Zooplankton biomass around marine protected islands in the tropical Atlantic Ocean

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ABSTRACT

Zooplankton biomass (as wet weight) was studied around marine protected islands in the tropical Atlantic Ocean. The study was based on 96 zooplankton samples collected during a 3-year period; specifically, 2010 was considered a year of thermal stress, and 2012 and 2014 were considered years without thermal stress. The analysis showed that zooplankton biomass varied significantly among protected areas, where the smallest and most isolated archipelago among the tropical islands, Saint Peter and Saint Paul Archipelago (SPSP), had approximately twice the biomass of Fernando de Noronha Archipelago (FN) and three times that of Rocas Atoll (RA). The position of SPSP near the equatorial divergence zone, the seasonal occurrences of phytoplankton blooms east of the Equator, the contribution of the productive waters that SPSP receives from the African coast under the influence of the South Equatorial Current (SEC) system and the local upwelling effect induced by the presence of the island were considered to be the factors responsible for the high pelagic productivity in this remote archipelago. Differences between day and night were also recorded. The high nocturnal biomass was considered an effect of the capture of larger-sized animals, which are considered to be strong migrators. The lowest zooplankton biomass was recorded in 2010 and was considered an apparent effect of the high sea surface temperature observed in that year. However, the interaction between spatial and interannual factors showed that, in FN and SPSP, the zooplankton biomass was lower in the year under thermal stress (2010). In contrast, RA presented a higher biomass value in this period. We suggest that this increase in zooplankton biomass is the result of the contribution of autochthonous sources (*e.g.*, as a consequence of local physical events, such as current wakes, recorded during this period at RA and responsible for the increase in local planktonic productivity) and allochthonous sources (*e.g.*, organisms supplied by FN *via* the zonal current).

1. Introduction

Marine zooplankton play a central role in structuring the pelagic trophic web and the biogeochemical cycling of carbon in the oceans (Piontkovski et al., 2003); these zooplankton contribute to the transfer of energy through the food chain and connect primary producers to higher trophic levels (Escribano, 2006). Biomass measurements can be a quantitative indicator of the productive potential of aquatic ecosystems (Piontkovski and Castellani, 2009). Thus, understanding the distribution of zooplankton biomass in the world's oceans is essential for estimating its contribution to energy flow through pelagic food webs (Duarte et al., 2014). The distribution of zooplankton biomass varies

with spatial and temporal scales (Brodeur et al., 1996), generating heterogeneous patches. Worldwide, much of this heterogeneity is the result of seasonal and geographic variations in nutrient availability, mixed layer depth and solar radiation. However, localized and transient abiotic mechanisms (*e.g.*, upwelling, wind and tide mixing) may increase productivity (Brodeur et al., 1996). Furthermore, biotic factors that are considered intrinsic characteristics of the zooplankton community (*e.g.*, physiology and growth, buoyancy and behavior) directly influence the distribution of zooplankton biomass in the world's oceanic ecosystems (Arashkevich et al., 2002).

Oceanic regions in tropical areas have been subjected to substantial environmental changes mainly as a result of the effect of climate change

(Piontkovski and Castellani, 2009), which causes interannual variability in the physical, biological and biogeochemical characteristics of the oceans, affecting their ecological function and ecosystem services. Despite strong evidence of systematic changes in biomass, abundance and planktonic community structure in recent decades in many areas of the world (Hays et al., 2005), there is a lack of information available for the tropical Atlantic due to logistical and funding restrictions that make it prohibitive to undertake long-term studies on zooplankton.

The tropical Atlantic is oligotrophic because of the permanent and deep thermocline typical of warm oceans, which limits biological productivity because of limited nutrient availability (Macedo-Soares et al., 2009). However, there are zones especially close to banks and islands that are an "oasis of life in an oceanic desert" (McClain, 2007). These "oases" are the consequence of the "mass island effect" (Doty and Oguri, 1956), a process that allows enriched subsurface waters to fertilize surface waters, promoting an increase in planktonic biomass (primary and secondary production) and fishery resources in the areas surrounding these islands. The interaction of currents with the topography of the islands and the existence of physical instability, which mainly induce downstream turbulence effects such as eddies, are known to affect the distribution of nutrients, Chlorophyll-a, primary production and fish larvae. There are areas of high zooplankton biomass favoring the retention of zooplankton in the areas downstream of oceanic islands (Rodríguez et al., 2001; Tchamabi et al., 2017). Another increase in zooplankton biomass is expected at night in tropical marine ecosystems, mainly due to the typical pattern of daily vertical migration (DVM) carried out by zooplankton. This DVM directly influences the higher trophic levels by displacing a substantial amount of biomass in the upper water column (Lira et al., 2014; Melo et al., 2012).

The marine protected areas (MPAs) of Fernando de Noronha Archipelago (FN), Rocas Atoll (RA) and Saint Peter and Saint Paul Archipelago (SPSP) are located in the Brazilian Marine Economic Exclusive Zone. These islands located in the tropical region of the South Atlantic are areas of special importance for biodiversity, and they deliver important ecosystem services (Soares et al., 2017). These MPAs are under serious regional (*e.g.*, fishing, plastic pollution and introduction of exotic species) and global (*e.g.*, global warming and acidification) impacts; thus, effective protection measures are needed (de Oliveira Soares, 2018). Studies of tropical oceanic waters off northeastern Brazil indicate that zooplankton biomass decreases from island locations to offshore locations (Campelo et al., 2018; Jales et al., 2015; Lira et al., 2014; Melo et al., 2012; Neumann-Leitão et al., 2008). The goal of our study was to investigate the spatial (FN *vs.* RA *vs.* SPSP), interannual (thermal stress *vs.* no thermal stress), time of day (day *vs.* night) and transect (upstream *vs.* downstream) differences around the MPAs of the tropical Atlantic Ocean. In the present study, we considered zooplankton biomass (mg.m^{-3} wet weight) as an indicator of the productive potential of the marine protected areas of FN, RA and SPSP.

2. Materials and methods

2.1. Study area

Sampling was carried out around three tropical Atlantic island systems (FN, RA, and SPSP) (Fig. 1). These islands are marine protected areas (MPAs) that were created in June 1986 and cover an area of 79,706 ha (Alves and Castro, 2006). The South Equatorial Current (SEC) is the main current that transports warm oligotrophic water to the tropical Atlantic oceanic region and bifurcates into the North Brazil Current (NBC) and the Brazil Current (Brazil C.) (Stramma et al., 2005) (Fig. 2). The flow portion located between the South Equatorial Undercurrent and the South Equatorial Countercurrent (SECC) is called the central SEC (cSEC); the south flow of the SECC, known as the South SEC (sSEC), and the Brazil Current are the main currents that reach the island areas being studied (Assunção et al., 2016) (Fig. 2).

The Fernando de Noronha Archipelago (3°50′24″S and 32°24′48″W) (Fig. 1) consists of 21 islands and islets, including rocks. It has a total area of 26 km^2, with its largest extension in the NNE-SSW direction (Assunção et al., 2016). There are two seasons: a rainy period from March and July and a dry period from August and January. The tidal regime is semidiurnal, with a range from 2 to 3.2 m, and the prevailing winds are the southeast trade winds, which vary to the northeast, with an average intensity of 4.8 ms^{-1}, from the surface to the level of 750 millibars (Mohr et al., 2009).

The Rocas Atoll (3°51′S and 33°49′W) (Fig. 1) is the top of an underwater mountain whose base is 4000 m deep. This reef covers an area of 7.5 km^2 (Gherardi and Bosence, 2005). The RA has volcanic origin and carbonate formation in the reef (Soares et al., 2011). Between June and August (winter in the Southern Hemisphere), SE winds occur on 35% of the days, and the frequency of E winds is 15% in the same period. Between December and April (summer in the Southern Hemisphere), SE winds and E winds occur on approximately 20% of the days (Kikuchi and Schobbenhaus, 2002).

The Saint Peter and Saint Paul Archipelago (00°53′-00°58′N and 29°16′-29°24′W) (Fig. 1) is Brazil's closest point to the African continent, with a distance of 937 km to Guiné-Bissau in Africa. It is formed by 15 islands (Becker, 2001) and is located north of the Equator and formed principally by mantle rocks. The SPSP region is under the influence of the Intertropical Convergence Zone (ITCZ) from January to May (rainy season). In the second half of the year, from June to September, the ITCZ moves to the north, and rainfall decreases (dry season). The prevailing winds are the southeast trade winds, with a constant intensity of approximately 7 ms^{-1} (Souza et al., 2013).

2.2. Sampling strategy

The expeditions were performed aboard the NHOc Cruzeiro do Sul of the Brazilian Navy as part of the "Camadas finas" project. Data were collected in July/August 2010 (thermal stress), September 2012 and August 2014 (no thermal stress) at FN, RA and SPSP (Fig. 1). Sampling was performed during the day (05:00 AM to 04:59 PM) and night (05:00 PM to 04:59 AM). A total of 96 samples were collected, of which 36 samples were from RA and SPSP and 24 samples were from FN. Mechanical problems with the ship made sampling FN in 2014 impossible. An ADCP was used to obtain the current direction and velocity, and this information was used to establish two transects: one upstream of the island and one downstream of the island in relation to the predominant surface current. We identified three equidistant stations along each transect.

2.3. Remotely sensed data

To describe the climatic and hydrological variability, we used remote sensing temperature, chlorophyll-*a*, wind and current velocity data for a region of the tropical Atlantic (60°W-20°W and 10°S-10°N). Chlorophyll-*a* data were extracted from the Copernicus database (http://marine.copernicus.eu/) with a spatial resolution of 4 km from 2008 to 2016; these data created a long data series that could be compared with our observations. We extracted monthly sea surface temperature (SST) and surface zonal wind (U) from the NCEP-NCAR reanalysis data (http://www.esrl.noaa.gov/psd/data/gridded/). The monthly chlorophyll-*a* data were obtained by merging MERIS, MODIS/ AQUA, and VIIRS and SeaWiFS data at a resolution of 4 km using an advanced retrieval based on fitting an in-water bio-optical model to the merged set of observed normalized water-leaving radiances.

2.4. Zooplankton sampling and analyses

To obtain the zooplankton biomass, oblique trawls were conducted using a bongo net (mouth opening of 0.6 m^2, mesh size of 300 μm). The oblique trawls were made in "V", extending from the surface to a
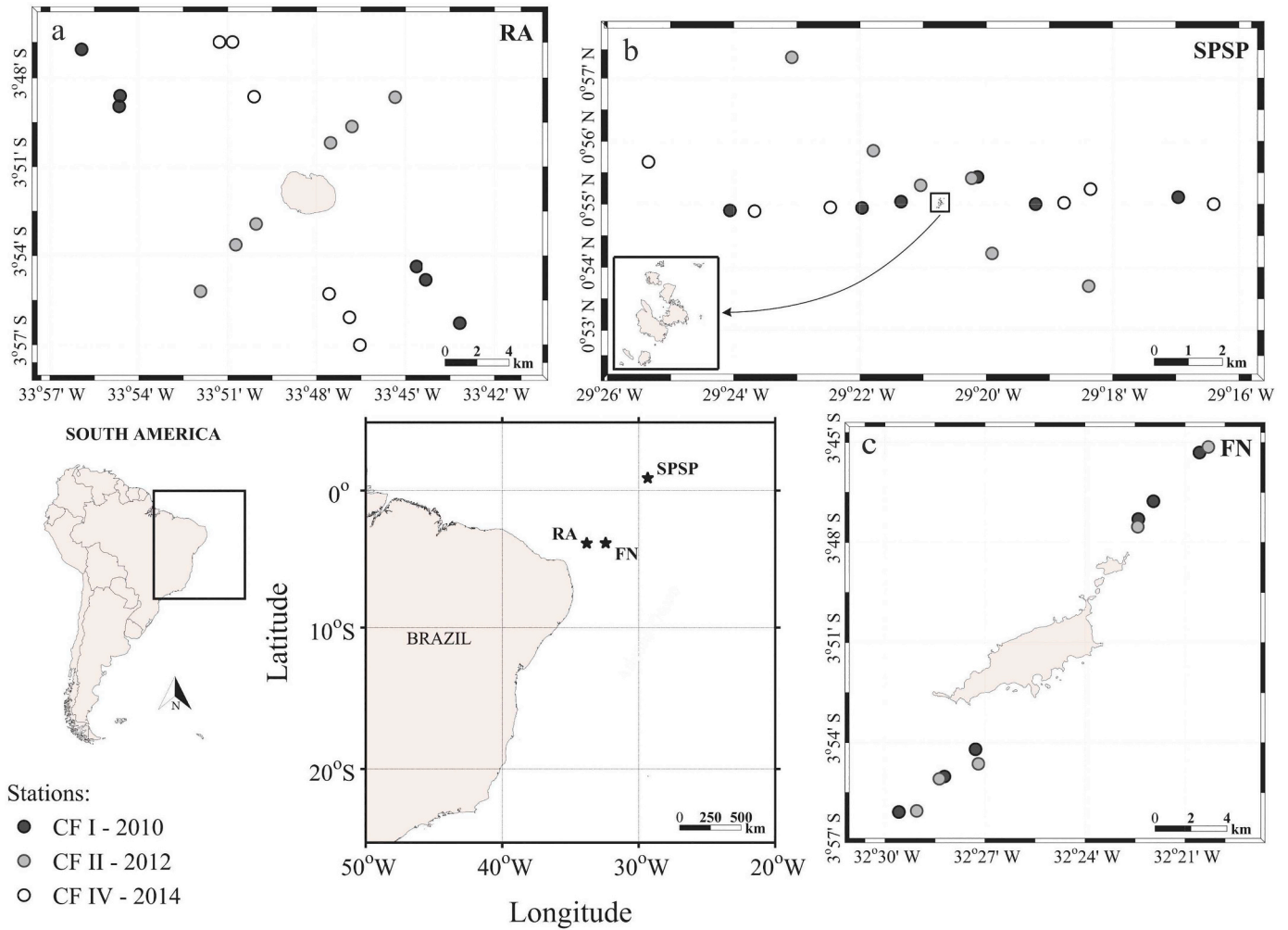
Fig. 1. Sampling stations in islands of the tropical Atlantic. (a) RA – Rocas Atoll; (b) SPSP – Saint Peter and Saint Paul Archipelago and (c) FN – Fernando de Noronha Archipelago as part of the project: CFI – 2010 ("Camadas Finas I"); CFII – 2012 ("Camadas Finas II") and CFIV – 2014 ("Camadas Finas IV").

maximum depth not exceeding 200 m and then back to the surface, maintaining a wire angle close to 45°. At stations shallower than 80 m, the bongo net was released up to 75% of the local depth. The sampling depth varied between 75 m at FN and 2288 m at RA. The towing speed was 1.5 to 2.5 knots. A flowmeter was mounted in the mouth of the net to estimate the volume of water filtered through the net. Zooplankton samples were preserved immediately in a 5% buffered formalin-sea-water solution.

In the laboratory, each sample was filtered in accumulators with a mesh size of 100 μm that were previously weighed on a scale with 0.001 mg precision for determination of the wet-weight (Harris et al., 2000). To avoid the effect of large particles that are not part of the plankton, elements such as macroalgae, pieces of ships' paint and microplastics were removed.
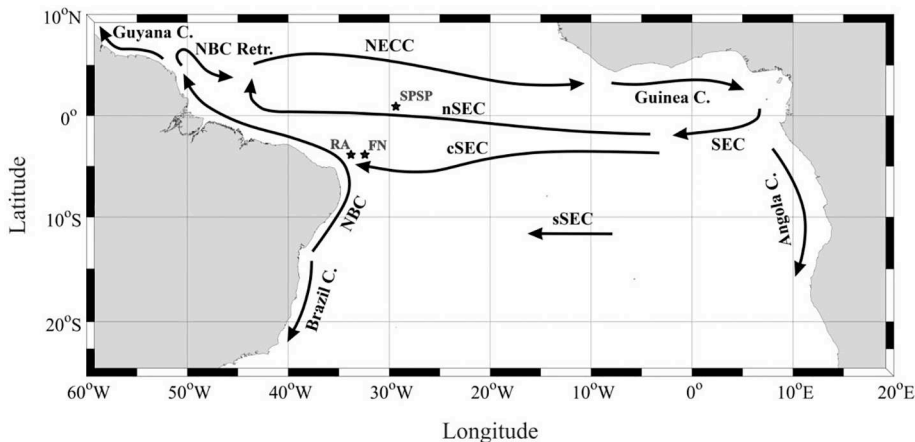

Fig. 2. Surface currents in the studied areas. FN – Fernando de Noronha Archipelago, RA – Rocas Atoll and SPSP – Saint Peter and Saint Paul Archipelago, including the North Equatorial Current (NEC), North Equatorial Counter Current (NECC), Northern South Equatorial Current (nSEC), Central South Equatorial Current (cSEC) and Southern South Equatorial Current (sSEC) branches of the South Equatorial Current (SEC), and the North Brazil Current and its retroflection (NBC Retr.) (Adapted from Lumpkin and Garzoli, 2005).

2.5. Data analysis

The interaction effect of factors, *i.e.*, spatial (FN *vs.* RA *vs.* SPSP), temporal (thermal stress *vs.* no thermal stress), time of day (day *vs.* night) and transect (upstream *vs.* downstream), on zooplankton biomass were tested using multifactorial analysis of variance (MANOVA). Data were transformed to the natural logarithm of $(X + 1)$ to stabilize the variance and reduce heteroscedasticity. The heterogeneity of variances was evaluated using Levene's test. When the biomass data satisfied the assumption of normality and MANOVA results indicated significant effects, a Bonferroni *post hoc* test was applied to identify the factors for which significant differences existed ($p < .05$). The parametric statistical analysis followed that in Zar (1996).

3. Results

3.1. Climatic and hydrological conditions

The anomalies of wind speed (0.2 degree of spatial resolution), sea surface temperature SST (with 1 °C of resolution) and current velocity U (with 1/3 of resolution variability) between 2008 and January 2016 are shown in Fig. 3. We highlight 2010, 2012 and 2014, which correspond to the sampling years of this study (Fig. 3).

In 2010, we observed a significant effect of the El Niño-Southern Oscillation (ENSO) connections in the tropical Atlantic on wind (Fig. 3a) and SST (Fig. 3c). In the first months of 2010 (January to March), a weakening of the zonal winds was observed in FN, RA and SPSP relative to the same period in the following years (2012 and 2014) (Fig. 3a).

Lower means of chlorophyll-*a* anomalies (Fig. 3b) were associated with higher positive SST anomalies from January to May 2010 (Fig. 3c), which corresponded to the period of response to the 2009 El Niño in the tropical Atlantic Ocean. The decrease in chlorophyll-*a* anomalies from positive to negative values (0 to -0.1 mg Chla.m^3) was pronounced and was associated with the positive SST after the El Niño event in 2010. An opposite pattern was observed in later years (2012 and 2014), while the negative SST anomalies were associated with positive chlorophyll-*a* anomalies, with a strong trend particularly around SPSP island.

SST anomalies were positive for the three islands (FN, RA and SPSP) in 2010 relative to the negative anomalies that were predominant in 2012 and 2014 (Fig. 3c). The higher SST anomaly in 2010 (Fig. 3c) was associated with the increasing wind anomaly, from -1.4 to 1.6 m.s^{-1} (Fig. 3a). The association of SST with increasing wind was only apparent after the El Niño event of 2009.

The circulation around FN and RA was mainly from east to west, driven by the South Equatorial Current (SEC). SPSP is under the influence of the SEC and NECC, as can be observed in Fig. 2. The NECC flows from the Brazilian coast to the African coast, presenting positive zonal current values. A reduction of zonal current was observed in FN, RA and SPSP through the decrease in the zonal current U anomalies values (0.1 to -0.3 m.s^{-1}) that occurred in the period from January to March 2010 (Fig. 3d) as a consequence of the weakening zonal winds. An opposite trend of zonal current U anomaly values (-0.1 to 0.1 m.s^{-1}) was observed during the same period of the years without the influence of El Niño, *i.e.*, in 2012 and 2014.

In the tropical Atlantic, the zonal wind is mostly driven from east to west for the three islands of FN, RA and SPSP (Fig. 4a). The average chlorophyll-a is ~ 0.11 mg.m^{-3} near the FN and RA islands, slightly lower than the average value registered at SPSP of ~ 0.15 mg.m^{-3} (Fig. 4b). We observe a wake region in RA and FN in Fig. 4b, at the location of the light blue dots, which corresponds to the islands' positions, with chlorophyll-a ~ 0.11 mg.m^{-3}. The average SST shows that the SST variability is $\sim$27 °C near the FN, RA and SPSP islands (Fig. 4c). All these islands are subjected to zonal U current influence flowing from east to west (Fig. 4d), with negative values under the influence of the
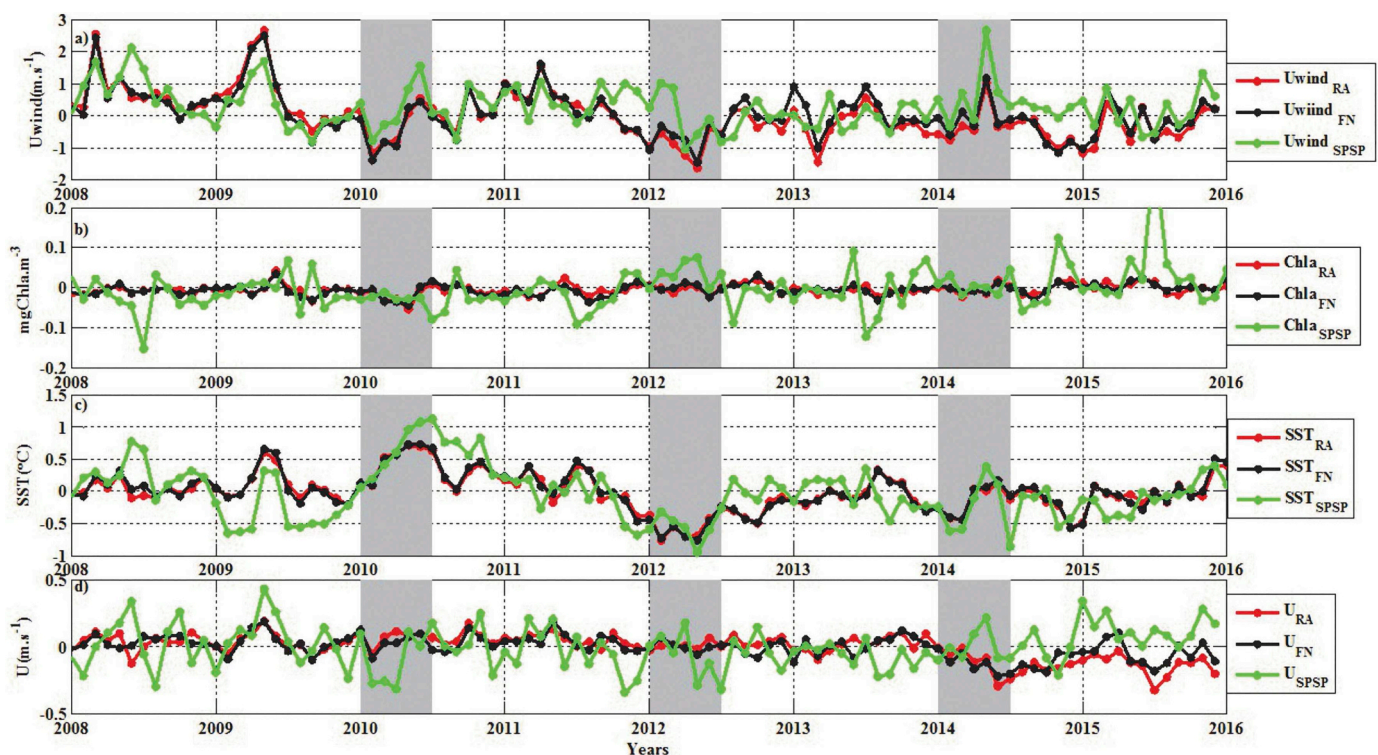

Fig. 3. Time series (2008 to 2016) describing the climatic and hydrological variability in the tropical Atlantic Ocean. (a) zonal wind U (m.s^{-1}) anomalies, (b) chlorophyll-a (mgChla.m^{-3}) anomalies, (c) sea surface temperature (°C) anomalies and (d) zonal current U (m.s^{-1}) anomalies represented in red for RA, black for FN and in green for SPSP. Shaded areas indicate sampling years in the region of the tropical southwestern Atlantic. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)
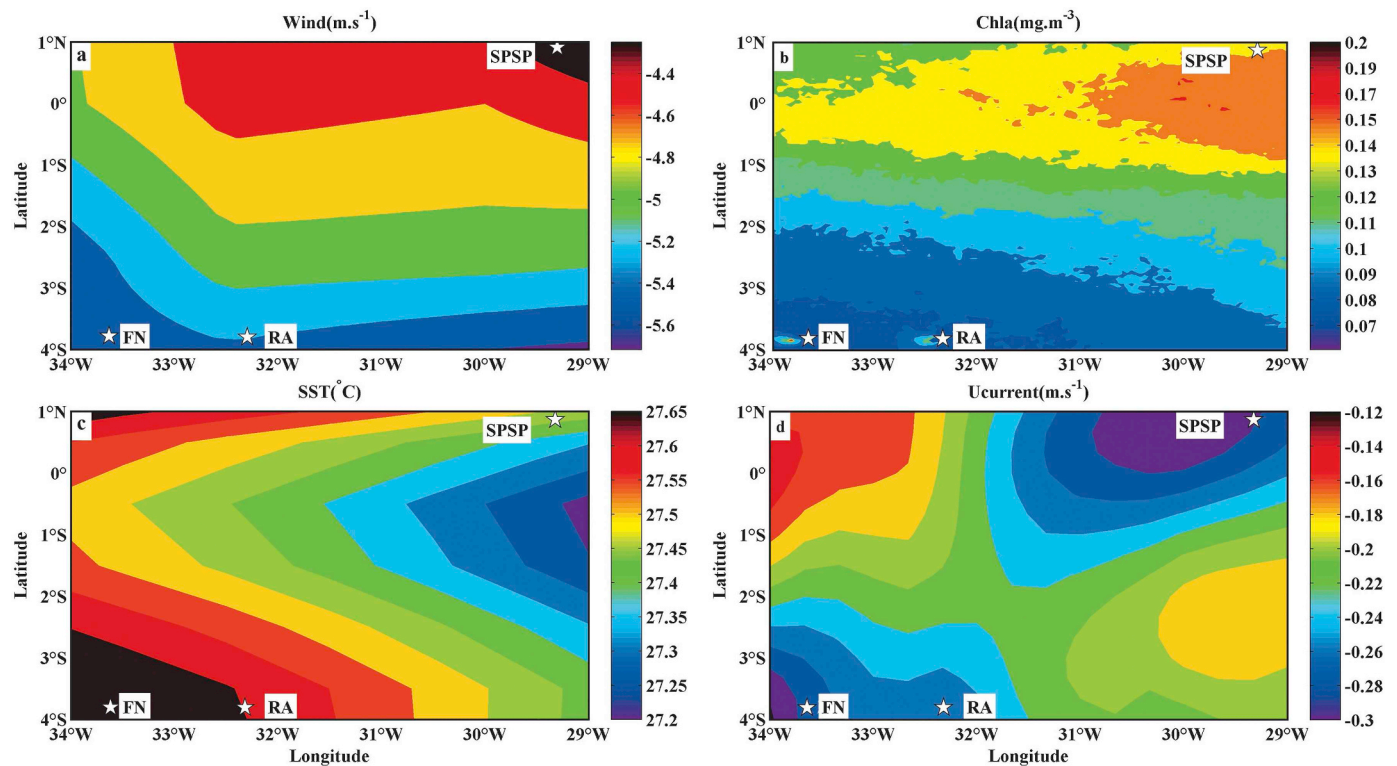
Fig. 4. Average zonal wind U (m.s^{-1}) (a), Chl a (mg.m^{-3}) (b), sea surface temperature (Celsius degree)(c), and zonal current U (m.s^{-1}) (d) in regional areas, which include FN, RA, and SPSP, between 2008 and 2016. The light blue dots in Fig. 4b represent wake regions in RA and FN. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

zonal components of nSEC (SPSP) and cSEC (FN and RA).

3.2. Zooplankton biomass

Zooplankton biomass differed among the islands ($F_{2, 70} = 10.24$, $p < .001$) (Fig. 5a), and SPSP (74.04 ± 60.54 mg.m^{-3}) had approximately twice the biomass of FN (37.29 ± 23.22 mg m^{-3}) and three times that of RA (24.02 ± 16.13 mg.m^{-3}). Differences between day and night were also recorded (Fig. 5b). The nighttime average (60.88 ± 56.76 mg.m^{-3}) was significantly higher ($F_{1, 70} = 11.64$, $p \leq .001$) than that of daytime (32.85 ± 26.23 mg.m^{-3}).

The interannual effect was verified on zooplanktonic biomass ($F_{1, 70} = 5.57$, $p < .01$), with a low value (30.51 ± 17.33 mg.m^{-3}) recorded in the period of thermal stress, corresponding to a biomass loss of 54.81% compared to that in the period without thermal stress (55.66 ± 54.01 mg.m^{-3}). An interaction effect was detected among the spatial and temporal factors for zooplankton biomass ($F_{2, 70} = 4.40$, $p < .01$) (Fig. 5c) (Table 1). The Bonferroni test showed that the thermal stress caused a reduction in zooplankton biomass in the islands of FN and SPSP, but in RA, zooplankton biomass was higher during the period of higher sea surface temperature (Fig. 5c, Table 1). In addition, the test detected that, regardless of the climatic condition, the biomass in SPSP was significantly higher than that in the other island systems that were studied (Fig. 5c, Table 1).

Regarding the transects, it was verified that in FN, the zooplankton biomass ranged from 6 to 102 mg.m^{-3}, both of which were registered downstream of the island (Fig. 6a and b). On the other hand, in the RA, the zooplankton biomass showed a concentration ranging from 1.15 to 70 mg.m^{-3}, both of which were registered on the upstream side (Fig. 6e and c). The highest values of this parameter were recorded in SPSP, ranging between 10 on the upstream side to 275 mg.m^{-3} on the downstream side of the island (Fig. 6g and h). In general, the average value downstream was equivalent to 49.37 ± 54.90 mg.m^{-3}, while the average upstream value was 43.88 ± 35.56 mg.m^{-3}.

4. Discussion

4.1. Climatic and hydrological conditions in the tropical Atlantic

The 2010 post-ENSO event caused a low concentration of chlorophyll-*a*, which was associated with increased SST at the beginning of the boreal spring season (January–February) relative to the values recorded in the same period in 2012 and 2014. ENSO weakened the zonal wind in 2010. Marengo et al. (1993) observed that during El Niño years, the ITCZ (Intertropical Convergence Zone) is anomalously farther north of its normal position; thus, the trade winds are weaker. A significant positive relationship between the percentage of coral bleaching and the corresponding anomaly of SST HotSpot was recorded by satellite and buoys, as a consequence of ENSO, and observed by Ferreira et al. (2013) in Fernando de Noronha and Rocas Atoll.

Regionally, the chlorophyll-*a* concentration varied between 0.11 and 0.15 mg.m^3 near FN, RA and SPSP. This result is similar to that found by Da-Cunha and Buitenhuis (2013) and Tchamabi et al. (2017) and is considered low when compared to the Brazilian shelf and its coastal zone (> 2 mg m^{-3}) (Mafalda Jr and Souza, 2007). The higher chlorophyll-*a* concentration obtained around the SPSP island than that near the FN and RA islands may be explained by the occurrence of equatorial upwelling processes (Grodsky et al., 2008; Longhurst, 1993; Peterson and Stramma, 1991) associated with the depth-integrated chlorophyll-*a* supplied to the surface waters (Pérez et al., 2005) around SPSP, where its position (00°53′- 00°58′N and 29°16′- 29°24′W) is nearer to the equator than those of the FN and RA islands.

4.2. Zooplankton biomass

The present study provides the first information about the spatial heterogeneity of tropical Atlantic island environments, where the smallest and most isolated archipelago of the tropical islands of the planet (SPSP) presented a significantly higher zooplankton biomass
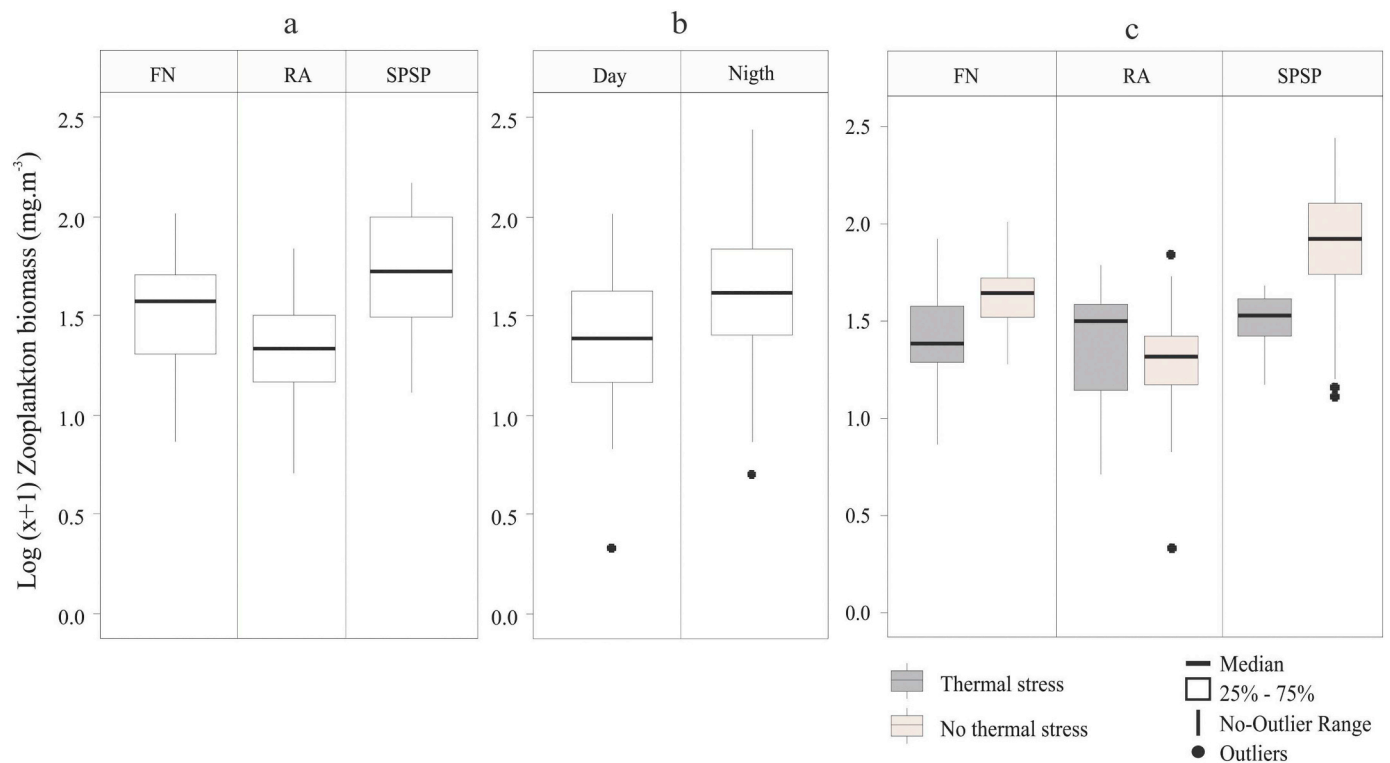
Fig. 5. Box plots (median and quartiles) representing the distribution of the zooplankton biomass. (a) spatial distribution (FN – Fernando de Noronha Archipelago *vs.* RA – Rocas Atoll *vs.* SPSP – Saint Peter and Saint Paul Archipelago), (b) time of day distribution (day *vs.* night) and (c) temporal distribution (thermal stress *vs.* no thermal stress).

than that of the Fernando de Noronha Archipelago and the Rocas Atoll. Patterns of biomass accumulation or increased production near islands have been frequently described (*e.g.,* Duarte et al., 2014; Hamner and Hauri, 1981; Lavaniegos et al., 1998; Lira et al., 2014). In general, the zooplankton biomass recorded near the islands of FN, RA and SPSP is considered high in relation to that of the open ocean off Northeast Brazil (Mafalda Jr and Souza, 2007; Neumann-Leitão et al., 2008), and corroborating studies show the surroundings of these areas are true "oases of life in the desert ocean" (Soares et al., 2017; Tchamabi et al., 2017). The oligotrophy of the tropical Atlantic is a consequence of a permanent thermocline; however, some areas, such as those located around the islands, have resurgence spots and tropical gyres that favor an increase in pelagic, benthic and nektonic productivity (Table 2).

The high zooplankton biomass recorded in SPSP is an indicator of high biological productivity, which is associated with the fact that SPSP represents an important area for highly migratory pelagic species that find refuge and food for their growth and survival in this environment (Morato et al., 2010). The high biological productivity has led this island system to be considered an ecologically or biologically significant area (EBSA), in accordance with the Convention on Biological Diversity (Soares and Lucas, 2018).

Some hypotheses were suggested by von Bröckel and Meyerhöfer (1999) to justify the high biological productivity existing around SPSP: **(1)** The fact that certain species of fish (*e.g.,* flying fish) search the rocks during the spawning season to obtain substrate for their eggs (information corroborated by our results because a considerable number of fish eggs were observed in the samples, contributing to an increase in zooplanktonic biomass - non-quantified data); additionally, **(2)** other species of fish feed on the benthic community, which provides favorable conditions because of the supply of material caused by the strong influence of local currents. This hypothesis was reinforced by Díaz et al. (2009) in a study that recorded high values of zooplankton biomass occurring in SPSP, and these high values were attributed to the reproductive processes of benthic and nektonic organisms with larval

phases in the plankton, verified by the high abundance of Brachyura zoeas and fish larvae. Finally, **(3)** nutrient enrichment events are responsible for pelagic and benthic life productivity around SPSP.

According to Araujo and Cintra (2009), this enrichment occurs constantly below a depth of 90 m, promoting the increase in nutrients at the base of the photic layer (100 m deep). This constant contribution results from subsurface action, occurring through the interaction of the Equatorial Undercurrent (EUC) with the topography of the island (W–E), causing instability downstream of the EUC's influence, forming eddies and causing upward and downward vertical movements of fluids. Upward vertical movements on the east side of the SPSP indicated small areas of potential submerged topographic upwelling (Araujo and Cintra, 2009). The sampling of the present study in the SPSP occurred in the dry season. During this period, the ITCZ moves farther north of the archipelago due to the intensification of the SE trade winds, which strengthens the SEC. The EUC is also directly influenced by the SE trade winds, becoming deeper and stronger from June to September (Macena and Hazin, 2016). Therefore, we suggest that the largest zooplanktonic biomass recorded for SPSP is a result of the local upwelling effect induced by the presence of the island contributing to an increase in biological productivity around the SPSP. Our results are supported by Pérez et al. (2005), who justified the high concentrations of chlorophyll-*a* occurring between June and August in the SPSP area as the influence of local circulation and the displacement of the ITCZ to the north, which reduces the cloud cover over the area.

In 2005, Díaz et al. (2009) carried out zooplankton sampling in SPSP during the dry and rainy seasons, registering the highest values of zooplanktonic biomass during the rainy season (January to May). During this period, the SE trade winds weakened, reducing the intensity of the westward flowing SEC in the area (Macena and Hazin, 2016) and creating favorable conditions for the retention/recruitment of larvae near SPSP, contributing to the increase in the zooplankton biomass (Araujo and Cintra, 2009). This increase in the concentration of organisms in the rainy season around SPSP attracts large pelagic filters,

Table 1

Multifactorial analysis of variance (MANOVA) results for natural logarithm of Log (x + 1) transformation was used to meet the assumptions of heterogeneity of data (Levene's test) of zooplankton biomass. Differences are considered significant if $p < .05$ (in bold).

(A) Factorial MANOVA

Source	Df	MS	F	p
		Zooplankton biomass (mg.m^{-3})		
Spatial (1)	2	4.55	10.24	**< 0.05**
Interannual (2)	1	2.48	5.57	**< 0.05**
Time of day (3)	1	5.18	11.64	**< 0.05**
Transect (4)	1	0.004	0.01	> 0.05
Spatial * Interannual	2	1.95	4.40	**< 0.05**
Spatial * Time of day	2	0.15	0.34	> 0.05
Interannual * Time of day	1	0.35	0.80	> 0.05
Spatial * Transect	2	0.51	1.15	> 0.05
Interannual * Transect	1	0.31	0.71	> 0.05
Time of day * Transect	1	0.05	0.12	> 0.05
Spatial * Interannual * Time of day	2	0.10	0.22	> 0.05
Spatial * Interannual * Transect	2	0.39	0.89	> 0.05
Spatial * Time of day * Transect	2	0.46	1.04	> 0.05
Interannual * Time of day * Transect	1	0.05	0.11	> 0.05
1 * 2 * 3 * 4	2	0.11	0.25	> 0.05
Error	70	0.44		

(B) Bonferroni *post hoc*	
FN	Thermal stress < No thermal stress
RA	Thermal stress > No thermal stress
SPSP	Thermal stress < No thermal stress
Thermal stress	RA < FN < SPSP
No thermal stress	RA < FN < SPSP

The factors tested were (a) spatial (FN *vs.* RA *vs.* SPSP), interannual (thermal stress *vs.* no thermal stress), time of day (day *vs.* night) and transect (upstream *vs.* downstream) effects on zooplankton biomass, and (b) Bonferroni tests on significant interaction terms for zooplankton biomass. *p* values in bold are significant.

such as the whale shark (*Rhincodon typus*) (Macena and Hazin, 2016). Melo et al. (2012) investigated the zooplankton biomass during the rainy season, which is considered a productive period in SPSP, but the average recorded by the authors (53.85 ± 30.65 mg m^{-3}) was lower than that observed in our study. We suggest that this difference may be related to the sampling method (subsurface trawls) and net mouth diameter (30 cm) used by Melo et al. (2012). It is difficult to directly compare the results from different studies because of the differences in sampling methods (*e.g.*, net mesh size, net mouth diameter), timing (*e.g.*, day/night) and natural fluctuations of the zooplankton community (Dias et al., 2010; Wu et al., 2011).

High concentrations of phosphate around SPSP are also considered an important source of energy input for this remote archipelago, although this water enrichment occurs seasonally and on a small spatial scale. In the plutonic rocks of the SPSP, abundant excrements from seabirds are deposited, and these seabirds use the island to feed and reproduce, including species such as the booby (*Sousa leucogaster*), the black noddy (*Anous minutus*) and the brown noddy (*Anous stolidus*) (Vaske-Jr et al., 2010). These seabirds act as biological pumps between the marine and terrestrial ecosystems, and their excrements are recognized as "guano", a material rich in phosphorus (P) (Otero et al., 2018). During the period of increased precipitation at SPSP caused by the ITCZ, a high input of phosphorus to the sea from leaching contributes to an enhanced primary and secondary productivity of the marine areas adjacent to the SPSP (Schaefer et al., 2009).

The proximity of the SPSP to the equatorial divergence zone, a high productivity area, and the seasonal occurrences of phytoplankton blooms in the eastern Equatorial Atlantic affect local pelagic and benthic productivity (Hastenrath and Lamb, 2004). There are also effects on the allochthonous contributions that SPSP receives, where at 28°W, a fresh water wedge found between 0 and 10°N up to 75 m in depth was linked to the intrusion of the Gulf of Guinea's rivers advected by the northern branch of the South Equatorial Current (nSEC) (Longhurst, 1995). All of these effects and interactions are also considered probable explanations for the high productivity of this small and remote island system.

It is clear that climate change has serious repercussions on the dynamics of coastal and marine ecosystems, as well as associated economic impacts (Rossi and Soares, 2017). In the present study, the period under thermal stress (2010) was associated with a significantly lower biomass than the period without thermal stress (2012 and 2014). A downward trend in zooplankton biomass in the Gulf of Guinea has been suggested as a result of the impact of climate change (Wiafe et al., 2008). Piontkovski and Castellani (2009) registered a decreasing trend of zooplankton biomass in the tropical Atlantic, pointing mainly to two factors: (1) the expansion of tropical species distribution due to the extension of the 'tropical belt' and (2) the reduction in primary productivity as a consequence of the thinning of the thermocline in response to global warming. Although our study has too few years to draw definitive conclusions regarding the climate connections, it points to significant interannual variability in zooplankton biomass around marine protected islands in the tropical Atlantic Ocean. Thus, the lower biomass recorded in the period with thermal stress indicates an impact on the zooplankton biomass stock and may affect the abundance and distribution of fish around FN, RA and SPSP in the future, with important regional impacts on secondary productivity and fisheries.

The Rocas Atoll presented a high biomass value in the period with thermal stress, contrary to what was observed for FN and SPSP in the same period. Observational data and numerical modeling were used to investigate oceanic current wakes surrounding Fernando de Noronha Island and Rocas Atoll (Tchamabi et al., 2017). FN and RA are under the influence of the flow to the west of the central branch of the South Equatorial Current (cSEC) (see Fig. 2). Sampling in 2010 occurred at the end of July and beginning of August, a period in which the cSEC strengthens over the islands (Tchamabi et al., 2017). The result of cSEC strengthening, flowing westward and being interrupted by FN and RA generated a current wake, with the formation of eddies downstream of these islands. This process acts to cool waters at the base of the mixed layer depth, inducing high productivity downstream of these islands (Tchamabi et al., 2017). The accumulation of mesozooplankton in a wake area as a causative mechanism of the "island-mass effect" was verified in the coastal waters around the Canary Islands (Hernández-León, 1991). The ecological connectivity between FN and RA has already been demonstrated, showing the role of RA as a stepping-stone and reservoir for marine organism species to be transported from FN (Rocha, 2003; Sampaio et al., 2004; Tchamabi et al., 2018). The sampling at FN in 2010 occurred in a period of maximum retention of larvae, with organisms transported towards RA as a consequence of the cSEC intensification and maximum recruitment in RA, thus enabling the development of individuals in this productive area (Tchamabi et al., 2018). Fernando de Noronha Archipelago is considered the largest archipelago in Brazil, covering a shallow platform area equivalent to 160.5 km^2 (Hachich et al., 2015). Rocas Atoll is 124 km from the Fernando de Noronha Archipelago and 700 km from the Saint Peter and Saint Paul Archipelago (Hachich et al., 2015). Thus, we suggest that the highest zooplankton biomass recorded in RA in the period with thermal stress originates from autochthonous sources (*e.g.*, as a consequence of local physical events such as current wakes recorded during this period in the area and responsible for the increase in local planktonic productivity) and allochthonous sources (*e.g.*, organisms supplied by FN *via* zonal currents) (Russell et al., 2005).
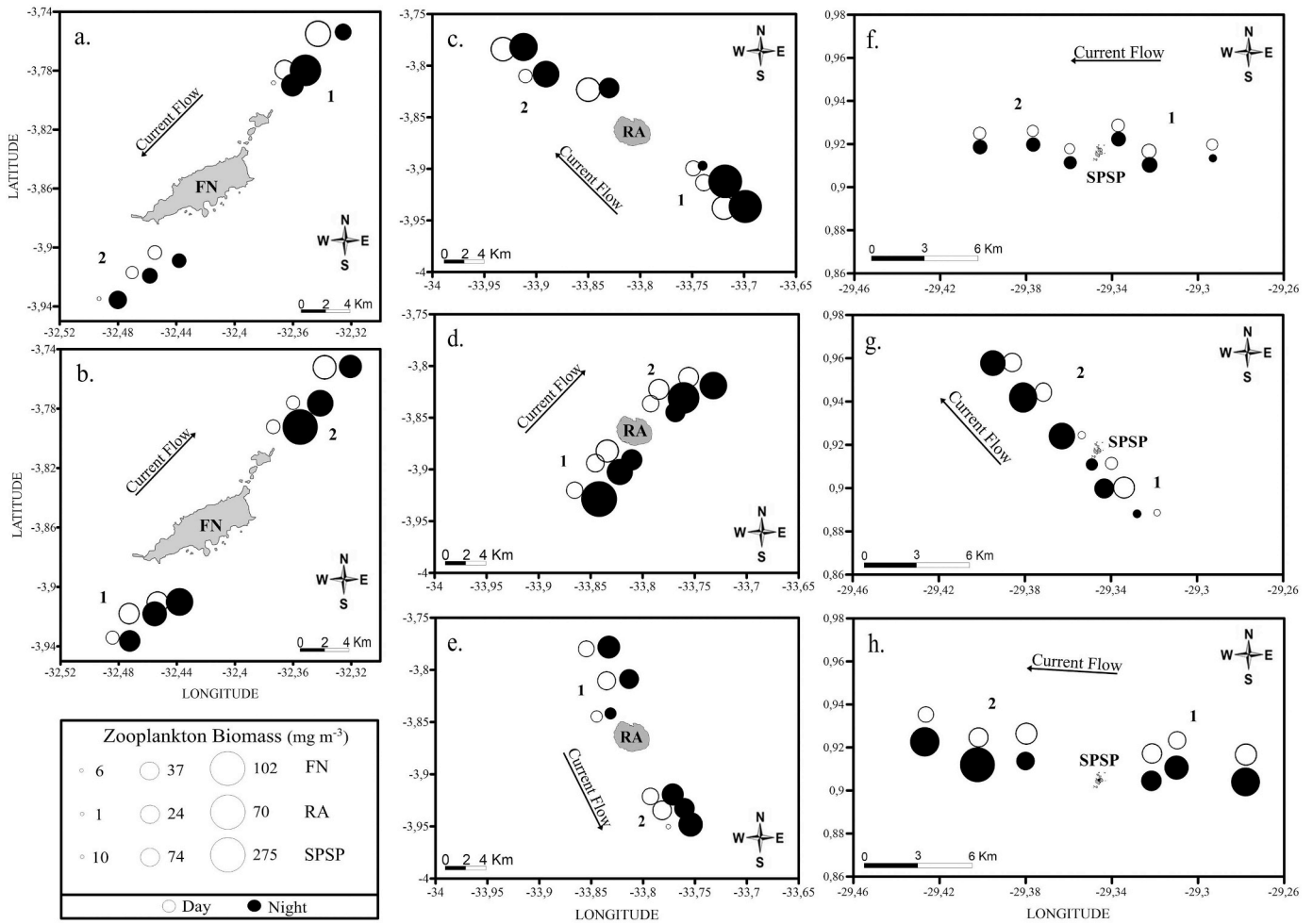
Fig. 6. Spatial distribution of the zooplanktonic biomass (mg.m^{-3}) around the marine protected islands of the tropical Atlantic: (a) and (b) / FN - Fernando de Noronha Archipelago in 2010 (thermal stress) and 2012 (no thermal stress); (c); (d); (e) / RA - Rocas Atoll in 2010 (thermal stress), 2012 and 2014 (no thermal stress); (f); (g) and (h) / SPSP - Saint Peter and Saint Paul Archipelago in 2010 (thermal stress), 2012 and 2014 (no thermal stress). 1 (upstream transect) and 2 (downstream transect).

Table 2
Zooplankton wet biomass (mg.m^{-3}) (average ± SD) recorded for some tropical environments.

Study area	Hauls	Mesh size (µm)	N	Average (± sd)	Seasonal period	Time period
[1]FN	Oblique	300	12	29.85 ± 21.81	Dry	July/August 2010
[1]FN	Oblique	300	12	44.73 ± 23.00	Dry	July 2012
[1]RA	Oblique	300	12	28.19 ± 19.53	Dry	July/August 2010
[1]RA	Oblique	300	12	28.68 ± 16.86	Dry	July 2012
[1]RA	Oblique	300	12	15.87 ± 8.49	Dry	August 2014
[1]SPSP	Oblique	300	12	32.14 ± 9.41	Dry	July/August 2010
[1]SPSP	Oblique	300	12	72.74 ± 58.72	Dry	July 2012
[1]SPSP	Oblique	300	12	15.87 ± 8.49	Dry	August 2014
[2]FN	Neuston	500	72	19.16 ± 14.73	Dry	July/August 2010
[3]SPSP	Subsurface	300	20	78.40 ± 38.80	Rainy	May and June 2005
[3]SPSP	Subsurface	300	36	118.80 ± 116.20	Dry	September and October 2005
[4]SPSP	Subsurface	300	20	53.85 ± 30.65	Rainy	May 2008
[5]South Atlantic gyre	Vertical or oblique	178 and 200	118	79.00 ± 62.00	Summer–autumn	1968 to 1992 (June to November)
[5]Eastern tropical Atlantic	Vertical or oblique	178 and 200	115	132.00 ± 66.00	Summer–autumn	1968 to 1992 (June to November)
[5]Western tropical Atlantic	Vertical or oblique	178 and 200	96	212.00 ± 202.00	Winter–spring	1968 to 1992 (December to May)
[5]Tropical gyre	Vertical or oblique	178 and 200	75	379.00 ± 461.00	Winter–spring	1968 to 1992 (December to May)

Source –[1]Present study; [2]Lira et al. (2014); [3]Díaz et al. (2009); [4]Melo et al. (2012); [5]Finenko et al. (2003).

Our collections found higher zooplankton biomass during nighttime than in daytime. We believe that the vertical migration performed by zooplankton was the main factor responsible for these differences. Hays et al. (2001) suggested the existence of a significant movement of organisms away from the surface of the ocean as a result of the diel vertical migration (DVM) of zooplankton. Changes in daily biomass of different size fractions revealed that the DVM was stronger in larger animals (Hays et al., 2001). This observation is explained by the greater susceptibility of larger animals to visual predators and, therefore, the need for these animals to descend into deeper and darker ocean waters (Rodriguez and Mullin, 1986). Thus, our results are consistent with the evidence presented because the differences found for the zooplankton biomass in the present study may be the result of the mesh size we used (300 μm), favoring the capture of larger animals. Our hypothesis is reinforced by recording a considerable increase in the occurrence of siphonophores (non-quantified data) in the nighttime samples of the present study. Lira et al. (2014) studied the zooneuston community with a 500-μm mesh size net in tropical Atlantic island environments and found that the neustonic biomass was significantly higher at night. Thus, the results of these studies support our hypothesis that the differences in zooplankton biomass between day and night in the studied islands are caused by the contribution of animals with larger body sizes at night.

5. Conclusion

This study represents the first comparative analysis of the productive potential of important marine protected islands of the tropical Atlantic. Nevertheless, the task of objectively differentiating the spatial, interannual and time-of-day heterogeneity causes identified in our results remains difficult because it requires long sampling programs. The findings described here, including the high zooplanktonic biomass recorded for the remote St. Peter and St. Paul, explains remarkable aggregations of pelagic fish species, particularly tuna (*Thunnus albacares*) and wahoo (*Acanthocybium solandri*), in that region, which makes it a target for industrial fisheries, either legal or illegal (Macena and Hazin, 2016). For this reason, intense debates between the Brazilian government and the scientific community took place and seem far from reaching an appropriate resolution (see Soares and Lucas, 2018; Giglio et al., 2018). It is important to highlight the lower zooplankton biomass observed in 2010 (thermal stress), which is considered an apparent effect of the increase in SST (°C) recorded in this year, but a long-term time series (preferably > 10 years) is needed to further expand the present findings. Differences between day and night were also recorded. The verified high nocturnal biomass was suggested as a result of the vertical migration performed by organisms with a larger body size, which are considered strong migrants. However, it is important to conduct studies with vertical sampling aiming to investigate the day/night variation in zooplankton size spectra. Thus, our results represent particularly useful tools to improve strategic plans for sustainable island management.

Declaration of Competing Interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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