

1 **Traits and depth: what do hydroids tell us about morphology and life-history strategies**
2 **in the deep sea?**

3

4 **Running title:** Functional traits and depth

5

6 **Abstract**

7 **Aim:** Traits affect the survival and reproduction of individuals in different habitat conditions,
8 ultimately altering their fitness. The bathymetric gradient in the ocean is associated with large
9 changes in environmental conditions that may influence the occurrence of specific traits.
10 Therefore, characterizing trait variation with depth can illuminate drivers related to the
11 distribution of diversity of forms, functions, and life histories. Our aim was to investigate
12 patterns of variation in the diversified life histories and morphologies of hydroids with depth,
13 integrating these patterns with the natural history of the group and ecological principles of the
14 deep sea.

15 **Location:** the Atlantic Ocean and adjacent polar seas, from 50 m to 5,330 m deep.

16 **Major taxa studied:** Hydrozoa.

17 **Methods:** Analyses were based on 14 traits collected for a total of 4,668 specimens of hydroids,
18 belonging to 438 species. Records were divided into 12 depth strata for comparisons. We
19 evaluated: how each trait varies with depth; whether variation in some traits is affected by the
20 presence of other traits; and how traits covary. Similarities in trait compositions among depth
21 strata were also investigated using PCoA.

22 **Results:** Traits of hydroids vary with depth, with more pronounced differences for regions
23 deeper than 1,000 m. Hydroids are generally smaller, infertile, solitary, meroplanktonic, and
24 devoid of protective structures with increasing depth. The relationship, however, is not always
25 linear. Also, some covariation and correlation between traits was evident. For example, depth
26 may affect size differently according to the presence of specific traits such as structures
27 protecting against predation. The lower proportion of fertile specimens recorded in the deep
28 sea suggests that chances for genetic recombination are reduced in deep-sea populations,
29 ultimately leading to slower rate of evolution.

30 **Main conclusions:** We identified novel trends in hydroid trait variation with depth by
31 combining observations on morphology, ecology, and life history, clarifying selection
32 pressures on hydroids in the deep sea.

33

34 **Keywords:** Atlantic ocean, bathymetric gradients, deep-sea benthos, fertility, Hydrozoa, life-
35 history strategies, size, traits

36

37 **Introduction**

38

39 Macroecological inferences aim to characterize broad patterns in the distribution of
40 biodiversity – for example, in richness, abundances, range sizes, and body sizes – and
41 understand the processes that underlie them across large temporal and geographic scales
42 (Brown, 1995; Gaston & Blackburn, 2000; Keith et al., 2012; Witman & Roy, 2009). Trait-
43 based approaches are increasingly being used to help understand the processes that regulate
44 large-scale diversity patterns (e.g. Lamanna et al. 2014. PNAS 111:13745-13750; Schumm et
45 al. 2019. Proc Roy Soc B: 286:20190745). Traits affect the abilities of individuals and species
46 to occur in different habitats by mediating responses to biotic and abiotic conditions. Thus,
47 they impact the capacities of individuals to grow, survive and reproduce, ultimately influencing
48 spatial variations in species composition (Bolam et al., 2017; Brun, Payne & Kjørboe, 2016;
49 Mlambo, 2014; Violle et al., 2007). Biological traits may vary either between or within species,
50 since developmental regulation by environmental signals may produce phenotypes adapted to
51 the prevailing conditions (Bosch et al., 2014; Gilbert, 2012). Therefore, it is important to
52 incorporate intraspecific variation into macroecological studies because it relates to niche
53 occupation by individuals or populations of the same species (Messier et al. 2010. Ecology
54 Letters 13:838-848). In general, analyses of trait variations across large spatial and
55 environmental gradients has the potential to reveal mechanisms not evident from species
56 richness alone (Bremner, 2008; Connell & Irving, 2009; Barton et al., 2013; Stahl et al., 2014;
57 Violle et al., 2014; Monro & Marshall, 2015; Frainer, et al., 2017; Henriques et al., 2017;
58 Lamanna et al. 2014. PNAS 111:13745-13750; Schumm et al. 2019. Proc Roy Soc B:
59 286:20190745).

60 In the oceans a number of environmental variables change with bathymetry, which can
61 lead to changes in functional and life history traits along this gradient (McClain, Rex & Etter,
62 2009; Ramirez-Llodra et al., 2010). For example, sunlight is rapidly filtered as depth increases
63 (Stewart, 2006), which leads to a lack of primary production in the deep sea. The input of
64 organic matter from surface waters, the primary source of carbon in the deep oceans, leads to
65 a decreasing gradient of food availability with depth, except for chemosynthetic environments
66 such as hydrothermal vents (Ramirez-Llodra et al., 2010; Smith, De Leo, Bernardino,
67 Sweetman & Arbizu, 2008). Limited food supply is followed by a pattern of decreasing faunal

68 biomass and population densities from the continental shelf towards the abyssal plains (Rex et
69 al., 2006; Sanders & Hessler, 1969), favoring the occurrence of organisms with specific body
70 sizes according to their trophic, reproductive or metabolic characteristics, enabling them to
71 exploit available resources more efficiently (Gambi et al., 2017; McClain, Allen, Tittensor &
72 Rex, 2012; Ramirez-Llodra et al., 2010; Rex & Etter, 1998; van der Grient & Rogers, 2015).
73 Another example is the sudden faunal variation between the edge of the continental shelf and
74 the slope, related to the change in sediment type from hard substrata to muddy bottoms typical
75 of the deep sea (Clark, Consalvey & Rowden, 2016; Jamieson, 2015). Therefore, variation in
76 the diversity of forms, functions and life histories with depth are most likely related to unique
77 drivers of evolution and adaptation. However, patterns of trait variations along bathymetry still
78 remain poorly quantified for most marine organisms.

79 Trait-based approaches are also potentially relevant for conservation of deep-sea
80 biodiversity. Specifically, they may help identify species particularly vulnerable to direct
81 anthropogenic impacts and climate change (Bremner, 2008; Stuart-Smith et al., 2015). For
82 example, deep-sea mining and bottom trawling fishing activities may reduce the availability of
83 hard substrata and impact species differently according to substratum use (Gollner et al., 2017;
84 Jones et al., 2017; Puig et al., 2012; Vanreusel, Hilario, Ribeiro, Menot & Arbizu, 2016).
85 Furthermore, changes in oxygenation, temperature, pH, and flow of organic matter to the ocean
86 floor affect the distribution of deep-sea species according to their traits (Danovaro et al., 2017;
87 Sweetman et al., 2017; Perez et al., 2018). Better information about the distribution of traits
88 along bathymetric gradients could, therefore, help model future response of the deep-sea fauna
89 to anthropogenic changes and guide its management.

90 Here, we investigated patterns of trait variations with depth in hydroids. Hydroids are
91 morphologically and ecologically diverse medusozoans (cnidarians that typically include a
92 medusa in their life cycle) that occur from shallow to hadal depths (Calder, 1996; 1998; Kramp,
93 1956). These modular organisms exhibit a wide array of biologically relevant traits, including
94 variation in size, shape, coloniality, and life cycle, that likely influence the exploitation of
95 environmental resources and exposure to predators, making them a well suited group for
96 studying trait diversity patterns (Cornelius, 1995a, 1995b; Cunha, Maronna & Marques, 2016;
97 Marfenin, 1997). For example, their typical life cycles include benthic polyps that bud off
98 medusae bearing gametes (after fertilization, the larva settles and metamorphoses into a new
99 polyp stage) (Cornelius, 1995a). However, different levels of reduction of the medusa stage,
100 up to its complete absence, occur among the different lineages of hydrozoans and are
101 interpreted to be advantageous or disadvantageous depending on the conditions in which the

102 individual/population/species lives (Calder, 1992, 2000; Cornelius, 1992). Hydroids also
103 undertake a large repertoire of modes of asexual reproduction that may be triggered by the
104 environment and may help populations survive in conditions where chances for sexual
105 reproduction are limited (Gili & Hughes, 1995).

106 We describe trait variation with depth in terms of 14 biological traits of hydroids that
107 influence their distributions in different habitats (see Table 1) and relate the patterns with the
108 biology of the group and deep-sea ecology.

109

110 **Material & methods**

111

112 *Study area, data sampling, and identification*

113

114 Our analyses were based on hydroid stages (excluding the hypercalcified Milleporidae
115 and Stylasteridae, and Limnomedusae) from depths below 50 m (maximum depth was 5,330
116 m) of the Atlantic Ocean and adjacent Arctic and Antarctic waters (Fig. 1). The material studied
117 belongs primarily to museum collections (National Museum of Natural History, Smithsonian
118 Institution; Museum of Comparative Zoology at Harvard University; Naturalis Biodiversity
119 Center; Royal Ontario Museum; Canadian Museum of Nature; Museum of Zoology of the
120 University of São Paulo and National Museum of the Federal University of Rio de Janeiro)
121 with geographic and depth data. MOF and ACM examined all material to check or to make
122 identifications and to gather morphological and biological data, enhancing uniformity within
123 the data set. The specimens were identified based on current literature specific to each taxon.
124 In total, we studied 4,668 records of hydroids belonging to 606 taxa used in the analyses, of
125 which 438 are identified at the species level (some records could not be identified to species
126 level but were included in the analyses if their respective trait data could be collected). A total
127 of 615 new species occurrence records were made for their respective regions.

128

129 *Functional and morphological traits*

130

131 We collected data for 14 traits from the material, seven related to the species as a whole
132 (e.g., life cycle and presence of exoskeleton), and seven related to the specimens (e.g., height
133 and substratum use) (Table 1; see Appendix S1 in Supporting Information). Information about
134 species life cycle and sexual reproduction was compiled from the primary literature. When the
135 life cycle was unknown for a specific species, we used the information for its genus or family

136 – except when extensive intra-genus or intra-family variation are known to occur – and
137 recorded the basis for approximation. Species reported as “benthic with swimming gonophore”
138 and “benthic with eumedusoid” life cycles were all considered “benthic” in the analysis, due
139 to the limited medusa/gonophore dispersive capacities (Boero & Bouillon, 1989; Migotto &
140 Marques, 1999). Likewise, the “dioecious” *Nemertesia antennina* (Linnaeus, 1758) was
141 considered to be ecologically “monoecious” in the analysis, because its gregarious growing
142 habit approximates male and female gametes (Hughes, 1977). Similarly, “absent” and
143 “shallow” hydranth exoskeletons, “phylactocarp”/“coppinia” and “corbula”/“pseudocorbula”
144 gonophore protections were considered to be single traits due to their biological similarities.

145

146 *Analyses of size variation with depth*

147

148 Records were divided into 12 depth strata (50 – 100 m; 101 – 200 m; 201 – 300 m; 301
149 – 400 m; 401 – 500 m; 501 – 600 m; 601 – 800 m; 801 – 1,000 m; 1,001 – 1,500 m; 1,501 –
150 2,000 m; 2,001 – 3,000 m and 3,001 – 5,330 m strata – records at depths between classes were
151 included in the deeper strata, e.g. 100.5 m is within the 101 – 200 m stratum) for comparisons.
152 To evaluate if size (height of the specimens) varies with depth, variations in size within and
153 between depth strata were summarized in boxplots, and differences analyzed by permutational
154 ANOVA using the ‘aov’ function from the ‘lmPerm’ package in R (Wheeler & Torchiano,
155 2016), followed by pairwise comparisons with the ‘pairwisePermutationTest’ function in the
156 ‘rcompanion’ R package (Mangiafico, 2017). In addition, sizes were plotted against depth at
157 which they were collected, for all specimens together and separately for those species with
158 more than 50 records. A linear relationship between size and depth was tested using the ‘lm’
159 function in the ‘stats’ R package on the standardized data for equal sampling across depths (R
160 Core Team, 2017). To infer if variation in size along depth is trait dependent, the standardized
161 data set was plotted with different colors for each trait category and linear models were fitted
162 to test for significant relationships between size and depth for each subdivision. Regression
163 lines were plotted only for significant relationships. Broken specimens were excluded from all
164 analyses regarding size.

165

166 *Analyses of other trait variation with depth*

167

168 To evaluate how the relative abundance of each trait category varies with depth, we
169 calculated the proportion of records and species within each trait category per depth stratum.

170 Proportions were used to allow comparisons between unequally sampled depth strata. To
171 describe the heterogeneity of sampling effort among depths, the total number of records
172 computed for each trait was indicated per depth stratum. For each trait, only records whose
173 trait information could be collected were computed. Trait records scored as ‘unknown’ were
174 excluded from the analyses. We used the Pearson’s Chi-square test to search for significant
175 differences in traits’ proportions with depth (‘chisq.test’ function in ‘stats’ R package; R Core
176 Team, 2017). A post-hoc z-test on the adjusted Pearson residuals allowed for the identification
177 of data strongly contributing to significant differences, i.e., values higher (positive) or lower
178 (negative) than expected (critical z-value), for a 0.05 significance level with Bonferroni
179 correction for multiple testing. Life cycle variation with depth was further investigated
180 regarding differences within coloniality, fertility, and substratum use categories. In the analyses
181 regarding species, only taxa identified to species level were used – three of them were
182 characterized as unique morphotypes and included in the species analyses, although their
183 specific names are uncertain, namely *Acaulis* cf. *rosae* (Verrill, 1878), *Euphysora* ?*bigelowi*
184 Maas, 1905, and *Millardiana* sp.

185 Principal coordinates analysis (PCoA) was used to assess similarities in the 14 traits
186 compositions among depths (‘cmdscale’ function; R Core Team, 2017). Records scored as
187 ‘unknown’ were removed from the analysis. The resemblance matrix was calculated using the
188 Gower’s dissimilarity index (‘gowdis’ function in the ‘FD’ package, R Core Team, 2017),
189 which allows including continuous, categorical and ordinal variables in the dissimilarity
190 measure, and considers a normalized distance between quantitative traits (Gower, 1971;
191 Podani, 1999). To visualize the directions towards which the traits change in the ordination,
192 trait vectors with correlations $R > 0.5$ were fitted and their lengths scaled according to their
193 correlation values (‘envfit’ function in the ‘vegan’ R package). Finally, the spatial medians of
194 each depth strata were calculated and plotted in the PCoA ordination to better visualize traits
195 similarities among depths (‘betadisper’ function, ‘vegan’ R package).

196

197 **Results**

198

199 The heights of the specimens were significantly different between depth strata ($p <$
200 0.0001; Fig. 2). Differences are more prominent between depth strata deeper and shallower
201 than 1,000 m, with deep-sea specimens being smaller, on average. In general, differences were
202 found between shallower (50 – 1,000 m deep) and deeper (1,000 – 5,330) depth strata, with
203 few exceptions (Fig. 2; see Appendix S2). From 50 to 1,000 m deep, hydroids varied greatly

204 in size, with both small and large specimens found, but variation decreases when deeper than
205 1,000 m deep, where mostly small specimens were found (Figs. 2–3). Similar trends were
206 found within species, especially for *Lytocarpia myriophyllum*, *Acryptolaria conferta*, and
207 *Billardia subrufa* (Fig. 3B–H).

208 No simple linear relationship exists between height and depth (Fig. 4A), except for
209 some selected trait categories (plotted regression lines in Fig. 4; see Appendix S3). Our data
210 do show that some traits covary with the height of the specimens. For example, basal diameter
211 and orders of branching increase with the height of the specimen, and taller specimens are more
212 often polysiphonic. Also, fertile specimens are frequently larger than infertile ones (Fig. 4B,
213 D, E, L; Fig. 8). Finally, specimens of benthic taxa are larger than those of meroplanktonic taxa
214 (Fig. 4J).

215 All 14 traits varied significantly with depth in terms of the proportion of records in each
216 trait category ($p < 0.001$), and nearly all varied in proportion of species, the exceptions being
217 for life cycle and sexual reproduction (Figs. 5–6, see Appendix S4 for all p -values). However,
218 larger proportions of meroplanktonic and monoecious species occur below 1,500 m deep (Fig.
219 5).

220 As with size, many other traits vary prominently below 1,000 m. The presence of
221 exoskeleton on hydrocauli decreases notably below 1,000 m deep, for both records and species;
222 the proportion of records with no exoskeleton on hydranth increases between 1,500 and 3,000
223 m; and proportion of records with an operculum decreases below 2,000 m. A decrease in
224 records of exoskeleton enveloping the gonophore is also notable – a substantial number of
225 records (more than 25%) have no gonophore protection between 1,000 and 3,000 m, in contrast
226 to only a few records from 50 to 500 m (less than 5%). Similarly, records with nematophores
227 significantly decrease below 2,000 m deep (less than 20%, compared to 40 – 50% in shallower
228 depths). Regarding life cycle, the proportion of meroplanktonic records increases below 1,500
229 m. There is a substantial increase in both records (~10 – 30%, in contrast to less than 5% in
230 shallower strata) and species (~15 – 25%, in contrast to less than 5% in shallower strata) of
231 solitary forms below 1,000 m. The proportion of fertile specimens decreases from 1,000 to
232 3,000 m. Finally, the use of biogenic substrata decreases below 1,000 m, with increased use of
233 both soft and non-biogenic hard substrata (see Figs. 5–6 for all proportions; see Appendix S5).
234 Soft substrata were frequently colonized at all depth strata by both solitary and colonial species
235 (see Appendix S6). Hydrocauli are significantly wider basally (> 1 mm) and tend to be
236 polysiphonic from 400 to 1,000 m (Figs. 6B, D; see Appendix S5). Alternatively, considerably

237 more monosiphonic colonies, with more basal annulations, were found in the 50 – 100 m depth
238 stratum (see Appendix S5 for all significance values).

239 Life-cycle variation with depth was related to other traits (Fig. 7). For example, there
240 was minor variation in life cycle with depth for colonial records and species, with a ~10%
241 increase in those meroplanktonic below 3,000 m (Fig. 7A, B). For solitary taxa, on the other
242 hand, there were conspicuously more of those that are meroplanktonic between 500 and 3,000
243 m deep (60 – 90% of the records, in contrast to only 0 – 20% in shallower strata; Fig. 7A, B).
244 Meroplanktonic specimens were more often infertile than benthic specimens, especially with
245 increasing depth, and there was increased use of soft substrata by meroplanktonic specimens
246 with depth (see Fig. 7C, D for proportions).

247 The distribution of some traits is dependent on or correlated to the distribution of other
248 traits since there is some covariation with traits (Fig. 8). The lower incidence of gonophore
249 protection in the deeper strata is followed by a lower incidence of nematophores, both
250 protective structures. Similarly, higher colonies in the 100 – 1000 m strata are correlated with
251 greater fertility, base diameter, branching and polysiphony (Fig. 8, see Appendix S7).

252

253 **Discussion**

254

255 The analyses presented here reveal previously undocumented bathymetric trends in
256 hydroid traits by combining observations on morphology, ecology, and life history, thereby
257 providing an avenue for understanding selection pressures that impact diversification and
258 evolution of hydrozoans in the deep-sea. Our analyses suggest that biological traits of hydroids
259 vary with depth, with more pronounced differences below 1,000 m. Hydroids were more
260 frequently smaller, meroplanktonic, solitary, lacking exoskeletons and nematophores, and
261 infertile with increasing depth, although the relationships are not always linear. These patterns
262 indicate that conditions in the deep-sea favour specific morphological and life-history
263 characteristics of individuals and species and that these traits are most likely facilitating the
264 exploitation of environmental resources in deep-sea habitats.

265 A particularly important trait that varies with depth is body size, probably associated
266 with the decreased availability of organic matter to the deep-sea benthos. It has been proposed
267 that this selective pressure affects the deep-sea fauna differently depending on other organismic
268 traits, such as feeding type and mobility. While there is a reduction in the average size of many
269 organisms with depth, an opposite pattern of larger individuals in the deep sea occurs in mobile
270 scavengers (i.e. animals that search for deadfalls), deposit feeders and detritivores (i.e. animals

271 that obtain food from the accumulated organic matter at the seafloor), and species living in
272 specialized habitats (e.g., close to hydrothermal vents and cold seeps; Hessler & Jumars, 1974;
273 Ramirez-Llodra et al., 2010; Rex et al., 2006; Sanders & Hessler, 1969). Our results show that
274 the size of hydroids decreases below 1,000 m. The larger specimens of hydroids occurring
275 above 1,000 m often belong to species with wide bathymetric distributions, with individuals
276 found in deeper waters being smaller (Fig. 3). This suggests that individuals/colonies have a
277 different growth rate in deep-sea environments, probably related to diminishing food supply
278 with increasing depth, which would hinder the growth of larger organisms in deeper waters.
279 Hydroids are suspension feeders and, thus, the smaller sizes of the hydroid community are
280 likely related to the scarcity of food in the plankton. In contrast, the gigantic (more than 2 m in
281 height) benthic solitary hydroid *Branchiocerianthus imperator* has the unusual habit of
282 sweeping the bottom with its tentacles to feed on deposited material, likely allowing higher
283 growth (Foell & Pawson, 1986; Omori & Vervoort, 1986). This species was not sampled in
284 this study but has been recorded for the Atlantic, Indian, and Pacific oceans up to 5,307 m deep
285 (Allman, 1888; Omori & Vervoort, 1986; Vervoort, 1966). Declines in the input of particulate
286 organic matter to the deep seafloor caused by climatic changes may, therefore, have an impact
287 on the composition of deep-sea hydroid assemblages (Sweetman et al., 2017). Smaller sizes
288 may also be related to temperature and its influences on metabolism. Cold deep-sea
289 temperatures limit metabolic rates, which in turn may constrain energy availability for growth
290 (Childress, Cowles, Favuzzi & Mickel, 1990; McClain, Allen, Tittensor & Rex, 2012),
291 although lower growth rates do not necessarily result in smaller sizes (Angilletta, Steury &
292 Sears, 2004). In general, temperature may not be a good predictor of size, because the
293 relationship depends on the specifics of the physiologies of individual taxa (Angilletta &
294 Dunham, 2003; Brown, Gillooly, Allen, Savage & West, 2004; McClain et al., 2015).

295 Despite the clear size differences between hydroids along the depth strata, the
296 relationship between size and depth is not linear, probably due to the presence of small-sized
297 hydroids all along the gradient (Figs. 3A, 4A). Within some trait categories, however, size and
298 depth are significantly associated (Fig. 4), suggesting that depth may affect size differently
299 according to the presence of other traits. For specimens with a protective exoskeleton
300 enveloping hydrocauli, hydranths, and gonophores, for instance, size and depth are associated,
301 but for specimens without an exoskeleton there is no apparent association (Fig 4 F-H).
302 Similarly, the size of colonial specimens significantly decreases with depth, but this is not
303 evident for solitary species (Fig. 4M). This pattern is probably related to colonial species being
304 capable of growing by adding modules or reducing in size by module reabsorption, which

305 confers them greater plasticity in response to environmental changes than for solitary species
306 (Marfenin, 1997). Exceptionally, monoecious specimens significantly increase in size with
307 depth (Fig. 4K). This could be related to a scenario of lower population densities with
308 increasing depth: while dioecious species would need to allocate energy to increase population
309 numbers to ease mating, monoecious specimens – with gametes of both sexes in the same
310 individual/colony – could allocate more energy for individual growth. Conflicting patterns for
311 size variation with depth were previously found for other taxa and have been related to species'
312 life-history traits or regions of occurrence (e.g., Gambi, Vanreusel & Danovaro, 2003; McClain
313 et al., 2015; Olabarria & Thurston, 2003; Ramirez-Llodra et al., 2010; Rex & Etter, 1998; van
314 der Grient & Rogers, 2015).

315 Smaller sized hydroids are expected to be more vulnerable to predation by several
316 animal taxa that feed on hydroids (Gili & Hughes, 1995). Given that nematophores and
317 exoskeletons are traits that are likely related to their protection (Gili & Hughes, 1995;
318 Mendoza-Becerril et al., 2016), one might expect their incidence to increase in the deep sea.
319 However, our data show that reduction of deep-sea hydroid sizes is not accompanied by
320 enhanced strategies for protection. We observe a higher proportion of species lacking
321 protective structures below 1,000 m – exoskeletons enveloping hydrocauli, hydranths, and
322 gonophores – and below 2,000 m – nematophores and opercula (Figs. 5A–H; 8). This suggests
323 that hydroids are likely less affected by predation pressure in deep habitats, even though
324 predation is considered an important structuring driver in many deep-sea communities
325 (Gallucci, Fonseca & Soltwedel, 2008; Micheli et al., 2002; Rex, 1976; Stevenson, Mitchell &
326 Davies, 2015).

327 Fertile specimens are more frequent shallower than 1,000 m (Fig. 6F), indicating
328 constraints not only on size in the deep sea but also on sexual reproduction, possibly due to
329 lower population densities in the deep sea. Sexual reproduction has been reported to be less
330 frequent in lower population densities for one well-studied species of hydroid (Danko,
331 Schaible, Pijanowska & Danko, 2018). The pattern may be evidence that deep-sea hydroid
332 populations are functioning under a source-sink dynamics, in which the deep sea would
333 function as a sink for some shallower water species, and where low nutrient input and low
334 population densities would not sustain reproductive populations immigrating from shallower
335 sources (Rex et al., 2005). Indeed, most hydroid species in the Atlantic Ocean have depth
336 ranges extending from shallower to deeper waters, and only a few species are restricted to
337 bathyal or abyssal depths (Fernandez & Marques, 2018; Gil & Ramil, 2017). Hydroids,
338 however, have a vast repertoire of modes of asexual reproduction (Gili & Hughes, 1995) that

339 could help maintain populations in deep-sea conditions, even if constrained by food
340 availability. In both cases, however, the lower proportion of fertile specimens in the deep sea
341 would decrease chances of genetic recombination in deep-sea populations, ultimately leading
342 to slower evolution. Further, the pattern may be evidence of low mortality of individuals in the
343 deep-sea. The selection of life-history traits such as body size, lifespan and reproductive
344 investment usually depends on the mortality risk of juveniles and adults, and low fecundity is
345 generally related to decreased juvenile mortality (Kindsvater, Mangel, Reynolds & Dulvy,
346 2016).

347 Solitary hydroid species, although rare in the group (ca. 6% of the species) (Cartwright
348 & Nawrocki, 2010; Schuchert, 2012; WoRMS, 2017), seem to be favored by the environmental
349 conditions below 1,000 m deep. The large increase in the proportion of records and species of
350 solitary rather than colonial with depth (Fig. 5M, N) could be a reflection of the increased
351 availability of soft substrata as sand and mud with depth, which is often the habitat for solitary
352 hydroids (Schuchert, 2012). The detritus deposited on the seafloor is often resuspended by deep
353 bottom currents (Bonnin, Haren, Hosegood & Brummer, 2006), which could favor suspension
354 feeding of solitary hydroids inhabiting soft bottoms. Colonial forms, on the other hand, more
355 often depend on hard substrata, biogenic or not, to settle and grow (Gili & Hughes, 1995).
356 However, increased use of soft substrata with depth was observed by both solitary and colonial
357 forms (Fig. 6G; see Appendix S6). The colonies frequently exhibited adaptations for
358 attachment in the sand, like developing root-like hydrorhizae. This ability of colonial hydroids
359 to grow on soft sediments has been reported rarely, and only for a few species (*e.g.*, Calder,
360 2017; Di Camillo et al., 2013; Gili & Hughes, 1995), but seems to be an important adaptation
361 allowing several hydroid species to occupy unconsolidated substrata of the deep sea (see
362 Appendix S6) where hard substrata are scarce. The decreasing use of biogenic substrata below
363 1,000 m deep (Fig. 6G) may be related to its lower availability, since abundances of species
364 that could potentially be used as substrata are, evidently, lower (McClain, Rex & Etter, 2009).
365 The capability to settle and grow on a variety of substrata would certainly allow hydroids to
366 survive in an increased number of habitats and thus has important consequences for dispersal
367 and colonization of new environments. For example, such hydroid species are less likely to be
368 affected by the reduced availability of hard substrata due to deep-sea mining or bottom trawling
369 fishing activities (Gollner et al., 2017; Jones et al., 2017; Puig et al., 2012; Vanreusel, Hilario,
370 Ribeiro, Menot & Arbizu, 2016). In addition, it could potentially decrease the need for long-
371 distance dispersal.

372 The increased proportion of meroplanktonic (able to release a medusa) records at
373 greater depth, especially in strata deeper than 1,500 m (Fig. 5I), seems counterintuitive.
374 Releasing a medusa and increasing gamete dispersal seems disadvantageous in an environment
375 with low population densities for cross-fertilization. Moreover, releasing a medusa requires
376 more energy to be allocated for reproduction, despite low food availability. On the other hand,
377 greater dispersal could help individuals get away from conspecifics to avoid competition in an
378 environment with scarce resources (Comita, 2017) and/or decrease chances of predation and
379 parasitism. In fact, species that release medusae usually have wider geographical ranges than
380 benthic species (Gibbons, Buecher, Thibault-Botha & Helm, 2010; Gibbons, Janson, Ismail &
381 Samaai, 2010; Rodriguez et al., 2017), although the opposite was found in the family
382 Hydractiniidae (Miglietta & Cunningham, 2012). A reasonable explanation for the increased
383 proportion of meroplanktonic records would be that the medusae released in deep-sea
384 environments are monoecious, an advantageous condition in an environment with scarce food,
385 allowing for greater dispersal and colonization of new environments along with ease of sexual
386 reproduction in an environment with low population densities. This plasticity was
387 demonstrated for hydroids, triggered by colder temperatures (Carré & Carré, 2000). It is
388 important to note, however, that patterns inferred in this study are for depths below 50 m deep.
389 Globally, around 74% of hydroid species are benthic and 26% meroplanktonic (holoplanktonic
390 species excluded; Gibbons, Janson, Ismail & Samaai, 2010). Therefore, disregarding
391 differences across depths, the total proportion of meroplanktonic species reported here (5%) is
392 much lower than that expected for entire oceans – either because the proportion of
393 meroplanktonic species in the Atlantic Ocean is lower than in other oceans, or, more likely,
394 because the proportion of meroplanktonic species is actually lower at depths greater than 50
395 m.

396 Other traits that vary with depth and may be related to deep-sea environmental
397 conditions are orders of branching, base diameter and polysiphony. Orders of branching
398 decrease with depth, (Fig. 6E), perhaps as a consequence of scarcity of food resources. Under
399 increased food availability, colonies may increase branching to maximize food consumption
400 (Marfenin, 1997). Increased base diameter and polysiphony from 400 to 1,000 m deep (Figs.
401 6B, D; see Appendix S5) may indicate a response to increased water circulation in the upper
402 slope, as a means for avoiding breakage or detachment, since survival in more exposed and
403 hydrodynamic habitats would demand more robust and flexible hydrocauli (Gili & Hughes,
404 1995).

405 Some traits, however, are correlated with each other. Correlations may be related either
406 to phylogenetic constraints or to trade-offs on resource allocation (Braendle, Heyland & Flatt,
407 2011). In conditions of limited resources, the allocation of the resource to one function may
408 restrict investment in another, resulting in trade-offs among optimal traits for survival and
409 reproduction (Braendle et al.; Stearns, 1989; Tökölyi et al., 2016). For example, benthic species
410 are larger than meroplanktonic species, which require more energy to release a medusa (Fig.
411 4J). Other examples are the greater proportion of meroplanktonic life cycles among solitary
412 species and the increased use of soft substrata by meroplanktonic species with depth (Fig. 7).
413 Curiously, fertile specimens studied here were larger, regardless of depth (Fig. 4L), perhaps
414 suggesting that hydroids do not develop reproductive structures until they reach a certain size.
415 Some covariations with traits were also found, and may be related to phylogenetic constraints.
416 For instance, the presence of gonophore protection and nematophores, both traits related to
417 protection, covary with depth (Fig. 8). These traits are related to species identities, often
418 changing across major clades and invariable among specimens of the same species. On the
419 other hand, traits that vary among specimens of the same species are less likely to be
420 phylogenetically constrained. Height and base diameter, for example, are traits that vary with
421 size, and their covariation may be more related to physical constraints (Fig. 8).

422 Despite our effort to collect trait data from deeper strata, there is a clear decrease in the
423 number of samples studied with depth (Figs. 5, 6). The lower numbers of specimens available
424 in museum collections with increasing depth may reflect both the challenges of sampling in
425 the deep sea and the decrease in faunal density with depth (Clark, Consalvey & Rowden, 2016).
426 The broad data collection presented here allowed comparisons and patterns to emerge. Unequal
427 sampling, however, may be hiding some of the variations in trait compositions (Fernandez &
428 Marques, 2017).

429 Most of the biological traits of hydroids in this study vary with depth, with specimens
430 being more frequently smaller, meroplanktonic, solitary, infertile, and devoid of exoskeleton
431 and nematophores with increasing depth. We present possible explanations for how these traits
432 may be impacting survival and reproduction in deep-sea conditions. Future studies relating trait
433 distribution patterns with specific deep-sea environmental conditions can help to test some of
434 the hypotheses presented here. We also show that the distribution of some traits may covary or
435 be correlated to others, possibly related to phylogenetic constraints or to trade-offs in resource
436 allocation. Patterns described here using a trait-based approach may also help to predict the
437 potential effects that increasing anthropogenic impacts may have on the deep-sea hydroid
438 fauna.

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682

683 **Data Availability Statement**

684 Biological traits data for the 606 identified taxa analysed in this study are available in the
685 Supporting Information file. Traits data collected for the specimens are available from the
686 corresponding author upon reasonable request.

687

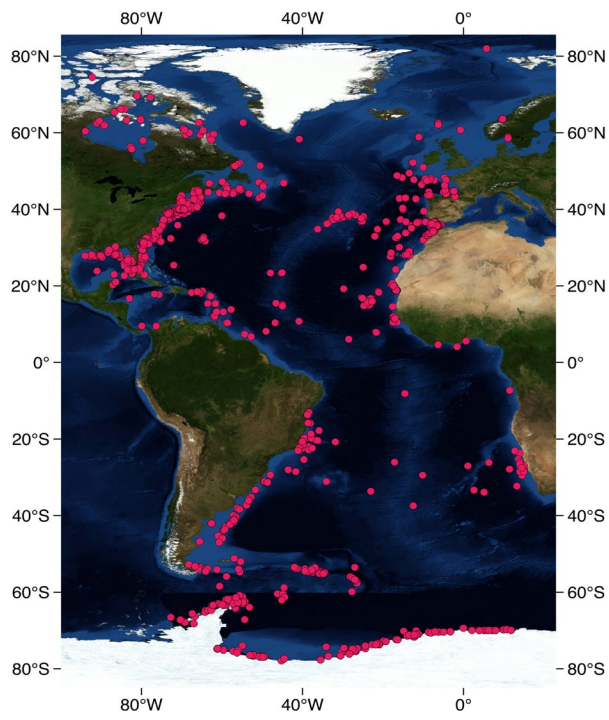
690 **Table 1.** Biological traits, their respective categories used in the analyses, and rationale for
 691 trait selection. Traits related to species identity (i.e., invariable among specimens) are indicated
 692 by asterisk (*).

Traits and categories	Rationale
Height of the specimen	Hydroids exhibit wide variation in size with species ranging from less than a millimeter to more than a meter (e.g. Cornelius, 1995a, 1995b; Millard, 1975; Schuchert, 2012). Increasing depth may favor specific body sizes, associated to the decreasing availability of organic matter
0.15 – 5 mm	
5.1 – 20 mm	
21 – 50 mm	
51 – 100 mm	
> 100 mm	
Diameter at the base of the specimen	Variable diameter of the hydrocauli (upright stems) in the region where they uplift from the stolon may confer robustness to individuals/colonies
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	Hydrocauli may have variable numbers of annulations, which confer flexibility (Cornelius, 1995a, 1995b; Gili & Hughes, 1995)
zero	
1 to 10	
> 10	
Basal arrangement	Hydrocauli may be composed of single (monosiphonic) or multiple (polysiphonic) tubes, conferring robustness to colonies (Cornelius, 1995a, 1995b)
monosiphonic	
polysiphonic	
Orders of branching	Hydroids stems branch with different patterns, including intraspecific variation in response to environmental conditions (Gili & Hughes, 1995)
stolonial / solitary	
erect, unbranched	
erect, with primary branching	
erect, with secondary branching	
erect, with tertiary branching	
erect, with quaternary branching or more	
Hydrocaulus exoskeleton (*)	A tubular exoskeleton protects hydrocauli to different extents (Mendoza-Becerril, Marian, Migotto & Marques, 2017)
absent	
filmy perisarc	
present	
Hydranth exoskeleton (*)	A protective exoskeleton may extend to the hydranths (feeding modules of the colony), which may be further
absent / shallow	

present with operculum	closed by opercular flaps in some species (Cornelius, 1995a)
Gonophore protection (*)	Gonophores (reproductive modules) may be enveloped
absent	by the exoskeleton only or by extra protective structures
enveloped by exoskeleton	– phylactocarps, coppinia, corbulae, and
phylactocarp / coppinia	pseudocorbulae (Cornelius, 1995a, 1995b; Millard,
corbula / pseudocorbula	1975)
Nematophore (*)	Nematophores – modified defensive polyps armed with
absent	nematocysts – may stop predation or larval settlement
present	(Cornelius, 1995a)
Life cycle (*)	Benthic (without medusa) or meroplanktonic (with
benthic	medusa) life cycles may be advantageous or
meroplanktonic	disadvantageous depending on the conditions in which
unknown / variable	the individuals lives (Cornelius, 1992)
Sexual reproduction (*)	Benthic hydroids may be monoecious or dioecious.
monoecious	Some species are variable, with both types of colonies
dioecious	recorded (Bouillon, Gravili, Pagès, Gili & Boero, 2006;
variable	Millard, 1975). Different strategies may relate to the
unknown	ease of finding a mate at different population densities
medusa	
Fertility	Specimens were checked regarding the presence (fertile)
fertile	or absence (infertile) of structures for sexual
infertile	reproduction
Coloniality (*)	Most hydroids are colonial, although some species are
colonial	solitary (Schuchert, 2012)
solitary	
Substratum	The nature of the substratum affects distribution of
biogenic	hydroids. Larvae generally settle and grow on hard or
hard (abiogenic)	biogenic substrata, with few specimens inhabiting soft
soft	bottoms (Ansín Agís, Ramil & Vervoort, 2001; Calder,
	1998; Fernandez, Navarrete & Marques, 2014)

694 **Figures**

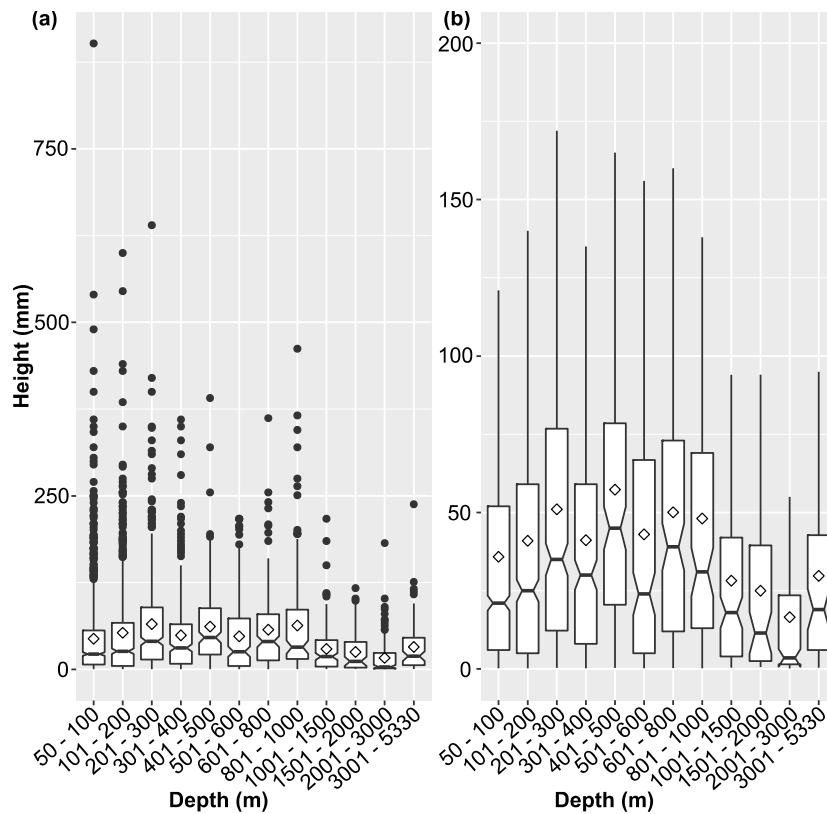
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696

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

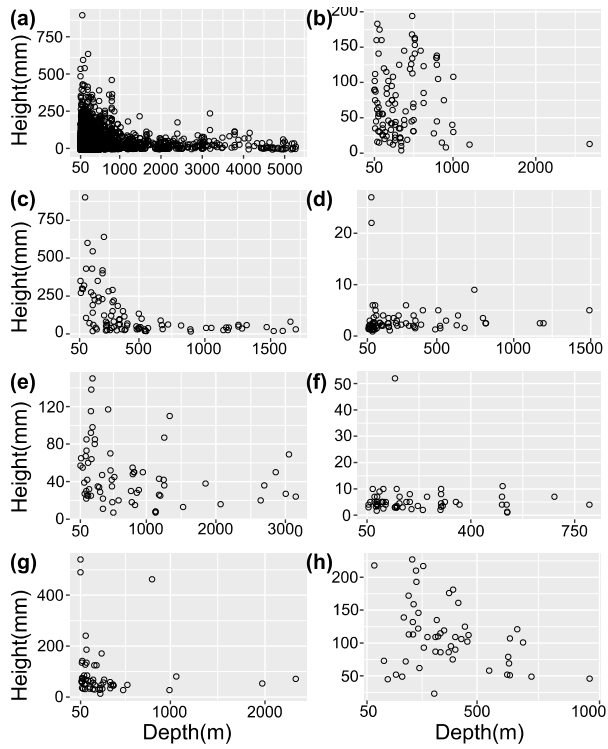
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700

701 **Figure 2.** Variation in height of the specimens along depth strata in the Atlantic Ocean
 702 including all data **(a)** and excluding outliers **(b)**. Boxplots summarize the interquartile range
 703 (boxes), the largest and smallest observations within a maximum of 1.5 times the interquartile
 704 range (whiskers), outliers (points), medians (notches inside the boxes), and averages
 705 (diamonds).

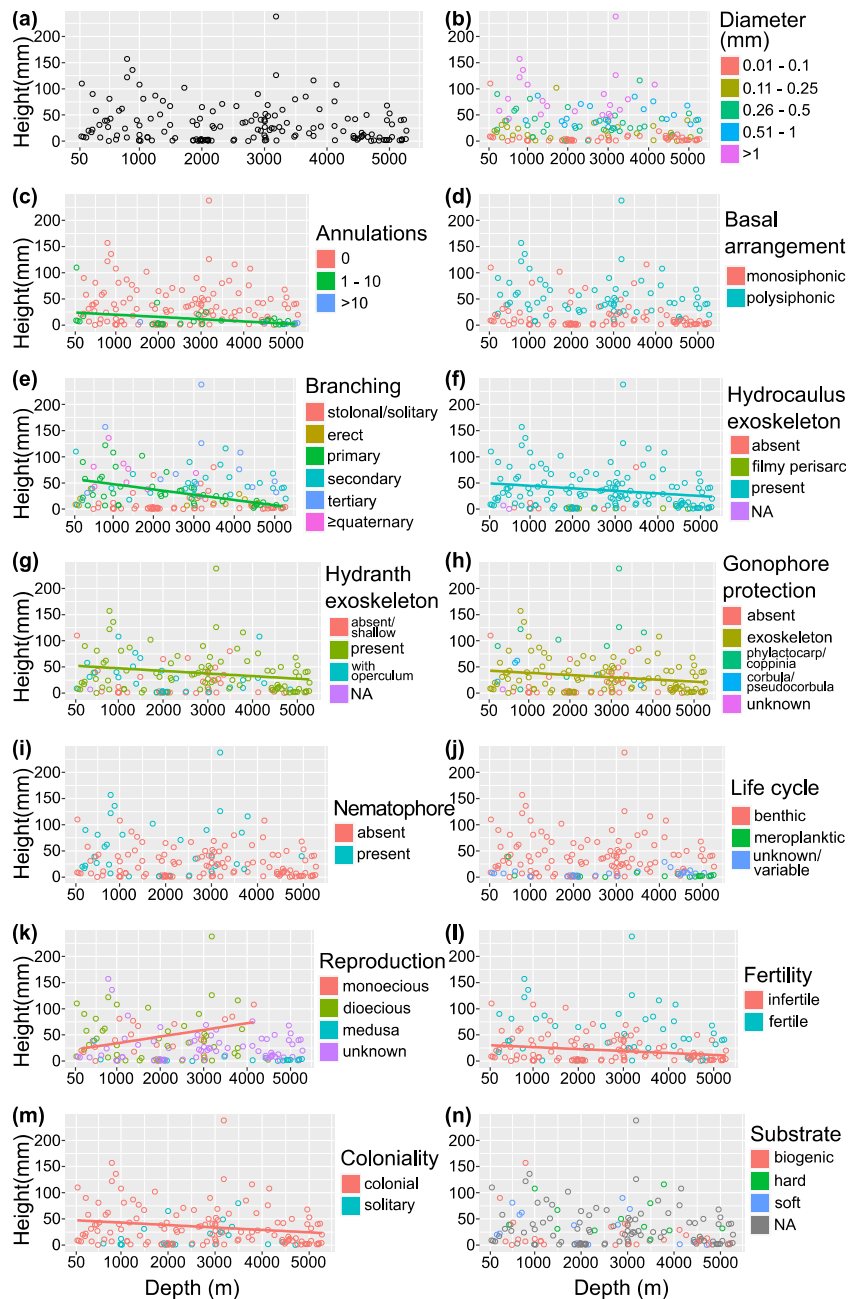
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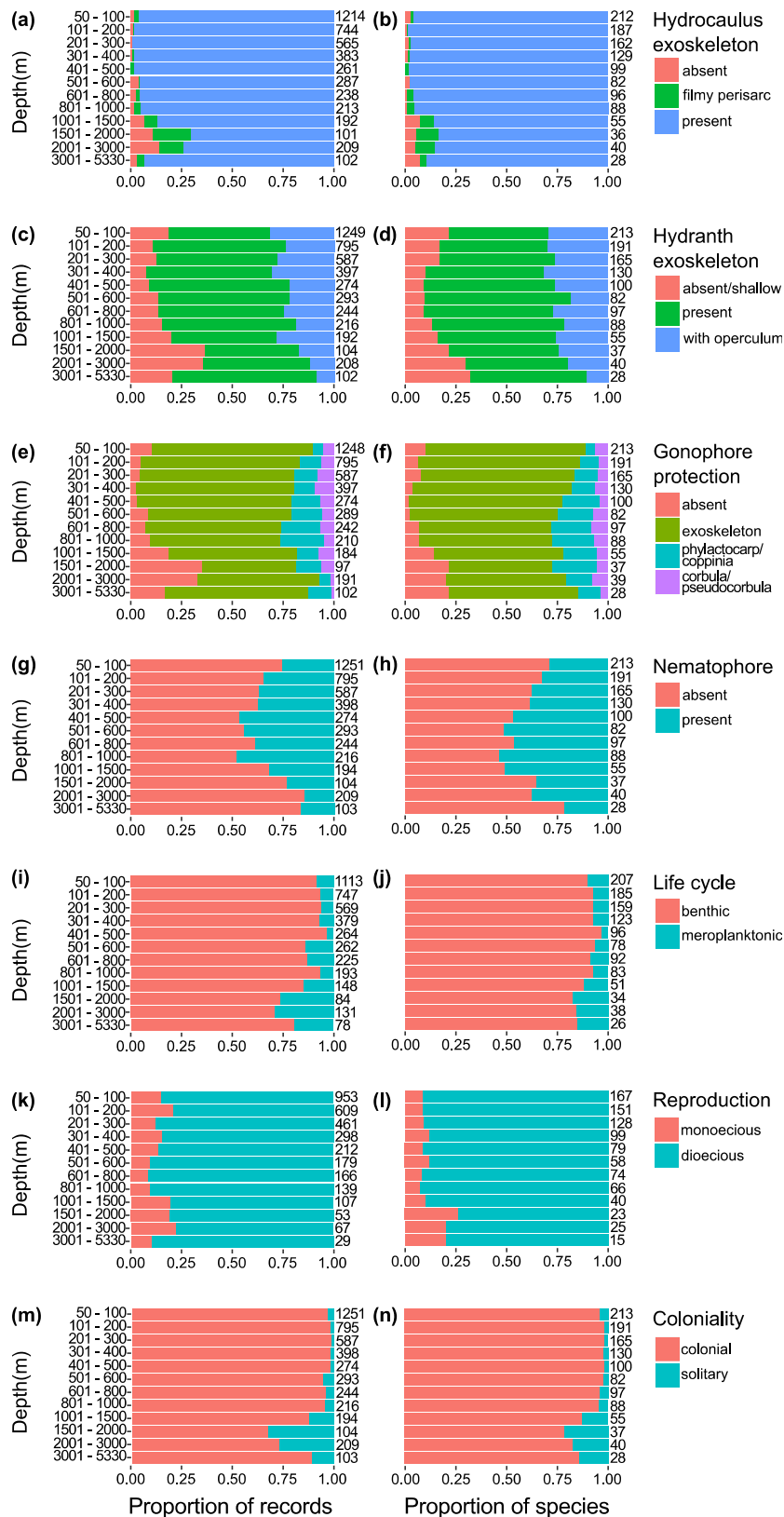
708 **Figure 3.** Relationship between height and depth for all studied specimens (a), and specific
 709 relationships for the specimens of *Sertularella gayi* (b), *Lytocarpia myriophyllum* (c),
 710 *Modeeria rotunda* (d), *Acryptolaria conferta* (e), *Campanularia hincksii* (f), *Nemertesia*
 711 *antennina* (g), and *Billardia subrufa* (h).

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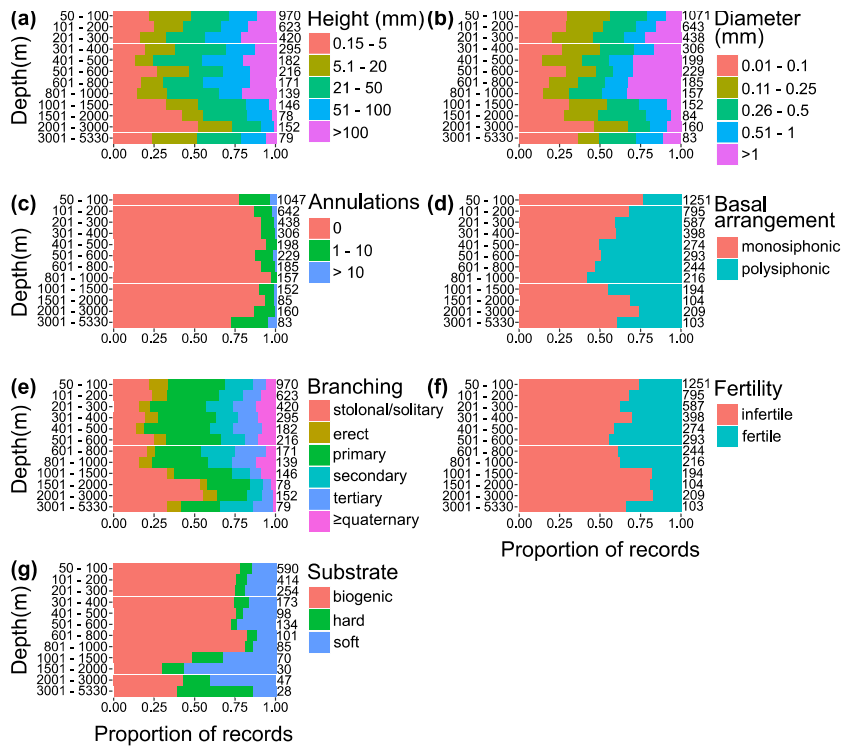
714 **Figure 4.** Relationship between height of the specimens and depth in the Atlantic Ocean, for
 715 the entire dataset (a), and divided by trait categories marked by different colors (b – n). Data
 716 was standardized for equal sampling across depths. Regression lines were plotted only for
 717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



718

719 **Figure 5.** Variation in the proportion of records (left column: **a, c, e, g, i, k, m**) and species
 720 (right column: **b, d, f, h, j, l, n**) for each trait category along depth strata in the Atlantic Ocean,
 721 for those traits considered to be invariable within species. Numbers of samples used per depth

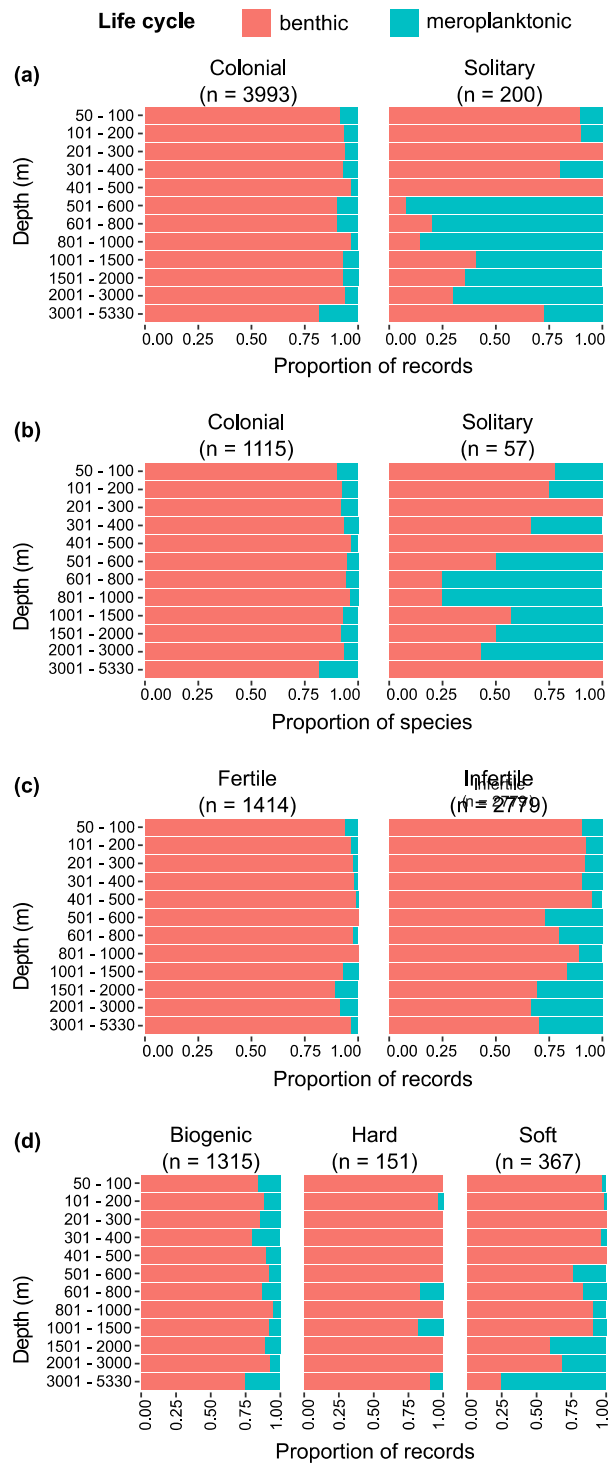
722 stratum are shown on the right of each bar. Only records whose trait information could be
723 collected were used in the analysis.



724

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

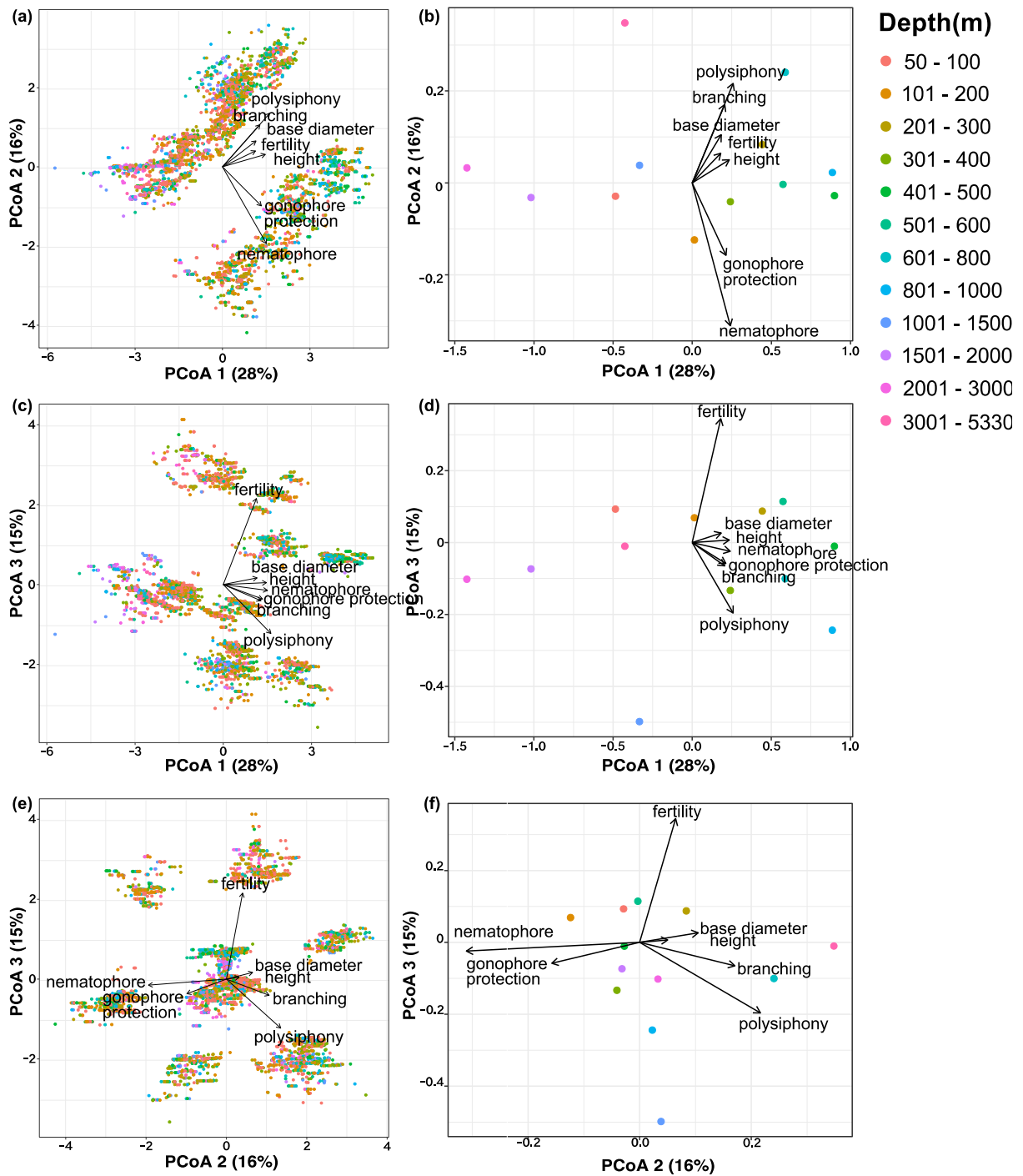
729



730

731 **Figure 7.** Life-cycle variation across depth strata in the Atlantic Ocean according to the
 732 categories of coloniality (**a**, **b**), fertility, and substratum use (**d**), in proportion of records (**a**, **c**,
 733 **d**) and species (**b**). Numbers of samples considered per trait category are shown on top of the
 734 chart. Only records whose trait information could be collected were used.

735



736

737 **Figure 8.** PCoA ordination plots of the 4,668 records from the Atlantic Ocean, coloured by

738 depth strata, based on the 14 studied biological traits (a, c, e) and the same ordinations

739 displaying only the spatial medians of each depth strata (b, d, f). The three first axes combined

740 explain 59% of the variation. Vectors are the explanatory variables.