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Community structure of the benthic macrofauna along the continental slope of Santos Basin and São Paulo plateau, SW Atlantic.

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ABSTRACT

Continental margins usually have a high degree of environmental heterogeneity, which, in turn, promotes high benthic biodiversity. The South-Southeast regions concentrate the most well-mapped areas of the Brazilian continental margin regarding seafloor geomorphology and physical oceanography. However, the structure of the soft-sediment benthic fauna of the continental slope is still unknown. Characterization and understanding of the Brazilian continental slope biota are imperative since human activities are increasing in the last decades, especially after the discovery of the pre-salt reservoir in Santos Basin. In this study, we aimed to establish a baseline of the spatial distribution of the benthic macrofaunal communities regarding their latitudinal and bathymetric patterns in the Santos Basin to support future environmental monitoring activities in the region. As part of the Santos Project – The Santos Basin Regional Environmental Characterization (PCR-BS) – coordinated by CENPES/PETROBRAS, a benthic oceanographic cruise was carried out in 2019. Sediment samples were collected using a GOMEX-type box corer in 47 stations distributed in eight transects (400–2,400 m depth range). In total, 12 additional stations (1,300–2,200 m) were defined to cover an area where oil and gas are exploited. Our results showed that macrofaunal assemblages of the Santos Basin present strong depth zonation related to changes in organic matter input, as well as to temperature, carbonate, and grain size. At local scale, the northern sector stood out for having a higher abundance of macrofauna in the upper slope (400 m) and it probably reflects the oceanographic processes and the organic enrichment caused by the upwelling events that occur at Cabo Frio region. The zonation pattern and the dominance of some polychaete, peracarid crustacean, and bivalve families were similar to other SE Brazilian continental margins.

Keywords: Brazilian margin, Baseline study, Deep-sea, Macrobenthos, Self-Organizing Map

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INTRODUCTION

Continental margins comprise the continental shelf and slope regions and represent approximately 15% of the ocean floor (Menot et al., 2010). Although they seem to be homogeneous environments, continental margins are influenced by a wide bathymetric gradient, different substrate types, and biological interactions between benthic communities (Menot et al., 2010; Ramirez-Llodra et al., 2010). Furthermore, geological, physical, and geochemical conditions of the ocean floor and water column generate a high degree of environmental heterogeneity (Ramirez-Llodra et al., 2010), which, in turn, promotes high benthic biodiversity. Continental margins also perform essential ecological services such as nursery grounds, nutrient remineralization, and long-term carbon sink (Levin and Sibuet, 2012). Among the benthic organisms, the macrofauna is used as an important food resource by benthic megafauna and fishes, contributing to biogeochemical cycles by remobilization of the sediment (bioturbation), or secondary production processes of marine ecosystems (Gage et al., 1991; Gray and Elliott, 2009).

Most macrofaunal species have little or no adult mobility and their depth and latitudinal distributions are frequently associated with different types of sediment, organic matter, and distribution patterns of water masses (Puerta et al., 2020). Although sediment characteristics (e.g., grain size and carbonate content) are traditionally suggested as the main driving factors of sediment macrofauna distribution (Gray and Elliott, 2009), other environmental characteristics have stood out as important drivers of the deep-sea benthic biodiversity, some of which may be directly or indirectly related to the characteristics of water masses such as temperature, dissolved oxygen, organic matter flow, and circulation patterns (Puerta et al., 2020). Benthic diversity usually decreases with increasing depth or latitude (Rex et al., 2006). Since water masses properties also covary with depth, as many other environmental variables (e.g., particulate organic matter), it is difficult to distinguish the role of each of these factors independently and the relationships between benthic diversity and those environmental factors can change from one continental margin to other.

Although the volume of biological data available from the continental margins of both the North and the Equatorial Atlantic is more expressive when compared to the South Atlantic (Levin and Gooday, 2003), initiatives in partnership with oil industries have been successful in increasing the knowledge in the last 15 years in the SW Atlantic, especially in the Northeast (Guimarães et al., 2020) and Southeast Brazil (Lavrado et al., 2010, 2017; Bernardino et al., 2016). The continental slope of Southeast-South Brazil concentrates more than 90% of the country’s oil reserves and production (Viana et al., 1998; Mohriak, 2003; Falcão et al., 2017), and the growth of oil and natural gas exploitation in the ocean floor has stimulated the development of environmental characterization and monitoring studies in Campos and Espírito Santo Basins over the last 15 years (Lavrado et al., 2010, 2017; Bernardino et al., 2016).

Different from the continental shelf, where information on benthic macrofauna has been developed since the 1980s (Capítoli and Bonilha, 1991; Sumida and Pires-Vanin, 1997; Seeliger et al., 1998), data available from the continental slope of Santos Basin are still incipient. The “Program for the Assessment of the Sustainable Potential of Living Resources in the Brazilian Exclusive Economic Zone” (REVIZEE – Score Sul) stands out as the most comprehensive investigation of the benthic fauna of the Southeast-South Brazilian continental margin, with stations collecting samples down to 808 m depth (Amaral et al., 2004). However, information on the deep benthic macrofauna was restricted to the upper slope at a maximum depth of 600 m. For instance, it was not possible, to observe the biodiversity unimodal trend along a depth gradient, as generally described for several groups of benthic invertebrates in the deep sea (Menot et al., 2010). Additional studies in the region have mostly focused on the benthic community structure of specific habitats on the middle and lower slopes, such as coral mounds associated with pockmarks, whale carcasses, and sunken wood (Sumida et al., 2004; 2016; Shimabukuro et al., 2017; 2019; Saaedi et al., 2019).

However, to date, knowledge about the patterns of the benthic fauna along a broader bathymetric gradient is still scarce, mainly considering the regions of the continental slope of Santos Basin and São Paulo plateau. This could be a serious issue as the increasing human footprint on that continental margin might compromise its biodiversity even before it is completely known. Among the main environmental risks to the deep sea worldwide are deep-sea fishing, oil and gas extraction, marine mineral extraction, and climate change (Glover and Smith, 2003). Deep-sea basins in Brazil have been the target of the oil and gas industry in the last decades, and Almada and Bernadino (2017) have already stressed the need for identifying vulnerable deep-sea habitats (EBSAs) in the Brazilian continental margin. Considering the increasing human activities from depths of 1,000 and 2,000 m, especially after the discovery of the pre-salt reservoir in Santos Basin, it is essential to characterize and to understand the Brazilian continental slope biota (Almada and Bernardino, 2017). Moreover, developing projects of a broad and multidisciplinary nature in those continental slopes is essential to subsidize future conservation and monitoring programs. In this context, as part of the "Santos Project – The Santos Basin Regional Environmental Characterization (PCR-BS)", coordinated by CENPES/PETROBRAS, this study focuses on characterizing the macrobenthic communities of the continental slope, on a regional scale basis, to understand the structure of this continental margin, providing subsidies for the planning and environmental management in the future. This study aims to (1) characterize the benthic macrofaunal community structure of Santos Basin; (2) determine the latitudinal and bathymetric distribution of macrobenthic communities, and (3) identify the main environmental variables determining the macrofauna distribution.

METHODS

Study site

The Santos Basin (23°S–28°S) comprises the coastal regions of the Brazilian states of Rio de Janeiro, São Paulo, Paraná, and Santa Catarina, covering an area of more than 350,000 km^2. Generally, the continental slope presents muddy bottoms with the occurrence of sandy muddy areas closer to the continental shelf break, especially at the central portion of the basin (Figueiredo Jr and Madureira, 2004).

From the coastline, the Santos Basin extends to the outer limit of the São Paulo Plateau, at the eastern, from 2,000 to 2,800 m depth. The plateau is 120–250 km wide, and its irregular surface is composed of a package of muddy sediments above the salt layer (Almeida and Kowsmann, 2016).

According to Silveira et al. (2023), the main water masses present along the continental slope were the South Atlantic Central Water (SACW), flowing southward from 150 to 500 m depth, Antarctic Intermediate Water (AAIW), the Upper Circumpolar Water (UCPW) from 500 to 1,300 m, and the North Atlantic Deep Water (NADW), flowing southward from 1,300 to 3,500 m.

The region is influenced by the meandering pattern of the Brazilian Current along the shelf-break and slope, which also induces the formation of mesoscale eddies that possibly leads to remobilization and resuspension of fine material down to 800 m or deeper (Mahiques et al., 2002).

In the northernmost sector of the Santos Basin, near the Cabo Frio region, upwelling events are frequent in the summer, driven by North-Northeast winds associated with the region topography, allowing the intrusion of SACW on the continental shelf and shelf break (Valentin, 2001; Coelho-Souza et al., 2012). These upwelling events promote seawater temperature variations and high nutrient inputs that often increase local primary and secondary productivities, especially on the outer shelf, which is about 100 m deep (Sumida et al., 2005; Brandini et al., 2018).

Field Sampling

A Winter Deep-sea Benthic Campaign (SANSED1-4) was carried out from June to August 2019 onboard the R/V Ocean Stalwart. In total, eight transects were evenly established off Santa Catarina to Rio de Janeiro, over six isobaths (400, 700, 1,000, 1,300, 1,900, and 2,400 m) in both continental slope and the São Paulo plateau. Furthermore, 12 stations were defined to cover a sampling gap with concentration of oil and gas exploitation (1,300–2,200 m), totaling 60 sampling stations (Figure 1). Detailed information on the georeferenced location and depth for each station is presented in Moreira et al. (2023). The sediment was collected in triplicates at each station using a GOMEX-type box-corer (0.25 m^2 surface area), except for stations A07 (one replicate), D08, G09, and P01 (two replicates). A modified van Veen grab (0.75 m^2 surface area) was used in stations A06 and H06, where the substrate was coarser. Due to operational sampling constraints caused by the bottom characteristics (e.g., hard substrate), station G11 could not be sampled. For macrofauna, each replicate consisted of nine 10 cm^2 corers (total area: 900 cm^2) sliced into three layers: 0–2, 2–5, and 5–10 cm. The samples were fixed onboard in a 10% formaldehyde solution buffered with borax.

A multiparameter profiler (CTD) was used to determine the pH, temperature, and salinity of the bottom seawater in each station. Sediment was also collected for carbonate content (0–2 cm), organic carbon, and grain-size analysis (0–2 and 2–10 cm), and frozen (–20°C) after sampling.

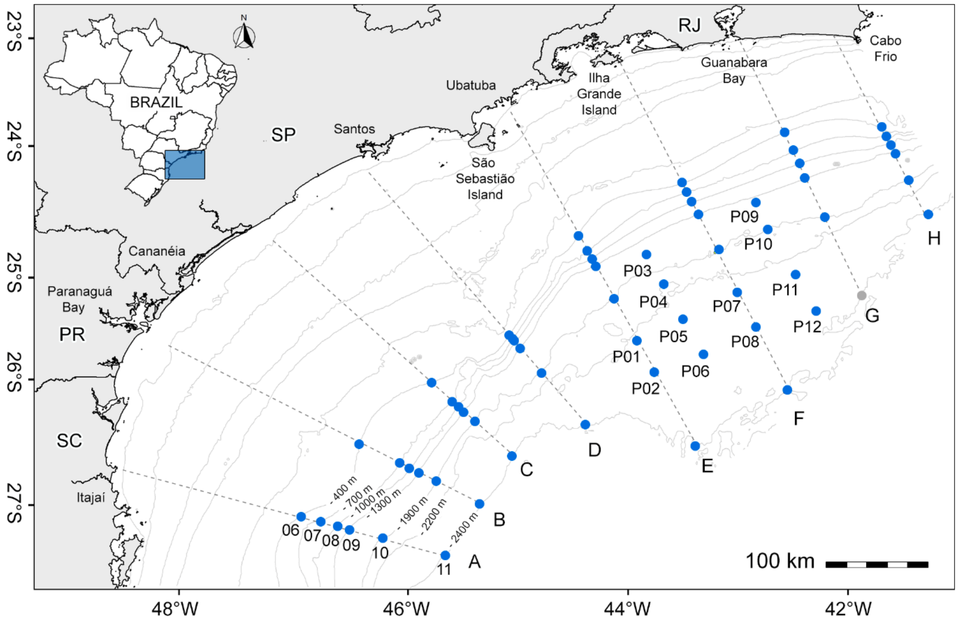

Figure 1. Distribution of sampling stations (blue dots) during the winter benthic cruise (SANSED 1-4) along the slope and São Paulo plateau in the Santos Basin, SW Atlantic. G11 station (gray dot) was not sampled. Capital letters A-H indicate each transect and numbers 06-11 represent depths (400–2,400 m). In stations P01-P12, sampling occurred at 2,200 m, except for P09 (1,300 m), P03, and P10 (1,900 m). Abbreviations: SC - Santa Catarina State, PR - Paraná State, SP - São Paulo State, and RJ - Rio de Janeiro State.

LABORATORY PROCEDURES

Regarding macrofauna, the sediment was washed through a 300 μm mesh sieve, and the organisms retained were preserved in 70% alcohol. That mesh size is often used for sampling deep-sea macrofauna, as the organisms are usually smaller than those found in shallow waters (Hessler and Jumars, 1974). Specimens were sorted, counted, and identified under a stereomicroscope. For the most abundant groups of the macrofauna (Polychaeta, Crustacea, and Mollusca), identification was initially made at family level and the specimens were later referred to several Brazilian specialists for subsequent taxonomic refinement. In the case of Mollusca, only organisms with intact shells and soft parts were considered in the analyses. Biomass was estimated by wet weight using an analytical balance (accuracy: 0.0001 g) for each group. All these procedures were done by Benthos Instituto de Pesquisa Ambiental.

For grain size analyses, a dried fraction of sediment was subjected to a laser grain sizer and larger particles (1-2 mm) were weighed separately and added later. To estimate carbonate content, another fraction of sediment was subjected to acid (HCl) treatment.

Chlorophyll-a and phaeopigments contents were determined by spectrophotometry. The protein content of the sediment was determined by colorimetry. The content of total carbohydrates was also determined by colorimetry assay based on the reaction between sugars and phenol with concentrated acid (H_2S0_4). Absorbances were determined by spectrophotometry and the results were quantified by a calibration curve. The biopolymeric carbon (BPC) was estimated based on the sum of the C equivalents obtained from relative standard analyses of carbohydrates, proteins, and lipids of the sediment. Sediment samples were processed for environmental variables at the Laboratório de Geologia Marinha (LAGEMAR/UFF) and the Laboratório de Estudos Marinhos e Ambientais (LabMAM/PUC-Rio). Further information on each analytical method and data from the sediment composition and organic matter can be found in Figueiredo Jr. et al. (2023) and Carreira et al. (2023).

Data and Statistical Analysis

Taxa abundances of the whole sediment column (0–10 cm) were converted to individuals per square meter and biomass was estimated in g wet weight m^{-2}. In this study, taxa were analyzed at family level, as many deep-sea species are still unknown to science and their identification is a very time-consuming process. That taxonomic resolution has been considered useful and sufficient for distinguishing natural spatial patterns of macrofauna assemblages in coastal and even in deep-sea (De Smet et al., 2017; Washburn et al., 2021; Kokesh et al., 2022) as it optimizes both effort and taxonomic expertise for future monitoring programs. Moreover, it is usually robust to damaged specimens, a particular issue with polychaetes, the dominant macrofauna group in deep-sea (Van Der Grient and Rogers, 2021).

Other primary community descriptors such as taxonomic richness (S), Shannon-Wiener diversity index (H'$\log_2$), Pielou evenness index (J´), and Hurlbert's rarefaction (ES_n) were calculated for each sample using PRIMER 6.1.16 & Permanova+ 1.6.0. (Clarke et al., 2001).

One-way analysis of variance (ANOVA) was performed to detect significant differences in density and community descriptors among depth or transects as the sampling design was unbalanced (e.g., only stations P have 2,200 m depth). Tukey's test was performed to detect statistically different mean pairs. Data were verified for normality using the Shapiro-Wilk test and for homogeneity of variances using Levene's test. All variables were log-transformed to achieve ANOVA assumptions. This routine was performed using the Statsoft Statistica 8.0 program.

For the multivariate analysis, abundance data was 4th-root transformed to downweigh the most abundant taxa. The resemblance matrix was obtained using Bray-Curtis distances and subjected to a non-metric multidimensional scaling (nMDS) to examine assemblages relationships from different depths using PRIMER 6.1.16 & Permanova+ 1.6.0. Differences in macrofauna community structure between depths were investigated by a one-way permutational ANOVA (PERMANOVA). A test for the homogeneity of multivariate dispersions was performed using the PERMDISP routine (Anderson et al., 2008).

An unsupervised self-organizing map (SOM) analysis (Kohonen, 2001) is a neural-network model and was used to classify the benthic assemblages sampled across depths and transects for a comprehensive view of the macrofauna spatial patterns at Santos Basin. The SOM analysis was applied to the 4th-root transformed taxa mean density dataset following the parameters described in Fonseca and Vieira (2023) in the iMESc 2.1.0.1 application interface (Vieira and Fonseca, 2022). After training 10 times, the model with the least topographic errors was selected. The results obtained after the SOM analysis were subjected to a hierarchical clustering using Ward's linkage method to reduce the number of groups. The optimal number of groups was determined by clustering.

A canonical correspondence analysis (CCA) was performed to identify the environmental variables that explain the macrofaunal assemblages distribution using the biological matrix with the most abundant (> 0.1%) and frequent (> 5%) taxa and a standardized environmental matrix. Latitude, longitude, bottom seawater temperature, mean grain size, sediment sorting, clay content, gravel content, carbonate content, biopolymeric carbon, protein:carbohydrate ratio, phaeopigments:chlorophyll-a ratio, and dinosterol were considered as environmental variables for the analysis. Longitude and gravel content were not indicated after performing forward ordistep selection, and thus, were excluded. All 10 variables indicated were kept considering the variance inflation factor (VIF < 5.0). Data analysis was performed using the Vegan 2.5-7 package (Oksanen et al., 2020), and visualization was generated using the package ggplot2 (Wickham, 2016) both in R Studio environment (R Core Team, 2021).

RESULTS

In total, 35,674 individuals belonging to 203 taxa of the macrofauna *stricto sensu* (excluding nematodes, copepods, and ostracods) were found, with average densities ranging from 241–12,959 ind.m^{-2}. The most abundant groups were Annelida, Crustacea, and Mollusca, accounting for 70%, 17.5%, and 6.5% of the total macrofauna, respectively. The remaining invertebrate groups, mainly composed of Sipuncula, Nemertea, and Echinodermata, were classified as "others" and corresponded to approximately 6% of the total abundance of the macrofauna.

The mean density decreased with depth for all major groups (Figure 2A). Higher densities occurred on the upper slope, at 400 m, decreasing towards 2,400 m depth (Figure 3E). Transect H, located north of the Santos Basin, aligned to the Cabo Frio upwelling region, had the highest density values for Annelida (2,831±1,161 ind.m^{2}) and Crustacea (772±219 ind.m^{2}). The mean density of Mollusca was exceptionally higher at the Transect F at 400 m (432±345 ind.m^{-2}) (Figure 2B), where Kellielidae bivalves represented 13.4% of the total macrofauna. In general, Spionidae, Paraonidae, Syllidae, Cirratulidae, and Pilargidae were the most numerically dominant and frequent families of Polychaeta (Table 1). However, Paraonidae dominated in the upper slope (400–700 m) while Spionidae mostly dominated the mid-lower slope and most stations down to the São Paulo plateau (1,000-2,400 m) (Table SM3, Supplementary Material). The families Colletteidae, Typhlotanaidae (Tanaidacea), and Desmosomatidae (Isopoda) were among the most abundant crustacean taxa, especially in the mid and lower slope. For the mollusks, Yoldiidae, Kellielidae (Bivalvia), and Chaetodermatidae (Caudofoveata) were the most representative abundant taxa (Table 1; Table SM4).

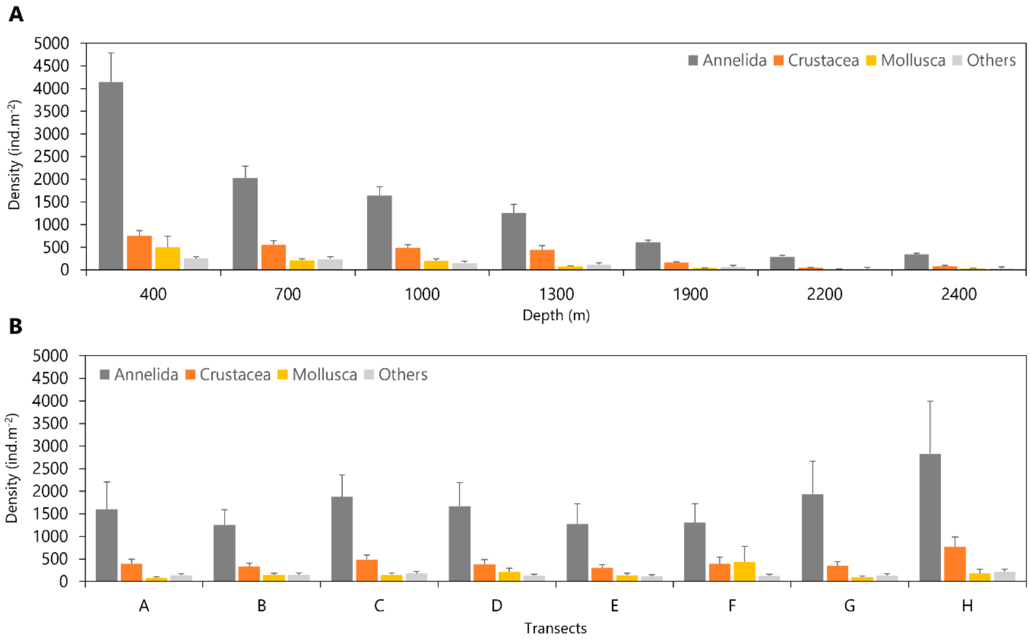

Figure 2. Mean densities (ind.m^{-2}) ±SE of the macrofaunal major taxa (Annelida, Crustacea, Mollusca, and other invertebrate groups) on the continental slope of Santos Basin and the São Paulo plateau. (A) Variation with depth. (B) Variation from south (Transect A) to north (Transect H).

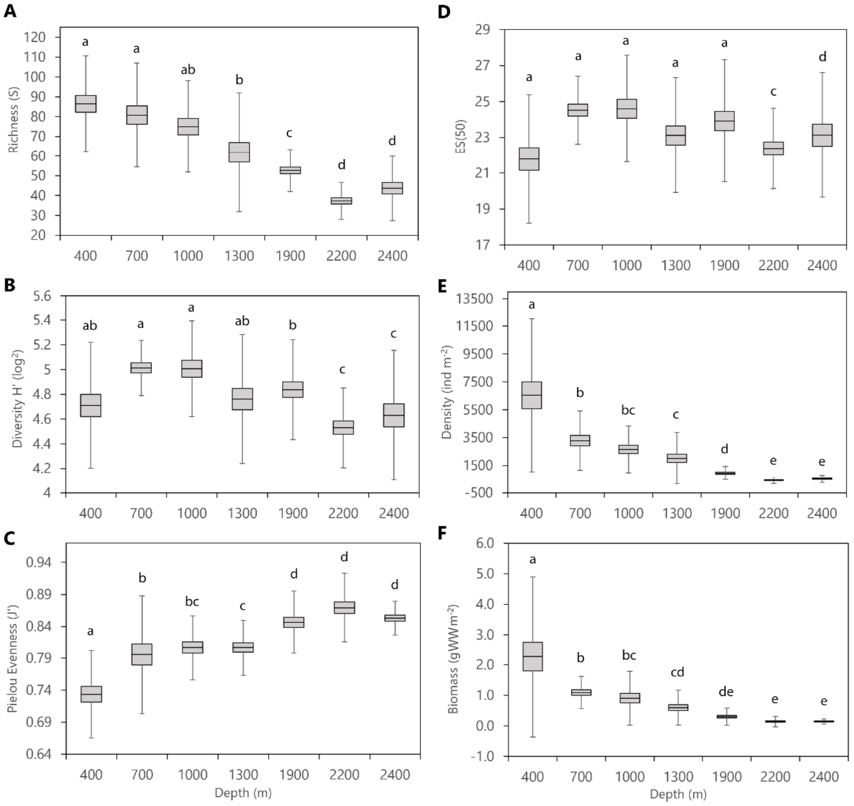

Figure 3. Mean values of (A) taxonomic richness (S), (B) Shannon-Wiener diversity (H'log2), (C) Pielou evenness (J'), (D) Hurlbert rarefaction (ES50), (E) density (ind.m^{-2}) (N), and (F) biomass (g wet weight m^{-2}) of the macrofaunal communities of the continental slope of Santos Basin (400-1,900 m) and São Paulo plateau (2,200–2,400 m) depth. Box limits = Mean±SE, Bars = Mean±2*SD. One-way ANOVA: richness – F: 101.0, p=0.00; diversity – F: 35.74, p=0.00; evenness – F: 68.29, p=0.00; rarefaction – F: 32.51, p=0.00; density – F: 172.2, p=0.00; biomass – F: 47.21, p =0.00. Lowercase letters above each bar indicate statistical significance according to Tukey pairwise test for unequal n (alpha = 0.05).

Table 1. Relative abundance (%) and frequency of occurrence (%) of the 10 top families of the major groups of the benthic macrofauna from Santos Basin and the São Paulo Plateau, 400–2,400 m depth. N = Total individuals. Total samples = 137. For Crustacea, Peracarida: (T) Tanaidacea, (I) Isopoda, (A) Amphipoda; for Mollusca: (B) Bivalvia, (C) Caudofoveata, (S) Scaphopoda.

Polychaeta			Crustacea			Mollusca		
Family	Rel. Abund.	Freq.	Family	Rel. Abund.	Freq.	Family	Rel. Abund.	Freq.
	N=22,964			N=5,819			N=2,290	
Spionidae	16.8	99.3	Colletteidae (T)	22.0	93.4	Yoldiidae (B)	19.3	49.6
Paraonidae	15.4	95.6	Desmosomatidae (I)	12.7	89.8	Kelliellidae (B)	15.2	28.5
Syllidae	8.3	90.5	Typhlotanaidae (T)	11.0	51.1	Chaetodermatidae (C)	5.6	24.1
Cirratulidae	8.0	98.5	Anarthruridae (I)	7.1	68.6	Entalinidae (S)	4.5	22.6
Pilargidae	6.3	38.0	Pseudotanaidae (T)	5.1	67.2	Nuculidae (B)	4.1	39.4
Nereididae	4.3	46.0	Akanthophoreidae (T)	4.2	70.1	Nuculanidae (B)	3.9	10.2
Amphinomidae	4.2	80.3	Apseudidae (T)	4.0	54.7	Prochaetodermatidae (C)	3.0	20.4
Capitellidae	3.9	83.9	Tanaellidae (T)	3.2	53.3	Cuspidariidae (B)	2.4	37.2
Sabellidae	3.2	94.2	Apseudidae (T)	3.0	40.9	Thyasiridae (B)	2.4	11.7
Ampharetidae	3.2	91.2	Phoxocephalidae (A)	2.5	40.1	Lasaeidae (B)	2.0	14.6

Mean taxa richness varied from 86.5±4.2 at 400 m to 37.3±1.5 at 2,200 m (Figure 3A). On the other hand, both taxonomic diversity indices (H' and ES$_{50}$) were higher in the mid-slope (700-1,000 m) (Figure 3B, 3D). Evenness increased with depth, with the highest value at 2,200 m (Figure 3C). No significant differences were found among transects for those indices (Figure SM1).

Macrofaunal biomass ranged from 0.06 to 5.34 g wet weight m^{-2}, with significant highest mean values in the transects at 400 m depth (F=47.65; p=0.00), reflecting the macrofauna abundance (Figure 3F). A significant difference between transects (F=3.596; p=0.002) was found, with higher biomass at Transect H (Figure SM1F). The groups with the highest biomass estimates were Annelida, followed by Mollusca, and Crustacea, respectively. The relative contribution of other macrofaunal invertebrate groups to the biomass was less relevant (Tables SM1 and SM2).

A clear depth zonation pattern was detected in the nMDS analysis, with almost all isobaths significantly differing from each other except for 1,000–1,300 m and 2,200–2,400 m (PERMANOVA, Pseudo-F=7.2769; p=0.001) (Figure 4). A greater spatial variability was observed at São Paulo plateau stations (2,200–2,400 m) when compared to slope depths (PERMDISP, Pseudo-F=4.8242, p=0.005) (Table SM5), showing that assemblages present at the São Paulo plateau are different regarding location and dispersion from the slope macrofauna.

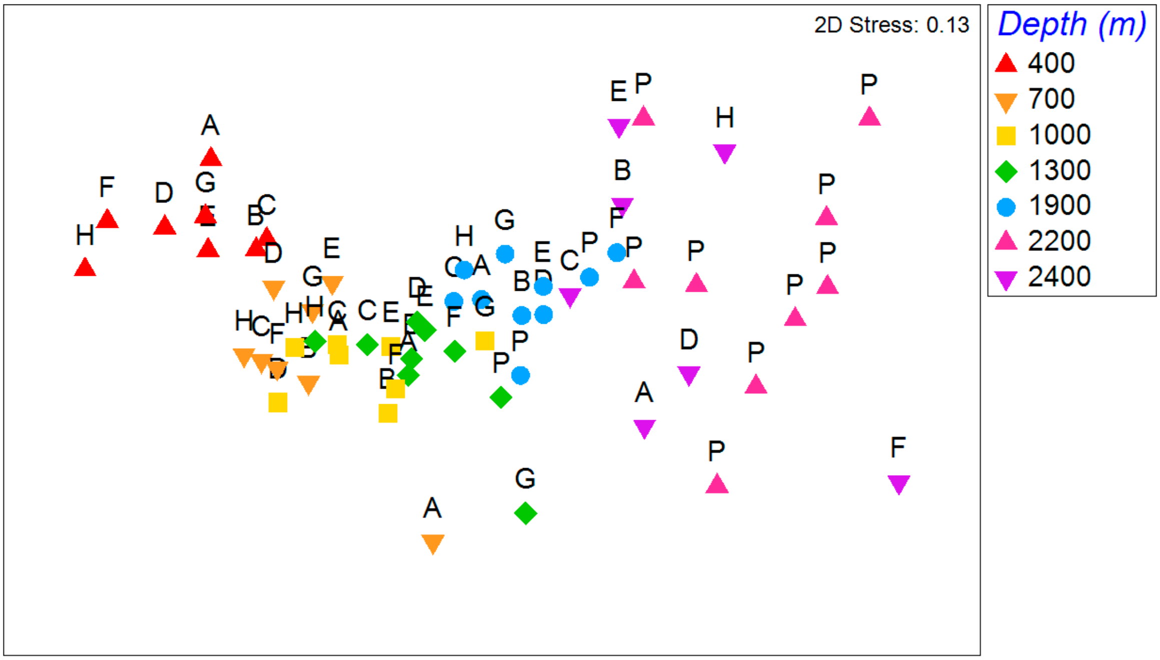

Figure 4. Non-metric multidimensional scaling ordination plot based on a Bray-Curtis distance matrix of the mean abundance of all macrofaunal taxa along the transects (A-H) and additional stations (P) in the continental slope of Santos Basin (400–1,900 m) and the São Paulo plateau (1,900–2,400 m). Abundance data were 4th-root transformed.

The network generated by the SOM analysis (quantization and topographic errors = 34.36 and 0.22, respectively) was composed of 36 nodes in a 6 × 6 hexagonal grid, in which the stations were plotted with taxa representing the 10 best correlations (Figure 5). Generally, four macrofaunal assemblages across Santos Basin were detected after clustering the SOM results mostly corresponding to four depth zones: the upper slope (400 m), middle slope (700–1,300 m), lower slope (1,900 m), and the São Paulo plateau (2,200–2,400 m), without clear latitudinal differences (Figure 6).

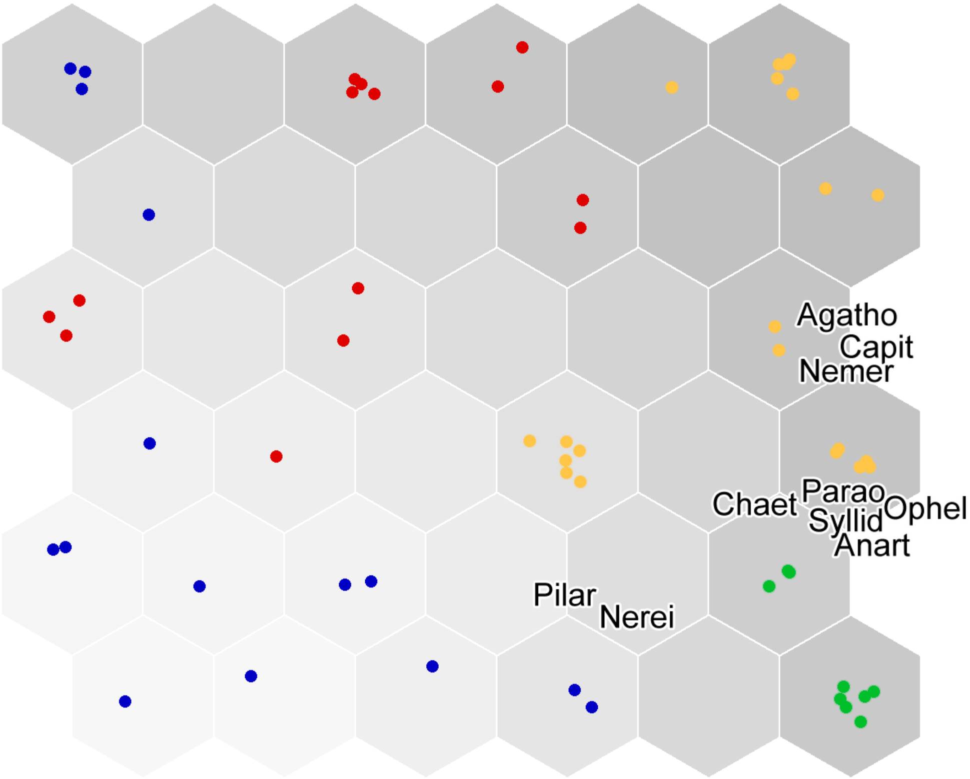

Figure 5. Two-dimensional mapping configuration obtained after the SOM analysis based on macrofaunal assemblages mean density data along the transects (A-H) and additional stations off Santos Basin. Dots represent each station. The 10 best correlations are shown. Annelida, Polychaeta: Capit (Capitellidae), Parao (Paraonidae), Syllid (Syllidae), Ophel (Opheliidae), Pilar (Pilargidae), Nerei (Nereididae); Crustacea, Tanaidacea: Agatho (Agathotanaidae), Anar (Anarthuridae); Mollusca, Caudofoveata: Chaet (Chaetodermatidae); Nemer (Nemertea). Abundance data were 4th-root transformed.

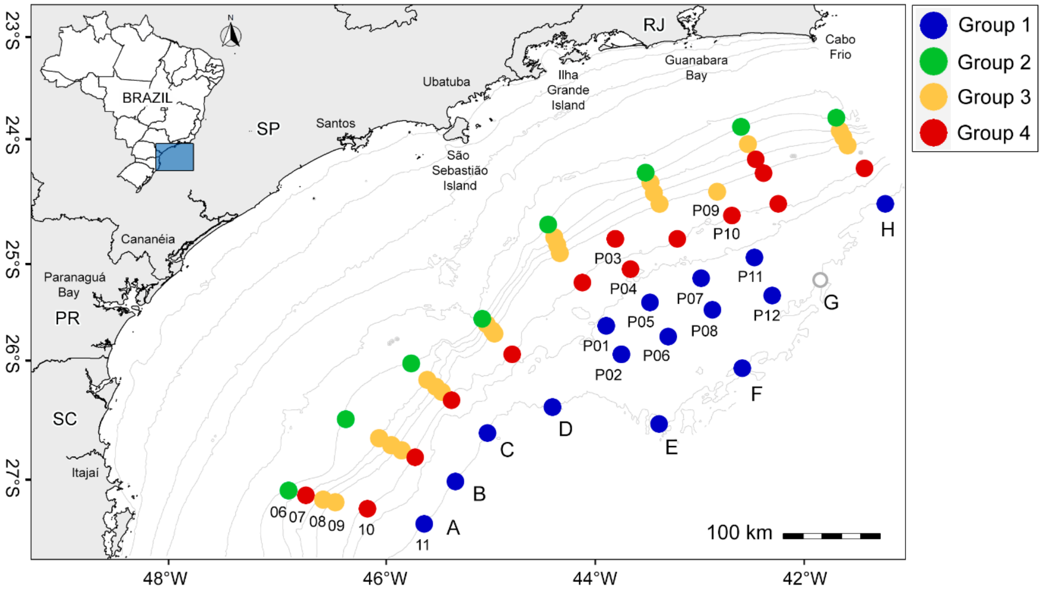

Figure 6. Benthic macrofaunal assemblages along the continental slope of Santos Basin and the São Paulo plateau after clustering the SOM results.

The influence of environmental characteristics on macrofauna assemblages was shown in CCA analysis. The first two significant axes explained 65.07% of the total data variance (Figure 7, Table SM6). Seawater temperature, protein:carbohydrate ratio, and mean particle size have the highest negative correlations with Axis 1 (43.22% of total variance), separating the upper slope (400 m) from the deeper stations. Magelonid polychaetes were associated with stations A06 and H06, where sediment was coarser. On the other hand, biopolymeric carbon, and clay content were the variables with the highest positive correlations with both axes (Figure 7, Table 2), where most of the stations of the middle-slope were found. Dinosterol was positively correlated with axis 2 (17.61% of total variance) while a negative correlation was found for carbonate content, with higher levels found at lower slope and plateau. Sabellid polychaetes and desmosomatid isopods were associated to these deeper stations.

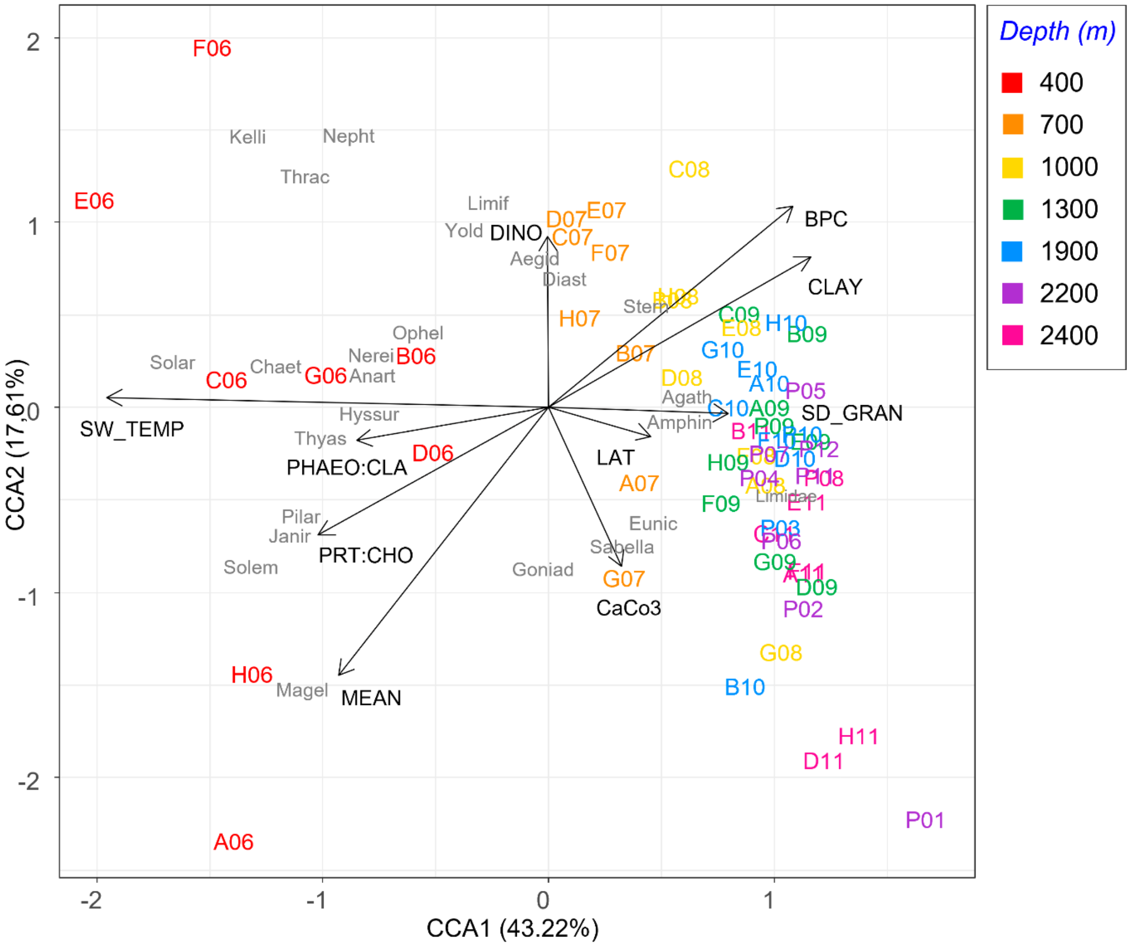

Figure 7. Canonical Correspondence Analysis (CCA) based on the abundance matrix of macrofaunal taxa. DINO = dinosterol (μg.g−1), BPC = biopolymeric carbon (mg.g-1), CLAY = clay content (%), SD_GRAN = grain sorting, LAT = latitude (°S), CaCO3 = total carbonate content (%), MEAN = mean grain size (mm), PRT:CHO = protein:carbohydrate ratio, PHAEO:CLA = Phaeopigments:Chlorophyll-a ratio; SW_TEMP = bottom seawater temperature (°C),. Annelida: Polychaeta - Amphin (Amphinomidae), Eunic (Eunicidae), Goniad (Goniadidae), Magel (Magelonidae), Nepht (Nephtyidae), Nerei (Nereididae); Ophel (Opheliidae), Sabelli (Sabellidae), Sabella (Sabellariidae), Stern (Sternaspidae); Crustacea: Amphipoda – Steno (Stenothoidae); Cumacea: Dias (Diastylidae); Isopoda: Aegid (Aegidae), Hyssur (Hyssuridae), Janir (Janiridae), Tanaidacea: Agath (Agathotanaidae), Anart (Anarthruridae); Mollusca, Bivalvia: Kelli (Kellielidae), Thyas (Thyasiridae), Thrac (Thraciidae), Yold (Yoldiidae); Caudofoveata: Chaet (Chaetodermatidae), Limif (Limifossoridae); Gastropoda: Solar (Solariidae).

Table 2. Minimum, maximum, and mean values of the main environmental variables from sediment samples of the continental slope and the São Paulo plateau, in Santos Basin, SW Atlantic, used in the Canonical Correspondence Analysis (CCA). Detailed information is present in Carreira et al. (2023) and Figueiredo Jr. et al. (2023).

	Abbreviation	Min	Max	Mean
Seawater temperature (°C)	SW_TEMP	2.5290	15.5960	4.6810
Mean particle size (mm)	MEAN	6.2130	90.7080	28.1700
Biopolymeric carbon (mg g^{-1})	BPC	1.5370	4.7560	2.8800
Carbonate content (%)	CaCO3	16.580	73.0100	41.5600
Protein:Carbohydrate	PRO:CHO	0.2700	0.7944	2.2331
Phaeopigments:Chlorophyll a	PHAEO:CLA	2.0620	16.4720	5.7010
Grain sorting	SD_GRAN	2.9370	10.2160	6.0720
Dinosterol (µg g^{-1})	DINO	0.0090	0.5170	0.1379
Latitude (°S)	LAT	23.7700	27.5400	25.5300
Clay content (%)	CLAY	2.5880	16.3740	9.1740

DISCUSSION

The bathyal macrofauna of the Santos Basin (SB) presented distribution patterns, regarding abundance and taxonomic composition, in line with the pattern already found for other regions of the Brazilian continental margin (Bernardino et al., 2016; Lavrado et al., 2017; Guimarães et al., 2020) and similar to those of other known deep-sea regions worldwide (Cosson et al., 1997; Galéron et al., 2000; Tyler, 2003; Buhl-Mortensen et al., 2012); Carvalho et al., 2013).

Regarding taxonomic composition, the dominance of polychaetes in Santos Basin (55–65% of total macrofauna) has also been recorded in several deep-sea regions worldwide, where that group can reach up to 90% of the total macrofauna (Cosson et al., 1997; Galéron et al., 2001, 2009; Ingole et al., 2010; Abdul-Jaleel, 2012). Similar dominance values (from 45 to 75%) are also found in Espírito Santo, Campos, and Sergipe-Alagoas Basins (Bernardino et al., 2016; Lavrado et al., 2017; Guimarães et al., 2020). Polychaete species present a wide range of feeding types and life modes (Jumars et al., 2015), including surface and subsurface deposit feeders that can efficiently exploit the organic matter accumulated on the top sediment layers along the continental slope (Thistle, 2003; Jumars et al., 2015). The main polychaete families found in Santos Basin (Spionidae, Paraonidae, Cirratulidae, and Syllidae) also predominate on the continental slope of Campos Basin (Lavrado et al., 2017) and are among the most abundant macrofauna taxa of Espírito Santo (Bernardino et al., 2016) and Sergipe-Alagoas Basins (Guimarães et al., 2020), as well as in other Atlantic continental margins (Shields and Blanco-Perez, 2013). The first three families comprise mainly surface and subsurface-feeder species, which usually feed on phytodetritus. Among Polychaete, Spionidae could reach up to 40% of total abundance in some deep-sea regions as in the mid-Atlantic ridge (Shields and Blanco-Perez, 2013). Spionidae is one of the most common polychaeta families in the deep sea (Glover et al., 2002; Hughes and Gage, 2004; Shields and Hughes, 2009) and evidence suggests that some spionid species can act as surface deposit or suspension feeders, depending on the levels of suspended organic matter in the water column (Taghon et al., 1980). Syllidae, on the other hand, is composed of omnivorous/carnivorous species, and they can be important predators of benthic foraminifera (Würzberg et al., 2011).

About 30% of the invertebrate taxa found were rare, occurring only once or represented by a single individual, a common trend in deep-sea macrofauna (Grassle and Maciolek, 1992). The same pattern was found in the Southeast Brazilian margin, in which Lavrado et al. (2017) reported that almost 37% of macrofauna species are extremely rare in Campos Basin slope. Even at higher taxonomic level ca. 39% of the families found in Sergipe-Alagoas continental slope occurred in less than three sites (Guimarães et al., 2020). The causes of the rarity of species in the deep sea are still poorly understood and it is a challenge for understanding the role of those species in the ecosystem functioning. Gage (2004) considers the possibility that the rare species represent a pool of transient immigrants that can settle when there are favorable conditions. However, further studies are needed to clarify this common pattern in the deep sea. The total macrofauna density decreased with depth as it is usually observed in other continental margins worldwide (Tselepides et al., 2000; Levin and Gooday, 2003; Pabis et al., 2019). In Brazil, density estimates of the upper slope at Santos Basin were lower than those found in the upper slope of Espírito Santo Basin (up to 15,396 ind.m^{-2} at 400 m). On the other hand, these estimates were similar to those found on the oligotrophic regions of Campos Basin margin (ca. 7,700 ind.m^{-2} in average at the upper slope (Lavrado et al., 2017)), although higher densities can also be attained in the northern sector, off Cabo Frio (> 10,000 ind.m^{-2} at Transect H). Depth variation of abundance and biomass is another common trend in the deep sea as those variables usually respond to changes in quantity or quality of organic matter, as well as the organic matter flux to the bottom, which can vary among different continental margins (Thistle, 2003) and it is considered as one of the main factors driving macrofauna depth distribution.

Along the continental slope of Santos Basin, a strong zonation pattern of macrofauna can be found, and at least three slope zones are distinguishable (upper: 400–700 m, middle: 1,000–1,300 m, and lower: 1,900 m) besides the area of the São Paulo plateau (2,200–2,400 m). The upper slope (400 m) stands out from the rest of the margin because of the higher abundance of macrofauna, with a marked presence of some groups of carnivorous or omnivorous polychaete families, which are also abundant in this depth zone, such as Syllidae, Pilargidae, and Nereididae. This same zonation pattern was observed in the Campos Basin (Lavrado et al., 2017), Espírito Santo Basin (Bernardino et al., 2016), and Sergipe-Alagoas Basin (Guimarães et al., 2020), where macrofauna assemblages differed with depth; notably the upper slope (400 m) always stands out from the middle and lower slopes. According to these authors, macrofauna zonation was primarily explained by differences in organic matter contents available in the sediment (TOC and phytopigments), as well as carbonate and temperature (as proxy of water masses). In this study, biopolymeric carbon (BPC) explained most of the bathymetric variation found in middle slope compared to upper slope, confirming the importance of organic matter input to determine macrofauna abundance and community structure.

On the other hand, higher temperatures of the SACW waters and coarser sediments were relevant factors determining macrofauna assemblages at the upper slope. However, the sediment carbonate content explains part of the variation of macrofauna and of the meiofauna on the lower slope and São Paulo plateau (Galucci et al., 2023). Temperature might be one of the environmental factors responsible for large-scale diversity patterns due to differences in the physiological tolerance of invertebrates. Generally, the benthic diversity response to temperature is unimodal with a peak occurring from 5to 10 °C (Yasuhara and Danovaro, 2014). Regarding the Santos Basin, the average temperature in the upper slope is ca. 11°C (Table 2) corresponding to the presence of SACW in this bathymetric range. Below 400 m colder water masses are found and species turnover is accentuated. The association between benthic fauna and the properties of water masses has been reported for sessile benthic organisms such as corals and sponges (Arantes et al., 2009; Davies et al., 2009; Davison et al., 2019), or for vagile fauna such as decapods (Cartes et al., 2013), and may also explain the macrofauna zonation along the slope since it is composed of many sedentary and small species. The depth distribution of macrofauna also seems to be related to the differences in environmental conditions provided by the water masses present along the slope, especially regarding temperature. In this study, the boundaries of the benthic zones found coincide with the range of the main water masses present along the slope (SACW: 400 m, AAIW: 700-1,300 m, NADW: > 1,300 m), except for the São Paulo plateau and lower slope (1,900 m), where differences in macrofaunal assemblages were detected despite the influence of the same water mass (NADW). This relationship between the macrofauna depth zones and water masses has also been observed on other continental margins such as the Campos Basin (Lavrado et al., 2017) and the Eastern Pacific (Palma et al., 2005). However, the causes for that relationship are still unclear. Besides temperature, water masses may control the larval supply transported from other regions by currents (Buhl-Mortensen et al., 2020) and could be responsible for differences in taxa composition along the slope. For instance, to the north of the Santos bifurcation (~28°S), SACW is transported southeastwards by the Brazil Current while the Intermediate Western Boundary Current (IWBC) flows northeastward, transporting AAIW (Belo and Silveira, 2013).

Regarding taxonomic diversity, the highest values of Shannon indices were found from 700 to 1,000 m in the Santos Basin, similar in depth ranges found in the Campos (1,000 m) and Espírito Santo Basin (1,000–1,300 m) slopes (Lavrado et al., 2017); Bernardino et al., 2016). Nevertheless, the taxa richness did not present such pattern, decreasing with depth as it is strongly influenced by the abundance rarefaction as a function of the decreasing food supply. Therefore, evenness increased along the depth gradient. When species richness is normalized to 50 individuals, the curve becomes more similar to that of Shannon diversity, both suggesting a parabolic function. The increase in family diversity at slope intermediate depths found in the Santos and Espírito Santo Basins (Bernardino et al., 2016) was equivalent to that obtained with data at species level at Campos Basin (Lavrado et al., 2017), suggesting that family level can also a good surrogate of diversity patterns in Brazilian margins. One advantage of macrofauna identification at family level is that this process is often standardized across taxonomists, suffering less from individual bias and uncertainty than identification at species level, which is hindered by the diversity of different groups and by the high number of undescribed species in the deep sea (Washburn et al., 2021).

The peak of diversity in this depth range differs from that mostly found on some continental margins of the Atlantic and Pacific Oceans (Menot et al., 2010). Although some studies verified that the diversity maximum of macrofauna and megafauna in the North Atlantic occurred from 1,900 to 2,800 m (Rex, 1981; Stuart and Rex, 2009), this apparently does not occur in the Southwestern Atlantic or even in the Gulf of Mexico, where the peak of diversity occurs in the shallower zone of the continental slope (Menot et al., 2010). These variations in the maximum diversity depth between continental margins may be mainly related to differences in carbon flux derived from surface pelagic production to the bottom, however, it can also respond to temperature, water masses properties, or even dissolved oxygen levels. For instance, an inverted pattern of diversity can occur in OMZ zones (500–1,000 m) with the minimum diversity in the middle slope (Palma et al., 2005), which is not the case of Santos Basin.

On the other hand, some authors consider that diversity could be related to productivity (Stuart and Rex, 2009) and data analysis based on assemblages of polychaetes, bivalves, and gastropods in the Gulf of Mexico showed a parabolic relationship between diversity and productivity with maximum diversity found at intermediate productivity levels (Menot et al., 2010). Although Carreira et al. (2023) have observed an increase in TOC and BPC from 700to 1,300 m, its origin in the southern section of Santos Basin is still undetermined. However, even in the absence of fresh and labile organic matter, many benthic taxa can benefit from organic matter in decay due to its enrichment by microbial communities (Danovaro et al., 1993). The higher protein:carbohydrate ratio at 400 m suggested that bacterial biomass can be related to the degradation of the organic matter on the bottom, but further investigation is needed to clarify that relationship.

The south and north upper slope regions at Santos Basin showed a slight but significant difference, comprised mainly by high abundance and biomass of macrofauna near Cabo Frio upwelling region (Transect H). These higher densities occur due to indirect effects of the upwelling events at the coastal region of Cabo Frio. Sumida et al. (2005) suggested the primary productivity of the Cabo Frio system may sustain the high microbial biomass and detritivore macrofauna, especially at outer shelf (100 m). It is reasonable that some part of the particulate organic matter could also reach the upper slope by some transport mechanism. Other than the fact that the continental shelf is narrower in this region and the slope is also steeper, some authors consider that transport may occur by influence of the eddies and meanders of the Brazilian Current (Oliveira et al., 2013) and then some transport of the organic matter from the outer shelf to the upper slope may occur. However, further investigation is necessary to clarify the benthic-pelagic coupling in the northern sector of Santos Basin.

On a regional scale, the spatial and bathymetric distribution of macrofauna in the Santos Basin, when analyzed at higher taxonomic levels (from family to phylum), is quite similar to that already found along the SE Brazilian continental margin, as well as the main environmental variables determining its distribution. Evidence suggests that macrofaunal spatial patterns found using data of taxa identified at higher taxonomic levels are consistent with these described for all macrofauna identified in species. Therefore, genera or families of macrofaunal organisms can be used as indicator groups for environmental monitoring purposes (Sallorenzo, 2013; Kokesh et al., 2022). However, local differences may exist in species composition, and only after the taxonomic refinement in progress, this issue can be better explained, as well as the detection of new species or endemic taxa in Santos Basin continental slope.

CONCLUSION

Macrofaunal assemblages of the Santos Basin continental slope and the São Paulo plateau are strongly related to depth, which is a proxy of changes in organic matter input, temperature (as an indicator of water masses), carbonate, and grain size on this margin. In total, four depth zones for macrofauna were clearly detected: upper slope (400 m), middle-slope (700–1,300 m) lower slope (1,900 m), and the São Paulo plateau (2,200–2,400 m). At local scale, the northern sector differed from the rest of the Santos Basin regarding macrofauna abundance, especially in the upper slope (400 m), reflecting the oceanographic processes and the organic enrichment due to the upwelling events that occur at Cabo Frio region. The zonation pattern and the dominance of some polychaetes, peracarid crustacean, and bivalve families were similar to other SE Brazilian continental margins. However, regional differences may arise when analyzing the macrofauna species composition. Therefore, caution is needed before making decisions regarding the management and conservation of each Brazilian margin. The taxonomic refinement in progress may bring complementary information regarding the structure and the functioning of macrobenthic sediment communities in the studied region.

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AUTHOR CONTRIBUTIONS

R.B.M.: Investigation; Formal analysis; Writing – original draft; Writing - review & editing;

A.G.D.: Investigation; Formal analysis; Writing – original draft; Writing - review & editing;

I.A.S.: Laboratory methodology; Writing – review;

D.L.M.: Conceptualization; Funding; Methodology, Project administration, Writing – review;

H.P.L.: Conceptualization; Supervision; Investigation; Methodology; Formal analysis; Writing – original draft; Writing - review & editing.

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