Marina de Oliveira Fernandez

Diversidade de hidroides (Cnidaria) do Atlântico profundo sob uma perspectiva macroecológica

Diversity of deep-sea Atlantic hydroids (Cnidaria) under a macroecological perspective

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Para meus pais, irmã e Felipe

“… joy and amazement at the beauty and grandeur of this world of which man can just form a faint notion.”

Albert Einstein, *The World as I see it*

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Índice

Introdução Geral

A macroecologia estuda a relação dos organismos com o ambiente onde vivem em grandes escalas espaciais, a partir da caracterização de padrões de distribuição da diversidade, como riqueza, abundância, amplitudes de distribuição ou tamanhos corporais (Brown & Maurer, 1989; Brown, 1995; Gaston & Blackburn, 2000; Witman & Roy, 2009; Keith *et al*., 2012). A distribuição atual da diversidade decorre de eventos históricos de origens, expansões, diversificações e extinções das espécies, e relaciona-se à capacidade de seus indivíduos e populações ocuparem diferentes nichos (Valentine, 1973; Jablonski *et al*., 1985, 2006; Sexton *et al*., 2009; Lomolino *et al*., 2017). Características funcionais dos organismos (= "*traits*" em inglês) estão relacionadas a suas respostas a fatores bióticos ou abióticos, afetando suas capacidades de crescimento, sobrevivência e reprodução em habitats distintos, assim influenciando diretamente a variação espacial na composição de espécies e podendo contribuir com o entendimento da seleção natural e do funcionamento de ecossistemas (Soininen *et al*., 2007; Violle *et al.,* 2007; Bremner, 2008; Connell & Irving, 2009; Webb *et al*., 2009; Brun *et al.,* 2016).

A variação batimétrica nos oceanos, com seus gradientes e mudanças ambientais associados, como queda de temperatura, luminosidade, disponibilidade de matéria orgânica e de substratos consolidados, e aumento da pressão hidrostática, impõem limites à distribuição de espécies (Somero, 1990, 1992; Smith *et al*., 1997; McClain & Hardy, 2010; Rex & Etter, 2010; Brown & Thatje, 2011; Talley *et al*., 2011; Jamieson, 2015), levando à ocorrência de indivíduos com diferentes formas, funções e histórias de vida de acordo com a profundidade (McClain, 2004; McClain *et al*, 2005; Rex *et al*., 2006; Ramirez-Llodra *et al.,* 2010). Por outro lado, o aumento da profundidade leva a condições ambientais mais homogêneas, reduzindo barreiras ao fluxo gênico e levando a uma maior uniformidade da fauna (McClain & Hardy, 2010; Rex & Etter, 2010). A variação ambiental no fluxo de matéria orgânica particulada para o bentos profundo é considerada um fator importante influenciando mudanças faunais ao longo da profundidade, e estruturando as comunidades em mar profundo (Carney, 2005; Rex & Etter, 2010; Wei *et al*., 2010; McClain *et al*., 2012; McClain & Rex, 2015; Woolley *et al*., 2016).

Hidroides, os estágios polipoides, geralmente bentônicos, das espécies de Hydroidolina (exceto Siphonophorae) (Cornelius, 1995; Cartwright *et al*., 2008; Schuchert, 2012), são ecologicamente diversos e apresentam grande variação intra e interespecífica de formas e tamanhos nos diferentes ambientes (Gili & Hughes, 1995; Cunha *et al*., 2016). Vivem desde águas rasas até profundidades hadais (Kramp, 1956; Calder, 1996; 1998), alimentando-se de matéria em suspensão e usando seus nematocistos para capturar pequenos organismos planctônicos (Gili & Hughes, 1995). Geralmente colonizam substratos consolidados, mas também ocorrem em substratos não-consolidados (Gili & Hughes, 1995; Bouillon *et al.*, 2006; Schuchert, 2012). Reproduzem-se sexuada e assexuadamente (Gili & Hughes, 1995). Suas espécies podem ou não liberar medusas ao longo dos ciclos de vida. Arquetipicamente, pólipos brotam medusas dioicas, portadoras dos gametas que, após fertilizados, desenvolvem-se em larvas plânulas, as quais se metamorfoseiam novamente em pólipos bentônicos (Cornelius, 1995). Há, porém, diferentes níveis de redução da fase de medusa nas diferentes linhagens, até sua completa supressão em ~74% das espécies (Gibbons *et al.*, 2010), nas quais o pólipo porta os gametas em gonóforos fixos.

Os primeiros registros de hidroides em profundidades maiores do Atlântico foram obtidos por expedições do final do século XIX, a partir da coleta de novas espécies e também estendendo as amplitudes de distribuição de espécies de áreas mais rasas (*e.g.*, Allman, 1874; Smith & Harger, 1874; Verrill, 1874). No entanto, apesar da importância de compreender os efeitos da variação batimétrica na distribuição da biodiversidade marinha, há apenas inferências pontuais ou regionais da distribuição de hidroides de mares profundos, e com diferentes focos (*e.g.*, Calder, 1998; Henry *et al.*, 2008). Na realidade, o conhecimento atual sobre os padrões de distribuição no mar profundo é escasso para a maioria dos táxons de invertebrados marinhos, com poucas sínteses do conhecimento de táxons superiores em oceanos como um todo (Allen & Sander, 1996; Rex *et al.*, 1993, 2000, 2005, 2006; Rex & Etter, 2010; Woolley *et al.*, 2016).

Objetivo Geral

Este estudo tem o objetivo de inferir padrões de distribuição de hidroides no Oceano Atlântico e mares árticos e antárticos adjacentes com mais de 50 m de profundidade, melhorando nossa compreensão da diversificação e estruturação associadas à batimetria que propiciaram a ocupação dos diferentes ambientes pelo grupo.

Organização da Tese

À parte esta introdução geral, essa tese é apresentada em 4 capítulos principais e uma seção de considerações finais.

O Capítulo 1 apresenta um extenso levantamento bibliográfico de registros de hidroides, em toda a área estudada, com o objetivo de descrever a distribuição batimétrica das espécies. Investigamos as relações das amplitudes de distribuição batimétrica com as regiões, latitudes e profundidades médias de ocorrência, assim como com a taxonomia do grupo. Por fim, examinamos a influência de fatores históricos nos padrões de profundidades de ocorrência sob um contexto filogenético.

O Capítulo 2 caracteriza a distribuição de uma série de características funcionais das espécies (= "*traits*") e indivíduos de hidroides ao longo da profundidade, contrastando-as com o conhecimento sobre a biologia do grupo e a ecologia de mar profundo.

No Capítulo 3 inferimos padrões de distribuição das espécies de hidroides em todo o Oceano Atlântico e mares polares circundantes considerando a variação batimétrica e latitudinal, buscando reconhecer limites e gradientes de distribuição.

O Capítulo 4 é um artigo publicado em resposta a Chaudhary *et al.* (2016), abordando a complexidade dos padrões de distribuição de espécies e o viés gerado pela heterogeneidade amostral nos dois hemisférios.

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Capítulo 1

Putting together bathymetry, latitude and phylogeny to understand the distribution of deep Atlantic hydroids (Cnidaria, Hydrozoa)

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Abstract

Depth is associated with significant environmental changes and gradients that, together with biotic, geological, and evolutionary processes, defines bathymetric ranges of individuals, populations, species, and even communities. However, inferences on bathymetric ranges of marine invertebrates are usually based on a few taxa or on restricted regional scales. In this study, we present a comprehensive literature survey of hydroids for the Atlantic Ocean and adjacent Arctic and Antarctic seas for records deeper than 50 m deep. These records were used in bathymetrical analyses along latitude, and major patterns were compared under an evolutionary framework. The Atlantic hydroid-bearing species are mainly eurybathic, but vertical distribution proved to be taxonomically and regionally dependent. Eurybathy is reduced in "Antarctic" species but increased in "Tropical" and "Subtropical North" regions. Bathymetric ranges increase along with mean depths of the species for both families and regions. There are no exclusively bathyal or abyssal benthic hydroidolinan supraspecific taxa in the Atlantic. Our results show that colonization of the deep sea and wide bathymetric distributions occurred early in the evolution of the group. Records of Atlantic hydroids are unevenly distributed; Equatorial and southern Tropical latitudes have few records, likely due to uneven sampling efforts, and future collections shall increase depth ranges of the species. We conclude that hydroid-bearing species are important inhabitants of the deep sea, and more studies are necessary to investigate the relationship between traits of the species with their depths of occurrence and habitat conditions, allowing to recognize processes involved in the formation of the patterns.

Resumo

A profundidade está associada a mudanças e gradientes ambientais significativos que, juntamente com processos bióticos, geológicos e evolutivos, definem amplitudes batimétricas de indivíduos, populações, espécies e até comunidades. No entanto, as inferências sobre as amplitudes batimétricas de invertebrados marinhos são geralmente baseadas em poucos táxons ou em escalas regionais restritas. Neste estudo, apresentamos um levantamento abrangente da literatura de hidroides para o Oceano Atlântico e os mares adjacentes do Ártico e da Antártida para registros a mais de 50 m de profundidade. Esses registros foram utilizados em análises batimétricas ao longo da latitude, e os principais padrões foram comparados sob um quadro evolutivo. As espécies com fase de hidroide do Atlântico são principalmente euribatiais, mas a distribuição vertical provou ser taxonômica e regionalmente dependente. Euribatialidade é reduzida em espécies "Antárticas", mas aumentou nas regiões "Tropical" e "Subtropical Norte". As amplitudes batimétricas aumentam juntamente com a profundidade média das espécies para famílias e regiões. Não há táxons supraespecíficos de Hydroidolina bentônicos exclusivamente batiais ou abissais no Atlântico. Nossos resultados mostram que a colonização do mar profundo e amplas distribuições batimétricas ocorreram no início da evolução do grupo. Os registros de hidroides do Atlântico são distribuídos de forma desigual; latitudes equatoriais e tropicais do Sul têm poucos registros, provavelmente devido a esforços de amostragem desiguais, e coleções futuras devem aumentar as amplitudes batimétricas das espécies. Concluímos que as espécies com fase de hidroide são habitantes importantes do mar profundo e que são necessários mais estudos para investigar a relação entre as características das espécies com suas profundidades de ocorrência e condições do habitat, permitindo reconhecer os processos envolvidos na formação dos padrões.

Introduction

Depth variation and associated environmental variables set limits to the tridimensional distribution of species (McClain & Hardy, 2010; Rex & Etter, 2010). However, inferences on bathymetric ranges of marine invertebrates are usually based on few taxa and/or on restricted regional scales (*e.g.* Pineda, 1993; Allen & Sanders, 1996; Brey *et al.*, 1996; Altuna, 2007;

Peña Cantero, 2004; Downey *et al.*, 2012). This is the first study synthesizing the knowledge on bathymetrical distribution of hydroids of the Atlantic Ocean and adjacent polar seas, contrasting these patterns with their taxonomy/phylogeny and Atlantic regions.

A multitude of biotic and abiotic processes influences the geographical and bathymetrical ranges of the species (Rex, 1977; Sexton *et al.*, 2009; Louthan *et al.*, 2015). The environment changes markedly along ocean depth. Temperature decreases up to becoming relatively constant below the permanent thermocline (usually between 200 m and 1,000 m deep), and there is no solar irradiance in areas deeper than 1,000 m (Talley *et al.*, 2011). Availability of organic matter decreases along depth and distance from the coast, except in chemosynthetic-based habitats (Lampitt & Antia, 1997; Smith *et al.*, 1997; Levin *et al.*, 2016). Hydrostatic pressure increases ~1 atm every 10 m; salinity varies non-uniformly in different parts of the oceans, as well as oxygen concentrations that vary from anoxia to saturation (Talley *et al.*, 2011). Substrates are typically muddy at abyssal plains, but hard substrates are found on the slope, seamounts and at the mid-ocean ridges (Jamieson, 2015). All these environmental heterogeneities may act as barriers to dispersal of individuals/colonies, isolating populations at different depths (McClain & Hardy, 2010; Rex & Etter, 2010). Sea surface and sea floor constrain distributions, and maximum depth ranges depend on the mean depth of occurrences of the species (Pineda, 1993). Therefore, benthic shallow water species would have ranges restricted by a combination of both, sea surface boundary and marked environmental changes along depth (Pineda, 1993).

Tolerance to temperature and hydrostatic pressure – and interactions between these two factors –, have been shown as important in limiting the bathymetric distribution of organisms (Menzies *et al.*, 1973; Somero, 1990, 1992; Gage & Tyler, 1991; Brown & Thatje, 2011; Mestre *et al.*, 2013). Hydrostatic pressure variation modulates physiological processes by causing changes in volume, affecting gene expression, and reducing fluidity of the lipid bilayer of cell membranes (Somero, 1992; Pradillon & Gaill, 2007; Morris *et al.*, 2015), therefore affecting biological systems. Adaptations regulating these processes are important for the survival of individuals and maintenance of populations at different depths. Differences in pressure may, therefore, work as a barrier restricting the occurrence of both shallow and deep water species along the water column (Somero, 1992). Apparently, depth related variations would be responsible for greater divergences between populations separated vertically than between those separated horizontally (Rex & Etter, 2010). However, processes seem to impose limits in both directions: those species with wider ranges of bathymetric distribution are also widely geographically distributed, and those species restricted to abyssal depths are usually more endemic (Vinogradova, 1997; Harley *et al*., 2003).

Physiological tolerance to depth may vary along the life cycle, with different answers in embryos, larvae, and adults. Many Echinodermata embryos and larvae, for example, potentially tolerate higher hydrostatic pressure than their respective adults (Tyler & Young, 1998; Tyler *et al*., 2000; Benitez Villalobos *et al*., 2006), and a shallow water neogastropod can survive up to 400 atm pressure, with its tolerance varying during ontogeny (Smith & Thatje, 2012). Some species, however, do not colonize certain depths because they cannot survive until reproduction (Tyler *et al*., 2000). Still, marine invertebrates may also expand their geographical distribution without long lasting dispersive stages (Young *et al*., 1997a; Winston, 2012). Dispersal distances and connectivity in deep-sea invertebrates, although variable among taxa and life-history traits, are generally comparable to those of shallower waters (Etter & Bower, 2015; Baco *et al*., 2016).

The capacity of individuals and populations to colonize and survive at different depths may vary geographically in relation to environmental and geological peculiarities. For instance, alternation between glacial and interglacial periods during the Pleistocene in Antarctica (Anderson *et al*., 2002; Ingólfsson, 2004) would have led to greater eurybathy of benthic Antarctic invertebrates (Brey *et al*., 1996). The impact of the ice on the continental shelf would have extinguished the coastal fauna during glacial periods, and species with greater physiological tolerances, for which populations could colonize deeper waters or refuges on the continental shelf, would have survived and recolonized the continental shelf after retraction of the ice (Thatje *et al*., 2005, 2008). In the Arctic, the continental shelf fauna would have been extinguished during glacial periods as well (Piepenburg, 2005). The Arctic, however, is more recent and less biogeographically isolated than the Antarctic, allowing faunal exchanges with boreal regions (Clarke & Crame, 1989; Clarke *et al*., 2004; 2005; Piepenburg, 2005), and making the Arctic fauna little endemic (Stepanjants, 1989; Piepenburg, 2005; Ronowicz *et al*., 2015), different from Antarctic (Clarke, 1996; Piepenburg, 2005). Consequently, part of the Arctic fauna may have survived glacial periods taking refuge in more southern latitudes, therefore not requiring tolerance to deep habitats.

In the late nineteenth century, deep-sea expeditions dredged the first records of hydroids (Cnidaria, Hydrozoa) in the Atlantic Ocean, unraveling new species but also extending the bathymetric range of many shallow water species (*e.g.* Allman, 1874; Smith & Harger, 1874; Verrill, 1874). Hydroids are the polypoid stages, usually benthic, of the hydrozoans Leptothecata, non-monophyletic "Anthoathecata", and Limnomedusae (Collins, 2000;

Marques & Collins, 2004; Collins *et al.*, 2006; Cartwright *et al.*, 2008). Their life cycles often include planktonic medusae (Marques & Collins, 2004). Presently, hydroids are known to be well represented in the deep-sea benthos (Vervoort, 1966; Calder & Vervoort, 1998). It has been suggested that their bathymetric ranges may be wider at higher latitudes, because tropical shallow water species would not survive in colder and deeper waters (Calder, 1998). Studies on bathymetric distribution of hydroids, however, focused on few taxa and restricted areas (Cornelius, 1979; Stepanjants, 1989; Calder, 1998; Peña Cantero, 2004; Altuna, 2007), without general descriptions of ranges of bathymetric distribution in an ocean wide scale.

This is the first study presenting an extensive literature survey at the oceanic scale, and this data is used to infer comprehensive patterns of bathymetric distribution of Atlantic hydroids. We focus our analysis on the relationships between bathymetric ranges, depths of occurrence, regions, latitudes, and taxonomic/phylogenetic structure.

Material and methods

Study area

The study area was the Atlantic Ocean and its adjacent Arctic and Antarctic seas deeper than 50 m (Fig. 1). Boundaries were established as: SE – 24˚E to the South of Africa, SW – line between 60˚W at the Antarctic Peninsula and Argentina / Chile border, NE – 30˚E to the North of Norway and 5.5˚W at the Strait of Gibraltar, and NW – to the West of Baffin Bay (Baffin and Hudson bays were included).

Literature survey

We compiled 8,978 records of hydroids (except for Milleporidae, Stylasteridae, and Limnomedusae) from 127 references published from 1874 to the present (see Supplementary Material, Table S1, for complete list of references). In the case of duplicate records, we assumed the one from the first published reference. We checked every record for information updates, corrected misidentifications based on the recent literature (see Supplementary Material for a complete list of checked references), and standardized the taxonomy based on the *World Register of Marine Species* (WoRMS Editorial Board, 2017). Every checked record was then classified in supraspecific taxonomic groups based on phylogenetic literature (Maronna *et al.*, 2016; Mendoza Becerril, 2015; Cunha *et al.*, 2017) whenever possible. We excluded from the analyses dubious records and those not identified up to the species level, as well as those species belonging to phylogenetic unstable lineages, remaining 8,162 records. For those records collected within intervals of coordinates or depths (*e.g.*, in trawl collections), we adopted average positions between initial and final points. Records without coordinates were georeferenced by using Google Earth (Google, 2017) based on the published information concerning the collection site.

Patterns of bathymetric distribution

The ranges of bathymetric distribution of the species were inferred for those species with more than one record of occurrence, using their shallowest and deepest records to delimit their ranges. Patterns of bathymetric ranges were inferred by plotting the depth ranges for all species, and estimating supraspecific variation by families.

To investigate if bathymetric ranges of the species vary among latitudes, we calculated new depth ranges for each 10˚ latitudinal band for each species and region. Regions were defined as "Arctic" (north of 58˚N), "Subtropical North" (58˚N–23.437˚N), "Tropical" (23.437˚N–23.437˚S), "Subtropical South" (23.437˚S–58˚S) and "Antarctic" (south of 58˚S). Effects of unequal sampling efforts between regions were reduced by constructing downscaled geographical sets of analyses composed by the same number of records for each region, after randomly subsampling the records of the original data set. These downscaled sets were used to estimate comparable bathymetric ranges of the species among regions by using permutational analyses of variance with the "aovp" function in the "lmPerm" R package (Wheeler & Torchiano, 2016), and subsequent permutational pairwise comparisons by using the "pairwisePermutationTest" function in the "rcompanion" R package (Mangiafico, 2017). We also analyzed the frequency distributions of bathymetric ranges of the species for each region.

Variability of the data within families, latitudes, and regions were inferred by plotting sets of records using boxplots. We also compared the total numbers of records compiled among latitudinal bands to evaluate differences in sampling efforts. Additionally, we calculated the mean depth of occurrence of each species as "(maximum depth – minimum depth)/2", and by plotting these values with the bathymetric ranges of the species we examined if the species bathymetric ranges are dependent on the depth where they occur (Pineda, 1993). Different colors were used to indicate the number of regions where each species was recorded to verify if bathymetric ranges were related to geographical distribution ranges.

We categorized the bathymetric ranges of the species by classifying them as eurybathic (*i.e.*, range of bathymetric distribution ≥300 m; Menzies *et al.*, 1973) or stenobathic (*i.e.*, range of bathymetric distribution <300 m), then comparing the number of species within each category among families and regions, taking into account the geographical differences in sampling effort.

Finally, the component related to the phylogenetic structure present in the deep-sea species was inferred by plotting the records by depth and region of occurrence on a phylogenetic hypothesis for the benthic Hydroidolina (Leptothecata and the non-monophyletic "Anthoathecata"). This approach allows to discuss whether living in the deep sea is a phylogenetic trend in a lineage or something else, like and adaptive response.

Results

Richness and distribution in the Atlantic

Our survey totaled 582 hydroid-bearing species, belonging to 33 families (Supplementary Material, Table S1). Records were unevenly distributed in the area, concentrated nearby land masses and at some specific areas, like North American and European continental shelves, Arctic Ocean, and Patagonia–Antarctic Peninsula region (Fig. 1).

Around 21% of the species were recorded deeper than 1,000 m, with 20 and 11 species exclusively recorded for ≥1,000 m and ≥2,000 m (*viz.*, *Aglaophenia octodonta*, A*glaophenopsis verrilli*, *Bouillonia cornucopia sensu* Petersen, 1990, *Branchiocerianthus imperator*, *Branchiocerianthus norvegicus*, *Cladocarpus crenatus*, *Clathrozoella abyssalis*, *Halecium dubium*, *Halecium profundum*, *Hydractinia ingolfi*, and *Staurotheca abyssalis*), respectively. *Aglaophenia latecarinata* presented both the deepest record and the greatest bathymetric range, from 52.5 m to 5,159 m deep (Supplementary Material, Table S1).

Patterns of bathymetric distribution

There are 422 species (29 families) with more than one depth record, for which we estimated the bathymetric ranges (Fig. 2, Table S1). Most species have bathymetric ranges of 0–500 m, with frequency distribution decreasing in a unimodal pattern (Fig. 3). Also, most species are eurybathic (251, or 59% of the total), *i.e.*, they have bathymetric ranges ≥300 m, 92 (22%) ≥1,000 m, and 38 (9%) ≥2,000 m.

The greater bathymetric ranges occurred for those species with deeper records, and ranges in general decrease following decreases in maximum depths of occurrence (Fig. 2). Indeed, only 3 out of 111 species recorded deeper than 1,000 m are stenobathic. Deep species extend their bathymetric distributions to shallower waters, with few exceptions (Fig. 2). Bathymetric ranges increase as mean depth of occurrence also increases, until a maximum range, and then decrease at abyssal depths. Narrow bathymetric ranges were found for species occurring at all depths, but wider ranges were only found for species at intermediate depths. There is no clear relationship between bathymetric and geographic ranges, although several species with the largest bathymetric ranges were found in more than one region. Several species with ranges restricted to lower bathyal, and most of those restricted to abyssal depths, were found in one region only (Fig. 4).

Taxonomic variation related to depths of occurrence and bathymetric ranges

Wider bathymetric ranges for species with greater maximum depths of occurrences is a general pattern across families (Fig. 5), but these occurrences are unequally distributed among families (Fig. 5, 10). Some families have no (*e.g.*, families of Capitata) or few (*e.g.*, Campanulariidae, Staurothecidae, Schizotrichidae, Kirchenpaueriidae) species occurring deeper than 1,000 m, while others have large proportions of species at those depths (*e.g.*, Lafoeidae, Sertulariidae, Aglaopheniidae). This indicates that none of the families of the Atlantic is typically deep water, that is, even families whose species extend their distributions to abyssal depths also have species at the continental shelf.

Bathymetric ranges of species are variable among families as well (Figs. 5–6). Lafoeidae, Laodiceidae, Campanulariidae, Staurothecidae, Thyroscyphidae, Sertulariidae, and Aglaopheniidae have at least twice more eurybathic than stenobathic species, whereas other families have higher proportions of stenobathic species (Fig. 5). Average bathymetric ranges of the species vary from a few meters (*e.g.*, Pandeidae, Corynidae, Oceaniidae) to more than a 1,000 m – the highest averages found in Tubulariidae, Lafoeidae, Laodiceidae, and Clytiidae (Fig. 6). Medians of bathymetric ranges and variation of species ranges within families were also variable (Fig. 6).

Geographic variation related to depths of occurrence and bathymetric ranges

Tendencies of increasing bathymetric ranges with increasing maximum depth of occurrence are present in all Atlantic regions (Fig. 7). However, bathymetric ranges of the species vary regionally ($p = 0.0048$; Figs. 7–8, 10). Significant differences were found in the pairwise comparisons “Antarctic” vs. “Subtropical North” ($p = 0.0202$), “Antarctic” vs.

"Tropical" (p = 0.0135), and "Subtropical South" vs. "Tropical" (p = 0.0360) depth ranges. The deepest occurrences and widest bathymetric ranges were found in the "Tropical" and "Subtropical North" (Figs. 3, 7–8) regions, even after data was downscaled to the same number of records (Fig. 7b, 8b). The "Tropical" region has also the highest proportion of eurybathic species, but at the "Subtropical North" region most species are stenobathic (Fig. 7b), despite some have wide ranges. Contrarily, most of the "Antarctic" species are stenobathic (Fig. 7b). On average, bathymetric ranges are larger and more variable in the "Tropical" region and smaller and less variable in the "Antarctic" (Figs. 3, 8b). All regions presented a unimodal pattern of decreasing numbers of species for larger depth ranges, although proportions of species with different ranges vary. The "Antarctic", for example, has no species with bathymetric ranges >1,500 m, while all species with ranges >2,000 m are in the "Subtropical North" and "Tropical" regions (Fig. 3).

Number of records was uneven in the different latitudinal bands, from 3 (10°S–20°S) and 6 (0°-10°S) records to 2,706 records (60°N–70°N). The number of deep records and the bathymetrical range of the species usually increase accompanying the total number of records (Fig. 9).

Phylogenetic and regional variation in depths of occurrence

Records of taxa are unevenly distributed across regions and depths (Fig. 10). Different taxa account for the patterns of bathymetric distributions in each region. Aplanulata, Staurothecidae, and Aglaopheniidae, for example, are responsible for all records below 1,500 m deep in the "Subtropical South" region; just a few taxa account for all records in the "Antarctic" region; and Thyroscyphidae, for example, was not recorded in the polar regions.

Under a phylogenetic perspective, bathymetric and geographic distribution patterns vary among related taxa. For instance, Aplanulata, sister group of all other Hydroidolina, has a wide bathymetric and geographic distribution; Capitata (represented by Corynidae, Pennariidae, Solanderiidae, and Zancleidae) is restricted to shallower waters; and the sister groups Oceaniidae and Bougainvilliidae have considerably different bathymetric ranges.

Discussion

The 582 hydroid-bearing species surveyed represent ~16.5% of the 3,519 all accepted benthic and planktonic hydroidolinan species (WoRMS Editorial Board, 2017). This is the most comprehensive dataset of deep-sea hydrozoans, or even cnidarians, to date. About 21% of the species in the studied area was recorded deeper than 1,000 m – this is a large proportion considering the peculiar deep-sea habitat, as well as the fragmentary knowledge for the area when compared to shallower waters (Levin *et al.*, 2001; Ramirez-Llodra *et al.*, 2010).

Sampling efforts in the abyssal depths are much lower and spatially heterogeneous when compared to continental shelves and slopes. This limited collection makes the bathymetric ranges of the species underestimated, and hampers some comparisons among the different regional patterns. Future samples and records shall increase the proportion of eurybathic species, as well as our knowledge about deep-sea Atlantic biodiversity. Presently, we believe there is a sufficient amount of records that, together with standardization procedures, are helpful to propose hypotheses based on consistent patterns, as well as to diagnose gaps/deficiencies in the present biodiversity knowledge.

A large proportion of the species have vertical ranges between 0–500 m, with decreasing numbers of species with larger ranges. Similar patterns were found for gastropods and polychaetes (Pineda & Caswell, 1998), and for benthic medusozoans in the Bay of Biscay (Altuna, 2007). Actually, hydroid-bearing fauna in the area is primarily characterized by eurybathic species, with most species presenting depth ranges ≥300 m. These wide vertical ranges must be associated with a high capacity of vertical dispersal and tolerance to the depth-related environmental changes, many derived from the hydrostatic pressure. Comparative data from the Bay of Biscay showed that only 34% of the species of Medusozoa (mostly Hydrozoa) were eurybathic (Altuna, 2007). However, it is important to highlight that our data is restricted to records deeper than 50 m, and shallow water species (*i.e.*, <50 m) tend to be stenobathic because of the uniquely high dynamics of the superficial depth zone. The greater variation in species composition associated to rapid environmental shifts would result in smaller bathymetric ranges. On the other hand, minor or slower environmental variations in deeper waters also help to explain the less than 3% of stenobathic species recorded in areas deeper than 1,000 m. This is also related to the fact that bathymetric ranges increase together with the increasing mean depths of occurrence, a pattern found among families and regions. However, this relation may not be merely related to the more uniform environmental conditions in the deep regions. The distribution is already expected to be wider for species occupying intermediate depths, because any range would be affected by the constraining that both surface and ocean floor boundaries apply to a random distribution (Pineda, 1993). Our results show this clear constraint at surface limits, but a weak symmetrical counterpart at lower bathyal and abyssal depths, since records closer to ocean floor are rare. Indeed, vertical boundary constraints cannot solely explain all bathymetric ranges, because it is expected that many species do not reach their maximum possible vertical distribution in relation to their mean depths of occurrences, *i.e.*, many distributions do not reach the boundaries, and must then be limited by other processes (Pineda & Caswell, 1998).

General bathymetric patterns are not universal among families. Ranges of distribution are variable, and there are families predominantly eurybathic or stenobathic. An association between unique evolutionary histories, different physiological tolerances, and habitat suitability (Stillman & Somero, 2000; Hall & Thatje, 2009) may be partly responsible for the varied patterns of bathymetric distributions. Differences in depths of occurrences between groups of Hydroidolina were reported in the Antarctic in a comparison between Leptothecata and "Anthoathecata" (non-monophyletic), the latter more represented in shallow waters (Peña Cantero, 2004). Differences were suggested to be caused by evolutionary and ecological factors, as well as destructive samplings biases (Peña Cantero, 2004). By not possessing polyps enveloped by exoskeleton, the fragile "anthoathecates" would suffer more damage during sampling and consequently be more difficult to identify, consequently decreasing their number of records in deeper waters (Peña Cantero, 2004). Our comparison of the differences in depths of occurrence based on a phylogenetic hypothesis has shown that the so-called "anthoathecates", composed by unrelated groups, have varied depth distributions. Capitata (herein represented by Corynidae, Pennariidae, Solanderiidae, and Zancleidae) is a taxon restricted to shallow waters in the Atlantic Ocean, while Aplanulata, Eudendriidae, Hydractiniidae, and Bougainvilliidae were recorded in both shallow and deep waters, with varied proportions across geographic regions (Figs. 3, 8). All these groups would be equally prone to be damaged during samplings, therefore suggesting that the different proportions of leptothecates and "anthoathecates" along depth is ecological and/or evolutionary rather than a sampling artefact, and that the processes shaping distributions generally act within the order taxonomic level, such as in families.

We found no exclusive bathyal or abyssal supraspecific taxa in the Atlantic. Depth distributions of families were usually extensions from shallower waters with a few species strictly occurring in deeper habitats. This pattern may reflect the deep-sea colonization by the species bearing hydroids, arising in shallower habitats before submerging into deeper waters. If so, the colonization of deep waters would have occurred early in the evolution and diversification of the group, because many taxa presently occur at great depths. The phylogeny would support that wide bathymetric distributions appeared basally among the Hydroidolina with some apical reversals, rather than a condition independently evolved in many taxa.

However, evolutionary processes related to the origin of the deep-sea fauna, such as invasions of the habitat followed by diversification, are still poorly studied (Rex & Etter, 2010). It was suggested that new taxa would have originated coastally and colonized deeper waters during the Phanerozoic (Jablonski *et al.*, 1983; Jablonski & Bottjer, 1991). Detritivore echinoids, for example, were hypothesized to have migrated to the deep sea after a greater organic carbon influx to the deep-sea habitats in the late Cretaceous (Smith & Stockley, 2005). Several other hypotheses on the origin of the deep-sea fauna assumed that temperature tolerance would limit the distribution of organisms. Therefore, deep-sea regions in low latitudes would have been populated between the Mesozoic and Early Cenozoic, when the water column was warm and isothermal (Madsen, 1961; Menzies *et al.*, 1973; Benson, 1975), subsequently gradually adapting to colder waters (Tyler & Young, 1998), while cold and isothermal waters at high latitudes would have been more easily colonized (Kussakin, 1973; Menzies *et al.*, 1973; Young *et al.*, 1997b). Alternative hypotheses proposed that a few deep-sea taxa arose and diversified in the deep sea, subsequently emerging to shallower waters (Hessler & Thistle, 1975; Lindner *et al.*, 2008). Processes of colonization of environments at different depths, however, might have been unique, and the faunal composition of an area may result from colonization, radiation and extinction from both shallow and deep waters (Brandt, 1992; Brandt *et al.*, 2007; Rex & Etter, 2010).

Bathymetric ranges and proportions of eurybathic species vary among regions. Geographic variation in eurybathy could be influenced by local evolution on the condition associated to local favorable environments. Interestingly, the high latitude and geological history of "Antarctic" apparently does not benefit higher eurybathy; our results showed reduced eurybathy for Antarctic species compared to other regions, with bathymetric ranges significantly lower than those of "Tropical" and "Subtropical North" regions. Indeed, this pattern is also different from those observed for other (mostly mobile) marine invertebrates – polychaetes, echinoderms, mollusks and crustaceans – for which there is an extended eurybathy in the Antarctic (Brey *et al.*, 1996; Martín-Ledo & López-González, 2014). However, sessile Antarctic sponges also have limited eurybathy, varying between classes and families (Downey *et al.*, 2012). In fact, environmental or geological conditions leading to eurybathy may have different effects in different groups, because physiological and life-history traits – *e.g.*, reproduction, dispersal capabilities, feeding modes, substrate use – may also be different between and within groups (Young *et al.*, 1997a, 1997b; Calder, 1998; Ramirez-Llodra *et al.*, 2010; Moreau *et al.*, 2017), affecting the capacity to survive at different depths.

Previous studies on bathymetric distribution of Antarctic hydroids reported several deep records restricted to the continental shelf, that may reach 500–1,000 m deep, deeper than the average 200 m continental shelves elsewhere (Clarke, 2003; Peña Cantero, 2004). A large proportion of the species extend their distribution over the continental shelf break (Peña Cantero, 2004). Our compilation revealed only three species with records over 1,000 m deep in the "Antarctic", suggesting that most deeper records of hydroids might be in areas outside the geographical scope of this study.

"Subtropical North" and "Tropical" regions have species with the deepest records and largest bathymetric ranges. The largest proportion of eurybathic species was also found in the tropics. This pattern is counterintuitive because variation of temperature and oxygen concentration along depth is greater and more abrupt in the tropics (Talley *et al*., 2011). Assuming temperature is an important variable delimiting species distribution, the historical window to surpass this barrier occurred during the Mesozoic and Cenozoic, when waters were warm and isothermal in the tropics (Madsen, 1961; Menzies *et al*., 1973; Benson, 1975). It is important to regard that distribution patterns of marine biodiversity are spatially and temporally dynamic, thus present distributions may not be readily interpreted as caused by recent past conditions. Marine distribution patterns may shift due to dispersal (Matthyesen, 2012; Grantham *et al*., 2003), tectonic events (Renema *et al*., 2008; Leprieur *et al*., 2016; Zaffos *et al*., 2017), and other biotic and abiotic processes (Sexton *et al*., 2009). This could explain the non-significant differences in the bathymetric distributions of the species between "Arctic" and "Antarctic", despite their distinctive geological histories. An alternative explanation would be similar ecological demands, in which ecology would overcome phylogeny, and the capacity of colonizing different depths would be a peculiarity of the populations within a species.

Species from abyssal depths with narrow vertical ranges are endemic to one region (with one exception, *Bouillonia cornucopia sensu* Petersen, 1990) and species with wider bathymetric ranges have wider geographical ranges. Similar patterns were observed for other taxa (review in Vinogradova, 1997) and might be a consequence of the ecophysiological tolerance of the species, that constrain their distributions both vertically and horizontally. For hydroids, luminosity, hydrodynamics, food availability, and temperature are important constraints to the distribution of the populations/species (Millard, 1978; Boero, 1984; Gili & Hughes, 1995; Schuchert, 2000; Mendoza Becerril & Marques, 2013), and especially associated with depth. However, little is known about the biology of deep-sea hydroid-bearing species, *i.e.*, their dispersal, reproduction, ecophysiological adaptations to depth and temperature, duration of larval stages, etc., making it difficult an integrated understanding of the processes that generated these patterns. Also, present species identifications are usually exclusively based on morphological criteria, and future population genetics studies might reveal cryptic species and, maybe, more segmented bathymetric ranges (Gooch & Schopf, 1972; Moura *et al.*, 2008; Zhou *et al.*, 2013; Cunha *et al.*, 2015, 2017; Schuchert, 2014). This expected population divergence driven by bathymetry still has to be explored for Hydroidolina and most taxa (Rex & Etter, 2010).

The distribution of a given species is shaped by processes acting on morphological, physiological, and life-history traits that may be variable between populations and/or individuals (Usseglio-Polatera *et al.*, 2000; Witman & Roy, 2009; Soininen *et al.*, 2016). Future studies shall have a better perspective when investigating how depth-associated habitat conditions favor specific traits of hydroids, ultimately defining their population, species, and community patterns of distribution. Dispersal, for example, a basic component of the distribution, is related to the different stages of the life cycle of a given lineage – planula/actinula larvae, polyp (by rafting or detachment of asexual propagules), or medusa (Gravier-Bonnet, 1992; Cornelius, 1995; Gili & Hughes, 1995; Gibbons *et al.*, 2010). Therefore, studies focusing on the relation of traits and distributions must be intensified to better understanding the processes involved in the diversification of hydroidolinans in general.

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Figures

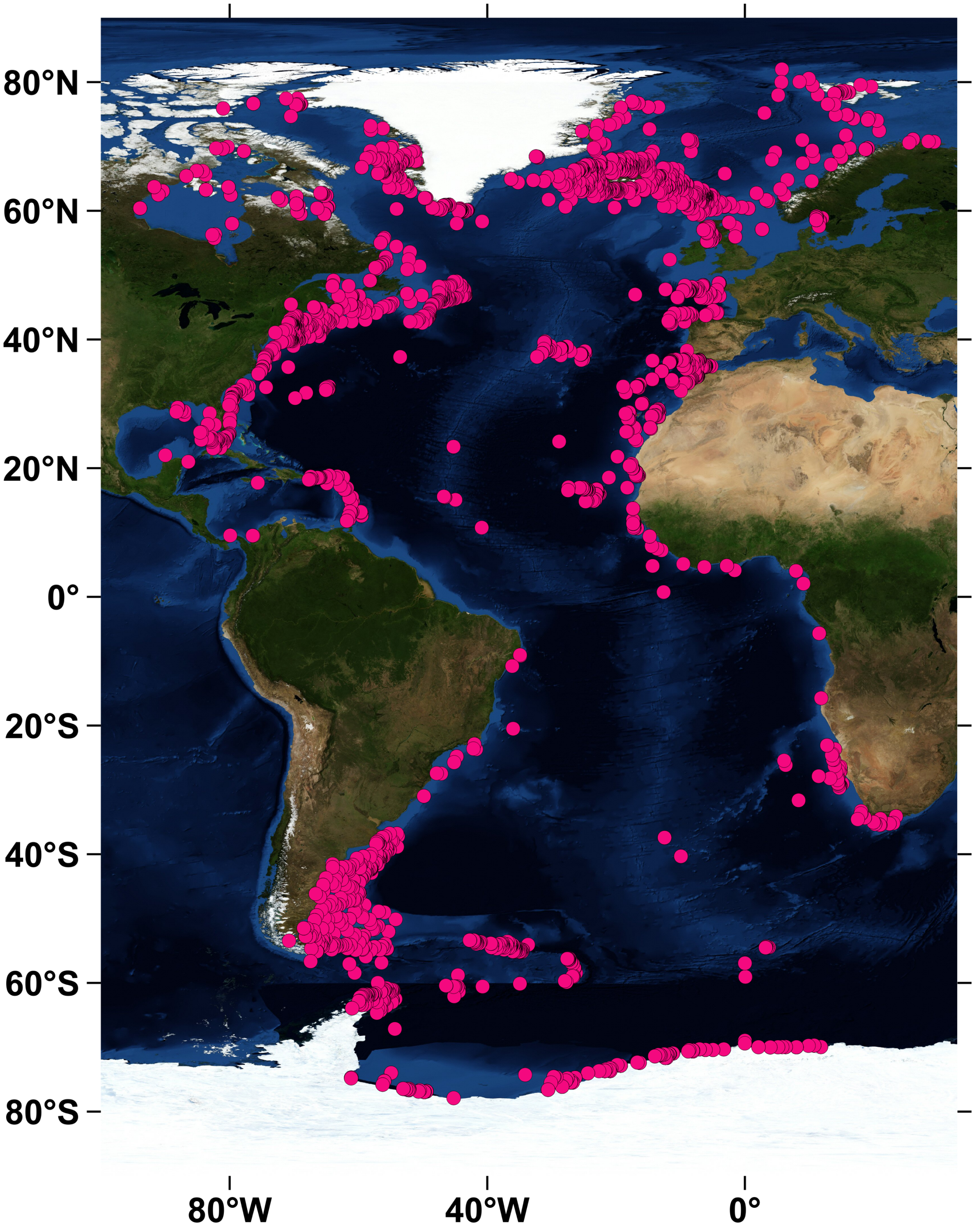

Figure 1. Geographic distribution of the records used to estimate bathymetric patterns in this study.

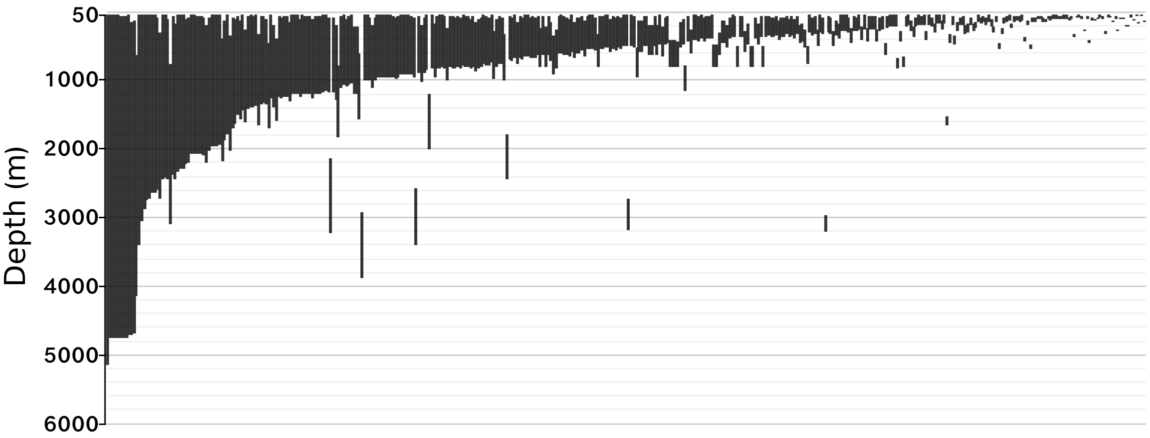

Figure 2. Bathymetric distribution of hydroids in the Atlantic Ocean and adjacent polar seas in waters deeper than 50 m, ordered from the largest to the smallest range. Each column represents one species. Species with ranges smaller than 20 meters not plotted.

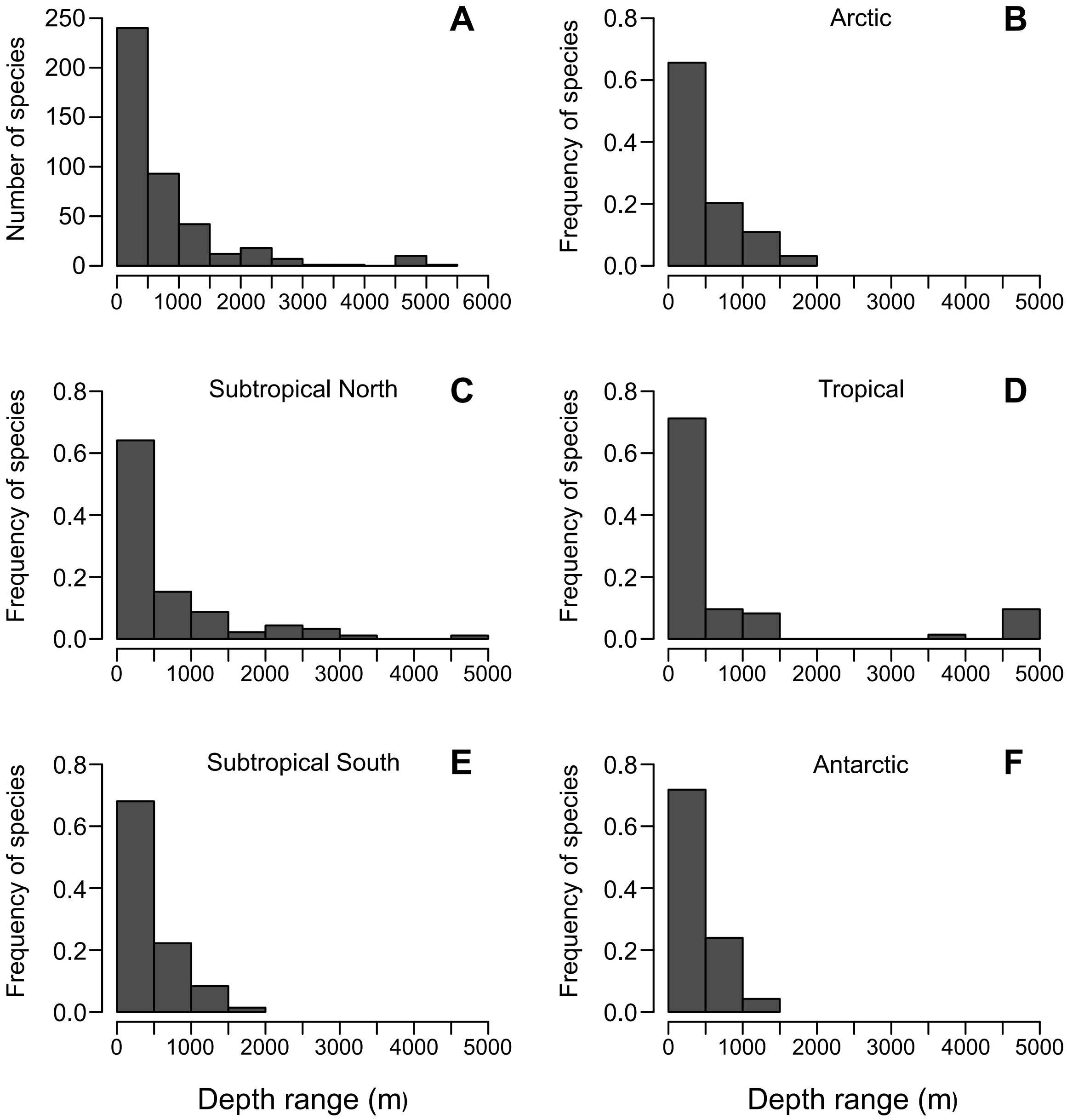

Figure 3. Frequency distribution of bathymetric ranges for hydroid-bearing species in the Atlantic Ocean and adjacent polar seas deeper than 50 m (**A**), and for each region of this study, *viz*., Arctic (**B**), Subtropical North (**C**), Tropical (**D**), Subtropical South (**E**), and Antarctic (**F**).

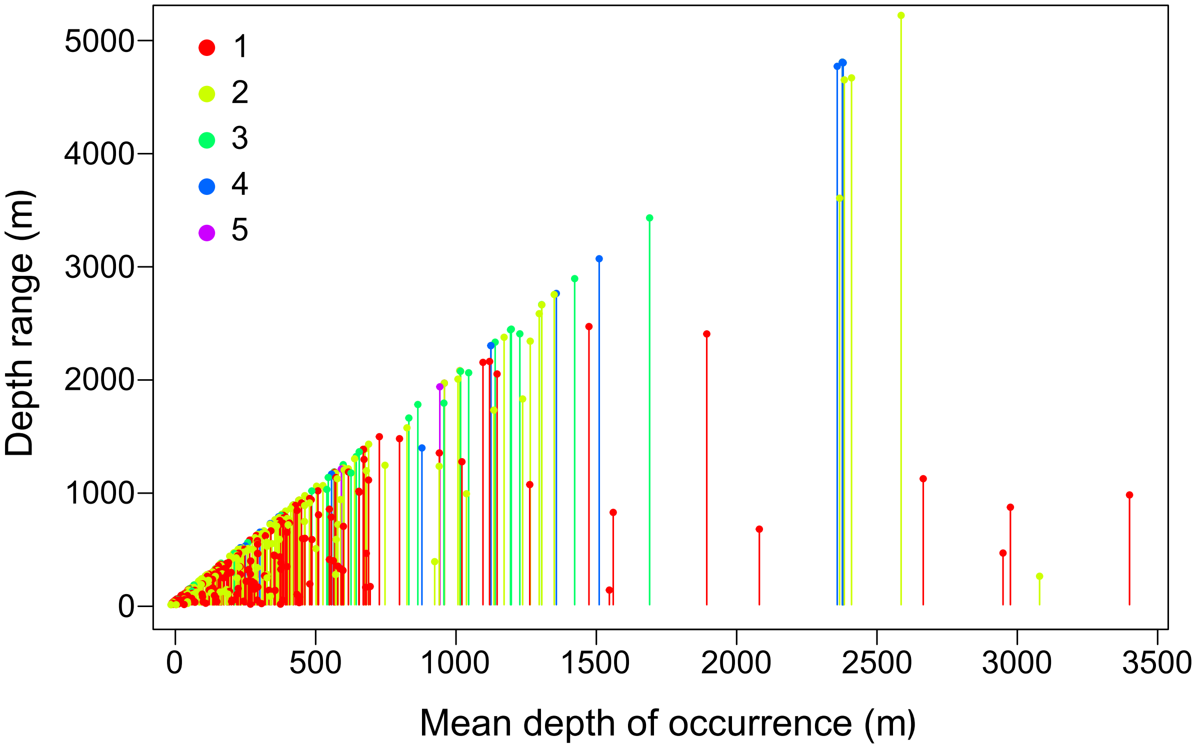

Figure 4. Relationship between mean depth of occurrence and bathymetric range of the hydroid-bearing species in the Atlantic Ocean and adjacent polar seas deeper than 50 m . Colors represent the number of regions each species occur (from 1 to 5).

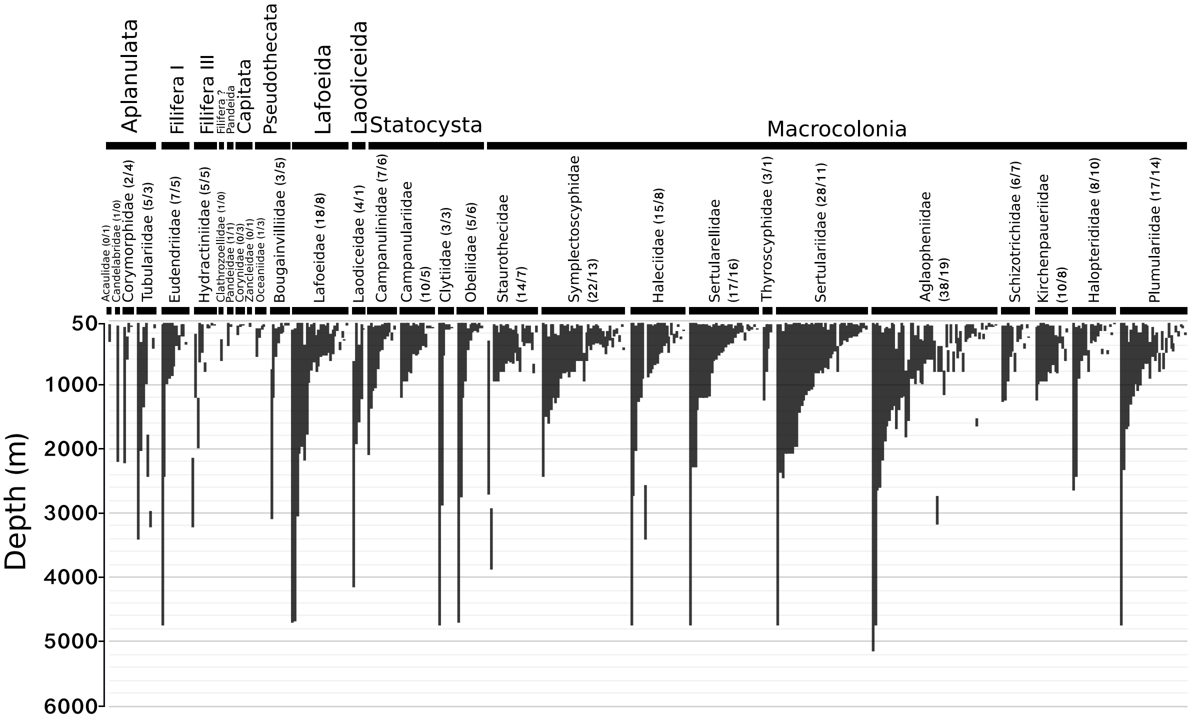

Figure 5. Bathymetric distribution of the species within each family of benthic Hydroidolina in the Atlantic Ocean and adjacent polar seas deeper than 50 m, organized by families and orders, ordered from the largest to the smallest ranges for each taxa. Each column represents one species. Species with ranges smaller than 20 meters not plotted. Total number of species classified as eurybathic (*viz.*, range of bathymetric distribution ≥300 m; Menzies *et al.*, 1973) and stenobathic (*viz.*, <300 m) in each family are indicated in the parentheses.

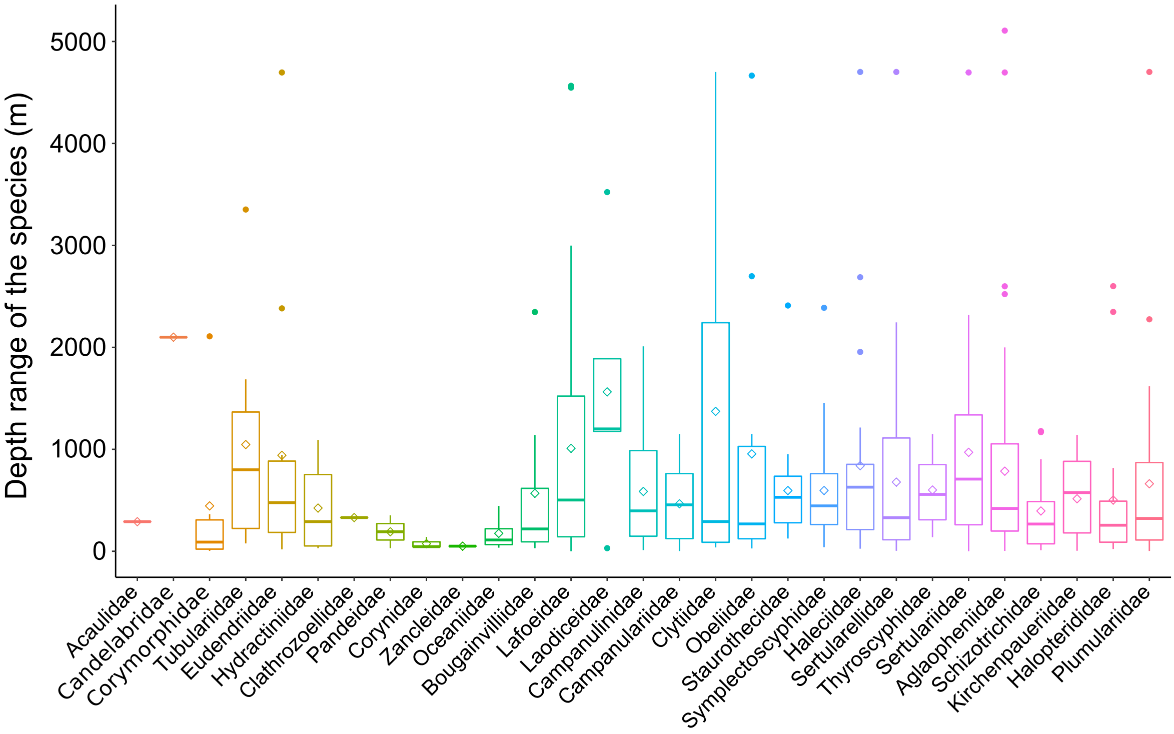

Figure 6. Variation in depth ranges of the species within each family of benthic Hydroidolina in the Atlantic Ocean and adjacent polar seas deeper than 50 m. Legend for boxplots: boxes – range between first and third quartiles; vertical lines – largest and smallest observations within a maximum of 1.5 times the interquartile range; points – outliers; horizontal lines inside boxes - medians; diamonds – averages.

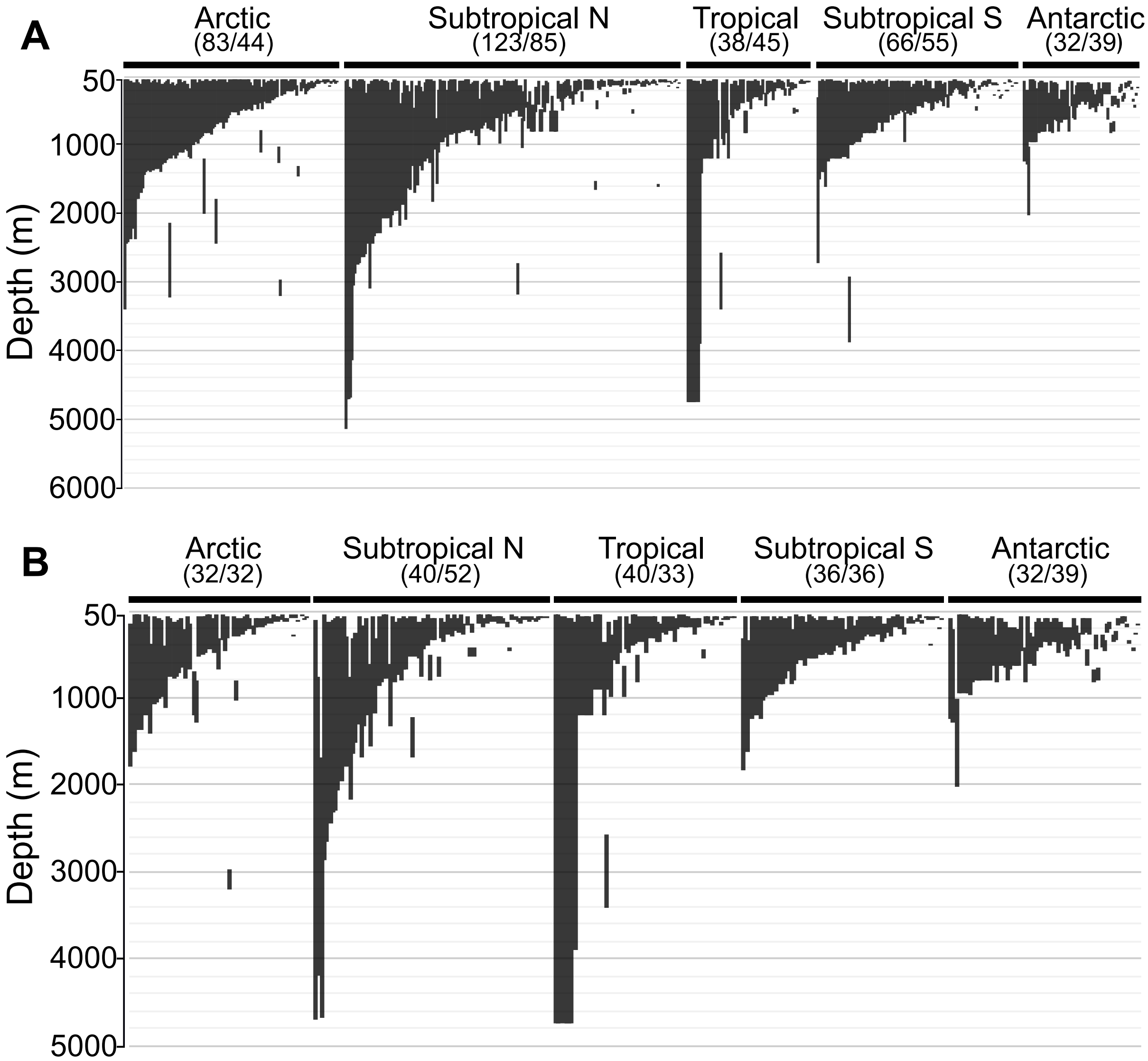

Figure 7. Bathymetric ranges of hydroids in the Atlantic Ocean and adjacent polar seas deeper than 50 m, ordered from the largest to the smallest ranges within each region, based on all available data (**A**), and data standardized by the number of records (**B**). Each column represents one species. Species with ranges smaller than 20 meters not plotted. In brackets is total number of species classified as eurybathic (*viz.*, range of bathymetric distribution ≥ 300 m; Menzies *et al.*, 1973) and stenobathic (*viz.*, < 300 m) for each region are indicated in the parentheses.

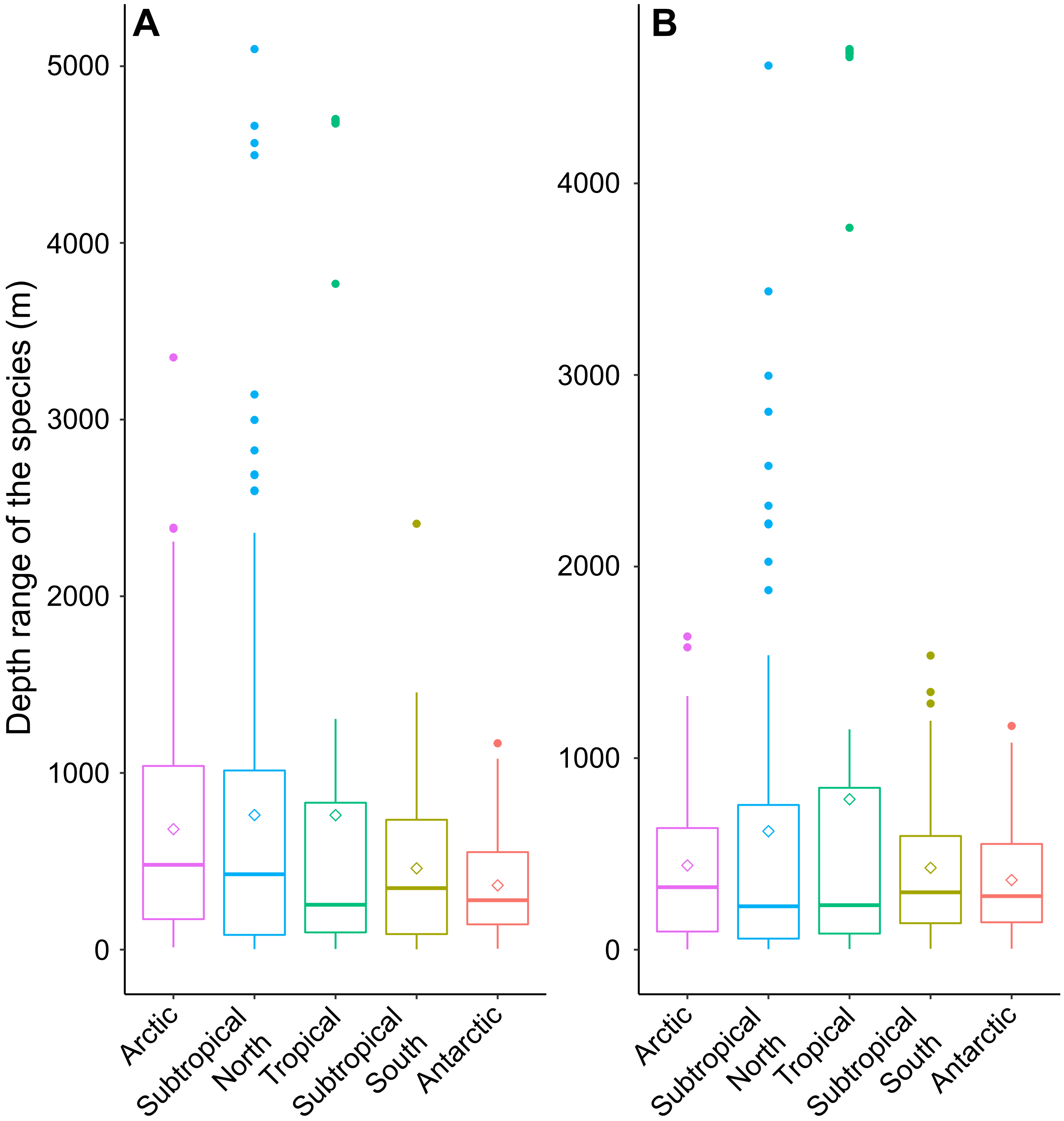

Figure 8. Bathymetric ranges of hydroid-bearing species in relation to different regions of the Atlantic Ocean and adjacent polar seas deeper than 50 m, for all (**A**) and the standardized (**B**) data. Legend for boxplots: boxes – range between first and third quartiles; vertical lines – largest and smallest observations within a maximum of 1.5 times the interquartile range; points – outliers; horizontal lines inside boxes - medians; diamonds – averages.

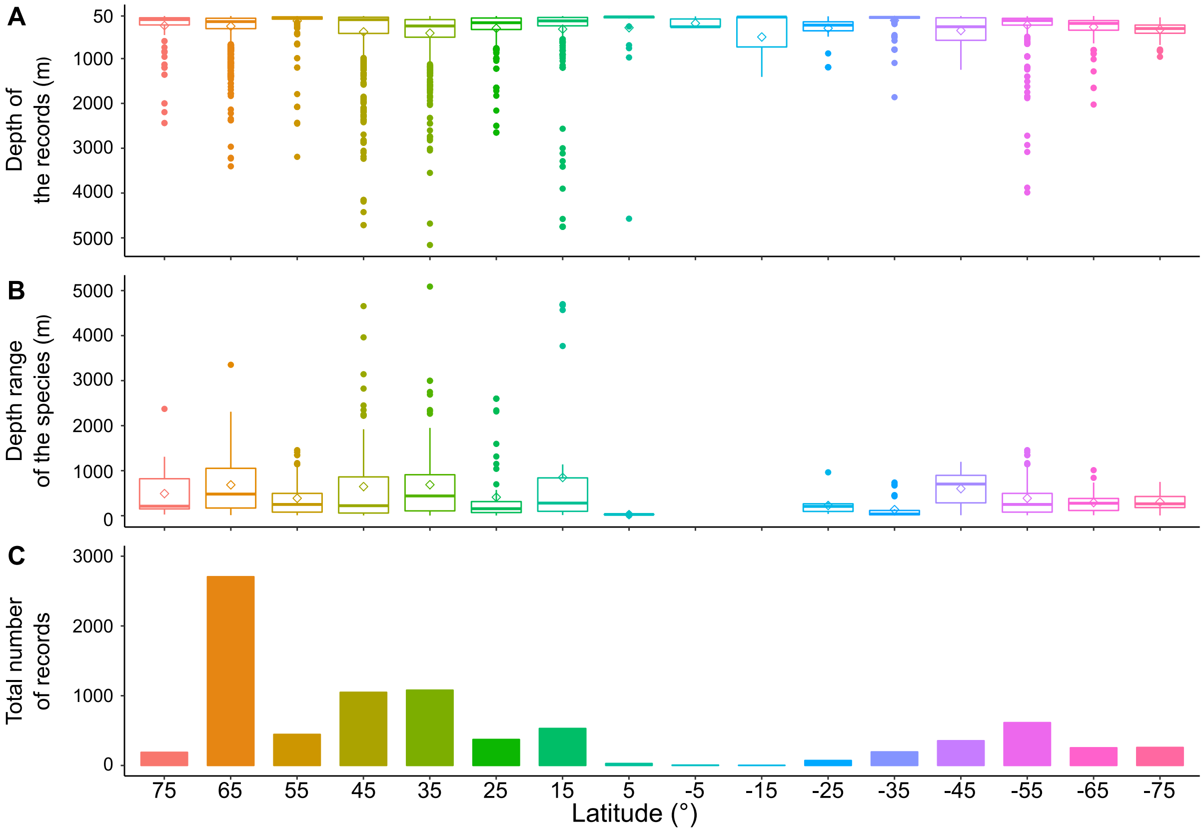

Figure 9. Variation in depths of occurrence for all records (**A**); variation in bathymetric ranges for the species (**B**); and total number of records (**C**) by 10˚ latitudinal bands (represented by the midpoint of each band) of hydroids from the Atlantic Ocean and adjacent polar seas deeper than 50 m deep. Legend for boxplots: boxes – range between first and third quartiles; vertical lines – largest and smallest observations within a maximum of 1.5 times the interquartile range; points – outliers; horizontal lines inside boxes - medians; diamonds – averages. 75˚ latitudinal band also include three records exceeding 80˚.

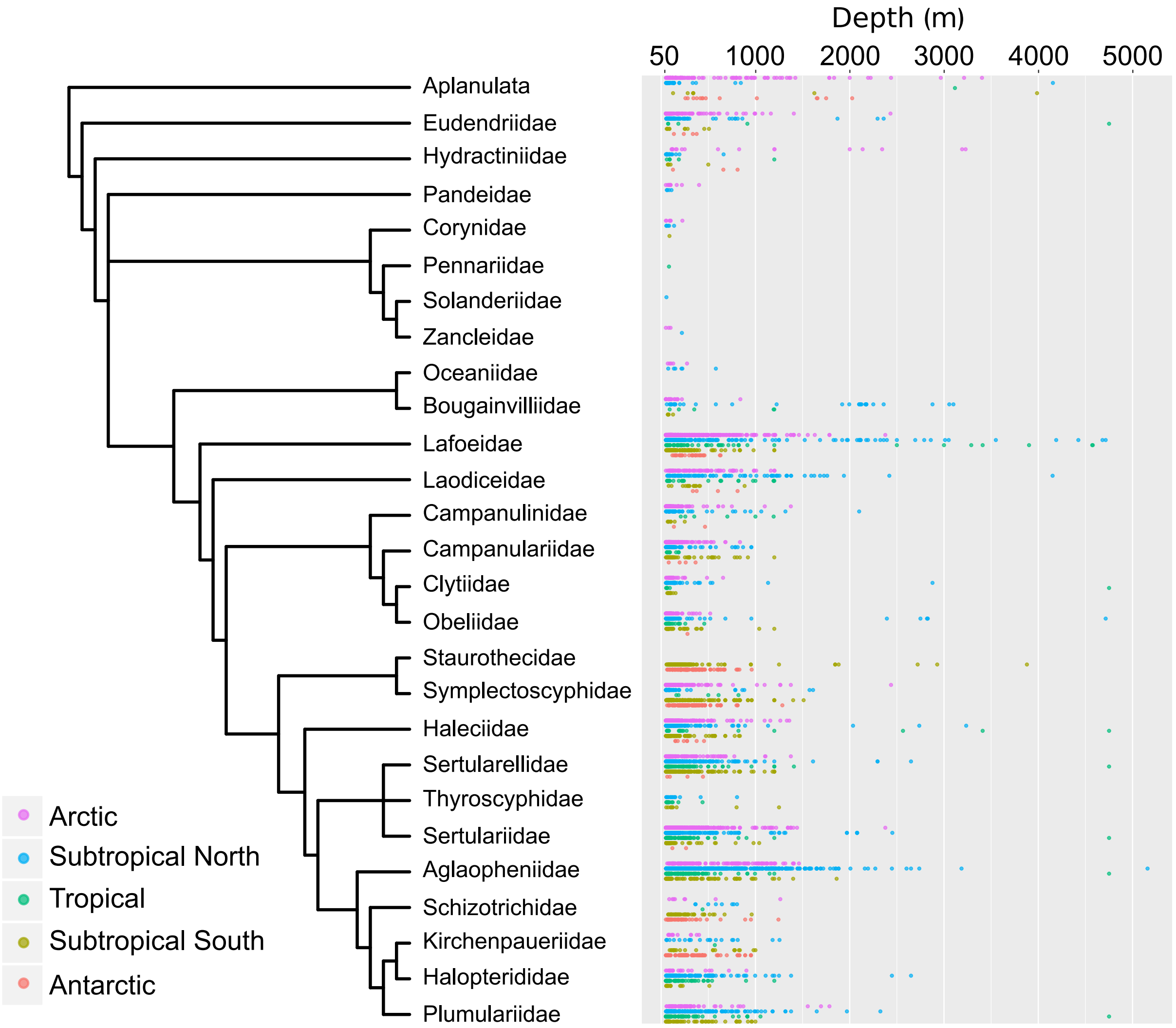

Figure 10. Depth of occurrence of the records within benthic Hydroidolina taxa distributed across the five regions used in this study. The phylogenetic hypothesis of Hydroidolina is a working hypothesis derived from the analyses by Maronna *et al*. (2016); Cunha *et al*. (2017), and Mendoza Becerril (2015), pruned to include only the taxa present in our survey. Cytaeididae, Clathrozoellidae, and Rosalindidae were not included due to their uncertain position.

Supplementary Material

Table S1. Depth distributions of the Hydroidolina species. Shallowest and deepest records, calculated depth range, and literature references from where the species records were obtained. Species are ordered by depth range within each family.

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Order: Aplanulata				
Acaulidae				
Acaulis primarius Stimpson, 1854	59	349	290	107
Candelabridae				
Candelabrum phrygium (Fabricius, 1780)	95	2195	2100	19, 20, 23, 27
Candelabrum austrogeorgiae (Jäderholm, 1904)	281	281	0	55
Monocoryne gigantea (Bonnevie, 1898)	95	95	0	27
Corymorphidae				
Corymorpha groenlandica (Allman, 1876)	114	2222	2108	19, 20, 23, 24, 107, 113
Corymorpha microrhiza (Hickson & Gravely, 1907)	257.5	621	363.5	113
Corymorpha pendula L. Agassiz, 1862	52.1	192	139.9	40, 43, 49, 118, 119
Corymorpha glacialis M. Sars, 1860	75	115	40	20, 107
Corymorpha nutans M. Sars, 1835	51.2	65.8	14.6	23, 24
Euphysa aurata Forbes, 1848	55	59	4	28, 107
Branchiocerianthus imperator (Allman, 1888)	4155	4155	0	75
Branchiocerianthus norvegicus Brattström, 1956	3987	3987	0	124
Branchiocerianthus reniformis Broch, 1918	768.1	768.1	0	24
Corymorpha nana Alder, 1857	232	232	0	19
Gymnogonos crassicornis Bonnevie, 1898	209	209	0	107
Gymnogonos obvolutus (Kramp, 1933)	175	175	0	62
Tubulariidae				
Ectopleura larynx (Ellis & Solander, 1786)	51.2	3403	3351.8	19, 23, 36, 49, 63, 105, 112
Bouillonia denhartogi Svoboda, Stepanjants & Ljubenkov, 2006	340	2026	1686	114
Tubularia regalis Boeck, 1860	100	1359	1259	19, 20, 23, 54, 60, 107
Tubularia indivisa Linnaeus, 1758	52.1	995	942.9	9, 10, 20, 23, 43, 49, 103, 105, 107, 110, 118, 119
Bouillonia cornucopia (Bonnevie, 1898)	1783	2438	655	19, 20, 54
Bouillonia cornucopia sensu Petersen, 1990	2966	3213	247	114
Zyzzyzus parvula (Hickson & Gravely, 1907)	281.5	435	153.5	113

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Tubularia couthouyi L. Agassiz, 1862	54.9	131.7	76.8	49, 72
Ectopleura crocea (L. Agassiz, 1862)	60.4	60.4	0	49
Hybocodon prolifer L. Agassiz, 1860	400	400	0	19
Order: Filifera I				
Eudendriidae				
Eudendrium ramosum (Linnaeus, 1758)	54.9	4751	4696.1	1, 9, 11, 23, 25, 40, 49, 50, 51, 52, 101, 105, 107, 110, 118, 126, 127
Eudendrium rameum (Pallas, 1766)	50	2432.3	2382.3	8, 10, 19, 23, 25, 27, 55, 57, 59, 61, 63, 103, 105, 107, 112, 125, 126
Eudendrium album Nutting, 1898	50	995	945	34, 41, 43, 49, 60, 61, 107
Eudendrium annulatum Norman, 1864	50	914.4	864.4	61, 100, 107
Eudendrium capillare Alder, 1856	50	861.4	811.4	2, 9, 23, 27, 49, 63, 105, 107, 110, 118, 126
Eudendrium carneum Clarke, 1882	84.1	724.2	640.1	49
Eudendrium caricum Jäderholm, 1908	85	398	313	61
Eudendrium antarcticum Stechow, 1921	240	457	217	82, 97, 112
Eudendrium laxum Allman, 1877	68	256	188	2, 48, 124
Eudendrium exiguum Allman, 1877	73.2	248.7	175.5	2, 48, 49
Eudendrium generale von Lendenfeld, 1885	336	376.5	40.5	111
Eudendrium dispar L. Agassiz, 1862	64	82.3	18.3	49
Eudendrium arbuscula Wright, 1859	57.5	57.5	0	27
Eudendrium attenuatum Allman, 1877	109.7	109.7	0	2
Eudendrium bathyalis Marques & Calder, 2000	283	283	0	65
Eudendrium cyathiferum Jäderholm, 1904	281	281	0	55
Eudendrium fruticosum Allman, 1877	246.9	246.9	0	2
Eudendrium rugosum Fraser, 1940	139	139	0	46
Eudendrium scotti Puce, Cerrano & Bavestrello, 2002	135	135	0	97
Order: Filifera III				
Hydractiniidae				
Hydractinia ingolfi Kramp, 1932	2137	3229	1092	61
Schuchertinia allmanii (Bonnevie, 1898)	220	1203	983	19, 54, 107
Hydractinia arctica (Jäderholm, 1902)	1200	2000	800	54, 61
Hydractinia echinata (Fleming, 1828)	53	662	609	23, 34, 43, 49, 103, 105, 112
Hydrocorella africana Stechow, 1921	70	500	430	112, 126
Hydractinia angusta Hartlaub, 1904	659.5	810.5	151	83
Hydractinia polyclina L. Agassiz, 1862	60.4	118.9	58.5	110, 119
Hydractinia parvispina Hartlaub, 1905	75	125	50	55

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Podocoryna carnea M. Sars, 1846	51.2	87	35.8	49, 112
Hydractinia paucispinata Vervoort, 2006	60	90	30	126
Clava multicornis (Forsskål, 1775)	54.9	54.9	0	105
Clavactinia serrata (Kramp, 1943)	165	165	0	61
Hydractinia carica Bergh, 1887	110	110	0	19
Hydractinia cytaeiformis Vervoort, 2006	1200	1200	0	126
Hydractinia monocarpa Allman, 1876	55	55	0	27
Hydractinia proboscidea (Hincks, 1868)	187.5	187.5	0	126
Hydractinia sarsii (Steenstrup, 1850)	120	120	0	63
Hydractinia valens Fraser, 1943	56.7	56.7	0	47
Podocoryna borealis (Mayer, 1900)	115	115	0	107
Order: Filifera?*				
Clathrozoellidae				
Clathrozoella medeae Peña Cantero, Vervoort & Watson, 2003	295	625.5	330.5	98
Clathrozoella abyssalis Peña Cantero, Vervoort & Watson, 2003	3083.5	3083.5	0	98
Cytaeididae				
Perarella clavata (Jäderholm, 1905)	360	360	0	55
Order: Pandeida				
Pandeidae				
Leuckartiara octona (Fleming, 1823)	50	402	352	19, 34, 49, 54, 103, 105
Neoturris pileata (Forsskål, 1775)	70	100	30	34, 103
Halitholus cirratus Hartlaub, 1913	95	95	0	34
Neoturris abyssi (G.O. Sars, 1874)	165	165	0	19
Order: Capitata				
Corynidae				
Coryne hincksi Bonnevie, 1898	84.5	225	140.5	27, 107
Sarsia tubulosa (M. Sars, 1835)	55	100	45	27, 50
Coryne pusilla Gaertner, 1774	54.9	95	40.1	27, 44, 124
Coryne eximia Allman, 1859	50	50	0	59
Sarsia pulchella (Allman, 1865)	137.2	137.2	0	105
Stauridiosarsia producta (Wright, 1858)	73.2	73.2	0	105
Pennariidae				
Pennaria disticha Goldfuss, 1820	83	83	0	126
Rosalindidae				
Rosalinda incrustans (Kramp, 1947)	225	225	0	64

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Rosalinda williami Totton, 1949	438.9	438.9	0	116
Solanderiidae				
Solanderia gracilis Duchassaing & Michelin, 1846	56	56	0	35
Zancleidae				
Zanclea implexa (Alder, 1856)	50	100	50	103
Zanclea sessilis (Gosse, 1853)	220	220	0	126
Order: Pseudothecata				
Bougainvilliidae				
Garveia arborea (Browne, 1907)	753.5	3100	2346.5	25, 101, 125, 126
Bougainvillia muscus (Allman, 1863)	60	1200	1140	8, 20, 52, 103, 105, 112, 126
Garveia nutans Wright, 1859	137.2	580	442.8	25, 101
Dicoryne conferta (Alder, 1856)	100	367.6	267.6	23, 49, 103, 107
Rhizorhagium roseum M. Sars, 1874	50	220	170	41, 60, 61, 103, 107
Bimeria vestita Wright, 1859	90	200	110	25, 101, 126
Bougainvillia muscoides (Sars, 1846)	50	90	40	103
Bougainvillia pyramidata (Forbes & Goodsir, 1853)	50	80	30	103
Bougainvillia macloviana Lesson, 1830	73.2	73.2	0	58
Bougainvillia meinertiae Jäderholm, 1923	73.2	73.2	0	58
Oceaniidae				
Turritopsis dohrnii (Weismann, 1883)	135	580	445	101
Merona cornucopiae (Norman, 1864)	128	274.3	146.3	23
Corydendrium parasiticum (Linnaeus, 1767)	75	150	75	30, 101
Rhizogeton nudus Broch, 1910	70	105	35	60, 107
Oceania armata Kölliker, 1853	215.8	215.8	0	48
Turritopsis nutricula McCrady, 1857	225	225	0	64
Order: Lafoeida				
Lafoeidae				
Cryptolarella abyssicola (Allman, 1888)	150	4715	4565	4, 25, 36, 101, 112, 125
Acryptolaria longitheca (Allman, 1877)	133.5	4681	4547.5	2, 32, 36, 37, 39, 48, 124, 126
Acryptolaria conferta (Allman, 1877)	52	3050	2998	2, 8, 17, 22, 24, 31, 37, 38, 39, 48, 49, 64, 99, 101, 107, 111, 112, 124, 125, 126
Lafoea dumosa (Fleming, 1820)	50	2078	2028	1, 2, 4, 8, 9, 10, 19, 20, 21, 24, 25, 26, 34, 38, 40, 41, 43, 44, 48, 49, 51, 52, 53, 54, 55, 56, 57, 59, 60, 61, 62, 63, 69, 70, 78, 82, 89, 97, 99, 100, 101, 103, 104, 106, 107, 110, 111, 112, 115, 118, 120, 124, 125, 126

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Filellum serpens (Hassall, 1848)	50	1970	1920	1, 9, 17, 20, 21, 22, 24, 25, 26, 34, 38, 40, 43, 44, 49, 53, 54, 55, 59, 60, 61, 63, 64, 78, 106, 107, 110, 112, 122, 124, 125
Acryptolaria crassicaulis (Allman, 1888)	392	2175	1783	4, 101, 125
Grammaria abietina (M. Sars, 1850)	50	1784.9	1734.9	1, 4, 19, 20, 21, 24, 26, 36, 38, 41, 43, 49, 55, 56, 59, 60, 61, 62, 63, 70, 104, 107, 110, 118, 119, 124, 127
Acryptolaria operculata Stepanjants, 1979	98	980	882	38, 111
Filellum antarcticum (Hartlaub, 1904)	72	775	703	13, 17, 38, 51, 78, 89, 104
Hincksella formosa (Fewkes, 1881)	53	652.9	599.9	39, 73
Acryptolaria pulchella (Allman, 1888)	228.6	801	572.4	48, 49
Lafoea symmetrica Bonnevie, 1899	150	717	567	8, 19, 20
Filellum serratum (Clarke, 1879)	60	570	510	8, 11, 17, 31, 37, 38, 48, 68, 107
Synthecium protectum Jäderholm, 1903	55	550	495	11, 18, 38, 48, 51, 104, 124
Grammaria borealis (Levinsen, 1893)	87	557	470	24, 61, 107, 124
Synthecium tubithecum (Allman, 1877)	51.2	504.7	453.5	31, 39, 49, 73
Filellum magnificum Peña Cantero, Svoboda & Vervoort, 2004	205	630	425	89
Synthecium evansi (Ellis & Solander, 1786)	144	523	379	101
Lafoea coalescens Allman, 1877	75	256	181	2, 31
Grammaria immersa Nutting, 1901	50	179.2	129.2	24, 26, 57, 59, 61, 107
Lafoea gaussica Vanhöffen, 1910	335	460	125	89
Acryptolaria abies (Allman, 1877)	171.9	281.6	109.7	39, 48
Lafoea benthophila Ritchie, 1909	293.5	324.5	31	111
Grammaria gracilis Stimpson, 1854	50	75	25	43
Lafoea grandis Hincks, 1874	170	182.9	12.9	53, 59
Hincksella cylindrica (Bale, 1888)	73	73.2	0.2	31, 45
Acryptolaria elegans (Allman, 1877)	278	278	0	2
Acryptolaria flabellum (Allman, 1888)	713.2	713.2	0	4
Filellum annulatum (Watson, 1973)	250	250	0	38
Filellum bouvetensis Marques, Peña Cantero, Miranda & Migotto, 2011	128	128	0	82
Grammaria elegans Fraser, 1943	210.3	210.3	0	48
Grammaria rigida Fraser, 1943	182.9	182.9	0	48
Lafoea intorta Calder, 2013	87	87	0	35
Synthecium marginatum (Allman, 1877)	592.5	592.5	0	48
Synthecium subventricosum Bale, 1914	80	80	0	112
Order: Laodiceida				
Laodiceidae				

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Stegolaria geniculata (Allman, 1888)	629.5	4152	3522.5	36, 101, 125, 126
Stegopoma plicatile (M. Sars, 1863)	50	1938.5	1888.5	19, 20, 24, 26, 38, 49, 52, 56, 60, 61, 83, 103, 107, 111, 120, 124
Stegopoma bathyale Vervoort, 1966	392	1592	1200	101, 126
Modeeria rotunda (Quoy & Gaimard, 1827)	62.5	1238.1	1175.6	1, 8, 21, 25, 38, 46, 49, 52, 59, 82, 101, 103, 106, 107, 111, 112, 122, 124, 126
Laodicea undulata (Forbes & Goodsir, 1853)	120	150	30	8, 25, 101
Stegopoma giganteum Ramil & Vervoort, 1992	1523	1523	0	101
Order: Statocysta				
Campanulariidae				
Campanularia tulipifera Allman, 1888	50	1200	1150	38, 55, 111, 124
Campanularia volubilis (Linnaeus, 1758)	50	956.5	906.5	20, 21, 24, 26, 40, 41, 44, 49, 53, 57, 59, 60, 61, 63, 103, 106, 107, 110
Rhizocaulus verticillatus (Linnaeus, 1758)	50	956.5	906.5	20, 21, 24, 26, 40, 43, 44, 49, 56, 60, 61, 72, 106, 107, 110, 118, 119
Campanularia hincksii Alder, 1856	50	812	762	8, 9, 20, 24, 25, 31, 38, 49, 51, 52, 63, 64, 67, 101, 103, 106, 107, 110, 122, 126
Bonneviella grandis (Allman, 1876)	75	836	761	19, 20, 24, 107
Campanularia agas Cornelius, 1982	70	550	480	38, 51
Campanularia crenata Allman, 1876	50	530	480	26, 40, 74, 107
Campanularia hicksoni Totton, 1930	80	535	455	38, 89, 111
Campanularia groenlandica Levinsen, 1893	50	470.5	420.5	21, 24, 26, 40, 43, 49, 59, 61, 107, 124
Orthopyxis integra (MacGillivray, 1842)	50	410	360	24, 26, 41, 43, 49, 52, 59, 60, 61, 62, 63, 107
Campanularia macroscypha Allman, 1877	215.8	418.8	203	2, 39, 48
Orthopyxis hartlaubi El Beshbeeshy, 2011	80	125	45	11, 38
Campanularia lennoxensis Jäderholm, 1903	91	119	28	50, 124
Campanularia gracilis Allman, 1876	100	125	25	20, 112
Campanularia africana Stechow, 1923	100	102	2	112
Campanularia antarctica Ritchie, 1913	365	365	0	89
Orthopyxis caliculata (Hincks, 1853)	86	86	0	21
Orthopyxis tincta (Hincks, 1861)	73.2	73.2	0	58
Silicularia rosea Meyen, 1834	252.5	252.5	0	111
Campanulinidae				
Racemoramus panicula (G.O. Sars, 1874)	90	2100	2010	52, 101, 103, 107
Calycella syringa (Linnaeus, 1767)	50	1375.3	1325.3	20, 21, 24, 26, 40, 43, 44, 49, 53, 57, 59, 60, 61, 63, 103, 104, 106, 107, 110, 124

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Egmundella producta (G.O. Sars, 1874)	100	1099	999	20, 49, 107, 109, 110
Cirrholovenia tetranema Kramp, 1959	75	1062	987	31, 36, 101
Plicatotheca anitae Calder & Vervoort, 1986	75	761	686	5, 31, 35, 52, 126
Mitrocomella polydiademata (Romanes, 1876)	80	486	406	1, 25, 34, 60, 61, 64, 101, 106, 112
Lafoeina longitheca Jäderholm, 1904	69	465	396	55, 89, 97
Cuspidella procumbens Kramp, 1911	50	300	250	26, 59, 61, 62
Lafoeina maxima Levinsen, 1893	50	260	210	24, 26, 56, 59, 60, 61, 107
Tetrapoma quadridentatum (Hincks, 1874)	52.5	200	147.5	24, 26, 53, 60
Lafoeina tenuis Sars, 1874	182.9	315	132.1	53, 64, 126
Phialella chilensis (Hartlaub, 1905)	80	143.5	63.5	38, 55
Phialella quadrata (Forbes, 1848)	107.5	118.9	11.4	63, 106
Calycella oligista Ritchie, 1910	100	100	0	112
Egmundella fasciculata Fraser, 1942	182.9	182.9	0	46
Egmundella grandis Fraser, 1943	288	288	0	47
Egmundella modesta Millard & Bouillon, 1975	1000	1000	0	126
Egmundella superba Stechow, 1921	75	75	0	31
Oplorhiza parvula Allman, 1877	541.3	541.3	0	2
Clytiidae				
Clytia paulensis (Vanhöffen, 1910)	50	4751	4701	52, 67, 101, 126
Clytia hemisphaerica (Linnaeus, 1767)	52.5	2878	2825.5	8, 9, 10, 20, 24, 25, 34, 41, 49, 54, 63, 67, 72, 74, 103, 106, 107, 110, 112, 120, 125
Clytia gracilis (M. Sars, 1850)	53	544	491	41, 50, 63, 64, 67, 68, 101, 106, 107, 112, 117, 122
Clytia noliformis (McCrady, 1859) sensu Calder, 1991	54.9	146	91.1	41, 49, 112
Clytia linearis (Thorneley, 1900)	63	150	87	8, 67, 101
Clytia arborescens Pictet, 1893	100	137.5	37.5	8, 67
Clytia paradoxa (Stechow, 1923)	100	100	0	112
Obeliidae				
Obelia dichotoma (Linnaeus, 1758)	50	4715	4665	8, 9, 22, 38, 41, 49, 50, 52, 63, 67, 99, 101, 103, 107, 112, 125, 126
Obelia bidentata Clark, 1875	52.5	2750	2697.5	2, 8, 9, 38, 49, 50, 51, 52, 67, 82, 101, 111, 122, 124, 126
Obelia geniculata (Linnaeus, 1758)	50	1200	1150	21, 24, 38, 49, 50, 52, 61, 67, 69, 112
Gonothyraea loveni (Allman, 1859)	50	956.5	906.5	20, 24, 26, 49, 60, 61, 63, 106, 107, 110, 120
Hartlaubella gelatinosa (Pallas, 1766)	131.7	461.5	329.8	48, 49
Laomedea angulata Hincks, 1861	59.4	327.4	268	49, 104, 106
Obelia longissima (Pallas, 1766)	53	187.5	134.5	9, 20, 24, 28, 38, 49, 51, 60, 63, 106, 107, 124
Laomedea pseudodichotoma Vervoort, 1959	52.5	180	127.5	67, 101, 122

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Laomedea calceolifera (Hincks, 1871)	70	187.5	117.5	67, 112
Laomedea neglecta Alder, 1856	50	131.7	81.7	43, 49
Laomedea flexuosa Alder, 1857	91.4	118.9	27.5	106
Obelia irregularis Fraser, 1943	457.2	457.2	0	48
Obelia striata Clarke, 1907	200	200	0	123
Order: Macrocolonia				
Aglaopheniidae				
Aglaophenia latecarinata Allman, 1877	52.5	5159	5106.5	2, 33, 39, 48, 122, 124
Lytocarpia myriophyllum (Linnaeus, 1758)	54.9	4751	4696.1	1, 7, 8, 10, 19, 20, 22, 24, 25, 52, 64, 99, 101, 102, 106, 107, 110, 112, 122, 124, 126
Aglaophenia lophocarpa Allman, 1877	51.2	2650	2598.8	2, 7, 37, 39, 48, 49, 52, 71, 101, 102, 126
Cladocarpus formosus Allman, 1877	80.5	2602.4	2521.9	1, 6, 24, 49, 57, 60, 61, 71, 107, 121
Streptocaulus corneliusi (Ramil & Vervoort, 1992)	194.5	2194	1999.5	7, 101, 102, 125
Aglaophenopsis cornuta (Fewkes, 1881)	135	1882	1747	6, 24, 26, 38, 49, 57, 60, 61, 107, 121, 124
Streptocaulus pectiniferus (Allman, 1883)	113	1645.9	1532.9	3, 7, 24, 101, 102, 107
Cladocarpus sigma (Allman, 1877)	134	1572.8	1438.8	2, 8, 48, 71, 99, 101, 102, 124
Lytocarpia canepa (Blanco & Bellusci de Miralles, 1971)	53	1400	1347	11, 15, 38, 51
Cladocarpus integer (Sars, 1873)	64	1329	1265	6, 24, 26, 57, 61, 71, 107, 121
Cladocarpus boucheti Ramil & Vervoort, 1992	452	1691	1239	101
Nematocarpus ramuliferus (Allman, 1874)	198.5	1407	1208.5	1, 6, 24, 107
Aglaophenia tubulifera (Hincks, 1861)	52	1200	1148	3, 4, 7, 8, 9, 22, 24, 52, 64, 99, 101, 102, 106, 126
Lytocarpia distans (Allman, 1877)	90	1182	1092	2, 7, 37, 38, 124
Cladocarpus flexuosus Nutting, 1900	788	1829	1041	29, 71
Cladocarpus diana Broch, 1918	606.5	1568	961.5	6, 24
Aglaophenia acacia Allman, 1883	50	914.4	864.4	3, 4, 7, 8, 15, 38, 51, 99, 100, 124, 126
Streptocaulus pulcherrimus Allman, 1883	52.5	914.4	861.9	3, 7, 100, 126
Streptocaulus caboverdensis Ansin Agís, Ramil & Vervoort, 2001	235	995	760	7
Cladocarpus septatus Nutting, 1900	87.8	786.4	698.6	71
Aglaophenia elongata Meneghini, 1845	291	985.7	694.7	1, 123
Aglaophenopsis cartieri (Bedot, 1921)	318	997	679	36, 99
Aglaophenopsis bonnevieae (Jäderholm, 1909)	87	683	596	19, 61, 107
Aglaophenia trifida Agassiz, 1862	57	620	563	37, 49, 71, 117
Macrorhynchia grandis (Clarke, 1879)	93.3	620	526.7	37, 49, 71
Cladocarpus dolichotheca Allman, 1877	95.1	620	524.9	2, 37, 48, 71
Cladocarpus paradiseus Allman, 1877	318.2	804.7	486.5	2, 39, 48, 71, 124

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Aglaophenopsis verrilli Nutting, 1900	2737.7	3185.8	448.1	71
Aglaophenopsis hirsuta Fewkes, 1881	413	804.7	391.7	39, 48, 49, 71, 124
Cladocarpus carinatus Nutting, 1900	413	804.7	391.7	48, 71, 124
Cladocarpus paraventricosus Ramil & Vervoort, 1992	789.5	1163	373.5	101, 107
Aglaophenia parvula Bale, 1882	70	429	359	52, 112
Cladocarpus grandis Nutting, 1900	470.9	804.7	333.8	48, 71
Aglaophenia rhynchocarpa Allman, 1877	54.9	365.8	310.9	33, 39, 48, 49, 71
Lytocarpia benedicti (Nutting, 1900)	493.8	804.7	310.9	71
Macrorhynchia clarkei (Nutting, 1900)	58	367.6	309.6	7, 49, 71, 126
Lytocarpia bispinosa (Allman, 1877)	285.3	592.5	307.2	2, 48
Aglaophenia insignis Fewkes, 1881	173.7	479.1	305.4	39, 48
Lytocarpia normani (Nutting, 1900)	507.5	804.7	297.2	48, 71
Gymnangium sinuosum (Fraser, 1925)	85	335	250	7, 33, 71
Cladocarpus flexilis Verrill, 1885	58.5	305.4	246.9	49, 71
Aglaophenia dubia Nutting, 1900	60	274.3	214.3	2, 33, 37, 39, 71
Macrorhynchia allmani (Nutting, 1900)	60	210.3	150.3	33, 48, 49, 71
Cladocarpus bicuspis (Sars, 1873)	124.4	252.4	128	24
Streptocaulus chonae Ansin Agís, Ramil & Vervoort, 2001	1523	1650	127	7, 101
Cladocarpus tenuis Clarke, 1879	184.7	298.1	113.4	37, 48
Aglaophenia pluma (Linnaeus, 1758)	52.5	146.3	93.8	7, 9, 69, 106
Streptocaulus sinuosus (Vervoort, 1966)	208	300	92	7, 52
Cladocarpus campanulatus Ritchie, 1912	80.5	142.6	62.1	24, 61, 107
Aglaophenia kirchenpaueri (Heller, 1868)	52.5	102	49.5	7, 126
Aglaophenia svobodai Ansin Agís, Ramil & Vervoort, 2001	60	107.5	47.5	7
Streptocaulus dollfusi (Billard, 1924)	77	114	37	7, 122
Macrorhynchia filamentosa (Lamarck, 1816)	54	80	26	69, 112
Gymnangium speciosum (Allman, 1877)	65	73	8	33
Gymnangium montagui (Billard, 1912)	60	65	5	9
Gymnangium allmani (Marktanner-Turneretscher, 1890)	58.5	62.2	3.7	3, 4, 71
Aglaophenia bicornuta Nutting, 1900	320	320	0	71
Aglaophenia constricta Allman, 1877	54.9	54.9	0	2
Aglaophenia octodonta Heller, 1868	2447.5	2447.5	0	7
Aglaophenia picardi Svoboda, 1979	580	580	0	101
Aglaophenia robusta Fewkes, 1881	160.9	160.9	0	39, 48
Aglaophenia tubiformis Marktanner-Turneretscher, 1890	59	59	0	102
Cladocarpus compressus Fewkes, 1881	208.5	208.5	0	39

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Cladocarpus crenatus (Fewkes, 1881)	2271.4	2271.4	0	39
Cladocarpus obliquus Nutting, 1900	365.8	365.8	0	71
Cladocarpus paraformosus Schuchert, 2000	904	904	0	107
Cladocarpus stechowi Ramil & Vervoort, 1992	1861	1861	0	124
Cladocarpus ventricosus Allman, 1877	182.9	182.9	0	2
Macrorhynchia ramosa (Fewkes, 1881)	173.7	173.7	0	39
Streptocaulus gracilis Fraser, 1937	438.9	438.9	0	45
Haleciidae				
Halecium beanii (Johnston, 1838)	50	4751	4701	4, 9, 11, 19, 24, 38, 40, 42, 49, 50, 51, 52, 57, 63, 67, 69, 99, 102, 103, 104, 106, 107, 108, 110, 112, 122
Halecium muricatum (Ellis & Solander, 1786)	50	2737.7	2687.7	19, 20, 21, 24, 26, 40, 41, 44, 49, 53, 54, 56, 57, 59, 60, 61, 63, 76, 103, 106, 107, 118, 119, 124, 127
Halecium mediterraneum Weismann, 1883	80	2035	1955	67, 101
Halecium halecinum (Linnaeus, 1758)	50	1263.7	1213.7	9, 10, 20, 24, 49, 63, 67, 76, 103, 106, 107, 108, 122, 124
Halecium tenellum Hincks, 1861	50	1200	1150	8, 9, 35, 37, 38, 40, 42, 52, 55, 60, 61, 63, 64, 67, 99, 101, 102, 103, 104, 106, 107, 110, 112, 120, 122, 126
Halecium scutum Clark, 1876	50	910	860	24, 26, 63, 108
Halecium profundum Calder & Vervoort, 1998	2565	3410	845	36
Halecium sessile Norman, 1866	56.7	890	833.3	8, 9, 20, 25, 49, 101, 102, 120, 126, 127
Halecium jaederholmi Vervoort, 1972	72	825	753	38, 55, 124
Halecium sibogae marocanum Billard, 1934	83	765	682	67, 101, 102
Halecium groenlandicum Kramp, 1911	59.5	700	640.5	26, 59, 60, 61
Halecium delicatulum Coughtrey, 1876	51.2	680	628.8	8, 13, 38, 48, 49, 52, 78, 122
Halecium minutum Broch, 1903	50	530	480	20, 24, 26, 40, 41, 49, 107
Halecium curvicaule Lorenz, 1886	50	500.5	450.5	24, 26, 41, 43, 59, 60, 61, 107
Halecium labrosum Alder, 1859	50	410	360	9, 20, 24, 26, 53, 59, 60, 61, 63, 99, 106, 107, 108, 110
Halecium irregulare Bonnevie, 1899	90	350	260	20
Halecium filicula Allman, 1877	256	507.5	251.5	2, 8, 48
Halecium textum Kramp, 1911	51.2	225	173.8	24, 26, 34, 49, 59, 107, 108
Halecium macrocephalum Allman, 1877	219.5	360.3	140.8	2, 39, 48
Halecium pallens Jäderholm, 1904	160	281	121	55
Halecium speciosum Nutting, 1901	60	106	46	26
Halecium incertus Naumov & Stepanjants, 1962	253.5	293.5	40	82, 111
Halecium telescopicum Allman, 1888	155	180	25	99
Halecium antarcticum Vanhöffen, 1910	253.5	253.5	0	82
Halecium articulosum Clark, 1875	56.7	56.7	0	72

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Halecium banzare Watson, 2008	275	275	0	97
Halecium dubium Fraser, 1943	3235.1	3235.1	0	47
Halecium dyssymetrum Billard, 1929	73	73	0	31
Halecium elegantulum Watson, 2008	376.5	376.5	0	111
Halecium exaggeratum Peña Cantero, Boero & Piraino, 2013	275	275	0	97
Halecium interpolatum Ritchie, 1907	454.5	454.5	0	78
Halecium laeve Kramp, 1932	365	365	0	60
Halecium lankesterii (Bourne, 1890)	167	167	0	52
Halecium pseudodelicatulum Peña Cantero, 2014	240	240	0	97
Halecium secundum Jäderholm, 1904	150	150	0	55
Halecium stoloniferum Soto Àngel & Peña Cantero, 2015	286.5	286.5	0	111
Halecium tensum Fraser, 1943	245.1	245.1	0	47
Halopterididae				
Antennella secundaria (Gmelin, 1791)	50	2650	2600	7, 8, 9, 22, 33, 52, 99, 101, 102, 112, 126
Polyplumaria flabellata G.O. Sars, 1874	100	2447.5	2347.5	1, 3, 7, 8, 24, 36, 64, 99, 101, 106, 107, 123
Polyplumaria gracillima (G.O. Sars, 1873)	87	904	817	24, 71, 103, 107
Halopteris geminata (Allman, 1877)	137.2	643.7	506.5	2, 39, 48, 71
Halopteris catharina (Johnston, 1833)	50	544	494	7, 24, 34, 52, 63, 68, 71, 101, 103, 106, 107, 124
Monostaechas quadridens (McCrady, 1859)	58	541.3	483.3	2, 7, 39, 48, 71, 126
Calvinia mirabilis Nutting, 1900	470.9	804.7	333.8	48, 71
Antennella quadriaurita Ritchie, 1909	54	365.8	311.8	33, 69, 71, 112
Diplopteroides quadricornis (Nutting, 1900)	54.9	320	265.1	49, 71
Halopteris clarkei (Nutting, 1900)	87	332.8	245.8	35, 71
Antennella siliquosa (Hincks, 1877)	50	252.5	202.5	7, 9, 101, 102, 122
Halopteris carinata Allman, 1877	64	160.9	96.9	2, 48
Antennella confusa Ansin Agís, Ramil & Vervoort, 2001	450	540	90	7
Antennella gracilis Allman, 1877	87	175.6	88.6	2, 35, 39
Diplopteroides grandis (Nutting, 1900)	470.9	537.7	66.8	48, 71
Halopteris diaphana (Heller, 1868)	60	100	40	8, 9
Corhiza fascicularis (Allman, 1883)	201.2	228.6	27.4	3, 4
Halopteris alternata (Nutting, 1900)	51	73	22	7, 33
Diplopteroides longipinna (Nutting, 1900)	365.8	365.8	0	71
Gattya humilis Allman, 1885	70	70	0	112
Halopteris pseudoconstricta Millard, 1975	54	54	0	69
Halopteris tuba (Kirchenpauer, 1876)	100	100	0	112
Halopteris valdiviae (Stechow, 1923)	100	100	0	112

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Halopteris vervoortii Galea, 2008	51	51	0	7
Kirchenpaueriidae				
Kirchenpaueria bonnevieae (Billard, 1906)	113	1255	1142	7, 8, 19, 99, 101, 102, 107
Oswaldella herwigi El Beshbeeshy, 2011	90	1000	910	38, 94
Oswaldella shetlandica Stepanjants, 1979	50	952	902	78, 79, 94, 97
Oswaldella vervoorti Peña Cantero & García Carrascosa, 1998	50	952	902	82, 94
Oswaldella incognita Peña Cantero, Svoboda & Vervoort, 1997	70	952	882	85, 94, 97
Kirchenpaueria pinnata (Linnaeus, 1758)	54.9	812	757.1	7, 9, 20, 25, 63, 102, 103, 106
Oswaldella rigida Peña Cantero, Svoboda & Vervoort, 1997	80	830	750	85
Oswaldella erratum Peña Cantero & Vervoort, 1997	80	696	616	77, 82, 85, 94
Oswaldella grandis Peña Cantero, Svoboda & Vervoort, 1997	235	810.5	575.5	83, 85
Oswaldella obscura Peña Cantero, Svoboda & Vervoort, 1997	265	830	565	85
Oswaldella stepanjantsae Peña Cantero, Svoboda & Vervoort, 1997	80	368.5	288.5	85, 94
Oswaldella encarnae Peña Cantero, Svoboda & Vervoort, 1997	252	440	188	85, 94
Oswaldella bifurca (Hartlaub, 1904)	450	630	180	85
Oswaldella elongata Peña Cantero, García Carrascosa & Vervoort, 1995	131	200	69	78, 79
Kirchenpaueria altitheca (Nutting, 1900)	493.8	512.1	18.3	71
Oswaldella delicata Peña Cantero, Svoboda & Vervoort, 1997	435	440	5	85, 94
Oswaldella garciacarrascosai Peña Cantero, Svoboda & Vervoort, 1997	330	335	5	85
Oswaldella antarctica (Jäderholm, 1904)	150	150	0	55, 90
Oswaldella billardi Briggs, 1938	412	412	0	94
Oswaldella crassa Peña Cantero & Vervoort, 1998	891	891	0	92
Oswaldella curiosa Peña Cantero & Vervoort, 1998	891	891	0	92
Oswaldella gracilis Peña Cantero, Svoboda & Vervoort, 1997	440	440	0	85
Oswaldella medeae Peña Cantero & Vervoort, 2004	215	215	0	94
Oswaldella monomammillata Peña Cantero & Vervoort, 2004	265	265	0	94
Oswaldella niobae Peña Cantero & Ramil, 2006	810.5	810.5	0	83
Oswaldella tottoni Peña Cantero & Vervoort, 1996	400	400	0	85
Plumulariidae				
Pseudoplumaria marocana (Billard, 1930)	50	4751	4701	5, 7, 52, 101, 102

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Nemertesia antennina (Linnaeus, 1758)	50	2325	2275	1, 7, 8, 9, 20, 24, 25, 36, 48, 49, 57, 60, 61, 71, 100, 101, 102, 106, 107, 122, 123, 124, 125
Nemertesia norvegica (G.O. Sars, 1874)	77	1695	1618	7, 19, 20, 25, 107, 122
Nemertesia falcicula (Ramil & Vervoort, 1992)	335	1650	1315	5, 7, 101
Plumularia filicula Allman, 1877	157.3	1318	1160.7	2, 48, 49, 71, 101
Nemertesia ramosa (Lamarck, 1816)	50	1182	1132	7, 8, 9, 15, 20, 22, 24, 25, 36, 39, 52, 63, 99, 100, 101, 102, 106, 107, 122, 126
Nemertesia vervoorti El Beshbeeshy, 2011	79	1000	921	11, 38
Plumularia attenuata Allman, 1877	192	1103	911	2, 8, 39, 48
Pseudoplumaria sabinae Ramil & Vervoort, 1992	194.5	1022.5	828	102
Plumularia setacea (Linnaeus, 1758)	50	753.5	703.5	7, 8, 9, 11, 15, 22, 24, 25, 33, 38, 49, 50, 51, 52, 69, 99, 101, 102, 103, 106, 107, 112
Nemertesia simplex (Allman, 1877)	65	682.1	617.1	2, 35, 71
Nemertesia americana (Nutting, 1900)	84.1	682.1	598	49, 71
Plumularia variabilis Quelch, 1885	349	914.4	565.4	19, 100
Nemertesia ventriculiformis (Marktanner-Turneretscher, 1890)	100	580	480	7, 101, 126
Plumularia megalocephala Allman, 1877	228.6	643.7	415.1	48, 71
Hippurella annulata Allman, 1877	195.7	517.6	321.9	2, 39, 71
Nemertesia geniculata (Nutting, 1900)	499.3	804.7	305.4	71
Nemertesia ciliata Bale, 1914	176	475	299	52
Plumularia caulitheca Fewkes, 1881	499.3	760.8	261.5	39, 71
Plumularia insignis Allman, 1883	274.3	507	232.7	3, 51, 124
Nemertesia perrieri (Billard, 1901)	50	273	223	7, 8, 10, 101, 122
Hippurella elegans Fraser, 1937	237.7	438.9	201.2	45
Nemertesia hippuris (Allman, 1877)	356.6	481	124.4	2, 39, 71
Nemertesia belini Bedot, 1916	91	187.5	96.5	7
Plumularia lagenifera Allman, 1885	167	247	80	52
Plumularia pulchella Bale, 1882	54	100	46	69, 112
Plumularia leloupi Blanco & Bellusci de Miralles, 1971	87	125	38	11, 16, 38
Plumularia stylifera Allman, 1883	201.2	228.6	27.4	3, 4
Plumularia margaretta (Nutting, 1900)	57	73	16	33, 117
Nemertesia rugosa (Nutting, 1900)	77	84.1	7.1	22, 71
Plumularia floridana Nutting, 1900	70	73	3	33
Nemertesia anonyma Ansin Agís, Ramil & Vervoort, 2001	83	83	0	7
Nemertesia cymodocea (Busk, 1851)	71	71	0	124
Nemertesia dissimilis (Fraser, 1943)	507.5	507.5	0	48

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Nemertesia distans (Nutting, 1900)	210.3	210.3	0	71
Nemertesia longicorna (Nutting, 1900)	373.1	373.1	0	71
Nemertesia nigra (Nutting, 1900)	221.3	221.3	0	71
Plumularia annuligera Quelch, 1885	914.4	914.4	0	100
Plumularia macrotheca Allman, 1877	823	823	0	2
Plumularia paucinoda Nutting, 1900	221.3	221.3	0	71
Plumularia spinulosa Bale, 1882	54	54	0	69
Sibogella erecta Billard, 1911	493.8	493.8	0	71
Schizotrichidae				
Schizotricha frutescens (Ellis & Solander, 1786)	85.5	1263.7	1178.2	24, 25, 34, 63, 101, 102, 103, 107
Schizotricha multifurcata Allman, 1883	76	1244	1168	38, 78, 82, 96, 112
Schizotricha turqueti Billard, 1906	50	952	902	77, 78, 84, 96, 97
Schizotricha unifurcata Allman, 1883	80	567	487	15, 84, 96, 112
Schizotricha crassa Peña Cantero & Vervoort, 2004	107	485	378	95
Schizotricha southgeorgiae Peña Cantero & Vervoort, 2004	324.5	672.5	348	111, 95
Schizotricha profunda (Nutting, 1900)	499.3	804.7	305.4	71
Schizotricha anderssoni Jäderholm, 1904	75	342	267	55, 78, 91, 96
Schizotricha nana Peña Cantero, Svoboda & Vervoort, 1996	80	291.5	211.5	77, 84, 96
Schizotricha falcata Peña Cantero, 1998	73	152	79	78, 96
Schizotricha dichotoma Nutting, 1900	365.8	438.9	73.1	48, 71
Schizotricha vervoorti Peña Cantero, 1998	66.5	117.5	51	78, 96
Schizotricha jaederholmi Peña Cantero & Vervoort, 1996	252.5	281	28.5	91, 96, 111
Schizotricha discovery Soto Àngel & Peña Cantero, 2015	366.5	376.5	10	111
Schizotricha glacialis (Hickson & Gravely, 1907)	630	630	0	84
Schizotricha heteromera Peña Cantero & Vervoort, 2005	107	107	0	96
Schizotricha parvula Nutting, 1900	643.7	643.7	0	71
Sertularellidae				
Sertularella gayii (Lamouroux, 1821)	50	4751	4701	1, 8, 9, 10, 12, 20, 24, 25, 36, 39, 48, 49, 52, 64, 66, 70, 73, 101, 103, 104, 106, 107, 110, 112, 122, 123, 124, 126
Sertularella polyzonias (Linnaeus, 1758)	50	2295.1	2245.1	1, 4, 8, 9, 20, 24, 25, 26, 38, 42, 43, 49, 53, 55, 58, 60, 63, 64, 66, 73, 99, 101, 103, 106, 107, 110, 118, 119, 126
Sertularella tenella (Alder, 1857)	50	2295.1	2245.1	20, 24, 26, 34, 36, 43, 48, 49, 53, 58, 73, 103, 104, 106, 107
Sertularella diaphana (Allman, 1885)	58.5	1408.2	1349.7	4, 31, 39, 48
Sertularella blanconae El Beshbeeshy, 2011	55	1200	1145	11, 38
Sertularella gaudichaudi (Lamouroux, 1824)	55	1200	1145	38, 52, 124

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Sertularella argentinica El Beshbeeshy, 2011	60	1200	1140	38, 111
Sertularella unituba Calder, 1991	61	1200	1139	4, 31, 66, 99, 126
Sertularella vervoorti El Beshbeeshy, 2011	80	1182	1102	38, 111, 124
Sertularella jorgensis El Beshbeeshy, 2011	100	835	735	38, 111
Sertularella sanmatiasensis El Beshbeeshy, 2011	64.5	638.5	574	38, 77, 78, 82, 111
Sertularella fuegonensis El Beshbeeshy, 2011	50	610	560	38, 124
Sertularella hermanosensis El Beshbeeshy, 2011	75	550	475	38, 124
Sertularella cruzensis El Beshbeeshy, 2011	68	515	447	38, 124
Sertularella ellisii (Deshayes & Milne Edwards, 1836)	55	497.4	442.4	24, 42, 66, 106, 126
Sertularella striata Stechow, 1923	80	429	349	52, 112
Sertularella robusta Coughtrey, 1876	71	380	309	11, 38, 55, 111, 124
Sertularella fusiformis (Hincks, 1861)	70	365.8	295.8	112, 127
Sertularella quadrata Nutting, 1895	122.5	354.8	232.3	73
Sertularella areyi Nutting, 1904	86.5	274.3	187.8	35, 73
Sertularella gigantea Hincks, 1874	50	220	170	24, 49, 59, 60, 61, 110, 112
Sertularella conica Allman, 1877	50	187	137	2, 12, 37, 40, 49, 51, 68, 73, 112
Sertularella antarctica Hartlaub, 1901	80	198	118	38, 70, 124
Sertularella leiocarpa (Allman, 1888)	201.2	318	116.8	4, 52
Sertularella flabellum (Allman, 1885)	54	155	101	69, 112
Sertularella xantha Stechow, 1923	80	178	98	112
Sertularella goliathus Stechow, 1923	100	155	55	112
Sertularella arbuscula (Lamouroux, 1816)	54	100	46	69, 112
Sertularella quadrifida Hartlaub, 1901	128	150	22	55, 73
Sertularella ornata Broch, 1933	75	92	17	66, 126
Sertularella mediterranea Hartlaub, 1901	54	60	6	9, 69
Sertularella rugosa (Linnaeus, 1758)	54.9	59.4	4.5	24, 76, 106
Calamphora solitaria (Nutting, 1904)	652.9	652.9	0	48
Sertularella annulata (Allman, 1888)	150	150	0	112
Sertularella calderi Galea, 2013	75	75	0	31
Sertularella catena (Allman, 1888)	713.2	713.2	0	4
Sertularella clausa (Allman, 1888)	1097.3	1097.3	0	4, 73
Sertularella fraseri Galea, 2010	329.2	329.2	0	45
Sertularella humilis Fraser, 1943	228.6	228.6	0	48
Sertularella inconstans Billard, 1919	57	57	0	117
Sertularella megastoma Nutting, 1904	305.4	305.4	0	73
Sertularella megista Stechow, 1923	54	54	0	69

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Sertularella pulchra Stechow, 1923	70	70	0	112
Sertularella undulitheca Vervoort, 1959	65	65	0	122
Sertulariidae				
Diphasia margareta (Hassall, 1841)	54.9	4751	4696.1	1, 4, 8, 9, 10, 22, 25, 36, 52, 64, 66, 99, 101, 106, 107, 112, 122, 126
Tamarisca tamarisca (Linnaeus, 1758)	60	2377.4	2317.4	9, 19, 20, 21, 24, 25, 34, 61, 63, 106, 107, 124
Thuiaria hippuris Allman, 1874	168.2	2452	2283.8	1, 57, 124
Sertularia robusta (Clark, 1877)	50	2078	2028	26, 49, 61, 124
Diphasia fallax (Johnston, 1847)	54.9	2078	2023.1	1, 19, 20, 21, 24, 49, 61, 63, 103, 106, 107, 110, 119, 124
Thuiaria laxa Allman, 1874	54.9	2078	2023.1	1, 20, 24, 26, 41, 43, 49, 57, 59, 61, 107, 124
Thuiaria thuja (Linnaeus, 1758)	54.9	2078	2023.1	20, 21, 24, 26, 38, 41, 49, 60, 61, 63, 73, 107, 124
Abietinaria abietina (Linnaeus, 1758)	50	1970	1920	1, 4, 9, 20, 21, 24, 25, 26, 34, 40, 43, 54, 57, 60, 61, 63, 103, 106, 107, 110, 124, 125
Hydrallmania falcata (Linnaeus, 1758)	50	1970	1920	1, 9, 19, 20, 24, 25, 49, 61, 63, 73, 101, 106, 107, 110, 112, 125
Sertularia similis Clark, 1877	50	1441.1	1391.1	24, 26, 43, 49, 107
Diphasia attenuata (Hincks, 1866)	60	1344.2	1284.2	8, 9, 24, 52, 63, 64, 66, 101, 106
Diphasia delagei (Billard, 1912)	65	1250	1185	9, 66, 101
Thuiaria articulata (Pallas, 1766)	53	1155.8	1102.8	1, 24, 26, 40, 49, 63, 69, 99, 103, 106, 107, 110, 124
Thuiaria carica Levinsen, 1893	70	1102	1032	24, 26, 107
Sertularia tenera G.O. Sars, 1874	50	1077.2	1027.2	9, 20, 21, 24, 26, 34, 53, 57, 60, 63, 106, 107, 124
Amphisbetia operculata (Linnaeus, 1758)	53.9	1040	986.1	9, 11, 38, 52, 55, 73, 97, 112, 124
Sertularia mirabilis (Verrill, 1873)	50	835	785	20, 24, 26, 40, 43, 49, 57, 61, 107, 110
Sertularia distans (Lamouroux, 1816)	52.5	826	773.5	8, 9, 37, 39, 66, 69, 101
Sertularia argentea Linnaeus, 1758	50	786.4	736.4	9, 40, 41, 43, 49, 103, 106, 107, 110, 118
Diphasia alata (Hincks, 1855)	115	823	708	4, 8, 24, 25, 99, 101
Abietinaria filicula (Ellis & Solander, 1786)	52.1	749.8	697.7	24, 63, 106, 107
Abietinaria pulchra (Nutting, 1904)	146.5	773.5	627	60, 107
Sertularia marginata (Kirchenpauer, 1864)	54	592.5	538.5	2, 4, 8, 66, 69, 117, 122
Diphasia rosacea (Linnaeus, 1758)	54.9	521	466.1	24, 41, 49, 73, 76, 101, 106
Sertularia fabricii Levinsen, 1893	50	497.4	447.4	20, 24, 26, 43, 49, 57, 60, 61, 107
Diphasia paarmanni Nutting, 1904	413	804.7	391.7	48, 73, 124
Salacia desmoides (Torrey, 1902)	61	400	339	35, 66, 126
Diphasia digitalis (Busk, 1852)	52.5	389.5	337	49, 73, 122
Dynamena dalmasi (Versluys, 1899)	50	310.9	260.9	31, 49, 66, 122
Abietinaria fusca (Johnston, 1847)	75	334	259	1, 20, 63, 107
Sertularia cupressina Linnaeus, 1758	50.3	274.3	224	4, 20, 24, 26, 28, 41, 49, 57, 63, 99, 106, 110, 118, 119, 124

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Sertularia schmidti Kudelin, 1914	50	274	224	26, 107
Dynamena quadridentata (Ellis & Solander, 1786)	57	256	199	49, 69, 117
Dynamena disticha (Bosc, 1802)	57.5	256	198.5	8, 52, 66, 73
Thuiaria alternitheca Levinsen, 1893	87.8	220	132.2	24, 57, 60, 107, 124
Idiellana pristis (Lamouroux, 1816)	52.5	182.9	130.4	49, 122
Sertularia latiuscula Stimpson, 1854	52	126.2	74.2	28, 49, 110, 118
Diphasia nigra (Pallas, 1766)	90	148	58	9, 10, 25
Dynamena pumila (Linnaeus, 1758)	54.9	55	0.1	38, 106
Abietinaria interversa (Pictet & Bedot, 1900)	240	240	0	99
Abietinaria thuiarioides (Clark, 1877)	373.5	373.5	0	107
Amphisbetia bidens (Bale, 1884)	54	54	0	69
Amphisbetia bispinosa (Gray, 1843)	92.4	92.4	0	73
Amphisbetia minima (Thompson, 1879)	54	54	0	69
Amphisbetia norte El Beshbeeshy, 2011	80	80	0	38
Amphisbetia rectitheca (Ritchie, 1907)	118.9	118.9	0	104
Dictyocladium coactum Stechow, 1923	155	155	0	112
Diphasia robusta Fraser, 1943	461.5	461.5	0	48
Diphasia tropica Nutting, 1904	73	73	0	31
Sertularia flowersi Nutting, 1904	274.3	274.3	0	73
Sertularia gracilis Hassall, 1848	130	130	0	99
Sertularia plumosa (Clark, 1876)	57.5	57.5	0	26
Thuiaria arctica (Bonnevie, 1899)	146.3	146.3	0	24
Thuiaria obsoleta (Lepechin, 1781)	64	64	0	57
Thuiaria pinaster (Lepechin, 1783)	350	350	0	20
Thuiaria sachalini Kudelin, 1914	111	111	0	107
Staurothecidae				
Staurotheca vervoorti (El Beshbeeshy, 2011)	310	2720.5	2410.5	38, 93
Staurotheca abyssalis Peña Cantero & Vervoort, 2003	2928	3879.5	951.5	93
Staurotheca compressa Briggs, 1938	68	951.5	883.5	18, 70, 77, 78, 93, 97, 111
Staurotheca pachyclada (Jäderholm, 1904)	92	951.5	859.5	55, 77, 78, 93
Staurotheca polarsterni Peña Cantero, Svoboda & Vervoort, 1997	181	960	779	70, 86
Staurotheca dichotoma Allman, 1888	63	799	736	18, 78, 82, 93, 111, 86
Staurotheca undosiparietina (Stepanjants, 1979)	74.5	810.5	736	78, 83, 93, 111, 86
Staurotheca glomulosa Peña Cantero, Svoboda & Vervoort, 1997	74	672	598	93, 86

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Staurotheca frigida Peña Cantero, Svoboda & Vervoort, 1997	58	638.5	580.5	55, 77, 78, 93, 111, 86
Staurotheca antarctica Hartlaub, 1904	118.9	661	542.1	18, 104, 115, 86
Staurotheca amphorophora Naumov & Stepanjants, 1962	143	672.5	529.5	70, 93, 111
Staurotheca jaederholmi Stechow, 1920	76	500	424	38, 93
Staurotheca nonscripta Peña Cantero, Svoboda & Vervoort, 1997	206	630	424	86
Staurotheca australis Peña Cantero, Svoboda & Vervoort, 1997	432	813	381	86
Staurotheca multifurcata Peña Cantero, García Carrascosa & Vervoort, 1999	58	342	284	78, 81, 93
Staurotheca cornuta Peña Cantero, García Carrascosa & Vervoort, 1999	125.5	405	279.5	81, 93
Staurotheca densa Peña Cantero & Vervoort, 2003	92	368.5	276.5	77, 78, 93
Staurotheca vanhoeffeni (Peña Cantero & García Carrascosa, 1994)	92	368.5	276.5	77, 78, 93, 86
Staurotheca juncea (Vanhöffen, 1910)	200	465	265	86
Staurotheca plana Peña Cantero, Svoboda & Vervoort, 1997	672	830	158	86
Staurotheca affinis (Jäderholm, 1904)	75	200	125	55, 78
Staurotheca profunda Peña Cantero & Vervoort, 2003	1845.5	1845.5	0	93
Staurotheca stolonifera (Hartlaub, 1904)	262	262	0	86
Symplectoscyphidae				
Symplectoscyphus tricuspidatus (Alder, 1856)	50	2438	2388	19, 20, 21, 24, 26, 28, 40, 41, 43, 49, 53, 57, 59, 60, 61, 63, 70, 76, 99, 104, 107, 110, 118, 119, 124
Symplectoscyphus milneanus (D'Orbigny, 1842)	55	1511	1456	11, 38, 73, 124
Symplectoscyphus bathyalis Vervoort, 1972	252.5	1611	1358.5	24, 36, 66, 107, 111
Symplectoscyphus vervoorti El Beshbeeshy, 2011	55	1400	1345	38, 124
Symplectoscyphus filiformis (Allman, 1888)	55	1200	1145	11, 12, 38, 51, 70, 78, 104, 115, 124
Symplectoscyphus naumovi Blanco, 1969	205	1285.5	1080.5	83, 88
Symplectoscyphus salvadorensis El Beshbeeshy, 2011	225	1200	975	38
Symplectoscyphus chubuticus El Beshbeeshy, 2011	60	920	860	38
Symplectoscyphus valdesicus El Beshbeeshy, 2011	60	835	775	38
Symplectoscyphus pinnatus (Clark, 1877)	87.5	835	747.5	26, 38
Symplectoscyphus flexilis (Hartlaub, 1901)	70	800	730	11, 124
Symplectoscyphus amphoriferus (Allman, 1877)	160.9	882	721.1	2, 8, 37, 48, 73
Symplectoscyphus curvatus (Jäderholm, 1917)	92	799	707	77, 78, 88, 97
Symplectoscyphus glacialis (Jäderholm, 1904)	118	810.5	692.5	55, 78, 83, 88, 97, 111

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Antarctoscyphus spiralis (Hickson & Gravely, 1907)	63	630	567	77, 78, 82, 87, 111
Antarctoscyphus elongatus (Jäderholm, 1904)	75	630	555	55, 82, 87, 124
Symplectoscyphus exochus Blanco, 1982	80	634	554	88, 97
Symplectoscyphus paraglacialis El Beshbeeshy, 2011	515	960	445	38
Symplectoscyphus anae Peña Cantero, Svoboda & Vervoort, 2002	200	630	430	88
Symplectoscyphus magellanicus (Marktanner-Turneretscher, 1890)	55	403	348	38, 124
Symplectoscyphus plectilis (Hickson & Gravely, 1907)	128	457	329	78, 82, 88, 97, 112
Symplectoscyphus vanhoeffeni Totton, 1930	80	385	305	77, 78, 88
Symplectoscyphus cumberlandicus (Jäderholm, 1905)	69	366.5	297.5	55, 97, 111
Antarctoscyphus grandis (Blanco, 1977)	80	365	285	87, 97
Symplectoscyphus weddelli Peña Cantero, Svoboda & Vervoort, 2002	119	385	266	88
Fraseroscyphus macrogonus (Trebilcock, 1928)	167	429	262	52
Symplectoscyphus nesioticus Blanco, 1977	260	522	262	88, 111
Symplectoscyphus frigidus Peña Cantero, Svoboda & Vervoort, 2002	170.5	402	231.5	78, 88
Symplectoscyphus singularis El Beshbeeshy, 2011	90	310	220	38
Antarctoscyphus gruzovi (Stepanjants, 1979)	279	414	135	87, 111
Antarctoscyphus asymmetricus Peña Cantero, García Carrascosa & Vervoort, 1997	144	247.5	103.5	80, 97
Antarctoscyphus encarnae Peña Cantero, García Carrascosa & Vervoort, 1997	118	210	92	80
Symplectoscyphus liouvillei (Billard, 1914)	240	330	90	14, 88
Symplectoscyphus leloupi El Beshbeeshy, 2011	55	115	60	38
Symplectoscyphus sofiae Peña Cantero, Svoboda & Vervoort, 2002	425	465	40	88
Antarctoscyphus admirabilis Peña Cantero, Svoboda & Vervoort, 1999	80	80	0	87
Antarctoscyphus biformis (Jäderholm, 1905)	360	360	0	55
Antarctoscyphus fragilis Peña Cantero, Svoboda & Vervoort, 1999	465	465	0	87
Symplectoscyphus magnificus Peña Cantero & Vervoort, 2009	264	264	0	97
Thyroscyphidae				
Parascyphus repens (Jäderholm, 1904)	100	1250	1150	38, 55, 124

Species	Shallowest record (m)	Deepest record (m)	Depth range (m)	References
Thyroscyphus marginatus (Allman, 1877)	54.9	804.7	749.8	4, 31, 49, 74, 117
Thyroscyphus ramosus Allman, 1877	73.2	438.9	365.7	48, 49
Sertularelloides cylindritheca (Allman, 1888)	62	200	138	8, 52, 64, 66, 101, 122
Parascyphus simplex (Lamouroux, 1816)	54	54	0	69
Thyroscyphus aequalis Warren, 1908	73.2	73.2	0	58

* Families of unresolved phylogenetic position within any of the monophyletic Filifera Orders were classified as "Filifera?".

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Capítulo 2

Functional traits of hydroids (Cnidaria, Hydrozoa) vary with depth

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Abstract

Functional traits affect survival and reproduction of individuals in different habitat conditions, ultimately altering their fitness. Ocean depth has unique related biotic and abiotic gradients, such as food availability, temperature, and population densities, that by its turn may influence the occurrence of specific traits. Characterizing patterns of trait variation along depth helps to infer evolutionary drivers related to diversity of marine forms, functions, and life-histories. Hydroids have diversified life histories and morphologies and occur from shallow to hadal depths, but have been poorly investigated concerning the relationship of depth and variation of traits. Here, we investigated patterns of variation of functional traits along depth for Atlantic hydroids, contrasting these patterns with the natural history of the group and ecological principles of the deep sea. Our results show that functional traits of hydroids vary with depth, and variation is more pronounced for regions deeper than 1,000 m. Hydroids are frequently smaller, meroplanktonic, solitary, infertile, and devoid of exoskeletons and nematophores with increasing depth. Limited food resources in the deep sea is proposed to be an important driver shaping patterns, especially for its influence in growth and reproduction.

Resumo

Características funcionais afetam a sobrevivência e a reprodução de indivíduos em diferentes condições de habitat, alterando sua aptidão. A profundidade do oceano possui gradientes bióticos e abióticos relacionados únicos, como disponibilidade de alimentos, temperatura e densidades populacionais, que por sua vez podem influenciar a ocorrência de características específicas. Caracterizar os padrões de variação de características ao longo da profundidade ajuda a inferir fatores evolutivos relacionados à diversidade de formas, funções e histórias de vida marinhas. Hidroides têm histórias de vida e morfologias diversificadas e ocorrem de profundidades superficiais a hadais, mas foram pouco investigados quanto à relação da profundidade com a variação de características. Aqui, investigamos padrões de variação de características funcionais ao longo da profundidade para as hidroides do Atlântico, contrastando esses padrões com a história natural do grupo e princípios ecológicos do mar profundo. Nossos resultados mostram que características funcionais de hidroides variam com a profundidade e que a variação é mais pronunciada para regiões a mais de 1.000 m de profundidade. Hidroides são frequentemente menores, meroplanctônicos, solitários, inférteis e desprovidos de exoesqueletos e nematóforos com o aumento da profundidade. A limitação de recursos alimentares no mar profundo é proposta como um fator importante moldando padrões, especialmente por sua influência no crescimento e na reprodução.

Introduction

Macroecological inferences aim to characterize broad patterns in the distribution of biodiversity – for example, in richness, abundances, range sizes and body sizes – and understand the processes that underlie them across large temporal and geographic scales (Brown, 1995; Gaston & Blackburn, 2000; Witman & Roy, 2009; Keith *et al*., 2012). Macroecological reasoning is based on the premise that functional traits of individuals may affect their fitness in different habitats by mediating responses to biotic and abiotic conditions by impacting capacity to grow, survive and reproduce, and ultimately affecting the spatial variation of species composition (Soininen *et al*., 2007a, 2007b; Violle *et al.,* 2007; Webb *et al*., 2009; Brun *et al.,* 2016; Beauchard *et al.,* 2017; Bolam *et al.,* 2017). Functional traits may vary either between or within species, since developmental regulation by environmental signals may produce appropriate phenotypes according to the conditions in which the individuals live (Gilbert, 2012; Bosch *et al*., 2014). Therefore, studying how traits vary in relation to the environment may help in understanding both natural selection and ecosystem functioning, in a way that the study of the distribution of species identities alone would not allow (Bremner, 2008; Connell & Irving, 2009).

Environmental gradients associated with ocean depth may influence the occurrence of different traits (McClain *et al.,* 2009; Ramirez-Llodra *et al.,* 2010). Sunlight is rapidly filtered as depth increases (Stewart, 2006). In the absence of light for photosynthesis, there is no phytoplankton, the primary food source in the ocean. Input of organic matter from surface waters leads to a decreasing gradient of food availability along depth, except for chemosynthetic environments such as hydrothermal vents (Smith *et al*., 2008; Ramirez-Llodra *et al*., 2010). The organic matter not consumed by the plankton during its fall settles to the bottom forming a layer of sedimented organic matter (Ramirez-Llodra *et al*., 2010). Temperature also decreases quickly, until it stabilizes around 1,000 m deep (Stewart, 2006). Hard substrates are rare in the deep sea, and abyssal plains are mostly formed by muddy bottoms (Jamieson, 2015; Clark *et al*., 2016). These general trends, however, may vary across regions.

Diversity of forms, functions and life-histories vary with depth, most likely related to unique drivers of evolution and adaptation. For instance, limited food supply constrains biomass and population densities in the deep sea (Sanders & Hessler, 1969; Rex *et al*., 2006), which may favor specific body sizes according to trophic, reproductive or metabolic functions towards more efficient resource exploitation (Rex & Etter, 1998; Ramirez-Llodra *et al*., 2010; McClain *et al*., 2012; van der Grient & Rogers, 2015; Gambi *et al*., 2017). Larger invertebrates would be favored by a lower energetic cost per unit of mass in a food deprived environment such as the deep sea, which would result in lower populations densities, diminishing the probability of finding mates for sexual reproduction (Peters, 1983; Rex & Etter, 1998; Ramirez-Llodra *et al*., 2010). Smaller sizes would, therefore, allow for higher abundances and increased chances of sexual reproduction (Thiel, 1979; Ramirez-Llodra *et al*., 2010). Thus, evidences of populations in the deep-sea benthos being largely structured by food availability indicate that trade-offs between life history traits are necessary (Thiel, 1979).

Hydroids – hydrozoans encompassing the polypoid stages of Limnomedusae, Leptothecata and "Anthoathecata" (Cartwright *et al*., 2008; Van Iten *et al*., 2014; Maronna *et al*., 2016; Cunha *et al*., 2017) – are morphologically and ecologically diverse, occurring from shallow to hadal depths (Kramp, 1956; Calder, 1996; 1998). These taxa with hydroid stages, particularly Leptothecata, encompass the vast majority of the species richness of Medusozoa (cnidarians that typically including a medusa in their life cycle). High diversity in hydroid containing taxa is also seen in the wide breadth of biologically relevant traits. Among these traits, species have evident variations in size, ranging from less than a millimeter to tens of centimeters (e.g. Millard, 1975; Cornelius, 1995; Schuchert, 2012). Most hydroids are colonial, branching off in different patterns, although some species are solitary (Schuchert, 2012). As modular organisms, many colonial hydroids easily vary their size and shape, therefore enhancing the exploitation of environmental resources, an advantageous phenotypic plasticity for sessile organisms (Marfenin, 1997; Cunha et al., 2016). These colonies are often polymorphic, composed by feeding (gastrozooid), reproductive (gonozooid) and defensive (nematozooid) modules (Millard, 1975). Some kind of exoskeleton, varying in extent from absent to enclosing the entire colony, is another typical trait of the group (Mendoza-Becerril *et al.*, 2017), including exoskeletons in the form of gonothecae, phylactocarps, coppiniae, corbulae and pseudocorbulae, that may function as extra protective structures (Millard, 1975; Cornelius, 1995). Stems and hydrocauli may be composed by single (monosiphonic) or multiple (polysiphonic) tubes, with variable numbers of annulations (Cornelius, 1995). Suspensivory is common in sites with constant water circulation, in which flow increases encounters with suspended matter (Genin *et al.*, 1986), and the use of nematocysts to kill planktonic prey aids survival in less hydrodynamic waters at abyssal depths (Calder, 1996). Their larvae generally settle and grow on hard substrates of abiogenic, biogenic, or artificial origin, but some individuals/colonies colonize soft bottoms (Bennett *et al.*, 1994; Ansín Agís *et al.*, 2001; Fernandez *et al.*, 2014; Blanco *et al.*, 2013; Watson, 2017).

The fundamental life-cycle of hydroid-bearing species is complex and comprises a succession of stages. Reproductive polyps bud off dioecious medusae bearing gametes; after fertilization, the embryo develops into a planula larva that settles and metamorphoses into a new benthic polyp stage (Cornelius, 1995), which undertakes a large repertoire of modes of asexual reproduction (Gili & Hughes, 1995). Variations to this fundamental life cycle occur among the different lineages of hydrozoans, such as different levels of reduction of the medusa stage, up to its complete absence, and suppression/variable life span of the planula larvae. Benthic (without medusa) or meroplanktonic (with medusa) life-cycles are interpreted to be advantageous or disadvantageous depending on the conditions in which the individual/population/species lives (Cornelius, 1992). For instance, apparently, there is a smaller proportion of meroplanktonic species at higher latitudes, and a similar pattern has been hypothesized for the deep-sea (Calder, 1992, 2000). The benthic stage is more often dioecious, but monoecious species occur (Millard, 1975).

Patterns and drivers of trait variations, however, are poorly investigated and understood for hydroids (and for medusozoans in general), especially in relation to depth, a chief factor for understanding marine biodiversity. Abiotic and biotic factors varying along depth, including resource limitations and gradients of physicochemical parameters, make the unique conditions of deep-sea habitats driving determinant effects on functional traits that would enable growth, survival, and reproduction of individuals/colonies. In this study, we investigated patterns of variation of functional traits of hydroid-bearing species along depth, contrasting these with the biology of the group and deep-sea ecology.

Material & methods

Study area, data sampling, and identification

Our analysis was based on hydroid stages (with the exception of the hypercalcified Milleporidae and Stylasteridae, and Limnomedusae) from depths below 50 m (maximum depth was 5,330 m) of the Atlantic Ocean and adjacent Arctic and Antarctic waters (Fig. 1). The material studied consists of 4,194 lots, belonging primarily to museum collections (National Museum of Natural History, Smithsonian Institution; Museum of Comparative Zoology at Harvard University; Naturalis Biodiversity Center; Royal Ontario Museum; Canadian Museum of Nature; Museum of Zoology of the University of São Paulo and National Museum of Rio de Janeiro) with geographic and depth data. We personally examined all material to check or to make identifications and to gather morphological and biological data, enhancing uniformity within the data set. The specimens were identified based on current literature specific to each taxon.

Functional traits

We collected data related to 14 functional traits from the material, seven related to the species (*e.g.*, life cycle and presence of exoskeleton), and seven related to the specimens (*e.g.*, height and substrate use) (Tables 1 and S1). Information on species life cycle and sexual reproduction was based on the best knowledge of the primary literature. Whenever the life cycle was unknown for a specific species, we used approximation data for its genus or family, except when extensive intra-genus or intra-family variation are known to occur, and recorded the basis for approximation. Species reported as "benthic with swimming gonophore" and "benthic with eumedusoid" life cycles were all considered "benthic" in the analysis, due to the limited medusa/gonophore dispersive capacities (Boero & Bouillon, 1989; Migotto & Marques, 1999). Likewise, the "dioecious" *Nemertesia antennina* (Linnaeus, 1758) was considered to be functionally “monoecious” in the analysis, because its gregarious growing habit approximates male and female gametes (Hughes, 1977). Similarly, “absent” and “shallow” hydranth exoskeletons, “phylactocarp”/“coppinia” and “corbula”/“pseudocorbula” gonophore protections were considered to be single traits due to their functional similarities.

Data analyses of size variation with depth

To evaluate if size (*viz.* height of the specimens) varies with depth, records were divided into 12 depth ranges (*viz.*, 50 – 100 m; 101 – 200 m; 201 – 300 m; 301 – 400 m; 401 – 500 m; 501 – 600 m; 601 – 800 m; 801 – 1,000 m; 1,001 – 1,500 m; 1,501 – 2,000 m; 2,001 – 3,000 m and 3,001 – 5,330 m strata), and an equal number of records was randomly selected for each range, standardizing comparisons among all depth strata. Variations in size within and between depth strata were summarized in boxplots, and differences analyzed by permutational ANOVA using the “aovp” function from the “lmPerm” package in R (Wheeler & Torchiano, 2016), followed by pairwise comparisons with the “pairwisePermutationTest” function in the “rcompanion” R package (Mangiafico, 2017). The height of all specimens was plotted against depth to visualize correlations between them. Similarly, correlations within species were searched for those species with more than 50 records. Linear relationship between size and depth was tested using the “lm” function in the “stats” R package on the standardized data (R Core Team, 2017). To infer if variation in size along depth is trait dependent, the standardized data set was plotted with different colors for each trait category and linear models were fitted to test for significant relationships between size and depth for each category. Regression lines were plotted only for significant relationships. Broken specimens were excluded from all analyses regarding size.

Data analyses of trait variation with depth

To evaluate how each of the 14 traits vary with depth, we calculated the proportion of records and species within each trait category per depth range. Proportions were adopted to balance unequal sampling across depth. For each trait, only records whose trait information could be collected were computed. We used the Pearson’s Chi-square test to search for significant differences in traits’ proportions along depth (“chisq.test” function in “stats” R package; R Core Team, 2017). A post-hoc z-test on the adjusted Pearson residuals allowed for identification of data majorly contributing to significant differences, *i.e.*, values higher (positive) or lower (negative) than expected (critical z-value), for a 0.05 significance level with Bonferroni correction for multiple testing. Life cycle variation along depth was further investigated regarding differences within coloniality, fertility and substrate use categories. In the analyses regarding species, only taxa identified to species level were used – three of them were characterized as unique morphotypes and included in the species analyses, although their specific names are dubious, namely *Acaulis* cf. *rosae* (Verrill, 1878), *Euphysora ?bigelowi* Maas, 1905, and *Millardiana* sp.

Results

We studied a total of 4,668 records of hydroids (some lots contained more than one hydroid specimen) representing 606 taxa used in the analyses, of which 438 were identified at the species level. A total of 615 new species occurrence records were made for their respective regions.

Size varies with depth

The height of the specimens was significantly different between depth strata ($p < 0.0001$; Fig. 2). Pairwise comparisons indicate differences mostly between depth strata deeper and shallower than 1,000 m, deep-sea specimens being smaller on average. No differences were found for depth strata from 50 to 1,000 m. In general, differences were found between shallower (50 – 1,000 m deep) and deeper (1,000 – 5,330) depth strata, with few exceptions (Fig. 2, Table 2). From 50 to 1,000 m deep, hydroids varied greatly in size, with both small and large specimens found, but variation decreases when deeper than 1,000 m deep, where mostly small specimens were found (Figs. 2–3). Similar patterns were found within species, especially for *Lytocarpia myriophyllum*, *Acryptolaria conferta*, and *Billardia subrufa* (Fig. 3B–H).

No general linear relationship was found between height and depth (Fig. 4A), except for some selected trait categories (plotted regression lines in Fig. 4; linear regression R^2 and p values in Table 3). Plotted data also show that some traits vary with the height of the specimens. Basal diameter and orders of branching increase with the height of the specimen (Fig. 4B, E), and higher specimens are more often polysiphonic (Fig. 4D). Also, fertile specimens are frequently larger than infertile ones (Fig. 4L). Finally, specimens of benthic taxa are larger than those of meroplanktonic taxa (Fig. 4J).

All traits vary with depth

All 14 traits varied significantly with depth in terms of proportion of records, and nearly all (12) varied in proportion of species, the exceptions being for life cycle and sexual reproduction (Figs. 5–6, Table 4). However, larger proportions of meroplanktonic and monoecious species occur below 1,500 m deep (Fig. 5).

Besides size, many other traits vary prominently below 1,000 m deep. The presence of exoskeleton on hydrocauli decreases notably below 1,000 m deep, for both records and species; proportion of records with no exoskeleton on hydranth increases between 1,500 and 3,000 m deep; and proportion of records with an operculum decreases below 2,000 m deep. A decrease in records of exoskeleton enveloping the gonophore is also notable – many records have no gonophore protection between 1,000 and 3,000 m deep, in contrast to only a few records from 50 to 500 m deep. Similarly, records with nematophores significantly decrease below 2,000 m deep. Regarding life cycle, the proportion of meroplanktonic records increases below 1,500 m deep. There is a substantial increase in both records and species of solitary forms below 1,000 m deep. The proportion of fertile specimens decreases from 1,000 to 3,000 m deep. Finally, use of biogenic substrates decreases below 1,000 m, with both hard and soft substrates being more often colonized (Figs. 5–6, and Tables 5–23 for all test results).

Hydrocauli are significantly wider basally (> 1 mm) and tend to be polysiphonic from 400 to 1,000 m (Figs. 6B, D; Tables 18, 20). Alternatively, considerably more monosiphonic colonies, with more basal annulations, were found in the 50 – 100 m depth range (Tables 18, 20).

Life cycle variation with depth was related to other traits (Fig. 7). For example, there was minor variation in life cycle with depth for colonial records and species, with a slight increase in those meroplanktonic below 3,000 m deep. For solitaries, on the other hand, there were conspicuously more of those meroplanktonic between 500 and 3,000 m deep (Fig. 7A, B). Meroplanktonic specimens were more often infertile than benthic, especially with increasing depth, and there was an increased use of soft substrates by meroplanktonic specimens with depth (Fig. 7C, D).

Discussion

Our analyses suggest that functional traits of hydroids vary with depth, with more substantial differences below 1,000 m deep. Hydroids were more frequently smaller, meroplanktonic, solitary, lacking exoskeletons and nematophores, and infertile with increasing depth.

Hydroids varied in size with depth, with both small and large specimens occurring shallower than 1,000 m deep, although significantly smaller specimens occurred deeper than that depth (Figs. 2–3). The larger specimens occurring shallower than 1,000 m deep often belong to species with wide bathymetric distributions whose specimens are smaller in deeper waters (Fig. 3), suggesting that individuals/colonies are not growing as well in deep sea environments, probably because of limited food supply (Sanders & Hessler, 1969; Hessler & Jumars, 1974; Ramirez-Llodra *et al.*, 2010). Since hydroids feed mostly on zooplankton, a resource diminishing with increasing depth, larger organisms could have metabolic constraints hindering survival in deeper waters. An opposite pattern apparently occurs in several non-hydroid taxa, for which larger individuals may be found in the deep sea, but these animals are usually deposit feeders and detritivores (*i.e.*, getting food from accumulated organic matter at the seafloor), or species living in restricted oases, *e.g.*, close to hydrothermal vents and cold seeps (Ramirez-Llodra *et al.*, 2010). An exception to the pattern observed here is the gigantic (more than 2 m in height) benthic solitary hydroid *Branchiocerianthus imperator*, but it was not observed in this study. Nevertheless, it has been recorded for the Atlantic, Indian, and Pacific oceans to 5,307 m deep (Allman, 1888; Vervoort, 1966; Omori & Vervoort, 1986). This remarkable species, besides regularly feeding on plankton, has the unique habit of sweeping the bottom with its tentacles to feed on material deposited in or on the sediment, which likely allows for its enormous growth (Foell & Pawson, 1986; Omori & Vervoort, 1986). Thus, the lower abundances and dimensions of the suspension feeding hydroid community are likely related to the scarcity of food, contrary to the dominance of deep sea deposit feeders (scavengers and detritivores) (Sanders & Hessler, 1969; Hessler & Jumars, 1974).

Smaller sized hydroids are expected to be more vulnerable to predation by several animal taxa that feed on hydroids (Gili & Hughes, 1995), but nematophores and exoskeletons could be traits related to their protection (Gili & Hughes, 1995; Mendoza-Becerril *et al.*, 2016). Contrary to this scenario, reduction of deep sea hydroid sizes is not accompanied by enhanced strategies for protection. We observe a higher proportion of species without exoskeletons enveloping hydrocauli, hydranths, and gonophores below 1,000 m deep, as well as a lack of nematophores and opercula below 2,000 m deep (Fig. 5A–H). This suggests that hydroids may be less affected by predation pressure in deep habitats, even though predation is considered an important structuring driver in many deep-sea communities (Rex, 1976; Micheli *et al*., 2002; Gallucci *et al*., 2008a,b; Thistle *et al*., 2008; Stevenson *et al*., 2015). However, although nematophores are part of defensive zooids with high nematocyst concentration, nematocysts are also spread over other parts of individuals. Cnidome complexity (*i.e.*, the different sets of nematocysts types from each species) is presumed to primarily improve protection (Weill, 1934; Mariscal, 1974), and could be an alternative strategy against predation, but this trait was not investigated in this study and so we cannot assess it here.

Absolute smaller sizes, as well narrow ranges of size variation below 1,000 m deep (Fig. 2), coincide with the absolute lower and narrow ranges of variation of temperatures below the thermocline. Temperature may ultimately be related to size since it influences metabolism, and therefore energy demand/availability for growth (Childress *et al*., 1990; McClain *et al*., 2012), although lower growth rates do not necessarily result in final smaller sizes (Angilletta *et al*., 2004). Temperature, however, is usually not a good predictor for size, because the relationship depends on organisms' physiological particularities (Angilletta & Dunham, 2003; Brown *et al*., 2004; McClain *et al*., 2015). Oxygen availability is often better regarded as a good predictor for size (Chapelle & Peck, 1999; McClain *et al*., 2009), and carbon flux is considered the main determinant (McClain *et al*., 2009).

Despite the clear size differences between hydroids along the depth strata, the relationship between size and depth is not linear, probably influenced by the presence of small-sized hydroids all along the gradient (Figs. 3A, 4A). Within some other trait categories, however, size and depth are significantly associated (Fig. 4), suggesting that depth may affect size differently according to the presence of specific functional traits. For specimens with an exoskeleton enveloping hydrocauli, hydranths, and gonophores, for instance, size and depth are associated, but for specimens without an exoskeleton there is no apparent association (Fig 4 F-H). Similarly, size of colonial specimens significantly decreases with depth, but this does not happen for solitary species (Fig. 4M). Monoecious specimens significantly increase in size with depth (Fig. 4K), which could be a strategy to successfully promote encounters of gametes in habitats of low population density – in this scenario, less energy would be allocated for both reproduction and to increase population numbers to ease mating, therefore monoecious specimens would be able to allocate more energy for individual growth. Conflicting patterns were previously found for size variation with depth for other taxa (Rex & Etter, 1998, Gambi *et al*., 2003; Olabarria & Thurston, 2003; McClain *et al*., 2015), perhaps due to other species' life history traits or regions of occurrence (Ramirez-Llodra *et al*., 2010; van der Grient & Rogers, 2015).

Size patterns discussed to this point refer to the height (*i.e.*, vertical size) of the specimens. However, conditions of limited food resources may not hamper colonies from growing horizontally by hydrorhizal extension, resulting in shorter but more numerous and spaced stems/polyps, as is seen in *Laomedea flexuosa* (Berrill, 1950; Crowell, 1957; Marfenin, 1997). A flat growing strategy would allow for colonizing larger areas, increasing and the likelihood of food capture. Solitary hydroids and colonial hydroids with stolonal growth, on the other hand, are not able to vary their heights by adjusting the number of modules according to food availability. Horizontal breadth of the specimens, however, could not be measured, because hydrorhizae connecting stems were often broken in studied specimens.

Developmental plasticity allows colonies to vary their shapes (*i.e.*, sizes and branching) according to the environment (Marfenin, 1997). Under increased food availability colonies may also increase branching to maximize food consumption (Marfenin, 1997). Although not significant, decreasing orders of branching along depth (Fig. 6E) may indicate scarcity of food resources. Also, survival in more exposed and hydrodynamic habitats would demand more robust and flexible hydrocaulus (Gili & Hughes, 1995). Increased base diameter and polysiphony from 400 to 1,000 m deep in the specimens studied here (Figs. 6B, D; Tables 18, 20) may, therefore, indicate a response to increased water circulation in the upper slope, as a means for avoiding breakage or detachment.

Some traits, however, may be correlated to each other and may not vary independently among specimens, therefore they cannot be readily interpreted as a response to environmental conditions in the deep sea. This may happen because the expression of a single trait may be combined with and/or limited by the expression of other traits, as a consequence of either physical, developmental, or historical constraints (Usseglio-Polatera *et al*., 2000; Braendle *et al*., 2011). Among these traits, there are the greater proportion of meroplanktonic life cycles among solitary species and the increased use of soft substrates by meroplanktonic species along depth (Fig. 7). Actually, larger sizes of benthic in comparison to meroplanktonic specimens may be related either to phylogenetic constraints or to trade-offs on resource allocation (Braendle *et al*., 2011). In conditions of limited resources, the allocation of the resource to one function may restrict investment in another, resulting in trade-offs among optimum traits for survival and reproduction (Stearns, 1989; Braendle *et al*., 2011; Tökölyi *et al*., 2016). Curiously, fertile specimens studied here were larger, regardless of depth (Fig. 4L), maybe suggesting that hydroids do not develop reproductive structures until they reach a certain size.

Alternatively, local variation in habitat conditions could favor growth and fecundity at the same time.

Larger proportions of fertile specimens shallower than 1,000 m deep (Fig. 6F) may indicate that limitation of resources in the deep sea could be constraining both size and sexual production. The pattern may be evidence that deep-sea hydroid populations are functioning under a source-sink dynamic, in which the deep sea would function as a sink for some shallower water species, and where low nutrient input and low population densities would not sustain reproductive populations immigrating from shallower sources (Rex *et al.*, 2005). Indeed, most hydroid species in the Atlantic Ocean have depth ranges extending from shallower to deeper waters, and only a few species are restricted to bathyal or abyssal depths (Fernandez & Marques, 2017a[1]). Hydroids, however, have a vast repertoire of modes of asexual reproduction (Gili & Hughes, 1995) that could help maintain populations in deep-sea conditions, even if constrained by food availability. Because we did not quantify asexual reproduction, this hypothesis cannot be tested. A single hypothesis is not likely to explain patterns of distribution for all the species, and this complex synthesis is, indeed, a composite of different diversities (Fernandez & Marques, 2017b[2]). In both cases, however, the lower proportion of fertile specimens in the deep sea would decrease chances of genetic recombination in deep sea populations, ultimately leading to slower evolution.

The increased proportion of meroplanktonic records at greater depth, especially in strata deeper than 1,500 m (Fig. 5I), is counterintuitive, because releasing a medusa and increasing gamete dispersion seems disadvantageous in an environment with low population densities for cross-fertilization (see speculation in Boero & Bouillon, 1989). Moreover, releasing a medusa requires more energy to be allocated for reproduction, despite low food availability. On the other hand, greater dispersion could help individuals get away from conspecifics to avoid competition in an environment with scarce resources (Comita, 2017) and/or decrease chances of predation and parasitism. In fact, species that release medusae usually have wider geographical ranges than benthic species (Gibbons *et al.* 2010a, 2010b; Rodriguez *et al.*, 2017), although the opposite was found in the family Hydractiniidae (Miglietta & Cunningham, 2012). A reasonable explanation for the increased proportion of meroplanktonic records would be possible when medusae released in deep-sea environments are monoecious, an advantageous condition in an environment with scarce food, allowing for greater dispersion and colonization

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[1] Capítulo 1.

[2] Capítulo 4.

of new environments along with ease of sexual reproduction in an environment with low population densities. This plasticity was demonstrated for hydroids, triggered by temperature (Carré & Carré, 2000), but maybe it could also be triggered by depth. Few meroplanktonic specimens in our data, however, were fertile (Fig. 7C), therefore the hypothesis of low sexual reproduction in deep sea habitats still has to be considered. Also, although we observed an increase in the proportion of meroplanktonic records at greater depths, there was no significant variation in the proportion of species.

Patterns inferred in this study are for depths below 50 m deep. Globally, around 74% of hydroid-bearing hydrozoan species are benthic and 26% meroplanktonic (holoplanktonic species excluded; Gibbons *et al*., 2010b). Therefore, disregarding differences across depths, the total proportion of meroplanktonic species reported here (5%) is much lower than that expected for entire oceans. Therefore, either the proportion of meroplanktonic species is lower for species living deeper than 50 m than for those in shallower waters, or the proportion of meroplanktonic species in the Atlantic Ocean is lower than in other oceans.

Although solitary hydroid species are rare in the group (ca. 6% of the species) (Cartwright & Nawrocki, 2010; Schuchert, 2012; WoRMS, 2017), they seem to be favored by the environmental conditions below 1,000 m deep. There is a large increase in the proportion of records and species of solitary rather than colonial (Fig. 5M, N). One explanation for this pattern would be the increased availability of soft substrates along depth, which is often the habitat for solitary hydroids. Similarly, decreasing use of biogenic substrates below 1,000 m deep (Fig. 6G) may be related to its lower availability, since abundances of species that could be potentially used as substrata are, evidently, lower (McClain *et al*., 2009). Many solitary forms can live in soft substrates as sand or mud (Schuchert, 2012). Detritus deposited on the seafloor is often resuspended by deep bottom currents (Bonnin *et al*., 2006), and may favor suspension feeding of solitary hydroids inhabiting soft bottoms. Colonial forms, on the other hand, more often depend on hard substrates, biogenic or not, to settle and grow (Gili & Hughes, 1995). An increased use of soft substrates was observed (Fig. 6G), by both solitary and colonial forms, frequently including adaptations for attachment in the sand like developing root-like hydrorhizae. The classical view that hydroids occupy mostly hard substrates may be related to sampling bias and should be, at least, better tested for the deep sea, where hard substrates are scarce. The ability of colonial hydroids to grow on soft sediments has been rarely reported, and only for a few species (Gili & Hughes, 1995; Di Camillo *et al*., 2013; Calder, 2017), but seems to be an important adaptation allowing hydroids to occupy muddy plains of the deep sea, with important potential consequences for dispersion and colonization of new environments.

In conclusion, our data show that the hydroid fauna is not uniform across depth. Most of the functional traits of hydroids vary with depth, and a typical deep-sea hydroid is small, meroplanktonic, solitary, infertile, and devoid of exoskeleton and nematophores. This large-scale study reports thus far undocumented trends in hydroid traits along depth by combining collections-based observations on morphology, ecology, and life-history, thereby providing an avenue for understanding selection pressures on hydrozoan diversification and evolution in the deep-sea. Although we understand that patterns of trait distribution may be constrained by historical factors (Leclère *et al.*, 2007; Cartwright & Nawrocki, 2010; Fine, 2015), the ability of species to occupy specific niches also modulates their final distribution (McClain & Hardy, 2010; Brun *et al.*, 2016). Patterns described here using a trait-based approach may also help to predict the potential effects that increasing anthropic activities may have on the deep-sea hydroid fauna (Bremner, 2008; Coro *et al.*, 2016). Substrate use, for example, may be affected by reduced availability of hard substrates through deep-sea mining or bottom trawling fishing activities (Puig *et al.*, 2012; Vanreusel *et al.*, 2016; Gollner *et al.*, 2017; Jones *et al.*, 2017), and climate change may cause declines in particulate organic matter on deep seafloor (Sweetman *et al.*, 2017) – aspects that may have enormous impacts on hydroids' distribution patterns.

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Figures

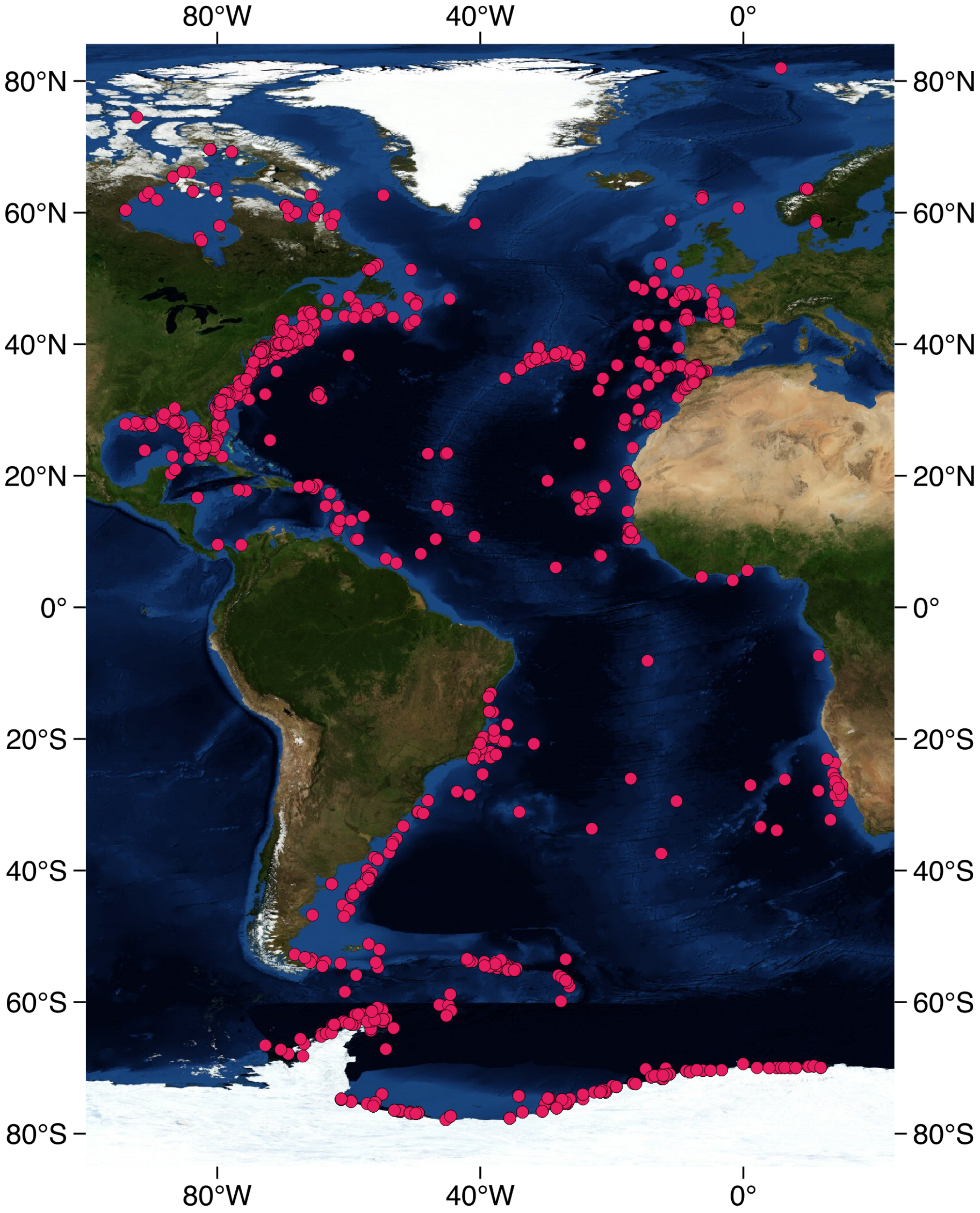

Figure 1. Geographic distribution of the material studied. The points may contain more than one species record.

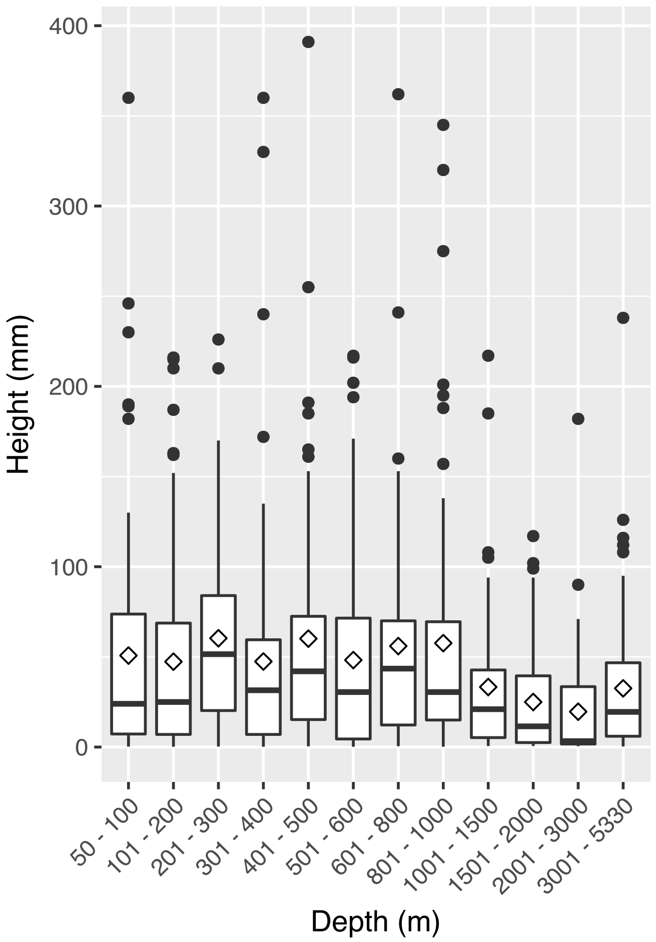

Figure 2. Variation in height of the specimens along depth strata in the Atlantic Ocean. Boxplots summarize the interquartile range (boxes), the largest and smallest observations within a maximum of 1.5 times the interquartile range (whiskers), outliers (points), medians (horizontal lines inside the boxes), and averages (diamonds).

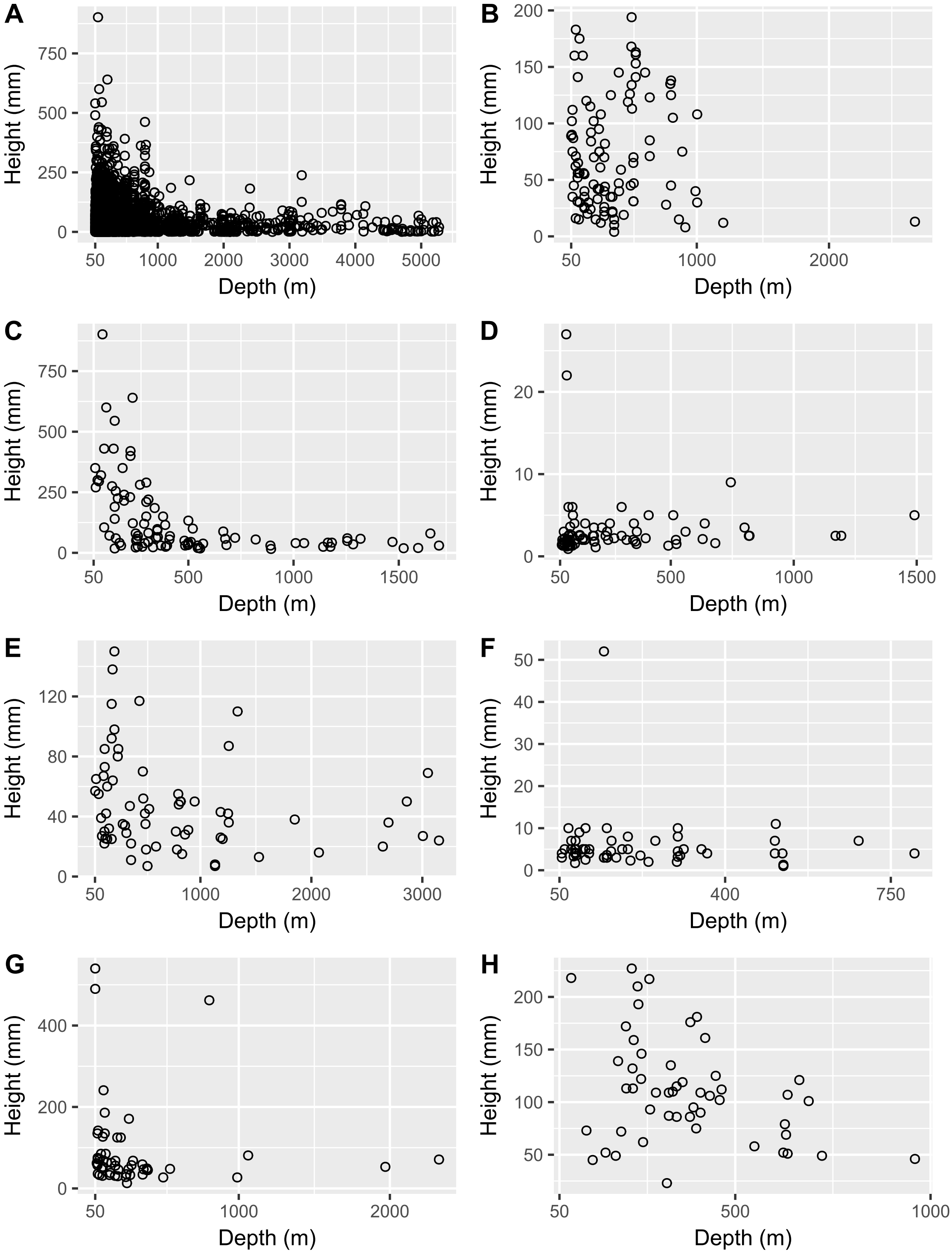

Figure 3. Relationship between height and depth for all studied specimens (**A**), and specific relationships for the specimens of *Sertularella gayi* (**B**), *Lytocarpia myriophyllum* (**C**), *Modeeria rotunda* (**D**), *Acryptolaria conferta* (**E**), *Campanularia hincksii* (**F**), *Nemertesia antennina* (**G**), and *Billardia subrufa* (**H**).

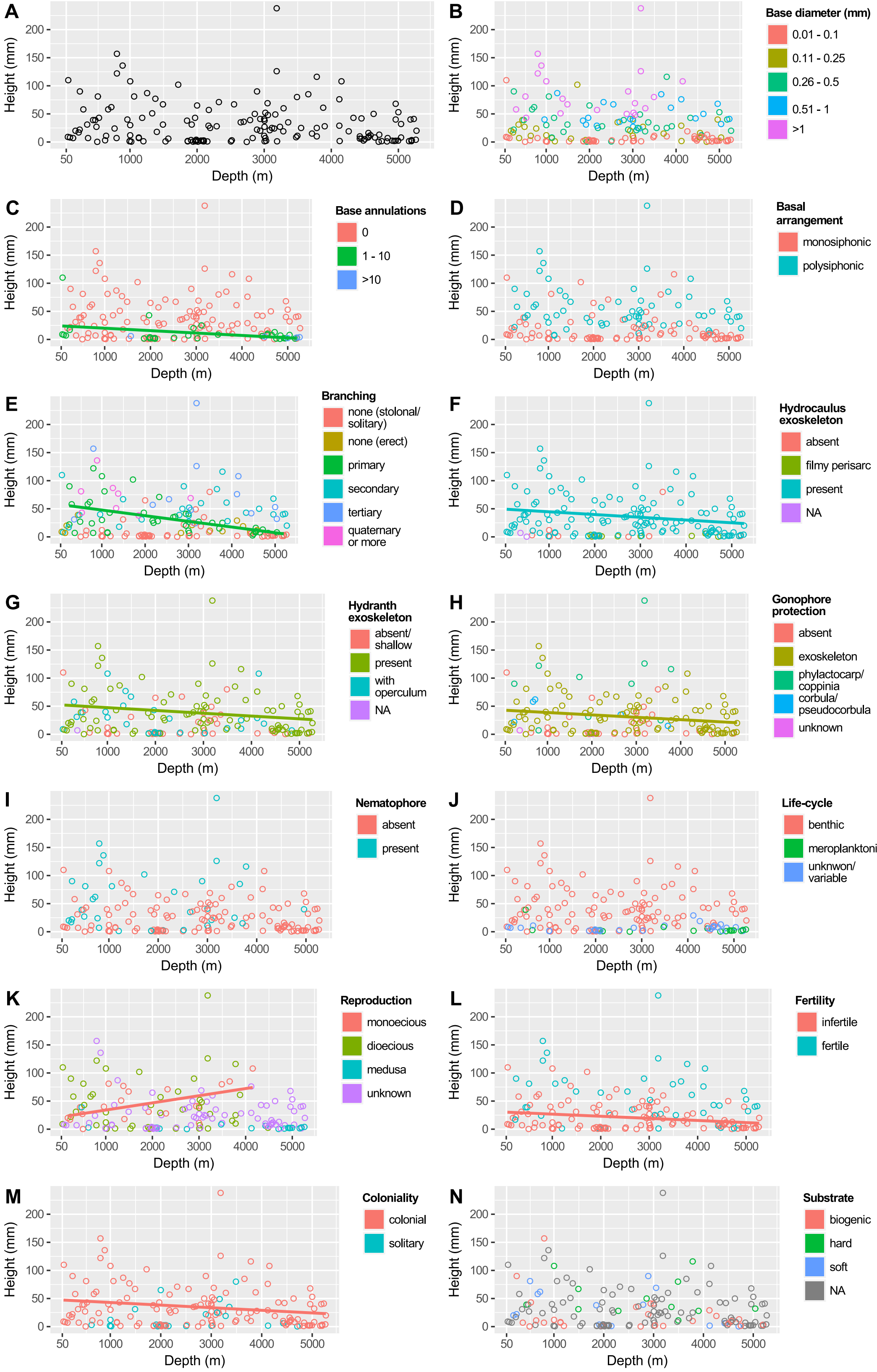

Figure 4. Relationship between height of the specimens and depth in the Atlantic Ocean, for the entire dataset (**A**), and divided by trait categories marked by different colors (**B – N**). Data was standardized for equal sampling across depths. Regression lines were plotted only for significant relationships.

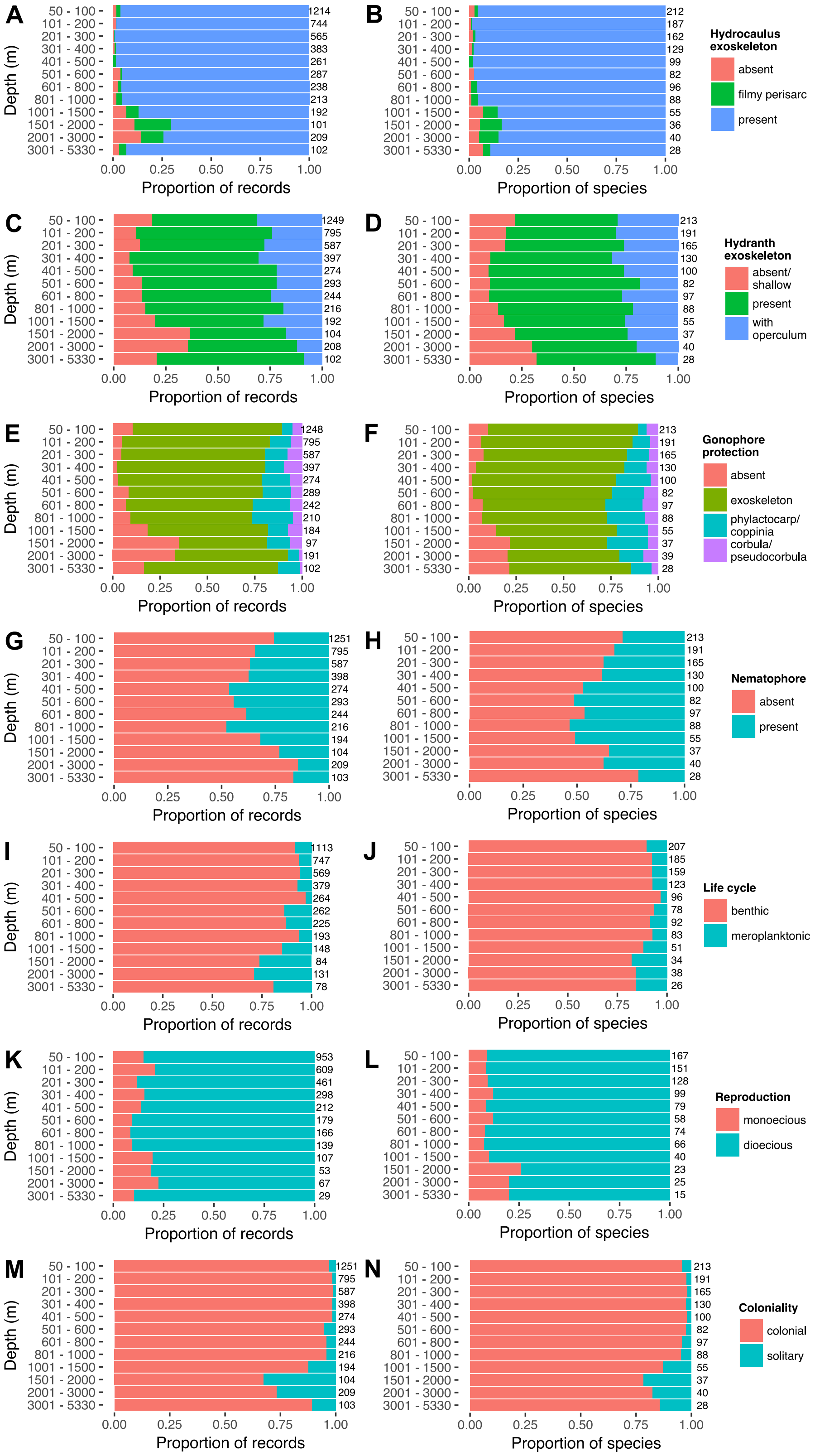

Figure 5. Variation in the proportion of records (left column: **A**, **C**, **E**, **G**, **I**, **K**, **M**) and species (right column: **B**, **D**, **F**, **H**, **J**, **L**, **N**) for each trait category along depth strata in the Atlantic Ocean, for those traits considered to be invariable within species. Numbers of samples used per depth stratum are shown on the right of each bar. Only records whose trait information could be collected were used in the analysis.

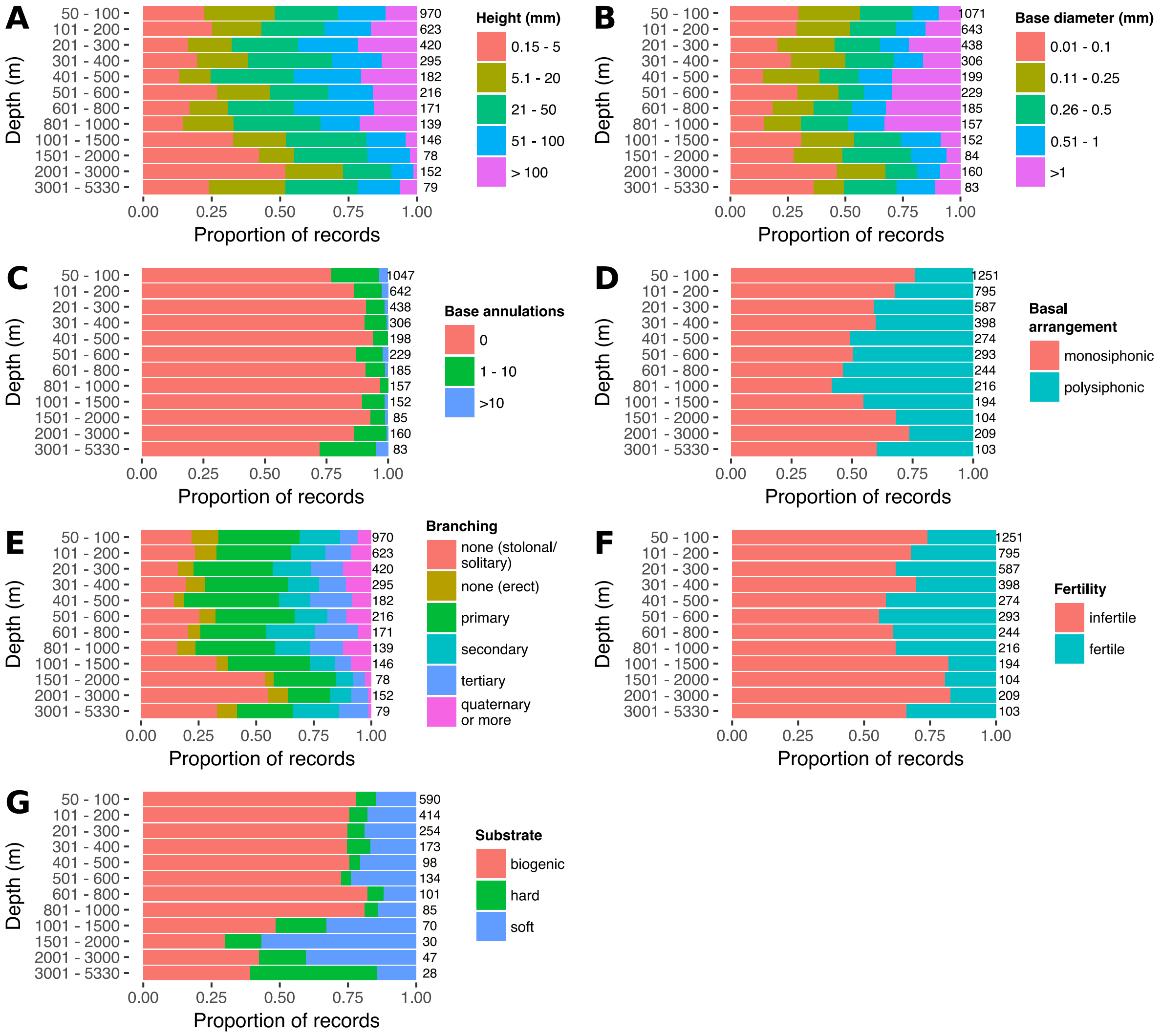

Figure 6. Variation in proportion of records for each trait category along depth ranges in the Atlantic Ocean, for those traits considered to be variable within species. Numbers of samples used per depth stratum are shown on the right of each bar. Only records whose trait information could be collected were used in the analysis.

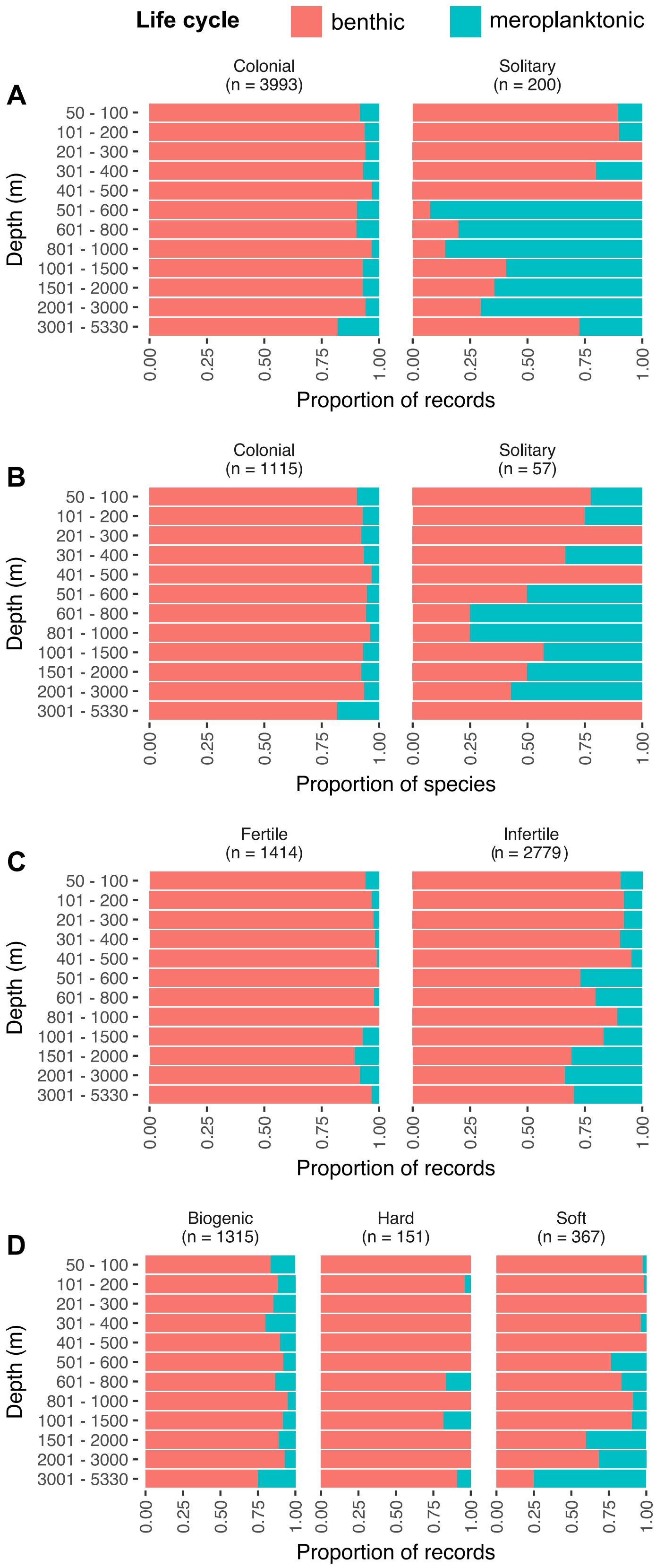

Figure 7. Life-cycle variation across depth strata in the Atlantic Ocean according to the categories of coloniality (**A**, **B**), fertility I, and substrate use (**D**), in proportion of records (**A**, **C**, **D**) and species (**B**). Numbers of samples considered per trait category are shown on top of the chart. Only records whose trait information could be collected were used.

Tables

Table 1. Functional traits and their respective categories used in the analyses. Traits related to species identity (*i.e.*, invariable among its specimens) are indicated by asterisk (*).

Traits and categories
Height of the specimen
0.15 – 5 mm
5.1 – 20 mm
21 – 50 mm
51 – 100 mm
> 100 mm
Diameter at the base of the specimen
0.01 – 0.1 mm
0.11 – 0.25 mm
0.26 – 0.5 mm
0.51 – 1 mm
> 1 mm
Number of annulations at the base of the specimen
zero
1 to 10
> 10
Basal arrangement
monosiphonic
polysiphonic
Orders of branching
stolonal / solitary
erect, unbranched
erect, with primary branching
erect, with secondary branching
erect, with tertiary branching
erect, with quaternary branching or more
Hydrocaulus exoskeleton (*)
absent
filmy perisarc
present
Hydranth exoskeleton (*)
absent / shallow
present
with operculum
Gonophore protection (*)
absent
enveloped by exoskeleton

Traits and categories
phylactocarp / coppinia
corbula / pseudocorbula
Nematophore (*)
absent
present
Life cycle (*)
benthic
meroplanktonic
unknown / variable
Sexual reproduction (*)
monoecious
dioecious
variable
unknown
medusa
Fertility
fertile
infertile
Coloniality (*)
colonial
solitary
Substrate
biogenic
hard (abiogenic)
soft

Table 2. Results of pairwise comparisons testing differences in the height of the specimens between depth strata. Significant differences in bold ($p \leq 0.05$).

Comparison – depth ranges (m)	**stat**	**p-value**
50 – 100 - 101 – 200	0.3454	0.7298
50 – 100 - 201 – 300	-1.008	0.3136
50 – 100 - 301 – 400	0.3146	0.753
50 – 100 - 401 – 500	-0.8899	0.3735
50 – 100 - 501 – 600	0.2564	0.7976
50 – 100 - 601 – 800	-0.5238	0.6004
50 – 100 - 801 – 1000	-0.6299	0.5288
50 – 100 - 1001 – 1500	**1.979**	**0.04783**
50 – 100 - 1501 – 2000	**3.066**	**0.002169**
50 – 100 - 2001 – 3000	**3.654**	**0.000258**
50 – 100 - 3001 – 5330	**2.062**	**0.03922**
101 – 200 - 201 – 300	-1.488	0.1369
101 – 200 - 301 – 400	-0.01099	0.9912
101 – 200 - 401 – 500	-1.3	0.1937
101 – 200 - 501 – 600	-0.09776	0.9221
101 – 200 - 601 – 800	-0.9348	0.3499
101 – 200 - 801 – 1000	-1.005	0.3149

Comparison – depth ranges (m)	stat	p-value
101 – 200 - 1001 – 1500	1.774	0.076
101 – 200 - 1501 – 2000	**3.012**	**0.002592**
101 – 200 - 2001 – 3000	**3.678**	**0.0002349**
101 – 200 - 3001 – 5330	1.867	0.06184
201 – 300 - 301 – 400	1.366	0.172
201 – 300 - 401 – 500	0.02247	0.9821
201 – 300 - 501 – 600	1.393	0.1636
201 – 300 - 601 – 800	0.4943	0.6211
201 – 300 - 801 – 1000	0.2769	0.7819
201 – 300 - 1001 – 1500	**3.549**	**0.0003865**
201 – 300 - 1501 – 2000	**4.91**	**9.127e-07**
201 – 300 - 2001 – 3000	**5.516**	**3.476e-08**
201 – 300 - 3001 – 5330	**3.641**	**0.000272**
301 – 400 - 401 – 500	-1.212	0.2257
301 – 400 - 501 – 600	-0.07997	0.9363
301 – 400 - 601 – 800	-0.8614	0.389
301 – 400 - 801 – 1000	-0.9391	0.3477
301 – 400 - 1001 – 1500	1.63	0.1031
301 – 400 - 1501 – 2000	**2.727**	**0.006387**
301 – 400 - 2001 – 3000	**3.337**	**0.0008482**
301 – 400 - 3001 – 5330	1.715	0.08638
401 – 500 - 501 – 600	1.214	0.2246
401 – 500 - 601 – 800	0.4182	0.6758
401 – 500 - 801 – 1000	0.2319	0.8166
401 – 500 - 1001 – 1500	**3.029**	**0.002454**
401 – 500 - 1501 – 2000	**4.134**	**3.559e-05**
401 – 500 - 2001 – 3000	**4.682**	**2.847e-06**
401 – 500 - 3001 – 5330	**3.109**	**0.001876**
501 – 600 - 601 – 800	-0.8425	0.3995
501 – 600 - 801 – 1000	-0.9216	0.3567
501 – 600 - 1001 – 1500	1.894	0.05823
501 – 600 - 1501 – 2000	**3.143**	**0.001671**
501 – 600 - 2001 – 3000	**3.807**	**0.0001407**
501 – 600 - 3001 – 5330	**1.987**	**0.0469**
601 – 800 - 801 – 1000	-0.1585	0.874
601 – 800 - 1001 – 1500	**2.781**	**0.005413**
601 – 800 - 1501 – 2000	**4.005**	**6.189e-05**
601 – 800 - 2001 – 3000	**4.61**	**4.035e-06**
601 – 800 - 3001 – 5330	**2.869**	**0.004114**
801 – 1000 - 1001 – 1500	**2.625**	**0.008668**
801 – 1000 - 1501 – 2000	**3.663**	**0.0002498**
801 – 1000 - 2001 – 3000	**4.201**	**2.662e-05**
801 – 1000 - 3001 – 5330	**2.703**	**0.006881**
1001 – 1500 - 1501 – 2000	1.506	0.132
1001 – 1500 - 2001 – 3000	**2.449**	**0.01432**
1001 – 1500 - 3001 – 5330	0.1188	0.9054
1501 – 2000 - 2001 – 3000	1.183	0.2366
1501 – 2000 - 3001 – 5330	-1.374	0.1695
2001 – 3000 - 3001 – 5330	**-2.322**	**0.02021**

Table 3. Results of the linear regression analyses testing for relationships between height of the specimens and depth, alternatively considering height regardless of other traits and height regarding each trait category. Significant relationships in bold ($p \leq 0.05$).

Trait	**R^2**	p-value
Height (all)	0.02116	0.06729
Base diameter (mm)		
0.01 – 0.1	0.03198	0.1792

Trait	**R^2**	**p-value**
0.11 – 0.25	0.008083	0.6556
0.26 – 0.5	0.01928	0.4486
0.51 – 1	0.002656	0.8244
> 1	0.002221	0.8393
Base annulations		
0	0.001054	0.7225
1 – 10	**0.1408**	**0.03434**
> 10	0.6252	0.1112
Basal arrangement		
monosiphonic	0.02616	0.1173
polysiphonic	0.02469	0.215
Branching		
none (stolonal/solitary)	0.0001514	0.9276
none (erect)	0.01524	0.7023
primary	**0.2796**	**0.0002673**
secondary	0.006531	0.6947
tertiary	0.02509	0.6053
quaternary or more	0.04083	0.6313
Hydrocaulus exoskeleton		
absent	0.06867	0.4106
filmy perisarc	0.0263	0.6544
present	**0.04241**	**0.01698**
Hydranth exoskeleton		
absent/shallow	0.02096	0.3792
present	**0.04207**	**0.04984**
with operculum	0.03688	0.3372
Gonophore protection		
absent	0.01269	0.526
exoskeleton	**0.05218**	**0.01796**
phylactocarp/coppinia	0.08012	0.399
corbula/pseudocorbula	0.3047	0.3347
Nematophore		
absent	0.0112	0.2382
present	0.005643	0.6778
Life-cycle		
benthic	0.001392	0.7015
meroplanktonic	0.1486	0.0764
unknown/variable	0.05461	0.2224
Sexual reproduction		
monoecious	**0.2541**	**0.0198**
dioecious	0.0002332	0.9216
medusa	0.1486	0.0764
Fertility		
infertile	**0.05724**	**0.01035**
fertile	0.03583	0.213
Coloniality		
colonial	**0.03872**	**0.02373**
solitary	0.05162	0.2544
Substrate		
biogenic	0.08122	0.1496
hard	0.02301	0.6379
soft	0.1284	0.2085

Table 4. Pearson's Chi-square test results for differences in proportion of trait categories with depth. Significant results in bold (p ≤ 0.05).

	Records			**Species**		
Traits	**Pearson's Chi-Square**	**df**	**p-value**	**Pearson's Chi-Square**	**df**	**p-value**
Hydrocaulus exoskeleton	**437.15**	**22**	**< 0.0001**	**56.241**	**22**	**< 0.0001**
Hydranth exoskeleton	**231.73**	**22**	**< 0.0001**	**43.749**	**22**	**0.0038**
Gonophore protection	**423.6**	**33**	**< 0.0001**	**76.493**	**33**	**0.008**
Nematophore	**152.91**	**11**	**< 0.0001**	**38.134**	**11**	**< 0.0001**
Life-cycle	**148.94**	**11**	**< 0.0001**	14.002	11	0.2329
Sexual reproduction	**38.254**	**11**	**< 0.0001**	12.857	11	0.3027
Coloniality	**487.99**	**11**	**< 0.0001**	**62.944**	**11**	**0.0002**
Height	**260.03**	**44**	**< 0.0001**	–	–	–
Base diameter	**270.97**	**44**	**< 0.0001**	–	–	–
Base annulations	**136.84**	**22**	**< 0.0001**	–	–	–
Basal arrangement	**235.45**	**11**	**< 0.0001**	–	–	–
Branching	**271.24**	**55**	**< 0.0001**	–	–	–
Fertility	**119.08**	**11**	**< 0.0001**	–	–	–
Substrate	**159.44**	**22**	**< 0.0001**	–	–	–

Table 5. Post-hoc z-test on the adjusted Pearson residuals results for the hydrocaulus exoskeleton trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.19695).

	Hydrocaulus exoskeleton – records		
Depth (m)	**absent**	**filmy perisarc**	**present**
50 - 100	-2.3346	-0.6758	2.1741
101 - 200	-2.0297	**-4.1513**	**4.4032**
201 - 300	**-3.2556**	**-3.3930**	**4.7599**
301 - 400	-2.2933	-2.1568	3.1884
401 - 500	-2.6927	-0.9391	2.6201
501 - 600	1.4240	-1.9446	0.3359
601 - 800	-0.0296	-0.7408	0.5439
801 - 1000	-0.6378	0.4124	0.1730
1001 - 1500	**3.7910**	**3.5702**	**-5.2742**
1501 - 2000	**5.3775**	**10.9133**	**-11.6061**
2001 - 3000	**11.0840**	**8.7992**	**-14.2644**
3001 - 5330	0.2532	1.0198	-0.9033

Table 6. Post-hoc z-test on the adjusted Pearson residuals results for the hydrocaulus exoskeleton trait comparison based on species. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.19695).

	Hydrocaulus exoskeleton – species		
Depth (m)	**absent**	**filmy perisarc**	**present**
50 - 100	0.6588	-0.9517	0.2198
101 - 200	-1.1640	-1.7548	2.0919
201 - 300	-0.3451	-0.9763	0.9494
301 - 400	-0.5488	-1.2255	1.2737
401 - 500	-1.5658	-0.1980	1.2532
501 - 600	0.1367	-1.4409	0.9431
601 - 800	-0.8186	0.5568	0.1786
801 - 1000	-0.7185	0.7155	-0.0070
1001 - 1500	2.5986	2.5112	**-3.6551**
1501 - 2000	1.3761	**3.5727**	**-3.5544**
2001 - 3000	1.2107	**3.2963**	**-3.2376**
3001 - 5330	1.7857	0.4512	-1.5918

Table 7. Post-hoc z-test on the adjusted Pearson residuals results for the hydranth exoskeleton trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.19695).

	Hydranth exoskeleton – records		
Depth (m)	**absent/ shallow**	**present**	**with operculum**
50 - 100	**3.3774**	**-7.3578**	**5.4905**
101 - 200	**-3.9229**	**3.9944**	-1.2478
201 - 300	-2.0939	0.5204	1.1500
301 - 400	**-4.5874**	1.3365	2.2984
401 - 500	-3.0189	**3.5259**	-1.4696
501 - 600	-0.9184	2.0470	-1.5452
601 - 800	-0.8898	1.0035	-0.3930
801 - 1000	-0.1061	2.2617	-2.4607
1001 - 1500	1.6637	-1.9332	0.7988
1501 - 2000	**5.9810**	-2.6515	-1.9723
2001 - 3000	**8.1649**	-1.9196	**-4.6083**
3001 - 5330	1.4252	2.4444	**-3.9365**

Table 8. Post-hoc z-test on the adjusted Pearson residuals results for the hydranth exoskeleton trait comparison based on species. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.19695).

	Hydranth exoskeleton – species		
Depth (m)	**absent/ shallow**	**present**	**with operculum**
50 - 100	2.4574	-2.7204	1.0067
101 - 200	0.5297	-1.4575	1.1941
201 - 300	0.3703	-0.1949	-0.0894
301 - 400	-1.9700	0.1939	1.4215
401 - 500	-1.9893	1.5486	-0.0819
501 - 600	-1.5938	2.7101	-1.7138
601 - 800	-1.8787	1.2983	0.1068
801 - 1000	-0.6245	1.4003	-1.0510
1001 - 1500	0.0780	0.0790	-0.1535
1501 - 2000	0.9497	-0.4517	-0.2835
2001 - 3000	2.4587	-0.9979	-0.9263
3001 - 5330	2.3598	-0.0568	-1.8995

Table 9. Post-hoc z-test on the adjusted Pearson residuals results for the gonophore protection trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.279024).

	Gonophore protection – records			
Depth (m)	**absent**	**exoskeleton**	**phylactocarp/ coppinia**	**corbula/ pseudocorbula**
50 - 100	1.9108	**4.6406**	**-7.1519**	-1.5904
101 - 200	**-4.7089**	2.9346	0.2036	0.0422
201 - 300	**-4.1025**	1.0175	0.9593	1.8438
301 - 400	**-4.8000**	1.9006	-0.5356	2.9894
401 - 500	**-3.6937**	0.7099	2.2070	0.3120
501 - 600	-0.5229	-1.2647	2.4304	-0.1819
601 - 800	-1.1848	-2.6072	**4.5687**	0.3202
801 - 1000	0.1851	**-3.4804**	**5.4362**	-0.8464
1001 - 1500	**4.4692**	**-3.3186**	-0.1300	0.8528
1501 - 2000	**8.9315**	**-6.2927**	0.5674	0.0227
2001 - 3000	**11.6541**	**-4.6406**	-2.2253	-2.6832
3001 - 5330	2.6559	-0.8163	0.3811	-2.1927

Table 10. Post-hoc z-test on the adjusted Pearson residuals results for the gonophore protection trait comparison based on species. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.279024).

	Gonophore protection – species			
Depth (m)	**absent**	**exoskeleton**	**phylactocarp/ coppinia**	**corbula/ pseudocorbula**
50 - 100	1.2699	1.9931	**-3.8726**	0.2691
101 - 200	-0.7455	2.1081	-1.4939	-0.9888
201 - 300	-0.1435	0.7405	-0.5052	-0.5151
301 - 400	-1.9015	1.3846	-0.4327	0.2284
401 - 500	-2.3489	0.6168	1.6482	-0.7707
501 - 600	-1.9599	-0.0460	1.2200	0.6473
601 - 800	-0.3549	-1.9600	2.1099	1.1201
801 - 1000	-0.4783	-1.6478	2.2549	0.4631
1001 - 1500	1.7688	-1.6744	0.8261	-0.0849
1501 - 2000	3.0361	-3.0800	1.6466	-0.0822
2001 - 3000	2.8627	-2.0700	0.0163	0.5409
3001 - 5330	2.5934	-1.1025	-0.3244	-0.4942

Table 11. Post-hoc z-test on the adjusted Pearson residuals results for the nematophore trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.078088).

	Nematophore – records	
Depth (m)	**absent**	**present**
50 - 100	**6.6226**	**-6.6226**
101 - 200	-0.8855	0.8855
201 - 300	-2.0251	2.0251
301 - 400	-1.9138	1.9138
401 - 500	**-4.7965**	**4.7965**
501 - 600	**-4.2262**	**4.2262**
601 - 800	-1.8429	1.8429
801 - 1000	**-4.6577**	**4.6577**
1001 - 1500	0.3508	-0.3508
1501 - 2000	2.2006	-2.2006
2001 - 3000	**5.8977**	**-5.8977**
3001 - 5330	**3.6229**	**-3.6229**

Table 12. Post-hoc z-test on the adjusted Pearson residuals results for the nematophore trait comparison based on species. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.078088).

	Nematophore – species	
Depth (m)	**absent**	**present**
50 - 100	**3.4072**	**-3.4072**
101 - 200	2.0132	-2.0132
201 - 300	0.4000	-0.4000
301 - 400	0.1303	-0.1303
401 - 500	-1.7140	1.7140
501 - 600	-2.3508	2.3508
601 - 800	-1.5579	1.5579
801 - 1000	-2.8789	2.8789
1001 - 1500	-1.8547	1.8547
1501 - 2000	0.4880	-0.4880
2001 - 3000	0.1963	-0.1963
3001 - 5330	1.9273	-1.9273

Table 13. Post-hoc z-test on the adjusted Pearson residuals results for the life-cycle trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.078088).

	Life-cycle – records	
Depth (m)	**benthic**	**meroplanktonic**
50 - 100	0.9304	-0.9304
101 - 200	2.9745	-2.9745
201 - 300	2.9698	-2.9698
301 - 400	1.4243	-1.4243
401 - 500	**3.5563**	**-3.5563**
501 - 600	-2.6728	2.6728
601 - 800	-2.0095	2.0095
801 - 1000	1.4400	-1.4400
1001 - 1500	-2.4637	2.4637
1501 - 2000	**-5.4812**	**5.4812**
2001 - 3000	**-8.0216**	**8.0216**
3001 - 5330	**-3.1243**	**3.1243**

Table 14. Post-hoc z-test on the adjusted Pearson residuals results for the sexual reproduction trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.078088).

	Sexual reproduction – records	
Depth (m)	**monoecious**	**dioecious**
50 - 100	-0.0275	0.0275
101 - 200	**4.3302**	**-4.3302**
201 - 300	-2.0102	2.0102
301 - 400	0.2048	-0.2048
401 - 500	-0.5699	0.5699
501 - 600	-2.1311	2.1311
601 - 800	-2.4415	2.4415
801 - 1000	-1.9147	1.9147
1001 - 1500	1.3520	-1.3520
1501 - 2000	0.7878	-0.7878
2001 - 3000	1.7023	-1.7023
3001 - 5330	-0.7094	0.7094

Table 15. Post-hoc z-test on the adjusted Pearson residuals results for the coloniality trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.078088).

	Coloniality – records	
Depth (m)	**colonial**	**solitary**
50 - 100	**3.3204**	**-3.3204**
101 - 200	**4.8053**	**-4.8053**
201 - 300	**4.6108**	**-4.6108**
301 - 400	**3.2399**	**-3.2399**
401 - 500	2.6880	-2.6880
501 - 600	-0.2290	0.2290
601 - 800	0.5555	-0.5555
801 - 1000	0.4731	-0.4731
1001 - 1500	**-4.9909**	**4.9909**
1501 - 2000	**-13.3824**	**13.3824**
2001 - 3000	**-15.1285**	**15.1285**
3001 - 5330	-2.7914	2.7914

Table 16. Post-hoc z-test on the adjusted Pearson residuals results for the coloniality trait comparison based on species. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.078088).

	Coloniality – species	
Depth (m)	**colonial**	**solitary**
50 - 100	0.3233	-0.3233
101 - 200	1.8253	-1.8253
201 - 300	1.8566	-1.8566
301 - 400	1.3411	-1.3411
401 - 500	1.3129	-1.3129
501 - 600	0.9841	-0.9841
601 - 800	0.2562	-0.2562
801 - 1000	0.0480	-0.0480
1001 - 1500	-2.9114	2.9114
1501 - 2000	**-4.9790**	**4.9790**
2001 - 3000	**-3.9247**	**3.9247**
3001 - 5330	-2.4500	2.4500

Table 17. Post-hoc z-test on the adjusted Pearson residuals results for the height trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.341479).

	Height (mm) – records				
Depth (m)	**0.15 – 5**	**5.1 – 20**	**21 – 50**	**51 – 100**	**>100**
50 - 100	-0.9915	**5.5137**	-1.4072	-0.5573	-2.7613
101 - 200	1.2339	-1.3129	-1.0433	-0.8264	2.2153
201 - 300	**-3.5565**	-2.1507	-0.2341	2.0823	**4.7839**
301 - 400	-1.5486	-0.5556	2.5379	-0.0188	-0.6085
401 - 500	-3.3175	-2.8964	1.7573	2.4234	2.5000
501 - 600	1.2723	-0.1653	-1.2139	-0.7120	0.9363
601 - 800	-2.0137	-1.9638	-0.2397	**3.9208**	0.6675
801 - 1000	-2.5385	-0.3540	1.9259	-1.1330	2.3554
1001 - 1500	2.7942	-0.2168	1.3457	-1.1640	**-3.5338**
1501 - 2000	**4.0144**	-1.5799	0.4502	-0.6095	-2.9541
2001 - 3000	**8.5486**	0.3708	-2.0406	-3.3179	**-4.6223**
3001 - 5330	0.1581	1.7954	0.3822	-0.6590	-1.9995

Table 18. Post-hoc z-test on the adjusted Pearson residuals results for the base diameter trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.341479).

	Base diameter (mm) – records				
Depth (m)	**0.01 – 0.1**	**0.11 – 0.25**	**0.26 – 0.5**	**0.51 – 1**	**> 1**
50 - 100	2.2931	3.2298	2.8090	-1.8090	**-7.7473**
101 - 200	1.2260	-0.0710	-0.0055	-0.1358	-1.2447
201 - 300	-3.2277	0.8467	-0.2423	-0.1353	3.2463
301 - 400	-0.2080	0.1077	0.3852	-0.0080	-0.2797
401 - 500	**-4.2166**	0.4608	-1.0806	0.7881	**4.9260**
501 - 600	0.8031	-1.9875	**-3.5703**	-0.2494	**5.3262**
601 - 800	-2.7031	-1.7970	-1.1544	0.7674	**5.7765**
801 - 1000	**-3.5560**	-2.2289	0.0997	1.2142	**5.5356**
1001 - 1500	1.1190	-0.0757	0.1020	1.6398	-2.8080
1501 - 2000	0.0846	-0.4062	2.2433	0.7548	-2.7108
2001 - 3000	**5.6155**	-0.6212	-2.0405	-1.0696	-2.8161
3001 - 5330	1.9034	-2.1862	0.6491	1.1345	-1.4921

Table 19. Post-hoc z-test on the adjusted Pearson residuals results for the base annulation trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.19695).

	Base annulations – records		
Depth (m)	**0**	**1 – 10**	**> 10**
50 - 100	**-9.5379**	**8.3697**	**4.1691**
101 - 200	0.5247	-0.9896	0.9669
201 - 300	**3.4727**	-3.1909	-1.1936
301 - 400	2.5469	-1.8953	-1.8811
401 - 500	**3.4257**	-2.7210	-2.1420
501 - 600	0.5643	-0.6224	0.0408
601 - 800	2.0603	-1.7528	-1.0253
801 - 1000	**4.0827**	**-3.5332**	-1.8962
1001 - 1500	1.3788	-1.1576	-0.7211
1501 - 2000	1.9435	-1.8054	-0.6239
2001 - 3000	0.2276	0.3567	-1.3572
3001 - 5330	**-3.5056**	3.0019	1.7004

Table 20. Post-hoc z-test on the adjusted Pearson residuals results for the basal arrangement trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.078088).

	Basal arrangement – records	
Depth (m)	**monosiphonic**	**polysiphonic**
50 - 100	**10.9233**	**-10.9233**
101 - 200	2.8734	-2.8734
201 - 300	-2.2848	2.2848
301 - 400	-1.4694	1.4694
401 - 500	**-4.9266**	**4.9266**
501 - 600	**-4.7755**	**4.7755**
601 - 800	**-5.6177**	**5.6177**
801 - 1000	**-6.7183**	**6.7183**
1001 - 1500	-2.5244	2.5244
1501 - 2000	1.0849	-1.0849
2001 - 3000	**3.2168**	**-3.2168**
3001 - 5330	-0.6388	0.6388

Table 21. Post-hoc z-test on the adjusted Pearson residuals results for the branching trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.391763).

	Branching – records					
Depth (m)	**none (stolonal/ solitary)**	**none (erect)**	**primary**	**secondary**	**tertiary**	**quaternary or more**
50 - 100	-1.4872	**4.1480**	1.4069	2.0847	**-3.6605**	-2.9885
101 - 200	-0.0560	0.5546	-0.5048	-0.5363	0.2153	0.8621
201 - 300	**-3.9743**	-1.3114	0.3878	0.7227	2.2612	3.3576
301 - 400	-1.8414	-0.0710	0.9452	-0.9492	0.5961	1.8997
401 - 500	-3.0631	-2.0727	2.2795	-0.6648	3.2549	0.1337
501 - 600	0.6358	-0.8890	0.2608	-0.4697	-1.2205	1.4941
601 - 800	-1.0139	-1.5904	-1.3626	2.0700	**3.4007**	-1.0553
801 - 1000	-2.2232	-0.2885	0.2764	-0.1208	1.3768	1.8871
1001 - 1500	2.6701	-1.6706	0.5672	-1.5404	-1.5823	0.4208
1501 - 2000	**6.3380**	-1.5111	-1.2355	-1.9215	-1.6395	-1.7854
2001 - 3000	**9.3660**	-0.0148	**-4.0157**	-2.1827	-1.4587	-3.1008
3001 - 5330	1.9519	0.0884	-1.7909	1.1890	0.5281	-2.2278

Table 22. Post-hoc z-test on the adjusted Pearson residuals results for the fertility trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.078088).

	Fertility – records	
Depth (m)	**infertile**	**fertile**
50 - 100	**4.9238**	**-4.9238**
101 - 200	-0.4590	0.4590
201 - 300	**-3.6129**	**3.6129**
301 - 400	0.6114	-0.6114
401 - 500	**-3.7068**	**3.7068**
501 - 600	**-4.8930**	**4.8930**
601 - 800	-2.5635	2.5635
801 - 1000	-2.0896	2.0896
1001 - 1500	**4.1255**	**-4.1255**
1501 - 2000	2.7266	-2.7266
2001 - 3000	**4.5492**	**-4.5492**
3001 - 5330	-0.5452	0.5452

Table 23. Post-hoc z-test on the adjusted Pearson residuals results for the substrate use trait comparison based on records. Values higher (positive) and lower (negative) than expected, for a 0.05 significance level, in bold (critical z-value = -3.19695).

		Substrate – records	
Depth (m)	**biogenic**	**hard**	**soft**
50 - 100	2.7984	-0.4270	-2.8765
101 - 200	1.0786	-1.1311	-0.4407
201 - 300	0.4965	-0.9860	0.1187
301 - 400	0.3269	0.4165	-0.6583
401 - 500	0.4582	-1.4236	0.4644
501 - 600	-0.3067	-1.8364	1.6167
601 - 800	2.0237	-0.7339	-1.7864
801 - 1000	1.6350	-1.1028	-1.0909
1001 - 1500	**-4.8142**	**3.3914**	3.1125
1501 - 2000	**-5.4425**	1.1235	**5.3919**
2001 - 3000	**-4.8679**	2.3631	**3.8840**
3001 - 5330	**-4.1339**	**7.6394**	-0.5941

Supplementary Material

Table S1. Functional traits considered in the study for the 606 identified taxa. * Taxa without hydrocaulus or in which this information was unavailable due to damage are regarded as “NA”. ** Taxa with unavailable information due to damage are regarded as “NA”.

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Abietinaria abietina (Linnaeus, 1758)	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Abietinaria filicula (Ellis & Solander, 1786)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Abietinella operculata (Jäderholm, 1903)	benthic	species	unknown	family (variable)	colonial	present	present, with operculum	coppinia	present
Acaulis primarius Stimpson, 1854	benthic	species	dioecious	species	solitary	filmy perisarc	absent	absent	absent
Acaulis cf. *rosae* (Verrill, 1878)	benthic	family (all known)	dioecious	family (all known)	solitary	filmy perisarc	absent	absent	absent
Acauloides ilonae (Brinckmann-Voss, 1966)	benthic	species	dioecious	species	solitary	absent	absent	absent	absent
?*Acauloides* sp.	benthic	family (all known)	dioecious	family (all known)	solitary	filmy perisarc	absent	absent	absent
Acryptolaria abies (Allman, 1877)	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Acryptolaria conferta (Allman, 1877)	benthic	species	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Acryptolaria crassicaulis (Allman, 1888)	benthic	species	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Acryptolaria elegans (Allman, 1877)	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Acryptolaria longitheca (Allman, 1877)	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Acryptolaria operculata Stepanjants, 1979	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Acryptolaria ?*operculata* Stepanjants, 1979	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Acryptolaria rectangularis (Jarvis, 1922)	benthic	family (all known)	unknown	family (variable)	colonial	present	present	coppinia	absent
Acryptolaria sp.	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
?*Acryptolaria* sp.	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
Aglaophenia acacia Allman, 1883	benthic	species	dioecious	species	colonial	present	present	corbula	present
Aglaophenia dubia Nutting, 1900	benthic	species	dioecious	species	colonial	present	present	corbula	present
Aglaophenia ?dubia Nutting, 1900	benthic	genus (mostly)	dioecious	species	colonial	present	present	corbula	present
Aglaophenia insignis Fewkes, 1881	benthic	genus (mostly)	dioecious	genus (all known)	colonial	present	present	corbula	present
Aglaophenia kirchenpaueri (Heller, 1868)	benthic	genus (mostly)	dioecious	species	colonial	present	present	corbula	present
Aglaophenia latecarinata Allman, 1877	benthic	species	dioecious	species	colonial	present	present	corbula	present
Aglaophenia lophocarpa Allman, 1877	benthic	genus (mostly)	dioecious	species	colonial	present	present	corbula	present
Aglaophenia octodonta (Heller, 1868)	benthic	genus (mostly)	dioecious	species	colonial	present	present	corbula	present
Aglaophenia rhynchocarpa Allman, 1877	benthic	genus (mostly)	dioecious	species	colonial	present	present	corbula	present
Aglaophenia sp.	benthic	genus (mostly)	dioecious	genus (all known)	colonial	present	present	corbula	present
Aglaophenia svobodai Ansin Agís, Ramil & Vervoort, 2001	benthic	genus (mostly)	dioecious	species	colonial	present	present	corbula	present
Aglaophenia trifida L. Agassiz, 1862	benthic	genus (mostly)	dioecious	genus (all known)	colonial	present	present	corbula	present
Aglaophenia tubiformis Marktanner-Turneretscher, 1890	benthic	genus (mostly)	dioecious	species	colonial	present	present	corbula	present
Aglaophenia tubulifera (Hincks, 1861)	benthic	genus (mostly)	dioecious	species	colonial	present	present	corbula	present
Aglaophenia ?tubulifera (Hincks, 1861)	benthic	genus (mostly)	dioecious	species	colonial	present	present	corbula	present
Aglaopheniidae indet.	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Aglaophenopsis cartieri (Bedot, 1921)	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	phylactocarp	present
Aglaophenopsis cornuta (Verril, 1879)	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	phylactocarp	present
Aglaophenopsis distans Nutting, 1900	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	phylactocarp	present
Aglaophenopsis hirsuta Fewkes, 1881	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	phylactocarp	present
Aglaophenopsis verrilli Nutting, 1900	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	phylactocarp	present

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Amphisbetia operculata (Linnaeus, 1758)	benthic with swimming gonophores	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Antarctoscyphus asymmetricus Peña Cantero, García-Carrascosa & Vervoort, 1997	benthic	genus (all known)	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Antarctoscyphus elongatus (Jäderholm, 1904)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Antarctoscyphus fragilis Peña Cantero, Svoboda & Vervoort, 1999	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Antarctoscyphus grandis (Blanco, 1977)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Antarctoscyphus gruzovi (Stepanjants, 1979)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Antarctoscyphus spiralis (Hickson & Gravely, 1907)	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Antennella confusa Ansin Agís, Ramil & Vervoort, 2001	benthic	family (all known)	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Antennella gracilis Allman, 1877	benthic	family (all known)	monoecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Antennella secundaria (Gmelin, 1791)	benthic	species	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Antennella siliquosa (Hincks, 1877)	benthic	family (all known)	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Antennella sp.	benthic	family (all known)	monoecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Anthoathecata indet. 1	unknown	–	unknown	–	solitary	filmy perisarc	absent	absent	absent
Anthoathecata indet. 2	unknown	–	unknown	–	colonial	present	absent	absent	absent
Anthoathecata indet. 3	unknown	–	unknown	–	solitary	absent	absent	absent	absent
Anthoathecata indet. 4	unknown	–	unknown	–	solitary	NA	absent	unknown	absent
Anthohebella communis (Calder, 1991)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Bedotella armata (Pictet & Bedot, 1900)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	present
Billardia subrufa (Jäderholm, 1904)	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Bimeria sp.	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Bimeria vestita Wright, 1859	benthic	species	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Bougainvillia ?carolinensis (McCrady, 1859)	meroplanktonic	genus (mostly)	medusa	genus (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Bougainvillia muscus (Allman, 1863)	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Bougainvillia sp.	meroplanktonic	genus (mostly)	medusa	genus (mostly)	colonial	present	present	unknown	absent
Bougainvilliidae indet. 1	variable	family (variable)	unknown	family (variable)	colonial	present	present	unknown	absent
Bougainvilliidae indet. 2	variable	family (variable)	unknown	family (variable)	solitary	present	present	unknown	absent
Bougainvilliidae indet. 3	variable	family (variable)	unknown	family (variable)	colonial	present	present	unknown	absent
Bouillonia cornucopia sensu Svoboda et al., 2006 (= *B. cornucopia* sensu Petersen, 1990)	benthic	species	unknown	genus (all known)	solitary	present	absent	absent	absent
Bouillonia denhartogi Svoboda, Stepanjants & Ljubenkov, 2006	benthic	species	unknown	genus (all known)	solitary	present	absent	absent	absent
Bouillonia sp.	benthic	genus (all known)	unknown	genus (all known)	solitary	present	absent	absent	absent
Calvinia mirabilis Nutting, 1900	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	present
Calycella syringa (Linnaeus, 1767)	benthic	species	monoecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Campanularia antarctica Ritchie, 1913	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Campanularia crenata Allman, 1876	benthic	species	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Campanularia groenlandica Levinsen, 1893	benthic	species	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Campanularia hicksoni Totton, 1930	benthic	species	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Campanularia hincksii Alder, 1856	benthic	species	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Campanularia lennoxensis Jäderholm, 1903	benthic	species	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Campanularia macroscypha Allman, 1877	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Campanularia sp.	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Campanularia volubilis (Linnaeus, 1758)	benthic	species	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Campanulariidae indet.	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Campanulina pumila (Clark, 1875)	benthic	species	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
?*Campanulina* sp.	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Campanulinidae indet.	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Candelabrum phrygium (Fabricius, 1780)	benthic	species	dioecious	species	solitary	absent	absent	absent	absent
Candelabrum serpentarii Segonzac & Vervoort, 1995	benthic	genus (all known)	monoecious	species	solitary	absent	absent	absent	absent
Cirrholovenia tetranema Kramp, 1959	meroplanktonic	species	medusa	species	colonial	present	present, with operculum	enveloped by exoskeleton	present
Cladocarpus boucheti Ramil & Vervoort, 1992	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus carinatus Nutting, 1900	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus compressus Fewkes, 1881	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus dolichotheca Allman, 1877	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus flexilis Verrill, 1885	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus flexuosus Nutting, 1900	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus grandis Nutting, 1900	benthic	genus (all known)	dioecious	species	colonial	present	present	phylactocarp	present
Cladocarpus integer (G. O. Sars, 1874)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus paradiseus Allman, 1877	benthic	genus (all known)	dioecious	species	colonial	present	present	phylactocarp	present
Cladocarpus paraformosus Schuchert, 2000	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus paraventricosus Ramil & Vervoort, 1992	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus pourtalesii Verrill, 1879	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus septatus Nutting, 1900	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
Cladocarpus sigma (Allman, 1877)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus tenuis Clarke, 1879	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Cladocarpus ventricosus Allman, 1877	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Clathrozoella abyssalis Peña Cantero, Vervoort & Watson, 2003	benthic	genus (all known)	unknown	family (all known)	colonial	present	present	enveloped by exoskeleton	present
Clathrozoella medeae Peña Cantero, Vervoort & Watson, 2003	benthic	genus (all known)	unknown	family (all known)	colonial	present	present	enveloped by exoskeleton	present
Clytia arborescens Pictet, 1893	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Clytia gigantea (Hincks, 1866)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Clytia cf. *gracilis* (M. Sars, 1850)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Clytia hemisphaerica (Linnaeus, 1767)	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Clytia cf. *hemisphaerica* (Linnaeus, 1767)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Clytia hummelincki (Leloup, 1935)	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Clytia linearis (Thornely, 1900)	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Clytia macrotheca (Perkins, 1908)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Clytia paulensis (Vanhöffen, 1910)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Clytia sp.	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
?*Clytia* sp.	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Corydendrium parasiticum (Linnaeus, 1767)	benthic	species	dioecious	species	colonial	present	absent	enveloped by exoskeleton	absent
Corydendrium cf. *parasiticum* (Linnaeus, 1767)	benthic	species	dioecious	species	colonial	present	absent	enveloped by exoskeleton	absent
Corymorpha glacialis M. Sars, 1860	benthic	species	dioecious	species	solitary	absent	absent	absent	absent
Corymorpha groenlandica (Allman, 1876)	benthic	species	dioecious	species	solitary	filmy perisarc	absent	absent	absent
Corymorpha microrhiza (Hickson & Gravely, 1907)	benthic	species	dioecious	genus (all known)	solitary	filmy perisarc	absent	absent	absent

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
Corymorpha pendula L. Agassiz, 1862	benthic	species	dioecious	genus (all known)	solitary	filmy perisarc	absent	absent	absent
Corymorpha sp.	unknown	genus (variable)	unknown	family (variable)	solitary	filmy perisarc	absent	absent	absent
Corymorphidae indet.	unknown	family (variable)	unknown	family (variable)	solitary	filmy perisarc	absent	absent	absent
Coryne pusilla Gaertner, 1774	benthic	species	dioecious	species	colonial	present	absent	absent	absent
Coryne ?pusilla Gaertner, 1774	benthic	species	dioecious	species	colonial	present	absent	absent	absent
Corynidae indet.	unknown	family (variable)	unknown	family (variable)	colonial	absent	absent	absent	absent
Cryptolarella abyssicola (Allman, 1888)	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Cryptolaria pectinata (Allman, 1888)	benthic	family (all known)	dioecious	species	colonial	present	present	coppinia	present
Cryptolaria ?pectinata (Allman, 1888)	benthic	family (all known)	unknown	family (variable)	colonial	present	present	coppinia	present
Cuspidella grandis Hincks, 1868	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
?*Cuspidella grandis* Hincks, 1868	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
?*Cuspidella procumbens* Kramp, 1911	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Cuspidella sp.	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Dicoryne conferta (Alder, 1856)	benthic with swimming gonophores	species	dioecious	species	colonial	present	absent	enveloped by exoskeleton	absent
Diphasia attenuata (Hincks, 1866)	benthic	species	dioecious	genus (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Diphasia delagei Billard, 1912	benthic	genus (all known)	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Diphasia digitalis (Busk, 1852)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Diphasia fallax (Johnston, 1847)	benthic	species	variable	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Diphasia margareta (Hassall, 1841)	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Diphasia paarmanni Nutting, 1904	benthic	genus (all known)	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
Diphasia pinastrum (Cuvier, 1830)	benthic	species	dioecious	genus (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Diphasia rosacea (Linnaeus, 1758)	benthic	species	dioecious	genus (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Diphasia sp.	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Diplopteroides grandis (Nutting, 1900)	benthic	family (all known)	unknown	family (variable)	colonial	present	present	phylactocarp	present
Dynamena dalmasi (Versluys, 1899)	benthic	genus (all known)	dioecious	family (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Dynamena disticha (Bosc, 1802)	benthic	species	dioecious	family (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Dynamena quadridentata (Ellis & Solander, 1786)	benthic	species	dioecious	family (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Ectopleura dumortierii (van Beneden, 1844)	meroplanktonic	species	medusa	species	solitary	present	absent	absent	absent
Egmundella fasciculata Fraser, 1942	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	present
Egmundella grandis Fraser, 1943	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	present
Egmundella modesta Millard & Bouillon, 1975	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	present
?*Egmundella producta* (G. O. Sars, 1874)	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	present
Egmundella superba Stechow, 1921	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	present
?*Egmundella superba* Stechow, 1921	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Eudendriidae indet.	benthic	family (all known)	dioecious	family (mostly)	colonial	present	absent	absent	absent
Eudendrium album Nutting, 1896	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium annulatum Norman, 1864	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium arbuscula Wright, 1859	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium capillare Alder, 1856	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium cf. *capillare* Alder, 1856	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	absent	absent	absent
Eudendrium carneum Clarke, 1882	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Eudendrium dispar Agassiz, 1862	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium exiguum Allman, 1877	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	absent	absent	absent
Eudendrium eximium Allman, 1877	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium fruticosum Allman, 1877	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium laxum Allman, 1877	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium rameum (Pallas, 1766)	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium cf. *rameum* (Pallas, 1766)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	absent	absent	absent
Eudendrium ?*rameum* (Pallas, 1766)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	absent	absent	absent
Eudendrium ramosum (Linnaeus, 1758)	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium rugosum Fraser, 1940	benthic	genus (all known)	dioecious	species	colonial	present	absent	absent	absent
Eudendrium sp.	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	absent	absent	absent
Euphysa aurata Forbes, 1848	meroplanktonic	species	medusa	species	solitary	filmy perisarc	absent	absent	absent
Euphysa sp.	meroplanktonic	genus (mostly)	medusa	genus (mostly)	solitary	filmy perisarc	absent	absent	absent
?*Euphysa* sp.	unknown	family (variable)	unknown	family (variable)	solitary	present	present	unknown	absent
Euphysa sp. 2	meroplanktonic	genus (mostly)	medusa	genus (mostly)	solitary	absent	absent	absent	absent
Euphysora ?*bigelowi* Maas, 1905	meroplanktonic	genus (all known)	medusa	genus (all known)	solitary	filmy perisarc	absent	absent	absent
Euphysora sp. 1	meroplanktonic	genus (all known)	medusa	genus (all known)	solitary	filmy perisarc	absent	absent	absent
Euphysora sp. 2	meroplanktonic	genus (all known)	medusa	genus (all known)	solitary	absent	absent	absent	absent
Euphysora sp. 3	meroplanktonic	genus (all known)	medusa	genus (all known)	solitary	NA	absent	absent	absent
Filellum annulatum (Watson, 1973)	benthic	family (all known)	monoecious	genus (mostly)	colonial	NA	present	enveloped by exoskeleton	absent
Filellum antarcticum (Hartlaub, 1904)	benthic	species	monoecious	genus (mostly)	colonial	NA	present	coppinia	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Filellum magnificum Peña Cantero, Svoboda & Vervoort, 2004	benthic	family (all known)	monoecious	genus (mostly)	colonial	NA	present	coppinia	absent
Filellum serpens (Hassall, 1848)	benthic	family (all known)	monoecious	species	colonial	NA	present	coppinia	absent
Filellum ?serpens (Hassall, 1848)	benthic	family (all known)	monoecious	genus (mostly)	colonial	NA	present	enveloped by exoskeleton	absent
Filellum serratum (Clarke, 1879)	benthic	species	monoecious	genus (mostly)	colonial	NA	present	coppinia	absent
Filellum cf. *serratum* (Clarke, 1879)	benthic	family (all known)	monoecious	genus (mostly)	colonial	NA	present	enveloped by exoskeleton	absent
Filellum sp.	benthic	family (all known)	monoecious	genus (mostly)	colonial	NA	present	enveloped by exoskeleton	absent
Filifera indet. 1	unknown	order (variable)	unknown	order (variable)	solitary	present	present	unknown	absent
Filifera indet. 2	unknown	order (variable)	unknown	order (variable)	colonial	NA	absent	unknown	absent
Filifera indet. 3	unknown	order (variable)	unknown	order (variable)	solitary	present	absent	unknown	absent
Filifera indet. 4	unknown	order (variable)	unknown	order (variable)	solitary	present	absent	absent	absent
Filifera indet. 5	unknown	order (variable)	unknown	order (variable)	colonial	present	absent	absent	absent
Filifera indet. 6	unknown	order (variable)	unknown	order (variable)	colonial	absent	absent	absent	absent
Garveia annulata Nutting, 1901	benthic	species	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Garveia arborea (Browne, 1907)	benthic	species	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
Garveia sp.	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	unknown	absent
?*Garveia* sp.	variable	family (variable)	unknown	family (variable)	colonial	present	present	unknown	absent
Gonothyraea loveni (Allman, 1859)	benthic	species	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Grammaria abietina (M. Sars, 1850)	benthic	family (all known)	monoecious	species	colonial	present	present	coppinia	absent
Grammaria immersa Nutting, 1901	benthic	family (all known)	unknown	family (variable)	colonial	present	present	coppinia	absent
Grammaria sp.	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Gymnangium allmani (Marktanner-Turneretscher, 1890)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Gymnangium sinuosum (Fraser, 1925)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Gymnangium sp.	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
?*Gymnangium* sp.	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Gymnangium speciosum (Allman, 1877)	benthic	species	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Gymnogonos sp.	benthic	genus (all known)	dioecious	family (all known)	solitary	filmy perisarc	absent	absent	absent
Haleciidae indet.	benthic	family (mostly)	dioecious	family (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium articulosum Clark, 1875	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium beanii (Johnston, 1838)	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium cf. *beanii* (Johnston, 1838)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium bermudense Congdon, 1907	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium calderi Galea, 2010	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium cf. *lankesterii* (Bourne, 1890)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium curvicaule Lorenz, 1886	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium delicatulum Coughtrey, 1876	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium cf. *delicatulum* Coughtrey, 1876	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium cf. *dichotomum* Allman, 1888	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium dubium Fraser, 1941	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium dyssymetrum Billard, 1929	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium filicula Allman, 1877	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
Halecium fruticosum Fraser, 1943	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium gracile Verrill, 1874	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium groenlandicum Kramp, 1911	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium halecinum (Linnaeus, 1758)	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium ?halecinum (Linnaeus, 1758)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium incertus Naumov & Stepanjants, 1962	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium jaederholmi Vervoort, 1972	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium labrosum Alder, 1859	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium ?labrosum Alder, 1859	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium liouvillei Billard, 1934	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium macrocephalum Allman, 1877	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium minutum Broch, 1903	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium muricatum (Ellis & Solander, 1786)	benthic	species	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium nanum Alder, 1859	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium ovatum Totton, 1930	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium ?ovatum Totton, 1930	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium pallens Jäderholm, 1904	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium profundum Calder & Vervoort, 1998	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium scutum Clark, 1876	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium sessile Norman, 1867	benthic	species	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Halecium sibogae Billard, 1929	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium ?sibogae Billard, 1929	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium sp. 1	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium sp. 2	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium speciosum Nutting, 1901	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium tenellum Hincks, 1861	benthic	species	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium cf. *tenellum* Hincks, 1861	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium tensum Fraser, 1943	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	shallow	enveloped by exoskeleton	absent
Halecium textum Kramp, 1911	benthic	genus (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	absent
Halisiphonia arctica Kramp, 1932	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Halisiphonia sp.	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Halitholus cirratus Hartlaub, 1913	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Halopterididae indet.	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	present
Halopteris alternata (Nutting, 1900)	benthic	family (all known)	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Halopteris catharina (Johnston, 1833)	benthic	family (all known)	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Halopteris clarkei (Nutting, 1900)	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
Halopteris diaphana (Heller, 1868)	benthic	family (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	present
Halopteris geminata (Allman, 1877)	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
Halopteris polymorpha (Billard, 1913)	benthic	species	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Halopteris sp.	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Hebella dyssymetra Billard, 1931	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Hebella plana Ritchie, 1907	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Hebella scandens (Bale, 1888)	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Hebella cf. *scandens* (Bale, 1888)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Hebella sp.	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Hebella venusta (Allman, 1877)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Hincksella cylindrica (Bale, 1888)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
Hincksella formosa (Fewkes, 1881)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
Hippurella annulata Allman, 1877	benthic	genus (all known)	dioecious	family (mostly)	colonial	present	present	phylactocarp	present
Hydractinia arge (Clarke, 1882)	meroplanktonic	species	medusa	species	colonial	absent	absent	absent	absent
Hydractinia cytaeiformis Vervoort, 2006	benthic with eumedusoid	species	dioecious	species	colonial	absent	absent	absent	present
Hydractinia echinata (Fleming, 1828)	benthic	species	dioecious	species	colonial	absent	absent	absent	present
Hydractinia cf. *echinata* (Fleming, 1828)	benthic	species	dioecious	species	colonial	absent	absent	absent	present
Hydractinia ingolfi Kramp, 1932	benthic	species	dioecious	species	colonial	absent	absent	absent	absent
Hydractinia monocarpa Allman, 1876	benthic	species	dioecious	species	colonial	absent	absent	absent	absent
Hydractinia paucispinata Vervoort, 2006	benthic	species	dioecious	species	colonial	absent	absent	absent	absent
Hydractinia ?proboscidea (Hincks, 1868)	variable	genus (variable)	unknown	genus (variable)	colonial	absent	absent	absent	present
Hydractinia sp. 1	variable	genus (variable)	unknown	genus (variable)	colonial	absent	absent	absent	present
Hydractinia sp. 2	variable	genus (variable)	unknown	genus (variable)	colonial	absent	absent	absent	absent
Hydractinia vallini Jäderholm, 1926	benthic	species	dioecious	genus (all known)	colonial	absent	absent	absent	absent
Hydractiniidae indet.	variable	family (variable)	unknown	family (variable)	colonial	absent	absent	absent	absent

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
Hydrallmania falcata (Linnaeus, 1758)	benthic	species	dioecious	family (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Hydrocorella africana Stechow, 1921	benthic	species	dioecious	species	colonial	absent	absent	absent	present
Hydrodendron arboreum (Allman, 1888)	benthic	species	dioecious	family (all known)	colonial	present	shallow	coppinia	present
Hydrozoa indet. 1	unknown	–	unknown	–	colonial	NA	NA	unknown	absent
Hydrozoa indet. 2	unknown	–	unknown	–	colonial	present	NA	unknown	absent
Idiellana pristis (Lamouroux, 1816)	benthic	genus (all known)	dioecious	family (mostly)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Kirchenpaueria altitheca (Nutting, 1900)	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Kirchenpaueria bonnevieae (Billard, 1906)	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Kirchenpaueria pinnata (Linnaeus, 1758)	benthic	species	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Kirchenpaueria triangulata (Totton, 1930)	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Lafoea coalescens Allman, 1877	benthic	family (all known)	monoecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
Lafoea dumosa (Fleming, 1820)	benthic	family (all known)	monoecious	species	colonial	present	present	coppinia	absent
Lafoea gaussica Vanhöffen, 1910	benthic	family (all known)	monoecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
Lafoea intorta Calder, 2013	benthic	family (all known)	monoecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
Lafoea sp.	benthic	family (all known)	monoecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
?*Lafoea* sp.	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Lafoeidae indet.	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Lafoeina longitheca Jäderholm, 1904	unknown	species	unknown	species	colonial	present	present, with operculum	enveloped by exoskeleton	present
Lafoeina maxima Levinsen, 1893	benthic	species	unknown	species	colonial	present	present, with operculum	enveloped by exoskeleton	present
Lafoeina tenuis G. O. Sars, 1874	unknown	species	unknown	species	colonial	present	present, with operculum	enveloped by exoskeleton	present
Lafoeina ?*tenuis* G. O. Sars, 1874	unknown	species	unknown	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Laodicea undulata (Forbes & Goodir, 1853)	meroplanktonic	species	medusa	species	colonial	NA	present, with operculum	enveloped by exoskeleton	absent
?*Laodicea undulata* (Forbes & Goodir, 1853)	meroplanktonic	family (all known)	medusa	family (all known)	colonial	NA	present, with operculum	enveloped by exoskeleton	absent
Laomedea calceolifera (Hincks, 1871)	benthic	species	variable	species	colonial	present	present	enveloped by exoskeleton	absent
Laomedea pseudodichotoma Vervoort, 1959	benthic	species	variable	species	colonial	present	present	enveloped by exoskeleton	absent
Leptothecata indet.	unknown	–	unknown	–	colonial	present	present	enveloped by exoskeleton	absent
Leuckartiara octona (Fleming, 1823)	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Lovenella clausa (Lovén, 1836)	meroplanktonic	species	medusa	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Lytocarpia benedicti (Nutting, 1900)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	corbula	present
Lytocarpia bispinosa (Allman, 1877)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	corbula	present
Lytocarpia canepa (Blanco & Bellusci de Miralles, 1971)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	corbula	present
Lytocarpia distans (Allman, 1877)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	corbula	present
Lytocarpia myriophyllum (Linnaeus, 1758)	benthic	species	dioecious	species	colonial	present	present	corbula	present
Lytocarpia cf. *myriophyllum* (Linnaeus, 1758)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	corbula	present
Lytocarpia normani (Nutting, 1900)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	corbula	present
Macrorhynchia allmani (Nutting, 1900)	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	pseudocorbula	present
Macrorhynchia clarkei (Nutting, 1900)	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	pseudocorbula	present
Macrorhynchia grandis (Clarke, 1879)	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	pseudocorbula	present
Macrorhynchia philippina Kirchenpauer, 1872	variable	species	variable	species	colonial	present	present	phylactocarp	present
?*Merona cornucopiae* (Norman, 1864)	variable	family (variable)	unknown	family (variable)	colonial	present	absent	absent	absent
Millardiana sp.	benthic	genus (all known)	unknown	family (variable)	colonial	present	absent	unknown	absent
Mitrocomella polydiademata (Romanes, 1876)	meroplanktonic	species	medusa	species	colonial	NA	present, with operculum	enveloped by exoskeleton	absent

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
?*Mitrocomella polydiademata* (Romanes, 1876)	meroplanktonic	family (all known)	medusa	family (all known)	colonial	NA	present, with operculum	enveloped by exoskeleton	absent
?*Mitrocomella* sp.	meroplanktonic	family (all known)	medusa	family (all known)	colonial	NA	present, with operculum	enveloped by exoskeleton	absent
Modeeria rotunda (Quoy & Gaimard, 1827)	meroplanktonic	species	medusa	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
cf. *Modeeria rotunda* (Quoy & Gaimard, 1827)	unknown	family (variable)	unknown	order (variable)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Moerisia inkermanica Paltschikowa-Osroumowa, 1925	meroplanktonic	species	medusa	species	solitary	filmy perisarc	absent	absent	absent
Monocoryne gigantea (Bonnevie, 1898)	benthic	species	monoecious	species	solitary	absent	absent	absent	absent
Monostaechas quadridens (McCrady, 1859)	benthic	family (all known)	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Nemertesia americana (Nutting, 1900)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia anonyma Ansin Agís, Ramil & Vervoort, 2001	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia antennina (Linnaeus, 1758)	benthic	species	dioecious, but gregarious	species	colonial	present	present	enveloped by exoskeleton	present
Nemertesia belini Bedot, 1916	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia ciliata Bale, 1914	benthic	genus (all known)	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Nemertesia distans (Nutting, 1900)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia falcicula (Ramil & Vervoort, 1992)	benthic	species	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Nemertesia geniculata (Nutting, 1900)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia longicorna (Nutting, 1900)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia nigra (Nutting, 1900)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia norvegica (G. O. Sars, 1874)	benthic	species	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia ramosa (Lamarck, 1816)	benthic	species	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia rugosa (Nutting, 1900)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia simplex (Allman, 1877)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Nemertesia sp.	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Nemertesia ventriculiformis (Marktanner-Turneretscher, 1890)	benthic	genus (all known)	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Nemertesia vervoorti El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Neoturris ?abyssi (G. O. Sars, 1874)	meroplanktonic	genus (all known)	medusa	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
Neoturris pileata (Forsskal, 1775)	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Obelia bidentata Clark, 1875	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
?*Obelia bidentata* Clark, 1875	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Obelia cf. *dichotoma* (Linnaeus, 1758)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Obelia geniculata (Linnaeus, 1758)	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
Obelia irregularis Fraser, 1943	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Obelia longissima (Pallas, 1766)	meroplanktonic	species	medusa	species	colonial	present	present	enveloped by exoskeleton	absent
?*Obelia longissima* (Pallas, 1766)	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Obelia sp.	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Oceania armata Kölliker, 1853	meroplanktonic	species	medusa	species	colonial	present	absent	absent	absent
Oceaniidae indet. 1	variable	family (variable)	unknown	family (variable)	solitary	present	absent	absent	absent
Oceaniidae indet. 2	variable	family (variable)	unknown	family (variable)	colonial	present	absent	absent	absent
Opercularella lacerata (Johnston, 1847)	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Opercularella sp.	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
?*Opercularella* sp.	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Orthopyxis caliculata (Hincks, 1853)	benthic with eumedusoid	species	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Orthopyxis hartlaubi El Beshbeeshy, 2011	benthic	species	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Orthopyxis sp.	unknown	family (variable)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Oswaldella antarctica (Jäderholm, 1904)	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella bifurca (Hartlaub, 1904)	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella billardi Briggs, 1938	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella delicata Peña Cantero, Svoboda & Vervoort, 1997	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella elongata Peña Cantero, García-Carrascosa & Vervoort, 1995	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella encarnae Peña Cantero, Svoboda & Vervoort, 1997	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella erratum Peña Cantero & Vervoort, 1997	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella garciacarrascosai Peña Cantero, Svoboda & Vervoort, 1997	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella gracilis Peña Cantero, Svoboda & Vervoort, 1997	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella grandis Peña Cantero, Svoboda & Vervoort, 1997	benthic	family (all known)	dioecious	species	colonial	present	shallow	enveloped by exoskeleton	present
Oswaldella herwigi El Beshbeeshy, 2011	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella incognita Peña Cantero, Svoboda & Vervoort, 1997	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella medeae Peña Cantero & Vervoort, 2004	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella monomammillata Peña Cantero & Vervoort, 2004	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella obscura Peña Cantero, Svoboda & Vervoort, 1997	benthic	family (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	present
Oswaldella rigida Peña Cantero, Svoboda & Vervoort, 1997	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella shetlandica Stepanjants, 1979	benthic	family (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	present
Oswaldella sp.	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella stepanjantsae El Beshbeeshy, 1991	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Oswaldella tottoni Peña Cantero & Vervoort, 1996	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Oswaldella vervoorti Peña Cantero & García Carrascosa, 1998	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Pachycordyle sp.	benthic	genus (mostly)	dioecious	genus (all known)	colonial	present	absent	unknown	absent
Pandea clionis (Vanhöffen, 1910)	meroplanktonic	species	medusa	species	colonial	present	absent	absent	absent
?Pandeidae indet. 1	variable	order (variable)	unknown	order (variable)	colonial	present	present	unknown	absent
?Pandeidae indet. 2	variable	order (variable)	unknown	order (variable)	colonial	absent	absent	absent	absent
Phialella belgicae (Hartlaub, 1904)	meroplanktonic	species	medusa	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Phialella quadrata (Forbes, 1848)	meroplanktonic	species	medusa	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Plicatotheca anitae Calder & Vervoort, 1986	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Plicatotheca sp.	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
?*Plicatotheca* sp.	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Plotocnide borealis Wagner, 1885	meroplanktonic	species	medusa	species	solitary	absent	absent	absent	absent
Plumularia attenuata Allman, 1877	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumularia caulitheca Fewkes, 1881	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumularia filicula Allman, 1877	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumularia gaimardi (Lamouroux, 1824)	benthic	genus (mostly)	dioecious	species	colonial	present	present	enveloped by exoskeleton	present
Plumularia insignis Allman, 1883	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumularia leloupi Blanco & Bellusci de Miralles, 1971	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumularia margaretta (Nutting, 1900)	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumularia paucinoda Nutting, 1900	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumularia setacea (Linnaeus, 1758)	benthic	species	variable	species	colonial	present	present	enveloped by exoskeleton	present

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
Plumularia cf. *setacea* (Linnaeus, 1758)	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumularia sp.	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
?*Plumularia* sp.	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumularia cf. *warreni* Stechow, 1919	benthic	genus (mostly)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	present
Plumulariidae indet.	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Polyplumaria armata Nutting, 1900	benthic	genus (all known)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Polyplumaria flabellata G. O. Sars, 1874	benthic	species	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Polyplumaria ?flabellata G. O. Sars, 1874	benthic	genus (all known)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Proboscidactyla sp.	meroplanktonic	genus (all known)	medusa	genus (all known)	colonial	absent	absent	absent	absent
Protohydra leuckarti Greeff, 1870	benthic	species	dioecious	species	solitary	absent	absent	absent	absent
Pseudoplumaria marocana (Billard, 1930)	benthic	genus (all known)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Pseudoplumaria sabinae Ramil & Vervoort, 1992	benthic	genus (all known)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Pseudoplumaria sp.	benthic	genus (all known)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Ptychogena lactea A. Agassiz, 1865	meroplanktonic	species	medusa	species	colonial	NA	present, with operculum	enveloped by exoskeleton	absent
Racemoramus panicula (G. O. Sars, 1874)	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
?*Racemoramus panicula* (G. O. Sars, 1874)	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Rhizocaulus verticillatus (Linnaeus, 1758)	benthic	species	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Rhizorhagium roseum M. Sars, 1874	benthic	species	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Rosalinda incrustans (Kramp, 1947)	meroplanktonic	genus (all known)	medusa	genus (all known)	colonial	absent	absent	absent	absent
Rosalinda sp.	meroplanktonic	genus (all known)	medusa	genus (all known)	colonial	absent	absent	absent	absent
Salacia desmoides (Torrey, 1902)	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Sarsia tubulosa (M. Sars, 1835)	meroplanktonic	species	medusa	species	colonial	present	absent	absent	absent
Scandia gigas (Pieper, 1884)	benthic	species	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Schizotricha anderssoni Jäderholm, 1904	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha crassa Peña Cantero & Vervoort, 2004	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha falcata Peña Cantero, 1998	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha frutescens (Ellis & Solander, 1786)	benthic	species	dioecious	species	colonial	present	present	enveloped by exoskeleton	present
Schizotricha glacialis (Hickson & Gravely, 1907)	benthic	family (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	present
Schizotricha jaederholmi Peña Cantero & Vervoort, 1996	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha multifurcata Allman, 1883	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha ?multifurcata Allman, 1883	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha nana Peña Cantero, Svoboda & Vervoort, 1996	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha parvula Nutting, 1900	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha profunda (Nutting, 1900)	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha southgeorgiae Peña Cantero & Vervoort, 2004	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha sp.	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha turqueti Billard, 1906	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha unifurcata Allman, 1883	benthic	family (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	present
Schizotricha vervoorti Peña Cantero, 1998	benthic	family (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	present
Sertularella areyi Nutting, 1904	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella argentinica El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella catena (Allman, 1888)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Sertularella clausa (Allman, 1888)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella conica Allman, 1877	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella cruzensis El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella cylindritheca (Allman, 1888)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella diaphana (Allman, 1885)	benthic	genus (all known)	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella cf. *dubia* Billard, 1907	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella ellisii (Deshayes & Milne Edwards, 1836)	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella gaudichaudi (Lamouroux, 1824)	benthic	genus (all known)	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella gayi (Lamouroux, 1821)	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella ?gayi (Lamouroux, 1821)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella gigantea Hincks, 1874	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella hermanosensis El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella jorgensis El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella leiocarpa (Allman, 1888)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella megastoma Nutting, 1904	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella polyzonias (Linnaeus, 1758)	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella cf. *polyzonias* (Linnaeus, 1758)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella quadrata Nutting, 1895	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella sanmatiasensis El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella sp.	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Sertularella striata Stechow, 1923	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella tenella (Alder, 1856)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella cf. *tenella* (Alder, 1856)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella unituba Calder, 1991	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella ?unituba Calder, 1991	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularella vervoorti El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia argentea Linnaeus, 1758	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia cupressina Linnaeus, 1758	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia cf. *cupressina* Linnaeus, 1758	benthic	genus (mostly)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia distans (Lamouroux, 1816)	benthic	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia fabricii Levinsen, 1893	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia marginata (Kirchenpauer, 1864)	benthic with swimming gonophores	species	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia mirabilis (Verril, 1873)	benthic	genus (mostly)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia schmidti Kudelin, 1914	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia similis Clark, 1876	benthic	genus (mostly)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia sp.	benthic	genus (mostly)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia tenera G. O. Sars, 1874	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Sertularia turbinata (Lamouroux, 1816)	benthic	genus (mostly)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Solanderia gracilis Duchassaing & Michelin, 1846	benthic	species	dioecious	genus (all known)	colonial	present	absent	absent	absent
Staurotheca abyssalis Peña Cantero & Vervoort, 2003	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Staurotheca affinis (Jäderholm, 1904)	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca amphorophora Naumov & Stepanjants, 1962	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca antarctica Hartlaub, 1904	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca australis Peña Cantero, Svoboda & Vervoort, 1997	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca compressa Briggs, 1938	benthic	genus (all known)	variable	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca cornuta Peña Cantero, García Carrascosa & Vervoort, 1999	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca densa Peña Cantero & Vervoort, 2003	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca dichotoma Allman, 1888	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca frigida Peña Cantero, Svoboda & Vervoort, 1997	benthic	genus (all known)	variable	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca glomulosa Peña Cantero, Svoboda & Vervoort, 1997	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca jaederholmi Stechow, 1920	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca multifurcata Peña Cantero, García Carrascosa & Vervoort, 1999	benthic	genus (all known)	variable	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca nonscripta Peña Cantero, Svoboda & Vervoort, 1997	benthic	genus (all known)	variable	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca pachyclada (Jäderholm, 1904)	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca plana Peña Cantero, Svoboda & Vervoort, 1997	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca polarsterni Peña Cantero, Svoboda & Vervoort, 1997	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca sp.	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca ?stolonifera (Hartlaub, 1904)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca undosiparietina (Stepanjants, 1979)	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Staurotheca vanhoeffeni (Peña Cantero & García Carrascosa, 1994)	benthic	genus (all known)	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Staurotheca vervoorti (El Beshbeeshy, 2011)	benthic	genus (all known)	dioecious	genus (mostly)	colonial	present	present	enveloped by exoskeleton	absent
Stegella lobata (Vanhöffen, 1910)	benthic	species	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Stegolaria geniculata (Allman, 1888)	benthic	species	monoecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
?*Stegolaria geniculata* (Allman, 1888)	unknown	family (variable)	unknown	family (variable)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Stegopoma bathyale Vervoort, 1966	unknown	family (variable)	unknown	family (variable)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Stegopoma giganteum Ramil & Vervoort, 1992	meroplanktonic	species	medusa	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Stegopoma plicatile (M. Sars, 1863)	meroplanktonic	species	medusa	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
?*Stegopoma plicatile* (M. Sars, 1863)	unknown	family (variable)	unknown	family (variable)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Stegopoma sp.	unknown	family (variable)	unknown	family (variable)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
?*Stegopoma* sp.	unknown	family (variable)	unknown	family (variable)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Streptocaulus caboverdensis Ansin Agís, Ramil & Vervoort, 2001	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Streptocaulus chonae Ansin Agís, Ramil & Vervoort, 2001	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Streptocaulus corneliusi (Ramil & Vervoort, 1992)	benthic	genus (all known)	dioecious	species	colonial	present	present	phylactocarp	present
Streptocaulus dollfusi (Billard, 1924)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Streptocaulus gracilis Fraser, 1937	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Streptocaulus pectiniferus (Allman, 1883)	benthic	genus (all known)	dioecious	species	colonial	present	present	phylactocarp	present
Streptocaulus pulcherrimus Allman, 1883	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
Streptocaulus sinuosus (Vervoort, 1966)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	phylactocarp	present
?*Streptocaulus* sp.	benthic	family (mostly)	dioecious	family (mostly)	colonial	present	present	enveloped by exoskeleton	present
Symplectoscyphus amphoriferus (Allman, 1877)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Symplectoscyphus anae Peña Cantero, Svoboda & Vervoort, 2002	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus bathyalis Vervoort, 1972	benthic	genus (all known)	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus chubuticus El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus curvatus (Jäderholm, 1917)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus exochus Blanco, 1982	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus ?exochus Blanco, 1982	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus filiformis (Allman, 1888)	benthic	genus (all known)	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus frigidus Peña Cantero, Svoboda & Vervoort, 2002	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus glacialis (Jäderholm, 1904)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus hero Blanco, 1977	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus leloupi El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus liouvillei (Billard, 1914)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus ?liouvillei (Billard, 1914)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus magnificus Peña Cantero & Vervoort, 2009	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus naumovi Blanco, 1969	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus nesioticus Blanco, 1977	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus paraglacialis El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus plectilis (Hickson & Gravely, 1907)	benthic	genus (all known)	dioecious	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus singularis El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus sofiae Peña Cantero, Svoboda & Vervoort, 2002	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
Symplectoscyphus ?sofiae Peña Cantero, Svoboda & Vervoort, 2002	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus sp.	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus tricuspidatus (Alder, 1856)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus unilateralis (Lamouroux, 1824)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus valdesicus El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus vanhoeffeni Totton, 1930	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus cf. *vanhoeffeni* Totton, 1930	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus vervoorti El Beshbeeshy, 2011	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Symplectoscyphus weddelli Peña Cantero, Svoboda & Vervoort, 2002	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Synthecium evansi (Ellis & Solander, 1786)	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
Synthecium tubithecum (Allman, 1877)	benthic	species	dioecious	species	colonial	present	present	enveloped by exoskeleton	absent
Tamarisca tamarisca (Linnaeus, 1758)	benthic	species	variable	species	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Tetrapoma quadridentatum (Hincks, 1874)	unknown	family (all known)	unknown	family (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Thuiaria alternitheca Levinsen, 1893	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Thuiaria articulata (Pallas, 1766)	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Thuiaria carica Levinsen, 1893	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Thuiaria laxa Allman, 1874	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Thuiaria sp.	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Thuiaria thuja (Linnaeus, 1758)	benthic	species	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Thyroscyphus marginatus (Allman, 1877)	benthic	species	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent

Species	Life cycle	Life cycle information basis	Sexual reproduction	Sexual reproduction information basis	Coloniality	Hydrocaulus exoskeleton *	Hydranth exoskeleton **	Gonophore protection	Nematophore
Thyroscyphus ramosus Allman, 1877	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present, with operculum	enveloped by exoskeleton	absent
Thyroscyphus sp.	benthic	genus (all known)	dioecious	genus (all known)	colonial	present	present	enveloped by exoskeleton	absent
Tubularia couthouyi L. Agassiz, 1862	benthic	species	dioecious	species	solitary	present	absent	absent	absent
Tubularia indivisa Linnaeus, 1758	benthic	species	dioecious	species	solitary	present	absent	absent	absent
Tubularia cf. *indivisa* Linnaeus, 1758	benthic	genus (all known)	dioecious	genus (mostly)	solitary	present	absent	absent	absent
Tubularia sp. 1	benthic	genus (all known)	dioecious	genus (mostly)	solitary	absent	absent	absent	absent
Tubularia sp. 2	benthic	genus (all known)	dioecious	genus (mostly)	solitary	present	absent	absent	absent
Turritopsis dohrnii (Weismann, 1883)	meroplanktonic	species	medusa	species	colonial	present	absent	enveloped by exoskeleton	absent
?*Turritopsis* sp.	variable	family (variable)	unknown	family (variable)	solitary	present	absent	absent	absent
Zanclea cf. *alba* (Meyen, 1834)	meroplanktonic	genus (all known)	medusa	genus (all known)	colonial	present	absent	absent	absent
Zanclea sp.	meroplanktonic	genus (all known)	medusa	genus (all known)	colonial	present	absent	absent	absent
Zygophylax africana Stechow, 1923	benthic	family (all known)	dioecious	species	colonial	present	present	coppinia	present
Zygophylax cf. *africana* Stechow, 1923	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	coppinia	present
Zygophylax biarmata Billard, 1905	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	coppinia	present
Zygophylax ?*biarmata* Billard, 1905	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
Zygophylax cf. *bifurcata* Billard, 1942	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	coppinia	present
Zygophylax brownei Billard, 1924	benthic	species	unknown	genus (variable)	colonial	present	present	coppinia	present
Zygophylax ?*brownei* Billard, 1924	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
Zygophylax convallaria (Allman, 1877)	benthic	family (all known)	monoecious	species	colonial	present	present	coppinia	present
Zygophylax ?*convallaria* (Allman, 1877)	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
Zygophylax crassicaulis (Fraser, 1943)	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present

Species	**Life cycle**	**Life cycle information basis**	**Sexual reproduction**	**Sexual reproduction information basis**	**Coloniality**	**Hydrocaulus exoskeleton ***	**Hydranth exoskeleton ****	**Gonophore protection**	**Nematophore**
Zygophylax echinata Calder & Vervoort, 1998	benthic	species	unknown	genus (variable)	colonial	present	present	coppinia	present
Zygophylax elegans (Fewkes, 1881)	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	absent
Zygophylax elongata Ramil & Vervoort, 1992	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	coppinia	present
Zygophylax leloupi Ramil & Vervoort, 1992	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
Zygophylax levinseni (Saemundsson, 1911)	benthic	family (all known)	monoecious	species	colonial	present	present	enveloped by exoskeleton	present
Zygophylax ?levinseni (Saemundsson, 1911)	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
Zygophylax parabiarmata Vervoort, 2006	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
Zygophylax pinnata (Sars, 1874)	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	absent
?*Zygophylax pinnata* (Sars, 1874)	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Zygophylax profunda Quelch, 1885	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	coppinia	present
Zygophylax sibogae Billard, 1918	benthic	family (all known)	dioecious	species	colonial	present	present	coppinia	present
Zygophylax sp.	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
?*Zygophylax* sp.	benthic	family (all known)	unknown	family (variable)	colonial	present	present	enveloped by exoskeleton	absent
Zygophylax ?tottoni Rees & Vervoort, 1987	benthic	family (all known)	unknown	genus (variable)	colonial	present	present	enveloped by exoskeleton	present
Zyzzyzus parvula (Hickson & Gravely, 1907)	benthic	species	unknown	genus (variable)	solitary	filmy perisarc	absent	absent	absent

Capítulo 3

Latitude and depth gradients explain distribution patterns of hydroids (Cnidaria) in the deep Atlantic Ocean

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Abstract

The diversity of historical and environmental factors that in concert shape species distributions is ultimately reflected in the geographical patterns of assemblage compositions. Therefore, spatial variation in species composition should be related both to species histories in space and time, and to the ability of individuals to occupy specific habitats. Here, we infer distribution patterns of hydroids in the deep Atlantic Ocean and adjacent polar seas from the characterization of species compositions along latitude and depth. Our results suggest that distribution patterns of hydroids in the deep Atlantic Ocean may be explained by historical factors related to the formation of the Southern Ocean and by environmental gradients associated to depth and latitude. Assemblages are primarily differentiated between those to the north and south of 40°S, regardless of depth, with an internal separation between Patagonian and Antarctic assemblages. Northwards of 40°S, assemblages gradually differentiate along both, depth strata and latitude, although a faunal turnover occurs at 1,000 m deep. Finally, assemblages at the 1,001–5,330 m stratum tend to be more similar to each other than those at shallower strata, suggesting deep-sea connectivity along great distances. We also raise the problem of largely unequal sampling in the Atlantic Ocean across depths and latitudes, especially in the southern hemisphere and below 1,000 m deep.

Resumo

A diversidade de fatores históricos e ambientais que, em conjunto, configuram as distribuições de espécies reflete-se nos padrões geográficos de composição de assembleias. Portanto, variação espacial na composição de espécies deve estar relacionada tanto com a história das espécies no espaço e no tempo, quanto com a capacidade dos indivíduos de ocupar habitats específicos. Aqui, inferimos padrões de distribuição de hidroides no Oceano Atlântico profundo e mares polares adjacentes a partir da caracterização de composições de espécies ao longo da latitude e da profundidade. Nossos resultados sugerem que padrões de distribuição de hidroides no Oceano Atlântico profundo podem ser explicados por fatores históricos relacionados à formação do Oceano Austral e por gradientes ambientais associados à profundidade e à latitude. As assembleias são primeiramente diferenciadas entre as ao norte e ao sul de 40°S, independentemente da profundidade, com uma separação interna entre as assembleias Patagônicas e Antárticas. Ao norte de 40°S, as assembleias se diferenciam gradualmente ao longo de ambos, estratos de profundidade e latitude, embora uma mudança de fauna ocorra a 1000 m de profundidade. Finalmente, as assembleias no estrato de 1.001–5.330 m tendem a ser mais parecidas entre si do que as de estratos mais rasos, sugerindo conectividade em mar profundo ao longo de grandes distâncias. Também levantamos o problema da amostragem amplamente desigual no Oceano Atlântico em profundidades e latitudes, especialmente no hemisfério sul e abaixo de 1000 m de profundidade.

Introduction

The geographical distribution of each individual species is shaped by evolutionary and ecological processes, and ultimately define biogeographical patterns when analyzed together with the overlapping ranges of other species (Valentine, 1973; Jablonski *et al.*, 1985; Morrone, 2009). Gradual or rapid shifts in species composition are therefore consequences of the evolutionary history of the species, and may be caused by physical or environmental barriers to dispersal and survival (Valentine, 1973, Lomolino *et al.*, 2017). Theoretically, physical variables such as topography, currents, water masses, heterogeneities in temperature and oxygen, or biological variables like food availability, would work as putative barriers to the distribution of marine invertebrates (Levin *et al.*, 2001; Carney, 2005; Gooday *et al.*, 2010; McClain & Hardy, 2010). At the population level, similarly, geographical distance may impair, even ceasing, gene flow among populations, gradually leading to faunal differentiation resulted from speciation (Soininen *et al*., 2007b; McClain *et al*., 2012; Postaire *et al*., 2017).

However, evolution in the deep sea points out to a different scenario. Barriers to dispersal are difficult to be recognized in deep-sea habitats, although they supposedly could be inferred from patterns of geographical distribution of the species communities (Zezina, 1997; Van Dover *et al*., 2002; McClain & Hardy, 2010; McClain *et al*., 2012). Also, greater environmental homogeneity found at bathyal and abyssal depths would enlarge species' geographic ranges, decreasing biogeographic differentiation (Zezina, 1997). Indeed, molecular analyses suggest continuous gene flow along great distances in the deep sea (Eilertsen & Malaquias, 2015; Dambach *et al*., 2016; Everett *et al*., 2016), even for disconnected and patchy ecosystems such as hydrothermal vents or cold seeps (Van Dover *et al*., 2002; Won *et al*., 2003; Beedessee *et al*., 2013; Teixeira *et al*., 2013; De Groote *et al*., 2017). However, although the assumption of tenuous or no existent barriers and presumed environmental homogeneity at the deep-sea floor would favor cosmopolitan distributions of the species, limited gene flow among populations and metapopulations is also documented (Vrijenhoek, 2010; LaBella *et al*., 2017), 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 (McClain & Barry, 2010; Vanreusel *et al*., 2010; McClain *et al*., 2011; Zeppilli *et al*., 2014; Judge & Barry, 2016). At the regional scale, however, β-diversity is more influenced by environmental variations in temperature and particulate organic carbon (POC) flux to the seafloor (UNESCO, 2009; Wei *et al*., 2010; Watling *et al*., 2013; McClain & Rex, 2015; Woolley *et al*., 2016), two key drivers that would structure communities along depth (Carney, 2005; Rex *et al*., 2005; Rex & Etter, 2010). 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 (review in Carney, 2005).

Knowledge on biogeographical patterns of the deep-sea communities is scant when compared to terrestrial and coastal marine ecosystems (UNESCO, 2009; Watling *et al*., 2013). Inferences are generally based on few taxa (*e.g.* Rex *et al*., 2010; Eilertsen & Malaquias, 2015). For hydroids, there are only regional synthesis mostly focusing on shallow water habitats (*e.g.* Henry *et al*., 2008; Genzano *et al*., 2009; Antsulevich, 2015; Miranda *et al*., 2015; Ronowicz *et al*., 2015; Peña Cantero *et al*., 2017). However, hydroid-bearing species are broadly distributed both in shallow and deep-sea habitats (Kramp, 1956; Calder, 1998; Gebruk *et al*., 2000; Henry *et al*., 2008), with great intra and interspecific variation across environments (review in Cunha *et al*., 2016; Fernandez & Marques, 2017a[a]; Fernandez *et al*., 2017[b]). Our aim in this study is to infer distribution patterns of hydroids in the deep Atlantic Ocean and adjacent polar seas based on the composition of species along depth and latitude, recognizing geological and environmental limits and gradients.

Material & 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 checked or made by the authors, improving uniformity within the data set by avoiding usual variable taxonomical interpretation, making the database unique and solid. 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 (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 (Fig. 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).

Data analyses

Only taxa identified to species level were used in the analyses. *Acaulis* cf. *rosae* (Verrill, 1878); *Euphysora ?bigelowi* Maas, 1905; and *Millardiana* sp. were also included for being recognized 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 number of occurrences of each species per area were used for multivariate analyses. Data was standardized by the total abundance of each area, because

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[a] Capítulo 1.

[b] Capítulo 2.

sampling efforts among areas are not comparable (Clarke & Warwick, 2001). Analyses were based on Bray-Curtis dissimilarities of the fourth-root transformed data.

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 resulted 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 areas as a fixed factor with 9,999 unrestricted permutations of the raw data and Type III sum of squares to consider unbalanced replicates per sample. Pairwise tests were implemented for significant differences. PERMANOVA analyses were made using all sampled sites in each area, allowing comparisons of differences within and between areas. Each site was characterized by unique coordinates and depth. The same standardization and transformation from previous analyses were used.

Analyses were performed in R (R Core Team, 2017), except for PERMANOVA, performed in PRIMER v6 (Clarke & Gorley, 2006) and PERMANOVA v1.0.5 (Anderson *et al.*, 2008).

Results

General data

Data analyzed totaled 3,699 records belonging to 432 unique species, at 1,444 unique sites (see list of taxa in Fernandez *et al.*, 2017[a]). 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 (Figs. 1-2, Table 1). However, even these best sampled areas have a rising tendency in the rarefaction curves, resulting in higher total richness estimates (Fig. 2). In general, the 50–200

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[a] Capítulo 2.

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 worst 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 (Figs. 1-2, Table 1).

Species composition in relation to latitudinal bands and depth strata

Species composition and abundance of hydroid assemblages are different among areas (PERMANOVA, P(perm) = 0.0001). The only pair of assemblages not differentiated by the PERMANOVA pairwise tests was the contiguous 0˚–20˚S and 21˚–40˚S bands at 50–200 m depth, all others being significantly different (Table 2).

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 (Fig. 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 (Figs. 1, 3).

Northwards of 40˚S, NMDS ordination shows a somewhat 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 (Fig. 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 201–1000 m stratum) than those in shallower strata, despite great latitudinal variation (Fig. 3). Assemblages within 50–200 m and 201–1,000 m strata gradually differentiate along latitude (Fig. 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 at the NMDS ordination (Fig. 3).

Discussion

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

Species composition

The variation in species composition across the Atlantic Ocean may be explained by a combination of both latitude and depth, and its associated factors acting at different time and spatial scales. The first clear separation is at latitude 40˚S, between southernmost (Patagonian and Antarctic) and northernmost areas (Fig. 3). The southernmost cluster may be explained by the shared geological history of South America and Antarctic, subsequently isolated from each other after the formation of the Antarctic Circumpolar Current (Thomson, 2004; Poulin *et al.*, 2014). Biologically, this relationship is represented by the high endemicity of many Southern Ocean taxa (Brandt *et al.*, 2004, 2007a, 2007b), including hydroids (Peña Cantero & García Carrascosa, 1999; Marques & Peña Cantero, 2010; Miranda *et al.*, 2015; Casares *et al.*, 2017).

Differently, relationships among areas to the north of 40˚S are more complex, apparently less affected by isolation and with environmental gradients playing an important role in the origin of its species' distributions. Assemblages in those areas presented an initial separation dominantly driven by depth, in which the deep-sea assemblages (1,001–5,330 m stratum) have differentiated from shallower ones (50–200 m and 201–1,000 m strata) (Fig. 3). This pattern corroborates previous hypothesis of faunal turnover at 1,000 m deep, suggested to be correlated to temperature shifts and limiting dispersal across this barrier (Carney, 2005). Greater environmental homogeneity in the deep sea, on the other hand, would allow a greater connectivity (Zezina, 1997; Dambach *et al.*, 2016; Everett *et al.*, 2016). 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 (Fig. 3). Unfortunately, there is no data in our analysis concerning the 1,001–5,330 m stratum south of 40˚S, but future data may 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 were already reported for different taxa, and associated to different dispersal capabilities (Brandt *et al.*, 2007a).

On the other hand, the shallower species assemblages gradually differentiated across a combination of both depth and latitude (Fig. 3). Significant clustering between 50–200 m and 201–1,000 m strata from the same latitudinal band (Fig. 3B) supports interconnectivity between populations from 50 to 1,000 m deep. Interestingly, once this group is established, its complexity is then highly driven by a latitudinal gradient, creating a somewhat gradual pattern of slightly different communities from north to south. This pattern was never described in such a large latitudinal scale before.

Gradual differentiation of hydroid assemblages may also be observed along depth (Fig. 3A), a result of 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, where only a few species are exclusively bathyal or abyssal (Fernandez & Marques, 2017a[a]), suggesting that the observed pattern resulted from the reduction of the range extensions limited by depth. Similar patterns have been observed in other taxa, suggesting that, although populations are able to get to the deep sea coming from shallower waters, these individuals would not get established (Rex *et al*., 2005), probably because of the limited POC flux (Stuart *et al*., 2017).

Spatial variation in species composition may also be related to the ability of individuals to occupy specific niches, promoted by the presence of particular functional traits (Soininen *et al*., 2007a, 2007b; Violle *et al.,* 2007; Webb *et al*., 2009; Brun *et al.,* 2016; Beauchard *et al.,* 2017; Bolam *et al.,* 2017). Similarity between deep-sea assemblages, for example, may be related to specific traits that allow survival and reproduction in a food deprived environment with low population densities (Fernandez *et al*., 2017[b]). Similarly, Southern Ocean endemism is usually associated to dispersal capabilities (Brandt *et al*., 2007a). Hydroid-bearing species have varied life cycles, related to a medusa release, that are associated to different dispersions and may result in different patterns of endemism (Gibbons *et al*. 2010a, 2010b; Rodriguez *et al*., 2017).

Sampling effort and species richness

Data collection for such a large area is difficult to be exhaustive. Our data sample broadly comprehends material for the region, with the unique advantage of being taxonomically standardized for comparison purposes. Available data is majorly located close to continental margins, except for the Scotia Arc region and few samples at the Mid-Atlantic Ridge (Fig. 2). There are important gaps in data coverage/knowledge (Fig. 2, Table 1), with areas almost with

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[a] Capítulo 1.

[b] Capítulo 2.

no records, as in the Southern Hemisphere and in the 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). Those areas urge to be better explored, since deep-sea ecosystems are becoming more and more impacted by direct and indirect anthropic activities even before they are properly studied (Ramirez-Llodra *et al.*, 2011; Courtene-Jones, *et al.*, 2017; Danovaro *et al.*, 2017; Jones *et al.*, 2017). Increased sampling effort in the Northern Hemisphere may cause a biased notion of highest richness in those areas, although similar diversities are proposed to exist in both hemispheres for most taxa (Chaudhary *et al.*, 2017; Fernandez & Marques, 2017b[a]). The 21˚–40˚N band is the best sampled latitude as a reflection of the historical greater sampling effort in the area for both sides of the Atlantic and in the Mid Atlantic Ridge region (*e.g.*, Nutting, 1900, 1904, 1915; Ramil & Vervoort, 1992; Medel & Vervoort, 1998, 2000; Ramil *et al.*, 1998; Ansín Agís *et al.*, 2001; Vervoort, 2006). Similarly, many Antarctic expeditions in the last decades contributed to enhance sampling in the area (61˚–80˚S), mostly in the 201–1,000 m stratum (*e.g.*, Peña Cantero & García Carrascosa, 1995; Peña Cantero & Vervoort, 2003; 2009; Peña Cantero *et al.*, 2004; Peña Cantero & Ramil, 2006; Peña Cantero, 2008). Although poor sampling may hamper estimates of total species richness and obscure biogeographical patterns, distribution patterns of our analysis have a strong internal coherence, despite unequal sampling.

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 zone, in a parabolic relationship (Sanders, 1968; Rex, 1973, 1981; Etter & Grassle, 1992; Levin & Gage, 1998; McClain & Etter, 2005; Costello & Chaudhary, 2017). 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 *et al.*, 2016).

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[a] Capítulo 4.

Conclusion

This study provides evidence on different drivers structuring the distribution patterns of hydroids in the deep Atlantic Ocean. Patterns of species assemblages suggest that both historical factors (*i.e.*, related to the geological history of the Southern Ocean) and environmental gradients related to latitudinal and depth variation significantly support most of the distributions.

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Figures

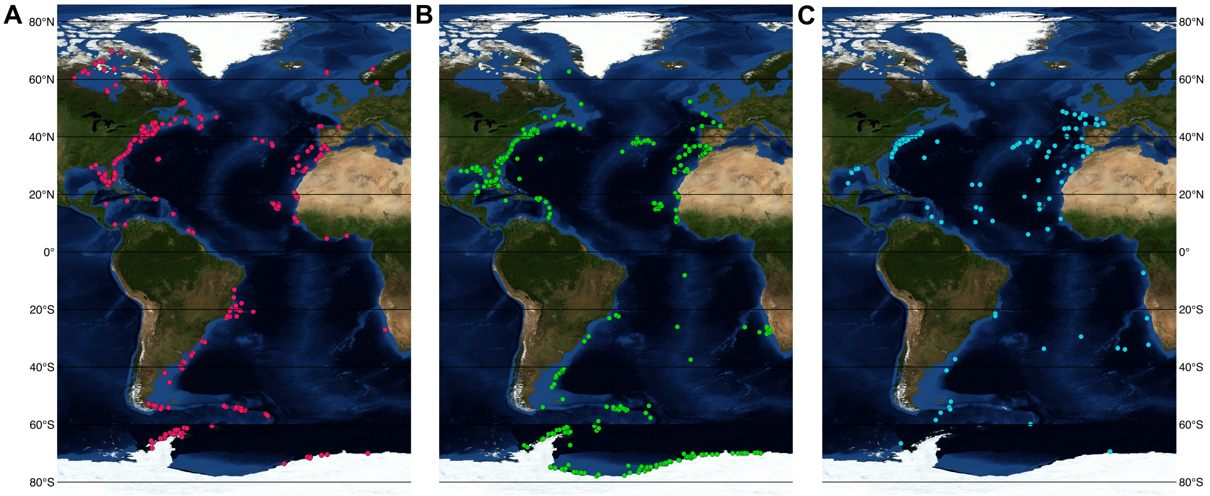

Figure 1. Geographic distribution of the material studied in the 50–200 m (**A**), 201–1,000 m (**B**), and 1,001–5,330 m (**C**) depth strata of the Atlantic Ocean. Maps are divided into latitudinal bands according to the studied areas. Each point may contain more than one record of species.

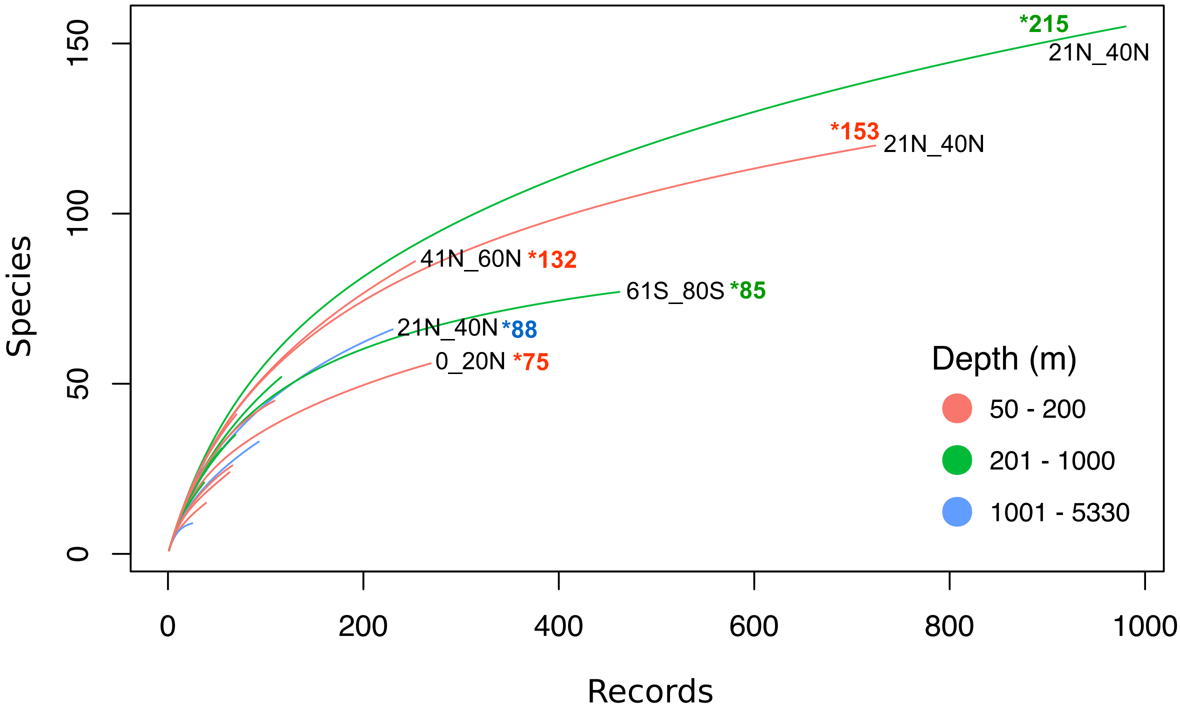

Figure 2. Individual-based rarefaction curves for the 18 studied areas of the Atlantic Ocean. Colors represent depth strata. Areas with more than 200 records are annotated with estimated richness (*).

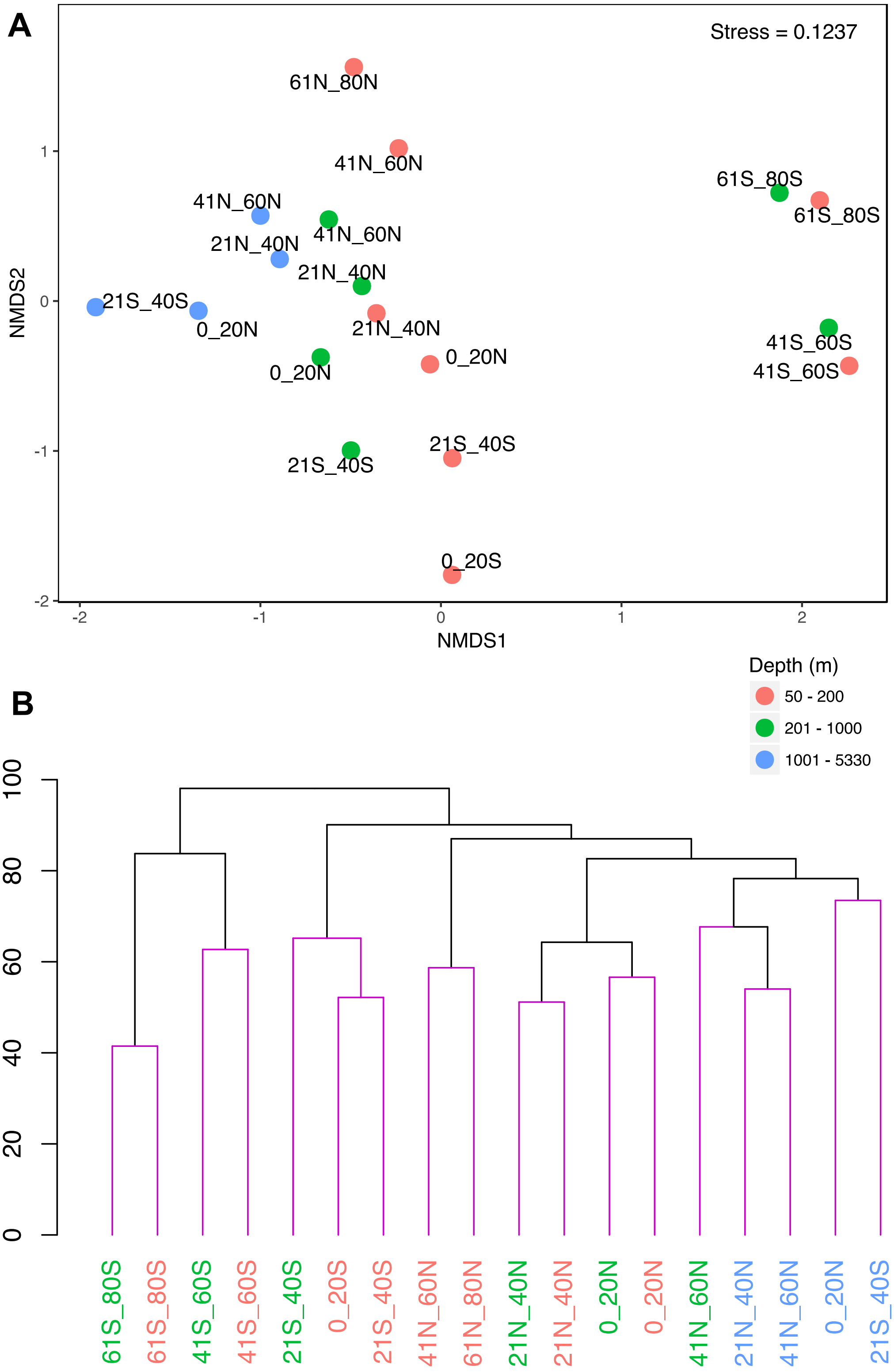

Figure 3. NMDS ordination plot showing relationships in species composition among assemblages of hydroids for the 18 studied areas of the Atlantic Ocean (**A**) and dendrogram resulting from the hierarchical clustering analysis for the same data, with significant clusters resulting from similarity profile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

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*

Table 2. PERMANOVA pairwise tests results for differences in species composition among assemblages of hydroids in the 18 studied areas of the Atlantic Ocean. Assemblage not significantly differentiated (P ≥ 0.05) in bold.

Groups	t	P(perm)	Unique perms
0_20N_1001_5330, 0_20S_50_200	1,6071	0,0001	6818
0_20N_1001_5330, 21S_40S_50_200	1,5966	0,0005	9896
0_20N_1001_5330, 41N_60N_50_200	1,6983	0,0001	9858
0_20N_1001_5330, 41S_60S_201_1000	1,6092	0,0001	9881
0_20N_1001_5330, 41S_60S_50_200	2,0592	0,0002	9872
0_20N_201_1000, 0_20N_1001_5330	1,6041	0,0001	9871
0_20N_201_1000, 0_20S_50_200	1,601	0,0003	9852
0_20N_201_1000, 21S_40S_50_200	1,8625	0,0001	9843
0_20N_201_1000, 41N_60N_50_200	2,0138	0,0001	9864
0_20N_201_1000, 41S_60S_201_1000	1,8407	0,0001	9834
0_20N_201_1000, 41S_60S_50_200	2,4388	0,0001	9866
0_20N_50_200, 0_20N_1001_5330	2,0815	0,0001	9879
0_20N_50_200, 0_20N_201_1000	1,8232	0,0001	9881
0_20N_50_200, 0_20S_50_200	1,7004	0,0002	9911
0_20N_50_200, 21S_40S_50_200	2,1955	0,0001	9880
0_20N_50_200, 41N_60N_50_200	2,8506	0,0001	9879
0_20N_50_200, 41S_60S_201_1000	2,3755	0,0001	9868
0_20N_50_200, 41S_60S_50_200	2,9996	0,0001	9876
21N_40N_1001_5330, 0_20N_1001_5330	1,6745	0,0002	9891
21N_40N_1001_5330, 0_20N_201_1000	2,1019	0,0001	9869
21N_40N_1001_5330, 0_20N_50_200	3,0907	0,0001	9884
21N_40N_1001_5330, 0_20S_50_200	1,7262	0,0004	9886
21N_40N_1001_5330, 21N_40N_50_200	3,1156	0,0001	9868
21N_40N_1001_5330, 21S_40S_201_1000	1,6391	0,0003	9908
21N_40N_1001_5330, 21S_40S_50_200	2,0905	0,0001	9894
21N_40N_1001_5330, 41N_60N_201_1000	1,9808	0,0001	9883
21N_40N_1001_5330, 41N_60N_50_200	2,7097	0,0001	9855
21N_40N_1001_5330, 41S_60S_201_1000	2,0662	0,0001	9861
21N_40N_1001_5330, 41S_60S_50_200	2,7956	0,0001	9872
21N_40N_1001_5330, 61S_80S_201_1000	3,7652	0,0001	9846
21N_40N_1001_5330, 61S_80S_50_200	2,5111	0,0001	9891
21N_40N_201_1000, 0_20N_1001_5330	1,7596	0,0002	9862
21N_40N_201_1000, 0_20N_201_1000	1,6473	0,0001	9845

Groups	t	P(perm)	Unique perms
21N_40N_201_1000, 0_20N_50_200	2,8009	0,0001	9880
21N_40N_201_1000, 0_20S_50_200	1,686	0,0001	9881
21N_40N_201_1000, 21N_40N_1001_5330	2,4502	0,0001	9880
21N_40N_201_1000, 21N_40N_50_200	2,4193	0,0001	9844
21N_40N_201_1000, 21S_40S_201_1000	1,5419	0,0001	9870
21N_40N_201_1000, 21S_40S_50_200	2,0954	0,0001	9871
21N_40N_201_1000, 41N_60N_201_1000	1,9486	0,0001	9865
21N_40N_201_1000, 41N_60N_50_200	2,7135	0,0001	9848
21N_40N_201_1000, 41S_60S_201_1000	2,0725	0,0001	9854
21N_40N_201_1000, 41S_60S_50_200	2,854	0,0001	9871
21N_40N_201_1000, 61S_80S_201_1000	4,0755	0,0001	9846
21N_40N_201_1000, 61S_80S_50_200	2,5542	0,0001	9849
21N_40N_50_200, 0_20N_1001_5330	1,7515	0,0001	9880
21N_40N_50_200, 0_20N_201_1000	1,7704	0,0001	9867
21N_40N_50_200, 0_20N_50_200	2,6467	0,0001	9867
21N_40N_50_200, 0_20S_50_200	1,6365	0,0002	9882
21N_40N_50_200, 21S_40S_201_1000	1,5406	0,0004	9874
21N_40N_50_200, 21S_40S_50_200	1,9771	0,0001	9888
21N_40N_50_200, 41N_60N_201_1000	2,0388	0,0001	9875
21N_40N_50_200, 41N_60N_50_200	2,2665	0,0001	9874
21N_40N_50_200, 41S_60S_201_1000	2,0898	0,0001	9867
21N_40N_50_200, 41S_60S_50_200	2,8547	0,0001	9854
21N_40N_50_200, 61S_80S_50_200	2,559	0,0001	9879
21S_40S_1001_5330, 0_20N_1001_5330	1,6349	0,0013	9010
21S_40S_1001_5330, 0_20N_201_1000	1,9305	0,0001	9895
21S_40S_1001_5330, 0_20N_50_200	2,2597	0,0001	9904
21S_40S_1001_5330, 0_20S_50_200	1,9141	0,0008	6951
21S_40S_1001_5330, 21N_40N_1001_5330	1,9236	0,0001	9901
21S_40S_1001_5330, 21N_40N_201_1000	2,032	0,0001	9863
21S_40S_1001_5330, 21N_40N_50_200	2,0501	0,0001	9876
21S_40S_1001_5330, 21S_40S_201_1000	1,7832	0,0001	8971
21S_40S_1001_5330, 21S_40S_50_200	1,9585	0,0001	9886
21S_40S_1001_5330, 41N_60N_1001_5330	1,573	0,0026	9792
21S_40S_1001_5330, 41N_60N_201_1000	1,9105	0,0001	9828
21S_40S_1001_5330, 41N_60N_50_200	1,9945	0,0001	9868
21S_40S_1001_5330, 41S_60S_201_1000	1,944	0,0001	9740
21S_40S_1001_5330, 41S_60S_50_200	2,2616	0,0001	9897
21S_40S_1001_5330, 61N_80N_50_200	1,9065	0,0001	9891
21S_40S_1001_5330, 61S_80S_201_1000	2,3575	0,0001	9875
21S_40S_1001_5330, 61S_80S_50_200	2,1075	0,0001	9904
21S_40S_201_1000, 0_20N_1001_5330	1,4366	0,0002	9512
21S_40S_201_1000, 0_20N_201_1000	1,434	0,0007	9858
21S_40S_201_1000, 0_20N_50_200	1,9005	0,0001	9899
21S_40S_201_1000, 0_20S_50_200	1,4512	0,0032	5327
21S_40S_201_1000, 21S_40S_50_200	1,4676	0,002	9884
21S_40S_201_1000, 41N_60N_50_200	1,4868	0,0004	9867
21S_40S_201_1000, 41S_60S_201_1000	1,5109	0,0002	9866
21S_40S_201_1000, 41S_60S_50_200	1,9423	0,0002	9885
21S_40S_50_200, 0_20S_50_200	**0,94359**	**0,5549**	**9807**
41N_60N_1001_5330, 0_20N_1001_5330	1,6559	0,0002	9886
41N_60N_1001_5330, 0_20N_201_1000	2,198	0,0001	9884
41N_60N_1001_5330, 0_20N_50_200	3,0058	0,0001	9887
41N_60N_1001_5330, 0_20S_50_200	1,752	0,0005	9048
41N_60N_1001_5330, 21N_40N_1001_5330	2,0908	0,0001	9907
41N_60N_1001_5330, 21N_40N_201_1000	2,6876	0,0001	9860
41N_60N_1001_5330, 21N_40N_50_200	2,8329	0,0001	9845
41N_60N_1001_5330, 21S_40S_201_1000	1,6334	0,0004	9820
41N_60N_1001_5330, 21S_40S_50_200	2,067	0,0001	9883
41N_60N_1001_5330, 41N_60N_201_1000	1,9562	0,0001	9881
41N_60N_1001_5330, 41N_60N_50_200	2,4246	0,0001	9860
41N_60N_1001_5330, 41S_60S_201_1000	2,0422	0,0001	9867
41N_60N_1001_5330, 41S_60S_50_200	2,6772	0,0001	9883
41N_60N_1001_5330, 61N_80N_50_200	2,0139	0,0001	9871

Groups	t	P(perm)	Unique perms
41N_60N_1001_5330, 61S_80S_201_1000	3,3245	0,0001	9886
41N_60N_1001_5330, 61S_80S_50_200	2,4106	0,0001	9896
41N_60N_201_1000, 0_20N_1001_5330	1,5825	0,0002	9867
41N_60N_201_1000, 0_20N_201_1000	1,8095	0,0001	9877
41N_60N_201_1000, 0_20N_50_200	2,4522	0,0001	9886
41N_60N_201_1000, 0_20S_50_200	1,621	0,0007	9077
41N_60N_201_1000, 21S_40S_201_1000	1,4647	0,0008	9858
41N_60N_201_1000, 21S_40S_50_200	1,8082	0,0001	9861
41N_60N_201_1000, 41N_60N_50_200	1,5707	0,0001	9889
41N_60N_201_1000, 41S_60S_201_1000	1,7342	0,0001	9851
41N_60N_201_1000, 41S_60S_50_200	2,3151	0,0001	9857
41N_60N_201_1000, 61S_80S_50_200	2,0481	0,0001	9859
41N_60N_50_200, 0_20S_50_200	1,6361	0,0003	9850
41N_60N_50_200, 21S_40S_50_200	1,8566	0,0001	9853
41N_60N_50_200, 41S_60S_201_1000	1,8646	0,0001	9857
41N_60N_50_200, 41S_60S_50_200	2,593	0,0001	9861
41S_60S_201_1000, 0_20S_50_200	1,6301	0,0003	9417
41S_60S_201_1000, 21S_40S_50_200	1,8131	0,0001	9867
41S_60S_201_1000, 41S_60S_50_200	1,6646	0,0008	9897
41S_60S_50_200, 0_20S_50_200	1,9007	0,0002	9872
41S_60S_50_200, 21S_40S_50_200	2,2697	0,0001	9899
61N_80N_50_200, 0_20N_1001_5330	1,5723	0,0001	9846
61N_80N_50_200, 0_20N_201_1000	1,7915	0,0001	9856
61N_80N_50_200, 0_20N_50_200	2,301	0,0001	9852
61N_80N_50_200, 0_20S_50_200	1,6135	0,0001	9829
61N_80N_50_200, 21N_40N_1001_5330	2,0242	0,0001	9868
61N_80N_50_200, 21N_40N_201_1000	2,0072	0,0001	9888
61N_80N_50_200, 21N_40N_50_200	1,9898	0,0001	9858
61N_80N_50_200, 21S_40S_201_1000	1,4986	0,0001	9846
61N_80N_50_200, 21S_40S_50_200	1,8026	0,0001	9873
61N_80N_50_200, 41N_60N_201_1000	1,659	0,0001	9862
61N_80N_50_200, 41N_60N_50_200	1,5252	0,0001	9853
61N_80N_50_200, 41S_60S_201_1000	1,6672	0,0001	9852
61N_80N_50_200, 41S_60S_50_200	2,2	0,0001	9879
61N_80N_50_200, 61S_80S_201_1000	2,5065	0,0001	9881
61N_80N_50_200, 61S_80S_50_200	1,9577	0,0001	9850
61S_80S_201_1000, 0_20N_1001_5330	2,2432	0,0001	9872
61S_80S_201_1000, 0_20N_201_1000	2,8982	0,0001	9861
61S_80S_201_1000, 0_20N_50_200	3,7143	0,0001	9873
61S_80S_201_1000, 0_20S_50_200	1,9479	0,0001	9882
61S_80S_201_1000, 21N_40N_50_200	3,9936	0,0001	9859
61S_80S_201_1000, 21S_40S_201_1000	2,0598	0,0001	9877
61S_80S_201_1000, 21S_40S_50_200	2,5095	0,0001	9875
61S_80S_201_1000, 41N_60N_201_1000	2,7151	0,0001	9887
61S_80S_201_1000, 41N_60N_50_200	3,3737	0,0001	9852
61S_80S_201_1000, 41S_60S_201_1000	2,4423	0,0001	9866
61S_80S_201_1000, 41S_60S_50_200	2,955	0,0001	9885
61S_80S_201_1000, 61S_80S_50_200	2,0766	0,0001	9896
61S_80S_50_200, 0_20N_1001_5330	1,8465	0,0001	9868
61S_80S_50_200, 0_20N_201_1000	2,1676	0,0001	9876
61S_80S_50_200, 0_20N_50_200	2,745	0,0001	9884
61S_80S_50_200, 0_20S_50_200	1,7631	0,0005	9884
61S_80S_50_200, 21S_40S_201_1000	1,71	0,0001	9894
61S_80S_50_200, 21S_40S_50_200	2,0597	0,0001	9885
61S_80S_50_200, 41N_60N_50_200	2,2673	0,0001	9853
61S_80S_50_200, 41S_60S_201_1000	1,7885	0,0001	9884
61S_80S_50_200, 41S_60S_50_200	2,321	0,0001	9895

Capítulo 4

Diversity of diversities: a response to Chaudhary, Saeedi, and Costello

Fernandez, M.O.[1] & Marques, A.C.[1,2]. 2017. Trends in Ecology & Evolution 32: 232–234[a]

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Chaudhary, Saeedi, and Costello (Chaudary *et al.*, 2016) argued against the paradigm of a unimodal richness pattern for marine species that peaks at the equator. They demonstrated that many marine taxa have a bimodal richness-distribution pattern that peaks close to tropical latitudes, and that richness is usually greater in the northern hemisphere (*i.e.*, the pattern is asymmetric). Indeed, the unimodal pattern is often uncritically assumed for marine species, most likely by analogy with terrestrial patterns. However, we believe that important caveats regarding the reasoning of Chaudhary *et al.* must be addressed: (i) a generalization that contrasts uni- and bimodal patterns may be an oversimplification for sets of taxa with complex and diverse biological functions and evolutionary histories; (ii) latitude is not a physical variable per se, and can be decomposed into many factors that actually drive diversification; (iii) the bimodal and asymmetric pattern may be an artifact of highly heterogeneous sampling and biased databases, at variance with the arguments advanced by Chaudhary *et al.* (2016).

First, the resulting bimodal pattern peaking in mid-latitudes is challenging and stimulates one to consider alternatives to classical patterns, but it consists of a synthetic chimera of several different distribution patterns, each with a particular shape and position of the peak or peaks (Figures S1–S4 in Chaudhary *et al.*, 2016), including unimodal or bimodal patterns with peaks at lower or higher latitudes. Patterns do not covary between groups, and cannot be transposed from one taxon to another. In addition, biological differences are found between or within taxa, for instance among species of the same taxon that live in different habitats (*e.g.*, benthic and pelagic, coastal and deep sea), in different oceans, and have different sizes and trophic levels (Hillebrand, 2004; Tittensor *et al.*, 2010; Powell *et al.*, 2012; Woolley *et al.*, 2016). Obviously, higher taxa comprise species with complex and non-uniform ecophysiologies, dispersal abilities, and life cycles, and these species cannot be expected to

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[a] Published in response to Chaudhary *et al.* (2016).

have similar habitat preferences. Moreover, ecological and historical diversifications interact, and may be equally important in shaping current biodiversity patterns. The richness of a region is a combination of the origins, extinctions, and changes in range distributions of species following changes in past environmental conditions (Jablonski *et al*., 2006). Therefore, different evolutionary histories may constrain current species distributions despite the existence of adequate environmental conditions. Explanations for the distribution of taxa may, therefore, combine their particular histories, biological functions, and habitat suitability/preference, which may or may not be directly correlated with latitude. A single summarizing pattern ignores and obscures the diversity of data inherent to biological systems, sometimes that are not even logically comparable (such as plankton vs benthos distribution).

Second, the quest for latitudinal patterns ignores the fact that this diversity of patterns is not driven by latitude *per se*, but by a multitude of variables. Differences in temperature and productivity are correlated with species distributions, and are major ecological drivers for both speciation and maintenance of diversity (Brayard *et al*., 2005; Tittensor *et al*., 2010; Woolley *et al*., 2016). Although these factors may generally approximate latitudinal patterns, they do not covary monotonically with the distance from the equator. Indeed, latitude is a position variable, not a factor determining species richness (Gaston, 2000). Solar irradiance is partially correlated with latitude, and may be an important driver of seasonal richness, abundance, and other physiological traits (*e.g.*, body sizes, energy requirements (Gaston, 2000)), but oversimplifying its associated mechanisms may prevent us from understanding their diversity.

Third, the uneven sampling effort around the globe is a fact, even though Chaudhary *et al*. (2016) disregarded this problem. They argued that the greater species richness in the northern hemisphere is related to the size of the continental shelf and consequent habitat availability (Chaudhary *et al*., 2016). However, sampling efforts in the northern hemisphere have historically been much greater, especially at particular latitudes, for both extant and fossil data {(Jablonski *et al*., 2006, Mittelbach *et al*., 2007), Ocean Biogeographic Information System (OBIS; iobis.org), Intergovernmental Oceanographic Commission (IOC) of UNESCO}. The OBIS data used for their analysis also reflect the greater effort expended by North American and European institutions to digitalize records for the same areas (Table 1). Therefore, it is not surprising to find higher marine species richness close to these biased latitudes. Chaudhary *et al*. (2016) supported their conclusion by mentioning that a meta-analysis found higher peaks of richness in the northern hemisphere than at the equator (Powell *et al*., 2012), and that this was not due to sampling effort. The data of Powell *et al*. (2012) show a larger number of studies in northern latitudes, and that although in general the location of diversity peaks is not a consequence of sampling bias, the number of peaks in other latitudes increases when potentially biased studies are included in the analysis. Therefore, if the data are not standardized by reference to the sampling effort, it is not possible to distinguish whether the patterns are biased or not. Moreover, the general latitudinal diversity pattern found by Chaudhary *et al*. (2016) does not account for different species richness across taxa – more diverse and better-sampled taxa may be shaping the synthesis curve. We argue that the use of absolute numbers of species for the analysis may mask the real patterns, and we suggest that standardizing species numbers in relation to sampling effort, or the number of records, would better test the different hypotheses.

It is indeed important to see the forest, but not all the trees follow the pattern of the forest. A universal and synthetic pattern does not necessarily fully explain all types of diversity. In sum, Chaudhary *et al*. (2016) and the increasing number of studies on marine species distributions are revealing multiple geographical patterns and explanations across taxa and habitats. It is legitimate to question whether a single overall latitudinal pattern can adequately synthesize complex evolutionary histories, or if we should instead be looking for a mosaic of patterns.

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Table

Table 1. Number of datasets, number of records, and accumulated sum of records added to OBIS database by OBIS nodes located in the Northern, Southern, or both hemispheres.[a]

Hemisphere	OBIS node name	Number of datasets	Number of records	Accumulated sum (%)
North	EurOBIS	620	18,448,018	39.68
	OBIS-USA	107	7,658,340	56.15
	OBIS Canada	168	4,172,311	65.13
	ArCOD	67	315,322	65.80
	OBIS Japan	6	300,807	66.45
	Caribbean OBIS	8	74,668	66.61
	OBIS China	10	69,241	66.76
	Korea OBIS	1	26,201	66.82
	MedOBIS	4	5,017	66.83
	Arctic OBIS	1	1,029	66.83
South	South Western Pacific OBIS	41	1,422,105	69.89
	Antarctic OBIS	139	1,232,069	72.5
	OBIS Australia	58	948,321	74.58
	OBIS Argentina	16	203,875	75.02
	Western South Atlantic OBIS	43	158,942	75.36
	Eastern South Pacific OBIS	10	33,182	75.43
Mixed	Not associated with an OBIS Node	33	3,609,575	83.19
	AfrOBIS	42	3,544,229	90.82
	OBIS-SEAMAP	644	2,519,007	96.23
	MicrOBIS	1	889,179	98.15
	FishBase OBIS	8	659,288	99.57
	IndOBIS	50	117,592	99.89
	Hexacorals	1	64,216	99.96
	SeamountsOnline	1	18,625	100
	SEAOBIS	2	1,594	100
	HAB OBIS	8	15	100
Total		2,089	46,492,768	

[a] Data from OBIS (http://www.iobis.org/indicators/).

Considerações Finais

Este estudo é pioneiro nas inferências de padrões de distribuição da diversidade de hidroides no Oceano Atlântico e mares polares circundantes em relação às variações batimétrica e latitudinal. Foram estudadas as amplitudes de distribuição batimétrica das espécies (Capítulo 1), a variação de características funcionais de indivíduos e espécies com a profundidade (Capítulo 2), e a distribuição da composição de espécies ao longo da profundidade e da latitude (Capítulo 3). Os padrões indicam que a distribuição de hidroides no Atlântico profundo é mediada tanto por fatores históricos – conforme sugerido pelo isolamento da fauna Patagônica e Antártica e pelas diferenças em amplitudes de distribuição batimétrica entre táxons e regiões –, quanto por gradientes ambientais associados à variação latitudinal e batimétrica. Tamanhos reduzidos e baixa fertilidade em mar profundo sugerem que a colonização e a evolução de hidroides ao longo da profundidade são principalmente influenciadas pela disponibilidade de alimento e pelas baixas densidades populacionais, enquanto a maior proporção de espécies com indivíduos solitários em mar profundo e maior uso de substratos não-consolidados também por formas coloniais sugerem influência da disponibilidade de substrato (Ramirez-Llodra *et al.*, 2010).

As amplas distribuições batimétricas e a tendência de maior uniformidade da fauna abaixo de 1.000 m de profundidade devem ser causadas pela grande capacidade de dispersão vertical e horizontal, assim como certamente inclui a tolerância às mudanças ambientais associadas à variação batimétrica (Young *et al.*, 1997a, 1997b). Da mesma forma, maiores amplitudes de distribuição geográfica para espécies com maiores amplitudes de distribuição batimétrica também devem resultar de tolerâncias fisiológicas e capacidades dispersivas.

Os dados sugerem que a colonização de hidroides no Atlântico profundo ocorre em um sistema de fonte-sumidouro, no qual as populações de profundidade seriam sustentadas pela imigração de indivíduos de águas mais rasas (Rex *et al.*, 2005). As extensões das amplitudes de distribuição das espécies, geralmente do raso para o fundo, com raras espécies estritamente batiais ou abissais, e a menor proporção de espécies férteis abaixo de 1.000 m de profundidade, apontam para taxas mais baixas de reprodução sexuada em estratos batimétricos profundos. Ainda, a proporção de espécies capazes de liberar medusa abaixo de 50 m é geralmente mais baixa do que em águas rasas costeiras – apesar de a proporção aumentar com a profundidade, principalmente abaixo de 1500 m. A liberação de medusa seria desvantajosa em um ambiente com baixas densidades populacionais, por diminuir a chance de fecundação devido ao aumento da dispersão de gametas, e ainda despender mais energia para reprodução em um ambiente com poucos recursos energéticos. No entanto, apesar do aumento de grupos meroplanctônicos com o aumento da profundidade, seus baixos índices de fertilidade adicionam evidências para a hipótese de fonte-sumidouro (Rex *et al*., 2005).

Algo importante deste estudo é que lidamos com um esforço amostral desigual ao longo do Oceano Atlântico, menor em latitudes tropicais sul e em profundidades abaixo de 1.000 m. Dados estão disponíveis principalmente próximos às margens continentais, com um hiato no conhecimento nas extensas planícies abissais. Isso demonstra a necessidade de melhores amostragens no futuro. O maior número de registros profundos nas latitudes mais bem amostradas é a base para afirmar que há subestimativa de riqueza de dados biológicos associados para diversas áreas – ou pior, nenhuma área está, de fato, adequadamente amostrada. A alta diversidade que já é conhecida para o grupo em mar profundo pode revelar-se ainda maior com futuras coletas direcionadas às áreas menos estudadas e a diferentes habitats, como por exemplo os de substratos não-consolidados, que tem grande potencial de riqueza.

O caminho a seguir para o estudo de macroecologia de hidroides de mar profundo inclui maximizar o rendimento dos dados já coletados e um maior apoio e dedicação à amostragem de áreas profundas, principalmente do Atlântico Sul. Derivando diretamente desta tese, é de particular interesse um estudo que relacione as características funcionais de hidroides tanto com as amplitudes de distribuição batimétrica quanto com as variações latitudinais e batimétricas de composição de espécies, com o objetivo de revelar a influência de características funcionais, principalmente relacionadas ao tamanho e reprodução, na distribuição de espécies. Por fim, investigações futuras integrando variáveis ambientais e filogenias devem contribuir com o entendimento dos processos micro e macroevolutivos envolvidos nos padrões aqui observados (Leclère *et al*., 2007; Cartwright & Nawrocki, 2010; Fine, 2015).

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Resumo

A variação batimétrica nos oceanos e suas mudanças ambientais associadas impõem limites à distribuição de espécies, modulando a ocorrência de indivíduos com diferentes formas, funções e histórias de vida de acordo com a profundidade, e sendo, portanto, importante para o entendimento de padrões da biodiversidade marinha. Este estudo objetiva inferir padrões de distribuição de hidroides no Oceano Atlântico e mares árticos e antárticos adjacentes a mais de 50 m de profundidade, buscando contribuir para o entendimento da diversificação e estruturação associadas à variação batimétrica que propiciaram a ocupação dos diferentes ambientes pelo grupo. Apresentamos pela primeira vez inferências das amplitudes de distribuição batimétrica das espécies, da variação de características funcionais de indivíduos e espécies com a profundidade e da distribuição da composição de espécies ao longo da profundidade e da latitude. Em conjunto, os resultados indicam que a distribuição de hidroides no Atlântico profundo está relacionada a fatores históricos e a gradientes ambientais associados às variações latitudinal e batimétrica. Os tamanhos reduzidos e a baixa fertilidade em mar profundo sugerem que a colonização e a evolução de hidroides ao longo da profundidade são principalmente influenciadas pela disponibilidade de alimento e pelas baixas densidades populacionais. Ainda, a maior proporção de espécies e indivíduos solitários em mar profundo e o maior uso de substratos não-consolidados sugerem influência da disponibilidade de substrato. A proporção de espécies capazes de liberar medusas abaixo de 50 m é geralmente menor que em águas rasas costeiras, mas a proporção aumenta com a profundidade, principalmente abaixo de 1.500 m. A liberação de medusas seria desvantajosa em um ambiente com baixas densidades populacionais, por aumentar a incerteza da fecundação dada pela dispersão de gametas, e despender mais energia para reprodução em um cenário de poucos recursos alimentares. Amplas distribuições batimétricas sugerem capacidade de dispersão vertical e alta tolerância às mudanças ambientais associadas à variação batimétrica. Os resultados indicam também que a colonização de hidroides em mar profundo ocorre em um sistema de fonte-sumidouro, no qual as populações de mar profundo seriam sustentadas por imigração de águas mais rasas. Mostramos neste estudo que hidroides são importantes habitantes do mar profundo e que o entendimento da diversidade do grupo neste ambiente se beneficiará de investigações em áreas ainda pouco amostradas, como latitudes tropicais sul e profundidades abaixo de 1.000 m.

Palavras-chave: Macroecologia marinha, mar profundo, Hydrozoa

Abstract

The bathymetric variation in the oceans and associated environmental changes impose limits on the distribution of species, modulating the occurrence of individuals with different forms, functions and life histories according to depth, and is therefore important for the understanding of marine biodiversity patterns. This study aims to infer patterns of hydroid distribution in the Atlantic Ocean and adjacent Arctic and Antarctic seas at more than 50 m deep, seeking to contribute to the understanding of the diversification and structuring associated with the bathymetric variation that favored the occupation of the different environments by the group. We present for the first time inferences on the bathymetric ranges of distribution of the species, on the variation of functional traits of individuals and species with depth, and on the distribution of the species composition along depth and latitude. Together, the results indicate that the distribution of hydroids in the deep Atlantic is related to historical factors and to the environmental gradients associated with latitudinal and bathymetric variations. Reduced sizes and low fertility in deep sea suggest that colonization and evolution of hydroids along depth are mainly influenced by food availability and low population densities. Also, the greater proportion of solitary species and individuals in the deep sea and the greater use of unconsolidated substrates suggest influence of substrate availability. The proportion of species capable of releasing medusae below 50 m deep is generally lower than in shallow coastal waters, but the proportion increases with depth, especially below 1,500 m. The release of medusae would be disadvantageous in an environment with low population densities, by increasing the uncertainty of fertilization given by the dispersion of gametes, and expending more energy for reproduction in a scenario of few food resources. Wide bathymetric distributions suggest vertical dispersal capacity and high tolerance to the environmental changes associated to the bathymetric variation. The results also indicate that colonization of hydroids in the deep sea occurs in a source-sink system in which deep-sea populations would be sustained by shallower water immigration. We show in this study that hydroids are important inhabitants of the deep sea and that the understanding of the diversity of the group in this environment will benefit from investigations in areas still poorly sampled, such as southern tropical latitudes and depths below 1,000 m.

Keywords: Marine macroecology, deep sea, Hydrozoa