

BENTHIC FORAMINIFER ASSEMBLAGES FROM NORWEGIAN COLD-WATER CORAL REEFS

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ABSTRACT

Quantitative investigations on the total (living + dead) benthic foraminiferal assemblages were performed on 32 surface-sediment samples (0–2 cm, >63-µm size fraction) from water depths ranging from 110–600 m ("on-reef") to >2000 m ("off-reef") in the Oslo Fjord (Skagerrak Basin), the mid-Norwegian slope (Sula, Røst, and Trænadjupet reefs), and the northern coral-reef areas in Norway (Korallen, LoppHAVet, Stjærnsundet, and Sveinsgrunnen reefs). Seven other samples were investigated for their living (stained) and dead (unstained) assemblages. Hierarchical cluster analysis allows the recognition of five benthic species groups linked to foraminiferal microhabitats from on- and off-reef environments as follows: I) shallow "off-reef" areas of the Oslo Fjord, II) deep-sea >1800-m water depth, and III) bathyal between 800–1800 m, and "on-reef" areas of IV) the Skagerrak and V) the shelf and upper continental slope of the mid- and northern Norwegian margin. The benthic foraminiferal fauna associated with the declining coral reefs in the Oslo Fjord suggests that a low amount of labile organic matter and/or nutrients reach the sea floor making the environment unfavorable for coral growth, reconfirming the previous results on direct measurements of the organic matter. This study indicates that foraminifers can be used as a tool for the characterization of cold-water coral-reef environments.

INTRODUCTION

Cold-water coral (CWC) ecosystems have worldwide occurrences, and along the European margin form widespread reefs. They were first documented from Norway in the 18th century (Pontoppidan, 1755; Linnaeus, 1758). Since these pioneering investigations, CWC reefs have been reported in the Mediterranean Sea (Zibrowius, 1980; Taviani and others, 2005; Margreth and others, 2011), the Gulf of Cadiz (e.g., Pinheiro and others, 2001; Foubert and others, 2008; Wienberg and others, 2009), and along the Irish margin (e.g., Hovland and others, 1994; de Mol and others, 2002; Kenyon and others, 2003; van Rooij and others, 2003) up to northern Norway (e.g., Mortensen and others, 1995; Freiwald and others, 1997; Hovland and others, 1998; Freiwald and others, 1999; Fosså and others, 2002; Lindberg and Mienert, 2005).

Lophelia pertusa (Linnaeus), a colonial, reef-forming scleractinian coral, is one of the dominant species in these ecosystems (Roberts and others, 2009). Along the Irish

margin *L. pertusa* forms large coral carbonate mounds, which originated in the late Pliocene/early Pleistocene (de Mol and others, 2002; Kano and others, 2007). On the Norwegian continental shelf, since the end of the last glacial stage at ~10,900 ka (López Correa and others, 2012), *L. pertusa* has built elongated reef-like structures on elevated hard substrates that can reach heights of 40 m and lengths of several km (Freiwald and others, 1997, 1999, 2002; Lindberg and others, 2007). Here cold-water-coral distribution is controlled by pre-existing topographic highs on the sea floor, such as moraine ridges and iceberg plough-mark levees (Freiwald and others, 1999, 2002; Mortensen and others, 2001; Fosså and others, 2005). Living corals colonize the top and the upper slopes of the highs, developing reefs, and preferentially occur at water depths between 150–400 m with the exception of a few shallower occurrences in fjord settings. In situ dead corals are generally present along the steep reef flanks, while bio-eroded coral rubble accumulates around their bases.

These reefs provide abundant and diverse microhabitats for benthic organisms (Mortensen and others, 1995) compared to the surrounding coral-free environments (Henry and Roberts, 2007). This is especially true for suspension and filter feeders (e.g., sponges, mollusks, brachiopods, cnidarians, bryozoans, ophiuroids, and crinoids; Mortensen and others, 2001). Foraminiferal assemblages associated with these ecosystems are not well known.

Freiwald and Schönfeld (1996) described the carnivore species *Hyrrokkin sarcophaga* Cedhagen feeding on polyps of *L. pertusa*. Hawkes and Scott (2005) described the foraminiferal assemblage of CWCs near the Nova Scotia peninsula, Canada. They found that *Discanomalina semipunctata* Asano is consistently abundant on the coral but uncommon on the margin itself, making it a possible indicator of past cold-water coral *Primonnoa resedaeformis* (Gunnerus) habitat. Recent studies on CWC mounds in the Rockall Bank and the Porcupine Seabight have shown that numerous epifaunal, benthic foraminiferal species colonize these habitats (Rüggerberg and others, 2005, 2007; Margreth and others, 2009; Schönfeld and others, 2011) and that the benthic species *Discanomalina coronata* (Parker and Jones) is generally associated with living CWC reefs (Margreth and others, 2009) or coral rubble in the reefs (Schönfeld and others, 2011). The latter authors documented that the foraminiferal diversity on the Porcupine Seabight (Galway and Propeller mounds) was no higher than in adjacent areas at 500–1300-m water depth.

This study focuses on benthic CWC foraminiferal assemblages in different on- and off-reef localities from northern Norway south to the Oslo Fjord (Fig. 1) and compares those occurrences with results from the Rockall Bank and Porcupine Basin off Ireland.

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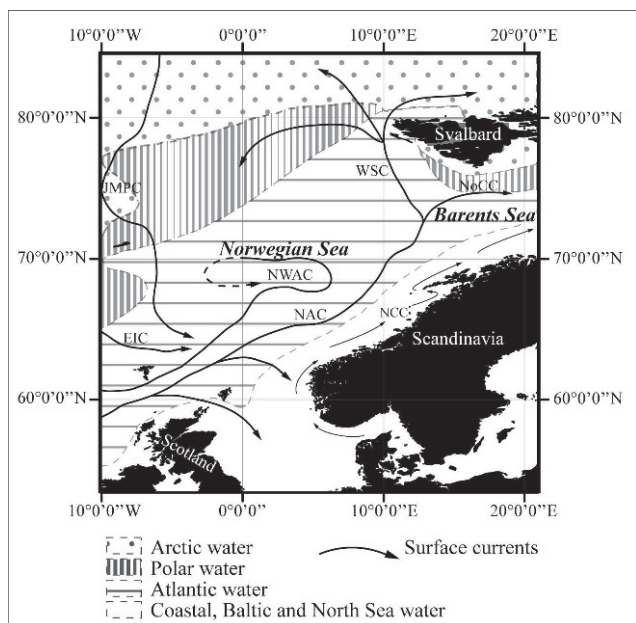


FIGURE 2. Circulation pattern in the North Atlantic and along the Norwegian margin. Currents in the Norwegian Sea and the surrounding seas modified from Yndestad and others (2008); water masses according to Mosby (1968). Surface currents: East Icelandic Current (EIC), Jan Mayen Polar Current (JMPC), North Atlantic Current (NAC), Norwegian Coastal Current (NCC), North Cape Current (NoCC), Norwegian Atlantic Current (NWAC), West Spitsbergen Current (WSC).

MATERIALS AND METHODS

Samples were collected at a relatively wide range of water depths, between 170–330 m at the northern coral reefs (Korallen, Stjærnsundet, Lophavet, and Sveinsgrunnen), between 300–2100 m on on- and off-reef sites at the mid-Norwegian margin (Sula Reef, Røst Reef, and Trænadjupet), and between 90–300 m in the Oslo Fjord (Table 1; Figs. 1, 2). The grab sampler operated by the submarine JAGO, a Giant Box corer, and Van-Veen grab were used to sample during six different cruises (Table 1). These cruises were not focused on sampling for foraminifers, and samples were not stained with rose Bengal or fixed in preservative. Only the seven samples recovered during cruise Poseidon 391, when part of the cruise was devoted to foraminifer sampling, were preserved in a 2 g l⁻¹ rose Bengal (stained) >70% ethanol mixture (Table 1), and their volume defined in the laboratory. Norwegian reefs are protected, and sampling with standard methods such as a box corer is forbidden. Thus, these seven samples from the uppermost 2 cm of sediment in between coral branches were retrieved with a special submarine-operated small sampler especially developed on board to avoid reef damage. When small pieces of coral branches were present in samples, benthic foraminifers were removed with a brush and stored.

Samples were dried at room temperature, weighed, and washed over a 63-µm sieve. The 32 unstained samples were investigated for their total (living + dead) foraminiferal content. The seven stained samples were investigated also for their unstained (dead) and stained (living) assemblages following Alve and Murray (1995). Each sample was split

to obtain at least 500 specimens. If a sample contained fewer specimens, all were counted. Stained specimens were counted separately from unstained. Video records obtained by a Remotely Operated Vehicle (ROV) and images taken with the submersible JAGO were used to characterize the seafloor.

To identify significant differences in foraminiferal assemblages, multivariate statistical analysis was performed on the quantitative foraminiferal data provided in Appendix I with the PRIMER software (version 6.1.9; Clarke, 1993). Relative percent abundance of foraminifers has been double square-root transformed to limit the contribution of the most abundant, ubiquitous species and simplify the interpretation (Field and others, 1982). The resulting similarity matrix was used to obtain the non-metric Multidimensional Scaling (nMDS) plot (Kruskal, 1964). Similarity Percentage Analysis (SIMPER) was obtained to highlight the contribution of each species to the total average (dis-) similarity between different groups and within one group (e.g., Kruskal, 1964).

RESULTS

SURFACE SEDIMENTS

Observations from the submersible JAGO, ROV underwater imaging, and the recovered sediments contributed to differentiate five sedimentary facies. Their descriptions integrated with the previous ones of Mortensen and others (1995, 2001), Freiwald and others (2002), and Rüggeberg and others (2011) are summarized in Table 2 and represented in Figure 3.

BENTHIC FORAMINIFERA

Two hundred and thirty benthic species were identified (Appendix 1). Their distribution along a bathymetric transect of four “on-reef” and five “off-reef” stations across the mid-Norwegian shelf at 67°N is shown in Figure 4. The hierarchical cluster analysis dendrogram shows clusters I–V separating at 50% of the Bray-Curtis Similarity (Fig. 5). Cluster I includes “off-reef” samples from the Oslo Fjord (northern Skagerrak Basin, 287–326-m water depth). Cluster II includes the deepest bathyal and abyssal samples from the mid-Norwegian continental slope (1824 m, 2098 m). Cluster III includes shallower bathyal samples from the mid-Norwegian slope (889–1514 m). Cluster IV includes “on-reef” samples from the Oslo Fjord (91–140 m), and Cluster V includes samples from the reefs on the shelf and on the upper continental slope in the Norwegian Atlantic (278–761 m).

DISCUSSION

DIFFICULTIES AND LIMITATIONS

During the processing of samples some limitations were encountered, which had to be considered before data interpretation. Many samples were received dry; thus assessment of living assemblages was not possible. Dead assemblages represent the mixing of tests from a succession of previously living assemblages that have been modified by taphonomic processes (Murray, 2000), and reflect

TABLE 1. List of samples (number and name), collecting device, geographic coordinates, water depth, region, mound region, facies, and species number for stained and unstained samples used for the foraminiferal study. Hermi = Hermione cruise, POS = RV *Poseidon*, PS = RV *Polarstern*, AL = RV *Alkor*.

Sample no.	Sample/cruise name	Collecting device	Latitude N	Longitude E	Depth (m)	Region	Facies	No. of species (unstained)	No. of species (stained)
1	Hermi-1-1	Grab	70°27.71	21°12.77	300	Lopphavet	<i>coral-rubble</i>	50	-
2	POS325 455	Giant box corer	70°16.13	22°29.46	270	Stjærnsundet	<i>coral-rubble</i>	49	-
3	PS70/011-1	Giant box corer	69°44.21	16°33.27	327	Sveinsgrunnen	<i>coral-rubble</i>	56	-
4	PS70/023-3	van Veen Grab	66°58.12	11°07.79	324	Trænadjupet	<i>coral-rubble</i>	50	-
5	PS70/002-2	Giant box corer	67°30.40	9°25.55	304	Røst Reef	<i>sediment-clogged coral framework</i>	55	-
6	PS70/029-3	Giant box corer	67°35.23	9°28.92	604	Røst Reef	<i>pebbly sand</i>	54	-
7	PS70/028-2	Giant box corer	67°38.05	9°26.98	761	Røst Reef	<i>pebbly sand</i>	39	-
8	PS70/037-2	Giant box corer	67°35.15	9°19.22	889	continental slope	<i>mud (deep)</i>	39	-
9	PS70/038-2	Giant box corer	67°37.77	9°10.30	1214	continental slope	<i>mud (deep)</i>	34	-
10	PS70/039-2	Giant box corer	67°40.15	9°03.00	1514	continental slope	<i>mud (deep)</i>	35	-
11	PS70/033-2	Giant box corer	67°43.00	8°55.00	1824	continental slope	<i>mud (deep)</i>	37	-
12	PS70/032-2	Giant box corer	67°52.22	8°30.72	2098	continental slope	<i>mud (deep)</i>	24	-
13	AL316-320	van Veen Grab	64°06.30	8°04.80	296	Sula Reef	<i>pebbly sand</i>	31	-
14	AL316 321	van Veen Grab	64°05.88	8°05.35	278	Sula Reef	<i>coral-rubble</i>	35	-
15	AL 232 1022	Giant box corer	58°59.88	10°57.80	91	Oslo Fjord	<i>coral-rubble</i>	55	-
16	AL 232 1025	Giant box corer	58°25.88	10°31.05	326	Oslo Fjord	<i>mud (shallow)</i>	47	-
17	AL 232 1026	Giant box corer	58°27.75	10°30.31	287	Oslo Fjord	<i>mud (shallow)</i>	36	-
18	AL 232 1155	Giant box corer	59°04.71	10°43.90	106	Oslo Fjord	<i>sediment-clogged coral framework</i>	49	-
19	POS 391 534-1	van Veen Grab	70°55.26	22°10.71	214	Korallen	<i>pebbly sand</i>	33	-
20	POS 391 535-1	van Veen Grab	70°55.14	22°11.26	201	Korallen	<i>coral-rubble</i>	39	-
21	POS 391 539-1	van Veen Grab	70°56.09	22°11.00	247	Korallen	<i>pebbly sand</i>	19	19
22	POS 391 544-2	van Veen Grab	70°56.03	22°12.35	172	Korallen	<i>coral-rubble</i>	32	32
23	POS 391 550-1	JAGO Grab	70°26.72	21°10.36	233	Lopphavet	<i>living coral framework</i>	54	-
24	POS 391 555-1	van Veen Grab	70°26.58	21°10.01	232	Lopphavet	<i>coral rubble</i>	46	-
25	POS 391 556-2	van Veen Grab	70°26.64	21°11.61	320	Lopphavet	<i>coral rubble</i>	37	22
26	POS 391 558-1	van Veen Grab	70°28.29	21°11.48	330	Lopphavet	<i>pebbly sand</i>	52	-
27	POS 391 559-1	van Veen Grab	70°26.93	21°11.10	230	Lopphavet	<i>pebbly sand</i>	42	32
28	POS 391 562-1	van Veen Grab	64°04.40	08°01.20	287	Sula Reef	<i>coral-rubble</i>	55	-
29	POS 391 567-1	JAGO Grab	59°06.78	10°47.46	140	Oslo Fjord	<i>sediment-clogged coral framework</i>	47	-
30	POS 391 570-2	van Veen Grab	59°05.62	10°47.95	110	Oslo Fjord	<i>coral-rubble</i>	51	32
31	POS 391 571-1	JAGO Grab	59°05.96	10°47.67	117	Oslo Fjord	<i>living coral framework</i>	59	18
32	POS 391 584-1	Giant box corer	59°03.96	10°48.37	290	Oslo Fjord	<i>mud (shallow)</i>	38	11

TABLE 2. Description of facies identified in a typical cold-water coral reef at LoppHAVet, northern Norway (N), compared with facies identified in the Porcupine Basin (PB).

Facies type	Description	Position in reef	Samples
<i>Living coral framework (N) = living coral facies (PB)</i>	Large deposits of dead <i>L. pertusa</i> (up to 2-m thick), with living corals at their periphery. Living corals are white or orange and covered by translucent mucus.	Top of the CWC reefs	23, 31
<i>Sediment-clogged coral framework (N) = sand wave and dead coral facies (PB)</i>	The in situ and dislocated coral framework is filled with silty clay or sandy deposits enriched in skeletal elements of bivalves and bio-eroded organisms.	Slopes	5, 18, 29
<i>Coral rubble (N) = dead coral facies (PB)</i>	Dead coral debris with trapped mud and silt. It appears as a detrital soft-sediment substratum with remains of mollusks and echinoids. Coral debris is thinner and finer away from the reef.	Lower flanks and/or at the base of the living reefs. Inclination generally between 5°–25°	1–4, 14, 15, 20, 22, 24, 25, 28, 30
<i>Pebbly sand (N) = sand wave and dropstone facies (PB)</i>	Sandy-silty sediments, sometimes rippled and containing dropstones. Bryozoans, mollusks, and coral fragments may be present.	Transitional area between the external reef facies and the “off-reef” mud-facies	6, 7, 13, 19, 21, 26, 27.
<i>Mud facies (deep) (N) = off-mound facies (PB)</i>	Fine-grained hemipelagic sediments with abundant foraminifers, echinoids, mollusks, and various terrigenous components.	Water deeper than 800 m off the mid-Norwegian shelves and influenced by the NSDW	8–12
<i>Mud facies (shallow) (N) = off-mound facies (PB)</i>	Fine-grained sediments containing foraminifers, echinoids, mollusks, and various terrigenous components. A color change marks the boundary between the thin oxygenated surface layer and the underlying dysoxic sediments.	Oslo Fjord (Skagerrak)	16, 17, 32

time-integrated environmental conditions commonly spanning several years (e.g., Bouchet and others, 2012). Therefore, in this case the total fauna may be considered as a good time-averaged assemblage (e.g., Saher and others, 2009).

The sampling procedure for the present study was hindered because grab or box-core sampling in living coral facies is forbidden for conservation reasons (Fosså and others, 2002). Only seven small samples from the reefs could be taken specifically for foraminiferal studies and were available for protoplasmic staining.

To identify living foraminifers rose Bengal was used to stain the cytoplasm (Walton, 1952). Although used in many ecological studies, its limitations are well-known. Rose Bengal is a protein stain that can be degraded slowly under certain circumstances (e.g., anoxic environments); thus, the living assemblages may be sometimes overestimated (Schönfeld and others, 2012). However, for the time being this procedure remains the most useful to identify living foraminifers (see Jorissen and others, 2007, and Schönfeld and others, 2012).

Since most samples were received already dried, monothalamous and soft-shelled foraminiferal species (e.g., Gooday and Hughes, 2002) are not considered in this study even if they are important assemblage components. Although some authors have also found that abyssal agglutinated foraminifer tests may be destroyed after drying (Schröder and others, 1988; Klitgaard Kristensen and others, 2002), Bouchet and others (2012) demonstrated that a significant positive correlation exists between the diversity of wet-picked and dry-picked assemblages from the Skagerrak (Oslo Fjord).

COLD-WATER CORAL ECOSYSTEMS

Cold-water corals occur exclusively in environments characterized by strong currents (e.g., Frederiksen and others, 1992; Freiwald and others, 2002; Rüggeberg and others, 2007) and input of large amounts of organic matter

in the form of phytoplankton detritus (Duineveld and others, 2004). The strong currents transport food to the coral polyps and prevent them from getting smothered by fine sediment (Duineveld and others, 2004; Freiwald and others, 2004; Thiem and others, 2006; White, 2007). The organic matter feeds the zooplankton, which is also a main food source for CWCs in the form of fresh and labile organic matter (Mortensen, 2001; Freiwald and others, 2002; Duineveld and others, 2007). Lateral advection and/or resuspension of fresh particles derived from production higher on the bank represent an additional food source for corals (Frederiksen and others, 1992; White and others, 2005; Duineveld and others, 2007).

Table 3 summarizes some of the most important parameters measured in Porcupine Seabight, Rockall Bank, the Norwegian margin, and Oslo Fjord. It shows that on the Norwegian continental margin and shelf conditions for cold-water-coral ecosystem development are generally met and are consistent with those in other North Atlantic cold-water coral sites. The modern plankton blooms and high nutrient transport caused by seasonal upwelling and eddies contribute to the high primary production at the surface, which contributes to high food flux to the sea floor. All cold-water coral sites in the North Atlantic have comparable current velocities, with mean values between 7–15 cm/s and temporary peaks up to 45 cm/s, and good bottom-water oxygenation.

AUTECOLOGY OF BENTHIC FORAMINIFERS

Benthic foraminifers show conspicuous patterns of habitat segregation in virtually all marine basins (e.g., Mackensen and others, 1985). The reason for this partitioning is a combination of many ecological parameters such as temperature, salinity, hydrodynamics, oxygen concentration of bottom waters, organic matter flux in different environments, and substrate (e.g., Sen Gupta, 1999; van der Zwaan and others, 1999; Gooday,

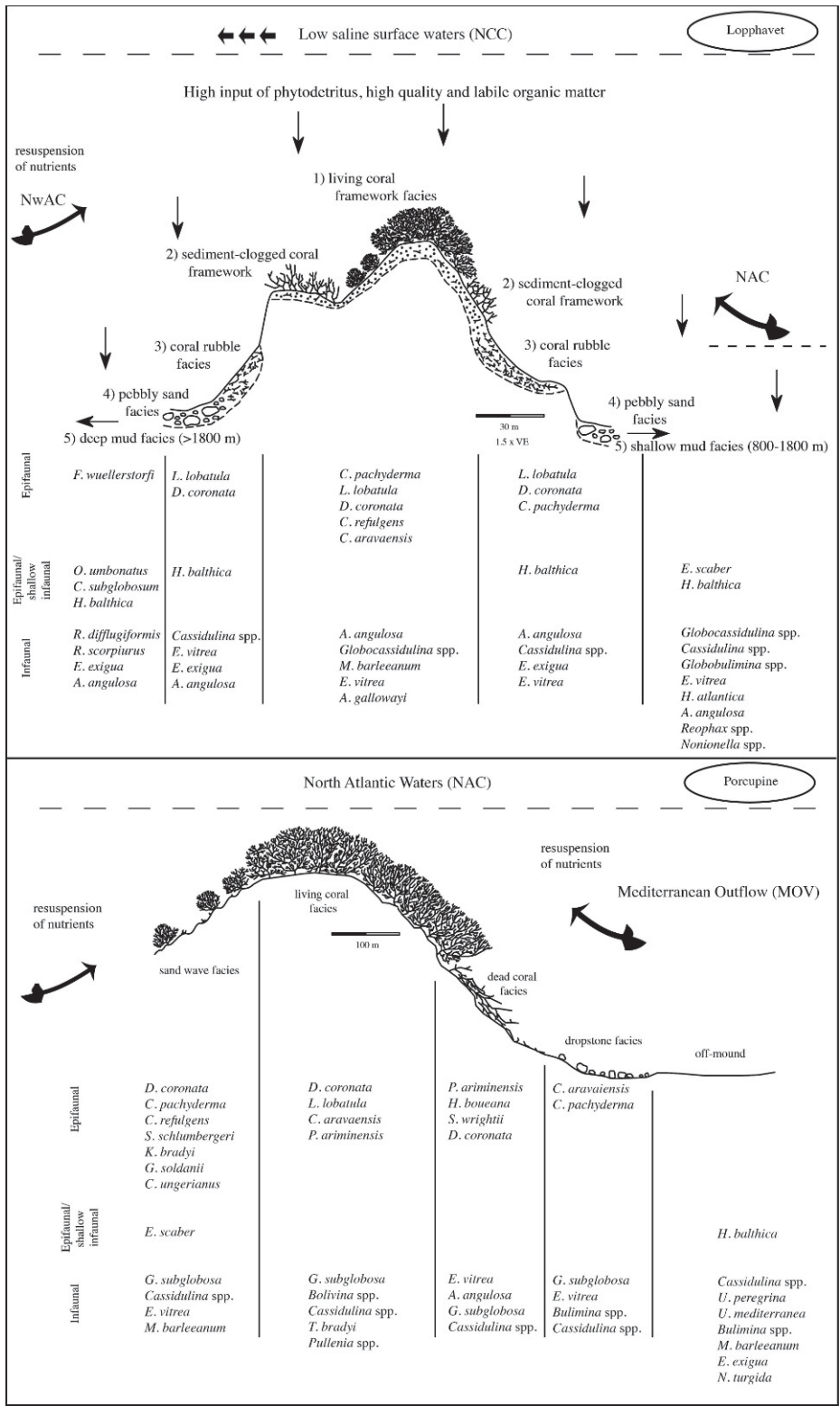


FIGURE 3. Models and distribution of benthic foraminifers on a typical cold-water coral reef at Lopphavet, northern Norway (facies model from Freiwald and others, 2002), and on cold-water coral mounds in the Porcupine Basin (modified after Margreth and others, 2009). Interpretation derived from literature data and direct observation from the submersible JAGO, GEOMAR, Kiel, Germany.

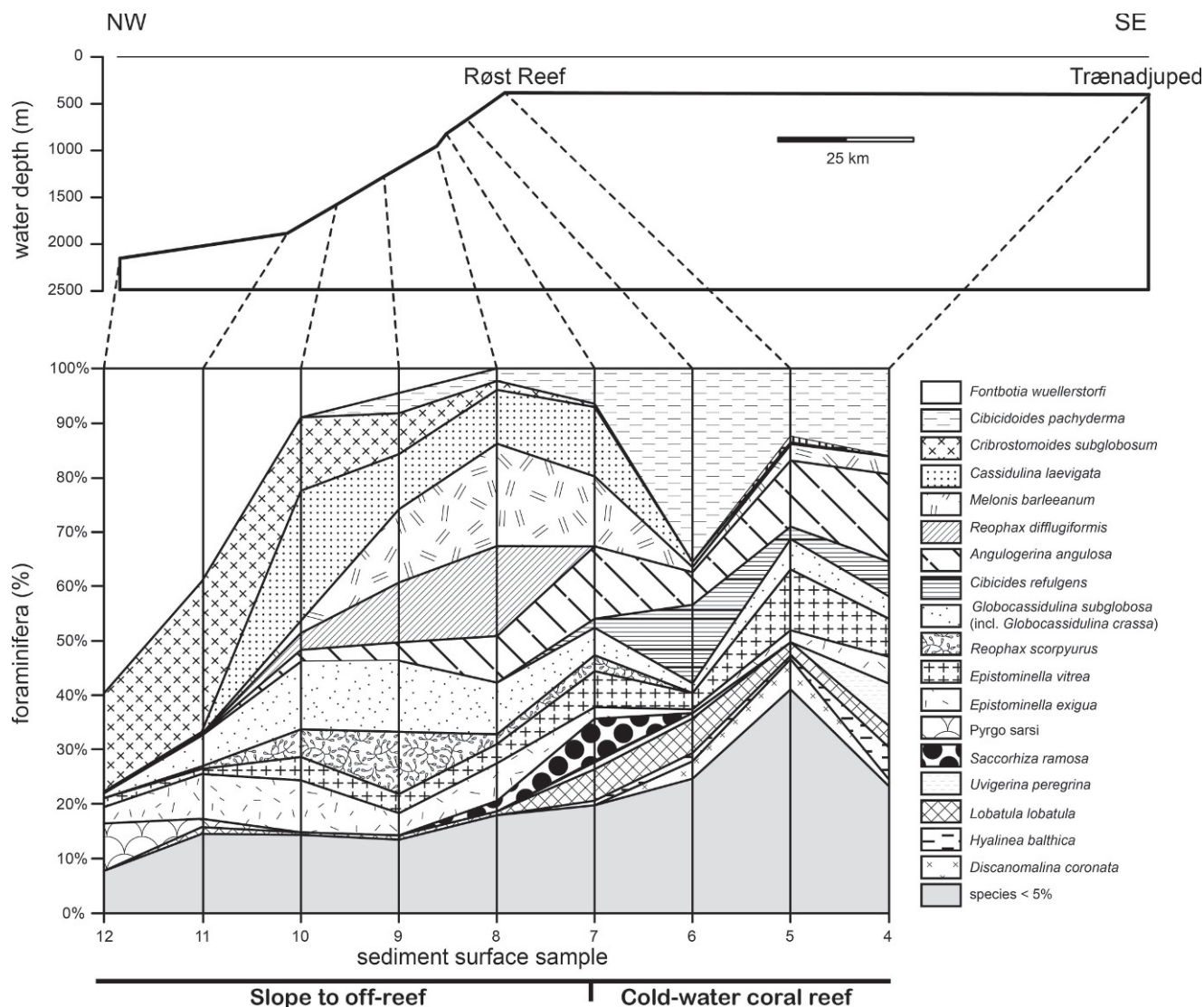


FIGURE 4. Percent distribution of the most abundant benthic foraminiferal species (>5%) along a bathymetric transect across the mid-Norwegian shelf at 67°N comprising five off-reef stations (11 and 12, Cluster II; 8–10, Cluster III) and four reef associated stations (4–7, parts of Cluster V).

2003; Murray 2006). A summary of the autecology of selected benthic foraminifer species is given in Table 4.

CHARACTERIZATION OF “ON-” AND “OFF-REEF” SITES

Distribution patterns of benthic foraminifers from CWC ecosystems along the Norwegian margin are here linked to temperature, substrate, surface productivity, facies, hydrodynamic system, surface water conditions, and organic-matter fluxes. Schönfeld and others (2011) found that benthic foraminifer diversity is similar on carbonate mounds and in adjacent areas in the Porcupine Seabight and that the distribution of some species such as *Cibicides refulgens* de Montfort, *Discanomalina coronata*, and *Uvigerina mediterranea* Hofker is controlled by their specific ecological demands and microhabitat availability. The statistical treatment of our data clearly shows that benthic foraminiferal assemblages from Norwegian “off-reef” sites are different from “on-reef” sites and have lower diversity (Table 1, Fig. 3).

Clusters I–III group samples from the “Mud Facies” (deep and shallow) are characterized by fine-grained bioclastic and terrigenous sediment (Figs. 5a, b). Cluster I groups samples come from the shallow facies within the Skagerrak Basin in the Oslo Fjord. This region is the major sink for fine-grained sediments derived from the North Sea (e.g., van Weering and others, 1987; Kuijpers and others, 1993; Rodhe and Holt, 1996), and is generally bathed by Atlantic waters (Fig. 2). Dominant in Cluster I are infaunal species *Globobulimina affinis* (d’Orbigny), *Eggerelloides scaber* (Williamson), *Hyalinea balthica* (Schröter), *Bigenerina cylindrica* (Cushman), *Textularia earlandi* Parker, *Bulimina marginata* d’Orbigny, *Stainforthia fusiformis* (Williamson), *Melonis* spp., and *Bolivina* spp. This assemblage is tolerant of dysoxic conditions and may also feed on low quality and refractory organic matter (Fontanier and others, 2003, 2005, 2008; Murray, 2003, 2006; Alve, 2010; Alve and Goldstein, 2010; Table 4). It suggests an environment characterized by high organic-matter flux and low oxygenation, indicating that oxygenated Atlantic

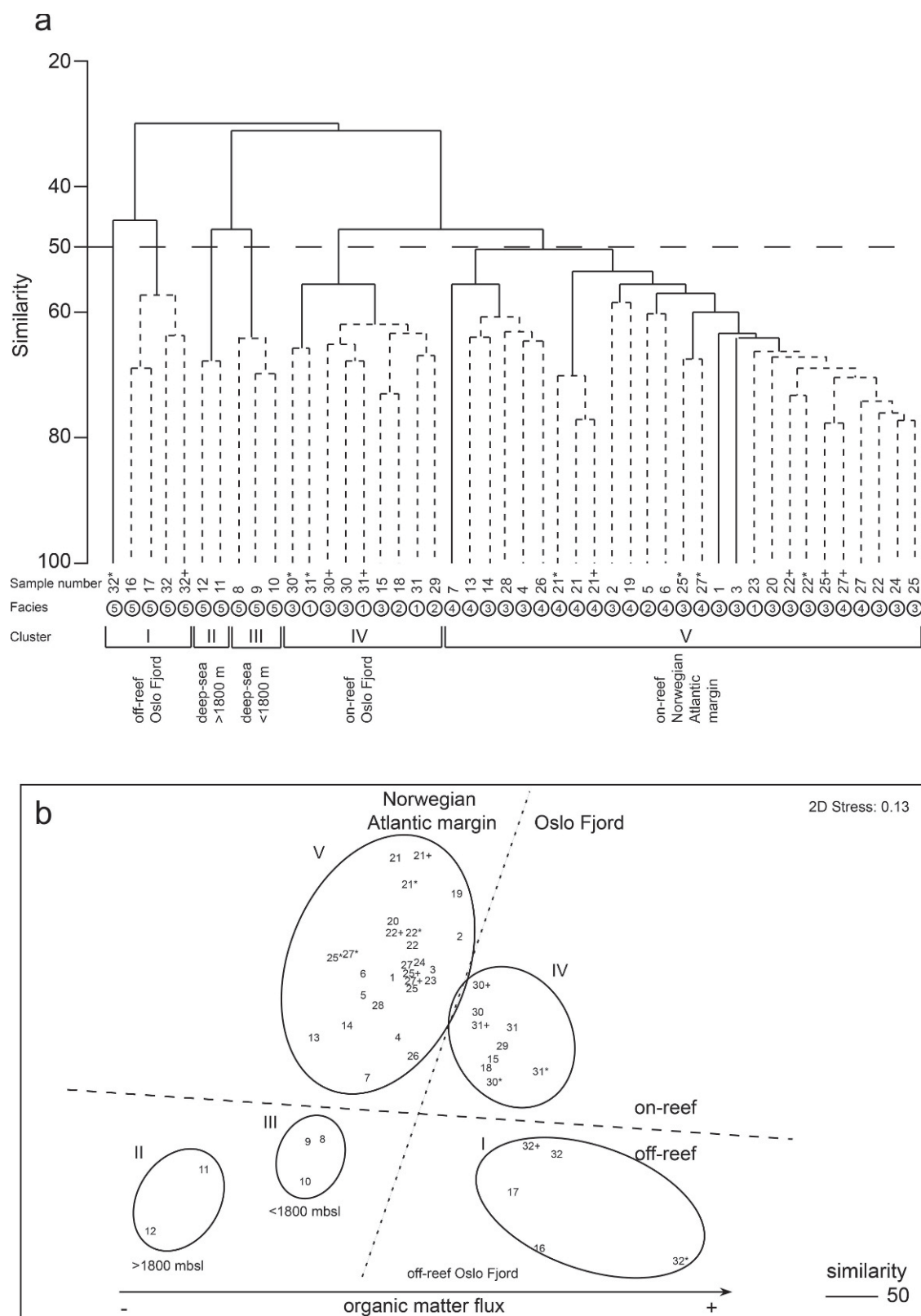


FIGURE 5. a) Hierarchical Cluster Analysis based on the Bray-Curtis similarity matrix of benthic foraminifers compositional data. Clusters I–V separate at 50% Bray-Curtis Similarity. Dashed lines indicate non-significantly differing samples (SIMPROF $p > 0.05$). Non-metric MultiDimensional Scaling (nMDS) ordination obtained from Bray-Curtis similarity matrix of benthic foraminifers compositional data. The three off-reef clusters are ordered according to the “organic matter gradient” as indicated at the bottom. Lower in Cluster II (>1800 m) and higher in Cluster I (Oslo Fjord). Samples marked with * = stained (living), + = unstained (dead).

TABLE 3. Oceanographic parameters that influence the cold-water coral ecosystems in the North Atlantic according to the most recent literature.

Parameter	Porcupine Seabight	Rockall Bank	Norwegian margin	Oslo Fjord—Skagerrak	Reference
Temperature (°C)	9.24–9.89	(6.2)8.57–9.28(9.8)	(6.2)8.57–9.28(9.8)	6.5–8.5	Alve and Murray (1995); Mienis and others (2007); Rüggeberg and Form (2007); Dullo and others (2008); Flögel and others (2011); Rüggeberg and others (2011); Wagner and others (2011)
Salinity	35.29–35.57	35.13–35.4	34.9–35.2	35.1–35.4	Mortensen (2001); Mienis and others (2007); Dullo and others (2008); Flögel and others (2011); Rüggeberg and others (2011); Wagner and others (2011)
Dissolved oxygen (ml/l)	3.76–4.60	4.57–.18	6.52–6.64	6.3–6.6	Alve and Murray, (1995); Dullo and others (2008)
Organic matter—type and/or amount	fresh particles	available to benthic consumers = 1.54 C mg g ⁻¹ in the CWC area	no data	mostly refractory at 280 m	Dauwe and Middleburg (1998); Krönke and others (2004); Morigi and others (2012)
Current velocity (cm/s)	9–30, mean 8–10	≤45 mean 10–15	7–44 at Sula	30 cm/s at depths <100 m, lower (<10 cm/s) in deeper parts	Eide (1979); Larsson and Rodhe (1979); Alve and Murray (1995); Duineveld and others (2007); Mienis and others (2007, 2009); Morigi and others (2012)
δ ¹⁵ N of <i>L. pertusa</i> /feeding strategy	8.6–8.8 = corresponding to filter feeding; predation observed in laboratory	8.7± 0.2 = corresponding to filter feeding; predation observed in laboratory	filter feeding	no data	Mortensen (2001); Duineveld and others (2007); van Oevelen and others (2009)
Surface productivity	phytoplankton blooms	induced by wind-mixing nutrient upwelling	phytoplankton blooms	high and human induced	Berner and Wefer (1994); Alve and Murray (1995); Sætre (1999); Lampitt and others (2001); Mitchelson-Jacob and Sundby (2001); White and others (2005); Duineveld and others (2007)

waters do not reach this part of the Oslo Fjord and/or that the dysoxic layer in the sediment is close to the sea surface.

Cluster II group samples come from a water depth >1800 m. This region is influenced by the NSDW and AwAC, which are generally well oxygenated with >87% saturation (Svansson, 1975; Bakker and Helder, 1993) and enter the Oslo Fjord in its deeper part (~200 m; e.g., Alve and Murray, 1997). However, at the location sampled a bathymetrically guided flow of the NSDW onto the inner shelf enables coral colonization between 90–140 m. Assemblages are dominated by *Fontbotia wuellerstorfi* (Schwager), *Cribrostomoides subglobosum* (Cushman), *Oridorsalis umbonatus* (Reuss), *Pyrgo sarsi* (Schlumberger), *H. balthica*, *Reophax* spp., and *Epistominella exigua* (Brady) (Table 5; Figs. 3, 5). Based on the ecology of these benthic foraminifers (Table 4), this cluster possibly indicates a nutrient-poor deep-sea environment, which may be influenced by strong currents (*F. wuellerstorfi*), cold waters (*H. balthica*), and periodic pulses of fresh phytodetritus to the sea floor (*F. wuellerstorfi*, *E. exigua*, *Reophax* spp.).

Cluster III group samples come from the continental slope between 800–1800-m water depth. Dominant foraminifers include *Globocassidulina subglobosa* (Brady), *E. exigua*, *Cassidulina laevigata* d'Orbigny, *Cassidulina* spp., *Reophax* spp., *Melonis barleeanum* (Williamson), and rarer *C. subglobosum* (Table 5; Figs. 3, 5). Benthic assemblages of this cluster suggest high nutrient input possibly related to periodic pulses of phytodetritus.

Cluster IV group samples are from the coral reefs in the Oslo Fjord. Dominant are *Lobatula lobatula* (Walker and Jacob), *Cassidulina* spp., *Melonis* spp., *Cibicidoides pachyderma* (Rzehak), and *B. marginata*. This cluster suggests

environments with strong bottom currents, high oxygen levels, and an elevated organic matter flux to the sea floor (Table 4).

Cluster V groups samples include the Atlantic Norwegian CWC reefs. The benthic foraminiferal fauna is dominated by *C. pachyderma*, *Globocassidulina* spp., *D. coronata* (Fig. 6), *C. refulgens*, *L. lobatula*, *Angulogerina angulosa* (Williamson), *M. barleeanum*, and *Epistominella vitrea* Parker. This cluster seems to indicate an environment characterized by strong bottom currents, elevated oxygen levels, and a high flux of organic matter including phytodetritus. Both Clusters IV and V apparently represent similar on-reef environments, characterized by varying abundances of epifaunal species (e.g., *L. lobatula*, *C. refulgens*, *C. pachyderma*).

The clustering of samples in separate areas of the MDS ordination suggests that conditions in the Oslo Fjord are different from those along the rest of the Norwegian margin. Direct observations from the JAGO submersible showed extensive living-reef complexes on the Norwegian margin (Freiwald and others, 2004; and authors' personal observations). However, cold-water coral ecosystems in Oslo Fjord, consisting only of small patches of living *L. pertusa* surrounded by muddy and sandy off-reef sediments, indicate that conditions for the growth of CWCs are probably not optimal.

The abundance of dead corals in the Oslo Fjord may be due to the nature of the organic matter. Kiriakoulakis and others (2008) showed that cold-water corals feed on high quality organic matter with elevated proportions of essential nutrients composed mainly of fresh and unaltered phytoplankton remains. Mortensen (2001) demonstrated

TABLE 4. Autecology of selected species of benthic foraminifera encountered in this study.

Species	Facies	Preferred substrate	Living strategy	Feeding strategy/ preference	Oxygen	Other ecological preferences	References
<i>E. exigua</i>	deep mud and pebbly sand facies	mud	infaunal	fresh phytodetritus feeder, seasonal food fluxes	—	opportunistic, tolerant of varying organic flux, low energy	Goody (1988, 1994); Smart and others (1994); Thomas and others (1995); Thomas and Goody (1996); Loubere and Fariduddin (1999)
<i>E. vitrea</i>	dead coral facies, shallow mud, pebbly sand facies	mud	infaunal	fresh phytodetritus	oxic	opportunistic, phyto-detritus, low water energy	Jorissen and others (1992); Murray (2006)
<i>C. refulgens</i>	sand wave, dropstone, and living coral facies	hard substrate	epifaunal attached	passive suspension feeder	oxic	stable physico-chemical conditions, high energy	van der Zwaan (1982); Kaiho (1994, 1999); Kouwenhoven (2000); Murray (2006)
<i>C. aravaensis</i>	sand wave, dropstone, and living coral facies	hard substrate	epifaunal attached	passive suspension feeder	oxic	stable physico-chemical conditions, high energy	Murray (2006); Margreth and others (2009)
<i>C. pachyderma</i>	sand wave, dropstone, and living coral facies	hard substrate	epifaunal-shallow infaunal	passive suspension feeder, prefers labile components of organic matter (e.g., fresh diatoms)	oxic	oligotrophic environments, stable physico-chemical conditions, high energy	Miao and Thunell (1993); Almogi-Labin and others (2000); Schmiedl and others (2000); Fontanier and others (2002); Murray (2006); Margreth and others (2009)
<i>L. lobatula</i>	living coral facies	hard substrates, coarse sediments	epifaunal attached	passive suspension feeder	oxic	high energy	Murray (1971); Lutze and Thiel (1989); Schönfeld (2002); Murray (2006)
<i>A. angulosa</i>	dead coral facies	sand	infauna	—	—	withstands permanent winnowing	Sejrup and others (1981); Hald and Vorren (1984); Mackensen (1985); Schönfeld (2002)
<i>H. balhica</i>	shallow, deep mud and pebbly sand facies	mud-silt	epifaunal-shallow infaunal	prefers fresh organic matter	suboxic-oxic	temperature 4–7.5°C. Mean bottom salinities 34.0–35.0 psu	Elliott and others (1991); Kaiho (1994); Schmiedl and others (2000); Norman (2001); Murray (2003, 2006); Husum and Hald (2004)
<i>M. barilecanum</i>	shallow mud and living coral facies	mud-silt	infaunal	may feed on low and intermediate quality organic matter	dysoxic	<10°C, lives in high productivity waters, lives on the redox front	Murray (1973, 2006); Corliss (1985); Goody (1986); Caralp (1989); Loubere (1991); Fontanier and others (2005, 2008); Koho and others (2008); Morigi and others (2012)
<i>C. subglobosum</i>	deep mud facies	mud-silt	epifaunal or shallow infaunal	strongly linked to fresh food availability	oxic and well ventilated	sensitive to changing environment	Murray (2006); Jorissen and others (2009)
<i>C. laevigata</i>	living coral facies, off-reef	sand	infaunal	dependent on labile organic matter	can tolerate dysoxia	high carbon fluxes	Mackensen and Hald (1988); Murray (2003, 2006); Alve (2010)
<i>G. subglobosa</i>	living coral and dropstone facies	mud	infaunal	phytodetritus feeder, preferentially ingest fresh diatoms	—	oligotrophic	Corliss (1979); Goody (1994); Mackensen and others (1995); Fariduddin and Loubere (1997); Suhr and others (2003); Murray (2006)
<i>Reophax</i> spp.	deep mud facies	mud-sand	shallow infauna	may feed on refractory organic matter, thrive in presence of fresh organic matter	may withstand dysoxia	organic-matter rich sediments	Fontanier and others (2003, 2005); Alve (2010)

TABLE 4. Continued.

Species	Facies	Preferred substrate	Living strategy	Feeding strategy/ preference	Oxygen	Other ecological preferences	References
<i>O. unbonatus</i>	deep mud facies	mud-sand	-	associated to fresh phytodetritus, but can thrive in nutrient-poor waters	prefers well- oxygenated waters	cold-water species	Mackensen and others (1985); Gooday (1988, 1993)
<i>F. wuellerstorfi</i>	deep mud facies, off-reef	mud-sand	generally epifaunal, rarely shallow infaunal	suspension feeder, associated to fresh phytodetritus	oxic	tolerates temperatures below 0°C, strong currents	Gooday (1988; 1994) Wollenburg and Mackensen (1998); Saidova (2011)
<i>E. scaber</i>	sand-wave facies	fine sand	Infaunal, may be epiphytic on seagrass	detrivore, does not depend on labile organic matter	—	eutrophic environments	Debenay (2000); Fontanier and others (2002); Duijnste and others (2004); de Nooijer and others (2008); Alve and Goldstein (2010)
<i>B. marginata</i>	coral rubble, mud, sediment-clogged and living coral facies	mud	deep infaunal in anoxic regions, also shallow infaunal	may feed on low quality organic matter	may tolerate dysoxia- anoxia	in Norway it lives in temperature of 4–13°C, is a high productivity taxon, low energy	Jorissen and others (1998); Jorissen and Wittling (1999); Fontanier and others (2002); Hustum and Hald (2004); Murray (2006)
<i>B. cylindrica</i>	deep mud facies	fine-grained sedi- ments	shallow infauna	prefer high quality organic matter	dysoxic, tolerant of anoxia	organic-rich sediments	Schmiedl and others (2000); Fontanier and others (2002); Koko and others (2008)
<i>T. earlandi</i>	shallow off-reef, sediment clogged coral facies	mud and sand	free-living	—	well-adapted to dysoxia	cosmopolitan	Murray (2003, 2006); Alve and Goldstein (2010)
<i>G. affinis</i>	shallow off-reef	mud	intermediate- deep infaunal	can feed on low and intermediate quality organic matter	zero oxygen level, anoxic, tolerates dysoxia	organic-matter rich sediments	Fontanier and others (2005, 2008)
<i>D. coronata</i>	sand wave and living coral facies	coarse	epifaunal attached	—	oxic	attached on hydroids and octocorals, strong bottom currents ≤26–50 cm/s	Schönfeld (2002); Hawkes and Scott (2005)
<i>S. fusiformis</i>	shallow off-reef	mud	infaunal	may feed of refractory organic matter variable food flux	dysoxic, can tolerate anoxia suboxic	opportunistic	Alve (2003, 2010); Murray (2006)
<i>Pullenia</i> spp.	living coral facies	mud	infaunal	—	—	high carbon-flux rates	Corliss and Chen (1988); Loubere (1998); Sen Gupta and Thomas (1999); Murray (2006)
<i>A. gallowayi</i> <i>N. iridea</i>	Sand-wave facies off-reef	mud and sand mud	infaunal infaunal	dependent on labile organic matter	— suboxic-dysoxic	strong bottom currents —	Wollenburg and Mackensen (1998) Kaiho (1994); Murray (2006); Alve (2010)

TABLE 5. List of benthic species and statistical parameters associated with the similarity in Clusters I–V. The average abundance (Av. Ab.), average similarity (Av. Sim.), contribution (%), and cumulative contribution (Cum. %) to the total similarity are given for each species.

Cluster I				
Average similarity: 54.53				
Species	Av. Ab.	Av. Sim.	Contrib. %	Cum.%
<i>Cassidulina</i> spp.	3.21	7.21	13.23	13.23
<i>Hyalinea balthica</i>	3.68	6.84	12.54	25.77
<i>Eggerelloides scaber</i>	2.41	5.15	9.44	35.21
<i>Bolivina</i> spp.	3	4.29	7.87	43.08
<i>Melonis barleeaanum</i>	1.89	3.66	6.72	49.79
<i>Bulimina marginata</i>	1.92	3.51	6.43	56.22
<i>Textularia earlandi</i>	1.81	3.27	5.99	62.21
<i>Pullenia</i> spp.	2.12	2.87	5.27	67.48
<i>Haplophragmoides robertsoni</i>	1.44	2.81	5.16	72.64
<i>Globobulimina</i> spp.	2.72	2.45	4.49	77.13
<i>Stainforthia fusiformis</i>	1.46	1.58	2.9	80.03
Cluster II				
Average similarity: 67.85				
Species	Av. Ab.	Av. Sim.	Contrib. %	Cum.%
<i>Fontbotia wuellerstorfi</i>	6.99	18.61	27.43	27.43
<i>Cribrostomoides subglobosum</i>	4.74	12.57	18.53	45.97
<i>Epistominella exigua</i>	2.35	5.34	7.87	53.83
<i>Oridorsalis umbonatus</i>	1.47	4.13	6.08	59.92
<i>Pyrgo</i> spp.	2.04	3.57	5.27	65.19
<i>Fissurina</i> spp.	1.02	2.92	4.31	69.49
<i>Lobatula lobatula</i>	1.01	2.67	3.93	73.43
<i>Epistominella vitrea</i>	1.05	2.66	3.93	77.35
<i>Cassidulina</i> spp.	1.06	2.39	3.52	80.87
Cluster III				
Average similarity: 66.14				
Species	Av. Ab.	Av. Sim.	Contrib. %	Cum.%
<i>Cassidulina</i> spp.	3.95	7.94	12.01	12.01
<i>Reophax</i> spp.	4.01	7.93	11.98	23.99
<i>Globocassidulina</i> group	3.41	7.58	11.46	35.45
<i>Epistominella exigua</i>	2.61	5.32	8.04	43.49
<i>Melonis barleeaanum</i>	3.17	5.19	7.85	51.34
<i>Epistominella vitrea</i>	1.94	4.4	6.66	57.99
<i>Cribrostomoides subglobosum</i>	2.6	4.37	6.61	64.6
<i>Pullenia</i> spp.	1.77	4.05	6.12	70.72
<i>Angulogerina angulosa</i>	2.04	3.66	5.53	76.25
<i>Cibicidoides pachyderma</i>	1.25	1.89	2.86	79.11
<i>Paratrochammina challenger</i>	1.01	1.76	2.67	81.77
Cluster IV				
Average similarity: 60.75				
Species	Av. Ab.	Av. Sim.	Contrib. %	Cum.%
<i>Lobatula lobatula</i>	3.5	5.73	9.43	9.43
<i>Cassidulina</i> spp.	2.96	4.89	8.04	17.48
<i>Melonis barleeaanum</i>	2.83	4.5	7.41	24.89
<i>Cibicidoides pachyderma</i>	2.93	4.21	6.93	31.82
<i>Melonis pompilioides</i>	2.53	4.03	6.64	38.46
<i>Bulimina marginata</i>	2.11	3.1	5.1	43.55
<i>Hyalinea balthica</i>	1.84	2.84	4.68	48.23
<i>Gavelinopsis</i> spp.	1.69	2.43	4	52.22
<i>Astrononion gallowayi</i>	1.5	2.42	3.98	56.2
<i>Cibicides refulgens</i>	1.91	2.09	3.44	59.64
<i>Angulogerina angulosa</i>	1.34	2.07	3.4	63.04
<i>Pullenia</i> spp.	1.36	1.8	2.97	66.01
<i>Globocassidulina</i> group	1.12	1.74	2.87	68.88
<i>Epistominella exigua</i>	1.28	1.71	2.81	71.7
<i>Spiroplectinella wrightii</i>	1.12	1.55	2.56	74.25
<i>Discorbinella bertheloti</i>	1.29	1.45	2.39	76.64
<i>Cibicidoides aravaensis</i>	1.02	1.12	1.85	78.49
<i>Hanzawaia boueana</i>	0.9	1.09	1.8	80.29

TABLE 5. Continued.

Cluster V				
Species	Average similarity: 56.45			
	Av. Ab.	Av.Sim.	Contrib. %	Cum. %
<i>Cibicidoides pachyderma</i>	4.19	7.55	13.37	13.37
<i>Globocassidulina</i> group	2.56	4.61	8.16	21.53
<i>Discanomalina coronata</i>	2.97	4.41	7.81	29.35
<i>Cibicides refulgens</i>	2.49	4	7.09	36.44
<i>Lobatula lobatula</i>	2.36	3.93	6.97	43.41
<i>Angulogerina angulosa</i>	2.5	3.89	6.89	50.3
<i>Cassidulina</i> spp.	2.09	3.6	6.37	56.67
<i>Melonis barleeanum</i>	1.73	3.04	5.38	62.05
<i>Epistominella vitrea</i>	1.61	2.21	3.91	65.96
<i>Cibicidoides aravaensis</i>	1.39	1.97	3.49	69.45
<i>Pullenia</i> spp.	1.16	1.65	2.92	72.37
<i>Astrononion gallowayi</i>	1.06	1.47	2.61	74.98
<i>Fissurina</i> spp.	1.01	1.42	2.52	77.5
<i>Gavelinopsis</i> spp.	1	1.29	2.28	79.78
<i>Epistominella exigua</i>	0.95	1.2	2.13	81.91

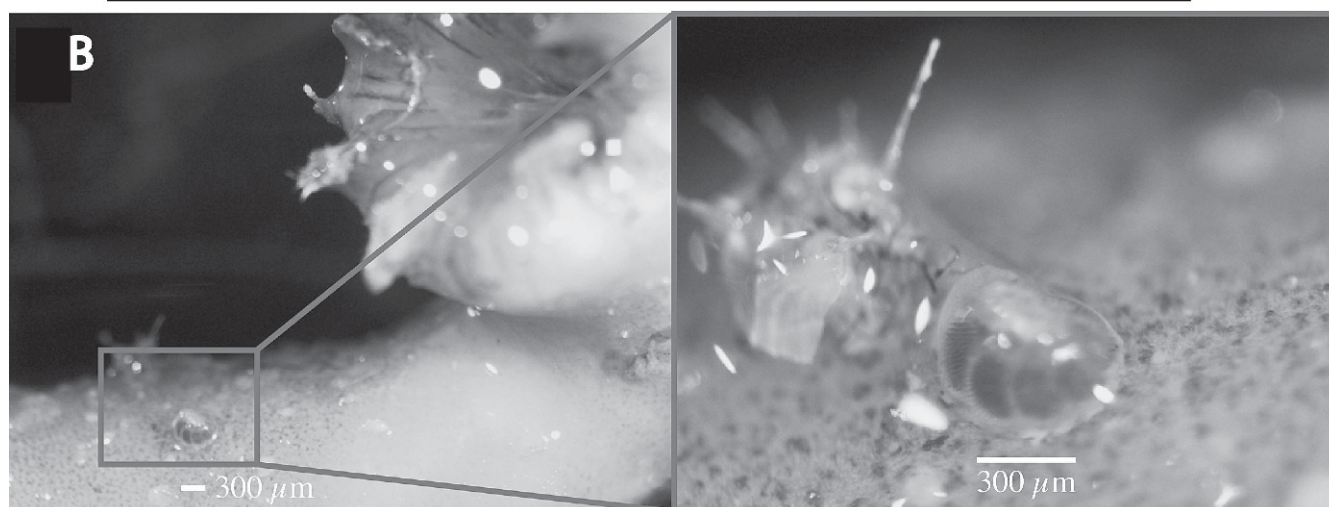
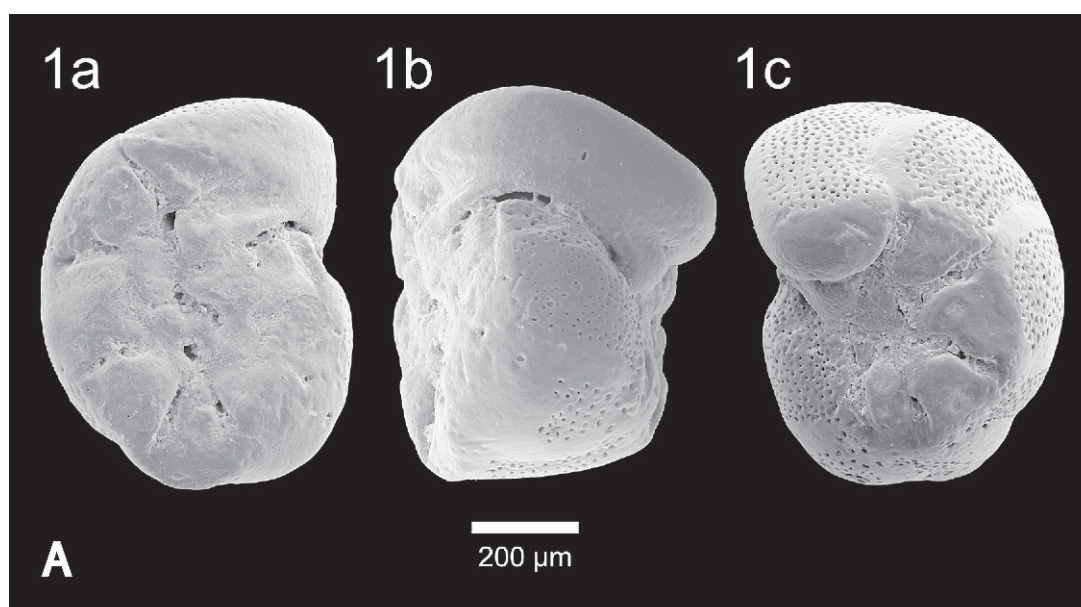


FIGURE 6. **A** *Discanomalina coronata*, SEM photomicrographs. **B** Living *D. coronata* attached to a *Lophelia pertusa* branch. Sampling was done by JAGO Dive 1051 at Sula Reef during cruise AL316.

that *Lophelia* could feed on small organic particulates as well as on live zoobenthos and zooplankton. The Danish slope of the Skagerrak Basin is a site with high benthic fertility caused by high abundance of particulate organic matter reaching the sea floor (Alve and Murray, 1997). However, van Weering and others (1987), Dauwe and Middleburg (1998), and Krönke and others (2004) observed that the Skagerrak sediments, while relatively rich in organic matter, are of low average quality because of extensive degradation prior to deposition, and cannot support a thriving coral population.

A recent experiment of Alve (2010) on foraminiferal species collected from 320-m water depth in the Skagerrak Basin demonstrated that they do not depend on a regular supply of fresh organic matter but instead feed on degraded refractory organic matter. Based on her experiment, Alve (2010) states, "The overall moderate response to lack of fresh phytodetritus was probably due to the fact that the assemblage already was adapted to an environment dominated by poor quality food particles."

Only a few species (e.g., allogromiids, *C. laevigata* and *Nonionella iridea* Heron-Allen and Earland) are strongly dependent on a supply of fresh phytodetritus to maintain their populations (Alve, 2010). In Clusters I and IV group samples from the Skagerrak, *C. laevigata* and *N. iridea* are rare compared to other sites, thus suggesting that in this region, although species diversity is comparable to other areas of the Norwegian margin, the organic matter is of lower quality, confirming the biochemical results of van Weering and others (1987), Dauwe and Middleburg (1998), and Krönke and others (2004). The low quality of organic matter prevents the proliferation of organisms living within the coral framework (such as benthic meiofauna; Bongiorni and others, 2010), and therefore, the food source for corals, explaining the high abundance of dead cold-water corals in the Oslo Fjord ecosystem.

COLD-WATER CORAL FACIES DISTRIBUTION AND HABITATS OF BENTHIC FORAMINIFERS: NORWEGIAN REEFS AND IRISH MOUNDS

Schönfeld and others (2011) showed that nutritional demands, microhabitat preferences, and ecology largely drive species abundance and distribution in the Porcupine Seabight. They observed that most of the species in the dead and living assemblages are epibenthic and that *D. coronata* is associated with coral-rubble facies, *C. refulgens* prefers off-mound sand veneer, and *U. mediterranea* maximum abundance is in the main depositional area on the southern flank of Galway Mound. Morigi and others (2012), on the contrary, showed that sediments surrounding the living CWCs on the Logachev Mound, Rockall Bank slope, were characterized by higher foraminiferal abundance and biodiversity than in open-slope sediments from the same area.

Margreth and others (2009) recorded abundant epifauna and benthic infauna in the living-coral-framework ecosystems from the Porcupine Basin. In particular, infaunal *M. barleeanum*, *G. subglobosa*, *Cassidulina* spp., and *Gavelinopsis* spp. live in the finer-sediment fraction between coral branches. Similarly along the Norwegian margin (Table 4;

Fig. 3), infaunal species are also present in the muddy-sandy sediments trapped by the living coral framework. In this region epifaunal benthic species are also present in the sediment-clogged coral and pebbly sand facies where dropstones and dead corals provide them with ecological niches. Uvigerinids abundant in the mud facies of the Porcupine Basin are rarer in the off-reef Norwegian study sites. This is consistent with Schönfeld and Altenbach (2005), who reported the absence of this group from the Norwegian-Greenland Sea. They relate this absence to the grazing activity of zooplankton that inhibits the deposition of the spring phytoplankton bloom in the Norwegian Sea (Bathmann and others, 1990; von Bodungen and others, 1995). Based on benthic foraminiferal distribution and sediment characterization (Table 2; Fig. 3), we find a near 1:1 correlation of sedimentary facies along the Norwegian margin (N) in this study with those in the Porcupine Basin (PB; Margreth and others, 2009) as shown in Table 2.

In summary, cold-water-coral facies distribution is controlled by the variability of physical, chemical, and biological parameters (temperature, pressure, oxygen availability, and currents; Roberts and others, 2006), nutrient supply, availability of fresh labile organic matter (Davies and others, 2009), and salinity and density (Dullo and others, 2008), which differ in adjacent regions (e.g., Dorschel and others, 2007; Wienberg and others, 2009). The distribution of benthic foraminifers and their microhabitats is controlled by geological and environmental parameters (e.g., Jorissen and others, 1995; Fontanier and others, 2002) very similar to those controlling cold-water-coral facies distribution such as oxygen, nutrients, substrate, and current patterns. Facies and benthic foraminiferal microhabitats are similar along the Irish and Norwegian margins, although species composition and abundance may vary. In the Porcupine Basin off Ireland both microhabitats and facies can extend over hundreds of meters (Margreth and others, 2009), whereas along the Norwegian margin they can change within tens of meters or even within meters (Freiwald and others, 2002; Hühnerbach and others, 2008) (Fig. 3).

CONCLUSIONS

Cluster and nMDS analyses of benthic foraminifers along the Norwegian margin have been used to characterize the cold-water coral (CWC) ecosystems. Our results show that on the Norwegian continental margin and shelf, the conditions for CWC ecosystem development are generally met and are consistent with those in other North Atlantic CWC sites.

Analysis of relative abundance data allows recognition of 5 clusters: I) shallow "off-reef" areas of the Skagerrak Basin; II) deep-sea >1800-m water depth; III) bathyal between 800–1800 m; IV) "on-reef" areas of the Skagerrak; and V) "on-reef" areas on shelf and upper-continental slope in the Norwegian Atlantic.

The benthic fauna provides information on environmental parameters, such as substratum, currents, oxygenation, and organic matter content. In particular, benthic fauna from deep and shallow mud facies suggests high nutrient input at the sea floor, strong currents, and cold waters.

Benthic foraminifers associated with living CWC reefs indicate an environment characterized by high energy and well-oxygenated waters with high amounts of fresh organic matter (derived from phytoplankton blooms) reaching the sea floor. The benthic foraminiferal fauna associated with coral reefs in the Skagerrak indicates that, although the flux of organic matter is high, the labile component usable for CWC growth is low, and may explain the extensive occurrence of dead corals in this area.

Benthic foraminiferal assemblages from the Porcupine Basin and the Norwegian margin show that their living strategies and microhabitats are similar, although species composition may vary. In the Porcupine Basin both microhabitats and facies can extend over hundreds of meters, whereas along the Norwegian margin they can change within tens of meters.

TAXONOMIC NOTE

In this research we retain the species concepts of *Discanomalina coronata*, *Discanomalina japonica* Asano, and *Rosalina semipunctata*. Medioli and Scott (1978) lumped together the planispiral *D. coronata* and *D. japonica* with the trochospiral *R. semipunctata*, stating that their morphologic differences are due to intraspecific variation resulting from different current energy, and their attached life style. Furthermore, the *Discanomalina* morphotypes are restricted to the shelf, and the spines of *R. japonica* are teratological features. However, they did not undertake a morphometrical study to support their hypothesis. After a careful analysis of their article we conclude that their specimens do not clearly show evidence of transitions between planispiral and trochospiral coiling, partly because the three standard SEM images of spiral, lateral, and umbilical views are not shown for all specimens that seem to be mostly trochospiral. Recent research has shown that *D. coronata* is also a deep-sea form, not restricted to the shelf, and it is abundant in cold-water coral ecosystems (e.g., Margreth and others, 2009; Schönfeld and others, 2011). It occurs together with *D. japonica* and *R. semipunctata* in the same environment.

We may argue that the two planispiral species could be lumped together under the senior synonym *D. coronata*. However, the clearly trochospiral form should be kept separate. Therefore, with the current lack of DNA evidence and/or a morphometric revision, we keep the three forms separated and retain the generic attribution for *D. coronata*, *D. japonica*, and *R. semipunctata*.

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APPENDIX 1

Species list and quantitative data of benthic foraminifera. Generic names follow Loeblich and Tappan (1987). This Appendix can be found on the Cushman Foundation website in the JFR Article Data Repository (<http://www.cushmanfoundation.org/jfr/index.html>) as item number JFR2013001.