Spatial patterns in planktonic cnidarian distribution in the western boundary current system of the tropical South Atlantic Ocean

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Abstract :

In marine western boundary systems, strong currents flowing coastward spread oceanic water masses over the continental shelves. Here we propose to test the hypothesis according to which oceanic cnidarian species may dominate western boundary system regions even in coastal waters. For that purpose we use a set of data collected above the shelf, slope and around oceanic seamounts and islands in the Western Tropical South Atlantic. Samples were acquired with a plankton net with 300 μm mesh size over 34 stations during an oceanographic cruise carried out in October 2015. Results reveal a diverse cnidarian assemblage in the area, extending the known distribution of many species. In addition, the Fernando de Noronha Chain and most of the narrow continental shelf presented a typical oceanic cnidarian community, dominated by holoplanktonic siphonophores. In this western boundary system, this condition was likely driven by the strong currents, which carry the oceanic tropical water and associated planktonic fauna toward the coast. A specific area with reduced influence of oceanic currents presented typical coastal species. The pattern we observed with the dominance of oceanic plankton communities up to coastal areas may be typical in western boundary systems characterized by a narrow continental shelf.

Keywords : medusae, siphonophores, tropical Atlantic Ocean, South Equatorial Current, North Brazil Undercurrent, Fernando de Noronha chain, Northeast Brazil

Introduction

In marine environments, the distribution of planktonic cnidarian species is closely related to water-masses and the inshore-offshore gradient (Pagès and Gili, 1992; Pagès *et al.*, 2001; Nogueira Júnior *et al.*, 2014). While holoplanktonic siphonophores are often more abundant in the open ocean, the dependence on rigid substrates for hydroids restricts the oceanic distribution of meroplanktonic hydromedusae, which are more common over the continental shelf (Bouillon, 1999; Mapstone, 2014). In addition to these meso-scale distribution patterns, circulation, turbulence, food availability, temperature, salinity and oxygen influence the distribution and abundance of planktonic organisms along a wide range of scales (Gili *et al.*, 1988; Gibbons and Buecher, 2001; Luo *et al.*, 2014; Bertrand *et al.*, 2014).

Due to their high fragility, which difficult fixation, and complicated taxonomy, typical zooplankton ecological studies often set cnidarians aside or simply include all species in a single category (e.g. Lane *et al.*, 2008; García-Comas *et al.*, 2011). However, in recent decades the group has received more attention due to their significant role in ecosystem functioning as active predators with high feeding rates and (often underestimated) prey for higher trophic levels (e.g. Hays *et al.*, 2018; Eduardo *et al.*, 2020). In adequate conditions, planktonic cnidarians may proliferate very fast, sometimes leading to large population blooms, which may control the pelagic community and collapse fisheries and other human activities (Purcell *et al.*, 2007; Pitt *et al.*, 2009; Purcell, 2012; Roux *et al.*, 2013; Hays *et al.*, 2018). In the Western South Atlantic, knowledge on planktonic cnidarians ecology is almost restricted to latitudes higher than 18°S (Vannucci, 1963; Nogueira and Oliveira Jr., 1991; Nogueira Júnior *et al.*, 2014, 2015; Nagata *et al.*, 2014) and fewer is known at lower latitudes (Vannucci, 1957; Gusmão *et al.*, 2014). This feature is not exclusive of the Western South Atlantic since tropical areas are less studied than mid- to high latitudes ecosystems worldwide (e.g. Boltovskoy *et al.*, 2003; Boltovskoy and Valentin, 2018; Menegotto and Rangel, 2018).

In western boundary systems such as the Western Tropical South Atlantic, strong currents flowing coastward typically results in massive intrusions of oligotrophic oceanic water masses over the continental shelves (Loder *et al.*, 1998; Piontkovski *et al.*, 2003; Moreno-Ostos *et al.*, 2010). In the western boundary system of the Tropical South Atlantic off Northeast Brazil (~5-10°S) strong trade winds and the presence of the North Brazil Undercurrent (NBUC) originated from the bifurcation of the southern South Equatorial Current (sSEC) drive the northward transport of oligotrophic saline tropical water along the Northeastern Brazilian continental shelf (Stramma and Schott, 1999; Lumpkin and Garzoli, 2005; Assunção *et al.*, 2020; Dossa *et al.*, 2021). Although nutrient-rich estuarine plumes and local upwelling events may enhance primary production in western boundary systems (Smith and Demaster, 1996),

the continental drainage is low in the Northeastern Brazilian continental shelf, not reaching beyond 16 km offshore (Castro *et al.*, 2006). This results in the lowest primary productivity on the Brazilian coast, even with occasional anti-cyclonic eddies causing upwelling events near the shelf break (Ekau and Knoppers, 1999; Castro *et al.*, 2006; Dossa *et al.*, 2021). Moreover, in this area the continental shelf is narrow (<50 km wide), also contributing to the high influence of oligotrophic oceanic water over most of the shelf (Brandini *et al.*, 1997; Loder *et al.*, 1998).

Although circulation dynamics and oceanic intrusions have potential to drive distribution and abundance of zooplanktonic communities in western boundary systems, this issue rarely was addressed properly (e.g. Thibault-Botha *et al.*, 2004; Dai *et al.*, 2016), mainly when concerning planktonic cnidarians and Northeast Brazil, since previous studies in the area did not considered this subject (Vannucci, 1957; Gusmão *et al.*, 2014). In this context, we propose to test the hypothesis according to which oceanic cnidarian species may dominate western boundary system regions even in coastal waters. For that purpose we use a comprehensive set of data collected above the shelf, slope and around oceanic seamounts and islands of the Fernando de Noronha Chain in the Western Tropical South Atlantic. More specifically, we evaluate how the structure and distribution patterns of the planktonic cnidarian community respond to ocean currents, the inshore-offshore gradient and physicochemical conditions.

Materials and methods

Data

Data were obtained during the "Acoustics along the Brazilian coast" survey (ABRACOS 1; Bertrand, 2015), carried out on September-October 2015, on board the French R/V ANTEA along the Northeast Brazilian continental shelf and slope between 5°S and 9°S, and around oceanic seamounts and islands from Fernando de Noronha Chain (FNC), including the Fernando de Noronha Archipelago itself and the Rocas Atoll up to 3°S, 38°W (Fig. 1).

Zooplankton samples were collected at 34 stations over the shelf (bottom depth <90 m, except shallow stations around oceanic islands), slope (bottom depth between 90 and 3500 m, except stations in this range around oceanic islands) and offshore around the FNC (bottom depth >3500 m and shallower station around oceanic islands), through oblique hauls, with a Bongo net 300 μm mesh size and 0.6 m mouth opening. The water column was sampled from near bottom to surface over the continental shelf, and from 200 m to the surface in the offshore. The net was towed at approximately 2 knots, at various times of day and night. The net was fitted with a calibrated mechanical flowmeter (Hydro-Bios) to estimate the volume

filtered during each haul. Samples were fixed with 4% formaldehyde buffered with sodium tetraborate (0.5 g.l^{-1}).

In laboratory, whole zooplankton samples were analyzed under stereomicroscope and cnidarian specimens were identified (mainly according to Bouillon, 1999; Pugh, 1999) and counted. Abundances were standardized in number of individuals per 100 m^{-3} for medusae and number of colonies per 100 m^{-3} for siphonophores. For calycophorans, the number of anterior nectophores was used for estimating the polygastric stage abundance, and eudoxid bracts for the eudoxid stage abundance (e.g. Hosia and Båmstedt, 2007; Hosia et al., 2008a). For physonects and Hippopodidae, number of colonies were roughly estimated by dividing the number of nectophores by 10 (Pugh, 1984).

Vertical profiles of temperature (°C), salinity and fluorescence were obtained with a CTD-O$_2$ profiler Seabird SBE911+. Conductivity, temperature and pressure accuracies were estimated at 0.0003 S/m, 10^{-3}°C and 0.7 dbar, respectively. Along-track current profiles were recorded with an 'Ocean Surveyor' ship-mounted acoustic Doppler current profiler (SADCP) operating at a frequency of 75 kHz with a depth range of 15-700 m. SADCP data were processed and edited using the Common Ocean Data Access System (CODAS) software package developed at the University of Hawaii (http://currents.soest. hawaii.edu). The relative velocities were rotated from the transducer to the Earth reference frame using the ship gyrocompass. The global positioning system (GPS) was used to retrieve the absolute current velocities. The orientation of the transducer relative to the gyroscopic compass and an amplitude correction factor for the SADCP were determined by standard calibration procedures. Finally, velocity profiles were averaged hourly, providing profiles in the 19-600 m range. SADCP data located over the shelf (bathymetry shallower than 70 m) were often affected by spurious reflections on the bottom, so the data coverage was only partial in these shallow areas. To describe current patterns, data from upper layer (0-70 m depth) were integrated each 0.1 square degree.

To better illustrate areas not covered by the SADCP data, surface current velocity field during sampling period where obtained from EU Copernicus marine environment monitoring Service reprocessed model derived from multi-satellite Geostrophic surface currents and modelled Ekman currents at the surface and 15 m depth with 0.25 square degree resolution (id MULTIOBS_GLO_PHY_REP_015_004; Rio et al., 2014).

Data analysis

To dampen effects of dominant species, abundance data was transformed by log (x+1). A Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson et al., 2016) was

used to test for diel differences among the community structure of planktonic cnidarians. Since no significant difference were observed (Pseudo-F = 0.93842, $P = 0.451$) the pooled set of day and night data was used. Analysis of Variance (ANOVA) were performed to test for differences in hydromedusae and siphonophores richness and total abundance, and the abundance of the most abundant (abundance >1%) planktonic cnidarian species, according to the domain (shelf, slope and FNC). Tukey post-hoc test was used to identify the domains that differed when ANOVA was significant. Spatial patterns in planktonic cnidarian community abundance were identified by hierarchical cluster analysis using Bray-Curtis similarity matrix. The validity of the groups defined by the cluster analysis was tested though SIMPROF test (5% significance level). A Similarity Percentage (SIMPER) analysis was performed to identify representative species and their contribution to similarity within the groups defined by the cluster analysis.

We performed a constrained ordination analysis to identify associations between the most abundant planktonic cnidarian species (>1% of total abundance) and the environmental variables. The following continuous explanatory variables were used in the analysis: (i) sea surface temperature (SST), (ii) sea surface salinity (SSS), (iii) the temperature gradient (maximum value–minimum value/depth sampled) over the 200 m water column (or whole column over the continental shelf), (iv) maximum value of fluorescence (as an indirect measure of biological productivity) in the first 200 m of the water column, (v) bottom depth, (vi) the zonal component of ADCP data integrated over the first 70 m depth, and (viii) the meridional component of ADCP data integrated over the first 70 m depth. Detrended Canonical Correspondence Analysis (DCCA) revealed a small length of variable gradients (<3), indicating that a linear method was more appropriate to use on this occasion, and thus Redundancy Analysis (RDA) was selected (Lepš and Šmilauer, 2003). Surface temperature was high correlated with surface salinity and bottom depth was high correlated with fluorescence and temperature gradient index. We also tested eliminating these variables from the analysis, however, since no significant influences were observed in the results, all variables were included in the model for a better perspective of species ecological niche (Lepš and Šmilauer, 2003).

Distribution maps were produced in Ocean Data View 5.0 (Schlitzer, 2020) and QGIS 3.4 (QGIS Development Team, 2020). ANOVA was performed in Statistica 10 (StatSoft, 2011). Cluster, SIMPROF, SIMPER and PERMANOVA analysis were performed in Primer v.6 + PERMANOVA (Clarke and Gorley, 2006). DCCA and RDA were performed in CANOCO 4.5 (Lepš and Šmilauer, 2003).

Results

Species composition

A total of 73 taxa of planktonic cnidarians was observed in the area, corresponding to three scyphomedusae, 27 hydromedusae and 43 siphonophores (Table 1). In addition, many unidentified cerinula and ephyrae were collected. *Aglaura hemistoma* and *Liriope tetraphylla* were the most frequent and abundant hydromedusae in the area, respectively being present in 100% and 94.1% of the samples and representing 61.5% and 18.3% of the total hydromedusae collected. Among siphonophores, *Eudoxoides spiralis*, *Abylopsis tetragona*, *Bassia bassensis*, *Chelophyes appendiculata*, *Diphyes bojani* and *Sulculeolaria chuni* were present in more than 90% of samples. When considering siphonophores abundance, the most representative species were *C. appendiculata* (18.4%), *D. bojani* (16.7%) and *B. bassensis* (16.4%). *Annatiara affinis*, *Cunina frugifera*, *Bougainvillia muscus*, *Proboscidactyla ornata*, *Nausithoe aurea* and *Vogtia pentacantha* were recorded for the first time in the area (Table 1).

Spatial distribution patterns

Hydromedusae diversity was low all over the study area (Fig. 2). Over the continental shelf, only two stations presented more than four species. In the slope and FNC it was slightly higher, reaching up to 9 species at station 49, however most stations did not exceeded six species. Hydromedusae total abundance was highly variable, ranging from 2.4 to 308 ind.100 m^{-3}, with no clear pattern between shelf, slope and FNC stations (Fig. 2). No significant differences were observed in hydromedusae richness and total abundance among the three environments (Table 2). The two dominant hydromedusa species presented distinct distribution patterns (Fig. 3). *A. hemistoma* was widespread over the area, occurring in high abundance in the shelf, slope and FNC. Although also widespread, *L. tetraphylla* was clearly more abundant over the continental shelf and slope, especially south of 7.5°S (Fig. 3). This species significantly differed among the domains (Table 2).

Siphonophores diversity and total abundance was globally higher than that of hydromedusae (Fig. 2). However, its diversity was also significantly lower in stations over the continental shelf (Table 2), where it averaged 9.1±4.3 species per station contrasting the 19.1±2.3 and 17.7±3.5 found in the slope and FNC, respectively. Siphonophores abundance was variable with no clear patterns between shelf, slope and FNC domains, ranging from 37.9 to 421.4 colonies per 100 m^{-3} (Fig. 2). Among dominant species, *C. appendiculata, D. bojani*, *B. bassensis*, *E. spiralis*, *A. tetragona* and *A. eschscholtzii* were widespread over the area. However, abundances of the former three species were much lower at neritic stations south of 7.5°S. *D. bojani* was more abundant in the remaining neritic stations and over the slope but

differences were not significant (Table 2). Otherwise, *Eudoxoides mitra* was much more abundant, in the FNC stations, occurring in low abundances over the continental shelf and slope (Tables 1, 2). Similarly, *Lensia meteori* distribution was restricted to the slope and FNC with higher abundance in the slope stations on the north of the area. On the opposite, unlike other dominant siphonophores, *Muggiaea kochii* occurred almost exclusively in neritic stations, especially in the south of the study area (Fig. 4).

Community structure

The cluster analysis depicted two main groups A and B with low similarity between each other (Fig. 5a). Still, SIMPROF analysis performed on the results of the cluster analysis considered as valid, six groups of stations (Fig. 5a) with group B split into five sub-groups.

Group A, the most specific, was represented by four stations over the shelf (bottom depth ranging from 26 to 34 m) in the southernmost part of the study area (Fig. 5a, b). The SIMPER analysis indicated an average similarity of 69% within the group, which was mainly characterized by the large abundance of *M. kochii* (almost exclusive of this group), *A. hemistoma* and *L. tetraphylla* and differed from the other groups by the absence or low abundance of siphonophores such as *D. bojani*, *B. bassensis*, *A. tetragona*, *C. appendiculata* and *E. mitra* (Table 3).

Group B, was subdivided into five subgroups and one outlier, the station 49. B1 (72% similarity) was represented by the remaining neritic stations (22 to 61 m depth), B2 (72% similarity) by most stations over the slope (546 to 2969 m depth; Fig. 5a, b), B3 (7% similarity) by remaining stations over the slope (1231 to 3327 m depth; Fig. 5a, b), and B4 and B5 (74 and 68 % similarity, respectively) corresponded to stations from the FNC (576 to 4274 and 997 to 4223 m depth, respectively).

Both subgroups B1 and B2 presented high abundances of the siphonophores *D. bojani*, *C. appendiculata*, *B. bassensis*, *E. spiralis*, *A. tetragona* and of the hydromedusa *A. hemistoma*. Divergences between these subgroups were associated to the siphonophore *L. meteori*, which did not occur in neritic stations of B1 and *L. tetraphylla*, which occurred in higher abundances there (Table 3). The siphonophores *C. appendiculata*, *B. bassensis, A. tetragona* and *D. bojani* also were dominant in subgroup B3. Distinctions with subgroup B2 were associated to the lower abundances of species such as *A. hemistoma*, *L. tetraphylla* and *D. bojani*. Subgroups B4 and B5 presented outstanding higher abundances of *E. mitra*, other species were similar to B3 (Table 3), differences between B4 and B5 were mainly in the abundance of species, which were slightly lower in B5.

Environmental data

Sharp thermocline and halocline were observed between ~78 and 160 m depth in offshore stations of subgroups B4 and B5 (FNC), where temperature and salinity varied respectively from 26°C and 36.2 (Tropical Water) to less than 13°C and ~35.1 (South Atlantic Central Water; see Assunção *et al.*, 2020 for a comprehensive description of the thermohaline structure). Thermohaline structure was quite distinct and the clines were less abrupt and more variable over the slope (subgroups B2 and B3). In these stations, thermocline and halocline started at a maximum of 50 m depth and extended down to ~250 m. A sub-surface fluorescence maximum layer (~100 m) was observed within the thermocline at all FNC and slope stations.

In the stations over the continental shelf, both group A and subgroup B1 presented similar temperature and salinity patterns, around 27°C and 35.5, respectively. Otherwise, while fluorescence was low in the entire water column of most stations at subgroup B1, all stations at group A presented a significant increase near the sea bottom. However, it was always lower than the sub-surface fluorescence maximum observed within the thermocline in the slope and FNC stations (Fig. 6).

SADCP data and Satellite velocity field model (Fig. 7) showed the Central branch of the South Equatorial Current (cSEC) flowed westward over all the study area (with its core around FNC), feeding the North Brazil Undercurrent (NBUC) and surface currents (both flowing north/northwestward) when reaching the slope and continental shelf (see Stramma *et al.*, 1995; Stramma and England, 1999; Dossa *et al.*, 2021). Overall, cSEC and NBUC was much more intense north of 7.5°S, where they spread over the continental shelf. South of 7.5°S, surface current speed weakened over the slope and almost dissipated over the continental shelf. Stations of group A were in this area. Although the surface current from satellite model were coherent with in situ SADCP data in the FNC region, finer scale circulation over the continental shelf were not observed in the data resolution of the former and discrepancies in both methods were observed in this area. This was more evident in the stations of group A where some eastward flow was observed in SADCP data, with coastal waters extending offshore (Fig. 7).

Species responses to environmental gradient

The four canonical axes of the RDA explained 42.7% of species variance. Monte Carlo test showed that the first (F-ratio = 7.408, P-value = 0.008) and all four canonical axes together (F-ratio = 2.586, P-value = 0.002) were significant (Table 4). Axis 1 explained 22.9% of the

variance and was negatively correlated to bottom depth, fluorescence, vertical temperature gradient and westward currents (negative zonal component, representing mainly cSEC). Axis 1 was positively related to SST, SSS and eastward currents (positive zonal component, representing oceanward currents). These variables were correlated since neritic stations presented higher surface temperature and salinity. Thus, axis 1 was mainly associated to the inshore-offshore gradient. Axis 2 explained additional 13.3% and was positively related northwards currents (positive meridional component, representing NBUC and surface currents); Table 4; Fig. 8).

Eudoxoides mitra was highly related with bottom depth due the higher abundance of the species in FNC stations (Subgroup B4 and B5), were higher fluorescence and thermal stratification occurred (negative portion of axis 1). Other abundant siphonophores, such as *C. appendiculata*, *D. bojani*, *B. bassensis*, *A. tetragona*, and *E. spiralis*, which occurred in both shelf, slope and FNC (group B), were related to the positive portion of axis 2 and northwards currents (NBUC and surface currents). The siphonophores *L. meteori*, *A. eschscholtzii* and *Sulculeolaria chuni* were related to the negative portion of axis 1 and positive portion of axis 2, indicating these species were more abundant in deeper stations under high influence of northward currents, such as the slope in the north of the study area. The hydromedusae *A. hemistoma* and *L. tetraphylla*, abundant in all the neritic stations, were positively related to both axis and consequently to higher SST and SSS and shallow depths. *M. kocchii* with almost exclusive occurrence in the neritic stations south of 7.5°S (group A) was associated with higher SST and the eastwards currents spreading coastal waters (Fig. 8).

Discussion

The continental shelf and offshore areas in the Western Tropical South Atlantic Ocean off Northeast Brazil presented a diverse cnidarian community. With 73 taxa, we observed a high species richness, which was expected considering the large spatial coverage of this study, resembling other studies with similar scale around the world (Thibault-Botha *et al.*, 2004; Hosia *et al.*, 2008b; Chen and Liu, 2010; Morita *et al.*, 2017). Among the new occurrences we propose for the area, we extend northward the distribution of *A. affinnis*, *C. frugifera* and *N. aurea* (previous northmost occurrences off Southeast Brazil around 20~23°S; Oliveira *et al.*, 2016) in more than 1500 km. Already known from Northeast Brazil (Oliveira *et al.*, 2016), we extend northward the known distribution of *B. muscus* (9.8°S) and *P. ornata* (16°S) by ca. 400 and 900 km, respectively. *V. pentacantha* was previously known from the Amazon River plume, around the equator (Oliveira *et al.*, 2016), and was now observed near Fernando de Noronha, 1700 km eastward.

Most of the region, including above the continental shelf, presented a typical oceanic assemblage, dominated by holoplanktonic species. Indeed, all stations over the continental shelf north of 8.3°S, slope and FNC (all subgroups of group B) presented high resemblance with similar dominant species, in particular the siphonophores *C. appendiculata*, *B. bassensis* and *A. tetragona*. This result was not necessarily expected since the three domains present significantly different thermohaline structure (Fig. 6; Assunção et al. 2020). Still, due to their holoplanktonic lifestyle, these species are typically present in open ocean superficial layers from all ocean basins (Lo and Biggs, 1996; Pugh *et al.*, 1997; Lo *et al.*, 2012; Grossmann *et al.*, 2015) as observed in the FNC. However, they usually do not dominate the community over the continental shelf, that are usually dominated by meroplanktonic medusae and/or other holoplanktonic species acclimated to this environment (Vannucci, 1957; Buecher and Gibbons, 1999). Two characteristics of the continental shelf off Northeast Brazil can explain such result. First, freshwater runoff from large rivers, which usually grant low salinity and high nutrient input to coastal water are absent in the area, thus waters are highly saline and oligotrophic, with low primary production (Ekau and Knoppers, 1999; Castro *et al.*, 2006). Second, in this western boundary system with narrow continental shelf, surface and sub-surface currents (cSEC, NBUC system) flow towards the continental shelf carrying oligotrophic oceanic water and its associated oceanic plankton fauna.

This substantiates the hypothesis we propose according to which the dominance of oceanic species was driven by the western boundary circulation system. Interestingly, Group A, the most specific in terms of communities, was located in the region of the Pernambuco Plateau, which has a particular topography and circulation with reduced influence of western boundary currents over the shelf (Buarque *et al.*, 2016) and is a hotspot for biodiversity (e.g. Eduardo *et al.*, 2018, 2020). Although the water characteristics from these stations were very similar to group B1, with no signs of reduced salinity or enhanced primary production due to freshwater and nutrients runoff, the typically oceanic siphonophores were absent or with much reduced abundance. On the contrary, the community was dominated by the siphonophore *M. kocchii*, a known coastal species that may even be found inside estuaries (Sanvicente-Añorve *et al.*, 2007; Touzri *et al.*, 2012; Nogueira Júnior *et al.*, 2014, 2018). The divergent patterns may be explained by the current field in the area that has a specific topography due to the presence of the Pernambuco plateau (Buarque *et al.*, 2016). In stations from group B1 the NBUC system shoves oceanic tropical water over the continental shelf, while in the south (group A) this influence was locally reduced. Indeed, an oceanward flow transported coastal water (also oligotrophic). It was likely due to the presence of an anticyclonic eddy with its core located at 8.9°S, 34.1°W that affected locally the NBUC system

(Dossa *et al*., 2021). Cnidarians, particularly siphonophores, are known as good indicators of water masses (Pagès and Gili, 1991; Pagès, 1992; Nogueira Júnior *et al.*, 2014), our results indicate they also are good tracers of coastal waters, even when distinctions are not easily perceptible by classic physical and chemical water characteristics.

Similar results, with oceanic species dominating the cnidarian community over the continental shelf, would be expected in other western boundary systems, particularly in tropical and subtropical environments with strong western boundary currents, narrow shelf and low continental drainage. Other western boundary systems with these physical characteristics are the east and northeast coast of Africa in the Indian Ocean and the coast of East Taiwan, Luzon, Mindanao and Southeast Australia in the Pacific (Loder *et al.*, 1998). These systems were never evaluated in terms of planktonic cnidarian community or dominant species. However, Thibault-Botha et al. (2004) examined the siphonophore assemblage from the narrow continental shelf off East South Africa, also under influence of western boundary currents, but with higher continental drainage (Loder *et al.*, 1998). There, almost the entire length of the continental shelf, under influence of the Agulhas Current, was dominated by the same oceanic species we found in this study (Thibault-Botha *et al.*, 2004). Comparable results in both studies reinforce the hypothesis according to which it could be a classic pattern in western boundary systems with narrow continental shelves. Interestingly, results similar to what we observed in the specific region of the Pernambuco Plateau (stations of group A) were also observed in specific coastal areas in East South Africa where Agulhas Current influence was reduced and a local upwelling present (Thibault-Botha *et al.*, 2004). This area was dominated by *Muggiaea atlantica* (Chun, 1897) a congeneric with similar niche requirements of *M. kocchii* (Mapstone, 2014)*,* which dominated group A.

On the other hand, in western boundary systems with larger continental shelf, such as the southeast coast off Brazil and the east coast off China (Loder *et al.*, 1998), typical coastal/neritic cnidarian species such as *Muggiaea* spp. were spread and dominant over the shelf (note that the East China Sea is also under the large freshwater discharge of the Yangtze River) and oceanic species were more abundant nearby the core of western boundary current over the outer shelf and slope (Nogueira and Oliveira Jr., 1991; Xu, 2006, 2009; Xu and Lin, 2006).

The holoplanktonic siphonophores *D. bojani* and *E. spiralis* and the holoplanktonic hydromedusae *A. hemistoma* and *L. tetraphylla*, although widespread over the area, were more abundant (significant differences for *L. tetraphylla*; Table 2) over the continental shelf and slope. *D. bojani* and *A. hemistoma* are typically present in both neritic and oceanic habitats, occurring in a wide range of temperatures and salinities (Vannucci, 1957; Hosia *et al.*,

2008b; Nogueira Júnior *et al.*, 2014, 2018; Grossmann *et al.*, 2015). The specific features of the continental shelf off Northeast Brazil discussed above may favor these species with apparently high adaptive capacity. *L. tetraphylla*, although also common in oceanic waters, is abundant in neritic habitats at South, Southeast and Northeast Brazil, being also very abundant even in brackish estuarine ecosystems (Vannucci, 1957; Nogueira Júnior *et al.*, 2014, 2015; Nagata *et al.*, 2014), thus its common occurrence was expected in the area.

On the other hand, the siphonophore *E. mitra* was abundant in the FNC (subgroups B4 and B5), an area characterized by a sharp thermocline and pycnocline between ~78 and 160 m depth (Fig. 6; Assunção *et al.*, 2020). This species was less abundant over the slope and the continental shelf. Although the species may be found in neritic environments (Morales-Ramírez and Nowaczyk, 2006; Sanvicente-Añorve *et al.*, 2007), it typically occurs in larger abundances in the upper layers of tropical and subtropical open ocean (Lo and Biggs, 1996; Suarez-Morales *et al.*, 2002; Martell-Hernández *et al.*, 2014). Thus, the reduced abundance over the continental shelf and slope is probably associated to niche preference since the FNC indeed presents current dynamics and a thermohaline structure significantly different from the coast and slope area (Assunção *et al.*, 2020; Dossa *et al.*, 2021). Further studies in finer scales are necessary for a better understanding of its distribution patterns in the Western Tropical South Atlantic.

L. meteori was present exclusively in the slope and FNC stations (subgroups B2, B3, B4 and B5). Generally with low abundance in tropical areas, this species typically occur below 50~100 m depth in the oceanic environment (Batistić *et al.*, 2004; Lučić *et al.*, 2005, 2011; Grossmann *et al.*, 2015). Stratified sampling would be necessary to confirm the vertical distribution of the species in our study area, but if this species distributes exclusively at depths below the shelf break, its absence over the continental shelf would be expected. Moreover, *L. meteori* was clearly more abundant in stations over the slope in the north of the area (Fig.4; Table 1; 2), where currents were typically stronger. This pattern may indicate that these organisms were pushed by the currents accumulating over the slope. *A. tetragona* abundance was also significantly higher over the slope (Fig.4; Table 1; 2), mainly in the north of the study area. Although not significant, the abundance of other siphonophores were also slightly higher over the slope (Table 2), indicating that aggregations over the slope may occur even in species presenting wide distribution in the upper layers of the water column. Although this process was never observed in cnidarians, many studies reported patch aggregation of other planktonic organisms in sloping topography associated to circulation, and species vertical distribution (Cotté and Simard, 2005; Sourisseau *et al.*, 2006; Hazen *et al.*, 2009). It is an important process in the formation of feeding hot spots for large zooplankton predators in

temperate environments (Cotté and Simard, 2005; Sourisseau *et al.*, 2006; Hazen *et al.*, 2009), however, its ecological significance in tropical areas are still unknown.

Conclusion

In conclusion, our results evinced that the continental shelf and offshore areas in the Western Tropical South Atlantic Ocean off Northeast Brazil presented a diverse cnidarian community and extended the known distribution of some species. We also conclude that the western boundary systems with narrow continental shelf from the tropical continental shelf off Northeast Brazil under influence of the cSEC and NBUC present a typical oceanic cnidarian community, dominated by holoplanktonic siphonophores (e.g. *D. bojani*, *C. appendiculata*, *B. bassensis*, *E. spiralis*) confirming our initial hypothesis and similar results are expected in analogous systems. Moreover, areas with reduced influence of western boundary currents present typical coastal species such as *M. kocchii*. The current pattern also seems to influence the distribution of *L. meteori* and *A. tetragona*, pushing and aggregating them toward the continental slope, and the inshore-offshore gradient drove the distribution of species such as *E. mitra,* which were more abundant in open ocean waters.

Conflict of Interest: The authors declare that they have no conflict of interest.

Ethical approval: The authors followed all applicable international, national, and/or institutional guidelines for animal testing, animal care and use of animals.

Sampling and field studies: The authors have obtained all necessary permits for sampling and observational field studies from the competent authorities.

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Figures

Figure 1. Geographic location of the study area in the Northeast Brazilian continental shelf (bottom depth <90 m, except shallow stations around oceanic islands), slope (bottom depth between 90 and 3500 m, except stations in this range around oceanic islands) and offshore around the Fernando de Noronha Chain (bottom depth >3500 m and shallower station around oceanic islands) in the Western Tropical South Atlantic, showing the sampled stations.
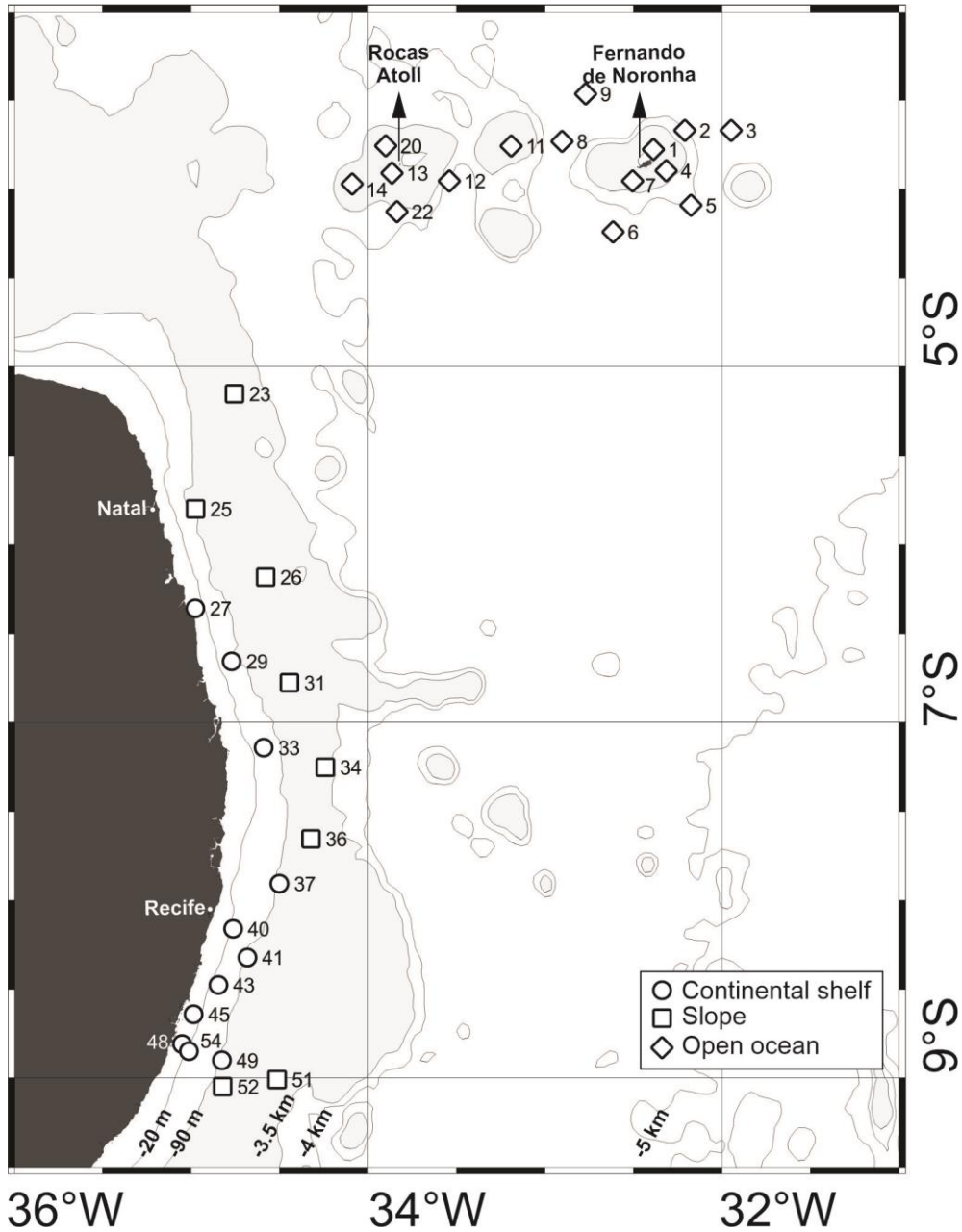
Figure 2. Geographic distribution of number of species and total abundance of hydromedusae and siphonophores in the first 200 m of the water at October 2015.
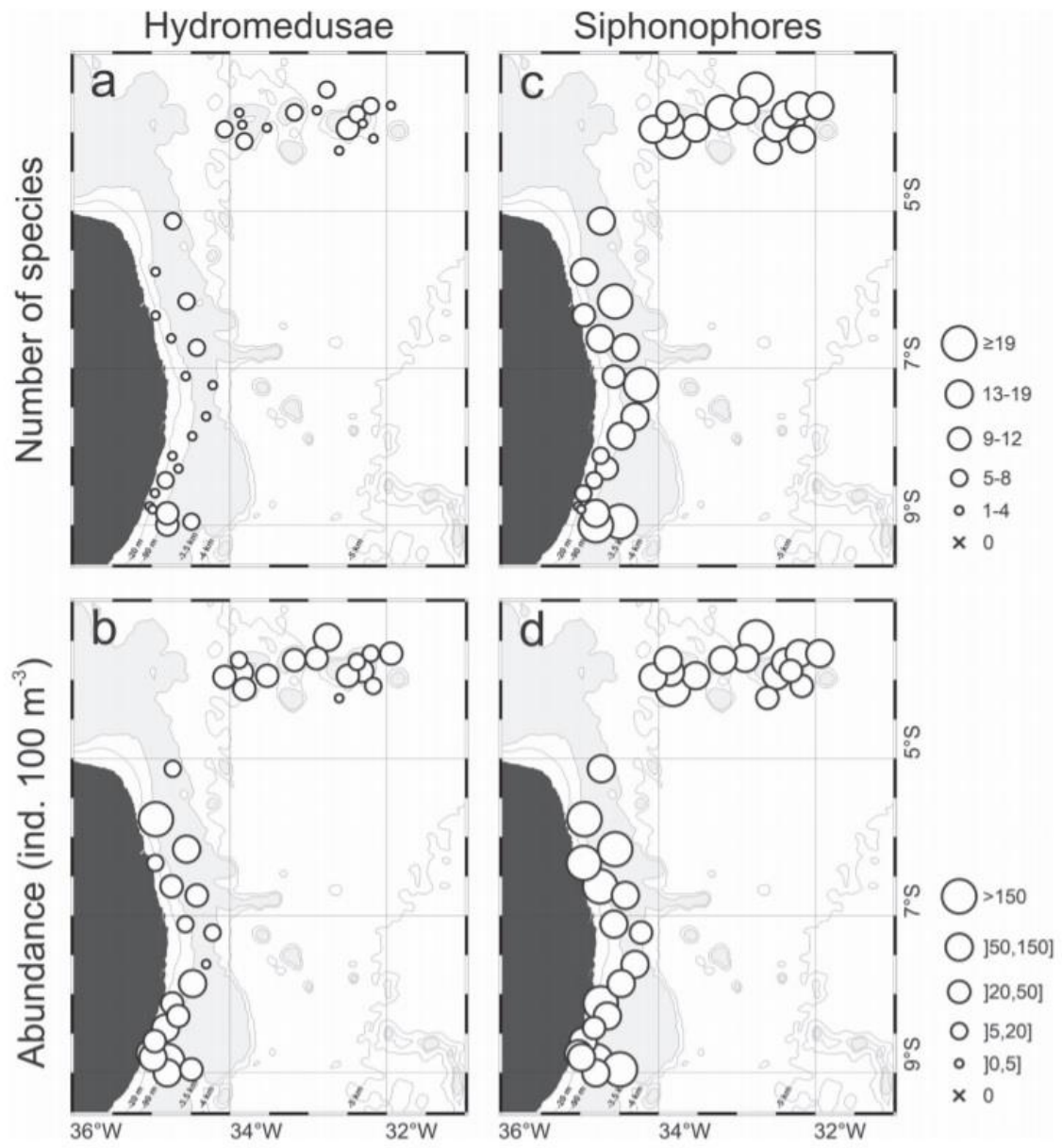
Figure 3. Geographic distribution and abundance of the dominant hydromedusae in the first 200 m of the water column at October 2015.
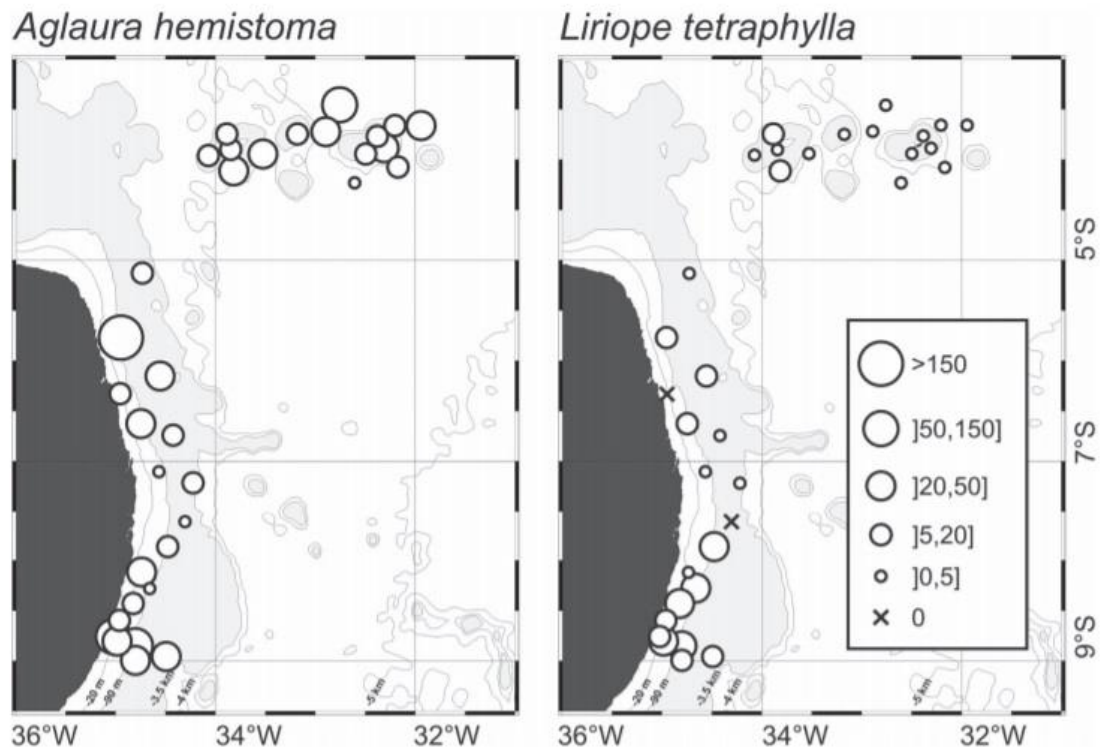
Figure 4. Geographic distribution and abundance of the dominant siphonophores in the first 200 m of the water column at October 2015.
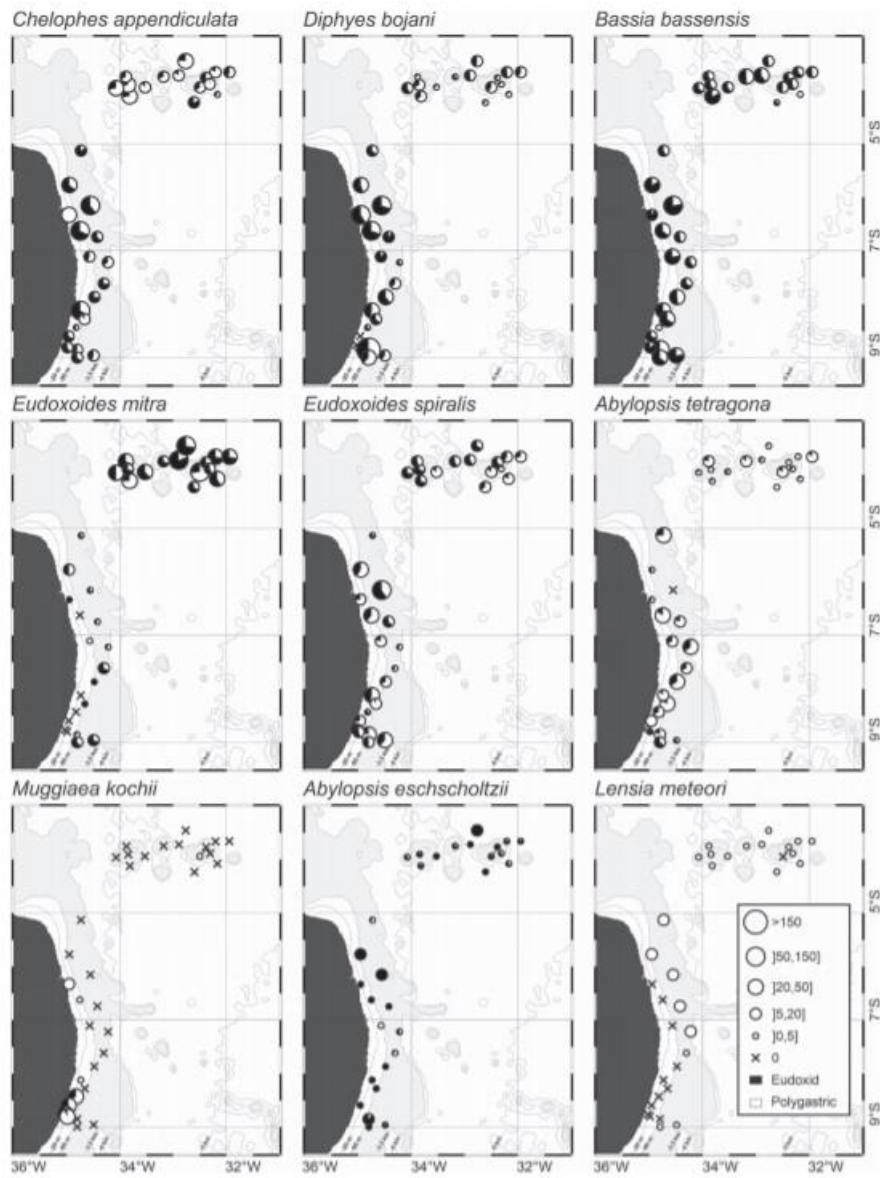
Figure 5. (a) Cluster analysis dendrogram indicating three main groups and subgroups of stations with similar planktonic cnidarian communities in the Western Tropical South Atlantic Ocean, dashed lines are significant groups in the SIMPROF analysis. (b) Map indicating location of the groups and subgroups arranged in the cluster analysis.
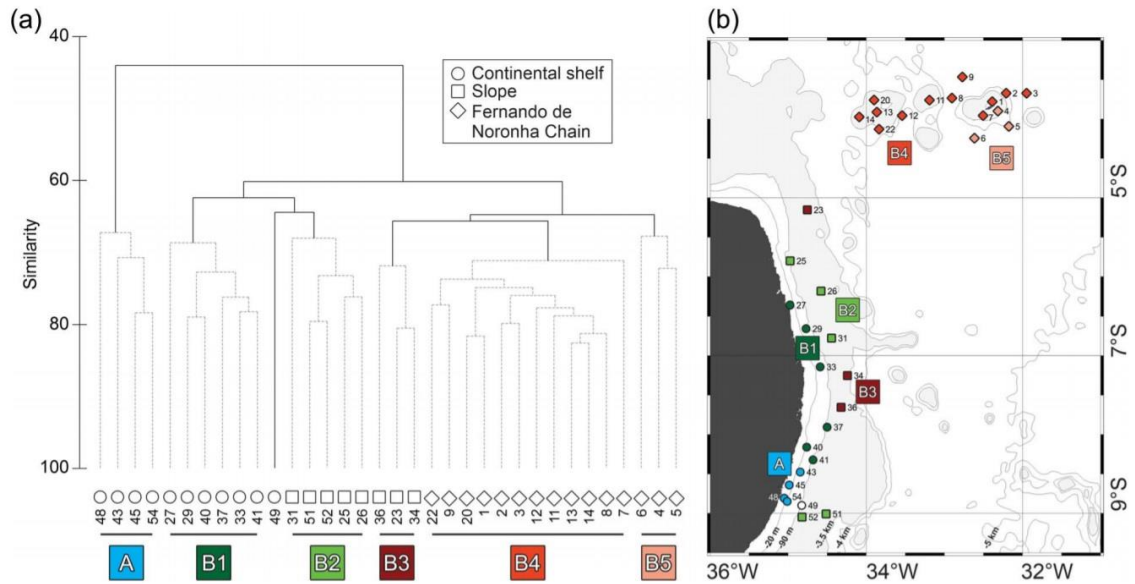
Figure 6. Vertical profiles of temperature, salinity and fluorescence in the 34 stations sampled, lines indicate station profiles and fill the range inside each group arranged in the cluster analysis (Fig. 5).
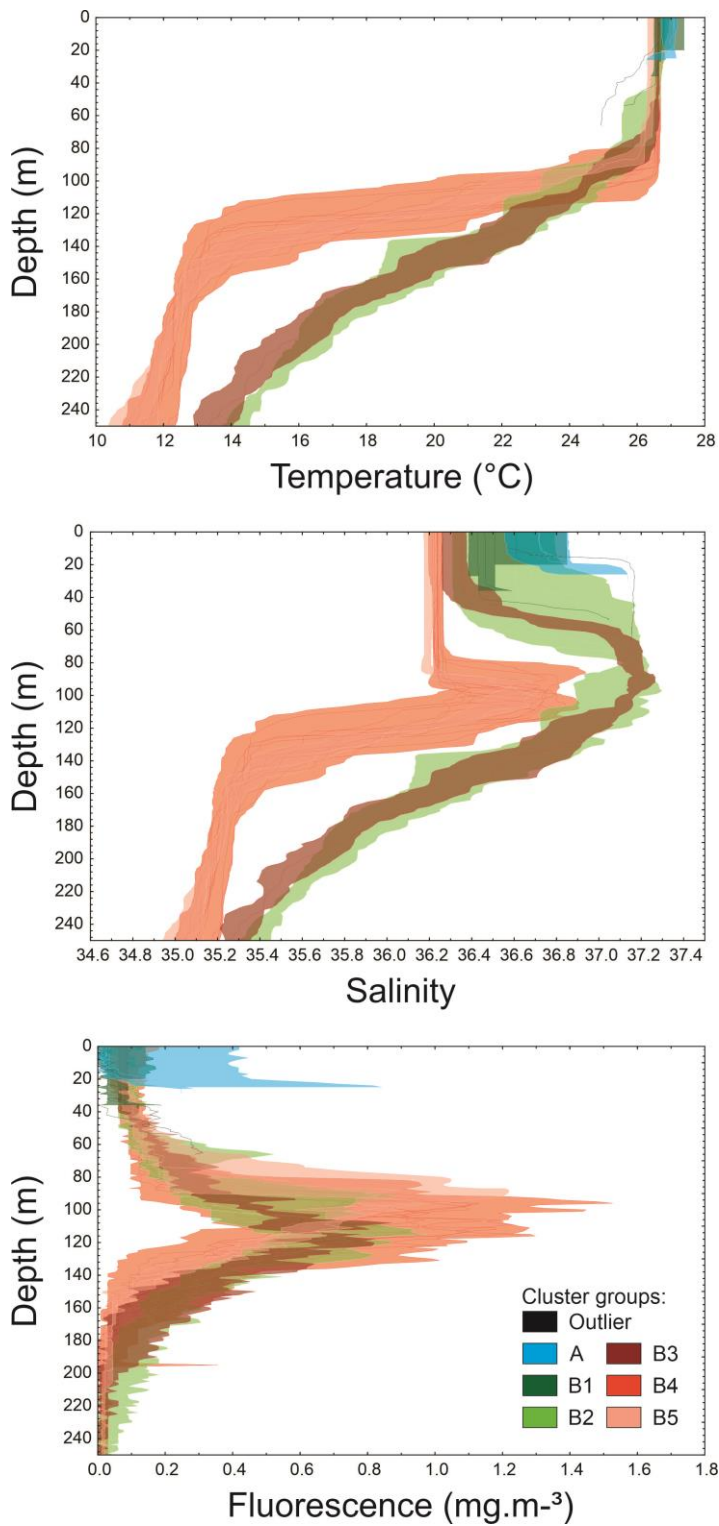
Figure 7. Surface currents vectors of satellite model (light blue) and ADCP data (dark blue) and indicators of the predominant current in the area (NBUC = North Brazil Undercurrent; cSEC = Central branch of the South Equatorial Current).
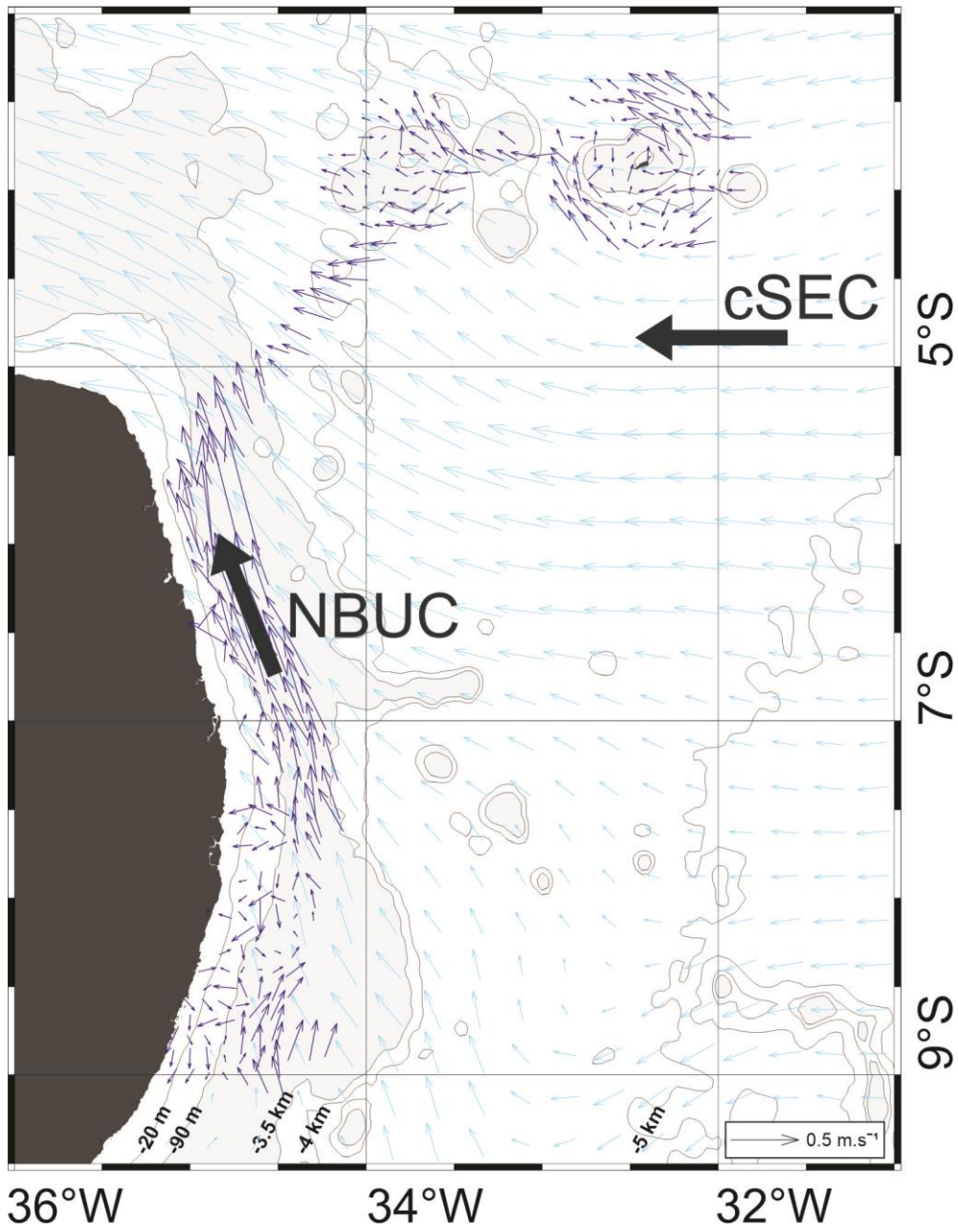
Figure 8. Redundancy analysis relating the 12 most abundant planktonic cnidarian species to environmental gradients in the Western Tropical South Atlantic Ocean. Species codes: *Eud_mit = Eudoxoides mitra, Aby_esc = Abylopsis eschscholtzii, Sul_chu = Sulculeolaria chuni, Len_met = Lensia meteori, Che_app = Chelophyes appendiculata, Bas_bas = Bassia bassensis, Aby_tet = Abylopsis tetragona, Dip_boj = Diphyes bojani, Eud_spi = Eudoxoides spiralis, Agl_hem = Aglaura hemistoma, Lir_tet = Liriope tetraphylla and Mug_koc = Muggiaea kocchii.* Environmental codes: SST = Sea surface temperature, SSS = Sea surface salinity, U = Surface currents zonal component, V = Surface currents meridional component, Fluor = Fluorescence, Tempchange = Temperature change index and Bdepth = Bottom depth.
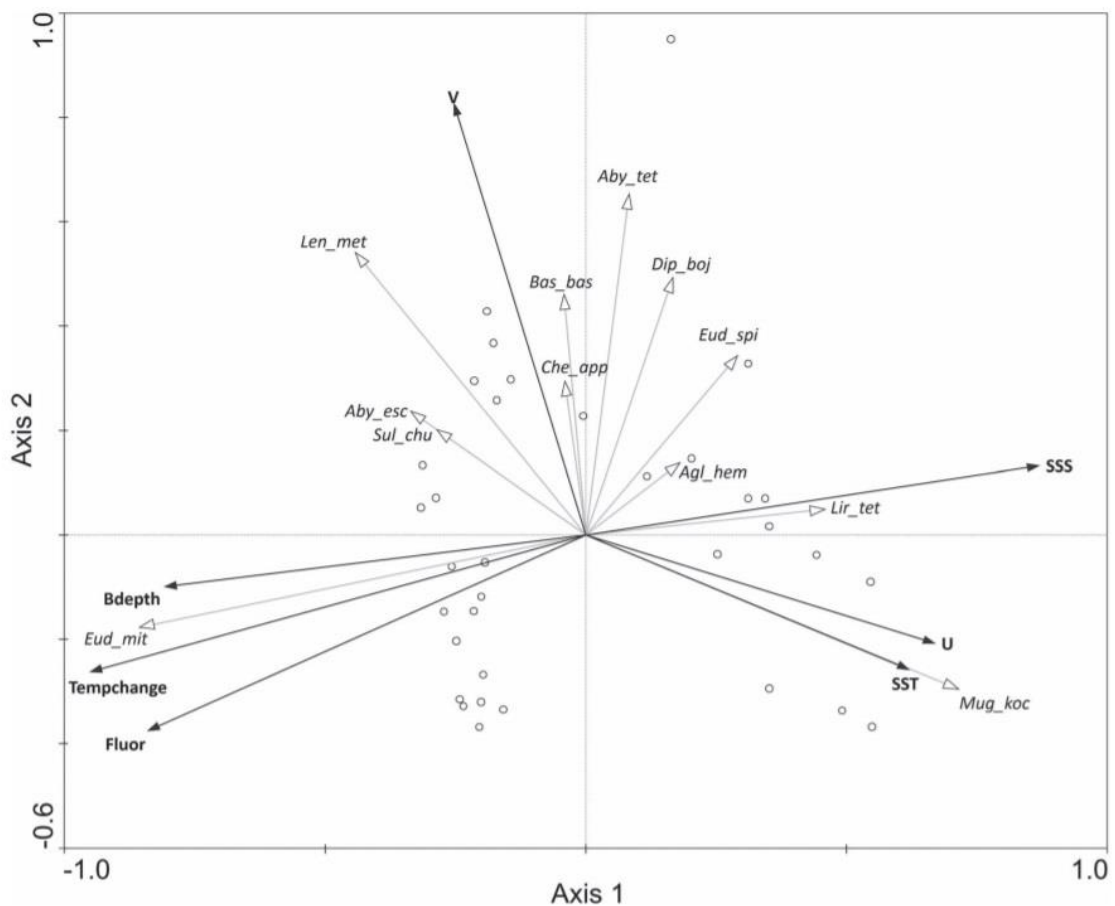
Table 1. Basic statistics of planktonic cnidarian species from shelf, slope and Fernando de Noronha Chain (FNC) domains in the Western Tropical South Atlantic Ocean off Northeast Brazil. Mean abundance (ind. 100 m^{-3}) per station and standard deviation, range of abundance , frequency of occurrence (f; considering all domains) and species life-cycle (LC; H = Holoplanktonic; M = Meroplanktonic). Bold species are new records in the area.

Species	Shelf		Slope		FNC		f (%)	LC
	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances		
Siphonophores								
Eudoxoides spiralis (Bigelow, 1911)	15.43 ± 10.64	4.78 - 37.89	17.33 ± 15.64	2.86 - 53.91	8.51 ± 3.8	2.73 - 15.44	100	H
Abylopsis tetragona (Otto, 1823)	9.61 ± 8.65	0.83 - 24.84	17.38 ± 9.34	5.34 - 32.65	3.9 ± 2.48	0.57 - 11.55	97.06	H
Bassia bassensis (Quoy & Gaimard, 1833)	22.4 ± 19.03	0.96 - 64.96	29.37 ± 27.37	2.33 - 97.64	13.22 ± 8.88	1.15 - 29.23	97.06	H
Chelophyes appendiculata (Eschscholtz, 1829)	26.05 ± 27.31	1.91 - 99.99	26.24 ± 27.24	8.18 - 94.65	17.89 ± 12.03	1.52 - 43.18	97.06	H
Diphyes bojani (Eschscholtz, 1825)	39.06 ± 55.75	2.87 - 199.67	22.55 ± 24.12	3.9 - 82.69	5.49 ± 3.57	1.24 - 12.93	91.18	H
Sulculeolaria chuni (Lens & van Riemsdijk, 1908)	1.15 ± 1.02	0.46 - 3.02	3.77 ± 4.22	0.17 - 13.48	2.22 ± 1.71	0.33 - 6.99	91.18	H
Abylopsis eschscholtzii (Huxley, 1859)	2.34 ± 2.91	0.46 - 10.51	2.91 ± 2.27	0.64 - 6.96	4 ± 3.74	0.66 - 16.78	88.24	H
Eudoxoides mitra (Huxley, 1859)	0.84 ± 1.42	0.46 - 4.52	7.1 ± 4.7	1.85 - 17.36	30.32 ± 14.35	3.59 - 54.27	82.35	H
Agalma okenii Eschscholtz, 1825	0.16 ± 0.33	0.83 - 0.9	0.58 ± 0.57	0.17 - 1.71	0.46 ± 0.27	0.12 - 0.99	67.65	H
Lensia meteori (Leloup, 1934)	-	-	7.66 ± 5.67	0.29 - 16.37	1.24 ± 1.14	0.33 - 4.46	64.71	H
Lensia spp.	0.09 ± 0.27	0.96 - 0.96	1.05 ± 0.88	0.13 - 3.19	1.33 ± 1.22	0.31 - 3.77	58.82	H
Sulculeolaria turgida (Gegenbaur, 1854)	0.2 ± 0.36	0.4 - 0.96	0.67 ± 0.63	0.36 - 2.12	0.23 ± 0.33	0.12 - 1.49	47.06	H
Agalma elegans (Sars, 1846)	0.08 ± 0.26	0.9 - 0.9	0.15 ± 0.22	0.29 - 0.64	0.27 ± 0.34	0.12 - 1.45	44.12	H
Nanomia bijuga (Delle Chiaje, 1844)	0.34 ± 0.6	0.83 - 1.91	0.46 ± 0.82	0.13 - 2.55	0.15 ± 0.15	0.12 - 0.35	44.12	H
Cordagalma ordinatum (Haeckel, 1888)	0.52 ± 0.84	0.4 - 2.48	0.55 ± 0.69	0.18 - 1.92	0.11 ± 0.16	0.19 - 0.48	41.18	H
Praydae spp.	-	-	0.83 ± 0.67	0.13 - 2.97	0.18 ± 0.26	0.21 - 1.29	41.18	H
Ceratocymba leuckartii (Huxley, 1859)	0.08 ± 0.18	0.4 - 0.52	0.92 ± 0.64	0.52 - 1.71	0.15 ± 0.28	0.25 - 1.72	38.24	H

Table 1. Continuation

Species	Shelf		Slope		FNC		f (%)	LC
	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances		
Diphyes dispar Chamisso & Eysenhardt, 1821	0.54 ± 0.94	0.79 - 3.24	1.3 ± 2.04	0.49 - 6.59	2.56 ± 9.41	0.34 - 37.77	38.24	H
Lensia subtilis (Chun, 1886)	0.16 ± 0.34	0.83 - 0.96	0.34 ± 0.4	0.13 - 1.2	0.17 ± 0.27	0.23 - 1.29	38.24	H
Dimophyes arctica (Chun, 1897)	-	-	-	-	0.45 ± 0.59	0.19 - 2.98	26.47	H
Sulculeolaria biloba (Sars, 1846)	1.82 ± 5.77	20.06 - 20.06	2.7 ± 3.01	0.13 - 8.85	0.02 ± 0.08	0.33 - 0.33	26.47	H
Muggiaea kochii (Will, 1844)	12.93 ± 15.24	0.79 - 42.67	-	-	0.01 ± 0.05	0.21 - 0.21	23.53	H
Vogtia glabra Bigelow, 1918	-	-	0.04 ± 0.1	0.3 - 0.3	0.14 ± 0.16	0.19 - 0.43	23.53	H
Lensia subtiloides (Lens & van Riemsdijk, 1908)	0.52 ± 1.65	5.73 - 5.73	0.12 ± 0.22	0.29 - 0.65	0.09 ± 0.19	0.34 - 0.67	17.65	H
Amphicaryon ernesti Totton, 1954	-	-	0.21 ± 0.37	0.85 - 0.86	0.07 ± 0.16	0.21 - 0.55	14.71	H
Lensia fowleri (Bigelow, 1911)	-	-	0.07 ± 0.13	0.29 - 0.3	0.06 ± 0.12	0.26 - 0.34	14.71	H
Lensia hardy Totton, 1941	-	-	0.15 ± 0.27	0.6 - 0.64	0.05 ± 0.1	0.21 - 0.28	14.71	H
Forskalia contorta (Milne Edwards, 1841)	-	-	0.1 ± 0.21	0.13 - 0.64	0.04 ± 0.09	0.23 - 0.31	11.76	H
Hippopodius hippopus (Forsskål, 1776)	-	-	0.19 ± 0.33	0.65 - 0.85	0.03 ± 0.08	0.12 - 0.31	11.76	H
Amphicaryon acaule Chun, 1888	-	-	0.03 ± 0.09	0.26 - 0.26	0.04 ± 0.11	0.28 - 0.34	8.82	H
Lensia cossack Totton, 1941	-	-	0.14 ± 0.28	0.3 - 0.85	0.02 ± 0.08	0.33 - 0.33	8.82	H
Lensia hotspur Totton, 1941	0.08 ± 0.26	0.9 - 0.9	0.28 ± 0.75	2.27 - 2.27	0.06 ± 0.22	0.91 - 0.91	8.82	H
Lychnagalma utricularia (Claus, 1879)	-	-	-	-	0.05 ± 0.1	0.23 - 0.28	8.82	H
Sulculeolaria monoica (Chun, 1888)	-	-	0.04 ± 0.12	0.35 - 0.35	0.09 ± 0.26	0.28 - 1.35	8.82	H
Abyla sp.	-	-	0.05 ± 0.14	0.49 - 0.49	0.02 ± 0.08	0.31 - 0.31	5.88	H
Abyla trigona Quoy & Gaimard, 1827	-	-	0.04 ± 0.08	0.17 - 0.18	-	-	5.88	H
Athorybia rosacea (Forsskål, 1775)	-	-	-	-	0.04 ± 0.1	0.23 - 0.34	5.88	H

Table 1. Continuation

Species	Shelf		Slope		FNC		f (%)	LC
	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances		
Hippopodidae sp.	-	-	0.02 ± 0.06	0.17 - 0.17	0.02 ± 0.09	0.35 - 0.35	5.88	H
Lensia conoidea (Keferstein & Ehlers, 1860)	-	-	-	-	0.03 ± 0.08	0.12 - 0.34	5.88	H
Ceratocymba dentata (Bigelow, 1918)	-	-	-	-	0.01 ± 0.03	0.12 - 0.12	2.94	H
Forskalia edwardsii Kölliker, 1853	0.04 ± 0.11	0.4 - 0.4	-	-	-	-	2.94	H
Halistemma rubrum (Vogt, 1852)	-	-	-	-	0.02 ± 0.06	0.25 - 0.25	2.94	H
Vogtia pentacantha Kölliker, 1853	-	-	-	-	0.01 ± 0.03	0.12 - 0.12	2.94	H
Hydromedusae								
Aglaura hemistoma Péron & Lesueur, 1810	31.65 ± 38.05	3.61 - 134.71	50.09 ± 83.28	1.39 - 267.71	20.1 ± 16.93	1.97 - 69.59	100	H
Liriope tetraphylla (Chamisso & Eysenhardt, 1821)	19.57 ± 15.18	0.61 - 43.95	6.91 ± 7.16	1.25 - 19.48	2.87 ± 1.88	0.19 - 6.99	94.12	H
Solmundella bitentaculata (Quoy & Gaimard, 1833)	0.66 ± 1.81	0.96 - 6.33	0.7 ± 0.6	0.17 - 1.69	0.58 ± 0.74	0.33 - 2.52	47.06	H
Cytaeis spp.	0.61 ± 1.92	6.69 - 6.69	0.24 ± 0.3	0.13 - 0.85	0.16 ± 0.2	0.21 - 0.69	35.29	M
Aequorea spp.	0.26 ± 0.82	2.87 - 2.87	0.18 ± 0.38	0.3 - 1.14	0.09 ± 0.13	0.21 - 0.34	23.53	M
Clytia spp.	8.67 ± 27.17	0.83 - 94.58	0.37 ± 0.98	2.96 - 2.96	2.11 ± 6.97	1.65 - 28.75	17.65	M
Rhopalonema velatum Gegenbaur, 1857	-	-	0.12 ± 0.21	0.13 - 0.64	0.1 ± 0.23	0.26 - 0.86	17.65	H
Annatiara affinis (Hartlaub, 1914)	0.17 ± 0.55	1.91 - 1.91	0.36 ± 0.47	0.85 - 1.14	-	-	11.76	M
Cirrholovenia tetranema Kramp, 1959	1.31 ± 3.6	0.83 - 12.64	0.08 ± 0.21	0.64 - 0.64	-	-	11.76	M
Corymorpha gracilis (Brooks, 1883)	0.55 ± 0.96	0.52 - 3.02	-	-	-	-	11.76	M
Cunina frugifera Kramp, 1948	-	-	-	-	0.16 ± 0.33	0.21 - 1.14	11.76	H
Bougainvillia muscus (Allman, 1863)	-	-	0.07 ± 0.14	0.17 - 0.49	-	-	5.88	M

Table 1. Continuation

Species	Shelf		Slope		FNC		f (%)	LC
	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances		
Laodiceidae spp.	-	-	-	-	0.03 ± 0.09	0.19 - 0.33	5.88	M
Pegantha clara R.P. Bigelow, 1909	-	-	0.04 ± 0.09	0.29 - 0.29	0.03 ± 0.11	0.43 - 0.43	5.88	H
Porpita porpita (Linnaeus, 1758)	-	-	0.26 ± 0.7	2.12 - 2.12	0.08 ± 0.31	1.23 - 1.23	5.88	H
Proboscidactyla ornata (McCrady, 1859)	0.75 ± 1.93	1.58 - 6.69	-	-	-	-	5.88	M
Sminthea eurygaster Gegenbaur, 1857	-	-	0.07 ± 0.18	0.53 - 0.53	0.01 ± 0.05	0.21 - 0.21	5.88	H
Teissiera polypofera Xu, Huang & Chen, 1991	0.35 ± 1.1	3.82 - 3.82	0.05 ± 0.14	0.42 - 0.42	-	-	5.88	M
Amphinema sp.	-	-	-	-	0.01 ± 0.05	0.21 - 0.21	2.94	M
Anthomedusa sp.1	0.17 ± 0.55	1.91 - 1.91	-	-	-	-	2.94	M
Anthomedusa sp.2	-	-	0.05 ± 0.14	0.42 - 0.42	-	-	2.94	M
Cirrholovenia sp.	-	-	-	-	0.01 ± 0.05	0.21 - 0.21	2.94	M
Ectopleura sp.	0.17 ± 0.55	1.91 - 1.91	-	-	-	-	2.94	M
Eirenidae sp.	-	-	-	-	0.09 ± 0.34	1.37 - 1.37	2.94	M
Eutima mira McCrady, 1859	-	-	-	-	0.02 ± 0.08	0.33 - 0.33	2.94	M
Lovenelidae spp.	-	-	0.08 ± 0.21	0.64 - 0.64	-	-	2.94	M
Orchistoma sp.	0.61 ± 1.93	6.72 - 6.72	-	-	-	-	2.94	M
Scyphomedusae								
Nausithoe spp.	0.78 ± 2.47	8.6 - 8.6	0.49 ± 0.64	1.23 - 1.43	0.59 ± 1.3	0.25 - 5.33	35.29	M
Nausithoe aurea Silveira & Morandini, 1997	0.21 ± 0.36	0.46 - 0.96	0.18 ± 0.28	0.29 - 0.82	0.03 ± 0.12	0.57 - 0.57	20.59	M
Nausithoe punctata Kölliker, 1853	0.07 ± 0.23	0.79 - 0.79	-	-	0.16 ± 0.54	0.33 - 2.14	8.82	M

11   **Table 1**. Continuation

Species	Shelf		Slope		FNC		f (%)	LC
	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances	Mean ± SD	Range of non-zero abundances		
Ephirae	3.22 ± 7.11	0.61 - 25.01	3.51 ± 5.97	0.29 - 17.67	0.11 ± 0.17	0.12 - 0.46	41.18	M
Anthozoa								
Cerinula	0.07 ± 0.23	0.79 - 0.79	0.07 ± 0.12	0.26 - 0.3	0.75 ± 1.69	0.21 - 6.92	35.29	M

12

13

14   **Table 2.** Results of the Analysis of Variance testing differences in community indicators and
15   abundance of representative planktonic cnidarian species among the shelf, slope and
16   Fernando de Noronha Chain (FNC) domains and Tukey post-hoc test. Significant p-values are in
17   bold. Letters indicate difference among the domains in the Tukey test.

Indicator/Species	F	p	Tukey test		
			Shelf	Slope	FNC
Hydromedusae richness	1.2790	0.2930	-	-	-
Hydromedusae total abundance	1.5000	0.2390	-	-	-
Siphonophores richness	**26.0480**	**0.0000**	a	b	b
Siphonophores total abundance	1.2130	0.3110	-	-	-
Abylopsis eschscholtzii	0.8230	0.4480	-	-	-
Abylopsis tetragona	**9.1780**	**0.0010**	a	b	a
Aglaura hemistoma	0.9620	0.3930	-	-	-
Bassia bassensis	2.0220	0.1500	-	-	-
Chelophyes appendiculata	0.5410	0.5870	-	-	-
Diphyes bojani	2.8600	0.0720	-	-	-
Eudoxoides mitra	**29.3430**	**0.0000**	a	a	b
Eudoxoides spiralis	2.3430	0.1130	-	-	-
Lensia meteori	**17.0960**	**0.0000**	a	b	a
Liriope tetraphylla	**9.4270**	**0.0010**	a	b	b
Muggiaea kochii	**7.5310**	**0.0020**	a	b	b
Sulculeolaria chuni	2.4880	0.1000	-	-	-

18

19   **Table 3.** Results of SIMPER analysis, showing the relative contribution of planktonic cnidarian
20   species in the formation of the groups defined in the Cluster analysis.

Species	A	B1	B2	B3	B4	B5
Abylopsis eschscholtzii	-	-	-	-	4.8	7.9
Abylopsis tetragona	-	11.1	9.7	11.7	6.8	-
Aglaura hemistoma	22.1	9.8	11	7.5	11.6	12.8
Bassia bassensis	-	15.5	10.1	13.7	11	8.6
Chelophyes appendiculata	-	15.7	9.3	14.5	12.4	12.2
Diphyes bojani	-	16.2	8.8	10.5	7.3	7.2
Eudoxoides mitra	-	-	6.2	7.8	15	22.3
Eudoxoides spiralis	14.3	13.1	9.4	9	9.8	11.2
Lensia meteori	-	-	4	7.7	-	-
Liriope tetraphylla	20.9	-	6.1	-	5.8	-
Muggiaea kochii	25.5	-	-	-	-	-
Sulculeolaria chuni	-	-	4.3	-	-	-

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22

23 **Table 4.** Summary of the Redundancy Analysis (RDA) performed between the cnidarian
24 representative taxa and environmental explanatory variables from the Northwestern Brazilian
25 continental shelf, slope and Fernando de Noronha Chain

	Axis 1	Axis 2	Axis 3	Axis 4
Eigenvalues	0.229	0.128	0.035	0.024
Species-environment correlations	0.917	0.636	0.632	0.52
Cumulative variance (%):				
Of species data	22.9	35.6	39.1	41.5
Of species-environment relation	52.6	82	90.1	95.5
Correlations of explanatory variables:				
Surface currents zonal component	0.6658	-0.2062	0.3627	-0.0974
Surface currents meridional component	-0.2512	0.8221	-0.3436	-0.369
Bottom depth	-0.8035	-0.0985	-0.1235	0.0204
Sea surface temperature	0.6165	-0.2562	-0.596	-0.3553
Sea surface salinity	0.8655	0.1319	-0.3494	0.1466
Temperature change index	-0.9463	-0.2613	-0.1016	0.0675
Fluorescence	-0.8359	-0.3738	-0.1532	-0.1098

26