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Benthic foraminifera in a deep-sea high-energy environment: the Moira Mounds (Porcupine Seabight, SW of Ireland)

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Abstract

Cold-water coral ecosystems represent unique and exceptionally diverse environments in the deep-sea. They are well developed along the Irish margin, varying broadly in shape and size. The Moira Mounds, numerous small-sized mounds, are nestled in the Belgica Mound Province (Porcupine Seabight, North-East Atlantic). The investigation of living (Rose Bengal stained) and dead benthic foraminiferal assemblages from these mounds allowed to describe their distribution patterns and to evaluate their response to environmental variability. Quantitative data was statistically treated to define groups of species/genera associated to specific habitats. The Moira Mounds differ from their larger neighbours by the reduced spatial variability of benthic foraminiferal assemblages, living assemblages only distinguishing coral-rich and coral-barren areas. The ecological needs of corals are highlighted by the abundance of *Alabaminella weddellensis* and *Nonionella iridea*, phytodetritus-feeding species in coral supporting sediments. Living foraminifera in sediments from the Moira Mounds concentrate in the upper first centimetre. Infaunal species may be affected by bioturbation and/or reworking by the strong currents in the area. Dead foraminiferal assemblages from the Moira Mounds resemble those described for the sandwave facies in adjacent giant mounds, suggesting similar processes in facies deposition.

Keywords Benthic foraminifera · Cold-water corals · Carbonate mounds · Bio-sedimentary facies

1 Introduction

In recent years cold-water coral (CWC) ecosystems have been studied in the Mediterranean Sea (Fink et al. 2013; Lo Iacono et al. 2014), on the Norwegian shelf (Freiwald et al. 2002; Rüggeberg et al. 2011; Stalder et al. 2014), along the

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Moroccan margin (Foubert et al. 2008; Wienberg et al. 2009) and off Mauritania (Eisele et al. 2014). However, the most intensively studied area remains the Irish margin (Hovland et al. 1994; De Mol et al. 2002; Beyer et al. 2003; Mohn et al. 2014; Hebbeln et al. 2016, and references therein). Offshore Ireland, CWCs composed of *Lophelia pertusa* and *Madrepora oculata* and hosting complex ecosystems characterize the seafloor (e.g., Freiwald et al. 2004; Vertino et al. 2015).

The Belgica Mound Province is located on the eastern margin of the Porcupine Seabight (PS), a shallow to deep-water north–south trending embayment in the northeast Atlantic continental margin (De Mol et al. 2002; Wheeler et al. 2007; Huvenne et al. 2009a). It is 45 km long and 10 km wide (Fig. 1), and hosts active or buried CWC mounds from 550 to 1030 m water depth. Mound size varies from giant representatives, e.g., Challenger or Galway Mound, reaching approximately 150 m in height (Ferdelman et al. 2005; Dorschel et al. 2007b; Foubert and Henriet 2009) to small-sized structures, e.g., the 256 Moira Mounds (MM) offshore western Ireland (Fig. 1) (Foubert
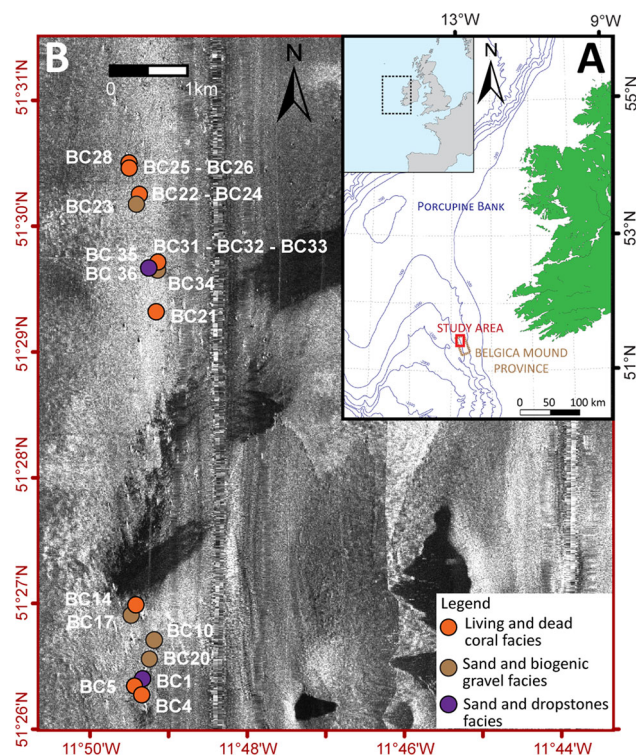
Fig. 1 (A) Location of the Belgica Mound Province (brown box) and the study area (red box). (B) Detailed 30 kHz side-scan sonar (TOBI) mosaic of the study area showing the location of the 20 box cores (BC) together with their facies classification (mod. from Wheeler and Science Party 2011)

et al. 2011; Wheeler et al. 2011; Lim et al. 2017, 2018). Based on video surveys, Wheeler et al. (2011) described a downslope area (Fig. 1) characterized by 143 small mounds between 900 and 1150 m water depth. These mounds have ovoid shapes, diameters of 20–50 m, heights of up to 11 m, slope gradients ranging between 15° and 20°, and their long-axis are oriented parallel to the dominant north–south flowing current (Wheeler et al. 2005, 2011; Foubert et al. 2011). Foubert et al. (2011) suggested that the midslope MM may represent the initial start-up phase of mound formation or an example of mound formation under stressed conditions.

The northward circulating Eastern North Atlantic Water (ENAW) and the Mediterranean Outflow Water (MOW) influence the PS. The ENAW, extending down to 800 m, overlays the MOW, which extends from around 800–1100 m depth (Rice et al. 1991; White 2007). The MOW is highly saline and its upper limit corresponds to the permanent thermocline (White 2007). It flows from the Gulf of Cadiz along the Portuguese margin, forming a contour current with a cyclonical pattern around the PS (Rice et al. 1991; Van Aken and Becker 1996; Dorschel et al. 2007b). In the Belgica Mound Province, Dorschel et al. (2007a) and White (2007) recorded a constant north-westward directed residual bottom flow, with velocities

between 5 and 15 cm s^{-1} originating from internal and tidal period baroclinic waves (White 2007). Peak velocities of 60 cm s^{-1} were measured in the Belgica Mound Province (White 2007; Dorschel et al. 2007a). Lim et al. (2018) calculated a residual current of 36–40 cm s^{-1} in the MM. Current-induced sedimentary structures demonstrate the action of these currents, e.g., east–west directed sediment waves, ripple marks and dunes (Foubert et al. 2011) (Online Resource 1).

Benthic foraminiferal abundance and diversity depends on the input of organic matter, oxygenation and hydro-sedimentary processes at the seafloor (Jorissen et al. 2007) making them useful tools to understand past and recent CWC environments (Rüggeberg et al. 2007; Margreth et al. 2009; Schönfeld et al. 2011; Morigi et al. 2012; Stalder et al. 2015). Margreth et al. (2009) proposed a model linking specific benthic foraminiferal assemblages to sedimentary facies, which has since been compared to a number of different CWC mounds (Schönfeld et al. 2011; Morigi et al. 2012; Spezzaferri et al. 2013; Smeulders et al. 2014). The aims of this study are: (1) to assess living benthic foraminiferal diversity in sediments from the MM, (2) to identify epifaunal and infaunal benthic foraminiferal distribution patterns and compare them to facies variations and (3) to better constrain the interaction between nutrient fluxes and the coral framework.

2 Materials and methods

Twenty surface samples collected during Eurofleets Cruise CWC-Moira (Spezzaferri et al. 2012) on the RV Belgica (2–7 June 2012) were investigated (Fig. 1, Table 1). They were recovered using a NIOZ-type box corer (50 cm diameter and a 55 cm penetration in sediments) equipped with a global acoustic positioning system (GAPS) for seafloor positioning (Spezzaferri et al. 2012). Sampling sites were identified in video surveys acquired during the VENTURE cruise (Wheeler and Science Party 2011).

Samples for micropaleontology were collected and processed following the FOBIMO protocol (Schönfeld et al. 2012), although no replicates were taken. Corals and other macrofauna were removed before sampling. Three subcores (10 cm diameter) were taken from box cores BC26, BC34 and BC35 and sliced down to 15 cm at 1 cm resolution. All were placed in an ethanol Rose Bengal solution (Walton 1952; Schönfeld et al. 2012). They were washed through 250, 125 and 63 μm mesh sieves, dried and weighed. Residues were dry picked for Rose Bengal stained (living) and unstained (dead) benthic foraminifera. At least 300 dead individuals and all living individuals were randomly picked. Only living benthic foraminifera were investigated for the three subcores. Large clasts (e.g.,

Table 1 Sample number, coordinates, water depth and surface description of investigated box cores (Spezzaferri et al. 2012)

Sample	Latitude (N)	Longitude (E)	Depth (m)	Surface description
BC1	51°26,433′	11°49,512′	1057	Sand with dropstones
BC4	51°26,304′	11°49,385′	1062	Coral rubble and sand
BC5	51°26,331′	11°49,402′	1069	Coral framework and sand
BC10	51°29,697′	11°49,140′	970	Rippled sand
BC14	51°26,959′	11°49,451′	1064	Coral rubble and sand
BC17	51°26,951′	11°49,462′	1057	Sand
BC20	51°26,560′	11°49,213′	1062	Rippled sand
BC21	51°29,312′	11°49,120′	980	Coral rubble and muddy sand, rare dropstones
BC22	51°30,189′	11°49,395′	952	Coral rubble and muddy sand
BC23	51°30,213′	11°49,379′	951	Sand with abundant biogenic fragments
BC24	51°30,227′	11°49,390′	942	Coral rubble and muddy sand
BC25	51°30,502′	11°49,486′	933	Coral rubble and muddy sand
BC26	51°30,519′	11°49,481′	949	Coral framework and sand
BC28	51°30,527′	11°49,499′	949	Coarse to medium sand and coral
BC31	51°29,689′	11°49,145′	962	Coral framework and sand
BC32	51°29,672′	11°49,118′	972	Coral framework and sand
BC33	51°29,672′	11°49,137′	962	Coral rubble and muddy sand
BC34	51°29,671′	11°49,132′	975	Silty sand and biogenic fragments
BC35	51°29,650′	11°49,149′	966	Medium to fine sand and dropstones
BC36	51°29,657′	11°49,050′	970	Sand and dropstones

dropstones and/or coral fragments) were also scrutinized at the stereomicroscope to record still attached specimens. Plummer cells were mounted and ordered to document all recognized species.

Living benthic foraminiferal data were standardized for 50 cm^3 of sediment whereas dead benthic foraminiferal data were standardized to percentages and statistically treated separately using the software PAST 3.12 (Hammer et al. 2001). The Similarity Percentage Analysis (SIMPER) was obtained with the PRIMER 6 software (Clarke and Gorley 2006). The Diversity Shannon index was calculated for all samples. Data for non-metric MultiDimensional Scaling (nMDS) analysis were not transformed. Clusters identified in the nMDS plot, both based on the Bray–Curtis Dissimilarity, underwent a non-parametric MANOVA test (NPMANOVA) and SIMPER. The SIMPER allowed to reveal the contribution of each species to the total dissimilarity/similarity, their individual contribution to each group (Clarke and Gorley 2006), and to highlight ecological differences in benthic foraminiferal assemblages. The ratio between the average contribution of a species ($\overline{\delta}_i$) and the standard deviation of the species average contribution [SD ($\overline{\delta}_i$)], defined as follows: $\overline{\delta}_i/\text{SD}(\overline{\delta}_i)$ (Clarke and Gorley 2006) was used to recognize discriminating species, e.g., the higher the value, the better the species is as a discriminator.

To analyse foraminiferal distribution within the sediments, the average living depth or ALD (Jorissen et al. 1995) for the infaunal component of the assemblage was calculated following the equation:

$$\text{ALD}_x = \sum_{i=0,x}(n_i D_i)/N$$

where x is the lowest boundary of the deepest sample, n_i is the number of specimens in interval i, D_i is the midpoint of sample interval i, and N is the total number of individuals for all levels. Calculation of the ALD$_{(6)}$(infauna) was performed on infaunal species: *Bolivina pseudopunctata*, *Bolivina difformis*, *Bulimina marginata*, *Globocassidulina subglobosa*, *Melonis barleeanum*, *Nonionella iridea*, *Nonionella labradorica*, *Pullenia bulloides*, *Pullenia subcarinata*, *Trifarina angulosa*, *Trifarina bradyi*, *Uvigerina mediterranea* and *Uvigerina peregrina*. In the case of the MM, the choice of investigated subcores enabled to decipher the main responses of the infaunal communities to surface sediment variability.

Total organic carbon (TOC) content (in weight%) was measured on 100 mg of surface bulk sediment by Rock-Eval6 at the University of Lausanne.

3 Results

3.1 Facies classification and description

Facies were described on board (Spezzaferri et al. 2012; Vertino et al. 2015). Examples of the three defined facies

are illustrated in the Online Resource 1 and in Spezzaferri et al. (2012). The living and dead coral facies is characterized by dense coral cover of live and/or dead colonies of corals together with sandy to muddy sandy sediments (Vertino et al. 2015). It is observed in box cores 4, 5, 14, 21, 22, 24, 25, 26, 28, 31, 32 and 33 (Fig. 1, Online Resource 1). Among these, two box cores (33 and 28) show contribution also from the sand and biogenic gravel facies. The sand and biogenic gravel facies is characterized by sandy to muddy sediment and/or bioclastic gravel. Sandy sediments are often rippled. This facies is present in box cores 10, 17, 20, 23 and 34 (Fig. 1, Online Resource 1). The sand and dropstones facies is characterized by sandy to muddy sediments and heterometric dropstones. This facies is represented by box cores 1, 35 and 36 (Fig. 1, Online Resource 1).

3.2 Distribution of living benthic foraminifera

Eighty-seven species were recognized (Online Resource 2). Multivariate analysis performed on the complete and standardized dataset reveals variations in the total number of individuals from one sample to another. Species contributing to the average dissimilarity/similarity and their individual abundances are listed in Online Resource 3.

The nMDS plot allowed to identify one main cluster (Cluster L) composed of 11 samples (Fig. 2a) and an outlier group. Cluster L groups all samples from the living coral and dead coral facies, except for BC33 that shares characteristics from the sand and biogenic gravel facies. Cluster L is hereafter referred to as the "Coral Assemblage". All nine outliers represent the sand and biogenic gravel facies, and sand and dropstone facies; except for BC33. The nine outlier samples are hereafter indicated as part of the "No-Coral Assemblage" (Fig. 2a).

The Coral Assemblage is characterized by the epibenthic *Alabaminella weddellensis* and the infaunal *T. bradyi*. Both species contribute to more than 15% of the total abundance. Less contributing species (from 6 to 11%) are *Hanzawaia boueana*, *T. angulosa*, *N. iridea*, and *G. subglobosa* (Online Resource 3). Epifaunal taxa represent 44.3% (against 40.8% when coral is absent) of the entire assemblage, infaunal taxa 39.8% (against 47.1% when coral is absent). In the No-Coral Assemblage the most important species (about 19% of the total abundance) are *H. boueana* and *T. bradyi*; other species (from 6 to 12%) are *T. angulosa*, *G. subglobosa*, *Hoeglundina elegans* and *Cibicides refulgens*. They represent together 15.4% of the total abundance (Online Resource 3). Benthic foraminifera characterizing the living assemblage are illustrated in Fig. 3.
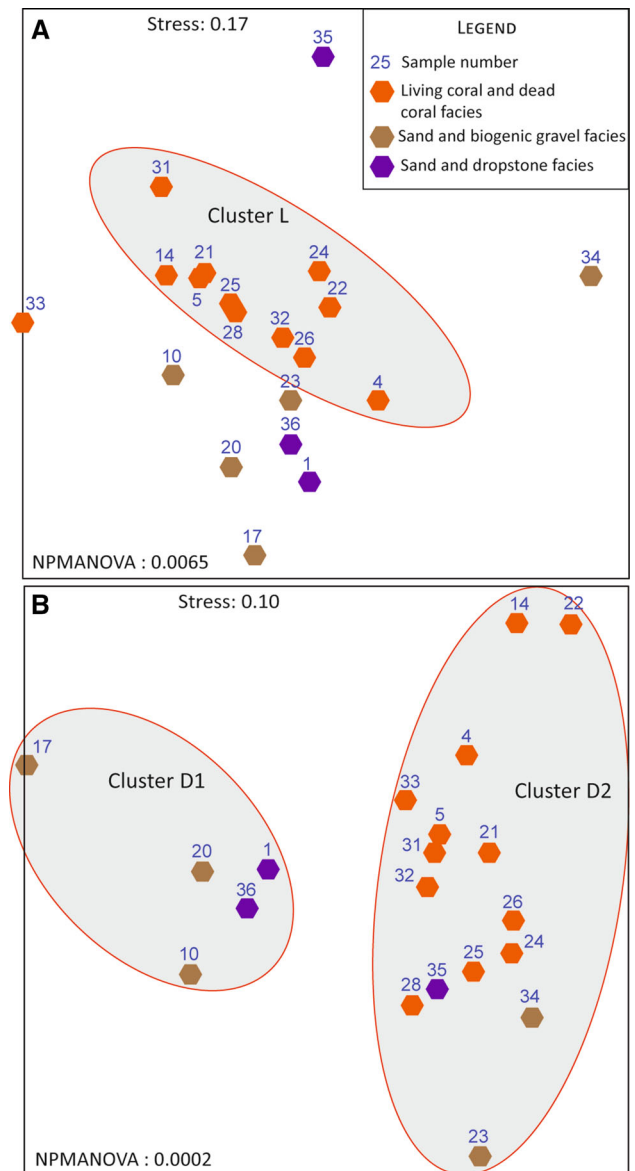

Fig. 2 Non-metric MultiDimensional Scaling (nMDS) plots based on Bray–Curtis similarity matrix of living (**a**) and dead (**b**) benthic foraminiferal assemblages. The clusters discussed in the text are represented by the grey filled ovals. Non-parametric MANOVA tests values (based on Bray–Curtis dissimilarity measures) are indicated along with the 2D stress values

Alabaminella weddellensis and *N. iridea* have the highest $\overline{\delta}_i$/SD ($\overline{\delta}_i$) ratios, demonstrating that they are good discriminating species between the Coral and No-Coral assemblages. The Coral Assemblage is more diverse than the No-Coral Assemblage (2.85 and 2.43 Shannon index, respectively) and yields approximately double the number of individuals (230/50 vs 117/50 cm^3).

The non-parametric MANOVA test, used to test the separation between the Coral Assemblage and the No-Coral Assemblage produced a *p* value of 0.0065 (Fig. 2a).
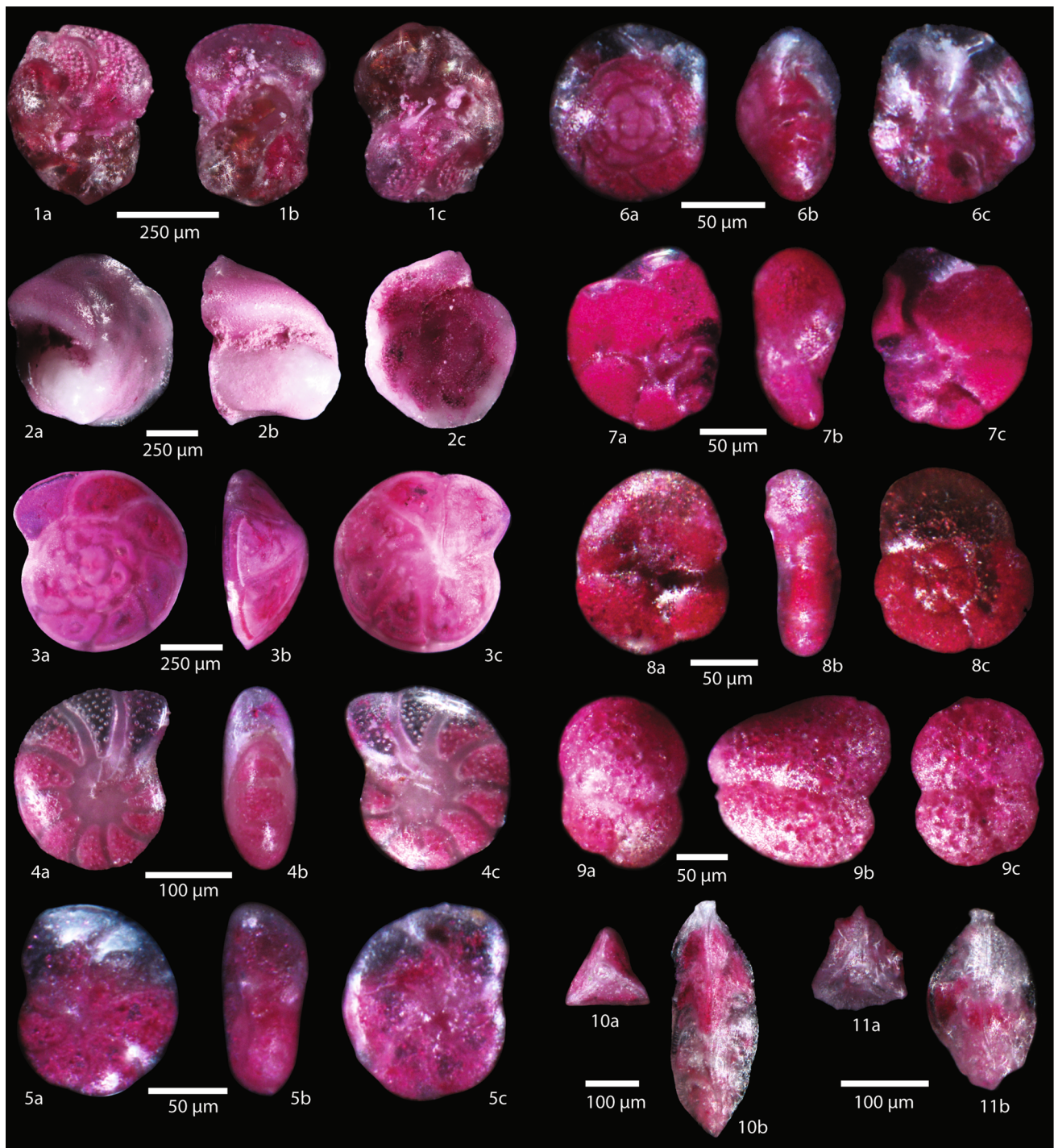
Fig. 3 Important living (stained) benthic foraminifera species identified in the Moira Mounds: **1a–c** *Discanomalina coronata* (Parker and Jones, 1857). **2a–c** *Cibicides refulgens* (de Monfort, 1808). **3a–c** *Hoeglundina elegans* (d'Orbigny, 1826). **4a–c** *Melonis barleeanum* (Williamson, 1858). **5a–c** *Hanzawaia boueana* (d'Orbigny, 1846). **6a–c** *Alabaminella weddellensis* (Saidova, 1975). **7a–c** *Nonionella iridea* (Heron-Allen and Earland, 1932). **8a–c** *Paratrochammina globorotaliformis* (Zheng, 1988). **9a–c** *Adercotryma wrightii* (Brönnimann and Whittaker, 1987). **10a–c** *Trifarina bradyi* (Cushman, 1923). **11a–c** *Trifarina angulosa* (Williamson, 1858)

3.3 Distribution of dead benthic foraminifera

One hundred and forty-three dead benthic foraminiferal species were recognized (Online Resource 2). The nMDS allows to separate two clusters: Cluster D1 (5 samples) and Cluster D2 (15 samples) (Fig. 2b). Cluster D1 groups three samples from the sand and biogenic gravel facies and two from the sand and dropstone facies. Cluster D1 groups the

samples that show clear rippled surfaces (BC20 and 10). Cluster D2 groups the remaining samples, essentially associated to the living coral and dead coral facies (Fig. 2b).

Cibicides kullenbergi, Sigmoilopsis schlumbergeri and Cassidulina teretis dominate Cluster D1 (contribution values above 19%, Online Resource 3). Cibicides kullenbergi is the most dominant species (over 28% of the average similarity). In Cluster D2, C. teretis and C. kullenbergi are also dominant (both contributing over 10%). However, in contrast with Cluster D1, C. teretis contributes more than C. kullenbergi (22 vs 10.9%). Less contributing species (between 6 and 7%) are Cassidulina crassa, Elphidium subarcticum, S. schlumbergeri and D. coronata (Online Resource 3).

Sigmoilopsis schlumbergeri and C. kullenbergi strongly contribute to the average dissimilarity (33.2%) between Cluster D1 and D2 (Online Resource 3). Sigmoilopsis schlumbergeri and C. kullenbergi also show high $\overline{\delta}_i/\mathrm{SD}(\overline{\delta}_i)$ values, together with C. crassa, Bolivina spathulata and U. mediterranea. The dissimilarity analysis confirms that C. kullenbergi and S. schlumbergeri are the species distinguishing the best between Cluster D1 and D2. Uvigerina mediterranea, more abundant in Cluster D1, and B. spathulata and C. crassa, more abundant in Cluster D2, also contribute to a lesser extent to the separation between the two clusters.

Cluster D1 has a lower Shannon Diversity Index value (2.5) than cluster D2 (3.1). The non-parametric MANOVA test, comparing Cluster D1 with Cluster D2, produced a p-value of 0.0002 (Fig. 2b).

3.4 Distribution of foraminifera in the sediments

Forty-four species were identified in the three subcores (Online Resource 2); the distribution of dominant species is illustrated in Fig. 4. Foraminiferal abundances rapidly decline downcore. However, in the presence of corals (BC26), foraminifera are more abundant in the first two centimetres of sediment, reaching over 350 individuals/ 50 cm^3 and accounting for approximately 93% of the total assemblage (Fig. 4). In absence of corals, benthic foraminifera are rarer in the first two centimetres, ranging from 150/50 cm^3 (74% of the total assemblage) for BC35 to 35/50 cm^3 (71.6% of the total assemblage) for BC34 (Fig. 4). Infaunal species represent approximately 47% of the assemblage in BC26 whereas they represent approximately 60% in BC34 and only 21% in BC35. Epibenthic species are mainly represented by H. boueana, Cibicides aravaensis, C. refulgens and C. kullenbergi, whereas infaunal species are mainly represented by T. angulosa, T. bradyi, M. barleeanum and B. pseudopunctata (Fig. 4).

Epifaunal species, such as A. weddellensis or H. boueana, are found in sediments at 6 cm downcore in BC26 and 3 cm downcore in BC34 and BC35, respectively (Fig. 4).

Although shallow in all three subcores, the ALD$_{(6)}$(infauna) is slightly shallower in presence of corals [ALD$_{(6)}$ = 1.07 cm] and slightly deeper in absence of corals [ALD$_{(6)}$ = 1.60 cm for BC34, ALD$_{(6)}$ = 2.04 cm for BC35] (Fig. 5).

3.5 Total organic carbon (TOC) in the sediments

The TOC content shows overall low values, ranging from 0.02 to 0.29% (Fig. 6). No distinct relation between TOC content, facies and benthic foraminiferal assemblages is observed (Fig. 6).

4 Discussion

The distribution of benthic foraminifera follows a complex interplay between oxygenation and food availability, which are related to the depth in the sediments and current dynamics (Fontanier et al. 2002; Schönfeld 2002; Jorissen et al. 2007). It is well known that bottom currents shape CWC mounds (Dorschel et al. 2005; Van Rooij et al. 2007; Huvenne et al. 2009b; Foubert et al. 2011; Hebbeln et al. 2016) and that the presence of coral build-ups may locally affect sedimentation (Foubert et al. 2011). This interaction creates distinct ecological niches for benthic foraminifera and other organisms (Roberts et al. 2006; Margreth et al. 2009).

4.1 Facies associated to the living benthic foraminiferal assemblage

Stefanoudis et al. (2016) demonstrated that abyssal hills influence benthic foraminiferal diversity. Similarly, the topographic highs provided by the small MM may induce higher diversity. Food sources available to foraminifera and produced by the diverse macro-organisms living within CWCs, e.g., the coral mucus itself (Wild et al. 2009), may also account for their higher diversity compared to adjacent areas. On Galway Mound, living epifauna in CWCs is more abundant (Schönfeld et al. 2011) than in the MM, where epifaunal and infaunal species are equally distributed suggesting less differentiated environments than on Galway Mound. However, Schönfeld et al. (2011) only studied the > 250 μm size fraction, thus underestimating small infaunal species (N. iridea, T. bradyi, T. angulosa, Bulimina spp. and Bolivina spp.). This different approach may account for discrepancies with the present study.

Diversity patterns in the MM also disagree with Morigi et al. (2012), who observed extremely low diversity in absence of corals on the Rockall Bank. The high currents
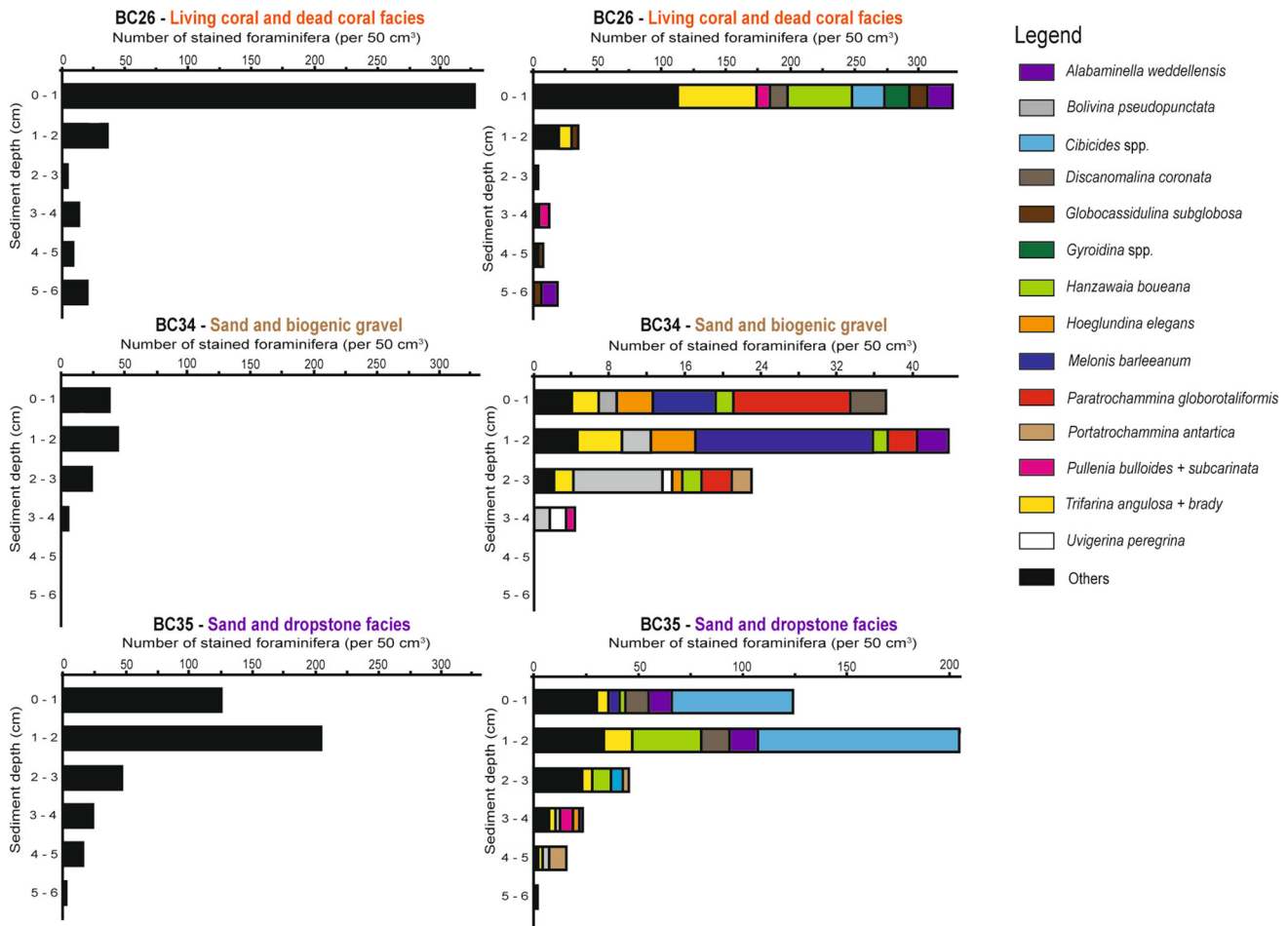
Fig. 4 Foraminiferal distribution in the sediments of box cores (BC) 26, 34 and 35. Left: total foraminiferal abundance from 0 to 6 cm depth, x axis is identical for all three samples. Right: dominant foraminiferal distribution in the sediments from 0 to 6 cm depth, attention has to be payed to the scale of the x axis
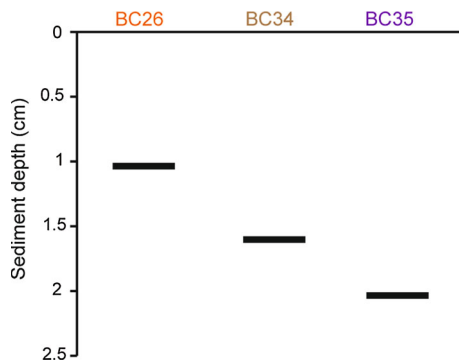

Fig. 5 Average living depth(6) (ALD) of infaunal foraminifera in box cores (BC) 26, 34 and 35. BC26: living coral and dead coral facies, BC34: sand and biogenic gravel facies, BC35: sand and dropstone facies

Fig. 6 Total organic carbon (TOC) content in box core (BC) surface sediments. Orange bars: living coral and dead coral facies; brown bars: sand and biogenic gravel facies; purple bars: sand and dropstone facies

recorded at the Rockall Bank (from 30 to 75 cm s^{-1}) and the lack of investigation of large sized debris for attached foraminifera are two explanations offered by Morigi et al. (2012) for the low diversity they observed. The abundance
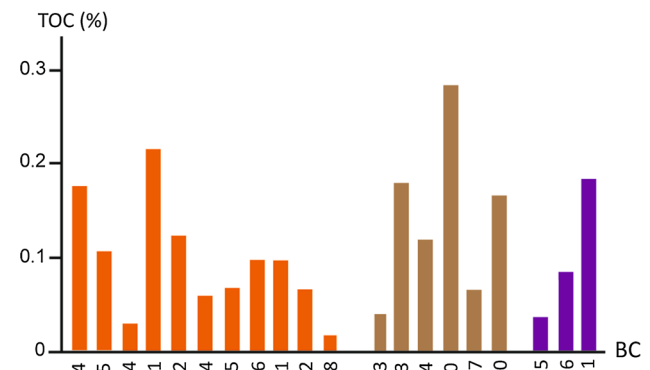
of infaunal species in the MM confirms the observations of Margreth et al. (2009) who also reported typical infaunal species on-mound.

The high abundance of the epifaunal phytodetritus-feeding *A. weddellensis* (Gooday 1993; Fariduddin and Loubere 1997; Gooday and Hughes 2002; Murray 2006; Sun et al. 2006) in the Coral Assemblage, together with the infaunal phytodetritus-feeding *N. iridea*, (Duchemin 2005; Murray 2006; Duffield et al. 2015), suggests that CWCs can trap phytodetritus that would otherwise not settle in an open setting, due to the intense currents (Fig. 7). Thus, coral and associated benthic foraminifera thrive in areas where currents are sufficiently strong to deliver phytodetritus, but are not strong enough to prevent the particulate organic matter from settling. This hypothesis is supported by Lim et al. (2017) who noticed that on the Piddington Mound in the MM area, living corals are concentrated on the lee-side of the mound. The settling of corals in these favourable areas would stabilize sediment waves and through sediment baffling, promote mound growth (Dorschel et al. 2005; Mienis et al. 2007; Huvenne et al. 2009a; Eisele et al. 2014).

High abundances of *N. iridea* and *A. weddellensis* in the Coral Assemblage may also be related to higher phytodetritus input shortly before sampling in the first week of June. Although blooms mainly occur during early to mid-spring, they may also extend to late spring in the North East Atlantic (LeBlanc et al. 2009; Van Oostende et al. 2012), producing brief high abundances of *N. iridea* and *A. weddellensis* that may not reflect the environment over a longer period of time.

In absence of corals, *C. refulgens*, associated to the sandwave facies by Margreth et al. (2009), is observed attached to dropstones in open settings, in agreement with Schönfeld et al. (2011).

4.2 Facies associated to the dead benthic foraminiferal assemblage

Dead benthic foraminiferal assemblages on the MM resemble those associated to the sandwave facies identified by Margreth et al. (2009). *Sigmoilopsis schlumbergeri* and *C. kullenbergi* dominate Cluster D1. *Sigmoilopsis schlumbergeri* positively correlates with high organic matter in the Adriatic Sea (Jorissen 1987) and in CWC environments it is considered as preferring the sandwave facies (Margreth et al. 2009). *Cibicides kullenbergi* dwells on shallow hard-substrates and mud (e.g., Corliss 1985; Schmiedl et al. 2000). It is associated to the off-mound facies in the PS, characterized by sediments containing sand-sized foraminifera, echinoids, molluscs and
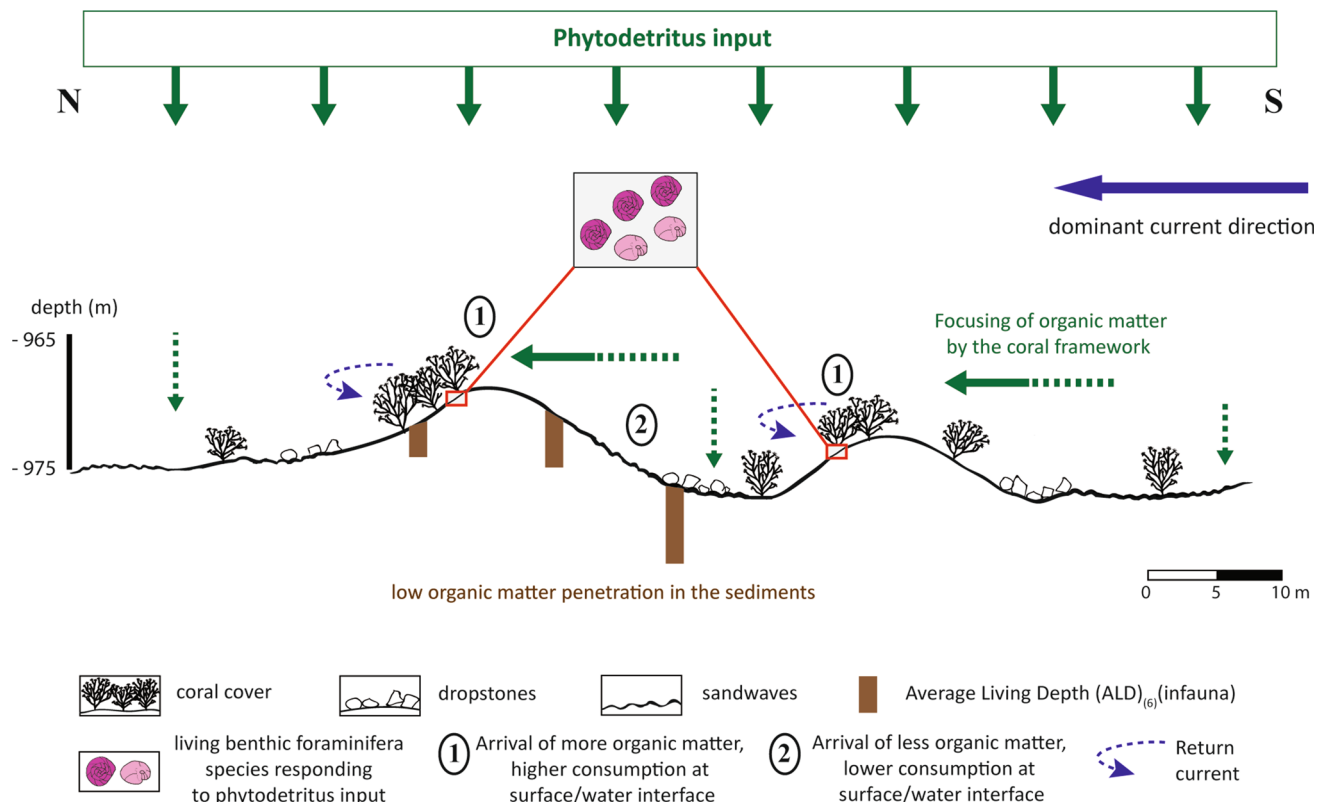

Fig. 7 Simplified ecological model of the Moira Mounds. This model represents typical mound sizes observed in the Moira Mounds. Coral distribution on the mounds is based on observations made by Lim et al. (2017). Only the mounds are to scale. Average living depth(6)(infauna) (ALD) are not to scale but proportions have been respected

terrigenous components (Margreth et al. 2009). The relatively high contribution and the high $\overline{\delta}_i/\text{SD}$ ($\overline{\delta}_i$) value of *U. mediterranea*, a shallow infaunal species typical of off-mound settings in the PS (Margreth et al. 2009; Schönfeld et al. 2011), would confirm that Cluster D1 can be related to the sandwave, dropstone and off-mound facies of Margreth et al. (2009). This observation implies different spatial distributions of benthic foraminiferal assemblages between large and small mounds. The facies model developed by Margreth et al. (2009) is based on large mounds where foraminiferal distribution is consistent with facies that develop over a large area. The MM are considerably smaller and their sedimentary facies develop within meters and/or centimetres, creating reduced microenvironments. Therefore, Cluster D1 cannot be matched to a specific facies described for large mounds; it represents instead a relatively diverse open environment.

Following the classification of Margreth et al. (2009), the higher contribution of *D. coronata* and *B. spathulata* in Cluster D2 implies a closer relationship to the living coral and sandwave facies. High abundances of *C. crassa* and *G. subglobosa* are associated to CWCs in dead assemblages from the Rockall Bank compared to off-mound settings (Morigi et al. 2012). This would suggest a close affinity of Cluster D2 to the coral facies (Fig. 2b).

4.3 Living foraminiferal assemblages in sediments

Several studies show that infaunal foraminiferal assemblages are related to food and oxygen availability (e.g., Jorissen et al. 1995; Fontanier et al. 2002; Hess et al. 2005). The TROX-model (Jorissen et al. 1995) suggests that in eutrophic areas, oxygen is the limiting factor, whereas food is the limiting factor in oligotrophic areas. The deepest penetration of benthic foraminifera in sediments is in mesotrophic conditions, where neither oxygen nor nutrient values are at a minimum. Based on infaunal foraminiferal distribution (Fig. 4) and the low TOC content in the sediments of the MM (Fig. 6), the main limiting factor appears to be food availability. In the MM benthic fauna concentrates in the upper two centimetres of sediment (Fig. 4) and consists of shallow infauna, e.g., *T. angulosa* and *H. elegans* (Hess and Jorissen 2009; Duros et al. 2011) or shallow to intermediate infaunal e.g., *M. barleeanum*, *U. peregrina* and *Gyroidina* spp. (Schmiedl et al. 2000; Fontanier et al. 2008). The slightly shallower ALD$_{(6)}$(infauna) in the presence of corals (Fig. 5) would demonstrate that food is rapidly consumed by the filtering suspension feeders (Wehrmann et al. 2009), causing limited accumulation down in the sediment, or alternatively, that it is oxidized in the upper part of the sediments. Low food

availability in the sediment would encourage shallow infaunal species such as *T. angulosa* and *T. bradyi* (e.g., Duros et al. 2011) and shallow to intermediate infaunal species such as *Gyroidina* spp. (Fontanier et al. 2002) to migrate upwards. The high foraminiferal abundance only in the first centimetre of sediment (Fig. 4), may suggest decoupling between the productive coral bearing sediments and the sediments below, the filtering suspension feeders acting as a sink for organic matter (Wehrmann et al. 2009).

Dropstones in BC35 and coral framework in BC26 offer suitable substrate for epibenthic species e.g., *Cibicides* spp. (Fig. 4), whereas the abundance of infauna in BC34 can be related to the absence of both dropstones and coral (Fig. 4). The infaunal *Pullenia* spp., *H. elegans* and *B. pseudopunctata* (Geslin et al. 2004; Murray 2006; Wollenburg and Mackensen 2009) are found below the first two/three centimetres of sediment (Fig. 4). The relative high abundances of *M. barleeanum* in the upper two centimetres, together with *Paratrochammina globorotaliformis*, characterizes BC34 (Fig. 4). *Melonis barleeanum* has been described as an intermediate infaunal species dependent on aerobic and anaerobic bacterial stocks that degrade refractory organic matter (Schmiedl et al. 2000; Fontanier et al. 2002, 2005). The ecology of *P. globorotaliformis* is not well constrained, however, a related species, *Paratrochammina haynesi*, is documented attached to gravel and shells, in crevices or ribs in current swept areas such as channels (Murray and Alve 1993; Murray 2006), suggesting similar preferences for *P. globorotaliformis* in the MM. The intense currents that sweep the MM may confirm a similar ecological preference. Box core 34 is situated on the south current facing side of the Piddington Mound (Lim 2017), where strong currents and the absence of baffling organisms (e.g., corals) may create a habitat relatively depleted in fresh organic matter. This may favour the proliferation of *M. barleeanum* and *P. globorotaliformis*, whilst reducing total foraminiferal abundance.

Foraminifera can quickly respond to changes in the microhabitat (Fontanier et al. 2008). Kiriakoulakis et al. (2004) propose that large echiuran worms may produce intense bioturbation in the Darwin Mounds. Bioturbation may deeply shape microhabitats where some benthic species can adapt to live after transport (Fontanier et al. 2008; Duros et al. 2011). In the Whittard Canyon, Duros et al. (2011) observed the shallow infaunal *T. angulosa* and *B. spathulata* at 10 cm sediment depth, living in the more oxygenated internal surface of burrows. In BC35, *T. angulosa* occurs from the surface down to a depth of 5 cm in the sediment. In contrast, *Pullenia* spp. prefers a specific depth from 3 to 4 cm in the sediments (Fig. 4). The continuous presence of *T. angulosa* at different depths could confirm the ability of this species to colonize burrows. The presence of *G. subglobosa* and *A. weddellensis* in the sediments between 5 and 6 cm

depth in BC26 may also be the result of bioturbation. Indeed, *A. weddellensis* is an epibenthic species (Gooday 1993; Gooday and Hughes 2002; Murray 2006; Sun et al. 2006), whilst *G. subglobosa* is as a shallow infaunal species living in the first two centimetres of sediment (Mackensen and Douglas 1989; Enge et al. 2012). Remobilization of sediments by currents could also displace benthic foraminifera in the sediments. Huvenne et al. (2009a) recognized the possible existence of "benthic storms" (Hollister and McCave 1984) with current velocities reaching up to 30 cm s^{-1} in the Darwin Mounds (Northern Rockall Trough). Lim (2017) calculated velocities of up to 40 cm s^{-1} in the MM region. In such high-energy environments, currents could easily displace the upper first centimetres of sediment and mobilize foraminifera.

5 Conclusion

This study suggests that high abundances of living *N. iridea* and *A. weddellensis* can be related to the coral framework's ability to capture phytodetritus in the Moira Mounds. Corals and associated benthic foraminifera thrive where currents are strong enough to mobilize nutrients, but not so strong as to be harmful for the ecosystem. This equilibrium may trigger mound growth through sediment baffling. Foraminifera are essentially present in surface sediments due to higher food availability. Benthic foraminiferal distribution in depth is shallow and is possibly impacted by bioturbation and the strong currents influencing the area. Higher abundances and diversity of living benthic foraminifera are observed in the living and dead coral facies. The Moira Mounds differ from larger adjacent mounds by lower spatial variability in foraminiferal assemblages. Clear facies distinction can only be based on living foraminiferal assemblages, and can only be made according to presence vs absence of corals.

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