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Cold-water coral reef frameworks, megafaunal communities and evidence for coral carbonate mounds on the Hatton Bank, north east Atlantic.

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Abstract

Offshore banks and seamounts sustain diverse megafaunal communities including framework reefs formed by cold-water corals. Few studies have quantified environmental effects on the alpha or beta diversity of these communities. We adopted an interdisciplinary approach that used historical geophysical data to identify topographic highs on Hatton Bank, which were surveyed visually. The resulting photographic data were used to examine relationships between megafaunal communities and macrohabitat, the latter defined into six categories (mud, sand, cobbles, coral rubble, coral framework, rock). The survey stations revealed considerable small-scale variability in macrohabitat from exposed Late Palaeocene lava flows to quiescent muddy habitats and coral-built carbonate mounds. The first reported evidence for coral carbonate mound development in UK waters is presented, which was most pronounced near present day or former sites of topographic change suggesting that local current acceleration favoured coral framework growth and mound initiation. Alpha diversity varied significantly across macrohabitats, but not between rock and coral rubble, or between smaller-grain sized categories of cobbles, sand and mud. Community composition differed between most macrohabitats, and variation in beta diversity across Hatton Bank was largely explained by fine-scale substratum. Certain megafauna were clearly associated with particular macrohabitats, with stylasterid corals notably associated with cobble and rock habitats and coral habitats characterised by a diverse community of suspension-feeders. The visual surveys also produced novel images of deep-water megafauna including a new photographic record of the gorgonian coral *Paragorgia arborea,* a species not previously reported from Rockall Plateau. Further interdisciplinary studies are needed to interpret beta diversity across these and other environmental gradients on Hatton Bank. It is clear that efforts are also needed to improve our understanding of the genetic connectivity and biogeography of vulnerable deep-water ecosystems and to develop predictive models of their occurrence that can help inform future conservation measures.

Keywords

Biodiversity; Deep-sea coral; *Paragorgia arborea*; *Lophelia pertusa*; Marine protected area; Seismic survey

Introduction

The Hatton Bank is a major offshore bank in the north east Atlantic formed from continental crust which, along with Rockall Bank and the intervening Hatton Basin, forms the Rockall Plateau. Figure 1 shows the regional setting of the Rockall Plateau overlaid with verified occurrences of reef framework-forming cold-water corals. These corals are typically found on the continental slope and on offshore banks and seamounts where recent work has shown how they can develop to form large reefs and carbonate mounds (Roberts et al. 2006). In the north east Atlantic such structures are intimately related to reef frameworks formed primarily by the scleractinian coral *Lophelia pertusa* (Freiwald 2002; Roberts et al. 2003). Here, occurrences of this coral on the continental shelf vary from small patch reefs, such as those described by Wilson (1979) on Rockall Bank, to the larger deep-water reef complexes characteristic of the Norwegian continental margin (Mortensen et al. 2001; Freiwald et al. 2002). Over the last decade, deep-water geophysical surveys have revealed large seabed mounds on the continental slope (Hovland et al. 1994; Kenyon et al. 2003). These are now known to be coral carbonate mounds. They form clusters, or ‘provinces’, with notable examples in the north east Atlantic from the Porcupine Seabight (De Mol et al. 2002; Huvenne et al. 2005; Wheeler et al. 2005), southern Rockall Trough (Akhmetzhanov et al. 2003; Kenyon et al. 2003) and west Africa (Colman et al. 2005). Large deep-water coral accumulations and ‘lithoherms’ have also been reported in the western Atlantic along the Florida-Hatteras Slope (Stetson 1962; Neumann 1977), and are now the subject of increased research activity (Reed and Ross 2005; Reed et al. 2006; Ross and Quattrini 2007).

Figure 1
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Shallow-water coral reefs are renowned for their biodiversity but our understanding of the biodiversity of cold-water coral reefs is limited by their remoteness. Existing information comes from two sources: (1) visual surveys based on video and/or stills images gathered by drop cameras, manned submersibles or remotely operated vehicles and (2) identification of species present in samples recovered from the reef habitat. Data from visual surveys are restricted to megafaunal animals large enough to identify in seabed photographs and studies consistently illustrate enhanced megafaunal diversity on-reef versus off (e.g. Mortensen et al. 1995; Jonsson et al. 2004). Similarly, studies of species diversity in samples of reef habitat show high diversities associated with coral framework samples (Jensen and Frederiksen 1992) and evidence of characteristic reef species (Henry and Roberts 2007). Thus while virtually all reports of cold-water coral reefs and carbonate mounds note that these habitats sustain diverse animal communities, most remain descriptive studies that compile lists of species reported from these habitats. For example, Rogers (1999) compiled literature showing 889 species associated with *Lophelia pertusa* reefs in the north east Atlantic, a total that had increased to just over 1300 species following a pan-European research project between 2000 and 2003 (Roberts et al. 2006). Such totals will certainly increase as new areas are investigated and new species described (e.g. Henry and Roberts 2007).

In this study we present geophysical evidence for carbonate mounds and outcropping bedrock on Hatton Bank and discuss this in terms of previous understanding of the regional geology of this offshore bank and its implications in terms of the diversity of substrata that are likely to occur. We use a large archive of seabed photographs taken during a baseline habitat mapping exercise to investigate whether cold-water coral habitats had quantifiable effects on the alpha and beta diversity of communities in a deep-water continental slope setting. For a recent summary of the oceanographic regime of this region see Due et al. (2006) and references therein. We integrate this information and consider the importance of understanding small-scale variability in marine habitats, its effects on biodiversity and some implications for habitat conservation and the design of deep-water marine reserves.

Methods

The results described in this paper stem from a series of geophysical and habitat-characterisation research cruises carried out between 1998 and 2006 that are summarised below.

Geophysical surveys

The single channel data seismic lines presented here were gathered through a joint British Geological Survey, oil industry initiative (‘Rockall Consortium’) using 2 x 40 and 4 x 40 cubic inch airgun arrays, and 1 and 2 kJ sparkers to carry out reconnaissance mapping of the Rockall-Hatton region between 1992 and 2006 (Hatton Bank from 1998). Airgun and sparker profiling was run simultaneously to allow high resolution near surface as well as deeper acoustic penetration. The programme aimed to establish the structure of the region, the extent of Early Cenozoic igneous cover and the thickness and stratigraphy of the post-Eocene sediments. It also identified windows in the basalt cover revealing Mesozoic sediments (Hitchen 2004). The grid of geophysical profiles was established to cover igneous centres identified from gravity and magnetic data as well as giving a regular spatial distribution (profiles gathered using a Coda acquisition system, CodaOctopus Products Ltd.). Initial shipboard interpretation allowed the inclusion of additional survey lines to improve mapping of selected features. Some surveys also had higher frequency devices that contributed to the interpretation of the seabed morphology such as single and multibeam echosounders, and a pinger (Brett and Smith 2000; Jacobs 2006; Smith 2002; 2006).

Visual surveys

Visual seabed surveys were conducted over a five day period in late August 2005 as part of Strategic Environmental Assessment (SEA) surveys by the UK Department of Trade and Industry (since renamed as Department for Business, Enterprise and Regulatory Reform). Both video and digital still images were recorded using a deep-water camera system (Seatronics DTS 6000 incorporating a 5 mega pixel Kongsberg Maritime Ltd OE14-208 digital still camera giving an oblique view of the seabed) deployed from the SV *Kommandor Jack* (Offshore Survey and Engineering). A series of 13 photographic stations was established on the Hatton Bank (Table 1) using existing British Geological Survey seismic data indicating topographic highs or on the basis of newly acquired multibeam bathymetry. The length of individual deployments varied depending upon weather conditions and equipment reliability and photographs were taken approximately every two minutes or where distinct changes in habitat were seen. The positions of the photographic stations and any intersecting BGS seismic lines are shown in Figure 2. In this paper we describe these photographic surveys and examine the difference in megafaunal species diversity and composition between macrohabitats. To our knowledge, these are the first *in situ* reports of benthic megafaunal communities from the Hatton Bank.

Figure 2
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We adopt the clearly defined ecological community terms as outlined by Fauth et al. (1996). Thus a community is defined as a ‘collection of species occurring in the same place at the same time’ and assemblages refer to ‘phylogenetically related groups within a community’. In terms of defining habitat types we adopt the approach described by Greene et al. (1999) where the Hatton Bank can be considered a megahabitat at the scale of kilometres to tens of kilometres. We present geological evidence for a variety of mesohabitats at the scale of tens of metres to a kilometre within the areas of Hatton Bank surveyed. Finally, we define a series of macrohabitats on the scale of one to tens of metres to investigate the effect of macrohabitat on megafaunal biodiversity.

Our photographic analysis was based on presence/absence of megafauna in the still images because the photographs were not standardised to a known area of seafloor. While this prevents abundance counts, it is worth noting that many of the megafauna recorded in these surveys were colonial epifauna and it is hard, if not impossible, to discriminate individuals in seafloor photographs. Presence or absence of the megafauna listed in Table 2 were noted from each still image so that a score of one corresponded to one or more occurrences in an image and a score of zero to a taxon that was absent. Any images that were obscured by resuspended sediment were excluded from the analysis. Each image was assigned to a dominant macrohabitat, based on the predominant substratum observed (mud, sand, cobbles, coral rubble, coral framework or rock, Figure 3). In total 633 images were scored.

Figure 3
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Statistical analyses

Alpha diversity

Alpha diversity was estimated as the richness (number) of distinct taxa observed in each image. Richness was compared across macrohabitat categories using a one-way analysis of variance (ANOVA) with *post-hoc* multiple comparison tests performed with Bonferroni corrections using the online GraphPad Software (http://graphpad.com) to identify statistically significant differences between pairwise macrohabitats.

Beta diversity of megafaunal communities

Multivariate ordinations and analyses were performed using PRIMER v6 (Clarke and Gorley 2006). Similarity of percentages (SIMPER) was used to estimate beta diversity and to identify taxa that characterised each macrohabitat. Beta diversity was estimated as the mean similarity between communities within each macrohabitat category. Species that contributed most to the overall similarity of communities within this macrohabitat were then listed. Following this, a triangular dissimilarity matrix of pairwise Sörensen measures based on presence/absence data was generated after the addition of a dummy variable with a value of one (included to counter cases where images contained no visible megafauna, which would greatly skew similarity estimates). Communities across different macrohabitat types were compared using analysis of similarity (ANOSIM), and the taxa that contributed most to the dissimilarity across macrohabitats were listed. Variation in beta diversity across macrohabitats was quantified in relation to environmental variables (depth, fine- and local-scale substratum) and geo-spatial location (latitude and longitude). Depth is implied here to represent a composite factor that could reflect a suite of variables such as current velocity, particle flux and sedimentation. The 'fine-scale' dominant substratum observed in an image was scored into a numeric metric as: 1 – mud, 2 – sand, 3 – cobbles, 4 – coral rubble, 5 – rock, 6 – coral framework, which roughly followed a gradient of increasing grain size. 'Local-scale' substratum was estimated as the frequency of occurrence of each substratum category in a station. These frequency data were normalized, and the resulting matrix used in a principal components analysis (PCA). The resulting axes with eigenvalues > 1 were used to ordinate all stations into a PCA plot according to these scores. The scores from each axis were then used as separate, but related, variables as estimates of local-scale substratum.

A new environmental/geo-spatial matrix was created that included $\log_{10}$ transformed depth, universal transverse mercator (UTM) coordinates in metres, the numeric measure of the fine-scale substratum and all three scores from the PCA representing local-scale substratum, for each image. Environmental data were normalized, and the BEST routine was run using the BIOENV method on Euclidean distances between the similarity matrices and all available variables. BEST finds the best match between the species similarity matrix and the environmental/geo-spatial variable matrix (Clarke and Gorley 2006). BEST estimates the Spearman's rank correlation metric ρ, a measure of the degree to which species' distributions correspond to the environmental and geo-spatial data, and its statistical significance. It also identifies the best combination of variables that maximize the explanatory power.

Megafaunal co-occurrences

We investigated the co-occurrences of all megafaunal taxa by calculating Sörensen measures estimated between pairwise combinations of variables i.e., taxa, and ordinating these measures into a non-metric multidimensional scaling (nMDS) plot to visualize the data.

Results

Representative images of each macrohabitat and megafaunal taxon are given in Figures 3 and 4 respectively. Here we summarise the characteristics of each station before considering the relationship between megafaunal community and macrohabitat.

Figure 4 here

Survey Stations

The seismic profiles across Hatton Bank revealed an irregular topography with local highs several tens of metres above the surrounding seafloor (Figure 5). The seismic profiles showed that some of these highs related to the outcropping of acoustic basement (Figures 5b and 5d), interpreted as Late Palaeocene igneous rocks, predominantly lava flows. Some highs related to cliffs formed by tectonic activity leading to vertical displacement (Figures 5c and 5e). Several compressional events have been noted in the Faroe-Hatton region during the Cenozoic with the major event being intra Late Eocene (Johnson et al. 2005). However, some of the topographic highs appeared as sedimentary features developed within the Cenozoic post igneous activity (Figure 5f). These were often located above topographic changes in the buried igneous surface.

Figure 5 here

Station G. This was the deepest of the photographic stations at just over 1 km water depth, on the eastern flank of Hatton Bank (Figure 2). The seabed surveyed was composed of soft, muddy sediments. One image showed a swept seabed with fractured cover, suggesting that recent sediments were not present throughout and that firmer sediments (possibly cemented) were at or close to the seabed. Multibeam surveys showed the flank of Hatton Bank to have numerous hollows up to 2 km in diameter. Xenophyophore tests (probably *Syringammina fragilissima*, see Figure 4 image 28) and echinothurid urchins were the most notable megafauna. No seismic lines intersected this station, although nearby lines indicated that erosion and infill of hollows up to 100 m deep occurred on a regular basis. This was reflected in multibeam-derived seabed topography images showing a scalloped surface.

Station A. This station ranged in depth from 537-591 m. Substrata varied from sandy, shelly material through coral rubble, with occasional live colonies of *L. pertusa* (Figure 4 image 1), to expanses of exposed rock and occasional boulders. Some rocky areas were steeply sloping and colonised in places by scleractinian, gorgonian and antipatharian corals. Coral rubble was noticeably rich in attached epifauna. No seismic lines intersected this station.

Station K. This station ranged in depth from 740-772 m on the western flank of Hatton Bank and the visual surveys revealed habitats dominated by coral rubble, reef framework and sediment-filled reef framework. The coral habitats supported rich epifaunal communities including large antipatharian corals (*Bathypathes*) along with frequent colonies of the smaller characteristically spiral-shaped antipatharian *Stichopathes* (Figure 4 image 9), probably *S. gravieri* after Molodtsova

(2006). In one of the photographs from this station a large gorgonian coral most likely to be *Paragorgia arborea* was seen. The distribution of this species is described by Tendal (1992) and it has not been previously reported from the Rockall Plateau. Station K is located close to seismic line 00/01-23 (Figure 2) where acoustic basement assumed to be Palaeocene igneous rock outcrops at 750 m water depth with small infilled basins of sediments, ~20 m thick (Figure 5b).

Station L. This station ranged in depth from 645-652 m. Substrata varied between a coarse sandy seabed with shelly debris and scattered coral rubble to patches of coral framework. Mobile holothurians (*Stichopus*, probably *S. tremulus*, see Figure 4 image 16) were common on the sandy sediments and the coral framework was colonised by suspension-feeding epifauna. Station L was located close to seismic line 00/01-27 (Figure 2) where an acoustically transparent peak occurred above a displacement in the acoustic basement, overlying an acoustically layered unit 40-50 msec thick with parallel reflectors. These reflectors and the basement were displaced vertically ~50 msec, above which a ridge-shaped mound 30 m high, 500 m wide and up to 1 km in length was seen (Figure 5c) with its axis trending south west-north east following the underlying tectonic geometry. A smaller, wider mound occurred upslope but there was no indication that it developed above any evidence of displacement.

Figure 6
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Station Q. This station ranged in depth from 622-642 m. Substrata were similar to those seen at equivalent depths at Station L with coarse, sandy sediments interspersed with patches of coral rubble and reef framework. Echiuran proboscoides were seen extending from burrows in sediment (Figure 4 image 25) and some areas of sediment-draped rock were also present. Seismic line 00/01-28 intersected a series of symmetrical sediment wave-like features up to 30 m in height at 1-2 km spacing along the survey line (Figure 5e). They occurred above a sub-horizontal reflector that represented acoustic basement and was interpreted as Late Palaeocene lavas. This reflector showed a displacement of approximately 50 m beneath one sediment wave about 2 km south west of station Q. There were a series of sediment wedges against this vertical displacement suggesting that it was exposed as a cliff for a significant period of time. The core of the topographic highs had a chaotic acoustic character, which may indicate either that the bedding seen between the highs was too steep at the sediment wave or there was a genuine change in physical properties. However the multibeam image (Figure 6c) shows that these are not waves but a series of topographic highs and ridges extending southwestwards into deep water on the western flank of Hatton bank. The largest of these topographic highs was located above the former cliff and so it may be assumed that this buried cliff has a similar orientation. The photographic evidence from station Q supported the interpretation of the lack of rocky outcrop and that the mound is an accumulation built up from coral and reworked sediments.

Station C-D. This station ranged in depth from 476-539 m making it the second shallowest station surveyed. The seabed was composed of sandy sediment with frequent, scattered pebbles and larger boulders. The latter were heavily colonised by epifauna, notably the stylasterid *Pliobothrus* (probably *P. symmetricus*, see Figure 4 image 11) and the sessile holothorian *Psolus* (probably *P. squamatus*, see Figure 4 image 15). Extensive rocky habitat was also seen including steeply sloping rock ledges with crevices and overhangs. Large colonies of antipatharian coral were seen on the sloping rock faces (Figure 4 image 10). Scattered coral fragments (*L. pertusa*) were also evident. A solitary peak with steep sides was located on seismic line 00/01-38 (Figure 5a) with its southwestern flank 75 m high and an apparent gradient of 20°. The cliff was so steep that the bottom tracking facility failed to lock as the line was surveyed from southwest to northeast. The subsequent multibeam survey showed the mound was located on a northeast-southwest trending cliff (Figure 6a). This cliff may be part of an extensive tectonic displacement as similar features were seen on nearby lines and stations M and P. It is variously orientated northeast-southwest to east-west creating a south-facing cliff. In front of the cliff at station C-D is a north east-south west orientated trough deepening to the south west (Figure 6a). A fan of material up to 40 m thick is located in the trough at the foot of the mound and appears as a wedge of sediment overlying a horizontal reflector on the seismic record (Figure 5a). The seabed photographs from station C-D suggest the mound bedrock outcrops occasionally, showing evidence of jointing.

Station M. This station, located 4 km northwest of station C-D, ranged in depth from 514-582 m. The survey revealed areas of coarse sandy habitat with mobile holothurians (probably *Stichopus tremulus*) close to areas of rock, with patchy fine sediment drape. In places the rock sloped steeply with rapid increases in depth noted as the camera frame tracked the bottom. Exposed rock surfaces were frequently colonised by *Psolus* holothurians and *Pliobothrus* stylasterids with small patches of live scleractinian framework (*L. pertusa*). The airgun record close to station M (line 00/01-01) showed a topographic high within a sequence of easterly dipping reflectors (see Figure 9b in Hitchen 2004). These were interpreted as landward dipping lava flows extruded along an incipient spreading axis at the time of continental break up rather than from one of the volcanic centres noted in the area (Hitchen 2004). No sparker record was available due to technical problems when crossing this station. The multibeam image shows that station M is a similar mound to that seen at station C-D though there is little or no evidence for a fan shaped mound of material at the foot of the topographic high. The photographs from station M show a traverse rising 75 m from the centre of the trough to near the top of the high. This may be the site of a tectonic displacement as similar features were seen on nearby lines suggesting a north east-south west orientation including stations C-D and P creating a south-facing cliff.

Station R. This station ranged in depth from 518-526 m. The seabed surveyed was predominantly rippled sediment with occasional patches of coarser cobble material. Some areas of exposed rock colonised by *L. pertusa* and other sessile epifauna were seen. No seismic lines intersected this station.

Station N. This station ranged in depth from 530-650 m. Isolated rocks colonised by sessile epifauna were seen with some showing evidence of current scouring pointing to an active near-bed current regime. Areas of exposed rock and coral framework were also seen with the latter again supporting a diverse assemblage of suspension-feeders. Transitions between habitats were frequently abrupt indicating the high level of habitat heterogeneity at small scales of between one and ten metres. No seismic lines intersected this station.

Station P. This station ranged in depth from 556-643 m. The survey was dominated by areas of coral reef framework along with expanses of sediment-draped rock and areas of steeply sloping cliff-like topography. Large *Phelliactis* sea anemones were conspicuous colonists on dead coral framework (Figure 4 image 12). Profile 06/02-06 showed that the steeply sloping topography seen at station P consisted of outcropping acoustic basement interpreted as part of the igneous suite. The cliff face, locally more than 80 m high, is the same tectonic structure seen at stations M and C-D, 15 and 20 km to the west respectively. At P its strike is oriented approximately east to west (Figure 6d). The igneous rocks, acoustic basement for the sparker, that comprise the cliff face, dip to the north and were overlaid by at least two periods of sedimentation (Figure 5f). A well-layered unit was seen below the seabed with an acoustically transparent unit infilling hollows in the igneous surface below. The dip of the well-layered reflectors was interrupted at station S where a moat is developed on the upslope (southern) flank of a 30 m high feature (Figure 5f). Multibeam data collected simultaneously with the sparker profile showed the feature to be near conical with a base area of 300 x 500 m (Figure 6e).

Station S. This station ranged in depth from 682-730 m. The visual surveys were taken down the flank of a near conical mound (Figure 5f). The sparker profile and multibeam data showed evidence of scouring at the base of the southern (the regional upslope) flank of the feature. The mound was 30 m above the surrounding seafloor, 50 m above the base of the adjacent scoured hollow (Figure 5f) and 300-500 m in diameter. Seabed substrata varied from coarse sandy material through to coral framework and rock. In some areas expanses of sloping rocky topography were evident. The internal structure of this mound was strongly reminiscent of a carbonate mound, similar to features described in the Porcupine Seabight (Hovland et al. 1994; De Mol et al. 2002; Huvenne et al. 2005; Wheeler et al. 2005). Station S appeared to have developed above a topographic change in the acoustic basement and grown as acoustically well-layered sediments were deposited on the flank of Hatton Bank. Sedimentation rates are greatly reduced within the scour zone immediately southeast of Station S (Figures 5f and 6e). These sediments were thought to be mid to late Cenozoic in age based on the regional setting.

Station E-F. This station ranged in depth from 798-855 m. At these greater depths finer, muddy sediments were colonised by xenophyophores and ophiuroids (Figure 4 images 28 and 19 respectively). Areas with scattered cobbles and larger rocks colonised by sessile epifauna were also found. Expanses of rock were recorded, with some sloping topography and rocky overhangs. No seismic lines intersected this station or were within 1 km.

Station H. This station ranged in depth from 466-482 m. At this the shallowest station surveyed, the seabed was predominantly composed of exposed rock or rock with a thin drape of coarse sediments and cobbles. Once again, exposed rock was characteristically colonised by the sessile holothurian *Psolus* and stylasterid coral *Pliobothrus*. No seismic lines intersected this station.

Alpha diversity

A total of 34 distinct megafaunal taxa were recorded across the 13 stations. All megafaunal taxa recorded in the visual surveys are listed in Table 2 and sample images are provided in Figure 4. The number of photographs assigned to each habitat class, total number of taxa and total occurrences recorded by macrohabitat are given in Table 3. Histograms showing the percent occurrence of each taxon by habitat are given in Figure 7. Taxon richness varied across stations, ranging from five taxa observed in station G, to 31 taxa observed in station Q. Stations P, K, N and S were also particularly rich.

Figure 7 here

Richness significantly differed across macrohabitat categories ($p < 0.05$, Table 4). Bonferroni corrected multiple comparisons demonstrated that richness usually differed significantly between pairwise macrohabitats ($p < 0.05$, Table 4), but not between rocks and coral rubble, or between the macrohabitat categories corresponding to smaller grain sizes i.e., between cobbles, sand or mud (Table 4).

Beta diversity

Table 6 summarises average community similarity and thus beta diversity in each macrohabitat and lists the taxa that best characterised each category. Muddy macrohabitats were best characterised by ophiuroids, polychaete feeding tubes and xenophyophores. Sand showed the lowest within macrohabitat similarity and was best characterised by deposit-feeders such as the holothurian *Stichopus* and echinoids. However, suspension-feeding taxa were also found in sandy habitats. This was often associated with the presence of hard substrata (cobbles or fragments of coral rubble) in predominantly sandy areas reflecting the heterogeneity of substrata at a fine scale. Cobble macrohabitat was best characterised by the stylasterid coral *Pliobothrus*, encrusting sponges and the suspension-feeding sessile holothurian *Psolus*. Coral rubble was characterised predominantly by suspension-feeding corals, anemones and sponges but galatheid crustaceans that use the coral rubble for shelter were also an important and characteristic group. Similarly, coral framework was best characterised by suspension-feeding corals, anemones and sponges. Finally, rock macrohabitat supported the most homogeneous fauna, which were best characterised by the sessile holothurian *Psolus*, encrusting sponges, the stylasterid *Pliobothrus*, galatheid crustaceans, the antipatharian coral *Stichopathes* and the scleractinian coral *Lophelia pertusa*.

A *post-hoc* Analysis of Similarities routine (ANOSIM) in PRIMER reported statistically significant differences in the community composition between most macrohabitats (Table 5). We adopted a somewhat conservative approach to this routine, given the positive relationship between the large sample size of images (633) that would necessarily increase the type I error rate. Thus, we considered ANOSIM test statistic values $R > 0.4$ with $p < 0.001$ to represent statistically significant differences in community composition between macrohabitats. This approach generally restricted differences to occur between mud and those substrata with coarser grain size i.e., coral rubble, rock and framework ($R = 0.425, 0.681, 0.793$, respectively). It also identified differences in community composition between coral framework and rocks ($R = 0.558$), the two largest grain-sized macrohabitats.

PCA permitted the identification of three components of substrata that could be used to characterise local-scale substrata. These components cumulatively explained 77.9% of the variation in substrata frequency of occurrence between stations (Table 7, Figure 8). The first PC (explaining 31% of the variation) was most associated with the frequency of occurrence of coral rubble and sand, corresponding to the highest PC scores seen in stations L, Q and K. The second PC (explaining 26% of the variation) was associated with the frequency of occurrence of cobbles, rock and sand, which corresponded to the highest PC scores for stations C-D, N and H. The third PC (explaining 21% of the variation) was associated with the frequency of occurrence of coral framework and cobbles, corresponding to the highest PC scores in stations N, P, K.

Figure 8 here

BEST measured the highest ρ between the megafaunal community similarity matrix and fine-scale substratum ($\rho = 0.394$) when all possible combinations of environmental variables were considered (Table 8), including the local-scale substrata scores estimated by PCA. Depth was the next most correlated variable, but was three times less correlated with the community similarity matrix than fine-scale substratum ($\rho = 0.129$). Therefore, beta diversity in the study area on Hatton Bank varied depending on the fine-scale substratum on which a megafaunal community was found.

Megafaunal co-occurrences

Using the nMDS to illustrate the associations between megafaunal taxa, some of these overall patterns are evident (Figure 9). The stylasterid *Pliobothrus* and sessile holothurian *Psolus* group closely along with encrusting sponges and serpulid polychaetes. These are all taxa that colonise

Figure 9 here

exposed rock, dropstones and cobbles. Similarly suspension-feeding species typically found with coral reef framework (e.g. *Lophelia pertusa*, *Madrepora oculata*, *Phelliactis*, *Stichopathes*) are grouped. On the other hand taxa associated with soft sediments (e.g. bonelliid echiurans, *Stichopus*, xenophyophores) are separated in the nMDS plot. Interestingly taxa commonly recorded in crevices in coral reef framework such as the galatheid crustaceans have grouped with characteristic reef fauna. While only relatively low numbers of fish were observed (66 observations in total), these mobile taxa plot some distance from the tight group of reef-associated suspension-feeders suggesting that the fish observed in this study may not be intimately associated with reef habitat. However, the effect of the camera frame and lights used in this study on fish behaviour are not known and we are therefore unable to draw any conclusions from this observation.

Discussion

Geological context

The general sedimentary structure and setting of the north east Atlantic is discussed by Laberg et al. (2005) and Stoker et al. (2005). Much of the Hatton High is composed of thick successions of Mesozoic (or older) sediments, overlaid by Cenozoic lavas and sediments. This situation contrasts with that at Rockall High where evidence for inversion (relative uplift of previously basinal area) suggests any Mesozoic succession will have been removed and metamorphic basement crops out close to the seabed (Hitchen 2004). The seismic data presented here show that Hatton Bank is in some areas characterised by an irregular topography developed by tectonic displacement exposing Late Palaeocene rocks that appear as acoustic basement on sparker profiles (Figure 5d). Other topographic highs appear to be features developed within sedimentary sequences after the Cenozoic igneous activity (Figure 5c). The evidence that several of these are carbonate mounds formed by successive periods of coral framework growth and sedimentation (Roberts et al. 2006; Williams et al. 2006; Rüggeberg et al. 2007) is compelling. Thus the basic geology of the Hatton Bank with both sediments and rock at the seabed, along with the development of carbonate mounds and biogenic reefs of cold-water corals, explain the diverse seabed facies revealed in this study.

Present-day coral carbonate mounds on the European continental slope were first reported in the mid-1990s by Hovland et al. (1994) and later by Henriet et al. (1998) who hypothesised that they were associated with faults and the seepage of light hydrocarbons. This stimulated intensive mapping and further geological investigations (summarised by Wheeler et al. 2007). There is now evidence for several carbonate mound provinces in the north east Atlantic from (1) south west Ireland: the Hovland (Hovland et al. 1994; De Mol et al. 2002), Magellan (Huvenne et al. 2002, 2007) and Belgica provinces (De Mol et al. 2002; Van Rooij et al. 2003), (2) southern Rockall Bank: Logachev Mounds (Kenyon et al. 2003; van Weering et al. 2003), (3) western Rockall Bank (Wienberg et al. 2008) and (4) north west flanks of Porcupine Bank: Pelagia mounds (Kenyon et al. 2003; van Weering et al. 2003). The Darwin Mounds reported by Masson et al. (2003) at 1000 m depth in the northern Rockall Trough are small sand mounds (up to 75 m diameter and 5 m high) colonised by cold-water corals. Their formation is not well understood and was interpreted by Masson et al. as related to fluid escape causing sand mounds to form, rather than successive generations of coral reef development that leads to coral-built carbonate mounds (Roberts et al. 2006). Studies of the stable isotopic composition of coral skeleton and tissue have not supported a seep-based food chain (Duineveld et al. 2004) and analyses of lipid biomarkers and stable nitrogen isotopes of *Lophelia pertusa* and *Madrepora oculata* point to a diet derived from primary productivity at the surface (Kiriakoulakis et al. 2005). Thus to date evidence for a relationship between coral growth and light hydrocarbon seepage has not been found and the mounds are thought to develop through periods of interglacial coral framework growth interspersed with periods of glacial sedimentation over timescales of 1 to 2 million years (Roberts et al. 2006; Kano et al. 2007). The focussed flow of hydrocarbons supporting microbial communities can lead to localised hardground or 'chemoherm' formation (Roberts and Aharon 1994) but the origin of the hard settlement substratum at the base of carbonate mounds has remained elusive (Huvenne et al. 2007).

The distribution of mounds in the Hatton area is associated with either present day or former sites of topographic change. We suggest that currents forced up such features (e.g. cliffs) created favourable conditions that initiated cold-water coral reef development forming a mound that has continued to grow even if the cliff had subsequently become buried by sediments. It should be noted that these sediments could include carbonate debris derived from the mound. At a larger scale the importance of current regime in shaping carbonate mound development is becoming apparent with evidence that the strongest near-bed current direction correlates with the orientation of mound clusters where enhanced diurnal tidal currents have been measured in the east Porcupine Seabight (Belgica mounds) and south east Rockall Bank (Logachev mounds) (White et al. 2007). At the smaller scale of an individual carbonate mound, abundant live coral patches are found in areas with locally enhanced bottom currents, notably on the summit of the Galway Mound (Dorschel et al. 2007) and on the south western and south eastern margins of Rockall Trough where living coral on carbonate mounds was related to internal waves and tidal currents (Mienis et al. 2007).

Megafaunal biodiversity across macrohabitats

While many recent studies have examined the broad distribution of megafauna in cold-water coral ecosystems, few have taken a quantitative approach to examine the influence of small-scale habitat class on megafaunal communities. The present study benefited from access to a large archive of high resolution seafloor images from transects that crossed a variety of habitats from mud, sand, cobbles and rock to coral rubble and reef framework. Presence/absence analysis of the megafauna recorded in these photographs revealed clear trends: both alpha and beta diversity varied between macrohabitats, with the richest communities associated with coral-structured (rubble and framework) and rocky macrohabitats. Beta diversity was highest in sandy macrohabitats, which was likely related to higher substratum heterogeneity due to the presence of coral rubble and cobbles. Beta diversity was lowest on rocks and coral framework, indicating more homogeneous communities within each of these categories. Beta diversity on Hatton Bank varied accordingly, with differences in fine-scale substratum (i.e., the macrohabitat identified as dominant in each image) explaining nearly 40% of this variation.

Characteristic taxa within muddy macrohabitats included xenophyophores. These giant testate protists are likely to have been *Syringammina fragillisima*, a species recorded in high densities at 1100 – 1300 m depth on the Scottish continental shelf (Roberts et al. 2000) and at 1000 m depth in the N Rockall Trough (Masson et al. 2003). They are known to provide significant localised structural habitat, altering small-scale community composition (Levin 1991; Gooday et al. 1993; Hughes and Gooday 2004). Cobble macrohabitats were best characterised by the stylasterid coral *Pliobothrus*, the sessile holothorian *Psolus* and a variety of encrusting sponges. *Pliobothrus* also characterised exposed rock macrohabitats, a finding that supports Cairns (1992) overall interpretation of stylasterids as species that are most commonly found on hard substrata off small land masses such as oceanic islands, atolls, or on seamounts and ridges where sediment input and nutrients are low and salinity varies little. Interestingly *Pliobothrus* was not seen in either coral framework or coral rubble macrohabitats lending further credence to Cairns' suggestion that scleractinian corals, which have far larger polyps and better sediment-shedding abilities than stylasterid corals, may out-compete stylasterids. Furthermore, as discussed by Cairns, Ostarello (1973) noted that stylsterid planulae tend to settle preferentially on vertical surfaces avoiding the deleterious effects of sedimentation. It is interesting to note that many of the *Pliobothrus* colonies seen in the present study were associated with the steeply sloping, cliff-like facies likely to be outcropping Late Palaeocene igneous rocks.

Coral rubble and coral framework macrohabitats were characterised by abundant suspension-feeding taxa including *Stichopathes* antipatharian coral, actinians, *Lophelia pertusa*, crinoids, erect sponges, *Phelliactis* sea anemones, other antipatharians, ophiuroids, octocorals and *Madrepora oculata*. It is noteworthy that the occurrence of antipatharian corals was important in discriminating between macrohabitats (Table 6) even though they are generally regarded as a group largely restricted to more southerly latitudes. Indeed the first reports of *Stichopathes* and *Bathypathes* species north of 52° N were only made very recently (Molodtsova 2006). The images of these species presented in Figure 4 are among the first *in situ* images available. It is likely that the *Stichopathes* species seen in these photographs is *S. gravieri* (pers. comm. T. N. Molodtsova, species described by Molodtsova 2006). This study also suggests that the large octocoral *Paragorgia arborea* has a wider distribution than previously thought. A single photograph from station K (58° 44 N) showed an octocoral likely to be *P. arborea* (enlarged in Figure 10), which would make this the southernmost record of a species generally found north of 60° N in the north east Atlantic (Tendal, 1992) and the first record from Rockall Plateau. In the northwest Atlantic, *P. arborea* extends further south to the Gulf of Maine at approximately 44° N (pers. comm. L. Watling).

Figure 10 here

Macrohabitats dominated by mud and cobbles were characterised by the fewest taxa, with three in each case corresponding to 90% of the similarity, followed by rocky macrohabitats with six taxa. The alpha diversity of coral rubble and framework macrohabitats was reinforced by the higher numbers of characterising taxa, 11 and 12 respectively. Higher similarity (and thus lower beta diversity) between samples from reef framework versus off-reef samples was also reported on the carbonate mounds of the Porcupine Seabight (Henry and Roberts 2007) and might relate to the greater spatial ‘predictability’ over a horizontal area of well-developed reef. Sandy macrohabitats were characterised by a greater number of taxa (12), but recall that the low percentage similarity within this category (and thus the higher beta diversity) reflects the heterogeneity of this habitat, which was frequently mixed with small patches of hard substrata in the form of cobbles or isolated patches of rock and/or coral.

Variation in the alpha and beta diversity of megafauna observed over the various stations and macrohabitats on Hatton Bank suggest that species turnover should closely relate to environmental gradients in this area. Future work on the megafaunal communities on Hatton Bank, and other comparable banks and seamounts, could integrate textural results from geophysical surveys (e.g. multibeam and sidescan sonar) and local-scale hydrographic data to generate an even wider suite of environmental variables to more tractably partition the variation in community composition amongst variables such as substratum, current speed and aspects of habitat complexity. Beta diversity may also be a significant influence on total diversity across marine habitats. This was recently demonstrated in shallow-waters by Hewitt et al. (2005) who found that small biogenic shell debris patches significantly affected beta diversity by enhancing and maintaining biodiversity on soft sediments in a New Zealand marine reserve.

This study demonstrated that alpha and beta diversity varies significantly across macrohabitats on Hatton Bank, and that there is a degree of predictability in the taxa associated with each macrohabitat. It is also clear that seamounts and offshore banks such as Hatton Bank support a diverse range of habitats from relatively quiescent fine sediment areas to submarine cliffs, exposed rock and coral reef framework. Habitats may vary and change across small spatial scales with concomitant change in megafaunal assemblages but further work to quantify the beta diversity of offshore banks and seamounts is needed. In addition to wide-area seismic and bathymetric survey and small-scale photographic survey intermediate scale mapping using both multibeam backscatter analysis and high resolution sidescan sonar will prove valuable. This spatial variability should be considered in the design of offshore marine conservation areas. Recent years have seen growing concern over the damage emergent deep-water benthic communities can suffer from bottom trawl fishing prompting the United Nations General Assembly to call upon member states to close vulnerable marine ecosystems, including seamounts, hydrothermal vents and cold-water corals to bottom fishing where they are known or are likely to occur, based on the best available scientific information (Davies et al. 2007). Thus while there is now a clear consensus that bottom trawling in vulnerable, long-lived ecosystems such as cold-water coral reefs is unsustainable, society lacks a clear indication of where these ecosystems are found and how they are linked in terms of genetic dispersal and biogeography. Without this information, offshore reserve design becomes simply a matter of designating features that happen to have been discovered and surveyed. The United

Nations use of the word ‘likely’ is significant here since it puts a clear emphasis on the precautionary principle and indicates that the likelihood of a vulnerable ecosystem’s occurrence is sufficient to merit protection. There is clear need to develop our ecological understanding of these habitats in terms of their distribution, connectivity and beta diversity so that predictive models of their occurrence can be used to inform reserve design.

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Table 1

Positions and depths of photographic survey stations listed by survey date.

n, number of images analysed.

Date	Station	Start position	End position	Depth range	*n*
27-8-05	G	58° 42.520 N 17° 22.854 W	58° 42.453 N 17° 22.946 W	1096 – 1108 m	16
27-8-05	A	58° 42.773 N 18° 21.594 W	58° 42.643 N 18° 21.439 W	537 – 591 m	76
27-8-05	K	58° 43.938 N 18° 39.671 W	58° 43.805 N 18° 39.477 W	740 – 772 m	60
28-8-05	L	58° 40.983 N 18° 31.959 W	58° 41.051 N 18° 32.054 W	645 – 652 m	21
28-8-05	Q	58° 42.676 N 18° 29.614 W	58° 42.720 N 18° 29.142 W	622 – 642 m	65
28-8-05	C-D	58° 44.288 N 18° 08.007 W	58° 44.190 N 18° 08.020 W	476 – 539 m	40
28-8-05	M	58° 45.571 N 18° 04.778 W	58° 45.331 N 18° 04.268 W	514 – 582 m	36
31-8-05	R	58° 44.866 N 18° 13.904 W	58° 44.879 N 18° 13.396 W	518 – 526 m	42
31-8-05	N	58° 49.319 N 17° 57.295 W	58° 49.105 N 17° 57.011 W	530 – 650 m	79
1-09-05	P	58° 48.088 N 17° 50.006 W	58° 47.871 N 17° 49.985 W	556 – 643 m	76
1-09-05	S	58° 52.507 N 17° 50.020 W	58° 52.404 N 17° 49.823 W	682 – 730 m	36
1-09-05	E-F	58° 57.209 N 17° 41.967 W	58° 56.877 N 17° 41.810 W	798 – 855 m	52
1-09-05	H	59° 09.763 N 17° 06.344 W	59° 09.616 N 17° 06.160 W	466 – 482 m	34

Table 2

Megafaunal categories included in presence/absence analysis of still images with cross-reference to example images in Figure 4. Question marks signify possible species identification. *n*, number of occurrences scored.

Major Group	Category	Description and image reference (depth)	*n*
Cnidaria	*Lophelia*	Colony of the reef framework-forming cold-water hexacoral *Lophelia pertusa* (Scleractinia). Fig. 4.1 (658 m)	154
	Madrepora	Colony of the secondary reef framework-forming hexacoral *Madrepora oculata* (Scleractinia). Fig. 4.2 (557 m)	64
	Solitary coral	Solitary hexacoral (Scleractinia). Image probably *Desmophyllum dianthus.* Fig. 4.3 (541 m)	25
	Anthomastus	Colony of the octocoral *Anthomastus ?grandiflorus* (Alcyonacea). Fig. 4.4 (623 m)	28
	Gorgonian	Colony of a gorgonian octocoral (Gorgonacea). Image probably *Callogorgia verticillata.* Fig. 4.5 (520 m)	31
	Bamboo	Colony of a bamboo octocoral (Isididae). Image probably *Acanella.* Fig. 4.6 (741 m)	26
	Nephtheid coral	Colony of nephtheid octocoral (Alcyonacea). Fig. 4.7 (740 m)	13
	Other octocoral	Colony of other uncategorised octocoral. Fig. 4.8 (757 m)	36
	Stichopathes	Colony of hexacoral *Stichopathes ?gravieri* (Antipatharia). Fig. 4.9 (518 m)	139
	Other Antipatharia	Colony of other uncategorised antipatharian. Image probably *Leiopathes*. Fig. 4.10 (508 m)	41
	Pliobothrus	Colony of the hydrozoan *Pliobothrus ?symmetricus* (Stylasteridae). Fig. 4.11 (548 m)	106
	Phelliactis	Large sea anemone *Phelliactis ?hertwigi* (Actiniaria). Fig. 4.12 (613 m)	103
	Other Actinia	Other uncategorised actinian. Image possibly *Bolocera*. Fig. 4.13 (632 m)	160
	Sediment-dwelling anthozoan	Small sediment-dwelling actinian or ceriantharian. Fig. 4.14 (1102 m)	51
Echinodermata	*Psolus*	Sessile suspension-feeding holothorian, proably *Psolus squamatus.* Fig. 4.15 (518 m)	201
	Stichopus	Mobile deposit-feeding holothorian, probably *Stichopus tremulus*. Fig. 4.16 (646 m)	36
	Cidaris	Large echinoid (Cidaridae). Fig. 4.17 (626 m)	60
	Other echnoid	Other uncategorised echinoid. Fig. 4.18 (533 m)	23
	Ophiuroidea	Uncategorised ophiuroid. Fig. 4.19 (831 m)	78
	Crinoid	Uncategorised crinoid. Fig. 4.20 (740 m)	52
	Brisingid	Basket star, possibly *Novodinia* sp. Fig. 4.21 (697 m)	23
Crustacea	Galatheid	Small anomuran ‘squat lobsters’ (Galathoidea). Fig. 4.22 (704 m)	155
	Decapod	Uncategorised decapod ‘crab’. Image probably *Chaceon affinis*. Fig. 4.23 (741 m)	51
	Prawn	Uncategorised decapod ‘prawn’. Fig. 4.24 (638 m)	26
Echiura	Bonelliid echiuran	Feeding proboscoides of large echiuran worm, probably *Bonellia viridis*. Fig. 4.25 (623 m)	15
Annelida	Serpulidae	Tube-dwelling serpulid polychaete worm. Fig. 4.26 (836 m)	25
	Sabellidae	Tube-dwelling sabellid polychaete worm. Fig. 4.27 (698 m)	47
	Polychaete feeding tubes	Polychaete feeding tubes emerging from sediment.	28
Foraminifera	Xenophyophore	Large testate foraminiferans, probably *Syringammina fragillisima*. Fig. 4.28 (798 m)	15
Porifera	Encrusting sponge	Sponge encrusting rock or dead coral. Fig. 4.29 (708 m)	172
	Erect sponge	Erect sponge growing from rock or dead coral. Fig. 4.30 (557 m)	87
	Aphrocallistes	Glass sponge, probably *Aphrocallistes bocagei* (Hexactinellida). Fig. 4.31 (756 m)	39
Pisces	*Lepidion*	Probably *Lepidion eques* (Moridae). Fig. 4.32 (646 m)	35
	Other fish	Other fish. Example images show *Helicolinus dactylopterus*, Fig. 4.33 (479 m). *Chimaera monstrosa*, Fig. 4.34 (641 m) and *Galeus malastomas*, Fig. 4.35 (542 m).	31

Table 3

Number of megafaunal taxa and total occurrences found with each macrohabitat. Subsequent analysis was based on presence/absence scoring where a score of one corresponded to one or more occurrences in an image and a score of zero to a taxon that was absent.

n = number images analysed.

	Mud	**Sand**	**Cobbles**	**Coral rubble**	**Coral framework**	**Rock**
Number of taxa	16	24	19	34	31	33
Total occurrences	61	197	60	570	621	667
Occurrences per image	1.49	1.06	1.94	4.16	6.68	4.63
n	*41*	*187*	*31*	*137*	*93*	*144*

Table 4

One-way ANOVA results and multiple comparisons made by Bonferroni corrections of the differences in megafaunal richness between macrohabitats. (* $p < 0.05$)

ANOVA source of variation	**SS**	**df**	**MS**	**F**
Between groups	2526.990	5	505.398	137.477 *
Residual	2312.355	629	3.6762	
Total	4839.345	634		

Pairwise comparison	**Bonferroni t-value**
Coral framework, Sand	23.117 *
Coral framework, Mud	14.439 *
Coral framework, Cobbles	11.926 *
Coral framework, Coral rubble	9.902 *
Coral framework, Rock	8.156 *
Rock, Coral rubble	2.059
Rock, Cobbles	7.023 *
Rock, Mud	9.177 *
Rock, Sand	16.717 *
Coral rubble, Cobbles	5.760 *
Coral rubble, Mud	7.749 *
Coral rubble, Sand	14.301 *
Cobbles, Mud	0.981
Cobbles, Sand	2.372
Mud, Sand	1.314

Table 5

Analysis of Similarities (ANOSIM) by macrohabitat. (* *R* > 0.4)

Habitats compared	**Average dissimilarity**	***R* statistic**	**p**
Mud, Sand	97.6	0.097	0.001
Mud, Cobbles	95.5	0.296	0.001
Mud, Coral rubble	94.7	0.425	0.001 *
Mud, Coral framework	96.3	0.793	0.001 *
Mud, Rock	93.7	0.681	0.001 *
Sand, Cobbles	96.2	-0.009	0.592
Sand, Coral rubble	95.7	0.216	0.001
Sand, Coral framework	96.4	0.336	0.001
Sand, Rock	94.1	0.387	0.001
Cobbles, Coral rubble	90.8	0.212	0.001
Cobbles, Coral framework	92.9	0.706	0.001 *
Cobbles, Rock	78.9	0.152	0.025
Coral rubble, Coral framework	77.7	0.069	0.001
Coral rubble, Rock	81.4	0.271	0.001
Coral framework, Rock	82.7	0.558	0.001 *

Table 6

Percent similarity of taxa by macrohabitat.

Habitat	**Average similarity**	**Taxa (cumulative % contribution)**
Mud	18.6	Ophiuroidea (64.1), Polychaete feeding tubes (78.6), Xenophyophore (92.1)
Sand	3.62	*Stichopus* (30.4), Other echinoid (43.1), Other fish (55.0), *Psolus* (65.4), *Cidaris* (72.1), Encrusting sponge (75.4), Sediment-dwelling Actinia (78.6), Other Actinia (81.7), Polychaete feeding tubes (84.8), Bonelliid echiuran (87.5), *Lophelia* (89.7), *Lepidion* (91.2)
Cobbles	13.9	*Pliobothrus* (34.7), Encrusting sponge (67.2), *Psolus* (90.1)
Coral rubble	18.0	*Lophelia* (17.0), Other Actinia (33.7), *Psolus* (43.9), Galatheid (52.5), *Stichopathes* (60.9), Erect sponge (68.7), *Phelliactis* (75.6), Encrusting sponge (80.4), Sediment-dwelling Actinia (84.0), Ophiuroidea (87.1), Sabellidae (90.1)
Coral framework	36.2	*Stichopathes* (20.2), Other Actinia (37.7), *Lophelia* (54.8), Galatheid (67.1), Crinoid (72.0), Erect sponge (76.3), *Phelliactis* (79.8), Other Antipatharia (82.7), Ophiuroidea (84.6), Prawn (86.6), Other octocoral (88.4), *Madrepora* (90.1)
Rock	37.3	*Psolus* (40.29), Encrusting sponge (66.2), *Pliobothrus* (79.5), Galatheid (87.0), *Stichopathes* (88.8), *Lophelia* (90.6)

Table 7

PCA results ordinating frequency of occurrence of substrata to explain the variation in macrohabitats between stations. The symbol * indicated PC axes with eigenvalues >1, the scores that were used to characterise local-scale substratum for each station.

1. Eigenvalues

PC axis	*Eigenvalues*	*% Variation*	*Cumulative % variation*
1 *	1.86	31.0	31.0
2 *	1.55	25.9	56.9
3 *	1.26	21.0	77.9
4	0.85	14.2	92.1
5	0.47	7.9	100.0

2. Eigenvectors

Variable	*PC1*	*PC2*	*PC3*	*PC4*	*PC5*
Mud	-0.462	-0.482	-0.251	-0.424	0.140
Sand	0.392	0.342	-0.585	0.238	0.333
Cobbles	-0.246	0.465	0.514	-0.173	0.640
Rock	-0.499	0.442	0.048	0.321	-0.550
Coral rubble	0.495	0.206	0.240	-0.624	-0.394
Coral framework	0.280	-0.444	0.520	0.492	0.043

Table 8

BEST analysis ranking combinations of environmental variables that correlate to the megafaunal assemblages. The symbol * indicates the variable that best correlates to taxa occurrence among all possible combinations of environmental variables.

Spearman *ρ*	**Variable(s)**
0.394 *	fine-scale substratum
0.127	depth
0.113	PCA axis 2 (local-scale substratum)
0.093	PCA axis 3 (local-scale substratum)
0.091	longitude
0.058	PCA axis 1 (local-scale substratum)
0.043	latitude

Figure 1

Chart showing regional setting of Rockall Plateau including Hatton Bank. Points correspond to literature occurrences of framework-forming cold-water corals (*Lophelia pertusa* and *Madrepora oculata*, data courtesy M. Wisshak and A. Freiwald). Marked square corresponds to area enlarged in Figure 2. ADS, Anton Dohrn Seamount; BB, Bill Bailey's Bank; FB, Faroe Bank; GBB, George Bligh Bank; HB, Hatton Bank; LB, Lousy Bank; PB, Porcupine Bank; RB, Rockall Bank; Ros. B, Rosemary Bank; WTR, Wyville Thomson Ridge.

Figure 2

Chart showing the location of photographic stations and any intersecting BGS seismic lines. Regional setting of this area is shown in Figure 1. Isobaths taken from GEBCO represent generalised interpretation of the bathymetry. The recent SEA surveys indicate that the seafloor is considerably more complex and there are differences of more than 100 m in some places. For correct station depths refer to Table 1.

Figure 3

Photographs of macrohabitat categories with descriptions of fauna present in each image.

a. Mud with many ophiuroids, a xenophyophore (probably *Syrangammina fragilissima*) and a cut-throat eel (*Synaphobranchus kaupi*). Scour formed around perimeter of xenophyophore test suggests active near bed current regime (799 m depth).

b. Sand with shell debris and fragments of coral rubble. Sparse fauna with brachiopod and mobile holothurian (*Stichopus*) visible (646 m depth).

c. Cobble with many small stones and sparse coral rubble. Stones colonised by encrusting sponges and stylasterid coral (*Pliobothrus*) (650 m depth).

d. Rock apparently steeply sloping with sizeable colony of antipatharian coral (probably *Leiopathes*), stylasterid corals (*Pliobothrus*), holothurians (*Psolus squamatus*) and large *Phelliactis* anemone. Fissures in rock contain galatheid crustaceans (508 m depth).

e. Coral framework with live *Lophelia pertusa*. Epifauna include large *Phelliactis*, yellow gorgonian, hydroids, seafan gorgonians, antipatharians, corkscrew-shaped antipatharians (*Stichopathes*) and unidentified anemones. Decapod crustaceans and prawns also visible (633 m depth).

f. Coral rubble with encrusting blue sponge, *Cidaris* urchin and galatheids (642 m depth).

Figure 4

Photographs illustrating the megafaunal categories listed in Table 2. See Table for description and depth of each image.

Figure 5

British Geological Survey seismic reflection profiles that coincide with photographic survey stations on Hatton Bank. (a) sparker line 00/01-38 (Stn. C-D), (b) sparker line 00/01-23 (Stn. K), (c) sparker line 00/01-27 (Stn. L), (d) airgun line 00/01-1 (Stn. M), (e) sparker line 00/01-28 (Stn. Q), (f) sparker line

06/02-6 (Stns. S and P). The vertical scale is two-way travel time in milliseconds, 100 ms =~75 m in water. Seismic profiles vertically exaggerate seabed topography and an estimate of this vertical exaggeration at the seabed is given in the lower right hand corner of each panel.

Figure 6

Bathymetric charts derived from multibeam sonar at the survey stations intersected by seismic lines. (a) Stns. C-D and M, (b) Stn. K, (c) Stns. L and Q, (d) Stns. P and S, (e) enlargement of Stn. S to show probable carbonate mound and scour depression to the east. Table gives the minimum depths plotted in red and maximum depths plotted in blue for each chart. Isobaths are at 10 m intervals apart from chart (d) where isobaths are at 20 m intervals. Seismic lines are shown using red lines and the positions of photographic survey stations using green dots.

Figure 7

Percentage occurrence of fauna by macrohabitat. Final dataset of each histogram ('Photos') shows the percentage of total photographs analysed that were categorised to each macrohabitat type.

Figure 8

Ordination of the three principal axes that explain the most variation in substrata frequency of occurrence across stations. Note the labels for stations K and N overlap one another in this figure.

Figure 9

Multi-dimensional scaling plot illustrating the grouping of megafaunal taxa by macrohabitat. Some taxa plot closely together so their labels overlap to some extent.

Figure 10

Enlargement of portion of an image from station K showing an octocoral likely to be *Paragorgia arborea* (58° 43.886 N 18° 39.586 W, 759 m depth). While impossible to make a definitive identification from this photograph alone, this would represent the southernmost extent of this species in the north east Atlantic and to our knowledge the first record from Rockall Plateau.