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Impact of bottom water currents on benthic foraminiferal assemblages in a cold-water coral environment: The Moira Mounds (NE Atlantic)

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ABSTRACT

Strong bottom currents play a key role in cold-water coral environments by shaping their morphology and providing the necessary food for the corals to thrive. This study investigates the differences between living and dead benthic foraminiferal assemblages in such environments, more precisely on the Moira Mounds (NE Atlantic). A specific focus is to understand the role of currents and their influence on the taphonomy of benthic foraminiferal assemblages. Here, we analyze high-resolution sediment grain size distributions coupled with benthic foraminiferal assemblage composition to assess how much deep-sea bottom currents affect benthic foraminiferal assemblages. We suggest that the dead benthic foraminiferal assemblage consists of a reworked glacial fauna associated with contemporary species. Reworked glacial species (*Elphidium excavatum*, *Sigmoilopsis schlumbergeri*) are the most abundant. Dominant species that are present almost exclusively in the living assemblage (*Alabaminella weddellensis*, *Nonionella iridea*, *Trifarina* spp.) are associated with high phytodetritus input, possibly as a response to the later phase of the North-east Atlantic spring bloom. Dead assemblages are further characterized by the scarcity of organic-walled agglutinated foraminifera in comparison to living assemblages. Sediment grain size distributions show that the downslope Moira Mounds consist of well-sorted fine sand, typical of contourite deposits in the area. Grain size distributions and the average Shannon diversity of living and dead foraminiferal assemblages indicate that the coral cover offers a sheltered environment, baffling eroded sediment and preventing post-mortem transport of dead foraminifera. We conclude that cold-water coral environments provide a valuable paleoenvironmental archive by trapping sediment in an otherwise non-depositional system.

1. Introduction

Cold-water coral (CWC) environments occur worldwide and are biologically diverse (Freiwald et al., 2004; Roberts et al., 2009; Freiwald, 2017). Strong bottom water currents play a key role in providing suspension feeding CWCs with the necessary food to thrive whilst limiting sediment smothering (Duineveld et al., 2004; Freiwald et al., 2004; White, 2007; Mienis et al., 2009a; Hebbeln et al., 2016). The coral framework is capable of baffling particles and of modifying local hydrodynamics (Mienis et al., 2009a; Foubert et al., 2011). This can over time lead to the build-up of CWC mounds reaching over 300 m high (De Mol et al., 2002; Dorschel et al., 2005; Mienis et al., 2009b). Among the number of organisms inhabiting CWC environments,

benthic foraminifera are a main faunal component in terms of abundance, as in most marine environments (Gooday, 2003). These protists are useful in understanding present and past environments (Gooday, 2003; Jorissen et al., 2007). Indeed, they are highly diverse, possess a good fossilization potential and respond rapidly to changing environmental conditions (Murray, 2006; Jorissen et al., 2007). Despite this, benthic foraminifera can be strongly affected by taphonomic processes (Jorissen and Whittling, 1999; Murray, 2006). A number of these have been proposed to explain differences between living foraminiferal (biocoensis) assemblages (LAs) and dead foraminiferal (thanatocoensis) assemblages (DAs) at the sediment surface (Murray, 2006 and references therein). Life processes, such as species-specific reproduction rates and seasonality, explain in part these disparities (Murray, 2006;

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Martins et al., 2018). Post-mortem processes, such as test transport, physical breakage, dissolution, bioerosion and bioturbation also have an important impact. Post-mortem transport of foraminifera is governed by current regimes, and is also influenced by the size and shape of foraminiferal tests (Kontrovitz et al., 1978; Snyder et al., 1990; Murray, 2006; Duros et al., 2012). Foraminiferal tests are known in places to accumulate in deep sea dunes and to form the main component of these sedimentary structures (Lonsdale and Malfait, 1974; Rebesco et al., 2014). The living strategy of foraminifera also plays a role, for example epibenthic foraminifera, living at the sediment-water interface, are particularly prone to transport (Jorissen and Whittling, 1999; Murray, 2006). In areas dominated by strong current regimes, such as estuaries or coastal lagoon mouths, differences between DAs and LAs are known to be considerable (Alve and Murray, 1995; Martins et al., 2018). Therefore, this study documents, for the first time, the differences between LAs and DAs and the impact of current dynamics on foraminiferal distributions in a CWC environment. We also address how disparities between LAs and DAs can provide insights on the sedimentary processes governing the Moira Mounds.

2. Study area

The Belgica Mound Province (BMP) is a CWC province (De Mol et al., 2002) located on the eastern margin of the Porcupine Seabight (PS). In this area, the dominant water mass between approximately 600 and 1100 m water depth is the highly saline Mediterranean Outflow Water (MOW). The MOW forms a contour current following a cyclonic pattern around the PS (Rice et al., 1991; Dorschel et al., 2007). Above the MOW flows the less saline Eastern North Atlantic Water (ENAW) (Rice et al., 1991; White et al., 2005). The PS is a north-south trending embayment on the Irish continental margin (De Mol et al., 2002; Shannon et al., 2007; Wheeler et al., 2007; Huvenne et al., 2009a). It is 45 km long and 10 km wide and hosts active or buried CWC mounds from 550 to 1030 m water depth (De Mol et al., 2002; Foubert et al., 2005; Wheeler et al., 2005). Mound size varies from small-sized structures, such as the Moira Mounds (MM; Fig. 1) (Foubert et al., 2011; Wheeler et al., 2011a; Lim et al., 2018) to giant counterparts, e.g., Challenger, Therese or Galway Mound, that reach approximately 150 m in height (De Mol et al., 2007; Kano et al., 2007; Thierens et al., 2010; Ferdelman et al., 2005; Dorschel et al., 2007; Foubert and Henriot, 2009). The MM have diameters of 20 to 50 m, heights of up to 11 m, slope gradients ranging between 15 and 20°, and ovoid shapes with their long-axis oriented parallel to the dominant north-south flowing current (Wheeler et al., 2005; Wheeler et al., 2011a). In addition, with approx. 23 mounds per km², they possess the highest CWC mound density ever documented (Lim et al., 2018). Wheeler et al. (2011a) proposed that the MM, through coalescing, may lead to the formation of giant mounds. Thus, the MM may represent the start-up phase for the formation of larger mounds (Wheeler et al., 2011a). Based on their geographic distribution, the MM are divided into 4 distinct areas: upslope, downslope, mid-slope and northern area (Wheeler et al., 2011a). Foubert et al. (2011) suggested that the mid-slope MM represent an example of mounds shaped by “sediment stressed” conditions, whilst mounds in the upslope and northern areas are considered dormant (Wheeler et al., 2011a). This study focuses on the most active downslope MM area (dMM) which hosts 143 small mounds situated between 900 and 1150 m water depth (Wheeler et al., 2011a; Fig. 1).

3. Current velocities recorded on Northeast Atlantic cold-water coral mounds

Mean measured bottom current velocities vary from approximately 6 to 16 cm s⁻¹ in the BMP (Dorschel et al., 2007; White et al., 2007), and between 5 and 17 cm s⁻¹ at the Southwest Rockall Trough margin (Mienis et al., 2009a). Within the vicinity of mounds, currents would be generally higher than 15 cm s⁻¹ for about 10% of the time at the BMP

(White et al., 2007) and for over 30% of the time at the Southwest Rockall Trough margin (Mienis et al., 2009a). Peak velocities reach up to 70 cm s⁻¹ at the summit of the Galway Mound in the BMP (Dorschel et al., 2007) and 51 cm s⁻¹ at the summit of Propeller Mound in the nearby Hovland mound province (Roberts et al., 2005). In other areas, peak velocities reach up to 35 cm s⁻¹ at the Darwin Mounds (Northern Rockall Trough) (Huvenne et al., 2009a) and 30 cm s⁻¹ at the Galicia Bank (Northwest Spain) (Duineveld et al., 2004) and Rockall Bank mounds (Duineveld et al., 2007). At the dMM, Lim et al. (2018) calculated an average current velocity of 35–40 cm s⁻¹. Agreeing with these current speed calculations, the seabed at the dMM develops typical current-induced sedimentary features, such as sediment waves, ripple marks and dunes (Fig. 2). Large scour pits, situated predominantly around the south-facing side of the mounds, may suggest the existence of low-frequency higher magnitude current events, such as dense water cascade events common on the Irish margin (Lim et al., 2018).

4. Material and methods

4.1. Sample collection and classification

Thirty-one box core samples collected during Eurofleets Cruise CWC-Moira (Spezzaferri and Vertino, 2012) on board RV Belgica between the 2nd and the 7th of June 2012 (Fig. 1; Table 1) are used in this study. The NIOZ-type box corer was equipped with a Global Acoustic Positioning System (GAPS) USBL (Ultra Short Baseline) for accurate seafloor positioning. Only surface sediment samples (top 1 cm) were analyzed. Samples were taken separately for grain size (ca. 10 cm³) and micropalaeontological (ca. 50 cm³) analysis. Samples were classified according to box core sediment surface characteristics. Previously defined bio-sedimentary facies were deemed unsuitable for the aim of this research (e.g. Spezzaferri and Vertino, 2012; Vertino et al., 2014; Fentimen et al., 2018). Here, we utilize a bio-sedimentary facies classification that differentiates between the facies' ability to alter the hydrodynamic or sedimentological regime. As such, all samples can be divided into presence or absence of coral framework (the main sediment bafflers) (Table 1). This classification follows a simplified approach and does not aim to encompass the extreme heterogeneity of CWC habitats.

4.2. Grain size analysis

All samples were measured for grain size of both bulk material and the siliciclastic fraction using the Malvern Mastersizer 3000 at the department of Geology of Ghent University. Before undertaking any measurement, large clasts (> 1 cm) such as coral fragments or dropstones were removed and samples were placed in 35% H₂O₂ to remove organic matter. In addition to this step, samples analyzed for the siliciclastic fraction were boiled in 10% HCl for 2 min to dissolve CaCO₃. Prior to measurement, samples were placed in 2% sodium hexa-aetaphosphate and boiled to assure complete disaggregation. Any particle larger than 2 mm was sieved off before measurement. Ultrasonification was not used in order to avoid breakage of foraminiferal tests whilst measuring bulk material. Each sample was measured three times and then averaged. Mean grain size, sorting, skewness and kurtosis were calculated using the Folk and Ward method (Folk and Ward, 1957) with the rysgran package for R (Gilbert et al., 2015; R Core Team, 2018).

4.3. Benthic foraminiferal assemblages

Twenty box core samples from the thirty-one analyzed for particle size analysis were also investigated for living and dead benthic foraminiferal assemblages (Fig. 1, Table 1). Samples for micropalaeontological analysis were collected and processed following the

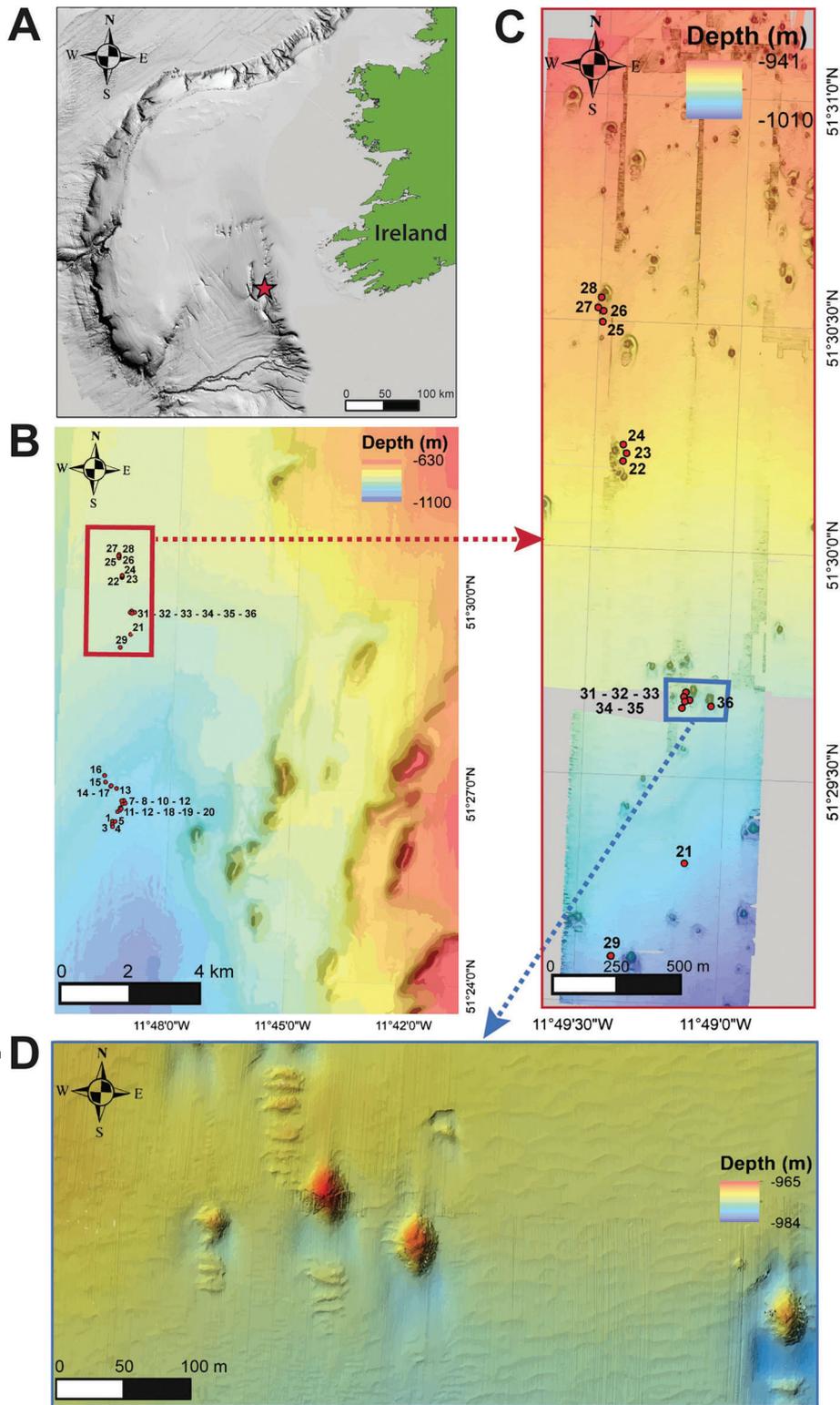


Fig. 1. A) General location of the Moira Mounds (red star) within the Porcupine Seabight off the coast of Ireland and the Propeller Mound in the Hovland mound province; B) Location of the investigated samples within the downslope Moira Mound area; C) Close-up of the northern sample sites (red box) showing the density of mound cover at the seafloor; D) Close-up of the Piddington Mound area (blue box) illustrating typical current induced sedimentary features (scours at the front of the mounds and sediment ripples off-mound). Map A is based on the GEBCO_2019 gridded bathymetric data. Maps B, C and D were acquired through Multibeam Bathymetry (MBES) during the QuERCi 1 cruise in 2015 (Wheeler et al., 2015) on board the RV Celtic Explorer. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

FOBIMO protocol (Schönfeld et al., 2012). Similar to the particle-size analyses, only surface sediment samples (top 1 cm) were analyzed. In order to distinguish between living and dead benthic foraminifera, all samples were placed in a Rose Bengal Ethanol solution for one month (2 g of Rose Bengal for 1 l of 90% ethanol) (Walton, 1952; Schönfeld et al., 2012). After determining the total sample volume, they were washed through 250, 125 and 63 μm mesh sieves, dried and weighed. Residues were dry picked for stained (living) and unstained (dead)

benthic foraminifera. Foraminifera were considered as living when all chambers except the last one were stained. At least 300 dead individuals and all living foraminifera were picked per fraction. Large clasts (e.g. coral fragments, dropstones) were investigated at the Stereo Microscope to document attached living foraminifera. In order to compare datasets, dead benthic foraminiferal assemblages were converted to percentages whilst living benthic foraminiferal assemblages were standardized for 50 cm^3 of sediment and then also converted to

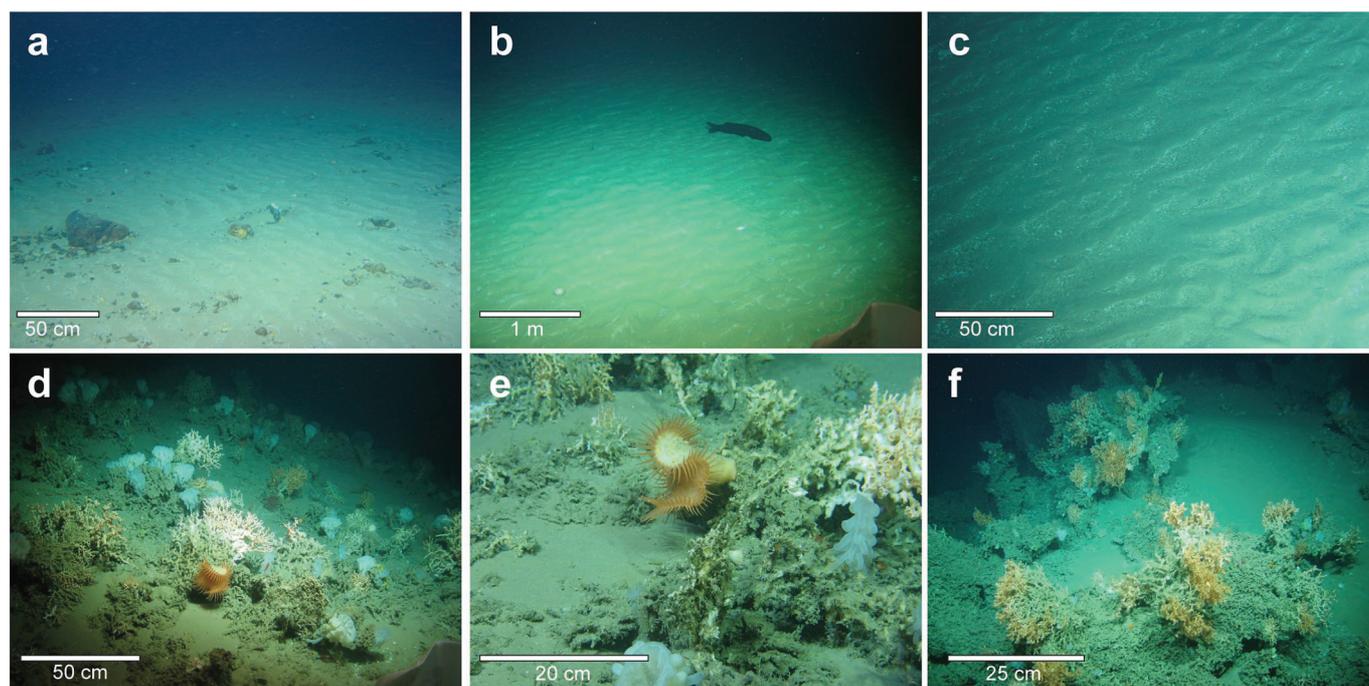


Fig. 2. Examples of facies variability and current induced sedimentary features at the downslope Moira Mound area. a) Rippled sand and dropstones, b) Rippled sand, c) Close-up of rippled sandy sediment, d) Side of a mound colonized by the cold-water coral *Lophelia pertusa*, sponges and sea-anemones, e) Close-up of living and dead coral cover. Notice the sediment accumulating within the dead coral framework and the absence of ripples in between coral cover, f) Dead and living coral cover at a downslope Moira Mound illustrating the patchiness of coral distribution. Images were acquired using the Remotely Operated Vehicle Holland 1 (ROV) on board the RV Celtic Explorer during cruises VENTuRE (Wheeler et al., 2011b) and QuERCi 1 (Wheeler et al., 2015).

Table 1

Number, coordinates, water depths and presence/absence of coral cover of surface samples investigated in this study. Bold font indicates the twenty samples considered for micropaleontological analysis.

| Sample | Latitude (N) | Longitude (E) | Water depth (m) | Coral cover |
|-------------|-------------------|-------------------|-----------------|-------------|
| BC1 | 51°26,433' | 11°49,512' | 1057 | Absence |
| BC3 | 51°26,315' | 11°49,384' | 1065 | Presence |
| BC4 | 51°26,304' | 11°49,385' | 1062 | Presence |
| BC5 | 51°26,331' | 11°49,402' | 1069 | Presence |
| BC7 | 51°29,715' | 11°49,202' | 969 | Absence |
| BC8 | 51°29,686' | 11°48,098' | 960 | Absence |
| BC10 | 51°29,697' | 11°49,140' | 970 | Absence |
| BC11 | 51°26,527' | 11°49,366' | 1054 | Absence |
| BC12 | 51°26,665 | 11°49,158 | 1062 | Absence |
| BC13 | 51°26,892 | 11°49,316 | 1062 | Absence |
| BC14 | 51°26,959' | 11°49,451' | 1064 | Presence |
| BC15 | 51°26,998 | 11°49,597 | 1062 | Absence |
| BC16 | 51°27,087' | 11°49,631' | 1056 | Absence |
| BC17 | 51°26,951' | 11°49,462' | 1057 | Absence |
| BC19 | 51°26,587' | 11°49,204' | - | Absence |
| BC20 | 51°26,560' | 11°49,213' | 1062 | Absence |
| BC21 | 51°29,312' | 11°49,120' | 980 | Presence |
| BC22 | 51°30,189' | 11°49,395' | 952 | Presence |
| BC23 | 51°30,213' | 11°49,379' | 951 | Absence |
| BC24 | 51°30,227' | 11°49,390' | 942 | Presence |
| BC25 | 51°30,502' | 11°49,486' | 933 | Presence |
| BC26 | 51°30,519' | 11°49,481' | 949 | Presence |
| BC27 | 51°30,548' | 11°49,488' | 952 | Presence |
| BC28 | 51°30,527' | 11°49,499' | 949 | Absence |
| BC29 | 51°29,104' | 11°49,372' | 983 | Absence |
| BC31 | 51°29,689' | 11°49,145' | 962 | Presence |
| BC32 | 51°29,672' | 11°49,118' | 972 | Presence |
| BC33 | 51°29,672' | 11°49,137' | 962 | Presence |
| BC34 | 51°29,671' | 11°49,132' | 975 | Absence |
| BC35 | 51°29,650' | 11°49,149' | 966 | Absence |
| BC36 | 51°29,657' | 11°49,050' | 970 | Absence |

percentages. The live to dead ratios (L/D) (Jorissen and Whittling, 1999) were calculated for all samples. The Shannon diversity index ($-\sum_{i=1}^S p_i \ln p_i$) was calculated for each sample, and was performed for each fraction taken separately (63–125 μm , 125–250 μm and > 250 μm) and for the combined data from all size fractions (Shannon and Weaver, 1949). These calculations were carried out for both living and dead assemblages. The average diversity for samples with coral cover and without coral cover was then calculated. Furthermore, to illustrate the relationship between dead and living assemblages, a non-metric Multi-Dimensional Scaling (nMDS) based on the Bray-Curtis similarity matrix was performed on the non-transformed dead and living benthic foraminiferal assemblage datasets. All statistical analyses were undertaken with the PRIMER6 software (Clarke and Gorley, 2006).

4.4. Radiocarbon dating

Radiocarbon dating was performed on 9 well-preserved and cleaned *Lophelia pertusa* coral fragments at the ETH-Zürich. The samples were first dissolved in phosphoric acid. The resulting extracted CO_2 was then converted to graphite and measured by Accelerator Mass Spectrometry (AMS) technique. A more detailed description can be found in Hajdas et al. (2004). Results were corrected for ^{13}C and calibrated using the software OxCal v4.2.4 curve (Reimer et al., 2013), the Marine13 calibration curve (Reimer et al., 2013) and a reservoir age of 400 years. Sample details and ages are given in Table 2.

5. Results

5.1. Grain size distribution

5.1.1. Bulk material

Box core samples with coral cover mostly consist of well-sorted fine sands with a limited “tail” of silt size particles. They show a narrow unimodal grain size distribution with a sharp peak at approximately 160 μm reaching 10 to 15% volume (Fig. 3). Samples 3 and 4 differ: they

Table 2
Radiocarbon ^{14}C ages and sample details of analyzed cold-water coral fragments.

| Sample | Sediment depth (cm) | Material | Sample ID | ^{14}C age BP (years) | 1σ (years) | cal. age BP (years) |
|--------|---------------------|-------------------|-----------|--------------------------------|-------------------|---------------------|
| BC3 | 2 | <i>L. pertusa</i> | ETH-68758 | 6754 | 23 | 6354 |
| BC3 | 17 | <i>L. pertusa</i> | ETH-68759 | 6617 | 23 | 6217 |
| BC3 | 20 | <i>L. pertusa</i> | ETH-68760 | 6563 | 23 | 6163 |
| BC3 | 27 | <i>L. pertusa</i> | ETH-68761 | 2852 | 22 | 2452 |
| BC5 | 2 | <i>L. pertusa</i> | ETH-68762 | 858 | 21 | 458 |
| BC5 | 6 | <i>L. pertusa</i> | ETH-68763 | 807 | 21 | 407 |
| BC31 | 2 | <i>L. pertusa</i> | ETH-68764 | 797 | 21 | 397 |
| BC32 | 3 | <i>L. pertusa</i> | ETH-68765 | 903 | 21 | 503 |
| BC33 | 4 | <i>L. pertusa</i> | ETH-68766 | 611 | 21 | 211 |

have a trimodal distribution with peaks in the colloid (0.3 μm), silt (8 μm) and fine sand (160 μm) fractions (Fig. 3). The coral fragments present in these two samples present the particularity of being embedded in the sediment. Moreover, the coral fragments did not form a framework as in the other box cores with coral cover. These observations mainly explain the trimodal grain size distribution noticed for samples 3 and 4. Grain size distributions among samples without coral cover have unimodal and trimodal distributions (Fig. 3). Unimodally distributed samples also consist of well-sorted fine sands with a limited “tail” of silt sized particles (Fig. 3). Trimodal distributions also show peaks in the colloid (0.3 μm), silt (8 μm) and fine sand (160 μm) fraction (Fig. 3). Samples without coral cover generally show lower % volume of fine sand and more fine material (Fig. 3). Average mean grain size is higher when coral cover is absent (206 μm as opposed to 155 μm when coral cover is present) (Table 3). Average sorting (1.35 ϕ without coral cover opposed to 1.02 ϕ with), skewness (0.15 ϕ without coral cover opposed to 0.04 ϕ with) and kurtosis (1.18 without coral cover opposed to 1.06 ϕ with) are also higher in samples where coral cover is absent (Table 3). The high standard deviation of the average mean grain size when coral cover is absent (128 μm as opposed to 59 μm in presence of coral cover) illustrates the higher sediment heterogeneity among these samples (Table 3). The higher positive skewness and higher mean grain size for samples devoid of coral cover is well-illustrated in the sand fraction (Fig. 4a). Our interpretations will predominantly be based on the sand fraction, as it reflects the influence of current dynamics on the dMM and corresponds to the size fraction containing foraminifera. Mean grain size, sorting, skewness and kurtosis values for all samples are listed in Annex 1.

5.1.2. Siliciclastic fraction

Grain size distributions for the siliciclastic fraction follow near-identical trends to those from the bulk material (Fig. 3). Thus, readers are referred to section 3.1.2. for the description of grain size distributions. Similar to bulk material, the average mean grain size is noticeably higher when coral cover is absent (206 μm) as opposed to when coral cover is present (150 μm) (Table 3). Average sorting (1.30 without coral cover as opposed to 0.95 ϕ with), skewness (0.19 ϕ without coral cover as opposed to 0.11 ϕ with) and kurtosis (1.12 without coral cover as opposed to 1.04 ϕ with) are also lower in samples with coral cover (Table 3). These results closely follow trends observed in bulk material (Table 3) and are clear in the sand fraction (Fig. 4b). Standard deviations also follow the same trends as for bulk material (Table 3). Mean grain size, sorting, skewness and kurtosis values for all box core samples are listed in Annex 1.

5.2. Benthic foraminiferal assemblages

5.2.1. Diversity

A total of 87 living and 143 dead benthic foraminifera species in all

considered fractions were recognized (Annex 2). More precisely, 20 living and 88 dead benthic foraminifera species were identified in the > 250 μm fraction, 43 living and 101 dead benthic foraminifera in the 125–250 μm fraction, and 68 living and 85 dead benthic foraminifera species in the 63–125 μm fraction (Annex 3). Average Shannon diversity of the living assemblage (LA: biocoensis) is the highest in the presence of coral cover and in the fraction 63–125 μm , whilst it is the lowest in the absence of coral and in the fraction > 250 μm (Fig. 5). Average Shannon diversity of the dead assemblage (DA: thanatocoensis) is the highest in the presence of coral cover and in the fraction 125–250 μm , whilst it is the lowest in the absence of coral and in the fraction > 250 μm (Fig. 5). When considering all size fractions combined, the DA show an average Shannon diversity of 2.98 ± 0.25 in the presence of coral cover and of 3.00 ± 0.34 in the absence of coral cover (Fig. 5). Living assemblages have an average diversity of 2.86 ± 0.30 in the presence of coral cover and of 2.42 ± 0.18 in the absence of coral cover (Fig. 5). Thus, Shannon diversity is higher among the DA than among the LA. Furthermore, the difference in average Shannon diversity between the LA and DA is greater when coral cover is absent than when coral cover is present (Fig. 5).

5.2.2. Assemblage composition

Dead and living assemblages show important differences in composition. The nMDS plot (Fig. 6) shows a clear separation between the LA and the DA. Furthermore, it demonstrates that similarity between samples from the LA is lower than similarity between samples from the DA (Fig. 6). The L/D further highlights the strong composition differences between the LA and DA: only 38% of species are common to the LA and DA (Annex 4). Moreover, dead benthic foraminifera show a much higher abundance than living foraminifera, living foraminiferal abundance representing ca. 1% of the dead foraminiferal abundance (Fig. 7). Fig. 8 summarizes the distribution of the most abundant species in the DA and LA. The 5 most abundant species in the LA are *Trifarina bradyi* (11.9% av. abundance), *Hanzawaia boueana* (10.8% av. abundance), *Alabaminella weddellensis* (8.8% av. abundance), *Trifarina angulosa* (7.4% av. abundance) and *Globocassidulina subglobosa* (5.5% av. abundance) (Fig. 8). These species show much lower average abundances in the DA (0.5%, 1%, 1.5%, 1.3% and 3.4% respectively). The 5 most abundant species in the DA are *Cassidulina teretis* (18.4% av. abundance), *Cibicides kullenbergi* (13.8% av. abundance), *Sigmoilopsis schlumbergeri* (8.3 av. abundance), *Discanomalina coronata* (6.3% av. abundance) and *Elphidium excavatum* (5.6 av. abundance) (Fig. 8). These species are noticeably less abundant in the LA (0.1%, 1.3%, 0%, 2.5% and 0% respectively).

Small agglutinated species, such as *Adercotryma wrighti*, *Paratrochammina globorotaliformis* and *Trochammina globigeriniformis*, are almost exclusively present in the LA. The L/D demonstrates that this trend applies to other agglutinated species such as *Haplophragmoides robertsoni*, *Reophax scorpionus*, *Textularia* spp. and *Trochammina* spp. (Annex 4). Contrary to the previously cited species, *S. schlumbergeri* does not follow this trend and is present in the DA in all samples, whilst completely absent in the LA (Fig. 8). The larger agglutinated *Karreriella bradyi* and *Gaudryina rudis* are also associated in most samples with the DA rather than with the LA (L/D = 0) (Annex 4). In contrast to small agglutinated foraminifera, the small perforates *C. crassa* (5.2% av. abundance), *C. teretis* and *E. excavatum* are almost uniquely present in the DA (Fig. 8). Interestingly, the distribution of these species is relatively homogeneous between samples. *Nonionella iridea* and *Hoeglundina elegans* have higher abundances in the LA (Fig. 8). Other species, such as *Cibicides aravaensis*, *Gyroïdina* spp., *Melonis barleeianum*, *Pullenia subcarinata* and *Uvigerina mediterranea* are present in similar numbers in the LA and DA (Fig. 8).

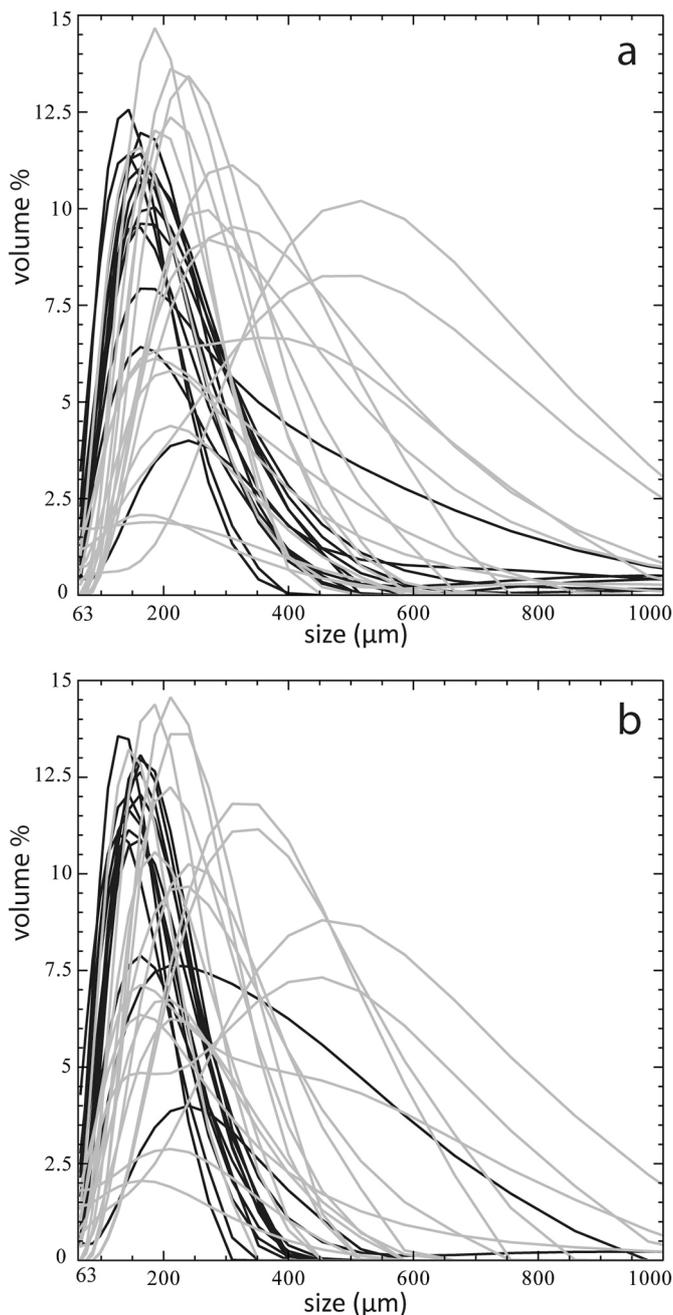


Fig. 4. Combined grain size distribution spectra of the sand fraction (63–1000 μm) for all 31 surface samples. a) bulk material b) siliciclastic fraction. Black curves: presence of coral cover. Grey curves: absence of coral cover.

5.3. Coral age distribution

All 9 measured coral fragments have Holocene ages. Six coral fragments in the top 6 cm were analyzed (Table 2). The age of 6354 ± 23 yr at 2 cm depth in BC3 is older than the 3 ages obtained for corals retrieved deeper in the box core (Table 2). A coral fragment at 27 cm depth in BC3 produced an age of 2452 ± 22 yr., i.e. approximately 4000 yr. younger than the 3 coral fragments dated at 2, 17 and 20 cm depth. Such age reversals are commonly observed in CWC environments and can be attributed to reworking or phases of mound collapse (Dorschel et al., 2007; White, 2007; Frank et al., 2009; Raddatz et al., 2011). The 5 other measured ages ranging from 211 ± 21 yr. (BC33) to 503 ± 21 yr. (BC32) are in agreement with ages obtained for surface coral fragments from other mounds in the area (Schröder-

Table 3

Average values and standard deviations of mean grain size (μm), sorting (ϕ), skewness (ϕ) and kurtosis (ϕ) for samples with and without coral cover. Bulk material (top) and siliciclastic fraction (bottom) are separated.

| Coral cover | Average Mean (μm) (St. Deviation) | Av. Sorting (ϕ) (St. Deviation) | Av. Skewness (ϕ) (St. Deviation) | Av. Kurtosis (ϕ) (St. Deviation) |
|-------------------------------|--|--|---|---|
| Bulk material | | | | |
| Absence | 206 (128) | 1.35 (0.91) | 0.15 (0.25) | 1.18 (0.55) |
| Presence | 155 (59) | 1.02 (0.72) | 0.04 (0.20) | 1.06 (0.21) |
| Siliciclastic fraction | | | | |
| Absence | 207 (104) | 1.30 (0.82) | 0.19 (0.27) | 1.12 (0.50) |
| Presence | 150 (52) | 0.95 (0.71) | 0.11 (0.20) | 1.04 (0.24) |

Ritzrau et al., 2005).

6. Discussion

6.1. Impact of taphonomic processes on benthic foraminiferal assemblages

6.1.1. Influence of the North East Atlantic bloom

Benthic foraminiferal standing stocks are strongly influenced by seasonality (Jorissen and Whittling, 1999; Murray, 2006). Cold-water coral environments are known to thrive in areas with high nutrient supply (Freiwald et al., 2004; Rüggeberg et al., 2014). The Porcupine Seabight, where the MM are nested, is affected by North East Atlantic blooms. The impact of such an important input of phytodetritus on benthic communities, and in particular benthic foraminifera, is striking (Gooday, 1988; Gooday and Lamshead, 1989; Gooday and Hughes, 2002). Benthic foraminiferal standing stocks vary accordingly with bloom periods (Gooday, 1988; Gooday and Lamshead, 1989; Gooday and Hughes, 2002). The spring bloom in the North East Atlantic, mainly consisting of diatoms, starts in March–April and follows a northward propagating pattern (Robinson et al., 1993; Leblanc et al., 2009). During the month of May, the spatial coverage of the North East Atlantic bloom and the Chlorophyll *a* concentrations at the Porcupine Seabight are at their highest (LeBlanc et al., 2009). In June, when the material for this study was collected (2nd – 7th of June), Chlorophyll *a* concentrations are lower than during the main bloom period of April–May but remain higher than in July (LeBlanc et al., 2009; Van Oostende et al., 2012). Additionally, timing of the North East Atlantic bloom varies from year to year as a function of meteorological conditions (Follows and Dutkiewicz, 2002). Internal tidal mixing and mixed layer shoaling will also affect the impact of the North East Atlantic bloom at the seafloor (Van Oostende et al., 2012). Although our samples were collected after the main North East Atlantic bloom period, an influence on foraminiferal standing stocks cannot be ruled out. Indeed, Lamshead and Gooday (1990) noticed a 0.5 cm thick phytodetritus surface layer in cores recovered in July 1982 at the Porcupine Seabight, associated with increased abundances of *A. weddellensis* and *Trifarina pauperata*. Thus, the high abundances in this study of *Trifarina angulosa*, *Trifarina bradyi* and *A. weddellensis* in the LA and their low abundances in the DA may be connected to such a bloom event. Other authors report that *N. iridea* and *A. weddellensis* show an opportunistic response to phytodetritus input (Gooday, 1993; Fariduddin and Loubere, 1997; Murray, 2006; Sun et al., 2006; Alve, 2010; Smart et al., 2019), although *N. iridea* may not be entirely dependent on phytodetritus availability (Duffield et al., 2014; Duffield et al., 2015). Indeed, it may also possibly feed on refractory degraded organic matter and associated bacteria (Duffield et al., 2014; Duffield et al., 2015). However, the joint observation of *N. iridea* and *A. weddellensis* at the dMM, would further suggest that the later phase of the North East Atlantic bloom could

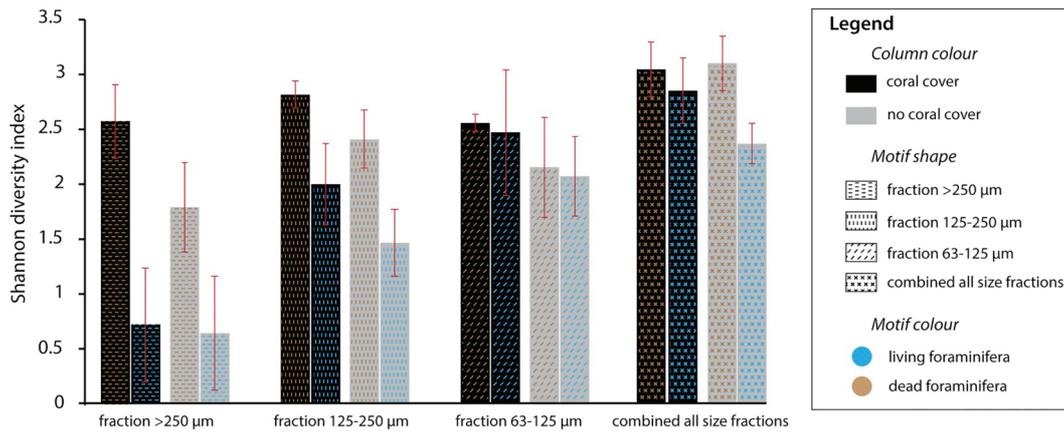


Fig. 5. Average Shannon diversity index (H) of benthic foraminiferal assemblages for the different size fractions (63–125 μm , 125–250 μm and > 250 μm) and for combined benthic foraminiferal assemblages from all size fractions. Samples are grouped in function of the presence (black columns) or absence of coral cover (grey columns). The column's motif shape and colour indicate the considered size fraction and the type of foraminiferal assemblage (see Legend). Standard deviations are also indicated (red segments; $n = 20$). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

induce high abundances of these species in the LA and their near absence in the DA (Fig. 8). Despite not reported to be a species responding to high phytodetritus input, the high abundance of *Hanzawaia boueana* in the LA and its low abundance in the DA may also reflect an impact of the later phase of the North East Atlantic bloom on this species. These combined observations suggest that seasonality has a strong impact on living benthic foraminiferal standing stocks in CWC environments at the BMP.

6.1.2. Physico-chemical destruction of benthic foraminiferal tests

The physical and/or chemical destruction of agglutinated benthic foraminifera and their consequent absence in DAs has been well-documented (Denne and Sen Gupta, 1989; Murray, 2006; Duros et al., 2012). The near absence of small agglutinated species (e.g. *Adercotryma wrighti*, *Reophax scorpiurus*, *Paratrochammina* spp. and *Trochammina* spp.) in the DA and their higher abundance in the LA (Fig. 8, Annex 2)

could be testimony to the post-mortem destruction of these species. The presence of *Trochammina* spp. and *Reophax* spp. only in LAs was previously documented in the Whittard Canyon (Duros et al., 2012) and in the Porcupine Abyssal Plain (Stefanoudis et al., 2017). Stefanoudis et al. (2017) also observed the presence of *Adercotryma* spp. only in LAs. The loss of agglutinated tests in DAs was also observed in CWC environments at the SE Rockall Bank (Morigi et al., 2012). The little amount of organic material cementing these agglutinated tests would favour post-mortem destruction, whilst agglutinated species possessing calcitic cement, such as *Sigmoilopsis schlumbergeri*, would be better preserved and would not disappear in DAs. However, delicate agglutinated species (e.g. *Saccorhiza ramosa*) were observed at Norwegian CWC reefs in DAs (Spezzaferri et al., 2013). Thus, the higher abundance of fragile agglutinated forms in LAs may also be a response to the later phase of the North East Atlantic bloom, rather than (or in combination with) the post-mortem destruction of these species. Dissolution of calcareous tests

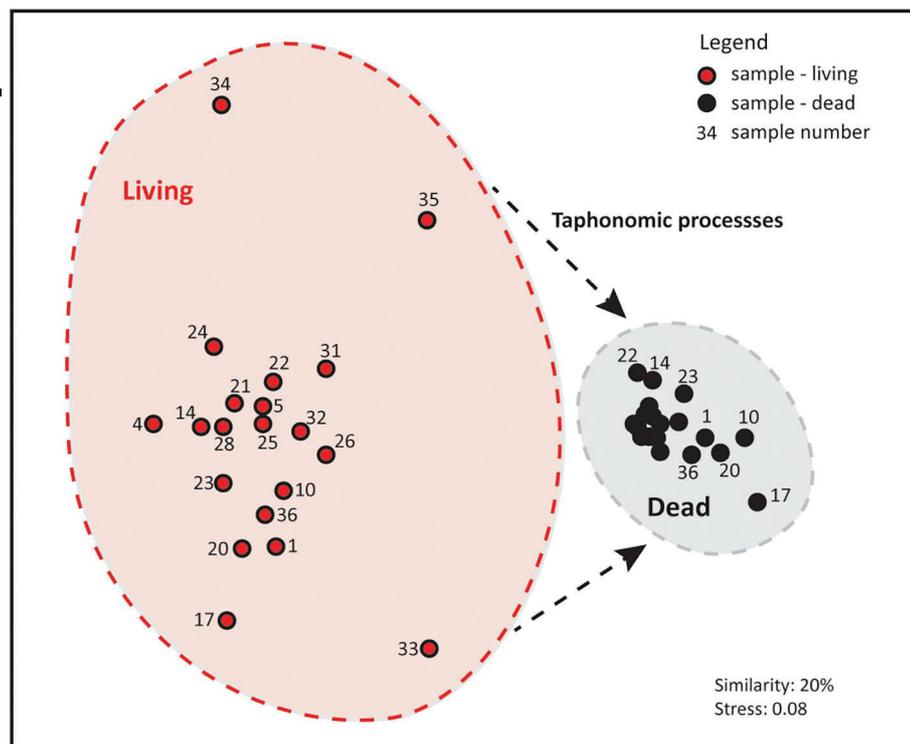


Fig. 6. Non-Metric Multidimensional Scaling (nMDS) plot of live (red circles) and dead (black circles) benthic foraminiferal assemblages based on Bray-Curtis similarity matrix. Note the higher similarity between samples from the dead assemblage, attributed to the effect of taphonomic processes. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

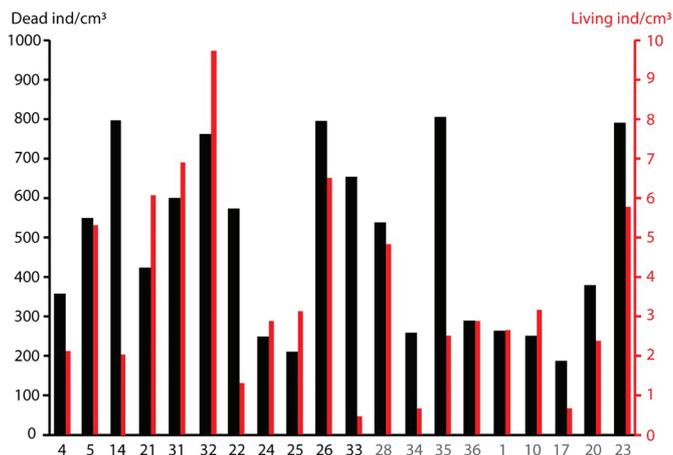


Fig. 7. Total abundance of dead (black columns) and living (red columns) benthic foraminifera combined from all size fractions for 1 cm³ of sediment. Sample numbers are indicated on the x axis. Black sample numbers: presence of coral cover. Grey sample number: absence of coral cover. Attention has to be paid to the double y axis. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and bioerosion can also influence preservation of DAs, yet the MM are situated far above the CCD and calcareous tests show no indications of typical signs of dissolution, such as test wall etching, or translucent or opaque appearance of normally transparent hyaline walls (Murray and Wright, 1970). Moreover, dissolution of CaCO₃ is generally not a notable process in carbonate rich environments (Kotler et al., 1992). Bioerosion by other organisms (e.g. fungi, bacteria, algae, microfaunal and macrofaunal predators) can also lead to etching and finally complete destruction of foraminiferal tests (Hickman and Lipps, 1983; Lipps, 1988). The presence of holes/punctures in foraminiferal tests have been associated to predation by macrofauna such as nematodes (Sliter, 1971), gastropods (Cedhagen, 1996), other foraminifera (e.g. *Hyrrokkinn sarcophaga*) (Parker and Jones, 1865), as well as bacteria-induced carbonate degradation (Freiwald, 1995). No important etching was observed on foraminiferal tests at our study site. Thus, these arguments would suggest that dissolution and bioerosion probably do not play a major role on the preservation of dead foraminiferal tests in the dMM.

6.1.3. Post-mortem transport of benthic foraminifera

Dead benthic and planktonic foraminifera can be considered as hollow diversely shaped sediment grains. Living benthic foraminifera can resist erosion by burrowing or by attaching themselves to the substratum by means of their pseudopodia. However, once dead, they become mobile and can be transported. A number of arguments suggest that the DA at the dMM are strongly impacted by transport processes.

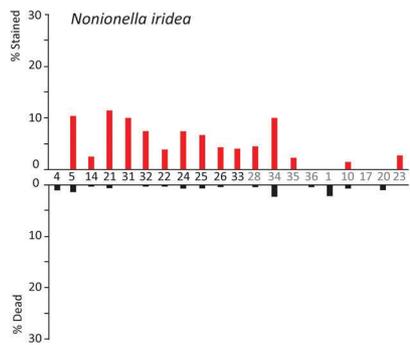
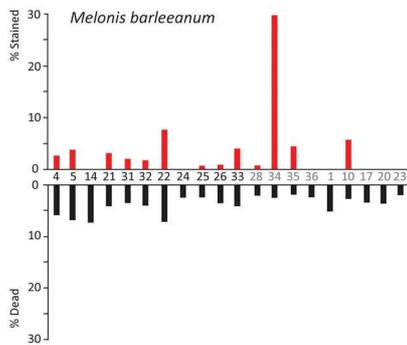
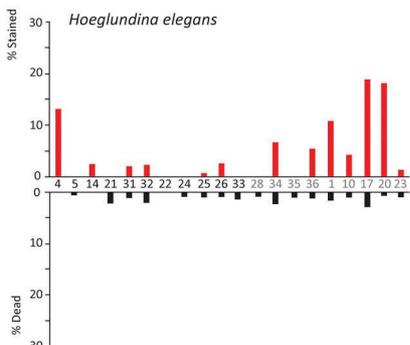
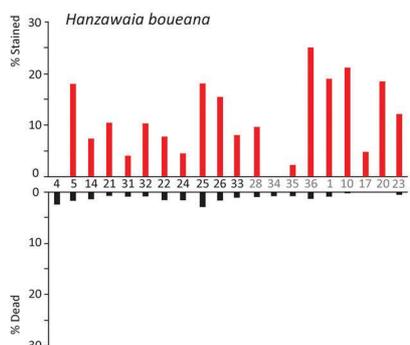
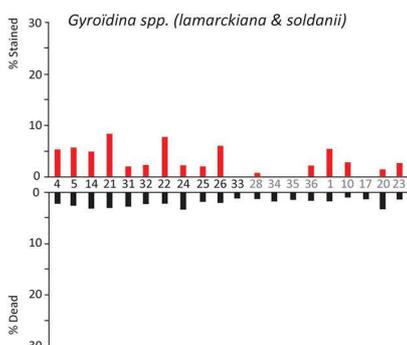
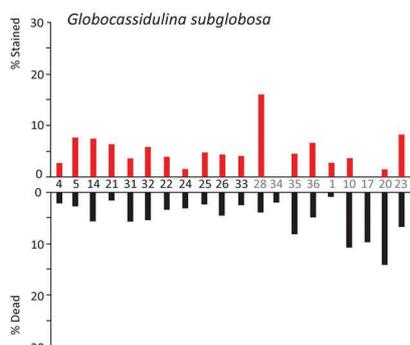
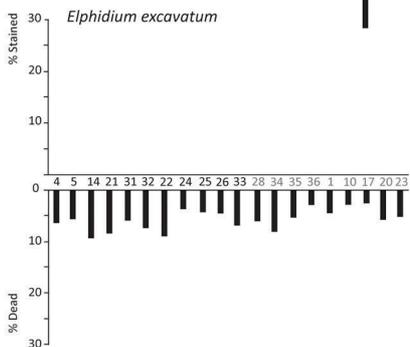
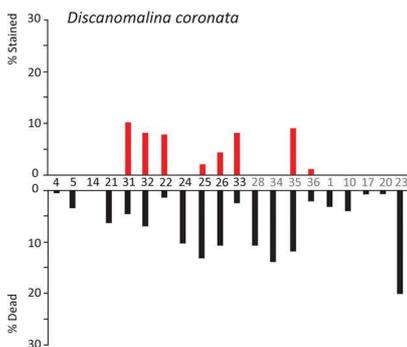
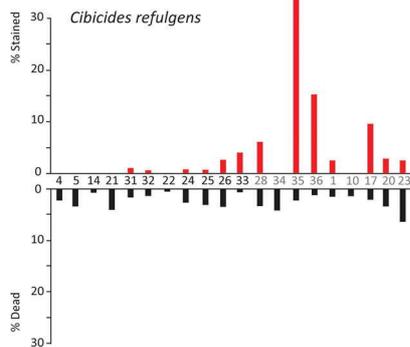
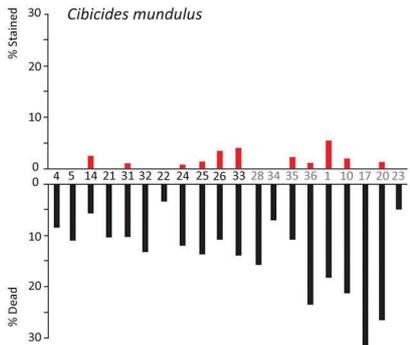
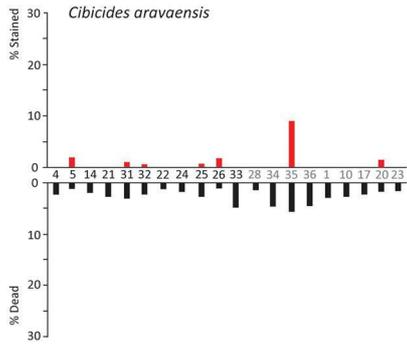
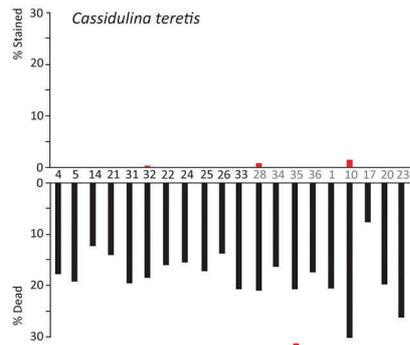
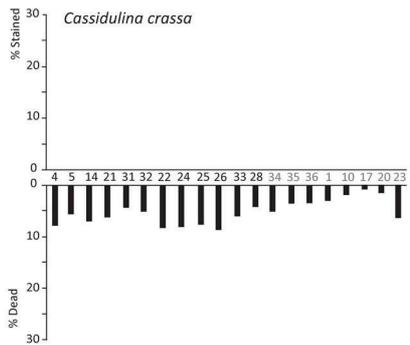
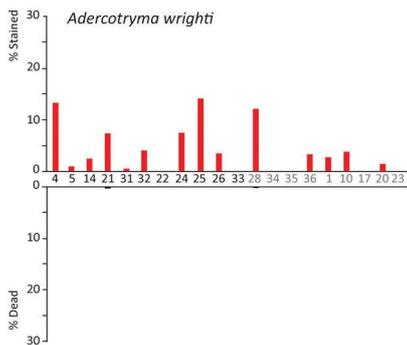
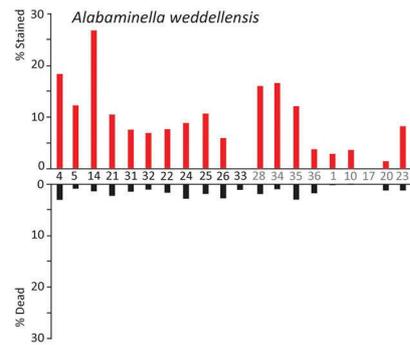
- (1) Diversity is higher in the DA than in the LA (Fig. 5). This is consistent with observations made by Alve and Murray (1994) in the Hamble estuary (southern England) that attribute higher diversity in the DA to the input of exotic transported species. However, the destruction of small agglutinated species, which contribute strongly to the LA, could also lead to comparatively higher diversity in the DA.
- (2) *Elphidium* spp. are generally considered near shore shallow-water species (Horton, 1999; Mojtahid et al., 2016) and are often considered allochthonous at deeper depths in recent times (Schönfeld et al., 2011; Duros et al., 2012). The complete absence of any living *Elphidium* spp. and their dominance in the DA at the dMM would confirm these observations. Moreover, the most abundant species at the dMM, *E. excavatum*, is frequent in glacier-proximal environments (Jennings and Weiner, 1996; Darling et al., 2016). It is

opportunistic and geographically widespread, showing higher standing stocks in the Arctic (Darling et al., 2016). Shallow dwelling foraminifera can be transported to deeper areas through ice-rafting during times of major ice shedding (Dieckmann et al., 1987; Ishman and Webb, 2003). This phenomenon incorporates benthic foraminifera when in contact with the sediment surface and at a later stage releases them at a new location through ice melting. Mojtahid et al. (2017) observed a dominance of *Elphidium* spp. at the Celtic margin during Heinrich Event 1. The authors associate this to a high release of icebergs at this specific period. High abundances of *Elphidium* spp. were also noticed at Propeller Mound (PS) during the Last Glacial Maximum (Rüggeberg et al., 2007). Thus, reworking of glacial sediments may result in a high abundance of *Elphidium* spp. in the DA, and in particular of *E. excavatum*, at the dMM. These foraminifera would have been transported through ice rafting together with the numerous dropstones present at the dMM (Fig. 2). Morigi et al. (2012) proposed that a number of other dead foraminifera at CWC mounds at the SE Rockall Bank, such as *Cassidulina* spp. and *Cibicides* spp., would be reworked glacial relics. Rüggeberg et al. (2007) defined *C. kullenbergi*, *C. teretis* and *Sigmoilopsis woodi* as part of a “glacial assemblage” in Propeller Mound (PS), whilst *Sigmoilopsis schlumbergeri* and *Cassidulina* spp. are present in DAs but absent in LAs at the surface of Galway Mound (Schönfeld et al., 2011). Furthermore, Grunert et al. (2015) observed higher abundances of *C. teretis* during the Last Glacial Maximum along the southwest Iberian Margin. These matching observations from different authors (Rüggeberg et al., 2007; Schönfeld et al., 2011; Morigi et al., 2012; Grunert et al., 2015) could confirm that most dominant species in the DA at the dMM (e.g. *Elphidium* spp., *C. kullenbergi*, *C. teretis*, *C. crassa* and *S. schlumbergeri*) are part of a reworked glacial fauna.

- (3) The well-sorted fine sands at the dMM are typically deposited in high current regimes and can be interpreted as sandy contourites (Fig. 4) (Huvenne et al., 2009a; Rebesco et al., 2014). The strong similarity between grain size distribution and sorting for both the bulk and siliciclastic fractions would indicate that carbonate and siliciclastic material is transported in the same way along with dead foraminifera. At the Darwin mounds (Northern Rockall Trough), Huvenne et al. (2009b) calculated erosional velocities of approximately 23 cm s⁻¹ for foraminifera (63–500 μm size fraction). Thus, the average current velocity of 35–40 cm s⁻¹ at the dMM calculated by Lim et al., 2018 would likely lead to transport of dead benthic foraminifera.

6.2. Implications on the dynamics and archive potential of the Moira Mounds

Foubert et al. (2011) observed, in shallow push cores taken in furrows from the midslope MM area, that Holocene sediments formed only a thin 10 cm veneer above the underlying glacial deposits. The Holocene veneer was composed by sand-sized material whilst the glacial deposits consisted of finer clay-dominated material (Foubert et al., 2007; Van Rooij et al., 2007a,b). Similarly, within the scour pits around the dMM, dropstones are regularly observed (Lim et al., 2018) (Fig. 2a). This suggests that the thin veneer of sand at the study site is also Holocene in age and is subject to erosion, exposing the underlying glacial deposits. The grain size distributions presented in this study reflect these observations. Samples with bimodal distributions evidencing fine material and poorer sorting would correspond to areas where glacial deposits are uncovered by erosion. These uncovered glacial deposits could be the source of the observed “glacial” foraminifera in the DA (e.g. *C. teretis*, *E. excavatum*, *S. schlumbergeri*), although samples with bimodal distributions do not show significant higher amounts of potential “glacial” benthic foraminifera (Fig. 8). This homogeneous distribution of “glacial” benthic foraminifera across samples can be attributed to the constant reworking taking place in the area. In contrast,



(caption on next page)

Fig. 8. Distribution of most abundant benthic foraminifera species (combined from all size fractions) in both living (red columns) and dead assemblages (black columns). Sample numbers are indicated on the x axis. Black sample numbers: presence of coral cover. Grey sample number: absence of coral cover. Note the strong disparity between living and dead foraminifera distributions. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

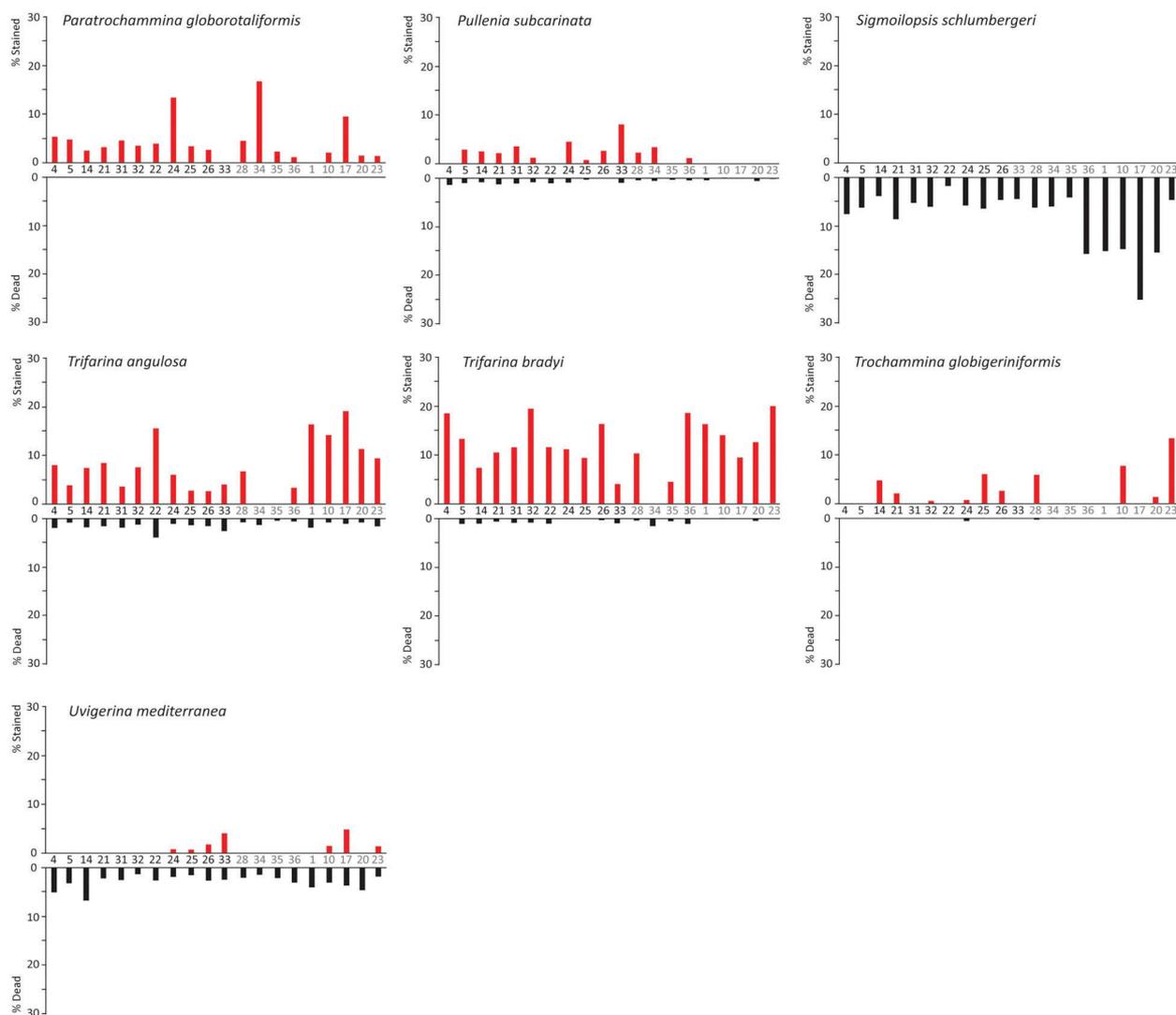


Fig. 8. (continued)

samples with unimodal well-sorted fine sand would correspond to non-erosive areas and/or areas of accumulated Holocene material. Interestingly, coral barren areas are generally richer in clay-dominated material (Fig. 3) which would confirm that erosion is predominant in open settings (Fig. 9). Moreover, cold-water corals are known to locally reduce current velocity through the creation of frictional drag, leading to the deposition of current-suspended particles (Mienis et al., 2009a; Foubert et al., 2011; Hebbeln et al., 2016). The lower mean grain size distribution of the sand fraction in the presence of coral (Fig. 4) suggests that coral framework at the dMM also locally reduces hydrodynamics and leads to reduced erosion and/or the deposition of transported material in the coral framework.

Thus, the coral framework, through sediment baffling, accumulates sediments derived from non-depositional settings, which will affect benthic foraminiferal assemblages (Fig. 9). The difference in diversity between the LA and the DA is less in the presence of coral cover (Fig. 5), where the coral framework acts as an obstacle, sheltering sediments

from erosion, and providing a variety of different microhabitats for benthic foraminifera. This “shelter” effect was also observed on a nearby MM, where only small deposits of sorted-sediments remained in the sheltered lee side of mounds (Lim et al., 2017). The sheltered environment offered by the framework would prevent the transport of foraminifera after their death, post-mortem transport that would preferentially take place in nearby open settings (Fig. 9). Hence, the action of the coral framework and its interaction with current dynamics is twofold: (1) accumulation of current suspended foraminifera from open settings and (2) preventing loss of recently dead benthic foraminifera in the shelter of the framework itself. Consequently, the coral framework, by acting as a natural sediment trap, would provide a useful paleoenvironmental archive for such current-driven environments. Indeed, it emerges as a depositional area in an otherwise non-depositional system. However, the framework may potentially accumulate sediments from a variety of sources, the relative contribution of each sediment source possibly shifting through time with varying

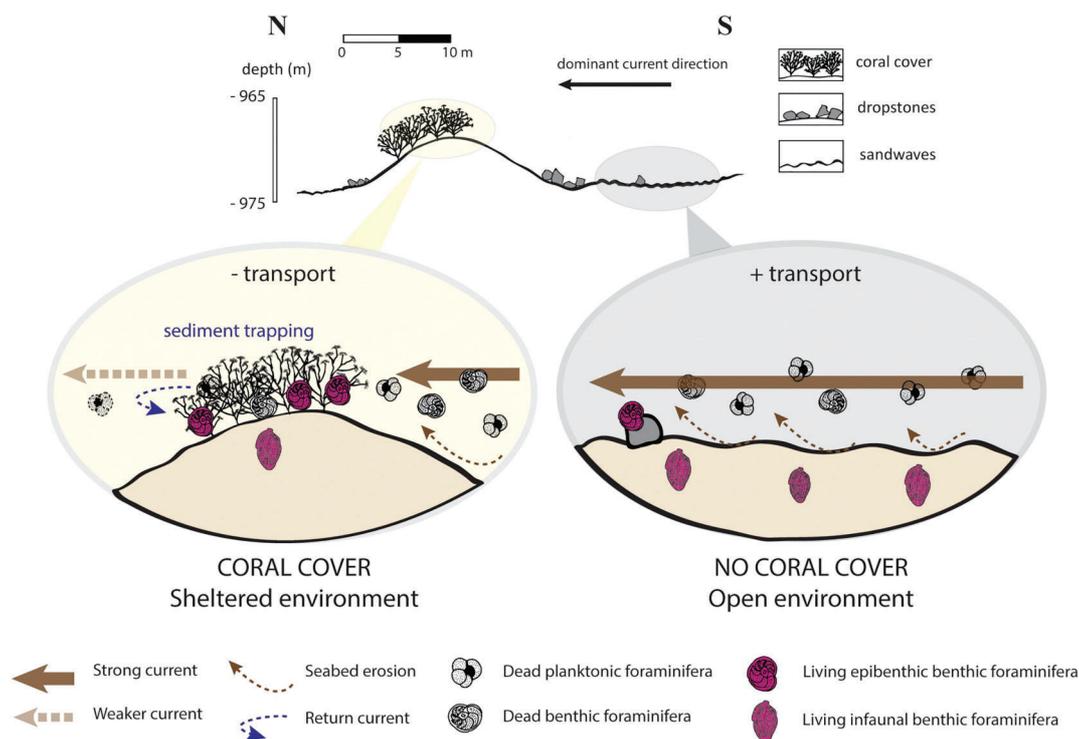


Fig. 9. Simplified model illustrating the differences in erosion and foraminiferal transport between environments with and without coral cover. Right bubble: open environment in which seabed erosion and foraminiferal transport is important. Left bubble: sheltered environment provided by coral cover. The coral framework locally reduces current speed, baffling transported sediment and foraminifera whilst preventing erosion. The foraminifera illustrated are not intended to reflect precisely assemblages described for the downslope Moira Mounds. The illustrated mound is to scale, all other elements are not.

hydrodynamic regimes. Thus, the number of reworked foraminifera in the coral framework is likely to be important, as suggested by the strong differences between LAs and DAs (Fig. 8). This reworking would also prove not to be constant, varying through time with changes in current velocity.

7. Conclusions

Dead and living benthic foraminiferal assemblages at the downslope Moira Mounds show important compositional differences. A number of phytodetritus feeding species, such as *Alabaminella weddellensis* and *Nonionella iridea*, were predominant in the living assemblage whilst nearly absent in the dead assemblage. The high abundance of these species may be explained by the influence of the later phase of the North East Atlantic bloom at our sampling site during the early month of June. The later phase of the North East Atlantic bloom may also have resulted in high abundances of *Trifarina bradyi* and *Trifarina angulosa* in the living assemblage. Low abundances of organic cemented agglutinated species (e.g. *Trochammina* spp., *Paratrochammina* spp., *Adercotryma* spp.) in the dead assemblage is probably a result of post-mortem destruction of these fragile forms and/or a seasonal response of these species to the later phase of the North East Atlantic bloom. Dominant species among the dead assemblage (*C. crassa*, *C. kullenbergi*, *C. teretis*, *E. excavatum* and *S. schlumbergeri*) are attributed to be typical of glacial periods. Transport through ice rafting during ice shedding events at the end of the Last Glacial Maximum could explain the high abundances of *Elphidium excavatum* in surface sediments at the Moira Mounds. We suggest that reworking of glacial deposits by the strong currents dominating the area may have an important impact on the composition of the dead assemblage. The dead assemblage is thus a result of mixing between relic glacial and contemporary foraminifera. Diversity differences between living and dead assemblages were less in the presence of coral cover than in its absence. The grain size distribution trends and the strong differences between living and dead

assemblages reflect the alternation between erosion and deposition in the downslope Moira Mounds. Such processes are typical of contouritic environments. The coral framework, by acting as a natural barrier and shelter, would accumulate sediments eroded from surrounding areas. This, together with the observed diversity differences, suggests that cold-water corals provide a useful record for paleoenvironmental reconstructions, better than surrounding open settings. However, this study highlights that benthic foraminifera in the cold-water coral framework may originate from the framework itself but also from transported material. Thus, paleoenvironmental reconstructions based on cold-water coral mound records need to be developed in consequence.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marmicro.2019.101799>.

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