Planktonic cnidarian responses to contrasting thermohaline and circulation seasonal scenarios in a tropical western boundary current system

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Abstract. In western boundary current systems (WBCS), strong currents flow coastward carrying oceanic water masses and their associated planktonic fauna. Variation in the intensity of these currents and in the continental runoff may affect the dynamic interplay between oceanic and coastal communities. In addition, changes in the continental runoff and the thermohaline structure modulate the primary production, adding complexity to the dynamics of these oligotrophic systems. These dynamics likely shape the planktonic cnidarian communities. To further understand such relationships, we used a comprehensive dataset encompassing samples collected above the shelf, slope and around oceanic seamounts and islands of the Fernando de Noronha Ridge in the Western Tropical South Atlantic, in two seasons characterized by distinct thermohaline structure and circulation patterns. Results show that in this WBCS, coastward currents spread oceanic waters and their associated cnidarian species over the continental shelf. However, while both costal and oceanic communities co-occur when the continental runoff is notable, oceanic species dominate almost the entire shelf during the dry season characterized by a stronger boundary current intensity. We also conclude that when the mixed-layer depth and associated nutricline is shallower, the enhanced primary productivity supports larger populations of planktonic cnidarian species through a bottom-up control.

1 Introduction

Planktonic cnidarians are predators of zooplankton present in most marine environments. Due their high feeding rates and capacity to reproduce fast and bloom, under specific favorable conditions they have the capacity to control the entire pelagic community with potential impacts on human activities such as fisheries (Boero, 2013; Yilmaz, 2015). Historically, this group was considered a dead-end in the pelagic food web due the low proportion of carbon in their gelatinous tissues. However, recent studies appointed then as a significant food source for many higher trophic level groups, from crustaceans to marine turtles (Ayala et al., 2018; Hays et al., 2018). These factors, associated to a concern that gelatinous populations could be

globally increasing due anthropogenic pressure (Condon et al., 2012; Mills, 2001; Nogueira Júnior et al., 2022; Purcell et al., 2007) enhanced the scientific and popular interest in the dynamics of the group and their role in ecosystem functioning.

The distribution patterns of planktonic cnidarians are closely related to physical processes. Distinct water-masses typically present characteristic species (Pagès, 1992; Pagès et al., 2001; Nogueira Júnior et al., 2014). Oceanic circulation features (e.g. currents, eddies and upwelling/downwelling) transporting these water-masses also convey the associated cnidarian fauna, shaping their meso-scale distribution patterns (Tosetto et al., 2021). Local resource availability and seawater characteristics such as temperature, salinity, and food availability are important factors controlling cnidarian species abundance and distribution, usually at smaller scales (Gibbons and Buecher, 2001; Gili et al., 1988; Luo et al., 2014). Due to these close relationships, among zooplankton communities, planktonic cnidarians are excellent model organisms to understand the complex dynamics between oceanic processes and marine life.

In western boundary current systems (WBCS), strong currents flow coastward carrying oceanic water masses and their associated planktonic fauna over the continental shelf (Dossa et al., 2021; Neumann-Leitão et al., 1999; Thibault-Botha et al., 2004; Tosetto et al., 2021). Under specific conditions (e.g. narrow shelves and low continental drainage), oceanic intrusions may reach coastal areas with oceanic species dominating the entire continental shelf (Tosetto et al., 2021; Thibault-Botha et al., 2004). In the WBCS of the tropical South Atlantic, such circumstance was observed in spring, when the continental runoff is reduced and the western boundary current flow is intense (Tosetto et al., 2021). In austral autumn, continental rainfall and temperature are higher and winds are weaker in the area comparing to spring, leading to distinct circulation and thermohaline structure scenarios (Assunção et al., 2020; Dossa et al., 2021). The North Brazilian Undercurrent (NBUC), which flows northwards parallel to the coast and is responsible for the oceanic intrusions over the continental shelf in spring, is weaker and has its core further from the shelf break in autumn (Dossa et al., 2021). Such circumstance, associated to the higher continental discharge, has the potential to reduce the influence of the oceanic species over the continental shelf and favor the spread of coastal species. However, the effects of the variability in western boundary currents intensity, intrusions of tropical water and river runoff over the continental shelf in zooplankton distribution and abundance are still to be tested.

Offshore, in the Fernando de Noronha Ridge (FNR), a strong stratification occurs. Still, due to wind mixing and the shear between the near-surface eastward flowing of the central South Equatorial Current (cSEC) and the sub-surface westward South Equatorial Undercurrent (SEUC), the mixed-layer depth is shallower in autumn than in spring (Assunção et al., 2020). A shallower mixed-layer increase nutrient input to the photic layer, enhancing primary production and phytoplankton biomass (Farias et al., 2022). The role of the stratification, mixing and light penetration in the modulation of the primary production is relatively well known (Farias et al., 2022; Mignot et al., 2014; Polovina et al., 1995; Signorini et al., 1999) and it was for instance related with increased production of zooplankton (Farstey et al., 2002; Hadfield and Sharples, 1996; Polovina et al., 1995). However, the effects of such changes in zooplankton communities, particularly cnidarians, from highly stratified and oligotrophic tropical systems is still unknown.

In this context, here we test two main hypotheses. First, an increase in continental runoff and a reduction in western boundary currents intensity would increase the presence of coastal and reduce the presence of oceanic cnidarian species over the

65   continental shelf in WBCS. Second, the shallower the mixed-layer depth, the greater the abundance of planktonic cnidarian communities. For that, we compared the spatial patterns in planktonic cnidarian distribution and abundance from data collected above the shelf, slope and around oceanic seamounts and islands of the FNR in the Western Tropical South Atlantic in spring (Tosetto et al., 2021) with a new dataset collected in autumn.

2 Materials and methods

70   ### 2.1 Data

Data were collected during two "Acoustics along the Brazilian coast" surveys (Bertrand, 2015, ABRACOS 1 and ABRACOS 2; 2017) performed along the Northeast Brazilian continental shelf and slope between 5 and 9°S, and around oceanic seamounts and islands from FNR, including the Fernando de Noronha Archipelago itself and the Rocas Atoll (Fig. 1). The surveys were carried out on board the French oceanographic vessel R/V ANTEA in austral spring (September-October 2015) and autumn
75   (April-May 2017). Planktonic cnidarians were sorted from zooplankton samples collected at 34 and 45 stations in spring and autumn, respectively (Fig. 1). Samples were collected 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 (Table 1). The net was fitted with a calibrated mechanical flowmeter (Hydro-Bios) to estimate the volume filtered during each haul. Samples were
80   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 Pugh, 1999; Bouillon, 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.
85   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-O2 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)
90   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
95   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. The analyses of the data obtained by ship-mounted Acoustic Doppler Current Profiler (SADCP) are discussed in Dossa et al. (2021) and Costa da Silva et al. (2021).

100   **2.2 Data analysis**

For the data analysis, stations were grouped in three systems (Fig. 1): Continental Shelf, WBCS (offshore stations adjacent to coast, mainly over the slope) and South Equatorial Current system (SECS; stations along the FNR). WBCS and SECS present distinct thermohaline structure (Assunção et al., 2020). Stations A2_39 and A2_54 were located in the transition zone between WBCS and SECS and thus removed for the comparative analysis. To dampen effects of dominant species, abundance data was

105   transformed by log (x+1) in all analyses. A Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson et al., 2008) was used to test for diel differences in the community structure of planktonic cnidarians at both seasons. Since no significant differences were observed (Pseudo-F = 0.93842 and 0.86812, P = 0.451 and 0.509, for spring and autumn, respectively) the pooled set of day and night data was used.

Factorial Analysis of Variance (ANOVA) were performed to test for differences in hydromedusae and siphonophores richness

110   and total abundance, and the abundance of the most abundant (abundance >1%) species, according to the region (shelf, WBCS and SECS), the season, and the interactions between these factors. When ANOVA was significant, Tukey post-hoc test was used to identify the levels (seasons and regions) that differed among each other.

Spatial patterns in planktonic cnidarian community abundance in autumn 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%

115   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. This procedure was previously performed by Tosetto et al. (2021) for the spring dataset.

Distribution maps were produced QGIS 3.20 (QGIS Development Team, 2022). Factorial ANOVA was performed in Statistica 10 (StatSoft Inc., 2011). Cluster, SIMPROF, SIMPER and PERMANOVA analysis were performed in Primer v.6 +

120   PERMANOVA (Clarke and Gorley, 2006).

3 Results

3.1 Environmental background

Whatever the season, surface (0-70 m) SADCP data showed the Central branch of the South Equatorial Current (cSEC) flowing westward in the open ocean with its core around FNR (Fig. 2). This westward flow feeds the NBUC, that flows northward

125   over the continental slope with intrusions over the continental shelf. The core of both currents meet up in the northwest part of the study area (around 3.5°S, 35°W) forming the North Brazil Current (Bourles et al., 1999; Dossa et al., 2021; Stramma and England, 1999).

Although the NBUC was weaker south of 7.5°S in both seasons, it was even weaker in spring 2015 due the presence of an anticyclonic eddy. Thus, intrusions over the shelf were greatly reduced in the region of the Pernambuco Plateau (Tosetto et al.,
130   2021; Fig. 2a; Dossa et al., 2021). Such feature was not observed in autumn and thus intrusions over the shelf were observed all along the coast. North of 7.5°S, in spring, the NBUC core was stronger and deeper (upper limit at ~105 m). Otherwise, in autumn the core was less intense but shallower (upper limit at ~80 m), thus surface currents were similar in both seasons (Fig. 2; Dossa et al., 2021). For a detailed description and discussion of circulation patterns and seasonal variability of NBUC and thermohaline structure in the area see Dossa et al. (2021).

135   In both seasons, the WBCS (over the slope) and the SECS (FNR) presented distinct thermohaline structure (Fig. 3b, c, e, f). While the thermocline and halocline were sharp in the SECS (Fig. 3c, f), with the South Atlantic Central Water mass (SACW; <13°C) being present in the first 150 m of the water column, they were less abrupt in WBCS (Fig. 3b, c) and the SACW was only observed below 250 m (Fig. 3 in Silva et al., 2021; Fig. 3 in Dossa et al., 2021). In both offshore areas, the upper limit of the mixed-layer depth (MLD) was shallower in autumn. However, the difference was much more pronounced in the SECS (90
140   m and 46 m in spring and autumn, respectively; Fig. 3c,f) than in the WBCS (53 m and 39 m in spring and autumn, respectively; Assunção et al., 2020). Sea surface temperature and salinity were higher in autumn in offshore areas and over the continental shelf (Fig. 3). For a detailed description and discussion of the seasonal variability of thermohaline structure see Assunção et al. (2020).

Over the continental shelf, although presenting high variability, fluorescence was higher in the surface layer in autumn (Fig.
145   3g), coinciding with period of larger continental discharge and nutrient input. In both the WBCS and the SECS, the peak of florescence reached similar values within the thermocline in both seasons (Fig. 3h, i). However, in the surface layer, while in the WBCS florescence were also similar in both seasons (note the small difference at the MLD), in the SECS it was higher in autumn when the MLD and the nutricline were shallower (Fig. 3h, i; Assunção et al., 2020; Silva et al., 2021; Farias et al., 2022).

150   **3.2 Species composition**

In total, 93 taxa of planktonic cnidarians were sampled in the area, corresponding to 42 hydromedusae, 51 siphonophores, and 3 scyphomedusae. A similar number of taxa were present at each season: 73 in spring and 74 in autumn, with 18 and 19 exclusive species, respectively. In addition, many unidentified larval stages (cerinula, ephyrae and athorybia) were collected (Supplementary table S1; Table 1 in Tosetto et al., 2021). In both seasons, the most frequent and abundant species were almost
155   the same. Among hydromedusae, *Aglaura hemistoma* and *Liriope tetraphyla* occurred in more than 85% of the samples. However, while *A. hemistoma* was the most abundant in spring, *L. tetraphyla* dominated in autumn. Among siphonophores, *Abylopsis eschscholtzii*, *Abylopsis tetragona*, *Bassia bassensis*, *Chelophyes appendiculata*, *Diphyes bojani*, *Eudoxoides mitra* and *Sulculeolaria chuni* were present in more than 80% of the samples in both seasons and *Eudoxoides spiralis* in spring. *B. bassensis*, *C. appendiculata*, *D. bojani* and *E. mitra* were also the most abundant siphonophores in both cruises, representing
160   46.5% of the total catch in spring and 36.9% in autumn (Supplementary table S1; Table 1 in Tosetto et al., 2021).

3.3 Spatial and seasonal patterns in diversity and abundance

Hydromedusae species richness was similar all over the study area, with no significant differences among areas or seasons, and averaging 4.5 ± 2.3 and 4.1 ± 1.5 species per station in spring and autumn, respectively (Table 2, Fig. 4). However, while, in spring, the total hydromedusae abundance was similar in all areas, averaging 49.9 ± 66.2 ind. 100 m^{-3}; in autumn it was
165 significantly higher over the continental shelf where it reached up to 1067.6 ind. 100 m^{-3} (383.4 ind. 100 m-3 in average; Table 2, Figs. 4, 5; Fig. 2 in Tosetto et al., 2021). No significant seasonal changes were observed in total hydromedusae abundance in the open ocean.

Siphonophores richness was significantly higher in the two oceanic areas than over the continental shelf, especially in the WBCS where it was also significantly higher in spring (reaching 23 species, 19.5 ± 2.9 in average) than in autumn (13.3 ± 1.5
170 species in average). No differences among seasons were observed over the shelf and in the SECS (Table 2, Fig. 4). The total abundance of siphonophores was similar between seasons over the continental shelf (137.2 and 169.5 ind. 100 m^{-3} in average in spring and autumn, respectively). Meanwhile, a contrasting pattern was observed in the oceanic areas: in spring it was higher in the WBCS (not statically significant), averaging 153.4 ind. 100 m^{-3}, while in autumn significantly higher abundances were observed in the SECS (245.2 ind. 100 m-3 in average; Table 2, Fig. 4; Fig. 2 in Tosetto et al., 2021).

175 The two dominant hydromedusae, *L. tetraphylla* and *A. hemistoma*, were widespread over the area. *L. tetraphylla* presented higher abundance over the continental shelf in both seasons. However, in autumn it was one order of magnitude higher than in spring in average, reaching up to 770.3 ind. 100 m^{-3} (Table 2, Figs. 5, 6; Fig. 3 in Tosetto et al., 2021). In both seasons, *A. hemistoma* was more evenly distributed than *L. tetraphylla*, with high abundances occurring both over the continental shelf and in the open ocean. But as occurred with *L. tetraphylla*, it was significantly higher over the continental shelf in autumn
180 (Table 2, Figs. 5, 6; Fig. 3 in Tosetto et al., 2021). The third more abundant hydromedusa taxa, *Aequorea* spp., occurred in low abundances over the area in spring. However, in autumn its abundance was significantly higher in the SECS, reaching up to 38.3 ind. 100 m^{-3} and was nearly absent over the shelf and in the WBCS (Table 2, Figs. 5, 6).

Although most dominant siphonophores were widespread over the area, distinct seasonal and spatial patterns were observed. *E. mitra* was more abundant in the SECS in both seasons. However the pattern was more pronounced in autumn when this
185 species reached up to 109.5 ind. 100 m^{-3}. *A. eschscholtzii*, which occurred in similar abundances in the three areas in spring, was significantly more abundant in the SECS in autumn, reaching up to 67.6 ind. 100 m^{-3}. In the WBCS, average abundances of *E. mitra* and *A. eschscholtzii* were similar in spring and autumn (Table 2, Figs. 5 , 6; Fig. 4 in Tosetto et al., 2021). Otherwise, over the continental shelf and in the WBCS, *D. bojani* and *B. bassensis* were more abundant in spring than in autumn, while in the SECS the opposite was observed and these species were significantly more abundant in autumn (Table 2, Figs. 5, 6; Fig.
190 4 in Tosetto et al., 2021).

In spring, *C. appendiculata* was slightly more abundant over the continental shelf and in the WBCS than in the SECS. Although, in autumn its abundance was higher over the continental shelf and lower in the two oceanic areas, seasonal changes were not significant (Table 2, Figs. 5, 6; Fig. 4 in Tosetto et al., 2021). Otherwise, *A. tetragona* and *E. spiralis* were more

abundant over the continental shelf and in the WBCS than in the SECS in spring. Conversely, in autumn they were less abundant in the shelf and WBCS than in autumn and the abundances of these species were similar in the three systems (Table 2, Figs. 5, 6; Fig. 4 in Tosetto et al., 2021).

Distinctly from other dominant siphonophores, in both seasons *M. kocchii* occurred almost exclusively over the continental shelf. However, while in spring the species was restricted to few stations in the south of the area, in autumn it occurred in higher abundances and was distributed over most of the continental shelf, except a few stations in the outer shelf (Table 2, Figs. 5, 6; Fig. 4 in Tosetto et al., 2021). No spatial and temporal patterns were identified in the abundance of *S. chuni.*

3.4 Community structure

In spring, two main groups of stations were depicted in the Cluster analysis. Group A was represented by four stations over the shelf in the southernmost part of the study area (Fig. 7b). It was mainly characterized by the large abundances of *M. kochii*, *A. hemistoma* and *L. tetraphylla*. It also differed from the other groups by the absence or low abundance of other dominant siphonophores. Group B was represented by the remaining neritic stations and all stations of the WBCS and the SECS where siphonophores such as *D. bojani*, *B. bassensis*, *A. tetragona*, *C. appendiculata* and *E. mitra* were more abundant. This group was further subdivided in several subgroups, which differed among each other in the abundance of dominant species. For a detailed description and discussion of the cnidarian community structure in the area in spring, see Tosetto et al. (2021).

Similarly, two main groups were depicted in autumn (Fig. 7c). Group X was composed by shallow stations (bottom depth <25 m) over the continental shelf. SIMPER analysis indicated an average similarity of 63.1%. It was mainly characterized by the occurrences in large or medium abundance of *L. tetraphylla*, *M. kocchii*, *A. hemistoma*, *A. eschscholtzii*, *C. appendiculata* and *B. bassensis*. One outlier was present in this branch (station autumn_3) and it differed from the main branch due the absence of *A. hemistoma*, *A. eschscholtzii*, *C. appendiculata* and *B. bassensis* (Table 3).

Group Y was composed by the deeper stations over the continental shelf and all stations in the WBCS and the SECS. This group was subdivided in two large branches and several outliers. Subgroup Y1 was composed by most stations of WBCS over the slope. SIMPER analysis indicated an average similarity of 73.4% within the group (Table 3). It was represented by the species *C. appendiculata*, *D. bojani*, *E. mitra*, *B. bassensis*, *A. tetragona*, *A. hemistoma*, *L tetraphylla*, *A. eschscholtzii*, *Lensia meteori*, and *E. spiralis*, occurring in high or medium abundances. Subgroup Y2 (average similarity of 78.1%) included most stations in SECS, represented by the species *D. bojani*, *B. bassensis*, *E. mitra*, *A. eschscholtzii*, *A. hemistoma*, *C. appendiculata*, *A. tetragona*, *S. chuni*, *Cordagalma ordinatum* and *Aequorea* spp (Table 3). Subgroup Y2 differed from Y1 due the higher abundance of *A. eschscholtzii*, *B. bassensis*, *Aequorea* spp., *D. bojani*, *A. hemistoma*, *E. mitra* and *C. ordinatum*, and the lower abundance of *L. meteori* and *C. appendiculata*.

4 Discussion

Here, we describe contrasting seasonal patterns in the planktonic cnidarian community in response to ecological and physical
225   forcing in the Western Tropical South Atlantic. Although the species composition of the cnidarian community was similar in
spring and autumn, with almost the same species dominating each specific area, the distribution and abundance of species both
over the continental shelf and in the oceanic WBCS and SECS were different. We associate these difference to distinct
scenarios in the thermohaline structure, circulation and continental runoff.

In spring, over the continental shelf, intrusions of oceanic water masses caused by the coastward currents characteristic of the
230   WBCS (NBUC and cSEC), reached coastal areas. Most of samples were then dominated by cnidarian species that typically
dominante in the open ocean, such as the siphonophores *C. appendiculata*, *D. bojani*, *B. bassensis* and *A. tetragona*. In the
Western Tropical South Atlantic, the dominance of such oceanic communities over the continental shelf is not exclusive in
cnidarians and has been observed for other zooplanktonic groups such as Copepods, Chaetognaths, Thaliaceans and fish larvae
(Neumann-Leitao et al., 2008; Neumann-Leitão et al., 1999; Santana et al., 2020; Schwamborn et al., 1999). Meanwhile, the
235   coastal community (group A), with high abundance of *Muggiaea kocchii* and *L. tetraphylla*, and absence or reduced abundance
of the siphonophores mentioned above, was restricted to a particular area over the Pernambuco Plateau. In this area, oceanic
intrusions were likely reduced due the presence of an anticyclonic eddy centered at 8.9°S, 34.1°W that locally dampened the
NBUC system that favoured the oceanward flow of coastal waters (Tosetto et al., 2021; Fig. 7b; Dossa et al., 2021).

In autumn, although the average velocity and water transport of the NBUC system was weaker, the core of the current was
240   shallower than in spring. Thus no remarkable differences were observed in surface currents between spring and autumn (Fig.
8b; Dossa et al., 2021). Thus, similar to spring, the dominance of oceanic planktonic cnidarian species over the continental
shelf would be expected. However, autumn is also the rainy season in Northeast Brazil. With higher continental runoff, the
characteristic coastal water can further spread over the continental shelf, potentially enhancing the extent to which coastal
waters species can reach. The combination of these two antagonist processes produced an interesting response in the structure
245   of the cnidarian community. The sharp outline between "coastal" and "oceanic like" communities present in spring (group A
and subgroup B1) was not observed in autumn. Instead, both communities merged and characteristic species of both
environments (e.g. *M. kocchii*, *L. tetraphylla*, *A. eschscholtzii*, *C. appendiculata* and *B. bassensis*) coexisted in most stations
over the continental shelf (group X). Exception was the closest to the coast (station autumn_3), where oceanic species were
absent or occurred in low abundance; and stations in the outer shelf, which presented the typical oceanic community and were
250   included at group Y. A typical coastal community spreading along the Northeast Brazilian coast was also observed in other
zooplankton groups such as copepods, chaetognaths and appendicularians, with large concentrations of larvae from mangrove
organisms as well (Ekau et al., 1999; Neumann-Leitao et al., 2008; Neumann-Leitão et al., 1999; Schwamborn et al., 1999).
These coastal communities usually spreads from 7 up to ~30 km offshore, sometimes merging with the oceanic community,
as we also observed in planktonic cnidarians in autumn. This extension is likely affected by the physical constraints discussed
255   above and by species ecological niche. Thus, our first hypothesis was partially correct: with an increase in continental runoff

and a reduction in western boundary currents intensity, the range of coastal cnidarian species were indeed increased. But the reduction in the current intensity was not enough to reduce the presence of oceanic cnidarian species over the continental shelf, thus both communities merged and species co-occurred.

The dynamic interaction between oceanic water mass intrusions and the spread of coastal waters and continental runoff is
260 likely to be the main factor affecting the distribution of planktonic cnidarians over the continental shelf in WBCS. In narrow continental shelves, when the continental discharge is reduced and intrusions are strong, oceanic communities may dominate almost the entire continental shelf. This circumstance was observed in our spring data (Tosetto et al., 2021) and similar patterns were observed in the west coast of Africa (Thibault-Botha et al., 2004). When the continental discharge is enhanced and intrusions are strong, the mixing of both water masses may allow the coexistence of species from both environments (although
265 species niche restrictions may act as well). Such circumstances were observed in our data in autumn and in the continental shelf off Southeast and South Brazil, and off South Africa in some seasons (Nogueira and Oliveira Jr., 1991; Nogueira Júnior et al., 2014; Thibault-Botha et al., 2004). Meanwhile, in WBCS with wider continental shelves and larger river discharge, such as the east coast off China (Yangtze River), typical coastal cnidarian species (mainly represented by *Muggiaea* spp.) may spread and dominate the almost entire shelf. Oceanic species are then restricted to the core of the WBC over the outer shelf
270 and slope (Xu, 2006, 2009; Xu and Lin, 2006).

To further support this hypothesis, unlike WBCS, in the eastern margin of ocean basins, currents typically flow away to the coast. The oceanward flow free up space for the spread of coastal waters over the continental shelf and upwelling of deeper water masses (Carr and Kearns, 2003). Thus, contrastingly to the patterns observed in WBCS, coastal cnidarian species such as *Mugiaea* spp., *L tetraphylla* and *Obelia* spp. typically dominate the community inhabiting the entire continental shelves,
275 sometimes also spreading beyond the shelf break, while other siphonophores are absent or occur in low abundance. Such circumstances were observed in eastern boundary systems from the South Atlantic (e.g. Pagès and Gili, 1991; Pagès et al., 1991; Pagès and Gili, 1992), South Pacific (e.g. Apablaza and Palma, 2006; Rodríguez and Ruiz, 2019; Palma G and Rosales G, 1995) and North Pacific (e.g. Segura-Puertas et al., 2010; Gamero-Mora et al., 2015). The patterns observed in both margins of ocean basins reinforce the major role of ocean circulation in the distribution of planktonic cnidarians both trough advection
280 of oceanic species over the continental shelf and/or the spread of coastal species to the outer shelf.

Back to the Western Tropical South Atlantic, apart from the spread of coastal cnidarian species, the higher freshwater runoff observed in autumn provides an important supply of nutrients to a continental shelf that is quite oligotrophic during most of the year (Brandini et al., 1997; Castro et al., 2006; Ekau and Knoppers, 1999). These nutrients support greater primary production in the rainy season, noted by the general increase in the fluorescence over the continental shelf in our CTDO data
285 in autumn cruise (Fig. 3g). High primary production may lead to a general increase in the abundance and biomass of organism though trophic web (bottom-up control) and this is likely behind the increase in the abundance of many dominant cnidarian species, such as *M. kocchii*, *L. tetraphylla*, *A. hemistoma*, *C. appendiculata* and *A. eschscholtzii*, in autumn (compared to spring) over the continental shelf.

A similar process was observed in the oceanic SECS as well. There, the increase in the supply of nutrients that enhanced
290 primary production in autumn occurred because the cline between the oligotrophic Tropical Water and the nutrient rich South
Atlantic Central Water was shallower than in spring (Fig. 3; Assunção et al., 2020; Silva et al., 2021). Thus, more nutrients
present in the later reached photic layers, becoming available to phytoplankton (Fig. 3i; Farias et al., 2022). The relation
between changes in mixing of water masses and light penetration with primary production in tropical systems is dynamic and
in some circumstances, a large mixed layer favors the supply of nutrients to photic layers (Mignot et al., 2014; Polovina et al.,
295 1995; Signorini et al., 1999). However, the opposite was observed in our area, likely due the high stratification in the system
(Farias et al., 2022). Anywise, the increase in primary production due changes in mixed layer generally reflects in coupled
increase in secondary production of zooplankton (Polovina et al., 1995). In the SECS, this process and the consequently
increase in food availability likely increase the abundance of most dominant cnidarian species as well (e.g. *Aequorea* spp., *D.
bojani*, *B. bassensis*, *E. mitra* and *A. eschscholtzii*). Thus, our results support our second hypothesis that the enhanced primary
300 productivity caused by the shallower mixed layer depth in oligotrophic systems supports more abundant planktonic cnidarian
communities.

In WBCS, with a thicker thermocline and less pronounced seasonal changes in the depth of mixed layer (Assunção et al.,
2020), such increase did not occur neither in primary production (Fig 3h), nor in the abundance of the species referred above
(Fig. 5). Instead, species that were dominant over the continental slope in spring, such as *A. tetragona*, *E. spiralis* and *L.
305 meteori*, were significantly less abundant in autumn (Fig.5). One hypothesis yet to be tested to explain these differences is that
in the spring the organisms were pushed by the currents towards the slope, accumulating there. In spring the core of the NBUC
was weaker and more diffuse, under these circumstances the accumulation of organisms may have not occurred. Accumulation
of organisms associated to circulation and sloping topography is not rare among zooplankton (e.g. Cotté and Simard, 2005;
Hazen et al., 2009; Sourisseau et al., 2006), but was never observed in cnidarians. Further approaches considering stratified
310 samples and/or other methods such active acoustics may help to better understanding the interaction among the behavior of
these and other species, oceanic currents and bottom topography in the Western Tropical South Atlantic.

5 Conclusions

In conclusion, we observed contrasting seasonal patterns in the planktonic cnidarian community in response to ecological and
physical processes associated to changes in the thermohaline structure and circulation in the western boundary system of
315 tropical South Atlantic. We concluded that in western boundary systems with narrow continental shelves, coastward currents
spread oceanic waters and its associated cnidarian species, such as *C. appendiculata*, *D. bojani*, *B. bassensis* and *A. tetragona*,
over the continental shelf. However, when the intensity of western boundary currents is weaker and under higher continental
runoff, costal (e.g. *M. kocchii* and *L. tetraphylla*) and oceanic communities merge and co-occur, while in dry seasons, oceanic
species may dominate the entire shelf. We also conclude that the enhanced primary productivity in oligotrophic systems caused

320 by changes in the depth of mixed layer that uplift nutrient rich water masses to photic layers, supports larger populations of planktonic cnidarian species through bottom up control.

Author contribution: Conceptualization: AB, SNL; taxonomy: EGT, MNJ; data analysis: EGT; writing - original draft preparation: EGT; writing - contributions, review and editing: all authors. All authors have read and agreed to the published

325 version of the manuscript.

Data availability: The authors confirm that the data supporting the findings of this study are available within the article and its supplementary materials.

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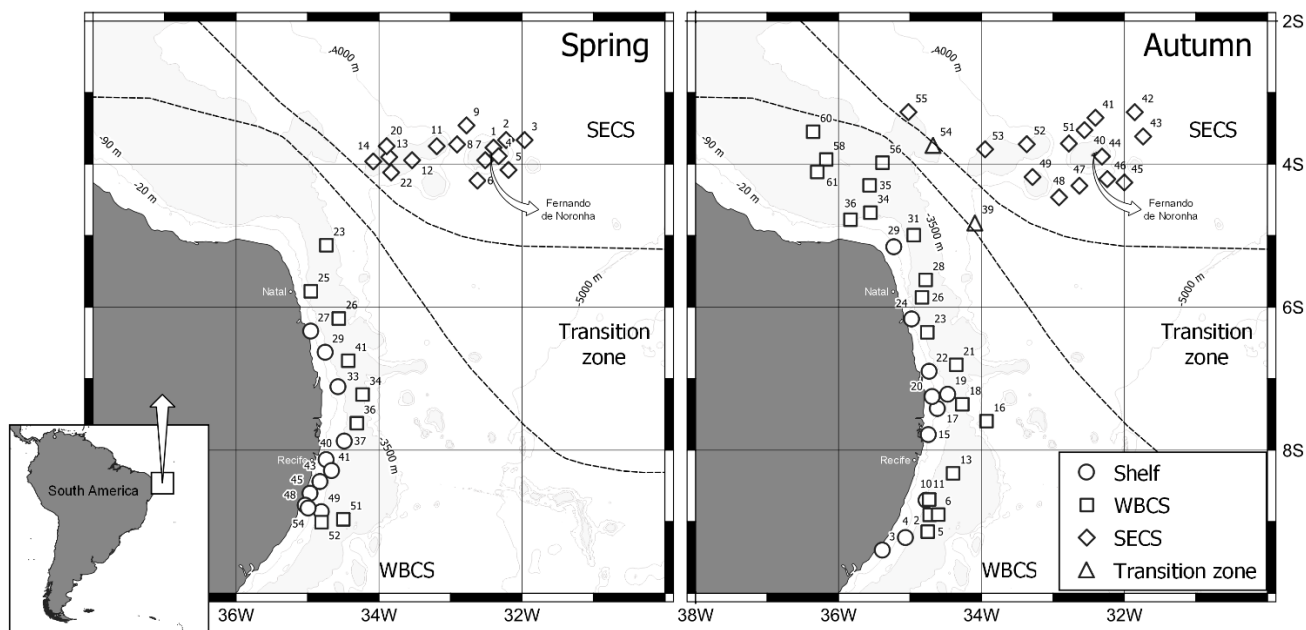


Figure 1: Geographic location of the study area in the Western Tropical South Atlantic, showing the sampled stations during (a) spring 2015 and (b) autumn 2017.

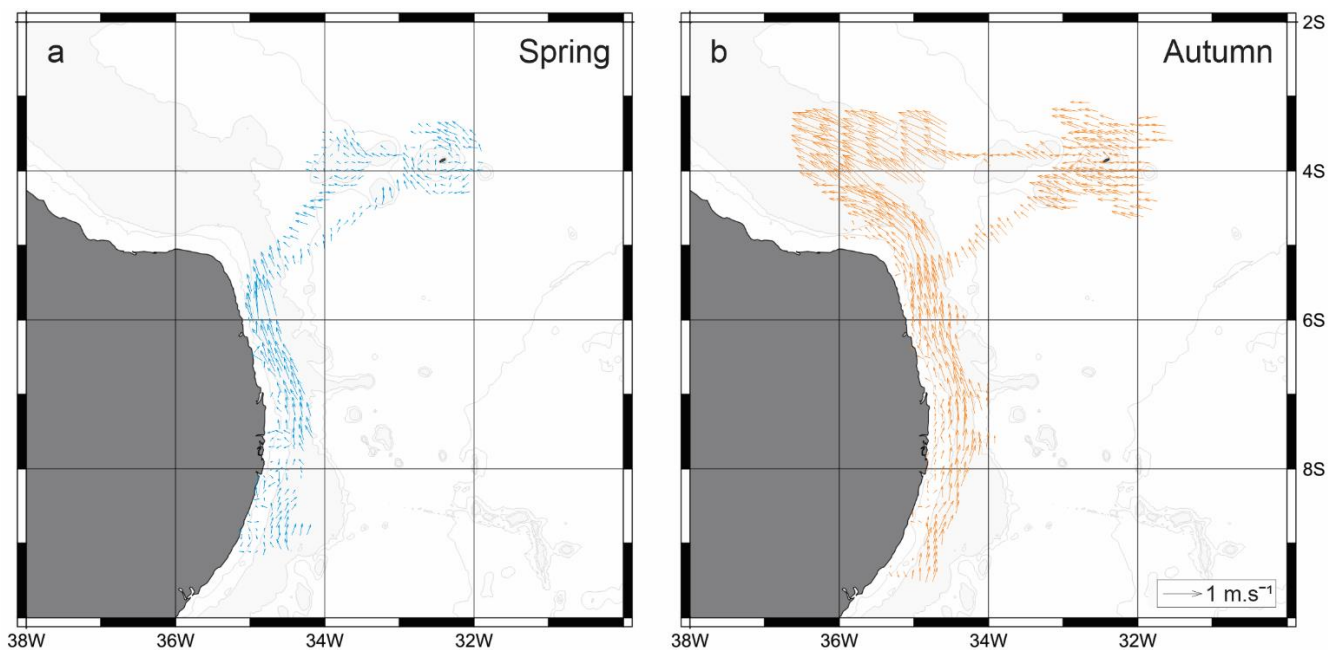



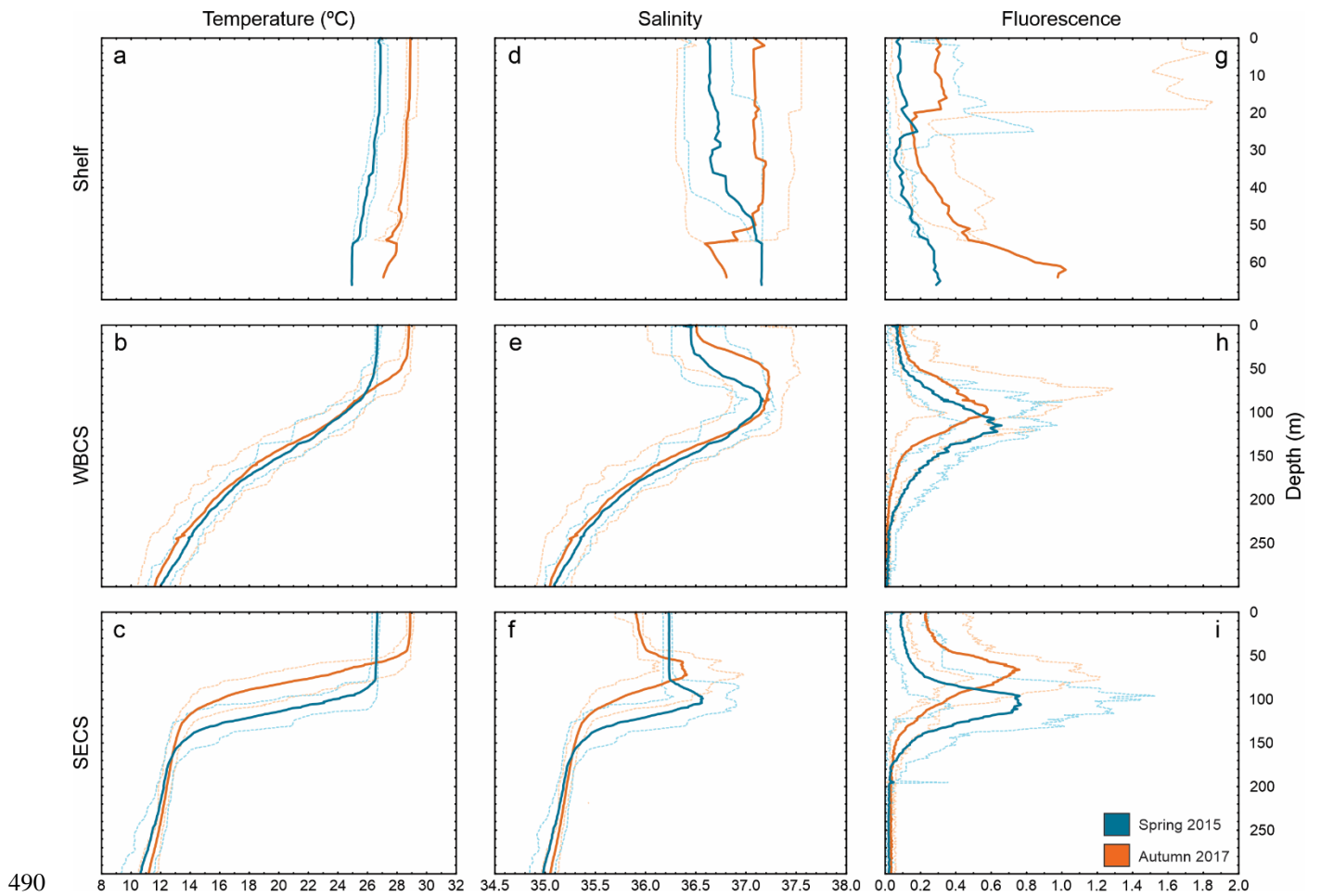
Figure 2: Surface (0 - 70 m) current vectors of ADCP data during (a) spring 2015 and (b) autumn 2017.

490

Figure 3: Vertical profiles of temperature (a, b, c), salinity (d, e, f) and fluorescence (g, h, i) during spring 2015 (blue) and autumn 2017 (orange) in three distinct areas from the Western Tropical South Atlantic. Solid lines are the average among stations and dashed lines are the maximum and minimum, in each season/area.

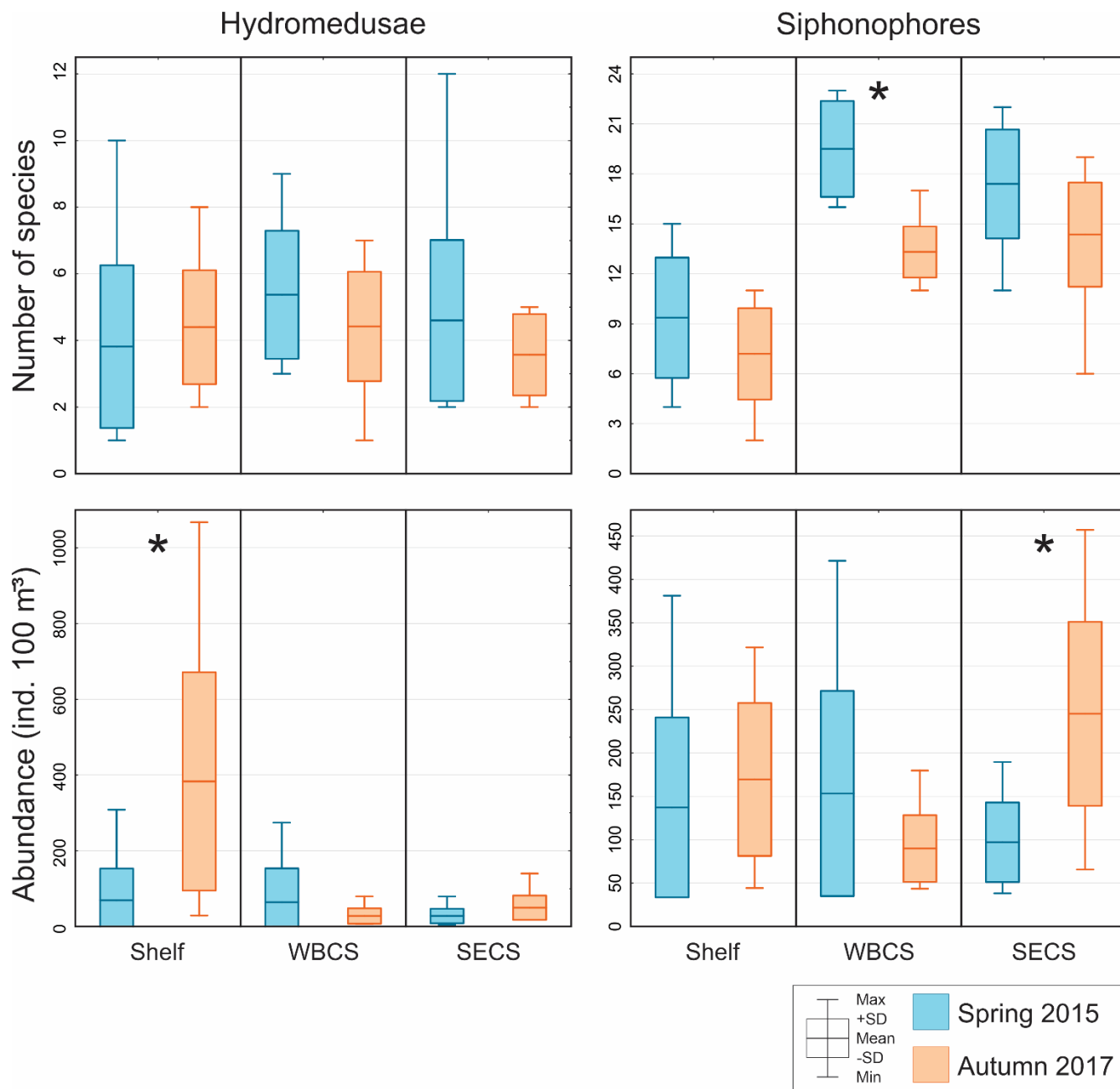



Figure 4: Comparison of average number of species and total abundance of hydromedusae and siphonophores during spring 2015 (blue) and autumn 2017 (orange) in three distinct areas from the Western Tropical South Atlantic.

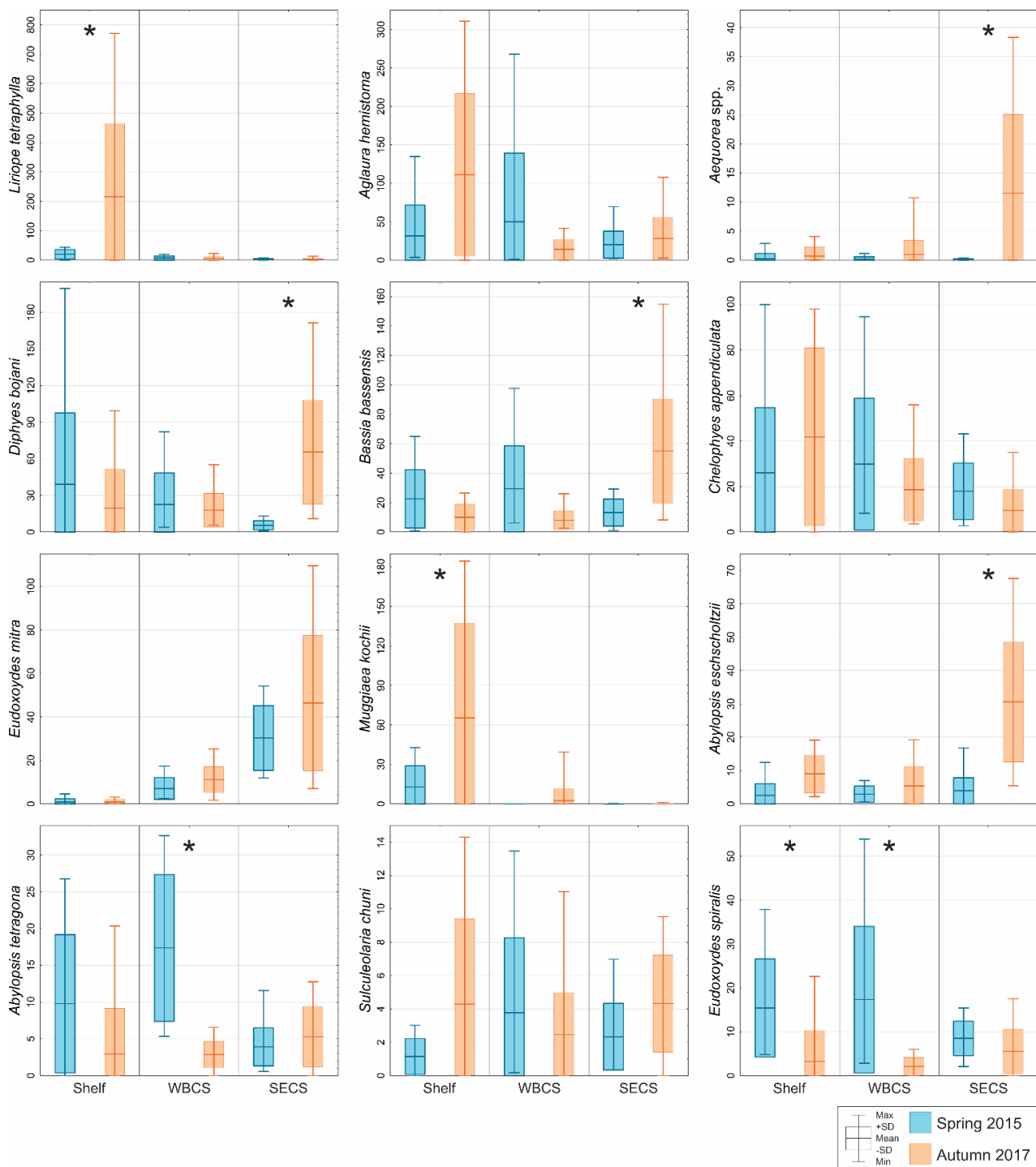



Figure 5: Comparison of average abundance of representative species of hydromedusae and siphonophores during spring 2015 (blue) and autumn 2017 (orange) in three distinct areas from the Western Tropical South Atlantic.

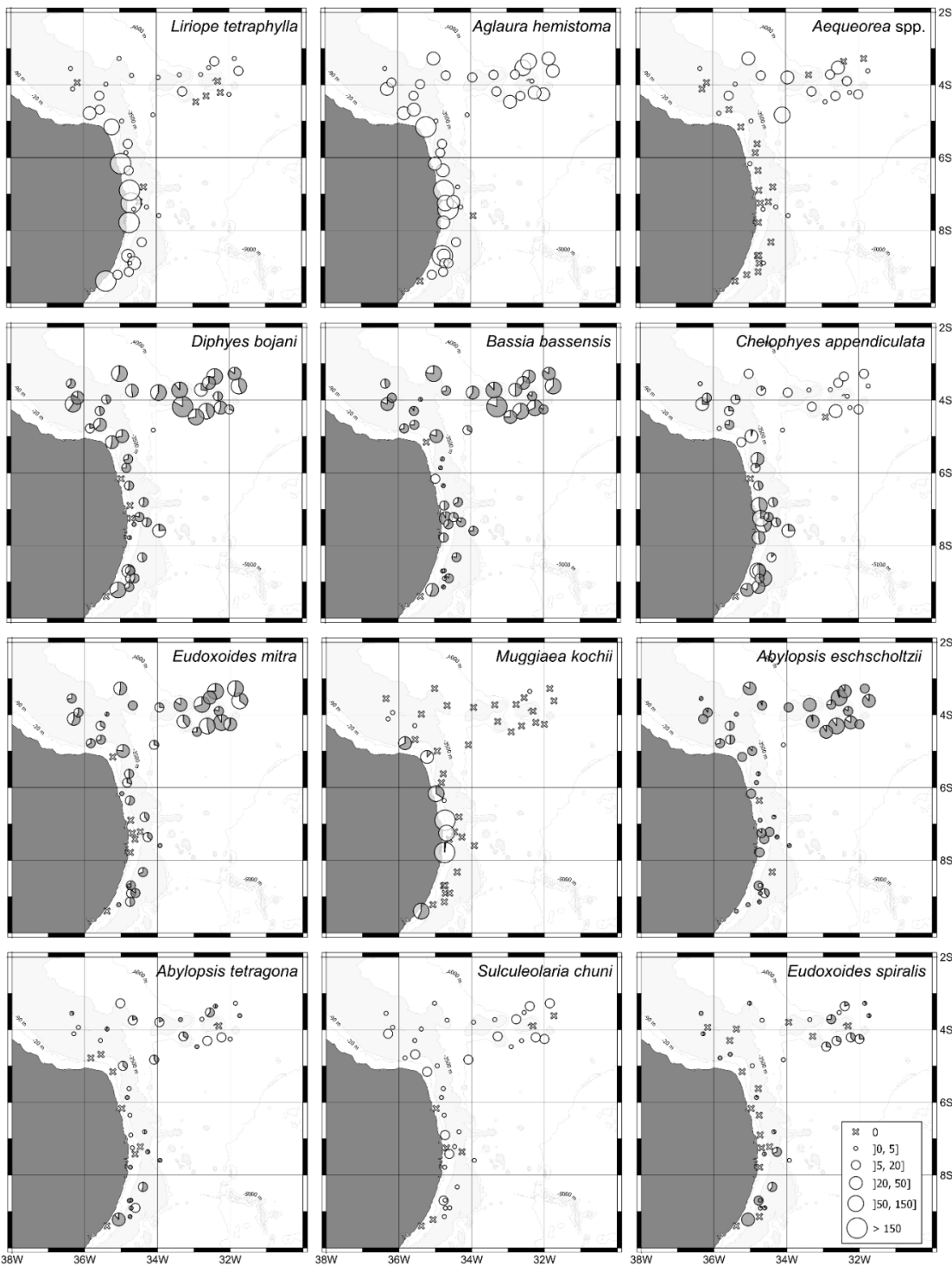
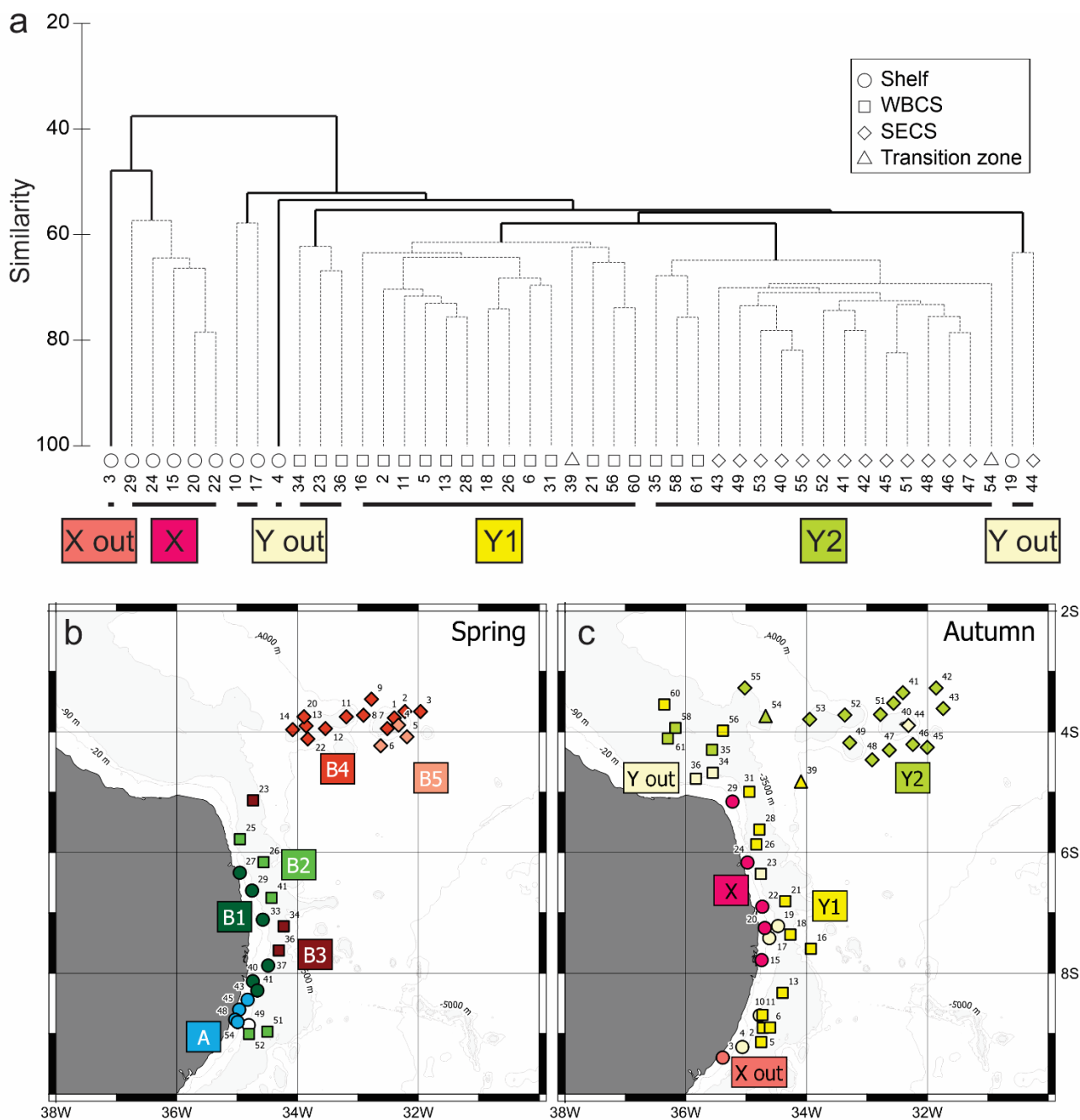



Figure 6: Geographic distribution of representative species of hydromedusae and siphonophores in the first 200 m of the water in Autumn 2017. For calycophoran siphonophores, black represents polygastric stage and white eudoxid stage.

510   **Table 1: Summary of field and laboratory proceedings**

Method	Description
Biological sampling	
Gear	Bongo zooplankton net
Mesh size	300 μm
Mesh opening	60 cm
Trawl depth	200 m or station depth when shallower
Physical sampling	
Temperature, salinity and fluorescence profiles	CTD-O_2 profiler Seabird SBE911+
Along-track current profiles	'Ocean Surveyor' acoustic Doppler current profiler (SADCP)
Laboratory proceedings	
Sample fraction analyzed	100%
Species identification	(Bouillon, 1999; Pugh, 1999)
Medusae abundance standardizing	Individuals per 100 m^3
Siphonophores abundance standardizing	Colonies per 100 m^3
Estimative of the number of calycophorans polygastric colonies	Number of anterior nectophores
Estimative of the number of calycophorans eudoxid colonies	Number of bracts
Estimative of the number of physonects and Hippopodidae colonies	Number of nectophores/10

Table 2: Results of the factorial analysis of variance testing differences in community indicators and abundance of representative planktonic cnidarian species among seasons (spring and autumn) and areas (shelf, WBCS and SECS). Significant P-values are in bold.

Indicator/species	Seasons		Areas		Seasons x Area	
	F	p	F	p	F	p
Hydromedusae richness	1.05	0.31	1.36	0.26	1.26	0.29
Total hydromedusae abundance	13.96	**0.00**	19.98	**0.00**	15.20	**0.00**
Siphonophores richness	31.62	**0.00**	56.56	**0.00**	3.10	**0.05**
Total siphonophores abundance	4.01	0.05	2.32	0.11	10.67	**0.00**
Liriope tetraphylla	9.49	**0.00**	12.04	**0.00**	9.05	**0.00**
Aglaura hemistoma	1.97	0.17	5.46	**0.01**	6.87	**0.00**
Aequorea spp.	8.94	**0.00**	6.79	**0.00**	7.12	**0.00**
Diphyes bojani	2.36	0.13	1.38	0.26	10.81	**0.00**
Bassia bassensis	0.30	0.59	5.95	**0.00**	18.77	**0.00**
Chelophyes appendiculata	0.06	0.81	5.17	**0.01**	2.49	**0.09**
Eudoxoides mitra	3.43	**0.07**	42.85	**0.00**	1.92	0.15
Muggiaea kochii	8.34	**0.01**	15.40	**0.00**	6.84	**0.00**
Abylopsis eschscholtzii	32.31	**0.00**	17.32	**0.00**	14.19	**0.00**
Abylopsis tetragona	24.36	**0.00**	6.03	**0.00**	12.46	**0.00**
Sulculaeolaria chuni	3.04	0.09	0.24	0.79	3.14	0.05
Eudoxoides spiralis	30.20	**0.00**	0.93	0.40	4.39	**0.02**

Table 3: Results of SIMPER analysis, showing the relative contribution of planktonic cnidarian species in the formation of the groups defined in the Cluster analysis during autumn 2017.

Species	X	Y1	Y2
Abylopsis eschscholtzii	11.2	5.6	11.6
Aequorea spp.	-	-	3.7
Abylopsis tetragona	-	8.3	5.6
Aglaura hemistoma	19.8	7.9	11.2
Bassia bassensis	6.2	11.2	13.6
Chelophyes appendiculata	7.8	15.2	7.3
Cordagagalma ordinatum	-	-	3.9
Diphyes bojani	-	14.5	15.3
Eudoxoides mitra	-	13.7	12.4
Eudoxoides spiralis	-	1.1	3.6
Lensia meteori	-	4.9	-
Liriope tetraphylla	26.1	5.8	-
Muggiaea kochii	21	-	-
Sulculeolaria chuni	-	-	5

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