



Community structures and Taphonomic controls on benthic foraminiferal community from an Antarctic Fjord (Edisto Inlet, Victoria Land)

Giacomo Galli^{1,2,3}, Francesca Caridi⁴, Patrizia Giordano⁵, Caterina Morigi², Anna Sabbatini⁴, Leonardo Langone⁵

¹Department of Environmental Science Informatics and Statistics, Ca' Foscari University of Venice, via Torino 155, 30172, Venice, Italy

²Department of Earth Sciences, University of Pisa, via Santa Maria 56, 56126, Pisa, Italy

³Climate Geochemistry Department, Max Planck Institute for Chemistry, Mainz, Hahn-Meitner-Weg 1, 55128, Germany

⁴Department of Life and Environmental Sciences, Polytechnic University of Marche, via delle Brecce Bianche, 60131, Ancona, Italy

⁵Istituto di Polar Sciences, National Research Council (CNR), Via Piero Gobetti 101, 40129, Bologna, Italy

Correspondence to: Giacomo Galli (giacomo.galli@unive.it)

Abstract. Benthic foraminiferal assemblages are key indicators for reconstructing past environmental conditions due to their ecological preference and preservation potential. This study investigates the hard-shelled benthic foraminifera of Edisto Inlet; an Antarctic fjord located on the Northern Victoria Land Coast (Ross Sea). The Inlet is characterized by a well-preserved Holocene laminated sedimentary sequence, providing an invaluable tool to reconstruct local and regional environmental changes. Living and fossil assemblages from the upper 5 cm of sediment were analysed across five sites along an inner-to-outer fjord transect to assess their ecological preferences and preservation patterns. Sites located on the inner fjord are characterized by high accumulation rates, low dry densities, fine grain sizes, and elevated content of organic carbon, indicative of high phytodetrital input and anoxic, reducing conditions probably derived by the burial of fresh organic matter. The surface ~~sediments~~ at these sites host low-diversity low-densities living assemblages but are abundant in dead specimens, suggesting substantial mortality events probably linked to post-sea-ice breakup, high organic matter flux to the bottom, and oxygen depletion associated with low current activity. Total assemblages are dominated by calcareous (*Globocassidulina bitor*, *G. subglobosa*) and agglutinated (*Paratrochammina bartrami*, *Paratrochammina antarctica*) taxa, reflecting sluggish circulation along with a high input of fresh organic matter. A sharp decline in calcareous forms points to intense carbonate dissolution caused by the low redox ~~potential inside the sediment~~ that develops during the year. In contrast, transitional and outer sites show more diverse and better-preserved assemblages, including *Trifarina angulosa*, *Nodulina dentaliniformis*, *Reophax scoriurus* and *Globocassidulina* spp. among others, consistent with stronger bottom currents and more oxygenated conditions of the outer bay in respect to the inner fjord sites. The site located at the fjord mouth ~~reveal~~ distinct fossil faunas, likely shaped by ecological succession and/or dissolution, highlighting the high environmental variability of this setting. Resistant agglutinated species (*Pseudobolivina antarctica*, *Paratrochammina bipolaris*, *Miliammina arenacea*) dominate these areas, underscoring their potential value for **paleoenvironmental reconstruction**. Comparison with the succession of the palaeocommunity collected in a nearby marine sediment core (TR17-08) suggests recent improvements in bottom conditions and organic matter content, though key taxa have not recovered to Late Holocene (3600-1500 years BP) levels. These findings highlight the sensitivity of benthic foraminiferal communities to sea-ice dynamics, organic matter input, and hydrographic conditions in Antarctic fjord systems.



1. Introduction

How organisms distribute and what are the underlying causes of their spatial patterns is a long-standing question in ecology. Local studies are crucial to gain insight of the extant ecological patterns that could be lost due to climate change or anthropogenic activities especially in sensitive areas, such as the polar regions (Gutt et al., 2021; Ingels et al., 2012). Antarctica's remoteness and isolation make it an almost pristine environment in respect of the anthropogenic pressure; thus, an ecological characterization of this area might highlight the natural processes acting on the extant community as well as giving a background natural level for future monitoring studies.

In this study, we focus on the distribution of the living and recent benthic foraminifera, an important meiofaunal component of all aquatic ecosystems (Gooday, 1993; Langlet et al., 2023; Nomaki et al., 2008). Benthic foraminifera are marine unicellular eukaryotes capable of forming a shell (test) that covers the cytoplasm (Sen Gupta, 2003). Fossil assemblages of hard-shelled benthic foraminifera communities are especially important for paleoenvironmental studies due to their excellent preservation potential (Gooday, 2003; Murray, 2006). The composition of these communities is influenced by water masses characteristics, the nature and availability of Organic Matter (OM) at the seafloor, and the dissolved oxygen concentration, which makes benthic foraminifera reliable tracers of past marine environmental conditions (Gooday, 2003). In coastal Antarctica, these assemblages have been used to infer past changes in the water circulation pattern, glacial discharge regime, and sea-ice cover making them a valuable tool to gain insight on the connectivity between the cryosphere and the ocean (Kyrmanidou et al., 2018; Li et al., 2000; Majewski et al., 2018; Majewski & Anderson, 2009; Peck et al., 2015). Thus, the ecological preference of the modern foraminiferal community offers key information on the associations between the species and their environmental significance, which is crucial to constrain the past environmental evolution of a region. Furthermore, the comparison with the modern fauna and the fossil one is crucial to underpin the taphonomic controls that might hinge on the preservation on these key environmental tracers.

In Antarctica, study that analysed benthic foraminifera over the continental shelf have focused on the Antarctic Peninsula, along the western sector of the continent, and on the Weddell Sea (Bernasconi et al., 2019; Cornelius & Gooday, 2004; Ishman & Szymcek, 2003; Lehrmann et al., 2025; Mackensen et al., 1990; Majewski et al., 2023). One of the most studied areas are the sub-Antarctic Island, especially Admiralty Bay; a shallow fjord that has been extensively investigated for its benthic foraminiferal content (< 200 m water depth) (Majewski, 2010). In the Ross Sea, research was largely carried out on the southernmost edge of Victoria Land, especially McMurdo Sound and Terra Nova Bay (Gooday et al., 1996; Violanti, 2000). Moreover, studies that focussed on the continental shelf of this basin have been limited to sites located along the main troughs (Capotondi et al., 2018, 2020; Gooday et al., 1996; Violanti, 2000).

The focus of this study is Edisto Inlet a little fjord located on the northwestern tip of the Ross Sea, and what could it be a key site to investigate palaeoceanographic changes occurring throughout the Holocene (Fig. 1, Battaglia et al., 2024, Galli et al., 2025). In addition, the presence of a 3600-year long record of benthic foraminiferal assemblage provides a robust baseline for assess the ecological context of the modern communities by characterizing the changes in relative abundance of key



indicator species with known environmental succession that affected the benthic fauna throughout this interval (Dillon et al., 2022; Galli et al., 2025).

Hence, the main aspects of this study will be to 1) to characterise the differences between living and the fossil benthic foraminiferal assemblages, with the goal of identifying the key environmental drivers of their distribution and preservation, and 2) to contextualize the modern environmental state of the fjord by comparing recent communities with the succession of different paleo communities reconstructed from sedimentary records.

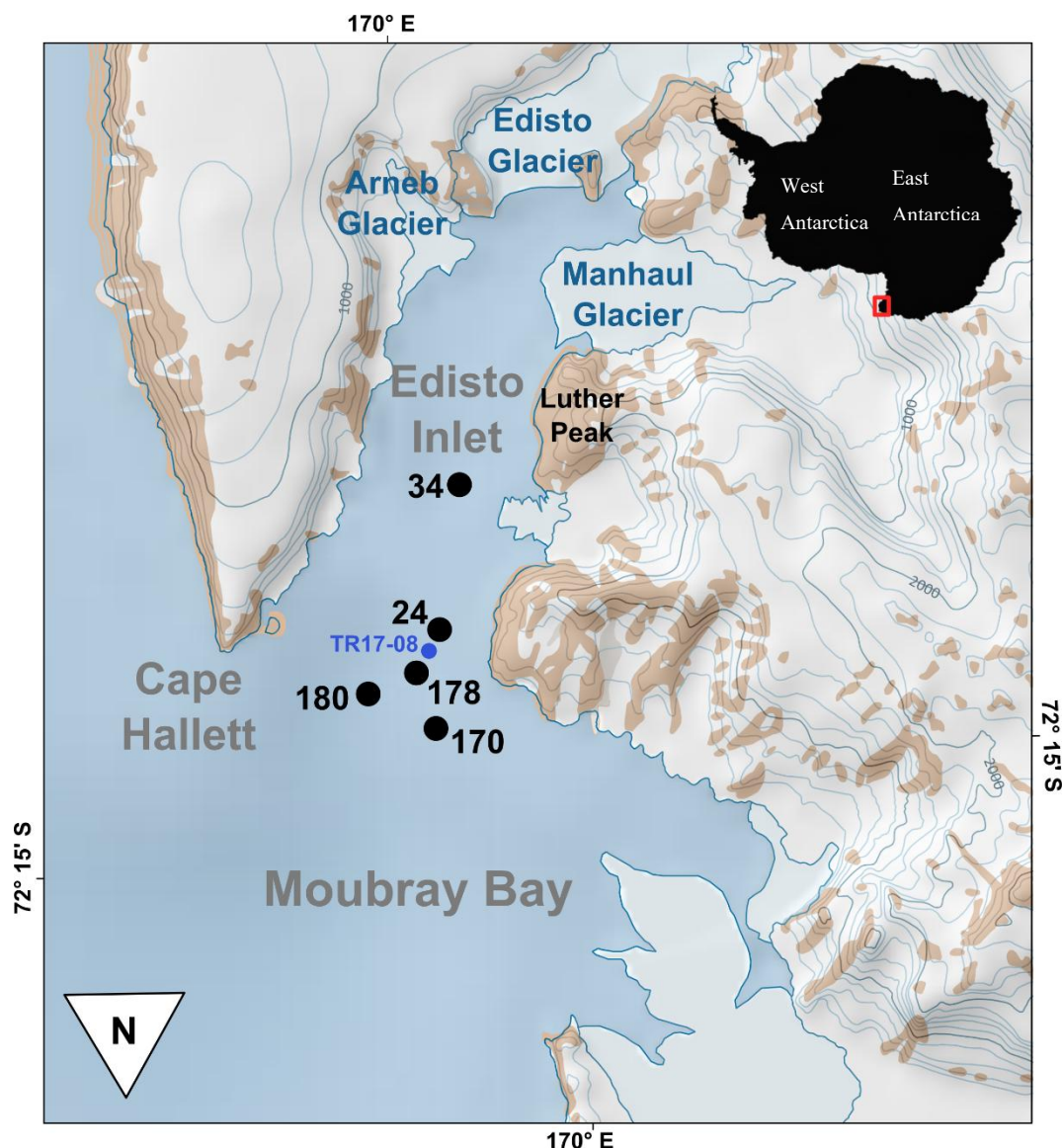


Figure 1. Location of the Edisto Inlet (red square) respect to Antarctica and relative location of site of sediment core retrieval inside the inlet (black dots). The previously investigated marine sediment core for the benthic assemblages (TR17-08) is indicated in blue.



80 1.1 Environmental Context

Edisto Inlet is narrow fjord located along the northern Victoria Land coast, in the northwestern part of the Ross Sea. The fjord is surrounded by 4 glaciers: Arneb Glacier, Manhaul Glacier, Edisto Glacier and a minor glacier next to Luther Peak (Fig. 1). The Inlet depth is between 400 and 500 m, and it is divided from the Moubray Bay by a sill with a height of about 100 m that shows a steeper flank on the eastern side ~~than the western one~~ (Battaglia et al., 2024).

85 The inlet is characterized by a seasonal cycle of landfast sea-ice: during the austral winter the sea-ice forms and covers the Inlet, and, over the beginning of the warming seasons, it thaws (Tesi et al., 2020). Differences in this seasonal behaviour can have a profound effect on the local benthic fauna: from 2-1.55 kyrs BP (Before Present: 1950 CE) the brittle stars *Ophionotus victoriae* was thriving, associated with stable interannual cycle of freezing and thawing of the sea-ice cover (Galli et al., 2024). Variability of these environmental patterns are also reflected in lamination structures observed in
 90 sediments, characterized by alternating dark and light laminae of different thickness (Galli et al., 2023; Tesi et al., 2020). These sedimentary features have been connected to first sea-ice break up over the spring (dark lamina), and ice-free conditions over the summer (light lamina) (Finocchiario et al., 2005; Tesi et al., 2020). This is further supported by the presence of two very distinct diatom associations: after the first break-up, diatom of the *Fragilariopsis* genus blooms, and a dark lamina is deposited. If ice-free conditions persist during the austral summer, reduced vertical mixing may further limit
 95 nutrient replenishment in surface waters, favouring the dominance of oligotrophic species like *Corethron pennatum* thus resulting in the deposition of light-colored laminae (Tesi et al., 2020). However, the Edisto Inlet does not open every year, as sea ice cover can persist even during the summer season (Tesi et al., 2020). As a result of this variability (interannual and seasonal), very few oceanographic studies have been carried out in the area due to its remoteness and the limited accessibility. When investigated, a two-layer stratification was observed, with water masses below the thermocline being
 100 saltier than those above (Battaglia et al., 2024).

High sedimentation rates, typical of fjord embayment, are inferred from age-depth models derived from marine sediment cores as well as sedimentary structures reflecting an expanded Holocene laminated sequence, mostly composed of diatomaceous ooze (Finocchiario et al., 2005; Battaglia et al., 2024).

2. Material and Methods

105 2.1 Sampling activities

To investigate the benthic foraminiferal assemblages and their distribution related to the environmental parameter in Edisto Inlet, 5 sediment cores were collected with a multicorer Oktopus MC08-12"series (12 x Ø; 100 mm x 610 mm) aboard on the *R/V Laura Bassi* during the 38th Italian Antarctic Expedition in the framework of the LASAGNE project (Fig. 1, Table 1).



Core	Latitude (° S)	Longitude (° E)	Depth (m)	Date of retrieval (dd/mm/yyyy)	SAR (cm yr ⁻¹)
34	72.3507	170.0139	496	13/02/2024	/
24	72.3081	170.056	475	10/02/2023	0.169
178	72.2979	170.0932	470	12/02/2023	0.119
180	72.2941	170.1464	419	11/02/2023	0.073
170	72.2791	170.0978	460	12/02/2023	0.036

Table 1. Core number, site coordinates, depth and date of retrieval. The Sediment Accumulation Rate (SAR) is calculated from the age-depth model reconstructed with the excess activity of ²¹⁰Pb.

2.2 Sedimentological analysis

Different analytical approaches were adopted to characterize the sedimentological properties of the uppermost 5 cm of the cores. Redox potential (Eh) was measured directly on board immediately after core recovery using a pre-calibrated Metrohm punch-in pH/Eh electrode. Measurements were taken with a vertical resolution of 1 cm. Following retrieval, the sediment cores were stored at +4 °C in a refrigerated ISO20 container and transported to Italy for further laboratory analyses. Magnetic susceptibility (MS; SI × 10⁻⁶) was measured at 1 cm resolution using an MS2F Surface Point Probe (Bartington Instruments Ltd., UK). Each sediment core was split lengthwise into two halves. One half was sub-sampled at 1 cm intervals, and each slice was divided into multiple aliquots for water content, biogeochemical, and stable isotope analyses. The remaining half was used for non-destructive analyses: it was photographed and x-rayed to identify sedimentary structures, variations in density and texture, and bioturbation features. This archive half was subsequently stored at +4 °C. Dry density (g cm⁻³) and water content (%) were determined by measuring weight loss after drying sediment samples overnight at 55 °C to constant weight. A particle density of 2.5 g cm⁻³ was assumed, following the method described by Langone et al. (2012). An aliquot of each sample was dried, weighed, and wet-sieved at 63 µm to estimate the proportion of sand-sized particles in the sediment. The sand fraction (%) was calculated as the ratio between the dry weight of the > 63 µm fraction and the total dry weight (g) of the sample, following the methodology for the dead assemblages (Section Micropaleontological analysis). For organic carbon (OC, wt%) analyses, an aliquot of freeze-dried sediment was homogenized using an agate mortar, acidified with 1.5 M HCl to remove carbonates, and analyzed using a Thermo Fisher FLASH 2000 CHNS/O Elemental Analyzer coupled to a Thermo Fisher Scientific Delta Q isotope ratio mass spectrometer (IRMS) (Tesi et al., 2012). The analysis of organic carbon (OC) was performed only for three sites (24, 34, and 180). A second freeze-dried and powdered aliquot was used for radionuclide analyses. ²¹⁰Pb activities were assessed through measurement of its daughter ²¹⁰Po by alpha spectrometry, using a silicon barrier detector connected to a multichannel analyzer. ²¹⁰Po activity was assumed to be in secular equilibrium with its grandparent ²²⁶Ra, following the method described in Frignani et al., (2005). Sediment accumulation rates (SARs; cm yr⁻¹) were calculated using the Constant Flux: Constant Sedimentation (CF:CS) model based on the decay profile of unsupported ²¹⁰Pb (half-life: 22.3 years).



2.3 Micropaleontological analysis

Sediment cores for living foraminiferal assemblages were split vertically into two halves. Each half was horizontally sectioned onboard: every 0.5 cm down to 2 cm depth, and then in 1 cm intervals down to 5 cm. The cores used for analysing dead assemblages were stored at -20°C onboard and later sliced into 1 cm sections down to 5 cm in the laboratory.

140 In the laboratory, one half of the prepared core was treated with Rose Bengal (RB) and fixed in a 4% formalin buffer with sodium borate solution for 72h. After staining, samples were sieved through 125 µm mesh. Residues were kept wet, hand-sorted and counted in water using a binocular microscope. Hard-shelled foraminifera were collected in micropaleontological slides. For what concerns the analysis of the dead assemblages, samples were dried and washed with distilled water with a 63 µm sieve and collected in filter paper. Samples were dried overnight at 40°C, and further dry sieved at 125 µm. The analysis
 145 focuses on the >125 µm fraction, while the 63-125 µm fraction was only collected. If the number of tests in a sample was estimated by sight to be well above 300 tests, the sample was split using a dry Microsplitter and one fraction was counted and picked. The use of the > 125 µm enables the comparison with the benthic foraminiferal assemblages to reconstruct paleoenvironmental evolutions of an area since coarser size fractions are commonly employed for that analysis and more suited for the scope of this study. However, it is important to acknowledge that finer fractions can bear different indicator
 150 species than coarser fraction (Lo Giudice-Capelli et al., 2018; Majewski et al., 2023).

From both living and fossils analysis, fragments of branching and tubular foraminifera (i.e., *Hyperammina* and *Rhizammina*) were collected but not included in the community data analysis because their fragile, easily breakable tests can mislead the correct determination of their occurrence and their abundance.

Taxonomy for hard-shelled benthic foraminifera (agglutinated and calcareous taxa) followed Loeblich & Tappan, (1988) for
 155 the genus-level identification, and other reference studies (Anderson, 1975; Capotondi et al., 2020; Galli et al., 2023; Igarashi et al., 2001; Ishman & Szymcek, 2003; Majewski et al., 2005, 2016, 2023; Melis & Salvi, 2009; Sabbatini et al., 2007). Foraminifera were recognised at the species level, when possible. A Scanning Electron Microscope (SEM, Hitachi TM3030plus Scanning Electronic Microscope) was used to gain images of surface texture of specimens and diagnostic details for species recognition. The total density of the specimens was calculated as the number of individuals per 50 cm³
 160 (Area of the core = 69.4 cm²). Relative abundances were calculated as the number of individuals of the same species normalized to the total number of benthic foraminiferal tests. Density of planktic foraminifera (expressed in n°/ g of dry sediment) was estimated by the ratio between the total number of tests and the total dry weight.

2.4 Statistical analysis

All the statistical analyses were conducted in the R environment (R Core Team, 2024). Figures and plots were computed
 165 using the package *ggplot2* (Wickham, 2011). Correlations between the environmental variables were assessed using the function *ggcorrplot* from the *ggcorrplot* package (Kassambra, 2022). All the code used to compute the figure and the statistical analysis is reported in the Supplementary Material.



To compare the results from living assemblages with the fossil ones, the assemblage composition of the first 2 centimetres was merged as a 1-cm thick sample to resemble the sample step of 1 cm of the dead assemblage.

170 To understand the ecological gradient that affected the communities, a non-Metric Multidimensional Scaling (nMDS) was computed using Wisconsin transformed relative abundances of species that showed a maximum relative abundances >5% and appeared in at least two samples, with a Bray-Curtis distance (function *monoMDS* in the package *vegan*; Oksanen et al., 2024). nMDS is conservative in respect of the dissimilarity between each sample, making it easier to detect the presence of ecological gradients (Kruskal, 1964; Prentice, 1977). In addition, convex hulls (polygons) were used to investigate the relationship between each station using the function *chull*.

175 Lastly, for comparing ~~each~~ different paleocommunities with the recent ones, the average relative abundance of selected species of different periods were pairwise compared using a non-parametric wilcoxon-test using the function *geom_pwc* of the *scales* package (Wicham et al., 2025). A significant p-value threshold of 0.05 was used to reject the null hypothesis of no differences between the groups. The data used for the comparison is the one of the TR17-08 (Galli et al., 2025), while, for 180 the core selected, only the assemblages at sites 24 and 34 were used because of the vicinity from the sediment core (Fig. 1).

3. Results

3.1 Geochemical characteristics of the sediments

The Sediment Accumulation Rate (SAR) derived from the ^{210}Pb excess activity is higher at sites 24 and 178 than the one characterizing the outer sites (170, 180) (Table 1, Fig. 2a). Core 34 did not yield a usable profile to compute the age-depth 185 model (Fig. S4).

Samples collected at sites 34 and 24 are characterized by low dry density, low magnetic susceptibility (MS), a low sand content and a high-water content (Fig. 2a). By contrast, sites on the outer part of the fjord, namely 170 and 180, are characterized by the opposite trend: high dry densities as well as a high MS and sand content, along with a low water content (Fig. 2a). Site 178, located at the fjord mouth, shows a mixture signal between the geochemical parameters at the inner and 190 outer sites (Fig. 2a). ~~For what it concerns the Red-ox potential (Eh),~~ site 34 has the most negative values, while sites 178, 170 and 180 show a similar reduction pattern down core with the presence of positive values only at the most surficial layer (Fig. 2a). Site 24 has positive values throughout, except for the deepest interval (Fig. 2a).

Since this study focus on the benthic foraminiferal distribution, planktic foraminifera test (only of *Neogloboquadrina pachyderma*) are used as indicator for primary productivity regimes. In the surface samples, sites 34 and 24 are characterised 195 by the highest concentration of planktic test, while outer stations are characterised by the almost complete absence of the latter (Fig. 2b).

Positive relationship between the dry densities, MS, the sand content and the Eh, are present, while the water is negatively with every other parameter, except with the planktic foraminifera (Fig. 2c). The only non-significant relationship is between the Eh and the planktic foraminifera content.

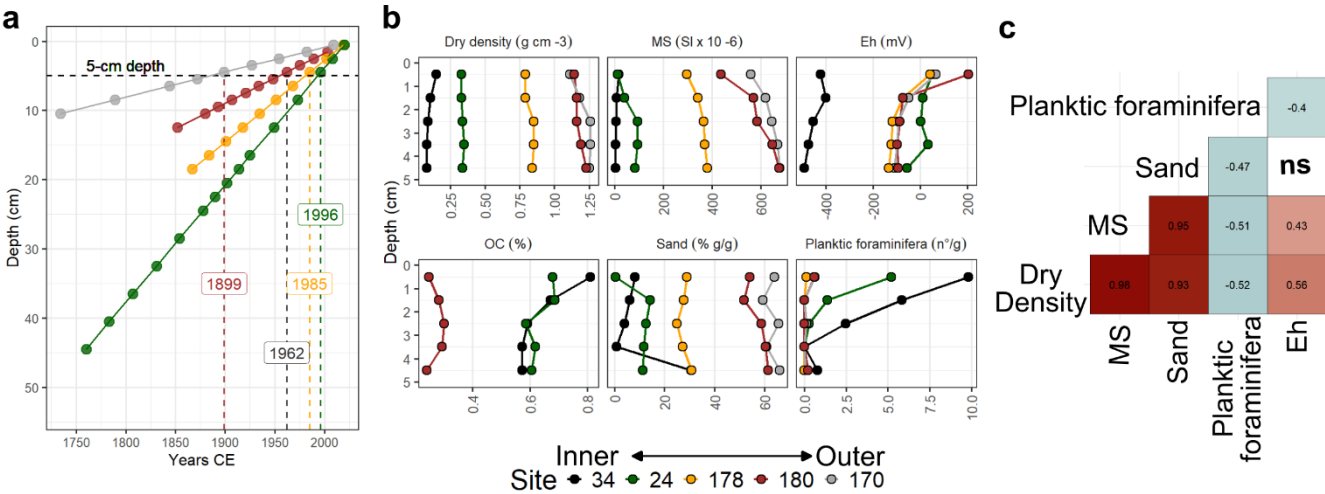


Figure 2. Sedimentological characteristics of the sediment cores retrieved in Edisto Inlet. a) Age-depth model derived from the ^{210}Pb excess activity for every core collected in the sites. The core 34 yield a not usable profile, thus it is not plotted (Fig. S1). The dashed horizontal black line highlights the upper 5 cm used in this study, while the color-coded vertical dashed line highlights how much do the upper section spans time (in yrs CE). b) Sedimentological, geochemical characteristics measured on the uppermost 5 cm, along with planktic foraminiferal densities, retrieved from the fossil assemblage. MS = Magnetic Susceptibility; Eh = Redox potential; OC = Organic Carbon. c) Pearson's relationship between the features of panel b. The strength of the relationship relationship is indicated by both the labels inside the square and by the color: Red color = positive relationship, Blue = negative relationship; White = no significant relationship.

3.2 Benthic foraminiferal fauna from Edisto Inlet

A total of 49 species were recognised in the living (stained) assemblages with a total counted test of 1589 tests, with the first half centimetre from 170 holding most specimens, for a total 496. Across the dead assemblages, 55 species were identified, and 5639 tests were counted, with the first centimetre of the 170 holding a total of 796 tests. Only one planktic species, *Neogloboquadrina pachyderma*, was found in the fossil assemblage.

Total densities and community composition of the most common species are reported in Fig. 3 and Fig. 4, while a list of all the benthic species identified is presented in Table S2 in the supplementary material, along with the counted specimens Supplementary Material.

A comparison between the living and dead assemblage is also reported in Fig. 5, highlighting the differences in the total densities between the two assemblages, and the different content of the agglutinated and calcareous test.

Scanning Electron Microscope (SEM) photos of selected species are presented in the Appendix section.

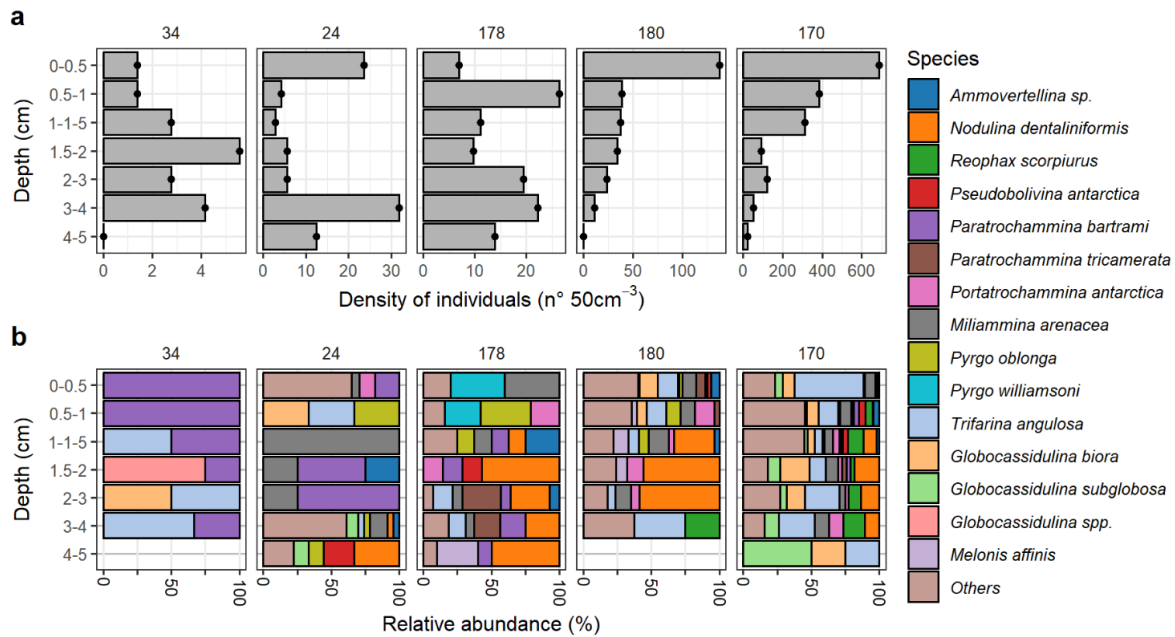


Figure 3. Living (Rose-Bengal stained) benthic foraminifera community in Edisto Inlet. a) Total densities (n°/50 cm³) of stained benthic foraminifera test counted. The x-axis is scaled differently for each station. b) Assemblage composition of the species that appears more than 20%. A threshold of 20% was used because of the low number of individuals at sites 34, 24 and 178 (< 30 n° ind./50 cm³). Sites names are reported on top of each plot and are arranged from the innermost (34) to the outermost site (180). Species are reported in alphabetical order.

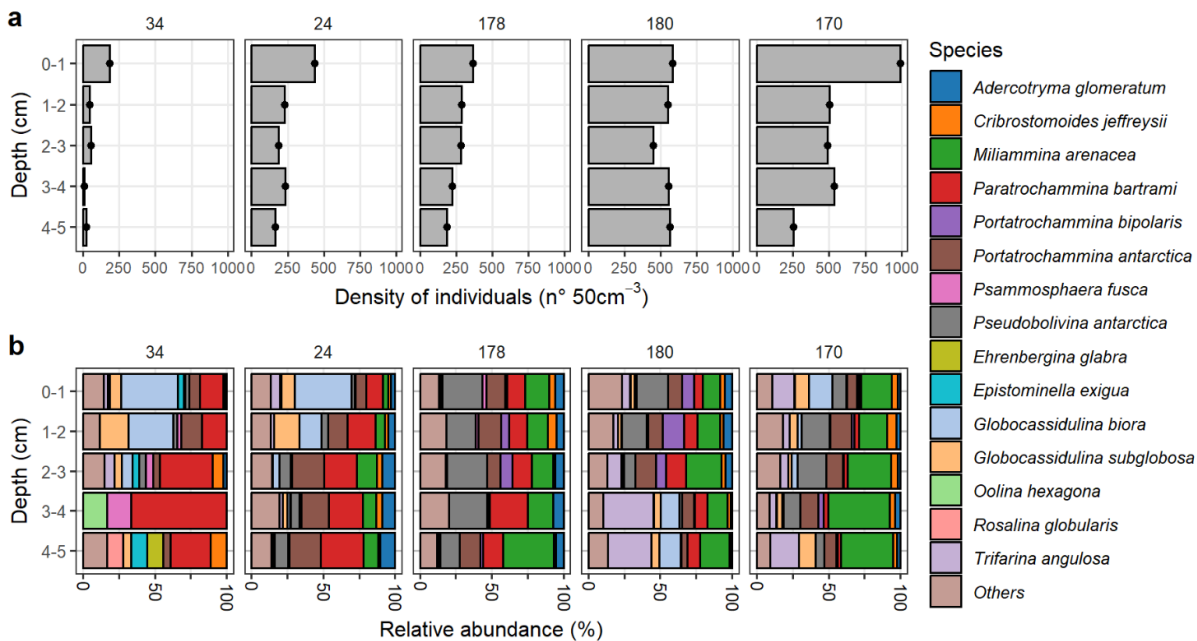




Figure 4. Fossil benthic foraminiferal community in Edisto Inlet. a) Total densities ($n^\circ/50\text{ cm}^3$) of foraminifera test counted in the dead assemblage. b) Assemblage composition of the species that appears more than 10% and at least in one station. Species are reported in alphabetical order.

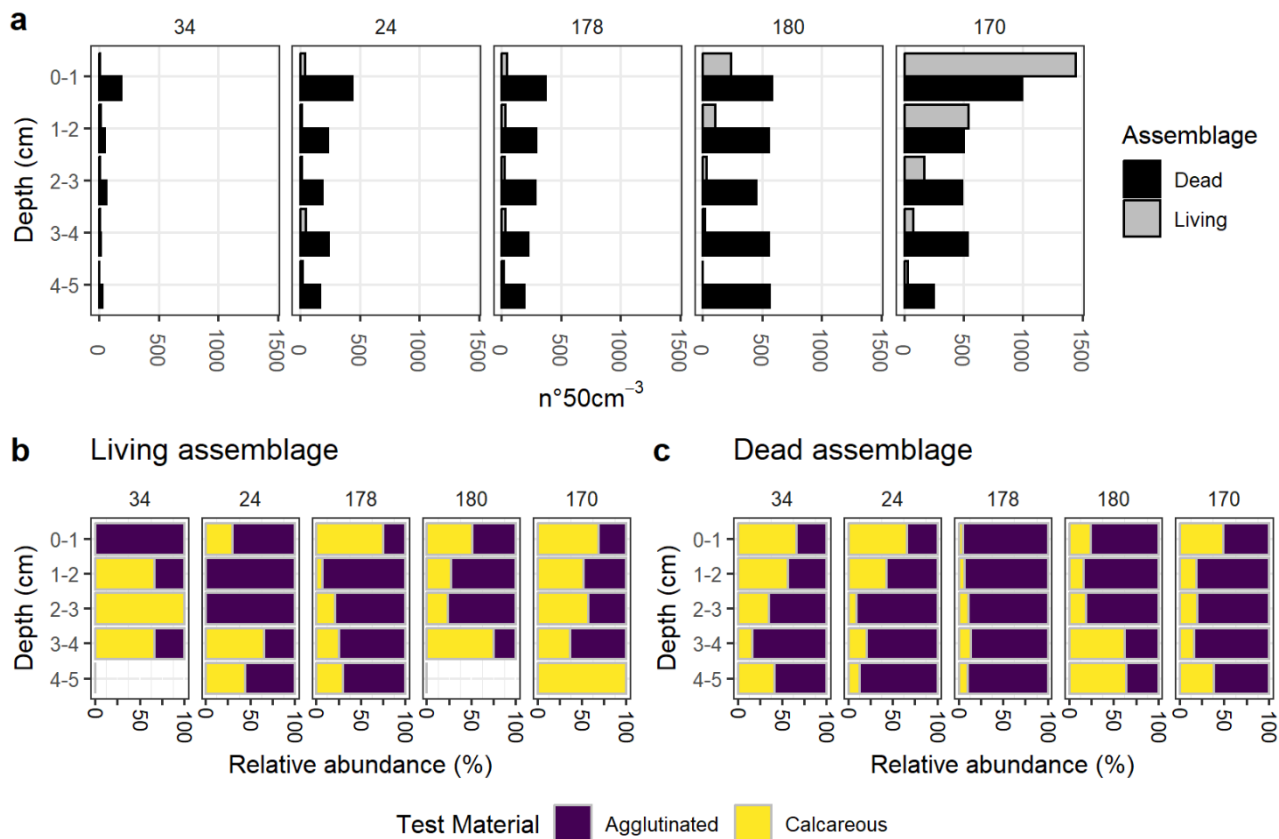


Figure 5. Comparison between the living and fossil benthic foraminifera assemblage. a) Total densities ($n^\circ / 50\text{ cm}^3$) of the living (grey) and dead (black) assemblages. To compare the total densities of the living with the one of the dead, samples that were sliced at 0.5 cm were merged. b) Relative abundances of calcareous (yellow) and agglutinated (dark purple) benthic foraminifera of the living (b) and dead assemblage (c) assemblage.

3.3 Multivariate analysis

The 2-dimension nMDS models are characterised by values < 0.2 (Fig. 6, Fig. 7), indicating that the ecological gradients in Edisto Inlet are well represented in a two-dimensional space (Dexter et al., 2018). The living benthic foraminiferal fauna shows a higher degree of overlap among sites than the dead assemblage (Fig. 6). Notably, site 34 appears as an outlier in both assemblages, so a second nMDS was computed excluding the latter (Fig. 7).

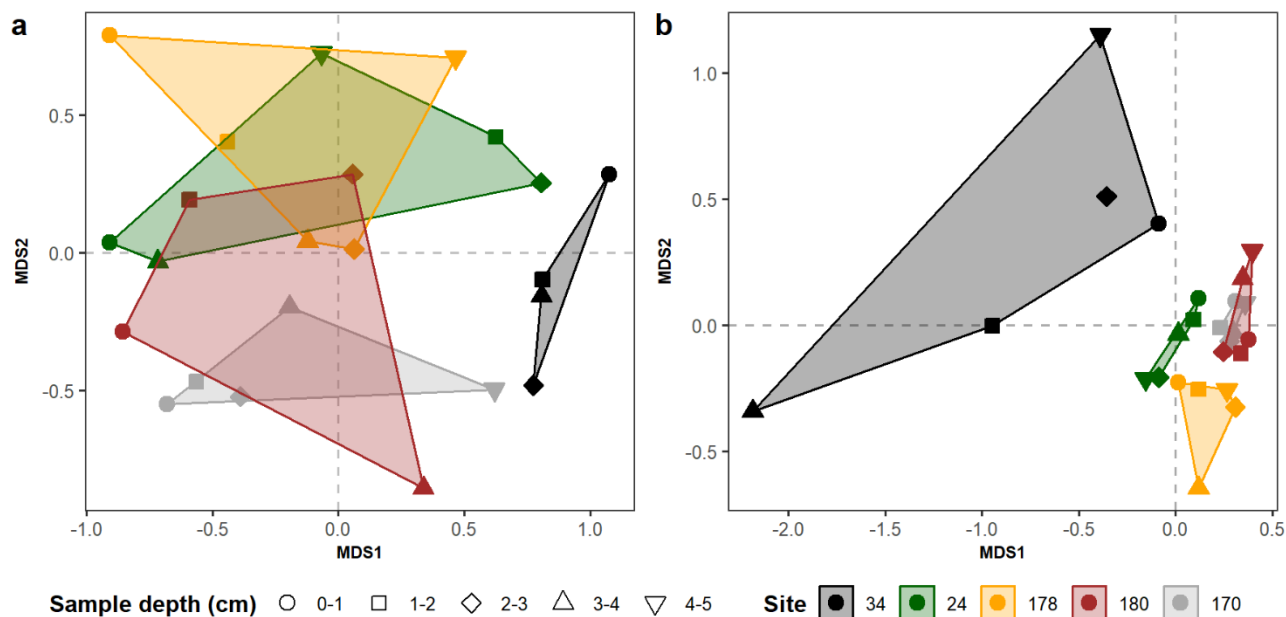


Figure 6. 2-dimension nMDS models computed on the community composition of the living (a) and the dead (b) benthic assemblages. Both models show Site 34 as an outlier. In the legend, the sites are reported from the innermost to the outermost part of the fjord.

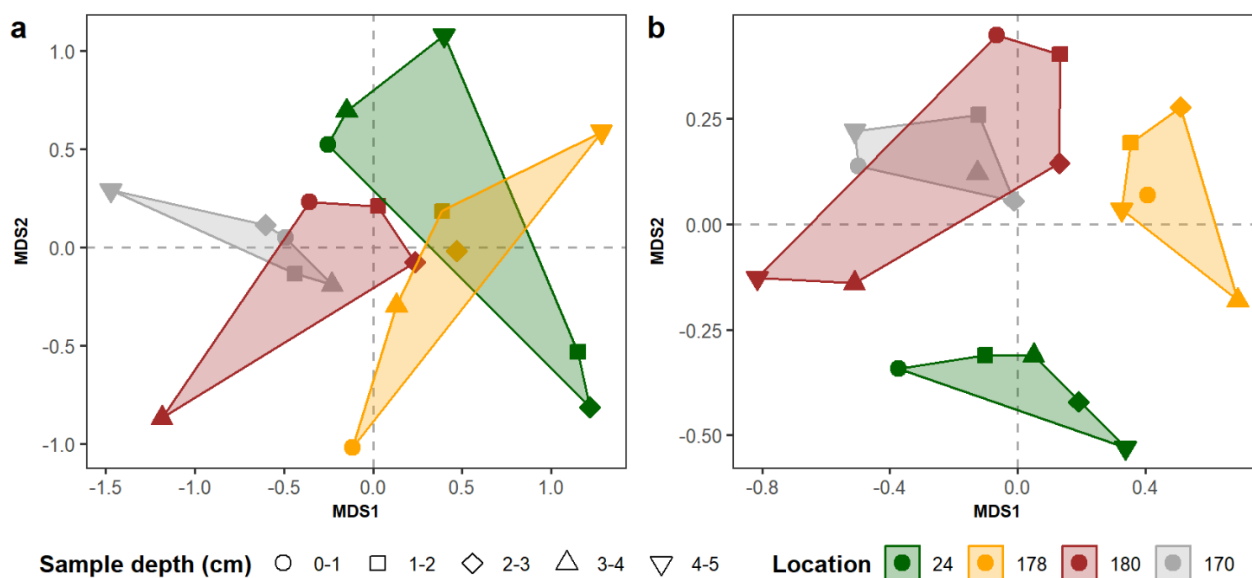


Figure 7. 2-dimension nMDS models computed on the community composition of the living (a) and the fossil (b) benthic assemblages computed without site 34. Notice the change in the community structure of site 178: in the living assemblages overlaps sites 24 (a), while on the fossil assemblage mostly overlaps site 180 (b).



250

After removing site 34, the living assemblage shows more overlapping features than the fossil one (Fig. 7). Of notes, the relative location of the polygon of site 178 (the site located at the sill, Fig. 1) changes quite substantially: in the living assemblage it overlaps site 24 (Fig. 7a), while on the fossil ones it is completely detached from it (Fig. 7b). Lastly, the fossil community at site 24 is much more distant from the outer and entrance site than the living one (Fig. 7), being the only site showing only negative MDS2 values (Fig. 7b).

255

3.4 Paleocommunities comparison

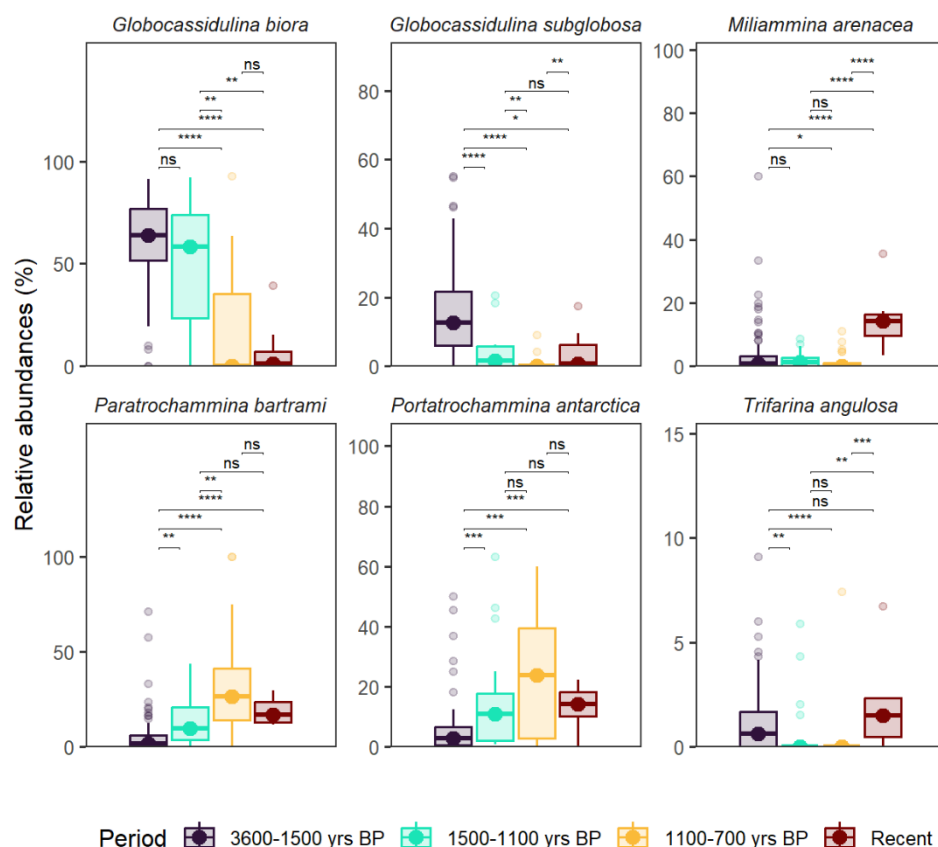


Figure 8. Comparison between the assemblages highlighted in the sediment core TR17-08 (black, cyan and yellow) and the one retrieved from site 24 and 178 (in brown). Significance thresholds of the pairwise comparison between periods are reported above the brackets as ns = $p > 0.05$; * = $p < 0.05$; ** = $p < 0.01$; *** = $p < 0.001$ and **** = $p < 0.0001$.

260

The palaeocommunities analysed from the TR17-08 were divided according to the environmental phases of Galli et al., (2025) with emphasize on the fjord-like behaviour (3600 – 1500 years Before Present (0 BP =1950 CE)), Transitional warming phase (1500 – 1100 years BP), Cooling phase (1100 - 700). The data used from site 24 and 178 is considered “recent”



because they span a relative long period as shown in Figure 2a. All the pairwise comparison and significance are reported in Figure 8. For simplicity, we comment only the comparison of the recent period with the others. All the species relative abundances are significantly different from the 3600 – 1500 years BP period except for *Trifarina angulosa*. Similarly, significant differences are present from the 1500-1100 period, except for *Globocassidulina subglobosa*, *Paratrochammina bartrami* and *Portatrochammina antarctica*. Content of *G. biora*, *P. bartrami*, *P. antarctica* shows no significance difference from the 1100-700 years BP period, *G. subglobosa*, *Miliammina arenacea* and *T. angulosa*, are characterized by an increase in their relative abundances in respect to the latter.

4. Discussion

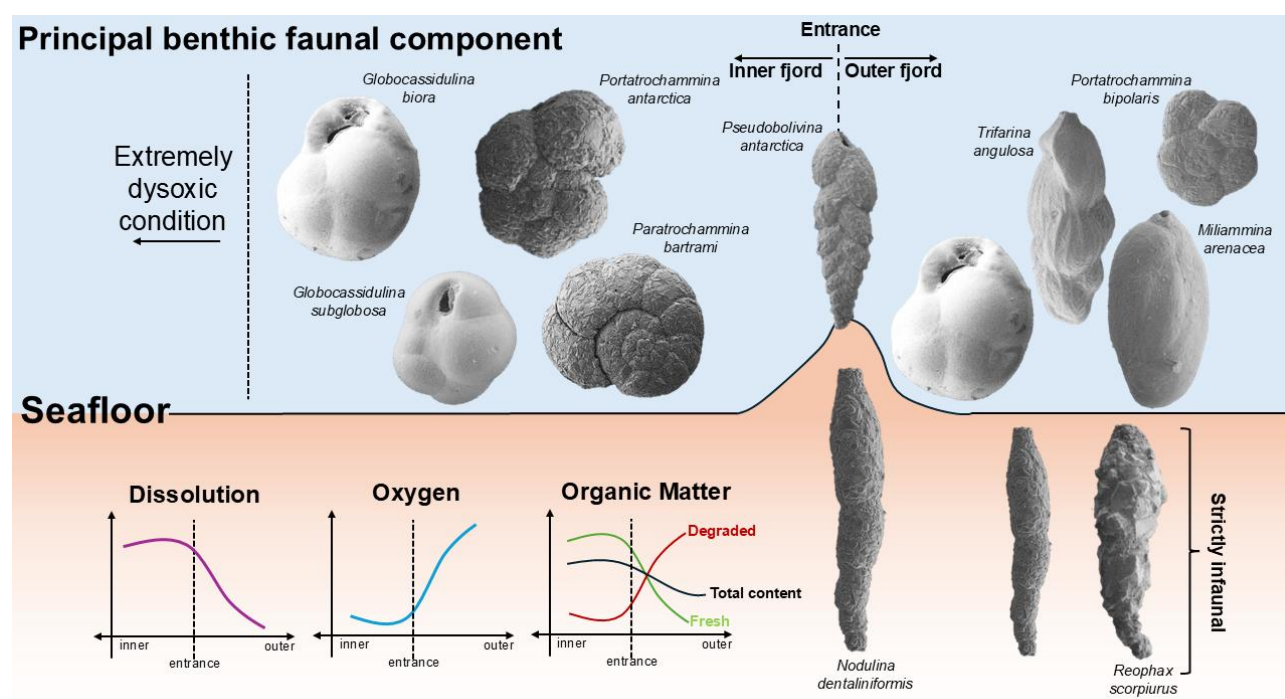


Figure 9. Conceptual cartoon of the Edisto Inlet benthic foraminiferal fauna and the major environmental factors (**Dissolution, Oxygen, Organic Matter**) that affects the benthic community and how they are distributed along the fjord transect, from innermost to outermost part. Species that have been found only below 1-cm were considered as strictly infaunal and are depicted inside the sediments. For a more detailed discussion readers are referred to the section 4.2. SEM photos of selected foraminifera are not in scale.

4.1 Environmental gradient across the fjord transects

From the sedimentological and geochemical analysis, it is evident that the fjord is characterized by an extremely well-defined gradient of benthic environmental conditions going from the inner to the outermost part (Fig. 2, Fig. 9). The main factor that shapes this pattern might be related to the amount of Organic Matter (OM) that arrives at the bottom probably



exerting a first order control on the amount of dissolved oxygen that is present at the bottom. Low MS, reduced sand content, high OC at the inner sites support this interpretation, along with the extremely low Eh values found at the innermost sites (Fig. 2b, Arndt et al., 2013; Hoogakker et al., 2024; LaRowe et al., 2020). Furthermore, the extremely low values of Eh at site 34, in conjunction with the elevated OC content, and the lower dry density, reflecting a high porosity, (Fig. 2b) suggest that the OM delivered to the bottom is efficiently buried within the sediments, generating a strong redox potential and a very harsh within the seafloor (Hoogakker et al., 2024). In addition, higher sedimentation rates characterize the innermost sites and can be attributed to the extreme seasonality that this fjord experiences (Table 1). In the Edisto Inlet, the presence of a landfast sea-ice cover that forms and thaws over the summer have been regarded as the first order control on depositional signal, since most of the primary productivity happens after the sea-ice break up (Finocchiaro et al., 2005; Tesi et al., 2020). This can be seen by the higher concentrations of planktic foraminifera in the upper first centimetre on the inner stations, indicating a high surface productivity (Fig. 2b). In addition, the almost completely absence of a bottom current activity in the fjord might enhance the amount of OM present in the sediment (Arndt et al., 2013; Battaglia et al., 2024).

On the other hand, sites located outside of the fjord are characterized by a complete opposite condition from the ones that characterized the inner fjord (Fig. 2b). Despite being lower, OC values on the outer stations are still quite high (> 0.3), implying that a significant amount of OM is still delivered to the bottom. However, the presence of higher values of Eh, higher MS, and higher sand content suggests the presence of a more dynamical regime and less dysoxic conditions, while also implying an increase in the detrital material arriving at the bottom respect to the inner site (Fig. 9).

Site 178, situated near the entrance of the fjord, bridges the gap between the innermost and the outermost conditions, showing values comprising between these two endmembers (Fig. 2b, Fig. 9).

Hence, it is reasonable to hypothesis that most of the benthic conditions in the Edisto Inlet are shaped by the type of OM that arrives at the seafloor and how much of this fresh OM is buried into sediments which is highly regulated by the bottom hydrographic conditions. These environmental conditions are probably exerting a first order control on the dissolved oxygen present at the sediment-water interface and deeper in the sediments (Fig. 9)

4.2 Benthic foraminiferal communities and their relationship with the environment

To better frame the differences in the benthic foraminiferal fauna that shapes the living assemblages and what control the preservation potential of the hard-shelled fauna, it is possible to define three important habitats within the studied sites by comparing it with the environmental gradients: innermost part of the fjord (34, 24), the entrance (178) and the outermost bay (170, 180) (Fig. 9). It is, however, important to stress that the living RB-stained assemblage represents an estimation of the living community, as well as snapshots of the whole benthic foraminifera community, while the fossil community represents a time averaged community, affected by both environmental and taphonomical controls on their compositions (Van Der Zwaan et al., 1999).

4.2.1 Inner fjord (sites 34 and 24)

The living community at this site shows very extremely low abundances and very low diversity, indicative of very harsh environmental conditions ~~inferring on~~ the populations (Fig. 3). However, a very sharp contrast between the amount of dead test and the presence of **very high dissolution conditions** going down core is testified by a sharp decay of calcareous test going down cores (Fig. 5). The presence of these extreme conditions can be further inferred from the nMDS models, both showing that the community at the inner sites are far more diverse than the one at the entrance and the one found on the outer bay (Fig. 6 and Fig. 7). This is evident for site 34 (Fig. 6, Fig. 7a). **At both sites**, the fossil community is dominated by the presence of four major component: the calcareous *Globocassidulina biora* and *Globocassidulina subglobosa*, while the agglutinated fauna is mainly composed by *Paratrochammina bartrami* and *Portatrochammina antarctica* (Fig. 9). The latter two are indicative of locations with high carbonate dissolution, and elevated organic matter (OM) accumulation on the seafloor, and, because of their fragile test material, to sluggish circulation regimes, all of which are consistent with the environmental features derived from the sedimentological properties (Fig. 9, Anderson, 1975; Capotondi et al., 2020; Majewski, 2010; Majewski et al., 2023; Majewski & Anderson, 2009; Melis & Salvi, 2009; Violanti, 2000). Anoxic (or suboxic) conditions can lead to the death of most benthic organisms, including foraminifera, with only a few opportunistic taxa capable of surviving in low-oxygen environments, such as *G. biora* and *G. subglobosa* (Gooday, 2003; Levin et al., 2009). Thus, the presence of these species, known for their tolerance to low oxygen condition, opportunistic behavior and rapid reproduction, supports the hypothesis of oxygen-depleted bottom conditions while highlighting the influence of organic-rich, poorly oxygenated microenvironments **hinging** on the living foraminiferal community structure (Fig. 4b). The presence in the fossil assemblage of the phytodetritivorous species *Epistominella exigua* further corroborates this view of enhanced OM fluxes, that might be associated with the seasonal break-up of the sea-ice cover (Mackensen et al., 1993; Smart et al., 1994; Gooday, 1999; Lehrmann et al., 2025). However, the preservation of this faunal component seems to be severely limited by the high dissolution conditions that develops deeper in the sediments and probably later in the year (Fig. 5 and Fig. 9). By these considerations, it is plausible that ~~this~~ discrepancies between the living and fossil assemblages over the innermost site are representative of a substantial mortality events following the sea-ice break up. The date of retrieval of the core was late in the austral summer (Table 1), well after the first break-up of the sea-ice, aligning with this explanation. Thus, the presence of relatively high fluxes of OM could exert a double control on the population. First, the break-up of the sea-ice cover enriches the seafloor of OM due to enhanced primary productivity because of the light availability. Afterwards, the absence of a strong circulation regime can increase the remineralization and oxidation potential of this food bank, providing a ~~suiting~~ explanation of the ~~discussed discrepancy~~ (Smith et al., 2015). While this makes the foraminiferal prone to ~~dissolute~~, it also stresses the importance of considering fjord as efficient hotspot of OC burial (Smith et al., 2015).



4.2.2 Entrance part (site 178)

In terms of geochemical and sedimentological parameters, this site is comprised between the innermost and the outermost station (Fig. 2b, Fig. 9). Interestingly, the living benthic foraminiferal community is characterized by being similar to the ones that are inside of the fjord, in both the total number of specimens and community structures (Fig. 3, Fig. 7). However, in the fossil assemblages the separation of this site from the innermost ones is more evident (Fig. 4, Fig. 7b). On the surface, the living community is characterized by calcareous miliolid of the epifaunal genus *Pyrgo* (*Pyrgo oblonga* and *P. williamsoni*) and by the presence of the agglutinated miliolid *Miliammina arenacea*; going downcore, the community is replenished by the agglutinated uniserial *Nodulina dentaliniformis*, the trochospiral *Paratrochammina tricamerata* and *P. bartrami* (Fig. 3b). On the other hand, the fossils community is characterized by a striking similar composition throughout, mostly composed *Pseudobolivina antarctica*, *Potratrochammina antarctica*, *Miliammina arenacea* and *Paratrochammina bartrami*, all of which are agglutinated forms (Fig. 4b). While dissolution conditions might affect the fossil assemblage, as evidenced by the discrepancies between the content of calcareous test on the first cm, the community is dominated by agglutinated forms in both assemblages going downcore (Fig. 5). The high content of *Pseudobolivina antarctica* in the fossil assemblage is particularly remarkable since, in the living one, it is found in only one sample at a depth of 3 cm (Fig. 3b), hinting to a different ecological preference rather than an increase in its concentration produced by dissolution alone. Site 178 is located at mouth of the fjord, where most variability in both oceanographical and sedimentological parameters happen in enclosed basin, due to water mass exchange with the outer bay and because landfast sea-ice being more prone to be broken because of the increasing distance from its anchored coastal part (Cottier et al., 2010; Fraser et al., 2023; Howe et al., 2010; Zhao et al., 2022). Hence, while dissolution cannot be fully ruled out as a major component affecting the preservation potential at this site, the presence of a different ecological succession of benthic fauna over the year can also be seen as concurring factor in shaping the community structure (Alve, 1999). However, more studies need to be done to fully understand and frame these peculiar discrepancies.

As what these species indicates, they align with the “mixture” of environmental conditions that the microhabitat at this site experiences (Fig. 2, Fig. 9). The presence of miliolids in the first cm of the living assemblages, as well as the presence of strictly infaunal species (*N. dentaliniformis*) throughout the core are indicative of more oxygen, more salinity variation but with conspicuous content of labile OM that is degraded by enhanced microbial activity (Kender & Kaminski, 2017; Lukina, 2001; Majewski, 2005). These environmental signals seem to be preserved in the fossil community even if the indicator species changes: *Pseudobolivina antarctica* has been found in OM-enriched-mud deposits, while *M. arenacea* is indicative of oxic to suboxic conditions and/or dissolution conditions (Capotondi et al., 2018; Lehrmann et al., 2025; Majewski et al., 2023; Rodrigues et al., 2013; Violanti, 2000; Ward et al., 1987). Presence of *P. bartrami* and *Portatrochammina antarctica* further supports the high OM content flux at the bottom (Majewski et al., 2023).



4.2.3 Outer Bay (site 170 and 180)

The outer sites constitute the other environmental end member for the analysed transect (Fig. 2, Fig. 9). An ameliorant of the microhabitat conditions respect to the inner station can be inferred by the increased number of specimens (Fig. 3a). Moreover, going deeper into the core, the fossil assemblage is characterized an increase in the calcareous component of the fauna, thus indicating a reduction in the dissolution conditions (Fig. 5c). The presence of a more dynamical and less severe environmental bottom conditions is reflected in both the living and fossils assemblage (Fig. 3, Fig. 4). The living assemblage is mainly composed by *Globocassidulina biora*, *Globocassidulina subglobosa*, *Trifarina angulosa* and *Miliammina arenacea*; downcore appearances of *Nodulina dentaliniformis* and *Reophax scorpiurus* are visible (Fig. 3b). While the presence of *G. biora* and *G. subglobosa* can be indicative of the still high, but lower, OC content (> 0.3 , Fig. 2b, Majewski, 2005, 2010; Majewski et al., 2019), the presence of *T. angulosa* aligns with the presence of coarser grain size, that can be indicative of higher hydrodynamical conditions at the bottom (Melis & Salvi, 2009; Murray & Pudsey, 2004; Violanti, 2000). Moreover, the stable presence of both *T. angulosa* and *G. biora* going downcore suggesting a facultative infaunal behaviour of these taxa.

The higher content of *M. arenacea* at this station might be caused by an increase in the oxygen content rather than dissolution (Lehrmann et al., 2025). In addition, the downcore presence the deep infaunal species *N. dentaliniformis* and *R. scorpiurus* further corroborates this view, since both have been associated with presence of labile OM and are resistant to change in salinity, suggesting higher hydrodynamic conditions (Kender & Kaminski, 2017). Similarly, the fossils community is characterized by the prominent presence of *G. biora*, *G. subglobosa* and *T. angulosa*, with a higher component of the agglutinated specimens (Fig. 4b). *M. arenacea*, is still present but its more prominent, while *Pseudobolivina antarctica* along with *Portatrochammina antarctica* and *P. bipolaris* become much more common going throughout (Fig. 4b). However, it is worth noting that the two deep infaunal species (*N. dentaliniformis* and *R. scorpiurus*) do not constitute a significant proportion of this assemblage at this site, probably because of the elongated test being susceptible to easily break (Majewski, 2005; Majewski & Pawlowski, 2010). Still, the fossil assemblage at these outer sites is closely related to the living one, suggesting high carbonate preservation potential on the outer bay.

4.3 Comparison with the paleocommunities from the Late Holocene

In coastal Antarctica, the presence of sea-ice affects almost every aspect of the water column (Fraser et al., 2023). Generally, after the first sea-ice break-up, light availability increases and this, along with the presence of a nutrient input, translates into higher surface productivity as well as increased OM fluxes to the seafloor (Arrigo & van Dijken, 2004; Misic et al., 2024). In the Edisto Inlet, paleoenvironmental reconstruction from the nearby piston core TR17-08 using benthic foraminiferal communities had highlighted the role of fast-ice in shaping the benthic community (Galli et al., 2023, 2024, 2025). Along the transect analysed in this study, the benthic foraminiferal community in Edisto are affected by the sedimentation rate, the quantity of OM at the bottom and the hydrographic regime (Fig. 9), all of which are closely related to the presence of a



seasonal cycle of freezing and thawing of the sea-ice cover (Fraser et al., 2012, 2023). Similar to the communities in the Arctic, this suggests that the benthic foraminiferal community in Antarctica, even at deep sites (> 200 m b.s.l.), are sensitive to different seasonal sea-ice conditions (Fossile et al., 2020; Lohrer et al., 2013; Seidenkrantz, 2013). Hence, by comparing the composed record of the fossil assemblage at two nearest site (24 and 178) with the faunal succession collected along the core TR17-08, it might be possible to give a broader and more general context of the modern environmental settings derived from the benthic foraminifera information. This comparison can be done because the core collected at site 24 and 178 spans ca. 60 years (Fig. 2a) making the fossil assemblage collected over the 5 cm a time frame long enough to be comparable to a longer baseline, in this case the last 3600 years BP. Although Galli et al., (2025) used a size fraction > 150 µm, while this study focussed on the > 125 µm, it is unlikely that the 25 µm difference have significantly influenced the differences between the communities (Fig. 8, Weinkauf & Milker, 2018).

Briefly, a typical Antarctic fjord environment was hypothesized between 3600-1500 years BP because of the dominance of *Globocassidulina bitor*, *G. subglobosa*, and the presence of *Portatrochammina antarctica* and *Paratrochammina bartrami*, which are commonly found in other inlet and enclosed basins across different Antarctic coastal sites (Galli et al., 2025; Majewski, 2010; Rodrigues et al., 2013). From 1500-1100 years BP, a transitional period with prolonged summer free-ice conditions along with an increase in the glacial discharge closed the fjord from the general circulation. From 1500-1100 a cooling period, culminating with the transition from a calcareous dominated fauna to an agglutinated dominated one was detected (Galli et al., 2023). The latter was followed by another 700 years interval of very low benthic foraminifera abundances, probably related to substantial increase in the sea-ice cover period (Galli et al., 2023; Di Roberto et al., 2023; Tesi et al., 2020). Additionally, to *G. bitor*, *G. subglobosa*, *P. antarctica* and *P. bartrami*, we also compare the content of *Trifarina angulosa* as an indicator of hydrodynamic conditions at the bottom and *Miliammina arenacea* to address the dissolution and/or suboxic to oxic conditions at the bottom (Fig. 8). As evidenced by the fjord-like community, the fjord as not fully recovered to the late Holocene state (3600-1500 years BP), and benthic fauna is similar the one from the cold transitional state, a period in which the foraminiferal community was severely stressed (Galli et al., 2025). Only *G. subglobosa* increased significantly in respect to the cooling transitional periods, thus suggesting an increase in the OM content at the bottom, probably due an increase in the seasonal regime of the sea-ice recover and more warmer conditions, like the ones characterizing the 1500-1100 years BP interval (Galli et al., 2023, 2025). Interestingly, there is an increase in the *T. angulosa* content that suggest increase of the hydrodynamical bottom conditions, which aligns with the significant increase of *M. arenacea* respect to both transitional periods (Fig. 8). *M. arenacea* content is also similar the one derived from the 3600-2700 years BP, which corresponds to a period in which the presence of higher salinity water masses was more prominent in the Inlet (in Fig. 9 this is highlighted by the presence of outlier points, Galli et al., 2025). Thus, it is possible that benthic foraminiferal community that inhabit the fjord have yet to recovered from the two highly stressful period (1500-1100 years BP; 1100 -700 years BP), but an ameliorant of the bottom conditions can be hypothesized by the changes in the major component of the benthic foraminiferal fauna.



5. Conclusions

By comparing the geochemical properties and the benthic foraminiferal fauna of the upper 5 cm of five sediment cores retrieved in Edisto Inlet, it was possible to understand the main distributional pattern of the benthic meiofaunal components within this Antarctic fjord and understand what drives their ecological preference and their preservation potential. Two distinct environmental settings were identified, the inner part of the fjord (sites 34 and 24) and the outer fjord (sites 170, 180). The entrance site (178) showed mixed properties between these two endmembers. Inner stations were characterized by low dry densities, low MS, **high sediment accumulation rates**, low Eh and lower sand content, all which are indicative of oxygen-depleted sediments with a high fresh OM content efficiently buried within the sediments. On the other hand, outer stations are characterized by low sedimentation rates, high dry densities and lower organic carbon content, indicative of a higher oxygen content at the bottom associated with less OM, but still a high overall content of the latter, probably due to a higher hydrodynamical regime at the bottom.

Both living and dead assemblage of the benthic foraminiferal community reflects these differences. The Rose-Bengal stained “living” assemblage on the inner part of the fjord **are** characterized by the lowest number of individuals and a higher number of dead, suggesting the presence of substantial mortality events **caused by sea-ice break up**. Due to the onset of a stressful environment after the first sea-ice break up, a sluggish circulation regime in concomitance with high fluxes of OM, might severely deplete the water column of oxygen and increase the dissolution condition at the bottom. Inner stations are also characterized by a release of these stressful environmental conditions going near the fjord-head. The hard-shelled benthic foraminifera community is mainly composed by *Globocassidulina bitor* and *Globocassidulina subglobosa* along with the agglutinated species such as *Paratrochammina bartrami* and *Portatrochammina antarctica*, resembling a high OM setting with sluggish circulation regimes, aligning with the geochemical parameters. In addition, the overall decrease of calcareous forms in the fossil assemblage that characterized the deeper parts of the cores suggest high dissolution conditions.

At the sill, the dominant faunal component of the first centimeter are miliolids, while, going deeper into the sediments, specimens deep infaunal species such as *Nodulina dentaliniformis* appears, indicating a higher hydrographic regime, in conjunction with a less oxygen-depleted environment with less OM content. The fossil assemblage is highly dissimilar from the living one, with the prominent presence of *Pseudobolivina antarctica* and with a lesser degree, *Miliammina arenacea*. While dissolution cannot be fully ruled out as an explanation of **these discrepancies**, it is possible that this agglutinated community might reflects different period of an ecological succession that develops later in the year.

On the outer fjord, living and dead assemblages are more similar. Both assemblages are constituted by *Trifarina angulosa*, indicating higher bottom current activity, while the presence of *Nodulina dentaliniformis* and *Reophax scorpiurus* resembles the presence of labile OM at the **bottom**. On the outer stations, calcareous species such as *Trifarina angulosa* and *Globocassidulinds*, along with the agglutinated *M. arenacea* align with coarser grain size that reflects these higher hydrodynamic conditions and a general higher oxygen content **in-respect** to the inner part.



470 Lastly, by comparing the relative abundances from the nearby piston cores TR17-08 of *G. bitor*, *G. subglobosa*, *P. batrami*,
Portatrochammina antarctica, *T. angulosa* and *M. arenacea* with the ones derived from the nearby sites (24 and 178) it was
possible to determine a more general context of this benthic communities: while the fjord-like community have yet to be
recovered to Late Holocene values, the presence of a significant increase in *T. angulosa* and *M. arenacea* from the 1500-
1100 years BP interval suggest an ameliorant from the harsh and stressful conditions that developed during that cooling
475 period.

480

485

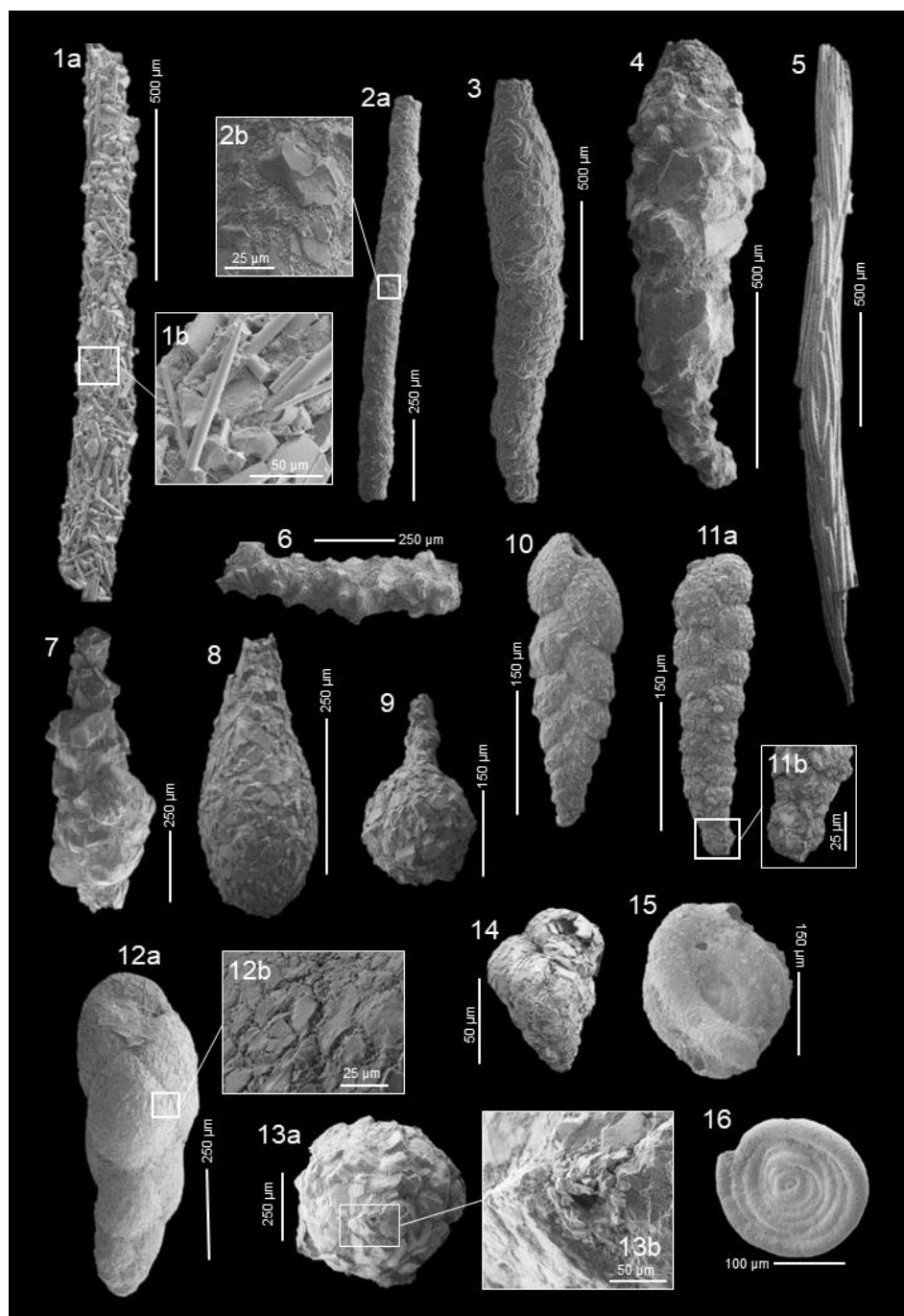
490

495

500



Appendix A – Taxonomic plate



505 Plate A1. 1a-b) *Rhabdammina* sp. 1; 2a-b) *Rhabdammina* sp. 2; 3) *Nodulina dentaliniformis*; 4) *Reophax scorpiurus*; 5) *Reophax spiculifer*; 6) Agglutinated tubular fragment; 7) *Lagenammina difflugiformis*; 8) *Lagenammina* sp. 1; 9) *Lagenammina* sp. 2; 10) *Pseudobolivina antarctica*; 11a-b) *Spiroplectammina biformis*; 12a-b) *Eggerelloides* sp. 13 a-b) *Psammospheara fusca*; 14) *Rhumlerella* sp.; 15) *Ammovertillina* sp.; 16) *Ammodiscus incertus*.

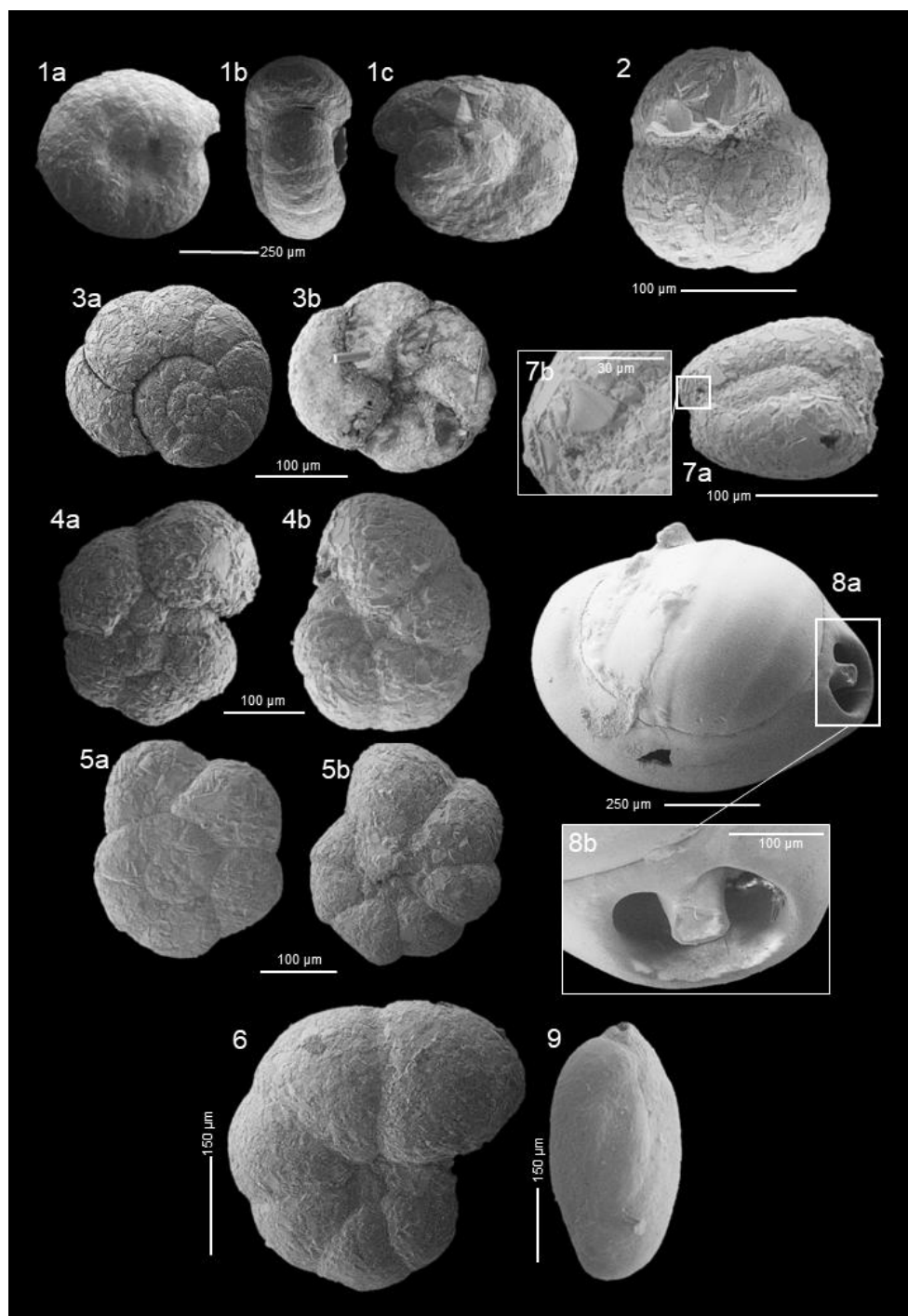


Plate A2. 1a-c) *Recurvoides contortus*; 2) *Paratrochammina tricamerata*; 3) *Paratrochammina bartrami*; 4) *Portatrochammina antarctica*; 5) *Portatrochammina bipolaris*; 6) *Cribrostomoides jeffreysii*; 7) *Adercotryma glomeratum*; 8a-b) *Pyrgo elongata*; 9) *Miliammina arenacea*.

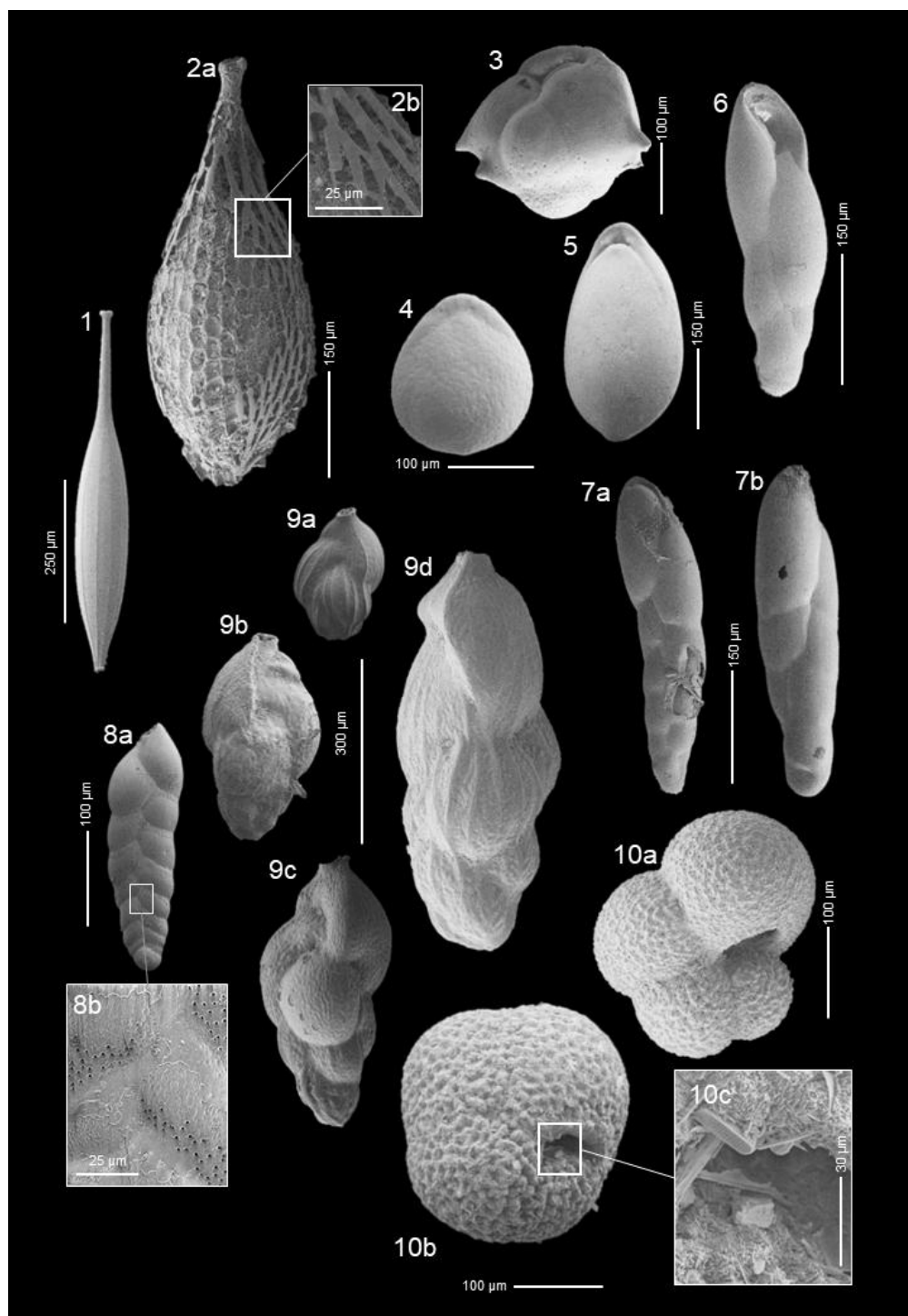
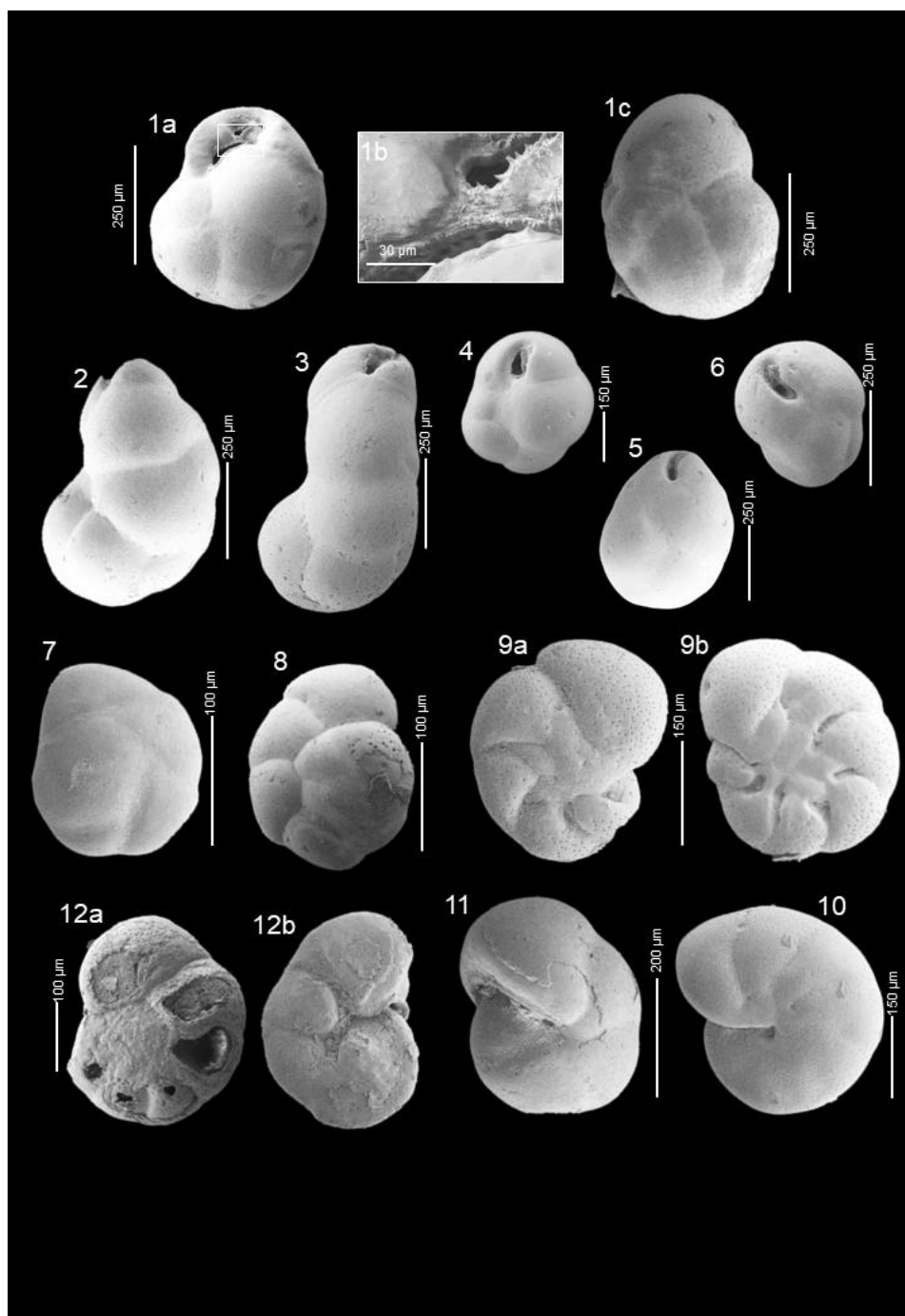


Plate A3. 1) *Hyalinometrion gracilium*; 2a-b) *Lagena substriata*; 3) *Ehrenbergina glabra*; 4) *Parafissurina* sp. 5) *Parafissurina fusiformis*; 6) *Stainforthia concava*; 7a-b) *Fursenkoina subacuta*; 8a-8b) *Bolivinellina pseudopunctata*; 9a-d). *Trifarina angulosa*.



515 Plate 4.1a-1c) *Globocassidulina bora*; 2-3) *Cassidulinoides porrectus*; 4-6) *Globocassidulina subglobosa*; 7) *Epistominella exigua*; 8) *Ioanella tumidula*; 9a-b) *Astrononion antarcticus*; 10) *Astrononion echolsi*; 11) *Pullenia quinqueloba*; 12a-b) *Rosalina globularis*.



Code and Data availability

All the data and codes used for this study are reported in the supplementary material to the article.

520 Author contribution

G.G.: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Visualization, Writing (original draft preparation); F.C and P.G.: Data curation, Investigation, Methodology, Validation, Writing (review and editing); C.M and A.S.: Investigation, Validation, Writing (review and editing); L.L.: Funding acquisition, Project administration, Resources, Writing (review and editing).

525 Competing interests

The authors declare that they have no conflict of interest.

Acknowledgements

We sincerely thank the crew of R/V *Laura Bassi* and the OGS technicians for their support during the sampling activities carried out as part of Leg 2 of the PNRA XXXVIII Antarctic Expedition. Special thanks go to Dr. Riccardo Scipinotti for his
 530 invaluable logistical assistance. This work is a contribution to the PNRA19_00069 LASAGNE project. We also acknowledge Laura Bellentani and Alessandro Sartini for their invaluable help in the sample preparations.

References

- Alve, E. (1999). Colonization of new habitats by benthic foraminifera: a review. *Earth-Science Reviews*, 46(1–4), 167–185.
[https://doi.org/10.1016/S0012-8252\(99\)00016-1](https://doi.org/10.1016/S0012-8252(99)00016-1)
- 535 Anderson, J. B. (1975). Ecology and Distribution of Foraminifera in the Weddel Sea of Antarctica. *Micropaleontology*, 21, 69–96. <https://doi.org/10.2307/1485156>
- Arndt, S., Jørgensen, B. B., LaRowe, D. E., Middelburg, J. J., Pancost, R. D., & Regnier, P. (2013). Quantifying the degradation of organic matter in marine sediments: A review and synthesis. In *Earth-Science Reviews* (Vol. 123, pp. 53–86). <https://doi.org/10.1016/j.earscirev.2013.02.008>
- 540 Arrigo, K. R., & van Dijken, G. L. (2004). Annual changes in sea-ice, chlorophyll a, and primary production in the Ross Sea, Antarctica. *Deep Sea Research Part II: Topical Studies in Oceanography*, 51(1–3), 117–138.
<https://doi.org/10.1016/j.dsr2.2003.04.003>



- Battaglia, F., De Santis, L., Baradello, L., Colizza, E., Rebesco, M., Kovacevic, V., Ursella, L., Bensi, M., Accettella, D.,
 Morelli, D., Corradi, N., Falco, P., Krauzig, N., Colleoni, F., Gordini, E., Caburlotto, A., Langone, L., & Finocchiaro,
 545 F. (2024). The discovery of the southernmost ultra-high-resolution Holocene paleoclimate sedimentary record in
 Antarctica. *Marine Geology*, 467, 107189. <https://doi.org/10.1016/j.margeo.2023.107189>
- Bernasconi, E., Cusminsky, G., & Gordillo, S. (2019). Distribution of foraminifera from South Shetland Islands (Antarctic):
 Ecology and taphonomy. *Regional Studies in Marine Science*, 29. <https://doi.org/10.1016/j.rsma.2019.100653>
- Capotondi, L., Bergami, C., Giglio, F., Langone, L., & Ravaioli, M. (2018). Benthic foraminifera distribution in the Ross
 550 Sea (Antarctica) and its relationship to oceanography. *Bollettino Della Società Paleontologica Italiana*, 57(3), 187–
 202. <https://doi.org/10.4435/BSPI.2018.12>
- Capotondi, L., Bonomo, S., Budillon, G., Giordano, P., & Langone, L. (2020). Living and dead benthic foraminiferal
 distribution in two areas of the Ross Sea (Antarctica). *Rendiconti Lincei. Scienze Fisiche e Naturali*, 31(4), 1037–1053.
<https://doi.org/10.1007/s12210-020-00949-z>
- 555 Cornelius, N., & Gooday, A. J. (2004). ‘Live’ (stained) deep-sea benthic foraminiferans in the western Weddell Sea: trends
 in abundance, diversity and taxonomic composition along a depth transect. *Deep Sea Research Part II: Topical Studies
 in Oceanography*, 51(14–16), 1571–1602. <https://doi.org/10.1016/j.dsr2.2004.06.024>
- Cottier, F. R., Nilsen, F., Skogseth, R., Tverberg, V., Skardhamar, J., & Svendsen, H. (2010). Arctic fjords: A review of the
 oceanographic environment and dominant physical processes. *Geological Society Special Publication*, 344, 35–50.
 560 <https://doi.org/10.1144/SP344.4>
- Dillon, E. M., Pier, J. Q., Smith, J. A., Raja, N. B., Dimitrijević, D., Austin, E. L., Cybulski, J. D., De Entrambasaguas, J.,
 Durham, S. R., Grether, C. M., Halder, H. S., Kocáková, K., Lin, C.-H., Mazzini, I., Mychajliw, A. M., Ollendorf, A.
 L., Pimiento, C., Regalado Fernández, O. R., Smith, I. E., & Dietl, G. P. (2022). What is conservation paleobiology?
 Tracking 20 years of research and development. *Frontiers in Ecology and Evolution*, 10.
 565 <https://doi.org/10.3389/fevo.2022.1031483>
- Finocchiaro, F., Langone, L., Colizza, E., Fontolan, G., Giglio, F., & Tuzzi, E. (2005). Record of the early Holocene
 warming in a laminated sediment core from Cape Hallett Bay (Northern Victoria Land, Antarctica). *Global and
 Planetary Change*, 45(1–3), 193–206. <https://doi.org/10.1016/j.gloplacha.2004.09.003>
- Fossile, E., Pia Nardelli, M., Jouini, A., Lansard, B., Pusceddu, A., Moccia, D., Michel, E., Péron, O., Howa, H., &
 570 Mojtahid, M. (2020). Benthic foraminifera as tracers of brine production in the Storfjorden “sea ice factory.”
Biogeosciences, 17(7), 1933–1953. <https://doi.org/10.5194/bg-17-1933-2020>
- Fraser, A. D., Massom, R. A., Michael, K. J., Galton-Fenzi, B. K., & Lieser, J. L. (2012). East Antarctic Landfast Sea Ice
 Distribution and Variability, 2000–08. *Journal of Climate*, 25(4), 1137–1156. <https://doi.org/10.1175/jcli-d-10-05032.1>
- 575 Fraser, A. D., Wongpan, P., Langhorne, P. J., Klekociuk, A. R., Kusahara, K., Lannuzel, D., Massom, R. A., Meiners, K. M.,
 Swadling, K. M., Atwater, D. P., Brett, G. M., Corkill, M., Dalman, L. A., Fiddes, S., Granata, A., Guglielmo, L., Heil,



- P., Leonard, G. H., Mahoney, A. R., ... Wienecke, B. (2023). Antarctic Landfast Sea Ice: A Review of Its Physics, Biogeochemistry and Ecology. In *Reviews of Geophysics* (Vol. 61, Issue 2). John Wiley and Sons Inc. <https://doi.org/10.1029/2022RG000770>
- 580 Frignani, M., Langone, L., Ravaioli, M., Sorgente, D., Alvisi, F., & Albertazzi, S. (2005). Fine-sediment mass balance in the western Adriatic continental shelf over a century time scale. *Marine Geology*, 222–223, 113–133. <https://doi.org/10.1016/j.margeo.2005.06.016>
- Galli, G., Hansen, K. E., Morigi, C., Di Roberto, A., Giglio, F., Giordano, P., & Gariboldi, K. (2025). Edisto Inlet as a sentinel for Late Holocene environmental changes over the Ross Sea: insights from foraminifera turnover events. *Climate of the Past*, 21(9), 1661–1677. <https://doi.org/10.5194/cp-21-1661-2025>
- 585 Galli, G., Morigi, C., Melis, R., Di Roberto, A., Tesi, T., Torricella, F., Langone, L., Giordano, P., Colizza, E., Capotondi, L., Gallerani, A., & Gariboldi, K. (2023). Paleoenvironmental changes related to the variations of the sea-ice cover during the Late Holocene in an Antarctic fjord (Edisto Inlet, Ross Sea) inferred by foraminiferal association. *Journal of Micropalaeontology*, 42(2), 95–115. <https://doi.org/10.5194/jm-42-95-2023>
- 590 Galli, G., Morigi, C., Thuy, B., & Gariboldi, K. (2024). Late Holocene echinoderm assemblages can serve as paleoenvironmental tracers in an Antarctic fjord. *Scientific Reports*, 14(1). <https://doi.org/10.1038/s41598-024-66151-5>
- Gooday, A. J. (1993). Deep-sea benthic foraminiferal species which exploit phytodetritus: Characteristic features and controls on distribution. *Marine Micropaleontology*, 22, 187–205. [https://doi.org/10.1016/0377-8398\(93\)90043-W](https://doi.org/10.1016/0377-8398(93)90043-W)
- 595 Gooday, A. J. (2003). Benthic Foraminifera (Protista) as Tools in Deep-water Palaeoceanography: Environmental Influences on Fauna Characteristics. *Advance in Marine Biology*, 46, 1–90. [https://doi.org/10.1016/s0065-2881\(03\)46002-1](https://doi.org/10.1016/s0065-2881(03)46002-1)
- Gooday, A. J., Bowser, S. S., & Bernhard, J. M. (1996). Benthic foraminiferal assemblages in Explorers Cove, Antarctica: A shallow-water site with deep-sea characteristics. *Progress in Oceanography*, 37(2), 117–166. [https://doi.org/10.1016/S0079-6611\(96\)00007-9](https://doi.org/10.1016/S0079-6611(96)00007-9)
- 600 Gutt, J., Isla, E., Xavier, J. C., Adams, B. J., Ahn, I. Y., Cheng, C. C., Colesie, C., Cummings, V. J., di Prisco, G., Griffiths, H., Hawes, I., Hogg, I., McIntyre, T., Meiners, K. M., Pearce, D. A., Peck, L., Piepenburg, D., Reisinger, R. R., Saba, G. K., ... Wall, D. H. (2021). Antarctic ecosystems in transition - life between stresses and opportunities. *Biol Rev Camb Philos Soc*, 96(3), 798–821. <https://doi.org/10.1111/brv.12679>
- Hoogakker, B., Ishimura, T., de Nooijer, L., Rathburn, A., & Schmiedl, G. (2024). A review of benthic foraminiferal oxygen and carbon isotopes. *Quaternary Science Reviews*, 342. <https://doi.org/10.1016/j.quascirev.2024.108896>
- 605 Howe, J. A., Austin, W. E. N., Forwick, M., Paetzel, M., Harland, R., & Cage, A. G. (2010). Fjord systems and archives: a review. *Geological Society, London, Special Publications*, 344(1), 5–15. <https://doi.org/10.1144/sp344.2>
- Igarashi, A., Numanami, H., Tsuchiya, Y., & Fukuchi, M. (2001). Bathymetric distribution of fossil foraminifera within marine sediment cores from the eastern part of Lützow-Holm Bay, East Antarctica, and its paleoceanographic implications. *Marine Micropaleontology*, 42(3–4), 125–162. [https://doi.org/10.1016/S0377-8398\(01\)00004-4](https://doi.org/10.1016/S0377-8398(01)00004-4)
- 610



- Ingels, J., Vanreusel, A., Brandt, A., Catarino, A. I., David, B., De Ridder, C., Dubois, P., Gooday, A. J., Martin, P., Pasotti, F., & Robert, H. (2012). Possible effects of global environmental changes on Antarctic benthos: A synthesis across five major taxa. *Ecology and Evolution*, 2(2), 453–485. <https://doi.org/10.1002/ece3.96>
- 615 Ishman, S. E., & Szymcek, P. (2003). Foraminiferal Distributions in the Former Larsen-A Ice Shelf and Prince Gustav Channel Region, Eastern Antarctic Peninsula Margin: A Baseline for Holocene Paleoenvironmental Change. In *Antarctic Peninsula Climate Variability: Historical and Paleoenvironmental Perspectives* (pp. 239–260). <https://doi.org/10.1029/AR079p0239>
- Kassambra, A. (2022). ggcorrplot: Visualization of a correlation Matrix using “ggplot2.” *R Package Version 0.1.4.999*.
- 620 Kender, S., & Kaminski, M. A. (2017). Modern deep-water agglutinated foraminifera from IODP Expedition 323, Bering Sea: ecological and taxonomic implications. *Journal of Micropalaeontology*, jmpaleo2016-026. <https://doi.org/10.1144/jmpaleo2016-026>
- Kruskal, J. B. (1964). Nonmetric multidimensional scaling: a numerical method. *Psychometrika*, 29(2), 115–119. <https://doi.org/https://doi.org/10.1007/BF02289694>
- 625 Kyrmanidou, A., Vadman, K. J., Ishman, S. E., Leventer, A., Brachfeld, S., Domack, E. W., & Wellner, J. S. (2018). Late Holocene oceanographic and climatic variability recorded by the Perseverance Drift, northwestern Weddell Sea, based on benthic foraminifera and diatoms. *Marine Micropaleontology*, 141, 10–22. <https://doi.org/10.1016/j.marmicro.2018.03.001>
- Langlet, D., Mermillod-Blondin, F., Deldicq, N., Bauville, A., Duong, G., Konecny, L., Hugoni, M., Denis, L., & Bouchet, V. M. P. (2023). Single-celled bioturbators: benthic foraminifera mediate oxygen penetration and prokaryotic diversity in intertidal sediment. *Biogeosciences*, 20(23), 4875–4891. <https://doi.org/10.5194/bg-20-4875-2023>
- 630 LaRowe, D. E., Arndt, S., Bradley, J. A., Estes, E. R., Hoarfrost, A., Lang, S. Q., Lloyd, K. G., Mahmoudi, N., Orsi, W. D., Shah Walter, S. R., Steen, A. D., & Zhao, R. (2020). The fate of organic carbon in marine sediments - New insights from recent data and analysis. In *Earth-Science Reviews* (Vol. 204). Elsevier B.V. <https://doi.org/10.1016/j.earscirev.2020.103146>
- 635 Lehrmann, A. A., Totten, R. L., Wellner, J. S., Hillenbrand, C.-D., Radionovskaya, S., Comas, R. M., Larter, R. D., Graham, A. G. C., Kirkham, J. D., Hogan, K. A., Fitzgerald, V., Clark, R. W., Hopkins, B., Lepp, A. P., Mawbey, E., Smyth, R. V., Miller, L. E., Smith, J. A., & Nitsche, F. O. (2025). Recent benthic foraminifera communities offshore of Thwaites Glacier in the Amundsen Sea, Antarctica: implications for interpretations of fossil assemblages. *Journal of Micropalaeontology*, 44(1), 79–105. <https://doi.org/10.5194/jm-44-79-2025>
- 640 Li, B., Yoon, H., & Park, B. (2000). Foraminiferal assemblages and CaCO₃ dissolution since the last deglaciation in the Maxwell Bay, King George Island, Antarctica. *Marine Geology*, 169, 239–257. [https://doi.org/10.1016/S0025-3227\(00\)00059-1](https://doi.org/10.1016/S0025-3227(00)00059-1)
- Loeblich, A. R., & Tappan, H. (1988). *Foraminiferal Genera and Their Classification*. Springer US. <https://doi.org/10.1007/978-1-4899-5760-3>



- 645 Lohrer, A. M., Cummings, V. J., & Thrush, S. F. (2013). Altered Sea Ice Thickness and Permanence Affects Benthic
 Ecosystem Functioning in Coastal Antarctica. *Ecosystems*, 16(2), 224–236. <https://doi.org/10.1007/s10021-012-9610-7>
- Lukina, T. G. (2001). Foraminifera of the Laptev Sea. *Protistology*, 2(2), 105–122.
- Mackensen, A., Grobe, H., Kuhn, G., & Fütterer, D. K. (1990). Benthic foraminiferal assemblages from the eastern Weddell
 Sea between 68 and 73° S: distribution, ecology and fossilization potential. *Marine Micropaleontology*, 16, 241–283.
 650 [https://doi.org/10.1016/0377-8398\(90\)90006-8](https://doi.org/10.1016/0377-8398(90)90006-8)
- Majewski, W. (2005). Benthic foraminiferal communities: distribution and ecology in Admiralty Bay, King George Island,
 West Antarctica. *Polish Polar Research*, 26(3), 159–214.
- Majewski, W. (2010). Benthic foraminifera from West Antarctic fiord environments: An overview. *Polish Polar Research*,
 31(1), 61–82. <https://doi.org/10.4202/ppres.2010.05>
- 655 Majewski, W., & Anderson, J. B. (2009). Holocene foraminiferal assemblages from Firth of Tay, Antarctic Peninsula:
 Paleoclimate implications. *Marine Micropaleontology*, 73(3–4), 135–147.
<https://doi.org/10.1016/j.marmicro.2009.08.003>
- Majewski, W., Bart, P. J., & McGlannan, A. J. (2018). Foraminiferal assemblages from ice-proximal paleo-settings in the
 Whales Deep Basin, eastern Ross Sea, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 493, 64–81.
 660 <https://doi.org/10.1016/j.palaeo.2017.12.041>
- Majewski, W., Pawłowski, J., & Zajączkowski. (2005). Monothalmous foraminifera from West Spitsbergen fjords, Svalbard: a
 brief overview. *Polish Polar Research*, 26(4), 269–285.
- Majewski, W., & Pawłowski, J. (2010). Morphologic and molecular diversity of the foraminiferal genus Globocassidulina in
 Admiralty Bay, King George Island. *Antarctic Science*, 22(3), 271–281. <https://doi.org/10.1017/s0954102010000106>
- 665 Majewski, W., Stolarski, J., & Bart, P. J. (2019). Two rare pustulose/spinose morphotypes of benthic foraminifera from
 eastern Ross Sea, Antarctica. *Journal of Foraminiferal Research*, 49(4), 405–422.
<https://doi.org/10.2113/gsjfr.49.4.405>
- Majewski, W., Szczuciński, W., & Gooday, A. J. (2023). Unique benthic foraminiferal communities (stained) in diverse
 environments of sub-Antarctic fjords, South Georgia. *Biogeosciences*, 20(3), 523–544. <https://doi.org/10.5194/bg-20-523-2023>
 670
- Majewski, W., Wellner, J. S., & Anderson, J. B. (2016). Environmental connotations of benthic foraminiferal assemblages
 from coastal West Antarctica. *Marine Micropaleontology*, 124, 1–15. <https://doi.org/10.1016/j.marmicro.2016.01.002>
- Melis, R., & Salvi, G. (2009). Late Quaternary foraminiferal assemblages from western Ross Sea (Antarctica) in relation to
 the main glacial and marine lithofacies. *Marine Micropaleontology*, 70(1–2), 39–53.
 675 <https://doi.org/10.1016/j.marmicro.2008.10.003>
- Misic, C., Bolineši, F., Castellano, M., Olivari, E., Povero, P., Fusco, G., Saggiomo, M., & Mangoni, O. (2024). Factors
 driving the bioavailability of particulate organic matter in the Ross Sea (Antarctica) during summer. *Hydrobiologia*,
 851(11), 2657–2679. <https://doi.org/10.1007/s10750-024-05482-w>



- Murray, J. W. (2006). *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press.
 680 <https://doi.org/10.1017/CBO9780511535529>
- Murray, J. W., & Pudsey, C. J. (2004). Living (stained) and dead foraminifera from the newly ice-free Larsen Ice Shelf, Weddell Sea, Antarctica: Ecology and taphonomy. *Marine Micropaleontology*, 53(1–2), 67–81.
<https://doi.org/10.1016/j.marmicro.2004.04.001>
- Nomaki, H., Ogawa, N. O., Ohkouchi, N., Suga, H., Toyofuku, T., Shimanaga, M., Nakatsuka, T., & Kitazato, H. (2008).
 685 Benthic foraminifera as trophic links between phytodetritus and benthic metazoans: Carbon and nitrogen isotopic evidence. *Marine Ecology Progress Series*, 357, 153–164. <https://doi.org/10.3354/meps07309>
- Oksanen, J., Simpson, G. L., Blanchet, F. G., Kindt, R., Legendre, P., Minchin, P. R., O'Hara, R. B., Solymos, P., Stevens, M. H. H., Szoecs, E., Wagner, H., Barbour, M., Bedward, M., Bolker, B., Borcard, D., Carvalho, G., Chirico, M., De Caceres, M., Durand, S., ... Weedon, J. (2024). vegan: Community Ecology Package. In *CRAN: Contributed*
 690 *Packages*. <https://doi.org/10.32614/CRAN.package.vegan>
- Peck, V. L., Allen, C. S., Kender, S., McClymont, E. L., & Hodgson, D. A. (2015). Oceanographic variability on the West Antarctic Peninsula during the Holocene and the influence of upper circumpolar deep water. *Quaternary Science Reviews*, 119, 54–65. <https://doi.org/10.1016/j.quascirev.2015.04.002>
- Prentice, I. C. (1977). Non-Metric Ordination Methods in Ecology. *The Journal of Ecology*, 65(1), 85.
 695 <https://doi.org/10.2307/2259064>
- R Core Team, V. A. (2024). *R: A Language and Environment for Statistical Computing* (4.3.3). R Foundation for Statistical Publishing. <<https://www.R-project.org/>>
- Rodrigues, A. R., Eichler, P. P. B., & Eichler, B. B. (2013). Foraminifera in Two Inlets Fed by a Tidewater Glacier, King George Island, Antarctic Peninsula. *The Journal of Foraminiferal Research*, 43(3), 209–220.
 700 <https://doi.org/10.2113/gsjfr.43.3.209>
- Sabbatini, A., Morigi, C., Negri, A., & Gooday, A. J. (2007). Distribution and biodiversity of stained monothalamous foraminifera from Tempelfjord, Svalbard. *The Journal of Foraminiferal Research*, 37(2), 93–106.
<https://doi.org/10.2113/gsjfr.37.2.93>
- Seidenkrantz, M.-S. (2013). Benthic foraminifera as palaeo sea-ice indicators in the subarctic realm – examples from the
 705 Labrador Sea–Baffin Bay region. *Quaternary Science Reviews*, 79, 135–144.
<https://doi.org/10.1016/j.quascirev.2013.03.014>
- Sen Gupta, B. K. (2003). *Modern Foraminifera*. Springer Netherlands. <https://doi.org/10.1007/0-306-48104-9>
- Smith, R. W., Bianchi, T. S., Allison, M., Savage, C., & Galy, V. (2015). High rates of organic carbon burial in fjord sediments globally. *Nature Geoscience*, 8(6), 450–453. <https://doi.org/10.1038/ngeo2421>
- 710 Tesi, T., Belt, S. T., Gariboldi, K., Muschitiello, F., Smik, L., Finocchiaro, F., Giglio, F., Colizza, E., Gazzurra, G., Giordano, P., Morigi, C., Capotondi, L., Nogarotto, A., Köseoglu, D., Di Roberto, A., Gallerani, A., & Langone, L.



- (2020). Resolving sea ice dynamics in the north-western Ross Sea during the last 2.6 ka: From seasonal to millennial timescales. *Quaternary Science Reviews*, 237. <https://doi.org/10.1016/j.quascirev.2020.106299>
- 715 Tesi, T., Langone, L., Gofri, M. A., Wheatcroft, R. A., Miserocchi, S., & Bertotti, L. (2012). Early diagenesis of recently deposited organic matter: A 9-yr time-series study of a flood deposit. *Geochimica et Cosmochimica Acta*, 83, 19–36. <https://doi.org/10.1016/j.gca.2011.12.026>
- Van Der Zwaan, G. J., Duijnste, I. A. P., Den Dulk, M., Ernst, S. R., Jannink, N. T., & Kouwenhoven, T. J. (1999). Benthic foraminifers: proxies or problems? A review of paleocological concepts. In *Earth-Science Reviews* (Vol. 46). www.elsevier.com/locate/earscirev
- 720 Violanti, D. (2000). Morphogroup Analysis of Recent Agglutinated Foraminifers off Terra Nova Bay, Antarctica (Expedition 1987–1988). *Ross Sea Ecology*, 479–492. https://doi.org/10.1007/978-3-642-59607-0_34
- Ward, B. L., Barret, P. J., & Vella, P. (1987). Distribution and ecology of benthic foraminifera in McMurdo Sound, Antarctica. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 58(3–4), 139–153. [https://doi.org/10.1016/0031-0182\(87\)90057-5](https://doi.org/10.1016/0031-0182(87)90057-5)
- 725 Weinkauf, M. F. G., & Milker, Y. (2018). The Effect of Size Fraction in Analyses of Benthic Foraminiferal Assemblages: A Case Study Comparing Assemblages From the >125 and >150 μm Size Fractions. *Frontiers in Earth Science*, 6. <https://doi.org/10.3389/feart.2018.00037>
- Wicham, H., Pedersen, T. L., & Seidel, D. (2025). scales: Scale Functions for Visualizations. *R Package Version 1.4.0*.
- Wickham, H. (2011). ggplot2. *WIREs Computational Statistics*, 3(2), 180–185. <https://doi.org/10.1002/wics.147>
- 730 Zhao, K. X., Stewart, A. L., & McWilliams, J. C. (2022). Linking Overturning, Recirculation, and Melt in Glacial Fjords. *Geophysical Research Letters*, 49(15). <https://doi.org/10.1029/2021GL095706>

735

740

745