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1 **Intermediate ocean circulation and cryosphere dynamics in**
2 **the Northeast Atlantic during Heinrich Stadials: benthic**
3 **foraminiferal assemblage response**

4 Pauline DEPUYDT^{1,*}, Meryem MOJTAHID¹, Christine BARRAS¹, Fatima Zohra
5 BOUHDAYAD^{1,2}, Samuel TOUCANNE³

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7
8 ¹ Univ Angers, Nantes Université, Le Mans Université, CNRS, UMR 6112, Laboratoire
9 de Planétologie et Géosciences, F-49000 Angers, France

10 ² Presently at: Institute of Geology and Mineralogy, Faculty of Mathematics and Natural
11 Sciences, University of Cologne, Cologne, Germany

12 ³ Univ Brest, CNRS, Ifremer, Geo-Ocean, F-29280 Plouzane, France

13
14 * Corresponding author: pauline.depuydt@univ-angers.fr

15 **Abstract**

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

32

33 **Keywords**

34 Intermediate water masses, AMOC, European Ice Sheet, Glacial Eastern Boundary
35 Current (GEBC), Channel River, Benthic foraminifera

36

37 **1. Introduction**

38 The last glacial-interglacial cycle is a critical period to understand the natural climate
39 variability and its abrupt transitions (*e.g.* Bond *et al.*, 1993; Wang *et al.*, 2001; Clark *et al.*,
40 2012; Denton *et al.*, 2021). Orbital forcing (solar radiation), and the feedbacks implying the
41 atmosphere, the ocean, and the cryosphere are the main factors explaining the recorded
42 centennial to multi-millennial climate variability over this period (Broecker and Denton, 1990;
43 McManus *et al.*, 1999; Denton *et al.*, 2010; Lynch-Stieglitz, 2017). In the Northern Hemisphere,
44 the climate of the last glacial period was punctuated by cold (stadials) and warm intervals
45 (interstadials), that were coeval with periods of weakened and accelerated Atlantic Meridional
46 Overturning Circulation (AMOC), respectively (*e.g.* Kissel *et al.*, 2008; Böhm *et al.*, 2015;
47 Henry *et al.*, 2016; Toucanne *et al.*, 2021). Amongst the cold intervals, the most drastic are
48 certainly the Heinrich Stadials (HSs), encompassing the Heinrich events (HEs), *i.e.* armadas of
49 icebergs discharge issued from the dislocation of the Hudson Strait Ice stream of the Laurentide
50 Ice Sheet (LIS) that ultimately caused the deposition of ice-rafted debris (IRD) rich sediments
51 in the subpolar North Atlantic (Hemming, 2004). It is hypothesized that HEs were triggered by
52 sub-surface heat (700–1100 m depth), 1-2 ka after the decline of the AMOC (Shaffer *et al.*,
53 2004; Marcott *et al.*, 2011; Alvarez-Solas *et al.*, 2013). The initial AMOC slowdown likely
54 requires precursor melting of North Atlantic–adjacent ice sheets and it is now accepted that the
55 European Ice sheet (EIS) was a critical source for AMOC destabilization and the initiation of
56 HSs conditions (Peck *et al.*, 2006; Eynaud *et al.*, 2012; Boswell *et al.*, 2019; Toucanne *et al.*,
57 2015, 2021, 2022).

58 The present work investigates the evolution of northeast Atlantic intermediate water depth
59 environments and their interaction with EIS dynamics during the last glacial and deglaciation
60 periods, with a focus on HSs. This is achieved through the study of marine sediment core
61 BOBGEO-CS05 retrieved at ~1000 m water depth in the northern Bay of Biscay (BoB) (Figure
62 1a & 1c). This record covers the past ~32-14 ka cal BP, thus encompassing the last three HSs
63 (HS1, HS2 and HS3). During the last glacial period and the last deglaciation, BOBGEO-CS05
64 site was located off the Channel River, that drained EIS sediment-laden meltwaters to the
65 northern BoB (Zaragosi *et al.*, 2001; Bourillet and Lericolais, 2003; Toucanne *et al.*, 2009,
66 2010) (Figure 1b). At the time, the core site was also on the pathway of the Glacial Eastern
67 Boundary Current (GEBC), the glacial analogue of the northward-flowing European Slope
68 Current, that represents the easternmost portion of the upper branch of the AMOC (Toucanne

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

71 The present study focuses on fossil benthic foraminifera as one of the very few biological
72 indicator groups that are able to record the history of events on the seafloor by integrating the
73 cumulative impacts of the changing physico-chemical habitats (*e.g.* Schmiedl and Mackensen,
74 1997; Wollenburg *et al.*, 2001; Rodriguez-Lazaro *et al.*, 2017). A particular interest is found in
75 documenting HS2 and HS3, which are not covered by the nearby recent foraminiferal studies
76 (Mojtahid *et al.*, 2017; Pascual *et al.*, 2020). In addition, our aim is to establish to what extent
77 information previously obtained from sedimentary, geochemical and surface water proxies on
78 the interaction between the AMOC and the EIS during the HSs are consistent with our benthic
79 biotic data. More specifically, the approach uses here foraminiferal diversity and density, and
80 the ecological requirements of specific species to interpret several aspects of the environment
81 on the seafloor (*e.g.* organic matter flux, bottom-water oxygenation, current, transport, water
82 masses properties). Our findings highlight strong foraminiferal species-specific responses,
83 particularly during HSs, with some species associations able to discriminate between
84 EIS/continental impact and ocean circulation changes.

85

86 **2. Core location, present and past sedimentological and hydrographical** 87 **settings**

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

97 Today, the sedimentation on the slope is governed by the European Slope Current (ESC),
98 flowing along the upper slope (~500-2000 m water depth) from the northern Iberian Peninsula
99 to the Faroe-Shetland Channel (Marsh *et al.*, 2017; Clark *et al.*, 2021; Moritz *et al.*, 2021)
100 (Figure 1a). This current, driven by both the steep topography of the European margin and

101 large-scale meridional density gradients (Huthnance, 1984; Pingree and Cann, 1990; Friocourt
102 *et al.*, 2007), is largely recruited from the eastern North Atlantic and is connected, north of
103 $\sim 55^\circ\text{N}$ (*i.e.* Rockall Trough), to the upper part of the North Atlantic Current (NAC; that is the
104 eastern limb of the subpolar gyre). This forms the bulk of the upper branch of the AMOC (down
105 to ~ 1500 m; Lozier *et al.*, 2019; Huthnance *et al.*, 2020). The latter (to which the ESC
106 contributes by $\sim 25\%$; Berx *et al.*, 2013) finally reaches the Nordic Seas convection region,
107 where it cools and sinks to form a deeper southward return flow, the North Atlantic Deep Water
108 (NADW), mainly found along the eastern continental margin of North America and transported
109 by the Deep Western Boundary Current (*e.g.* Dickson and Brown, 1994) (Figure 1a).

110 The main water mass transported by the NAC into the BoB forms the Eastern North Atlantic
111 Central Water (ENACW), found down to ~ 600 m water depth (Pollard and Pu, 1985). Below,
112 the Mediterranean Outflow Water (MOW) is present between ~ 600 and 1500 m, flowing
113 northward from the Gulf of Cadiz and largely entrained by the ESC north of $\sim 45^\circ\text{N}$ (*e.g.* Pingree
114 *et al.*, 1999; van Aken, 2000). Deeper, the Labrador Sea Water (LSW), centered at ~ 2000 m
115 water depth and corresponding to the upper NADW, dominates (van Aken, 2000a). fcapture of
116 the (southward-flowing) LSW by the above (eastward-flowing) Gulf Stream – NAC system in
117 the north-western North Atlantic (Buckley and Marshall, 2016; Zou *et al.*, 2017) (Figure 1a).

118 During the last glacial maximum (LGM) ca. 23-18 ka cal BP (Mix *et al.*, 2001), the Gulf
119 Stream – NAC system and more generally the upper branch of the AMOC certainly had a
120 different geometry (*i.e.* positioned southward) because of the (southward) expansion of ice
121 sheets over North America (Keffer *et al.*, 1988; Otto-Bliesner *et al.*, 2006; Brady and Otto-
122 Bliesner, 2011; Löffverström *et al.*, 2014) (Figure 1b). The NADW was likely replaced by a
123 shallower, northern-sourced nutrient-poor water mass, namely the Glacial North Atlantic
124 Intermediate Water (GNAIW), dominant above 2000 m depth and overlaying a more nutrient-
125 rich water of southern origin below 2000 m (*i.e.* a glacial analog of Antarctic Bottom Water)
126 (*e.g.* Lynch-Stieglitz *et al.*, 2007). The recirculation of the GNAIW by the glacial Gulf Stream
127 – NAC system certainly explains GNAIW signatures recorded in the NE Atlantic basin and the
128 BoB basin during the last glacial period (Zahn *et al.*, 1997; Peck *et al.*, 2006, 2007a; Toucanne
129 *et al.*, 2021). At the same time, the Mediterranean-Atlantic water exchange was reduced by
130 $\sim 50\%$, and the MOW was certainly restricted to the southern Iberian margin (*e.g.* Rogerson *et*
131 *al.*, 2012). On the other hand, the presence of Antarctic Intermediate waters (AAIW) along the
132 European margin as far north as the South Iceland Rise was hypothesized (Rickaby and
133 Elderfield, 2005; Thornalley *et al.*, 2010) but the recent studies of Thornalley *et al.* (2015) then

134 Crocker *et al.* (2016) concluded that mid-depth in the NE Atlantic was never ventilated by
135 southern-sourced waters during the last glacial period. During late HS1 (~17 ka cal BP), and
136 the near shutdown of the AMOC (McManus *et al.*, 2004; Ng *et al.*, 2018), Mojtahid *et al.* (2017)
137 recorded low foraminiferal Sr/Ca ratios (*i.e.* carbonate system proxy; Yu *et al.*, 2014; Allen *et*
138 *al.*, 2016; Keul *et al.*, 2017), indicative of a change in water mass chemistry and origin in the
139 BoB. At the same time, Mojtahid *et al.* (2017) recorded increasing benthic foraminiferal Mg/Ca
140 ratios, indicating a warming of intermediate water masses. This is interpreted as the northward
141 conveyance of the subsurface warming originating from the low latitudes (Rühlemann *et al.*,
142 2004; Shaffer *et al.*, 2004) by the glacial NAC (GNAC) and the GEBC (Figure 1b) (Toucanne
143 *et al.*, 2021). This reinforces the view that the water mass structure in the glacial NE Atlantic
144 could have changed rapidly through time.

145

146 **3. Materials and Methods**

147 **3.1. Chronology**

148 The chronostratigraphic framework of core BOBGEO-CS05 (Figure 2) is detailed in
149 Toucanne *et al.* (2021). In short, the final age model is based on XRF-Ca/Ti data
150 synchronization with the nearby well-dated core MD95-2002 (Figure 2a). Twenty-one XRF tie-
151 points based on the recognition of millennial-scale oscillations were determined. The final age
152 model indicates that core BOBGEO-CS05 covers a period extending from ca. 32 to
153 14 ka cal BP (Figure 2), thus encompassing the end of MIS 3 (ca. 57-29 ka cal BP) and MIS 2
154 (ca. 29-14.7 ka cal BP). The accuracy of the age model is supported first by the good match
155 between the percentages of the polar planktonic taxon *N. pachyderma* in core BOBGEO-CS05
156 and MD95-2002 (Figure 2c), and second, by the overall concordance with the new radiocarbon
157 dates (n=12; Table 1; Figure 2b). The top core ¹⁴C dates show older ages (~15.7 cal ka BP) than
158 the final XRF-Ca/Ti based age model (~14 cal ka BP) (Figure 2b). The low percentages of the
159 polar taxon *N. pachyderma* at the core top (Figure 2c) indicate that we are out of the Heinrich
160 Stadial, making the core top ¹⁴C ages unreliable. Such incoherencies in ¹⁴C dates (including the
161 few outliers; Figure 2b) are certainly linked to physical sediment mixing and bioturbation that
162 are common in contourite deposits.

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

166 to the significant sea-level rise and the embayment of the English Channel (e.g., Bourillet *et al.*,
167 2003; Toucanne *et al.*, 2012).

168 Core BOBGEO-CS05 shows sedimentation rates of 50-150 cm.ka⁻¹ (Figure 2b). As such,
169 core BOBGEO-CS05 offers a unique opportunity to study at high time resolution the later part
170 of the last glacial period and the last three HSs.

171

172 **3.2. Foraminiferal analyses**

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

192 The relative abundances of benthic species (% of the total foraminiferal abundances) were
193 calculated for the >150 µm fraction for the 56 samples and for the >63 µm fraction (63-150 µm
194 + >150 µm) for the selected 16 samples. The error bars of the relative abundances were
195 computed with the binomial standard error $\sqrt{(p(1-p))/n}$ (Buzas, 1990; Fatela and Taborda,
196 2002), where p is the species proportion estimate (number of counted individuals for a given
197 species/n). The diversity of the 56 samples (>150 µm) was calculated with the Shannon index
198 (entropy, H; Hayek and Buzas, 1997) using the PAST software (PAleontological STatistics;

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

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

211

212 **4. Results**

213 Average BFAR values from the >150 μm fraction are $\sim 12 \cdot 10^3 \text{ ind.cm}^{-2} \cdot \text{ka}^{-1}$ and from the
214 >63 μm are $\sim 7.5 \cdot 10^6 \text{ ind.cm}^{-2} \cdot \text{ka}^{-1}$ (Figure 3a). The values from the >150 μm fraction are
215 minimal during the three HSs ($\sim 1 \cdot 10^3 \text{ ind.cm}^{-2} \cdot \text{ka}^{-1}$) and are more important during the
216 interstadial periods ($\sim 30 \cdot 10^3 \text{ ind.cm}^{-2} \cdot \text{ka}^{-1}$). From ~ 32 to 14 ka cal BP, the Shannon (H) index
217 (Figure 3b) shows an overall increase of diversity, with values ranging from ~ 2 to 3.2.

218 The eight most dominant species (>10 %) showing the highest variability are illustrated in
219 Plate 1 and their relative abundances are presented in Figure 3 (c-j). *Elphidium* spp.,
220 *Cassidulina crassa* and *Cibicides lobatulus* are dominant along the record and account together
221 for 12.7 to 74.3 % of the total fauna. In this study, *Elphidium* spp. includes mainly *E. excavatum*
222 (*i.e.* *E. excavatum* f. *clavatum*) with pyritized shells (Plate 2a) and other species of the genus
223 *Elphidium* (e.g., *E. gerthi*, *E. macellum*). *Elphidium* spp. show maximum values (>30 %)
224 between 30.7 and 28.9 ka cal BP (*i.e.* HS3) and minimum values (<10 %) between 17.5 and
225 16.5 ka cal BP (*i.e.* Early HS1; Figure 3c). Before HS2, *C. crassa* accounts in average for about
226 ~ 21 % of the total fauna (Figure 3d). The highest values are recorded during HS2, with
227 maximum percentages (40 %) just before HE2 followed by a sharp decrease. After HS2, the
228 relative density of this species remains stable around ~ 8 %. *Cibicides lobatulus* exhibits a
229 different pattern in comparison with the previously mentioned species. Generally, this species
230 is present with lower proportions during HS periods (around 5-10 %), except at 24.2 ka cal BP

231 (during HE2) and 17.2 ka cal BP (during HS1). Between HS3 and HS2 (ca. 29-26 ka cal BP)
232 and during the LGM (ca. 23-18 ka cal BP), *C. lobatulus* accounts for ~22 % of the total fauna
233 (Figure 3e). *Trifarina angulosa* shows the same trend as *C. lobatulus* (Figure 3f) but with
234 overall lower proportions (maximum values around 10 %). The remaining dominant species
235 (>10 %) present a discontinuous evolution. *Cassidulina carinata*, *Bolivina* spp. and
236 *Globobulimina* spp. exhibit high relative abundances (up to 42 %, 24 % and 18 % respectively),
237 with high variability, during early HS1 (Figure 3g, 3h & 3i). Before HS1, *Globobulimina*
238 species are almost absent except in samples from HS3 and HS2 (average of ~5 % and 7.5 %,
239 respectively). *Cibicidoides pachyderma* is also present mainly during the three HSs reaching
240 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
241 around 10 % at ~HS1 (Figure 3j). Here, *C. pachyderma* encompasses several morphotypes
242 spanning from *C. pachyderma* sensu stricto (pronounced carina) to *Cibicidoides kullenbergi*
243 sensu stricto (less pronounced carina) (Plate 2b). The presence of several intermediate
244 morphotypes hampered the taxonomical differentiation between *C. pachyderma* and *C.*
245 *kullenbergi*, and as such were lumped together as *C. pachyderma*.

246 The evolution through time of the minor species (*i.e.* present only few times with percentages
247 >5 %) is represented in **Erreur ! Source du renvoi introuvable.** *Gavelinopsis praegeri* and
248 *Planorbulina mediterranensis* mainly appear just after 24.2 ka cal BP, between HE2 and the
249 end of HS2. *Chilostomella oolina*, *Pullenia quinqueloba*, *Textularia sagittula* occur just one
250 time with relative densities >5 % at 16.8 ka cal BP, 16.5 ka cal BP, 17.2 ka cal BP respectively
251 while *Hoeglundina elegans* occurs only at 14 ka cal BP. *Nonionella turgida* become dominant
252 only after HE1 (~6 %).

253 In the small fraction (63-150 μ m), the identified species were similar to the ones found in
254 the larger size fraction (>150 μ m). When considering the small and large fractions together
255 (>63 μ m), six major species >5 % are present: *Elphidium* spp., *C. crassa*, *C. lobatulus*, *C.*
256 *carinata*, *Bolivina* spp. and *T. angulosa*. These species, also identified as major species when
257 considering only the >150 μ m size fraction, exhibit approximately similar trends (black dashed
258 line; Fig. 3 c-h). Only *C. crassa* presents much higher proportions in the >63 μ m fraction with
259 abundances ranging from 15 to 60 % of the total fauna.

260

261 **5. Discussion**

262 **5.1. Regional inter-comparison of benthic foraminiferal faunas**

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

269

270 **5.1.1. High-energy indicator species**

271 *Cibicides lobatulus* (also known as *Lobatula lobatula*) is highly dominant in our record (~4-
272 30 %). This species is also present, but with overall lower percentages (~10 %), at site MD99-
273 2328, north of our study site (Figure 1), that covers the time interval from 23 to 16 ka cal BP
274 (Mojtahid *et al.*, 2017) (Figure 3). However, this epibenthic species is absent today from the
275 BoB modern foraminiferal communities at ~1000 m depth (*e.g.* Fontanier *et al.*, 2002;
276 Fontanier *et al.*, 2006; Mojtahid *et al.*, 2010; Duros *et al.*, 2011, 2012). This discrepancy can be
277 explained by different environmental conditions (*e.g.* food source, hydrodynamics) during the
278 last glacial period allowing their settlement at intermediate water depths in the area. Indeed, *C.*
279 *lobatulus* is a suspension-feeder that inhabits moderate-to-strong hydrodynamic environments
280 of the modern northeast Atlantic. These include shelf environments (*e.g.* Basque shelf; Pascual
281 *et al.*, 2008) and upper slope settings swept by strong bottom currents and characterized by
282 coarse substrate and/or cold-water coral mounds and reefs trapping abundant food particles (*e.g.*
283 Gulf of Cadiz, Porcupine and Rockall Banks; Schönfeld, 1997, 2002a, 2002b; Margreth *et al.*,
284 2009; Spezzaferri *et al.*, 2015). As such, the high presence of *C. lobatulus* in the BOBGEO-
285 CS05 glacial record might indicate stronger currents than today. The depicted link between *C.*
286 *lobatulus* and strong energy environments is further supported in our record by its co-variation
287 with: i) the abundance of *Trifarina angulosa* ($r^2 = 0.78$) (Figure 3e & 3f) which is commonly
288 associated with shelf-edge to upper-slope areas swept by vigorous bottom currents (*e.g.*
289 southwest Norway, Rockall Trough ; Mackensen *et al.*, 1985; Austin and Evans, 2000; Gooday
290 and Hughes, 2002), and ii) the “sortable silt” mean size \overline{SS} (*i.e.* the mean grain size of the
291 carbonate-free terrigenous silt fraction) at BOBGEO-CS05 (Figure 4f; Toucanne *et al.*, 2021)
292 that provides a direct constraint on the rate of past bottom flows (McCave *et al.*, 1995). As such,
293 our biotic data independently support the presence of strong bottom currents on the upper slope

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

299

300 **5.1.2. Glacier-proximal species**

301 The high dominance (up to ~40 % in the late MIS 3 and ~20 % thereafter) of elphidiids in
302 core BOBGEO-CS05 is peculiar as this group is presently found in coastal, shelf and estuarine
303 environments of the northeast Atlantic (*e.g.* Pujos, 1976; Murray, 2014; Mojtahid *et al.*, 2016).
304 In the modern benthic foraminiferal assemblage of the upper Whittard region (northern BoB,
305 ~1000 m depth; Duros *et al.*, 2012), *Elphidium* spp. are found only in the dead faunas, and as
306 such, were considered as transported from shallower settings. Mojtahid *et al.* (2017) report
307 high abundances of *Elphidium* spp. in core MD99-2328 especially during the late HS1 (16.7-
308 16 ka cal BP; up to ~70 %) and hypothesized their transport to these intermediate depths by the
309 EIS icebergs and/or shelf ice. This would be also a possibility for BOBGEO-CS05 since
310 *Elphidium* shells show pyritization marks (Plate 2a) that may indicate a potential reworking and
311 transport. However, it is interesting to note that modern elphidiids may extend their habitats to
312 deeper settings (several hundred meters) in cold, arctic environments, usually in connection
313 with freshwater river outflow (*e.g.* Bergsten, 1994; Polyak *et al.*, 2002). Therefore, another
314 explanation for the high abundance of elphidiids in the glacial BOBGEO-CS05 record could
315 simply be an adaptation to cold glacial conditions and meltwater inputs in the BoB. This is
316 supported by the presence of *E. excavatum* f. *clavatum*, the dominant elphidiids species in our
317 assemblages (~75 %), frequently found today in glacier-proximal environments (*e.g.* Jennings
318 *et al.*, 2004; Murray, 2006; Darling *et al.*, 2016; Fossile *et al.*, 2020). The modern conditions in
319 the polar regions where this species lives today are close to the conditions prevailing during the
320 last glacial period in our study area since the EIS invaded the western European shelf (cf. ice-
321 sheet and polar fronts limits in Figure 1) and the Channel River channeled huge amounts of
322 meltwaters to the northern BoB.

323 *Cassidulina crassa* occurs concomitantly to *E. excavatum* f. *clavatum* in our record ($r^2 =$
324 0.85). Similarly to *Elphidium* spp., modern upper slope foraminiferal studies from the BoB
325 reported that *C. crassa* is either only encountered in the dead faunas or very rarely present in

326 the living faunas (*e.g.* Fontanier *et al.*, 2002 , 2006; Mojtahid *et al.*, 2010; Duros *et al.*, 2012).
327 It is therefore probable that this species has been transported to the study site, although *C. crassa*
328 tests are rather intact (Plate 1) compared to *E. excavatum* f. *clavatum* (Plate 2a). It must be noted
329 that the morphospecies identified here as *C. crassa* (d'Orbigny, 1839) has a variant that is very
330 close morphologically and was described first as *Cassidulina crassa* var. *reniforme* Nørvang,
331 1945, and later elevated to the species rank as *C. reniforme*. *Cassidulina reniforme*
332 morphospecies is mainly reported from arctic regions as typical of near-glacier environments
333 (Hansen and Knudsen, 1995; Korsun *et al.*, 1995; Murray, 2006). Thus, it is highly possible
334 that *C. crassa* from BOBGEO-CS05 is actually the same morphospecies than the one reported
335 from arctic regions. We therefore assume that the *C. crassa* - *E. excavatum* f. *clavatum*
336 association in our record is coherent with near-glacier environments. This is further
337 corroborated by the absence of these species in the upper slope glacial record PP10-12 from the
338 southeast BoB (Pascual *et al.*, 2020), far from both the ice sheet extent limit and the Channel
339 River mouth. Based on the above, we summed the percentages of *E. excavatum* f. *clavatum* and
340 *C. crassa* to constitute the group of glacier-proximal indicator species. The latter will be used
341 to examine the EIS dynamics (*cf.* Section 5.2).

342

343 **5.1.3. Holocene indicator species**

344 One of the most striking features of our benthic foraminiferal record is the absence of
345 uvigerinids (*e.g.* *U. peregrina*, *U. mediterranea*), whereas they dominate the modern benthic
346 foraminiferal assemblages of the BoB between ~500 and 2000 m water depth (*e.g.*, Schönfeld,
347 2006; Barras *et al.*, 2010; Mojtahid *et al.*, 2010; Duros *et al.*, 2011, 2012). This absence is also
348 the case in the glacial part of the MD99-2328 record (Mojtahid *et al.*, 2017). We assume
349 therefore that uvigerinids might not be tolerant to the glacial-related conditions on the BoB
350 seafloor (Mojtahid *et al.*, 2013; Pascual *et al.*, 2020; Rodriguez-Lazaro *et al.*, 2017). Schönfeld
351 and Altenbach (2005) hypothesized a widespread change from glacial to modern surface
352 productivity configuration (*e.g.* nature of primary producers, seasonality in phytoplankton
353 blooms) that may have triggered the Holocene settlement of *U. peregrina* in the northeast
354 Atlantic. It is also interesting to note that *U. peregrina* and *U. mediterranea* are very abundant
355 in bathyal depths (~200-1500 m) of the Mediterranean and the BoB bathed by the MOW (*e.g.*
356 De Rijk *et al.*, 2000; Schmiedl *et al.*, 2000; Fontanier *et al.*, 2003). The possible link between
357 water masses and specific fauna has been progressively abandoned in favor of organic matter
358 and oxygen as major controlling environmental parameters (Jorissen *et al.*, 2007). Yet, the

359 settlement of uvigerinids in the BoB in the end of deglaciation - early Holocene (Garcia *et al.*,
360 2013; Mojtahid *et al.*, 2013; Pascual *et al.*, 2020) seems to coincide with the significant increase
361 in the influx of the MOW into the North Atlantic and along the European margin (Rogerson *et*
362 *al.*, 2012; Lebreiro *et al.*, 2018). This is coherent with what Mojtahid *et al.* (2017) observed in
363 core MD99-2328 where they record the appearance of uvigerinids (although with low
364 abundances) only in the Holocene portion of the record.

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

371

372 ***5.2. Environmental particularities of Heinrich Stadials depicted by benthic*** 373 ***foraminifera***

374 **5.2.1. What do the last three Heinrich Stadials have in common in the Bay of** 375 **Biscay?**

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

391 BOBGEO-CS05 and at many sites along the French Atlantic margin (Toucanne *et al.*, 2021).
392 As such, biotic and sedimentological data indicate reduced near-bottom flow speed (*i.e.*
393 weakened GEBC) and, by extension, a sluggish AMOC during the three HSs.

394 The glacier-proximal species (*E. excavatum* f. *clavatum*. and *C. crassa*), although present all
395 along the BOBGEO-CS05 record, display the highest percentages during the HSs, especially
396 during HS3 and HS2 (Figure 4b). In their modern habitats in the Arctic fjords, these species are
397 impacted by seasonal melting of marine-terminating glaciers (Schroder-Adams *et al.*, 1990;
398 Wollenburg and Mackensen, 1998; Wollenburg and Kuhnt, 2000; Wollenburg *et al.*, 2004).
399 Since enhanced EIS meltwaters influx to the BoB are described during HSs (Toucanne *et al.*,
400 2015), increased densities of these species might be indicative of such meltwater inputs. The
401 concomitant presence of meso-oligotrophic species (*e.g.* *C. pachyderma*) indicates a low to
402 moderate export of organic matter to the seafloor, especially during HS2 and HS3. This will be
403 further discussed when addressing the specificities of each HS (*cf.* Sections 5.2.2. and 5.3).

404

405 **5.2.2. The difference between the early HS1 and the other HSs**

406 In core BOBGEO-CS05, HS1 is very distinct from HS2 and HS3 by displaying a high
407 presence (~60 %) of opportunistic and high-organic flux indicator species (*C. carinata* and
408 *Bolivina* spp.; Schmiedl *et al.*, 1997; Fontanier *et al.*, 2003; Duros *et al.*, 2011) during its early
409 phase *ca.* ~18-16.7 ka cal BP (Figure 4d). This is coherent with the findings of Mojtahid *et al.*
410 (2017) at the same time period at site MD99-2328. Conversely, during HS2 and HS3, these
411 species were present with much lower abundances (< 10 %; Figure 4d). Thus, we assume that
412 limited organic material inputs reached the BOBGEO-CS05 site during HS3 and HS2, then
413 substantially increased during the early HS1. This difference is further corroborated by the
414 positive correlation between the abundance of the high-organic flux indicator species during
415 early HS1 at our site and both the BIT index at site MD95-2002 (Figure 4c; Ménot *et al.*, 2006)
416 and the turbidite (*i.e.* flood-related deposits) flux in the deep BoB (Zaragosi *et al.*, 2006;
417 Toucanne *et al.*, 2008, 2012). It has been suggested that these differences in organic material
418 inputs through time could result from complex interactions between climate conditions, and ice
419 and vegetation cover (Ménot *et al.*, 2006). Our data cannot resolve this issue, but it certainly
420 highlights the paroxysmal phase of EIS melting in response to increasing boreal insolation
421 during HS1, and the concomitant rapid progradation of a large outer-shelf delta that ultimately
422 improved the connection between the BOBGEO-CS05 site and the Channel River system
423 (Toucanne *et al.*, 2012). That said, because *C. carinata* and *Bolivina* spp. are very abundant in

424 shallower settings in the BoB (140-550 m depth; Duros *et al.*, 2011 ; Fontanier *et al.*, 2003), we
425 cannot discard that their presence in our record is a result of downslope transport. Even so, the
426 abundance of these species still indicates increased organic fluxes in their source habitats.

427 Interestingly, in the upper slope BOBGEO-CS05 and MD99-2328 cores, the dominance of
428 the anoxia indicator species (representing the sum of *Globobulimina* spp. and *Chilostomella*
429 *oolina*) at HS1 occurs early within this interval, before HE1 event *sensu stricto* (Figure 4i).
430 According to Mojtahid *et al.* (2017), the presence of these indicator species during early HS1
431 is indicative of organically-enriched and/or oxygen-depleted benthic environments, and their
432 absence during HE1 event, together with high \overline{SS} (Figure 4i & 4f) indicate well-ventilated
433 intermediate waters. In deeper sediment cores from the BoB (>2000 m depth), the HE1 event
434 is characterized by the presence of authigenic carbonates indicating anoxic bottom waters (*e.g.*
435 Auffret *et al.*, 1996; Toucanne *et al.*, 2015). Because these anoxia markers are not observed in
436 the shallower cores BOBGEO-CS05 and MD99-2328 and because all proxies (\overline{SS} and
437 foraminifera; Figure 4) indicate well-ventilated bottom waters, we can hypothesize a
438 decoupling between a vigorous intermediate water depth circulation during HE1 and a still
439 sluggish circulation at >2000 m in the northeast Atlantic, as reported by the Bermuda rise
440 $^{231}\text{Pa}/^{230}\text{Th}$ data from the deep northwest Atlantic (Figure 4e). A similar pattern is found in the
441 equatorial Atlantic where a better ventilation of mid-depth waters in late HS1 is recorded while
442 the deep sites remained poorly ventilated (Chen *et al.*, 2015).

443

444 **5.3. Foraminiferal evidence for mid-HS2 re-ventilation event**

445 During HS2 (Figure 5), the overall meso-oligotrophic conditions and the low bottom-water
446 ventilation depicted by both the low BFAR and the *C. pachyderma* - *Globobulimina* spp.
447 association (*i.e.* meso-oligotrophic species) were interrupted around 24.3 ka cal BP (Figure 5d
448 & 5e). At the same time, low percentages of the polar planktonic species *N. pachyderma* (Figure
449 5a) indicate a a warming of the sea-surface conditions and therefore a cessation of meltwater
450 input in the northern BoB. This surface water warming is recorded in several sedimentary
451 records along the European margin (*e.g.* Scourse *et al.*, 2009; Austin *et al.*, 2012; Waelbroeck
452 *et al.*, 2019). This warm event interrupting HS2 seems to be coeval with a well-known
453 atmospheric decrease in dust flux at high latitudes (Rasmussen *et al.*, 2008; Austin *et al.*, 2012).
454 During this sea-surface warming event, the re-appearance of the high-energy indicator species
455 (Figure 5c) and the drop in the anoxia indicator species (Figure 5f) strongly suggests a

456 reactivation of bottom water currents at site BOBGEO-CS05. This is supported by the increase
457 in the \overline{SS} values at our site and, more generally, in the northern part of the French Atlantic
458 margin (Figure 5b). Our biotic data, although covering this millennial-scale event at low
459 sampling resolution, thus indicate, together with the \overline{SS} proxy, enhanced vigor of the GEBC
460 and, by extension, of the AMOC during the mid-HS2. This re-acceleration of the GEBC
461 continues to about 100 yrs before the iceberg debacle of the LIS (*i.e.* HE2 *sensu stricto* at
462 24.2 ka cal BP), when our biotic and sedimentological proxies show a rapid return to meso-
463 oligotrophic conditions at the sea-floor and weak bottom currents.

464

465 **6. Conclusions**

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

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

480 Detailed investigation of the benthic foraminifera reveals some specificities of the HSs in
481 the northeast Atlantic. First, the high abundance of high-organic flux indicator species
482 (*Cassidulina carinata* and *Bolivina* spp.) during early HS1, compared to their near absence
483 during HS2 and HS3, reveals a millennial-scale peak in terrestrial organic material in the BoB
484 resulting from the significant EIS melting and Channel River meltwater floods. Second, benthic
485 foraminiferal species depict a short-term mid-depth re-ventilation event during HS2, indicated
486 by a decrease in the proportions of anoxia indicator species and an increase in the abundance
487 of high-energy indicator species. This short-term reactivation of the GEBC along the French

488 Atlantic margin, and of the AMOC, is coherent with the cessation of the EIS meltwater input
489 in the northern BoB, and more generally, with a warming of the sea-surface conditions in the
490 northeast Atlantic. This result strongly emphasizes the connection between the intermediate
491 ocean circulation and the cryosphere dynamics in the northeast Atlantic during the Heinrich
492 Stadials.

493

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505

506 **8. References**

507 Allen, K.A., Hönisch, B., Eggins, S.M., Haynes, L.L., Rosenthal, Y., Yu, J., 2016. Trace
508 element proxies for surface ocean conditions: A synthesis of culture calibrations with planktic
509 foraminifera. *Geochimica et Cosmochimica Acta* 193, 197–221.
510 <https://doi.org/10.1016/j.gca.2016.08.015>

511 Altenbach AV, Pflaumann U, Schiebel R et al. 1999. Scaling percentages and
512 distributional patterns of benthic Foraminifera with flux rates of organic carbon. *Journal of*
513 *Foraminiferal Research* 29: 173–185.

514 Alvarez-Solas, J., Robinson, A., Montoya, M., Ritz, C., 2013. Iceberg discharges of the
515 last glacial period driven by oceanic circulation changes. *PNAS* 110, 16350–16354.
516 <https://doi.org/10.1073/pnas.1306622110>

517 Auffret, G.A., Boelaert, A., Vergnaud-Grazzini, C., Müller, C., Kerbrat, R., 1996.
518 Identification of Heinrich Layers in core KS 01 North-Eastern Atlantic (46 °N, 17 °W),
519 implications for their origin. *Marine Geology, Ice Rafting and Paleocengraphy of the Northeast*
520 *Atlantic Ocean Selected papers presented at the 7th European Union of Geosciences* 131, 5–
521 20. [https://doi.org/10.1016/0025-3227\(95\)00141-7](https://doi.org/10.1016/0025-3227(95)00141-7)

522 Auffret G, Zaragosi S, Dennielou B et al. 2002. Terrigenous fluxes at the Celtic margin
523 during the last glacial cycle. *Marine Geology* 188: 79–108.

524 Austin, W.E.N., Evans, J.R., 2000. NE Atlantic benthic foraminifera: modern
525 distribution patterns and palaeoecological significance. *Journal of the Geological Society* 157,
526 679–691. <https://doi.org/10.1144/jgs.157.3.679>

527 Austin, W.E.N., Hibbert, F.D., Rasmussen, S.O., Peters, C., Abbott, P.M., Bryant, C.L.,
528 2012. The synchronization of palaeoclimatic events in the North Atlantic region during
529 Greenland Stadial 3 (ca 27.5 to 23.3 kyr b2k). *Quat. Sci. Rev.* 36, 154–163.
530 <https://doi.org/10.1016/j.quascirev.2010.12.014>

531 Barras, C., Fontanier, C., Jorissen, F., Hohenegger, J., 2010. A comparison of spatial
532 and temporal variability of living benthic foraminiferal faunas at 550m depth in the Bay of
533 Biscay. *Micropaleontology* 56, 275–295.

534 Bergsten, H., 1994. Recent benthic foraminifera of a transect from the North Pole to the
535 Yermak Plateau, eastern central Arctic Ocean. *Marine Geology*, 4th International Conference
536 on Paleoceanography (ICP IV) 119, 251–267. [https://doi.org/10.1016/0025-3227\(94\)90184-8](https://doi.org/10.1016/0025-3227(94)90184-8)

537 Bernhard JM. 1992. Benthic foraminiferal distribution and biomass related to pore-
538 water oxygen content: central California continental slope and rise. *Deep Sea Research Part A.*
539 *Oceanographic Research Papers* 39: 585–605.

540 Bernhard JM, Sen Gupta BK. 2003. Foraminifera of oxygen-depleted environments. In
541 *Modern Foraminifera*, Sen Gupta BK (ed). Springer Netherlands:Dordrecht; 201–216.

542 Berx, B., Hansen, B., Østerhus, S., Larsen, K.M., Sherwin, T., Jochumsen, K., 2013.
543 Combining in situ measurements and altimetry to estimate volume, heat and salt transport
544 variability through the Faroe–Shetland Channel. *Ocean Science* 9, 639–654.
545 <https://doi.org/10.5194/os-9-639-2013>

546 Böhm, E., Lippold, J., Gutjahr, M., Frank, M., Blaser, P., Antz, B., Fohlmeister, J.,
547 Frank, N., Andersen, M.B., Deininger, M., 2015. Strong and deep Atlantic meridional
548 overturning circulation during the last glacial cycle. *Nature* 517, 73–76.
549 <https://doi.org/10.1038/nature14059>

550 Bond, G., Broecker, W., Johnsen, S., McManus, J., Labeyrie, L., Jouzel, J., Bonani, G.,
551 1993. Correlations between climate records from North Atlantic sediments and Greenland ice.
552 *Nature* 365, 143–147. <https://doi.org/10.1038/365143a0>

553 Boswell, S.M., Toucanne, S., Pitel-Roudaut, M., Creyts, T.T., Eynaud, F., Bayon, G.,
554 2019. Enhanced surface melting of the Fennoscandian Ice Sheet during periods of North
555 Atlantic cooling. *Geology* 47, 664–668. <https://doi.org/10.1130/G46370.1>

556 Bourillet, J.-F., 2009. BOBGEO cruise, Pourquoi pas? R/V.
557 <https://doi.org/10.17600/9030060>

558 Bourillet, J.-F., Lericolais, G., 2003. Morphology and Seismic Stratigraphy of the
559 Manche Paleoriver System, Western Approaches, in: Mienert, J., Weaver, P. (Eds.), *European*

560 Margin Sediment Dynamics: Side-Scan Sonar and Seismic Images. Springer, Berlin,
561 Heidelberg, pp. 229–232. https://doi.org/10.1007/978-3-642-55846-7_37

562 Bourillet JF, Reynaud JY, Baltzer A, Zaragosi S. 2003. The ‘Fleuve Manche’: The
563 submarine sedimentary features from the outer shelf to the deep-sea fans. *Journal of Quaternary*
564 *Science* 18: 261–282.

565 Brady, E.C., Otto-Bliesner, B.L., 2011. The role of meltwater-induced subsurface ocean
566 warming in regulating the Atlantic meridional overturning in glacial climate simulations. *Clim*
567 *Dyn* 37, 1517–1532. <https://doi.org/10.1007/s00382-010-0925-9>

568 Broecker, W.S., Denton, G.H., 1990. The role of ocean-atmosphere reorganizations in
569 glacial cycles. *Quaternary Science Reviews* 9, 305–341. [https://doi.org/10.1016/0277-](https://doi.org/10.1016/0277-3791(90)90026-7)
570 [3791\(90\)90026-7](https://doi.org/10.1016/0277-3791(90)90026-7)

571 Buckley, M.W., Marshall, J., 2016. Observations, inferences, and mechanisms of the
572 Atlantic Meridional Overturning Circulation: A review. *Reviews of Geophysics* 54, 5–63.
573 <https://doi.org/10.1002/2015RG000493>

574 Buzas, M.A., 1990. Another look at confidence limits for species proportions. *Journal*
575 *of Paleontology* 64, 842–843. <https://doi.org/10.1017/S002233600001903X>

576 Chen, T., Robinson, L.F., Burke, A., Southon, J., Spooner, P., Morris, P.J., Ng, H.C.,
577 2015. Synchronous centennial abrupt events in the ocean and atmosphere during the last
578 deglaciation. *Science*. <https://doi.org/10.1126/science.aac6159>

579 Clark, C.D., Hughes, A.L.C., Greenwood, S.L., Jordan, C., Sejrup, H.P., 2012. Pattern
580 and timing of retreat of the last British-Irish Ice Sheet. *Quaternary Science Reviews, Quaternary*
581 *Glaciation History of Northern Europe* 44, 112–146.
582 <https://doi.org/10.1016/j.quascirev.2010.07.019>

583 Clark, M., Marsh, R., Harle, J., 2021. Weakening and warming of the European Slope
584 Current since the late 1990s attributed to basin-scale density changes (preprint). *Shelf-sea*
585 *depth/Data Assimilation/Shelf Seas/Transports/cycling (nutrients, C, O, etc.)/Ocean-shelf*
586 *interactions*. <https://doi.org/10.5194/os-2021-60>

587 Corliss BH. 1991. Morphology and microhabitat preferences of benthic foraminifera
588 from the northwest Atlantic Ocean. *Marine Micropaleontology* 17: 195–236.

589 Corliss BH, Emerson S. 1990. Distribution of rose bengal stained deepsea benthic
590 foraminifera from the Nova Scotian continental margin and Gulf of Maine. *Deep Sea Research*
591 *Part A. Oceanographic Research Papers* 37: 381–400.

592 Crocker, A.J., Chalk, T.B., Bailey, I., Spencer, M.R., Gutjahr, M., Foster, G.L., Wilson,
593 P.A., 2016. Geochemical response of the mid-depth Northeast Atlantic Ocean to freshwater
594 input during Heinrich events 1 to 4. *Quaternary Science Reviews* 151, 236–254.
595 <https://doi.org/10.1016/j.quascirev.2016.08.035>

596 Darling, K.F., Schweizer, M., Knudsen, K.L., Evans, K.M., Bird, C., Roberts, A.,
597 Filipsson, H.L., Kim, J.-H., Gudmundsson, G., Wade, C.M., Sayer, M.D.J., Austin, W.E.N.,

598 2016. The genetic diversity, phylogeography and morphology of Elphidiidae (Foraminifera) in
599 the Northeast Atlantic. *Marine Micropaleontology* 129, 1–23.
600 <https://doi.org/10.1016/j.marmicro.2016.09.001>

601 De Rijk, S., Jorissen, F.J., Rohling, E.J., Troelstra, S.R., 2000. Organic flux control on
602 bathymetric zonation of Mediterranean benthic foraminifera. *Marine Micropaleontology* 40,
603 151–166. [https://doi.org/10.1016/S0377-8398\(00\)00037-2](https://doi.org/10.1016/S0377-8398(00)00037-2)

604 de Stigter HC 1996. Recent and fossil benthic foraminifera in the Adriatic Sea:
605 distribution patterns in relation to organic carbon flux and oxygen concentration at the seabed.
606 *Faculteit Aardwetenschappen*.

607 de Stigter HC, Jorissen FJ, van der Zwaan GJ. 1998. Bathymetric distribution and
608 microhabitat partitioning of live (Rose Bengal stained) benthic Foraminifera along a shelf to
609 bathyal transect in the southern Adriatic Sea. *Journal of Foraminiferal Research* 28: 40–65.

610 Denton, G., Anderson, R., Toggweiler, J.R., Edwards, R., Schaefer, J., Putnam, A.,
611 2010. The Last Glacial Termination. *Science (New York, N.Y.)* 328, 1652–6.
612 <https://doi.org/10.1126/science.1184119>

613 Denton, G.H., Putnam, A.E., Russell, J.L., Barrell, D.J.A., Schaefer, J.M., Kaplan,
614 M.R., Strand, P.D., 2021. The Zealandia Switch: Ice age climate shifts viewed from Southern
615 Hemisphere moraines. *Quaternary Science Reviews* 257, 106771.
616 <https://doi.org/10.1016/j.quascirev.2020.106771>

617 Dickson, R.R., Brown, J., 1994. The production of North Atlantic Deep Water: Sources,
618 rates, and pathways. *Journal of Geophysical Research: Oceans* 99, 12319–12341.
619 <https://doi.org/10.1029/94JC00530>

620 Dorst S, Schönfeld J. 2013. Diversity of benthic foraminifera on the shelf and slope of
621 the NE Atlantic: analysis of Datasets. *Journal of Foraminiferal Research* 43: 238–254.

622 Dorst S, Schönfeld J, Walter L. 2015. Recent benthic foraminiferal assemblages from
623 the Celtic Sea (South Western Approaches, NE. Atlantic). *Paläontologische Zeitschrift* 89:
624 287–302.

625 Duros, P., Fontanier, C., de Stigter, H.C., Cesbron, F., Metzger, E., Jorissen, F.J., 2012.
626 Live and dead benthic foraminiferal faunas from Whittard Canyon (NE Atlantic): Focus on
627 taphonomic processes and paleo-environmental applications. *Marine Micropaleontology* 94–
628 95, 25–44. <https://doi.org/10.1016/j.marmicro.2012.05.004>

629 Duros, P., Fontanier, C., Metzger, E., Pusceddu, A., Cesbron, F., de Stigter, H.C.,
630 Bianchelli, S., Danovaro, R., Jorissen, F.J., 2011. Live (stained) benthic foraminifera in the
631 Whittard Canyon, Celtic margin (NE Atlantic). *Deep Sea Research Part I: Oceanographic*
632 *Research Papers* 58, 128–146. <https://doi.org/10.1016/j.dsr.2010.11.008>

633 Duros P, Silva Jacinto R, Dennielou B et al. 2017. Benthic foraminiferal response to
634 sedimentary disturbance in the Capbreton canyon (Bay of Biscay, NE Atlantic). *Deep Sea*
635 *Research Part I: Oceanographic Research Papers* 120: 61–75.

636 Eynaud, F., Malaizé, B., Zaragosi, S., Vernal, A. de, Scourse, J., Pujol, C., Cortijo, E.,
637 Grousset, F.E., Penaud, A., Toucanne, S., Turon, J.-L., Auffret, G., 2012. New constraints on
638 European glacial freshwater releases to the North Atlantic Ocean. *Geophysical Research Letters*
639 39. <https://doi.org/10.1029/2012GL052100>

640 Fatela, F., Taborda, R., 2002. Confidence limits of species proportions in microfossil
641 assemblages. *Marine Micropaleontology* 45, 169–174. [https://doi.org/10.1016/S0377-](https://doi.org/10.1016/S0377-8398(02)00021-X)
642 [8398\(02\)00021-X](https://doi.org/10.1016/S0377-8398(02)00021-X)

643 Fontanier, Christophe, Jorissen, F., Anschutz, P., Chaillou, G., 2006. Seasonal
644 variability of benthic foraminiferal faunas at 1000 m depth in the Bay of Biscay. *Journal of*
645 *Foraminiferal Research* 36, 61–76. <https://doi.org/10.2113/36.1.61>

646 Fontanier C, Jorissen FJ, Chaillou G et al. 2005. Live foraminiferal faunas from a 2800m
647 deep lower canyon station from the Bay of Biscay: Faunal response to focusing of refractory
648 organic matter. *Deep Sea Research Part I: Oceanographic Research Papers* 52: 1189–1227.

649 Fontanier, C., Jorissen, F.J., Chaillou, G., David, C., Anschutz, P., Lafon, V., 2003.
650 Seasonal and interannual variability of benthic foraminiferal faunas at 550m depth in the Bay
651 of Biscay. *Deep Sea Research Part I: Oceanographic Research Papers* 50, 457–494.
652 [https://doi.org/10.1016/S0967-0637\(02\)00167-X](https://doi.org/10.1016/S0967-0637(02)00167-X)

653 Fontanier, C., Jorissen, F.J., Licari, L., Alexandre, A., Anschutz, P., Carbonel, P., 2002.
654 Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and
655 microhabitats. *Deep Sea Research Part I: Oceanographic Research Papers* 49, 751–785.
656 [https://doi.org/10.1016/S0967-0637\(01\)00078-4](https://doi.org/10.1016/S0967-0637(01)00078-4)

657 Fontanier C, Jorissen FJ, Michel E et al. 2008. Stable oxygen and carbon isotopes of
658 live (stained) benthic foraminifera from cap-ferret canyon (bay of biscay). *Journal of*
659 *Foraminiferal Research* 38: 39–51.

660 Fossile, E., Nardelli, M.P., Jouini, A., Lansard, B., Pusceddu, A., Moccia, D., Michel,
661 E., Péron, O., Howa, H., Mojtahid, M., 2020. Benthic foraminifera as tracers of brine production
662 in the Storfjorden “sea ice factory.” *Biogeosciences* 17, 1933–1953. [https://doi.org/10.5194/bg-](https://doi.org/10.5194/bg-17-1933-2020)
663 [17-1933-2020](https://doi.org/10.5194/bg-17-1933-2020)

664 Friocourt, Y., Levier, B., Speich, S., Blanke, B., Drijfhout, S.S., 2007. A regional
665 numerical ocean model of the circulation in the Bay of Biscay. *Journal of Geophysical*
666 *Research: Oceans* 112. <https://doi.org/10.1029/2006JC003935>

667 Garcia J, Mojtahid M, Howa H et al. 2013. Benthic and Planktic Foraminifera as
668 Indicators of Late Glacial to Holocene Paleoclimatic Changes in a Marginal Environment: An
669 Example from the Southeastern Bay of Biscay. *Acta Protozoologica* 52: 161–180.

670 Gooday, A.J., 2003. Benthic foraminifera (protista) as tools in deep-water
671 palaeoceanography: Environmental influences on faunal characteristics, in: *Advances in*
672 *Marine Biology*. Academic Press, pp. 1–90. [https://doi.org/10.1016/S0065-2881\(03\)46002-1](https://doi.org/10.1016/S0065-2881(03)46002-1)

673 Gooday, A.J., Hughes, J.A., 2002. Foraminifera associated with phytodetritus deposits
674 at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a
675 comparison of stained and dead assemblages. *Marine Micropaleontology* 46, 83–110.
676 [https://doi.org/10.1016/S0377-8398\(02\)00050-6](https://doi.org/10.1016/S0377-8398(02)00050-6)

677 Grousset FE, Pujol C, Labeyrie L et al. 2000. Were the North Atlantic Heinrich events
678 triggered by the behavior of the European ice sheets? *Geology* 28: 123–126.

679 Gupta AK. 1999. Latest Pliocene through Holocene paleoceanography of the eastern
680 Indian Ocean: benthic foraminiferal evidence. *Marine Geology* 161: 63–73.

681 Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological Statistics
682 Software Package for Education and Data Analysis 9.

683 Hansen, A., Knudsen, K.L., 1995. Recent foraminiferal distribution in Freemansundet
684 and Early Holocene stratigraphy on Edgeøya, Svalbard. *Polar Research* 14, 215–238.
685 <https://doi.org/10.3402/polar.v14i2.6664>

686 Hayek, L.-A., Buzas, M., 1997. *Surveying Natural Populations: Quantitative Tools for*
687 *Assessing Biodiversity, Surveying Natural Populations.* Columbia University Press.
688 <https://doi.org/10.7312/haye14620>

689 Hemming, S.R., 2004. Heinrich events: Massive late Pleistocene detritus layers of the
690 North Atlantic and their global climate imprint. *Reviews of Geophysics* 42.
691 <https://doi.org/10.1029/2003RG000128>

692 Henry, L.G., McManus, J.F., Curry, W.B., Roberts, N.L., Piotrowski, A.M., Keigwin,
693 L.D., 2016. North Atlantic ocean circulation and abrupt climate change during the last
694 glaciation. *Science* 353, 470–474. <https://doi.org/10.1126/science.aaf5529>

695 Herguera, J.C., Berger, W.H., 1991. Paleoproductivity from benthic foraminifera
696 abundance: Glacial to postglacial change in the west-equatorial Pacific. *Geology* 19, 1173–
697 1176. [https://doi.org/10.1130/0091-7613\(1991\)019<1173:PFBFAG>2.3.CO;2](https://doi.org/10.1130/0091-7613(1991)019<1173:PFBFAG>2.3.CO;2)

698 Hess S, Jorissen FJ. 2009. Distribution patterns of living benthic foraminifera from Cap
699 Breton canyon, Bay of Biscay: Faunal response to sediment instability. *Deep Sea Research Part*
700 *I: Oceanographic Research Papers* 56: 1555–1578.

701 Hess S, Jorissen FJ, Venet V et al. 2005. Benthic Foraminiferal recovery after recent
702 turbidite deposition in Cap Breton Canyon, Bay of Biscay. *Journal of Foraminiferal Research*
703 35: 114–129.

704 Huthnance, J.M., 1984. Slope Currents and “JE BAR.” *Journal of Physical*
705 *Oceanography* 14, 795–810. [https://doi.org/10.1175/1520-0485\(1984\)014<0795:SCA>2.0.CO;2](https://doi.org/10.1175/1520-0485(1984)014<0795:SCA>2.0.CO;2)

707 Huthnance, J.M., Inall, M.E., Fraser, N.J., 2020. Oceanic Density/Pressure Gradients
708 and Slope Currents. *Journal of Physical Oceanography* 50, 1643–1654.
709 <https://doi.org/10.1175/JPO-D-19-0134.1>

710 Jennings, A.E., Weiner, N.J., Helgadottir, G., Andrews, J.T., 2004. Modern
711 foraminiferal faunas of the southwestern to northern Iceland Shelf: oceanographic and
712 environmental controls. *Journal of Foraminiferal Research* 34, 180–207.
713 <https://doi.org/10.2113/34.3.180>

714 Jones R, Brady H. 1994. *The challenger foraminifera*. Oxford University Press

715 Jorissen FJ. 1987. The distribution of benthic foraminifera in the Adriatic Sea. *Marine*
716 *Micropaleontology* 12: 21–48.

717 Jorissen FJ. 1999. Benthic foraminiferal microhabitats below the sediment-water
718 interface. In *Modern Foraminifera*, Sen Gupta BK (ed). Springer Netherlands: Dordrecht; 161–
719 179.

720 Jorissen FJ, Wittling I, Peypouquet JP et al. 1998. Live benthic foraminiferal faunas off
721 Cape Blanc, NW-Africa: Community structure and microhabitats. *Deep Sea Research Part I:*
722 *Oceanographic Research Papers* 45: 2157–2188.

723 Jorissen, F.J., Fontanier, C., Thomas, E., 2007. Chapter Seven Paleooceanographical
724 Proxies Based on Deep-Sea Benthic Foraminiferal Assemblage Characteristics, in: Hillaire–
725 Marcel, C., De Vernal, A. (Eds.), *Developments in Marine Geology, Proxies in Late Cenozoic*
726 *Paleoceanography*. Elsevier, pp. 263–325. [https://doi.org/10.1016/S1572-5480\(07\)01012-3](https://doi.org/10.1016/S1572-5480(07)01012-3)

727 Keffer, T., Martinson, D.G., Corliss, B.H., 1988. The Position of the Gulf Stream During
728 Quaternary Glaciations. *Science* 241, 440–442. <https://doi.org/10.1126/science.241.4864.440>

729 Keul, N., Langer, G., Thoms, S., de Nooijer, L.J., Reichart, G.-J., Bijma, J., 2017.
730 Exploring foraminiferal Sr/Ca as a new carbonate system proxy. *Geochimica et Cosmochimica*
731 *Acta* 202, 374–386. <https://doi.org/10.1016/j.gca.2016.11.022>

732 Kissel, C., Laj, C., Piotrowski, A.M., Goldstein, S.L., Hemming, S.R., 2008. Millennial-
733 scale propagation of Atlantic deep waters to the glacial Southern Ocean. *Paleoceanography* 23.
734 <https://doi.org/10.1029/2008PA001624>

735 Koho, K.A., Piña-Ochoa, E., Geslin, E., Risgaard-Petersen, N., 2011. Vertical
736 migration, nitrate uptake and denitrification: survival mechanisms of foraminifera
737 (*Globobulimina turgida*) under low oxygen conditions. *FEMS Microbiology Ecology* 75, 273–
738 283. <https://doi.org/10.1111/j.1574-6941.2010.01010.x>

739 Korsun, S.A., Pogodina, I.A., Forman, S.L., Lubinski, D.J., 1995. Recent foraminifera
740 in glaciomarine sediments from three arctic fjords of Novaja Zemlja and Svalbard. *Polar*
741 *Research* 14, 15–32. <https://doi.org/10.3402/polar.v14i1.6648>

742 Lebreiro SM, Antón L, Reguera MI et al. 2018. Paleooceanographic and climatic
743 implications of a new Mediterranean Outflow branch in the southern Gulf of Cadiz. *Quaternary*
744 *Science Reviews* 197: 92–111.

745 Löffverström, M., Caballero, R., Nilsson, J., Kleman, J., 2014. Evolution of the large-
746 scale atmospheric circulation in response to changing ice sheets over the last glacial cycle.
747 *Climate of the Past* 10, 1453–1471. <https://doi.org/10.5194/cp-10-1453-2014>

748 Lozier, M.S., Li, F., Bacon, S., Bahr, F., Bower, A.S., Cunningham, S.A., Jong, M.F.
749 de, Steur, L. de, deYoung, B., Fischer, J., Gary, S.F., Greenan, B.J.W., Holliday, N.P., Houk,
750 A., Houpert, L., Inall, M.E., Johns, W.E., Johnson, H.L., Johnson, C., Karstensen, J., Koman,
751 G., Bras, I.A.L., Lin, X., Mackay, N., Marshall, D.P., Mercier, H., Oltmanns, M., Pickart, R.S.,
752 Ramsey, A.L., Rayner, D., Straneo, F., Thierry, V., Torres, D.J., Williams, R.G., Wilson, C.,
753 Yang, J., Yashayaev, I., Zhao, J., 2019. A sea change in our view of overturning in the subpolar
754 North Atlantic. *Science* 363, 516–521. <https://doi.org/10.1126/science.aau6592>

755 Lynch-Stieglitz, J., 2017. The Atlantic Meridional Overturning Circulation and Abrupt
756 Climate Change. *Annu. Rev. Mar. Sci.* 9, 83–104. [https://doi.org/10.1146/annurev-marine-](https://doi.org/10.1146/annurev-marine-010816-060415)
757 [010816-060415](https://doi.org/10.1146/annurev-marine-010816-060415)

758 Lynch-Stieglitz, J., Adkins, J.F., Curry, W.B., Dokken, T., Hall, I.R., Herguera, J.C.,
759 Hirschi, J.J.-M., Ivanova, E.V., Kissel, C., Marchal, O., Marchitto, T.M., McCave, I.N.,
760 McManus, J.F., Mulitza, S., Ninnemann, U., Peeters, F., Yu, E.-F., Zahn, R., 2007. Atlantic
761 Meridional Overturning Circulation During the Last Glacial Maximum. *Science* 316, 66–69.
762 <https://doi.org/10.1126/science.1137127>

763 Mackensen, A., Sejrup, H.P., Jansen, E., 1985. The distribution of living benthic
764 foraminifera on the continental slope and rise off southwest Norway. *Marine*
765 *Micropaleontology* 9, 275–306. [https://doi.org/10.1016/0377-8398\(85\)90001-5](https://doi.org/10.1016/0377-8398(85)90001-5)

766 Marcott, S.A., Clark, P.U., Padman, L., Klinkhammer, G.P., Springer, S.R., Liu, Z.,
767 Otto-Bliesner, B.L., Carlson, A.E., Ungerer, A., Padman, J., He, F., Cheng, J., Schmittner, A.,
768 2011. Ice-shelf collapse from subsurface warming as a trigger for Heinrich events. *Proc. Natl.*
769 *Acad. Sci. U.S.A.* 108, 13415–13419. <https://doi.org/10.1073/pnas.1104772108>

770 Margreth, S., Rüggeberg, A., Spezzaferri, S., 2009. Benthic foraminifera as bioindicator
771 for cold-water coral reef ecosystems along the Irish margin. *Deep Sea Research Part I:*
772 *Oceanographic Research Papers* 56, 2216–2234. <https://doi.org/10.1016/j.dsr.2009.07.009>

773 Marsh, R., Haigh, I.D., Cunningham, S.A., Inall, M.E., Porter, M., Moat, B.I., 2017.
774 Large-scale forcing of the European Slope Current and associated inflows to the North Sea.
775 *Ocean Sci.* 13. <https://doi.org/10.5194/os-13-315-2017>

776 McCave, I.N., Manighetti, B., Beveridge, N. a. S., 1995. Circulation in the glacial North
777 Atlantic inferred from grain-size measurements. *Nature* 374, 149–152.
778 <https://doi.org/10.1038/374149a0>

779 McManus, J.F., Oppo, D.W., Cullen, J.L., 1999. A 0.5-Million-Year Record of
780 Millennial-Scale Climate Variability in the North Atlantic. *Science* 283, 971–975.
781 <https://doi.org/10.1126/science.283.5404.971>

782 McManus JF, Francois R, Gherardi J-M et al. 2004. Collapse and rapid resumption of
783 Atlantic meridional circulation linked to deglacial climate changes. *Nature* 428: 834–837.

784 Mendes I, Dias JA, Schönfeld J et al. 2012. Distribution of living benthic foraminifera
785 on the northern gulf of Cadiz continental shelf. *Journal of Foraminiferal Research* 42: 18–38.

786 Ménot, G., Bard, E., Rostek, F., Weijers, J.W.H., Hopmans, E.C., Schouten, S., Damsté,
787 J.S.S., 2006. Early Reactivation of European Rivers During the Last Deglaciation. *Science* 313,
788 1623–1625. <https://doi.org/10.1126/science.1130511>

789 Milker Y, Schmiedl G. 2012. A taxonomic guide to modern benthic shelf foraminifera
790 of the western Mediterranean Sea. *Palaeontologica Electronica* 15: 1–134.

791 Mix AC, Bard E, Schneider R. 2001. Environmental processes of the ice age: land,
792 oceans, glaciers (EPILOG). *Quaternary Science Reviews* 20: 627–657.

793 Mojtahid M, Jorissen F, Lansard B et al. 2009. Spatial distribution of live benthic
794 foraminifera in the Rhône prodelta: Faunal response to a continental–marine organic matter
795 gradient. *Marine Micropaleontology* 70: 177–200.

796 Mojtahid, M., Griveaud, C., Fontanier, C., Anschutz, P., Jorissen, F.J., 2010. Live
797 benthic foraminiferal faunas along a bathymetrical transect (140–4800m) in the Bay of Biscay
798 (NE Atlantic). *Revue de Micropaléontologie, Foraminiferal Geobiology* 53, 139–162.
799 <https://doi.org/10.1016/j.revmic.2010.01.002>

800 Mojtahid, M., Jorissen, F.J., Garcia, J., Schiebel, R., Michel, E., Eynaud, F., Gillet, H.,
801 Cremer, M., Diz Ferreiro, P., Siccha, M., Howa, H., 2013. High resolution Holocene record in
802 the southeastern Bay of Biscay: Global versus regional climate signals. *Palaeogeography,*
803 *Palaeoclimatology, Palaeoecology* 377, 28–44. <https://doi.org/10.1016/j.palaeo.2013.03.004>

804 Mojtahid, M., Geslin, E., Coynel, A., Gorse, L., Vella, C., Davranche, A., Zozzolo, L.,
805 Blanchet, L., Bénéteau, E., Maillet, G., 2016. Spatial distribution of living (Rose Bengal
806 stained) benthic foraminifera in the Loire estuary (western France). *Journal of Sea Research,*
807 *Recent and past sedimentary, biogeochemical and benthic ecosystem evolution of the Loire*
808 *Estuary (Western France)* 118, 1–16. <https://doi.org/10.1016/j.seares.2016.02.003>

809 Mojtahid, M., Toucanne, S., Fentimen, R., Barras, C., Le Houedec, S., Soulet, G.,
810 Bourillet, J.-F., Michel, E., 2017. Changes in northeast Atlantic hydrology during Termination
811 1: Insights from Celtic margin’s benthic foraminifera. *Quaternary Science Reviews* 175, 45–
812 59. <https://doi.org/10.1016/j.quascirev.2017.09.003>

813 Morigi C, Jorissen FJ, Gervais A et al. 2001. Benthic foraminiferal faunas in surface
814 sediments off nw africa: relationship with organic flux to the ocean floor. *Journal of*
815 *Foraminiferal Research* 31: 350–368.

816 Moritz, M., Jochumsen, K., Kieke, D., Klein, B., Klein, H., Köllner, M., Rhein, M.,
817 2021. Volume Transport Time Series and Variability of the North Atlantic Eastern Boundary
818 Current at Goban Spur. *Journal of Geophysical Research: Oceans* 126, e2021JC017393.
819 <https://doi.org/10.1029/2021JC017393>

820 Murray JW. 1970. Foraminifers of the Western Approaches to the English Channel.
821 *Micropaleontology* 16: 471–485.

822 Murray, J.W., 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge
823 University Press.

824 Murray, J.W., 2014. Ecology and Palaeoecology of Benthic Foraminifera. Routledge.

825 Ng HC, Robinson LF, McManus JF et al. 2018. Coherent deglacial changes in western
826 Atlantic Ocean circulation. Nature Communications 9: 2947.

827 Otto-Bliesner, B.L., Brady, E.C., Clauzet, G., Tomas, R., Levis, S., Kothavala, Z., 2006.
828 Last Glacial Maximum and Holocene Climate in CCSM3. Journal of Climate 19, 2526–2544.
829 <https://doi.org/10.1175/JCLI3748.1>

830 Pascual, A., Rodriguez-Lazaro, J., Martín-Rubio, M., Jouanneau, J.-M., Weber, O.,
831 2008. A survey of the benthic microfauna (foraminifera, Ostracoda) on the Basque shelf,
832 southern Bay of Biscay. Journal of Marine Systems, Oceanography of the Bay of Biscay 72,
833 35–63. <https://doi.org/10.1016/j.jmarsys.2007.05.015>

834 Pascual, A., Rodríguez-Lázaro, J., Martínez-García, B., Varela, Z., 2020.
835 Palaeoceanographic and palaeoclimatic changes during the last 37,000 years detected in the SE
836 Bay of Biscay based on benthic foraminifera. Quaternary International, Quaternary Research
837 in Spain: Environmental Changes and Human Footprint 566–567, 323–336.
838 <https://doi.org/10.1016/j.quaint.2020.03.043>

839 Peck, V.L., Hall, I.R., Zahn, R., Elderfield, H., Grousset, F., Hemming, S.R., Scourse,
840 J.D., 2006. High resolution evidence for linkages between NW European ice sheet instability
841 and Atlantic Meridional Overturning Circulation. Earth and Planetary Science Letters 243,
842 476–488. <https://doi.org/10.1016/j.epsl.2005.12.023>

843 Peck, V.L., Hall, I.R., Zahn, R., Grousset, F., Hemming, S.R., Scourse, J.D., 2007. The
844 relationship of Heinrich events and their European precursors over the past 60ka BP: a multi-
845 proxy ice-rafted debris provenance study in the North East Atlantic. Quaternary Science
846 Reviews 26, 862–875. <https://doi.org/10.1016/j.quascirev.2006.12.002>

847 Phleger FB, Parker FL, Peirson JF. 1953. North Atlantic foraminifera. Reports of the
848 Swedish Deep-Sea Expedition 7: 1–122

849 Pina-Ochoa, E., Hogslund, S., Geslin, E., Cedhagen, T., Revsbech, N.P., Nielsen, L.P.,
850 Schweizer, M., Jorissen, F., Rysgaard, S., Risgaard-Petersen, N., 2010. Widespread occurrence
851 of nitrate storage and denitrification among Foraminifera and Gromiida. Proceedings of the
852 National Academy of Sciences 107, 1148–1153. <https://doi.org/10.1073/pnas.0908440107>

853 Pingree, R.D., Cann, B.L., 1990. Structure, strength and seasonality of the slope currents
854 in the Bay of Biscay region. Journal of the Marine Biological Association of the United
855 Kingdom 70, 857–885. <https://doi.org/10.1017/S0025315400059117>

856 Pingree, R.D., Sinha, B., Griffiths, C.R., 1999. Seasonality of the European slope
857 current (Goban Spur) and ocean margin exchange. Continental Shelf Research 19, 929–975.
858 [https://doi.org/10.1016/S0278-4343\(98\)00116-2](https://doi.org/10.1016/S0278-4343(98)00116-2)

859 Pollard, R.T., Pu, S., 1985. Structure and circulation of the Upper Atlantic Ocean
860 northeast of the Azores. Progress in Oceanography 14, 443–462. [https://doi.org/10.1016/0079-6611\(85\)90022-9](https://doi.org/10.1016/0079-6611(85)90022-9)

861

862 Polyak, L., Korsun, S., Febo, L.A., Stanovoy, V., Khusid, T., Hald, M., Paulsen, B.E.,
863 Lubinski, D.J., 2002. Benthic foraminiferal assemblages from the southern Kara Sea, a river-
864 influenced Arctic marine environment. *Journal of Foraminiferal Research* 32, 252–273.
865 <https://doi.org/10.2113/32.3.252>

866 Pujos, M., 1976. *Ecologie des foraminifères benthiques et des thecamoebiens de la*
867 *Gironde et du plateau continental Sud-Gascogne: application à la connaissance du quaternaire*
868 *terminal de la région Ouest-Gironde (Thèse de doctorat). Université Bordeaux-I, 1971-2013,*
869 *France.*

870 Rasmussen, S.O., Andersen, K.K., Svensson, A.M., Steffensen, J.P., Vinther, B.M.,
871 Clausen, H.B., Siggaard-Andersen, M.-L., Johnsen, S.J., Larsen, L.B., Dahl-Jensen, D., Bigler,
872 M., Röthlisberger, R., Fischer, H., Goto-Azuma, K., Hansson, M.E., Ruth, U., 2006. A new
873 Greenland ice core chronology for the last glacial termination. *Journal of Geophysical*
874 *Research: Atmospheres* 111. <https://doi.org/10.1029/2005JD006079>

875 Rasmussen SO, Seierstad IK, Andersen KK et al. 2008. Synchronization of the NGRIP,
876 GRIP, and GISP2 ice cores across MIS 2 and palaeoclimatic implications. *Quaternary Science*
877 *Reviews* 27: 18–28.

878 Rasmussen, S.O., Bigler, M., Blockley, S.P., Blunier, T., Buchardt, S.L., Clausen, H.B.,
879 Cvijanovic, I., Dahl-Jensen, D., Johnsen, S.J., Fischer, H., Gkinis, V., Guillevic, M., Hoek,
880 W.Z., Lowe, J.J., Pedro, J.B., Popp, T., Seierstad, I.K., Steffensen, J.P., Svensson, A.M.,
881 Vallelonga, P., Vinther, B.M., Walker, M.J.C., Wheatley, J.J., Winstrup, M., 2014. A
882 stratigraphic framework for abrupt climatic changes during the Last Glacial period based on
883 three synchronized Greenland ice-core records: refining and extending the INTIMATE event
884 stratigraphy. *Quaternary Science Reviews, Dating, Synthesis, and Interpretation of*
885 *Palaeoclimatic Records and Model-data Integration: Advances of the INTIMATE*
886 *project (INTEgration of Ice core, Marine and TERrestrial records, COST Action ES0907)* 106,
887 14–28. <https://doi.org/10.1016/j.quascirev.2014.09.007>

888 Reimer PJ, Austin WEN, Bard E et al. 2020. The IntCal20 Northern Hemisphere
889 Radiocarbon Age Calibration Curve (0–55 cal kBP). *Radiocarbon* 62: 725–757.

890 Rickaby, R.E.M., Elderfield, H., 2005. Evidence from the high-latitude North Atlantic
891 for variations in Antarctic Intermediate water flow during the last deglaciation. *Geochemistry,*
892 *Geophysics, Geosystems* 6. <https://doi.org/10.1029/2004GC000858>

893 Risgaard-Petersen, N., Langezaal, A.M., Ingvarsdén, S., Schmid, M.C., Jetten, M.S.M.,
894 Op den Camp, H.J.M., Derksen, J.W.M., Piña-Ochoa, E., Eriksson, S.P., Peter Nielsen, L., Peter
895 Revsbech, N., Cedhagen, T., van der Zwaan, G.J., 2006. Evidence for complete denitrification
896 in a benthic foraminifer. *Nature* 443, 93–96. <https://doi.org/10.1038/nature05070>

897 Rodriguez-Lazaro, J., Pascual, A., Cacho, I., Varela, Z., Pena, L.D., 2017. Deep-sea
898 benthic response to rapid climatic oscillations of the last glacial cycle in the SE Bay of Biscay.
899 *Journal of Sea Research, Changing Ecosystems in the Bay of Biscay: Natural and*
900 *Anthropogenic Effects* 130, 49–72. <https://doi.org/10.1016/j.seares.2017.06.002>

901 Rogerson, M., Rohling, E.J., Bigg, G.R., Ramirez, J., 2012. Paleoceanography of the
902 Atlantic-Mediterranean exchange: Overview and first quantitative assessment of climatic
903 forcing. *Reviews of Geophysics* 50. <https://doi.org/10.1029/2011RG000376>

904 Rühlemann, C., Mulitza, S., Lohmann, G., Paul, A., Prange, M., Wefer, G., 2004.
905 Intermediate depth warming in the tropical Atlantic related to weakened thermohaline
906 circulation: Combining paleoclimate data and modeling results for the last deglaciation.
907 *Paleoceanography* 19. <https://doi.org/10.1029/2003PA000948>

908 Schmiedl G, Mackensen A. 1997. Late Quaternary paleoproductivity and deep water
909 circulation in the eastern South Atlantic Ocean: Evidence from benthic foraminifera.
910 *Palaeogeography, Palaeoclimatology, Palaeoecology* 130: 43–80.

911 Schmiedl, G., Mackensen, A., Müller, P.J., 1997. Recent benthic foraminifera from the
912 eastern South Atlantic Ocean: Dependence on food supply and water masses. *Marine*
913 *Micropaleontology* 32, 249–287. [https://doi.org/10.1016/S0377-8398\(97\)00023-6](https://doi.org/10.1016/S0377-8398(97)00023-6)

914 Schmiedl, G., de Bovée, F., Buscail, R., Charrière, B., Hemleben, C., Medernach, L.,
915 Picon, P., 2000. Trophic control of benthic foraminiferal abundance and microhabitat in the
916 bathyal Gulf of Lions, western Mediterranean Sea. *Marine Micropaleontology* 40, 167–188.
917 [https://doi.org/10.1016/S0377-8398\(00\)00038-4](https://doi.org/10.1016/S0377-8398(00)00038-4)

918 Schmiedl G, Mitschele A, Beck S et al. 2003. Benthic foraminiferal record of ecosystem
919 variability in the eastern Mediterranean Sea during times of sapropel S5 and S6 deposition.
920 *Palaeogeography, Palaeoclimatology, Palaeoecology* 190: 139–164.

921 Schönfeld, J., 1997. The impact of the Mediterranean Outflow Water (MOW) on benthic
922 foraminiferal assemblages and surface sediments at the southern Portuguese continental
923 margin. *Marine Micropaleontology* 29, 211–236. [https://doi.org/10.1016/S0377-8398\(96\)00050-3](https://doi.org/10.1016/S0377-8398(96)00050-3)

924

925 Schönfeld, J., 2002a. A new benthic foraminiferal proxy for near-bottom current
926 velocities in the Gulf of Cadiz, northeastern Atlantic Ocean. *Deep Sea Research Part I:*
927 *Oceanographic Research Papers* 49, 1853–1875. [https://doi.org/10.1016/S0967-](https://doi.org/10.1016/S0967-0637(02)00088-2)
928 [0637\(02\)00088-2](https://doi.org/10.1016/S0967-0637(02)00088-2)

929 Schönfeld, J., 2002b. Recent benthic foraminiferal assemblages in deep high-energy
930 environments from the Gulf of Cadiz (Spain). *Marine Micropaleontology* 44, 141–162.
931 [https://doi.org/10.1016/S0377-8398\(01\)00039-1](https://doi.org/10.1016/S0377-8398(01)00039-1)

932 Schönfeld J. 2006. Taxonomy and distribution of the *Uvigerina peregrina* plexus in the
933 tropical to northeastern Atlantic. *Journal of Foraminiferal Research* 36: 355–367.

934 Schönfeld, J., Altenbach, A.V., 2005. Late Glacial to Recent distribution pattern of
935 deep-water *Uvigerina* species in the north-eastern Atlantic. *Marine Micropaleontology* 57, 1–
936 24. <https://doi.org/10.1016/j.marmicro.2005.05.004>

937 Schroder-Adams, C., Cole, F., Medioli, F., Mudie, P., Scott, D., Dobbin, L., 1990.
938 Recent Arctic shelf Foraminifera: seasonally ice covered vs. perennially ice covered areas.

- 939 Journal of Foraminiferal Research - J FORAMIN RES 20, 8–36.
940 <https://doi.org/10.2113/gsjfr.20.1.8>
- 941 Scourse, J.D., Haapaniemi, A.I., Colmenero-Hidalgo, E., Peck, V.L., Hall, I.R., Austin,
942 W.E.N., Knutz, P.C., Zahn, R., 2009. Growth, dynamics and deglaciation of the last British–
943 Irish ice sheet: the deep-sea ice-rafted detritus record. *Quaternary Science Reviews* 28, 3066–
944 3084. <https://doi.org/10.1016/j.quascirev.2009.08.009>
- 945 Shaffer, G., Olsen, S.M., Bjerrum, C.J., 2004. Ocean subsurface warming as a
946 mechanism for coupling Dansgaard-Oeschger climate cycles and ice-rafting events. *Geophys.*
947 *Res. Lett.* 31, L24202. <https://doi.org/10.1029/2004GL020968>
- 948 Spezzaferri, S., Rüggeberg, A., Stalder, C., Margreth, S., 2014. Taxonomic notes and
949 illustrations of benthic foraminifera from cold-water coral ecosystems. *Cushman Foundation*
950 *Special Publication* 49–140.
- 951 Thornalley DJR, Elderfield H, McCave IN. 2010. Intermediate and deep water
952 paleoceanography of the northern North Atlantic over the past 21,000 years. *Paleoceanography*
953 25: PA1211.
- 954 Thornalley, D.J.R., Bauch, H.A., Gebbie, G., Guo, W., Ziegler, M., Bernasconi, S.M.,
955 Barker, S., Skinner, L.C., Yu, J., 2015. A warm and poorly ventilated deep Arctic
956 Mediterranean during the last glacial period. *Science* 349, 706–710.
957 <https://doi.org/10.1126/science.aaa9554>
- 958 Toucanne, S., Zaragosi, S., Bourillet, J.F., Naughton, F., Cremer, M., Eynaud, F.,
959 Dennielou, B., 2008. Activity of the turbidite levees of the Celtic–Armorican margin (Bay of
960 Biscay) during the last 30,000 years: Imprints of the last European deglaciation and Heinrich
961 events. *Marine Geology* 247, 84–103. <https://doi.org/10.1016/j.margeo.2007.08.006>
- 962 Toucanne, S., Zaragosi, S., Bourillet, J.F., Cremer, M., Eynaud, F., Van Vliet-Lanoë,
963 B., Penaud, A., Fontanier, C., Turon, J.L., Cortijo, E., Gibbard, P.L., 2009. Timing of massive
964 ‘Fleuve Manche’ discharges over the last 350kyr: insights into the European ice-sheet
965 oscillations and the European drainage network from MIS 10 to 2. *Quaternary Science Reviews*
966 28, 1238–1256. <https://doi.org/10.1016/j.quascirev.2009.01.006>
- 967 Toucanne, S., Zaragosi, S., Bourillet, J.-F., Marieu, V., Cremer, M., Kageyama, M., Van
968 Vliet-Lanoë, B., Eynaud, F., Turon, J.-L., Gibbard, P.L., 2010. The first estimation of Fleuve
969 Manche palaeoriver discharge during the last deglaciation: Evidence for Fennoscandian ice
970 sheet meltwater flow in the English Channel ca 20–18ka ago. *Earth and Planetary Science*
971 *Letters* 290, 459–473. <https://doi.org/10.1016/j.epsl.2009.12.050>
- 972 Toucanne, S., Zaragosi, S., Bourillet, J.-F., Dennielou, B., Jorry, S.J., Jouet, G., Cremer,
973 M., 2012. External controls on turbidite sedimentation on the glacially-influenced Armorican
974 margin (Bay of Biscay, western European margin). *Marine Geology* 303–306, 137–153.
975 <https://doi.org/10.1016/j.margeo.2012.02.008>
- 976 Toucanne, S., Soulet, G., Freslon, N., Jacinto, R.S., Dennielou, B., Zaragosi, S., Eynaud,
977 F., Bourillet, J.-F., Bayon, G., 2015. Millennial-scale fluctuations of the European Ice Sheet at

- 978 the end of the last glacial, and their potential impact on global climate. *Quaternary Science*
979 *Reviews* 123, 113–133.
- 980 Toucanne, S., Soulet, G., Riveiros, N.V., Boswell, S.M., Dennielou, B., Waelbroeck,
981 C., Bayon, G., Mojtahid, M., Bosq, M., Sabine, M., Zaragosi, S., Bourillet, J.-F., Mercier, H.,
982 2021. The North Atlantic Glacial Eastern Boundary Current as a Key Driver for Ice-Sheet—
983 Amoc Interactions and Climate Instability. *Paleoceanography and Paleoclimatology* 36,
984 e2020PA004068. <https://doi.org/10.1029/2020PA004068>
- 985 Toucanne, S., Naughton, F., Rodrigues, T., Vázquez-Riveiros, N., Sánchez Goñi, M.F.,
986 2022. Chapter 25 - Abrupt (or millennial or suborbital) climatic variability: Heinrich
987 events/stadials, in: Palacios, D., Hughes, P.D., García-Ruiz, J.M., Andrés, N. (Eds.), *European*
988 *Glacial Landscapes*. Elsevier, pp. 181–187. [https://doi.org/10.1016/B978-0-12-823498-
989 *3.00062-5*](https://doi.org/10.1016/B978-0-12-823498-3.00062-5)
- 990 van Aken, H.M., 2000. The hydrography of the mid-latitude Northeast Atlantic Ocean:
991 II: The intermediate water masses. *Deep Sea Research Part I: Oceanographic Research Papers*
992 47, 789–824. [https://doi.org/10.1016/S0967-0637\(99\)00112-0](https://doi.org/10.1016/S0967-0637(99)00112-0)
- 993 Van der Zwaan GJ, Jorissen FJ. 1991. Biofacial patterns in riverinduced shelf anoxia.
994 *Geological Society, London, Special Publications* 58: 65–82.
- 995 Vénec-Peyré M-T, Le Calvez Y. 1988. Les Foraminifères épiphytes de l'herbier de
996 Posidonies de Banyuls-sur-Mer (Méditerranée occidentale): étude des variations spatio-
997 temporelles du peuplement. *Cahiers de Micropaléontologie* 3: 21–40.
- 998 Waelbroeck, C., Lougheed, B.C., Vazquez Riveiros, N., Missiaen, L., Pedro, J.,
999 Dokken, T., Hajdas, I., Wacker, L., Abbott, P., Dumoulin, J.-P., Thil, F., Eynaud, F., Rossignol,
1000 L., Fersi, W., Albuquerque, A.L., Arz, H., Austin, W.E.N., Came, R., Carlson, A.E., Collins,
1001 J.A., Dennielou, B., Desprat, S., Dickson, A., Elliot, M., Farmer, C., Giraudeau, J., Gottschalk,
1002 J., Henderiks, J., Hughen, K., Jung, S., Knutz, P., Lebreiro, S., Lund, D.C., Lynch-Stieglitz, J.,
1003 Malaizé, B., Marchitto, T., Martínez-Méndez, G., Mollenhauer, G., Naughton, F., Nave, S.,
1004 Nürnberg, D., Oppo, D., Peck, V., Peeters, F.J.C., Penaud, A., Portillo-Ramos, R. da C.,
1005 Repschläger, J., Roberts, J., Rühlemann, C., Salgueiro, E., Sanchez Goni, M.F., Schönfeld, J.,
1006 Scussolini, P., Skinner, L.C., Skonieczny, C., Thornalley, D., Toucanne, S., Rooij, D.V.,
- 1007 Wang, Y.J., Cheng, H., Edwards, R.L., An, Z.S., Wu, J.Y., Shen, C.-C., Dorale, J.A.,
1008 2001. A High-Resolution Absolute-Dated Late Pleistocene Monsoon Record from Hulu Cave,
1009 China. *Science* 294, 2345–2348. <https://doi.org/10.1126/science.1064618>
- 1010 Wollenburg, J.E., Kuhnt, W., 2000. The response of benthic foraminifers to carbon flux
1011 and primary production in the Arctic Ocean. *Marine Micropaleontology* 40, 189–231.
1012 [https://doi.org/10.1016/S0377-8398\(00\)00039-6](https://doi.org/10.1016/S0377-8398(00)00039-6)
- 1013 Wollenburg, J.E., Mackensen, A., 1998. Living benthic foraminifers from the central
1014 Arctic Ocean: faunal composition, standing stock and diversity. *Marine Micropaleontology* 34,
1015 153–185. [https://doi.org/10.1016/S0377-8398\(98\)00007-3](https://doi.org/10.1016/S0377-8398(98)00007-3)

1016 Wollenburg JE, Mackensen A. 2009. The ecology and distribution of benthic
1017 foraminifera at the Håkon Mosby mud volcano (SW Barents Sea slope). *Deep Sea Research*
1018 *Part I: Oceanographic Research Papers* 56: 1336–1370.

1019 Wollenburg JE, Kuhnt W, Mackensen A. 2001. Changes in Arctic Ocean
1020 paleoproductivity and hydrography during the last 145 kyr: The benthic foraminiferal record.
1021 *Paleoceanography* 16: 65–77.

1022 Wollenburg, J.E., Knies, J., Mackensen, A., 2004. High-resolution paleoproductivity
1023 fluctuations during the past 24 kyr as indicated by benthic foraminifera in the marginal Arctic
1024 Ocean. *Palaeogeography, Palaeoclimatology, Palaeoecology* 204, 209–238.
1025 [https://doi.org/10.1016/S0031-0182\(03\)00726-0](https://doi.org/10.1016/S0031-0182(03)00726-0)

1026 Yu, J., Elderfield, H., Jin, Z., Tomascak, P., Rohling, E.J., 2014. Controls on Sr/Ca in
1027 benthic foraminifera and implications for seawater Sr/Ca during the late Pleistocene.
1028 *Quaternary Science Reviews* 98, 1–6. <https://doi.org/10.1016/j.quascirev.2014.05.018>

1029 Zahn R, Schönfeld J, Kudrass H-R et al. 1997. Thermohaline instability in the North
1030 Atlantic during meltwater events: Stable isotope and ice-rafted detritus records from Core
1031 SO75-26KL, Portuguese Margin. *Paleoceanography* 12: 696–710.

1032 Zaragosi, S., Eynaud, F., Pujol, C., Auffret, G.A., Turon, J.-L., Garlan, T., 2001.
1033 Initiation of the European deglaciation as recorded in the northwestern Bay of Biscay slope
1034 environments (Meriadzek Terrace and Trevelyan Escarpment): a multi-proxy approach. *Earth*
1035 *and Planetary Science Letters* 188, 493–507. [https://doi.org/10.1016/S0012-821X\(01\)00332-6](https://doi.org/10.1016/S0012-821X(01)00332-6)

1036 Zaragosi, S., Bourillet, J.-F., Eynaud, F., Toucanne, S., Denhard, B., Van Toer, A.,
1037 Lanfumeu, V., 2006. The impact of the last European deglaciation on the deep-sea turbidite
1038 systems of the Celtic-Armorican margin (Bay of Biscay). *Geo-Mar Lett* 26, 317–329.
1039 <https://doi.org/10.1007/s00367-006-0048-9>

1040 Zou, S., Lozier, S., Zenk, W., Bower, A., Johns, W., 2017. Observed and modeled
1041 pathways of the Iceland Scotland Overflow Water in the eastern North Atlantic. *Progress in*
1042 *Oceanography* 159, 211–222. <https://doi.org/10.1016/j.pocean.2017.10.003>

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

Core label	Depth (cm)	Lab. Number ^a	Species	^{14}C age (yr BP)	error (1 σ)	Reservoir correction ^b (^{14}C yr)	error ^b (1 σ)	^{14}C age corrected for reservoir ^c (^{14}C yr BP)	error ^d (1 σ)	Calendar age range ^e (yr BP, 2 σ)
BOBGEO-CS05	0	Poz-73846	<i>N. pachyderma</i>	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	<i>G. bulloides</i>	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	<i>G. bulloides</i>	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	<i>G. bulloides</i>	19680	60	400	200	19280	209	22885-23789
BOBGEO-CS05	933-935	Beta-478196	<i>G. bulloides</i>	20430	70	400	200	20030	212	23727-24665
BOBGEO-CS05	1030-1033	Beta-478197	<i>G. bulloides</i>	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	<i>N. pachyderma</i>	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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Table 2. Taxonomic reference list, microhabitat and ecological preferences for the dominant benthic species (>5 %) and the corresponding bibliographic references.

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

<i>Species</i>	References with images	Microhabitat	<i>Ecological preferences</i>	Plate 1	Plate 2
<i>Globobulimina</i> spp.		Deep infaunal (John W. Murray, 2006)	<i>Globobulimina</i> spp. live in organically-enriched and/or oxygen-depleted sediments (e.g. Jorissen, 1999; Schmiedl <i>et al.</i> , 2003; Mojtahid <i>et al.</i> , 2010). They can live in anoxic sediments by respiring nitrates (Risgaard-Petersen <i>et al.</i> , 2006).	3	
<i>Gavelinopsis praegeri</i> Heron-Allen & Earland, 1913	Jorissen (1987), pl. 3, Fig. 13	Epifaunal (Jorissen, 1987)	<i>Gavelinopsis praegeri</i> is an epiphytic species living in a wide range of water depths in marine environments (John W. Murray, 2006). They are found down to 1200m water depth (de Stigter, 1996) and prefers more oxic conditions (Dorst <i>et al.</i> , 2015).	16	
<i>Hoeglundina elegans</i> d'Orbigny, 1826	Milker and Schmiedl, (2012), pl. 19, Fig. 15	Epifaunal; shallow infaunal (Jorissen <i>et al.</i> , 1998; Fontanier <i>et al.</i> , 2002)	<i>Hoeglundina elegans</i> is described as indicator of low organic carbon environments (Fontanier <i>et al.</i> , 2002; Morigi <i>et al.</i> , 2001).	17	
<i>Nonionella turgida</i> Williamson, 1858	Milker and Schmiedl, (2012), pl. 26, Figs. 1-5	Deep infaunal (Corliss, 1991)	<i>Nonionella turgida</i> is an opportunistic species, tolerant to low oxygen conditions and high nutrient level (Van der Zwaan and Jorissen, 1991).	2	
<i>Planorbulina mediterraneensis</i> d'Orbigny, 1826	Jones and Brady (1994), pl. 92, Fig. 1	Epifaunal (Murray, 2006)	<i>Planorbulina mediterraneensis</i> is an epiphytic species and lives at shallow depths (Murray, 2006).	15	
<i>Pullenia quinqueloba</i> Reuss, 1851	Jones and Brady (1994), pl. 84, Fig. 14	Intermediate infaunal (Corliss, 1991; C. Fontanier <i>et al.</i> , 2008)	<i>Pullenia quinqueloba</i> can live in low-organic carbon conditions (Gupta, 1999).	18	
<i>Textularia sagittula</i> DeFrance, 1824	Jorissen (1987), pl. 3, Fig. 12	Epifaunal (Murray, 2006)	<i>Textularia sagittula</i> is an agglutinated species (Murray, 2006). They are dominant in shallow water depths, on sandy sediments (Murray, 2014)	1	
<i>Trifarina angulosa</i> Williamson, 1858	Jones and Brady (1994), pl. 74, Fig. 15	Shallow infaunal (Hess and Jorissen, 2009)	<i>Trifarina angulosa</i> have been observed in phytodetritus-enriched sediment (e.g. Hess and Jorissen, 2009; Duros <i>et al.</i> , 2011). They are often associated with <i>C. lobatulus</i> to strong bottom currents and can be observed until 1000m water depth (Mackensen <i>et al.</i> , 1985).	14	

1052

1053 **9. Tables caption**

1054 **Table 3.** ^{14}C dates of core BOBGEO-CS05.

1055 **Table 4.** Taxonomic reference list, microhabitat and ecological preferences for the dominant
1056 benthic species (>5 %) and the corresponding bibliographic references.

1057

1058 **10. Figures caption**

1059 **Figure 1.** Location of the study area. a) 3D representation (N-S, W-E and in water depth) of
1060 the modern oceanic circulation in the North Atlantic representing the main currents (acronyms
1061 written in black), water masses (acronyms written in colors) and the Subpolar (in blue) and
1062 Subtropical (in red) gyres in the North Atlantic. b) Bathymetric map representing the
1063 paleogeographic and paleoceanographic configuration (i.e. ice sheets, the Channel River,
1064 currents, and water masses) of the North Atlantic during the Last Glacial Stadials according to
1065 Toucanne et al. (2021). The angulous shapes represent the icebergs. c) Bathymetric map
1066 focussing on the study area and showing the location of our study core BOBGEO-CS05 (violet
1067 star), together with nearby cores at 1000 m water depth (black stars): MD95-2002 (Eynaud et
1068 al., 2012; Ménot et al., 2006; Toucanne et al., 2015), MD99-2328 (Mojtahid et al., 2017), PP10-
1069 12 (Pascual et al., 2020). For the detailed description of the general modern and glacial
1070 circulation in the North Atlantic and in the study area, the reader is referred to the text (Section
1071 2). LGM: Last Glacial Maximum.

1072 **Figure 2.** Age model of core BOBGEO-CS05. a) Chronostratigraphic framework of core
1073 BOBGEO-CS05 based on the synchronisation of XRF-Ca/Ti ratios with cores MD95-2002 and
1074 MD99-2328 (Zaragosi et al., 2006; Mojtahid et al., 2017; Toucanne et al., 2021). b) Sediment
1075 Accumulation Rate (SAR; full line) and ^{14}C dates (orange triangles) with associated errors in
1076 core BOBGEO-CS05. The ^{14}C dates represented by empty triangles are outliers (cf. section
1077 3.1. for further details). In red is represented the final age model based on XRF-Ca/Ti
1078 synchronisation (cf. Fig. 2a). c) Test of the robustness of the age model with the percentages of
1079 the polar planktonic species *N. pachyderma* in core BOBGEO-CS05 (this study) with core
1080 MD95-2002 (Grousset et al., 2000) and MD99-2328 (Mojtahid et al., 2017). d) NGRIP $\delta^{18}\text{O}$
1081 (GICCS05 chronology; Rasmussen et al., 2006, 2014). f) X-Ray photographs (cf.
1082 Supplementary material S1 for the whole core) showing the four observed facies. Blue triangles:
1083 ^{14}C dates of core MD95-2002 (Toucanne et al., 2021); Orange and empty triangles: ^{14}C dates

1084 of core BOBGEO-CS05; Blue bands: Heinrich Stadials (HSs); Gray bands: Heinrich Events
1085 (HEs); Greenland Interstadial (GI); Last Glacial Maximum (LGM); Marine Isotope Stage
1086 (MIS).

1087 **Figure 3.** Benthic foraminiferal data from core BOBGEO-CS05. a) Benthic Foraminiferal
1088 Accumulation Rates (BFAR; ind.cm⁻³.ka⁻¹) for the >150 µm (full line) and the >63 µm fraction
1089 (dashed line). b) Shannon index (H). c-j) Relative abundances (%) of the eight most
1090 representative benthic foraminiferal species (>10 %). Full lines and dashed lines represent
1091 respectively the > 150 µm and >63 µm fractions. Brown lines represent data from the >150 µm
1092 fraction of core MD99-2328 (Mojtahid et al., 2017). Yellow bands: Greenland Interstadials
1093 (GI); gray bands: Heinrich Events (HEs); blues bands: Heinrich Stadial (HSs). Marine Isotope
1094 Stage (MIS). The vertical dashed grey line represents the limit between early HS1 (ca. 18.2 -
1095 16.7 cal ka BP) and late HS1 (ca. 16.7 – 14.7 cal ka BP). To better highlight the variations of
1096 the different species groups, the scale of the ordinate axis is not constant.

1097
1098 **Figure 4.** Benthic foraminiferal response to ice-sheet/AMOC dynamics. a) Relative abundance
1099 of *N. pachyderma* in core BOBGEO-CS05. b) Relative abundances of glacier-proximal
1100 indicator species (% *Elphidium excavatum* f. *clavatum* + % *C. crassa*) in core BOBGEO-CS05.
1101 c) BIT-index at site MD95-2002 as a proxy for continental-derived material input (Ménot et al.,
1102 2006). d) Relative abundances of high-organic flux indicator species (% *C. carinata* +
1103 % *Bolivina* spp.) in core BOBGEO-CS05. e) Bermuda Rise ²³¹Pa/²³⁰Th compilation as a proxy
1104 for AMOC export at >2 000 m depth (McManus et al., 2004; Böhm et al., 2015; Henry et al.,
1105 2016). f) XRF-Zr/Rb (violet line) and \overline{SS} (pink line) composite records from the northeast
1106 Atlantic including BOBGEO-CS05 as proxies for the reconstruction of GEBIC flow speed
1107 changes (Toucanne et al., 2021). g) Relative abundances of high-energy indicator species (% *C.*
1108 *lobatulus* + % *T. angulosa*) in core BOBGEO-CS05. h) Relative abundances of meso-
1109 oligotrophic indicator species (% *C. pachyderma*) in core BOBGEO-CS05. i) Relative
1110 abundances of anoxia indicator species (% *Globobulimina* spp. + % *C. oolina*). To better
1111 highlight the variations of the different species groups, the scale of the ordinate axis is not
1112 constant. The main events and climatic phases are reported similarly to Figure 3.

1113
1114 **Figure 5.** Focus on HS2. a) Relative abundances of the planktonic species *N. pachyderma* in
1115 core BOBGEO-CS05 (black line; this study) and MD95-2002 (blue line; Grousset et al., 2000).

1116 b) XRF-Zr/Rb (violet line) and \overline{SS} (pink line) composite records from the northeast Atlantic
1117 (including BOBGEO-CS05) as proxies for the reconstruction of GEBC flow speed changes
1118 (Toucanne et al., 2021). c) Relative abundances of high-energy indicator species (% *C.*
1119 *lobatulus* + % *T. angulosa*) in core BOBGEO-CS05. d) Benthic Foraminiferal Accumulation
1120 Rates (BFAR; ind.cm⁻³.ka⁻¹) for the >150 μ m in core BOBGEO-CS05. e) Relative abundances
1121 of meso-oligotrophic indicator species (% *C. pachyderma*) in core BOBGEO-CS05. f) Relative
1122 abundances of anoxia indicator species (% *Globobulimina* spp. + % *C. oolina*) in core
1123 BOBGEO-CS05. Dashed vertical line: Heinrich Event 2 (HE2) sensu stricto according to the
1124 regional Ca/Ti synchronisation (cf. Table S2 in Toucanne et al., 2021); blue bands: the HS2a,b
1125 cold events (Bard et al., 2000); yellow band: the mid-HS2 re-ventilation event. To better
1126 highlight the variations of the different species groups, the scale of the ordinate axis is not
1127 constant.

1128

1129 **11. Plates caption**

1130 **Plate 1.** SEM photographs of the dominant benthic species (>5 % in at least one sample): 1)
1131 *Textularia sagittula* ; 2) *Nonionella turgida* ; 3) *Globobulimina affinis* ; 4) *Chilostomella oolina*
1132 ; 5) *Bolivina subaenariensis*; 6) *Bolivina albatrossi*; 7) *Cassidulina carinata*; 8) *Cassidulina*
1133 *crassa*; 9) *Elphidium gerthi* ; 10) *Elphidium excavatum* f. *clavatum* ; 11) *Cibicidoides*
1134 *pachyderma* ; 12) *Cibicides lobatulus*; 13) *Trifarina angulosa*; 14) *Planorbulina*
1135 *mediterraneensis*; 15) *Gavelinopsis praegeri* ; 16) *Hoeglundina elegans* ; 17) *Pullenia*
1136 *quineloba*. Scale bar = 100 μ m.

1137

1138 **Plate 2.** a) Natural light photographs of *Elphidium excavatum* f. *clavatum* showing pyritised
1139 and altered shells. b) SEM photographs showing the variability of the morphotypes (in lateral
1140 view) lumped into *Cibicidoides pachyderma* in this study.

1141

1142 **12. Supplementary materials caption**

1143 **S1.** X-Ray imagery of core BOBGEO-CS05

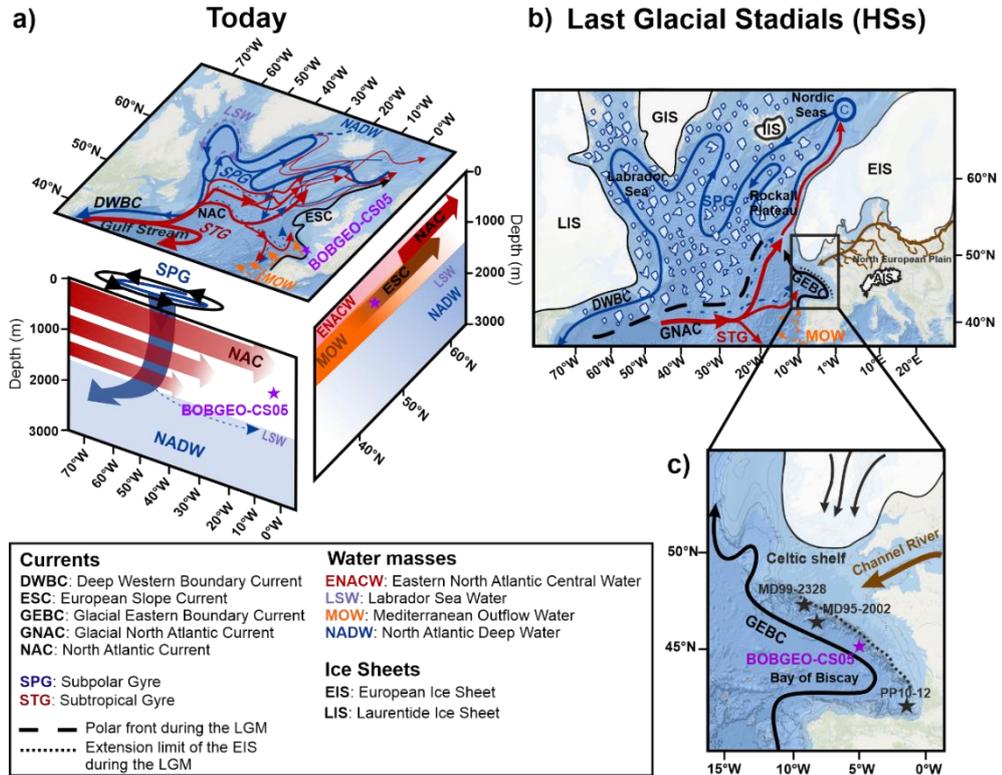
1144 **S2.** Figure representing the relative abundances of taxa present between 5 and 10 % in at least
1145 one sample

1146 **S3.** Raw foraminiferal counts

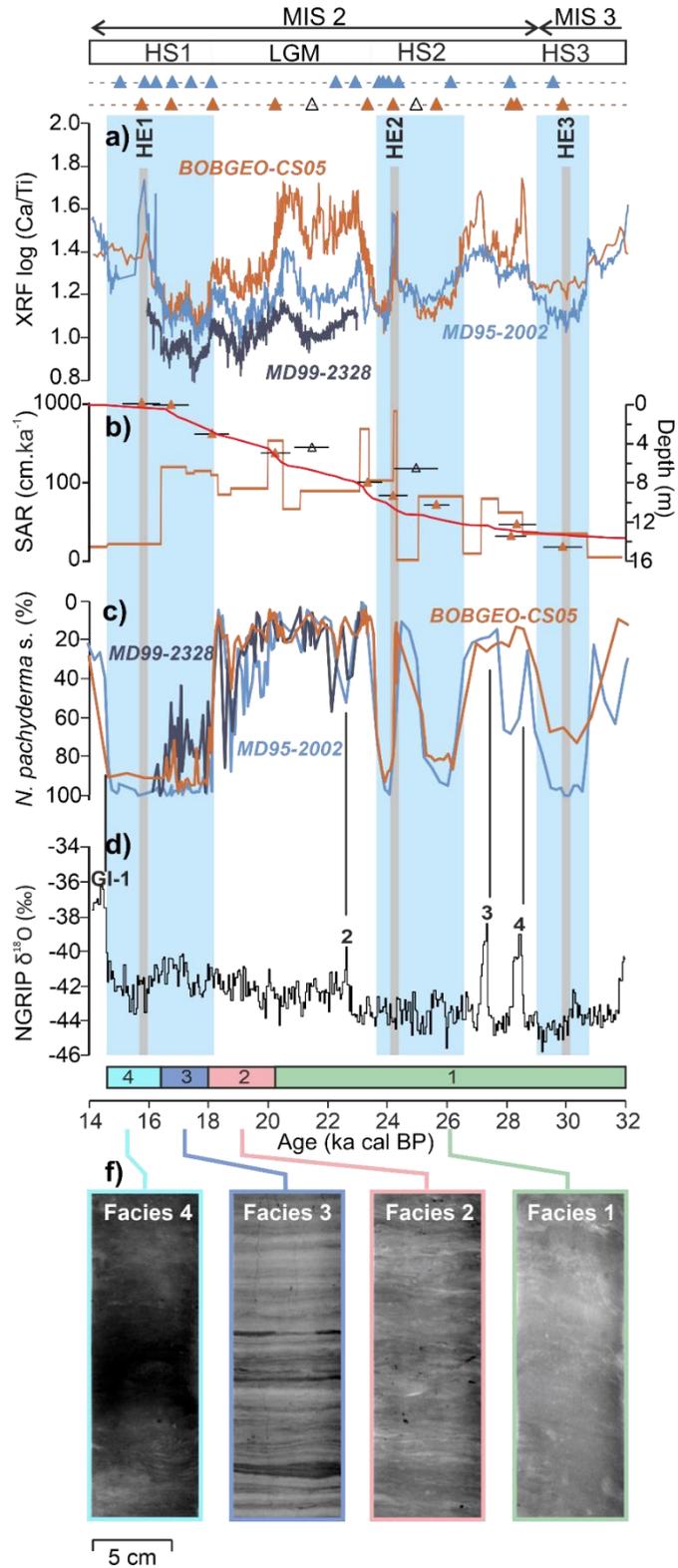
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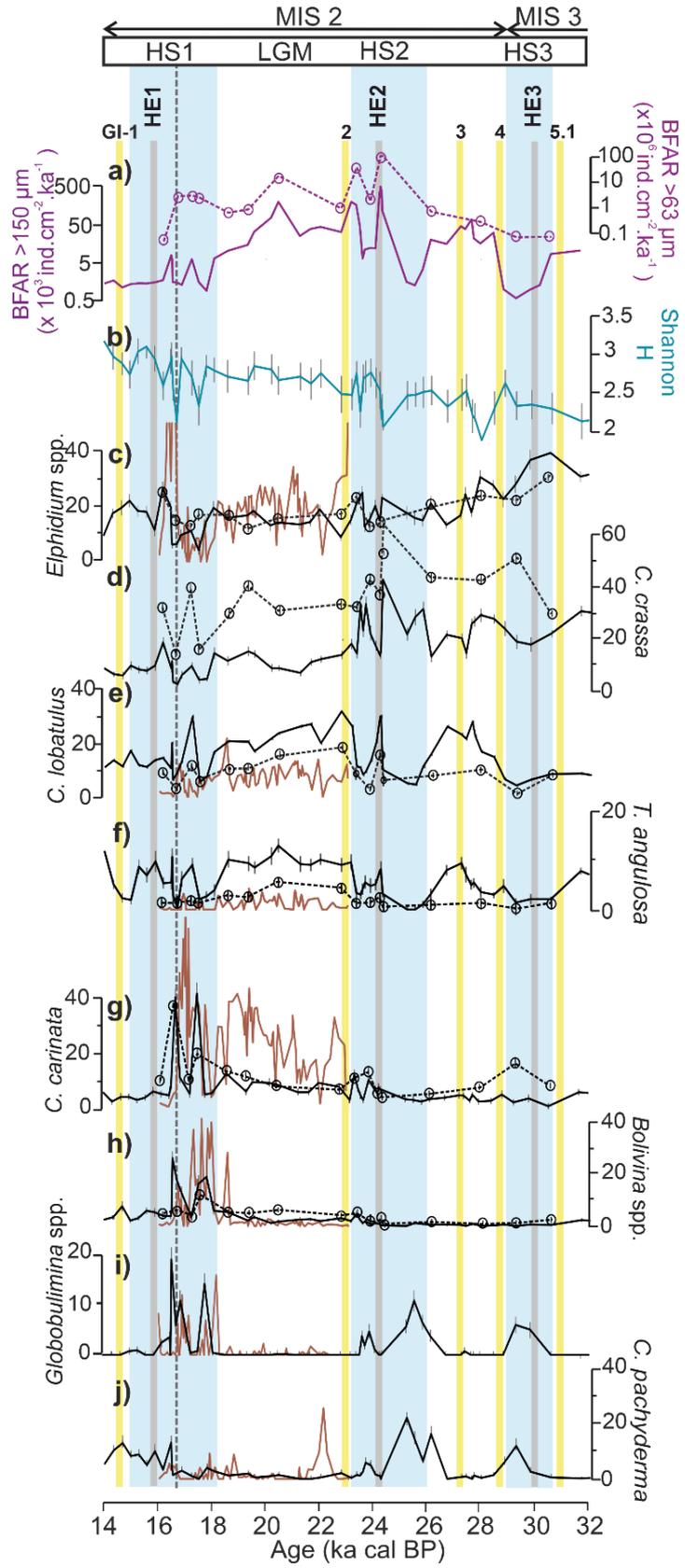
Figure 1



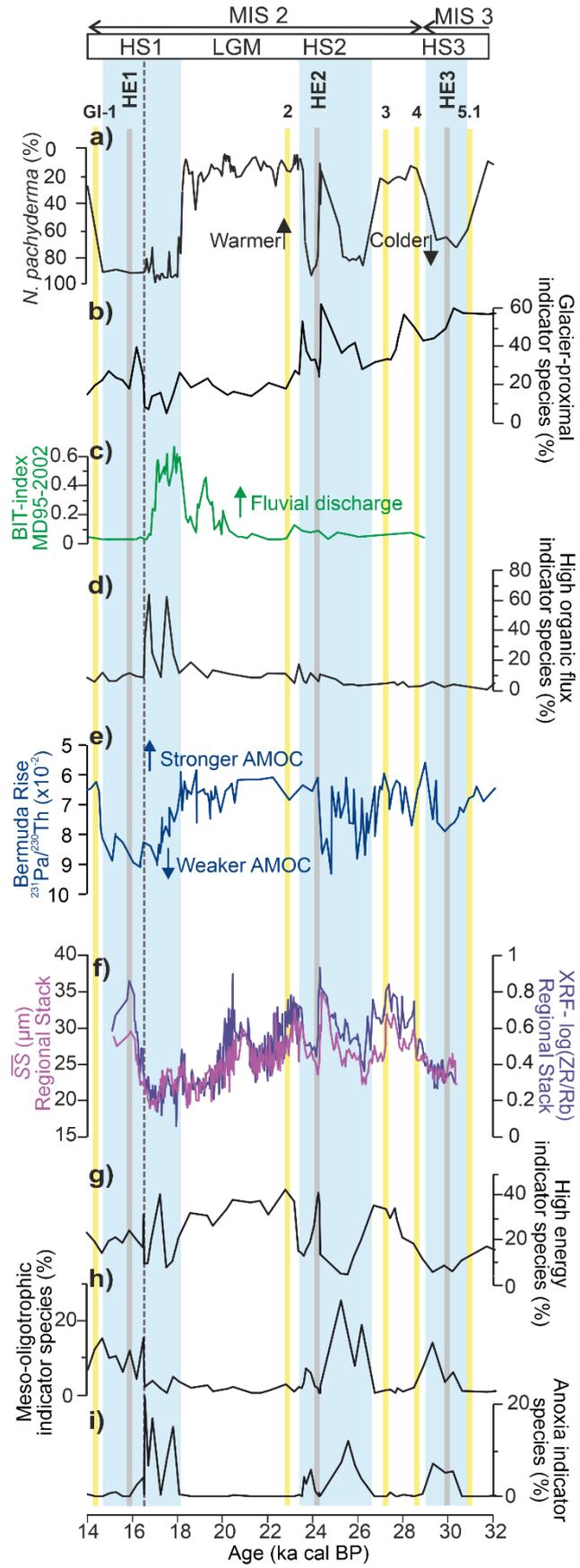
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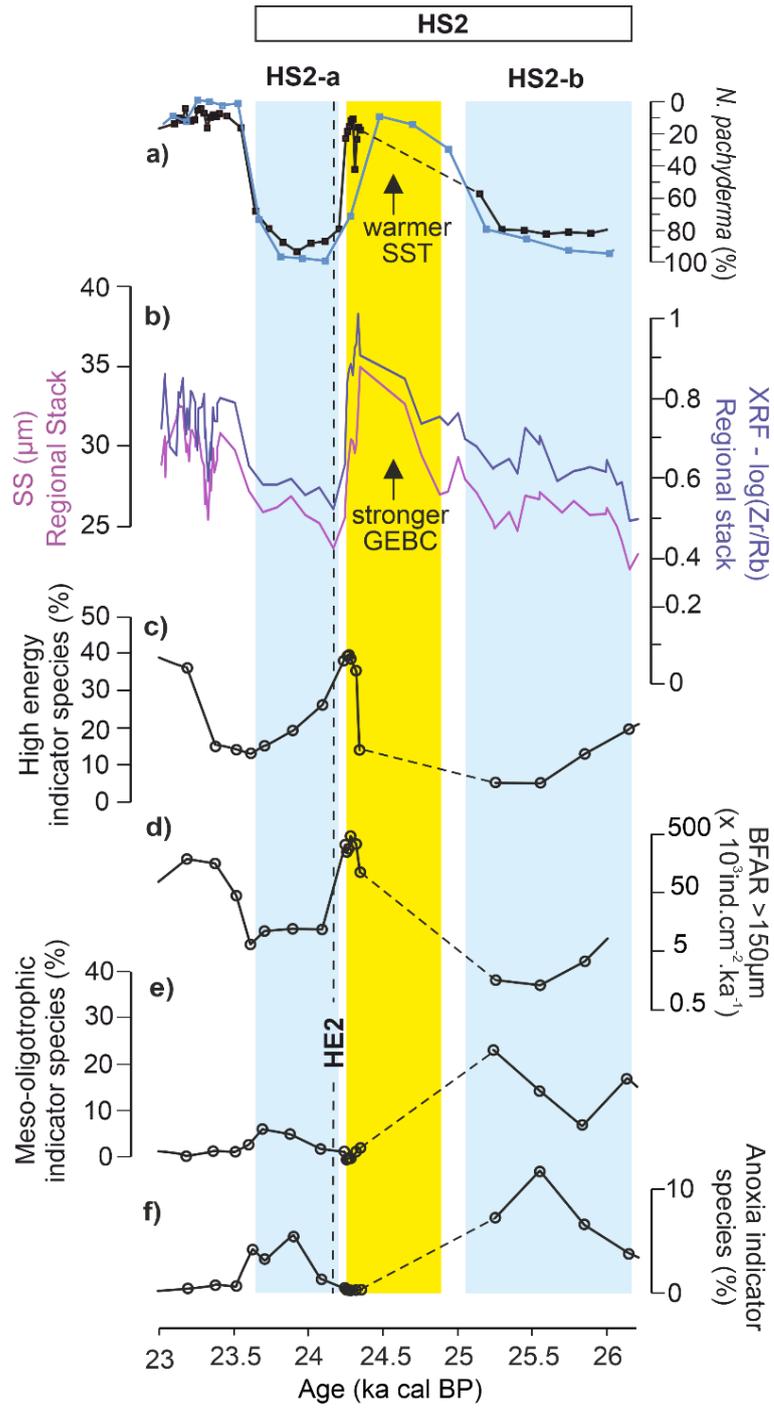
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Figure 5

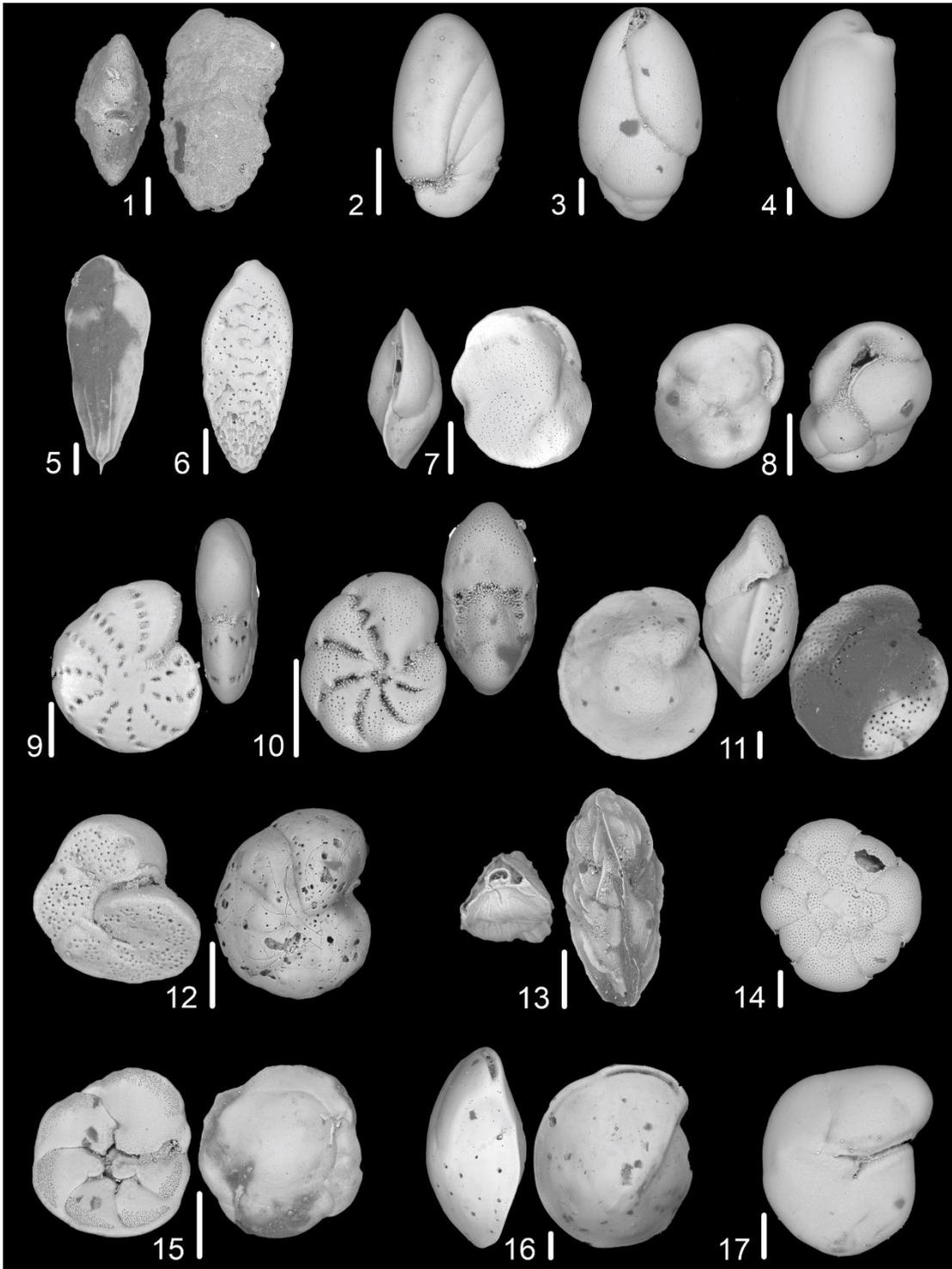


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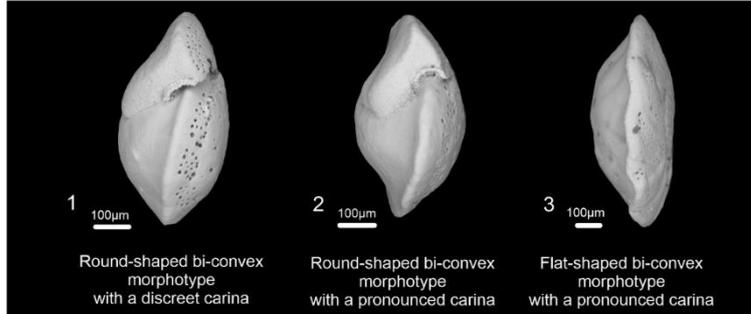
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Plate 2

a) *Elphidium excavatum* cf. *clavatum*



b) Morphotypes of *C. pachyderma*



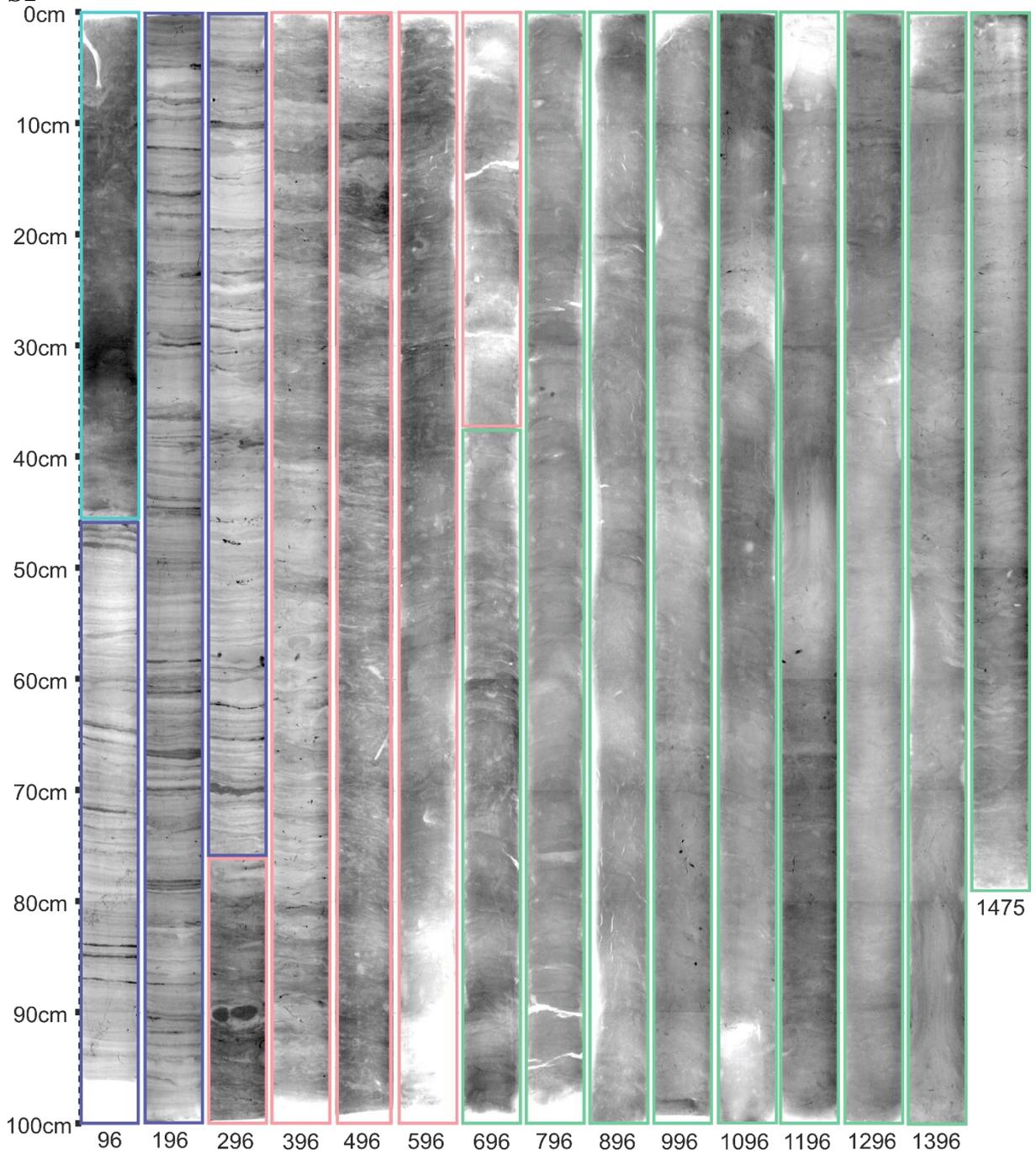
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1180 **Supplementary material**

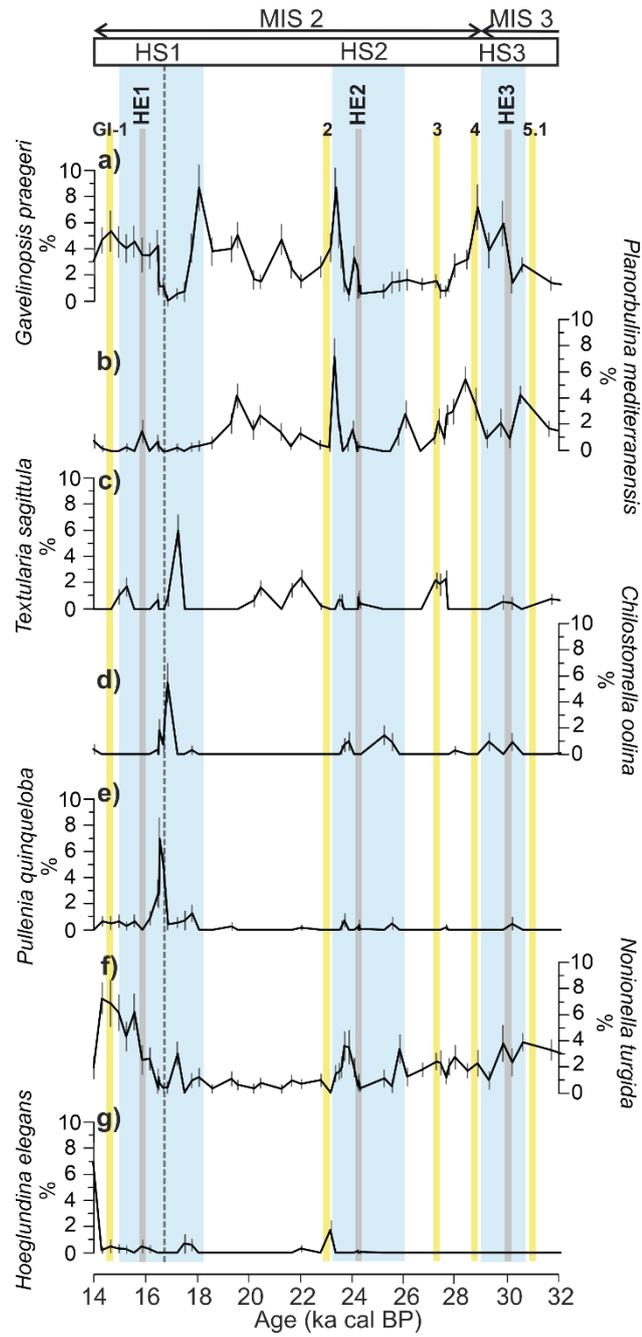
1181 **S1**



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S2



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S3. Raw foraminiferal counts available in <https://doi.org/10.17882/88029>