



Megafaunal distribution and biodiversity in a heterogeneous landscape: the iceberg-scoured Rockall Bank, NE Atlantic

Katleen Robert^{1,*}, Daniel O. B. Jones², Veerle A. I. Huvenne²

¹School of Ocean and Earth Science, University of Southampton, Waterfront Campus, European Way, Southampton SO14 3ZH, UK

²National Oceanography Centre, European Way, Southampton SO14 3ZH, UK

ABSTRACT: Species distributions are influenced by spatial structure in environmental factors, but the scales at which these dependencies occur and the effect of habitat patch diversity, connectivity and spatial arrangement have rarely been investigated in deep-sea settings. In this study, spatially limited photographic transects collected from Rockall Bank, NE Atlantic, were combined with sidescan and multibeam sonar maps to model spatial patterns in species distribution and biodiversity. Sediment interpretation maps were created and canonical ordination techniques were used to examine relationships between fine-scale sediment characteristics extracted from the digital stills as well as landscape metrics describing the patch mosaic structure of the surrounding areas. Fine-scale sediment characteristics explained 45.1 and 63.8% of the variation in species composition and biodiversity, respectively. This survey effectively captured variation in species distribution resulting from iceberg ploughmarks, occurring at a scale of <50 m — which would normally go undetected by traditional ship-based studies. Our study suggests that fine-scale environmental information is required to capture the spatial heterogeneity of complex seafloor areas in sufficient detail to model species distributions and biodiversity.

KEY WORDS: Landscape ecology · Deep sea · Megabenthic invertebrates · Spatial heterogeneity · Biodiversity

INTRODUCTION

Long-term stability in the deep sea was initially suggested as an explanation for observed species richness that was higher than expected (Sanders 1968). However, the importance of spatial heterogeneity (the uneven distribution of environmental variables over space) was soon recognized (Jumars 1976). In a heterogeneous environment, a higher number of niches are available — which allows resource partitioning to occur, thereby reducing competitive exclusion between species (Williams 1964). The hypothesis that increased spatial heterogeneity leads to higher species richness has been examined in terrestrial (Pickett & Cadenasso 1995, Tews et al. 2004) and shallow water environments (Hewitt et al. 2005, Mellin et

al. 2012), but for many deep-sea areas, spatial heterogeneity has not yet been mapped at sufficient resolution to represent fine-scale biodiversity patterns over large spatial extents (Thrush et al. 2008, Levin & Sibuet 2012). Yet this information would confer a significant advantage for the implementation of management measures, where precautionary decisions may have to be made based on limited evidence. In this case, seafloor heterogeneity, which can be rapidly described via acoustic surveys, could be employed as a proxy for biological diversity or conservation priority, reducing the significant time investment associated with biological data collection, identification and manual quantification (Schoening et al. 2012).

Spatial patterns in species distribution can arise from interactions between organisms (e.g. intraspeci-

*Corresponding author: kr2e11@soton.ac.uk

fic: reproduction or recruitment; and interspecific: predation or competition) or be induced by spatial structures exhibited by environmental factors (Legendre 1993). Characterizing the relationships between environmental factors and species distributions is a first step in accurately predicting species distributions and creating fine-scale habitat maps. Environmental variables vary over different spatial scales to form a mosaic of interspersed habitat patches on the seafloor (Jumars 1976). However, in the deep sea the scales at which these factors influence species distributions have not yet been thoroughly investigated. At broader spatial scales (i.e. 100 to 1000 km), deep-sea studies on the relationships between environmental variables and biodiversity have showed that water mass and current-related factors (e.g. oxygen and temperature), as well as flux of organic material have the strongest influence on biodiversity (Levin et al. 2001, Sellanes et al. 2010, Williams et al. 2010). At medium scales (i.e. 1 to 10s of km), the presence of large geomorphological features such as submarine canyons, nodule fields or habitat forming biological structures are significant (Henry & Roberts 2007, Sellanes et al. 2010, Vetter et al. 2010). The importance of sediment properties (e.g. hardness, grain size), food resources (e.g. organic matter content) and disturbance rate appears only at finer spatial scales (i.e. m to km) (Vetter & Dayton 1999, Gutt & Piepenburg 2003, McClain & Barry 2010).

The spatial relationships between habitat patches and their effects on the distribution and composition of the deep-sea benthic fauna has even more rarely been examined (Wedding et al. 2011). The field of 'landscape ecology', developed in terrestrial environments, has focused on creating metrics to describe the geometry and spatial arrangement of habitat patches and their relationships to ecological processes (Turner & Gardner 1991). Class metrics are used to describe properties of patches from a single substratum type, while landscape metrics consider all patches present within a landscape (McGarigal et al. 2012). In shallow marine environments, a landscape approach has been used to examine the effects of habitat fragmentation in seagrass beds (Jackson et al. 2006), the importance of patch size and connectivity in coral reefs (Grober-Dunsmore et al. 2007), spatial patterns in rocky benthic species assemblages (Garrabou et al. 1998) as well as the multi-scale influence of landscape structure on the spatial distribution of fish species (Pittman et al. 2004, Monk et al. 2011). Metrics such as fractal dimension have also been found useful in describing irregular shapes such as spatial patterns within mussel beds (Com-

mito & Rusignuolo 2000) and the morphology of marine branching sessile organisms (Kaandorp 1999). Although application of spatial metrics in deeper marine ecosystems had been limited owing to difficulties associated with underwater mapping, it was successful in explaining fine-scale (<1 m) benthic species assemblages in the Antarctic (Teixidó et al. 2002, Teixidó et al. 2007). In deeper sites, the landscape is often characterized by sediment type, and not by vegetation or biogenic structures (with the exception of cold-water corals, carbonate mounds and sponge aggregations (Klitgaard 1995, Howell et al. 2011), resulting in more subtle changes in seafloor structure which makes it inherently difficult to delineate benthic habitats (Zajac 2008). However, recent studies in automated seabed classification based on sidescan or multibeam sonar backscatter have greatly facilitated the creation of high resolution sediment interpretation maps (Wilson et al. 2007, Lucier 2008, Brown et al. 2012). Analysis of these maps from a landscape perspective has the potential to increase the amount of ecologically meaningful information extracted. Since no additional data collection is required, this approach has the potential to reduce the time needed to gather sufficient information to address management issues.

As the anthropogenic footprint of activities such as trawling extends deeper into our oceans, detailed descriptions of seafloor habitats and the species they harbour become increasingly important in order to establish the baseline state of this ecosystem (Levin & Sibuet 2012). As the environmental variables responsible for spatial structuring in species distribution vary over different scales, choice of resolution and spatial extent will affect the ecological processes that can be examined (Levin 1992). We must find sampling resolutions that retain enough fine-scale variation to describe species distributions while remaining coarse enough to be economically feasible (Przeslawski et al. 2011).

This study used a hierarchical survey to examine a highly heterogeneous seafloor area characterized by iceberg ploughmarks on Rockall Bank, NE Atlantic (200 to 400 m depth). A fine-scale analysis of photographic transects was first carried out to identify megafaunal species and map their distribution and biodiversity. A landscape approach was then used to examine whether the inclusion of metrics describing the spatial arrangement of habitat patches could improve the explanatory power of models using environmental variables to describe species composition and distributions. The amount of variation explained by survey techniques of varying resolutions was also

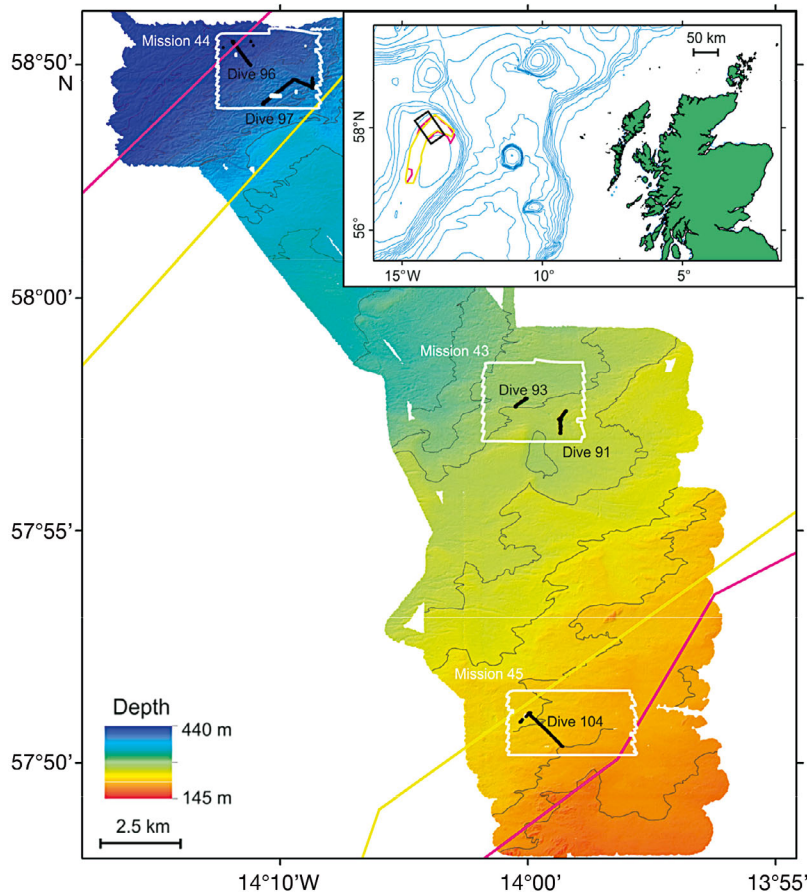


Fig. 1. Hierarchical survey carried out on Rockall Bank, Northeast Atlantic. Ship-based bathymetry displayed with superimposed outlines of the sidescan sonar data (white) collected during 3 autonomous underwater vehicle (AUV) missions. The 5 remotely operated vehicle (ROV) imagery transects are shown in black. Insert shows the position of Rockall Bank in relation to Scotland; the black rectangle represents the location of the survey. The boundaries of the 2007 Fisheries Closure area and candidate for 'Special Area of Conservation' are illustrated in yellow and pink, respectively. Background bathymetry of the Northeast Atlantic from GEBCO (General Bathymetric Chart of the Oceans; IOC IHO and BODC 2003)

examined, and the scale of variation in the biological data was used to identify the process potentially responsible for the spatial structure captured by the survey.

MATERIALS AND METHODS

Study site

Rockall Bank, NE Atlantic (Fig. 1) is a shallower part of the larger Rockall Plateau, a subsided and submerged microcontinent which includes Hatton-Rockall Basin and Hatton Bank to the northwest, and which is separated from the Scottish continental mar-

gin by Rockall Trough (Roberts 1971, 1975). The seabed of the Rockall Bank has a long history of investigation (Thomson 1874). The shallower areas of the western bank have a heterogeneous seabed, including partly buried rock outcrops, boulder and cobble fields as well as large areas of carbonate sand cover (Roberts 1975). The deeper western and southern flanks (250 to 450 m water depth) are incised with deep scours (<8 m) from iceberg keels having ploughed the seabed during periods of Quaternary low sea levels (Sacchetti et al. 2012). Over time, soft sediment filled the centre of the ploughmarks while coarse debris remained at the scar edges. The presence of dispersed hard substratum has allowed colonization by the cold-water coral *Lophelia pertusa* (Wilson 1979a,b, Rogers 1999). A high diversity of organisms has been reported associated with *L. pertusa* patches (Jensen & Frederiksen 1992, Wienberg et al. 2008) but there has been little investigation of the fauna of the softer sediments (Wilson & Desmond 1986). In 2007, the North East Atlantic Fisheries Commission established a Fisheries Closure on the north-western flank of Rockall Bank. In 2010, a nearly overlapping area was proposed by the Joint Nature and Conservation Committee (JNCC), an adviser group to the UK Government, as a candidate 'Special Area of Conservation' (SAC) under the EU Habitats Directive, with the aim to protect the cold-water coral communities from extensive deep-water fishing activities (Howell et al. 2009, JNCC 2010a)

Survey design and data collection

Map creation

A nested seafloor survey of the northwestern flank of Rockall Bank (Fig. 1) (200 to 400 m depth) was carried out during the RRS 'James Cook' 060 cruise in May and June 2011 as part of the 'Marine Environmental Mapping Programme' (MAREMAP: www.maremap.ac.uk/index.html) and the 'Complex Deep-sea Environments: Mapping habitat heterogeneity As Proxy for biodiversity' project (CODEMAP: www.codemap.eu/). Three missions (M43, M44 and

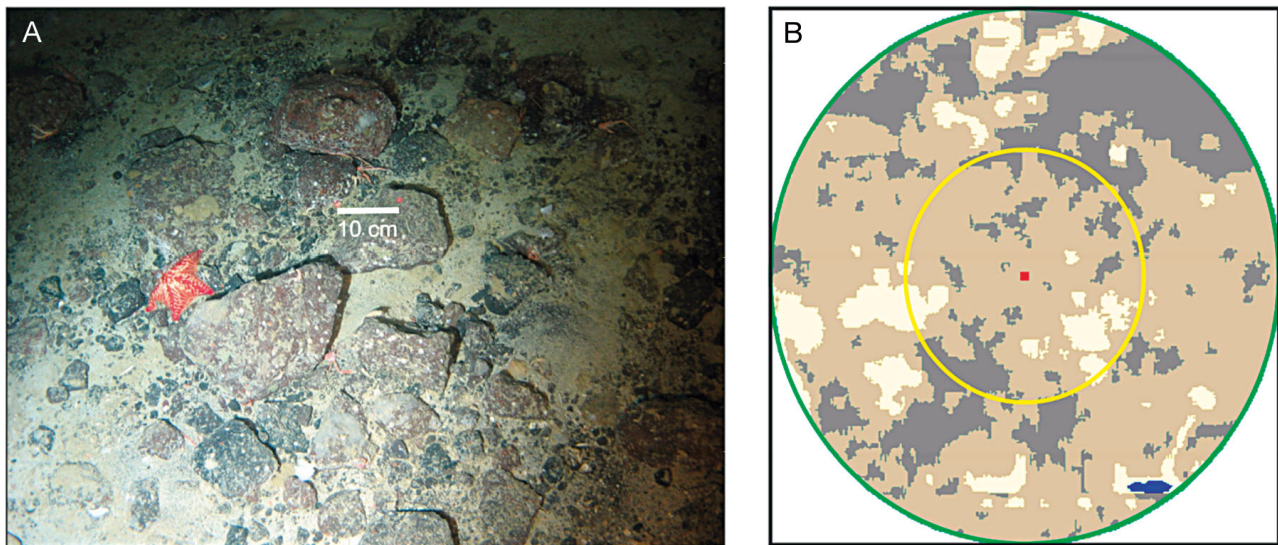


Fig. 2. (A) Image acquired via remotely operated vehicle illustrating megabenthic organisms and a mixed substratum. Laser beams are separated by 10 cm. (B) Associated circular areas (green and yellow; 75 m and 30 m radii) as represented by the sediment interpretation map. Soft, mixed and hard substratum types are represented in grey, tan and cream, respectively, while coral stand are shown in blue. The red square illustrates the approximate area covered by the image

M45) by the autonomous underwater vehicle (AUV) Autosub6000 were carried out, mapping 3 distinct areas of seafloor (12.0, 12.0 and 13.0 km², respectively) using an EdgeTech high frequency (410 kHz) high-resolution (resulting pixel size of 0.5 × 0.5 m) sidescan sonar. These were located in areas within (M43) and immediately outside (M44 and M45) the Fisheries Closure, but still within the candidate SAC (Fig. 1). Ship-board bathymetry of the surrounding area (380 km²) was also collected using a Kongsberg EM710 multibeam echosounder (128 beams; resulting pixel size of 20 × 20 m).

Thematic maps representing seafloor substratum composition were produced, based on an unsupervised classification of the sidescan sonar backscatter. Unsupervised classification attempts to identify structure within the data and segment it into units without prior recourse to *in situ* reference points (Brown et al. 2012). This classification used mean backscatter, average grey level difference, and variance within a 9 × 9 pixel moving window to assign each pixel to 1 of 6 classes: soft, mixed or hard substratum, coral stand or rubble, and exposed bedrock. Mean backscatter represented substratum hardness while variance at fine spatial scales was indicative of more complex substratum structures such as coral stands, where strong contrasts occur between the high backscatter of the corals in combination with the low backscatter caused by their shadows (Huvette et al. 2002). Sediment patches of less than 12

pixels were filtered out; those pixels were assigned to the sediment class represented by the majority of neighbouring pixels.

Biological imagery

Within the areas surveyed by the AUV, 5 remotely operated vehicle (ROV) photographic transects (Stns 91, 93, 96, 97 and 104) were conducted using a SAAB SeaEye Lynx. Digital stills (Fig. 2) were taken every ~40 s using an oblique mounted downward-looking Kongsberg OE14-208 camera (focal length: 7.188 mm and maximum aperture: *f*/2) equipped with parallel lasers for scale (10 cm separation), and used for analysis of megabenthic invertebrates. Using the image processing software Image J (<http://rsbweb.nih.gov/ij/>), all images from a transect were imported using the 'Image Sequence' function to form a 'stack' (multiple images displayed consecutively in a single window); each organism was identified, marked and its pixel position recorded to avoid risks of double counting. Images of suboptimal quality were removed as well as those collected when ROV altitude varied beyond the 1 to 2.25 m range. Each image was then georeferenced using the ROV's ultra-short baseline (USBL) navigation system which also recorded its depth and altitude. The ROV position was estimated based on a moving average of the navigation with a 4-reading subset, correspon-

ding to 1 s. See Table 5 for average depth, transect lengths and number of images collected per transect. The ROV was also equipped with a SeaKing CTD which showed average bottom temperatures of 9.26°C (SD = 0.10°C) and salinities of 34.8‰ (SD = 0.025‰).

When species-level identification would have required sample collection, visually distinctive taxa were identified to the lowest possible taxonomic unit and assigned to morphospecies. The use of morphospecies is somewhat problematic, as cryptic species will be considered under a single grouping while other groups showing greater morphological variation (e.g. sponges) may be split into more groups, but their use is common in marine studies where imagery is used as the main sampling tool (Soltwedel et al. 2009, Schlacher et al. 2010, Compton et al. 2013). Although the use of higher taxonomic levels is another option to estimate biodiversity (Roy et al. 1996), these tend to be more useful when investigating broader scale patterns—and in the case of our dataset, even family-level identification of sponges is problematic without specimen collection. As such, the diversity measures presented are likely underestimated, but represent the closest estimates that can be achieved. Consultation with the image catalogue compiled by Howell & Davies (2010) for morphospecies encountered in the surrounding area was carried out, and a set of voucher images was assembled. This set of images was deposited in the publicly available SERPENT media archive (<http://archive.serpentproject.com/>). In the case of encrusting species, individual colonies were counted. For community analysis, only morphospecies for which at least 10 individuals were observed and a presence recorded in at least 10 images were retained, but every record was retained for biodiversity calculations (Shannon index of diversity, H' , Shannon 1948). To examine the effect that cryptic species may have on estimates of biodiversity, a percentage (5% and 20%) of the number of taxa listed in OBIS (Ocean Biogeographic Information System, www.iobis.org/) for the North Atlantic Ocean was used as a potential number of present, but undistinguishable cryptic species. When 2 or more specimens of a morphospecies of ascidians, bryozoans, cerianthids, cormatulids, sponges, ophiuroids, sabellid worms or sipuncula worms were observed within an image, each individual was randomly assigned, with replacement, to a potential cryptic species, and biodiversity estimates were recalculated. This analysis was conducted in order to determine whether the uncertainty created by the use of morphospecies was high

enough to effect the conclusions of the study. However, as the trends observed did not change, we argue that the use of morphospecies is appropriate for this study (results presented in Supplement 1 at www.int-res.com/articles/suppl/m501p067_supp.pdf).

Imagery-derived environmental variables

Composition of the substratum was visually assessed in each image based on grain size classes: soft sediment, gravel, pebbles (4 to 64 mm), cobbles (64 to 256 mm) and boulders (>256 mm) (Wentworth 1922). Pebbles of 4 mm could be measured in the imagery, but only a visual distinction in texture could be used to separate soft sediments from gravel. The overall composition was first assigned to 1 of 7 seabed facies: sand, sand and pebbles or gravel, sand and cobbles, cobble-dominated, coral stand, coral rubble and exposed bedrock (example images are provided in Supplement 2 at www.int-res.com/articles/suppl/m501p067_supp.pdf). To obtain a quantitative description of substratum composition, percentage covers were obtained by importing images in the freely available statistical software R (R Development Core Team 2011) and drawing 100 randomly located points for each image. Using a custom-made R code with an interactive prompt, the substratum (grain size class, exposed bedrock, coral rubble or coral stand) at each location was recorded.

Sonar-derived environmental variables

The spatial structure (e.g. size, shape, composition, spatial arrangement and diversity) of the seafloor habitat patches represented in the sediment interpretation of the sidescan sonar maps (complete extent figures are available in Supplement 3 at www.int-res.com/articles/suppl/m501p067_supp.pdf) was described using the class and landscape metrics listed in Table 1. Metrics were grouped into 5 general groups 'area and edge', 'shape', 'core area', 'diversity' (Peng et al. 2010, McGarigal et al. 2012). The first group is related to size of the patches and amount of edge, the second group is used to characterize the geometry of the different patches and the third grouping examines patch sizes when the edge cells (only the first one in this study) are removed. Spatial arrangement of patches to each other is described by the fourth group, while diversity measures (only available for landscape analysis) form the last group. Refer to McGarigal et al. (2012) for a thorough description of

Table 1. Class and landscape level metrics considered in the analysis. Class metrics were calculated for each of the 6 substratum classes present in the sediment interpretation maps: soft, mixed or hard substratum, coral stand or rubble, and exposed bedrock. For formulas and descriptions see McGarigal et al. (2012)

Class metrics	Landscape metrics
Area and edge metrics	Area and edge metrics
Patch number	Patch number
Total area	Patch density
Patch density	Edge length
Edge length	Mean patch area
Edge density	Smallest patch area
Mean patch area	Largest patch area
Smallest patch area	Shape metrics
Largest patch area	Landscape shape index
Shape metrics	Largest patch index
Landscape shape index	Mean shape index
Largest patch index	Minimum shape index
Perimeter area fractal dimension	Maximum shape index
Mean perimeter area ratios	Core area metrics
Minimum perimeter area ratio	Total core area
Maximum perimeter area ratio	Mean core area
Mean shape index	Smallest core area
Minimum shape index	Largest core area
Maximum shape index	Mean core area index
Core area metrics	Aggregation metrics
Total core area	Proportion of like adjacencies
Mean core area	Aggregation index
Smallest core area	Landscape division index
Largest core area	Splitting index
Aggregation metrics	Effective mesh size
Proportion of like adjacencies	Patch cohesion index
Aggregation index	Diversity metrics
Landscape division index	Patch richness
Splitting index	
Effective mesh size	
Patch cohesion index	

each measure and equations. In the present study, circular areas of seafloor (1, 5, 10, 20, 30, 40, 50, 75 and 100 m in radius) were delimited around each image (Fig. 2). Within those circular areas, class and landscape metrics were computed using the 'SDM-Tools' (Species Distribution Modelling Tools) package in R. Compared with the seafloor visible in the fine-scale imagery, these class and landscape metrics provided a description of the broader seabed surrounding each image. The use of increasingly larger area sizes was carried out in order to determine which one would be most appropriate for the calculation of class and landscape metrics as explanatory variables for species composition and biodiversity. Using the statistical techniques described below (redundancy analysis or linear regression with forward selection), metrics were selected for each circle size, and the amount of variation explained was calculated. Varia-

tion partitioning (explained below) was used to select which 2 circle sizes provided the most appropriate metrics to describe the biological variation observed.

For each image, the statistical mean and variance in backscatter as obtained from the original sidescan sonar maps were calculated based on all pixels present within the 2 circular areas. Area-weighted averages for slope, curvature, aspect, surface-area ratio and bathymetric position index (BPI) were calculated for the 4 m surrounding the position of each image. The layers were derived from a 20 × 20 m resolution base surface of the multibeam data (spatial reference: World Geodetic System '84 Universal Transverse Mercator Zone 28N). As BPI varies depending on neighbourhood size, 2 layers were created: coarse and fine, based on 10 pixels and 2 pixels neighbourhood radii (Wilson et al. 2007). Layers were generated in ArcGIS using the 'Spatial Analyst Extension' as well as the 'Land Facet Corridor Tools' and 'DEM Surface Tools' developed by Jenness Enterprises (Jenness 2012a,b).

Statistical analysis

Owing to the number of statistical methods employed, only a general description is provided below; additional details are provided in Supplement 4 at www.int-res.com/articles/suppl/m501p067_supp.pdf. Analyses were carried out in the statistical software R using the libraries 'vegan', 'labdsv' and 'gstat'. A methodological flowchart is also presented (Fig. 3) with each major step (as described below) represented by numbers (1 through 9). An extensive review of statistical techniques for spatial analysis of community data, including the ones employed in this study, is available in Dray et al. (2012).

Environmental variable selection

To determine which explanatory variables (e.g. sediment percentage cover, class and landscape metrics, and multibeam sonar-derived layers) could best explain morphospecies distribution, (1) redundancy analysis (RDA) was used. RDA is a type of constrained ordination which allows the regression

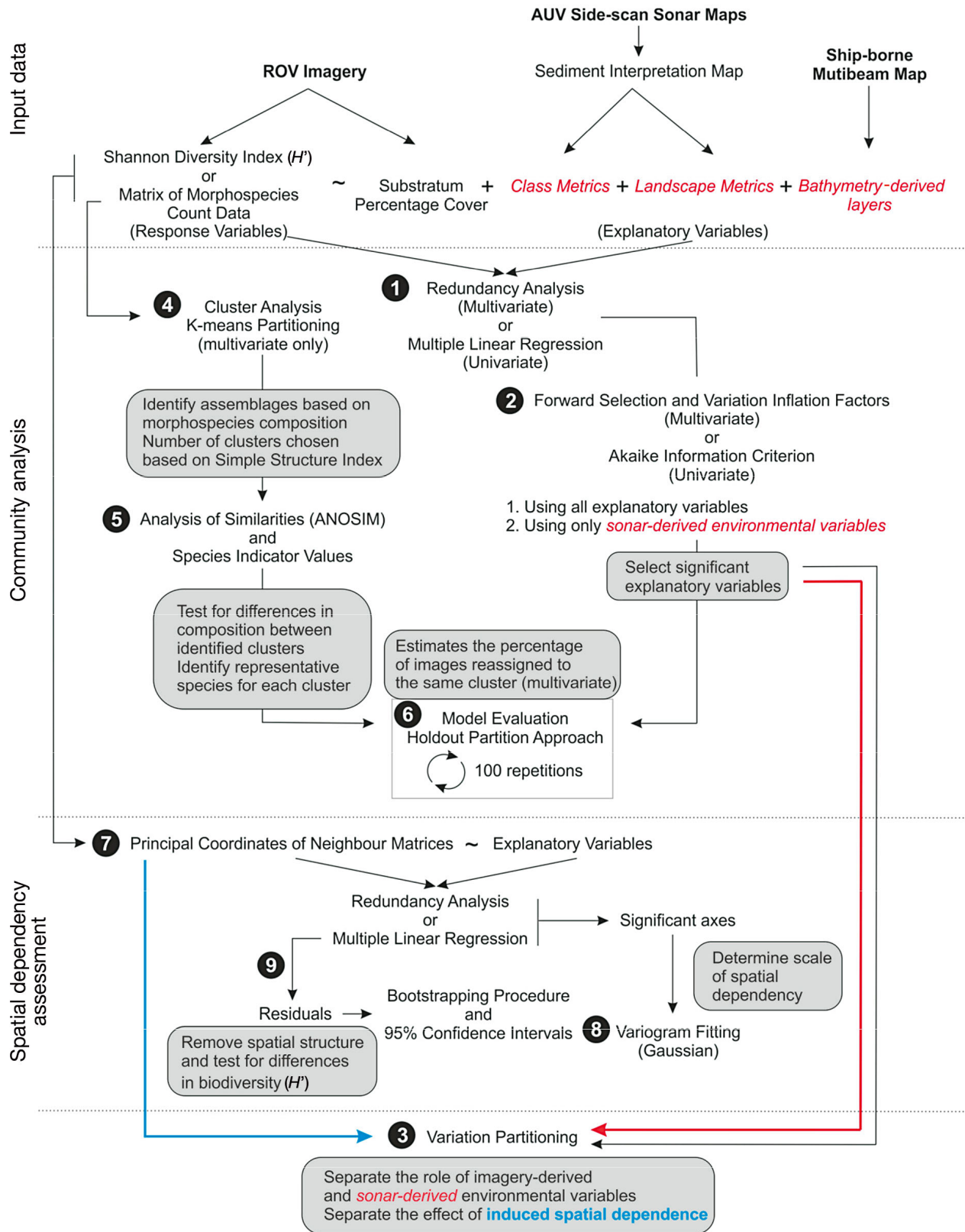


Fig. 3. Methodological flow chart representing the statistical analysis. Rounded rectangles contain short descriptions of the aims of specific steps. Elements in red show the steps involved for sonar-derived environmental variables while elements in blue show the steps involved to separate the effect of induced spatial dependence

concept to be applied to a multivariate response variable (such as a species matrix) (Legendre & Legendre 1998). The morphospecies abundance matrix was $\log_{10}(x + 1)$ transformed before the analysis to reduce the influence of abundant species (Clarke & Warwick 2001). (2) Forward selection was carried out to obtain the most parsimonious model and variance inflation factors (VIF) were used to exclude additional explanatory variables that showed strong collinearity with others present within the model (Borcard et al. 2011). To compare the information obtained from sampling tools of differing resolution (ROV images: <1 m, versus acoustic maps: 1 to 20 m), this step was carried out once using all explanatory variables and once using only sonar-derived environmental variables. As only lower resolution survey methods are generally available over large extents, (3) variation partitioning (Peres-Neto et al. 2006) was used to examine the amount of variation that was no longer captured when imagery-derived environmental variables (e.g. sediment percentage cover) were no longer available. The amount of variation in species composition and biodiversity explained by the sediment class present at the location of the image and the values of the multibeam-derived layers was also calculated. This determined whether the inclusion of landscape metrics increased explanatory power when compared to the use of sediment interpretation maps as abiotic proxies for species assemblages. These steps were also carried out using the Shannon index of diversity (H') (Shannon 1948) as a response variable, but linear regression was used instead of RDA as the response variable was now univariate.

Species assemblages

To identify clusters of images of similar morphospecies composition, (4) K-means partitioning was employed. This method aims at separating observations into a predefined number of clusters by minimizing the distance between individual samples and the center of their assigned cluster (Hartigan & Wong 1979). The optimal number of cluster was selected using the 'simple structure index' (Dimitriadou et al. 2002). (5) ANOSIM was used to assess significant differences in morphospecies composition between clusters and representative species for each cluster were identified based on 'species indicator values' (Dufrene & Legendre 1997).

Model evaluation

As an additional independent dataset was not available, (6) model evaluation was carried out using a 'holdout partition' approach. A subset of the data (300 randomly selected images) was removed from the original dataset and the RDA parameters were recomputed. The removed data points were then reclassified, and the percentage of data points re-assigned the same cluster was calculated. This process was repeated 100 times to estimate variability in the results obtained. Marine benthic studies employing similar methodological approaches include Hewitt et al. (2004), Teixidó et al. (2007) and Verfaillie et al. (2009)

Spatial dependency assessment

To determine how much of the spatial structure present in the species dataset can be explained by spatial structuring of environmental variables (induced spatial dependence), (7) principal coordinates of neighbour matrices (PCNM) were used (Borcard & Legendre 2002, Dray et al. 2006). This approach yielded synthetic representations of potential spatial structures based on distances between sampling sites. These synthetic representations were then compared to the spatial structure present in the species dataset, and those found to be accurate representations were included in the variation partitioning Step (3) to assess how well the environmental variables described the biological spatial structures modelled. (8) Gaussian variogram creation of the selected spatial representations was used to determine the scale of variation captured (the distance required for 2 points to be considered independent). As PCNM represent the spatial structure present within the species dataset, they can also be used to alleviate issues associated with autocorrelation. This property was used to compare differences in biodiversity at a broader scale, between transects and substratum facies.

Broader-scale spatial patterns

In order to assess broader-scale patterns, class and landscape metrics were calculated within a 200 m buffer around each transect line. Linear regressions of diversity, organism abundance and substratum percentage cover observed in each image were carried out against depth. To examine differences in

biodiversity (between transects and between seabed facies), we first accounted for spatial autocorrelation by filtering out the spatial structure previously modelled (9). The biodiversity indices were first regressed against the significant PCNMs, and the residuals were used as response variables in the analysis. Because transects length differed, data resampling with replacement was carried out to obtain 75 images from each transect. The 95% confidence intervals around the mean residual biodiversity for each transect were built using a bootstrapping procedure with 999 repetitions. For the seabed facies, the same bootstrapping procedure was applied, but sample size was standardized to 30 images.

RESULTS

In the 1222 images analysed, a total of 7267 individual organisms were observed from 81 morphospecies (for a complete list see Supplement 5 at www.int-res.com/articles/suppl/m501p067_supp.pdf). Many of these were rare, and only 35 morphospecies were seen in more than 10 images (Fig. 4). The squat lobster *Munida sarsi* made up the largest percentage (33.0%) of the organisms observed and was the dominant species in all transects with the exception of Transect 96, which was dominated by the holothurian *Parastichopus tremulus* (40.3% of fauna). However, across all transects, *P. tremulus* only represented 2.6% of the total observations. Only the bryozoan *Reteporella* sp. (13.1%) and colonies of yellow (9.8%) and white (6.2%) encrusting sponges composed more than 5% of the total observations.

The class and landscape metrics calculated at varying scales showed that the most variation was captured using a radius of 40 m for both morphospecies composition and biodiversity. However, when 2 circle sizes were considered, the highest variation explained was achieved using metrics derived from areas with radii of 30 m and 75 m for morphospecies composition, and 20 m and 75 m for biodiversity (results included in Supplement 6 at www.int-res.com/articles/suppl/m501p067_supp.pdf). For simplicity, sonar-derived metrics calculated at 30 m and 75 m were used for the analysis.

Following forward selection, a large number of environmental variables (substratum percentage cover, class and landscape metrics as well as backscatter and bathymetric variables) significantly explained morphospecies composition and biodiversity (Tables 2 & 3). The most parsimonious models including all environmental variables explained 45.1%

($p = 0.001$) and 63.8% ($p < 0.001$) of the variation for morphospecies composition and biodiversity, respectively. When models relied solely on sonar-derived environmental characteristics, lower percentages of variation were explained: 24.7% ($p = 0.001$) and 40.6% ($p < 0.001$) for morphospecies composition and biodiversity, respectively. However, these percentages were much higher than what was obtained when only the sediment interpretation class and multibeam-derived information were employed: variation explained 13.0% ($p = 0.001$) for morphospecies composition and 22.9% ($p < 0.001$) for biodiversity.

The first 14 axes of the redundancy analysis were significant, but only the first 2 axes are illustrated in the ordination graphs. Substratum percentage cover, as obtained from the imagery, best explained variation in the morphospecies count data (Fig. 5A). The first canonical axis illustrates a gradient in images dominated by soft to hard substrata, while the second axis represents the presence of coral rubble and stands. The vectors representing species scores (Fig. 5B) separate into 3 subgroups: upper right quadrant, characterized by squat lobsters *Munida sarsi*, a species of Actiniaria, yellow encrusting sponges and Sabellid worms; lower right quadrant, showing predominance of other small encrusting sponge colonies and bryozoan species as well as the asteroid *Porania pulvillus*; and lower left quadrant, represented by the holothurian *Parastichopus tremulus*. K-means partitioning showed a similar trend by identifying an optimum of 3 clusters. However, the use of 4 clusters allowed the separation of species occurring on both corals and hard substratum from those more closely associated with live coral stands. As the 4 clusters differed significantly in their morphospecies composition based on ANOSIM analysis ($R = 0.85$, $p = 0.001$), they were retained.

Between 3 and 15 morphospecies were representative for each cluster, as determined by indicator species analysis (Table 4). However, no morphospecies significantly represented the cluster associated with soft sediment habitats, although this is likely a result of the low densities of organisms observed in this habitat. There was a clear separation in ordination space of images assigned to each K-means cluster (Fig. 6). At the transect level, morphospecies associated with soft sediments only represented 5.3% of total organisms observed, while coral-associated morphospecies represented 18.9%. The remainder of the organisms recorded represented hard bottom (40.1%) or more generalist morphospecies (e.g. associated with hard substratum, coral stand and rubble;

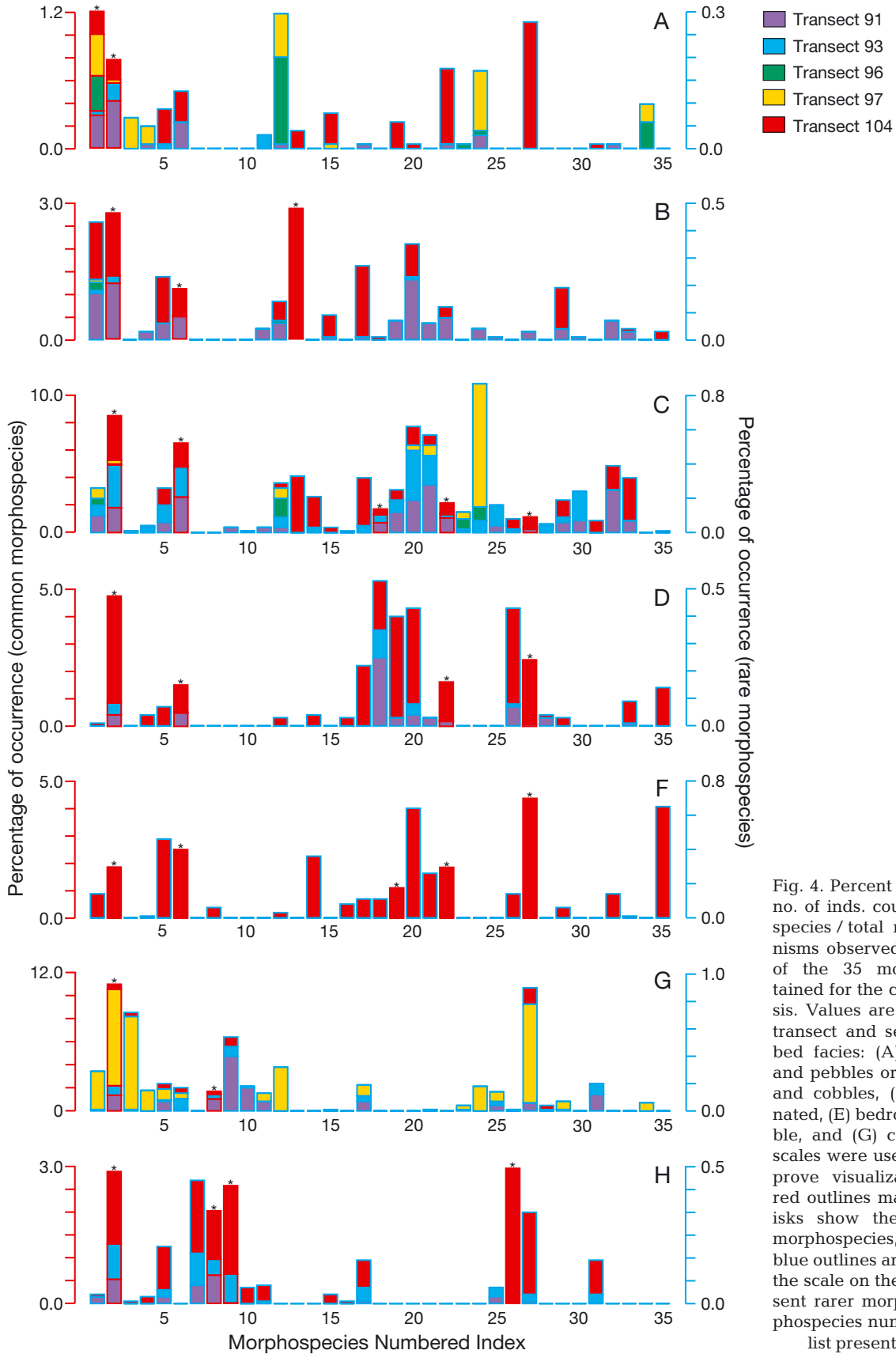


Fig. 4. Percent occurrence (total no. of inds. counted for a given species / total no. of ind. organisms observed \times 100) for each of the 35 morphospecies retained for the community analysis. Values are colour-coded by transect and separated by seabed facies: (A) sand, (B) sand and pebbles or gravel, (C) sand and cobbles, (D) cobble dominated, (E) bedrock, (F) coral rubble, and (G) coral stands. Two scales were used in order to improve visualization: bars with red outlines marked with asterisks show the more common morphospecies, while bars with blue outlines are associated with the scale on the right and represent rarer morphospecies. Morphospecies numbers refer to the list presented in Table 4

Table 2. Selected environmental variables for the most parsimonious models (with and without including fine-scale imagery-derived information) for the morphospecies count matrix. α = class metrics, β = landscape metrics, γ = sidescan sonar, δ = multi-beam sonar, ϵ = ROV imagery-derived variables

	Sonar	Imagery and sonar
Explanatory variables	β Number of patches (75 m)	ϵ Percentage cover cobbles
	α Proportion of like adjacencies sand (30 m)	ϵ Percentage cover rubble
	α Total area coral (30 m)	ϵ Percentage cover live coral
	γ Mean backscatter (30 m)	ϵ (Percentage cover cobbles) ²
	α Mean shape index coral (75 m)	ϵ Rock (factor)
	α Effective mesh size bedrock (30 m)	ϵ Rock - sand (factor)
	δ Aspect	ϵ Sand - cobbles (factor)
	β Mean shape index (75 m)	ϵ Cobbles - sand (factor)
	α Minimum patch core area coral (30 m)	α Proportion of like adjacencies sand (30 m)
	α Patch density bedrock (30 m)	α Mean shape index coral (75 m)
	α Patch density rubble (30 m)	ϵ Percentage cover boulder
	α Landscape shape index mixed (30 m)	α Minimum patch core area coral (30 m)
	β Largest patch index (30 m)	ϵ (Percentage cover rubble) ²
	α Proportion of like adjacencies sand (75 m)	α Proportion of like adjacencies sand (75 m)
	α Largest patch index coral (75 m)	α Effective mesh size bedrock (30 m)
	α Mean shape index bedrock (30 m)	α Total area coral (30 m)
	α Minimum patch area bedrock (75 m)	α Landscape shape index sand (30 m)
	β Mean core area index (75 m)	ϵ Percentage cover gravel
	α Mean shape index mixed (75 m)	α Patch density bedrock (75 m)
	α Mean patch core area hard (75 m)	α Mean shape index bedrock (30 m)
	α Maximum shape index sand (75 m)	α Landscape shape index hard (30 m)
	γ Mean backscatter (75 m)	α Landscape division index mixed (75 m)
	β Maximum shape index (30 m)	α Patch density rubble (30 m)
	α Landscape shape index sand (30 m)	ϵ Pebbles (factor)
	γ Variance backscatter (75 m)	δ Aspect
	α Minimum shape index sand (75 m)	α Maximum shape index sand (75 m)
	α Mean patch area sand (75 m)	α Mean patch core area mixed (30 m)
α Mean patch core area mixed (30 m)	α Largest patch index coral (75 m)	
α Mean shape index hard (30 m)	β Number of patches (75 m)	
α Minimum patch core area rubble (75 m)	α Landscape shape index mixed (30 m)	
	α Mean shape index mixed (75 m)	
	β Maximum core area index (75 m)	
	α Patch cohesion index hard (75 m)	
	β Patch cohesion index (30 m)	
Adjusted R²	24.7 %	45.1 %
F-value	12.1, df = 36, 1185	26.1, df = 40, 1181
p-value	0.001	0.001

38.3%). High percentages of hard bottom-associated morphospecies were recorded for Transects 91 (49.0%) and 104 (46.9%). Organisms representing morphospecies associated with corals ranged between 16.7 and 18.9% of the observations for Transects 91, 93 and 104, but fell below 5% for Transects 96 and 97. Morphospecies associated with soft sediments represented 54.5% and 14.2% of total observations for Transect 96 and 97, respectively, but less than 5% in the remaining transects. Morphospecies associated with the use of multiple sediment types (hard substratum, coral stand and rubble) ranged between 30.4 and 73.3% of total observations. Characteristic substrata and morphospecies images for each observed assemblage are presented (Fig. 7).

In the case of the Shannon biodiversity index, percentage cover of sand and gravel had the strongest association ($p < 0.001$) to lower biodiversity indices (Table 3). Sites classified as containing cobbles, exposed bedrock and pebbles had significantly higher biodiversity ($p < 0.001$). Number of patches ($p < 0.001$) and patch cohesion, an index indicative of greater connectivity (full model: $p < 0.001$, sonar-only model: $p < 0.05$), also significantly increased biodiversity, while metrics indicative of large sandy areas (e.g. proportion of like adjacencies) were associated with a decrease in biodiversity (both models: $p < 0.001$). Percentage cover of corals, and a few associated indices indicative of larger, more closely located patches (e.g. aggregation index [both mod-

Table 3. Selected environmental variables for the most parsimonious models (with and without including fine-scale imagery-derived information) for the Shannon diversity index (H'). α = class metrics, β = landscape metrics, γ = sidescan sonar, δ = multibeam sonar, ϵ = ROV imagery-derived variables. *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$, 'p < 0.1

	Sonar		Imagery and sonar	
	Shannon diversity index	Coefficient	Shannon diversity index	Coefficient
Explanatory variables	α Aggregation index coral (75 m)	0.003 ***	ϵ Percentage cover sand	-0.454 ***
	α Proportion of like adjacencies sand (30 m)	-0.456 ***	ϵ Sand - cobbles (factor)	0.668 ***
	α Proportion of like adjacencies coral (30 m)	0.188 *	α Aggregation index coral (75 m)	0.003 ***
	γ Mean backscatter (30)	<0.001 ***	ϵ Percentage cover gravel	-0.455 ***
	α Patch cohesion index hard (75 m)	-0.188	ϵ Rock - sand (factor)	0.927 ***
	δ Aspect	NA	ϵ Rock (factor)	0.950 ***
	α Mean shape index mixed (75 m)	-0.193 **	ϵ (Percentage cover rubble)^2	-1.712 ***
	α Effective mesh size bedrock (30 m)	0.000 **	ϵ Cobbles - sand (factor)	0.634 ***
	α Effective mesh size coral (75 m)	0.039 **	α Mean patch area sand (75 m)	<0.001
	β Patch cohesion index (75 m)	0.271 *	β Patch cohesion index (75 m)	0.237 ***
	α Mean perimeter area ratio hard (75 m)	-0.076 *	β Patch richness (75 m)	-0.102 ***
	β Number of patches (30 m)	0.012 ***	α Proportion of like adjacencies sand (30 m)	-0.263 ***
	α Minimum patch core area rubble (75 m)	0.003 *	ϵ Percentage cover rubble	0.011
	α Landscape shape index sand (30 m)	-0.044 *	α Minimum patch area coral (75 m)	0.001 *
	α Mean patch area sand (75 m)	<0.001 ***	ϵ Pebbles (factor)	0.169 ***
	γ Mean backscatter (75 m)	-0.001 ***	ϵ Percentage cover coral	0.300 **
	α Minimum patch area coral (75 m)	0.002 *	ϵ Rubble (factor)	0.121 **
	α Proportion of like adjacencies sand (75 m)	-0.433 *	α Maximum perimeter area ratio sand (75 m)	0.014 *
	α Minimum patch core area mixed (30 m)	<0.001 *	α Mean perimeter area ratio hard (30 m)	0.026 *
	β Mean core area index (30 m)	0.918 **	β Mean shape index (30 m)	0.091
	α Number of patches sand (75 m)	0.003	α Minimum patch core area rubble (75 m)	0.002 .
	α Mean patch area bedrock (75 m)	<0.001	α Proportion of like adjacencies coral (30 m)	0.088
	β Division index (75 m)	-0.191	δ Slope	0.004
	δ Bathymetric position index (coarse)	0.012 .		
	α Maximum perimeter area ratio sand (30 m)	0.012 *		
	α Patch cohesion index mixed (30 m)	-0.136		
	α Mean perimeter area ratio hard (30 m)	0.036 *		
	γ Variance backscatter (75 m)	<0.001		
	Adjusted R²	40.6%		63.8%
	F-value	25.6, df = 34, 1187		94.54, df = 23, 1198
p-value	<0.001		<0.001	

els: $p < 0.001$], portion of like adjacencies [sonar-only model: $p < 0.05$], mean core area index [sonar-only model: $p < 0.01$] and effective mesh size [sonar-only model: $p < 0.01$]), were also associated with increased biodiversity. Second-order relationships to percentage cover of rubble were also significant ($p < 0.001$), indicating that they can increase biodiversity when present in intermediate quantities.

Variation partitioning of the models allowed for the separation of the amount of variation explained by imagery versus sonar-derived environmental variables. When the model considering all environmental parameters was partitioned between imagery and sonar-derived environmental variables, fine-scale characterization of substratum percentage cover obtained from the imagery explained the most variation, contributing to a total of 38.6% for community composition and 59.0% for biodiversity (Fig. 8). Of those percentages, 16.4 and 31.0%, respectively,

were also explained by the selected class and landscape metrics. However, as the full models explained 45.1 and 63.8% of the variation in community composition and biodiversity respectively, it is clear that the variation explained by the class and landscape metrics was almost entirely captured by the imagery-derived substratum percentage cover. Forward selection of PCNMs resulted in 2 sets of 50 PCNMs, which identified 31.1 and 36.0% of the variation in the morphospecies matrix and biodiversity index, respectively, as resulting from spatial structuring (see Supplement 7 at www.int-res.com/articles/suppl/m501p067_supp.pdf). Of these percentages associated with spatial structuring, only 5.9% (morphospecies composition) and 2.0% (H') could not be explained by the environmental variables. This variation could be the result of unmeasured environmental variables or spatial autocorrelation resulting from biological interactions. Gaussian variogram fitting of

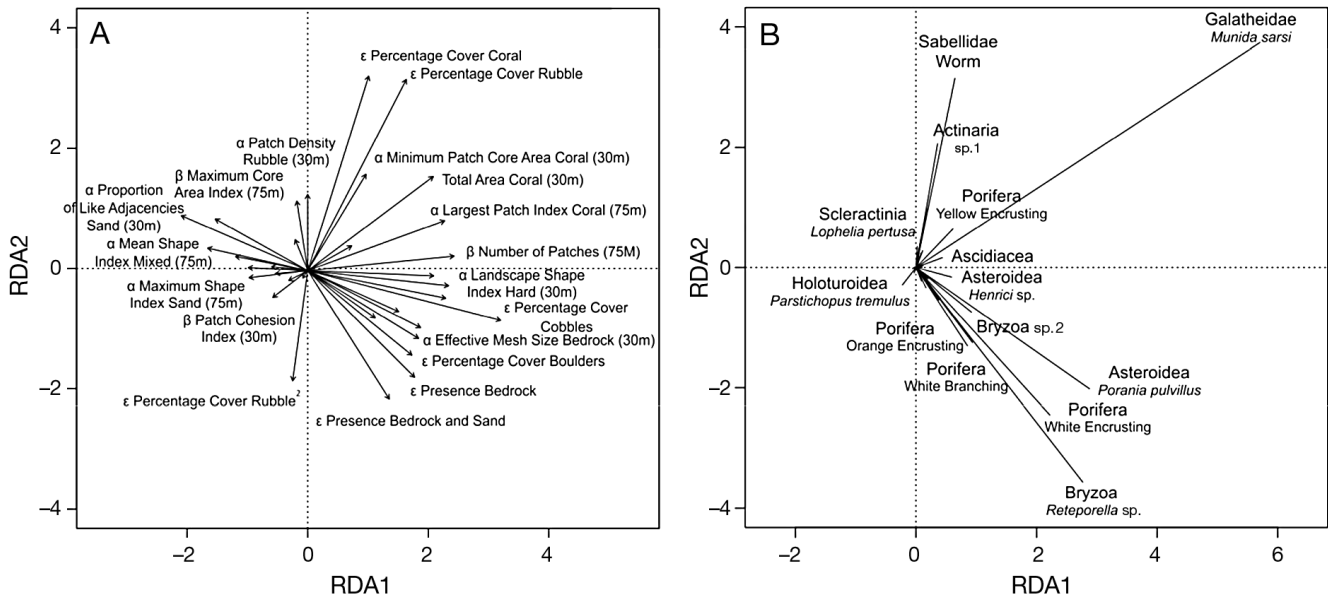


Fig. 5. Redundancy analysis using all significant environmental predictors. For clarity, the triplot is illustrated in 3 separate graphs (A,B and Fig. 6A), and only environmental variables and morphospecies with the strongest effects are labelled. (A) Environmental variables: α = class metrics, β = landscape metrics; derived from γ = sidescan sonar, δ = multibeam sonar and ϵ = ROV imagery. (B) Morphospecies

site scores for significant canonical axes indicated that ranges in the spatial structure modelled varied between 20 and 50 m.

When model validity was assessed following 100 repetitions, on average 81.1% (SD = 2.5%) of the 300 images removed were assigned to the same cluster as

originally computed using the full model. When only sonar-derived environmental information was used, values of 71.8% (SD = 3.9%) were obtained.

At the broader scale, transects varied in morpho-species composition, diversity and substratum composition. The 95% confidence intervals for Transects

Table 4. Total counts based on 1222 images, K-means partitioning cluster association as well as indicator values and significance for the operational taxonomic units observed. Cluster 1: soft sediments, Cluster 2: hard substratum, Cluster 3: coral associated and Cluster 4: occurring on hard substratum, coral stand and rubble. Bold numbers indicate morphospecies presented in Fig. 4. ***p < 0.001, **p < 0.01, *p < 0.05, 'p < 0.1

Morphospecies	Count	Cluster	Indicator value	Morphospecies	Count	Cluster	Indicator value
1 <i>Parastichopus tremulus</i>	185	1	0.06	4 <i>Asterias rubens</i>	28	3	0.02
24 <i>Caryophyllia</i> sp. 1	92	1	0.03	5 <i>Henricia</i> spp.	117	3	0.24***
34 <i>Echinus</i> sp. 3 (possibly <i>E. elegans</i>)	11	1	0.01	7 <i>Lophelia pertusa</i>	39	3	0.53***
6 <i>Reteporella</i> sp.	942	2	0.72***	8 Sabellidae	272	3	0.93***
14 Brown cup sponge	942	2	0.72***	9 Actinaria sp. 1	227	3	0.72***
16 <i>Echinus</i> sp. 2	10	2	0.04**	10 <i>Echinus</i> sp. 1 (possibly <i>E. acutus</i>)	19	3	0.24***
18 Cyclostomatida sp. 1	175	2	0.37***	11 Portunidea sp. 1	24	3	0.08***
19 Orange encrusting sponge	138	2	0.29***	15 <i>Hippasteria</i> sp.1	19	3	0.06**
20 White branching sponge	152	2	0.43***	17 Translucent tunicate	96	3	0.09**
21 Brown lamellated sponge	69	2	0.16***	25 Yellow columnar sponge	28	3	0.10***
22 White encrusting sponge	445	2	0.69***	26 Ophiuroidea	263	3	0.16***
27 Yellow encrusting sponge	705	2	0.54***	31 Hydroidae	35	3	0.21***
28 <i>Porania pulvillus</i>	10	2	0.01	2 <i>Munida sarsi</i>	2373	4	0.32***
29 Blue encrusting sponge	38	2	0.04*	3 <i>Cidaris cidaris</i>	59	4	0.05
30 Orange branching sponge	19	2	0.05**	12 Shrimp sp. 1	80	4	0.03
32 Tan columnar sponge	48	2	0.10***	13 Orange worm sp. 1	233	4	0.04
33 Yellow spherical sponge	36	2	0.12***	23 Brown anemone	13	4	0.01
35 Red encrusting sponge	60	2	0.08***				

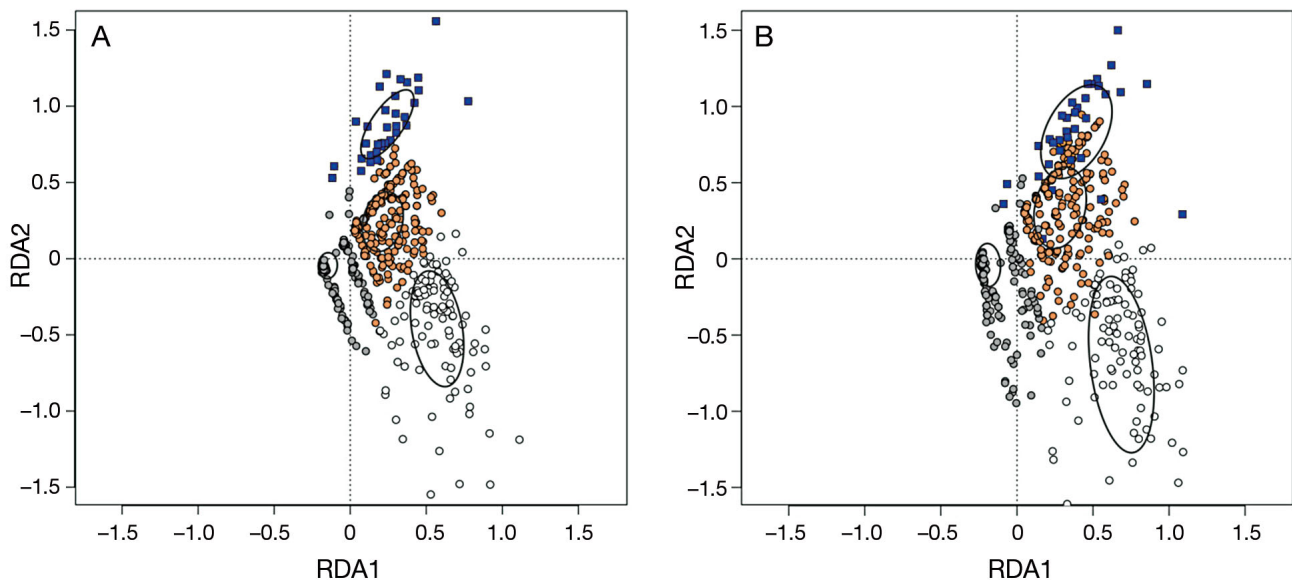


Fig. 6. Position of each image in ordination space (plotted as 'weighted averages of species scores' for the first 2 canonical axes) following redundancy analysis using (A) both imagery and sonar-derived environmental variables, and (B) only sonar-derived variables. Sites are colour-coded based on their association to K-means partitioning clusters: soft (grey), mixed (brown) and hard (white) substratum and coral stands (rectangles). Black ellipses indicate the standard deviation surrounding the centroid of each cluster

96 and 97 indicated a significantly lower biodiversity than for the other 3 transects (Fig. 9A). Biodiversity was lowest in soft sediment or rubble-dominated images and highest when cobbles, bedrock or corals were present (Fig. 9B). Significant negative relationships were observed between diversity ($R^2 = -0.167$, $p < 0.001$) and organism abundance ($R^2 = -0.159$, $p < 0.001$) versus depth. Percentage cover of hard substratum ($R^2 = -0.079$, $p < 0.001$) and coral stands ($R^2 = -0.027$, $p < 0.001$) also diminished with depth. Landscape metrics showed similarities across all 5 transects, but class metrics displayed greater variation. At the transect level (200 m buffer), patch sizes averaged 256 m² (SD = 41 m²), but greater differences were apparent when separated by sediment grain size classes: 9178 m² (soft), 537 m² (hard), 160 m² (mixed), 21 m² (bedrock), 14 m² (rubble) and 20 m² (coral). Soft sediments comprised the largest proportion of the landscape, while exposed bedrock, rubble fields and coral stands were rarely encountered. Exposed bedrock was only recorded along Transects 91 and 104, while large rubble fields were only identified in the sonar maps of Mission 44. Live coral stands of *Lophelia pertusa* were recorded along Transects 91, 93 and 104. Estimates of the proportion of landscape occupied by each substratum class were highly dependent on the resolution of the observation method. Greater differences were observed when comparing the high resolution imagery to the

sediment interpretation maps covering various extents (Table 5). Based on the imagery, soft sediments represented the dominant substratum class in all transects, but Transects 91 and 104 had mixed sediments as their dominant class if sediment interpretation maps were used instead.

DISCUSSION

This study employed community and landscape analysis approaches traditionally employed in terrestrial settings to examine species-environment relationships based on remotely acquired data of Rockall Bank, NE Atlantic. This represents one of the first applications of these techniques to a deep-sea environment, and the results obtained suggest potential applications for management and conservation requiring fine-scale species distribution and biodiversity information.

Megafaunal distribution and biodiversity

A strong association between morphospecies distributions and substratum types was observed, yielding 3 distinct assemblages: soft bottom, hard bottom and coral-associated. Although not forming an independent group, the addition of a fourth cluster en-

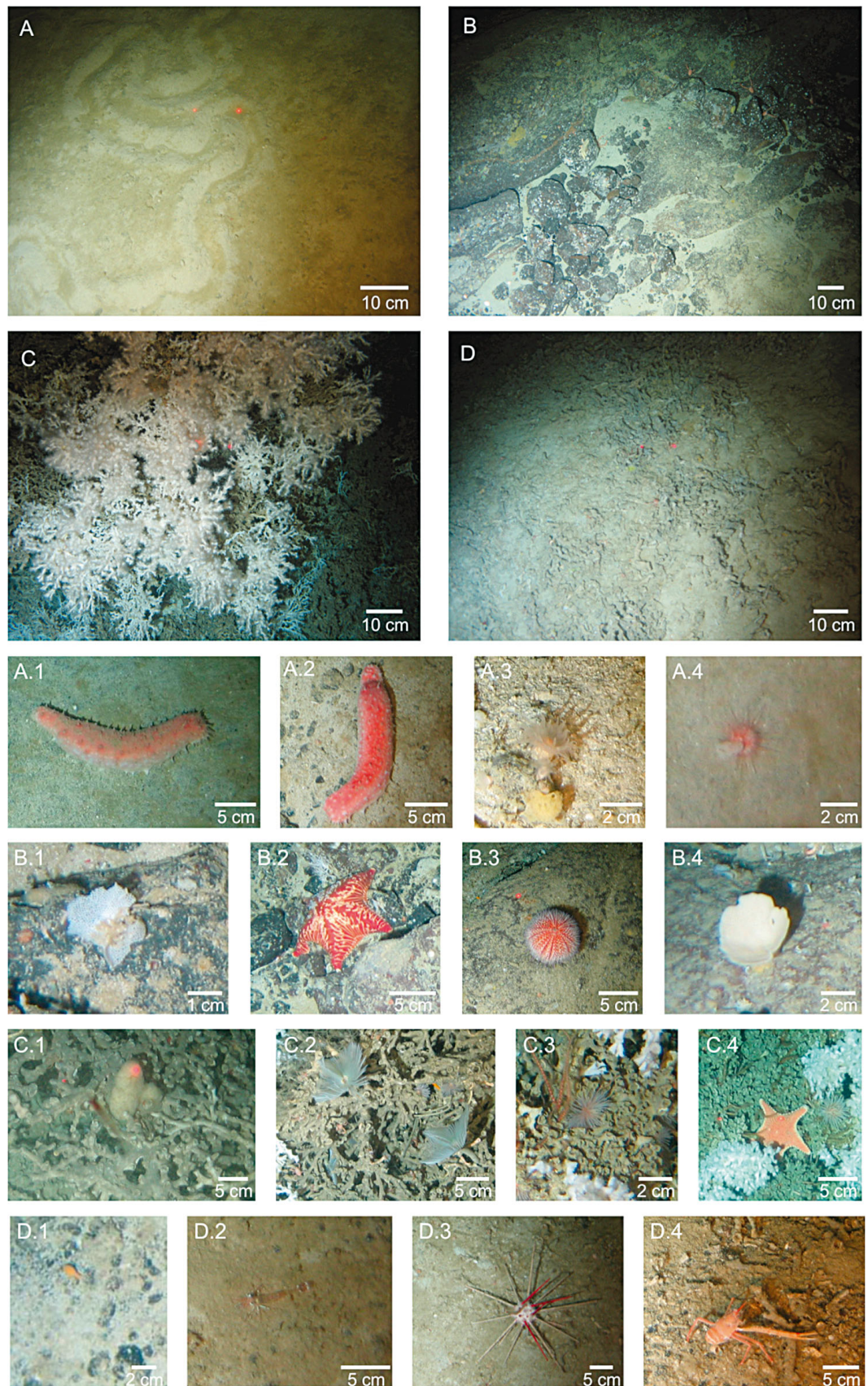


Fig. 7. Characteristic images for substratum classes and associated morpho-species. (A) Soft sediments; (A.1) and (A.2): *Parastichopus tremulus*, (A.3): *Caryophyllia* sp. 1, (A.4): *Echinus* sp. 3 (possibly *E. elegans*). (B) Hard substratum; (B.1): *Reteporella* sp., (B.2): *Porania pulvillus*, (B.3): *Echinus* sp. 2, (B.4): Porifera (cup sp. 1). (C) Coral stands; (C.1): Porifera (yellow columnar sp. 1), (C.2): *Sabellidea* sp. 1, (C.3): Actiniaria sp. 1, (C.4): *Hippasteria* sp. 1. (D) Coral rubble; (D.1): *Sipuncula* sp. 1, (D.2): *Caridea* sp. 1, (D.3): *Cidaris cidaris*, (D.4): *Munida sarsi* (species also frequently present on hard substratum and live coral stands)

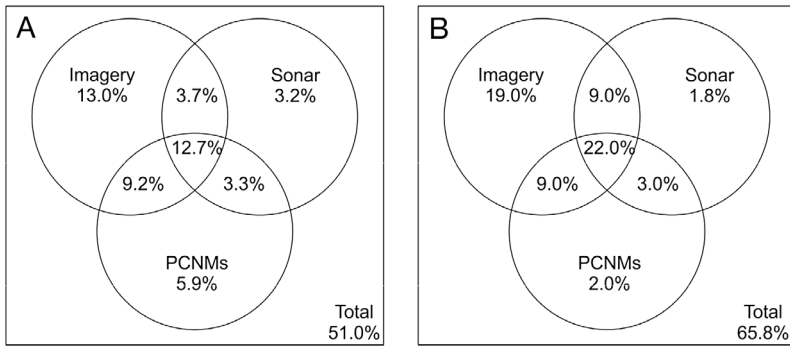


Fig. 8. Venn diagram showing, for the full model, percentages of variation in species composition and biodiversity explained by selected environmental variables extracted from the imagery (% substratum cover), the sonar maps (backscatter, bathymetry, class and landscape metrics) and the principal coordinates of neighbour matrices (PCNMs). (A) Morphospecies count matrix and (B) Shannon diversity index (H')

abled the separation of morphospecies occurring in multiple substratum classes (hard bottom, coral stands and rubble) from those more closely associated with live coral stands. No morphospecies were significantly associated with soft bottoms, but assemblages dominated by the sea cucumber *Parastichopus tremulus* have been reported for sandy flat areas by Howell (2010) in Rockall Trough, and Buhl-Mortensen et al. (2012) in northern Norway. Howell (2010) also reported the concurrent occurrence of the pencil sea urchin *Cidaris cidaris*, but in our study this species was mostly observed in coral rubble fields. In

this study, cup corals *Caryophyllia* spp. were also observed on isolated cobbles or boulders in soft sediment-dominated areas. The majority of morphospecies in the second assemblage were similar to descriptions of the rocky reef habitat of the central and eastern flanks of Rockall Bank (Howell et al. 2009). Being mostly dominated by encrusting sponge colonies as well as bryozoan species (*Cyclostomatida* and *Reteporella* sp.), taxonomic identification was not possible without sample collection and rendered comparisons between studies difficult. As previously reported from other surveys of the region, squat lobsters *Munida* spp. were commonly

observed associated with coarse sediments (gravel and cobbles) (Howell et al. 2009, Howell 2010) as well as on live coral stands and rubble (JNCC 2010a). Finally, sabellid worms and unidentified morphospecies of Actiniaria and Ophiuroidea were repeatedly observed in high densities on live coral stands. Association of suspension feeders (i.e. actinarians, hydroids, hexactinellids and demosponges as well as crinoids and brisingiids) with *Lophelia pertusa* has been described for the Franken Mound area on western Rockall Bank (Wienberg et al. 2008) and the nearby, though deeper Rockall Trough (Masson et al.

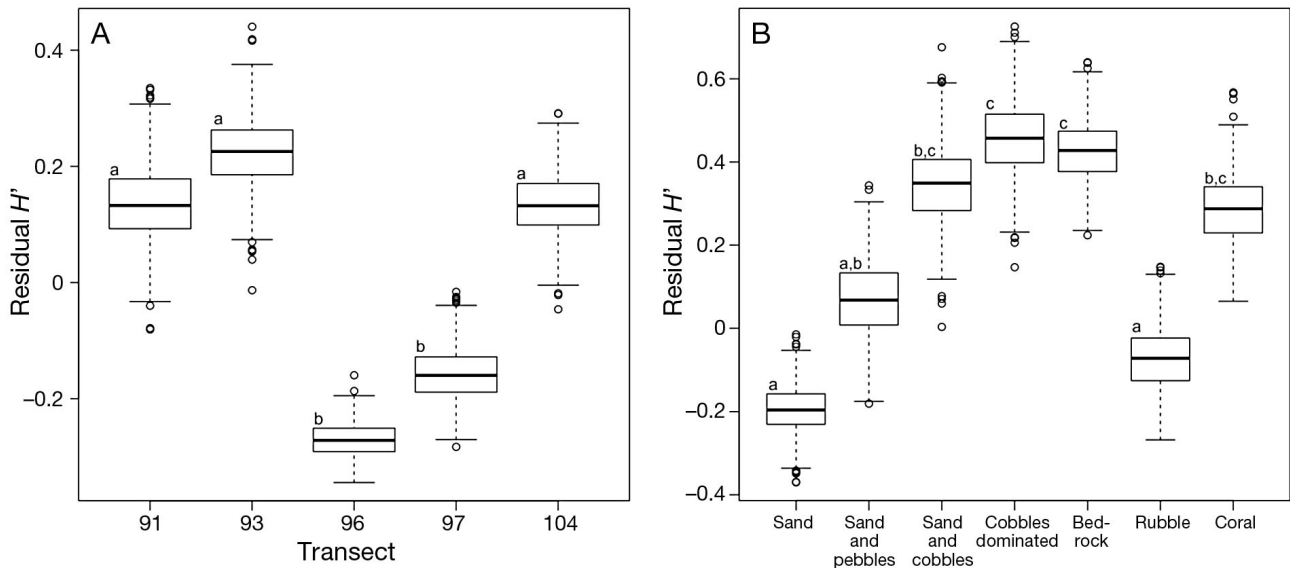


Fig. 9. Difference in residuals between (A) the 5 imagery transects and (B) the seabed facies, after filtering out the spatial structure of the Shannon diversity indices (H') using significant principal coordinates of neighbour matrices. A bootstrapping procedure was used to standardize sample length. The box shows the median (thick line) as well as the first (lower edge) and third (upper edge) quartiles while the whiskers show the minimum and maximum value excluding any outliers which are illustrated as circles. Letters indicate factors which are not significantly different based on 95% confidence intervals

Table 5. Averaged characteristics for the 5 transects. Substratum percentage cover for each sediment grain size class is given as obtained from the imagery, the circular (5 m radius) area surrounding each image and the 200 m buffer surrounding each transect. Gra: gravel; Peb: pebbles; Cob: cobbles; Bou: boulders; Bed: bedrock; Rub: rubble; Cor: coral; Mix: mixed

Tran- sect	No. images	Length (m)	Depth (m)	Imagery					Thematic maps															
				Sand	Gra	Peb	Cob	Bou	Bed	Rub	Cor	Soft	Mix	Hard	Bed	Rub	Cor							
91	211	970	217.5	81.4	0.4	3.2	3.4	2.3	4.9	4.3	41.0	46.1	12.0	0.0	0.0	0.0	1.0	40.0	45.1	14.2	0.0	0.0	0.7	
93	100	575	227.7	64.9	0.6	6.7	10.6	0.0	0.0	8.8	8.3	45.4	33.0	20.1	0.0	0.0	0.0	1.5	48.3	33.5	16.6	0.0	0.0	1.6
96	160	1200	317.3	98.6	0.0	0.4	0.6	0.1	0.0	0.4	0.0	55.8	22.7	20.6	0.0	0.8	0.0	0.0	51.6	22.3	24.7	0.0	1.5	0.0
97	369	2810	297.6	82.2	0.0	0.2	1.1	0.1	0.0	15.9	0.4	42.5	22.7	31.9	0.0	2.9	0.0	0.0	51.2	20.2	26.1	0.0	2.5	0.0
104	382	2490	188.6	44.7	7.1	25.6	6.0	0.8	8.3	2.1	5.4	22.0	42.0	20.8	14.2	0.0	1.0	1.0	18.6	49.7	21.9	9.8	0.0	0.0

2003). The distribution of similar habitats occupied by many of the same species has been reported for the nearby Hatton Bank (Roberts et al. 2008).

The assemblages observed in this study showed similarities to others described in areas characterized by iceberg reworking of the seabed (Gutt et al. 1996, Gutt & Piepenburg 2003, Jones et al. 2007a). During the Quaternary Period, the majority of the western and southern flanks of Rockall Bank were left covered in scours averaging 2 to 2.3 km in length, ranging between 50 and 200 m in width and up to 8 m in depth (Sacchetti et al. 2012). As found in other areas of the northwest European continental margin (Freiwald et al. 1999, Wheeler et al. 2007), iceberg debris provided hard ground for cold-water coral colonies to establish. Association of coral colonies with hard substratum originating from iceberg activity has also been observed on the continental margin off Nova Scotia and Newfoundland in the northwest Atlantic (Edinger et al. 2011). Fine-scale distinctions in morphospecies assemblages between the coarser and finer sediments dominating, respectively, the edges and centre sections of iceberg ploughmarks have been reported for other NE Atlantic areas such as Hatton Basin (JNCC 2012), the Wyville Thomson Ridge (JNCC 2010b) and northwest of Shetland (Bett 2001). However, studies in areas of active iceberg formation (Arctic and Antarctic) have shown that the observed patterns in benthic species assemblages and biodiversity are highly dependent on the time elapsed since iceberg disturbance, particularly with respect to slow growing organisms (e.g. sponges and corals) whose presence can affect distributions of associated species (Gutt et al. 1996, Gutt & Piepenburg 2003). Higher diversity on ploughmark edges dominated by hard sediments has also been reported for the Fimbul ice shelf region, Antarctica, and dominance of bryozoans and encrusting sponge colonies was mostly observed in less disturbed areas (Jones et al. 2007a). At broader spatial scales, when higher diversity is observed in areas of medium iceberg activity levels, it often results from the coexistence of various stages of succession and recovery (Jones et al. 2007b, Teixidó et al. 2007). In the case of Rockall Bank, this high diversity is more likely the result of a spatial dependence of distinct species assemblages on substratum type which varies over fine spatial scales.

Much variation in species-depth relationships occurs at local scales. However, over regional scales, reductions in faunal densities and biomass attributed to a diminishing organic matter supply, and unimodal responses in diversity have frequently been reported

(Rex et al. 2006). In the current study, the depth range encountered was relatively small (~100 m), and showed strong collinearity with other environmental variables. For example, higher number of coral colonies and presence of exposed bedrock were observed along the shallower transect, while the deeper transects located at the northern end of the study area were characterized by large expenses of coral rubble fields (likely resulting from previous trawling activities). Those deeper transects had the lowest Shannon diversity index. Cold-water coral stands increase habitat complexity by providing 3-dimensional structures to which fishing activities such as trawling can cause damage (Fosså et al. 2002). As many species are associated with cold-water corals, their destruction is expected to impact composition and diversity of benthic fauna (Roberts & Hirshfield 2004, Henry & Roberts 2007). Our study indicated that coral rubble fields did not appear to be exploited by specific morphospecies assemblages, and megabenthic diversity was generally reduced. This contrasts with results obtained by Roberts et al. (2008), who found high diversity of epifauna associated with areas of naturally occurring coral rubble on Hatton Bank. Although images where coral stands were present did not have a significantly higher biodiversity than images dominated by cobbles or bedrock, corals did harbour a specific morphospecies assemblage whose positive influence on diversity was visible at the transect level. Much of the diversity associated with cobbles or bedrock substrata was composed by hard-to-distinguish small encrusting sponge colonies, while large fish aggregations were seen surrounding coral patches but were not included in this analysis.

Landscape approach and environmental variables

The importance of different environmental variables depended on whether multivariate morphospecies distributions or a diversity index were considered. In both cases, environmental variables with the highest resolution (~1 cm), such as substratum percentage cover as obtained from imagery were most useful in explaining the variation observed. The use of landscape metrics explained 24.7% of the variation in morphospecies distribution — values similar to those reported by Teixidó et al. (2007) using similar analyses. Using canonical correspondence analysis to examine structural patterns (characterized by landscape metrics) of successional stages of iceberg disturbance and their effects on an Antarctic benthic community, they found that the 2 first axes explained

11% of the observed variation. In our study, although sonar backscatter maps were available at high resolutions (0.5 × 0.5 m pixel size), the presence of small, single-coral colonies or isolated boulders which were observed within pictures could not be identified in the backscatter. However, their presence within areas of homogeneous soft sediment did affect megafaunal composition. In this environment, these small seafloor features may represent 'keystone structures' (Tews et al. 2004) whose importance could only be captured through ROV imagery. This difference in resolution caused estimates of substratum percentage cover to vary more between acquisition methods than between the different spatial extents considered for the sediment interpretation maps. Hence, in this highly heterogeneous setting, the sole availability of high resolution acoustic surveys (even if covering larger extent) would result in a ~35 to 45% decrease in the amount of biological variation that could otherwise be explained by cm-scale substratum type information. Similarly, the classification of substratum types that was achieved visually provided additional information that is not yet achievable via automated seabed classification of backscatter data. The accuracy of the sediment class assigned is also likely to be higher when based on photographs.

High-resolution sidescan sonar was effective in mapping seafloor heterogeneity resulting from iceberg reworking, and highlighting a similar spatial pattern in megafaunal distribution indicative of spatial induced dependence. Indeed, the ranges identified by variogram fitting (20 to 50 m) were consistent with iceberg ploughmark widths and patch sizes observed over the larger transect extents (200 m buffer). Taking into account this seafloor heterogeneity by examining the surroundings of each image collected using class and landscape metrics resulted in an additional 12 to 17% of variation explained over the use of only sediment interpretation maps and bathymetry-derived information as proxies for morphospecies assemblages or biodiversity.

The comparatively low resolution (20 × 20 m pixel size), small bathymetric gradient (~100 m), limited extent considered and absence of topographic features may explain why other bathymetry-derived variables showed poor predictive abilities. However, in other seafloor regions where sediment characteristics do not exhibit the high spatial heterogeneity observed in this study, and where geomorphology shows greater complexity, bathymetric parameters such as slope, curvature and BPI may reveal significant broad-scale patterns in species assemblages (Jones & Brewer 2012).

The majority of the metrics selected when morphospecies distributions were considered described patch area and shape, whereas metrics describing areas of greater spatial heterogeneity, such as aggregation metrics, were selected more often when describing variation in biodiversity. In northern Norway, diversity increased in areas of mixed sediment (Buhl-Mortensen et al. 2012). In our study, this increase in diversity resulted from very fine-scale partitioning of the seabed based on sediment hardness. This fine-scale partitioning could be described by substratum percentage cover analysis of the digital stills, but was often lost in the sediment interpretation of the backscatter, yielding a transition zone of mixed sediment class with higher biodiversity, but of insufficient resolution to describe morphospecies assemblages. Effects of patch edges and transition zones on species composition and abundance have also been frequently documented in terrestrial systems, showing positive, negative and neutral relationships (Ries et al. 2004). However, this important concept of landscape ecology has very rarely been examined in marine benthic ecosystems (but see Zajac et al. 2003 for macrobenthos and Anderson et al. 2009 for deep-water demersal fishes). Landscape metrics will only provide valuable information if the spatial patterns they describe can be linked to specific ecological mechanisms, and the development of marine-specific metrics will be required (Wedding et al. 2011). Three-dimensional metrics taking into account the structure of the overlying water masses affecting benthic-pelagic linkages would be one area of potential research. Experimental manipulation of landscape characteristics would also be required to establish links between landscape spatial patterns and specific ecological processes.

CONCLUSION

Our study showed that for the Rockall Bank area, a strong association exists between morphospecies distribution and sediment characteristics resulting from past iceberg activity. The identified relationships were stronger when fine-scale (<1 m) imagery-derived sediment percentage cover information was available. However, taking into account the surrounding (30 m and 75 m) spatial context in which sediment patches were located, using class and landscape metrics nearly doubled the amount of variation in morphospecies composition and biodiversity that could be explained when compared to the use of sediment interpretation maps and bathymetry alone. As

the inclusion of this approach does not require that additional time be spent collecting data, it shows potential for increasing our understanding of the links between environmental structure and ecological processes, and may become a useful concomitant step for informing management decisions.

Although we currently do not have the possibility to describe large extents of seafloor to <1 m scale resolution levels, the scale (20 to 50 m) of the ecological process described in this study clearly indicates that most ship-based surveys, which for the depth considered are often processed to pixels sizes of 20 to 50 m in resolution, would be inadequate to capture the variation observed. For example, the European Nature Information System (EUNIS) classification (Connor et al. 2004) describes the western flank of the Rockall Bank area as mixed sediments separated by depth zones (deep circalittoral and upper slope). Although accurate for the spatial extent and resolution considered, finer scale studies are still required to understand how much of the biological complexity might be underrepresented, and inform conservation measures — particularly those aimed at specific species such as cold-water corals.

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