

The metazoan meiofauna associated with a cold-water coral degradation zone in the Porcupine Seabight (NE Atlantic)

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Abstract. The metazoan meiofauna associated with *Lophelia pertusa* reef degradation zones in the Belgica Mound province (Porcupine Seabight, North-East Atlantic) was studied in the framework of the Atlantic Coral Ecosystem Study (ACES; EC Fifth Framework Research Program). Attention was focused on the influence of and differences between different microhabitat types: dead coral fragments, glass sponge skeletons and the underlying sediment. This study demonstrates the importance of dead *Lophelia pertusa* framework and associated substrates for meiofauna along the European continental margins. The presence of these large biogenic structures on the seafloor of the continental margin (1) enables more taxa to be present and (2) particularly favours harpacticoid copepods, naupliar larvae and polychaetes. The meio-epifaunal community on these substrates significantly differs from the meio-infaunal community in the underlying sediment. This is mainly due to a much lower dominance of nematodes and a higher relative abundance of most other taxa, especially harpacticoids, naupliar larvae and polychaetes, in the latter habitat. This situation is comparable to that of epiphytic assemblages. Dominance of nematodes is low. The meio-infaunal assemblage in the underlying sediment is characterized by low densities. There are clear indications that cold-water coral degradation zones are biologically very diverse, in terms of species richness as well as equitability. Of all microhabitat types, coral fragments support the most diverse communities, whereas the underlying sediment is the least diverse.

Keywords. Cold-water corals, dead coral framework, meiofauna, community structure, microhabitats, biodiversity

Introduction

Meio-epifauna: a new chapter in cold-water coral research

Although the existence of cold-water corals was known to science since the 18th century (Pontoppidan 1755), the associated fauna has by no means been studied as

intensely as for tropical corals. Most preceding studies dealing with real epifauna on either living or dead *Lophelia pertusa* (Linnaeus, 1758) have focused on the macrofauna; some studies dealt with the associated fauna in a broader sense and examined the animals that could be identified on live images or photographs from ROV, defined as megafauna (Dons 1944; Le Danois 1948; Burdon-Jones and Tambs-Lyche 1960; Jensen and Frederiksen 1992; Mortensen et al. 1995; Fosså and Mortensen 1998; Rogers 1999; Van Gaever 2001; De Backer 2002). Until the present-day, there is almost no knowledge on the composition and diversity of the smaller fraction, known as meiofauna, associated with *Lophelia pertusa* reefs (except for the study of Jensen and Frederiksen 1992). Obviously, this is an important hiatus in our understanding of cold-water coral associated fauna. Meiofauna is known to play an important role in the marine benthic ecosystem (Heip et al. 1985; Coull 1988) and it serves as food for other organisms (Thiel 1983; Coull 1988). Furthermore, as meiofaunal organisms occur in high abundances and because they are characterized by high species richness (Heip et al. 1985; Lambshead 1993), they are very suitable for biodiversity studies.

For the first time, the meiofauna associated with cold-water corals has been intensively studied. Three years of study on this topic will be presented here, highlighting the most important and striking aspects of this formerly unknown fauna and underlining its particular nature and relevance.

The present study deals only with metazoan meiofauna. In this paper, meiofauna is defined as the fauna that passes through a 1 mm mesh sieve but that is retained on a 32 μm mesh sieve. The 32 μm limit is used primarily in deep-sea studies because of the smaller size of deep-sea meiofauna (Thiel 1975; Thiel 1983; Pfannkuche 1985; Soetaert and Heip 1989). Next to the interstitial and mud-dwelling meiofauna (here referred to as meio-infauna), there is a large group of meiofauna living epifaunally on well-defined surfaces from diverse origin, ranging from large biogenic debris to seagrasses, macro-algae, larger coral fragments, sponge skeletons, manganese nodules and pebbles, to name a few. The term *meio-epifauna* will be used here to cover this unit of the meiofauna. For meiofauna living on seagrasses and macro-algae, the terms “epiphytic” and “foliicolous” have already been used in literature. A suitable substrate for meio-epifauna (1) should be a discrete and well-defined structure of at least about 5 mm in diameter and (2) should not be completely covered with sediment, implying that at least a part of the surface area remains in contact with the water column. Although it is expected that these surfaces will provide higher numbers of typical epifaunal taxa than any other habitat, there is of course no exclusive relationship in either way. This is because the surfaces are always in close contact with the sediment to a certain extent (physical contact with sediment surface, infill from sedimentation and resuspension), and because several typical epifaunal taxa (e.g., representatives from the epifaunal nematode families Epsilonematidae and Draconematidae: Fig. 4) are also found in coarse and poorly sorted sediments. Recently, a representative of the family Epsilonematidae (*Glochinema bathyperuvensis* Neira, Gad, Arroyo and Decraemer, 2001) has even been found living in fluffy, muddy sediments (Neira et al. 2001). In the present

study suitable surfaces for meio-epifauna are found on dead coral fragments of the framework builder *Lophelia pertusa* (Linnaeus, 1758) and skeletons of the glass sponge *Aphrocallistes bocagei* Schultze, 1886, both abundantly present in the cold-water coral degradation zones.

Most preceding studies on marine meiofauna have focused on the meio-infauna. The few studies that dealt with meio-epifauna focused on the fauna associated with macro-algae and seagrasses (e.g., Lewis and Hollingworth 1982; Coull et al. 1983; Bell et al. 1984; Hall and Bell 1993; Jarvis and Seed 1996; De Troch et al. 2001). The present study focuses on dead coral fragments and the dead glass sponge skeletons that are associated with them. Living coral is assumed not to be a suitable substrate for meiofauna, although the absence of meiofauna has not yet been verified. It was observed that the healthy coral responds to the settlement of sessile organisms by (1) an increase in mucus production and (2) selective sclerenchyme precipitation (Freiwald and Wilson 1998). These protective properties have proven to be rather successful antifouling measures against macrofauna (Mortensen 2000).

Location and environmental conditions

The information compiled in this study is based on three box core samples. The box cores were taken on the top and slope of a single seabed mound at depths between 972 and 1005 m (Table 1; Fig. 1). This mound is located in the Belgica Mound province of the Porcupine Seabight. The Porcupine Seabight is a large embayment of the European continental slope, located in the North-East Atlantic Ocean, southwest of Ireland. It is bordered by the Slyne Ridge in the north, the Goban Spur in the south, the Porcupine Bank in the west and the Irish Mainland shelf in the east. In this area numerous seabed mounds occur, grouped in three so called "mound provinces": the Hovland Mound province, the Magellan Mound province and the Belgica Mound province (Fig. 1). The Belgica Mound province is the most southern of all seabed mound provinces. It is characterized by large outcropping or buried, conical (sometimes composite) mounds with well-exposed downslope sides (De Mol et al. 2002), aligned in four along-slope-trending ridges (Van Rooij et al. 2003). In total, 21 outcropping mounds are present. These mounds are known to be associated with deep-water coral banks, mainly constructed by the framework builder *Lophelia pertusa* (Linnaeus, 1758) and associated fauna such as the glass sponge *Aphrocallistes bocagei* Schultze, 1886. These cold-water corals are present only on the basinward flanks of the mounds (De Mol et al. 2002). The presence of these mounds as well as the reefs that are associated with them alters the local hydrodynamic and sedimentary regime.

The presence of transversal sand dunes in the Belgica Mound region indicates very high current velocities, up to 100 cm/s (De Mol 2002). These very high velocities are probably exceptional but normal current speeds are still rather high (about 10-25 cm/s (White submitted) or even 40-50 cm/s (V. Huvenne pers. comm.)). High current speeds are attributed to the combination of strong, northward along-slope bottom currents, internal tides and waves, and the presence of mounds (Rice et al. 1991; Van Rooij et al. 2003; Wheeler et al. submitted; White submitted). Strong current activity is known to affect meiofaunal abundance and community structure

Table 1 An overview of the exact sampling location and depth, as well as the observed and calculated densities of the sediment-dwelling meiofauna found in the underlying sediment of the present study and in sediments from nearby localities at a comparable depth. Artificial values for the respective depths were calculated using the function $Y = 2241 - 227 \cdot \ln \text{depth}$ (Vincx et al. 1994: Fig. 4)

	Area	Coordinates		Depth [m]	Observed density [ind/10cm ²]	Calculated density [ind/10cm ²]
		Latitude	Longitude			
Box IV 2000	Porcupine Seabight	51°24'48.2"N	11°45'55.4"W	1005	376 ± 54	672
Box V 2000	Porcupine Seabight	51°24'49.4"N	11°45'55.9"W	1000	328 ± 178	673
Box IV 2001	Porcupine Seabight	51°25'7.7"N	11°46'9.3"W	972	291	679
Station 511-03 (Pfannkuche 1985)	Porcupine Seabight	51°47'0"N	13°08'36"W	960	1593 ± 143	682
Station 511-04 (Pfannkuche 1985)	Porcupine Seabight	51°21'24"N	13°03'18"W	1492	943 ± 127	582
Vanreusel et al. (1995)	Porcupine Seabight	51°46'12.8"N	13°13'2.4"W	900	1523 ± 267	697
Vanreusel et al. (1995)	Porcupine Seabight	51°39'2.4"N	12°59'1.8"W	1200	1500 ± 270	632
Station I (Vanaverbeke et al. 1997)	Goban Spur	49°24'43.2"N	11°31'51.6"W	670	612 ± 76	764
Station B (Vanaverbeke et al. 1997)	Goban Spur	49°21'59.4"N	11°48'5.4"W	1034	619 ± 47	665
Station II (Vanaverbeke et al. 1997)	Goban Spur	49°11'12.0"N	12°49'10.8"W	1425	509 ± 72	593

(Aller 1989; Aller 1997; Thistle and Levin 1998; Thistle et al. 1999). Currents are less vigorous upslope, to the east of the mounds (Van Rooij et al. 2003).

According to De Mol et al. (2002) and Van Rooij et al. (submitted) the upper 10 cm of the sediment in the Belgica Mound region can be defined as Foraminifera-rich silty sand or soupy, foraminiferal sand, with a high sand content decreasing towards a depth of 10 cm. Below this, the sediment becomes more clayey (pers. obs.), defined as olive grey silty clay by Van Rooij et al. (submitted). In the vicinity of the mounds, the sediment becomes littered with coral fragments and other biogenic debris (see below).

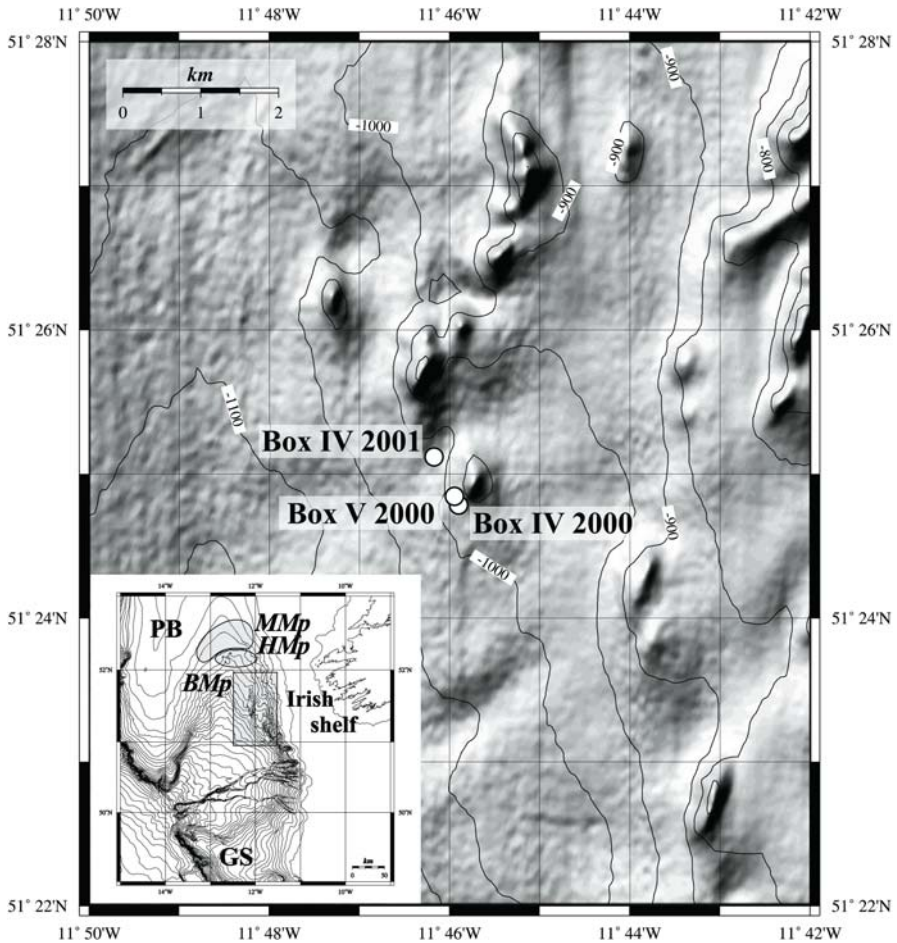


Fig. 1 Map of the Porcupine Seabight area, with a detail showing the ridge of mounds in the Belgica Mound province where the analysed samples originate from (bathymetry after Beyer et al. 2003). Boxcore locations are indicated. (PB = Porcupine Bank; *MMp* = Magellan Mound province; *HMp* = Hovland Mound province; *BMp* = Belgica Mound province; GS = Goban Spur)

The Porcupine Seabight is known to be subject to substantial phytodetrital deposition (Billett et al. 1983; Lampitt 1985; Gooday et al. 1996). The detritus itself as well as the Bacteria and Protozoa that rapidly colonize it are the main food source for deep-sea meiofauna. Taking into account both timing of surface blooms in 2000 and 2001, as well as sinking rates, it was calculated that phytodetritus should have been present on the bottom at both sampling occasions. It is however difficult to judge whether this material already had a relevant impact on the meiobenthos as response speed by benthic organisms may be taxon-specific, or even guild-specific: smaller species that utilize the organic matter directly show a more rapid response than larger species on a higher trophic level (Graf et al. 1982; Gooday et al. 1996).

Next to this, it is not even clear if this deposited material was available for the benthic fauna in the Belgica Mound region, an area subject to strong bottom currents. These currents will certainly cause resuspension and relocation of the material. Down-slope and along-slope variability of phytodetrital deposition in this region makes generalizations even more difficult (D. Billett pers. comm.).

Food supply is known to influence meiofaunal abundance and biomass (Graf et al. 1982; Pfannkuche and Thiel 1987; Gooday and Lamshead 1989; Thiel et al. 1990; Pfannkuche 1993; Vanreusel et al. 1995a; Gooday 2002), metabolic activity (Graf et al. 1982; Pfannkuche 1993; Gooday 2002), community structure (Gooday 1988), reproductive cycles (Gooday et al. 1996; Gooday 2002) and size spectra (Thiel 1975; Soetaert and Heip 1989; Vanreusel et al. 1995a; Soltwedel et al. 1996) in the deep-sea. Our samples did not show any evidence of a detrital layer covering the sediment or the large biogenic substrates (pers. obs.).

Cold-water coral degradation zones

As already mentioned above, this study deals mainly with dead coral skeletons. These structures are the result of a bioerosion process that starts with the death of *Lophelia pertusa* colonies due to persistent attack by fouling organisms. The progress of this bioerosion process is visible in the zonation of the deep-water reef mound environment. Although each reef has its own characteristic zonation pattern with its own succession of typical facies (Freiwald et al. 1997; Freiwald et al. 2002), the two zones described by Mortensen et al. (1995) can be distinguished in most cases: according to these authors, a cold-water bioherm can be divided into two zones of approximately equal height: (1) a living coral zone on the summit and the upper flanks, and (2) a lower zone of dead corals. The centre of a deep-water bioherm indeed consists of living coral framework. According to Freiwald and Wilson (1998), the *Lophelia pertusa* bioerosion process starts with the formation of a microbial biofilm and endolithic fungal infestation, followed by colonisation of the coral skeleton by sessile invertebrates such as sponges and octocorals. The microbial biofilm might serve as a food source for small microvores including some meiofauna. As already mentioned above, this meiofauna is a food source for higher trophic levels (macrofauna and megafauna). Thus, the development of such a biofilm might enable an entirely new food web to be established, although there is still no evidence for this. In the reef's zonation pattern the living coral framework is flanked by the dead coral framework.

In a next stage, locally intense sponge excavation results in skeletal loss, and the *in situ* collapse of the dead *Lophelia pertusa* framework. Conversely, the encrusting sponge communities also speed up the closure of the gaps in the open coral framework and catalyse sediment-trapping, resulting in the strengthening of the framework architecture and the origin of large topographic features (De Mol et al. 2002). The dead coral framework gradually changes into a zone composed of smaller and more biodegraded coral skeletons with a rich associated fauna. The gaps between the skeletons and their branches are filled up with sediment (Freiwald et al. 2002). Our samples were taken in this type of habitat (sediment-clogged coral

framework). However, the sediment infill in our samples seemed rather limited, probably due to the high current velocities and the resulting resuspension of the sediment (see above). Because of the dynamic origin of this habitat, it is more generally referred to as a "coral degradation zone" in the present study.

In a final stage, intensified bioerosion will result in accumulations of centimetre-sized coral debris. This so-called coral rubble pavement (Freiwald et al. 1997) then grades into the soft bottom background. The diversity of megafauna living in this *Lophelia pertusa* rubble zone has been found to be lower than that of the zones with living or dead coral colonies (Mortensen et al. 1995). Dead coral colonies accommodate the most diverse macro- and megafauna (Jensen and Frederiksen 1992; Mortensen et al. 1995). This can be attributed to the sheltering function and higher habitat diversity of branched dead coral skeletons (framework) in contrast to the very small fragments in the *Lophelia pertusa* rubble zone.

In the immediate vicinity of the seabed mound examined in this study, every stage between dead coral framework and the coral rubble pavement is present. The dead framework however occurs only in small patches. Live coral framework in this region is present on the ridge directly to the north of the examined mound, from the nearby Therèse Mound to Galway Mound farther north (A. Foubert pers. comm.). As the seabed mound in question is considered to be the most southern mound of this ridge, it is expected that this structure also contains live coral patches.

The present paper aims to describe the metazoan meiofaunal community structure associated with cold-water coral degradation zones for the first time, investigate the importance of different microhabitats for meiofauna in this area by checking for habitat preferences and compare the observed community structure with the composition of epiphytic assemblages. In addition, densities of the meio-infauna in the underlying sediment will be compared with available data from preceding studies on meiofauna in the northeast Atlantic and the biodiversity of this formerly unknown fauna will be extensively discussed.

Methods used to study the meiofauna

Sampling procedure

Material was obtained by means of a NIOZ (Netherlands Institute for Sea Research) box corer (\varnothing 32 cm). In total, three box cores were examined. Two box cores were taken during the 9-19 June 2000 sampling campaign on the RV Belgica. A third box core was taken on the same location and brought to the surface during the 2-11 May 2001 sampling campaign on the same vessel (Fig. 1). In all cases, the surface of the sediment was partly or entirely covered with several fragments of dead corals (*Lophelia pertusa* (Linnaeus, 1758)) and dead sponge skeletons (*Aphrocallistes bocagei* Schultze, 1886). Only a very small amount of living coral was present. The larger sponge and coral fragments were collected separately. After removal of the large biogenic substrates three sediment cores (10 cm²) were pushed into the underlying sediment of each box core. All material was fixed with 4 % neutralised formalin.

Microhabitats

The main aim of this study is to examine the differences in community structure due to the presence of different microhabitat types. Obviously, for meiofaunal organisms the conditions within the sediment are clearly different from those on a complex elevated structure on the seafloor, and this in terms of food supply and food quality as well as in terms of the physical influence of strong bottom currents. These differences should have their effect on the presence and abundance of meiofaunal taxa. Next to this obvious distinction between large biogenic substrates and the underlying sediment as a habitat, small differences in microhabitat structure should also influence meiofaunal community composition as meiofauna is known to respond acutely to minor environmental changes. In this respect the rough surface of the branches of *Lophelia pertusa* (Linnaeus, 1758), sometimes covered with a thin layer of bryozoan colonies, is quite dissimilar from the complex three-dimensional build-up of spicules in the glass sponge *Aphrocallistes bocagei* Schultze, 1886 (Fig. 2).

In total, 28 subsamples were examined: 18 subsamples were collected in the first box core (2000), six subsamples in the second box core (2000) and another four subsamples in the box core from 2001. After thorough examination of their contents, the subsamples were classified into one of the following groups, each of them representing a microhabitat type (Fig. 2): (1) coral fragments, (2) sponge skeletons (i.e., the two large biogenic substrates), (3) the underlying sediment and (4) a mixed substrate. Subsamples belonging to the *mixed substrate* group contained coral fragments as well as sponge skeletons. The underlying sediment consisted of fine to medium sand (median 194.9 μm) with a small fine silt fraction and a high amount of globigerine forams. It was observed that this was a poorly-sorted sediment, also containing small fragments of both large biogenic substrates, as well as some small mollusc shells and echinoid radiolas (Fig. 2E). The second sample

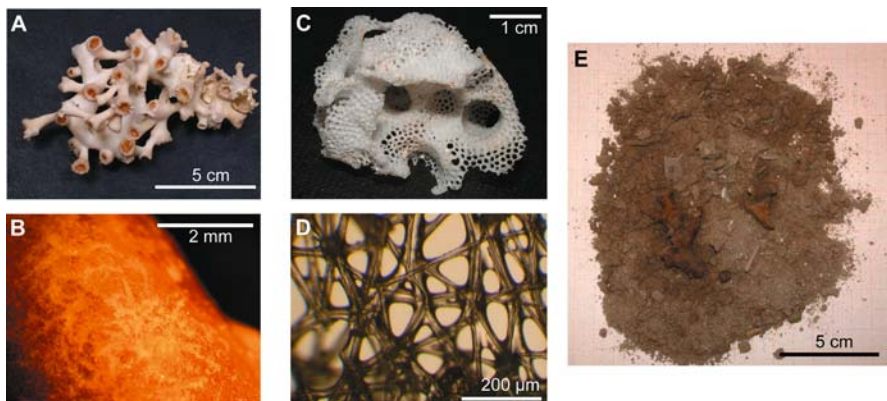


Fig. 2 An overview of the three major microhabitat types: **A** a dead *Lophelia pertusa*-fragment; **B** detail of the fragment's surface; **C** a dead *Aphrocallistes bocagei*-skeleton; **D** detail of the complex three-dimensional sponge spicule framework; **E** the underlying sediment. Note that small coral and sponge debris is present in the underlying sediment, as well as small bivalve and gastropod shells and echinoid radiolas

from 2000 did not yield any “sponge skeletons” subsamples and the sample from the 2001-campaign did not yield any “mixed substrate” subsamples.

Laboratory analyses

Each *Lophelia* and *Aphrocallistes* fragment was rinsed thoroughly over a 1 mm and a 32 μm sieve to separate the macrofauna from the meiofauna fraction. Meiofauna extraction from the underlying or remaining sediment was done by density gradient centrifugation, using Ludox (a colloidal silica polymer; specific gravity 1.18) as a flotation medium (Heip et al. 1985; Vincx 1996). All metazoan meiofauna was stained with Rose Bengal, counted in small counting trays and identified up to higher taxonomic level under a stereomicroscope. Meiofauna was classified into several taxonomic groups, ranging from orders to phyla. Most larvae however were difficult to associate with a single taxon and therefore they were referred to by using the name of their larval stage: nauplii (Crustacea), zoea (Crustacea), metazoea (Crustacea) and trochophora larvae (Polychaeta).

Volumes of all examined large biogenic substrates were measured by immersion. This method only provides a value for the volume of each substrate and not its surface area, but volume can be used as a proxy for surface area: only an extra mathematical factor describing branching complexity of corals or three-dimensional structure of sponge skeletons is needed. The use of volume estimates results from the absence of such a factor and the lack of other good alternatives. Each sediment subsample represented 10 cm^2 of sediment.

Statistical analyses

The PRIMER5 software package was used for most statistical analyses. With this software Bray-Curtis (dis)similarities between all subsamples are calculated, ultimately resulting in a test statistic reflecting within-microhabitat as well as between-microhabitat similarities. The resulting similarity matrix was applied to perform a non-metric multidimensional scaling analysis (MDS; stress 0.11). The stress value gives a measurement of goodness-of-fit of the MDS ordination. A low stress value (<0.2) indicates a good ordination with no real prospect for a misleading interpretation (Clarke 1993). ANalysis Of SIMilarities (ANOSIM) was used to test the statistic for significant differences ($p < 0.05$) between meiofaunal community structure in the different microhabitats and to investigate which taxa were responsible for these differences (SIMilarity of PERcentages: SIMPER). In this study all absolute data were square root transformed prior to the analysis.

Indicator species analysis (ISA; Duf re and Legendre 1997) was performed using the PC-ORD4 software. For this type of analysis absolute data were used without any transformation. Calculated indicator values were tested for statistical significance using the Monte Carlo test.

Parametric (one-way ANOVA) and non-parametric (Kruskal-Wallis) analysis of variance were performed using the STATISTICA6 software. Bartlett’s and Cochran’s test were used to verify the homogeneity of variances prior to the analysis.

Several biodiversity indices were calculated to obtain an extensive overview of taxon diversity of the analysed samples. The Shannon-Wiener index H' and Pielou’s

evenness J (Pielou 1975) are mainly included for reasons of comparability with other studies. Hill's diversity numbers (Hill 1973) gradually change from indices of species richness to indices of dominance with increasing number: N_0 is identical to the number of species, $N_1 = \exp(H')$ and N_∞ reflects evenness. The *expected number of taxa* for a theoretical sample of 100 individuals $ET(100)$ was derived from the *expected number of species* (Hurlbert 1971).

Associated meiofauna: community structure, densities and the influence of suitable substrates

As mentioned above, only the metazoan meiofauna was considered in this study. It is however relevant to mention that intact ciliates and foraminiferans were encountered in our samples.

In this study a total of 16547 metazoan meiofaunal organisms was counted, divided into 16 phyla and 33 groups (i.e., taxonomic groups as well as larval stages). The number of phyla represented here is quite high, especially taking into account that only 22 metazoan phyla (in the traditional sense) have representatives in the meiobenthos (Coull 1988). Because a full taxon list is seldom given in literature, it is difficult to compare the number of taxa. In total, only 31 of the 33 groups were included in the analysis: Hydrozoa and Calanoida were excluded for different reasons. A large number of hydrozoans was found: either individual polyps or branched pieces of hydrocaulus with several polyps still attached. It was reasoned that large branched colonies of Hydrozoa would be withheld on a 1 mm sieve and that therefore the number of individual polyps counted as meiofauna was not an accurate reflection of the natural situation. Calanoida on the other hand are pelagic copepods that have an aggregated spatial distribution in the water column. Therefore, their occurrence in the overlying water of a box core is highly coincidental. As a result, the presence of 29 Calanoida in two subsamples from the same box core and their absence in all the other subsamples indicates that these 29 individuals originated from a swarm of calanoids in the overlying water of this box core and can therefore be considered as contamination. It should be remarked here that a large number of other taxa found in our samples is also capable of permanent or temporary residence in the overlying water (e.g., Chaetognatha, Cladocera, and most larvae), especially when the high current velocities in the region (see above) are taken into account.

A considerable number of larvae or juveniles were encountered. Next to the crustacean and polychaete larvae already mentioned above, an unknown juvenile arthropod, which is probably a recently hatched juvenile amphipod, was encountered. It should be mentioned here that direct development resulting in hatching as a juvenile, i.e., without a nauplius larva, is a feature of all Peracarida (e.g., Amphipoda, Isopoda, Tanaidacea, and Cumacea) and of Cladocera (Williamson 1982). This means that the nauplii encountered in our samples are either from harpacticoid copepods, ostracods or from crustaceans that belong to the macrofauna. Therefore, unlike most other studies, nauplii will be considered separately from harpacticoid copepods here. Judging by their size, the zoea and metazoea are larvae from crustaceans of macrofaunal size and in this respect they are regarded as temporary

meiofauna. Loricifera, Tantulocarida and Bivalvia were only represented by their larvae (Loricifera: "Higgins-larvae"; Tantulocarida: "Tantulus-larvae") or juveniles (Bivalvia).

An overview of the relative abundances and overall average densities of the meiofaunal taxa and larvae associated with cold-water coral degradation zones is given in Table 2A. Overall, the meiofaunal population was dominated by nematodes which made up 67.0 % of the total metazoan meiofaunal community on average. Harpacticoida constituted the second most abundant taxon, comprising 12.6 % of all meiofauna on average. Nauplii were the third most abundant group: they accounted for 7.1 % of the total meiofauna. These results correspond relatively well with the available information on deep-sea meio-infaunal community composition (compiled by Vincx et al. 1994 and Soltwedel 2000), although the observed relative abundance of nematodes is lower than for the meio-infauna in the Porcupine Seabight (Pfannkuche 1985). This relative abundance varies strongly, between 32.7 and 94.7 %, which is due to differences in the type and amount of large biogenic substrates present in the subsamples. These substrates accommodate a community characterized by a significantly lower dominance of nematodes (see below) and higher relative abundances of most other taxa. When only the underlying sediment is considered, nematodes comprise between 71.6 and 94.7 % of the total meiofaunal community, a situation more similar to that of the deep-sea meiobenthos not associated with large biogenic structures on the seafloor (Vincx et al. 1994). Moreover, there are no relevant differences between the meiofaunal community composition on higher taxon level in the underlying sediment of this study and in other deep-sea soft sediments not covered by dead coral framework, at least not for the most abundant taxa.

Next to the three taxa already mentioned, only polychaetes, tardigrades and gastrotrichs have a relative importance of more than 1 %. According to Vincx et al. (1994), polychaetes are indeed the third most abundant taxon in the northeast Atlantic deep-sea meio-infauna (after nematodes and the combined harpacticoids-nauplii).

Only the densities of the meio-infauna in the underlying sediment could be compared with existing data, because no comparable density measurements (ind/l) were made for meio-epifauna in preceding studies and because the accumulation of sedimented material on the substrates obscures the concept of total available surface area for meio-epifaunal organisms. The overall meio-infaunal density of 346 ind/10 cm² found in the present study is below that expected for a depth of 1000 m as indicated by the 'best regression' in Vincx et al. (1994: Fig. 4). This is even more obvious when applying the function given by the same authors, describing the relationship between metazoan meio-infaunal density and depth in the northeast Atlantic, and given as $Y = 2241 - 227 \cdot \ln \text{depth}$. The mean densities (and standard deviations) of the meio-infauna for each examined box core, compared with calculated values for the respective depths, are given in Table 1. It is clear that the observed values are consistently far below the calculated values. Moreover, the mean densities in the Porcupine Seabight area (given as areas 1 and 2 in the considered

graph) appear to have a position far above the 'best regression' trendline depicted in Vincx et al. (1994: Fig. 4), indicating that this area is normally characterized by very high densities. In a final attempt to confirm that the densities found in the present study are exceptionally low, they are compared with data from three studies dealing with samples from the Porcupine Seabight and nearby Goban Spur at a similar depth (Pfannkuche 1985; Vanreusel et al. 1995b; Vanaverbeke et al. 1997). For optimal comparison, it was attempted each time to select the stations from each study that are most comparable in depth with the samples from the present study, i.e., around 1000 m. The average densities, standard deviations and the corresponding calculated values are given in Table 1. The highest mean density in our samples (376 ind/10 cm²: Box IV 2000) is still markedly lower than the lowest value found in literature (509 ind/10 cm²: station II in Vanaverbeke et al. 1997). Moreover, station II in Vanaverbeke et al. (1997) is situated much deeper (1425 m) than Box IV 2000 (1005 m) and therefore the low observed densities in the former are probably due to an effect of depth-related density decrease. Vanaverbeke et al. (1997) attributed their lower density values compared to sites in the Porcupine Seabight to (1) a difference in deposited amount of phytodetritus and (2) differences in sampling gear. Indeed, the Porcupine Seabight is considered an area with exceptionally high organic food input (Billett et al. 1983; Lampitt 1985; Gooday et al. 1996), resulting in very high meiofaunal densities. This contrasts sharply with the low densities observed in our study. Without taking in consideration the current uncertainty about the extent of phytodetrital deposition in the Belgica Mound region, there are several potential explanations for this discrepancy.

Differences in sampling gear and the low efficiency of box corers in collecting meiobenthos may be of importance here, as the studies of Pfannkuche (1985) and Vanreusel et al. (1995b) are based on multiple corer samples. On the other hand, the coral and sponge fragments present at the sample site might act as a sediment trap, preventing resuspension of the sediment and therefore limiting the bow-wave effect generated by box corers. The relative limpidity of the overlying water seems to confirm this last hypothesis. In this case, the presence of large biogenic structures on the seafloor affects the meio-infaunal densities on the sampling site in a positive way. However, their presence may also cause a decline in meiofaunal densities in the underlying sediment as it is thought that the collapsed coral framework and associated substrates act as a kind of 'net', successfully trapping most of the seasonally supplied phytodetritus and in this way limiting the amount of food supplied to the underlying sediment. The high amount of food trapped by the biogenic structures is made unavailable for the fauna in the underlying sediment. It has already been mentioned that meiobenthic densities decrease with decreasing food availability.

Although these large biogenic structures are thought to protect the underlying meio-infauna from physical erosion and removal by strong currents and enable other taxa to dwell among the coral branches, it is not clear to what extent they are able to reduce the impact of strong currents on the underlying sediment. Strong bottom flow may not be adequately decreased under the sediment-clogged cold-

water coral framework. Lower meio-infaunal abundances may therefore be an effect of physical removal of the meiofauna in the upper sediment layers (keeping the fauna in suspension until a time of decreased flow) or an effect of lower microbial biomass due to decreased deposition of food. The relative limpidity of the overlying water as argued above, as well as the presence of a well-established meio-epifaunal community associated with the *Lophelia pertusa* framework as proven by the present study, are however inconsistent with this idea. One should always keep in mind that because of the diurnal and semi-diurnal nature of tidal currents (Rice et al. 1991) the impact on meiobenthos will fluctuate on a short time-scale. This is because the frequently changing current speeds will result in periodic cycles of erosion and deposition. During the latter periods, sediment, food and organisms are redeposited on the seabed and meiofaunal abundances will increase (Aller 1989, 1997).

The presence of small biogenic structures (coral fragments, sponge skeletons, sponge spicules, echinoid radiolas, gastropod and bivalve shells) in the sediment may also have its effect on meiofaunal density. The coarsening of the sediment might particularly affect typical interstitial taxa, such as the dominant nematodes and gastrotrichs, because of its influence on the dimensions of interstitial free space and because the biogenic structures are probably obstacles for organisms crawling between the sand grains. A decrease in nematode density will then directly affect total meiofaunal density. Decreased meiobenthic densities in the underlying sediment can also be explained by high predation pressure by the abundant and diverse macrofaunal community found in association with the sediment-clogged coral framework (Jensen and Frederiksen 1992). A more intense comparison with background sediments is needed to confirm or falsify these and other hypotheses.

In contrast with the underlying sediment, the sediment-clogged coral framework itself is thought to be more densely populated. Because this framework is able to trap sedimented organic food, it can be regarded as a hotspot of abundant food in a generally food-limited environment. Limitation of food is not proven here: on the contrary, fast flows should provide a constant supply of food. It is argued however that fast flows may also interfere with deposition of food and that sediment resuspension due to strong currents makes deposited food less accessible for meiobenthos (see also: Lampitt 1985). This is based on the observed decrease in microbial biomass due to faster flow (Thistle and Levin 1998). As complex biogenic structures may also provide shelter against predation, conditions should be ideal for the development of a rich meio-epifaunal community: low disturbance, low predation pressure and abundant food enable a specific community to be established on and in between the coral branches and sponge skeletons.

Habitat preferences

Within this relatively protected habitat significant differences in meiofaunal community structure were found between the different microhabitats that were distinguished. Only twelve taxa occurred in all four microhabitats (Table 2B). Moreover, on a total of 31 taxa, five taxa were found exclusively on coral fragments, although not in all subsamples. In contrast, only three were found exclusively in the sediment, two on the mixed substrate and not a single taxon was restricted to

sponge skeletons. There were no taxa showing an obligate association with a certain microhabitat in the sense that when a taxon occurred in only one microhabitat it was never found in all subsamples.

The MDS graph given in Figure 3 plots all subsamples relative to each other. There is a high degree of overlap between the different microhabitats in terms of community composition, although on the MDS plot a trend from the upper left corner to the lower right corner (coral fragments - sponge skeletons - underlying sediment) is present. Overall, the image seems however rather complex.

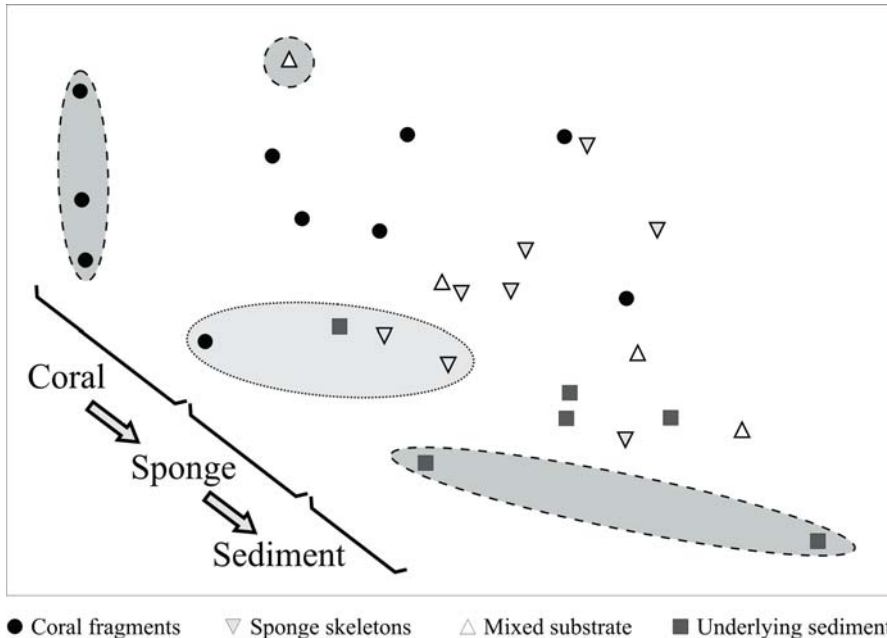


Fig. 3 Multidimensional Scaling (MDS) two-dimensional plot (stress: 0.11) of all subsamples. The subsamples in a pale field surrounded by a dotted line are from the 2001-box core. The subsamples in a darker field surrounded by a dashed line are from the second box core taken in 2000. The trend mentioned in the text is visualized in the lower left corner

ANOSIM showed highly significant ($p = 0.005$) overall differences between the microhabitats. Pairwise tests were carried out and revealed significant differences between the coral microhabitat and all other microhabitats in terms of community composition. It can therefore be concluded that the coral microhabitat houses a very typical and rather unique meiofaunal community. Very highly significant differences ($p = 0.001$) were found between the coral microhabitat and the underlying sediment. This result is in good agreement with the number of taxa found exclusively in each of these microhabitats and the image given by the MDS analysis: the coral fragment subsamples can be clearly separated from the sediment subsamples on the ordination graph.

At this point attention will be focused only on these two extremes. Average dissimilarity (29.7 %) is low, probably because of the large differences between the subsamples within one microhabitat type. More than 50 % of this dissimilarity is caused by four taxa: Harpacticoida (16 %), Nematoda (14 %), nauplii (13.5 %) and Polychaeta (8.5 %). Only nematodes had a significantly higher average relative abundance ($p = 0.0007$) in the sediment subsamples compared to the coral subsamples; all other taxa were relatively more abundant on coral fragments. An indicator species analysis was carried out on all subsamples (including the sponge and mixed subsamples) to elucidate habitat preferences. This yielded three taxa with significant indicator values for coral fragments: nauplii (IV = 74); Harpacticoida (IV = 53) and Polychaeta (IV = 47). Kinorhyncha was the only significant indicator for the sediment subsamples (IV = 40). Nematodes were not identified as indicators for the sediment, although this was put forward by SIMPER and the observed significantly lower relative abundance of this taxon on coral fragments. This is due to the fact that nematodes were still the dominant group on this substrate.

Although nematodes are the dominant group in all microhabitats, they are relatively more important in sedimentary habitats. Because most nematodes are long and slender organisms, they are morphologically more adapted to move between the sand grains than to crawl over a large surface (Giere 1993). Moreover, the presence of interstitial microniches is essential for nematode colonization (Danovaro and Fraschetti 2002). So the presence of sediment is probably essential to ensure a well-developed nematode community. Only those nematodes belonging to the epifaunal families Epsilonematidae and Draconematidae are morphologically adapted to “walk” over hard substrates. These nematodes are known to have a looper caterpillar-like locomotion using ventral setae (*ambulatory setae*: Epsilonematidae) or tubes (*posterior adhesion tubes*: Draconematidae) on their posterior body region, sometimes together with tubes on or near the head capsule (*cephalic adhesion tubes*: Draconematidae) (Fig. 4). A predominance of representatives of these two families on dead *Lophelia pertusa* fragments has been observed (Raes and Vanreusel pers. obs.). The lower dominance of nematodes on coral fragments results in a higher relative abundance of all other taxa. Although some of these taxa are known to be typically interstitial (e.g., Gastrotricha and Tardigrada), only kinorhynchs were found to have a clear habitat preference for the underlying sediment. According to Higgins (1988), kinorhynchs are frequently found in the interstia of medium to coarse sand or gravel. On the other hand, Coull (1988) stated that Kinorhyncha, being for the most part burrowing organisms in muddy sediments, are excluded from interstitial habitats.

The fact that nematodes are still the dominant group on the coral substrate is mainly attributed to the sediment infill between the fragments and coral branches, these substrates are still in close association with the underlying sediment. The community composition of meio-epifauna on cold-water coral fragments is therefore in a broad sense somewhat comparable to the composition of the infauna, however with some important differences as already argued above. On higher taxon level, a meio-epifaunal community is composed of a sediment-dwelling

background community (predominantly nematodes) but with several groups that are more adapted to a life on large biogenic surfaces than nematodes (evidently Harpacticoida, naupliar larvae and Polychaeta from our Indicator Species Analysis),

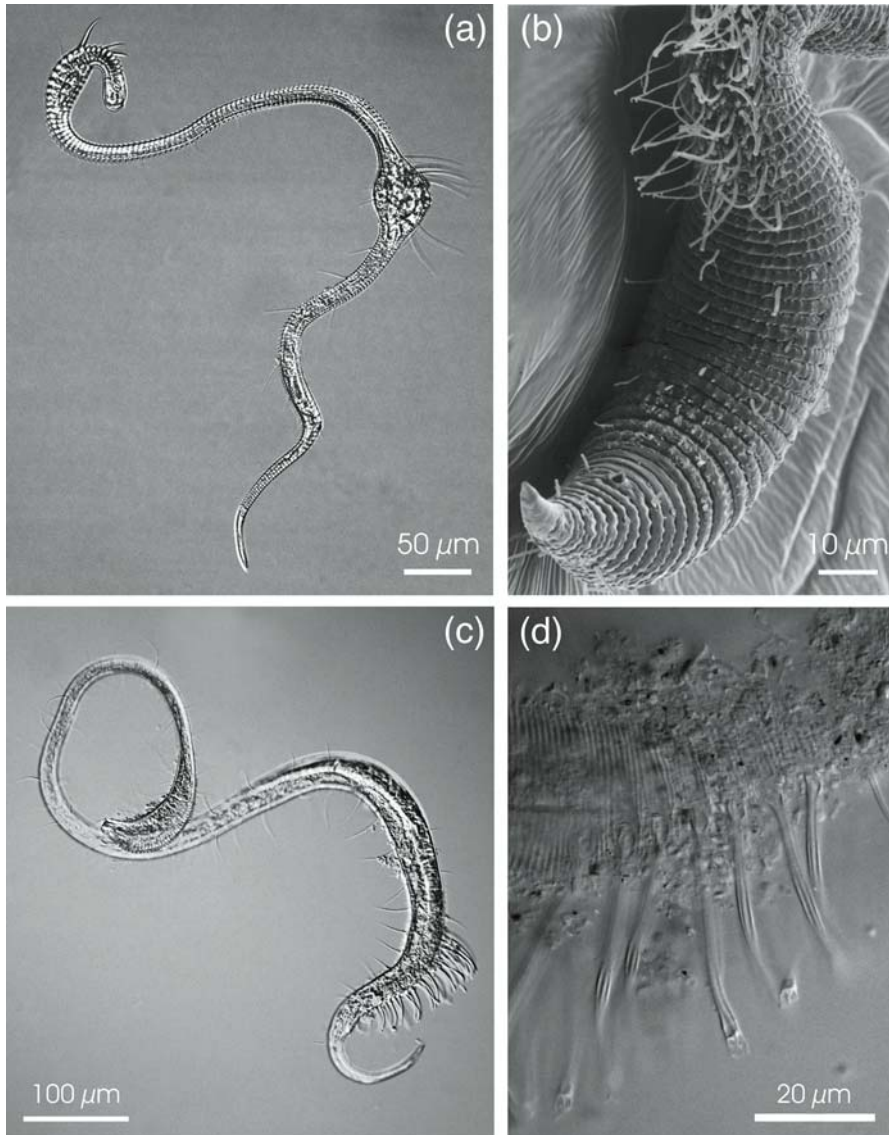


Fig. 4 Some representatives of the nematode families Epsilonematidae and Draconematidae found in the Porcupine Seabight area, and their morphological adaptations to an epifaunal life strategy. **(a)** *Glochinema trispinatum* Raes, Vanreusel and Decraemer, 2003: habitus; **(b)** *Bathyepsilonema lopheliae* Raes, Vanreusel and Decraemer, 2003: ambulatory setae; **(c)** *Tenuidraconema* sp. n.: habitus; **(d)** *Cygnonema* sp. n.: posterior adhesion tubes

showing a significantly increased importance. Although communities found in the sediment are significantly different from those on cold-water coral fragments (see above), it is almost impossible to distinguish between “typical interstitial” and “typical epifaunal” taxa on a higher taxonomic level.

Some dead coral structures may be partly covered with a felty layer of bryozoan colonies that very effectively traps sedimented material. It can be stated that the coral substrate provides a complex habitat for meiofauna because it can possibly be subdivided into even smaller microhabitats: the felty bryozoan encrustation probably combines sediment-dwelling and substrate-crawling taxa; the sediment infill between branches harbours an interstitial fauna; the coral surface is covered with a microbial biofilm and will therefore mainly attract obligate microbial-feeding meio-epifauna, and the cavities within the coral fragments (e.g., those constructed by *Eunice norvegica* (Linné, 1767)) are maybe home to still other communities. These differences within one microhabitat type (dead coral fragments) could then explain the scattered distribution of the coral subsamples in the MDS ordination graph. Analysis of all these very specific microhabitats should be a subject for future research. In the present study, relatively fine-tuned habitat preferences on family-level have been found for nematodes (families Epsilonematidae, Draconematidae) and harpacticoid copepods (families Tegastidae and Laophontidae (H. Gheerardyn pers. comm.)).

Several studies dealing with epiphytic meio-epifauna revealed that this fauna was often dominated by nematodes. In those cases, their relative abundances were rather low, especially compared to infaunal communities (Lewis and Hollingworth 1982; De Troch et al. 2001). Harpacticoida and naupliar larvae are always abundant in epiphytic communities (Lewis and Hollingworth 1982; Jarvis and Seed 1996; De Troch et al. 2001) and several authors reported a shift to a predominance of these two groups in epiphytic samples, especially on seagrass leaves and on macro-algae (Coull et al. 1983; Bell et al. 1984; Hall and Bell 1993 and authors cited herein). These results confirm the observed importance of these two groups as indicator epifauna. The high abundance of naupliar larvae (and copepodites) in seagrass beds has also been attributed to a potential nurseries function (Lewis and Hollingworth 1982; Hall and Bell 1993). It is difficult to say whether this is also the case for cold-water coral degradation zones, although the assumed low disturbance, low predation pressure and abundant food might provide a suitable habitat for larvae and juveniles. Most meiofaunal taxa, and especially nematodes, turned out to be associated with the filamentous epiphytic flora covering the macro-algae and seagrasses (Lewis and Hollingworth 1982; Bell et al. 1984; Hall and Bell 1993; Jarvis and Seed 1996). Algae that accumulate sediment and detritus have a richer nematode community because the sediment provides the interstitial microniches that are crucial for nematodes (Heip et al. 1985). This is an interesting idea, especially when applied to cold-water coral fragments where the coral surface is sometimes covered with a felty layer of bryozoans.

Finally, a comparison between soft-bottom and hard-bottom meiofauna carried out in a shallow environment on the Mediterranean coast (Danovaro and Fraschetti 2002) produced SIMPER-results that are comparable with ours: harpacticoid

copepods were identified as the taxon characterising hard-bottom assemblages and nematodes were identified as responsible for the differences between hard- and soft-bottom community composition.

From the MDS graph given in Figure 3 it is clear that the community structure on sponge skeletons is intermediary between that from coral fragments and that from the sediment, indicating the presence of both infaunal and epifaunal organisms. Because of their intricate structure, these sponge skeletons are able to trap a lot of sediment, in this way stimulating the presence of interstitial taxa. On the other hand, the sponge spicules may act as a substrate for epifaunal forms or as a three-dimensional maze for crawling taxa.

The high number of taxa encountered in this study is attributed to the presence of a large number of different microhabitats that were extensively discussed above. It is hypothesized here that each of these microhabitats favours a community with a different life style and a different composition. The sum of all these separate communities results in a high number of taxa.

Biodiversity

The statement by Jensen and Frederiksen (1992) that the associated fauna of *Lophelia pertusa* is as rich and diverse as that of hermatypic branching species of coral has led to increased efforts to describe the biological diversity of cold-water coral reefs. Although the correctness of this idea is not yet fully proven, for example because tropical coral reefs are much older than cold-water coral reefs and because their diversity is increased by the presence of a higher number of coral species, the presence of coralline algae and a higher diversity in food sources, cold-water coral reefs are without doubt diversity hotspots in the deep-sea. Mortensen et al. (1995) found that diversity is three times higher on the reefs than in the surrounding soft-bottom. In the present study attention is only focused on the dead *Lophelia pertusa* and associated substrates. According to both Jensen and Frederiksen (1992) and Mortensen et al. (1995), the diversity of fauna associated with living *Lophelia* colonies is generally lower than that on dead colonies.

In the foregoing, some strong indications for high taxon diversity, as well as a number of favourable conditions promoting high biodiversity have already been put forward:

1. A total number of 33 groups (taxa and larvae) was identified. This high taxon richness is attributed to the cumulative effect of different communities associated with a large number of different microhabitats due to the process of niche segregation, and due to the lower dominance of nematodes. A possible effect on an even smaller scale (microhabitats within microhabitats) opens up even more perspectives on this subject.
2. Low dominance of the most abundant taxon, Nematoda, and the resulting higher relative abundances of all other taxa was observed. This is thought to be due to the preference of nematodes for interstitial habitats resulting from their morphological (slender body shape) and ecological (feeding strategy, locomotion) adaptations to a life between the sandgrains.

3. It is hypothesized that cold-water coral degradation zones are characterized by high habitat complexity for meiofauna, and that each of the large number of microhabitats favours a certain lifestyle among meiofauna. As each of these lifestyles requires some highly specialized morphological adaptations, several habitat-specific taxa were found, at least on the family level (Nematoda: Epsilonematidae, Draconematidae; Harpacticoida: Tegastidae, Laophontidae).
4. The Porcupine Seabight is an area known to be subject to exceptionally high organic food input (Billett et al. 1983; Lampitt 1985; Gooday et al. 1996). Abundant food might support a higher number of individuals as well as a higher number of taxa. It is however still not clear whether this is also the case for the Belgica Mound region.
5. Large biogenic structures might also act as an efficient food trap. This leads to the idea that cold-water coral degradation zones are possible food hotspots, but associated with an impoverished underlying sediment. Although high food concentrations may support enriched, diverse communities, they can also have a negative effect on biodiversity by creating intensified competitive exclusion of species. According to Lambshead (1993), the occurrence of a spatiotemporal mosaic of small-scale patches, low disturbance and a low amount of nutrients keeps evenness high and prevents competitive exclusion of species, thus resulting in a high regional species pool. In the underlying sediment these three conditions are fulfilled, implying that this sediment may be home to a very diverse meiobenthic community.
6. Moreover, the food deposited in cold-water coral degradation zones will become patchily distributed between the substrate fragments, in this way adding to the process of niche segregation.
7. These biogenic structures are also thought to provide a low-disturbance environment in which the meiofauna is protected against physical erosion (currents) and predation from higher trophic levels. Frequent large-scale disturbances resulting from strong bottom currents might lead to (1) a high-dominance community or (2) destruction of life and/or habitats. High predation intensity will result in competitive exclusion and therefore a community characterized by high dominance.
8. Turnover is known to be very high in meiofauna, especially in nematodes. High turnover rates are attributed to the limited mobility and conservative reproductive method (i.e., lack of larvae with dispersive capacities) in nematodes, characterizing them as biogeographically localized organisms with high speciation rates (Castillo-Fernandez and Lambshead 1990). Combined with the presence of a whole spectrum of small-scale patches within and in between coral and sponge fragments, this could ultimately lead to a high number of species on a small or medium spatial scale.

In conclusion, there is a lot of evidence indicating that cold-water coral degradation zones constitute a highly diverse habitat for deep-sea meiofauna.

Diversity values for the entire meiofauna community associated with this habitat (on higher taxon level) are given in Table 3. At present, no diversity measurements on higher taxonomic level are present for comparison.

Another interesting question is which microhabitat type harbours the most diverse meiofaunal community. A whole spectrum of biodiversity indices, ranging from indices of taxon richness (N_0) to indices of evenness (N_∞ and J), is given in Table 3. An obvious difference in taxon richness between the different microhabitats can also be seen on Table 2B. The exact number of taxa per microhabitat type is given by the overall (b) N_0 in Table 3. Although there are of course differences in microhabitat volume, N_0 gives a good first impression of differences in terms of taxon richness. Clearly, coral fragments house the highest number of taxa ($N_0 = 23$) whereas sponge skeletons are characterized by the lowest number of taxa ($N_0 = 15$). The expected number of taxa for 100 individuals $ET(100)$, an index not influenced by differences in sample size, is also highest on coral fragments. The same is true for H' . Differences between microhabitats are visualized by Box and Whisker plots for H' and J in Fig. 5. As expected, equitability (J) is highest on coral fragments and lowest in the underlying sediment, where nematodes exhibit a high dominance. Except for N_0 , all indices indicate that the sediments are the least diverse and that coral fragments support the most diverse communities. All differences were statistically highly or very highly significant, with the exception of N_0 and $ET(100)$.

It is also very conspicuous that the entire community has much more taxa than either of the separate microhabitats. This result confirms the statement that

Table 3 Biodiversity indices: Hill's diversity numbers N_0 , N_1 , N_2 and N_∞ , the expected number of taxa for 100 individuals $ET(100)$, the Shannon-Wiener diversity index H' and Pielou's evenness J . Under (a) the average value over all subsamples with its standard deviation is given. Under (b) the value for the total community associated with the respective microhabitat is given. (NS): not significant; (**): highly significant; (***): very highly significant

		N_0	$ET(100)$	N_1	H'	N_2	J	N_∞
Coral fragments	(a)	11.30 ± 3.65	7.96 ± 1.58	3.97 ± 1.28	1.33 ± 0.34	2.82 ± 1.00	0.55 ± 0.10	1.90 ± 0.57
	(b)	23	9.65	4.89	1.59	3.24	0.51	2.00
Sponge skeletons	(a)	8.75 ± 2.05	6.25 ± 1.23	2.32 ± 0.33	0.83 ± 0.15	1.63 ± 0.17	0.39 ± 0.06	1.30 ± 0.08
	(b)	15	7.06	2.40	0.88	1.58	0.32	1.27
Mixed substrate	(a)	10.50 ± 6.46	6.81 ± 3.55	2.56 ± 1.36	0.84 ± 0.52	1.68 ± 0.60	0.36 ± 0.14	1.30 ± 0.25
	(b)	20	8.04	2.46	0.90	1.56	0.30	1.26
Underlying sediment	(a)	10.00 ± 2.37	5.93 ± 1.65	1.92 ± 0.60	0.61 ± 0.29	1.37 ± 0.28	0.26 ± 0.11	1.17 ± 0.12
	(b)	19	6.76	2.10	0.74	1.42	0.25	1.20
Entire community		31	8.70	3.46	1.24	2.11	0.36	1.49
p-level		0.52 (NS)	0.16 (NS)	0.0057 (**)	0.0011 (**)	0.0015 (**)	0.000051 (***)	0.0018 (**)

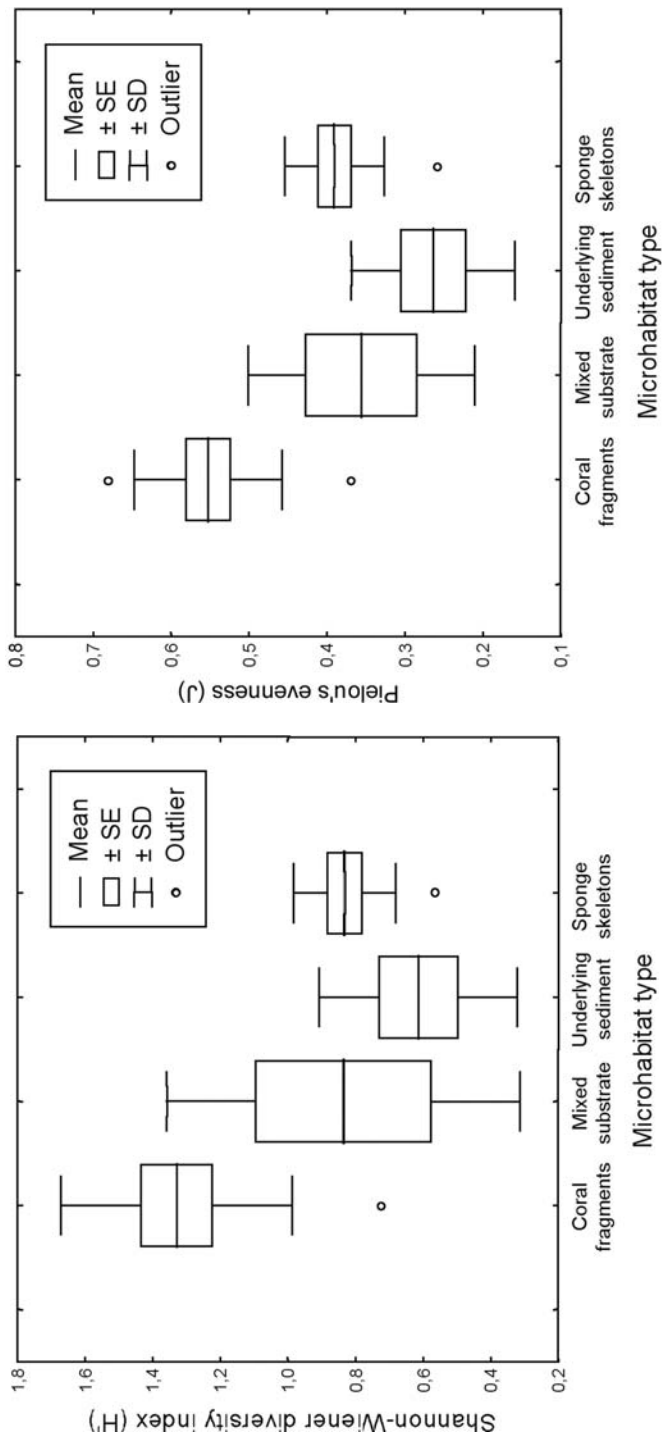


Fig. 5 Box and Whisker plots comparing the microhabitats for the Shannon-Wiener diversity index (H') and Pielou's evenness J , a typical equitability index

the combination of all separate communities results in a high number of taxa (see above).

Conclusions

1. The presence of large biogenic structures on the seafloor of the continental margin (1) enables more taxa to be present and (2) particularly favours harpacticoid copepods, naupliar larvae and polychaetes. The nematode community responds by a shift to a predominance of typical epifaunal nematodes on the coral fragments.
2. The large biogenic substrates are characterized by a meio-epifaunal community that is significantly dissimilar from the meio-infaunal community in the underlying sediment.
3. The meio-epifaunal community is composed of a sediment-dwelling background community (predominantly nematodes); however with several groups that are more adapted to a life on large biogenic surfaces showing a significantly increased importance.
4. The meio-infaunal community in the underlying sediment is characterized by low densities.
5. Cold-water coral degradation zones are assumed to be biologically diverse. This high biodiversity is attributed to:
 - a) lower physical disturbance by strong bottom currents and lower predation pressure by higher trophic guilds.
 - b) a high microhabitat diversity resulting in a high degree of niche segregation. Combined, the communities associated with each microhabitat type give rise to high taxon richness.
 - c) low dominance of nematodes.
 - d) assumed abundant food from seasonally deposited phytodetritus, partly resulting from the suggested efficient food trapping function of the biogenic substrates.
6. Of all four microhabitat types, coral fragments support the most diverse communities, whereas the underlying sediments are the least diverse.

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