



# Benthic foraminifera as bioindicator for cold-water coral reef ecosystems along the Irish margin

Stephan Margreth<sup>a,\*</sup>, Andres Rüggeberg<sup>b,1</sup>, Silvia Spezzaferri<sup>a</sup>

<sup>a</sup> University of Fribourg, Department of Geosciences, Chemin du Musée 6, 1700 Fribourg, Switzerland

<sup>b</sup> Leibniz-Institute of Marine Sciences, IFM-GEOMAR, Wischhofstrasse 1-3, 24148 Kiel, Germany

## ARTICLE INFO

### Article history:

Received 4 November 2008

Received in revised form

6 July 2009

Accepted 20 July 2009

Available online 19 August 2009

### Keywords:

Benthic foraminifera

Faunal assemblage

Cold-water coral facies

Carbonate mound

*Discanomalina coronata*

## ABSTRACT

Cold-water coral ecosystems building cold-water carbonate mounds occur worldwide and are especially developed along the European margin, from northern Norway to the Gulf of Cadiz. A remarkable mound province is documented southwest of Ireland along the Porcupine and Rockall Banks. In this area carbonate mounds are formed in water depths between 500 and 1200 m and are often densely settled by cold-water coral ecosystems offering many ecological niches for benthic foraminifera. We investigated total (unstained) benthic foraminiferal assemblages from surface sediments (0–1 cm, >63 µm size fraction) of this region with the aim to trace their distribution patterns and to test if they can be used as bioindicators for facies characterization in different parts of carbonate mound systems. Our quantitative data were further statistically treated with non-metric multidimensional scaling (nMDS) based on Bray–Curtis similarity matrix to highlight community patterns that were not readily apparent. Our results indicate that different benthic foraminiferal assemblages characterize different facies along cold-water carbonate mounds and are related to the environmental conditions and available substrates. The following facies can be described: (1) the *Off-Mound Facies* is dominated by uvigerinids and other infaunal species; (2) the *Dropstone Facies* is characterized by infaunal *Globocassidulina subglobosa* and attached-epifaunal *Cibicidoides* sp.; (3) the *Dead Coral Facies* is characterised by epifaunal species (e.g., *Planulina ariminensis*, *Hanzawaia boueana*) and infaunal species (*Spiroplectinella wrightii*, *Angulogerina angulosa*, *Epistominella vitrea*); (4) the *Living Coral Facies* includes both infaunal and epifaunal species, but is dominated by the epifaunal *Discanomalina coronata*; and (5) the *Sandwave Facies* contains high abundances of epifaunal species including *D. coronata*. Based on this distribution, we propose *D. coronata*, as an indicator species to identify active mounds and/or living cold-water coral ecosystems. Our results also emphasise the importance of studying the small size fractions that yield many infaunal species. A causal link exists between distribution patterns of benthic foraminifera and cold-water coral facies, thus providing an independent tool to identify and describe the different facies in this setting.

© 2009 Elsevier Ltd. All rights reserved.

## 1. Introduction

Cold-water coral ecosystems occur worldwide and are developed along the European margin, from northern Norway (Fosså et al., 2002; Freiwald et al., 1997, 1999; Hovland et al., 1998; Lindberg and Mienert, 2005;

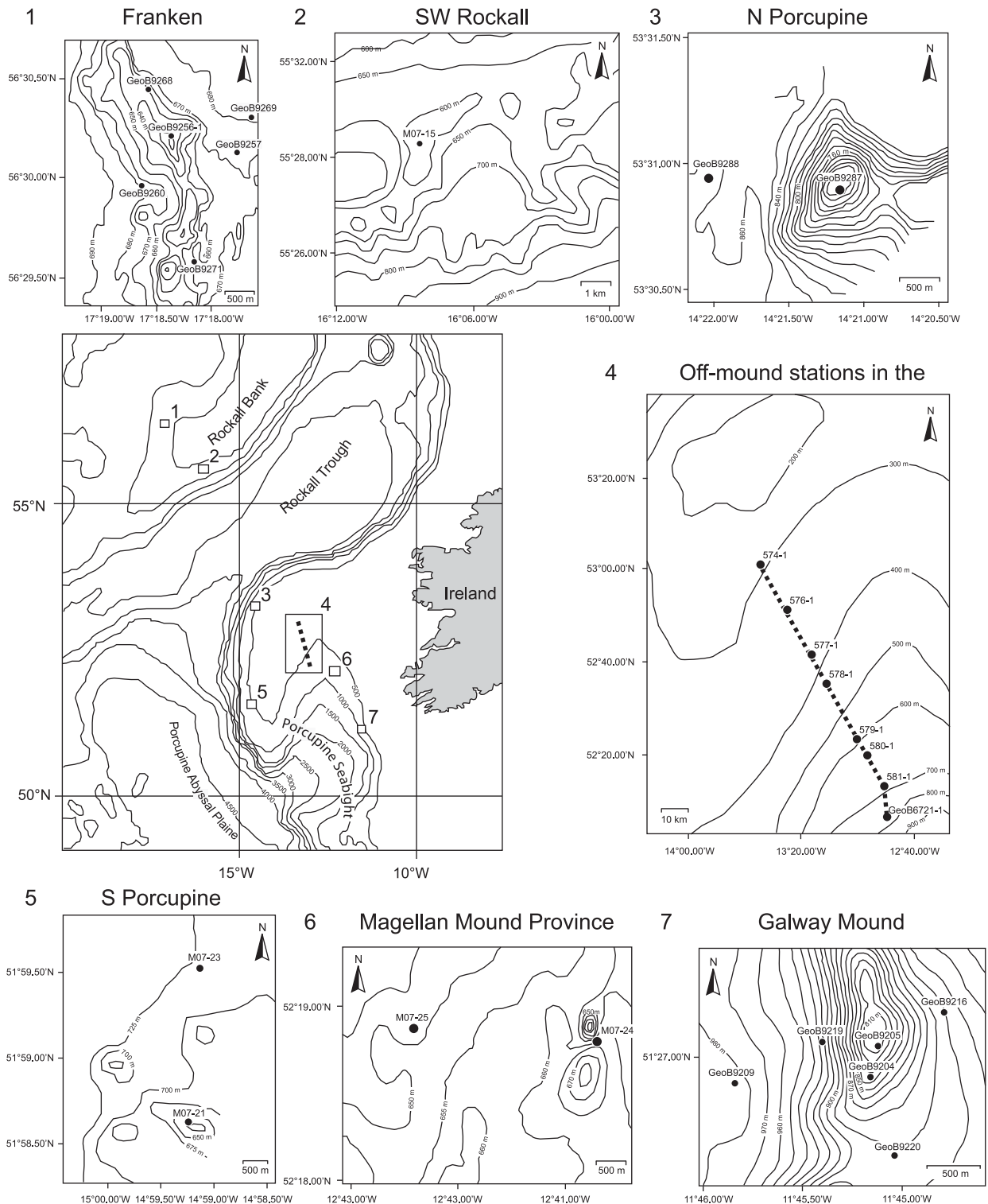
\* Corresponding author.

E-mail address: [stephan.margreth@unifr.ch](mailto:stephan.margreth@unifr.ch) (S. Margreth).

<sup>1</sup> Present address: Renard Centre of Marine Geology, Ghent University, Krijgslaan 281, S-8, 9000 Gent, Belgium.

Mortensen et al., 1995) along the Irish margin (De Mol et al., 2002; Hovland et al., 1994; Kenyon et al., 2003; Van Rooij et al., 2003) down to the Gulf of Cadiz (Pinheiro

et al., 2003; Somoza et al., 2003), and in the Mediterranean Sea (Taviani et al., 2005; Zibrowius, 1980). These ecosystems have been known since the last century. Cold-water



**Fig. 1.** Location map of the surface sediment samples investigated in this study. The different carbonate mound provinces along the Rockall Bank (1, 2), the Porcupine Bank (3, 5), and the Porcupine Seabight (4, 6, 7) are highlighted.

corals were collected and successively studied by Duncan (1870, 1873, 1878), Gravier (1915, 1920), and mapped by Joubin (1922a, b, 1923). The investigation of these ecosystems proceeded more quickly in Norway where cold-water corals were more easily accessible. However, research accelerated only in the last two decades after Hovland et al. (1994) described a group of seabed mounds, suspected to be modern bioherms off western Ireland. Since then, research has progressed quickly within the framework of several European and international projects (ECOMOUND, GEOMOUND, ACES, MOUNDFORCE, MICRO-SYSTEM, HERMES).

On the Rockall and Porcupine Banks, cold-water corals, particularly the scleractinians *Lophelia pertusa* and *Madrepora oculata*, build up carbonate mounds. These mounds considerably differ in size and some are partially or fully buried (De Mol et al., 2002; Huvenne et al., 2003). Recent investigations in this area revealed that successive phases of coral growth might be superimposed on fossil coral debris building mounds up to a few hundred meters in height (Wheeler et al., 2007). The amount of living corals is presently used as the main parameter for “activity” of cold-water carbonate mounds. If living corals are abundant, the mound is considered to be in a growing state – a so-called “active” or “active growing” mound (Henriet et al., 2002; Rüggeberg et al., 2007). If living corals are absent and pelagic sediment covers the mound, it is then defined as a “buried” mound and is only visible on seismic sections (De Mol et al., 2002; Freiwald, 2002).

Presently, cold-water coral mounds are described and classified based on their sedimentary facies and type of coral coverage. Foubert et al. (2005) introduced 12 different facies for seabed classification and used them for interpreting ROV video surveys in the Belgica Mound Province. The study of Dorschel et al. (2007a), focused on Galway Mound, reduced the number of the different facies to seven from mound top down to the basin: (1) dense coral coverage (mostly alive); (2) dense coral coverage (mostly dead); (3) sediment clogged dead coral framework and/or coral rubble; (4) patchy distribution of mostly live (or dead) coral on un-rippled seabed; (5) patchy distribution of mostly dead coral on rippled seabed; (6) sandwaves covered with corals (overgrown sandwaves); (7) patchy distribution of dropstones. Dorschel et al. (2007a) also demonstrated that the spatial distribution of the different facies correlates with different small-scale environmental settings and in particular, with local hydrodynamic regimes.

However, until now only a few studies targeted foraminiferal assemblages and their relation to cold-water coral ecosystems along the European continental margin (e.g., Freiwald and Schönfeld, 1996; Hawkes and Scott, 2005; Rüggeberg et al., 2007). The present study focuses on the distribution patterns of total (unstained) benthic foraminiferal assemblages that are associated with different cold-water coral mounds on the Rockall and Porcupine Bank area (Fig. 1). The aims of this study are to: (a) identify the distribution patterns of benthic foraminifera on cold-water coral mounds in the investigated area; (b) relate these to the different facies; and (c) propose a model for assemblage versus facies distribution that can be applied to other carbonate mounds in similar settings.

## 2. Study area

The Porcupine and the Rockall Banks are situated in the Northeast Atlantic west of Ireland (Fig. 1). Steep flanks characterize the Rockall Trough, a deep-sea channel between the Porcupine Bank to the east and the Rockall Bank to the west. The Porcupine Bank and the Irish Mainland Shelf delimit a small basin, the Porcupine Seabight, which opens to the west onto the Porcupine Abyssal Plain. Along the flanks of the Porcupine Bank and Porcupine Seabight numerous carbonate mounds of different sizes are documented (e.g., De Mol et al., 2002; Foubert et al., 2007; Huvenne et al., 2002, 2003; Mienis et al., 2006). In particular, three carbonate mound provinces are located along the margin of the Porcupine Seabight: (a) the Belgica Mound Province, which is located along the steep eastern slope, (b) the Hovland Mound Province along the margin of the central Porcupine Seabight and (c) the Magellan Mound Province north of the Hovland Mound Province (De Mol et al., 2002; Henriet et al., 1998; Huvenne et al., 2003; Van Rooij et al., 2003).

Several mounds from the Porcupine and Rockall Bank region have been investigated for the present study (Fig. 1). (1) The Franken Mound is situated on the steep western slope of the Rockall Bank at 600–675 m water depth. Its summit rises 80–100 m above the surrounding seafloor. It is 2.5 km long and 600–700 m wide. It has a more irregular shape compared to the ovate shape of the Galway and the Propeller mounds in the Porcupine Seabight (Wienberg et al., 2007). (2) Single mounds on the southeastern Rockall margin, up to 1–2 km in diameter and 50–100 m of elevation. They are all located in a water depth between 650 and 900 m (Akhmetzhanov et al., 2003; Mienis et al., 2006; Rogers, 1999; Van Weering et al., 2003). (3) The Connaught Mound located on the steep slope of the Northern Porcupine Bank. It is orientated north–south, about 3 km long and 1.7 km wide with an elevation above the seafloor of 180 m and a water depth at the summit of 680 m. (4) The Propeller Mound is situated in the Hovland Mound Province. Its summit is at a water depth of 680 m, its elevation above the surrounding seafloor is 140 m (Dorschel et al., 2005, 2007b; Rüggeberg et al., 2005, 2007). (5) Unnamed mound from the western Porcupine Bank discovered in 2008 during the ‘Pelagia’ cruise M07II. (6) Unnamed half buried mounds from the Magellan Mound Province (De Mol et al., 2002; Huvenne et al., 2003). (7) The Galway Mound, which is part of the Belgica Mound Province. Its summit is at 782 m water depth and its elevation above the seafloor is 160 m (Dorschel et al., 2007a). It belongs to an “active” and “growing” mound chain with a dense coverage of living corals (De Mol et al., 2002; Foubert et al., 2005; Huvenne et al., 2005; Wheeler et al., 2005).

## 3. Material and methods

During four different cruises (RV ‘Meteor’ cruise M61-3, RV ‘Poseidon’ cruises P265, and P292, and RV ‘Pelagia’ cruise M07II) carbonate mounds and pelagic sediments were sampled at 27 stations in the Rockall and Porcupine

Bank region (Table 1). A giant box corer with a sampling area of  $50 \times 50$  cm allowed a maximum 50 cm penetration into the sediments. All retrieved samples were taken from cold-water coral mounds and/or the adjacent pelagic sediments. Samples P292/564-1, P292/576-1, P292/577-1, P292/578-1, P292/579-1, P292/580-1, P292/581-1, and GeoB6721-1 were retrieved along a bathymetric transect from the Porcupine Bank at ~200 m down to the Porcupine Seabight at ~750 m (Fig. 1). A sample from the uppermost two centimetres of each box core was taken with a teflon spatula and stored in plastic containers. Additionally, video records obtained by an underwater video camera or a Remotely Operated Vehicle (ROV 'Quest' and 'Cherokee' of MARUM, University Bremen) were used to characterize the seafloor, together with descriptions of cores from unpublished cruise reports (De Haas, 2007; Freiwald et al., 2000; Freiwald and Shipboard Party, 2002; Ratmeyer and Shipboard Party, 2004).

Sediment samples for micropaleontological analyses were processed at the University of Fribourg following Spezzaferri and Coric (2001). Samples were washed through a set of 250, 125 and  $63 \mu\text{m}$  mesh sieves to obtain three size fractions. The obtained residues were dried at room temperature and weighted. If the residue contained more than 400 foraminiferal specimens in one fraction, the volume was reduced by splitting. A maximum of 200 benthic specimens per fraction (600 specimens per sample) were picked, collected in Plummer cell-slides, sorted at species level, fixed with glue, and counted. In the case of samples containing less than 100 specimens per fraction, all specimens were counted. The 124 benthic foraminiferal species identified are listed in Appendix A.

Multivariate statistical treatment on the compositional faunal data was performed with the software PRIMER 5 (Clarke, 1993; Clarke and Warwick, 2001). Data were double-square root transformed in order to limit the contribution of most abundant, ubiquitous species (Field et al., 1982). Bray–Curtis (dis-)similarities were calculated following Clifford and Stephenson (1975). The resulting similarity matrix was used to obtain the nMDS plot (non-metric MultiDimensional Scaling; Kruskal, 1964; Kruskal and Wish, 1978). The nMDS plot has no dimensions and no axes and can be arbitrarily scaled, rotated, located or inverted as it gives simply the relationship of samples relative to each other (Clarke and Warwick, 2001; Warwick and Clarke, 1991). Based on the clusters given in the nMDS plot, the Similarity Percentage Analysis (SIMPER) was obtained to highlight the contribution of each species to the total average (dis-) similarity between different groups and within one group (e.g., Basso and Spezzaferri, 2000; Clarke and Warwick, 2001; Kruskal, 1964; Kruskal and Wish, 1978). Taxonomic notes, census data, and compositional data of the benthic foraminiferal taxa used for multivariate statistic are given in Appendices A and B.

## 4. Results

### 4.1. Facies description

Field observations (video images taken on board with underwater video camera, ROV camera, and core description) and sediments recovered in core samples allowed to identify five different facies types (Table 1):

**Table 1**

Sample number, geographical position, water depth, region, mound region and facies of the investigated samples.

Station	Latitude (°N)	Longitude (°W)	Depth (m)	Region	Mound region	Facies
GeoB 9220	51°26.69	11°45.04	892	Porcupine Seabight	Belgica	Sandwave
GeoB 9209-2	51°26.89	11°45.81	982	Porcupine Seabight	Belgica	Sandwave
GeoB 9204-1	51°26.94	11°45.16	838	Porcupine Seabight	Belgica	Living coral
GeoB 9205-1	51°27.04	11°45.12	810	Porcupine Seabight	Belgica	Living coral
GeoB 9219-1	51°27.05	11°45.40	920	Porcupine Seabight	Belgica	Living coral
GeoB 9216-1	51°27.09	11°44.81	890	Porcupine Seabight	Belgica	Living coral
M07-21	51°58.65	14°59.18	627	Porcupine Seabight	SW Porcupine Bank	Dead coral
M07-23	51°59.54	14°59.05	721	Porcupine Seabight	SW Porcupine Bank	Off-mound
GeoB 6721-1	52°09.22	12°46.31	696	Porcupine Seabight	Hovland	Off-mound
P292/581-1	52°13.40	12°50.24	736	Porcupine Seabight		Off-mound
M07-24	52°18.86	12°40.78	663	Porcupine Seabight	Magellan	Dead coral
M07-25	52°18.87	12°42.42	647	Porcupine Seabight	Magellan	Off-mound
P292/580-1	52°20.46	12°56.72	630	Porcupine Seabight		Off-mound
P292/579-1	52°23.62	13°01.56	554	Porcupine Seabight		Off-mound
P292/578-1	52°35.67	13°10.74	450	Porcupine Seabight		Off-mound
P292/577-1	52°41.78	13°16.43	356	Porcupine Seabight		Off-mound
P292/576-1	52°51.40	13°25.39	249	Porcupine Seabight		Off-mound
P292/574-1	53°00.80	13°34.04	202	Porcupine Seabight		Off-mound
GeoB 9287	53°30.91	14°21.16	696	Porcupine Bank	N Porcupine Bank	Living coral
GeoB 9288	53°31.06	14°21.77	870	Porcupine Bank	N Porcupine Bank	Dropstones
M07-15	55°29.18	16°08.24	552	Rockall Bank	SE Rockall Trough	Living coral
GeoB 9271	56°29.58	17°18.16	664	Rockall Bank	SW Rockall Bank	Dropstones
GeoB 9260	56°29.98	17°18.63	683	Rockall Bank	SW Rockall Bank	Dropstones
GeoB 9257	56°30.13	17°17.77	678	Rockall Bank	SW Rockall Bank	Dropstones
GeoB 9256-1	56°30.20	17°18.37	629	Rockall Bank	SW Rockall Bank	Dead coral
GeoB 9269	56°30.28	17°17.63	686	Rockall Bank	SW Rockall Bank	Dropstones
GeoB 9268	56°30.44	17°18.62	656	Rockall Bank	SW Rockall Bank	Dead coral



- (1) *Off-Mound Facies*: the distal parts of the cold-water carbonate mounds, the fine-grained pelagic sediments contain sand-sized benthic and planktonic foraminifera, echinoids, molluscs, and terrigenous components.
- (2) *Dropstone Facies*: large mounds (e.g., Galway Mound) are flanked by erosional moats formed by bottom currents (De Mol et al., 2002). These moats consist of sandy and silty sediments, sometimes rippled, containing dropstones up to 10 cm in diameter. Fragments of bryozoans, molluscs, and corals, generally characterize this facies.
- (3) *Dead Coral Facies*: this facies consists mainly of dead coral debris accumulating at the lower flanks and/or base of the mounds. Fine-grained sediments, mud and silt, trapped by the coral debris, are deposited to form a soft-sediment substratum containing pieces of molluscs and echinoids. The amount of coral debris decreases towards the distal parts of this facies.
- (4) *Living Coral Facies*: mainly developed on the upper flanks of the mounds and partially on their summits, this facies consists of a dense cover of living cold-water corals, mainly *L. pertusa* and *M. oculata*. Corals may colonize a hard substratum composed of dead coral debris or coarse sand. Also in this facies, muddy and silty sediments are trapped by the coral build-ups. However, the trapped sediments can be finer than in the *Dead Coral Facies*.
- (5) *Sandwave Facies*: the sandwave facies can co-exist with all the other facies. However, this facies is generally developed on the mound flanks (e.g., Galway and Franken Mounds) or close to the summit (Propeller Mound) within or close to the *Living Coral Facies* (Rüggeberg et al., 2007). Single branches or small patches of living cold-water corals colonize the sandy sediments and/or fragments of dead corals.

#### 4.2. Benthic foraminiferal assemblages in surface sediments

A total of 124 (unstained) benthic foraminiferal species belonging to 75 genera were identified in the studied region (Appendix A). The samples collected along the bathymetric transect (water depths between 202 and 736 m) from the Porcupine Bank into the Seabight document the variation of benthic foraminiferal assemblages with depth in this area (Figs. 1 and 2; Table 1).

In the shallowest part of the Porcupine Bank (202, 249 and 356 m) *Cassidulina carinata* dominates the assemblage (50% at 202 m, 24.9% at 249 m, and 10.7% at 356 m, respectively). The accompanying species at 202 m include abundant *Globocassidulina subglobosa* (up to 14.9%), and at 249 m abundant *Cibicidoides pachyderma* (20.5%). The abundances of uvigerinids increase with increasing depth reaching a maximum of 40.6% at 554 m, but they show abundances still around ~30% down to 736 m. *Hyalinea balthica* and *Bulimina marginata* are abundant in the whole transect with a maximum between 356 and 630 m water depth. Below 450 m water depth *Melonis barleeanum*, *Epistominella vitrea* and *Epistominella exigua* are important

representatives of the community. Other deep-water taxa are present in lower amounts. For example, the highest abundance of *Angulogerina angulosa* (9.3%) is recorded at 356 m. Sample GeoB6721-1 is located within the Hovland mound region on the summit of a cold-water coral mound. In comparison to other mounds in this region the sediment does not contain coral rubble, dropstones or sandwaves, indicating no recent settling of *L. pertusa*. Therefore we classify it as off-mound sediment but relatively close to cold-water corals. Transport could be the reason for the abundance of epifaunal-attached foraminiferal species like *Planulina ariminensis*, *Discanomalina coronata*, *Cibicidoides ungerianus*, and *Fontbotia wuellerstorfi*.

#### 4.3. Statistical treatment

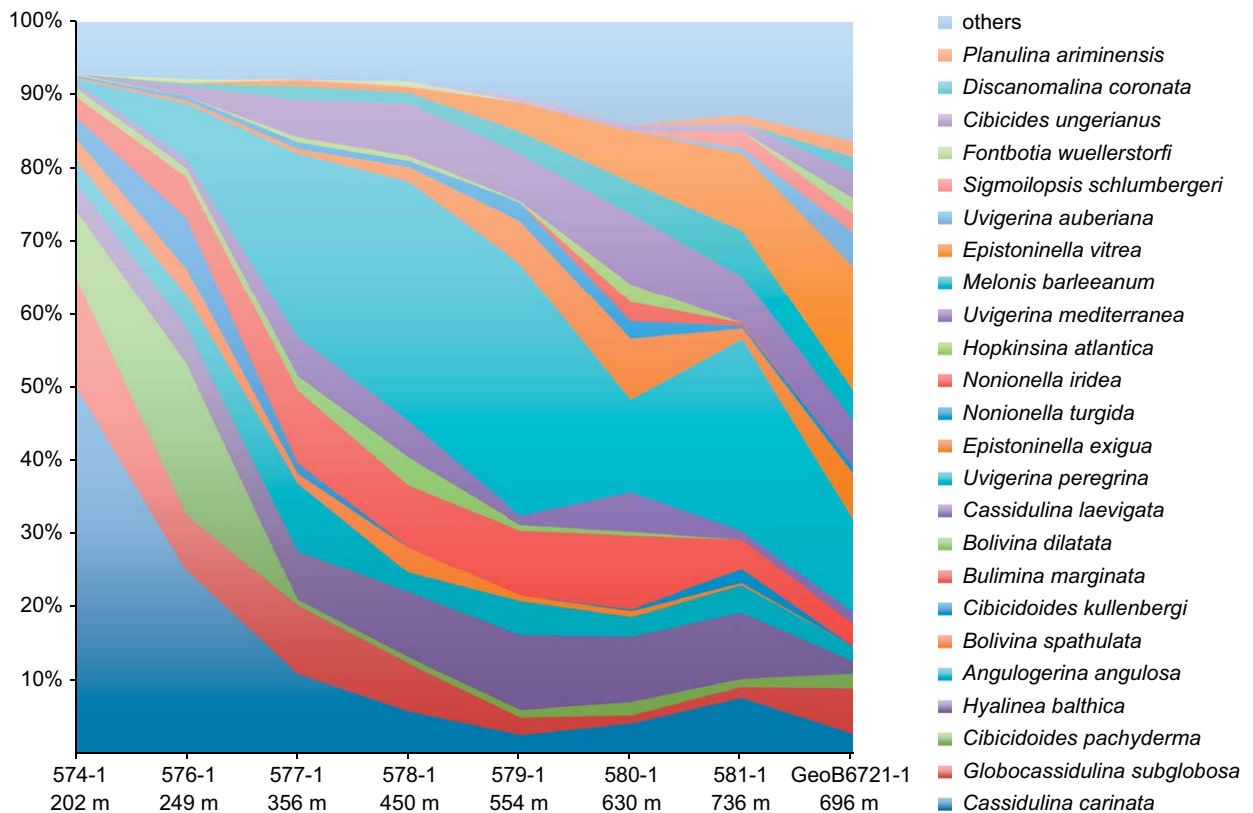
Since patterns of community structures are often not readily apparent (Clarke and Warwick, 2001), we have applied the Bray–Curtis Similarity clustering to our data, which is an excellent method to treat community data in order to highlight patterns in benthic foraminiferal distribution (Kenkel and Orloci, 1986). At the 100% of Bray–Curtis Similarity, 5 clusters (1–5) can be distinguished. On the basis of the same similarity matrix samples are ordinated by non-metric MultiDimensional-nMDS (Kruskal, 1964; Kruskal and Wish, 1978), with a stress value of 0.19 (Fig. 3, Table 3).

Cluster 1 groups samples 574-1, 576-1, 577-1, 578-1, 579-1, 580-1, 581-1, GeoB6721-1, M07-23, and M07-25 (Bray–Curtis Similarity 49%). Eleven species and/or groups account for 90.4% of the average similarity of this cluster (Table 3). Cluster 2 combines samples 9257, 9269, 9260, 9271, and 9288 (Bray–Curtis Similarity 58%). Ten species and/or groups account for 91.1% of the average similarity of this cluster (Table 3). Cluster 3 groups samples M07-21, M07-24, 9256-1, and 9268 (Bray–Curtis Similarity 51.1%). Eleven species and/or groups account for 90.2% of the average similarity of this cluster (Table 3). Cluster 4 assembles samples 9204-1, 9205-1, 9216-1, 9219-1, 9287, and M07-15 (Bray–Curtis Similarity 51.1%). Fourteen species and/or groups account for 90.9% of the average similarity of this cluster (Table 3). Cluster 5 combines only two samples, 9209-2 and 9220 (Bray–Curtis Similarity 49.5%). Eleven species and/or groups account for 90.4% of the average similarity of this cluster (Table 3).

## 5. Discussion

### 5.1. Potential indicator species

We investigated total (unstained) assemblages from surface sediments recovered in the Porcupine Seabight and Rockall Bank carbonate mound systems. A total assemblage may result from complex interaction of environmental parameters, including the original microhabitat of the living forms, reworking, winnowing, dissolution, and bacterial decomposition of organic test components, which create differences between the live and dead components (Licari and Mackensen, 2005;



**Fig. 2.** Percent distribution of the most abundant species (>2%) along a bathymetric transect comprising 8 off-mound-station in the Porcupine Seabight. (in colour for web- and print version).

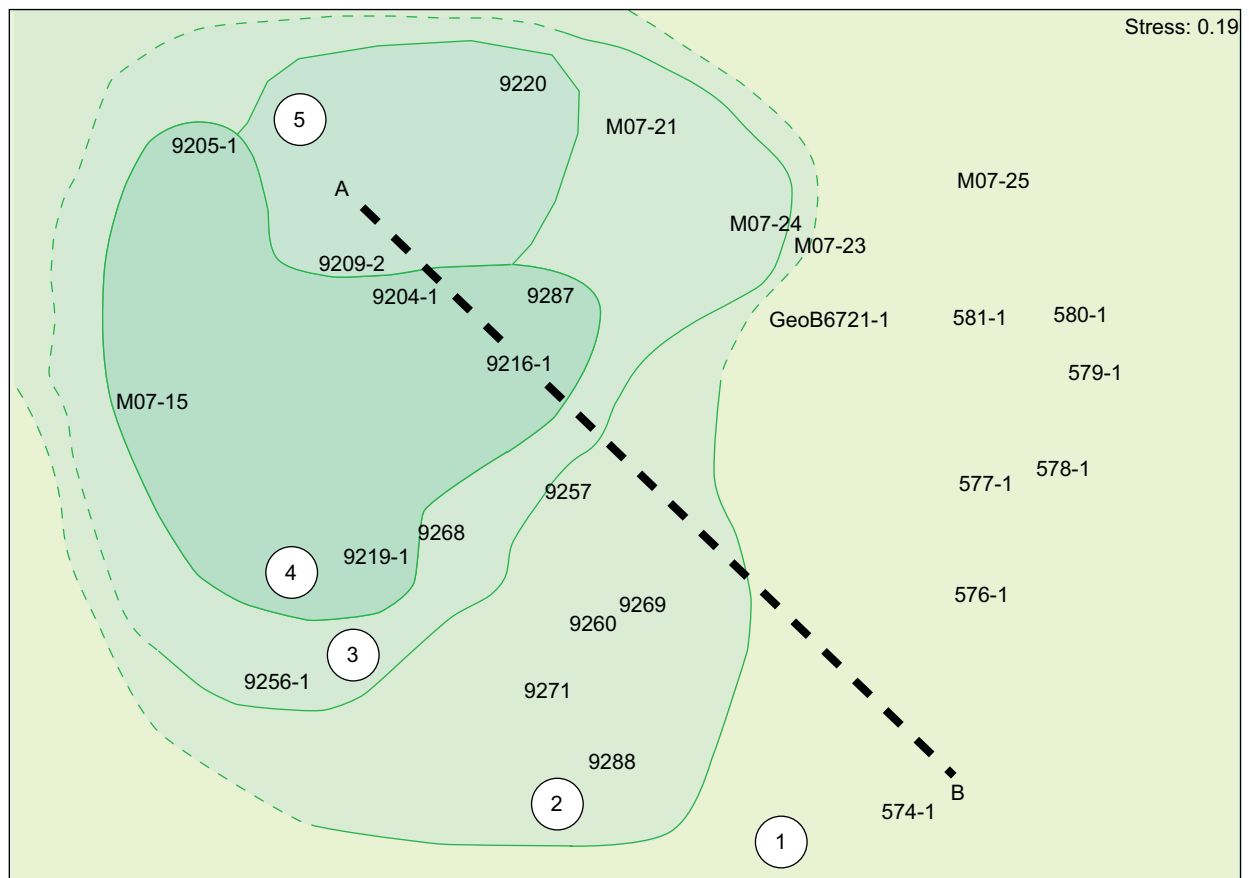
Loubere, 1989; Mackensen and Douglas, 1989). For this reason we probably miss some of the monothalamous and soft-shelled foraminiferal species (Gooday and Hughes, 2002). Nevertheless, the aim of this study is to define benthic foraminiferal assemblages that can help to identify different mound facies in the paleo-record. We therefore exclude soft-shelled species since they are rarely preserved in the fossil record. Although monothalamous and soft-shelled species are very important components of cold-water coral ecosystems, they are rarely preserved in the fossil record and are not treated in the present study.

## 5.2. Environmental interpretation

The spatial distribution of benthic foraminifera is controlled by a combination of environmental parameters (e.g., Gooday 2003; Grimsdale and van Morkhoven, 1955; Gupta, 1997; Jorissen et al., 2007; Lutze and Coulbourn, 1984; Murray, 1991, 2006; Natland, 1933; Pflum and Frerichs, 1976; Schönfeld, 2002a,b; Van der Zwaan et al., 1999; Table 2). Among the most important parameters controlling the distribution of these organisms in the deep sea are the organic flux to the seafloor and the bottom water oxygenation (e.g. Jorissen, 1988; Lutze and Coulbourn, 1984; Mackensen et al., 1990, 1995; Miller and Lohmann, 1982; Schmiedl and Mackenesen, 1997).

The quality of the organic matter, and the degree of seasonality in its delivery to the seafloor, are also important (Fontanier et al., 2002, 2005). Where current velocities are high, bottom flow, together with substrate characteristics, play a central role in the distribution of benthic foraminiferal assemblages (Schönfeld 1997, 2002a, b).

Weston (1985) compared living and dead foraminiferal assemblages (>125 µm) from surface samples south of 51°50'N in the Porcupine Seabight, the area where big cold-water coral mounds on elevated substrates were originally discovered (Hovland et al., 1994; Rüggeberg et al., 2007). The assemblages of Weston (1985) show zonation with respect to water depth. In particular, Weston found high numbers of *B. marginata* and *C. carinata* above 700 m water depth and attached living species, e.g. *Lobatula lobatula*, *Cibicides refugens*, below this depth. In the area that we investigated, benthic foraminiferal assemblages are dominated by infaunal species. In particular, *G. subglobosa*, *Uvigerina peregrina*, *Uvigerina mediterranea*, *E. vitrea*, *C. carinata*, *Cassidulina laevigata*, *A. angulosa*, and *B. marginata* are generally very abundant (Appendix B). Clear depth-related patterns in these assemblages, of the kind observed by Weston (1985), are not obvious (Fig. 1, Appendix B). Instead, benthic foraminiferal distribution patterns reveal a link between assemblages and facies. In particular, the infaunal uvigerinids and cassidulinids display the highest



**Fig. 3.** Non-metric MultiDimensional Scaling (nMDS) plot obtained from Bray–Curties similarity matrix of benthic foraminifera compositional data. The different clusters (1–5) are illustrated in different greyscales. The cluster arrangement corresponds to the facies distribution of an active cold-water coral mound. Transect A–B is illustrated in Fig. 4. The stress represents the distortion involved in compressing the data from a multidimensional space into a smaller number of dimensions (Field et al., 1982). (in colour for web version and black and white for print version).

abundance in off-mound surface sediments, whereas *G. subglobosa* and *E. vitrea* dominate on-mound. The most remarkable feature is the high occurrence of the epibenthic species *D. coronata* in on-mound sediments and its absence in the off-mound sediments.

The nMDS plot provides an overview of the similarities between assemblages (Clarke and Warwick, 2001; Everitt, 1978). This method is particularly suitable for the analysis of coral mound faunas, where the boundaries between different facies are often gradual (Clarke and Warwick, 2001). Our samples have been collected from different mounds at different water depth and from different facies in the Porcupine–Rockall Bank region (Table 1). The clustering of samples in the nMDS plot based on species corresponds to the distribution of facies on a typical mound in this area (e.g., Galway Mound, Fig. 4). The nMDS ordination (Fig. 3) and SIMPER analysis (Tables 3 and 4), together with information about the ecology of individual species and species groups (e.g., Table 2), leads to the following interpretations of the five clusters.

Cluster 1 groups 10 samples from the *Off-Mound Facies* (Fig. 3; Tables 2 and 4). The sediment varies from sandy silt to coarse sand. The water depths at which

samples were taken range between 202 and 736 m (Table 1). Cluster 1 is represented by the infaunal species *U. peregrina*, *U. mediterranea*, *H. balthica*, *M. barleeianum*, *E. exigua* and *Cassidulina* spp. (*C. carinata* and *C. laevigata*), *Bulimina* spp. (*B. aculeata*, *B. marginata*, and *B. striata*), and *Nonionella* spp. (*N. iridea*, *N. labradorica*, and *N. turgida*). These species are known to be typical for muddy/silty to sandy substrata, to prefer high organic matter input, and to thrive under suboxic-dysoxic conditions (e.g., Fontanier et al., 2002; Jorissen et al., 2007; Murray, 2006; Schönfeld and Altenbach, 2005). In particular, uvigerinids require high quantity and quality of nutrients supplied to the seafloor (Jorissen et al., 1998; Schönfeld and Altenbach, 2005).

Cluster 2 combines 5 samples from the *Dropstone Facies*. Sediment consists of a sandy fraction with dropstones indicating strong bottom currents (De Mol et al., 2002). *G. subglobosa* is highly abundant in these samples. This infaunal species (e.g., Fariduddin and Loubere, 1997; Murray, 2006) is characteristic for oligotrophic areas with high bottom current velocities (Jorissen, 1988; Mackensen et al., 1995). *Cibicidoides* sp., the dominant epibenthic species, appears to be specialised to this high-energy environment.

**Table 2**

Living strategy, preferred substratum and other ecological attributes of selected benthic foraminifera according to the literature.

Species	Facies	Living strategy	Preferred substratum	Comments	Reference
<i>Hyalinea balthica</i>	Off-mound	Epifaunal	Mud to silt		Murray (2006)
<i>Epistominella exigua</i>	Off-mound	Epifaunal, shallow infaunal	Mud	Opportunistic, phytodetritus feeder, seasonal food fluxes, large tolerance to varying organic flux	Gooday (1988), Gooday et al. (1993), Loubere and Fariduddin (1999), Murray (2006), Smart (2008), Smart et al. (1994), Thomas et al. (1995), Thomas and Gooday (1996)
<i>Cibicidoides kullenbergi</i>	Off-mound	Epifaunal, shallow infaunal		Passive suspension feeder, deep sea habitat, oligotrophic environment, oxic, stable physico-chemical conditions	Fariduddin and Loubere (1997), Jorissen (1988), Morigi et al. (2001), Murray (2006), Schmiedl et al. (2000), Woodruff et al. (1980)
<i>Uvigerina mediterranea</i>	Off-mound	Shallow infaunal	Mud	Rich supply of labile organic matter, superior competitor in food- and oxygen-rich sediments, less tolerant to suboxic conditions than <i>U. peregrina</i>	Altenbach et al. (1999), De Stigter et al. (1998), Fontanier et al. (2002), Murray (2006)
<i>Uvigerina peregrina</i>	Off-mound	Shallow infaunal	Mud	Rich supply of labile organic matter and high concentration of bacteria	Altenbach et al. (1999), Altenbach and Sarnthein (1989), Fontanier et al. (2002)
<i>Nonionella iridea</i>	Off-mound	Infaunal	Mud	Opportunistic, suboxic, reacts fast to phytodetritus blooms	Duchemin et al. (2007), Murray, (2006)
<i>Nonionella turgida</i>	Off-mound	Infaunal	Mud	Suboxic, dysoxic	Kaiho (1994), Murray (2006)
<i>Bulimina</i> spp.	Off-mound	Infaunal	Mud to fine sand	High carbon flux rates; tolerates low oxygen	Brüchert et al. (2000), Mackensen et al. (1993), Mackensen et al. (1990), Mullins et al. (1985), Murray (2006), Seidenkrantz et al. (2000)
<i>Hanzawaia boueana</i>	Dead coral facies	Epifaunal attached	Hard substrates	Oxic	Murray (2006), Spezzaferri and Coric (2001)
<i>Planulina ariminensis</i>	Dead coral facies	Epifaunal attached		Suspension feeder	Lutze and Thiel (1987), Schönfeld (2002a)
<i>Spiroplectinella wrightii</i>	Dead coral facies	Epifaunal, attached			Gross (2000)
<i>Angulogerina angulosa</i>	Dead coral facies	Infaunal	Sand	High energy areas, can withstand permanent winnowing and redeposition	Hald and Vorren (1984), Jarke (1960), Mackensen et al. (1985), Murray (1971), Qvale and Van Weering (1985), Schönfeld (2002a), Sejrup et al. (1981)
<i>Epistominella vitrea</i>	Dead coral facies	Infaunal	Mud	Opportunist, high food availability, low water energy, hypoxic	Jorissen et al. (1992), Murray (2006), Osterman et al. (2005)
<i>Gavelinopsis praegeri</i>	Living coral facies	Epifaunal attached, mobile	Hard substrates		Murray (2006)
<i>Lobatula lobatula</i>	Living coral facies	Epifaunal, attached	Hard substrates, coarse sediments	Suspension feeder, high energy areas	Lutze and Thiel (1989), Murray (1971), Murray (2006), Schönfeld (2002a)
<i>Cassidulina carinata</i>	Living coral facies, off-mound	Shallow infaunal, epifaunal		Opportunistic, moderate to high carbon flux rates, preference for high quality food	Altenbach et al. (1999), Gupta and Thomas (1999), Hess et al. (2005), Jorissen et al. (2007); Nomura (1983a,b)
<i>Cassidulina laevigata</i>	Living coral facies, off-mound	Infaunal	Sand	High carbon flux rates, tolerates low oxygen	Mackensen and Hald (1988), Murray (2003), Murray (2006)



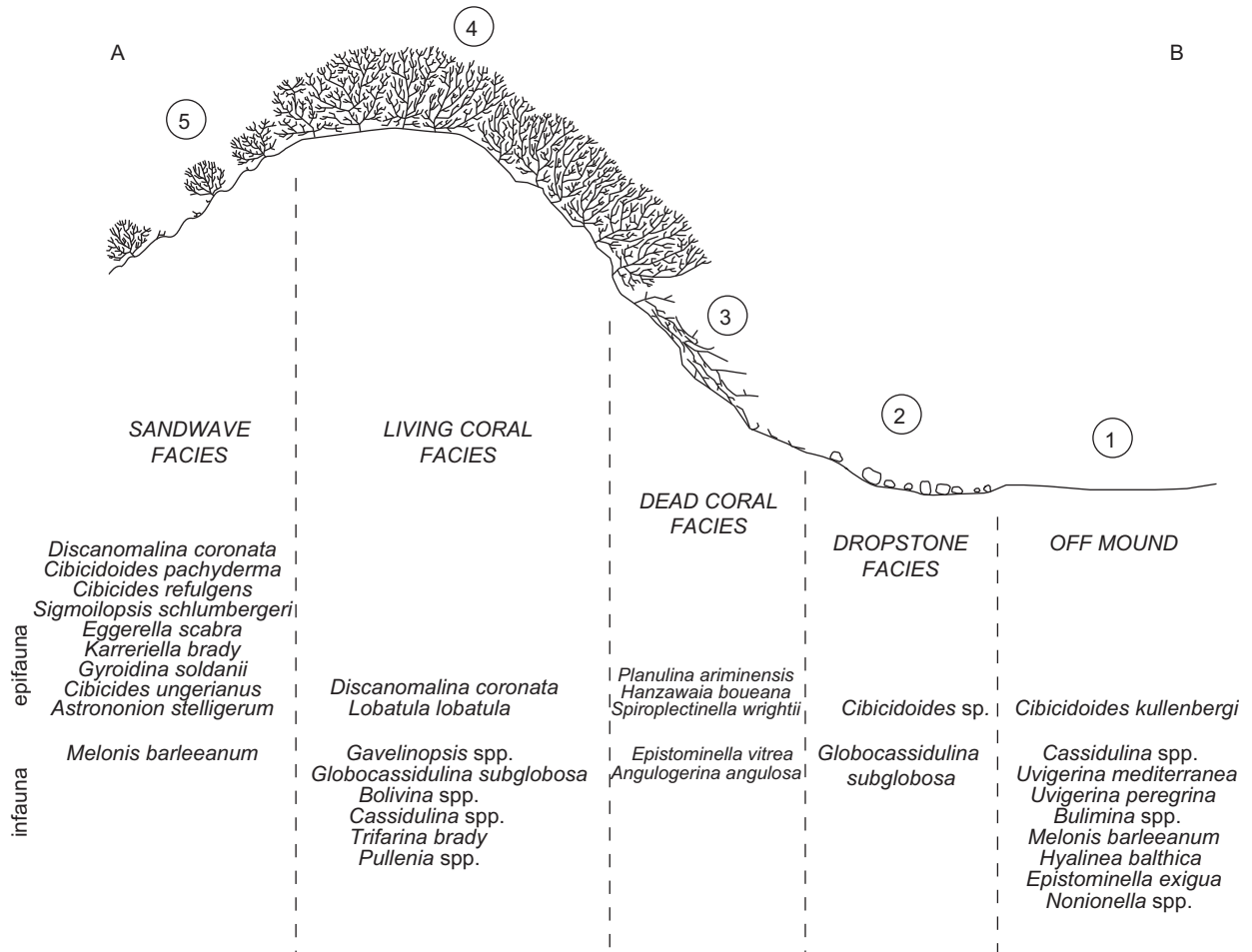
Table 2 (continued)

Species	Facies	Living strategy	Preferred substratum	Comments	Reference
<i>Bolivina</i> spp.	Living coral facies	Infaunal	Mud	High carbon flux rates, tolerates low oxygen	Loubere (1996), Mackensen et al. (1995), Mullins et al. (1985), Murray (2006), Seidenkrantz et al. (2000)
<i>Pullenia</i> spp.	Living coral facies	Infaunal	Mud	High carbon flux rates, low oxygen, variable food flux	Corliss and Chen (1988), Gupta and Thomas (1999), Loubere (1998), Murray (2006)
<i>Trifarina brady</i>	Living coral facies	Infaunal		Facultative anaerob	Gupta (1997)
<i>Globocassidulina subglobosa</i>	Living coral facies, dropstone facies	Infaunal	Mud	Phytodetritus feeder, preferentially ingest fresh diatoms, oligotrophic	Corliss (1979), Fariduddin and Loubere (1997), Gooday (1994), Mackensen et al. (1995); Murray (2006); Suhr et al. (2003)
<i>Discanomalina coronata</i>	Sandwave facies, living coral facies	Epifaunal attached		Strong bottom currents, attached to hydroids and octocorals	Hawkes and Scott (2005), Schönfeld (1997, 2002a, b)
<i>Cibicides refulgens</i>	Sandwave facies	Epifaunal attached	Hard substrates	Passive suspension feeder, high energy, oxic, stable physico-chemical conditions	Kaiho (1994, 1999), Kouwenhoven (2000), Murray (2006), Van der Zwaan (1982)
<i>Astrononion</i> spp.	Sandwave facies	Epifaunal attached, infaunal	Mud	Passive suspension feeder, high energy, oxic, stable physico-chemical conditions	Jorissen et al. (2007), Kaiho (1994, 1999), Kouwenhoven (2000), Murray (2006), Van der Zwaan (1982)
<i>Cibicides ungerianus</i>	Sandwave facies	Epifaunal, shallow infaunal	Mud	Passive suspension feeder, preferentially ingest fresh diatoms, oligotrophic environment, high energy, oxic, stable physico-chemical conditions	Almogi-Labin et al. (2000), Miao and Thunell (1993), Murray (2006), Schmiedl et al. (2000)
<i>Cibicidoides pachyderma</i>	Sandwave facies	Epifaunal, shallow infaunal		Eutrophic environments, does not depend on labile organic matter	De Nooijer et al. (2008), Duijnsteet et al. (2003), Ernst (2002), Ernst et al. (2005)
<i>Eggerella scabra</i>	Sandwave facies	Infaunal	Fine sand		Murray (2006)
<i>Karreriella brady</i>	Sandwave facies	Epifaunal	Mud to silt		
<i>Melonis barleeanum</i>	Sandwave facies, off-mound	Infaunal	Mud to silt	< 10 °C, high POM, lives in high productivity waters, lives on the redox front	Caralp (1989), Corliss (1985), Gooday (1986), Koho et al. (2008), Loubere (1991), Murray (2006)
<i>Gyroidina soldanii</i>	Sandwave facies	Epifaunal	Mud	Suboxic, dysoxic	Mullins et al. (1985), Murray (2006)

The five facies identified in this study are also plotted.

Clusters 3, 4, and 5 represent the facies types typical of cold-water carbonate mounds. The boundaries between these facies types are gradual. Some species are repre-

sented in all of them, although their relative abundance varies. Attached-epifaunal foraminiferal species are considerably more abundant on- than off-mound.



**Fig. 4.** Model representing the distribution of benthic foraminiferal assemblages, based on the nMDS ordination, along the A-B transect. Numbers 1–5 refer to the five clusters estimated in the nMDS and representing the different facies on an active cold-water coral mound. For each cluster the most important benthic foraminifera are listed according to their living strategy and preference (Table 3).

**Table 3**

List of species and statistical parameters associated with the similarity in clusters 1–5.

Species	Average similarity: 49.49%			
	Av.Abund	Av.Sim	Contrib%	Cum.%
<b>Group 1</b>				
<i>U. peregrina</i>	17.69	11.04	22.31	22.31
<i>Cassidulina</i> spp.	14.51	7.55	15.26	37.56
<i>Bulimina</i> spp.	7.18	4.97	10.04	47.6
<i>H. balthica</i>	6.49	4.6	9.29	56.89
<i>U. mediterranea</i>	10.09	4.52	9.12	66.01
<i>A. angulosa</i>	4.05	2.9	5.87	71.88
<i>G. subglobosa</i>	5.39	2.8	5.67	77.55
<i>E. vitrea</i>	5.92	2.26	4.56	82.11
<i>Bolivina</i> spp.	3.45	1.94	3.92	86.03
<i>M. barleeaanum</i>	2.53	1.29	2.6	88.63
<i>C. pachyderma</i>	3.73	0.87	1.75	90.38

Table 3 (continued)

Species	Average similarity: 57.80%			
	Av.Abund	Av.Sim	Contrib%	Cum.%
<b>Group 2</b>				
<i>G. subglobosa</i>	29.74	25.51	44.14	44.14
<i>E. vitrea</i>	10.25	6.34	10.97	55.1
<i>Cibicidoides</i> sp.	7.47	4.98	8.62	63.72
<i>Cassidulina</i> spp.	8.13	3.99	6.9	70.62
<i>Bulimina</i> spp.	4.55	3.37	5.83	76.45
<i>A. angulosa</i>	4.92	2.97	5.13	81.59
<i>C. pachyderma</i>	2.46	1.67	2.89	84.48
<i>U. peregrina</i>	4.44	1.45	2.51	86.99
<i>L. lobatula</i>	1.56	1.26	2.18	89.16
<i>P. ariminensis</i>	2.24	1.1	1.91	91.07
Species	Average similarity: 51.10%			
	Av.Abund	Av.Sim	Contrib%	Cum.%
<b>Group 3</b>				
<i>E. vitrea</i>	16.88	13.16	25.75	25.75
<i>G. subglobosa</i>	20.52	12.88	25.21	50.97
<i>A. angulosa</i>	9.16	4.79	9.38	60.35
<i>Cassidulina</i> spp.	6.37	4.08	7.99	68.34
<i>P. ariminensis</i>	4.62	2.46	4.81	73.15
<i>H. boueana</i>	2.54	1.93	3.78	76.93
<i>Discanomalina</i> spp.	2.64	1.62	3.16	80.09
<i>U. peregrina</i>	4.65	1.59	3.12	83.21
<i>U. mediterranea</i>	3.14	1.51	2.96	86.17
<i>Bulimina</i> spp.	2.89	1.06	2.08	88.25
<i>L. lobatula</i>	1.44	0.99	1.94	90.19
Species	Average similarity: 51.10%			
	Av.Abund	Av.Sim	Contrib%	Cum.%
<b>Group 4</b>				
<i>G. subglobosa</i>	19.67	15.51	30.36	30.36
<i>Bolivina</i> spp.	10.15	7.47	14.62	44.98
<i>Cassidulina</i> spp.	11.09	7.33	14.35	59.33
<i>Discanomalina</i> spp.	9.03	4.28	8.38	67.71
<i>P. ariminensis</i>	3.02	1.89	3.71	71.41
<i>L. lobatula</i>	2.14	1.3	2.55	73.96
<i>Cibicidoides</i> sp.	2.13	1.29	2.53	76.49
<i>E. vitrea</i>	4.27	1.29	2.52	79.01
<i>A. stelligerum</i>	2.11	1.18	2.31	81.32
<i>Bulimina</i> spp.	2.48	1.17	2.28	83.61
<i>A. angulosa</i>	3.32	1.09	2.14	85.75
<i>U. peregrina</i>	2.13	0.91	1.79	87.53
<i>T. bradyi</i>	1.47	0.87	1.69	89.23
<i>Gavelinopsis</i> spp.	1.88	0.86	1.67	90.9
Species	Average similarity: 49.19%			
	Av. Abund	Av. Sim	Contrib%	Cum.%
<b>Group 5</b>				
<i>G. subglobosa</i>	12.1	11.29	22.95	22.95
<i>Discanomalina</i> spp.	14.11	10.48	21.31	44.26
<i>Cassidulina</i> spp.	10.08	5.65	11.48	55.74
<i>E. vitrea</i>	6.05	4.03	8.2	63.93
<i>A. stelligerum</i>	4.44	2.42	4.92	68.85
<i>Bolivina</i> spp.	3.63	2.42	4.92	73.77
<i>U. mediterranea</i>	4.84	1.61	3.28	77.05
<i>K. brady</i>	2.42	1.61	3.28	80.33
<i>L. lobatula</i>	2.42	1.61	3.28	83.61
<i>M. barleeanum</i>	2.02	1.61	3.28	86.89
<i>H. boueana</i>	1.61	1.61	3.28	90.16

Average similarity within the group of station, average abundance, average similarity, contribution (%), and cumulative contribution (%) are given for each species with respect to the total similarity for each cluster.

**Table 4**

List of species and statistical parameter associated with the dissimilarity between each pair of clusters 1–5.

Species	Average dissimilarity=68.0					Species	Average dissimilarity=58.9				
	Group 1	Group 4					Group 3	Group 5			
		Av.Abund	Av.Abund	Av.Diss	Contrib %			Cum.%	Av.Abund	Av.Abund	Av.Diss
<i>U. peregrina</i>	17.7	2.1	8.0	11.8	11.8	<i>Discanomalina</i> spp.	2.6	14.1	5.8	9.8	9.8
<i>G. subglobosa</i>	5.4	19.7	7.3	10.8	22.5	<i>E. vitrea</i>	16.9	6.1	5.4	9.2	19.0
<i>Cassidulina</i> spp.	14.5	11.1	5.1	7.4	29.9	<i>G. subglobosa</i>	20.5	12.1	5.1	8.7	27.7
<i>Discanomalina</i> spp.	0.2	9.0	4.4	6.5	36.4	<i>A. angulosa</i>	9.2	0.0	4.6	7.8	35.5
<i>U. mediterranea</i>	10.1	2.0	4.4	6.5	42.9	<i>C. pachyderma</i>	0.0	8.9	4.5	7.6	43.1
<i>Bolivina</i> spp.	3.5	10.2	3.6	5.3	48.2	<i>Cassidulina</i> spp.	6.4	10.1	2.8	4.8	47.9
<i>E. vitrea</i>	5.9	4.3	3.1	4.5	52.7	<i>U. peregrina</i>	4.7	0.4	2.2	3.8	51.7
<i>H. balthica</i>	6.5	0.9	2.9	4.2	57.0	<i>C. refulgens</i>	1.5	4.4	1.9	3.3	54.9
<i>Bulimina</i> spp.	7.2	2.5	2.7	3.9	60.9	<i>A. stelligerum</i>	0.6	4.4	1.9	3.3	58.2
<i>C. pachyderma</i>	3.7	0.0	1.9	2.8	63.6	<i>U. mediterranea</i>	3.1	4.8	1.8	3.1	61.3
<i>A. angulosa</i>	4.1	3.3	1.7	2.5	66.1	<i>P. ariminensis</i>	4.6	2.4	1.8	3.0	64.3
<i>P. ariminensis</i>	0.3	3.0	1.4	2.1	68.1	<i>S. schlumbergeri</i>	0.0	3.2	1.6	2.8	67.0
<i>E. exigua</i>	2.5	0.0	1.3	1.9	70.0	<i>S. wrightii</i>	2.6	0.0	1.3	2.3	69.3
<i>Nonionella</i> spp.	2.5	0.1	1.2	1.8	71.8	<i>Bulimina</i> spp.	2.9	1.2	1.3	2.1	71.4
<i>M. barleeanum</i>	2.5	0.7	1.1	1.7	73.4	<i>Bolivina</i> spp.	2.0	3.6	1.1	1.9	73.3
<i>C. kullenbergi</i>	2.0	1.3	1.1	1.6	75.0	<i>K. brady</i>	0.3	2.4	1.1	1.8	75.1
<i>Cibicidoides</i> spp.	0.1	2.1	1.0	1.5	76.5	<i>E. scabra</i>	1.4	2.0	1.0	1.7	76.9
<i>A. stelligerum</i>	0.9	2.1	1.0	1.5	78.0	<i>G. soldanii</i>	0.4	1.6	0.8	1.4	78.2
<i>L. lobatula</i>	0.3	2.1	1.0	1.4	79.5	<i>C. kullenbergi</i>	1.6	0.0	0.8	1.4	79.6
<i>Gavelinopsis</i> spp.	0.3	1.9	0.8	1.2	80.7	<i>L. lobatula</i>	1.4	2.4	0.6	1.0	80.6
Species	Average dissimilarity=64.0					Species	Average dissimilarity=64.3				
	Group 1	Group 3					Group 1	Group 2			
		Av.Abund	Av.Abund	Av.Diss	Contrib%	Cum.%		Av.Abund	Av.Abund	Av.Diss	Contrib%
<i>G. subglobosa</i>	5.4	20.5	7.8	12.2	12.2	<i>G. subglobosa</i>	5.4	29.7	12.2	19.0	19.0
<i>U. peregrina</i>	17.7	4.7	7.0	11.0	23.2	<i>U. peregrina</i>	17.7	4.4	7.2	11.1	30.1
<i>E. vitrea</i>	5.9	16.9	5.9	9.2	32.4	<i>U. mediterranea</i>	10.1	5.7	5.5	8.5	38.6
<i>Cassidulina</i> spp.	14.5	6.4	4.9	7.6	40.0	<i>Cassidulina</i> spp.	14.5	8.1	5.4	8.4	47.0
<i>U. mediterranea</i>	10.1	3.1	4.0	6.3	46.3	<i>E. vitrea</i>	5.9	10.3	3.9	6.1	53.1
<i>A. angulosa</i>	4.1	9.2	3.3	5.1	51.5	<i>Cibicidoides</i> spp.	0.1	7.5	3.7	5.7	58.8
<i>H. balthica</i>	6.5	0.5	3.0	4.7	56.2	<i>H. balthica</i>	6.5	0.2	3.1	4.9	63.7
<i>Bulimina</i> spp.	7.2	2.9	2.6	4.0	60.2	<i>C. pachyderma</i>	3.7	2.5	2.0	3.1	66.8
<i>P. ariminensis</i>	0.3	4.6	2.2	3.4	63.6	<i>Bulimina</i> spp.	7.2	4.6	1.9	3.0	69.8
<i>C. pachyderma</i>	3.7	0.0	1.9	2.9	66.6	<i>Bolivina</i> spp.	3.5	1.6	1.4	2.2	72.0
<i>Bolivina</i> spp.	3.5	2.0	1.3	2.1	68.7	<i>A. angulosa</i>	4.1	4.9	1.4	2.1	74.1
<i>S. wrightii</i>	0.6	2.6	1.3	2.1	70.7	<i>E. exigua</i>	2.5	0.0	1.3	2.0	76.1
<i>E. exigua</i>	2.5	0.0	1.3	2.0	72.7	<i>Nonionella</i> spp.	2.5	0.2	1.2	1.9	77.9
<i>Discanomalina</i> spp.	0.2	2.6	1.3	2.0	74.7	<i>P. ariminensis</i>	0.3	2.2	1.1	1.6	79.6
<i>C. kullenbergi</i>	2.0	1.6	1.2	1.9	76.5	<i>C. kullenbergi</i>	2.0	1.7	1.0	1.6	81.1
<i>Nonionella</i> spp.	2.5	0.2	1.2	1.9	78.4						
<i>H. boueana</i>	0.4	2.5	1.1	1.7	80.1						
Species	Average dissimilarity=55.3					Species	Average dissimilarity=53.6				
	Group 4	Group 3					Group 4	Group 2			
		Av.Abund	Av.Abund	Av.Diss	Contrib%	Cum.%		Av.Abund	Av.Abund	Av.Diss	Contrib%
<i>E. vitrea</i>	4.3	16.9	6.4	11.6	11.6	<i>G. subglobosa</i>	19.7	29.7	5.4	10.0	10.0
<i>G. subglobosa</i>	19.7	20.5	5.2	9.4	21.1	<i>Discanomalina</i> spp.	9.0	0.2	4.4	8.3	18.3
<i>Bolivina</i> spp.	10.2	2.0	4.2	7.6	28.7	<i>Bolivina</i> spp.	10.2	1.6	4.4	8.2	26.5
<i>A. angulosa</i>	3.3	9.2	3.7	6.8	35.4	<i>E. vitrea</i>	4.3	10.3	4.0	7.4	33.9
<i>Discanomalina</i> spp.	9.0	2.6	3.4	6.2	41.6	<i>Cassidulina</i> spp.	11.1	8.1	3.7	6.8	40.7
<i>Cassidulina</i> spp.	11.1	6.4	3.2	5.7	47.3	<i>U. mediterranea</i>	2.0	5.7	3.1	5.8	46.5
<i>U. peregrina</i>	2.1	4.7	2.2	4.0	51.3	<i>C. lopjanicus</i>	2.1	7.5	2.8	5.1	51.6
<i>P. ariminensis</i>	3.0	4.6	1.5	2.7	54.0	<i>U. peregrina</i>	2.1	4.4	2.2	4.0	55.6
<i>Bulimina</i> spp.	2.5	2.9	1.5	2.7	56.6	<i>A. angulosa</i>	3.3	4.9	2.0	3.6	59.2
<i>S. wrightii</i>	0.1	2.6	1.3	2.4	59.0	<i>Bulimina</i> spp.	2.5	4.6	1.6	2.9	62.1
<i>U. mediterranea</i>	2.0	3.1	1.3	2.4	61.4	<i>C. pachyderma</i>	0.0	2.5	1.2	2.3	64.4
<i>C. kullenbergi</i>	1.3	1.6	1.0	1.9	63.3	<i>P. ariminensis</i>	3.0	2.2	1.0	1.9	66.3
<i>Cibicidoides</i> sp.	2.1	0.2	1.0	1.8	65.1	<i>C. kullenbergi</i>	1.3	1.7	1.0	1.8	68.1
<i>A. stelligerum</i>	2.1	0.6	1.0	1.7	66.8	<i>A. stelligerum</i>	2.1	1.2	0.9	1.6	69.7

Table 4 (continued)

Species	Average dissimilarity=55.3					Species	Average dissimilarity=53.6				
	Group 4	Group 3					Group 4	Group 2			
		Av.Abund	Av.Abund	Av.Diss	Contrib%			Cum.%	Av.Abund	Av.Abund	Av.Diss
<i>C. refulgens</i>	1.2	1.5	0.9	1.5	68.4	<i>C. refulgens</i>	1.2	0.6	0.8	1.4	71.1
<i>H. boueana</i>	1.1	2.5	0.8	1.5	69.9	<i>T. bradyi</i>	1.5	0.0	0.7	1.4	72.5
<i>Gavelinopsis</i> spp.	1.9	0.6	0.8	1.4	71.3	<i>M. barleeaanum</i>	0.7	1.6	0.7	1.4	73.8
<i>M. barleeaanum</i>	0.7	1.8	0.8	1.4	72.7	<i>Gavelinopsis</i> spp.	1.9	1.3	0.7	1.3	75.2
<i>E. scabra</i>	0.0	1.4	0.7	1.3	74.0	<i>Pullenia</i> spp.	1.4	0.0	0.7	1.3	76.5
<i>L. lobatula</i>	2.1	1.4	0.7	1.3	75.3	<i>L. lobatula</i>	2.1	1.6	0.7	1.3	77.7
<i>T. bradyi</i>	1.5	0.3	0.7	1.2	76.5	<i>C. tenellus</i>	1.3	0.3	0.6	1.2	78.9
<i>C. tenellus</i>	1.3	0.0	0.6	1.2	77.7	<i>S. schlumbergeri</i>	0.9	1.0	0.6	1.1	80.0
<i>Fissurina</i> spp.	0.8	0.8	0.6	1.0	78.7	<i>H. boueana</i>	1.1	0.5	0.5	1.0	81.0
<i>Pullenia</i> spp.	1.4	0.5	0.6	1.0	79.7						
<i>H. balthica</i>	0.9	0.5	0.5	0.9	80.6						
Species	Average dissimilarity=68.5					Species	Average dissimilarity=49.5				
	Group 1	Group 5					Group 3	Group 2			
		Av.Abund	Av.Abund	Av.Diss	Contrib%			Cum.%	Av.Abund	Av.Abund	Av.Diss
<i>U. peregrina</i>	17.7	0.4	8.7	12.7	12.7	<i>G. subglobosa</i>	20.5	29.7	6.5	13.1	13.1
<i>Discanomalina</i> spp.	0.2	14.1	7.0	10.2	22.8	<i>E. vitrea</i>	16.9	10.3	4.2	8.4	21.5
<i>Cassidulina</i> spp.	14.5	10.1	4.9	7.1	29.9	<i>Cibicidoides</i> sp.	0.2	7.5	3.7	7.4	28.8
<i>C. pachyderma</i>	3.7	8.9	4.6	6.7	36.6	<i>A. angulosa</i>	9.2	4.9	3.3	6.6	35.5
<i>U. mediterranea</i>	10.1	4.8	3.9	5.7	42.3	<i>U. mediterranea</i>	3.1	5.7	3.2	6.5	42.0
<i>G. subglobosa</i>	5.4	12.1	3.6	5.3	47.6	<i>Cassidulina</i> spp.	6.4	8.1	2.9	5.9	47.9
<i>H. balthica</i>	6.5	0.4	3.0	4.4	52.0	<i>U. peregrina</i>	4.7	4.4	2.4	4.9	52.8
<i>Bulimina</i> spp.	7.2	1.2	3.0	4.4	56.4	<i>P. ariminensis</i>	4.6	2.2	1.6	3.3	56.1
<i>E. vitrea</i>	5.9	6.1	2.7	3.9	60.3	<i>Bulimina</i> spp.	2.9	4.6	1.5	3.1	59.2
<i>C. refulgens</i>	0.5	4.4	2.1	3.1	63.4	<i>S. wrightii</i>	2.6	0.0	1.3	2.7	61.8
<i>A. angulosa</i>	4.1	0.0	2.0	3.0	66.4	<i>C. pachyderma</i>	0.0	2.5	1.2	2.5	64.3
<i>A. stelligerum</i>	0.9	4.4	1.9	2.8	69.2	<i>Discanomalina</i> spp.	2.6	0.2	1.2	2.5	66.8
<i>S. schlumbergeri</i>	0.7	3.2	1.6	2.4	71.5	<i>C. kullenbergi</i>	1.6	1.7	1.1	2.2	69.0
<i>E. exigua</i>	2.5	0.0	1.3	1.9	73.4	<i>H. boueana</i>	2.5	0.5	1.0	2.1	71.1
<i>Nonionella</i> spp.	2.5	0.0	1.2	1.8	75.2	<i>Bolivina</i> spp.	2.0	1.6	1.0	1.9	73.0
<i>P. ariminensis</i>	0.3	2.4	1.2	1.8	76.9	<i>C. refulgens</i>	1.5	0.6	0.8	1.6	74.6
<i>Bolivina</i> spp.	3.5	3.6	1.1	1.6	78.6	<i>M. barleeaanum</i>	1.8	1.6	0.7	1.5	76.0
<i>K. brady</i>	0.3	2.4	1.1	1.6	80.2	<i>E. scabra</i>	1.4	0.0	0.7	1.5	77.5
						<i>A. stelligerum</i>	0.6	1.2	0.6	1.2	78.6
						<i>Fissurina</i> spp.	0.8	0.8	0.6	1.2	79.8
						<i>S. schlumbergeri</i>	0.0	1.0	0.5	1.1	80.8
Species	Average dissimilarity=52.4					Species	Average dissimilarity=61.6				
	Group 4	Group 5					Group 5	Group 2			
		Av.Abund	Av.Abund	Av.Diss	Contrib%			Cum.%	Av.Abund	Av.Abund	Av.Diss
<i>Discanomalina</i> spp.	9.0	14.1	4.8	9.1	9.1	<i>G. subglobosa</i>	12.1	29.7	8.8	14.3	14.3
<i>C. pachyderma</i>	0.0	8.9	4.5	8.5	17.6	<i>Discanomalina</i> spp.	14.1	0.2	7.0	11.3	25.6
<i>G. subglobosa</i>	19.7	12.1	4.4	8.4	26.0	<i>C. pachyderma</i>	8.9	2.5	4.4	7.2	32.8
<i>Bolivina</i> spp.	10.2	3.6	3.5	6.6	32.6	<i>U. mediterranea</i>	4.8	5.7	3.7	6.0	38.8
<i>Cassidulina</i> spp.	11.1	10.1	3.0	5.8	38.4	<i>Cassidulina</i> spp.	10.1	8.1	3.4	5.6	44.4
<i>E. vitrea</i>	4.3	6.1	2.5	4.7	43.1	<i>Cibicidoides</i> sp.	0.8	7.5	3.3	5.4	49.8
<i>U. mediterranea</i>	2.0	4.8	2.0	3.9	46.9	<i>E. vitrea</i>	6.1	10.3	3.2	5.2	55.0
<i>C. refulgens</i>	1.2	4.4	2.0	3.9	50.8	<i>A. angulosa</i>	0.0	4.9	2.5	4.0	59.0
<i>A. angulosa</i>	3.3	0.0	1.7	3.2	54.0	<i>C. refulgens</i>	4.4	0.6	2.1	3.5	62.4
<i>S. schlumbergeri</i>	0.9	3.2	1.6	3.1	57.1	<i>U. peregrina</i>	0.4	4.4	2.1	3.4	65.8
<i>A. stelligerum</i>	2.1	4.4	1.4	2.7	59.8	<i>Bulimina</i> spp.	1.2	4.6	1.7	2.7	68.6
<i>P. ariminensis</i>	3.0	2.4	1.3	2.4	62.2	<i>S. schlumbergeri</i>	3.2	1.0	1.6	2.6	71.2
<i>E. scabra</i>	0.0	2.0	1.0	1.9	64.1	<i>A. stelligerum</i>	4.4	1.2	1.6	2.6	73.8
<i>U. peregrina</i>	2.1	0.4	1.0	1.9	66.0	<i>Bolivina</i> spp.	3.6	1.6	1.2	2.0	75.8
<i>K. brady</i>	0.5	2.4	1.0	1.9	67.9	<i>P. ariminensis</i>	2.4	2.2	1.2	2.0	77.8
<i>Cibicidoides</i> sp.	2.1	0.8	0.9	1.7	69.6	<i>E. scabra</i>	2.0	0.0	1.0	1.6	79.4
<i>Bulimina</i> spp.	2.5	1.2	0.8	1.6	71.2	<i>K. brady</i>	2.4	0.5	1.0	1.5	80.9
<i>G. soldanii</i>	0.0	1.6	0.8	1.5	72.7						
<i>Gavelinopsis</i> spp.	1.9	0.8	0.8	1.5	74.2						
<i>M. barleeaanum</i>	0.7	2.0	0.8	1.4	75.6						



Table 4 (continued)

Species	Average dissimilarity=52.4					Species	Average dissimilarity=61.6				
	Group 4		Group 5				Group 5		Group 2		
	Av.Abund	Av.Abund	Av.Diss	Contrib%	Cum.%		Av.Abund	Av.Abund	Av.Diss	Contrib%	Cum.%
<i>M. pompilioides</i>	0.9	0.8	0.7	1.3	77.0						
<i>L. lobatula</i>	2.1	2.4	0.7	1.2	78.2						
<i>C. kullenbergi</i>	1.3	0.0	0.6	1.2	79.4						

For each pair of clusters the average dissimilarity is shown. For each species the average abundance, average dissimilarity, contribution (%), and cumulative contribution (%) to the total similarity is also given.

Cluster 3 groups 4 samples from the *Dead Coral Facies*. A variety of different sediment types are associated with this facies. The framework created by the coarse coral debris traps fine sediment. Coral debris offers substrates favourable for the proliferation of epifaunal-attached species such as *P. ariminensis*, *Hanzawaia boueana*, and *Spiroplectinella wrightii* (Gross, 2000; Lutze and Thiel, 1989; Murray, 2006). *Angulogerina angulosa* and *E. vitrea* are very abundant in this facies. *Angulogerina angulosa*, a small infaunal species often associated with strong bottom currents, is typical for coarse grained sediments (Mackensen et al., 1985; Schönfeld, 2002a). *Epistominella vitrea* is an opportunistic species that responds to high food availability and occurs in muddy sediments under hypoxic conditions (e.g., Jorissen et al., 1992; Murray, 2006; Osterman et al., 2005). It dominates in microhabitats that are more protected from high current velocities (Mackensen et al., 1995).

Cluster 4 groups 6 samples from the *Living Coral Facies*. Living corals grow on debris and/or pebbly mud that is clogged by fine-grained sediments (mud and silt). Foraminiferal assemblages from this facies mainly comprise *G. subglobosa*, *Bolivina* spp., *Cassidulina* spp., *Tifarina bradyi*, and *Pullenia* spp., species that are generally considered to be infaunal (e.g., Gooday, 2003; Murray, 2006; Jorissen et al., 2007). According to Jorissen (1988), *G. subglobosa* prefers more oligotrophic environments than the uvigerinids. Since *G. subglobosa* dominates the *Living Coral Facies* on-mound and uvigerinids dominate the *Off-Mound Facies* we can interpret this distribution pattern as related to the current hydrography. In particular, the higher current energy probably keeps the organic particles in suspension in the water column, and therefore unavailable to the infaunal species *G. subglobosa*. On the other hand corals feed on high amounts of fresh organic matter (Duineveld et al., 2007), which may influence the quantity and/or quality of the flux material reaching the sea floor.

The epifaunal-attached species in the *Living Coral Facies* consist of *D. coronata*, *L. lobatula*, and *Gavelinopsis praegeri*, which are characteristic for active mounds (Rüggeberg et al., 2007). *Discanomalina coronata* lives attached to dead biogenic fragments that make up the substratum in the *Living Coral Facies*. The high density of *L. pertusa* in this facies offers wide habitats for *D. coronata*.

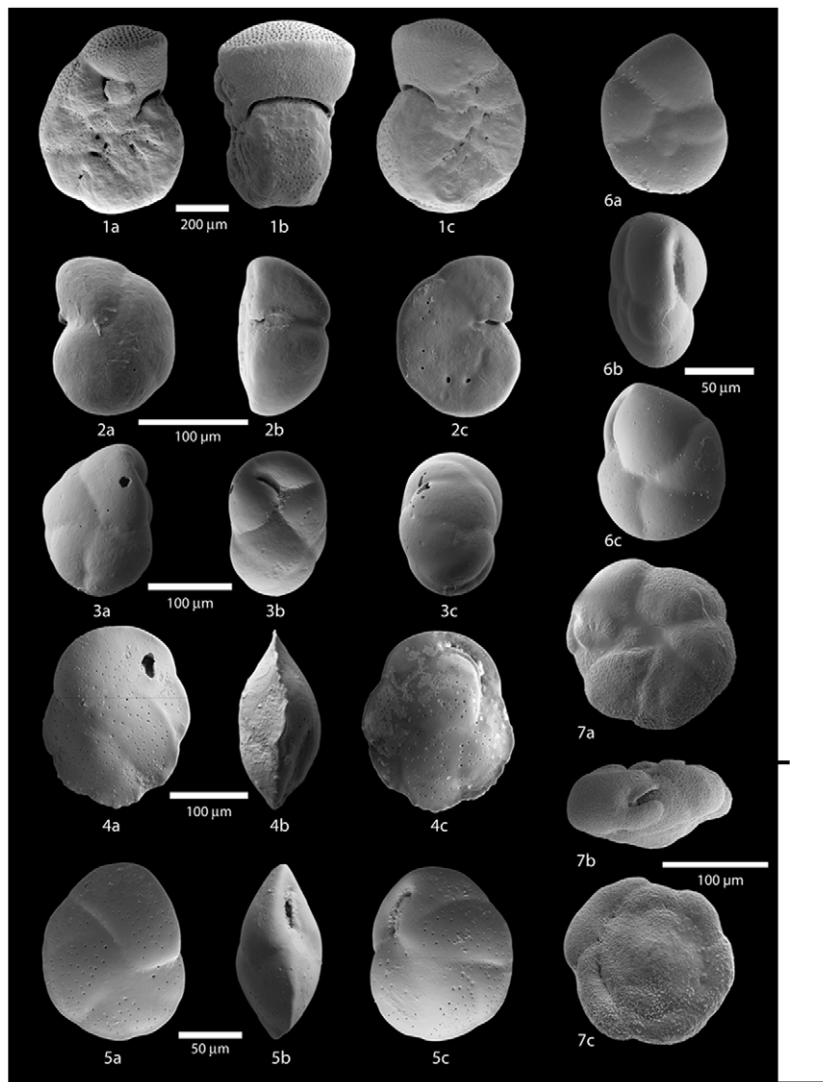
Cluster 5 groups 2 samples from the *Sandwave Facies*. In this facies sandwaves are the result of bottom currents. The sandwaves are colonized by patches of living corals and a highly diverse fauna, including hydroids, sponges, soft corals, and bivalves (Wienberg et al., 2007). Typical

for this facies are high abundances of epifaunal species such as *C. pachyderma*, *Karrerella bradyi*, *Gyroidina soldanii*, *C. ungerianus*, *Astrononion stelligerum* and epifaunal-attached forms like *C. refulgens* (e.g., Miao and Thunell, 1993; Murray, 2006; Schmiedl et al., 2000). *Discanomalina coronata* is a very abundant component of this cluster and dominates the epifaunal group (Rüggeberg et al., 2007; Schönfeld 1997, 2002a). Infaunal species are dominated by *G. subglobosa*, *Cassidulina* spp., *M. barleeianum* and *Eggerella scabra*.

In summary, cold-water carbonate mounds generally develop in environments with high current velocities (e.g., De Mol et al., 2002; White et al., 2005) and high nutrient flux (Kiriakoulakis et al., 2004). Various types of elevated substrata provide different ecological niches for epifaunal foraminifera. The epifauna in the *Living Coral Facies* has a distinctive composition compared to other facies. In particular, *D. coronata* is the dominant epifaunal species in the *Living Coral Facies* and in the *Sandwave Facies* and seems to occupy the ecological niches made available by dead fragments of cold-water corals (Jensen and Frederiksen, 1992) (Plate 1).

## 6. Conclusion

- (1) Benthic foraminiferal assemblages provide an independent tool to identify different facies of cold-water coral mounds in the Porcupine-Rockall Bank region. The *Off-Mound Facies* is dominated by uvigerinids and other infaunal species. The *Dropstone Facies* is characterized by both infaunal (*G. subglobosa*) and epifaunal-attached (*Cibicidoides* sp.) species. The *Dead Coral Facies* is characterized by a combination of infaunal (*A. angulosa*, *E. vitrea*) and epifaunal (*P. ariminensis*, *H. boueana*, *S. wrightii*) species. The *Living Coral Facies* is characterized by epifauna and infauna. The species typical of this facies is *D. coronata*. The *Sandwave Facies* contains high abundances of epifauna and *D. coronata*.
- (2) A potential problem in environmental interpretation is the fact that most of the indicator species (e.g., phytodetritus feeders) are small-sized (63–125 µm) and therefore have not been studied very often (Jorissen et al., 2007). Our results underline the importance of studying the small fraction to highlight the contribution of small-sized species.
- (3) *Discanomalina coronata* is present and abundant only in sediments associated with cold-water coral mounds and is not present in off-mound. The fact that



**Plate 1.** Important species collected on cold-water coral mounds at the Rockall and Porcupine Bank: (1a–c) *Discanomalina coronata* (Parker and Jones, 1857), sample M07-15. (2a–c) *Cibicoides* sp., sample 9260. (3a–c) *Globocassidulina subglobosa* (Brady, 1881), sample 9260. (4a–c) *Cassidulina carinata* (Silvestri, 1896), sample 574-1. (5a–c) *Cassidulina laevigata* (d'Orbigny, 1826), sample 577-1. (6a–c) *Epistominella exigua* (Brady, 1884), sample 580-1. (7a–c) *Epistominella vitrea* (Parker, 1953), sample 9256-1. a=spiral views, b=side views, c=umbilical views.

it is mainly found in the Living Coral and *Sandwave Facies* makes this species useful as an indicator for active cold-water coral mounds.

- (4) Foraminiferal species associated with cold-water coral carbonate mounds provide potentially useful indicators for these environments in the fossil record.

## Acknowledgements

This research is funded by the Swiss National Foundation (200021-103482). AR acknowledges funding by European Commission FP6 Integrated Project HERMES (Hotspot Ecosystem Research on the Margin of European Seas) Contract No. GOCE-CT-2005-511234-1. The authors are grateful to captains, crews, chief scientists and scientific

parties of the research cruises with RV 'Meteor' (M61-3), RV 'Poseidon' (P265 and P292), and RV 'Pelagia' (M07II). We warmly thank Hans Pirlet and Jean-Pierre Henriët for their fruitful advices and discussion and for providing box core material, and Dierk Hebbeln and Claudia Wienberg for advices and support for the development of this research. We also thank Michael P. Bacon, Joachim Schönfeld, Andrew J. Gooday and an anonymous reviewer for their constructive comments, criticisms and helpful reviews.

## Appendix A. Supplementary materials

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.dsr.2009.07.009](https://doi.org/10.1016/j.dsr.2009.07.009).

## References

- Akhmetzhanov, A.M., Kenyon, N.H., Ivanov, M., Wheeler, A.J., Shashkin, P.V., Van Weering, T.C.E., 2003. Giant carbonate mounds and current-swept seafloors on the slopes of the southern Rockall Trough. In: Mienert, J., Weaver, P. (Eds.), *European Margin Sediment Dynamics*. Springer, Berlin, pp. 203–209.
- Almogi-Labin, A., Schmiedl, G., Hemleben, C., Siman-Tov, R., Segl, M., Meischner, D., 2000. The influence of the NE winter monsoon on productivity changes in the Gulf of Aden, NW Arabian Sea, during the last 530 ka as recorded by foraminifera. *Mar. Micropaleontol.* 40, 295–319.
- Altenbach, A.V., Pflaumann, U., Schiebel, R., Thies, A., Timm, S., Trauth, M., 1999. Scaling percentages and distributional patterns of benthic foraminifera with flux rates of organic carbon. *J. Foraminif. Res.* 29 (3), 173–185.
- Altenbach, A.V., Sarnthein, M., 1989. Productivity Record in Benthic Foraminifera. In: Berger, W.H., Smetacek, V.S., Wefer, G. (Eds.), *Productivity of the Oceans: Present and Past, Dahlem Conferences*, pp. 255–269.
- Basso, D., Spezzaferri, S., 2000. The distribution of living (stained) benthic foraminifera in Iskenderun Bay: a statistical approach. *Boll. Soc. Paleont. It.* 29, 356–370.
- Brüchert, V., Perez, M.E., Lange, C.B., 2000. Coupled primary production, benthic foraminiferal assemblage, and sulfur diagenesis in organic-rich sediments of the Benguela upwelling system. *Mar. Geol.* 163, 27–40.
- Caralp, M.H., 1989. Size and morphology of the benthic foraminifer *Melonis barleeanum*: relationships with marine organic matter. *J. Foraminif. Res.* 19 (3), 235–245.
- Clarke, K., 1993. Non-parametric multivariate analyses of changes in community structure. *Aust. J. Ecol.* 18, 117–143.
- Clarke, K., Warwick, R., 2001. *Change in Marine Communities: an Approach to Statistical Analysis and Interpretation*. PRIMER-E, Plymouth.
- Clifford, D.H.T., Stephenson, W., 1975. *An Introduction to Numerical Classification*. Academic Press, New York.
- Corliss, B.H., 1979. Quaternary Antarctic bottom-water history: deep-sea benthonic foraminiferal evidence from the Southeast Indian Ocean – Inferred bottom-water routes and ecological implications. *Mar. Geol.* 31, 115–138.
- Corliss, B.H., 1985. Microhabitats of benthic foraminifera within deep-sea sediments. *Nature* 314, 435–438.
- Corliss, B.H., Chen, C., 1988. Morphotype Patterns of Norwegian Sea Deep-Sea Benthic Foraminifera and Ecological Implications. *Geology* 16 (8), 716–719.
- De Haas, H., 2007. *RV Pelagia cruise M07II (64PE276), Galway – Galway*. Unpublished report.
- De Mol, B., Van Rensbergen, P., Pillen, S., Van Herreweghe, K., Van Rooij, D., McDonnell, A., Huvenne, V., Ivanov, M., Swennen, R., Henriët, J.P., 2002. Large deep-water coral banks in the Porcupine Basin, south-west of Ireland. *Mar. Geol.* 188, 193–231.
- De Nooijer, L.J., Duijnste, I.A.P., Bergman, M.J.N., Van der Zwaan, G.J., 2008. The ecology of benthic foraminifera across the Frisian Front, southern North Sea. *Estuar. Coast. Shelf Sci.* 78 (4), 715–726.
- De Stigter, H.C., Jorissen, F.J., Van der Zwaan, G.J., 1998. Bathymetric distribution and microhabitat partitioning of live (Rose Bengal stained) benthic foraminifera along a shelf to bathyal transect in the southern Adriatic Sea. *J. Foraminif. Res.* 28 (1), 40–65.
- Dorschel, B., Hebbeln, D., Rüggeberg, A., Dullo, W.-Chr., Freiwald, A., 2005. Growth and erosion of a cold-water coral covered carbonate mound in the Northeast Atlantic during the Late Pleistocene and the Holocene. *Earth and Plan. Sci. Lett.* 233, 33–44.
- Dorschel, B., Hebbeln, D., Foubert, A., White, M., Wheeler, A.J., 2007a. Hydrodynamics and cold-water coral facies distribution related to recent sedimentary processes at Galway Mound west of Ireland. *Mar. Geol.* 244, 184–195.
- Dorschel, B., Hebbeln, D., Rüggeberg, A., Dullo, C., 2007b. Carbonate budget of a deep water coral mound: Propeller Mound, Porcupine Seabight. *Int. J. Earth Sci.* 96, 73–83.
- Duchemin, G., Fontanier, C., Jorissen, F.J., Barras, C., Griveaud, C., 2007. Living small-sized (63–150 µm) foraminifera from mid-shelf to mid-slope environments in the Bay of Biscay. *J. Foraminif. Res.* 37 (1), 12–32.
- Duijnste, I.A.P., Ernst, S.R., Van der Zwaan, G.J., 2003. Effect of anoxia on the vertical migration of benthic foraminifera. *Mar. Ecol. Prog. Ser.* 246, 85–94.
- Duineveld, G.C.A., Lavaleye, M.S.S., Bergman, M.J.N., Stigter, H.C.d., Mienis, F., 2007. Trophic structure of a cold-water coral Mound community (Rockall Bank, NE Atlantik) in relation to the near-bottom particle supply and current regime. *Bull. Mar. Sci.* 81 (3), 449–467.
- Duncan, P.M., 1870. A description of the *Madreporaria* dredged up during the expeditions of HMS Porcupine. *Proc. Roy. Soc. London* 18, 289–301.
- Duncan, P.M., 1873. A description of the *Madreporaria* dredged up during the expeditions of HMS Porcupine in 1869 and 1870. *Trans. Zool. Soc. Lond.* Part 1 8, 303–344.
- Duncan, P.M., 1878. A description of the *Madreporaria* dredged up during the expeditions of HMS Porcupine in 1869 and 1870. *Trans. Zool. Soc. Lond.* Part 2 10, 235–249.
- Ernst, S.R., 2002. An experimental study on the proxy value of benthic foraminifera-The impact of physical disturbance, oxygen depletion and organic flux. Unpublished Ph.D. Thesis, University of Utrecht, Netherlands.
- Ernst, S.R., Bours, R., Duijnste, I., Van der Zwaan, B., 2005. Experimental effects of an organic matter pulse and oxygen depletion on a benthic foraminiferal shelf community. *J. Foraminif. Res.* 35 (3), 177–197.
- Everitt, B., 1978. *Graphical Techniques for Multivariate Data*. Heinemann, London.
- Fariduddin, M., Loubere, P., 1997. The surface ocean productivity response of deeper water benthic foraminifera in the Atlantic Ocean. *Mar. Micropaleontol.* 32 (3–4), 289–310.
- Field, J.G., Clarke, K.R., Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Mar. Ecol. Prog. Ser.* 8, 37–52.
- Fontanier, C., Jorissen, F.J., Chaillou, G., Anschutz, P., Gremare, A., Griveaud, C., 2005. Live foraminiferal faunas from a 2800 m deep lower canyon station from the Bay of Biscay: faunal response to focusing of refractory organic matter. *Deep Sea Res.* 1 52 (7), 1189–1227.
- Fontanier, C., Jorissen, F.J., Licari, L., Alexandre, A., Anschutz, P., Carbonel, P., 2002. Live benthic foraminiferal faunas from the Bay of Biscay: faunal density, composition, and microhabitats. *Deep Sea Res.* 1 49, 751–785.
- Fosså, J.H., Mortensen, P.B., Furevik, D.M., 2002. The deep-water coral *Lophelia pertusa* in Norwegian waters: distribution and fishery impacts. *Hydrobiologia* 471, 1–12.
- Foubert, A., Beck, T., Wheeler, A.J., Opderbeke, J., Grehan, A., Klages, M., Thiede, J., Henriët, J.-P., the Polarstern ARK-XIX/3a Shipboard Party, 2005. New view of the Belgica Mounds, Porcupine Seabight, NE Atlantic: preliminary results from the Polarstern ARK-XIX/3a ROV cruise. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, Heidelberg, New York, pp. 403–415.
- Foubert, A., Van Rooij, D., Blamart, D., Henriët, J.-P., 2007. X-ray imagery and physical core logging as a proxy of the content of sediment cores in cold-water coral mound provinces: a case study from Porcupine Seabight, SW of Ireland. *Int. J. Earth Sci.* 96, 141–158.
- 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 Verlag, Berlin, Heidelberg, New York, pp. 365–385.
- Freiwald, A., Dullo, C., Shipboard Party, 2000. *RV Poseidon Cruise 265, Thórshavn – Galway – Kiel*. Unpublished report.
- Freiwald, A., Heinrich, R., Pätzold, J., 1997. Anatomy of a deep-water coral reef mound from Stjernsund, West-Finnmark, northern Norway. In: James, N., Clarke, J. (Eds.), *Cool-water Carbonates*. SEPM Special Publication, pp. 141–161.
- Freiwald, A., Schönfeld, J., 1996. Substrate pitting and boring pattern of *Hydrokkin sarcophaga* Cedhagen, 1994 (Foraminifera) in a modern deep-water coral reef mound. *Mar. Micropaleontol.* 28, 199–207.
- Freiwald, A., Shipboard Party, 2002. *RV Poseidon Cruise 292, Reykjavik – Galway*. Unpublished report.
- Freiwald, A., Wilson, J.B., Heinrich, R., 1999. Grounding Pleistocene icebergs shape recent deep-water coral reefs. *Sed. Geol.* 125, 1–8.
- Gooday, A.J., 1986. Meiofaunal foraminiferans from the bathyal Porcupine Seabight (northeast Atlantic): size structure, standing stock, taxonomic composition, species diversity and vertical distribution in the sediments. *Deep Sea Res.* 1 33 (10), 1345–1373.
- Gooday, A.J., 1988. A response by benthic foraminifera to the deposition of phytodetritus in the deep sea. *Nature* 322, 70–73.
- Gooday, A.J., 1994. The biology of deep-sea foraminifera: a review of some advances and their applications in paleoceanography. *Palaios* 9, 14–31.
- Gooday, A.J., 2003. Benthic foraminifera (Protista) as tools in deep-water palaeoceanography: environmental influences on faunal characteristics. *Adv. Mar. Biol.* 46, 1–90.

- Gooday, A.J., Bett, B.J., Pratt, D.N., 1993. Direct observation of episodic growth in an abyssal xenophyophore (Protista). *Deep Sea Res.* 40 (11/12), 2131–2143.
- 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.
- Gravier, C., 1915. Note préliminaire sur les *Madréporaires* recueillis au cours des croisières de la Princesse-Alice et de l'Hirondelle II, de 1893 à 1913 inclusivement. *Bull. Inst. Océanogr. Monaco* 12 (304), 1–22.
- Gravier, C., 1920. *Madréporaires* provenant des campagnes des yachts Princesse Alice et Hirondelle II (1893–1913). Résultats des Campagnes Scientifiques du Prince Albert Ier de Monaco 55 (1–123).
- Grimsdale, T.F., van Morkhoven, F.P.C.M., 1955. The ratio between pelagic and benthonic foraminifera as a means of estimating depth of deposition of sedimentary rocks. 4th World Petroleum Congress, pp. 473–491.
- Gross, O., 2000. Influence of temperature, oxygen and food availability on the migrational activity of bathyal benthic foraminifera: evidence by microcosm experiments. *Hydrobiologia* 426, 123–137.
- Gupta, A.K., 1997. Paleocceanographic and paleoclimatic history of the Somali Basin during the Pliocene-Pleistocene: Multivariate analyses of benthic foraminifera from DSDP Site 241 (Leg 25). *J. Foraminif. Res.* 27 (3), 196–208.
- Gupta, A.K., Thomas, E., 1999. Latest Miocene through Pleistocene paleocceanographic evolution of the northwestern Indian Ocean (DSDP Site 219): global and regional factors. *Paleoceanography* 14, 62–73.
- Hald, M., Vorren, T., 1984. Modern and Holocene foraminifera and sediments on the continental shelf off Troms, North Norway. *Boreas* 13, 133–154.
- Hawkes, A.D., Scott, D.B., 2005. Attached benthic Foraminifera as indicators of past and present distribution of the coral *Primnoa resedaeiformis* on the Scotian Margin. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, Heidelberg, New York, pp. 881–894.
- Henriet, J.P., De Mol, B., Pillen, S., Vanneste, M., Van Rooij, D., Versteeg, W., Croker, P.F., Shannon, P.M., Unnithan, V., Bourliak, S., Chachkine, P., 1998. Gas hydrate crystals may help build reefs. *Nature* 391, 648–649.
- Henriet, J.P., Guidard, S., Team, O.P., 2002. Carbonate mounds as a possible example for microbial activity in geological processes. In: Wefer, G., Billew, D., Hebbeln, D., Jørgensen, B.B., Schlüter, M., Van Weering, T.C.E. (Eds.), *Ocean Margin Systems*. Springer Verlag, Berlin, Heidelberg, New York, pp. 437–455.
- Hess, S., Jorissen, F.J., Venet, V., Abu-Zied, R., 2005. Benthic foraminiferal recovery after recent turbidite deposition in Cap Breton Canyon (Bay of Biscay). *J. Foraminif. Res.* 35, 114–129.
- Hovland, M., Croker, P.F., Martin, M., 1994. Fault-associated seabed mounds (carbonate knolls?) off western Ireland and north-west Australia. *Mar. Pet. Geol.* 11 (2), 232–246.
- Hovland, M., Mortensen, P.B., Brattegard, T., Strass, P., Rokoengen, K., 1998. Ahermatypic coral banks of mid-Norway: evidence for a link with seepage of light hydrocarbons. *Palaios* 13, 189–200.
- Huvenne, V.A.I., Beyer, A., De Haas, H., Dekindt, K., Henriet, J.P., Kozachenko, M., Olu-Le Roy, K., Wheeler, A.J., Participants, T.P.A.C.C., 2005. The seabed appearance of different coral bank provinces in the Porcupine Seabight, NE Atlantic: results from sidescan sonar and ROV sea-bed mapping. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, Heidelberg, New York, pp. 535–569.
- Huvenne, V.A.I., Blondel, P., Henriet, J.-P., 2002. Textural analyses of sidescan sonar imagery from two mound provinces in the Porcupine Seabight. *Mar. Geol.* 189 (3–4), 323–341.
- Huvenne, V.A.I., De Mol, B., Henriet, J.-P., 2003. A 3D seismic study of the morphology and spatial distribution of buried coral banks in the Porcupine Basin, SW of Ireland. *Mar. Geol.* 198, 5–25.
- Jarke, J., 1960. Beitrag zur Kenntnis der Foraminiferenfauna der mittleren und westlichen Barents-See. *Int. Rev. Ges. Hydrobiol.* 45, 581–654.
- Jensen, A., Frederiksen, R., 1992. The fauna associated with the bank-forming deepwater coral *Lophelia pertusa* (Scleractinaria) on the Faroe shelf. *Sarsia* 77, 53–69.
- Jorissen, F.J., 1988. Benthic foraminifera from the Adriatic Sea; principles of phenotypic variation. *Utr. Micropaleontol. Bull.* 37, 176.
- Jorissen, F.J., Barmawidjaja, D.M., Puskaric, S., Van der Zwaan, G.J., 1992. Vertical distribution of benthic foraminifera in the Northern Adriatic Sea. The relation with high organic flux. *Mar. Micropaleontol.* 19, 131–146.
- Jorissen, F.J., Fontanier, C., Thomas, E., 2007. Paleocceanographical proxies based on deep-sea benthic foraminiferal assemblage characteristics. In: Hillaire-Marcel, C., de Vernal, A. (Eds.), *Proxies in late Cenozoic Paleocceanography*. Elsevier, pp. 263–325.
- Jorissen, F.J., Wittling, I., Peyrouquet, J.P., Rabouille, C., Relexans, J.C., 1998. Live benthic foraminiferal faunas off Cape Blanc, NW-Africa: Community structure and microhabitats. *Deep Sea Res.* 45 (45), 2157–2188.
- Joubin, L., 1922a. Les coraux de mer profonde nuisibles aux chalutiers. Notes et Mémoires. Ov. Sci. Tech. Pêches Maritimes 18 (5–16).
- Joubin, L., 1922b. Distribution géographique de quelques coraux abyssaux dans les mers occidentales européennes. *Comp. R. Acad. Sci. Paris* 175, 930–933.
- Joubin, L., 1923. Les coraux de mer profonde du plateau continental atlantique. Rapports et procès-verbaux des réunions. International Council for the Exploration of the Sea, Copenhagen, Denmark, pp. 43–46.
- Kaiho, K., 1994. Benthic foraminiferal dissolved-oxygen index and dissolved-oxygen levels in the modern ocean. *Geology* 22, 719–722.
- Kaiho, K., 1999. Effect of organic carbon flux and dissolved oxygen on the benthic foraminiferal oxygen index (BFOI). *Mar. Micropaleontol.* 37, 67–76.
- Kenkel, N.C., Orloci, L., 1986. Applying metric and nonmetric multidimensional scaling to some ecological studies: some new results. *Ecology* 67 (919–928).
- Kenyon, N.H., Akhmetzhanov, A.M., Wheeler, A.J., Van Weering, T.C.E., de Hass, H., Ivanov, M.K., 2003. Giant carbonate mud mounds in the southern Rockall Trough. *Mar. Geol.* 195, 5–30.
- Kiriakoulakis, K., Bett, B.J., White, M., Wolff, G.A., 2004. Organic biogeochemistry of the Darwin Mounds, a deep-water coral ecosystem, of the NE Atlantic. *Deep Sea Res.* 151 (12), 1937–1954.
- 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.
- Kouwenhoven, T.J., 2000. Survival under stress: benthic foraminiferal patterns and Cenozoic biotic crises. *Geol. Ultraetina* 186, 1–206.
- Kruskal, J.B., 1964. Multidimensional scaling by optimizing goodness of fit to a nonmetric hypothesis. *Psychometrika* 29, 1–27.
- Kruskal, J.B., Wish, M., 1978. *Multidimensional Scaling*. Sage Publication, Beverly Hills, CA.
- Licari, N., Mackensen, A., 2005. Benthic foraminifera off West Africa (1°N to 32°S): do live assemblages from the topmost sediment reliably record environmental variability? *Mar. Micropaleontol.* 55, 205–233.
- Lindberg, B., Mienert, J., 2005. Sedimentological and geochemical environment of the Fugløy Reef off northern Norway. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, Heidelberg, New York, pp. 633–650.
- Loubere, P., 1989. Bioturbation and sedimentation rate control of benthic microfossil taxon abundances in surface sediments: a theoretical approach to the analysis of species microhabitats. *Mar. Micropaleontol.* 14, 317–325.
- Loubere, P., 1991. Deep-sea benthic foraminiferal assemblage response to a surface ocean productivity gradient: a test. *Paleoceanography* 6 (2), 193–204.
- Loubere, P., 1996. The surface ocean productivity and bottom water oxygen signals in deep water benthic foraminiferal assemblages. *Mar. Micropaleontol.* 28, 247–261.
- Loubere, P., 1998. The impact of seasonality on the benthos as reflected in the assemblages of deep-sea foraminifera. *Deep Sea Res.* 45 (2–3), 409–432.
- Loubere, P., Fariduddin, M., 1999. Quantitative estimation of global patterns of surface ocean biological productivity and its seasonal variation on timescales from centuries to millennia. *Global Biogeochem. Cy.* 13 (1), 115–133.
- Lutze, G.F., Coulbourn, W.T., 1984. Recent benthic foraminifera from the continental margin of northwest Africa: community structure and distribution. *Mar. Micropaleontol.* 8, 361–401.
- Lutze, G.F., Thiel, H., 1987. *Cibicides wuellerstorfi* and *Planulina ariminensis*, elevated epibenthic foraminifera. *Berichte SFB* 313 6, 17–30.
- Lutze, G.F., Thiel, H., 1989. Epibenthic foraminifera from elevated microhabitats: *Cibicides wuellerstorfi* and *Planulina ariminensis*. *J. Foraminif. Res.* 19 (2), 153–158.
- Mackensen, A., Douglas, R.G., 1989. Down-core distribution of live and dead deep-water benthic foraminifera in box cores from the Weddell

- Sea and the California continental borderland. *Deep Sea Res. I* 36 (6), 879–900.
- Mackensen, A., Fütterer, D.K., Grobe, H., Schmiedl, G., 1993. Benthic foraminiferal assemblages from the eastern South Atlantic Polar Front region between 35° and 57°S: distribution, ecology and fossilization potential. *Mar. Micropaleontol.* 22 (1993), 33–69.
- Mackensen, A., Grobe, H., Kuhn, G., Fütterer, D.K., 1990. Benthic foraminiferal assemblages from the eastern Weddell Sea between 68 and 73°S: distribution, ecology and fossilization potential. *Mar. Micropaleontol.* 16, 241–283.
- Mackensen, A., Hald, M., 1988. *Cassidulina teretis* TAPPAN and *C. laevigata* d'ORBIGNY: their modern and late quaternary distribution in Northern seas. *J. Foraminifer. Res.* 18 (1), 16–24.
- Mackensen, A., Schmiedl, G., Harloff, J., Giese, M., 1995. Deep-sea foraminifera in the South Atlantic Ocean: ecology and assemblage generation. *Micropaleontology* 41 (4), 342–358.
- Mackensen, A., Sejrup, H., Jansen, E., 1985. The distribution of living benthic foraminifera on the continental slope and rise off Southwest Norway. *Mar. Micropaleontol.* 9 (7), 275–306.
- Miao, Q., Thunell, R.C., 1993. Recent deep-sea benthic foraminiferal distributions in the South China and Sulu Seas. *Mar. Micropaleontol.* 22, 1–32.
- Mienis, F., Van Weering, T.C.E., de Haas, H., de Stigter, H., Huvenne, V.A.I., Wheeler, A., 2006. Carbonate mound development at the SW Rockall Trough margin based on high resolution TOBI and seismic recording. *Mar. Geol.* 233 (1–4), 1–19.
- Miller, K.G., Lohmann, G.P., 1982. Environmental distribution of Recent benthic foraminifera on the northeast United States continental slope. *Geol. Soc. Am. Bull.* 93, 200–206.
- Morigi, C., Jorissen, F.J., Gervais, A., Guichard, S., Borsetti, A.M., 2001. Benthic foraminiferal faunas in surface sediments off NW Africa: relationship with organic flux to the ocean floor. *J. Foraminifer. Res.* 31 (4), 350–368.
- Mortensen, P.B., Hovland, M.T., Brattegard, T., Farestveit, R., 1995. Deep water bioherms of the scleractinian coral *Lophelia pertusa* (L.) at 64°N on the Norwegian shelf: structure and associated megafauna. *Sarsia* 80, 145–158.
- Mullins, H.T., Thompson, J.B., McDougall, K., Vercoutere, T.L., 1985. Oxygen minimum zone edge effect: evidence from the Central California coastal upwelling system. *Geology* 13, 491–494.
- Murray, J.W., 1971. *An Atlas of Recent Foraminiferids*. Heinemann Educational Books, London.
- Murray, J.W., 1991. *Ecology and Palaeoecology of Benthic Foraminifera*. Longman Scientific & Technical, Essex.
- Murray, J.W., 2003. Patterns in the cumulative increase in species from foraminiferal time-series. *Mar. Micropaleontol.* 48, 1–21.
- Murray, J.W., 2006. *Ecology and Applications of Benthic Foraminifera*. Cambridge University Press, Cambridge.
- Natland, M.L., 1933. The temperature- and depth-distribution of some Recent and fossil foraminifera in the Southern California Region. *Bull. Scripps Inst. Oceanogr.* 3, 225–230.
- Nomura, R., 1983a. *Cassidulinidae* (foraminiferida) from the uppermost Cenozoic of Japan (part 1). *Sci. Rep. Tohoku. Univ.* 2 Ser. Geol. 53, 1–101.
- Nomura, R., 1983b. *Cassidulinidae* (foraminiferida) from the uppermost Cenozoic of Japan (part 2). *Sci. Rep. Tohoku. Univ.* 2 Ser. Geol. 54, 1–93.
- Pflum, C.E., Frerichs, W.E., 1976. Gulf of Mexico Deep-Water Foraminifers. *Spec. Publ. Cushman Foundation For.* 14, 125.
- Pinheiro, L.M., Ivanov, M.K., Sautkin, A., Akhmanov, G., Magalhães, V.H., Volkonskaya, A., Monteiro, J.H., Somoza, L., Gardner, J., Hamouni, N., Cunha, M.R., 2003. Mud volcanism in the Gulf of Cadiz: results from the TTR-10 cruise. *Mar. Geol.* 195, 131–151.
- Osterman, L.E., Poore, R.Z., Swarzenski, P.W., Turner, R.E., 2005. Reconstructing a 180 yr record of natural and anthropogenic induced low-oxygen conditions from Louisiana continental shelf sediments. *Geology* 33 (4), 329–332.
- Qvale, G., Van Weering, T.C.E., 1985. Relationship of surface sediments and benthic foraminiferal distribution patterns in the Norwegian Channel (northern North Sea). *Mar. Micropaleontol.* 9, 469–488.
- Ratmeyer, V., and Shipboard Party, 2004. Meteor-Berichte 06–2, Cruise No. 61, Leg 3, Cork – Ponta Delgada. Unpublished report.
- Rogers, A.D., 1999. The biology of *Lophelia pertusa* (Linnaeus 1758) and other deep-water reef forming corals and impact from human activities. *Int. Rev. Hydrobiol.* 84, 315–406.
- Rüggeberg, A., Dorschel, B., W.-Chr., D., Hebbeln, D., 2005. Sedimentary patterns in the vicinity of a carbonate mound in the Hovland Mound Province, northern Porcupine Seabight. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, Heidelberg, New York, pp. 87–112.
- Rüggeberg, A., Dullo, C., Dorschel, B., Hebbeln, D., 2007. Environmental changes and growth history of Propeller Mound, Porcupine Seabight: evidence from benthic foraminiferal assemblages. *Int. J. Earth Sci.* 96, 57–72.
- Schmiedl, G., Bovée, F. de, Buscail, R., Charrière, B., Hemleben, C., Medernach, L., Picon, P., 2000. Trophic control of benthic foraminiferal abundance and microhabitat in the bathyal Gulf of Lions, western Mediterranean Sea. *Mar. Micropaleontol.* 40, 167–188.
- Schmiedl, G., Mackensen, A., 1997. Late Quaternary paleoproductivity and deep water circulation in the Eastern South Atlantic Ocean: evidence from benthic foraminifera. *Palaeogeogr. Palaeoclimatol. Palaeoecol.* 130, 43–80.
- Schönfeld, J., 1997. The impact of the Mediterranean Outflow Water (MOW) on benthic foraminiferal assemblages and surface sediments at the southern Portuguese continental margin. *Mar. Micropaleontol.* 29 (1997), 211–236.
- Schönfeld, J., 2002a. Recent benthic foraminiferal assemblages in deep high-energy environments from the Gulf of Cadiz (Spain). *Mar. Micropaleontol.* 44, 141–162.
- Schönfeld, J., 2002b. A new benthic foraminiferal proxy for near-bottom current velocities in the Gulf of Cadiz, northeastern Atlantic Ocean. *Deep Sea Res. I* 49, 1853–1875.
- Schönfeld, J., Altenbach, A.V., 2005. Late Glacial to Recent distribution pattern of deep-water *Uvigerina* species in the north-eastern Atlantic. *Mar. Micropaleontol.* 57, 1–24.
- Seidenkrantz, M.-S., Kouwenhoven, T.J., Jorissen, F.J., Shackleton, N.J., Van der Zwaan, G.J., 2000. Benthic foraminifera as indicators of changing Mediterranean–Atlantic water exchange in the late Miocene. *Mar. Geol.* 163, 387–407.
- Sejrup, H.P., Fjærø, T., Hald, M., Beck, L., Hagen, J., Miljeteig, I., Morvik, I., Norvik, O., 1981. Benthic foraminifera in surface samples from the Norwegian continental margin between 62°N and 65°N. *J. Foraminifer. Res.* 11, 277–295.
- Smart, C.W., 2008. Abyssal NE Atlantic benthic foraminifera during the last 15 kyr: relation to variations in seasonality of productivity. *Mar. Micropaleontol.* 69 (2), 193–209.
- Smart, C.W., King, S.C., Gooday, A.J., Murray, J.W., Thomas, E., 1994. A benthic foraminiferal proxy of pulsed organic matter paleofluxes. *Mar. Micropaleontol.* 23, 89–99.
- Somoza, L., Díaz-del-Río, V., Leon, R., Ivanov, M., Fernandez-Puga, M.C., Gardner, J.M., Hernandez-Molina, F.J., Pinheiro, L.M., Rodero, J., Lobato, A., 2003. Seabed morphology and hydrocarbon seepage in the Gulf of Cádiz mud volcano area: acoustic imagery, multibeam and ultra-high-resolution seismic data. *Mar. Geol.* 195, 153–176.
- Spezzaferri, S., Coric, S., 2001. Ecology of Karpatian (early Miocene) foraminifers and calcareous nannoplankton from Laa an der Thaya, Lower Austria: a statistical approach. *Geol. Carpathica* 52 (6), 361–374.
- Suhr, S.B., Pond, D.W., Gooday, A.J., Smith, C.R., 2003. Selective feeding by benthic foraminifera on phytodetritus on the western Antarctic Peninsula shelf: evidence from fatty acid biomarker analysis. *Mar. Ecol. Prog. Ser.* 262, 153–162.
- Taviani, M., Remia, A., Corselli, C., Freiwald, A., Malinverno, E., Mastrototaro, F., Savini, A., Tursi, A., 2005. First geo-marine survey of living cold-water *Lophelia* reefs in the Ionian Sea (Mediterranean basin). *Facies* 50, 409–417.
- Thomas, E., Booth, L., Maslin, M., Shackleton, N.J., 1995. Northeastern Atlantic benthic foraminifera during the last 45,000 years: changes in productivity seen from the bottom up. *Paleoceanography* 10 (3), 545–562.
- Thomas, E., Gooday, A.J., 1996. Cenozoic deep-sea benthic foraminifers: tracers for changes in oceanic productivity?. *Geology* 24 (4), 355–358.
- Van der Zwaan, G.J., 1982. Paleoeecology of Late Miocene Mediterranean foraminifera. *Utr. Micropaleontol. Bull.* 25, 1–202.
- Van der Zwaan, G.J., Duijnste, I.A.P., Dulk, M.d., Ernst, S.R., Jannink, N.T., Kouwenhoven, T.J., 1999. Benthic foraminifers: proxies or problems? A review of paleoecological concepts. *Earth Sci. Rev.* 46, 213–236.
- Van Rooij, D., De Mol, B., Huvenne, V.A.I., Ivanov, M., Henriët, J.-P., 2003. Seismic evidence of current-controlled sedimentation in the Belgica mound province, upper Porcupine slope, southwest of Ireland. *Mar. Geol.* 195, 31–53.
- Van Weering, T.C.E., de Haas, H., De Stigter, H.C., Lykke-Anderson, H., Kouvaev, I., 2003. Structure and development of giant carbonate mounds at the SW and SE Rockall Trough margins, NE Atlantic Ocean. *Mar. Geol.* 198, 67–81.



- Warwick, R.M., Clarke, K.R., 1991. A comparison of methods for analysing changes in benthic community structure. *J. Mar. Biol. Ass. UK* 71, 225–244.
- Weston, J.F., 1985. Comparison between Recent benthic foraminiferal faunas of the Porcupine Seabight and Western Approaches Continental Slope. *J. Micropalaeontol.* 4 (2), 165–183.
- Wheeler, A.J., Beck, T., Thiede, J., Klages, M., Grehan, A., Monteys, F.X., the Polarstern ARK-XIX/3a Shipboard Party, 2005. Deep-water coral mounds on the Porcupine Bank, Irish Margin: preliminary results from the Polarstern ARK-XIX/3a ROV cruise. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, Heidelberg, New York, pp. 393–402.
- Wheeler, A.J., Beck, T., Thiede, J., Klages, M., Grehan, A., Monteys, F.X., Party, P.A.X.a.S., 2005. Deep-water coral mounds on the Porcupine Bank, Irish Margin: preliminary results from the Polarstern ARK-XIX/3a ROV cruise. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, Heidelberg, New York, pp. 393–402.
- Wheeler, A.J., Beyer, A., Freiwald, A., de Haas, H., Huvenne, V.A.I., Kozachenko, M., Olu-Le Roy, K., 2007. Morphology and Environment of Deep-water Coral Mounds on the NW European Margin. *Int. J. Earth Sci.* 96, 37–56.
- White, M., Mohn, C., de Stigter, H., Mottram, G., 2005. Deep-water coral development as a function of hydrodynamics and surface productivity around the submarine banks of the Rockall Trough, NE Atlantic. In: Freiwald, A., Roberts, J.M. (Eds.), *Cold-water Corals and Ecosystems*. Springer-Verlag, Berlin, Heidelberg, New York, pp. 503–514.
- Wienberg, C., Beuck, L., Heidkamp, S., Hebbeln, D., Freiwald, A., Pfannkuche, O., Monteys, X., 2007. Franken Mound: facies and biocoenoses on a newly-discovered “carbonate mound” on the western Rockall Bank, NE Atlantic. *Facies* 54 (1), 1–24.
- Woodruff, F., Savin, S.M., Douglas, R.G., 1980. Biological fractionation of oxygen and carbon isotopes by recent benthic foraminifera. *Mar. Micropaleontol.* 5, 3–11.
- Zibrowius, H., 1980. *Les Scléractiniaires de la Méditerranée et de l'Atlantique nord-oriental*. Mémoires de l'Institut océanographique, Monaco.