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From river mouth to reef: benthic foraminifera assemblages reveal ecological dynamics in a mixed carbonate–siliciclastic Brazilian continental shelf

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Abstract. The recent benthic foraminiferal assemblages have been considered to be a very useful tool as analogues for understanding environmental changes in the past oceans. In order to identify distribution patterns, the benthic foraminiferal assemblages (total fauna, $> 63\,\mu m$), along with sedimentological data, have been investigated on the continental shelf of the Espírito Santo Basin (ESB, between 18°20′ and 21°20′ S). The ESB is distinguished from the other Brazilian basins due its geomorphologically diverse continental shelf and slope; this is apart from it being economically important for oil exploration. Seafloor samples (0–2 cm) from 18 to 150 m were distributed in seven transects arranged perpendicularly to the coast. The density, taxonomic diversity, and assemblage of the total biota composition have changed significantly along the Espírito Santo continental shelf (ESCS). This study identified five main benthic foraminiferal assemblages along the ESCS, each associated with distinct sedimentary and environmental characteristics. The cluster analysis reveals five groups which were named after the abbreviation of the main species or genera. Group M–C is characterized by the marked presence of *Miliamina subrotunda* and *Cibicides* spp., as well as by high values of diversity and richness, indicating a stable environment. Group H–Q is dominated by *Hanzawaia boueana* and *Quinqueloculina* spp. in areas with terrigenous sediments and biogenic carbonate deposits. Group G–T is associated with high organic matter content and a marked presence of *Globocassidulina rossensis* and *Trifarina angulosa*. Group Q–B is linked to high-energy environments with bioclastic sediments and is dominated by *Quinqueloculina cuvieriana* and *Bigenerina textularioidea*. Group A–P is found on the Abrolhos Shelf, characterized by high abundances of porcelaneous symbiotic foraminifera, such as *Articulina sulcata* and *Peneroplis planatus*, in carbonate sediments. The distribution of these assemblages is primarily controlled by sediment composition, grain size, organic matter flux, and hydrodynamic conditions. Sediments rich in carbonate seem to favor symbiotic-bearing foraminifera species adapted to oligotrophic environments, while regions with higher organic matter content support opportunistic and infaunal species. The results highlight the interplay between sedimentary and oceanographic processes and ecological factors in structuring benthic foraminiferal assemblages along the ESCS.

1 Introduction

Several studies have explored the relationship between foraminiferal distributions and environmental drivers such as riverine chemical and sediment inputs and distinct oceanographic forcings (tides, waves, and currents) (e.g., Debenay et al., 2001; Majewski et al., 2023; Fouet et al., 2024; Jorissen et al., 2022; Castelo et al., 2022). The abundance and diversity of benthic foraminiferal communities are closely tied to sediment grain size, organic matter input, and oxygen concentration in the marine sediments, reflecting seafloor hydrodynamics (Murray, 2006; Jorissen et al., 2007; Hyams-Kaphzan et al., 2008). These factors influence species composition, vertical distribution in sediments, and overall community structure, making benthic foraminifera valuable proxies for both past (Murray, 2006; Díaz et al., 2014; Mello et al., 2017; Rodrigues et al., 2018) and current environmental changes, including anthropogenic impacts (Culver and Buzas, 1995; Cearreta et al., 2002; Geslin et al., 2002; McGann et al., 2025). Furthermore, modern foraminiferal distributions play a fundamental role in determining assemblage composition and inferring paleoecological, paleobathymetric, and paleoceanographic conditions using modern analogs (Gooday, 1993; Sen Gupta, 1999; Hayward et al., 2004; Ruschi et al., 2024).

The distribution patterns of benthic foraminifera along the Brazilian continental shelf have been thoroughly documented in several key regions, notably in proximity to major coastal economic centers, including the margins of major metropolitan areas such as São Paulo and Rio de Janeiro (Eichler et al., 2003; Donnici et al., 2012; Díaz et al., 2014; Eichler et al., 2014), on the Amazon shelf (Vilela, 2003) and in northeastern Brazil on the carbonate shelf (Araújo and Machado, 2008; Eichler et al., 2024; Barbosa et al., 2025). However, certain areas remain unknown, requiring further investigation to identify recent assemblages and to refine our understanding of these organisms along the western South Atlantic continental shelf.

The Espírito Santo Continental Shelf (ESCS) exhibits a complex sedimentary and morphological characteristic due to its mixed sediment composition, width variability, and riverine sediment input. The shelf is characterized by areas with siliciclastic sedimentation and areas dominated by carbonate sedimentation, with rhodolith beds throughout the entire outer shelf (Bastos et al., 2015; D'Agostini et al., 2019; Bourguignon et al., 2018; Vieira et al., 2019; Oliveira et al., 2020). The Doce River delta plays a significant environmental role in the sedimentary and ecological dynamics of the Espírito Santo shelf (Quaresma et al., 2015; Leite et al., 2016; Aguiar et al., 2023). In light of this complexity, the distribution of benthic foraminifera may be indicative of a gradient between environments characterized by distinct sedimentary regimes. This observation emphasizes the necessity for detailed mapping to support climate and oceanographic studies related to continental margin changes and potential anthropogenic impacts.

The present study aims to investigate the distribution of recent benthic foraminifera assemblages along the ESCS and to infer the predominant environmental factors that control their microfauna distribution. This study area covers a region later impacted by the 2015 Fundão Dam collapse (the world's largest mining disaster), which released over $60 \times 10^6\,m^3$ of iron-rich tailings into the Doce River basin, affecting over 600 km of terrestrial, freshwater, and estuarine ecosystems (Queiroz et al., 2022). Furthermore, this study endeavors to verify if the benthic foraminifera assemblages are in some way related to the three distinct morphologic compartments previously established in the ESCS (Bastos et al., 2015; Vieira et al., 2019) and if they are thereby related to different sedimentary regimes and their potential use to monitor human activity in the coastal environment.

2 Study area

The ESCS, located along the eastern Brazilian margin between the latitudes of 18°20′ and 21°18′ S, is characterized by three sedimentary facies: terrigenous, mixed, and carbonate (Costa Júnior et al., 2022). The ESCS can be divided into three sectors based on sedimentary and morphological characteristics (Fig. 1): the Paleovalley, the Doce River, and the Abrolhos Continental Shelf (Bastos et al., 2015). Each sector exhibits distinct sedimentary regimes, morphology, oceanographic influences, and ecological dynamics, which are crucial for understanding the distribution of benthic foraminifera.

2.1 Paleovalley Continental Shelf

The Paleovalley Continental Shelf (south of the study area) is characterized by an accommodation regime, presenting an irregular morphology marked by paleovalleys and hard grounds and the presence of estuaries (Bastos et al., 2015; Vieira et al., 2019). This region is predominantly composed of carbonate sediments and topographic formations shaped during periods of seafloor exposure (Ximenes Neto et al., 2024). The presence of rhodolith beds and bioconstructions along paleochannel margins further highlights the unique sedimentary and ecological features of this sector (Oliveira et al., 2020).

2.1.1 Environmental protection area

The multiple-use "Costa das Algas" Environmental Protection Area (EPA) and the no-take Santa Cruz Wildlife Refuge (WR) are adjacent and form part of UNESCO's Mata Atlântica Biosphere Reserve. Established in 2010 by Brazil's Federal Government, these marine protected areas aim to protect marine biodiversity and local culture. They marked important milestones in safeguarding rhodolith beds

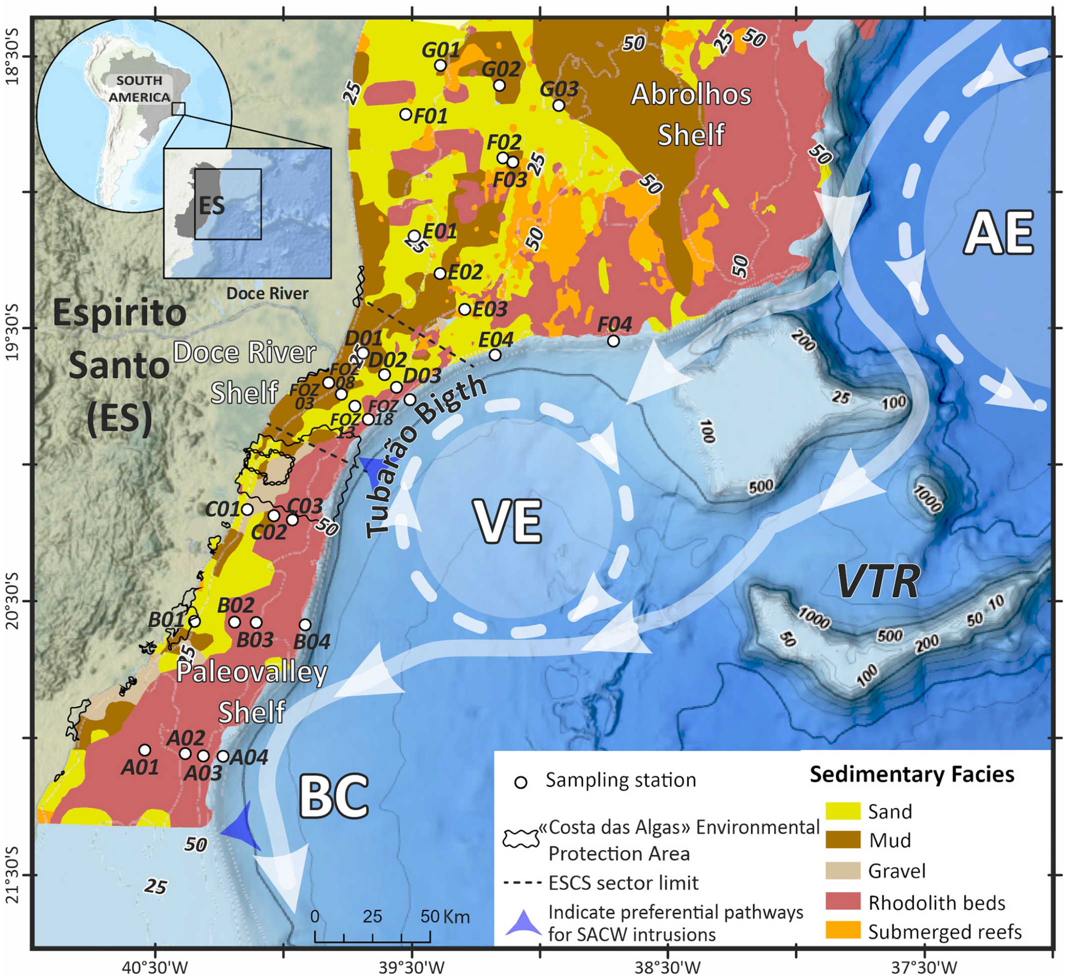

Figure 1. Sedimentary facies distribution along the ESCS obtained from Bastos et al. (2015) and Vieira et al. (2019). Schematic surface circulation of the Brazil Current (BC), the Abrolhos Eddy (AE), and the Vitória Eddy (VE) is based on de Almeida et al. (2022) and samples distributed over the ESCS (transects A to G). The areas of SACW intrusion into the ESCS were based on Palóczy et al. (2016).

from large-scale exploitation for fertilizer production by the Brazilian Institute of Environment and Renewable Natural Resources (IBAMA, 2006). Both areas hold great ecological and socioeconomic significance and safeguard vital habitats that protect the coastal zone from erosion and support the sustainability of artisanal fisheries, which is a key economic activity in the region (ICMBio, 2023).

2.2 Doce River Continental Shelf

The Doce River Continental Shelf, located in the central-northern ESCS, is driven by a high input of terrigenous sediments from the Doce River, with an estimated discharge of approximately 148 $t\,km^{-2}\,yr^{-1}$ (Souza and Knoppers, 2003). This sector exhibits a smooth seafloor, corresponding to the delta front and prodelta of the Doce River delta (Bastos et al., 2015; Quaresma et al., 2015). The dominance of terrigenous sediments in this region reflects the direct influence of the Doce River as the primary source of sedimentary material. The deltaic environment is marked by modern sediments, with deposition extending to depths of approximately 30 m (Quaresma et al., 2015).

2.3 Abrolhos Continental Shelf

At the northernmost extent of the ESCS, the southern Abrolhos Continental Shelf represents a broadening of the eastern Brazilian Continental Shelf. This sector is characterized by a mixed siliciclastic–carbonate depositional system, with terrigenous sediments dominating the inner continental shelf and carbonate sedimentation prevailing offshore (Bastos et al., 2015; Vieira et al., 2019). The presence of isolated biogenic reefs, extensive rhodolith beds, and a broader continental shelf distinguishes this region from the other sectors. The transition from terrigenous to carbonate sediments is gradual, reflecting the interplay between terrigenous input and marine processes.

2.4 Oceanographic influences

The present-day ESCS is influenced by intricate interactions between large-scale circulation, mesoscale eddies, and local wind forcing. The Brazil Current (BC), formed by the bifurcation of the South Equatorial Current (SEC) near 18.6° S, exerts a strong influence on shelf dynamics, particularly to the south of the Vitória–Trindade Ridge (VTR). Mesoscale features, such as the Vitória Eddy and semi-permanent anticyclones, are frequently observed in this area (Soutelino et al., 2011; Arruda et al., 2013; Palóczy et al., 2016; Silveira et al., 2020).

Although the warm and saline Tropical Water (TW) is the dominant water mass along the shelf throughout the year, the South Atlantic Central Water (SACW), which is colder and fresher, sporadically intrudes near the bottom, especially during summer when a strong thermocline develops (Castro and Miranda, 1998). These episodic intrusions of nutrient-rich SACW have been identified as one of the triggers responsible for surface water nutrient enrichment, thereby influencing benthic assemblages (Bernardino et al., 2016; de Almeida et al., 2022, 2023).

Wind forcing drives southwestward currents along the shelf, with coastal upwelling being intensified by internal tides near the southern Abrolhos Bank (AB) (Pereira et al., 2005). Numerical studies suggest that, in the Tubarão Bight (TB), wind-driven Ekman transport dominates over topographic effects, accounting for over 75 % of vertical transport (Rodrigues and Lorenzzetti, 2001; Mazzini and Barth, 2013).

3 Material and methods

3.1 Sample collection

Surface sediment samples were collected during the development of the Espirito Santo Basin Assessment Project (AMBES, CENPES/PETROBRAS), which systematically sampled the Espirito Santo Basin (ESB) and the northern Campos Basin (NCB) between 2008 and 2014. We analyzed 30 sediment samples (0–2 cm), collected with a Van-Veen (stations shallower than 100 m) and box corer (stations deeper than 100 m) during an oceanographic cruise in 2013. Samples were stored in a plastic container (∼ 20 cm^3). As the samples were not stained with Bengal Rose after the collection, the dataset counts are based on total fauna, giving a larger-scale time picture, avoiding seasonal variations in the foraminifera population. It is also known that the utilization of total fauna may be indicative of a mixture of autochthonous and allochthonous foraminifera (Hayward et al., 2004). Therefore, our data represent the overall faunal composition and distribution at ESCS. The samples were evenly distributed across seven transects on the shelf at water depths of 25, 40, 50, and 150 m and one transect at water depths from 18 to 50 m on the Doce River mouth (Fig. 1). The position of the stations can be accessed in the Supplement (https://doi.org/10.5281/zenodo.17313920).

3.2 Sedimentological data

The sedimentological dataset used in this study is a compilation of data analyzed and published by Maia et al. (2015) in the AMBES project report. The data encompass grain size, calcium carbonate (% $CaCO_3$), and organic matter (% OM) content. As those authors' analyses were carried out in replicates, we opted to use the median values for each parameter. The gravel and sand fractions were analyzed via standard wet-sieving methods, while mud fractions were assessed through pipetting (Suguio, 1973; Dias, 2004). The % $CaCO_3$ was determined by measuring the calcium carbonate loss through dissolution in 10 % HCl using a modified Bernard Calcimeter (Soares, 2017). The % OM was determined post-combustion at 450 °C by measuring the difference between dry weight and ash-free dry weight.

3.3 Total foraminiferal analysis

Sediment samples for foraminiferal analysis were processed at CENPES/PETROBRAS laboratory (Rio de Janeiro, Brazil). After drying the samples at 60 °C, an aliquot of dry sediment for each sample (∼ 20 g) was gently washed with tap water through a 63 µm sieve to remove the mud fraction. The coarse fraction retained on the sieve was dried, weighed, and dry-sieved using 500, 125, and 63 µm to facilitate the species classification in the distinct grain sizes.

All benthic foraminifera specimens were picked from the 500 µm fraction. The fractions of 63–125 and 125–500 µm were divided using a microsplitter to ensure the presence of at least 300 specimens of benthic specimens for both fractions together. All picked specimens were placed on plummer slides for taxonomic identification. The total absolute number of foraminifera for each sample was standardized to 20 g.

The tubular agglutinated forms, including genera such as *Rhabdammina*, *Rhizammina*, and *Saccorhiza*, were quantified based on the presence of standardized fragments. Every set of five fragments (approximately 0.3 cm in length) was counted as one single individual, following de Almeida et al. (2022, 2023). Juvenile forms were identified when the specimens had a large proloculum and a whole small test (125–63 µm fraction) without enough features to be identified to the species level. Due to their large number of species and ecological similarity, members of the genera *Fissurina*, *Lagena*, *Oolina*, and *Parafissurina* (Nodosariata) were grouped and nominated to be "unilocular", according to Patterson and Richardson (1987).

Taxonomic classification and identification were conducted following Boltovskoy et al. (1980), Loeblich and Tappan (1988, 1994), Boersma (1984), van Morkhoven et al. (1986), Bolli et al. (1994), Jones (1994), Kaminski and

Gradstein (2005), and Holbourn et al. (2013). The species names were updated according to the World Register of Marine Species (WoRMS Editorial Board, 2022). The main species (up to 140) were compared with the holotypes and syntypes of the Cushman Foraminifera and other collections held at the National Museum of Natural History (NMNH), Smithsonian Institute (USA). All figured specimens are reposited in the Laboratory of Marine Geosciences (LaboGeo) collection at the Department of Oceanography and Ecology at the Universidade Federal do Espirito Santo (Brazil).

In addition to benthic taxa, planktic foraminiferal tests were also recorded during the picking process using the > 125 µm size fraction. This fraction was selected based on its ability to capture the majority of adult planktic species (Peeters et al., 1999; Tapia et al., 2022).

3.4 Statistical analysis

The benthic foraminifera density (density = number of tests / dry sediment gram) was calculated for each sample, as well as the percentage of agglutinated tests (% AGGLU) representing the subclass Textulariana (class Globothalamea) and the class Monothalamea, porcelaneous forams (% PORC) that represent the class Tubothalamea, and calcareous hyaline forams (% HYAL) that represents the subclass Rotaliana (class Globothalamea) and the class Nodosariata (Pawlowski et al., 2013).

The microhabitat preference (epifaunal vs. infaunal) was differentiated based on the morphotypes of the tests as proposed by Corliss (1985), Corliss and Chen (1988), Kaminski et al. (1995), and Murray (2006). Species diversity is expressed in terms of species richness (S), equitability (J), and Shannon–Wiener (H) and Fisher's α indexes (Magurran, 2004). The calculations of these indexes were performed using PAST 4.10 software (Hammer et al., 2001).

The relative abundance of all taxa identified was analyzed through Q-mode cluster analysis in order to help define foraminiferal assemblages. The Bray–Curtis distance was used to measure the proximity between samples, and Ward's method was used to arrange samples into a hierarchical dendrogram.

The Indicator Species Analysis (IndVal) (Dufrene and Legendre, 1997) was used to determine exactly which parameters (species and environmental factors) were unique to each group, with important differences in community assemblage. The IndVal was determined by first calculating the relative abundance and relative frequency of each foraminifera species within each group formed through the Q-mode cluster. Those scores were then multiplied to yield the final indicator value. The statistical significances (p values) of the indicator values are estimated by means of 9999 random reassignments (permutations) of sites across groups. The resulting p value represents the probability that the calculated indicator value for any species or factor was bigger than that found by chance (Table 1).

Table 1. Example of how the IndVal data are expressed.

Factors and main taxa[1]	Average[2]	Freq. (%)[3]	p (< 0.05)[4]	IndVal[5]
Example	x	80	0.05	y

[1] Factors and main taxa: the species or taxa, ecological indices, or environmental variables (e.g., sediment type, organic matter content) being evaluated for specific groups. [2] Average: the mean relative abundance of the species (or the value of another parameter) within a given group. [3] Freq. (%): the frequency of occurrence (%) of the factor across sites within the group. A frequency of > 80 % is often used as a threshold to identify reliable indicators. [4] p (< 0.05): the p value obtained from permutation tests. Values below 0.05 indicate that the factor is significantly associated with the group. [5] IndVal: the Indicator Value, ranging from 0 to 100. It reaches its maximum (100 %) when the factor occurs at all sites of only one group. Some factors (e.g., foraminiferal density, sand, or mud content) may be evenly distributed across sites, but differences in mean values can still result in significant indicator values.

The analyses were performed using software packages PAST 4.10c (Hammer et al., 2001), PRIMER v.5 (Clarke and Warwick, 1994), and STATISTICA v.7 (Statsoft, 2001).

4 Results

4.1 Sediment properties: grain size, calcium carbonate, and total organic matter content

The sedimentological results are presented in the Supplement (https://doi.org/10.5281/zenodo.17313920) and Fig. 2. In general, sediments from the ESCS are predominantly composed of carbonate sand and mud. According to Larsonneur's (1977) classification, sediments from the ESCS include terrigenous (< 30 % $CaCO_3$), mixed (30 %–75 % $CaCO_3$), and carbonate (> 75 % $CaCO_3$) facies. Terrigenous sediments were mainly observed in FOZ03, FOZ13, and D02 (16 to 41 m water depth). In these samples, the $CaCO_3$ content reflected a larger siliciclastic influence near to the Doce River mouth. Mixed sediments dominated across the continental shelf, while carbonate sediments were identified in A01, B01, and FOZ18, indicating carbonate-rich environments.

The highest mud content was observed at the Doce River mouth region (FOZ03 and D01), where terrigenous mud dominates, as well as in B01 and D04. In contrast, sandy sediments with minimal mud fractions (< 5 %) were recorded in C01, FOZ13, and G01. Furthermore, high gravel content (> 10 %) was predominantly present in FOZ18, F02, and E04.

The organic OM content exhibited a range from 1 % to 17 %, with elevated values typically correlating with fine-grained sediments. The highest OM content was recorded in FOZ03, D01, and D04, consistently with the predominance

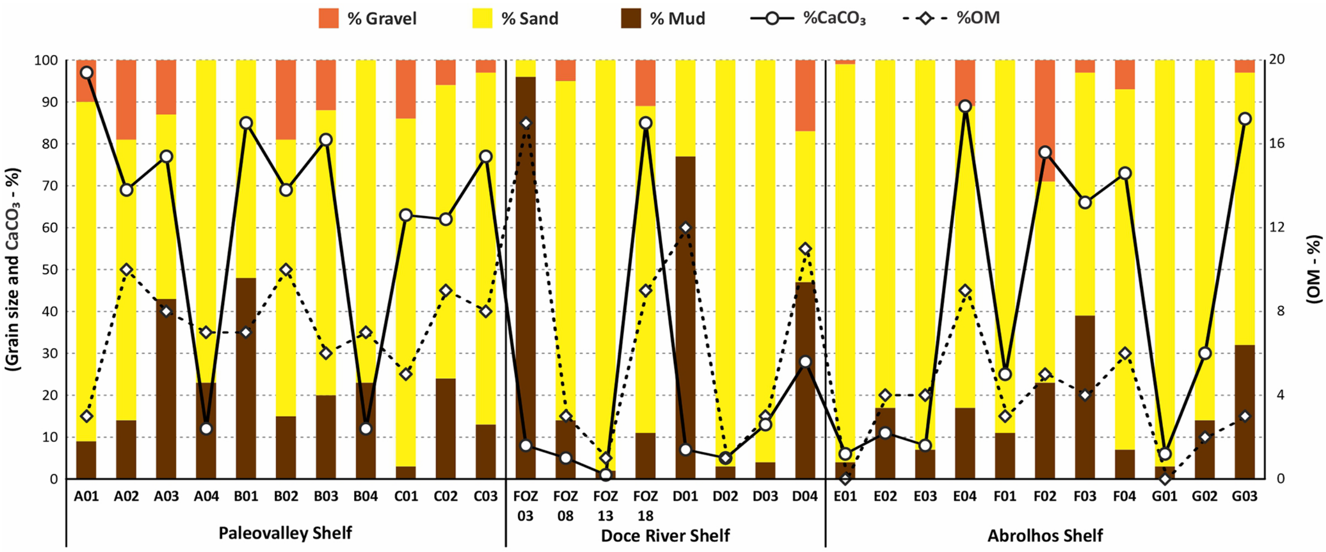

Figure 2. Sedimentological data (gravel, sand, mud, calcium carbonate, and total organic matter content) on the ESCS. Values expressed in percentages.

of muddy deposits, while the lowest values (< 2 %) were found in FOZ13 and D02.

4.2 Benthic foraminiferal composition: density, diversity, and relative abundance

A total of 274 benthic foraminiferal taxa were identified, comprising 237 species and 154 genera in the analyzed samples (see the Supplement – https://doi.org/10.5281/zenodo.17313920).

The total benthic density ranges from 11 to 10 083 tests per gram, with high values on transects A and B on the Paleovalley Shelf and on transects F and G on the Abrolhos Shelf. The species richness ranged from 26 to 99 species per sample, with the highest values being observed at transects A and B on the Paleovalley Shelf and at transect F on the Abrolhos Shelf. The Shannon–Wiener index (H) varied between 1.46 and 4.02, with elevated values at transects A, B, and G (B03: 4.02, G03: 3.69), indicating high species diversity in these areas. The Fisher α index, which reflects species richness relative to sample size, ranged from 3.34 to 13.93, with the highest values at transects B and FOZ. Equitability (J) values ranged from 0.39 to 0.88, demonstrating a generally well-distributed species community, particularly at transects B and G.

The distribution of hyaline, porcelaneous, and agglutinated foraminifera across the study area revealed distinct patterns (Fig. 3). The calcareous hyaline taxa dominated most of the transects (ranging from 20.2 % to 98.6 %), and were particularly dominant in the FOZ03 (98.6 %) and D01 (98.9 %). In contrast, porcelaneous taxa exhibited low abundances values (ranging from 0.8 % to 71.8 %), with the highest values being observed at G01 (71.8 %) and F01 (65.9 %). Agglutinated taxa were generally less abundant (ranging from 0 % to 38.1 %), with the highest values being recorded at C03 (38.1 %) and E01 (17.5 %).

The relative abundances of all species can be observed in the Supplement (https://doi.org/10.5281/zenodo.17313920), and those of the main species in Plates 1 and 2. The dominant taxa include the hyaline species *Globocassidulina rossensis*, with an average abundance of 8.4 %, and *Hanzawaia boueana*, with an average abundance of 7.8 %. Hyaline juvenile foraminifera were frequently abundant (average of 4.4 %). Additionally, the porcelaneous species *Quinqueloculina cuvieriana* and *Quinqueloculina lamarckiana* were also abundant (> 3 %) and frequently observed. Among the agglutinated species, *Bigenerina textularioidea* is the most abundant and frequent, with an average abundance of 3.36 %.

The presence of symbiont-bearing benthic foraminifera exhibited significant variability across the study area, as indicated by the occurrence of the genera *Amphistegina*, *Peneroplis*, and *Archaias*. The total relative abundance of these genera ranged from 0 % to 25 %, with the highest values observed along transect F on the Abrolhos Shelf. High relative abundances of these species were also recorded along transects B and C on the Paleovalley Shelf (C03: 14.0 %, B04: 12.1 %) and on the transect E on at the Doce River Shelf (E01: 11.5 %). The symbiont-bearing species were absent or had low abundance along the transects D and FOZ, except for D03 (18.0 %).

The distribution of epifaunal and infaunal foraminifera species across the study area varied, indicating that epifaunal taxa were more abundant on the Abrolhos Shelf and in some areas of the Paleovalley Shelf, while infaunal taxa were prevalent in the Doce River Shelf. Epifaunal taxa (ranging from 2.9 % to 83.6 %) reached their the highest abundances

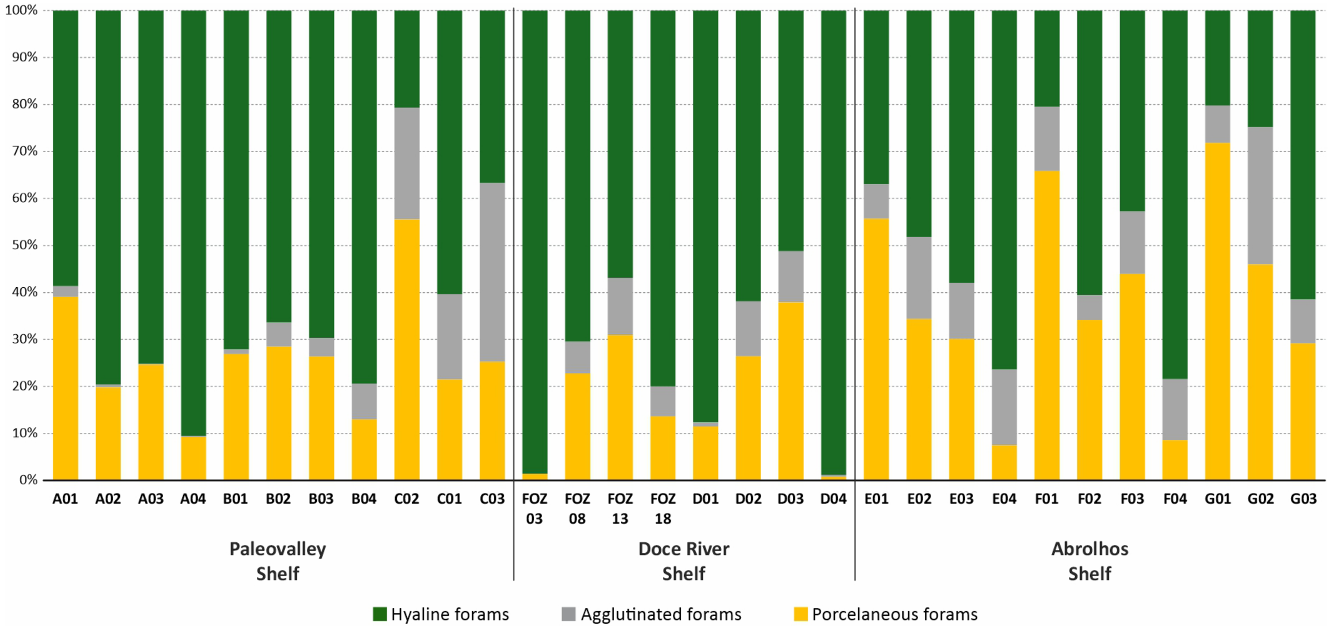

Figure 3. Relative abundance of hyaline, porcelaneous, and agglutinated taxa along the ESCS.

in samples G01 (83.6 %), F01 (80.3 %), and A01 (72.8 %). Infaunal taxa (ranging from 7.5 % to 93.5 %) achieved the highest values in samples D01 (93.5 %) and FOZ03 (67.9 %).

For a comprehensive summary of the ecological and taxonomic data, see Table 2 and the Supplement (https://doi.org/10.5281/zenodo.17313920).

4.3 Benthic foraminiferal assemblages

The dendrogram obtained from Q-mode cluster analysis identified five major groups (M–C, Q–B, H–Q, G–T, and A–P). The groups were analyzed further to determine their characteristics using IndVal analyses, and each group was named based on the abbreviation of its dominant taxa, representing five distinct benthic foraminiferal assemblages distributed along the ESCS (Fig. 4).

The predominant species and main factors in each group, which were used to name the groups, were determined based on the distribution of the main species across the study area and within the groups (Table 3).

Group *M–C (Miliolinella–Cibicides)* includes samples from the southern ESCS and the northern Campos Shelf (Paleovalley Shelf): A01, A02, A03, A04, B01, B02, B03, B04 and C02. The IndVal analysis indicated that *Miliolinella subrotunda* (8.4 %), *Discorbis viladeboeanus* (3.5 %), *Bolivina striatula* (2.3 %), *Cibicides* spp. (2.1 %), *Discorbinella bertheloti* (2.0 %), and *Cibicides aknerianus* (2.0 %) were characteristic taxa of this group. The analysis also showed that the highest averages of the richness (84 taxa per sample), Shannon–Wiener (3.7) and Fisher α (10.4) indexes, and equitability (0.8) were found to have a relevant role in distinguishing this group.

Other aspects that seem to be characteristic of the M–C group were the high density of benthic foraminifera (3755 tests per gram), the high abundance of *Cibicides* species (9.0 %), and the low abundance of agglutinated taxa (4.3 %). Sediment samples from this group exhibit the highest average content of gravel (8.8 %) and a high content of $CaCO_3$ (62.7 %).

Group Q–B (*Quinqueloculina–Bigerina*) includes samples C03 and C01, also located on the Paleovalley Shelf. The IndVal analysis indicated that *Quinqueloculina cuvieriana* (32.1 %), *Bigenerina textularioidea* (18.1 %), *Amphistegina radiata* (10.0 %), *Eponides cribrorepandus* (2.6 %), and *Sigmoilopsis schlumbergeri* (2.2 %) were the most characteristic taxa of this group. The analysis also showed that the highest average of epifaunal foraminifera (68.5 %) and the highest abundance of agglutinated foraminifera (31 %) were relevant in distinguishing this group.

Other aspects that seem to be characteristic of this group were the lowest average values in terms of the richness (38 taxa per sample), Shannon–Wiener (2.3) and Fisher's α indexes (4.4), and equitability (0.6). Sediment samples from this group exhibit a high average content of gravel (8.5 %) and the highest content of $CaCO_3$ (70.0 %), as well as the lowest content of mud (8.0 %).

Group G–T (*Globocassidulina–Trifarina*) includes samples FOZ03, FOZ18, D01, D04, F04, and E04, which encompass the Doce River Shelf and the southern portion of the Abrolhos Shelf. The IndVal analysis indicated that *Globocassidulina rossensis* (19.8 %), *Globocassidulina*

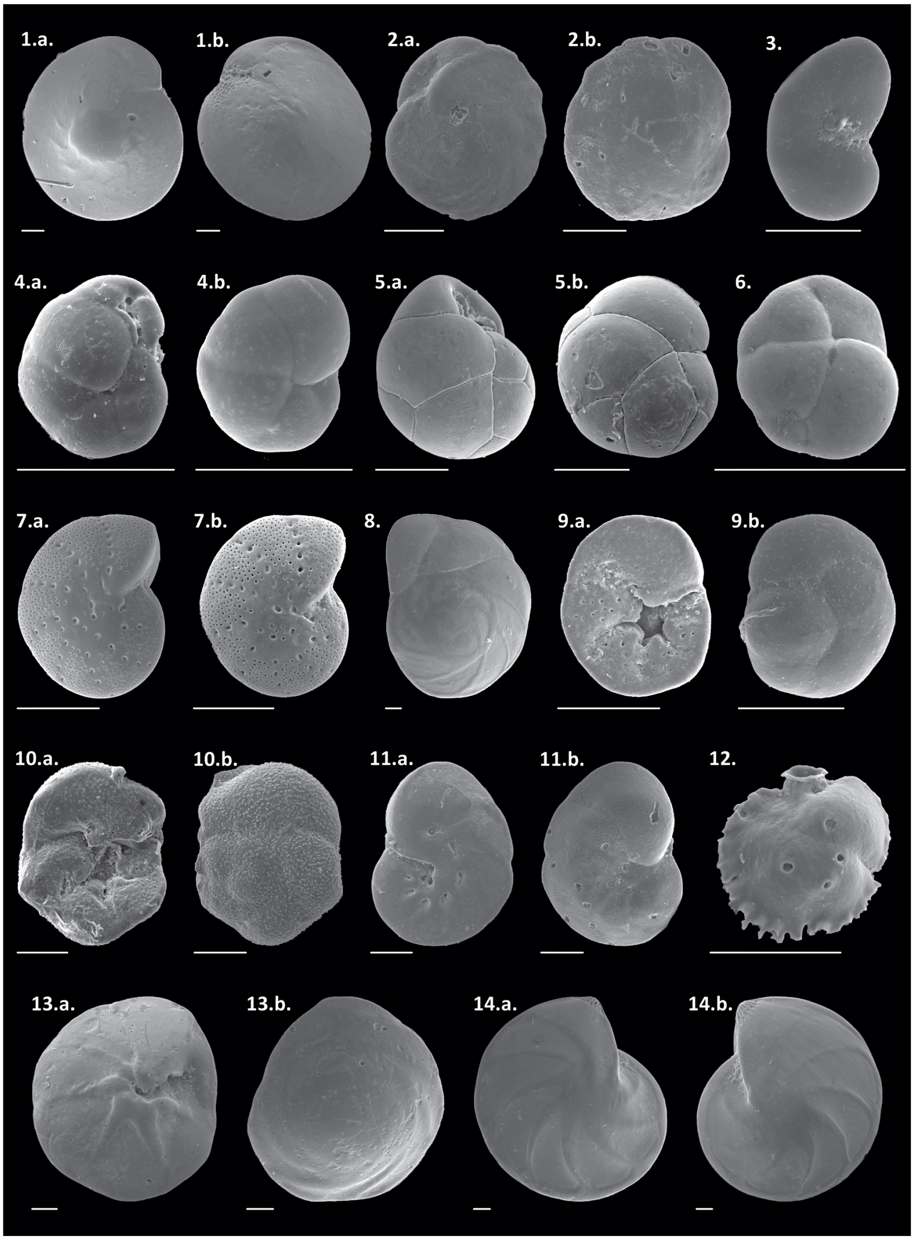

Plate 1. 1. a.–b. *Amphistegina radiata*, 2. a.–b. *Cassidulina laevigata*, 3. *Paracassidulina nipponensis*, 4. a.–b. *Globocassidulina crassa*, 5. a.–b. *Globocassidulina subglobosa*, 6. *Globocassidulina rossensis*, 7. a.–b. *Elphidium discoidale*, 8. *Eponides cribrorepanus*, 9. a.–b. *Discorbis viladeboeanus*, 10. a.–b. *Rosalina globularis*, 11. a.–b. *Hanzawaia boueana*, 12. *Siphonina bradyiana*, 13. a.–b. *Neoponides antillarum*, and 14. a.–b. *Lenticulina stephensoni*. Scale bar: 100 µm.

crassa (9.2 %), *Trifarina angulosa* (6.7 %), *Planulina foveolata* (3.4 %), *Globocassidulina subglobosa* (3.2 %), *Bolivina lowmani* (2.7 %), and *Cibicidoides mundulus* (2.6 %) were distinguishing taxa of this group. The highest averages of hyaline foraminifera (87 %), benthic foraminifera (83.1 %), infaunal (64 %), planktonic foraminifera (3.0 %), and fragmented planktonic foraminifera (19.2 %) were found to be relevant in distinguishing this group, as was the highest content of mud (42.5 %) and OM (10.7 %).

Another aspect that seems to be characteristic of this group was the lowest abundance of porcelaneous taxa (7.2 %).

Group *H–Q* (*Hanzawaia–Quinqueloculina*) includes samples E03, D03, FOZ13, FOZ08, E02, and D02, which also encompass the Doce River Shelf and the southern portion of the Abrolhos Shelf. The IndVal analysis indicated that *Hanzawaia boueana* (23.4 %), *Quinqueloculina* spp. (7.7 %), *Quinqueloculina lamarckiana* (5.4 %), and *Elphidium discoidale* (3.6 %) were characteristic taxa of this group. The

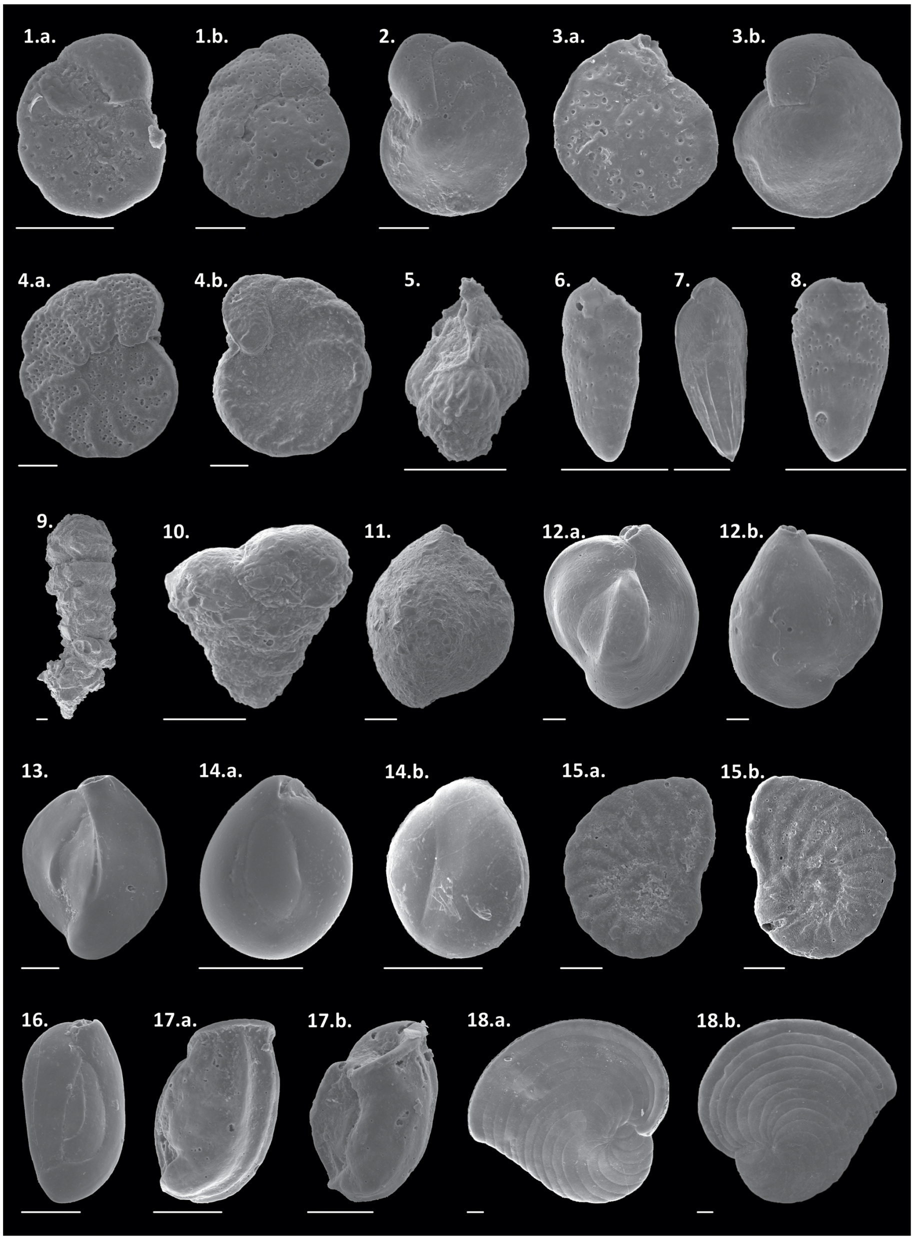

Plate 2. 1. a.–b. *Cibicides aknerianus*, 2. *Cibicidoides mundulus*, 3. a.–b *Cibicides fletcheri*, 4. a.–b. *Planulina foveolata*, 5. *Trifarina angulosa*, 6. *Bolivina dilatata*, 7. *Bolivina fragilis*, 8. *Bolivina lowmani*, 9. *Bigenerina textularioidea*, 10. *Textularia agglutinans*, 11. *Sigmoilopsis schlumbergeri*, 12. a.–b. *Quinqueloculina cuvieriana*, 13. *Quinqueloculina lamarckiana*, 14. a.–b. *Miliolinella subrotunda*, 15. a.–b. *Peneroplis planatus*, 16. *Quinqueloculina seminulum*, 17. a.–b. *Articulina sulcata*, and 18. a.–b. *Archaias angulatus*. Scale bar: 100 µm.

analysis also showed that the highest average of fragmented benthic foraminifera (58.2 %) was relevant in distinguishing this group, along with the highest sand content (91.3 %).

Other aspects that seem to be characteristic of this group were the lowest values in terms of density (798 tests per gram). Sediment samples from this group exhibit the lowest averages of gravel (0.8 %), OM (2.7 %), and $CaCO_3$ (7.2 %).

Group *A–P* (*Articulina–Peneroplis*) includes samples G03, G02, F03, F02, G01, F01, and E01, which collectively represent the majority of the Abrolhos Shelf. The IndVal analysis indicated that *Articulina sulcata* (8.6 %) and *Archaias angulatus* (3.9 %) were characteristic taxa of this group. The analysis also showed that the highest average in terms of the abundance of porcelaneous (49.5 %) and symbiont-bearing species (15.1 %).

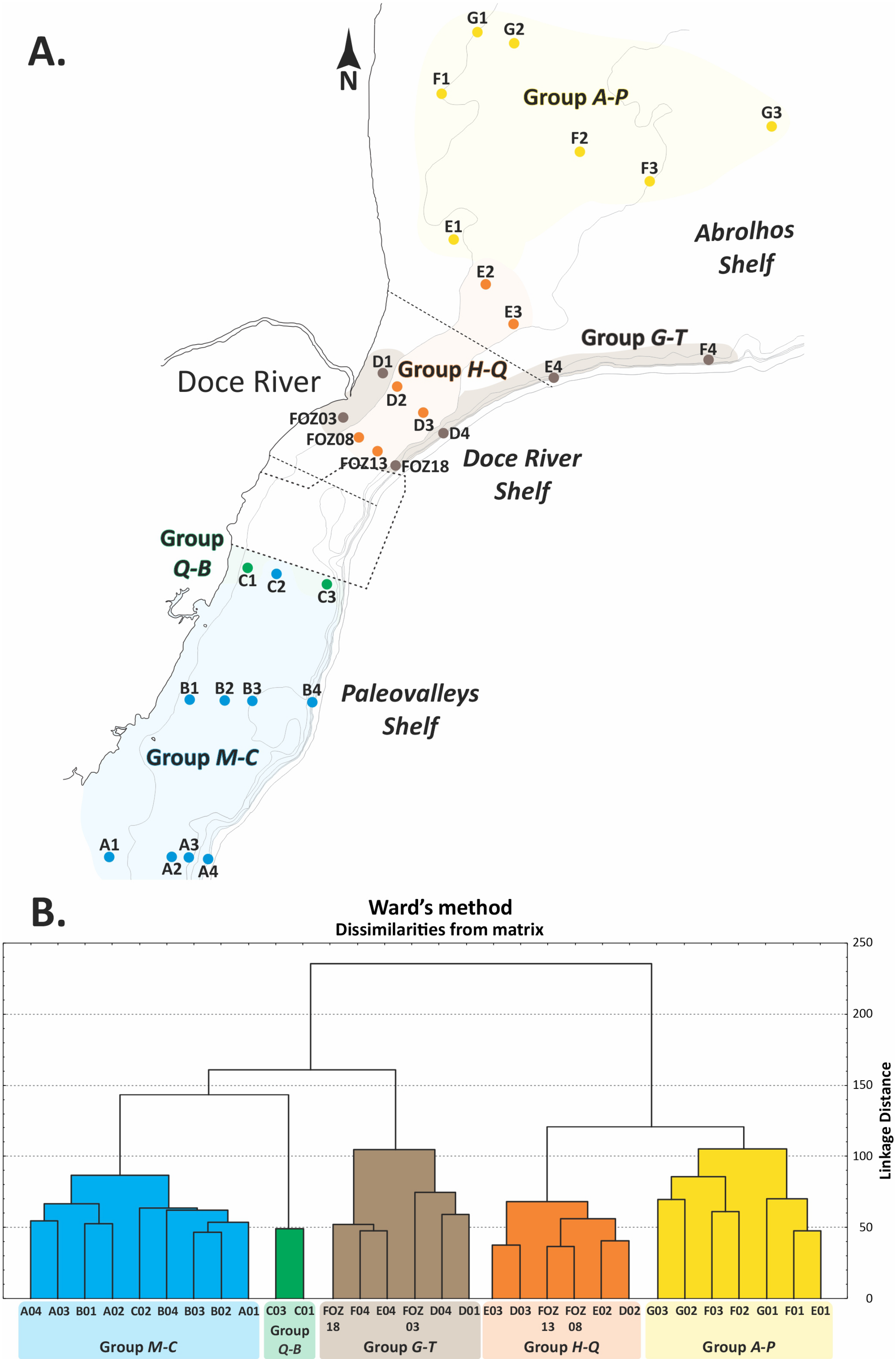

Figure 4. Distribution map of the five groups in the ESCS **(a)** based on the groups identified in the dendrogram classification (Q-mode) **(b)**.

Table 2. Benthic foraminiferal ecological indexes of the ESCS samples. The highest values are highlighted in bold and underlined, and the lowest are in bold and italics.

Shelf		Richness	Density per g	Symbiont-bearing benthic foraminifera	Epifaunal foraminifera	Infaunal foraminifera	Shannon–Wiener *H*	Fisher *α*	Equitability *J*
Paleovalley	A01	84	1255	2.8	72.8	17.1	3.67	11.28	0.82
	A02	85	4710	1.7	60.9	27.0	3.79	9.68	0.84
	A08	93	**10083**	0.2	58.3	29.9	3.55	9.87	0.78
	A04	76	5548	0.5	38.5	53.9	3.31	8.55	0.75
	B01	73	5023	1.0	56.7	29.8	3.62	8.04	0.84
	B02	78	559	9.7	56.2	32.3	3.75	11.99	0.85
	B03	88	3559	2.9	50.7	39.1	**4.02**	10.66	**0.88**
	B04	**99**	2002	12.1	46.1	45.9	3.85	12.93	0.83
	C01	***26***	544	6.2	54.1	43.1	1.86	***3.34***	0.57
	C02	75	1059	11.5	74.6	25.1	3.67	10.21	0.84
	C03	49	2635	14.0	62.4	30.7	2.82	5.45	0.72
Doce River	FOZ08	37	***11***	***0.0***	8.4	67.9	3.16	**13.93**	0.86
	FOZ08	36	450	***0.0***	29.9	60.0	2.61	4.93	0.72
	FOZ13	42	283	1.4	44.2	47.2	2.81	6.47	0.74
	FOZ18	82	1827	1.1	39.5	45.9	3.52	10.27	0.79
	D01	51	1690	0.0	12.7	60.6	3.03	6.11	0.76
	D02	47	83	6.8	***2.9***	**93.5**	3.31	9.65	0.85
	D03	45	117	18.0	40.8	57.2	2.91	8.25	0.76
	D04	41	3369	0.0	28.6	61.4	***1.46***	4.47	***0.39***
Abrolhos	E01	46	468	11.5	44.2	43.8	3.29	6.70	0.84
	E02	53	2966	6.2	47.9	44.6	3.28	5.96	0.82
	E03	63	890	2.4	61.1	22.0	3.19	8.44	0.76
	E04	56	399	5.2	48.6	40.4	3.22	8.46	0.79
	F01	53	9119	25.2	40.1	53.8	3.15	5.25	0.79
	F02	61	1491	8.4	80.3	9.6	3.08	7.69	0.74
	F03	84	4788	14.6	42.9	17.4	3.64	9.29	0.81
	F04	78	8487	4.4	55.8	30.0	3.53	8.34	0.80
	G01	53	1364	17.6	**83.6**	***7.5***	3.00	6.74	0.75
	G02	37	3114	**24.0**	54.8	44.4	2.71	3.92	0.75
	G03	71	5835	4.5	50.3	34.7	3.69	7.80	0.86

Other aspects that seem to be characteristic of this group were the highest abundance of *Peneroplis* species (17.8 %), the lowest abundance of infaunal taxa (24 %), and the high abundance of juvenile foraminifera. Sediment samples from this group exhibit a low content of OM (2.4 %).

5 Discussion

The ESCS compartments are distinguished by their distinct sediment composition, varied seafloor morphology, sedimentary regimes, and oceanographic characteristics. This section will provide a detailed discussion of the distribution of the defined benthic foraminiferal assemblages within each ESCS compartment previously defined by Bastos et al. (2015) and Vieira et al. (2019).

The ESCS's benthic foraminifera fauna include taxa commonly found in the Campos Basin continental shelf right in the south of our present study, as evidenced by the abundance of hyaline genera such as *Globocassidulina* (Vieira et al., 2015). There are several surveys that relate the benthic foraminiferal assemblages to the continental shelf in the Brazilian margin, but in Fig. 5, we selected some broad latitudinal-study examples in the south of our database, where the sedimentation pattern is much more siliciclastic than carbonate and where there is a constant presence of the hyaline genus of *Globocassidulina* species, *Uvigerina*, *Bulimina*, and *Bolivina* (and some *Brizalina*) (Eichler et al., 2012; Burone et al., 2011). There are also some examples in the north of our study area, until the equatorial margin, where the carbonate sedimentation pattern is more frequently marked by the abundance of miliolids and robust and symbiont-bearing foraminifera common to higher-energy and marine-driven environments, such as the genera *Quinqueloculina*, *Amphistegina*, and *Archaias* (Araújo and

Table 3. The Indicator Species Analyses (IndVal) based on the dendrogram classification. The indicator factor for each group has a p value of < 0.05. The highest values are highlighted in bold and underlined, and the lowest are in bold and italics.

Group	Factors and main taxa	Average	Freq. (%)	p (< 0.05)	IndVal
M–C	HYALINE SUM	72.5	100	0.012	25.53
	Miliolinella subrotunda	**8.4**	100	0.000	74.45
	Discorbis viladeboeanus	**3.5**	90	0.002	48.02
	HYALINE Un.ID.	***2.5***	80	0.000	56.73
	FRAGMENTED HYALINE Un.ID.	**2.3**	100	0.000	53.36
	Bolivina striatula	**2.3**	80	0.000	65.26
	Cibicides spp.	**2.1**	100	0.000	87.10
	Discorbinella bertheloti	**2.0**	80	0.005	46.51
	Cibicides aknerianus	**2.0**	80	0.002	50.59
	Cibicides fletcheri	**2.0**	80	0.000	68.81
	Rosalina globularis	**1.7**	100	0.000	69.92
	Cassidulina laevigata	**1.2**	80	0.000	71.31
	Quinqueloculina seminulum	**1.1**	100	0.033	33.18
	Amphistegina sp. (juv.)	**1.0**	100	0.000	73.67
	Elphidium spp.	**0.7**	100	0.000	53.03
	Siphonina bradyiana	**0.7**	80	0.044	28.26
	Amphistegina spp.	**0.7**	80	0.032	42.70
	Wisnerella auriculata	0.6	80	0.025	29.63
	Richness	**83.44**		0.000	29.39
	Shannon (H)	**3.69**		0.000	24.19
	Fisher's α	**10.36**		0.000	27.69
	Equitability (J)	**0.83**		0.003	21.93
Q–B	AGGLUTINATED SUM	**30.9**	100	0.005	47.18
	Quinqueloculina cuvieriana	**32.1**	100	0.000	77.22
	Bigenerina textularioidea	**18.1**	100	0.001	79.66
	Amphistegina radiata	**10.0**	100	0.003	71.11
	Eponides cribrorepandus	**2.6**	100	0.020	85.39
	Sigmoilopsis schlumbergeri	**2.2**	100	0.043	48.70
	Lenticulina stephensoni	**0.7**	100	0.004	86.29
	Sigmoilopsis sp.	**0.3**	100	0.003	100.00
	Neoponides antillarum	**0.1**	100	0.038	50.60
	Epifaunal forams	**68.51**		0.027	27.48
G–T	HYALINE SUM	**86.7**	100	0.000	30.54
	Globocassidulina rossensis	**19.8**	100	0.000	64.66
	Globocassidulina crassa	**9.2**	100	0.000	56.10
	Trifarina angulosa	**6.7**	100	0.001	56.84
	Planulina foveolata	**3.4**	83	0.001	72.87
	Globocassidulina subglobosa	**3.2**	83	0.015	47.79
	Bolivina lowmani	**2.7**	83	0.002	70.30
	Cibicidoides mundulus	**2.6**	83	0.008	47.58
	Unilocular forams	**1.4**	83	0.028	34.91
	Bolivina dilatata	**0.4**	83	0.000	70.04
	Bolivina fragilis	0.8	83	0.001	60.17
	Depth (m)	**90.00**		0.026	33.47
	Plankt forams frag. (%)	**19.21**		0.015	41.37
	Benthic forams (%)	**83.12**		0.018	24.28
	Plankt forams (%)	**2.97**		0.033	38.60
	Infaunal forams	**64.42**		0.000	32.27
	Mud (%)	**42.50**		0.004	42.22
	OM (%)	**10.67**		0.001	35.91

Table 3. Continued.

Group	Factors and main taxa	Average	Freq. (%)	p (< 0.05)	IndVal
H–Q	*Hanzawaia boueana*	**23.4**	100	0.000	64.62
	Quinqueloculina spp.	**7.7**	83	0.012	42.42
	Quinqueloculina lamarckiana	**5.4**	100	0.032	33.77
	Textularia agglutinans	5.0	83	0.009	44.31
	SUM *Elphidium* spp.	**4.7**	100	0.010	32.61
	Elphidium discoidale	**3.6**	83	0.000	60.97
	Paracassidulina nipponensis	1.1	100	0.006	47.43
	Forams bent. frag. (%)	**58.18**		0.016	32.54
	Foraminiferos planct. frag. (%)	18.86		0.035	32.49
	Sand (%)	**91.33**		0.016	24.79
A–P	PORCELANEOUS SUM	**49.5**	100	0.003	32.84
	Articulina sulcata	**8.6**	86	0.001	66.55
	Archaias angulatus	**3.9**	100	0.000	67.36
	Peneroplis planatus	**3.2**	86	0.007	46.02
	Quinqueloculina seminulum	**1.7**	86	0.027	36.80
	Benthic forams (%)	80.65		0.043	23.56
	SYM-BEA LBF	**15.13**		0.005	40.33

Machado, 2008; Araújo and Araújo, 2010; Bérgamo et al., 2024).

The following section will discuss the ESCS foraminiferal assemblages with regard to other studies along the Brazilian Margin and all over the world.

5.1 Paleovalley Continental Shelf assemblages: groups *M–C* and *Q–B*

The sedimentation regime at the Paleovalley Continental Shelf differs from that of adjacent areas. In this sediment-starved shelf (low terrigenous input), the carbonate sedimentation predominates in the middle and outer shelves. Species from group *M–C* (Fig. 4, Table 3) inhabit this shelf compartment, dominated by *M. subrotunda*, *Cibicides* sp., *Bolivina paula*, and *Discorbis vilardeboanus*. This group also presented elevated values of species diversity, indicating a well-established community (Frontalini and Coccioni, 2008). High diversity values are typically indicative of a balanced community of species, greater resilience to natural disturbances, and stable environmental conditions that support a diverse and functionally efficient benthic community (Hill, 1973; Buzas and Hayek, 1998). A sufficient supply of organic matter favors benthic foraminiferal species establishment and diversity (Jorissen et al., 2007; de Almeida et al., 2023).

In the ESCS, the BC incursion on the continental shelf has the potential to promote episodic intrusion of SACW along the Paleovalley Continental Shelf (Palóczy et al., 2016). This intrusion results in the upwellings of this cold and nutrient-rich water mass from the upper slope to the surface waters

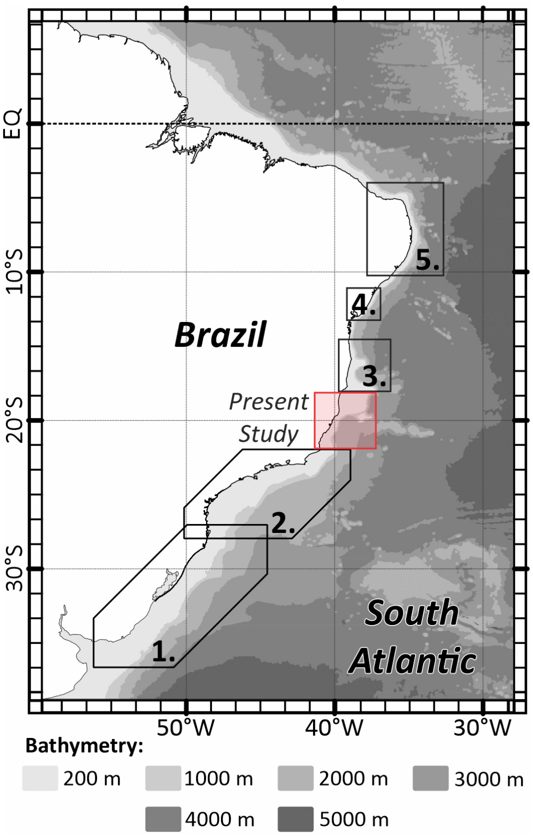

Figure 5. Map showing the distribution of some broad latitudinal studies along the Brazilian Margin. (1) Eichler et al. (2012), (2) Burone et al. (2011), (3) Araújo and Machado (2008), (4) Araújo and Araújo (2010), and (5) Bérgamo et al. (2024).

(Silveira et al., 2020). The nutrient enrichment on the surface waters induces an increase in local primary productivity and, consequently, an increase in the organic matter influx to the seafloor. As a result of this mechanism, the diversity and density of benthic foraminiferal populations might rise in environments characterized by elevated levels of oxygen (Cearreta, 1988; Debenay et al., 2001; Eichler et al., 2012). Eichler et al. (2012), in the south of the Brazil continental margin, related the presence of the SACW to *Uvigerina peregrina*, a species that was not particularly abundant in the ESCS but is an infauna species like *B. paula*. In addition, this condition seems to favor *M. subrotunda* and *D.* abundances in the ESCS. A similar assemblage was reported by Buosi et al. (2012) in the Mediterranean Sea. These authors found *Rosalina vilardeboanus* (= *Discorbis vilardeboanus*) and *M. subrotunda* in regions with increased organic input. Altenbach et al. (1993) describes how shallow infaunal *M. subrotunda* exhibits a unique adaptation by constructing dentritic tubes that lift its test several millimeters above the sediment surface, facilitating a temporary epibenthic lifestyle to feed. The high abundance of *M. subrotunda* in group *M–C* may highlight its potential role as an indicator of carbonate-rich sediments.

The infaunal species of the genus *Bolivina* were also found in high abundance on the lower slope of the Espírito Santo Basin (2500–3000 m) by de Almeida et al. (2022). *Bolivina* species have been demonstrated to serve as indicators of an increase in the availability of more refractory organic matter (Abu-Zied et al., 2008), eventually metabolized by anaerobic bacteria within the sediment (Jorissen and Wittling, 1999).

Species from group *Q–B* (Fig. 5, Table 3) are distributed near the "Costa das Algas" Environmental Protection Area (CA-EPA) (ICMBio, 2020). The CA-EPA is characterized by a diverse seafloor, featuring a wide variety of marine calcareous and non-calcareous macroalgae, such as rhodoliths (IBAMA, 2006; Holz et al., 2020). This region is characterized by the presence of biolithoclastic and lithoclastic sediments, which collectively create a mosaic of seafloor environments (Gastão et al., 2020; Longo and Amado Filho, 2014).

Group *Q–B* exhibited the lowest benthic foraminiferal density and diversity indexes and is dominated by *Q. cuvieriana* and *B. textularioidea*. The genus *Quinqueloculina* is widely distributed in marine sediments; however, it is notably more abundant in nearshore and reef or lagoonal environments characterized by phytal substrates. Similar patterns have been reported in reef and lagoonal habitats in Papua New Guinea (Langer and Lipps, 2003) and Bazaruto, East Africa (Langer et al., 2013). On Brazilian continental shelves, the frequency and high abundance of *Quinqueloculina* species are associated with coastal, high-energy, and warm-water carbonate environments (Araújo and Machado, 2008; Oliveira-Silva et al., 2005; Bérgamo et al., 2024; Eichler et al., 2024).

Disaró (2013) found *B. textularioidea* associated with sandy sediments, mainly composed of carbonate bioclasts on the outer continental shelf of the Campos Basin. Others studies found *B. textularioidea* in shallower sediments on the Abrolhos Shelf (Sanches et al., 1995; Araújo and Machado, 2008; Ruschi et al., 2024) and on the upper slope (150 m water depth) of the Potiguar Basin (Santa-Rosa et al., 2021). In this same basin, Disaró et al. (2022) reported *B. textularioidea* associated with sediments composed of 2 %–11 % of total organic matter (TOC) and > 70 % $CaCO_3$. In the ESCS, this species exhibited its highest abundance in bioclastic and coarser sediments, suggesting that *B. textularioidea* is well-adapted to carbonate environments with moderate to high energy, as reflected in its association with coarse-grained, poorly sorted sediments.

5.2 Doce River and southern Abrolhos Continental Shelf assemblages: groups *G–T* and *H–Q*

Groups *G–T* and *H–Q* (Fig. 4, Table 3) cover an extensive area of the ESCS, which contains terrigenous deposits in the vicinity of the Doce River mouth (Bastos et al., 2015; Quaresma et al., 2015) and a rhodolith bed on the outer shelf. The species belonging to group *G–T* inhabit this shelf compartment, distinguished by the high relative abundance of *Globocassidulina rossensis*.

The dominance of *Globocassidulina* (e.g., *G. rossensis* and *G. crassa*) in group *G–T* is consistent with its dominance on the upper slope of the Espírito Santo Basin (de Almeida et al., 2022). These authors found a distinct foraminiferal assemblage at 400 m water depth, containing a high abundance of *G. rossensis* and *Trifarina* spp. Both species are associated with a substantial flux of metabolizable organic matter, which is in agreement with the observed increased number of infaunal species. These aforementioned findings are in alignment with the results reported by Sousa et al. (2017) from the upper slope of Campos Basin. In the northern Campos Basin, *Globocassidulina* is associated with outer continental shelf environments, characterized by lower temperatures and high silt content (Vieira et al., 2015). Burone et al. (2011) investigated the southeastern Brazilian margin (from 23 to 28° S), highlighting the occurrence of *G. subglobosa* in regions influenced by upwelling phenomena, where mesotrophic conditions prevail, which, in group *G–T*, might be related to an SACW intrusion in the Tubarão Bight region (Palóczy et al., 2016). Such environments generally support a diverse benthic community, which is in contrast to those that are dominated by opportunistic assemblages. In a study of the Pleistocene–Holocene core from the Pelotas Basin, Rodrigues et al. (2018) found a positive correlation between the relative abundance of *T. angulosa* and TOC content. In the ESCS, *T. angulosa* is associated with mud sediments containing high OM content.

Group *H–Q* (Fig. 4, Table 3) is characterized by the high abundance of *H. boueana* and a notable presence of the porcelaneous foraminifera *Quinqueloculina* spp. and *Peneroplis planatus*. This assemblage comprises samples distributed from the Doce River Shelf to the southern portion of the Abrolhos Shelf. This region primarily consists of terrigenous sediments with localized occurrences of biogenic carbonate deposits (Vieira et al., 2019). The occurrence of the symbiont-bearing *P. planatus* is associated with warm-carbonate waters, such as biofacies reported by Ruschi et al. (2024) at the Abrolhos Depression on the southern Abrolhos Shelf.

Group H–Q appears to represent a transitional assemblage between group G–T, dominated by infaunal species in terrigenous muddy sediments with high OM, and group A–P (Fig. 4a), dominated by epifaunal species in warm-carbonate sandy sediments with low OM. Additionally, the frequency and abundance of *Quinqueloculina* spp. in group H–Q, along with samples characterized by low mud and OM content, align with one biofacies found by Ruschi et al. (2024), which is dominated by epifaunal species adapted to carbonate-rich and low-OM environments. Group H–Q contains a mixture of infaunal and epifaunal species, similarly to biofacies EH from Ruschi et al. (2024), where *Elphidium* spp. and *H. boueana* predominate. The relative abundance of *Elphidium* and *Criboelphidium* spp. is higher in group H–Q than in the other groups. This condition might reflect a transitional adaptation. The data presented in our study indicate that group H–Q constitutes a transitional foraminiferal assemblage, representing a transition zone between infaunal-dominated, terrigenous-rich environments (group G–T) and epifaunal-dominated, carbonate-rich environments (group A–P). These findings are indicative that benthic foraminiferal assemblages undergo changes in their composition under different latitudinal environments across the ESCS.

5.3 Abrolhos Continental Shelf assemblage: group *A*–*P*

Group A–P is defined by a high abundance and diversity of porcelaneous foraminifera, including symbiont-bearing species (Hallock et al., 2003), such as *Peneroplis* spp. and *Archaias* spp. These species are commonly found in warm and carbonate-rich waters. These genera are frequently documented in reef environments of the Brazilian continental shelves (e.g., Sanches et al., 1995; Santa-Rosa et al., 2021; Bérgamo et al., 2024) and worldwide (e.g., Langer and Lipps, 2003; Fajemila et al., 2015; A'ziz et al., 2021).

The carbonate sediments of the Abrolhos Continental Shelf include mud, bioclastic sand, rhodolith beds, and submerged reefs (Bastos et al., 2015; Vieira et al., 2019). The genus *Articulina*, which was also found in high abundance in group A–P, was identified in the Barrier Reef Tract and Lagoon in British Honduras (Cebulski, 1969). Additionally, agglutinated species such as *Textularia agglutinans* and *Sahulia barkeri* have been reported in significant numbers in Safaga Bay, a warm-water carbonate environment in the Red Sea along the Egyptian coast (Haunold, 1999).

The foraminiferal biota identified in this group appears to be largely influenced by two inversely related parameters on the seafloor: sediment grain size and organic matter input. The samples are predominantly sandy and exhibit a lower average content of OM, which may be associated with the presence of mesotrophic to oligotrophic and symbiont-bearing species.

The samples from this group vary from 25 and 50 m and showed a marked abundance of the cosmopolitan species *Ammonia* spp. (*A. parkinsoniana*, *A. tepida*, and juvenile forms), typical of inner and coastal marine environments. *Ammonia tepida*, a commonly reported species in Brazilian coastal environments (e.g., Debenay et al., 2001; Burone et al., 2007; Teodoro et al., 2009; Díaz et al., 2014), was observed in only three samples: G01, F01 (group A–P), and FOZ03 (group G–T). The FOZ03 sample, the shallowest in the dataset (13 m depth), is located near the Doce River mouth and showed the highest abundance of this species.

6 Conclusion

- The benthic foraminiferal assemblages found in this study are closely related to the distinct geomorphology compartments and sedimentary regimes of the ESCS. Each continental shelf compartment (Paleovalley, Abrolhos, and Doce River) supports distinct foraminiferal groups that reflect local sedimentary, geomorphological, and oceanographic conditions.

- The distribution of benthic foraminiferal assemblages along the ESCS reflects the current environmental mosaic and provides a framework for interpreting past environmental changes.

- Each assemblage identified in this study (M–C, Q–B, H–Q, G–T, and A–P) can serve as a valuable proxy for reconstructing paleoenvironmental conditions, such as sediment supply, organic matter flux, and oceanographic dynamics.

- The dominance of carbonate-associated species in the Paleovalley and Abrolhos shelves can be used to identify periods of carbonate sedimentation and reef development in the geological record.

- The presence of infaunal-dominated assemblages in the Doce River Shelf can indicate periods of increased terrigenous input and organic matter deposition.

- The transitional nature of group H–Q can help identify shifts between siliciclastic and carbonate-dominated environments, providing insights into past changes in sediment sources and oceanographic conditions.

Data availability. The data discussed in this paper are available in the Supplement (https://doi.org/10.5281/zenodo.17313920, Rodrigues, 2025).

Sample availability. All of the figured specimens have been placed in plummer slides, reposited in the Laboratory of Marine Geosciences (LaboGeo) collection at the Department of Oceanography and Ecology at the Universidade Federal do Espirito Santo (Brazil).

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Author contributions. ARR, FKA, and RMM conceived the study. ARR, FKA, and PPR performed the morphological identifications and the statistical analyses. PPR made the SEM images. CFG, VSQ, and KAJ organized the abiotic parameters. ARR, FKA, VSQ, PPR, CFG, RRM, KAJ, and ACB wrote the paper. ARR, FKA, VSQ, and KAJ created the figures.

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