

Paleoceanography and Paleoclimatology

RESEARCH ARTICLE

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Key Points:

- For the first time, drill holes in planktonic Foraminifera from the western South Atlantic were compared with paleoceanographic proxies
- Paleo productivity of the western South Atlantic was reconstructed using assemblage and geochemical indexes for the last 46 kyr
- Paleo productivity estimates and bioerosion rates of planktonic foraminiferal tests show a strong relation during late Quaternary

Supporting Information:

- Supporting Information S1
- Data Set S1
- Data Set S2
- Data Set S3
- Data Set S4

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Bioerosion on Late Quaternary Planktonic Foraminifera Related to Paleo productivity in the Western South Atlantic

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Abstract Planktonic Foraminifera are widely used in paleoceanographic reconstructions, although studies of their trophic interactions are still rare, especially those focusing on predation. Drilling holes are the most frequent traces of bioerosion in foraminifer tests, but environmental factors that control bioerosion are not yet understood. To determine if paleoceanographic variables are associated with bioerosion rates in late Quaternary planktonic foraminifers of the western South Atlantic, geochemical and assemblage analyses were made on a 46 kyr record from a piston core. An age model was constructed based on 10 AMS ¹⁴C dates. To reconstruct the paleo productivity, $\delta^{13}\text{C}$, benthic/planktonic foraminifer and the relative abundances of *Globigerina bulloides* and *Globigerinoides ruber* (high and low productivity, respectively) were used. Bioeroded tests were counted and found in 21 of the 25 identified species, with frequencies ranging from 8.84% to 16.7%. Bioerosion was different in two groups identified by cluster analysis, with a higher intensity during glacial times, showing a strong correlation with paleoceanographic fluctuations. Paleo productivity estimates and bioerosion rates show a significant correlation, suggesting that bioerosion is more frequent in eutrophic environments and more inhibited in oligotrophic conditions. However, even with a strong correlation between bioerosion and productivity, there is also a negative correlation with sea surface temperature in the study area. Since conditions that promote higher productivity are accompanied by a decrease in surface temperature, the precise distinction between the influence of both variables is hampered. Further research will allow us to explore the potential of planktonic foraminiferal bioerosion as a tool in paleoceanographic studies.

1. Introduction

The patterns of distribution and abundance of planktonic Foraminifera have often been associated with the resources necessary for their survival, reproduction, and fundamental niche; however, part of their realized niche includes predation and parasitism, which remain largely unexplored. To refer to the interactions that result in the ingestion of foraminifers, Hickman & Lipps (1983) introduced the term “foraminiferivory.”

This phenomenon occurs mainly in an accidental and nonselective way, and, due to the difficulty of observations both in situ and in a controlled environment, its evidence is almost always indirect, generally consisting of gut content analysis of invertebrates and vertebrates (Culver & Lipps, 2003). Another difficulty in recognizing foraminiferivory is the damage caused to the tests in this process. Such damage can be caused by the differential dissolution within the acidic stomach contents of consumers (Herbert, 1991), also by shell fragmentation by crushing (Berger, 1971; Gudmundsson et al., 2000), making them, sometimes, unrecognizable. There are also records of shells that can pass through the digestive tract of these organisms without suffering damage and even individuals that remain alive after this process (Goldbeck et al., 2005).

In an extensive review of several records of parasitism and predation in planktonic and benthic foraminifers over 100 years, Boltovskoy and Wright (1976) questioned the difficulty in knowing whether foraminifers are selectively chosen or accidentally ingested when their remains are found in the stomach contents of other organisms. In view of this, Lipps (1983) categorized the records of studies reporting the consumption of foraminifers between accidental or selective and noted that the activities of these accidental consumers can

drastically reduce the biomass of foraminiferal populations, although they constitute a small part of their food items. On the other hand, Culver and Lipps (2003) presented studies with species of scaphopods specialized in the consumption of foraminifers, which can sometimes become their exclusive source of food.

In addition to the accidental form, foraminiferivory can still leave traces more suggestive of an intentional interaction on the part of consumers than the stomach content: the boring holes. These drillings are bioerosional structures caused mainly by predators and parasites to penetrate the interior of the chambers and access the protoplasm (Boltovskoy & Wright, 1976). However, even in these cases, the protoplasm may not be the main target of bioeroders, who can simply seek refuge inside the chambers or a substrate to fix themselves on, characterized as an interaction different from predation and parasitism (Culver & Lipps, 2003).

The records of these traces are extremely rare for planktonic Foraminifera (Nielsen, 1999; Nielsen et al., 2003; Nielsen & Nielsen, 2001; Sliter, 1971), and this scarcity is even more evident when compared to the quantity of studies that report such marks of bioerosion in the tests of benthic foraminifers (e.g., Arnold et al., 1985; Collen, 1973; Douglas, 1973; Hickman & Lipps, 1983; Malumian et al., 2007; Nielsen, 2002; Reymont, 1966; Sengupta & Nielsen, 2009; Sliter, 1975).

From the bioerosion records, characterized by boring holes in planktonic foraminifers, only Nielsen et al. (2003) make an association between these traits and environmental variables, in this case for the late Pleistocene and Holocene. In general, this attempt to unveil patterns related to foraminiferivory has been carried out in a few studies with both fossil and recent Foraminifera (Malumian et al., 2007; Sliter, 1971, 1975).

According to McIlroy (2004), ichnofossils are important sources of information on animal behavior in response to their environment and are commonly specific to particular environmental conditions. In this way, paleoenvironmental reconstructions based on these features are possible but extremely difficult when the ecological interactions of the group are still not understood. Thus, here we present a case study of bioerosion on late Quaternary planktonic Foraminifera of the Pelotas Basin and its correlation with paleoproductivity and paleotemperature proxies for the last 46 ka at the southwest Atlantic Ocean.

2. Regional Setting

The Pelotas Basin is a Mesozoic basin formed during the opening of the South Atlantic Ocean (Miranda, 1970) and comprises the southernmost portion of the Brazilian Continental Margin, between the parallels 28°40'S and 34°S (Figure 1). This basin is influenced in the offshore portion by the Brazil Current (BC), a surface current that transports the warm ($T > 20^{\circ}\text{C}$) and saline ($S > 36$) tropical water (TW; Silveira et al., 2000). The BC flows along the South American Margin until it meets the Malvinas Current (MC), a surface current that detaches as a northward flowing branch of the Antarctic Circumpolar Current (ACC), carrying cool ($T < 15^{\circ}\text{C}$) and less saline ($S < 34.2$) water (Peterson & Stramma, 1991). The meeting of BC and MC reaches the Brazil-Malvinas Confluence (BMC) at approximately 39°S (Piola & Matano, 2001).

The BMC forms a large meander that separates to the south of the continental margin (Piola & Matano, 2019) and varies seasonally and interannually, reaching its northernmost position in the austral autumn and winter and its southernmost in spring and summer, thus influencing the distribution of nutrients along the continental shelf off the coasts of Argentina, Uruguay, and southern/southeastern Brazil (González-Silvera et al., 2006).

On the eastern South American Coast, there are two sources of freshwater and nutrients to the continental shelf benefiting plankton biomass growth (Figure 1). These sources are (i) the Río de la Plata Estuary (RPE) draining the second largest hydrographic basin in South America, and (ii) the largest lagoon complex in South America, the Patos-Mirim Lagoon system (PMLS) (Oliveira et al., 2015) with a 10 times smaller water discharge than the Río de la Plata (Marques et al., 2009). In the austral winter, the Río de la Plata plume flows northwards reaching the Santa Marta Cape (28°36'13.9"S) (Pimenta et al., 2005; Piola et al., 2005) or even lower latitudes, having been recorded as far north as 23°S under favorable wind conditions (Campos et al., 1999).

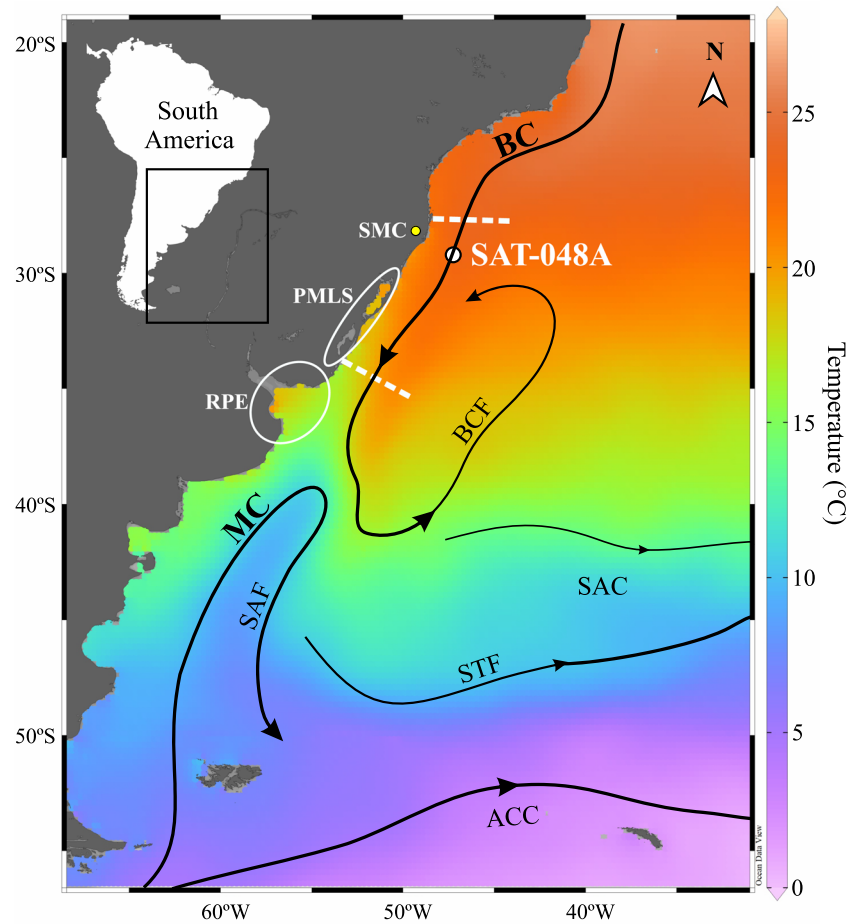


Figure 1. Study area at the western South Atlantic. Locations of the Pelotas Basin (delimited by dashed white lines); core SAT048A (white circle); the Patos-Mirim Lagoon System (PMLS); the Río de La Plata Estuary (RPE); the Santa Marta Cape (SMC). Mean annual sea surface temperature (SST, °C) (Locarnini et al., 2013) and main modern surface currents (modified from Peterson & Stramma, 1991). Brazil Current (BC); Malvinas Current (MC); Brazil Current Front (BCF); Subantarctic Front (SAF); Subtropical Front (STF); South Atlantic Current (SAC); Antarctic Circumpolar Current (ACC). Plotted with Ocean Data View (ODV, Schlitzer, 2020).

3. Materials and Methods

The SAT048A piston core was collected by FUGRO for the Brazilian National Petroleum Agency (ANP) and transferred to the *Laboratório de Oceanografia Geológica* at the *Universidade Federal do Rio Grande (FURG)*. The core was collected on the continental slope of the Pelotas Basin (29°11'52.110"S, 47°15'10.219"W; 1,542 m.b.s.l.; Figure 1), with a recovery of 315 cm. The core is composed mainly by hemipelagic mud rich in carbonates interlaced with thin layers rich in organic matter. Fifty samples of the core SAT048A were analyzed for foraminiferal assemblages and bioerosion. The slides containing the foraminifers are deposited at the *Laboratório de Microfósseis Calcários* of the *Departamento de Paleontologia e Estratigrafia* from the *Instituto de Geociências* of the *Universidade Federal do Rio Grande do Sul (LMC, IGeo, UFRGS)*.

3.1. Sample Preparation and Assemblage Analyses

Samples of approximately 10 cm³ of sediment were wet sieved through a 63 μm mesh, dried at < 60 °C, and sieved again to obtain the fraction greater than 150 μm. Sampling was performed with spacing ranging from 2.5 to 12 cm.

The planktonic foraminifer census counts were performed on 50 samples containing at least 300 planktonic specimens and counting benthic foraminiferal abundances as well. Subsequently, planktonic foraminifers were identified at a specific level and arranged in multicell slides. The taxonomic criteria for identification

followed Bé (1967), Bé et al. (1977), Bolli and Saunders (1985), Hemleben et al. (1989), and Schiebel and Hemleben (2017).

3.2. Stable Isotopes and Age Model

The age model for the core is based on 10 AMS ^{14}C dates using monospecific samples of planktonic Foraminifera (approximately 1,000 shells of *Globigerinoides ruber*) (see Supporting Information Text S1, Figure S1, and Table S1). Except for a few samples displaying less translucent shells suggesting dissolution and scarce scanning electron microscopy (SEM) images showing recrystallization, the shells were overall well preserved and with no significant evidence of overgrowth.

The radiocarbon dating was performed at the Radiocarbon Laboratory of the Physics Institute of Universidade Federal Fluminense (LAC-UFF). The ^{14}C ages were calibrated using the Calib 7.1 software (Stuiver & Reimer, 1993) and the Marine 13 calibration curve (Reimer et al., 2013), considering a ΔR of 54.0 ± 42.0 applied to the base correction data for Reservoir Effect (Marine Reservoir Correction Database) with ages from Nadal de Masi (1999), Angulo et al. (2005), and Alves et al. (2015).

Isotopic compositions of both oxygen and carbon ($\delta^{18}\text{O}$ and $\delta^{13}\text{C}$) of benthic foraminifers (*Uvigerina* spp.) were performed with approximately seven individuals larger than 250 μm from each sample. The analyses were performed with a Thermo Scientific MAT-253 mass spectrometer, coupled to a Kiel IV carbonate device, by the Laboratory of Stable Isotopes of the University of California, Santa Cruz (SIL-UCSC). All results are expressed relative to the Vienna Pee-Dee Belemnite (VPDB) standard.

3.3. Paleoproductivity and Paleotemperature Estimates

Indicators used for paleoproductivity estimates were (i) the relative abundance of *Globigerina bulloides* (related to high productivity; Sautter & Thunell, 1991; Conan & Brummer, 2000; Shrivastav et al., 2016) and *G. ruber* (associated with low productivity; Kroon et al., 1991; Conan et al., 2002; Toledo et al., 2008); (ii) the ratio between benthic and planktonic foraminifers (e.g., Berger & Diester-Haass, 1988; Loubere, 1991); and (iii) the benthic $\delta^{13}\text{C}$ isotopic curve (Sen Gupta, 2003). Relative abundances of the planktonic menardiiform plexus (*Globorotalia menardii*, *Globorotalia tumida*, and *Globorotalia flexuosa*) (Vicalvi, 1999), *Globigerinella calida* (Retailleau et al., 2011), and warm and cool species ratio (see Table S2) (Kucera, 2007) were used as indicators of warm waters and *Neogloboquadrina pachyderma* (Boltovskoy et al., 1996) relative abundances as a cool water species indicator.

Correlation tests between paleoproductivity estimates and bioerosion were performed using Pearson and Spearman's correlation coefficients, with a significance of $\alpha = 0.05$. The normality of the data was tested using the Shapiro-Wilk test.

It should be noted that such indicators are indirect and not exclusively dependent on productivity or temperature and may thus reflect other environmental and ecological variables.

3.4. Cluster Analysis

In order to identify similarities between the core samples, a cluster analysis (Mode Q) was performed. The similarity coefficient Bray-Curtis and UPGMA strategy (Unweighted Pair Group Method using Arithmetic Averages) with a data matrix of relative abundances of species with an abundance greater than 2% were used. The matrix variables were transformed with $\sqrt{x + 0.5}$ to avoid deviations from adjustment to the normal curve and reduce the heterogeneity of the variances. The cut-off level adopted was 0.12.

A multivariate analysis of variance with permutation (PERMANOVA; Anderson, 2001) was performed to test the differences between the groups identified based on a Bray-Curtis similarity matrix. The level of significance was set at $\alpha = 0.01$. To represent distance multivariate similarity between samples in a 2-D space, an nMDS (nonmetric multidimensional scaling) was performed. Before performing the nMDS, the original matrix of biological data was doubly transformed, initially dividing all values by the maximum abundance of the columns and later by the sample with the greatest abundance of foraminifers. These transformations were performed using the “decostand” function of the “vegan” package (Oksanen et al., 2019). nMDS was performed with the “metaMDS” function, configured for two dimensions ($k = 2$).

3.5. Bioerosion

Planktonic foraminifera containing traces of bioerosion were selected and separated from the samples for counting. Shells were checked for the presence of boring holes, characterized by complete opening of the wall (Figure 2a), and pits, generated by incomplete perforations that did not fully penetrate the wall (Figure 2b). The terminology used follows Nielsen and Nielsen (2001).

All analyses were performed with a Zeiss stereomicroscope, model Stemi 508, and fixed magnification of 100X, to prevent the alteration between the samples by using different lenses, magnifications, and illumination. Images were also obtained with a SEM at the Microscopy and Microanalysis Center (CMM) at UFRGS for a more detailed documentation of the bioerosion traces.

In addition to the aforementioned criteria, the selection of holes and pits with smooth and regular margins, circular to semicircular and oval to semioval, was used to distinguish traces of biotic origin from those caused by dissolution (Brom, 2014; Klompmaker et al., 2019; Kowalewski, 1993, 2002 and references therein) (Figures 2c–2e). The trace characteristics were used solely as a record of interaction between two organisms, without discussion of the nature of the interaction, being outside the scope of the present report, but should be addressed in upcoming studies. Therefore, for the purpose of comparison with other findings, it is assumed that the cause of bioerosion may be related to both predation and parasitism.

The frequency of bioeroded planktonic foraminiferal associations, which allows determining the potential rates of these interactions over time, was modified from the equation suggested by Kowalewski (2002): $EI: AF = \frac{\sum BA}{\sum TA} * 100$, where AF is the assemblage frequencies, BA is the number of planktonic foraminifer specimens in each sample with at least a trace of bioerosion, and TA is the total number of planktonic foraminifera per sample.

To define the correlation between the relative abundance of species in the samples and the proportion of bioerosion for each species, both in the groups formed by the cluster analysis and for species, the Pearson correlation coefficient (r) and the correlation coefficient of Spearman (ρ) were employed. The Shapiro-Wilk test was used to test the normality of the data, with the level of significance admitted for the $\alpha = 0.05$ correlations.

The Mann-Whitney U test was used to assess the association between pairs of groups defined in the cluster analysis and bioerosion rates and the Kruskal Wallis (KW) test for groups and subgroups. The significance value adopted was $\alpha = 0.05$.

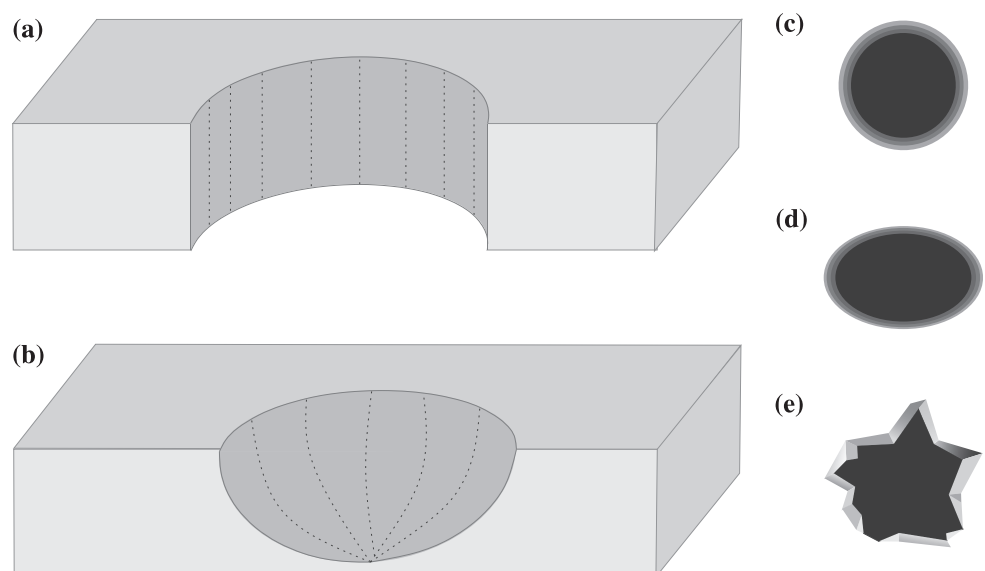


Figure 2. Schematic representation, in cross section, of holes (a) and pits (b) identified as traces of bioerosion, and representation of circular (c) and oval (d) holes with smooth edges characteristic of bioerosion, and holes with angular edges caused by dissolution (e).

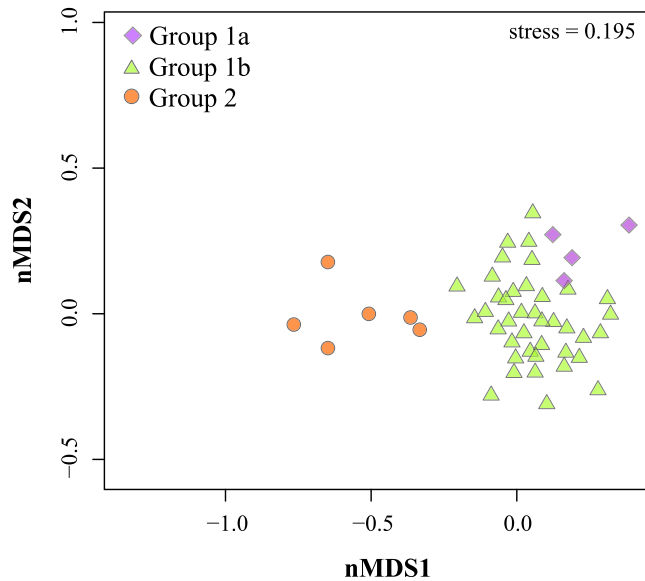


Figure 3. nMDS ordination comparing distinct groups and subgroups according to the assemblage composition of planktonic foraminifera. Symbols represent samples.

3.6. Analysis of Time Series

To determine whether the estimates related to paleoproductivity and bioerosion showed a trend, positive or negative, over time, and if such variations are statistically significant, the Mann-Kendall Test (S) was applied with a significance level of $\alpha = 0.05$. All statistical analyses were carried out using the language R (R Core Team, 2019).

4. Results

Of 20,216 individuals analyzed, 25 species belonging to 14 genera were identified. Overall, the most abundant species was *G. ruber* (34.44%), and another four species showed abundances greater than 10%, namely, *Globigerinita glutinata*, *G. bulloides*, *Neogloboquadrina incompta*, and *Globoconella inflata*. Three species obtained maximum relative abundances below 1%: *Turborotalita humilis*, *Candeina nitida*, and *Dentigloborotalia anfracta* (Table S3).

In 47 of the 50 samples analyzed, *G. ruber* dominated the planktonic foraminifer associations and reached up to 56.03% at 5.7 ka BP, obtaining smaller relative abundances in older samples, with a minimum of 22.41% at 45.4 ka BP. In the other three samples (ages of 25.9, 43.4, and 45.4 ka BP), *G. bulloides* presented relative abundance greater than *G. ruber* and, although it practically shares with

G. glutinata the second largest relative abundance, over time the relative abundance of *G. bulloides* displayed more expressive oscillations. This is evidenced by the difference of 32% between the minimum and maximum relative abundances of *G. bulloides* compared to 16% for the same parameter in *G. glutinata*.

4.1. Cluster Analysis

Two distinct groups were identified in the planktonic foraminiferal associations using cluster analysis (Figure S2b). The first and largest group includes samples from the older portion, corresponding to the late Pleistocene (~12 to 46 ka BP). This group can further be subdivided into two, with one of the subgroups comprising most of the samples from the glacial interval (~12 to 41 ka BP) and the other, small, including the oldest samples (~42 to ~45 ka BP). The second group corresponds to the youngest samples, from the Holocene (<12 ka BP) (Figure S2a). PERMANOVA demonstrated that the groups identified in the cluster analysis are significantly different ($F = 22.093$; $p < 0.001$), as well as the subgroups identified within group 1 ($F = 14.933$; $p < 0.001$). The nMDS, in Figure 3, represents dissimilarities in groups distinguished with cluster analysis in a low-dimensional space for simplified viewing.

4.2. Bioerosion

Traces of bioerosion were found in 21 of the 25 identified species. Only *Globigerinoides conglobatus*, *T. humilis*, *D. anfracta*, and *C. nitida* did not present bioerosion traits; however, these species together represent less than 0.4% of the total analyzed specimens. The total frequency of bioerosion was 14.45% (2,921/20,216), and throughout the core, the frequencies of bored individuals between samples varied from 8.84% to 16.7%, with an average of 10.6%.

Of the five species whose total relative abundances were greater than 5% (Figure 4), *G. glutinata* (687/3,081) recorded the highest proportion of bioerosion among all species and *G. ruber* (770/6,963) the lowest. The values of relative bioerosion rates, for the five most abundant species, are listed in Table 1.

The proportion of bored specimens per species did not increase or decrease significantly when compared to an increase in abundance of *G. bulloides* ($r = 0.22$; $p = 0.11$), *G. glutinata* ($\rho = -0.07$; $p = 0.59$), *N. incompta* ($r = 0.09$; $p = 0.5$), and *G. inflata* ($\rho = 0.0008$; $p = 0.99$) for all samples. *G. ruber* showed a significantly weak negative correlation ($\rho = -0.31$; $p = 0.026$), indicating that bioerosion decreases reasonably in this species when its abundance is high and vice versa. Using species with abundances greater than 5% in the entire core, no group showed significant correlation between species abundance and the proportion of bored

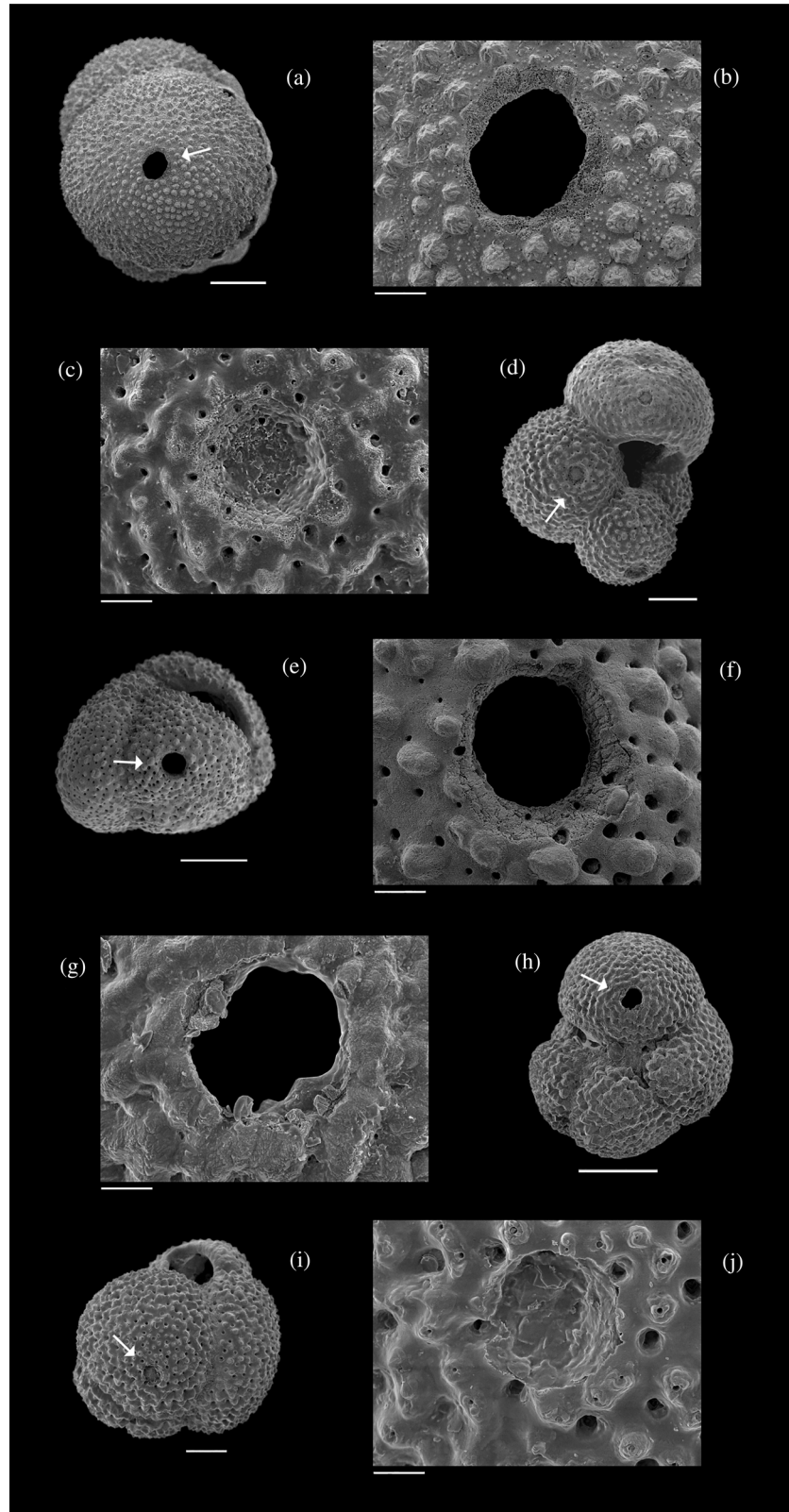


Figure 4. Traces of bioerosion in species with the highest frequencies of bored individuals, when abundances greater than 5% are considered. (a, b) *G. glutinata*; (c, d) *G. bulloides*; (e, f) *G. inflata*; (g, h) *N. incompta*; (i, j) *G. ruber*. Scale bars: panels (a), (d), and (i) = 50 μm ; panels (e) and (h) = 100 μm ; panels (b), (c), (f), (g), and (j) = 10 μm .

Table 1
Bioerosion Indicators for Species With Total Relative Abundance Greater Than 5%

Species	Relative bioerosion per species (%)			
	Total	Maximum	Average	Minimum
<i>Globigerinita glutinata</i>	22.30 (687/3,081)	37.5 (18/48)	22.7	12.2 (5/41)
<i>Neogloboquadrina incompta</i>	16.62 (263/1,582)	37.5 (6/16)	16.5	0 (0/3)
<i>Globigerina bulloides</i>	16.29 (491/3,014)	29.41 (5/17)	15.86	0 (0/34)
<i>Globoconella inflata</i>	13.58 (202/1,488)	100 (5/5)	14.8	0 (0/5)
<i>Globigerinoides ruber</i>	11.06 (770/6,963)	20 (18/90)	11.5	4.17 (8/192)

Note. From left to right, the columns represent the total relative bioerosion of each species (for the entire set of samples analyzed) and maximum, average, and minimum values (between samples). The *n* population is indicated in parentheses next to each data.

individuals: Group 2 ($\rho = -0.4$; $p = 0.51$) (Figure 5a); Group 1b ($r = -0.37$; $p = 0.53$) (Figure 5b); and Group 1a ($r = -0.41$; $p = 0.49$) (Figure 5c).

Bioerosion rates over time (Figure 6a) reveal a significant decreasing trend toward the recent ($S = 303$, $p = 0.011$), with peaks at 45 and 20 ka BP. The comparison of bioerosion rates between the groups distinguished in the cluster analysis revealed that Groups 2 and 1 are significantly distinct ($W = 2$; $p < 0.05$), as well as Group 2 and the Subgroups 1a and 1b ($H = 20.393$; $p \leq 0.05$) (Figure 7). Pairwise analyses between groups and subgroups (post-hoc Dunn's test < 0.05) showed all cluster units are different from each other.

4.3. Paleoproductivity and Paleotemperature Estimates

The relative abundances of the planktonic menardiiform plexus reveal an abrupt rise starting around 9 ka BP ($S = -365$; $p < 0.05$) (Figure 6h). *G. calida* ($S = -203$; $p < 0.05$) (Figure 6f) and the warm and cool species ratio ($S = -785$; $p < 0.05$) (Figure 6g) present a similar pattern, although indicating an earlier warming starting around

14 ka BP. The *G. bulloides* relative abundance (Figure 6d) shows a clear downward trend toward the younger samples ($S = 629$, $p < 0.05$); the same can be observed for the *N. incompta* relative abundance ($S = 413$, $p < 0.05$) (Figure 6i), but with small differences in the oldest samples. Such trend is also registered for the proportion of benthic foraminifers in relation to planktonic ones ($S = 573$, $p < 0.05$) (Figure 6c).

G. ruber relative abundances display a significant gradual increase toward the recent ($S = -709$; $p < 0.05$) (Figure 6e). The carbon isotope curve ($\delta^{13}\text{C}$) of *Uvigerina* spp. reveals a progressive increase in values toward the recent ($S = -389$, $p < 0.05$) with an expressive rise close to the beginning of the Holocene (Figure 6b).

When compared to bioerosion rates, throughout time, all estimates related to paleoproductivity were significant. The *G. bulloides* relative abundance shows a moderate positive correlation ($r = 0.59$; $p < 0.05$), while the *G. ruber* relative abundance, with an opposite pattern, shows a negative correlation ($\rho = -0.33$; $p = 0.02$). The benthic and planktonic foraminifer ratio has a significant, weak correlation ($\rho = 0.39$; $p = 0.005$), and the $\delta^{13}\text{C}_{\text{Uvi}}$ values are moderately correlated but in a negative way ($r = -0.4$; $p = 0.004$).

5. Discussion

Although it is not uncommon to find specimens of planktonic foraminifers with traces of bioerosion, this phenomenon has been little explored in the scientific literature, especially for this group. In fact, no work has been found using a quantitative approach to estimate bioerosion in planktonic foraminifers. Several studies citing bioerosion in planktonic foraminifers (e.g., Nielsen, 1999; Nielsen et al., 2003; Nielsen & Nielsen, 2001) present only the number of samples and individuals analyzed but not the number of bioeroded specimens. In this way, our outcomes are not likely possible to be compared with previous studies.

However, there are several studies that quantitatively analyze bioerosion in benthic foraminifers (e.g., Arnold et al., 1985; Shroba, 1993; Sliter, 1971). Although the processes that govern their distribution and abundance are different than in planktonic species (Sen Gupta, 2003), the comparison of bioerosion rates between planktonic and benthic groups can be performed, but only to compare the intensity of bioerosion in both communities.

It is worth mentioning that the possibility of these traces being produced by benthic organisms has already been considered. However, records of planktonic individuals containing holes, but already covered with a new layer of calcite with the same texture as the original wall (Nielsen et al., 2003), suggest that the healing process occur after the interaction (Bé & Spero, 1981). This reinforces that, in our case, it is likely an interaction that actually took place on the plankton.

On the other hand, almost the entire community settling from the upper water column is made up of empty tests from individuals that have undergone reproduction or died before this stage, with a portion consisting of organisms still with protoplasm (Schiebel & Hemleben, 2017). The hypothesis that the presence of

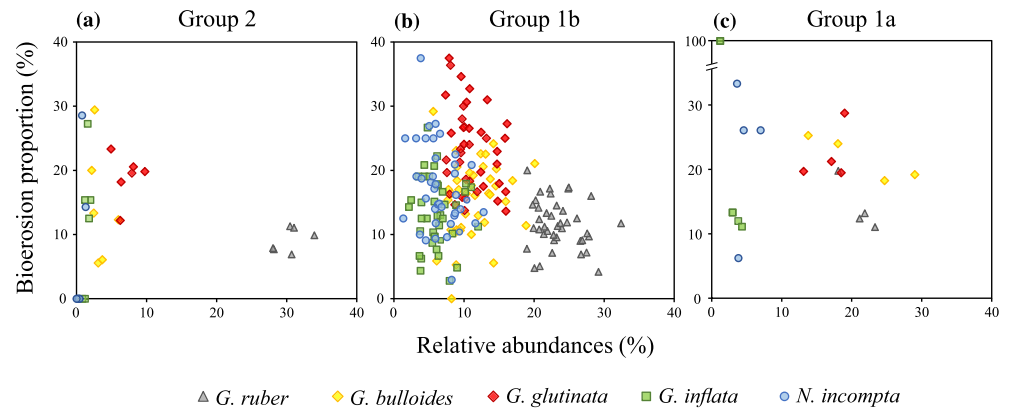


Figure 5. Relative abundances of species samples for (a) Group 2, (b) Group 1b, and (c) Group 1a versus the proportion of bioerosion in each species. Broken y axis in panel (c) was necessary for plotting a *G. inflata* sample where all (few) specimens were bioeroded.

protoplasm must mean that individuals who have lost buoyancy are still alive after reaching the bottom comes from the premise that decomposition is fast enough in the water column (Parker, 1954; Petró et al., 2018; Phleger, 1960).

However, Boltovskoy and Lena (1970), performing a series of experiments, found that the decomposition can last from weeks to months. This could allow the presence of partially intact organisms in places with shallow depth and high sedimentation rates, preventing this decomposition from occurring entirely in the water column. It seems unlikely that even if they were still alive, planktonic foraminifers that reach the bottom would maintain their metabolism long enough to heal the boring hole. Nevertheless, the hypothesis that part of the tests suffered bioerosion by detritivorous organisms after settling to the seafloor with the protoplasm still present cannot be ruled out.

Anyway, the focus of the present study is not on the process itself, but on the potential for paleoceanographic studies. Thus, in the next sections, assemblage composition variations, the observed bioerosion rates, and the relationship between bioerosion and paleoproductivity over time are discussed, respectively.

5.1. Assemblage Composition

The identification of the samples that comprise the Holocene (<11.7 ka BP) as a different group from the rest of the core, evidenced by the cluster analysis (Figure S2b), reveals how the distribution of local assemblages reflects the environmental variables associated with the characteristic fluctuations of the late Quaternary.

The core species composition, which varies over time with a characteristic alternating dominance between warm and cool water assemblages, suggests the influence of BC and MC in the study area (Boltovskoy et al., 1996). This alternating dominance can be better visualized in Figure 8. Just as on a seasonal scale, in glacial periods, there is a shift to the north of the BMC caused by the strengthening of the ACC from which the MC originates (Laprida et al., 2011). In this configuration, the BC, which brings the tropical and subtropical biotas, is weakened, thus the relative abundance of species coming from low latitudes decreases. Conversely, when the MC and/or Río de la Plata plume reach the south/southeast of Brazil, a significant increase in the relative abundance of cool to temperate foraminifers is expected (Boltovskoy et al., 1996), as indicated in samples from Group 1 (Figure S2b).

5.2. Bioerosion Rates in Planktonic Foraminifera

Several marine taxa with mineralized skeleton have been studied as to the possible perforations in their shells, which are generally attributed to predation or parasitism. The use of the frequency of these traits to estimate their intensity is widespread, and one of the most important tools for quantitative analysis for bioerosion in the fossil record (Kowalewski, 2002).

Vermeij (1987) characterized bioerosion intensity in bivalves as “frequent” when the predation rates in species with more than 20 individuals are greater than 10%. Analyzing modern benthic foraminifer species from

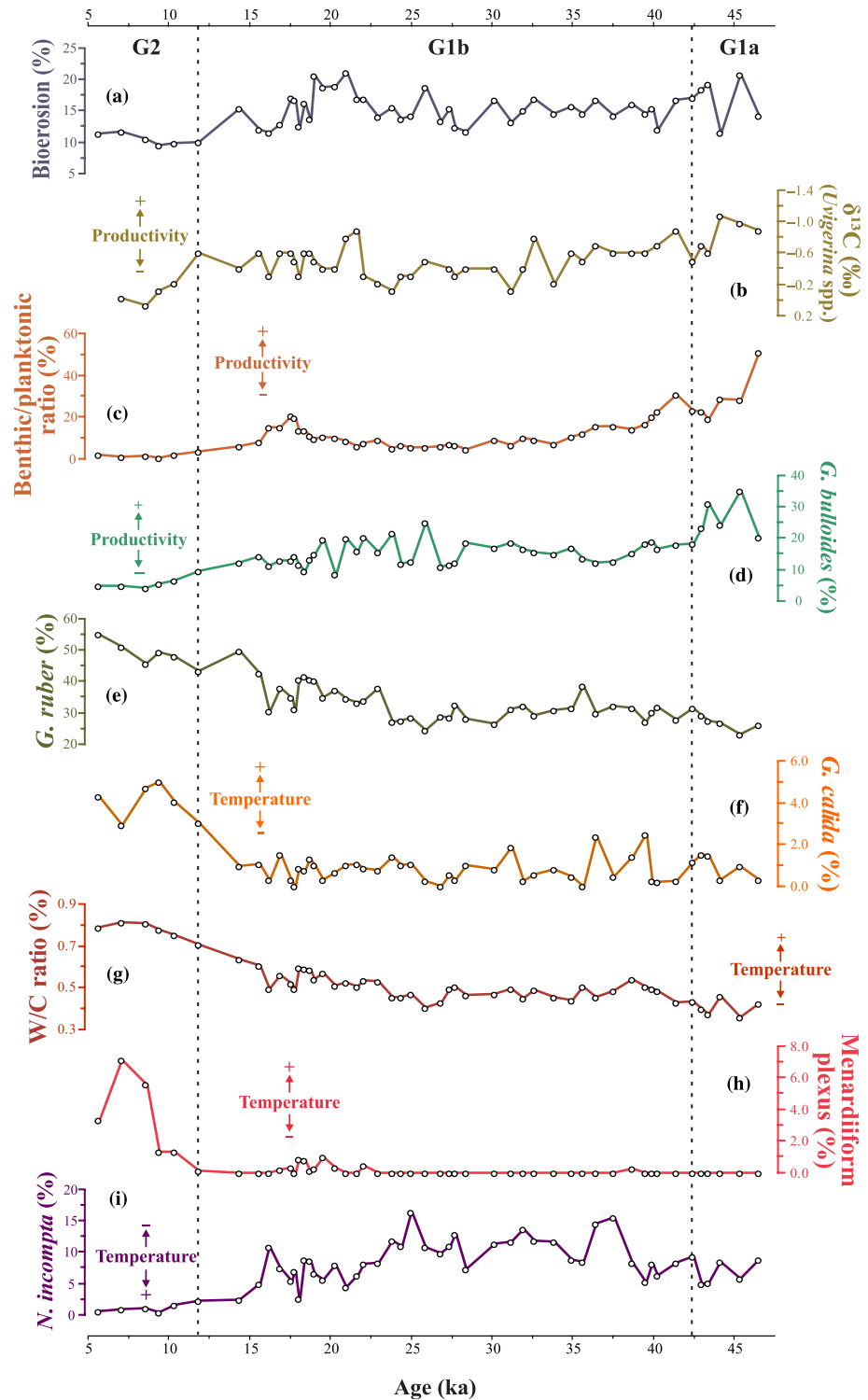


Figure 6. Proxies of paleoproductivity and paleotemperature plotted together with bioerosion through the time: (a) bioerosion frequencies; (b) $\delta^{13}\text{C}_{\text{Uvi}}$ (inverted scale); (c) benthic and planktonic foraminifer ratio; (d) *G. bulloides* relative abundance; (e) *G. ruber* relative abundance; (f) *G. calida* relative abundance; (g) warm and cool species ratio; (h) planktonic menardiiform plexus; and (i) *N. incompta* relative abundance. Dashed lines delimit groups and subgroups identified in the cluster analysis.

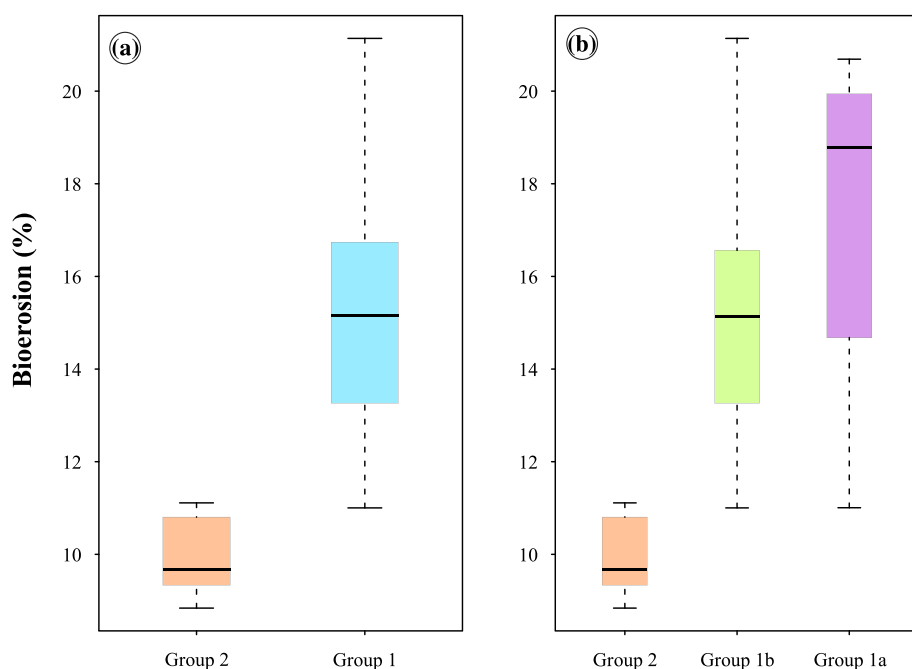


Figure 7. Box plots of the bioerosion frequencies between Groups 2 and 1 (a) and Group 2 in relation to Subgroups 1b and 1a (b). Colors correspond to each group and subgroups; center line, median; box limits, upper and lower quartiles; whiskers, lowest and highest data point still 1.5X interquartile range.

California, Sliter (1971) found predation frequencies of 6% to 8% in his samples, and comparing with samples from the Gulf of Mexico, he found frequencies of up to 16%. Malumian et al. (2007) characterized the frequency of 10% found for benthic foraminifers with predation holes as low, using the same criteria as Vermeij (1987).

If compared to the rates exposed above, the total frequency of bioerosion in this study of planktonic foraminifers (14.45%) can be classified as frequent, and even high for some samples (21.14%) or for some of the most abundant species (*G. glutinata*; 37.5%), mainly considering that bioerosion occurs much more intensely in benthic habitats (Allen & McAlister, 2007).

The analysis of the proportion of bioeroded individuals compared to the number of specimens per sample for the five most abundant species demonstrates that bioerosion does not occur preferably in high abundances. This is valid for the three sample groups (Figure 5). That is, the variations in the observed bioerosion rates do not represent an artifact of the sampling effort and bioerosion did not necessarily occur in the most abundant species.

In many studies on predation in marine invertebrates and benthic foraminifers (e.g., Arnold et al., 1985; Carriker & Yochelson, 1968; Malumian et al., 2007; Sliter, 1971), the abundance of predated populations is crucial for the intensity of bioerosion. This is because it is assumed that the encounter between the foraminifer and the bioeroding individual is more likely to take place when the density of the target population is high (Smith et al., 2018). When the most abundant species were analyzed separately, *G. ruber* was the only taxon that showed a significant correlation between taxon abundance and bioerosion rate, but a negative one. This suggests that the conditions that promote the presence of the bioeroding organism are probably not the same as those that favor the presence of this species.

5.3. Paleoproductivity and Paleotemperature

The bioerosion curve in planktonic foraminifers for the analyzed core (Figure 6a) indicates that this process was not constant over the last 46 ka and that bioerosion frequency is influenced by variables that fluctuate over time. With the separation of the bioerosion frequencies between the groups and subgroups, identified in the cluster analysis, it is possible to observe how the paleoceanographic and paleoclimatic fluctuations of this period were also decisive for bioerosion.

The last 40 ka in the subtropical Southwest Atlantic was marked by a trend of high productivity during the glacial periods and low productivity conditions during the Holocene (Pereira et al., 2018). The paleoproductivity estimates obtained for the SAT048A core (Figures 6b–6e) indicate that productivity in the Pelotas Basin started to decline

Planktonic foraminiferal provinces	Group 2	Group 1b	Group 1a
Tropical	24.18	13.88	6.74
Subtropical	53.46	35.88	31.78
Transitional	21.14	40.63	54.54
Subpolar-polar	1.21	9.62	6.94

Figure 8. Proportion of species (%) characteristic from each biogeographic planktonic foraminiferal province (Kucera, 2007) for each group defined in the cluster analysis. Color bars correspond to a graphical representation of the province's percentage in each cluster.

at the beginning of the Holocene and continued until 8 ka, as can also be seen in the bioerosion rates (Figure 6a). According to Voigt et al. (2015) and Gu et al. (2018), the position of the BMC was stable from the beginning of the Holocene to 8 ka BP, in a configuration further south than the present. This demonstrates that in addition to the variables associated with paleoproductivity, such as cooler sea surface temperatures (SSTs), a decrease in bioerosion since the Last Glacial Maximum could be mainly reflecting the low productivity conditions caused by the decrease in the influence of the Río de la Plata plume (Portillo-Ramos et al., 2019).

Bioerosion/predation in benthic and planktonic environments has been associated with productivity in some studies (e.g., Berger, 1971; Bohannan & Lenski, 2000; Leibold, 1989). This is observed because productivity is often the main factor influencing the size of the prey population; however, this is a complex relationship between variables that does not always correspond to the predicted model (Klompaker et al., 2019). According to Hemleben et al. (1989), there seem to be no exclusive consumers of planktonic foraminifers, so when productivity increases, it is likely that the natural number of possible predators will also increase, affecting the population of planktonic Foraminifera in that area by its consumption (Boltovskoy & Wright, 1976).

The correlation of bioerosion with the relative abundances of *G. bulloides* and *G. ruber*, proportion of benthic foraminifers, and carbon isotopes (Figures 6a–6e) suggest that their frequency is strongly influenced by the trophic conditions of seawater. Despite showing some limitations, these variables are widely used and are important indicators of paleoproductivity.

The $\delta^{13}\text{C}_{\text{Uvi}}$ showed a tendency to lower values at the older samples (Figure 6b). Smaller values of benthic $\delta^{13}\text{C}$ indicate that a greater proportion of the light isotope (^{12}C) is related to a greater supply of food to the seafloor as a consequence of a high primary productivity in the photic zone (Sen Gupta, 2003). The benthic and planktonic foraminifer ratio is another widespread way of inferring paleoproductivity conditions (e.g., Berger & Diester-Haass, 1988; Loubere, 1991). Along with the oxygenation of bottom waters, the supply of organic matter to the seafloor is the main controlling parameter in the structuring of benthic foraminiferal assemblages (Jorissen & Fontainer, 2007). When compared to bioerosion (Figures 6a and 6c), it can be seen that the main similarity of the curves resides on the oldest samples, where the bioerosion frequencies are higher.

The strongest correlation among the variables analyzed with bioerosion is the *G. bulloides* relative abundance. This is an opportunistic species that responds to organic particle increase and often dominates the planktonic foraminiferal assemblages in upwelling environments (Kucera, 2007; Schiebel & Hemleben, 2005). On the other hand, *G. ruber* has been used as an indicator for low-productivity conditions (Conan et al., 2002; Kroon et al., 1991; Toledo et al., 2008), and its relative abundance presents a negative correlation with bioerosion.

Our data indicate that bioerosion within the Pelotas Basin was primarily influenced by paleoproductivity, with negative correlations among warm water indicators and bioerosion rates. However, Nielsen et al. (2003) attributed temperature as the primary control on the presence of boring holes in cold water planktonic and benthic foraminifers. Therefore, we cannot rule out the fact that temperature may have some role to play on bioerosion of planktonic foraminiferal tests (Figure 6).

Furthermore, the negative correlation between the bioerosion frequency with the warm and cool species ratio (Figure 6g) and *G. ruber* relative abundance, along with the higher frequency of *G. calida* (Figure 6f) and planktonic menardiiform plexus (Figure 6h) (warm water indicators) and low *N. incompta* relative abundance (Figure 6i) (cool water indicator) in low bioerosion periods, indicates that bioerosion is inhibited in warm water conditions. Although the presence of the planktonic menardiiform plexus suggests warmer waters in the Holocene, it is also a reflection of a change in the configuration of global circulation that allowed it to reenter the Atlantic Ocean from the Indian Ocean as a whole (e.g., Peeters et al., 2004) and would not necessarily reflect a local temperature variation.

However, the decrease in temperature in the study region is usually associated with greater productivity, due either to the presence of cool waters from the MC or to the Río de la Plata plume, or even to seasonal upwelling processes. Thus, the influence of paleotemperature and paleoproductivity is difficult to disentangle.

6. Conclusions

Because bioerosion is commonly more intense at the sediment-water interface on the seafloor, it was expected that its frequency in planktonic foraminifers would be less expressive than in benthic ones. This demonstrates how the predation/parasitism pressure in planktonic species can be crucial for the standing crop of its populations, especially when observing the frequencies of individual species.

As the frequencies of bioerosion are not constant and do not seem to attend to a random distribution, it is natural to be related to processes that also oscillate. In addition to climate fluctuations in the Quaternary, the study area is affected by one of the largest fluctuations in temperature, salinity, and productivity in the South Atlantic.

The frequencies of bioerosion correspond, in general, to all tested paleoproductivity proxies. In two of them, the proportion of benthic foraminifers and $\delta^{13}\text{C}$ in *Uvigerina* spp., this correspondence could be observed only in the trend of the curves, but their oscillations seem to be out of sync. The *G. bulloides* relative abundance has a stronger correlation with bioerosion, oscillating in a similar way.

Paleoproductivity data may have noises that are primarily influencing bioerosion and masking the influence of other variables that fluctuate with it. As temperature is one of the factors that most influences the distribution and abundance of several taxa and fluctuates significantly in the study area over time, this variable could be determinant for bioerosion when not only the abundances of potential boring organisms are revealed but also the different species/groups to which they belong. In a period with warmer waters in the southwestern Atlantic, other communities may be occupying the study area in the Holocene that do not have foraminifers as a food source, a situation that would be reversed in glacial conditions.

Understanding the processes that govern bioerosion in planktonic Foraminifera can be crucial to assist in the inference of paleoenvironments when other data are scarce. However, such information should not be used in isolation, since carrying out paleoenvironmental reconstructions based on only one complex proxy, which depends on several variables, is at least risky.

Data Availability Statement

The data presented in this paper are available in 10.1594/PANGAEA.918325.

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