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RESEARCH ARTICLE

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Trait–environment relationships of hydroids (Cnidaria: Hydrozoa) across large spatial and environmental gradients in the Atlantic Ocean

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Abstract

Aim: The aim was to test trait–environment relationships in hydroids across large spatial and environmental gradients and to evaluate associations between traits, environmental variables, space and phylogeny.

Location: Atlantic Ocean and adjacent polar seas.

Time period: Present day.

Major taxa studied: Hydrozoa.

Methods: Trait–environment relationships and their spatial and phylogenetic contexts were assessed in hydroids by using a combination of a fourth-corner test and extended-RLQ approach, in a multivariate ordination method that uses five matrices: (1) species across sites, (2) environmental data across sites, (3) traits across species, (4) latitude and longitude for each site, and (5) phylogenetic distance among species. We based our analyses on 3680 records of 431 species distributed at 1440 sites, 16 species traits, nine environmental variables and a phylogenetic tree of the studied species.

Results: Hydroid traits are significantly correlated with environmental variables and geographical space, and hydroid phylogeny is correlated with the environment and geographical space. More evidently, we observed an increased presence of larger species (taller, more branched, with greater base diameter and polysiphonic) at sites richer in nitrate and silicate, with higher dissolved oxygen, lower temperatures, lower salinities and lower current velocities. The observation of phylogenetically related species with similar traits and distributions corroborates that historical processes interact with the environment in determining community assembly and explaining patterns of distribution of species traits.

Main conclusions: Several environmental variables combined affect the distribution of hydroid traits, which are also influenced by spatial and historical factors. In the first analysis of its kind for hydrozoans, we have provided an overview of how hydroids are distributed across environments according to their traits and revealed the spatial and phylogenetic components of these trait–environment relationships.

KEYWORDS
Atlantic Ocean, community assembly, hydrozoa, marine biogeography, marine macroecology, species traits, trait–environment relationship

1 | INTRODUCTION

Community assembly and species distribution patterns are influenced simultaneously by multiple and interrelated factors, such as environmental gradients, evolutionary histories, biotic interactions and morphological/life-history traits (Fernandez, Collins, Gittenberger, et al., 2020; Hillebrand, 2004; Roy et al., 2000; Tittensor et al., 2010). However, the particular effects of each factor are difficult to distinguish, and hypotheses about community assembly generally focus on a single or a few of these factors.

The variation of traits can affect the ability of the species to grow, survive and reproduce in different habitats, modulating, to a variable extent, the spatial distribution of the species (Beauchard et al., 2017; Bolam et al., 2017; Brun et al., 2016; Violle et al., 2007; Webb et al., 2009). Studies show significant trait–environment relationships in marine species (Fernandez, Collins, Gittenberger, et al., 2020; Jansen et al., 2018; McClain et al., 2020; Mindel et al., 2016). A study of trait–environment relationships in bryozoans found that colony shape varies with depth and substrate and that polymorphism varies with depth and oxygen levels (Schack et al., 2020). Likewise, life-history traits of marine fish, such as body length and growth, respond strongly to the environment (Beukhof et al., 2019). These approaches help us to understand the underlying processes that regulate the distribution of diversity (Beauchard et al., 2017), a fundamental question in biodiversity studies.

Species traits are also determined by the evolutionary history of the species (Felsenstein, 1985; Hawkins & Diniz-Filho, 2008; Quattrini et al., 2017; Webb et al., 2002). Evolutionary history can either favour or restrict the occurrence of taxa in certain environments by affecting their tolerance to environmental conditions owing to conserved traits (Quattrini et al., 2017; Thomas et al., 2016). According to the niche conservation theory, phylogenetically close species would tend to have more similar traits (Wiens et al., 2010). However, diversification followed by niche changes is frequent (e.g., Evans et al., 2009; Østbye et al., 2018). Therefore, it is important that studies investigating the relationship between species and their environments also consider the phylogenetic relationships between species, allowing results to be interpreted at an evolutionary scale (de Bello et al., 2015).

Hydroids have extensive geographical distributions, occurring from the intertidal zone to hadal depths. Hydroid species show great morphological and life-history variation (Cunha et al., 2020; Fernandez, Collins, Gittenberger, et al., 2020), and their phylogenetic relationships are relatively well established (e.g., Cunha et al., 2017; Maronna et al., 2016; Mendoza-Becerril et al., 2018; Moura et al., 2011). It is of great interest to gain a better understanding of the ecological and evolutionary processes that shape hydroid distributions. Despite being small and frequently overlooked, hydroids have extensive roles in ecosystems (Di Camillo et al., 2017). They are early substrate colonizers (Fernandez et al., 2014, 2015; Meyer-Kaiser et al., 2021; Migotto et al., 2001) and important predators of zooplanktonic and benthic populations (Gili & Hughes, 1995; Huang et al., 2020). Being among the first taxa to recolonize the substrate after disturbances, they are also important for the recovery of benthic communities (Al-Hababheh et al., 2020).

Although some studies have described significant trait–environment relationships in marine species (Beukhof et al., 2019; Fernandez, Collins, Gittenberger, et al., 2020; Jansen et al., 2018; McClain et al., 2020; Mindel et al., 2016; Schack et al., 2020), few have also addressed the contribution of evolutionary history to trait biogeography in the marine environment (McLean et al., 2021). By jointly analysing spatial, environmental, trait and phylogenetic data of the species, we aim to test trait–environment relationships in hydroids across large spatial and environmental gradients and to evaluate associations between traits, environmental variables, space and phylogeny. We expect that the comparative study of the different factors affecting a community assembly will help us to understand the processes that determine/influence the distribution of hydroids in a broad and integrative perspective.

2 | MATERIALS AND METHODS

2.1 | Species occurrence data

Hydroid distribution data from the Atlantic Ocean and adjacent Arctic and Antarctic oceans were obtained from 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 the Federal University of Rio de Janeiro). Museum specimens were collected by a variety of methods, such as dredging, bottom trawling, box corers, Van Veen grabs and submersibles. We made an effort to collected as much data as possible from less sampled areas, but hydroid sampling across the Atlantic Ocean is very unequal across depth and latitudes and temporally, being particularly scarce in the Southern Atlantic (Fernandez, Collins, & Marques, 2020). Therefore, our results reflect associations primarily in the best-sampled areas of the North Atlantic. Depth distributions of records for different regions of the studied area are shown in the Supporting Information (Figure S1), and all the sampled sites are indicated in Figure 1, giving an idea of sampling distribution. All identifications were verified by us (Fernandez, Collins, Gittenberger, et al., 2020; Fernandez, Collins, & Marques, 2020). Each site is a unique combination of longitude, latitude and depth. Records with missing geographical coordinates were georeferenced using Google Earth (Google, 2020) based on the collection site. Only records identified at the species level were used. Aplanulata indet., *Euphysora? bigelowi* Maas, 1905, *Millardiana* sp. and *Oceaniidae* indet. were also included for being identified as unique species/morphotypes (idem Fernandez, Collins, Gittenberger, et al., 2020). Our final dataset encompasses 3680 records of benthic hydroids belonging to 431 species at 1440 sites from 50 to 5330 m deep. The number of records per species varies greatly and is given in the Supporting Information (Table S1).

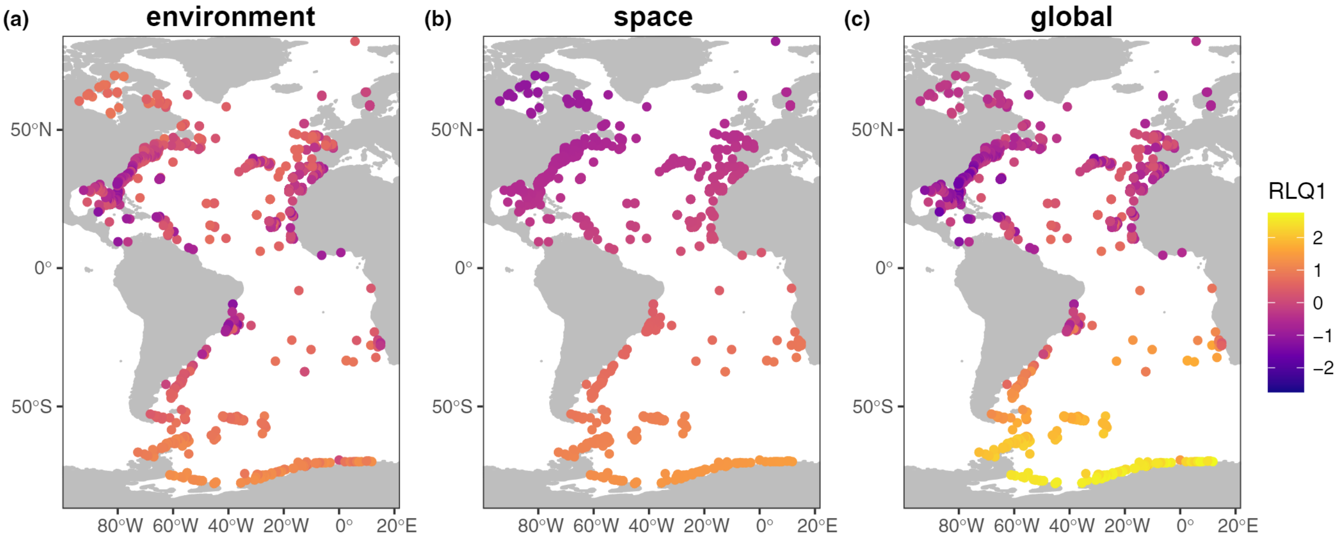

FIGURE 1 Results of the RLQ analysis visualized in space. Colours represent the values of the site scores on the first axis of the RLQ analysis. Global scores are the sum of a combination of environmental and spatial variables, exploring the relative influences of the environmental gradients and the spatial relationship between sites on the global site scores.

2.2 | Trait data

Sixteen traits (Table 1) were collected personally for every specimen during the examination of species samples at museum collections (Fernandez, Collins, Gittenberger, et al., 2020; Fernandez, Collins, & Marques, 2020). Trait information that could not be observed for every specimen (life cycle, sexual mode, number of tentacles, gonophore position and gonophore protection) was collected in the primary literature. Categorical species traits not available in the literature were established based on information from other species of the same genus or family only when little (<20% of the species) or no intragenus or intrafamily variation occurs; otherwise, the entry was left missing. Life cycle and sexual mode traits with intraspecific variation were treated as polymorphisms and considered analytically as missing data. Intraspecific variation in the number of tentacles was equalized by estimating the average number. Gonophores can be located either on the hydranth or elsewhere (hydrorhiza/hydrocaulus). Some gonophores, however, develop in atrophied hydranths (such as in some species of *Eudendrium* and *Hydractinia*) and in this case, they were considered functionally different from those of feeding hydranths, because feeding and reproductive functions would be in distinct zooids.

2.3 | Environmental data

Ten environmental variables were obtained for each site (Supporting Information Figure S2). Variables were chosen based on the hypothesis of trait–environment relationships regarding hydroids and other marine invertebrates (Table 1). The depth of each site was obtained from the museum specimen data. Average temperature (in degrees Celsius), dissolved oxygen (in millimoles per metre cubed), salinity (on the practical salinity scale), nitrate (in millimoles per metre cubed), phosphate (in millimoles per metre cubed), silicate (in millimoles per metre cubed), current velocity (in metres per second) and bathymetric slope (in degrees) were obtained from Bio-ORACLE v.2.1 (Assis et al., 2018; Tyberghein et al., 2012) and MARSPEC (Sbrocco & Barber, 2013) using benthic environmental layers (i.e., sea bottom data) with the “sdmpredictors” R package (Bosch & Fernandez, 2021). Particulate organic carbon (POC) flux to the bottom (in grams of organic carbon per metre squared per year) was obtained from the paper by Lutz et al. (2007). All environmental layers are bottom layers and have a 5 arcmin spatial resolution (*c*. 9.2 km at the Equator). Environmental values for each studied site were extracted from the bottom environmental layers by matching their spatial coordinates (latitude and longitude). Environmental values are, therefore, an approximation limited by the resolution of the layers, except for depth data, which were obtained directly from the museum specimen data. Given that our organismal sampling is based on museum collection data, species distribution data do not necessarily match environmental data in time.

We investigated collinearity in the studied environmental variables by plotting the values obtained for each site between pairs of variables. Phosphate was highly correlated with nitrate and was excluded from the analysis (Supporting Information Figure S2). Maps of the studied region showing the variation of depth and all the environmental variables used in the analysis are provided in the Supporting Information (Figure S3).

Given that environmental variables were mostly right skewed and required $\log_{10}$-transformation, all environmental data were $\log_{10}$-transformed to maintain consistency throughout the analysis. A constant was added to variables with zero or negative values

TABLE 1 Species traits of hydroids collected during this study, a rationale for trait selection, and expectations about specific trait–environmental relationships

Traits	Type	Attributes/units	Rationale for trait selection	Expectations
Height[a]	Q	Millimetres	There is wide size variation among hydroid species, ranging from <1 mm to >1 m (e.g., Cornelius, 1995a, 1995b; Schuchert, 2012). Temperature, dissolved oxygen concentration, organic matter availability and salinity can influence the size of marine invertebrates (e.g., Gili & Hughes, 1995; Hunt & Roy, 2006; McClain et al., 2012; McClain & Rex, 2001)	Occurrence of larger species at sites with decreasing temperatures and salinities and increasing dissolved oxygen and organic matter availability
Diameter at the base[a]	Q	Millimetres	Diameter at the base of individuals/colonies is used as an indicator of size and robustness	Species with greater base diameter at sites favouring the occurrence of larger species (decreasing temperatures and salinities and increasing dissolved oxygen and organic matter availability) and at sites with faster currents
Annulations[a]	Q	Count	Annulations confer flexibility (Cornelius, 1995a, 1995b; Gili & Hughes, 1995)	Species with more annulations at sites with faster currents
Branching[a]	O	0 = stolonal/solitary; 1 = erect, unbranched; 2 = erect, with primary branching; 3 = erect, with secondary branching; 4 = erect, with tertiary branching; 5 = erect, with quaternary branching or more	Orders of branching are used to indicate colony size (Gili & Hughes, 1995)	More branched species at sites favouring the occurrence of larger species (decreasing temperatures and salinities and increasing dissolved oxygen and organic matter availability)
Hydrotheca	O	0 = absence of hydrotheca; 1 = presence of hydrotheca; 2 = presence of hydrotheca and operculum	Hydrotheca confers protection to predation on hydranths (Cornelius, 1995a)	Weak or no relationship with environmental variables
Perisarc hydrocaulus[a]	O	0 = absent; 1 = filmy; 2 = present	Perisarc confers protection to coenosarc in the form of hydrocauli (Mendoza-Becerril et al., 2017)	Weak or no relationship with environmental variables
Number of tentacles	O	0 = ≤20; 1 = 21–50; 2 = 51–100; 3 = >100	Increased number of tentacles might facilitate food capture (Gili & Hughes, 1995)	More species with increased number of tentacles at sites with lower food availability (particulate organic carbon flux)
Basal arrangement[a]	F	Monosiphonic; polysiphonic	Basal arrangement is used as an indicator of colony size and robustness	More polysiphonic species at sites favouring the occurrence of larger species (decreasing temperatures and salinities and increasing dissolved oxygen and organic matter availability) and at sites with faster currents
Coloniality[a]	N	Colonial; solitary	Solitary hydroids have been found more often at greater depths (Fernandez, Collins, Gittenberger, et al., 2020)	More solitary species with increasing depth

(Continues)

TABLE 1 (Continued)

Traits	Type	Attributes/units	Rationale for trait selection	Expectations
Sexual mode	N	Hermaphroditic; gonochoristic	Different sexual strategies might ease reproduction at different population densities	Weak or no relationship with environmental variables
Life cycle	N	Benthic; meroplanktonic	Individuals of some species might release medusae exclusively in certain environmental conditions (e.g., Schierwater & Hadrys, 1998; Werner, 1955), locally affecting the medusa release of single species	Species with different life cycles occupy similar environmental conditions, because variation is mostly intraspecific
Nematophore[a]	N	With nematophore; without nematophore	These defensive polyps might stop predation or larval settlement (Cornelius, 1995a)	Weak or no relationship with environmental variables
Tentacle type[a]	M	Capitate; filiform	Capitate tentacles have nematocyst concentrations that might facilitate defence and/or food capture	More species with capitate tentacles at sites with lower food availability (particulate organic carbon flux)
Tentacle arrangement	M	Oral; aboral; scattered	Scattered tentacles might facilitate food capture	More species with scattered tentacles at sites with lower food availability (particulate organic carbon flux)
Gonophore position[a]	M	Hydranth; separated	Species with a gonophore on the hydranth accumulate the functions of feeding and reproduction in the same module, which might limit survival in specific environments	Wider environmental and geographical distributions of species with a gonophore separated from the hydranth
Gonophore protection[a]	M	Absent; gonotheca; coppinia; corbula; phylactocarp; pseudocorbula	Gonophores (reproductive modules) might be protected to different extents, enhancing defence (Cornelius, 1995a)	Weak or no relationship with environmental variables

Note: Type codes: F, fuzzy; M, multichoice; N, nominal; O, ordinal; Q, quantitative.

[a] Traits significantly correlated with the environment (and included in the RLQ analysis).

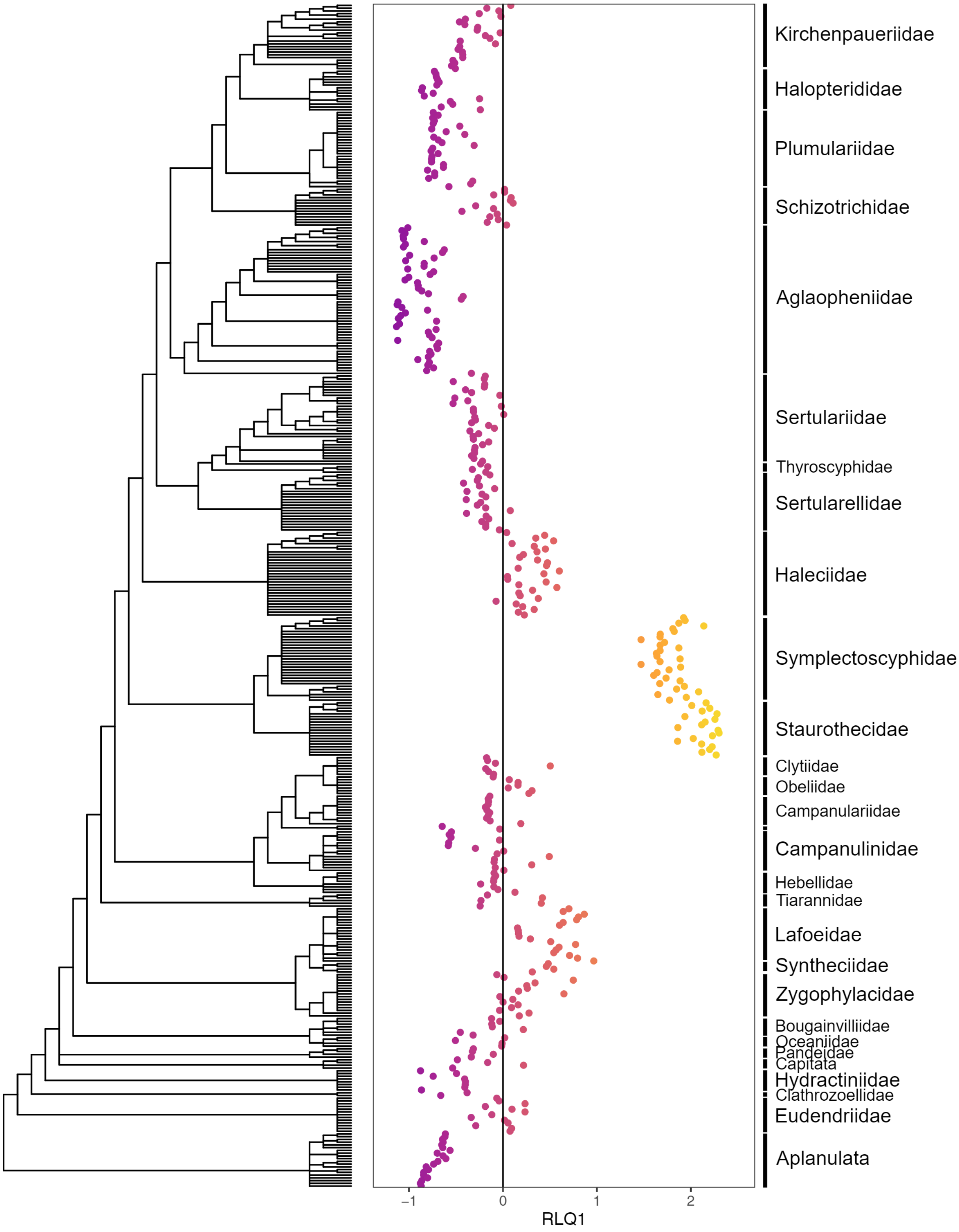

FIGURE 2 A phylogenetic tree of hydroids and the respective species scores plotted on the first axis of the RLQ analysis. For species names, see the Supporting Information (Figure S4).

present before $\log_{10}$-transformation. All variables were standardized to scale each variable to zero mean and unit variance (*z*-scores). Missing environmental data (1.75% of the total) were replaced by the mean of available data (zero) and are therefore non-informative (neutral) for the results.

2.4 | Phylogeny

A composite phylogenetic tree including all the studied species was constructed manually based on the available molecular phylogenies (e.g., Cunha et al., 2017; Maronna et al., 2016; Mendoza-Becerril et al., 2018) to be adopted as a working hypothesis to preserve both molecular and morphological information (Supporting Information Figure S4). We used the topology of Maronna et al. (2016: fig. 1) as the backbone topology of the hydroid tree. The relationships between families, genus and species were mainly based on this topology (Figure 2; Supporting Information Figure S4). The relationships within the suborder Proboscoida Broch, 1910 (including families Campanulariidae, Clytiidae and Obeliidae) were based on the work of Cunha et al. (2017), a study focusing on the group and therefore a wide sampling of taxa, corroborating results found in previous studies on the relationships of these three families of Hydrozoa. In addition, the phylogenetic position of the bougainvilliids within Hydrozoa was based on the work of Mendoza-Becerril et al. (2018). Species used in our analysis not represented in the existing molecular phylogenies were placed according to their position in non-molecular classifications (i.e., morphology-based taxonomic positions). The relationships of these species within their groups were established as unresolved. For this reason, a large number of polytomies is present at the species level in our topology (Figure 2; Supporting Information Figure S4). The lengths of the branches were set to one and subsequently ultrametricized using the software MESQUITE (Maddison & Maddison, 2021).

2.5 | Species by trait matrix

A species by trait matrix summarizing the information on 16 traits for each of the 431 species was constructed from the trait data collected. For continuous traits with intraspecific variation, entries are the average value for all the records of each species. For height and branching, averages are based on entire colonies only. For categorical traits with intraspecific variation, the frequencies of occurrences of each category were calculated and inserted as fuzzy variables (i.e., respective frequencies of specimens in each category were separated in two columns). Traits were separated by statistical type (fuzzy, multichoice, nominal, ordinal and quantitative).

Some trait categories had missing trait data (3.8% of trait values). However, the fourth-corner analysis (used to examine trait–environment relationships; see “Statistical analysis” below) runs only on complete datasets. Given that the missing trait data were not distributed evenly across species and to avoid excluding from the analysis many species with only one missing trait, the missing values were imputed (estimated) using the “MISSMDA” package in R (Josse & Husson, 2016). Principal components analysis (PCA) and multiple correspondence analysis (MCA) are methods that allow exploration of the association between two or more continuous (PCA) or categorical (MCA) variables. Continuous missing values were imputed with a PCA with the “imputePCA” function, and categorical missing values were imputed with an MCA with the “imputeMCA” function. These are iterative methods that impute missing values using the fitted PCA and MCA matrices, respectively, therefore considering links between variables and similarities between species to improve the estimation (Josse & Husson, 2016).

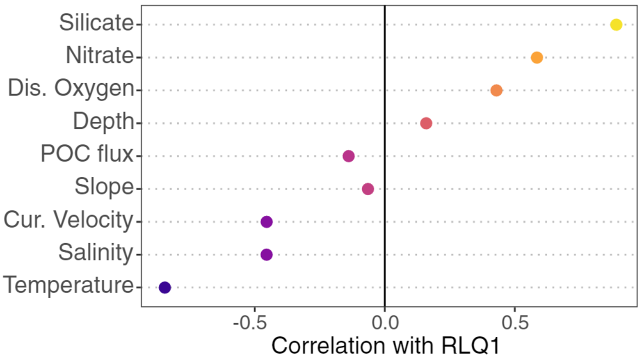

FIGURE 3 Pearson correlations between environmental variables and site scores on the first axis of the RLQ analysis.

Quantitative traits were $\log_{10}$-transformed to reduce skewness using $\log(x+1)$ because of zero values.

2.6 | Statistical analysis

Trait–environment relationships of hydroids and their spatial and phylogenetic contexts were assessed using a combination of the fourth-corner test (Dray et al., 2014; Dray & Legendre, 2008) and the extended-RLQ approach (Pavoine et al., 2011). We first evaluated whether there are significant associations between (1) traits and environmental variables, (2) traits and space, (3) phylogeny and environmental variables, and (4) phylogeny and space using the multivariate fourth-corner test and permutation model 6 (Dray et al., 2014; Dray & Legendre, 2008). Permutation model 6 performs two separate permutation tests, one permutating samples and one permutating species, to obtain a combined *p*-value (Dray et al., 2014; Dray & Legendre, 2008). The *p*-values were adjusted for multiple comparisons using the false discovery rate (FDR) method (Benjamini & Hochberg, 1995). The analysis was performed with the “fourthcorner2” function in the “ADE4” package. Only traits significantly correlated with the environment were included in the RLQ analysis (indicated by asterisks in Table 1).

The original RLQ method studies the relationship between traits and the environment across sites by the multivariate ordination of three matrices: (1) species across sites, (2) environmental data across sites, and (3) traits across species. The extended-RLQ adds two matrices to the original approach: (4) spatial data of latitude and longitude for each site and (5) phylogenetic distance of the species. The five matrices were constructed with the data described above. The first step of the RLQ analysis is to subject each matrix to a factorial analysis using functions in the “ADE4” package (Dray & Dufour, 2007). First, the community matrix (species by sites) was subjected to a correspondence analysis (CA). Then, for the following matrices, each analysis should be weighted by the sites (spatial and environmental matrices) and species (traits and phylogenetic matrices) weights from the CA (Dray et al., 2014; Pavoine et al., 2011). The spatial data matrix and the environmental data matrix (E) were subjected to PCA weighted by the rows (sites) of the community matrix after CA. To construct the species by traits matrix, containing the 11 significant selected

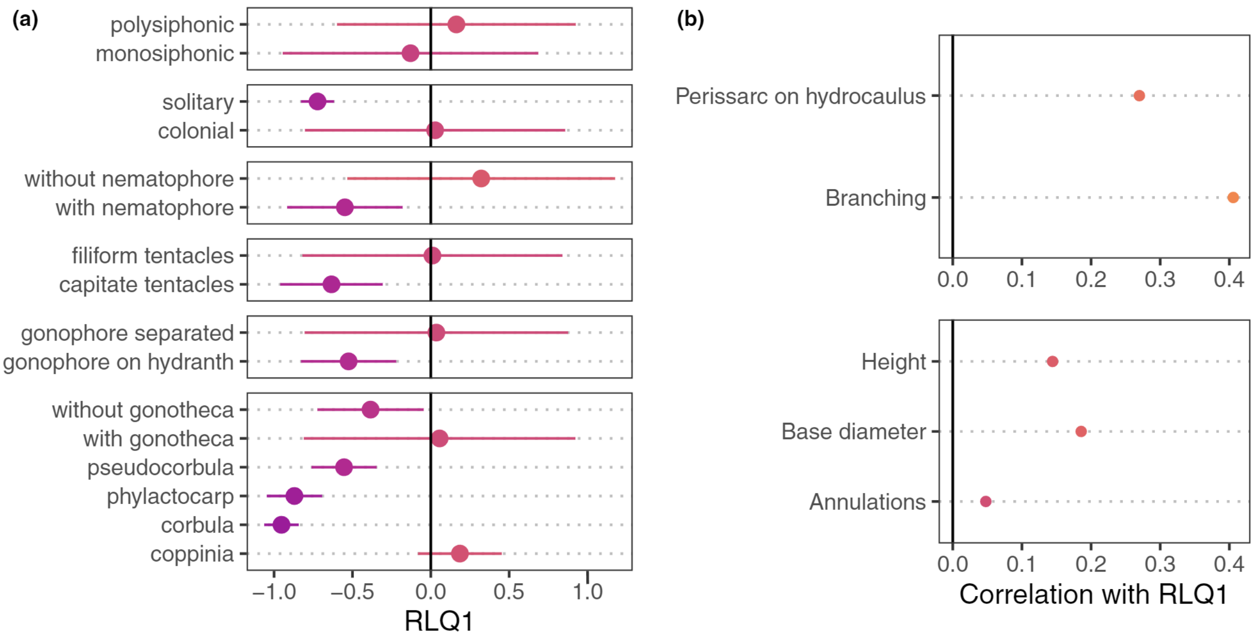

FIGURE 4 (a) Species scores for categorical traits along the first axis of the RLQ analysis. (b) Correlations between traits and species scores on the first axis of the RLQ analysis. Points in (a) are the average scores of all the species characterized by each trait, and segments are the standard deviation. Upper plots in (b) are Spearman correlations for ordinal traits and lower plots are Pearson correlations for continuous traits.

traits, the tables of fuzzy and binary traits were first prepared with the "prep.fuzzy" and "prep.binary" functions, respectively, to specify the number of attributes per trait. A distance matrix between species was then calculated based on the 11 significant selected traits using the mixed-variables coefficient of distance (Pavoine et al., 2009) implemented with the "dist.ktab" function in the "ADE4" package. The distances between species were then analysed by a principal coordinates analysis (PCoA) weighted by the columns (species) of the community matrix. Likewise, the phylogenetic distance matrix was analysed by PCoA weighted by the columns of the community matrix.

Finally, we ran the extended-RLQ analysis using the "rlqESLTP" function in the "ADIV" R package (Pavoine, 2020). The resulting site scores are the sum of a combination of the environmental variables and a combination of the spatial variables, whereas species scores are the sum of a combination of the trait variables and a combination of the phylogenetic variables.

Figures were prepared using "GGPLOT2" (Wickham, 2016), "GGPUBR" (Kassambara, 2020), "PATCHWORK" (Pedersen, 2020), "GGTREE" (Yu, 2020) and "APLOT" (Yu, 2021) R packages. The same range was used for colour gradients in all figures to allow comparisons between figures.

All datasets used in the analysis are available as supplementary files in the Supporting Information.

3 | RESULTS

Fourth-corner multivariate tests showed that hydroid traits were significantly correlated with environmental variables ($p = .002$) and with geographical space ($p = .001$) and that hydroid phylogenies were correlated with the environment ($p = .001$) and with geographical space ($p = .001$). From our original list of 16 traits, a subset of 11 traits was significantly correlated with the environment and was retained for the RLQ analysis (Table 1; Supporting Information Figure S5). The tentacle arrangement, number of tentacles, sexual mode, life cycle and hydrotheca traits were not significantly correlated with the environment (Supporting Information Figure S5).

The first axis of the extended-RLQ analyses, integrating spatial, environmental, trait and phylogenetic data, explained 71.9% of the total variation. The positive side of the axis corresponds to areas richer in nutrients (silicate and nitrate) and dissolved oxygen and with lower temperatures, salinities and current velocities (Figure 3). Most of those areas are located towards the polar regions, but especially in the Southern Ocean (see environmental scores in Figure 1). Species in those areas were more often polysiphonic, without nematophores, with perisarc on hydrocaulus, had higher orders of branching and had greater height, base diameter and number of annulations (Figure 4). They mostly correspond to Staurothecidae and Symplectoscyphidae species (Figure 2; Supporting Information Figure S4). The negative side of the axis corresponds to areas poorer in nutrients and dissolved oxygen, with higher temperatures, salinities and current velocities (Figure 3), mostly located near coastal areas of the tropical Atlantic and the North Atlantic (see environmental scores in Figure 1). Species in those areas were often of smaller height, base diameter and number of annulations and had fewer branching orders. Solitary species with capitate tentacles, gonophores on hydranths and without perisarc on hydrocaulus (essentially corresponding to Aplanulata species) were mostly found in those areas, but also species with nematophores or protection for the gonothecas (corbulas, pseudocorbulas or phylactocarps), corresponding mostly to Halopterididae, Plumulariidae and Aglaopheniidae (Figures 2 and 4; Supporting Information Figure S4).

4 | DISCUSSION

The results corroborate our general hypothesis that traits and lineages of hydroids are correlated with spatial and environmental gradients. The individual correlations between traits and environmental variables were identified, and the spatial and phylogenetic components of these relationships were characterized.

The most evident trait–environment relationship observed was the increase in the presence of taller, more branched, basally wider and polysiphonic species, mainly in nitrate- and silicate-rich sites with lower temperatures, salinities and current velocities and with greater dissolved oxygen (Figures 3 and 4). The occurrence of these larger species in lower-temperature regions of the Southern South Atlantic and the Southern Ocean, whereas smaller species occur in warmer tropical areas of the Atlantic, suggests that increased temperatures limit the distribution of larger species. However, the patterns also suggest that nutrient, dissolved oxygen, salinity and current velocity gradients are important factors affecting hydroid sizes, either by affecting growth or by restricting distributions according to species sizes.

Numerous studies have estimated that increasing the rearing temperatures leads to faster growth but significantly reduced adult sizes in most ectotherms, a pattern known as the temperature–size rule (Atkinson, 1994). Those findings indicate a phenotypically plastic response of the size of individuals in response to temperature, although no single mechanism is accepted to explain the relationship (Angilletta & Dunham, 2003). Additionally, palaeontological evidence indicates increases in ostracod body sizes during cooler periods (Hunt & Roy, 2006) and reductions in the body size of soil organisms during high-temperature periods (Smith et al., 2009). Interestingly, hydroid colonies tend to present these same size responses to temperature. Some studies also show that climate warming can affect community species composition by increasing the proportion of smaller species (Daufresne et al., 2009; Petchey et al., 1999). The patterns resulting from our analyses show that smaller colonies of hydroids are also in warmer locations, hence it is reasonable to assume that hydroids might also follow this trend in response to global warming.

A decrease in colony height with increasing temperature was observed previously in two species of hydroids, *Obelia geniculata* and *Silicularia bilabiata*, together with a decrease in branching in *O. geniculata* (Ralph, 1956). Rearing experiments in hydroids have shown that growth rates are also influenced by temperature, although the relationship varies across species. Slower growth of *Dynamena pumila* and slower stolonal growth of *Clava multicornis* were observed at increased temperatures (Dementyev & Marfenin, 2019; Kinne & Paffenhöfer, 1966), whereas faster growth at higher temperatures was observed for *Bougainvillia* sp. (Gili & Hughes, 1995). However, the optimal temperature ranges for growth vary across species (Gili & Hughes, 1995).

Dissolved oxygen concentration can also influence the size of marine benthic invertebrates. The maximum length of benthic amphipods measured world-wide is limited by oxygen availability (Chapelle & Peck, 1999), and the maximum size of deep-sea gastropods increases significantly with increasing dissolved oxygen concentration (McClain & Rex, 2001). Although previous studies relating dissolved oxygen availability to hydroid size are not available, those patterns are in accordance with our findings (Figures 3 and 4b).

Increased salinity was correlated with decreased hydroid size (Figures 3 and 4b). Differences in hydroid growth and morphology along salinity gradients have generally been identified in species that occur in low-salinity environments with sharper variation, such as estuaries (Folino-Rorem & Renken, 2018; Gili & Hughes, 1995). Smaller polyps and less branched hydrocauli were observed in *Cordylophora caspia* with an increase in salinity from 15 to 30‰ (Gili & Hughes, 1995). Although low-salinity environments were not included in the present study, variation in height and branching was observed even in relationship to the salinity range observed here.

The same morphological variation correlated with salinity was observed for current velocities. Decreased size and branching of hydroids were observed at increased current velocities (Figures 3 and 4b). Families with many plumose species, such as Plumulariidae, Halopterididae and Aglaopheniidae, occur more often at sites with faster currents (Figures 2 and 3). Plumose hydroids usually orientate their colonies towards water movement, increasing oxygenation and food capture (Boero, 1984; Svoboda, 1976), and the general pattern of smaller hydroids occurring in faster currents (Figures 3 and 4b) has been observed previously in colonies of some species (Bandel & Wedler, 1987; Boero, 1984). The pattern might be related to colony resistance, given the difficulty in maintaining larger colonies in strong water flows. However, with this reasoning, we would also expect species with more annulations to occur at sites with greater current velocity, but the opposite pattern was observed in our results (Figures 3 and 4b) and elsewhere (Silveira & Migotto, 1991). Hydroid morphology might also be determined by current direction, a factor we did not evaluate. Hydroids are usually pinnate in places with uni- or bidirectional water flow and tend to be irregularly and more branched in multidirectional water flows (Silveira & Migotto, 1991).

Depth, POC flux and slope gradients had a minor impact on shaping the distribution of hydroid traits throughout the Atlantic Ocean. Several traits of hydroids, including size, have been shown to vary with depth (Fernandez, Collins, Gittenberger, et al., 2020). However, trait variation with depth is often not linear, with variations at specific depths that would not be captured in our analyses. In addition, clearer trait–depth relationships are observed when intraspecific variation is considered (Fernandez, Collins, Gittenberger, et al., 2020). Some studies indicate that the use of average trait values for species with intraspecific trait variation might prevent retrieval of patterns of niche occupation by individuals or populations of a single species (Cianciaruso et al., 2009; Schleuter et al., 2010;

Violle et al., 2014). The analytical approach taken here, however, works at a different level, comparing patterns across species (Pavoine et al., 2011), preventing further discussion related to intraspecific variation in trait–environment relationships.

Despite the expected influence of the availability of organic energy on the traits of marine species (Danovaro et al., 2017; Gambi et al., 2017; McClain et al., 2012), no correlation was observed between the traits and the POC flux to the seafloor. However, the availability of silicates and nitrates, along with temperature, were the environmental variables that explained most of the variation in our data (Figure 3). Larger and more branched species were found mostly at sites richer in those nutrients. Food availability has already been shown to influence hydroid growth (e.g., Crowell, 1957) but, to our knowledge, this is the first study relating nutrient availability in the environment to the selection of hydroid species according to their traits.

Taller and more branched species were observed mainly in *Staurotheca*, *Antarctoscyphus* and *Symplectoscyphus* (Figures 2 and 4b). *Staurotheca* species of this study are endemic to the Southern Ocean region, whereas *Antarctoscyphus* and *Symplectoscyphus* are endemic to the SW Atlantic and Southern Ocean (Miranda et al., 2021). This suggests that the species traits of these genera, although correlated with the environment, are also evolutionarily conserved. We found a significant association between space and phylogeny, indicating that historical processes, such as the colonization of the Southern Ocean by those genera, interact with environmental variables in determining community assembly and explaining patterns of distribution of species traits.

Importantly, species scores (Figures 2 and 4) result from a combination of many traits. No single trait can be interpreted as responsible for the observed patterns. For example, although Aglaopheniidae species are correlated with the negative side of the RLQ axis, indicating that most species are small, some Aglaopheniidae are very large, such as *Lytocarpia myriophyllum*. Other traits, especially the presence of nematophores, corbulas and phylactocarps, ubiquitous in Aglaopheniidae species, drive their correlation with this side of the axis. Furthermore, many traits are not independent of each other because of trait correlations and phylogenetic constraints, leading to trait covariations along environmental variables. Therefore, the correlation of one specific trait with the environment can lead to correlation of another trait that might not necessarily be influenced by the same environmental factor, masking the trait–environment relationship (Wilkes et al., 2020).

The distribution of species with nematophores was mostly correlated with higher temperatures, fewer nutrients and lower dissolved oxygen. Nematophores are structures that enhance defence, making the distribution of species with nematophores probably more related to biotic factors than to the abiotic factors studied here. Likewise, an explanation for the association of gonophore position with high-temperature and nutrient-poor environments is unclear. Species with a gonophore on the hydranth accumulate the functions of feeding and reproduction in the same module, distinguished from those species where gonophores are separated from the hydranth. The latter species have wider environmental and geographical distributions (large standard deviation for "gonophores separated from the hydranth" in Figure 4a), indicating an occupation of a greater number of niches.

Five traits are not correlated with the environment: tentacle arrangement, tentacle number, sexual mode, life cycle and hydrotheca. Individuals of some species might release medusae only in certain environmental conditions (e.g., Schierwater & Hadrys, 1998; Werner, 1955). However, although environmental variation might affect the medusa release of a single species locally, our results suggest that species with different life cycles occupy similar niches and have similar global distributions. Furthermore, given that species with more tentacles or with tentacles arranged in more than one whorl can capture larger and more mobile prey more easily (Gili & Hughes, 1995), we would expect a variation in the number and arrangement of tentacles following gradients in food availability, assessed with data from POC flux, but no correlation between the arrangement and number of tentacles and the environmental variables was detected. Only tentacle type was significantly correlated with the environment. Species with capitate tentacles were found more often in warmer waters with fewer nutrients. However, many species with capitate tentacles are from the order Aplanulata, which have other traits associated with those same environmental variables; therefore, the pattern might be related, in part, to a phylogenetic constraint.

By analysing trait data from hundreds of hydroid species across the Atlantic Ocean, we have presented how several environmental variables combined affect the distribution of hydroid traits, which are also influenced by spatial and historical factors. Although our extended-RLQ analyses partitioned the influence of some important factors that affect community assembly, there are certainly other unconsidered factors that might influence hydroid distributions, such as barriers to dispersal that might restrict the distribution of some lineages despite environmental suitability, or species interactions. However, we were able to unravel many important factors to provide an overview of trait–environment relationships in hydroids and to reveal the spatial and phylogenetic components of these relationships. The main pattern observed was an increased presence of larger species (taller, more branched, with greater base diameter, and polysiphonic) at sites richer in nitrate and silicate, with lower temperatures, salinities and current velocities and with higher dissolved oxygen. It suggests that these environmental variables might either affect hydroid growth or restrict their distributions according to size. These new data, together with palaeontological and climate warming evidence that increased temperatures restrict the size of marine invertebrates (Daufresne et al., 2009; Hunt & Roy, 2006; Petchey et al., 1999), suggest that global warming will affect hydroid community composition by decreasing the occurrence of larger species.

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All the data used in the analysis are available in the Supporting Information.

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BIOSKETCHES

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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