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Living Benthic Foraminifera from the Surface and Subsurface Sediment Layers Applied to the Environmental Characterization of the Brazilian Continental Slope (SW Atlantic)

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Abstract: Living benthic foraminifera (>63 µm) were studied to characterize the continental slope of the Potiguar Basin (SW Atlantic). Foraminifers from the surface (0–2 cm), subsurface (2–5 cm), and integrated (0–5 cm) sediment layers were analyzed to verify their contribution to environmental characterization. It was also estimated if and which changes occur when the subsurface is added. Sampling stations were distributed in five transects in four isobaths (150, 400, 1000, and 2000 m). Sediment samples were fixed with 4% buffered formaldehyde and stained with Bengal rose. Were recorded 396 species in the surface layer, 228 in the subsurface, and 449 in integrating both layers. This study did not include tubular agglutinated species. The assemblages from 150 m isobath indicated the upper slope, from 400 m indicated the middle slope and the ones from the 2000 m indicated the lower slope. The surface layer's assemblage at 1000 m isobath was more similar to the middle slope; in contrast, its subsurface layer's assemblage had more similarity with the lower slope. Rarefaction curves, Permanova, and NMDS routines indicated a high resemblance between surface and integrated layers. Therefore, the first two centimeters were sufficient to characterize this region based on living benthic foraminifera.

Keywords: living benthic foraminifera; environmental characterization; vertical stratification; continental slope; Potiguar Basin; Rio Grande do Norte

1. Introduction

The study of Foraminifera is an important tool for environmental quality assessment, as they are abundant and easily collectible, have short life cycles, are sensitive to physical and chemical changes in the environment, and change the composition of their assemblages and their distribution in regions impacted by pollution [1–5]. The widespread use of these organisms promoted the establishment of guidelines for environmental monitoring of marine ecosystems and a protocol with standardized methods for soft-bottom benthic foraminiferal monitoring studies [6].

Benthic foraminifers do not live only at the sediment-water interface but can be found several centimeters deep in marine sediments. These microhabitats have a combination of physical, chemical, and biological characteristics. The species that inhabit superficial layers may differ from those inhabiting deeper layers forming assemblages with different faunal compositions [7]. However, microhabitats may change seasonally, and the species or genera can be found in different sediment layers according to favorable conditions or due to their development [8].

Foraminifera can be classified according to the depth they inhabit in marine sediments. Epifaunal, which live on the surface, shallow infaunal live in the range of 0–2 cm, intermediate infaunal live in the range of 1–4 cm, and deep infaunal live below 4 cm [9]. Although this classification is functional, the depth mentioned for these categories can be variable over time, influenced by seasonal events. Therefore, we should not consider the exact depth in the sediment but the relative position of one species among the others [7].

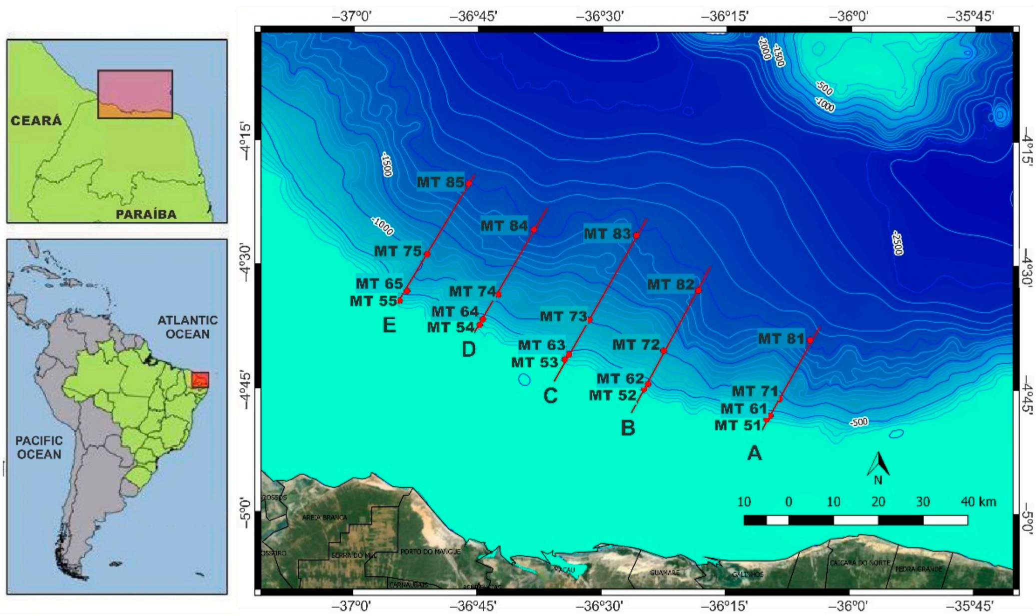
Several deep-sea studies have addressed the vertical distribution of foraminifera. Usually, up to 10 centimeters depth is analyzed in the sediments, and in general, the densities are higher at superficial layers, decreasing with increasing depth [10–18]. It is still unclear whether only the surface layer of the sediment is sufficient to characterize a region based on foraminifera. Further studies are necessary to evaluate subsurface habitats occupied by foraminifera in different world regions [18]. It is also unknown whether the results of bathymetric zoning of deep regions change by including the lower layers.

Licari and Mackensen [19] questioned whether neglecting foraminifers from subsurface layers would harm environmental characterization based on their assemblages, bringing inaccuracy to paleoenvironmental interpretations. These authors studied the similarities and differences between surface (0–1 cm) and surface-plus subsurface assemblages (0–5 cm) in the southeastern Atlantic. They found that there were no significant differences in the distribution and composition of the assemblages. However, they emphasized that the result may be different in other oceanic regions due to environmental peculiarities.

The main objective of this study is to investigate the living benthic foraminifera from the surficial sediment layer (0–2 cm) applied to the environmental characterization of the continental slope at the Brazilian Equatorial Margin. Moreover, to verify whether the incorporation of foraminifers from the subsurface sediment layer (2–5 cm) of the slope changes the observed pattern, influencing regional understanding.

2. Study Area

The Potiguar Basin is located at the eastern end of the Brazilian Equatorial Margin (Figure 1).



(**a**) (**b**)

Figure 1. Study area. (**a**) South America—Brazil in green; rectangle delimiting the northern coast of Rio Grande do Norte. (**b**) Location of sampling stations at the continental slope (•); transects signed with the red lines.

The continental shelf is narrow and very different from the south of Brazil and southeast continental shelves. At the Rio Grande do Norte (NW Brazil), there is a strong declivity beginning at ~70 m. The continental slope starts at depths that usually belong to the middle/outer continental shelf in other Brazilian or other world regions. According to Almeida et al. [20], the upper slope occupies the area between the shelf break, at 70 m, up to 300 m depth with a gradient of 15°, and the middle slope occupies between 300 m and 1300 m depth with a gradient of 6°. The abyssal plain begins at about 2000 m depth [21].

The vertical structure of the water column in the region is characteristic of the South Atlantic and composed of the following water masses: Tropical Water (TW), South Atlantic Central Water (SACW), Antarctic Intermediate Water (AIW), and North Atlantic Deep Water (NADW). TW has a higher temperature and salinity characteristics (>20 and >36 °C, respectively); SACW has temperatures between 6 and 20 °C, salinity ranging from 34.6–36, and a high concentration of nutrients; AIW has temperatures between 3 and 6 °C, salinity between 34.2 to 34.6, with high phosphate values; NADW has temperatures ranging between 3 and 4 °C, and salinity between 34.6 and 35 [22,23].

Systems of oceanic gyres and currents typify the ocean circulation in the South Atlantic; a subtropical anticyclonic gyre occupies the east-west extension of the ocean basin [22]. The South Equatorial Current (SEC) limits the Equatorial Gyre with the Subtropical Gyre of the South Atlantic [24]. The Cabo de São Roque region is divided into two Contour Currents: Brazilian Northern Subcurrent (BNS) in the north and Brazil Current (BC) in the south. These currents flow on the western continental margins of the ocean basins and are characterized by geophysical jets that present intense, narrow, and well-defined flows [25]. North of 5°S, the BNS is influenced in its superficial portion by the contribution of the SEC with its central (CSEC) and equatorial (ESEC) branches and configures the intense flow of the North Brazil Current (NBC) that crosses the Equator in a northwest direction, closing the Equatorial Gyre at its western edge [24,26].

According to Testa and Bosence [27], the continental shelf of Rio Grande do Norte is a windward shelf without bays, estuaries, or rivers with significant inflow. Exposed to the full force of the western flow of the SEC faces strong winds and a large tidal range, resulting in a high-energy shelf facing the open ocean. The coast of Rio Grande do Norte is very unstable around 5°S due to the abrupt change in the shelf orientation associated with the intensity of the BNS. Associated with the northward flowing North Brazil Undercurrent (NBUC), a quasi-stationary subsurface anticyclone, the Potiguar Eddy, extends vertically from 100 to 400 m in Potiguar Basin, with maximum velocities of 0.6 m s^{-1} at the study area [28].

3. Materials and Methods

3.1. Sediment Sampling

Samples were collected aboard the RV Seward Johnson in transects perpendicular to the coastline and parallel one to another, crossing the isobaths of 150 m, 400 m, 1000 m, and 2000 m totaling 20 sampling stations (Table 1). The stations were defined using characteristics of the water masses present in the region. Sediment samples were recovered using a box-core (2500 cm^2) and/or a modified Van Veen grab with the top opening (231 L). At each station, samples (10 cm × 10 cm × 10 cm) were taken from each sampler using a stainless-steel box. The presence or absence of an anoxic layer was recorded, as well as signs of bioturbation. The cores were sliced into the surface (0–2 cm) and subsurface (2–5 cm) sediment layers, totaling 40 samples (Figure 2). Each sample was fixed with a 4% formaldehyde solution buffered with sodium tetraborate and stained with Rose Bengal to differentiate between living and dead foraminifers [29]. The surface layer was used for sedimentological analysis.

Table 1. Data of sampling stations at the slope of the Potiguar Basin.

Sample	Lat	Long	Depth (m)	Water Mass
MT51	04°29′10″	36°06′02″	167	TW
MT52	04°27′01″	36°14′56″	203	TW
MT53	04°24′54″	36°20′41″	133	TW
MT54	04°22′23″	36°26′51″	128	TW
MT55	04°20′39″	36°32′40″	145	TW
MT61	04°28′55″	36°05′47″	400	SACW
MT62	04°26′39″	36°14′38″	422	SACW
MT63	04°24′32″	36°20′23″	394	SACW
MT64	04°21′59″	36°26′38″	409	SACW
MT65	04°19′57″	36°32′07″	408	SACW
MT71	04°27′41″	36°05′06″	998	AIW
MT72	04°24′12″	36°13′31″	1011	AIW
MT73	04°22′01″	36°18′55″	1100	AIW
MT74	04°20′11″	36°25′31″	983	AIW
MT75	04°17′17″	36°30′41″	970	AIW
MT81	04°23′26″	36°02′55″	2010	NADW
MT82	04°19′51″	36°11′01″	1992	NADW
MT83	04°15′52″	36°15′31″	1957	NADW
MT84	04°15′28″	36°22′57″	1983	NADW
MT85	04°12′08″	36°27′41″	2000	NADW

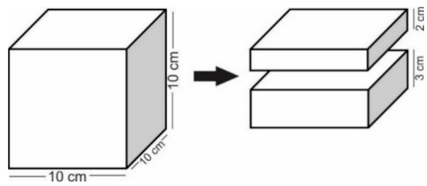


Figure 2. Schematic diagram of sampling sectioning (surface 0–2 cm and subsurface 2–5 cm) layers.

3.2. Granulometric Analysis

The granulometric analysis was performed at the Laboratório de Geografia Física (LabGeoFis/UFRN). The sediment grain size was determined by dry sieving following Folk [30], in an electromagnetic sieve shaker (Produtest brand), with different mesh openings (4 mm, 2 mm, 1 mm, 0.500 mm, 0.250 mm, 0.125 mm, 0.062 mm). The fine fraction was quantified by pipetting.

3.3. Foraminifera—Samples Processing

All samples had their wet volume standardized to 100 cm^3 and were washed under running water with a 63 µm mesh sieve and oven-dried below 60 °C. The sediments were hand sieved (63, 125, 250, 500, 850, and 1000 µm mesh) to improve the observation of different grain sizes. The ≥250 µm fraction was entirely observed and counted, while the <250 µm fraction was quartered. The $\frac{1}{4}$ examined was corrected to 100 cm^3. Each fraction was examined under a Zeiss SteREO Discovery.V8 microscope, 8:1 zoom range, 150× maximum magnification. All living foraminifera were collected and stored in micropaleontological slides. Tubular agglutinated species were not analyzed in this study. A difficulty encountered and raised by other authors (e.g., Fontanier et al. [16]) was the observation of the protoplasm in species with non-transparent tests such as some agglutinated and miliolid taxa. Using transmitted light, water, alcohol, and glycerin, we tried to see the protoplasm in these taxa. Nevertheless, the best way to overcome this problem was to break the tests after identification to confirm the status of living or dead.

Foraminiferal species were identified with the help of several publications (e.g., Ellis and Messina [31], Loeblich and Tappan [32,33], Hottinger et al. [34], Kaminski [35], Hayward et al. [36], Debenay [37], Kaminski and Cetean [38]; among others) and by comparison with material from museum collections, e.g., Museo Argentino de Ciencias Naturales “Bernardino Rivadavia”—Buenos Aires (Argentina), Smithsonian National Museum of Natural History—Washington D.C. (U.S.A.) and Natural History Museum-London (U.K.). Some of the specimens were imaged using a Scanning Electron Microscope and illustrated in the plates.

3.4. Statistical Treatment

Analyses were performed for three distinct data sets: surface layer (0–2 cm), subsurface layer (2–5 cm), and integrated layers (0–5 cm). These terms, as used hereafter, refer to the data sets of this study.

Diversity was assessed by species richness (S), Shannon’s index (H’), Pielou’s evenness (J’), and Dominance (D). H’, J’, and D were calculated only for densities higher than 50 ind./100 cm^3. The bootstrap [39], a non-parametric resampling method that allows estimating wealth, was also used; an original data set is repeatedly sampled, creating various combinations of observations; these observations are used to define the standard error [40]. Unidentified specimens were excluded from these analyses.

Although the sampling effort was similar in the two layers (0–2 and 2–5 cm), we estimated the species richness using rarefaction and extrapolation based on sample size [41] with the software R [42] and the iNEXT package [43]. This technique allows an inferential comparison of the diversity between groups with different sample sizes by constructing sampling curves for species richness. These curves are interpolated for smaller sample sizes or extrapolated to larger sample sizes [41,43]. These estimates should not be interpreted as representing the total richness or diversity of species at each depth interval, but rather as comparable estimates at the different depths (0–2 and 2–5 cm), as well as the comparison of these depths with the total evaluated layer (0–5 cm). In graphical representations, the shaded areas represent the confidence intervals calculated from the 95% bootstrap method.

Non-metric multidimensional scaling (NMDS) examines differences between areas and depths in species composition using Jaccard dissimilarities [44]. We performed the NMDS using the “metaMDS” function of the “vegan” package [45]. We used permutational multivariate analysis of variance (PERMANOVA, 9999 permutations) to determine differences in species composition by using the ‘adonis2’ routine available within the “vegan” package [45] and testing for significant clustering of depths across the post hoc test using “adonis.pair” routine available in the “EcolUtils” package [46].

Clustering analyses (Q mode) were applied using the hierarchical agglomerative clustering method (unweighted pair-group average—UPGMA) and the Bray-Curtis index to define foraminiferal assemblages [47]. For the curves, NMDS, PERMANOVA, and clustering analyses, only species with a relative frequency higher than or equal to 2% and occurrence in at least three samples were used. The Indicator Species Analysis [48] was applied to identify the significant species ($p < 0.05$) of each group of the superficial layer and their contribution within the group (Ind Val).

To correlate the abundance of species and environmental variables, a Canonical Correlation Analysis was performed, whose objective is to represent in its ordination axes the linear combinations between the data matrices [49]. To identify the correlations between foraminifera and environmental variables in the superficial layer, we used the biological matrix of indicator species and chlorophyll-a, pheophytin-a, dissolved oxygen, pH, temperature, organic matter, anoxic layer, and percentage of sand and clay.

The list of species with the original names is given in Supplementary Materials Table S1. Selected species are illustrated in Plates I-IV (Appendix A).

4. Results

4.1. Abiotic Data

Sediments from 150 m and 400 m contained larger grain size particles. The highest sand content was observed at MT54 and MT53 (94.21% and 91.48%, respectively). Stations from 1000 m and 2000 m were silt-dominated. The highest silt contents were registered in MT81 and MT84 (65.20% and 64.10%, respectively). Clay percentage was low, with maximum rates (27.13%) at MT82 (Figure 3).

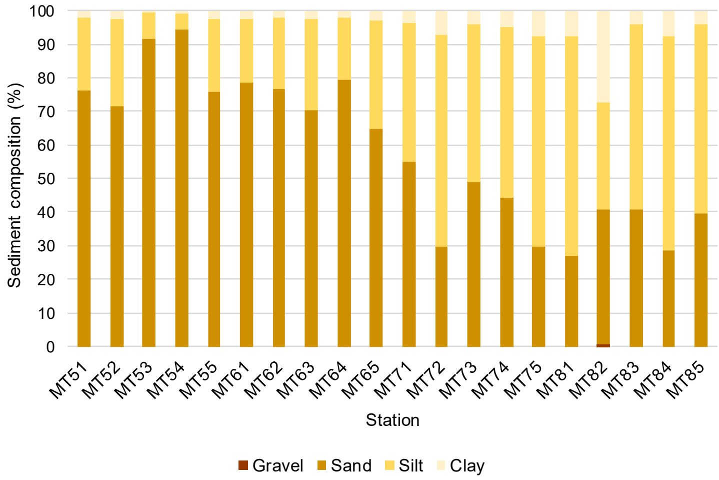


Figure 3. Sediments composition at the stations sampled at the Potiguar Basin Slope.

Anoxic layers were recorded at 400 m, at 4 and 5 cm deep in samples MT63 and MT64.

The average percentage of organic matter was lower in the 400 m and 150 m isobaths and higher in 1000 and 2000 m, varying from 6.93 ± 2.22 to 10.02 ± 1.77.

The parameters related to the water column are briefly described below. The mean temperature was higher in the 150 m isobath (21.36 ± 1.50) and decreased towards the deeper isobaths (400 m 8.38 ± 1.05; 1000 m 4.16 ± 0.05; 2000 m 3.40 ± 0.07).

Dissolved oxygen was on average higher in the 2000 m isobath (8.18 ± 0.16). In the other isobaths, it ranged from 5.66 ± 0.16 in 400 m to 6.05 ± 0.09 in 150 m.

On average, the pH was higher at 150 m (7.98 ± 0.10) and reached the lowest value in 1000 m (7.69 ± 0.06), increasing slightly in 2000 m (7.81 ± 0.05).

The percentage of chlorophyll-a and pheophytin-a were lower in the 400 m and 150 m isobaths and higher in 1000 and 2000 m. Chlorophyll-a ranged from 0.28 ± 0.10 in 400 m to 0.38 ± 0.16 in 1000 m. Pheophytin-a ranged from 0.12 ± 0.06 in 400 m to 0.19 ± 0.06 in 1000 m.

The main trends of abiotic data obtained during the project sampling are available in Supplementary Materials (Supplementary Figure S1).

4.2. Foraminifera

We recognized a total of 449 species and 193 genera in all samples. We recorded 396 species and 178 genera at the surface layer, and at the subsurface layer, 228 species and 127 genera. A total of 175 species were common to both layers, while 221 and 53 species were exclusive to the surface and subsurface layers, respectively.

We obtained 85.6% of the expected species from the surface layer, 84.26% of the expected species from the subsurface layer, with the same number of samples. Moreover, 86.36% of the expected species from the integrated layer at the study area (Table 2).

Table 2. The obtained and estimated richness (bootstrap) for the three studied layers of the Potiguar Basin Slope. S = richness observed; S(est) = Estimated richness.

Layer	S	S(est) 95% CI Lower Bound	S(est) 95% CI Upper Bound	Bootstrap	%
0–2 cm	396	376	416	463	85.60
2–5 cm	228	212	244	271	84.26
0–5 cm	449	428	470	520	86.36

The richness analysis based on the occurrence of the species showed that 449 species were observed across the analyzed depth (0–5 cm), while at a depth of 0–2 cm, 396 species were recovered, showing the ratio of the sampling effort concerning the total depth (0–5 cm) equivalent to 0.88 (interquartile range = 0.87–0.88); and in 2–5 cm, 228 species were found, with a sample effort ratio equivalent to 0.52 (interquartile range = 0.50–0.53) (Figure 4).

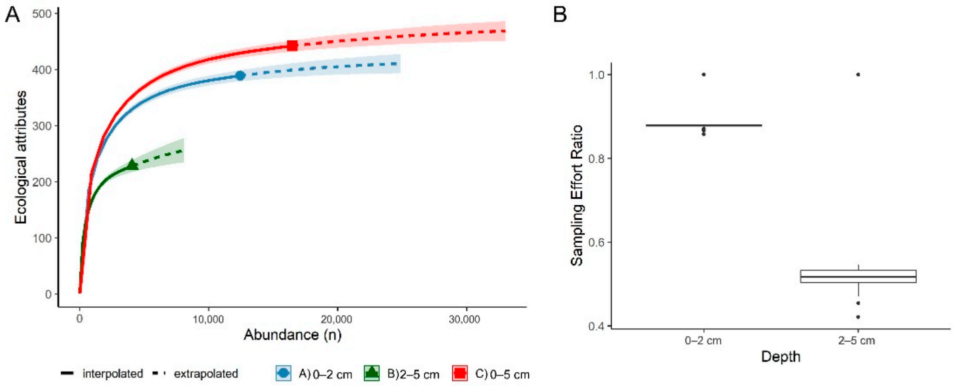
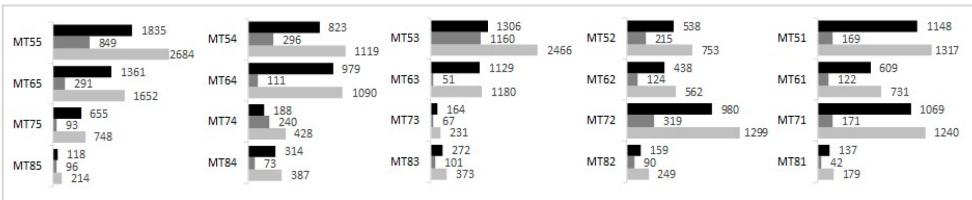


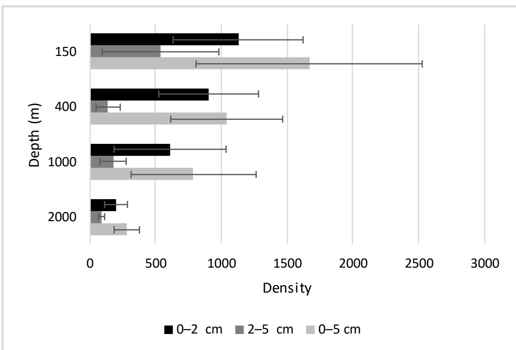
Figure 4. Richness analysis (**A**) Sampling curves for species richness comparing estimates at the different depths (0–2 and 2–5 cm) and comparing them with the total evaluated layer (0–5 cm). The shaded areas represent the confidence intervals. (**B**) Sampling effort ratio at integrated and subsurface layer.

4.2.1. Density

We recorded a total of 18,902 specimens in the study area, and the mean density was consistently higher on the surface than the subsurface layer. Foraminiferal densities varied between 118 (MT85) and 1835 (MT55) individuals/100 cm^3 in the surface (total = 14,222 specimens) compared to 42 (MT81) and 1160 (MT53) individuals/100 cm^3 in the subsuperficial layer (total= 4680 specimens). Only one station of the middle slope (1000 m) (MT74) presented a higher density at the subsurface layer (Figure 5a).



(**a**)



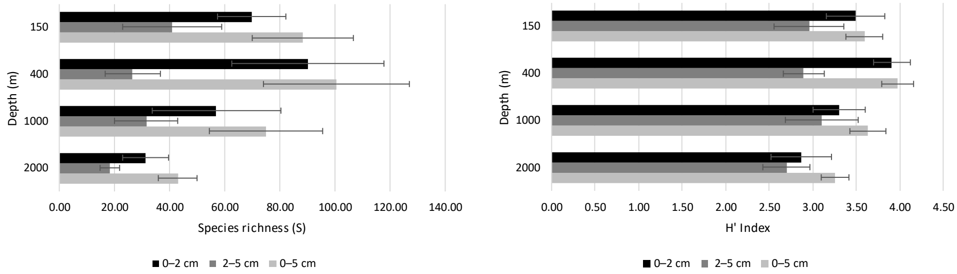
(**b**)

Figure 5. Density of foraminifera. (**a**) Per station at the layers. (**b**) Mean and standard deviation per isobath at the studied layers.

At the surface layer, the mean density was higher at 150 m (1130 ± 493.21 standard deviation), decreasing towards the deeper isobaths (400 m = 903.2 ± 377.25; 1000 m = 611.2 ± 426.20 and 2000 m = 200 ± 87.40). At the subsurface layer, the mean density was higher at 150 m (537.8 ± 442.34) and 1000 m (178 ± 104.07). The mean values were lower at 400 m and 2000 m with 139.8 ± 89.64 and 80.4 ± 23.92, respectively (Figure 5b).

4.2.2. Diversity

Species richness was predominantly higher at the surface, except for station MT74 (S = 29 surface; S = 41 subsurface). The highest surficial layer's S values occurred at 400 m ($\bar{x}$ = 90 ± 27.61), decreasing toward deeper isobaths. In the subsurface layer, the mean S was higher at 150 m ($\bar{x}$ = 41 ± 17.99), varying at 400 m and 1000 m, and the lowest values occurred at 2000 m in both layers, surface $\bar{x}$ = 31.2 ± 8.41 and subsurface $\bar{x}$ = 18.25 ± 3.59 (Figure 6a).

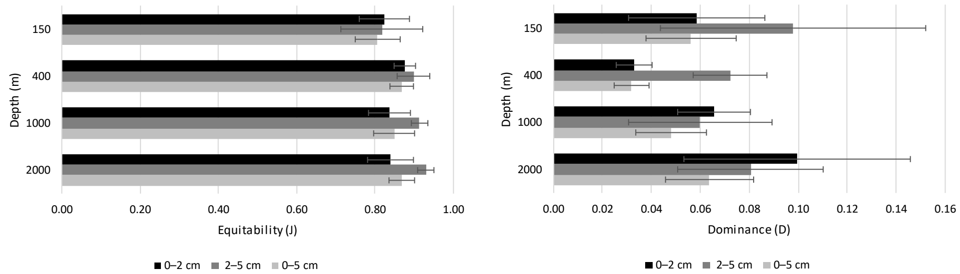


(**a**) (**b**)

Figure 6. The mean and standard deviation of foraminifera species diversity along the studied isobaths at the surface, subsurface, and integrated layer. (**a**) Species richness; (**b**) Shannon's index.

The higher H′ diversity index values occurred at the surface layer; the highest was registered at 400 m (H′= 4.18, MT65) while the lowest at 2000 m (H′ = 2.49, MT82) (Figure 6b). H′ diversity had few changes at the subsurface layer; the highest value occurred at 1000 m (H′ = 3.49, MT72), and the lowest at 2000 m (H′ = 2.31, MT84).

The subsurface layers showed higher equitability (J′) mean values, increasing towards the deep sea, except at 150 m, where both layers presented the same average ($\bar{x}$ = 0.82 ± 0.06 in surface and $\bar{x}$ = 0.82 ± 0.1 in subsurface). At the surface layer, the lower values were registered at 150 m (Figure 7a).



(**a**) (**b**)

Figure 7. The mean and standard deviation of foraminifera equitability (**a**) and dominance (**b**) along the isobaths at the studied layers.

The dominance (D) varied among layers and isobaths (Figure 7b). It was higher at 150 m on the subsurface layer ($\bar{x}$ = 0.10 ± 0.05). At the surface layer, its higher values were registered at 2000 m ($\bar{x}$ = 0.1 ± 0.04), and 1000 m ($\bar{x}$ = 0.07 ± 0.01).

After integrating the layers, in general, the patterns observed in the surface are maintained for the community structure. These values are presented in Supplementary Materials Table S2.

4.2.3. Composition of Assemblages: Major Taxa

At the surface layer, the dominant species (Rel.Freq. > 4%) at 150 m are *Bigenerina textularioidea*, *Angulogerina occidentalis* s.l., and *Sigmavirgulina tortuosa*; at 400 m are *Trifarina bradyi* and *Siphonina bradyana*; at 1000 m are *Epistominella* sp. 1, *Reophax spiculifer*, *Bolivina pseudoplicata* and *Bolivina albatrossi*; at 2000 m are *Karrerulina* sp. A, *Bolivina pseudoplicata*, *Repmanina charoides*, *Reophax hispidulus* and *Lituotuba lituiformis* (Figure 8).

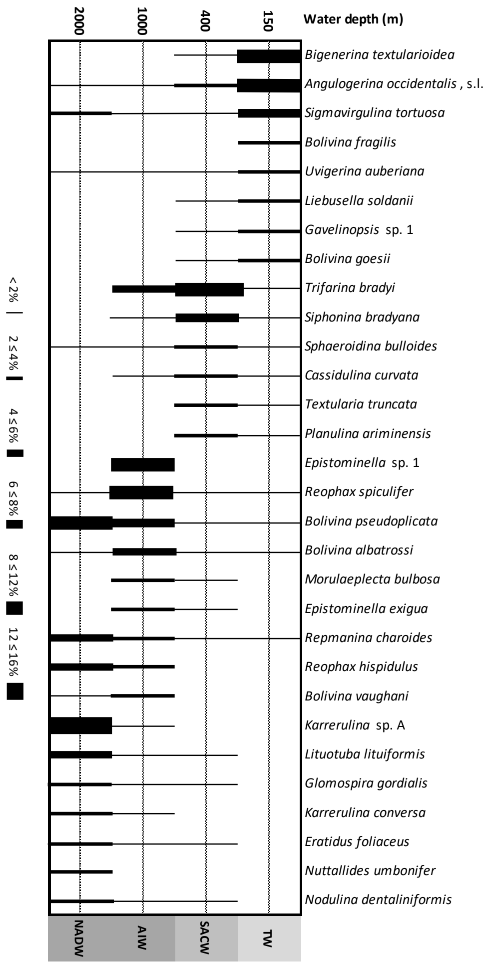


Figure 8. Species and their respective relative frequencies at the superficial layer.

At the subsurface layer, the dominant species (Rel.Freq. > 4%) at 150 m are *Bigenerina textularioidea*, *Liebusella soldanii*, *Angulogerina occidentalis* s.l., and *Sigmavirgulina tortuosa*; at 400 m are *Siphonina bradyana*, *Trifarina bradyi*, *Textularia truncata*, *Psammosphaera fusca* s.l., *Angulogerina occidentalis*, s.l., and *Lagenammina*? sp. 2; at 1000 m are *Repmanina charoides*, *Paratrochammina brasiliensis*, and *Nouria harrisii*; at 2000 m are *Gyroidina* sp. 2, *Paratrochammina brasiliensis*, *Nouria harrisii*, *Bolivina pseudoplicata*, *Pullenia* aff. *subcarinata*, *Bolivina vaughani*, *Nuttallides umbonifer* and Trochamminidae indet. 6 (Figure 9).

When layers are integrated, the species with relative frequency >4% at 150 m are *Bigenerina textularioidea*, *Angulogerina occidentalis*, s.l., and *Sigmavirgulina tortuosa*, but also *Liebusella soldanii* joins the group. *Trifarina bradyi* and *Siphonina bradyana* remain to represent the group at 400 m. At 1000 m, the species with relative frequency >4% are *Epistominella* sp. 1, *Reophax spiculifer* and *Bolivina pseudoplicata*. At the 2000 m depth, species with higher (>4%) relative frequency are *Karrerulina* sp. A, *Bolivina pseudoplicata* and *Paratrochammina brasiliensis* (Figure 10). All values are presented in Supplementary Materials Table S3.

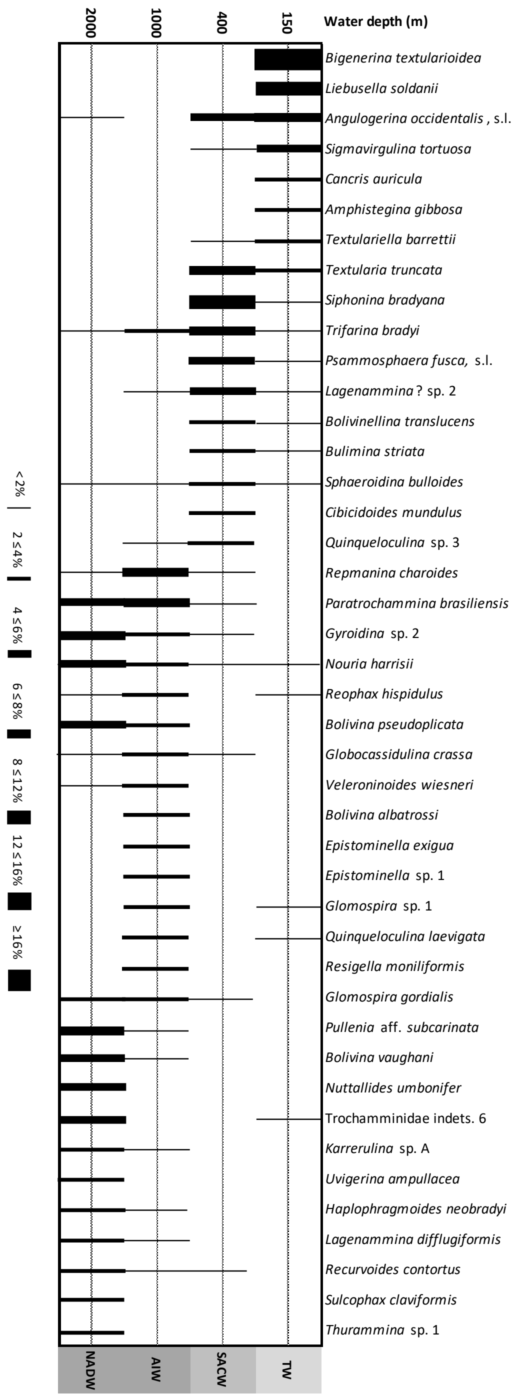


Figure 9. Species and their respective relative frequencies at the subsurface layer.

4.2.4. Comparison of Assemblages

The species composition significantly differed among depths (F = 1.705; $p = 0.0063$). The assemblage at 0–2 cm was statistically similar to that at 0–5 cm (F = 0.334; $p = 0.999$), while the assemblage at the depth of 2–5 cm was statistically different from the layers of 0–2 cm and 0–5 cm (F = 2.605, $p < 0.0001$; F = 2.658, $p < 0.0001$, respectively).

The NMDS revealed that 2–5 cm depth tree species composition did not represent the 0–5 cm depth assemblage as 0–2 cm represented it (Figure 11).

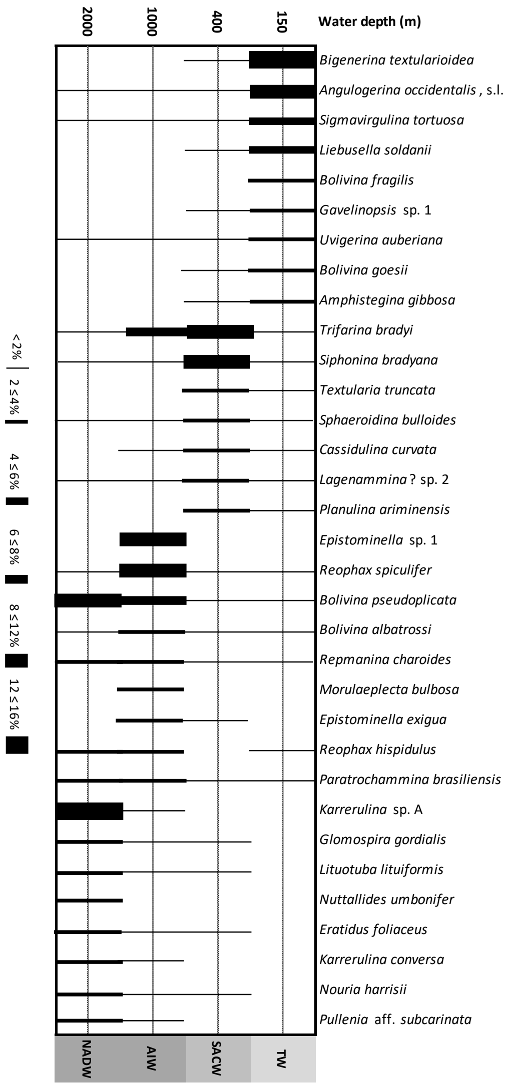


Figure 10. Species and their respective relative frequencies at the integrated layer.

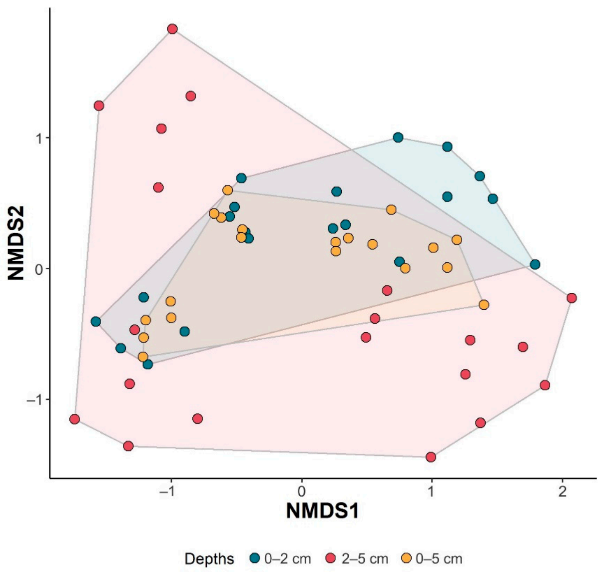


Figure 11. Non-metric multidimensional scaling (NMDS) of three study layers from the continental slope of Potiguar Basin based on the tree of foraminiferal species composition: blue—surface layer (0–2 cm); red—subsurface layer (2–5 cm); yellow—integrated layer (0–5 cm).

4.2.5. Cluster Analysis

Three distinct dendrograms based on foraminiferal assemblages are illustrated in Figure 12.

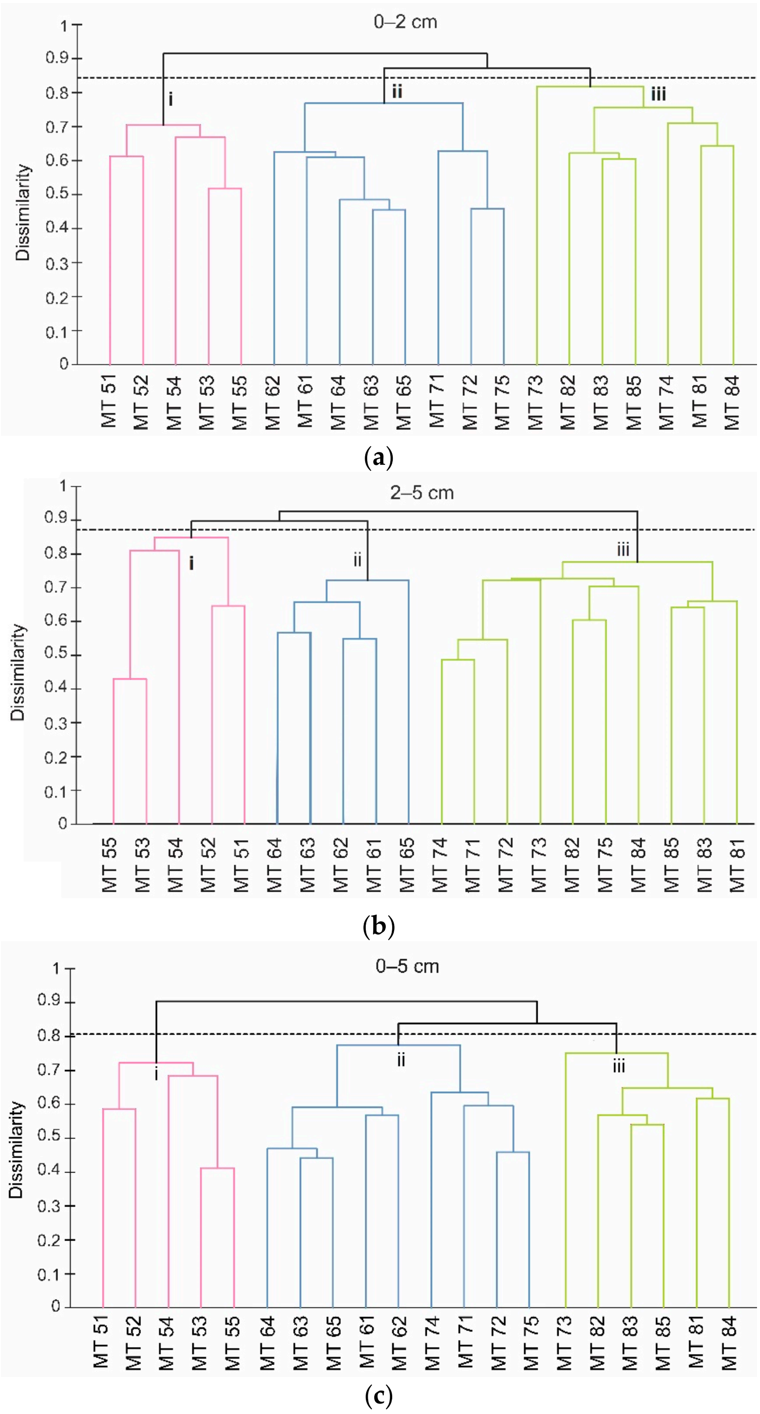


Figure 12. Dendrograms based on foraminiferal assemblages. (**a**) Surface layer. (**b**) Subsurface layer. (**c**) Integrated layer. Groups: (i) upper slope, (ii) middle slope, and (iii) lower slope.

Three main groups are identified at the dendrogram from the surface layer. Group I comprises all the samples from 150 m isobath, indicating the area of the upper slope. Group II joins all the samples from the 400 m isobath and three samples from 1000 m (MT71, MT72, and MT75), indicating the area of the middle slope. Group III joins all the samples from 2000 m isobath and two samples from 1000 m (MT73 and MT74), mostly indicating the lower slope (Figure 12a).

Three main groups are identified at the dendrogram from the subsurface layer. Group I comprises all the samples from 150 m isobath, indicating the area of the upper slope. Group II joins all the samples from 400 m, indicating the middle slope. Group III comprises all the samples from 1000 m and 2000 m, indicating middle to lower slope areas (Figure 12b).

The cluster produced by integrated layers shows a similar pattern to the observed in the surface layer analysis, with minor differences, especially within the samples from 400 and 1000 m. Three groups are observed. Group I comprises all the samples from 150 m, indicating the upper slope. Group II joins all the samples from 400 m and most samples from 1000 m, except for MT73, indicating the middle slope region. Sample MT73 belongs to Group III, with all samples from 2000 m, indicating the lower slope region (Figure 12c).

The main indicator species ($p < 0.05$; and IndVal > 0.6) of dendrogram from the surface layer are available in Supplementary Table S4 (Supplementary Materials).

4.2.6. Canonical Correspondence Analysis

The CCA showed that the species are correlated with the variables data ($p < 0.0001$) and explained 65.71% of the variance (Figure 13).

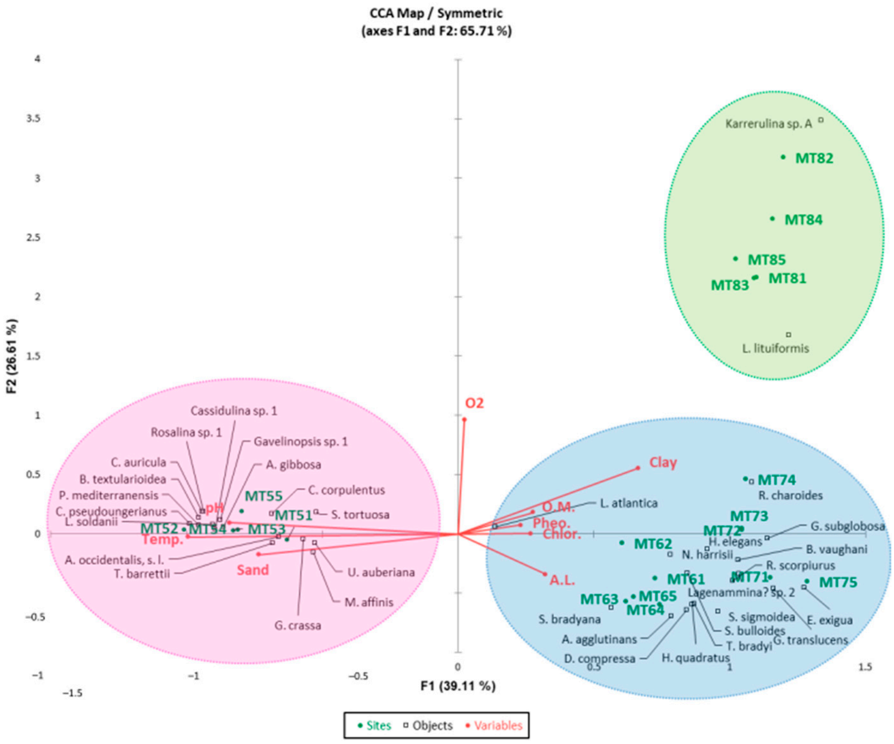


Figure 13. Ordering diagram with the result of CCA performed with indicator species of superficial layer and abiotic variables. Environmental descriptors in red. Temp.: Temperature; A.L.: Anoxic Layer; O.M.: Organic Matter; O_2: Dissolved Oxygen; Sand, Clay, Chlo: chlorophyll-a; Pheo: pheophytin-a, and pH. Ellipses: pink—upper slope, blue—middle slope; green—lower slope.

The three main regions are mentioned below and related to environmental parameters.

In the upper slope (150 m), the indicator species were: *Rosalina* sp. 1, *Bigenerina textularioidea*, *Liebusella soldanii*, *Amphistegina gibossa*, *Cibicidoides corpulentus*, *Angulogerina occidentalis*, s.l., *Globocassidulina crassa* and *Textulariella barretii*. Sands dominated the sediments, the pH and temperature were higher (on the diagram, highlighted in pink).

In the middle slope (400–1000 m), the indicator species were: *Reophax scorpiurus*, *Trifarina bradyii*, *Gavelinopsis translucens*, *Sphaeroidina bulloides*, *Hoeglundina elegans*, *Discammina compressa* and *Haplophragmoides quadratus*. At 400 m isobath sediments, we observed the lowest mean organic matter content, as lowest values of pheophytin-a, chlorophyll-a, dissolved oxygen, and the presence of an anoxic layer. At 1000 m isobath, the sediments were dominated by silt and clay fractions, and registered the highest mean organic matter content, as the values of pheophytin-a and chlorophyll-a (on the diagram, highlighted in blue)

In the lower slope (2000 m), the indicator species were *Karrerulina* sp. A and *Lituotuba lituiformis*. The sediments were dominated by silt and clay fractions. This isobath had the lowest temperature and highest dissolved oxygen concentration. The organic matter, pheophytin-a, and chlorophyll-a values were similar to those recorded at 1000 m (on the diagram, highlighted in green).

5. Discussion

The Brazilian continental margin has many carbonate areas dominating the continental shelf with sandy and gravel sediments usually well-oxygenated, especially in the northeastern region [50]. Sampling and sectioning the first centimeter at sandy and gravel bottom may be complicated sometimes, and a one-centimeter sampling layer might not adequately represent the foraminiferal assemblages. For that reason, most studies performed at the Brazilian shelves have been done with the first two surficial centimeters, aiming to study the epifaunal and the shallow infaunal species.

Schönfeld et al. [6] strongly suggest that replicates should be used in biocenosis studies, especially in environmental monitoring studies, to cover the heterogeneous distribution of foraminiferal assemblages.

This study is part of the environmental characterization of the Potiguar Basin slope area that aims for future monitoring activities. Although the other replicas were not used in this study, the sampling design was carried out on a regular grid and allowed five replicates per isobath, providing a consistent spatial pattern of the foraminiferal assemblages along the bathymetric gradient. Later on, other data may be evaluated, making it possible to discuss microhabitat variation and the variance within the foraminiferal assemblages. The bootstrap analysis indicated that more than 86% of the expected species were recovered, showing the spatial distribution of foraminiferal assemblages along the bathymetric gradient, and increasing the information available for the region. We also emphasize that the characterization of the foraminiferal assemblage using only the first two centimeters of sediment was enough to represent 88% of the species composition, being important evidence to reduce the sampling efforts.

Studies investigating foraminiferal distribution in space and time have described that they are distributed by pulsating patches [51]. In this study, it was not possible to evaluate the temporal distribution. The spatial distribution of foraminiferal density varied widely between stations of the same depth and between the two layers studied, showing the expected patchy distribution. Higher average densities occurred in the stations of the upper slope (150 m), decreasing towards the lower slope (2000 m), similar to the trends observed in other continental slope regions [13,52–56]. The superficial layer had the highest densities; 75.24% of the specimens occurred in this layer, while 24.76% occurred in the subsurface layer. In general, the highest concentration occurs in the first centimeter, with a decrease in density as it goes down vertically [12–15].

The area with the highest diversity at the surface layer was the middle slope (400 m). This region is under the influence of the SACW, rich in nutrients, and it probably influenced the foraminiferal assemblages. At the subsurface layer, the areas with the highest diversity values (S and H′) were the upper slope (150 m) and the middle slope (1000 m), respectively. The presence of sands and very poorly selected sediments at the 150 m isobath might have favored interstitial oxygenation at the subsurface layer, enhancing foraminiferal diversity and density.

Amphistegina gibbosa was recorded on the upper slope surface, and subsurface layers, and on the surface layer of the middle slope (400 m). The presence of living specimens of *A. gibbosa* at the slope is herein attributed to the transported material from the continental shelf, where this species is abundant. As commented before, the continental shelf is narrow at NE Brazil. It presents a strong declivity, beginning at ~70 m, favoring species from the continental shelf to be transported downwards to the slope by currents once the activity of the Potiguar Eddy also influences the hydrodynamics at a regional scale. The preservation of the protoplasm for a short period after death is not uncommon [57]. They can be stained by the Bengal Rose, artificially extending its distribution inadvertently to areas where they are not established.

The low values of density and diversity in the subsurface layer of the middle slope (400 m) are probably associated with an anoxic layer between 4 cm and 5 cm deep in the sedimentary column registered during sampling activities. Although *Trifarina bradyi* occurred in all isobaths with variable densities, it was the most abundant species in the middle slope (400 m) at the surficial layer and the second most abundant species in the subsurface (8.55% and 7.68%, respectively). *T. bradyi* is strongly associated with anoxia or dysoxia events and is usually known as a probably facultative species under those conditions [58,59]. The two stations with the great abundance of this species coincided with the presence of the anoxic layer.

The increase in diversity close to the middle slope is consistent with patterns recorded by Buzas and Gibson [60] and Gibson and Buzas [61] for the North Atlantic, and also by Hayward et al. [36] for the west coast of New Zealand. These authors observed an increase in diversity near the platform and a maximum in the upper bathyal region (between 200 m and 600 m), followed by a slight decline towards the abyssal areas. Disaró et al. [62] found the greater diversity of foraminifers at Potiguar Basin on the carbonate areas of the middle and outer shelf and at the middle slope (370 m). At the Campos Basin, southeastern Brazilian continental margin, the higher relative richness of foraminifers at the first two centimeters of the slope occurred at 400 m to 1000 m. In contrast, the lower values occurred from 1300 m to 3000 m (middle to lower slope) [63].

The subsurface layer had the most constant density, diversity, and evenness in the middle and lower slope. The dominance was usually higher in this layer. The most abundant species responsible for this dominance were *Bigenerina textularioidea* (21.55%) and *Liebusella soldanii* (8.68%) in the upper slope, and *Siphonina bradyana* (10.56%) and *Trifarina bradyi* (7.68%) in the middle slope (400 m).

Regarding the specific foraminiferal composition, we observed that in the upper slope, about 50% of the most abundant species were common to the surface and subsurface layers; at 400 m, this ratio was variable, and at 1000 m and 2000 m, there were about 35% of the most abundant species common to both layers. Calcareous hyaline and agglutinated foraminifera with a robust test (e.g., *Bigenerina textularioidea* and *Liebusella soldanii*) are among the dominant species of the upper slope. These species can live in higher energy environments, represented by the domain of gravel and sand fractions. The number of calcareous species decreased towards deeper stations, and fragile agglutinated species increased, including several species of *Reophax*, *Repmanina charoides*, and *Eratidus foliaceous* increase their densities where the silt and clay fractions dominate.

Regardless of which layer is used, the results show that the distribution of foraminiferal assemblages is strongly associated with the bathymetric gradient and bottom topography. The sedimentary properties also influenced the establishment of the assemblages. Sand fractions predominated in the upper slope, and silt and clay dominate deep regions (middle 1000 m and lower slope). The middle slope (400 m) is dominated by the sand fraction.

Data also indicate that the water masses influence the oxygen content, pH, and nutrients availability. The currents and Potiguar Eddy affect the upper and middle slope sediment deposition and other physicochemical properties [28,64]. The species *Bigenerina textularioidea*, *Angulogerina occidentalis*, s.l., *Sigmavirgulina tortuosa*, *Liebusella soldanii*, *Bolivina fragilis*, *Gavelinopsis* sp. 1, and *Uvigerina auberiana* were abundant throughout the upper slope. According to Murray [59], *Trifarina angulosa*, *Adercotryma glomeratum*, *Aschemonella ramuliformis*, *Cribrostomoides subglobosus*, *Cribrostomoides weddellensis* and *Hoeglundina elegans* are characteristic species of associations exposed to intense bottom currents.

The North Subcurrent of Brazil, with the influence of the South Equatorial Current, configure the North Brazilian Current, which exerts an intense flow in this area [25]. According to Mackensen et al. [65], *Angulogerina angulosa* is associated with larger grain size sediments and the influence of bottom currents in the eastern region of the South Atlantic, between 400 m and 700 m, and at more than 900 m depth. On the upper slope of Potiguar Basin, *Angulogerina occidentalis*, s.l., and on the middle slope (400 m), *Cribrostomoides subglobosus* and *Hoeglundina elegans* are probably responding to the broad influence of this current.

Epistominella spp. were especially abundant at 1000 m, mainly occurring at surficial layers. According to Schnitker [66] and Lohmann [67], the *Epistominella exigua* community is restricted to areas under the influence of the North Atlantic Deep Water in the Atlantic. *E. exigua* is a cosmopolitan species that feed opportunistically on phytodetritus deposited seasonally on the seafloor and is usually associated with elevated oxygen concentrations [68–70]. Comparing phytodetritus assemblages with other assemblages from his study area, Gooday [71] found relatively few species (11–15), low diversity, and high dominance values at the phytodetritus assemblages. In our study, the dominance was higher at the lower slope (surficial layer), and the diversity diminishes at the lower and middle slope (1000 m). *Epistominella* spp. dominate the superficial layers from the middle slope (1000 m), where organic matter, sedimentary phytoplankton chlorophyll, and phytodetritus content were higher. At the 1000 m isobath, *Adercotryma glomeratum*, *Oridorsalis umbonatus*, *Alabaminella weddellensis* and *Globocassidulina subglobosa* were also recorded to be associated with phytodetritus by Gooday [71]. Most of them were also associated with sedimentary phytodetritus at Santos Basin, Brazil [72]. The middle slope (1000 m) is the region most influenced by primary production (chlorophyll and phytodetritus) within the study area.

When comparing the data obtained in the surface and integrated layers, we observe the prevalence of the same patterns. The community structure of the integrated strata followed the same trend as the surficial layer. In both, there was a tendency for the density and diversity to decline towards the deeper slope areas. The highest density occurred in the upper slope, and the most notable diversity occurred in the middle slope (400 m). They also present the same patterns of dominance and equitability. Minor changes could be observed among the most abundant species of the shallow region (upper and middle slope 400 m) when comparing the integrated and the surficial layer. At the deeper stations, only the order of the most abundant species changed.

The data obtained in this study suggest that the foraminifera found in the surface layer accurately represents the environment, allowing reliable environmental characterization. The integration of foraminifers from the subsurface layer did not change the observed patterns. So, it is not necessary to study the double of the sedimentary volume. The increment of species when analyzing 200 cm^3 was 53 species, representing 12% of the recorded species. None occurred at a density greater than 20 individuals/100 cm^3, they are rare species with a relative frequency lower than 2% in the subsurface layer. Most analyses are based on species with more than 2% relative frequency, which means that they will be excluded from these analyses. Licari and Mackensen [19] concluded that the foraminiferal fauna of the surface layer (0–1 cm) coincided with what they found in the total column (0–5 cm). Even though observed minor differences in species composition and distribution, the authors concluded that most of the qualitative ecological information (absence/presence of species and geographic occurrences) is obtained by analyzing only the upper centimeter. The present study corroborates the main results of these authors.

6. Conclusions

The three main foraminiferal assemblages identified along the continental slope of the Potiguar Basin represented the upper slope (150 m isobath), the middle slope (400 m isobath if the subsurface layer is analyzed, or including the 1000 m isobath when surface and integrated layers are evaluated), and the lower slope (1000 m and 2000 m isobaths if the subsurface is analyzed, and only the 2000 m isobath when surface and integrated layers are evaluated).

The assemblages are controlled by bathymetry, sediment (grain size, organic matter, chlorophyll, and phytodetritus content), and by the water masses properties (oxygen, temperature, and nutrients), together with bottom geomorphology and currents.

Density and diversity trends showed higher values in the upper and middle slope (400 m) and lower values in the middle (1000 m) and lower slope, corroborating published data from other regions. The surface layer presented more abundance of foraminifera and more diverse assemblages than the subsurface layer.

Angulogerina occidentalis, s.l., *Adercotryma glomeratum*, *Cribrostomoides subglobosus* and *Hoeglundina elegans* indicate slope areas under the influence of stronger bottom currents (150 m and 400 m). *Trifarina bradyi* indicates anoxic or dysoxic zones as occurs in many other regions of the world.

Our results demonstrated that the efforts made to process and analyze samples from the surficial layer prove adequate for effective environmental characterization of the slope region based on foraminiferal assemblages in the area studied. The incorporation of foraminifers from the subsurface (2–5 cm) sediment layer did not change the pattern observed at the surficial layer. Our study at the slope of the western South Atlantic had the same effectiveness founded by Licari and Mackensen [19], studying the same organisms from the surface (0–1 cm) layer at the eastern South Atlantic.

Nevertheless, when time and technical resources are available, it is always interesting to obtain more information, especially from regions with little available data. Foraminifers of the surficial layer are sufficient bioindicators of the leading environmental conditions. However, the study of deeper layers adds knowledge about the ecology of these organisms and provides additional information about the environment, allowing for the registration of some species that are only found in the subsurface layer of the area.

Supplementary Materials: The following are available online at https://www.mdpi.com/article/10.3390/w13131863/s1, Supplementary Figure S1: Abiotic data of continental slope Potiguar Basin. (a) Temperature (°C); (b) Oxygen (mg/L); (c) pH; (d) Sedimentary organic matter (%); (e) Chlorophyll-a (µg/L); (f) Pheophytin-a (µg/L). Supplementary Table S1. List of recorded species on the continental slope of the Potiguar Basin, with their original designations. Genus or morphotypes with undefined species names are absent. Supplementary Table S2. Values of the ecological indices of foraminifera assemblages from the continental slope Potiguar Basin. Supplementary Table S3. Relative frequency of species (≥2%) from studied layers in the continental slope of the Potiguar Basin. Supplementary Table S4. Indicator species of the surface layer of the Potiguar Basin.

Author Contributions: Conceptualization, L.C.d.C.S.-R. and S.T.D.; data curation, L.C.d.C.S.-R., V.T. and S.W.; formal analysis, L.C.d.C.S.-R. and A.T.B.G.; funding acquisition, S.T.D.; Investigation, L.C.d.C.S.-R., S.T.D., V.T. and S.W.; methodology, L.C.d.C.S.-R. and A.T.B.G.; project administration, S.T.D.; software, L.C.d.C.S.-R. and A.T.B.G.; supervision, S.T.D.; validation, L.C.d.C.S.-R., S.T.D., V.T., S.W. and A.T.B.G.; visualization, L.C.d.C.S.-R.; Writing—original draft, L.C.d.C.S.-R., S.T.D., V.T. and A.T.B.G.; writing—review & editing, L.C.d.C.S.-R., S.T.D., V.T. and A.T.B.G. All authors have read and agreed to the published version of the manuscript.

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Data Availability Statement: The data presented in this study are available upon request to the project administration's author. Most data are not yet publicly known; they are subject to access restrictions and might be made available only with authorization from PETROBRAS S/A, the data holder.

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Conflicts of Interest: The authors declare no conflict of interest.

Appendix A. Plates

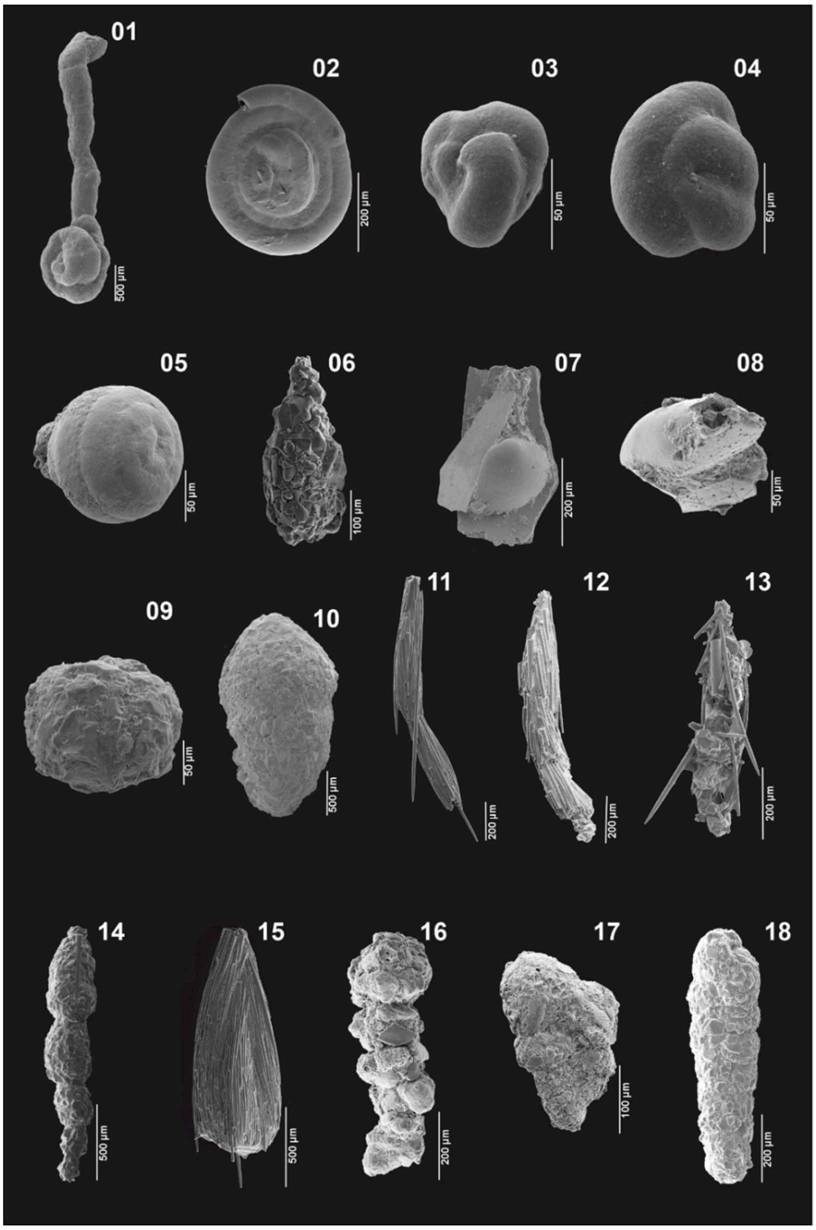

Figure A1. Plate I: 1—*Lituotuba lituiformis* (Brady, 1879), side view; 2—*Glomospira gordialis* (Jones &

Parker, 1860), side view; 3,4—*Glomospira* sp. 1, side views; 5—*Repmanina charoides* (Jones & Parker, 1860), side view; 6—*Lagenammina difflugiformis* (Brady, 1879), side view; 7,8 *Lagenammina*? sp. 2: 7, side view; 8 apertural view; 9—*Psammosphaera fusca* Schulze, 1875, s.l., side view; 10—*Liebusella soldanii* (Jones & Parker, 1860), side view; 11,12—*Reophax spiculifer* Brady, 1879, side views; 13—*Reophax hispidulus* Cushman, 1920, side view; 14—*Nodulina dentaliniformis* (Brady, 1881), side view; 15—*Nouria harrisii* Heron-Allen & Earland, 1914, side view; 16,17 *Bigenerina textularioidea* (Goës, 1894): 16 side view—adult specimen; 17 side view—juvenile specimen with only the biserial stage; 18—*Morulaeplecta bulbosa* Höglund, 1947, side view.

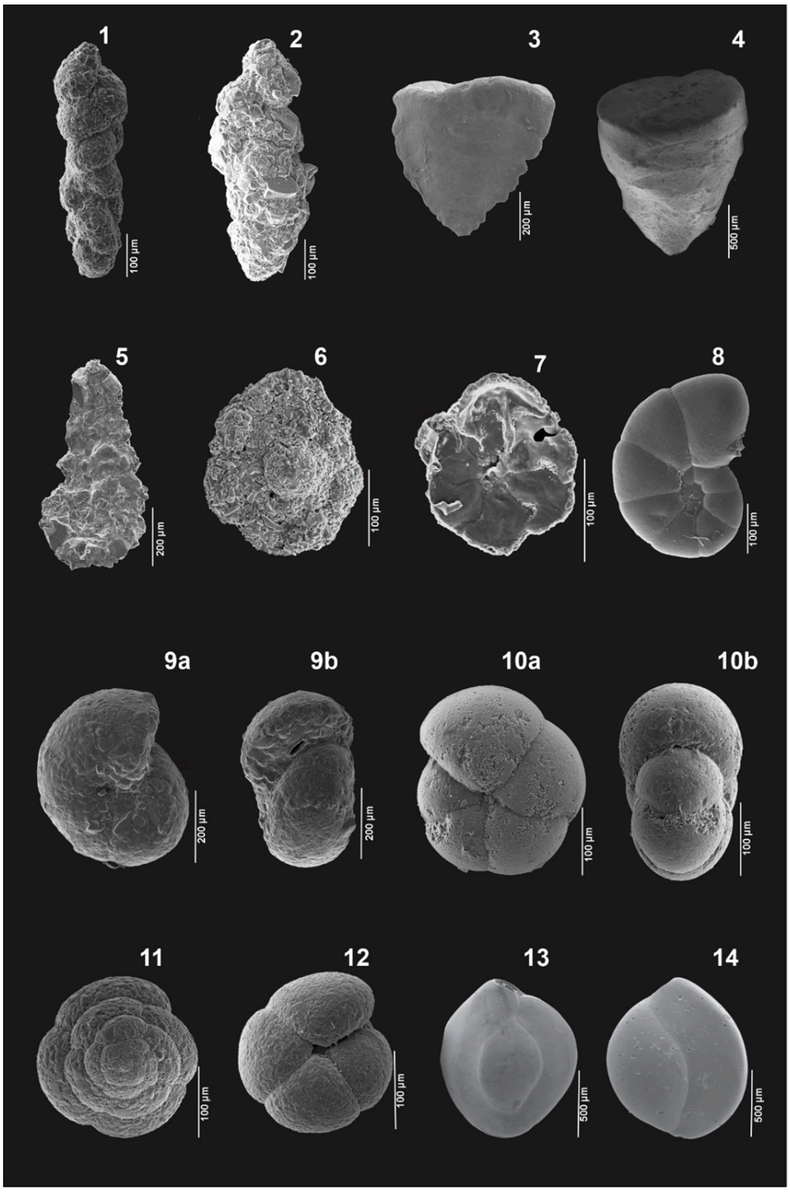

Figure A2. Plate II: 1—*Karrerulina conversa* (Grzybowski, 1901), side view; 2—*Karrerulina* sp. A, side view; 3—*Textularia truncata* Höglund, 1947, side view; 4—*Textulariella barrettii* (Jones & Parker, 1876), side view; 5—*Eratidus foliaceus* (Brady, 1881), side view; 6,7—Trochamminidae indet. 6: 6 spiral view; 7—umbilical view; 8—*Veleroninoides wiesneri* (Parr, 1950), side view; 9a,b—*Recurvoides contortus* Earland, 1934: a—side view; b—apertural profile; 10a,b—*Haplophragmoides neobradyi* Uchio, 1960: a—side view; b—apertural profile; 11,12—*Paratrochammina brasiliensis* (Brönnimann & Beurlen, 1977): 11—spiral view; 12—umbilical view; 13,14—*Quinqueloculina* sp. 3: 13—side view (4 chambers); 14—side view (3 chambers).

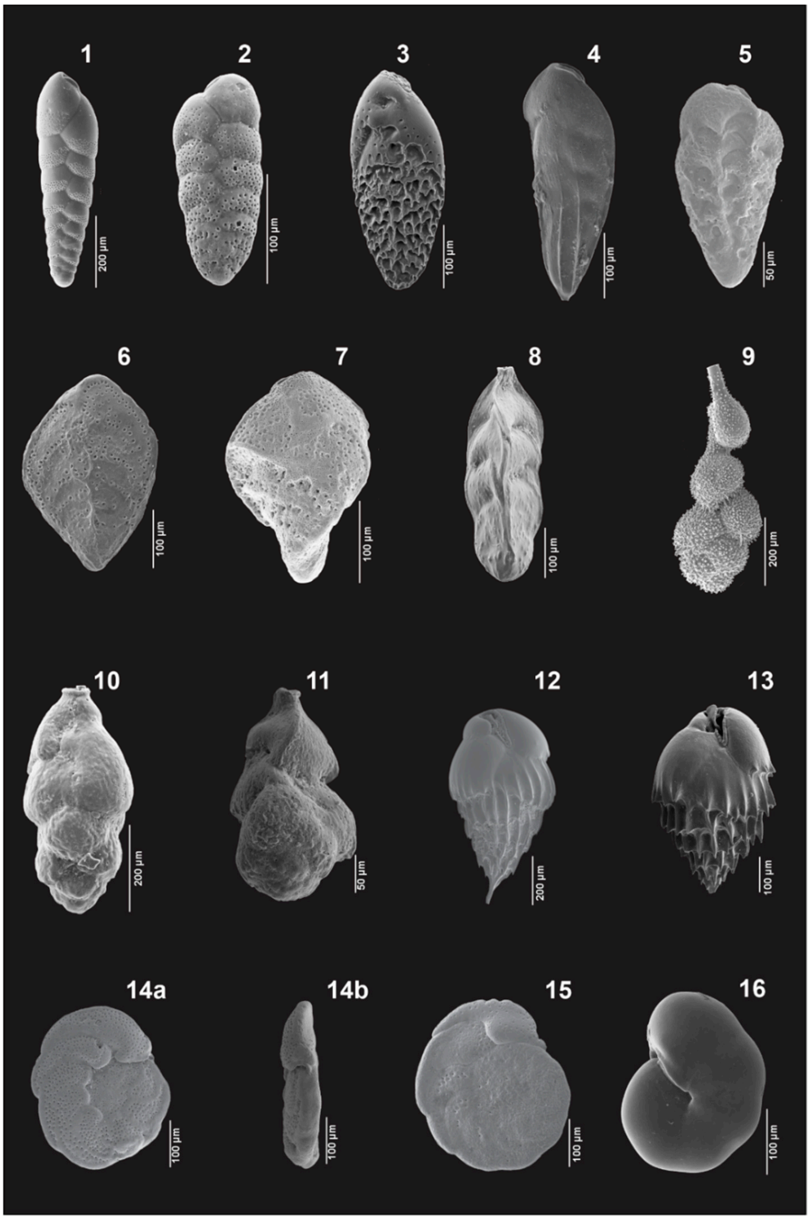

Figure A3. Plate III: 1—*Bolivinellina translucens* (Phleger & Parker, 1951), side view; 2—*Bolivina vaughani* Natland, 1938, side view; 3—*Bolivina albatrossi* Cushman, 1922, side view; 4—*Bolivina fragilis* Phleger & Parker, 1951, side view; 5—*Bolivina pseudoplicata* Heron-Allen & Earland, 1930, side view; 6—*Bolivina goesii* Cushman, 1922, side view; 7—*Sigmavirgulina tortuosa* (Brady, 1881), side view; 8—*Trifarina bradyi* Cushman, 1923, side view; 9—*Uvigerina ampullacea* Brady, 1884, side view; 10,11—*Angulogerina occidentalis* (Cushman, 1923), s.l., side views; 12,13—*Bulimina striata* d'Orbigny in Guérin-Méneville, 1832, side views; 14a,b,15—*Planulina ariminensis* d'Orbigny, 1826: 14a—umbilical view; 14b—apertural profile; 15—spiral view; 16—*Pullenia* aff. *subcarinata* (d'Orbigny, 1839), side view.

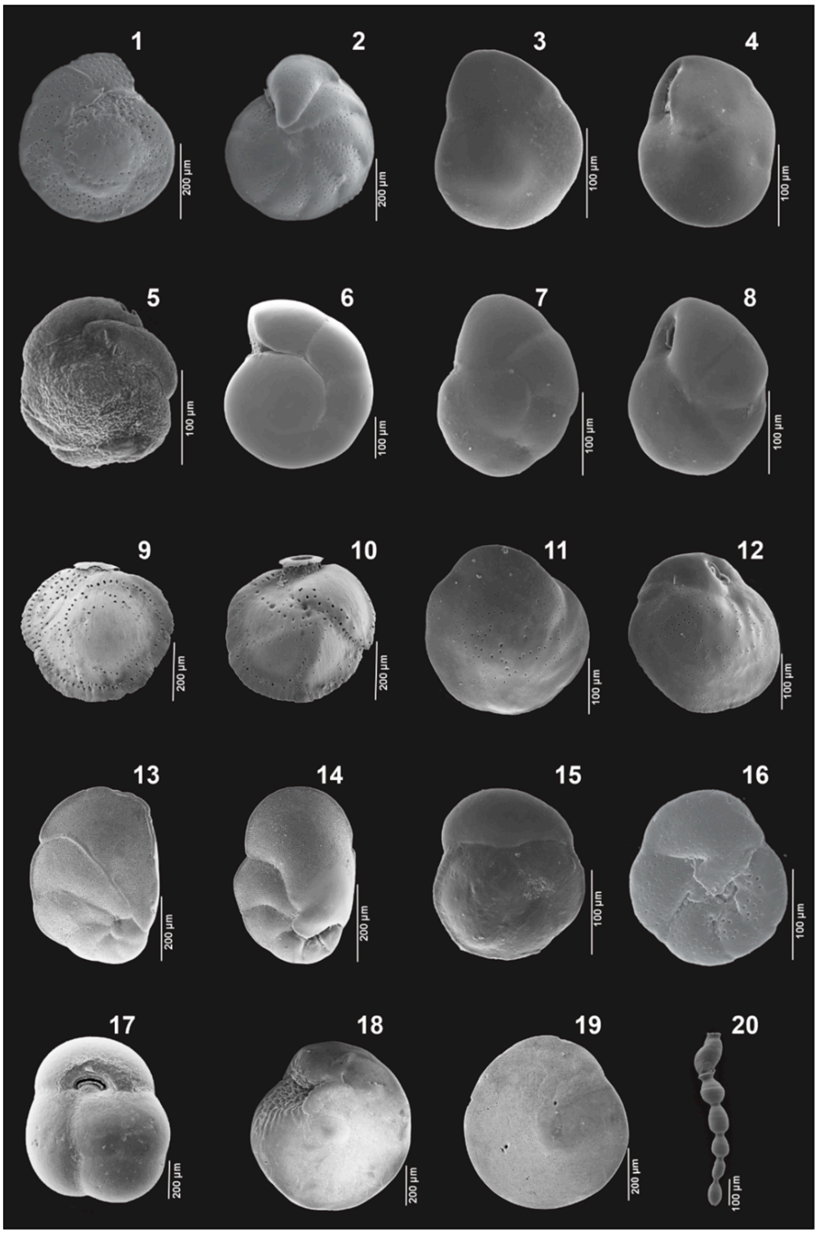

Figure A4. Plate IV: 1,2—*Cibicidoides mundulus* (Brady, Parker & Jones, 1888): 1—spiral view; 2—umbilical view; 3,4—*Epistominella exigua* (Brady, 1884): 3—spiral view; 4—umbilical view; 5—*Nuttallides umbonifer* (Cushman, 1933), spiral view; 6—*Gyroidina* sp. 2, spiral view; 7,8—*Epistominella* sp. 1, 7—spiral view; 8—umbilical view; 9,10—*Siphonina bradyana* Cushman, 1927, 9—spiral view; 10—umbilical view; 11,12—*Cassidulina curvata* Phleger & Parker, 1951: 11—side view; 12—side view showing the aperture; 13,14—*Cancris auricula* (Fichtel & Moll, 1798): 13—spiral view; 14—umbilical view; 15,16—*Gavelinopsis* sp. 1: 15—spiral view; 16—umbilical view; 17—*Sphaeroidina bulloides* d'Orbigny in Deshayes, 1828, apertural view; 18,19—*Amphistegina gibbosa* d'Orbigny, 1839, 18—side view showing the aperture; 19—side view; 20—*Resigella moniliformis* (Resig, 1982), side view.

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