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1 **FROM GLACIAL TIMES TO LATE HOLOCENE: BENTHIC**
2 **FORAMINIFERAL ASSEMBLAGES FROM COLD WATER CORAL**
3 **HABITATS OFF NORTHWEST SCOTLAND**

4

5 Meryem MOJTAHID^{1,*}, Magali SCHWEIZER¹, Mélanie DOUARIN¹, Justine
6 GABRIEL¹, Christophe COLIN², Nadine TISNÉRAT-LABORDE³, Mary ELLIOT¹

7

8 ¹ Univ Angers, Université de Nantes, CNRS, LPG, Laboratoire de Planétologie et
9 Géodynamique, UMR-CNRS 6112, 2 Bd Lavoisier, 49045 Angers Cedex F-49000 Angers, 2
10 rue de la Houssinière, BP 92208, 44322 Nantes Cedex 3, CNRS, France

11 ² Université Paris-Saclay, CNRS, GEOPS, 91405, Orsay, France

12 ³ Laboratoire des Sciences du Climat et de l'Environnement, LSCE/IPSL, CEA-CNRS-
13 UVSQ, Université Paris-Saclay, 91191 Gif-sur-Yvette, France

14 **Abstract**

15 Benthic foraminiferal assemblage data have been derived from a marine sediment core
16 collected in a cold-water coral (CWC) site off northwest Scotland (near the Wyville Thomson
17 Ridge - WTR). The record covers the last glacial period to the late Holocene. Our
18 reconstructions enable to better constrain the paleoenvironmental changes that took place in
19 the study area since the last glacial time and define the environmental conditions that allowed
20 the onset, formation and decline of CWCs in the area. The sedimentary record was
21 characterized by three distinct foraminiferal assemblages, dominant during the pre-coral time
22 interval (i and ii) and the coral period (iii): (i) the “Glacial” assemblage (> 13 cal ka BP) was
23 characterized by the dominance of *Cibicides refulgens* and *Discanomalina coronata*. Low
24 foraminiferal densities and diversities indicated unfavorable ecological conditions (i.e., low
25 temperature and food availability, coarse substrate) that were most likely related to the
26 extended British Ice Sheet; (ii) the “Deglacial-Early Holocene” assemblage (~13-9 cal ka BP)
27 was characterized by the cassidulinids-*Lobatula lobatula* association, indicating a progressive
28 increase of organic matter content and influx of warm and saline North Atlantic surface
29 waters. We hypothesize that these were the main environmental factors that thereafter allowed
30 the settlement of CWCs in the WTR area around 9 cal ka BP; (iii) the “Holocene” (< 9 cal ka
31 BP) assemblage was characterized by the cohabitation of diverse epifaunal species (e.g.,
32 *Rosalina globularis*) present when CWCs were highly abundant, and infaunal species (e.g.,
33 *Trifarina angulosa*) when corals were less frequent. The periods recording high presence of *T.*
34 *angulosa* after 9 ka cal BP were interpreted as indicating a higher contribution of Eastern
35 North Atlantic Waters during periods of retracted Subpolar Gyre (SPG), affecting probably
36 the efficiency of food export to the seafloor.

37

38 **Keywords:** NE Atlantic; Wyville Thomson Ridge; Epifauna; Infauna; Benthic foraminifera;

39 Cold-Water Corals

40

41 **Highlights:**

- 42 • Cold water and low food export to the seafloor during the glacial pre-coral period
- 43 • Increased organic carbon flux and influx of Atlantic waters as a trigger for coral settlement
- 44 • Varying Holocene epifaunal/infaunal species in consistency with high/low coral presence
- 45 • *Trifarina angulosa* as possible indicator of Eastern North Atlantic Water after 9 ka

46 **1- Introduction**

47 Present in all oceanic basins (e.g., Freiwald and Roberts, 2005; Roberts et al., 2009), cold-
48 water corals (CWCs) are particularly abundant and well described along the European
49 continental margin between ~100 and 1000 m water depth from the Gulf of Cadiz to northern
50 Norway (e.g., Freiwald et al., 2004; Freiwald and Roberts, 2005; Frank et al., 2011; Wienberg
51 and Titschack, 2017). In these settings, *Lophelia pertusa* (Linnaeus, 1758), recently assigned
52 to the genus *Desmophyllum* (Addamo et al., 2016) and called *Desmophyllum pertusum*
53 (Linnaeus, 1758), is the dominant species. *Desmophyllum pertusum* lives in waters between 4
54 and 14°C (Roberts et al., 2006) and thrives in moderately high energy environments that
55 provide it with the necessary food supplied by a variety of hydrographies such as currents,
56 internal tides and downwelling flows (e.g., White, 2006; Davies et al., 2009; Hebbeln et al.,
57 2016). *Desmophyllum pertusum* may form complex structures such as reefs and mounds, that
58 provide refuge and nursery areas for diverse living organisms (e.g., Henry and Roberts, 2007,
59 2017). The complex framework built by CWCs is capable of reducing current velocity (e.g.,
60 Mienis et al., 2019), leading to the deposition of current-suspended particles (e.g., Dorschel et
61 al., 2005; de Haas et al., 2009). On geological time scales, large carbonate mounds are formed
62 when coral growth and the resulting sediment accumulation exceed the background marine
63 sedimentation (e.g., Dorschel et al., 2005; Wienberg and Titschack, 2017; Hebbeln et al.,
64 2019). By acting as natural sediment traps, CWC mounds provide useful paleoenvironmental
65 and paleoclimate archives for such current-driven environments (e.g., Copard et al., 2010;
66 Pirlet et al., 2011; Copard et al., 2012; Thierens et al., 2012, 2013; Montero-Serrano et al.,
67 2011; Victorero et al., 2016; Bonneau et al., 2018; Colin et al., 2019; Elliot et al., 2019).

68 Beside the worldwide well known changes linked to glacial/interglacial climate variability,
69 paleostudies from the northeast (NE) Atlantic emphasize phases of CWC demise and re-
70 settlement on shorter timescales linked to rapid climate changes (e.g., Wienberg et al., 2010;

71 Frank et al., 2011; Douarin et al., 2013, 2014, 2016; Bonneau et al., 2018; Dubois-Dauphin et
72 al., 2019; Elliot et al., 2019). The specific environmental conditions that triggered regional
73 extinctions and re-occurrences of CWCs on such short-time periods have yet to be defined.
74 Although CWC aragonitic skeletons may appear as the logical prime signal carriers to identify
75 these environmental changes, they cannot inform us on these periods when the corals were
76 absent (e.g., Hebbeln et al., 2019).

77 Among the number of organisms inhabiting CWC environments, benthic foraminifera are a
78 main component in terms of abundance, as in most marine environments (Gooday, 2003),
79 with CWCs offering these microorganisms many ecological niches (see review in Spezzaferri
80 et al., 2015). Several studies in the NE Atlantic investigated recent foraminiferal communities
81 living in CWC environments, and especially southwest of Ireland along the Porcupine and
82 Rockall Banks (e.g., Margreth et al., 2009; Schönfeld et al., 2011; Morigi et al., 2012;
83 Spezzaferri et al., 2013, 2015; Smeulders et al., 2014; Fentimen et al., 2018, 2020b). These
84 studies document the high diversity and density of living benthic foraminifera in CWC
85 environments. Because of their short life cycle, species specific ecological requirements,
86 excellent preservation and their presence with high numbers in a small volume of sediment,
87 foraminifera are powerful tools to understand past CWC environments (e.g., Rüggeberg et al.,
88 2007; Stalder et al., 2014; Fentimen et al., 2020a). The increasing knowledge of the ecological
89 requirements of living, recent and sub-recent benthic foraminifera from different NE Atlantic
90 *D. pertusum* sites (e.g., Margreth et al., 2009, 2011; Schönfeld et al., 2011; Morigi et al.,
91 2012; Spezzaferri et al., 2013; Fink et al., 2013; Smeulders et al., 2014; Stalder et al., 2014;
92 Fentimen et al., 2018, 2020b) is the basis of our paleoecological interpretations inferred from
93 fossil assemblages.

94 In this study, we present benthic foraminiferal assemblage data from a marine sediment core
95 collected in a CWC mound off northwest Scotland (near the Wyville Thomson Ridge – WTR)

96 at the Hebridean shelf break that flanks the NE Rockall Trough (Fig. 1b). The objectives are:
97 i) better constrain the paleoenvironmental changes that took place in the WTR area since the
98 last glacial period, and ii) define the environmental characteristics that allowed the onset,
99 formation and decline of CWCs in the study site. Elliot et al (2019) documented on the same
100 core the evolution through time of the physical habitats of the WTR with the purpose of
101 relating changes in sediment sources and dynamic of transport with the appearance of the
102 CWC at this location. Our study further uses benthic foraminifera as biological indicators that
103 integrate the cumulative impacts of these changing physical habitats to better constrain
104 environmental changes. More specifically, the approach taken here consists of the use of the
105 abundance of taxa and their known ecology to interpret several aspects of the environment
106 around the WTR (e.g., flux of organic matter to the sea floor, bottom-water oxygenation,
107 current energy, transport, water masses properties).

108

109 **2- Study area**

110 ***2.1. Geographic features and CWC distribution near the Wyville Thomson Ridge***

111 The WTR is a bathymetric feature that forms the easternmost part of the Greenland-Scotland
112 ridge stretching across the northeastern part of the North Atlantic from Greenland to the
113 northern Scottish shelf (Fig. 1b). The WTR separates the Faroe–Shetland Channel to the north
114 from the Rockall Trough to the south (Fig. 1b). These are two deep water areas that separate
115 the Hebrides and West Shetland shelves from the Rockall Plateau and Faroes Shelf (Fig. 1b).

116 The WTR is a rocky plateau with extensive gravel, cobble and boulder fields (Stewart and
117 Davies, 2007), providing suitable substrates for most CWC larvae to settle (e.g., Roberts et
118 al., 2009). Data referring to *Desmophyllum pertusum* distribution in this region were initially
119 reported in the study of Wyville Thomson (1874). More recently, CWC presence in the study
120 area was reported in the light of several seismo-acoustic surveys of the seabed, including the

121 mapping survey onboard the MV British Enterprise Four during which our studied sediment
122 core was retrieved (Long et al., 1999). These studies report mound-like structures near the
123 WTR that were mostly interpreted as patches of *D. pertusum*, present from the shelf break
124 down to ~1000 m water depth (e.g., Long et al., 1999; Roberts et al., 2003; Masson et al.,
125 2003). Only dead (or undetermined status) CWCs were observed at our study site based on
126 trawl recovering corals (Long et al., 1999).

127

128 ***2.2. Hydrography and ocean circulation***

129 In the study area, warm (~7-11 °C) and saline (35.4–35.58 psu) Eastern North Atlantic Water
130 (ENAW) flows in the upper ~600-700 m of the water column (Johnson et al., 2010; McGrath
131 et al., 2012). The ENAW is carried poleward into the Nordic Seas by the North Atlantic
132 Current (NAC) and the Shelf Edge Current (SEC) (e.g., McCartney and Mauritzen, 2001;
133 New et al., 2001; Pollard et al., 2004; McGrath et al., 2012; Marsh et al., 2017) (Fig. 1b). In
134 addition, the Scottish Coastal Current (SCC) flowing on the shelf, carries cooler and fresher
135 waters from the Irish and Clyde Seas (Ellett and Edwards, 1983). The coolest and freshest
136 Atlantic Waters within the subpolar North Atlantic are those found to the northwest of the
137 northernmost branch of the NAC. These waters are a mixture of NAC-carried ENAW, and
138 Subarctic Intermediate Water (SAIW) found further to the west and north (Harvey and Arhan,
139 1988; Holliday, 2003). The term Modified North Atlantic Waters (MNAW) is usually used to
140 denote this water mass (e.g., New and Smythe-Wright, 2001) (Fig. 1). In the northern part of
141 the Rockall Trough, the SAIW (~6°C, 35.10 psu) is present between ~600 and 1200 m depth
142 together with the WTR Overflow Water (WTROW; ~5-9°C, 35-35.35 psu), a part of the
143 outflow from the Norwegian Sea, and recirculating Mediterranean influenced waters (Johnson
144 et al., 2010; McGrath et al., 2012). The relative composition of the NAC in the WTR area is
145 related to the strength and shape (expansion/contraction) of the Subpolar Gyre (SPG) (Hátún

146 et al., 2005; Inall et al., 2009) (Fig. 1c).

147

148 **2.3. Carbon and nutrient dynamics**

149 Cold-water corals in the NE Atlantic and the communities they support, including benthic
150 foraminifera, rely on surface productivity and the vertical and lateral supply of organic carbon
151 to the aphotic zone as their primary source of nutrition via various hydrographies (e.g.,
152 downwelling, tidal currents) (e.g., Kiriakoulakis et al., 2007; Mienis et al., 2007; Davies et al.,
153 2009; Soetaert et al., 2016). Phytoplankton growth in turn is mainly dependent on nutrients
154 availability (nitrogen, phosphorus, iron, silica) in the euphotic zone (e.g., Moore et al., 2013;
155 Birchill et al., 2019; Maier et al., 2020). Most studies on *D. pertusum* highlight its
156 opportunistic feeding preferences with a large variety of preys (zooplankton, phytodetritus,
157 bacteria) (e.g., Freiwald et al., 2004; Mienis et al., 2007; Davies et al., 2009), and some
158 studies imply a dependence on chemical nutrients (e.g., Findlay et al., 2014) and its ability to
159 feed directly on dissolved organic carbon (e.g., Mueller et al., 2014). Benthic foraminifera are
160 also heterotrophic organisms, feeding on various sources of organic carbon (e.g., dissolved
161 organic carbon, labile phytodetritus, degraded organic matter, bacteria) (e.g., DeLaca et al.,
162 1981; Goldstein and Corliss, 1994; Nomaki et al., 2006; Mojtahid et al., 2011). In our study
163 area, nutrients and the organic matter exported to the seafloor have two main sources:

164 a) Local source: primary production

165 In northwest (NW) Scottish waters, there is relatively little river inflow so that nutrient
166 budgets are dominated by supply from the ocean (with some from the West Scottish shelf)
167 (Huthnance et al., 2009). The hydrography of NW Scottish waters shows a marked salinity
168 boundary separating coastal and oceanic shelf waters (Savidge and Lennon, 1987). Increased
169 chlorophyll concentrations were observed adjacent to the salinity boundary, discontinuously
170 within the coastal waters, and also in the vicinity of the thermocline in the deeper off-shelf

171 water (Savidge and Lennon, 1987). More recently, a distinct biogeochemical divide was
172 observed, with Iron (Fe) deficient surface waters present beyond the shelf break, limiting
173 seasonally phytoplankton growth in our study area and greatly reducing the efficiency of the
174 biological carbon pump (Birchill et al., 2019). Along the shelf break and the upper slope, the
175 strong near-bed currents (e.g., Masson et al., 2002) provide the perfect conditions for the
176 development of rich benthic communities dominated by suspension-feeders (e.g., Davies et
177 al., 2009). Active internal tidal mixing on the shelf and deeper (e.g., in the WTR) can also
178 supply nutrients to the euphotic zone, with fronts between summer-stratified and mixed
179 waters particularly favoring phytoplankton growth (e.g., Pingree et al., 1978; Sherwin, 1991;
180 Frederiksen et al., 1992; Duineveld et al., 2007; Mienis et al., 2007; Roberts et al., 2009).
181 Over the Hebridean shelf break, the surface wind drives on-shelf flow creating a
182 compensating off-shelf downwelling circulation that has been shown to rapidly (<10 days)
183 transport diatom chains down the shelf slope to deep waters (>1500 m) (e.g., Holt et al., 2009;
184 Huthnance et al., 2009; Simpson and McCandliss, 2013; Birchill et al., 2019).

185 b) External source: water masses

186 Surface waters originating from south of the Rockall Trough (i.e., ENAW) bring less nutrients
187 than waters from the northwest (i.e., WNAW), which are modified by interactions with
188 nutrient rich sub-polar waters in the Iceland Basin (McGrath et al., 2012; Johnson et al.,
189 2013). Johnson et al. (2013) reported that between 1996 and the mid-2000s, the upper waters
190 (200–700 m) of the Rockall Trough became warmer saltier, and depleted in nitrate and
191 phosphate as the proportion of subpolar waters in the basin decreased from around 50% to
192 less than 20%. These changes are explained by the varying influence of southern versus
193 subpolar water masses in the basin as the SPG weakened and contracted (Sherwin et al., 2012;
194 Johnson et al., 2013). Hátún et al. (2017) further show clear evidence of a marked pre-bloom
195 silicate decline throughout the winter mixed layer during the last 25 years, which they

196 attributed to natural multi-decadal variability through decreased winter convection depths, a
197 weakening and retraction of the subpolar gyre and increased influence of nutrient-poor water
198 of subtropical origin.

199

200 **3- Material and Methods**

201 ***3.1. Core Sampling***

202 Vibrocore +59-07/293VE (named WTR Core hereafter; 59°43.40' N; 06°28.90' W) was
203 retrieved at 282 m water depth with a total recovery of 495 cm during a British Geological
204 Survey campaign in August 1984, at the junction with the WTR and the West Shetland
205 shelf/Hebridean shelf (Fig. 1b) onboard the MV British Enterprise Four (Long et al., 1999).
206 Prior to sub-sampling, the core was sliced into meter-length sections onboard, frozen and split
207 with a diamond bladed saw to avoid any shifting in the position and orientation of the coral
208 fragments and to preserve internal sedimentary structures of the cores (as described by
209 Dorschel et al., 2007; Douarin et al., 2013; Elliot et al., 2019). Once opened and defrosted, the
210 core was dissected into 1 cm-thick sediment slices at 1 to 10 cm intervals. These subsamples
211 were freeze dried and washed through 150, 1000 and 2000 μm mesh sieves. All size fractions
212 were then dried in an oven at 45°C. This core was previously studied for clay mineralogy, and
213 grain-size distribution complemented by $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ profiles of the planktonic foraminifer
214 *Globigerina bulloides* (Elliot et al., 2019).

215

216 ***3.2. Chronology and age model***

217 The methodology used for establishing the chronology of WTR Core is detailed in Elliot et al.
218 (2019). It is based on 43 U-Th and 17 AMS ^{14}C dates performed on the same pristine samples
219 of *D. pertusum*, 6 AMS ^{14}C dates measured on the benthic foraminifer *Cibicides refulgens* and
220 3 AMS ^{14}C dates on the bivalves *Venus* spp. (Fig. 2a). Despite this significant dating effort,

221 unexplained $^{14}\text{C}/\text{U-Th}$ anomalies preclude the use of an accurate age model as discussed in
222 Elliot et al. (2019). Elliot et al. (2019) hypothesized the presence of a diagenetic process that
223 standard quality tests have failed to highlight, affecting unevenly U-Th and ^{14}C dates. The
224 new foraminiferal data does however provide new additional constraints for the age model of
225 this sediment core. When U-Th dates indicate a rapid sediment deposition event between
226 160.5 and 61.5 cm depths (the layer of poorly preserved corals; Fig. 2), ^{14}C ages indicate a
227 rather continuous sedimentation rate in line with our foraminiferal data that seem to record
228 unchanged absolute abundances, diversities, and species composition (Figs. 3; 4) and show no
229 particular signs of shell alteration nor transport. Hence, foraminiferal data seem to preclude
230 any major reworking process involving a mix of sediments or transport from other settings in
231 this section. We cannot discard however the possible presence of hiatuses which is a common
232 feature in CWC habitats (e.g., López Correa et al., 2012). Pending further detailed studies on
233 the intracrystalline structure of the coral aragonite in this core that may give a final
234 explanation to the U-Th or ^{14}C inconsistencies, we use the independent age model of Elliot et
235 al. (2019) built from correlations of planktonic $\delta^{18}\text{O}_{G. \textit{bulloides}}$ profiles with a well-dated
236 sediment core from the Rockall Plateau (NA 87–22; Waelbroeck et al., 2001), identifying
237 three time periods (Glacial, Deglacial-Early Holocene and Holocene).

238

239 ***3.4. Benthic foraminiferal assemblages***

240 Benthic foraminiferal assemblages were investigated in 69 samples sampled at 5 to 10 cm
241 intervals from the $>150\ \mu\text{m}$ fraction (cf. raw dataset in Supplementary Material S1). Although
242 the $>150\ \mu\text{m}$ fraction provides valuable information on prevailing environmental conditions,
243 we are aware that there is a possible loss of information when discarding the small size
244 fraction as densities are generally higher, and some species are small sized in their adult forms
245 (e.g., Caille et al., 2014; Weinkauff and Milker, 2018; Lo Giudice Cappelli and Austin, 2019;

246 Fossile et al., 2020). In our case, there was no possibility to investigate the small size fraction
247 due its use for previous analyses. Foraminifera were picked under a stereomicroscope. For the
248 subsamples where foraminifera were very abundant, they were split with an Otto microsplitter
249 and the whole splits were counted until a minimum of 300 tests of benthic foraminifera was
250 obtained.

251 To confirm and/or help with taxonomical identification, Scanning Electron Microscope
252 (SEM) photographs were obtained at the SCIAM platform (University of Angers) using a
253 Zeiss EVO LS10 without prior coating and with low vacuum (Plates 1 and 2). Please refer to
254 the taxonomical appendix (Supplementary material S2) for a detailed description of the
255 dominant morphospecies and the knowledge gained from the genetic studies for some of these
256 taxa (e.g., Schweizer et al., 2005, 2008; Darling et al., 2016).

257 Diversity index (Shannon H), a Principal Component Analysis (PCA) and a multiple
258 correlation graph were performed using the software PAST (PAleontological STatistics;
259 Version 3.25; Hammer et al., 2001). Shannon H index (Shannon, 1948; Hayek and Buzas,
260 1997) was calculated following the equation ($H = -\sum_i p_i \ln(p_i)$) where p_i is the proportion
261 of the i th species ($p = \%/100$). H values for Atlantic assemblages are generally comprised
262 between a minimum of ~ 1.1 and a maximum of 3.8 (Murray, 2006). Input for the PCA
263 consisted of species' relative abundance data (correlation matrix). Only taxa occurring with
264 $\geq 5\%$ in at least one sample were retained in these statistical analyses.

265

266 **4- Results**

267 A total number of 88 benthic foraminiferal taxa were observed in WTR Core, among which
268 16 were dominant (i.e., showing relative abundances $\geq 5\%$ in at least one sample) (Figs. 3 and
269 4).

270 In order to facilitate examination of the large dataset obtained for WTR Core and to extract

271 the main foraminiferal ecological groups, a PCA was performed based on the percentage data
272 of the dominant taxa (Fig. 3a). Axes 1 and 2 account respectively for 46.26 % and 14.34% of
273 the total variance of the dataset. These axes were retained as the most meaningful according
274 to the scree plot graphical method proposed by Cattell (1966) showing a sharp change in slope
275 at the second eigenvalue. The PCA separates the assemblages into three main species groups
276 (see below (i), (ii) and (iii); Fig. 3a) each associated with changes in sediment properties
277 corresponding to one of the three time periods previously defined (Elliot et al., 2019):

278 (i) PCA Group 1 was abundant between ~480 and 400 cm depths, during the “Glacial”
279 part of the record (ages older than 13 cal ka BP) (Fig. 3b) and is dominated by *Cibicides*
280 *refulgens* (45.9 ± 5 % on average during this time-period) followed to a lesser extent by
281 *Discanomalina coronata* (6.6 ± 1.5 %) and only negligibly represented by *Cibicidoides* sp.
282 (2.3 ± 1.7 %), *Quinqueloculina seminulum* (2.8 ± 1.1), and *Bulimina aculeata* (2.1 ± 1.4 %)
283 (Fig. 4). Apart from *Cibicidoides* sp. that showed an inconsistent pattern, most of these
284 species showed overall decreasing relative abundances with minima values around 300 cm,
285 and then stabilized at very low values until the core top (Fig. 4).

286 (ii) PCA Group 2 was dominant between ~400 and 300 cm depths, marking the end of
287 the deglaciation and the early Holocene (13-9 cal ka BP) (Fig. 3b). This group is mainly
288 driven by *Textularia sagittula* (15.6 ± 5.1 % on average during this time-period), *Lobatula*
289 *lobatula* (11.6 ± 6.2 %) and *Elphidium clavatum* (10.4 ± 6.4 %) and only negligibly by
290 *Cassidulina laevigata* (5.3 ± 1.4 %) and *Melonis barleeanus* (3.2 ± 1.8 %) (Fig. 4). *Textularia*
291 *sagittula* and *E. clavatum* were present with very low abundances during the “Glacial” part of
292 the record, then increased rapidly above 400 cm core depth to attain maximum percentages at
293 ~350 cm and ~385 cm, respectively. *Melonis barleeanus* was present with low percentages
294 from 485 to 310 cm and was nearly absent in the top 300 cm section of the core (Fig. 4).
295 *Lobatula lobatula* and *C. laevigata* were nearly absent in the “Glacial” section. The

296 percentages of these species showed an overall stable trend after 400 cm around ~10 and 5%
297 respectively, apart from the upper 180 cm core section where *C. laevigata* percentages
298 increased from ~5 to 8-9 %.

299 (iii) PCA Group 3 was dominant in the upper 300 cm of the core, during the Holocene
300 sequence associated with CWC growth (after ~9 cal ka BP) (Fig. 3b). PCA 3 is composed of
301 *Trifarina angulosa* (20.5 ± 6.2 % on average during this time-period), *Globocassidulina*
302 *crassa* (16.1 ± 4.9 %), *Gavelinopsis praegeri* (7.9 ± 2.4 %), *Rosalina globularis* (4.0 ± 2.2
303 %), *Miliolinella subrotunda* (3.8 ± 1.7 %) and *Textularia agglutinans* (1.5 ± 1.3 %) (Fig. 4).
304 *Trifarina angulosa* was present continuously through the entire record with percentages >
305 10%. In the “Glacial” part, its contribution decreased progressively from ~20 to 10 %, then
306 increased in the “Deglacial/Early Holocene” part to reach ~20%. After 9 cal ka BP, the
307 relative abundances of *T. angulosa* showed an increasing trend with percentages ranging from
308 10 to 40 %. *Globocassidulina crassa* was nearly absent in the “Glacial” section. The
309 abundances of *G. crassa* increased progressively after 13 cal ka BP to reach maximum values
310 (~25 %) around 200 cm depth and decreased afterwards until the core top (~5 %).
311 *Gavelinopsis praegeri*, *R. globularis*, *M. subrotunda* and *T. agglutinans* were nearly absent
312 beneath 300 cm sediment depth and their percentages varied from low to high values in the
313 upper 300 cm core section (Fig. 4).

314 In the entire core, absolute foraminiferal abundances ranged between 77 and 2128 ind. g⁻¹ of
315 dry sediment (Fig. 3b). Low densities (average = 107 ± 16 ind. g⁻¹) were present in the older
316 part of the record from 485 to 400 cm sediment depth. Then, abundances increased and
317 stabilized at ~700 ind. g⁻¹ from 360 to 325 cm, followed by a rapid increasing trend to reach
318 maximum values of 2128 ind. g⁻¹ at 290 cm. After, abundances decreased until 250 cm and
319 oscillated around 626 ± 244 ind. g⁻¹ until the core top.

320 Shannon diversity (*H*) showed relatively low values from 480 to 410 cm of 2.0 ± 0.1 , then

321 increased to reach intermediate values of 2.4 ± 0.1 between 410 and 300 cm. From there, a
322 rapid increase was recorded to reach maximum values of 2.9 at 270 cm, followed by an
323 overall slow decreasing trend until the core top where we recorded values around 2.5 (Fig.
324 3b).

325

326 **5- Discussion**

327 ***5.1. Benthic foraminiferal-based comparison between NE Atlantic CWC sites***

328 Most of the foraminifera found in the “coral” part of our record are overall similar to the ones
329 of the modern CWC environments in the NE Atlantic (cf. review in Spezzaferri et al., 2015).
330 Some differences are yet present. For example, while *R. globularis*, *R. anomala*, *M.*
331 *subrotunda*, *H. balthica*, and the textulariids are dominant in our record, they are generally
332 absent or rare in the investigated NE Atlantic CWC environments (e.g., Margreth et al., 2009;
333 Schönfeld et al., 2011; Morigi et al., 2012; Smeulders et al., 2014; Spezzaferri et al., 2013;
334 Stalder et al., 2014; Fentimen et al., 2020a). This discrepancy can be partly explained by the
335 fact that most of the studied foraminiferal assemblages associated with CWC sites in the NE
336 Atlantic are deeper (~700-800 m depth) than our study sites (e.g., the Porcupine Seabight and
337 the Rockall Bank region). In open ocean deep-sea environments, and because of partial
338 remineralization in the water column, the flux of labile organic matter that reaches the
339 seafloor decreases with increasing water depth (e.g., Berger and Wefer, 1990; Herguera,
340 1992). Benthic foraminiferal assemblages are therefore distributed following this
341 bathymetric/trophic gradient, with some taxa inhabiting a large range of organic matter fluxes
342 (e.g., from shelf to lower slope: *M. barleeanus*) whereas others are dominant in a more
343 restricted depth range such as shelf and upper slope environments (e.g., *Rosalina* spp., *M.*
344 *subrotunda*, *H. balthica*) (e.g., Murray, 1973, 2006; Mojtahid et al., 2010). For the
345 textulariids, the ecological requirements are still poorly known. The dominant *T. sagittula* in

346 the study core is mostly reported from temperate shelf seas of the NE Atlantic with sandy or
347 muddy bottom sediments (e.g., Schönfeld, 1997; Murray, 2006; Pascual et al., 2008),
348 including the Hebridean Shelf (Murray, 2003). For *T. sagittula* and *T. agglutinans*, the
349 sediment is not only a habitat, but also a source of material for test building as it has been
350 evidenced that they are able to select and sort grain size (e.g., Armynot du Châtelet et al.,
351 2013). This suggests that these species are sensitive to the mineralogical composition of the
352 substrate (e.g., the proportion of quartz), beyond the fine or coarse nature of the sediment
353 (e.g., Armynot du Châtelet et al., 2013) and perhaps also beyond the quantity of organic
354 matter arriving to the seafloor.

355 CWCs create local ecological niches for foraminifera by providing a variety of habitats and
356 by trapping fine sediments and organic matter, so that the above-mentioned organic carbon
357 gradients may not apply to CWC habitats as in "normal marine conditions". This might be
358 corroborated by the fact that the late Quaternary 240 m deep record of Stalder et al. (2014)
359 north of Norway (about 70°N), even though at a comparable depth range as the core
360 investigated herein, is characterized by a rather different benthic assemblage, with the
361 dominance of species that are not found in our records (e.g., *Cassidulina teretis*, *Discorbinella*
362 *bertheloti*, *Pullenia subcarinata*). Furthermore, several studies report specific living benthic
363 foraminiferal communities for specific facies along CWC mounds (e.g., off-mound facies,
364 living coral facies, dead coral facies) and their distribution seems to be governed by the
365 ecological demands of the species, microhabitat availability and the nature of the substrates
366 (e.g., Margreth et al., 2009; Spezzaferri et al., 2013; Smeulders et al., 2014). The species
367 difference between our site and north of Norway (Stalder et al., 2014) might also be explained
368 by the possibility that the Norwegian site is located in a different benthic foraminiferal
369 biogeographic zone (i.e., "Arctic-Subarctic" province) than our study area (i.e., "Atlantic
370 temperate" province) (e.g., Boltovskoy and Wright, 1976; Culver and Buzas, 2003). Although

371 many benthic foraminiferal taxa seem to be ubiquitous, especially when looking at the
372 morphology only, some species might exhibit distinct biogeographic patterns that are not
373 dependent on the existence of suitable habitats (e.g., Gooday and Jorissen, 2011).

374 To summarize, it is very likely that the observed discrepancies between our site and the rest of
375 the other NE Atlantic CWC sites relies partly on the inherent interlink of the parameters
376 governing CWC habitats (e.g. nature of the substrate, abundance of corals, CWC related
377 microhabitats and facies, ...), but also on local physico-chemical processes (current strength
378 variability, organic carbon fluxes, water mass properties, oxygenation, ...) that further govern
379 the abundance and species composition of benthic foraminifera in these environments.

380

381 ***5.2. Glacial environmental conditions inferred from WTR benthic foraminifera***

382 Species from PCA Group 1 (referred to as “Glacial” species) were abundant in the coarse silts
383 characterizing the “Glacial” part of the record (ages older than ~13 cal ka BP) (Fig. 3b), and
384 described as mixed sediment deposits (i.e. glacio-marine and marine deposits) of glacial age
385 in the study of Elliot et al. (2019). The low abundances and diversities characterizing this
386 time-period (Fig. 3b) are indicative of unfavorable ecological conditions (e.g., low food
387 availability, coarse substrate, cold temperatures) for the reproduction and growth of many
388 benthic foraminifera. The dominant taxa *C. refulgens* and *D. coronata* are both epifaunal
389 species attached to elevated substrates in high-energy areas (e.g., Hawkes and Scott, 2005;
390 Murray, 2006; Margreth et al., 2009; Schönfeld et al., 2011). It is interesting to note that *T.*
391 *angulosa*, although belonging to PCA Group 3, was also present during this time-period (Fig.
392 4). In the literature, this species is commonly associated with shelf-edge–upper-slope areas of
393 sand to gravel sediment under the influence of strong bottom currents (e.g., Mackensen et al.,
394 1985; Austin and Evans, 2000; Gooday and Hughes, 2002), thus corroborating the
395 environment depicted by *C. refulgens* and *D. coronata*. In addition to these overall high

396 energy benthic environments, the low diversity and abundance of foraminifera may indicate
397 low food availability to which the species present in this glacial period might be tolerant. Low
398 organic matter input is coherent with the interpretations of Rüggeberg et al. (2007) from
399 glacial foraminiferal data from CWC mounds (Porcupine Seabight) and with the local
400 climatic conditions prevailing during the last glacial period. The British Ice Sheet (BIS)
401 extended close to the WTR core location (cf. BIS extent in Fig. 1b; Clark et al., 2004),
402 therefore preventing continental sediment input from reaching our site (as shown by the very
403 low sedimentation rate; Fig. 2a), and with it the supply of nutrients necessary for primary
404 production. In parallel, relative sea-level was lower, making the study site shallower and
405 closer to the surface processes (sea ice, freezing processes, brine formation, etc.) which might
406 have affected the development of benthic foraminifera. Furthermore, Elliot et al. (2019)
407 interpreted the poorly-sorted bimodal grain-size distribution and the presence of pebbles of
408 rock fragments (Fig. 2b) as indicating that ice-rafting was a likely sedimentation mechanism,
409 and that sluggish bottom current was unable to sort coarse glaciomarine deposits. Low-current
410 intensities under fully glacial conditions were also interpreted from the Porcupine Seabight
411 (~700 m depth) foraminiferal study of Rüggeberg et al. (2007). This appears to contradict our
412 interpretations drawn from the ecology of the dominant benthic species. One possibility is that
413 highly variable sedimentation regimes include episodes of increased current flow regimes
414 during this period, allowing the settlement of these species. Another explanation is that these
415 foraminifera might have lived onsite attached to glacial dropstones or the sandy shelly
416 substrate tolerating the cold and low food availability conditions and profiting from the low
417 competition. Alternatively, we are possibly recording highly variable conditions in time with
418 alternating episodes of ice rafting and others characterized by environments enabling these
419 species to settle, all mixed by high energy currents. At the transition between the “Glacial”
420 and the “Deglacial-Early Holocene” periods, there is a reduction in the relative abundance of

421 these “Glacial” species (Fig. 3b), most likely related to the progressive retreat of the BIS that
422 started around 23 cal ka BP (Clark et al., 2004; Fig. 1b). This further corroborates a strong
423 link of these two species with the glacial environmental conditions at the WTR.

424 An important observation is that *C. refulgens* and *D. coronata* were dominant in a period of
425 absence of *D. pertusum* in our site and only contributed very little to the total assemblages
426 after 9 cal ka BP when the corals were present. This seems to contradict the common current
427 knowledge about their ecology in CWC environments in the North Atlantic where they are
428 often found alive either attached on corals or living in the sandwaves around the coral mound
429 (e.g., Hawkes and Scott, 2005; Margreth et al., 2009; Schönfeld et al., 2011). Margreth et al.
430 (2009) further suggested the use of *D. coronata* as an indicator of CWC coral facies (on-
431 mound). The late Quaternary 240 m-deep record of Stalder et al. (2014) north of Norway and
432 the 700 m-deep record of Rüggeberg et al. (2007) in the Porcupine Seabight both show that *D.*
433 *coronata* was mostly found during coral-rich periods, whereas this species was dominant
434 during the pre-coral interval in our study site. In western Mediterranean CWC habitats, the
435 restricted presence of *D. coronata* during glacial times was interpreted as its preference for
436 cold waters (Stalder et al., 2018), and as such temperature may have also a strong influence in
437 the distribution of this species. Because there is increasing evidence that CWCs respond to
438 more variable environmental factors (e.g., oxygenation - Wienberg et al., 2018; Hanz et al.,
439 2019) than the ones classically cited (substrate type, temperature, salinity, currents, and food
440 availability - e.g., Freiwald, 2002; Davies et al., 2008; Brooke et al., 2013), our results suggest
441 that the variability of benthic foraminiferal species in CWCs habitats may also be higher than
442 previously assumed.

443

444 ***5.3. Transition from glaciomarine to open marine conditions***

445 Species from PCA Group 2 (referred to as “Deglacial-Early Holocene” species) were

446 dominant between ~13 and 9 cal ka BP, a period of transition from glaciomarine to open
447 marine sedimentation (Elliot et al., 2019). PCA group 2 is dominated by *T. sagittula*, *E.*
448 *clavatum* and *L. lobatula*. *Textularia sagittula* is an agglutinated species (Barmawidjaja et al.,
449 1992), mostly described from temperate shelf seas of the NE Atlantic with sandy or muddy
450 sediments (e.g., Schönfeld, 1997; Murray, 2006; Pascual et al., 2008). *Elphidium clavatum* is
451 particularly frequent in glacier-proximal environments (e.g., Jennings et al., 2004; Murray,
452 2006; Darling et al., 2016; Fossile et al., 2020), generally thrives in slightly fresher waters and
453 may withstand bottom temperatures of < -1°C (e.g., Hald and Korsun, 1997; Polyak et al.,
454 2002). Also, it is common in boreal waters of the Skagerrak, the Wadden Sea and North Uist
455 (Outer Hebrides) near our study site (Darling et al., 2016). Observations of CWC deposits off
456 northern Norway show that this species clusters with Arctic–Subarctic glaciomarine taxa
457 (Stalder et al. 2014), whereas its dominance in the glacial part of the Porcupine Seabight on-
458 mound record was considered as an indication of erosional processes from shallow shelf areas
459 (Rüggeberg et al., 2007). In modern CWC environments of the NE Atlantic, *T. sagittula* and
460 *E. clavatum* are either absent or rare (Margreth et al., 2009; Schönfeld et al., 2011; Morigi et
461 al., 2012; Spezzaferri et al., 2013; Fentimen et al., 2020b). Although not much is known about
462 the ecological requirements of *T. sagittula*, we believe that its association with *E. clavatum*
463 during the end of the deglaciation and the early Holocene might be indicative of the presence
464 of low salinity and cold waters in the study area. In the NE Atlantic, *L. lobatula* is usually
465 present in areas with strong currents and coarse sediments (e.g., Schönfeld, 1997, 2002a,
466 2002b; Murray, 2006). Its presence during this pre-CWC period might indicate a reactivation
467 of near-bed currents.

468 The concomitant presence of the infaunal *M. barleeanus* and *C. laevigata* from the same PCA
469 Group 2 together with *G. crassa* from PCA Group 1 might be further indicative of increased
470 organic matter flux, as reported from slope environments south of our study site (e.g., Koho et

471 al., 2008; Morigi et al., 2012; Garcia et al., 2013). In the study of Rüggeberg et al. (2007), *G.*
472 *crassa* (referred to as *C. reniforme*) clusters with the glacial group and is interpreted as an
473 indicator for cold and nutrient-poor bottom water conditions whereas *C. laevigata* makes part
474 of the Holocene assemblage indicating high flux of organic material to the sea-floor. In
475 subarctic waters however, studies report that the presence of *C. laevigata* is more consistent
476 with the flow of warm and saline Atlantic waters than with organic matter flux (Østby and
477 Nagy, 1982; Mackensen and Hald, 1988; Hald and Steinsund, 1992; Husum and Hald, 2004).
478 Østby and Nagy (1982) interpreted the association of the cassidulinids with *L. lobatula* as
479 indicative of increased current activity. Because this is a transitional period from glacial to
480 interglacial times, it is probable that the association of the cassidulinids (i.e., *G. crassa* and *C.*
481 *laevigata*) and *M. barleeanus* with *L. lobatula* indicates both increased influx of warm and
482 saline Atlantic waters to the study site, and increased influx of organic matter. These species-
483 based interpretations are coherent with the observed increase in foraminiferal absolute
484 abundances and diversities characterizing this time interval (Fig. 3b). This is indeed indicative
485 of more favorable environmental conditions for many benthic foraminifera (e.g., higher food
486 availability, finer sediments, and possibly higher temperatures and salinities).

487 At ~13 cal ka BP, there was a sharp transition marked by an increase in sedimentation rates
488 (Fig. 2a) and a reduction of smectite clay fraction (sourced from the weathering of basaltic
489 rocks from the Iceland and the Faroe-Shetland ridge area) in favor of an increase in illite
490 (sourced from the Scottish Irish continental shelves) (Elliot et al., 2019) (Fig. 3c). This is
491 indicative of an active northward transport of terrigenous material, probably by the NAC,
492 SEC and/or SCC, progressively reactivated after the meltdown of the northern ice sheets and
493 the gradual installation of modern-like circulation in the area (Elliot et al., 2019). Therefore,
494 we suggest that i) increased export production through the progressive settlement of modern-
495 like hydrographic structures (e.g., downwelling, tidal currents, salinity fronts, etc.) controlling

496 the vertical and lateral supply of organic carbon to the aphotic zone, and ii) more vigorous
497 currents (NAC, SEC and SCC) transporting warm and saline Atlantic waters between ~13 and
498 9 cal ka BP were the environmental factors that allowed the settlement and growth of *D.*
499 *pertusum* in the WTR area during most parts of the Holocene.

500

501 **5.4. Holocene environmental conditions inferred from WTR benthic foraminifera**

502 Species from PCA Group 3 (referred to as “Holocene” CWC-related species) were dominant
503 after ~9 cal ka BP, and concomitant with the settlement of *D. pertusum* (Fig. 3b). The overall
504 high absolute foraminiferal abundances and diversities (Fig. 3b) indicate highly favorable
505 environmental conditions for benthic foraminifera, most likely provided by the presence of
506 CWCs. These favorable conditions were probably the result of: i) the “shelter” effect of the
507 coral framework providing a variety of different microhabitats for foraminifera (e.g., Freiwald
508 et al., 2002; Margreth et al., 2009; Spezzaferri et al., 2013, 2015). This also results in the
509 accumulation of fine sediments that are generally rich in organic matter; ii) the high export
510 production to the seafloor that usually characterizes the recent CWC environments, which can
511 be directly coupled to high primary production and/or to secondary enrichment processes,
512 such as nepheloid layers and downwelling (e.g., Duineveld et al., 2004; Mienis et al., 2007;
513 Davies et al., 2009). Absolute foraminiferal abundances marked a peak centered around 9 cal
514 ka BP, followed by a sharp decrease (Fig. 3b). This might be the result of the settlement of a
515 diverse CWC ecosystem with a more complex trophic network constraining food resources
516 for foraminifera with competitors and decreasing their numbers with predators.

517 The “Holocene” period was characterized by the cohabitation of diverse epifaunal species (*L.*
518 *lobatula*, *G. praegeri*, *R. globularis* and *M. subrotunda*) together with infaunal species (*T.*
519 *angulosa*, *G. crassa*, *C. laevigata*, and *T. agglutinans*) (e.g., Altenbach et al., 1993; Linke and
520 Lutze, 1993; Margreth et al., 2009; Schönfeld et al., 2011; Spezzaferri et al., 2015) (Fig. 4).

521 Our data show that the abundance of epifaunal species is variable and seems to covary with
522 the abundance of coral fragments (Fig. 5a). We assume therefore that these epifaunal species
523 lived attached to CWCs (colonizing live corals or coral debris). This epifauna-CWC link is
524 interrupted between 110 and 70 cm depth representing the upper half of the poorly preserved
525 corals layer (160.5 - 61.5 cm) as defined by Elliot et al. (2019) (Fig. 5b). As such, the scarcity
526 of large (> 2 cm) well preserved coral fragments characterizing this interval and the poorly
527 preserved aspect (i.e., highly fragmented and eroded) of the remaining small (< 2 cm)
528 fragments might not be the consequence of a low presence of CWC at the time but rather the
529 result of the poor preservation of the coral skeletons. Because benthic foraminifera did not
530 show any particular sign of reworking and alteration, nor a major change in abundances or
531 diversities (Figs. 3b, 4) that may indicate a major modification of environmental conditions,
532 our results point to post-mortem diagenetic processes affecting preferentially the aragonitic
533 skeletons of CWCs (e.g., Beuck and Freiwald, 2005; Gómez et al., 2018). The poor
534 preservation of corals in that layer (160.5 - 61.5 cm) might be due to CWC carbonate
535 dissolution linked with the oxidation of organic matter, and/or the presence of more corrosive
536 waters (e.g., Pirlet et al., 2010; Andersson, 2015; Raddatz et al., 2016). Further investigation
537 of redox-sensitive elements incorporated into foraminiferal calcite might help defining the
538 diagenetic process responsible for this pattern.

539 Meanwhile, we observe a significant negative correlation between epifaunal and infaunal
540 species in this coral-period; the former being mostly driven by *R. globularis* and the latter by
541 *T. angulosa* (Fig. 5). Because the number of coral fragments is positively correlated with
542 epifaunal species, infaunal species, and particularly the dominant *T. angulosa*, should
543 therefore be negatively correlated to coral fragments, and yet no statistical correlation is found
544 between them (Fig. 5a). This lack of correlation is not ecologically related but rather due to i)
545 a mathematical bias by the long-term increasing trend of *T. angulosa* and ii) a diagenetic bias

546 in the poorly preserved coral layer (Fig. 5b). When detrending the *T. angulosa* long-term
547 trend record and removing the interval of poor coral preservation (110 - 70 cm depth) from
548 the analysis, we find a statistical negative correlation (pearson $r = -0.40$) with corals
549 fragments. In the literature, *T. angulosa* is very often associated with sandy shelf-edge–upper-
550 slope areas under the influence of strong bottom currents, regardless of the presence or not of
551 CWCs (e.g., Mackensen et al., 1985; Schönfeld, 2002; Gooday and Hughes, 2002; Murray,
552 2006). This makes the interpretation of its evolution through time at the opposite of *D.*
553 *pertusum* in our study area rather challenging. The first logical explanation for the observed
554 high variability of *T. angulosa* would be the effect of changing habitats inherent to the CWC
555 interruption and re-occurrence episodes that punctuated the coral-period of our record. With
556 the absence/low presence of CWCs and the related change in habitat, the epifauna had no
557 longer appropriate substrates for their settlement whereas *T. angulosa* may have found a more
558 suitable ecological niche, triggering its increase in absolute and relative densities (Fig. 5b).
559 These more favorable conditions might be due to the coral framework and its effect on current
560 velocities on the seafloor: when CWCs are absent, the regional current velocities can be lower
561 than during coral presence but at the seafloor still higher due to the lacking effect of the coral
562 framework, explaining perhaps the higher contribution of *T. angulosa* during these times.

563

564 ***5.5. Trifarina angulosa as an indicator of the presence of ENAW in the WTR during the*** 565 ***‘Holocene’ period?***

566 Besides the possible impact of the coral framework on the infaunal habitat of *T. angulosa*, we
567 cannot rule out that changing abundances of this species may have been a response to the
568 environmental factors that caused at the first place the intermittent CWC presence in our
569 study site. We observe a significant negative correlation between percentages of *T. angulosa*
570 and smectites sourced from the north (Iceland/Faroe-Shetland areas) (Fig. 5a), and by extent a

571 positive correlation with illites sourced from south (Elliot et al., 2019) (Fig. 5b). This link is
572 expressed mainly in the long-term trend evolution, and to a lesser extent in the short-term
573 variability with minima of *T. angulosa* (except minimum VI; Fig. 5b) being overall coeval
574 with periods of higher contribution of smectites (~10 % shift; Fig. 5c). The long-term increase
575 of illites in our sediments is coherent with the results of Colin et al. (2019) showing an overall
576 increasing contribution of the southern-sourced ENAW in the Rockall Trough from ~8 to 3 ka
577 BP and induced by a westward contraction of the SPG (Fig. 1c). Superimposed to this long-
578 term trend, the same study showed a millennial scale variability of the contribution of ENAW
579 in the Rockall Trough, which may echo the short-term variability observed in our
580 foraminiferal data. Because of the lower abundance of *T. angulosa* during periods of high
581 presence of coral fragments, this would imply that CWCs were more abundant during periods
582 of higher contribution of north-western sourced waters. A similar pattern was observed in the
583 late Holocene studies of Douarin et al. (2016) and Dubois-Dauphin et al. (2019) from the
584 Mingulay Reef Complex (Western British shelf) where CWCs were abundant either during
585 periods of the highest advection of cold waters under extended SPG or slightly preceding it.
586 However, Douarin et al. (2016) suggested that both parameters were not coeval but rather
587 successive in time with the initial increased advection of cold waters causing the following
588 progressive degradation of CWCs.

589 The idea that a benthic species is related to certain water masses has long been debated (e.g.,
590 Schnitker, 1974; Mackensen et al., 1993; Schmiedl et al., 1997). There is evidence that water
591 masses (via currents) transport propagules that ultimately settle, grow and reproduce when
592 they reach a suitable environment (e.g., Alve and Goldstein, 2002, 2010). In the case of *T.*
593 *angulosa*, this possibility seems to be unlikely since it was also present when CWCs were
594 abundant. It is more likely that *T. angulosa* may have responded positively to the
595 environmental/hydrological changes accompanying a higher presence of ENAW in the study

596 site. There is evidence that waters originating from the south (i.e., ENAW) are relatively
597 nutrient-poor compared to waters from the northwest (i.e., WNAW) (McGrath et al., 2012;
598 Johnson et al., 2013). As such, and depending on the SPG dynamics, the variations in the
599 contribution of either water masses may impact differently primary production by changing
600 the nature of the primary producers, the sustainable character of primary production through
601 the year, and the efficiency of the carbon pump (e.g., Hátún et al., 2017). Although a
602 relatively higher contribution of ENAW is present in the Rockall Trough during periods of
603 weak SPG (Sherwin et al., 2012; Johnson et al., 2013), the intensity of the SEC carrying a
604 significant portion of this water mass is lowered (e.g., Marsh et al., 2017). Because the SEC
605 plays an important role in physical exchange processes at the shelf break, it affects cross-shelf
606 fluxes (e.g. Huthnance, 1995, 1986) and as such the efficiency of food export to the seafloor.
607 Furthermore, because ENAW and WNAW have different salinity and temperature properties,
608 their either presence certainly affects the local hydrology (e.g., depth of the thermocline,
609 intensity of salinity fronts with shelf waters), which impacts also food fluxes to the aphotic
610 zone. Although it is still largely unanswered to what extent the known environmental factors
611 tolerated by CWCs (e.g., Davies et al., 2008) define tipping points leading to their
612 local/regional extinction (e.g., Hebbeln et al., 2019), there is increasing evidence that food
613 source might be a critical parameter for their key physiological processes (e.g., Naumann et
614 al., 2011). It is therefore conceivable that at our study site, the Holocene periods recording an
615 absence/low presence of *D. pertusum* may have been caused by an overall less intense SEC, a
616 less efficient biological pump and/or a change in their food source with a higher advection of
617 southern-sourced water masses. *Trifarina angulosa* may have a higher adaptability for such
618 changes by taking advantage of the new habitats left after the fall of the coral framework (e.g.,
619 less competition and predation, still high energy environment providing them with food, etc).
620 It should be however kept in mind that the hypothesized *T. angulosa*/ENAW connection

621 might be hampered by the fact that the small size fraction was not investigated in this study.
622 As such, the proposed hypotheses here are meant to be a basis for reflection in future research
623 topics that are necessary to improve our still limited knowledge on the link between CWCs,
624 foraminifera, and water masses properties in the region.

625

626 **6. Conclusions**

627 Amongst the prominent features observed in the benthic foraminiferal variability and
628 constituting the most important knowledge gain compared to the sedimentary study of Elliot
629 et al. (2019), we find that: i) foraminifera indicate increasing organic carbon flux to the sea-
630 floor and higher influx of Atlantic waters before the appearance of CWCs, which makes us
631 believe that these are the main environmental factors that allowed the settlement of corals in
632 the WTR area; and ii) the short-term variability of foraminifera during the coral-period might
633 have a link with the changing habitats due to the low/high abundance of corals and/or the
634 relative presence of ENAW vs WNAW affecting the hydrology of the basin and food export
635 to the aphotic zone.

636 From glacial time to the late Holocene, three distinct benthic foraminiferal assemblages stood
637 out matching the three periods (Glacial, Deglacial-Early Holocene and Holocene) defined by
638 Elliot et al. (2019) on the basis of sedimentological analyses:

639 i) During the “Glacial” part of the record (ages older than 13 cal ka BP), the low
640 absolute abundances and diversities were indicative of unfavorable ecological
641 conditions for the reproduction and growth of many benthic foraminifera. The
642 dominant taxa *C. refulgens* and *D. coronata* might have lived attached to glacial
643 dropstones or the sandy shelly substrate tolerating the cold and low food availability
644 conditions in a period of extended BIS.

645 ii) During the Deglacial-Early Holocene period (13-9 cal ka BP), the overall increase in

646 foraminiferal absolute densities and diversities are indicative of more favorable
647 environmental conditions (e.g., increased food availability). The cassidulinids-*L.*
648 *lobatula* association seems to indicate a progressive increase of organic matter content
649 and influx of the warm and saline ENAW. We believe that these are the main
650 environmental factors that allowed the settlement of *D. pertusum* in the WTR area
651 around 9 cal ka BP.

652 iii) During the “Holocene” part (after 9 cal ka BP), the benthic foraminiferal assemblage
653 was characterized by the cohabitation of epifaunal species (e.g., *R. globularis*)
654 together with infaunal species (e.g., *T. angulosa*). Our data show a great variability in
655 the abundance of epifaunal/infaunal species that seems to be related partly to the
656 high/low presence of corals and the subsequent changes in habitats.

657 iv) After 9 ka, the observed link between the high presence of *T. angulosa* and the high
658 proportions of southern-sourced illites led us to hypothesize that this species may also
659 respond to the presence of ENAW in the study site. How and to what ENAW property
660 this species responds exactly is still to be investigated. We propose a link with
661 nutrients content and the resulting effect on the efficiency of primary production
662 and/or with a change in the local hydrology (e.g., thermocline depth, salinity fronts)
663 affecting the export of food to the seafloor.

664

665 **7. Data availability**

666 The raw data are available as Supplementary Material S1 and on PANGAEA online
667 repository (<https://doi.pangaea.de/10.1594/PANGAEA.932647>).

668

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1219 **5. Figures captions**

1220 **Figure 1.** a) Overview map modified from Staines-Urías et al. (2013) showing modern North
1221 Atlantic Ocean surface circulation. Red arrows indicate warm currents and blue arrows
1222 indicate cold currents. Water masses are written in italics to be distinguished from currents,
1223 and gyres are underlined; b) Bathymetric map showing the location of our study core together
1224 with the main seabed topographic features. The location of Core NA 87-22 used for age
1225 model is indicated (cf. text for more detail). The extension limit of the British Ice Sheet at
1226 different times in the past is shown by the colored dotted lines after Clark et al. (2004) and a
1227 set of maps created by the University of Sheffield led by Professor Chris Clark
1228 (<https://www.donsmaps.com/icemaps.html>). In red are the main surface poleward water flows
1229 and in grey the main southward cold deep-water flows; c) Schematics showing the two main
1230 oscillating states of the SPG: eastward expanded and westward retracted. Red arrows indicate
1231 warm currents and blue arrows indicate cold currents.

1232 **Figure 2.** a) Published WTR core data from Elliot et al. (2019) showing age depth distribution
1233 in cal ka BP using U-Th and ^{14}C dates measured on *L. pertusa*, and ^{14}C dates measured on *C.*
1234 *refulgens* and marine bivalves (*Venus* spp.) and the number of coral fragments >2 cm; b)
1235 Synthetic lithological log of WTR core. The hatched surface indicates the sediment layer with
1236 poorly preserved corals.

1237 **Figure 3.** a) PCA analysis based on the percentages of the main benthic foraminiferal species
1238 in WTR Core (i.e., present with $\geq 5\%$ in at least one of the sediment samples); b) WTR Core
1239 plots of the cumulative percentages of the three PCA groups (cf. Figure 3a), absolute
1240 abundances of benthic foraminifera (AA/g of dry sediment), Shannon *H* diversity index of
1241 benthic foraminifera; c) Clay mineralogy from the study of Elliot et al. (2019). The dark grey
1242 band represents the “Glacial” period, and the light grey band represents the “Deglacial-Early
1243 Holocene” period (Deg./Early Hol.). The hatched surface indicates the sediment layer with

1244 poorly preserved corals as described in Elliot et al. (2019).

1245 **Figure 4.** Depth plots representing percentages (red) and absolute densities/g of dry sediment
1246 (grey) of the main benthic foraminiferal species (i.e., present with $\geq 5\%$ in at least one of the
1247 sediment samples). The dark grey band represents the “Glacial” period, and the light grey
1248 band represents the “Deglacial-Early Holocene” period (Deg./Early Hol.). The hatched
1249 surface indicates the sediment layer with poorly preserved corals as described in Elliot et al.
1250 (2019).

1251 **Figure 5.** a) Graph representing the results of linear multiple correlations between proxies in
1252 the upper 325 cm of WTR Core (% of the main benthic species, % of smectites, the mean
1253 grain size number of coral fragments > 2 cm, $\delta^{18}\text{O}$ and $\delta^{13}\text{C}$ of *G. bulloides*). Colors refer to
1254 Pearson correlation r , with blue/red referring to positive/negative correlation. The size and the
1255 color intensity of the round symbols are proportional to the strength of the correlation. Non-
1256 significant correlations ($p > 0.05$) are highlighted in grey; b) Depth plots for the upper 325 cm
1257 of the % of the benthic species *T. angulosa* and *R. globularis*. The number of coral fragments
1258 from Elliot et al. (2019) are indicated in dashed blue lines. Numbers I to VIII indicate minima
1259 of % of *T. angulosa*; c) Depth plot of % of smectites. Note the inverse x-axis for smectites.
1260 The horizontal grey bands are based on the minima of % *T. angulosa*. The red crosses indicate
1261 where there is a mismatch between % *T. angulosa* and % smectites (refer to the text for
1262 details). The dotted horizontal line indicates the limit at 9 cal ka BP between the defined
1263 glacial and deglacial-early Holocene periods (refer to the text for details). The hatched surface
1264 indicates the sediment layer with poorly preserved corals as described in Elliot et al. (2019).

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1266 **6. Plate captions**

1267 **Plate 1.** Scanning electron microscope (SEM) images of: 1 a-b. *Quinqueloculina seminulum*

1268 (Linnaeus, 1758); 2 a-b. *Miliolinella subrotunda* (Montagu, 1803); 3. *Spirillina vivipara*
1269 Ehrenberg, 1843; 4. *Spiroloculina tenuiseptata* Brady, 1884; 5 a-b. *Textularia sagittula*
1270 Defrance 1824; 6. *Textularia agglutinans* d'Orbigny, 1839; 7. *Bolivina spathulata*
1271 (Williamson, 1858); 8. *Bolivina earlandi* Parr, 1950; 9. *Ehrenbergina* sp.; 10. *Bulimina*
1272 *aculeata* d'Orbigny, 1826; 11. *Bulimina marginata* d'Orbigny, 1826; 12 a-b. *Globocassidulina*
1273 *crassa* (d'Orbigny, 1839); 13 a-d. *Cassidulina laevigata* d'Orbigny, 1826; 14 a-b.
1274 *Evolvocassidulina bradyi* (Norman, 1881); 15. *Lagenosolenia bradyiformata* (McCulloch,
1275 1977); 16. *Favulina squamosa* (Montagu, 1803); 17. *Lagena striata* (d'Orbigny, 1839); 18. a-
1276 d. *Discanomalina coronata* (Parker & Jones, 1865).

1277 **Plate 2.** SEM images of benthic foraminifera of: 18 a-b. *Amphicoryna scalaris* (Batsch,
1278 1791); 19. *Laevidentalina filiformis* (d'Orbigny, 1826); 20 a-b. *Globulina* sp.; 21 a-b.
1279 *Trifarina angulosa* (Williamson, 1858); 22. *Robertina arctica* d'Orbigny, 1846; 23. *Uvigerina*
1280 *mediterranea* Hofker, 1932; 24. *Uvigerina peregrina* Cushman, 1923; 25. *Ammonia batava*
1281 (Hofker, 1951); 26 a-b. *Rosalina bradyi* (Cushman, 1915); 27. a-c. *Elphidium clavatum*
1282 Cushman, 1930; 28. a-b. *Elphidium* sp.; 29 a-b. *Gavelinopsis praegeri* (Heron-Allen &
1283 Earland, 1913); 30. *Astrononion gallowayi* Loeblich & Tappan, 1953; 31. *Nonionella turgida*
1284 (Williamson, 1958); 32 a-b. *Melonis barleeanus* (Williamson, 1858); 33 a-c. *Osangulariella*
1285 *bradyi* (Earland 1934); 34 a-c. *Cibicides refulgens* Montfort, 1808; 35 a-c. *Lobatula lobatula*
1286 (Walker & Jacob, 1798); 36 a-c. *Cibicidoides* sp.