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Intermediate ocean circulation and cryosphere dynamics in the northeast Atlantic during Heinrich Stadials: benthic foraminiferal assemblage response

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Abstract :

The interaction between ocean circulation and ice-sheet dynamics plays a key role in the Quaternary climate. Compared with the surface and deep regions of the Atlantic Meridional Overturning Circulation (AMOC), the study of intermediate depths during key time periods, such as Heinrich Stadials (HSs), remains poorly documented, especially for the northeast Atlantic. Here we use benthic foraminiferal assemblage data to trace palaeoenvironmental changes from similar to 32 to 14 ka cal BP at similar to 1000 m depth in the Bay of Biscay. Our results highlight the high sensitivity of foraminifera, with species-specific responses, to continental (European Ice Sheet dynamics) and marine (AMOC) forcing factors during the last three HSs. In general, HSs were characterised by the concomitant presence of meso-oligotrophic and anoxia indicator species and the low abundance of high-energy indicator species. This confirms an overall sluggish intermediate circulation during the three HSs in the northeast Atlantic. HS1 is distinctive for its abundance of high-organic flux indicator species during its early phase. This is consistent with the fact that HS1 was by far the most important period of ice-sheet retreat and meltwater release into the ocean over the studied time interval. Finally, foraminifera depict the mid-HS2 reventilation event due to regional glacier instabilities.

Keywords : AMOC, benthic foraminifera, Channel River, European Ice Sheet, Glacial Eastern Boundary Current (GEBC), intermediate water masses

1. Introduction

The last glacial-interglacial cycle is a critical period to understand the natural climate variability and its abrupt transitions (e.g. Bond *et al.*, 1993; Wang et *al.*, 2001; Clark *et al.*, 2012; Denton *et al.*, 2021). Orbital forcing (solar radiation), and the feedbacks implying the atmosphere, the ocean, and the cryosphere are the main factors explaining the recorded centennial to multi-millennial climate variability over this period (Broecker and Denton, 1990; McManus *et al.*, 1999; Denton *et al.*, 2010; Lynch-Stieglitz, 2017). In the Northern Hemisphere, the climate of the last glacial period was punctuated by cold (stadials) and warm intervals (interstadials), that were coeval with periods of weakened and accelerated Atlantic Meridional Overturning Circulation (AMOC), respectively (e.g. Kissel *et al.*, 2008; Böhm *et al.*, 2015; Henry *et al.*, 2016; Toucanne *et al.*, 2021). Amongst the cold intervals, the most drastic are certainly the Heinrich Stadials (HSs), encompassing the Heinrich events (HEs), i.e. armadas of icebergs discharge issued from the dislocation of the Hudson Strait Ice stream of the Laurentide Ice Sheet (LIS) that ultimately caused the deposition of ice-rafted debris (IRD) rich sediments in the subpolar North Atlantic (Hemming, 2004). It is hypothesized that HEs were triggered by sub-surface heat (700–1100 m depth), 1-2 ka after the decline of the AMOC (Shaffer *et al.*, 2004; Marcott *et al.*, 2011; Alvarez-Solas *et al.*, 2013). The initial AMOC slowdown likely requires precursor melting of North Atlantic–adjacent ice sheets and it is now accepted that the European Ice sheet (EIS) was a critical source for AMOC destabilization and the initiation of HSs conditions (Peck *et al.*, 2006; Eynaud *et al.*, 2012; Boswell *et al.*, 2019; Toucanne *et al.*, 2015, 2021, 2022).

The present work investigates the evolution of northeast Atlantic intermediate water depth environments and their interaction with EIS dynamics during the last glacial and deglaciation periods, with a focus on HSs. This is achieved through the study of marine sediment core BOBGEO-CS05 retrieved at ~1000 m water depth in the northern Bay of Biscay (BoB) (Fig. 1a & 1c). This record covers the past ~32-14 ka cal BP, thus encompassing the last three HSs (HS1, HS2 and HS3). During the last glacial period and the last deglaciation, BOBGEO-CS05 site was located off the Channel River, that drained EIS sediment-laden meltwaters to the northern BoB (Zaragosi *et al.*, 2001; Bourillet and Lericolais, 2003; Toucanne *et al.*, 2009, 2010) (Fig. 1b). At the time, the core site was also on the pathway of the Glacial Eastern Boundary Current (GEBC), the glacial analogue of the northward-flowing European Slope Current, that represents the easternmost portion of the upper branch of the AMOC (Toucanne

et al., 2021) (Fig. 1b). As such, core BOBGEO-CS05 is ideally located to track EIS melting episodes and evaluate their impact/relation to the upper branch of the AMOC.

The present study focuses on fossil benthic foraminifera as one of the very few biological indicator groups that are able to record the history of events on the seafloor by integrating the cumulative impacts of the changing physico-chemical habitats (e.g. Schmiedl and Mackensen, 1997; Wollenburg *et al.*, 2001; Rodriguez-Lazaro *et al.*, 2017). A particular interest is found in documenting HS2 and HS3, which are not covered by the nearby recent foraminiferal studies (Mojtahid *et al.*, 2017; Pascual *et al.*, 2020). In addition, our aim is to establish to what extent information previously obtained from sedimentary, geochemical and surface water proxies on the interaction between the AMOC and the EIS during the HSs are consistent with our benthic biotic data. More specifically, the approach uses here foraminiferal diversity and density, and the ecological requirements of specific species to interpret several aspects of the environment on the seafloor (e.g. organic matter flux, bottom-water oxygenation, current, transport, water masses properties). Our findings highlight strong foraminiferal species-specific responses, particularly during HSs, with some species associations able to discriminate between EIS/continental impact and ocean circulation changes.

2. Core location, present and past sedimentological and hydrographical settings

Core BOBGEO-CS05 (46°18.850'N, 5°56.988'W, 1473 cm length, 1015 m water depth) was extracted from the upper continental slope of the northern BoB (northeast Atlantic) during the BOBGEO cruise (doi.org/10.17600/9030060; R/V Pourquoi pas?; Bourillet, 2009) (Fig. 1). Core BOBGEO-SC05 is mostly composed of contourite deposits (Toucanne *et al.*, 2021), i.e. sediments deposited or substantially reworked by the persistent action (e.g. selective deposition, winnowing, erosion) of bottom currents (Facies 1 and 2; Fig. 2). Silty-clayey laminations characterized the early part of the deglaciation (early HS1), ca. 18-16.7 ka (Facies 3; Fig. 2), and IRD (Facies 4; Fig. 2) allowed the recognition of the Heinrich layers (cf. Supplementary material S1 for the complete X-Ray radiographs).

Today, the sedimentation on the slope is governed by the European Slope Current (ESC), flowing along the upper slope (~500-2000 m water depth) from the northern Iberian Peninsula to the Faroe-Shetland Channel (Marsh *et al.*, 2017; Clark *et al.*, 2021; Moritz *et al.*, 2021) (Fig. 1a). This current, driven by both the steep topography of the European margin and large-scale meridional density gradients (Huthnance, 1984; Pingree and Cann, 1990; Friocourt

et al., 2007), is largely recruited from the eastern North Atlantic and is connected, north of ~55°N (i.e. Rockall Trough), to the upper part of the North Atlantic Current (NAC; that is the eastern limb of the subpolar gyre). This forms the bulk of the upper branch of the AMOC (down to ~1500 m; Lozier *et al.*, 2019; Huthnance *et al.*, 2020). The latter (to which the ESC contributes by ~25 %; Berx *et al.*, 2013) finally reaches the Nordic Seas convection region, where it cools and sinks to form a deeper southward return flow, the North Atlantic Deep Water (NADW), mainly found along the eastern continental margin of North America and transported by the Deep Western Boundary Current (e.g. Dickson and Brown, 1994) (Fig. 1a).

The main water mass transported by the NAC into the BoB forms the Eastern North Atlantic Central Water (ENACW), found down to ~600 m water depth (Pollard and Pu, 1985). Below, the Mediterranean Outflow Water (MOW) is present between ~600 and 1500 m, flowing northward from the Gulf of Cadiz and largely entrained by the ESC north of ~45°N (e.g. Pingree *et al.*, 1999; van Aken, 2000). Deeper, the Labrador Sea Water (LSW), centered at ~2000 m water depth and corresponding to the upper NADW, dominates (van Aken, 2000). The upper NADW in the eastern North Atlantic and the BoB reflects recirculation processes, i.e. capture of the (southward-flowing) LSW by the above (eastward-flowing) Gulf Stream – NAC system in the north-western North Atlantic (Buckley and Marshall, 2016; Zou *et al.*, 2017) (Fig. 1a).

During the last glacial maximum (LGM) ca. 23-18 ka cal BP (Mix *et al.*, 2001), the Gulf Steam – NAC system and more generally the upper branch of the AMOC certainly had a different geometry (i.e. positioned southward) because of the (southward) expansion of ice sheets over North America (Keffer *et al.*, 1988; Otto-Bliesner *et al.*, 2006; Brady and Otto-Bliesner, 2011; Löfverström *et al.*, 2014) (Fig. 1b). The NADW was likely replaced by a shallower, northern-sourced nutrient-poor water mass, namely the Glacial North Atlantic Intermediate Water (GNAIW), dominant above 2000 m depth and overlaying a more nutrient-rich water of southern origin below 2000 m (i.e. a glacial analog of Antarctic Bottom Water) (e.g. Lynch-Stieglitz *et al.*, 2007). The recirculation of the GNAIW by the glacial Gulf Stream – NAC system certainly explains GNAIW signatures recorded in the NE Atlantic basin and the BoB basin during the last glacial period (Zahn *et al.*, 1997; Peck *et al.*, 2006, 2007; Toucanne *et al.*, 2021). At the same time, the Mediterranean-Atlantic water exchange was reduced by ~50 %, and the MOW was certainly restricted to the southern Iberian margin (e.g. Rogerson *et al.*, 2012). On the other hand, the presence of Antarctic Intermediate waters (AAIW) along the European margin as far north as the South Iceland Rise was hypothesized (Rickaby and Elderfield, 2005; Thornalley *et al.*, 2010) but the recent studies of Thornalley *et al.* (2015) then

Crocker *et al.* (2016) concluded that mid-depth in the NE Atlantic was never ventilated by southern-sourced waters during the last glacial period. During late HS1 (~17 ka), and the near shutdown of the AMOC (McManus *et al.*, 2004; Ng *et al.*, 2018), Mojtahid *et al.* (2017) recorded low foraminiferal Sr/Ca ratios (i.e. carbonate system proxy; Yu *et al.*, 2014; Allen *et al.*, 2016; Keul *et al.*, 2017), indicative of a change in water mass chemistry and origin in the BoB. At the same time, Mojtahid *et al.* (2017) recorded increasing benthic foraminiferal Mg/Ca ratios, indicating a warming of intermediate water masses. This is interpreted as the northward conveyance of the subsurface warming originating from the low latitudes (Rühlemann *et al.*, 2004; Shaffer *et al.*, 2004) by the glacial NAC (GNAC) and the GEBC (Fig. 1b) (Toucanne *et al.*, 2021). This reinforces the view that the water mass structure in the glacial NE Atlantic could have changed rapidly through time.

3. Materials and Methods

3.1. Chronology

The chronostratigraphic framework of core BOBGEO-CS05 (Fig. 2) is detailed in Toucanne *et al.* (2021). In short, the final age model is based on XRF-Ca/Ti data synchronization with the nearby well-dated core MD95-2002 (Fig. 2a). Twenty-one XRF tie-points based on the recognition of millennial-scale oscillations were determined. The final age model indicates that core BOBGEO-CS05 covers a period extending from ca. 32 to 14 ka cal BP (Fig. 2), thus encompassing the end of MIS 3 (ca. 57-29 ka cal BP) and MIS 2 (ca. 29-14.7 ka cal BP). The accuracy of the age model is supported first by the good match between the percentages of the polar planktonic taxon *N. pachyderma* in core BOBGEO-CS05 and MD95-2002 (Fig. 2c), and second, by the overall concordance with the new radiocarbon dates (n=12; Table 1; Fig. 2b). The top core ^{14}C dates show older ages (~15.7 cal ka BP) than the final XRF-Ca/Ti based age model (~14 cal ka BP) (Fig. 2b). The low percentages of the polar taxon *N. pachyderma* at the core top (Fig. 2c) indicate that we are out of the Heinrich Stadial, making the core top ^{14}C ages unreliable. Such incoherencies in ^{14}C dates (including the few outliers; Fig. 2b) are certainly linked to physical sediment mixing and bioturbation that are common in contourite deposits.

The final age model clearly shows a sedimentary hiatus after ~14 cal ka BP, in concordance with previous studies in similar environments in the BoB (Mojtahid *et al.*, 2017; Toucanne *et al.*, 2021). The lack of sedimentation is due to increased erosion of the shelf deposits in response

169 to the significant sea-level rise and the embayment of the English Channel (e.g., Bourillet *et al.*,
170 2003; Toucanne *et al.*, 2012).

171 Core BOBGEO-CS05 shows sedimentation rates of 50-150 cm.ka^{-1} (Fig. 2b). As such, core
172 BOBGEO-CS05 offers a unique opportunity to study at high time resolution the later part of
173 the last glacial period and the last three HSs.

174

175 ***3.2. Foraminiferal analyses***

176 For benthic foraminiferal analyses, 56 samples were investigated (~320 years resolution). The
177 samples were washed through 63 and 150 µm mesh size sieves. The >150 µm fraction was
178 splitted with a dry Otto microsplitter (when necessary) until obtaining at least 250-300
179 specimens in the final split. Then, all foraminifera were picked out from the split and mounted
180 on Plummer cell slides for taxonomic determination. To verify the relevance of small-sized
181 benthic species, 16 out of the 56 samples were investigated from the 63-150 µm size fraction.
182 Foraminifera were picked out from 3 out of the 16 samples, put in Plummer cell slides and
183 determined taxonomically. For the rest of the 63-150 µm samples, foraminifera were counted
184 and determined directly under the stereomicroscope. Similarly to the >150 µm fraction, samples
185 (63-150 µm) were splitted with a dry Otto microsplitter until obtaining at least 250-300
186 specimens in the final split. The benthic foraminiferal accumulation rate (ind.cm^{-2}.ka^{-1})
187 (BFAR), used as paleo-productivity proxy (Herguera and Berger, 1991; Herguera, 1992;
188 Gooday, 2003; Jorissen *et al.*, 2007), was calculated for both the >150 µm and >63 µm (63-150
189 + >150 µm) fractions as: number of individuals per gram of dry sediment × linear sedimentation
190 rate (cm.ka^{-1}) × Dry Bulk Density (g.cm^{-3}) (Herguera and Berger, 1991). The Dry Bulk Density
191 (DBD) was calculated following the relation: DBD = 2.65 x (1.024 – D_{wet})/(1.024-2.65), where
192 2.65 g.cm^{-3} is the grain density and 1.024 g.cm^{-3} is the interstitial water density (Auffret *et al.*,
193 2002). Wet bulk densities (D_{wet}) were derived from gamma-ray attenuation density
194 measurements obtained from a 'Geotek Multi Sensor Core Logger' (MSCL).

195 The relative abundances of benthic species (% of the total foraminiferal abundances) were
196 calculated for the >150 µm fraction for the 56 samples and for the >63 µm fraction (63-150 µm
197 + >150 µm) for the selected 16 samples. The error bars of the relative abundances were
198 computed with the binomial standard error $\sqrt{(p(1-p))/n}$ (Buzas, 1990; Fatela and Taborda,
199 2002), where p is the species proportion estimate (number of counted individuals for a given
200 species/n). The diversity of the 56 samples (>150 µm) was calculated with the Shannon index

(entropy, H; Hayek and Buzas, 1997) using the PAST software (PAleontological STatistics; Version 2.14; Hammer *et al.*, 2001). Error bars representing 95 % confidence interval were computed with a bootstrap procedure. In this study, we discuss mainly the most dominant species with relative abundance >10 % showing the highest variability. All species with relative abundance between 5 and 10 % in at least one sample are presented in supplementary material S2, and their ecological interpretations summarized in Table 2. The complete raw data set is available as supplementary material S3 and in SEANOE data repository (https://doi.org/10.17882/88029). Scanning Electron Microscope (SEM) photographs were obtained at LPG (Angers University, France) using a Tabletop Microscope Hitachi TM4000Plus.

For the counts of the planktonic taxon *N. pachyderma*, the >150 µm fraction were used and the relative abundances were determined using a minimum of 300 planktonic foraminiferal tests from single sample splits. Counting was performed at University of Bordeaux (France).

4. Results

Average BFAR values from the >150 µm fraction are ~12.10^3 ind.cm^{-2}.ka^{-1} and from the >63 µm are ~$7.5.10^6$ ind.cm^{-2}.ka^{-1} (Fig. 3a). The values from the >150 µm fraction are minimal during the three HSs (~1.10^3 ind.cm^{-2}.ka^{-1}) and are more important during the interstadial periods (~30.10^3 ind.cm^{-2}.ka^{-1}).

From ~32 to 14 ka cal BP, the Shannon (H) index (Fig. 3b) shows an overall increase of diversity, with values ranging from ~2 to 3.2.

The eight most dominant species (>10 %) showing the highest variability are illustrated in Plate 1 and their relative abundances are presented in Figure 3 (c-j). *Elphidium* spp., *Cassidulina crassa* and *Cibicides lobatulus* are dominant along the record and account together for 12.7 to 74.3 % of the total fauna. In this study, *Elphidium* spp. includes mainly *E. excavatum* (i.e. *E. excavatum* f. *clavatum*) with pyritized shells (Plate 2a) and other species of the genus *Elphidium* (e.g. *E. gerthi*, *E. macellum*). *Elphidium* spp. show maximum values (>30 %) between 30.7 and 28.9 ka cal BP (i.e. HS3) and minimum values (<10 %) between 17.5 and 16.5 ka cal BP (i.e. Early HS1; Fig. 3c). Before HS2, *C. crassa* accounts in average for about ~21 % of the total fauna (Fig. 3d). The highest values are recorded during HS2, with maximum percentages (40 %) just before HE2 followed by a sharp decrease. After HS2, the relative density of this species remains stable around ~8 %. *Cibicides lobatulus* exhibits a different

pattern in comparison with the previously mentioned species. Generally, this species is present with lower proportions during HS periods (around 5-10 %), except at 24.2 ka cal BP (during HE2) and 17.2 ka cal BP (during HS1). Between HS3 and HS2 (ca. 29-26 ka cal BP) and during the LGM (ca. 23-18 ka cal BP), *C. lobatulus* accounts for ~22 % of the total fauna (Fig. 3e). *Trifarina angulosa* shows the same trend as *C. lobatulus* (Fig. 3f) but with overall lower proportions (maximum values around 10 %). The remaining dominant species (>10 %) present a discontinuous evolution. *Cassidulina carinata, Bolivina* spp. and *Globobulimina* spp. exhibit high relative abundances (up to 42 %, 24 % and 18 % respectively), with high variability, during early HS1 (Figs. 3g, 3h & 3i). Before HS1, *Globobulimina* species are almost absent except in samples from HS3 and HS2 (average of ~5 % and 7.5 %, respectively). *Cibicidoides pachyderma* is also present mainly during the three HSs reaching 12.5 % at 29.3 ka cal BP (i.e. during HS3), 20 % at 25.3 ka cal BP (i.e. during HS2) and varying around 10 % at ~HS1 (Fig. 3j). Here, *C. pachyderma* encompasses several morphotypes spanning from *C. pachyderma* sensu stricto (pronounced carina) to *Cibicidoides kullenbergi* sensu stricto (less pronounced carina) (Plate 2b). The presence of several intermediate morphotypes hampered the taxonomical differentiation between *C. pachyderma* and *C. kullenbergi*, and as such were lumped together as *C. pachyderma.*

The evolution through time of the minor species (i.e. present only few times with percentages >5 %) is represented in supplementary material S2. *Gavelinopsis praegeri* and *Planorbulina mediterranensis* mainly appear just after 24.2 ka cal BP, between HE2 and the end of HS2. *Chilostomella oolina, Pullenia quinqueloba, Textularia sagittula* occur just one time with relative densities >5 % at 16.8 ka cal BP, 16.5 ka cal BP, 17.2 ka cal BP respectively while *Hoeglundina elegans* occurs only at 14 ka cal BP. *Nonionella turgida* become dominant only after HE1 (~6 %).

In the small fraction (63-150 µm), the identified species were similar to the ones found in the larger size fraction (>150 µm). When considering the small and large fractions together (>63 µm), six major species >5 % are present: *Elphidium* spp., *C. crassa, C. lobatulus, C. carinata, Bolivina* spp. and *T. angulosa.* These species, also identified as major species when considering only the >150 µm size fraction, exhibit approximately similar trends (black dashed line; Fig. 3 c-h). Only *C. crassa* presents much higher proportions in the >63 µm fraction with abundances ranging from 15 to 60 % of the total fauna.

5. Discussion

5.1. Regional inter-comparison of benthic foraminiferal faunas

Most of the dominant foraminiferal taxa in core BOBGEO-CS05 (e.g. *C. pachyderma*, *C. carinata*, *C. crassa*, *Bolivina* spp., *Globobulimina* spp.) inhabit the modern upper slope environments of the BoB (e.g. Murray, 1970; Fontanier *et al.*, 2006; Mojtahid *et al.*, 2010; Duros *et al.*, 2011, 2012; Dorst and Schönfeld, 2013), and/or are found in the regional benthic fossil (i.e. last glacial) records of intermediate waters depths (Fig. 1c; Mojtahid *et al.*, 2017; Pascual *et al.*, 2020). However, some discrepancies are observed and detailed hereafter:

5.1.1. High-energy indicator species

Cibicides lobatulus (also known as *Lobatula lobatula*) is highly dominant in our record (~4-30 %). This species is also present, but with overall lower percentages (~10 %), at site MD99-2328, north of our study site (Fig. 1), that covers the time interval from 23 to 16 ka cal BP (Mojtahid *et al.*, 2017) (Fig. 3). However, this epibenthic species is absent today from the BoB modern foraminiferal communities at ~1000 m depth (e.g. Fontanier *et al.*, 2002; Fontanier *et al.*, 2006; Mojtahid *et al.*, 2010; Duros *et al.*, 2011, 2012). This discrepancy can be explained by different environmental conditions (e.g. food source, hydrodynamics) during the last glacial period allowing their settlement at intermediate water depths in the area. Indeed, *C. lobatulus* is a suspension-feeder that inhabits moderate-to-strong hydrodynamic environments of the modern northeast Atlantic. These include shelf environments (e.g. Basque shelf; Pascual *et al.*, 2008) and upper slope settings swept by strong bottom currents and characterized by coarse substrate and/or cold-water coral mounds and reefs trapping abundant food particles (e.g. Gulf of Cadiz, Porcupine and Rockall Banks; Schönfeld, 1997, 2002a, 2002b; Margreth *et al.*, 2009; Spezzaferri *et al.*, 2015). As such, the high presence of *C. lobatulus* in the BOBGEO-CS05 glacial record might indicate stronger currents than today. The depicted link between *C. lobatulus* and strong energy environments is further supported in our record by its co-variation with: i) the abundance of *Trifarina angulosa* ($r^2 = 0.78$) (Figs. 3e & 3f) which is commonly associated with shelf-edge to upper-slope areas swept by vigorous bottom currents (e.g. southwest Norway, Rockall Trough; Mackensen *et al.*, 1985; Austin and Evans, 2000; Gooday and Hughes, 2002), and ii) the "sortable silt" mean size $\overline{SS}$ (i.e. the mean grain size of the carbonate-free terrigenous silt fraction) at BOBGEO-CS05 (Fig. 4f; Toucanne *et al.*, 2021) that provides a direct constraint on the rate of past bottom flows (McCave *et al.*, 1995). As such, our biotic data independently support the presence of strong bottom currents on the upper slope

of the BoB, and by extent the presence of the GEBC along the French Atlantic margin (Toucanne *et al.*, 2021). Based on the above, we summed the percentages of *C. lobatulus* and *T. angulosa* to constitute the group of high-energy indicator species. The latter will be used to examine the hydrodynamics variability in the study area throughout the ca. 32-14 ka cal BP interval, and more specifically during the HSs (cf. section 5.2).

5.1.2. Glacier-proximal species

The high dominance (up to ~40 % in the late MIS 3 and ~20 % thereafter) of elphidiids in core BOBGEO-CS05 is peculiar as this group is presently found in coastal, shelf and estuarine environments of the northeast Atlantic (e.g. Pujos, 1976; Murray, 2014; Mojtahid *et al.*, 2016). In the modern benthic foraminiferal assemblage of the upper Whittard region (northern BoB, ~1000 m depth; Duros *et al.*, 2012), *Elphidium* spp. are found only in the dead faunas, and as such, were considered as transported from shallower settings. Mojtahid *et al.* (2017) report high abundances of *Elphidium* spp. in core MD99-2328 especially during the late HS1 (16.7-16 ka cal BP; up to ~70 %) and hypothesized their transport to these intermediate depths by the EIS icebergs and/or shelf ice. This would be also a possibility for BOBGEO-CS05 since *Elphidium* shells show pyritization marks (Plate 2a) that may indicate a potential reworking and transport. However, it is interesting to note that modern elphidiids may extend their habitats to deeper settings (several hundred meters) in cold, arctic environments, usually in connection with freshwater river outflow (e.g. Bergsten, 1994; Polyak *et al.*, 2002). Therefore, another explanation for the high abundance of elphidiids in the glacial BOBGEO-CS05 record could simply be an adaptation to cold glacial conditions and meltwater inputs in the BoB. This is supported by the presence of *E. excavatum* f. *clavatum*, the dominant elphidiids species in our assemblages (~75 %), frequently found today in glacier-proximal environments (e.g. Jennings *et al.*, 2004; Murray, 2006; Darling *et al.*, 2016; Fossile *et al.*, 2020). The modern conditions in the polar regions where this species lives today are close to the conditions prevailing during the last glacial period in our study area since the EIS invaded the western European shelf (cf. ice-sheet and polar fronts limits in Fig. 1) and the Channel River channeled huge amounts of meltwaters to the northern BoB.

Cassidulina crassa occurs concomitantly to *E. excavatum* f. *clavatum* in our record (r^2 = 0.85). Similarly to *Elphidium* spp., modern upper slope foraminiferal studies from the BoB reported that *C. crassa* is either only encountered in the dead faunas or very rarely present in the living faunas (e.g. Fontanier *et al.*, 2002 , 2006; Mojtahid *et al.*, 2010; Duros *et al.*, 2012).

It is therefore probable that this species has been transported to the study site, although *C. crassa* tests are rather intact (Plate 1) compared to *E. excavatum* f. *clavatum* (Plate 2a). It must be noted that the morphospecies identified here as *C. crassa* (d'Orbigny, 1839) has a variant that is very close morphologically and was described first as *Cassidulina crassa* var. *reniforme* Nørvang, 1945, and later elevated to the species rank as *C. reniforme*. *Cassidulina reniforme* morphospecies is mainly reported from arctic regions as typical of near-glacier environments (Hansen and Knudsen, 1995; Korsun *et al.*, 1995; Murray, 2006). Thus, it is highly possible that *C. crassa* from BOBGEO-CS05 is actually the same morphospecies than the one reported from arctic regions. We therefore assume that the *C. crassa* - *E. excavatum* f. *clavatum* association in our record is coherent with near-glacier environments. This is further corroborated by the absence of these species in the upper slope glacial record PP10-12 from the southeast BoB (Pascual *et al.*, 2020), far from both the ice sheet extent limit and the Channel River mouth. Based on the above, we summed the percentages of *E. excavatum* f. *clavatum* and *C. crassa* to constitute the group of glacier-proximal indicator species. The latter will be used to examine the EIS dynamics (cf. section 5.2).

5.1.3. Holocene indicator species

One of the most striking features of our benthic foraminiferal record is the absence of uvigerinids (e.g. *U. peregrina*, *U. mediterranea*), whereas they dominate the modern benthic foraminiferal assemblages of the BoB between ~500 and 2000 m water depth (e.g., Schönfeld, 2006; Barras *et al.*, 2010; Mojtahid *et al.*, 2010; Duros *et al.*, 2011, 2012). This absence is also the case in the glacial part of the MD99-2328 record (Mojtahid *et al.*, 2017). We assume therefore that uvigerinids might not be tolerant to the glacial-related conditions on the BoB seafloor (Mojtahid *et al.*, 2013; Pascual *et al.*, 2020; Rodriguez-Lazaro *et al.*, 2017). Schönfeld and Altenbach (2005) hypothesized a widespread change from glacial to modern surface productivity configuration (e.g. nature of primary producers, seasonality in phytoplankton blooms) that may have triggered the Holocene settlement of *U. peregrina* in the northeast Atlantic. It is also interesting to note that *U. peregrina* and *U. mediterranea* are very abundant in bathyal depths (~200-1500 m) of the Mediterranean and the BoB bathed by the MOW (e.g. De Rijk *et al.*, 2000; Schmiedl *et al.*, 2000; Fontanier et al., 2003). The possible link between water masses and specific fauna has been progressively abandoned in favor of organic matter and oxygen as major controlling environmental parameters (Jorissen *et al.*, 2007). Yet, the settlement of uvigerinids in the BoB in the end of deglaciation - early Holocene (Garcia *et al.*,

2013; Mojtahid *et al.*, 2013; Pascual *et al.*, 2020) seems to coincide with the significant increase in the influx of the MOW into the North Atlantic and along the European margin (Rogerson *et al.*, 2012; Lebreiro *et al.*, 2018). This is coherent with what Mojtahid *et al.* (2017) observed in core MD99-2328 where they record the appearance of uvigerinids (although with low abundances) only in the Holocene portion of the record.

In summary, we have shown that the upper slope benthic foraminifera assemblage found at site BOBGEO-CS05 reflect the complex, highly dynamic and variable environmental conditions in the northern BoB during the last glacial period, including high bottom water currents, glacier-proximal settings, and southern retreat of the MOW. Since benthic foraminifera respond greatly to these various environmental parameters, they present a great potential to better constrain glacial intermediate bottom water characteristics during HSs.

5.2. Environmental particularities of Heinrich Stadials depicted by benthic foraminifera

5.2.1. What do the last three Heinrich Stadials have in common in the Bay of Biscay?

In general, HS3 (~31-29 ka cal BP), HS2 (~26-23 ka cal BP) and HS1 (~18-15.5 ka cal BP) in core BOBGEO-CS05 are characterized by a systematic drop in BFAR values (Fig. 3a). This may indicate unfavorable conditions (e.g. low quality/quantity of the organic matter, low oxygenation) for the growth and reproduction of foraminifera. In the same intervals, we record the highest occurrence of *Cibicidoides pachyderma* and *Globobulimina* spp. (Figs. 3j & 3i). C*ibicidoides pachyderma* is usually found in meso-oligotrophic open-slope environments, as in the modern BoB (Schmiedl *et al.*, 2000; Mojtahid *et al.*, 2010; Duros *et al.*, 2012). *Globobulimina* spp., on the other hand, are deep infaunal species that tolerate hypoxia and anoxia (Risgaard-Petersen *et al.*, 2006; Pina-Ochoa *et al.*, 2010; Koho *et al.*, 2011). Hence, we interpret the *C. pachyderma* - *Globobulimina* spp. association (i.e. meso-oligotrophic species; see Fig. 4h) during HSs, together with the low BFAR, as indicating meso-oligotrophic conditions, with moderate to low export of organic matter to the seafloor, and reduced bottom-water ventilation. The latter is supported by the concomitant decrease in the proportions of high-energy indicator species *T. angulosa* and *C. lobatulus* during each of the HSs (Fig. 4g). The weak hydrodynamics during the HSs is independently supported by the low $\overline{SS}$ values at BOBGEO-CS05 and at many sites along the French Atlantic margin (Toucanne *et al.*, 2021).

As such, biotic and sedimentological data indicate reduced near-bottom flow speed (i.e. weakened GEBC) and, by extension, a sluggish AMOC during the three HSs.

The glacier-proximal species (*E. excavatum* f. *clavatum*. and *C. crassa*), although present all along the BOBGEO-CS05 record, display the highest percentages during the HSs, especially during HS3 and HS2 (Fig. 4b). In their modern habitats in the Arctic fjords, these species are impacted by seasonal melting of marine-terminating glaciers (Schroder-Adams *et al.,* 1990; Wollenburg and Mackensen, 1998; Wollenburg and Kuhnt, 2000; Wollenburg *et al.*, 2004). Since enhanced EIS meltwaters influx to the BoB are described during HSs (Toucanne *et al.,* 2015), increased densities of these species might be indicative of such meltwater inputs. The concomitant presence of meso-oligotrophic species (e.g. *C. pachyderma*) indicates a low to moderate export of organic matter to the seafloor, especially during HS2 and HS3. This will be further discussed when addressing the specificities of each HS (cf. sections 5.2.2. and 5.3)

5.2.2. The difference between the early HS1 and the other HSs

In core BOBGEO-CS05, HS1 is very distinct from HS2 and HS3 by displaying a high presence (~60 %) of opportunistic and high-organic flux indicator species (*C. carinata* and *Bolivina* spp.; Schmiedl *et al.,* 1997; Fontanier *et al.,* 2003; Duros *et al.,* 2011) during its early phase ca. ~18-16.7 ka cal BP (Fig. 4d). This is coherent with the findings of Mojtahid *et al.* (2017) at the same time period at site MD99-2328. Conversely, during HS2 and HS3, these species were present with much lower abundances (< 10 %; Fig. 4d). Thus, we assume that limited organic material inputs reached the BOBGEO-CS05 site during HS3 and HS2, then substantially increased during the early HS1. This difference is further corroborated by the positive correlation between the abundance of the high-organic flux indicator species during early HS1 at our site and both the BIT index at site MD95-2002 (Fig. 4c; Ménot *et al.,* 2006) and the turbidite (i.e. flood-related deposits) flux in the deep BoB (Zaragosi *et al.,* 2006; Toucanne *et al.,* 2008, 2012). It has been suggested that these differences in organic material inputs through time could result from complex interactions between climate conditions, and ice and vegetation cover (Ménot *et al.*, 2006). Our data cannot resolve this issue, but it certainly highlights the paroxysmal phase of EIS melting in response to increasing boreal insolation during HS1, and the concomitant rapid progradation of a large outer-shelf delta that ultimately improved the connection between the BOBGEO-CS05 site and the Channel River system (Toucanne *et al.,* 2012). That said, because *C. carinata* and *Bolivina* spp. are very abundant in shallower settings in the BoB (140-550 m depth; Duros *et al.,* 2011 ; Fontanier *et al.,* 2003), we cannot discard that their presence

in our record is a result of downslope transport. Even so, the abundance of these species still indicates increased organic fluxes in their source habitats.

Interestingly, in the upper slope BOBGEO-CS05 and MD99-2328 cores, the dominance of the anoxia indicator species (representing the sum of *Globobulimina* spp. and *Chilostomella oolina*) at HS1 occurs early within this interval, before HE1 event *sensu stricto* (Fig. 4i). According to Mojtahid *et al.* (2017), the presence of these indicator species during early HS1 is indicative of organically-enriched and/or oxygen-depleted benthic environments, and their absence during HE1 event, together with high $\overline{SS}$ (Fig. 4i & 4f) indicate well-ventilated intermediate waters. In deeper sediment cores from the BoB (>2000 m depth), the HE1 event is characterized by the presence of authigenic carbonates indicating anoxic bottom waters (e.g. Auffret *et al.*, 1996; Toucanne *et al.*, 2015). Because these anoxia markers are not observed in the shallower cores BOBGEO-CS05 and MD99-2328 and because all proxies ($\overline{SS}$ and foraminifera; Fig. 4) indicate well-ventilated bottom waters, we can hypothesize a decoupling between a vigorous intermediate water depth circulation during HE1 and a still sluggish circulation at >2000 m in the northeast Atlantic, as reported by the Bermuda rise $^{231}Pa/^{230}Th$ data from the deep northwest Atlantic (Fig. 4e). A similar pattern is found in the equatorial Atlantic where a better ventilation of mid-depth waters in late HS1 is recorded while the deep sites remained poorly ventilated (Chen *et al.*, 2015).

5.3. Foraminiferal evidence for mid-HS2 re-ventilation event

During HS2 (Fig. 5), the overall meso-oligotrophic conditions and the low bottom-water ventilation depicted by both the low BFAR and the *C. pachyderma* - *Globobulimina* spp. association (i.e. meso-oligotrophic species) were interrupted around 24.3 ka cal BP (Fig. 5d & 5e). At the same time, low percentages of the polar planktonic species *N. pachyderma* (Fig. 5a) indicate a a warming of the sea-surface conditions and therefore a cessation of meltwater input in the northern BoB. This surface water warming is recorded in several sedimentary records along the European margin (e.g. Scourse *et al*., 2009; Austin *et al*., 2012; Waelbroeck et al., 2019). This warm event interrupting HS2 seems to be coeval with a well-known atmospheric decrease in dust flux at high latitudes (Rasmussen *et al.*, 2008; Austin *et al.*, 2012). During this sea-surface warming event, the re-appearance of the high-energy indicator species (Fig. 5c) and the drop in the anoxia indicator species (Fig. 5f) strongly suggests a reactivation of bottom water currents at site BOBGEO-CS05. This is supported by the increase in the $\overline{SS}$ values at our site and, more generally, in the northern part of the French

Atlantic margin (Fig. 5b;). Our biotic data, although covering this millennial-scale event at low sampling resolution, thus indicate, together with the $\overline{SS}$ proxy, enhanced vigor of the GEBC and, by extension, of the AMOC during the mid-HS2. This re-acceleration of the GEBC continues to about100 yrs before the iceberg debacle of the LIS (i.e. HE2 *sensu stricto* at 24.2 ka cal BP), when our biotic and sedimentological proxies show a rapid return to meso-oligotrophic conditions at the sea-floor and weak bottom currents.

6. Conclusions

Benthic foraminiferal assemblage data allowed us to reconstruct the paleoenvironmental evolution of the upper slope of the BoB (site BOBGEO-CS05) over the ca. 32-14 ka cal BP period. In general, species-specific responses reflect the complex, highly dynamic and variable environmental conditions in the northern BoB during the last glacial period, including fluctuations in the bottom water current and the GEBC, changes in organic matter fluxes and Channel River discharges, and latitudinal changes of the MOW.

The three HSs (HS3, HS2 and HS1) present some common features. They are all characterized by an overall low proportion of high-energy indicator species (i.e. *Cibicides lobatulus* and *Trifarina angulosa*), and a significant presence of meso-oligotrophic indicator species (*Cibicidoides pachyderma*), anoxia indicator species (*Globobulimina* spp. and *C. oolina*), and glacier-proximal species (*E. excavatum* f. *clavatum* and *Cassidulina crassa*). In agreement with previously published sedimentological and geochemical proxies, this reflects overall low organic matter fluxes to the seafloor and a low bottom water ventilation during the HSs.

Detailed investigation of the benthic foraminifera reveals some specificities of the HSs in the northeast Atlantic. First, the high abundance of high-organic flux indicator species (*Cassidulina carinata* and *Bolivina* spp.) during early HS1, compared to their near absence during HS2 and HS3, reveals a millennial-scale peak in terrestrial organic material in the BoB resulting from the significant EIS melting and Channel River meltwater floods. Second, benthic foraminiferal species depict a short-term mid-depth re-ventilation event during HS2, indicated by a decrease in the proportions of anoxia indicator species and an increase in the abundance of high-energy indicator species. This short-term reactivation of the GEBC along the French Atlantic margin, and of the AMOC, is coherent with the cessation of the EIS meltwater input in the northern BoB, and more generally, with a warming of the sea-surface conditions in the northeast Atlantic. This result strongly emphasizes the connection between the intermediate

ocean circulation and the cryosphere dynamics in the northeast Atlantic during the Heinrich Stadials.

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1000 **Table 1.** ^{14}C dates of core BOBGEO-CS05.

Core label	Depth (cm)	Lab. Number[a]	Species	^{14}C age (yr BP)	error (1σ)	Reservoir correction[b] (^{14}C yr)	error[b] (1σ)	^{14}C age corrected for reservoir[c] (^{14}C yr BP)	error[d] (1σ)	Calendar age range[e] (yr BP, 2σ)
BOBGEO-CS05	0	Poz-73846	*N. pachyderma*	14100	80	970	200	13130	215	15133-16357
BOBGEO-CS05	10	Poz-42911	bulk planktonic	14770	70	970	200	13800	212	16132-17333
BOBGEO-CS05	305-309	Beta-478193	*G. bulloides*	15270	40	400	200	14870	204	17550-18661
BOBGEO-CS05	446	SacA-29355	bulk planktonic	18090	60	400	200	17690	209	20890-22026
BOBGEO-CS05	500-505	Beta-478194	*G. bulloides*	17140	50	400	200	16740	206	19773-20716
BOBGEO-CS05	660	SacA-29356	bulk planktonic	21140	200	400	200	20740	283	24238-25672
BOBGEO-CS05	796-800	Beta-478195	*G. bulloides*	19680	60	400	200	19280	209	22885-23789
BOBGEO-CS05	933-935	Beta-478196	*G. bulloides*	20430	70	400	200	20030	212	23727-24665
BOBGEO-CS05	1030-1033	Beta-478197	*G. bulloides*	21830	70	400	200	21430	212	25220-26049
BOBGEO-CS05	1230	Poz-45912	bulk planktonic	24510	240	400	200	24110	312	27726-28959
BOBGEO-CS05	1350	SacA-29357	bulk planktonic	24220	100	400	200	23820	224	27624-28628
BOBGEO-CS05	1460	Poz-73848	*N. pachyderma*	26130	230	400	200	25730	305	29237-30490

a: Poz- (Poznan Radiocarbon Lab., Poland); Beta- (Beta Analytic, USA); SacA- (SMA Artemis, France)

b: Reservoir correction inferred from Stern et Lisieki (2013); see Toucanne et al. (2015) for details

c: Corrected ^{14}C ages are obtained by subtracting the reservoir correction to the original ^{14}C age

d: Errors associated to the corrected ^{14}C were propagated through the quadratic sum

e: Corrected ^{14}C ages were calibrated using the atmospheric calibration curve IntCal20 (Reimer et al., 2020)

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1004 **Table 2.** Taxonomic reference list, microhabitat and ecological preferences for the dominant
1005 benthic species (>5 %) and the corresponding bibliographic references.

Species	References with images	Microhabitat	Ecological preferences	Plate 1	Plate 2
Bolivina spp.		Shallow infaunal (Murray, 2006)	*Bolivina* spp. have opportunistic behaviour (Schmiedl *et al.*, 2000) and ecological preferences for phytodetritus enriched deposits (Duros *et al.*, 2017, 2011)	5-6	
Cassidulina carinata Silvestri, 1896	Phleger *et al.* (1953), p1. 9, Figs. 32–37	Epifaunal to shallow infaunal (Jorissen, 1987; Altenbach *et al.*, 1999)	*Cassidulina carinata* is an opportunistic species (Fontanier *et al.*, 2003; Duros *et al.*, 2011) that lives in OM-enriched sediments (Hess *et al*., 2005; Hess and Jorissen, 2009).	7	
Cassidulina crassa d'Orbigny, 1839	Jorissen (1987), pl. 1, Fig. 3	Shallow infaunal (de Stigter *et al*., 1998; Fontanier et al., 2005)	In our case, *Cassidulina crassa* could be a morphospecies of *Cassidulina reniforme*. This latter is often transported from the continental shelf, and redeposited on glacial marine sediments (Mackensen *et al*., 1985), until 1000m water depth in Arctic (Wollenburg and Mackensen, 2009).	8	
Cibicides lobatulus Walker and Jacob, 1798	Jones and Brady (1994), pl. 93, Fig. 1	Epifaunal (Murray, 2006)	*Cibicides lobatulus* live at shallow depth, attached on seagrass and algae (Vénec-Peyré and Le Calvez, 1988; Murray, 2006). Even if, they were described as transported species, they can be found alive in deep and high energy environments (e.g. Schönfeld, 1997, 2002b, 2002a; Margreth *et al.*, 2009; Spezzaferri *et al.*, 2015)	13	
Cibicidoides pachyderma Rzehak, 1886	Jones and Brady (1994), pl. 94, Fig. 9	Shallow infaunal (Fontanier *et al.*, 2003, 2002)	*Cibicidoides pachyderma* live in meso-oligotrophic conditions (Fontanier *et al.*, 2003; Mojtahid *et al.*, 2009). They prefer low nutrients waters (Schmiedl *et al.*, 2000).	11-12	b
Chilostomella oolina Schwager, 1878	Jones and Brady (1994), pl. 55, Fig. 12-14	Deep Infaunal (Corliss and Emerson, 1990; Bernhard, 1992; Jorissen *et al.*, 1998)	*Chilostomella oolina* is adapted to anoxic or suboxic conditions (Fontanier *et al*., 2002; Bernhard and Sen Gupta, 2003). They may be replaced by *Globobulimina* spp. when the degraded OM quality decreases (Fontanier *et al.*, 2002)	4	
Elphidium clavatum Cushman, 1930	Darling *et al.* (2016), Fig. 4, S4	Infaunal–epifaunal (Murray, 2006)	*Elphidium clavatum* is a widespread taxon, mainly distributed in the Arctic, and frequent in glacier-proximal environments. It is found living down to several hundreds of meters depths in the Arctic and in the Baltic (Jennings *et a*l., 2004; Murray, 2006; Darling *et al*., 2016; Fossile *et al.*, 2020). In the nearby study of Mojtahid *et al.* (2017), *Elphidium* species found at 1000 m depth during the last deglaciation were interpreted as being possibly transported from shallower settings.	10	a
Elphidium gerthi van Voorthuysen, 1957	Mendes *et al. (*2012), Fig. 4, 8		*Elphidium gerthi* is a subtidal to intertidal species, very coommon along the western European coasts . In the nearby study of Mojtahid *et al.* (2017), *Elphidium* species found at 1000 m depth during the last deglaciation were interpreted as being possibly transported from shallower settings.	9	
Globobulimina spp.		Deep infaunal (Murray, 2006)	*Globobulimina* spp. live in organically-enriched and/or oxygen-depleted sediments (e.g. Jorissen, 1999; Schmiedl *et al*., 2003; Mojtahid *et al.*, 2010). They can live in anoxic sediments by respiring nitrates (Risgaard-Petersen *et al*., 2006).	3	
Gavelinopsis praegeri Heron-Allen & Earland, 1913	Jorissen (1987), pl. 3, Fig. 13	Epifaunal (Jorissen, 1987)	*Gavelinopsis praegeri* is an epiphytic species living in a wide range of water depths in marine environments (Murray, 2006). They are found down to 1200m water depth (de Stigter, 1996) and prefer~~s~~ more oxic conditions (Dorst *et al.*, 2015).	16	

Hoeglundina elegans d'Orbigny, 1826	Milker and Schmiedl, (2012), pl. 19, Fig. 15	Epifaunal; shallow infaunal (Jorissen *et al*., 1998; Fontanier *et al.*, 2002)	*Hoeglundina elegans* is described as indicator of low organic carbon environments (Fontanier *et al.*, 2002; Morigi *et al*., 2001).	17	
Nonionella turgida Williamson, 1858	Milker and Schmiedl, (2012), pl. 26, Figs. 1-5	Deep infaunal (Corliss, 1991)	*Nonionella turgida* is an opportunistic species, tolerant to low oxygen conditions and high nutrient level (Van der Zwaan and Jorissen, 1991).	2	
Planorbulina mediterranensis d'Orbigny, 1826	Jones and Brady (1994), pl. 92, Fig. 1	Epifaunal (Murray, 2006)	*Planorbulina mediterranensis* is an epiphytic species and lives at shallow depths (Murray, 2006).	15	
Pullenia quinqueloba Reuss, 1851	Jones and Brady (1994), pl. 84, Fig. 14	Intermediate infaunal (Corliss, 1991; Fontanier *et al*., 2008)	*Pullenia quinqueloba* can live in low-organic carbon conditions (Gupta, 1999).	18	
Textularia sagittula Defrance, 1824	Jorissen (1987), pl. 3, Fig. 12	Epifaunal (Murray, 2006)	*Textularia sagittula* is an agglutinated species (Murray, 2006). They are dominant in shallow water depths~~,~~ on sandy sediments (Murray, 2014)	1	
Trifarina angulosa Williamson, 1858	Jones and Brady (1994), pl. 74, Fig. 15	Shallow infaunal (Hess and Jorissen, 2009)	*Trifarina angulosa* have been observed in phytodetritus-enriched sediment (e.g. Hess and Jorissen, 2009; Duros *et al.*, 2011). They are often associated with *C. lobatulus* to strong bottom currents and can be observed until 1000m water depth (Mackensen *et al*., 1985).	14	

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9. Table caption

Table 1. ^{14}C dates of core BOBGEO-CS05

Table 2. Taxonomic reference list, microhabitat and ecological preferences for the dominant benthic species (>5 %) and the corresponding bibliographic references.

10. Figures Caption

Figure 1. Location of the study area. a) 3D representation (N-S, W-E and in water depth) of the modern oceanic circulation in the North Atlantic representing the main currents (acronyms written in black), water masses (acronyms written in colors) and the Subpolar (in blue) and Subtropical (in red) gyres in the North Atlantic. b) Bathymetric map representing the paleogeographic and paleoceanographic configuration (i.e. ice sheets, the Channel River, currents, and water masses) of the North Atlantic during the Last Glacial Stadials according to Toucanne *et al.* (2021). The angulous shapes represent the icebergs. c) Bathymetric map focussing on the study area and showing the location of our study core BOBGEO-CS05 (violet star), together with nearby cores at 1000 m water depth (black stars): MD95-2002 (Eynaud *et al.*, 2012; Ménot *et al.*, 2006; Toucanne *et al.*, 2015), MD99-2328 (Mojtahid *et al.*, 2017), PP10-12 (Pascual *et al.*, 2020). For the detailed description of the general modern and glacial circulation in the North Atlantic and in the study area, the reader is referred to the text (Section 2). LGM: Last Glacial Maximum.

Figure 2. Age model of core BOBGEO-CS05. a) Chronostratigraphic framework of core BOBGEO-CS05 based on the synchronisation of XRF-Ca/Ti ratios with cores MD95-2002 and MD99-2328 (Zaragosi *et al.*, 2006; Mojtahid *et al.*, 2017; Toucanne *et al.*, 2021). b) Sediment Accumulation Rate (SAR; full line) and ^{14}C dates (orange triangles) with associated errors in core BOBGEO-CS05. The ^{14}C dates represented by empty triangles are outliers (cf. section 3.1. for further details). In red is represented the final age model based on XRF-Ca/Ti synchronisation (cf. Fig. 2a). c) Test of the robustness of the age model with the percentages of the polar planktonic species *N. pachyderma* in core BOBGEO-CS05 (this study) with core MD95-2002 (Grousset *et al.*, 2000) and MD99-2328 (Mojtahid *et al.*, 2017). d) NGRIP δ^{18}O (GICCS05 chronology; Rasmussen *et al.*, 2006, 2014). f) X-Ray photographs (cf. Supplementary material S1 for the whole core) showing the four observed facies. Blue triangles:

^{14}C dates of core MD95-2002 (Toucanne *et al.*, 2021); Orange and empty triangles: ^{14}C dates of core BOBGEO-CS05; Blue bands: Heinrich Stadials (HSs); Gray bands: Heinrich Events (HEs); Greenland Interstadial (GI); Last Glacial Maximum (LGM); Marine Isotope Stage (MIS).

Figure 3. Benthic foraminiferal data from core BOBGEO-CS05. a) Benthic Foraminiferal Accumulation Rates (BFAR; ind.cm^{-3}.ka^{-1}) for the >150 µm (full line) and the >63 µm fraction (dashed line). b) Shannon index (H). c-j) Relative abundances (%) of the eight most representative benthic foraminiferal species (>10 %). Full lines and dashed lines represent respectively the > 150 µm and >63 µm fractions. Brown lines represent data from the >150 µm fraction of core MD99-2328 (Mojtahid *et al.*, 2017). Yellow bands: Greenland Interstadials (GI); gray bands: Heinrich Events (HEs); blues bands: Heinrich Stadial (HSs). Marine Isotope Stage (MIS). The vertical dashed grey line represents the limit between early HS1 (ca. 18.2 - 16.7 cal ka BP) and late HS1 (ca. 16.7 – 14.7 cal ka BP). To better highlight the variations of the different species groups, the scale of the ordinate axis is not constant.

Figure 4: Benthic foraminiferal response to ice-sheet/AMOC dynamics. a) Relative abundance of *N. pachyderma* in core BOBGEO-CS05. b) Relative abundances of glacier-proximal indicator species (% *Elphidium excavatum* f. *clavatum* + % *C. crassa*) in core BOBGEO-CS05. c) BIT-index at site MD95-2002 as a proxy for continental-derived material input (Ménot *et al.*, 2006). d) Relative abundances of high-organic flux indicator species (% *C. carinata* + % *Bolivina* spp.) in core BOBGEO-CS05. e) Bermuda Rise ^{231}Pa/^{230}Th compilation as a proxy for AMOC export at >2000 m depth (McManus *et al.*, 2004; Böhm *et al.*, 2015; Henry *et al.*, 2016). f) XRF-Zr/Rb (violet line) and $\overline{SS}$ (pink line) composite records from the northeast Atlantic including BOBGEO-CS05 as proxies for the reconstruction of GEBC flow speed changes (Toucanne *et al.*, 2021). g) Relative abundances of high-energy indicator species (% *C. lobatulus* + % *T. angulosa*) in core BOBGEO-CS05. h) Relative abundances of meso-oligotrophic indicator species (% *C. pachyderma*) in core BOBGEO-CS05. i) Relative abundances of anoxia indicator species (% *Globobulimina* spp. + % *C. oolina*). To better highlight the variations of the different species groups, the scale of the ordinate axis is not constant. The main events and climatic phases are reported similarly to Fig. 3.

Figure 5. Focus on HS2. a) Relative abundances of the planktonic species *N. pachyderma* in core BOBGEO-CS05 (black line; this study) and MD95-2002 (blue line; Grousset *et al.*, 2000). b) XRF-Zr/Rb (violet line) and $\overline{SS}$ (pink line) composite records from the northeast Atlantic (including BOBGEO-CS05) as proxies for the reconstruction of GEBC flow speed changes (Toucanne *et al.*, 2021). c) Relative abundances of high-energy indicator species (% *C. lobatulus* + % *T. angulosa*) in core BOBGEO-CS05. d) Benthic Foraminiferal Accumulation Rates (BFAR; ind.cm^{-3}.ka^{-1}) for the >150 µm in core BOBGEO-CS05. e) Relative abundances of meso-oligotrophic indicator species (% *C. pachyderma*) in core BOBGEO-CS05. f) Relative abundances of anoxia indicator species (% *Globobulimina* spp. + % *C. oolina*) in core BOBGEO-CS05. Dashed vertical line: Heinrich Event 2 (HE2) sensu stricto according to the regional Ca/Ti synchronisation (cf. Table S2 in Toucanne et al., 2021); blue bands: the HS2a,b cold events (Bard et al., 2000); yellow band: the mid-HS2 re-ventilation event. To better highlight the variations of the different species groups, the scale of the ordinate axis is not constant.

11. Plates caption

Plate 1. SEM photographs of the dominant benthic species (>5 % in at least one sample): 1) *Textularia sagittula* ; 2) *Nonionella turgida* ; 3) *Globobulimina affinis* ; 4) *Chilostomella oolina* ; 5) *Bolivina subaenariensis*; 6) *Bolivina albatrossi*; 7) *Cassidulina carinata*; 8) *Cassidulina crassa*; 9) *Elphidium gerthi* ; 10) *Elphidium excavatum* f. *clavatum* ; 11) *Cibicidoides pachyderma* ; 12) *Cibicides lobatulus*; 13) *Trifarina angulosa*; 14) *Planorbulina mediterranensis*; 15) *Gavelinopsis praegeri* ; 16) *Hoeglundina elegans* ; 17) *Pullenia quinqueloba*. Scale bar = 100µm.

Plate 2. a) Natural light photographs of *Elphidium excavatum* f. *clavatum* showing pyritised and altered shells. b) SEM photographs showing the variability of the morphotypes (in lateral view) lumped into *Cibicidoides pachyderma* in this study.

12. Supplementary material caption

S1. X-Ray radiographs of core BOBGEO-CS05

S2. Figure representing the relative abundances of taxa present between 5 and 10 % in at least one sample

S3. Raw foraminiferal counts

Figure 1

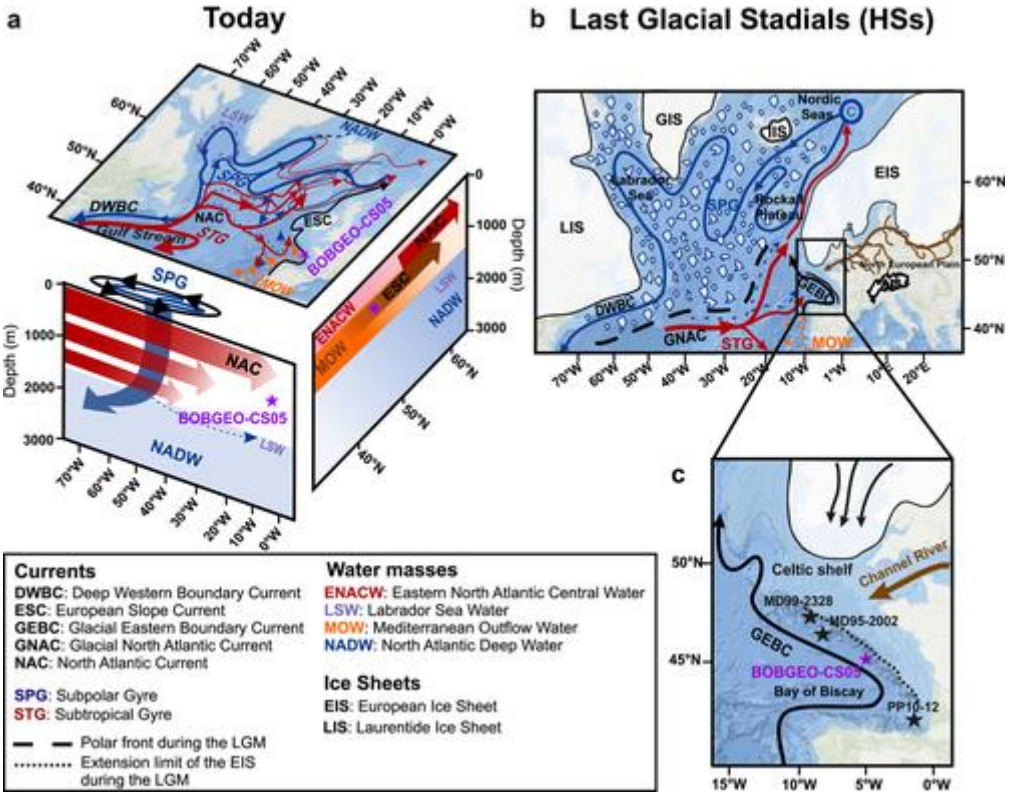

a
Today
b
Last Glacial Stadials (HSs)
c
DWBC
NAC
Gulf Stream
STG
SPG
ESC
MOW
LSW
NADW
BOBGEO-CS05
ENACW
Depth (m)
GIS
LIS
EIS
Nordic Seas
Labrador Sea
Rockall Plateau
GEBC
GNAC
Celtic shelf
Channel River
MD99-2328
MD95-2002
Bay of Biscay
PP10-12
Currents
DWBC: Deep Western Boundary Current
ESC: European Slope Current
GEBC: Glacial Eastern Boundary Current
GNAC: Glacial North Atlantic Current
NAC: North Atlantic Current
SPG: Subpolar Gyre
STG: Subtropical Gyre
Polar front during the LGM
Extension limit of the EIS during the LGM
Water masses
ENACW: Eastern North Atlantic Central Water
LSW: Labrador Sea Water
MOW: Mediterranean Outflow Water
NADW: North Atlantic Deep Water
Ice Sheets
EIS: European Ice Sheet
LIS: Laurentide Ice Sheet

Figure 2

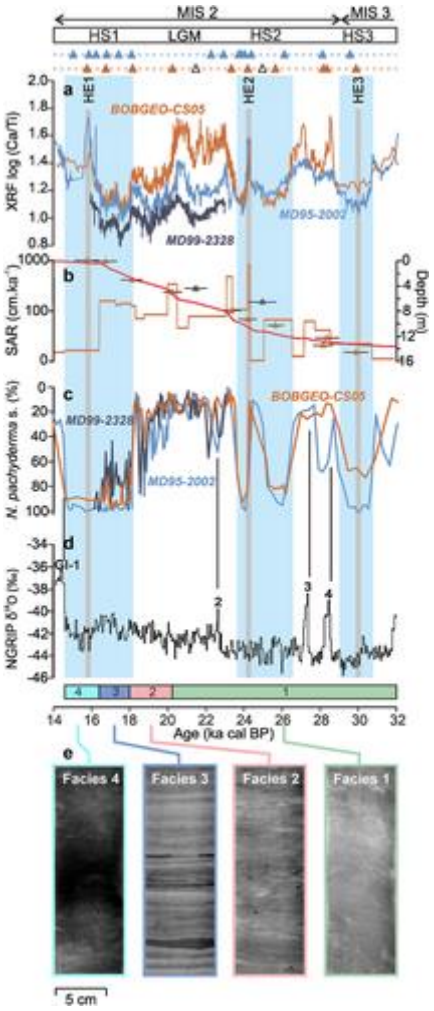

MIS 2
MIS 3
HS1
LGM
HS2
HS3
a
HE1
HE2
HE3
BOBGEO-CS05
MD95-2002
MD99-2328
XRF log (Ca/Ti)
b
SAR (cm.ka⁻¹)
Depth (m)
c
MD99-2328
BOBGEO-CS05
MD95-2002
N. pachyderma s. (%)
d
GI-1
2
3
4
NGRIP δ¹⁸O (‰)
4
3
2
1
Age (ka cal BP)
e
Facies 4
Facies 3
Facies 2
Facies 1
5 cm

Figure 3

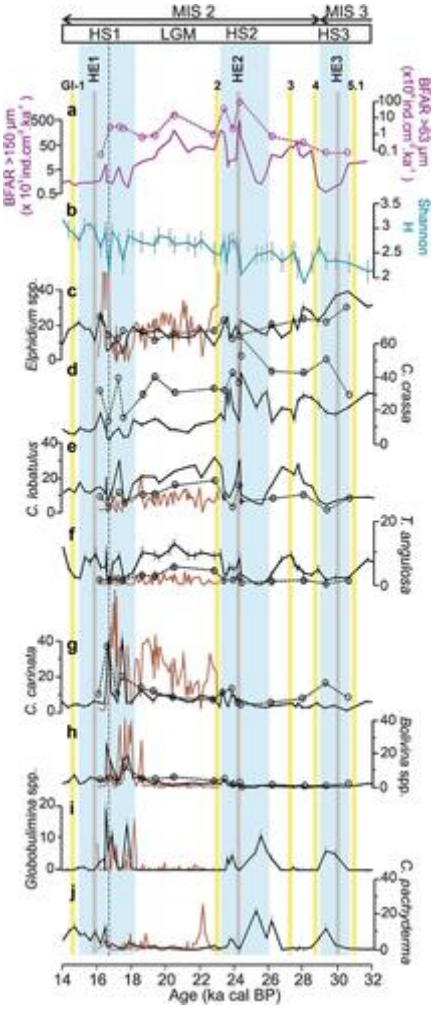

MIS 2
MIS 3
HS1
LGM
HS2
HS3
HE1
HE2
HE3
GI-1
2
3
4
5.1
BFAR >150 µm (x 10³ ind.cm⁻².ka⁻¹)
BFAR >63 µm (x10⁶ ind.cm⁻².ka⁻¹)
Shannon H
Elphidium spp.
C. crassa
C. lobatulus
T. angulosa
C. carinata
Bolivina spp.
Globobulimina spp.
C. pachyderma
Age (ka cal BP)

Figure 4

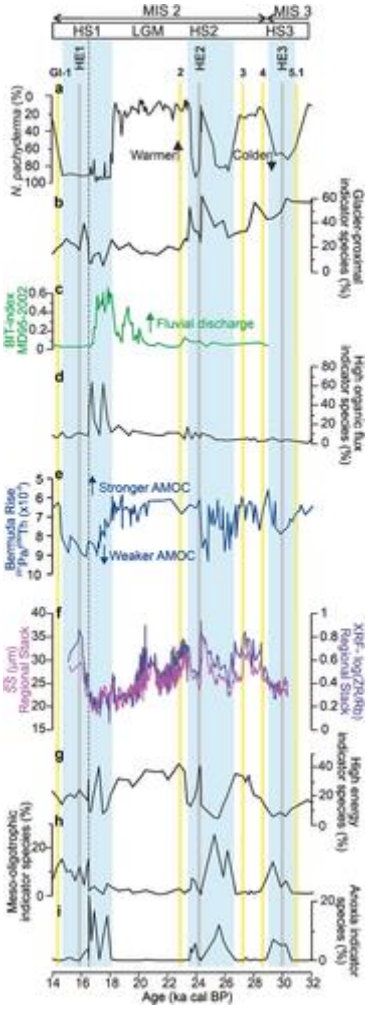

MIS 2
MIS 3
HS1
LGM
HS2
HS3
GI-1
HE1
2
HE2
3
4
HE3
5.1
a
N. pachyderma (%)
Warmer
Colder
b
Glacier-proximal indicator species (%)
c
BIT-index MD95-2002
Fluvial discharge
d
High organic flux indicator species (%)
e
Stronger AMOC
Weaker AMOC
Bermuda Rise $^{231}Pa/^{230}Th$ (x10^{-1})
f
ξS (um) Regional Stack
XRF- log(ZR/Rb) Regional Stack
g
High energy indicator species (%)
h
Meso-oligotrophic indicator species (%)
i
Arzoxia indicator species (%)
14
16
18
20
22
24
26
28
30
32
Age (ka cal BP)

Figure 5

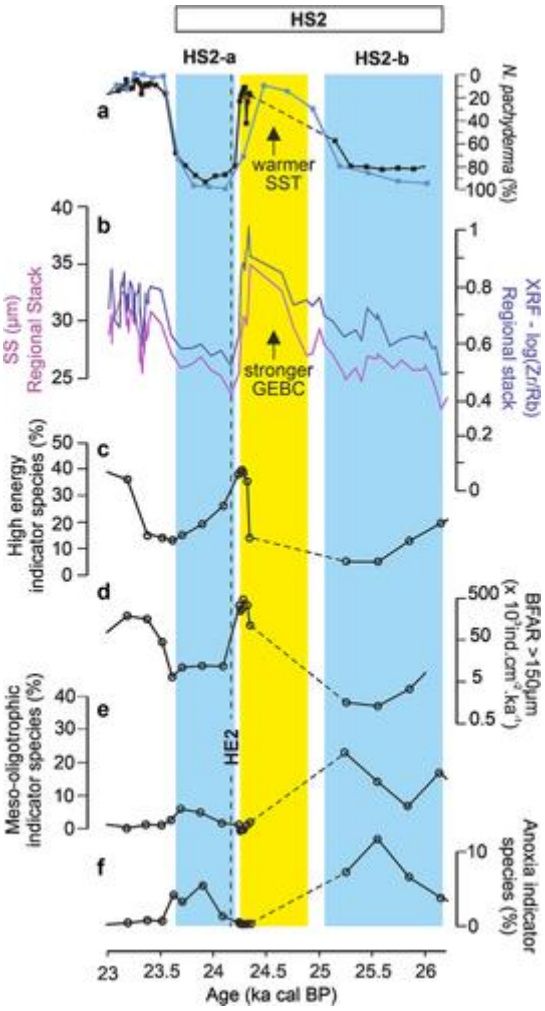

HS2
HS2-a
HS2-b
a
N. pachyderma (%)
warmer SST
b
SS (µm) Regional Stack
XRF - log(Zr/Rb) Regional stack
stronger GEBC
c
High energy indicator species (%)
d
BFAR >150µm (x 10³ind.cm⁻².ka⁻¹)
e
Meso-oligotrophic indicator species (%)
HE2
f
Anoxia indicator species (%)
Age (ka cal BP)

Plate 1

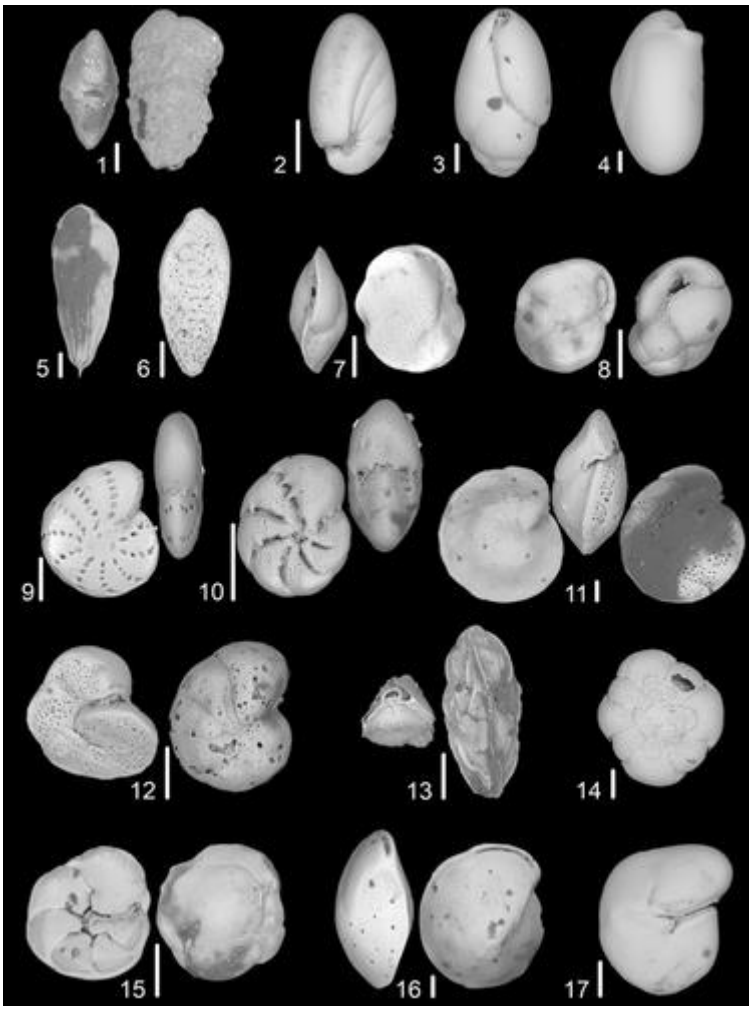
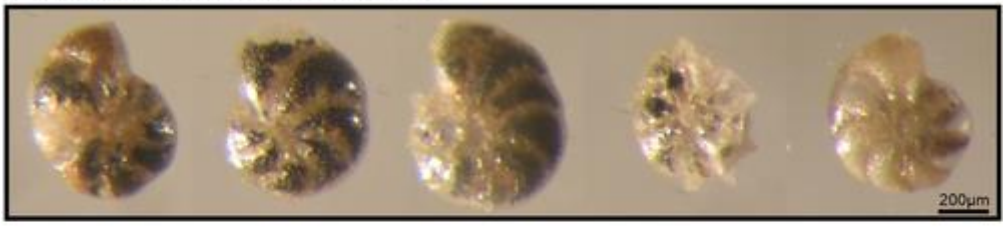


Plate 2

a ***Elphidium excavatum* cf. *clavatum***



b **Morphotypes of *C. pachyderma***