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Environmental controls on the distribution of living (stained) benthic foraminifera on the continental slope in the Campos Basin area (SW Atlantic)

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Abstract

Living (stained) benthic foraminifera from deep-sea stations in the Campos Basin, southeastern Brazilian continental margin, were investigated to understand their distribution patterns and ecology, as well as the oceanographic processes that control foraminiferal distribution. Sediments were collected from 1050 m to 1950 m of water depth during the austral winter of 2003, below the Intermediate Western Boundary Current (IWBC) and the Deep Water Boundary Current (DWBC). Based on statistical analysis, vertical flux of particulate organic matter and the grain size of sediment seem to be the main factors controlling the spatial distribution of benthic foraminifera. The middle slope (1050 m deep) is characterized by relatively high foraminiferal density and a predominance of phytodetritus-feeding foraminifera such as *Epistominella exigua* and *Globocassidulina subglobosa*. The occurrence of these species seems to reflect the Brazil Current System (BCS). The above-mentioned currents are associated with the relatively high vertical flux of particulate organic matter and the prevalence of sandy sediments, respectively. The lower slope (between 1350 and 1950 m of water depth) is marked by low foraminiferal density and assemblages composed of *Bolivina* spp. and *Brizalina* spp., with low particulate organic matter flux values, muddy sediments, and more refractory organic matter. The distribution of this group seems to be related to episodic fluxes of food particles to the seafloor, which are influenced by the BCS at the surface and are deposited under low deep current activity (DWBC).

Keywords: benthic foraminiferal ecology; benthic foraminiferal distribution; Intermediate Western Boundary Current; Deep Water Boundary Current; particulate matter flux; grain size

1. Introduction

In deep-sea environments, benthic foraminifera are a major element of the soft sediment and hard-substrate communities, accounting for approximately 50% or more of the eukaryotic biomass (Gooday et al., 1992). Due to their central role in deep ocean ecosystems, these protists have been extensively studied for a better understanding of their contribution to the organic matter recycling and the impact of biological processes (Nardelli et al., 2010).

Benthic foraminiferal abundance, community structure, and distribution are determined by the relationship between trophic conditions (*i.e.*, vertical and horizontal organic matter fluxes) and oxygen availability, resulting from the interaction between oceanographic processes and bottom morphology (Schmiedl et al., 1997; Schmiedl et al., 2000; Morigi et al., 2001; Jorissen et al., 2007; Fontanier et al., 2008; Koho et al., 2008; Hess and Jorissen, 2009; Burone et al., 2011; Yamashita et al., 2016).

In well-oxygenated bottom water environments, the quantity and quality of the organic matter reaching the seafloor are the two most important factors controlling the density and diversity of benthic foraminiferal assemblages (e.g., Schmiedl et al., 1997; Den Dulk et al., 1998; Jorissen et al., 1998; Van der Zwaan et al., 1999; De Rijk et al., 2000; Schönfeld, 2001; Fontanier et al., 2002, 2003; Jorissen et al., 2007; Fontanier et al., 2008, 2016; Koho et al., 2007, 2008).

Fontanier et al. (2016), for example, observed high foraminiferal species richness in two different locations, at 530 m and 780 m of water depth off Madagascar, in fine sediments enriched in highly degraded organic matter, and characterized by low amino-acid bioavailability and reduced chlorophyllic freshness. The highest densities were observed at 780 m deep site, where dominant *Bolivina alata*, *Bulimina marginata*, *Haplophragmoides bradyi* and *Nouria compressa* were considered bioindicators of enhanced organic matter burial and eutrophic conditions. In contrast, at 530 m of water depth, dominant species *Uvigerina hispida* and *Uvigerina semiornata* were associated with mesotrophic conditions.

The organic carbon flux to the seafloor is determined by the export production, a fraction of primary productivity which survives loss due to mineralization processes in the water column and circulation patterns (Altenbach and Struck, 2001; Millero, 2005). Thus, this parameter varies with water depth and reflects temporal and spatial oscillations of primary production in surface waters (Berger and Wefer, 1990; Fontanier et al., 2002), particulate organic matter sources and oceanic circulation patterns (Millero, 2005).

In oligotrophic areas, a small quantity of organic matter is observed in deeper basins, accompanied by a reduction of the living foraminiferal density and biomass (e.g., Altenbach and Struck, 2001; Fontanier et al., 2002, 2016; Eberwein and Mackensen, 2006). Hence, the abundance and biomass of benthic foraminifera in the oligotrophic systems covary with the quantity and quality of the organic matter exported from the euphotic zone (Altenbach and Struck, 2001; Fontanier et al., 2003). The accumulation of organic matter and, hence, the food availability for benthic foraminifera dwelling on open slopes in oligotrophic environments is also highly dependent on sedimentary dynamics (e.g., Jorissen et al., 1994; Schmiedl et al., 2000; Hess et al., 2005; Fontanier et al., 2005; Koho et al., 2007; Fontanier et al., 2008; Hess and Jorissen, 2009).

This study focuses on the Campos Basin, which is located on the southwestern margin of the South Atlantic Ocean and is considered to be an oligotrophic basin with oxygenated bottom water (Suzuki et al., 2015; Sousa et al., 2006). Therefore, the ecosystem variability in the area is expected to reflect mainly changes in food supply reaching the seafloor (Gooday, 1988; 1993). In addition to this, the Campos Basin is of high scientific interest since the deep-sea benthic foraminiferal assemblages in this region are poorly known. Although Petróleo Brasileiro S/A (PETROBRAS) has been undertaking intense oil exploration and production activities in the Campos Basin, the area did not suffer anthropic impact (in terms of pollutants) (Carreira et al., 2010; Wagener et al., 2017). Hence, the main food supply in the basin should come from the organic matter exported from primary production (Carreira et al., 2010).

In this context, the main objectives of this work are (1) to study the spatial variability of living benthic foraminifera along bathymetric transects (from 1050 m to 1950 m of water depth) in the Campos Basin slope and (2) to understand the influence of environmental factors (i.e., particulate organic carbon fluxes, bottom-water dissolved oxygen content, sediment grain size and geochemical composition—calcium carbonate, organic carbon, total nitrogen and total lipid contents) on the living benthic foraminiferal assemblages, in terms of density, diversity, and assemblage composition.

2. Study area

The study area is situated between latitude 21°S and 23°S in the Campos Basin, specifically off the São Tomé Cape-East/Southeast Brazilian coast (Figure 1). The continental slope displays a convex profile to the north and a concave one to the south. The area is cut by the Itapemirim Canyon (Figure 1), which is an immature canyon, since no turbidite deposits are observed in this system (Kowsmann et al., 2016).

The Campos Basin exhibits remarkable features related to the vertical structure of water masses, ocean circulation, and coastal and oceanic fronts. Based on past studies performed on the west coast of the South Atlantic Ocean, the vertical structure of the water column is basically composed of five main water masses: The Tropical Water (TW), the South Atlantic Central Water (SACW), the Antarctic Intermediate Water (AAIW), the Upper Circumpolar Water (UCW), and the North Atlantic Deep Water (NADW) (Reid, 1989; Weatherly, 1993). The TW [temperature (T)>20°C; salinity (S)>36.2] occupies an oceanic mixed layer, restricted to the upper 150 m (Mémery et al., 2000) (Figure 2). Beneath the TW, the SACW (T=10°C to 20°C; S =34.8 to 36.2) extends vertically from 150 m to approximately 400 m of water deep (Silveira et al., 2008). Between 400 m and approximately 1070 m, the AAIW (T=4°C to 10°C; S =34.2 to 34.8) is characterized by a marked salinity minimum (Figure 2). The UCW (T=3.3°C to 3.5°C; S= 34.4 to

34.6) occurs down to 1200 m of water depth. Below the 1200 m, the NADW ($T=2.0^{\circ}\text{C}$ to 3.3°C ; $S=34.6$ to 34.9) flows southwards reaching 3000 m of water depth (Reid, 1989; Weatherly, 1993) (Figure 2).

Three currents are present in the Campos Basin: The Brazil Current (BC), the Intermediate Western Boundary Current (IWBC) and the Deep Western Boundary Current (DWBC) (Reid, 1989; Böebel et al., 1999; Stramma and England, 1999). The BC and IWBC together represent the Brazil Current System, which is characterized by meanders and eddies (Mascarenhas et al., 1971; Signorini, 1978; Campos et al., 2000; Palóczy et al., 2013). The BC is detected from the surface down to intermediate waters and flows south-southwestward, reaching speeds up to $0.80\text{ m}\cdot\text{s}^{-1}$, transporting TW and SACW. The Intermediate Western Boundary Current occurs from 500 m to 1200 m of water depth and carries the AAIW with contribution of the upper UCW to the north-northeast (Figure 2). This current has a swift core of velocities centered at a depth of 800 m that exceed $0.30\text{ m}\cdot\text{s}^{-1}$ (Böebel et al., 1999; Silveira et al., 2004). Below 2000 m of water depth, the Deep Western Boundary Current (DWBC) flows south-southwestward and transports NADW with contribution of the lower UCW (Figure 2). The presence of the São Paulo Plateau shifts the DWBC core offshore, reducing the interaction of the western boundary current system (BC and IWBC) with DWBC (Sousa et al., 2006).

The Campos Basin is characterized by the occurrence of a transient coastal upwelling, shelf break upwelling, coastal front, and meanders and eddies associated with the instability of the BC (Castro and Miranda, 1998; Palóczy et al., 2013). The wind is the main factor forcing the coastal upwelling off the São Tomé Cape at 22°S (Palóczy et al., 2013). Based on numerical simulation, Calado et al. (2010) recognized that near the São Tomé Cape, the coastal and oceanic systems interact and that the presence of the BC and its cyclonic meanders could cause an enhancement of coastal upwelling. According to the authors, eddy-induced upwelling may intensify the prevalent coastal upwelling due to wind and topographic effects.

In the Cabo Frio coastal region and continental shelf chlorophyll-*a* concentrations in surface waters vary up to 2 mg m^{-3} in winter and up to 25.5 mg m^{-3} in summer (Moser and Giancesella-Galvão, 1997). The organic matter flux to the

seafloor as well as sedimentary processes are controlled by the Brazil Current meandering, eddy formation, coastal and shelf break upwelling and Ekman transport (Mahiques et al., 2002, 2004). Offshore transport of shelf waters driven by eddy-like BC meanders are likely to be the most important mechanisms promoting the exchange between the shelf and the deep ocean (Mahiques et al., 2002, 2004).

The basin bottom topography is derived from tectonic evolution and/or evolution of the sedimentary basin, which is locally affected by the intensity of bottom currents (Viana et al., 2007; Viana, 2008). Sediment deposition induced by bottom currents may result in morphological features, which act as sediment traps or gateways that can displace sediments (Viana, 2008). The sedimentary cover of the upper slope in the study area consists of fine sand (Viana et al., 1998b) or sandy mud (Caddah et al., 1998). Reworked sand is deposited by BC in the upper slope (Viana et al., 1998a). The middle slope (550-1200 m of water depth) presents iron-rich laminated indurated fine sands and deep-water coral mounds (Viana et al., 1998b). Below 1200 m of water depth, a thin (<10 cm thick) Holocene calcareous ooze (a mixed coccolithophores/nanoplankton-foraminiferal ooze) occurs, overlying the iron-rich crust (Viana et al., 1998b).

3. Materials and Methods

3.1 Sediment sampling

Twenty sediment samples were collected during the austral winter of 2003 (Figure 1, Table 1), between 1050 and 1950 m of depth, using a modified Usnel Spade Corer MK (50 x 50 x 50 cm). At each station, sections (10 cm long x 10 cm wide x 20 cm high) were taken from each box core using a stainless-steel box. The cores were sliced down to 15 cm with 4 subsamples taken at 0-2 cm, 2-5 cm, 5-10 cm and 10-15 cm. We did not observe signs of bioturbation and disturbance due to the retrieval by the sampling gear. However, it is important to note that although sediment surface in box cores may appear completely undisturbed, this type of sampling gear may cause some loss of superficial sediment, influencing the protozoan composition of the meiobenthos (Bett et al., 1994). The sampling

program in 2003 did not include replicate collection for each station. We are aware that analysis based on replicates is established as mandatory for environmental monitoring (Schönfeld et al., 2012), which is however not the focus of our study. Nevertheless, it should be noted that our samples may potentially have a limited representation of the spatial variability (Schönfeld et al., 2012).

3.2. Sediment grain size and bulk geochemistry data

Sedimentological (grain-size analysis) and geochemical (calcium carbonate, organic carbon, total nitrogen and total lipid contents) data were obtained from surface sediments (0-2 cm). The grain-size analysis was undertaken using laser diffraction (Shimadzu model SALD-3101). Calcium carbonate (CaCO_3) was determined by the difference in weight of the sediment prior to and after acidification with 1.0 N HCl. Values are reported as percentages of dry weight (Mahiques et al., 2004). Organic carbon (C_{org}) and total nitrogen (N_t) were determined by a CHNS/O PerkingElmer analyzer (2400 series II) prior to and after acidification of the sediment with 1.0 N HCl solution to eliminate carbonates. Total lipid content was obtained using gas chromatography mass spectrometry (GC/MS; Finnigan Focus DSQ GC/MS system) while fatty acids (FAs, as fatty acid methyl esters “FAMES” after reaction with BF_3/MeOH at 85°C for 2 h) were analyzed using GC with flame ionization detection (GC-FID; Hewlett–Packard 6890). Laboratory blanks showed no contamination during sample processing.

3.3 Dissolved oxygen data

Bottom water samples were collected using a Niskin and GO-FLO sampler linked to conductivity, temperature and depth sensor in the rosette. The dissolved oxygen (DO) content was determined using the Winkler method modified by Grasshoff (1983).

3.4 Vertical flux estimation of particulate organic matter

The determination of the particulate organic flux to the seafloor was based on the Dunne et al. (2005) models. Some of the following factors were considered: the role of the pelagic trophic chain; the controlling mechanisms for aggregation and disaggregation of phytoplankton cells; the role of minerals (calcite and aragonite), both as ballast of the particle or as a protective agent for organic material; the metamorphosis of organic matter during downward transport in the water column; the influence of hydrodynamics and the characteristics of water mass (Boyd and Trull, 2007). The model was fed with satellite data (MODIS and SeaWiFS). To determine the fraction of nanoplankton and picoplankton (the input data for the model provided by Dunne et al., 2005), we used the model proposed by Ciotti et al. (2002).

The chosen study period was 24 days before the vertical flux of particulate organic matter reached the ocean floor, since the remote sensing data used in the SeaWiFS sensor had a temporal resolution of 8 days. The time response of benthic foraminifera (density and species composition) to particulate organic flux contribution was based on the study of Heinz et al. (2002), who estimated a response of approximately 22 days.

3.5 Geostrophic velocity

Monthly mean dynamic topography maps were obtained by averaging satellite products of absolute dynamic topography fields. The final product (DT-GLOBAL-TWOSAT-MADT-H), available in a 0.25° grid, was created by merging the data of altimetry sensors from two satellites. The mean geostrophic streamline function (ψ) was calculated using η , following the approach of Kundu and Cohen (2011). The altimeter products were produced by Ssalto/Duacs and distributed by Aviso, with support from Cnes (<http://www.aviso.altimetry.fr/duacs/>).

For the period from May 2002 to June 2003, surface streamline function fields and geostrophic velocities were plotted for a quantitative analysis of the BC axis

position and meandering patterns. Considering in total a set of 14 analyzed images, we selected seven images to display the geostrophic velocity snap shots for June 2002 (Figure 3a), August 2002 (Figure 3b), October 2002 (Figure 3c), December 2002 (Figure 3d), February 2003 (Figure 4d), April 2003 (Figure 4d), and June 2003 (Figure 4d).

3.6 Benthic foraminifera

For foraminiferal analyses, each subsample was stained with a 4% formalin solution of rose Bengal, immediately after sampling to differentiate between living and dead foraminifera (Walton, 1952). The sediment was homogenized and an aliquot of 10 cm³ was carefully washed in the laboratory through a >63 µm sieve. The remaining residues were dried, and living (stained) specimens of benthic foraminifera were picked and stored on slides for analysis using a stereomicroscope (80X). All living specimens present in each sample were summed, and the total living assemblage (abundance and composition) in 15 cm of the cores (0-2 cm, 2-5 cm, 5-10 cm and 10-15 cm) below the water-sediment interface was analyzed in this study. Such methodology was considered since a significant number of species/specimens were found living in the first 15 centimeters below the water-sediment interface. Therefore, the foraminiferal density (FD) at each station corresponds to a number of specimens per 40 cm³ of the sediment (each subsample corresponding to 10 cm³). The chosen sample preparation method did not allow inclusion of the organic-walled taxa, which shrink and become unrecognizable during picking of dried samples (Fontanier et al., 2016).

Tubular fragments were considered to be equivalent to one-third of a specimen (Harloff and Mackensen, 1997, Kurbjeweit et al., 2000; Heinz and Hemleben, 2003) to avoid overestimation of tubular specimens. Specimens were identified following the generic classification and taxonomy based on Boltovskoy et al. (1980), van Morkhoven et al. (1986), Loeblich and Tappan (1987) and Jones (1994). Some species were imaged using a digital Scanning Electron Microscope (SEM) (Plate 1). Assemblage data were evaluated using the Shannon-Wiener

diversity (H' ; using \log_e) (Shannon, 1948), Pielou evenness (J') (Pielou 1975), and species richness (S) (Clarke and Gorley, 2006). Indices H' and J' were calculated only for densities higher than 100 ind./40 cm³.

3.7 Statistical data analysis

Spearman correlation analyses were performed considering $p < 0.05$ as significant. The foraminiferal indices (S , J' and H') and the relative abundance of representative species (present in 10% of the samples with abundance $> 2\%$ per station) were correlated with the sand and mud content, C_{org} , N_t , $CaCO_3$, total lipids, and particulate organic matter flux to the sea floor. The relative abundance of representative benthic foraminiferal species was used for classification and ordination analyses. The Bray-Curtis similarity index based on the abundance similarity matrix was also used (Bray and Curtis, 1957). Cluster analysis was performed by agglomerative hierarchical clustering, using the unweighted pair group method with arithmetic mean (UPGMA) and ordination analysis was performed using the non-metric multidimensional scaling (nMDS).

The subset of environmental variables that were best related to representative species was obtained using the Biota and/or Environmental Matching (BEST) procedure in PRIMER v6.1.16. The method used was Biotic-Environmental Matching (BIOENV), based on the Spearman correlation between the Bray-Curtis similarity matrix (biological data) and the resemblance matrices obtained by environmental variables. The variables considered for this analysis included the sand and mud content, C_{org} , N_t , $CaCO_3$, total lipids, particulate organic matter flux to the sea floor and DO. All data were standardized by natural $\log(x+1)$. To determine which benthic foraminiferal species contributed the most to the nMDS dissimilarities, a SIMPER (*similarity percentage breakdown*) analysis using the Bray-Curtis similarity was performed in PAST (Hammer et al., 2001).

4. RESULTS

4.1. Sediment grain size and bulk geochemistry

Grain size analysis showed that sandy sediments were predominant at 1000 m deep (Figure 5a). High mud contents (up to 69%) occurred at all the stations located between 1300 m and 2000 m of water depth (Table 1). The calcium carbonate content in the sediment varied between 24% and 50% in the study area. Lower CaCO_3 values (24 to 39%) characterized the middle slope and water depths <900 m (Table 1; Figure 5b).

The C_{org} concentrations, N_t content and total lipid content showed heterogeneous pattern in the study area, with some trends described below. The C_{org} concentrations ranged between 4.9 mg g^{-1} and 18 mg g^{-1} (Figure 5c). Three of the four sandy sediments showed the lowest C_{org} contents in samples/stations of the middle slope. An increase in C_{org} was observed in the muddy sediments, both in the middle and lower slope. The N_t content varied between 0.9 mg.g^{-1} and 1.8 mg.g^{-1} (Figure 5d; Table 1), and its distribution pattern was mostly similar to that of C_{org} (Figure 5c), that is, in 11 stations out of 16 that presented higher values of C_{org} showed higher values of N_t . The highest values of total lipid content were observed at northern stations (middle-lower slope) and varied between $1132 \text{ } \mu\text{g g}^{-1}$ and $1065 \text{ } \mu\text{g g}^{-1}$ (Table 1; Figure 5e).

4.2. Dissolved oxygen

The dissolved oxygen concentration in the bottom water varied between 4.5 mL L^{-1} and 5.5 mL L^{-1} , which can be verified at Table 1. The higher concentration (5.5 mL L^{-1}) was observed at deep stations on the lower slope (Table 1).

4.3. Vertical flux of particulate organic matter

The model-based estimation of the particulate organic matter flux showed values between $14.6 \text{ mgC m}^{-2}\text{day}^{-1}$ and $24.4 \text{ mgC m}^{-2}\text{day}^{-1}$, which are represented

in Figure 5f. The map shows that the highest values ($24\text{-}25 \text{ mgC m}^{-2}\text{day}^{-1}$) occurred at the southern stations, mainly in the shallower regions (Table 1).

4.4. Geostrophic velocity

Images showing the variation of mean geostrophic stream function associated with mesoscale surface movement were presented for the average conditions throughout 2002 (Figures 3a-June; 3b- August; 3c- October; 3d- December), and 2003 (Figures 4a-February; 4b-April; 4d- June).

According to Figure 3a, in June/2002 the BC axis was closer to the stations sampled in the south. In August/2002 (Figure 3b), the BC axis displaced offshore. In June/2002 and August/2002 the BC showed relative more meandering than October/2002 and December/2002 (Figure 3c and 3d respectively). In February/2003 (Figure 4a), the BC axis was displaced toward the 100 m isobath, becoming less convoluted.

In April/2003 (Figure 4b), the BC axis overruled the region delimited by the 100 m isobath. In June/2003 (Figure 4c) the BC was positioned beyond the offshore continental shelf.

4.5. Benthic foraminifera assemblage characteristics

In the study area, calcareous foraminifera of the order Rotaliida had the highest relative abundance of up to 98% of the assemblage. Other calcareous orders such as Miliolida, Lagenida, Robertinida and Spirillinida reached the highest percentages at stations 53 and 60 (19%), located at 1910 m and 1055 m, respectively. Agglutinated foraminifera (Astrorhizida, Lituolida, and Textulariida) were poorly represented in the study area with abundances $\leq 5\%$.

A total of 63 genera and at least 87 living benthic foraminiferal species were recorded in the Campos Basin slope, with some of them illustrated in Plate 1. It should be noted that some species were unidentified due to a large number of small individuals. The most frequent species are reported in Table 2.

Foraminiferal density varied between 62 and 2208 individuals/40 cm³ (474 ind./40 cm³ on average) and two stations, the northernmost one and the one in the south, had exceptionally high densities (Figure 6a). Species richness (S) varied between 8 and 43 (Figure 6b) with 16 on average. Index J' showed a range between 0.50 and 0.82 with 0.7 on average (Figure 6c), while H' varied between 1.29 and 2.97 with 1.9 as a mean value (Figure 6d). All indices showed relatively high values in the middle-lower slope stations (Table 2).

4.6. Statistical analysis

The nMDS and cluster analysis allowed for the identification of three main groups of stations reflecting a depth gradient. The Group I clustered together the middle-lower slope stations, while Group II grouped together the lower slope stations. Finally, Group III was composed of only station 56, representing a lower slope outlier (Figures 7 and 8). The SIMPER analysis showed an average dissimilarity of 83.12% (Table 3). The species, which showed the highest dissimilarity included *Globocassidulina subglobosa* (31.48%), *Bolivina* spp./*Brizalina* spp. (6.58%), and *Epistominella exigua* (6.95%). Among the taxa, the most contributive species to the Group I were *G. subglobosa* (Figure 9a) and *E. exigua* (Figure 9b), whereas Group II and Group III had the greatest contributions by *Bolivina* spp./*Brizalina* spp. (Figure 9c) and *Cibicidoides* spp. (Figure 9d), respectively. According to the BIOENV analysis (correlation of 0.53), the particulate organic matter flux and sand percentage were the main variables controlling the distribution of living benthic foraminifera in the studied samples. Table 4 shows the Spearman correlation matrix among biotic and abiotic parameters. The particulate organic matter flux correlated positively with the percentage of sand (0.56) and negatively with the CaCO₃ content (-0.56) and mud fraction (-0.47). The percentage of sand was negatively correlated with N_t (-0.51). Organic carbon showed significant positive correlations values with the CaCO₃ (0.53) and N_t (0.62) contents. Foraminiferal density was positively correlated with the percentage of sand (0.7)

and particulate organic matter flux (0.79). A significant correlation was also found between S and the particulate organic matter flux (0.49), as well as both *Bolivina albatrossi* (0.52) and *E. exigua* (0.67) significantly correlated with particulate organic matter flux. Significant positive correlations were noted of C_{org} and N_t with the frequency of *Cibicidoides* spp. (0.51 and 0.55, respectively).

5. Discussion

5.1. Sedimentological and geochemical features

The grain size and geochemical data show a heterogeneous distribution pattern distribution in the middle-lower slope of the Campos Basin. These abiotic parameters seem to be controlled by hydrodynamics (i.e. geostrophic currents) and the bottom physiography (continental slope, Plateau of São Paulo and Itapemirim canyon) (Kowsmann and Carvalho, 2002). The relatively high percentages of sand along the middle slope, mainly in the south (Figure 5a), could be due to the bed-load transfer of sand from the shelf to the middle-lower slope. According to Viana et al. (1998b), this sector of the slope is characterized by remobilization of the bottom sediments by the BC, and it is known that this current contributes to the formation of sandy deposits on the shelf edge. These deposits are transferred to the middle-lower slope and are further remobilized by eddies.

No significant positive correlations between the mud content in the sediments and the total lipids, C_{org} , N_t , and particulate organic matter flux were observed. This suggests that the deposition of the sedimentary organic matter components is influenced by seafloor bottom topography as well as by hydrographic and sedimentary regimes. Additionally, no correspondence was observed between the particulate organic matter flux and the spatial distribution of sedimentary total lipids, C_{org} and N_t contents. However, a correlation of 0.62 was observed between N_t and C_{org} , possibly indicating high levels of inorganic nitrogen contributing to the sedimentary organic matter composition of the Campos Basin slope, according to Meyers (1997).

The absence of correlation between the particulate organic matter flux and the total lipids might indicate the occurrence of other lipid compounds in sediments besides the ones derived from phytoplankton, and/or the presence of lipids with high resistance to degradation (Volkman, 2006; Carreira et al., 2010). We argue that there may be “a time scale discrepancy” between estimated particulate organic matter flux and geochemical components measured in the surface sediments. For the Holocene, sedimentation rates in the upper and middle slope of the Campos Basin are estimated to be approximately 14 cm ky^{-1} in the north and 7 cm ky^{-1} in the south (Viana et al., 1998b). Therefore, surface sediment samples represent a temporal mixture of hundreds of years, and the geochemical composition of the Campos Basin sediments has a temporal resolution limit when applied as a tool for the recognition of contemporary oceanographic processes, if compared to particulate organic matter flux in the same period.

In the study area, vertical particulate organic matter flux can be influenced by meanders and the BC eddies (Schmid et al., 1995), providing a supply of phytodetritus to deeper regions (Figures 3 and 4). Although the periodicity of the surface water algal blooms in the Campos Basin is still unknown, the blooms are probably enhanced by eddy-induced upwelling off the São Tomé Cape (Palóczy et al., 2013).

In relation to the calcium carbonate content in the sediment, deeper stations showed an increase of CaCO_3 in the sediment, mainly in the southern area, which is related to the occurrence of the carbonate ooze in the Campos Basin from 1200 m of water depth (Viana et al., 1998b) because of the reduced supply of siliciclastic materials to the deeper slope areas of the Campos Basin. With the preservation of calcium carbonate and presence of the carbonate ooze (Viana et al., 1998a, b), oxygen penetration can be relatively deep in the sediment.

5.2. Living foraminifera and environmental factors

5.2.1. Controls on foraminiferal abundance and diversity

The UPGMA and nMDS identified three principal groups of stations: middle-lower slope stations (Group I), lower slope stations (Group II) and the lower slope outlier, station 56 (Group III). In general, Group I was characterized by higher foraminiferal density, higher richness and higher diversity of species, as well as exhibited higher vertical particulate organic matter fluxes and sand content. The lower slope stations of Group II were commonly characterized by low particulate organic matter flux and associated with fine grained sediments, likely reflected in lower density, lower richness and lower diversity values. The distinguished groups are likely to reflect the BCS variability, which influences both the distribution of particulate organic matter flux and sedimentation regime.

The high diversity of deep-sea benthic communities can be explained by the presence of organic-rich patches on the ocean floor (Grassle and Morse-Porteous, 1987; Snelgrove et al., 1996; Levin et al., 2001), sporadic and discrete disturbance events, and the lack of barriers, which all may influence the dispersion of living organisms (Levin et al., 2001).

The specific differences in the distribution of benthic foraminiferal density, diversity, richness and evenness in the study area (station 60 and 75) might be linked to local environmental variability related to the BCS. Such local variability may be associated with surface and bottom currents, meanders, eddies, the position of the axis of the Brazil Current, lateral flux, as well as bottom morphology, sedimentation rate, and degradation of particulate organic matter in the water column (Thiel et al., 1990; Klaas and Archer, 2002; Boyd and Trull, 2007; Yamashita et al., 2016), predation, resource partitioning, competitive exclusion, and facilitation (Levin et al., 2001). Although it is known that foraminiferal assemblages have generally patchy distributions due to food control (Hohenegger et al., 1993), several studies have demonstrated that seasonal changes of foraminiferal assemblages may cause patchiness as well (e.g., Silva et al., 1996; Fontanier et al., 2002, 2003; Eberwein and Mackensen, 2006; Burone et al., 2011).

5.2.2. Controls on species assemblages

In the deep-sea benthic environments the oxygen concentration may be a limiting factor for the establishment of an infaunal living benthic foraminifera community (e.g., Alve and Bernhard, 1995; Schönfeld, 2002; Gooday, 2003). The values of dissolved oxygen concentration in the Campos Basin bottom waters are between 4.5 and 5.5. mL.L⁻¹ (Table 1), revealing the presence of oxic conditions (Kaiho, 1994). Pore waters of surface sediments should also be oxic, mainly in the middle slope in the southern region, due to the high porosity and permeability of the sandy sediments (Armstrong and Brasier, 2005). Therefore, we propose that there is no oxygen restriction for the proliferation of shallow infaunal and epifaunal benthic foraminifera in the study area, as proposed by Sousa et al. (2006).

The benthic foraminiferal species that contributed the most for the dissimilarity of nMDS groups was *G. subglobosa*. This species was observed mainly in the south. This species is known to thrive in environments with input of phytodetritus and oxic bottom waters (Gooday, 1993; Sousa et al., 2006). Thus, it can be used as an indicator of the presence of food pulses in the marine environment (Gupta, 2010). Moreover, *G. subglobosa* was reported as able to adapt to environments characterized by enhanced bottom current velocities (Mackensen et al., 1995; Schmiedl et al., 1997). The occurrence of *G. subglobosa* in the Campos Basin, under the domain of IWBC (exceeding 0.30 m.s⁻¹) with an input of food originating from an upwelling region (Palóczy et al., 2013), corroborates the ecological preferences of this species, as described in the literature. *Globocassidulina subglobosa* has also been associated with increased phytodetritus input, feeding selectively on specific components of seasonally deposited phytodetritus in the slope (560 m of w.d.) off the western Antarctic Peninsula. Higher amounts of polyunsaturated fatty acids were found inside the species, indicating its preference for phytodetrital food sources (Suhr et al., 2003). In our study, no correlation between *G. subglobosa* and total lipids in the sediment was observed. This again suggests that some of the lipids contained in the total lipids fraction may be refractory, and are not used as food by most living organisms (Volkman, 2006; Carreira et al., 2010).

In the middle slope stations (1050 m deep; Group I), the second species that highly contributed to the dissimilarity of nMDS groups was *E. exigua*. This species and *Uvigerina* spp. have been considered by Fontanier et al. (2003) as the first species to respond to labile organic matter inputs in an ecosystem. The positive correlation between *E. exigua* and particulate organic matter flux may reflect a phytodetritus input in the middle slope stations out the southern region of the study area. *Epistominella exigua* has been regarded as an opportunistic species, able to thrive and reproduce rapidly in the presence of phytoplankton floccules following important surface water bloom periods (Gooday, 1988, 1993; Loubere, 1998; Fontanier et al., 2003). The presence of *E. exigua* and *G. subglobosa* together seems to be related to the presence of relatively high particulate organic matter vertical flux and sandy sediments (oxic pore water conditions) due to the Brazil Current System (BCS) and IWBC activity in the study area.

In Group II (1350-1950 m deep stations), the higher contribution of *Bolivina* spp./*Brizalina* spp. to the dissimilarity of this group seems to confirm the input of food to the lower slope of the Campos Basin (Mill et al., 2015). Due to the Brazil Current meanders and eddies, eddy-induced upwelling off the São Tomé Cape activities can provide food resources to deeper regions in the basin. *Bolivina* spp. show several peculiarities: they are considered shallow infaunal protists (Gooday, 1994), a deposit feeder species, a proxies of food availability (see Corliss, 1985; Corliss and Chen, 1988; Debenay and Redois, 1997; Schmiedl et al., 1997); and are characteristic of organic-rich environments (Lutze and Coulbourn, 1984). Although this taxon indicates food availability in the environment, it seems to be less dependent on the pulses of phytodetritus. These species should feed on products resulting from the decomposition of organic matter by bacteria, and may reach high densities in sedimentary deposits with more refractory organic matter which occur in the Campos Basin slope. Indeed, according to Carreira et al. (2010), a fraction of lipids associated with more refractory organic matter tend to become higher with increasing water depth. This increase in our study might be related to the low DWBC current activity as confirmed by the presence of muddy sediment.

In Group III (depth of 1350 m), *Cibicidoides* was the taxon which highly contributed to the dissimilarity. It is noteworthy that Group III is formed only by the station 56 and is located at the mouth of the Itapemirim Canyon (Schreiner et al., 2008). Lower values of foraminiferal density, and higher values of C_{org} and N_t , were observed, compared to other stations located at the same depth (~ 1300 m). This difference may be explained by the sedimentary dynamics and variability of the organic matter accumulation between the canyon and open slope environments (Schmiedl et al., 2000; Hess et al., 2005; Koho et al., 2007; 2008; Hess and Jorissen, 2009). At the same time, more samples would be necessary to better understand and evaluate the environmental system associated with Group III and the mouth of the Itapemirim Canyon.

The foraminiferal community structure observed in the Campos Basin agrees well with the data obtained for food-limited systems, e.g., the abyssal North Atlantic (Gooday and Rathburn, 1999; Ohkushi and Natori, 2001; Enge et al., 2012), and Mozambique Channel (Fontanier et al., 2016). On the other hand, the observed community pattern contrasts with the faunal density and composition observed in meso-eutrophic systems, e.g., the Bay of Biscay (Fontanier et al., 2002).

6. Conclusions

Live (rose Bengal-stained) foraminiferal faunas show major changes in community structure (density, diversity, richness and evenness) in the middle and lower slopes of the Campos Basin, southeastern Brazilian coast. The particulate organic matter vertical flux and grain size of the sediment driven by hydrodynamics seem to be the main controlling factors in the spatial distribution and structural community of benthic foraminifera in the basin.

Living benthic foraminiferal assemblages from the Campos Basin slope that were investigated in this study presented decreasing density as the depth increased. The distribution of foraminiferal assemblages in the basin seems to be related to changes in environmental conditions, primarily driven by the particulate organic matter flux and the sediments texture and composition. These parameters

are driven by hydrodynamics, that is, by BCS variability and by the eddy-induced upwelling off the São Tomé Cape

Despite the spatial variability in the abundance and distribution of the main species of living benthic foraminifera, two main assemblages were recognized. In middle-lower slope stations, characterized by higher vertical particulate organic matter fluxes and well oxygenated environments, it was found higher foraminiferal density, richness and diversity of species. In this zone, the assemblages are dominated by species that respond to phytodetritus seasonal input, such as *E. exigua* and *G. subglobosa*. In the lower slope stations, less affected by the seasonal flow of phytodetritus, fine-grained sediments were found along with relatively high organic matter content but with less quality to be used as food. In these stations, foraminiferal assemblages characterized by lower density, richness and diversity were dominated by *Bolivina* spp.

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Table 1: Sampling localities, water depth, sedimentological and oceanographic data.

Station	Latitude (S)	Longitude (W)	Depth (m)	Mud (%)	Sand (%)	CaCO ₃ (%)	C _{org} (mg.g ⁻¹)	N _t (mg.g ⁻¹)	Flux (mgC.m ⁻² .day ⁻¹)	Total lipids (µg g)	DO (mL.L ⁻¹)
46	39.8168	-22.1821	1336	95	5	42	10.4	1.3	20.1	6263	4.7
47	39.7846	-22.1845	1654	97	3	35	11.5	1.4	21.5	8074	4.7
48	39.7291	-22.1879	1968	93	7	43	9.5	1.0	15.5	8665	5.1
51	39.8680	-22.0761	1299	80	20	31	13.3	1.5	18.3	8259	5.0
52	39.7754	-22.0789	1643	93	7	36	12.8	1.6	17.5	7847	4.8
53	39.7172	-22.0795	1910	82	18	49	12.3	1.3	17.5	10351	4.5
56	39.8270	-21.9543	1357	94	6	32	14.9	1.8	16.5	7465	4.5
57	39.7955	-21.9543	1587	91	9	30	11.8	1.7	18.4	7550	4.6
58	39.6760	-21.9574	1942	86	14	43	12.6	1.0	15.7	5447	5.5
60	39.8618	-21.8806	1055	61	39	27	7.0	1.0	19.1	6035	4.9
70	40.1480	-22.5845	1043	87	13	39	11.8	1.4	23.5	3471	4.8
71	40.0706	-22.6482	1342	90	10	41	12.9	1.0	21.3	8685	5.1
72	40.0155	-22.6843	1623	95	5	44	13.7	1.4	16.7	1871	4.9
73	40.0125	-22.6931	1906	93	7	48	14.3	1.4	14.6	5741	5.5
75	40.064	-22.5245	1043	52	48	47	18.0	1.4	23.9	2999	4.9
76	40.0028	-22.5682	1337	91	9	42	11.6	1.3	21.3	6126	4.9
77	39.9652	-22.6009	1670	93	7	45	12.8	1.5	16.2	1132	4.7

(Montfort, 1808)	0	4	0	0	0	9	0	7	0	3	0	0	0	5	0	0	0	0	0	0
	0	0	0	0	0	6	0	9	0	6	0	0	0	4	0	0	0	0	0	0
<i>Miliolinella</i>	0.	0.	3.	0.	3.	1.	0.	0.	2.	8.	0.	0.	0.	0.	4.	0.	0.	1.	1.	5.
<i>subrotunda</i>	0	0	3	4	1	0	0	5	9	1	0	0	0	0	3	0	3	0	6	8
(Montagu, 1803)	0	0	1	1	3	0	0	5	0	9	0	0	0	0	6	0	6	2	8	1
								1												
	0.	0.	0.	0.	0.	0.	0.	1.	1.	0.	0.	0.	0.	1.	0.	0.	0.	0.	0.	0.
	0	5	6	0	0	5	0	1	5	0	0	0	0	5	0	0	3	0	0	0
<i>Miliolinella</i> spp.	0	5	6	0	0	0	0	0	9	0	0	0	0	4	0	0	6	0	0	0
								1												
	0.	0.	0.	0.	0.	0.	0.	0.	0.	5.	0.	0.	0.	0.	3.	0.	0.	0.	0.	0.
	0	0	0	0	0	0	0	0	0	3	8	0	0	0	8	0	0	0	0	0
<i>Neoeponides</i> spp.	0	0	0	0	0	0	0	0	0	0	4	0	0	0	7	0	0	0	0	0
	0.	0.	0.	7.	0.	0.	0.	0.	0.	0.	6.	3.	4.	0.	0.	2.	5.	4.	6.	0.
<i>Nonionella turgida</i>	0	0	0	0	0	0	0	0	0	2	7	3	8	0	0	6	7	0	7	0
(Williamson, 1858)	0	0	0	1	0	0	0	0	0	4	2	6	2	0	0	8	8	8	2	0
				1																
	0.	4.	0.	9.	7.	0.	0.	0.	0.	0.	0.	0.	0.	0.	5.	2.	0.	0.	0.	0.
	0	4	0	7	1	0	0	0	0	0	0	0	0	0	3	8	0	0	0	0
<i>Paracassidulina</i> spp.	0	0	0	9	4	0	0	0	0	0	0	0	0	0	7	9	0	0	0	0
	0.	0.	0.	0.	0.	0.	0.	8.	0.	0.	3.	0.	4.	0.	0.	0.	0.	0.	0.	0.
<i>Trifarina angulosa</i>	0	0	0	0	0	0	0	7	0	0	4	0	8	0	0	0	0	0	0	0
(Williamson, 1858)	0	0	0	0	0	0	0	9	0	0	5	0	2	0	0	0	0	0	0	0
	0.	8.	0.	3.	7.	0.	0.	0.	0.	1.	0.	3.	4.	0.	3.	8.	0.	0.	0.	0.
<i>Uvigerina peregrina</i>	0	7	0	3	1	0	0	0	0	0	8	7	8	0	8	0	3	0	0	9
Cushman, 1923	0	9	0	0	4	0	0	0	0	8	4	8	2	0	7	5	6	0	0	7

Table 3: Result of SIMPER analysis: Av. dissim= average dissimilarity; and Contrib.= contribution.

Taxon	Av. dissim	Contrib. %	Cumulativ e %	Mean 2	Mean 1	Mean 3
					285.0	
<i>Globocassidulina subglobosa</i>	26.17	31.48	31.48	52.40	0	8.00
<i>Bolivina</i> spp./ <i>Brizalina</i> spp.	5.47	6.58	38.07	42.50	9.78	0.00
<i>Epistominella exigua</i>	4.95	6.95	44.02	0.00	75.20	0.00
<i>Bolivina albatrossi</i>	2.81	3.38	47.40	0.10	31.80	0.00
<i>Nonionella turgida</i>	2.49	3.00	50.40	1.20	20.40	0.00
<i>Bolivina doniezi</i>	2.48	2.98	53.38	0.00	35.60	0.00
<i>Paracassidulina</i> spp.	2.29	2.75	56.13	2.40	15.10	0.00
<i>Cassidulinoides parkeriana</i>	2.04	2.45	58.59	0.00	42.70	0.00
<i>Miliolinella subrotunda</i>	1.97	2.37	60.95	1.80	35.00	0.00
<i>Uvigerina peregrina</i>	1.89	2.27	63.22	4.00	20.20	0.00
<i>Neoeponides</i> spp.	1.87	2.25	65.48	0.00	45.20	0.00
Unidentified, fragmented or juveniles	1.76	2.12	67.59	0.80	30.90	0.00
<i>Cibicidoides</i> spp.	1.63	1.97	69.56	3.30	3.22	28.00
<i>Cibicides kullenbergi</i>	1.49	1.79	71.35	0.10	17.90	0.00
<i>Trifarina angulosa</i>	1.29	1.56	72.91	2.40	7.11	0.00
<i>Bolivina striatula</i>	1.20	1.45	74.35	4.00	5.33	0.00
<i>Fissurina laevigata</i>	1.15	1.38	75.73	4.80	7.11	0.00
<i>Gavelinopsis</i> spp.	1.08	1.30	77.03	6.40	1.78	0.00
<i>Eponides</i> spp.	1.08	1.30	78.33	2.00	2.00	16.00
<i>Discorbinella nitida</i>	1.07	1.28	79.61	1.70	6.22	0.00
<i>Fissurina orbignyana</i>	1.05	1.26	80.87	0.00	4.56	0.00
<i>Brizalina</i> sp1.	1.00	1.20	82.07	0.00	1.78	16.00
<i>Uvigerina bradyana</i>	0.92	1.10	83.18	0.00	12.00	0.00
<i>Hoeglundina elegans</i>	0.89	1.07	84.25	4.60	7.00	1.00
<i>Cibicides</i> spp.	0.89	1.07	85.32	0.40	0.89	16.00
<i>Pyrgoella irregularis</i>	0.83	1.00	86.32	0.30	15.90	0.00
<i>Fursenkoina squamosa</i>	0.73	0.87	87.19	0.00	14.20	0.00
<i>Bolivinellina translucens</i>	0.67	0.81	88.01	0.80	1.78	9.00
<i>Cassidulina laevigata</i>	0.64	0.77	88.78	0.80	6.00	0.00
<i>Criboelphidium</i> sp1.	0.62	0.75	89.52	0.00	8.00	0.00
<i>Bulimina aculeata</i>	0.59	0.72	90.24	0.00	4.78	0.00
<i>Lenticulina cultrata</i>	0.56	0.67	90.91	4.10	0.89	0.00
<i>Siphouvigerina proboscidea</i>	0.54	0.65	91.56	1.60	6.33	0.00
<i>Oridorsalis umbonatus</i>	0.53	0.64	92.2	0.00	11.60	0.00
<i>Alabaminella weddellensis</i>	0.53	0.63	92.84	3.30	0.89	0.00
<i>Bolivina aenariensis</i> var. <i>multicostata</i>	0.50	0.60	93.44	0.00	10.70	0.00
<i>Astacolus</i> spp.	0.45	0.54	93.98	0.00	2.67	0.00
<i>Nonion</i> spp.	0.44	0.53	94.5	3.20	0.00	1.00

<i>Nonionoides</i> spp.	0.41	0.50	95,00	1.60	1.78	0.00
<i>Pseudotriloculina laevigata</i>	0.29	0.35	95.35	0.10	5.67	0.00
<i>Uvigerina</i> sp1.	0.27	0.33	95.68	0.10	3.33	0.00
<i>Pseudononion</i> spp.	0.26	0.31	95.99	0.00	3.67	0.00
<i>Bolivina</i> sp1.	0.23	0.28	96.27	0.00	6.00	0.00
<i>Miliolinella</i> spp.	0.22	0.27	96.53	1.40	0.11	0.00
<i>Cibicides wuellerstorfi</i>	0.22	0.26	96.80	0.00	2.00	0.00
<i>Sigmoilina sigmaidea</i>	0.21	0.26	97.06	0.20	2.67	0.00
<i>Glaphyrammina americana</i>	0.18	0.22	97.27	0.00	3.56	0.00
<i>Reophax scorpiurus</i>	0.18	0.22	97.49	0.00	3.56	0.00

Taxon	Av. dissim	Contrib. %	Cumulative %	Mean 2	Mean 1	Mean 3
<i>Rhabdammina</i> spp.	0.15	0.19	97.68	0.50	1.56	0.00
<i>Reophax subfusiformis</i>	0.14	0.17	97.85	0.30	0.67	1.00
<i>Bolivina simplex</i>	0.14	0.16	98.01	0.00	3.56	0.00
<i>Hyalinea balthica</i>	0.14	0.16	98.17	0.00	3.56	0.00
<i>Bolivina</i> sp1.	0.14	0.16	98.34	0.00	3,56	0.00
<i>Pullenia bulloides</i>	0.13	0.16	98.50	0.00	2.22	0.00
<i>Cibicoides</i> sp1.	0.12	0.15	98.65	1.00	0.00	0.00
<i>Eggerella bradyi</i>	0.08	0.10	98.75	0.20	0.44	0.00
<i>Pullenia</i> spp.	0.08	0.09	98.84	0.40	0.22	0.00
<i>Rhizammina</i> spp.	0.07	0.08	98.92	0.40	0.44	0.00
<i>Lagena sulcata</i>	0.06	0.07	98.99	0.40	0.11	0.00
<i>Trifarina</i> spp.	0.06	0.07	99.06	0.10	0.00	1.00
<i>Pyrgo lucernula</i>	0.05	0.06	99.12	0.00	1.00	0.00
<i>Ehrenbergina spinea</i>	0.05	0.06	99.18	0.00	0.00	1.00
<i>Lagena radiata</i>	0.05	0.06	99.24	0.00	0.00	1.00
<i>Lagenammina</i> spp.	0.05	0.06	99.3	0.00	0.00	1.00
<i>Hormosina</i> sp1.	0.05	0.06	99.36	0.40	0.00	0.00
<i>Bolivinita quadrilatera</i>	0.05	0.06	99.41	0.00	1.22	0.00
<i>Reophax</i> sp1.	0.05	0.06	99.47	0.00	0.44	0.00
<i>Lagenammina</i> sp.	0.05	0.05	99.52	0.00	0.89	0.00
<i>Sphaeroidina bulloides</i>	0.04	0.04	99.57	0.30	0.00	0.00
<i>Karrerella baccata</i>	0.03	0.04	99.61	0.00	0.89	0.00
<i>Hemirobulina</i> sp1.	0.03	0.04	99.65	0.00	0,89	0.00
<i>Sagrinella subspinescens</i>	0.03	0.04	99.69	0.00	0,89	0.00
<i>Bulimina truncana</i>	0,03	0.04	99.73	0.00	0,89	0.00
<i>Oolina stelligera</i>	0,03	0.03	99.77	0.00	0.22	0.00
<i>Biloculinella globula</i>	0.03	0.03	99.80	0.00	0.67	0.00
<i>Triloculina tricarinata</i>	0.02	0.03	99.83	0.00	0.11	0.00
<i>Chilostomella oolina</i>	0.02	0.03	99.85	0.00	0.22	0.00
<i>Fissurina alveolata</i>	0.02	0.02	99.87	0.00	0.11	0.00

<i>Spirulina</i> spp.	0.01	0.02	99.89	0.10	0.00	0.00
<i>Goesella cylindrica</i>	0.01	0.02	99.91	0.10	0.00	0.00
<i>Paratrochammina pseudotricamerata</i>	0.01	0.02	99.92	0.10	0.00	0.00
<i>Lagena striata</i>	0.01	0.02	99.94	0.10	0.00	0.00
<i>Robertinoides</i> spp.	0.01	0.02	99.95	0.10	0.00	0.00
<i>Planulina</i> spp.	0.01	0.02	99.97	0.10	0.00	0.00
<i>Lagenosolenia lagenoides</i>	0.01	0.02	99.99	0.00	0.33	0.00
<i>Pyrgo murrhina</i>	0.01	0.01	100.00	0.00	0.11	0.00

Table 4: Correlation of biotic and abiotic variables. Bold values indicate correlations with significance level $p < 0.05$. where: FD= total individuals; S=number of species; J'= Pielou's evenness; and H'=Shannon-Wiener diversity index.

Variable	Flux	Total lipids	Mud	Sand	CaCO ₃	C _{org}	N _t
Flux	1.00	-0.28	-0.47	0.56	-0.56	-0.44	-0.30
Total lipids	-0.28	1.00	0.18	-0.18	0.10	0.04	0.06
Mud	-0.47	0.18	1.00	-0.89	0.23	0.21	0.44
Sand	0.56	-0.18	-0.89	1.00	-0.28	-0.33	-0.51
CaCO ₃	-0.56	0.10	0.26	-0.28	1.00	0.53	0.09
C _{org}	-0.44	0.04	0.21	-0.33	0.53	1.00	0.62
N _t	-0.30	0.06	0.44	-0.51	0.09	0.62	1.00
FD	0.80	-0.31	-0.65	0.70	-0.48	-0.37	-0.30
S	0.49	-0.17	-0.36	0.28	-0.51	-0.34	0.06
J'	0.07	-0.10	-0.25	0.34	-0.21	0.11	0.09
H'	0.38	-0.06	-0.38	0.43	-0.53	-0.20	0.03
<i>Bolivina aenariensis</i> var. <i>multicostata</i>	0.27	-0.24	-0.44	0.44	-0.04	0.05	-0.12
<i>Bolivina albatrossi</i>	0.52	-0.42	-0.50	0.45	-0.32	-0.19	-0.01
<i>Bolivina doniezi</i>	0.44	-0.42	-0.55	0.55	-0.23	-0.15	-0.27
<i>Bolivina</i> spp./ <i>Brizalina</i> spp.	-0.10	0.44	0.46	-0.29	0.12	-0.25	-0.09
<i>Bolivina striatula</i>	-0.12	0.10	-0.06	0.23	-0.16	0.00	0.11
<i>Cassidulina laevigata</i>	-0.04	-0.14	-0.24	0.18	-0.06	-0.26	-0.38
<i>Cassidulinoides parkeriana</i>	0.43	-0.29	-0.59	0.59	-0.31	-0.25	-0.37
<i>Cibicides kullenbergi</i>	0.45	-0.32	-0.49	0.46	-0.53	-0.68	-0.56
<i>Cibicides wuellerstorfi</i>	0.24	-0.21	-0.26	0.22	-0.28	-0.29	-0.12
<i>Cibicidoides</i> spp.	-0.44	0.12	0.65	-0.67	0.24	0.51	0.55
<i>Discorbinella nitida</i>	-0.02	0.17	-0.08	0.02	-0.19	0.18	0.33
<i>Epistominella exigua</i>	0.67	-0.54	-0.70	0.69	-0.40	-0.34	-0.39
<i>Eponides</i> spp.	-0.19	-0.01	0.47	-0.56	0.12	0.30	0.27
<i>Fissurina laevigata</i>	-0.02	0.30	0.37	-0.19	0.13	-0.01	-0.16
<i>Fissurina orbignyana</i>	0.17	0.32	-0.18	0.14	-0.13	0.15	-0.05
<i>Gavelinopsis</i> spp.	-0.61	0.14	0.10	-0.18	0.66	0.11	-0.13
<i>Globocassidulina subglobosa</i>	-0.05	-0.02	0.12	-0.24	0.41	0.15	-0.09
<i>Hoeglundina elegans</i>	-0.33	0.04	0.02	-0.14	0.04	-0.17	-0.02
<i>Lenticulina cultrata</i>	-0.07	0.26	0.06	-0.10	-0.04	-0.15	0.12
<i>Miliolinella</i> spp.	-0.48	0.10	0.21	-0.31	0.29	-0.04	0.01
<i>Miliolinella subrotunda</i>	0.06	-0.07	-0.61	0.52	-0.17	-0.30	-0.33
<i>Nonionella turgida</i>	0.15	-0.16	-0.23	0.15	-0.11	0.02	-0.02

<i>Neoeponides</i> spp.	0.36	-0.32	-0.43	0.41	-0.10	-0.04	-0.08
<i>Paracassidulina</i> spp.	0.03	0.13	0.19	-0.25	-0.13	0.06	0.40
<i>Trifarina angulosa</i>	0.11	-0.25	0.11	-0.17	-0.10	0.04	0.31
<i>Uvigerina peregrina</i>	0.43	-0.13	0.05	-0.14	-0.15	0.09	0.12

ACCEPTED MANUSCRIPT

Highlights

- Main controlling factors: particulate organic matter vertical flux and grain size.
- Middle slope is characterized by *E. exigua* and *G. subglobosa*.
- Lower slope is marked by *Bolivina* spp./*Brizalina* spp.

ACCEPTED MANUSCRIPT

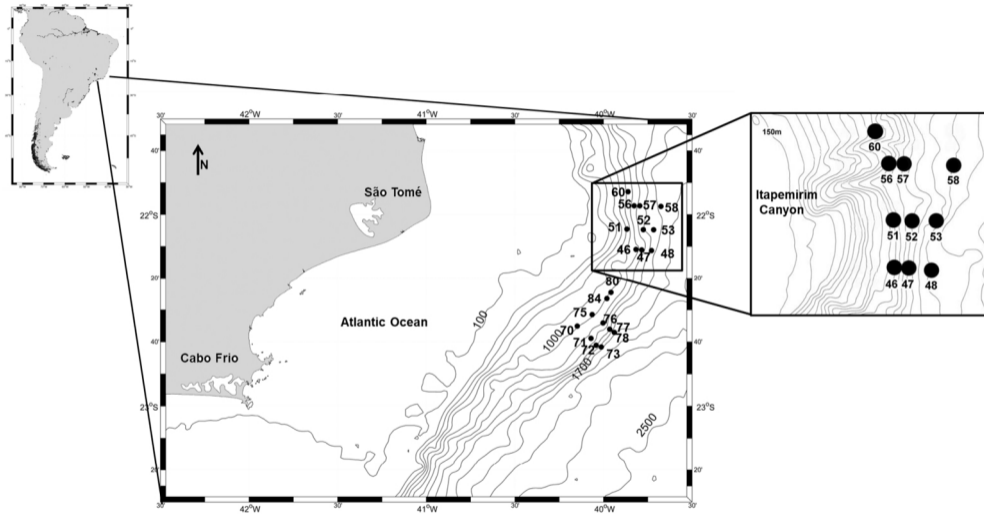


Figure 1

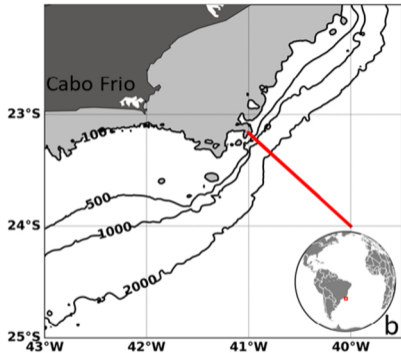
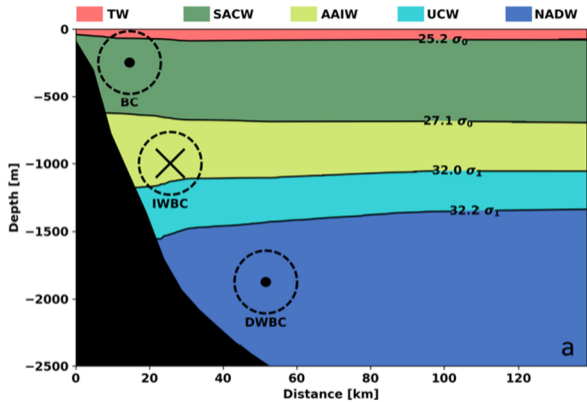


Figure 2

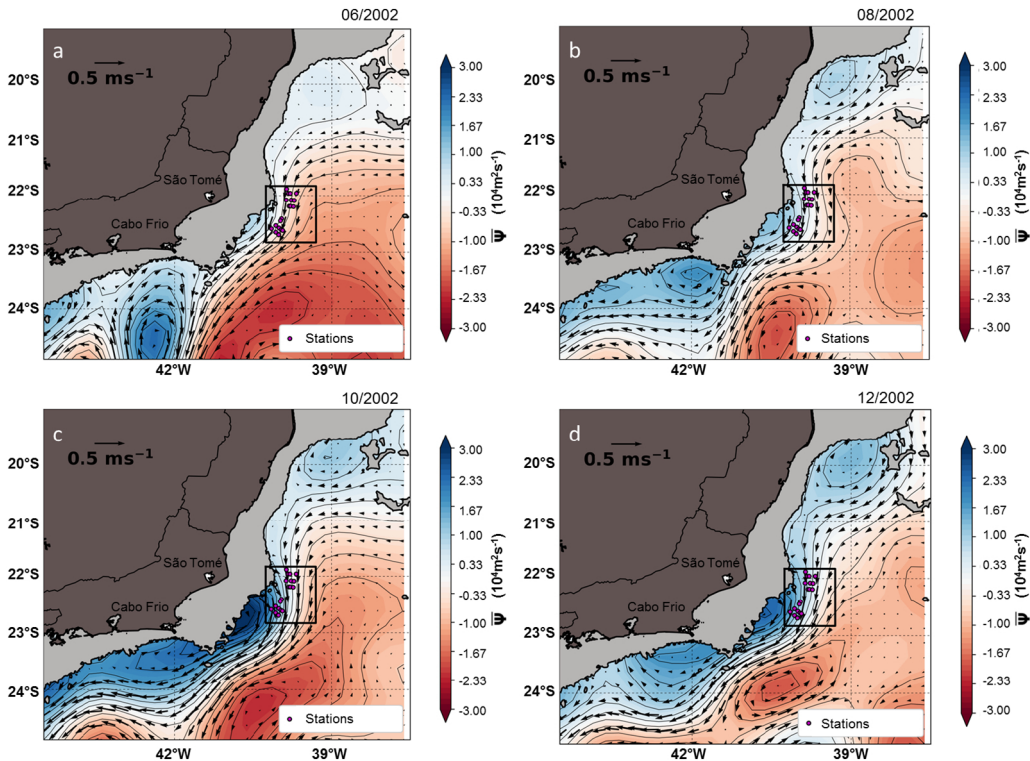


Figure 3

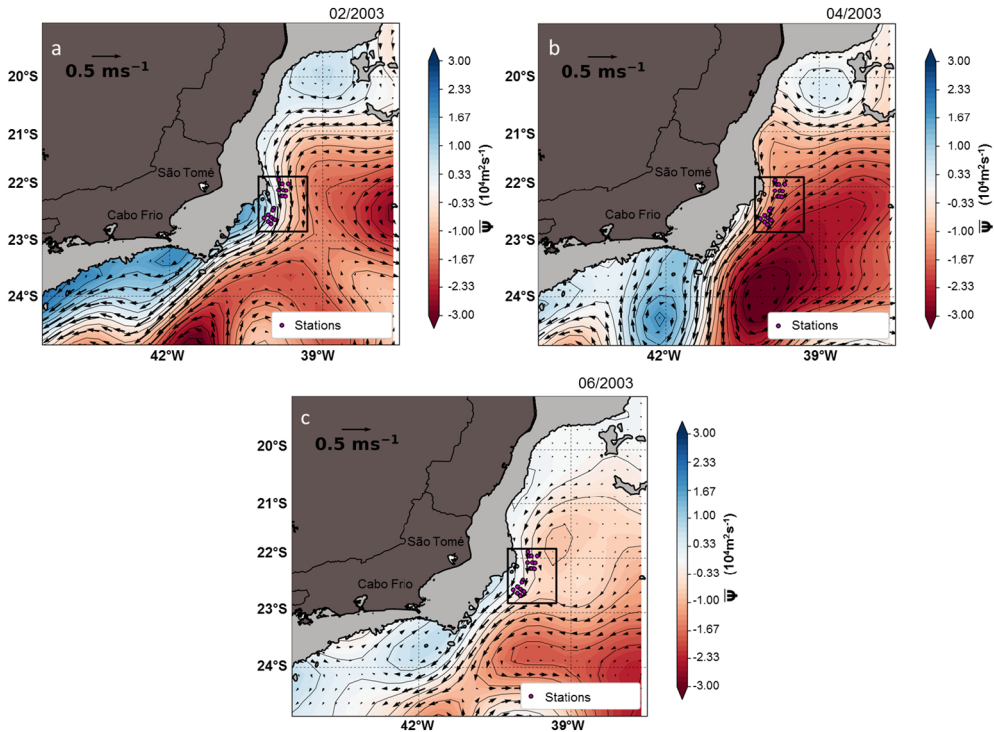


Figure 4

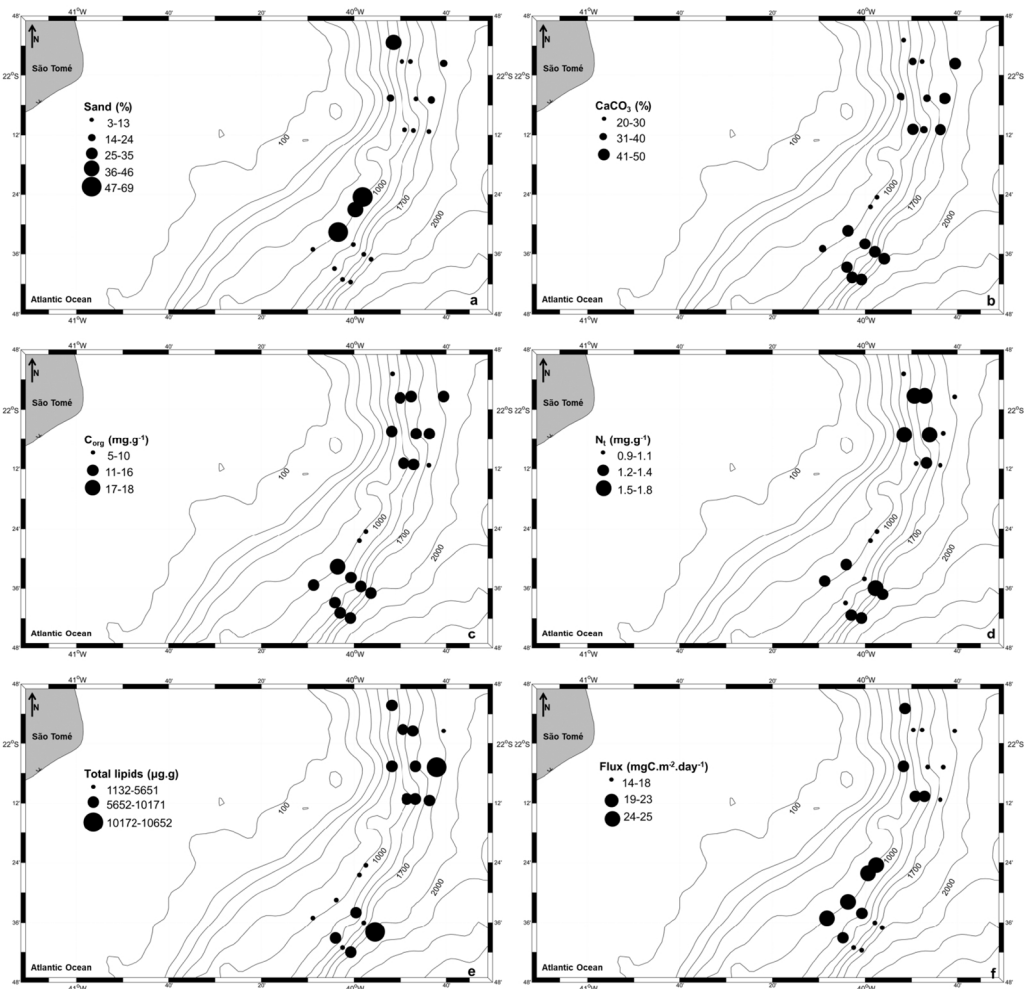


Figure 5

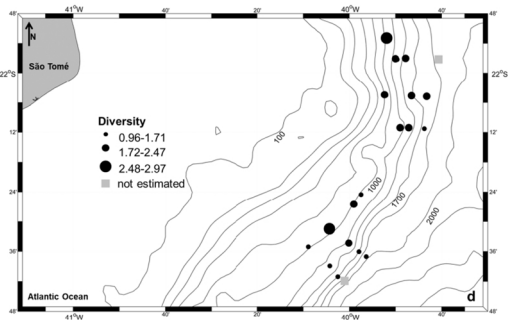
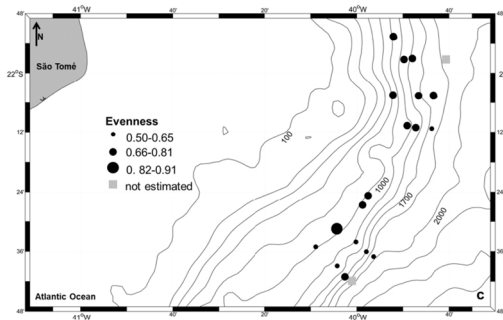
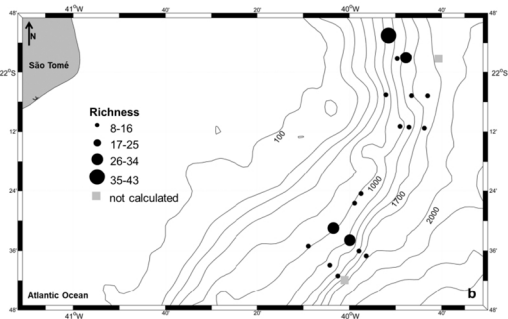
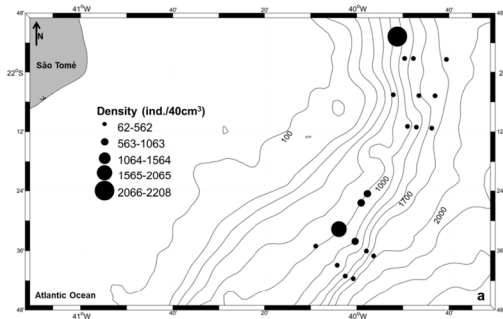


Figure 6

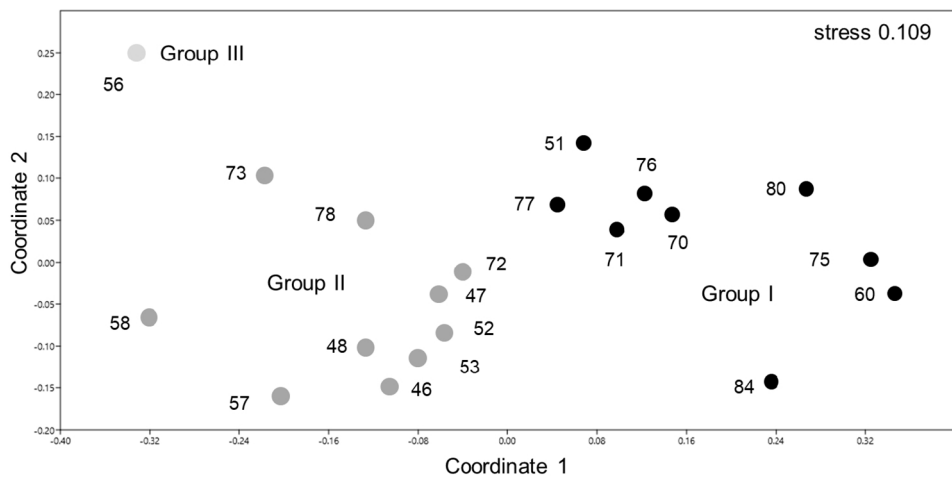
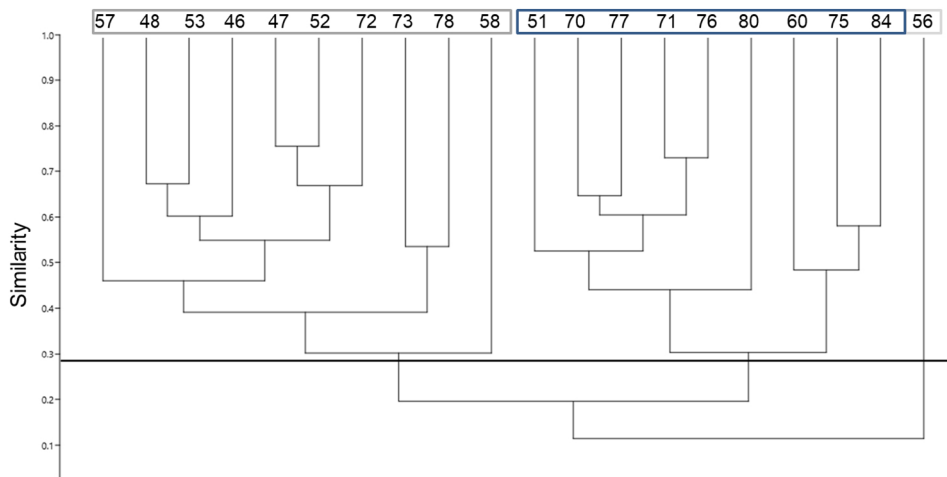


Figure 7

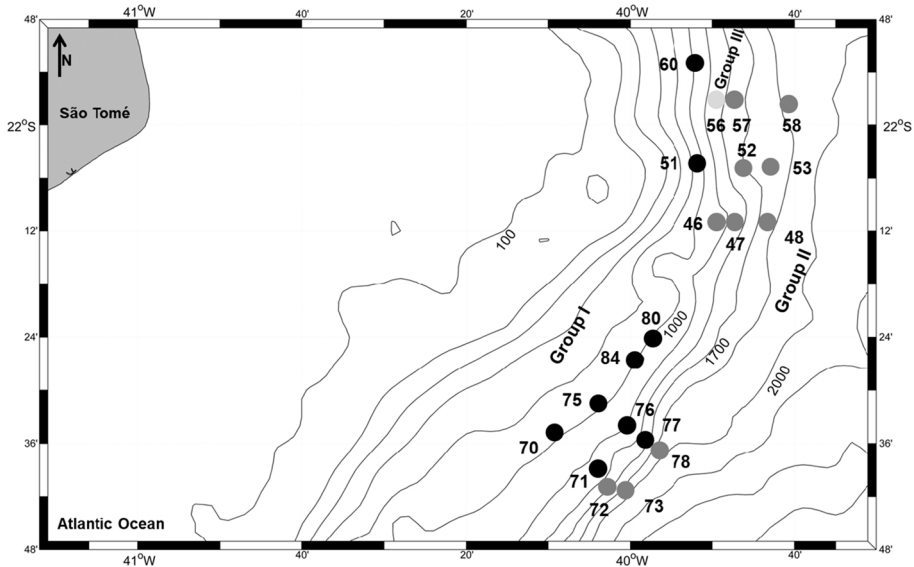


Figure 8

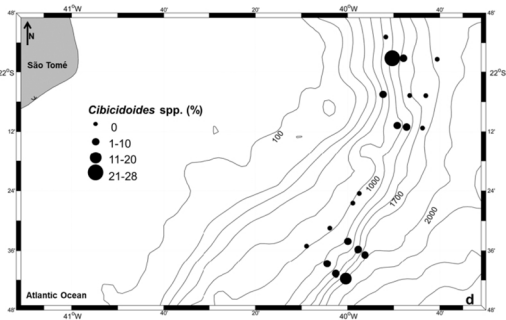
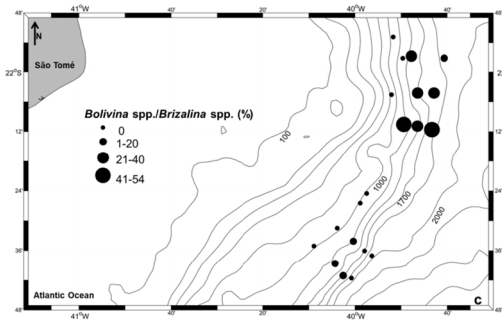
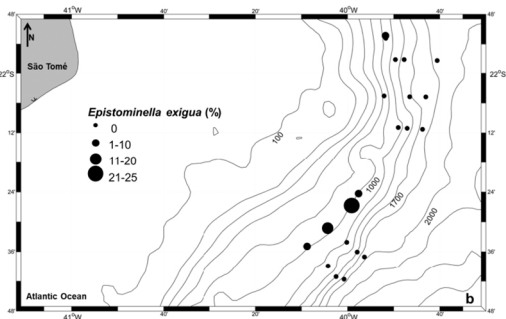
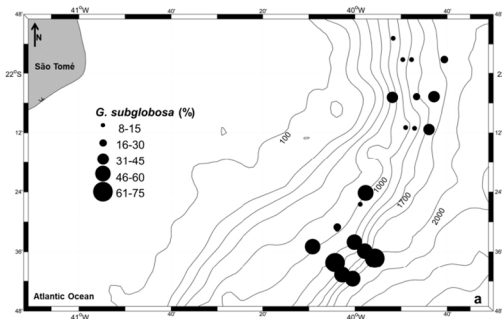


Figure 9