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Deep-sea living (stained) benthic foraminifera from the continental slope and São Paulo Plateau, Santos Basin (SW Atlantic): ecological insights

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ABSTRACT

This study aimed to characterize the spatial distribution and composition of living Benthic Foraminifera (BF) and to comprehend how environmental conditions (e.g., organic matter) can affect communities of these protozoa in the northern and southern sectors of the Santos Basin (SB), in the continental slope and São Paulo Plateau. In this context, 23 stations (65 samples including replicates at each station) were collected between 400 and 2,400 m water depth. Multivariate analyses revealed that the ecological structure of the community changes mainly along the bathymetric gradients. Stations located between 400 and 700 m, both in northern and southern sectors, are characterized by the presence of indicator species of high intensity of currents, such as *Globocassidulina subglobosa* and *Trifarina bradyi*. These stations are also mainly marked by the occurrence of *Epistominella exigua,* a phytodetritivore species. The stations at 1,000 and 1,300 m depth, in both sectors, are characterized by high accumulation of organic matter in the sediments, which favors the development of agglutinated foraminifera species, such as those of the genus *Reophax*. Finally, the lower slope and the São Paulo Plateau, in both sectors, are oligotrophic regions, with pulses of labile organic carbon, probably low current velocities and the presence of *Alabaminella weddellensis*. The quantity and quality of food, which are closely related to hydro-sedimentary dynamics and bentho-pelagic coupling in the slope and São Paulo Plateau, are the main factors that influence the distribution of living BF assemblages in the SB.

Keywords: Pelagic-benthic coupling, Food availability, Continental slope, Oceanographic processes, Southwest atlantic

INTRODUCTION

In deep-sea environments, the spatial dynamics of benthic foraminifera (BF) (Adl et al., 2005, 2012) are controlled by many physicochemical parameters, such as food supply and redox conditions in the sediment (Gooday, 1988; Jorissen et al., 2007; Fontanier et al., 2012, 2016; Yamashita et al., 2016). Jorissen et al. (1995) summarized the role of food supply and oxygen availability on the benthic foraminifera in the so-called TROX-model (Trophic-Oxygen-Microhabitat-Reaction) and validated it for many marine ecosystems (e.g., Licari et al., 2003; Nardelli et al., 2010;

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Burone et al., 2011; Mello et al., 2014). In well-oxygenated deep-sea ecosystems, the availability of sedimentary organic matter is the factor controlling BF community density and structure, and the BF microhabitat (with predominance of epifaunal specimens) (e.g., Jorissen et al., 1995; Nardelli et al., 2010; Burone et al., 2011; Mello et al., 2014). In eutrophic and depleted oxygen environments, densities are higher whereas diversity is usually low. In the mesotrophic settings, where the oxygen can penetrate deep in the sediment layers and the organic compounds are available, the diversity can reach maximum values (Jorissen et al., 1995; Fontanier et al., 2002, 2006; Singh et al., 2021).

In deep-sea, different sources of organic matter to the seafloor have been recognized, but the vertical flux of particulate organic matter from the sea surface primary productivity is considered the most important (e.g., Altenbach and Struck, 2001; Henson et al., 2015). Studies in the deep sea have noticed the increase in density and biomass of bacteria and eukaryotic organisms in the sediments after phytoplankton blooms (Gooday, 1988; Franco et al., 2007; Veit-Köhler et al., 2011; Mello et al., 2014). Regarding BF, studies have shown positive correlations between their densities and biomass and the flux of organic matter (e.g., Rijk et al., 2000; Altenbach and Struck, 2001; Gooday, 2002; Fontanier et al., 2003; Vicente et al., 2021). Moreover, the BF community structure is closely related to the nutritional quality of organic matter (Fontanier et al., 2005; Nardelli et al., 2010).

The influence of hydrodynamic processes on the BF community has been demonstrated in other studies. In environments characterized by the occurrence of gravity flows, the community shows low densities and high dominance (e.g., Koho et al., 2007; Nardelli et al., 2010; Duros et al., 2011). Furthermore, differences in hydrodynamic conditions promoted by water masses, their surface fronts, eddies, and bottom current intensity can determine energy conditions that interfere with the input of organic matter, sediments texture and oxygen availability in the environment, changing the ecological parameters of BF assemblages (Mello et al., 2014; Yamashita et al., 2016, 2018, 2020; Vicente et al., 2021). Moreover, the competition for microhabitat and resources are also important controlling factors of the foraminiferal dynamics (Boltovskoy and Wright, 1976; Murray, 1991, 2006).

Therefore, the structure of a living BF community results from a complex interplay of abiotic and biotic parameters and hydro-sedimentary processes. In addition, these protists can be considered environmental sentinels due to their short reproductive and life cycle, abundance, and high degree of specialization (Kramer and Botterweg, 1993; Schönfeld et al., 2012; Sousa et al., 2020), and can be used as environmental monitoring tools in marine systems, such as continental margins (e.g. Barras et al., 2014; Alve et al., 2016), abyssal regions (Gooday et al., 2012), canyons (Bella et al., 2019), areas of natural gas exudations (Fontanier et al., 2014), and oil exploration regions (Jorissen et al., 2009; O'Malley et al., 2021).

The Santos Basin (SB), located at the southeastern Brazilian continental margin, has one of the largest oil provinces in the world, known as pre-salt, since it is located below a 2 km thick layer of salt (Gouveia, 2010). This large sedimentary basin is an important oil and gas exploration complex and is considered one of the most profitable regions in the exploration of non-renewable marine resources (Gouveia, 2010).

The literature (Lorenzzetti and Gaeta, 1996; Mahiques et al., 2002; Calado et al., 2008; Eichler et al., 2016; Yamashita et al., 2016) demonstrates the hydrodynamic complexity of the BS in its coastal regions, continental shelf, and continental slope. The upwelling off Cape Frio, in the northern sector of the basin, and the presence of eddies caused by the meandering of the Brazil Current are some of the hydrodynamic processes that make the SB a dynamic ecosystem. The continental shelf and upper continental slope of the southern region of the SB are characterized by more homogeneous sedimentation environments, where muddy sediments predominate (Mahiques et al., 2004). The southern region also shows high primary productivity, mainly in Cape Santa Marta (Campos et al., 2013). At 29° S, below Cape Santa Marta, the upwelling of South Atlantic Central Water (SACW) on the continental shelf is documented, as well as the La Plata River Plume (RdlP), which reaches the shelf in winter (Mahiques et al., 2004; Piola and Romero, 2004; Piola et al., 2008) and the upper continental slope (~200 m) (Matano et al., 2014; Razik et al., 2015) up to 24° S. According to Tura and Brandini (2020), the outer shelf of the SB is characterized by oceanographic features typical of a meso-oligotrophic western boundary system, which depends on mesoscale physical processes for seawater fertilization. Moreover, these processes are essential for phytoplankton production in offshore waters (Castro et al., 2006).

Currently, by using remote sensing methods, it is relatively easy and fast to estimate the phytoplankton productivity of surface waters (Laws et al., 2000; Zscheischler et al., 2017). However, it is often difficult to understand how much of what is produced in the surface ocean reaches the ocean bottom and becomes available to the benthic fauna, and also to comprehend the oceanographic processes that enable the fertilization in deep sea environments. One of the most sensitive groups to these changes are the benthic foraminifera (Jorissen et al., 1995; Gooday, 2003; Burone et al., 2011; Yamashita et al., 2016, 2018, 2020; Vicente et al., 2021). Thus, this study aimed to characterize the spatial distribution and composition of living BF in the northern and southern sectors of SB, on the continental slope and São Paulo Plateau, and to understand how the abiotic factors (e.g., organic supply) and the hydro-sedimentary can influence the BF community in remote regions.

The study by Yamashita et al. (2016) on living BF present up to 1,000 m depth, from São Sebastião and Ilha Grande, is the only found on the slope of the SB. Therefore, our work is a pioneering study, which also contributes to the Santos Project—Santos Basin Environmental Characterization—coordinated by Petróleo Brasileiro S.A. (Moreira et al., 2023). This is part of a larger study that aims to understand the environmental processes that influence the benthic communities in SB.

METHODS

Sediment Sampling

In total, 65 sediment samples, including replicates from each of the 23 stations, were collected on the continental slope and São Paulo Plateau, in the Santos Basin during the 2019 winter (Figure 1) between 400 and 2,400 m of water depth, using a box corer (50×50×50 cm). At A06 and H06 sampling stations, collection was carried out with a Van Veen grab sampler due to sandy sediments, which made it impossible for the box corer to penetrate and collect sediment. This study analyzes samples of four transects: the transects A and B, with six stations each, located in the south sector; and the transects G and H, with five and six stations, respectively, situated in the north sector of the basin.

At each sampling location three replicates of sediment were taken for foraminiferal analysis, following Schönfeld et al. (2012). The upper 0–2 cm of each core was sliced for living (stained) benthic foraminifera. The samples were stored in plastic containers with a 10% formaldehyde buffered with borax with Rose Bengal (2 gL^{-1}) solution, to evidence the presence of protoplasm in living individuals at the time of collection (Walton, 1952; Schönfeld et al., 2012). The faunas were washed in 63 µm sieve since the deep ocean community of BFs is best represented in this fraction (Schroeder et al., 1987; Schmiedl et al., 1997). The license to collect, store, and transport biological material, number 1119/2019, was provided by the Brazilian Institute for the Environment and Renewable Natural Resources.

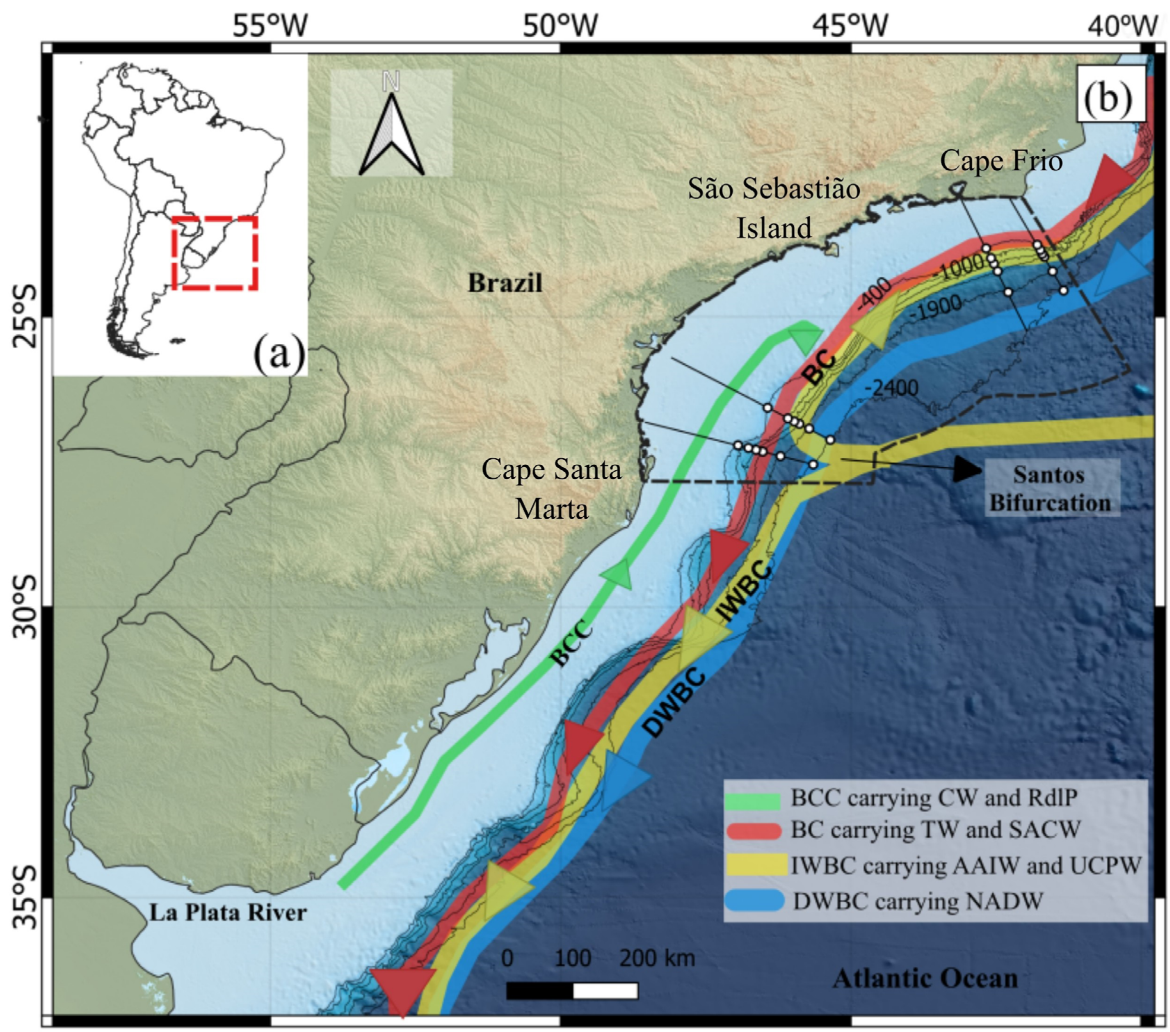

Figure 1. (a) South America (b) Schematic representation of Brazilian Coastal Current (BCC), Brazil Current (BC), Intermediate Western Boundary Current (IWBC), Deep Western Boundary Current (DWBC), and oceanographic stations location (White circle).

Sediment grain size and bulk geochemistry data

Grain size data (gravel and calcium carbonate) were obtained from Figueiredo Jr. et al. (2023), which describes the methodology used. The geochemical analysis was carried out at Pontifical Catholic University of Rio de Janeiro, coordinated by Renato Carreira. The methodology used to analyze the parameters total organic carbon (TOC), chlorophyll *a* sediment (chlo *a* sediment), phaeopigments, and biopolymers [carbohydrate (CHO), lipid (LIP), and protein (PTN)] were detailed by Carreira et al. (2022). The total biopolymeric carbon (BPC, sum of CHO, PTN, and LIP), used to recognize if the organic matter is refractory or labile (Danovaro et al., 1993), was also estimated.

Living benthic foraminifera analysis

Assemblage data were evaluated using density (FD) (number of individuals/50 cm^3 of sediment), richness (S), index of Shannon (H’)

(Shannon, 1948), Pielou evenness index (J') (Pielou, 1975). These ecological parameters were estimated using PRIMER v6 (Clarke and Gorley, 2006).

For species identification, many bibliographic references were used, such as Boltovskoy et al. (1980), van Morkhoven et al. (1986), Loeblich and Tappan (1988), Jones (1994), Debenay (2012) and Holbourn et al. (2013). The status of the species names followed the online dataset (WoRMS Editorial Board, 2023). Some species were photographed using a digital camera attached to the stereomicroscope (SteREO Discovery.V12). Plate 1 shows the photographs.

Multivariate analyses

The multivariate analyses of clustering were performed with PAST 4.05 program (Hammer et al., 2001). The Bray-Curtis similarity with the UPGMA was used for clustering, considering species with at least 2% of relative abundance. To determine which benthic foraminiferal species contributed the most to the groups formed in the cluster analysis, a SIMPER (similarity percentage breakdown) analysis using the Bray-Curtis similarity was performed in PAST (Hammer et al., 2001).

Spearman correlation analyses were performed considering $p < 0.05$ as significant. The foraminiferal indexes (S, FD, J', and H') and main species selected by Simper analysis with relative abundance—higher than 2%—were correlated with sea surface chlorophyll (chlo *a* surface), gravel, calcium carbonate content, phytopigments (phaeopigments and chlo *a* sediment), TOC, BPC, CHO, PTN, LIP, PTN:CHO, and the declivity using STATISTICA® version 10.

Remote sensing data: Surface chlorophyll *a*

Surface chlorophyll *a* concentrations were estimated to verify a possible relationship between surface primary production and the BF community. For that, chlo *a* surface (mg/m^3) images and algorithms acquired by remote sensing, from the MODIS-Aqua satellite, and available on NASA's Giovanni portal (https://giovanni.gsfc.nasa.gov/giovanni/) were used. The temporal resolution of the MODIS-Aqua satellite was one month, and the spatial resolution was 4 km. Thus, 16 km radius circles were made around each sampling point. In this way, data on the average concentration of chlo *a* surface in these circumferences were acquired over three months prior to collection (March to May). This period was selected considering the life cycle of foraminifera, in general, and the time required for the establishment of the community changes, depending on the flux of organic carbon to the bottom (Fontanier et al., 2003).

RESULTS

Living benthic foraminifera

The FD ranges from 166 (at the A07 station) to 1,910 (H08 station) specimens per 50 cm^3 of sediment (Figure 2a). A total of 669 benthic foraminiferal species was identified in the study area. The species that reached higher relative abundance (up to 4%) were *Globocassidulina subglobosa* and *Epistominella exigua*.

The highest richness was detected at station H08 (307) and the lowest at station A07 (97) (Figure 2b). The stations in the north sector of SB (G06, H07 and H08) showed the highest diversity values (H' = 4.7), while the lowest ones were detected in the south sector at A10 (H' = 3.7) (Figure 2c). Regarding the evenness, São Paulo Plateau PSP stations (B11 and H11) showed the highest values (J' = 0.9) and station A06 the lowest value (J' = 0.7) (Figure 2d). Density, identification of benthic foraminifera, and the ecological indices, can be found in Tables S1 and S2 (Supplementary Material).

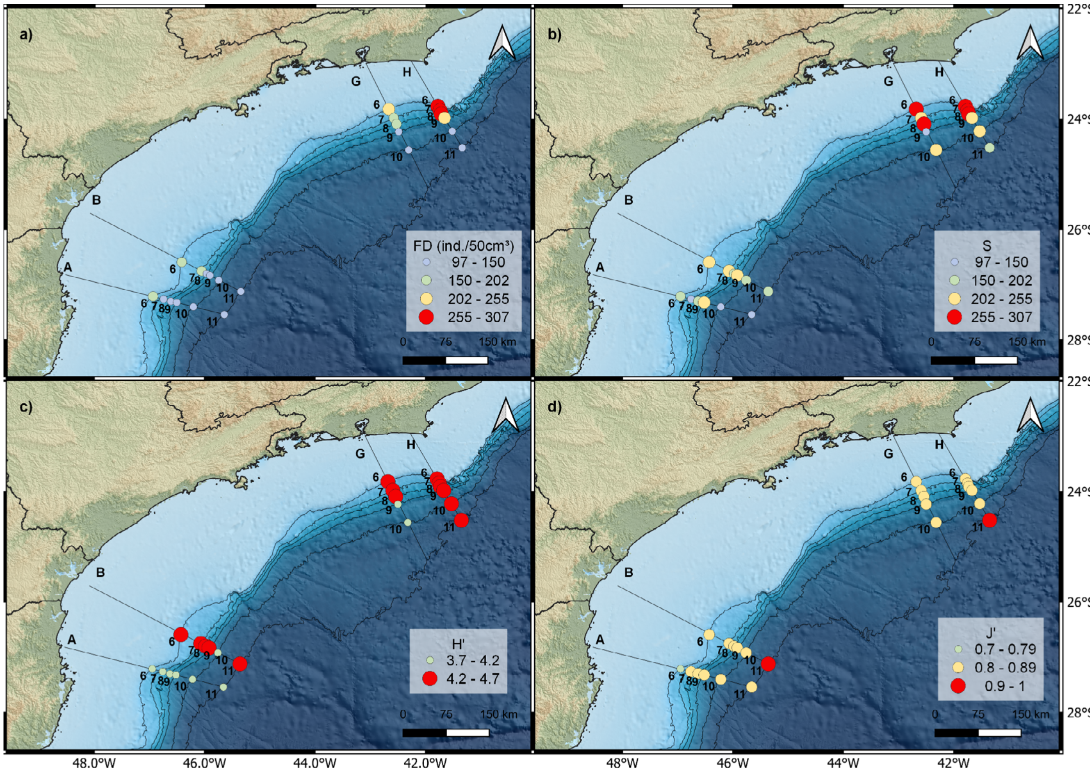

Figure 2. a) Distribution of foraminiferal density (FD, ind./50 cm³) in the study area; b) Distribution of species richness (S) in the study area; c) Distribution of Shannon-Wiener diversity index (H`) in the study area; d) Distribution of Pielou's evenness (J`) in the study area.

Environmental parameters

Average Grain Size (AGS) of all sampling stations was 49.7 µm. The station A09, located at 1,300 m depth in the south sector, presented the finest grains (8.6 µm), while station H11, situated at 2,400 m depth in the north sector had the coarsest grains (175.2 µm).

The average content of calcium carbonate was 42.8%. Some sampling stations located in the northern sector, at 700 m (A07) and 2,100 m depth (B11), presented carbonate peaks > 65 %. In the southern sector, the stations G08, G09, H08, G10, and H11 showed $CaCO_3$ > 50 %.

The average TOC content was 6.28 mg g^{-1} at the analyzed stations and ranged from 1.08 mg g^{-1} (A07) to 10.20 mg g^{-1} (A09). There was an increase in TOC contents up to 1,300 m depth, followed by a decrease towards the lower continental slope (1,900 m) and São Paulo Plateau (2,400 m). The CHO average was 1.55 mg g^{-1}; highest and lowest CHO contents were recorded at the stations B09 (2.79 mg g^{-1}) and A06 (0.46 mg g^{-1}), respectively. The average concentration of PTN was 1.15 mg g^{-1} in SB; the highest and lowest PTN contents were found at A08 and B06 (1.98 mg g^{-1} for both stations) and H11 (0.63 mg g^{-1}), respectively. Average LIP content was 0.31 mg g^{-1}; the highest and lowest concentrations were found at H08 (0.78 mg g^{-1}) and at H11 (0.14 mg g^{-1}), respectively.

In most sampling stations, the BPC reached the highest contents in the continental slope, between 700 m and 1,300 m depth. The PTN:CHO reached the highest values (>1) at stations A06, A07, B06, B10, and G06.

The lowest value (0.16 µg g^{-1}) of chlo *a* sediment content was found at station H06, while station B11 presented the highest one (0.94 µg g^{-1}). Station A11 presented the lowest sedimentary phaeopigment concentration (0.75 µg g^{-1}) and B09 showed the highest one (4.4 µg g^{-1}).

Remote sensing data: sea surface chlorophyll *a*

Sea surface chlorophyll *a* concentration (Figure 3) ranges from 0.10 mg m^{-3} (stations A11 and H11) and 0.20 mg m^{-3} (station A07). In the Santos Basin, a general pattern of gradual increase in chlo *a* surface concentration is observed in the coastal region and on the continental shelf from south towards north (Figure 3).

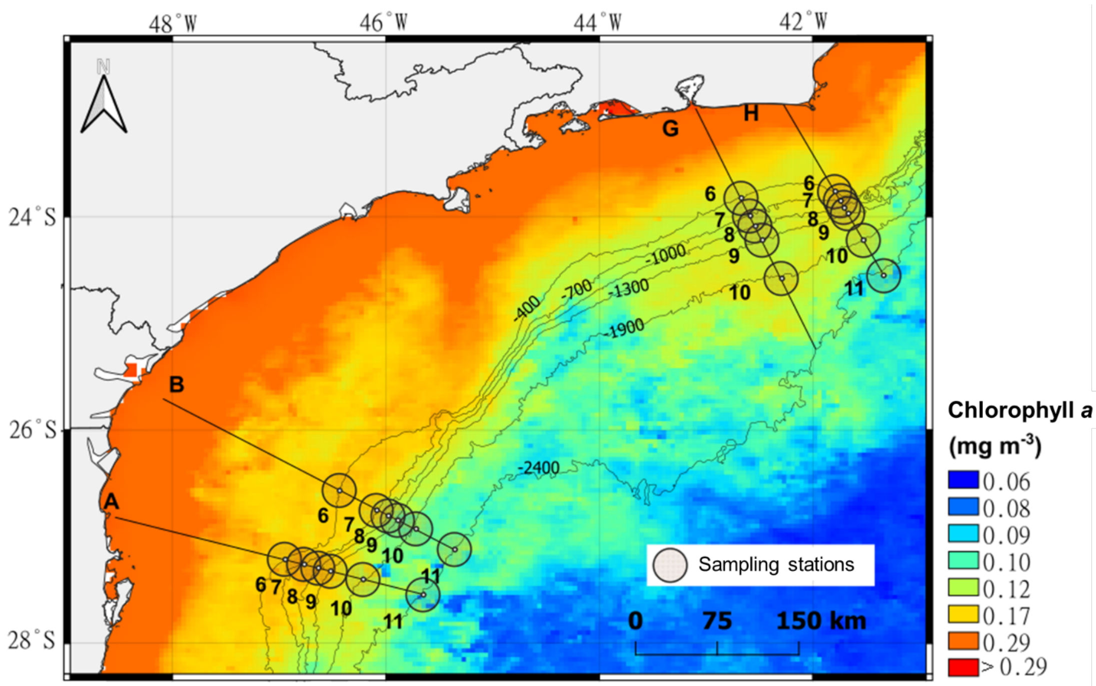

Figure 3. Sea surface chlorophyll *a* concentration at the study area (monthly average between March and May) from MODIS Aqua.

Statistical analyses

The FD showed a statistically significant correlation between chlo *a* surface and phytopigments, while the S presented a significant correlation with phytopigments (Figure 4). The cluster analysis (Figures 5 and 6) differentiated the species into five different groups: upper slope stations (Group I), middle-lower slope stations (Group II), lower slope stations in the southern sector (Group III), middle slope (station A07, Group IV), and lower slope and São Paulo Plateau stations (Group V).

Group I included the shallowest stations of the slope (400 m depth – stations A06, B06, G06, and H06). According to SIMPER analysis, hyaline species such as *Trifarina bradyi*, *Siphonina bradyana,* and *G. subglobosa* were the most important in this group. Group II was composed of stations on the continental slope, between 700 and 1,300 m depth (stations H07, H08, and H09). The most representative species in this group at these depths (Table S1, Supplementary Material) were *G. subglobosa* (at 700 m), and *E. exigua* (at 1,300 m), respectively. Group III was composed of stations between 700 and 1,300 m depth in the southern sector (A08, A09, B07, B08, and B09 stations) and the north sector (G07, G08, and G09 stations) and was characterized by the presence of *Reophax* sp. 1, and *E. exigua*. Group IV is composed only of A07; according to SIMPER, the most abundant species in this station were *Uvigerina auberiana* and *T. bradyi*. The stations at the lower continental slope (1,900 m) and PSP (2,400 m), which compose of Group V (stations A10, A11, B10, B11, G10, H10, and H11) have as most representative species, according to SIMPER analysis, *Alabaminella weddellensis* and *Reophaxopsis* aff. *elegans*.

	FD	S	*J'*	*H'*	Ee	Gspp	Gs	Rsc	Rsp	Rspp	Rsu	Re	Sb	Tb	Ua	Up
TOC	0.17	0.25	**-0.47**	0.00	0.17	0.28	0.01	0.14	0.01	0.22	0.24	-0.02	-0.16	0.03	-0.03	0.19
Chl-a s	-0.05	-0.01	-0.03	0.18	-0.22	-0.22	-0.24	-0.15	**0.52**	0.16	-0.06	**0.46**	-0.30	-0.35	-0.35	-0.09
Chl-a rs	**0.50**	0.31	-0.41	-0.06	**0.42**	**0.51**	**0.57**	**0.49**	-0.26	0.25	0.22	-0.40	**0.43**	**0.70**	**0.58**	**0.47**
Phaeo	**0.48**	**0.47**	-0.23	0.31	0.34	**0.58**	0.34	**0.47**	0.06	0.33	0.38	-0.26	0.24	0.36	0.16	**0.49**
Phito	**0.45**	**0.44**	-0.25	0.30	0.32	**0.52**	0.28	**0.44**	0.12	0.32	0.36	-0.19	0.18	0.28	0.09	**0.47**
CHO	**-0.43**	**-0.44**	-0.12	**-0.46**	-0.12	-0.32	-0.36	-0.41	0.17	0.07	0.05	0.18	**-0.52**	-0.35	-0.23	-0.30
PTN	-0.29	-0.40	-0.16	**-0.44**	-0.16	-0.04	-0.09	-0.12	-0.21	0.10	-0.11	0.01	-0.24	-0.01	0.05	-0.01
LIP	0.23	0.39	-0.12	0.30	0.19	**0.49**	0.22	0.30	-0.12	0.23	0.18	-0.22	0.08	0.25	0.16	0.21
BPC	-0.33	-0.36	-0.19	-0.39	-0.08	-0.08	-0.19	-0.19	0.01	0.18	0.06	0.05	-0.40	-0.14	-0.06	-0.16
Gravel	-0.37	-0.24	0.23	-0.08	-0.32	**-0.45**	-0.28	**-0.45**	-0.19	**-0.47**	**-0.52**	0.23	-0.23	-0.23	0.01	**-0.67**
PTN/CHO	0.16	0.09	-0.06	0.04	-0.02	0.33	0.30	0.32	**-0.48**	-0.02	-0.13	-0.26	0.32	0.41	0.35	0.25
CaCO3	-0.14	-0.07	0.25	0.08	-0.07	-0.41	-0.37	-0.26	0.08	**-0.51**	-0.39	**0.44**	-0.25	-0.27	-0.12	-0.24
Declivity	0.21	0.34	0.22	0.40	0.25	0.29	0.10	0.39	-0.16	-0.34	0.18	-0.21	0.19	0.23	0.05	0.20

Color scale: 1, 0, -1

Figure 4. Heat map with Spearman's correlation between biotic parameters and the main species/taxa of living foraminifera and abiotic parameters: Richness (*S*), Living benthic foraminifera density (FD; ind/50 cc), Pielou's evenness (*J'*), Diversity (*H'*), mainly species (Ee – *Epistominella exigua*; Gspp – *Globocassidulina* spp.; Gs – *Globocassidulina subglobosa*; Rsc – *Reophax scorpiurus; Rsp – Reophax spiculifer; Rspp – Reophax* spp.; Rsu – *Reophax subfusiformis*; Re – *Reophaxopsis aff. elegans*; Sb – *Siphonina bradyana*; Tb – *Trifarina brady*; Ua – *Uvigerina auberiana*; and Up – *Uvigerina peregrina*), organic parameters (TOC – Total Organic Carbon; Chl-a[rs] – Surface chlorophyll-a; Chl-a[s] – Chlorophyll-a in the sediment; Phaeo – Phaeopigments; Phyto – Phytopigments; CHO – Carbohydrates; PTN – Proteins; LIP – Lipids; BPC – Biopolymeric Carbon; PTN/CHO – Protein/Carbohydrates); Gravel (Grain size); $CaCO_3$ – Carbonate and Declivity. Where: [rs]: data retrieved from remote sensing and [s]: data obtained from sediment analysis; bold values – significant correlations, $p < 0.05$.

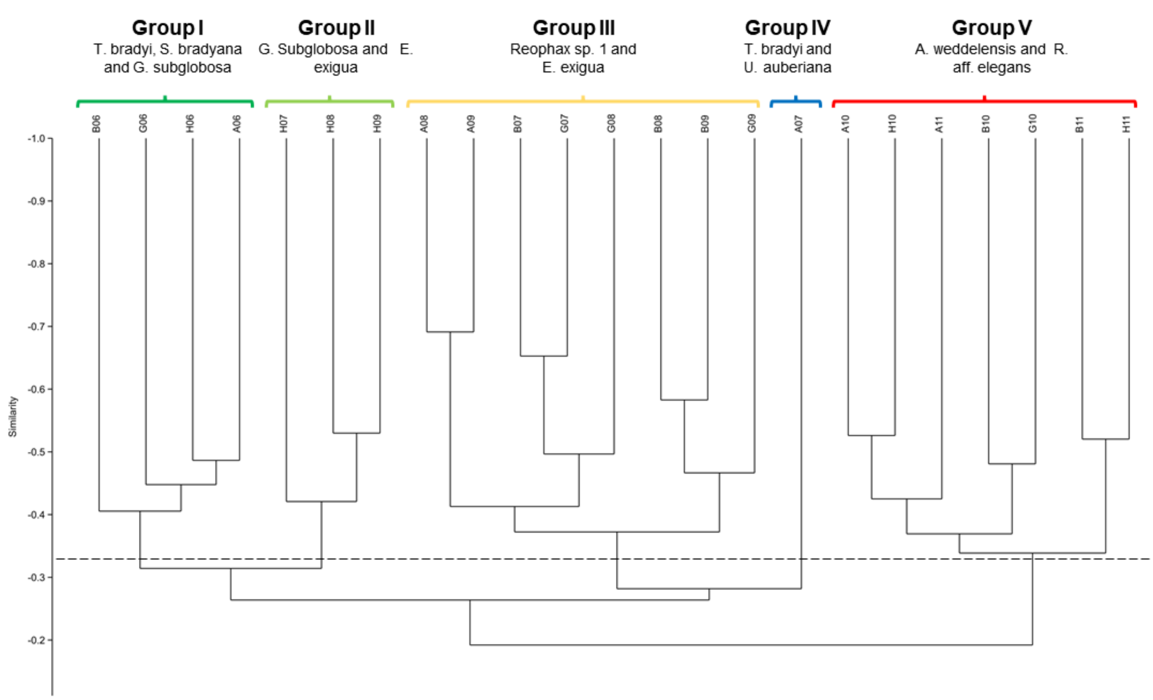

Figure 5. Cluster analysis (UPGMAxWard) based on the foraminiferal density: Group I (middle slope-dark green), Group II (Middle-lower slope of H's stations-light green), Group III (lower slope-orange), Group IV (lower slope outlier-blue), and Group V (lower slope and Paulo Plateau stations -red). Representative species of each group are listed.

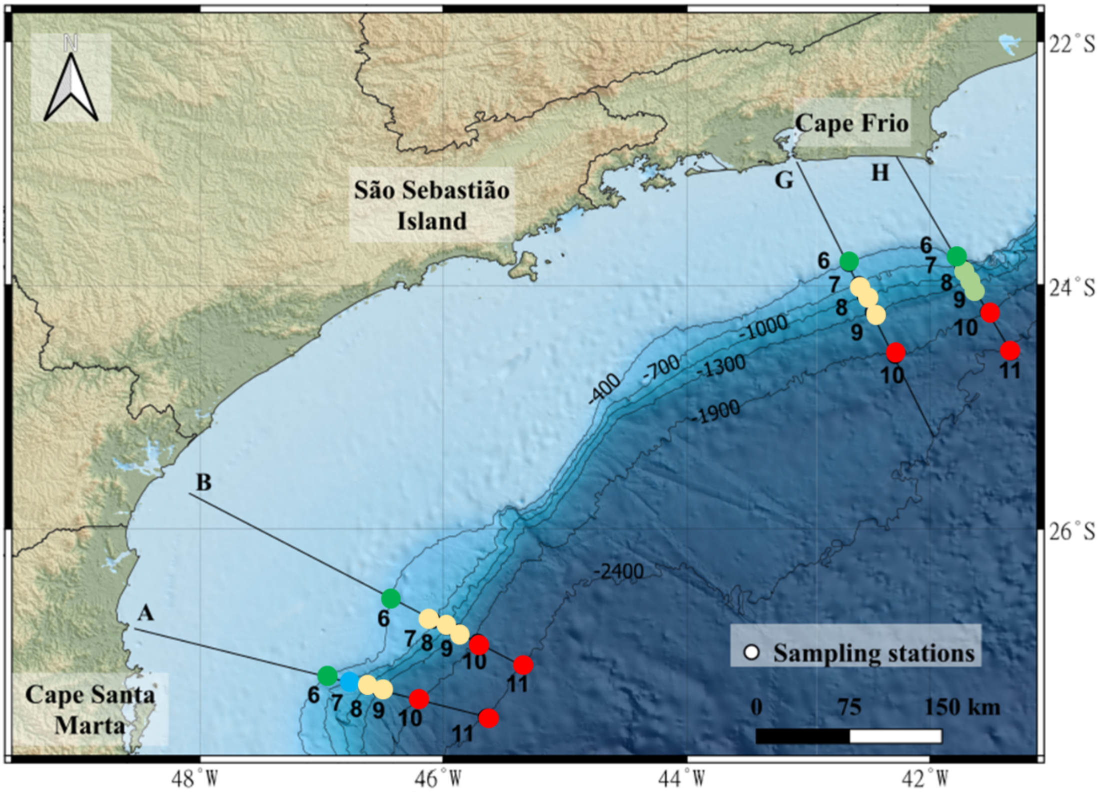

Figure 6. Location of the five groups identified via cluster analysis (UPGMA).

DISCUSSION

The correlation between FD and chlo *a* surface (Figure 4) indicates a benthic-pelagic coupling mediated interaction in the study area. The chlo *a* surface concentration can indirectly provide information about the pelagic-benthic coupling system (McTigue et al., 2015). Studies have demonstrated that high surface concentrations of chlo *a* are associated with increased primary productivity and organic carbon export; this situation stimulates the trophic web and, generally, provides higher supply of organic matter to the bottom (Altenbach and Struck, 2001; Ducklow et al., 2001; Vicente et al., 2021). Our data show a relationship between the input of phytodetritus and the increase in the number of two species (*E. exigua and G. subglobosa*), considered opportunistic species (r-strategists) (Gooday, 1988, 1993), corroborating the observations of Duchemin et al. (2007) and Almeida et al. (2022). It was also observed that species richness is positively correlated with phytopigments, which may indicate a preference for phytoplanktonic food (also protein-rich). This confirms the influence of organic carbon pulses derived from the primary productivity in the surface sediments and benthic foraminiferal community in the basin.

However, no correlation was observed between chlo *a* surface and the sediment contents in TOC, phytopigment, LIP, CHO, BPC, and chlol *a* sediment. Some factors may explain the non-correlation of the data, such as the consumption of a large part of what is produced in the ocean surface and along the water column or high nutrient utilization/recycling rates, (Maier-Reimer, 1993; Lyle and Lyle, 2006; Griffith et al., 2021) or its transport to other areas by bottom currents or its burial in deeper layers of sediment, caused by bioturbation or other phenomena. In contrast, we should consider that positive correlations between protein, PTN:CHO ratio and chlo *a* surface concentrations, and between species richness and phytopigments are observed, which indicate the influence of more labile organic matter in the sediment on the benthic foraminiferal community in the basin.

The upper continental slope group (Group I), shows high values of FD, richness and diversity. The main species of this group are *G. subglobosa*, *T. bradyi*, and *S. bradyana*, which are considered opportunistic species (Gooday, 1991, 1993; Murray, 2006). These species are known to thrive in environments with seasonal input of phytodetritus (Gooday, 1993; Hayward et al., 2002; Sousa et al., 2006; Gupta and Smith, 2010; Yamashita et al., 2016, 2018, 2020; Vicente et al., 2021), and strong bottom current velocities (Mackensen et al., 1995; Schmiedl et al., 1997; Sousa et al., 2006; Yamashita et al., 2016, 2018, 2020; Vicente et al., 2021). The sediments of these stations presented low TOC, CHO, LIP, and chlorophyll *a* contents, but displayed the highest PTN and PTN:CHO ratio values. Notably, according to Danovaro et al. (1993) PTN:CHO ratio values > 1 are tracers of fresh organic matter. Therefore, higher PTN:CHO and chlo *a* sediment values reveal the presence of high quality food for BF. However, the lowest TOC, CHO, LIP, and chlo *a* sediment contents in surface sediments, may be related to the influence of the high bottom velocities of the Brazil Current (Silveira et al., 2008), that may be responsible for the low retention of O.M. on the substrate. Despite the high bottom velocities of the Brazil Current (Silveira et al., 2004, 2008), these opportunistic species are able to respond rapidly to input of labile O.M. (Diz, 2004; Duchemin et al., 2007; Yamashita et al., 2016, 2018, 2020; Vicente et al., 2021); the increase in their relative abundance in the BF community is an indicator of intermittent inputs of high-quality food in the upper slope of the basin.

Group II consists only of samples from transect H (H07, H08, and H09), which is located off Cape Frio, at the northern sector of Santos Basin. The faunal composition presented the highest values of density, richness, diversity, and evenness among the five analyzed groups, which is probably related to the availability of fresh food, which was assumed from the high chlo *a* sediment concentrations and by the PTN:CHO ratios > 1, in stations H08 and H09. The most abundant species in these stations were *E. exigua* and *G. subglobosa*. It is well known that *E. exigua* is an opportunistic species that reproduces rapidly in the presence of fresh phytodetritus, especially in regions with a large seasonal supply of nutrients, as in upwelling areas (Gooday and Turley, 1990; Gooday, 1993). *Epistominella exigua* has the ability to colonize places at different depths, and to respond quickly to nutrient supply from the sea surface (Fontanier et al., 2002). Thus, their relative abundance in the BF community can be considered an indicator of the presence of labile organic matter in the sediment (Jorissen et al., 1995; Fontanier et al., 2003; Murray, 2006; Sun et al., 2006). The presence of a heterogeneous bottom morphology (Nagai et al., 2014), with high declivity of the slope, which can intensify the Intermediate Water Boundary Current (IWBC) (Zembruscki, 1979; Mahiques et al., 2022), must have a great influence on the stations of Group II. Furthermore, the high declivity of the slope could also favor food transportation from the upper continental slope to greater depths by mass flow (Murray, 2006; Nardelli et al., 2010). These environmental conditions benefit the presence of *G. subglobosa,* which can thrive in environments with phytodetritus input and oxic conditions (Gooday, 1993; Sousa et al., 2006) and high bottom current velocities (Mackensen et al., 1995; Schmiedl et al., 1997). Therefore, it can also be used as an indicator of the presence of food pulses in the marine environment (Gupta and Smith, 2010) associated with active currents.

Group III presents stations from the northern and southern middle slope of Santos Basin (A08, A09, B07, B08, B09 G07, G08, and G09), located between 700 m and 1,300 m water depth. The ecological indices had lower values than those found in the upper slope, although higher TOC, CHO, and LIP contents were found in these depths. One of the main species found in these stations was *E. exigua*, which shows significant positive correlation to chlo *a* surface concentrations. This species is directly associated with phytodetritus pulses, it blooms during seasonal increases in phytodetritus to the seafloor (Gooday, 1988; Gooday and Turley, 1990). Carreira et al. (2022) found high concentrations of BPC, notably in the southern sector of the SB, between 700 and 1,900 m isobaths, suggesting that on the middle-lower slope the O.M. still has nutritional quality to benthic organisms. However, these authors suggest that the O.M. contained in surface sediment is degraded since most of these samples presented PTN:CHO ratios near or below the threshold of 1.0. The other main species observed in the Group III (Figure 5) is *Reophax* sp. 1, which has not been described yet. Species of *Reophax* has been considered first recolonizers of physically unstable environments, due to the action of currents, internal waves, internal tides, benthic storms, turbidite deposition, among others (Kaminski, 1985; Kaminski and Schroder, 1987; Koho et al., 2007; Hess and Jorissen, 2009; Duros et al., 2011; Martins et al., 2012). Nevertheless, no correlation between the distribution of the species *Reophax* sp. 1 and the average grain size was found.

A07 (700 m depth) is the sole station in Group IV and it seems to be located at a deep-sea coral reefs region (Sumida et al., 2004). Lower values of FD, S, and H', highest value of $CaCO_3$ (Figueiredo Jr. et al., 2023), and high declivity of the continental slope (Zembruscki, 1979; Mahiques et al., 2022) characterize the environmental conditions in this region. The species *U. auberiana* and *T. bradyi*, which highly contributed to the dissimilarity of this group, presented positive correlation to chlo *a* surface concentrations. According to Vicente et al. (2021) *U. auberiana* is a species that indicate carbon flux in Campos Basin. *Trifarina bradyi* is a common species in environments with phytodetritus inputs and lability of the particulate organic matter (Gooday, 1993; Hayward et al., 2002; Sousa et al., 2006; Gupta and Smith, 2010; Yamashita et al., 2016, 2018, 2020; Vicente et al., 2021). The PTN:CHO ratio values > 1 confirm the presence of labile organic matter in the station A07. However, *U. auberiana* is also usually associated with low-oxygen (Jian et al., 1999; Kuhnt et al., 1999), associating this particularity to the location of station A07. However, more samples should be analyzed to better understand and evaluate the environmental characteristics of this area.

Group V, composed of the deepest stations, is characterized by the lowest values of FD, richness, and diversity. *Alabaminella weddellensis*, *Reophax* aff. *elegans, Ioanella tumidula,* and *Reophax agglutinatus* were some examples of the taxa that contributed to the dissimilarity of this group. The species *A. weddellensis* is an indicator of seasonal phytoplankton blooms (Kender et al., 2019) in the environment. Moreover, *Reophax* aff. *elegans* is positively correlated with chlo *a* sediment and $CaCO_3$ contents. However, the species *R. agglutinatus* is essentially found in deep ocean environments with refractory organic matter (Dessandier et al., 2016). *I. tumidula* is considered a species sensitive to organic enrichment, present in places with low TOC values (Alve et al., 2016). The species is also present in fine sediments and abundant at great depths (Martins and Gomes, 2004). These facts, associated with low values of ecological indices, suggest that Group V is present in the most oligotrophic region of the study area and with low-quality organic matter, occurring seasonal inputs of phytodetritus.

Thus, the input of more labile food, derived from the pelagic sources, from the upper to the lower slope of both sectors of the basin, has a great influence on the benthic foraminiferal community in the Santos basin. Moreover, the Brazil Current System dynamics (Lorenzzetti and Gaeta, 1996; Sumida et al., 2005; Eichler et al., 2016; Calil et al., 2021), can play a role in transporting and delivering organic matter to deep ocean regions in the basin (Marone et al., 2010; Mahiques et al., 2017; Tura and Brandini, 2020)

CONCLUSION

In the northern region of the SB, species richness, and diversity are higher than in the south, which is due to the greater availability of fresh food supplied to the sea floor. The lower slope and São Paulo Plateau, however, are similar in both regions. Despite the spatial variability of foraminiferal assemblages composition, we found that species richness (S) is correlated with phytopigment concentration and FD with chlo *a* surface concentration.

For the establishment of living BF faunas in SB, it seems that the quality of the organic matter present in the substrate is more important than the quantity of this parameter. It is essential to better understand the bentho-pelagic coupling and/or decoupling and the dynamics of the vortices in the SB, as they are oceanographic features with the potential to induce the production and transport of food to deep ocean regions.

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AUTHOR CONTRIBUTIONS

B.D.A.: Conceptualization; Formal analysis; Investigation; Methodology; Writing – original draft;

C.Y.: Investigation; Writing – original draft; Writing – review & editing;

A.C.A.S., C.C.P., M.V.A.M.: Investigation; Writing – review & editing;

A.V.R.: Writing – original draft; Writing – review & editing;

T.M.V.: Writing – review & editing; Project administration;

R.N.M.M.: Writing – review & editing;

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