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Biodiversity and ecological composition of macrobenthos on cold-water coral mounds and adjacent off-mound habitat in the bathyal Porcupine Seabight, NE Atlantic

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Abstract

The cold-water scleractinian corals *Lophelia pertusa* and *Madrepora oculata* form mound structures on the continental shelf and slope in the NE Atlantic. This study is the first to compare the taxonomic biodiversity and ecological composition of the macrobenthos between on- and off-mound habitats. Seven box cores from the summits of three mounds and four cores from an adjacent off-mound area in the Belgica Mound Province in the Porcupine Seabight yielded 349 species, including 10 undescribed species. On-mound habitat was three times more speciose, and was richer with higher evenness and significantly greater Shannon's diversity than off-mound. Species composition differed significantly between habitats and the four best discriminating species were *Pliobothrus symmetricus* (more frequent off-mound), *Crisia* nov. sp, *Aphrocallistes bocagei* and *Lophelia pertusa* (all more frequent on-mound). Filter/suspension feeders were significantly more abundant on-mound, while deposit feeders were significantly more abundant off-mound. Species composition did not significantly differ between mounds, but similarity within replicates decreased from Galway Mound < Thérèse Mound < off-mound. We propose that, despite having greater vertical habitat heterogeneity that supports higher biodiversity, coral mounds have a characteristic "reef fauna" linked to species' biology that contrasts with the higher horizontal habitat heterogeneity conferred by the action of deposit feeders and a varied seabed sedimentary facies off-mound. Standardisation of equipment and restriction of analyses to higher taxonomic levels would facilitate prospective comparative analyses of cold-water coral biodiversity across larger spatio–temporal scales.
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1. Introduction

The cold-water scleractinian corals *Lophelia pertusa* and *Madrepora oculata* form conspicuous patches, reefs and mounds along the European continental margin (Freiwald, 2002). Clusters of mounds form three mound "provinces" in the bathyal (∼600–1000 m) region of this area off the Irish margin: the Hovland (Hovland et al., 1994; De Mol et al., 2002), Magellan (Huvenne et al., 2002, 2003) and Belgica (De Mol et al., 2002; Van Rooij et al., 2003) mound provinces.

The Belgica mound province (BMP) supports the highest number of mounds, many of which are

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topped by *L. pertusa* and *M. oculata* from the summits down to the flanks. Periods of mound growth are punctuated by significant hiatuses concomitant with glacial cycles, which would have eliminated most reef fauna including the corals (Roberts et al., 2006). Present-day mounds in the BMP are largely asymmetrical and conical in shape (Huvenne et al., 2005) and range in extent from tens to hundreds of metres high and several kilometres across (Wheeler et al., 2005a). Mounds appeared to have been initiated at least 1.65 MYA (Expedition Scientists, 2005) and their evolution reflects interactions between hydrography, sedimentary regime and the accumulation of carbonate from the coral skeletons (Dorschel et al., 2005; De Mol et al., 2005).

Coral mounds in the Porcupine Seabight occur predominantly on topographic ridges influenced by a strong hydrodynamic regime of enhanced currents and seabed erosion that provide hard substrata for benthic recruits (Wheeler et al., 2005a; White, 2006). Intense currents and circulation patterns around coral banks in the region increase surface productivity and enhance rapid transport of fresh organic material for mound fauna while preventing sediments from smothering and burying the corals (White et al., 2005; Kiriakoulakis et al., 2006; White, 2006). The shallow, warm Eastern North Atlantic Water mass interfaces with the deeper, more saline Mediterranean Outflow Water (MOW) mass at about 600–700 m water depth in the vicinity of the coral mounds. MOW dominates the hydrographic setting of the coral mounds in the BMP and presents a salinity maximum/oxygen minimum at about 950 m (Pollard et al., 1996).

The number and spatial extent of the mounds in the BMP, and the habitat complexity associated with the reefs they support, make these structures optimal areas for the development of diverse benthic assemblages. There have been some studies of the mound megabenthos (Wheeler et al, 2005a), macrobenthos (Van Gaever, 2001; De Backer, 2002) and meiobenthos (Raes et al., 2003; Raes and Vanreusel, 2005, 2006) in the BMP. Video observations combined with the sparse quantitative information on the intra-provincial variation in mega- and macrobenthos suggest that significant biological heterogeneity exists within the BMP (Foubert et al., 2005 and references therein; Wheeler et al., 2005a). In this paper, we specifically address the paucity of information regarding intra-provincial variation by comparing macrobenthic biodiversity between on- and off-mound habitats. We also report preliminary data regarding intra-mound variability in biodiversity, and discuss solutions to mitigate difficulties surrounding the measurement of biodiversity in these ecosystems.

2. Materials and methods

2.1. Coral mounds in the BMP

The BMP is the southernmost of the three coral mound provinces in the Porcupine Seabight (Fig. 1). Several mounds (Galway Mound, the Moira Mounds and Thérèse Mound) in the western region of the BMP were investigated during the R.V. *Polarstern* expedition ARK XIX/3a in June 2003, a cruise jointly organized by the Alfred-Wegener-Institut für Polar- und Meeresforschung (AWI) and l'Institut français de recherche pour l'exploitation de la mer (IFREMER) (Table 1, Fig. 2). "Off-mound" areas were characterised either by a dropstone facies, or by occasional dropstones on either a rippled or an unrippled seabed, the appearance of which suggested a generally northward directed slope current (Foubert et al., 2005).

The Galway Mound is a giant double-peaked carbonate mound approximately 100 m in height, over 1.6 km long and 800 m across. The summits and flanks of this mound are topped by dense reefs
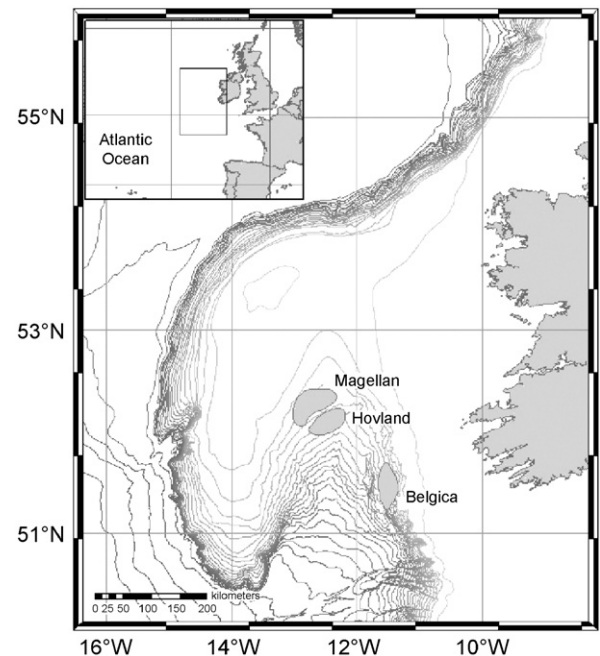

Fig. 1. Location of the three mound "provinces" in the Porcupine Seabight, southwest of Ireland.

Table 1
Summary of box core stations obtained from the BMP in June 2003 (adapted from Klages et al., 2004)

Box core	On/off mound	Latitude/ longitude	Depth (m)	Core description
254-1	GM	51°26.970′N/ 11°45.002′W	857	*M. oculata*, *L. pertusa*, glass sponges, coral rubble
254-2	GM	51°27.144′N/ 11°45.079′W	852	*M. oculata*, *L. pertusa*, glass sponges
254-3	GM	51°27.282′N/ 11°45.039′W	875	*M. oculata*, *L. pertusa*, hydroids, bryozoans
254-4	GM	51°27.056′N/ 11°45.142′W	798	*M. oculata*, dead *L. pertusa*, crab, shrimp, glass sponges, fine coral debris
258-1	OM	51°26.541′N/ 11°44.681′W	910	*M. oculata*, hydrocorals, glass sponge fragments, medium to coarse sand
263-1	OM	51°26.130′N/ 11°43.970′W	921	Hydrocorals, urchin, dead *L. pertusa*, mollusc shell debris, coarse sands, dropstones 1–30 cm diameter
263-2	OM	51°25.990′N/ 11°44.346′W	927	Hydrocorals, molluscs, coarse to fine sand, dropstones 1–10 cm diameter, pebbles/lag
263-3	OM	51°25.895′N/ 11°45.025′W	942	Coral rubble, pebbles <5 cm, coarse sand with shell fragments, muddy clay below
270-1	MM	51°25.960′N/ 11°45.280′W	942	*M. oculata*, molluscs, glass sponges, medium grained sand with forams, shell fragments and coral debris
271-1	TM	51°25.750′N/ 11°46.180′W	900	Glass sponges, octocorals, hydroids, bryozoans, dead large *L. pertusa* colonies
271-2	TM	51°25.766′N/ 11°46.253′W	919	Glass sponges, octocorals, coral rubble, polychaetes

GM = Galway Mound, MM = Moira Mound, TM = Thérèse Mound, OM = Off-mound.

of *L. pertusa* and *M. oculata*, and thus it is termed a fully "active" mound (Huvenne et al., 2005).

The Moira Mounds are clusters of hundreds of small, mostly subcircular-shaped mounds, about 5–10 m high and 15–40 m across (Wheeler et al., 2005b). They occur in areas of active sediment transport on rippled sand sheets, with glacial dropstones and corals scattered between mounds (Foubert et al., 2005; Wheeler et al., 2005b). These mounds may represent the "incipient" early developmental stage of large carbonate mounds (Wheeler et al., 2005b) and have probably formed relatively recently (Huvenne et al., 2005).

Thérèse Mound is another giant carbonate mound, reaching heights of 100–140 m high and about 1.3 km long and 650 m across. The seabed facies consists mostly of live and dead coral, or occasionally sandy sediments and rippled sands (Huvenne et al., 2005; De Mol et al., 2005). Thérèse Mound is another example of an active mound, with dense coverage of *L. pertusa* and *M. oculata* at the mound summits.

2.2. Box coring

Samples were collected 7–9 June 2003 during the ARK XIX/3a expedition. A single 0.25 m^2 spade box

core was deployed at each of 11 sites (Table 1) following a reconnaissance survey by the remotely operated vehicle (ROV) *VICTOR 6000*. On-mound box coring targeted the mound summits. All core contents were photographed (Fig. 3), washed through 1000, 500 and 250 μm sieves, fixed in 10% borax-buffered formalin made with filtered seawater and transferred later into industrial methylated spirit. Macrobenthos (>500 μm) were enumerated and identified to the lowest possible taxonomic level.

2.3. Statistical analyses

2.3.1. Taxonomic biodiversity

Four univariate biodiversity measures were estimated on untransformed data using "DIVERSE" in PRIMER version 5 (Clarke and Gorley, 2001). The total number of distinct species identified (s) was enumerated for each box core. Richness (d) was estimated using Margalef's index as $d = (s - 1)/\log N$, where N is the total number of individuals in the sample. Shannon's diversity (H') was estimated as $H' = -\Sigma_i p_i(\log_{10} p_i)$ and where p_i is the relative abundance of the ith species in a sample. Pielou's evenness (J') was estimated as $J' = H'_{obs}/H'_{max}$, where $H'_{obs} = H'$ and H'_{max} is the highest possible H' if all species are equally abundant. Colonial
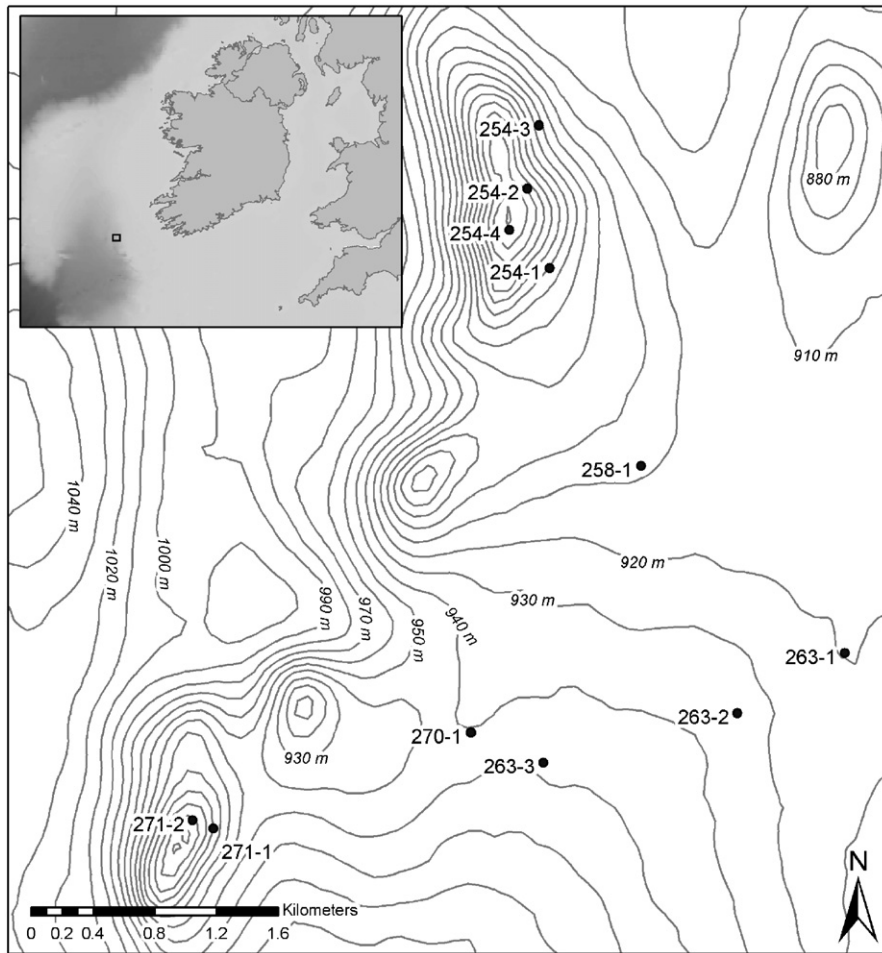
Fig. 2. Sampling locations of the 11 box cores collected by the ARK XIX/3a expedition. Refer to Table 1 for station co-ordinates and box core contents.

macrobenthos (i.e., "pseudo-colonial" sponges and colonial anthozoans, hydroids, bryozoans) frequently fragment and detach from their substrata during box coring and processing. Thus, only the presence or absence of these animals was enumerated and for this reason they were excluded from d, H' and J' estimates. Differences in univariate measures between the on- and off-mound habitats were evaluated using two-tailed non-parametric Mann–Whitney U-tests.

Two methods of surveying distributional patterns in macrobenthic biodiversity were examined using PRIMER. First, sample-based species accumulation curves were visually contrasted using "species–area plot". Because species density varied between box cores, it was not possible to compare richness between the curves (Gotelli and Colwell, 2001). Instead, we compared curves in order to examine

the rate at which new species were encountered in each habitat. Second, a cumulative k-dominance curve was constructed using "dominance plot" based on the abundances of solitary (non-colonial) species in order to visually contrast species dominance between habitats.

Multivariate ordination and analyses were performed using PRIMER. "SIMILARITY" generated a matrix of pairwise Sörensen indices based on presence/absence data that were ordinated into a non-metric multi-dimensional scaling (nMDS) and a cluster plot. Differences between on- and off-mound habitats were examined using analysis of similarity percentages ("ANOSIM") that estimates R, the degree to which species composition differed between habitats. Similarity of percentages ("SIMPER") was used to identify species that could potentially discriminate between habitats.
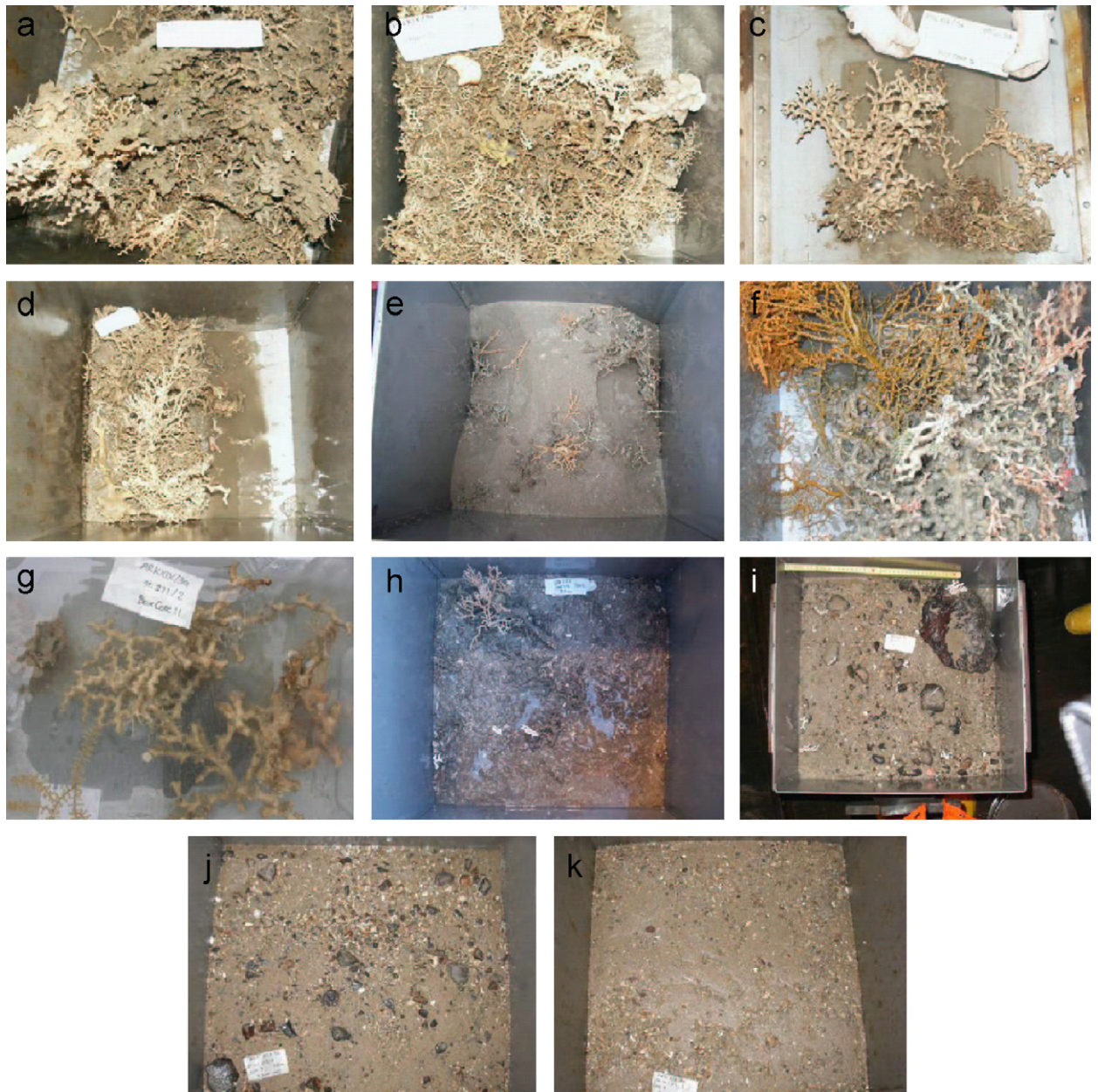
Fig. 3. Box core contents from on- and off-mound habitats in the BMP. Live and dead coral densely colonized by epifauna were typical components of box cores on GM (a–d), MM (e) and TM (f and g). Dropstones, pebbles and coarse to fine sandy sediments colonized by the hydrocoral *Pliobothrus symmetricus* were commonly found in cores obtained off-mound (h–k). All photos credited to the shipboard party of the R.V. *Polarstern* cruise ARK XIX/3a.

2.3.2. Ecological composition

Macrobenthos encompassed all the animals that use coral framework or rubble as habitat, whether it is live or dead, as well as the fauna found in underlying sediments, or on hard inert substrata. Thus, we expected there to be differences in the ecology of macrobenthos between habitats. When the biology of a species was well understood (e.g., a bryozoan is a filter/suspension feeder), this species was categorized into a feeding guild according to feeding methods and source of food: carnivores, detritivores, deposit feeders, omnivores, and filter/suspension feeders, similar to the approach of Jonsson et al. (2004). One off-mound box core

contained only four species, all sessile filter/suspension feeders: thus, this outlier was omitted from these analyses to prevent skewing of the results. As colonial animals and sponges were not enumerated beyond presence/absence, analyses included these animals but their abundances were binomially transformed i.e., one or zero. Thus, the proportions of filter/suspension feeders and sessile species were conservatively estimated. Differences in the feeding and mobility guild composition of macrobenthos were examined using two-tailed Mann–Whitney U-tests on abundances of each guild standardised to the total abundance between habitats.

Statistical significance in all cases was set *a priori* at $p = 0.05$.

2.4. Environmental context

Macrobenthic sampling was complemented with short-term *in situ* monitoring of the near-bed current and sedimentary regime experienced on Galway Mound using a benthic "photolander". The photolander supported several still cameras, a transmissometer, light scattering sensor, fluorometer, and a three-dimensional recording current metre with a CTD and temperature logger. A video transect was run across Galway Mound by the ROV *VICTOR 6000*. The photolander was deployed at 51°27.09′N, 11°45.24′W at 824 m water depth by lowering it to within 20 m of the seabed, and releasing the mooring using an acoustic release. The photolander was deployed 8 June 2003 and recovered by the R.V. *Celtic Voyager* on 9 July 2003 (Roberts et al., 2005).

Initial photolander analyses demonstrated an intense current and dynamic sedimentary regime on the mound with a maximum recorded velocity of $70 \, \text{cm s}^{-1}$. The residual northwesterly current flow of $13.6 \, \text{cm s}^{-1}$ exceeded $50 \, \text{cm s}^{-1}$ on all diurnal tidal cycles 2–3 days either side of spring tides. Maximum mean daily currents occurred at diurnal spring tides and the minimum at neap tides (Roberts et al., 2005).

3. Results

3.1. Species

A total of 349 species from 16 phyla was identified from the 11 box cores (313 on-mound, 102 off-mound). Of these, 18% occurred in both habitats, and over one third (36%) occurred only on Galway Mound. Overall, annelids, crustaceans, molluscs and cnidarians were the richest groups (Table 2 and Appendix A). Most species had bathyal, temperate affinities and coastal, boreal and arctic species represented a minor component of the faunas. At least 10 of the species, eight of which inhabit Galway Mound, are undescribed (Appendix A). The number of new species is likely to increase as more material is studied by taxonomic specialists.

3.2. Biodiversity

Box core contents from Galway Mound suffered varying degrees of washing out upon recovery, as large coral fragments prevented cores from being fully sealed. Yet s and d on-mound were still nearly double that found off-mound, although these differences were not statistically significant ($U = 19.5$, $p = 0.315$ and $U = 18.0$, $p = 0.527$, respectively) (Fig. 4). Although solitary species were always more speciose on-mound, the reduction in the proportion of colonial species from 30% on-mound to 18% off-mound contributed to the lower number of species off-mound.

Both H' and J' were higher on-mound than off ($U = 26.0$, $p = 0.024$ and $U = 20.0$, $p = 0.315$, respectively) although only the former was significantly greater. Off-mound, the most common species was the nematode *Synonchus* cf *acuticaudata*

Table 2
Taxonomic composition of macrobenthos identified from all box cores

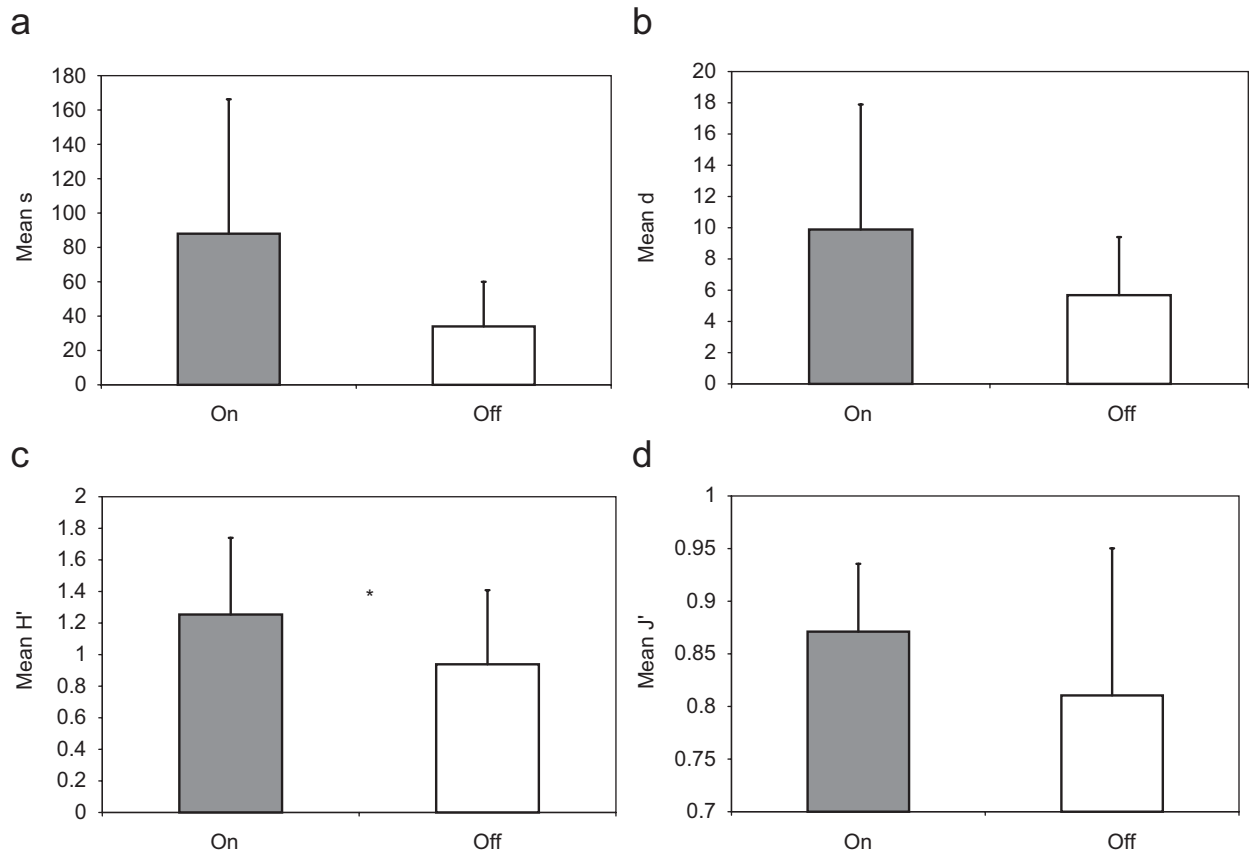| Taxonomic group	Number of species
Annelida	81
Crustacea	75
Cnidaria	52
Mollusca	47
Bryozoa	17
Porifera	17
Echinodermata	11
Nematoda	11
Sipuncula	10
Foraminifera	7
Indeterminate	7
Brachiopoda	5
Echiura	3
Acari	2
Pycnogonida	2
Chaetognatha	1
Hemichordata	1

a

b

c

d

Fig. 4. Taxonomic diversity (a. richness, b. Margalef's, Shannon's diversity, d. Pielou's evenness) between on- and off-mound areas. Error bars represent + one standard deviation. The symbol "*" indicates statistical significance at $p = 0.05$.

making up 17% of the individuals. In contrast, the most common species on-mound was an unidentified paraonid polychaete comprising only 6% of all individuals.

The number of new species encountered by successive sampling increased more rapidly on-mound than off (Fig. 5). The on-mound curve was not punctuated by "jumps" in the number of accumulated species as a new mound was sampled. Both curves seem to reach an asymptote, at least within the vicinity of the approximately 16 km^2 study area.

Dominance was lower in on-mound than in off-mound habitats (Fig. 6). The isopod *Janira maculosa*, the bivalve *Delectopecten vitreus*, the unidentified paraonid polychaete, the bivalve *Asperarca nodulosa* and the polychaete *Syllidia armata* were the five proportionally most abundant on-mound animals. The nematodes *Synonchus* cf *acuticaudata* and *Cylicolaimus* cf *magnus*, the amphipod *Haploops setosa*, the unidentified paraonid polychaete

and the pycnogonid *Pantopipetta armoricana* were the most abundant animals off-mound.

The hexactinellid sponge *Aphrocallistes bocagei*, the unidentified paraonid polychaete, *Crisia* nov. sp., *Lophelia pertusa* and the hydroid *Eudendrium* sp. 1 were the most common animals in on-mound habitats. In contrast, off-mound habitat was characterised by the stylasterid hydrocoral *Pliobothrus symmetricus*, the pycnogonid *Pantopipetta armoricana*, the nematodes *Synonchus* cf *acuticaudata* and *Cylicolaimus* cf *magnus* and the unidentified paraonid polychaete. Habitats differed significantly in their taxonomic composition ($R = 0.323$, $p = 0.033$). The first four discriminating species were *Pliobothrus symmetricus* (more frequent off-mound), *Crisia* nov. sp., *Aphrocallistes bocagei* and *Lophelia pertusa* (all more frequent on-mound) (Fig. 7). These species explained less than 5% of the variance between habitats, and on-mound sites were more speciose (313 species) than those off-mound (102 species); thus it was simply the presence or
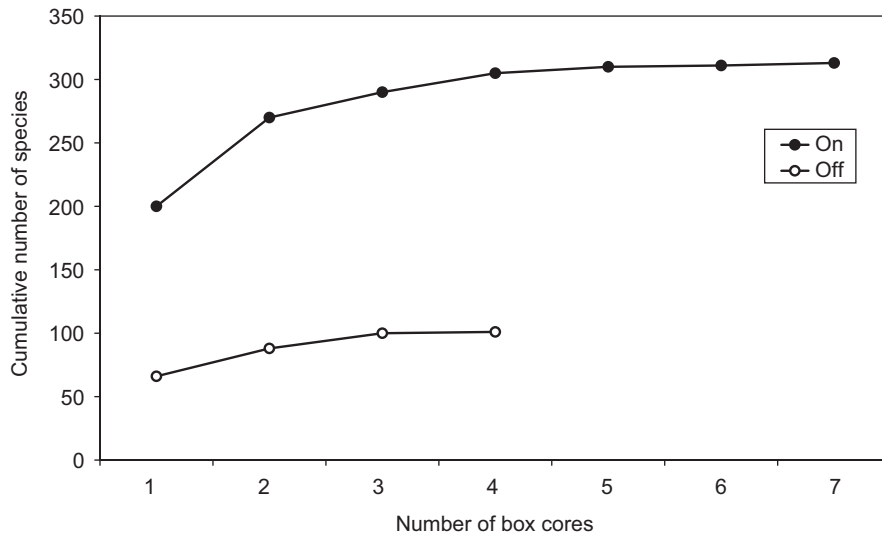
Fig. 5. Species accumulation curves demonstrate the considerably steeper increases in the number of new macrobenthic species encountered on- versus off-mound.
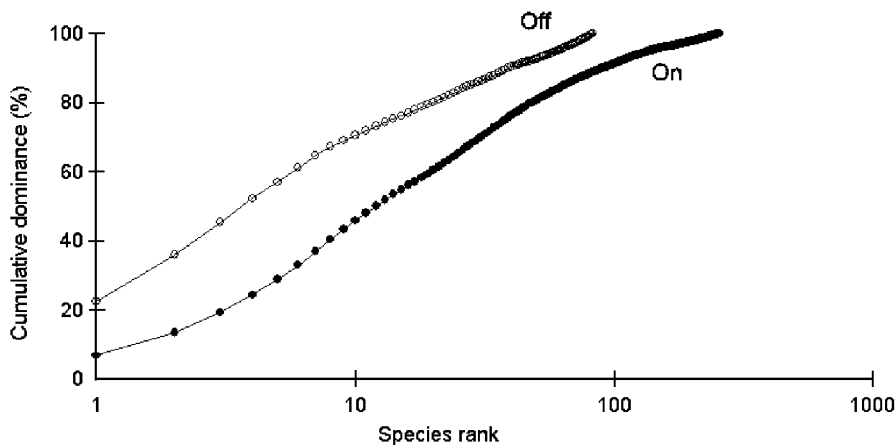

Fig. 6. *k*-dominance curve for solitary macrobenthos contrasted between on- and off-mound habitats.

absence of most species that generated the significant difference between habitats. A *post-hoc* SIMPER analysis of the similarity among replicates from each mound and in the off-mound habitat showed the following sequence of decreasing similarity: Galway Mound > Thérèse Mound > off-mound habitat (46%, 30%, to 18% similarity, respectively). A *post-hoc* multivariate dispersion (MVDISP) analysis in PRIMER (Warwick and Clarke, 1993) also showed greatest variability among replicates (i.e., higher "relative dispersion") off-mound, and Galway Mound replicates were comparatively less variable in comparison to

those on Thérèse Mound and off-mound (i.e., the "index of multivariate dispersion" approaches -1, Table 3). The lack of replicates for the Moira Mound precluded it from analysis. SIMPER and MVDISP results are supported by the nMDS and cluster ordinations (Fig. 8).

3.3. Ecological composition

3.3.1. Feeding guilds

Relative proportions of carnivorous and filter/suspension feeding species were higher on-mound, but this was only significant for filter/suspension
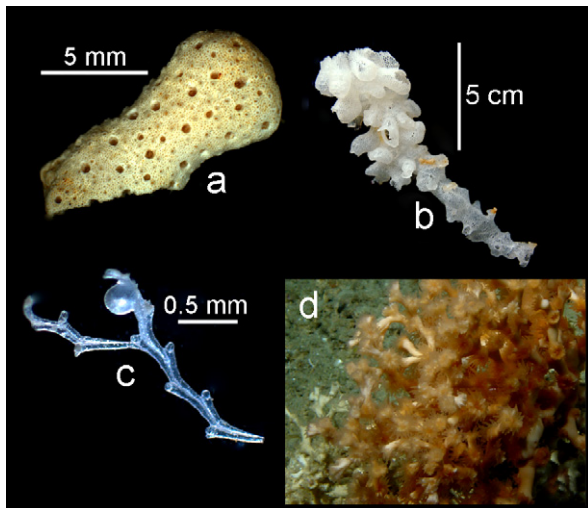
Fig. 7. Species that best discriminated between on- and off-mound habitats: the hydrocoral *Pliobothrus symmetricus* (a), the hexactinellid sponge *Aphrocallistes bocagei* (b), a new bryozoan species *Crisia* nov. sp. (c) and the scleractinian coral *Lophelia pertusa* (d) (no scale available, photo credited to AWI and IFREMER).

Table 3
Multivariate dispersion between mounds and off-mound habitat

Area	Relative dispersion
Galway Mound	0.548
Thérèse Mound	1.286
Off-mound	1.405
Pairwise comparison	Index of multivariate dispersion
Galway Mound, Off-mound	−0.889
Galway Mound, Thérèse Mound	−1
Off-mound, Thérèse Mound	0.333

feeders ($U = 13.0$, $p = 0.666$ and $U = 21.0$, $p = 0.0167$, respectively, Fig. 9). The five most characteristic on-mound filter/suspension feeders were *Aphrocallistes bocagei*, *Crisia* nov. sp, *Lophelia pertusa*, *Eudendrium* sp. 1 and *Asperarca nodulosa*. Relative proportions of detritivores, omnivores and deposit feeders were higher off- than on-mound, but these differences were statistically significant only for deposit feeders ($U = 13.0$, $p = 0.666$, $U = 11.0$, $p = 1$ and $U = 21.0$, $p = 0.017$, respectively, Fig. 9). Recall that the deposit-feeding nematodes *Synonchus* cf *acuticaudata* and *Cylicolaimus* cf *magnus* were the numerically dominant species off-mound.

3.3.2. Mobility guilds

Sessile fauna (characterised by *Aphrocallistes bocagei*, *Crisia* nov. sp., *Lophelia pertusa*, *Eudendrium* sp. 1 and *Sertularella tenella*) were proportionally more abundant on-mound than off-mound. Mobile fauna (characterised by *Synonchus* cf *acuticaudata* and *Cylicolaimus* cf *magnus*, *Lumbrineris tetraura* and *Glycera* sp. 1 and *Pantopipetta armoricana*) constituted a greater proportion of the fauna off-mound than on-mound. However, no significant differences in mobility guild composition was detected between habitats, at least not at $p = 0.05$ ($U = 19.0$, $p = 0.067$ and $U = 19.0$ and $p = 0.067$, respectively).

4. Discussion

4.1. Trends in biodiversity

Higher s, total abundance, and a more equitable distribution of specimens among species explain the higher values of d, H' and J', (Fig. 4), the greater rate of species accumulation (Fig. 5), and the lower dominance of species in these samples (Fig. 6) on-mound. Despite these differences, no species approached the level of dominance encountered in shallow-water habitats (often $> 80\%$), a result that is consistent with the low relative abundance of individual species (usually $< 10\%$) reported on coral mounds in the BMP (De Backer, 2002) and in other deep-sea habitats (Grassle and Maciolek, 1992).

Interestingly, we did not observe "jumps" in the number of new species encountered as a new mound was sampled. The potential for large coral/sponge fragments to trap sediments in a box core sample (after Raes and Vanreusel, 2005) and thereby limit displacement of surficial sediments and fauna (Bett et al., 1994) is unclear. In the case of Galway Mound, sampling of the sediment-dwelling macrofauna was not strictly quantitative. Yet despite the washing out of sediment-dwelling biota from cores on Galway Mound, this mound appeared to be one of the most highly biodiverse in the BMP, and may possibly serve as a source of larvae for other mounds in various developmental stages. Many species found exclusively on-mound are capable of long-distance dispersal e.g., *Delectopecten vitreus* (Dijkstra and Gofas, 2004), which was also one of the most numerically abundant species on Galway Mound (up to 66 individuals/0.25 m^2). The widespread distribution of corals, reefs and mounds on
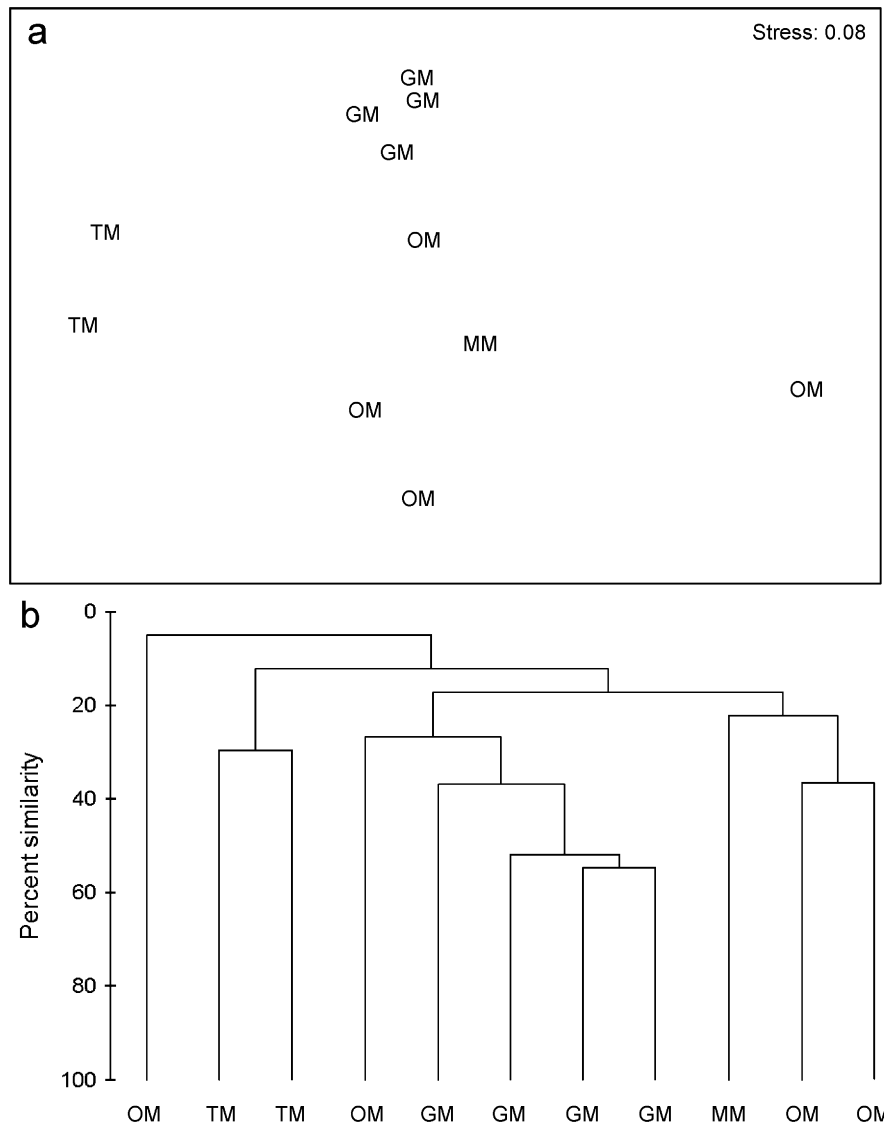
Fig. 8. nMDS (a) and cluster (b) ordinations of macrobenthic assemblages from on-mound (GM = Galway Mound, MM = Moira Mound, TM = Thérèse Mound) and off-mound (OM) habitats.

the European continental shelf and slope could also have significant consequences for the biogeography of deep-water faunas with more restricted dispersal. This is suggested by the fact that many of the species identified in the present study also live amongst deep-water corals in geographically distant regions (e.g., Henry and Roberts, 2006), implying that they may be using coral substrata to colonize successively more distant locations where their habitat requirements (e.g., exposure to sedimentation, predation, competition) are met. Thus, the continuity of coral mound fauna is likely to be controlled by

larger-scale regional effects over geological time-scales such as species differentiation and landscape ecology, but refined by the effects of local-scale factors governed on ecological timescales, such as habitat conditions (Gage, 2004; Witman et al., 2004).

Despite the potential for mound macrobenthos to disperse between distant locations, the dominant megabenthos in the BMP coral mounds differed from other European cold-water coral reefs. Images from the photolander demonstrated conspicuous megabenthos of the BMP to include octocorals,
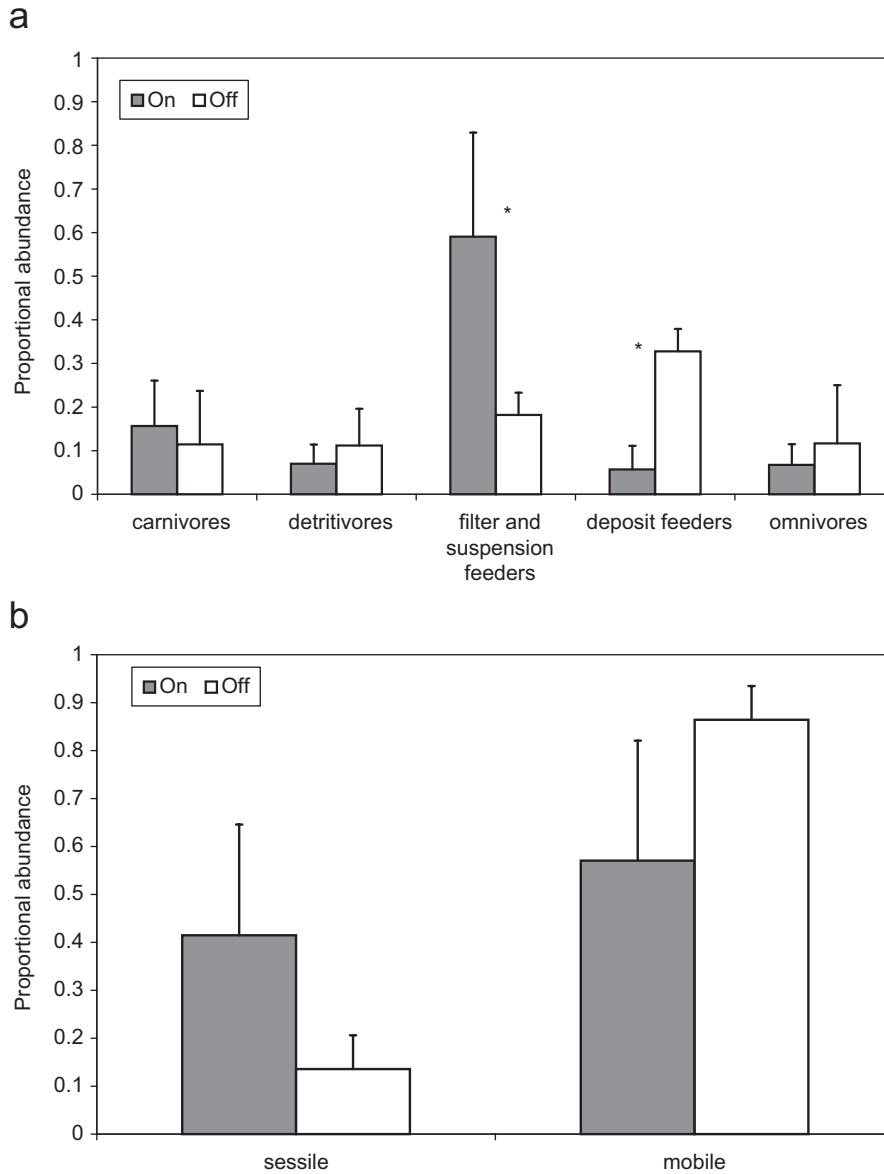
a

b

Fig. 9. Ecological diversity (a. trophic guild composition, b. mobility guild composition) between on- and off-mound areas. Error bars represent + one standard deviation. The symbol "*" indicates statistical significance at $p = 0.05$.

black corals (*Stichopathes* sp.), anemones and hexactinellid sponges (also reported by Olu-Le Roy et al., 2002; Klages et al., 2004; Foubert et al., 2005; Wheeler et al., 2005a). Crinoids and ascidians dominated the macro- and megafauna in a shallow Swedish fjord (Jonsson et al., 2004), while gorgonians and demosponges dominated reefs in Norwegian fjords (Mortensen et al., 1995). Differences could be attributed to variability in hydrography, topography and the biological traits of the species themselves, all of which mediate effects of

reef/mound size and habitat complexity (Ricklefs and Lovette, 1999). Once the variation in sampling methodology and analyses are resolved (discussed later), the effects of large- and smaller-scale factors on cold-water coral biodiversity can be tested.

We demonstrated significant differences in the taxonomic composition of assemblages between habitats. The epilithic stylasterid hydrocoral *Pliobothrus symmetricus* best characterised off-mound habitat, and best discriminated between habitats (Fig. 7). Stylasterid distribution is linked to the

presence of hard substrata such as dropstones and the absence of spatial competitors such as azooxanthellate scleractinians (Cairns, 1992; Tendal et al., 2005) (Table 1), conditions met in the off-mound habitat. Interestingly, pycnogonid larvae were reported in the gastric cavities of gastrozooids of *P. symmetricus* in the western Atlantic (Zibrowius and Cairns, 1992). This symbiosis may explain the high incidence of species co-occurrence (72.7%) estimated *post-hoc* between *P. symmetricus* and the pycnogonid *Pantopipetta armoricana*.

We also reported increasing dissimilarity and relative dispersion between assemblages moving from on- to off-mound habitats (Table 3). On-mound cores were geographically more clustered than off-mound cores (Fig. 2); thus, a higher dissimilarity or dispersion would be expected. However, increasing dissimilarity with increasing distance from the reef was also evident between more equidistant transects of *L. pertusa* reefs in Swedish fjords (Fig. 6 in Jonsson et al., 2004), although this trend was not discussed. We predict that dissimilarity or dispersion increases from the mound summit to the flanks and to the off-mound habitat, in proportion to a decrease in vertical habitat heterogeneity but an increase in horizontal habitat heterogeneity conferred by local fauna and a varied low relief seabed facies (discussed later).

As mentioned earlier, we identified mound assemblages as consisting primarily of *L. pertusa*, glass sponges, and other colonial epifauna. Many other animals were found exclusively on-mound, their associations with corals and sponges being highly predictable. Restricted on-mound distribution of the gnathiid isopods *Caecognathia abyssorum* and *Gnathia dentata* might reflect their affinities for the hexactinellid sponges that characterised the on-mound habitat (Klitgaard, 1991). Hexactinellid sponges and their shed spicules may also enhance benthic biodiversity (Bett and Rice, 1992). Porifera were noticeably absent from the off-mound habitat, which may be partly explained by the lack of dead coral framework upon which these mostly calcareous sponges settle in the bathyal Porcupine Seabight (Könnecker and Freiwald, 2005). Entire families also demonstrated strong associations with the coral mounds. Ten out of 12 species of syllid polychaetes, a family commonly living symbiotically with sponges and corals (Martin and Britayev, 1998; López et al., 2001; Martin et al., 2002) including *L. pertusa* (Flach et al., 2002), were found solely on-mound. Another coral-symbiont, the eunicid polychaete *Eunice norvegica*, was also found exclusively on-mound and seems to exploit *L. pertusa* as habitat by aggregating coral fragments and contributing to reef growth (Roberts, 2005). Thus, although mound fauna are not locally endemic but typically derived from regional species pools, a characteristic yet facultative reef fauna distinguishes coral mounds from other habitats in the BMP.

4.2. Trends in ecological composition

Differences in trophic and mobility guilds between habitats in the BMP (Fig. 9) were similar to those reported by Flach et al. (2002) and Jonsson et al. (2004) for *Lophelia* reefs on Galicia Bank at 770 m depth and in a shallow Swedish fjord; a higher abundance of filter/suspension feeders and sessile fauna occurred on-mound, while a higher abundance of deposit-feeders and mobile fauna occurred off-mound (although the latter was statistically insignificant in the present study). Deep-water corals, reefs and mounds occur in areas of fast currents and internal waves (Frederiksen et al., 1992; White et al., 2005; White, 2006) where particle encounter rates are highest (Thiem et al., 2006). Greater resuspension of particulate organic matter (POM) and low sediment deposition in high-energy habitats in the NE Atlantic could explain the significantly greater proportion of filter/suspension feeders on-mound. Conversely, weaker currents and higher POM sedimentation rates may sustain proportionally more deposit feeders off-mound (Flach and Thomsen, 1998; Flach et al., 1998, 2002; Lavaleye et al., 2002; Witbaard et al., 2005). Deposit feeders may have profound effects on the structure of local assemblages in off-mound habitat. Their bioturbation and burrowing activities are sufficient to agitate sediments in bathyal environments (Lampitt et al., 1986; Smith et al., 1986), disturbances that could increase species dominance in the deep-sea (Grassle and Maciolek, 1992). Thus, the abundance and more widespread activities of deposit feeders off-mound may explain the dominance of a few species not observed on the coral mounds (Fig. 6). Alternatively, a higher proportion of deposit feeders off-mound could reflect the loss of sediment-dwelling animals such as nematodes from cores on Galway Mound. However, neither mean abundance nor diversity (*s*, *d*, *H'* or *J'*) of the nematode fauna differed between habitats (*p* all > 0.05, measured *post-hoc* by Mann–Whitney *U* tests).

The significantly greater proportion of filter/suspension feeders in the on-mound habitat must be interpreted cautiously, given the *a priori* decision to binomially transform the abundances of colonial epifauna that were fragmented by the box core. Nevertheless, we consider our trends to represent genuine differences in the relative abundance of filter/suspension feeders between habitats for two reasons. First, sessile fauna (85% of which were filter/suspension feeders) were over twice as proportionally abundant on-mound than off-mound (Fig. 9). Second, the mean number of colonial species (100% of which were filter/suspension feeders) was nearly five times greater on-mound (29 species) than off (six species). The distribution and diversity of sessile colonial fauna are inherently related to the greater occurrence of skeletal framework and hard substrata in general found on-mound versus off (seen in Fig. 3).

4.3. Effects of vertical versus horizontal habitat heterogeneity on reef fauna

We propose that, within the area sampled by the box core, coral mounds in the BMP have high vertical habitat heterogeneity (living/dead coral, rubble, sediment-clogged framework, etc.) and thus high biodiversity, which foster a predictable or "characteristic" reef fauna. This situation contrasts with higher horizontal habitat heterogeneity in the off-mound habitat, which would experience greater disturbance from the action of deposit feeders and was characterised by a varied seabed facies of glacial dropstones and rippled sands over a low relief horizontal gradient that would not have been sampled in its entirety by the $0.25 \, \text{m}^2$ box core.

4.4. Future sampling considerations

The largest scale comparison of biodiversity of cold-water coral ecosystems was conducted by the EU-funded Atlantic Coral Ecosystem Study (ACES). This study examined trends in reef biodiversity from the Sula Ridge (Norway) to Galicia Bank (west of Spain) (Roberts et al., 2006). Differences could not solely be attributed to regional effects. In particular, this study recommended that future comparisons adhere to strict standardisation of sampling and taxonomic protocols to address major disparities in methodologies used by different partners. Specifically, sampling

protocol and equipment should be standardised by using equipment with integrated video to locate and adequately penetrate coral habitat with limited washing out of sediment. Initial sorting could be concentrated in one or two laboratories to improve faunal identification, while taxonomic accuracy could be achieved through the creation of a network of participant experts. Where the same equipment has not been used, comparisons could be made by restricting data to attached epifauna standardised to coral volume or biomass, transforming data to presence/absence, or confining data to higher taxonomic levels. These measures should all be complemented by environmental data obtained by instrumented moorings and *in situ* long-term observatories (Linke et al., 2006) to understand factors affecting the biodiversity and ecology of these ecosystems.

Appendix A

List of macrofaunal species identified from box cores in the vicinity of the carbonate mounds of the Belgica Mound Province in the Porcupine Seabight from the R.V. *Polarstern* cruise ARK XIX/3a. Phyla are listed from the most speciose to the least speciose.

Phylum Annelida
Acanthicolepis asperimma (M. Sars, 1861)
Amparete sp. 1
Amparete sp. 2
Ampharetidae sp. 1
Annelida sp. 1
Antinoella finmarchica (Malmgren, 1867)
Apistobranchus sp. 1
Autolytus sp. 1
Autolytus sp. 2
Capitellidae sp. 1
Capitellidae sp. 2
Cirratulidae sp. 1
Eunice norvegica (Linnaeus, 1767)
Eunice torquata Quatrefages, 1867
Eunicidae sp. 1
Eupolymnia nebulosa (Montagu, 1818)
Eurysyllis tuberculata Ehlers, 1862
Exogone sp. 1
Fimbriosthenelais zetlandica (McIntosh, 1876)
Glycera sp. 1
Goniadides aciculata Hartmann-Schröder, 1960
Haplosyllis spongicola (Grube, 1855)
Harmothoe sp. 1
Hemipodus sp. 1
Leocrates atlanticus (McIntosh, 1885)
Lumbrineris cf *latreilli* (Audouin and Milne-Edwards, 1834)
Lumbrineris tetraura (Schmarda, 1861)
Lysidice nov. sp.
Maldane cf *sarsi* Malmgren, 1865
Maldanidae sp. 1
Maldanidae sp. 2
Maldanidae sp. 3
Maldanidae sp. 4
Nereimyra punctata (O. F. Müller, 1788)
Nothria cf *conchylega* (Sars, 1835)
Odontosyllis gibba Claparède, 1863
Oligochaeta sp. 1
Ophiodromus flexuosus (Delle Chiaje, 1825)
Paraonidae sp. 1
Paraonidae sp. 2
Paraonidae sp. 3

Petta pusilla
cf *Pionosyllis* nov. sp.
Pisione sp. 1
Polychaeta sp. 1
Polychaeta sp. 2
Polychaeta sp. 3
Polychaeta sp. 4
Polychaeta sp. 5
Polychaeta sp. 6
Polychaeta sp. 7
Polychaeta sp. 8
Polychaeta sp. 9
Polynoidae sp. 1
Polynoidae sp. 2
Proceraea sp. 1
Sabellidae sp. 1
Sabellidae sp. 2
Sabellidae sp. 3
Sabellidae sp. 4
Sabellidae sp. 5
Sabellidae sp. 6
Sabellidae sp. 7
Serpulidae sp. 1
Serpulidae sp. 2
Sigalonidae sp. 1
Sigalonidae sp. 2
Sigalonidae sp. 3
Syllidae sp. 1
Syllidae sp. 2
Syllidae sp. 3
Syllidia armata Quatrefages, 1866
Terebellidae sp. 1
Terebellomorpha sp. 1
Terebellomorpha sp. 2
Terebellomorpha sp. 3
Terebellomorpha sp. 4
Terebellomorpha sp. 5
Trypanosyllis coelaica Claparède, 1868
Typosyllis cf *vittata* (Grube, 1840)
Websterinereis glauca (Claparède, 1870)
Phylum Arthropoda
Acari sp. 1
Acari sp. 2
Ampelisca macrocephala Liljeborg, 1852
Ampelisca sp. 1
Ampeliscidae sp. 1
Amphipoda sp. 1
Amphipoda sp. 2
Amphipoda sp. 3
Amphipoda sp. 4
Amphipoda sp. 5
Aoridae sp. 1

Aoridae sp. 2
Apseudes spinosus (M. Sars, 1858)
Apseudidae sp. 1
Caecognathia abyssorum (G.O. Sars, 1852)
Campylaspis rubicunda (Liljeborg, 1855)
Campylaspis sp. 1
Campylaspis costata (Sars, 1865)
Caprella septentrionalis Krøyer, 1838
Caprella sp. 1
Caprella unica Mayer, 1903
Caprellidae sp. 1
Cirrepedia sp. 1
Cirrepedia sp. 2
Bathylasma sp. 1
Copepoda sp. 1
Copepoda sp. 2
Copepoda sp. 3
Copepoda sp. 4
Cressa dubia (Bate, 1857)
Cressa minuta Boeck, 1871
Bathynectes sp. 1
Eurycope sp. 1
Gitana sarsi Boeck, 1871
Gnathia dentata (G.O. Sars, 1872)
Gnathia maxillaris (Montagu, 1804)
Haploops setosa Boeck, 1871
Harpinia laevis Sars, 1891
Harpinia pectinata Sars, 1891
Ischyrocerus megacheir (Boeck, 1871)
Janira maculosa Leach, 1814
Jassa falcata (Montagu, 1808)
Jassa pusilla (Sars, 1894)
Laetomatophilus tuberculatus Bruzelius, 1859
Leptognathia sp. 1
Leucon nasica (Krøyer, 1841)
Leucon nov. sp. A
Leucon nov. sp. B
Liljeborgia pallida (Bate, 1857)
Lysianassidae sp. 1
Malacostraca sp. 1
Malacostraca sp. 2
Metopella sp. 1
Microdeutopus stationis Della Valle, 1893
Munida sp. 1
Munna kroyeri Goodsir, 1842
Munna minuta Hansen, 1916
Munna sp. 1
Natatolana borealis (Lilljeborg, 1851)
Normanion sp. 1
Oedicerotidae sp. 1
Ostracoda sp. 1
Ostracoda sp. 2

Pandalus sp. 1
Paraphoxus oculatus (Sars, 1879)
Perioculodes longimanus (Bate & Westwood, 1868)
Phoxocephalidae sp. 1
Sphyrapus sp. 1
Stenothoe marina (Bate, 1856)
Tanaidacea sp. 1
Tanaidacea sp. 2
Tanaidacea sp. 3
Tanaidacea sp. 4
Urothoe elegans (Bate, 1857)
Urothoe sp. 1
Westwoodilla caecula (Bate, 1857)
Phylum Cnidaria
Acanthogorgia armata Verrill, 1878
Acryptolaria conferta (Allman, 1877)
Actinaria sp. 1
Actinaria sp. 2
Actinaria sp. 3
Actinaria sp. 4
Antennella secundaria (Gmelin, 1791)
Anthomastus grandiflorus Verrill, 1878
Athecata sp. 1
Bedotella armata (Pictet and Bedot, 1900)
Bougainvilliidae nov. sp.
Bougainvilliidae sp. 1
Bougainvilliidae sp. 2
Campanularia hincksii Alder, 1856
Campanulinidae sp. 1
Clavulariidae sp. 1
Clytia sp. 1
Coronatae sp. 1
Corydendrium nov. sp.
Edwardsiella loveni (Carlgren, 1893)
Eudendrium sp. 1
Eudendrium sp. 2
Euphysa sp. 1
Filellum serpens (Hassall, 1848)
Filellum serratum (Clarke, 1879)
Haleciidae nov. gen. nov. sp.
Halecium tenellum Hincks, 1861
Hebellinae sp. 1
Kirchenpaueria bonnevieae (Billard, 1906)
Lafeoe dumosa (Fleming, 1820)
Lafoeidae sp. 1
Lafoeina tenuis Sars, 1874
Lophelia pertusa (Linnaeus, 1758)
Madrepora oculata Linnaeus, 1758
Nemertesia ramosa (Lamarck, 1816)
Octocorallia sp. 1
Octocorallia sp. 2

Octocorallia sp. 3
*Paraedwardsia sarsii (*Düben and Koren, 1847)
Plexauridae sp. 1
Plexauridae sp. 2
Pliobothrus symmetricus Pourtalès, 1868
Plumulariidae sp. 1
Protanthea sp. 1
Schizotricha frutescens (Ellis and Solander, 1786)
Sertularella gayi robusta Allman, 1873
Sertularella polyzonias (Linnaeus, 1758)
Sertularella tenella (Alder, 1857)
Stegopoma plicatile (M. Sars, 1863)
Telestula septentrionalis Madsen,1944
Virgularia sp. 1
Zoanthid sp. 1
Phylum Mollusca
Abra longicallus (Scacchi, 1834)
Acanthomenia sp. 1
Alvania cimicoides (Forbes, 1844)
Alvania jeffreysi (Waller, 1864)
Alvania zetlandica (Montagu, 1815)
Amphissa acuticostata (Philipi, 1844)
Anatoma aspera (Philipi, 1844)
Antalis cf *entalis* (Linnaeus, 1758)
Asperarca nodulosa (O.F. Müller, 1776)
Berthella sp. 1
Boreotrophon clavatus (G.O. Sars, 1878)
Cadulus jeffreysi (Monterosato, 1875)
Calliostoma sp.
Chlamys sulcata (O.F. Müller, 1776)
Clio sp. 1
Cuspidaria sp. 1
Delectopecten vitreus (Gmelin, 1791)
Diacria cf *trispinosa* (Lesueur, 1821)
Dorymenia sp. 1
Emarginula sp. 1
Fissurisepta granulosa Jeffreys, 1883
Gregorioiscala sarsi (Kobelt, 1904)
Hanleya cf *hanleyi* (Bean in Thorpe, 1844)
Heteranomia squamula (Linnaeus, 1758)
Iphitus tuberatus Jeffreys, 1883
Ischnochitonidae sp. 1
Kelliella abyssicola (Forbes, 1844)
Kruppomenia sp. 1
Ledella messanensis (Jeffreys, 1870)
Limea sarsi Lovén, 1846
Macellomenia sp. 1
Melanella sp. 1
Neomeniomorpha nov. gen. nov. sp.
Neomeniomorpha sp. 1
Opistobranch sp. 1
Pedicularia sp. 1

Phyllomeniidae sp. 1
Pruvotinidae sp. 1
Pruvotinidae sp. 2
Pseudamussium sulcatum (O.F. Müller, 1776)
Pseudosetia turgida (Jeffreys, 1870)
Rugulina fragilis (G.O. Sars, 1878)
Skenea cf *peterseni* (Friele, 1877)
Solariella amabilis (Jeffreys, 1865)
Talassia dagueneti (de Folin, 1873)
Thyasira cf *succisa* (Jeffreys, 1876)
Yoldiella sp. 1
Phylum Bryozoa
Bicrisia abyssicola Kluge, 1862
Bryozoa sp. 1
Cheilostomata sp. 1
Cheilostomata sp. 2
Cheilostomata sp. 3
Cheilostomata sp. 4
Cheilostomata sp. 5
Cheilostomata sp. 6
Cribrilina annulata (O. Fabricius, 1780)
Crisia nov. sp.
Ctenostomata sp. 1
Cyclostomata sp. 1
Cyclostomata sp. 2
Cyclostomata sp. 3
Hippothoa flagellum Manzoni, 1870
Lichenopora verrucaria (O. Fabricius, 1780)
Tubulipora penicillata (O. Fabricius, 1780)
Phylum Porifera
Aphrocallistes bocagei Schulze, 1886
Characella pachastrelloides (Carter, 1876)
Cladorhiza gelida Lundbeck, 1905
Clathrina ascandroides Borojevic, 1971
Cyamon spinispinosum (Topsent, 1904)
Erylus nummulifer Topsent, 1892
Geodia barretti Bowerbank, 1858
Hertwigia falcifera Schmidt, 1880
Janulum spinispiculum (Carter, 1876)
Lissodendoryx diversichela Lundbeck, 1905
Lyssacinosida sp. 1
Plocamionida ambigua (Bowerbank, 1866)
Porifera sp. 1
Porifera sp. 2
Rossellidae sp. 1
Soleneiscus olynthus (Borojevic & Boury-Esnault, 1987)
Thrombus abyssi (Carter, 1873)
Phylum Echinodermata
Amphipholis pentacantha H.L. Clark, 1915
Amphiuridae sp. 1
Echinus acutus var norvegicus de Lamarck, 1816

Echinus sp. 1
Hemiaster expergitus Lovén, 1874
Holothuroidea sp. 1
Spatangoida sp. 1
Spatangoida sp. 2
Ophiacantha bidentata (Retzius, 1805)
Ophiactis abyssicola M. Sars, 1861
Ophioscolex glacialis J. Müller & Troschel, 1842
Phylum Nematoda
Cylicolaimus cf *magnus* (Villot, 1875)
Enoplida sp. 1
Enoplus sp. 1
Mesacanthion sp. 1
Metacylicolaimus sp. 1
Phanodermatidae sp. 1
Synonchus cf *acuticaudata* (Jägerskjöld, 1901)
*Synonchu*s sp. 1
Synonchus sp. 2
Thoracostoma sp. 1
Thoracostoma sp. 2
Phylum Sipuncula
Aspidosiphon muelleri Diesing, 1851
Aspidosiphon sp. 1
Golfingia iniqua (Sluiter, 1912)
Golfingia sp. 1
Golfingia sp. 2
Golfingia sp. 3
Onchnesoma squamatum (Koren & Danielssen, 1875)
Phascolion tuberculosum Theel, 1875
Sipuncula sp. 1
Sipuncula sp. 3
Phylum Foraminifera
Foraminifera sp. 1
Foraminifera sp. 2
Foraminifera sp. 3
Foraminifera sp. 4
Foraminifera sp. 5
Foraminifera sp. 6
Foraminifera sp. 7
Indeterminate phyla
Unknown sp. 1
Unknown sp. 2
Unknown sp. 3
Unknown sp. 4
Unknown sp. 5
Unknown sp. 6
Unknown sp. 7
Phylum Brachiopoda
Brachiopoda sp. 1
Brachiopoda sp. 2
Brachiopoda sp. 3

Eucalathis tuberata (Jeffreys, 1878)
Macandrevia cranium (O. F. Müller, 1776)
Phylum Echiura
Bonnellidae sp. 1
Echiura sp. 1
Echiura sp. 2
Phylum Pyconogonida
Pantopipetta armoricana Stock, 1963
Pycnogonum nov. sp.
Phylum Chaetognatha
Chaetognatha sp. 1
Phylum Chordata
Tunicata sp. 1

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