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# Spatial and temporal changes in biomass, production and assemblage structure of mesozooplanktonic copepods in the tropical south-west Atlantic Ocean

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*We examined the spatial and temporal variations of coastal and oceanic epipelagic copepods (rainy–dry seasons of 2009) in a tropical area of the south-west Atlantic. Zooplankton samples were obtained at 48 stations along six transects perpendicular to the coast, in the subsurface water between the 25 and 3000 m isobaths, by horizontal hauls using a Multinet. Abundance (42–64,753 ind. $m^{-3}$), biomass (0.08–113 mg C $m^{-3}$) and daily copepod production (0.17–163.20 mg C $m^{-3}$ $d^{-1}$) showed longitudinal and latitudinal variability. The highest values were observed over the southern continental shelf during the dry season. Temoridae,* Undinula vulgaris *and* Paracalanus quasimodo *dominated the biomass and daily copepod production during the rainy season; while* Calanoides carinatus, Calanopia americana, *Clausocalanidae, Temoridae, Paracalanidae and Subeucalanidae dominated during the dry season. The copepod assemblages formed four different groups: rainy season–continental shelf (1), dry season–continental shelf (2), rainy season–continental slope (3) and dry season–continental slope (4). Temperature, salinity, chlorophyll-*a *and suspended particulate matter explained 45% of the productivity distribution of the dominant copepod species. This study is the first attempt to examine the biomass and daily copepod production in oceanic waters in the south-west Atlantic Ocean, and it showed that copepod biomass and production in a tropical region can be relatively high compared with other regions of the world's oceans.*

**Keywords:** Mesozooplanktonic copepods, biomass, biological production, seasonal variations, tropical environment, south-eastern Brazil

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## INTRODUCTION

In general, marine productivity is expected to be higher in the high-latitude seas around the poles. Waters in high latitudes have higher nutrient concentrations, and the marine organisms reach larger body sizes than in low latitudes. Conversely, tropical species breed continuously throughout the year, in contrast to their intra- and interspecific relatives at higher latitudes (Bauer, 1989). The high abundance of organisms and the marked lack of seasonality in tropical regions might allow an increase in productivity to levels comparable to the productivity of larger-bodied organisms at high latitudes.

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In marine environments, copepods (Crustacea) comprise over 70% of the mesozooplankton abundance and biomass (Kiørboe & Nielsen, 1994; Leandro *et al.*, 2007), and are the main primary consumers and secondary producers in these systems (Chisholm & Roff, 1990a; Miyashita *et al.*, 2009). Because of this dominance, copepods can be used as a model to understand the distribution pattern of secondary production of mesozooplankton assemblages. Most of the available information on copepod production is derived from studies in temperate coastal areas and polar regions, and is usually restricted to the dominant species (Miyashita *et al.*, 2009). In the south-west Atlantic, estimates of zooplankton/copepod biomass and production rates are still incipient, with little available data on growth and production (Ara, 2004; Lopes *et al.*, 2007), mainly for oceanic areas. Few studies have been conducted in estuarine systems and neritic waters or reef areas along the Brazilian coast. On the central coast of Brazil, the influence of nutrients on the diel and seasonal variations in abundance, stage, sex composition, body length, dry weight, chemical composition, biomass and production rate of the planktonic copepods were studied in estuarine systems and on the adjacent inner shelf (Ara, 2001a, b, 2002; Miyashita *et al.*, 2009). These studies showed that the annual copepod biomass and productivity in tropical and subtropical estuaries can be relatively high compared with other estuarine and neritic waters of the world.

The Campos Basin is a petroleum-rich area located off the coast of the state of Rio de Janeiro, Brazil. The local oceanographic dynamics impose specific conditions on the local water mass, i.e. horizontal vortices and vertical movements (upwelling and downwelling) associated with the influence of the winds and the morphology of the deep ocean floor (Stramma *et al.*, 1990). Despite these water movements and the continental influence from the Paraíba do Sul River, which act to enrich the region, Campos Basin waters are oligotrophic. Most of the few studies in this area have examined the composition and abundance of zooplankton species down to the 200-m depth in the region of Cabo Frio (Valentin, 1984; Valentin *et al.*, 1987). Information on the mesopelagic and bathypelagic community is non-existent, except for copepods (Dias *et al.*, 2010).

In this study, we examined the spatial and temporal changes in abundance, biomass, production and assemblage structure of copepods living in the subsurface water between the 25- and 3000-m isobaths in a tropical area in the southwest Atlantic Ocean. We also examined the relationship of the copepod production and assemblage structure with the environmental factors (temperature, salinity, chlorophyll-*a* and suspended particulate matter).

## MATERIALS AND METHODS

### Study area

The Campos Basin is located between 20.5 and 24°S off the central Brazilian coast (Figure 1) and covers an area of approximately 100,000 km². In this region, the continental shelf has a mean width of 100 km, and the shelf break is located between the 80- and 130-m isobaths in the northern and southern portions, respectively. The slope extends over a width of 40 km and has a mean declivity of 2.5°. Its base is shallower at the northern limit (about 1500 m), and deeper near the southern limit (about 2000 m; Viana *et al.*, 1998). The regional climate is warm and humid, with a rainy summer season and a dry winter.

This region is influenced by different water masses with distinct properties (e.g. temperature, salinity and dissolved oxygen) that provide different potential habitats for pelagic species. The upper depth levels, the nutrient-poor subsurface water (Subsurface Water – SS) is registered. Below it, the relatively cold, nutrient-rich South Atlantic Central Water (SACW, 142–567 m depth), with temperatures and salinities below 20°C and 36.4, is recorded.

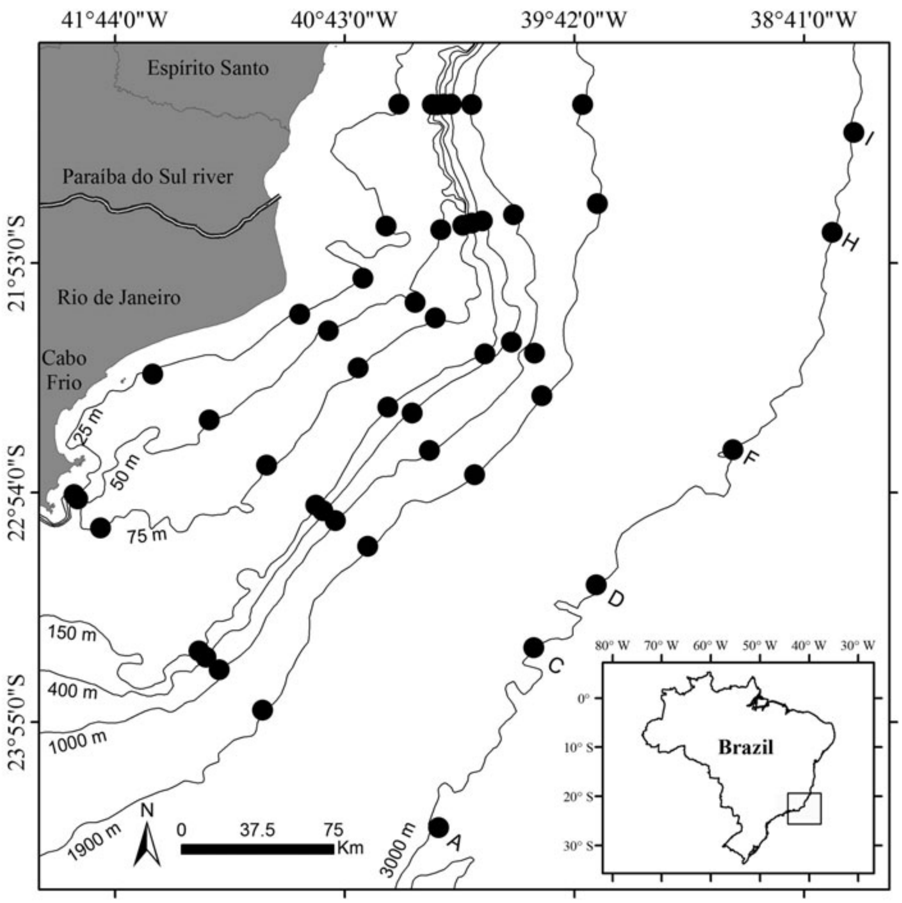


**Fig. 1.** Map of the study area showing the location of sampling stations.

To the south end of the study area, the Cabo Frio region has climatic peculiarities, which have been explained by factors such as the emergence of the SACW on a coast dominated by warm currents (upwelling phenomenon). This phenomenon results in attenuation of precipitation and climate dynamics during the months of January and February (Barbiére, 1975). This upwelling is intermittent and is intensified by strong north-east winds, especially in the spring and summer. Because of the coastal upwelling, the southern area of the Campos Basin has been the focus of most studies, mainly on circulation, nutrients, microplankton and epipelagic mesoplankton (Valentin, 1984; Valentin *et al.*, 1987).

## Sampling method and treatment of samples

The biological material was obtained as part of a project to study the zooplankton and ichthyoplankton of the Habitats Project – Campos Basin Environmental Heterogeneity by CENPES/PETROBRAS. Sampling was carried out during two oceanographic cruises in 2009, one in the rainy season (25 February to 13 April) and the other in the dry season (5 August to 17 September). The stations were distributed along six transects perpendicular to the coast (A, C, D, F, H and I) in the south–north direction. Each transect contained eight sampling stations distributed across the shelf, from the 25- to 3000-m isobaths (25, 50, 75, 150, 400, 1000, 1900 and 3000 m), four on the continental shelf and four on the slope (Figure 1).

Water temperature and salinity at 1 m depth were determined using a Rosette system with a Sea-Bird® Electronics Inc. CTD profiler attached (Bellevue, Washington, USA). Water samples at 1 m depth were collected using a GO–FLO bottle for analysis of suspended particulate matter (SPM) and chlorophyll-*a*.

To estimate the chlorophyll-*a* concentration, 2-L water subsamples were filtered through cellulose membrane filters (Millipore HAWP 0.45 μm) under low vacuum, and stored in liquid nitrogen. The filters were extracted overnight in 90% acetone at 4°C, and analysed with a Turner TD-700 fluorometer (Parsons *et al.*, 1984). For suspended particulate matter (SPM), a 4-L water subsample was filtered through a Whatman GF/F filter pre-combusted at 510°C for 4 h, and weighed to an accuracy of ± 0.0001 g. SPM was obtained from the difference between the initial weight of the sample and the weight after drying at 40°C for 4 days.

To study the abundance, biomass and copepod production, the zooplankton samples were collected by horizontal subsurface hauls (1 m depth). The hauls were made using a *MultiNet*® (Hydro-Bios, 200 μm mesh) fitted with a digital flowmeter attached to the inner net mouth and also an external meter to assess the filtration efficiency (filtered water volume: rainy season range, 61–240 $m^3$ and mean, 133.06 $m^3$; dry season range, 60–280 $m^3$ and mean, 132.26 $m^3$). In the dry season, no samples were collected on the 3000-m isobath of transects H and I, due to logistical problems. A total of 94 samples were analysed, 48 in the rainy season and 46 in the dry season.

The samples were fixed and preserved in 4% buffered formalin. All samples were collected at night, from 18:18 p.m. to 05:08 a.m. during the rainy season and from 17:57 p.m. to 05:46 a.m. during the dry season.

In the laboratory, the preserved samples were divided into fractions between one and ten times with a Folsom Plankton Splitter (Hydro-Bios) (McEwen *et al.*, 1957) to provide subsamples, which were then identified. Taxon abundance per cubic metre and copepod species composition were determined in all samples, according to Bradford-Grieve *et al.* (1999) and Dias & Araujo (2006). The total abundance of each species was estimated from adult and juvenile forms.

## Calculation of biomass and daily copepod production

Immediately after they were identified, the copepods were inspected under a stereomicroscope; about 20 organisms of each taxon were measured using the Image–Pro Plus 6.1 software. When the taxon was rare (<20) in the samples, we measured all individuals present. We estimated the dry mass (DM) of each copepod species from its prosome length, using length–weight equations for marine tropical copepods proposed by Chisholm & Roff (1990b) and Webber & Roff (1995). Taxon-specific equations were used whenever possible. Weights of taxa for which no equations exist were estimated by applying the regression for a taxon with similar body proportions and size range. The general regressions for calanoids were used for the younger forms. For Harpacticoida, in which the prosome and urosome are not clearly discriminated, we used the following allometric equation:

$$CM = 2.65 \times 10^{-6} \times TL^{1.95}$$

where CM is the body carbon mass (μg C $ind^{-1}$) and TL is the total length (μm) (Uye *et al.*, 2002).

The dry mass was calculated as the product of weight multiplied by the number of individuals (ind. $m^{-3}$).

We converted DM of Calanoida to carbon mass, assuming the carbon content of copepods to be 44.7% of DM (Bamstedt, 1986). The carbon content of Cyclopoida was assumed to be 42.5% (James & Wilkinson, 1988) and Poecilostomatoida, 53%. Nishibe & Ikeda (2008) reported carbon contents of Poecilostomatoida of 49–57% of DM, and we used the mean of this range.

We calculated the biomass of the total copepod assemblage from the sum of the carbon mass of the individuals at each sampling station.

We estimated the production rate (Pc, mg C $m^{-3}$ $d^{-1}$) by the following equation:

$$Pc = \sum N \times Wc \times G$$

where N is abundance (ind. $m^{-3}$), Wc is the individual carbon weight (mg C) and G is the individual weight-specific growth rate ($d^{-1}$). Here, G was estimated using the model proposed by Hirst & Sheader (1997), where the growth rate is dependent on carbon weight (Wc) and temperature, expressed as:

$$G = 1.0583^{T} \times Wc^{-0.2962} \times 13.6616^{-1}.$$

According to the authors, this equation may be the most appropriate for estimation of growth and production for suites of organisms when growth-rate data are lacking. The global model without chlorophyll-*a* was chosen because we preferred not to exclude species that are known to be entirely carnivorous (e.g. *Candacia* spp.), feed by piercing and sucking metazoan prey (e.g. *Corycaeus* spp.) or feed on aggregates or macroscopic particles (e.g. *Oncaea* spp.).

Secondary and tertiary production rates were calculated separately on the basis of the feeding habits of each genus. Suspension feeders (e.g. *Acrocalanus*, *Calanoides*, *Calanopia*, *Clausocalanus*, *Ctenocalanus*, *Paracalanus* and *Temora*) and detritivores (e.g. *Corycaeus*, *Oncaea* and *Scolecithrix*) were assigned to secondary production. Carnivores (e.g. *Candacia*, *Euchaeta* and *Heterorhabdus*) were assigned to tertiary production.

## Data analysis

We tested the effect of the region (continental shelf and slope) along each transect (A, C, D, F, H and I) on the copepod biomass and production, using a non-parametric factorial multivariate analysis of variance (np MANOVA). To perform the np MANOVA, the isobaths on each transect were paired according to proximity. In the dry season, due to missing samples for the last isobaths (transects H and I), the data for the previous isobaths were used. The variance analyses (np MANOVA) were performed in the PERMANOVA program.

The relationship between the major species contributing to the daily copepod production (seven species, representing about 50% of the daily copepod production) and the environmental parameters, was determined by Canonical Correspondence Analysis (CCA), using the PC ORDER program. Data on the most-productive copepod species were used, as abundance transformed as log (x + 1). Data for temperature, salinity, chlorophyll-*a* and suspended particulate matter (SPM) were used as environmental parameters. The Monte Carlo test using 999 unrestricted permutations was performed to test the significance of the correlations.

We calculated the Shannon diversity index (H') and richness to evaluate the degree of organization of the copepod assemblage. We used the Analysis of Similarity (ANOSIM) to assess whether the copepod assemblage structure varied according to the sampling region (continental shelf and slope) and the sampling period (rainy and dry season). The SIMPER (similarity of percentages) test was used to identify those species that contributed most to similarities within groups. These analyses were done using the statistical package Primer 5.

# RESULTS

## Hydrography

The water temperature ranged from 24.82 to 28.50 °C during the rainy season and from 19.94 to 24.89 °C during the dry season. Salinity showed low variation in both sampling periods, ranging from 35.44 to 37.28 during the rainy season and from 35.71 to 37.11 during the dry season (Figure 2). Temperature and salinity were lower in the dry season, mainly at stations located in the southern part of the study area, over the continental shelf near Cabo Frio; and in the northern part, under the continental influence of the Paraíba do Sul River. The highest values were found over the slope (mean temperature 27.96 ± 0.56°C during the rainy season and 23.26 ± 0.94°C during the dry season; mean salinity 37.00 ± 0.17 during the rainy season and 36.74 ± 0.7 during the dry season). Over the continental shelf, the mean temperatures were 26.67 ± 1.04°C during the rainy season and 21.66 ± 0.93°C during the dry season, and the mean salinities were 36.45 ± 0.55 during the rainy season and 36.20 ± 0.28 during the dry season.

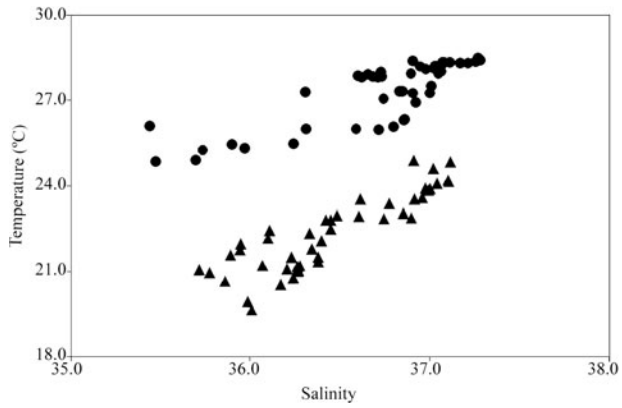


**Fig. 2.** Temperature–salinity diagram of the water masses found in the Campos Basin (Rainy season, circles; Dry season, triangles).

Chlorophyll-*a* concentration reached its lowest levels during the rainy season, ranging from 0.03 to 1.26 μg $L^{-1}$. During the dry season the concentration ranged from 0.06 to 5.93 μg $L^{-1}$. Chlorophyll-*a* concentrations showed a decreasing gradient from coastal to oceanic areas, varying from 0.14 to 1.26 μg $L^{-1}$ and 0.06 to 5.93 μg $L^{-1}$ in the coastal region during the rainy and dry seasons, respectively. In the oceanic area, chlorophyll-*a* varied between 0.33 and 0.79 μg $L^{-1}$ in both periods (Figure 3). The same pattern was recorded for the suspended particulate matter (SPM) concentration, which varied from 0.29 to 3.99 mg $L^{-1}$ during the rainy season and from 0.15 to 6.50 mg $L^{-1}$ during the dry season. The highest values of these parameters were found at stations located in the southern part of the study area, over the continental shelf near Cabo Frio; and in the northern part, under the continental influence of the Paraíba do Sul River during both sampling periods.

## Abundance, biomass, production and assemblage structure of Copepoda

In SS, abundance, biomass and daily copepod production were about three times higher in the dry season than in the rainy season (Table 1; Figures 4–6). In both sampling periods, about 60% of the sampling stations showed low values of daily copepod production (<5 mg C $m^{-3}$ $d^{-1}$).

Copepod abundance, biomass and production decreased toward the offshore region and showed latitudinal variability (between transects; Figures 4–6). The maximum values of these parameters were found at stations located in the southern part of the study area (more than 8000 ind. $m^{-3}$, 15 mg C $m^{-3}$ and 20 mg C $m^{-3}$ $d^{-1}$, respectively) during the rainy season, and in the southern and northern parts (more than 60,000 ind. $m^{-3}$, 100 mg C $m^{-3}$ and 150 mg C $m^{-3}$ $d^{-1}$, respectively) during the dry season (Figures 4–6). Abundance, biomass and daily copepod production showed a longitudinal variation (continental shelf × slope) on all transects during both sampling periods (np MANOVA test, $P < 0.05$), except abundance during the rainy season. In this period, abundance

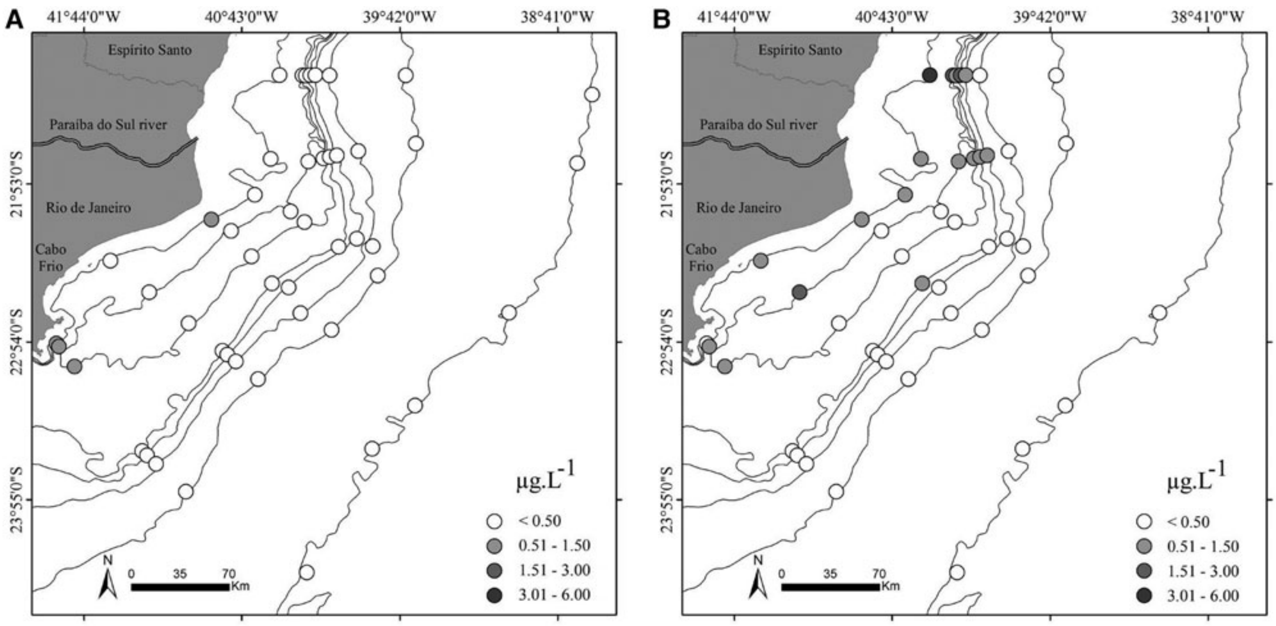


**Fig. 3.** Study area, showing the seasonal variation of chlorophyll-*a* ($\mu g.L^{-1}$). (A) rainy season, (B) dry season.

showed a significant difference only on transect A (in the southern part of the study area near Cabo Frio).

With respect to daily copepod production, secondary production varied from 0.01 to 66.23 $mg\,C\,m^{-3}\,d^{-1}$ (overall mean: 4.56 $\pm$ 12.21 $mg\,C\,m^{-3}\,d^{-1}$), and from 0.01 to 157.64 $mg\,C\,m^{-3}\,d^{-1}$ (overall mean: 14.22 $\pm$ 32.33 $mg\,C\,m^{-3}\,d^{-1}$) during the rainy and dry season, respectively. Secondary production constituted 98.28–98.68% of the entire copepod production for both sampling periods. Copepod tertiary production (carnivores) varied from 0.004 to 3.34 $mg\,C\,m^{-3}\,d^{-1}$ (overall mean: 0.49 $\pm$ 0.89 $mg\,C\,m^{-3}\,d^{-1}$) during the rainy season, and from 0.02 to 5.95 $mg\,C\,m^{-3}\,d^{-1}$ (overall mean: 1.36 $\pm$ 2.15 $mg\,C\,m^{-3}\,d^{-1}$) during the dry season.

One hundred and one copepod taxa were identified during the study period: 73 Calanoida, 4 Cyclopoida, 17 Poecilostomatoida, 6 Harpacticoida and 1 Monstrilloida; 71 of these are widely distributed species. Eight taxa and 35 species were recorded exclusively in the rainy and dry season, respectively (Table 2). Over the continental shelf, 48 species were found, and over the slope, ~40 species. The maximum number of species was found in the dry season over the slope (58 species) and the minimum in the rainy season over the continental shelf (36 species).

The species diversity index (H') showed a similar pattern to the number of species. Species diversity was higher over the slope than over the continental shelf, with a peak in the dry season (rainy season: continental shelf, mean: 2.71, and slope, mean: 2.86; dry season: continental shelf, mean: 2.69, and slope, mean: 3.09).

The contributions of Calanoida, Poecilostomatoida, Cyclopoida and Harpacticoida to total copepod abundance were 80–92%, 18–6%, 0.4–2% and 1–0.3% during the rainy and dry seasons, respectively. Monstrilloida occurred during the rainy season, but their contribution was small (<0.001%). The number of unidentified copepods was also small (<3% of the entire copepod assemblage).

The most numerous copepods were the calanoids *Paracalanus quasimodo* Bowman, 1971, *Clausocalanus furcatus* (Brady, 1883), *Ctenocalanus citer* Heron & Bowman, 1971, *Temora turbinata* (Dana, 1849), *Temora stylifera* Dana, 1849, *Calanopia americana* F. Dahl, 1894, *Calanoides carinatus* (Krøyer, 1849), *Oncaea venusta* Philippi, 1843 and *Farranula gracilis* (Dana, 1849) (Table 2). *Paracalanus quasimodo*, *T. turbinata*, *C. furcatus* and *F. gracilis* (52%) were the most abundant taxa during the rainy season, and *P. quasimodo*, Clausocalanidae, *C. furcatus* and Paracalanidae (48%) during the dry season (Figure 7).

Biomass and copepod production of the four copepod orders followed the same pattern as abundance; Calanoida was the dominant order (92–96% and 88–95% of the total copepod biomass and production, respectively). The contribution of Poecilostomatoida was 8–3% and 12–5%, Cyclopoida was 0.1–0.3% and 0.2–0.6%, and Harpacticoida was 0.2–0.1% and 0.4–0.1%, for copepod biomass and production during the rainy and dry seasons, respectively (Figure 7).

**Table 1.** Variations of biotic variables during the rainy and dry seasons in the study area.

| Biotic variables | Rainy season | | | Dry season | | |
|---|---|---|---|---|---|---|
| | Min | Max | Mean/SD | Min | Max | Mean/SD |
| Density ($m^{-3}$) | 41.68 | 22,945.19 | 2357.18 $\pm$ 3648.31 | 60.03 | 64,752.94 | 10,518.75 $\pm$ 19085.01 |
| Biomass ($mg\,C\,m^{-3}$) | 0.08 | 26.98 | 4.44 $\pm$ 4.93 | 0.09 | 112.88 | 18.1 $\pm$ 32.07 |
| Daily production ($mg\,C\,m^{-3}\,d^{-1}$) | 0.17 | 58.16 | 8.31 $\pm$ 9.79 | 0.17 | 163.2 | 26.94 $\pm$ 46.90 |

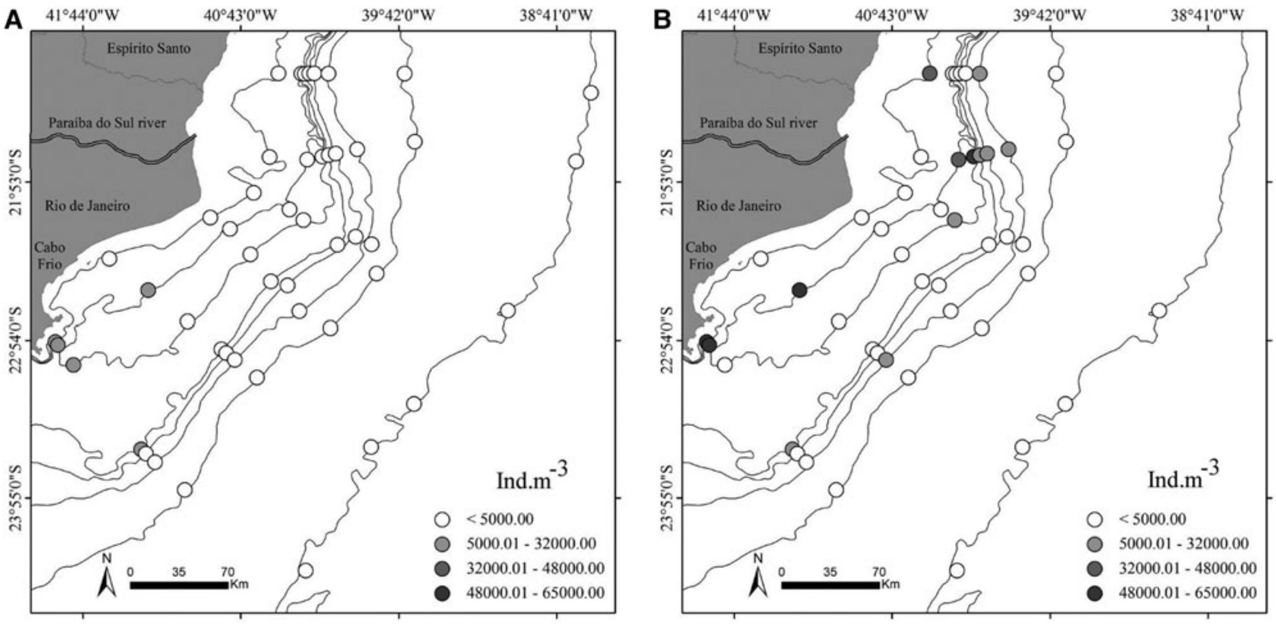


**Fig. 4.** Study area, showing the seasonal variation of copepod abundance (ind. $m^{-3}$). (A) rainy season, (B) dry season.

In terms of copepod biomass and production, the dominant taxa were *C. carinatus*, *T. stylifera*, *P. quasimodo*, *C. furcatus*, *Undinula vulgaris* (Dana, 1849) and *C. americana* (Table 2). The percentage contributions of the different taxa to the total biomass and copepod production varied between seasons. The main contributors to biomass and copepod production during the rainy period were Temoridae (*T. turbinata* and *T. stylifera*), *U. vulgaris* and *P. quasimodo* (biomass ~60% and copepod production ~55%). During the dry period, the main contributors included Clausocalanidae, *C. carinatus*, Temoridae (*T. turbinata* and *T. stylifera*), Paracalanidae, Subeucalanidae and *C. americana* (biomass and copepod production ~70%).

During the study period, the copepod assemblage comprised mainly small individuals: on average, individuals <1000 μm in total prosome length contributed 94% (93.6–94.1%, rainy and dry season, respectively) of the total copepod abundance. The contribution of individuals <1000 μm to total copepod abundance was higher than to biomass (63.8–71.3%) and copepod production (75.21–80.89%).

ANOSIM analyses demonstrated that the distribution patterns of copepod communities could be separated into four significantly different groups (Table 3). Each group was well separated from the others in relation to the sampling season and the longitudinal variation: rainy season–continental

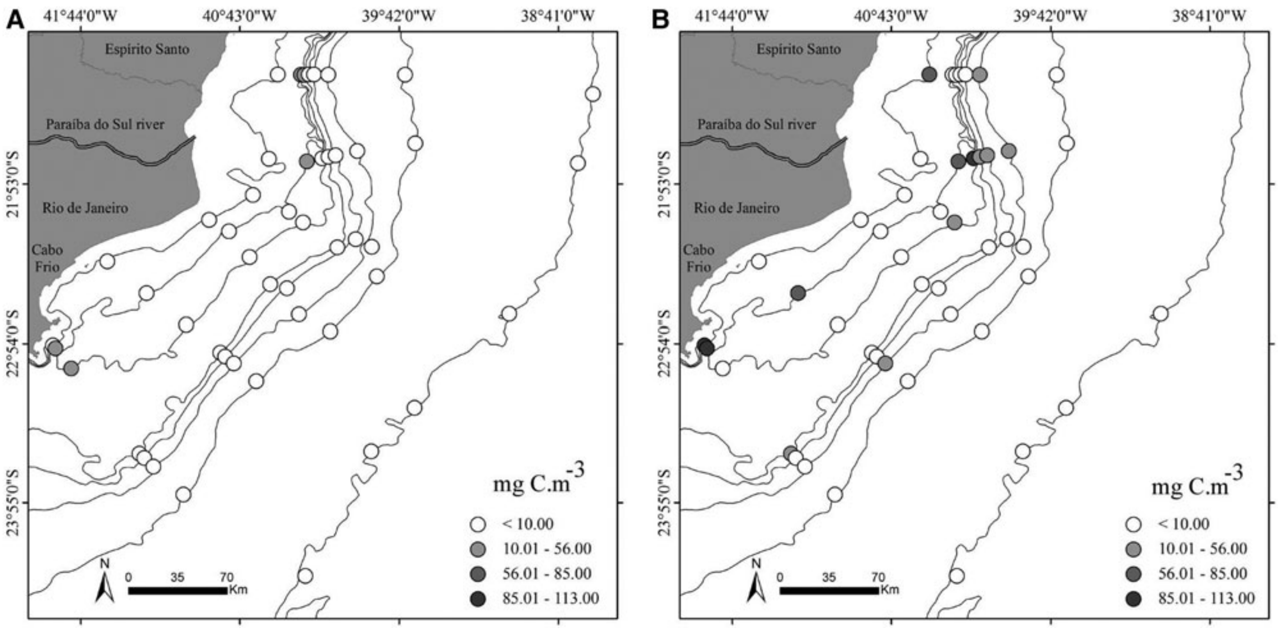


**Fig. 5.** Study area, showing the seasonal variation of copepod biomass (mg C $m^{-3}$). (A) rainy season, (B) dry season.

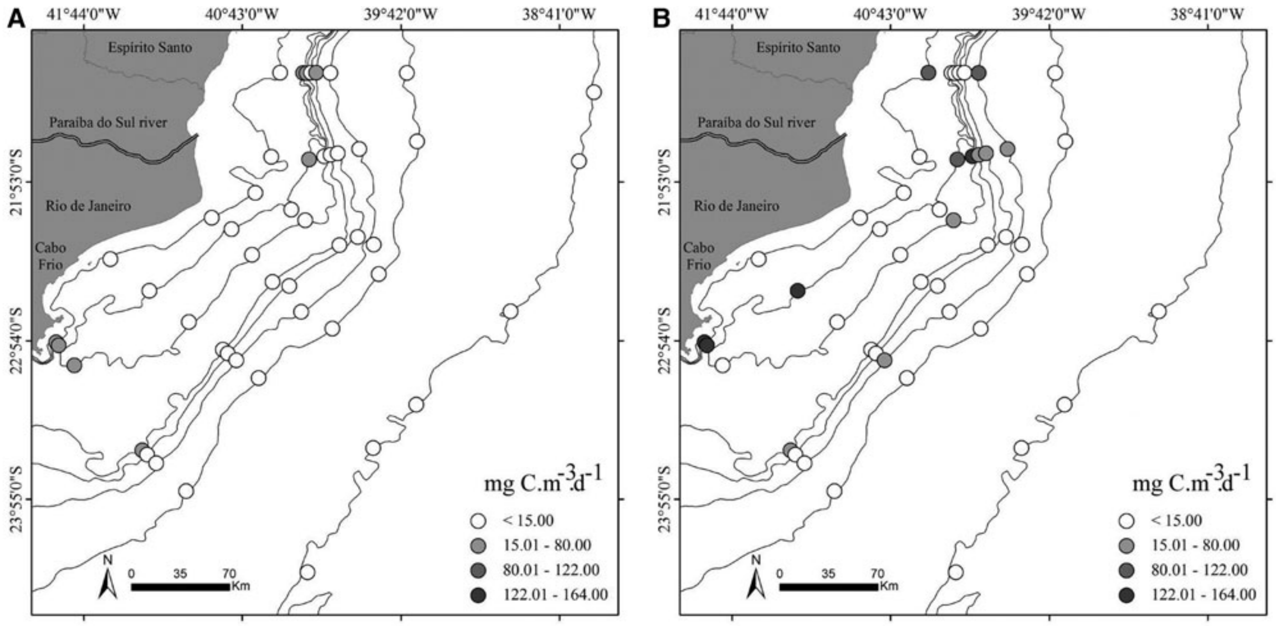


**Fig. 6.** Study area, showing the seasonal variation of the daily copepod production (mg C $m^{-3}$ $d^{-1}$). (A) rainy season, (B) dry season.

shelf (1), dry season–continental shelf (2), rainy season–slope (3) and dry season–slope (4). Epipelagic–mesopelagic species contributed, mostly, to the similarity of the groups (SIMPER test, Table 4). *Clausocalanus furcatus*, *T. stylifera*, *O. venusta* and *Corycaeus* (*Onychocorycaeus*) *giesbrechti* F. Dahl, 1894 were important in all copepod assemblages. *Nannocalanus minor* (Claus, 1863) and *U. vulgaris* were important in all groups except the continental-shelf group during the dry season, when *C. carinatus* and *C. citer* were important in this area.

## Association of assemblage structure with environmental parameters

Temperature, salinity, chlorophyll-*a* and SPM explained 45% of the variance of the distribution of the seven copepod species that showed the highest daily production (axis 1 = 28%, axis 2 = 11%, axis 3 = 6%). The Monte Carlo test showed that the environmental parameters analysed were correlated with the daily copepod production data. The daily production of *C. americana*, *P. quasimodo* and *T. turbinata* was positively correlated with the highest chlorophyll-*a* and SPM values. *Calanoides carinatus* was inversely correlated with temperature (Figure 8), while the daily production of *T. stylifera* and, mainly, *U. vulgaris* was correlated with the highest temperature and salinity. *Clausocalanus furcatus* showed a positive correlation with salinity, and inverse correlations with the other parameters (Figure 8).

## DISCUSSION

Coastal and oceanic epipelagic species of copepods, typical of the tropical and subtropical southwest Atlantic, were identified in the sampling area. The oceanic copepod assemblage was low in abundance but showed high species diversity. The species richness observed in this study was higher than that found off the central coast of Brazil, in the region of the Vitória–Trindade chain, off the north-eastern Brazil coast and over the continental shelf of northern and north-eastern Brazil, where species richness did not exceed 70 species (Dias, 1994, 1996; Gusmão *et al.*, 1997; Lopes *et al.*, 1999; Cavalcanti & de Larrazabal, 2004; Dias *et al.*, 2010). However, caution is needed in comparing richness in different environments, because the heterogeneity of environments, the sampling effort and the gear used should be considered.

The species *Paracalanus quasimodo*, *Clausocalanus furcatus*, *Temora turbinata* and *Farranula gracilis* can be considered resident populations in the subsurface layer in the study area, where the shelf and oceanic regions are affected by the presence of warm waters. A similar species composition has frequently been observed at the same site (e.g. Lopes *et al.*, 1999; Dias *et al.*, 2010), in other oceanic regions along the coast of Brazil (e.g. Dias, 1996; Cavalcanti & Larrazábal, 2004; Lopes *et al.*, 2006) and in tropical regions elsewhere (Chisholm & Roff, 1990a, b; Webber & Roff, 1995).

Clausocalanidae, Paracalanidae, Calanidae and Temoridae were the most important families in terms of abundance, biomass and daily copepod production. These copepod families are highly adapted to oligotrophic conditions, and can exploit other forms of food besides phytoplankton (Miyashita *et al.*, 2009). They can affect the microbial food webs, serving as a link between the micro- and nanozooplankton, and the larger zooplankton and fish larvae (Sommer & Stibor, 2002). These copepods were proportionally more important in the rainy season, when conditions were apparently more oligotrophic than in the dry season.

*Clausocalanus furcatus* comprised 51% of the members of this genus, with a peak of abundance in the dry season; the population increased gradually to the 1300 m isobath, and then decreased sharply toward the 1900 and 3000 m isobaths. *Clausocalanus furcatus* is a warm-water species and its distribution is typically superficial, above the thermocline

**Table 2.** List of copepod taxa from the study area, with the values for density (ind. $m^{-3}$), biomass (mg C $m^{-3}$), daily copepod production (mg C $m^{-3}$ $d^{-1}$) and length–weight regressions applied for biomass calculation of different copepod taxa. Blank cell: biomass and production were not calculated.

| Species | Rainy season | | | Dry season | | | Regression | Authors |
|---|---|---|---|---|---|---|---|---|
| | Density (Ind $m^{-3}$) | Biomass (mg C $m^{-3}$) | Production (mg C $m^{-3}$ $d^{-1}$) | Density (Ind $m^{-3}$) | Biomass (mg C $m^{-3}$) | Production (mg C $m^{-3}$ $d^{-1}$) | | |
| Calanoida | 4068.9 | 4.92 | 6 | 72,344.09 | 87.55 | 157.64 | In W = 2.74 ln L – 16.41 | Chisholm & Roff (1990a, b) |
| *Acartia danae* | 91.27 | 0.16 | 0.31 | 1.2 | 0.002 | 0.001 | In W = 3.09 ln L – 19.19 | Chisholm & Roff (1990a, b) |
| *Acartia lilljeborgi* | 0 | 0 | 0 | 743.92 | 0.61 | 1.22 | In W = 3.09 ln L – 19.19 | Chisholm & Roff (1990a, b) |
| *Acartia longiremis* | 0 | 0 | 0 | 4.79 | 0.004 | 0.01 | In W = 3.09 ln L – 19.19 | Chisholm & Roff (1990a, b) |
| *Acartia* spp. | 5.57 | 0.01 | 0.02 | 0 | 0 | 0 | In W = 3.09 ln L – 19.19 | Chisholm & Roff (1990a, b) |
| *Euaugaptilus* sp. | 1.92 | 0.002 | 0.001 | 0 | 0 | 0 | In W = 4.27 In L – 29.00 | Webber & Roff (1995) |
| *Haloptilus longicornis* | 0 | 0 | 0 | 5.64 | 0.01 | 0.02 | In W = 4.27 In L – 29.00 | Webber & Roff (1995) |
| Calanidae | 740.24 | 1.66 | 3.51 | 13,928.85 | 31.24 | 46.69 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Calanoides carinatus* | 21.37 | 0.26 | 0.34 | 11,368.04 | 136.4 | 123.8 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Nannocalanus minor* | 1460.61 | 7.16 | 12.24 | 1442.21 | 7.07 | 9.15 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Neocalanus gracilis* | 0 | 0 | 0 | 9.83 | 0.59 | 0.38 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Neocalanus robustior* | 0 | 0 | 0 | 11.51 | 0.4 | 0.29 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Undinula vulgaris* | 4548.43 | 49.28 | 66.23 | 1738.25 | 18.83 | 19.38 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Candacia bipinnata* | 49.61 | 0.87 | 0.99 | 395.36 | 6.91 | 5.11 | In W = 3.38 ln L – 20.48 | Webber & Roff (1995) |
| *Candacia ethiopica* | 0 | 0 | 0 | 6.56 | 0.14 | 0.12 | In W = 3.38 ln L – 20.48 | Webber & Roff (1995) |
| *Candacia pachydactyla* | 142.32 | 3.03 | 3.34 | 49.66 | 1.06 | 0.89 | In W = 3.38 ln L – 20.48 | Webber & Roff (1995) |
| *Candacia simplex* | 11.11 | 0.1 | 0.13 | 0 | 0 | 0 | In W = 3.38 ln L – 20.48 | Webber & Roff (1995) |
| *Candacia* spp. | 179.29 | 0.21 | 0.53 | 2714.16 | 3.18 | 5.95 | In W = 3.38 ln L – 20.48 | Webber & Roff (1995) |
| Centropagidae | 62.44 | 0.1 | 0.21 | 4.79 | 0.01 | 0.01 | In W = 3.68 ln L – 22.86 | Chisholm & Roff (1990a, b) |
| *Centropages furcatus* | 455.18 | 0.46 | 1.07 | 6254.79 | 6.28 | 12.86 | In W = 3.68 ln L – 22.86 | Chisholm & Roff (1990a, b) |
| *Centropages violaceus* | 27.91 | 0.37 | 0.48 | 7.26 | 0.1 | 0.09 | In W = 3.68 ln L – 22.86 | Chisholm & Roff (1990a, b) |
| Clausocalanidae | 6153.33 | 6.67 | 16.69 | 55,586.98 | 60.21 | 113.54 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Clausocalanus arcuicornis* | 0 | 0 | 0 | 605.69 | 1.19 | 2.24 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Clausocalanus brevipes* | 0 | 0 | 0 | 5.31 | 0.02 | 0.03 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Clausocalanus furcatus* | 10,714.94 | 11.35 | 28.99 | 53,657.33 | 56.86 | 112.72 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Ctenocalanus citer* | 0 | 0 | 0 | 10,456.55 | 19.28 | 29.54 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Ctenocalanus vanus* | 0 | 0 | 0 | 164.17 | 0.77 | 0.97 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| Eucalanidae | 0 | 0 | 0 | 33.88 | 0.01 | 0.03 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| Subeucalanidae | 266.67 | 1.33 | 1.92 | 9346.55 | 46.79 | 54.58 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Subeucalanus crassus* | 0 | 0 | 0 | 169.48 | 4.23 | 3.76 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Subeucalanus pileatus* | 0 | 0 | 0 | 9758.95 | 35.82 | 45.80 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Euchaetidae* | 11.11 | 0.06 | 0.1 | 434.85 | 2.53 | 3.16 | In W = 3.00 In L – 17.82 | Webber & Roff (1995) |
| *Euchaeta marina* | 19.98 | 0.77 | 0.73 | 6.63 | 0.26 | 0.18 | In W = 3.00 In L – 17.82 | Webber & Roff (1995) |
| *Heterorhabdus papilliger* | 8.47 | 0.21 | 0.21 | 0 | 0 | 0 | In W = 3.68 ln L – 22.86 | Chisholm & Roff (1990a, b) |
| *Heterorhabdus spinifrons* | 45.41 | 0.68 | 0.82 | 61.61 | 0.92 | 0.9 | In W = 3.68 ln L – 22.86 | Chisholm & Roff (1990a, b) |
| *Heterorhabdus* spp. | 0 | 0 | 0 | 8.21 | 0.01 | 0.02 | In W = 3.68 ln L – 22.86 | Chisholm & Roff (1990a, b) |
| *Lucicutia flavicornis* | 69.49 | 0.06 | 0.17 | 1352.15 | 1.12 | 2.52 | In W = 3.68 ln L – 22.86 | Chisholm & Roff (1990a, b) |
| *Lucicutia* spp. | 16.23 | 0.01 | 0.03 | 947.13 | 0.53 | 1.45 | In W = 3.68 ln L – 22.86 | Chisholm & Roff (1990a, b) |
| *Pleuromamma abdominalis* | 5.65 | 0.08 | 0.09 | 333.48 | 4.48 | 4.81 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Pleuromamma gracilis* | 0 | 0 | 0 | 916.78 | 2.86 | 3.88 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Pleuromamma piseki* | 11.96 | 0.03 | 0.06 | 364.04 | 0.94 | 1.55 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |

| | | | | | | | | |
|---|---|---|---|---|---|---|---|---|
| *Pleuromamma xiphias* | 0 | 0 | 0 | 6.21 | 0.48 | 0.28 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Pleuromamma* spp. | 18.46 | 0.02 | 0.06 | 508.54 | 0.67 | 1.41 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| Paracalanidae | 6344.01 | 2.76 | 8.66 | 49,913.58 | 21.73 | 50.94 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Acrocalanus* spp. | 0 | 0 | 0 | 3.56 | 0.01 | 0.01 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Acrocalanus gracilis* | 0 | 0 | 0 | 3.66 | 0.01 | 0.01 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Acrocalanus longicornis* | 2725.94 | 4.13 | 9.86 | 2588.92 | 3.92 | 7.14 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Calocalanus contractus* | 0 | 0 | 0 | 83.22 | 0.14 | 0.24 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Calocalanus pavo* | 611.28 | 0.34 | 1.1 | 17.38 | 0.01 | 0.03 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Calocalanus pavoninus* | 1336.59 | 1.47 | 3.85 | 1183.15 | 1.3 | 2.53 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Calocalanus* spp. | 749.45 | 0.56 | 1.66 | 21.68 | 0.02 | 0.04 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Mecynocera clausi* | 4.77 | 0.01 | 0.03 | 81.68 | 0.2 | 0.33 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Paracalanus aculeatus* | 1493.86 | 2.48 | 5.37 | 827.29 | 1.37 | 2.42 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Paracalanus parvus* | 989.92 | 1.77 | 3.69 | 2330.83 | 4.16 | 6.67 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Paracalanus quasimodo* | 25,541.98 | 20.48 | 52.36 | 71,422.3 | 57.28 | 114.29 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| Phaennidae | 0 | 0 | 0 | 3.46 | 0.03 | 0.04 | In W = 3.57 In L – 21.36 | Webber & Roff (1995) |
| Pontellidae | 16.32 | 0.01 | 0.03 | 501.96 | 0.31 | 0.66 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Calanopia americana* | 38.32 | 0.13 | 0.22 | 17,949.4 | 60.46 | 78.82 | In W = 2.67 ln L – 15.47 | Chisholm & Roff (1990a, b) |
| *Labidocera acutifrons* | 75.05 | 8.45 | 5.73 | 0 | 0 | 0 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Labidocera* spp. | 73.59 | 1.07 | 1.22 | 0 | 0 | 0 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Pontellina plumata* | 0 | 0 | 0 | 6.84 | 0.02 | 0.03 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| *Pontellopsis villosa* | 0.15 | 0.01 | 0.005 | 0 | 0 | 0 | In W = 3.65 ln L – 22.89 | Chisholm & Roff (1990a, b) |
| Rhincalanidae | 0 | 0 | 0 | 533.33 | 1.13 | 1.65 | In W = 4.27 In L – 29.00 | Webber & Roff (1995) |
| *Rhincalanus cornutus* | 32.6 | 0.11 | 0.21 | 2175.59 | 7.23 | 10.43 | In W = 4.27 In L – 29.00 | Webber & Roff (1995) |
| Scolecitrichidae | 114.55 | 0.32 | 0.65 | 1105.14 | 3.11 | 4.61 | In W = 3.57 In L – 21.36 | Webber & Roff (1995) |
| *Lophothrix frontalis* | 0 | 0 | 0 | 5.87 | 0.74 | 0.33 | In W = 3.57 In L – 21.36 | Webber & Roff (1995) |
| *Scolecithrix danae* | 218.57 | 3.42 | 4.17 | 15.39 | 0.24 | 0.23 | In W = 3.57 In L – 21.36 | Webber & Roff (1995) |
| *Scolecithricella minor* | 0 | 0 | 0 | 125.63 | 0.34 | 0.5 | In W = 3.57 In L – 21.36 | Webber & Roff (1995) |
| *Scolecithricella tenuiserrata* | 0 | 0 | 0 | 39.08 | 0.53 | 0.51 | In W = 3.57 In L – 21.36 | Webber & Roff (1995) |
| Spinocalanidae | 0 | 0 | 0 | 957.54 | 4.24 | 4.98 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Spinocalanus* sp. | 0 | 0 | 0 | 9.39 | 0.03 | 0.04 | In W = 2.78 In L – 16.52 | Webber & Roff (1995) |
| *Temora turbinata* | 12,374.36 | 22.46 | 44.21 | 12,280.55 | 22.29 | 35.52 | In W = 3.34 ln L – 19.59 | Chisholm & Roff (1990a, b) |
| *Temora stylifera* | 6643.03 | 35.22 | 54.56 | 13,254.73 | 70.28 | 85.99 | In W = 3.34 ln L – 19.59 | Chisholm & Roff (1990a, b) |
| *Oithona plumifera* | 166.01 | 0.07 | 0.24 | 4490.03 | 1.87 | 4.55 | In W = 1.68 ln L – 10.20 | Webber & Roff (1995) |
| *Oithona setigera* | 0 | 0 | 0 | 1051.62 | 0.44 | 1.08 | In W = 1.68 ln L – 10.20 | Webber & Roff (1995) |
| *Oithona similis* | 297.45 | 0.08 | 0.32 | 1535.11 | 0.41 | 1.18 | ln W = 1.10 ln L – 7.07 | Chisholm & Roff (1990a, b) |
| *Oithona* spp. | 24.52 | 0.004 | 0.02 | 439.37 | 0.08 | 0.23 | ln W = 1.10 ln L – 7.07 | Chisholm & Roff (1990a, b) |
| Corycaeidae | 1560.48 | 0.79 | 2.47 | 2287.89 | 1.16 | 2.92 | ln W = 1.70 ln L – 9.92 | Chisholm & Roff (1990a, b) |
| *Corycaeus flaccus* | 0 | 0 | 0 | 12.14 | 0.02 | 0.04 | ln W = 1.70 ln L – 9.92 | Chisholm & Roff (1990a, b) |
| *Corycaeus giesbrechti* | 2732.12 | 1.91 | 5.32 | 7175.28 | 5.03 | 11.15 | ln W = 1.70 ln L – 9.92 | Chisholm & Roff (1990a, b) |
| *Corycaeus lautus* | 84.01 | 0.25 | 0.49 | 26.95 | 0.08 | 0.12 | ln W = 1.70 ln L – 9.92 | Chisholm & Roff (1990a, b) |
| *Corycaeus limbatus* | 132.3 | 0.09 | 0.28 | 121.02 | 0.08 | 0.19 | ln W = 1.70 ln L – 9.92 | Chisholm & Roff (1990a, b) |
| *Corycaeus speciosus* | 444.54 | 0.8 | 1.82 | 99.92 | 0.18 | 0.32 | ln W = 1.70 ln L – 9.92 | Chisholm & Roff (1990a, b) |
| *Corycaeus typicus* | 0 | 0 | 0 | 14.7 | 0.03 | 0.05 | ln W = 1.70 ln L – 9.92 | Chisholm & Roff (1990a, b) |
| *Farranula gracilis* | 10,655.84 | 7.83 | 22.88 | 2848.15 | 2.09 | 4.79 | In W = 2.72 In L – 16.19 | Webber & Roff (1995) |
| *Lubbockia squillimana* | 0 | 0 | 0 | 153.34 | 0.52 | 0.82 | In W = 2.10 In L – 11.63 | Webber & Roff (1995) |
| *Lubbockia* spp. | 0 | 0 | 0 | 10.61 | 0.04 | 0.05 | In W = 2.10 In L – 11.63 | Webber & Roff (1995) |

*Continued*

Table 2. Continued

| Species | Rainy season Density (Ind m$^{-3}$) | Biomass (mg C m$^{-3}$) | Production (mg C m$^{-3}$ d$^{-1}$) | Dry season Density (Ind m$^{-3}$) | Biomass (mg C m$^{-3}$) | Production (mg C m$^{-3}$ d$^{-1}$) | Regression | Authors |
|---|---|---|---|---|---|---|---|---|
| Oncaeidae | 174.29 | 0.15 | 0.43 | 1280.72 | 1.12 | 2.21 | $\ln W = 2.10 \ln L - 11.63$ | Webber & Roff (1995) |
| *Oncaea media* | 719.67 | 0.69 | 1.84 | 1819.98 | 1.75 | 3.42 | $\ln W = 2.10 \ln L - 11.63$ | Webber & Roff (1995) |
| *Oncaea venusta* | 3457.21 | 4.47 | 11.14 | 10615.75 | 13.71 | 25.29 | $\ln W = 2.10 \ln L - 11.63$ | Webber & Roff (1995) |
| *Oncaea* spp. | 70.08 | 0.06 | 0.18 | 5.31 | 0 | 0.01 | $\ln W = 2.10 \ln L - 11.63$ | Webber & Roff (1995) |
| *Triconia conifera* | 222.03 | 0.3 | 0.76 | 1624.24 | 2.17 | 4.09 | $\ln W = 2.10 \ln L - 11.63$ | Webber & Roff (1995) |
| *Copilia mirabilis* | 32.64 | | | 10.77 | | | | |
| *Sapphirina nigromaculata* | 86.55 | | | 15.28 | | | | |
| *Euterpina acutifrons* | 0 | 0 | 0 | 487.62 | 0.1 | 0.31 | | |
| *Macrosetella gracilis* | 1171.8 | 0.44 | 1.64 | 261.14 | 0.1 | 0.28 | | |
| *Microsetella rosea* | 0 | 0 | 0 | 5.82 | 0.001 | 0.003 | | |
| *Clytemnestra scutellata* | 6.78 | 0.002 | 0.01 | 499.51 | 0.12 | 0.33 | | |
| *Clytemnestra* sp. | 0 | 0 | 0 | 6.21 | 0.002 | 0.01 | | |
| *Miracia efferata* | 2.41 | 0.004 | 0.01 | 0 | 0 | 0 | | |
| Monstrilloida | 0.01 | | | 0.01 | | | | |
| Damage | 2511.8 | | | 13767.41 | | | | |

(Paffenhöfer & Mazzocchi, 2003), in the surface layers of the CW + TW. Previous studies have reported that *C. furcatus* occurs predominantly in the TW (Lopes *et al.*, 1999).

In the south-west Atlantic, *Paracalanus* is one of the most important genera in the neritic region off the Brazilian coast. They are common copepods off this coast, as has been reported by Valentin & Monteiro-Ribas (1993), Dias (1996), Vega-Pérez & Hernandez (1997), Lopes *et al.* (1999), |Neumann-Leitão *et al.* (1999, 2008), Dias *et al.* (2010) and Miyashita *et al.* (2009). In the present study, *P. quasimodo* was the dominant and most frequent species. Their mean densities remained high out to the 75-m isobath, and decreased from the 350- to the 3000-m isobaths. *Paracalanus quasimodo* has been cited as the most abundant copepod species associated with coastal, neritic and shelf waters of tropical regions (Campaner, 1985; Vega-Pérez & Hernandez, 1997; Lopes *et al.*, 1999; Araujo, 2006).

One of the most characteristic aspects of the copepod assemblage structure in this area was the size composition: small individuals (<1000 μm in prosome length) accounted for much of the total copepod abundance, biomass and copepod production. This pattern has been observed not only in tropical and subtropical regions (Hopcroft *et al.*, 1998; Ara, 2004), but also in high-latitude regions (Hopcroft *et al.*, 2001). Off south-eastern Brazil (Ara, 2004) and in Kingston Harbor, Jamaica (Hopcroft *et al.*, 1998), individuals <450 μm (including nauplii) contributed over 55% of the total copepod biomass and production. In oligotrophic waters, the dominance of small copepods is explained by their greater efficiency than larger species in capturing pico- and nanoplankton. The dominance of small planktonic marine copepods is due to their feeding ecology and aspects of their reproductive biology which allow sufficient reproductive success to counter predation losses (Turner, 2004).

The daily production of the dominant species was the highest over the continental shelf, with the exception of *Undinula vulgaris*. The same pattern was observed for copepod abundance and biomass. The highest levels of these parameters occurred in the southern part of the area, near the Cabo Frio region; and in the north, in the area of continental influence from the Paraíba do Sul River plume during the dry season. In this period, biomass and production were more than three times higher than in the rainy season. The high levels of copepod abundance, biomass and production in the area off the Paraíba do Sul River were associated with the potential area of influence of its plume on the inner continental shelf. This area forms a cone that extends north and south from the mouth and reaches out to the 50-m isobath (Souza *et al.*, 2010). In the Cabo Frio region, the high values found in the southern part of the study area can be attributed to the influence of an upwelling event that occurred before the sampling period. Upwelling is an important fertilizing mechanism in this region, and could have positively influenced copepod productivity. Although water temperatures were lower during the dry season, we did not observe an SACW intrusion over the continental shelf during the sampling period. The presence of *Ctenocalanus citer* and *Calanoides carinatus* in the continental-shelf assemblage during the dry season supports this scenario. *Ctenocalanus citer* is found in coastal and oceanic cold waters and upwelling areas in subtropical regions (Dias & Araujo, 2006). *Calanoides carinatus* is widespread in the tropical neritic zones of the Atlantic, Pacific and Indian oceans and in the western

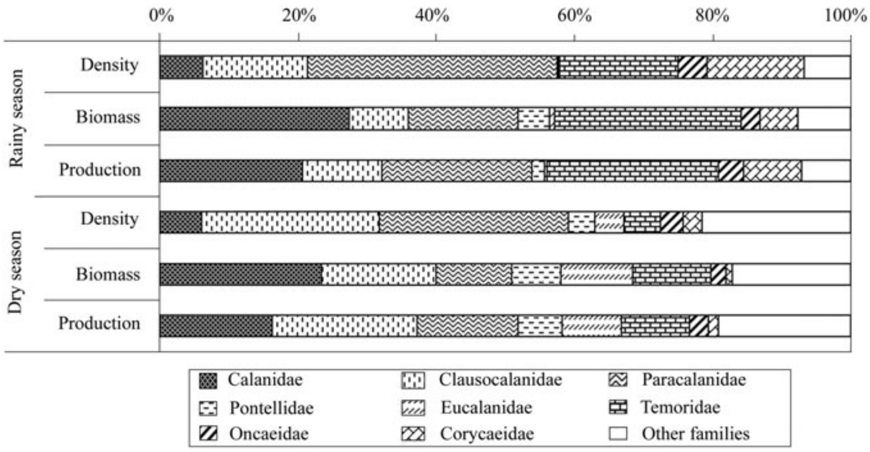


**Fig. 7.** Composition of copepod families in relation to abundance (ind. $m^{-3}$), biomass (mg C $m^{-3}$) and daily copepod production (mg C $m^{-3}$ $d^{-1}$) for the rainy and dry seasons.

Mediterranean. It is considered an indicator of subtropical-water upwelling off Brazil, and has been studied in upwelling areas off western Africa (Campaner & Honda, 1987 and references therein; Avila *et al.*, 2009). This species was among those responsible for the higher copepod production observed during the dry season.

Production can be defined as the amount of tissue or biomass generated in a certain area within a period of time, and is expressed as mg C $m^{-3}$ $d^{-1}$ (Rigler & Downing, 1984). The methodology employed to determine the animal growth rate is the major problem in estimating production. In general terms, the degrees of influence of temperature, food deprivation and size of organisms are used as factors affecting the growth rate (Avila *et al.*, 2012). Here, because we used the entire copepod assemblage, including carnivores, we preferred to use a global model with temperature. Differences in estimated production levels using different standardized mathematical methods to estimate the zooplankton growth rate (G) have been reported elsewhere. Ara (2001a), in his study of a Brazilian estuarine system, using three models with few easily measurable parameters (temperature, individual weight and abundance), estimated significantly higher production values using the Ikeda-Motoda and Huntley-Lopez models than with the Hirst-Sheader model. Ara (2001a) suggested that the first two models may have overestimated the production rates. This possibility was also pointed out by Hirst & Sheader (1997), Leandro *et al.* (2007) and Miyashita *et al.* (2009). Therefore, differences among the estimation capacity of the mathematical models can be expected. The mathematical model employed in the present study is a reliable tool to estimate production, since this model includes ecologically important parameters such as biomass and growth rate, which have been studied for longer periods.

**Table 3.** ANOSIM analyses of similarity between sampling groups in the Campos Basin.

| Sampling groups | R statistic |
|---|---|
| Rainy season/shelf – rainy season/Slope | 0.18 |
| Rainy season/shelf – dry season/Shelf | 0.31 |
| Rainy season/slope – dry season/Slope | 0.30 |
| Dry season/shelf – dry season/Slope | 0.24 |

R, strength of the difference between groups (significant differences to $P<0.05$).

No previous study has evaluated the biomass and production of the copepod assemblage in the oceanic region of the south-west Atlantic or in any other oceanic region along the Brazilian coast. In studies of biomass and secondary production in estuarine systems and neritic waters off the north-eastern (Neumann-Leitão, 2010) and central Brazilian coasts (Ara, 2004; de Melo Junior, 2009), the production ranged from 1.13 to 17 mg C $m^{-3}$ $d^{-1}$. It is generally expected that tropical oceanic areas will support a lower rate of secondary production than tropical neritic waters, because of the low food level and the dominance of small-sized phytoplankton, which are not directly available to copepods, in tropical oceanic areas (Miyashita *et al.*, 2009).

Copepod biomass and production in tropical and subtropical waters have historically been believed to be lower than in temperate waters (e.g. Raymont, 1983). Although there are many reports on seasonal variation in biomass and/or production of planktonic copepods in temperate coastal waters, it is difficult to strictly compare the values for biomass and production obtained in the present study with other reports. This difficulty is due to differences in the characteristics of the animals targeted (size, species, developmental stage), collection methods (frequency, mesh size, type of net tows, etc.), techniques, times, frequencies and estimation (calculation) of biomass and production, and units for expressing the values. Nonetheless, the biomass and production rates (means: 4.44 mg C $m^{-3}$ and 8.31 mg C $m^{-3}$ $d^{-1}$, respectively, during the rainy season; and 18.10 mg C $m^{-3}$ and 26.94 mg C $m^{-3}$ $d^{-1}$, respectively, during the dry season) obtained in the present study were similar to or higher than those in other highly productive waters in temperate regions. For instance, in the western Seto Inland Sea of Japan, the maximum biomass was 44.6 mg C $m^{-3}$ and the mean production rate was 5.28 mg C $m^{-3}$ $d^{-1}$; Koga, 1986); and in Osaka Bay, Japan, the biomass ranged from 9.5 to 11.10 mg C $m^{-3}$ and copepod production ranged from 0.98 to 4.48 mg C $m^{-3}$ $d^{-1}$ (Joh & Uno, 1983). Ara & Hiromi (2007), off the central coast of Japan, found biomass levels ranging from 0.95 to 81.50 mg C $m^{-3}$ (mean = 8.85 mg C $m^{-3}$) and copepod production rates ranging from 0.097 to

**Table 4.** Species contribution (%) to the community similarity during the rainy and dry seasons, over the continental shelf and slope in the study area (SIMPER).

| Continental shelf/rainy season species | % | Slope/rainy season species | % |
|---|---|---|---|
| *Clausocalanus furcatus* | 17.18 | *Farranula gracilis* | 17.48 |
| *Temora stylifera* | 13.42 | *Clausocalanus furcatus* | 14.80 |
| *Farranula gracilis* | 8.98 | *Oncaea venusta* | 13.93 |
| *Paracalanus quasimodo* | 8.19 | *Acrocalanus longicornis* | 9.69 |
| *Paracalanus aculeatus* | 8.02 | *Undinula vulgaris* | 9.38 |
| *Acrocalanus longicornis* | 7.55 | *Temora stylifera* | 9.10 |
| *Oncaea venusta* | 7.15 | *Nannocalanus minor* | 4.97 |
| *Corycaeus giesbrechti* | 6.64 | *Macrosetella gracilis* | 4.32 |
| *Undinula vulgaris* | 5.91 | *Corycaeus giesbrechti* | 4.08 |
| *Temora turbinata* | 4.04 | *Calocalanus pavoninus* | 3.18 |
| *Nannocalanus minor* | 3.63 | | |
| **Continental shelf/dry season species** | **%** | **Slope/dry season species** | **%** |
| *Clausocalanus furcatus* | 16.53 | *Clausocalanus furcatus* | 20.20 |
| *Paracalanus quasimodo* | 16.11 | *Oncaea venusta* | 13.96 |
| *Temora turbinata* | 10.27 | *Farranula gracilis* | 8.81 |
| *Temora stylifera* | 9.85 | *Paracalanus quasimodo* | 8.22 |
| *Centropages furcatus* | 6.50 | *Temora stylifera* | 6.29 |
| *Calanoides carinatus* | 6.28 | *Lucicutia flavicornis* | 5.20 |
| *Oncaea venusta* | 5.68 | *Undinula vulgaris* | 4.81 |
| *Corycaeus giesbrechti* | 5.13 | *Corycaeus giesbrechti* | 3.56 |
| *Subeucalanus pileatus* | 3.21 | *Nannocalanus minor* | 3.10 |
| *Paracalanus parvus* | 3.20 | *Acrocalanus longicornis* | 2.93 |
| *Paracalanus aculeatus* | 2.47 | *Macrosetella gracilis* | 2.29 |
| *Ctenocalanus citer* | 2.44 | *Triconia conifera* | 2.03 |
| *Oithona plumifera* | 2.07 | *Temora turbinata* | 2.00 |
| *Oncaea media* | 2.00 | *Oncaea media* | 1.80 |
| | | *Oithona plumifera* | 1.74 |
| | | *Calocalanus pavoninus* | 1.57 |
| | | *Oithona similis* | 1.44 |
| | | *Subeucalanus pileatus* | 1.32 |

7.77 mg C $m^{-3}$ $d^{-1}$ (mean = 0.94 mg C $m^{-3}$ $d^{-1}$), based on samples collected with nets of the same mesh size (200 μm). Uye *et al.* (1987), in the Inland Sea of Japan, and Uye and Liang (1998), in Fukuyama Harbor, Japan, found similar copepod production levels (4.90 and 6.85 mg C $m^{-3}$ $d^{-1}$, respectively), using a plankton net with a smaller mesh size (<100 μm). The possible combination of an abundant food supply, attributed to the influence of an upwelling event prior to the sampling period; and a scarcity of large predators may account for the high copepod biomass and production. In addition, it is expected that different production levels will be found in years when upwellings do not occur.

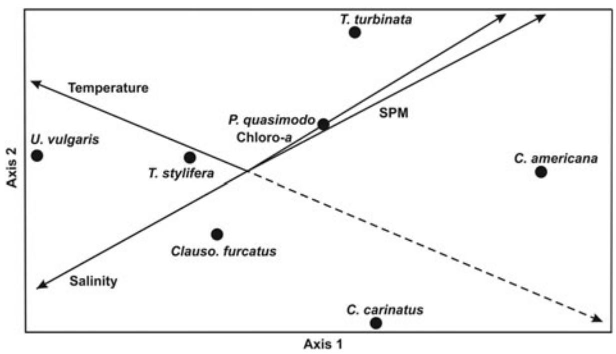


**Fig. 8.** CCA analyses of the major species contributing to the daily copepod production, with respect to the environmental parameters (temperature, salinity, chlorophyll-*a* and suspended particulate matter – SPM). Individual species in the plot: *T. stylifera*, *Temora stylifera*; *T. turbinata*, *Temora turbinata*; *U. vulgaris*, *Undinula vulgaris*; *C. americana*, *Calanopia americana*; *C. carinatus*, *Calanoides carinatus*; *Clauso. furcatus*, *Clausocalanus furcatus*.

The present study is the first attempt to examine the copepod biomass and daily production in oceanic waters in the south-west Atlantic Ocean. This study showed that copepod biomass and production in a tropical region can be relatively high compared with other regions of the world. Future studies should be directed to dominant copepod populations and also to the definition of a copepod growth model specific to this ecosystem.

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