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Copepod distribution and production in a Mid-Atlantic Ridge archipelago

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ABSTRACT

The Saint Peter and Saint Paul Archipelago (SPSPA) are located close to the Equator in the Atlantic Ocean. The aim of this study was to assess the spatial variations in the copepod community abundance, and the biomass and production patterns of the three most abundant calanoid species in the SPSPA. Plankton samples were collected with a 300 µm mesh size net along four transects (north, east, south and west of the SPSPA), with four stations plotted in each transect. All transects exhibited a tendency toward a decrease in copepod density with increasing distance from the SPSPA, statistically proved in the North. Density varied from 3.33 to 182.18 ind.m⁻³, and differences were also found between the first perimeter (first circular distance band) and the others. The total biomass varied from 15.25 to 524.50 10⁻³ mg C m⁻³ and production from 1.19 to 22.04 10⁻³ mg C m⁻³d⁻¹. The biomass and production of *Undinula vulgaris* (Dana, 1849), *Acrocalanus longicornis* Giesbrecht, 1888 and *Calocalanus pavo* (Dana, 1849) showed differences between some transects. A trend of declining biodiversity and production with increasing distance from archipelago was observed, suggesting that even small features like the SPSPA can affect the copepod community in tropical oligotrophic oceanic areas.

Key words: oligotrophic, plankton, St. Peter and St. Paul archipelago, tropical, upwelling.

INTRODUCTION

The tropical ocean region is made up of oligotrophic waters characterized by low primary productivity and consequently a low secondary productivity (Boltovskoy 1981). Despite low densities, tropical zooplanktonic communities have as their primary characteristic a high species richness, which in turn results in a large network of trophic interactions in

which this community participates (Piontkovski and Landry 2003).

Within this complex network of interactions, copepods play a significant role in the transfer of energy and organic material from primary producers to the higher trophic levels in pelagic ecosystems (Verity and Smetacek 1996, Satapoomin et al. 2004) accounting for as much as 80% of the biomass of planktonic metazoans in the marine environment (Kiørboe 1998). Several studies have addressed the

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importance of this group in terms of community structure, biological processes and their behavioral mechanisms (Wiggert et al. 2005, Berasategui et al. 2005, Hirst and Kiørboe 2002, Strickler 1984), including discussion on the importance of copepod in the diet of fish species of commercial interest (Champalbert and Pagano 2002, Möllmann et al. 2004, Catalán et al. 2007) and the reasons underlying its success in the marine environment (Kiørboe 2011). The copepods are considered the most abundant and diverse components of mesozooplankton in marine environments and the most important secondary producers in marine food webs (Shimode et al. 2006, Gallienne and Robins 2001).

Variations in the abundance, distribution and interactions within the community of planktonic copepods are strongly related to the hydrographic characteristics of the marine environment (Kang and Hong 1995), determining its structure and function (Haury et al. 1990). The presence of islands and seamounts is responsible for modifications in the hydrodynamics of the environments where these features occur, generating a diversity of physical and ecological processes, influencing the structure of several local communities (Boehlert and Genin 1987, Genin 2004, Rogers 1994) and promoting the creation of unique habitats for many species (De Forest and Drazen 2009).

Typical oceanic species are less common above seamounts than in open ocean (Wilson and Boehlert 1993, Genin et al. 1994). Therefore, the interactions between the physical forcing and animal behaviors such as vertical migrations are key factors in the formation and maintenance of aggregations in regions of abrupt topography, still affecting the spatial distribution of such plankton aggregations in these areas (Genin 2004, Leis 1982).

Within this context, the present study tested the hypothesis that the abundance of copepod and the biomass and production of dominant calanoids vary around the Saint Peter and Saint Paul Archipelago according to the distance from the feature.

MATERIALS AND METHODS

STUDY AREA

The archipelago is formed by a group of rocky islands and is located north of Equator ($0^{\circ}55'06''\text{N}$ and $29^{\circ}20'48''\text{W}$), lying approximately 960 km off the northeast coast of Brazil (Edwards and Lubbock 1983) (Fig. 1). The SPSPA rises from the Mid-Atlantic Ridge, 4000 meters deep, to a maximum altitude of 18 m (Vaske Jr. et al. 2005). The three larger islands (Belmonte, St. Peter and St. Paul) form a horseshoe cove with average depth of 8 m. These islands are separated by narrow channels that promote strong water currents (Pinheiro 2004).

According to Araujo and Cintra (2009), the ocean dynamics that act on the SPSPA are subject to the influence of the north branch of the South Equatorial Current (nSEC) and the Equatorial Undercurrent (EUC) (Fig. 1). Near the surface, the nSEC is shifted northwestward under the action of the Southwestern tradewinds shear, whereas the EUC flows eastward over the equator just beneath the surface (Stramma 1991, Stramma et al. 2003, Giarolla et al. 2005, Lumpkin and Garzoli 2005, Brandt et al. 2006). The interaction between the abrupt topography of the SPSPA and these currents results in the production of vortices, disturbances of the thermohaline structure and possibly local mechanisms of resurgence (Araujo and Cintra 2009).

Because of its long distance from the coast and its strategic position in the middle of the Equatorial Atlantic Ocean, the SPSPA is of great importance, being a migratory stop and feeding location for a large number of species of fish, and constitutes an important fishing area in the Exclusive Economic Zone (EEZ) of northeastern Brazil with an emphasis on fishing for tuna, mackerel, sharks and flying fish (Vaske Jr. et al. 2005). The SPSPA also displays a high degree of endemism among reef fishes (Campos 2004).

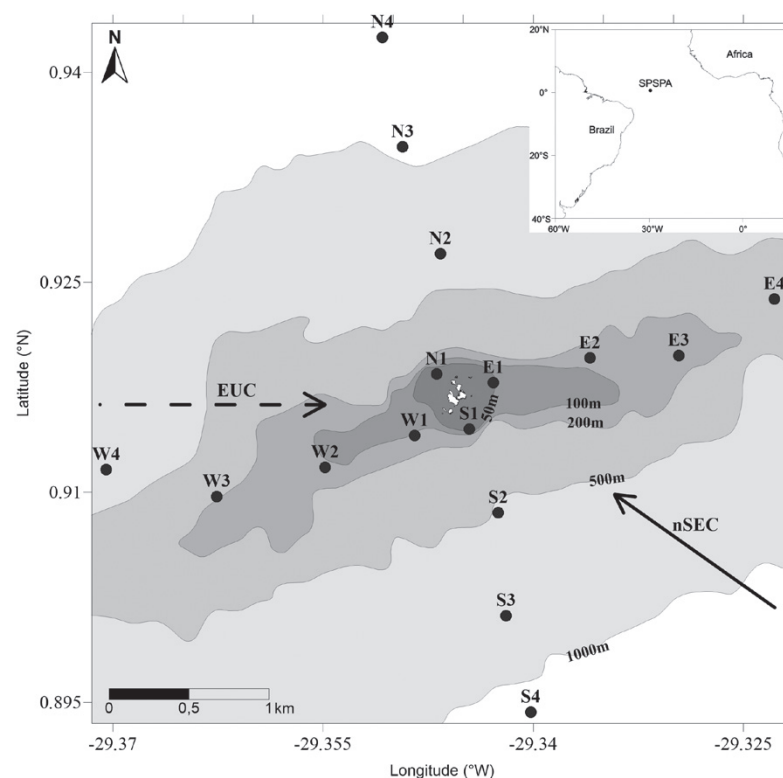


Figure 1 - Sampling stations at Archipelago of Saint Peter and Saint Paul, Brazil. The north branch of the South Equatorial Current (nSEC) and the Equatorial Undercurrent (EUC) flows are indicated in the figure.

SAMPLING STRATEGY AND LABORATORY PROCEDURES

Diurnal collections of plankton samples were performed and water surface temperatures were measured between 07:00 and 10:00 h at 16 stations around the SPSPA (Fig. 1). These stations were arranged along perpendicular transects to represent four circular distance bands (perimeters) from the SPSPA, lying approximately 325 (perimeter 1 - P1), 1250 (perimeter 2 - P2), 2175 (perimeter 3 - P3) and 3100 m (perimeter 4 - P4) from the archipelago. The transects were oriented to the north (N), south (S), east (E) and west (W). The stations were codified based on transect orientation and distance bands (e.g. N1 – Transect north, first band). The samples were collected during the rainy season (May 2008).

Mesozooplankton samples were collected with a plankton net with a mesh size of 300 μm and a 0.30 m mouth diameter, coupled with a

flowmeter. Due to logistical problems associated to the extreme environmental conditions, it was not possible to replicate the samples. Subsurface hauls were conducted for 10 minutes at a speed of 2 to 3 knots. The samples were placed in 250 mL plastic bottles and fixed with 4% neutralized formaldehyde with borax (5 g L⁻¹) according to the procedure described by Newell and Newell (1963).

In the laboratory, each sample was placed in a beaker, diluted to 250 mL with distilled water and homogenized. Three subsamples of 5 mL were taken with a Hensen Stempel pipette and then analyzed under a binocular compound microscope. Five additional subsamples were inspected to search rare species. Copepods were identified to the lowest taxonomic level possible. The sestonic biomass was determined on the basis of the wet weight by weighing the sample on a precision balance, as described in Omori and Ikeda (1984).

DRY WEIGHT, BIOMASS AND PRODUCTION OF COPEPODS

Copepod production was estimated for the three most abundant and frequent calanoid species (*Undinula vulgaris*, *Acrocalanus longicornis* and *Calocalanus pavo*). As a criterion for the selection of the focal species, the frequency (>85%) and dominance/abundance (> 30% in more than one sample) of the species were considered.

For each species, the length of the prosome of 30 individuals, chosen at random, independently of its developmental stage, were measured per sample. These measurements were used for the calculation of dry weight (DW) through linear regressions between prosome length and body weight, according to Webber and Roff (1995). Dry weight (DW) was then converted into carbon (C), assuming that $C = 0.40 \cdot DW$ (Postel et al. 2000).

To obtain the biomass of each species (B ; mg C m^{-3}), the equation $B = DW \cdot 10^{-3} \cdot D$ was used, where DW (μg) was the average dry weight in C and D was the density (ind m^{-3}) of each species.

Unfortunately it was not possible to carry out any incubation technique to estimate copepod growth/egg production, due to the complete isolation and prohibitive conditions of the scientific station of the archipelago. For this reason, we choose the Hirst-Lampitt model (Hirst and Lampitt 1998), to estimate the instantaneous growth rate (g). This model was developed based on a data set that includes studies conducted at temperatures ranging from -2.3 to 29.0°C , polar to tropical regions, highly eutrophic to oligotrophic waters, and estuarine to offshore waters. The used H-L model considers the water temperature (T) and the dry weight in carbon to calculate the growth rate, where $\text{Log}_{10} g = 0.0208[T] - 0.3221[\text{Log}_{10}C] - 1.1408$. Production ($\text{mg C m}^{-3} \text{d}^{-1}$) was calculated as the product of g and B .

DATA AND STATISTICAL ANALYSIS

The Shannon index (H') was applied to estimate the diversity of the community (Shannon 1948), and the evenness (J') was calculated according to Pielou (1977).

Statistical analyses were based on data density, biomass and production, where samples were compared using a Kruskal-Wallis. The Student-Newman-Keuls test was used as an *a posteriori* comparison when significant differences were found. Before the analyses, all data were transformed using $\log(x+1)$. Spearman's correlation coefficient was applied to verify the degree of association between the values of sestonic biomass and the biomasses of the 3 focal species. The statistical tests were conducted using the statistical package BioEstat 5.0 (Ayres et al. 2007), and values of $p < 0.05$ were considered to represent significant differences.

RESULTS

COPEPOD STRUCTURE AND RICHNESS

The copepod community in the SPSPA was composed of 38 taxa, of which 22 were Calanoida, 12 Cyclopoida and four were Harpacticoida. Of these, 35 were identified to the level of species; one, to genus; one, to family; and one, to the order level (Table I). The calanoids were represented by 11 families, dominated by Paracalanidae with five species, followed by Calanidae (4 species), Pontellidae (3 species) and Euchaetidae (2 species). Among the cyclopoids, the most well-represented taxa were Sapphirinidae and Corycaidae (four species each) and Oncaeidae (two species). In harpacticoids, Miraciidae was represented by two species, and the other families were represented by only one species.

Calanoids were the most abundant group, followed by cyclopoids and harpacticoids. Calanoids represented more than 50% of the total density in all samples.

The total density of copepods ranged between 3.33 and $182.18 \text{ ind m}^{-3}$, averaging $26.9 \pm 42.5 \text{ ind m}^{-3}$. This high average and large amplitude was marked primarily by a high density at N1, which was 5.5 times greater than the observed value at the point with the second highest density (E1) (Fig. 2).

TABLE I
List of copepod taxa, relative abundance (by transect) and frequency
of occurrence (FO) (for sample) at the Archipelago of Saint Peter and
Saint Paul, Brazil. S: South; W: West; N: North; E: East.

TAXA	Relative Abundance				FO (%)
	S	W	N	E	
<i>Nannocalanus minor</i> (Claus, 1863)	0.00	0.00	6.87*	0.00	13%
<i>Neocalanus gracilis</i> (Dana, 1849)	0.95	0.00	5.11*	0.00	19%
<i>Neocalanus robustior</i> (Giesbrecht, 1888)	0.00	0.00	0.55	0.00	6%
<i>Undinula vulgaris</i> (Dana, 1849)	6.30*	16.11*	3.92	43.75***	100%
<i>Calocalanus pavo</i> (Dana, 1852)	21.75**	28.03**	3.26	5.41*	100%
<i>Calocalanus plumulosus</i> (Claus, 1863)	0.00	0.00	0.05	0.00	6%
<i>Paracalanus aculeatus</i> Giesbrecht, 1888	0.00	0.00	0.05	10.07*	13%
Paracalanidae (others)	0.00	0.00	1.09	0.00	6%
<i>Acrocalanus longicornis</i> Giesbrecht, 1888	37.37***	15.55*	9.30*	11.62*	88%
<i>Clausocalanus furcatus</i> (Brady, 1883)	1.72	0.86	1.19	0.00	31%
<i>Euchaeta marina</i> (Prestandrea, 1833)	0.00	0.00	6.57*	0.00	13%
<i>Paraeuchaeta pubera</i> (Sars, 1907)	0.00	0.00	3.58	0.00	13%
<i>Scolecithrix danae</i> (Lubbock, 1856)	0.00	0.41	28.24**	0.18	31%
<i>Lucicutia flavicornis</i> (Claus, 1863)	0.00	0.00	0.55	0.00	6%
<i>Haloptilus angusticeps</i> Sars, 1907	0.00	0.00	0.27	0.00	6%
<i>Pleuromamma piseki</i> Farran, 1929	0.00	0.00	0.55	0.00	6%
<i>Centropages violaceus</i> (Claus, 1863)	0.00	0.41	1.12	0.10	31%
<i>Candacia pachydactyla</i> (Dana, 1849)	0.00	1.73	4.76	0.80	50%
<i>Pontella atlantica</i> (Milne Edwards, 1840)	0.00	0.45	0.64	1.22	38%
<i>Pontellina plumata</i> (Dana, 1849)	3.88	0.45	1.27	6.54*	69%
<i>Labidocera nerii</i> (Krøyer, 1849)	0.00	3.04	1.04	0.73	69%
Calanoida (others)	0.00	1.31	0.09	0.00	19%
<i>Corycaeus (Corycaeus) speciosus</i> Dana, 1849	3.25	1.66	6.97*	1.17	75%
<i>Corycaeus (Corycaeus) clausi</i> Dahl, 1894	0.00	0.41	0.49	0.25	31%
<i>Corycaeus (Onychocorycaeus) latus</i> Dana, 1849	2.38	2.07	1.38	1.17	88%
<i>Farranula gracilis</i> (Dana, 1849)	6.18*	2.89	1.57	2.41	94%
<i>Farranula</i> sp.	1.95	0.86	0.00	0.00	31%
<i>Oithona plumifera</i> Baird, 1843	2.11	2.48	0.52	0.00	50%
<i>Oncaea venusta</i> Philippi, 1843	4.05	5.96*	0.49	1.49	75%
<i>Oncaea media</i> Giesbrecht, 1891	4.48	6.39*	5.71*	7.36*	100%
<i>Copilia mirabilis</i> Dana, 1849	1.15	2.48	1.02	0.43	38%
<i>Copilia lata</i> Giesbrecht, 1891	0.00	0.00	0.00	0.18	6%
<i>Sapphirina nigromaculata</i> Claus, 1863	0.96	2.10	0.56	1.79	75%
<i>Sapphirina opalina-darwinni</i> Dana, 1849	0.00	0.00	0.32	0.00	13%
<i>Macrosetella gracilis</i> (Dana, 1847)	0.47	1.69	0.15	0.75	44%
<i>Microsetella rosea</i> (Dana, 1849)	0.00	0.00	0.09	0.19	13%
<i>Miracia efferata</i> Dana, 1849	1.06	1.28	0.50	2.37	56%
Harpacticoida (others)	0.00	1.35	0.14	0.00	19%

Non-rare species are in bold.

The density of copepods showed a gradient between the archipelago and the open ocean, with higher values on the perimeter closer to the archipelago that decreased with increasing distance

from the islands (Fig. 2). All transects showed a decrease in density of copepods towards open ocean, but only the north transect was significantly different from the others (K-W, $H = 28.77$, $p < 0.0001$; *SNK*,

NxS: $q = 1.87$, $p < 0.01$; NxW: $q = 2.17$, $p < 0.01$; NxE: $q = 1.50$, $p < 0.01$). When comparing the four distances from the archipelago, significant differences were found (K-W, $H = 20.25$, $p = 0.0002$) between P1 and P2 (SNK , $q = 1.48$, $p = 0.0182$), P1 and P3 (SNK , $q = 1.70$, $p = 0.0003$), and P1 and

P4 (SNK , $q = 2.08$, $p < 0.0001$), which indicates an immediate effect of distance from SPSPA on the community. The largest density variations occurred between the two closest distance bands (P1 and P2), with P3 and P4 showing low variability between different transects ($SD = 2.5 \text{ ind m}^{-3}$).

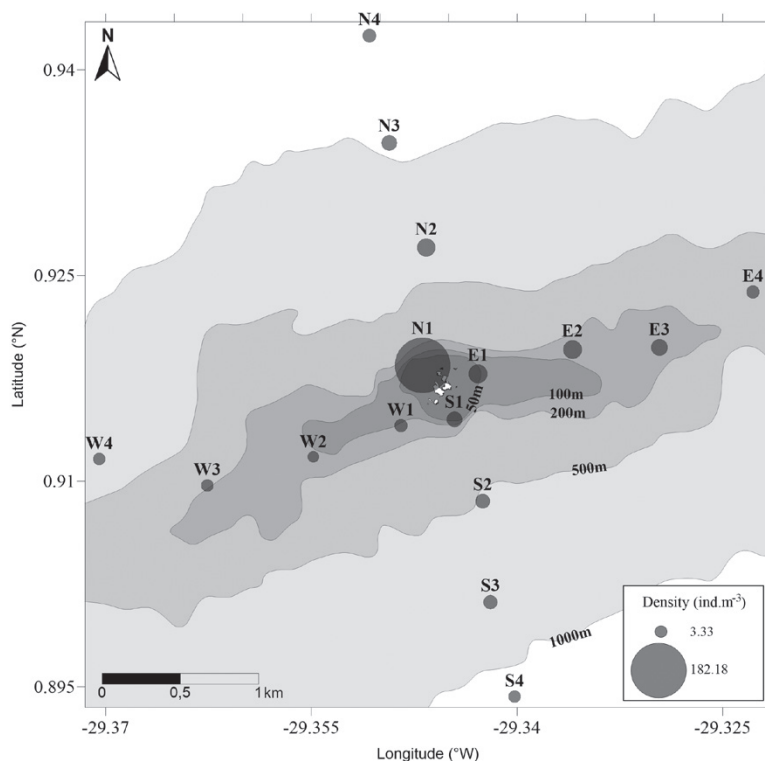


Figure 2 - Copepod density spatial variation in the Archipelago of Saint Peter and Saint Paul, Brazil.

The north transect exhibited the highest variation in density, with significant differences between the stations (K-W, $H = 19.12$, $p = 0.0003$). These differences were found between N1 and N3 (SNK , $q = 2.32$, $p = 0.0008$), N1 and N4 (SNK , $q = 2.53$, $p < 0.0001$) and between stations N2 and N4 (SNK , $q = 0.67$, $p = 0.0242$). The other transects did not show significant differences in density between their stations, being relatively homogeneous.

The relative abundance of species by transect (Table I) highlighted the large number of rare species. No species shows more than 50% of relative abundance. The species *Undinula vulgaris*, *Acrocalanus longicornis* and *Scolecithrix danae*

were abundant in transects E, S and N, and *Calocalanus pavo* dominated in S and W. *U. vulgaris* was the dominant species at E4 station.

Nine species (23.7% of the total) were observed in more than 75% of the samples, including three species (*U. vulgaris*, *C. pavo* and *Oncaea media*) that were present in all samples (Table I). The mean diversities observed in the transects were 3.50 ± 0.25 (N) 2.48 ± 0.26 (E), 2.76 ± 0.37 (S) and 3.00 ± 0.33 (W) bits ind^{-1} , ranging from 2.08 (E4) to 3.85 bits ind^{-1} (N2). No clear pattern of diversity related to proximity to the archipelago was observed. Community evenness followed the same trend as diversity, varying from 0.58 to 0.91.

BIOMASS AND PRODUCTION OF DOMINANT COPEPODS

Undinula vulgaris showed the highest average biomass ($80.2 \pm 108.8 \cdot 10^{-3} \text{ mg C m}^{-3}$), followed by *A. longicornis* ($42.2 \pm 35.6 \cdot 10^{-3} \text{ mg C m}^{-3}$) and *C. pavo* ($11.9 \pm 5.8 \cdot 10^{-3} \text{ mg C m}^{-3}$) (Table II). Significant differences were found between the species (K-W, $H = 10.94$, $p = 0.0042$). Although *A. longicornis* exhibited higher biomass values than *U. vulgaris* in the south transect (Fig. 3), no significant differences were observed between them. *C. pavo* was significantly lower in biomass than the two mentioned species (SNK , $q = 2.36$, $p = 0.0019$; $q = 1.42$, $p = 0.0111$, respectively).

U. vulgaris biomass was not significantly different in the various distance bands; however, differences were observed among the transects (K-W, $H = 11.71$, $p = 0.0084$). These differences were found between north and west (SNK , $q = 4.57$, $p = 0.0175$), east and west (SNK , $q = 2.45$, $p = 0.0023$), and east and south (SNK , $q = 2.09$, $p = 0.0259$). For this species, high biomass was recorded at three stations, which reflects different conditions for the community. At N1, high abundances of copepodites were observed, which were present in low abundances or absent in the other stations. The biomass of *A. longicornis* and *C. pavo* was not significantly different amongst transects and distance bands.

The total biomass for the three species (Table II) exhibited significant differences only between transects (K-W, $H = 9.90$, $p = 0.0194$).

These differences were between the north and west transects (SNK , $q = 4.89$, $p = 0.0175$) and the east and west transects (SNK , $q = 5.46$, $p = 0.0038$), with higher biomasses north and east of the SPSPA. A positive correlation was observed between the values of total and sestonic biomass (Spearman; $r_s = 0.794$ and $p < 0.001$).

The production showed the same pattern that was observed for biomass, and although *U. vulgaris* exhibited a higher mean value ($4.3 \pm 5.1 \cdot 10^{-3} \text{ mg C m}^{-3} \text{ d}^{-1}$), followed by *A. longicornis* ($2.9 \pm 2.4 \cdot 10^{-3} \text{ mg C m}^{-3} \text{ d}^{-1}$) and *C. pavo* ($1.0 \pm 0.5 \cdot 10^{-3} \text{ mg C m}^{-3} \text{ d}^{-1}$), no differences in production were observed between species.

The production of *U. vulgaris* showed significant spatial differences (K-W, $H = 9.90$, $p = 0.0194$) between the east and south transects (SNK , $q = 6.82$, $p = 0.0175$) and east and west transects (SNK , $q = 7.23$, $p = 0.0038$). Among the distance bands, no differences were found. *A. longicornis* and *C. pavo* did not exhibit any type of difference between transects or distance bands.

The total production of the three species also showed significant differences (K-W, $H = 8.44$, $p = 0.0376$) between the north and west transects (SNK , $q = 4.42$, $p = 0.0213$) and the east and west transects (SNK , $q = 5.49$, $p = 0.0075$) (Fig. 4, Table II).

DISCUSSION

Typical epipelagic copepod assemblages characterized the waters around the SPSPA, dominated

TABLE II
Total density (ind m^{-3}), Biomass ($10^{-3} \text{ mg C m}^{-3}$) and Production ($10^{-3} \text{ mg C m}^{-3} \text{ d}^{-1}$) of the total three main Copepod species by transect and distance band at the Archipelago of Saint Peter and Saint Paul, Brazil.

	Transect				Distance band			
	N	E	S	W	P1	P2	P3	P4
Density	244.82	100.80	57.06	27.92	245.89	82.53	66.10	36.06
Biomass	825.79	805.05	331.10	144.00a	941.42	553.29	364.72	246.52
Production	41.90	52.79	26.21	10.60b	51.77	37.98	24.95	16.79

^a Significantly different from N (K-W, $H = 9.90$, $p = 0.0175$) and E (K-W, $H = 9.90$, $p = 0.0038$)

^b Significantly different from N (K-W, $H = 8.44$, $p = 0.0213$) and E (K-W, $H = 8.44$, $p = 0.0075$)

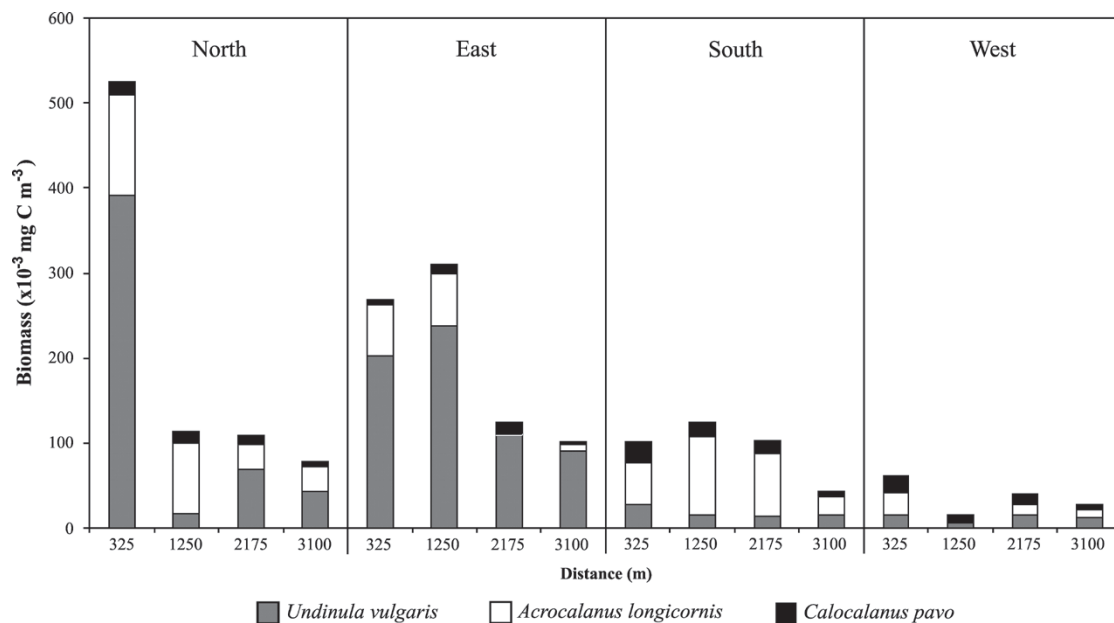


Figure 3 - Biomass values (10^3 mg C m^{-3}) of the three main copepod species by station in the Archipelago of Saint Peter and Saint Paul, Brazil.

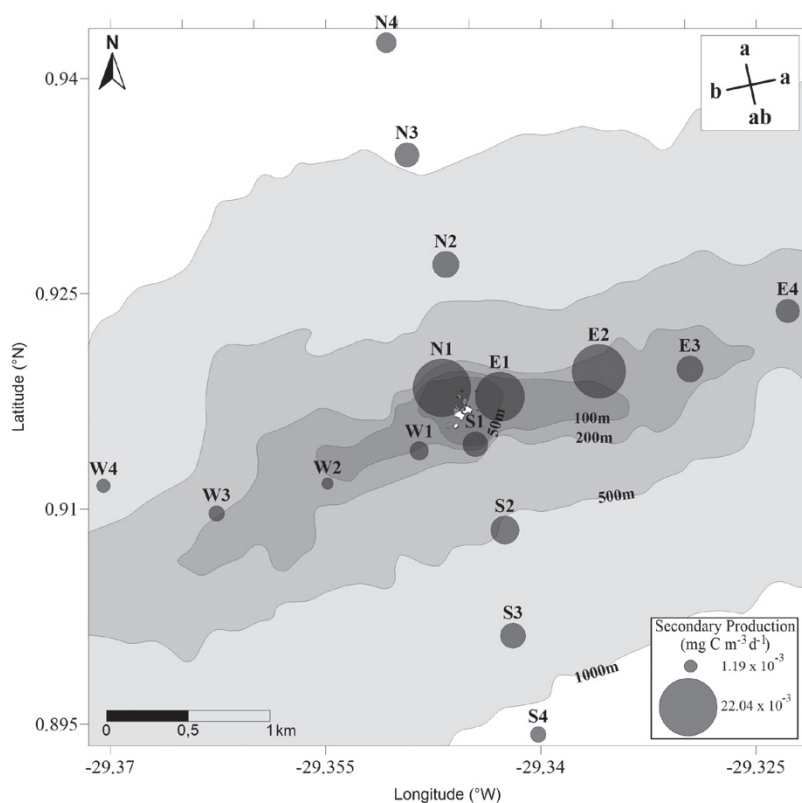


Figure 4 - Production spatial variation ($\text{mg C m}^{-3} \text{ day}^{-1}$) of the three main copepod species in the Archipelago of Saint Peter and Saint Paul, Brazil. The letters on the upper panel indicate significant differences (Kruskal-Wallis; $p < 0.05$; posteriori Student-Newman-Keuls) between transects.

mainly by calanoids species. Several authors report that in tropical and subtropical waters, calanoids often contribute over 50% of the community of copepods in meshes over 200 μm , as was observed in this study (Webber and Roff 1995, Champalbert et al. 2005). The ratio of the different orders of copepods indicated the dominance of calanoids, which is typical of subtropical and tropical waters (Miyashita et al. 2009, Schnack-Schiel et al. 2010), but in deeper layers, several studies have shown that the calanoid concentrations tend to decrease, resulting in a reversal of that dominance with increasing depth (Roman et al. 1995) and they can occasionally be replaced by cyclopoids, such as Oncaeidae (McKinnon et al. 2012).

All species considered by Björnberg (1981) as indicators of the tropical water (a superficial water mass with salinities and temperatures >36 and >20 $^{\circ}\text{C}$, respectively), were found in our study, where the most common in the archipelago were the calanoids *Undinula vulgaris*, *Calocalanus pavo*, *Paracalanus aculeatus*, *Acrocalanus longicornis*, and the cyclopoids *Farranula gracilis*, *Oncaea venusta*, *Corycaeus* (*Corycaeus*) *speciosus*, *Corycaeus* (*Onychocorycaeus*) *latus*, *Oncaea media* and *Sapphirina nigromaculata*. The others species were considered rare, which is a typical feature of tropical and subtropical oceanic waters (Piontkovski et al. 2003, Lo et al. 2004). The most abundant and frequent species were *U. vulgaris*, *A. longicornis* and *C. pavo*. Neumann-Leitão et al. (2008) also observed *C. pavo* and *U. vulgaris* to be the two most abundant species in the oceanic area of Northeastern Brazil and to have wide distributions in this area. Several authors highlight *U. vulgaris* as common species in tropical oceanic areas, and it can be regarded as the dominant species of the shelf and oceanic waters of Northeastern Brazil (Champalbert et al. 2005, Cavalcanti and Larrazábal 2004). *Acrocalanus longicornis* is also a common species in tropical surface waters (Stephen 1984, Cornils et al. 2010).

The species richness observed in this study is related to some important factors: (i) the size of the mesh used (300 μm), (ii) the small diameter of the net's mouth (0.30 m) than that used in oceanic areas, and (iii) the depth sampled. In tropical/subtropical communities, there is a dominance of small species of copepods (Webber and Roff 1995, McKinnon et al. 2008), which may not be efficiently sampled by a plankton net with a large mesh size. For instance, the Oithonidae, a typical and common family of small copepods in tropical Atlantic ocean (Neumann-Leitão et al. 2008), was represented by just one species (*O. plumifera*), probably indicating this mesh selectivity. On the other hand, the diameter of the plankton net mouth may have contributed to an underestimation of the large and sparse copepod species, since in oligotrophic waters the size of the net's mouth may have to be increased to collect a reasonable sample size of animals (Sameoto et al. 2000). Besides, large species tend to occur mostly in deeper waters that are rich in phytoplankton and smaller species more numerous near the surface (Deevey and Brooks 1977, Webber and Roff 1995). This pattern of vertical distribution of species explains the lower species richness reported in studies of mesozooplankton compared to studies carried out with smaller mesh size or with studies with vertical hauls.

Other studies in tropical oceans have observed similar biodiversity trends. Brugnano et al. (2010), for instance, recorded a greater number of species at depths of 20-40 m (87 species) and 40-60 m (78 species) compared to the superficial layer (0-20 m), the latter depth having only 19 species. Woodd-Walker (2001), studying the Atlantic equatorial, found 41 copepod genera; however, these genera were collected in vertically integrated hauls (from a 200 m depth to the surface) encompassing a greater diversity of genera, because in the equatorial, tropical and subtropical Atlantic, the diversity of copepod increases down to 200 m depth (Piontkovski

et al. 2003). Lo et al. (2004) observed less species richness on the surface (11), with a gradual increase with depth, reaching almost 40 species at 200 m. Thus, the richness recorded for the SPSPA in our study (38 species and 27 genera) can be considered high, similar to other studies in similar conditions (Lo et al. 2004, Schnack-Schiel et al. 2010). Our data, obtained from sub-surface hauls, suggest a potential for high biodiversity in deeper layers in the SPSPA. This could be corroborated by P.A.M.C. Melo, Unpublished data, who observed 3 times more species from 0-20 to 80-100 m.

Another possible explanation for the biodiversity values found, can be related with the vortices, disturbances of the thermohaline structure and possibly local mechanisms of resurgence (Araujo and Cintra 2009). The instability generated by these physical forces is consistent with the intermediate disturbance hypothesis (Connell 1978), which suggests that the maximum diversity of a community may not be found in a more stable system, but at intermediate disturbance levels (Sommer et al. 1993, Flöder and Sommer 1999). At the SPSPA, possible upwelling mechanisms resulting from the interaction of the current with the topography can cause a superficial increase in diversity in the vicinity of the archipelago. The diversity in the east and south transects exhibited lower values, probably because of the arrival of nSEC at the forefront of the SPSPA (Araujo and Cintra 2009), which could cause a homogenization of the community in this sector. Studies linking biodiversity assessments with physical oceanography in the area are necessary to elucidate this process.

COPEPOD ABUNDANCE

Copepod abundance in the archipelago was similar to other tropical environments (Hwang et al. 2007, López and Anadón 2008), with a great variation between stations, as shown by other authors for tropical Atlantic environments (Schnack-Schiel et al. 2010, Champalbert et al. 2005).

The archipelago appears to have a major impact on the zooplankton community in the area. A marked decrease in density should be noted with increasing distance from the SPSPA, with the first distance band already significantly different from the second, and further bands. Such trends of density reduction can be observed in all transects; however, the pattern is statistically significant only for the north transect. It is interesting to observe that after the third distance band, a reduction in variability among the different transects, characterizing the environment around the SPSPA as homogeneous from a 2 km distance, a smaller scale effect than has been suggested by the authors cited earlier. This disagrees with Dower and Mackas (1996), who suggest that the community changes only at distances greater than 30 km from a seamount. According to these authors, this may be caused by changes in the depth of the mixed layer and the shoaling of the seamount topography.

Studies show that changes in the zooplankton community occur along the axis of the current (Mackas et al. 1991). Since the cSEC is the main stream acting in the surface layer of the SPSPA waters (Araujo and Cintra 2009), probably the primary change in the community structure should occur along an E-W axis. However, what is actually observed is a greater variation in the north direction, confirming that the nSEC's interaction with the SE tradewinds causes a surface transport to the northwest, justifying the high values of density in this direction and the absence of patterns in the S and W.

The observed abundance in N1 was high when compared to other stations. However, Melo et al. (2012) studying the SPSPA bay and the area immediately adjacent, registered average density values of $185.25 \text{ ind m}^{-3}$. The main opening of the bay faces north toward station N1, causing an increase in density at this station directly and/or indirectly, through the input of organic matter. These values observed in N1 are very high, even when compared to a tropical upwelling area, which

presented values of nearly 100 ind m⁻³ in the surface layer (Lo et al. 2004). Thus, the observed values may also be related to a mechanism of concentration resulting from the relationship between topography and hydrodynamics, as suggested by Araujo and Cintra (2009) for the archipelago and observed elsewhere (Hunt and Pakhomov 2003).

In this study, higher densities were observed for *C. pavo* and *U. vulgaris* with a greater participation of the last one, like observed by Neumann-Leitão et al. (2008) in the oceanic region of northeastern Brazil. This dominance of *U. vulgaris* was also observed in another important area of the tropical Atlantic, where a high concentration of tuna was found (Champalbert and Pagano 2002), as well as in the archipelago. Hassett and Boehlert (1999), in a study on the distribution of *U. vulgaris* in the Hawaiian archipelago, noticed a declining trend with distance from the islands, as was noted for our east transect. Woodd-Walker (2001), studying the equatorial Atlantic at a generic level, found the same pattern, with a greater importance of *Calocalanus* in relation to *Undinula*, recording densities of 1.3 and 0.4 ind m⁻³, respectively.

BIOMASS AND PRODUCTION

The biomass and production values obtained for the three most abundant species of copepod (> 300 µm) around the SPSPA showed a similar pattern to that seen in studies of biomass of zooplankton communities in the vicinity of seamounts (Saltzman and Wishner 1997, Martin and Nellen 2004, Martin and Christiansen 2009). The biomass enrichment and increased production around seamounts are of great importance for higher trophic levels, such as the small and medium-sized pelagic fish that feed on this high primary productivity, which are subsequently captured by larger species such as tuna (Sund et al. 1981). This effect along the trophic web makes the areas around islands, banks and seamounts important fishing sites for pelagic fish of commercial

importance, as is the case for the SPSPA in the Atlantic (Vaske Jr. et al. 2006). It is noteworthy that the fishing in the SPSPA occurs in the west (Vaske Jr. et al. 2006), the lowest production transect, but productive enough to sustain this activity in the area. Often, low values of biomass can be observed as a result of intense grazing by predators (Martin and Christiansen 2009).

Several problems concerning the use of global models to estimate copepod growth have been discussed in recent studies (Liu and Hopcroft 2006a, b, Leandro et al. 2007). Although most of the data compiled to build Hirst-Lampitt model was originated from temperate areas, this model was developed based on data from polar to tropical regions, with temperatures ranging from -2.3 to 29.0 °C (Hirst and Lampitt 1998). However, because this model is based on log transformed data for warmer areas (mainly tropical regions), it usually gives overestimated growth rates. Another problem is related to the fact that most of the growth rate data used to create this model came from moult rate experiments, which may generate biased growth rates (Hirst et al. 2005). On the other hand, as no “ideal” model covering all variables exist, and no standard method has been widely accepted (Muxagata et al. 2012), these global models are still widely used to estimate copepod production (e.g., Dvoretsky and Dvoretsky 2012, Hernández-León et al. 2010, Miyashita et al. 2009, Muxagata et al. 2012).

Compared to other species, *U. vulgaris* exhibited high numbers of juveniles, directly affecting their values of biomass and production. Neumann-Leitão et al. (2008) observed a high abundance of young stages of *U. vulgaris* in superficial oceanic samples, a pattern also observed in this study except at N1, where there was a dominance of adult forms. Moore and O'Berry (1957) reported that this species has a moderate diurnal vertical migration, observed at 25 m depths in daytime samples and on the surface only at night, a fact also described by Hassett and Boehlert

(1999). Therefore, the large amount of adults in N1 is possibly related to the intrusion of sub-superficial water into the surface layer.

Acrocalanus longicornis and *C. pavo* fluctuated in biomass consistently with the variation in abundances, and dry weight values exhibited little variation, primarily because both species were observed almost exclusively as adults. Gusmão and McKinnon (2009) observed biomass and production values of *Acrocalanus gracilis* that were higher than those observed for *A. longicornis* in the present study. The values reflect the high abundance observed for *A. gracilis* in the Timor Sea, Australia (108.14 ind m⁻³). However, the growth rate of *A. longicornis* was higher than that found for adults of *A. gracilis* (0.17 and 0.15 d⁻¹, respectively).

Melo Júnior (2009) noted that the copepod production in a subtropical area from Brazil (Ubatuba) was dominated by very frequent taxa, which accounted for 72.3% of the total production and were thus important indicators of the total productivity of the environment. In the present study, the selected species of copepod appear to reflect the patterns of production of the SPSPA.

Despite the lack of replication in our study and the scarcity of studies in this area, a trend of declining biodiversity and production with increasing distance from archipelago was observed, suggesting that even small features like the SPSPA can affect the copepod community in tropical oligotrophic oceanic areas.

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RESUMO

O arquipélago de São Pedro e São Paulo (ASPSP) está localizado próximo ao Equador, no oceano Atlântico. O objetivo deste estudo foi avaliar variações espaciais nos padrões de abundância da comunidade de Copepoda, e da biomassa e produção das três espécies de Calanoida mais abundantes no ASPSP. Amostras de plâncton foram coletadas com rede com 300 µm de abertura de malha, ao longo de quatro transectos (norte, leste, sul e oeste do ASPSP), com quatro estações cada. Todos os transectos exibiram uma tendência de redução da densidade dos Copepoda com o aumento da distância do ASPSP, provado estatisticamente para o Norte. A densidade variou de 3,33 a 182,18 ind.m⁻³, e diferenças também foram observadas entre o primeiro perímetro (primeira faixa de distância circular) e os demais. A biomassa total variou de 15,25 a 524,50 10⁻³ mg C m⁻³ e a produção de 1,19 a 22,04 mg C m⁻³.d⁻¹. A biomassa e produção de *Undinula vulgaris* (Dana, 1849), *Acrocalanus longicornis* Giesbrecht, 1888 e *Calocalanus pavo* (Dana, 1849) apresentaram diferenças entre alguns transectos. Uma tendência de declínio da biodiversidade e produção com o aumento da distância do arquipélago foi observada, sugerindo que pequenas feições como o ASPSP podem afetar a comunidade em áreas oceânicas oligotróficas tropicais.

Palavras-chave: oligotrófico, plâncton, Arquipélago de São Pedro e São Paulo, tropical, ressurgência.

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