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Foraminiferal biodiversity associated with cold-water coral carbonate mounds and open slope of SE Rockall Bank (Irish continental margin—NE Atlantic)

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ABSTRACT

Cold-water coral (CWC) ecosystems are hotspots of macro- and microfaunal biodiversity and provide refuge for a wide variety of deep-sea species. We investigated how the abundance and biodiversity of 'live' (Rose Bengal stained) foraminifera varies with, and is related to, the occurrence of CWC on the Rockall Bank (NE Atlantic). Qualitative and quantitative analyses were performed on 21 replicate samples from 8 deep-sea stations, including 4 stations on CWC-covered carbonate mounds at depths of 567–657 m, and 4 stations on the adjacent slope at depths of 469–1958 m where CWC were absent. This sampling strategy enabled us to demonstrate that sediments surrounding the living CWC were characterised by higher foraminiferal abundance and biodiversity than open-slope sediments from the same area. A total of 163 foraminiferal species was identified. The dominant species in CWC sediments were: *Spirillina vivipara*, *Allogromioid* sp. 1, *Globocassidulina subglobosa*, *Adercotryma wrighti*, *Eponides pusillus*, *Ehrenbergina carinata*, *Planulina ariminensis*, *Trochammina inflata* and *Paratrochammina challengerii*. Foraminifera were nearly absent in adjacent open slope areas subject to strong tidal currents and characterised by coarse grained deposits. We suggest that CWC create a heterogeneous three-dimensional substrate offering microhabitats to a diverse benthic foraminiferal community.

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1. Introduction

Logachev Mounds is an area located on Rockall Bank between water depths of 550 and 900 m. The Logachev Mounds consist of a complex of mounds with abundant cold-water corals (CWC) present on the mound summits. Living CWC lack symbiotic algae and depend on the supply of current-transported particulate organic matter and zooplankton for their nutrition. For this reason, areas with high densities of living corals are characterised by strong bottom currents (Dorschel et al., 2010). To capture the food efficiently, CWC produce tree-like branching structures supporting colonies of polyps sharing a common calcium carbonate frame. These complex three-dimensional structures provide a multitude of micro-habitats for associated faunal communities, thereby enriching local biodiversity (Freiwald et al., 2004). The OSPAR (Convention for the Protection of the Marine Environment of the North-East Atlantic)

commission included CWC and carbonate mounds in the list of threatened and/or declining species and habitats to ensure their protection from human activities. In particular, the Logachev Mounds are included in the Marine Protected Area by the North East Atlantic Fisheries Commission. The study of this highly vulnerable environment is important to understand its complex relationship with deep marine biodiversity.

Although, CWC have been known to science since the 18th century, their ecological requirements have only been investigated in recent years (review by Freiwald and Roberts, 2005). Most studies dealing with CWC have focused on mega- and macrofauna (Jensen and Frederiksen, 1992; Mortensen et al., 1995), fishes (Auster, 2005) and metazoan meiofauna (Raes and Vanreusel, 2005; Bongiorno et al., 2010), whereas few have targeted foraminiferal assemblages. Cedhagen (1994) described *Hyrrokkin sarcophaga* (up to 6 mm diameter), a new genus and species of parasitic calcareous foraminifera that lives on various biogenic substrates including deep-sea corals such as *Lophelia pertusa*, *Madrepora oculata* and *Primnoa resedaeformis* (Freiwald and Schönfeld, 1996). Hawkes and Scott (2005) studied benthic

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foraminifera (63–500 μm fraction) attached to the deep-sea gorgonian coral *P. resedaeformis* from the Scotian Margin (Canada). They found 29 species, five of which (*Cibicides lobatulus*, *Cribrorostomoides crassimargo*, *Cyclogyra involvens*, *Discanomalina semipunctata* and *Rosalina* sp.) occurred on all analysed coral specimens. Zibrowius and Taviani (2005) found the epibenthic calcareous foraminifera *Planogypsina?* (> 2 mm) living on CWC collected in the Strait of Sicily (Italy). Buhl-Mortensen and Mortensen (2005) recorded 17 species of benthic foraminifera (> 250 μm) attached to deep-sea gorgonian corals collected in the Labrador Sea; the most common species were *Discanomalina vermiculata*, *D. coronata*, *Cibicides refulgens* and *C. lobatulus*. Margreth et al. (2009) studied the total (unstained) benthic foraminiferal assemblages (> 63 μm) from surface sediment samples collected on CWC mounds in the Porcupine Seabight and on the Rockall Bank. They identified five different benthic foraminiferal associations related to the different environmental conditions that characterised five facies, one of them being living CWC. Schönfeld et al. (2010), who studied living and dead (> 250 μm fraction) assemblages, found that foraminiferal diversity on Galway and Propeller Mounds in the Porcupine Seabight on the Irish continental margin was not higher than in the adjacent off-mound area. Although these studies indicated that benthic foraminifera are abundant on CWC and in the sediment around CWC, there has been no comprehensive study of the live benthic foraminiferal assemblage (soft-shelled and hard-shelled foraminifera).

Here, we describe the abundance, diversity and taxonomic composition of the 'live' (Rose-Bengal-stained) benthic foraminiferal assemblages in an area with an exceptionally dense coverage on CWC on the SE Rockall Bank (Logachev Mounds—NE Atlantic). We compare the biodiversity in the sediment underneath living corals with that of the neighbouring open-slope sediments, both at a similar depth and across a bathymetric transect down the slope (from 500 m to 1900 m water depth). We address the following questions:

- Do CWC influence benthic foraminiferal assemblages, and if how? More specifically, does the CWC habitat promote a higher foraminiferal biodiversity?
- Are foraminiferal abundance patterns at CWC consistent with those reported for the metazoan meiofauna?
- Are some foraminiferal species typical of CWC habitat or endemic to it?
- Is the composition of the living assemblage reflected by the thanatocoenosis in this area influenced by strong bottom currents?

2. Materials and methods

2.1. The study site

The mound on which this study is focused forms part of the Logachev Mounds province, a large group of giant carbonate mounds spread out between 500 and 900 m depth along the SE flank of Rockall Bank (Mienis et al., 2007). Rockall Bank is located between 53°30' and 58°30'N on the Irish continental margin, approximately 400 km to the west of Ireland. It is separated from the European shelf by the Rockall Trough (Fig. 1). Mounds of the Logachev group occur in clusters of several kilometres in length and width, and reach heights ranging from several tens of metres to more than 300 m. Mound clusters are separated by gullies that are oriented perpendicular to the overall trend of the slope. The summits of the mounds are densely covered with live coral framework (Fig. 2), whereas isolated corals and coral rubble are found further down the slopes of the mounds. The flat areas in

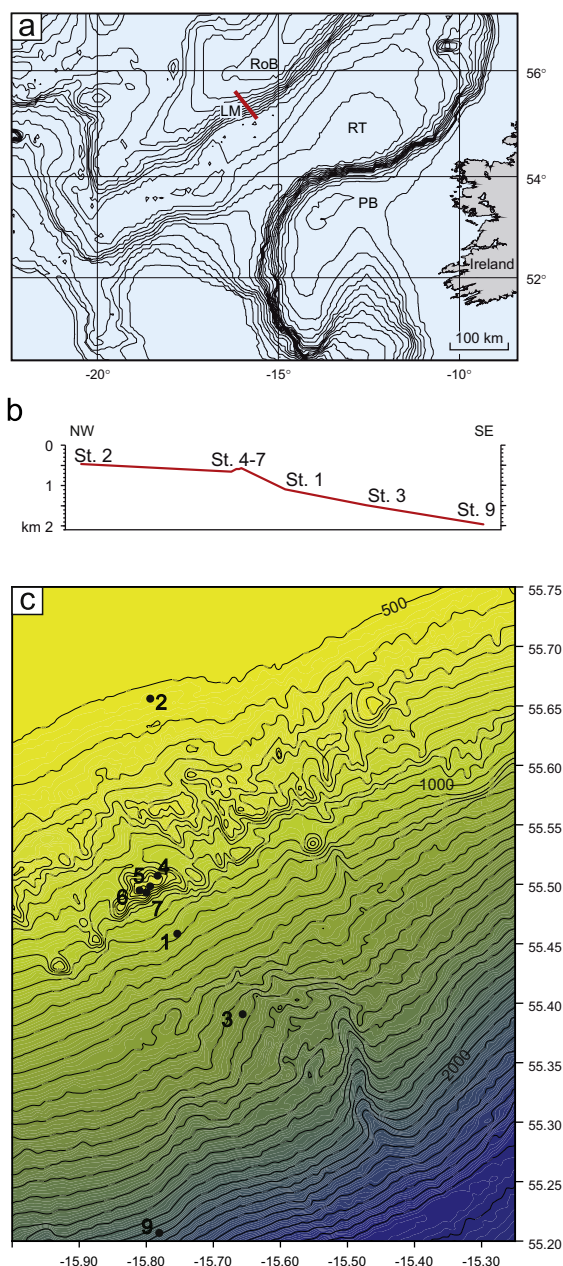


Fig. 1. (a) Map of the Irish margin showing the Rockall Bank (RoB) that hosts the Logachev Mounds province (LM), the Rockall Trough (RT) and the Porcupine Bank (PB). Contour interval is 200 m. Bold line shows the studied area; (b) depth profile with location of the stations corresponds to the red bold line in (a); (c) location of the eight sampling sites. Contour interval is 50 m.

between the mounds are covered with winnowed sand and pavements of ice-rafted pebbles and rocks (Fig. 2, Sts. 1 and 2), washed out from glacial sediments by strong currents. Bottom-water temperature on the Rockall Bank exhibits a daily variation of ca. 2 °C, reflecting the alternation of deep, cold water flowing upslope and warmer water flowing downslope under the influence of internal tides (Duineveld et al., 2007; Mienis et al., 2007). It has been hypothesised by White et al. (2005) that enhanced surface water primary productivity over Rockall Bank is related to the formation of a cold water patch over the bank during winter (Shapiro et al., 2003). This dome of nutrient-rich and less saline water causes a spring bloom early in the year, creating locally enhanced surface productivity (White et al., 2005; Mienis et al., 2007). Sea-surface chlorophyll-a concentrations in June 2006

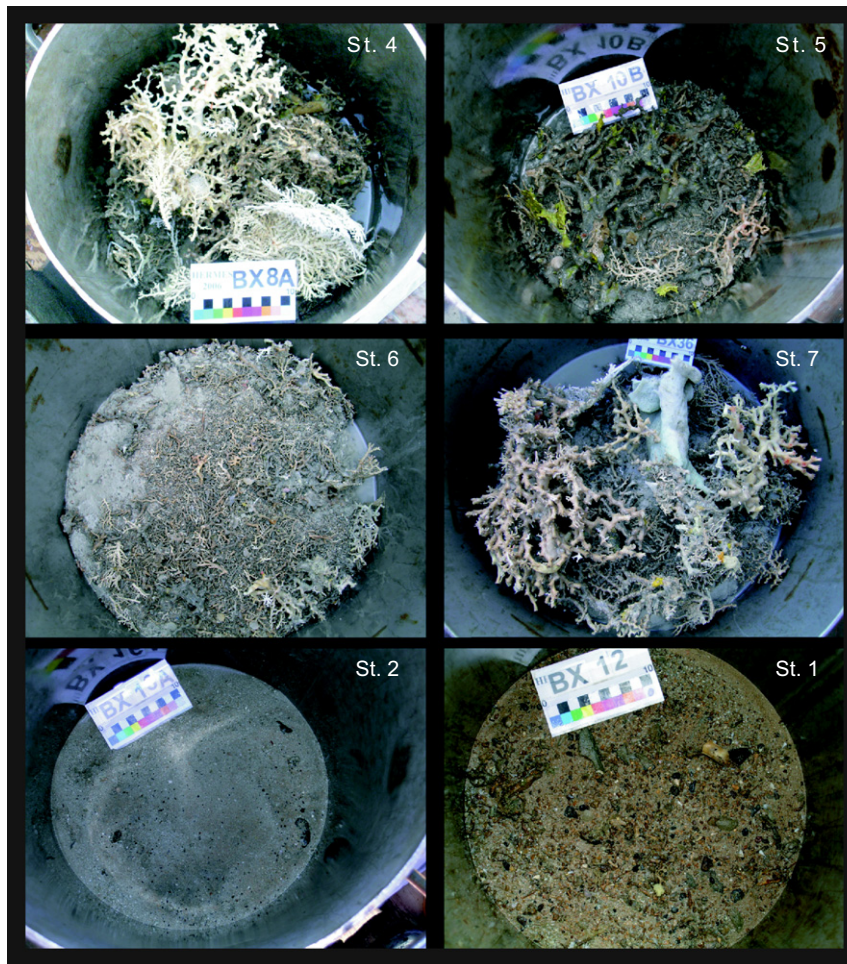


Fig. 2. Box-cores collected during the cruise 64PE249.

(during sampling time) were within the range $3\text{--}5\text{ mg m}^{-2}$ (<http://seawifs.gsfc.nasa.gov>).

Most of the samples for this study were collected on the so-called 'Haas Mounds', a relatively isolated mound cluster at the margin of the Logachev Mound province, which reaches a height of more than 300 m above the surrounding seabed. This cluster comprises of two relatively flat summits at 550 m depth, separated by shallow gullies. The summits have a dense coverage of cold-water corals, *L. pertusa* (Linnaeus, 1758) and *M. oculata* (Linnaeus, 1758), and sponges (*Hexadella*, *Higginsia* and *Asconema*).

Current speed at 1 m above bottom was measured with a current meter (Nortek Aquadopp) mounted on a benthic lander deployed near the top of the mound, i.e. stations 4–7. The average and maximum speeds were 9 and 30 cm s^{-1} , respectively. Current measurements from a point immediately south of the coral mound, ca. 2 nm north of station 1, indicated a maximum speed of 65 cm s^{-1} and an average speed of 16 cm s^{-1} . These were measured during a period of 9 days (23 June–2 July 2006) at 3 m above the bottom by a FSI current meter. Data published in Mienis et al. (2009) indicated that at station M2005-33 (55.4890°N , 16.1416°W , 557 m water depth), located 28 km SW of our St. 2 in an analogue setting up-slope of the carbonate mounds, current speeds were above 15 cm s^{-1} for 30% of the time of the measurements and peaked at up to 75 cm s^{-1} . Mienis et al. (2007) reported current speeds exceeding 45 cm s^{-1} down-slope of the carbonate mounds at the SW Rockall Trough margin, located 5 km distance from our St. 3. We do not have current speeds measured directly above the St. 9 site. However, according to White et al. (2007), the average current speed

is less than 5 cm s^{-1} at the base of the slope of the Rockall Bank area.

The biopolymeric C content (BPC—quantity of organic matter available to benthic consumers measured on dry weight of surface sediment) in the studied area varied between 0.51 C mg g^{-1} at the open slope stations and 1.54 C mg g^{-1} in the CWC area (see Bongiorno et al., 2010 for details of biochemical methods). Protein to carbohydrate ratios, indicating the quality of the organic matter (Pusceddu et al., 2009), varied between 0.22 at the open slope stations and 0.31 in the CWC area.

2.2. Sampling

Sediment samples were collected at 8 sites during cruise 64PE249 of R.V. *Pelagia* (19 June–7 July 2006) within the framework of the HERMES project (Duineveld and shipboard scientific crew, 2006). Samples containing live CWC were collected at four stations at water depths of 567–657 m (Sts. 4–7), and samples without CWC were collected at four stations, characterised by a coarse-grained lag deposit of ice-rafted debris and winnowed sand, along a bathymetric transect across the SE Rockall Bank between 469 and 1958 m water depth. One of these slope stations (St. 2) was located up-slope of the mound, whereas the other three (Sts. 1, 3, 9) were located further down-slope (Table 1 and Fig. 1). The samples were collected using a NIOZ-boxcorer with a 50-cm diameter cylindrical coring barrel and a top valve preventing washout of the core. After removing the larger pieces of live and dead corals and other large fauna lying loosely on the

Table 1

List of stations along the depth transect, with official station number given in brackets, latitude, longitude, water depth, number of replicates, average current speed, peak current speed and sediment facies. For current data see text for more detailed explanations and references. na=not available.

Station	Latitude	Longitude	Water depth (m)	Number of replicates	Average current (cm s^{-1})	Current peak (cm s^{-1})	Sediment facies
St. 2 (BX16A)	55.65000 N	15.79855 W	469	3	~15	75	Winnowed sand
St. 4 (BX8A)	55.50333 N	15.78592 W	657	3	9	30	CWC
St. 5 (BX10B)	55.49988 N	15.79893 W	591	3	9	30	CWC
St. 6 (BX28A)	55.49790 N	15.81007 W	588	3	9	30	CWC
St. 7 (BX36)	55.49515 N	15.80933 W	567	3	9	30	CWC
St. 1 (BX12)	55.45180 N	15.76608 W	1091	2	16	65	Coarse grained lag-deposit
St. 3 (BX30A)	55.38068 N	15.65310 W	1488	3	na	45	Coarse grained lag-deposit
St. 9 (BX79A)	55.20755 N	15.77933 W	1958	1	~5	na	na

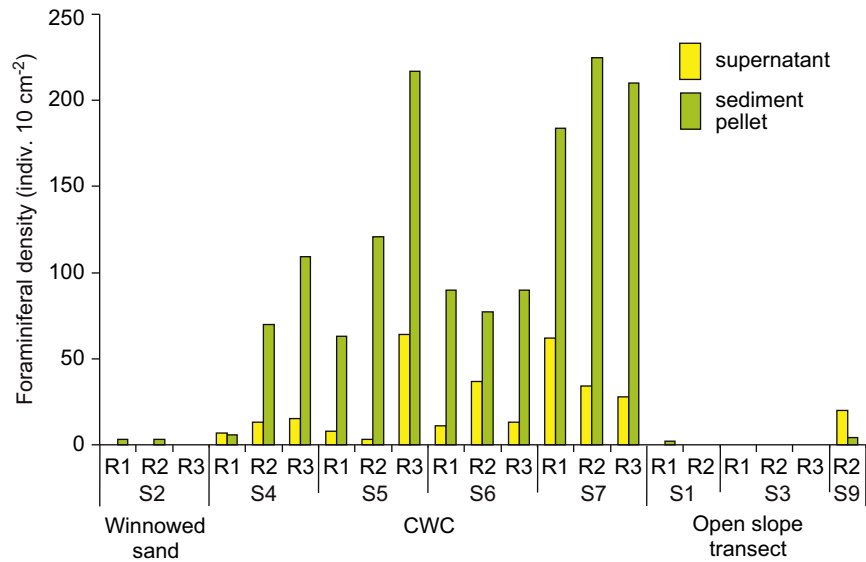


Fig. 3. Number of 'live' benthic foraminifera per 10 cm^2 (indiv. 10 cm^{-2}) in the supernatant (LUDOX fraction) and sediment pellet.

sediment surface, replicate subcores were taken using a PVC coring tube (3.6 cm internal diameter) (Table 1). Subcores were frozen at -20°C , which still enabled the identification of all organisms, including the soft-shelled foraminifera (Danovaro, 2010), until analysis in the laboratory.

2.3. Foraminiferal analyses

This study is based on the analysis of 'live' (Rose Bengal stained) and dead (unstained) benthic foraminifera from the top 1 cm of the replicate subcores. After extraction, subcore slices were preserved in a buffered 4% formalin solution until further processing in the laboratory. In order to compare patterns of foraminiferal and metazoan meiofaunal diversity (Bongiorno et al., 2010) the sediment samples were shared. The samples were washed through screens with a mesh size of $1000 \mu\text{m}$ and $20 \mu\text{m}$. The residue remaining on the latter sieve was resuspended and centrifuged three times with LUDOX HS40 (density 1.31 g cm^{-3}), and stained for 24 h with Rose Bengal. After the metazoans had been removed (Bongiorno et al., 2010), the two fractions, i.e. the sediment residue (LUDOX retained fraction, hereafter termed the 'sediment pellet') and the floated residue (supernatant), were sieved over a $63\text{-}\mu\text{m}$ sieve and sorted separately in water under a stereomicroscope for stained benthic foraminifera. LUDOX extractions ($n=3$) typically have an efficiency $>98\%$ for metazoan meiofauna (Danovaro, 2010) but a lower efficiency for foraminifera (Burgess, 2001; Sabbatini et al., 2002), due to the fact that many benthic foraminifera have heavy tests. In

Table 2

Extraction efficiency of LUDOX for different groups of foraminifera.

Taxon	N	Mean extraction efficiency (%)	SD
Soft-walled taxa	13	84.9	18.2
MAF	13	0.4	1.2
Miliolids	10	0	–
Calcareous perforate taxa	16	4.1	12.6

MAF=multilocular agglutinated foraminifera; SD=standard deviation; N=number of replicates in which each group of foraminifera was identified.

the present study, this problem was solved by manually picking out the foraminifera remaining in the sediment pellet after extraction in the density gradient. Most of the foraminifera with mineralised test (agglutinated and calcareous) remained in the sediment pellet after centrifugation, whereas the majority of the soft-shelled foraminifera floated in the supernatant (Fig. 3). The efficiency of LUDOX extraction technique was ca. 85% for the soft-shelled foraminifera, ca. 4% for the calcareous perforate foraminifera, 0.4% for multilocular agglutinated foraminifera and 0% for miliolids (Table 2). Heavier monothalamous foraminifera with predominately agglutinated walls (*Lagenammina*, *Psammospaeridae* and *Saccamminidae*), were mainly found in the sediment pellet. The counts from the supernatant and sediment pellet were combined and normalised to 10 cm^2 for subsequent data interpretation.

The picked specimens were stored on micropaleontological slides (hard-shelled species) or in glycerol on cavity slides (soft-shelled species). In the case of calcareous species, only individuals in which most chambers were stained were regarded as having been alive when collected. In the case of multilocular agglutinated and miliolid species, where no stained protoplasm was visible from the exterior, the test was broken in order to establish the presence or absence of stained cytoplasm. The protoplasm of soft-shelled taxa such as allogromiids often contained numerous stercomata and sediment grains and therefore did not stain as clearly as that of calcareous species. However, because the delicate organic or agglutinated wall is likely to decompose rapidly after death, all intact individuals that displayed some degree of staining were recorded as live. Tubular Astrorhizida (mainly *Hyperammina* and *Rhizammina*) were usually fragmented. We counted fragments separately and excluded them from all statistical analyses. The dead benthic and planktonic foraminiferal assemblage of one replicate subcore (R2, 0–1 cm interval) from each station was analysed after all stained foraminifera had been removed. The sample was dried in an oven at 40 °C, and then split with a microsplitter in order to obtain a subsample containing about 250 specimens.

Foraminiferal specimens were identified when possible to the species level in both the 'live' and dead assemblages, based largely upon the taxonomic concepts of Loeblich and Tappan (1994), Gooday and Hughes (2002) and Cornelius and Gooday (2004). Small specimens in which distinctive features were not clearly developed were counted as 'juvenile'. The category 'indeterminate' was used when the genus could not be determined; however, within this category, taxa were distinguished based on test morphology and included in calculations of diversity indices.

2.4. Diversity indices and data processing

The following diversity indices were calculated: (a) Foraminiferal species richness was calculated as the total number of species identified in each replicate subcore; (b) Standardised species richness was calculated as the expected number of species $E(S_x)$ for a theoretical sample of 51 specimens (Hurlbert, 1971); (c) Species diversity (H' , using log-base e) was measured by the Shannon–Wiener information function and Fisher α index. All indices reported above were calculated using PAST v. 1.86b (Hammer et al., 2001).

For the calcareous species, we calculated L/D ('live'/dead) ratios from percentages re-calculated after removing all non-calcareous taxa (i.e. all the soft-shelled foraminifera and agglutinated foraminifera).

Canonical correspondence analysis (CCA) was performed using PAST v. 1.86b (Hammer et al., 2001). We selected 7 environmental parameters, water depth, average current speed, protein, carbohydrate, lipid, biopolymeric organic C (BPC), phytopigments (from Bongiorni et al., 2010), and 31 benthic foraminiferal species, each of which representing > 3% of the total 'live' foraminiferal abundance in at least one sample. Data from Sts. 1–3 were not included due to the low number of living foraminifera.

3. Results

3.1. Abundance, taxonomic composition and diversity of the 'live' assemblage

CWC sediment samples (Sts. 4–7) yielded an average stained foraminiferal density of 135 ± 67 indiv. 10 cm^{-2} (Fig. 4), of which

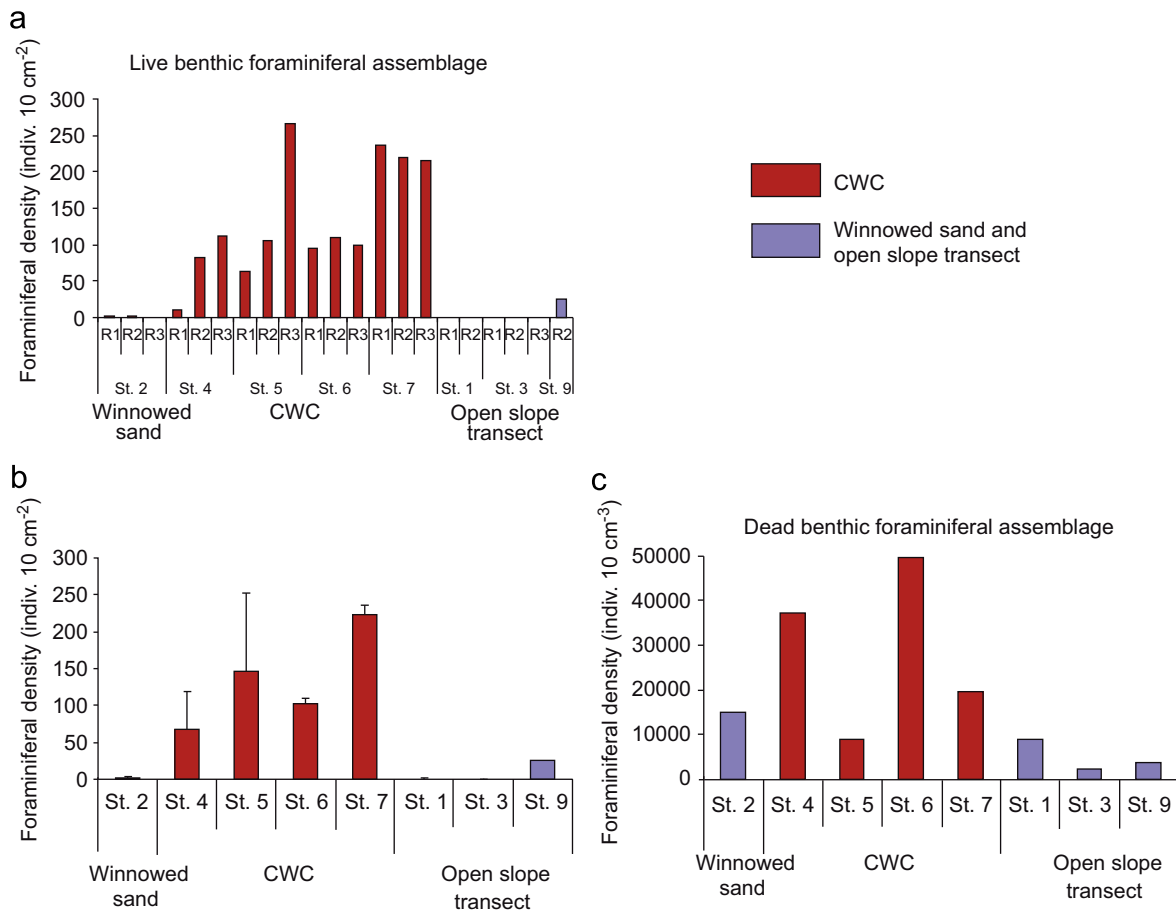


Fig. 4. (a) Abundance of 'live' foraminifera (indiv. 10 cm^{-2}) in all the 21 replicates, (b) abundance (average values with standard deviation) of 'live' foraminifera in the 8 stations (indiv. 10 cm^{-2}) and (c) dead foraminifera (indiv. 10 cm^{-3}) in the 8 stations.

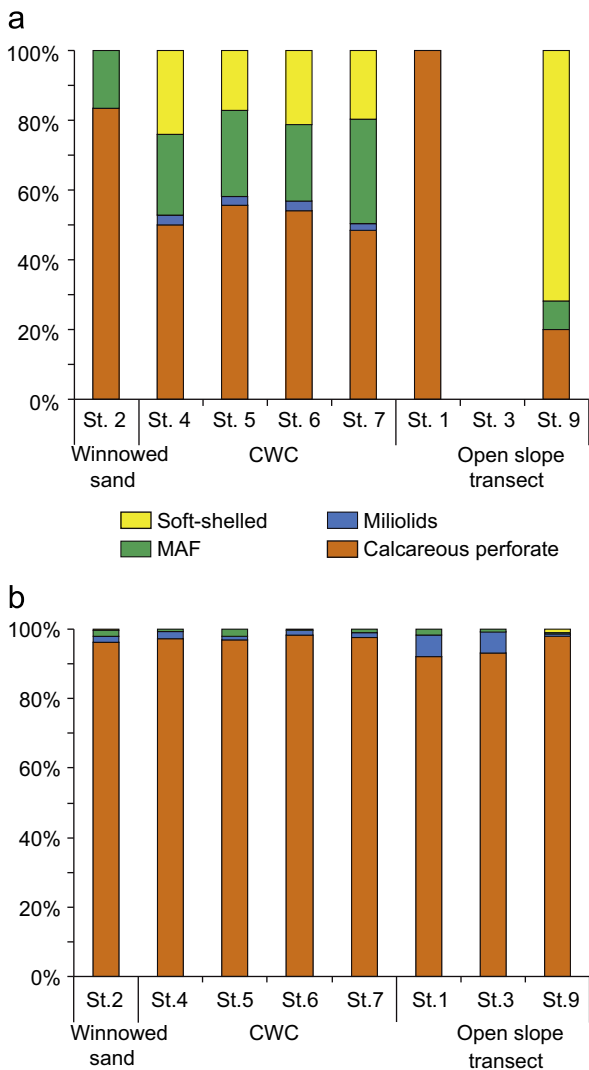


Fig. 5. Proportions of the main groups of foraminifera in (a) the 'live' and (b) the dead foraminiferal assemblages; multilocular agglutinated foraminifera (MAF).

20% belonged to soft-shelled taxa, 26% to multilocular agglutinated taxa, 2% to miliolids and 52% to calcareous taxa (Fig. 5). Several tubular fragments of *Hyperammia* and *Rhizammina*, and two different species of *Gromia* (a group related to the foraminifera), were excluded when calculating densities (Fig. 6). Three species, *Allogromiid* sp. 1, *Spirillina vivipara* and *Eponides pusillus*, were most abundant in the CWC area and *Adercotryma wrighti*, *Discoanomalina coronata* and *Globocassidulina subglobosa* appeared among the top 10 most abundant species in three out of the four CWC stations (Table 3). Among soft-shelled taxa, *Allogromiid* sp. 1, *Allogromiid* sp. 9, *Allogromiid* sp. A and *Saccamminid* sp. 5 were the most abundant (Fig. 7). A significant proportion (~10%) of allogromiids, saccamminids and psammosphaerids could not be separated easily into morphospecies and therefore were considered as indeterminate.

Foraminifera were virtually absent along the bathymetric transect on the open slope (Sts. 1, 3 and St. 9) and at the winnowed sandy site (St. 2). None of the replicates from St. 3, or from St. 1 (R2) and St. 2 (R3), yielded any 'live' foraminifera. The other samples, from St. 2 (R1 and R2), St. 1 (R1) and St. 9 (R2), yielded an average density of 7 ± 12 indiv. 10 cm^{-2} , of which 55% were soft-shelled foraminifera, 9% multilocular agglutinated foraminifera (*Eggerella bradyi*) and 36% were calcareous perforate species (*Hoeglundina elegans*, *Nonionella iridea* and *C. refulgens*) (Fig. 5a). Soft-shelled taxa were found only at St. 9, where *Allogromiid* sp. 1 was dominant; *Allogromiid* sp. 9 also occurred here, together with typical deep-sea taxa (*Nodellum*, *Resigella polaris*, *Saccamminid* sp. 5 and 'silver' *Saccamminid*) (Table 3 and Fig. 7).

A total of 163 benthic foraminiferal species belonging to 71 genera was identified in the sediment samples. Species richness (number of species/station) varied from 0 (St. 3) to a maximum of 89 species at St. 7 (Table 4). CWC stations contained 67–89 species, while only 1–15 species were found at sites along the bathymetric transect (Table 4). The Shannon–Wiener diversity index (H') had its highest value (> 3.0) in the CWC area. Values of $E(S_{51})$ in the CWC area ranged from 22 (St. 5 R3) to 33 (St. 4 R3).

3.2. Abundance, taxonomic composition and diversity of the dead assemblage

The average density of dead foraminifera was higher in the CWC samples than in samples from the bathymetric transect

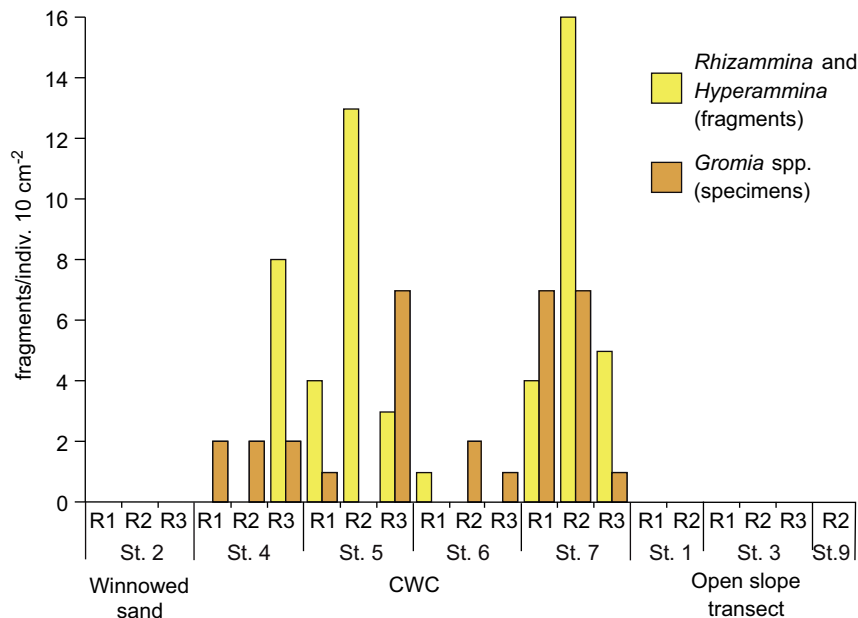


Fig. 6. Abundance of tubular foraminifera (*Rhizammina* and *Hyperammia*) (fragments per 10 cm^{-2}) and *Gromia* spp. (indiv. 10 cm^{-2}) at the study sites.

Table 3
Top 10 species in the 'live' and dead assemblages.

'LIVE' ASSEMBLAGE													
Coral area = CWC			St. 4			St. 5			St. 6			St. 7	
Name	N	%	Name	N	%	Name	N	%	Name	N	%		
Saccamminid sp. 5	18	8.8	<i>Spirillina vivipara</i>	51	11.7	Allogromiid sp. 1	33	10.8	<i>Spirillina vivipara</i>	82	12.2		
<i>Spirillina vivipara</i>	14	6.9	<i>Globocassidulina subglobosa</i>	42	9.6	<i>Globocassidulina subglobosa</i>	26	8.5	Allogromiid sp. 1	59	8.8		
<i>Labrospira jeffreysii</i>	9	4.4	<i>Ehrenbergina carinata</i>	32	7.3	<i>Adercotryma wrighti</i>	21	6.9	<i>Paratrochammina challengeri</i>	45	6.7		
<i>Leptohalysis gracilis</i>	9	4.4	Allogromiid sp. 1	29	6.6	<i>Spirillina vivipara</i>	21	6.9	<i>Adercotryma wrighti</i>	37	5.5		
<i>Melonis barleeanus</i>	9	4.4	Allogromiid sp. A	25	5.7	<i>Trochammina inflata</i>	19	6.2	<i>Reophax spiculifer</i>	34	5.1		
<i>Discoanomalina coronata</i>	8	3.9	<i>Adercotryma wrighti</i>	23	5.3	<i>Planulina ariminensis</i>	14	4.6	<i>Planulina ariminensis</i>	33	4.9		
<i>Eponides pusillus</i>	7	3.4	<i>Trochammina inflata</i>	21	4.8	<i>Ehrenbergina carinata</i>	11	3.6	<i>Globocassidulina subglobosa</i>	27	4.0		
<i>Anomalinoidea minimus</i>	7	3.4	<i>Eponides pusillus</i>	21	4.8	<i>Eponides pusillus</i>	10	3.3	<i>Haplophragmoides bradyi</i>	24	3.6		
Allogromiid sp. 1	6	2.9	<i>Trochammina sp. 3</i>	14	3.2	<i>Discoanomalina coronata</i>	10	3.3	<i>Eponides pusillus</i>	24	3.6		
<i>Adercotryma glomeratum</i>	4	2.0	<i>Discoanomalina coronata</i>	9	2.1	Saccamminid sp. 5	9	3.0	Saccamminid sp. 2	21	3.1		
Total	91 (204)	44.6	Total	267 (437)	61.1	Total	174 (305)	57.0	Total	386 (672)	57.4		
Open slope stations			St. 2			St. 1			St. 3			St. 9	
Name	N	%	Name	N	%	Name	N	%	Name	N	%		
<i>Hoeglundina elegans</i>	5	83.3	<i>Cibicides refulgens</i>	1.0	100.0				Allogromiid sp. 1	8	32.0		
<i>Eggerella bradyi</i>	1	16.7							Saccamminid sp. 5	2	8.0		
									"Silver" Saccamminid	2	8.0		
									<i>Nonionella iridea</i>	2	8.0		
									Allogromiid sp. 9	1	4.0		
									<i>Nodellum</i> like sp. 1	1	4.0		
									<i>Nodellum</i> like sp. 2	1	4.0		
									<i>Resigella polaris</i>	1	4.0		
									Saccamminid sp. 7	1	4.0		
									Saccamminid sp. 8	1	4.0		
Total	6 (6)	100.0	Total	1 (1)	100.0	Total	0.0	0.0	Total	20 (25)	80.0		
DEAD ASSEMBLAGE													
Coral area = CWC			St. 4			St. 5			St. 6			St. 7	
Name	N	%	Name	N	%	Name	N	%	Name	N	%		
<i>Cassidulina crassa</i>	227	38.9	<i>Cassidulina crassa</i>	109	39.5	<i>Cassidulina crassa</i>	122	31.4	<i>Cassidulina crassa</i>	268	43.6		
<i>Globocassidulina subglobosa</i>	95	16.3	<i>Globocassidulina subglobosa</i>	42	15.2	<i>Globocassidulina subglobosa</i>	73	18.8	<i>Globocassidulina subglobosa</i>	82	13.3		
<i>Cassidulina laevigata</i>	50	8.6	<i>Cassidulina laevigata</i>	19	6.9	<i>Cassidulina laevigata</i>	27	7.0	<i>Cassidulina laevigata</i>	66	10.7		
<i>Eponides pusillus</i>	34	5.8	<i>Eponides pusillus</i>	12	4.3	<i>Eponides pusillus</i>	23	5.9	<i>Epistominella exigua</i>	21	3.4		
<i>Stainforthia fusiformis</i>	22	3.8	<i>Epistominella exigua</i>	11	4.0	<i>Epistominella exigua</i>	18	4.6	<i>Stainforthia fusiformis</i>	12	2.0		
<i>Epistominella exigua</i>	17	2.9	<i>Bulimina marginata</i>	6	2.2	<i>Trifarina angulosa</i>	13	3.4	<i>Eponides pusillus</i>	11	1.8		
<i>Bolivina pseudopunctata</i>	16	2.7	<i>Fissurina</i> spp.	6	2.2	<i>Stainforthia fusiformis</i>	11	2.8	<i>Gavelinopsis lobatulus</i>	11	1.8		
<i>Gavelinopsis lobatulus</i>	13	2.2	<i>Stainforthia fusiformis</i>	6	2.2	<i>Bolivina difformis</i>	9	2.3	<i>Hanzawaia</i> sp.	11	1.8		
<i>Fissurina</i> spp.	10	1.7	<i>Trifarina angulosa</i>	5	1.8	<i>Bulimina marginata</i>	8	2.1	<i>Spirillina vivipara</i>	10	1.6		
<i>Bulimina marginata</i>	9	1.5	<i>Astrononion allowayi</i>	4	1.4	<i>Gavelinopsis lobatulus</i>	8	2.1	<i>Bolivina spathulata</i>	9	1.5		
Total	493 (583)	84.6	Total	220 (276)	79.7	Total	312 (388)	80.4	Total	501 (615)	81.5		

Table 3 (continued)

DEAD ASSEMBLAGE				St. 1			St. 3			St. 9		
Open slope stations				N	%	Name	N	%	Name	N	%	Name
Cibicides refulgens	75	31.8	Cibicides refulgens	58	23.7	Rupertia stabilis	30	20.1	Cassidulina crassa	77	33.3	
Cassidulina crassa	26	11.0	Cassidulina crassa	30	12.2	Cibicides wuellerstorffi	18	12.1	Cassidulina laevigata	31	13.4	
Trifarina angulosa	25	10.6	Globocassidulina subglobosa	24	9.8	Cassidulina crassa	16	10.7	Rupertia stabilis	28	12.1	
Cibicides lobatulus	22	9.3	Cibicides lobatulus	14	5.7	Cassidulina laevigata	11	7.4	Cibicides wuellerstorffi	14	6.1	
Cassidulina laevigata	11	4.7	Cassidulina laevigata	13	5.3	Trifarina angulosa	9	6.0	Globocassidulina subglobosa	10	4.3	
Globocassidulina subglobosa	10	4.2	Carpenteria proteiformis	11	4.5	Cibicides refulgens	6	4.0	Cyroidina laevigata	9	3.9	
Cibicides pseudoungertianus	8	3.4	Rupertia stabilis	11	4.5	Astronotium gallowayi	4	2.7	Bolivina difformis	8	3.5	
Eponides pusillus	5	2.1	Carpenteria monticularis	8	3.3	Carpenteria proteiformis	4	2.7	Gavelinopsis lobatulus	6	2.6	
Discoanomalina coronata	5	2.1	Mitrolimella subrotunda	8	3.3	Epistominella exigua	4	2.7	Eponides pusillus	5	2.2	
Planulina ariminensis	5	2.1	Ehrenbergina serrata	7	2.9	Cibicides lobatulus	3	2.0	Cibicides refulgens	5	2.2	
Total	192 (236)	81.4	Total	184 (245)	75.1	Total	105 (149)	70.5	Total	193 (231)	83.5	

(Fig. 4c). Calcareous species, mainly rotaliids, accounted for 90% or more of all specimens in the dead assemblages (Fig. 5b) and the other orders were relatively much less abundant in the dead than in the 'live' assemblage. In particular, allogromiids, saccamminids and psammosphaerids, important components of the 'live' fauna, were virtually absent. The dead assemblages from the four CWC sites were very similar (Sts. 4–7; Table 3). At all sites, the three dominant species were *Cassidulina crassa*, *G. subglobosa* and *Cassidulina laevigata*. Another three species, *E. pusillus*, *Epistominella exigua* and *Stainforthia fusiformis*, were among the 10 most abundant dead species in all samples. *Gavelinopsis lobatulus* and *Bulimina marginata* also were abundant in three out of the four CWC samples examined.

The dead assemblages in the samples collected along the bathymetric transect (Sts. 1, 3 and St. 9) and at the winnowed sand station (St. 2) were quite different from those collected in the CWC area. Perforate calcareous species characterised by robust, trochospiral tests, such as *C. refulgens*, *Rupertia stabilis*, *Carpenteria proteiformis*, and *C. monticularis*, were among the most abundant in at least two samples. These species had poorly preserved shells and were probably reworked specimens of glacial age. *C. crassa*, *C. laevigata*, *C. lobatulus* and *G. subglobosa* were also abundant in dead assemblage.

A total of 97 benthic foraminiferal species belonging to 64 genera was identified in the dead assemblages. Species richness (number of species/station) varied from 33 (St. 9) to a maximum of 47 species at St. 7. Sediments from CWC contained 40–47 species, whilst 33–39 species were found at sites along the bathymetric transect. The Shannon–Wiener diversity index (*H'*) was fairly constant in all the samples, varying between 2.33 and 3.01. Values of *E*(*S*₅₁) in the CWC area ranged from 15 to 17, and in the slope samples from 16 to 22 (Table 5).

3.3. 'Live' vs. dead assemblage

The dead assemblages in the CWC area yielded substantially fewer species, and had consistently lower values for all diversity indices, compared to the 'live' assemblages (Tables 2 and 5). In contrast, the dead assemblages of the open slope transect had consistently higher values for all the diversity indices compared to the 'live' assemblages. The L/D ratios varied from zero for species that present only in the dead assemblages to values < 1 for species with higher relative abundance in the dead than the 'live' assemblages, and higher values (1–50) for species that were much more abundant in the 'live' assemblages. The L/D ratios (Table 6) varied widely between species. In summary, in the CWC area *C. crassa*, *C. laevigata*, *E. exigua* and *G. subglobosa*, had consistently lower percentages in the 'live' than in the dead fauna, whereas *A. minimus*, *E. carinata*, *M. barleeanus*, *P. ariminensis* and *S. vivipara* had consistently higher percentages in the 'live' than in the dead fauna. At the four bathymetric transect stations, all species showed lower percentages in the 'live' than in the dead assemblage, except for *Trifarina angulosa*.

3.4. Canonical correspondence analysis

The output of the CCA performed on the live benthic assemblages, revealed that the linear combination of the tested explanatory variables (i.e. water depth, average current speed, protein, carbohydrate, lipid, BPC and phytopigments) explained 77% of the variation in the living foraminiferal assemblage composition (Fig. 8 and Table 7). The first axis accounted 55% of the variation, positive values were mainly influenced by depth and negative values by average current speed, BPC and protein. The four CWC stations had negative values on axis 1, whereas St. 9 had a

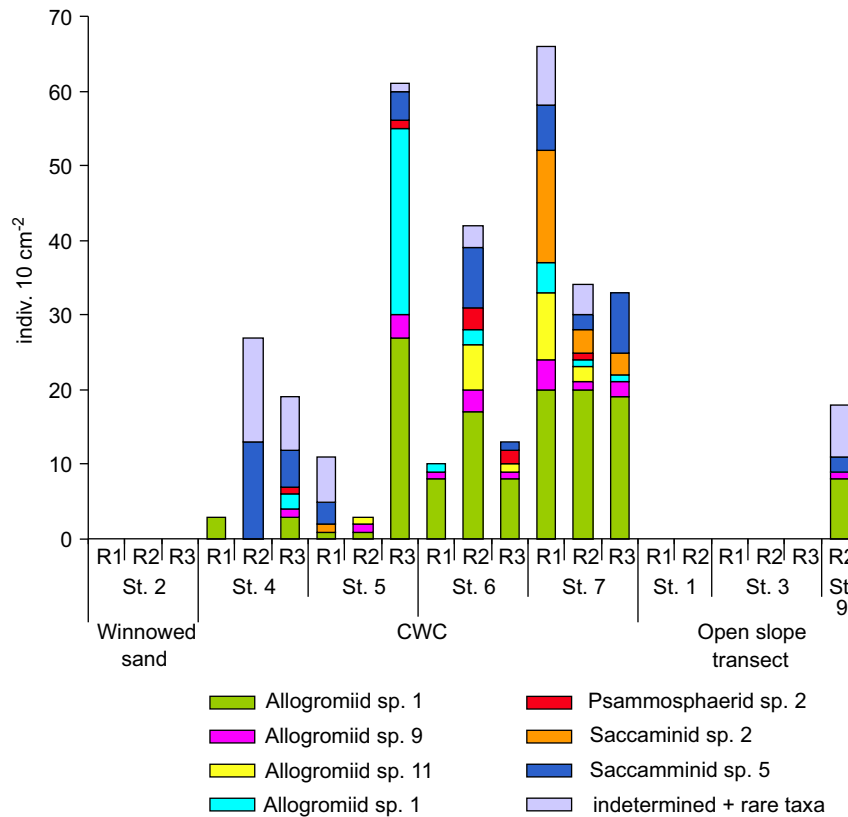


Fig. 7. Abundance (indiv. 10 cm^{-2}) of different taxa and indeterminate forms, in the 'live' soft-shelled foraminiferal assemblage.

Table 4
Diversity indices for the 'live' assemblage: S =species richness, N =number of specimens, $H'(\log_e)$ =Shannon–Wiener index, Fisher α , $E(S_{51})$ =expected number of species, nd=not determined.

Site	Replica	Sediment facies	S	N	$H'(\log_e)$	Fisher α	$E(S_{51})$
St. 2	R1	Winnowed sand	1	3	0.00	0.53	nd
	R2		2	3	0.64	2.62	nd
	R3		0	0	nd	nd	nd
St. 4	R1	CWC	7	11	1.85	8.29	nd
	R2		29	82	3.01	16.00	22.93 ± 1.73
	R3		52	111	3.71	38.13	32.91 ± 2.28
St. 5	R1	CWC	32	64	3.19	25.47	27.82 ± 1.49
	R2		37	106	3.11	20.19	24.01 ± 2.16
	R3		46	267	3.15	16.02	21.80 ± 2.35
St. 6	R1	CWC	33	96	3.16	17.78	24.48 ± 1.91
	R2		42	110	3.30	24.82	26.89 ± 2.23
	R3		33	99	3.13	17.33	24.16 ± 1.93
St. 7	R1	CWC	61	237	3.64	26.59	28.61 ± 2.52
	R2		53	219	3.31	22.23	24.58 ± 2.51
	R3		48	216	3.18	19.13	23.24 ± 2.39
St. 1	R1	Coarse grained lag-deposit	1	1	0.00	0.00	nd
	R2		0	0	nd	nd	nd
St. 3	R1	Coarse grained lag-deposit	0	0	nd	nd	nd
	R2		0	0	nd	nd	nd
	R3		0	0	nd	nd	nd
St. 9	R2	nd	15	25	2.39	15.83	nd

positive loading on the first axis. The second axis accounted 22% of the total variation and was mainly influenced by the biochemical composition of the organic matter in the sediment. In particular, positive values indicate higher amount of carbohydrates (St. 4), whereas negative values indicates higher amount of phytopigments (St. 7).

4. Discussion

4.1. Abundance of 'live' foraminifera

Foraminiferal abundance is closely related to food availability when severe oxygen depletion is not a limiting ecological factor

Table 5

Diversity indices for the dead assemblages: *S*=species richness, *N*=number of specimens, *H*(log_e)=Shannon–Wiener index, Fisher α , *E*(*S*₅₁)=expected number of species and % of *Neoglobobulimina pachyderma* left-coiling in the planktonic foraminiferal assemblage.

Site	Replica	Sediment facies	S	N	<i>H</i> (log _e)	Fisher α	<i>E</i> (<i>S</i> ₅₁)	% <i>N. pachyderma</i> left-coiling
St. 2	R2	Winnowed sand	34	236	2.58	10.9	17.00 ± 2.12	49
St. 4	R2	CWC	41	583	2.37	10.1	15.13 ± 2.19	1
St. 5	R2	CWC	45	276	2.50	15.3	17.46 ± 2.38	2
St. 6	R2	CWC	40	388	2.57	11.2	16.92 ± 2.20	2
St. 7	R2	CWC	47	615	2.33	11.8	15.51 ± 2.33	1
St. 1	R2	Coarse grained lag-deposit	37	245	2.88	12.1	19.74 ± 2.18	50
St. 3	R2	Coarse grained lag-deposit	39	149	3.01	17.2	22.23 ± 2.28	80
St. 9	R2	nd	33	231	2.49	10.5	16.20 ± 2.08	14

Table 6

Percentages of 'live' and dead, and L/D ('live'/dead) ratios, for the most common calcareous species. L/D ratios were calculated from percentages re-calculated after removing all non-calcareous taxa from the 'live' and dead assemblages.

	St. 2			St. 4			St. 5			St. 6			St. 7			St. 1			St. 3			St. 9			
	L	D	L/D	L	D	L/D	L	D	L/D	L	D	L/D	L	D	L/D	L	D	L/D	L	D	L/D	L	D	L/D	
<i>Anomalinoidea minimus</i>				6.5	0.3	21.7	1.6	0.4	4.0	1.2	0.0		2.1	0.0											
<i>Cassidulina crassa</i>	0.0	11.3	0.0	0.0	39.2	0.0	1.2	40.4	0.0	4.0	31.5	0.1	1.2	44.0	0.0	0.0	12.4	0.0	0.0	10.8	0.0	0.0	33.8	0.0	
<i>Cassidulina laevigata</i>	0.0	4.8	0.0	0.0	8.6	0.0	0.0	7.0	0.0	0.0	7.0	0.0	0.0	1.8	0.0	0.0	5.4	0.0	0.0	7.4	0.0	0.0	13.6	0.0	
<i>Cibicides lobatulus</i>	0.0	9.5	0.0	1.9	0.7	2.7	0.0	0.4	0.0	0.6	0.8	0.8	2.4	0.8	3.0	0.0	5.8	0.0	0.0	2.0	0.0	0.0	0.4	0.0	
<i>Cibicides refulgens</i>	0.0	32.5	0.0	0.9	0.2	4.5							0.3	0.0		100.0	24.1	4.1	0.0	4.1	0.0	0.0	2.2	0.0	
<i>Ehrenbergina carinata</i>	0.0	0.4	0.0	3.7	0.3	12.3	12.6	0.4	31.5	6.4	0.3	21.3	3.6	0.2	18.0	0.0	2.9	0.0							
<i>Epistominella vitrea</i>				0.9	2.9	0.3	1.2	4.1	0.3	0.6	4.7	0.1	1.5	3.4	0.4	0.0	1.2	0.0	0.0	2.7	0.0	0.0	2.2	0.0	
<i>Eponides pusillus</i>	0.0	2.2	0.0	6.5	5.9	1.1	8.3	4.4	1.9	5.8	5.9	1.0	7.1	1.8	3.9	0.0	1.2	0.0	0.0	1.4	0.0	0.0	2.2	0.0	
<i>Globocassidulina subglobosa</i>	0.0	4.3	0.0	2.8	16.4	0.2	16.5	15.6	1.1	15.0	18.9	0.8	8.0	13.5	0.6	0.0	10.0	0.0	0.0	1.4	0.0	0.0	4.4	0.0	
<i>Melonis barleeanus</i>	0.0	0.4	0.0	8.3	0.0		0.4	0.0		4.0	0.0		3.0	0.2	15.0	0.0	1.2	0.0	0.0	0.7	0.0	0.0	0.9	0.0	
<i>Planulina ariminensis</i>	0.0	2.2	0.0	2.8	0.9	3.1	2.8	1.1	2.5	8.1	1.6	5.1	9.8	1.1	8.9	0.0	2.1	0.0							
<i>Rupertia stabilis</i>																0.0	4.6	0.0	0.0	20.3	0.0	0.0	12.3	0.0	
<i>Spirillina vivipara</i>				13.0	0.0		20.1	0.4	50.3	12.1	0.3	40.3	24.3	1.6	15.2	0.0	0.4	0.0							
<i>Stainforthia fusiformis</i>				1.9	3.8	0.5	0.0	2.2	0.0	0.0	2.8	0.0	0.3	2.0	0.2				0.0	1.4	0.0				
<i>Trifarina angulosa</i>	0.0	10.8	0.0	0.0	0.9	0.0	3.5	1.9	1.8	1.7	3.4	0.5	5.3	1.3	4.1	0.0	2.1	0.0	0.0	6.1	0.0	20.0	1.8	11.1	

(Morigi et al., 2001). Live foraminifera were more abundant in CWC samples where a higher amount of organic matter was present than in the open slope sediments (Fig. 9), where biochemical values were consistently low. CCA revealed that the amount of organic matter explained between-station variability along axis 1. In particular, CWC stations had high negative values on axis 1, that corresponded to high amount of organic matter (higher values of all biochemical compounds) (Figs. 8 and 9), whereas St. 9 was characterised by positive values of axis 1, which were negatively correlated with the quantity of organic matter and positively related to water depth. This is consistent with evidence that the coral framework promotes the sedimentation of fine particles and organic matter and creates a relatively sheltered environment in which trapped organic detritus is available to associated biota (Mienis et al., 2009; De Haas et al., 2009).

Comparisons between our results and previous studies on samples taken at comparable water depth and environmental conditions in North Atlantic are hampered by the use of different size sieves (150 or 250 μm compared to 63 μm in the present study; see Table 8 for references), the fact that our samples were sorted wet, and the inclusion of the soft-shelled tests that are routinely overlooked in geologically oriented studies. The foraminiferal densities obtained from the CWC area (68–224 indiv. 10 cm^{-2}) were slightly lower than those reported from the 63 to 150 μm fraction along an open slope transect in the Bay of Biscay (550–2000 m, ~75–400 indiv. 10 cm^{-2} ; Duchemin et al., 2007) and much lower than the high values reported by Gooday and Hughes (2002) in the nearby Rockall Trough (> 63 μm , 1913–

1980 m, 830–2379 indiv. 10 cm^{-2}) (Table 8). Nardelli et al. (2010) found lower foraminiferal density (> 63 μm , 959–1002 m, 40–78 indiv. 10 cm^{-2}) at open slope stations on the Portuguese margin, an area characterised by the same concentration of phytopigments and BPC in the sediments. The very low densities that we obtained from the winnowed sand and open-slope stations are very unusual for bathyal continental margin settings. The open slope stations (Sts. 1–3) are influenced by strong currents (Table 1) and characterised by coarse-grained lag deposits, indicating either a lack of sedimentation or an erosive regime (De Haas et al., 2009). St. 9, the deepest site (1958 m), experienced more oligotrophic conditions, as the labile component of the organic matter rapidly diminishes with water depth, and its deposition can be strongly influenced by lateral advection (Morigi et al., 2001). The flux of organic matter to the deep-sea floor is the main parameter structuring benthic foraminiferal faunas, controlling their density and species composition (Jorissen et al., 2007). Thus, a reduced organic matter flux can sustain only a small standing stock of benthic foraminifera.

It appears, therefore, that foraminiferal densities at the CWC sites are not enhanced compared to normal open slopes of similar water depth, but rather that the open slope sites in the present study area are severely impoverished. The negative effect that strong currents have on benthic foraminiferal assemblages is to some extent reduced by the presence of the CWC that creates different protected niches and hence hotspots of benthic foraminiferal abundance.

The trend in the abundance of sediment-dwelling foraminifera followed that of the metazoan meiofauna (data from Bongiorno

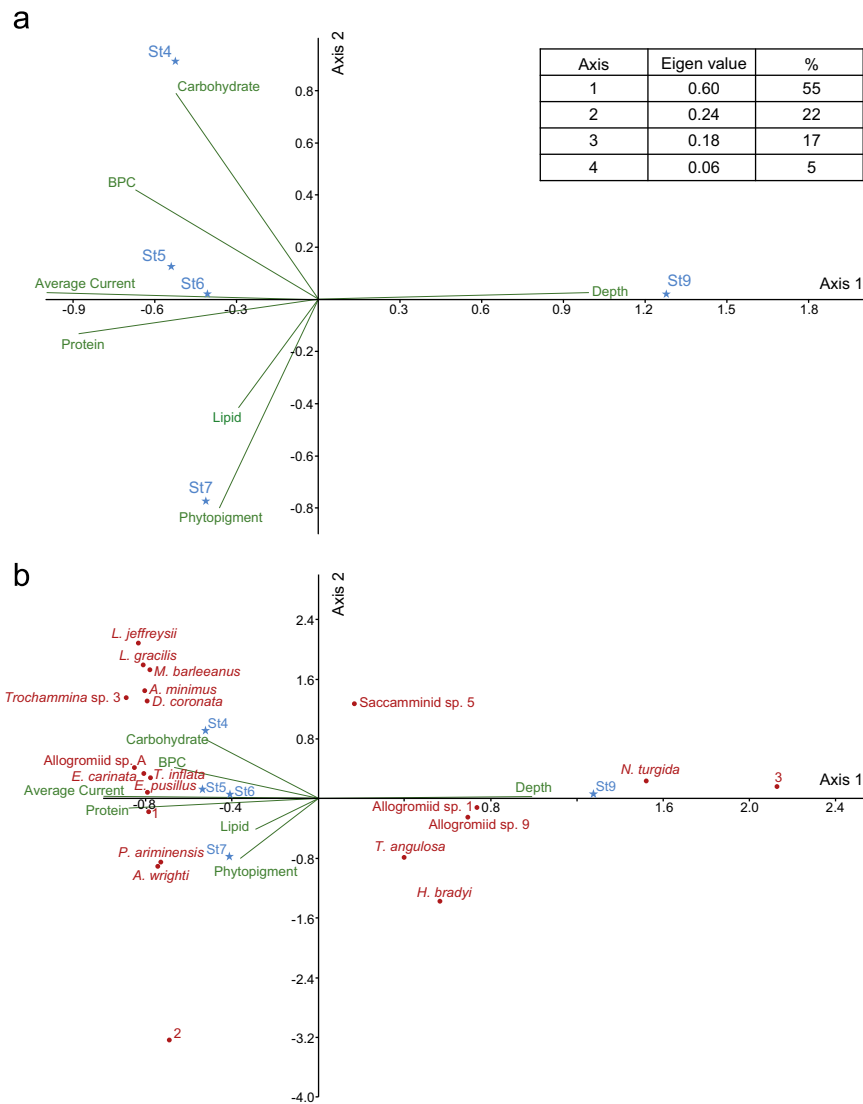


Fig. 8. (a) CCA plot showing the distribution of stations (stars) and the environmental parameters along axes 1 and 2; (b) CCA plot showing the distribution of the stations (stars) and the 'live' species (dots) along axes 1 and 2. 1 = *Globocassidulina subglobosa*, *Spirillina vivipara*; 2 = *Paratrochammina challengerii*, *Reophax spiculifer*, Saccamminid sp. 2; 3 = *Haplophragmoides* sp., *Nodellum*-like sp.1, *Nodellum*-like sp. 2, *Nonionella iridea*, *Resigella polaris*, 'silver' Saccamminid, Saccamminid sp. 7; Saccamminid sp. 8.

et al., 2010), although the metazoans outnumbered foraminifera at all sites. Foraminifera constituted ~15% of the total meiofauna in the CWC area whereas on the open slope the percentage decreased to only 0–0.4%, except at the deepest site (St. 9), where the percentage was again 15% (Fig. 9). This suggests that the metazoan meiofauna coped better with strong currents than the foraminifera. The nematodes, in particular, seem to do well in high energy environments (Bongiorni et al., 2010). Similarly, Garcia et al. (2007) found that in the energetic upper and middle sections of the Nazaré canyon on the Portuguese margin were characterised by lower foraminiferal and metazoan densities, but a higher proportion of nematodes.

4.2. Biodiversity and taxonomic composition of 'live' assemblage

4.2.1. Biodiversity

Biodiversity (number of species, H' and Fisher α) was higher in the CWC area than at the winnowed sand and the open-slope sites and it was higher than that reported in many other studies (see Table 8 for comparison). We believe that this reflects the inclusion of both soft-shelled and hard-shelled species, and the analysis of finer

size fraction. On the other hand, we probably underestimated the number of species occupying the CWC habitat, since we analysed only the first centimetre of sediment and not the deeper-dwelling infaunal foraminifera or the epibenthic taxa living on the coral branches. Buhl-Mortensen et al. (2010) suggested that the live tissue of deep-water scleractinian corals prevents attachment of sessile epibenthic foraminiferal species. Only the parasite foraminifera *H. sarcophaga* has direct contact with live coral tissue (Cedhagen, 1994; Buhl-Mortensen and Mortensen, 2004). Several other species can live on dead coral skeletons. Schönfeld et al. (2010) recorded more than 26 species of attached epibenthic foraminifera (> 63 μm) in the coral area of Galway Mound, Porcupine Seabight. Among them, four species (*C. lobatulus*, *C. refulgens*, *D. coronata* and *P. ariminensis*) also occurred in our samples. According to Buhl-Mortensen et al. (2010), the highest diversity of associated organisms (metazoan meiofauna, fishes, etc.), is found in the zone with dead coral blocks, where the coral skeletons are exposed and create a more complex three dimensional structure than the rubble zone surrounding the coral reef. Carbonate mounds on the Rockall Bank are covered by a thick layer of dead coral framework and living polyps were usually found on top of the dead framework. This implies that we may have

Table 7

Results of the canonical correspondence analysis (CCA) considering 31 benthic foraminiferal species representing > 3% of the total 'live' foraminiferal abundance in at least one sample of the 5 stations and 7 environmental parameters: water depth, average current speed, protein, carbohydrate, lipid, phytopygments, biopomeritic organic carbon (BPC).

Parameters	Axis 1	Axis 2	Axis 3	Axis 4
Allogromiid sp.1	0.73	-0.14	-0.18	-0.41
Allogromiid sp. 9	0.69	-0.25	-0.59	-0.93
Allogromiid sp. A	-0.85	0.42	-1.52	2.92
Like <i>Nodellum</i> sp. 1	2.13	0.16	-0.04	0.34
Like <i>Nodellum</i> sp. 2	2.13	0.16	-0.04	0.34
<i>Resigella polaris</i>	2.13	0.16	-0.04	0.34
Saccamminid sp. 2	-0.69	-3.24	2.33	0.91
Saccamminid sp. 5	0.17	1.26	1.09	-0.23
Saccamminid sp. 7	2.13	0.16	-0.04	0.34
Saccamminid sp. 8	2.13	0.16	-0.04	0.34
Silver Saccamminid	2.13	0.16	-0.04	0.34
<i>Adercotryma wrighti</i>	-0.75	-0.91	-0.81	-1.13
<i>Haplophragmoides bradyi</i>	0.56	-1.36	0.80	-0.29
<i>Haplophragmoides</i> sp.	2.13	0.16	-0.04	0.34
<i>Labrosira jeffreysii</i>	-0.84	2.08	2.38	1.20
<i>Leptohalysis gracilis</i>	-0.82	1.79	1.76	-0.06
<i>Paratrochammina challengeri</i>	-0.69	-3.24	2.33	0.91
<i>Reophax spiculifer</i>	-0.69	-3.24	2.33	0.91
<i>Trochammina inflata</i>	-0.78	0.27	-1.58	-1.32
<i>Trochammina</i> sp. 3	-0.89	1.35	-1.29	4.15
<i>Eponides pusillus</i>	-0.79	0.08	-0.01	0.59
<i>Anomalinooides minimus</i>	-0.81	1.46	1.43	-0.10
<i>Discoanomalina coronata</i>	-0.80	1.32	0.54	-1.01
<i>Ehrenbergina carinata</i>	-0.81	0.34	-1.10	0.68
<i>Globocassidulina subglobosa</i>	-0.78	-0.14	-1.42	-0.41
<i>Melonis barleeanus</i>	-0.78	1.72	1.90	-1.92
<i>Nonionella iridea</i>	2.13	0.16	-0.04	0.34
<i>Nonionella turgida</i>	1.52	0.23	-0.63	1.36
<i>Planulina ariminensis</i>	-0.73	-0.85	-0.02	-1.71
<i>Spirillina vivipara</i>	-0.79	-0.15	0.13	0.65
<i>Trifarina angulosa</i>	0.39	-0.80	-0.11	0.74
St. 4	-0.53	0.91	0.68	0.01
St. 5	-0.54	0.13	-0.54	0.32
St. 6	-0.41	0.02	-0.35	-0.44
St. 7	-0.41	-0.78	0.42	0.05
St. 9	1.28	0.03	-0.01	0.02
Water depth	0.99	0.02	-0.03	0.06
Average current speed	-1.00	0.03	-0.05	0.06
Protein	-0.88	-0.13	0.31	0.31
Carbohydrate	-0.52	0.79	0.15	0.41
Lipid	-0.29	-0.42	0.61	0.52
Phytopygment	-0.36	-0.80	0.09	0.35
BPC	-0.67	0.42	0.41	0.57

missed a substantial number of epifaunal foraminifera and consequently underestimated the biodiversity of the CWC habitat. In contrast, the stations along the slope (Sts. 1–3) had a very low number of species, much lower than other open-slope stations (Table 8). Unfortunately, the very low number of living foraminifera found in the open slope stations does not allow us to include Sts. 1–3 in the CCA. Nevertheless, the highest current speeds (average and maximum values) were recorded at these three stations (Table 1). The current velocity at 50 cm above the seafloor varied between 3 and 30 cm/s with peaks of 65 cm/s (Table 1). The absence of arborescent foraminifera at the slope stations (Fig. 6) also suggests that these sites are impacted by strong currents. These delicate forms thrive in relatively stable environments characterised by lower current velocities (Koho et al., 2007) and may be damaged by enhanced current flow (Altenbach, 1988). These findings are consistent with the results of other studies (Mackensen et al., 1990, 1993; Schönfeld, 2002), which indicated that physical parameters, especially currents, can strongly affect the benthic foraminiferal assemblages, creating oligotypic associations dominated by few resistant species (i.e. *C. lobatulus*, *C. refulgens* and *T. angulosa*).

4.2.2. The soft-shelled component (Fig. 10)

Soft-shelled taxa contributed 20% of the 'live' foraminiferal assemblage (average density 135 indiv. 10 cm⁻²) in the CWC stations and 72% at St. 9 on the open slope (Fig. 5a). Several of the most common species have never been found before, either in the Northeast Atlantic or in CWC habitats. Most are undescribed, but several belong to known genera (*Nodellum*, *Resigella* and *Tinogullmia*). Some resemble species reported from other locations, although the conspecificity of these morphologically simple forms is difficult to establish without molecular data. The most abundant species, Allogromiid sp. 1 (Fig. 10-1), is similar to Allogromiid sp. 1 from the Porcupine Seabight (Gooday, 1986, Fig. 3b therein) and the central Equatorial and North Pacific (Gooday et al., 2004, Fig. 5e therein). Pancotti (2011) discovered a similar morphotype in the deep Western Mediterranean Sea. Allogromiid sp. 9 (Fig. 10-2) closely resembles a species with the same numerical designation from much shallower depths in the North Adriatic (Sabbatini et al., 2010, Pl. 1, Fig. 5 therein). A similar organic-walled allogromiid is also present at abyssal depths in the Mediterranean basin (Pancotti, 2011). Allogromiid sp. A (Fig. 10-3), an organic-shelled form with two apertures, is common in our CWC samples. This form ranges from spindle-shaped to cylindrical and contains numerous stercomata (waste pellets). Saccamminid sp. 5 (Fig. 10-7), which has one terminal aperture, represents a morphotype that is common in the deep North Atlantic, Indian and Pacific Oceans (=Saccamminid sp. 5 in Gooday 1994, Fig. 3F; Gooday et al., 2004, Fig. 6D–G). It is also very similar to a form reported from the upper bathyal (~900 m water depth) western Mediterranean (Heinz, 1999) and the abyssal Alboran Sea (Western Mediterranean) (Pancotti, 2011). A 'silver saccamminid' (Fig. 10-8), a morphotype reported at deep-water sites in the Northeast Atlantic and North and Western Equatorial Pacific Oceans (Saccamminid sp. 2 in Gooday et al., 2004, Fig. 6A–C) as well as the Mediterranean (Pancotti, 2011), occurs at Sts. 7 and 9. The sparse 'live' assemblage at St. 9 is dominated by soft-shelled taxa. Some forms with brownish, organic-walled tests (*Nodellum* spp. and *R. polaris*, Figs. 5-5 and 10-6) found exclusively at St. 9, are polythalamous. Pancotti (2011) reported similar morphotypes from the abyssal Mediterranean and the Atlantic off the Straits of Gibraltar. These small forms are common in deep-sea sediments world-wide and probably a ubiquitous component of deep-sea faunas (Gooday et al., 2004).

4.2.3. The 'live' hard-shelled component (Fig. 11)

More than 60% of the foraminifera in our samples belong to hard-shelled taxa (Fig. 5a). Epifaunal species (*D. coronata*, *P. ariminensis* and *S. vivipara*), shallow infaunal species that are either often (*E. pusillus*) or sometimes (*G. subglobosa*) associated with phytodetritus (Gooday and Lamshead, 1989; Gooday, 1993; Gooday and Hughes, 2002) and taxa typical of high energy environment (*T. angulosa* and *E. carinata*) (Mackensen et al., 1990; Schönfeld, 2002), are the most abundant species in our samples (Table 3 and Fig. 12). Schönfeld et al. (2010) reported that living epifaunal specimens of *D. coronata* and *P. ariminensis* occurred in surface sediment samples collected from Galway Mound. *D. coronata* was also suggested by Margreth et al. (2009) as a useful indicator to identify living CWC facies together with *C. lobatulus* (reported as *Lobatula lobatula*). *S. vivipara*, one of the most abundant 'live' species in our CWC samples, occurs on the Galway Mounds in very low numbers, likely due to the different studied size fraction (> 250 μm in Schönfeld et al., 2010).

The CCA revealed that the quality of organic matter influenced the distribution of the benthic foraminifera. Axis 1 is indicative of the bioavailable organic matter quantity, whereas axis 2 reflects the nutritional quality of the organic matter. The labile carbon content increased towards the negative values of axis 2; a higher content of carbohydrates, generally considered to be refractory compounds (Pusceddu et al., 2009), are suggested by the positive score of

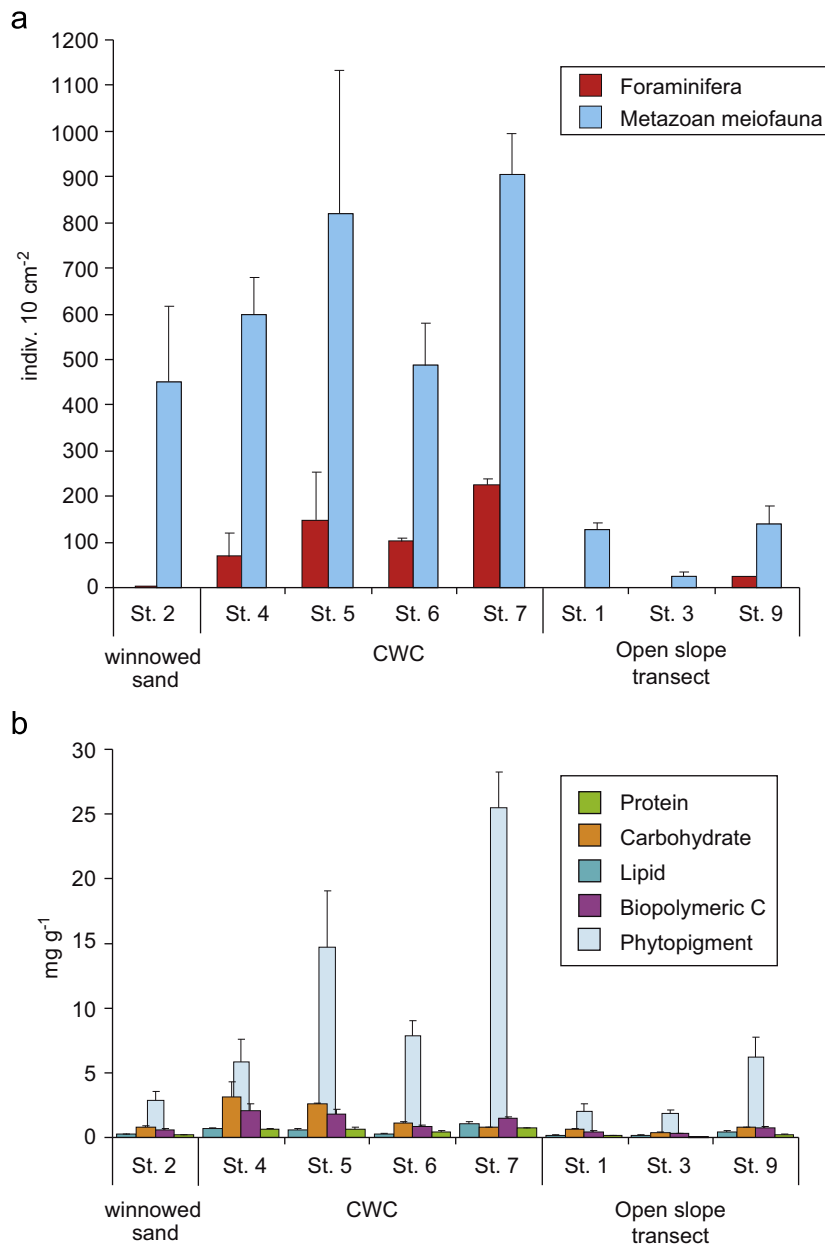


Fig. 9. (a) Abundance of 'live' foraminiferal and metazoan meiofauna (indiv. 10 cm⁻²) in the 8 stations and (b) biochemical composition of organic matter in the sediment (data from Bongiorni et al., 2010) in the 8 stations. Bars indicate standard deviations.

Melonis barleeanus, a species that appears to be adapted to somewhat degraded organic matter (Caralp, 1989). Decreasing values along axis 2 reflect more labile organic matter (a higher content of protein and phytopigments), as indicated also by the increasing proportion of *E. pusillus* and *G. subglobosa* (Gooday and Hughes, 2002; Suhr et al., 2003). *E. pusillus*, known as a phytodetritus species, is common in this part of the Atlantic Ocean, where it colonises and feeds on aggregates of phytodetritus (Gooday, 1993; Gooday and Hughes, 2002). The ecological requirements of *P. challengerii*, *R. spiculifer* and *Saccamminid* sp. 2, which had the highest negative scores on axis 2, are unknown, but we speculate that the abundance of these species may be strongly influenced by the presence of a seasonal phytodetritus input.

Although apparently thriving in the CWC habitat, the hard-shelled species associated with CWC (*D. coronata*, *E. carinata*, *E. pusillus*, *G. subglobosa*, *P. ariminensis*, *S. vivipara* and *T. angulosa*) are also known from other habitats, and therefore do not appear to be endemic to the CWC sites.

4.3. Live/dead ratios

Differences in 'live' and dead assemblages reflect a combination of biological and taphonomic processes. In particular, differences in test production rates, bioturbation by mega and macro-fauna, dissolution of calcareous tests, disintegration of organic tests and agglutinated tests with organic cement, and transport of small-sized tests (Mackensen et al., 1990, 1993; de Stigter et al., 1999; Jorissen and Wittling, 1999; Murray, 2006) can enhance the abundance in the dead assemblage of the more resistant and high productivity species. For example, most of the agglutinated and soft-shelled taxa are absent from the thanatocoenoses. This illustrates the progressive post-mortem destruction of the test due to degradation of the organic cement (e.g., Mackensen et al., 1990, 1993; de Stigter et al., 1999). The dead assemblages from the CWC and the adjacent slope were very different. *C. crassa* and *C. laevigata* were very abundant in the dead faunas, but absent in

Table 8

Comparison of abundance and diversity of foraminiferal microfauna from the Rockall Bank and other open slope and high energy sites.

Area	Water depth (m)	Method	Sieve (μm)	Sample depth (cm)	S (min–max)	N (ind. 10 cm^{-2}) (min–max)	H' (\log_e)	Fisher α	Notes on the study area	Ref.
Bay of Biscay	550–2000	RB	63–150	0–1	39–57	~75–400	na	na	Open slope	Duchemin et al. (2007)
Celtic margin	515–1939	RB	> 150	0–10	19–49	9–231	1.88–3.34	na	Canyon area	Duros et al. (2011)
Rockall Trough	1913–1980	RB	> 63	0–1	158–176	830–2379	na	33–38.5	Bathyal area	Gooday and Hughes (2002)
Portuguese margin	344–927	RB	> 150	0–5	30–54	18–32	na	na	Canyon terrace	Koho et al. (2007)
Portuguese margin	959–1002	RB	> 63	0–1	40–42	40–78	na	na	Open slope	Nardelli et al. (2010)
Gulf of Cadiz	496	RB	250–2000	Uppermost cm	na	2–41	na	na	High energy	Schönfeld (2002)
Galway Mound	810–982	RB	> 250	Uppermost cm	4–33	na	na	4.9–15.7	CWC	Schönfeld et al. (2010)
Rockall bank	567–657	RB	63–1000	0–1	29–61	68–224	1.85–3.71	16–38.1	CWC	This study
Rockall bank	469–1958	RB	63–1000	0–1	0–15	0–25	0–2.39	0.53–15.8	High energy	This study

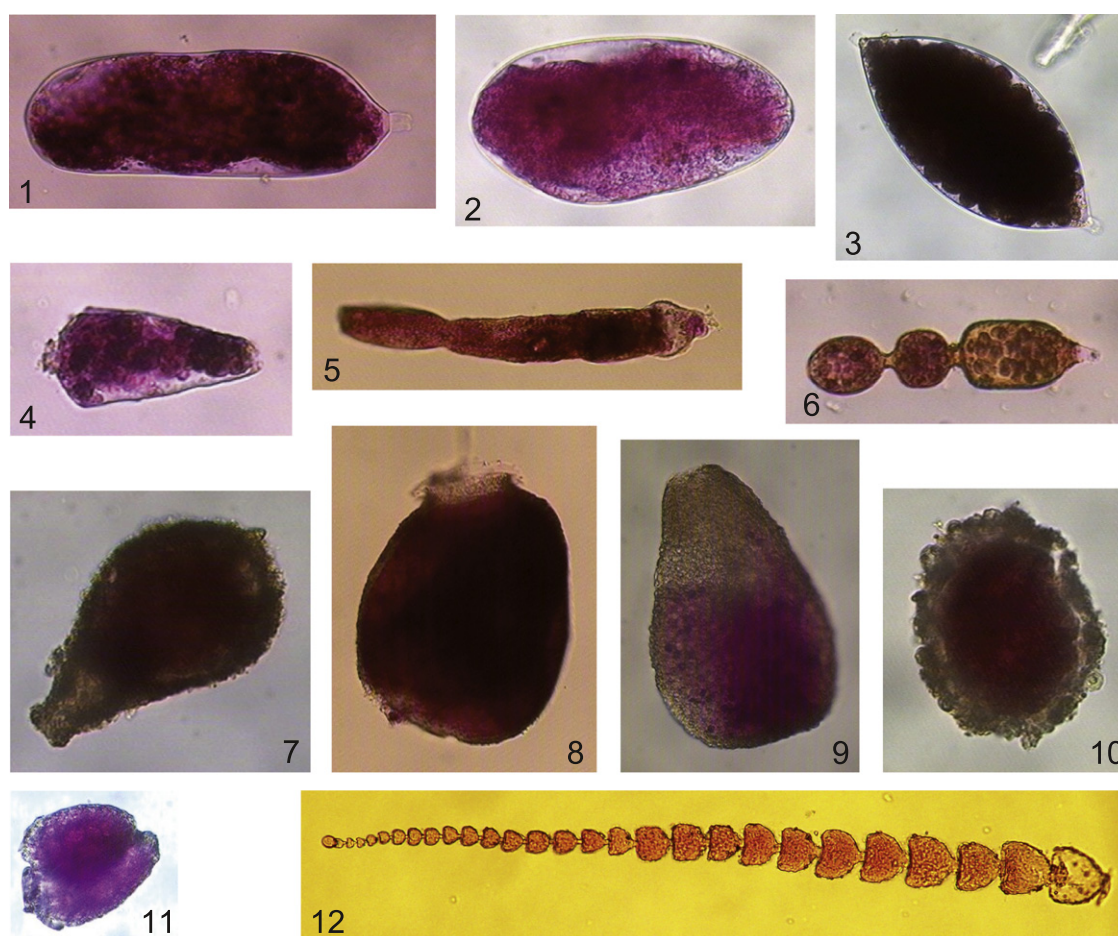
RB=Rose Bengal; S=species richness, N=number of specimens, H' (\log_e)=Shannon–Wiener index, na=not available. (min–max)=minimum and maximum values.

Fig. 10. Soft-shelled foraminifera photographed under a transmitted light microscope. The maximum length is indicated for each specimen. 1. Allogromiid sp. 1 from St. 7 R1, 171 μm ; 2. Allogromiid sp. 9 from St. 5 R3, 155 μm ; 3. Allogromiid sp. A from St. 4 R3, 182 μm ; 4. Allogromiid sp. 11 from St. 6 R2, 75 μm ; 5. *Nodellum*-like from St. 9 R2, 320 μm ; 6. *Resigella polaris* from St. 9 R2, 115 μm ; 7. Saccamminid sp. 5 from St. 4 R2, 132.5 μm ; 8. 'Silver' saccamminid from St. 7 R1, 205 μm ; 9. Saccamminid sp. 2 from St. 5 R1, 180 μm ; 10. Psammosphaerid sp. 2 from St. 4 R3, 100 μm ; 11. *Adercotryma glomeratum* from St. 4 R2, 110 μm ; 12. *Leptohalysis gracilis* from St. 4 R3, 700 μm .

the living assemblages. This reflects opportunistic behaviour leading to rapid test production in these species, which have also been observed to dominate living faunas in other high productivity open slope area (Morigi et al., 2001). As already observed by

Gooday and Hughes (2002) for other cassidulinids, one possible explanation is that the test production in these species occurs later in the summer, perhaps as part of a successional sequence following phytodetritus deposition in spring. *E. pusillus* and

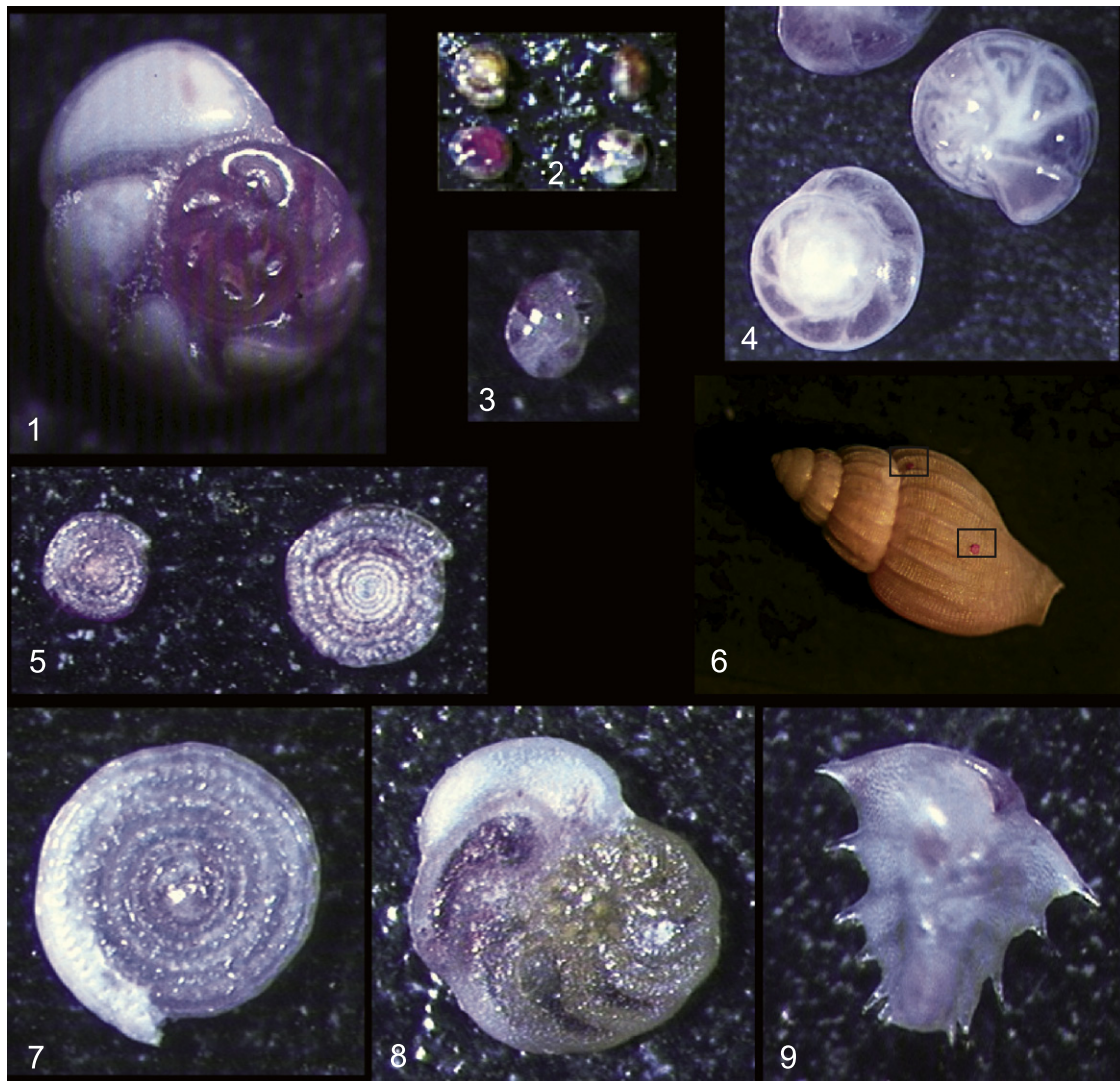


Fig. 11. Calcareous polythalamous foraminifera photographed under a stereomicroscope. The maximum length is indicated for each specimen. 1. *Stomartobina concentrica* from St. 5 R2, 838 μm ; 2. *Eponides pusillus* from St. 4 R3, 106.4–120 μm ; 3. *Globocassidulina oblonga* from St. 4 R2, 186 μm ; 4. *Hoeglundina elegans* from St. 2 R1, 769.5–883 μm ; 5. *Spirillina vivipara* from St. 4 R1, 173–279 μm ; 6. Gastropods with *Spirillina vivipara* from St. 5 R2; 7. *Spirillina grossoperforata* from St. 4 R1, 465 μm ; 8. *Planulina ariminensis* from St. 4 R3, 2 mm; 9. *Ehrenbergina carinata* from St. 4 R3, 505 μm .

E. exigua, which are considered to be proxies for pulsed inputs of organic matter to the sea floor (phytodetritus species) (Gooday, 1993), showed low L/D ratios, suggesting that the bulk of test production is likely concentrated at another time of the year, but that these species maintained their relatively high abundance in the 'live' assemblage, despite considerable fluctuation in absolute numbers. In addition, the high abundance of these species in the dead assemblages indicated that the phytodetrital signal is recorded in the dead fauna. The same high L/D value is shown by *G. subglobosa*. This species has been found living in phytodetrital lumps, but not nearly as often as typical phytodetritus species, such as *E. pusillus* and *E. exigua* (Gooday and Lambshead 1989; Gooday, 1988, 1993).

The dead assemblages from our samples were different from the dead assemblage reported in previous CWC studies (Margreth et al., 2009; Schönfeld et al., 2010). In particular Margreth et al. (2009) found that uvigerinids and cassidulinids displayed the highest abundance in off-mound surface sediment. Uvigerinids are absent in our samples, whereas cassidulinids (*C. crassa* and *C. laevigata*), together with *G. subglobosa*, had higher abundances on-mound in the CWC area. In the case of *C. refulgens*, our results diverge from those of Schönfeld et al. (2010), who found high densities of live

specimens in the sand belt around the CWC mounds and a lower proportion in the dead assemblage. We had exactly the opposite result; specimens of *C. refulgens* were virtually absent in the 'live' assemblage and abundant in the dead assemblages (especially in Sts. 1 and 2). The presence of this suspension feeder in high-energy environments on the open slope and at winnowed stations is consistent with the strong near-bottom currents measured in these areas. We found low percentages of *D. coronata* at the CWC stations, as well as at the two stations around the mound (Sts. 1 and 2), whereas Margreth et al. (2009) and Schönfeld et al. (2010) indicated this to be the most frequent species in the on-mound assemblage. Although not a dominant species, *D. coronata* could be a useful proxy for the CWC habitat if found in association with other epifaunal species (*P. ariminensis* and *S. vivipara*), species associated with high amounts of labile organic matter (*E. pusillus* and *G. subglobosa*), and high energy species (e.g. *T. angulosa*).

4.4. Possible glacial relics?

Large (> 250 μm), typically epibiontic taxa with robust tests (*Rupertia* spp., *Carpenteria* spp. and *C. refulgens*) were present in significant numbers in the dead assemblage at the open slope

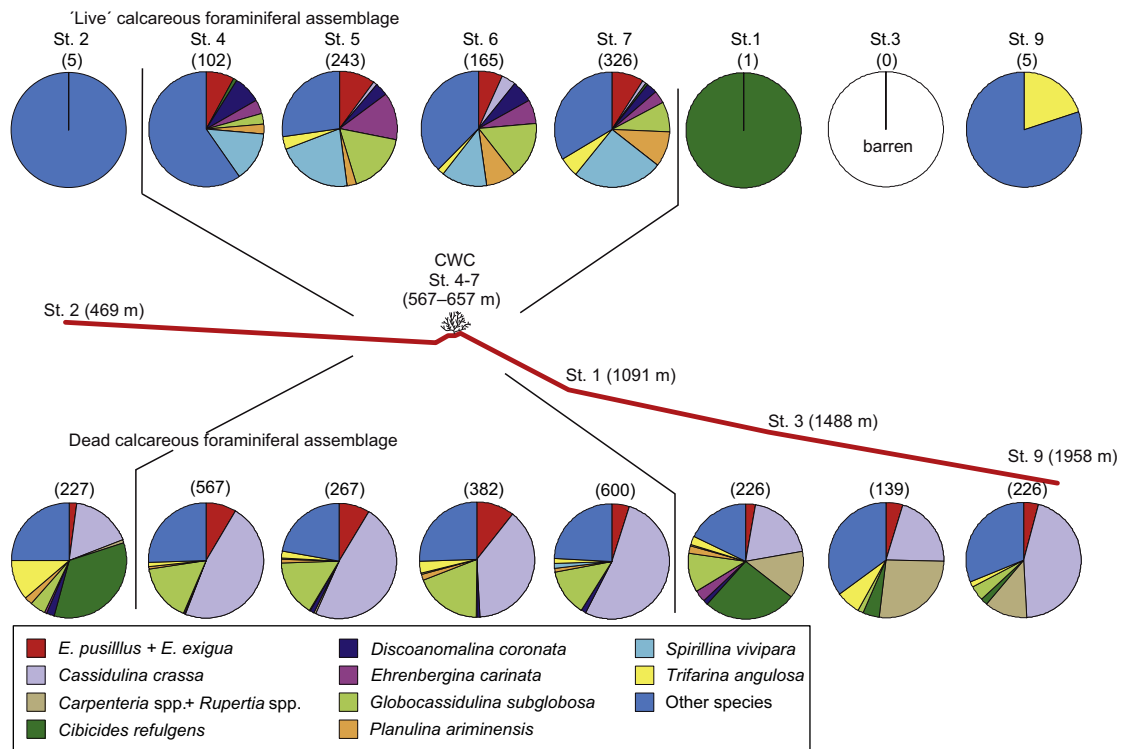


Fig. 12. Distribution of the 10 dominant calcareous perforate foraminiferal species in the 'live' and dead assemblages of the Rockall Bank area. Percentages are calculated based only on the calcareous perforate foraminiferal assemblage. The number in bracket indicates the calcareous specimens counted in each station.

stations (Sts. 1, 3 and to a lesser extent St. 9) but rare or absent at the CWC sites (Fig. 12). The winnowed lag deposit constituting the surface sediment layer at the open slope sites is mainly composed of ice-rafted sediment of glacial age, and planktonic foraminifera from these sites include a considerable percentage of left-coiled *N. pachyderma* (Table 5), which also indicates a glacial origin. It seems likely that the robust epibenthic species, which have poorly preserved tests, represent reworked glacial fauna. This interpretation is strengthened by the fact that no stained specimens of these 3 taxa occurred in the open slope sites. An alternative interpretation is that *Rupertia* spp., *Carpenteria* spp. and *C. refulgens* live attached to stones and other firm substrata, and therefore were missed in the present study, where only the > 63 μm fraction of the first centimetre of sediment was analysed.

5. Conclusions

This study of foraminiferal biodiversity on CWC and open slope sites on the Rockall Bank (NE Atlantic) leads to the following conclusions:

- Sediments at the upper bathyal (567–657 m) CWC sites are characterised by significantly higher foraminiferal abundance and species richness than samples from coarse-grained lag deposits and winnowed sands on the adjacent slope (469–1958 m). Some replicate samples from the open slope sites were even barren of living specimens.
- High-velocity bottom currents at the open slope sites apparently prevent the deposition of fine-grained sediment and organic material, creating a hostile environment that epifaunal and shallow infaunal foraminifera are unable to colonise. In contrast, on carbonate mounds, where CWC framework provides

a sheltered and heterogeneous habitat, foraminiferal assemblages are characterised by high biodiversity and abundance.

- Foraminifera are less abundant than metazoan meiofauna at both the CWC and open slope sites. However, in both the groups, higher abundance and diversity is associated with the presence of CWC.
- No foraminiferal species were endemic to the Rockall Bank. The CWC area is characterised by a combination of epifaunal (*D. coronata*, *P. ariminensis* and *S. vivipara*), shallow infaunal (*E. pusillus*, *A. minimus* and *G. subglobosa*) and high energy (*E. carinata* and *T. angulosa*) species that can be used as indicators of CWC habitat in paleoenvironmental reconstructions.

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Appendix A. Supplementary material

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.dsr.2011.10.004.

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