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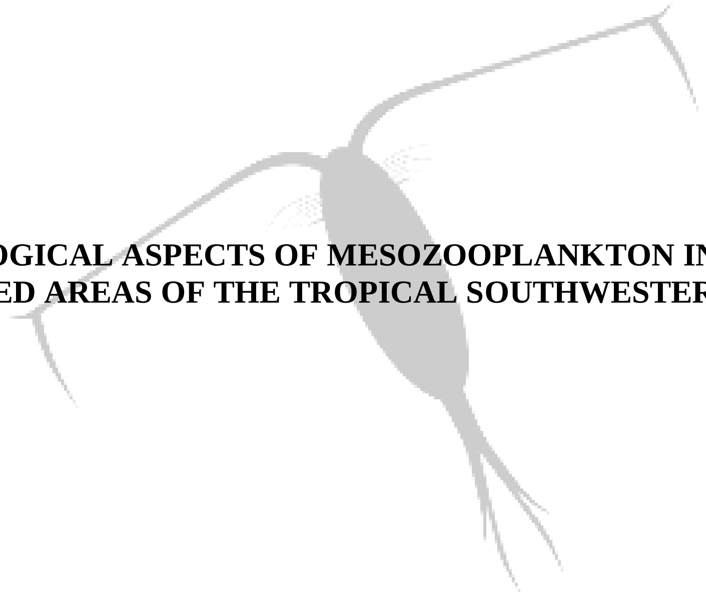
**RENATA POLYANA DE SANTANA CAMPELO**



# ECOLOGICAL ASPECTS OF MESOZOOPLANKTON IN MARINE PROTECTED AREAS OF THE TROPICAL SOUTHWESTERN ATLANTIC

FORTALEZA
2019

RENATA POLYANA DE SANTANA CAMPELO

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Tese apresentada ao Programa de Pós-Graduação em Ciências Marinhas Tropicais da Universidade Federal do Ceará, como parte dos requisitos para obtenção do título de Doutor em Ciências Marinhas Tropicais.

Orientador: Prof. Dr. Luis Ernesto Arruda Bezerra
Coorientadores: Profa. Dra. Sigrid Neumann Leitão & Prof. Dr. Mauro de Melo Junior.

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Aprovada em: ____/_____/_____

## BANCA EXAMINADORA

____________________________________________

Prof. Dr. Luis Ernesto Arruda Bezerra (Orientador)
Universidade Federal do Ceará (UFC)

____________________________________________

Prof$^{a}$. Dra. Cristina de Almeida Rocha Barreira (Interno)
Universidade Federal do Ceará (UFC)

____________________________________________

Prof. Dr. Marcelo de Oliveira Soares (Interno)
Universidade Federal do Ceará (UFC)

____________________________________________

Prof$^{a}$. Dra. Xiomara Franchesca Garcia Diaz (Externo)
Universidade Federal Rural da Amazônia (UFRA)

____________________________________________

Dra. Tatiane Martins Garcia (Externo)
Universidade Federal do Ceará (UFC)

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# RESUMO

A biomassa zooplanctônica (BZ), estrutura da assembleia de copépodes e a abundância e biovolume do mesozooplâncton são importantes descritores ecológicos no manejo e conservação dos recursos marinhos. No presente estudo, o efeito dos fatores espacial, interannual, turno de amostragem e posição dos transectos foram testados sobre os referidos descritores. Os resultados foram baseados em 96 amostras de zooplâncton coletadas em três anos (Julho/2010, Setembro/2012 e Agosto/2014) no entorno do Arquipélago de Fernando de Noronha (AFN), Atol das Rocas (AR) e Arquipélago de São Pedro e São Paulo (ASPSP). A BZ ($mg.m^{-3}$) variou significativamente no espaço, onde o ASPSP apresentou um valor médio significativamente maior comparado ao AFN e o AR. O efeito do turno de amostragem também influenciou a BZ, onde a média noturna foi maior que a diurna. O ano de 2010 registrou o menor valor significativo da BZ, onde sugerimos que possa ser uma séria repercussão associada à alta temperatura da superfície do mar registrada em várias partes do mundo e especialmente no Oceano Atlântico Tropical. A composição taxonômica foi representada por 195 espécies de copépodes freqüentemente encontrados em águas tropicais e subtropicais do mundo. A hipótese de heterogeneidade espacial foi comprovada, demonstrando que o ASPSP apresenta a maior abundância ($ind.m^{-3}$) de copépodes e a menor riqueza de espécies quando comparado aos outros sistemas insulares estudados. O aumento significativo na abundância de copépodes a jusante foi sugerido como consequência do "*Efeito de Massa insular*"**. A**mostras foram analisadas usando o sistema *ZooScan*. Um total de cinco classes de tamanho foram estabelecidas: 0,3 a 1 mm; 1 a 2 mm; 2 a 3 mm; 3 a 4 mm; 4 a 5 mm e > 5 mm. Os resultados mostram a resposta da abundância e biovolume ($mm.m^{-3}$) do mesozooplancton ao efeito espacial, cujos valores médios foram elevados no remoto ASPSP. Destacamos também que a fração (0,3 a 1 mm) dominou no ASPSP, o que indica que esta é a ilha biologicamente mais produtiva. Os menores valores de abundância e biovolume do mesozooplancton foram verificados em julho/2010. A alta contribuição de organismos de maior volume corporal à noite foi explicada pela alta abundância das classes de tamanho: 1 a 2 mm; 4 a 5 mm e > 5 mm, o que corresponde ao tamanho de organismos considerados fortes migradores. Além disso, é importante considerar que a menor fração (0,3 a 1 mm) não respondeu ao efeito do turno de amostragem, tampouco em relação à abundância ou biovolume, o que pode ser explicado pela predação ou ausência de migração vertical.

**Palavras-chave**: Distribuição. Biomassa. Abundância. Biovolume. Mesozooplancton. Ilhas.

# ABSTRACT

The zooplankton biomass (BZ), copepod assemblages structure, abundance, biovolume and size of mesozooplankton are important ecological descriptors in the management and conservation of marine resources. In the present study, the spatial, interannual, sampling time and transect positions effect were tested on these descriptors. The results were based on 96 samples of zooplankton collected in three years (July/2010, September/2012 and August/2014) in the surroundings of the Fernando de Noronha Archipelago (FNA), Rocas Atoll (RA) and St. Peter and St. Paul (SPSPA). The ZB ($mg.m^{-3}$) varied significantly in space, where SPSPA had a significantly higher average value compared to FNA and RA. The effect of the sampling time also influenced the ZB, where the nighttime average was higher than the daytime. The year 2010 registered the lowest significant value of ZB, where we suggest that it could be a serious repercussion associated with the high temperature of the sea surface registered in several parts of the world and especially in the Tropical Atlantic Ocean. The hypothesis of spatial heterogeneity was demonstrated, showing that the SPSPA has the highest copepods abundance ($ind.m^{-3}$) and the lowest species richness when compared to the other island systems studied. The significant increase in copepods abundance downstream was suggested as a consequence of the *"Island Mass Effect*". Samples were analyzed using the *ZooScan* system. A total of five size classes were established: 0.3 to 1 mm; 1 to 2 mm; 2 to 3 mm; 3 to 4 mm; 4 to 5 mm and > 5 mm. The results show the abundance and biovolume ($mm.m^{-3}$) response of mesozooplankton to the spatial effect, whose average values were elevated in the remote SPSPA. We also highlight that the fraction (0.3 to 1 mm) dominated in the SPSPA, indicating that this is the biologically most productive island. The lowest values of abundance and biovolume of mesozooplankton were verified in July / 2010. The high contribution of organisms with higher body volume at night was explained by the high abundance of size classes: 1 to 2 mm; 4 to 5 mm and > 5 mm, which corresponds to the size of organisms considered to be strong migrators. Furthermore, it is important to consider that the smaller fraction (0.3 to 1 mm) did not respond to the effect of sampling time, nor in relation to abundance neither biovolume, which can be explained by the predation or absence of vertical migration.

**Keywords:** Distribution. Biomass. Abundance. Biovolume. Mesozooplankton. Islands.

# LISTA DE FIGURAS

## Caphter 1

Figure 1. Sampling stations in islands of the Tropical Atlantic. (a) RA – Rocas Atoll; (b) SPSP – Saint Peter and Saint Paul Archipelago; (c) FN – Fernando de Noronha Archipelago along two transects: 1 - upstream transect and 2 downstream transect as part of the project: CFI – 2010 (Camadas Finas I); CFII – 2012 (Camadas Finas II) and CFIV (Camadas Finas IV)........................................................................... 30

Figure 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, central and southern branches of the South Equatorial Current (SEC), and the North Brazil Current and its retroflection (NBC Retr.) (Adapted from Lumpkin and Garzoli, 2005). .......................................................................................................... 31

Figure 3. Anomalies. (a) zonal Wind U ($m.s^{-1}$), (b) Chl-a ($mg.m^{-3}$), (c) Sea Surface temperature (degree) and (d) zonal current U ($m.s^{-1}$) from 2008 to 2016 represented in red for RA, in black for FN and green for SPSP. Shaded areas indicate sampling years in the region of the Tropical Atlantic. ......................................................................... 34

Figure 4. Mean average. (a) zonal wind U ($m.s^{-1}$); (b) Chl-a ($mg.m^{-3}$); (c) Sea Surface temperature (degree) and (d) zonal current U ($m.s^{-1}$) in regional area which include FN, RA, SPSP between 2008 and 2015. ............................................................................ 35

Figure 5. Distribution. Box-Plot (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)......................................................................... 36

Figure 6. Transect position. Spatial distribution of the zooplanktonic biomass ($mg. m^{-3}$) on the around the protected marine islands of the Tropical Atlantic: (a) FN - Fernando de Noronha Archipelago in 2010 (thermal stress) and (b) Fernando de Noronha Archipelago in 2012 (no thermal stress); (c) RA - Rocas Atoll in 2010 (thermal stress); (d) RA - Rocas Atoll in 2012 (no thermal stress) and (e) RA – Rocas Atoll in 2014 (no thermal stress); (f) SPSP – Saint Peter and Saint Paul Archipelago in 2010 (thermal

stress); (g) SPSP – Saint Peter and Saint Paul Archipelago in 2012 (no thermal stress) and (h) SPSP - Saint Peter and Saint Paul Archipelago in 2014 (no thermal stress)...... 37

**Capther 2**

Figure 1 a) Sampling in the Marine Ecoregions (Tropical Southwestern Atlantic ocean) as part of the project: CFI – 2010 (Camadas Finas I - Circle in dark gray); CFII – 2012 (Camadas Finas II - Circle in light gray) and CFIV (Camadas Finas IV - White circle); b) Sampling stations in RA – Rocas Atoll; c) SPSP – St. Peter and St. Paul's Archipelago and d) FN – Fernando de Noronha Archipelago along two transects: 1 (transect upstream) and 2 (transect downstream) in relation to the prevailing surface current. ........................................................................................................ 56

Figure 2 Relative abundance (%) of copepod assemblages in FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSP (Saint Peter and Saint Paul Archipelago). Copepods classified according to body-sized: Small-sized (0.3 - 1.0 mm), Medium-sized (1 - 2mm) and Large-sized (> 2mm). ................................................. 60

Figure 3 Box-Plot (median and quartiles) representing difference on copepod abundance: a) Spatial variability of copepods abundance in Fernando de Noronha Archipelago (FN), Rocas Atoll (RA) and St. Peter and St. Paul's (SPSP); b) Transection position variability of copepods abundance. .............................................................. 61

Figure 4 Box-Plot (median and quartiles) representing difference in diversity index in the islands of the Fernando de Noronha Archipelago (FN), Rocas Atoll (RA) and St. Peter and St. Paul's (SPSP): a) Spatial variability of Margalef's richness; b) Spatial variability of Shannon-Winer diversity; c) Time of day variability of Shannon-Winer diversity. ....................................................................................................... 62

Figure 5 MDS ordination of the copepod assemblages in response to the: a) Spatial factor (FNA – Fernando de Noronha Archipelago (Light gray circle), RA - Rocas Atoll (Yellow circle) and SPSP – St. Peter and St. Paul Archipelago (Blue circle): b) Interannual factor (2010 - (Light gray circle); 2012 (white circle); 2014 (Black circle) in the Tropical Southwestern Atlantic Ocean. ................................................................ 66

Figure 6 Interannual difference on the most abundant species: a) *A. longicornis*; b) *S. danae*; c) *C. speciosus*; d) *N. minor*; e) *O. plumifera*; f) *F. gracilis*, g) *U. vulgaris*; h) *C. furcatus*; i) *E. marina*; j) *O. media* and k) *C. pavo* in the context of project *Camadas* *finas oceânicas* I (2010), II (2012) and III (2014) in FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago). ...... 67

**Caphter 3**

Figure 1 Sampling stations in the islands : a) RA – Rocas Atoll; b) SPSPA – Saint Peter and Saint Paul Archipelago; c) FNA – Fernando de Noronha Archipelago along two transects: 1 - upstream transect and 2 downstream transect as part of the project: CFI – July/2010; CFII – September/2012 and CFIV – August/2014. .................................... 96

Figure 2 Relative abundance (a) and relative biovolume (b) of dominant taxonomic groups in Marine Protected Area located in the Tropical Southwestern Atlantic - FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago). ........................................................................................ 99

Figure 3 Relative abundance (a) and relative biovolume (b) of dominant copepods in Marine Protected Area located in the Tropical Southwestern Atlantic - FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago). ......................................................................................... 100

Figure 4 Box-Plot (median and quartiles) representing the spatial distribution of abundance and biovolume. (a) Spatial *vs.* temporal interaction of abundance and biovolume (b) of mesozooplankton; Spatial distribution of abundance (c) and biovolume (d) of established size classes in FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago). ......................... 102

Figure 5 Box-Plot (median and inter-quartil range) representing the temporal distribution of abundance and biovolume. (a) temporal distribution of mesozooplankton abundance; (b) response of abundance of main taxa to the temporal effect; (c) temporal distribution of mesozooplankton biovolume and (d) response of biovolume of main taxa to the temporal effect. ........................................................................... 104

Figure 6 Box-Plot (median and quartiles). Representing the temporal distribution of abundance of size classes: (0.3 to 1.0 mm); (1 to 2 mm); (2 to 3 mm); (4 to 5 mm) and (> 5 mm). ......................................................................................... 105

Figure 7 Median and interquartile range of night/day mesozooplankton abundance and biovolume. (a) response of abundance of main taxa to the night/day effect; (b) response of mesozooplankton biovolume to the night/day effect; (c) response of biovolume of main taxa to the night/day effect ........................................................................ 106

Figure 8 Box-Plot (median and interquartile range). Night/day distribution of abundance (a) and biovolume (b) of size classes (0.3 to 1.0 mm); (1 to 2 mm); (2 to 3 mm); (4 to 5 mm) and (> 5 mm)........................................................................ 107

# LISTA DE TABELAS

## Capther 1

Table 1. Multifactorial Analysis of Variance (ANOVA) results for natural logarithm of Log (x + 1) transformation was used to meet assumptions of heterogeneity of data (Levene-test) of Zooplankton biomass........................................................................ 37

Table 2. Zooplankton wet biomass (mg.m$^{-3}$) (Mean ± SD) recorded for some tropical environments. ............................................................................................................ 43

## Capther 2

Table 1 Characteristics of the Marine Ecoregions (Tropical Southwestern Atlantic ocean): FNA (Fernando de Noronha Archipelago); RA (Rocas Atoll) and St. Peter and St. Paul's (SPSPA). (Modified from Barroso et al., 2016). ......................................... 55

Table 2 Summary of the: a) PERMANOVA, this analysis tests differences in quantitative taxonomic composition of copepods assemblage considering spatial, interannual, transect and time of day as factors. Differences are considered significant if *P (perm)* <0.01 (in bold). *d.f* = degrees of freedom; MS = average squares; P = probability associated with the Pseudo F statistic; b) Parwise comparisons for the significant spatial x interannual term for copepod assemblages. P (MC) = probability associated with the Monte Carlo randomization procedure. ......................................... 64

Table 3 Results of parwise test for copepod assemblage structure between the sampling year for island in the FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul's Archipelago. P(MC) = probability associated with the Monte Carlo randomization procedure.Symbol (*) = Data not sampled. ...................... 64

Table 4 One-way Anova and *pos-hoc* Tukey-HSD results for total abundance of the main copepods species in response to the interannual factor in FN (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSP (Saint Peter and Saint Paul Archipelago). ............................................................................................................ 65

**Caphter 3**

Table 1 Taxonomic composition of mesozooplankton (a) and copepods (b) identified from the Zooscan image system through samples collected around the Marine Protected Area of the Tropical Southwestern Atlantic: FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago). .......................... 108

Table 2 (a) Factorial ANOVAs testing the effects of space (FN *vs.* RA *vs.* SPSP), sampling time (day *vs.* night), temporal (2010 *vs.* 2012 *vs.* 2014) and transect to (upstream *vs.* downstream) on (i) mesozooplankton abundance and (ii) mesozooplankton biovolume, and (b) Tukey - HSD tests on significant interaction terms for (i) mesozooplankton abundance and (ii) mesozooplankton biovolume. ................ 111

Table 3 One-way Anova results for total abundance (a) and biovolume (b) of the main groups of the mesozooplankton in response to the spatial, temporal, sampling time and transection factors. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s (not significante). ...... 112

Table 4 Abundance and biovolume of mesozooplankton size classes in relation to the factors tested: a (spatial and transect) and b (temporal and sampling time). ............... 113

Table 5 One-way Anova results for total abundance (a) and biovolume (b) of mesozooplankton size classes in response to the spatial, temporal, sampling time and transection factors. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$........................................ 114

# SUMÁRIO

**GENERAL INTRODUCTION** .......... **17**

REFERENCES .......... 23

**CHAPTER 1 - Zooplankton biomass around Marine Protected Islands in the Tropical Atlantic Ocean** .......... **25**

ABSTRACT .......... 26
1. INTRODUCTION .......... 27
2. MATERIALS AND METHODS .......... 29
   2.1. Study Area .......... 29
   2.2. Sampling strategy .......... 31
   2.3. Remotely sensed data .......... 31
   2.4. Zooplankton sampling and analyses .......... 32
   2.5. Data analysis .......... 32
3. RESULTS .......... 33
   3.1. Climatic and hydrological conditions .......... 33
   3.2. Zooplankton biomass .......... 35
4. DISCUSSION .......... 38
   4.1. Climatic and hydrological conditions in the Tropical Atlantic .......... 38
   4.2. Zooplankton biomass .......... 39
5. CONCLUSIONS .......... 43
6. ACKNOWLEDGMENTS .......... 44
7. REFERENCES .......... 44

Supplementary material .......... 49

**CHAPTER 2 - Copepod assemblages in island environments from the Tropical Southwestern Atlantic: An explanation of distribution and diversity** .......... **50**

ABSTRACT .......... 51
1. INTRODUCTION .......... 52
2. MATERIAL AND METHODS .......... 54
   2.1. Study Area .......... 54
   2.2. Sampling strategy .......... 56
   2.3. Sampling and laboratory analyses .......... 57
   2.4. Data analysis .......... 57
3. RESULTS .......... 58
   3.1. Species composition .......... 58
   3.2. Total abundance of Copepods (ind. $m^{-3}$) .......... 60
   3.3. Species diversity .......... 61
   3.4. Copepods assemblage structure .......... 62
   3.5. Indicator species .......... 68
4. DISCUSSION .......... 69
   4.1. Copepod assemblage structure .......... 72
   4.2. Species diversity .......... 73
   4.3. Indicator species .......... 76
5. CONCLUSIONS .......... 77
6. ACKNOWLEDGEMENTS .......... 78
7. REFERENCES .......... 79

**CHAPTER 3 - Mesozooplankton abundance, biovolume and size in Marine Protected Areas in the Tropical Southwestern Atlantic .......................................... 89**

ABSTRACT .......... 90
1. INTRODUCTION .......... 91
2. MATERIALS AND METHODS .......... 94
  2.1. Study Area .......... 94
  2.2. Sample design .......... 96
  2.3. Field sampling and laboratory procedures .......... 97
  2.4. Zooscan analysis .......... 97
  2.5. Data analyses .......... 98
3. RESULTS .......... 98
  3.1. Mesozooplankton taxonomic composition .......... 98
  3.2. Hypothesis 1: Spatial heterogeneity .......... 100
  3.3. Hypothesis 2: Temporal heterogeneity .......... 103
  3.4. Hypothesis 3: The vertical migration effect .......... 105
  3.5. Hypothesis 4: The Island Mass Effect .......... 107
4. DISCUSSION .......... 111
  4.1. Mesozooplankton taxonomic composition .......... 111
  4.2. Hypothesis 1: Spatial heterogeneity .......... 112
  4.3. Hypothesis 2: Temporal heterogeneity .......... 116
  4.4. Hypothesis 3: The vertical migration effect .......... 118
5. CONCLUSIONS .......... 120
6. ACKNOWLEDGEMENTS .......... 121
7. REFERENCE .......... 121

**FINAL CONSIDERATIONS .......... 133**

**APPENDIX .......... 134**

Appendix I – Small-sacale distribution of the mesozooplankton in a Tropical insular system; .......... 134
Appendix II - Morphological abnormalities in *Corycaeus speciosus* Dana, 1849 (Copepoda, Cyclopoida) on an Equatorial Atlantic Island; .......... 134
Appendix III - Book chapter published in commemoration to the 20 years of research carried out in the Saint Peter and Saint Paul Archipelago .......... 134
I – Small-scale distribution of the mesozooplankton in a tropical insular system .......... 135
II - Morphological abnormalities in *Corycaeus speciosus* Dana, 1849 (Copepoda, Cyclopoida) on an Equatorial Atlantic Island .......... 149
III - Book chapter published in commemoration to the 20 years of research carried out in the Saint Peter and Saint Paul Archipelago .......... 153

# GENERAL INTRODUCTION

Zooplankton plays a key role in the structuring the pelagic ecosystem, (1) controlling phytoplankton production, (2) food source for higher trophic levels, (3) representing an important link between the classic trophic chain and the microbial loop (4) export particulate organic matter (POM), used by bacteria, and (5) excrete nutrients that can be recycled by phytoplankton (Figure 1) (Havens, 1998; Rivero, 2014).

These organisms are characterized by very short life cycles, which can last from weeks to months and are therefore considered as excellent indicators of changes caused by anthropic or climatic impacts (Hays *et al.,* 2005). Thus, according to their life cycle zooplankton is classified as meroplankton (those organisms that are planktonic only for a part of their life cycle, usually eggs and larvae, such as fish, echinoderms, cnidarians or molluscs) and holoplankton (those that are planktonic during their entire life cycle, e.g., copepods, ostracods, euphausiids) (Rivero, 2014). The most important representatives of the holoplankton are the copepods, small crustaceans dominant in the pelagic environment of several marine ecosystems, comprising 55-95% of the abundance and up to 80% of the total biomass of mesozooplankton (Brandini *et al.,* 1997).

Understanding the processes that create the distribution patterns of marine zooplankton has become increasingly important in the face of continued threats of habitat destruction, pollution, invasion of species and climate change (Robinson *et al*., 2011). There is great evidence that the ecological impacts of recent climate change and the responses of flora and fauna already reach a variety of ecosystems and organizational hierarchies, from species to community levels. This rapid change should to affect plankton growth with a significant impact on its distribution, diversity, abundance, biomass and size (Gorsky *et al.,* 2010). Therefore, continuous research projects on plankton will act as sentinels to identify current and future changes in marine ecosystems.

Estimates of abundance and biomass are indirect ways of identifying zooplankton production and are of fundamental importance to understand the ecological role of planktonic organisms in an ecosystem (Rodriguez and Mullin, 1986). The present thesis show the results on the distribution of zooplankton biomass, distribution of abundance, diversity and structure of epipelagic copepod assemblages, as well as the aspects related to the size/biovolume of mesozooplankton in protected tropical Atlantic island systems: Fernando de Noronha Archipelago, Rocas Atoll and St.Peter and St. Paul Archipelago. All this information were organized in chapters written according to the norms of the journals in which the articles will be submitted.

The body size limits prey-predator interactions and physiology, therefore plankton size spectra were named as synthetic descriptors of the structure and functioning of the planktonic community. The results of the intra-individual size spectrum (metabolism, growth, natural death) and inter-individual processes (predation, grazing, reproduction), lead to the transfer of energy from the smallest to the largest organism in a community (Zhou, 2006). Recently image systems and supervised classification tools have been developed to provide measurements of the size of any object. The semi-automatic Zooscan system provides robust estimates of zooplankton biovolume. The great technological innovation of the present study was the analysis involving the semi - automated measurement (*Zooscan*) of different morphological attributes of zooplankton organisms.

The waters of Tropical Southwestern Atlantic are characteristically oligotrophic and of low biological productivity, except in places where upwelling occur as in the surroundings of seamounts and oceanic islands (Lira *et al.,* 2014). Since these topographic features change the local hydrodynamics, through the combination of recirculation currents and upwelling, causing the “island-effect” (Doty and Ogury, 1956). This event contributes to an increase in planktonic productivity around these areas (which act as true "hotspots" of biodiversity) in the midle of the oligotrophic ocean (Boehlert, 1988). Thus, the presence of these features can cause retention of the plankton in the areas mainly downstream of the islands (Tchamabi *et al.,* 2017). In this way, the present study considered the position of the transects as an important factor in the distribution of ecological attributes of zooplankton in the islands of the tropical Atlantic.

The spatial, seasonal, interannual and day/night patterns of the distribution of marine zooplankton inspired ecological research in the Tropical Southwestern Atlantic. However, there is still a scarcity of information for the oceanic region of Northeast Brazil. Investigations on epipelagic copepods off the oceanic islands of the Tropical Southwestern Atlantic were reviewed by Brandini *et al.* (1997), these began in the late 1900s during the NOc cruise "Victor Hensen" within JOPS-II. Cavalcanti and Larrazabal (2004) provided information on macrozooplankton (with emphasis on

Copepoda) of the Exclusive Economic Zone of Northeast Brazil within the REVIZEE / NE II project. Neumann-Leitão *et al.* (2008) studied the distribution of mesozooplankton abundance and diversity (also highlighting the epipelagic copepods) in the neritic and oceanic region of the Tropical Southwestern Atlantic. Production data and abundance of copepod species considered key in the pelagic environment were provided by Miyashita *et al.* (*2009*) and Melo *et al.* (2012, 2014).

The present thesis is the result of the cooperation of two research projects: ***Camadas Finas Oceânicas ao largo do Nordeste do Brasil*** whose objective is to evaluate how the spatial-temporal heterogeneity of tropical marine environments can determine the response patterns of these environments and its resilience to climate change that will affect north-northeast Brazil in this century. The second project to which this thesis is linked is titled: ***Study of the balance of the carbon cycle in the coastal region and its potential ocean transport – with emphasis on the coast of Pernambuco*** (CaReCos) whose objective is to increase knowledge about the carbon cycle in the coastal region of Pernambuco and São Paulo, especially in the metropolitan region of Recife and Cananéia coast, with reference to the Fernando de Noronha Archipelago, a protected area in the Tropical Atlantic. The results presented in the thesis within the context of the CaReCos are referring to the beaches of the northern coast of the Island of Fernando de Noronha.

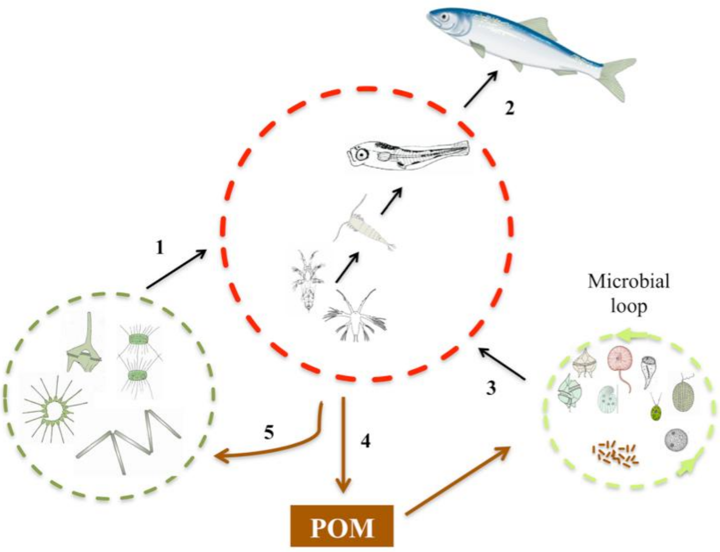

Figure 1. The importance of zooplankton in the marine ecosystem (Source: Rivero, 2014)

# Chapter 1

*Status - Submitted to Journal of Sea Research*

## General objective:

To assess the spatial (FN *vs.* RA *vs.* SPSP), temporal (Thermal stress *vs.* No thermal stress), time of day (Day *vs.* Night) and transection (Upstream *vs.* Downstream) differences around the protected marine islands of the Tropical Atlantic Ocean.

## Hypothesis:

- **Hypothesis 1**: The environmental characteristics of the island of St. Peter and St. Paul contribute to this remote archipelago presenting a zooplankton biomass significantly higher than Fernando de Noronha and Rocas Atoll;

- **Hypothesis 2**: The high sea surface temperature recorded in 2010 (thermal stress) in various parts of the world affected planktonic productivity around the protected marine islands in the tropical Atlantic;

- **Hypothesis 3**: The elevation of zooplankton biomass at night around the tropical islands occurs in response to the typical vertical migration behavior of zooplankton;

- **Hypothesis 4**: The protected side of the wind (downstream) of insular systems are areas of retention of the plankton thus increasing the biomass of zooplankton.

## Chapter 2

_Status - To be submitted to the Hydrobiology_

### General objective:

To determine the patterns of abundance, diversity and structure of pelagic copepod assemblages taking into account the geographic characteristics of the islands, years of sampling, time of day and position of the transects.

### Hypothesis:

- **Hypothesis 1**: The smallest and most isolated Archipelago of tropical islands in the world (SPSPA) presents a differentiated taxonomic composition, high abundance and low richness and diversity of epipelagic copepods in comparison to the Fernando de Noronha Archipelago and Rocas Atoll;

- **Hypothesis 2**: Interannual fluctuation of ecological estimators: abundance, diversity, richness and structure of epipelagic copepod assemblages are indicative of periods of increased productivity around the islands of the Tropical Southwestern Atlantic;

- **Hypothesis 3:** An increase in abundance, diversity, richness and differentiation in the taxonomic similarity of epipelagic copepod assemblages is expected at night as a response to vertical migration;

- **Hypothesis 4:** Downstream of tropical islands, there is a high abundance, a reduction in the diversity and richness, and a differentiated taxonomic composition of epipelagic copepod assemblages.

# Chapter 3

*<u>Status - To be submitted to the Journal of Marine Systems</u>*

## General objective:

The aim of the present study was to investigate the spatial, temporal, sampling time, and transect variability of the mesozooplankton abundance, biovolume, and size in Marine Protected Areas**.**

## Hypothesis:

- **Hypothesis 1:** There is high abundance and biovolume of small mesozooplankton, indicative of high productivity in surroundings of the island systems;

- **Hypothesis 2:** Temporal fluctuations of abundance and biovolume of mesozooplankton distribution are indicative of periods of higher or lower secondary productivity in surroundings of the island systems;

- **Hypothesis 3:** High abundance, biovolume, and body size of mesozooplankton occur during night because of vertical migration;

- **Hypothesis 4:** Downstream the Tropical Southwestern Atlantic Islands are places of plankton retention, implying higher abundances, and biovolume, especially from small mesozooplankton.

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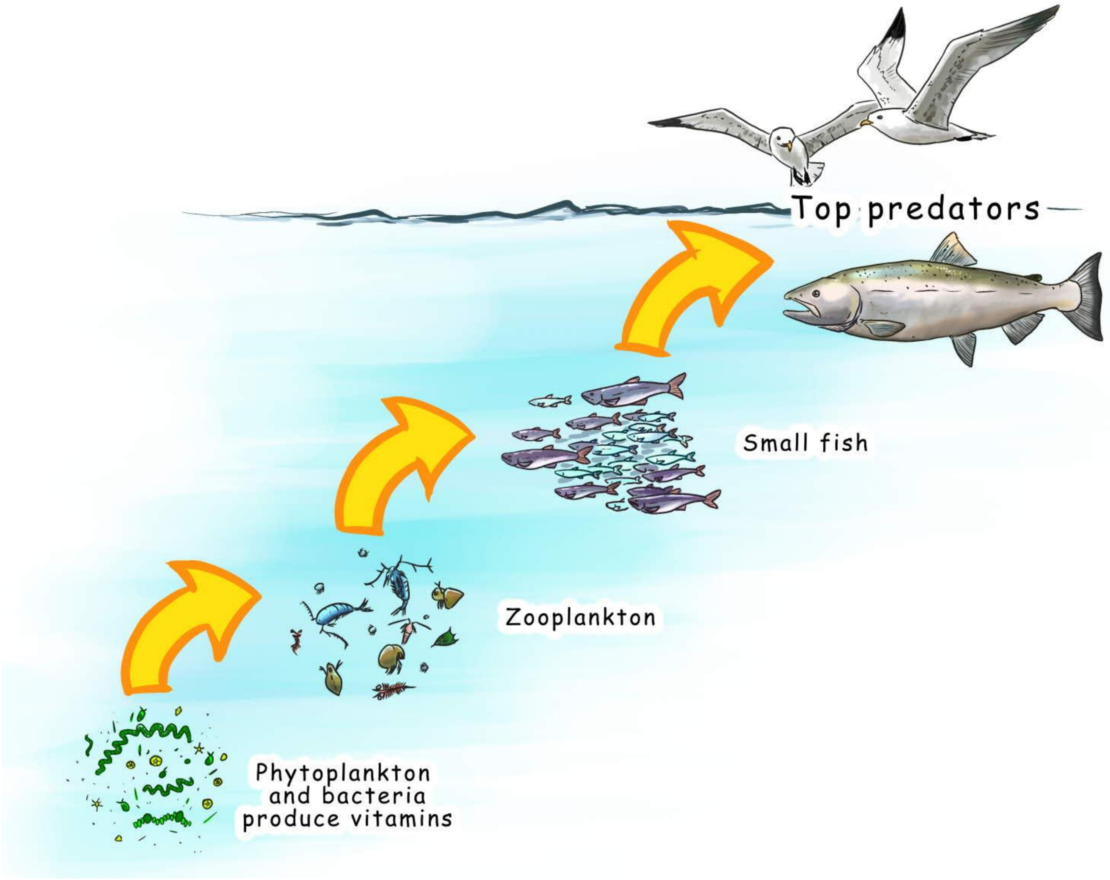
# CHAPTER 1 - Zooplankton biomass around Marine Protected Islands in the Tropical Atlantic Ocean



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# Zooplankton biomass around marine protected islands in the Tropical Atlantic Ocean

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## ABSTRACT

Zooplankton biomass (as wet weight) was studied around protected marine islands in the Tropical Atlantic Ocean. The results were based on 96 zooplankton samples collected during a 3-year period, where 2010 was considered the year under thermal stress, and 2012 and 2014 were considered as the years without thermal stress. The analysis of the data set showed that zooplankton biomass responded significantly to the spatial factor, where the smallest and most isolated archipelago of the tropical islands of the planet, Saint Peter and Saint Paul Archipelago (SPSP) corresponds to about twice the biomass of Fernando de Noronha Archipelago (FN) and three times that of Rocas Atoll (RA). The position of SPSP near the retroflection zone of the Amazon River plume, animal retention mechanisms and local hydrodynamic characteristics are pointed to as the main factors responsible for high pelagic productivity in this remote archipelago. The effect of time of day factor also influenced zooplanktonic biomass in these islands, where the nighttime mean was significantly higher than daytime. This increase was associated with the mesh size used in the present study (300 µm), which favors the capture of larger sized animals considered to be strong migrators. The year 2010 (period under thermal stress) recorded the lowest significant value of zooplankton biomass, which suggests that it is a serious repercussion associated with high sea surface temperature recorded in several parts of the world, and especially in the Tropical Atlantic Ocean, as a consequence of El Niño.

**Keywords:** Productivity, Island, “Oases”, Sea surface temperature

# 1. INTRODUCTION

Marine zooplankton plays a central role in the structuring of the pelagic trophic web and the biogeochemical cycling of carbon in the oceans (Piontkovski et al., 2003), contributing to the transfer of energy through the food chain, connecting the primary producers to the organisms of high 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 ocean is a requirement to estimate its contribution to global organic matter and energy flow through planktonic webs (Duarte et al., 2014).

The zooplankton biomass distribution varies on a scale of time and space (Brodeur et al., 1996), generating heterogeneous patches. Worldwide, much of this heterogeneity is the result of seasonal and geographic variations in nutrient availability, depth of the mixing layer 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 considered intrinsic characteristics of the zooplankton community (physiology and growth, buoyancy and behavior) also directly influence the distribution of zooplankton biomass in the world's oceanic ecosystems (Arashkevich et al., 2002).

Oceanic regions of tropical areas have suffered substantial environmental changes mainly caused by the effect of climate change (Piontkovski and Castellani, 2009), causing 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), in the Tropical Atlantic there is a lack of information due to logistic and funding restrictions, which inhibits the execution of long-term studies on plankton.

The Tropical Atlantic follows the oligotrophic pattern of warm oceans due to the permanent and deep thermocline that limits biological productivity, mainly by limiting the availability of nutrients (Macêdo et al., 2009). However, there are zones especially close to banks and islands that are an "oasis of life in an oceanic desert" (McClain, 2008). 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 of planktonic biomass (primary and secondary production) and fishery resources in the surroundings of these islands.

The interaction of the current with the topography of the islands and the existence of physical instability, inducing mainly downstream turbulences such as eddies, are known to affect the distribution of nutrients, Chlorophyll-a, primary production and fish larvae. Downstream of the oceanic islands there are areas of high zooplankton biomass favoring the retention of zooplankton (Rodríguez et al., 2001; Tchamabi et al., 2017). Another increase in zooplankton biomass is also expected at night in tropical marine ecosystems, due mainly 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 along the water column (Melo et al., 2012; Lira et al., 2014).

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. The FN archipelago presents the largest Brazilian area in oceanic islands, representing an area of extreme importance for conservation and constituting a great bank of food and reproduction for the marine fauna of the South Atlantic (Campelo et al., 2018a). The RA is the only atoll in the South Atlantic and one of the smallest on the planet, housing the main colony of seabirds and the second largest population of green turtles in the South Atlantic (Soares et al., 2011).

In terms of Brazilian environmental legislation, the Rocas Atoll was the first Marine Biological Reserve of Brazil, created in 1979, involving an area of approximately 360 km$^2$, which is set aside only for research and which is considered by UNESCO to be a natural world heritage site (Villaça et al., 2010). Saint Peter and Saint Paul is the smallest and most isolated Brazilian archipelago and plays a significant role in the life cycle of several species that spend an important stage of their migratory routes in this environment, either as a breeding area or as a feeding zone (Porto, 2006).

The few studies in tropical oceanic waters off Northeastern Brazil shows a biomass decrease from the island to offshore (Neumann-Leitão et al., 1999; 2000; Koettker et al., 2010; Tiburcio et al., 2011; Brandão et al., 2012; Macedo-Soares et al., 2012; Melo et al., 2012; Lira et al., 2014; Jales et al., 2015; Campelo et al., 2018b). In the present study, we considered zooplankton biomass (mg.m$^{-3}$) as an indicator of the productive potential of the marine protected areas of FN, RA and SPSP. Thus, our goal was to assess the spatial (FN *vs.* RA *vs.* SPSP), temporal (Thermal stress *vs.* No thermal stress), time of day (Day *vs.* Night) and transection (Upstream *vs.* Downstream) differences around the protected marine islands of the Tropical Atlantic Ocean.

## 2. MATERIALS AND METHODS

### 2.1. Study Area

Sampling was carried out in three tropical Atlantic island systems (FN, RA, SPSP) (Figure 1). These islands are Marine Protected Areas, created in June 1986, covering an area of 79.706 ha (Alves and Castro, 2006). The Equatorial South Current is the main current that transports warm and oligotrophic water to the tropical Atlantic oceanic region and bifurcates into the Northern Brazil Current (NBC) and the Brazilian Current (BC) (Stramma et al., 2005). The flow portion located between the Equatorial South Undercurrent and the Equatorial South 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 studied (Assunção et al., 2016) (Figure 2).

The Fernando de Noronha Archipelago (FN) (3º50’24”S and 32º24’48”W) (Figure 1) is constituted by 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: the rainy, between March and July, and the dry, between August and January. The tidal regime is semidiurnal, with a range of 2 to 3.2 m, and the prevailing winds are the Southeast trade, varying to the northeast with a mean intensity of 4.8 m.s$^{-1}$, from the surface to the level of 750 millibars (Mohr et al., 2009).

The Rocas Atoll (RA) (3°51’S and 33°49’W) (Figure 1) constitutes the top of an underwater mountain whose base is 4,000 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). Wind direction data indicate that prevailing winds occur throughout the year, with a mean frequency of 45% of measured days. 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 about 20% of the days (Kikuchi, 2002).

The Saint Peter and Saint Paul Archipelago (SPSP) (00°53’- 00°58’N and 29°16’- 29°24’W) (Figure 1) is the point belonging to Brazil closest to the African continent, at its closest point 937 km from Guiné-Bissau in Africa. It is formed by 15 islands (Becker, 2001), located above the line of the Equator and formed essentially 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 constant intensity of about 7 ms$^{-1}$ (Souza et al., 2013).

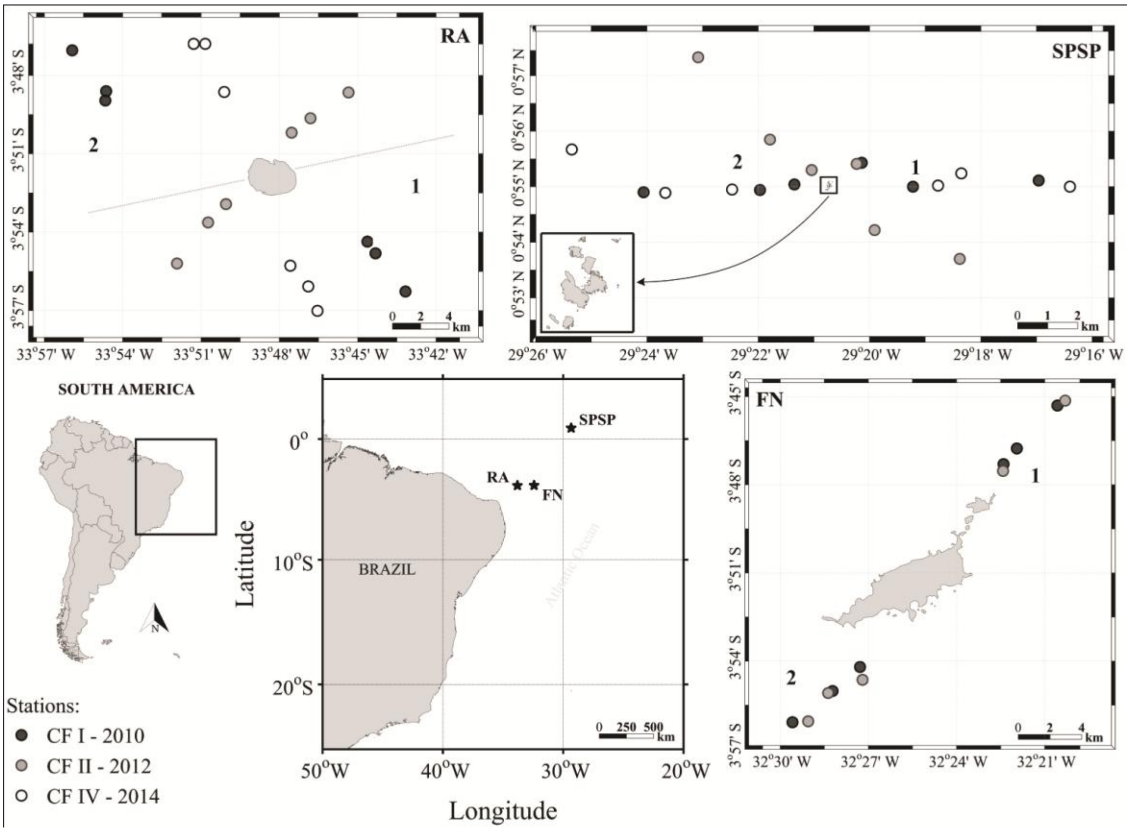

**Figure 1. Sampling stations in islands of the Tropical Atlantic.** (a) RA – Rocas Atoll; (b) SPSP – Saint Peter and Saint Paul Archipelago; (c) FN – Fernando de Noronha Archipelago along two transects: 1 - upstream transect and 2 downstream transect as part of the project: CFI – 2010 (Camadas Finas I); CFII – 2012 (Camadas Finas II) and CFIV (Camadas Finas IV).

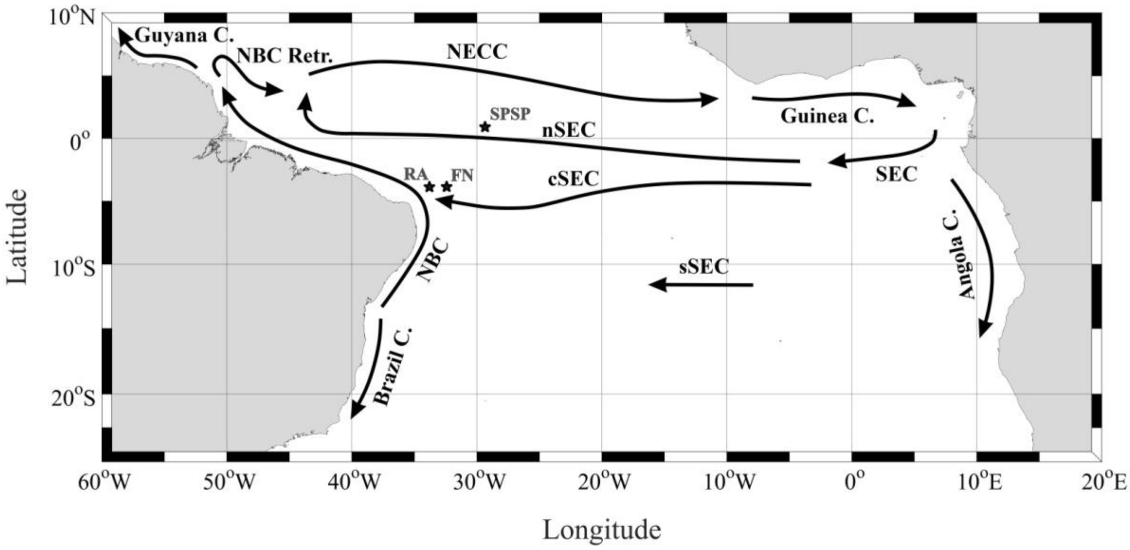

**Figure 2. Surface currents in the studied areas.** FN – Fernando de Noronha Archipelago, RA – Rocas Atoll and SPSP – Saint Peter and Saint Paul Archipelago, including the North Equatorial Current (NEC), North Equatorial Counter Current (NECC), northern, central and southern branches of the South Equatorial Current (SEC), and the North Brazil Current and its retroflection (NBC Retr.) (Adapted from Lumpkin and Garzoli, 2005).

### 2.2. Sampling strategy

The expeditions were carried out aboard the NHOc Cruzeiro do Sul of the Brazilian Navy, as part of the project "*Camadas finas*". Data were collected in July 2010 (thermal stress), September 2012 and August 2014 (No thermal stress) at FN, RA and SPSP (Figure 1). Sampling was performed during the day and night periods. Ninety-six samples were collected during the expeditions. An ADCP was used to obtain the current direction and velocity, and this information was used to establish two transects (1) upstream (before the island) and transect (2) downstream (after the island) in relation to the predominant surface current (Figure 1). In each transect three equidistant stations were marked.

### 2.3. Remotely sensed data

To describe the climatic and hydrological variability, the remote sensing data of temperature, chlorophyll-*a*, winds and current velocity were assessed in the region of Tropical Atlantic (60W-20W and 10S-10N). The Chlorophyll-*a* data was extracted from Copernicus database (http://marine.copernicus.eu/) with 4 km of resolution from 2008 to 2015 in order to have long data series for comparison. We extracted monthly Sea Surface Temperature (SST), surface zonal wind U (http://www.esrl.noaa.gov/psd/data/gridded/); these products are NCEP-NCAR reanalysis. The monthly products were obtained by the merging of MERIS, MODIS/AQUA, and VIIRS and SeaWiFS data in the 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 hauls were made using a "Bongo" cylindrical-conical net (mouth opening 0.6 $m^2$, mesh size 300 μm). The oblique trawls were made in "V", extending up to a depth of 75% of the local depth, or at most up to 200 m deep. A Hydro-Bios 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 5% buffered formalin-seawater solution.

In the laboratory all the samples were filtered in accumulators with mesh opening equivalent to 100 μm previously weighed on a scale with 0.001 mg precision for determination of the wet-weight (Newell and Newell, 1963). To avoid the effect of large particles that are not part of the plankton environment, such as macroalgae, pieces of ships paint and microplastics, these elements were removed from the samples before weighing.

### 2.5. Data analysis

Interaction effect of factors: spatial (FN *vs.* RA *vs.* SPSP), temporal (Thermal stress *vs.* No thermal stress), time of day (Day *vs.* Night) and transection (Upstream *vs.* Downstream) on zooplankton biomass were tested using the Multifactorial Analysis of Variance (ANOVA). Due to uneven spatial distribution of zooplankton the biomass data were transformed to the natural logarithm of $(X + 1)$ to stabilize the variance and reduce heteroscedasticity. The heterogeneity of variances was verified with the Levene test. When the biomass data satisfied the normality assumption and ANOVA results indicated significant effects, a Bonferroni *post-hoc* test was applied to identify where significant differences existed ($p < 0.05$). The parametric statistical analysis followed 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° of resolution), and current velocity U (with 1/3 of resolution variability) between 2008 and January 2016 are shown in Figure 3. We highlight 2010, 2012 and 2014, which correspond to the sampling years for different islands (Figure 3).

Spring 2010 was the period of significant effect of the El Nino-Southern Oscillation (ENSO) connections in the tropical Atlantic where was observed a weakening of the wind in relation of the wind variation for the previous year in the three islands (Figure 3a) lower concentration of chlorophyll-a (Figure 3b) associated to higher SST (Figure 3c).

We observed 1°C of positive SST anomaly from January to May 2010, and this value is the highest SST of the whole period of study in this region mainly at the three islands (FN, RA and SPSP) (Figure 3c). The higher anomaly of SST in 2010 is combined with a positive anomaly of wind (-1 to 3 m/s of anomaly) (Figure 3c and 3a). This pattern on SST associated to the wind is only observed after the El Ninõ of 2009. Lower means of Chlorophyll-a anomalies (Figure 3b) are associated with higher positive anomalies of SST from January to May 2010 (Figure 3c), which corresponds to the period of response of El Niño 2009 in the Tropical Atlantic ocean, especially for the islands.

We observed the alternance condition while the negative anomalies of SST are actually associated with the positive Chl-a, with a strong trend mainly around SPSP islands. The circulation around FN and RA is mainly from Eastern to Western, driven by the South Equatorial Current (SEC). Relatively negative values of zonal current U were observed (Figure 3d). SPSP is under the influence of the SEC and NECC, as can be observed in schematic Figure 2. The NECC flows from the Brazilian coast to the African coast, presenting positive values of zonal current.

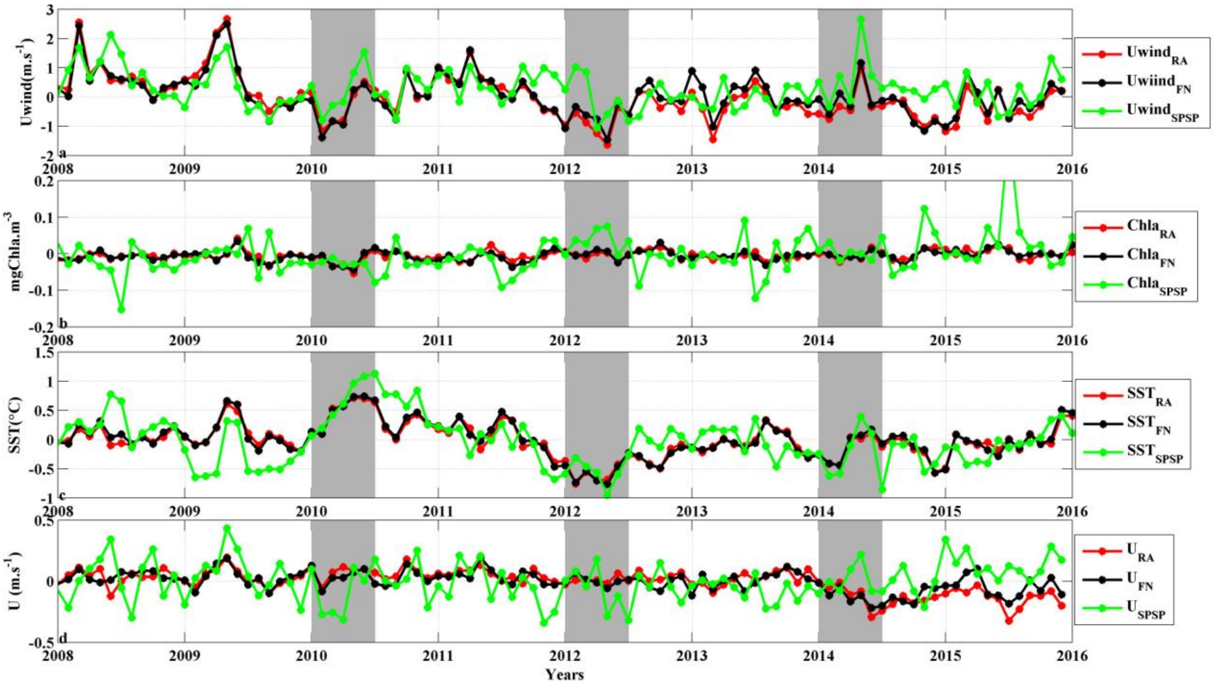

**Figure 3. Anomalies.** (a) zonal Wind U (m.s$^{-1}$), (b) Chl-a (mg.m$^{-3}$), (c) Sea Surface temperature (degree) and (d) zonal current U (m.s$^{-1}$) from 2008 to 2016 represented in red for RA, in black for FN and green for SPSP. Shaded areas indicate sampling years in the region of the Tropical Atlantic.

The means of zonal wind, zonal current, Chlorophyll-a and SST are presented in this section from 2008 to 2015 (Figure 4). In the Tropical Atlantic, the zonal wind is mostly negative for the three islands FN, RA and SPSP (Figure 4a). The dominant values of the W are mostly negative for FN, RA and SPSP, and this result confirms that the wind direction is essentially from the east to western.

The mean chl-a is ~ 0.1 mg.m$^{-3}$ around FN and RA islands, slightly lower than the concentration of Chl-a at SPSP island. We can observe the wake region in RA and FN in Figure 4b at the location of the white dot, which corresponds to the islands' position with Chl-a > 0.12 mg.m$^{-3}$. The two islands (FN and RA) have lower Chl-a values than the mean value in SPSP (~0.25 mg.m$^{-3}$) (Figure 4b). The mean SST shows that the SST variability of the region of three islands is ~27°C near FN, RA and SPSP islands (Figure 4c).

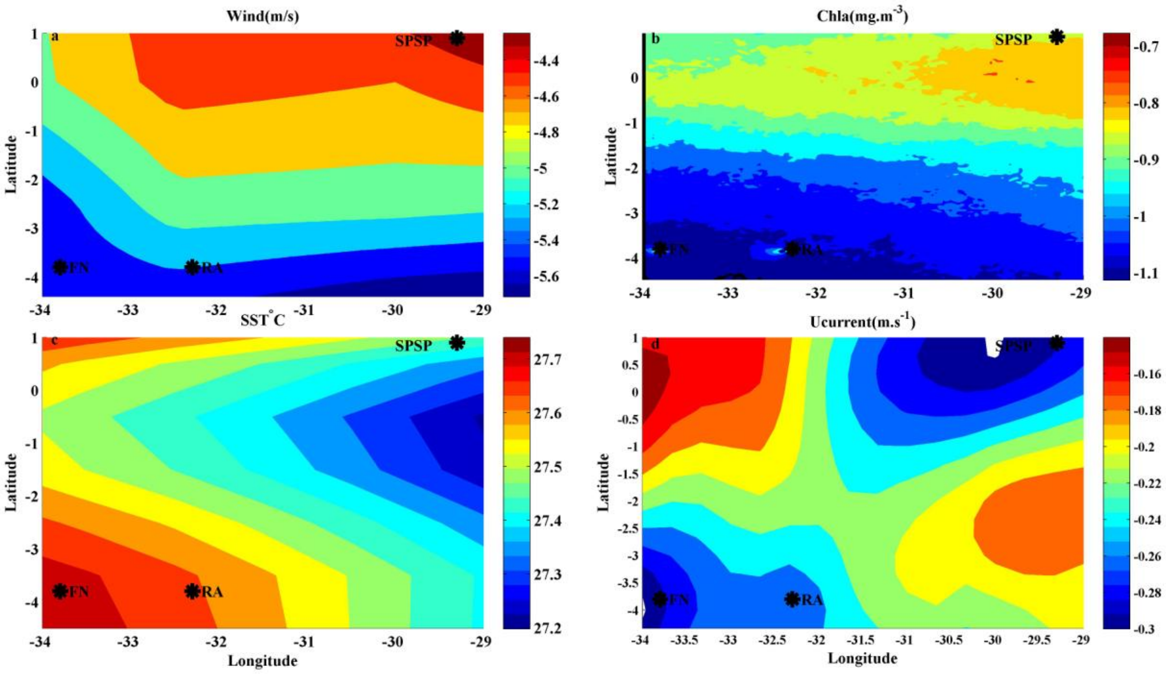

**Figure 4. Mean average.** (a) zonal wind U (m.s$^{-1}$); (b) Chl-a (mg.m$^{-3}$); (c) Sea Surface temperature (degree) and (d) zonal current U (m.s$^{-1}$) in regional area which include FN, RA, SPSP between 2008 and 2015.

### 3.2. Zooplankton biomass

The islands sampled differ in relation to zooplanktonic biomass ($F_{2, 70} = 10.24$ p $< 0.0001$) (Figure 5a), where SPSP (74.04 ± 60.54 mg.m$^{-3}$) corresponds to about twice the biomass of FN (37.29 ± 23.22 mg.m$^{-3}$) and three times that of RA (24.02 ±16.13 mg.m$^{-3}$) (Supplementary data I). Differences between day and night were also recorded (Figure 5b). The nighttime mean (60.88 ± 56.76 mg.m$^{-3}$) was significantly higher ($F_{1, 70} = 11.64$, $p = 0.001$) than that of daytime (32.85 ± 26.23 mg.m$^{-3}$).

The time of year under thermal stress (30.51 ± 17.33 mg.m$^{-3}$) caused a significant reduction in biomass ($F_{1, 70} = 5.57$ $p = 0.002$), as observed when comparing 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 $< 0.01$) (Figure 5c, Table 1). The Bonferroni test showed that the thermal stress caused a reduction in zooplanktonic biomass in the islands of FN and SPSP, but in RA this was higher during the period of higher sea surface temperature (Figure 5c, Table 1). In addition, the test detected that, regardless of the climatic condition, the biomass in SPSP was significantly higher in comparison to the other island systems studied (Figure 5c, Table 1).

Regarding the transects, it was verified that in FN the zooplankton biomass ranged from 6 mg.m$^{-3}$/day/ thermal stress/downstream to 102 mg.m$^{-3}$/night/no thermal stress/upstream of the island (Figure 6a and 6b). In the RA the zooplankton biomass showed a concentration ranging from 1.15 mg.m$^{-3}$/day/no thermal stress to 400 mg.m$^{-3}$/night/thermal stress, both registered upstream of the island (Figure 6e and 6c). The highest values of this parameter were recorded in SPSP, ranging between 10 mg.m$^{-3}$/day/no thermal stress/upstream to 275 mg.m$^{-3}$/night/no thermal stress/downstream (Figure 6g and 6h). In general, the average value downstream was equivalent to (49.37 ± 54.90 mg.m$^{-3}$), while upstream it was (43.88 ± 35.56 mg. m$^{-3}$), but statistical differences were not observed.

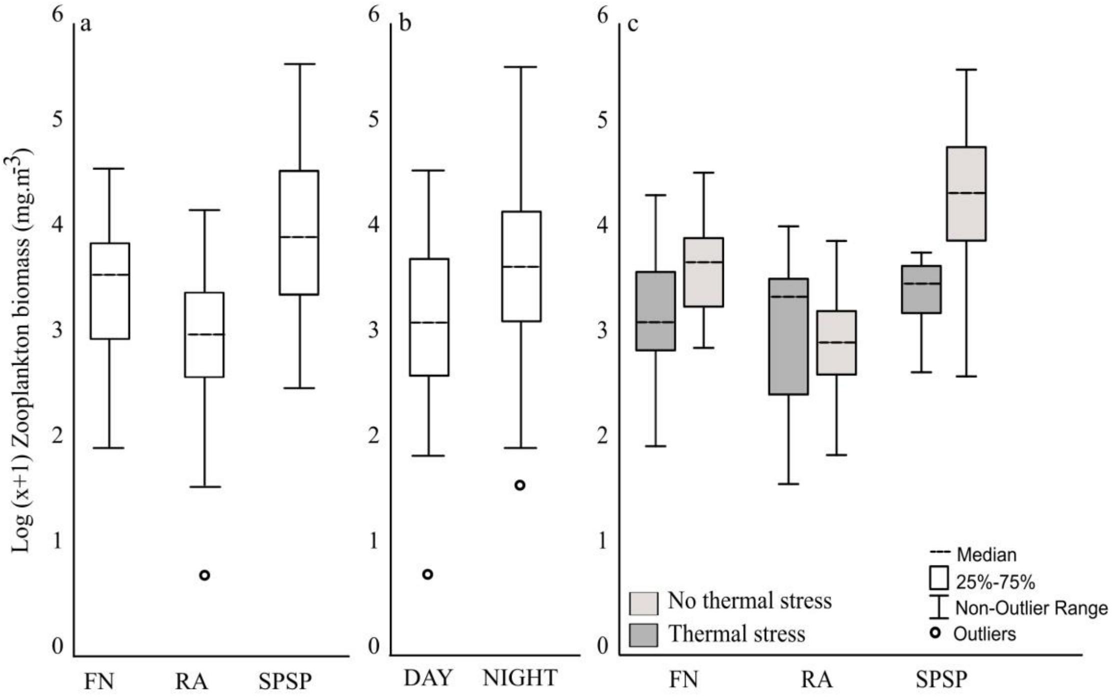

**Figure 5. Distribution.** Box-Plot (median and quartiles) representing the distribution of the zooplankton biomass. (a) Spatial distribution (FN – Fernando de Noronha Archipelago *vs.* RA – Rocas Atoll *vs.* SPSP – Saint Peter and Saint Paul Archipelago), (b) Time of day distribution (Day *vs.* Night) and (c) Temporal distribution (Thermal stress *vs.* No thermal stress).

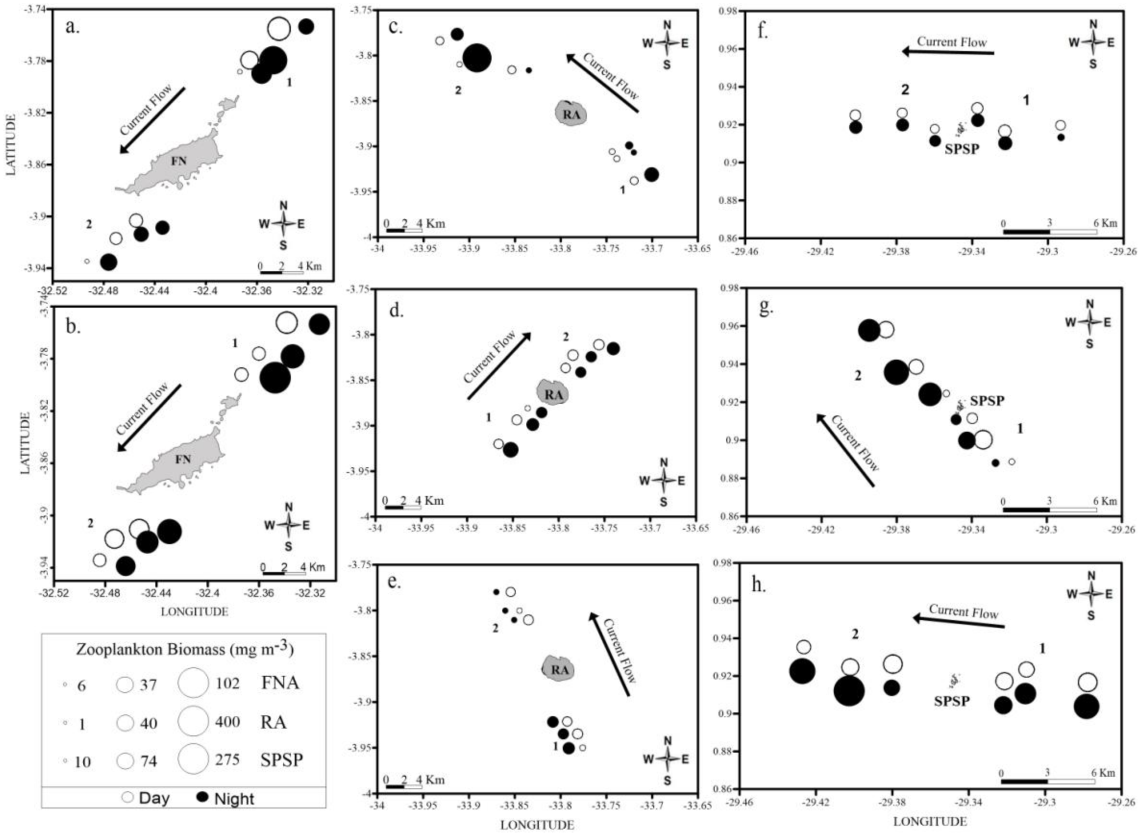

**Figure 6. Transect position.** Spatial distribution of the zooplanktonic biomass (mg. $m^{-3}$) on the around the protected marine islands of the Tropical Atlantic: (a) FN - Fernando de Noronha Archipelago in 2010 (thermal stress) and (b) Fernando de Noronha Archipelago in 2012 (no thermal stress); (c) RA - Rocas Atoll in 2010 (thermal stress); (d) RA - Rocas Atoll in 2012 (no thermal stress) and (e) RA – Rocas Atoll in 2014 (no thermal stress); (f) SPSP – Saint Peter and Saint Paul Archipelago in 2010 (thermal stress); (g) SPSP – Saint Peter and Saint Paul Archipelago in 2012 (no thermal stress) and (h) SPSP - Saint Peter and Saint Paul Archipelago in 2014 (no thermal stress).

**Table 1.** Multifactorial Analysis of Variance (ANOVA) results for natural logarithm of Log (x + 1) transformation was used to meet assumptions of heterogeneity of data (Levene-test) of Zooplankton biomass.

**(A) Factorial Anova**

| | | Zooplankton biomass (mg.$m^{-3}$) | | |
|---|---|---|---|---|
| Source | df | MS | *F* | *p* |
| Spatial (1) | 2 | 4.55 | 10.24 | **< 0.0001** |
| Temporal (2) | 1 | 2.48 | 5.57 | **0.002** |
| Time of day (3) | 1 | 5.18 | 11.64 | **0.001** |
| Transection (4) | 1 | 0.004 | 0.01 | 0.91 |
| Spatial * Temporal | 2 | 1.95 | 4.40 | **0.01** |
| Spatial * Time of day | 2 | 0.15 | 0.34 | 0.70 |

**Continuation table 1**

| | | | | |
|---|---|---|---|---|
| Temporal * Time of day | 1 | 0.35 | 0.80 | 0.37 |
| Spatial * Transection | 2 | 0.51 | 1.15 | 0.32 |
| Temporal * Transection | 1 | 0.31 | 0.71 | 0.40 |
| Time of day * Transection | 1 | 0.05 | 0.12 | 0.72 |
| Spatial * Temporal * Time of day | 2 | 0.10 | 0.22 | 0.79 |
| Spatial * Temporal * Transection | 2 | 0.39 | 0.89 | 0.41 |
| Spatial * Time of day * Transection | 2 | 0.46 | 1.04 | 0.35 |
| Temporal * Time of day * Transection | 1 | 0.05 | 0.11 | 0.73 |
| 1 * 2 * 3 * 4 | 2 | 0.11 | 0.25 | 0.77 |
| Error | 70 | 0.44 | | |

**(B) Bonferroni *post-hoc***

| | |
|---|---|
| FNA | Thermal stress < No thermal stress |
| RA | Thermal stress > No thermal stress |
| SPSPA | Thermal stress < No thermal stress |
| | |
| Thermal stress | RA < FNA < SPSPA |
| No thermal stress | RA < FNA < SPSPA |

The factors tested were: (a) spatial (FN *vs.* RA *vs.* SPSP), annual (Thermal stress *vs.* No thermal stress), time of day (Day *vs.* Night) and transection (Upstream *vs.* Downstream) effects on zooplankton biomass, and (b) Bonferroni tests on significant interaction terms for zooplankton biomass. p values in bold are significant.

## 4. DISCUSSION

### 4.1. Climatic and hydrological conditions in the Tropical Atlantic

A long-term time series of zonal wind, zonal current, Chlorophyll-*a* and sea surface temperature (SST) anomalies were presented from the period 2008 to 2015, aiming to describe the climatic and hydrological conditions of the tropical Atlantic region, with emphasis on the sampling years of 2010, 2012 and 2014.

Data extracted at FNA, RA, and SPSP islands showed a slightly seasonal variation associated with the interannual variability. We highlighted the occurrence of El Nino-Southern Oscillation (ENSO) in the year 2010. This ENSO event caused a low concentration of Chlorophyll-*a*, associated with an increase in SST at the beginning of the boreal spring season (January-February), in contrast to the same period in the years 2012 and 2014. This process 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, so the trade winds of SE and NE are weaker. A significant positive relationship between the percentage of coral bleaching and the corresponding anomaly of SST HotSpot recorded by satellite and buoys, as a consequence of (ENSO), was verified by Ferreira et al. (2013) in Fernando de Noronha and Rocas Atoll, indicating that warming observed in ocean waters was followed by warming in the reefs.

The FN, RA, SPSP island locations are subject to higher SST values with low variability during the year (Bonou et al., 2016). In boreal spring 2010, after the special event of El Ninõ of 2009, the SST was higher than expected for the period. This event has been associated with the weakening processes of the wind in 2010, and this is one of the processes that contributed to making the event of 2010 different from other events (Lefèvre et al., 2013).

Regionally, the Chlorophyll-*a* concentration has variability in the range of 0.1 and 0.25 mg.m$^{-3}$ around the three islands. This is similar to that found by Da-Cunha et al. (2013) and Tchamabi et al. (2017) and considered low when compared to the Brazilian shelf and its coastal zone (> 2 mg.m$^{-3}$). It is clearly observed that the chl-a concentration near SPSP (~0.2 mg.m$^{-3}$) is slightly higher around FN and RA (~0.1 mg.m$^{-3}$) (Figure 5b). This feature is explained by the main currents influencing this region, i.e. the SEC and NBC, flowing at the surface, and the EUC flowing at the subsurface (Peterson and Stramma, 1991).

During the retroflection period, the coastal water masses of the Amazon plume are transported towards the African coast, reaching from 50° W to 25° W during the peak flow of the North Equatorial Countercurrent (NECC) (Subramaniam et al., 2008; Lefèvre et al., 2010). As SPSP is located close to the retroflection zone, the high chlorophyll-a water masses from the coastal area can reach SPSP through spatial propagation (Figure 4b). This is one of the key findings of this work.

### 4.2. Zooplankton biomass

The present study provides the first information about the spatial heterogeneity of tropical island environments, where the smallest and remote SPSP presented a significantly higher zooplankton biomass compared to the Fernando de Noronha Archipelago and the Rocas Atoll.

The high biological productivity, associated with the fact that SPSP represents an important area for highly migratory pelagic species that find refuge and food in this environment for their growth and survival (Morato et al., 2010) has led this island system to be considered as an Ecologically or Biologically Significant Area (EBSA), in accordance with the Convention on Biological Diversity (Soares and Lucas, 2018).

Some hypotheses have been 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 the eggs (which justifies our results, since a considerable number of fish eggs were observed in the samples, contributing to an increase in zooplanktonic biomass - non-quantified data); **(2)** Other species of fish feed on the base of the benthic community, which finds favorable conditions because of the supply of material by the strong influence of local currents, and **(3)** The occurrence has not yet been well understood, but probable nutrient enrichment events are responsible for pelagic and benthic life productivity around SPSP.

According to Araújo and Cintra (2009), this enrichment occurs constantly below 90 meters of depth, promoting the increase of nutrients at the base of the photic layer (100 meters 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 vertical movements and subsidence.

The values recorded for the zooplanktonic biomass in the present work are superior to those observed by Melo et al. (2012). The author carried out sampling in the winter season in SPSP. Sampling of the present study occurred between winter and spring, when the ITCZ (*Intertropical Convergence Zone)* is further north, enhancing surface winds and surface currents like Equatorial South Current (SEC) and EUC weakening. As a result, a faster process of larval propagation is observed, which reduces the potential for retention of larvae in SPSP (Araújo and Cintra, 2009). In the year 2005, Diaz (2009) carried out zooplankton sampling in the SPSP during the summer and winter seasons, registering the highest values of zooplanktonic biomass occurring during the summer and these high values are 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.

During the summer the ITCZ is further south, where weakening of the SEC and intensification of the EUC is observed. In this situation the SPSP meets the conditions for the retention of larvae supplementing the recruitment of the local benthic fauna (Araújo and Cintra, 2009). Our observations point to a significant effect of the temporal factor, where the period considered under thermal stress (2010) presented a significantly lower biomass than the period considered without thermal stress (2012 and 2014). However, the connection with climate is not clear, and other factors like seasonality (D'Alcalà et al., 2004), winds (Aristegui et al., 1989), current dynamics (Lavaniegos et al., 1998) and predation (Piontkovski and Castellani, 2009) must be considered, since they influence the zooplankton biomass stock in Tropical environments.

Serious repercussions of climate change associated with El Ninõ on the dynamics of coastal and marine ecosystems, as well as the associated economic impacts, are very evident (Rossi and Soares, 2007). During the 1982-83 El Niño, zooplankton biomass recorded in the Gulf of California did not show a significant reduction (Chavez et al., 1984), contrary to what was recorded in the waters of Peru and the California Current (McGowan, 1983). Piontkovski and Castellani (2009) registered a decreasing trend of zooplankton biomass in the Tropical Atlantic, pointing mainly to two factors: (1) expansion of Tropical species distribution due to extension of the 'Tropical belt' and (2) reduction of primary productivity as a consequence of the thinning of the thermocline as a response to global warming. However, some areas such as those located around the islands, resurgence spots and tropical gyres favor an increase in pelagic, benthic and nektonic productivity (Table 2).

The Rocas Atoll presented a high biomass value in the period considered under thermal stress, contrary to what was observed for FN and SPSP for the same period. RA is under the influence of the flow to the west of the central branch of the South Equatorial Current (cSEC) (Tchamabi et al., 2017). Sampling in 2010 occurred at the end of July and beginning of August, a period of cSEC intensification at RA. Tchamabi et al. (2017) used models of climatological simulation for the area and found that the result of cSEC strengthening, flowing westward and being interrupted by RA, generated current wake with formation of eddies downstream of these islands. The resulting perturbation induces mixing by cooling downstream of the Atoll. This effect acts by cooling waters at the base of the mixture layer depth, causing an increase in the productivity downstream of these islands. Information from the thermohaline structure of RA for the year 2010 reinforces the modeling results of Tchamabi et al. (2017), showing that the mean temperature in the SE transect varied from 26.23 to 27.84 ºC, and in the NW transect the temperature decreased considerably, exhibiting low values at the depth of the mixture layer, equivalent to 23.23°C (Jales et al., 2015). According to the author, this reduction of the temperature at the base of the mixture layer is a result of the influence of the central water of the South Atlantic, providing nutrients for the increase in planktonic productivity on the NW side of the Rocas Atoll, thus contributing to an increase in zooplanktonic biomass.

The effect of time of day on the zooplanktonic biomass was observed with a significantly higher value in the nighttime. The vertical migration performed by zooplankton was the main factor responsible for the differences between day and night. Hays et al. (2001) suggested the existence of a significant loss of material near the surface of the ocean, mediated by the diel vertical migration (DVM) of zooplankton, although direct quantification of this rate is problematic.

Changes in daily biomass of different size fractions revealed that DVM occurred more strongly 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, since the differences found for the zooplanktonic biomass in the present study may be the result of the mesh size we used (300µm), favoring the capture of larger animals. Our hypothesis is reinforced by recording a considerable increase in 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 net in tropical Atlantic island environments and found that the neustonic biomass was significantly higher at night. Thus, all 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 of larger body size at night.

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

| Study area | Hauls | Mesh size (μm) | N | Mean (± SD) | Seasonal Period | Time Period |
|---|---|---|---|---|---|---|
| [1]FN | Oblique | 300 | 12 | 29.85 ± 21.81 | rainy | July/August, 2010 |
| [1]FN | Oblique | 300 | 12 | 44.73 ± 23 | rainy | July, 2012 |
| [1]RA | Oblique | 300 | 12 | 28.19 ± 19.53 | rainy | July/August, 2010 |
| [1]RA | Oblique | 300 | 12 | 28.68 ± 16.86 | rainy | July, 2012 |
| [1]RA | Oblique | 300 | 12 | 15.87 ± 8.49 | rainy | August, 2014 |
| [1]SPSP | Oblique | 300 | 12 | 32.14 ± 9.41 | rainy | July/August, 2010 |
| [1]SPSP | Oblique | 300 | 12 | 72.74 ± 58.72 | rainy | July, 2012 |
| [1]SPSP | Oblique | 300 | 12 | 15.87 ± 8.49 | rainy | August, 2014 |
| [2]FN | Neuston | 500 | 72 | 19.16 (± 14.73) | rainy | July/August, 2010 |
| [3]SPSP | Subsurface | 300 | 20 | 78.4 (± 38.8) | rainy | May and June, 2005 |
| [3]SPSP | Subsurface | 300 | 36 | 118.8 (± 116.2) | rainy | 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 (± 62) | Summer–autumn | 1968 to 1992 (June to November) |
| [5]Eastern tropical Atlantic | Vertical or oblique | 178 and 200 | 115 | 132 (± 66) | Summer–autumn | 1968 to 1992 (June to November) |
| [5]Western tropical Atlantic | Vertical or oblique | 178 and 200 | 96 | 212 (±202) | Winter–spring | 1968 to 1992 (December to May) |
| [5]Tropical gyre | Vertical or oblique | 178 and 200 | 75 | 379 (±461) | 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).

## 5. CONCLUSIONS

The changes in zooplanktonic biomass observed around the protected marine islands in the Tropical Atlantic were mainly related to the spatial, temporal and time of day factors. In summary, our results show: (1) The Saint Peter and Saint Paul Archipelago presented the largest zooplanktonic biomass in comparison to Fernando de Noronha and Rocas Atoll. The position of SPSP near the retroflection zone of the Amazon River plume, animal concentration mechanisms and local hydrodynamic features are presumably the main factors responsible for the distribution of zooplanktonic biomass in SPSP; however, further investigation is necessary since these represent important fishing sites where fish eggs and larvae remain around the island, increasing the local zooplankton biomass. **(2)** The high nighttime value of the zooplanktonic biomass observed for tropical Atlantic islands is a reflection of the size of the mesh used in the present study, favoring the capture of larger animals considered as strongly migratory. **(3)** The increase in the SST (°C) in 2010 as a consequence of El Niño is suggested as the stressor responsible for the low productivity recorded in the Atlantic Tropical Islands. An important future recommendation is that research should be carried out over a long time period to prove this evidence and to understand the response patterns of these environments and their resilience to a possible increase in El Niño occurrence in the coming decades.

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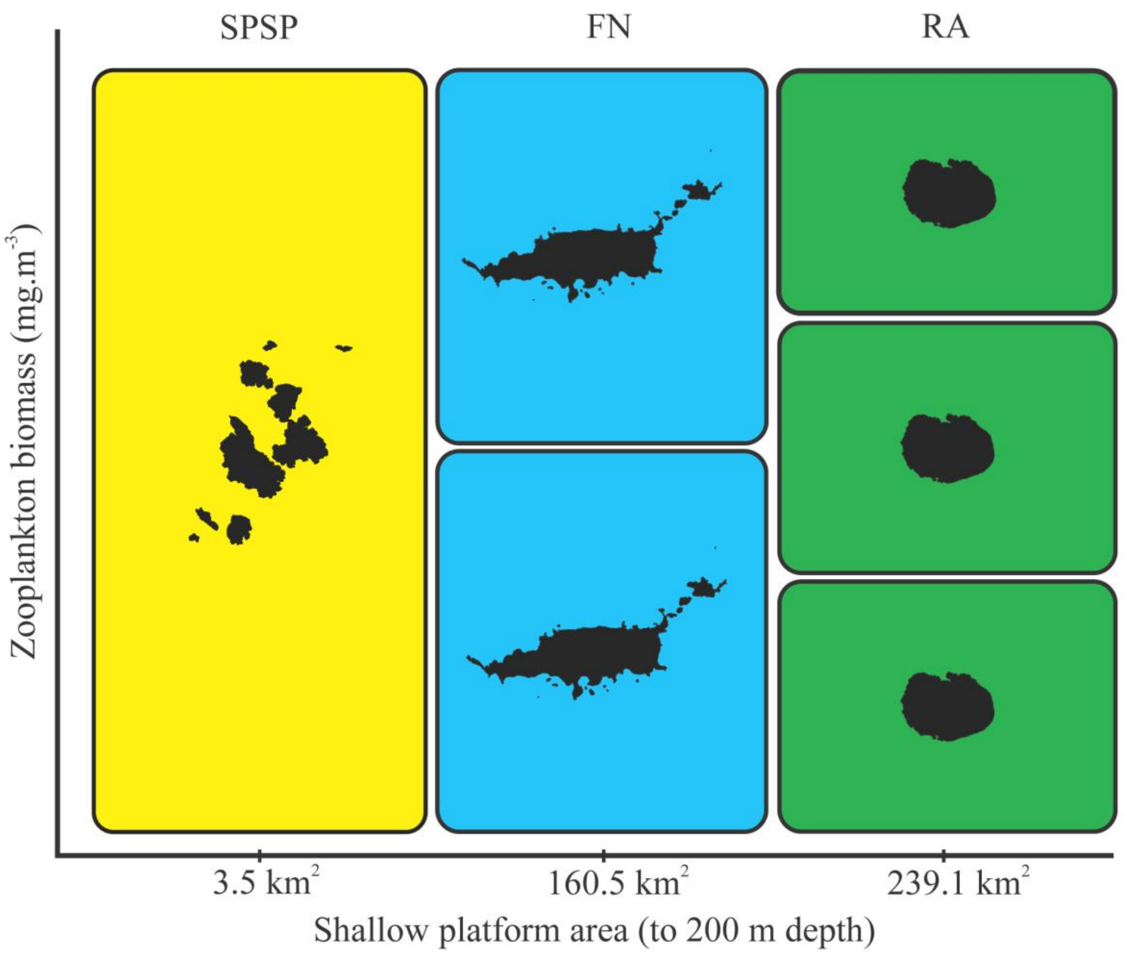
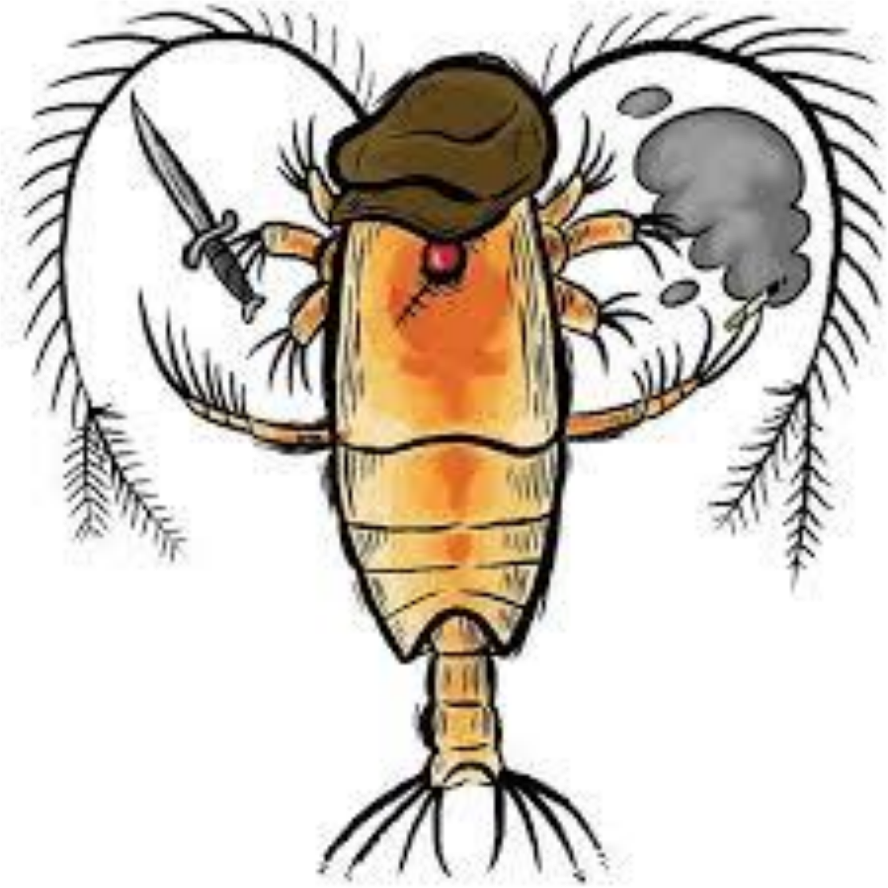
# Supplementary material

Proportion of the zooplankton biomass in relation to the shallow platform area in the Tropical Atlantic (SPSP - Saint Peter and Saint Paul; FN – Fernando de Noronha Archipelago and RA – Rocas Atoll)



# CHAPTER 2 - Copepod assemblages in island environments from the Tropical Southwestern Atlantic: An explanation of distribution and diversity



Fonte: https://deskgram.net/explore/tags/racscal

# Copepod assemblages in island environments from the Tropical Southwestern Atlantic: An explanation of distribution and diversity

## ABSTRACT

Patterns of abundance, diversity and structure of the epipelagic Copepoda assemblage are showed for the poorly known in island environments from the Tropical Southwestern Atlantic. Hypotheses considering the factors: spatial (Fernando de Noronha Archipelago-FN *vs.* Rocas Atoll-RA *vs.* St. Peter and St. Paul Archipelago-SPSP), interannual (July 2010 *vs.* September 2012 *vs.* August 2014), time of day (Day *vs.* Night) and transect position (Upstream *vs.* Downstream) were tested. The results were based on 96 zooplankton samples. The taxonomic composition was represented by 195 species often found in tropical and subtropical waters around the world, with a high contribution (69%) in terms of the relative abundance of small-sized copepods for the SPSP. A greater similarity between the quali-quantitative composition of the copepod assemblage was verified between FNA and RA, which is explained by the proximity of the islands since these are located at the same geographical latitude. The SPSP remote is the island whose standing-stock of copepods abundance is higher and species richness is lower. The highest diversity of copepod species was verified for the RA Biological Reserve. The significant increase in downstream copepod abundance was suggested because of the *"Island Mass Effect"* which seems to control zooplankton retention sites. In addition, multivariate analysis demonstrated differences in the structure of copepod assemblages between spatial, interannual and time of day factors. The Indval analysis detected indicator species of mesoscale events such as: wake in FN in 2010, influence of South Atlantic Central Water Masses in RA and upwelling in SPSP in 2014. Copepods considered strong migrators were also excellent indicators of the nocturnal period. Our results reinforce the need to consider issues of dispersal capacity of organisms, proximity and isolation of habitats as well as identify productive sides of the island when planning marine protected area so that conservation objectives can be achieved.

**Keywords:** Abundance, biodiversity, refuge, Island Mass Effect, Tropical Island

## 1. INTRODUCTION

Since the main knowledge of Charles Darwin and Alfred Russel Wallace, the biota of island systems has been the focus of evolutionary and ecological research (Trewick & Cowie, 2008). The main interest of ecologists is to understand how the maintenance and dispersion of populations occurs in island environments (MacArthur & Wilson, 1967). Furthermore, the biota (planktonic, benthic and nektonic) living in surrounding of island systems are a vital component of oceanic food webs, besides many of these represent early life-history stages of ecologically and economically important species (Landeira et al., 2013).

The heterogeneous distribution of zooplankton in marine ecosystems is affected by physical phenomena in different spatial and interannual scales that mainly include hydrographic events such as currents and predominant wind (Cowie & Holland, 2006). Furthermore, the increase in sea surface temperature in response to global warming in the Atlantic temperate and Pacific oceans and in the subtropical Mediterranean Sea is pointed as the main factor responsible for regime change in pelagic ecosystems (Vandromme et al., 2011; Mackas et al., 2012). Associated with the changes there is still strong evidence of systematic changes in the distribution of abundance, diversity and structure of the plankton community in the last decades in many areas of the world (Hays et al., 2005; Beaugrand, 2009).

The insular systems of Fernando de Noronha Archipelago (FNA), Rocas Atoll (RA) and St. Peter and St. Paul’s Archipelago (SPSPA) are considered Marine Ecoregions and integrate the territory known as "Blue Amazon", located in the Tropical Southwestern Atlantic Ocean. They are Marine Protected Areas covering an area of 79.706 ha. The marked endemism, biological fragility and great genetic diversity made them be considered by UNESCO as natural patrimony of Humanity and are part of the Biosphere Reserve of the Atlantic Forest (Soares, 2018). Around these islands, there are the same highly oligotrophy waters of the Atlantic Ocean, due to a permanent thermocline (Souza et al., 2013). However, the surroundings of these oceanic islands are recognized as “Oases” of life in an oceanic desert (Tchamabi et al., 2017), in reason of an increase in biological productivity in response to current interaction with the topography of islands and seamounts known as *“Island Mass Effect”* (Doty & Oguri, 1956). The interaction of the current with the topography of the island may cause at downstream zone eddies production and consequently enrichment (nutrients upwelling from the depths of the ocean), concentration (internal convergent flow) and retention (closed recirculation) which are associated with favorable habitat for breeding and recruitment of many fish species (Condie & Condie, 2016). Thus, downstream areas of oceanic islands are sites of high planktonic abundance and biomass (Araujo & Cintra, 2009; Jales et al., 2015).

Variations in the abundance, diversity and interactions within the zooplanktonic community are strongly related to the time of day (Lo et al., 2004; Melo et al., 2014). In typical diel vertical migration behavior, the zooplankton can to transfer energy available in the euphotic layer to deeper layers in a process known as biological pump (Wetzel, 2001), and the most prominent group in this flow of energy are the copepods (Thorisson, 2006). Copepoda representing up to 80% of the biomass of planktonic metazoan in the marine environment (Kiørboe, 1998), act as important link between the primary producers and the upper trophic levels of the aquatic trophic web (Christou, 1998) and may be used as an integrative measure of biological productivity (Hopcroft et al., 1998). They play an important role as a vehicle for transporting carbon from the surface of the ocean to the depths limiting the amount of $CO_2$ in the atmosphere that heats the planet (Hays et al., 2005; Jónasdóttir et al., 2015).

Geographic features such as island size and degree of isolation strongly influence planktonic, benthic and nektonic communities of island environments (Mazaris et al., 2010; Hachich et al., 2015; Barroso et al., 2016). Studies in islands have registered that changes in diversity, abundance and structure of the copepod assemblage is not only determined by the physical and chemical conditions of the aquatic environment, but also in response to geographical factors (Rezai et al., 2005, Saitoh et al., 2011). It is surprising that there are not interannual series of abundance measurements (ind. $m^{-3}$) and diversity of copepods to the Tropical Southwestern Atlantic, which reinforces the importance of the present study that although it is a short time scale (three years), is the only one performed so far for this area. The few available literatures for the zooplankton of the oceanic islands of Southwestern Atlantic primarily concerns about taxonomy, abundance, diel vertical migration and productivity (Brandão, 2012; Macedo-Soares, 2012; Melo, 2012; 2014; Lira, 2014).

In this study, we tested the effects of environmental heterogeneity (Island *vs.* Atoll *vs.* Seamount), interannual (2010 *vs.* 2012 *vs.* 2014), time of day (day *vs.* night) and transection (upstream *vs.* downstream) on the abundance, diversity and richness of epipelagic copepods on three islands of the Tropical Southwestern Atlantic. We predicted that (a) The island of greater environmental heterogeneity would be the St. Peter and St. Paul Archipelago presenting a differentiated taxonomic composition, greater abundance and less richness of copepod species, (b) connected environments would have a quali-quantitative composition, diversity and similar richness due to their greater similarity in environmental conditions and greater dispersal rates, (c) Interannual fluctuation in the abundance, diversity and richness of copepod assemblages would be indicative of periods of increased productivity, (d) The abundance, diversity and richness of copepods may be higher at night as a response to vertical migration behavior, and (e) Downstream of oceanic islands are places of high abundance, diversity and richness of copepod species.

## 2. MATERIAL AND METHODS

### 2.1. Study Area

The Fernando de Noronha Archipelago (FNA), Rocas Atoll (RA) and St. Peter and St. Paul's Archipelago (SPSPA) were classified as their own marine ecoregion due to the great distance separating them from the mainland and by the presence of endemic species of fish, birds and turtles (Stattersfield et al., 1998). These islands are in the western portion of the South Atlantic and are respectively 345, 266 and 1000 km distant from the Brazilian coast (Barroso, 2016) (Table 1). Fernando de Noronha Archipelago (Figure 1) (03°45'-03°57' S, 32°19'-32°41' W) and the Rocas Atoll (Figure 1) (03°48'-03°59' S, 33°34'-33°59' W) are part of seamounts alignment developed along the Fernando de Noronha Fracture Zone of the meso-Atlantic Ridge (Almeida, 2006). FNA is considered the largest Archipelago in Brazil covering a shallow platform area equivalent to 160.5 km$^2$ (Hachich et al., 2015) (Table 1). Rocas Atoll is the only atoll in the South Atlantic Ocean and one of the smallest in the world (Kikuchi & Leão, 1997). It has a shallow platform area of approximately 239.5 km$^2$ (Barroso, 2016) distant 124 km from the Fernando de Noronha Archipelago (Kikuchi & Leão, 1997) (Table 1). The same zonal current influences both islands: The South Equatorial Current (SEC), which dominates this region with its east-west direction (Becker, 2001). This current has three large branches, besides an equatorial branch, being the central branch of the SEC (cSEC) the one with greatest influence on these islands in the surface region. In the subsurface layer, the dominant current is the Equatorial South Undercurrent (sSEC) in the east-west direction (Assunção et al., 2016). St. Peter and St. Paul's Archipelago (SPSPA) (Figure 1) is formed by a group of rocky islands located north of equator (0°55'06" N and 29°20'48" W), being approximately about 1.800 km from the African coast and 630 km from FNA (Edwards & Lubbock, 1983). The SPSPA is the smallest (shallow platform area equivalent to 3.5 km$^2$) and more isolated group of oceanic islands in the world (Hachich et al., 2015) (Table 1). It is an outcrop of the sub-oceanic mantle that emerges from depth above 4000 m, and the archipelago constitutes the top of a transformant fault of the Meso-Atlantic Chain, when it crosses the equator (Luiz et al., 2015). This fault extends practically in the East-West direction, the same of the Equatorial South Current. The SPSPA is inserted in a complex current system directly associated with the Southeast trade winds, favoring a very particular hydrological dynamic (Becker, 2001). The main zonal currents flowing westward in the surface layer of this region are the Equatorial North Current (NEC) and the South Equatorial Current (SEC). The NEC presents a relatively broad and continuous flow, while the SEC is formed by three zonal branches, separated by counter-currents of relatively weak intensity (Stramma, 1991). Another current of substantial importance is the Equatorial Undercurrent (EUC), which profiles the equator and flows to the East, just below the surface, with its core positioned approximately 80 m deep (Brandt et al., 2006).

**Table 1** Characteristics of the Marine Ecoregions (Tropical Southwestern Atlantic ocean): FNA (Fernando de Noronha Archipelago); RA (Rocas Atoll) and St. Peter and St. Paul's (SPSPA). (Modified from Barroso et al., 2016).

| Island | Age (Ma) | Shallow platform area (to 200 m depth (km$^2$) | Distance from continent (km) | Isolation from nearest reef (km) |
|---|---|---|---|---|
| FNA | 8-12$^{(2)}$ | 160.5 $^{(3)}$ | 345$^{(4)}$ | 124$^{(5)}$/RA |
| RA | > 8 - 12$^{(2)}$ | 239.5$^{(4)}$ | 266$^{(4)}$ | 124$^{(5)}$/FNA |
| SPSPA | 8 - 9 $^{(1)}$ | 3.5$^{(3)}$ | 1000$^{(4)}$ | 630$^{(3)}$/FNA |

(1)Hekinian et al. (2000); (2)Lopes & Ulbrich (2015); (3)Hachich et al. (2015); (4)Barroso et al. (2016) (5)Kikuchi and Leão (1997).

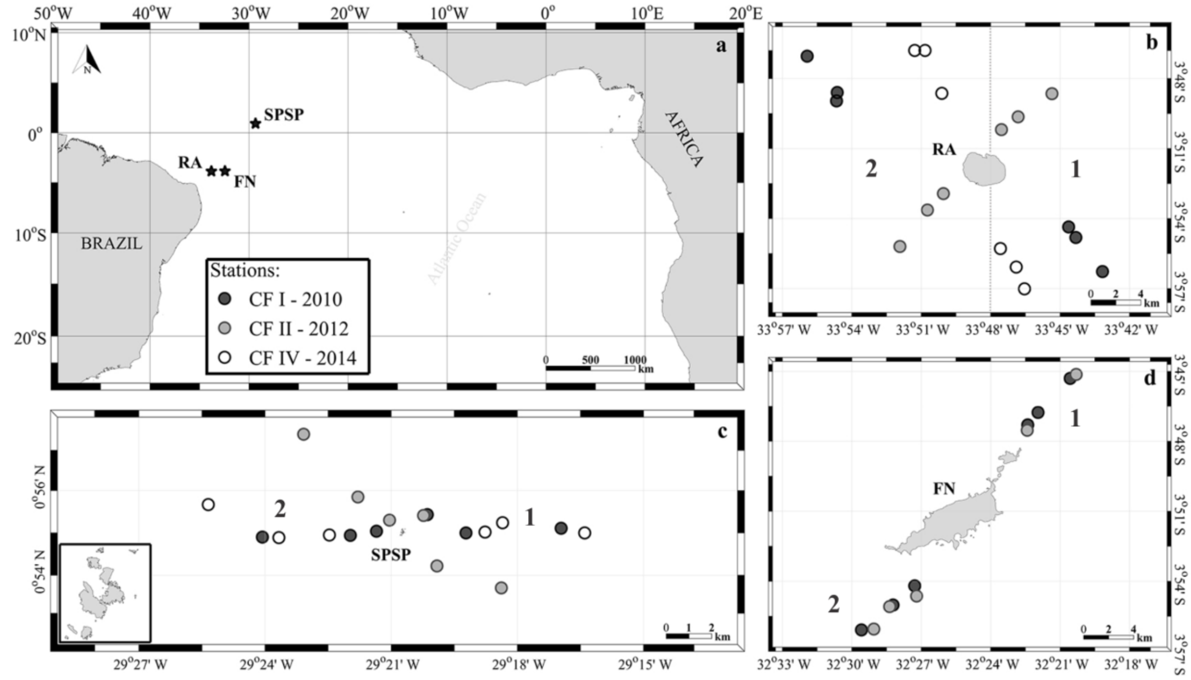


**Figure 1** a) Sampling in the Marine Ecoregions (Tropical Southwestern Atlantic ocean) as part of the project: CFI – 2010 (Camadas Finas I - Circle in dark gray); CFII – 2012 (Camadas Finas II - Circle in light gray) and CFIV (Camadas Finas IV - White circle); b) Sampling stations in RA – Rocas Atoll; c) SPSP – St. Peter and St. Paul's Archipelago and d) FN – Fernando de Noronha Archipelago along two transects: 1 (transect upstream) and 2 (transect downstream) in relation to the prevailing surface current.

## 2.2. Sampling strategy

The sampling campaigns were made in the context of project "*Camadas finas oceânicas ao largo do Nordeste do Brasil*". The expeditions were carried out aboard the NHOc Cruzeiro do Sul from the Brazilian Navy in the Tropical Southwestern Atlantic island systems (FNA, RA and SPSPA). Samples were carried out in July 2010 (Camadas finas I), September 2012 (Camadas finas II) and August 2014 (Camadas finas IV). A total of 96 samples were collected being 36 in RA and SPSPA and 24 samples in FNA. The loss in field of the bongo net in the year 2014 in FNA did not allow for sampling. Day and night samplings were carried out in each investigated insular system. Two transects were defined from the identification of the predominant surface current with an ADCP. A transect upstream (1) and downstream (2) of the islands were determined and three stations defined in each transect.

## 2.3. Sampling and laboratory analyses

Zooplankton samples were collected through oblique hauls using a "Bongo" with cylindrical-conical net (mouth area 0.6 $m^2$, mesh size 300 µm). We used the 300 µm mesh to facilitate the comparison of the data of the present study with other works carried out in the Tropical Southwestern Atlantic (there is a historical use of larger mesh sizes, such as 300 and 500 µm, in this region; Díaz et al., 2009; Melo et al., 2012; Melo et al., 2014, Lira et al., 2014). The oblique hauls were made in "V", extending up to a depth of 75% of the local depth, or at most up to 200 m deep. Filtered volume was measured with a calibrated flowmeter, and samples preserved in saline 4% buffered formaldehyde solution.

In laboratory, the samples were fractionated in aliquots of 1/32 or 1/64, using a Motoda splitter (Omori and Ikeda, 1984), containing at least 300 copepods (Frontier, 1981). The specimens were identified and inspected using Bogorov counting chambers under a Zeiss Discovery V8 stereomicroscope. The copepods identification mainly followed Björnberg (1981), Bradford-Grieve et al. (1999), Pinto Silva et al. (2018), https://copepodes.obs-banyuls.fr/

## 2.4. Data analysis

**Univariate approach.** Main effects ANOVA was used to analyze the first-order (non-interactive) effects of multiple independent variables: spatial (FN *vs.* RA *vs.* SPSP), interannual (2010 *vs.* 2012 *vs.* 2014), time of day (Day *vs.* Night) and transection (Upstream *vs.* Downstream) on response variables: (1) total abundance of copepods and (2) dominant species of copepods (with more than 2% of total abundance). The normality of the data was investigated through the Kolmogorov-Smirnov test and the heterogeneity of variances was verified with the Levene test. When necessary, the data were transformed to the natural logarithm of (x+1). Once the significance was verified ($P < 0.05$), the Tukey-HSD a *pos-hoc* test was applied. Parametric statistical analysis followed Zar (1996).

**Sampling effort**. Since diversity is a measure directly related to the sampling effort, we consider only the years 2010 and 2012 for data analysis. Mechanical problems on the ship did not make it possible sampling in 2014 in FN. The structure of copepod assemblages was described from the diversity index (Margalef's richness index (*d′*) and Shannon-Wiener diversity index (H′)). Main effects ANOVA was used to analyze the first-order (non-interactive) effects of multiple independent variables: spatial (FN *vs.* RA *vs.* SPSP), interannual (2010 *vs.* 2012), time of day (Day *vs.* Night) and transection (Upstream *vs.* Downstream) on the diversity indexes mentioned. All the indexes were Log (x +1) transformed.

**Multivariate approach.** The copepod assemblage structure was analyzed using multivariate analyses. Permutational multivariate analysis of variance (PERMANOVA) was used to test the hypothesis that the assemblage structure of copepods changes in response to space, interannual, time of the day and transects, and interactions among these four factors. The Monte Carlo *P values* were used for all analyses, and 9.999 random permutations were tested. In case of significant differences, a pairwise test (the multivariate version of the t statistic) between different levels of significant factor(s) was performed. To identify patterns of similarity between the samples and, therefore, possible changes in the distribution of the copepods assemblage the multi-dimensional scaling (NMDS) was used to represent the Bray-Curtis matrix graphically in a two-axis space. Both the PERMANOVA and the MDS were based on a Bray-Curtis similarity matrix constructed on the log (X+1) transformed abundance of species with frequency of occurrence greater than 50%.

To detect non-random distributions of species (indicator species) between spatial, interannual, time of day and transects factors, the Indicator Species Analysis developed by Dufrêne and Legendre (1997) was used. This coefficient combines the relative abundance of the species (specificity) with its frequency of occurrence (fidelity) in a defined group. Only the species that presented values of indicators (Indval) ≥ 50% were considered excellent indicators of the factors tested. The statistical significance of the species indicator values was evaluated using the Monte Carlo test (1.000 permutations). The level of significance was set at $P < 0.05$ for all analyses.

## 3. RESULTS

### 3.1. Species composition

The taxonomic composition of the marine islands from the Tropical Southwestern Atlantic was represented by three orders, one suborder, 26 families, 57 genera, one subgenus and 195 species (see Supplementary data 1). A total of 133 taxa were recorded in FNA (see Supplementary data 1), with the orders Calanoida, Cyclopoida and Harpacticoida represented by 85, 32 and 5 species, respectively. Small-sized copepods, such as those with size between 0.3 - 1.0 mm (*Acrocalanus longicornis*, *Clausocalanus furcatus*, *Oithona plumifera*, *Oncaea venusta* and *Farranula gracilis*) contributed around 32% for total relative abundance of copepods (Figure 2). Those of medium body size (size between 1- 2mm) (*Nannocalanus minor*, *Undinula vulgaris* and *Corycaeus speciosus*) contributed with 39% and large body size copepods (size > 2mm) such as (*Euchaeta marina*, *Scolecithrix danae* and *Lucicutia longicornis*) corresponded to 29% of the total relative abundance of copepods at the FNA (Figure 2).

A total of 181 taxa were recorded in RA, where the main orders Calanoida, Cyclopoida and Harpacticoida were represented by 84, 32 and 3 species, respectively (see Supplementary data 1). The same abundant species in FNA also dominated the assemblage of copepods at the RA, where the copepods of small body size corresponded to 39%, those of medium body size to 33% and the large body size to 28% of the total relative abundance of copepods (Figure 2).

In St. Peter and St. Paul’s Archipelago 129 taxa have been registered, where the order Calanoida was represented by 84 species; Cyclopoida by 29 species and Harpacticoida by 4 species (see Supplementary data 1). In the SPSP, small-sized copepods (*Calocalanus pavo*, *Clausocalanus furcatus*, *Oithona plumifera*, *Oncaea media*, *Oncaea venusta* and *Farranula gracilis*) represented 65% of the total relative abundance of copepods, while the medium body size (*Nannocalanus minor*, *Undinula vulgaris* and *Corycaeus speciosus*) corresponded to 25% and those of larger body size (*Euchaeta marina*) represented about 10% of the total relative abundance of copepods at the SPSP (Figure 2).

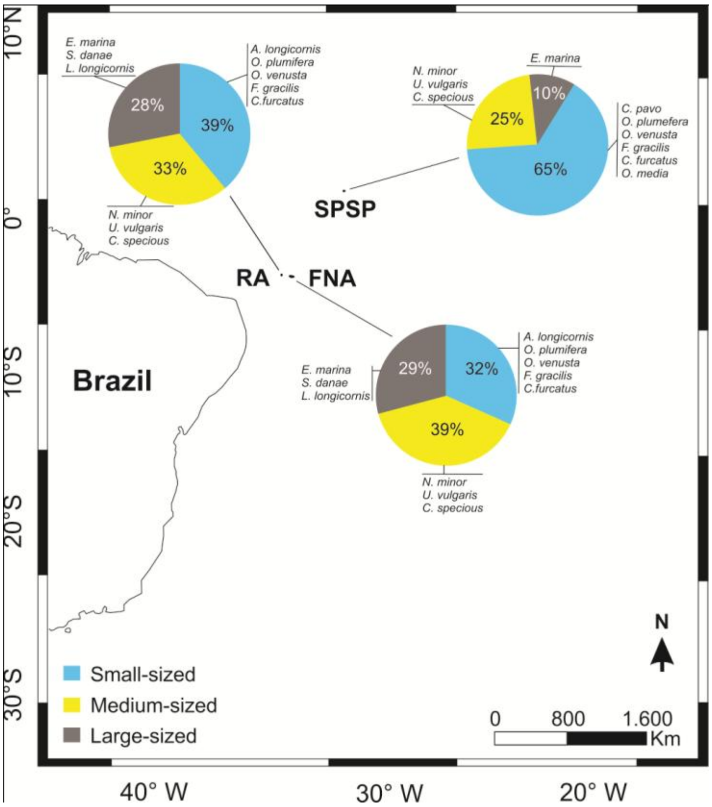


**Figure 2** Relative abundance (%) of copepod assemblages in FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSP (Saint Peter and Saint Paul Archipelago). Copepods classified according to body-sized: Small-sized (0.3 - 1.0 mm), Medium-sized (1 - 2mm) and Large-sized (> 2mm).

### 3.2. Total abundance of Copepods (ind. $m^{-3}$)

In general, the average abundance of the planktonic copepods of the Tropical Island of the Southwestern Atlantic was greater than 50 ind. $m^{-3}$ in the sampling of the years 2010, 2012 and 2014. Spatially the islands differ in terms of abundance of copepods (Anova, F (2, 89) = 13.13, $p < 0.0001$) (Figure 3a) where the average recorded for the SPSP (114.8 ± 76.4 ind.$m^{-3}$) is around twice that recorded for RA (57.2 ± 80.3 ind.$m^{-3}$) and three times that recorded in FN (47.37 ± 24.29 ind.$m^{-3}$). The *pos-hoc* test showed that FNA and RA did not differ in terms of total copepod abundance. The opposite was observed for SPSP, where it presented significantly different average values of FNA (Tukey-HSD, p = 0.0008) and RA (Tukey-HSD, p = 0.0001).

Interannual differences were not observed, with the average values recorded in 2010, 2012 and 2014 higher than 70 ind. $m^{-3}$. The total abundance of copepods did not differ between times of day, but the average daytime was equivalent to 64.30 ± 54.36 ind. $m^{-3}$ and the nighttime to 86.08 ± 89.20 ind. $m^{-3}$. The effect of position of the transects was verified on total copepods abundance (Anova, F (1, 90) = 5.57, p = 0.02)

(Figure 3b) whose the value recorded downstream was significantly higher 94.19 ± 94.69 ind.m$^{-3}$ than that to upstream 55.83 ± 37.12 ind.m$^{-3}$.

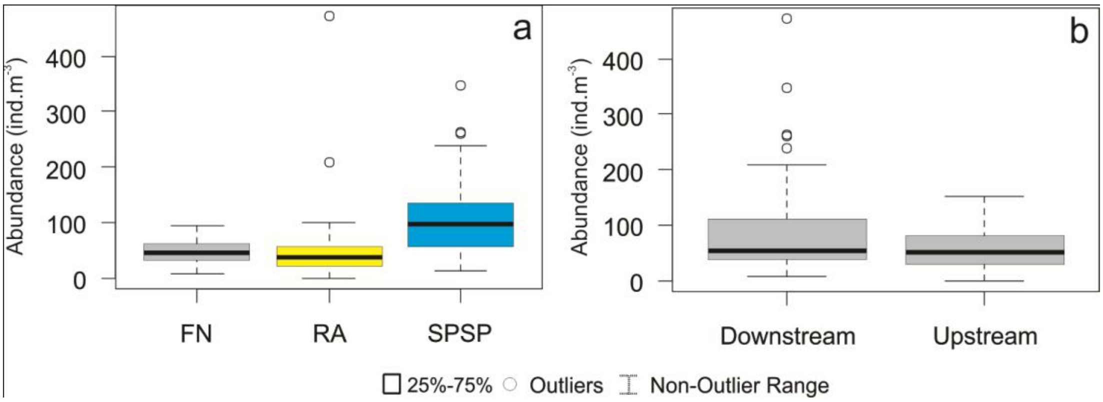


**Figure 3** Box-Plot (median and quartiles) representing difference on copepod abundance: a) Spatial variability of copepods abundance in Fernando de Noronha Archipelago (FN), Rocas Atoll (RA) and St. Peter and St. Paul's (SPSP); b) Transection position variability of copepods abundance.

### 3.3. Species diversity

The average values of species diversity indices (Margalef's species richness ( *d'*) and Shannon–Wiener index (*H'*), observed in the islands of the Tropical Southwestern Atlantic due to the factors tested (spatial, interannual, time of day and transects) indicate high taxonomic diversity with low variation. However, these island complexes differ in richness of copepod species (Anova, F (2, 64) = 4.98, p = 0.009) (Figure 4a), with the highest richness observed in FN (larger in size) (10.0 ± 3.41) and the lowest in SPSP (smaller and more isolated) (7.6 ± 1.98).

The RA registered an average richness equivalent to 8.5 ± 3.0. This difference is confirmed by the *pos-hoc* test where it was shown that FN > RA (Tukey-HSD, p = 0.04) and > SPSP (Tukey-HSD, p = 0.003). Although the year 2014 has not been considered to investigate the differences, the mean values will be presented. Regarding the interannual distribution of Margalef richness index, in 2010 this was equivalent to 8.33 ± 2.89; 2012 to 9.22 ± 3.11 and 2014 to 8.72 ± 4.14. The nighttime average was equivalent to 9.0 ± 3.10 and the daytime to 8.54 ± 3.52. Regarding the position of transects was recorded to average richness of 9.0 ± 3.51 upstream and 8.54 ± 3.12 downstream of the islands.

The islands differ significantly (Anova, F (2, 64) = 5.35 p = 0.007) in terms of diversity, where the Shannon-Winer index at FN registered an average of 3.71 ± 0.44; RA 3.89 ± 0.36 and SPSP 3.57 ± 0.63 (Figure 4b). The Tukey-HSD *pos-hoc* test showed that the difference in diversity occurs between AR > SPSP (Tukey-HSD, p = 0.01).

In interannual terms the average (3.84 ± 0.31; 3.61 ± 0.61 and 3.90 ± 0.43) were registered respectively for the years 2010, 2012 and 2014. The time of day effect was registered on the diversity (Anova, F (1, 64) = 4.17, p= 0.04) (Figure 4c), while the nighttime average (3.91 ± 0.39) of the Shannon-Winer index was significantly higher than the daytime average (3.58 ± 0.53). Statistical differences were not verified for the transect factor, but the average diversity verified to upstream of the island was 3.61 ± 0.43 and downstream 3.88 ± 0.41.

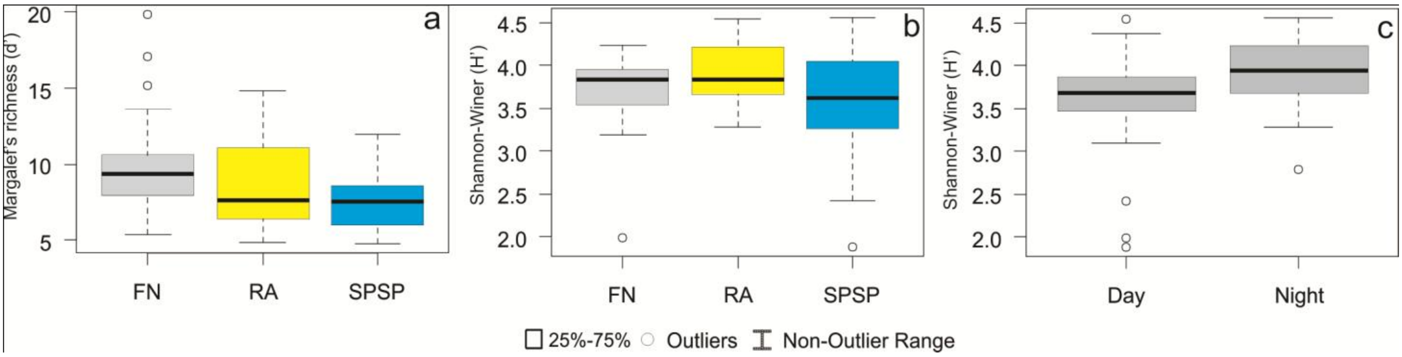


**Figure 4** Box-Plot (median and quartiles) representing difference in diversity index in the islands of the Fernando de Noronha Archipelago (FN), Rocas Atoll (RA) and St. Peter and St. Paul's (SPSP): a) Spatial variability of Margalef's richness; b) Spatial variability of Shannon-Winer diversity; c) Time of day variability of Shannon-Winer diversity.

### 3.4. Copepods assemblage structure

The PERMANOVA indicated that the structure of copepods assemblage differs according to the spatial, interannual and time of day factors, but not according to the transects (Table 2a). There was a significant interaction between the spatial *vs.* interannual factors (Table 2a). The *pairwise* tests for the spatial factor showed that the three island systems differ significantly in quantitative taxonomic composition of copepods assemblage (Table 2b), but the SPSP has a lower average similarity between groups when compared to FNA and RA (Table 2b). For the interannual factor, the results of the *pairwise* tests showed that the assemblage structure differs between the three years of samplings (Table 2b) but has a lower average similarity between groups of the years 2010 and 2012 (Table 2b). The NMDS graphically represents the differences recorded by PERMANOVA in the structure of the copepod assemblage between marine ecoregions (Figure 5a), as well as marked differences among the sampling years (Figure 5b).

Table 3 shows the *parwise* comparisons for interaction (spatial *vs.* interannual). The results indicate that changes in the structure of the copepod assemblages ($p < 0.01$) in FNA were more important between the years 2010 *vs.* 2012 (Table 3). In RA, these differences were more important between the years 2010 *vs.* 2012 and 2010 *vs.* 2014 (Table 3).

The effects of the interannual factor on the most abundant species at the insular systems studied are shown in Figure6. The one-way Anova results (Table 4) indicated that in FN, the epipelagic copepods *A. longicornis, S. danae* and *C. speciosus* presented their values of abundance significantly higher in 2010 (Figure 6a, Figure 6b, Figure 6c), respectively. The species *N. minor* (Figure 6d), *O. plumifera* (Figure 6f) and *F. gracilis* (Figure 6g) dominated significantly in 2012. For RA all copepod species that are significantly dominant (*A. longicornis, S. danae, C. speciosus, N. minor, O. plumifera, F. gracilis, U. vulgaris, C. furcatus, E. marina*) registered their high abundance in 2010 (Figure 6a-i).

Important changes in the structure of copepod assemblages in SPSP occurred between 2010 *vs.* 2012; 2010 *vs.* 2014 and 2012 *vs.* 2014 (Table 4). The species *C. speciosus, F. gracilis, C. furcatus* and *O. media* showed average values of abundance significantly higher in 2012. However, three species had their average abundance values significantly higher in 2014 (*U. vulgaris, C. pavo* and *E. marina*).

**Table 2** Summary of the: a) PERMANOVA, this analysis tests differences in quantitative taxonomic composition of copepods assemblage considering spatial, interannual, transect and time of day as factors. Differences are considered significant if *P (perm)* <0.01 (in bold). *d.f* = degrees of freedom; MS = average squares; P = probability associated with the Pseudo F statistic; b) Parwise comparisons for the significant spatial x interannual term for copepod assemblages. P (MC) = probability associated with the Monte Carlo randomization procedure.

**a) PERMANOVA**

| Source | *df* | MS | *Pseudo-F* | *P(perm)* |
|---|---|---|---|---|
| Spatial (S) | 2 | 7727.1 | **10.91** | **0.001** |
| Interannual (I) | 2 | 6731.8 | **95.11** | **0.001** |
| Transect (T) | 1 | 1758.7 | 2.48 | 0.015 |
| Time of day (Td) | 1 | 2983.3 | **42.15** | **0.002** |
| **S x I**** | 3 | 4471.6 | **63.18** | **0.001** |
| S x T | 2 | 1017.3 | 14.37 | 0.09 |
| S x Td | 2 | 688.67 | 0.97 | 0.47 |
| IN x T | 2 | 1084.9 | 15.32 | 0.07 |
| IN x Td | 2 | 690.36 | 0.97 | 0.47 |
| T x Td | 1 | 1604.4 | 2.26 | 0.02 |
| S x IN x T | 3 | 1267.4 | 17.90 | 0.01 |
| S x IN x Td | 3 | 711.69 | 10.05 | 0.43 |
| S x T x Td | 2 | 681.56 | 0.96 | 0.48 |
| IN x T x Td | 2 | 777.79 | 1.09 | 0.32 |
| S x IN x T x Td | 3 | 440.62 | 0.62 | 0.92 |
| Residual | 61 | 707.74 | | |
| Total | 92 | | | |

**b) Pairwise comparisons of copepods assemblage**

| Factor | Level | Interaction | *t* | P(MC) |
|---|---|---|---|---|
| Spatial | FNA | RA *vs.* FNA | 2.38 | 0.001 |
| | RA | RA *vs.* SPSPA | **3.68** | **0.001** |
| | SPSPA | FNA *vs.* SPSPA | **3.28** | **0.001** |
| Interannual | 2010 | 2010 *vs.* 2012 | **3.83** | **0.001** |
| | 2012 | 2010 *vs.* 2014 | 2.58 | 0.001 |
| | 2014 | 2012 *vs.* 2014 | 2.56 | 0.001 |

**Table 3** Results of parwise test for copepod assemblage structure between the sampling year for island in the FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul's Archipelago. P(MC) = probability associated with the Monte Carlo randomization procedure.Symbol (*) = Data not sampled.

| | **FNA** | | **RA** | | **SPSPA** | |
|---|---|---|---|---|---|---|
| Groups | *t* | P(MC) | *t* | P(MC) | *t* | P(MC) |
| **2010 x 2012** | 2.99 | 0.001 | 4.17 | 0.001 | 2.72 | 0.001 |
| **2010 x 2014** | * | * | 3.31 | 0.001 | 2.16 | 0.002 |
| **2012 x 2014** | * | * | 2.03 | 0.005 | 2.79 | 0.001 |

**Table 4** One-way Anova and *pos-hoc* Tukey-HSD results for total abundance of the main copepods species in response to the interannual factor in FN (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSP (Saint Peter and Saint Paul Archipelago).

| | | | | | *Pos-hoc* (Tukey – HSD) | | |
|---|---|---|---|---|---|---|---|
| Source | df | MS | F | P | 2010 x 2012 | 2010 x 2014 | 2012 x 2014 |
| **Interannual<br>2010 x 2012<br>FN** | ***Acrocalanus longicornis*** | | | | | | |
| | 1 | 9.90 | 16.87 | < 0.01 | - | - | - |
| | ***Scolecithrix danae*** | | | | | | |
| | 1 | 5.50 | 10.17 | < 0.01 | - | - | - |
| | ***Corycaeus speciosus*** | | | | | | |
| | 1 | 7.97 | 14.6 | < 0.01 | - | - | - |
| | ***Nannocalanus minor*** | | | | | | |
| | 1 | 3.12 | 6.37 | 0.01 | - | - | - |
| | ***Oithona plumifera*** | | | | | | |
| | 1 | 3.91 | 10.6 | 0.03 | - | - | - |
| | ***Farranula gracilis*** | | | | | | |
| | 1 | 8.04 | 19.59 | < 0.01 | - | - | - |
| **Interannual<br>2010 x 2012 x 2014<br>RA** | ***Acrocalanus longicornis*** | | | | | | |
| | 2 | 10.08 | 28.76 | < 0.01 | < 0.01 | < 0.01 | - |
| | ***Scolecithrix danae*** | | | | | | |
| | 2 | 2.84 | 9.13 | < 0.01 | < 0.01 | < 0.01 | - |
| | ***Nannocalanus minor*** | | | | | | |
| | 2 | 6.85 | 23.31 | < 0.01 | < 0.01 | < 0.01 | 0.04 |
| | ***Undinula vulgaris*** | | | | | | |
| | 2 | 3.62 | 8.39 | < 0.01 | < 0.01 | < 0.01 | - |
| | ***Clausocalanus furcatus*** | | | | | | |
| | 2 | 4.04 | 8.32 | < 0.01 | < 0.01 | - | 0.02 |
| | ***Euchaeta marina*** | | | | | | |
| | 2 | 7.60 | 19.85 | < 0.01 | < 0.01 | < 0.01 | - |
| | ***Oithona plumifera*** | | | | | | |
| | 2 | 5.66 | 10.32 | < 0.01 | - | < 0.01 | 0.03 |
| | ***Corycaeus speciosus*** | | | | | | |
| | 2 | 3.91 | 13.78 | < 0.01 | < 0.01 | - | 0.02 |
| | ***Farranula gracilis*** | | | | | | |
| | 2 | 6.07 | 25.23 | < 0.01 | < 0.01 | < 0.01 | - |
| **Interannual<br>2010 x 2012 x 2014<br>SPSP** | ***Clausocalanus furcatus*** | | | | | | |
| | 2 | 9.45 | 12.23 | < 0.01 | < 0.01 | - | 0.01 |
| | ***Oncaea media*** | | | | | | |
| | 2 | 17.34 | 19.42 | < 0.01 | < 0.01 | 0.01 | < 0.01 |
| | ***Corycaeus speciosus*** | | | | | | |
| | 2 | 2.26 | 5.19 | 0.01 | - | 0.02 | 0.02 |
| | ***Farranula gracilis*** | | | | | | |
| | 2 | 4.11 | 7.90 | < 0.01 | < 0.01 | - | - |
| | ***Undinula vulgaris*** | | | | | | |
| | 2 | 5.90 | 14 | < 0.01 | 0.01 | - | < 0.01 |
| | ***Calocalanus pavo*** | | | | | | |
| | 2 | 2.75 | 5.92 | < 0.01 | - | 0.03 | < 0.01 |
| | ***Euchaeta marina*** | | | | | | |
| | 2 | 5.80 | 17.84 | < 0.01 | < 0.01 | | < 0.01 |

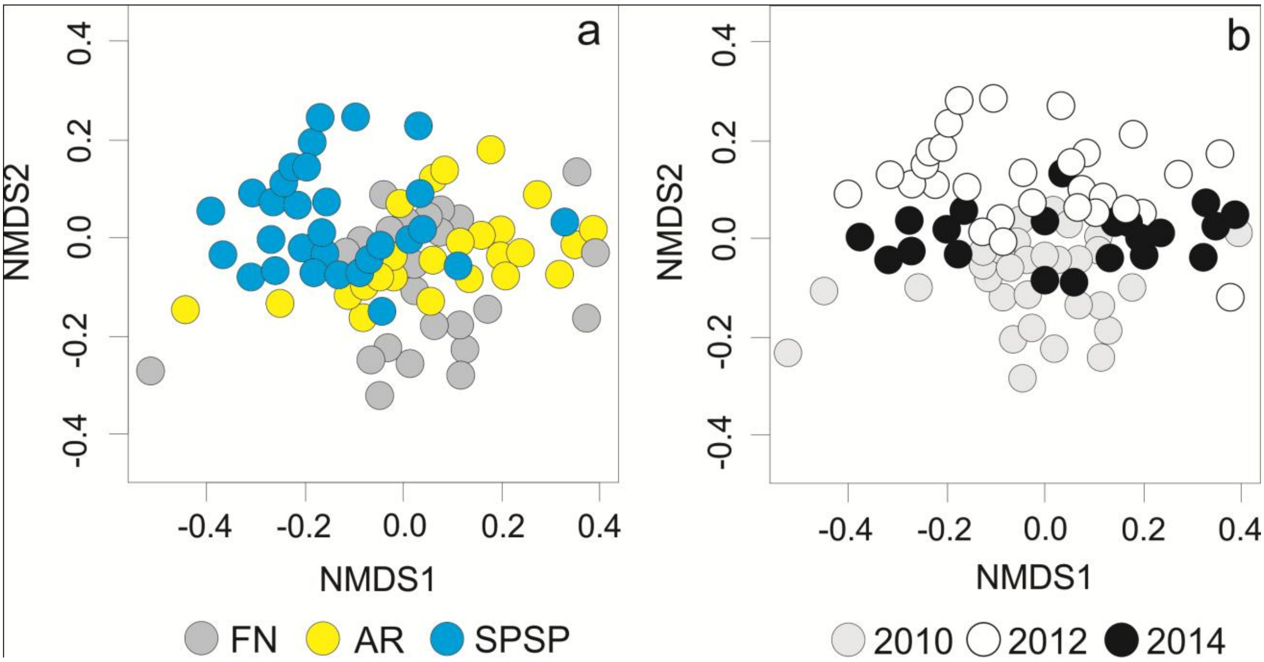


**Figure 5** MDS ordination of the copepod assemblages in response to the: a) Spatial factor (FNA – Fernando de Noronha Archipelago (Light gray circle), RA - Rocas Atoll (Yellow circle) and SPSP – St. Peter and St. Paul Archipelago (Blue circle): b) Interannual factor (2010 - (Light gray circle); 2012 (white circle); 2014 (Black circle) in the Tropical Southwestern Atlantic Ocean.

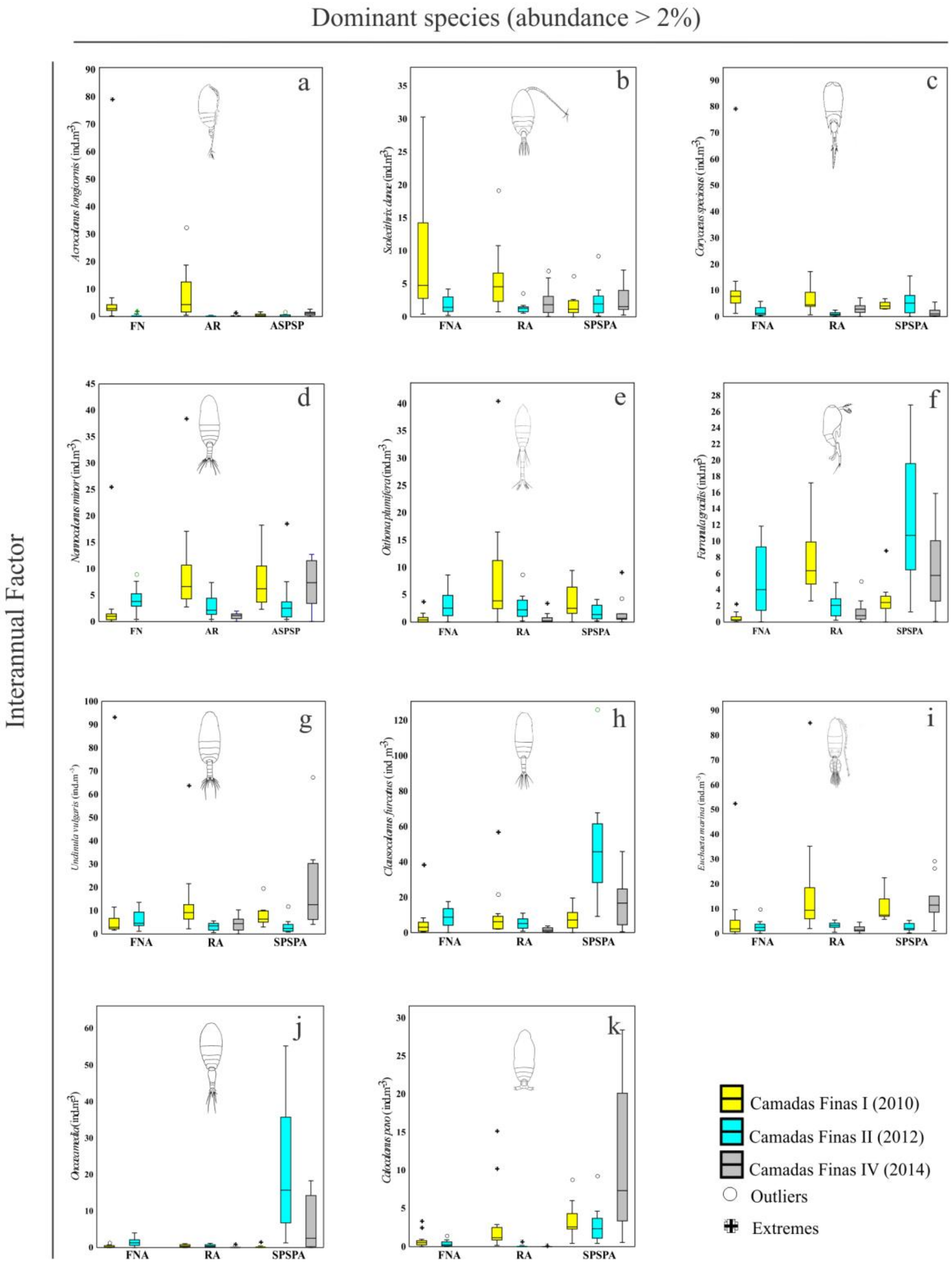


**Figure 6** Interannual difference on the most abundant species: a) *A. longicornis*; b) *S. danae*; c) *C. speciosus*; d) *N. minor*; e) *O. plumifera*; f) *F. gracilis*, g) *U. vulgaris*; h) *C. furcatus*; i) *E. marina*; j) *O. media* and k) *C. pavo* in the context of project *Camadas finas oceânicas* I (2010), II (2012) and III (2014) in FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago).

## 3.5. Indicator species

The Indval analysis allowed the identification of species indicator of physical events of mesoscale (wakes, influence of masses of water and upwelling) in the studied island environments. Furthermore, the analysis showed species considered important migrants that contribute to the vertical particles flow in the tropical Atlantic.

Therefore, FN was represented by three significant indicator (characteristic) species. Indicator Values (IndVal) of more than 50% were found for the species*:* *Euchaeta marina* (Juvenile) (IndVal = 87%; p = 0.005), *Acrocalanus gracilis* (IndVal = 69%; p = 0.005), *Corycaeus* (*Onychocorycaeus*) *ovalis* (IndVal = 66%; p = 0.005) and *Scolecithrix danae* (IndVal = 54%; p = 0.005). *Lucicutia clausii* (IndVal = 50%; p = 0.04) was the only species considered by the analysis as indicator of the RA. Two species were associated to the SPSPA, with Indicator Values of more than 50%: *Subeucalanus longiceps* (IndVal = 69%; p = 0.005) and *Oncaea scottodicarloi* (IndVal = 58%; p = 0.005).

The group of species that were strongly related to the year 2010 were: *Euchaeta marina* (Juvenile) (IndVal = 80%; p = 0.005), *Acrocalanus gracilis* (IndVal = 64%; p = 0.005) and *Corycaeus* (*Onychocorycaeus*) *ovalis* (IndVal = 61%; p = 0.005). *Aetideus acutus* (IndVal = 59%; p = 0.005) was considered an indicator species of 2012. On the other hand, *Subeucalanus longiceps* (IndVal = 79%; p = 0.005), *Candacia varicans* (IndVal = 64%; p = 0.005) and *Candacia cheirura* (IndVal = 54%; p = 0.005) were considered indicative of the year 2014.

Regarding to the time of day factor, seven species showed Indicator Values of more than 50%, being strongly related to the nocturnal period: *Pleuromamma borealis* (IndVal = 82%; p = 0.005), *Pleuromamma* spp. (Juvenile) (IndVal = 81%; p = 0.005), *Lucicutia longicornis* (IndVal = 80%; p = 0.005), *Pleuromamma gracilis* (IndVal = 76%; p = 0.005), *Pleuromamma abdominalis* (IndVal = 71%; p = 0.005), *Pleuromamma robusta* (IndVal = 526%; p = 0.005) and *Pontellina plumata* (IndVal = 525%; p = 0.01). The species *Oncaea mediterranea* was the only considered indicator of the upstream transect (IndVal = 69%; p = 0.005).

## 4. DISCUSSION

The study of the abundance, diversity and structure of the epipelagic copepods in the islands of the Tropical Southwestern Atlantic indicated a remarkable change in the spatial distribution of copepod assemblages, where a high abundance and a low richness were verified for the remote St. Peter and St. Paul's Archipelago. The insular systems of FN and RA present homogeneity of the quali-quantitative composition of planktonic copepods. In addition, the single and smallest atoll of the South Atlantic Ocean (RA) presented the greatest diversity of copepods and this showed no differences in relation to FN, but was higher than that recorded in SPSP.

The copepod assemblages were dominated by species often found in tropical and subtropical waters of the world (Satapoomin et al., 2004; Hidalgo et al., 2010). Although the present study used 300 µm mesh size net to high contribution in terms of the relative abundance of small-sized copepods for SPSP and RA corresponding respectively to 65% and 39%.

The importance of small-sized copepods at shelf, open ocean and oceanic island off Southwestern Brazil was pointed out by many authors (e.g. Neumann-Leitão et al., 2008; Miyashita et al., 2009; Melo et al., 2012; 2014; Melo Junior et al., 2016), whose dominance in oligotrophic waters is explained by the high efficiency of nanoplankton capture compared to larger size phytoplankton species (Zervoudaki et al., 2011). The dominance in terms of abundance and biomass of small-sized copepods was also recorded in oligotrophic waters of the Mediterranean Sea (Zervoudaki et al., 2007). This is explained because in oligotrophic areas small-sized copepods are critical intermediates between the classical and the microbial food web (Turner, 2004).

The hypothesis of spatial differences on total copepod abundance was verified in the present study, where SPSP showed a significantly higher average value compared to the Fernando de Noronha Archipelago and Rocas Atoll, but the values of average abundance registered for the islands from the Tropical Southwestern Atlantic are considered like others registered in Tropical environments (Hwang et al., 2007; López & Anadón, 2008). These results were reinforced by PERMANOVA, which indicated a quantitative taxonomic composition difference among the islands, showing that the SPSP has a lower average similarity between the groups when compared to FN and RA.

The value of abundance recorded in SPSP was considered higher than those recorded in the Egadi Island Archipelago (central Mediterranean) (Brugnano et al., 2010), Gulf Stream (Wishner and Allison, 1986) and Southeastern Taiwan Strait (Lo et al., 2004), but it was lower than that observed in the El Bajo Espiritu Santo seamount (González-Armas et al., 2002).

A greater similarity between the quali-quantitative composition of the copepod assemblages between FN and RA can be explained by the proximity of the islands since these are located at the same geographical latitude probably forming a metacommunity. The ecological connectivity between FN and RA has already been demonstrated, where papers show the role of RA as a "Stepping stones" for marine species transported from FN to RA (Rocha, 2003; Sampaio et al., 2004; Tchamabi et al., 2018).

The similarity found between the species of the fauna of FN and RA is probably due to the presence of shallow oceanic banks located between the two islands and the local hydrodynamic mechanisms as the strong influence in both the areas of the westward flow of the Central South Equatorial Current (cSEC) (Tchamabi et al., 2017). Planktonic copepods utilize ocean currents to help their dispersal, besides the currents acting as gene-exchange corridors (Teschima et al., 2016). Thus, the FN Island provides species of copepods to RA via currents systems.

Seamounts are characterized as areas of high biomass and diversity in relation to the surrounding benthic and pelagic habitats, where due to their high topography are conceptualized as islands of habitats in the deep sea (Denda et al., 2016). The few works carried out in SPSP, in the physical and biological context, showed that the production of phytoplankton and zooplankton increases during the rainy season (Araújo & Cintra, 2009). The sampling of the present study occurred between winter and spring when the average value of abundance registered was very close and many times higher than those registered at the time considered productive in SPSP by Díaz et al. (2009) and Melo et al. (2012; 2014).

Araújo & Cintra (2009), performing a modeling study in SPSP, suggested that the integrated action of physical mechanisms (subsurface action) and trophically subsidized enrichment mechanism (surface action) both functioning independently could be contributing to sustain the high ecological productivity in the surroundings of SPSP. According to this author the physical mechanism is characterized by the displacement of the ITCZ (*Intertropical Convergence Zone)* further north favoring the intensification of the trade winds (SE) to the surface, causing an increase in EUC (*Equatorial*

*Undercurrent*) intensity and weakening of the SEC (*South Equatorial Current*) surface. The sampling of the present work occurred during this period. The interaction of the EUC (W-E) with the topography of the island generates instability downstream of the EUC's influence on the SPSP. These disturbances occur strongly from 100m to 250m deep. With the average positioning of the end of the euphotic layer at 100m depth, it is believed that the punctual, but constant, processes observed to the east of the SPSP can contribute to the nutrient enrichment at the base of the photic layer (Araújo & Cintra, 2009). This enrichment increases planktonic productivity, especially the copepod assembly in this period.

Although geographically isolated, the SPSPA is not independent, therefore we suggest that in association with these biotic (aggregation) and abiotic (nutrient enrichment) factors the high copepods abundance may also be caused by the influence of another island system (nearest refuge hypotheses). According to this hypothesis, habitats far away and isolated from neighboring habitats, would be colonized more quickly because the animals use any habitat to establish themselves, since they are far from other refugees (Virnstein & Curran, 1986).

These evidences are growing, demonstrating high abundance of copepods in isolated habitats that present high richness and abundance of seagrass and brown algae (Russell et al., 2005). Rudorff et al. (2009) demonstrated by modeling the dispersal of spiny lobster larvae in the Tropical Atlantic, where the virtual larvae released on Ascension Island in the middle of the South Atlantic arrive at the SPSPA via cSEC, reinforcing our hypothesis that the SPSPA functions as a refuge for these larvae in the middle of the ocean.

The enrichment phenomenon downstream of the islands was verified in the present study, where the significant increase in copepod abundance was considered an indicative of the "*Island Mass Effect*". Similar result was recorded for the Canary Islands where the presence of eddies downstream of the islands suggest that accumulation was the causative mechanism for the presence of high zooplankton biomass (Hernandez-Leon et al., 2001). A mechanism of larval retention downstream in the inner coastal zone of Fernando de Noronha was also considered as a response to the *"Island Mass Effect"*, as suggested by Santana et al. (2018). Evidence provided by Jales et al. (2015), confirms the significant increase in chlorophyll-a and nutrient concentration downstream of RA when the temperature in the mixed layer was reduced due to the influence of the South Atlantic Central Water.

### 4.1. Copepod assemblage structure

The hypothesis that the assemblage of copepods differs between the sampling years has been proven through the Permanova with significant interaction between spatial *vs.* interannual factors. The species of copepods that dominated the insular complex of FN and RA are considered common in tropical surface waters (Champalbert et al., 2005; Cornils et al., 2010) and have already been registered occurring in high abundance in the neritic and oceanic regions of the Southwestern Tropical Atlantic (Neumann-Leitão et al., 2008; Dias & Bonecker, 2009; Díaz et al., 2009; Melo, 2012; 2014; Melo Junior et al., 2016). In 2010, the islands were sampled at the end of July, beginning of August, when the central branch of the South Equatorial Current (cCSE) presents higher intensity (Richardson & McKee, 1984). The thermohaline structure of FN in 2010, during higher intensity of the cSEC presented an isolines ascendance able of destabilizing the thermohaline structures in the SW transect, downstream of the island (Tchamabi et al., 2017). The author also confirmed through simulation models that during the strengthening period of the SEC, flowing westward and interrupted by FN and RA, occurs the formation of current wake with formation of wake eddies downstream. This effect acts by cooling waters in the base of the mixture layer depth, biologically impacting around of these islands causing an increase in the productivity.

The expedition of the year of 2012 in the SPSP occurred in a period of intensification of the South Equatorial Current (SEC) and minimum intensification of the northern branch of the South Equatorial Current (nCSE) (Brandt et al., 2006). Turbulent processes generated due to the strong action of a current can cause indirect effects on the availability of food for copepods (Alcaraz, 1997). Small-sized copepods dominated the assemblage in SPSP in 2012. In oligotrophic regions small copepods are important components, where the microbial community dominates (Turner, 2004). In islands and slopes of seamounts the main source of ammonia for autotrophic cells comes from regeneration in the pelagic microbial food web (Cordeiro et al., 2013). Studies on microplanktonic community performed in the SPSP based on samples of vertical hauls revealed a high abundance, highly diversified composed of tintinids, radiolarians and heterotrophic dinoflagellates, being these important ammonia producers in tropical oligotrophic waters (Costa et al., 2018). Thus, the high abundance of epipelagic copepods registered for the years 2012 in the SPSP is probably sustained by this important contribution of the microbial loop and the link that it establishes with the classic food web.

### 4.2. Species diversity

There is a consensus and almost a law in ecology that the number of species observed (micro and macroscopic communities) increases with the area investigated (Triantis et al., 2012). Historical and biogeographic characteristics (insulation, reef type, geomorphological characteristics and age) of the island systems from the Tropical Southwestern Atlantic make these habitats unique, presenting different dynamics when compared to the Indo-Pacific and Caribbean (Longo et al., 2015).

The SPSP is considered the smallest (3.5 $Km^2$) and most isolated (further from the nearest reef 630 Km de Fernando de Noronha) Archipelago of tropical islands in the world and further from the continent (1,010 km) (Luis et al., 2015). Although SPSP (129 taxa registered) has presented a richness of copepod species lower than FN and RA, it is important to note that the values showed in the present study were higher than that observed in this environment by Melo et al. (2014), but were associated to the sampling method and effort. A total of 38 copepod taxa were identified through subsurface hauls conducted for 10 minutes with a 300 μm mesh size net and a mouth diameter of 30 cm. Likewise, our results were also higher than those recorded in the El Bajo Espiritu Santo seamount, in the Southern Gulf of California (González-Armas et al., 2002).The author recorded 46 copepod species sampled through cylindrical-conical plankton net with a 60 cm diameter mouth and a 505 mm mesh net.

On the other hand, Fernando de Noronha was the Archipelago where it was registered the greatest species richness (133 taxa registered), this was eight times higher than the number of taxa observed in the coastal area of FNA; subsurface trawls with 300 μm mesh size net (Campelo et al., 2018) and 1.2 times higher than recorded in Canary Island; subsurface trawls, with 475 μm mesh size net (Hernández-León, 1998).

The FN Archipelago is larger in size (160.5 $km^2$), located 350 km off the Brazilian coast and is closer to Rocas Atoll 124km (Barroso et al., 2016). Quantitative studies of copepod assemblages in FN are scarce, mainly due to logistic issue (Neumann-Leitão et al., 2008; Larrazabal et al., 2009; Campelo et al., 2018). The greatest richness recorded in FNA may also be associated with the connection with the continent through the chain of submarine mounts increasing the rate of immigration according to the theory of the biogeography of the islands (Barroso et al., 2016).

The relationship between richness of copepod species and the area, insulation or age of an island has received limited attention on the islands of the Southwest Atlantic Ocean, being studied and verified for other marine groups in the same geographic area (Luiz et al., 2015; Hachich et al., 2015; Barroso et al., 2016). The results of these studies verified a high endemism (reflection of the insulation effect) and low species richness of gastropods, reef fish and seaweed for SPSP, with the increase of species richness of these groups in islands that had a larger area (FN). The results of Hachich et al. (2015) reinforce the strong effect of island size showing that the geographic insulation in Atlantic Ocean areas seems not to be a limiting factor in the richness of groups with high dispersion capacity (Kinlan & Gaines, 2003).

Zooplankton, specifically copepods, have a high dispersal capacity mainly via ocean currents, thus our data suggest that the lowest value of average copepods richness occurs in response to a smaller shallow platform area (3.5 km$^2$) observed for the SPSP in comparison to the RA and FN, being these reinforced by previous studies which proved that species of pelagic or coastal microcrustacean have a significant species-area relationship (Dodson, 1992; Fryer, 1985; Rezai et al. 2005; Saitoh et al. 2011). According to Longato et al. (2018) the relationship between zooplankton richness and area in Brazilian lakes depend both on the size and type of the environments. Browne, (1981) found a significant species-area power curve for crustacean zooplankton in 13 lakes in central New York. Thus, we consider important that other studies investigate the effect of the size of the area of the Tropical Southwestern Atlantic islands on planktonic copepod richness.

Biodiversity is a key biological parameter influencing multiple aspects of ecosystem structure and function (Hooper et al., 2005). In the present study, the greatest diversity of copepods was recorded for the biogenic reef of the Rocas Atoll. The Atoll is the island that has the most extensive shallow platform area (239.5 km2), consequently generating a greater amount of microhabitats. The biogenic reef of Rocas can be considered an oceanic Atoll for presenting an elliptical platform to circulate, a reef ring made of calcareous algae, developed at the top of submerged volcanic hills, whose base is more than 4000 m deep in the ocean floor, has a shallow lagoon, sandy islands and a greater width of the reef ring in the windward portion (Soares et al., 2011).

All these characteristics define the Rocas Atoll as an environment of great heterogeneity due to its complexity of vertical and horizontal structure leading us to suggest that the greatest diversity of copepods registered for this island is based on the hypothesis of "environmental heterogeneity" (Connor & McCoy, 1979) where the increase in the number of habitats and its structural complexity leads to a greater diversity of species.

We also consider that in the present work the diversity of FN was considered similar to that of RA, which we reinforce, that is in response to the connectivity of these environments. The difference in diversity occurred between RA and the remote SPSP. However it is important to note that our data are based on the Shannon-Winer diversity index of and this is a reflection of alpha diversity (local diversity) (Bonecker et al., 2013). Other diversity metrics have been applied to investigate faunistic composition and richness/diversity, such as the estimation of beta diversity (Baselga, 2010). It measures the heterogeneity of the community in a given environment (Nogueira et al., 2018). However, the degree of spatial connectivity between environments directly influences the measure of beta diversity that may reflect two different phenomena: spatial species turnover and nestedness of assemblages (Baselga, 2010).

Communities that are highly connected (such as FN and RA) by hydrological connections and smaller distance between habitats have lower beta diversity index due to the high exchange of individuals between these communities via active or passive dispersion (Lopes et al., 2014). A fruitful avenue for further research would be to extend the approach used here to test specific correlates of zooplankton beta diversity patterns in FN, RA and SPSP Islands, aiming mainly the realization of conservation strategies (Lopes et al., 2014).

From the integrated analysis of the data we recorded a greater diversity at night. This is result of the typical vertical migration behavior of zooplankton which allows, for example, species to ascend from deep layers to the surface at night, mainly in search of food. This movement displaces a large amount of biomass and it contributes to that species occurring in mesopelagic regions are registered on the surface, thus influencing an increase in diversity in this oceanic region at night (Diaz et al., 2009; Melo et al., 2012; 2014).

### 4.3. Indicator species

Variations in the meteorological regime, regional geomorphological characteristics and anthropogenic impacts together establish the particular hydrographic regime of each region and consequently the taxonomic characteristics and temporal-spatial dynamics of the copepod assemblage (Brandini et al., 1997). Several studies have attempted to recognize indicator species of coastal and oceanic environments, seasonality or impacted areas in the waters of the Tropical Southwestern Atlantic (Sarmento & Santos, 2012; Campos et al., 2017; Campelo et al., 2018; Neumann-Leitão et al., 2018). Results of the climatological simulation performed by Tchamabi et al. (2017) for the FN show the occurrence of wake in the island. These mesoscale structures have a strong influence on the thermodynamic properties that surrounds this insular complex, contributing to the increase of planktonic productivity (Tchamabi et al., 2017). We considered that the species *E. marina*, *A. gracilis* and *C.* (Onychocorycaeus) *ovalis* (Campelo et al., 2018) were favored by the increase of the planktonic productivity registered in the surroundings of FN in 2010 as a consequence of wake.

The *Lucicutia clausii* copepod indicative of the biogenic reef of the RA is a species classified as mesopelagic and migratory (Lo et al., 2004; Melo et al., 2014). Dias et al. (2010) registered this species through vertical hauls on the northern coast of Rio de Janeiro, Brazil occurring in the South Atlantic Central Water Masses (SACW). Therefore, the high frequency of occurrence this species in the Rocas Atoll represents a reinforcement of the influence of SACW verified in this island by Tchamabi et al. (2017) and Jales et al. (2015).

The species *Subeucalanus longiceps* stood out as a good indicator of SPSP as well as the year 2014. Members of the Eucalanidae family occur across the world's oceans in the epipelagic and mesopelagic layer in both neritic and oceanic regions (Bradford-Grieve et al., 1999). They are mainly primary consumers ingesting small particles, phytoplankton cells, and exhibiting wide forms of feeding (Goetze, 2003). Dias et al. (2010) registered this species occurring in the Intermediate Antarctic Water (IAW) in an area of occurrence of upwelling in Southeast Brazil, but some species of the Eucalanidae family were verified by Kasyi (2006) and Ohman et al. (1998), also occurring in upwelling systems. Evidence of upwelling in SPSP is not confirmed

(Travassos et al., 1999; Macedo et al., 2009), but species of copepods indicative of this phenomenon as *Phaenna spinifera* (Melo, 2012) and of species typically nocturnal dominating daytime samples (*Pleurommama* spp. and *Heterorhabdus* spp.) were mentioned by Díaz et al. (2009). Thus, the high frequency of occurrence of *Subeucalanus longiceps* in SPSP reinforces the hypothesis of an upwelling effect in the area.

The four most common species in the South Atlantic oceanic islands (*Pleuromamma abdominalis*, *Pleuromamma borealis*, *Pleuromamma gracilis* and *Pleuromamma robusta*) were recognized by the analysis as indicators of the nocturnal period. This species are considered to be strong vertical migrators which remain at depth (>200 m) during the daytime and perform night excursions to the surface layer (justifies their high frequency of occurrence at night) (Melo et al., 2012; 2014). Thus, these migrants play an important role in the active transport of carbon, nitrogen, and phosphorous out of the euphotic zone and into the deep sea, where they excrete their lipid reserves (lipid pump hypothesis; Teuber et al., 2014; Jónasdóttir et al., 2015).

In relation to transects, *Oncaea mediterranea* was the only species that best characterized downstream conditions off the investigated island systems. An inspection of the oral cavity of *Oncaea* copepodites led to the assumption that they could feed on material located on the surface (Paffenhofer, 1993). Nauplius, copepodites or adults of *Oncaea mediterranea* do not create feeding current, limited swimming performance and the encounter with food must be created by both the food particle and the copepod jumping repeatedly to locate a food-rich environment (Paffenhofer, 1993). Therefore, the high frequency of these specimens upstream of the islands may be associated with the formation of eddies as a result of the encounter of contraries flows of currents and countercurrents that act in the islands. These eddies generate turbulence that promotes selection of phytoplankton life forms, increasing the availability of prey to the *Oncaea mediterranea* which is a species of low swimming ability.

## 5. CONCLUSIONS

In conclusion, we show that the taxonomic composition, abundance, diversity and richness of copepods are mainly associated to mechanisms of ecological connectivity and probably to the size of the habitat in the islands of the Tropical Southwestern Atlantic, thus:

(a) The smallest and remote SPSP Archipelago showed a taxonomic composition different from FN and RA, highest abundance and the lower species richness of copepods. All these findings show SPSP as the island environment of greater environmental heterogeneity, as a result of the strong influence of local currents that promotes a high productivity around the island;

(b) The greater similarity between the quali-quantitative composition and the copepods diversity between FN and RA is a result of the degree of connectivity between the environments, leading us to suggest that both comprise a single conservation unit;

(c) In July 2010, the islands of FN and RA were influenced by wakes, which resulted in an increase in planktonic productivity around these environments. We highlight in particular the high significant abundance of all species considered dominant in RA in July 2010, which was considered as a response to this increase of productivity on the island. In SPSP a higher number of copepod species showed high abundance values in September 2012. In this period the island is under strong intensity of the trade-winds and of the South equatorial current (SEC), promoting the formation of eddies and vertical mixing in the water.

(d) The participation of important vertical migrants such as: *P. abdominalis*, *P. borealis*, *P. gracilis* and *P. robusta* identified by the Indval analysis as indicators of the nocturnal period, justifies the increase in the diversity of copepod species at night between 0 - 200 m depth;

(e) The greater abundance of copepods to downstream is a result of the influence of surface and subsurface currents that wash the island by transporting and retaining the copepods on the protected side.

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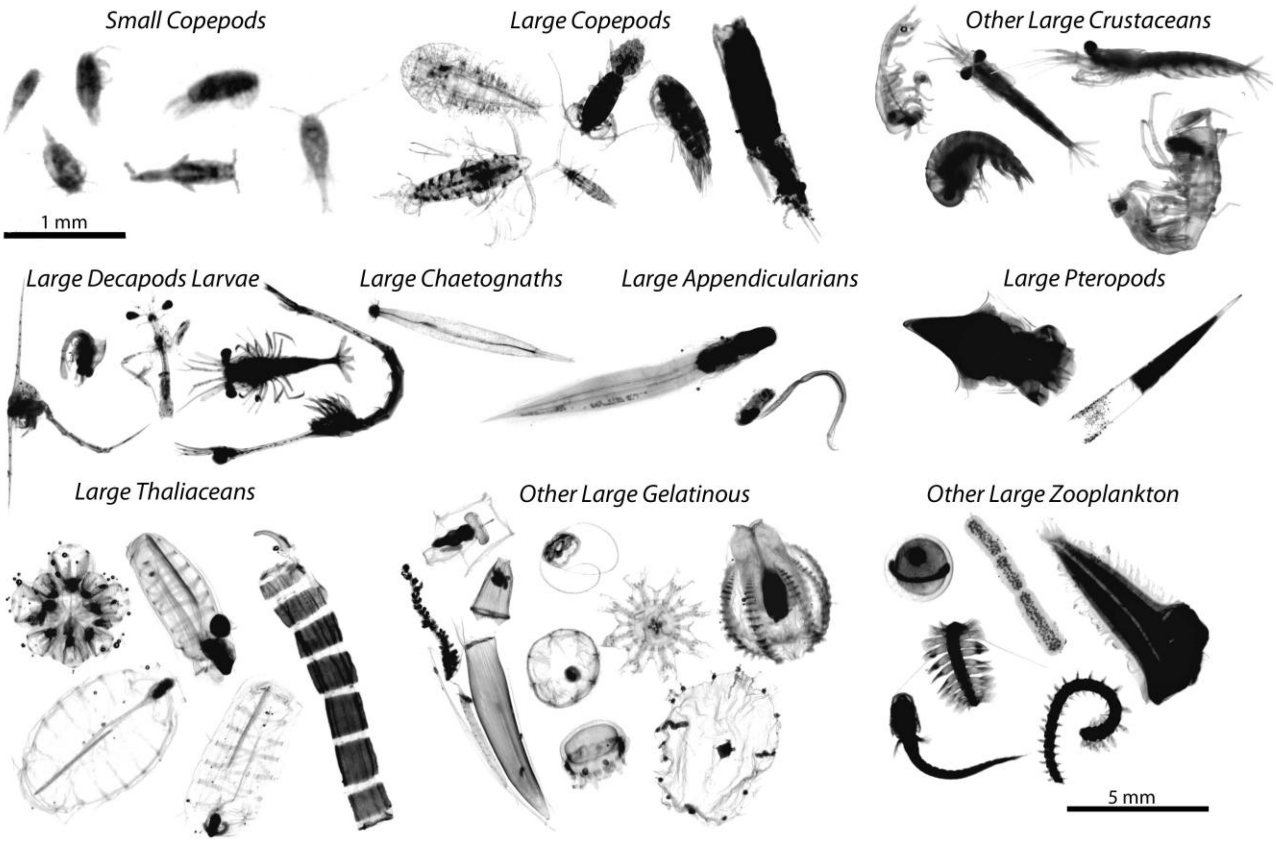
# CHAPTER 3 - Mesozooplankton abundance, biovolume and size in Marine Protected Areas in the Tropical Southwestern Atlantic



Fonte: Vandromme et al., 2011

**To be submitted to Journal of Marine Systems**

# Mesozooplankton abundance, biovolume and size in Marine Protected Areas in the Tropical Southwestern Atlantic

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## ABSTRACT

Abundance and biovolume are considered important indicators of ecosystem status and are particularly useful for marine resources management. The present study investigated the spatial (Fernando de Noronha archipelago *vs.* Rocas Atoll *vs.* St. Peter and St. Paul archipelago), temporal (July/2010 *vs.* September/2012 *vs.* August/2014), sampling time (Day *vs.* Night) and transect (Upstream *vs.* Downstream) changes on established ecological indicators. Samples were analyzed using the semi-automated system ZooScan. A total of five size classes were established: 0.3 to 1 mm; 1 to 2 mm; 2 to 3 mm; 3 to 4 mm; 4 to 5 mm and > 5 mm. Results show the effect of the spatial factor on abundance and biovolume of mesozooplankton, whose average values were significantly elevated in the remote St. Peter and St. Paul archipelago (SPSPA). The high abundance of the smaller size class (0.3 to 1 mm) and the highest contribution in biovolume in organism > 5 mm in all the island systems is a typical characteristic of tropical oligotrophic environments. We also highlight that the smaller fraction was dominant in the SPSPA, which indicates that it is likely to be the most productive island and also represents an important refuge for migratory species. The lowest average values of abundance and biovolume were verified in July/2010. Highest values occurred in August / 2014 with an important contribution in biovolume from organisms larger than 5 mm. Our results suggest that the low productivity in July/2010 could be a response to thermal stress as a consequence of the El Ninõ event. On the other hand, the high productivity in August/2014 should be a response to increases in local hydrodynamism in the area, caused by local currents flow increase and vertical mixing. Important vertical migrants were Ostracoda, Euphausiacea, Decapoda, Mollusca, and Cnidaria, which had higher abundances during the night due to diel vertical migration. These were also organisms with a higher body volume, especially in the size classes: 1 to 2 mm; 4 to 5 mm and > 5 mm. These large organisms are considered to be strong migrators and important vehicles in the biological carbon pump. In addition, it is important to consider that the smaller organisms (0.3 to 1 mm) did not respond to the effect of the sampling time, which can be explained either by predation or by the absence of vertical migration. The hypothesis of the "*Island Mass effect*" has not been statistically proven, although there a general tendency towards higher mesozooplankton size, abundance and biovolume over the downstream side off all islands.

**Keywords**: Island Mass Effect, Brazil, productivity, temporal distribution, vertical migration

## 1. INTRODUCTION

The South Atlantic Ocean is extremely important in global climate change because there are a number of key zones where oceanic signals on intraseasonal to decadal scales occur (Silva et al., 2009). The oligotrophy of Tropical Southwestern Atlantic is a consequence of a permanent thermocline, however, the surroundings of oceanic islands are known as true "hotspots of life in an oceanic desert" (Tchamabi et al., 2017). The occurrence of eddies and turbulence in islands, atolls, and seamounts causes an outcropping of subsurface enriched waters to the surface layer causing increases in plankton productivity, mass and energy fluxes along the trophic chain (Oxenford et al., 1993).

The island systems of Fernando de Noronha Archipelago, Rocas Atoll, and St. Peter and St. Paul Archipelago are important Marine Protected Area (MPA's) located in the Tropical Southwestern Atlantic that integrate the "Blue Amazon". This territory is rich in biodiversity and ecosystem services and similar in extension to our terrestrial tropical rainforest (Soares et al., 2017). These islands are Environmental Protected Areas, created in June 1986, covering an area of 79,706 ha (Alves and Castro, 2006). Their geographic (size, isolation, and distance from the mainland) and biological features (biomass, diversity and richness of planktonic, benthic, nektonic communities and the presence of tropical reefs.) make these marine habitats unique (Luiz et al., 2015, Soares, 2018).

These MPA's are subject to anthropogenic pressures of local, regional, and global order such as global warming, predatory fishing, marine pollution, acidification, and introduction of exotic species (Soares, 2018). These pressures have the potential to cause serious impacts on marine ecosystem functioning, changing the structure of the pelagic trophic web, particularly the zooplankton. Zooplankton are critical to the functioning of ocean food webs since they: (1) control phytoplankton production; (2)

are food source for higher trophic levels; (3) represent an important link between the classic trophic chain and the microbial loop; (4) export particulate organic matter (POM) used by bacteria, and (5) excrete nutrients that can be recycled by phytoplankton (Lowry et al., 2004; Wassmann et al., 2006; Richardson, 2008; Dai et al., 2016).

Zooplankton abundance and biovolume vary across a wide range of time and spatial scales and are highly useful estimators for marine resource management (Basedow et al., 2010; Brucet et al., 2010; Gaedke, 1992; Marcolin et al., 2015a; Medellín-Mora and Escribano, 2013; Thompson et al., 2013). These fluctuations occur in ocean systems in response to oceanographic conditions (winds, currents, and upwelling) as well as in response to organisms life cycles, migration, reproductive strategies, feeding approach, size, and intra-interspecific relationships (Heath, 1995; Zhou, 2006; Zhou and Huntley, 1997; Leandro, 2007).

In addition to abundance and biovolume, the body size has been appointed as important descriptors of plankton community structure and functioning (Vandromme et al., 2012), besides being an important indicator of the transfer of energy up the trophic web, influenced the mechanisms of carbon export and sequestration (San Martin et al., 2006). Quantitative functional traits such as zooplankton size, body composition, or physiological measurement of respiration rate, excretion, egestion, and growth directly affect the stock and flow of matter in an ecosystem (Hébert et al., 2016). Furthermore, corporeal size is associated with the competitive capacity of organisms within a population, implying species coexistence, predation, and niche selection (Chase et al., 2002).

The dichotomy between top-down and bottom-up forces acting on zooplankton communities has motivated research in ecology once that have consequences on organism size structure (Suthers et al., 2006; Marcolin et al., 2013; Marcolin et al., 2015; Sato, et al., 2015; Dai et al., 2016). This is because the heterogeneity of zooplankton community distribution is also controlled by bottom-up (changes in the physical environment and/or food resource) and top-down (changes in predation) mechanisms (Ji and Sterget, 2013).

Many studies have reported the high abundance of zooplankton of smaller size in high productivity ecosystems (Champalbert et al., 2005; Finlay et al., 2011; Vergara et al., 2017; Sato et al., 2015; Zhou, 2006). In the zooplankton community the herbivores occupy the first trophic level and transfer the biomass of phytoplankton to the zooplankton community which generally occupies a smaller body size, this can be clearly observed in the biovolume spectrum (Zhou et al., 2009). Since the productivity of the zooplankton community can be assessed by its slope, a greater amount of herbivores will produce a steeper slope, indicating a greater productive potential (Zhou and Huntley, 1997; Zhou, 2006). On the other hand the predation on zooplankton, especially by fish, has an important effect on temporal variation in community body size, resulting in increased dominance of zooplankton of small body size (Bonecker et al., 2011; Finlay et al., 2011; Hambright, 2008).

Manual classification is still a method used to obtain data on the mesozooplankton community size structure (Heidelberg et al., 2010; Nakajima et al., 2014; Nakajima et al., 2017), although it requires intensive laboratory work, and the number of samples and organisms processed is very limited (Vandromme et al., 2012). To obtain a rapid form of information regarding the abundance and biovolume, semi-automated imaging tools (Zooscan) were designed. Abundance and biovolume data can be quickly estimated through the ZooScan system. This is based on the analysis of scanned images where through standard methods of recognition quantifies, measures and classifies the organisms of net zooplankton samples (Grosjean et al., 2004).

Our current knowledge on the zooplankton size structure of Tropical South Atlantic environments is limited (Marcolin et al., 2013; Marcolin et al., 2015a; 2015b). Most studies in this area usually focused on taxonomic information, diversity, and spatio-temporal variability of zooplankton community abundance (Neumann-Leitão et al., 2008; Brandão, 2012; Melo, 2012; 2014; Lira et al., 2014; Campelo et al., 2018a). In this context, the aim of the present study was to investigate the spatial, temporal, sampling time, and transect variability of the mesozooplankton abundance, biovolume, and size in Marine Protected Areas. Specifically, we hypothesized that:

Hypothesis 1: There is high abundance and biovolume of small mesozooplankton, indicative of high productivity in surroundings of the island systems;

Hypothesis 2: Temporal fluctuations of abundance and biovolume of mesozooplankton distribution are indicative of periods of higher or lower secondary productivity in surroundings of the island systems;

Hypothesis 3: High abundance, biovolume, and body size of mesozooplankton occur during night because of vertical migration;

Hypothesis 4: Downstream the Tropical Southwestern Atlantic Islands are places of plankton retention, implying higher abundances, and biovolume, especially from small mesozooplankton.

## 2. MATERIALS AND METHODS

### 2.1. Study Area

The Fernando de Noronha Archipelago (FNA) (3º50’24”S and 32º24’48”W) and the Rocas Atoll (3°51’S and 33°49’W) are located at approximately the same geographical latitude (Figure1), where they are in alignment with seamounts developed along the Fernando de Noronha Fracture Zone, in the meso-Atlantic Ridge (Almeida, 2006). The FNA is the largest oceanic island in Brazil, and it is extremely important for conservation because it is a great source of food and reproduction area for the marine fauna in the Tropical South Atlantic (Hachich et al., 2015). Rocas Atoll (RA) (Figure1) is the only atoll in the South Atlantic, it has a volcanic origin and coraline formation (Soares, 2018). This reef covers an area of 7.5 $km^2$ and it is the top of an underwater mountain whose base is 4,000 m deep. It is one of the smallest atolls in the world (Gherardi and Bosence, 2005). Rocas Atoll was the first Marine Biological Reserve of Brazil, created in 1979, involving an area of approximately 360 $km^2$, which is destined only for research and which is considered by UNESCO to be a natural patrimony of Humanity (Soares, 2018).

FNA and RA are under the influence of the central branch of the South Equatorial Current (cSEC) in the upper waters. This zonal current flows west-ward to join the North Brazil current (NBC) close to the Brazilian shore. The subsurface FNA and RA are impacted by the east-ward flow of the South Equatorial Undercurrent (SEUC) (Tchamabi et al., 2017).

In FNA the temperature recorded in July/2010, September/2012 and August/2014 remained constant (25°C) in both transects sampled and in depths between 60 meters downstream (July/2010) and 100 meters upstream (September/2012). A small variation of salinity was recorded between the years in the depths of 65 to 110 meters. The observed values were around 35.7 both upstream and downstream the island. Chlorophyll-a recorded values ranging from 1.5 $mg.m^{-3}$ upstream in July/2010 to 0.5 $mg.m^{-3}$ upstream in August/2014 (Silva, 2018, Personal communication).

In the Atol the temperature recorded its highest value (26.25°C) in September/2012 to 30 meters deep in the upstream transect and 85 meters downstream. The lowest temperature (23.23°C) was recorded in July/2010 between 90-117 meters upstream the Atol. The salinity of 34.95 was recorded in both transects, upstream (125-160 meters) and downstream (120-180 meters) in September/2012, while the value of 35.5 was observed in the other years in the transects sampled. Chlorophyll-a showed a higher concentration (1.5 mg.m$^{-3}$) in July/2010 in 55 meters upstream of the island (Silva, 2018, Personal communication).

The St. Peter and St. Paul Archipelago (SPSPA) (00°53'- 00°58'N and 29°16'-29°24'W) (Figure 1) is formed by a group of rocky islands located at 960 km off São Roque Cape, northeastern coast of Brazil, and 1890 km south-west off Senegal, West Africa (Luiz et al., 2015). It is one of the word's smallest and most isolated tropical islands (Soares and Lucas, 2018).

The SPSPA is part of a multiple-use Marine Protected Area (APA of the Fernando de Noronha – Rocas – St. Peter and St. Paul) characterizing it as an important habitat because it represents a migratory route for many pelagic species, with high endemism and high biological productivity (Campelo et al., 2018b). All of these significant biological and ecological characteristics of the SPSPA establishes it as an *"Ecologically or Biologically Significant Area"* – EBSA according to the Convention on Biological Diversity (CBD) (Soares and Lucas, 2018).

The presence of the seamount (SPSPA) directly influences the local hydrodynamic conditions and consequently the biological communities that live in its surroundings (Campelo et al., 2018b). The ocean dynamics that act on SPSPA is conditioned by the influence of the South Equatorial Current (SEC) flowing westward on the surface layer of this region and the Equatorial Undercurrent (EUC) that profiles the equator and flows east just below the surface, with its core positioned approximately 80 m deep. The interaction of the currents acting with the topography of the seamount causes the production of eddies, disturbances in the thermohaline structure and possible local mechanisms of resurgence (Araujo and Cintra, 2009).

The values of temperature, salinity and chlorophyll-a recorded in SPSPA were obtained from Silva, 2018, Personal communication. The temperature value of 25°C was observed in July/2010, September/2012 and August/2014 and in both transects studied at depths ranging from 47 meters downstream in August /2014 and 100 meters downstream and upstream in July/2010. Salinity around 36 PSU was observed in

September/2012 and August/2014 on both sides of the island. The highest chlorophyll-a values occurred in July/2010, but the maximum record was downstream of SPSPA 2.2 mg.m$^{-3}$ and 0.7 mg.m$^{-3}$ downstream in August/2014.

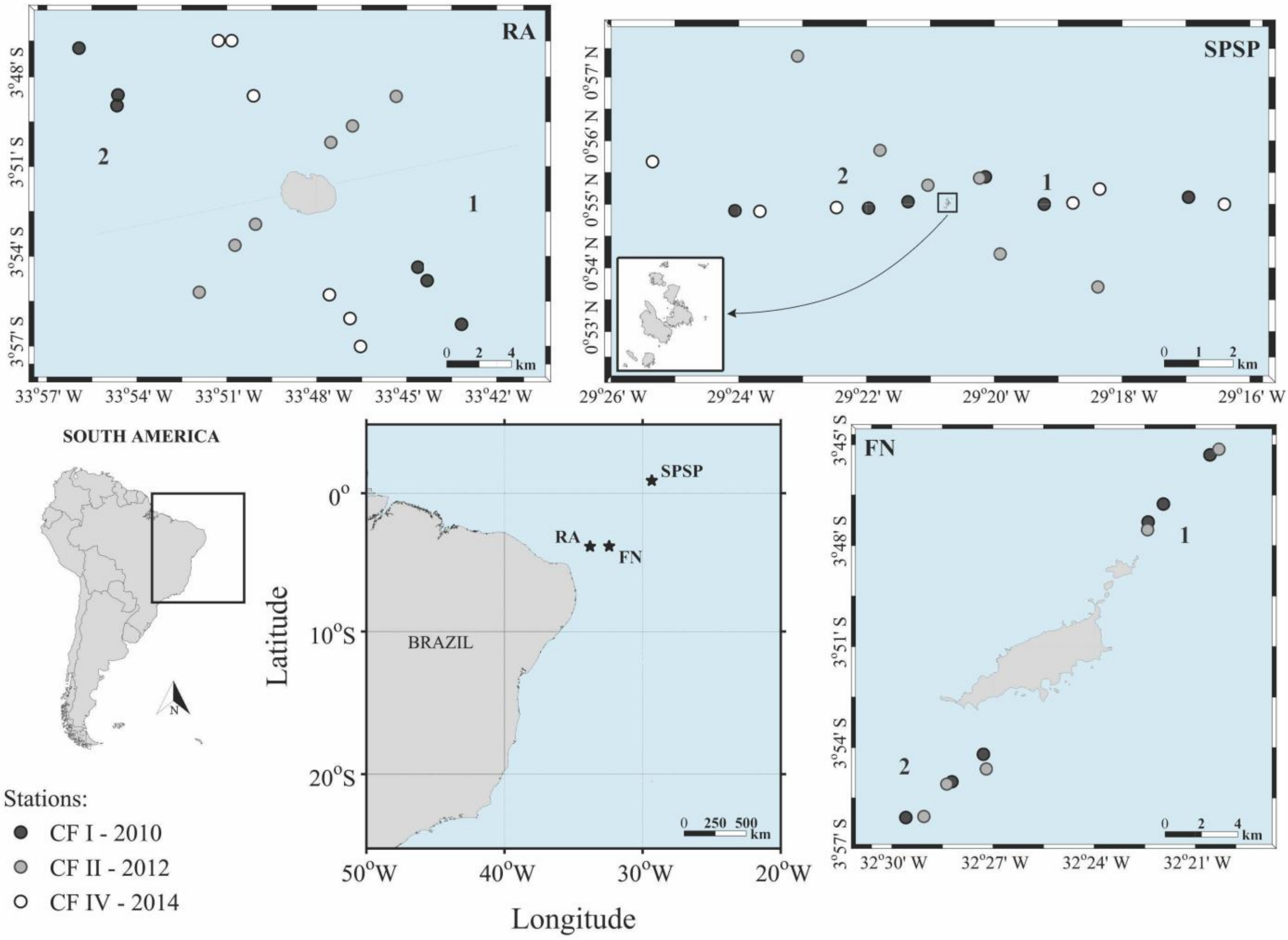

**Figure 1** Sampling stations in the islands : **a)** RA – Rocas Atoll; **b)** SPSPA – Saint Peter and Saint Paul Archipelago; **c)** FNA – Fernando de Noronha Archipelago along two transects: **1 -** upstream transect and **2** downstream transect as part of the project: CFI – July/2010; CFII – September/2012 and CFIV – August/2014.

## 2.2. Sample design

The field survey was performed in July 2010, September 2012 and August 2014 at FNA, RA, and SPSPA on board the hydrographic ship *Cruzeiro do Sul*. Forty-eight stations were sampled during the day and night periods. Ninety-six samples were collected during expeditions. An ADCP was used to obtain the currents direction and velocity, used to establish two transects (1) upstream (before the island) and transect (2) downstream (after the island) in relation to the predominant surface current. In each transect three stations were marked. Temperature and salinity profiles were recorded using a Seabird CTD from up to 200 m (or up to 75% of the local depth) to the surface. CTD data was used to characterize the thermohaline structure of the water column and to determine the depth of the thermocline.

### 2.3. Field sampling and laboratory procedures

Zooplankton samples were collected by means of oblique hauls with a "Bongo" cylindrical-conical net (mouth opening 0.6 $m^2$, mesh size 300 μm). Samplings were made in "V", extending from up to a depth of 75% of the local depth, or at most up to 200 m deep to the surface. A Hydro-Bios 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 5% buffered formalin-seawater solution.

In the laboratory, each sample was separated into two size fractions (> 500µm and < 500µm). The main objective of this separation was to avoid underestimating large individuals (less abundant) (Gorsky et al., 2010). We used a Motoda box splitter (Motoda, 1959) to subsample each size-fraction (Vandromme et al., 2012); aliquots were usually between 1/2 and 1/64, which were then scanned with the ZooScan.

### 2.4. Zooscan analysis

Zooplankton aliquots were scanned with the Zooscan system (Hydroptic model ZSCAN03) at a resolution of 2400 dpi, in accordance with the protocol established by Grosjean et al. (2004) in http://www.zooscan.obs-vlfr.fr/. Sample imaging was done using the Zooprocess software (Version 7.19), which is a plugin for ImageJ (https://imagej.nih.gov/ij/). After processing the samples with Zooprocess each detected particle was segmented into vignettes. In the Plankton Identifier (version 1.3.4) the vignettes were automatically classified according to a previously built learning set and then corrections for eventual misclassified particles were made manually. By default, only particles having an equivalent spherical diameter (ESD) < 300 μm were detected and processed (Gorsky et al., 2010; Grosjean et al., 2004). Size parameters were converted from pixels to micrometers, according to the scanner resolution (1 pixel: 10.58 μm).

### 2.5. Data analyses

The abundance (ind.$m^{-3}$) for each taxonomic group was obtained by the following formula: Abundance = number of organisms$*$ splitting ratio/filtered volume. The biovolume ($mm^3.m^{-3}$) of organisms was estimated assuming an ellipsoidal form for the zooplankton, as in Vandromme et al. (2012), following the formula: Ellipsoidal volume ($mm^3.m^{-3}$) = $4/3*\pi*(Major/2)*(Minor/2)^2*$splitting ratio/ filtered volume; where “Major” corresponds to the primary axis of the best fitting ellipse for the object and “Minor” corresponds to the secondary axis of the best fitting ellipse for the object.

To analyze the effect of spatial (FN *vs.* RA *vs.* SPSP), temporal (July/2010 *vs.* Sep/2012 *vs.* Aug/2014), sampling time (Day *vs.* Night) and transection (Upstream *vs.* Downstream) factors on the dependent variables (mesozooplankton abundance and biovolume, and the following size classes – 0.3 to 1, 1 to 2, 3 to 4, 4 to 5, and > 5 mm ESD) by means of factorial ANOVA and one-way, respectively. The dependent variables were transformed to the natural logarithm of (x + 1). The heterogeneity of variances was verified with the Levene test. When the data satisfied the normality assumption and the ANOVA results indicated significant effects, Tukey's HSD *post-hoc* tests were applied ($p < 0.05$).

## 3. RESULTS

### 3.1. Mesozooplankton taxonomic composition

We identified 51 zooplankton groups (Table 1). The relative abundance of different taxa varied between the islands (Table 1), although copepods were by far the most important group in terms of numerical abundance (Table 1b). In general, the zooplankton groups numerically abundant in FNA, RA, and SPSPA were Copepoda (69.27%, 62.76%, and 68.82%), followed by Chaetognatha (10%, 6.20%, and 2.94%) and Euphausiacea (2.77%, 4.66%, and 12.45%) (Figure 2a). In terms of relative biovolume, other taxa stood out. In FNA, the most important taxa in biovolume were Copepoda (29.31%), Decapoda (20.23%), Chaetognatha (16.68%), and Teleostei (larvae) (15.90%), whereas in RA Teleostei (larvae) (24.83%), Copepoda (22.97%), Tunicata (16.88%), Chaetognatha (10.57%), and Euphausiacea (10.14%) (Figure 2b). In the SPSPA, Copepoda was the most prominent group corresponding to 51.24% of the total relative biovolume, posteriorly Cnidaria, Chaetognatha and Euphausiacea contributed their respective values (15.50%, 10.74% and 8.35%) (Figure 2b).

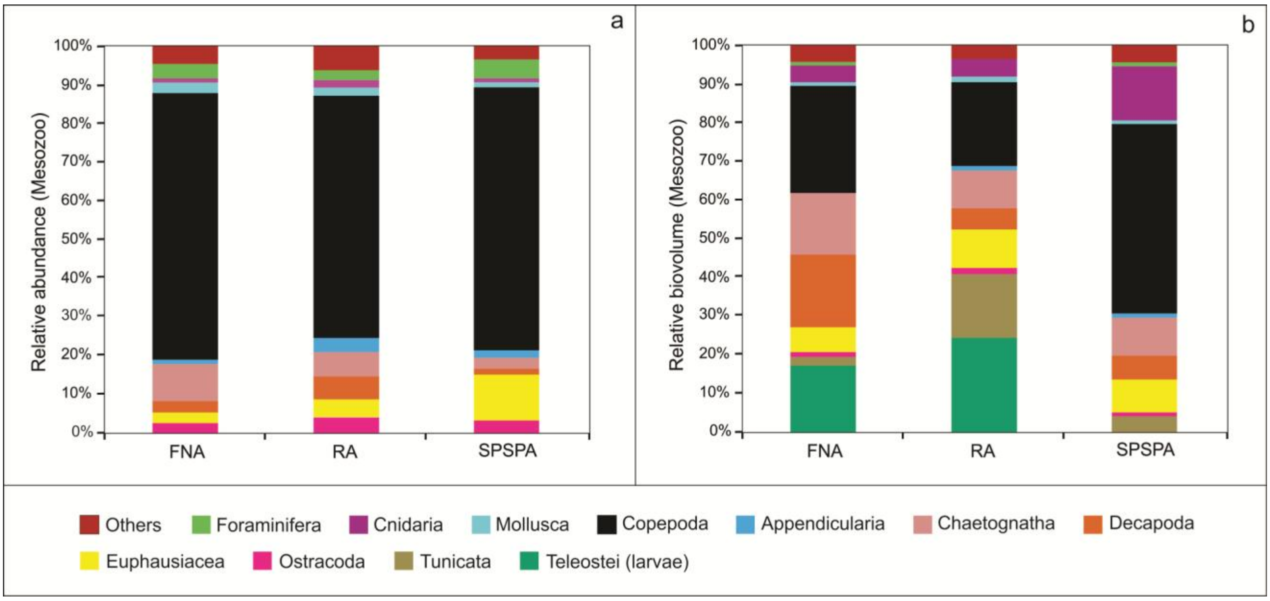

**Figure 2** Relative abundance (a) and relative biovolume (b) of dominant taxonomic groups in Marine Protected Area located in the Tropical Southwestern Atlantic - FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago).

We identified 37 taxonomic categories of Copepoda using the Zooscan system (Table 1b), 14 of them were dominant in the region (Figure 3a). Unidentified Calanoida, *Undinula vulgaris*, *Clausocalanus*, *Euchaeta*, Paracalanidae, *Scolecitrix*, *Corycaeus*, *Farranula*, *Oithona*, and *Oncaea* contributed with > 80% relative abundance in the MPA's (Figure 3a). In terms of relative biovolume we recorded a high contribution (22.41%; 21.58%; 16.93% and 15.5211%) of *Euchaeta*, *Scolecithrix*, *U. vulgaris* and other Calanoida in FNA (Figure3b), while in RA these same species also stood out corresponding to 22.89%; 7.01%; 16.20% and 20.77% respectively (Figure 3b). In the SPSPA, the genus *Subeucalanus* corresponded to 24.14% of the total biovolume, followed by *Euchaeta* (14.85%), other Calanoida (16.32%), and *Pleuromamma* (13.31%) (Figure 3b).

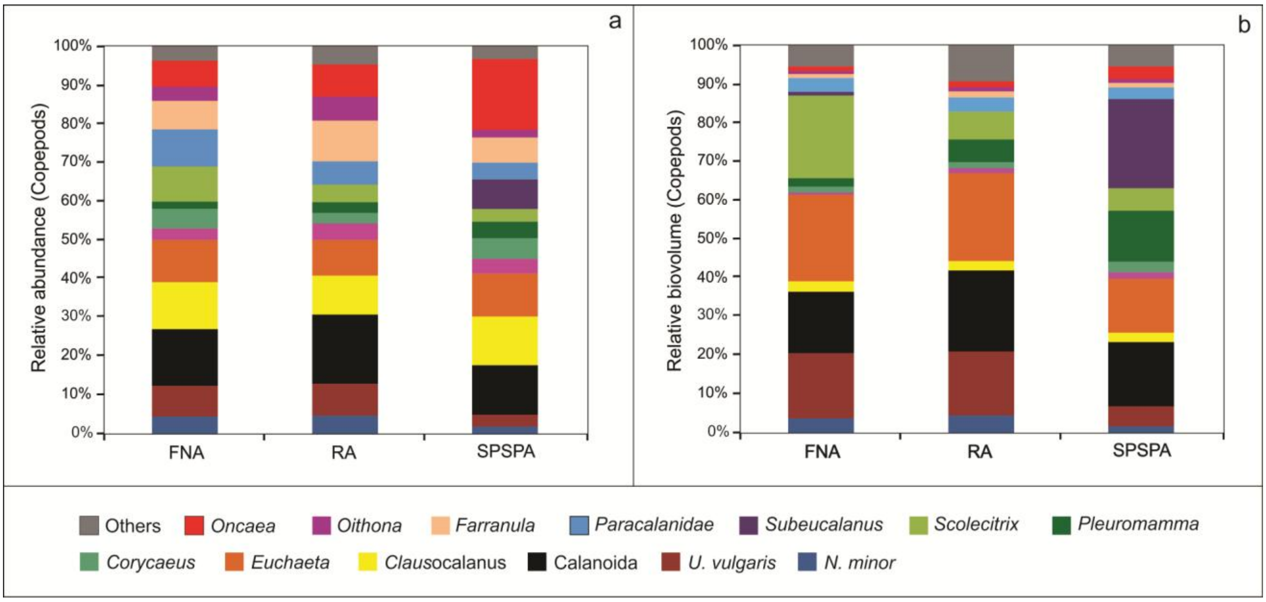

**Figure 3** Relative abundance (a) and relative biovolume (b) of dominant copepods in Marine Protected Area located in the Tropical Southwestern Atlantic - FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago).

### 3.2. Hypothesis 1: Spatial heterogeneity

Mesozooplankton abundance ranged from 0.77 ind.m$^{-3}$ in RA/Day/September 2014/Upstream to 13142.19 ind.m$^{-3}$ in SPSPA/Night/September 2014/Downstream. The mesozooplankton biovolume ranged from 0.49 mm$^{3}$.m$^{-3}$ in RA/Day/September 2014 /Upstream to 1043.40 mm$^{3}$.m$^{-3}$ in SPSPA/Night/September 2014/Upstream the island. In general, average abundance and biovolume were higher in SPSPA (594.13 ± 2255.80 ind.m$^{-3}$; 457.41 ± 1832.55 mm$^{3}$.m$^{-3}$) compared to FNA (71.67 ± 48.56 ind.m$^{-3}$; 93.67 ± 191.96 mm$^{3}$.m$^{-3}$) and RA (70.82 ± 53.24 ind.m$^{-3}$; 91.31 ± 238.86 mm$^{3}$.m$^{-3}$) (Table 2a).

The hypothesis of spatial heterogeneity was verified for the mesozooplankton abundance (Factorial Anova, $F_{1, 60} = 36.28$, $p < 0.01$) and biovolume (Factorial Anova, $F_{1,60} = 13.12$, $p < 0.01$) (Table 2a). A significant 2-way interaction for abundance (spatial *vs.* temporal interaction, $F_{3,60} = 3.18$, $p = 0.03$) and biovolume (spatial *vs.* temporal interaction, $F_{3,60} = 5.78$, $p < 0.01$) was detected (Table 2a). The Tukey-HSD *posteriori* test showed that the highest values of abundance in July 2010, September 2012 and August 2014 were recorded in SPSPA in comparison to FNA and RA (Table 2b; Figure 4a).

In relation to the biovolume, in general the same pattern is observed, especially the highest averages being recorded in September 2012 and August 2014 in SPSPA (

Figure4b). The spatial effect also significantly influenced the abundance of the following groups: Copepoda, Foraminifera, Euphausiacea, and Appendicularia. All of these taxa had their average abundances significantly higher in SPSPA (Tukey-HSD, $p < 0.01$) (Table 1a; Table 3a).

The average biovolume of Copepoda in SPSPA was also higher in relation to FNA (Tukey-HSD, $p = 0.01$) and RA (Tukey-HSD, $p < 0.01$) (Table1a; Table 3b). Tunicata also responded to the spatial effect with a significantly higher average biovolume in SPSPA compared to FNA (Tukey-HSD, $p < 0.01$) and RA (Tukey-HSD, $p = 0.01$) (Table 1a; Table 3b). Differences in Chaetognatha biovolume were only found between SPSPA and RA (Tukey-HSD, $p = 0.0007$) (Table 1a and Table 3b).

A significant variation of total abundance of the size classes was recorded between the MPA's it was highest for SPSPA, followed by RA and FNA (Table 4a). Total abundance was due to the dominance of the 0.3 to 1 mm size class for all islands (Figure 4c), but this was significantly more abundant in SPSPA (Figure 4c; Table 5a). For the size classes: 1 to 2 mm; 2 to 3 mm; 3 to 4 mm and > 5mm the highest abundances were also observed in SPSPA (Figure 4c; Table 5a).

Total biovolume exhibited a pattern similar to that of total abundance (Table 4a). The size class > 5 mm dominated in biovolume in all the island systems (Table 4a). The highest biovolume recorded in SPSPA occurred due to the size class domain > 5 mm (Figure 4d; Table 5a). In general the size classes: 0.3 to 1; 1 to 2 mm; 2 to 3 mm; 3 to 4 mm; 4 to 5 mm and > 5mm showed a significantly higher biovolume also in SPSPA (Figure 4d; Table 5a).

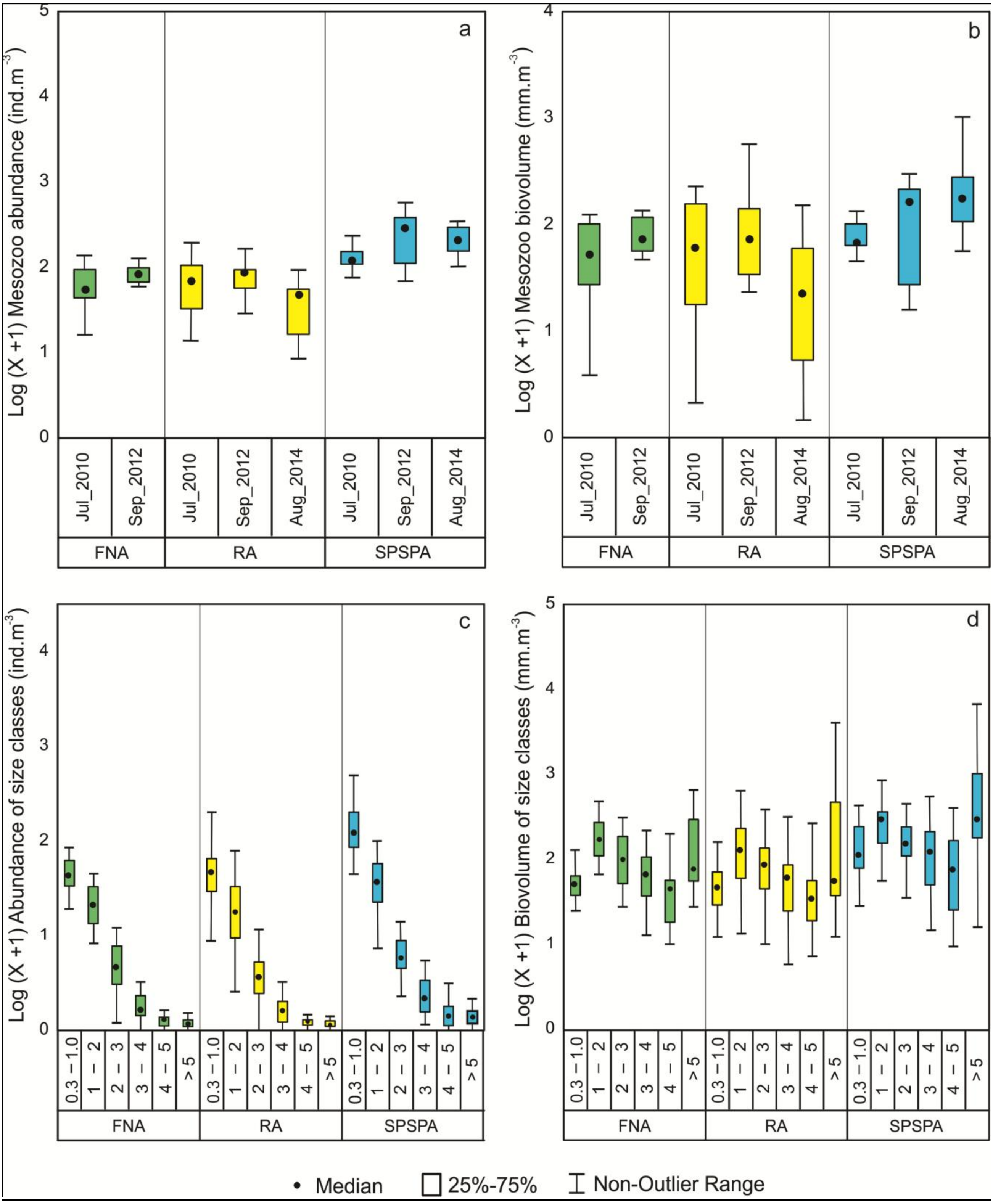

**Figure 4 Box-Plot (median and quartiles) representing the spatial distribution of abundance and biovolume.** (a) Spatial *vs.* temporal interaction of abundance and biovolume (b) of mesozooplankton; Spatial distribution of abundance (c) and biovolume (d) of established size classes in FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago).

### 3.3. Hypothesis 2: Temporal heterogeneity

We verified the temporal variability of the mesozooplankton abundance (Factorial Anova, $F_{1, 60}$ = 4.04, p = 0.04) and biovolume (Factorial Anova, $F_{1,60}$ = 4.06, p = 0.04) (Table 2a). The average abundance of mesozooplankton in July 2010 (88.14 ± 53.66 ind.m$^{-3}$) was significantly lower than that recorded in September 2012 (144.96 ± 130.88 ind.m$^{-3}$) (Figure5a). In August 2014 the average abundance was 684.11 ± 2717.48 ind.m$^{-3}$. Ostracoda, Euphausiacea, Decapoda, and Mollusca also varied temporally (Table 3a). Their average abundances in July 2010 (1.31 ± 2.24 ind.m$^{-3}$; 3.02 ± 4.03 ind.m$^{-3}$; 1.45 ± 1.51 ind.m$^{-3}$ and 0.67 ± 0.71 ind.m$^{-3}$) were significantly lower than those recorded in September 2012 (3.72 ± 3.40 ind.m$^{-3}$; 4.82 ± 5.58 ind.m$^{-3}$; 4.43 ± 8.84 ind.m$^{-3}$ and 4.01 ± 4.13 ind.m$^{-3}$) and August 2014 (19.26 ± 82.52 ind.m$^{-3}$; 102.77 ± 456.30 ind.m$^{-3}$; 8.24 ± 28.42 ind.m$^{-3}$ and 6.87 ± 24.31 ind.m$^{-3}$) (Figure 5b).

The temporal distribution of biovolume followed the same pattern of the abundance; in July 2010 the average was lower (76.94 ± 58.61 mm$^{3}$.m$^{-3}$) than that in September 2012 (141.11 ± 161 mm$^{3}$.m$^{-3}$), which was lower than that in August 2014 (143.41± 225 mm$^{3}$.m$^{-3}$) (Figure 5c). Only Decapoda and Tunicata responded significantly to the temporal effect (Table 3b). Both taxa showed a significantly lower average biovolume in July 2010 (3.09 ± 3.44 mm$^{3}$.m$^{-3}$; 1.65 ± 4.33 mm$^{3}$.m$^{-3}$) compared to September 2012 (17.58 ± 51.91 mm$^{3}$.m$^{-3}$; 21.84 ± 76.32 mm$^{3}$.m$^{-3}$) and August 2014 (36.69 ± 120.39 mm$^{3}$.m$^{-3}$; 214.24 ± 857 mm$^{3}$.m$^{-3}$) (Figure 5d).

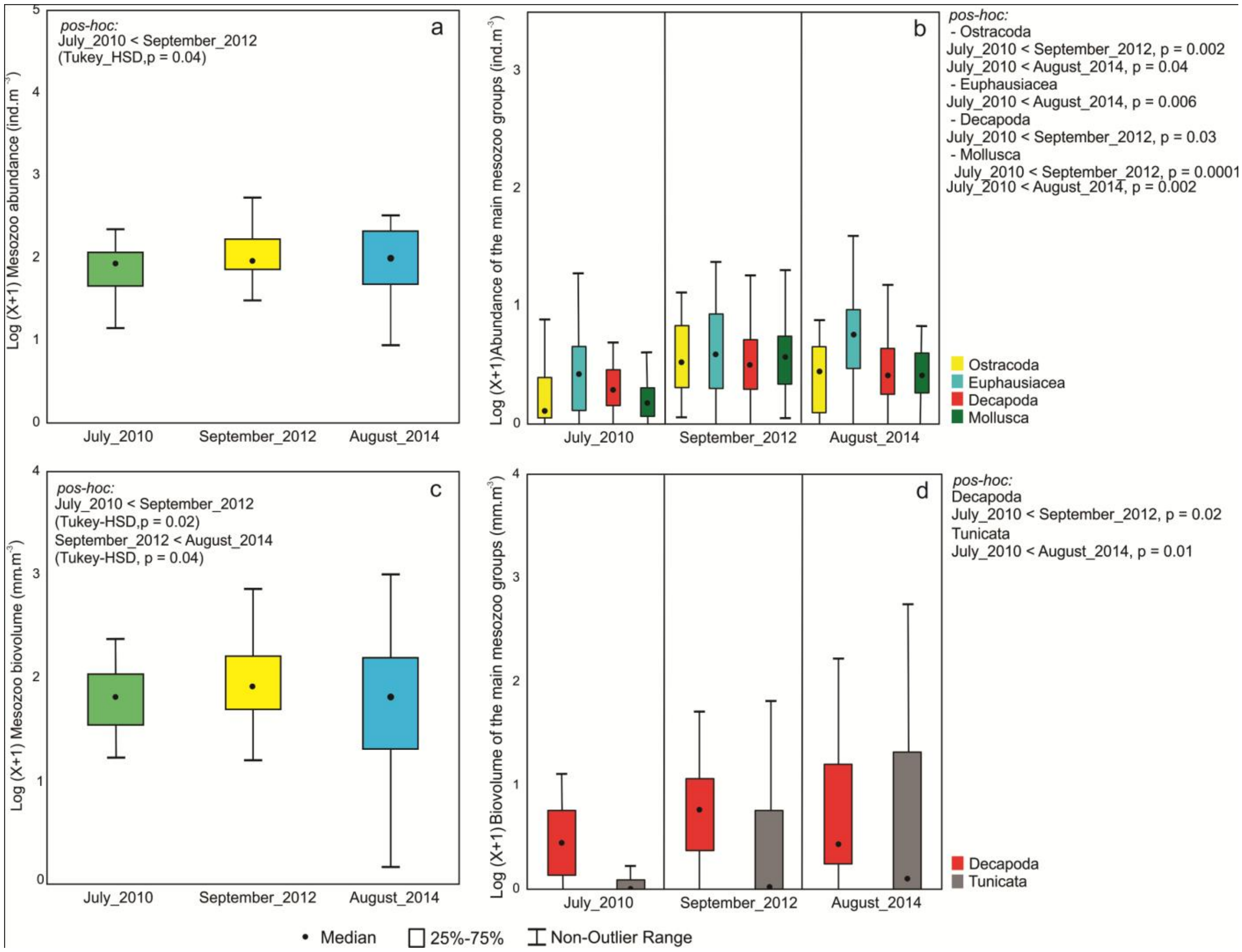

**Figure 5** Box-Plot (median and inter-quartil range) representing the temporal distribution of abundance and biovolume. (a) temporal distribution of mesozooplankton abundance; (b) response of abundance of main taxa to the temporal effect; (c) temporal distribution of mesozooplankton biovolume and (d) response of biovolume of main taxa to the temporal effect.

Temporally, size classes had average values of abundance ranging from a maximum of 473.80 ± 1848.4 ind. m$^{-3}$ (0.3 to 1mm) in August 2014 to a minimum of 0.20 ± 0.14 ind. m$^{-3}$ (> 5mm) in July 2010 (Table 4b). Already total biovolume varied from 2200.5 ± 7886.4 mm$^{3}$ m$^{-3}$ (> 5 mm) to 41.90 ± 225.37 mm$^{3}$ m$^{-3}$ (4 to 5 mm) in July 2010 (Table 4b). There were no significant variations in the abundance of size classes: 0.3 to 1 mm; 1 to 2 mm; 2 to 3 mm; 3 to 4 mm and 4 to 5 mm. Only the class > 5 mm responded significantly to the temporal factor, with a higher abundance value in August 2014 (Figure 6; Table 5a). Differences in biovolume of established size classes were not recorded.

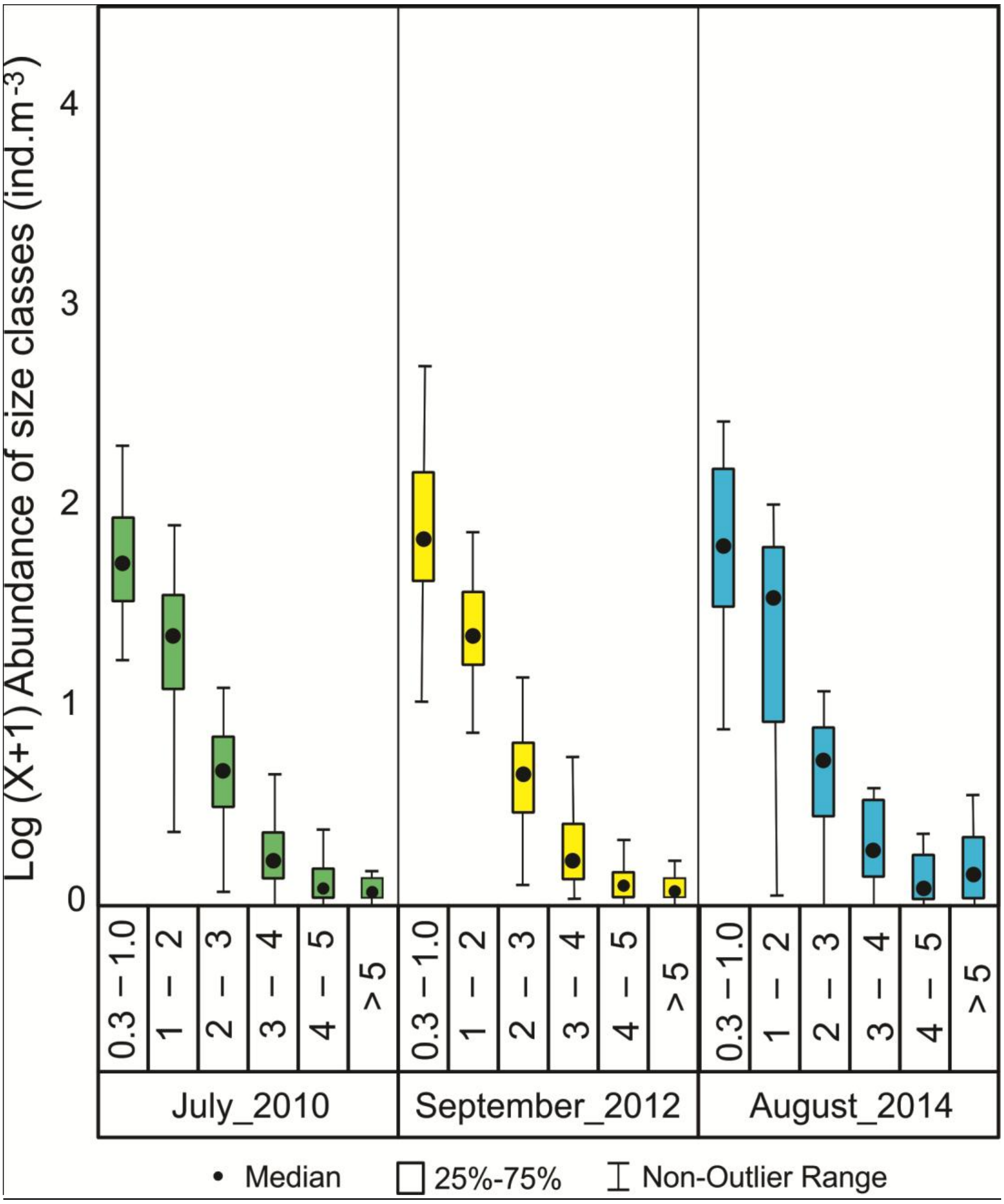

**Figure 6** Box-Plot (median and quartiles). Representing the temporal distribution of abundance of size classes: (0.3 to 1.0 mm); (1 to 2 mm); (2 to 3 mm); (4 to 5 mm) and (> 5 mm).

### 3.4. Hypothesis 3: The vertical migration effect

Day–night comparisons of the zooplankton abundance were not significantly different (nighttime: 132 ± 119.14 ind.m$^{-3}$; daytime: 102 ± 79.63 ind.m$^{-3}$). However, the average nighttime abundances of Ostracoda (11.82 ± 57.60 ind.m$^{-3}$), Euphausiacea (53 ± 319 ind.m$^{-3}$), Decapoda (6.03 ± 19.96 ind.m$^{-3}$), Mollusca (5.13 ± 17.18 ind.m$^{-3}$), and

Cnidaria (6.71 ± 31.41 ind.m$^{-3}$) were significantly higher when compared to their respective daytime values: 1.38 ± 1.76 ind.m$^{-3}$; 3.12 ± 5.67 ind.m$^{-3}$; 2.46 ± 7.55 ind.m$^{-3}$; 1.79 ± 2.58 ind.m$^{-3}$, and 0.44 ± 0.61 ind.m$^{-3}$, respectively (Figure 7a). A high significant contribution (Factorial Anova, $F_{1,60}$ = 13.93, p = 0.001) (Table 2a) of taxa with high body volume was observed in the nighttime (172. 49 ± 198.56 mm$^{3}$.m$^{-3}$) in relation to daytime (61.67 ± 46.35 mm$^{3}$.m$^{-3}$) (Figure7b). In terms of biovolume, only three taxa differed according to the sampling time (Figure 7c; Table 3b). The average biovolume of Euphausiacea, Decapoda, and Teleostei (larvae) were statistically higher during night (24.50 ± 139 mm$^{3}$.m$^{-3}$; 17.15 ± 49.92 mm$^{3}$.m$^{-3}$; 24.74 ± 90.68 mm$^{3}$.m$^{-3}$) compared to daytime (12.84 ± 19.38 mm$^{3}$.m$^{-3}$; 16.85 ± 84.17; 1.35 ± 5.79) (Figure 7c).

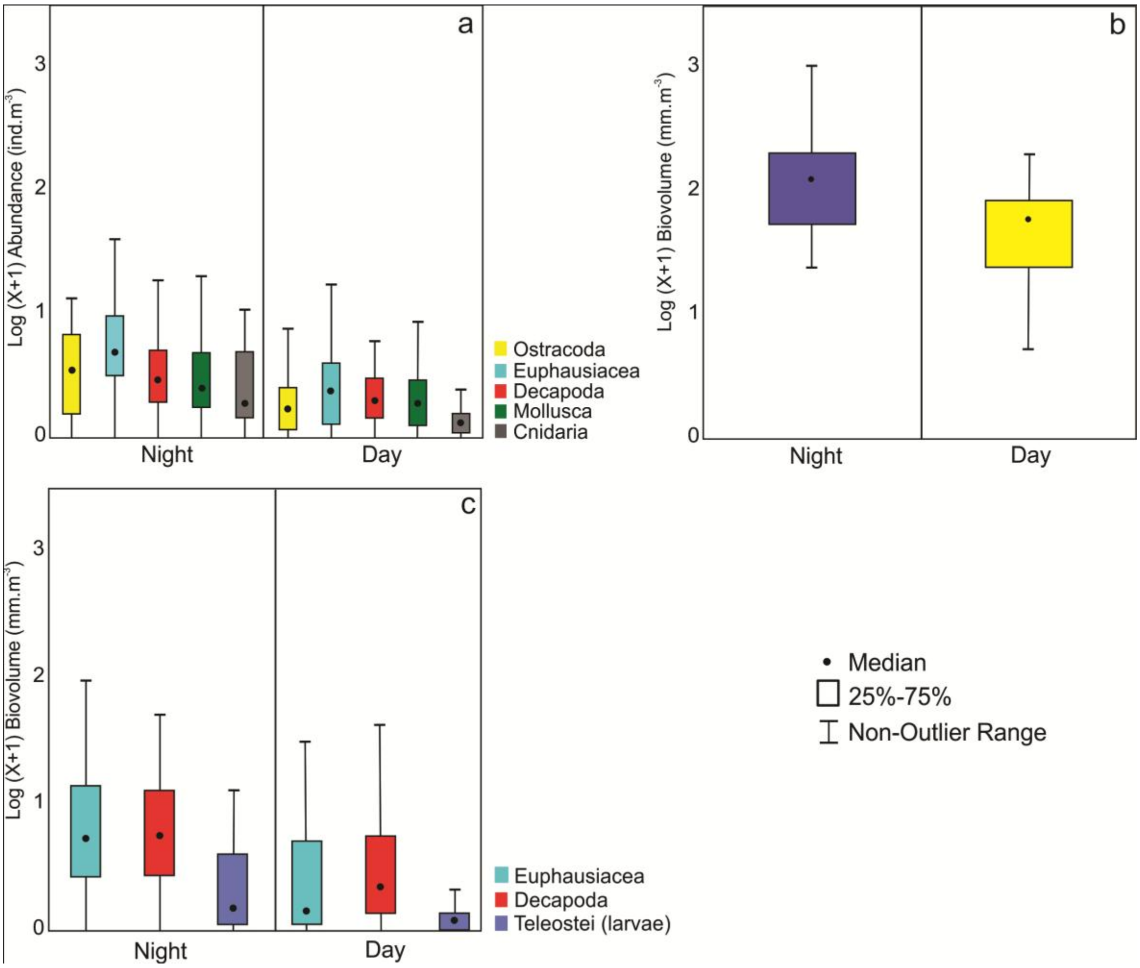

**Figure 7 Median and interquartile range of night/day mesozooplankton abundance and biovolume**. (a) response of abundance of main taxa to the night/day effect; (b) response of mesozooplankton biovolume to the night/day effect; (c) response of biovolume of main taxa to the night/day effect

Our results show that the class (0.3 to 1 mm) was the only one that did not respond to the effect of the sampling time factor (Figure 8; Table 5a and 5b).

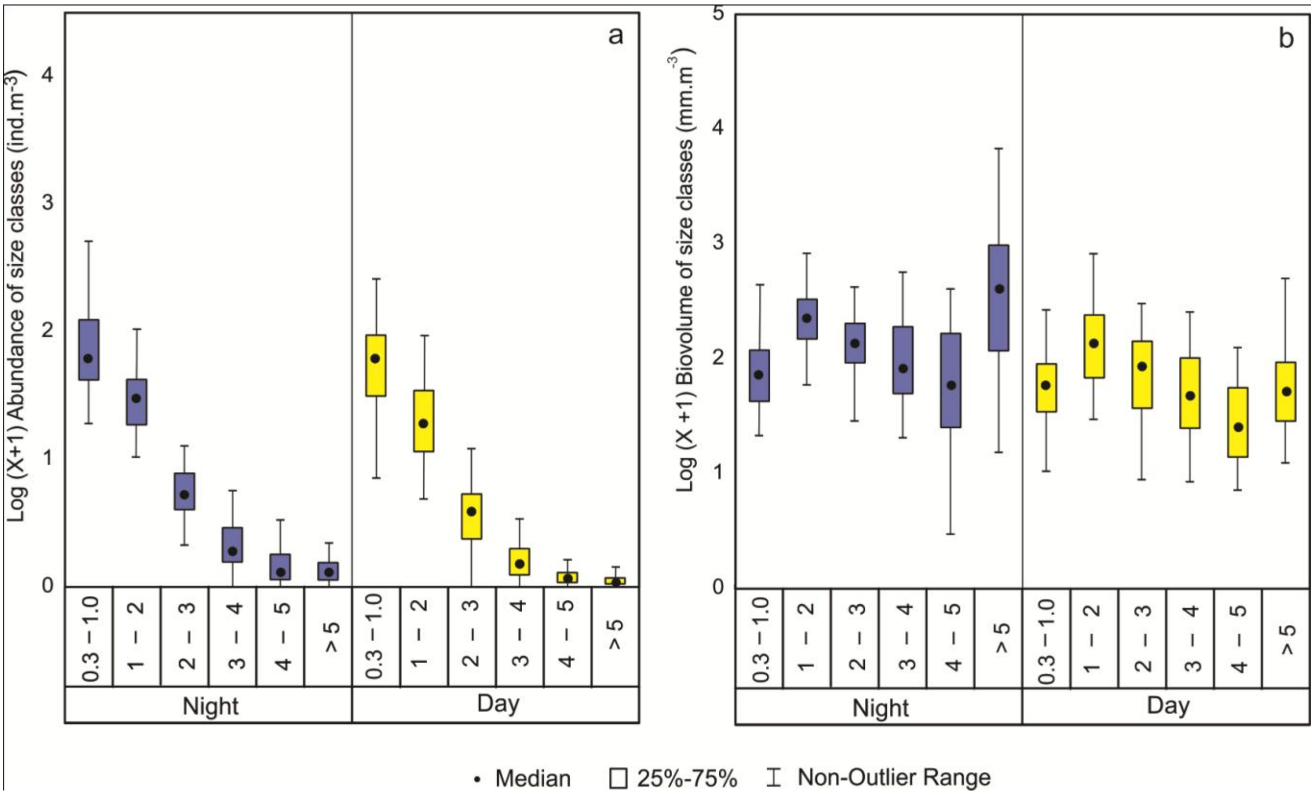

**Figure 8** Box-Plot (median and interquartile range). Night/day distribution of abundance (a) and biovolume (b) of size classes (0.3 to 1.0 mm); (1 to 2 mm); (2 to 3 mm); (4 to 5 mm) and (> 5 mm).

### 3.5. Hypothesis 4: The Island Mass Effect

The *'Island Mass effect'* was not verified on the abundance, biovolume and size classes of mesozooplankton. However, the average abundance downstream (129.27 ± 112.66 ind.m$^{-3}$) was numerically higher than the upstream (104.80 ± 89.63 ind.m$^{-3}$) off the island environments of the Southwest Atlantic. The greater dispersion of biovolume data around the mean was responsible for the absence of statistical differences. Thus, the average recorded downstream was (128 ± 150 mm$^{3}$.m$^{-3}$) and upstream (107.97 ± 159.51 mm$^{3}$.m$^{-3}$). In general for abundance, the dominants size classes corresponded to 0.3 to 1 mm followed by 1 to 2 mm both mainly downstream (Table 4a). For the biovolume the fraction of size > 5 mm and 1 to 2 mm were also highlighted in the downstream transect (Table 4a).

**Table 1** Taxonomic composition of mesozooplankton (a) and copepods (b) identified from the Zooscan image system through samples collected around the Marine Protected Area of the Tropical Southwestern Atlantic: FNA (Fernando de Noronha Archipelago), RA (Rocas Atoll) and SPSPA (St. Peter and St. Paul Archipelago).

| **(a) Mesozooplankton** | Ind.m$^{-3}$ ± S.D (Relative abundance %) | | | mm$^3$.m$^{-3}$ ± S.D (Relative biovolume %) | | |
|---|---|---|---|---|---|---|
| | FNA | RA | SPSPA | FNA | RA | SPSPA |
| Foraminifera | 2.74 ± 4.80 (3.85%) | 1.80 ± 3.24 (2.54%) | 28.62 ± 58.35 (4.75%) | 0.22 ± 0.39 (0.23%) | 0.08 ± 0.18 (0.09%) | 2.45 ± 4.88 (0.54%) |
| Cnidaria | 0.63 ± 0.85 (0.89%) | 1.33 ± 2.25 (1.87%) | 8.29 ± 37.50 (1.37%) | 4.99 ± 11.96 (5.34%) | 4.66 ± 10.58 (5.10%) | 69.14 ± 304.69 (15.50%) |
| Polychaeta | 0.28 ± 0.27 (0.39%) | 0.34 ± 0.36 (1.48%) | 1.03 ± 3.61 (0.17%) | 0.72 ± 1.59 (0.77%) | 0.75 ± 1.68 (0.82%) | 8.44 ± 31.78 (1.89%) |
| Mollusca | 1.91 ± 2.59 (2.67%) | 1.63 ± 2.23 (2.29%) | 6.63 ± 20.39 (1.10%) | 0.30 ± 0.34 (0.32%) | 0.92 ± 4.44 (1.01%) | 1.60 ± 3.72 (0.35%) |
| Copepoda | 49.74 ± 24.42 (69.27%) | 47.25 ± 21.84 (62.76%) | 415.24 ± 1546.59 (70.3%) | 27.95 ± 17.63 (29.89%) | 20.99 ± 18.32 (22.97%) | 228.54 ± 1001.23 (51.24%) |
| Ostracoda | 1.56 ± 1.90 (2.18%) | 2.39 ± 3.09 (3.36%) | 15.05 ± 68.76 (2.50%) | 0.31 ± 0.38 (0.33%) | 0.51 ± 0.74 (0.56%) | 3.81 ± 17.48 (0.85%) |
| Amphipoda | 0.41 ± 0.32 (0.58%) | 0.20 ± 0.21 (0.88%) | 3.99 ± 17.67 (0.66%) | 2.04 ± 4.79 (2.18%) | 0.88 ± 1.56 (0.96%) | 5.45 ± 15.77 (1.30%) |
| Euphausiacea | 1.97 ± 1.56 (2.77%) | 3.31 ± 3.46 (4.66%) | 74.90 ± 380.80 (12.45%) | 6.33 ± 9.01 (6.77%) | 9.27 ± 21.32 (10.14%) | 37.27 ± 161.72 (8.35%) |
| Decapoda | 1.91 ± 2.09 (2.67%) | 4.21 ± 7.02 (5.93%) | 6.08 ± 23.73 (1.01%) | 19.29 ± 62.13 (20.63%) | 4.95 ± 7.25 (5.49%) | 28.12 ± 101 (6.30%) |
| Chaetognatha | 7.84 ± 4.43 (11.05%) | 4.40 ± 3.65 (6.20%) | 17.72 ± 57.27 (2.94%) | 15.60 ± 12.43 (16.68%) | 9.66 ± 7.84 (10.57%) | 47.94 ± 153.82 (10.74%) |
| Appendicularia | 0.58 ± 0.55 (0.82%) | 2.82 ± 4.33 (3.97%) | 8.60 ± 12.21 (1.43%) | 0.09 ± 0.14 (0.10%) | 0.31 ± 0.47 (0.34%) | 1.83 ± 2.17 (0.41%) |
| Tunicata (Salpa and *Doliolum*) | 0.06 ± 0.11 (0.09%) | 0.08 ± 0.13 (1.11%) | 2.96 ± 13.63 (0.49%) | 0.22 ± 0.51 (0.23%) | 15.42 ± 74.48 (16.88%) | 19.9 ± 24.69 (1.89%) |
| Teleostei (eggs) | 1.75 ± 4.32 (2.45%) | 0.64 ± 0.89 (1.90%) | 4.06 ± 11.90 (0.67%) | 0.45 ± 1.27 (0.48%) | 0.22 ± 0.44 (0.24%) | 1.99 ± 2.78 (0.44%) |
| Teleostei (larvae) | 0.29 ± 0.35 (0.41%) | 0.42 ± 0.54 (1.05%) | 0.96 ± 3.39 (0.16%) | 15.16 ± 69.39 (16.05%) | 22.69 ± 89.56 (24.83%) | 0.93 ± 6.82 (0.20%) |
| **Total** | **71.67 ± 48.56 (100%)** | **70.82 ± 71.74 (100%)** | **594.13 ± 2255.80 (100%)** | **93.67 ± 191.96 (100%)** | **91.31 ± 238.86 (100%)** | **457.41 ± 1832.55 (100%)** |
| **(b) Copepods** | | | | | | |
| *Nannocalanus minor* | 1.56 ± 1.43 (3.15%) | 1.35 ± 1.53 (3.03%) | 3.26 ± 4.22 (0.78%) | 1.06 ± 1.16 (3.81%) | 0.001 ± 1.88 (4.77%) | 2.37 ± 3.52 (1.03%) |
| *Neocalanus* | 0.04 ± 0.19 (0.08%) | 0.03 ± 0.11 (0.07%) | - | 0.02 ± 0.13 (0.10%) | 0.06 ± 0.26 (0.32%) | - |
| *Undinula vulgaris* | 3.83 ± 2.96 (7.75%) | 3.78 ± 3.14 (8.48%) | 9.84 ± 17.39 (2.37%) | 4.73 ± 4.34 (16.92%) | 3.4 ± 3.39 (16.20%) | 12.87 ± 35.29 (5.63%) |
| *Acartia* | 0.05 ± 0.07 (0.11%) | 0.03 ± 0.08 (0.07%) | 1.50 ± 7.25 (0.36%) | 0.008 ± 0.02 (0.03%) | 0.002 ± 0.007 (0.01%) | 0.14 ± 0.61 (0.06%) |
| *Acrocalanus* | - | 0.002 ± 0.01 (0.005%) | - | - | 0.0004 ± 0.002 (0.001) | - |
| Calanidae | 0.14 ± 0.71 (0.29%) | 0.08 ± 0.52 (0.19%) | - | 0.2 ± 0.99 (0.72%) | 0.09 ± 0.57 (0.46%) | - |

**Continuation table 1**

| | | | | | | |
|---|---|---|---|---|---|---|
| Calanoida | 7.35 ± 4.26 (14.87%) | 8.04 ± 8.26 (18.02%) | 55.55 ± 193.31 (13.42%) | 4.33 ± 2.57 (15.52%) | 4.36 ± 4.86 (20.77%) | 37.3 ± 151.70 (16.32%) |
| *Calocalanus* | 0.005 ± 0.02 (0.01%) | 0.43 ± 1.06 (0.97%) | | 0.0006 ± 0.003 (0.002%) | 0.03 ± 0.09 (0.18%) | - |
| *Candacia* | 0.36 ± 0.49 (0.74%) | 0.55 ± 0.61 (1.24%) | 6.10 ± 30.74 (1.47%) | 0.41 ± 0.61 (1.46%) | 0.58 ± 0.70 (2.78%) | 6.62 ± 30.98 (2.89%) |
| *Centropages* | 0.22 ± 0.29 (0.46%) | 0.13 ± 0.18 (0.30%) | 0.56 ± 0.69 (0.13%) | 0.13 ± 0.18 (0.46%) | 0.11 ± 0.16 (0.54%) | 0.35 ± 0.45 (0.15%) |
| *Clausocalanus* | 6.22 ± 5.80 (12.53%) | 4.78 ± 5.70 (10.71%) | 52.65 ± 107.85 (12.71%) | 0.69 ± 0.70 (2.47%) | 0.53 ± 0.58 (2.55%) | 5.84 ± 10.92 (2.55%) |
| Eucalanidae | - | 0.07 ± 0.25 (0.16%) | - | - | 0.004 ± 0.01 (0.02%) | - |
| *Euchaeta* | 5.70 ± 5.66 (11.54%) | 4.27 ± 4.26 (9.59%) | 49.04 ± 230.06 (11.84%) | 6.26 ± 7.97 (22.41%) | 4.8 ± 4.98 (22.89%) | 33.94 ± 132.83 (14.85%) |
| *Gaetanus* | 0.02 ± 0.09 (0.07%) | 0.03 ± 0.10 (0.07%) | - | 0.006 ± 0.02 (0.02%) | 0.02 ± 0.12 (0.14%) | - |
| *Haloptilus* | 0.11 ± 0.17 (0.23%) | 0.20 ± 0.35 (0.45%) | 0.10 ± 0.19 (0.02%) | 0.15 ± 0.30 (0.54%) | 0.22 ± 0.40 (1.04%) | 0.16 ± 0.49 (0.07%) |
| *Heterorabdus* | 0.03 ± 0.06 (0.03%) | 0.06 ± 0.14 (0.14%) | 2.46 ± 13.70 (0.59%) | 0.01 ± 0.04 (0.06%) | 0.04 ± 0.11 (0.20%) | 0.93 ± 4.97 (0.40%) |
| *Labidocera* | 0.07 ± 0.15 (0.14%) | 0.05 ± 0.15 (0.11%) | 0.009 ± 0.041 (0.002%) | 0.16 ± 0.39 (0.60%) | 0.16 ± 0.51 (0.80%) | 0.005 ± 0.02 (0.002%) |
| *Lucicutia* | 0.86 ± 0.80 (1.75%) | 1.39 ± 1.48 (3.13%) | 11.90 ± 60.65 (2.87%) | 0.17 ± 0.14 (0.61%) | 0.24 ± 0.25 (1.17%) | 2.81 ± 14.49 (1.23%) |
| Paracalanidae | 2.65 ± 2.23 (5.37%) | 1.37 ± 1.89 (3.08%) | 23.90 ± 88.87 (5.77%) | 0.48 ± 0.40 (1.71%) | 0.23 ± 0.31 (1.11%) | 5.19 ± 21.67 (2.27%) |
| *Pleuromamma* | 0.68 ± 1.03 (1.39%) | 1.26 ± 1.75 (2.83%) | 18.73 ± 96.14 (4.52%) | 0.64 ± 1.23 (2.30%) | 1.3 ± 1.93 (6.20%) | 30.42 ± 163.78 (13.31#) |
| *Pontella* | - | 0.01 ± 0.06 (0.18%) | - | - | 0.004 ± 0.02 (0.01%) | - |
| *Rhincalanus* | 0.08 ± 0.15 (0.18%) | 0.21 ± 0.25 (0.49%) | 0.82 ± 3.40 (0.19%) | 0.15 ± 0.21 (0.54%) | 0.43 ± 0.56 (2.09%) | 3.38 ± 17.08 (1.48%) |
| *Scolecitrix* | 4.74 ± 7.17 (9.59%) | 2.19 ± 1.78 (4.92%) | 12.99 ± 62.02 (3.13%) | 6.03 ± 10.22 (21.72%) | 1.47 ± 1.50 (7.01%) | 13.59 ± 67.37 (5.94%) |
| *Subeucalanus* | 0.10 ± 0.20 (0.21%) | 0.02 ± 0.05 (0.05%) | 33.05 ± 167.61 (7.98%) | 0.14 ± 0.28 (0.50%) | 0.03 ± 0.09 (0.17%) | 55.17 ± 283.58 (24.14%) |
| *Temora* | - | 0.002 ± 0.05 (0.006%) | 0.04 ± 0.11 (0.009%) | - | 0.0005 ± 0.003 (0.002%) | 0.01 ± 0.04 (0.006%) |
| *Copilia* | 0.04 ± 0.07 (0.09%) | 0.05 ± 0.12 (0.12%) | 0.07 ± 0.15 (0.01%) | 0.03 ± 0.06 (0.13%) | 0.08 ± 0.33 (0.42%) | 0.08 ± 0.22 (0.03%) |
| *Corycaeus* | 4.82 ± 3.97 (9.76%) | 2.92 ± 2.42 (6.54%) | 20.85 ± 76.13 (5.03%) | 1.13 ± 0.99 (4.07%) | 0.73 ± 0.68 (3.51%) | 5.53 ± 21.67 (2.42%) |
| Cyclopoida | - | 0.006 ± 0.03 (0.01%) | - | - | 0.0004 ± 0.002 (0.001%) | - |
| *Farranula* | 3.58 ± 4.79 (7.26%) | 4.34 ± 6.86 (9.74%) | 23.37 ± 63.72 (5.64%) | 0.30 ± 0.40 (1.09%) | 0.34 ± 0.52 (1.63%) | 2.05 ± 5.78 (0.90%) |
| *Lubockia* | - | 0.01 ± 0.08 (0.03%) | - | - | 0.001 ± 0.009 (0.009%) | - |
| *Oithona* | 2.11 ± 2.90 (4.26%) | 3.06 ± 7.02 (6.86%) | 5.98 ± 19.79 (1.44%) | 0.11 ± 0.15 (0.42%) | 0.13 ± 0.28 (0.66%) | 0.38 ± 1.24 (0.16%) |
| *Oncaea* | 3.38 ± 2.69 (6.84%) | 3.68 ± 4.21 (8.25%) | 79.53 ± 319.39 (19.21%) | 0.32 ± 0.25 (1.17%) | 0.38 ± 0.38 (1.85%) | 8.81 ± 39.60 (3.85%) |

**Continuation table 1**

| | | | | | | |
|---|---|---|---|---|---|---|
| *Saphiirina* | 0.07 ± 0.17 (0.15%) | 0.05 ± 0.11 (0.13%) | 0.09 ± 0.23 (0.02%) | 0.05 ± 0.16 (0.21%) | 0.06 ± 0.13 (0.31%) | 0.17 ± 0.67 (0.07%) |
| *Clytemnestra* | - | - | 0.02 ± 0.05 (0.006%) | - | - | 0.002 ± 0.005 (0.001%) |
| *Macrosetella gracilis* | 0.01 ± 0.04 (0.02%) | 0.009 ± 0.03 (0.02%) | 0.01 ± 0.04 (0.002%) | 0.0009 ± 0.003 (0.003%) | 0.001 ± 0.005 (0.006%) | 0.0008 ± 0.003 (0.0.164%) |
| *Microsetella* | 0.01 ± 0.04 (0.03%) | 0.007 ± 0.02 (0.01%) | 0.01 ± 0.03 (0.003%) | 0.002 ± 0.005 (0.007%) | 0.0005 ± 0.002 (0.002%) | 0.002 ± 0.007 (0.001%) |
| *Miracia* | 0.44 ± 0.76 (0.90%) | 0.001 ± 0.008 (0.003%) | 1.42 ± 3.90 (0.34%) | 0.11 ± 0.20 (0.39%) | 0.0004 ± 0.002 (0.169%) | 0.3 ± 0.67 (0.13%) |
| **Total** | **49.27 ± 49.36 (100%)** | **44.46 ± 54.66 (100%)** | **413.84 ± 1567.67 (100%)** | **27.82 ± 34.12 (100%)** | **19.83 ± 25.63 (100%)** | **228.42 ± 1009.63 (100%)** |

Values are: abundance_Ind.m$^{-3}$_mean ± standard deviation, numbers in parentheses indicates the relative abundance (%) and biovolume_mm$^{3}$.m$^{-3}$_mean ± standard deviation, where numbers in parentheses indicate the relative biovolume (%).

**Table 2** (a) Factorial ANOVAs testing the effects of space (FN *vs.* RA *vs.* SPSP), sampling time (day *vs.* night), temporal (2010 *vs.* 2012 *vs.* 2014) and transect to (upstream *vs.* downstream) on (i) mesozooplankton abundance and (ii) mesozooplankton biovolume, and (b) Tukey - HSD tests on significant interaction terms for (i) mesozooplankton abundance and (ii) mesozooplankton biovolume.

| (a) ANOVA | | (i) Mesozooplankton abundance | | | (ii) Mesozooplankton biovolume | | |
|---|---|---|---|---|---|---|---|
| Effect | df | MS | F | p | MS | F | p |
| Spatial (1) | 1 | 5.27 | 36.28 | *** | 2.50 | 13.12 | ******* |
| Sampling time (2) | 1 | 0.40 | 2.86 | 0.094 | 3.12 | 13.93 | ******* |
| Temporal (3) | 1 | 0.58 | 4.04 | * | 0.77 | 4.06 | ***** |
| Transect (4) | 1 | 0.44 | 3.14 | 0.079 | 0.10 | 0.47 | 0.492 |
| Spatial *vs.* Sampling time | 1 | < 0.01 | < 0.01 | 0.968 | 0.51 | 2.68 | 0.10 |
| Spatial *vs.* Temporal | 3 | 0.46 | 3.18 | * | 1.10 | 5.78 | ****** |
| Sampling time *vs.* Temporal | 1 | < 0.01 | 0.01 | 0.906 | 0.19 | 1.00 | 0.319 |
| Spatial *vs.* Transect | 1 | 0.20 | 1.43 | 0.236 | 0.46 | 2.43 | 0.124 |
| Sampling time *vs.* Transect | 1 | 0.01 | 0.05 | 0.812 | 0.002 | 0.01 | 0.922 |
| Temporal *vs.* Transect | 1 | < 0.01 | < 0.01 | 0.975 | 0.04 | 0.23 | 0.629 |
| 1 *vs.*2 *vs.*3 | 3 | 0.23 | 1.64 | 0.189 | 0.28 | 1.49 | 0.225 |
| 1 *vs.* 2 *vs.* 4 | 1 | 0.07 | 0.54 | 0.461 | 0.11 | 0.60 | 0.439 |
| 1 *vs.* 3 *vs.* 4 | 3 | 0.02 | 0.15 | 0.925 | 0.05 | 0.26 | 0.849 |
| 2 *vs.* 3 *vs.* 4 | 1 | 0.282 | 1.94 | 0.168 | 0.65 | 3.43 | 0.068 |
| 1 *vs.* 2 *vs.* 3 *vs.* 4 | 3 | 0.03 | 0.26 | 0.847 | 0.007 | 0.03 | 0.989 |
| Error | 60 | 0.14 | | | 0.19 | | |

| (b) *pos-hoc* | (i) Tukey - HSD, *p-level* | (ii) Tukey - HSD, *p-level* |
|---|---|---|
| | SPSPA (2012) > FNA (2010) - ****** | SPSPA (2012) > RA (2014) - ****** |
| | SPSPA (2014) > FNA (2010) - ******* | SPSPA (2014) > FNA (2010) - ***** |
| | SPSPA (2014) > FNA (2012) - ****** | SPSPA (2014) > RA (2014) - ******* |
| | SPSPA (2012) > RA (2010) - ***** | FNA (2012) > RA (2014) - ****** |
| | SPSPA (2014) > RA (2010) - ****** | |
| | SPSPA (2014) > RA (2012) - ***** | |
| | SPSPA (2010) > RA (2014) - ****** | |
| | SPSPA (2012) > RA (2014) - *** | |
| | SPSPA (2014) > RA (2014) - *** | |

p values in bold are significant. Abundance and biovolume data were log (x + 1) transformed. Significance level: *p < 0.05, **p < 0.01, ***p < 0.001.

**Table 3** One-way Anova results for total abundance (a) and biovolume (b) of the main groups of the mesozooplankton in response to the spatial, temporal, sampling time and transection factors. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$, n.s (not significante).

| **(a) Abundance (ind.m$^{-3}$)** | **Spatial** | **Temporal** | **Sampling time** | **Transection** |
|---|---|---|---|---|
| Ostracoda | n.s | F (2, 89) = 6.40, p = ** | F (1, 90) = 12.41, p = *** | n.s |
| Euphausiacea | F (2, 89) = 9.37, p = *** | F (2, 89) = 4.98, p = ** | F (1, 90) = 14.25, p = *** | n.s |
| Decapoda | n.s | F (2, 89) = 3.53, p = * | F (1, 90) = 7.45, p = ** | n.s |
| Chaetognatha | F (2, 89) = 6.41, p = ** | n.s | n.s | n.s |
| Appendicularia | F (2, 89) = 28.43, p = *** | n.s | n.s | n.s |
| Copepoda | F (2, 89) = 20.13, p = *** | n.s | n.s | n.s |
| Mollusca | F (2, 89) = 4.19, p = * | F (2, 89) = 15.7, p = *** | F (1, 90) = 4.86, p = * | n.s |
| Cnidaria | n.s | n.s | F (1, 90) = 18.13, p = *** | n.s |
| Foraminifera | F (2, 89) = 26.80, p = *** | n.s | n.s | n.s |
| **(b) Biovolume (mm$^3$.m$^{-3}$)** | **Spatial** | **Temporal** | **Sampling time** | **Transection** |
| Euphausiacea | n.s | n.s | F (1, 90) = 10.76, p = ** | n.s |
| Decapoda | n.s | F (2, 89) = 3.63, p = * | F (1, 90) = 6.66, p = * | n.s |
| Chaetognatha | F (2, 89) = 7.38, p = ** | n.s | n.s | n.s |
| Copepoda | F (2, 89) = 13.15, p = *** | n.s | n.s | n.s |
| Cnidaria | n.s | n.s | n.s | n.s |
| Tunicata | F (2, 89) = 6.14, p = ** | F (2, 89) = 3.95, p= * | n.s | n.s |
| Teleostei (Larvae) | n.s | n.s | F (1, 90) = 8.07, p = ** | n.s |

**Table 4** Abundance and biovolume of mesozooplankton size classes in relation to the factors tested: a (spatial and transect) and b (temporal and sampling time).

| (a) Parameter | Spatial | | | Transect | |
|---|---|---|---|---|---|
| | FNA | RA | SPSPA | Upstream | Downstream |
| Abundance (ind. $m^{-3}$) | | | | | |
| 0.3 to 1 mm | 43.84 ± 21.99 | 55.16 ± 46.79 | 427.27 ± 1543.3 | 73.71 ± 71.97 | 292.89 ± 1307.6 |
| 1 to 2 mm | 22.45 ± 12.36 | 20.23 ± 16.75 | 133.88 ± 531.5 | 27.33 ± 22.14 | 94.36 ± 449.1 |
| 2 to 3 mm | 4.48 ± 3.14 | 2.80 ± 2.37 | 26.10 ± 117.3 | 4.15 ± 3.25 | 18.72 ± 99 |
| 3 to 4 mm | 0.80 ± 0.62 | 0.67 ± 0.75 | 4.13 ± 16.7 | 0.88 ± 0.76 | 2.97 ± 14.1 |
| 4 to 5 mm | 0.22 ± 0.30 | 0.17 ± 0.31 | 1.01 ± 3.3 | 0.23 ± 0.32 | 0.72 ± 2.8 |
| >5 mm | 0.11 ± 0.15 | 0.12 ± 0.15 | 2.05 ± 10.1 | 0.21 ± 0.40 | 1.38 ± 8.5 |
| **Total** | **71.90 ± 38.56** | **79.15 ± 67.12** | **594.44 ± 2222.2** | **106.51 ± 98.84** | **411.04 ± 1881.1** |
| Biovolume (mm3 $m^{-3}$) | | | | | |
| 0.3 to 1 mm | 50.52 ± 26.2 | 53.42 ± 37.43 | 484.2 ± 1885.7 | 75.29 ± 68 | 333.46 ± 1595.3 |
| 1 to 2 mm | 198.36 ± 120.3 | 155.39 ± 134.18 | 1096 ± 4490.8 | 220.35 ± 191.2 | 775.53 ± 3792 |
| 2 to 3 mm | 119.16 ± 85.1 | 90.80 ± 80.21 | 924.4 ± 4261.4 | 129.19 ± 102.1 | 653.82 ± 3594.3 |
| 3 to 4 mm | 74.40 ± 57.3 | 67.22 ± 75.98 | 448.4 ± 1839.3 | 87.81 ± 81.7 | 318.81 ± 1553.4 |
| 4 to 5 mm | 35.69 ± 46.6 | 33.39 ± 62.12 | 181 ± 563.4 | 44.72 ± 61.4 | 127.34 ± 479.1 |
| >5 mm | 302.84 ± 1073.4 | 348.21 ± 906.62 | 1622.5 ± 6644.3 | 642.26 ± 1447.9 | 938.22 ± 5558.7 |
| **Total** | **780.97±1408.9** | **748.43±1296.54** | **4756.5±19684.9** | **1199 ± 1952.3** | **3147.18 ± 16572.8** |

| (b) Parameter | Temporal | | | Sampling time | |
|---|---|---|---|---|---|
| | July/2010 | September/2012 | August/2014 | Day | Night |
| Abundance (ind. $m^{-3}$) | | | | | |
| 0.3 to 1 mm | 65.84 ± 46.89 | 112.76 ± 114.07 | 473.80 ± 1848.4 | 75.24 ± 63.95 | 286.92 ± 1294.9 |
| 1 to 2 mm | 24.47 ± 16.54 | 26.74 ± 15.78 | 169.44 ± 633.5 | 23.73 ± 21.10 | 96.26 ± 444.1 |
| 2 to 3 mm | 4.13 ± 3.16 | 4.24 ± 3.02 | 33.80 ± 139.8 | 3.32 ± 2.96 | 19.17 ± 97.8 |
| 3 to 4 mm | 0.79 ± 0.77 | 0.92 ± 0.93 | 5.22 ± 19.9 | 0.57 ± 0.62 | 3.21 ± 13.9 |
| 4 to 5 mm | 0.38 ± 0.37 | 0.45 ± 0.55 | 2.23 ± 6.14 | 0.13 ± 0.16 | 0.81 ± 2.8 |
| >5 mm | 0.20 ± 0.14 | 0.23 ± 0.19 | 5.91 ± 17.65 | 0.06 ± 0.09 | 1.49 ± 8.4 |
| **Total** | **95.81 ± 67.87** | **145.34 ± 134.54** | **690.4 ± 2665.3** | **103.05 ± 88.88** | **407.86 ± 1861.9** |
| Biovolume (mm3 $m^{-3}$) | | | | | |
| 0.3 to 1 mm | 66.30 ± 40.46 | 105.16 ± 102.9 | 570.7 ± 2254 | 73.63 ± 62.77 | 329.6 ± 1579 |
| 1 to 2 mm | 213.30 ± 1458.16 | 190.83 ± 109.3 | 1410.2 ± 5349.6 | 189.66 ± 178.64 | 792.1 ± 3749.5 |
| 2 to 3 mm | 125.90 ± 72.81 | 127.80 ± 98 | 1208.2 ± 5078.4 | 95.27 ± 82.51 | 674 ± 3553.2 |
| 3 to 4 mm | 73.14 ± 65.97 | 101.02 ± 112.4 | 561.5 ± 2191.2 | 58.14 ± 64.96 | 341.2 ± 1533.8 |
| 4 to 5 mm | 41.90 ± 225.37 | 76.43 ± 99 | 169.5 ± 672.3 | 22.99 ± 31.63 | 145.5 ± 472.7 |
| >5 mm | 105.67 ± 61.91 | 536.99 ±1224.7 | 2200.5 ± 7886.4 | 52.07 ± 99.75 | 1473.1 ± 5593.6 |
| **Total** | **626.21± 1924.68** | **1138.23 ± 1746.3** | **6120.6 ± 23431.9** | **491.76 ± 520.26** | **3755.5 ± 16481.8** |

Values are: abundance_Ind.m$^{-3}$_mean ± standard deviation and biovolume_mm$^{3}$.m$^{-3}$_mean ± standard deviation

**Table 5** One-way Anova results for total abundance (a) and biovolume (b) of mesozooplankton size classes in response to the spatial, temporal, sampling time and transection factors. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

| a) Abundance (ind.m$^{-3}$) | **Spatial** | **Temporal** | **Sampling time** | **Transection** |
|---|---|---|---|---|
| 0.3 to 1.0 mm | $F_{(2,89)} = 22.90$, p < ** | n.s | n.s | n.s |
| 1.0 to 2.0 mm | $F_{(2, 89)} = 7.68$, p < ** | n.s | $F_{1,90} = 5.50$, p < * | n.s |
| 2.0 to 3.0 mm | $F_{(2, 85)} = 5.70$, p < ** | n.s | $F_{1,86} = 6.88$, p = ** | n.s |
| 3.0 to 4.0 mm | $F_{(2, 79)} = 4.12$, p = ** | n.s | $F_{1,80} = 6.94$, p = ** | n.s |
| 4.0 to 5.0 mm | n.s | n.s | $F_{1,61} = 5.85$, p = ** | n.s |
| > 5.0 mm | $F_{(2,52)} = 3.47$, p < * | $F_{(2, 52)} = 4.43$, p = ** | $F_{1,53} = 4.15$, p < * | n.s |
| b) Biovolume (mm.m$^{-3}$) | | | | |
| 0.3 to 1.0 mm | $F_{(2, 89)} = 19.41$, p < ** | n.s | n.s | n.s |
| 1.0 to 2.0 mm | , $F_{(2, 89)} = 5.97$, p < ** | n.s | $F_{1,90} = 5.41$, p < * | n.s |
| 2.0 to 3.0 mm | $F_{(2, 85)} = 5.52$, p < ** | n.s | $F_{1,86} = 8.84$, p < ** | n.s |
| 3.0 to 4.0 mm | $F_{(2, 79)} = 4.58$, p = * | n.s | $F_{1,80} = 7.05$, p < ** | n.s |
| 4.0 to 5.0 mm | $F_{(2, 60)} = 3.76$, p < * | n.s | $F_{1,61} = 7.95$, p < ** | n.s |
| > 5.0 mm | $F_{(2,52)} = 3.55$, p < * | n.s | $F_{1,53} = 22.70$, p < ** | n.s |

# 4. DISCUSSION

The present study provides evidence that the Marine Protected Areas of the Tropical Southwestern Atlantic (FNA, RA and SPSPA) differ in terms of abundance, biovolume and size classes of the mesozooplankton community. Other works have already pointed out differences between these oceanic islands in terms of the diversity of benthic and nektonic groups, and these are related to habitat size (e.g., FNA the largest) and distance from the mainland (e.g., SPSPA more isolated) (Barroso et al., 2017; Hachich et al., 2015;  Luiz et al., 2015; Soares et al., 2017), but the present study was the first to compare these habitats in terms of important ecological indicators (mesozooplankton abundance, biovolume, and size) that can be used to subside management and conservation policies in these areas. The spatial difference hypothesis was supported, where we highlight the productive potential of the smallest and most isolated archipelago of tropical islands of the planet (SPSPA). In addition, the hypothesis of temporal fluctuation for the abundance and biovolume of mesozooplankton was accepted signaling July / 2010 as a period whose zooplankton productivity was considered low. Curiously, we found that the size class (0.3 to 1 mm) was the only that did not respond to the sampling time effect neither in terms of abundance nor biovolume. This may be associated with the absence of vertical migration or high predation pressure over this size fraction.

## 4.1. Mesozooplankton taxonomic composition

A high number of taxonomic categories were identified with the ZooScan system. The dominance of Copepoda, Chaetognatha, and Euphausiacea in the Tropical Southwestern Atlantic has already been described (Neumann-Leitão et al., 2008), as well as in the Philippines region, in the western tropical North Pacific (Dai et al., 2017), and in the southern California Current System (Ohman et al., 2012).

The copepods considered dominant in the present study such as, Unidentified Calanoida, *U. vulgaris*, *Clausocalanus*, *Euchaeta*, Paracalanidae, *Scolecitrix*, *Corycaeus*, *Farranula*, *Oithona* and *Oncaea* occur worldwide in high abundances (Campos et al., 2017; Campelo et al., 2018c; Melo et al. 2012; 2014; Melo-Junior et al., 2016; Suárez-Morales & Gasea, 1997). However, we observed that these had maximum relative abundance in SPSPA, with highlight on smaller copepods, such as *Oncae*. High abundance of *Oncae* species was recorded in areas of upwelling such as Cabo Frio, Rio de Janeiro, Brazil (Mureb et al., 1976; Rosa et al., 2016) and off Chile (Vergara et al., 2017).

We recorded a high participation in biovolume of *Euchaeta*, *Scolecithrix*, *U. vulgaris* and Calanoida in FNA and RA. These are large body size copepods (Benedetti et al., 2015), which represent a considerable fraction of the total biomass of the assemblage in tropical and subtropical environments (Webber and Roff, 1995; Melo et al., 2014; Melo-Júnior et al., 2016). In the SPSPA, the *Subeucalanus* genus had a highlighted importance, corresponding to 24.14% of the total relative biovolume. Species of *Subeucalanus* are herbivorous and were considered dominant grazer in highly productive coastal upwelling systems (Hidalgo et al., 2005; Madhupratap et al., 1990; Vergara et al., 2017).

The taxonomic groups that contributed the most to the relative biovolume, we highlight Copepoda, Decapoda (larvae), Chaetognatha, Teleosteo (larvae), Cnidaria and Tunicata (Salpa and Doliolum). Spatial changes in biovolume in the North Pacific also recorded the high contribution of these taxa to the total biovolume, which is different from the proportion based on abundance (Dai et al., 2016;2017). Off Ubatuba (São Paulo, Brazil), these taxa were considered as the ones that contributed the most in biomass also reflecting their high individual sizes (Marcolin et al., 2015a).

### 4.2. Hypothesis 1: Spatial heterogeneity

Abundance and biovolume are important quantitative indices for zooplankton studies (Sato et al., 2015; Dai et al., 2016, 2017). The lowest abundance and biovolume that we found in RA is about 45 and 8.7 times lower than the range observed in the subtropical North Pacific (Dai et al., 2016) and 16.8 and 4.5 times lower than in the neighboring waters of Japan (Sato et al., 2015). Conversely, the high abundance and biovolume observed in SPSPA signaled it as a productive region, where these values were 28 and 4.5 times higher than those observed in the subtropical North Pacific (Dai et al., 2015) and 12 and 1.04 times higher than in the Northwest Pacific Ocean (Sato et al., 2015) .

Investigations about the mesozooplankton community are scarce in FNA, RA, and SPSPA, mainly due to logistical issues. Recently, the first study on the spatial and temporal fluctuations of the mesozooplankton in the coastal area of Fernando de Noronha was published; sampling was carried out with subsurface hauls, 300-µm-mesh-size plankton net. The author identified 37 taxa, especially Copepoda (Campelo et al., 2018a). The zooneuston community, with special interest in Decapoda, was studied in the surroundings of FNA; 500-µm-mesh-size plankton net (Lira et al., 2014). In both studies abundances were lower than those we recorded in FNA in the present study. The scarcity of information is greater over the RA; there is only one study about zooplankton in general (Pinto et al., 1997) and on study about the tintinids community (Nogueira et al. 2008; Nogueira and Sassi, 2011).

There is a greater number of information on taxonomic composition, spatial and vertical distribution, and mesozooplankton production in the SPSPA, mainly with emphasis on copepods (Melo et al., 2012; Melo et al., 2014; Díaz et al., 2009; Campelo et al., 2018b) because of the Proarquipelago program, which in association with the Brazilian Navy supports research in the seamount area. It is important to emphasize that SPSPA had a higher standing stock than other important areas such as the subtropical North Pacific (206.6 ± 128.6 ind. $m^{-3}$) (Dai et al., 2016), which is a highly diverse region (Tittensor et al., 2010), comparable to subarctic (431 ind. $m^{-3}$) and subtropical (278 ind.$m^{-3)}$ waters in the North Pacific (Matsuno and Yamaguchi 2010).

The high abundance and biovolume in SPSPA, emphasizes their role as "Oases of life" in the midst of an oceanic desert, which supports the hypothesis of seamounts as highly biologically productive sites (Rowden et al., 2010). Spatial contrasts on the mesozooplankton that inhabit seamounts are driven by a better food supply to the organisms (Genin et al., 1986). The SPSPA supports high abundances of planktonic, benthic and nektonic organisms (Barroso et al., 2016; Luiz et al., 2015; Magalhães et al., 2015;; Macena and Hazin 2016; Mendonça et al., 2018). Due to the abrupt topography (Barroso et al., 2016) aggregations of organisms are expected, caused by different physical mechanisms such as strong mixing, internal wave interactions, eddies, and recirculation (Mullin, 1993).

According to Travassos et al. (1999) the SPSPA is located within a complex current system characterized by a surface westward flow of the South Equatorial Current (SEC) and a subsurface eastward flow of the Equatorial Undercurrent (EUC). Vertical mixing between the SEC and the EUC can promote disruption in the water column pushing some water vertically. The author studying the thermohaline structure in the surroundings of the SPSPA informed that their results did not provide clear evidence of upwelling in the area. However, Araujo and Cintra (2009) using modeling data of nutrient and plankton dispersion in the same area verified disturbances in the thermocline associated with vertical transport induced by eddies. As the main effect of the currents' interaction with the island topography is the formation of eddies, these can be trapped over seamounts and form closed cells of anticyclonic circulation known as Taylor column (White and Mohn, 2005).

The Taylor column may be responsible for aggregations of zooplankton and micronekton in seamounts as well as changes in the pelagic food chain (Genin, 2004). Araujo and Cintra (2009) suggest the occurrence of a Taylor column in the SPSPA, but explain the need for a longer time series, covering different seasonal moments to confirm the possibility of upwelling in the area beyond the Taylor column.

The spatial distribution pattern of the abundance and biovolume size classes (ESD) were very similar over the MPAs. The high contribution of the 0.3 to 1 mm fraction  in the MPAs is indicated as a characteristic of highly stable and oligotrophic tropical environments (Hopcroft et al., 2001; Van der Lingen, 2006). In addition, the effect of mesh size used in the present study (300µm) also contributed to the results achieved. Studies on the vertical distribution of the plankton size spectrum above the Abrolhos Bank and in adjacent oceanic areas off Eastern Brazil (Marcolin et al., 2013) and on the subtropical shelf off Brazil (Marcolin et al., 2015b) also recorded a greater contribution in abundance of smaller organisms. Both works used 200 µm mesh net. Reinforcing this information, vertical samplings carried out in the subtropical North Pacific during winter 2012 (Dai et al., 2016) and in the western tropical North Pacific during autumn 2014 (Dai et al., 2017) using 160 and 200 µm mesh nets respectively, also recorded a greater contribution in the abundance of mesozooplankton of smaller body size.

Size is an important feature in the structuring of the planktonic community and according to Garcia-Comas et al. (2016) in East China Sea and Basedow et al. (2010) in Northwestern Barents Sea food availability is the more important factor in modeling zooplankton size structure. The high mesozooplankton abundance in the smaller fraction (0.3 to 1 mm) reaffirms  SPSPA as a greater secondary productivity area, which can sustain a whole megadiversa fauna  in its surroundings.  *Clasusocalanus* copepods, Paracalanidae and  Cyclopoida (*Oncae*, *Farranula*, and *Corycaeus*) were particularly relevant in the area, accounting for over 50% of the total abundance in SPSPA (Campelo et al. Unpublished). Cyclopoida copepods were also relatively more abundant offshore the Abrolhos Bank, in oceanic areas (Marcolin et al., 2013). Besides the influence of the mesh size discussed previously, the dominance of small copepods in oligotrophic systems is explained by their high efficiency in capturing flagellate phytoplankton species and microzooplankton (Hopcroft et al., 2001; Paffenhoefer, 1998). In fact, there is an abundant and diverse microzooplanktonic community of tintinids, radiolarians, and heterotrophic dinoflagellates, which are important ammonia producers in the tropical oligotrophic waters of SPSPA (Costa et al., 2018). The main source of ammonia in seamounts comes from regeneration processes in the pelagic microbial food web (Cordeiro et al., 2013).

Hydrographic features, such as pycnocline, upwelling, eddies, and vertical mixing are typical examples of physical mechanisms that provide bottom-up control. According to von Bröckel and Meyerhöfer (1999) its occurrence has not yet been well understood, but probable nutrient enrichment events are responsible for the high pelagic and benthic productivity around the SPSPA. The > 5 mm high biovolume dominated in all island systems because of a greater contribution of large-sized taxa such as large copepods – (*e.g., Pleuromamma*), Decapoda, Chaetognatha, Teleostei (larvae), Cnidaria (mainly Siphonophora), and Tunicata (mainly *Doliolum*). Although Sato et al. (2015) have found higher biovolume in smaller size classes (0.5 – 1 mm), comprised by small copepods (*Paracalanus parvus* and Poecilostomatoida) in the Kuroshio extension in the Northern Japan Sea, Okhotsk Sea, and subarctic Western North Pacific the higher contribution was in the 4 to 5 mm size class, because of macrozooplankton such as amphipods, euphausiids, and chaetognaths (Sato et al., 2015). In addition, in the surroundings of the Canary islands the small size fraction (100–200 µm) also displayed lowest average biomass values, whith greater biomass in the > 1000-µm size fraction (Hernández-León et al., 2001).

Seamounts are considered areas of intense predation (Genin et al., 1988, 1994; Haury et al., 2000). According to Brooks and Dodson (1965) predation and competition are important structuring the zooplankton community. When the predation pressure by fish is intense, larger zooplankton will be removed from the community and small zooplankton will dominate. For instance, whale sharks off Mafia Island, Tanzania, target zooplankton patches characterized by a higher biomass, larger mean size and dominated by macrozooplankton compared with non-feeding areas (Rohner et al., 2015). The SPSPA is a migratory route of important species that use this area for breeding and feeding (Hazin et al., 2008). This small island complex is home to one of the greatest diversities of mobulid ray (Mendonça et al., 2018), and has the highest occurrence of Whale Shark (*Rhincodon typus*), in relation to FNA and RA (Macena & Hazin 2016). The occurrence of *R. typus* and increased abundance of mobulids, mainly *Mobula tarapacana,* is seasonal in the SPSPA and occurs when specific oceanographic conditions favor reproductive processes of fish and invertebrates in the region (Mendonça et al., 2018; Macena and Hazin 2016). *R. typus* and *M. tarapacana* are large filter feeders, consuming mainly euphausiids, copepods, and decapods (Macena and Hazin, 2016; Mendonça et al., 2018). Therefore, we suggest that the intense predation pressure exerted by these elasmobranchs and planktivorous fish in SPSPA may reduce the competitive effect among the size classes, thus promoting the development of smaller-sized populations (Brooks and Dodson, 1965).

### 4.3. Hypothesis 2: Temporal heterogeneity

A temporal trend of significant increase of the abundance and biovolume of mesozooplankton was shown. However, it is important to carry out longer series (> 5 years) to reveal the possible impacts that climatic events such as El Niño of 2010 (Kim et al., 2011) and La Niña of 2012 (Rodrigues & McPhaden, 2014) can cause in the composition, abundance, biomass and productivity of the mesozooplanktonic community of island environments of the Tropical Southwestern Atlantic.

Zooplankton are important indicators of changes of both climatic and anthropogenic order (Taylor et al., 2002) because they are (1) poikilothermic (Mauchline, 1998); (2) have short life cycle (Hays et al., 2005), and (3) are not commercially exploited so that the changes in their community are not confused with exploitation trends (Vandrome et al., 2011). In 2010, unusually high sea surface temperatures (SST) associated with the El Ninõ event were recorded in several parts of the world and caused coral bleaching and mortality (Krishnan et al., 2011). In the Atlantic Ocean, the NOAA Coral Reef Watch (CRW) satellite product (NOAA, 2000) recorded a thermal stress in the region between latitudes 0°_S and 8°_S (Ferreira et al., 2013). The authors recorded the percentage of bleached corals persisting after the subsidence of the thermal stress, and disease prevalence increased through 2010, after two periods of thermal stress in FNA and RA.

Our results showed changes in abundance and biovolume between the studied periods, where values of the respective indices significantly lower in July 2010, which may be a response to the thermal stress recorded for this year. However, seasonality, winds, current dynamics and predation must be considered, since they influence the zooplankton abundance and biomass stocks in Tropical environments (Aristegui et al., 1989; D'Alcalà et al., 2004; Lavaniegos et al.,1998; Piontkovski and Castellani, 2009).

Changes in copepod species composition between El Niño 1997-1998 and La Niña 1998-1999, following trends in oceanographic conditions was recorded off Baja California (Jiménez-Pérez and Lavaniegos, 2004). Low zooplankton biomass was recorded during El Niño 1997-1998 from Vancouver Island to 50°N, 145°W, off the Canadian coast (Mackas & Galbraith 2002) and off southern California (Hayward, 2000, Lavaniegos & Ohman 2003). The probable effect of the thermal increase in 2010 was pointed out as possible responsible for the low concentration of zooplanktonic biomass verified in FNA, RA and SPSPA in July / 2010 (Campelo et al., Unpublished).

Our abundance and biovolume data (776% and 186%, respectively, higher in August/2014 when compared to July/2010) supports the hypothesis of a thermal increase effect. Also, it is important to highlight the increase in abundance of omnivores, carnivory/detritivores, and filter-feeding (Ostracoda, Euphausiacea, Decapoda and Mollusca) (1470%, 3402%, 568% an1025%d, respectively) and in biovolume, particularly of carnivore and filter-feeding organisms such as Tunicata and Decapoda (1187% and 12, 98%, respectively). When the water temperature is > 25° it can alter the growth of individuals and consequently the body size of zooplankton (Moore & Folt, 1993). The high contribution in biovolume of Tunicata in August/2014 is another evidence of warmer temperatures since it is an important component of the herbivorous zooplankton in warm seas, because it rapidly colonizes sites of high primary productivity competing with as copepods (Alldredge and Madin, 1982).

In August/2014 the islands were strongly influenced by the southeast trade winds (Campelo et al., Unpublished), and important local currents such as the South Equatorial Undercurrent (SEUC) in FNA and RA and the Equatorial Undercurrent (EUC) in SPSPA had maximum flows (Brandt et al., 2011; Tchamabi et al., 2017). As a consequence vertical mixing is expected, which is an important driver of plankton productivity via nutrient input and exposure of phytoplankton cells to light (Demers et al., 1986). Indeed, chlorophyll concentrations indicated vertical mixing in August /

2014. Also, high numbers of fish species were recorded in August as a consequence of the increased chlorophyll concentration in SPSP (Macedo et al., 2012).

Our results indicate that the islands of the Southwest Tropical Atlantic met favorable conditions in August/2014, which resulted in increase productivity since there was an increase tendency in smaller mesozooplankton and a significant increase in biovolume of the > 5 mm organisms. Changes in plankton size structure during increased productivity and consequent phytoplankton blooms were also observed in the central Cantabrian sea (Zarauz et al., 2009). The authors verified that in the oceanic stations both small and large cells contributed to the biomass increase, although large cells increased faster and had a larger contribution that resulted in the final size structure.

### 4.4. Hypothesis 3: The vertical migration effect

The diel vertical migration (DVM) is a typical behavior performed by zooplankton where hypotheses such as: predator-evasion (Dagg et al., 1997), changes in light intensity (Dodson et al., 1997), light-protection (Manuel and O'Dor, 1997) and food-availability (Dagg et al., 1997) were elaborated to explain zooplankton ascendance into the surface water at night and return to deep layers during the day (Steinberg et al., 2000). Our findings did not show any day-night differences for integrated mesozooplankton abundance data, which was also recorded in Cato island (Suthers et al., 2010) and over seamounts in the eastern Mediterranean (Rhodes Basin, Anaximander Mountains, northern Levantine Basin) (Denda and Christiansen, 2011). However, specific groups such as: Ostracoda, Euphausiacea, Decapoda, Mollusca, and Cnidaria were more abundant during the night, probably exerting DVM. Mathew et al. (1996) found a pronounced vertical migration of ostracods, with significant higher abundances during night in the Arabian Sea and Bay of Bengal. This group was also an important biomass source in the Abrolhos Bank in comparison to the copepods that dominated only in abundance (Marcolin et al., 2013).

Vertical migration is common in most euphausiids species (Antezana, 2010) and high concentrations may occur on abrupt topographies, such as continental shelf-breaks, ridges and seamounts (Genin 2004; Letessier et al., 2009) as a result of the interaction of currents with the island topography (Barange et al., 1991). In the Canary current system, euphausiids and decapods were the most important groups in terms of biomass displacement between the mesopelagic layer and surface waters (Pugh, 1974, Rudyakov, 1979, Hernández-León, et al., 2001). Significant differences in the abundance of decapod larvae during nighttime, when these become dominant were already observed in SPSPA (Koettker et al., 2010).

The high abundance of mollusks at night recorded in the present study occurred due to the high contribution of the representatives of the order Pteropoda present in the samples analyzed. These important components of macrozooplankton comprising species larger than 5 mm in size (Larrazabal and Oliveira, 2003). High abundance of *Limacina inflata* and *Creseis virgula* were recorded at night in the surface waters of the Fernando de Noronha Chain, which was independent of the depth, mesh size and temperature. (Larrazabal and Oliveira, 2003). We found especially siphonophores, which are among the most abundant and efficient carnivores in the ocean preying strongly on small copepods (Haddock and Dunn, 2005). The high and significant abundance of gelatinous zooplankton, especially siphonofores, in the upper mixed layer during night was registered in a Subtropical Stratified Ecosystem (South Brazilian Bight) (Junior et al., 2015), reinforcing the strong pressure of predation performed by this group. Thus, Ostracoda, Euphausiacea, Decapoda, Mollusca and Cnidaria play an important role as vehicles for the removal of organic carbon in surface water to the deeper regions, contributing strongly to the vertical flow of particles around tropical island environments.

Although the analysis of the integrated data of the average abundance of mesozooplankton did not show differences between day and night the biovolume responded significantly. The high contribution of organisms of higher body volume at night is explained by the important contribution of size classes: 1 to 2 mm; 4 to 5 mm and > 5 mm registered in the present study. Furthermore, it is important to consider that the smaller fraction (0.3 to 1mm) did not respond to the effect of the sampling time, neither in abundance nor in biovolume. This probably occurs because this smaller fraction is food of larger sized mesozooplankton organisms and another explanation would be the fact that this smaller fraction corresponds to non-migratory organisms (Denda and Christiansen, 2014).

In terms of biovolume the size classes that stood out at night were: 1 to 2 mm; 2 to 3 mm; 3 to 4; 4 to 5 mm and > 5 mm. We suggest that these classes are probably represented by the taxa: Euphausiacea, Decapoda, Mollusca and Cnidaria already discussed in the present work as important top-dow controllers of the zooplankton smaller fraction. In addition, individuals such as Chaetognatha, Thaliacea and Teleosteo (larvae) also identified in the present study contribute to this greater participation in size and consequently in biomass at night. Chaetognatha contributed to the highest percentage of total zooplankton biomass due to its high individual size (mean of 1.43 mm ESD) off Ubatuba, Brazil (Marcolin et al., 2015a). The study of the vertical distribution of biomass in the Canary Islands recorded a high biomass of larger organisms in 500 meters of depth during the day. These concentrations reduced the night and the biomass in the 200 m upper increased due to rising of the larger sized individuals (Hernández-León et al., 2001).

## 5. CONCLUSIONS

Changes in abundance, biovolume and mesozooplankton size in Marine Protected Areas of the Tropical Southwestern Atlantic were related to the effect of spatial, temporal, and sampling time:

(1) The remote St. Peter and St. Paul archipelago (SPSPA) was the most productive island, with higher mesozooplankton abundance and biovolume. Furthermore, small mesozooplankton (0.3 to 1 mm) was dominant, reinforcing the high productive potential of this small and remote archipelago. We suggest that this high productivity is sustained by bottom-up mechanisms provoked by nutrient enrichment events;

(2) Temporal changes in the mesozooplankton community show July / 2010 as a much less productive period. Although we believe that this may be a response to the rising sea surface temperature as a consequence of El Niño, whose influencing planktonic productivity, seasonality, wind, and currents should be considered;

(3) The high abundance of important vertical migrants during nighttime such as Ostracoda, Euphausiacea, Decapoda, Mollusca, and Cnidaria, contributed to significant increases on the average biovolume. Likewise, both abundance and biovolume of the larger size classes responded to the sampling time effect. These signs indicate that diel vertical migration should be an important behavior in this region, contributing to biological carbon pump. The lack of differences between day-night in the size class 0.3 - 1 mm suggests high predation pressure or no vertical migration behavior in small mesozooplankton;

(4) Although the "*Island Mass effect*" has not been proven, our data point to a trend in zooplankton retention downstream the island.

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# FINAL CONSIDERATIONS

- High zooplankton biomass, abundance of copepods, abundance of mesozooplankton, abundance of the smaller size class (0.3 to 1 mm) and the highest contribution in biovolume in organism > 5 mm were recorded in the smallest and most isolated Tropical Islands Archipelago of the planet - SPSP, highlighting it as the biologically most productive insular system, thus reinforcing the need for efficient policies for the conservation and protection of marine biodiversity in this remote environment;

- A reduction of zooplankton biomass, abundance and biovolume of mesozooplankton was observed in 2010, a period considered under thermal stress, as a consequence of the El-nino event. These results provide evidence of commitment of growth and zooplankton secondary productivity surrounding of the island systems studied during this event;

- The typical vertical migration behavior of zooplankton, especially those of larger body size, was responsible for the high values of zooplankton biomass and biovolume of mesozooplankton in the surrounding of the tropical islands studied. Through this behavior the migrators contribute to the vertical flow of particles and remove the carbon from the surface layer, transporting them to the deeper regions, contributing to the biological carbon pump;

- In general, we recorded high average values of zooplankton biomass, copepod abundance, abundance and biovolume of the mesozooplankton occurring downstream of the islands studied. However, the only statistically significant difference was for the copepods abundance. These high downstream values are a consequence of the "*Island Mass effect*", whose interaction of the surface current with the topography of the island causes downstream turbulence and plankton retention mechanisms.

# APPENDIX

Appendix I – Small-sacale distribution of the mesozooplankton in a Tropical insular system;

Appendix II - Morphological abnormalities in *Corycaeus speciosus* Dana, 1849 (Copepoda, Cyclopoida) on an Equatorial Atlantic Island;

Appendix III - Book chapter published in commemoration to the 20 years of research carried out in the Saint Peter and Saint Paul Archipelago.

ORIGINAL ARTICLE / ARTIGO ORIGINAL BJOCE

# Small-scale distribution of the mesozooplankton in a tropical insular system

*Renata Polyana de Santana Campelo*[1,3]*, *Xiomara Franchesca Garcia Diaz*[1], *Gleice Santos*[1], *Pedro Augusto Mendes de Castro Melo*[1], *Mauro Melo Junior*[2], *Lucas Guedes Pereira Figueiredo*[1], *Andrea Pinto Silva*[1], *Luis Ernesto Arruda Bezerra*[2], *Manuel de Jesus Flores Montes*[1], *Sigrid Neumann-Leitão*[1]

[1] Universidade Federal de Pernambuco, Centro de Tecnologia e Geociências Museu de Oceanografia, Laboratório de Zooplâncton.
(Av. Arquitetura s/n, Cidade Universitária, 50.740-550, Recife, Pernambuco, Brazil)
[2] Universidade Federal Rural de Pernambuco Departamento de Biologia, Laboratório de Ecologia de Plâncton.
(Rua Dom Manuel de Medeiros, s/n, Dois Irmãos, 52.171-900, Recife, Pernambuco, Brazil)
[3] Universidade Federal do Ceará Instituto de Ciências do Mar
(Av. da Abolição, 3207, Meireles, 60165-081, Fortaleza, Ceará, Brazil)

*Corresponding author: renatapolyanadesantanacampelo@gmail.com

## ABSTRACT

In the present work, spatial and seasonal fluctuations of the abundance and diversity of mesozooplankton are presented, with special attention being given to copepod assemblages from coastal area of the Fernando de Noronha Archipelago (FNA) (3°50'24"S and 32°24'48"W). Sampling was carried out during the dry and rainy seasons of two consecutive years (July and December 2013) and (June and November 2014). A total of 37 mesozooplankton taxa were recorded, being the copepods the most diversified group (15 taxa). The Subclass Copepoda dominated in both periods sampled, comprising 53% and 86% of the total abundance in the dry and rainy season respectively. The species considered abundant were: *Calanopia americana, Undinula vulgaris, Oithona plumifera* and *Corycaeus speciosus*. The rainy season favored a significant increase in the abundance of mesozooplankton and copepods. However, a low value of the Shannon-Wiener diversity index was observed in this same seasonal period. This was explained by the dominance of the species *C. americana* and *U. vulgaris* in the studied area. Spatial differences have not been verified. The copepod assemblages was composed mostly by species considered as predator-carnivours of greater importance on the pelagic trophic web, indicators of oligotrophic conditions and components of a major portion of fish food items. Thus, we suggest that a spatially homogeneous mesozooplankton community characterizes the coastal area of Fernando de Noronha Archipelago with variations related mainly to the seasonal factor.

**Descriptors:** Community structure, Copepoda, Sazonality, Functional traits.

## RESUMO

Neste presente trabalho, são apresentadas as flutuações espacial e sazonal da abundância e diversidade do mesozooplâncton, com especial atenção para assembleia de copépodes da área costeira do Arquipélago de Fernando de Noronha (AFN) (3°50'24"S and 32°24'48"W). A amostragem foi realizada durante as estações seca e chuvosa de dois anos consecutivos (julho e dezembro de 2013) e (junho e novembro de 2014). Um total de 37 taxa do mesozooplâncton foram registrados, sendo os copépodes o grupo mais diversificado (15 taxa). A Subclasse Copepoda dominou em ambos os períodos amostrados, com valores de abundância relativa equivalentes a 53% e 86%, respectivamente, nas estações seca e chuvosa. As espécies consideradas abundantes foram: *Calanopia americana, Undinula vulgaris, Oithona plumifera e Corycaeus speciosus*. A estação chuvosa favoreceu um aumento significativo na abundância do mesozooplâncton e copépodes. No entanto, um baixo valor do índice de diversidade de Shannon-Wiener foi observado para este mesmo período sazonal. Isso foi explicado pelo domínio das espécies *C. americana* e *U. vulgaris* na área estudada. Diferença espacial não foi verificada. A assembleia de copépodes apresentou um maior número de espécies consideradas carnívoro-predador de grande importância na teia trófica pelágica, indicadoras de condições oligotróficas e componente de grande porção dos itens alimentares dos peixes. Assim, sugerimos que a área costeira do Arquipélago de Fernando de Noronha é caracterizada por uma comunidade do mesozooplâncton espacialmente homogênea, onde as mudanças observadas estão principalmente relacionadas ao fator sazonal.

**Descritores:** Estrutura da Comunidade, Copepoda, Sazonalidade, Características funcionais.

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# INTRODUCTION

The zooplankton community plays a key role in the pelagic environment including the export of ocean surface carbon, energy transfer and organic matter to higher trophic levels, influencing primary producers (top-down effect) and predators (Falkowski et al., 1998; Barton et al., 2013).

Spatial and seasonal patterns of species distribution have motivated ecological research (Gause, 1934; Hutchinson, 1957). Understanding the processes that create these patterns has become increasingly important in the face of continuing threats of habitat destruction, pollution, species invasion and climate change (Robinson et al., 2011). Thus, the driving processes of the spatial distribution of organisms (local topography, current patterns, winds and physico-chemical characteristics of water masses) can provide insights into the possible mechanisms responsible for the complexity and maintenance of natural diversity and provide critical information for conservation priorities (Cowie and Holland, 2006).

In tropical seas, the seasonal dynamics of zooplankton ecological attributes are difficult to identify and are much less marked than those observed in temperate aquatic ecosystems (Dias et al., 2010). The zooplankton community structure of the Brazilian Northeastern region is directly influenced by rainy and dry periods and regional oceanographic phenomena (Neumann-Leitão et al., 1999). In addition to abiotic factors (seasonality and spatiality), the structure and composition of ecosystems are governed by biotic factors inherent to community such as the life cycles of organisms, migration, reproductive strategies, feeding approach, size and intra-interspecific relationships (Björnberg, 1981). Some zooplankton species, with well known tolerance levels to different environmental conditions can be used to describe the main characteristics of the water masses in which they occur (Wickstead, 1979; Rice and Stewart, 2016).

Despite their important in marine food web, few papers have been published about zooplankton in tropical coastal marine waters of Northeastern Brazil (Neumann-Leitão et al., 1999; Neumann-Leitão et al., 1999; 2008) and to insular milieus (Mafalda Jr. et al., 2007; Diaz et al., 2009; Larrazabal et al., 2009; Melo et al., 2012). Insular environments in tropical oceans are hotspots for pelagic fauna, amidst the most nutrient-poor waters of the Atlantic Ocean, where occurs intensive fisheries. Analyses of species-diversity patterns of remote islands have been crucial to the development of ecological processes enriching production and to envisage the health quality of these environments.

In ocean, the holoplankton dominates numerically (Neumann-Leitão et al., 2008), and among all taxa, the copepods correspond to the most abundant (60 to 90% of the total abundance of zooplankton) and diverse group (Piontkovski et al., 2003). Furthermore, copepods play an important role in the functioning and maintenance of marine ecosystems. Thus the identification of functional groups based on species with similar responses to ecosystem functions and/or similar response to environmental conditions is a pressing need (Benedetti et al., 2015).

In spite of the above mentioned, our hypothesis was that abundance and diversity attributes of the mesozooplankton community fluctuate spatial and seasonally in a tropical insular system. Thus, the main objectives of our study are (i) To describe seasonal and spatial variations in the mesozooplankton community in a tropical oceanic Archipelago in Brazilian Northeastern; (ii) To provide data on seasonal and spatial changes of abundance and diversity of the main group (copepods); and (iii) To identify the functional traits of dominant copepod species from this tropical area.

# MATERIAL AND METHODS

## STUDY AREA

The Fernando de Noronha Archipelago (FNA) (Figure 1) lies in a National Marine Park (created by Decree No. 96.693 of September 14, 1988), as well as a State protected area (created by Decree 92.755 of June 5, 1986) (Almeida, 1955), being located in the Equatorial Atlantic (Tropical). The park covers 21 islands, islets and rocks, encompassing part of the FNA and a chain of seamounts located at 3°50’24”S and 32°24’48”W. The FNA is located approximately 545 km from the capital of Pernambuco (Recife), 2.600 km from the African coast and 360 km from the South American continent (Lira et al., 2014).

Due to the morphological configuration of the main island, two coasts have been formed opposite to each other, one on the southeast side and the other on the northwest side. The area is characterized by the tropical climate (Köeppen, 1948) having two well-defined seasons: a dry (August-February) and a rainy season (March to July). The mean annual rainfall is about 1.400 mm, and the annual mean temperature 25°C (Serafini et al., 2010). The Archipelago is subject to a complex system of currents and

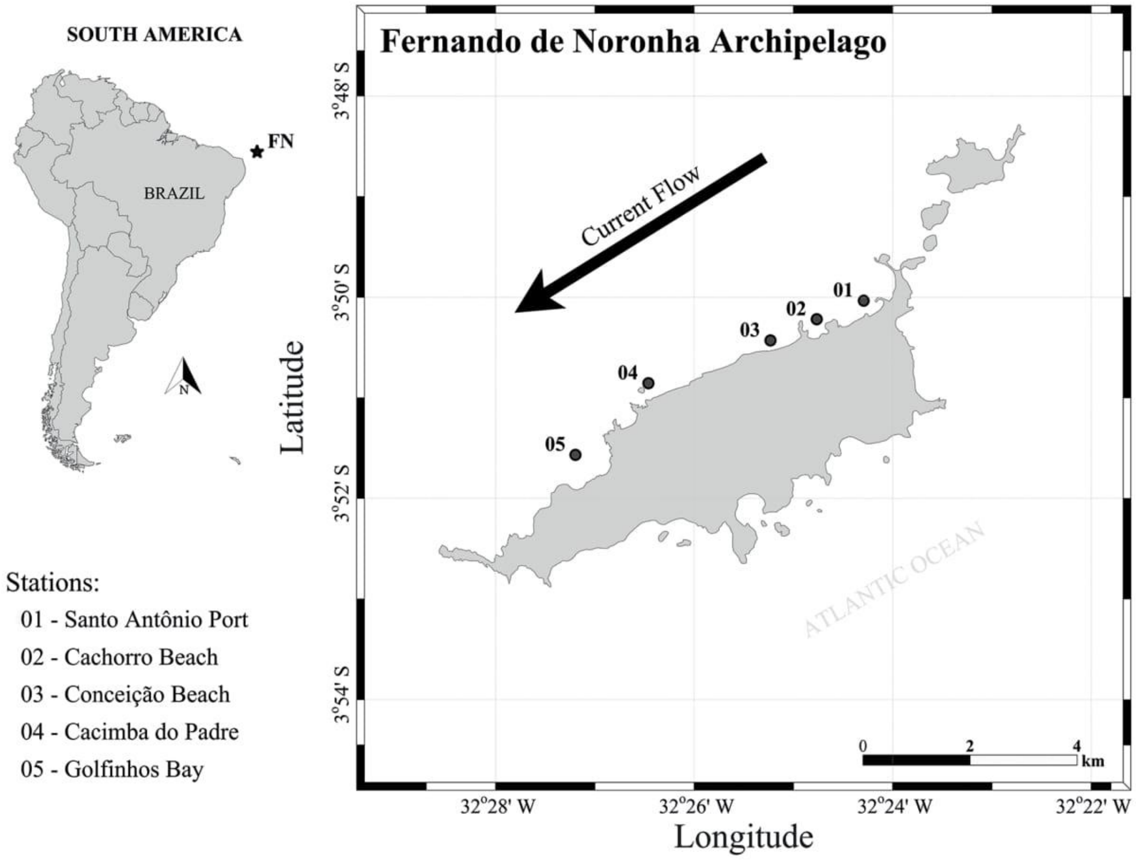

**Figure 1.** Study area showing the collection stations off the Fernando de Noronha Archipelago (3°50'24''S and 32°24'48''W), State of Pernambuco, Northeastern Brazil. Santo Antonio Port (1), Cachorro Beach (2), Conceição Beach (3), Cacimba do Padre (4) and Golfinhos Bay (5).

undercurrents that flow mainly in an East-West direction along the equator, usually under the influence of the South Equatorial Current (SEC) in the surface layer of the water column. The prevailing winds are the southeasterly trades, varying to northeasterly, with a mean intensity of 4.8 m $s^{-1}$, from the surface to the level of 750 mb (Assunção et al., 2016).

## Sampling strategy

Sampling was carried out during four diurnal oceanographic expeditions along the western coast of FNA during the dry and rainy seasons of two consecutive years (July and December 2013 and June and November 2014). A total of 19 samples were collected. Five stations were determined being to the north: Santo Antonio Port (1), Cachorro Beach (2) and Conceição Beach (3) and to the south: Cacimba do Padre (4) and Golfinhos Bay (5) (Figure 1). The stations presented different local depths (ranging from 2 to 30 meters, with a mean of 16.6 m) due to variations in the tide and the climatic periods throughout the study.

## Sampling and laboratory analyses

Zooplankton samples were collected by horizontal subsurface hauls that were performed with a cylindrical-conical net (mouth area 0.6 $m^2$, mesh size 300 μm) during 10 minutes. To obtain the water volume filtered, a flowmeter was coupled at the net mouth. After collection, the samples were transferred to plastic bottles and immediately preserved in formaldehyde solution (4%), buffered with sodium tetraborate.

In the laboratory, the samples were fractionated in aliquots of 1/32 or 1/64, using a Motoda splitter (Omori & Ikeda, 1984) provided that a minimum number of 200 individuals were analyzed (Frontier, 1981). The specimens were identified and inspected under a Zeiss Discovery V8 stereomicroscope.

The copepods identification mainly followed Björnberg (1981), Bradford-Grieve et al. (1999) and Dias and Araújo (2006). The overall abundance of each species was estimated for juvenile and adult copepodites. All the specimens found were deposited in the zooplankton collection of the Museum of Oceanography at UFPE.

In this study, only the species of copepods were classified according to their functional characteristics, such as: body size (<1100 µm; 1000-1300 µm; 1500-3300 µm and >1700 µm), trophic group (herbivorous, suspensivores, omnivorous, detritivores and carnivorous), spawning strategy (broadcast spawner and sac-spawner) and vertical distribution (epipelagic, mesopelagic, epipelagic to mesopelagic and epipelagic to bathypelagic). The functional characteristics were obtained from the literature (Boltovskoy, 1981; 1999; Benedetti et al., 2015; Pomerleau et al., 2015).

### STATISTICAL ANALYSIS

The Shannon-Wiener index (H′) was applied on copepod assemblages as the measure of diversity. Main effects ANOVA was used to analyze the first-order (non-interactive) effects of multiple categorical independent variables (spatial and seasonal) on biotic variables (abundance of mesozooplankton, abundance of copepods, dominant species of copepods (with more than 2% of total abundance) and Shannon-Wiener diversity index).

The heterogeneity of variances was verified through the Levene test and normality tested using the Shapiro Wilk's test. The data were transformed by the Log (X + 1) when necessary. Multivariate procedures included: (i) Permutational Multivariate analysis of variance (PERMANOVA) (Anderson, 2001; Mcardle and Anderson, 2001) was performed (with 999 permutations) based on the dissimilarity of Bray-Curtis (data transformed with Log X + 1). This analysis was used to determine whether there were significant differences in the structure of the mesozooplankton community between the dry and rainy seasons (seasonal factor) and among sampling stations (spatial factor). The interaction of these two factors was also tested. Only species that presented more than 2% of relative abundance were considered in this analysis. (ii) Multi-dimensional scaling (MDS) was used to represent the Bray-Curtis matrix graphically in a two-axis space (Sarmento and Santos, 2012). The significance of the PERMANOVA was assessed by the *p* value. (iii) In case of significant differences, SIMPER (Similarity of percentages) test was used to identify the taxa that contributed most to the dissimilarity between the groups. (iv) Classification (cluster analysis) of the sample-copepod species data matrix based on the Sorensen coefficient and weighted pair group method was used with the averaging clustering method built on four functional characteristics (body size, trophic group, spawning strategy and vertical distribution).

The indicator value analysis (Indval) was calculated to classify the fidelity of taxa in relation to the tested factors (seasonal and spatial), and tests for the statistical significance of the associations by permutation (Dufrêne and Legendre, 1997; Legendre and Legendre, 1998). The values varied from 0% (no indication) to 100% (perfect indication). It was considered those taxa occurring with more than 20% of frequency of occurrence. Only the taxa that presented values of indicators (Indval) ≥50% were considered indicators of the factors tested. The indicator value (Indval) of a species has been used to show species status as ecological indicator.

The Shannon-Wiener index, SIMPER analyze, MDS and PERMANOVA were applied using the software Primer_v.6. The Main effects ANOVA test was calculated using the software STATISTICA 7.0. The Indval value was calculated using the software R-Studio (available at https://cran.r-project.org/) within the R-Studio (v.0.99) user interface (available at http://www.rstudio.com/). The level of significance was set at $p<0.05$ for all analyses. Parametric statistical analysis followed Zar (1996).

## RESULTS

### SEASONAL VARIATION

Altogether, 37 taxa were identified (Table 1). Holoplankton dominated with 97% of all taxa. In general, copepods dominated in both periods sampled, comprising 53% of the zooplankton community in the dry season and 86% in the rainy season (Figure 2a and 2b). 15 species of Copepoda where recorded (Table 1); the most abundant species were *Calanopia americana, Undinula vulgaris, Oithona plumifera* and *Corycaeus speciosus* (Figure 2c and 2d). Among the copepods, *C. americana* was considered dominant, representing 35% (dry season) and 79.33% (rainy season) of the total copepods (Figure 2c and 2d).

The second most abundant holoplankton group was Appendicularia, with 12.76% in the dry and 0.88% in the rainy season (Figure 2a and 2b). The meroplankton consisted of larval gastropods, with 4.59% in the dry and 1.25% in the rainy season and fish (eggs and larvae) with 2.17% in the dry and 5.81% in the rainy season (Figure 2a and 2b).

**Table 1.** Total abundance of mesozooplankton (ind.m$^{-3}$) identified in the stations: Santo Antonio Port (1), Cachorro Beach (2), Conceição Beach (3), Cacimba do Padre (4) and Golfinhos Bay (5) located on Fernando de Noronha Archipelago during the rainy and dry seasons of two consecutive years (July and December 2013 and June and November 2014). In bold type the copepod species considered dominant (Abundance ≥2%).

| | **RAINY SEASON** | | | | | **DRY SEASON** | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Stations** | **1** | **2** | **3** | **4** | **5** | **1** | **2** | **3** | **4** | **5** |
| Taxa | | | | | | | | | | |
| Foraminifera (Others) | 0.00 | 0.00 | 9.82 | 19.71 | 0.45 | 1.13 | 0.01 | 2.30 | 4.60 | 1.91 |
| *Globigerinoides* sp. | 0.50 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Siphonophorae | 0.38 | 0.00 | 0.00 | 4.64 | 0.15 | 0.68 | 0.02 | 0.58 | 1.16 | 0.81 |
| Bivalvia | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 | 0.32 | 0.64 | 0.00 |
| Gastropoda (Veliger and Juvenile) | 0.38 | 2.58 | 3.93 | 6.57 | 0.07 | 0.92 | 0.02 | 0.51 | 1.03 | 0.43 |
| Bryozoa | 0.25 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 |
| Polychaeta (Larvae) | 0.00 | 0.83 | 0.00 | 0.00 | 0.00 | 0.02 | 0.01 | 0.06 | 0.13 | 0.00 |
| Ostracoda | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 |
| Calanoida | 0.00 | 0.00 | 2.95 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Calanoida (Copepodite) | 3.05 | 5.81 | 0.00 | 105.12 | 3.71 | 0.45 | 0.05 | 0.00 | 0.00 | 0.55 |
| Calanidae | 0.00 | 0.00 | 0.00 | 0.00 | 7.95 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Undinula vulgaris* | 5.41 | 6.08 | 2.95 | 13.53 | 1.74 | 1.41 | 0.07 | 0.81 | 1.62 | 0.85 |
| *Calocalanus pavo* | 0.00 | 1.22 | 0.98 | 6.57 | 0.07 | 0.45 | 0.01 | 0.00 | 0.00 | 0.22 |
| *Calocalanus* (Copepodite) | 0.00 | 1.55 | 0.00 | 0.00 | 3.62 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Paracalanus aculeatus* | 0.25 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Acrocalanus longicornis* | 5.20 | 20.73 | 14.73 | 6.57 | 0.00 | 0.45 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Acrocalanus* (Copepodite) | 0.00 | 0.00 | 0.00 | 6.57 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.11 |
| *Clausocalanus furcatus* | 0.00 | 0.05 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Euchaeta marina* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.10 | 0.00 |
| *Metridia* spp. (Copepodite) | 0.00 | 0.00 | 0.00 | 0.00 | 0.30 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Centropages velificatus* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.33 | 0.00 |
| *Candacia pachydactyla* | 0.00 | 0.00 | 0.00 | 2.84 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 0.00 |
| ***Calanopia americana*** | **25.14** | **84.52** | **50.08** | **519.03** | **0.52** | **1.63** | **0.12** | **0.14** | **0.28** | **1.56** |
| ***Oithona plumifera*** | **1.01** | **1.66** | **2.95** | **6.57** | **0.22** | **3.47** | **0.26** | **0.63** | **1.26** | **0.91** |
| *Oncaea mediterranea* | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.01 | 0.00 |
| *Oncaea venusta* | 0.63 | 0.29 | 0.98 | 0.00 | 0.07 | 0.69 | 0.04 | 0.02 | 0.04 | 0.32 |
| ***Corycaeus speciosus*** | **0.50** | **3.25** | **0.00** | **2.32** | **0.60** | **2.27** | **0.17** | **0.08** | **0.16** | **1.07** |
| *Agetus flaccus* | 0.00 | 0.00 | 0.00 | 0.00 | 3.62 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| *Farranula gracilis* | 2.29 | 9.90 | 5.89 | 28.60 | 0.22 | 2.31 | 0.07 | 0.08 | 0.15 | 0.86 |
| Stomatopoda | 0.00 | 0.00 | 0.00 | 1.16 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Decapoda | 0.84 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Mysidacea | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.47 | 0.00 | 0.00 | 0.15 | 0.00 |
| Amphipoda | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.05 | 0.00 |
| Chaetognatha | 3.26 | 0.00 | 0.00 | 19.32 | 0.97 | 1.13 | 0.15 | 0.01 | 0.02 | 1.71 |
| *Flaccisagitta enflata* | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.43 |
| Appendicularia | 0.38 | 0.00 | 7.86 | 0.00 | 1.27 | 4.08 | 0.07 | 0.00 | 0.00 | 4.06 |
| Teleostei (Eggs and Larvae) | 40.96 | 1.66 | 6.87 | 13.14 | 0.00 | 1.13 | 0.06 | 0.00 | 0.00 | 0.88 |
| Mean | 2.44 | 3.79 | 2.97 | 20.60 | 0.69 | 0.61 | 0.03 | 0.14 | 0.31 | 0.45 |
| STD (±) | 7.76 | 14.18 | 8.63 | 86.10 | 1.59 | 1.00 | 0.05 | 0.41 | 0.82 | 0.80 |

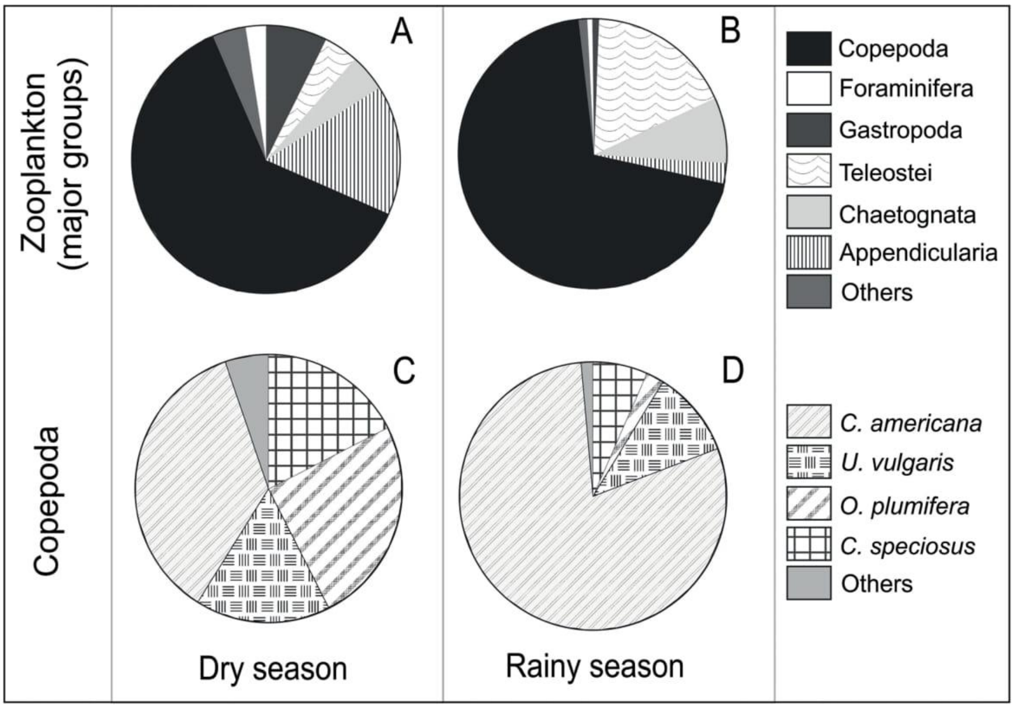

**Figure 2.** Relative abundance of the mesozooplankton community (abundance > 2%) during the dry (A) and rainy (B) seasons. Relative abundance of the dominant copepod species (abundance > 2%) in the dry season (C) and rainy season (D) from the months of July and December/2013 and June and November/2014 in the coastal area of the Fernando de Noronha Archipelago in northeastern Brazil.

The effect of seasonality on the total abundance of mesozooplankton, total abundance of copepods, *Calanopia americana*, *Undinula vulgaris* (dominant species copepods) and Shannon-Wiener diversity is illustrated in Figure 3a, 3b, 3c, 3d and 3 e, respectively.

The mean abundance of mesozooplankton and of copepods for dry season were: 13.04±19.39 ind.m$^{-3}$; 7.53±14 ind.m$^{-3}$ and for rainy season: 72.83±73.02 ind.m$^{-3}$; 108.63±161.92 ind.m$^{-3}$ respectively (Table 2b). The Anova indicated the significant effect of the seasonal factor on the mean abundance of mesozooplankton (*F* (*1, 13*)=15.82, *p-level*=0.001) and mean abundance of copepods (*F* (*1, 13*)=15.78, *p-level*=0.001) (Table 2a).

Among the copepod species considered to be dominants only *C. americana* (F (*1, 10*)=23.39, *p-level*=0.006) and *U. vulgaris* (F (*1, 12*)=17.73, *p-level*=0.001) responded to the seasonal factor (Table 2a), whose mean abundance value was significantly higher in the rainy season 97±123.93 ind.m$^{-3}$ and (3.30±2.26 ind.m$^{-3}$) respectively in comparison to dry season 3.84±9.79 ind.m$^{-3}$ and (0.72±0.74 ind.m$^{-3}$) respectively (Table 2b).

The Shannon-Wiener diversity of copepods differed significantly between the seasonal periods investigated (F (*1, 13*)= 6.66, *p-level*=0.02) (Table 2a), presenting a higher mean diversity during the dry season (2.19±0.57 bits.ind$^{-1}$) compared to the mean recorded in the rainy season (1.46±0.69 bits.ind$^{-1}$) (Table 2b).

## SPATIAL VARIATION

The mean abundance of mesozooplankton in stations 1, 2, 3, 4 and 5 were respectively: 28.52 ± 21.58 ind.m$^{-3}$, 35.69 ± 63.88 ind.m$^{-3}$, 61.56 ± 50.13 ind.m$^{-3}$, 194.60 ± 257.98 ind.m$^{-3}$ and 11.41 ± 6.07 ind.m$^{-3}$ equivalent to: 14.15±17.02 ind.m$^{-3}$ at the station 1, 33.96±61 ind.m-3 at the station 2, 44.36±38 ind.m$^{-3}$ at the station 3, 175.30±237.90 ind.m$^{-3}$ at the station 4 and 7.29±8.28 ind.m$^{-3}$ at the station 5 (Figure 4a).

The Shannon-Wiener diversity had a higher mean numerical value at station 2 (Cachorro beach) and a lower value at station 4 (Cacimba do Padre) (Figure 4b). The

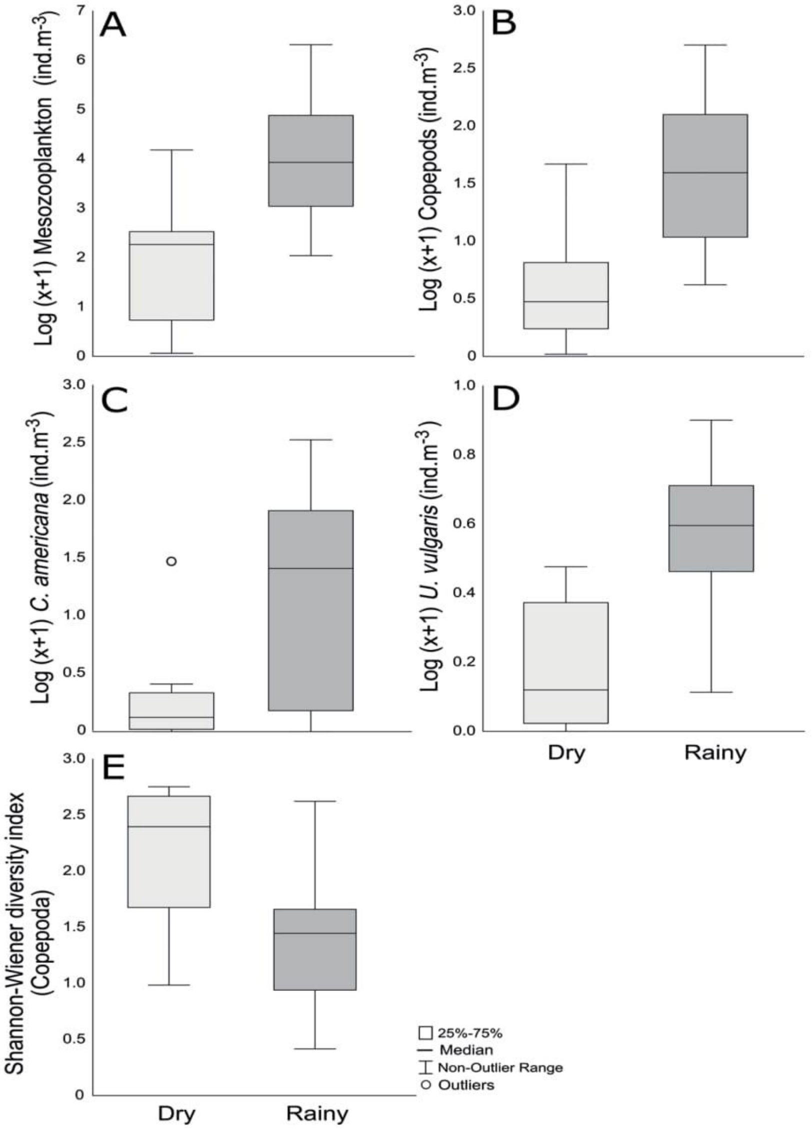

**Figure 3.** Box-Plot (median and quartiles) representing the Log (X + 1) of: (A) Mesozooplankton (ind.m$^{-3}$); B) copepods (ind.m$^{-3}$); (C) *C. americana* (ind.m$^{-3}$) and (D) *U. vulgaris* (ind.m$^{-3}$) between the seasonal periods (DRY vs RAINY) in the coastal area of the Fernando de Noronha Archipelago in northeastern Brazil.

mean values of Shannon-Wiener diversity recorded for the stations 1, 2, 3, 4 and 5 were: 2.02±0.63 bits.ind$^{-1}$, 2.09±0.43 bits.ind$^{-1}$, 2.03±0.62 bits.ind$^{-1}$ , 1.19±0.86 bits.ind$^{-1}$ and 1.95±0.86 bits.ind$^{-1}$ respectively (Figure 4b).

There were no significant differences among the stations sampled in terms of total abundance of mesozooplankton, total abundance of copepods and Shannon-Wiener diversity.

All copepod species considered dominant: *Calanopia americana* (129.82±164 ind.m$^{-3}$)*, Undinula vulgaris* (3.78±3.49 ind.m$^{-3}$)*, Oithona plumifera* (1.95±3.11 ind.m$^{-3}$) *and Corycaeus speciosus* (0.93±1.07 ind.m$^{-3}$) also recorded numerically highest mean values at station four (Cacimba do Padre), but statistical differences were not verified among the sampling stations. The species *Calanopia americana* dominated spatially in both seasonal periods sampled, but its abundance values were

**Table 2.** Main effects ANOVA results for abundance of: (i) Mesozooplankton; (ii) Copepods; (iii) *Undinula vulgaris*; (iv) *Calanopia americana* and (v) Shannon-Wiener diversity in response to the seasonal factor (as between dry vs rainy) and spatial factor (as between stations) on Fernando de Noronha Archipelago in northeastern Brazil.

| a) ANOVA | | (i) Mesozooplankton abundance | | | | (ii) Copepods abundance | | | |
|---|---|---|---|---|---|---|---|---|---|
| Source | df | MS | F | *p* | Source | df | MS | F | *p* |
| Spatial (ST) | 4 | 2.84 | 1.92 | 0.16 | Spatial (ST) | 4 | 0.54 | 1.67 | 0.21 |
| Seasonal (S) | 1 | 23.38 | 15.81 | 0.001 | Seasonal (S) | 1 | 5.17 | 15.78 | 0.001 |
| Residual | 13 | 1.47 | | | Residual | 13 | 0.32 | | |
| | | | (iii)<br>*Undinula vulgaris* | | | | | (iv)<br>*Calanopia americana* | |
| Spatial (ST) | 4 | 0.38 | 1.78 | 0.19 | Spatial (ST) | 4 | 3.39 | 1.73 | 0.21 |
| Seasonal (S) | 1 | 3.80 | 17.73 | **0.001** | Seasonal (S) | 1 | 23.39 | 11.96 | **0.006** |
| Residual | 12 | 0.21 | | | Residual | 10 | 1.95 | | |
| | | | (v) Shannon-Wiener diversity (H′) | | | | | | |
| Spatial (ST) | 4 | 0.53 | 1.49 | 0.26 | | | | | |
| Seasonal (S) | 1 | 2.38 | 6.66 | **0.02** | | | | | |
| Residual | 13 | 0.35 | | | | | | | |

| b) BIOTIC VARIABLES | Dry season | | Rainy season | |
|---|---|---|---|---|
| | Mean | SD | Mean | SD |
| Total abundance of Zooplankton (ind.m$^{-3}$) | 13.04 | ±19.39 | 126.13 | ±173.88 |
| Total abundance of Copepods (ind.m$^{-3}$) | 7.53 | ±14.00 | 108.63 | ±161.92 |
| *Undinula vulgaris* (ind.m$^{-3}$) | 0.72 | ±0.74 | 3.30 | ±2.26 |
| *Calanopia americana* (ind.m$^{-3}$) | 3.84 | ±9.79 | 97 | ±123.93 |
| Shannon-Wiener diversity (H′) | 2.19 | ±0.57 | 1.46 | ±0.69 |

Significant ($p<0.05$) - *p* values in bold.

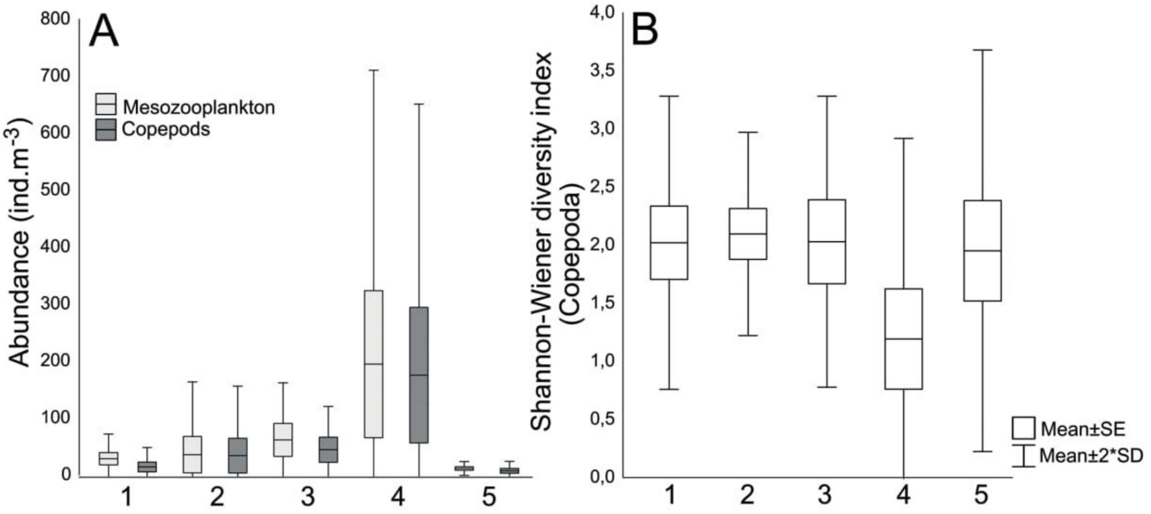

**Figure 4.** Box-Plot (mean and standard deviation) representing the spatial variation of: (A) Mesozooplankton (light gray) and Copepods (dark gray) and (B) Shannon-Wiener diversity index (for copepods) at stations: Santo Antonio Port (1), Cachorro Beach (2), Conceição Beach (3), Cacimba do Padre (4) and Golfinhos Bay (5) in the coastal area of the Fernando de Noronha Archipelago in northeastern Brazil.

much higher in the rainy period (more than 250 ind.m$^{-3}$) (Figure 5).

### Mesozooplankton community structure

MDS analyses indicated differences in the structure of the mesozooplankton community of the Fernando de Noronha Archipelago between dry and rainy seasons (Figure 6), but differences among the five sampling stations were not verified. The pattern illustrated in the MDS ordination was confirmed by PERMANOVA. Significant differences in the structure of the mesozooplankton community of the Fernando de Noronha Archipelago were detected between seasons (dry *vs.* rainy) ($p=0.02$) (Table 3). The interaction between factors (stations x seasons) did not show statistical difference (Table 3). The observed differences between seasons were examined through of the average dissimilarity (SIMPER) among the two sets of data (mesozooplankton abundance), which was equivalent to 76.84%. The greatest dissimilarity between dry and rainy seasons is generated by *Calanopia americana* (as shown in Table 4).

### Indicator value and functional traits

The rainy season was represented by two significant indicator (characteristic) species. Indicator values (Indval) of more than 50% were found for species: *Undinula vulgaris* (Indval=85%; $p=0.01$) and *Calanopia americana* (Indval=86%; $p=0.03$).

The Appendicularia Class was the only spatial indicator associated with the combination between stations 3 (Conceição beach) and 5 (Golfinhos Bay) (Indval = 86%; $p=0.005$).

Cluster analysis for functional features of copepods assemblage showed two main groups (Figure 7): the first composed of broadcast spawners and the second, composed mostly of sac-spawners. Each group is subdivided in two subgroups. Subgroup 1 contained the greater number of species and consisted of calanoid copepods with clearly herbivorous trend predominance. The species of this group contained calanoids with mean body sized of 1300 to 1700 µm (*Acrocalanus longicornis, Calocalanus pavo*, *Clausocalanus furcatus*, *Paracalanus aculeatus* and *Calanopia americana*). Subgroup 2 included fewer species, consisting of larger-sized copepods (>1700 µm) as *Candacia pachydactyla, Centropages velificatus* (both carnivorous) and *Undinula vulgaris* (herbivorous). Subgroup 3 consisted of copepods with body size of (1110 up to 1300 µm) such as the Calanoida: *Euchaeta marina* (carnivorous) and the Cyclopoida copepods *Agetus flaccus* and *Corycaeus speciosus*. Subgroup 4 was characterized by cyclopoids copepods (*Farranula gracilis*, *Oncaea venusta, Oithona plumifera* and *Oncaea mediterranea*), classified as small omnivores (<1100 µm) (exhibiting mixed feeding strategies depending on the availability of food items), and occurring from the epipelagic to the mesopelagic domain of the oceanic environment.

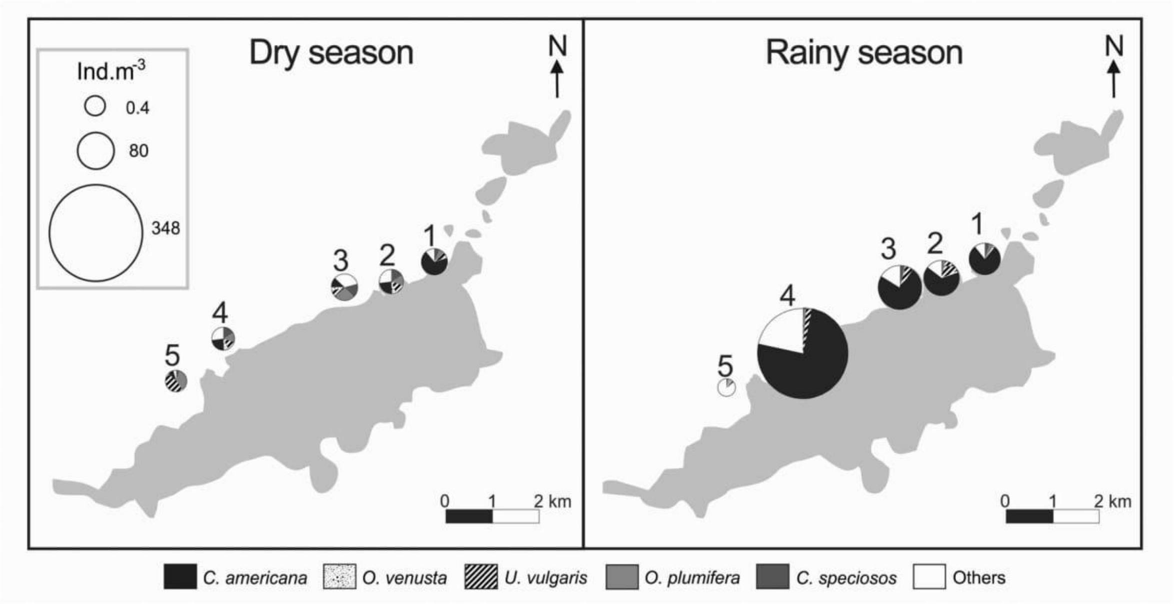

**Figure 5.** Seasonal (dry and rainy) and spatial (sampling stations) distribution of copepods (Abundance >2%) in: Santo Antônio Port (1), Cachorro Beach (2), Conceição Beach (3), Cacimba do Padre (4) and Golfinhos Bay (5) in the coastal area of the Fernando de Noronha Archipelago in northeastern Brazil.

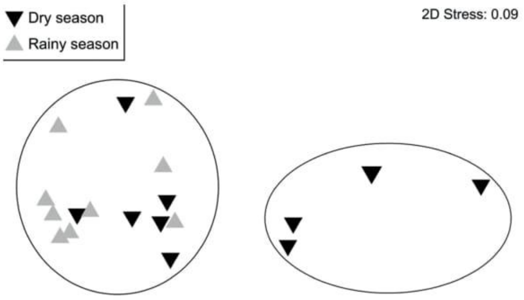

**Figure 6.** MDS ordination of the mesozooplankton community in response to the seasonal factor: Dry season (Black triangle) and rainy season (Gray triangle) in the coastal area of the Fernando de Noronha Archipelago in northeastern Brazil.

**Table 3.** Summary of PERMANOVA results for the mesozooplankton community structure of the Fernando de Noronha Archipelago in response to the spatial (as between stations) and seasonal (as between dry *vs*. rainy) factors.

| Source | df | MS | Pseudo-F | *p*(perm) |
|---|---|---|---|---|
| Spatial (ST) | 4 | 2802.8 | 1.012 | 0.483 |
| Seasonal (S) | 1 | 7102.1 | 2.564 | 0.028 |
| ST x S | 4 | 2239.5 | 0.809 | 0.788 |
| Residual | 9 | 2769.8 | | |
| Total | 18 | | | |

## DISCUSSION

The study of the abundance, diversity and structure of the mesozooplankton community (with emphasis on copepods) in the years 2013 and 2014 corresponds to the first work carried out in the coastal area of Fernando de Noronha Archipelago, a south-western Atlantic Ocean tropical island. The results indicated a remarkable change in the seasonal distribution of the mesozooplankton community, copepod assemblages and diversity of copepods, but a greater similarity between the quali-quantitative composition was verified between sampling stations, which is explained by the proximity between them.

Previous studies on zooplankton from tropical islands in Brazilian oceanic waters are relatively recent (Cavalcanti and Larrazabal, 2004; Lira et al., 2014), but some have also demonstrated the effect of seasonality on the ecological attributes of the mesozooplankton community (Diaz et al., 2009; Melo et al., 2012). The hypothesis of difference between dry and rainy seasons was verified in the present study, where the mean abundance of mesozooplankton and copepods were significantly higher in the rainy season. Thus, our data suggest a seasonal effect on the ecological attributes of mesozooplankton, but the long-term time series (preferably >10 years) is needed to further expand the present findings.

Variations in the meteorological regime, regional geomorphological characteristics and anthropogenic impacts together establish the particular hydrographic regime of each region and, consequently, the taxonomic characteristics and temporal-spatial dynamics of the copepods assemblage (Brandini et al., 1997). Coastal and oceanic epipelagic species of copepods, typical of the tropical and subtropical southwestern Atlantic were identified in the study area, but the numerically dominant species were *Calanopia americana, Corycaeus speciosus, Undinula vulgaris* and *Oithona plumifera*. In particular, the species *U. vulgaris* (suspensivore) and *C. americana* (herbivore) responded significantly to the seasonal factor, presenting high abundance in the rainy season. Both species were considered by the results of the Indval analysis as indicators of the environmental conditions presented in the rainy season on Fernando de Noronha Archipelago.

The distribution of *U. vulgaris* in lagoon systems was positively related to the abundance of organic (particulate) nitrogen sources and abundant food sources may be critical for this species (Renon, 1993). According to Gerber and Gerber (1979) the daily metabolic losses of carbon by *U. vulgaris* are very high, so considerable productivity is required to keep these populations abundant. Therefore, the high, and for that reason, abundance of this specie verified in the rainy season in the present study reinforces an increase of the productivity in “Inner Sea” of FNA during this seasonal period.

*Calanopia americana* occurs mainly in coastal regions (Bowman, 1971). This species makes vertical migrations in both shallow coastal environments and in deeper locations, being more frequently found in surface waters at night compared to day period (Clarke, 1934; Bowman, 1971; Turner et al., 1979; Cohen and Forward, 2002; Melo et al., 2010; Pessoa et al., 2014). The high abundance of *C. americana* in diurnal samples of FNA could be explained by hydrodynamic effects since the stations are shallow. In addition, the occurrence of swell in some of the sampling periods of the years 2013 and 2014, resuspending bottom sediment and organisms associated with it. Several studies showed the importance of this event in the called surf-zone fauna, where a group of invertebrate species inhabit sandy beach surf zones (Mees and Jones, 1997). This is reforced in our results by the lesser abundance of the *C. americana* in Golfinhos Bay, a deeper station.

**Table 4.** Summary of SIMPER showing the contribution of taxa (abundance >2%) for the differences between the dry and rainy seasons, in the coastal area of Fernando de Noronha Archipelago. The Variable "Taxonomic composition" had a dissimilarity average between dry and rainy seasons of 76.84%.

| AR (%) >2% | Rainy Season | Dry Season | | | |
|---|---|---|---|---|---|
| Taxa | Av.Abund | Av.Abund | Av.Diss | Contrib% | Cum.% |
| *Calanopia americana* | 2.7 | 0.66 | 17.25 | 22.46 | 22.46 |
| *Undinula vulgaris* | 1.32 | 0.42 | 9.66 | 12.58 | 35.03 |
| Calanoida (Copepodite) | 1.1 | 0.24 | 9.02 | 11.74 | 46.77 |
| Teleostei (eggs and larvae) | 1.08 | 0.19 | 7.91 | 10.29 | 57.07 |
| *Farranula gracilis* | 1.19 | 0.27 | 7.24 | 9.42 | 66.48 |
| *Acrocalanus longicornis* | 1.1 | 0.27 | 6.66 | 8.67 | 75.15 |
| Chaetognatha | 0.75 | 0.38 | 6.63 | 8.63 | 83.78 |
| Foraminifera (Others) | 0.64 | 0.63 | 6.45 | 8.4 | 92.18 |

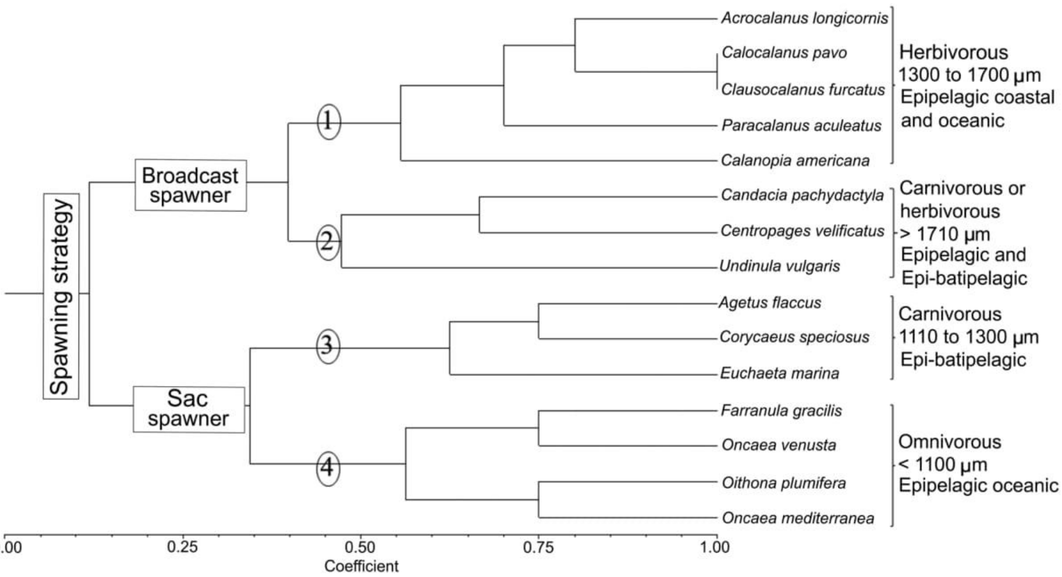

**Figure 7.** Functional groups of 15 species of copepod identified in the coastal area of the Fernando de Noronha Archipelago based on the Sorensen coefficient and weighted pair group *method* with averaging clustering method built on four functional characteristics (spawning strategy, trophic group, body size, and vertical distribution).

According to Assunção et al. (2016) the mean precipitation levels recorded for both the years of 2013 and 2014 was higher than usual for the rainy season. The intensification of the hydrological cycle caused salinity reduction, but a water surface heating was identified during the rainy season (June and July) in comparison to dry season. The author also reports that nutrient concentrations exhibited values characteristic of an oligotrophic area, but in general, these values were slightly higher in the rainy season, specifically in the bottom stratum.

Seasonal changes in nutrient concentration are followed by changes in planktonic productivity (Hawes, 1983). The increase in biological productivity in the surrounding islands has been reported in several studies as a consequence of the island mass effect (Doty and Oguri, 1956; Palacios, 2002). Patterns of plankton biomass accumulation or productivity increase near the FNA have been frequently described (Lira et al., 2014; Tchamabi et al., 2017) and related as a consequence of the island effect. Once, "Inner Sea" of FNA is dependent on the region of its surroundings where the input of macro and micronutrients from island runoff (Perissinotto et al., 2000) and contributions from benthic processes (Signorini et al., 1999) stand out as the main mechanisms contributing to high productivity during the rainy season. Furthermore, the occurrence of rainfall allows the excrement of seabirds, present in the several elevations (hills) of FNA and especially in the island Rata, (considered the largest deposit of guano and consequent phosphate in Brazil) arrived the waters of the Archipelago more quickly, also contributing to a significant response of planktonic productivity and consequently of the abundance of mesozooplankton and copepods observed in the rainy season in FNA.

In general, the abundance data of mesozooplankton community and copepod assemblages registered for the coastal area of Fernando de Noronha Archipelago are considered low. It is important to emphasize that in the present work, we performed subsurface hauls, with a net of 300 µm mesh size. Many researches with Copepoda has shown that the abundance of copepods collected with plankton net using smaller mesh size (<100 µm) has nearly two or more orders of degree higher than those obtained with larger mesh size plankton net. These differences are chiefly due to the loss of small-sized copepods in the samples obtained with bigger mesh plankton net (Araujo et al., 2008; Wu et al., 2011). The mean value of the Shannon-Wiener diversity index for copepod assemblages was also considered low in the present study. Significant differences were observed between the seasonal periods investigated, where the mean of season diversity was significantly higher than the values recorded in rainy season. Thus, the lower value recorded for the rainy season can be a consequence of the dominance of the copepods *U. vulgaris* and *C. americana* observed in this seasonal period in the present study. Cavalcanti and Lazzarabal (2004) studying the mesozooplankton of the northeast Brazilian Exclusive Economic zone during the dry season, through oblique hauls with a bongo net (mesh size of 300 µm) in the stratum of 0-200 m, showed that the species diversity of the copepod assemblages presented values ranging from very low to high. The authors explained the fact as a response to the dominance of *U. vulgaris* and *C. americana* in some sampling stations. Then, in order to compare diversity in different environments, considerations must be made regarding the heterogeneity of environments, the sampling effort and the equipment used in sampling (Dias et al., 2010).

## FUNCTIONAL FEATURES OF THE COPEPOD COMMUNITY

In this study two groups were formed according to their reproductive characteristics (broadcast spawner and sac-spawner), and they could be classified in four functional subgroups. Subgroup 1 brought together numerically important calanoids in the epipelagic layer of coastal environments and tropical Atlantic Ocean, some of which, such as *C. americana,* are strong vertical migrants (Neumann-Leitão et al., 2008; Pessoa et al., 2014).

Particularly, *C. americana* had high participation and dominance in practically all the samples. Peaks of abundance occurred mainly in the rainy season. This fact may have occurred due the intensification of the trade winds in this seasonal period, exhibiting higher intensity from July to September (11 ms$^{-1}$) (Manso et al., 2011). Thus, we suggest that the intensification of the trade winds caused an increase in the intensity of the waves and resuspension of the bottom, considering the benthic habit during the day and planktonic behavior at night of *C. americana* specie (Cohen and Forward, 2002). In several studies that performed daytime sampling this species is cited (Dias and Bonecker, 2009; Dias et al., 2010), but rarely with high abundance (as recorded in the present work). However, high values of abundance have already been recorded for *C. americana* in nocturnal sampling (Melo et al., 2010; Pessoa et al., 2014). This subgroup also included the Paracalanidae (*Acrocalanus longicornis*, *Calocalanus pavo* and *Paracalanus aculeatus*), a family of great importance in terms of abundance, biomass and daily production, besides being highly adapted to the oligotrophic conditions and having the ability to exploit other forms of food besides the phytoplankton (Miyashita et al., 2009; Melo Júnior et al., 2016). However, in FNA its participation in terms of abudance was low, caused by the selectivity of the plankton net mesh size used (300µm).

The species *Candacia pachydactyla*, *Centropages velificatus* and *Undinula vulgaris* formed the second subgroup within this cluster, composed of larger copepods. Interesting studies of the tropical oceanic zooplankton have shown *U. vulgaris* presenting high values of relative abundance and frequency of occurrence in Northeastern Brazil (Neumann-Leitão et al., 1999; 2008). *Candacia pachydactyla* and *Centropages velificatus* together within the subgroup 3 include the carnivorous species. *Euchaeta marina*, known as among the most common mesozooplankton predators in the planktonic food web, prey on smaller copepods such as *Oncaea* and *Oithona* as well as the larger *Calanoides acutus* (Øresland, 1991), doliolids (Takahashi et al., 2013), larvaceans (Ohtsuka and Onbé, 1989) and fish larvae (Yen, 1987); and *Corycaeus speciosus* and *Agetus flaccus* which despite being classified as medium-sized carnivores also have the feeding behavior of cruising detritivores, moving to great depths to decompose particulate organic matter and contributing to epipelagic secondary production (Benedetti et al., 2015). *Corycaeus speciosus* is also typical of the Brazil Current and is an indicator of oligotrophic areas (Björnberg, 1981). This species is very frequent and abundant in oceanic waters with temperatures and salinities around 26°C and of 35, respectively, also having wide tropical and subtropical distribution (Bradford-Grieve et al., 1999).

Subgroup 4 grouped together small marine planktonic copepods (*Farranula gracilis*, *Oncaea venusta, Oncaea mediterranea* and *Oithona plumifera*). *Oithona* spp. are small, active ambush-feeding omnivores that carry their eggs and has been described as the most ubiquitous and abundant copepod in the world's (Gallienne and Robins, 2001). *Oncaea* spp. are mainly cruise detritivores, epipelagic and found associated with appendicularians "houses" (Alldredge, 1972; Steinberg et al., 1994). *Farranula gracilis* is a typical species of the west-central Gulf of Mexico, and of the surface oceanic waters of the Caribbean Sea. It may be associated with the mixed oligotrophic waters of the Caribbean (López-Salgado et al., 2000).

In general, the copepod assemblages of the western coast of Fernando de Noronha Archipelago presented a larger number of species considered as predator-carnivours (*Euchaeta marina, Candacia pachydactyla, Corycaeus speciosus, Agetus flaccus, Centropages velificatus* and *Farranula gracilis*). Thus, actual dominance of predator with preference for smaller or larger prey will influence the number of steps in the food chains (number of trophic levels) and thereby determine whether primary production is efficiently passed to larger organisms or remineralized (Hansen et al., 1994).

## CONCLUSIONS

We suggest that changes in the structure of the mesozooplankton community (with emphasis on copepods) of the coastal area of Fernando de Noronha Archipelago ("Inner Sea") was mainly related to the seasonal factor where: (1) The rainy season (considered a period of increased productivity) favored a significant increase in the abundance of mesozooplankton. (2) *Undinula vulgaris* and *Calanopia americana* were considered indicators of the environmental conditions presented in the rainy season, recording high values of abundance in this seasonal period. The high abundance of *C. americana* in practically all sampled stations is an evidence of coastal influence, as well it indicates the effects of hydrodynamism inducing the species dominance in all shallow stations, leading to the conclusion that *C. americana* is a key species for the study area. (3) The mean values of Shannon–Wiener diversity of the copepod assemblages indicate a low taxonomic diversity, mainly in the rainy season. This low diversity was explained by the high dominance of *C. americana* and *U. vulgaris* in the samples.

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# II - Morphological abnormalities in *Corycaeus speciosus* Dana, 1849 (Copepoda, Cyclopoida) on an Equatorial Atlantic Island

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## Morphological abnormalities in *Corycaeus speciosus* Dana, 1849 (Copepoda, Cyclopoida) from the area of an Equatorial Atlantic Island

Renata P.S. CAMPELO[1,2], Mauro de MELO JÚNIOR[3], Claudeilton S. SANTANA[2], Luis E. BEZERRA[1]
and Sigrid NEUMANN-LEITÃO[2]
*(1) Universidade Federal do Ceará, Instituto de Ciências do Mar, Av. da Abolição, 3207, Meireles,*
*60.165-081, Fortaleza, Ceará, Brazil. E-mail: renatapolyanadesantanacampelo@gmail.com*
*(2) Universidade Federal de Pernambuco, Departamento de Oceanografia, Av. Arquitetura, s/n, Cidade Universitária,*
*50.670-901, Recife, Pernambuco, Brazil*
*(3) Universidade Federal Rural de Pernambuco, Departamento de Biologia, Rua Dom Manuel de Medeiros, s/n,*
*Dois Irmãos, 52.171-900, Recife, Pernambuco, Brazil*

**Abstract:** Taxonomic and ecological studies of a large number of specimens can lead to the finding of morphological anomalies. Thus, based on 800 specimens of *Corycaeus speciosus* in different developmental stages (juvenile and adult copepodites) this study was carried out to assess for the first time anomalies in Equatorial Atlantic specimens. Samples were collected around the St. Peter and St. Paul Archipelago (Equatorial Atlantic). Anomalies were found at the end of the prosome in two female specimens, one recorded in the juvenile copepodite stage V and was characterized by a left-side rounded prosome tip, while in the adult the anomaly was characterized by a rounded prosome inner the tip in the left-side. The causes of the malformations remain unknown, but the results are indicative that they are probably genetic in character, transmitted on reproduction. However, experimental tests are necessary to confirm such conclusions and their effect on the population structure of this ecologically important species.

**Résumé :** *Anomalies morphologiques chez* Corycaeus speciosus *Dana, 1849 (Copepoda: Cyclopoida) dans la region d'une île de l'Atlantique équatorial.* Les études taxonomiques et écologiques d'un grand nombre de spécimens peuvent conduire à la découverte d'anomalies morphologiques. Ainsi, à partir de 800 spécimens de *Corycaeus speciosus* de stades de développement différents (copepodites juvéniles et adultes), cette étude a été réalisée pour examiner, pour la première fois, des anomalies sur des spécimens d'Atlantique équatorial. Les échantillons ont été recueillis autour de l'archipel de St. Pierre et St. Paul (Atlantique équatorial). Des anomalies ont été trouvées à la pointe du prosome chez deux spécimens femelles, l'une sur le stade copepodite V, caractérisée par une pointe de prosome arrondie du côté gauche, tandis que chez une adulte l'anomalie était caractérisée par un prosome arrondi à l'intérieur de la pointe sur le côté gauche. Les causes de ces malformations restent encore inconnues, mais les résultats indiquent qu'elles sont probablement de nature génétique, transmises lors de la reproduction. Cependant, des tests expérimentaux sont nécessaires pour confirmer ces conclusions et leurs effets sur la structure de la population de ces espèces écologiquement importantes.

*Keywords: Corycaeus speciosus* ● Equatorial Atlantic ● Isolated island ● Marine copepods ● Morphological abnormalities

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are rarely observed and discussed (Bhandare & Ingole, 2008; Mantha et al., 2013). However, for the order Calanoida these records are well documented (Brylinski, 1984; Behrends et al., 1997; Barthélémy et al., 1998; Omair, 1999; Gusmão & Mckinnon, 2009; Martinelli-Filho et al., 2009; Pombo & Martinelli-Filho, 2012; Melo et al., 2014). Different degrees of morphological alterations to the last pair of spines on the prosome were observed for both male and female in *Acartia lilljeborgii*. Some of these suggested that the anomalies registered are due to congenital defects, since the area of study (Caraguatatuba Bay, on the southeastern Brazilian coast) suffers from high anthropogenic disturbance, which increases the possibilities of induced morphological changes due to environmental factors (Pombo & Martinelli-Filho, 2012). Other species of calanoid copepods, such as those belonging to the family Candacidae, have different prosome extensions, considered secondary sex characters, indicating sexual dimorphism for this family (Boltovskoy, 1999). However, this is not the case for the Corycaeidae, since the characteristic of the family is to present both sides of the prosome sharply defined by Boltovskoy (1999), and these abnormalities are likely to occur equally in males and females.

The morphological malformations in these last stages of development in *C. speciosus* have never been reported before (Figs 2 & 4). It is unlikely that such anomalies arose during the ontogeny process, but rather during the process of embryonic development in the case of congenital defects (e.g., Björnberg, 1972; Crisafi & Crescenti, 1977). Abnormality affecting the embryonic stage, causing morphological deformities in the early stages of copepods (nauplius and copepodite), can have serious consequences for the survival of individuals and for the recruitment of any population with a high incidence of anomalies. These anomalies interfere in the process of development, hatching, swimming and reduction in physical fitness (Poulet et al., 1995).

Anomalies described in *Clausocalanus mastigophorus* occurring in the same area (SPSPA) are probably genetic in character, being transmitted on reproduction (Melo et al., 2014). The frequency of occurrence of these anomalies in *C. speciosus* and other specimens of copepods from the SPSPA need to be better investigated, and this alert for factors that need to be considered as a cause, since teratogenic anomalies have been observed in copepods (Pandourski & Evtimova, 2009).

Despite being an isolated archipelago that is not directly influenced by anthropogenic action, microplastics have been found in the SPSPA, which may have an indigenous origin, have been transported long distances by currents, or have originated from a fishing fleet of small boats (Ivar Do Sul et al., 2013). These microplastics can be a potential transfer vector of persistent organic compounds causing deleterious effects on marine biota (Thompson et al., 2004). Laboratory experiments have verified the intake of microplastics by calanoid copepods, reaffirming the ability of zooplankton to ingest microplastics (Wilson, 1973) and, consequently, perpetuate in the marine food web and attain predators such as *Corycaeus* species that can consume microplastic passively with prey (or in the prey itself) (Taylor et al., 2016). The diversity and anomalies of cyclopoid copepods were investigated along the hydrothermal vent at Kueishantao Island, north-eastern Taiwan and it was verified that pelagic cyclopoid copepods do ample vertical migrations along the water column (Lo et al., 2004). These migrations were related to additional searches of food sources in the form of bacteria (Burd & Thomson, 1994), being the pelagic copepods considered as opportunistic feeders that consume the excessive alimentary vent bacteria and organic carbon near hydrothermal vents. However, at these sites, these copepods were exposed to high concentrations of potentially toxic chemicals (Peng et al., 2011) and metals (Kondoh et al., 2003). Thus, pelagic cyclopoid copepods (eg, *Corycaeus* and *Oncaea*) can be transported to toxic environments through streams and may be exposed to toxic concentrations of metals and gases that weaken their exoskeletons (Mantha et al., 2013).

In this way, both the frequency of occurrence and the features of such morphological anomalies in isolated island areas can be tools for the assessment of impacts and to help distinguish between natural and anthropogenic changes, as well as assisting in environmental monitoring activities.

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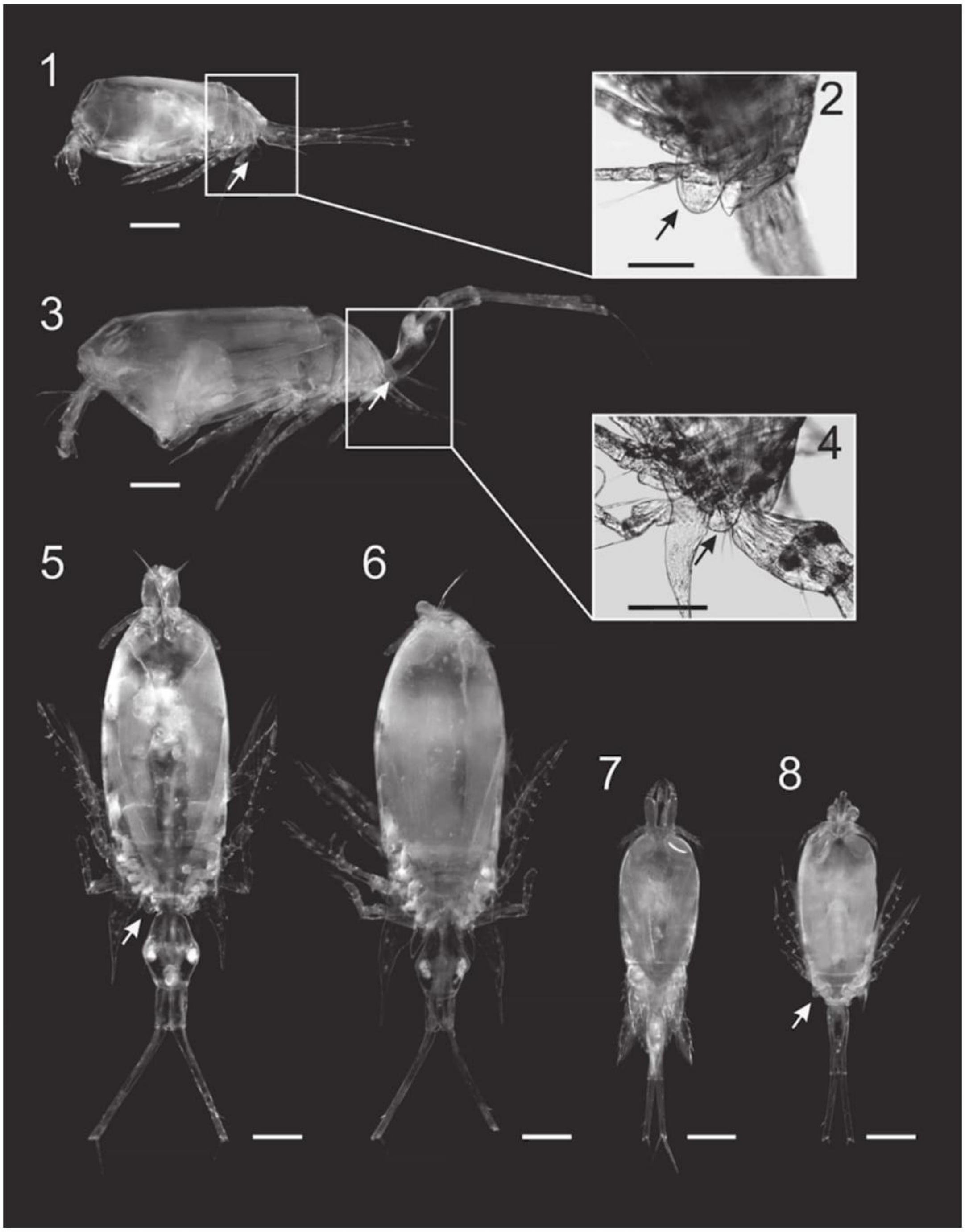

**Figures 1-8. 1.** Lateral view of *Corycaeus speciosus*, female in the Copepodite V stage of development, with anomaly at the tip of the third thoracic segment. **2.** Photo featured of the anomaly, characterized by a rounded tip on the left side at the end of the third thoracic segment in Copepodite female of *Corycaeus speciosus* V stage of development. **3.** Lateral view in adult female of *Corycaeus speciosus* with the presence of the anomaly at the prosome inner tip in the left-side. **4.** Photo featured of the anomaly, characterized by a rounded prosome inner tip in the left-side in adult female of *Corycaeus speciosus*. **5.** Dorsal view in adult female of *Corycaeus speciosus* with the presence of the anomaly at the prosome inner tip in the left-side. **6.** Dorsal view in adult female of *Corycaeus speciosus* without the presence of the anomaly at the prosome inner tip and at the end of the third thoracic segment. **7.** Dorsal view of *Corycaeus speciosus* female in the Copepodite V stage of development without the presence of the anomaly at the end of the third thoracic segment. **8.** Dorsal view of *Corycaeus speciosus*, female in the Copepodite V stage of development with anomaly at the tip of the third thoracic segment. All the specimens were collected on the St. Peter and St. Paul Archipelago, Tropical Atlantic Ocean. Figures 1 & 3-8 have a scalebar with length of 200 µm. Figure 2 with a scalebar length of 100 µm. The anomalies were indicated at figures by arrows. The figures 1, 3, 5-8 are proportional in size.

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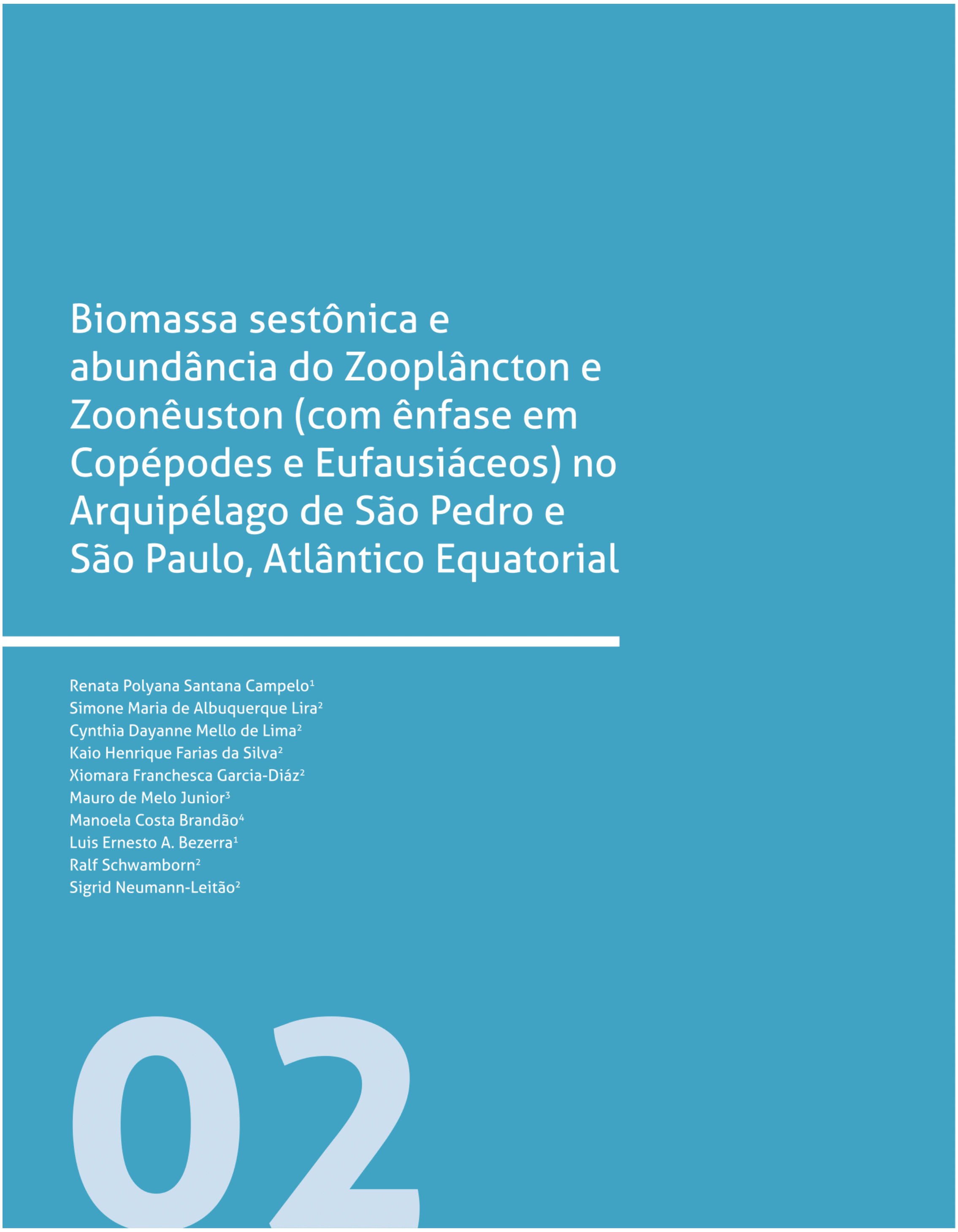
# III - Book chapter published in commemoration to the 20 years of research carried out in the Saint Peter and Saint Paul Archipelago



## Biomassa sestônica e abundância do Zooplâncton e Zoonêuston (com ênfase em Copépodes e Eufausiáceos) no Arquipélago de São Pedro e São Paulo, Atlântico Equatorial

Renata Polyana Santana Campelo[1]
Simone Maria de Albuquerque Lira[2]
Cynthia Dayanne Mello de Lima[2]
Kaio Henrique Farias da Silva[2]
Xiomara Franchesca Garcia-Diáz[2]
Mauro de Melo Junior[3]
Manoela Costa Brandão[4]
Luis Ernesto A. Bezerra[1]
Ralf Schwamborn[2]
Sigrid Neumann-Leitão[2]

02

## Abstract

Tropical oceanic regions have a permanent thermocline, which prevents the mixing of surface and nutrient-rich deep waters, thus showing low productivity and planktonic biomass. Seamounts are known to disrupt the vertical stability of the water column significantly increasing the availability of nutrients in the upper layers. The Saint Peter and Saint Paul Archipelago constitute a small isolated group of rocky islands surrounded by oligotrophic waters. The presence of the archipelago influences the hydrodynamic and potentially the local planktonic community. The present study gathered data from different sampling strategies at Saint Peter and Saint Paul Archipelago between 2010 and 2012. Our main aims were to access distribution patterns of the sestonic biomass, total abundance of copepods, total abundance of zooneuston, characterize the neustonic copepod assemblage, and describe the distribution of euphausiids around the archipelago. We focused on copepods and euphausiids due to the importance of these groups in terms of abundance and role in energy transfer between primary and higher trophic levels. Our results show higher sestonic biomass at night and downstream of the islands, attributed to diel vertical migration (DVM) and local hydrodynamics. Regarding the copepods, no significant spatial or diel distinction was observed in the community, which might have occurred due to the high predation rates by planktivorous fish. In turn, euphausiids were significantly more abundant at night, highlighting their DVM behavior. The neustonic copepod assemblage was depicted by species considered truly neustonic, as well as pelagic ones, which presence was associated with food availability.

## Introdução

O Zooplâncton desempenha um papel chave no controle da produção do fitoplâncton e são uma fonte de alimento para os níveis tróficos superiores, estruturando assim o ecossistema pelágico (HAVENS, 1998). Esses organismos são caracterizados por ciclos de vida bastante curtos, podendo durar de semanas até meses (DENMAN *et al.*, 1989) o que os caracterizam por exemplo, como excelentes indicadores de mudanças provenientes do impacto antrópico ou de ordem climática (HAYS *et al.*, 2005). Assim, de acordo com o ciclo de vida o zooplâncton é classificado em meroplâncton (organismos que passam parte do seu ciclo de vida no plâncton sendo representado por larvas e juvenis da maioria dos organismos do bentos e nécton) e holoplâncton (que passam todo o seu ciclo de vida como membros do plâncton). Os representantes mais importantes do holoplâncton são os copépodes, pequenos crustáceos dominantes no ambiente pelágico de

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1 Universidade Federal do Ceará;

2 Universidade Federal de Pernambuco (sigridnl@uol.com.br);

3 Universidade Federal Rural de Pernambuco;

4 Observatoire Océanologique de Villefranche-sur-Mer.

vários ecossistemas marinhos, compreendendo de 55 a 95% da abundância e até 80% da biomassa total do mesozooplâncton (BRANDINI *et al.*, 1997). Outro importante grupo do holoplâncton são os eufausídeos. Estes pequenos camarões desempenham um papel fundamental no ciclo global do carbono. Por serem considerados fortes migradores, se deslocam verticalmente a distâncias superiores a 200 m á noite, contribuindo desta forma, para a transferência de energia disponível na camada fótica para as camadas profundas através da bomba biológica do carbono (BRINTON *et al.*, 1999).

Os organismos zooplanctônicos ocupam diferentes zonas de profundidades no domínio pelágico dos oceanos. O nêuston é composto de organismos associados a interface oceano-atmosfera ocorrendo até um limite de 1 m de profundidade (PARANAGUÁ *et al.*, 2004). A comunidade neustônica é principalmente influenciada pela radiação solar, temperaturas extremas, variação de salinidade e vento (LIRA, 2013). Além disso, os organismos do zooplâncton são encontrados em estratos de grandes profundidades (cerca de 6.000 m) (LALLI e PARSON, 1993), porém as maiores concentrações de biomassa e abundância desses organismos ocorrem na camada epipelágica (que se estende em média até aos 200 m de profundidade, embora possa ser limitada pela termoclina) nos oceanos (LALLI e PARSON, 1993).

As águas do Nordeste brasileiro são caracteristicamente oligotróficas e de baixa produtividade biológica, exceto nos locais em que ocorrem ressurgências como no entorno de montes e ilhas oceânicas (LIRA *et al.*, 2014). Uma vez que essas feições topográficas mudam a hidrodinâmica local, através da combinação de correntes de recirculação e ressurgência, provocando o chamado "efeito ilha" (DOTY e OGURY, 1956). Este evento contribui para um incremento na biomassa planctônica ao redor dessas áreas (que atuam como verdadeiros 'Oásis' em meio ao oceano oligotrófico do Atlântico Sul) (BOEHLERT, 1988). Estimativas de abundância e biomassa são um meio indireto de identificar a produção zooplanctônica e são de fundamental importância para entender o papel ecológico dos organismos planctônicos num ecossistema (RODRIGUEZ e MULLIN, 1986).

Os padrões de distribuição da biomassa sestônica (DIAZ *et al.*, 2009) e da abundância do mesozooplâncton (DIAZ *et al.*, 2009; Melo *et al.*, 2012, 2014) e do zooneuston (LIRA, 2013; SANTANA, 2015) inspiraram pesquisas ecológicas no remoto Arquipelago de São Pedro e São Paulo, porém ainda existe uma escassez de informações para a região, sobretudo devido a dificuldade de acesso. Assim o presente estudo reúne dados de pesquisas com diferentes estratégias de amostragens realizadas no menor e mais isolado arquipélago do planeta no período entre 2010 à 2012, onde os principais objetivos foram: (1) Determinar os padrões de distribuição espacial (montante vs. jusante) e quanto ao turno (dia vs. noite) da biomassa sestônica, abundância total de copépodes e abundância total do zoonêuston; (2) Caracterizar a assembleia de copépodes neustônicos e (3) Descrever a composição e abundância total de Euphausiacea em resposta ao turno de amostragem no entorno do Arquipélago de São Pedro e São Paulo.

## Material e Métodos

### *Área de estudo*

O Arquipélago de São Pedro e São Paulo (ASPSP) (Figura 1) é um dos menores (área de plataforma rasa equivalente a 3,5 km$^2$) e mais isolado grupos de ilhas oceânicas. Localizado ao norte do equador (0°55'06"N e 29°20'48"W), dista aproximadamente 1.800 km da costa africana e 630 km de Fernando de Noronha (EDWARDS e LUBBOCK, 1983). O ASPSP está sob a influência do ramo norte da Corrente Sul Equatorial (CSE) que flui no sentido Leste-Oeste, carregando águas superficiais vindas do Golfo da Guiné e da região de Cabo Verde e Serra Leoa. Em sentido contrário e de ação subsuperficial, a Subcorrente Equatorial (SCE) carrega águas entre 40 e 150 m de profundidade (ARAUJO e CINTRA,

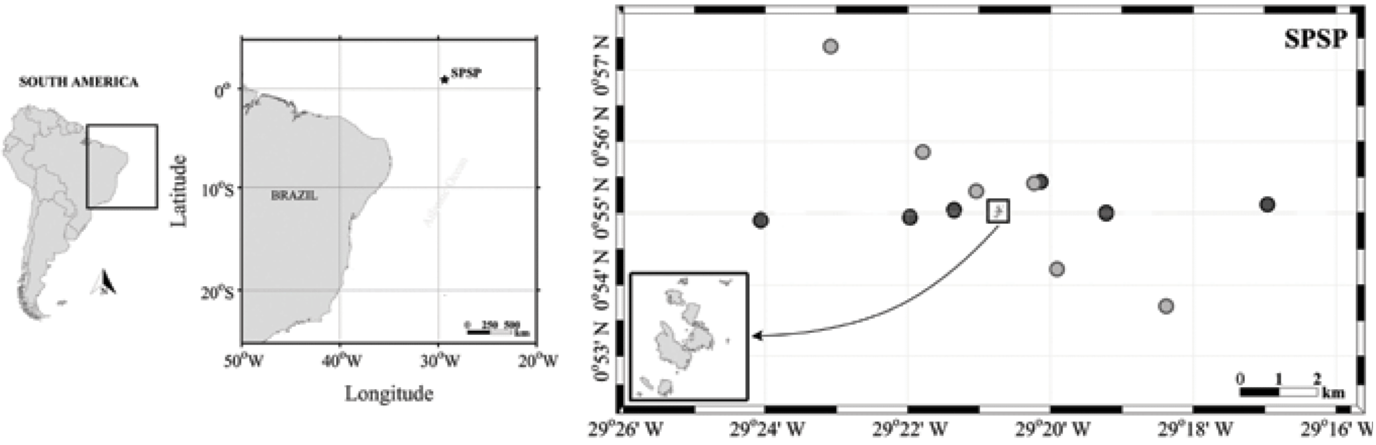

**Figura 1.** Posição dos transectos: E (Leste) - W (Oeste) (círculos cinza escuro – dados coletados em 2010) e SE (Sudeste) - Noroeste (NW) (círculos cinza-claros – dados coletados em 2012) e localização das estações de amostragens no ASPSP.
***Figure 1. Location of the transects: E (East) – W (West) (dark gray circles - data collected in 2010) and SE (Southeast) - Northwest (NW) (light gray circles - data collected in 2012) and location of the sampling stations at SPSPA.***

2009), originária da Corrente Norte do Brasil (CNB) (EDWARDS e LUBBOCK, 1983). A interação da topografia do rochedo com as correntes atuantes ocasiona a produção de vórtices, perturbações da estrutura termohalina e possíveis mecanismos locais de ressurgência (ARAUJO e CINTRA, 2009). Dessa forma, a presença do arquipélago influencia diretamente as condições hidrodinâmicas locais e consequentemente as comunidades biológicas que vivem no seu entorno.

### *Estratégia de amostragem*

O presente trabalho reúne dados de pesquisas sobre o zooplâncton insular desenvolvidas pelo laboratório de Zooplâncton Marinho da UFPE. Assim, as informações apresentadas sobre a biomassa sestônica (mg.m$^{-3}$), abundância total de copépodes (ind.m$^{-3}$) e abundância total do zoonêuston (ind.m$^{-3}$) foram obtidas através de expedições realizadas a bordo do Navio Hidroceanográfico Cruzeiro do Sul da Marinha do Brasil. Amostragens diurnas e noturnas ocorreram em julho de 2010 e 2012. Um ADCP foi usado para obter a direção e velocidade da corrente predominante e assim definir a posição dos dois transectos: Um transecto a montante da ilha (1) e outro a jusante da ilha (2). Em cada transecto foram definidas três estações.

Com o objetivo de estudar a distribuição vertical da assembleia dos Euphausideos foram realizadas amostragens noturnas e diurnas em junho de 2010, setembro e outubro de 2011. As amostras foram coletadas a partir de uma profundidade de 100 m até a superfície em duas estações fixas, uma a leste (S1) e uma a oeste (S2) do ASPSP (Figura 1).

### *Procedimento de campo*

Para obter informações da biomassa sestônica e da abundância total da assembleia de copépodes, arrastos oblíquos feitos em "V", estendendo-se a uma profundidade de 75% da profundidade local, ou no máximo 200 m de profundidade foram realizados utilizando uma armação do tipo "Bongo" com rede cilíndrico-cônica (diâmetro de boca de 0,6 m$^2$ e tamanho de malha de 300µm). Um total de 12 amostras foram coletadas. Um fluxômetro da marca Hydro-Bios foi posicionado na boca da rede para estimar o volume de água filtrada.

Para a coleta do Zoonêuston, arrastos de 20 minutos, em velocidade de 2 a 3 nós foram performizados. Estas coletas foram realizadas em um catamarã David Hempel de alumínio (Hydro-Bios) equipado com duas redes superpostas com boca retangular (nêuston inferior de 0-7,5cm) e (nêuston superior de 7,5-22,5cm), com malha de 500µm cada. Para obtenção do volume filtrado utilizou-se um fluxômetro acoplado a rede de plâncton do neuston inferior.

A assembleia de eufausiáceos foi amostrada através de arrastos verticais realizados com uma rede de fechamento tipo "Nansen" com diâmetro de boca de 0,28 m² e tamanho de malha de 200 µm. No total, 60 amostras de plâncton foram analisadas.

Após os arrastos acima descritos, as amostras foram transferidas para frascos plásticos e imediatamente fixadas a bordo em solução de formaldeído (4%), tamponado com tetraborato de sódio.

### *Procedimento laboratorial*

**Biomassa sestônica (mg.m$^{-3}$)** - esta foi estimada através da metodologia do peso-úmido. As amostras foram filtradas em acumuladores de tamanho de malha equivalente a 100µm previamente pesado em balança de precisão de 0,001mg (NEWELL e NEWELL, 1963). A amostra foi submetida a um tempo de secagem que variou entre 2 á 5 minutos (dependendo da quantidade de material amostrado) e posteriormente submetido a uma pesagem final. Para evitar o efeito do peso de partículas que não fazem parte do ambiente planctônico (como macroalgas, pedaços de tintas dos navios e microplásticos), foram removidos das amostras e pesados separadamente.

**Abundância total dos copépodes (ind.m-3)** - As amostras foram fracionadas em alíquotas de 1/32 ou1/64, utilizando um quarteador do tipo Motoda (OMORI e IKEDA, 1984), contendo pelo menos 300 copépodes (FRONTIER, 1981). Os espécimes foram identificados e inspecionados sob o estereomicroscópio Zeiss Discovery V8. Apenas os dados de abundância total da assembleia de copépodes são apresentados no presente estudo.

**Abundância total do Zooneuston (ind.m-3)** - As amostras foram fracionadas em alíquotas 1/2 ou 1/16, utilizando um quarteador do tipo Motoda (OMORI e IKEDA, 1984), contendo pelo menos 200 organismos. Os espécimes foram identificados e inspecionados sob o estereomicroscópio Zeiss Stemi SV6. Apenas os dados de abundância total dos grupos em grandes grupos e da assembleia de copépodes são apresentados no presente estudo.

**Abundância total dos Eufausiáceos (ind.m-3)** - As amostras foram triadas em sua totalidade e os eufausídeos foram separados de acordo com o estágio de desenvolvimento (caliptopis, furcilia e adulto) e identificados até o menor nível taxonômico possível, usando literatura disponível (MONTÚ, 1983; BAKER *et al.*, 1991). Indivíduos danificados que não puderam ser identificados foram classificados como "Euphausiacea n.id".

### *Análise dos dados*

A análise de variância (ANOVA Two-way) foi usada para examinar o efeito do turno (dia *vs.* noite) e espacial (montante *vs.* jusante) sobre a biomassa sestônica e abundância total de copépodes. Posteriormente, o teste SNK (Student-Newman-Keuls) foi usado para uma comparação a *posteriori* quando a interação entre os fatores foi significativa. Para o Zoonêuston além dos fatores associados ao turno, e lados da ilha, também foi testado o fator espacial: interface do nêuston (superior *vs.* inferior). Todos esses fatores comparando a comunidade neustônica foram testados através do teste T de Student e para testar os fatores espaciais e entre turnos associados aos eufasiáceos foi utilizado o teste Mann-Whitney. A heterogeneidade das variâncias foi investigada através do teste de Levene e os dados foram transformados através do logaritmo natural de (X + 1) antes da análise quando necessário. O nível de significância foi definido em $P<0,05$ para todas as análises.

## Resultados

### *Biomassa sestônica e Abundância total de copépodes*

No ano de 2012 a biomassa sestônica variou entre um valor mínimo de (10 mg.m$^{-3}$) no período diurno, transecto montante, estação a (insular) à um máximo de (185 mg.m$^{-3}$) no período noturno, transecto jusante, estação c (intermediária) (Figura 2A). O efeito do fator turno (Tabela I) foi verificado sobre a biomassa sestônica (Anova two-way F (1, 8) = 6,86, P = 0,03) onde a média noturna (98,66 ± 69,07 mg.m$^{-3}$) foi significativamente maior do quê a média diurna (46,83 ± 34,70 mg.m$^{-3}$) (Figura 3A). O efeito espacial (Tabela I) também foi verificado (Anova two-way F(1, 8) = 8,78, P = 0,01), cujo valor médio a jusante da ilha (102 ± 65 mg.m$^{-3}$) foi significativamente superior ao valor a montante (43,43 ± 36,03 mg.m$^{-3}$) (Figure 3B). Para a biomassa uma interação significativa entre os fatores (turno x espacial) foi detectada (Tabela I). O teste SNK mostrou o efeito do turno sobre a biomassa sestônica em ambos os transectos estudados, onde tanto no período diurno como noturno esta é significativamente maior a jusante da ilha. Ainda de acordo com o teste a *posteriori*, a montante do ASPSP a biomassa diurna mostrou-se maior do quê a noturna e no lado jusante a média diurna foi menor que a noturna (Tabela I).

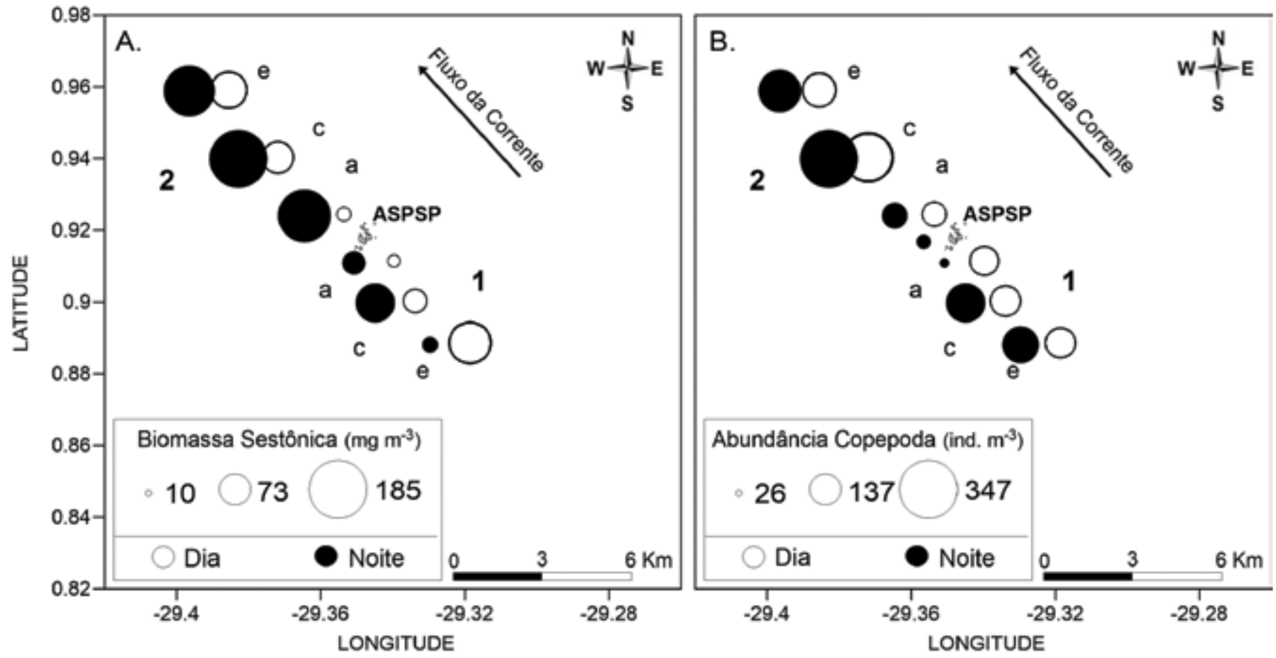

**Figura 2.** Distribuição espacial da: (A) Biomassa sestônica (mg.m$^{-3}$) e (B) Abundância de copépodes (ind.m$^{-3}$) no ASPSP em julho de 2012. As áreas dos círculos são proporcionais à biomassa sestônica (A) e abundância de copépodes (B) total em cada estação de amostragem. Os círculos em preto representam os dados amostrados no período noturno, e os círculos transparentes aos diurnos. O número 1 indica a posição do transecto sudeste (montante da ilha) e o número 2 a posição Noroeste (jusante da ilha). As estações são representadas pelas letras: a (insular), c (intermediária), e (oceânica).

***Figure 2. Spatial distribution of the: (A) Sestonic biomass (mg.m$^{-3}$) and (B) Abundance of copepods (ind.m$^{-3}$) at SPSPA in July 2012. The areas of the circles are proportional to total sestonic biomass (A) and total abundance of copepods (B) at each sampling station. The circles in black represent data sampled in the nocturnal period, and the transparent circles to the diurnal period. Number 1 indicates the position of the Southeast transect (upstream of the island) and number 2 represents the Northwest position (downstream of the island). The stations are represented by letters: a (insular), c (intermediate), e (oceanic).***

Em relação à abundância total de copépodes, os valores mínimos e máximos registrados foram respectivamente iguais a (26, 57 ind.m$^{-3}$) no período noturno, transecto montante, estação a (insular) e (347 ind.m$^{-3}$) no período noturno, transecto jusante, estação c (intermediária) (Figura 2B). A média noturna (151,32 ± 111 ind.m$^{-3}$) da abundância total de copépodes foi numericamente maior quê a média diurna (123 ± 69,9 ind.m$^{-3}$) (Figura 3C). A abundância de copépodes registrada a montante foi equivalente a (100 ± 43,45 ind.m$^{-3}$) e a jusante (173,88 ± 112,27 ind.m$^{-3}$) (Figura 3D). Não foi observado o efeito do turno e do espaço sobre a distribuição da abundância de copépodes no entorno do ASPSP (Tabela I).

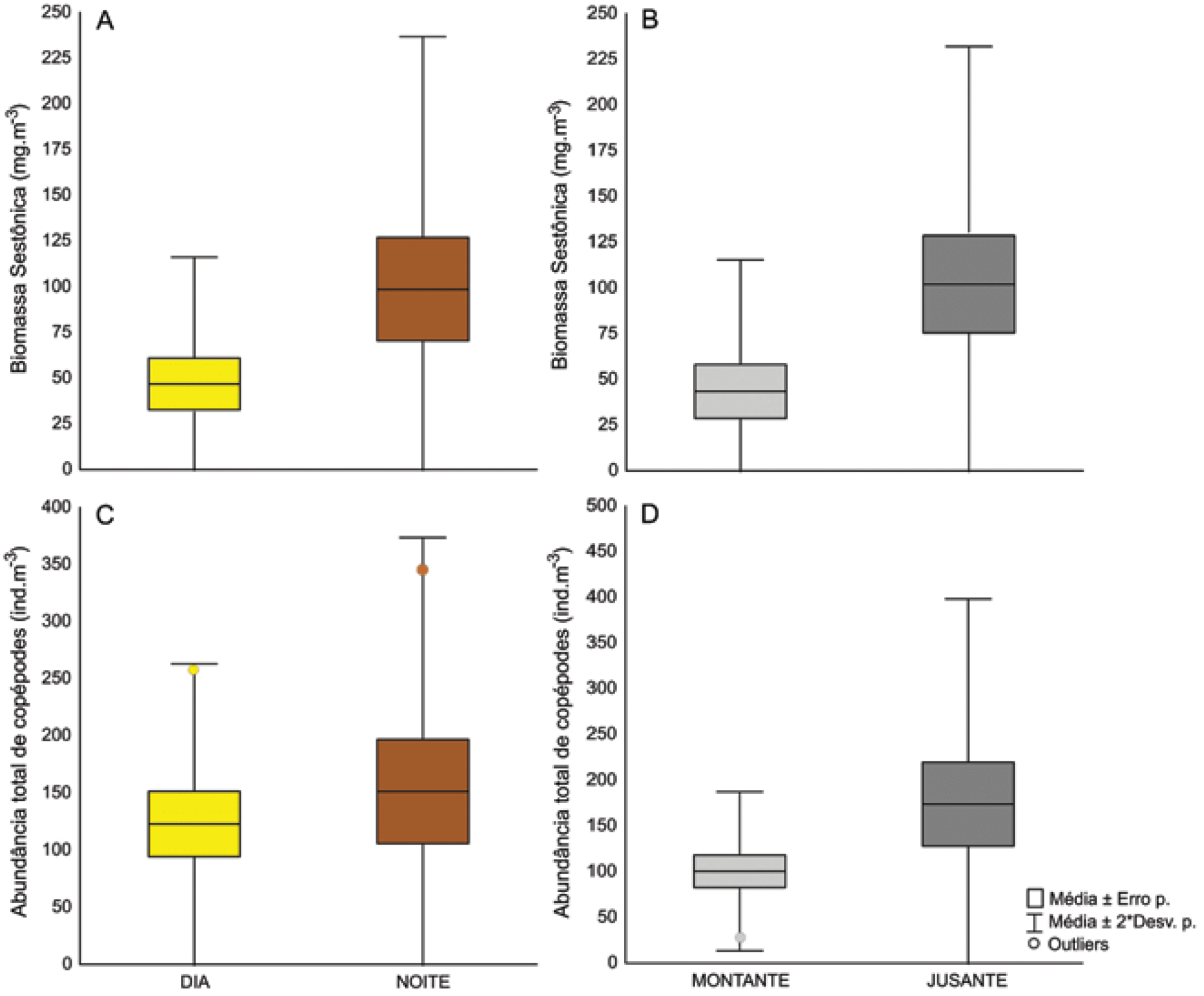

**Figura 3.** Box-Plot mostrando a média (± desvio padrão) da biomassa sestônica (mg.m$^{-3}$) e da abundância total de copépodes (ind.m$^{-3}$) em relação aos fatores testados, onde: A (biomassa sestônica *vs.* turno); B (biomassa sestônica *vs.* espacial); D (Abundância total de copépodes *vs.* turno); E (Abundância total de copépodes *vs* espacial) em Julho de 2012, no ASPSP.

***Figure 3. Box-Plot showing the mean (± standard deviation) of the sestonic biomass (mg.m$^{-3}$) and the total abundance of copepods (ind.m$^{-3}$) in relation to the factors tested, where: A (sestonic biomass*** **vs.** ***diel variation); B (sestonic biomass*** **vs.** ***spatial); D (total abundance of copepods*** **vs.** ***diel variation); E (total abundance of copepods*** **vs.** ***diel variation) in July 2012, at SPSPA.***

**Tabela I.** (A) ANOVA de dois fatores testando os efeitos do turno (dia *vs.* noite) e espacial (montante *vs.* jusante) sobre a (i) a biomassa sestônica e (ii) abundância total de copépodes; (B) testes SNK em termos de interação significativa para (i) biomassa sestônica. Os valores de p em negrito são significativos.

***Table I. (A) Two-way ANOVA testing the effects of diel variation (day* vs. *night) and spatial (upstream* vs. *downstream) on the (i) sestonic biomass and (ii) total copepods abundance; (B) SNK tests on significant interaction terms for (i) sestonic biomass. p values in bold are significant.***

| **A) ANOVA** | | (i) Biomassa sestônica | | | (ii) Abundância total de copépodes | | |
|---|---|---|---|---|---|---|---|
| Fatores | *df* | MS | *F* | p | MS | *F* | p |
| Turno (T) | 1 | 8058,43 | 54 | **0,03** | 2406,2 | 0,27 | 0,61 |
| Espacial (E) | 1 | 10311,69 | **7** | **0,01** | 16183,0 | 1,88 | 0,21 |
| T X E | 1 | 10181,96 | 9 | **0,01** | 1217,9 | 0,14 | 0,72 |
| Error | 8 | 1173,64 | | | 8605,3 | | |

| **B) SNK** | (i) Biomassa sestônica | | |
|---|---|---|---|
| **Turno** | | **Espacial** | |
| Dia | Montante < Jusante | Montante | Dia > Noite |
| Noite | Montante < Jusante | Jusante | Dia < Noite |

## *Zoonêuston*

A abundância total dos organismos planctônicos associados ao zoonêuston variou de um mínimo de 0,6 ind.m$^{-3}$ no nêuston superior durante o dia até o máximo 30,06 ind.m$^{-3}$ no nêuston inferior durante a noite. Foram registrados 19 táxons (Tabela II) em grandes grupos e 25 táxons de copépodes. Os Copepoda, Chaetognatha e Foraminifera foram os táxons mais abundantes tanto para o nêuston superior (NS) quanto para o nêuston inferior (NI) no ASPSP. A contribuição de Copepoda foi de 67% para o nêuston inferior e 65,15% para o nêuston superior, os Chaetognatha contribuiram com 14,03% e 17,74% e os Foraminifera com 7,76% e 6,60%, respectivamente. Os demais grupos se distribuiram com menores frequências e abundâncias com uma proporção semelhante entre as camadas superiores e inferiores do nêuston.

A assembleia de copépodes do zoonêuston foi composta por 25 espécies, com valores de média no NS equivalente a 3,2±6 ind.m$^{-3}$, enquanto que no NI foi de 0,9±1,4 ind.m$^{-3}$. As espécies *Undinula vulgaris* (Dana, 1849), *Euchaeta marina* (Prestandrea, 1833), *Pontellina plumata* (Dana, 1849), *Labidocera nerii* (Krøyer, 1849), *Corycaeus speciosus* (Dana, 1849) e *Farranula gracilis* (Dana, 1849) foram consideradas as mais abundantes (Figura 4). A espécie *Undinula vulgaris* (Figura 4a) dominou em termos de abundância relativa no neuston superior dia (17,25%) e noite (19,45%) e no neuston inferior dia (16,27%) e noite (24,50%).

**Tabela II.** Abundância relativa (AR) da comunidade zooneustônica do ASPSP, no período de julho a agosto de 2010. Nêuston superior (N.S.) e Nêuston inferior (N. I.).

***Table II. Relative abundance (AR) of the zooneustonic community from SPSPA, between July and August 2010. Epineuston (N.S.) and Hyponeuston (N. I.).***

| | **N.S** | **N.I** |
|---|---|---|
| **FORAMINIFERA** | | |
| Foraminifera | 6,60 | 7,76 |
| **CNIDARIA** | | |
| Hydrozoa | 1,65 | 1,70 |
| Anthozoa | 0 | 0,01 |
| **MOLLUSCA** | | |
| Gastropoda | 1,23 | 2,37 |
| Cephalopoda | 0 | 0,50 |
| **ANNELIDA** | | |
| Polychaeta | 0,36 | 0,25 |
| **HEXAPODA** | | |
| *Halobates* sp. | 0,04 | 0 |
| **CRUSTACEA** | | |
| Ostracoda | 0 | 0,006 |
| Copepoda | 65,16 | 67,00 |
| Mysidacea | 0,81 | 079 |
| Euphausiacea | 2,29 | 2,93 |
| Amphipoda | 0,69 | 0,56 |
| Decapoda total | 0,32 | 0,34 |
| Stomatopoda | 0,07 | 0,005 |
| **CHAETOGNATHA** | | |
| Chaetognatha | 17,74 | 14,03 |
| **CHORDATA** | | |
| Thaliacea | 0,80 | 0,10 |
| Appendicularia | 0,45 | 0,26 |
| Teleostei (larva) | 0,008 | 0,15 |
| Teleostei (ovos) | 1,75 | 1,66 |

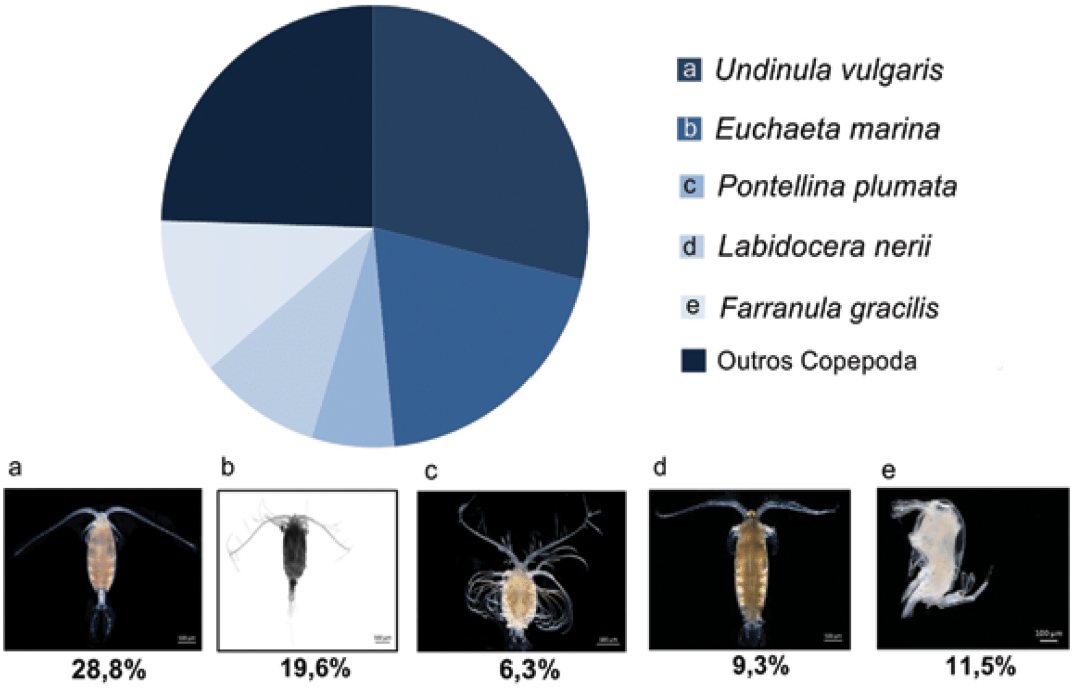

**Figura 4.** Abundância relativa da assembleia de copépodes associada ao Zoonêuston do Arquipélago de São Pedro e São Paulo em julho de 2010. a) *Undinula vulgaris*, b) *Euchaeta marina*, c) *Pontellina plumata*, d) *Labidocera nerii*, e) *Farranula gracilis*.

***Figure 4. Relative abundance of the copepods associated to the Zooneuston of the SPSPA in July 2010. a)* Undinula vulgaris*, b)* Euchaeta marina*, c)* Pontellina plumata*, d)* Labidocera nerii*, e)* Farranula gracilis.**

A variabilidade das comunidades em relação aos fatores turno da amostragem e aos fatores espaciais: interfaces do nêuston (superior e inferior) e lado da ilha (montante *vs.* jusante) apresentou diferença apenas para o fator turno, onde a abundância foi significativamente maior no período noturno (teste t, p< 0,05) (Figura 5). A distribuição da abundância total (ind.m$^{-3}$) em cada ponto de amostragem (Figura 6) não exibiu tendência em relação aos lados da ilha e nem com a interface do nêuston superior e inferior, entretanto, foi possível visualizar a diferença em relação aos horários noturnos e diurnos, com maiores valores bem maiores no período noturno.

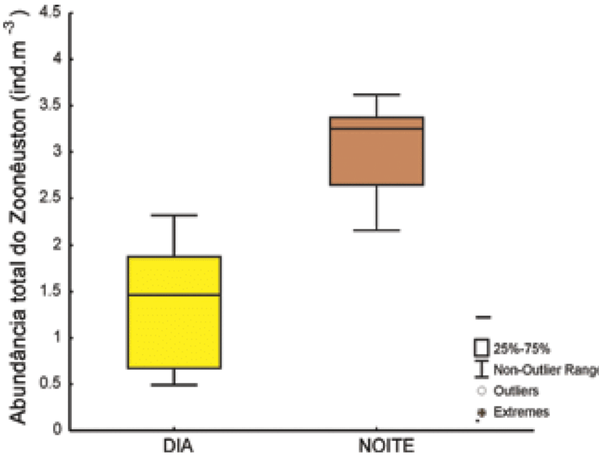

**Figura 5.** Box-Plot mostrando a mediana da abundância total do zoonêuston em relação ao dia e a noite em Julho-Agosto de 2010, no ASPSP.

***Figure 5. Box-Plot showing the median in relation to the factors tested, where: the total* abundance of zoonêuston in relation to day and night in July-August 2010, at SPSPA.**

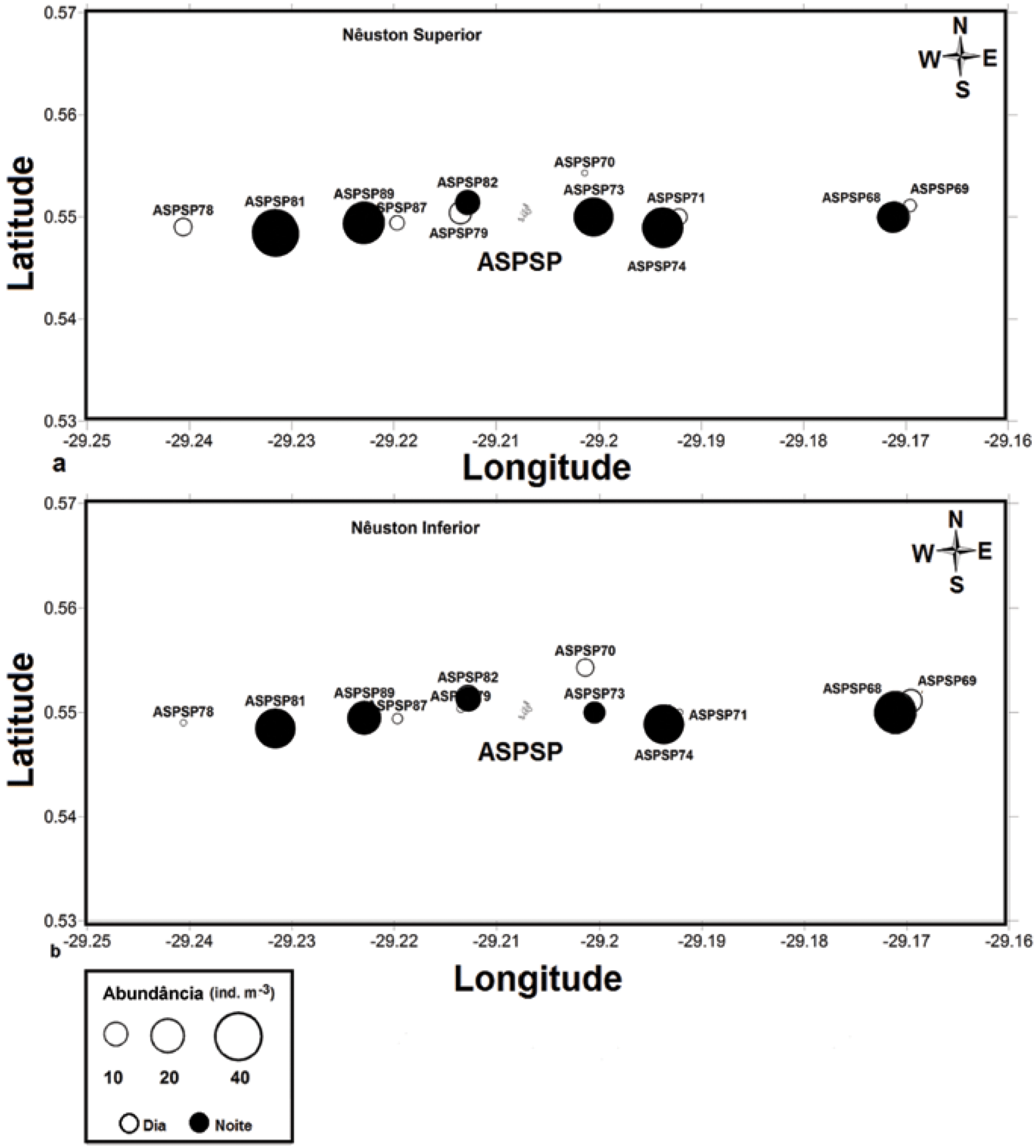

**Figura 6.** Distribuição da abundância total do Zoonêuston no Arquipélago de São Pedro e São Paulo em cada estação de amostragem em julho de 2010. As áreas dos círculos são proporcionais à abundância total de cada ponto amostrado. a) Nêuston Superior e b) Nêuston Inferior.

***Figure 6. Total abundance distribution of Zooneuston at Saint Peter and Saint Paul Archipelago at each sampling station in July 2010. The areas of the circles are proportional to total abundance of each sampled point. a) Epineuston and b) Hyponeuston.***

### ***Abundância total de Euphausiacea***

Foram identificados 948 indivíduos, com uma abundância média de 2,65 ind.m$^{-3}$ (até 30,4 ind.m$^{-3}$), pertencentes a doze espécies e quatro gêneros da família Euphausiidae: *Euphausia* Dana, 1850; *Nematoscelis* G. O. Sars, 1883; *Stylocheiron* G. O. Sars, 1883 e *Thysanopoda* Milne Edwards, 1830 (Tabela III). A comunidade de eufausiáceos foi composta principalmente por larvas (estágios caliptopis e furcília), contribuindo com mais de 80% de todos os indivíduos (43,4% e 37,6%, respectivamente). As larvas do gênero *Euphausia* foram as mais abundantes, com 56,4% de todos os indivíduos capturados (31,6% de caliptopis e 24,8% de furcília). Durante o dia, predominaram as larvas de Euphausia, apesar de apresentar abundâncias totais mais baixas (média: 0,4 ind.m$^{-3}$). A abundância de caliptopis variou de 0,1 á 14 ind.m$^{-3}$, com valores significativamente maiores à noite (Teste Mann-Whitney, U = 262, N1 = 30, N2 = 30, P = 0,005). Para as furcílias, a abundância variou entre 0,1 e 11,1 ind.m$^{-3}$, com valores mais altos também à noite (Teste Mann-Whitney, U= 271,5, N1= 30, N2= 30, P = 0.008). Os adultos representavam 24,5% da comunidade. Os táxons mais abundantes foram *Euphausia* spp. (30,8%), *E. americana* (23%), *S. carinatum* (19,1%), *E. tenera* (8,6%), *E. similis* (4,3%), e *S. suhmii* (4,3%) (Tabela III). Considerando todos os adultos, a abundância variou entre 0,1 e 2,8 ind.m$^{-3}$, com maior abundância à noite (Teste Mann-Whitney, U= 251, N1= 30, N2= 30, P = 0,003).

**Tabela III.** Abundância relativa (RA) e abundância média dos eufausiáceos coletados no Arquipélago de São Pedro e São Paulo, de junho/2010 a outubro/2011. n.id=não identificado.

***Table III. Relative abundance (RA) and mean abundance of euphausiids sampled at Saint Peter and Saint Paul Archipelago, Brazil, from June 2010 to October 2011. n.id.= not identified.***

| **Táxon** | **Estágio de desenvolvimento** | **AR (%)** | **ind.m$^{-3}$ Média** | | **ind.m$^{-3}$ Máximo** | |
|---|---|---|---|---|---|---|
| | | | Dia | Noite | Dia | Noite |
| *Euphausia* Dana, 1850 n. id | larva calyptopis | 31,6 | 0,45 | 1,20 | | |
| *Euphausia* n. id | larva furcilia | 24,8 | 0,35 | 0,90 | | |
| *Euphausia* n. id | adulto | 7,6 | 0,10 | 0,30 | | |
| *E. americana* Hansen, 1911 | adulto | 5,6 | < 0,01 | 0,29 | 0,17 | |
| *E. tenera* Hansen, 1905 | adulto | 2,1 | 0,05 | 0,07 | 1,36 | |
| *E. similis* G.O. Sars, 1885 | adulto | 1,1 | | 0,06 | | |
| *E. diomedeae* Ortmann, 1894 | adulto | 0,1 | | < 0.01 | | |
| *Nematoscelis* G. O. Sars, 1883 n. id | larva, adulto | 0,3 | | 0,01 | | |
| *N. atlantica* Hansen, 1916 | adulto | 0,6 | 0,02 | 0,02 | 0,17 | |
| *N. megalops* G.O. Sars, 1883 | adulto | 0,1 | 0,01 | | 0,17 | |
| *Stylocheiron* G. O. Sars, 1883 n. id | larva calyptopis | 0,2 | 0,01 | 0,01 | | |
| *Stylocheiron* n. id | larva furcilia | 3,8 | 0,08 | 0,12 | | |
| *Stylocheiron* n. id | adulto | 0,4 | | 0,02 | | |
| *S. abbreviatum* G.O. Sars, 1883 | adulto | 0,2 | 0,01 | | 0,17 | |
| *S. affine* Hansen, 1910 | adulto | 0,1 | < 0,01 | | 0,17 | |
| *S. carinatum* G.O. Sars, 1883 | larva, adulto | 6,2 | 0,05 | 0,30 | | |
| *S. carinatum* | furcilia larvae | 4,8 | 0,05 | 0,20 | | |
| *S. suhmi* G.O. Sars, 1883 | larva, adulto | 1,1 | 0,06 | 0,03 | 0,85 | |
| *Thysanopoda* Milne Edwards, 1830 n. id | larva, adulto | 0,6 | | 0,03 | | |
| *T. aequalis* Hansen, 1905 | larva, adulto | 0,6 | | 0,03 | | |
| *T. tricuspidata* Milne Edwards, 1837 | larva, adulto | 0,6 | < 0,01 | 0,03 | 0,17 | |
| Euphausiacea Dana, 1852 (others) | larvae | 6,5 | 0,07 | 0,27 | 0,66 | |
| Euphausiacea (total) | larva, adulto | 100 | 1,3 | 4,0 | | |

## Discussão

A heterogeneidade da distribuição da comunidade zooplanctônica epipelágica e neustônica do ASPSP respondeu apenas ao fator turno de amostragem, onde um significativo aumento no período noturno da biomassa sestônica, abundância total do zooneuston e abundância total de eufausiáceos foi verificada. Os padrões espaciais testados em relação às comunidades alvo mostrou-se menos importante neste pequeno e isolado sistema insular.

**Biomassa sestônica** - A média da biomassa sestônica registrada no presente estudo apresentou valores semelhantes aos observados por Díaz (2007) e ligeiramente maiores aos encontrados por Melo *et al.* (2012) com dados obtidos durante o período chuvoso na mesma área de estudo. A hipótese de diferenças da biomassa quanto ao fator turno foi verificada, onde a média noturna foi significativamente maior, sendo este resultado das agregações noturnas na região epipelágica como consequência da migração vertical diária (DVM) dos organismos. Mudanças na biomassa diária de frações de diferentes tamanhos revelaram que a DVM ocorreu mais fortemente em animais maiores (HAYS *et al.*, 2001). Logo, sugerimos que a diferença registrada no presente trabalho entre a biomassa sestônica diurna e noturna possa ocorrer em resposta ao tamanho da malha da rede utilizada (300μm) o que favoreceu a captura de organismos de tamanhos maiores, considerados fortes migradores. Espacialmente a biomassa sestônica registrada a jusante do ASPSP foi superior à verificada a montante da ilha. Segundo Condie e Condie (2016) a interação da corrente com a topografia da ilha pode causar a jusante: produção de vórtices, enriquecimento (nutrientes provenientes das profundezas do oceano) e retenção que estão associados com habitat favorável para a reprodução e recrutamento de muitas espécies de peixes. Assim, as áreas a jusante das ilhas oceânicas são locais de alta biomassa planctônica (ARAUJO e CINTRA, 2009).

**Abundância total de copépodes** - Os valores médios de abundância observados no presente trabalho são considerados similares a outros registrados em ambientes Tropicais (LÓPEZ e ANADÓN, 2008). Os poucos trabalhos realizados no ASPSP, no contexto físico (ARAUJO e CINTRA, 2009) e biológico, mostraram que a produção de fitoplâncton (DE QUEIROZ, 2014) e zooplâncton (DÍAZ *et al.*, 2009) aumentam durante a estação chuvosa. A amostragem do presente estudo ocorreu durante o fim de Julho e início de Agosto de 2012 (estação seca), onde o valor médio de abundância verificado foi muito próximo e muitas vezes superior aos registrados no período considerado produtivo no ASPSP (MELO *et al.*, 2012, 2014). Uma abundância de copépodes superior ao apresentado no referido estudo foi registrado por Macedo-Soares *et al.* (2009) e Diaz (2007) através de arrastos subsuperficiais realizados para investigar o mesozooplâncton no ASPSP.

A abundância total de copépodes não diferiu significativamente em relação aos turnos amostrados, embora sua média noturna tenha apresentado um valor numérico mais elevado do quê a diurna. A ausência de diferenças na distribuição da abundância de copépodes em relação ao turno de amostragem também foi observada por Melo *et al.* (2012), Melo *et al.* (2014) estudando a assembleia de copépodes no ASPSP. O aumento da abundância de copépodes durante a noite é um indicativo de agregações, provocado pela migração realizada por esses organismos (WIEBE, 1970). Porém, fatores bióticos como a pressão de predação realizada principalmente durante o dia por peixes zooplanctívoros que residem no ASPSP a exemplo das famílias Myctophidae, Scombridae, Hemiramphidae e Exocoetidae, corresponde a um importante controlador da abundância de copépodes (SANTANA, 2015). Diferenças estatísticas não foram registradas quanto ao fator espacial sobre a abundância, porém numericamente o valor à jusante da ilha foi maior quê o registrado a montante. Lira (2013) e Santana (2015) estudando o zooneuston com ênfase em decapoda e larvas/ovos de peixes respectivamente registraram uma abundância média elevada à jusante do ASPSP. Embora a hipótese de diferença espacial não tenha sido comprovada é importante ressaltar que o aumento da produtividade pelágica e bentônica principalmente a jusante do ASPSP é resultado da ação superficial da corrente sul equatorial (SEC) transportando larvas de organismos. Assim, o resultado da interação da SEC com a topografia do ASPSP cria um ambiente favorável para o recrutamento larval em águas oceânicas (ARAUJO e CINTRA, 2009).

**Zoonêuston** - A comunidade do zoonêuston no entorno do ASPSP foi caracterizada com 18 táxons em nível de grandes grupos, a maioria dos grupos já haviam sido previamente registrados na área (GARCIA-DIÁZ *et al.*, 2009; MELO *et al.*,; 2012, LIRA *et al.*, 2017) e também em outros sistemas insulares do Atlântico Tropical como o Atol das Rocas (PINTO *et al.*, 1997) e o Arquipélago de Fernando de Noronha (LIRA *et al.*, 2014, 2017). Destaca-se no presente trabalho, o registro do inseto pertencente ao gênero *Halobates*, o qual foi amplamente registrado nas águas tropicais do Oceano Atlântico Norte e Sul entre 40°N e 30–40°S para a espécie *Halobates micans* Eschscholtz, 1822 (CHENG e SCHULZ-BALDES, 1981) e provavelmente se trata da mesma espécie do ASPSP. Também foi verificada nessa comunidade o raro decápode *Amphionides reynaudii* (H. Milne Edwards, 1833) (LIRA *et al.*, 2017), representado por apenas um único exemplar. Dentre os grupos taxonômicos registrados na comunidade neustônica, a Subclasse Copepoda se destacou como a mais frequente e abundante em ambas as interfaces do nêuston. *Undinula vulgaris* foi à espécie que dominou em ambos os turnos e interfaces investigadas no entorno do ASPSP. *U. vulgaris* é um dos Calanoida mais abundantes e indicador de águas oceânicas, também ocorrendo em regiões neríticas, com ampla distribuição em águas tropicais e subtropicais dos oceanos Atlântico, Pacífico e Indico (NEUMANN-LEITAO *et al.*, 2008).

A variação diurna vs. noturna foi marcante na abundância total de indivíduos do zoonêuston, sendo significativamente maior no período noturno. Esse aumento da abundância total do plâncton subsuperficial no período noturno apesar ter sido corroborado para a comunidade de larvas de Decapoda no ASPSP (BRANDÃO *et al.*, 2013), não é um padrão facilmente registrado em ambientes insulares para grupos de zooplâncton no ASPSP (DIAZ, 2007; MELO *et al.*, 2012). Essa variabilidade entre as amostras é parcialmente explicada pela agregação dos organismos planctônicos na superfície e pela migração vertical noturna que é comum para as comunidades planctônicas e organismos maiores (BRANDÃO *et al.*, 2013).

**Abundância de Euphausiacea** - O presente estudo observou maior abundância de larvas de Euphausiacea (caliptopis e furcilia) em relação aos adultos. Isso pode ser explicado pelo processo contínuo de reprodução desses organismos, comum em áreas tropicais (FERNÁNDEZ *et al.*, 2002). As espécies de eufausiáceos (*E. americana*, *S. carinatum* e *E. tenera*) apresentaram altas abundâncias em regiões epipelágicas, especialmente à noite. Entre as espécies encontradas neste estudo, *E. americana* é endêmica do Atlântico e a mais abundante na camada superficial da costa leste brasileira (ANTEZANA e BRINTON, 1981). A maior abundância deste táxon à noite indica forte migração vertical, comportamento característico do grupo. Este pode ser uma resposta a vários fatores, como a disponibilidade de alimento e características físicas da coluna de água (ANTEZANA e BRINTON, 1981; GIBBONS *et al.*, 1999). O número de espécies (12) registradas para o ASPSP foi semelhante à riqueza de espécies registrada para ecossistemas altamente produtivos, como uma frente ao sul da Califórnia, com 11 espécies (LARA-LOPEZ *et al.*, 2012) e o ecossistema de ressurgência no

Chile com 10 espécies (FERNÁNDEZ *et al.*, 2002). Além disso, também foi superior à riqueza de espécies observada em latitudes mais altas, como na plataforma norueguesa, onde apenas cinco espécies foram registradas. Onze das espécies verificadas no presente estudo no ASPSP já haviam sido registradas anteriormente neste sistema insular (MACEDO-SOARES, *et al.*, 2009).

## Considerações Finais

- Sugerimos que o aumento significativo da biomassa sestônica verificada no período noturno no entorno do ASPSP no ano de 2012 seja reflexo do tamanho da malha da rede utilizada no presente estudo, favorecendo a captura de animais de tamanho corpóreo maior, sendo estes considerados fortes migradores;

- Uma maior biomassa sestônica foi registrada a jusante do ASPSP no ano de 2012. Mecanismos de concentração animal e características hidrodinâmicas locais são presumivelmente os principais responsáveis pela distribuição da biomassa sestônica no ASPSP, no entanto, são necessárias mais investigações, já que este representa um importante local de pesca onde os ovos e larvas de peixes permanecem no entorno da ilha, contribuindo para o aumento da produtividade pelágica, bentônica e da biomassa planctônica;

- A abundância de copépodes no entorno do ASPSP não diferiu entre os turnos de amostragens (dia vs. noite) nem espacialmente (jusante vs. montante), embora os valores tenham se apresentado numericamente maiores à noite e a jusante da ilha respectivamente. Isto pode ser resultado da alta taxa de predação provocada por peixes residentes no ASPSP (o que é comum em montes submarinos), interferindo no efeito da migração realizada pelos copépodes;

- A abundância total do Zoonêuston durante a noite no ASPSP é bem maior em relação ao período diurno;

- A comunidade neustônica do ASPSP é homogênea em relação a distribuição entre os lados da ilha e entre as interfaces do nêuston superior e inferior;

- A assembleia de copépodes neustônicos esteve representada por espécies consideradas pela literatura 'verdadeiramente 'neustônica' por apresentarem adaptações morfológicas para este ambiente (*Labidocera nerii* e *Pontellina plumata*) e por espécies pelágicas presentes no neuston, sobretudo pela oferta de alimento (*Undinula vulgaris*, *Euchaeta marina* e *Farranula gracilis*).

- Os dados referentes aos eufausiáceos demonstraram a forte migração vertical desse grupo, representados principalmente pelos gêneros *Euphausia* e *Stylocheiron* no ASPSP.

## Agradecimentos

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