



From glacial times to late Holocene: Benthic foraminiferal assemblages from cold water coral habitats off northwest Scotland

Meryem Mojtahid, Magali Schweizer, Mélanie Douarin, Justine Gabriel,
Christophe Colin, Nadine Tisnérat-Laborde, Mary Elliot

► To cite this version:

Meryem Mojtahid, Magali Schweizer, Mélanie Douarin, Justine Gabriel, Christophe Colin, et al.. From glacial times to late Holocene: Benthic foraminiferal assemblages from cold water coral habitats off northwest Scotland. *Marine Geology*, 2021, 440, pp.106581. 10.1016/j.margeo.2021.106581 . hal-03317921

HAL Id: hal-03317921

<https://hal.science/hal-03317921>

Submitted on 22 Aug 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution - NonCommercial 4.0 International License

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

Abstract

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

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

1- Introduction

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

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

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

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

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

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

2- Study area

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

The WTR is a bathymetric feature that forms the easternmost part of the Greenland-Scotland ridge stretching across the northeastern part of the North Atlantic from Greenland to the northern Scottish shelf (Fig. 1b). The WTR separates the Faroe–Shetland Channel to the north from the Rockall Trough to the south (Fig. 1b). These are two deep water areas that separate the Hebrides and West Shetland shelves from the Rockall Plateau and Faroes Shelf (Fig. 1b). The WTR is a rocky plateau with extensive gravel, cobble and boulder fields (Stewart and Davies, 2007), providing suitable substrates for most CWC larvae to settle (e.g., Roberts et al., 2009). Data referring to *Desmophyllum pertusum* distribution in this region were initially reported in the study of Wyville Thomson (1874). More recently, CWC presence in the study area was reported in the light of several seismo-acoustic surveys of the seabed, including the

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

2.2. Hydrography and ocean circulation

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

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

2.3. Carbon and nutrient dynamics

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

a) Local source: primary production

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

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

b) External source: water masses

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

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

3- Material and Methods

3.1. Core Sampling

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

3.2. Chronology and age model

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

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

3.4. Benthic foraminiferal assemblages

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

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

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

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

4- Results

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

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

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

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

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

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

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

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

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

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

5- Discussion

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

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

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

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

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

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

5.2. Glacial environmental conditions inferred from WTR benthic foraminifera

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

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

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

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

5.3. Transition from glaciomarine to open marine conditions

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

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

The concomitant presence of the infaunal *M. barleeanus* and *C. laevigata* from the same PCA Group 2 together with *G. crassa* from PCA Group 1 might be further indicative of increased 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

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

5.4. Holocene environmental conditions inferred from WTR benthic foraminifera

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

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

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

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

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

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

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

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

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

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

6. Conclusions

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

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

- i) During the “Glacial” part of the record (ages older than 13 cal ka BP), the low absolute abundances and diversities were indicative of unfavorable ecological conditions for the reproduction and growth of many benthic foraminifera. The dominant taxa *C. refulgens* and *D. coronata* might have lived attached to glacial dropstones or the sandy shelly substrate tolerating the cold and low food availability conditions in a period of extended BIS.
- ii) During the Deglacial-Early Holocene period (13-9 cal ka BP), the overall increase in

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

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

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

7. Data availability

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

8. Acknowledgments

We would like to thank the editor, Dr. Jürgen TITSCHACK, Dr. Andres RÜGGERBERG, and

the third anonymous reviewer for their thorough reviews and comments that helped improving the manuscript. We would like to thank the British Geological Survey (BGS) for granting access to sediment core material and the NERC support for access to facilities on the RRS James Cook. This study was funded by the French National Research Agency “Investissement d'Avenir” (ANR-10-LABX-0018), the HAMOC project ANR-13-BS06-0003, the INSU-LEFE-IMAGO program, and the *Région Pays de Loire* programs (New Research Group initiative and Rising Star project TANDEM). Salary and research support for MD were provided by fellowships from the Scottish Alliance for Geoscience, Environment and Society (SAGES), and the BGS. Original SEM micrographs of foraminiferal species (Plates 1 and 2) were performed by Romain Mallet at the SCIAM platform of the University of Angers. We thank Edwige Pons-Branchu for her constructive comments and discussion.

9. References

- Altenbach, A.V., Heeger, T., Linke, P., Spindler, M., Thies, A., 1993. *Miliolinella subrotunda* (Montagu), a miliolid foraminifer building large detritic tubes for a temporary epibenthic lifestyle. *Mar. Micropaleontol.* 20, 293–301. [https://doi.org/10.1016/0377-8398\(93\)90038-Y](https://doi.org/10.1016/0377-8398(93)90038-Y)
- Alve, E., Goldstein, S.T., 2010. Dispersal, survival and delayed growth of benthic foraminiferal propagules. *J. Sea Res.* 63, 36–51.
- Alve, E., Goldstein, S.T., 2002. Resting stage in benthic foraminiferal propagules: a key feature for dispersal? Evidence from two shallow-water species. *J. Micropalaeontology* 21, 95–96.
- Andersson, A.J., 2015. A fundamental paradigm for coral reef carbonate sediment dissolution. *Front. Mar. Sci.* 2. <https://doi.org/10.3389/fmars.2015.00052>
- Armynot du Châtelet, E., Bout-Roumazeilles, V., Coccioni, R., Frontalini, F., Guillot, F., Kaminski, M.A., Recourt, P., Riboulleau, A., Trentesaux, A., Tribovillard, N., Ventalon, S., 2013. Environmental control on shell structure and composition of agglutinated foraminifera along a proximal–distal transect in the Marmara Sea. *Mar. Geol.* 335, 114–128. <https://doi.org/10.1016/j.margeo.2012.10.013>
- Austin, W.E.N., Evans, J.R., 2000. NE Atlantic benthic foraminifera: modern distribution patterns and palaeoecological significance. *J. Geol. Soc.* 157, 679–691. <https://doi.org/10.1144/jgs.157.3.679>
- Barmawidjaja, D.M., Jorissen, F.J., Puskaric, S., Zwaan, G.J. van der, 1992. Microhabitat selection by benthic Foraminifera in the northern Adriatic Sea. *J. Foraminif. Res.* 22, 297–317. <https://doi.org/10.2113/gsjfr.22.4.297>
- Berger, W.H., Wefer, G., 1990. Export productivity: seasonality and intermittency, and paleoceanographic implications. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 9, 245–

- 254.
- Beuck, L., Freiwald, A., 2005. Bioerosion patterns in a deep-water *Lophelia pertusa* (Scleractinia) thicket (Propeller Mound, northern Porcupine Seabight), in: Freiwald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems, Erlangen Earth Conference Series. Springer, Berlin, Heidelberg, pp. 915–936. https://doi.org/10.1007/3-540-27673-4_47
- Birchill, A.J., Hartner, N.T., Kunde, K., Siemering, B., Daniels, C., González-Santana, D., Milne, A., Ussher, S.J., Worsfold, P.J., Leopold, K., Painter, S.C., Lohan, M.C., 2019. The eastern extent of seasonal iron limitation in the high latitude North Atlantic Ocean. *Sci. Rep.* 9. <https://doi.org/10.1038/s41598-018-37436-3>
- Boltovskoy, E., Wright, R., 1976. Recent Foraminifera. Dr. W. Junk Publishers, The Hague.
- Bonneau, L., Colin, C., Pons-Branchu, E., Mienis, F., Tisnérat-Laborde, N., Blamart, D., Elliot, M., Collart, T., Frank, N., Foliot, L., Douville, E., 2018. Imprint of Holocene Climate Variability on Cold-Water Coral Reef Growth at the SW Rockall Trough Margin, NE Atlantic. *Geochem. Geophys. Geosystems* 19, 2437–2452. <https://doi.org/10.1029/2018GC007502>
- Brooke, S., Ross, S.W., Bane, J.M., Seim, H.E., Young, C.M., 2013. Temperature tolerance of the deep-sea coral *Lophelia pertusa* from the southeastern United States. *Deep Sea Res. Part II Top. Stud. Oceanogr., Deep-Sea Biodiversity and Life History Processes* 92, 240–248. <https://doi.org/10.1016/j.dsr2.2012.12.001>
- Cattell, R.B., 1966. The Scree Test For The Number Of Factors. *Multivar. Behav. Res.* 1, 245–276. https://doi.org/10.1207/s15327906mbr0102_10
- Caulle, C., Koho, K.A., Mojtahid, M., Reichart, G.J., Jorissen, F.J., 2014. Live foraminiferal faunas (Rose Bengal stained) from the northern Arabian Sea: links with bottom-water oxygenation. *Biogeosciences* 10, 15257–15304. <https://doi.org/10.5194/bgd-10-15257-2013>
- Clark, C.D., Evans, D.J.A., Khatwa, A., Bradwell, T., Jordan, C.J., Marsh, S.H., Mitchell, W.A., Bateman, M.D., 2004. Map and GIS database of glacial landforms and features related to the last British Ice Sheet. *Boreas* 33, 359–375. <https://doi.org/10.1111/j.1502-3885.2004.tb01246.x>
- Colin, C., Tisnérat-Laborde, N., Mienis, F., Collart, T., Pons-Branchu, E., Dubois-Dauphin, Q., Frank, N., Dapoigny, A., Ayache, M., Swingedouw, D., Dutay, J.-C., Eynaud, F., Debret, M., Blamart, D., Douville, E., 2019. Millennial-scale variations of the Holocene North Atlantic mid-depth gyre inferred from radiocarbon and neodymium isotopes in cold water corals. *Quat. Sci. Rev.* 211, 93–106. <https://doi.org/10.1016/j.quascirev.2019.03.011>
- Copard, K., Colin, C., Douville, E., Freiwald, A., Gudmundsson, G., De Mol, B., Frank, N., 2010. Nd isotopes in deep-sea corals in the North-eastern Atlantic. *Quat. Sci. Rev., Special Theme: Case Studies of Neodymium Isotopes in Paleoceanography* 29, 2499–2508. <https://doi.org/10.1016/j.quascirev.2010.05.025>
- Copard, K., Colin, C., Henderson, G.M., Scholten, J., Douville, E., Sicre, M.-A., Frank, N., 2012. Late Holocene intermediate water variability in the northeastern Atlantic as recorded by deep-sea corals. *Earth Planet. Sci. Lett.* 313–314, 34–44. <https://doi.org/10.1016/j.epsl.2011.09.047>
- Culver, S.J., Buzas, M.A., 2003. Biogeography of neritic benthic Foraminifera, in: Sen Gupta, B.K. (Ed.), Modern Foraminifera. Springer Netherlands, Dordrecht, pp. 93–102. https://doi.org/10.1007/0-306-48104-9_6
- Darling, K.F., Schweizer, M., Knudsen, K.L., Evans, K.M., Bird, C., Roberts, A., Filipsson, H.L., Kim, J.-H., Gudmundsson, G., Wade, C.M., Sayer, M.D.J., Austin, W.E.N., 2016. The genetic diversity, phylogeography and morphology of Elphidiidae

- (Foraminifera) in the Northeast Atlantic. *Mar. Micropaleontol.* 129, 1–23.
<https://doi.org/10.1016/j.marmicro.2016.09.001>
- Davies, A.J., Duineveld, G.C.A., Lavaleye, M.S.S., Bergman, M.J.N., Haren, H. van, Roberts, J.M., 2009. Downwelling and deep-water bottom currents as food supply mechanisms to the cold-water coral *Lophelia pertusa* (Scleractinia) at the Mingulay Reef Complex. *Limnol. Oceanogr.* 54, 620–629. <https://doi.org/10.4319/lo.2009.54.2.0620>
- Davies, A.J., Wisshak, M., Orr, J.C., Murray Roberts, J., 2008. Predicting suitable habitat for the cold-water coral *Lophelia pertusa* (Scleractinia). *Deep Sea Res. Part Oceanogr. Res. Pap.* 55, 1048–1062. <https://doi.org/10.1016/j.dsr.2008.04.010>
- de Haas, H., Mienis, F., Frank, N., Richter, T.O., Steinacher, R., de Stigter, H., van der Land, C., van Weering, T.C.E., 2009. Morphology and sedimentology of (clustered) cold-water coral mounds at the south Rockall Trough margins, NE Atlantic Ocean. *Facies* 55, 1–26. <https://doi.org/10.1007/s10347-008-0157-1>
- DeLaca, T.E., Karl, D.M., Lipps, J.H., 1981. Direct use of dissolved organic carbon by agglutinated benthic foraminifera. *Nature* 289, 287–289. <https://doi.org/10.1038/289287a0>
- Dorschel, B., Hebbeln, D., Rüggeberg, A., Dullo, C., 2007. Carbonate budget of a cold-water coral carbonate mound: Propeller Mound, Porcupine Seabight. *Int. J. Earth Sci.* 96, 73–83. <https://doi.org/10.1007/s00531-005-0493-0>
- Dorschel, B., Hebbeln, D., Rüggeberg, A., Dullo, W.-C., Freiwald, A., 2005. Growth and erosion of a cold-water coral covered carbonate mound in the Northeast Atlantic during the Late Pleistocene and Holocene. *Earth Planet. Sci. Lett.* 233, 33–44. <https://doi.org/10.1016/j.epsl.2005.01.035>
- Douarin, M., Elliot, M., Noble, S.R., Moreton, S.G., Long, D., Sinclair, D., Henry, L.-A., Roberts, J.M., 2016. North Atlantic ecosystem sensitivity to Holocene shifts in Meridional Overturning Circulation. *Geophys. Res. Lett.* 43, 291–298. <https://doi.org/10.1002/2015GL065999>
- Douarin, M., Elliot, M., Noble, S.R., Sinclair, D., Henry, L.-A., Long, D., Moreton, S.G., Murray Roberts, J., 2013. Growth of north-east Atlantic cold-water coral reefs and mounds during the Holocene: A high resolution U-series and ¹⁴C chronology. *Earth Planet. Sci. Lett.* 375, 176–187. <https://doi.org/10.1016/j.epsl.2013.05.023>
- Douarin, M., Sinclair, D.J., Elliot, M., Henry, L.-A., Long, D., Mitchison, F., Roberts, J.M., 2014. Changes in fossil assemblage in sediment cores from Mingulay Reef Complex (NE Atlantic): Implications for coral reef build-up. *Deep Sea Res. Part II Top. Stud. Oceanogr., Biology and Geology of Deep-Sea Coral Ecosystems: Proceedings of the Fifth International Symposium on Deep Sea Corals* 99, 286–296. <https://doi.org/10.1016/j.dsr2.2013.07.022>
- Dubois-Dauphin, Q., Colin, C., Elliot, M., Dapoigny, A., Douville, E., 2019. Holocene shifts in sub-surface water circulation of the North-East Atlantic inferred from Nd isotopic composition in cold-water corals. *Mar. Geol.* 410, 135–145. <https://doi.org/10.1016/j.margeo.2019.01.004>
- Duineveld, G.C.A., Lavaleye, M.S.S., Berghuis, E.M., 2004. Particle flux and food supply to a seamount cold-water coral community (Galicia Bank, NW Spain). *Mar. Ecol. Prog. Ser.* 277, 13–23. <https://doi.org/10.3354/meps277013>
- Duineveld, G.C.A., Lavaleye, M.S.S., Bergman, M.J.N., de Stigter, H., Mienis, F., 2007. Trophic structure of a cold-water coral mound community (Rockall Bank, NE Atlantic) in relation to the near-bottom particle supply and current regime. *Bull. Mar. Sci.* 81, 449–467.
- Ellett, D.J., Edwards, A., 1983. Oceanography and inshore hydrography of the Inner Hebrides. *Proc. R. Soc. Edinb. Sect. B Biol. Sci.* 83, 144–160.

- <https://doi.org/10.1017/S0269727000013385>
- Elliot, M., Colin, C., Douarin, M., Pons-Branchu, E., Tisnérat-Laborde, N., Schmidt, F., Michel, E., Dubois-Dauphin, Q., Dapoigny, A., Foliot, L., Miska, S., Thil, F., Long, D., Douville, E., 2019. Onset and demise of coral reefs, relationship with regional ocean circulation on the Wyville Thomson Ridge. *Mar. Geol.* 416, 105969. <https://doi.org/10.1016/j.margeo.2019.105969>
- Fentimen, R., Feenstra, E., Rüggeberg, A., Vennemann, T., Hajdas, I., Adatte, T., Van Rooij, D., Foubert, A., 2020a. Cold-water coral mound archive provides unique insights into intermediate water mass dynamics in the Alboran Sea during the last deglaciation. *Front. Mar. Sci.* 7, 354. <https://doi.org/10.3929/ethz-b-000424338>
- Fentimen, R., Lim, A., Rüggeberg, A., Wheeler, A.J., Van Rooij, D., Foubert, A., 2020b. Impact of bottom water currents on benthic foraminiferal assemblages in a cold-water coral environment: The Moira Mounds (NE Atlantic). *Mar. Micropaleontol.* 154, 101799. <https://doi.org/10.1016/j.marmicro.2019.101799>
- Fentimen, R., Rüggeberg, A., Lim, A., Kateb, A.E., Foubert, A., Wheeler, A.J., Spezzaferri, S., 2018. Benthic foraminifera in a deep-sea high-energy environment: the Moira Mounds (Porcupine Seabight, SW of Ireland). *Swiss J. Geosci.* 111, 561–572. <https://doi.org/10.1007/s00015-018-0317-4>
- Findlay, H.S., Hennige, S.J., Wicks, L.C., Navas, J.M., Woodward, E.M.S., Roberts, J.M., 2014. Fine-scale nutrient and carbonate system dynamics around cold-water coral reefs in the northeast Atlantic. *Sci. Rep.* 4, 1–10. <https://doi.org/10.1038/srep03671>
- Fink, H.G., Wienberg, C., De Pol-Holz, R., Wintersteller, P., Hebbeln, D., 2013. Cold-water coral growth in the Alboran Sea related to high productivity during the Late Pleistocene and Holocene. *Mar. Geol.* 339, 71–82. <https://doi.org/10.1016/j.margeo.2013.04.009>
- Fossile, E., Nardelli, M.P., Jouini, A., Lansard, B., Pusceddu, A., Moccia, D., Michel, E., Péron, O., Howa, H., Mojtahid, M., 2020. Benthic foraminifera as tracers of brine production in the Storfjorden “sea ice factory.” *Biogeosciences* 17, 1933–1953. <https://doi.org/10.5194/bg-17-1933-2020>
- Frank, N., Freiwald, A., Correa, M.L., Wienberg, C., Eisele, M., Hebbeln, D., Rooij, D.V., Henriët, J.-P., Colin, C., Weering, T. van, Haas, H. de, Buhl-Mortensen, P., Roberts, J.M., Mol, B.D., Douville, E., Blamart, D., Hatté, C., 2011. Northeastern Atlantic cold-water coral reefs and climate. *Geology* 39, 743–746. <https://doi.org/10.1130/G31825.1>
- Frederiksen, R., Jensen, A., Westerberg, H., 1992. The distribution of the scleractinian coral *Lophelia pertusa* around the Faroe islands and the relation to internal tidal mixing. *Sarsia* 77, 157–171. <https://doi.org/10.1080/00364827.1992.10413502>
- Freiwald, A., 2002. Reef-Forming Cold-Water Corals, in: Wefer, G., Billett, D., Hebbeln, D., Jørgensen, B.B., Schlüter, M., van Weering, T.C.E. (Eds.), *Ocean Margin Systems*. Springer, Berlin, Heidelberg, pp. 365–385. https://doi.org/10.1007/978-3-662-05127-6_23
- Freiwald, A., Fossa, J.H., Grehan, A., Roberts, T.K. and J.M., 2004. Cold Water Coral Reefs: Out of Sight-No Longer Out of Mind, UNEP-WCMC. Biodiversity Series No 22. UNEP World Conservation Monitoring Centre (UNEP-WCMC).
- Freiwald, A., Hühnerbach, V., Lindberg, B., Wilson, J.B., Campbell, J., 2002. The Sula Reef Complex, Norwegian shelf. *Facies* 47, 179–200. <https://doi.org/10.1007/BF02667712>
- Freiwald, A., Roberts, J.M. (Eds.), 2005. Cold-Water Corals and Ecosystems, Erlangen Earth Conference Series. Springer-Verlag, Berlin Heidelberg. <https://doi.org/10.1007/3-540-27673-4>
- Garcia, J., Mojtahid, M., Howa, H., Michel, E., Schiebel, R., Charbonnier, C., Jorissen, F.J.,

2013. Benthic and planktic foraminifera as indicators of late glacial to Holocene paleoclimatic changes in a marginal environment: An example from the southeastern Bay of Biscay. *Acta Protozool.* 52, 161–180.
- Goldstein, S.T., Corliss, B.H., 1994. Deposit feeding in selected deep-sea and shallow-water benthic foraminifera. *Deep Sea Res. Part Oceanogr. Res. Pap.* 41, 229–241. [https://doi.org/10.1016/0967-0637\(94\)90001-9](https://doi.org/10.1016/0967-0637(94)90001-9)
- Gómez, C.E., Wickes, L., Deegan, D., Etnoyer, P.J., Cordes, E.E., 2018. Growth and feeding of deep-sea coral *Lophelia pertusa* from the California margin under simulated ocean acidification conditions. *PeerJ* 6. <https://doi.org/10.7717/peerj.5671>
- Gooday, A.J., 2003. Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: Environmental influences on faunal characteristics, in: *Advances in 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)
- Gooday, A.J., Hughes, J.A., 2002. Foraminifera associated with phytodetritus deposits at a bathyal site in the northern Rockall Trough (NE Atlantic): seasonal contrasts and a comparison of stained and dead assemblages. *Mar. Micropaleontol.* 46, 83–110. [https://doi.org/10.1016/S0377-8398\(02\)00050-6](https://doi.org/10.1016/S0377-8398(02)00050-6)
- Gooday, A.J., Jorissen, F.J., 2011. Benthic foraminiferal biogeography: controls on global distribution patterns in deep-water settings. *Annu. Rev. Mar. Sci.* 4, 237–262. <https://doi.org/10.1146/annurev-marine-120709-142737>
- Hald, M., Korsun, S., 1997. Distribution of modern benthic foraminifera from fjords of Svalbard, European Arctic. *J. Foraminifer. Res.* 27, 101–122. <https://doi.org/10.2113/gsjfr.27.2.101>
- Hald, M., Steinsund, P.I., 1992. Distribution of surface sediment benthic Foraminifera in the southwestern Barents Sea. *J. Foraminifer. Res.* 22, 347–362. <https://doi.org/10.2113/gsjfr.22.4.347>
- Hammer, O., Harper, D.A.T., Ryan, P.D., 2001. PAST: Paleontological statistics software package for education and data analysis. *Paleontol. Electron.* 4 (1): 1–9.
- Harvey, J., Arhan, M., 1988. The water masses of the central North Atlantic in 1983–84. *J. Phys. Oceanogr.* 18, 1855–1875. [https://doi.org/10.1175/1520-0485\(1988\)018<1855:TWMOTC>2.0.CO;2](https://doi.org/10.1175/1520-0485(1988)018<1855:TWMOTC>2.0.CO;2)
- Hátún, H., Azetsu-Scott, K., Somavilla, R., Rey, F., Johnson, C., Mathis, M., Mikolajewicz, U., Coupel, P., Tremblay, J.-É., Hartman, S., Pacariz, S.V., Salter, I., Ólafsson, J., 2017. The subpolar gyre regulates silicate concentrations in the North Atlantic. *Sci. Rep.* 7, 14576. <https://doi.org/10.1038/s41598-017-14837-4>
- Hátún, H., Sandø, A.B., Drange, H., Hansen, B., Valdimarsson, H., 2005. Influence of the Atlantic subpolar gyre on the thermohaline circulation. *Science* 309, 1841–1844. <https://doi.org/10.1126/science.1114777>
- Hawkes, A.D., Scott, D.B., 2005. Attached benthic Foraminifera as indicators of past and present distribution of the coral *Primnoa resedaeformis* on the Scotian Margin, in: *Freiwald, A., Roberts, J.M. (Eds.), Cold-Water Corals and Ecosystems*, Erlangen Earth Conference Series. Springer, Berlin, Heidelberg, pp. 881–894. https://doi.org/10.1007/3-540-27673-4_45
- Hayek, L.C., Buzas, M.A., 1997. *Surveying natural populations*. Columbia Univ. Press 563p.
- Hebbeln, D., Portilho-Ramos, R. da C., Wienberg, C., Titschack, J., 2019. The Fate of Cold-Water Corals in a Changing World: A Geological Perspective. *Front. Mar. Sci.* 6. <https://doi.org/10.3389/fmars.2019.00119>
- Hebbeln, D., Van Rooij, D., Wienberg, C., 2016. Good neighbours shaped by vigorous currents: Cold-water coral mounds and contourites in the North Atlantic. *Mar. Geol., The contourite log-book: significance for palaeoceanography, ecosystems and slope*

- instability 378, 171–185. <https://doi.org/10.1016/j.margeo.2016.01.014>
- Henry, L.A., Roberts, J.M., 2017. Global biodiversity in cold-water coral reef ecosystems, in: *Marine Animal Forests: The Ecology of Benthic Biodiversity Hotspots*. Springer International Publishing, Cham, pp. 235–256.
- Henry, L.-A., Roberts, J.M., 2007. Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic. *Deep Sea Res. Part Oceanogr. Res. Pap.* 54, 654–672. <https://doi.org/10.1016/j.dsr.2007.01.005>
- Herguera, J.C., 1992. Deep-sea benthic foraminifera and biogenic opal: Glacial to postglacial productivity changes in the western equatorial Pacific. *Mar. Micropaleontol.* 19, 79–98.
- Holliday, N.P., 2003. Air-sea interaction and circulation changes in the northeast Atlantic. *J. Geophys. Res. Oceans* 108. <https://doi.org/10.1029/2002JC001344>
- Holt, J., Wakelin, S., Huthnance, J., 2009. Down-welling circulation of the northwest European continental shelf: A driving mechanism for the continental shelf carbon pump. *Geophys. Res. Lett.* 36. <https://doi.org/10.1029/2009GL038997>
- Husum, K., Hald, M., 2004. A continuous marine record 8000–1600 cal. yr BP from the Malangenfjord, north Norway: foraminiferal and isotopic evidence. *The Holocene* 14, 877–887. <https://doi.org/10.1191/0959683604hl752rp>
- Huthnance, J.M., 1995. Circulation, exchange and water masses at the ocean margin: the role of physical processes at the shelf edge. *Prog. Oceanogr.* 35, 353–431. [https://doi.org/10.1016/0079-6611\(95\)80003-C](https://doi.org/10.1016/0079-6611(95)80003-C)
- Huthnance, J.M., 1986. The Rockall slope current and shelf-edge processes. *Proc. R. Soc. Edinb. Sect. B Biol. Sci.* 88, 83–101. <https://doi.org/10.1017/S0269727000004486>
- Huthnance, J.M., Holt, J.T., Wakelin, S.L., 2009. Deep ocean exchange with west-European shelf seas. *Ocean Sci.* 5, 621–634. <https://doi.org/10.5194/os-5-621-2009>
- Inall, M., Gillibrand, P., Griffiths, C., MacDougall, N., Blackwell, K., 2009. On the oceanographic variability of the North-West European Shelf to the West of Scotland. *J. Mar. Syst., Workshop on Coastal Observatories: Best Practice in the Synthesis of Long-Term Observations and Models* 77, 210–226. <https://doi.org/10.1016/j.jmarsys.2007.12.012>
- Jennings, A.E., Weiner, N.J., Helgadottir, G., Andrews, J.T., 2004. Modern foraminiferal faunas of the southwestern to northern Iceland shelf: oceanographic and environmental control. *J. Foraminifer. Res.* 34, 180–207. <https://doi.org/10.2113/34.3.180>
- Johnson, C., Inall, M., Häkkinen, S., 2013. Declining nutrient concentrations in the northeast Atlantic as a result of a weakening Subpolar Gyre. *Deep Sea Res. Part Oceanogr. Res. Pap.* 82, 95–107. <https://doi.org/10.1016/j.dsr.2013.08.007>
- Johnson, C., Sherwin, T., Smythe-Wright, D., Shimmield, T., Turrell, W., 2010. Wyville Thomson Ridge Overflow Water: Spatial and temporal distribution in the Rockall Trough. *Deep Sea Res. Part Oceanogr. Res. Pap.* 57, 1153–1162. <https://doi.org/10.1016/j.dsr.2010.07.006>
- Kiriakoulakis, K., Freiwald, A., Fisher, E., Wolff, G.A., 2007. Organic matter quality and supply to deep-water coral/mound systems of the NW European Continental Margin. *Int. J. Earth Sci.* 96, 159–170. <https://doi.org/10.1007/s00531-006-0078-6>
- Koho, K.A., García, R., de Stigter, H.C., Epping, E., Koning, E., Kouwenhoven, T.J., van der Zwaan, G.J., 2008. Sedimentary labile organic carbon and pore water redox control on species distribution of benthic foraminifera: A case study from Lisbon–Setúbal Canyon (southern Portugal). *Prog. Oceanogr.* 79, 55–82. <https://doi.org/10.1016/j.pocean.2008.07.004>

- 958 Linke, P., Lutze, G.F., 1993. Microhabitat preferences of benthic foraminifera—a static
959 concept or a dynamic adaptation to optimize food acquisition? *Mar. Micropaleontol.*
960 20, 215–234. [https://doi.org/10.1016/0377-8398\(93\)90034-U](https://doi.org/10.1016/0377-8398(93)90034-U)
- 961 Lo Giudice Cappelli, E., Austin, W.E.N., 2019. Size matters: Analyses of benthic
962 foraminiferal assemblages across differing size fractions. *Front. Mar. Sci.* 6.
963 <https://doi.org/10.3389/fmars.2019.00752>
- 964 Long, D., Roberts, J.M., Gillespie, E.J., 1999. Occurrences of *Lophelia pertusa* on the
965 Atlantic margin (Publication - Report), British Geological Survey. Natural
966 Environment Research Center, Nottingham, UK.
- 967 López Correa, M., Montagna, P., Joseph, N., Rüggeberg, A., Fietzke, J., Flögel, S., Dorschel,
968 B., Goldstein, S.L., Wheeler, A., Freiwald, A., 2012. Preboreal onset of cold-water
969 coral growth beyond the Arctic Circle revealed by coupled radiocarbon and U-series
970 dating and neodymium isotopes. *Quat. Sci. Rev.* 34, 24–43.
971 <https://doi.org/10.1016/j.quascirev.2011.12.005>
- 972 Mackensen, A., Fu tterer, D.K., Grobe, H., Schmiedl, G., 1993. Benthic foraminiferal
973 assemblages from the eastern South Atlantic Polar Front region between 35° and 57°S:
974 Distribution, ecology and fossilization potential. *Mar. Micropaleontol.* 22, 33–69.
975 [https://doi.org/10.1016/0377-8398\(93\)90003-G](https://doi.org/10.1016/0377-8398(93)90003-G)
- 976 Mackensen, A., Hald, M., 1988. *Cassidulina teretis* Tappan and *C. laevigata* d’Orbigny; their
977 modern and late Quaternary distribution in northern seas. *J. Foraminif. Res.* 18, 16–
978 24. <https://doi.org/10.2113/gsjfr.18.1.16>
- 979 Mackensen, A., Sejrup, H.P., Jansen, E., 1985. The distribution of living benthic foraminifera
980 on the continental slope and rise off southwest Norway. *Mar. Micropaleontol.* 9, 275–
981 306.
- 982 Maier, S.R., Bannister, R.J., van Oevelen, D., Kutti, T., 2020. Seasonal controls on the diet,
983 metabolic activity, tissue reserves and growth of the cold-water coral *Lophelia*
984 *pertusa*. *Coral Reefs* 39, 173–187. <https://doi.org/10.1007/s00338-019-01886-6>
- 985 Margreth, S., Gennari, G., R  ggeberg, A., Comas, M.C., Pinheiro, L.M., Spezzaferri, S.,
986 2011. Growth and demise of cold-water coral ecosystems on mud volcanoes in the
987 West Alboran Sea: The messages from the planktonic and benthic foraminifera. *Mar.*
988 *Geol., Special Issue on Cold-water Carbonate Reservoir systems in Deep*
989 *Environments - COCARDE* 282, 26–39. <https://doi.org/10.1016/j.margeo.2011.02.006>
- 990 Margreth, S., R  ggeberg, A., Spezzaferri, S., 2009. Benthic foraminifera as bioindicator for
991 cold-water coral reef ecosystems along the Irish margin. *Deep Sea Res. Part Oceanogr.*
992 *Res. Pap.* 56, 2216–2234. <https://doi.org/10.1016/j.dsr.2009.07.009>
- 993 Marsh, R., Haigh, I.D., Cunningham, S.A., Inall, M.E., Porter, M., Moat, B.I., 2017. Large-
994 scale forcing of the European Slope Current and associated inflows to the North Sea.
995 *Ocean Sci.* 13, 315–335. <https://doi.org/10.5194/os-13-315-2017>
- 996 Masson, D.G., Bett, B.J., Billett, D.S.M., Jacobs, C.L., Wheeler, A.J., Wynn, R.B., 2003. The
997 origin of deep-water, coral-topped mounds in the northern Rockall Trough, Northeast
998 Atlantic. *Mar. Geol.* 194, 159–180. [https://doi.org/10.1016/S0025-3227\(02\)00704-1](https://doi.org/10.1016/S0025-3227(02)00704-1)
- 999 Masson, D.G., Howe, J.A., Stoker, M.S., 2002. Bottom-current sediment waves, sediment
1000 drifts and contourites in the northern Rockall Trough. *Mar. Geol.* 192, 215–237.
1001 [https://doi.org/10.1016/S0025-3227\(02\)00556-X](https://doi.org/10.1016/S0025-3227(02)00556-X)
- 1002 McCartney, M.S., Mauritzen, C., 2001. On the origin of the warm inflow to the Nordic Seas.
1003 *Prog. Oceanogr.* 51, 125–214. [https://doi.org/10.1016/S0079-6611\(01\)00084-2](https://doi.org/10.1016/S0079-6611(01)00084-2)
- 1004 McGrath, T., Nolan, G., McGovern, E., 2012. Chemical characteristics of water masses in the
1005 Rockall Trough. *Deep Sea Res. Part Oceanogr. Res. Pap.* 61, 57–73.
1006 <https://doi.org/10.1016/j.dsr.2011.11.007>
- 1007 Mienis, F., Bouma, T.J., Witbaard, R., Oevelen, D. van, Duineveld, G.C.A., 2019.

- Experimental assessment of the effects of coldwater coral patches on water flow. *Mar. Ecol. Prog. Ser.* 609, 101–117. <https://doi.org/10.3354/meps12815>
- Mienis, F., de Stigter, H.C., White, M., Duineveld, G., de Haas, H., van Weering, T.C.E., 2007. Hydrodynamic controls on cold-water coral growth and carbonate-mound development at the SW and SE Rockall Trough Margin, NE Atlantic Ocean. *Deep Sea Res. Part Oceanogr. Res. Pap.* 54, 1655–1674. <https://doi.org/10.1016/j.dsr.2007.05.013>
- Mojtahid, M., Griveaud, C., Fontanier, C., Anschutz, P., Jorissen, F.J., 2010. Live benthic foraminiferal faunas along a bathymetrical transect (140–4800 m) in the Bay of Biscay (NE Atlantic). *Rev. Micropaléontologie* 53, 139–162. <https://doi.org/10.1016/j.revmic.2010.01.002>
- Mojtahid, M., Zubkov, M.V., Hartmann, M., Gooday, A.J., 2011. Grazing of intertidal benthic foraminifera on bacteria: Assessment using pulse-chase radiotracing. *J. Exp. Mar. Biol. Ecol.* 399, 25–34. <https://doi.org/10.1016/j.jembe.2011.01.011>
- Montero-Serrano, J.-C., Frank, N., Colin, C., Wienberg, C., Eisele, M., 2011. The climate influence on the mid-depth Northeast Atlantic gyres viewed by cold-water corals. *Geophys. Res. Lett.* 38. <https://doi.org/10.1029/2011GL048733>
- Moore, C.M., Mills, M.M., Arrigo, K.R., Berman-Frank, I., Bopp, L., Boyd, P.W., Galbraith, E.D., Geider, R.J., Guieu, C., Jaccard, S.L., Jickells, T.D., La Roche, J., Lenton, T.M., Mahowald, N.M., Marañón, E., Marinov, I., Moore, J.K., Nakatsuka, T., Oschlies, A., Saito, M.A., Thingstad, T.F., Tsuda, A., Ulloa, O., 2013. Processes and patterns of oceanic nutrient limitation. *Nat. Geosci.* 6, 701–710. <https://doi.org/10.1038/ngeo1765>
- Morigi, C., Sabbatini, A., Vitale, G., Pancotti, I., Gooday, A.J., Duineveld, G.C.A., De Stigter, H.C., Danovaro, R., Negri, A., 2012. Foraminiferal biodiversity associated with cold-water coral carbonate mounds and open slope of SE Rockall Bank (Irish continental margin—NE Atlantic). *Deep Sea Res. Part Oceanogr. Res. Pap.* 59, 54–71. <https://doi.org/10.1016/j.dsr.2011.10.004>
- Mueller, C.E., Larsson, A.I., Veuger, B., Middelburg, J.J., van Oevelen, D., 2014. Opportunistic feeding on various organic food sources by the cold-water coral *Lophelia pertusa*. *Biogeosciences* 11, 123–133. <https://doi.org/10.5194/bg-11-123-2014>
- Murray, J.W., 2006. *Ecology And Applications of Benthic Foraminifera*. Cambridge University Press.
- Murray, J.W., 2003. An illustrated guide to the benthic foraminifera of the Hebridean shelf, west of Scotland, with notes on their mode of life. *Palaeontol. Electron.* 5, art.1-[31pp].
- Murray, J.W., 1973. *Distribution and ecology of living Benthic foraminiferids*, Crane, Russak&Co. Inc. ed. New York.
- Naumann, M.S., Orejas, C., Wild, C., Ferrier-Pagès, C., 2011. First evidence for zooplankton feeding sustaining key physiological processes in a scleractinian cold-water coral. *J. Exp. Biol.* 214, 3570–3576. <https://doi.org/10.1242/jeb.061390>
- New, A.L., Barnard, S., Herrmann, P., Molines, J.-M., 2001. On the origin and pathway of the saline inflow to the Nordic Seas: insights from models. *Prog. Oceanogr., Dynamics of the North Atlantic Circulation: Simulation and Assimilation with High-Resolution Models (DYNAMO)* 48, 255–287. [https://doi.org/10.1016/S0079-6611\(01\)00007-6](https://doi.org/10.1016/S0079-6611(01)00007-6)
- New, A.L., Smythe-Wright, D., 2001. Aspects of the circulation in the Rockall Trough. *Cont. Shelf Res., The Marine Environment of the North East Atlantic Margin* 21, 777–810. [https://doi.org/10.1016/S0278-4343\(00\)00113-8](https://doi.org/10.1016/S0278-4343(00)00113-8)
- Nomaki, H., Heinz, P., Nakatsuka, T., Shimanaga, M., Ohkouchi, N., Ogawa, N.O., Kogure, K., Ikemoto, E., Kitazato, H., 2006. Different ingestion patterns of ¹³C-labeled

bacteria and algae by deep-sea benthic foraminifera. Mar. Ecol. Prog. Ser. 310, 95–108. <https://doi.org/10.3354/meps310095>

Østby, K.L., Nagy, J., 1982. Foraminiferal distribution in the western Barents Sea, Recent and Quaternary. Polar Res. 1982, 53–87. <https://doi.org/10.1111/j.1751-8369.1982.tb00472.x>

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

Pingree, R.D., Holligan, P.M., Mardell, G.T., 1978. The effects of vertical stability on phytoplankton distributions in the summer on the northwest European Shelf. Deep Sea Res. 25, 1011–1028. [https://doi.org/10.1016/0146-6291\(78\)90584-2](https://doi.org/10.1016/0146-6291(78)90584-2)

Pirlet, H., Colin, C., Thierens, M., Latruwe, K., Van Rooij, D., Foubert, A., Frank, N., Blamart, D., Huvenne, V.A.I., Swennen, R., Vanhaecke, F., Henriët, J.-P., 2011. The importance of the terrigenous fraction within a cold-water coral mound: A case study. Mar. Geol., Special Issue on Cold-water CARbonate Reservoir systems in Deep Environments - COCARDE 282, 13–25. <https://doi.org/10.1016/j.margeo.2010.05.008>

Pirlet, H., Wehrmann, L.M., Brunner, B., Frank, N., Dewanckele, J., Rooij, D.V., Foubert, A., Swennen, R., Naudts, L., Boone, M., Cnudde, V., Henriët, J.-P., 2010. Diagenetic formation of gypsum and dolomite in a cold-water coral mound in the Porcupine Seabight, off Ireland. Sedimentology 57, 786–805. <https://doi.org/10.1111/j.1365-3091.2009.01119.x>

Pollard, R.T., Read, J.F., Holliday, N.P., Leach, H., 2004. Water masses and circulation pathways through the Iceland Basin during Vivaldi 1996. J. Geophys. Res. Oceans 109. <https://doi.org/10.1029/2003JC002067>

Polyak, L., Levitan, M., Khusid, T., Merklin, L., Mukhina, V., 2002. Variations in the influence of riverine discharge on the Kara Sea during the last deglaciation and the Holocene. Glob. Planet. Change, Glaciation and reorganisation of Asia's network of drainage 32, 291–309. [https://doi.org/10.1016/S0921-8181\(02\)00072-3](https://doi.org/10.1016/S0921-8181(02)00072-3)

Raddatz, J., Liebetrau, V., Trotter, J., Rüggeberg, A., Flögel, S., Dullo, W.-C., Eisenhauer, A., Voigt, S., McCulloch, M., 2016. Environmental constraints on Holocene cold-water coral reef growth off Norway: Insights from a multiproxy approach. Paleoceanography 31, 1350–1367. <https://doi.org/10.1002/2016PA002974>

Roberts, J.M., Long, D., Wilson, J.B., Mortensen, P.B., Gage, J.D., 2003. The cold-water coral *Lophelia pertusa* (Scleractinia) and enigmatic seabed mounds along the north-east Atlantic margin: are they related? Mar. Pollut. Bull. 46, 7–20. [https://doi.org/10.1016/S0025-326X\(02\)00259-X](https://doi.org/10.1016/S0025-326X(02)00259-X)

Roberts, J.M., Wheeler, A., Freiwald, A., Cairns, S.D., 2009. Cold-Water Corals: The Biology and Geology of Deep-Sea Coral Habitats, Cambridge University Press. ed.

Roberts, J.M., Wheeler, A.J., Freiwald, A., 2006. Reefs of the deep: the biology and geology of cold-water coral ecosystems. Science 312, 543–547. <https://doi.org/10.1126/science.1119861>

Rüggeberg, A., Dullo, C., Dorschel, B., Hebbeln, D., 2007. Environmental changes and growth history of a cold-water carbonate mound (Propeller Mound, Porcupine Seabight). Int. J. Earth Sci. 96, 57–72. <https://doi.org/10.1007/s00531-005-0504-1>

Savidge, G., Lennon, H.J., 1987. Hydrography and phytoplankton distributions in north-west Scottish waters. Cont. Shelf Res. 7, 45–66. [https://doi.org/10.1016/0278-4343\(87\)90063-X](https://doi.org/10.1016/0278-4343(87)90063-X)

Schmiedl, G., Mackensen, A., Müller, P.J., 1997. Recent benthic foraminifera from the eastern South Atlantic Ocean: Dependence on food supply and water masses. Mar.

1108 Micropaleontol. 32, 249–287.

1109 Schnitker, D., 1974. West Atlantic abyssal circulation during the past 120,000 years. *Nature*

1110 248, 385–387. <https://doi.org/10.1038/248385a0>

1111 Schönfeld, J., 2002a. A new benthic foraminiferal proxy for near-bottom current velocities in

1112 the Gulf of Cadiz, northeastern Atlantic Ocean. *Deep Sea Res. Part Oceanogr. Res.*

1113 Pap. 49, 1853–1875. [https://doi.org/10.1016/S0967-0637\(02\)00088-2](https://doi.org/10.1016/S0967-0637(02)00088-2)

1114 Schönfeld, J., 2002b. Recent benthic foraminiferal assemblages in deep high-energy

1115 environments from the Gulf of Cadiz (Spain). *Mar. Micropaleontol.* 44, 141–162.

1116 [https://doi.org/10.1016/S0377-8398\(01\)00039-1](https://doi.org/10.1016/S0377-8398(01)00039-1)

1117 Schönfeld, J., 1997. The impact of the Mediterranean Outflow Water (MOW) on benthic

1118 foraminiferal assemblages and surface sediments at the southern Portuguese

1119 continental margin. *Mar. Micropaleontol.* 29, 211–236. [https://doi.org/10.1016/S0377-](https://doi.org/10.1016/S0377-8398(96)00050-3)

1120 [8398\(96\)00050-3](https://doi.org/10.1016/S0377-8398(96)00050-3)

1121 Schönfeld, J., Dullo, W.-C., Pfannkuche, O., Freiwald, A., Rüggeberg, A., Schmidt, S.,

1122 Weston, J., 2011. Recent benthic foraminiferal assemblages from cold-water coral

1123 mounds in the Porcupine Seabight. *Facies* 57, 187–213.

1124 <https://doi.org/10.1007/s10347-010-0234-0>

1125 Schweizer, M., Pawlowski, J., Duijnste, I.A.P., Kouwenhoven, T.J., van der Zwaan, G.J.,

1126 2005. Molecular phylogeny of the foraminiferal genus *Uvigerina* based on ribosomal

1127 DNA sequences. *Mar. Micropaleontol.* 57, 51–67.

1128 <https://doi.org/10.1016/j.marmicro.2005.07.001>

1129 Schweizer, M., Pawlowski, J., Kouwenhoven, T.J., Guiard, J., van der Zwaan, B., 2008.

1130 Molecular phylogeny of Rotaliida (Foraminifera) based on complete small subunit

1131 rDNA sequences. *Mar. Micropaleontol.* 66, 233–246.

1132 <https://doi.org/10.1016/j.marmicro.2007.10.003>

1133 Shannon, C.E., 1948. A mathematical theory of communication. *Bell Syst. Tech. J.* 27, 379–

1134 423, 623–656.

1135 Sherwin, T.J., 1991. Evidence of a deep internal tide in the Faeroe-Shetland channel, in: *Tidal*

1136 *Hydrodynamics*. John Wiley, New York, pp. 469–488.

1137 Sherwin, T.J., Read, J.F., Holliday, N.P., Johnson, C., 2012. The impact of changes in North

1138 Atlantic Gyre distribution on water mass characteristics in the Rockall Trough. *ICES*

1139 *J. Mar. Sci.* 69, 751–757. <https://doi.org/10.1093/icesjms/fsr185>

1140 Simpson, J.H., McCandliss, R.R., 2013. “The Ekman Drain”: a conduit to the deep ocean for

1141 shelf material. *Ocean Dyn.* 63, 1063–1072. [https://doi.org/10.1007/s10236-013-0644-](https://doi.org/10.1007/s10236-013-0644-y)

1142 [y](https://doi.org/10.1007/s10236-013-0644-y)

1143 Smeulders, G.G.B., Koho, K.A., de Stigter, H.C., Mienis, F., de Haas, H., van Weering,

1144 T.C.E., 2014. Cold-water coral habitats of Rockall and Porcupine Bank, NE Atlantic

1145 Ocean: Sedimentary facies and benthic foraminiferal assemblages. *Deep Sea Res. Part*

1146 *II Top. Stud. Oceanogr., Biology and Geology of Deep-Sea Coral Ecosystems:*

1147 *Proceedings of the Fifth International Symposium on Deep Sea Corals* 99, 270–285.

1148 <https://doi.org/10.1016/j.dsr2.2013.10.001>

1149 Soetaert, K., Mohn, C., Rengstorf, A., Grehan, A., van Oevelen, D., 2016. Ecosystem

1150 engineering creates a direct nutritional link between 600-m deep cold-water coral

1151 mounds and surface productivity. *Sci. Rep.* 6, 35057.

1152 <https://doi.org/10.1038/srep35057>

1153 Spezzaferri, S., Rüggeberg, A., Stalder, C., Margreth, S., 2015. Benthic foraminiferal

1154 assemblages from cold-water coral ecosystems, in: *Atlas of Benthic Foraminifera from*

1155 *Cold-Water Coral Reefs - Special Publication*, Cushman Foundation Special

1156 *Publication*, 44. pp. 20–48.

1157 Spezzaferri, S., Rüggeberg, A., Stalder, C., Margreth, S., 2013. Benthic foraminifer

- assemblages from Norwegian cold-water coral reefs. *J. Foraminifer. Res.* 43, 21–39.
<https://doi.org/10.2113/gsjfr.43.1.21>
- Staines-Uriás, F., Kuijpers, A., Korte, C., 2013. Evolution of subpolar North Atlantic surface circulation since the early Holocene inferred from planktic foraminifera faunal and stable isotope records. *Quat. Sci. Rev.* 76, 66–81.
<https://doi.org/10.1016/j.quascirev.2013.06.016>
- Stalder, C., El Kateb, A., Vertino, A., Rüggeberg, A., Camozzi, O., Pirkenseer, C.M., Spangenberg, J.E., Hajdas, I., Van Rooij, D., Spezzaferri, S., 2018. Large-scale paleoceanographic variations in the western Mediterranean Sea during the last 34,000 years: From enhanced cold-water coral growth to declining mounds. *Mar. Micropaleontol.* 143, 46–62. <https://doi.org/10.1016/j.marmicro.2018.07.007>
- Stalder, C., Spezzaferri, S., Rüggeberg, A., Pirkenseer, C., Gennari, G., 2014. Late Weichselian deglaciation and early Holocene development of a cold-water coral reef along the Lophavet shelf (Northern Norway) recorded by benthic foraminifera and ostracoda. *Deep Sea Res. Part II Top. Stud. Oceanogr., Biology and Geology of Deep-Sea Coral Ecosystems: Proceedings of the Fifth International Symposium on Deep Sea Corals* 99, 249–269. <https://doi.org/10.1016/j.dsr2.2013.07.009>
- Stewart, H.A., Davies, J.S., 2007. Habitat investigations within the SEA7 and SEA4 areas of the UK continental shelf (Hatton Bank, Rosemary Bank, Wyville Thomson Ridge and Faroe–Shetland Channel) (Publication - Report), British Geological Survey. British Geological Survey.
- Thierens, M., Browning, E., Pirlet, H., Loutre, M.-F., Dorschel, B., Huvenne, V.A.I., Titschack, J., Colin, C., Foubert, A., Wheeler, A.J., 2013. Cold-water coral carbonate mounds as unique palaeo-archives: the Plio-Pleistocene Challenger Mound record (NE Atlantic). *Quat. Sci. Rev.* 73, 14–30. <https://doi.org/10.1016/j.quascirev.2013.05.006>
- Thierens, M., Pirlet, H., Colin, C., Latruwe, K., Vanhaecke, F., Lee, J.R., Stuut, J.-B., Titschack, J., Huvenne, V.A.I., Dorschel, B., Wheeler, A.J., Henriët, J.-P., 2012. Ice-rafting from the British–Irish ice sheet since the earliest Pleistocene (2.6 million years ago): implications for long-term mid-latitudinal ice-sheet growth in the North Atlantic region. *Quat. Sci. Rev., Quaternary Glaciation History of Northern Europe* 44, 229–240. <https://doi.org/10.1016/j.quascirev.2010.12.020>
- Victorero, L., Blamart, D., Pons-Branchu, E., Mavrogordato, M.N., Huvenne, V.A.I., 2016. Reconstruction of the formation history of the Darwin Mounds, N Rockall Trough: How the dynamics of a sandy contourite affected cold-water coral growth. *Mar. Geol., The contourite log-book: significance for palaeoceanography, ecosystems and slope instability* 378, 186–195. <https://doi.org/10.1016/j.margeo.2015.12.001>
- Waelbroeck, C., Duplessy, J.C., Michel, E., Labeyrie, L., Paillard, D., Duprat, J., 2001. The timing of the last deglaciation in North Atlantic climate records. *Nature* 412, 724–727. <https://doi.org/10.1038/35089060>
- Weinkauf, M.F.G., Milker, Y., 2018. The Effect of Size Fraction in Analyses of Benthic Foraminiferal Assemblages: A Case Study Comparing Assemblages From the >125 and >150 μm Size Fractions. *Front. Earth Sci.* 6. <https://doi.org/10.3389/feart.2018.00037>
- White, M., 2007. Benthic dynamics at the carbonate mound regions of the Porcupine Sea Bight continental margin. *Int. J. Earth Sci.* 96, 1. <https://doi.org/10.1007/s00531-006-0099-1>
- Wienberg, C., Frank, N., Mertens, K.N., Stuut, J.-B., Marchant, M., Fietzke, J., Mienis, F., Hebbeln, D., 2010. Glacial cold-water coral growth in the Gulf of Cádiz: Implications of increased palaeo-productivity. *Earth Planet. Sci. Lett.* 298, 405–416. <https://doi.org/10.1016/j.epsl.2010.08.017>

1208 Wienberg, C., Titschack, J., 2017. Framework-Forming Scleractinian Cold-Water Corals
 1209 Through Space and Time: A Late Quaternary North Atlantic Perspective, in: Rossi, S.,
 1210 Bramanti, L., Gori, A., Orejas, C. (Eds.), Marine Animal Forests: The Ecology of
 1211 Benthic Biodiversity Hotspots. Springer International Publishing, Cham, pp. 699–732.
 1212 https://doi.org/10.1007/978-3-319-21012-4_16
 1213 Wyville Thomson, C., 1874. The depths of the sea; an account of the general results of the
 1214 dredging cruises of H.M. SS. “Porcupine” and “Lightning” during the summers of
 1215 1868, 1869 and 1870, under the scientific direction of Dr. Carpenter, J. Gwyn Jeffreys,
 1216 and Dr. Wyville Thomson., 2d. ed. ed. Macmillan and co., London.
 1217
 1218

5. Figures captions

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

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

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

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

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

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

6. Plate captions

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 praeegeri* (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.