

## SPATIAL AND NYCTHEMERAL DISTRIBUTION OF THE ZOONEUSTON OFF FERNANDO DE NORONHA, BRAZIL

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### ABSTRACT

Island environments drastically modify the hydrodynamics of ocean currents and generate strong vertical turbulence. This leads to an upward transport of nutrient-rich waters, thus increasing the biomass of plankton in these oceanic marine environments. The objective of this study was to assess the biomass and density of the zooneuston communities in relation to the upper and lower layers (epi-/hyponeuston), the nycthemeral variation (day/night), the currents in relation to the island (downstream vs upstream), and the distance from the island, focusing on the spatial variability. Samples were taken in July and August 2010 with a David-Hempel neuston net (Hydro-Bios) with a mesh size of 500  $\mu\text{m}$ . Twenty-one taxa were recorded. The most abundant taxa were Copepoda, Chaetognatha, Teleostei (eggs) and Hydrozoa. This is the first record of phoronid larvae for the waters of the Tropical Atlantic. For both layers, density and biomass were significantly higher at night. Density and biomass were always significantly higher in the upper (epineuston) layer than in the lower (hyponeuston) layer. This was probably due to a zooneuston aggregation at the surface and massive vertical migration from deep waters at night, leading to increased abundances at night in both neuston layers.

### RESUMO

Ambientes insulares são responsáveis pela modificação da hidrodinâmica das correntes oceânicas e por gerar turbulência vertical. Esta faz com que águas da camada inferior ricas em nutrientes sejam elevadas à região superior da coluna de água, aumentando a biomassa do plâncton local. O objetivo deste trabalho foi avaliar a biomassa e a densidade e das comunidades do zoonêuston em relação às camadas superior e inferior da coluna de água (epi/hiponêuston), à variação nictemeral (dia/noite), corrente superficial predominante (jusante/montante) e à distância da ilha, com foco na variabilidade espacial do plâncton. Amostras foram realizadas de julho a agosto de 2010 com uma rede de nêuston David-Hempel (Hydro-Bios) com malha de 500  $\mu\text{m}$ . Vinte e um táxons foram registrados, sendo os mais abundantes Copepoda, Chaetognatha, Teleostei (ovos) e Hydrozoa. Apresenta-se também o primeiro registro de larvas de Phoronida para o Atlântico Tropical. Para ambas as camadas, a densidade e a biomassa foram significativamente mais elevadas durante a noite e também significativamente maiores no epinêuston. Este fato provavelmente ocorreu devido à agregação do zoonêuston na superfície do oceano e à forte migração vertical a partir de camadas profundas durante a noite, levando a um aumento das abundâncias dos organismos nesse período, em ambas as camadas neustônicas.

Descriptors: Neuston, Island Mass Effect, Zooplankton, Phoronid Larvae, Small-Scale Vertical Distribution, Tropical Atlantic.

Descritores: Nêuston, Efeito Ilha, Zooplâncton, Larvas de Phoronida, Distribuição Vertical em Pequena Escala, Atlântico Tropical.

### INTRODUCTION

Oceanic island environments of the Tropical Atlantic have been intensively studied regarding their zooplankton diversity and productivity (HOLTHUIS et al., 1980; KOETTKER et al., 2010; BRANDÃO et al., 2012a, b; MACEDO-SOARES et al., 2012). These

studies have revealed a higher biomass and diversity of zooplankton in waters close to these islands as compared to those of open-water oceanic regions. Some of these studies have suggested that these spatial patterns in oligotrophic areas are due to an “island mass effect” (DOTY; OGURI, 1956). This term refers to a disturbance produced by an island

environment that changes the dynamics of ocean circulation around these areas, and causes the increase of the production of plankton biomass in these environments (DOTY; OGURI, 1956, HERNÁNDEZ-LEÓN, 1988, MACEDO-SOARES et al., 2012).

The biomass and diversity of plankton, besides being directly associated with the availability of nutrients, are related to various other physical, chemical and biological factors. These factors lead to specific horizontal and vertical distributions of these communities in oceanic environments (ANGER, 2001; GIBSON, 2003).

The community associated with the air-water interface and which comprises a surface layer of approximately 1 m depth is known as the neuston (ZAITSEV, 1971). This community has been mainly studied for its ichthyoneuston (fish larvae and eggs, ELDRIDGE et al., 1978; GRUBER et al., 1982; EKAU et al., 2001). Studies involving temperature, wave action, solar radiation and marine waste/pollution show a negative influence of these factors on the neuston community due to their extreme exposure (HOLDWAY; MADDOCK 1983; DAVENPORT; REES, 1993; RAWLINSON et al., 2005). In this context, research on the temporal and spatial structure of the zooneuston can provide the baseline for the comparative monitoring of the structure of these planktonic organisms and reflect changes in the environment.

The neuston of waters close to oceanic islands has only been studied for fish eggs and larvae (LESSA et al., 1999) and for the marine insect

*Halobates* sp. (CHENG; SCHMITT, 1982), thus this study contributes about the other groups of the zooneuston of these unique and highly productive environments. In the literature, there is no information on how neustonic invertebrates are distributed in the water column at different periods of the day off oceanic islands.

The objective of this study was to investigate the oceanic zooneuston communities off Fernando de Noronha, and to test the following hypotheses: that there is greater density and biomass during the night than in the daytime, at the ocean surface (epineuston) than in the subsurface layer (hyponeuston), downstream as compared to upstream, and higher close to the island, forming a community structure gradient around the island.

## MATERIAL AND METHODS

### Study Area

The Fernando de Noronha Archipelago (Figs 01 and 02) is located in the Tropical Atlantic, approximately 345 km off the Brazilian coast (03°51' S and 32°25' W). This island environment presents one main island and 20 other smaller islands and islets, being part of a complex system of currents and crosscurrents flowing mainly in an East-West direction, generally under the influence of the South Equatorial Current (RODRIGUES et al., 2006).

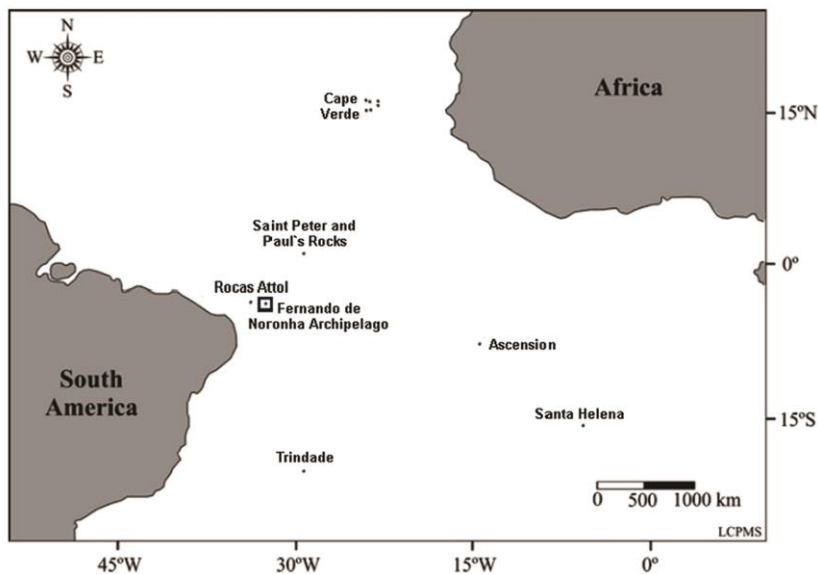


Fig. 1. Location of the Fernando de Noronha Archipelago and adjacent oceanic islands. Adapted from Brandão et al. (2012a).

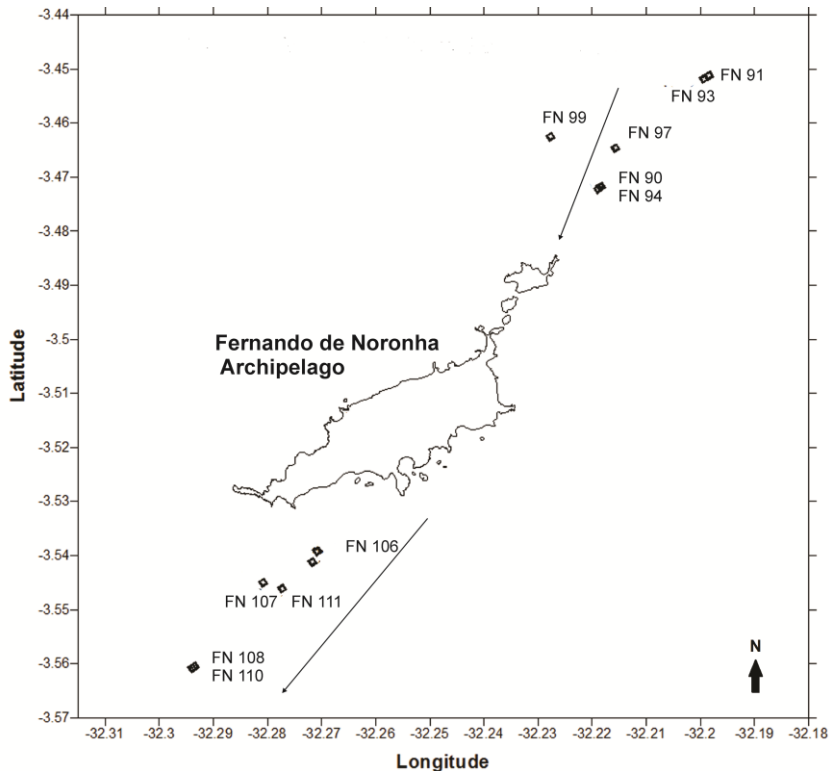


Fig. 2. Map of the Fernando de Noronha Archipelago with sampling stations along two transects: one transect downstream and one upstream in relation to the prevailing surface current (indicated by arrows), in July-August 2010.

#### Sampling Strategy

Samples were collected in July and August 2010 on board the Oceanographic Vessel *Cruzeiro do Sul* (of the Brazilian Navy). Dominant surface currents, as established from on-site ADCP data, were from northeast to southwest. To test the existence of an island effect, two transects were defined off the archipelago (Fig. 2): transect 1, which was upstream (before the island effect), and transect 2, which was downstream (after the island effect).

A David-Hempel aluminum catamaran (Hydro-Bios, Kiel, Germany) was equipped with two superposed nets, each with a rectangular mouth (two nets, each being 29.3 cm wide x 15.2 cm deep) and a 500  $\mu\text{m}$  mesh plankton net. Haul duration was always 20 minutes at a speed of 2-3 knots. The upper net was trimmed to be exactly centered at the air-water interface, and was thus sampling, on average, the epineuston (surface) layer from the surface to 7.6 cm depth, while the lower net sampled the hyponeuston (subsurface) layer from 7.6 cm to 22.8 cm depth. A flowmeter (Hydro-Bios) was placed in the center of the lower net to determine the towed distance and thus the water volume filtered by both nets. After each

haul, both samples were fixed separately with 4% formaldehyde that had previously been buffered with sodium tetraborate ( $0.5 \text{ g} \cdot \text{L}^{-1}$ ). Temperature and salinity data were obtained at each station with a CTD (Seabird 911-Plus).

#### Data Analysis

Biomass was calculated based on the wet weight of each sample (wet samples were weighed on preweighed 120 micron sieves, in g), divided by the filtered volume ( $V$ ) that was calculated by:  $V (\text{m}^3) = A (\text{m}^2) \cdot D (\text{m})$ . The mouth area ( $A$ ) of the lower net, that was totally submerged, was  $A_{\text{lower}} = 15.2 \text{ cm} \cdot 29.3 \text{ cm} = 0.045 \text{ m}^2$ . Since half of the upper (epineuston) net was kept above the water, the effective mouth area of this net was  $A_{\text{upper}} = 7.6 \text{ cm} \cdot 29.3 \text{ cm} = 0.022 \text{ m}^2$ . Towed distance  $D$  (m) was calculated based on the flowmeter's rotations.

Total density (sum of all individuals found in each sample / filtered volume) and biomass data were  $\log(x + 1)$  transformed to improve normality and homoscedasticity, as tested by Kolmogorov-Smirnov and Bartlett tests (ZAR, 1996). To test the hypotheses, one-way ANOVA, two-way ANOVA, and Student  $t$ -tests were performed using neuston total density and

biomass as dependent variables and combinations of several factors (epineuston vs hyponeuston, day vs night, upstream vs downstream, and three distances from the archipelago: D1: 1,946m - 2,600m, D2: 2,601m - 5,000m, D3: 5,100m - 8,665m). The Spearman correlation coefficient was used to verify possible correlations between abiotic variables (temperature and salinity) and neuston community descriptors (ZAR, 1996). A significance level of  $p < 0.05$  was required to reject the null hypotheses. All analyses were performed using STATISTICA (8.0).

## RESULTS

The zooneuston community was represented by 21 taxa that belonged to eight different phyla (Table 1). Hydrozoa, Copepoda and Chaetognatha occurred in all epineuston (surface layer) samples, while for the hyponeuston (subsurface layer), the groups recorded in all samples were Hydrozoa, Copepoda and Decapoda. Most taxa occurred in both vertical layers, except for bivalves, appendicularians and the marine insect *Halobates* sp., that occurred in the epineuston only.

Copepoda was the most abundant group in the epineuston and hyponeuston, with average densities of  $9.32 \pm 4.79$  and  $3.57 \pm 2.23$  ind  $m^{-3}$ , respectively, followed by Chaetognatha ( $4.49 \pm 2.53$  and  $0.91 \pm 0.99$  ind  $m^{-3}$ ), fish eggs ( $2.77 \pm 5.62$  and

$1.07 \pm 1.90$  ind.  $m^{-3}$ ) and Hydrozoa ( $1.96 \pm 1.12$  and  $0.88 \pm 0.79$  ind.  $m^{-3}$ ).

Phoronid larvae were recorded for the first time in the Tropical Atlantic in this study, albeit in very low abundance (average of  $0.006 \pm 0.02$  and  $0.001 \pm 0.005$  ind.  $m^{-3}$ , for epi- and hyponeuston, respectively, Table 1) and frequency, occurring at only two offshore stations on the upstream transect (stations 94 and 97). A total of only 5 individuals were found.

The total density of the zooneuston showed a mean of  $14.13 (\pm 10.19)$  ind. $m^{-3}$  and varied from the minimum of  $1.73$  ind. $m^{-3}$  at the hyponeuston during the day to a maximum value of  $37.66$  ind. $m^{-3}$  in the epineuston at nighttime. Biomass showed a mean of  $19.16 (\pm 14.73)$  mg. $m^{-3}$  and varied from a minimum of  $3.0$  mg. $m^{-3}$  in the hyponeuston during the day to a maximum of  $66.97$  mg. $m^{-3}$  in the epineuston at nighttime.

Significant ( $p < 0.05$ ) differences between the two vertical layers (epi- / hyponeuston) were detected for all community parameters (Table 2). Density and biomass showed higher values in the epineuston layer (Figs 3 and 4 - Box-Plot Chart), showing a significant accumulation at the air-water interface. Differences between day and night were significant for density and biomass (higher values at night, Table 2). The interactions between the two factors (day / night and the two layers) were not significant (Table 2), showing a constant accumulation on the air-water interface, that was independent of day and night.

Table 1. Mean density, maximum density, and relative abundance (%) of the Zooneuston community off Fernando de Noronha Archipelago (Tropical Atlantic) in July and August 2010. Samples were taken from the epineuston (surface to 7.6 cm depth) and from the hyponeuston layer (7.6 cm to 22.8 cm depth).

Taxa	Epineuston (0-7.6 cm)			Hyponeuston (7.6-22.8 cm)		
	Mean (ind. $m^{-3}$ )	Max. (ind. $m^{-3}$ )	RA (%)	Mean (ind. $m^{-3}$ )	Max. (ind. $m^{-3}$ )	RA (%)
Foraminifera	0.43	1.12	1.99	0.02	0.03	0.29
Hydrozoa	1.96	1.12	9.1	0.88	0.80	12
Anthozoa	0.21	0.27	0.95	0.01	0.02	0.14
Bivalvia	0.003	0.01	0.01	-	-	-
Gastropoda	0.60	0.48	2.8	0.17	0.29	2.3
Cephalopoda	0.007	0.02	0.03	0.0008	0.002	0.01
Polychaeta	0.07	0.08	0.32	0.007	0.02	0.10
<i>Halobates</i>	0.003	0.009	0.01	-	-	-
Copepoda	9.32	4.80	43	3.57	2.24	49
Isopoda	0.006	0.02	0.02	0.02	0.08	0.32
Mysidacea	0.25	0.39	1.15	0.03	0.09	0.41
Euphausiacea	0.41	0.47	1.90	0.14	0.19	1.91
Amphipoda	0.28	0.25	1.28	0.11	0.14	1.55
Decapoda	0.56	0.48	2.6	0.25	0.19	3.4
Stomatopoda	0.004	0.009	0.01	0.006	0.01	0.08
Thaliacea	0.18	0.30	0.81	0.04	0.06	0.60
Chaetognatha	4.49	3.53	21	0.91	0.99	12
Appendicularia	0.003	0.01	0.01	-	-	-
Phoronida	0.006	0.02	0.02	0.001	0.005	0.02
Teleostei (larvae)	0.05	0.08	0.25	0.03	0.04	0.43
Teleostei (eggs)	2.78	5.62	13	1.07	1.90	12

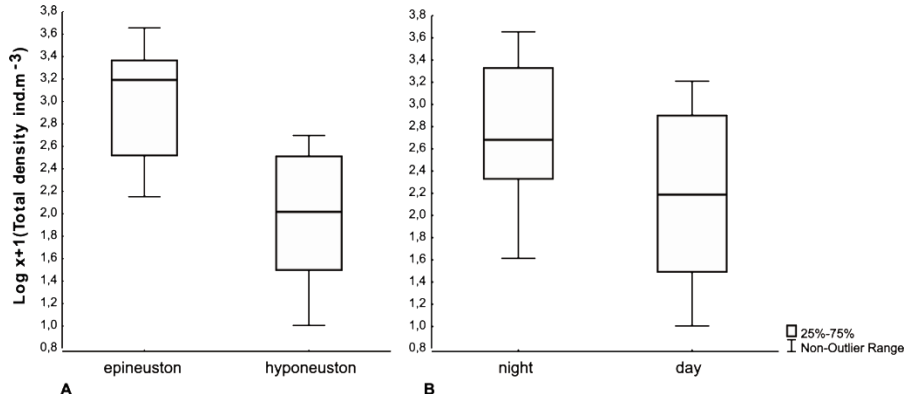


Fig. 3. Box-Plot (median and quartiles) representing the total density ( $\text{ind.m}^{-3}$ ) of the zooneuston community off Fernando de Noronha Archipelago from July to August 2010. Samples were taken from the epineuston (surface to 7.6 cm depth) and from the hyponeuston layer (7.6 cm to 22.8 cm depth) a): difference between the two vertical layers (epi- vs hyponeuston) b): nycthemeral variation (day vs night).

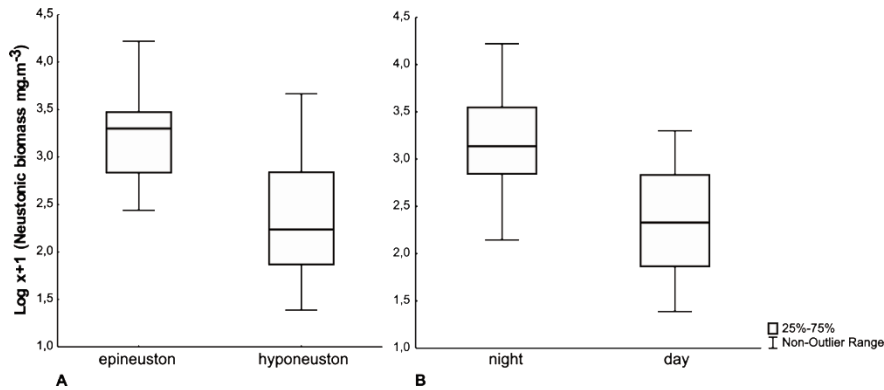


Fig. 4. Box-Plot (median and quartiles) representing the total biomass ( $\text{mg.m}^{-3}$ ) of the zooneuston community off Fernando de Noronha Archipelago from July to August 2010. Samples were taken from the epineuston layer (7.6 cm depth) and from the hyponeuston layer (7.6 cm to 22.8 cm depth) a): difference between the two vertical layers (epi- vs hyponeuston) b): nycthemeral variation (day vs night).

Table 2. Two-way ANOVA results for total biomass and total density of the neustonic community in relation to the vertical layers and the periods of the day. Samples were taken off the Fernando de Noronha Archipelago from July to August 2010. n.s.: not significant.

Factors	Community Parameters	F	p
	<b>Total Density</b>		
Layer (hypo. / epineuston)		31.29	< 0.001
Nycthemeral (day / night)		9.95	< 0.01
Layer x Nycthemeral		1.28	n.s.
	<b>Biomass</b>		
Layer (hypo. / epineuston)		24.38	< 0.001
Nycthemeral (day / night)		24.46	< 0.001
Layer x Nycthemeral		1.21	n.s.

The mesoscale spatial factors (upstream vs downstream and distance from the island) did not

show any significant effects on the community parameters tested (Figs 5 and 6). Biomass and total density were not correlated with temperature and salinity.

## DISCUSSION

One of the striking features of the zooneuston off the Fernando de Noronha Archipelago was the variation in biomass and density between neuston layers and different times of the day. This variability is partly explained by the aggregation of these planktonic organisms at the ocean surface and the nocturnal vertical migration, that is common in oceanic plankton communities (SCHLACHER; WOOLDRIDGE, 1995; RAWLINSON et al, 2005; BRANDÃO et al., 2012a, b).

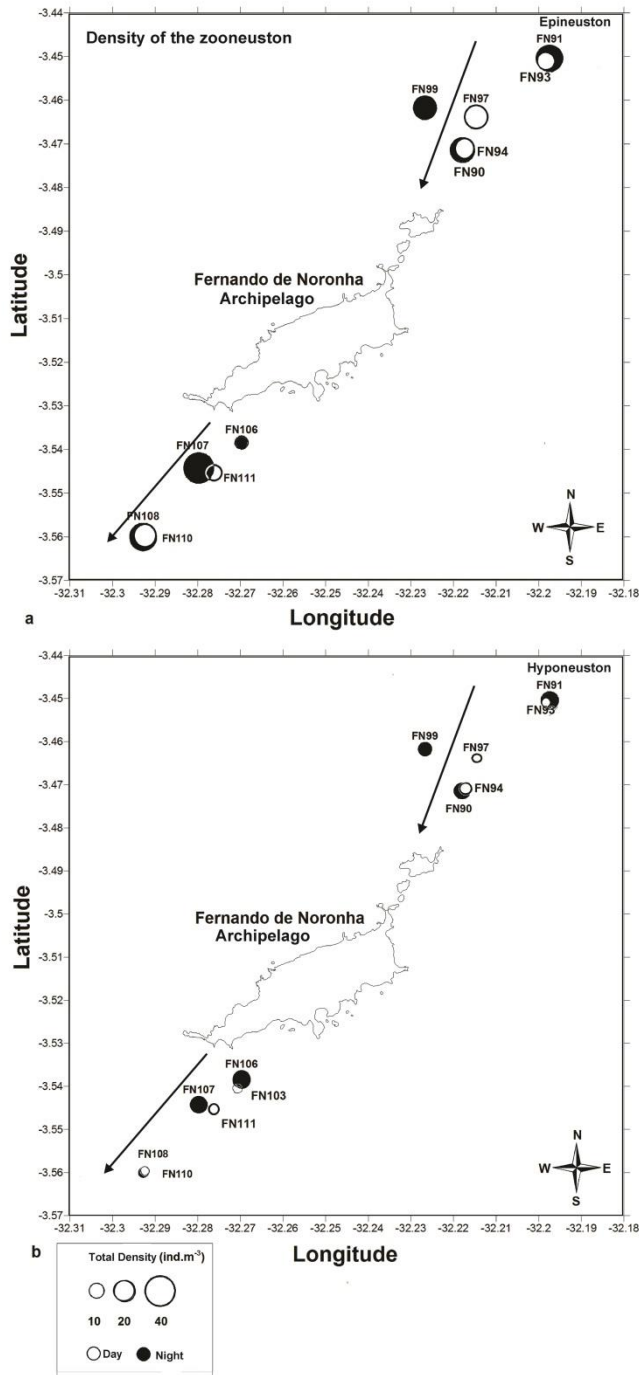


Fig. 5. Spatial distribution of the density of the zooneuston sampled off Fernando de Noronha Archipelago from July to August 2010. The areas of the circles are proportional to the total density of each sampled site. The arrows indicate the main current direction (averaged for 10 m depth) a): epineuston, b): hyponeuston.

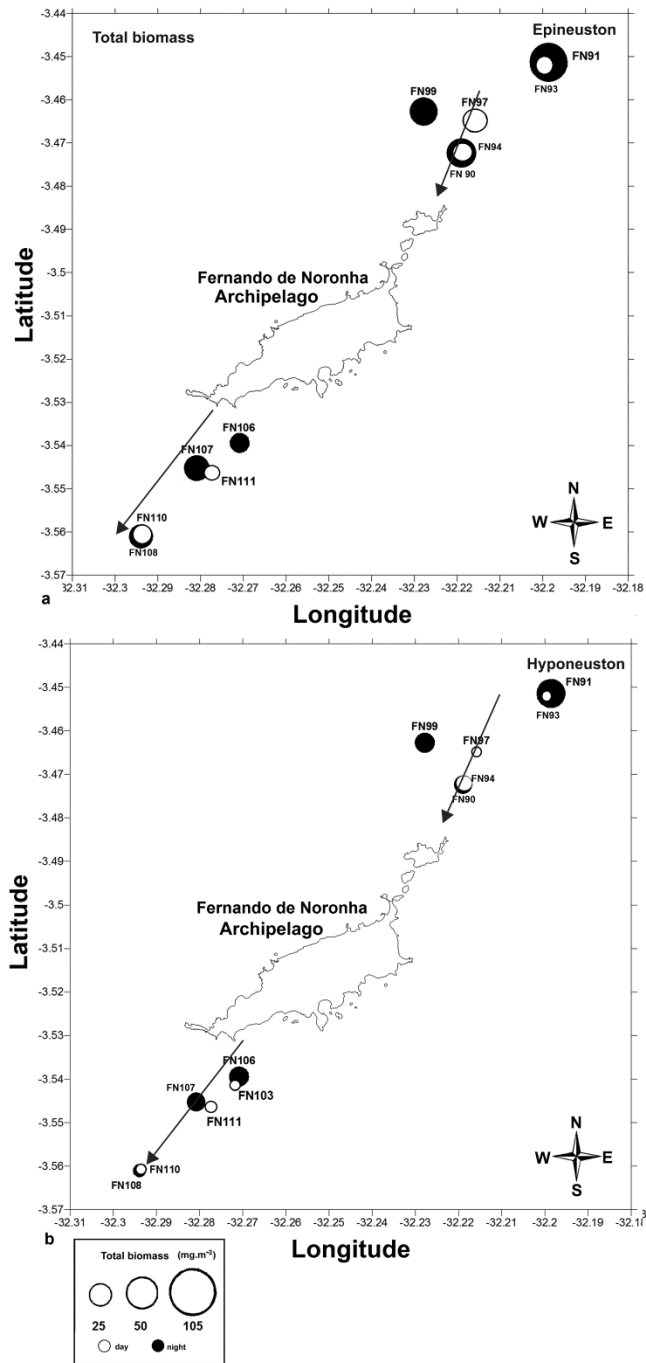


Fig. 6. Spatial distribution of the biomass of the zooneuston sampled off Fernando de Noronha Archipelago from July to August 2010. The areas of the circles are proportional to the total density of each sampled site. The arrows indicate the mainstream direction (averaged for 10 m depth). a): epineuston, b): hyponeuston.

This study was the first to quantify and test the variation in biomass and density between vertical layers for the zooneuston community. Much of the work on neuston compared these communities with those of other depths and the nycthemeral and seasonal variation, but not the differences between the two neuston layers (LOCKE; COREY, 1988; 1989; HASSETT; BOEHLERT, 1999; RAWLINSON et al., 2005). One detailed study on the small-scale vertical structure of the zooneuston was conducted by Olivar et al. (1998), who described vertical distributions in the epi- and hyponeuston layers for some selected fish and macrocrustacean taxa in the north-western Mediterranean. They showed specific vertical patterns for several fish species. Similarly to the present study, higher densities of portunid megalopae and isopods were found in the upper layer throughout their study. However, in contrast to the present study, they did not assess the whole community and did not apply any statistical tests to compare densities between layers or periods.

The vast majority of the taxa found in the neuston in this study have been previously recorded for the plankton of surrounding oceanic area, as off the Saint Peter and Saint Paul Archipelago (DIAZ et al., 2009; MELO et al., 2012) and Rocas Atoll (PINTO et al., 1997), which are oceanic island environments of the Tropical Atlantic, relatively close to the study area. However, plankton communities off these islands were sampled with other mesh sizes and at other depth strata than in the present study.

Phoronid larvae were recorded for the first time in the Tropical Atlantic in this study, albeit in very low abundance and frequency. This phylum has been cited for the plankton in the following areas of the subtropical Atlantic: São Paulo (Brazil) (FORNERIS, 1959) and Gran Canaria (Spain) (LANDEIRA, et al., 2009). The larvae of these organisms were also registered for the plankton off Reunion Island (Indian Ocean) and for the South China Sea and Black Sea (TEMEVERA, 2009). Records elsewhere in the Tropical Atlantic may not have been made before since the organisms are generally rare and occur at low abundances. Furthermore, there have been very few efforts of taxonomic identification directed towards these larvae.

The marine insect *Halobates* sp. had not been reported in previous studies conducted off the Saint Peter and Saint Paul Archipelago and Rocas Atoll, two other Brazilian oceanic islands in the Tropical Atlantic (PINTO et al., 1997; DIAZ et al., 2009; MELO et al., 2012). This is probably due to the use of plankton nets that were towed at subsurface, that thus do not sample the epineuston layer (DAVID, 1965). These sea-runners live exclusively in the habitat of the air-water interface and were thus recorded in the epineuston layer only. Despite being

the first record for the Fernando de Noronha Archipelago, the group had already been registered as a common species in research with oceanographic expeditions covering the waters of Tropical North and South Atlantic Ocean between 40°N and 30-40°S for the species *Halobates micans* Eschscholtz, 1822 (CHENG; SCHULZ-BALDESS, 1981; ANDERSEN; CHENG, 2004). Due to its wide distribution in oceanic waters the specimens found in this work probably are of the species *H. micans* (CHENG; SCHULZ-BALDES, 1981; ANDERSEN; CHENG, 2004). Bivalves and appendicularians were also found exclusively in the upper layer in this study, probably due to the accidental accumulation of gas bubbles in mantle cavities (bivalves), and mucous dwellings (appendicularians), which is probably a serious issue for many plankton and neuston organisms. We thus propose that some organisms may actually not be found at the surface due to an active adaptation, but rather accidentally. On the other hand, several taxa have been shown to be well adapted to the air-water interface and thus to inhabit only the epineuston layer, such as *Halobates* spp. and many gastropod and cnidarian species (CHENG; SCHMITT, 1982; CHURCHILL et al., 2011).

Copepods were the most common and abundant group in both neuston layers. These organisms generally dominate the surface waters of marine environments and are characterized as common animals in ocean ecosystems (NEUMANN-LEITÃO et al., 1999; PIONTKOVSKI et al., 2006), as corroborated for the Saint Peter and Saint Paul Archipelago (DIAZ et al., 2009; MELO et al., 2012) and Rocas Atoll (PINTO et al., 1997), relatively close to the study area. This group is always recorded as the dominant group in these environments and their high abundance and biomass is an indicator of the massive-island effect (MACEDO-SOARES et al., 2009). Even in different abiotic situations this group is dominant, such as in estuaries, neritic regions and other non-tropical regions (BOXSHALL, 1977; RAMAIAH; NAIR, 1997; NEUMANN-LEITÃO et al., 1999, 2008; PLOURDE et al., 2002; SILVA et al., 2003; CHAMPALBERT et al., 2005; RAWLINSON et al., 2005, KÂ; HWANG, 2011).

The most common and abundant groups after Copepoda were Chaetognatha, fish eggs and Hydrozoa. The Chaetognata and Hydrozoa, as well as Copepoda are holoplanktonic groups (BOXSHALL, 1977; NEUMANN-LEITÃO et al., 2008), which are those organisms that spend their whole life cycle in the water column (OMORI; IKEDA, 1984). These groups do not depend on spawning or export of larvae of benthic or nektonic organisms that inhabit the island, as occurs with meroplanktonic taxa, which are those organisms with larval stages in the water column and adults in other (e.g. benthic) habitats (OMORI;



IKEDA, 1984). The holoplanktonic groups that dominated the neuston community off the Fernando de Noronha Archipelago have also been observed elsewhere in the Atlantic Ocean (BOLTOVSKOY, 1999); the neritic and oceanic region off the Northeast of Brazil (CAVALCANTI; LARRAZABAL, 2004; NEUMANN-LEITÃO et al., 1999; 2008) and also off oceanic islands - as has been observed off the Saint Peter and Saint Paul Archipelago (DIAZ et al., 2009; MACEDO-SOARES et al., 2012; MELO et al., 2012) and Rocas Atoll (PINTO et al., 1997).

The high abundance of fish eggs may be related to the seasonal spawning period (July-August) of several fish species in this region. This is the spawning period for several species of Carangidae and Scaridae, two abundant families found between these and other oceanic islands of the Tropical Atlantic (SOUZA; MAFALDA Jr., 2008; SOUZA et al., 2010).

The Decapoda were also important in the zooneuston community. This group can be represented by meroplanktonic organisms such as brachyuran larvae and holoplanktonic decapod larvae like sergestids and luciferids (KOETTKER et al., 2010). The abundance of these larvae may increase during specific spawning periods, as has been recorded for the larvae of *Grapsus grapsus* (Brachyura: Grapsidae) that occur in the waters off Saint Peter and Saint Paul Archipelago (KOETTKER et al., 2010; BRANDÃO et al., 2012b).

Density and biomass of the zooneuston were significantly higher in the night period. This pattern has also been observed for decapod larvae off Saint Peter and Saint Paul Archipelago (KOETTKER et al., 2010; BRANDÃO et al., 2012a, b). However, other studies on the zooplankton community in this area have not shown a significant difference between densities at day and night (MELO et al., 2012). Nocturnal aggregation of zooplankton at the surface, as found in the present study, is a common feature of oceanic (e.g. ROE, 1974, FORWARD, 1988, RAWLINSON et al., 2005, MELO Jr. et al., 2007), inshore (LOCKE; COREY, 1988; 1989) and estuarine (e.g. SILVA et al., 2003, SCHLACHER; WOOLDRIDGE, 1995) waters. The most common explanation for this phenomenon is that zooplankton descend into the darkness in the daytime to avoid predation, and ascend during the night so as to feed in more productive surface layers (e.g. FORWARD, 1988).

The meso-scale spatial factors (upstream/downstream and distance from the coast) did not show any significant gradients in biomass and density. This may be due to mesoscale eddies formed close to oceanic islands, which disrupt any possible continuous gradients. Also, the maximum distance from the island may have been still too close to the islands to permit sampling of open-water oceanic

waters for comparison. This may, further, be due the large amount of holoplanktonic organisms (over 70%) recorded in this study, where the total biomass may not have been influenced by larvae and eggs that originated from the islands. A similar pattern has been observed in the Hawaiian Archipelago (HASSETT; BOEHLERT, 1999) that showed no significant difference in the plankton for the distances nor between the sides of the islands. Future analyses with emphasis on a detailed study of meroplanktonic taxa may be used to infer whether the input of such organisms from the islands exercises a positive influence on the waters downstream, as noted off the Canary Islands where the horizontal distribution of the groups of invertebrate larvae showed that the highest values of abundance occurred in an elongated zone around the island oriented in the general direction of the flow, on the downstream side of the island (LANDEIRA et al., 2009).

In conclusion, the zooneuston community in the study area presented a constant aggregation at the air-water surface (densities were always significantly higher in the epineuston layer than in the hyponeuston). Abundances were always higher at nighttime in both layers, probably due to vertical migration from deeper midwater layers.

Further studies are necessary to understand the distribution of specific taxonomic groups and species, to verify whether there is a retention and even a larval contribution originating from parental populations of benthic invertebrates from these islands, and to describe the life cycles of populations of oceanic islands.

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