

1 Biodiversity and biogeography of hydroids across marine ecoregions and provinces of
2 southern South America and Antarctica

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16 ABSTRACT

17 To better understand the polar connections between and among benthic communities of
18 southern South America and Antarctica (SSA & A) , we used hydroids as a model to
19 investigate marine assemblages by evaluating classic biodiversity-biogeographic
20 divisions at different spatial resolutions. Using a georeferenced dataset of 249 species
21 and multivariate analyses, we evaluated biodiversity and defined assemblages of
22 ecoregions and provinces for the area. Species' distributions, compositions and
23 biogeographic connectivity were investigated. Hotspots of rich biodiversity at risk of
24 depletion were defined according to specific biogeographic processes in the evolution of
25 the distribution and endemism of hydroids. Analyses of ecoregions have a more
26 stratified biogeographic structure, and reveal critical regions susceptible to loss of
27 faunistic and habitat diversity. Analyses of provinces show a clear division between
28 Atlantic-Pacific and Antarctic-Subantarctic assemblages, with high biogeographic
29 isolation of the Subantarctic islands. Depending on spatial resolution, the biogeographic
30 position of the Magellan area is spatially contradictory, clustering on the one hand with
31 SSA ecoregions, and on the other with Antarctic provinces. Our marine biogeographic

32 patterns appear to be driven by different combinations of processes and barriers,
33 reflected in the stratified distribution of hydroids. The high level of endemism and
34 concentration of species at the edge of distribution in the Magellan area and Scotia Arc
35 suggest that they are transitional in nature and particularly important for understanding
36 the historical and ecological connections between the Pacific, Atlantic and Southern
37 oceans.

38 **KEYWORDS:** marine biogeography, biodiversity, Hydrozoa, Southern Ocean,
39 community structure, endemism.

40 INTRODUCTION

41 The southern South America (SSA) coast extends from $\sim 22^{\circ}\text{S}$ to 56°S ,
42 encompassing $\sim 10,000$ km of coastline washed by the Atlantic and the Pacific oceans
43 (Miloslavich et al. 2011). It comprises several different geographic features and marine
44 ecosystems (e.g., archipelagos, channels, estuaries, lagoons, mangroves, rocky shores,
45 sandy beaches, seagrass beds), supporting a high, but still poorly known, marine
46 biodiversity (Acha et al. 2004; Costello et al. 2010; Miloslavich et al. 2011).
47 Historically, part of the marine fauna of the Atlantic and Pacific is shared with the
48 Southern Ocean due to the past connection between southern South America and
49 Antarctica (SSA & A). Antarctica, however, has been isolated for the last ~ 25 million
50 years contributing to the high incidence of endemic marine species (e.g., Lawver and
51 Gahagan 2003).

52 The region has been classified according to many biogeographic schemes based
53 on different taxa (e.g., Gibbons 1997; Linse et al. 2006; Griffiths et al. 2009), but
54 usually focusing on single oceans (e.g., Gibbons 1997; Douglass et al. 2014; Koubbi et
55 al. 2014; Acha et al. 2020) or on global studies (e.g., Costello et al. 2017; Watling et al.
56 2013; Sutton et al. 2017), obscuring detailed biogeographic patterns of the SSA & A.
57 The Marine Ecoregions of the World (MEOW) and the pelagic provinces of the world
58 (Spalding et al. 2007, 2012), however, provide nested systems of classification of the
59 oceans that combine small-scale spatial units, practical utility and strong databases,
60 facilitating biogeographic analyses along SSA & A. Both systems are complementary
61 and preserve many common elements of previous global/regional biogeographic
62 classifications (e.g., Briggs 1974), including different levels of endemism. Their
63 ecoregions and provinces are defined as cohesive units applicable to the broad life

64 history processes of most mobile, sedentary and dispersive species (e.g., cnidarians of
65 the class Hydrozoa; Spalding et al. 2007). As such, they are widely used for biodiversity
66 and biogeographic studies worldwide (Poore and Bruce 2012; Vilar et al. 2019;
67 Palomares et al. 2020; Summers and Watling 2021).

68 Along the SSA & A coasts, hydroids – the polyp stage of the cnidarian class
69 Hydrozoa (Cornelius 1992) – are abundant in benthic communities, being usually
70 among the first organisms to settle available space and having the capacity to grow
71 quickly on several natural and artificial substrates (Gili and Hughes 1995; Genzano et
72 al. 2009). Recent phylogenetic studies have identified several likely clades
73 corresponding roughly to the suborder or order level in hydrozoan classifications,
74 including Limnomedusae, Leptothecata, Aplanulata, Capitata, and Pseudothecata; the
75 latter three taxa along with a few other groups of “Filifera” are still united under a non-
76 monophyletic “Anthoathecata” (Collins et al. 2006; Cartwright et al. 2008; Leclère et al.
77 2009; Kayal et al. 2015; Maronna et al. 2016; Mendoza-Becerril et al. 2018).

78 Hydroids are widely-distributed in marine benthic substrates, occurring from
79 shallow coastal to abyssal habitats (Gili and Hughes 1995; Gravili 2016). Geographic
80 records of hydroids are directly related to the worldwide distribution of hydrozoan
81 taxonomists. The Mediterranean sea, for example, has a comparatively high richness of
82 known hydrozoan species but also concentrates a large number of specialists in
83 Hydrozoa and is one of the best studied areas of the world (González-Duarte et al. 2015;
84 Gravili et al. 2013; Gravili 2016). In contrast, the deep-sea, polar regions, and vast areas
85 of the South Atlantic and South Pacific have significant knowledge gaps (Henry et al.
86 2008; Genzano et al. 2009, 2017; Peña Cantero 2014; Ronowicz et al. 2015; Fernandez
87 and Marques 2018). Nevertheless, recent studies in these areas are building biodiversity
88 knowledge about Hydrozoa, allowing for reports on patterns of richness, endemism,
89 dispersal, and bathymetrical and latitudinal distributions (Genzano et al. 2009, 2017;
90 Gibbons et al. 2010a, b; Mercado Casares et al. 2017; Ronowicz et al. 2019; Fernandez
91 et al. 2020).

92 Wider or patchier geographic distributions of hydroids generally result from
93 different dispersal capabilities, biotic interactions, substrate availability and
94 environmental preferences (Cornelius 1992; Gili and Hughes 1995). Despite being
95 relatively well known since the 19th century in the Chilean Patagonia (from ~40°S to
96 56°S), the southeastern Brazilian and Buenos Aires coasts (from ~20°S to 40°S) and the
97 Antarctic Peninsula (from ~60°S to 75°S) (Peña Cantero 2014; Oliveira et al. 2016),

98 hydroids are still poorly known from the Argentinian Patagonia (from 40°S–55°S), and
99 along the east coast of Antarctica (from 60°S–70°S 0°–180°E). Many records are
100 associated with contradictory identifications or are referred to cryptic species (e.g.,
101 species of Campanulariidae and Sertulariidae; Moura et al. 2011; Cunha et al. 2015,
102 2017), and thus are likely to benefit from a taxonomic review prior to biogeographic
103 inferences. The first steps to minimize biases in biogeographic studies are defining the
104 species pool under study, intensive and careful field surveys (particularly in poorly
105 explored regions), and detailed cleaning and quality control of taxonomic and spatial
106 data (Yang et al. 2013; Khalighifar et al. 2020). The use of measures of biodiversity that
107 are highly dependent on equal sampling effort (e.g., richness) is challenging because
108 these measures may generate biased conclusions (Hortal et al. 2007; Clarke et al. 2014).
109 Alternative approaches employing taxonomic distinctness, which measures the
110 biodiversity at the taxonomic level, allow for the comparison of diversity between
111 unequal samples (Clarke et al. 2014). For conservation purposes, taxonomic distinctness
112 provides a high level of accuracy for the description of patterns of biodiversity, being
113 highly applicable for qualitative datasets and species lists with presence/absence data
114 (Clarke and Warwick 1998, 2001; Clarke et al. 2014).

115 The coasts of SSA & A were connected until at least ca. 30 Ma ago (Lawver and
116 Gahagan 2003). The distributions of biological communities along these continents
117 have been separated into different marine realms, provinces and ecoregions (viz.,
118 Spalding et al. 2007, 2012), encompassing the southwestern Atlantic, the southeastern
119 Pacific and the Southern Ocean. For hydroids, the area is classically divided in
120 Patagonia, the Antarctic region, and the Scotia Arc, the latter traditionally considered as
121 a biogeographic bridge between both continents (Mercado Casares et al. 2017). Recent
122 studies involving hydroid distributions show that the Scotia Arc has higher faunistic
123 affinity to Antarctica than to Patagonia, and they suggest that the Polar Front is an
124 important biogeographic barrier in the area (Soto Àngel and Peña Cantero 2017).
125 Studies with other marine taxa, however, suggest that the colonization of Antarctica was
126 not necessarily from the Magellan area via the Scotia Arc (Mühlenhardt-Siegel 1999),
127 implying that the connectivity of the latter is likely scale- and taxon-dependent (Moon et
128 al. 2017), and that the permeability of the Polar Front and the Antarctic Circumpolar
129 Current (ACC) is likely higher than once presumed (Sanches et al. 2016).

130 The area between SSA & A represents a complex and interesting biogeographic
131 laboratory to study the composition, biodiversity and distribution of marine species in

132 an ecological and historical context. Here, we study the marine hydroid fauna of SSA &
133 A in order to (1) update the taxonomic status of the species present, (2) evaluate species
134 endemism, (3) assess distribution patterns of species and community composition along
135 Spalding's ecoregions and provinces, and (4) assess the biogeographic connectivity
136 between SSA & A. We hypothesize that the biodiversity and faunistic composition of
137 assemblages are scale-dependent and vary across Spalding's ecoregions and provinces.
138 Also, taxonomic distinctness is likely to be higher in the better sampled areas, such as
139 the Southwestern Atlantic and the Antarctic Peninsula, and that endemism increases
140 southwards.

141 MATERIAL AND METHODS

142 Area of study

143 The study area comprises the marine benthic habitats of southern South America
144 (both the southwestern Atlantic and the southeastern Pacific oceans) and Antarctica
145 (including the Southern Ocean) from 20°S to 80°S, from shallow waters to ~5,000m
146 depth. The main oceanographic currents influencing the area are the Humboldt system
147 along the Pacific side, the Brazilian and Falklands/Malvinas currents along the Atlantic
148 side, and the Antarctic Circumpolar Current (ACC) of the Southern Ocean (Acha et al.
149 2004).

150 The area was divided in 25 ecoregions (Fig. 1a) and 10 provinces (Fig. 1b)
151 following the global biogeographic classification proposed by Spalding et al. (2007) –
152 the Marine Ecoregions of the World (MEOW) – and three additional Antarctic pelagic
153 provinces of Spalding et al. (2012) – used only for the Antarctic ecosystem because
154 several Antarctic and subantarctic records are beyond the coastal and shelf areas
155 presented by Spalding et al. (2007). Despite being proposed for pelagic waters, these
156 provinces agree with many Antarctic biogeographic benthic systems delimited for
157 different taxa (e.g., Linse et al. 2006; Clarke 2008; Griffiths 2010; Pierrat et al. 2013),
158 as well as with recent proposals included in the Biogeographic Atlas of the Southern
159 Ocean (De Broyer and Koubbi 2014). We chose these large-scale biogeographic
160 classification systems because they were developed under the same methodology for
161 both the ecoregions and provinces of SSA & A, enhancing the coherence and robustness
162 of our biogeographic analyses. Using both the ecoregions and provinces proposed by
163 Spalding et al. (2007, 2012), we approach the data from different biogeographic

164 perspectives – from smaller and larger scales, respectively – allowing for a more
165 complete understanding of the distribution data and the biodiversity of hydroids.

166 Data collection

167 Hydroid specimens (hydrocorals excepted) collected in the field and from
168 museum and university collections, from 1,360 geographic sites along the SSA & A
169 coasts, were examined. All specimens collected in the field were deposited in the
170 Marine Invertebrates Collection of the Museu de Zoologia of the University of São
171 Paulo. A qualitative approach was required due to (1) the lack of standardized
172 collections available at universities and museums, (2) the lack of knowledge of large
173 marine areas of SSA & A, (3) and the availability of unexamined and unpublished
174 records of hydroids in university and museum collections. While less suitable than
175 quantitative sampling for estimating the richness and abundance of species in
176 communities, qualitative surveys are advantageous in that they maximize the
177 exploration of poorly studied areas and uncover new records that increase knowledge of
178 species distributions (Hortal et al. 2007; Clarke et al. 2014). As our focus is to update
179 knowledge of the taxonomic composition of hydroid species in SSA & A and to use
180 these observations in order to make biogeographic inferences, we placed considerable
181 effort on maximizing the taxonomic quality of our presence/absence data.

182 We personally identified specimens and checked all collection and geographic
183 information in the literature, thereby guaranteeing taxonomic uniformity and geographic
184 accuracy; as required for large-scale biogeographic studies (Hortal et al. 2007; Santos et
185 al. 2010; Di Camillo et al. 2018). This approach is particularly essential for
186 taxonomically complex groups, given that available databases have non-uniform
187 identifications and extensive taxonomic revisions have recently been produced (e.g.,
188 Peña Cantero 2014; Oliveira et al. 2016). We compiled a list of the species studied and
189 their geographic distribution by ocean and/or sea of occurrence (Online Resource Table
190 S1); the endemic species were classified in eight categories of endemism along SSA &
191 A, and according to their distribution and traditional biogeographic classifications of the
192 area (Balech 1954; Palacio 1982): species endemic to (1) the whole area of study, i.e.,
193 from 22°S to 78°S, (2) tropical areas, i.e., from 22°S to 30°S, (3) tropical and
194 subtropical areas, i.e., from 22°S to ~43°S, (4) subtropical areas, i.e., from 30°S to
195 ~42°S, (5) subtropical and Magellan areas, i.e., from 30°S to 60°S, (6) the Magellan
196 area, i.e., from ~42°S to 60°S, (7) the Magellan and Antarctic areas, i.e., from ~42°S to

197 78°S, and (8) the Antarctic area, i.e., ~60°S to 78°S (Online Resource Table S1).
198 Literature records of hydroids were not herein listed, as this has already been done
199 elsewhere (Ronowicz et al. 2019; Oliveira et al. 2016). Exceptions are the Antarctic
200 records of *Corymorpha microrhiza* (Hickson & Gravely, 1907) and *Zyzyzus parvula*
201 (Hickson & Gravely, 1907) from Svoboda and Stepanjants (2001), which were included
202 after studying the specimens at the National Museum of Natural History, Smithsonian
203 Institution. The taxonomy of all species was standardized following the pertinent
204 literature to their area of occurrence (Oliveira et al. 2016 and references therein;
205 Ronowicz et al. 2019 and references therein; Schuchert 2021). Species were
206 phylogenetically classified according to Maronna et al. (2016), Mendoza-Becerril et al.
207 (2018) and Schuchert (2021).

208 Multivariate analyses

209 We included only georeferenced records that were identified to the species level
210 in the analyses. Records only to the genus or family level, (e.g., *Sphaerocoryne* sp.,
211 Eudendriidae not identified) and dubious records (e.g., *?Hybocon chilensis*, or *Hebella*
212 *?striata*) were excluded from the analyses. For the ecoregion analyses, records of
213 *Oswaldella gracilis*, *Staurotheca abyssalis* and *Symplectoscyphus liouvillei* collected
214 from outside coastal and shelf areas of SSA & A were excluded.

215 All multivariate analyses were conducted twice, comparing assemblages from
216 ecoregions and provinces. To compare species richness between equally large samples
217 and to evaluate sampling effort between assemblages, we calculated sample-based
218 rarefaction curves of estimated richness by sampling unit in each assemblage. Each
219 sampling unit is a geographic site, represented by a unique pair of latitude and longitude
220 coordinates, and may have one or more species records.

221 To compare the biodiversity of hydroids at different taxonomic levels between
222 assemblages, we used the average taxonomic distinctness (AvTD) and the variation in
223 taxonomic distinctness (VarTD). Both AvTD and VarTD are unbiased statistical
224 diversity measures, applicable to presence/absence data, and insensitive to sampling
225 effort, size and dominant species (Clarke et al. 2014). They use the Linnaean
226 classification relationships between species to test for biodiversity changes among
227 assemblages, qualitatively comparing their taxonomic distinctness given a master list of
228 species observed in an area (i.e., the “species pool” of SSA & A) (Clarke and Gorley
229 2015). The AvTD of an assemblage is a reflection of the taxonomic distance across the

230 taxonomic hierarchy of a master list of species observed for the whole area of study
231 (i.e., the species inventory), without the effect of species abundance distribution (Clarke
232 & Warwick 2014). It is defined as the ratio between the average taxonomic distance
233 (i.e., the expected path length in the classification tree between any two individuals
234 chosen at a random) and the Simpson diversity index (i.e., the probability that any two
235 individuals selected at a random belong to the same species) of a sample (Warwick and
236 Clarke 1995; Clarke et al. 2014). The VarTD is the variance of the taxonomic distances
237 between each pair of species, representing the unevenness of the classification tree (i.e.,
238 reflects different classification tree constructions) (Clarke and Warwick 2001; Clarke et
239 al. 2014). Both AvTD and VarTD of an assemblage can be tested from the master list of
240 species which encompasses the taxonomic boundaries of the classification tree related
241 to the inventory, and the suitable biogeographic limits from which the species were
242 documented. As taxonomic distinctness measures are independent of sampling effort, it
243 is possible to compare the AvTD and VarTD of a subset of species in an assemblage
244 with those of the master list to check if they represent the biodiversity expressed in the
245 full species inventory. Therefore, the AvTD and VarTD for the master list correspond to
246 the expected values for the whole faunal group (Clarke et al. 2014). Analyses of
247 taxonomic distinctness were performed using seven taxonomic levels (superorder,
248 order, suborder, infraorder, family, genus and species) and equal weights between them.

249 Hydroid distributions, compositions and biogeographic connectivity across
250 assemblages were investigated based on Bray-Curtis similarities of presence/absence
251 data. Assemblages were clustered using the group-average method, and the similarity
252 profile test (SIMPROF) was used to test for statistically significant clusters. To
253 identify the species that mostly contributed to the internal similarity within clusters, and
254 for the overall dissimilarity between clusters, the similarity percentages routine
255 (SIMPER) was used, with a cut-off value for low contributions of 70%. This method
256 compares two clusters at a time and identifies the most influential species for its
257 similarities, through the decomposition of the Bray-Curtis dissimilarity index between
258 the species (Clarke et al. 2014).

259 A non-metric multidimensional scaling (nMDS) with 50 interactions was also
260 performed to assess gradual faunistic changes between the assemblages. To test for
261 differences in species composition between assemblages, the one-way analysis of
262 similarity test (ANOSIM) with 999 permutations was calculated (Clarke and Green
263 1988). Finally, we used BVSTEP, a stepwise routine that searches for the smallest

264 subset of species contributing most for the nMDS pattern (Clarke et al. 2014). All
265 multivariate analyses were performed using the software Primer-e v. 7 (Clarke and
266 Gorley 2015).

267 RESULTS

268 A total of 5,622 records and 357 morphospecies of hydroids – representing 2
269 superorders, 8 orders, 5 suborders, 4 infraorders, 38 families, 83 genera, and 256
270 identified species – were documented for the 1,360 sampling sites along the SSA & A.
271 Seven singleton non-georeferenced records (i.e., *Acryptolaria crassicaulis*,
272 *Corydendrium parasiticum*, *Cryptolarella abyssicola*, *Filellum bouvetensis*, *Halecium*
273 *secundum*, *Sertularella uruguayensis*, *Zygophylax infundibulum*; Online Resource Table
274 S1) were excluded, reducing the number of analysed species to 249. Three species are
275 new records for the Southwestern Atlantic Ocean (*Nemertesia ciliata*, *Sertularella*
276 *leiocarpa*, and *Zygophylax sibogae*), and 128 are endemic to SSA & A, corresponding
277 to ~51% of the total species recorded (Fig. 2; Online Resource Table S1). Among the
278 endemic species, the proportion of endemism increases towards Antarctica (Fig. 3;
279 Online Resource Table S1).

280 Eighty-eight percent of the species (226 of 256) belong to the superorder
281 Leptothecata, 9% (24 of 256) to “Anthoathecata” (i.e., “Filifera”, Capitata and
282 Aplanulata), and 3% (6 of 256) to Pseudothecata. The majority of the species belong to
283 the order Macrocolonia (175 of 256 species); the most speciose families are
284 Symplectoscyphidae (30 species), Kirchenpaueriidae (29 species) and Staurothecidae
285 (23 species). The most speciose genera are *Oswaldella* (26 species), *Staurotheca* (24
286 species), *Symplectoscyphus* (21 species), *Sertularella* (14 species) and *Halecium* (12
287 species), which together encompass ~38% of the 256 identified species (Online
288 Resource Table S1).

289 Rarefaction curves do not reach a clear asymptote for any of the ecoregions and
290 provinces analysed, providing evidence that sampling effort along SSA & A is unequal
291 and still deficient (Figure 4). However, within all biogeographic units analysed,
292 ecoregions 180, 183, 185, 187, 220, 222, 223, 227, and 229 appear to be closer to
293 reaching an asymptote (Fig. 4a), as well as curves CHA, M, SS and WTSWA for
294 provinces (Fig. 4b).

295 Regarding taxonomic distinctness, eleven ecoregions have AvTD values within
296 the 95% interval of expectation of the master list, three ecoregions (180, 181 and 183)

297 have AvTD values above it, and ten have AvTD values below the expected (Fig. 5a;
298 Table 1). Most VarTD values were within the expected, with exceptions of above
299 expectation values for ecoregions 177, 222, 223, 227 and 229 (Fig. 5b; Table 1). For
300 provinces, most AvTD values were within or below the expected, except for WTSWA
301 (Fig. 6a; Table 2). The VarTD values were also mostly within the expected for each
302 area, except for above expected values for provinces A, CHA and SS (Fig. 6b; Table 2).

303 Bray-Curtis and SIMPROF analyses showed 17 statistically significant clusters
304 for the ecoregions (Fig. 7a) and 7 statistically significant clusters for the provinces (Fig.
305 8a). For both ecoregions and provinces, analyses divide the whole area of study between
306 southern South American (E10 to E17 and P1 to P2; Fig. 7a) and Antarctic assemblages
307 (E1 to E9 and P3 to P7; Fig. 8a). The Magellan area (ecoregions 185 to 187 and
308 province M; Fig. 1) clusters with SSA assemblages when ecoregions are analysed (Fig.
309 7a), but with Antarctic assemblages when provinces are considered (Fig. 8a). SIMPER
310 analyses show great variation in species composition within and between assemblages,
311 for both ecoregions and provinces (Online Resource Tables S2, S3).

312 Along the southwestern Atlantic coast, assemblages E11 and P2 in particular
313 (Fig. 1, 7a, 8a), have similar composition of non-endemic species widely distributed
314 along tropical and subtropical areas (e.g., *Dynamena* spp., *Sertularia* spp., among
315 others; Online Resource Tables S1–S3), including records for the Caribbean (cf. Calder,
316 1988, 1991). Endemic species along the southwestern Atlantic were found in
317 assemblage E17 (as well as other species widely distributed across the world), all of
318 them distributed among the categories tropical+subtropical, subtropical+Magellan and
319 Magellan+Antarctic (Fig. 1a, 7a; Online Resource Tables S1, S2). Along the Pacific
320 coast, SIMPER suggests that WTSEP (Fig. 1b, 7) as an assemblage with few endemic
321 species, distributed along the Subtropical (e.g., *Sertularella mixta*, *Thuiaria polycarpa*),
322 subtropical+Magellan (e.g., *Sertularella fuegonensis*) and Magellan+Antarctic (e.g.,
323 *Halecium interpolatum*) categories of endemism (Online Resource Tables S1, S3). The
324 presence of *Coryne eximia*, *Obelia dichotoma* and *Plumularia setacea* along the
325 northern Chilean coast (176, 177), the Chilean Patagonia (178, 188), the southern Brazil
326 (181) and the Río de La Plata Estuary (182), gather these ecoregions in assemblage E13,
327 with lower internal similarity value but connecting the Pacific and the Atlantic coasts of
328 SSA (Fig. 1a, 7a; Online Resource Table S2). The most dissimilar assemblage in SSA is
329 E14 (Fig. 1a, 7a; Online Resource Table S4), with a mix of endemic species from
330 tropical+subtropical (e.g., *Sertularella fuegonensis*), Magellan (e.g., *Sertularella*

331 *jorgensis*), and Magellan+Antarctic ranges (e.g., *Abietinella operculata*) (Online
332 Resource Tables S1, S2). Assemblage E16 corresponds to the Magellan area, composed
333 of endemic species from tropical+subtropical (e.g., *Corymorpha januarii*), Magellan
334 (e.g., *Orthopyxis hartlaubi*) and Magellan+Antarctic categories of endemism (e.g.,
335 *Halecium interpolatum*), in addition to some widely distributed species (Fig. 1a, 7a;
336 Online Resource Tables S1, S2).

337 Our results suggest that Antarctic assemblages are biogeographically divided
338 between the subantarctic islands (i.e., assemblages E2 and SI) and the Scotia Arc plus
339 the rest of the Antarctic ecosystem (assemblages E3 and P4) (Fig. 1a, 7a, 8a). E2
340 clusters Bouvet Island and Peter I Island by the presence of *Antarctoscyphus spiralis*
341 and *Staurotheca dichotoma* (Fig. 1a, 6a; Online Resource Table S2). SI gathers Bouvet,
342 Prince Edwards, Crozet, Kerguelen islands, being the most dissimilar assemblage of
343 provinces (Fig. 1b, 8a; Online Resource Table S5), composed of endemic species from
344 the Magellan+Antarctic category (e.g., *Oswaldella erratum*, *O. vervoorti*, *Schizotricha*
345 *vervoorti*, *Staurotheca dichotoma*, *S. vanhoeffeni*) but also by rare (e.g., *Staurotheca*
346 *echinocarpa*) and widely distributed species (e.g., *Symplectoscyphus subdichotomus*)
347 (Online Resource Tables S1, S3). South Georgia and South Sandwich Islands, which are
348 part of the Scotia Arc, are represented by assemblage E5, with most endemic species
349 from Magellan+Antarctic category (mainly *Antarctoscyphus* spp., *Oswaldella* spp., and
350 *Staurotheca* spp.) (Fig. 1a, 7a; Online Resource Tables S1, S2). The west coast of the
351 Antarctic Peninsula corresponds to assemblage E9 (Fig. 1a, 7a), composed of species
352 distributed in a few lower taxonomic levels (e.g., genus and family levels) and by a high
353 number of species endemic from Antarctica (e.g., *Antarctoscyphus* spp., *Oswaldella*
354 spp., *Clathrozoella medeae*, *Mixoscyphus antarcticus*, *Schizotricha crassa*, *S. nana*, *S.*
355 *vervoorti*, *Staurotheca antarctica*) (Online Resource Tables S1–S3). This faunistic
356 pattern was also found in P5, corresponding to the whole coast of Antarctica (Fig. 1b,
357 8a). APF is composed of endemic species from Magellan (e.g., *Acryptolaria* spp.,
358 *Clathrozoella abyssalis*, *Oswaldella elongata*, *Sertularella jorgensis*, *Staurotheca*
359 *abyssalis*, *S. profunda*, *S. vervoorti*) and Magellan+Antarctic categories (e.g.,
360 *Antarctoscyphus elongatus*, *Schizotricha vervoorti*, *Staurotheca jaederholmi*, *S.*
361 *pachyclada*), besides some worldwide distributed species (e.g., *Amphisbetia operculata*
362 and *Sertularella gaudichaudi*) (Online Resource Tables S1, S3).

363 The nMDS ordination plots reflect the same biogeographic division between the
364 assemblages of SSA & A found in the cluster and SIMPROF analyses (Fig. 7, 8).

365 Additionally, a gradual variation in species composition along the ecoregions and
366 provinces was observed (Fig. 7b, 8b). The adjacent ecoregions 76 and 180, for example,
367 have similar species composition, while ecoregion 186, although more isolated, is more
368 similar in species composition to ecoregions 187 and 188 (Fig. 1, 7b). The
369 geographically isolated province SI has a unique species composition, while adjacent S
370 and APF are more closely related to each other (Fig. 8b). The BVSTEP routine
371 identified five species (correlation 0.815) better matching the pattern of the nMDS
372 ordination of the ecoregions: *Antarctoscyphus spiralis*, *Billardia subrufa*, *Halecium*
373 *jaederholmi*, *Staurotheca dichotoma*, and *S. glomulosa*. For the province nMDS
374 patterns, BVSTEP identified 15 species (correlation 0.952): *Acryptolaria conferta*, *A.*
375 *operculata*, *Aglaophenia latecarinata*, *A. trifida*, *Antarctoscyphus grandis*,
376 *Clathrozoella abyssalis*, *Halecium pallens*, *Obelia dichotoma*, *Schizotricha vervoorti*,
377 *Sertularella gaudichaudi*, *S. mixta*, *S. polyzonias*, *Staurotheca antarctica*, *S. dichotoma*,
378 and *S. echinocarpa*.

379 Although R values are low, the ANOSIM global test resulted in significantly
380 different species composition among both ecoregions (R=0.192, p=0.1%) and provinces
381 (R=0.11, p=0.1%). Pairwise tests show significantly different faunistic composition
382 between most ecoregions and most provinces, with few exceptions (Online Resource
383 Tables S6, S7).

384 DISCUSSION

385 Despite the unavoidable unequal sampling along the ecoregions and provinces of
386 SSA & A, the patterns herein documented are related to the geographic scale, reflecting
387 its evolutionary and environmental aspects, and evidencing their biogeographic
388 connection. Also, the distribution of hydroids along SSA & A is driven by a
389 combination of barriers of varying intensity for different species, modulating dispersal
390 over long distances.

391 *Faunistic composition*

392 The 256 species of hydroids studied here represent ~7% of the total species of
393 Hydrozoa described in the world (Schuchert 2021), and ~30% of all species of hydroids
394 recorded for South America and Antarctica (Ronowicz et al. 2019; Oliveira et al. 2016).
395 Leptothecata (88% of the species) dominates over “Anthoathecata” and Pseudothecata

396 (9% and 3% of the species, respectively) – a similar proportion found in other parts of
397 the world, such as tropical (Calder 1993; Di Camillo et al. 2008) and subtropical areas
398 (Genzano et al. 2017; Ajala-Batista et al. 2020), the Mediterranean (Bouillon et al.
399 2004; Gravili et al. 2013), the Arctic (Ronowicz et al. 2015) and the Antarctic (Peña
400 Cantero 2014; Soto Àngel and Peña Cantero 2019; Peña Cantero 2021). The high
401 proportions of Leptothecata over Anthoathecata is at least partially due to the
402 destructive sampling of unprotected polyps (i.e., anthoathecates) (Peña Cantero, 2004),
403 although it may be more related to evolutionary and ecological factors than to sampling
404 biases (Fernandez and Marques 2018; Fernandez et al. 2020). Symplectoscyphidae is
405 the most speciose family in the study area (Online Resource Table S1) (cf. Soto Àngel
406 and Peña Cantero 2019; Peña Cantero 2021), although Haleciidae is the most speciose
407 hydrozoan family in South America (Oliveira et al. 2016). Among genera, *Oswaldella*,
408 *Staurotheca*, *Symplectoscyphus*, *Sertularella* and *Halecium* are the most speciose genera
409 for SSA &, corroborating previous findings (cf. Peña Cantero 2014; Oliveira et al.
410 2016; Soto Àngel and Peña Cantero 2019).

411 *Sampling effort, biodiversity and taxonomic distinctness*

412 Sampling effort along SSA & A is unequal and none of the rarefaction curves
413 reached an asymptote. Therefore the biodiversity of the region is underestimated,
414 hindering full biogeographic comparisons among the ecoregions and provinces.
415 However, exhaustive sampling effort for large-scale areas is challenging, and
416 geographical gaps in knowledge of taxa is the usual situation in studies making
417 biodiversity inferences (Hortal 2008; Fernandez et al. 2020).

418 Taxonomic distinctness (i.e., AvTD and VarTD) are useful measures to
419 characterize differences in taxonomic structure across SSA & A, revealing areas with
420 apparent losses or gains of biodiversity, or reduced habitat diversity (Clarke and
421 Warwick 2001; Clarke et al. 2014). High values of AvTD (e.g., ecoregions 180, 181,
422 183 and province WTSWA; Fig. 1, 5a, 6a; Tables 1, 2), for example, are related to gains
423 of biodiversity. This pattern suggests that the southeastern Brazilian and the Buenos
424 Aires coasts concentrate intensive efforts in studies of marine biodiversity, possibly
425 related to higher availability of suitable habitats for hydroid occurrence, such as hard
426 substrata and rocky shores, and the ease of access to shallow-water environments
427 (Miloslavich et al. 2011, 2016).

428 Low values of AvTD are related to loss of biodiversity, as evidenced for the
429 Antarctic and sub-Antarctic ecosystems (e.g., ecoregions 219 to 224, 226, 227, 229,
430 provinces A, CHA, S, SI, SS; Fig. 1, 5a, 6a; Tables 1, 2). The higher resolution analyses
431 (i.e., ecoregions) suggest that the Scotia Arc, the Antarctic Peninsula, the Weddel Sea,
432 the Ross Sea and Queen Maud Land are more susceptible to biodiversity loss. This
433 might be related to their geographic proximity to commercial fishery areas, implying
434 transportation of benthic exotic species on ship hulls from the northern oceans (Clarke
435 et al. 2005; Scott 2012). An example of possible anthropogenic impacts along the region
436 is the presence of the globally distributed *Lafoea dumosa* and *Obelia bidentata* in the
437 South Orkney Islands, as well as along other Antarctic areas (cf., Online Resource
438 Tables S1, S2).

439 High values of VarTD, on the other hand, reflect lower habitat diversity, as
440 found in ecoregion 177 and province WTSEP (Fig. 1, 5b, 6b; Tables 1, 2). These
441 regions correspond to the Chilean coast, historically socio-economically dependent on
442 marine resources, and with human activities commonly impacting different habitats
443 along the southeastern Pacific (Fernandez et al. 2000; Miloslavich et al. 2016). The
444 overexploitation of benthic resources, pollution by sewage discharges and oil spills from
445 ships are the main human impacts in the region, possibly associated with habitat
446 depauperation and consequently, loss of habitat diversity (Fernandez et al. 2000).

447 Ecoregions and provinces with low values of AvTD and high values of VarTD
448 (e.g., Antarctic Peninsula, Weddell and Ross seas, i.e., ecoregions 222, 223, 227, 229,
449 provinces A, CHA, SS; Fig. 5, 6; Tables 1, 2) are probably related to the presence of
450 species' pools that are unevenly distributed across the taxonomic classification tree and
451 which belong to a few high taxonomic groups (Clarke and Warwick 2001; Clarke et al.
452 2014; Ronowicz et al. 2015). These regions have a hydroid fauna concentrated in a few
453 families and/or genera (e.g., *Antarctoscyphus* spp. and *Oswaldella* spp.; Fig. 1, 7, 8;
454 Tables S1–S3). A similar pattern was documented for Arctic hydrozoans (Ronowicz et
455 al. 2015), presumably related to high speciation (Mayr 1963) and low rates of higher
456 taxa diversification along polar regions, also influenced by particular climatologic,
457 geologic and oceanographic events (Gillespie and Roderick 2014).

458 The other ecoregions and provinces have values of AvTD and VarTD within
459 expectation (i.e., within the 95% range of simulated values depart from the one of the
460 master list; Fig. 5, 6), meaning that the subsets of species observed in each

461 ecoregion/province have the same taxonomic diversity of the whole SSA & A (Fig. 5, 6;
462 Table 1, 2).

463 *Endemism, distribution and biogeographic patterns*

464 There is a statistically significant separation between SSA and Antarctic
465 assemblages, for both ecoregions and provinces (Fig. 7, 8; ANOSIM test; Online
466 Resource Tables S6, S7). This pattern has been shown for other benthic invertebrates
467 based on different biogeographic units and molecular inferences (González-Wevar et al.
468 2010; Figuerola et al. 2013; Griffiths and Waller 2016). However, the biogeographic
469 affinity of the Magellan area (including the Falkland/Malvinas Islands and the
470 Burdwood Bank) is scale dependent and muddies the picture somewhat. Magellan
471 ecoregions E16 and 186 are grouped with SSA assemblages, but province P7 is grouped
472 with Antarctic assemblages (Fig. 1, 7a, 8a). The Falkland/Malvinas Islands and
473 Burdwood Bank (assemblage 186; Fig. 1a, 7a) are currently part of the large
474 biogeographic region of Patagonia (42°S–56°S; Acha et al. 2004), which includes the
475 Magellan area (Mercado Casares et al. 2017). The Southern tip of South America, the
476 Falkland/Malvinas Islands and Burdwood Bank (viz., E16, P7 and 186) are composed
477 of species from the Magellan, Antarctic and Magellan+Antarctic categories of
478 endemism (Online Resource Tables S1, S2). Their faunistic composition is unique,
479 revealing a dissimilarity higher than 75% in relation to the other assemblages (Online
480 Resource Tables S4, S5), corroborating its distinct and complex biogeographic role as a
481 center of endemism and route for dispersal of benthic species (Schejter et al. 2016).

482 The nMDS plots also corroborate the conflicting biogeographic position of the
483 Magellan area, with the intermediate ecoregions 185, 186 and 187 between SSA & A.
484 Province S clusters with Antarctic provinces, and M occupies an intermediate position
485 between SSA & A (Fig. 1, 7b, 8b). Although conflicting, these patterns reinforce the
486 complex role of the Magellan area as a transition zone connecting the SE Pacific, the
487 SW Atlantic and the Southern Ocean. The high proportion of endemic species with
488 different ranges along the Magellan area (Fig. 3) and the high concentration of species
489 at the edge of their distributions (Online Resource Tables S1–S3) corroborate its
490 transitional nature. The Magellan, the Antarctic and the Magellan+Antarctic ranges of
491 endemism in particular (Fig. 3; Online Resource Table S1), reinforce the hypothesis
492 that the Magellan area is a biogeographic corridor for interchange of some species, but
493 also a barrier impacting the distribution of others (Balech 1954; Souto et al. 2014;

494 Sepulveda et al. 2016). This transition area results in species being either geographically
495 restricted or dispersed over long distances, mainly through the influence of the ACC.

496 The ACC plays a fundamental role in the biogeographic structuring of hydroids
497 from the Southern Hemisphere (Marques and Peña Cantero 2010; Miranda et al. 2013;
498 Soto-Àngel and Peña Cantero 2017; Mercado Casares et al. 2017), since its circulation
499 simultaneously connects the Southern Ocean biota with the rest of the adjacent oceans
500 but also isolates Antarctica promoting its high endemism (Sanches et al. 2016).

501 Therefore, it is a significant biogeographic barrier to the subtropical,
502 subtropical+Magellan and Magellan endemic hydroids, but does not influence the
503 distribution of the Magellan+Antarctic species. An example is the intermediate area
504 between the subantarctic and Antarctic waters (assemblage APF; Fig. 1b), directly
505 influenced by the ACC and more than 88% dissimilar to the assemblages of other
506 provinces, with a mixed composition of Subtropical (e.g., *Acryptolaria operculata*),
507 Magellan (e.g., *Clathrozoella abyssalis*, *Oswaldella elongata*, *Sertularella jorgensis*,
508 *Staurotheca abyssalis*, *S. profunda* and *S. vervoorti*) and Magellan+Antarctic endemic
509 species (e.g., *Antarctoscyphus elongatus*, *Schizotricha vervoorti*, *Staurotheca*
510 *jaederholmi*, *S. pachyclada*) (Online Resource Tables S1, S3, S5).

511 The southwestern Atlantic is also a transition zone characterized by widely
512 distributed tropical-subtropical species (assemblages E11 and P2; Fig. 1, 7a, 8a; Tables
513 S1–S3 – cf. Palacio 1982; Barroso et al. 2016 for other marine taxa). The Uruguay-
514 Buenos Aires shelf and the Atlantic Patagonia coast (assemblages E17; Fig. 1a, 7a) are
515 characterized by warmer temperate waters (Genzano et al. 2009) with widely distributed
516 species, and a few tropical+subtropical, subtropical+Magellan and southern South
517 America+Antarctica endemic species (Online Resource Tables S1, S2). The Uruguay-
518 Buenos Aires Shelf and the Atlantic Patagonia coasts are areas of endemism *per se*
519 (Miranda et al. 2015), although they have a low number of endemic species when
520 compared with the Antarctic assemblages (Online Resource Tables S1, S2).

521 The convergence zone of the Brazilian and Falkland/Malvinas currents is a
522 biogeographic barrier for some species (Miranda et al. 2015; Barroso et al. 2016), but
523 some subtropical and Magellan edges of species ranges might extend to latitudes lower
524 than 40°S (e.g., 35°–37°S; Genzano et al. 2009; Souto et al. 2014). This is particularly
525 supported by *Campanularia agas*, *C. subantarctica*, *Lytocarpia canepa*, *Phialella*
526 *chilensis*, *Sertularella cruzensis*, and *Symplectoscyphus magellanicus* (viz., E17 species
527 composition; Online Resource Table S1, S2), and is probably related to the adjacent

528 subantarctic waters and the cooler and more saline waters of the Falkland/Malvinas
529 current along the Argentinian continental shelf (Acha et al. 2004). The thermohaline
530 front produces flows northwards (Acha et al. 2004; Genzano et al. 2009) and explains
531 the presence of subantarctic species at lower latitudes (e.g., along 27°–30°S), such as
532 *Amphisbetia operculata*, *Lafoea dumosa*, *Stegolaria irregularis*, and *Symplectoscyphus*
533 *subdichotomus* (Online Resource Table S1).

534 The southeastern Pacific (WTSEP and part of E13 – ecoregion 177; Fig. 1, 7a)
535 has a unique set of endemic species from different categories: Tropical (*Sertularella*
536 *mixta*), Tropical+Subtropical (*Thuiaria polycarpa*), Magellan+Antarctic (*Halecium*
537 *interpolatum*) and southern South America+Antarctica (*Sertularella fuegonensis*).
538 *Sertularella mixta* and *Thuiaria polycarpa* for example, corroborate the “warm-
539 temperate north of 35°S” area defined for benthic macroinvertebrates of the
540 southeastern Pacific (Lancellotti and Vasquez 1999), while *Halecium interpolatum* is
541 more related to the “cold-temperate south of 48°S” area, reinforcing the position of the
542 southeastern Pacific as a mixed biogeographic area (Camus 2001) driven by the
543 Humboldt Current system and its upwelling zones. Although being the most isolated
544 province among the SSA assemblages (Fig. 8; Online Resource Tables S1, S3), WTSEP
545 might be considered a hotspot of biodiversity since it is suffering from loss of habitat
546 diversity (see the section above).

547 Despite the low internal similarity (29.8%; Online Resource Table S2), E13 is
548 connected to the Chilean coast (ecoregions 176 to 178 and 188), the southern Brazilian
549 coast (ecoregion 181) and the Río de La Plata Estuary (ecoregion 182) (Fig. 1a, 7) based
550 on the presence of the well-known and widely distributed – equatorial to subantarctic –
551 *Coryne eximia*, *Obelia dichotoma*, and *Plumularia setacea* (Oliveira et al. 2016; Online
552 Resource Table S2). This pattern reflects the Pacific-Atlantic connection driven by the
553 Humboldt Current system distributing species from the Pacific to the Atlantic through
554 the Cape Horn current (Fernandez et al. 2000; Sepulveda et al. 2016). Its role in shaping
555 biogeographic patterns along the Magellan-Antarctic area is poorly understood despite
556 the importance of the area as a marine hotspot (Fernandez et al. 2000; Scott 2012; Selig
557 et al. 2014; Schejter et al. 2016). The Cape Horn current flows through the Magellan
558 Strait, surrounds the tip of South America, and turns northeastwards to form the
559 Falkland/Malvinas current (Montiel et al. 2005; Souto et al. 2014; Sepulveda et al.
560 2016), which passes through the Scotia Arc and flows northwards meeting the warm
561 Brazilian current (at ~36°S–40°S) (Acha et al. 2004). Bio/phylogeographic models have

562 suggested that the formation of the Magellan Strait created a new pathway for faunistic
563 interchange between the Pacific and the Atlantic (Montiel et al. 2005; González-Wevar
564 et al. 2012; Souto et al. 2014). The intermediate role of the Scotia Arc along the area
565 includes dispersal events of species between the Atlantic and Southern oceans (Marques
566 and Peña Cantero 2010; Miranda et al. 2013; Mercado Casares et al. 2017).

567 The hydroid communities of South Georgia and South Sandwich (cluster E5;
568 Fig. 1a, 7) are highly (97+%) dissimilar to those of SSA, and more similar to those of
569 Antarctica (Online Resource Table S4). The South Sandwich+South Georgia
570 assemblage, therefore, is a unique mixture of Magellan and Magellan+Antarctic
571 endemic species (Online Resource Tables S1, S2), corroborating the role of these
572 islands as a biogeographic bridge between both continents (Montiel et al. 2005; Dalziel
573 et al. 2013; Maldonado et al. 2015; Mercado-Casares et al. 2017). The position of the
574 South Orkney Islands (ecoregion 221; Fig. 1a, 7) reinforces the bridge idea because of
575 its unique composition of Magellan+Antarctic and Antarctic species (Online Resource
576 Table S2), although the assemblage is more similar to that of the Antarctic Peninsula
577 (assemblage E9; Fig. 7; Online Resource Table S4).

578 Clustering between South Georgia and South Sandwich Islands has been
579 commonly demonstrated (Ramos-Esplá et al. 2005; Primo and Vásquez 2009), but
580 recent inferences based on hydroids clustered the South Sandwich Islands with Bouvet
581 Island, keeping South Georgia with Shag Rocks, although with low internal support
582 (Soto Àngel and Peña Cantero 2017). We recovered Bouvet Island with Peter I
583 (assemblage E2) despite low internal similarity (i.e., 36.4%; Online Resource Table S2;
584 Fig. 1a, 7a), but the analysis with the provinces includes Bouvet Island in SI (Fig. 1b,
585 8). The high concentration of endemic (e.g., Magellan+Antarctic and Antarctic) and rare
586 species (e.g., *Staurotheca echinocarpa*; Online Resource Tables S1–S3) around E2 and
587 SI suggests that their hydroid communities are truly highly isolated despite being poorly
588 known (Fig. 7, 8; Online Resource Tables S4, S5).

589 Queen Maud Land (assemblage 226; Fig. 1a) is the most isolated area of
590 Antarctica, with a fauna composed only of Magellan+Antarctic and Antarctic endemic
591 species of *Oswaldella* and *Staurotheca* (Online Resource Tables S2, S4). It is part of the
592 Eastern High Antarctica Zone, an Antarctic area of endemism characterized by an
593 impoverished fauna of hydroids with vast geographical gaps interrupted by scattered
594 records (Marques and Peña Cantero 2010). The faunistics of this area have been poorly
595 explored (De Broyer et al. 2011), hindering knowledge on biogeographic patterns, since

596 real absences and insufficient sampling effort are commonly treated together (Gili et al.
597 2016; Griffiths and Waller 2016).

598 The western Antarctic Peninsula (assemblage E9) has the strongest
599 biogeographic structure in the higher resolution analysis, and the whole coast of
600 Antarctica and the Scotia Arc (assemblage P5) in the lower resolution analysis (Fig. 1,
601 7, 8; Tables S2, S3). These assemblages have an endemic fauna of hydroids with the
602 highest internal similarity in relation to other assemblages (Tables S2, S3). The high
603 endemism of the Antarctic Peninsula is likely originated from isolation of an
604 epicontinental sea along its northern portion, which allowed a long standing evolution
605 of the fauna (Marques and Peña Cantero 2010; Miranda et al. 2013). The region is
606 known as a biodiversity hotspot (Grange and Smith 2013; Kerr et al. 2018), but
607 anthropogenic impacts are increasing, especially invasive species and tourism (Frenot et
608 al. 2005; Lynch et al. 2010).

609 Assemblage E7 encompass geographically disjointed Antarctic areas with
610 similar hydroid faunas, suggesting a connection between the Wilkes Land coast (at east
611 Antarctica) and the Weddell and the Ross seas (at west Antarctica) (Fig. 1a, 7; Online
612 Resource Table S2). This pattern was previously described for sponges (Downey et al.
613 2012) and is likely to be related to the opening of the trans-Antarctic passage ~60Ma
614 (early Cenozoic), connecting east and west Antarctica through populations of the
615 Weddell and the Ross seas, respectively (Linse et al. 2006; Marques and Peña Cantero
616 2010; Gili et al. 2016). The subsequent glacial event in Antarctica (~40-30 Ma; Lawver
617 and Gahagan 2003) might have contributed to the partial biogeographic isolation of
618 these areas and the formation of an endemic biota distributed in different categories of
619 endemism, as for the hydroids (Fig. 3; Online Resource Table S1).

620 BVSTEP results reinforce the importance of endemism in the biogeographic
621 history of hydroids along SSA & A and emphasize the importance of the Magellan area
622 as a center of endemism and transition area along the Pacific, Atlantic and Southern
623 oceans. The ordination results underscore that the biogeographic patterning of hydroids
624 along SSA & A is related to a combination of widely distributed species and those with
625 restricted distribution ranges across the area.

626 The hotspots of biodiversity herein proposed (e.g., the southeastern Pacific, the
627 Magellan area, and the Antarctic Peninsula) were inferred mainly through the presence
628 of endemic species and the level of environmental impact. Although endemism hotspots
629 are more successful in capturing a great proportion of endemic species, species richness

630 and threatened species (Orme et al. 2005), there is very low congruence among different
631 types of hotspots in their ability to be efficient for conservation efforts (Orme et al.
632 2005; Possingham and Wilson 2005; Thompson et al. 2020). The potential hotspots of
633 biodiversity of hydroids herein defined for the assemblages of SSA & A may facilitate
634 monitoring and conservation efforts within this broad region.

635 CONCLUSIONS

636 The hierarchical biogeographic patterns herein documented are scale dependent,
637 reflecting an interaction of evolutionary and environmental factors, but also making
638 them useful for investigating complex patterns of biodiversity (Willis and Whittaker
639 2002). For both spatial resolutions (i.e., ecoregions and provinces), we found a clear
640 separation between assemblages of SSA & A, as well as different levels of faunistic
641 affinities amongst their respective assemblages. The higher resolution analyses
642 (ecoregions) show a more stratified biogeographic structure, revealing critical regions
643 susceptible to loss of faunistic and habitat biodiversity (e.g., the southeastern Pacific
644 coast, the subantarctic islands, the east coast of Antarctica). The lower resolution
645 analyses (provinces) show a clear division between the Atlantic-Pacific, the Antarctic-
646 Subantarctic provinces, and the high biogeographic isolation of the subantarctic islands.
647 Both resolutions show the Magellan area and the Scotia Arc as an important transition
648 zone between SSA & A, although the Magellan area has a conflicting position
649 concerning its faunistic affinities (Fig. 7, 8).

650 Using hydroids as a model allowed us to successfully examine biogeographic
651 patterns and come to an improved understanding of species connectivity in the region.
652 Their wide bathymetric and latitudinal distributions, their associations with different
653 types of natural and artificial substrate, the high level of endemism across large-scale
654 areas, and the high variability in their life cycle strategies (Cornelius 1992; Gili and
655 Hughes 1995), make hydroids an interesting and useful model to explore biogeography,
656 connectivity, and endemism. Although exploring large-scale patterns through different
657 spatial resolutions of SSA & A, this study is focused on coastal benthic areas.
658 Additional integrative approaches involving data of the medusa stage and records from
659 greater depths will further improve the biogeographic knowledge of hydrozoans
660 inhabiting SSA & A. Similarly, expanding comparative studies to incorporate data from
661 South Africa and Oceania are necessary to more thoroughly understand hydrozoan
662 distributions in the southern hemisphere.

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REFERENCES

- Acha EM, Mianzan HW, Guerrero RA et al (2004) Marine fronts at the continental shelves of austral South America: physical and ecological processes. *J Marine Syst* 44:83–105. <https://doi.org/10.1016/j.jmarsys.2003.09.005>
- Acha EM, Viñas MD, Derisio C et al (2020) Large-scale geographic patterns of pelagic copepods in the southwestern South Atlantic. *J Marine Syst* 204:103281. <https://doi.org/10.1016/j.jmarsys.2019.103281>
- Ajala-Batista L, Lins DM, Haddad MA (2020) Diversity of estuarine and marine hydroids (Cnidaria, Hydrozoa) from subtropical ecosystems of Brazil. *Mar Biodivers* 50:97. <https://doi.org/10.1007/s12526-020-01133-0>
- Balech E (1954) División zoogeográfica del litoral sudamericano. *Rev Biol Mar* 4:184–195.
- Barroso CX, Lotufo TMC, Matthews-Cascon H (2016) Biogeography of Brazilian prosobranch gastropods and their Atlantic relationships. *J Biogeogr* 43:2477–2488. <https://doi.org/10.1111/jbi.12821>
- Bouillon J, Medel MD, Pagès F et al (2004) Fauna of the Mediterranean Hydrozoa. *Sci Mar* 68(Suppl 2):5–438. <https://doi.org/10.3989/scimar.2004.68s25>
- Briggs JC (1974) *Marine zoogeography*. McGrall-Hill, New York.
- Calder DR (1988) Shallow-water hydroids of Bermuda: the Athecatae. *Roy Ontario Mus Life Sci Contrs* 148:1–107.
- Calder DR (1991) Shallow-water hydroids of Bermuda: the Thecatae, exclusive of Plumularioidea. *Roy Ontario Mus Life Sci Contrs* 154:1–140.
- Calder DR (1993) Local distribution and biogeography of the hydroids (Cnidaria) of Bermuda. *Carib J Sci* 29:61–74.
- Camus PA (2001) Biogeografía marina de Chile continental. *Rev Chil Hist Nat* 74:587–617. <http://dx.doi.org/10.4067/S0716-078X2001000300008>
- Cartwright P, Evans NM, Dunn CW et al (2008) Phylogenetics of Hydroidolina (Hydrozoa: Cnidaria). *J Mar Biol Assoc UK* 88:1663–1672. <https://doi.org/10.1017/S0025315408002257>
- Clarke A (2008) Antarctic marine benthic diversity: patterns and processes. *J Exp Mar Biol Ecol* 366:48–55. <https://doi.org/10.1016/j.jembe.2008.07.008>
- Clarke KR, Gorley RN (2015) *Primer v7: user manual/tutorial*. 1st Edition. PRIMER-E, Plymouth.

- Clarke KR, Green RH (1988) Statistical design and analysis for a ‘biological effects’ study. *Mar Ecol* 46:213–226.
- Clarke KR, Warwick RM (1998) A taxonomic distinctness index and its statistical properties. *J Appl Ecol* 35:523–531.
- Clarke KR, Warwick RM (2001) A further biodiversity index applicable to species lists: variation in taxonomic distinctness. *Mar Ecol Prog Ser* 216:265–278. DOI: 10.3354/meps216265
- Clarke A, Barnes DKA, Hodgson DA (2005) How isolated is Antarctica? *Trends Ecol Evol* 20:1–3. <https://doi.org/10.1016/j.tree.2004.10.004>
- Clarke KR, Gorley RN, Somerfield PJ, Warwick RM (2014) Change in marine communities: an approach to statistical analysis and interpretation. 3rd Edition. PRIMER-e, Plymouth.
- Collins AG, Schuchert P, Marques AC et al (2006) Medusozoan phylogeny and character evolution clarified by new large and small subunit rDNA data and an assessment of the utility of phylogenetic mixture models. *Syst Biol* 55:97–115. <https://doi.org/10.1080/10635150500433615>
- Cornelius PFS (1992) Medusa loss in leptolid Hydrozoa (Cnidaria), hydroid rafting, and abbreviated life-cycles among their remote-island faunae: an interim review. In: Bouillon J, Boero F, Cicogna F, Gili J-M, Hughes RG (eds.) *Aspects of hydrozoan biology*, vol. 56. Scientia Marina, Barcelona, pp 245–261.
- Costello MJ, Coll M, Danovaro R et al (2010) A census of marine biodiversity knowledge, resources, and future challenges. *PLoS ONE* 5:e12110. <https://doi.org/10.1371/journal.pone.0012110>
- Costello MJ, Tsai P, Wong PS et al (2017) Marine biogeographic realms and species endemism. *Nat Commun* 8:1057. <https://doi.org/10.1038/s41467-017-01121-2>
- Cunha AF, Genzano GN, Marques AC (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:e0117553. <https://doi.org/10.1371/journal.pone.0117553>
- Cunha AF, Collins AG, Marques AC (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 Phylogenet Evol* 106:118–135.
<http://dx.doi.org/10.1016/j.ympev.2016.09.012>
- Dalziel IWD, Lawver LA, Norton IO, Gahagan LM (2013) The Scotia Arc: genesis, evolution, global significance. *Annu Rev Earth Pl Sc* 41:767–793.
<https://doi.org/10.1146/annurev-earth-050212-124155>
- De Broyer C, Danis B, with 64 SCAR-MarBIN Taxonomic Editors (2011) How many species in the Southern Ocean? Towards a dynamic inventory of the Antarctic marine species. *Deep-Sea Res II* 58:5–17.
<https://doi.org/10.1016/j.dsr2.2010.10.007>
- De Broyer C, Koubbi P (2014) The biogeography of the Southern Ocean. In: De Broyer C, Koubbi P, Griffiths HJ et al. (Eds.) *Biogeographic Atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, pp 2–9.
- Di Camillo CG, Bavestrello G, Valisano L, Puce S (2008) Spatial and temporal distribution in a tropical hydroid assemblage. *J Mar Biol Assoc UK* 88:1589–1599. <https://doi.org/10.1017/S0025315408002981>
- Di Camillo CG, Gravili C, De Vito D, et al (2018) The importance of applying Standardized Integrative Taxonomy when describing marine benthic organisms and collecting ecological data. *Invertebr Syst* 32:794–802.
<https://doi.org/10.1071/IS17067>
- Douglass LL, Turner J, Grantham HS et al (2014) A hierarchical classification of benthic biodiversity and assessment of protected areas in the Southern Ocean. *PLoS ONE* 9:e100551. <https://doi.org/10.1371/journal.pone.0100551>
- Downey RV, Griffiths HJ, Linse K, Janussen D (2012) Diversity and distribution patterns in high southern latitude sponges. *PLoS ONE* 7:e41672.
<https://doi.org/10.1371/journal.pone.0041672>
- Fernandez M, Jaramillo E, Marquet PA et al (2000) Diversity, dynamics and biogeography of Chilean benthic nearshore ecosystems: an overview and guidelines for conservation. *Rev Chil Hist Nat* 73:797–830.
<http://dx.doi.org/10.4067/S0716-078X2000000400021>
- Fernandez MO, Marques AC (2018) Combining bathymetry, latitude, and phylogeny to understand the distribution of deep Atlantic hydroids (Cnidaria). *Deep-Sea Res Pt I* 133:39–48. <https://doi.org/10.1016/j.dsr.2018.01.008>

- Fernandez MO, Collins AG, Marques AC (2020) Gradual and rapid shifts in the composition of assemblages of hydroids (Cnidaria) along depth and latitude in the deep Atlantic Ocean. *J Biogeogr* 47:1541–1551. <https://doi.org/10.1111/jbi.13853>
- Figuerola B, Gordon DP, Polonio V et al (2013) Cheilostome bryozoan diversity from the southwest Atlantic region: is Antarctica really isolated? *J Sea Res* 85:1–17. <http://dx.doi.org/10.1016/j.seares.2013.09.003>
- Frenot Y, Chown SL, Whinam J et al (2005) Biological invasions in the Antarctic: extent, impacts and implications. *Biol Rev* 80:45–72. <https://doi.org/10.1017/S1464793104006542>
- Genzano GN, Giberto D, Schejter L et al (2009) Hydroid assemblages from the Southwestern Atlantic Ocean (34–42°S). *Mar Ecol* 30:33–46. <https://doi.org/10.1111/j.1439-0485.2008.00247.x>
- Genzano GN, Bremec CS, Diaz-Briz L et al (2017) Faunal assemblages of intertidal hydroids (Hydrozoa, Cnidaria) from Argentinean Patagonia (Southwestern Atlantic Ocean). *Lat Am J Aquat Res* 45:177–187. <http://dx.doi.org/10.3856/vol45-issue1-fulltext-17>
- Gibbons MJ (1997) Pelagic biogeography of the South Atlantic Ocean. *Mar Biol* 129:757–768. <https://doi.org/10.1007/s002270050218>
- Gibbons MJ, Buecher E, Thibault-Botha D, Helm RR (2010a) Patterns in marine hydrozoan richness and biogeography around southern Africa: implications of life cycle strategy. *J Biogeogr* 37:606–616.
- Gibbons MJ, Janson LA, Ismail A, Samaai T (2010b) Life cycle strategy, species richness and distribution in marine Hydrozoa (Cnidaria: Medusozoa) *J Biogeogr* 37:441–448.
- Gili J-M, Hughes RG (1995) The ecology of marine benthic hydroids. *Oceanogr Mar Biol Ann Rev* 33:351–426.
- Gili J-M, Zapata-Guradiola R, Isla E et al (2016) Introduction to the special issue on the Life in Antarctica: boundaries and gradients in a changing environment (XIth SCAR Biology Symposium). *Polar Biol* 39:1–10. <https://doi.org/10.1007/s00300-015-1852-3>
- Gillespie RG, Roderick GK (2014) Geology and climate drive diversification. *Nature* 509:297–298. <https://doi.org/10.1038/509297a>
- González-Wevar CA, Nakano T, Cañete JI, Poulin E (2010) Molecular phylogeny and historical biogeography of *Nacella* (Patellogastropoda: Nacellidae) in the

- Southern Ocean. *Mol Phylogenet Evol* 56:115–124.
<https://doi.org/10.1016/j.ympev.2010.02.001>
- González-Wevar CA, Hüne M, Cañete JI et al (2012) Towards a model of postglacial biogeography in shallow marine species along the Patagonian Province: lessons from the limpet *Nacella magellana* (Gmelin, 1791). *BMC Evol Biol* 12:139-154.
<https://doi.org/10.1186/1471-2148-12-139>
- Grange LJ, Smith CR (2013) Megafaunal communities in rapidly warming fjords along the west Antarctic Peninsula: hotspots of abundance and beta diversity. *Plos ONE* 8:e77917. <https://doi.org/10.1371/journal.pone.0077917>
- Gravili C (2016) Zoogeography of Hydrozoa: past, present and a look to the future. In: Goffredo S, Dubinsky Z (eds) *The Cnidaria, past, present and future*, 1st edn. Springer, pp 95–107. <https://doi.org/10.1007/978-3-319-31305-4>
- Gravili C, Di Camillo C, Piraino S, Boero F (2013) Hydrozoan species richness in the Mediterranean Sea: past and present. *Mar Ecol* 34:41–62.
<https://doi.org/10.1111/maec.12023>
- Griffiths HJ, Branes DKA, Linse K (2009) Towards a generalized biogeography of the Southern Ocean benthos. *J Biogeogr* 36:162–177. <https://doi.org/10.1111/j.1365-2699.2008.01979.x>
- Griffiths HJ (2010) Antarctic marine biodiversity – what do we know about the distribution of life in the Southern Ocean? *PLoS ONE* 5:e11683.
<https://doi.org/10.1371/journal.pone.0011683>
- Griffiths HJ, Waller CL (2016) The first comprehensive description of the biodiversity and biogeography of Antarctic and Sub-Antarctic intertidal communities. *J Biogeogr* 43:1143–1155. <https://doi.org/10.1111/jbi.12708>
- Henry LA, Nizinski MS, Ross SW (2008) Occurrence and biogeography of hydroids (Cnidaria: Hydrozoa) from deep-water coral habitats off the southeastern United States. *Deep-Sea Res Pt I* 55:788–800. <https://doi.org/10.1016/j.dsr.2008.03.002>
- Hortal J (2008) Uncertainty and the measurement of terrestrial biodiversity gradients. *J Biogeogr* 35:1335–1336. <https://doi.org/10.1111/j.1365-2699.2008.01955.x>
- Hortal J, Lobo JM, Jiménez-Valverde A (2007) Limitations of biodiversity databases: case study on seed-plant diversity in Tenerife, Canary Islands. *Conserv Biol* 21:853–863. <https://doi.org/10.1111/j.1523-1739.2007.00686.x>

- Khalighifar A, Jiménez L, Nuñez-Penichet C et al (2020) Inventory statistics meet big data: complications for estimating numbers of species. *PeerJ* 8:e8872.
<https://doi.org/10.7717/peerj.8872>
- Kayal E, Bentlage B, Cartwright P et al (2015). Phylogenetic analysis of higher-level relationships within Hydroidolina (Cnidaria: Hydrozoa) using mitochondrial genome data and insight into their mitochondrial transcription. *PeerJ* 3:e1403.
<https://doi.org/10.7717/peerj.1403>
- Kerr R, Mata MM, Mendes, CRB, Secchi ER (2018) Northern Antarctic Peninsula: a marine climate hotspot of rapid changes on ecosystems and ocean dynamics. *Deep-Sea Res Pt II* 149:4–9. <https://doi.org/10.1016/j.dsr2.2018.05.006>
- Koubbi P, de Broyer C, Griffiths H et al (2014) Conclusions: present and future of Southern Ocean biogeography. In: De Broyer C, Koubbi P, Griffiths HJ et al. (eds) *Biogeographic atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, pp 470–475.
- Lancellotti DA, Vásquez JA (1999) Biogeographical patterns of benthic macroinvertebrates in the Southeastern Pacific littoral. *J Biogeogr* 26:1001–1006.
<https://doi.org/10.1046/j.1365-2699.1999.00344.x>
- Lawver LA, Gahagan LM (2003) Evolution of Cenozoic seaways in the circum-Antarctic region. *Palaeogeogr Palaeocl* 198:11–37. [https://doi.org/10.1016/S0031-0182\(03\)00392-4](https://doi.org/10.1016/S0031-0182(03)00392-4)
- Leclère L, Schuchert P, Cruaud C et al (2009) Molecular phylogenetics of Thecata (Hydrozoa, Cnidaria) reveals long-term maintenance of life history traits despite high frequency of recent character changes. *Syst Biol* 58:509-526.
<https://doi.org/10.1093/sysbio/syp044>
- Linse K (2006) New records of shelled marine molluscs at Bouvet Island and preliminary assessment of their biogeographic affinities. *Polar Biol* 29:120–127.
<https://doi.org/10.1007/s00300-005-0721-x>
- Linse K, Griffiths HJ, Barnes DKA, Clarke A (2006) Biodiversity and biogeography of Antarctic and sub-Antarctic mollusca. *Deep Sea Res II* 53:985–1008.
<https://doi.org/10.1016/j.dsr2.2006.05.003>
- Lynch HJ, Crosbie K, Fagan WF, Naveen R (2010) Spatial patterns of tour ship traffic in the Antarctic Peninsula region. *Antarct Sci* 22:123–130.
<https://doi.org/10.1017/S0954102009990654>

- Maldonado A, Dalziel IWD, Leat PT (2015) The global relevance of the Scotia Arc: an introduction. *Global Planet Change* 125:A1–A8.
<http://dx.doi.org/10.1016/j.gloplacha.2014.06.011>
- Maronna MM, Miranda TP, Peña Cantero AL et al (2016) Towards a phylogenetic classification of Leptothecata (Cnidaria, Hydrozoa). *Sci Rep* 6:18075.
<https://doi.org/10.1038/srep18075>
- Marques AC, Peña Cantero AL (2010) Areas of endemism in the Antarctic – a case study of the benthic hydrozoan genus *Oswaldella* (Cnidaria, Kirchenpaueriidae). *J Biogeogr* 37:617–623. <https://doi.org/10.1111/j.1365-2699.2009.02238.x>
- Mayr E (1963) *Animal species and evolution*. Harvard University Press, Cambridge.
- Mendoza-Becerril MM, Jaimes-Becerra AJ, Collins AG, Marques AC (2018). Phylogeny and morphological evolution of the so-called bougainvilliids (Hydrozoa, Hydroidolina). *Zool Scr* 47:608–622.
<https://doi.org/10.1111/zsc.12291>
- Mercado Casares B, Soto Àngel JJ, Peña Cantero AL (2017) Towards a better understanding of Southern Ocean biogeography: new evidence from benthic hydroids. *Polar Biol* 40:1975–1988. <https://doi.org/10.1007/s00300-017-2113-4>
- Miloslavich P, Klein E, Díaz JM et al (2011) Marine biodiversity in the Atlantic and Pacific coasts of South America: knowledge and gaps. *PLoS ONE* 6:e14631.
<https://doi.org/10.1371/journal.pone.0014631>
- Miloslavich P, Cruz-Motta JJ, Hernández A et al (2016) Benthic assemblages in South American intertidal rocky shores: biodiversity, services, and threats. In: Riosmena-Rodríguez R (ed) *Marine benthos: biology, ecosystem functions and environmental impact*. Nova Science Publishers, New York.
- Miranda TP, Peña Cantero AL, Marques AC (2013) Southern Ocean areas of endemism: a reanalysis using benthic hydroids (Cnidaria, Hydrozoa). *Lat Am J Aquat Res* 41:1003–1009. <https://doi.org/103856/vol41-issue5-fulltext-20>
- Miranda TP, Genzano GN, Marques AC (2015) Areas of endemism in the southwestern Atlantic Ocean based on the distribution of benthic hydroids (Cnidaria: Hydrozoa). *Zootaxa* 4033:484–506. <http://dx.doi.org/10.11646/zootaxa.4033.4.2>
- Montiel ASM, Gerdes D, Arntz WE (2005) Distributional patterns of shallow-water polychaetes in the Magellan region: a zoogeographical and ecological synopsis. *Sci Mar* 69:123–133. <http://dx.doi.org/10.3989/scimar.2005.69s2123>

- Moon KL, Chown SL, Fraser CI (2017) Reconsidering connectivity in the sub-Antarctic. *Biol Rev* <https://doi.org/10.1111/brv.12327>.
- Moura CJ, Cunha MR, Porteiro FM, Rogers AD (2011) The use of the DNA barcode gene 16S mRNA for the clarification of taxonomic problems within the family Sertulariidae (Cnidaria, Hydrozoa). *Zool Scr* 40:520–537. <https://doi.org/10.1111/j.1463-6409.2011.00489.x>
- Mühlenhardt-Siegel U (1999) On the biogeography of Cumacea (Crustacea, Malacostraca). A comparison between South America, the Subantarctic Islands and Antarctica: present state of art. *Sci Mar* 63(Suppl. 1):295–302. <https://doi.org/10.3989/scimar.1999.63s1295>
- Oliveira OMP, Miranda TP, Araújo EM et al (2016) Census of the Cnidaria (Medusozoa) and Ctenophora from South American marine waters. *Zootaxa* 4194:1–256. <http://doi.org/10.11646/zootaxa.4194.1.1>
- Orme CDL, Davies RG, Burgess M et al (2005) Global hotspots of species richness are not congruent with endemism or threat. *Nature* 436:1016–1019. <https://doi.org/10.1038/nature03850>
- Palacio FJ (1982) Revisión zoogeográfica marina del sur del Brasil. *Bol Inst Oceanogr* 31:69–92.
- Palomares MLD, Froese R, Derrick B et al (2020) Fishery biomass trends of exploited fish populations in marine ecoregions, climatic zones and ocean basins. *Estuar Coast Shelf S* 243:106896. <https://doi.org/10.1016/j.ecss.2020.106896>
- Peña Cantero AL (2004) How rich is the deep-sea Antarctic benthic hydroid fauna? *Polar Biol* 27:767–774. <https://doi.org/10.1007/s00300-004-0654-9>
- Peña Cantero AL (2014) Benthic hydroids (Cnidaria, Hydrozoa). In: De Broyer C, Koubbi P, Griffiths HJ et al (eds.) *Biogeographic Atlas of the Southern Ocean*. Scientific Committee on Antarctic Research, Cambridge, pp 103-106.
- Peña Cantero AL (2021) Biodiversity, distribution and community structure of benthic hydroids from Point Géologie Archipelago (Dumont d’Urville Sea, Adélie Land, Antarctica). *Polar Biol* 44:407–420. <https://doi.org/10.1007/s00300-021-02802-x>
- Pierrat B, Saucède T, Brayard A, David B (2013) Comparative biogeography of echinoids, bivalves and gastropods from the Southern Ocean. *J Biogeogr* 40:1374–1385. <https://doi.org/10.1111/jbi.12088>

- Poore GCB, Bruce NL (2012) Global diversity of marine isopods (except Asellota and crustacean symbionts). *PLoS ONE* 7:e43529.
<https://doi.org/10.1371/journal.pone.0043529>
- Possingham HP, Wilson KA (2005) Turning up the heat on hotspots. *Nature* 436:919–920. <https://doi.org/10.1038/436919a>
- Primo C, Vásquez E (2009) Antarctic ascidians: an isolated and homogeneous fauna. *Polar Res* 28:403–414. <https://doi.org/10.1111/j.1751-8369.2009.00110.x>
- Ramos-Esplá AA, Cárcel JA, Varela M (2005) Zoogeographical relationships of the littoral ascidiofauna around the Antarctic Peninsula, in the Scotia Arc and in the Magellan region. *Sci Mar* 69:215–223.
<https://doi.org/10.3989/scimar.2005.69s2215>
- Ronowicz M, Kukliński P, Mapstone GM (2015) Trends in diversity, distribution and life history strategy of Arctic Hydrozoa (Cnidaria). *PLoS ONE* 10:e0120204.
<https://doi.org/10.1371/journal.pone.0120204>
- Ronowicz M, Peña Cantero AL, Mercado Casares B et al (2019) Assessing patterns of diversity, bathymetry and distribution at the poles using Hydrozoa (Cnidaria) as a model group. *Hydrobiologia* 833:25–51. <https://doi.org/10.1007/s10750-018-3876-5>
- Sanches PF, Pellizzari F, Horta PA (2016) Multivariate analyses of Antarctic and sub-Antarctic seaweed distribution patterns: an evaluation of the role of the Antarctic Circumpolar Current. *J Sea Res* 110:29–38.
<http://dx.doi.org/10.1016/j.seares.2016.02.002>
- Santos AMC, Jones OR, Quicke DJ, Hortal J (2010) Assessing the reliability of biodiversity databases: identifying evenly inventoried island parasitoid faunas (Hymenoptera: Ichneumonoidea) worldwide. *Insect Conserv Diver* 3:72–82.
<https://doi.org/10.1111/j.1752-4598.2010.00079.x>
- Scott KN (2012). Conservation on the high areas: developing the concept of the high seas marine protected areas. *Int J Mar Coastal Law* 27:849–857.
<https://doi.org/10.1163/15718085-12341243>
- Selig ER, Turner WR, Troëng S et al (2014) Global priorities for marine biodiversity conservation. *PLoS ONE* 9:e82898. <https://doi.org/10.1371/journal.pone.0082898>
- Sepúlveda RD, Camus PA, Moreno CA (2016) Diversity of faunal assemblages associated with ribbed mussel beds along the South American coast: relative roles

- of biogeography and bioengineering. *Mar Ecol* 37:943–956.
<https://doi.org/10.1111/maec.12301>
- Schejter L, Rimondino C, Chiesa I et al (2016) Namuncurá Marine Protected Area: an oceanic hot spot of benthic biodiversity at Burdwood Bank, Argentina. *Polar Biol* 39:2373–2386. <https://doi.org/10.1007/s00300-016-1913-2>
- Schuchert P (2021) World Hydrozoa Database. Accessed through: World Register of Marine Species at <http://marinespecies.org/aphia.php?p=taxdetails&id=174552> Accessed on March 21st 2021.
- Soto Àngel JJ, Peña Cantero AL (2017) A new piece in the puzzle of the Antarctic biogeography: what do benthic hydroids tell us about the Scotia Arc affinities? *Polar Biol* 40:863–872. <https://doi.org/10.1007/s00300-016-2013-z>
- Soto Àngel JJ, Peña Cantero AL (2019) Benthic hydroids (Cnidaria, Hydrozoa) from the Weddell Sea (Antarctica). *Zootaxa* 4570:1–78.
<https://doi.org/10.11646/zootaxa.4570.1.1>
- Souto V, Escolar M, Genzano G, Bremec C (2014) Species richness and distribution patterns of echinoderms in the southwestern Atlantic Ocean (34–56°S). *Sci Mar* 78:269–280. <http://dx.doi.org/10.3989/scimar.03882.26B>
- Spalding MD, Fox H, Allen GR et al (2007). Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *BioScience* 57:573–583.
<https://doi.org/10.1641/B570707>
- Spalding MD, Agostini VN, Rice J, Grant SM (2012) Pelagic provinces of the world: a biogeographic classification of the world’s surface pelagic waters. *Ocean Coast Manage* 60:19–30. <https://doi.org/10.1016/j.ocecoaman.2011.12.016>
- Summers N, Watling L (2021) Upper bathyal Pacific ocean biogeographic provinces from octocoral distributions. *Prog Oceanogr* 191:102509.
<https://doi.org/10.1016/j.pocean.2020.102509>
- Sutton TT, Clark MR, Dunn DC et al (2017) A global biogeographic classification of the mesopelagic zone. *Deep-Sea Res Pt I* 126:85–102.
<http://dx.doi.org/10.1016/j.dsr.2017.05.006>
- Svoboda A, Stepanjants SD (2001) Redescription of two Antarctic Corymorphidae species and the reestablishment of the genus *Monocaulus* (Cnidaria: Hydrozoa). *Mar Ecol* 22:53–70. <https://doi.org/10.1046/j.1439-0485.2001.00742.x>

- Thompson MSA, Couce E, Webb TJ et al (2020) What's hot and what's not: making sense of biodiversity 'hotspots'. *Glob Change Biol* 27:521–535.
<https://doi.org/10.1111/gcb.15443>
- Yang W, Ma K, Kreft H (2013) Geographical sampling bias in a large distributional database and its effects on species richness-environment models. *J Biogeogr* 40:1415–1426. <https://doi.org/10.1111/jbi.12108>
- Vilar CC, Magris RA, Loyola R, Joyeux JC (2019) Strengthening the synergies among global biodiversity targets to reconcile conservation and socio-economic demands. *Aquatic Conserv Mar Freshw Ecosyst* 30:497–513.
<https://doi.org/10.1002/aqc.3269>
- Warwick RM, Clarke KR (1995) New 'biodiversity' measures reveal a decrease in taxonomic distinctness with increasing stress. *Mar Ecol Prog Ser* 129:301–305.
- Watling L, Guinotte J, Clark MR, Smith CR (2013) A proposed biogeography of the deep ocean floor. *Prog Oceanogr* 111:91–112.
<http://dx.doi.org/10.1016/j.pocean.2012.11.003>
- Willis KJ, Wittacker RJ (2002) Species diversity – scale matters. *Science* 295:1245–1248. <https://doi.org/10.1126/science.1067335>

Table 1 Richness, average taxonomic distinctness (AvTD) and variation in taxonomic distinctness (VarTD) estimated for each ecoregion analyzed. Refer to Fig. 1 for ecoregions numbers.

Ecoregion	Species	Genera	Families	Infraorders	Suborders	Orders	Superorders	AvTD	VarTD
76	23	19	13	9	9	4	2	79.39	413.34
176	2	2	2	2	2	2	1	85.71	0
177	14	8	8	6	6	4	2	68.29	815.44
178	6	5	5	5	5	3	2	80.95	453.51
180	85	46	26	14	12	7	2	79.80	466.02
181	14	12	11	9	8	6	2	86.34	353.95
182	10	9	9	9	8	5	2	86.03	258.40
183	47	29	21	15	13	8	2	80.84	392.50
184	35	22	16	12	11	6	2	78.03	438.31
185	45	24	18	11	10	6	2	74.92	496.57
186	20	11	9	6	5	3	1	68.72	476.02
187	58	25	19	13	10	6	2	74.47	435.45
188	9	7	7	6	6	3	2	79.76	401.08
217	5	3	3	2	2	1	1	54.29	522.45
218	6	5	5	3	3	2	1	66.67	426.30
219	16	4	4	2	2	1	1	48.57	552.38
220	17	4	4	2	2	1	1	44.33	580.07
221	25	10	8	6	6	4	2	63.67	581.25
222	69	16	13	9	9	6	2	63.62	548
223	59	17	16	9	9	6	2	67.58	607.45
224	30	12	12	8	8	5	2	66.93	530.07
226	9	2	2	2	2	1	1	26.98	564.37
227	38	9	9	8	8	5	2	61.80	734.58
229	34	11	10	7	7	4	2	65.98	604.01

Table 2 Richness, average taxonomic distinctness (AvTD) and variation in taxonomic distinctness (VarTD) estimated for each province analyzed. Refer to Fig. 1 for provinces acronyms.

Province	Species	Genera	Families	Infraorders	Suborders	Orders	Superorders	AvTD	VarTD
A	39	12	12	9	9	5	2	60.90	633.92
APF	15	9	8	5	5	3	2	68.03	635.66
CHA	60	13	12	10	10	5	2	62.74	640.34
M	81	35	22	14	11	7	2	75.67	449.51
S	25	15	12	7	6	3	1	66.90	502.66
SI	7	4	4	2	2	1	1	53.74	503.49
SS	86	21	17	11	11	7	2	65.80	593.23
TSWA	20	17	12	8	7	4	2	80.38	387.18
WTSEP	14	9	8	6	6	4	2	71.11	672.70
WTSWA	111	57	32	14	12	8	2	80.92	417.11

FIGURE CAPTIONS

Fig. 1 Ecoregions (a) and provinces (b) for southern South America and Antarctica (modified from Spalding et al. 2007, 2012). 76: eastern Brazil; 176: Humboldtian; 177: central Chile; 178: Araucanian; 180: southeastern Brazil; 181: Rio Grande; 182: Rio de La Plata; 183: Uruguay-Buenos Aires shelf; 184: north Patagonian gulfs; 185: Patagonian shelf; 186: Malvinas/Falklands; 187: channels and fjords of southern Chile; 188: Chiloense; 217: Bouvet Island; 218: Peter the First Islands; 219: South Sandwich Islands; 220: South Georgia; 221: South Orkney Islands; 222: South Shetlands Islands; 223: Antarctic Peninsula; 224: east Antarctic Wilkes Land; 226: east Antarctic Dronning Maud Land; 227: Weddell Sea; 229: Ross Sea; TSWA: Tropical Southwestern Atlantic; WTSWA: Warm Temperate Southwestern Atlantic; M: Magellan; WTSEP: Warm Temperate Southeastern Pacific; S: Subantarctic; APF: Antarctic Polar Front; A: Antarctic; SS: Scotia Sea; CHA: Continental High Antarctica; SI: Subantarctic Islands

Fig. 2 Distribution of the endemic and non-endemic species of hydroids sampled along southern South America and Antarctica. The graphics show the number of geographic locations (total: 1,360), non-endemic (total: 121) and endemic species (total: 128) examined by latitudinal band.

Fig. 3 Number of endemic species of hydroids in each of the eight categories of endemism recognized for the southern South America and Antarctica. “Total” is the total number of endemic species of hydroids recorded for the whole coast of SSA & A. The numbers in bold and between parenthesis are the percentages of endemic species of hydroids for each of the eight categories of endemism for the SSA & A in relation to the “Total”. See Online Resource Table S1 for details on the endemic species distribution.

Fig. 4 Sample-based rarefaction curves of species of hydroids from Southern South America and Antarctica ecoregions (a) and provinces (b). Refer to Fig. 1 for ecoregion numbers and provinces acronyms.

Fig. 5 Funnel plots for the (a) average taxonomic distinctness (AvTD) and (b) variation in taxonomic distinctness (VarTD) simulated for each southern South American and Antarctic ecoregion. Dashed lines indicate the AvTD and VarTD for the master list of

species of hydroids. Black lines show the 95% probability interval for simulated AvTD and VarTD. Blue triangles and red crosses represent the ecoregions of SSA & A, respectively. Refer to Fig. 1 for ecoregions numbers.

Fig. 6 Funnel plots for the (a) average taxonomic distinctness (AvTD) and (b) variation in taxonomic distinctness (VarTD) simulated for each southern South American and Antarctic province. Dashed lines indicate the AvTD and VarTD for the master list of species of hydroids. Black lines show the 95% probability interval for simulated AvTD and VarTD. Blue triangles and red crosses represent the provinces of SSA & A, respectively. Refer to Fig. 1 for provinces acronyms.

Fig. 7 (a) Dendrogram and SIMPROF test among ecoregions from southern South America and Antarctica. Black lines indicate statistically significant clusters: E1 to E9 for Antarctica, and E10 to E17 for SSA. (b) Non-metric multidimensional scaling (nMDS) ordination plot of southern South American (blue triangles) and Antarctic (red crosses) ecoregions. Refer to Fig. 1 for ecoregions numbers.

Fig. 8 (a) Dendrogram and SIMPROF test among provinces from southern South America and Antarctica. Black lines indicate statistically significant clusters: P1 and P2 for SSA, and P3 to P7 for Antarctica. (b) Non-metric multidimensional scaling (nMDS) ordination plot of southern South American (blue triangles) and Antarctic (red crosses) provinces. Refer to Fig. 1 for provinces acronyms.

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