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ECOSYSTEMS

# Seston biomass in plankton assemblages in the Southwestern Atlantic Ocean: spatial, vertical, and temporal variations

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**Abstract:** Bioseston is a heterogeneous assemblage of bacterioplankton, phytoplankton, zooplankton, and planktonic debris. A detailed knowledge of biosestons is essential for understanding the dynamics of trophic flows in marine ecosystems. The distributional features of seston biomass in plankton (micro- and mesoplankton) in the Southwest Atlantic Ocean (Rio de Janeiro State, Brazil) were analyzed using stratified samples gathered to a depth of 2,400 m during night time. The horizontal pattern of biomass distribution was analyzed vis-a-vis station depth during both wet and dry periods, with higher values recorded in the continental shelf than in the slope, confirming the terrestrial contribution of nutrient sources to the marine environment. This horizontal variation reinforces the occurrence of seasonal vortices in Cabo Frio and Cabo de São Tomé on the central coast of Brazil. Environmental variables reflect the hydrological signatures of the water masses along the Brazilian coast. The largest seston biomass was related to high temperatures, salinities, and low inorganic nutrient concentrations in tropical and South Atlantic central waters. The observed distribution patterns suggest that seston biomass in plankton in the region may be structured based on partitioned horizontal and vertical habitats and food resources.

**Key words:** Plankton, Seston biomass, Southwestern Atlantic Ocean, Spatial and temporal variations, Water mass.

## INTRODUCTION

Seston refers to living organisms (bioseston—plankton and nekton) and non-living matter (abioseston—detritus, mineral particles, and fecal pellets) swimming or floating in water bodies such as lakes and seas (Nakajima et al. 2010, Huguet 2015). Biosestons comprise heterogeneous assemblages of bacterioplankton, phytoplankton, zooplankton, and planktonic debris (Gladstone-Gallagher et al. 2016). Understanding the role of seston particles is essential for understanding trophic flow dynamics in marine ecosystems (Silva 2016). Changes in planktonic biomass are good indicators of global and local biogeochemical changes caused by anthropogenic activities. Anthropogenic sources include the potential impact of industrial fisheries on marine biogeochemistry, large-scale $CO_2$ emissions in the 21$^{st}$ century, and $CO_2$-induced warming (Getzlaff & Oschlies 2017); therefore, there is a need to expand our understanding of these changes throughout the marine environment in different regions of the world.

Studies on deepwater masses along the Brazilian coast are rare (Bonecker et al. 2017). Owing to the scarcity of food in the deep sea, these systems can only sustain a limited number of organisms (Nybakken & Bertness 2005).

Therefore, a decrease in biomass density and diversity is expected with the increase in depth (Weikert 1982, Robison 2004, Bonecker et al. 2009). In addition, heterogeneity in vertical distribution, particularly migration, is a phenomenon observed in different zooplanktonic organisms, which is directly associated with physiological responses triggered by environmental stimuli such as light and temperatures (Simoncelli et al. 2019). Thus, the quantification of planktonic biomass can serve as a tool for estimating the impacts of global warming.

By the end of the 1980s, with the beginning of oil exploration in deep waters, regular studies were conducted on plankton in the Campos Basin. Studies carried out in the Cabo Frio region (Rio de Janeiro State) reported that zooplankton biomass is significantly impacted by the intense local coastal upwelling typical of the summer period and that there is a strong relationship between phytoplankton biomass and that of microplankton (Valentin et al. 1987, McManus et al. 2007). Valentin and Monteiro-Ribas (1993) and Bonecker et al. (2017) reported an increase in biomass and a decrease in diversity with decreasing latitude. Neumann-Leitão et al. (1999) found that low zooplankton biomass and abundance off Northeastern Brazil correspond to oligotrophic water masses, which are affected by inshore mangroves, topographic upwelling offshore, or both. On oceanic islands in environmentally protected areas in the Northeast of Brazil, zooplankton biomass is impacted by the period of the day, increased water temperature, and the contribution of autochthonous sources generated by the effects of these islands in nutrient accumulation (Campelo et al. 2019). Owing to the importance of zooplankton biomass in maintaining fish stocks in Brazil (Duarte et al. 2014), studies on economically critical areas are necessary.

In the Campos Basin, previous studies have addressed aspects of mesozooplankton species richness and composition (Bonecker et al. 2014), diel variation in zooplankton and ichthyoplankton (Bonecker et al. 2018), and the occurrence and abundance of Appendicularia (Carvalho & Bonecker 2016) and Copepoda (Dias et al. 2015, 2019). However, aspects of seston biomass, such as variations in longitudinal, seasonal, and vertical distributions, have not been previously analyzed. This study aimed to answer two main questions to help fill these knowledge gaps regarding the distribution of plankton biomass in the Southwest Atlantic: 1) Is there a difference in the distribution of plankton biomass between the continental shelf and slope, considering the Cabo Frio coastal upwelling, and the impact of local rivers that can contribute to the input of nutrients and the possible advection of organisms and biogenic particles in different regions? 2) Are there differences in biomass distribution between the nuclei of each water mass in the region in the vertical direction (1–2,300 m), considering the different physical and chemical properties of each?

## MATERIALS AND METHODS

### Study area

The Campos Basin covers an area of approximately 100,000 km$^2$ (Viana et al. 1998). It is bordered offshore by the Vitória Arc (20.5 °S) on the north and the Cabo Frio Arc (24 °S) on the south (Carrasquilla & Ulugergerli 2006). 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 extended over a width of 40 km and had a mean declivity of 2.5°. Its base is relatively shallower at its Northern limit (~1,500 m) and deeper near its Southern limit (~2,000 m; Viana et al. (1998). The climate is humid, with a wet summer period (WP) and a relatively dry winter period (DP) (Lacerda et al. 2004). This region is characterized by its water column structure and water mass distribution over the continental shelf and slope (Dias et al. 2019). The different water masses in the area (Fig. 1) exhibit distinct temperatures, salinities, and dissolved oxygen (DO) levels, which provide varying habitats for pelagic species down to a depth of 3,000 m (Suzuki et al. 2015, Falcão et al. 2017, Dias et al. 2019).

The Northern offshore region of Rio de Janeiro contains five water masses. The upper reaches of the water column include the nutrient-poor Tropical Water (TW; temperatures >20 °C and salinity >36.20) and the relatively cold, nutrient-rich South Atlantic Central Water (SACW; 8.72 °C <temperatures <20 °C and 34.66 <salinity <36.20). At greater depths, there are the cold waters of the Antarctic Intermediate Water (AAIW, 567–1,060 m; 3.46 °C <temperature <8.72 °C and 34.42 <salinity <34.66), the Upper Circumpolar Deep Water (UCDW, 1,060–1,300 m; 3.31 °C <temperature <3.46 °C and 34.42 <salinity <34.66) and the North Atlantic Deep Water (NADW; 2.04 °C <temperature <3.31 °C and 34.59 <salinity <34.87) (Mémery et al. 2000, da Silveira et al. 2000, da Silveira, 2007). NADW is found below the UCDW, influencing the lower continental slope below a depth of 1,300 m (Mémery et al. 2000, da Silveira et al. 2000, da Silveira, 2007, Bonecker et al. 2012, 2014; Fig. 1).

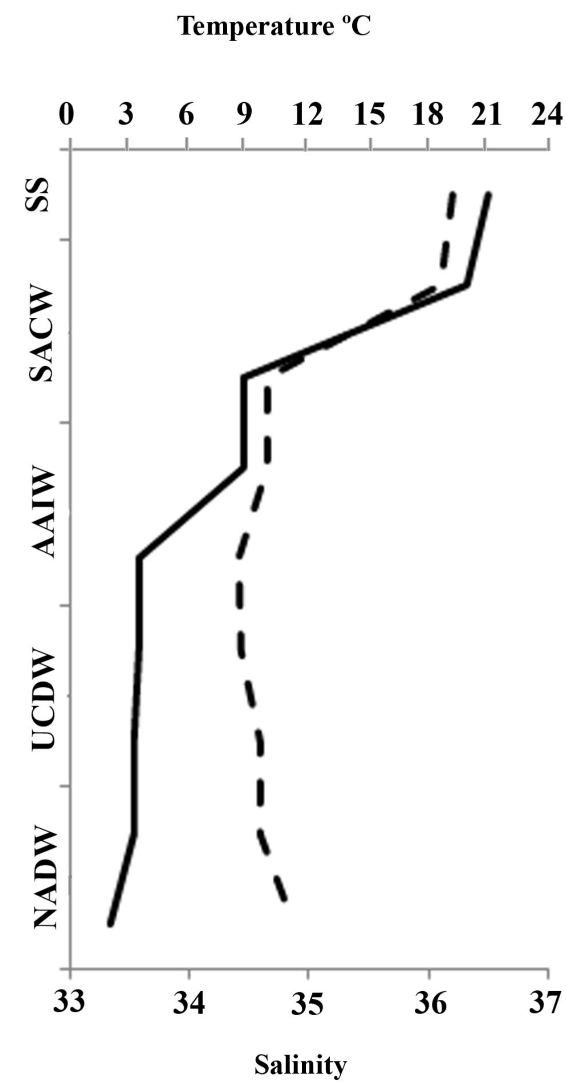

**Figure 1. Salinity and temperature of five water masses (0–3,260 m) in the Campos Basin, central Brazilian coast, as modified from (Bonecker et al. 2014). Solid line: temperature; dashed line: salinity; TW: Tropical Water (0–142 m); SACW: South Atlantic Central Water (142–567 m); AAIW: Antarctic intermediate Water (567–1,060 m); UCDW: Upper Circumpolar Deep Water (1,060–1,300 m); NADW: North Atlantic Deep Water (1,300–3,260 m).**

## Sampling method and treatment of samples

Biological materials were obtained as part of a subproject designed to study the zooplankton and ichthyoplankton under the Habitats Project – Campos Basin Environmental Heterogeneity coordinated by CENPES/ PETROBRAS. Sampling was conducted during two oceanographic cruises in 2009, one during the wet period (February 25 to April 13) and the other during the dry period (August 5 to September 17). The stations are distributed along six transects perpendicular to the coast (A, C, D, F, H, and I) from south (A) to north (I). Each transect contained eight sampling stations distributed across the shelf: 25- to 3,000-m isobaths (25, 50, 75, 150, 400, 1,000, 1,900, and 3,000 m), four on the continental shelf, and four on the slope (Fig. 2). All samples were collected between 6:18 pm and 5:08 am during the WP and between 5:57 pm and 5:46 am during the DP, Brasilia Standard Time (GMT-3).

Environmental data collected included: (a) water temperature and salinity at all sampling depths, namely, 1, 250, 800, 1,200, and 2,400 m, sampled using a commercially available rosette system of Sea-Bird Electronics Inc. (Bellevue, WA, USA); (b) DO levels measured continuously in the water column with a sensor coupling in the attached CTD profiler (Sea-Bird Electronics, USA); (c) concentrations of inorganic nutrients, determined using standard oceanographic methods (Grasshoff et al. 1999); and (d) suspended particulate matter (SPM) content, obtained from water samples collected using a GO-FLO bottle (General Oceanics, USA). 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. The SPM content was obtained from the difference between the initial weight of the sample and the weight after drying at 40 °C for 4 days. A detailed methodology and discussion of the hydrochemistry of the study area have been presented elsewhere (Rodrigues et al. 2014, Dias et al. 2015, Suzuki et al. 2015).

Micro- and mesoplankton samples were collected using horizontal hauls at the same stations and depths at which environmental parameters were recorded. The sampling depths represented the nuclei of each water mass. In

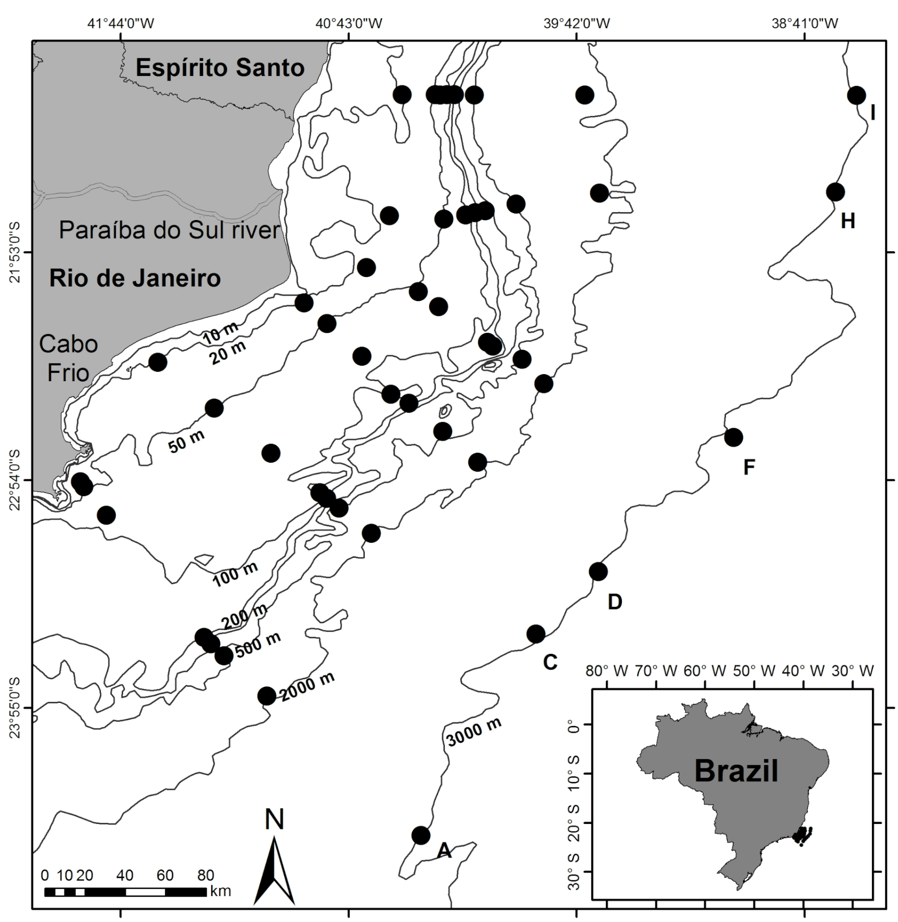


**Figure 2. Sampling stations and sites (solid black circles) in the study area.**

the DP, no samples were collected from the 3,000 m isobaths of transects H and I because of logistical problems. A total of 398 samples (210 in the WP and 188 in the DP) were collected using a Midi-type Hydro-Bios MultiNet® (HYDROBIOS, Germany; aperture 0.25 $m^2$ and dimensions of 80 cm × 90 cm × 95 cm) fitted with a set of two nets (mesh apertures 120 and 200 µm, for micro- and mesoplankton samples, respectively), with each water mass sampled separately to prevent cross-contamination. At each predetermined depth, hauls were performed at a speed of 2 knots using an open–close mechanism operated by electronically transmitted commands. MultiNet was equipped with a depth sensor, and a depressor was used to maintain the net stability. Five depths were sampled, and the haul depth was controlled during the entire procedure to ensure the net was towed horizontally. At 1 m depth, 5-min hauls were performed, and at 250, 800, 1,200, and 2,400 m depths, the net was towed for 10 min because of the lower number of organisms found in deeper waters than in shallower waters. Water volume and haul depth data were transmitted to a computer in real-time on the ship. The filtration efficiency and water volume were measured using two flowmeters: one mounted in front of the mouth of the net and the other fixed to the outer part of the net. The average water volumes filtered through the 120 µm mesh at 1, 250, 800, 1,200, and 2,400 m were 133 ± 57 $m^3$ (50 to 268 $m^3$; median 124 $m^3$), 131 ± 35 $m^3$ (55 to 182 $m^3$; median 138 $m^3$), 153 ± 52 $m^3$ (79 to 286 $m^3$; median 133 $m^3$), 158 ± 44 $m^3$ (88 to 263 $m^3$; median 151 $m^3$), and 140 ± 40 $m^3$ (88 to 207 $m^3$; median 136 $m^3$), respectively. Similarly, the average water volumes filtered through the 200 µm net at 1, 250, 800, 1,200, and 2,400 m were 133 ± 55 $m^3$ (60 to 280 $m^3$; median 127 $m^3$), 130 ± 34 $m^3$ (57 to 195 $m^3$; median 136 $m^3$), 152 ± 47 $m^3$ (83 to 269 $m^3$; median 141 $m^3$), 158 ± 41 $m^3$ (92 to 264 $m^3$; median 146 $m^3$), and 125 ± 48 $m^3$ (91 to 190 $m^3$; median 114 $m^3$), respectively. Samples were fixed immediately in 4% (v/v) buffered formalin.

### Seston biomass in plankton

In the laboratory, each sample of microplankton (collected using 120 µm mesh) and mesoplankton (collected 200 µm mesh) was filtered and washed with fresh water to remove salts and formaldehyde (Beers 1981), in sieves with a mesh size of 100 µm that were previously weighed individually on a scale with 0.001 mg precision (Ainsworth 21N) for the determination of the wet weight. The interstitial water was then gently removed with paper towels placed under the sieves for at least 1 h or until the towels no longer absorbed the liquid to remove the interstitial fluid. Finally, each sample was weighed on a precision balance to obtain the wet weight (Omori & Ikeda 1984). The material was resuspended and stored in 4% formaldehyde buffered with sodium tetraborate, and the original samples were collected. To avoid the effects of large particles, which were not part of the plankton, elements such as macroalgae, debris, and microplastics were removed. Seston biomass was obtained using the formula $SB = WW \times V^{-1}$, where SB is the total wet seston biomass (mg $m^{-3}$), WW is the wet weight (mg), and V is the filtered volume ($m^3$). The results for total wet seston biomass in plankton are expressed in g $m^{-3}$.

### Data analysis

A non-parametric multivariate analysis of variance (np-MANOVA) was used to test the effects of regions (continental shelf × slope) and transects (A, C, D, F, H, and I) at each sampling station in the subsurface layer (only in samples taken from a depth of 1 m) on seston biomass for microplankton and mesoplankton. To replicate the samples for the np-MANOVA, the isobaths in each transect were paired two-by-two according to proximity. Owing to the absence of samples from the last isobaths of transects H and I during the dry period, we duplicated the data from the previous isobaths. np-MANOVA was performed using permutational MANOVA (Anderson 2005). Total seston biomass (microplankton in relation to mesoplankton and WP in relation to DP) was tested using a Mann–Whitney *U*-test non-parametric corresponding analysis (Mann & Whitney 1947) at a significance level of $p$ <0.05 to identify statistical differences among the sampling periods (WP and DP). Differences in seston biomass for microplankton and mesoplankton among the five slope water masses (vertical variation) were verified using the Kruskal–Wallis H-test (Kruskal & Wallis 1952). All data were evaluated for normality and homogeneity before the analysis. These analyses were performed using the Statistica 7 software (TIBCO Software, Palo Alto, CA, USA).

Principal component analysis (PCA) was used to define the similarities between the samples based on environmental descriptors (continuous variables) and how the observed patterns were related to the environment. Highly correlated variables (nitrite and ammonia) were excluded from the analysis to minimize collinearity effects on the results (Zuur et al. 2009). Environmental descriptors included the concentrations of SPM, DO, nitrate, silicate, and orthophosphate, and temperatures and salinity. Before conducting PCA, the environmental variables were standardized and normalized for the different water masses (TW, SACW, AAIW, UCDW, and NADW). Seston biomasses for microplankton and mesoplankton were added as categorical supplements. A correlation matrix was used to calculate the eigenvectors and principal components (PCs), ranked in the order of significance. The broken-stick model, a method for estimating the number of statistically significant PCs (Jackson 1993), was used as the stopping rule in PCA. The scores of the retained PCA axes were used as new variables in ANOVA to determine whether the environmental data varied with depth. The results were considered significant at $p$ <0.05. These analyses were performed using R version 3.6.0 (R Development Core Team 2020) and the FactoMineR library (Lê et al. 2008).

## RESULTS

### Hydrography conditions

The analyzed samples were taken from the core of each water mass, and the values of the hydrological variables were highly diverse, as reflected in the characteristics of each water mass. Variations were observed in the spatial distribution of hydrological parameters on the continental shelf in the Cabo Frio (transect A) and Cabo de São Tomé (transects D and F) regions, where vortex formation was observed. These variations are typically greater in surface water than in the layers below. The vertical distribution of nutrients was typical of permanently stratified TW. Nutrients were scarce in TW, and their concentrations increased in deeper waters. In addition, higher nutrient values were observed on the continental shelf than in open waters in the slope region.

The water temperatures ranged from 24.82–28.50 °C and 19.64–24.89 °C in WP and DP, respectively. Salinity showed low variation during both sampling periods, ranging from 35.44–37.28 and 35.71–37.11 in WP and DP, respectively. Temperature and salinity were lower during DP than during WP, mainly at stations located in the Southern part of the study area, over the continental shelf near Cabo Frio (transect A), and in the Northern part, under the continental impact of the Paraíba do Sul River (transects H and I; Fig. 3a–3d). The vertical distributions of temperatures and salinity in the slope region

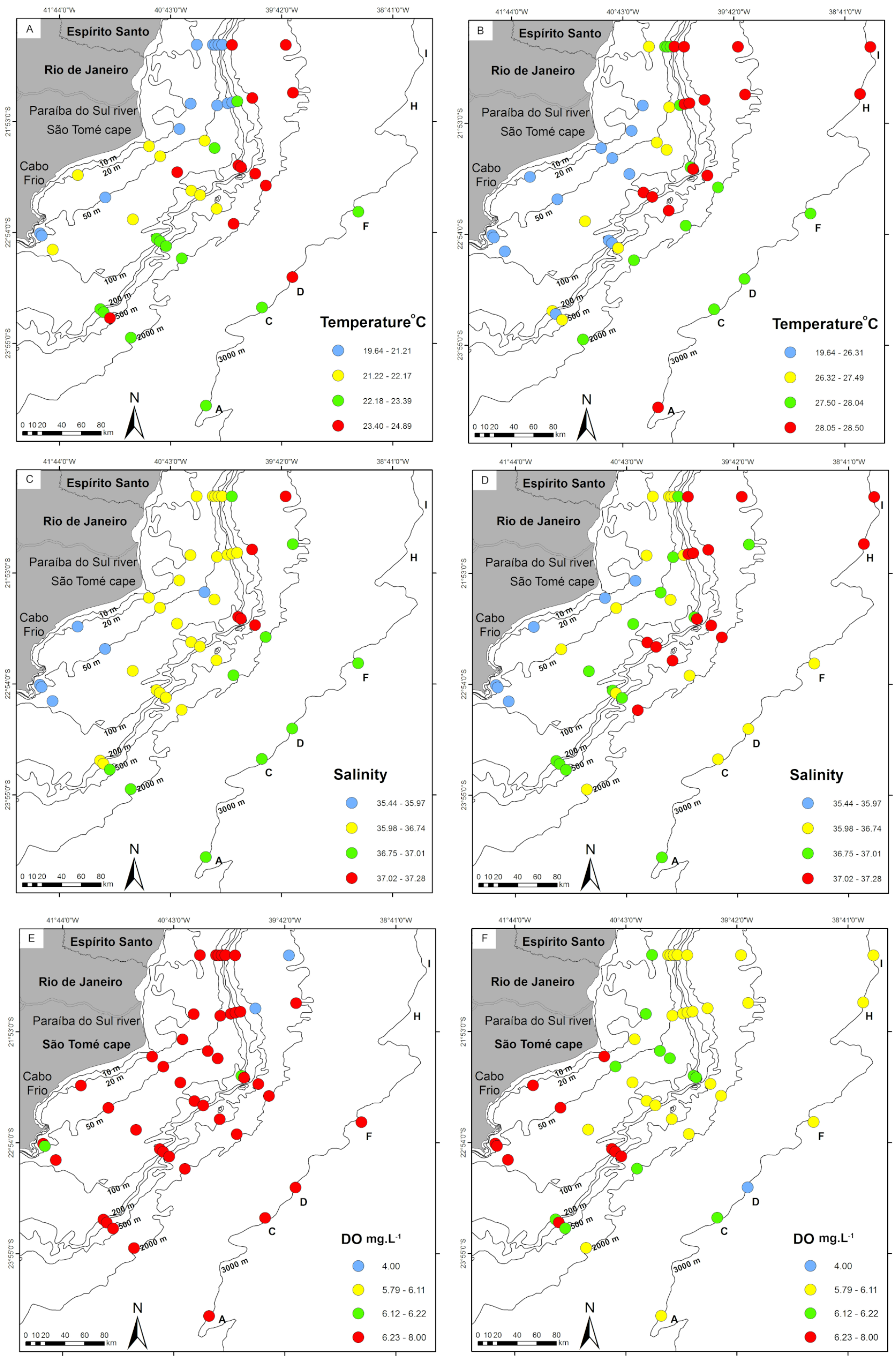


**Figure 3.** Spatial distribution of the values of hydrography parameters in the pelagic environment of the Campos Basin: a) temperature (°C) distribution values at 1 m depth in the wet period of 2009; b) temperature (°C) distribution values at 1 m depth in the dry period of 2009; c) salinity distribution values at 1 m depth in the wet period of 2009; d) salinity distribution values at 1 m depth in the dry period of 2009; e) dissolved oxygen (mg $L^{-1}$) distribution values at 1 m depth in the wet period of 2009; and f) dissolved oxygen (mg $L^{-1}$) values at 1 m depth in the dry period of 2009.

were relatively uniform at 800 m in AAIW and 1,200 m in UCDW (Fig. 4a, 4b).

The DO values varied between 4.36 mg $L^{-1}$ (DP, TW – 1 m) and 7.89 mg $L^{-1}$ (DP, NADW – 2,300 m). Regarding the spatial distribution at a depth of 1 m, the highest values of this parameter were observed in the Cabo Frio (transect A, WP) and Cabo de São Tomé (transects D, F, DP; Fig. 3e, 3f) regions, related to the highest values of nutrients in these same regions. The vertical profile of DO on the slope was characteristic of water mass values present in these regions,

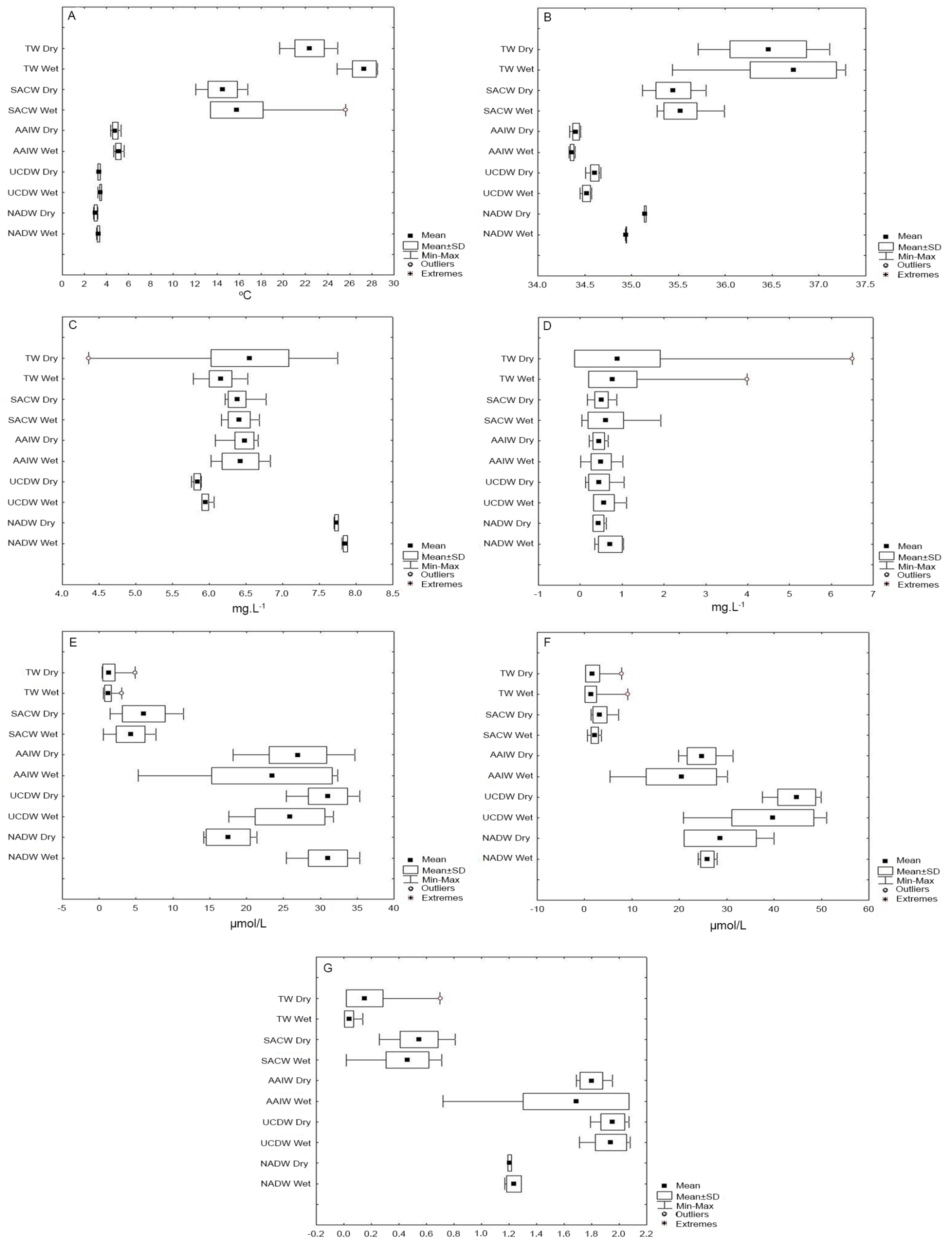


**Figure 4.** Vertical profile of the values of hydrography parameters in the dry and wet periods of 2009 in the pelagic environment of the Campos Basin: a) temperature (°C); b) salinity; c) dissolved oxygen (mg $L^{-1}$); d) suspended particulate matter (mg $L^{-1}$); e) nitrate (µmol/L); f) silicate (µmol/L); and g) orthophosphate (µmol/L).

similar in both sampling periods, except for the 1 m depth in DP, where a greater variation was observed in values than at other depths. The lowest values of this parameter were recorded for NADW during both sampling periods (Fig. 4c).

The values of SPM varied between 0.04 mg $L^{-1}$ (SACW – 250 m) and 7.89 mg $L^{-1}$ (TW – 1 m) in the WP and DP, respectively. The SPM values declined above the slope compared with that on the continental shelf during the two sampling periods (Fig. 5a, 5b). During DP, the highest SPM values were recorded in the Cabo Frio region (transect A) in the Southern part of the study area and in the Northern part under the continental impact of the Paraíba do Sul River (transects H and I; Fig. 5a, 5b). The SPM values decreased along the water column with increasing depths during both sampling periods (Fig. 4d).

Nitrate values oscillated between 0.37 (1 m depth – TW) and 35.33 µmol/L (1,200 m - NADW)

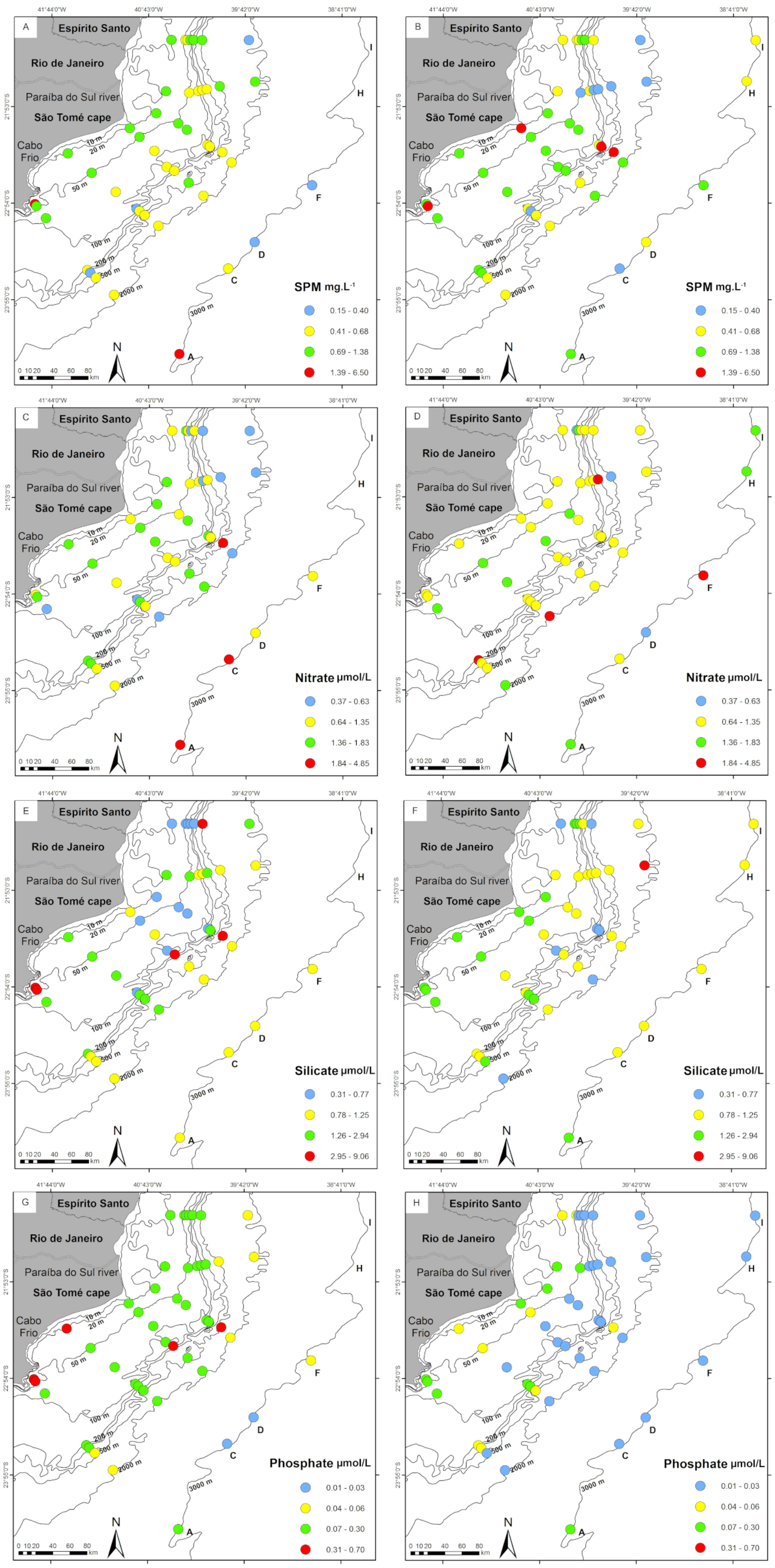

**Figure 5.** Spatial distribution of the values of hydrography parameters in the pelagic environment of the Campos Basin: a) suspended particulate matter (mg $L^{-1}$) distribution values at 1 m depth in the wet period of 2009; b) suspended particulate matter (mg L-1) distribution values at 1 m depth in the dry period of 2009; c) nitrate (µmol/L) distribution values at 1 m depth in the wet period of 2009; d) nitrate (µmol/L) distribution values at 1 m depth in the dry period of 2009; e) silicate (µmol/L) distribution values at 1 m depth in the wet period of 2009; f) silicate (µmol/L) distribution values at 1 m depth in the dry period of 2009; g) orthophosphate (µmol/L) distribution values at 1 m depth in the wet period of 2009; and h) orthophosphate (µmol/L ) distribution values at 1 m depth in the dry period of 2009.

during the DP. It was not possible to identify a pattern for the horizontal distribution of nitrate values during sampling (Fig. 5c, 5d). Regarding the vertical gradient in the 1 m depth layer, the results ranged from 0.56–3.09 µmol/L and 0.37–4.85 µmol/L in the WP and DP, respectively. The nitrate content was higher in the other water masses, mainly in the AAIW (Table I; Fig 4e).

Nitrite was present in small amounts during both seasons. Values observed at 1 m depth during WP ranged from close to the detection limit (0.01 µmol/L) to 0.35 µmol/L (Table I). Neither the regions nor transects differed in their nitrite distributions. The only areas with higher nitrite values were Cabo Frio (transect A) and Cabo de São Tomé (transects D and F), as reported for other nutrients. Generally, the vertical nitrite profile was almost entirely homogeneous with no major oscillations (Table I).

Similar to nitrite concentrations, the concentrations of ammonia were predominantly close to the detection limit of the analytical method employed (0.05 µmol/L N-$NH_3$/$NH_4^+$; Table I). Establishing criteria or standards for determining ammonia distribution was not feasible, resulting in time and space constraints, representing a different pattern from that of the other analyzed nutrients, as it was not possible to identify any horizontal, vertical, or temporal patterns observed with the other variables (Table I).

The silicate values varied between 0.31 µmol/L at 1 m depth (DP) and 51.11 µmol/L at 1,200 m depth (WP), with great variability in the results. The spatial patterns observed at a depth of 1 m were similar to those described for other nutrients, in which the highest silicate values were observed in the Cabo Frio (transect A) and Cabo de São Tomé (transects D and F) regions during both sampling periods (Fig. 5e, 5f). The vertical distribution of silicates followed a stratification pattern characteristic of nutrients in oceanic areas. In the upper layer (1 m depth) the values ranged between 0.41 and 9.06 µmol/L (WP), and between 0.31 and 7.89 µmol/L (DP). For the other water column extracts, the values increased with depth (Fig. 5f). Regarding the variation between sampling times, the biomass value obtained at 1 m in the DP was greater than

**Table I. Minimum and maximum values registered for parameters nitrate (µmol/L), nitrite (µmol/L), and ammonia concentrations (µmol/L) for samples collected in the water column of the Campos Basin during the wet and dry periods of 2009.**

| Depth | Sampling Periods | Nitrate (µmol/L) | | Nitrite (µmol/L) | | Ammonia (µmol/L) | |
|---|---|---|---|---|---|---|---|
| | | Min | Max | Min | Max | Min | Max |
| 1 m | Wet Period | 0.56 | 3.09 | 0.02 | 0.1 | 0.05 | 0.37 |
| | Dry Period | 0.37 | 4.85 | 0.02 | 0.35 | 0.05 | 0.25 |
| 250 m | Wet Period | 0.58 | 7.67 | 0.02 | 0.32 | 0.05 | 0.15 |
| | Dry Period | 1.48 | 11.41 | 0.02 | 0.14 | 0.05 | 0.39 |
| 800 m | Wet Period | 5.29 | 32.37 | 0.02 | 0.13 | 0.05 | 0.07 |
| | Dry Period | 18.18 | 34.72 | 0.02 | 0.08 | 0.05 | 0.32 |
| 1,200 m | Wet Period | 17.58 | 31.76 | 0.02 | 0.08 | 0.05 | 0.05 |
| | Dry Period | 25.42 | 35.33 | 0.02 | 0.1 | 0.05 | 0.48 |
| 2,300 m | Wet Period | 11.01 | 18.41 | 0.05 | 0.07 | 0.05 | 0.05 |
| | Dry Period | 14.16 | 21.38 | 0.02 | 0.05 | 0.05 | 0.08 |

that recorded in the WP. At other depths, silicate values exhibited low seasonal variability (Fig. 5f).

The orthophosphate values observed during the two sampling periods showed great variability, oscillating between 0.01 µmol/L at 1 m depth (TW) and 2.08 µmol/L at 1,200 m depth (UCDW), both recorded in the WP. As expected, in both seasons, the spatial distribution of orthophosphate at a depth of 1 m in the continental shelf area was greater than that recorded on the slope. The largest differences between seasons were at stations located near the coast, particularly in the Cabo Frio (transect A) and Cabo de São Tomé (transects D and F) regions during the WP, as well as throughout the continental shelf and part of the slope region during the DP (Fig. 5g, 5h). However, the vertical distribution of orthophosphate in the slope region showed a pattern typically observed for the distribution of nutrient elements in oceanic areas, with low values at the surface and increasing with depth (Fig. 4f).

## Plankton biomass

The seston biomass values for microplankton ranged from 0.001 (AAIW - 800 m) to 1.53 g $m^{-3}$ (TW - 1 m) and 0.001 (UCDW – 1,200 m) to 0.60 g $m^{-3}$ (TW - 1 m) in the WP and DP, respectively. The mesoplankton values ranged from 0.002 (UCDW – 1,200 m and NADW – 2,400 m) to 1.08 g $m^{-3}$ (TW - 1 m) during the WP and from 0.001 (UCDW – 1,200 m and NADW – 2,400 m) at 0.74 g $m^{-3}$ (TW - 1 m) during the DP.

The biomasses of microplankton (average 0.14 ± 0.23 and 0.12 ± 0.15 g $m^{-3}$ with a median of 0.03 and 0.04 $m^3$ in WP and DP, respectively) were higher than those of mesoplankton (average 0.12 ± 0.18 and 0.10 ± 0.14 g $m^{-3}$ with a median of 0.04 and 0.03 $m^3$ in WP and DP, respectively) in the two sampling periods. However, despite the higher values observed for microplankton than for mesoplankton, the differences between the two sampling methods (micro- and mesoplankton) were not significant (*U*-test: WP, $p$ = 0.87; *U*-test: DP, $p$ = 0.69). The biomasses of both microplankton (*U*-test, $p$ = 0.52) and mesoplankton (*U*-test, $p$ = 0.15) were higher during WP than during DP; the seasonal differences were not significant.

## Horizontal distribution

### *Microplankton*

The highest microplankton biomass values at 1 m depth were recorded in the continental shelf region in transect A (Cabo Frio region, WP, and DP), transect C (in the 50 m isobath between the Cabo Frio and São Tomé capes, DP), and in the slope region in transect H (at the height of the mouth of the Paraíba do Sul River, in the 200 m isobath, DP) (Fig. 6a, 6b). The horizontal distribution of microplankton biomass at a depth of 1 m was significantly different ($p$ <0.05), with higher values on the continental shelf than on the slope during both WP and DP in all six transects (Fig. 6a, 6b; Table II).

Based on the np-MANOVA analysis, there was significant variation in biomass between transects in both study periods ($p$ <0.05), regardless of the region, continental shelf, or slope (Table II).

### *Mesoplankton*

The highest biomass values at 1 m depth were recorded in the continental shelf region in transects A (below the 100 m isobath in the Cabo Frio region, WP), C (in the 50 m isobath between the Cabo Frio and São Tomé capes, DP), and H (height of the mouth of the Paraíba do Sul River, in the 100 m isobath, DP), and in the slope region in transect H (at the height of the mouth of the Paraíba do Sul River, in the 200 m isobath, DP) (Fig. 7a, 7b). The mesoplankton biomass was significantly different ($p$ <0.05) on

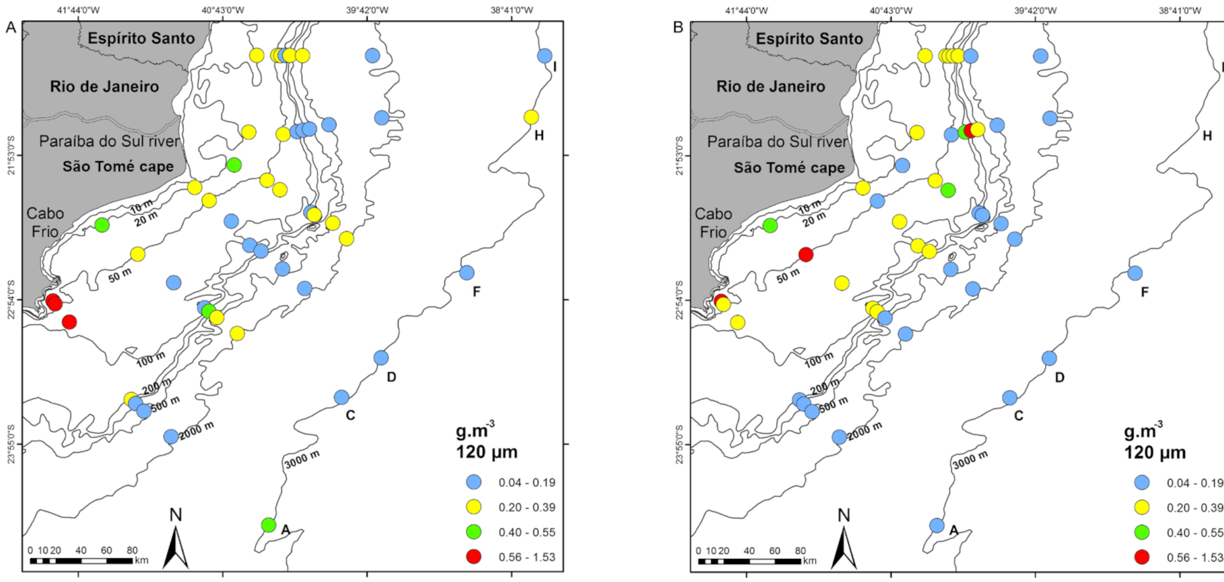


**Figure 6. Biomass distribution (g m$^{-3}$) of microplankton collected at 1 m depth during wet and dry periods. a) Biomass during the wet period and b) biomass during the dry period.**

the continental shelf than on the slope during the WP and DP in all six transects (Fig. 7a, 7b; Table III).

Based on the np-MANOVA analysis, similar to microplankton, there was a significant variation in biomass between transects in both periods (*p* <0.05) on both the continental shelf and slope (Table III).

## Vertical distribution

### *Microplankton*

The vertical distribution of the microplankton biomass was significantly different (H-test - *p* <0.05), with higher biomass values in TW (0.042–1.527 g m$^{-3}$ with an average value of 0.283 ± 0.276 g m$^{-3}$ and a median of 0.207 m$^3$ during WP and 0.038–0.608 g m$^{-3}$ with an average value of 0.231 ± 0.155 g m$^{-3}$ and a median of 0.191 m$^3$ during DP) than in the other water masses in both periods (Fig. 8a). In the same periods, SACW (0.007–0.041 g m$^{-3}$ with an average value of 0.019 ± 0.008 g m$^{-3}$ and a median of 0.017 m$^3$; and 0.005–0.046 g m$^{-3}$ with an average value of 0.016 ± 0.010 g m$^{-3}$ and a median of 0.013 m$^3$ during the WP and DP, respectively) also showed significantly different biomass values (H-test - *p* <0.05) from those observed in the UCDW (0.002–0.008 g m$^{-3}$ with an average value of 0.005 ± 0.002 g m$^{-3}$ and a median of 0.004 m$^3$; and 0.001–0.005 g m$^{-3}$ with an average value of 0.002 ± 0.001 g m$^{-3}$ and a median of 0.002 m$^3$ during the WP and DP, respectively; Fig. 8a).

### *Mesoplankton*

The mesoplankton showed significantly different biomass values (H-test, *p* <0.05) in TW (0.044–1.080 g m$^{-3}$ with an average value of 0.237 ± 0.206 g m$^{-3}$ and a median of 0.196 m$^3$ during WP and 0.025–0.740 g m$^{-3}$ with an average value of 0.195 ± 0.152 g m$^{-3}$ and a median of 0.165 m$^3$ during DP) compared with that in the other water masses in both periods (Fig. 8b). In WP, in addition to the differences observed between TW and the other water masses, SACW (0.007–0.137 g m$^{-3}$ with an average value of 0.028 ± 0.032 g m$^{-3}$ and a median of 0.016 m$^3$) also showed significantly different biomass values (H-test - *p* <0.05) from

**Table II.** **Average, minimum, and maximum values of biomass (g m−3) of the microplankton collected at 1 m depth in the six transects on the continental shelf and on the slope during the wet and dry periods.**

| | Continental shelf | | Slope | |
|---|---|---|---|---|
| | **Wet period** | **Dry period** | **Wet period** | **Dry period** |
| | **Transect A** | | | |
| Average biomass | 1.00 | 0.32 | 0.24 | 0.11 |
| (Min-Max) | (0.391-1.527) | (0.101-0.600) | (0.129-0.506) | (0.070-0.132) |
| | **Transect C** | | | |
| Average biomass | 0.31 | 0.40 | 0.27 | 0.11 |
| (Min-Max) | (0.169-0.550) | (0.213-0.572) | (0.106-0.468) | (0.068-0.195) |
| | **Transect D** | | | |
| Average biomass | 0.23 | 0.25 | 0.13 | 0.17 |
| (Min-Max) | (0.161-0.308) | (0.141-0.384) | (0.100-0.159) | (0.075-0.357) |
| | **Transect F** | | | |
| Average biomass | 0.25 | 0.23 | 0.25 | 0.08 |
| (Min-Max) | (0.126-0.466) | (0.064-0.410) | (0.061-0.393) | (0.040-0.129) |
| | **Transect H** | | | |
| Average biomass | 0.19 | 0.39 | 0.13 | 0.13 |
| (Min-Max) | (0.042-0.307) | (0.188-0.608) | (0.055-0.273) | (0.038-0.211) |
| | **Transect I** | | | |
| Average biomass | 0.24 | 0.35 | 0.16 | 0.23 |
| (Min-Max) | (0.194-0.277) | (0.317-0.387) | (0.083-0.221) | (0.118-0.388) |

those observed in NADW (0.002–0.003 g $m^{-3}$ with an average value of 0.003 ± 0.001 g $m^{-3}$ and a median of 0.003 $m^3$), with the highest biomass values observed in SACW (Fig. 8b).

## Influence of environmental variables

The first two axes of the PCA performed on the environmental factors accounted for 82% of the total variance. Only PC1 (eigenvalue = 4.59) was retained in the analyses to explain the data variability (66%). The PCA results showed that the five water masses were distinct, and samples were drawn (axis 1; Fig. 9). Temperatures and salinities accounted for negative separation (−0.96 and −0.93, respectively), whereas orthophosphate (0.99), nitrate (0.96), and silicate (0.92) showed positive separations. The TW and SACW (left side of the plot) were influenced by the highest temperatures and salinities and the lowest orthophosphate, nitrate, and silicate concentrations. The deeper water masses (AAIW, UCDW, and NADW; right side of the plot) exhibited an opposite trend to that of the shallower water masses (Fig. 9). The scores on axis 1 indicate significant differences between depths (GLM: $F = 816.82$; $df = 9$; $p << 0.05$). Therefore, the variables related to axis 1 varied depending on the water mass characteristics. In the TW and SACW, the seston biomass for microplankton and mesoplankton increased with an increase in temperature and salinity but had low inorganic nutrient concentrations (orthophosphate, nitrate, and silicate). Conversely, the biomass decreased with increasing inorganic nutrient

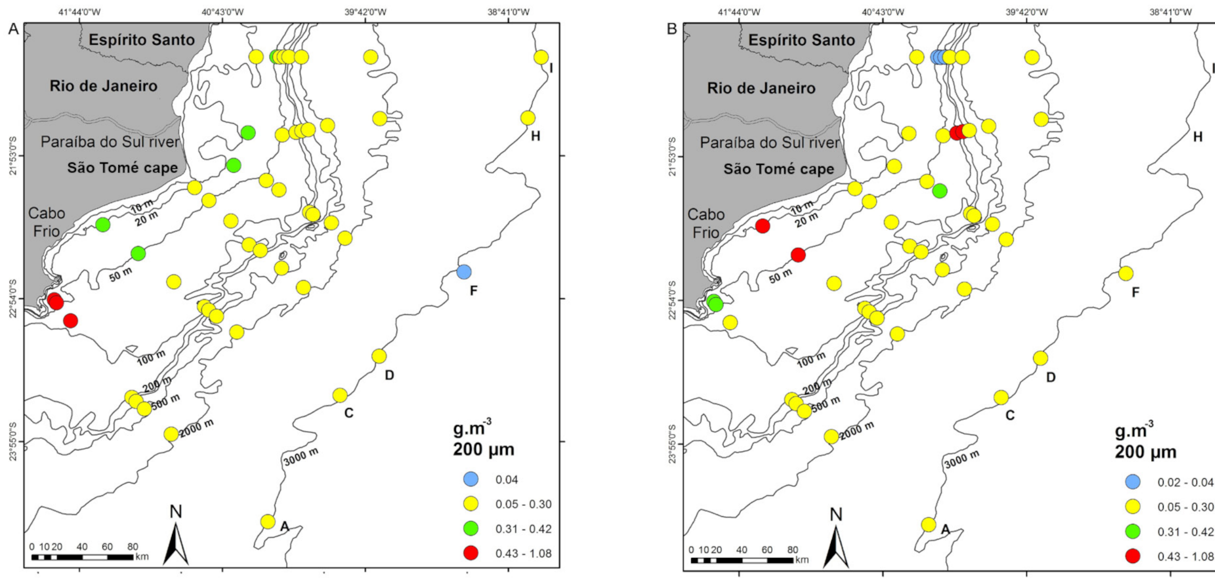


**Figure 7. Biomass distribution (g m$^{-3}$) of mesoplankton collected at 1 m during wet and dry periods. a) Biomass during the wet period and b) biomass during the dry period.**

concentrations in AAIW, UCDW, and NADW. Although DO and SPM were responsible for the formation of axis 2, this axis was not retained to explain PCA (*p* >0.05), and, therefore, the relationship between these two parameters and micro- and mesoplankton biomass was not included in this analysis.

## DISCUSSION

### Hydrography conditions

Horizontal variations related to the distance from the coastline were found, with higher amounts of dissolved nutrients in isobaths relatively closer to the continent than in the more distant isobaths, confirming that the terrestrial region is a source of nutrients for the marine environment (Andrade et al. 2004, Pedrosa et al. 2006, Suzuki et al. 2015). The observed horizontal variation reinforces the occurrence of SACW intrusion into the continental shelf in the Cabo Frio region and seasonal eddy formation in the Cabo de São Tomé region (Andrade et al. 2007, Suzuki et al. 2015). Higher concentrations of dissolved and particulate nutrients were observed in these areas than in the other regions.

In addition, classical profiles of the vertical distribution of dissolved and particulate nutrients in oceans relative to permanently stratified tropical ocean waters were observed during summer and winter in the Campos Basin. The oligotrophic characteristics of the waters of the Campos Basin (Andrade et al. 2004, Pedrosa et al. 2006, Suzuki et al. 2015) were confirmed in this study. The Campos Basin had overly low amounts of dissolved inorganic nutrients in surface layers, impacted by TW, and increasingly high amounts in biolytic layers (SACW, AAIW, UCDW, and NADW) during both periods. Oligotrophic conditions in tropical oceanic regions result from a lack of nutrient sources, specifically N and P, primarily consumed by the food chain (Moore et al. 2013). According to Suzuki et al. (2015), the Campos Basin is notable because the spatial distribution patterns (horizontal and vertical) of nutrients reveal differing patterns of limitations of N and P, particularly in the TW water mass. These authors reported that the nutrient supply is transient,

**Table III.** Average, minimum, and maximum values of biomass (g m−3) of the mesoplankton collected at 1 m depth in the six transects on the continental shelf and on the slope during the wet and dry periods.

| | Continental shelf | | Slope | |
|---|---|---|---|---|
| | **Wet period** | **Dry period** | **Wet period** | **Dry period** |
| | **Transect A** | | | |
| Average biomass | 0.78 | 0.26 | 0.16 | 0.11 |
| (Min-Max) | (0.276-1.080) | (0.126-0.413) | (0.093-0.279) | (0.073-0.140) |
| | **Transect C** | | | |
| Average biomass | 0.28 | 0.36 | 0.20 | 0.12 |
| (Min-Max) | (0.142-0.421) | (0.208-0.569) | (0.093-0.258) | (0.050-0.177) |
| | **Transect D** | | | |
| Average biomass | 0.21 | 0.22 | 0.11 | 0.12 |
| (Min-Max) | (0.163-0.276) | (0.181-0.238) | (0.080-0.132) | (0.049-0.194) |
| | **Transect F** | | | |
| Average biomass | 0.17 | 0.22 | 0.17 | 0.09 |
| (Min-Max) | (0.180-0.408) | (0.083-0.316) | (0.044-0.299) | (0.055-0.166) |
| | **Transect H** | | | |
| Average biomass | 0.17 | 0.46 | 0.10 | 0.18 |
| (Min-Max) | (0.055-0.302) | (0.271-0.740) | (0.059-0.197) | (0.103-0.237) |
| | **Transect I** | | | |
| Average biomass | 0.25 | 0.06 | 0.16 | 0.12 |
| (Min-Max) | (0.185-0.301) | (0.025-0.135) | (0.075-0.241) | (0.76-0.145) |

occurs at low concentrations in the biogenic layer, and originates from the decomposition of organic matter in the photic zone or from upwelling processes and continental inputs. Photosynthesis in the photic layer promotes the accumulation of particulate organic matter, resulting in high levels of particulate organic carbon and high amounts of N and P associated with this particulate organic matter (Suzuki et al. 2015). Considering the vertical distribution, nutrient partitioning indicates a slight limitation of N for primary producers. In the biolytic layer, the degradation of organic debris increases the concentrations of remobilized dissolved nutrients and reduces the particulate concentration. Dissolved organic and particulate materials indicate strong phosphate depletion and have N:P ratios, indicating the preferential degradation of N compounds over phosphate compounds (Suzuki et al. 2015).

The environmental variables described for the water column reflect the unique hydrological signatures of the water masses, typical of oligotrophic oceanic regions along the Brazilian coast (Dias et al. 2018). Temperature and salinity decrease from the subsurface to the deep waters, whereas inorganic nutrients are incrementally depleted from the surface to relatively deeper waters (Pedrosa et al. 2006, Rezende et al. 2007, Rodrigues et al. 2014, Suzuki et al. 2015). The pattern observed in the subsurface layer is characteristic of the nutrient-poor oceanic waters carried by the Brazil Current (Andrade et al. 2007, Rodrigues et al. 2014, Suzuki et al. 2015).

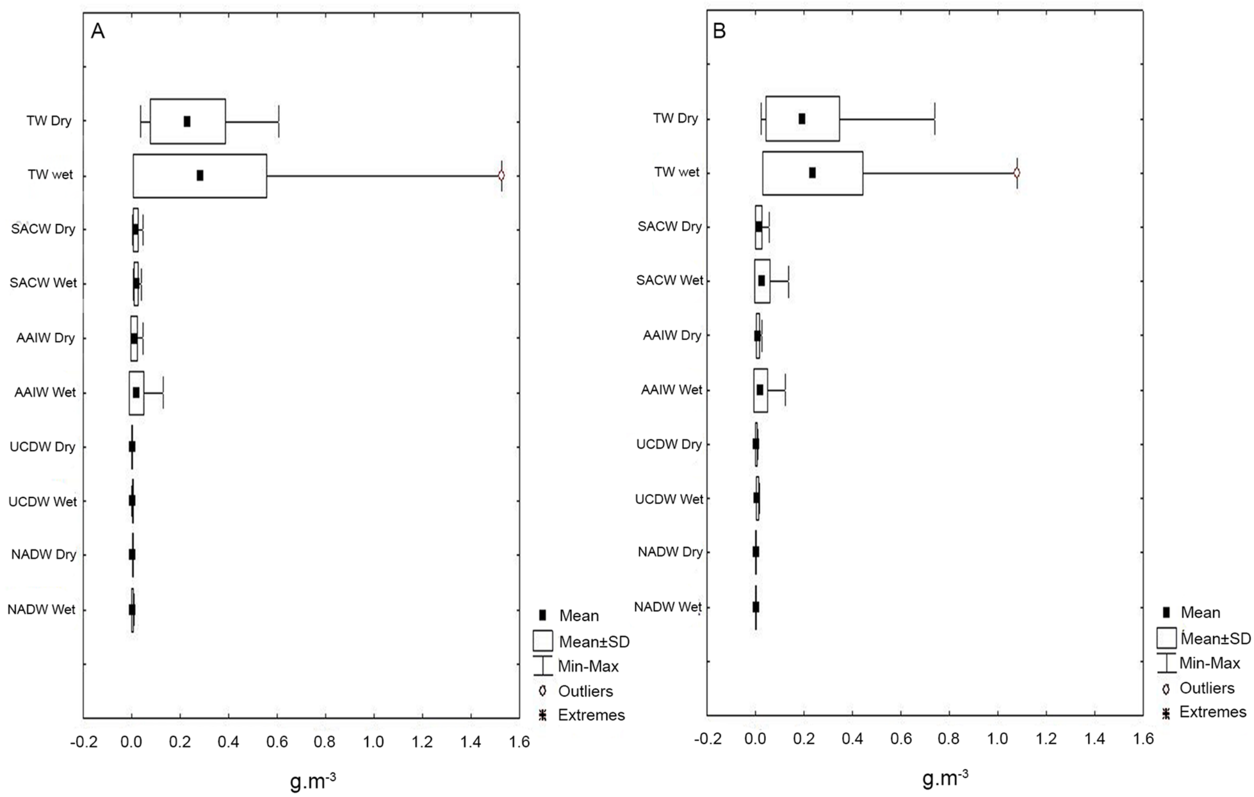


**Figure 8. Vertical profile of plankton biomass (g $m^{-3}$) in the dry and wet periods of 2009 in the pelagic environment of the Campos Basin: a) microplankton and b) mesoplankton.**

## Seston biomass in plankton: horizontal and vertical distribution

The distribution patterns of seston biomasses (micro- and mesoplankton) were similar when compared using the two different mesh sizes, although the values of seston biomass collected by the 120 μm mesh were higher than those captured using the 200 μm mesh size. The greater ability of relatively smaller-sized meshes than that of bigger-sized meshes to capture the biomass of planktonic organisms has been observed in the Pacific and Atlantic Oceans. In a study by Silva et al. (2016), conducted in the coastal and oceanic region of Northeast Brazil, significantly higher values of wet biomass and biovolume were observed in the 200 μm mesh compared to those in the 300 μm mesh. Similar to the findings reported in this study, these differences are not of great magnitude (20–40%), with the difference recorded between the relatively large-sized meshes (100 and 200 μm; Pakhomov et al. 2020). In communities and ecosystems, small organisms are generally more numerous reaching greater densities than large organisms can reach. Furthermore, small organisms exhibit a higher species richness than that of larger ones. Additionally, networks with a smaller mesh opening can accumulate organisms and particles identical to or larger than the size of the mesh (Stanley 1973, Silva et al. 2016).

Methodologies used for biomass estimation vary significantly. The question of the most appropriate strategy for estimating zooplankton biomass continues to be debated, including the type of net, mesh size, and trawl depth. Nevertheless, net trawls have been useful in defining large-scale patterns of zooplankton

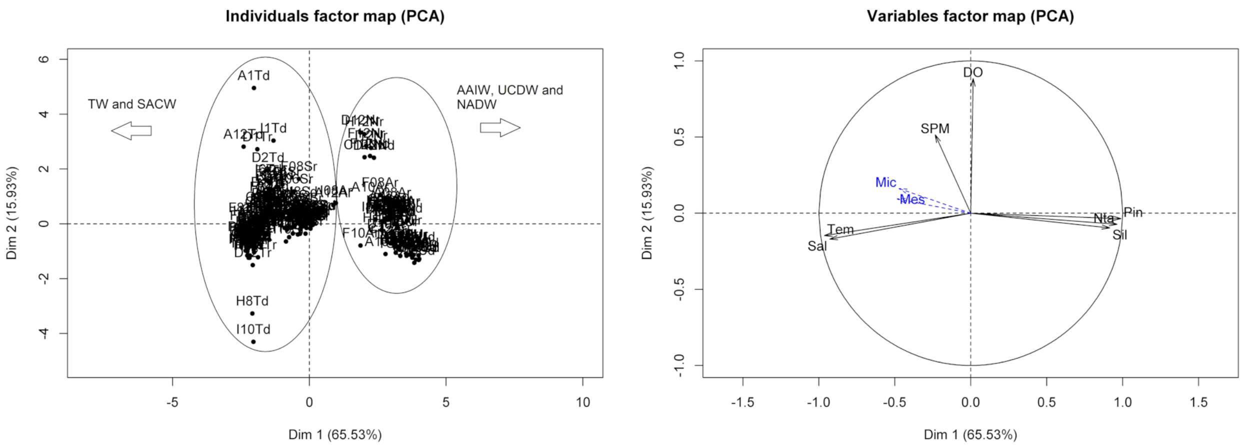


**Figure 9. Principal component analysis (PCA) was used to summarize environmental and biological variables. The abiotic variables included temperature (Tem), salinity (Sal), suspended particulate matter (SPM), dissolved oxygen (DO), nitrate (Nta), silicate (Sil), and orthophosphate (Pin). Microplankton (Mic) and mesoplankton (Mes) seston biomass were used as supplements. The samples collected from TW, SACW, AAIW, UCDW, and NADW were arranged based on the first two principal components.**

biomass (Landry & Swalethorp 2022). However, methodology selection depends on the availability of laboratory equipment, sample number, time, study objective, study environment, and group/community studied (Paggi & Paggi 1995, Blettler & Bonecker 2006).

The structure and dynamics of plankton communities in relation to biomass depend directly on the hydrographic characteristics of water masses and their regional and seasonal variations (Brandini et al. 1989, Brandini 1990). Material exported via river discharge and continental shelf-edge resurgence contributes to the productivity of the adjacent coastal region, justifying the high values of biomass and species density in relation to the oceanic region (Mafalda Jr et al. 2004, Melo Jr et al. 2007, Silva et al. 2016).

The data obtained in this study revealed a horizontal pattern of biomass distribution during both sampling periods, with higher values recorded on the continental shelf region. Bonecker et al. (2007) found that the average planktonic biomass density (200 m) was higher in autumn than in spring along the continental shelf of the Southern region of Bahia, Cabo de São Tomé, and close to the Abrolhos Bank. Owing to the continental drainage in the study area, the continental shelf has a higher concentration of nutrients than that observed in the oceanic region (Raymont 1983, Suzuki et al. 2017). This increased concentration of nutrients favors an increase in phytoplankton biomass and, consequently, in the biomass of the micro-and mesoplankton organisms that feed on it, showing a strong interaction between these two communities (Irigoien et al. 2004, Hoover et al. 2006). Associated with this natural enrichment, phenomena such as upwelling can further increase productivity in coastal regions. The upwelling phenomenon in the Cabo Frio region has been extensively documented in the literature and occurs mainly during the spring–summer period (Valentin et al. 1976, 1987, Valentin 1984, da Silva et al. 2006, Coe et al. 2007, McManus et al. 2007).

The upwelling makes the Cabo Frio region more productive than other tropical areas off the Brazilian coast (Valentin 1984, Valentin et al. 1987, da Silva et al. 2006). During the WP, the southernmost transect, located off the coast of Cabo Frio, was differentiated from the other transects. The outbreak of SACW, a characteristic of the upwelling phenomenon in the Cabo Frio region, was detected at a low intensity only in the DP. Despite this, the large planktonic biomass found during the WP and the high phytoplankton density observed simultaneously likely reflect a post-upwelling period (Tenenbaum et al. 2017). In addition to being rich in nutrients, SACW has a low temperature, and the area impacted by this water mass has the highest planktonic biomass. Although not the main focus of the current study, this result indicates that an increase in temperature, possibly caused by global warming, can negatively interfere with plankton biomass, as observed in several studies (Chust et al. 2014, Campelo et al. 2019), providing critical information for further research. In addition to the latitudinal differences associated with the upwelling phenomenon in the Southern region of the study area, the transects located further north differed from the central and Southern transects during the DP. The Northern region of the study area showed continental impact from the Paraíba do Sul River plume, which enriches the region (Dias et al. 2015). The potential area impacted by this plume on the inner continental shelf forms a cone that extends north and south from the mouth and reaches 50-m isobaths (Souza et al. 2010). The entry of nutrients into the aquatic environment promotes not only an increase in the density of producers but also in their size, leading to an increase in both the abundance and size of organisms, which in turn consume them, contributing positively in an indirect way to the overall biomass of consumers (Pomati et al. 2020).

Nutritional contribution serves as a basis for increasing the trophic chain length and, thus, the mesozooplankton biomass in the areas of Cabo Frio and the mouth of the Paraíba do Sul River areas. In addition, these regions are impacted by oceanographic features with physical dynamics likely promoting the advection of planktonic organisms and biogenic particles. Although our study could not prove this, mesozooplankton advection promoted the crucial contribution of these organisms, increasing their biomass by 12 times (Wassmann et al. 2019). Owing to their nutritional richness and hydrodynamics, these areas of the Campos Basin are crucial to the region, as the zooplankton biomass, with micro- and meso-biomass, is a food subsidy for other organisms and the balance of the marine environment in coastal and oceanic regions (Landry & Swalethorp 2022).

The primary productivity is directly related to the depth of the marine environment. The absence of light in the lower layers than in the surface layers restricts energy production by photosynthetic organisms (Lourenço & Junior 2002), with the main source of zooplankton biomass at these depths originating from the sinking of organisms from the surface layers (Hernández-León et al. 2020). The higher biomass values found in TW than in the other waters can be attributed to the close relationship between plankton and producers, as this water mass is the only one entirely within the photic zone (Stramma & England 1999). In the Abrolhos Bank ecosystem and adjacent oceanic areas (Eastern Brazil), shelf stations had higher particle concentrations and mesozooplankton biomass than vertically stratified oceanic stations, due to the impact of the cold and nutrient rich SACW (Marcolin et al. 2013). We must consider that our sampling was carried out mainly during the night, and that the local biomass can undergo large diel variations directly related to the periods of the day (day and night; McLachlan & Brown 2006, Campelo et al. 2019). The higher biomass values found in TW than in the other water masses may also be linked to the fact that the most efficient upward migration to the surface layers at night was by organisms of relatively large size and biomass. This variation was recently observed in Northern Brazil (Campelo et al. 2019). The abiotic parameters that differentiated UCDW from AAIW did not reflect the differentiation in plankton biomass (micro- and mesoplankton) during the two collection periods. In addition, plankton biomass may have been impacted by similar circulation patterns in the two water masses (Stramma & England 1999).

## CONCLUSIONS

The observed distribution patterns suggest that the seston biomass (micro- and mesoplankton) is mainly structured in the region based on the horizontal and vertical partitioning of habitats and food resources. As reported for many organisms at different trophic levels, plankton may suffer from global and local changes induced by human population growth. Although our study did not aim to assess the effects of anthropogenic activities on planktonic biomass, it serves as a knowledge base for further focused studies covering a wide area of the Brazilian coast and Southwestern Atlantic.

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