

1 **Gradual and rapid shifts in the composition of assemblages of hydroids (Cnidaria) along depth**  
2 **and latitude in the deep Atlantic Ocean**

3  
4 **Running title:** Turnover of hydroids along depth and latitude

5  
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35

36 **Abstract**

37 **Aim:** Despite growing knowledge on deep-sea benthic fauna, patterns of changes in species  
38 composition combining both bathymetric and latitudinal variation are still poorly known. In  
39 the first synthesis on the beta-diversity patterns of assemblages of hydroids across an entire  
40 ocean basin, our aim was to infer limits and gradients of species distribution along depth and  
41 latitude.

42 **Location:** Atlantic Ocean and adjacent polar seas.

43 **Taxon:** Hydrozoa.

44 **Methods:** Hydroids from 50 to 5,330 m deep were studied primarily based on museum  
45 collections. Identifications were made by the authors, improving uniformity within the dataset  
46 by avoiding variations in taxonomic interpretation. Data totaled 3,699 records belonging to 432  
47 species, at 1,444 unique sites. Records were assigned to three depth strata (50–200 m, 201–  
48 1,000 m, and 1,001–5,330 m) and 8 latitudinal bands of 20° each, totaling 24 sample areas. We  
49 conducted NMDS ordination, clustering, and PERMANOVA analyses of species compositions  
50 and abundances per area to examine differences and relationships in hydroid assemblages  
51 among areas.

52 **Results:** Assemblages primarily differentiate between those to the north and south of 40°S,  
53 regardless of depth, with southern ones separated between Patagonian and Antarctic.  
54 Northwards of 40°S, assemblages differentiate gradually along both depth and latitude,  
55 although a faunal turnover occurs at 1,000 m deep. Also, assemblages at 1,001–5,330 m deep  
56 tend to be more similar to each other than assemblages at shallower strata, suggesting  
57 significant connectivity over great distances in the deep sea. We note the problem of largely  
58 unequal hydroid sampling in the Atlantic Ocean across depths and latitudes, especially in the  
59 southern hemisphere and below 1,000 m deep.

60 **Main conclusions:** Assemblages of hydroids differentiate gradually along latitude and depth,  
61 with more rapid shifts in species composition occurring at 40°S, 60°S, and at 1,000 m deep.  
62 Greater similarity was found among deeper water assemblages.

63

64 **Keywords:** Atlantic Ocean, deep-sea benthos, depth, faunal changes, Hydrozoa, latitude,  
65 marine biogeography, turnover

66

## 67 **Introduction**

68

69 The geographical distribution of every species is shaped by evolutionary, ecological,  
70 and physiological processes, and when analyzed holistically over groups of species with  
71 overlapping ranges define global biogeographical patterns (Jablonski, Flessa, & Valentine,  
72 1985; Morrone, 2009; Valentine, 1973). Gradual or rapid shifts in species composition are a  
73 consequence of the evolutionary history of the species, and may be caused by physical or  
74 environmental factors that impact dispersal and survival (Lomolino, Riddle, & Whittaker,  
75 2017; Valentine, 1973). Theoretically, physical variables such as topography, currents, water  
76 masses, heterogeneity in temperature and oxygen, or biological variables like food availability,  
77 operate as putative barriers controlling the distributions of marine invertebrates (Carney, 2005;  
78 Gooday et al., 2010; Levin et al., 2001; McClain & Hardy, 2010). At the population level,  
79 geographical distance may impair, even stop, gene flow among populations, gradually leading  
80 to faunal differentiation via speciation (McClain, Stegen, & Hurlbert, 2012; Postaire, G lin,  
81 Bruggemann, Pratlong, & Magalon, 2017; Soininen, McDonald, & Hillebrand, 2007).

82 Evolution in the deep sea points to an alternative general scenario. Barriers to dispersal  
83 are difficult to identify in deep-sea habitats, although they presumably could be inferred from  
84 patterns of geographical distributions of the species making up deep-sea communities  
85 (McClain & Hardy, 2010; McClain, Stegen, & Hurlbert, 2012; Van Dover, German, Speer,  
86 Parson, & Vrijenhoek, 2002; Zezina, 1997). Also, greater environmental homogeneity found  
87 at bathyal and abyssal depths would enlarge species' geographic ranges, decreasing  
88 biogeographic differentiation (Zezina, 1997). Indeed, molecular analyses of numerous species  
89 suggest continuous gene flow along great distances in the deep sea (Dambach, Raupach, Leese,  
90 Schwarzer, & Engler, 2016; Eilertsen & Malaquias, 2015; Everett et al., 2016), even in  
91 disconnected and patchy ecosystems such as hydrothermal vents or cold seeps (Beedessee et  
92 al., 2013; Teixeira et al., 2013; De Groote, Hauquier, Vanreusel, & Derycke, 2017; Van Dover  
93 et al., 2002; Won, Young, Lutz, & Vrijenhoek, 2003). However, a general assumption of  
94 tenuous or non-existent barriers and presumed environmental homogeneity at the deep-sea  
95 floor favoring cosmopolitan distributions is contradicted in some cases, as indicated by limited  
96 gene flow among populations and metapopulations (LaBella, Van Dover, Jollivet, &  
97 Cunningham, 2017; Vrijenhoek, 2010), as well as highly endemic taxa restricted to abyssal  
98 depths and deep trenches (Vinogradova, 1979).

99 Faunal turnover related to local scale habitat heterogeneity is pervasive in the deep-sea  
100 benthos (Judge & Barry, 2016; McClain & Barry, 2010; McClain, Nekola, Kuhnz, & Barry,  
101 2011; Vanreusel et al., 2010; Zeppilli, Bongiorno, Santos, & Vanreusel, 2014). At the regional  
102 scale, however,  $\beta$ -diversity is more influenced by environmental variations in temperature and  
103 particulate organic carbon (POC) flux to the seafloor (McClain & Rex, 2015; UNESCO, 2009;  
104 Watling, Guinotte, Clark, & Smith, 2013; Wei et al., 2010; Woolley et al., 2016), two key  
105 drivers that would structure communities along depth (Carney, 2005; Rex & Etter, 2010; Rex

106 et al., 2005). Indeed, faunal turnovers with depth are particularly common at the shelf break,  
107 around 1,000 m deep, and between 2,000 and 3,000 m deep, mostly correlated with temperature  
108 and food supply shifts, although specific boundaries may vary across regions and latitudes  
109 (reviewed in Carney, 2005).

110 Knowledge on biogeographical patterns of deep-sea communities is scant when  
111 compared to terrestrial and coastal marine ecosystems (UNESCO, 2009; Watling, Guinotte,  
112 Clark, & Smith, 2013). Inferences are generally based on a single genus or species (e.g.  
113 Eilertsen & Malaquias, 2015; Rex, Stuart, Etter, & McClain, 2010). Few studies have  
114 investigated changes in faunal composition combining both depth and latitude. A study on  
115 protobranch bivalves in the Atlantic found greater species turnover along depth than between  
116 ocean basins, although changes were less marked at bathyal and abyssal depths than at the shelf  
117 break (Allen & Sanders, 1996). Similarly, assemblages of benthic molluscs in the Gulf of  
118 Mexico were found to be structured more by depth than by geographic distance, with greatest  
119 faunal changes occurring at the continental shelf break and at 3,000 m depth (Shantharam &  
120 Baco, 2020). Zonation of protobranchs along latitude was less clear at bathyal and abyssal  
121 depths, where cosmopolitan species are more frequent than at shallow depths (Allen & Sanders,  
122 1996). Biogeographical analysis of the ophiuroid fauna in the South Pacific, Indian, and  
123 Southern Ocean found that latitudinal changes in species composition were different at shelf  
124 and bathyal depths, and that the bathyal fauna gradually changes along latitude, with no clear  
125 biogeographical breaks (O'Hara, Rowden & Bax, 2011).

126 For hydroids, there are only regional biogeographical syntheses, mostly focusing on  
127 shallow-water habitats (e.g. Antsulevich, 2015; Genzano, Giberto, Schejter, Bremec, &  
128 Meretta, 2009; Henry, Nizinski, & Ross, 2008; Miranda, Genzano, & Marques, 2015; Peña  
129 Cantero, Ferrer, & Miranda, 2017; Ronowicz, Kuklinski, & Mapstone, 2015). However,  
130 hydroids are broadly distributed both in shallow and deep-sea habitats (Calder, 1998; Gebruk,  
131 Chevaldonné, Shank, Lutz, & Vrijenhoek, 2000; Henry et al., 2008; Kramp, 1956), with great  
132 intra and interspecific variation across environments (review in Cunha, Maronna, & Marques,  
133 2016; Fernandez & Marques, 2018; Fernandez, Collins, Gittenberger, Roy, & Marques, 2020).  
134 Our aim in this study was to infer patterns of change in species composition of hydroids along  
135 depth and latitude in the deep Atlantic Ocean and adjacent polar seas.

136

## 137 **Material and Methods**

138

### 139 *Study area and data collection*

140

141 Hydroids (Milleporidae, Stylasteridae and Limnomedusae excepted) from the Atlantic  
142 Ocean and adjacent Arctic and Antarctic seas, with geographic and depth data, from 50 to 5,330  
143 m deep, were studied primarily based on museum collections. Identifications were confirmed  
144 or made by the authors, improving the uniformity of taxonomic interpretation within the

145 dataset. Records were assigned to three depth strata comprising the lower continental shelf  
146 (50–200 m), the upper bathyal (201–1,000 m), and the lower bathyal and abyssal plains (1,001–  
147 5,330 m) and 8 latitudinal bands of 20° each (61°–80°N, 41°–60°N, 21°–40°N, 0°–20°N, 0°–  
148 20°S, 21°–40°S, 41°–60°S, and 61°–80°S), totaling 24 sample areas (Figure 1, Table 1). Six out  
149 of the 24 areas with 10 or less records were excluded from the analyses (*viz.*, 201–1,000 m for  
150 61°–80°N and 0°–20°S; and 1,001–5,330 m for 61°–80°N, 0°–20°S, 41°–60°S, and 61°–80°S).  
151 Depth strata were chosen considering the decreasing number of records with increasing depth  
152 and previous hypotheses of faunal turnover at the continental shelf break (~200 m) and at the  
153 depth of the permanent thermocline (~1,000 m), where temperatures become nearly constant  
154 (Carney, 2005). Latitudinal bands encompass equidistant intervals.

155

### 156 *Data analyses*

157

158 Only taxa identified to species level were used in the analyses. Aplanulata indet.;  
159 *Euphysora ?bigelowi* Maas, 1905; *Millardiana* sp.; and Oceaniidae indet. were also included  
160 as unique species. We built individual-based rarefaction curves by permutation using  
161 ‘rarecurve’ function in the ‘vegan’ package (Oksanen et al., 2017) to assess quality of  
162 samplings among areas. We calculated the Chao estimate of richness using the ‘estimateR’  
163 function in areas with more than 200 records.

164 Species compositions and abundances (i.e. number of records of each species) per area  
165 were used for multivariate analyses. Data were standardized by the total abundance of each  
166 area, dividing the abundance of each species by the total abundance in the area. Although not  
167 completely solving the problem of unequal sampling effort among areas, this standardization  
168 equalizes total abundances among areas while maintaining differences in species abundances  
169 within areas. Analyses were based on Bray-Curtis dissimilarities of the fourth-root transformed  
170 data, allowing both the most abundant and rarer species to exert some influence on the  
171 similarities between the areas.

172 Non-metric multidimensional scaling (NMDS) ordination was carried out to examine  
173 gradual differences among areas, using the ‘metaMDS’ function of the ‘vegan’ package  
174 (Oksanen et al., 2017), with 100 random starts. The ‘metaMDS’ function rotates the final  
175 ordination configuration and scales it to center the origin to the average of principal  
176 components axes and to place the greatest variance of points in the first axis, although it is the  
177 relative positions of the points in the ordination that matters (Kreft & Jetz, 2010; Oksanen et  
178 al., 2017).

179 We performed a hierarchical clustering analysis using UPGMA algorithm to investigate  
180 relationships in assemblages of hydroids among areas. The resulting clusters were tested for  
181 significance with a similarity profile analysis (1,000 permutations, 0.05 significance level),  
182 performed with ‘simprof’ function of the ‘clustsig’ package (Whitaker & Christman, 2014).

183 Statistical difference between areas was tested through a permutational multivariate  
184 analysis of variance (PERMANOVA; Anderson, 2001), using the ‘adonis’ function of the  
185 ‘vegan’ package (Oksanen et al., 2017), with 999 permutations. Depth and latitude were  
186 considered as crossed factors to test for interaction between their effects on the composition of  
187 the assemblages. Because there is a significant interaction between factors, pairwise  
188 comparisons were performed separately for levels of latitude within each depth and for levels  
189 of depth within each latitude. Pairwise comparisons were implemented using the  
190 ‘pairwise.perm.manova’ function of the ‘RVAideMemoire’ package (Hervé, 2019).  
191 PERMANOVA analyses were made using all sampled sites in each area, allowing comparisons  
192 of differences within and between areas. Each sample was characterized by unique coordinates  
193 and depth. The same standardization and transformation from previous analyses were used. All  
194 analyses were performed in R (R Core Team, 2017).

195

## 196 **Results**

197

### 198 *General data*

199

200 The data analyzed totaled 3,699 records belonging to 432 unique species, at 1,444  
201 unique sites (see Appendix S1 in Supporting Information). Sampling is unequal among areas,  
202 with best sampled areas at latitudinal band of 21°–40°N, and depth strata of 50–200 m and 201–  
203 1,000 m (Figures 1-2, Table 1). However, even these best sampled areas have rarefaction  
204 curves that are not approaching any obvious asymptotes, resulting in higher total richness  
205 estimates (Figure 2). In general, the 50–200 m and 201–1,000 m strata are better sampled than  
206 the 1,001–5,330 m stratum. The best sampled area for the 1,001–5,330 m stratum is also at the  
207 21°–40°N band. In this well-sampled band, highest richness is estimated to be in the 201–1,000  
208 m stratum, and lowest richness in the 1,001–5,330 m. The southern hemisphere is less well  
209 sampled than the northern hemisphere, except for the area at the 61°–80°S band and 201–1,000  
210 m stratum, corresponding to the Southern Ocean (Figures 1-2, Table 1).

211

### 212 *Species composition in relation to latitudinal bands and depth strata*

213

214 There is a significative interaction between depth and latitude (PERMANOVA,  $P =$   
215 0.001), meaning that variation on species composition with depth is not the same at all latitudes  
216 and variation on species composition with latitude is not the same at all depth strata. The  
217 pairwise comparisons for each factor (depth and latitude) within each level of the other factor  
218 revealed significant differences between all pairs of assemblages, except for the 201–1,000 m  
219 and 1,001–5,300 m strata at latitude 21°–40°S and the 50–200 m and 201–1,000 m strata at  
220 latitude 61°–80°S (see Appendix S2 in Supporting Information).

221 NMDS ordination and cluster analysis indicate that species' assemblages are primarily  
222 differentiated by those to the north and south of 40°S, regardless of depth (Figure 3). This  
223 southernmost group is then separated into assemblages to the north of 60°S (henceforth referred  
224 to as "Patagonian" assemblage) and to the south of 60°S (henceforth "Antarctic" assemblage),  
225 coinciding with the limits of South American and Antarctic continents (Figures 1, 3).

226 Northwards of 40°S, NMDS ordination shows a gradual differentiation across depth  
227 strata, from shallow to deep, the shallower assemblages being more similar to the Patagonian  
228 and Antarctic assemblages than the deeper ones (Figure 3A). Assemblages at the 1,001–5,330  
229 m strata tend to be more similar to each other (except by the non-significant intrusion of the  
230 41°–60°N band, at 201–1,000 m stratum) than those in shallower strata, despite great latitudinal  
231 variation (Figure 3). Assemblages within 50–200 m and 201–1,000 m strata gradually  
232 differentiate along latitude (Figure 3A). Additionally, all assemblages at the 201–1,000 m strata  
233 significantly clustered with 50–200 m strata assemblages from the respective latitudinal bands,  
234 with the only exception at the 41°–60°N band, although equivalent similarity can also be  
235 observed for this band in the NMDS ordination (Figure 3).

236

## 237 **Discussion**

238

239 The distribution of deep-sea Atlantic hydroids is structured by both biogeographical  
240 limits and gradients across depth and latitude, probably reflecting historical and ecological  
241 factors at regional and local scales. Patterns emerged despite the unequal sampling among areas  
242 across the Atlantic Ocean.

243

### 244 *Species turnover*

245

246 Variation in species composition across the Atlantic Ocean occurs gradually but  
247 exhibits clear transitions by latitude and depth. The first clear separation is at latitude 40°S,  
248 between southernmost (Patagonian and Antarctic) and northernmost areas (Figure 3). The  
249 southernmost cluster may be explained by the shared geological history of South America and  
250 Antarctica, subsequently isolated from each other after the formation of the Antarctic  
251 Circumpolar Current (Poulin, González-Wevar, Díaz, Gérard, & Hüne, 2014; Thomson, 2004).  
252 Biologically, this relationship is represented by the high endemism of many Southern Ocean  
253 taxa (Brandt, De Broyer, Gooday, Hilbig, & Thomson, 2004; Brandt, De Broyer, et al., 2007;  
254 Brandt, Gooday, et al., 2007), including hydroids (Casares, Soto Àngel, & Peña Cantero, 2017;  
255 Marques & Peña Cantero, 2010; Miranda, Genzano, & Marques, 2015; Peña Cantero & García  
256 Carrascosa, 1999). This subsequent isolation is reflected in the pronounced differentiation  
257 between Antarctic and Patagonian assemblages. These assemblages, however, are more similar  
258 across depth than are assemblages at other latitudes. The Antarctic assemblages, in particular,  
259 were not significantly differentiated between the 50–200 m and 201–1,000 m strata. A similar

260 pattern had been observed for ophiuroids in the Antarctic Peninsula, where turnover was  
261 detected between geographic regions, but not between depths of the continental shelf, a pattern  
262 that is probably related to the deeper continental shelf in the region (Ambroso, Böhmer, López-  
263 González & Teixidó, 2016).

264 Relationships among areas to the north of 40°S are more complex, apparently less  
265 affected by isolation, and with environmental gradients appearing to play important roles in  
266 explaining species' distributions. Assemblages in those areas gradually differentiate along the  
267 three depth strata (Figure 3A). This pattern may result from either species replacement (i.e.  
268 different species occurring at different depths) or limited depth ranges of the species. Indeed,  
269 most Atlantic hydroids have depth ranges that begin in shallow regions and extend into the  
270 deep; only a few are exclusively bathyal or abyssal (Fernandez & Marques, 2018). This  
271 suggests that the observed pattern results from the reduction of the range extensions limited by  
272 depth. Similar patterns have been observed in other taxa, indicating that populations are able  
273 to colonize the deep sea from shallower waters, but individuals are less likely to get established  
274 (Rex et al., 2005), probably because of the limited POC flux (Stuart et al., 2017). However,  
275 although there is a gradation in assemblage differentiation with depth, a more pronounced  
276 change in species composition occurs at 1,000 m, between the deeper (1,001–5,330 m stratum)  
277 and the shallower assemblages (50–200 m and 201–1,000 m strata) (Figure 3). This pattern  
278 corroborates a previous hypothesis of faunal turnover at ~1,000 m deep, suggested to be  
279 correlated to temperature shifts and limited dispersal across this barrier (Carney, 2005; Gage,  
280 Lamont, Kroeger, Paterson & Vecino, 2000), although turnover of starfish at ~1,100 m was  
281 attributed to variability in currents (Howell, Billett & Tyler, 2002). Turnover of hydroids at the  
282 shelf break (between 50–200 m and 201–1,000 m strata) was less pronounced, contrary to what  
283 has been observed for other benthic taxa (Allen & Sanders, 1996; Carney, 2005; Shantharam  
284 & Baco, 2020). Significant clustering between 50–200 m and 201–1,000 m strata at most  
285 latitudes (Figure 3B) supports interconnectivity between populations from 50 to 1,000 m deep.  
286 Interestingly, once this group is established (50–1,000 m), turnover in the assemblages is  
287 apparently driven by a latitudinal gradient, creating a somewhat gradual pattern of slightly  
288 different communities from north to south. Therefore, assemblages gradually differentiated  
289 across a combination of both depth and latitude (Figure 3). This pattern has never been  
290 described over such a large latitudinal scale before.

291 Greater environmental homogeneity in the deep sea would allow for greater  
292 connectivity (Dambach, Raupach, Leese, Schwarzer, & Engler, 2016; Everett et al., 2016;  
293 Zezina, 1997). In this way, the deep species assemblages (1,001–5,330 m stratum) became  
294 unique, with deep-sea populations interconnected even if separated by great geographical  
295 distances (Figure 3). Similar patterns of more widely distributed species with increasing depth  
296 were previously observed for other taxa. For example, no latitudinal zonation in species  
297 composition was found for protobranchs at bathyal and abyssal depths (Allen & Sanders,  
298 1996). Also, ophiuroids are more widely distributed at bathyal depths than at the continental



299 shelf (O'Hara, Rowden & Bax, 2011), and deep-sea species of benthic foraminiferans have  
300 wider ranges than shallow-water species (Gooday & Jorissen, 2012). Our results are consistent  
301 with the hypothesis that hydroid propagules are generally able to disperse and establish  
302 populations over great distances in the deep sea. In turn, this general dispersal ability would be  
303 likely to reduce rates of speciation in the deep sea. In fact, lower proportions of fertile hydroids  
304 have been recorded for the deep-sea (Fernandez, Collins, Gittenberger, Roy, & Marques,  
305 2020), indicating that sexual reproduction is lower, which would also reinforce the tendency  
306 for slower rates of speciation.

307         Unfortunately, there are no data in our analysis concerning the 1,001–5,330 m stratum  
308 south of 40°S, but future data should reveal if assemblages in those areas are either more related  
309 to the Patagonian/Antarctic assemblages (i.e. driven by their common geological history) or to  
310 those in the 1,001– 5,330 m stratum (i.e. expressing connectivity of deep-sea populations along  
311 the Atlantic Ocean). Both possibilities have been reported for different taxa, and associated  
312 with different dispersal capabilities (Brandt et al., 2007b).

313         Spatial variation in species composition may also be related to the ability of individuals  
314 to occupy specific niches, promoted by the presence of particular traits (Beauchard, Veríssimo,  
315 Queirós, & Herman, 2017; Bolam et al., 2017; Brun, Payne, & Kiørboe, 2016; Soininen,  
316 Lennon, & Hillebrand, 2007; Soininen, McDonald, & Hillebrand, 2007; Violle et al., 2007;  
317 Webb, Tyler, & Somerfield, 2009). The similarity between deep-sea assemblages and species  
318 turnover at 1,000 m may be related to the occurrence of species with specific traits that allow  
319 survival and reproduction in a food deprived environment with low population densities. For  
320 example, hydroids occurring deeper than 1,000 m are more frequently meroplanktonic,  
321 characterized by a medusa stage in the life-cycle (Fernandez, Collins, Gittenberger, Roy, &  
322 Marques, 2020). Hydroids have varied life cycles related to medusa production and release,  
323 which are associated with different dispersal abilities. Medusa release increases gamete  
324 dispersal, potentially expanding geographical ranges, which are generally wider for  
325 meroplanktonic than for benthic species of hydrozoans (Gibbons, Buecher, Thibault-Botha, &  
326 Helm, 2010; Gibbons, Janson, Ismail, & Samaai, 2010). The proportion of hydroids colonizing  
327 soft substrates also increases below 1,000 m (Fernandez, Collins, Gittenberger, Roy, &  
328 Marques, 2020), likely related to the scarcity of hard substrata and the presence of muddy  
329 bottoms characteristic of the deep-sea. The ability to colonize a greater variety of substrata may  
330 help hydroids to occupy a greater number of environments, potentially expanding geographic  
331 ranges. The increased proportion of monoecious specimens below 1,000 m may facilitate  
332 sexual reproduction at the low population densities of the deep sea, although deep-sea hydroids  
333 were also found to be less frequently fertile, suggesting that sexual reproduction is rare  
334 (Fernandez, Collins, Gittenberger, Roy, & Marques, 2020). That said, hydroids exhibit a wide  
335 variety of modes of asexual reproduction (Gili & Hughes, 1995), which probably helps  
336 maintain populations in the deep sea.

337

338 *Sampling effort and species richness*

339

340 Exhaustive data collection over such a large area is difficult to achieve. Available data  
341 are skewed toward continental margins, except for the Scotia Arc region and some samples at  
342 the Mid-Atlantic Ridge (Figure 2). There are important gaps in data coverage/knowledge  
343 (Figure 2, Table 1), with areas almost with no records, as in the Southern Hemisphere 1,000–  
344 5,330 m stratum (Table 1), despite the Atlantic Ocean lying mostly at depths between 4,000  
345 and 5,000 m (Levin & Gooday, 2003). It is essential that these areas be better explored because  
346 deep-sea ecosystems are becoming more and more impacted by direct and indirect  
347 anthropogenic activities (Courtene-Jones, Quinn, Gary, & Mogg, 2017; Danovaro, Corinaldesi,  
348 Dell'Anno, & Snelgrove, 2017; Jones et al., 2017; Ramirez-Llodra et al., 2011). Increased  
349 sampling effort in the Northern Hemisphere may cause a biased notion of higher richness in  
350 those areas, although similar diversities are proposed to exist in both hemispheres for most taxa  
351 (Chaudhary, Saeedi, & Costello, 2017; Fernandez & Marques, 2017). The 21°–40°N band is  
352 the best sampled latitude reflecting historically greater sampling effort in the area for both sides  
353 of the Atlantic and in the Mid Atlantic Ridge region (e.g., Ansín Agís, Vervoort, & Ramil,  
354 2001; Medel & Vervoort, 1998, 2000; Nutting, 1900, 1904, 1915; Ramil & Vervoort, 1992;  
355 Ramil, Vervoort, & Ansín, 1998; Vervoort, 2006). Similarly, many Antarctic expeditions in  
356 the last decades have enhanced sampling in the area (61°–80°S), mostly in the 201–1,000 m  
357 stratum (e.g., Peña Cantero, 2008; Peña Cantero & García Carrascosa, 1995; Peña Cantero &  
358 Ramil, 2006; Peña Cantero, Svoboda, & Vervoort, 2004; Peña Cantero & Vervoort, 2003; Peña  
359 Cantero & Vervoort, 2009). Despite the unequal sampling, our data sample covers material for  
360 the region broadly, with the unique advantage of being taxonomically standardized for  
361 comparison purposes. Biogeographical patterns have strong internal coherence, although  
362 biases may exist.

363 Species richness estimates could be adequately calculated for six areas. The 21°–40°N  
364 band is the only latitude where reasonable sampling exists along depth. The highest richness  
365 in the 201–1,000 stratum and low richness below 1,000 m deep corroborates previous findings  
366 of an increase in the number of species from the continental shelf towards the bathyal, reaching  
367 a peak at medium slope depths and subsequently declining towards the abyssal plains (Costello  
368 & Chaudhary, 2017; Etter & Grassle, 1992; Levin & Gage, 1998; McClain & Etter, 2005; Rex,  
369 1973, 1981; Sanders, 1968). For the three best sampled latitudes in the 50–200 m stratum,  
370 species richness was estimated to be lower in the 0°–20°N band than in more northern bands,  
371 corroborating, for this depth stratum, recent inferences of a dip in marine species richness near  
372 the equator (Chaudhary, Saeedi, & Costello, 2016).

373

374 *Conclusion*

375

376           This study provides evidence that the composition of assemblages of hydroids in the  
377 deep Atlantic Ocean changes gradually but exhibits defined biogeographical limits along  
378 latitude and depth. Patterns suggest that both historical factors (i.e., related to the geological  
379 history of the Southern Ocean) and environmental gradients related to latitude and depth  
380 underlie most of the distributions. Deficient sampling in many areas of the Atlantic Ocean,  
381 especially at greater depths and in the Southern Atlantic, limits our findings and future  
382 observations will certainly improve resolution of the patterns we have uncovered.  
383

384 **Tables**

385

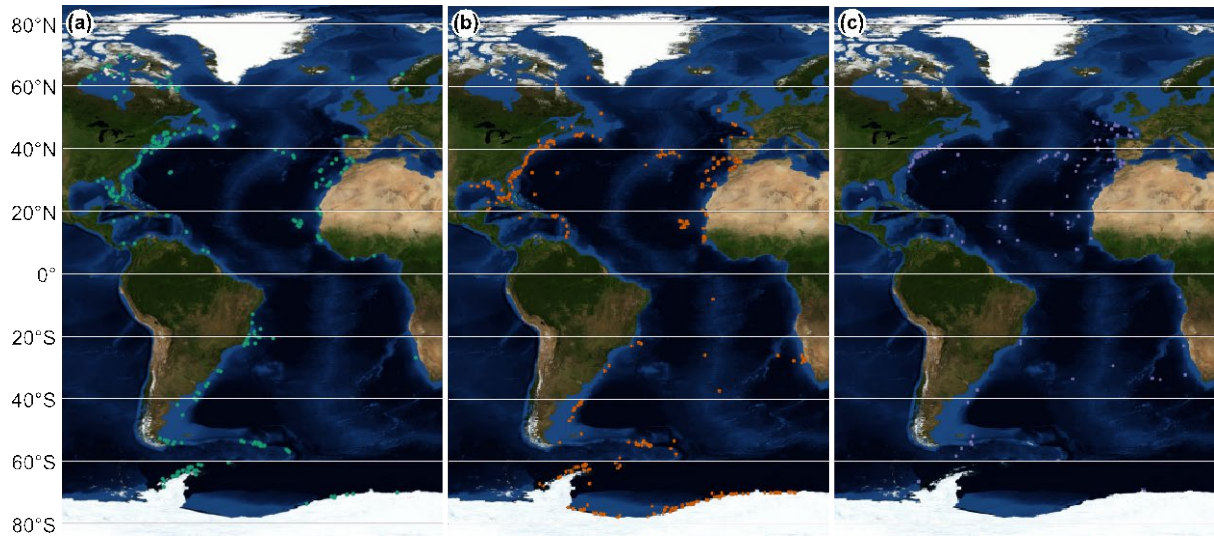
386 **Table 1.** Number of records and species studied by area of the Atlantic Ocean and adjacent  
 387 polar seas, organized by depth strata and latitudinal bands.

	50–200 m		201–1,000 m		1,001–5,330 m		<b>Total records</b>
	<b>records</b>	species	<b>records</b>	species	<b>records</b>	species	
<b>61°–80°N</b>	<b>70</b>	41	<b>3</b>	3	<b>0</b>	0	73
<b>41°–60°N</b>	<b>253</b>	86	<b>69</b>	35	<b>93</b>	33	415
<b>21°–40°N</b>	<b>724</b>	120	<b>980</b>	155	<b>230</b>	66	1934
<b>0°–20°N</b>	<b>269</b>	56	<b>116</b>	52	<b>39</b>	28	424
<b>0°–20°S</b>	<b>39</b>	15	<b>1</b>	1	<b>1</b>	1	41
<b>21°–40°S</b>	<b>63</b>	24	<b>37</b>	21	<b>25</b>	9	125
<b>41°–60°S</b>	<b>66</b>	26	<b>55</b>	31	<b>9</b>	6	130
<b>61°–80°S</b>	<b>109</b>	45	<b>462</b>	77	<b>2</b>	1	573
<b>Total</b>	<b>1593</b>		<b>1723</b>		<b>399</b>		<b>3715</b>

388

389 **Figures**

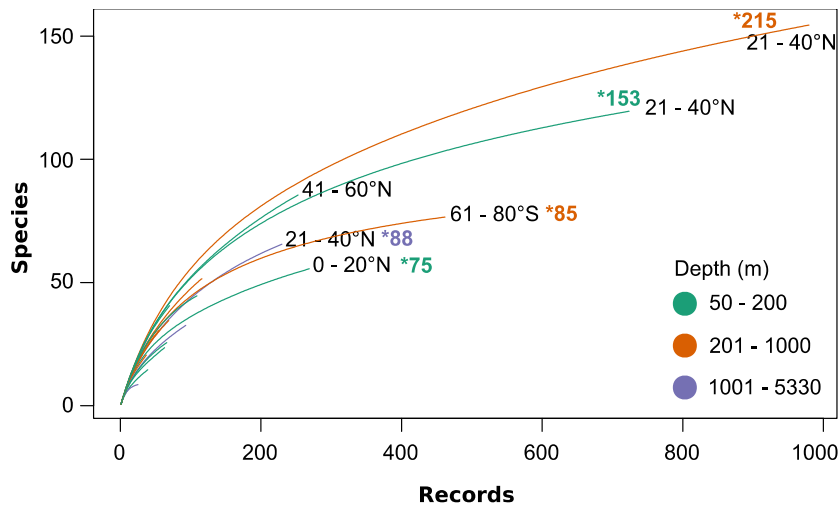
390



391

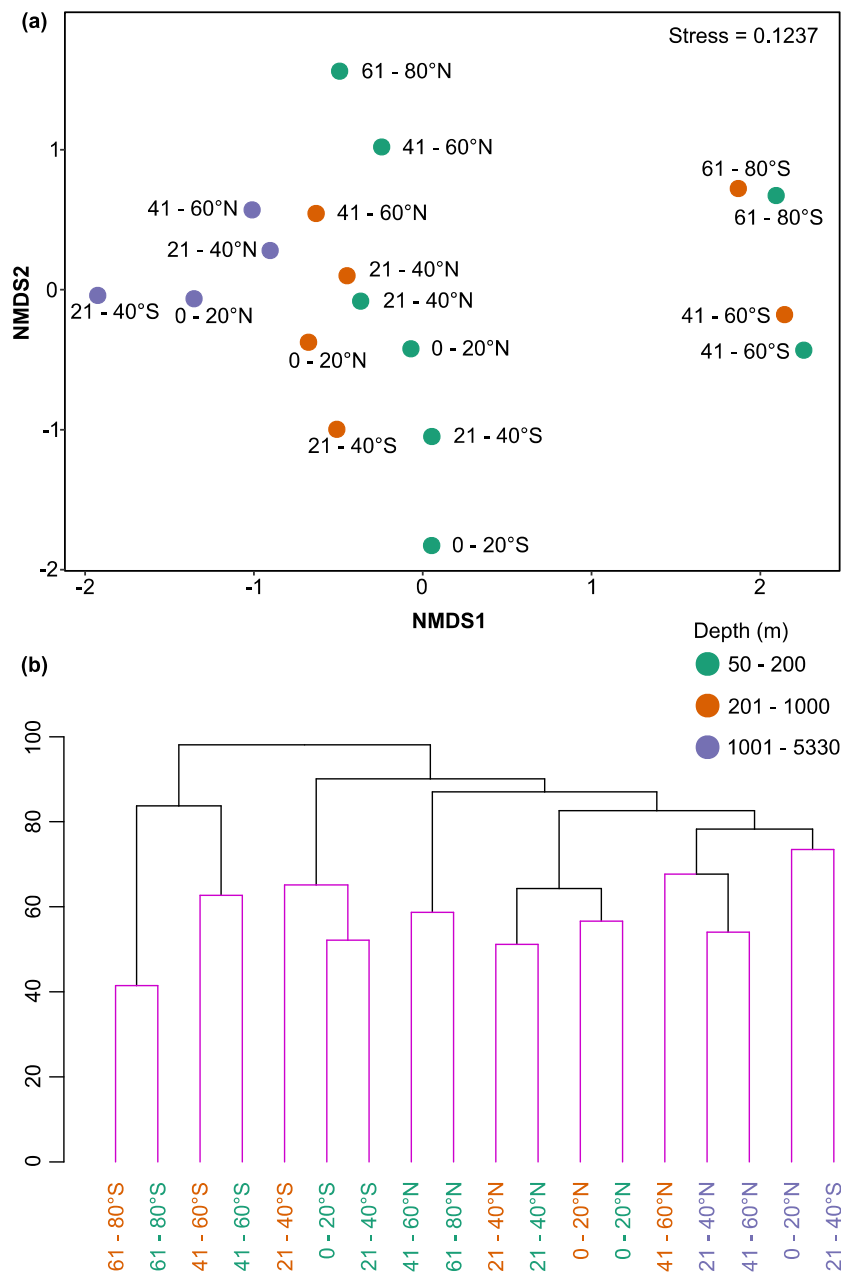
392 **Figure 1.** Geographic distribution of the material studied in the 50–200 m (a), 201–1,000 m  
 393 (b), and 1,001–5,330 m (c) depth strata of the Atlantic Ocean. Maps are divided into latitudinal  
 394 bands according to the studied areas. Each point may contain more than one record of species.

395



396

397 **Figure 2.** Individual-based rarefaction curves for the 18 studied areas of the Atlantic Ocean.  
 398 Colors represent depth strata. Areas with more than 200 records are annotated with estimated  
 399 richness (\*).



400

401 **Figure 3.** NMDS ordination plot showing relationships in species composition among  
 402 assemblages of hydroids for the 18 studied areas of the Atlantic Ocean (a) and dendrogram  
 403 resulting from the hierarchical clustering analysis for the same data, with significant clusters  
 404 resulting from similarity profile analysis in magenta (b).

405

406 **Data Availability Statement**

407 All the data used in the analyses are available in the Supporting Information file.

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