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Implication of size fraction on benthic foraminiferal-based paleo-reconstructions: A case study from the Bay of Biscay (NE Atlantic)

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ABSTRACT

Many paleoenvironmental studies based on benthic foraminiferal assemblages use different protocols for sample analysis. A standardized protocol has been recently established for biomonitoring applications, but for paleo-studies, the influence of size fraction on benthic foraminiferal composition and biodiversity is poorly documented. We studied fossil foraminiferal assemblages along two paleorecords (BOBGEO-CS05 and SU81–44) from the Bay of Biscay covering the last ~35 ka cal BP. We investigated diversity and community composition to compare the impact of each size fraction (63–150 μm , >150 μm , >63 μm) on environmental interpretations. Foraminiferal diversity was affected by the accumulation of small opportunistic species. In terms of faunal composition, both paleorecords displayed a different pattern depending on the size fraction selected. While in both cores, the 63–150 μm fraction blurred the signal of some rare indicator species, our results show that i) in BOBGEO-CS05, it yielded no extra ecological information compared to the large fraction whereas ii) in SU81–44, it contained small opportunistic species that were not present in the >150 μm , impacting therefore paleo-environmental interpretations. According to these findings, we recommend: i) to focus on the large fraction for a thorough taxonomic determination and a detailed analysis of benthic assemblages, and ii) to analyse the small fraction separately after a taxonomical identification of major species and strategic selection of studied samples. Although the 125 μm size limit was not tackled in this study, we recommend to use it for the limit between the small and large fractions instead of 150 μm for harmonization with the previously published standardized protocol for living faunas.

1. Introduction

Benthic foraminiferal assemblages are widely studied to characterize modern marine environmental conditions (e.g., Buzas, 1969; Alve, 1995; Jorissen, 1999; Murray, 2006; Bouchet et al., 2012; Pati and Patra, 2012) and to reconstruct past environments (e.g., Alve, 1999; Gooday and Rathburn, 1999; Van der Zwaan et al., 1999; Gooday, 2003; Jorissen et al., 2007), from estuaries to abyssal realms. For ecological studies, the analysis of benthic foraminiferal faunas implies some sieving procedures to remove clays and fine silts from the sample and extract foraminifera of a given size fraction from the sediment. Specimens smaller than the chosen threshold (i.e. size fraction) are ignored. The smaller the foraminifera, the more difficult it is to identify the species (Bé, 1959, 1960), or even impossible for juvenile benthic foraminifera <32 μm or propagules (i.e. dormant stages consisting of a proloculus or few chambers;

Alve and Goldstein, 2002, 2003, 2010). Different size fractions may be chosen depending on sampling regions, environmental characteristics, authors, and institutions e.g., >32 μm in Ohkawara et al., 2009; >63 μm in Thomas et al., 1995; Pascual et al., 2020; >100 μm in Seidenkrantz et al., 2007; Ivanova et al., 2008; >125 μm in Milker et al., 2009; Diz et al., 2020; >150 μm in Gupta et al., 2004; Milker et al., 2017; >250 μm in Schönfeld and Zahn, 2000; >500 μm in Renema, 2008) (see Fig. S1 for other examples). According to the review of Schönfeld (2012), the most frequently used fractions are >63 μm , >125 μm and > 150 μm . The variety of used size fractions in paleo-studies implies that different proportions of the total foraminiferal assemblage are considered and therefore it is challenging to compare data between publications. Several studies based on modern samples discuss the influence of foraminiferal size fraction on the environmental interpretations (Jennings and Helgadottir, 1994; Schroder-Adams et al., 1987; Bouchet et al.,

2012; Lo Giudice Cappelli and Austin, 2019; Fossile et al., 2022; Klootwijk and Alve, 2022). For example, Bouchet et al. (2012) and Klootwijk and Alve (2022) focused on the differences in diversity indices between the $>63\ \mu\text{m}$ and $>125\ \mu\text{m}$ fractions in samples from Skagerrak basin (northeast North Sea) and Norwegian fjords, respectively. They show that although the $>125\ \mu\text{m}$ size fraction describes the general trends in biodiversity and it is therefore enough for an overview of environmental changes, the smaller size fraction provides a less biased estimate of this diversity. Lo Giudice Cappelli and Austin (2019) reached similar conclusions while comparing the $63\text{--}150\ \mu\text{m}$ and $>150\ \mu\text{m}$ fractions in samples from Shetland Island (Scotland). They specified that a certain number of species were exclusively present in one of the two size fractions. Therefore, they proposed to combine the two fractions to obtain a statistically more robust reconstruction. Recently, Fossile et al. (2020) showed that similar foraminiferal-based biozones were identified in Storfjorden (Svalbard) whatever the considered size fraction (i.e. $63\text{--}150\ \mu\text{m}$, >63 or $>150\ \mu\text{m}$), although the $63\text{--}150\ \mu\text{m}$ fraction provides a more precise estimation of diversity. The authors recommended to neglect the $63\text{--}150\ \mu\text{m}$ fraction for future studies in this area considering the time-consuming character inherent to its analysis unless it is studied with the aim of answering some very specific questions. In the same logic, the standardized protocol proposed by the FOBIMO group for biomonitoring studies based on living benthic foraminifera recommended the use of the $>125\ \mu\text{m}$ fraction as the best compromise between processing time and precision in ecological interpretations (Schönfeld et al., 2012).

In paleoceanography, the choice of the most relevant size fraction is still debated. Initially, and for standardization purposes, the CLIMAP group recommended to use the $>149\ \mu\text{m}$ fraction to study planktonic foraminifera (CLIMAP Project Members, 1981, 1984; Kellogg, 1984), a limit that was probably adopted for benthic studies afterwards. This may explain why the $>150\ \mu\text{m}$ fraction is commonly used in paleo-records (e.g., Rohling et al., 1997; Jian et al., 2000; Huang et al., 2003; Gupta et al., 2004; Milker et al., 2017) although several studies are also based on the total $>63\ \mu\text{m}$ fraction (e.g., Thomas et al., 1995; Hayward et al., 2004, 2006; Kang et al., 2010; de Almeida et al., 2015). Few studies discuss the influence of size fraction on paleo-records interpretations and, to our knowledge, only Weinkauff and Milker (2018) precisely compared fossil assemblages and diversity data from two size fractions (i.e. >125 and $>150\ \mu\text{m}$). These authors conclude that the difference in term of biodiversity is small, and the reduction of the limit by $25\ \mu\text{m}$ only improves the representation of the total assemblage but the choice of the size fraction can have an influence on assemblage composition. To our knowledge, no statistical comparison exists between the most commonly used fractions in paleo-records ($>63\ \mu\text{m}$ vs $>150\ \mu\text{m}$).

The aim of this work is to contribute to filling this gap by comparing benthic fossil foraminiferal assemblages between the $>63\ \mu\text{m}$ and $>150\ \mu\text{m}$ size fractions, and as such, to highlight the potential implications on environmental interpretations. These two size limits are commonly used by paleoceanographers in the Bay of Biscay, northeast (NE) Atlantic (Thomas et al., 1995; Mojtahid et al., 2013, 2017; Rodriguez-Lazaro et al., 2017; Pascual et al., 2020; Depuydt et al., 2022; see Fig. S1). We believe that the obtained results are the first stepping-stones towards the building of a standardized protocol for future palaeoceanographic studies. To this end, we studied biodiversity and assemblage composition from two sedimentary cores collected from the Bay of Biscay, at similar water depths (i.e. $\sim 1000\ \text{m}$) (Fig. 1) and covering comparable time periods. Data from BOBGEO-CS05 core, located in the north of the Bay of Biscay and covering the 32–14 ka cal BP time interval, have been published in Depuydt et al. (2022). Core SU81–44 (original data) is located in the south part and covers the last 35 kyr. The objectives of this study are therefore: 1) to identify differences in major species assemblages depending on the size fraction by using multivariate statistical analyses, 2) to evaluate the *plus* value of including the smaller size fraction, 3) to compare the findings between the two different geographical sites and 4) to determine whether the choice of size

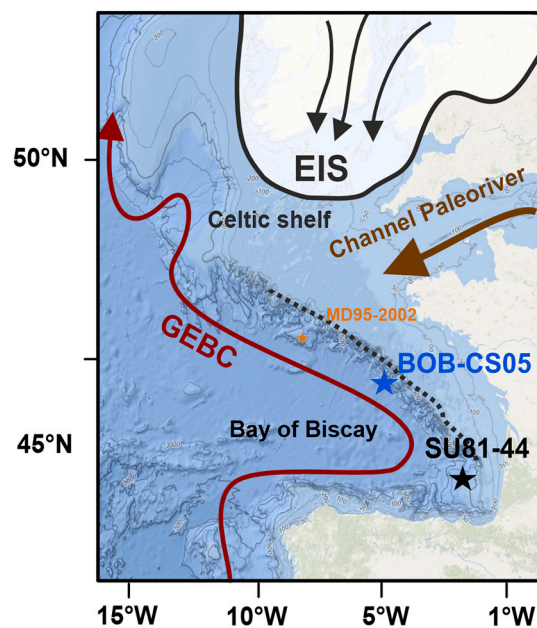


Fig. 1. Bathymetric map modified from Depuydt et al. (2022) representing the paleogeographic and paleoceanographic configuration (i.e. EIS: European Ice Sheet; the Channel Paleoriver; GEB: Glacial Eastern Boundary Current) of the Bay of Biscay during the Last Glacial Period and showing the location of our study cores: BOBGEO-CS05 (blue star; Toucanne et al., 2021; Depuydt et al., 2022) and SU81–44 (black star; this study) with a nearby core at 1000 m water depth (orange star) MD95–2002 (Ménot et al., 2006; Eynaud et al., 2012; Toucanne et al., 2015). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

fractions could effectively have an impact on environmental reconstructions. The results highlight that the discrepancy in the choice of size fraction may hamper the possibility of comparing paleo-records between published studies and call for a standardization of protocols in this field.

2. Materials and methods

2.1. Core locations, sampling and foraminiferal analyses

Two marine sediment cores from the Bay of Biscay (NE Atlantic) were investigated: core BOBGEO-CS05 ($46^{\circ}18.850'N$, $5^{\circ}56.988'W$, 1473 cm length, 1015 m water depth) retrieved during the BOBGEO cruise in 2009 (doi.org/10.17600/9030060; R/V Pourquoi pas?; Bourillet, 2009) and core SU81–44 ($44^{\circ}15.4'N$, $2^{\circ}41.7'W$, 436 cm length, 1173 m water depth) retrieved during the CEPAG cruise in 1981. Cores BOBGEO-CS05 and SU81–44 are located on the upper slope at about 200 km and 100 km from the French Atlantic coast, respectively (Fig. 1). A total of 56 and 65 samples were studied for core BOBGEO-CS05 (Depuydt et al., 2022) and SU81–44, respectively. These samples were washed with tap water through $63\ \mu\text{m}$ and $150\ \mu\text{m}$ mesh sieves, dried, and each fraction was analyzed separately ($63\text{--}150\ \mu\text{m}$ and $>150\ \mu\text{m}$). Note that no disaggregating agents were used for samples' processing. Due to high foraminiferal abundances from the $>150\ \mu\text{m}$ size fraction, the dry samples were split with an Otto microsplitter reaching, at least ~ 250 specimens from a single split. All sorted foraminifera were stored in Plummer cell slides. Wherever possible, we identified specimens to species level (cf. taxonomical list of major species in Fig. S2). For the $63\text{--}150\ \mu\text{m}$ fraction, 16 out of the 56 samples in core BOBGEO-CS05 and 15 out of the 65 samples in core SU81–44 were investigated. The depths of these samples were selected based on major changes of the foraminiferal assemblages observed in the $>150\ \mu\text{m}$ fraction. Dry samples were split with a dry Otto microsplitter to reach a minimum of ~ 250

specimens in the analyzed split. In three samples out of 16 and four samples out of 15 (cores BOBGEO-CS05 and SU81-44, respectively), foraminifera were picked out from the entire split, stored in Plummer cell slides and each specimen of the total assemblage was identified (Fig. S2). For this small fraction, in a few cases we combined species under their genus to avoid misrepresentation and/or misidentification of species. This is for example the case for *Globobulimina* spp. (gathering *G. affinis* and *G. pacifica*) or *Quinqueloculina* spp. where species level was not reached. Major species from the 63–150 µm fraction (>5% of the assemblage) were identified from these samples. For the rest of the 63–150 µm samples, no foraminifera were picked or stored in Plummer cell slides but the total assemblage was counted from the entire split. Moreover, major species were identified and counted separately whereas minor species (<5%) were counted altogether and gathered as ‘others’. The same operator performed all sample analyses and identification to avoid any operator bias. The complete raw data sets for SU81-44 are available as supplementary material in Table S1 and in the SEANOE data repository (<https://doi.org/10.17882/91758> for SU81-44). Raw data for BOBGEO-CS05 have been published in Depuydt et al. (2022) and are available in the SEANOE data repository (<https://doi.org/10.17882/88029>).

The diversity indices (Shannon and equitability) were determined for each size fraction using PAST software (Paleontological Statistics; Version 2.14; Hammer et al., 2001). For the small fraction, diversity indices were only calculated for the 3–4 samples per core that were picked and identified. The Shannon diversity index (H' ; Shannon, 1948) allows to characterize the structure of a community and the distribution of these individuals within this community. It is calculated according to the following formula:

$$H' = - \sum_{i=1}^S p_i \ln p_i$$

Where S is the total number of species (also called species richness) and p_i is the proportion of each species i in the community. It is important to note that the higher the H' value is, the higher is the diversity. The modern H' values for benthic communities in the Atlantic are often between ~1.1 and ~3.8 (Murray, 2006). The equitability index (J ; Pielou, 1966) indicates how similar are the proportion of the species of an assemblage and it is calculated according to:

$$J = \frac{H'}{\ln S}$$

J index varies between 0 and 1 where the maximum represents the most equal distribution of taxa in a given assemblage. As such, it was necessary to apply these diversity indices on fully picked samples (i.e. 3 samples and 4 samples for cores BOBGEO-CS05 and SU81-44, respectively).

The relative abundances of benthic species were calculated for each size fraction (i.e. 63–150 µm, >150 µm and their sum, i.e. >63 µm) and for all samples in both cores. We computed a binomial standard error according to the following formula (Buzas, 1990; Fatela and Taborda, 2002):

$$\text{Binomial standard error} = \frac{\sqrt{p^*(1-p)}}{n}$$

Where p is the species proportion estimate (number of counted individuals for a given species/ n) and n the total number of specimens counted. Several ecological groups that may indicate particular environmental conditions established in Depuydt et al. (2022) for core BOBGEO-CS05 were applied to core SU81-44 for comparison (Table 1).

2.2. Stratigraphic framework

The chronostratigraphic framework of core BOBGEO-CS05 is based on the synchronization of XRF-elements with those of the well dated

Table 1

Classification of major species from cores BOBGEO-CS05 and SU81-44 according to ecological indicators groups as proposed by Depuydt et al. (2022). (*) Species identified as major in core SU81-44 and added into the list published in Depuydt et al. (2022).

Ecological species groups	Major Species/Genera
Glacier-proximal indicator species	<i>Elphidium excavatum</i> f. <i>clavatum</i> <i>Cassidulina crassa</i> d'Orbigny, 1839 <i>Globobulimina</i> spp.
Low oxygen indicator species	<i>Chilostomella oolina</i> Schwager, 1878 <i>Alabaminella weddellensis</i> Earland, 1936* <i>Bolivina</i> spp.
High organic flux indicator species	<i>Cassidulina carinata</i> Silvestri, 1896 <i>Uvigerina mediterranea</i> Hofker, 1932* <i>Uvigerina peregrina</i> Cushman, 1923* <i>Gavelinopsis praegeri</i> Heron-Allen & Earland, 1913
Epiphytic species	<i>Planorbulina mediterraneensis</i> d'Orbigny, 1826
Meso-oligotrophic indicator species	<i>Cibicides pachyderma</i> Rzehak, 1886
High energy indicator species	<i>Cibicides lobatulus</i> Walker & Jacob, 1798 <i>Trifarina angulosa</i> Williamson, 1858

nearby core MD95-2002 (Toucanne et al., 2021). The counts of the polar planktonic taxon *Neogloboquadrina pachyderma* are published in Depuydt et al. (2022). For core SU81-44 and BOBGEO-CS05, *N. pachyderma* was used to identify the Deglacial/Holocene and the last glacial periods, as well as some remarkable events such as the Heinrich Stadials (HSs) (Fig. 2) (Eynaud et al., 2009). A minimum of ~300 specimens of planktonic foraminiferal tests were counted in the >150 µm fraction from a single sample split.

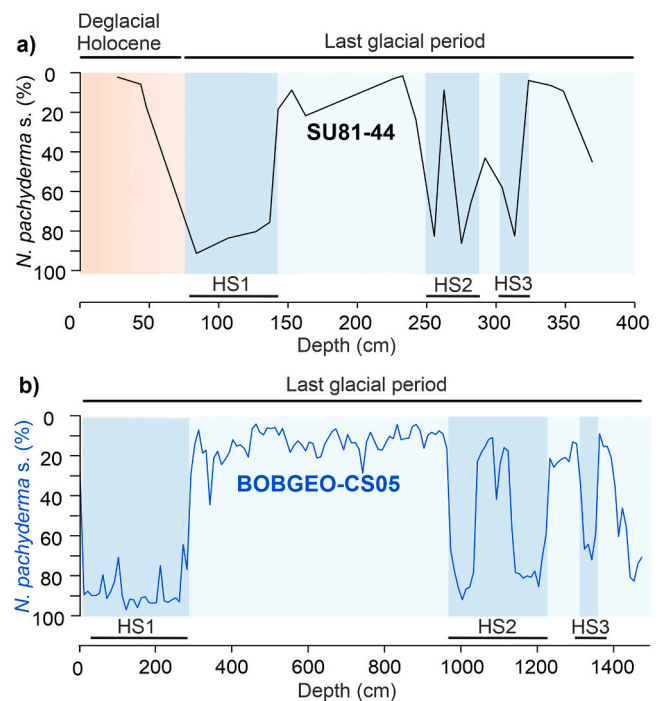


Fig. 2. Percentages of the polar planktonic species *N. pachyderma* according to sediment depths for a) core SU81-44 (black line, this study) and b) core BOBGEO-CS05 (blue line, Depuydt et al., 2022). Blue color represents the Last glacial period and the orange color represents the deglacial/Holocene period. The dark blue bands show Heinrich Stadials. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

2.3. Multivariate analyses

In order to get a visual comparison of the differences in major species compositions (*i.e.* relative abundance >5%) between size fractions (>63 μm and > 150 μm) for each core, a non-metric multidimensional scaling (nMDS) analysis (Taguchi and Oono, 2005) based on Bray-Curtis dissimilarity (Bray and Curtis, 1957) was performed using PAST software (Hammer et al., 2001). The species per sample matrix used for this analysis was based on the relative abundance of major species (>5%) of the 16 and 15 samples analyzed for both size fractions for cores BOBGEO-CS05 and SU81-44, respectively. The different species belonging to the genus *Globobulimina*, *Elphidium*, *Bolivina* and *Bulimina* were lumped together as “*spp.*” for comparison between both fractions of both cores. We chose to compare the results of >63 μm and > 150 μm fractions because the 63–150 μm fraction is rarely used for paleo-record interpretations on its own (supplementary information about the comparison between 63 and 150 μm and > 150 μm are available in Fig. S3 and Table S2). The quality of our nMDS is assessed according to a) stress values (Kruskal and Wish, 1978) that consider ordination as suspect (>0.2), correct (0.1–0.2), good (0.05–0.1) or excellent (<0.05), and b) Shepard's diagram (actual distances vs. ordination distances between samples) that shows a linear trend with little spread (Fig. S4). This visualization for each of the cores is accompanied by an ANOSIM statistical test to discuss the dissimilarity matrices (Clarke, 1993). This was done with 999 permutations on the Bray-Curtis dissimilarity matrices in each core using the *anosim()* function in the R package *vegan* (Oksanen et al., 2020), with the aim of comparing both size fractions to detect differences in major species composition. The ANOSIM test give an R value: if R is close to 1, the test suggests a strong dissimilarity between the fractions whereas an R close to 0 suggests that the distribution is equal between the fractions.

A similarity percentages breakdown (SIMPER) procedure (Clarke, 1993) was also applied to our species-by-sample matrix to identify the main contributing species to the Bray-Curtis dissimilarities detected between the samples of the two fractions studied. This analysis was performed using the *simper()* function of the R package *vegan* (Oksanen et al., 2020) giving an average contribution which we transformed into

percentage. Only the major species with the most influence on the dissimilarities between samples of the two fractions studied (*i.e.* representing ~90% cumulative contribution) were extracted and displayed on the nMDS biplot.

3. Results

3.1. Core SU81-44

Considering the four fully analyzed samples (*i.e.* assemblages picked out and identified in both fractions) from core SU81-44, the 63–150 μm and > 150 μm fractions show similar values of species richness varying between 15 and 25 species (Fig. 3a). Nevertheless, these fractions contain partly different species since the >63 μm fraction (*i.e.* >150 μm + 63–150 μm) exhibits a higher number of species varying between 25 and ~40. The Shannon (H') and equitability (J) indices exhibit different trends through time between the >150 μm fraction on one side and 63–150 μm and > 63 μm fractions on the other side, with a greater difference during the last glacial period at 350 cm depth. Indeed, this sample shows a higher diversity index values when considering only the >150 μm fraction.

In core SU81-44, foraminiferal fauna is characterized by a total of 22 major species (>5% of the total fauna): 8 species out of 22 species are present with >5% whatever the size fraction considered (*Bolivina spp.*, *Cassidulina carinata*, *Cibicidoides pachyderma*, *Cibicides lobatulus*, *Elphidium spp.*, *Gavelinopsis praegeri*, *Melonis affinis*, *Osangularia umbonifera*). Ten species out of 22 species are present with >5% when considering only the >150 μm size fraction (*Bulimina spp.*, *Cibicidoides robertsonianus*, *Cibicides wuellerstorfi*, *Globobulimina spp.*, *Gyroldina orbicularis*, *Quinqueloculina spp.*, *Sigmöilopsis schlumbergeri*, *Spiroloculina tenuiseptata*, *Uvigerina mediterranea*, *Uvigerina peregrina*). Four species are present only in the 63–150 μm size fraction (*Alabaminella weddellensis*, *Epistominella exigua*, *Nonionella turgida* and *Trifarina angulosa*).

The nMDS of core SU81-44 shows a good ordination with a Shepard plot having a linear trend without strong propagations and a stress value = 0.119 (Fig. S4a). The ordinations of this analysis are therefore representative and can be considered as reliable. The nMDS ordination

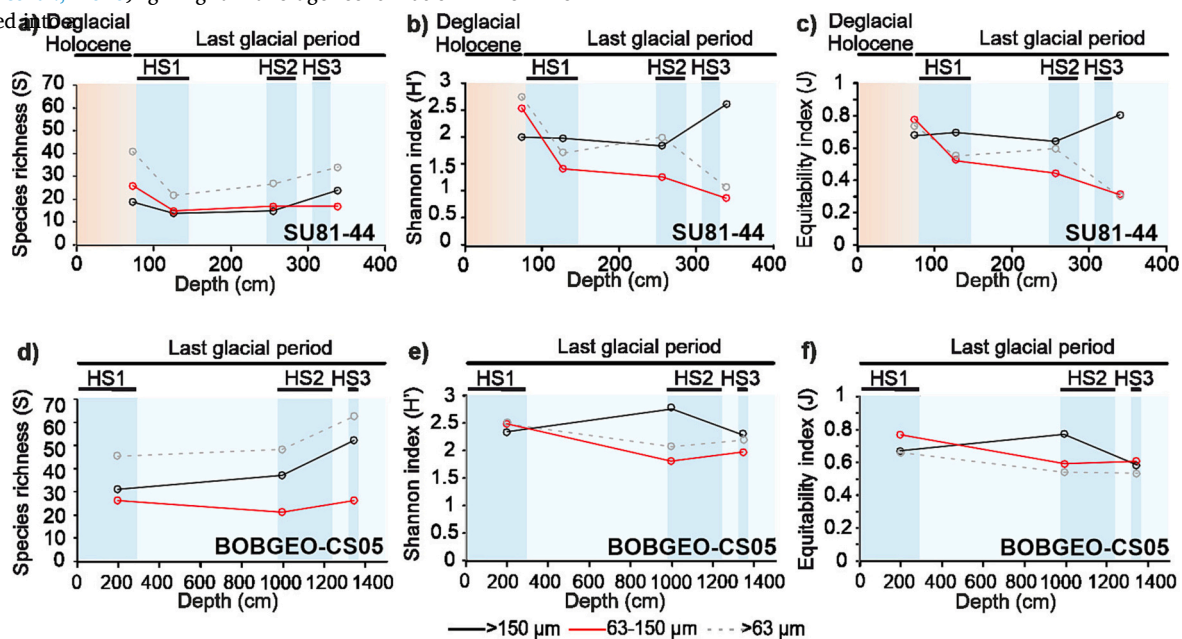


Fig. 3. Biodiversity indices based on benthic foraminiferal faunas calculated separately for the three size fractions: >150 μm (full black line), 63–150 μm (full red line) and > 63 μm fraction (dashed grey line) in a-c) core SU81-44 and d-f) core BOBGEO-CS05. Blue color represents the Last glacial period and the orange color represents the Deglacial/Holocene period. The dark blue bands show Heinrich Stadials. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

in core SU81–44 (Fig. 4a) shows that the first dimension (NMDS1) separates the >63 μm fraction from the >150 μm fraction while NMDS 2 clearly differentiates between deglacial/Holocene and the last glacial period (with HSs and without HSs). The polygonal areas of each convex hull of the size fractions do not overlap. This shows a significant difference between the two fractions, tested statistically by ANOSIM with an $R = 0.966$ ($p = 0.0001$). SIMPER analysis identified eight species contributing significantly ($p < 0.01$) to this observed difference: *Cibicides-pachyderma*, *C. wuellerstorfi*, *Bulimina* spp., *Gyroidina orbicularis*, *Sigmoilipsis schlumbergeri* correlated positively with NMDS1, and *Cassidulina carinata*, *Elphidium* spp., *Trifarina angulosa* correlated negatively with NMDS1. Despite their $p > 0.01$, *U. mediterranea*, *U. peregrina* and *M. affinis* correlate negatively with NMDS 2 and positively with NMDS1, and *A. weddellensis* correlates negatively with NMDS 1 and 2 (Fig. 4a, Table S3a).

The relative densities of major species show that the large fraction (i. e. >150 μm) is largely dominated by *C. pachyderma* with high values between 20 and 80% of the fauna during the last glacial period (Fig. 5b). This species was replaced by *U. peregrina* and *U. mediterranea* (about 20 and 40%, respectively) during the deglacial/Holocene period (Fig. 5c & d). In the small fraction, *C. carinata* dominated the faunas at ~65% during the last glacial period (Fig. 5a), and it was replaced by *A. weddellensis* and *E. exigua* varying around 35% together during the deglacial/Holocene period (Fig. 5e & f). *Alabaminella weddellensis*, *E. exigua* and *T. angulosa* (Fig. 5g) are the only species exclusively pre-sent in the 63–150 μm fraction.

The ecological groups based on indicator species (Fig. 6a) show that the meso-oligotrophic group dominates the large fraction whereas the high organic matter flux indicator group dominates the small fraction. Moreover, the low oxygen indicator group occurring during the HSs in the >150 μm are completely minimized in the >63 μm since they are almost absent in the 63–150 μm .

3.2. Core BOBGEO-CS05

In the three analyzed samples of core BOBGEO-CS05 (Fig. 3d), the species richness shows lower values in the 63–150 μm fraction (~30 species) than in the >150 μm fraction (~40 species). Overall, the values of Shannon and Equitability indices in both fractions are similar for two out of three samples, varying respectively around 2.2 and 0.65 (Fig. 3e-f). When considering only the >150 μm , the sample at ~1000 cm sediment depth is different with a higher diversity fraction.

Foraminiferal fauna is characterized by a total of fifteen major species (i.e. contributing with >5% to the total fauna): five species are found whatever the size fraction considered (*Bolivina* spp., *Cassidulina carinata*, *Cassidulina crassa*, *Cibicides lobatulus*, *Elphidium* spp.). Ten species are found only in the >150 μm fraction (*Cibicides-pachyderma*, *Chilostomella oolina*, *Gavelinopsis praegeri*, *Globobulimina* spp., *Hoe-glundina elegans*, *Nonionella turgida*, *Planorbulina mediterraneensis*, *Pullenia quinqueloba*, *Trifarina angulosa*, *Textularia sagittula*). No species is classified as major only in the 63–150 μm fraction.

The nMDS analysis shows a good ordination with Shepard plot and a

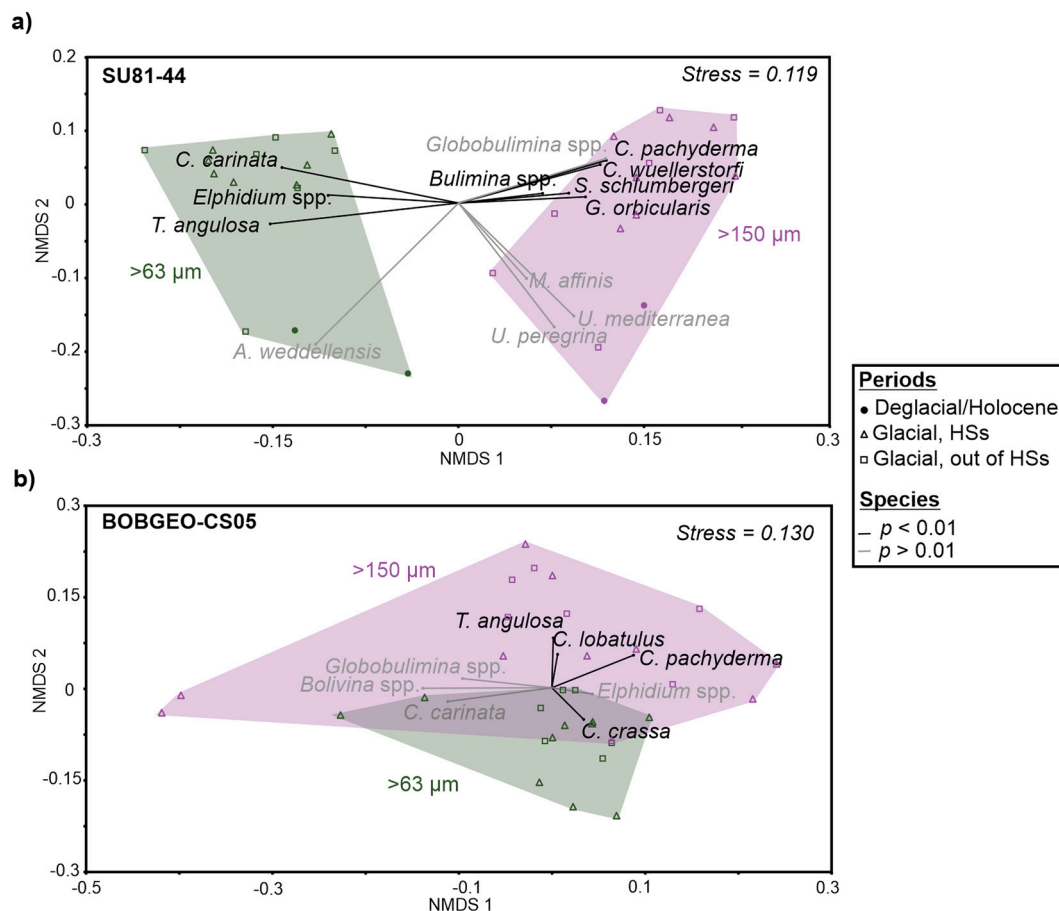


Fig. 4. Non-metric multidimensional scaling (nMDS) analysis (Bray-Curtis dissimilarity) calculated on relative densities of major species (>5%) considering two size fraction groups (>63 μm in green and > 150 μm in pink) for a) core SU81–44 and b) core BOBGEO-CS05. Triangles correspond to samples from the Heinrich Stadials, squares represent samples from the Last glacial period out of Heinrich Stadials, and circles represent the Deglacial/Holocene period. The convex hulls enclosed each size fraction group. The displayed vectors are the species explaining 90% of the dissimilarity between the groups based on SIMPER analysis, with $p < 0.01$ (black) and $p > 0.01$ (grey). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

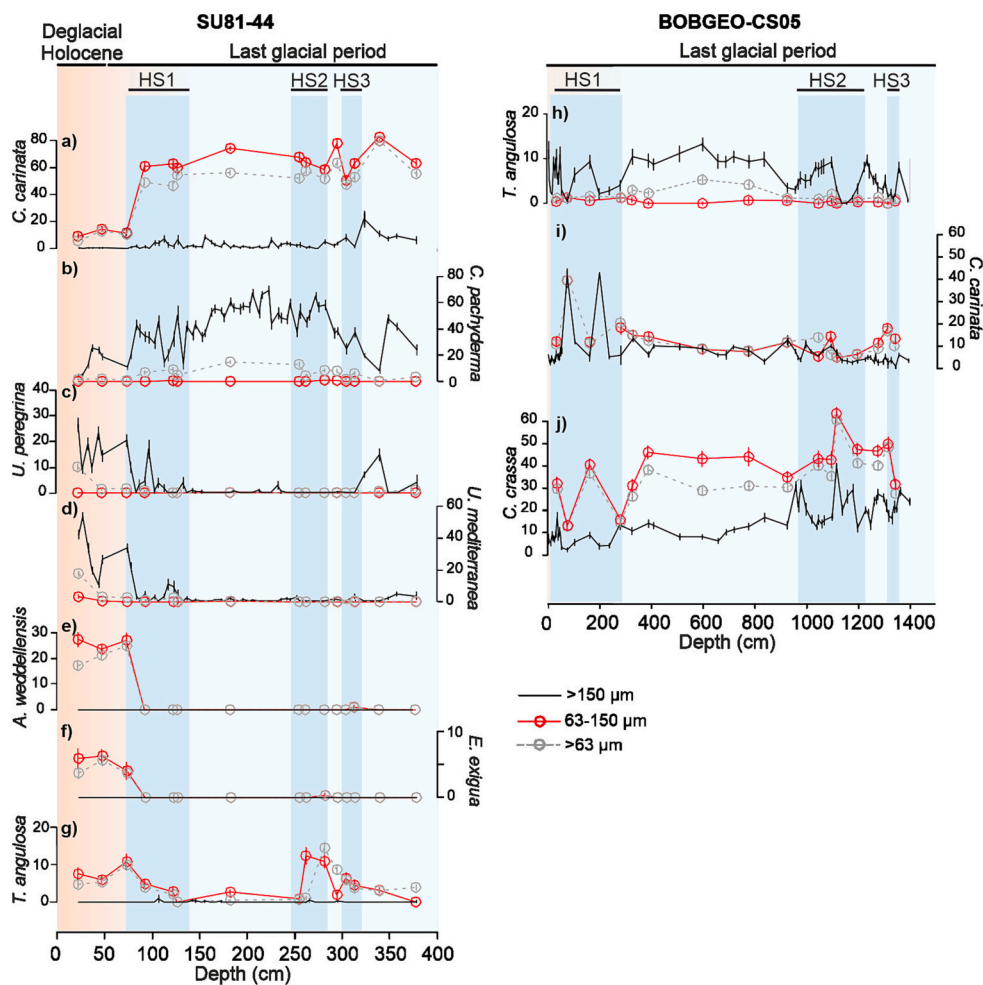


Fig. 5. Relative abundances (%) of benthic foraminiferal faunas from a-g) core SU81-44 (this study) and h-j) core BOBGEO-CS05 (Depuydt et al., 2022). Full black lines, full red lines and dashed grey lines represent respectively the >150 µm, 63–150 µm and > 63 µm. Blue color represents the Last glacial period and the orange color represents the Deglacial/Holocene period. The dark blue bands show Heinrich Stadials. To better highlight the variations of the different species, the scale of the ordinate axis is not constant. Error bars correspond to the binomial standard errors. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

stress value of 0.130 (Fig. S4b). In general, the faunal assemblages between size fractions are less distinct for BOBGEO-CS05 than for SU81-44 (Fig. 4b). For core BOBGEO-CS05, the different size fractions (*i.e.* >63 µm and > 150 µm) are separated on the NMDS2 ordination. Fig. 4b shows that the convex hulls identifying the two size fractions overlap. This result shows that, in core BOBGEO-CS05, dissimilarity between samples decreases when including the 63–150 µm fraction in addition to the >150 µm and the dissimilarity is not as marked as in core SU81-44. The ANOSIM test for this core shows an R of around 0.514 ($p = 0.0001$), which is lower than that of SU81-44. Moreover, the faunal assemblage variations between different sediment depths are enhanced when considering only the >150 µm fraction. Here, the SIMPER analysis identifies only four species contributing significantly ($p < 0.01$) to the difference between the two size fractions (Fig. 4b, Table S3b): *C. lobatulus*, *T. angulosa* and *C. pachyderma* correlates positively with NMDS2 (*i.e.* >150 µm fraction) and *C. crassa* correlates negatively with NMDS2, largely representing the 63–150 µm. Indeed, *C. crassa* dominated the faunal assemblage in the 63–150 µm fraction representing in average about 40% while it represented about 15% of the benthic composition in the large fraction (Fig. 5j). In contrast, *T. angulosa* is almost absent in the 63–150 µm fraction while it reaches about 10% along the record in the >150 µm fraction (Fig. 5h). *Cassidulina carinata* occurred with high percentages during HS1 in both size fractions (Fig. 5i). This species together with *Globobulimina* and *Bolivina* species is negatively correlated with NMDS1 (p value >0.01) showing a higher contribution to HS sample assemblages (Fig. 4b).

Finally, there is little change in the distribution of the ecological groups according to the size fraction (Fig. 6b). Indeed, the glacier-

proximal indicator group, high organic matter flux indicator group and high energy indicator group are well represented regardless of the size fraction. However, the percentages of the low oxygen group and the epiphytic group, are becoming very low when the small fraction is considered.

4. Discussion

4.1. Size fraction effect on foraminiferal biodiversity

In the present study, 15% of the total fossil foraminiferal abundance and 67% of the species richness is recorded in the >150 µm fraction compared to the >63 µm fraction. So considering the small fraction allows taking into account more individuals and species (Fig. 3a and d). According to the review of Schönfeld et al. (2012), only 27% of the living individuals in the deep-sea and 11% in the shallow waters are captured when only the >150 µm size fraction is studied compared to the >63 µm fraction. Regarding the number of species, the ratio is 47% in the deep-sea and 61% in shallow waters. Our results are therefore in the same range as for living foraminifera.

In addition, biodiversity indices show the same trend through time when considering the small fraction 63–150 µm alone or the >63 µm fraction (Fig. 3b-c and 3e-f) but the observed trend is different when considering the larger fraction alone. This indicates that the 63–150 µm does not co-evolve with the >150 µm and the small fraction (63–150 µm) drives the trend observed for the total fraction (*i.e.* >63 µm). In the literature, the addition of the small size fraction to the large one usually results in higher diversity indices (*e.g.*, >30 vs >125 µm in Kurbjewit

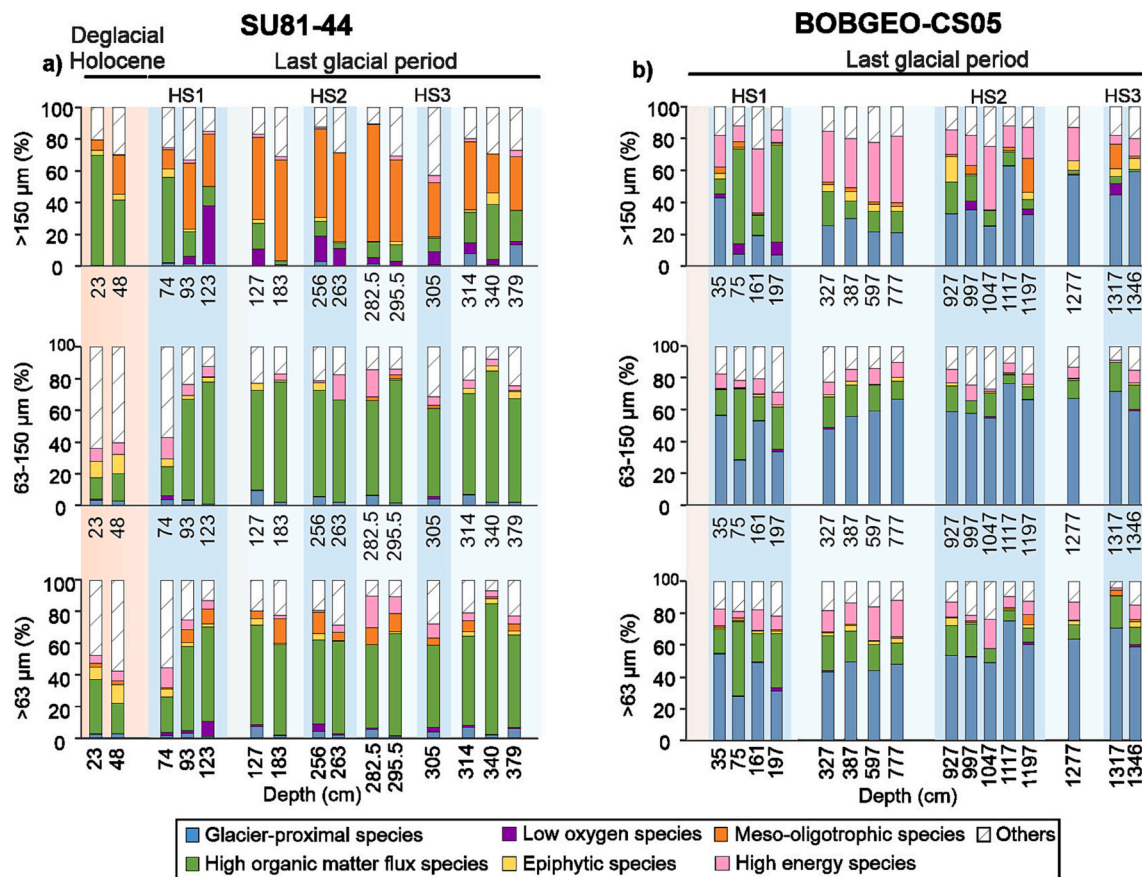


Fig. 6. Relative abundances (%) of benthic foraminiferal indicator groups in each size fraction (>150 µm, 63–150 µm and > 63 µm) for each sample from a) core SU81-44 and b) core BOBGEO-CS05. Blue color represents the Last glacial period and the orange color represents the Deglacial/Holocene period. The dark blue bands show Heinrich Stadials. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 2000; >63 vs >125 µm in Alve, 2010; Klootwijk and Alve, 2022); > 63 vs >150 µm in Schönfeld et al., 2012, Gooday and Goineau, 2019; >125 vs >150 µm in Weinkauff and Milker, 2018). This is not always the case in our dataset where the opposite is observed for half of the data points. Some authors report contrasted results in their study area as well. For instance, Fossile et al. (2020) recorded higher diversity and lower dominance in the >150 µm compared to the >63 µm in the deep basin of Storfjorden (Svalbard) and the opposite for the inner and outer fjord. Phipps et al. (2012) also show contrasting results along a bathymetric transect between stations at <1000 m water depths close to the Portuguese margin (i.e. higher diversity in the 63–150 µm fraction) and those at >1000 m water depths (i.e. higher diversity in >150 µm fraction). In both cases, the authors suggest that the driving parameter could be the availability or quality of organic matter. In our study, the lower diversity (and higher dominance) observed in the >63 µm fraction, driven by the 63–150 µm size fraction, is the result of high percentages of small opportunistic species (e.g., *Cassidulina carinata*, *Epistominella exigua*), probably developing in response to fluctuations in organic matter fluxes. These species, due to high reproduction potential and turnover rate usually would accumulate in fossil records and lead to amplified effect on diversity and equitability indices. This potential accumulation effect in response to population dynamics was suggested by Duros et al. (2012) to explain the higher percentages of opportunistic species observed in the dead assemblages compare to the living one in the Whittard canyon, north of site BOBGEO-CS05. Taphonomic processes such as loss of some non-fossilizing species (e.g., agglutinated species) or transport of tests could also influence the diversity indices. However, these taphonomic effects should affect both the small and large size fractions. More studies based on fossil fauna comparing biodiversity of different size fractions

would allow verifying if this observation is systematic and understanding the effects of seasonal variability and taphonomic mechanisms on size fraction records. Indeed, if the accumulation/removal of indicator species affect paleoenvironmental interpretations, this would hamper the possibility to compare studies based on different size fractions.

4.2. Environmental interpretations driven from assemblages according to the analyzed size fraction

4.2.1. Core SU81-44

In the southeastern Bay of Biscay foraminiferal record, the lower diversity and higher dominance driven by the small size fraction is mainly due to the high presence of *C. carinata* (>60% of the total > 63 µm assemblage) during the last glacial period (Fig. 5a) and *A. weddellensis* (about 30%) during the Holocene (Fig. 5e). These species were present only in low proportions or even absent in the large size fraction. This is supported by the nMDS analysis showing a clear difference between the faunal composition of the >63 µm and the >150 µm size fractions considering the major species (Fig. 4a).

In the Bay of Biscay, *C. carinata* (including *C. laevigata*) is abundant in recent living faunas in the 63–150 µm size fraction (10–15%; Fontanier et al., 2003). However, it reached up to 40% of the large fraction (>150 µm) during the last glacial and deglacial/Holocene periods in paleorecords from the Bay of Biscay (Mojtahid et al., 2013, 2017). This species can dominate the deepest areas of continental shelves exposed to high organic matter input (e.g., Hayward et al., 2002; Fontanier et al., 2003; Hess and Jorissen, 2009). *Alabaminella weddellensis* is a small species restricted to the 63–150 µm size fraction in our study and also

observed in the <125 μm fraction in the living fauna from the NE Atlantic (Gooday, 1988) and in fossil records in Antarctica (Thomas and Gooday, 1996). This species is usually found in association with *Epis-tominella exigua* responding to seasonal organic matter inputs (e.g., Thomas and Gooday, 1996; Gooday and Hughes, 2002; Sun et al., 2006; Smart, 2008; Smart et al., 2019). Opportunistic species, such as *Cassidulina* and *Epistominella* species are often found in small size fractions (Perez-Cruz and Machain-Castillo, 1990; Alve, 2003; Lo Giudice Cap-pelli and Austin, 2019). Some authors suggested that opportunistic species adopt a r-strategy lifestyle (e.g., Gooday et al., 1990; Gooday, 1993; Jorissen, 1988) responding to high organic matter inputs with fast growth and precocious reproductions to colonize rapidly their habitat (Phleger and Soutar, 1973; Gooday et al., 1990; Melki et al., 2010). Due to this strategy, opportunistic species are able to reach very high den-sities in the 63–150 μm fraction, influencing significantly the >63 μm assemblage.

Core SU81–44 is located on the Landes Plateau, influenced by important fluvial inputs from the Adour-Gironde river system (Koutsikopoulos and Le Cann, 1996), known for its strong seasonal variations (Coynel et al., 2005). Because river discharges bring a significant quantity of nutrients, they trigger strong primary production in surface waters (e.g., Nausch et al., 1999; Labry et al., 2001, 2002; Gohin et al., 2003; Guillaud et al., 2008). The benthic communities affected by these seasonal organic matter vertical fluxes may respond with a dominance of opportunistic species.

In the paleo-record of core SU81–44, interpretations in terms of environmental changes are definitely influenced by the size fraction considered. On one hand, when only the >150 μm fraction is considered, the faunal composition during the last glacial period is largely dominated by meso-oligotrophic species (e.g., *C. pachyderma*) (Fig. 5b, 6a). The deglacial/Holocene period is characterized by the presence of *Uvi-gerina* species which are identified as species living in organic-matter rich environments (Jorissen et al., 2007) suggesting a potential shift in surface productivity between the last glacial and Holocene periods (Schönfeld and Altenbach, 2005) (Fig. 5c & d). Moreover, the group of low oxygen tolerant species exhibit higher percentages in the last glacial period (during HSs in particular) compared to deglacial/Holocene samples (Fig. 6a). On the other hand, when the total > 63 μm assemblage is considered, the fauna is dominated by small opportunistic species indicative of high organic matter inputs throughout the record (Fig. 6a) whereas the meso-oligotrophic indicator species become poorly represented. Based on the total > 63 μm assemblage, the study area can be considered as an environment receiving high organic matter fluxes. This is coherent with the nearby study of Pascual et al. (2020), based on the >63 μm fraction, that showed an overall dominance of species appreciating high organic matter environments. In our >63 μm dataset, the transition between the last glacial and deglacial/Holocene periods can still be highlighted by the shift in major species composition (i.e. *C. carinata* vs *A. weddellensis*) (Fig. 5a & e) and the increase in diversity indices (Fig. 3b). However, the low oxygen indicator species group is not anymore usable to distinguish low ventilation events when the >63 μm fraction is considered. Indeed, the proportion of opportunistic species completely “overwrite” the information that could be taken from “rare” species which may be excellent environmental indicators.

4.2.2. Core BOBGEO-CS05

The results of the multivariate analyses for core BOBGEO-CS05 data, which covers only the last glacial period, are very different from SU81–44 data. The convex hulls overlap of the two size fractions show that the faunal assemblages are proportionally more similar between fractions in BOBGEO-CS05 than in SU81–44. The dissimilarity between both fractions is mainly driven by the presence of *Cassidulina crassa* in the small fraction. This species contributes in average to ~35% of the total fauna in the >63 μm fraction and only 15% in the >150 μm frac-tion. According to Depuydt et al. (2022), *C. crassa* responds to large amounts of organic material arriving to the study site during episodes of

EIS melting.

The dominant ecological groups, previously determined by Depuydt et al. (2022) in the same core, remain the same regardless of the size fraction studied (>150 μm and > 63 μm) (Fig. 6b), although the percentages are slightly changing. Indeed, whatever the size fraction considered, there is always a dominance of glacier-proximal indicator and high energy indicator species. Additionally, the addition of the small fraction (63–150 μm) dilutes the signal of the rare “large-size” species from the low oxygen indicator group (i.e. *Globobulimina* and *Chilostomella*) that are well represent by the >150 μm fraction during specific low ventilation events (i.e. HSs) (Mojtahid et al., 2017; Depuydt et al., 2022). This is also the case for the epiphytic group (Fig. 6b). This “dilution effect” is also highlighted by the nMDS results since the >150 μm fraction exhibits higher dissimilarity in the faunal community between samples, i.e. over time, than the >63 μm fraction (Fig. 4b).

4.3. Recommendations in the choice of the size fraction

Our results show that the impact of the used size fraction on paleo-environmental interpretations is not the same depending on the site location. This difference is probably due to the different environmental conditions (e.g., trophic conditions, proximity to the ice sheet influence, bottom-current velocity, nature of sediments) between the two study sites. Core BOBGEO-CS05 is located on a topographically steep slope, relatively well ventilated during the last glacial period due to the influence of the strong North Atlantic Glacial Eastern Boundary current, as testified by sedimentological and geochemical proxies (Toucanne et al., 2021). Core SU81–44, however, is located on a gentle slope and is composed of homogeneous fine sediments. This indicates a lower current velocity than at site BOBGEO-CS05 allowing the settlement of organic-rich fine sediments. This seems to be confirmed by the lower proportion of the “high energy indicator group” in core SU81–44 compared to core BOBGEO-CS05. Benthic foraminiferal community seems to respond differently between the two sites, by exhibiting a higher proportion of small opportunistic specimens in the organic-rich fine sediments of core SU81–44. It is also interesting to note that *Cassidulina carinata*, *Trifarina angulosa* and *Nonionella turgida*, three species present in both records, have different sizes depending on the location. These species are almost exclusively found in the 63–150 μm fraction in SU81–44 (99% of the total individuals of each species is found in the 63–150 μm) whereas they are more present in the >150 μm fraction in BOBGEO-CS05 (respectively 82%, 14% and 29% of the total individuals are found in the 63–150 μm). This behaviour may be explained by generally higher organic matter fluxes in the southern part of the Bay of Biscay which favour an opportunistic r-type strategy resulting in smaller individuals. Mojtahid et al. (2009) also observed a difference in size within the same species depending on the geographical location for *C. carinata*, *N. turgida*, *Rectuvigerina phlegeri* or *Nonion scaphum* in the Rhône prodelta. Smaller specimens of a given species were abundant in the area influenced by the river plume, whereas larger specimens were concentrated close to the river mouth. They suggested that it could be related to an earlier reproductive maturity in the ontogenetic stage in areas under strong organic matter influences. Several planktonic foraminiferal studies also showed a relationship between shell size and surrounding ecological conditions, where some species tend to be relatively larger under optimal conditions for reproduction (e.g., Hecht, 1976; Schmidt et al., 2003; Iwasaki et al., 2017).

Our results show that, even in the same geographic area (i.e. Bay of Biscay) and a similar water depth (i.e. 1000 m), it is still complicated to draw straightforward conclusions about the choice of the size fraction for benthic foraminiferal-based paleoenvironmental reconstructions. For sure, the addition of the 63–150 μm size fraction allows to include a greater number of specimens and species that are absent from the large fraction, and therefore be more representative of the “real” diversity as it has been shown in modern ecological studies (e.g., Schroder-Adams et al., 1987; Lo Giudice Cappelli and Austin, 2019; Klootwijk and Alve,

2022). However, paleoenvironmental interpretations cannot only be based on diversity indices because those are biased by taphonomic processes. Therefore, paleoenvironmental studies rely rather on distribution patterns of single species or groups of indicative species than on diversity indices. However, these patterns may be blurred by the dominance of small opportunistic species. For living foraminifera, Lo Giudice Cappelli and Austin (2019) recommended combining both fractions to achieve high-resolution environmental reconstructions. Our results based on fossil records highlight that the accumulation of opportunistic species shells may dilute the signal of other indicative taxa and therefore reduce the quality of the interpretations. We therefore suggest to systematically analyse both size fractions (63–150 μm and $> 150 \mu\text{m}$) separately to account for the signal provided 1) by rare large species and 2) by small-sized opportunistic species. In addition, this approach allows a more relevant comparison between studies using different size fractions. In fact, some studies on living assemblages had already considered to study the 63–150 μm fraction in a limited number of samples in addition to the $>150 \mu\text{m}$ fraction (e.g., Rathburn et al., 2001; Fontanier et al., 2008; Mojtahid et al., 2009; Gooday and Goineau, 2019). To our opinion, the $>150 \mu\text{m}$ size fraction should be done systematically and thoroughly to reach high time resolution, because it is less time consuming and requires less taxonomic expertise than the study of the small fraction. The small fraction (here 63–150 μm) should be analyzed following a strategic selection of samples depicting the environmental gradient encountered in the core (e.g., glacial/Holocene periods, specific periods as HSs, Bølling-Allerød, etc.). These samples would not necessarily need to be fully sorted/picked, and sample processing could be simplified by only counting major species, once they have been identified for this fraction separately. Depending on the relevance of the small fraction fauna for the paleoenvironmental interpretations, a more detailed analysis of the 63–150 μm may be essential.

These conclusions are based on a limit set at 150 μm for the large size fraction because this limit is traditionally used in the NE Atlantic and particularly in the Bay of Biscay for both living (e.g., Fontanier et al., 2003; Mojtahid et al., 2010; Duros et al., 2012) and fossil faunal studies (cf. Fig. S1). However, for other benthic foraminiferal paleo-studies (e.g., Fontanier et al., 1990; Schmiedl and Mackensen, 1997; Hayward, 2002; Kaminski et al., 2002; Gupta and Thomas, 2003; Diz and Barker, 2016; Das et al., 2021; see Fig. S1). Additionally, this size limit was already chosen as the best compromise for biomonitoring studies (Schönfeld et al., 2012) and Weinkauff and Milker (2018) showed that the $>125 \mu\text{m}$ size fraction better represents the total assemblages in fossil records than the $>150 \mu\text{m}$ fraction. Therefore, we suggest that a step forward, towards a more general homogenization of protocols dealing with benthic foraminifera, would benefit from the choice of the $>125 \mu\text{m}$ instead of $>150 \mu\text{m}$ for the large size fraction. However, conversely to biomonitoring objectives, the separate investigation of the input of the smaller size fraction would be mandatory in the case of paleoceanographic purposes.

5. Conclusions

Our results show that it is complex to process a unique size fraction to reconstruct accurately paleoenvironments. The inclusion of the small fraction allows to be closer to the real diversity when considering living fauna but the average image given by the fossil fauna, subject to taphonomic processes, may follow a different pattern. In terms of faunal assemblages, core BOBGEO-CS05 located in relatively well-dynamic environment, shows that the small fraction blurred the signal of rare indicator species from the $>150 \mu\text{m}$ fraction and provides no additional information compared to the large fraction. Core SU81–44 however, located in a calmer environment and influenced by seasonal inputs of organic matter, shows that it is essential to study the 63–150 μm fraction since the faunal composition from each fraction provides different

paleoenvironmental interpretations. Therefore, our research highlights the need to follow a harmonized protocol for paleoenvironmental studies based on benthic foraminifera as the one proposed by Schönfeld et al. (2012) for the biomonitoring studies. In view of our results in the NE Atlantic at 1000 m water depth and for harmonization of practices within the community working on living and fossil assemblages, our recommendations for the paleoenvironmental reconstructions are:

- 1) To separate the small fraction (preferentially 63–125 μm , or 63–150 μm) from the large fraction (preferentially $>125 \mu\text{m}$, or $> 150 \mu\text{m}$) during sample preparation and treatment;
- 2) To focus systematically on the large fraction (preferentially $>125 \mu\text{m}$, or $> 150 \mu\text{m}$) for high time resolution analysis of benthic assemblages;
- 3) To make a strategic choice in the selection of samples to study the small fraction (preferentially 63–125 μm , or 63–150 μm) for a complete analysis of foraminiferal faunas. This will highlight the relevance of this fraction and allow to identify major species;
- 4) Depending on the study purpose, a more detailed analysis of the small fraction might be essential, either by focusing on major species or on total fauna.

More studies comparing the difference between size fractions in other geographic areas, water depths and time intervals are necessary in order to validate or improve the above proposed procedure. Moreover, the systematic availability (in open databases) of distinct databases for each size fraction studied will definitely help to reach a standardized protocol for paleoenvironmental studies.

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marmicro.2023.102242>.

Declaration of Competing Interest

None.

Data availability

I have shared the link to my data at the attached file step

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