Polar Biology (2021) 44:1669–1689
https://doi.org/10.1007/s00300-021-02909-1

ORIGINAL PAPER

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

Thaís P. Miranda[1] · **Marina O. Fernandez**[2] · **Gabriel N. Genzano**[3,4] · **Álvaro L. Peña Cantero**[5] · **Allen G. Collins**[6] · **Antonio C. Marques**[2]

Received: 10 June 2020 / Revised: 14 June 2021 / Accepted: 16 June 2021 / Published online: 25 June 2021
© The Author(s), under exclusive licence to Springer-Verlag GmbH Germany, part of Springer Nature 2021

Abstract

To better understand the biodiversity-biogeographic polar connections between southern South America and Antarctica (SSA & A), we used benthic communities of hydroids as a model to investigate marine assemblages by evaluating classic spatial divisions at different geographical resolutions. Using a georeferenced dataset of 249 species and multivariate analyses, we investigated species' distribution, composition and biogeographic connectivity, and defined assemblages of ecoregions and provinces for the area. Hotspots of rich biodiversity at risk of depletion were defined. Analyses of ecoregions have a more stratified biogeographic structure, and reveal critical regions susceptible to loss of diversity. Analyses of provinces show a clear division between Atlantic-Pacific and Antarctic-Subantartic assemblages, with high biogeographic isolation of the Subantarctic islands. Depending on spatial resolution, the biogeographic position of the Magellan area is spatially contradictory, clustering on the one hand with SSA ecoregions and on the other with Antarctic provinces. Our patterns appear to be driven by different combinations of processes and barriers, reflected in the stratified distribution of hydroids. The high level of endemism and concentration of species at the edge of distribution in the Magellan area and Scotia Arc suggest their transitional nature and particular importance for understanding the historical and ecological connections between SSA & A.

Keywords Marine biogeography · Biodiversity · Hydrozoa · Southern Ocean · Community structure · Endemism

Introduction

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

The region has been classified according to many biogeographic schemes based on different taxa (e.g., Gibbons 1997; Linse et al. 2006; Griffiths et al. 2009), but usually focusing on single oceans (e.g., Gibbons 1997;

✉ Thaís P. Miranda
thaispmir@gmail.com

[1] Departamento de Biologia Animal e Vegetal, Centro de Ciências Biológicas, Universidade Estadual de Londrina, Londrina, PR, Brazil

[2] Departamento de Zoologia, Instituto de Biociências, Universidade de São Paulo, São Paulo, SP, Brazil

[3] Estación Costera J.J. Nagera, Universidad Nacional de Mar del Plata, Funes 3350, 7600 Mar del Plata, Argentina

[4] Instituto de Investigaciones Marinas y Costeras, Consejo Nacional de Investigaciones Científicas y Técnicas (IIMyC-CONICET), Mar del Plata, Argentina

[5] Instituto Cavanilles de Biodiversidad y Biología Evolutiva/Departamento de Zoologia, Universidad de Valencia, Valencia, Spain

[6] National Systematics Laboratory of NOAA's Fisheries Service, National Museum of Natural History, Smithsonian Institution, Washington, DC, USA

Douglass et al. 2014; Koubbi et al. 2014; Acha et al. 2020) or on global studies (e.g., Watling et al. 2013; Costello et al. 2017; Sutton et al. 2017), obscuring detailed biogeographic patterns of the SSA & A. The Marine Ecoregions of the World (MEOW) and the pelagic provinces of the world (Spalding et al. 2007, 2012), however, provide nested systems of classification of the oceans that combine small-scale spatial units and standardized datasets that provide practical utility, facilitating biogeographic analyses along SSA & A. Both systems are complementary and preserve many common elements of previous global and regional biogeographic classifications (e.g., Briggs 1974). Their ecoregions and provinces are defined as cohesive units applicable to the broad life history processes of most mobile, sedentary, and dispersive species (e.g., cnidarians of the class Hydrozoa; Spalding et al. 2007). As such, they are widely used for biodiversity and biogeographic studies wordwide (Poore and Bruce 2012; Vilar et al. 2019; Palomares et al. 2020; Summers and Watling 2021).

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

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

Wider or patchier geographic distributions of hydroids generally result from different dispersal capabilities, biotic interactions, substrate availability and environmental preferences (Cornelius 1992; Gili and Hughes 1995). Despite being relatively well known since the nineteenth century in the Chilean Patagonia (from ~ 40°S to 56°S), the southeastern Brazilian and Buenos Aires coasts (from ~ 20°S to 40°S) and the Antarctic Peninsula (from ~ 60°S to 75°S) (Peña Cantero 2014; Oliveira et al. 2016), hydroids are still poorly known from the Argentinian Patagonia (from 40°S–55°S), and along the east coast of Antarctica (from 60°S–70°S 0°–180°E). Many records are associated with contradictory identifications or are referred to cryptic species (e.g., species of Campanulariidae and Sertulariidae; Moura et al. 2011; Cunha et al. 2015, 2017), and thus are likely to benefit from a taxonomic review prior to biogeographic inferences. The first steps to minimize biases in biogeographic studies are defining the species pool under study, intensive and careful field surveys (particularly in poorly explored regions), and detailed cleaning and quality control of taxonomic and spatial data (Yang et al. 2013; Khalighifar et al. 2020). The use of measures of biodiversity that are highly dependent on equal sampling effort (e.g., richness) is challenging because these measures may generate biased conclusions (Hortal et al. 2007; Clarke et al. 2014). Alternative approaches employing taxonomic distinctness, which measures the biodiversity at the taxonomic level, allow for the comparison of diversity between unequal samples (Clarke et al. 2014). For conservation purposes, taxonomic distinctness provides a high level of accuracy for the description of patterns of biodiversity, being highly applicable for qualitative datasets and species lists with presence/absence data (Clarke and Warwick 1998, 2001; Clarke et al. 2014).

The distributions of biological communities along these continents have been separated into different marine realms, provinces and ecoregions (viz., Spalding et al. 2007, 2012), encompassing the southwestern Atlantic, the southeastern Pacific and the Southern Ocean. For hydroids, the area is classically divided in Patagonia, the Antarctic region, and the Scotia Arc, the latter traditionally considered as a biogeographic bridge between both continents (Mercado Casares et al. 2017). Recent studies involving hydroid distributions show that the Scotia Arc has higher faunistic affinity to Antarctica than to Patagonia, and they suggest that the Polar Front is an important biogeographic barrier in the area (Soto Àngel and Peña Cantero 2017). Studies with other marine taxa, however, suggest that the colonization of Antarctica was not necessarily from the Magellan area via the Scotia Arc (Mühlenhardt-Siegel 1999), implying that the connectivity of the latter is likely scale and taxon dependent (Moon et al. 2017), and that the permeability of the Polar Front and the Antarctic Circumpolar Current (ACC) is likely higher than once presumed (Sanches et al. 2016).

The area between SSA & A represents a complex and interesting biogeographic laboratory to study the composition, biodiversity and distribution of marine species in an ecological and historical context. Here, we study the marine hydroid fauna of SSA & A in order to (1) update the taxonomic status of the species present, (2) evaluate species endemism, (3) assess distribution patterns of species and community composition along Spalding's ecoregions and provinces, and (4) assess the biogeographic connectivity between SSA & A. We hypothesize that the biodiversity and faunistic composition of assemblages are scale-dependent and vary across Spalding's ecoregions and provinces, and also that endemism increases southwards.

Material and methods

Area of study

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

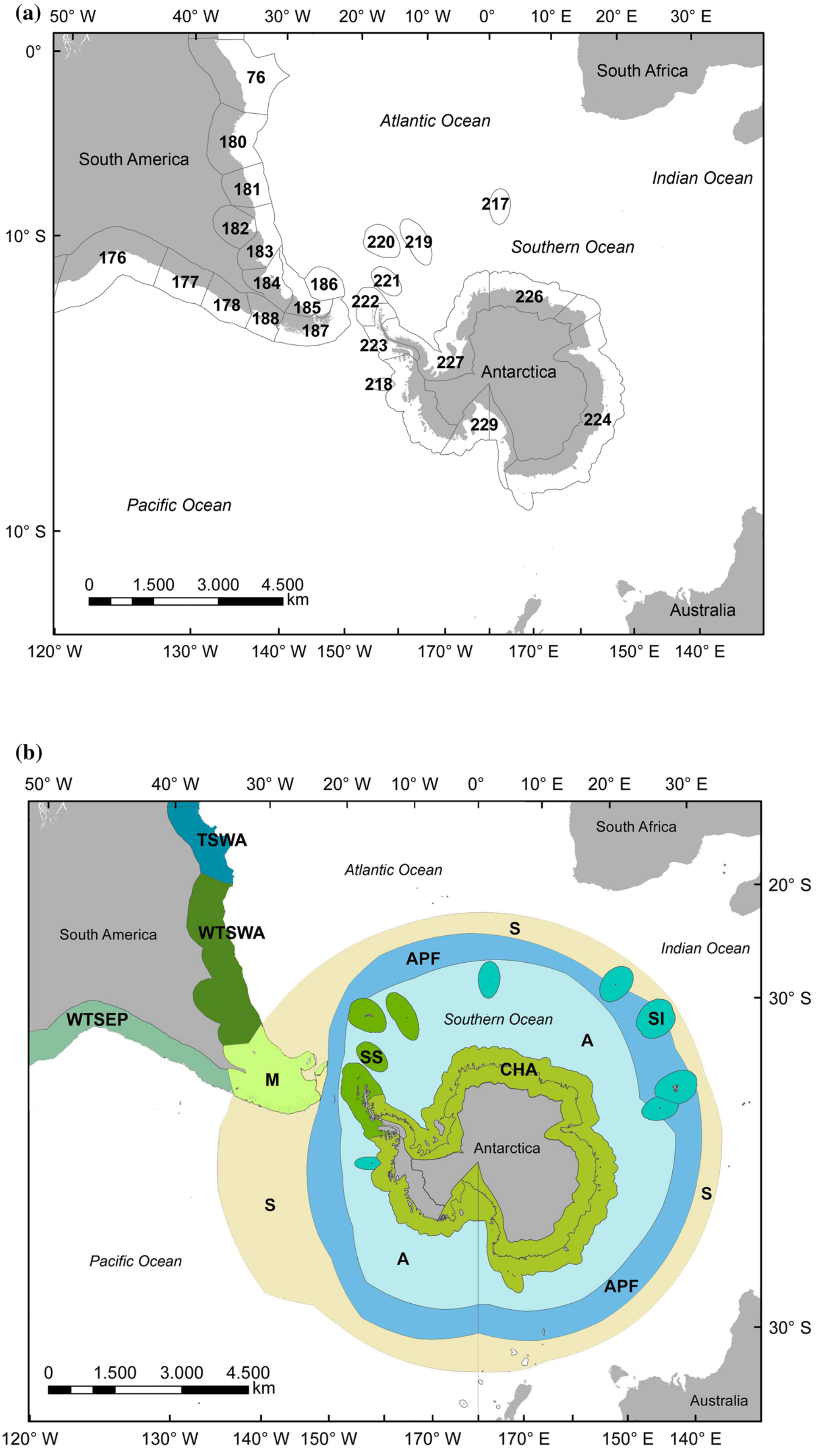
The area was divided in 25 ecoregions (Fig. 1a) and 10 provinces (Fig. 1b) following the global biogeographic classification proposed by Spalding et al. (2007)—the Marine Ecoregions of the World (MEOW)—and three additional Antarctic pelagic provinces of Spalding et al. (2012)—used only for the Antarctic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

Data collection

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

We personally identified specimens and checked all collection and geographic information in the literature, thereby guaranteeing taxonomic uniformity and geographic accuracy; as required for large-scale biogeographic studies (Hortal et al. 2007; Santos et al. 2010; Di Camillo et al. 2018). This approach is particularly essential for taxonomically complex groups, given that available databases have non-uniform identifications and extensive taxonomic revisions have recently been produced (e.g., Peña Cantero 2014; Oliveira et al. 2016). We compiled a list of the species studied and their geographic distribution by ocean and/or sea of occurrence (Online Resource Table S1); the endemic species

Fig. 1 Ecoregions (**a**) and provinces (**b**) for southern South America and Antarctica (modified from Spalding et al. 2007, 2012)



were classified in eight categories of endemicity along SSA & A, and according to their distribution and traditional biogeographic classifications of the area (Balech 1954; Palacio 1982): species endemic to (1) the whole area of study, *i.e.*, from 22°S to 78°S, (2) tropical areas, *i.e.*, from 22°S to 30°S, (3) tropical and subtropical areas, *i.e.*, from 22°S to ~ 43°S, (4) subtropical areas, *i.e.*, from 30°S to ~ 42°S, (5) subtropical and Magellan areas, *i.e.*, from 30°S to 60°S, (6) the Magellan area, *i.e.*, from ~ 42°S to 60°S, (7) the Magellan and Antarctic areas, *i.e.*, from ~ 42°S to 78°S, and (8) the Antarctic area, *i.e.*, ~ 60°S to 78°S (Online Resource Table S1). Literature records of hydroids were not herein listed, as this has already been done elsewhere (Oliveira et al. 2016; Ronowicz et al. 2019). Exceptions are the Antarctic records of *Corymorpha microrhiza* (Hickson and Gravely 1907) and *Zyzzyzus parvula* (Hickson and Gravely 1907) from Svoboda and Stepanjants (2001), which were included after studying the specimens at the National Museum of Natural History, Smithsonian Institution. The taxonomy of all species was standardized following the pertinent literature to their area of occurrence (Oliveira et al. 2016 and references therein; Ronowicz et al. 2019 and references therein; Schuchert 2021). Species were phylogenetically classified according to Maronna et al. (2016), Mendoza-Becerril et al. (2018) and Schuchert (2021).

Multivariate analyses

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

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

To compare the biodiversity of hydroids at different taxonomic levels between assemblages, we used the average taxonomic distinctness (AvTD) and the variation in taxonomic distinctness (VarTD). Both AvTD and VarTD are unbiased statistical diversity measures, applicable to presence/absence data, and unsensitive to sampling effort, size and dominant species (Clarke et al. 2014). They use the Linnaean classification relationships between species to test for biodiversity changes among assemblages, qualitatively comparing their taxonomic distinctness given a master list of species observed in an area (*i.e.*, the “species pool” of SSA & A) (Clarke and Gorley 2015). The AvTD of an assemblage is a reflection of the taxonomic distance across the taxonomic hierarchy of a master list of species observed for the whole area of study (*i.e.*, the species inventory), and is not impacted by species abudance distributions (Clarke and Warwick 2014). It is defined as the ratio between the average taxonomic distance (*i.e.*, the expected path length in the classification tree between any two individuals chosen at a random) and the Simpson diversity index (*i.e.*, the probability that any two individuals selected at a random belong to the same species) of a sample (Warwick and Clarke 1995; Clarke et al. 2014). The VarTD is the variance of the taxonomic distances between each pair of species, representing the unevenness of the classification tree (*i.e.*, reflects different classification tree constructions) (Clarke and Warwick 2001; Clarke et al. 2014). Both AvTD and VarTD of an assemblage can be calculated from the master list of species which encompasses the taxonomic boundaries of the classification tree related to the inventory, and the suitable biogeographic limits from which the species were documented. As taxonomic distinctness measures are independent of sampling effort, it is possible to compare the AvTD and VarTD of a subset of species in an assemblage with those of the master list to check if they represent the biodiversity expressed in the full species inventory. Therefore, the AvTD and VarTD for the master list correspond to the expected values for the whole faunal group (Clarke et al. 2014). Analyses of taxonomic distinctness were performed using seven taxonomic levels (superorder, order, suborder, infraorder, family, genus and species) and equal weights between them.

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

A non-metric multidimensional scaling (nMDS) with 50 interactions was also performed to assess gradual faunistic changes between the assemblages. To test for differences in species composition between assemblages, the one-way analysis of similarity test (ANOSIM) with 999 permutations was calculated (Clarke and Green 1988). Finally, we used BVSTEP, a stepwise routine that searches for the smallest subset of species contributing most for the nMDS pattern (Clarke et al. 2014). All multivariate analyses were performed using the software Primer-e v. 7 (Clarke and Gorley 2015).

Results

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

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

Rarefaction curves do not reach a clear asymptote for any of the ecoregions and provinces analyzed, providing

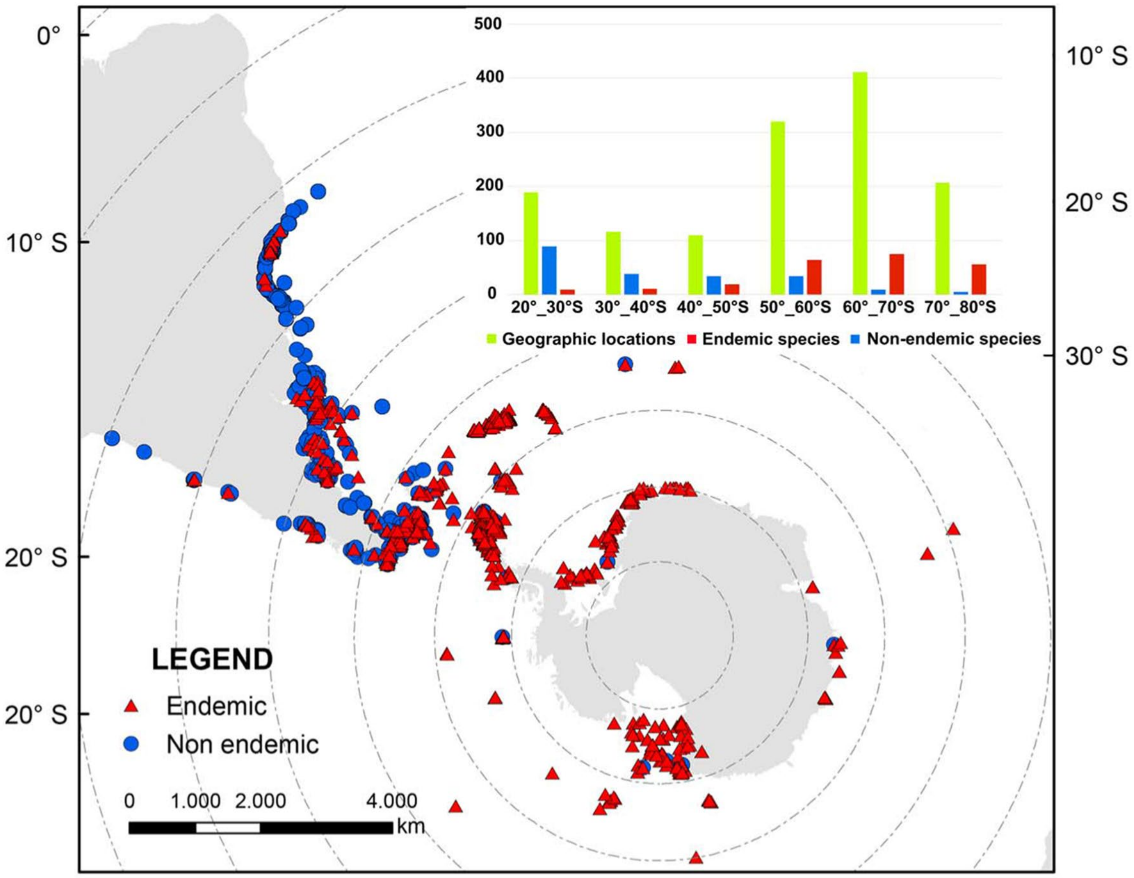


Fig. 2 Distribution of the endemic and non-endemic species of hydroids sampled along southern South America and Antarctica. The graphics show the number of geographic locations (total: 1,360), and non-endemic (total: 121) and endemic species (total: 128) examined by latitudinal band

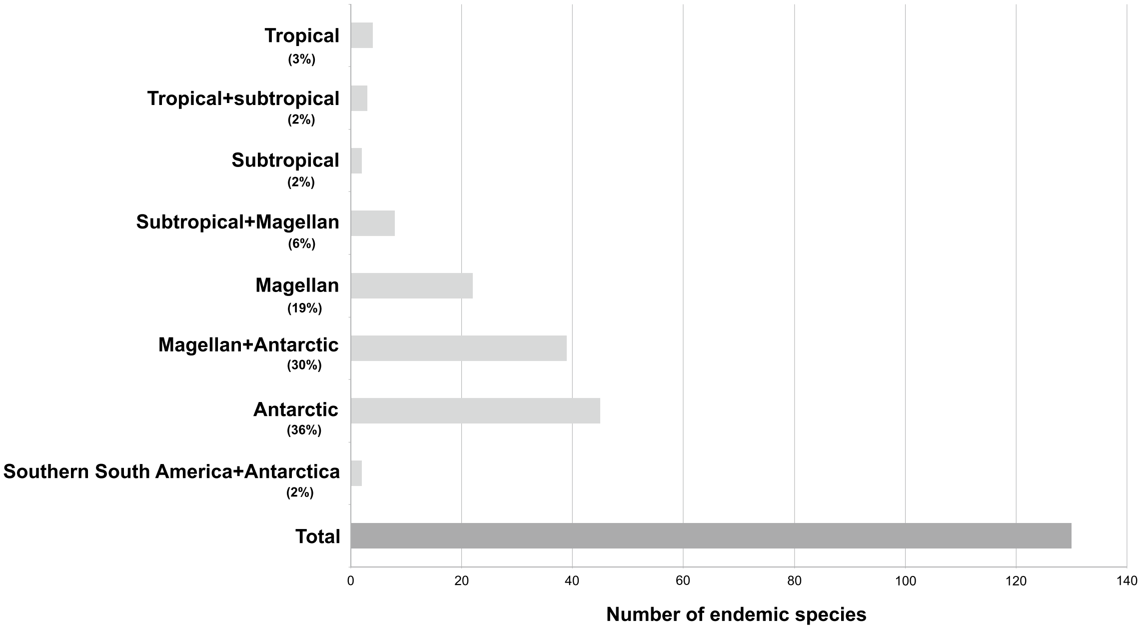


Fig. 3 Number of endemic species of hydroids in each of the eight categories of endemicity recognized for the southern South America and Antarctica. "Total" is the total number of endemic species of hydroids recorded for the whole coast of SSA & A. The numbers in bold and between parenthesis are the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

evidence that sampling effort along SSA & A is unequal and still deficient (Fig. 4). However, within all biogeographic units analyzed, ecoregions 180, 183, 185, 187, 220, 222, 223, 227, and 229 appear to be closer to reaching an asymptote (Fig. 4a), as well as curves CHA, M, SS and WTSWA for provinces (Fig. 4b).

Regarding taxonomic distinctness, eleven ecoregions have AvTD values within the 95% interval of expectation of the master list, three ecoregions (180, 181 and 183) have AvTD values above it, and ten have AvTD values below the expected (Fig. 5a; Table 1). Most VarTD values were within the expected, with exceptions of above expectation values for ecoregions 177, 222, 223, 227 and 229 (Fig. 5b; Table 1). For provinces, most AvTD values were within or below the expected, except for WTSWA (Fig. 6a; Table 2). The VarTD values were also mostly within the expected for each area, except for above expected values for provinces A, CHA and SS (Fig. 6b; Table 2).

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

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

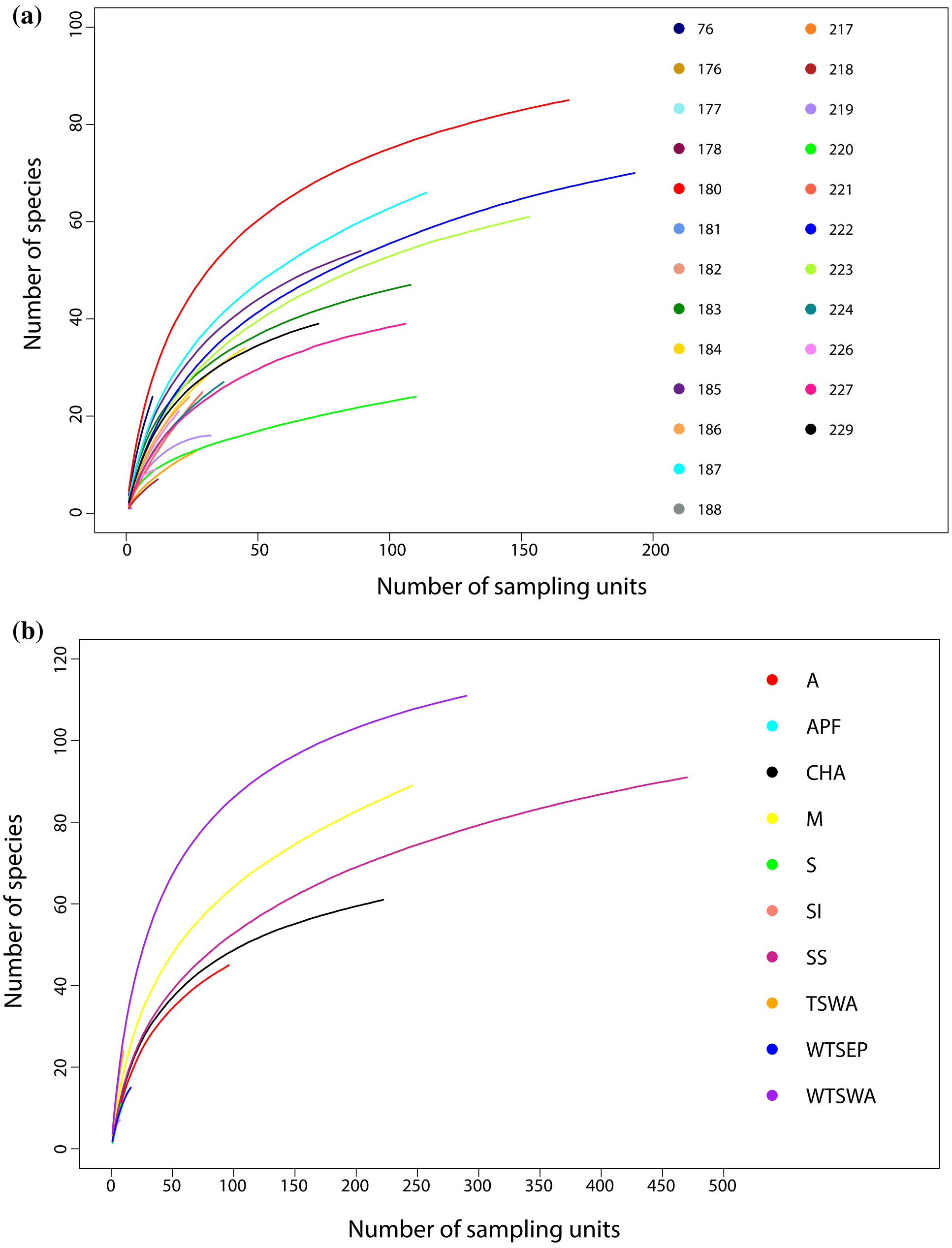


Fig. 4 Sample-based rarefaction curves of species of hydroids from southern South America and Antarctica ecoregions (**a**) and provinces (**b**). Refer to Fig. 1 for ecoregions numbers and provinces acronyms

SSA is E14 (Figs. 1a, 7a; Online Resource Table S4), with a mix of endemic species from tropical + subtropical (e.g., *Sertularella fuegonensis*), Magellan (e.g., *Sertularella jorgensis*), and Magellan + Antarctic ranges (e.g., *Abietinella operculata*) (Online Resource Tables S1, S2). Assemblage E16 correponds to the Magellan area, composed of endemic species from tropical + subtropical (e.g., *Corymorpha januarii*), Magellan (e.g., *Orthopyxis hartlaubi*) and Magellan + Antarctic categories of endemicity (e.g., *Halecium interpolatum*), in addition to some widely distributed species (Figs. 1a, 7a; Online Resource Tables S1, S2).

Our results suggest that Antarctic assemblages are biogeographically divided between the subantarctic islands (*i.e.*, assemblages E2 and SI) and the Scotia Arc plus the rest of the Antarctic ecosystem (assemblages E3 and P4) (Figs. 1a, 7a, 8a). E2 clusters Bouvet Island and Peter I Island by the presence of *Antarctoscyphus spiralis* and *Staurotheca dichotoma* (Figs. 1a, 6a; Online Resource Table S2). SI gathers Bouvet, Prince Edwards, Crozet, Kerguelen islands, being the most dissimilar assemblage of provinces (Figs. 1b, 8a; Online Resource Table S5), composed of endemic species from the Magellan + Antarctic category (e.g., *Oswaldella erratum*, *O. vervoorti*, *Schizotricha vervoorti*, *Staurotheca dichotoma*, *S. vanhoeffeni*) but also by rare (e.g., *Staurotheca echinocarpa*) and widely distributed species (e.g., *Symplectoscyphus subdichotomus*) (Online Resource Tables S1, S3).

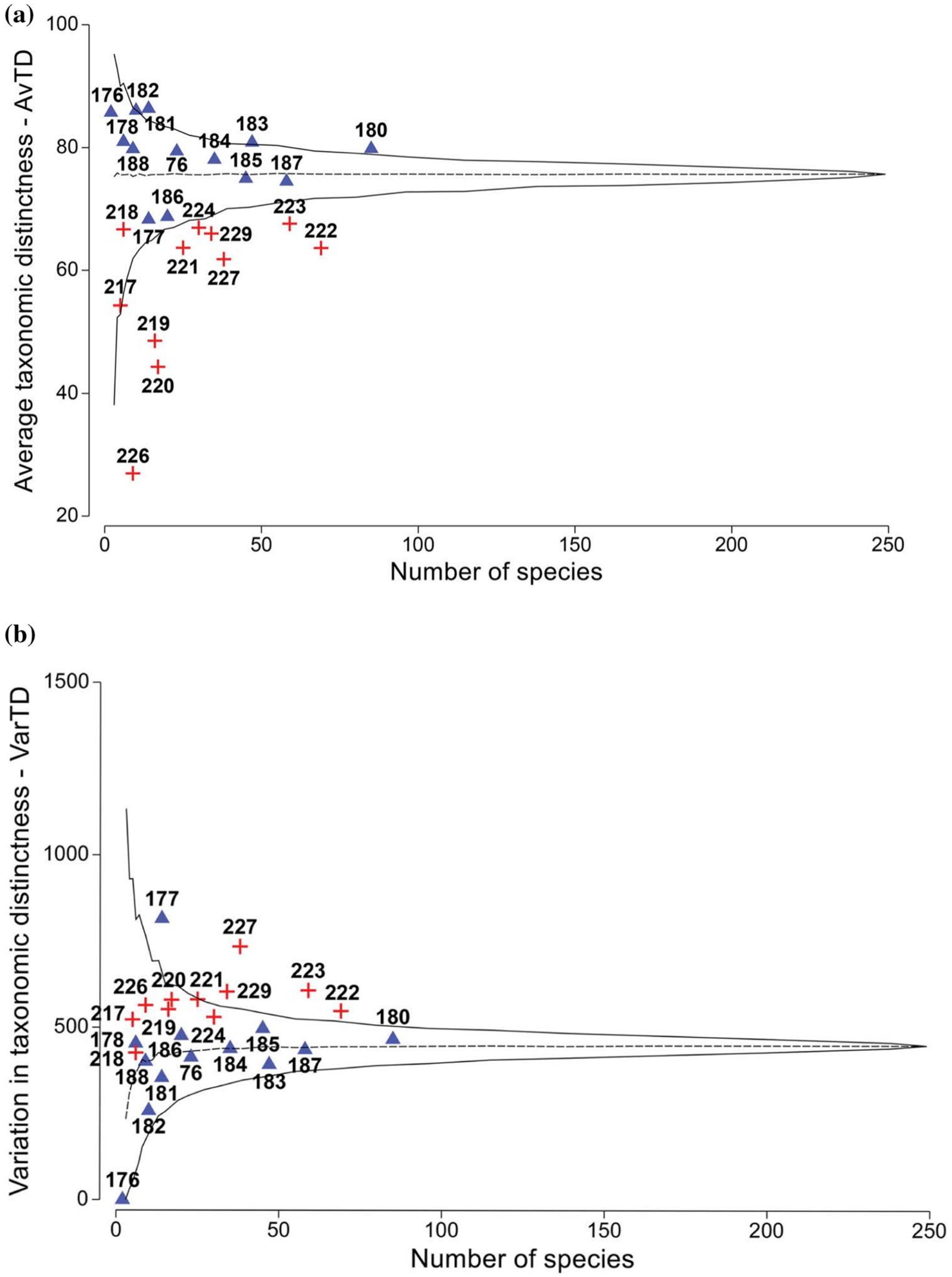


Fig. 5 Funnel plots for the (**a**) average taxonomic distinctness (AvTD) and (**b**) variation in taxonomic distinctness (VarTD) simulated for each southern South American and Antarctic ecoregion. Dashed lines indicate the AvTD and VarTD for the master list of species of hydroids. Black lines show the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

South Georgia and South Sandwich Islands, which are part of the Scotia Arc, are represented by assemblage E5, with most endemic species from Magellan + Antarctic category (mainly *Antarctoscyphus* spp., *Oswaldella* spp., and *Staurotheca* spp.) (Figs. 1a, 7a; Online Resource Tables S1, S2). The west coast of the Antarctic Peninsula corresponds to assemblage E9 (Figs. 1a, 7a), composed of species distributed in a few lower taxonomic levels (e.g., genus and family levels) and by a high number of species endemic from Antarctica (e.g., *Antarctoscyphus* spp., *Oswadella* spp., *Clathrozoella medeae*, *Mixoscyphus antarcticus*, *Schizotricha crassa*, *S. nana*, *S. vervoorti*, *Staurotheca antarctica*) (Online Resource Tables S1–S3). This faunistic pattern was also found in P5, corresponding to the whole coast of Antarctica (Figs. 1b, 8a). APF is composed of endemic species from Magellan (e.g., *Acryptolaria* spp., *Clathrozoella abyssalis*, *Oswaldella elongata, Sertularella jorgensis, Staurotheca abyssalis*, *S. profunda*, *S. vervoorti*) and Magellan + Antarctic categories (e.g., *Antarctoscyphus elongatus*, *Schizotricha vervoorti*, *Staurotheca jaederholmi*, *S. pachyclada*), besides some worldwide distributed species (e.g., *Amphisbetia operculata* and *Sertularella gaudichaudi*) (Online Resource Tables S1, S3).

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

The nMDS ordination plots reflect the same biogeographic division between the assemblages of SSA & A found in the cluster and SIMPROF analyses (Figs. 7, 8). Additionally, a gradual variation in species composition along the ecoregions and provinces was observed (Figs. 7b, 8b). The adjacent ecoregions 76 and 180, for example, have similar species composition, while ecoregion 186, although more isolated, is more similar in species composition to ecoregions 187 and 188 (Figs. 1, 7b). The geographically isolated province SI has a unique species composition, while adjacent S and APF are more closely related to each other (Figs. 8b). The BVSTEP routine identified five species (correlation 0.815) better matching the pattern of the nMDS ordination of the ecoregions: *Antarctoscyphus spiralis*, *Billardia subrufa*, *Halecium jaederholmi*, *Staurotheca dichotoma*, and *S. glomulosa*. For the province nMDS patterns, BVSTEP identified 15 species (correlation 0.952): *Acryptolaria conferta*, *A. operculata*, *Aglaophenia latecarinata*, *A. trifida*, *Antarctoscyphus grandis*, *Clathrozoella abyssalis*, *Halecium pallens*, *Obelia dichotoma*, *Schizotricha vervoorti*, *Sertularella gaudichaudi*, *S. mixta*, *S. polyzonias*, *Staurotheca antarctica*, *S. dichotoma*, and *S. echinocarpa*.

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

Discussion

Despite the unavoidable unequal sampling along the ecoregions and provinces of SSA & A, the patterns herein documented are related to the geographic scale of aggregation of hydroid occurrence data, but they help elucidate biotic and abiotic factors that impact their biogeographic distributions. In general, the distribution of hydroids along SSA & A appears to be driven by a combination of barriers of varying intensity for different species, modulating dispersal over long distances.

Faunistic composition

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

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

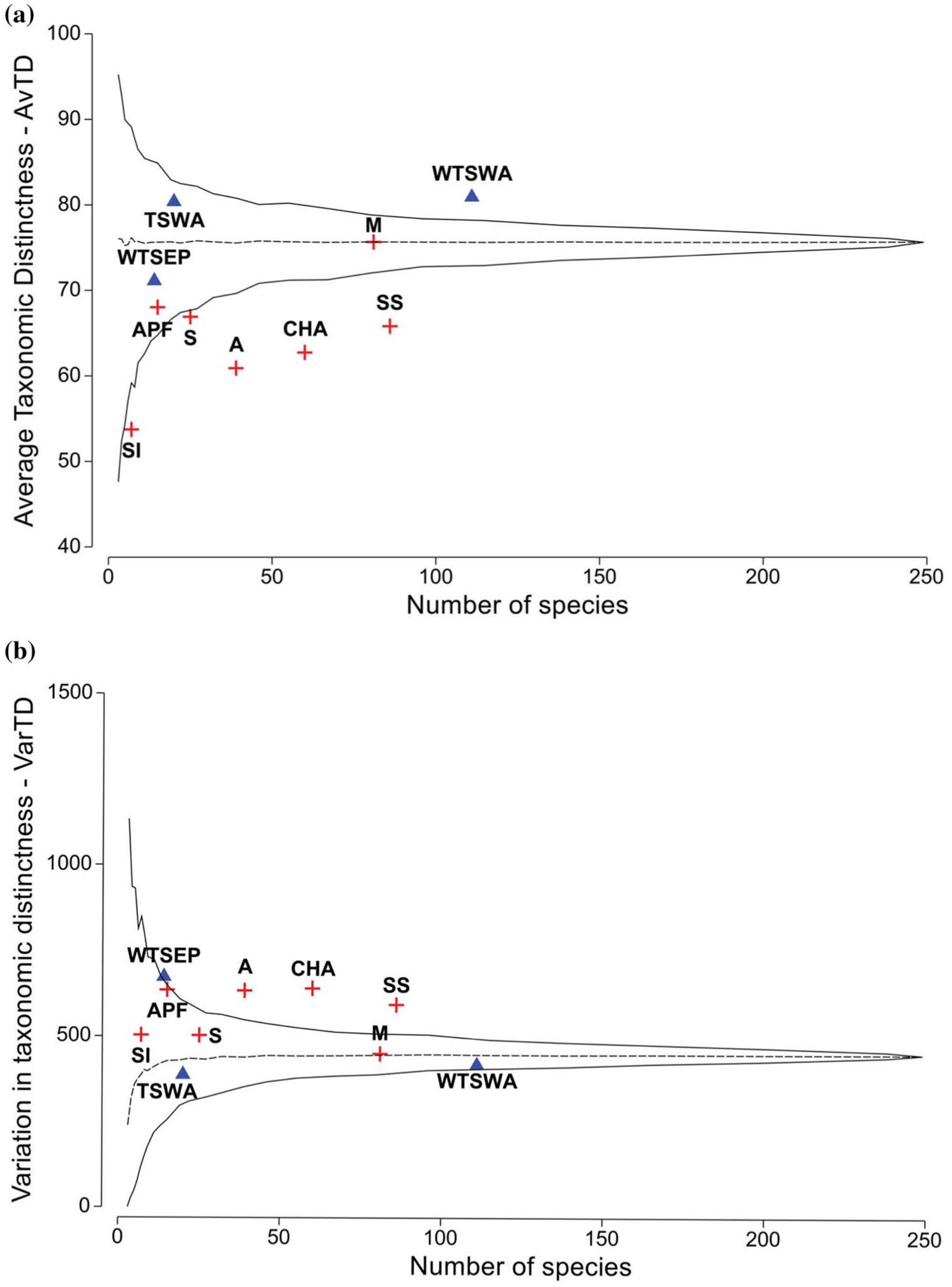


Table 2 Richness, average taxonomic distinctness (AvTD), and variation in taxonomic distinctness (VarTD) estimated for each province analyzed. Refer to Fig. 1 for provinces acronyms

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

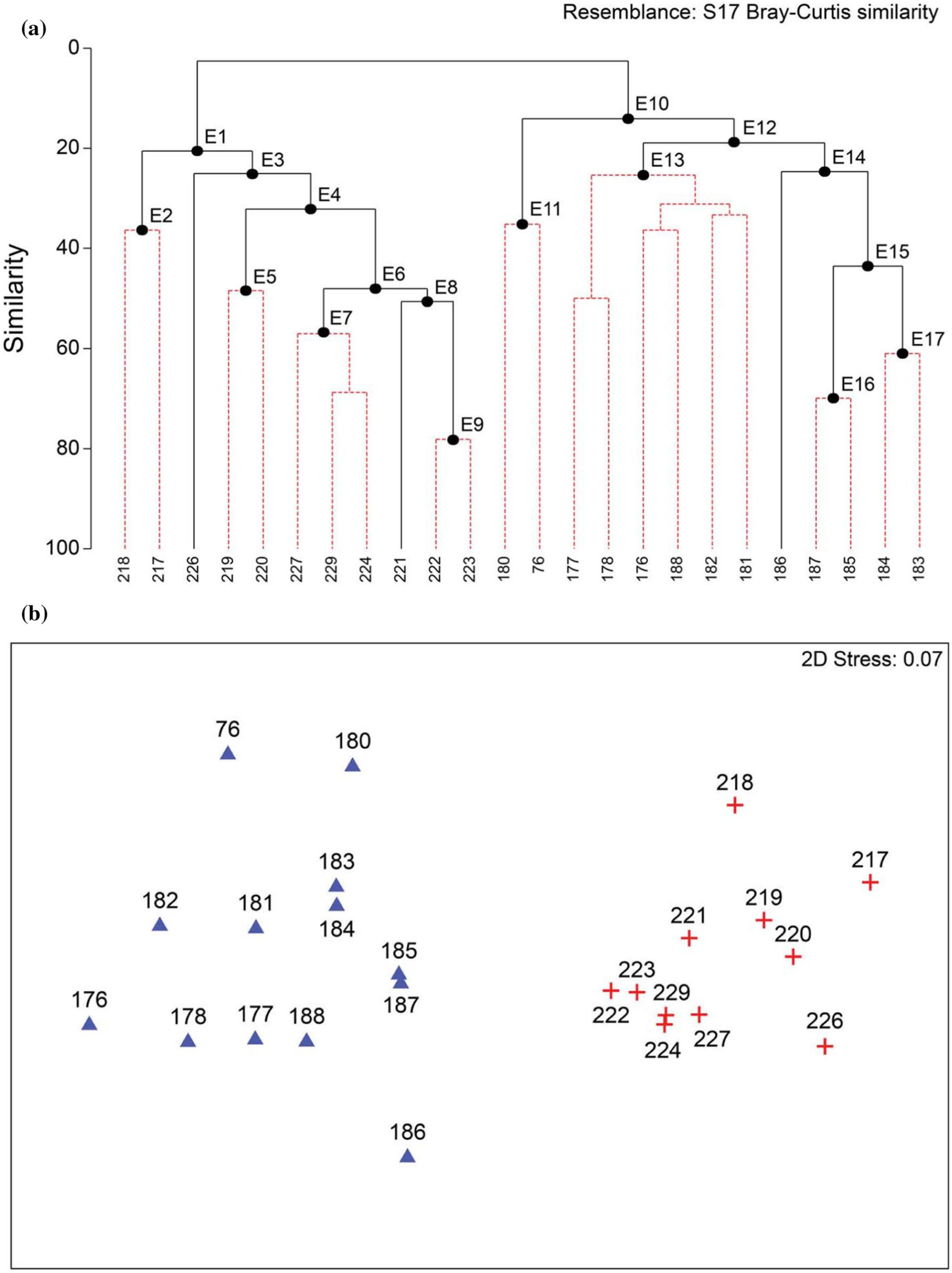


Fig. 7 (**a**) Dendrogram and SIMPROF test among ecoregions from southern South America and Antarctica. Black lines indicate statistically significant clusters: E1 to E9 for Antarctica, and E10 to E17 for SSA. (**b**) Non-metric multidimensional scaling (nMDS) ordination plot of southern South American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

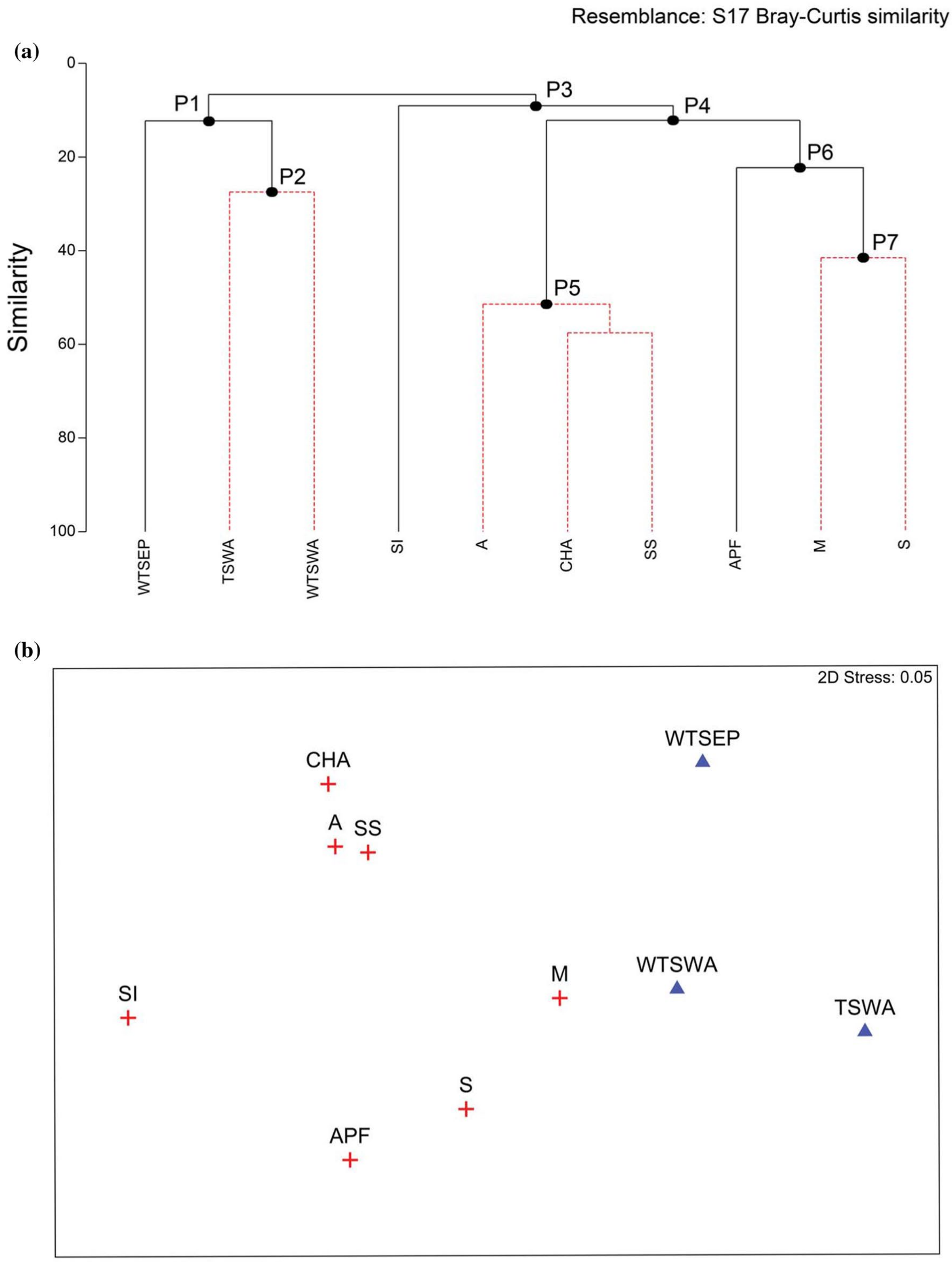


Fig. 8 (**a**) Dendrogram and SIMPROF test among provinces from southern South America and Antarctica. Black lines indicate statistically significant clusters: P1 and P2 for SSA, and P3 to P7 for Antarctica. (**b**) Non-metric multidimensional scaling (nMDS) ordination plot of southern South American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

species) dominates over "Anthoathecata" and Pseudothecata (9% and 3% of the species, respectively)—a similar proportion found in other parts of the world, such as tropical (Calder 1993; Di Camillo et al. 2008) and subtropical areas (Genzano et al. 2017; Ajala-Batista et al. 2020), the Mediterranean (Bouillon et al. 2004; Gravili et al. 2013), the Arctic (Ronowicz et al. 2015) and the Antarctic (Peña Cantero 2014; Soto Àngel and Peña Cantero 2019; Peña Cantero 2021). The high proportions of Leptothecata over Anthoathecata is at least partially due to the destructive sampling of unprotected polyps (*i.e.*, anthoathecates) (Peña Cantero 2004), although it also likely reflects true higher diversity of Leptothecata as compared to Anthoathecata (Fernandez and Marques 2018; Fernandez et al. 2020). Symplectoscyphidae is the most speciose family in the study area (Online Resource Table S1) (*cf.* Soto Àngel and Peña Cantero 2019; Peña Cantero 2021), although Haleciidae is the most speciose hydrozoan family in South America (Oliveira et al. 2016). Among genera, *Oswaldella*, *Staurotheca*, *Symplectoscyphus*, *Sertularella* and *Halecium* are the most speciose genera for SSA & A, corroborating previous findings (*cf.* Peña Cantero 2014; Oliveira et al. 2016; Soto Àngel and Peña Cantero 2019).

Sampling effort, biodiversity and taxonomic distinctness

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

Taxonomic distinctness (i.e., AvTD and VarTD) are useful measures to characterize differences in taxonomic structure across SSA & A, revealing areas with apparent losses or gains of biodiversity, or reduced habitat diversity (Clarke and Warwick 2001; Clarke et al. 2014). High values of AvTD (e.g., ecoregions 180, 181, 183 and province WTSWA; Figs. 1, 5a, 6a; Tables 1, 2), for example, are related to comparatively high biodiversity. This pattern suggests that the southeastern Brazilian and the Buenos Aires coasts have the hierarchy of their taxonomic units more finely partitioned, possibly as a result of environmental stability of the region over evolutionary and/or ecological time scales (Warwick and Clarke 1995).

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

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

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

The other ecoregions and provinces have values of AvTD and VarTD within expectation (*i.e.*, within the 95% range of simulated values depart from the one of the master list; Figs. 5, 6), meaning that the subsets of species observed in each ecoregion/province have the same taxonomic diversity of the whole SSA & A (Figs. 5, 6; Table 1, 2).

Endemism, distribution and biogeographic patterns

There is a statistically significant separation between SSA and Antarctic assemblages, for both ecoregions and provinces (Figs. 7, 8; ANOSIM test; Online Resource Tables S6, S7). This pattern has been shown for other benthic invertebrates based on different biogeographic units and molecular inferences (González-Wevar et al. 2010; Figuerola et al.

2013; Griffiths and Waller 2016). However, the biogeographic affinity of the Magellan area (including the Falkland/Malvinas Islands and the Burdwood Bank) is scale dependent and muddies the picture somewhat. Magellan ecoregions E16 and 186 are grouped with SSA assemblages, but province P7 is grouped with Antarctic assemblages (Figs. 1, 7a, 8a). The Falkland/Malvinas Islands and Burdwood Bank (assemblage 186; Figs. 1a, 7a) are currently part of the large biogeographic region of Patagonia (42°S–56°S; Acha et al. 2004), which includes the Magellan area (Mercado Casares et al. 2017). The Southern tip of South America, the Falkland/Malvinas Islands and Burdwood Bank (viz., E16, P7 and 186) are composed of species from the Magellan, Antarctic and Magellan + Antarctic categories of endemicity (Online Resource Tables S1, S2). Their faunistic composition is unique, revealing a dissimilarity higher than 75% in relation to the other assemblages (Online Resource Tables S4, S5), corroborating its distinct and complex biogeographic role as a center of endemism and route for dispersal of benthic species (Schejter et al. 2016).

The nMDS plots also corroborate the conflicting biogeographic position of the Magellan area, with the intermediate ecoregions 185, 186 and 187 between SSA & A. Province S clusters with Antarctic provinces, and M occupies an intermediate position between SSA & A (Figs. 1, 7b, 8b). Although conflicting, these patterns reinforce the complex role of the Magellan area as a transition zone connecting the SE Pacific, the SW Atlantic and the Southern Ocean. The high proportion of endemic species with different ranges along the Magellan area (Fig. 3) and the high concentration of species at the edge of their distributions (Online Resource Tables S1–S3) corroborate its transitional nature. The Magellan, the Antarctic and the Magellan + Antarctic ranges of endemicity in particular (Fig. 3; Online Resource Table S1), reinforce the hypothesis that the Magellan area is a biogeographic corridor for interchange of some species, but also a barrier impacting the distribution of others (Balech 1954; Souto et al. 2014; Sepulveda et al. 2016). This transition area results in species being either geographically restricted or dispersed over long distances, mainly through the influence of the ACC.

The ACC plays a fundamental role in the biogeographic structuring of hydroids from the Southern Hemisphere (Marques and Peña Cantero 2010; Miranda et al. 2013; Mercado Casares et al. 2017; Soto-Àngel and Peña Cantero 2017), since its circulation simultaneously connects the Southern Ocean biota with the rest of the adjacent oceans but also isolates Antarctica promoting its high endemism (Sanches et al. 2016). Therefore, it is a significant biogeographic barrier to the subtropical, subtropical + Magellan and Magellan endemic hydroids, but does not influence the distribution of the Magellan + Antarctic species. An example is the intermediate area between the subantarctic and Antarctic waters (assemblage APF; Fig. 1b), directly influenced by the ACC and more than 88% dissimilar to the assemblages of other provinces, with a mixed composition of Subtropical (e.g., *Acryptolaria operculata*), Magellan (e.g., *Clathrozoella abyssalis*, *Oswaldella elongata*, *Sertularella jorgensis*, *Staurotheca abyssalis*, *S. profunda* and *S. vervoorti*) and Magellan + Antarctic endemic species (e.g., *Antarctoscyphus elongatus*, *Schizotricha vervoorti*, *Staurotheca jaederholmi*, *S. pachyclada*) (Online Resource Tables S1, S3, S5).

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

The convergence zone of the Brazilian and Falkland/Malvinas currents is a biogeographic barrier for some species (Miranda et al. 2015; Barroso et al. 2016), but some subtropical and Magellan edges of species ranges might extend to latitudes lower than 40°S (e.g., 35°–37°S; Genzano et al. 2009; Souto et al. 2014). This is particularly supported by *Campanularia agas*, *C. subantarctica*, *Lytocarpia canepa*, *Phialella chilensis*, *Sertularella cruzensis*, and *Symplectoscyphus magellanicus* (viz., E17 species composition; Online Resource Fig S1, S2), and is probably related to the adjacent subantarctic waters and the cooler and more saline waters of the Falkland/Malvinas current along the Argentinian continental shelf (Acha et al. 2004). The thermohaline front produces flows northwards (Acha et al. 2004; Genzano et al. 2009) and explains the presence of subantarctic species at lower latitudes (e.g., along 27°–30°S), such as *Amphisbetia operculata*, *Lafoea dumosa*, *Stegolaria irregularis*, and *Symplectoscyphus subdichotomus* (Online Resource Table S1).

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

Despite the low internal similarity (29.8%; Online Resource Table S2), E13 is connected to the Chilean coast (ecoregions 176 to 178 and 188), the southern Brazilian coast (ecoregion 181) and the Río de La Plata Estuary (ecoregion 182) (Figs. 1a, 7) based on the presence of the well-known and widely distributed—equatorial to subantarctic—*Coryne eximia*, *Obelia dichotoma*, and *Plumularia setacea* (Oliveira et al. 2016; Online Resource Table S2). This pattern reflects the Pacific-Atlantic connection driven by the Humboldt Current system distributing species from the Pacific to the Atlantic through the Cape Horn current (Fernandez et al. 2000; Sepulveda et al. 2016). Its role in shaping biogeographic patterns along the Magellan-Antarctic area is poorly understood despite the importance of the area as a marine hotspot (Fernandez et al. 2000; Scott 2012; Selig et al. 2014; Schejter et al. 2016). The Cape Horn current flows through the Magellan Strait, surrounds the tip of South America, and turns northeastwards to form the Falkland/Malvinas current (Montiel et al. 2005; Souto et al. 2014; Sepulveda et al. 2016), which passes through the Scotia Arc and flows northwards meeting the warm Brazilian current (at ~ 36°S–40°S) (Acha et al. 2004). Bio/phylogeographic models have suggested that the formation of the Magellan Strait created a new pathway for faunistic interchange between the Pacific and the Atlantic (Montiel et al. 2005; González-Wevar et al. 2012; Souto et al. 2014). The intermediate role of the Scotia Arc along the area includes dispersal events of species between the Atlantic and Southern oceans (Marques and Peña Cantero 2010; Miranda et al. 2013; Mercado Casares et al. 2017).

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

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

Queen Maud Land (assemblage 226; Fig. 1a) is the most isolated area of Antarctica, with a fauna composed only of Magellan + Antarctic and Antarctic endemic species of *Oswaldella* and *Staurotheca* (Online Resource Tables S2, S4). It is part of the Eastern High Antarctica Zone, an Antarctic area of endemism characterized by an impoverished fauna of hydroids with vast geographical gaps interrupted by scattered records (Marques and Peña Cantero 2010). The faunistics of this area have been poorly explored (De Broyer et al. 2011), hindering knowledge on biogeographic patterns, since real absences and insufficient sampling effort are commonly treated together (Gili et al. 2016; Griffiths and Waller 2016).

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

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

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

The hotspots of biodiversity herein proposed (e.g., the southeastern Pacific, the Magellan area, and the Antarctic Peninsula) were inferred mainly through the presence of endemic species and the level of environmental impact. Although endemism hotspots are more successful in capturing a great proportion of endemic species, species richness and threatened species (Orme et al. 2005), there is very low congruence among different types of hotspots in their ability to be efficient for conservation efforts (Orme et al. 2005; Possingham and Wilson 2005; Thompson et al. 2020). The potential hotspots of biodiversity of hydroids herein defined for the assemblages of SSA & A may facilitate monitoring and conservation efforts within this broad region.

Conclusions

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

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

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00300-021-02909-1.

Acknowledgements We are thankful to André Morandini, Eduardo Hajdu, Fernando Jerep, Rosana Rocha, and Ricardo Pinto-da-Rocha for comments and suggestions on previous versions of this manuscript. Also to Amanda F. Cunha and María A. Mendoza-Becerril for their valuable help in clarifying some taxonomic and biogeographic questions about species of the families Campanulariidae and Bougainvilliidae, respectively. We are grateful to the curators and collection managers at Departamento de Zoologia da Universidade Federal do Paraná (Curitiba, Brazil), Fundação Zoobotânica do Rio Grande do Sul (Porto Alegre, Brazil), Great North Museum Hancock (Newcastle, UK), Instituto Nacional de Investigación y Desarollo Pesquero (Mar del Plata, Argentina), Museum d'Histoire Naturelle de la Ville de Genève (Geneva, Switzerland), Museo de La Plata (La Plata, Argentina), Museu Nacional da Universidade Federal do Rio de Janeiro (Rio de Janeiro, Brazil), Museu de Zoologia da Universidade de São Paulo (São Paulo, Brazil), Natural History Museum (London, UK), Naturalis Biodiversity Center (Leiden, Netherlands), Smithsonian National Museum of Natural History (Washington DC, USA), Zoologisches Museum Universität Hamburg (Hamburg, Germany), and Zoologische Staatssammlung München (Munich, Germany) for their permission and support in accessing specimens of hydroids and geographic data from South America and Antarctica. This manuscript was immensely improved by the contributions of Cristina G. Di Camillo, Mark J. Gibbons, and an anonymous reviewer, to whom we are grateful.

Author's contributions ACM and TPM conceived the ideas with assistance from AGC, GNG, and MOF; ACM, ALPC, GNG, and TPM collected the data; MOF and TPM analyzed the data; all authors led the writing.

Funding This study received financial support from CAPES-PDSE (Proc. BEX 9194/11-8), CNPq (Proc. 490348/2006-8, 142269/2010-7, 477156/2011-8, 445444/2014-2, 309995/2017-5, 429738/2018-8, 170969/2018-5), and FAPESP (Proc. 2010/06927–0, 2011/50242-5, 2012/21453-0, 2013/10821-1, 2014/24407-5, 2018/04257-0).

Availability of data and material The data and material are available in the Supporting Information (see Online Resource Table S1).

Declarations

Conflict of interest There is no conflict of interest or competing interests.

Consent to participate All authors of this manuscript agreed to participate in this study.

Consent for publication All authors give their consent for the publication of this manuscript.

References

Acha EM, Mianzan HW, Guerrero RA, Favero M, Bava J (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, Alemany D, Piola AR (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, Gili JM, Boero F, Gravili C (2004) Fauna of the Mediterranean Hydrozoa. Sci Mar 68:5–438. 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. https://doi.org/10.4067/S0716-078X2001000300008

Cartwright P, Evans NM, Dunn CW, Marques AC, Miglietta MP, Schuchert P, Collins AG (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. 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. https://doi.org/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. PRIMER-e, Plymouth

Collins AG, Schuchert P, Marques AC, Jankowski T, Medina M, Schierwater B (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 abhreviated 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, Halpin P, Ojaveer H, Miloslavich P (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 endemicity. 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. https://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 et al (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, Pica D, Piraino S, Puce S, Cerrano C (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, Kaiser S, Constable A, Nicoll R, Raymond B, Post A, Brandt A, Beaver D (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, Moreno CA, Navarrete SA, Ojeda FP, Valdovinos CR, Vasquez JA (2000) Diversity, dynamics and biogeography of Chilean benthic nearshore ecosystems: an overview and guidelines for conservation. Rev Chil Hist Nat 73:797–830. https://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, Cristobo J, Avila C (2013) Cheilostome bryozoan diversity from the southwest Atlantic region: is Antarctica really isolated? J Sea Res 85:1–17. https://doi.org/10.1016/j.seares.2013.09.003

Frenot Y, Chown SL, Whinam J, Selkirk PM, Convey P, Skotnicki M, Bergstrom DM (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, Bremec C, Meretta P (2009) Hydroid assemblages from the Souhwestern 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, Costello JH, Morandini AC, Miranda TP, Marques AC (2017) Faunal assemblages of intertidal hydroids (Hydrozoa, Cnidaria) from Argentinean Patagonia (Southwestern Atlantic Ocean). Lat Am J Aquat Res 45:177–187. https://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. https://doi.org/10.1111/j.1365-2699.2009.02237.x

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. https://doi.org/10.1111/j.1365-2699.2009.02226.x

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, Vaqué D, Barbosa A, García-Sancho L, Quesada A (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-Duarte MM, Megina C, De Vito D, Di Camillo CG, Puce S, Piraino S (2015) A unified assessment of marine Mediterranean assemblages: a lesson from benthic hydroids. Mar Ecol 37:155–163. https://doi.org/10.1111/maec.12271

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, Mansilla A, Nakano T (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, Cham, 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, Freeman B, Ingenloff K, Jiménez-García D, Peterson T (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, Yanagihara AA, Lindsay DJ, Hopcroft RR, Collins AG (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

Leclére L, Schuchert P, Cruaud C, Couloux A, Manuel M (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, 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. Glob Planet Chang 125:A1–A8. https://doi.org/10.1016/j.gloplacha.2014.06.011

Maronna MM, Miranda TP, Peña Cantero AL, Barbeitos MS, Marques AC (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

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. https://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. https://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 63:295–302. 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. https://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, Kukliński P, Soto Àngel JJ (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. https://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

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. World Register of Marine Species. http://marinespecies.org/aphia.php?p=taxdetails&id=174552 Acessed 21 March 2021

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

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. https://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 Manag 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. https://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, Grace M, Cooper KM, Schratzberger M (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. https://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

Publisher's Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.