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Title: Gradual and rapid shifts in the composition of assemblages of hydroids (Cnidaria) along depth and latitude in the deep Atlantic Ocean

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

Running title: Turnover of hydroids along depth and latitude

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Abstract

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

Location: Atlantic Ocean and adjacent polar seas.

Taxon: Hydrozoa.

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

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

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

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

Introduction

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

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

Faunal turnover related to local scale habitat heterogeneity is pervasive in the deep-sea benthos (Judge & Barry, 2016; McClain & Barry, 2010; McClain, Nekola, Kuhnz, & Barry, 2011; Vanreusel et al., 2010; Zeppilli, Bongiorni, Santos, & Vanreusel, 2014). At the regional scale, however, β-diversity is more influenced by environmental variations in temperature and particulate organic carbon (POC) flux to the seafloor (McClain & Rex, 2015; UNESCO, 2009; Watling, Guinotte, Clark, & Smith, 2013; Wei et al., 2010; Woolley et al., 2016), two key drivers that would structure communities along depth (Carney, 2005; Rex & Etter, 2010; Rex et al., 2005). Indeed, faunal turnovers with depth are particularly common at the shelf break, around 1,000 m deep, and between 2,000 and 3,000 m deep, mostly correlated with temperature and food supply shifts, although specific boundaries may vary across regions and latitudes (reviewed in Carney, 2005).

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

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

Material and Methods

Study area and data collection

Hydroids (Milleporidae, Stylasteridae and Limnomedusae excepted) from the Atlantic Ocean and adjacent Arctic and Antarctic seas, with geographic and depth data, from 50 to 5,330 m deep, were studied primarily based on museum collections. Identifications were confirmed or made by the authors, improving the uniformity of taxonomic interpretation within the dataset. Records were assigned to three depth strata comprising the lower continental shelf (50–200 m), the upper bathyal (201–1,000 m), and the lower bathyal and abyssal plains (1,001–5,330 m) and 8 latitudinal bands of 20° each (61°–80°N, 41°–60°N, 21°–40°N, 0°–20°N, 0°–20°S, 21°–40°S, 41°–60°S, and 61°–80°S), totaling 24 sample areas (Figure 1, Table 1). Six out of the 24 areas with 10 or less records were excluded from the analyses (*viz*., 201–1,000 m for 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). Depth strata were chosen considering the decreasing number of records with increasing depth and previous hypotheses of faunal turnover at the continental shelf break (~200 m) and at the depth of the permanent thermocline (~1,000 m), where temperatures become nearly constant (Carney, 2005). Latitudinal bands encompass equidistant intervals.

Data analyses

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

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

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

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

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

Results

General data

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

Species composition in relation to latitudinal bands and depth strata

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

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

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

Discussion

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

Species turnover

Variation in species composition across the Atlantic Ocean occurs gradually but exhibits clear transitions by latitude and depth. The first clear separation is at latitude 40˚S, between southernmost (Patagonian and Antarctic) and northernmost areas (Figure 3). The southernmost cluster may be explained by the shared geological history of South America and Antarctica, subsequently isolated from each other after the formation of the Antarctic Circumpolar Current (Poulin, González-Wevar, Díaz, Gérard, & Hüne, 2014; Thomson, 2004). Biologically, this relationship is represented by the high endemicity of many Southern Ocean taxa (Brandt, De Broyer, Gooday, Hilbig, & Thomson, 2004; Brandt, De Broyer, et al., 2007; Brandt, Gooday, et al., 2007), including hydroids (Casares, Soto Àngel, & Peña Cantero, 2017; Marques & Peña Cantero, 2010; Miranda, Genzano, & Marques, 2015; Peña Cantero & García Carrascosa, 1999). This subsequent isolation is reflected in the pronounced differentiation between Antarctic and Patagonian assemblages. These assemblages, however, are more similar across depth than are assemblages at other latitudes. The Antarctic assemblages, in particular, were not significantly differentiated between the 50–200 m and 201–1,000 m strata. A similar pattern had been observed for ophiuroids in the Antarctic Peninsula, where turnover was detected between geographic regions, but not between depths of the continental shelf, a pattern that is probably related to the deeper continental shelf in the region (Ambroso, Böhmer, López-González & Teixidó, 2016).

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

Greater environmental homogeneity in the deep sea would allow for greater connectivity (Dambach, Raupach, Leese, Schwarzer, & Engler, 2016; Everett et al., 2016; Zezina, 1997). In this way, the deep species assemblages (1,001–5,330 m stratum) became unique, with deep-sea populations interconnected even if separated by great geographical distances (Figure 3). Similar patterns of more widely distributed species with increasing depth were previously observed for other taxa. For example, no latitudinal zonation in species composition was found for protobranchs at bathyal and abyssal depths (Allen & Sanders, 1996). Also, ophiuroids are more widely distributed at bathyal depths than at the continental shelf (O’Hara, Rowden & Bax, 2011), and deep-sea species of benthic foraminiferans have wider ranges than shallow-water species (Gooday & Jorissen, 2012). Our results are consistent with the hypothesis that hydroid propagules are generally able to disperse and establish populations over great distances in the deep sea. In turn, this general dispersal ability would be likely to reduce rates of speciation in the deep sea. In fact, lower proportions of fertile hydroids have been recorded for the deep-sea (Fernandez, Collins, Gittenberger, Roy, & Marques, 2020), indicating that sexual reproduction is lower, which would also reinforce the tendency for slower rates of speciation.

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

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

Sampling effort and species richness

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

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

Conclusion

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

Tables

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

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

Figures

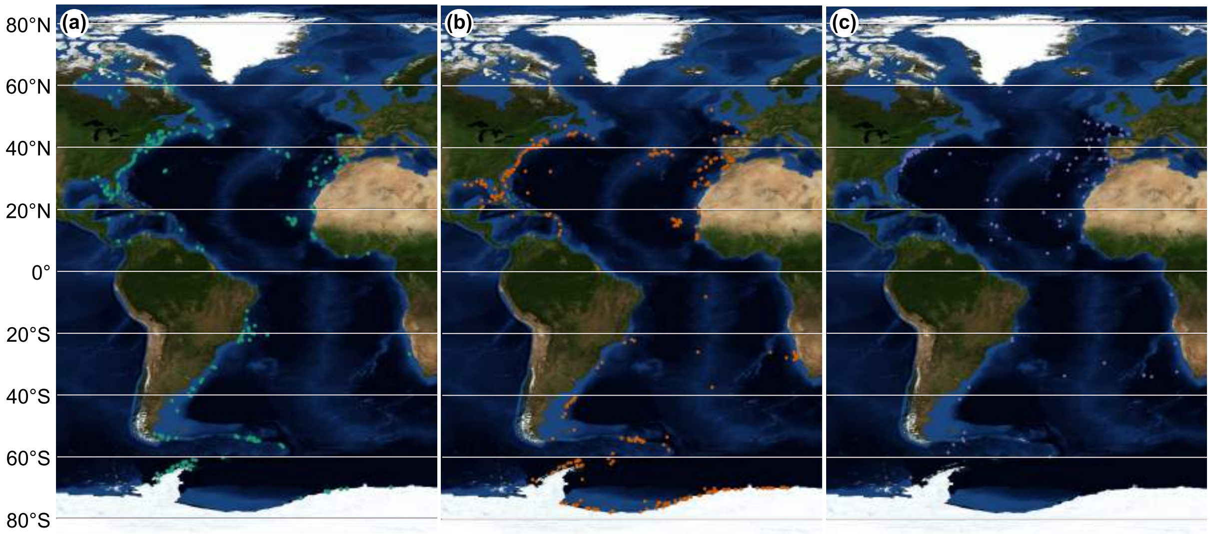

Figure 1. Geographic distribution of the material studied in the 50–200 m (**a**), 201–1,000 m (**b**), and 1,001–5,330 m (**c**) depth strata of the Atlantic Ocean. Maps are divided into latitudinal bands according to the studied areas. Each point may contain more than one record of species.

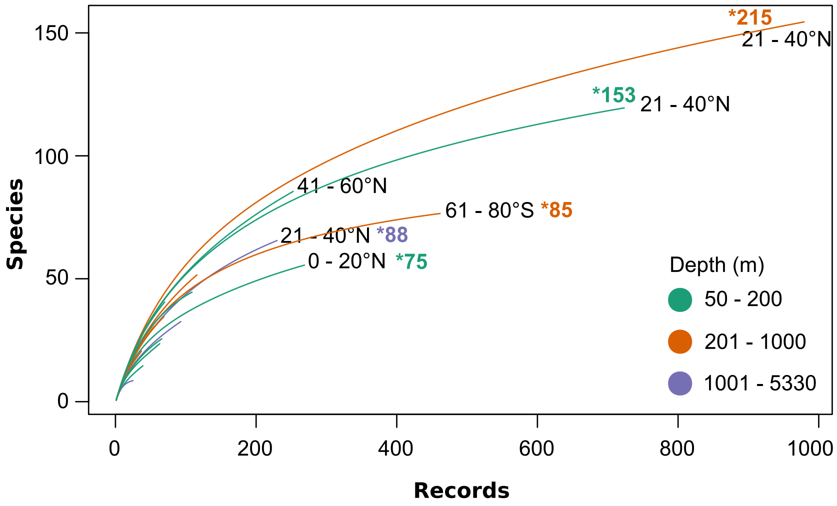

Figure 2. Individual-based rarefaction curves for the 18 studied areas of the Atlantic Ocean. Colors represent depth strata. Areas with more than 200 records are annotated with estimated richness (*).

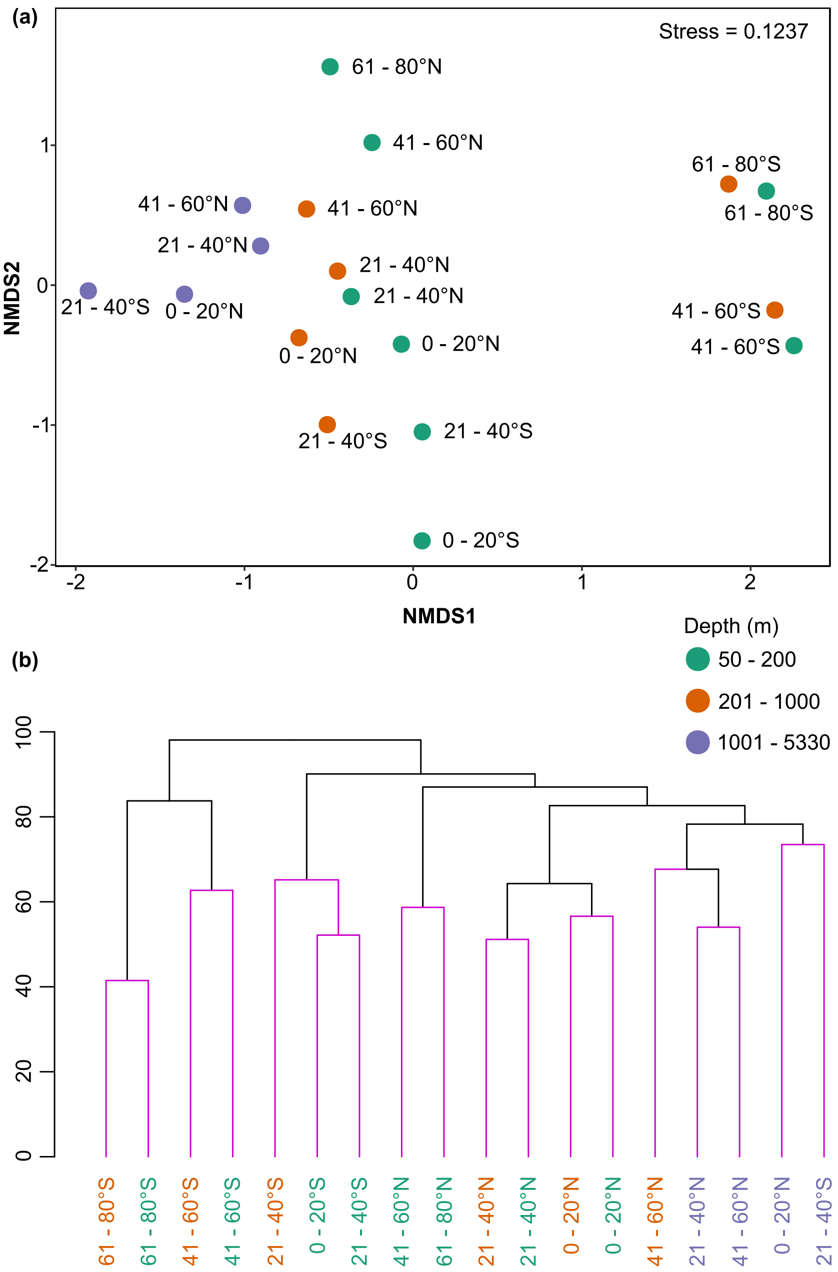

Figure 3. NMDS ordination plot showing relationships in species composition among assemblages of hydroids for the 18 studied areas of the Atlantic Ocean (**a**) and dendrogram resulting from the hierarchical clustering analysis for the same data, with significant clusters resulting from similarity profile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

Data Availability Statement

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

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