Recent benthic foraminiferal assemblages from cold-water coral mounds in the Porcupine Seabight

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Abstract Cold-water coral ecosystems are characterised by a high diversity and population density. Living and dead foraminiferal assemblages from 20 surface sediment samples from Galway and Propeller Mounds were analysed to describe the distribution patterns of benthic foraminifera on coral mounds in relation to different sedimentary facies. Hard substrates were examined to assess the foraminiferal microhabitats and diversities in the coral framework. We recognised 131 different species, of which 27 prefer an attached lifestyle. Epibenthic species are the main constituents of the living and dead foraminiferal assemblages. The frequent species *Discanomalina coronata* was associated with coral rubble, *Cibicides refulgens* showed preference to the off-mound sand veneer, and *Uvigerina mediterranea* displayed abundance maxima in the main depositional area on the southern flank of Galway Mound, and in the muds around Propeller Mound. The distribution of these species is rather governed by their specific ecological demands and microhabitat availability than by the sedimentary facies. Benthic foraminiferal assemblages from coral mounds fit well into basin-wide-scale distribution patterns of species along the western European continental margin. The diversity of the foraminiferal faunas is not higher on the carbonate mounds as in their vicinity. The living assemblages show a broad mid-slope diversity maximum between 500 and 1,300 m water depth, which is the depth interval of coral mound formation at the Celtic and Amorican Margin. The foraminiferal diversity maximum is about 700 m shallower than comparable maxima of nematodes and bivalves. This suggests that different processes are driving the foraminiferal and metazoan diversity patterns.

Keywords Benthic foraminifera · Epizoans ·
Cold-water coral ecosystems · Carbonate mound

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Introduction

Benthic foraminifera are widely used for palaeoenvironmental studies. A calibration of index species or faunal assemblages to scaling environmental parameters is required before application to the fossil record. Many studies on the recent distribution of living (Rose Bengal-stained) benthic foraminifera prove a substantial relationship with the flux of particulate organic matter to the sea floor (Lutze and Coulbourn 1984; Altenbach and Sarnthein 1989; Herguera and Berger 1991; Gooday 1994; Altenbach et al. 1999; Loubere and Fariduddin 1999), the quality of organic matter (Caralp 1989; Wollenburg and Mackensen

1998; Fontanier et al. 2005; Koho 2008), and the oxygen content of ambient bottom waters (Koutsoukos et al. 1990; Hermelin 1992; Alve 1995; Bernhard and Sen Gupta 1999). Water turbulence and near-bottom currents also exert a certain impact on benthic foraminiferal faunas. Changes in assemblage composition were recognised in places where water turbulence markedly decreases (Pujos 1971; Lutze 1980; Schiebel 1992; Debenay and Redois 1997). Elevated habitats or hard substrates are populated by epibenthic foraminifera with greater abundances under the impact of near-bottom flow regimes (Haward and Haynes 1967; Dobson and Haynes 1973; Mullineaux 1988; Schönfeld 1997, 2002). However, lateral displacement of empty foraminiferal tests is common in such settings, and environmental interpretations have to rely on the distribution pattern of the living fauna (Murray 1970; Murray et al. 1982; Williamson et al. 1984).

Cold-water coral ecosystems are biological and sedimentary facies that are often found in deep or cold high-energy environments. They are characterised by the occurrence of the frame-building corals *Lophelia pertusa* and *Madrepora oculata* that occur along the European continental margin from northern Norway, to the Gulf of Cadiz, and in the Mediterranean Sea at shallow to intermediate depths (Wilson 1979; Rogers 1999; Freiwald 2002; Taviani et al. 2005). The corals tend to form thickets, which are stabilised by sediment baffling forming bioherms (Dorschel et al. 2005; Roberts et al. 2006). Sedimentary facies and type of coral coverage characterise different stages of coral mound development (Foubert et al. 2005). The spatial facies distribution correlates with different small-scale variations of local hydrodynamical regimes (Dorschel et al. 2007). With a given variability of up to 12 different facies types, coral mounds are unique ecosystems with a high species richness and extraordinary population density as compared to the surrounding sea floor (see Mortensen et al. 1995 and Freiwald 2002 for a review). In having such different facies patterns, they are very similar to many shallow-water coral reefs known from the fossil record (Flügel and Flügel-Kahler 1992).

Coral mounds were classified as hotspot ecosystems, and were intensively studied by several, large-scale European projects (e.g. ECOMOUND, ACES, MOUND-FORCE, HERMES), but there were only a few investigations of benthic foraminifera from cold-water coral ecosystems (e.g. Freiwald and Schönfeld 1996; Hawkes and Scott 2005; Margreth et al. 2009). This was mainly due to the fact that surface sediments from these environments were difficult to sample (Weston 1982). The first investigations therefore concentrated on palaeoenvironmental implications of faunal assemblages from sediment cores (Coles et al. 1996; Rüggeberg et al. 2007). Significant progress has been made during the past decade

with the retrieval of well-preserved and reliable surface sediment samples by using dynamic positioning systems, detailed bathymetric maps from individual coral mounds, seabed images and video-controlled sampling, and the use of remotely operated vehicles (e.g. Dorschel et al. 2007). The aims of the present study are to: (a) describe the distribution patterns of benthic foraminifera on Galway and Propeller coral mounds in the Porcupine Seabight in relation to different facies, (b) to assess the foraminiferal microhabitats in the coral framework, (c) to trace the distribution of carbonate mound indicative species in foraminiferal assemblages outside the mound provinces, and (d) to compare the benthic foraminiferal diversity on the mounds with that of the ambient foraminiferal assemblages.

Study area and hydrography

Large cold-water coral carbonate mounds are common in the Porcupine Seabight, southwest of Ireland (Fig. 1), at depths between 600 and 1,200 m. They occur in clearly defined mound provinces, the Viking Mound Province, Hovland Mound Province, the Magellan Mound Province, the Enya Mound Province, and the Belgica Mound Province (Henriet et al. 1998; Van Rooij et al. 2007; Wheeler et al. 2007). The mounds have diameters of up to 5 km and grow up to 190 m above the ambient sea floor (De Mol et al. 2002). Smaller mounds are also common, and buried mounds have been reported on seismic profiles (Huvenne et al. 2007; Huvenne et al. 2003). In the following, we will concentrate on two mounds from Belgica and Hovland Mound Provinces.
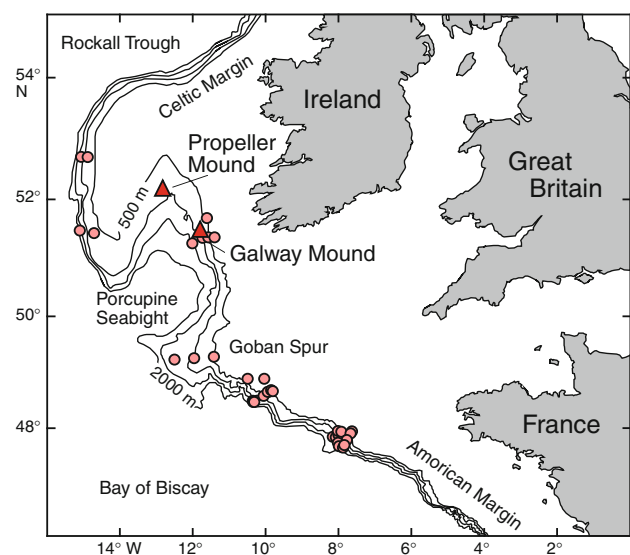

Fig. 1 Location of investigated coral mounds (*triangles*) and other surface sediment samples (*circles*, Weston 1985; Schönfeld 2006)

Galway Mound represents one of the largest mounds in the Belgica Mound Province (Fig. 2). The mound arises from 920 to 780 m water depth. A living coral framework covers the top and the western flank. A fringe of dead coral framework and rubble surrounds it. Coarse-grained sediments, sand waves, and coral patches are found in the ambient off-mound area (Dorschel et al. 2007; Noé et al. 2006). The Propeller Mound is part of a cluster of up to 150-m-high mounds in the Hovland Province. The top is mainly covered by coral rubble fringed by a girdle of sand with coral debris (Fig. 2). Mud with few coral patches is recorded in the off-mound area. A living coral framework occurs on the southern, upper flank of the mound around 700 m depth only (Dorschel et al. 2005; Rüggeberg et al. 2007).

The formation of Galway and Propeller Mounds is controlled by the oceanographic setting. At depth of recent coral growth, a water mass boundary occurs between the Eastern North Atlantic Water (ENAW, Pollard et al. 1996) and the Mediterranean Outflow Water (MOW). A weak eastern boundary slope current transports ENAW and MOW northwards (White 2007; Hackett and Roed 1998). Average bottom-current velocities range from 16 to 20 cm s^{-1} on the flanks of Galway Mound (Dorschel et al. 2007; Henry and Roberts 2007), and vary around 5 cm s^{-1} at Propeller Mound. Maximum velocities of up to 40 cm s^{-1} were recorded (White 2001). Much of the near-bottom current dynamics is induced by the breaking of internal waves and tidal baroclinic waves however (White 2007). It has been suggested that a strong gradient in density at the ENAW–MOW transition facilitates enrichment and spreading of fine-grained particles in this boundary layer, and that the corals benefit from this enrichment of food particles (White et al. 2005; Rüggeberg et al. 2007; Dullo et al. 2008). Sediment trap data and local

accumulation rates inferred that the majority of particles from pelagic settling is baffled by the coral mounds in the Belgica Mound Province (Harbers et al. 2010).

Materials and methods

Twenty sediment surface samples from Galway and Propeller Mound were used in this study (Table 1). They were recovered with an USNEL giant box corer with 50 × 50 cm surface area and a Van Veen grab sampler of 35 × 35 cm size during R/V Poseidon cruises PO265, PO292, and PO316, and legs 1 and 3 of RV Meteor cruise M61 (Freiwald et al. 2000, 2002; Pfannkuche and Utecht 2005; Hebbeln et al. 2006). A volume-defined sample from the uppermost centimetre of the surface sediment was taken with a spoon and immediately conserved and stained with a solution of 2 g Rose Bengal in 1 l ethanol (98%, technical quality) (Lutze and Altenbach 1991). This sample was used to study the living, shallow epi- and endobenthic foraminifers, and the dead assemblage in the surface sediment. A representative coverage of different microenvironments on the sediment surface was attempted wherever possible, including larger objects as coral fragments or dropstones. Samples M61/1-259 and PO316-525 recovered freestanding coral fragments. They were carefully removed from the box cores and conserved in a Rose Bengal–ethanol solution too. These objects were later examined for attached epibenthic foraminifers. The maximum height of the substrates or points of attachment above the ambient surface was recorded. As the coral fragments were partly embedded in the interstitial sediment, zero level for attachment height was assigned to a horizon from where below traces of fine sediment were still sticking to the object.

Fig. 2 Bathymetry, surface sediments, and biofacies around Propeller and Galway Mounds (after Harbers et al. 2010, and own observations)
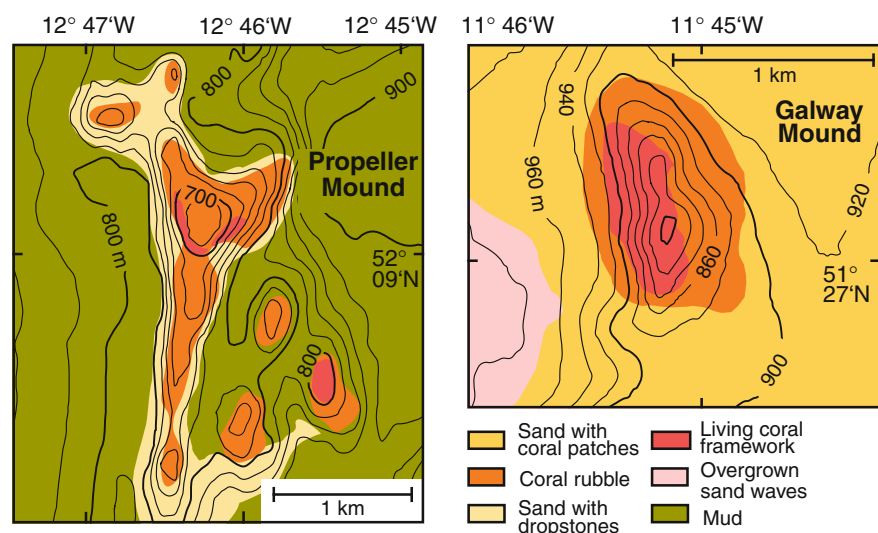
The samples for foraminiferal studies were washed on a 63-μm mesh screen. They were first passed through a 2,000-μm sieve to collect larger particles, which can be damaged if washed too long. The dried residues were further divided into the grain-size fractions 63–250 μm, and 250–2,000 μm. The objects >2,000 μm were examined for attached foraminifers. The size of the epibenthic specimens was measured with an eyepiece reticle so that they can be included in the faunal census of different grain-size fractions from the samples. Benthic foraminifers were analysed from the fraction >250 μm to make the data compatible to previous benthic foraminiferal studies in adjacent areas or comparable environments (Weston 1985; Schönfeld 1997, 2002; Schönfeld and Altenbach 2005). The samples were then picked for well-stained benthic foraminifers that are considered to have been living at the time of sampling (Murray and Bowser 2000). Arenaceous, and thick-walled miliolid species were either soaked with water to make their staining pattern more visible or crushed to see whether the test contained protoplasm. After the living forms were sorted out, an aliquot was made with an Otto microsplitter and picked for dead foraminifers. Living and dead assemblages from Galway Mound were collected in Plummer cell-slides, sorted at species level, fixed with glue, and counted by the first author. The samples from Propeller Mound contained only a few or were barren of living (stained) specimens. The sediment surface was apparently washed during box-corer recovery. Therefore, only the dead assemblages were analysed from these samples. The residues were further subdivided into the grain-size fractions 63–125 μm, 125–250 μm, 250–500 μm, 500–1,000 μm, and 1,000–2,000 μm to facilitate microscopic work. The benthic foraminiferal specimens were picked from aliquots made with an Otto microsplitter of the size fractions >125 μm, sorted at species level in single cell-slides, and counted by Steffi Schmidt for each size fraction. The census data of the size fractions >250 μm were put together to make the data comparable to the Galway Mound samples. Multivariate analyses were applied to the faunal census data by using the statistics program PAST v1.74 (Hammer et al. 2001). PAST was also used to calculate faunal diversity indices.

Results

Foraminiferal species and distribution

The foraminiferal fauna shows middle to upper bathyal characteristics and is similar to assemblages previously described from other cold-water coral ecosystems and adjacent parts of the eastern North Atlantic (Weston 1985; Coles et al. 1996; Margreth et al. 2009). One hundred and thirty-two different species are recognised in total

Table 1 Station number, coordinates, water depths, and sedimentary facies of samples from coral mounds considered in this study

Station	Latitude (N)	Longitude (W)	Depth (m)	Facies
(a) Galway mound				
GeoB9219-1	51° 27.05′	11° 45.40′	921	Fine sand with coral rubble and living corals
GeoB9218-1	51° 27.47′	11° 45.33′	889	Dead coral framework
Geob9209-2	51° 26.89′	11° 45.81′	982	Silty sand with corals and sponges
GeoB9206-1	51° 27.31′	11° 45.12′	857	Living corals and dead coral framework
GeoB9205-1	51° 27.04′	11° 45.12′	810	Living coral framework
GeoB9204-1	51° 26.94′	11° 45.16′	837	Living coral framework
PO316-525	51° 26.88′	11° 45.62′	957	Silty sand with coral rubble and sponges
M61/1-259	51° 27.30′	11° 45.26′	858	Coral rubble with living corals
(b) Propeller mound				
GeoB 9246-3	52° 8.99′	12° 46.20′	750	Coral framework
GeoB 6721-1	52° 9.22′	12° 46.31′	696	Sand with coral fragments
GeoB 8074-1	52° 8.43′	12° 45.88′	784	Sand with coral rubble
GeoB 8047-1	52° 9.34′	12° 46.40′	795	Sand with coral fragments
GeoB 9245-1	52° 8.84′	12° 46.14′	769	Silty sand
GeoB 8039-1	52° 8.19′	12° 46.09′	850	Dropstones with coral fragments
GeoB 6708-1	52° 9.25′	12° 46.19′	742	Silty sand
GeoB 8059-1	52° 9.20′	12° 46.88′	804	Sandy mud
GeoB 8073-1	52° 8.75′	12° 47.11′	761	Sandy mud
GeoB 6718-1	52° 9.58′	12° 45.00′	890	Mud

([Appendix 1](#)), of which 57 are Textulariina, 20 are Miliolina and 55 are Rotaliina. The living fauna at Galway Mound showed 58 different species ([Appendix 2](#)), of which 21 were not recorded in the dead assemblages. These were almost exclusively fragile arenaceous species with a low preservation potential. The dead assemblages showed 84 different species ([Appendix 3](#)), and 47 of them were not found in the living assemblages. These were bathyal foraminifera with robust tests, for instance *Pyrgo* species, which usually showed low-standing stocks in other areas. Only three species from the dead assemblages, namely *Elphidium excavatum*, *Elphidium incertum* and *Hyalinea balthica,* were reported living on the adjacent continental shelf and could be redeposited (e.g. Murray [1970](#)). The shelf species contribute at maximum 4.6% to the dead assemblages at Galway Mound. The dead assemblages at Propeller Mound showed 81 different species ([Appendix 4](#)). Even though this species number is comparable to the dead assemblages from Galway Mound, 36 arenaceous species were recognised at Propeller Mound, but only 24 were found at Galway Mound. The number of miliolid species is 10 and 15 respectively. Species that were probably redeposited from the continental shelf, *Buccella frigida, Elphidium excavatum,* and *Hyalinea balthica,* contribute between 1.1 and 11.2% to the dead assemblages at Propeller Mound. A comparison of the dead assemblage species compositions revealed that 34 and 31 species were only found on Galway and Propeller Mound respectively. In the following, we only considered the main faunal constituents because of the differences between Galway and Propeller Mound, and the differences between living and dead assemblage compositions.

Discanomalina coronata was the most frequent species at Galway Mound contributing on average 19.3 and 37.2% to the living and dead assemblages. *Placopsilina confusa* and *Cibicides lobatulus* were with 13.0 and 8.7% also very frequent in the living and dead assemblages. Other frequent species were *Cibicides refulgens, Cibicidoides pachyderma, Dorothia bradyana, Crithionina mamilla, Planulina ariminensis, Textularia hystrix,* and *Uvigerina mediterranea*. Each of these species contributes between 5 and 8% to the living and dead assemblages. With the exception of *Cibicidoides pachyderma, Dorothia bradyana,* and *Uvigerina mediterranea*, all frequent species at Galway Mound prefer an epibenthic lifestyle (Jones [1994](#); Schönfeld [1997](#), [2002](#)). The population densities varied between 4 and 31 living specimens per 10 cm^3, and they showed no pattern that could be related to the sedimentary facies distribution.

Uvigerina mediterranea was the most frequent species at Propeller Mound with on average 31.6% of the dead assemblages. *Uvigerina peregrina parva* and *Discanomalina coronata* were with 10.8 and 8.0% also very frequent.

Other common and frequent species were *Cibicidoides wuellerstorfi, Sigmoilopsis schlumbergeri,* and *Planulina ariminensis*. Each of these species contributed on average between 7.1 and 4.5% to the dead assemblages. Only half of the frequent species at Propeller Mound live epibenthic and they were not dominant here.

The local occurrence pattern of frequent foraminiferal species around Galway and Propeller Mounds was highly differentiated. The epibenthic *Hyrrokkin sarcophaga*, a species that preys from living coral tissue (Cedhagen [1994](#); Freiwald and Schönfeld [1996](#)), was found living only in Galway Mound samples from the living coral framework, or close to it, with very low proportions. *Hyrrokkin sarcophaga* was uniformly distributed in the dead assemblages on and around the mound with 2–4%, which indicates a later dispersal of the empty tests (Fig. [3](#)). The elevated epibenthic *Discanomalina coronata* showed the highest proportions of the living fauna in living coral thickets at the northern top of Galway Mound and on overgrown sandwaves to the west of the mound (Fig. [4](#)). In the dead assemblages, the proportions were with 40–67% consistently higher in samples from dead coral framework and coral rubble than in samples from the living coral thickets (22–33%) or the surrounding sand veneer (14–42%). *Discanomalina coronata* was less abundant in the dead assemblages from Propeller Mound, where it showed variable proportions between 5 and 22% in samples from coral rubble and the living framework, and 0.1–16% in the fringing sands (Fig. [4](#)). The species was almost absent from the muds that surround Propeller Mound.

The shallow epibenthic *Cibicides lobatulus* and *Cibicides refulgens* were rare in the living fauna of samples from the dead coral framework and coral thickets. The proportions were with 1–2% consistently lower than in the dead assemblages. On the sands surrounding Galway Mound however, the proportions of living *Cibicides refulgens* were with 24–35% higher by a factor of 10 than in samples from the coral habitats, whereas the proportions in the dead assemblages were similar (Fig. [4](#)). The same holds true for living *Cibicides lobatulus* on the ambient sands, but the proportions were with 5 and 15% considerably lower. *Cibicides refulgens* showed similar proportions of 2–5% of the dead assemblages in samples from coral rubble, living framework, and the sand belt around Propeller Mound. The species was very rare in samples from the ambient muds.

The shallow endobenthic *Uvigerina mediterranea* was recorded in the living fauna with 8 and 10% in two samples from the coral thicket at the southern flank of Galway Mound (Fig. [4](#)). The proportions of the dead assemblages were with 6–20% consistently higher on the sands to the south of the mound than in the coral habitats. *Uvigerina mediterranea* constituted 1–5% of the dead assemblages on
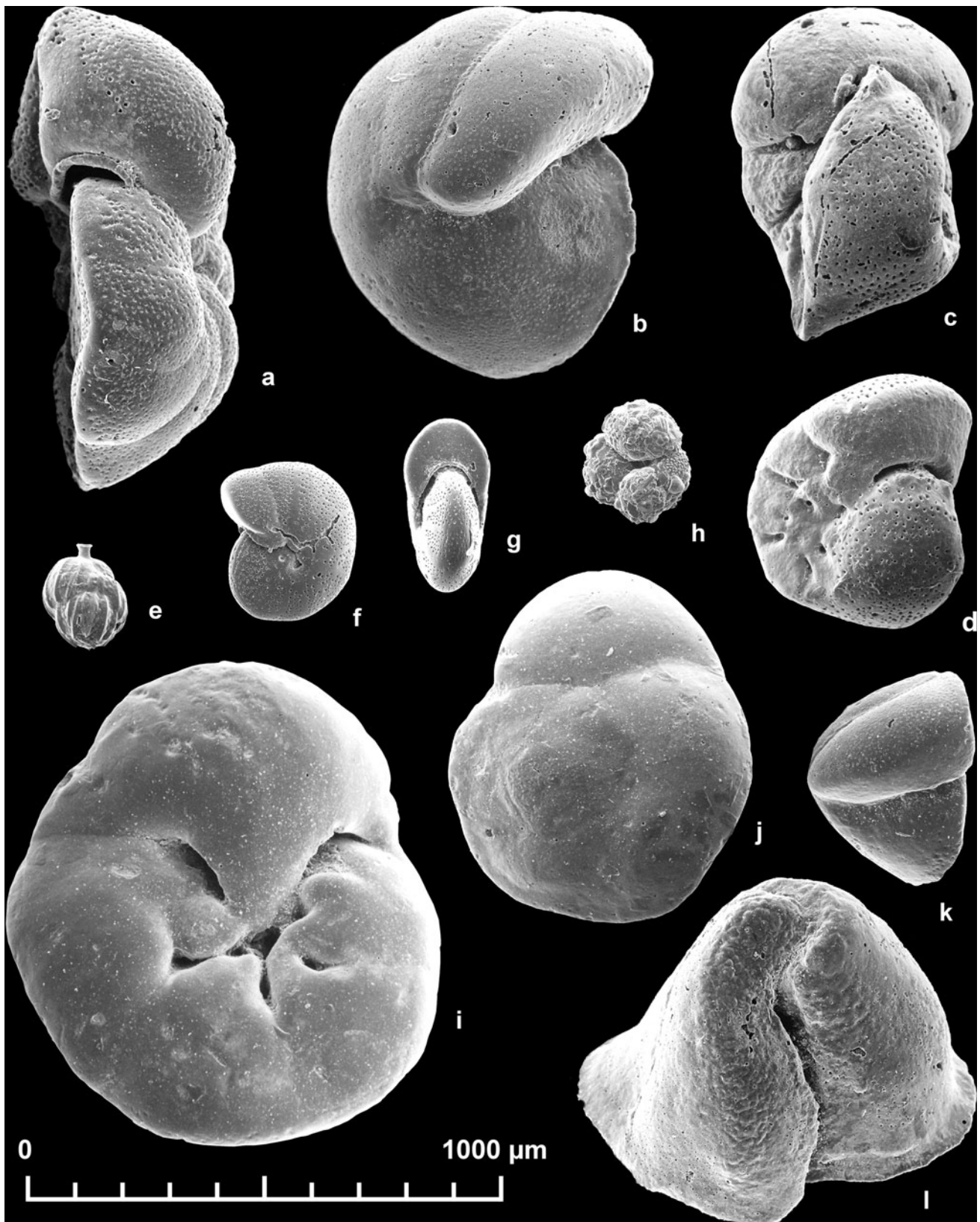
the southern side of Galway Mound, and it was rare or absent on the northern side. On Propeller Mound, *Uvigerina mediterranea* was with 10 to 81% much more frequent in the dead assemblages than on Galway Mound. A local distribution pattern was not recognised, though the species was with 20 and 22% less frequent to the south of the

◄ **Fig. 3** *Cibicides lobatulus*; **a** lateral view, **b** umbilical side view, sample GeoB8045-1, size fraction 500–1,000 μm. **c, d** *Discanomalina coronata*; **c** lateral view, **d** umbilical side view, sample GeoB8045-1, size fraction 250–500 μm. **e** *Uvigerina mediterranea*; sample GeoB8045-1, size fraction 125–250 μm. **f, g** *Melonis barleeanum*; **f** umbilical side view, **g** lateral view, sample GeoB8045-1, size fraction 125–250 μm. **h** *Trochammina globigeriniformis*; umbilical side view, sample GeoB8045-1, size fraction 125–250 μm. **i, j** *Hyrrokkin sarcophaga*; **i** umbilical side view, **j** spiral side view, sample GeoB8045-1, size fraction 500–1,000 μm. **k, l** *Cibicides refulgens*; **k** lateral view, sample GeoB8045-1, size fraction 250–500 μm. **l** umbilical side view, sample GeoB8045-1, size fraction 500–1,000 μm. Note the difference to *C. lobatulus* by the more conical geometry and the smoother test walls of *C. refulgens*

mound than on the mound itself, where the proportions were 10–36%. Off Propeller Mound, *Uvigerina mediterranea* was with 56 and 81% very frequent in the dead assemblages in the surrounding muds (Fig. 4).

The shallow to intermediate infaunal species *Melonis barleeanum* was recorded in the living fauna of three samples from Galway Mound with proportions of 1–4% (Appendix 2). The species was with 1–5% also rare in the dead assemblages (Appendix 3). *Melonis barleeanum* was evenly distributed on and around Galway Mound, and the abundances showed no systematic variability with

sedimentary facies. On Propeller Mound, *Melonis barleeanum* was with 3–9% more frequent in the dead assemblages on the mound than in the surrounding muds, where it showed 1% only (Appendix 4). Furthermore, the proportions increased with elevation, and the highest percentages were recorded in the living coral thicket near the summit.

Foraminiferal assemblages

To reduce the high species numbers to a practical size, only those species which occurred in at least one sample among the five ranked species were taken into consideration for multivariate analyses. This resulted in a reduction to 17 and 12 species at Galway Mound, which comprised 61.5–100% and 67.1–100% of the living and dead assemblage, respectively. At Propeller Mound, the reduction left 15 species, which comprised 67.7–97.4% of the dead assemblage.

Correspondence analyses and detrended correspondence analyses were applied to the reduced data sets in order to obtain species associations with distinct distributions or demands to certain environmental conditions. Factor
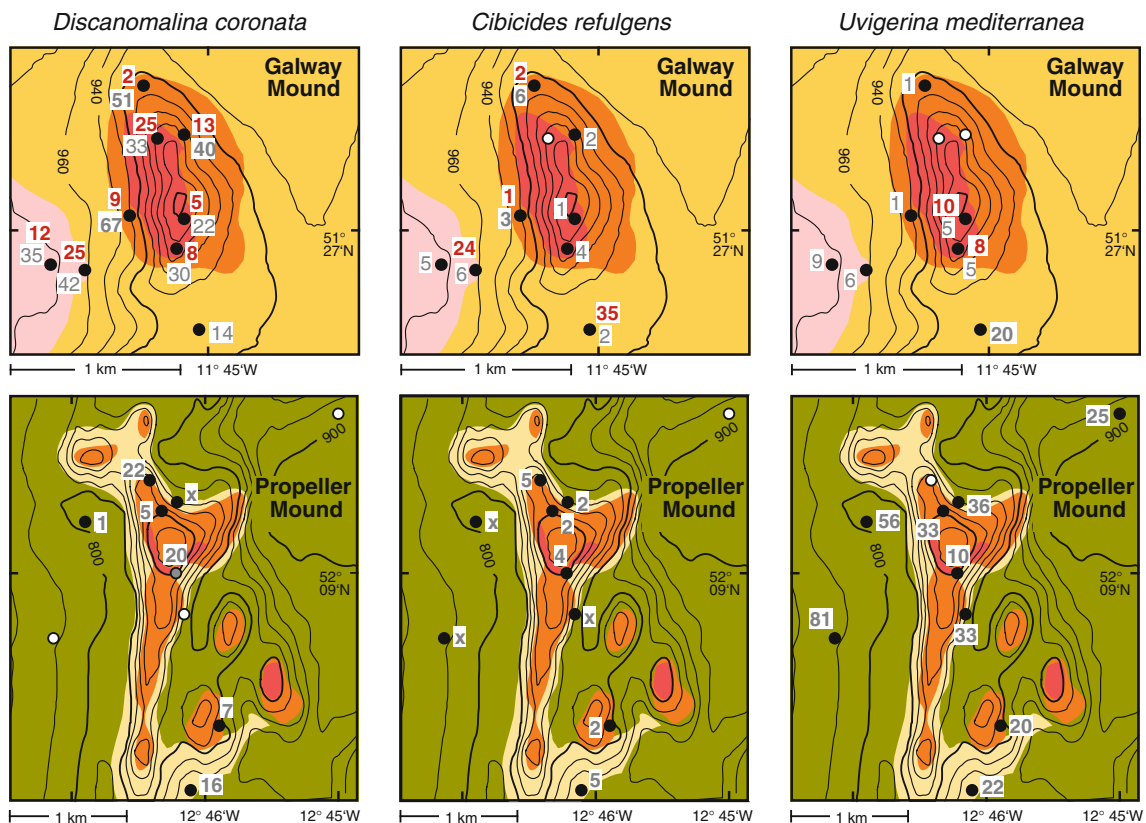

Fig. 4 Bathymetry, surface sediments, biofacies and distribution of dominant foraminiferal species around Galway and Propeller Mounds. *Grey numbers* indicate the proportion of the dead assemblage >250 μm (%), *red numbers* indicate the proportion of the living (rose Bengal stained) assemblage >250 μm (%), *x* proportion < 0.1%

analyses, which were successfully applied in previous investigations (Schönfeld 2002), were discarded in this study because the species number exceeds the number of samples from Galway or Propeller Mounds. Living and dead assemblages were analysed separately. Foraminiferal species were assigned to different associations following at first the analysis of the living assemblage, because the living fauna is considered to be in equilibrium with the ambient environmental parameters. For 17 frequent benthic foraminiferal species from ten samples from Galway Mound, the analysis extracted nine axes. The two-first ranked axes were clearly separated from the others by their variance proportion, and they accounted for 48.4% of the total data variability. The best resolution of faunal groups was displayed between Axes 1 and 2. The species scores inferred two main clusters that are assigned to Assemblages 1 and 2. There were also two outliers of single species, which are considered separately. The detrended correspondence analyses produced the same pattern though with a less pronounced separation of the faunal assemblages. The results from detrended analyses were therefore omitted in the following. Testing for absence—not recorded artefacts by replacing 0 by 0.001% for species that were not recorded in a given sample revealed no influence of zero values on correspondence analyses results of our data (Wartenberg et al. 1987).

Assemblage 1 was characterised by positive Axis 1 scores and positive Axis 2 scores. Assemblage 1 mainly contained endobenthic foraminifera, namely *Hoeglundina elegans, Pullenia bulloides, Reophax calcareus, Reophax spiculifer* and *Uvigerina mediterranea* (Fig. 5a). *Tholosina vesicularis* was the only epibenthic species in this assemblage. Assemblage 2 was characterised by low negative to positive Axis 1 scores and negative Axis 2 scores. This assemblage was composed predominantly by epibenthic foraminifera, in particular *Cibicides lobatulus, Crithionina mamilla, Placopsilina confusa, Spirillina decorata, Textularia hystrix*, and *Tritaxis fusca. Saccorhiza ramosa,* and *Saccammina sphaerica* were also clustered with Assemblage 2. These species were occasionally found attached to larger objects in samples from Galway Mound. *Dorothia bradyana* is considered as a free-living species though. Outlier species were the elevated epibenthic *Discanomalina coronata* and shallow epibenthic *Cibicides refulgens*, which showed highly negative Axis 1 and Axis 2 scores, respectively.

The correspondence analysis of the dead assemblages from Galway Mound extracted eight axes. The first two axes were clearly separated by their variance proportion, and they accounted for 83.2% of the total data variability. Again, the best resolution of faunal relationships was displayed between Axes 1 and 2. In contrast to the living assemblage, clustering is less clear. A group of *Cibicides*
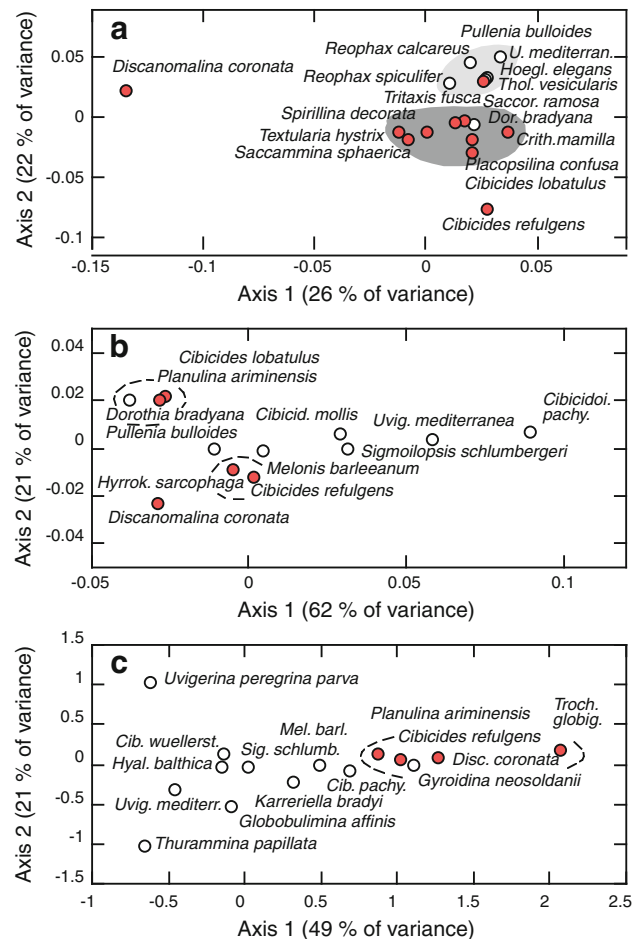
Fig. 5 Correspondence analysis of the relative abundances of the five ranked species. *Red dots* indicate epibenthic species. **Panel a** living assemblage, Galway Mound, the *light grey polygon* marks Assemblage 1 of mainly endobenthic species, the *dark grey polygon* encircles Assemblage 2 of mainly epibenthic species. **Panel b** dead assemblage, Galway Mound. **Panel c** dead assemblage, Propeller Mound

lobatulus, Planulina ariminensis, and *Dorothia bradyana* was separated from the other species by Axis 2 scores of >0.015 (Fig. 5b). Again, the free-living *Dorothia bradyana* was grouped with epibenthic species. Axis 2 scores between 0.006 and −0.002 confine the main group. It was composed of *Cibicidoides mollis, Cibicidoides pachyderma, Melonis barleeanum, Pullenia bulloides, Sigmoilopsis schlumbergeri*, and *Uvigerina mediterranea*. These are mainly endobenthic species, but *Cibicidoides mollis* was reported to prefer shallow substrates in the bottom nepheloid layer in places (Schönfeld 1997). A single living and attached *Cibicidoides pachyderma* was observed in this study, but the species was found to live in shallow endobenthic microhabitats elsewhere (Schönfeld 2001; Fontanier et al. 2002). A third group of species was separated by Axis 2 scores of < −0.008 (Fig. 5b). It comprises the epibenthic *Hyrrokkin sarcophaga* and *Cibicides refulgens,*

which have a quite different ecology. *Discanomalina coronata* again is an outlier with very low Axis 2 scores.

The dead assemblages from Propeller Mound exhibited an even more indistinct clustering. The first two axes of the correspondence analyses accounted for 69.6% of the total data variability. The majority of species gathered in a broad cluster between Axis 2 scores of 0.2 and −0.6. The cluster may be subdivided into a group of species with rather high individual distances at Axis 1 scores of < 0.7 (Fig. 5c). These are endobenthic species as *Cibicidoides pachyderma*, *Globobulimina affinis*, *Hyalinea balthica*, *Karreriella bradyi*, *Melonis barleeanum*, *Sigmoilopsis schlumbergeri* and the epibenthic *Cibicidoides wuellerstorfi*. The other group showed lower individual distances at Axis 1 scores >0.7 and comprised the epibenthic *Cibicides refulgens*, *Discanomalina coronata*, *Planulina ariminensis* and *Textularia hystrix*, as well as the endobenthic *Gyroidina neosoldanii*. It has to be noted that in contrast to the results from Galway Mound, *Discanomalina coronata* and *Cibicides refulgens* join other epibenthic foraminifera in one data subgroup at Propeller Mound. Outlier species were *Uvigerina peregrina parva* and *Thurammina papillata*, which showed highly positive and negative Axis 2 scores, respectively.

Colonisation structures

A total of 117 different hard substrates and other elevated objects from Galway Mound were examined, and 429 attached, living foraminifera were recorded, of which 364 were larger than 250 μm. Twenty-seven epibenthic foraminiferal species were recognised (Appendix 5). Seven species were found as free living specimens too, and thus used the attached lifestyle only facultatively. The substrates were mainly coral fragments, fragments of siliceous sponges, hydroids, pteropod shells, fragments of bivalves, gastropods and crustacean shells, balanid and echinoid plates, other biodetritus and dropstones. The size of the objects varied between a few and 90 mm, and was on average 10–20 mm. The population density was very variable and ranged from one to 43 living specimens per object. Clustering of two to four specimens of the same species and size was commonly observed. The recruitment on other epizoans, in particular hydroids was also frequent. The hydroids settle preferentially in and around ancient thecae of coral fragments, thus promoting a concentration of certain epibenthic species, in particular *Discanomalina coronata*, in these microenvironments (Fig. 6). Nonetheless, exposed edges were also preferred by many species. In one case, the assemblage displayed a distinct tiering in that the lower, sheltered side of a coral fragment was populated by *Placopsilina confusa*, and the upper, exposed side was inhabited by *Cibicides refulgens*. A determination of the attachment height above the ambient sediment surface was possible in

two samples only. The attached specimens concentrated at a height of 2–3 cm above the ambient sediment surface as defined by the mudline of interstitial sediment. *Discanomalina coronata*, *Discanomalina semipunctata*, *Dorothia goesi*, *Hyrrokkin sarcophaga*, *Patellina corrugata*, *Planulina ariminensis*, and *Spirillina decorata* depicted a preference for an elevated lifestyle. They recruited free-standing substrates, other epizoans, and they showed a higher population density at elevated positions. The elevated epibenthic foraminifera from Galway Mound comprise 7–95 and 15–75% of the living and dead assemblages. The shallow-living species contribute 5–85 and 5–27% to living and dead assemblages.

Discussion

Biological heterogeneity and sampling

A systematic distribution pattern of frequent benthic foraminiferal species was recognised around Galway Mound. This pattern raises the question, whether it is related to sedimentary facies distribution or macrofaunal populations, and whether it is influenced by patchiness at different scales. Data on patchiness of habitats on coral mounds and ambient environments are rare (Henry and Roberts 2007). Bottom photographs of coral thickets suggested an average lateral extension of macrofaunal habitats in the range of 0.5–2 metres (Hebbeln et al. 2006; Wienberg et al. 2008). The lateral variability is with more than a metre at a higher range in dead coral framework. On sand sheets, lateral changes in macrofaunal population and sediment coverage were observed over distances of 6–15 m (Hebbeln et al.

Fig. 6 Recruitment on other epizoans. Three specimens of *Discanomalina coronata* were attached to a hydroid that settled in the ancient theca of a coral fragment (Sample PO265-482, Propeller Mound)

2006). It is therefore conceivable that sampling with a box core of 0.5 × 0.5 m size represents a single facies type only. A small-scale patchiness of epibenthic foraminifera was observed on hard substrates. The recruitments varied over distances of a few centimetres as described above. We can only speculate about the lateral inhomogeneity of the endobenthic foraminiferal population, however, but the size of our samples from Galway Mound is considered to be sufficient to cover the different small-scale epibenthic microhabitats.
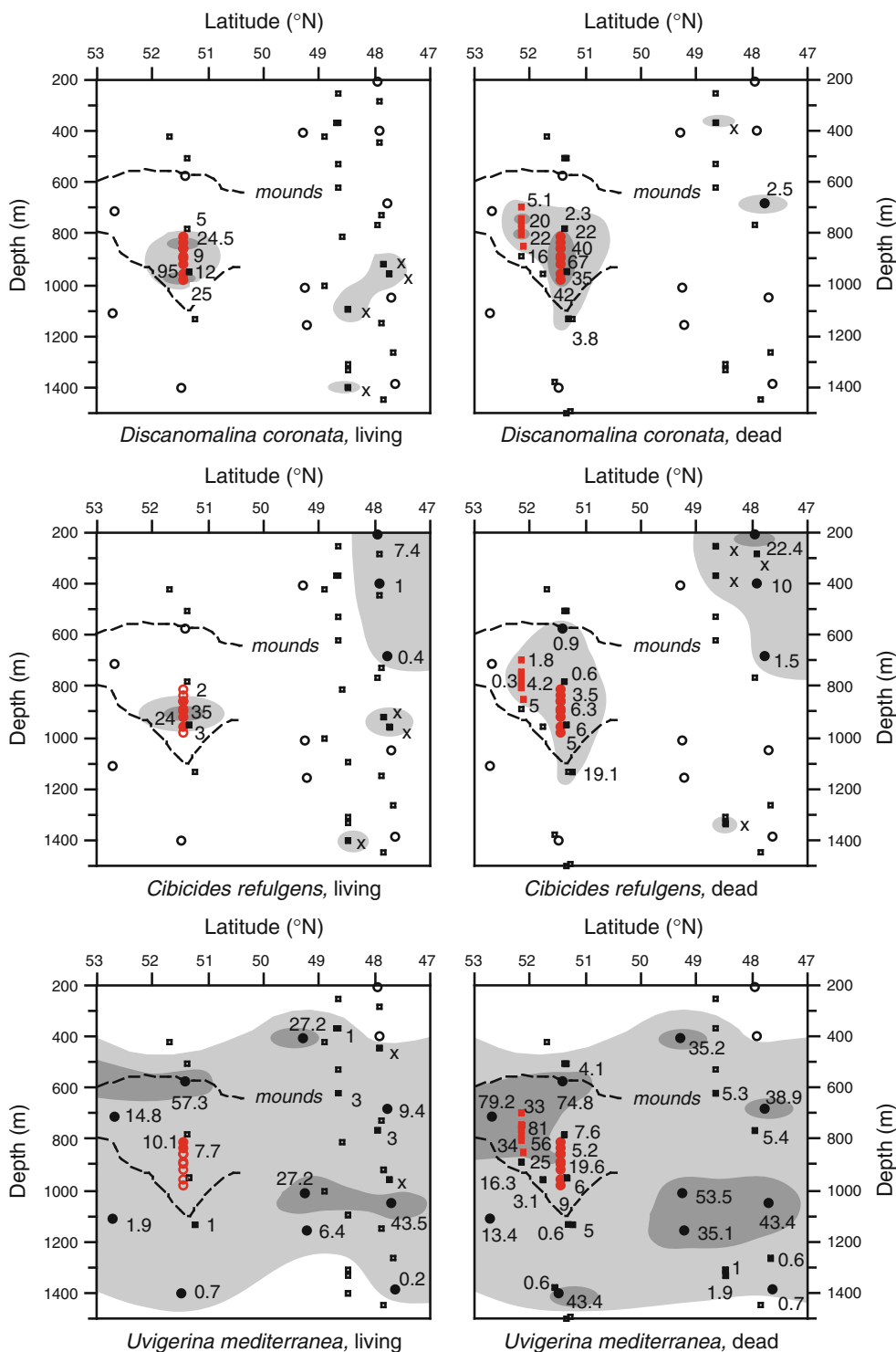
Identification of cold-water coral habitats
and related facies

The data from Galway Mound indicate that among the most frequent species *Discanomalina coronata* is associated with coral rubble, *Cibicides refulgens* shows preference to the off-mound sand veneer, and that *Uvigerina mediterranea* shows an abundance maximum in the main depositional area on the southern, exposed side of the mound. This raises the question whether these species can be used as indicator for cold-water coral habitats and related sedimentary facies. A survey of total assemblages >63 μm of several mounds from the Porcupine and Rockall Bank region depicted *Discanomalina coronata* as an indicator species to identify active mounds (Margreth et al. 2009). The depth distribution of *Discanomalina coronata* along the Celtic and Amorican margins indeed showed high abundances in the mound provinces, but there was another distribution patch between 47°N and 48°N (Appendix 6; Fig. 7). This occurrence is situated between 600 m and 1,200 m depth below La Chapelle Bank, from where deep-water corals were described (Reveillaud et al. 2008). *Discanomalina coronata* was also reported from various deep high-energy environments off southern Portugal, Galicia, in the Bay of Biscay, and elsewhere (Pujos 1970; Medioli and Scott 1978; Schönfeld 1997). These findings and the results from our study indicated that this species prefers fibrous elevated substrates when available, especially hydroids. The occurrence of flexible, tubular epizoans under high bottom-near currents and sufficient food supply are therefore considered as limiting boundary conditions for significant populations of *Discanomalina coronata*. These settings are not exclusively linked to cold-water coral habitats, they may occur on other hard substrates too. As such, *Discanomalina coronata* has to be used with caution for identifications of living cold-water coral ecosystems. Our data infer that *Hyrrokkin sarcophaga* could be a supplementary indicator as this species directly inhabits living cold-water corals (Freiwald and Schönfeld 1996), but it is redeposited off mound and comparatively rare in the dead assemblages from the study area.

Cibicides refulgens has been attributed to the sandwave facies around coral mounds (Margreth et al. 2009). Indeed, the proportions of this species from the living assemblages on the sand veneer around Galway Mound were substantially higher than in samples from the coral habitats, but the proportions in the dead assemblages were similar (Fig. 4). The depth distribution of *Cibicides refulgens* along the Celtic and Amorican margins indeed showed a broad distribution patch in the mound provinces with high abundances in the living fauna and rather low abundances in the dead assemblages (Fig. 7). Another distribution patch was recognised on the upper Amorican Margin between 47°N and 49°N at depths between 200 m and 1,000 m, which continued into extended occurrences of this species on the Celtic Sea shelf and Channel area (e.g. Le Calvez 1958; Lees et al. 1969; Giese 1991). *Cibicides refulgens* lives firmly attached to smooth and stable surfaces, for instance dropstones or bivalves. The species may use different nutrition strategies, in particular grazing and filter feeding by a specialised network of partially sheltered pseudopodia. By that, *Cibicides refulgens* can stand a very low and highly variable food supply under exposure to strong currents (Alexander and DeLaca 1987). It is conceivable that the recruitment and reproduction rates of this species may be much lower in such high-energy environments than those of the closely related *Cibicides lobatulus* (Wisshak and Rüggeberg 2005). This would offer an explanation of the eye-catching contrast between high population densities of *Cibicides refulgens* and low proportions in the dead assemblages. An exclusive relationship of this species to the sand belts around cold-water coral mounds is not given.

Sediment baffling by the coral thickets lead to the accumulation of fine-grained organic-rich interstitial sediment, which sustained a rich endobenthic foraminiferal fauna specialised to high food supply (Margreth et al. 2009). This process is mirrored in the present study by the occurrence pattern of *Uvigerina mediterranea* around Galway Mound, which was frequent on the southern side and rare on the northern side. Bottom currents deliver suspended particles from the south (Dorschel et al. 2007). *Uvigerina mediterranea* is common on the Celtic and Amorican margins above 1,400-m water depth (Fig. 7). The species shows regional patches of high abundances, which are typical for several deep-water *Uvigerina* species (Lutze 1986; Schönfeld 2006). The high abundance patches may be induced by locally enhanced flux rates of particulate organic matter to the seafloor by downslope transport or lateral advection (Altenbach et al. 2003; Schönfeld and Altenbach 2005). One of these *Uvigerina mediterranea* patches is centred on the Celtic margin between 51°N and 53°N at depths between 500 and 900 m. It includes the Magellan and Belgica Mound Provinces. It is therefore

Fig. 7 Latitudinal vs. depth distribution of foraminiferal species at the Irish and American continental margin. The *numbers* indicate percentages of the fauna >250 μm. The *light grey polygons* encircle the distribution patches, the *dark grey polygons* highlight the abundance maxima of >20%. *Dashed lines* depth limits of carbonate mounds

Discanomalina coronata, living

Discanomalina coronata, dead

Cibicides refulgens, living

Cibicides refulgens, dead

Uvigerina mediterranea, living

Uvigerina mediterranea, dead

justified to assign *Uvigerina mediterranea* as indicator for off-mound conditions, at least in the Porcupine Seabight.

Significance of epibenthic assemblages

The correspondence analyses of the five ranked species from living and dead assemblages identify epibenthic species as a consistent group. *Discanomalina coronata* and *Cibicides refulgens* were not affiliated with the epibenthic cluster because they were very frequent in single samples. The free-living *Dorothia bradyana* was included in the epibenthic group. This species was recorded from coarse sands from the upper slope off Scotland and on the outer shelf off northern Norway from 90 to 640 m water depth

by the first author, where *Dorothia bradyana* is adapted to high-energy environments. That would explain the affiliation of this species with the epibenthic cluster at Galway Mound (Fig. 5a).

The proportion of epibenthic species in living and dead assemblages showed no systematic distribution pattern around Galway Mound that would allow to characterise a specific sedimentary facies by epibenthos percentages. Furthermore, elevated epibenthic species showed their highest proportions in samples from the overgrown sandwaves, where *Discanomalina coronata* dominates the assemblages. Nonetheless, the abundance of epibenthic foraminifera is with 34–100%, on average 66.5% of the living assemblages at Galway Mound substantially higher than outside the Mound Provinces. To the south at Goban Spur, the same species comprise 5.1–9.4% of the living assemblages at similar water depths. Therefore, epibenthic foraminifera have to be considered as significant faunal constituents for cold-water coral environments. This corresponds to the ecological composition of the macrofauna where a higher abundance of filter and suspension feeders was recognised on the coral mounds whereas deposit feeders and mobile fauna occurred off-mound (Jonsson et al. 2004).

Trends in diversity

Coral mounds are ecosystems with a high diversity as compared to ambient environments (Henry and Roberts 2007). The diversity of benthic foraminiferal assemblages, as displayed by Fisher's alpha index, shows a high variability of values between 5 and 20 in the study area (Figs. 1, 8). The living assemblages from Galway Mound show two groups of different faunal structure. One group shows alpha indices between 9.6 and 15.7, which do not differ from samples outside the Mound Provinces at the same water depths. The other group are samples from

elevated substrates, where the diversity is with 0.9–4.9 significantly lower (Fig. 8). With reference to macrofaunal studies, this pattern is difficult to explain. One reason, which concurs with our observations, could be that coral rubble and living framework provides only a restricted number of niches and thus provides living space only for a limited number of species.

The Fisher's alpha indices of living benthic foraminiferal assemblages from the Celtic and Amorican margin including samples from Galway Mound follow a broad band with a distinct maximum at 500–1,200 m water depth. This depth interval matches the range of mound formation in the Porcupine Seabight (Fig. 8). A mid-slope diversity maximum is known from macrofaunal studies, and it is suggested to reflect an intersection of decreasing food availability and increasing environmental stability with depth (e.g. Gage et al. 2000). In the Porcupine Seabight however, comparable diversity maxima of nematodes and gastropods were recorded at 700-m greater depth than the foraminiferal diversity maximum (Paterson and Lambshead 1995; Olabarria 2005). This infers that different processes were involved.

Metazoan diversities often displayed a parabolic, unimodal relationship with environmental or spatial gradients (Pearson and Rosenberg 1978). The diversity was high when the intensity and frequency of biotic or physical disturbance was low (Huston 1979). Biological disturbances induced population fluctuations, which caused the expelling or even extinction of less-tolerant species and hence a lower diversity (Dayton and Hessler 1972). Physical stability facilitated a high degree of specialisation among potentially competing species in the deep sea, in a way that minimises their competition (Sanders 1968). Physical disturbance is created by a near-bottom flow regime, which maintains the habitat in an early successional state, in particular where the sediments are mobile. This affected the diversity of many groups. For instance,

Fig. 8 Diversity of benthic foraminifera (*left panel*) and metazoans (*right panel*) vs. water depth at the Irish and Amorican Margin. The foraminiferal samples with exceptional low diversity are from coral rubble at Galway Mound where the living assemblages are dominated by attached species. The *arrows* indicate the mid-slope diversity maxima
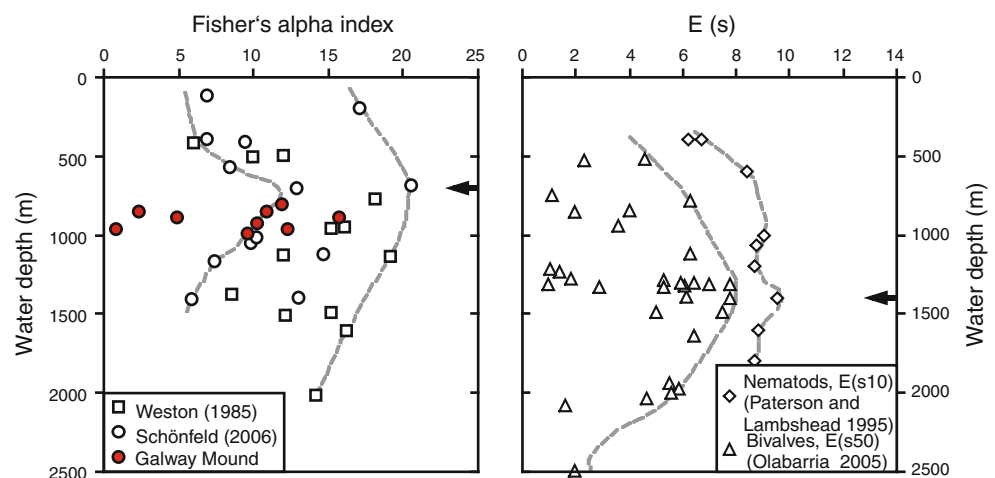
the diversity of polychaetes and bivalves was found to decrease at near-bottom current velocities of more than 30 cm s^{-1} (Gage 1997).

The diversity of foraminifera, however, was less influenced by physical disturbance (Gooday 1999). Food supply was a governing factor instead. For instance, a meridional survey in the Atlantic revealed a northward decrease in diversity that was seemingly coupled with northward increasing food availability and seasonality (Culver and Buzas 2000). A strong negative productivity-diversity relationship was reported from oxygen minimum zones where the flux of particulate organic matter to the sea floor is extraordinary high (Levin et al. 2000). Furthermore, the results from our investigation and selected foraminiferal microhabitat studies inferred that patchy food input and physical disturbance creates a patchiness to maintain the seafloor as a series of small-scale successional mosaics, which as a whole promote a comparatively high diversity (Grassle and Sanders 1973; Erbacher and Nelskamp 2006). This offers an explanation why the foraminiferal diversity at the Celtic and Amorican margin showed a maximum in the boundary layer between ENAW and MOW with a strong hydrodynamic environment and facies differentiation at different scales, while metazoan diversity maxima were established at depths below where the environmental stability was considerably higher.

Summary and conclusions

The benthic foraminiferal fauna at Galway and Propeller Mounds showed 132 different species. The assemblage composition differed between the mounds and also between living and dead assemblages. The proportion of redeposited species from the continental shelf not exceeds 11% of the dead assemblages, which reveals that the coral mound foraminiferal assemblages were largely autochthonous. Nonetheless, 35% of the living species were not preserved in the fossil record, which infers limitations to palaeoenvironmental interpretations from subsurface samples. Because of the differences between living and dead assemblages, and between Galway and Propeller Mounds, we only considered the main faunal constituents.

Discanomalina coronata, *Placopsilina confusa*, *Cibicides lobatulus*, *Cibicides refulgens*, and *Uvigerina mediterranea* were the most frequent species. Their occurrence pattern around the mounds was highly differentiated. The elevated epibenthic *Discanomalina coronata* showed the highest population densities in living coral thickets on top of Galway Mound and on overgrown sandwaves to the west of the mound. In the dead assemblages, the proportions were with higher in samples from coral rubble than from the other facies. Living *Cibicides refulgens* were very frequent on sands surrounding Galway Mound, and the species was rare in samples from the coral habitats. Both species show similar patterns in the dead assemblages around Propeller Mound, but they were very rare in samples from the ambient muds. The shallow endobenthic *Uvigerina mediterranea* showed the highest abundances on the southern side of Galway Mound, and it was rare on the northern side. On Propeller Mound, *Uvigerina mediterranea* showed no systematic local distribution pattern, but it was much more frequent in the dead assemblages of the ambient muds than on the mound itself.

The examination of colonisation structures on hard substrates from Galway Mound and literature information revealed that their nutritional demands, microhabitat preferences, and ecology largely drove the abundances of these frequent species. *Discanomalina coronata* prefers to recruit other flexible, tubular epizoans under high bottom-near currents and sufficient food supply. Around Galway Mound, hydroids were common in and around ancient thecae of coral fragments from coral framework or rubble, thus promoting high abundances of *Discanomalina coronata* in these microenvironments (Appendix 5; Fig. 6). As hydroids may occur on other hard bottom environments too, high abundances of *Discanomalina coronata* were not exclusively linked to cold-water coral habitats. This species is therefore considered to be of less diagnostic value in order to identify living cold-water coral ecosystems.

Cibicides refulgens was found firmly attached to smooth and stable surfaces of dropstones or biogenic fragments. The strong fixation and the ability to use different nutrition strategies enable the species to live under very low and highly variable food supply and strong near-bottom currents. Recruitment and reproduction rates of this species may therefore be much lower in such high-energy environments than those of other species. This would explain the observed disparity between high population densities of *Cibicides refulgens* on the sand belts around cold-water coral mounds and the low proportions in the dead assemblages. As their occurrence is defined by the availability of suitable substrates, an exclusive relationship of *Cibicides refulgens* to a certain facies, for instance to dropstone pavements, is not necessarily given.

Uvigerina mediterranea was frequent on the southern side and rare on the northern side of Galway Mound, and very frequent in muds around Propeller Mound. Bottom currents from the south lead to sediment baffling, the accumulation of organic-rich sediment on the southern side of Galway Mound. The high food supply sustained a rich endobenthic foraminiferal fauna with *Uvigerina mediterranea*. As with other deep-water uvigerinids, this species shows extended patches of high abundances at mid depth, one occurs on the Celtic margin between 51°N and 53°N and includes the Magellan and Belgica Mound Provinces.

High abundances of *Uvigerina mediterranea* may therefore indicate off-mound conditions in the Porcupine Seabight.

The correspondence analyses of living and dead assemblages exhibit epibenthic species as a consistent group on Galway and Propeller Mounds. Surprisingly, the cumulative percentages of epibenthic species showed no systematic pattern characterising a specific sedimentary facies around Galway Mound. However, the average abundances of living epibenthic foraminifera were substantially higher at Galway Mound than at Goban Spur, outside the Mound Provinces. Epibenthic foraminifera are therefore a significant faunal constituent for cold-water coral environments. This corresponds to the ecological composition of the macrofauna where filter and suspension feeders were frequent on coral mounds and deposit feeders and mobile fauna prevailed in off-mound habitats.

The diversity of the living benthic foraminiferal assemblages from Galway Mound falls in the range of Fisher's alpha indices from living assemblages outside the Mound Provinces. Samples from elevated substrates showed, however, a significantly lower diversity. We speculate that the coral framework provides only a restricted number of niches for a limited number of specialised foraminiferal species. In contrast, macrofaunal studies indicated a significantly higher diversity in the coral framework. The Fisher's alpha indices of living benthic foraminiferal assemblages from the Celtic and Amorican margin display a distinct maximum between 500 and 1,200 m water depth, which falls in the range of mound formation in the Porcupine Seabight. Comparable mid-slope diversity maxima of nematodes and gastropods were recorded at 700 m greater depth. Again, this discrepancy suggests that different processes were involved driving the foraminiferal and metazoan diversity patterns.

Appendix 1

Benthic foraminiferal species which are considered in this paper. Taxonomic references were given by Ellis and Messina (1940–2009) and Jones (1994). They are not included in the reference list.

Acervulina inhaerens Schultze 1854

Ammoassilina alveoliniformis (Milett) = *Massilina alveoliniformis* Milett 1898

Ammobaculites agglutinans (d'Orbigny) = *Spirolina agglutinans* d'Orbigny 1846

Ammodiscus tenuis Brady 1884

Ammolagena clavata (Jones and Parker) = *Trochammina irregularis* (d'Orbigny) var. *clavata* Jones and Parker 1860

Amphicoryna scalaris (Batsch) = *Nautilus (Orthoceras) scalaris* Batsch 1791

Aschemonella catenata (Norman) = *Astrorhiza catenata* Norman 1877

Astrorhiza crassatina Brady 1884

Bathysiphon capillare De Folin 1886

Bigenerina nodosaria d'Orbigny 1826

Bolivina subspinescens Cushman 1922

Botellina labyrinthica Brady 1881

Buccella frigida (Cushman) = *Pulvinulina frigida* Cushman 1921

Bulimina acanthia Costa 1856

Bulimina marginata d'Orbigny 1826

Bulimina striata mexicana Cushman = *Bulimina striata* d'Orbigny var. *mexicana* Cushman 1922

Carpenteria utricularis (Carter) = *Polytrema utriculare* Carter 1876

Cassidulina laevigata d'Orbigny 1826

Note: the taxon includes *Cassidulina carinata* of Margreth et al. (2009)

Cassidulina neoteretis Seidenkrantz 1995

Chilostomella ovoidea Reuss 1850

Note: *Chilostomella oolina* of Coles et al. (1996)

Cibicides lobatulus (Walker and Jacob) = *Nautilus lobatulus* Walker and Jacob 1798

Note: *Lobatula lobatula* of Margreth et al. (2009). The taxon includes the smaller variety without a distinct keel that was determined as *Cibicides ungerianus* by Margreth et al. (2009)

Cibicides refulgens Montfort 1808

Cibicidoides kullenbergi (Parker) = *Cibicides kullenbergi* Parker 1953

Cibicidoides pachyderma (Rzehak) = *Truncatulina pachyderma* Rzehak 1886

Note: *Cibicidoides pseudoungerianus* (Cushman 1922) of authors

Cibicidoides robertsonianus (Brady) = *Planorbulina (Truncatulina) robertsoniana* Brady 1881

Cibicidoides wuellerstorfi (Schwager) = *Anomalina wuellerstorfi* Schwager 1866

Cornuloculina sp

Cornuspira involvens (Reuss) = *Operculina involvens* Reuss 1850

Cribrostomoides nitidus (Goes) = *Haplophragmium nitidum* Goes 1896

Cribrostomoides scitulum (Brady) = *Lituola (Haplophragmium) scitulum* Brady 1881

Cribrostomoides subglobosum (Cushman) = *Haplophragmoides subglobosum* Cushman 1910

continued

Crithionina hispida Flint 1899

Crithionina mamilla Goes 1894

Cyclammina cancellata Brady 1879

Dendrophyra arborescens (Heron-Allen and Earland) = *Dendronina arborescens* Heron-Allen and Earland 1922

Discanomalina coronata (Parker and Jones) = *Anomalina coronata* 1857

Discanomalina semipunctata (Bailey) = *Rotalina semipunctata* 1851

Dorothia bradyana Cushman 1936

Note: Our specimens from Galway Mound and Hebrides Shelf are more coarsely agglutinated and slightly larger than the specimens figured by Brady (1884), Natural History Museum London collection no. 2F1462, but the other morphological features as the subrounded apertural face, whitish cement, and the straight and distinct sutures were found identical

Dorothia goesi (Cushman) = *Textularia goesi* Cushman 1911

Eggerella bradyi (Cushman) = *Verneuilina bradyi* Cushman 1911

Eggerella scabra (Williamson) = *Bulimina scabra* Williamson 1858

Elphidium excavatum (Terquem) = *Polystomella excavata* Terquem 1875

Elphidium incertum (Williamson) = *Polystomella umbilicatula* (Walker) var. *incerta* Williamson 1858

Fissurina marginata (Montagu) = *Vermiculum marginatum* Montagu 1803

Glandulina laevigata (d'Orbigny) = *Nodosaria (Glandulina) laevigata* d'Orbigny 1826

Glandulina rotundata Reuss 1850

Globobulimina affinis (d'Orbigny) = *Bulimina affinis* d'Orbigny 1839

Note: *Preaglobobulimina ovata* of Coles et al. (1996)

Globulina minuta (Roemer) = *Polymorphina minuta* Roemer 1838

Glomospira charoides (Jones and Parker) = *Trochammina squamata* Jones and Parker var. *charoides* Jones and Parker 1860

Gyroidina neosoldanii Brotzen 1936

Gyroidina orbicularis d'Orbigny 1826

Hanzawaia rhodiensis (Terquem) = *Truncatulina rhodiensis* Terquem 1878

Note: *Hanzawaia boueana* of Margreth et al. (2009)

Hanzawaia solei Colom 1957

Hoeglundina elegans (d'Orbigny) = *Rotalia (Turbinulina) elegans* d'Orbigny 1826

Hormosinella guttifera (Brady) = *Lituola (Reophax) guttifera* Brady 1881

Hyalinea balthica (Schröter) = *Nautilus balthicus* Schröter 1783

Hyperammina friabilis Brady 1844

Hyrrokkin sarcophaga Cedhagen 1994

Karreriella bradyi (Cushman) = *Gaudryina bradyi* Cushman 1911

Karreriella novangliae (Cushman) = *Gaudryina baccata* Schwager var. *novangliae* Cushman 1922

Labrospira jeffreysii (Williamson) = *Nonionina jeffreysii* Williamson 1858

Lagena sulcata (Walker and Jacob) = *Serpula sulcata* Walker and Jacob 1798

continued

Lagenammina arenulata (Skinner) = *Reophax difflugiformis* Brady var. *arenulata* Skinner 1961

Laminonion tumidum (Cushman and Edwards) = *Astrononion tumidum* Cushman and Edwards 1937

Lenticulina atlantica (Barker) = *Robulus atlanticus* Barker 1960

Lenticulina rotulata (Lamarck) = *Lenticulites rotulata* 1804

Lituotuba lituiformis (Brady) = *Trochammina lituiformis* Brady 1879

Melonis barleeanum (Williamson) = *Nonionina barleeana* Williamson 1858

Mississippina concentrica (Parker and Jones) = *Pulvinulina concentrica* Parker and Jones 1864

Note: *Stromatorbina concentrica* of Margreth et al. (2009)

Neolenticulina peregrina (Schwager) = *Cristellaria peregrina* Schwager 1866

Nummuloculina irregularis (d'Orbigny) = *Biloculina irregularis* d'Orbigny 1839

Oolina striata d'Orbigny 1839

Patellina corrugata Williamson 1858

Parafissurina ovata (Seguenza) = *Fissurina ovata* Seguenza 1862

Pelosina cylindrica Brady 1884

Pelosina rotundata Brady 1879

Placopsilina confusa Cushman 1920

Planulina ariminensis d'Orbigny 1826

Psammosphaera fusca Schultze 1875

Pseudomassilina australis (Cushman) = *Massilina australis* Cushman 1932

Pullenia bulloides (d'Orbigny) = *Nonionina bulloides* d'Orbigny 1846

Pullenia quinqueloba (Reuss) = *Nonionina quinqueloba* Reuss 1851

Pyrgo depressa (d'Orbigny) = *Biloculina depressa* d'Orbigny 1826

Pyrgo fornasinii Chapman and Parr 1935

Pyrgo lucernula (Schwager) = *Biloculina lucernula* Schwager 1866

Pyrgo murrhina (Schwager) = *Biloculina murrhina* Schwager 1866

Pyrgo rotalaria Loeblich and Tappan 1953

Pyrgo williamsoni (Silvestri) = *Biloculina williamsoni* Silvestri 1923

Quinqueloculina seminula (Linné) = *Serpula seminulum* Linné 1758

Reophax bilocularis Flint 1899

Reophax calcareus (Cushman) = *Proteonina difflugiformis* (Brady) var. *calcarea* Cushman 1947

Reophax scorpiurus Montfort 1808

Reophax spiculifer Brady 1879

Rhabdammina abyssorum Sars 1869

Rhizammina algaeformis Brady 1879

Robertina bradyi Cushman and Parker 1936

Rosalina anomala Terquem 1875

Rosalina obtusa d'Orbigny 1846

Saccammina catenulata Cushman = *Saccammina sphaerica* Brady var. *catenulata* Cushman 1917

continued

Saccammina sphaerica Brady 1871

Saccorhiza ramosa (Brady) = *Hyperammina ramosa* Brady 1879

Sigmoilopsis schlumbergeri (Silvestri) = *Sigmoilina schlumbergeri* Silvestri 1904

Sigmoilopsis woodi Atkinson 1968

Siphotextularia bermudezi Mikhaelevich 1978

Siphotextularia caroliniana Cushman = *Siphotextularia flintii* (Cushman) var. *caroliniana* Cushman 1922

Sphaeroidina bulloides d'Orbigny 1826

Spiculosiphon sp.

Spirillina decorata Brady 1884

Spiroloculina canaliculata d'Orbigny 1846

Spiroloculina depressa d'Orbigny 1826

Spiroloculina excavata d'Orbigny 1846

Spiroplectinella sagittula (Defrance) = *Textularia sagittula* Defrance 1824

Note: The taxon includes *Spiroplectinella wrighti* of Margreth et al. (2009)

Subreophax aduncus (Brady) = *Reophax aduncus* Brady 1882

Technitella melo Norman 1978

Technitella raphanus Brady 1884

Textularia hystrix Jones 1994

Note: *Gaudryina rudis* or *Dorothia rudis* of authors

Tholosina vesicularis (Brady) = *Placopsilina vesicularis* Brady 1879

Thurammina papillata Brady 1879

Tolypammina vagans (Brady) = *Hyperammina vagans* Brady 1879

continued

Trifarina angulosa (Williamson) = *Uvigerina angulosa* Williamson 1858

Note: *Angulogerina angulosa* of Margreth et al. (2009)

Triloculina tricarinata d'Orbigny 1826

Triloculina trigonula (Lamarck) = *Miliolites trigonula* Lamarck 1804

Tritaxis conica (d'Orbigny) = *Textularia conica* d'Orbigny 1839

Tritaxis fusca (Williamson) = *Rotalina fusca* Williamson 1858

Trochammina astrifica Rhumbler = *Trochammina squamata* Hero-Allen and Earland var. *astrifica* Rhumbler 1938

Trochammina globigeriniformis (Parker and Jones) = *Lituola nautiloidea* Lamarck var. *globigeriniformis* Parker and Jones 1865

Note: *Paratrochammina challengeri* of Margreth et al. (2009)

Trochammina squamata Jones and Parker 1860

Uvigerina auberiana d'Orbigny 1839

Uvigerina celtica Schönfeld 2006

Uvigerina mediterranea Hofker 1932

Uvigerina peregrina parva Lutze = *Uvigerina peregrina* forma *parva* Lutze 1986

Note: *Uvigerina bradyana* of Coles et al. (1996) and *Uvigerina peregrina* of Margreth et al. (2009)

Vulvulina pennatula (Batsch) = *Nautilus* (*Orthoceras*) *pennatula* Batsch 1791

Appendix 2

See Table 2.

Table 2 Foraminiferal census data of the living assemblages from Galway Mound

	GeoB9220–2	GeoB9219–1	GeoB9218–1	Geob9209–2	GeoB9206–1	GeoB9205–1	GeoB9204–1	PO316–525	PO316–525, 2–3 cm above surf.	M61/1–259
Ammobaculites agglutinans	–	1.3	–	–	–	1.7	–	2.4	–	–
Ammolagena clavata	–	1.3	–	4.2	2.8	2.2	–	1.2	–	–
Aschemonella catenata	5.0	3.8	2.1	–	–	1.7	–	–	–	–
Bathysiphon capillare	–	–	–	–	–	0.6	–	–	–	–
Cibicides lobatulus	15.0	2.6	2.1	–	–	5.6	–	4.9	1.3	8.5
Cibicides refulgens	35.0	1.3	2.1	–	–	–	–	24.4	2.5	–
Cibicidoides mollis	–	–	–	–	1.4	1.1	–	–	–	–
Cibicidoides pachyderma	–	–	–	–	–	–	7.7	–	–	–
Cribrostomoides nitidus	–	–	–	–	–	0.6	–	–	–	–
Cribrostomoides scitulum	–	–	–	–	–	1.7	7.7	–	–	–
Cribrostomoides subglobosum	–	3.8	–	–	–	3.4	–	–	–	–
Crithionina hispida	–	–	2.1	–	–	–	7.7	–	–	–
Crithionina mamilla	15.0	15.4	8.3	–	–	15.6	7.7	6.1	–	11.7
Cyclammina cancellata	–	–	–	–	–	–	–	2.4	–	–
Dendrophyra arborescens	–	–	–	–	–	0.6	–	–	–	–
Discanomalina coronata	–	9.0	2.1	25.0	12.7	5.0	7.7	12.2	95.0	24.5
Discanomalina semipunctata	–	–	–	–	–	–	–	–	–	2.1
Dorothia bradyana	5.0	6.4	6.3	–	4.2	0.6	7.7	2.4	–	–
Dorothia goesi	–	–	2.1	–	–	–	7.7	1.2	–	–
Eggerella bradyi	–	–	–	4.2	–	–	–	–	–	–

Table 2 continued

	GeoB9220–2	GeoB9219–1	GeoB9218–1	Geob9209–2	GeoB9206–1	GeoB9205–1	GeoB9204–1	PO316–525	PO316–525, 2–3 cm above surf.	M61/ 1–259
Eggerella scabra	–	–	–	–	1.4	–	–	–	–	–
Glandulina rotundata	–	–	–	–	1.4	–	–	–	–	–
Hoeglundina elegans	–	–	–	–	–	8.4	–	–	–	–
Hyrrokkin sarcophaga	–	1.3	–	–	1.4	0.6	–	–	–	–
Karreriella bradyi	–	–	–	–	–	–	–	1.2	–	–
Lagenammina arenulata	–	–	–	–	–	0.6	–	–	–	–
Lenticulina atlantica	–	–	–	–	–	–	–	1.2	–	–
Lenticulina rotulata	–	–	–	–	–	0.6	–	–	–	–
Lituotuba lituiformis	5.0	–	–	–	–	0.6	–	–	–	–
Melonis barleeanum	–	–	–	4.2	1.4	2.2	–	–	–	–
Neolenticulina peregrina	–	–	2.1	–	–	1.1	–	–	–	–
Placopsilina confusa	15.0	19.2	25.0	8.3	11.3	1.7	15.4	7.3	1.3	25.5
Planulina ariminensis	–	–	–	–	–	–	–	–	–	1.1
Pullenia bulloides	–	–	2.1	–	14.1	14.0	–	3.7	–	–
Pullenia quinqueloba	–	–	–	–	1.4	–	–	–	–	–
Reophax calcareus	–	2.6	4.2	4.2	25.4	3.9	7.7	1.2	–	–
Reophax scorpiurus	–	–	–	–	–	–	–	1.2	–	–
Reophax spiculifer	–	–	–	–	8.5	0.6	–	1.2	–	–
Rhabdammina abyssorum	–	2.6	–	4.2	–	1.7	7.7	2.4	–	–
Rhizammina algaeformis	–	–	–	–	–	–	–	1.2	–	–
Saccammina sphaerica	5.0	2.6	–	12.5	1.4	–	–	3.7	–	–
Saccorhiza ramosa	–	5.1	10.4	–	1.4	–	–	–	–	–
Spiculosiphon sp.	–	1.3	–	4.2	1.4	0.6	–	–	–	–
Spirillina decorata	–	2.6	4.2	–	1.4	1.1	–	4.9	–	21.3
Spiroloculina canaliculata	–	–	–	–	–	0.6	–	–	–	–
Spiroloculina excavata	–	–	–	–	1.4	–	–	–	–	–
Spiroplectinella sagittula	–	–	–	–	–	0.6	–	–	–	–
Technitella melo	–	–	–	–	–	1.7	–	–	–	–
Technitella raphanus	–	–	–	–	–	–	–	1.2	–	–
Textularia hystrix	–	6.4	4.2	20.8	–	–	7.7	8.5	–	2.1
Tholosina vesicularis	–	–	2.1	–	1.4	7.3	–	–	–	–
Tolypammina vagans	–	–	4.2	–	–	–	–	–	–	–
Triloculina trigonula	–	–	–	–	–	–	–	1.2	–	–
Tritaxis fusca	–	2.6	6.3	–	–	–	–	–	–	–
Trochammina astrifica	–	2.6	2.1	–	1.4	–	–	1.2	–	3.2
Trochammina squammata	–	5.1	–	–	1.4	–	–	–	–	–
Uvigerina mediterranea	–	–	–	–	–	10.1	7.7	–	–	–
Others	–	1.3	6.3	8.3	1.4	2.2	–	1.2	–	–
Counted specimens:	20	78	48	24	71	179	13	82	80	94
Sample volume (cm^3):	45	34	70	13	67	57	36	87	–	–
Split:	1	1	1	1	1	1	1	1	1	1
Standing stock (Ind./10 cm^3):	4.4	22.9	6.9	18.5	10.6	31.4	3.6	9.4	–	–
Species number:	8	22	21	11	22	33	12	25	4	9
Fisher's alpha:	4.9	10.2	15.7	9.6	10.9	11.9	–	12.3	0.9	2.5

The abundances are reported in percent of the living assemblage >250 μm. Species that occur in at least one sample among the first five ranked species are marked with *bold letters*

Appendix 3

See Table 3.

Table 3 Foraminiferal census data of the dead assemblages from Galway Mound

	GeoB9220-2	GeoB 9219-1	GeoB 9218-1	GeoB9209-2	GeoB 9206-1	GeoB9204-1	GeoB9205-1	PO316-525	M61/1-259
Acervulina inhaerens	–	0.3	–	0.6	–	–	–	–	–
Ammoassilina alveoliniformis	3.9	0.3	–	–	–	–	–	–	–
Ammobaculites agglutinans	–	0.9	–	1.9	0.6	–	–	–	–
Ammolagena clavata	–	–	–	1.3	–	–	–	–	–
Amphicoryna scalaris	–	–	–	–	–	–	–	0.3	–
Bulimina acanthia	0.7	–	–	–	–	–	–	–	–
Bulimina marginata	–	–	–	0.6	–	0.6	1.2	–	–
Bulimina striata mexicana	1.4	0.3	–	–	–	–	–	0.5	–
Cassidulina laevigata	–	–	–	–	–	–	0.6	–	–
Cassidulina neoteretis	–	–	–	–	–	0.6	–	–	–
Chilostomella ovoidea	–	–	–	–	–	–	0.6	–	–
Cibicides lobatulus	3.2	4.1	5.7	5.8	11.6	4.1	9.2	8.0	26.7
Cibicides refulgens	1.8	2.8	6.3	4.5	1.7	3.5	0.6	5.8	–
Cibicidoides mollis	4.9	0.3	–	–	0.6	0.6	2.3	0.3	–
Cibicidoides pachyderma	32.3	2.5	–	9.0	–	1.7	1.7	6.1	–
Cibicidoides robertsonianus	–	–	–	–	–	0.6	–	–	–
Cibicidoides wuellerstorfi	–	–	–	–	–	–	–	1.6	–
Cornuloculina sp	–	–	–	–	–	–	0.6	–	–
Cornuspira involvens	–	–	–	–	1.2	–	–	–	–
Cribrostomoides subglobosum	0.4	0.3	–	0.6	1.2	0.6	1.2	–	–
Cyclammina cancellata	–	–	0.6	–	–	–	–	–	–
Discanomalina coronata	13.7	66.9	50.6	35.3	40.1	30.2	22.0	42.4	33.3
Discanomalina semipunctata	–	0.3	–	–	2.3	–	1.2	–	–
Dorothia bradyana	–	3.8	8.2	–	6.4	10.5	3.5	0.8	20.0
Dorothia goesi	–	–	–	–	0.6	0.6	–	–	–
Eggerella bradyi	–	–	–	1.9	0.6	–	–	–	–
Elphidium excavatum	1.4	1.3	–	0.6	0.6	4.1	3.5	2.4	–
Elphidium incertum	0.4	–	–	–	–	–	–	–	–
Glandulina laevigata	–	–	0.6	–	–	–	–	–	–
Glandulina rotundata	–	–	–	–	–	–	0.6	–	–
Globobulimina affinis	0.4	–	–	0.6	–	1.2	1.2	–	–
Globulina minuta	–	–	–	0.6	–	0.6	–	–	–
Gyroidina neosoldanii	2.5	–	–	–	–	–	1.2	0.3	–
Gyroidina orbicularis	1.1	–	–	1.3	–	0.6	0.6	1.1	–
Hanzawaia solei	–	0.3	–	–	–	–	–	–	–
Hoeglundina elegans	–	–	–	–	–	1.7	2.3	–	–
Hyalinea balthica	0.7	–	–	0.6	–	–	1.2	0.8	–
Hyrrokkin sarcophaga	–	3.2	2.5	3.8	2.3	2.3	2.3	1.6	–
Karreriella bradyi	1.1	0.3	3.2	0.6	–	3.5	0.6	1.9	–
Labrospira jeffreysii	–	–	1.3	0.6	–	–	1.2	0.3	–
Lagena sulcata	–	0.3	–	–	1.2	0.6	1.7	–	–
Laminonion tumidum	–	–	0.6	–	1.2	–	1.2	–	–
Lenticulina atlantica	–	–	–	–	–	–	–	0.3	–
Lenticulina rotulata	–	–	–	–	0.6	–	0.6	–	–
Melonis barleeanum	2.1	1.3	1.3	1.9	2.9	1.2	5.2	1.9	–
Mississippina concentrica	–	–	0.6	–	0.6	–	–	–	–
Nummuloculina irregularis	–	–	0.6	1.3	–	1.7	1.2	1.1	–
Parafissurina ovata	–	–	–	–	–	0.6	–	–	–
Placopsilina confusa	–	0.3	2.5	–	–	0.6	–	–	–
Planulina ariminensis	1.1	2.5	4.4	5.1	10.5	10.5	8.7	3.4	20.0
Psammosphaera fusca	–	–	–	–	0.6	–	–	–	–
Pullenia bulloides	0.7	0.6	3.8	–	6.4	3.5	5.2	1.1	–

Table 3 continued

	GeoB9220-2	GeoB 9219-1	GeoB 9218-1	GeoB9209-2	GeoB 9206-1	GeoB9204-1	GeoB9205-1	PO316-525	M61/1-259
Pullenia quinqueloba	0.4	–	–	–	1.2	1.2	2.9	0.3	–
Pyrgo fornasinii	0.4	–	–	1.3	0.6	–	–	–	–
Pyrgo lucernula	–	–	–	0.6	–	1.2	–	–	–
Pyrgo murrhina	–	–	–	–	–	–	–	0.5	–
Pyrgo rotalaria	–	–	–	–	–	0.6	–	0.5	–
Pyrgo williamsoni	–	0.3	–	–	–	–	–	–	–
Quinqueloculina seminula	–	–	–	–	–	–	–	0.3	–
Reophax calcareus	–	–	–	–	–	–	1.2	–	–
Reophax scorpiurus	–	–	–	–	–	0.6	–	–	–
Rhabdammina abyssorum	–	–	–	–	–	0.6	1.2	–	–
Rosalina anomala	–	–	–	–	–	0.6	–	–	–
Rosalina obtusa	–	–	–	–	–	–	0.6	–	–
Saccammina sphaerica	0.4	0.9	–	1.3	1.7	–	0.6	1.9	–
Saccorhiza ramosa	–	–	1.3	–	1.2	–	–	–	–
Sigmoilopsis schlumbergeri	4.9	–	–	2.6	–	–	1.2	4.0	–
Sigmoilopsis woodi	0.7	–	–	0.6	–	–	1.2	–	–
Siphotextularia bermudezi	–	–	–	–	–	0.6	–	–	–
Siphotextularia caroliniana	–	0.3	–	0.6	–	–	–	–	–
Sphaeroidina bulloides	0.4	–	–	–	–	–	–	0.3	–
Spirillina decorata	–	1.3	–	–	1.2	–	1.2	0.3	–
Spiroloculina excavata	–	–	–	–	–	–	0.6	–	–
Spiroplectinella sagittula	–	0.6	–	–	–	–	–	–	–
Textularia hystrix	–	0.9	0.6	–	–	–	–	1.1	–
Tholosina vesicularis	–	–	–	–	–	–	0.6	–	–
Triloculina tricarinata	–	–	–	–	–	–	0.6	–	–
Tritaxis fusca	–	–	1.9	–	–	–	–	0.3	–
Trochammina squammata	–	0.3	0.6	–	–	0.6	–	0.5	–
Uvigerina auberiana	–	–	–	–	–	–	0.6	–	–
Uvigerina celtica	–	–	–	0.6	–	–	–	–	–
Uvigerina mediterranea	19.6	1.3	0.6	9.0	–	5.2	5.2	5.8	–
Uvigerina peregrina parva	–	–	–	0.6	–	1.7	–	1.1	–
Vulvulina pennatula	–	–	–	3.2	–	–	–	1.3	–
Others	–	0.9	1.9	0.6	0.6	1.2	–	0.3	–
Counted specimens:	285	317	158	156	172	172	173	377	15
Split:	0.032	0.03	0.014	0.03	0.065	0.064	0.25	0.03	1
Species number:	26	31	24	32	27	37	42	36	4

The abundances are reported in percent of the dead assemblage >250 µm. Species that occur in at least one sample among the first five ranked species are marked with *bold letters*

Appendix 4

See Table 4.

Table 4 Foraminiferal census data of the dead assemblages from Propeller Mound

	GeoB9246-3	GeoB6721-1	GeoB8074-1	GeoB8047-1	GeoB9245-1	GeoB8039-1	GeoB6708-1	GeoB8059-1	GeoB8073-1	GeoB6718-1
Ammobaculites agglutinans	0.3	<0.1	2.2	1.9	–	0.4	–	–	–	–
Ammodiscus tenuis	0.3	–	<0.1	–	–	–	–	–	–	–
Ammolagena clavata	0.6	0.4	3.8	2.4	<0.1	1.1	0.1	0.1	<0.1	–
Amphicoryna scalaris	0.5	1.7	–	–	0.7	–	0.3	–	–	–
Astrorhiza crassatina	–	–	–	–	–	–	–	–	–	1.1
Bigenerina nodosaria	0.8	2.4	0.1	2.1	<0.1	1.7	1.7	2.4	1.0	0.3
Bolivina subspinescens	–	–	–	0.2	–	–	–	–	–	–

Table 4 continued

	GeoB9246-3	GeoB6721-1	GeoB8074-1	GeoB8047-1	GeoB9245-1	GeoB8039-1	GeoB6708-1	GeoB8059-1	GeoB8073-1	GeoB6718-1
Botellina labyrinthica	–	–	<0.1	–	–	–	–	–	–	–
Buccella frigida	–	–	–	0.9	–	–	–	–	–	–
Bulimina acanthia	–	–	–	–	0.4	0.4	0.8	–	–	–
Bulimina marginata	0.5	0.3	–	2.1	0.7	1.6	0.8	1.0	0.6	0.9
Carpenteria utricularis	<0.1	0.1	<0.1	<0.1	0.2	0.1	<0.1	–	–	–
Cassidulina laevigata	–	–	–	–	–	–	–	–	0.2	–
Cibicides lobatulus	0.1	2.9	2.3	3.3	–	3.2	1.4	1.0	0.2	0.3
Cibicides refulgens	4.1	1.8	1.6	5.0	0.2	4.6	1.5	<0.1	0.2	–
Cibicidoides kullenbergi	0.3	1.0	–	2.1	0.2	0.4	–	–	0.2	–
Cibicidoides pachyderma	2.8	5.1	–	1.9	–	2.9	0.3	0.7	–	–
Cibicidoides wuellerstorfi	9.5	11.7	5.6	0.5	6.7	4.8	15.8	9.7	2.1	4.4
Cornuspira involvens	–	–	–	0.2	–	<0.1	–	–	–	–
Cribrostomoides scitulum	0.5	<0.1	4.2	<0.1	0.2	0.6	0.1	<0.1	–	0.9
Cribrostomoides subglobosum	0.3	–	–	1.4	<0.1	0.4	–	–	0.2	2.3
Cyclammina cancellata	0.5	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	<0.1	–	–
Discanomalina coronata	20.4	5.1	7.3	22.5	–	15.8	<0.1	0.7	–	–
Dorothia bradyana	1.4	–	–	–	–	–	–	–	–	–
Dorothia goesi	<0.1	<0.1	0.9	<0.1	<0.1	<0.1	–	–	–	-
Elphidium excavatum	0.3	0.3	0.4	–	–	–	–	–	–	–
Fissurina marginata	–	–	–	–	–	0.4	–	–	–	–
Glandulina rotundata	–	–	–	0.9	–	–	–	–	–	–
Globobulimina affinis	–	–	5.8	–	–	<0.1	–	<0.1	–	7.2
Glomospira charoides	–	–	1.3	–	–	–	–	–	–	–
Gyroidina neosoldanii	4.2	0.5	2.3	10.2	–	2.8	1.4	1.0	1.3	1.9
Hanzawaia rhodiensis	<0.1	0.7	1.3	–	–	–	0.3	–	–	0.3
Hoeglundina elegans	1.0	0.3	2.3	1.4	–	0.8	1.3	0.4	0.2	–
Hormosinella guttifera	–	–	–	–	–	–	–	–	–	1.2
Hyalinea balthica	0.8	2.7	1.7	3.8	4.9	2.9	4.9	3.8	3.7	11.2
Hyperammina friabilis	–	–	<0.1	–	–	–	–	–	<0.1	–
Hyrrokkin sarcophaga	0.8	–	<0.1	<0.1	–	1.9	–	–	–	–
Karreriella bradyi	1.1	2.9	2.8	3.1	0.4	3.4	1.9	0.3	0.4	6.9
Karreriella novangliae	–	–	–	–	–	–	<0.1	–	–	–
Lagena sulcata	–	–	0.9	–	–	–	0.5	–	0.2	–
Lenticulina rotulata	2.0	–	0.4	2.6	<0.1	0.4	0.3	–	<0.1	–
Melonis barleeanum	9.0	5.5	2.6	4.7	1.3	5.0	3.0	0.7	1.2	5.6
Oolina striata	–	–	0.4	0.9	–	–	0.3	–	–	–
Pelosina cylindrica	–	–	–	–	–	–	–	–	0.1	–
Pelosina rotundata	–	–	–	–	–	–	–	–	<0.1	–
Placopsilina confusa	–	<0.1	0.2	0.3	–	<0.1	0.3	–	–	0.2
Planulina ariminensis	9.0	5.4	5.8	11.3	2.7	7.0	0.8	2.8	0.2	–
Psammosphera fusca	–	–	2.0	4.6	<0.1	<0.1	0.1	<0.1	0.2	0.7
Pseudomassilina australis	–	–	–	0.2	–	–	–	–	–	–
Pullenia bulloides	0.3	–	0.4	–	–	–	–	–	–	–
Pullenia quinqueloba	0.3	0.7	1.7	–	–	–	0.3	0.3	–	–
Pyrgo depressa	<0.1	<0.1	<0.1	–	<0.1	<0.1	–	<0.1	–	–
Pyrgo fornasinii	–	–	–	<0.1	–	–	–	–	–	–
Pyrgo lucernula	<0.1	–	–	<0.1	–	–	0.3	–	–	–
Pyrgo rotalaria	<0.1	–	0.7	–	<0.1	<0.1	–	–	<0.1	–
Quinqueloculina seminulum	0.9	–	0.2	<0.1	<0.1	<0.1	–	–	–	–
Reophax bilocularis	–	–	1.8	–	–	–	–	–	0.3	–
Rhabdammina abyssorum	0.6	0.1	1.4	0.3	<0.1	0.4	<0.1	–	<0.1	–
Rhizammina algaeformis	–	<0.1	<0.1	–	<0.1	–	<0.1	<0.1	–	6.6
Robertina bradyi	–	0.3	–	–	–	–	–	–	–	–
Saccammina catenulata	–	–	–	<0.1	–	–	–	–	–	–
Saccammina sphaerica	<0.1	0.1	0.6	0.3	<0.1	<0.1	<0.1	<0.1	<0.1	0.4
Saccorhiza ramosa	–	<0.1	0.3	–	<0.1	–	–	–	0.4	2.7
Sigmoilopsis schlumbergeri	6.3	7.2	4.0	<0.1	3.3	9.0	7.6	3.7	2.1	5.6

Table 4 continued

	GeoB9246-3	GeoB6721-1	GeoB8074-1	GeoB8047-1	GeoB9245-1	GeoB8039-1	GeoB6708-1	GeoB8059-1	GeoB8073-1	GeoB6718-1
Sigmoilopsis woodi	–	–	–	–	–	–	–	0.3	0.2	–
Siphotextularia bermudezi	–	0.3	–	–	–	3.5	0.5	<0.1	–	1.2
Sphaeroidina bulloides	–	4.4	2.2	0.9	–	0.4	0.5	1.4	–	–
Spiroloculina depressa	–	–	0.5	–	–	–	–	–	–	–
Spiroplectinella sagittula	–	0.3	–	–	–	–	–	–	–	–
Subreophax aduncus	–	–	0.4	–	–	–	–	–	0.2	–
Textularia hystrix	0.3	<0.1	0.4	0.5	<0.1	0.2	<0.1	–	–	–
Tholosina vesicularis	–	–	<0.1	<0.1	–	–	–	–	–	–
Thurammina papillata	–	–	–	–	–	–	–	–	2.7	3.4
Trifarina angulosa	–	–	–	–	–	0.4	0.5	–	–	–
Tritaxis conica	–	–	0.4	–	–	–	–	–	–	–
Tritaxis fusca	–	–	0.1	–	<0.1	<0.1	<0.1	<0.1	–	–
Trochammina globigeriniform.	0.3	–	0.4	4.7	–	0.4	–	–	–	–
Uvigerina auberiana	<0.1	–	–	–	–	–	–	0.3	–	0.3
Uvigerina mediterranea	10.4	32.7	20.3	–	32.5	22.2	35.9	55.9	81.2	24.6
Uvigerina peregrina parva	7.7	2.8	2.3	–	45.4	0.6	16.0	13.1	<0.1	8.9
Vulvulina pennatula	1.4	<0.1	–	0.9	–	<0.1	<0.1	<0.1	–	–
Others	–	–	3.3	1.1	–	–	–	–	0.2	0.5
Counted specimens:	367	297	232	106	452	242	364	293	488	320
Split:	0.016	0.016	0.031	0.008	0.016	0.008	0.016	0.004	0.008	0.250
Species number:	45	40	54	50	32	47	42	31	37	27

The abundances are reported in percent of the dead assemblage >250 μm. Species that occur in at least one sample among the first five ranked species are marked with *bold letters*

Appendix 5

See Table 5.

Table 5 Recordings of attached epibenthic foraminifera >63 μm

Station	No. of objects >2,000 μm, grainsize	Substrate types	Specific colonisation structures	Hight (mm)	Maximum squattering density (#/object)	Ammolagena clavata	Aschemonella catenata[a]	Cibicides lobatulus	Cibicides refulgens	Cibicidoides pachyderma[a]	Crithionina hispida	Crithionina mamilla	Dendrophyra arborescens[a]	Discanomalina coronata
M61/1-259	6	Co, hyd, sco	Clus, sec	17–26	42	–	–	9	–	–	–	19	–	24
PO316-525	17	Co, spon, bal, ds	Exp		9	–	–	6	10	–	–	6	–	2
	250–2,000 μm	Co			1	1	–	–	–	–	–	1	–	–
PO316-525, 2–3 cm	2	Co	Sec, clus, exp	20–30	43	–	–	1	2	1	–	–	–	76
GeoB9204-1	2	Co			1	–	–	–	–	–	1	1	–	–
	250–2,000 μm	Co, spon			1	–	–	–	–	–	–	–	–	–
GeoB9205-1	11	Co, crus, ech	Clus		14	–	3	10	–	–	–	28	1	1
	250–2,000 μm	Co, sco, biv, pt, hyd	Sec		1	4	–	1	–	–	–	–	–	–
GeoB9206-1	10	Co, spon			2	–	–	–	–	–	–	–	–	–
	250–2,000 μm	Pt, for			1	2	–	–	–	–	–	–	–	–
GeoB9209-2	7	Spon, co, hyd, pt	Clus, sec		2	1	–	1	–	–	–	–	–	3
	250–2,000 μm	Spon, pt, hyd	Sec		1	–	1	–	–	–	–	–	–	1
GeoB9218-1	25	Co, spon, bal,	Exp		6	–	–	–	–	–	–	11	–	–
	250–2,000 μm	Co, spon			1	–	–	–	–	–	1	–	–	–
GeoB9219-1	31	Co, spon, biv, gast			3	–	3	3	1	–	–	11	–	–
	250–2,000 μm	Co, biv, gast			1	1	–	–	–	–	–	1	–	–
GeoB9220-2	6	Co	Tier		4	–	1	3	3	–	–	3	–	–
	250–2,000 μm	Co			1	–	–	–	1	–	–	–	–	–

Table 5 continued

Station	No. of objects >2,000 μm, grainsize	Substrate types	Specific colonisation structures	Hight (mm)	Maximum squattering density (#/object)	Discanomalina semipunctata	Dorothia goesi	Lituotuba lituiformis	Patellina corrugata	Placopsilina confusa	Planulina ariminensis	Reophax calcareus[a]	Saccammina sphaerica[a]	Saccorhiza ramosa[a]	Spiculosiphon sp.[a]	Spirillina decorata	Textularia hystrix	Tholosina vesicularis	Tolypammina vagans	Tritaxis fusca	Trochammina astrifica	Trochammina squammata	Others
M61/1-259	6	Co, hyd, sco	Clus, sec	17–26	42	2	1	–	12	24	1	–	–	–	–	35	2	–	–	–	5	–	–
PO316-525	17	Co, spon, bal, ds	Exp		9	–	1	–	–	5	–	1	–	–	–	4	2	–	–	–	1	–	–
PO316-525, 2–3 cm	250–2,000 μm	Co			1	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	1
GeoB9204-1	2	Co	Sec, clus, exp	20–30	43	–	–	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	1
	2	Co			1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
	250–2,000 μm	Co, spon			1	–	–	1	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
GeoB9205-1	11	Co, crus, ech	Clus		14	–	–	–	–	3	–	–	1	–	–	1	–	12	–	–	–	–	–
	250–2,000 μm	Co, sco, biv, pt, hyd	Sec		1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
GeoB9206-1	10	Co, spon			2	–	–	–	–	7	–	–	1	–	–	–	–	1	–	–	1	1	–
	250–2,000 μm	Pt, for			1	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–
GeoB9209-2	7	Spon, co, hyd, pt	Clus, sec		2	–	–	–	–	1	1	1	–	–	1	–	1	–	–	1	–	–	–
	250–2,000 μm	Spon, pt, hyd	Sec		1	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–
GeoB9218-1	25	Co, spon, bal,	Exp		6	–	–	–	–	12	–	–	–	4	–	2	–	1	–	1	2	–	2
	250–2,000 μm	Co, spon			1	–	–	–	–	1	–	–	–	1	–	–	–	–	–	2	–	–	1
GeoB9219-1	31	Co, spon, biv, gast			3	–	–	–	–	14	–	–	1	3	1	2	1	–	–	1	2	3	–
	250–2,000 μm	Co, biv, gast			1	–	–	1	–	2	–	–	1	–	–	–	–	–	–	–	–	–	1
GeoB9220-2	6	Co	Tier		4	–	–	–	–	2	–	–	–	–	–	–	–	–	–	–	2	–	–
	250–2,000 μm	Co			1	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–

[a] Species uses epibenthic lifestyle facultatively

Substrate types: *co* coral fragments, *hyd* hydroids, *sco* soft corals, *spon* siliceous sponges, *bal* balanid plates, *ds* dropstones, *crus* crustacean fragments, *ech* ecinoid plates, *biv* bivalves, *pt* pteropod shells, *for* foraminiferal tests, *gast* gastropod shell fragments

Colonisation structures: *clus* specimens tend to occur in a cluster, *sec* settling on other epizoans, mostly hydroids, *exp* specimens tend to occur on exposed edges of the substrate, *tier* attached assemblage shows a distinct tiering in that different species occur at different levels on the substrate

Appendix 6

See Table 6.

Table 6 Surface samples, depths and abundance of frequent benthic foraminiferal species from literature sources and new samples examined by the first author

Station	Latitude (°N)	Longitude (°W)	Water depth (m)	Discanomalina coronata, living	Discanomalina coronata, dead	Cibicides refulgens, living	Cibicides refulgens, dead	Uvigerina mediterranea, living	Uvigerina mediterranea, dead	Sum of counted specimens, dead	Sum of counted specimens, living	Reference
16219	52.704	15.050	1,114	–	–	–	–	1.9	13.4	372	107	b
16220	52.699	14.868	709	–	–	–	–	14.8	79.2	154	142	b
91	51.7712	13.1200	960	–	–	–	–	–	3.1	–	–	a
30	51.6833	11.6000	422	–	–	–	–	–	–	–	17	a
81	51.5600	12.4400	1,380	–	–	–	–	–	0.6	–	–	a
16221	51.469	15.088	1,398	–	–	–	–	0.7	43.4	166	141	b
16222	51.430	14.695	576	–	–	–	0.9	57.3	74.8	345	225	b
27	51.3607	11.4000	780	–	2.3	–	0.6	1	7.6	–	15	a
28	51.3607	11.5600	510	–	–	–	–	–	4.1	–	20	a
26	51.3500	11.7200	950	2	7.8	1	5.9	–	5.9	–	18	a
90	51.3358	13.9600	510	–	–	–	–	–	–	–	–	a
93	51.3357	13.1000	1,500	–	–	–	–	–	–	–	–	a
78	51.2917	11.7600	1,130	–	3.8	–	19.1	–	0.6	–	–	a
92	51.2733	13.2000	1,492	–	–	–	–	–	–	–	–	a
25	51.2537	12.0000	1,130	–	–	–	–	1	5	–	5	a
71	49.8050	10.6800	160	–	–	–	–	–	–	–	–	a
16901	49.285	11.416	410	–	–	–	–	27.2	35.2	364	268	b
16902	49.257	11.953	1,013	–	–	–	–	27.2	53.5	333	371	b
M30/1 433	49.237	12.493	1,158	–	–	–	–	6.4	35.1	205	234	b
89	48.8933	10.0283	1,002	–	–	–	–	–	–	–	–	a
88	48.8933	10.4933	420	–	–	–	–	–	–	–	–	a
58	48.6867	9.8417	370	–	–	–	–	–	–	–	–	a
46	48.6720	9.7883	255	–	–	–	x	–	–	–	69	a
106	48.6693	9.8400	370	–	x	–	x	1	–	–	79	a
47	48.6586	9.9000	530	–	–	–	–	–	–	–	5	a
48	48.6586	9.9333	620	–	–	–	–	3	5.3	–	36	a
59	48.5833	10.0500	810	–	–	–	–	–	–	–	–	a
113	48.4950	10.3417	1,400	x	–	x	–	–	–	–	–	a
52	48.4750	10.3283	1,310	–	–	–	–	–	1	–	16	a
54	48.4733	10.3267	1,330	–	–	–	x	–	1.9	–	1	a
112	48.4717	10.3050	1,095	x	–	–	–	–	–	–	–	a
111	47.9483	8.0117	765	–	–	–	–	3	5.4	–	29	a
PO201/10-755	47.944	7.632	207	–	–	7.4	22.4	–	–	254	108	b
110	47.9367	7.9167	287	–	–	–	x	–	–	–	–	a
109	47.9367	7.9167	442	–	–	–	–	x	–	–	–	a
PO201/10-754	47.903	7.665	398	–	–	1	9.9	–	–	425	105	b
49	47.8867	8.0000	725	–	–	–	–	–	–	–	19	a
50	47.8833	7.9867	1,150	–	–	–	–	–	–	–	–	a
57	47.8400	8.1517	1,450	–	–	–	–	–	–	–	2	a
64	47.8350	8.0717	920	x	–	x	–	–	–	–	–	a
PO201/10-753	47.784	7.765	684	–	2.5	0.4	1.5	9.4	38.9	275	117	b
108	47.7367	8.0183	960	x	–	x	–	x	–	–	–	a
PO201/10-752	47.691	7.833	1,050	–	–	–	–	43.5	43.4	152	504	b
107	47.6717	7.9833	1,260	–	–	–	–	–	0.6	–	26	a
PO201/10-750	47.647	7.876	1,387	–	–	–	–	0.2	0.7	289	510	b

Reference a: Weston (1985), living: no. of specimens >125 μm, x: presence in a non-quantitative sample, dead: >125 μm (%), x: presence in a non-quantitative sample.
Reference b: Schönfeld (2006; this study), living assemblage >250 μm (%), dead assemblage 250–2,000 μm (%)

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