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# Thaliacean community responses to distinct thermohaline and circulation patterns in the Western Tropical South Atlantic Ocean

Everton Giachini Tosetto, Barbara Barkokébas Silva, Xiomara Franchesca García Díaz,  
Sigrid Neumann-Leitão, Arnaud Bertrand

**Abstract** In western boundary current systems, strong currents transport oligotrophic oceanic waters towards the coast. Thaliaceans may have an advantage in these systems due their ability to filter small particles such as the bacterioplankton, typically responsible for the primary production in oligotrophic waters. Here, we evaluated the structure of the thaliacean community present in the tropical South Atlantic Ocean western boundary current system to test the

hypothesis that species distribution and abundance are structured by the circulation and thermohaline features. For that purpose, we used data collected through 40 mm mesopelagic trawls above the slope and around oceanic seamounts and islands. Results reveal distinct patterns in the thaliacean community structure. Over the continental slope, under the influence of the strong North Brazilian Undercurrent, *Pyrosoma atlanticum* was highly abundant. *Soestia zonaria* was also present but in a lesser amount. Off-shore, around oceanic islands and Seamounts under the influence of the central branch of South Equatorial Current, Doliolida spp. were the dominant thaliacean, co-occurring with *P. atlanticum* in lower abundance. Mesh selectivity is a potential drawback in these results since the coarse aperture may have lost smaller species and early life stages.

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**Keywords** *Pyrosoma atlanticum* · *Soestia zonaria* ·  
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Equatorial current · Gelatinous zooplankton

## Introduction

Holoplanktonic organisms of the class Thaliacea (Chordata: Tunicata) have a global distribution and a rich biodiversity with variations in size, morphology and behaviour, reflecting adaptations to their wide range of habitats (Harbison & Campenot, 1979; Govindarajan et al., 2011; Lucas et al., 2014).

Although some species are restricted to polar regions, the greatest diversity and biomass of thaliaceans is found in tropical and sub-tropical waters (Van Soest, 1975; Lucas et al., 2014). Many of these tropical systems are oligotrophic, with primary production typically dominated by bacterioplankton (Hagström et al., 1988; Zubkov et al., 2003). Thaliaceans are efficient filter-feeders, their characteristic barrel-shape body with circular musculature allows them to swim and simultaneously filter pico- and nanoparticles as small as 0.2  $\mu\text{m}$  such as bacteria (Piette & Lemaire, 2015; Dölger et al., 2019). Thanks to this strategy, they flourish and remove a large portion of primary production from the environment even in oligotrophic systems, particularly in tropical western boundary systems (Stone & Steinberg, 2016).

Under specific conditions, such as high temperatures and phytoplankton productivity, upwelling events and/or specific water mass intrusions, the high rates of asexual reproduction of thaliaceans, producing aggregated zooids, allows rapid population growth and occasional blooms (Deibel, 1982; Gibson & Paffenhöfer, 2000; Henschke et al., 2019). These large aggregations or swarms can compete and overlap other typically more abundant planktonic feeders such as copepods, changing the structure of marine food webs (Harbison & Gilmer, 1976). Historically, due to the high water content in their tissues and low caloric value, thaliaceans and other gelatinous organisms were considered irrelevant and even dead-ends in marine trophic networks. However, this concept has changed in recent decades as it has been observed that these organism are key components in the diet of groups such as crustaceans, fish and turtles (Henschke et al., 2016; Hetherington et al., 2019). Although their energetic content is indeed lower than other zooplankton organisms, due to their slow motion, predators expend less energy in the capture process making them an efficient food source (Henschke et al., 2016; Hetherington et al., 2019). Additionally, due to the combination of the efficient filter-feeding lifestyle and eventual large population blooms, thaliaceans are able to transform small particles they feed, into large faecal pellets, which quickly sink, as well as their carcass after death, promoting an important carbon input to the deep ocean (Iseki, 1981; Henschke et al., 2016; Köster & Paffenhöfer, 2016).

In the Western Tropical South Atlantic, the southern South Equatorial Current (sSEC) reaches

the continental slope around 10–20°S and bifurcates into two branches. The northern one feeds the strong North Brazil Undercurrent (NBUC), which flows northward along the Brazilian coast (Dossa et al., 2021). Meanwhile, the central South Equatorial Current (cSEC) transposes the Fernando de Noronha Ridge (FNR), composed by a series of islands and seamounts around 5°S, encountering the NBUC when reaching the Brazilian coast (Dossa et al., 2021). Differences in the intensity and direction of these currents affect the thermohaline structure of the Western Tropical South Atlantic and two areas were previously identified (Assunção et al., 2020): (i) area 1, along the continental slope and under the influence of NBUC, presenting thicker thermocline and weaker stratification, hereafter called Western Boundary Current System (WBCS); and (ii) area 2, offshore in the region of FNR under the influence of cSEC, with high stratification, hereafter called central South Equatorial Current system (SECS). Although nutrient-rich estuarine plumes and uplift may enhance primary production in western boundary systems, continental drainage is low in the Western Tropical South Atlantic, not reaching beyond 16 km offshore, and uplift events due anti-cyclonic eddies occurring near the shelf break are sporadic (Smith & Demaster, 1996; Castro et al., 2006; Dossa et al., 2021). Therefore, the region presents the lowest primary production along the Brazilian Coast (Ekau & Knoppers, 1999; Castro et al., 2006).

Although the particular characteristic of this system may benefit the thaliaceans filter-feeding behaviour on pico- and nanoparticles, knowledge on the species inhabiting the area is scarce (Carvalho & Bonecker, 2008; Díaz et al., 2008; Neumann-Leitao et al., 2008) and no study evaluated the structure of the thaliacean community. Here, we evaluated the composition, spatial distribution (horizontal and vertical) and abundance of the thaliacean community (Pyrosomatidae, Salpidae and Doliolidae) of the Western Tropical South Atlantic according to the characteristics of the physical environment. In particular, we test the hypothesis according to which differences in the circulation and thermohaline patterns of the WBCS and SECS shape the structure of the thaliacean community in the region.

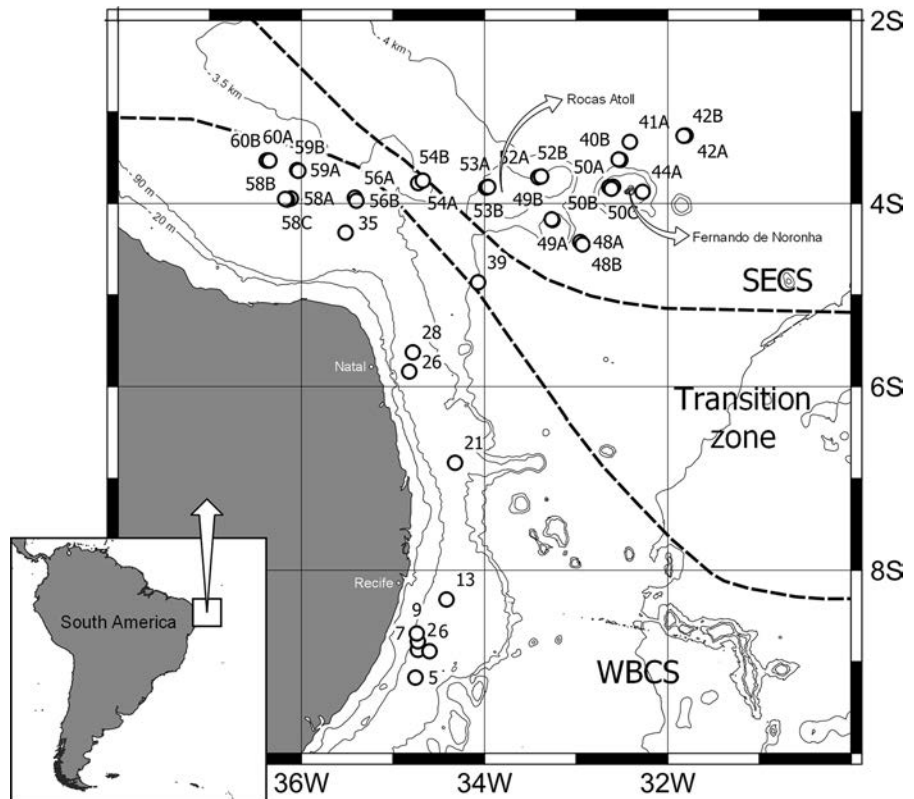
## Materials and methods

Data were collected during the ABRACOS 2 survey (Bertrand, 2017) on board the French R/V Antea from 9 April to 6 May 2017 (rainy season) in the Western Tropical South Atlantic Ocean along the continental slope of Northeastern Brazil (5–9°S) and around the Fernando de Noronha Ridge (between 3°S, 37°W and 5°S, 31°W; Fig. 1). Fifty samples were collected in 32 stations at day and night using a micronekton mesopelagic trawl (body mesh: 40 mm, cod-end mesh: 10 mm) at depths ranging from the surface to 1170 m, selected according to the presence of sound scattering layers detected with an echosounder (organisms were also captured during net descent and ascent phases). The net was hauled at 2–3 knots during approximately 30 min once the targeted depth was reached. Additional samples were obtained with a finer mesh (body mesh: 30 mm, cod-end mesh: 4 mm) around Fernando de Noronha. Specimens collected in these samples were used to improve species composition, only. Thaliaceans were sorted from the entire trawl

sample on board and fixed with 4% formaldehyde buffered with sodium tetraborate ( $0.5 \text{ g L}^{-1}$ ).

At each station, vertical profiles of temperature (°C), salinity, pressure and fluorescence were obtained with a CTD-O2 profiler Seabird SBE911+. Conductivity, temperature and pressure accuracies were estimated at  $0.0003 \text{ S m}^{-1}$ ,  $10\text{--}3 \text{ °C}$  and  $0.7 \text{ dbar}$ , respectively. Along-track current profiles were recorded with an ‘Ocean Surveyor’ ship-mounted acoustic Doppler current profiler (SADCP) operating at a frequency of  $75 \text{ kHz}$  with a depth range of  $15\text{--}700 \text{ m}$ . 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 the amplitude correction factor for the SADCP were determined by standard calibration procedures. Finally, velocity profiles were averaged

**Fig. 1** Geographic location of the study area in the Western Tropical South Atlantic, showing the sampled stations



hourly, providing profiles in the 19–600 m range. SADC 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 the upper (0–70 m depth) and mesopelagic (70–350 m) layers were integrated and averaged each 0.1 square degree.

To estimate the abundance of organisms, the volume of water filtered by the net was estimated from the distance covered and the area of the net's mouth. In the laboratory, samples with more than 200 thaliaceans were fractionated. The organisms of each subsample were identified (mainly following Esnal, 1999; Esnal & Daponte, 1999a, 1999b) and counted. The type of zooid was identified by differentiating oozoids (asexual solitary zooids) and blastozooids (hermaphrodite aggregated zooids) based on the number and arrangement of the body muscle bands, the position and form of the digestive tract and the shape of the tunic (Tavares, 1967). For Doliolidae, only unidentified rigid transparent tunics were recorded. Abundances were standardized in number of individuals or colonies per  $10^5 \text{ m}^{-3}$ .

Laboratory analyses were performed at the *Laboratório de Ecologia Aquática Tropical* (LECAT-UFRA, Belém-Brazil) and *Laboratório de Zooplâncton* of *Museu de Oceanografia* of *Universidade Federal de Pernambuco* (LABZOO-UFPE, Recife-Brazil). After laboratory analyses, samples and specimens were deposited at the *Museu de Oceanografia* of *Universidade Federal de Pernambuco*.

## Data analysis

For data analysis, the 32 stations were aggregated according to Assunção et al. (2020) in two areas with distinct thermohaline structure (Fig. 1): the WBCS, along the continental slope, corresponds to the western boundary current system dominated by the NBUC (Dossa et al., 2021), while the SECS encompasses the Rocas Atoll and part of Fernando de Noronha ridge seamounts and corresponds to the cSEC (Silva et al., 2021). For practical purpose, station 39, which was in the transition zone, was included in the SECS. To dampen effects of dominant species, abundance data were transformed by  $\log(x + 1)$  in all analysis. A bi-factorial

Permutational Multivariate Analysis of Variance (PERMANOVA; Anderson et al., 2008) was used to test for spatial (WBCS and SECS) differences among the thaliacean community structure. Additionally, bi-factorial Analysis of Variance (ANOVA) was performed to test for spatial differences among the dominant thaliacean species.

Spatial patterns in thaliacean community abundance were identified by hierarchical cluster analysis using Bray–Curtis similarity matrix. The validity of the groups defined by this analysis was tested through 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 analyses to identify associations between the thaliacean species and the environmental variables. The following continuous explanatory variables were used: (i) sea surface temperature (SST), (ii) sea surface salinity (SSS), (iii) maximum value of fluorescence (as an indirect measure of primary productivity) from the surface to maximum sampling depth in each station, (iv) bottom depth, (v) relative presence of Tropical Surface Water ( $\sigma_0 < 25.6$ ), South Atlantic Central Water ( $\sigma_0$  between 25.6 and 27) and Antarctic Intermediate Water ( $\sigma_0 > 27$ ) from the surface to maximum sampling depth in each station, (vi) the zonal component (westward/eastward) of ADCP data integrated over the first 70 m depth and between 70 and 350 m depth and (viii) the meridional component (southward/northward) of ADCP data integrated over the first 70 m depth and between 70 and 350 m depth. Detrended Canonical Correspondence Analyses (DCCA) revealed short 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 & Šmilauer, 2003).

Environmental and distribution maps were produced in Ocean Data View 5.0 (Schlitzer, 2020) and QGIS 3.4 (QGIS Development Team, 2022). ANOVA was performed in Statistica 10 (StatSoft Inc., 2011). Cluster, SIMPROF, SIMPER and PERMANOVA analyses were performed in Primer v.6 + PERMANOVA (Clarke & Gorley, 2006). DCCA and RDA were performed in CANOCO 4.5 (Lepš & Šmilauer, 2003).

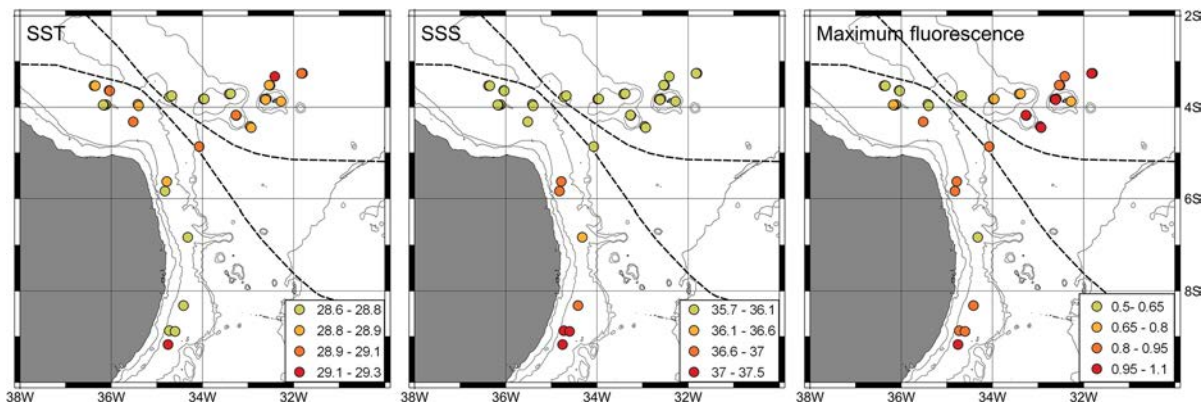
## Results

### Environmental background

SST ranged from 28.6 to 29.3 °C through the area. Shallower stations over the continental slope in the WBCS presented higher surface salinity ranging from 36.5 to 37.5, particularly over the Pernambuco Plateau in the south of the study area, where the highest values were observed (Fig. 2). In the open ocean (SECS), SSS was slightly lower and more stable, ranging from 35.7 to 36 with exception of station 39, in the transition zone. The region of seamounts in the north of the WBCS presented intermediate values around 36 (Fig. 2). Although the SECS presented higher values of maximum fluorescence in the water column, it was quite variable, with both areas

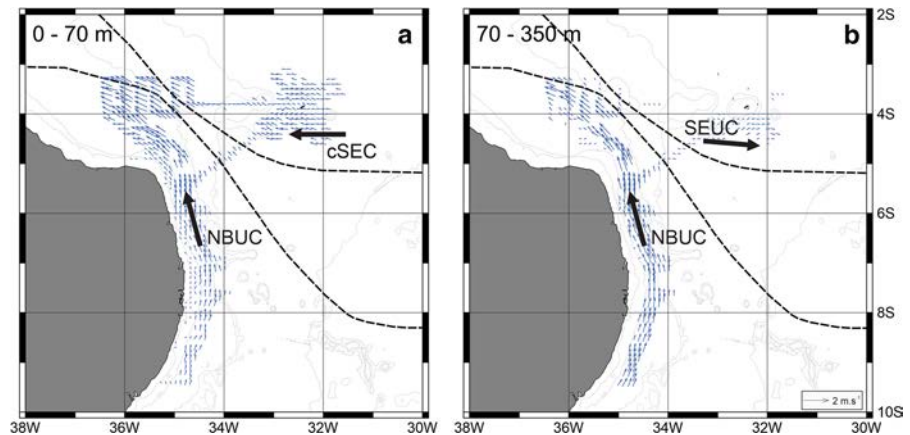
presenting high and low values. In the WBCS, it ranged from 0.56 to 1 and in the SECS from 0.5 to 1.1 (Fig. 2). For a detailed description of patterns of the thermohaline structure and phytoplankton biomass in the area, see Assunção et al. (2020) and Farias et al. (2022), respectively.

SADCP data integrated from 0 to 70 m depth showed the cSEC flowed westward over the open ocean (with its core around Fernando de Noronha Ridge), feeding the NBUC and surface currents (both flowing north/northwestward) when reaching the slope and continental shelf (Fig. 3). Overall, in the surface waters (0 to 70 m depth) cSEC and NBUC were 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 where



**Fig. 2** Sea surface temperature (SST, °C), sea surface salinity (SSS) and maximum fluorescence ( $\text{mg.m}^{-3}$ ) during autumn 2017 in the Western Tropical South Atlantic

**Fig. 3** Current vectors of ADCP data integrating 0–70 (a) and 70–350 (b) m depth. Large arrows indicate the predominant currents in the area (NBUC North Brazil Undercurrent, cSEC Central branch of the South Equatorial Current, SEUC South Equatorial Undercurrent)



some eastward flow was observed (Fig. 3). However, from 70 to 350 m depth, NBUC was intense all over the slope and seamounts of the WBCS (Fig. 3). In contrast, in the open ocean, cSEC almost dissipated in this depth and eastward flow of the South Equatorial Undercurrent SEUC was observed in the area (Fig. 3). For detailed description of the circulation in the study area see Stramma et al. (2010), Stramma & England (1999), Dossa et al. (2021) and Costa da Silva et al. (2021).

### Species composition

Seven species of thaliaceans were observed in pelagic waters of the Western Tropical South Atlantic, corresponding to six species from the order Salpida and one from the order Pyrosomatida (Table 1). Only tunicates from the order Doliolida were found, which were grouped in a single taxon as Doliolida spp. (Table 1). Overall, the most frequent and abundant species was *Pyrosoma atlanticum* Péron, 1804, which was present in 56.4% of the samples and represented 97.1% of the total specimens collected (Table 1). Although Doliolida spp. was present in 43.6% of the samples, it always occurred in low abundance, representing 2.2% of the total catch (Table 1). The most frequent and abundant species among Salpida was *Soestia zonaria* (Pallas, 1774) which was present in

30.8% of the samples and represented 0.7% of the total catch (Table 1).

### Spatial, vertical and diel distribution patterns

Overall, the thaliacean community presented highly significant differences according to the areas (PERMANOVA Pseudo-F=27.455,  $P = 0.001$ ). The dominant species, *P. atlanticum*, presented higher abundance over the continental slope and around oceanic seamounts (WBCS), reaching 700 col.  $10^5 \text{ m}^{-3}$  (Fig. 4, Table 1). Although also present in oceanic stations of the Fernando de Noronha Ridge (SECS), *P. atlanticum* was significantly (ANOVA  $F=18.33$ ,  $p=0.0001$ ) less abundant there (max: 3.4 col.  $10^5 \text{ m}^{-3}$ ; Fig. 4, Table 1). At daytime, the abundance of *P. atlanticum* was even in the different depths of the sampled water column. Contrastingly, at night, higher abundances were observed in the first 200 m (Figs. 4, 5).

Doliolida spp. occurred in low abundances in both areas, except for station 42A in the SECS, where it reached 27 ind.  $10^5 \text{ m}^{-3}$  (Fig. 4, Table 1). No significant differences among areas were observed (ANOVA  $F=0.069$ ,  $P=0.79$ ); however, Doliolida spp. was absent from most stations over the slope in the WBCS (Fig. 4). During the day, it was more abundant in deeper waters (400 to 850 m) while at night, higher abundances occurred in the first 200 m (Figs. 4, 5).

**Table 1** Species composition and basic statistics of thaliaceans from two areas (Assunção et al., 2020) in the Western Tropical South Atlantic Ocean off Northeast Brazil

| Species                              | WBCS                |                              | SECS            |                              | $f(\%)$ |
|--------------------------------------|---------------------|------------------------------|-----------------|------------------------------|---------|
|                                      | Mean $\pm$ SD       | Range of non-zero abundances | Mean $\pm$ SD   | Range of non-zero abundances |         |
| <i>Pyrosoma atlanticum</i> (colony)  | 206.42 $\pm$ 209.67 | 27.65–699.96                 | 0.36 $\pm$ 0.79 | 0.2–3.38                     | 56.41   |
| Doliolida spp.                       | 2.06 $\pm$ 4.17     | 0.33–12.42                   | 2.5 $\pm$ 5.89  | 0.37–27.04                   | 43.59   |
| <i>Soestia zonaria</i> (aggregate)   | 1.01 $\pm$ 1.44     | 0.54–4.7                     | 0.04 $\pm$ 0.11 | 0.33–0.39                    | 25.64   |
| <i>Soestia zonaria</i> (solitary)    | 0.39 $\pm$ 0.81     | 0.18–2.69                    | 0.02 $\pm$ 0.09 | 0.43                         | 17.95   |
| <i>Iasis cylindrica</i> (solitary)   | 0.08 $\pm$ 0.22     | 0.28–0.9                     | –               | –                            | 7.69    |
| <i>Salpa aspera</i> (solitary)       | 0.01 $\pm$ 0.04     | 0.18–0.18                    | 0.02 $\pm$ 0.09 | 0.43                         | 5.12    |
| <i>Salpa aspera</i> (aggregate)      |                     |                              | X               |                              |         |
| <i>Cyclosalpa pinnata</i> (solitary) | 0.02 $\pm$ 0.08     | 0.36–0.36                    | –               | –                            | 2.56    |
| <i>Salpa fusiformis</i> (solitary)   |                     |                              | X               |                              |         |
| <i>Cyclosalpa polae</i> (solitary)   |                     |                              | X               |                              |         |

Mean abundance (colonies or individuals  $10^5 \text{ m}^{-3}$ ) per station and standard deviation, range of abundance, frequency of occurrence ( $f$ ; considering both areas). X = Species present only in the additional samples and not included in the analysis

**Fig. 4** Geographic distribution of the abundance of *Pyrosoma atlanticum*, Doliolida spp. and Salpida species. s—solitary individuals, a—aggregates. Values standardized in number of individuals or aggregates per  $10^5 \text{ m}^{-3}$

*Soestia zonaria* was significantly more abundant in the WBCS (ANOVA  $F=8.66$ ,  $P=0.005$ ), particularly in the south of the study area where it reached  $7.4 \text{ ind. } 100 \text{ km}^{-3}$ . Only occasional catches were observed in the SECS. It was more abundant in stations sampled at night where it peaked in the first 200 m of the water column. During the day, *S. zonaria* was more abundant in samples with target depth between 400 and 600 m (Fig. 5). Other Salpida species occurred almost exclusively in the first 100 m of water column in stations over the slope in the south of the WBCS (Figs. 4, 5). It is noteworthy that mesh selectivity is a potential drawback in these results since the coarse aperture may have lost smaller species and early life stages.

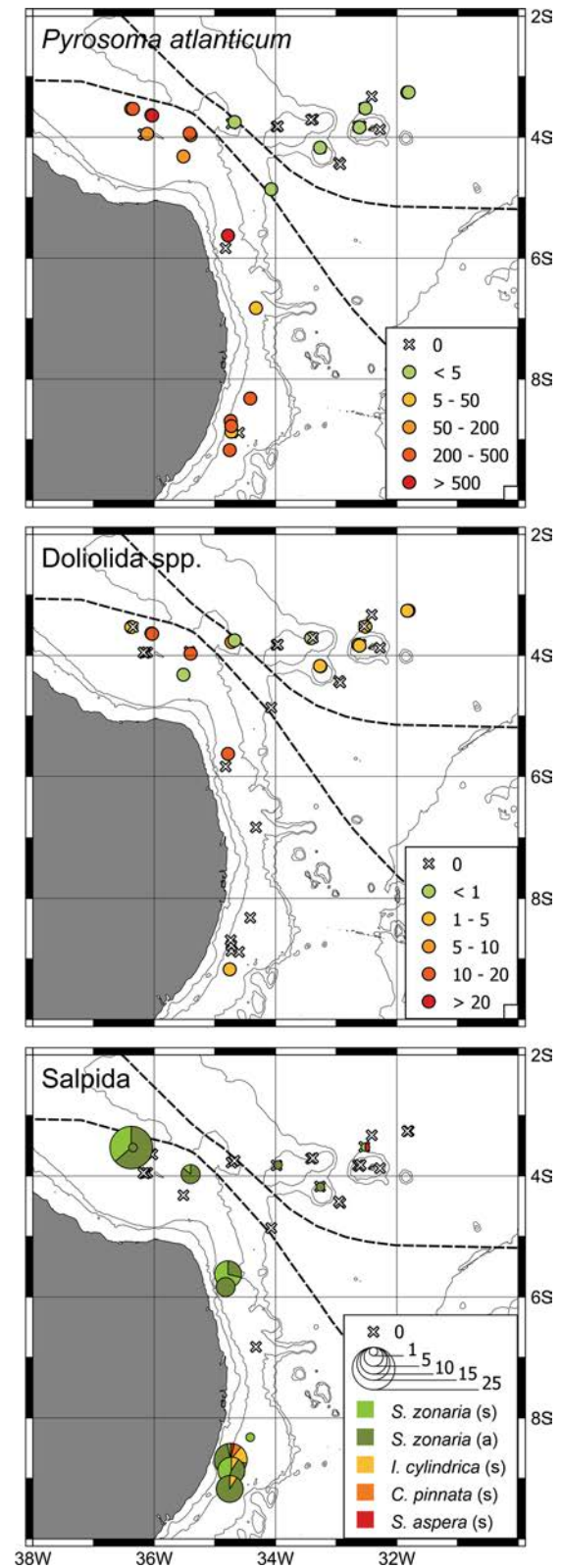
#### Community structure

The cluster analysis depicted three groups: A, B and C, with low similarity between each other (Fig. 6). SIMPROF analysis performed on the results of the cluster analysis considered the three groups as valid.

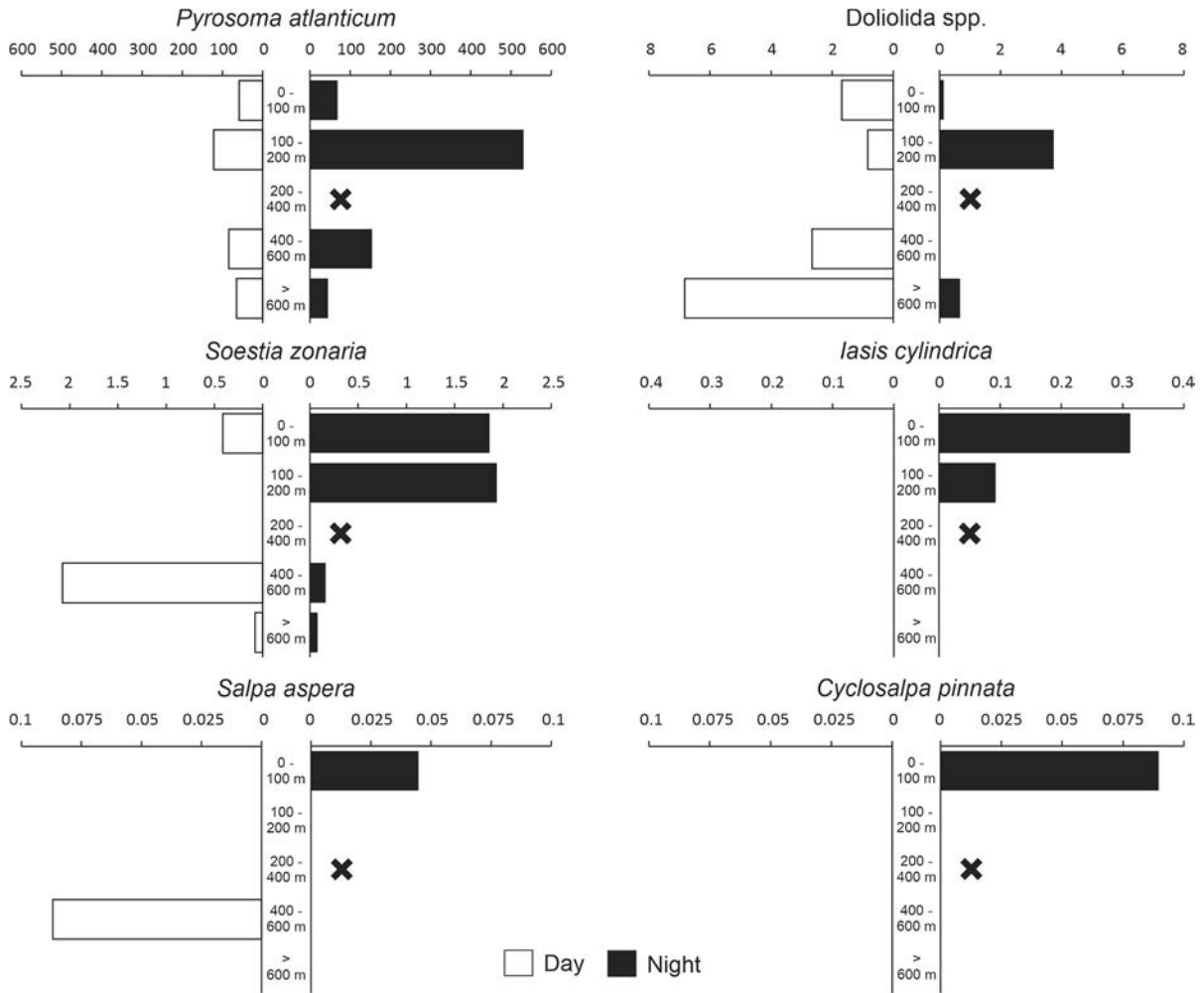
Group A, with 76.3% similarity within group, included most stations located in the WBCS (Fig. 6). High abundances of *P. atlanticum* were the main responsible for the similarity in the group. *S. zonaria* was also present in the samples of the group, but with a much lesser abundance (Table 2). Group B included only offshore stations from the SECS (Fig. 6). The group had 64.7% similarity and Doliolida spp. contributed for 90% of the similarity within the group (Table 2), although *P. atlanticum* was also present in low abundance. Group C was represented by samples from both areas (although more frequent in the SECS) where thaliaceans were found in very low abundances or completely absent (Figs. 4, 6, Table 2).

#### Species responses to environmental gradient

The two first canonical axes of the RDA explained 64.3% of species variance (Table 3). Monte Carlo test showed that the first ( $F\text{-ratio}=40.110$ ,  $P=0.002$ ) and all canonical axes together ( $F\text{-ratio}=4.902$ ,  $P=0.002$ ) were significant. Axis 1 explained 60.7%







**Fig. 5** Average relative abundance (individuals and aggregates per  $10^5 \text{ m}^{-3}$ ) per target depth strata (including net descent and ascent phases) and day period of *Pyrosoma atlanticum*, Doli-

olida spp. and Salpida species in the Western Tropical South Atlantic. x = Depth strata not sampled

of the variance and was positively related to northward currents (positive meridional component, representing NBUC) and SSS, and negatively related to westward currents (negative zonal component, representing cSEC), fluorescence and bottom depth (Fig. 7, Table 3). Axis 2 explained additional 3.6% and was positively related to SSS and the relative presence of SACW and AIW in the portion of the water column sampled and negatively related to the relative presence of TSW, SST and bottom depth (Fig. 7, Table 3).

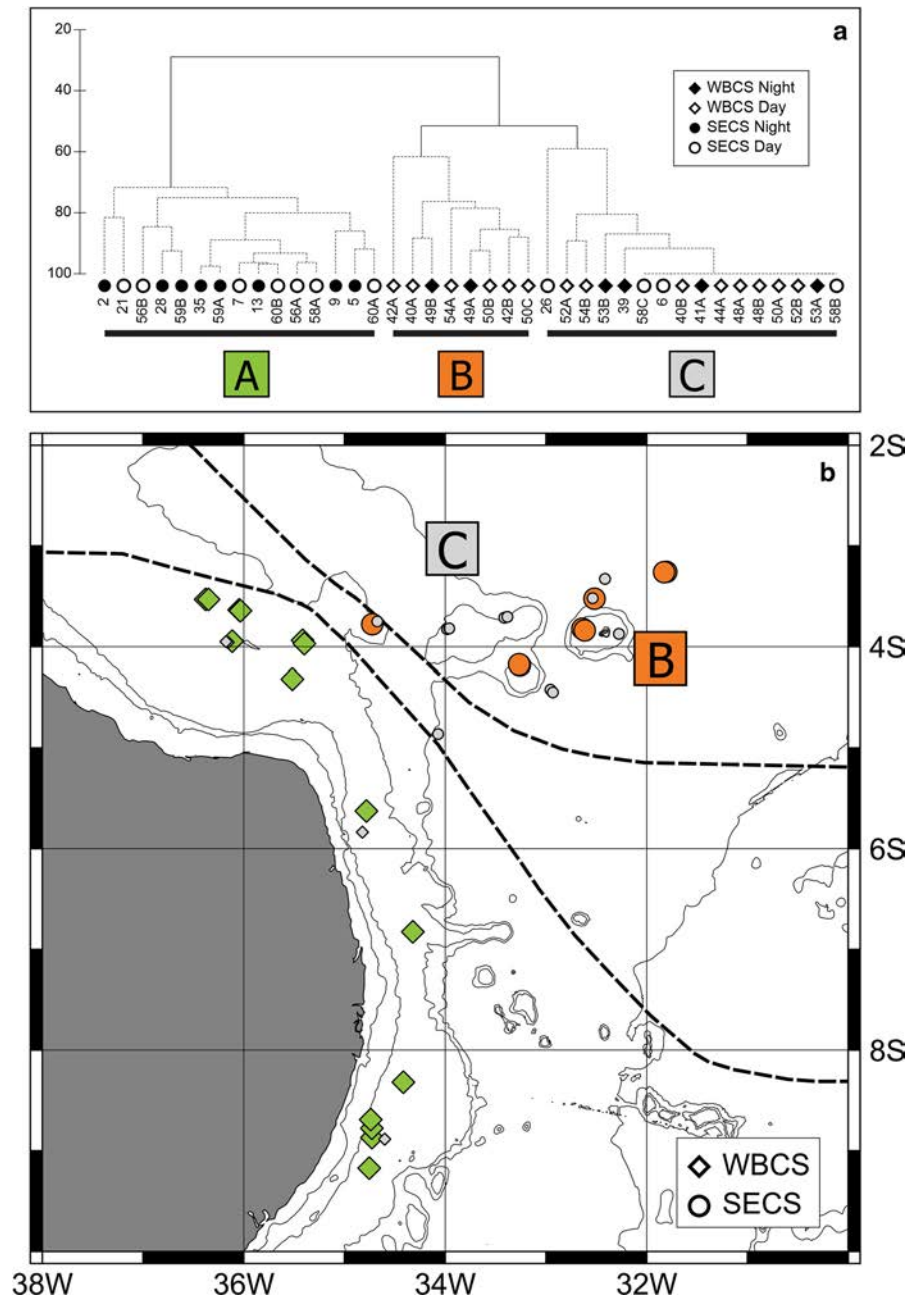
*Pyrosoma atlanticum* and *S. zonaria* were positively related to axis 1, indicating these species were more abundant in shallower samples under the influence of the NBUC with lower fluorescence and

higher salinity. Doliolida spp. was related to the negative portion of axis 2, indicating the taxa was more abundant in deeper stations, and related to higher SST and relative presence of TSW (Fig. 7).

## Discussion

Our results reveal that in the Western Tropical South Atlantic off Northeast Brazil, the thaliacean community structure presents different patterns according to the current system and associated thermohaline structure. This was not necessarily expected since in other gelatinous organisms, such as planktonic cnidarians,

**Fig. 6** **a** Cluster analysis dendrogram of data indicating three groups samples with similar thaliacean communities in the Western Tropical South Atlantic Ocean, dashed lines are significant groups in the SIMPROF analysis. **b** Map indicating distribution of the groups arranged in the cluster analysis



**Table 2** Results of SIMPER analysis, showing the relative contribution of thaliaceans taxa in the formation of the groups defined in the Cluster analysis

| Species                    | A    | B    | C    |
|----------------------------|------|------|------|
| <i>Pyrosoma atlanticum</i> | 93.1 | 9.4  | 30.5 |
| <i>Doliolida</i> spp.      |      | 89.8 | 45.7 |
| <i>Soestia zonaria</i>     | 4    |      | 23.8 |

the spread of oligotrophic oceanic waters over the coast led to typically homogeneous oceanic communities in the study area and other regions (Thibault-Botha et al., 2004; Tosetto et al., 2021).

In the WBCS, *P. atlanticum* and in a lesser extent *S. zonaria* were the most representative thaliacean species. These species were highly related to the NBUC, the strong western boundary subsurface

**Table 3** Summary of the RDA performed between the thaliacean taxa and environmental explanatory variables from the Western Tropical South Atlantic

|  | Axis 1   | Axis 2   |
|--|----------|----------|
| Eigenvalues                            | 0.607    | 0.036    |
| Species–environment correlations       | 0.843    | 0.578    |
| Cumulative variance (%)                |          |          |
| Of species data                        | 60.7     | 64.3     |
| Of species–environment relationships   | 92.9     | 98.3     |
| Correlations of explanatory variables  |          |          |
| 0–70 m currents zonal component        | – 0.3304 | 0.1006   |
| 0–70 m currents meridional component   | 0.6625   | 0.0678   |
| 70–350 m currents zonal component      | – 0.6243 | 0.0347   |
| 70–350 m currents meridional component | 0.7143   | 0.1054   |
| Bottom depth                           | – 0.1959 | – 0.1299 |
| Sea surface temperature                | 0.1365   | – 0.3367 |
| Sea surface salinity                   | 0.3739   | 0.2105   |
| Fluorescence                           | – 0.6734 | – 0.0143 |
| % of Tropical surface water            | 0.0506   | – 0.1276 |
| % of South Atlantic Central water      | – 0.028  | 0.099    |
| % of Antarctic intermediate water      | – 0.0608 | 0.1115   |

current that reaches up to  $1.2 \text{ ms}^{-1}$  and flows parallel to the coast (Dossa et al., 2021). In this area, *P. atlanticum* reached the highest abundances observed in the study (up to 700 col.  $10^5 \text{ m}^{-3}$ ). Massive occurrences of *P. atlanticum* were reported previously in areas with sloping topography under the influence of strong currents, such as the Northern California current and Guinea current. These studies associated the massive occurrences of the species with local changes in water temperature and salinity (Lebrato & Jones, 2009; Miller et al., 2019; Schram et al., 2020), but the relation of *P. atlanticum* with water circulation was not addressed properly by the authors. Tunic tissues of *P. atlanticum* are typically thicker than other thaliaceans (Hirose et al., 1999). This trait, associated with the larger sizes of the colonies, may grant them resistance to survive in strong boundary currents and the possibility to take advantage from local conditions of water and additional food supply. These organisms may also have been pushed by the coastward currents and accumulated over the slope. Although this process was never observed in thaliaceans, many studies reported the aggregation of other planktonic organisms in sloping topography induced by oceanic currents and

species vertical behaviour (Cotté & Simard, 2005; Sourisseau et al., 2006; Hazen et al., 2009).

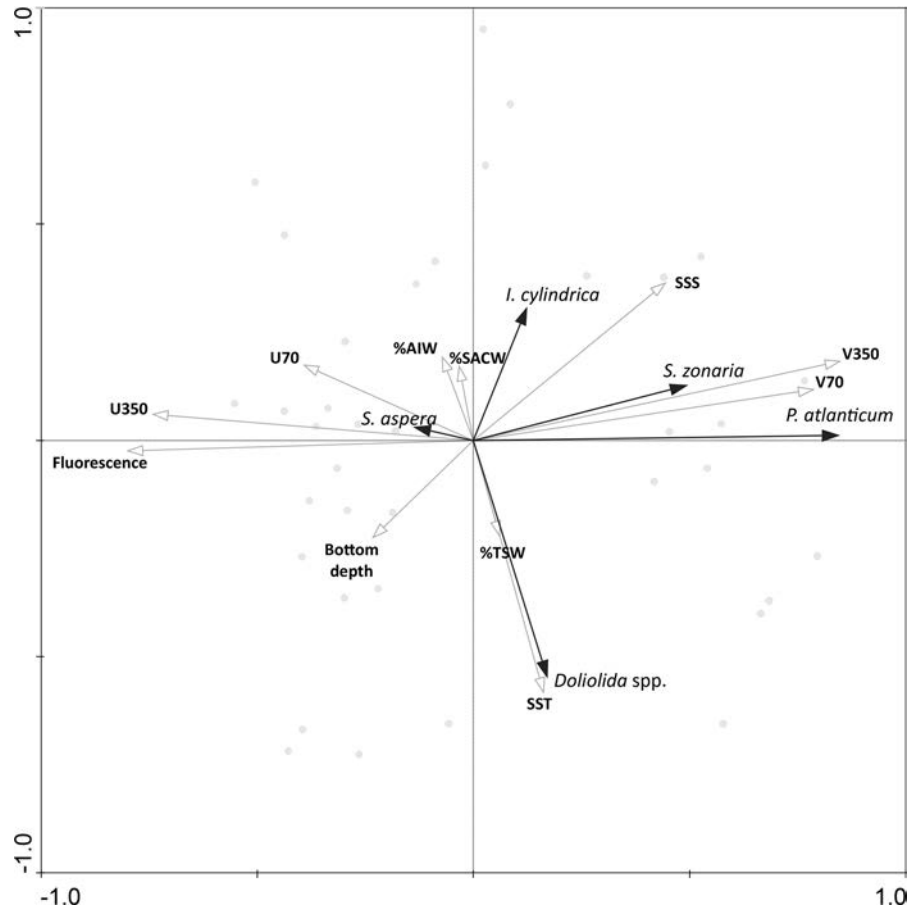
Additionally, *P. atlanticum* and *S. zonaria* were negatively related to fluorescence. Fluorescence is an indirect proxy of primary production and food availability. These species are efficient filter-feeders consuming pico- and nanoparticles including the bacterioplankton typically responsible for most primary production in oligotrophic systems such as the Western Tropical South Atlantic. Thus, the large abundance of *P. atlanticum* observed in this study may have contributed to the reduction of the chlorophyll stocks as previously observed in other ocean basins (Drits et al., 1992; Perissinotto et al., 2007).

Interestingly, the Salpida species *Iasis cylindrical* (Cuvier, 1804), *Salpa aspera* Chamisso, 1819, and *Cyclosalpa pinnata* (Forskål, 1775) occurred almost exclusively in stations in the south of the WBCS, where the Pernambuco Plateau is located (Buarque et al., 2016). The particular topography and circulation in the region reduces the influence of western boundary currents over the shelf and oceanward transport of coastal water is observed (Dossa et al., 2021; Tosetto et al., 2021). This hydrographic configuration has significant implications in the structure of pelagic communities and possibly the entire ecosystem (Eduardo et al., 2018; Tosetto et al., 2021).

Doliolida spp. dominated stations from group B, located exclusively in the SECS. Unfortunately, only tunics were found in our samples; thus, identification to species level was not possible. However, common doliolid species in waters of the Western Tropical South Atlantic are *Dolioletta gegenbauri* (Uljanin, 1884), *Dolioloides rarum* (Grobber, 1882), *Doliolum denticulatum* Quoy & Gaimard, 1834, and *Doliolum nationalis* Borgert, 1893 (EsnaI & Daponte, 1999a; Díaz et al., 2009). These are typical epipelagic warm water species (EsnaI & Daponte, 1999a); thus, the close positive relation of doliolid species observed in this study with tropical surface water mass (Fig. 7) is expected.

Although we did not perform depth stratified samples, our results suggest the three more frequent and abundant taxa performed diel vertical migrations. Higher abundances of *P. atlanticum* occurred in samplings carried out at night between 100 and 200 m depth. At daytime, this species was steadily abundant in the sampled water column. Since no tows were made below 1170 m depth, we cannot infer whether

**Fig. 7** RDA relating the thaliacean species to environmental gradients in the Western Tropical South Atlantic Ocean



during daytime these organisms were aggregated in deeper waters or were distributed evenly throughout the water column. Both hypotheses are possible since *P. atlanticum* is known to undertake large vertical migrations below 1000 m depth (Andersen & Sardou, 1994; Henschke et al., 2019). Both *Doliolida* spp. and *S. zonaria* were more abundant in samplings carried out down to 200 m depth during night, and below 400 during daytime. *S. zonaria* vertical migration was not studied previously; however, this is a common behaviour in other *Salpida* species (e.g. Wiebe et al., 1979; Madin et al., 1996; Nishikawa & Tsuda, 2001) and thus expected for *S. zonaria*. Differently, large vertical migration, as suggested by the larger abundances occurring in distinct depths during day and night, was never observed for doliolids, which often are reported in epipelagic waters (Esnal & Daponte, 1999a). Vertical migration is an important mechanism transporting carbon assimilated in the surface by epipelagic phytoplankton to deeper water masses across the

thermocline, particularly when considering large swarms as observed herein for *P. atlanticum*. Thus, future studies should use closing net devices to better describe the vertical migration of thaliacean species and quantify carbon fluxes.

Mesh selectivity is always a potential drawback when sampling pelagic organisms. While a coarse mesh may lose smaller species and early life stages, a small mesh may filter high rates of unwished particles, obstructing water passage and rapidly clogging the mesh (Riccardi, 2010; Tosetto et al., 2019). Studies focussing on thaliacean communities use wide range of mesh sizes, from fine plankton nets to large micronekton meshes (e.g. Li et al., 2011; Henschke et al., 2019; Miller et al., 2019). In this study, we used a relatively coarse mesh to sample the thaliacean community (40 mm in the main body and 10 mm in the cod-end). Still, with this gear, we could filter a large volume of water reaching deeper strata. The coarse meshes also reduce clogging and

bow wave effect, enabling the catch of large specimens and colonies (Vannucci, 1968). Thaliacea encompasses species with a wide range of sizes and no single method would allow a sampling all of them. The additional trawls we performed with the finer mesh (30 mm in the main body and 3 mm in the cod-end) collected two additional salp species (Table 1). Unfortunately, few tows were performed with this mesh, and we could not properly compare the effects of mesh selectivity on the structure and abundance of the thaliacean community in the Western Tropical South Atlantic, an important subject to be addressed in the future studies. Additionally, studies carried out with samples collected with a 300- $\mu$ m mesh size from 200 m depth to surface at the Archipelago of Saint Peter and Saint Paul, close to FNR, recorded eight thaliaceans species: *P. atlanticum*, *D. rarum*, *D. denticulatum*, *I. cylindrica* (as *Weelia cylindrical*), *Thalia democratica* (Forskål, 1775), *Thalia cicar* van Soest, 1973, *Pegea socia* (Bosc, 1802) and *Thalia* sp. (Díaz et al., 2009). Thus, at least three of the species collected with the finer mesh in Saint Peter and Saint Paul were not present in our samples.

In conclusion, we observed clearly distinct patterns in the thaliacean community in the Western Tropical South Atlantic likely related to the circulation and thermohaline structure in the area. Over the continental slope, where the strong NBUC flows northward, high abundances of *P. atlanticum*, and, to a lesser degree, *S. zonaria* were observed. Over the Pernambuco plateau, in the South of this area and where current intensity was lower, other less abundant salp species, such as *I. cylindrica*, *C. pinnata* and *S. aspera*, were present as well. Meanwhile, offshore around the Fernando de Noronha Ridge, Doliolida spp. were the dominant thaliacean, co-occurring with *P. atlanticum* in lower abundance.

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**Data availability** The data that support the findings of this study are available from the corresponding author, upon reasonable request.

**Conflict of interest** The authors declare they have no conflict of interests.

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