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REPORT

Beta diversity of cold-water coral reef communities off western Scotland

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Abstract Spatial heterogeneity in coral reef communities is well documented. This "species turnover" (beta diversity) on shallow warm-water reefs strongly conforms to spatial gradients in the environment as well as spatially autocorrelated biotic processes such as dispersal and competition. But the extent to which the environment and spatial autocorrelation create beta diversity on deep cold-water coral reefs such as those formed by *Lophelia pertusa* (Scleractinia) is unknown. The effects of remotely sensed and ground-truthed data were tested on the community composition of sessile suspension-feeding communities from the Mingulay Reef Complex, a landscape of inshore *Lophelia* reefs off the Scottish west coast. Canonical correspondence analysis determined that a statistically significant proportion (68%) of the variance in community composition could be explained by remotely sensed environmental variables (northerly and easterly aspect, seabed rugosity, depth), ground-truthed environmental variables (species richness and reef macrohabitat) and geospatial location. This variation was further partitioned into fractions explained by pure effects of the environment (51%), spatially structured environmental variables (12%) and spatial autocorrelation (5%). Beta diversity in these communities reflected the effects of both measured and unmeasured and spatially dependent environmental variables that vary across the reef complex, i.e., hydrography. Future work will quantify the significance and relative contributions of these variables in creating beta diversity in these rich communities.

Keywords Beta diversity · *Lophelia pertusa* · Cold-water corals · Acoustic remote sensing · Variance partitioning

Introduction

Spatial heterogeneity in coral reef communities

The distribution of species inhabiting coral reefs is often heterogeneous. Because species tend to occupy particular environmental niches, the spatial structure of reef communities is largely controlled by environmentally deterministic processes governed by species' traits. Thus, on shallow warm-water reefs, environmental gradients explain significant amounts of variation in community composition or "beta diversity" (Adjeroud 1997; Cleary and de Voogd 2007). Beta diversity itself can vary on these reefs and

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closely corresponds to the degree of environmental similarity and heterogeneity (Becking et al. 2006; Harborne et al. 2006; de Voogd et al. 2006).

Heterogeneous reef communities can also reflect the effects of spatial autocorrelation. In this instance, processes governed by species' traits (e.g., growth, predation, differential mortality) and/or random but spatially autocorrelated neutral processes (e.g., spatially limited dispersal) produce heterogeneous communities that vary across purely spatial gradients (Borcard et al. 1992; Hubbell 2001; Dray et al. 2006). Neutrality assumes demographic equality, whereby spatial autocorrelated communities are created through "spatially limited dispersal of species drawn at random from a metacommunity, plus possibly the appearance of newly evolved species in different areas" (Legendre et al. 2005). There is presently minor support for spatially autocorrelated coral reef communities (e.g., Schlacher et al. 1998), but it has been difficult to resolve whether this actually reflects spatial autocorrelation or the effects of unmeasured environmental variables that are often themselves spatially dependent (Becking et al. 2006; Cleary and de Voogd 2007), which confounds any pure spatially explicit effects on beta diversity. However, more studies are needed, and across a broader range of species, communities and regions that simultaneously test the significance and relative importance of these processes in order to refine the understanding of beta diversity on coral reefs worldwide.

Beta diversity on *Lophelia* reefs

Deep cold-water coral reefs formed by the colonial azooxanthellate scleractinian *Lophelia pertusa* are globally ubiquitous (Roberts et al. 2006, 2009a, b), but until recently their remoteness has meant that these habitats have received much less attention than their shallow warm-water counterparts. *Lophelia* is typically distributed 200–1,000 m deep and can form reefs tens of kilometres long, some of which have been growing sporadically since the early Pleistocene (Kano et al. 2007). Like shallow warm-water corals, *Lophelia* creates structural habitat that alters local hydrography (Davies et al. 2009). As such, *Lophelia* is an important "ecosystem engineer" (van Oevelen et al. 2009): it creates and modifies the abiotic environment in ways that favour colonisation of its reefs by species-rich fish and invertebrate communities, with the richness of some taxa rivalling that found on shallow warm-water coral reefs (Jensen and Frederiksen 1992; Henry et al. 2008; Gheerardyn et al. 2009).

Cyclical *Lophelia* reef growth produces a dynamic mosaic of habitats that results in the vertical zonation of four major "macrohabitats" and therefore zones of significant invertebrate species turnover ranging from the reef summit to its flank: (1) living coral framework, (2) sediment-clogged mostly dead coral framework, (3) coral rubble and (4) underlying sediments (Mortensen et al. 1995; Raes and Vanreusel 2005; Roberts et al. 2006). Beta diversity on *Lophelia* reefs is also created by gradients in live coral cover and depth (Jonsson et al. 2004; Raes and Vanreusel 2005; van Soest and Lavaleye 2005; Mortensen and Fosså 2006; Henry and Roberts 2007; van Soest et al. 2007; Roberts et al. 2008; Weinberg et al. 2008). Beta diversity on *Lophelia* reefs also varies, with communities becoming more dissimilar from each other as one moves from the reef summit to flank macrohabitats, and as one compares communities from increasingly dissimilar or distant environments (Jonsson et al. 2004; Mortensen and Fosså 2006; Henry and Roberts 2007; van Soest et al. 2007; Cordes et al. 2008; Roberts et al. 2008). However, none of these studies have tested the significance of spatial autocorrelation or the effects of remotely sensed environmental data in creating beta diversity in these habitats. These omissions present new opportunities for the cold-water coral reef research community to contribute to the knowledge about the mechanisms controlling beta diversity on such rich yet remote coral reefs.

Acoustic remote sensing of cold-water coral reefs

Remotely sensed environmental data can explain significant amounts of variation in invertebrate species composition and beta diversity itself on shallow warm-water coral reefs (Becking et al. 2006; Harborne et al. 2006; de Voogd et al. 2006; Cleary and de Voogd 2007; also see review by Knudby et al. 2007) and have also been used to predict and map beta diversity of coral reef species (Mumby et al. 2004; Harborne et al. 2006). But the measurement of environmental variables on an aphotic deep cold-water coral reef excludes the use of airborne or satellite-based remote sensing methods that are effective on shallow marine ecosystems. Measurements at the depths of most *Lophelia* reefs require shipboard, towed or underwater vehicle-mounted acoustic remote sensing devices such as multibeam echosounders and side-scan sonar to characterise seafloor properties. Acoustic remote sensing has been vital to the recent discovery, habitat mapping and geological characterisation of *Lophelia* reefs (Fosså et al. 2005; Foubert et al. 2005; Roberts et al. 2005a, 2008; Beyer et al. 2007), and has overall positive implications for conceptual and predictive modelling, cruise planning and overall conservation of coral reefs worldwide (Andréfouet and Riegl 2004). Bathymetric terrain features, e.g., depth, slope, aspect and rugosity, can all be predicted from acoustic data and have been used to model habitat associations of the cold-water corals themselves (Wilson et al. 2007; Davies et al. 2008; Dolan et al. 2008; Guinan et al. 2009).

An interdisciplinary approach combining ground-truthed (photographs, videos, benthic sampling) and acoustically acquired data allows one to test the effects of numerous bathymetric and seabed features on deep cold-water coral reef communities. The present study integrated these data into a model of community composition variance to test whether cold-water coral reef communities show significantly heterogeneous spatial structure, and the significance and relative importance of environmental and spatial autocorrelation in creating beta diversity.

Materials and methods

Study site

The Mingulay Reef Complex (MRC) is an inshore landscape of *Lophelia pertusa* reefs in the outer Hebrides off the west coast of Scotland in the northeast Atlantic (Fig. 1) and has been the subject of recent intensive study (Roberts et al. 2009a, b). Each reef is formed by seabed mounds up to five metres high that likely have been growing since the early Holocene (Roberts et al. 2005a). Reef invertebrates broadly conform to local habitat classes: these range from bioturbated muds inhabited by *Nephrops norvegicus*, seapens, crinoids and other burrowing megafauna, to rocky substrata encrusted by large erect sponges (*Phakellia* sp., *Axinella* sp.) and zoanthids, to living *Lophelia* reefs and coral rubble inhabited by diverse suspension-feeding communities (Roberts et al. 2005a). Sponges are particularly diverse on the MRC, with 70 species being recorded to date (Maier et al. 2006), at least one of which was new to science (van Soest and Beglinger 2008). Two of the reefs that were mapped in detail using multibeam bathymetry in June–July 2003, Mingulay Reef 1 and Mingulay Reef 5 North (Roberts et al. 2005a), are considered in the present study, and herein called MRC1 and MRC5. The survey was conducted using an EM2000 Multibeam Echo Sounder (MBES, Kongsberg-Simrad Ltd.) with hull-mounted transducers on the RV *Lough Foyle* (Roberts et al. 2005a).

Grab sampling and faunal identification

A total of 18 Day grab samples (each 100 cm^2) of invertebrates were collected from the reefs (Fig. 1). Latitude and longitude of each grab were recorded and based on the ship's differential GPS position. Macrohabitat data were ground-truthed, based on the predominant seabed type recovered in the grab (coral framework, coral rubble, rock or muddy

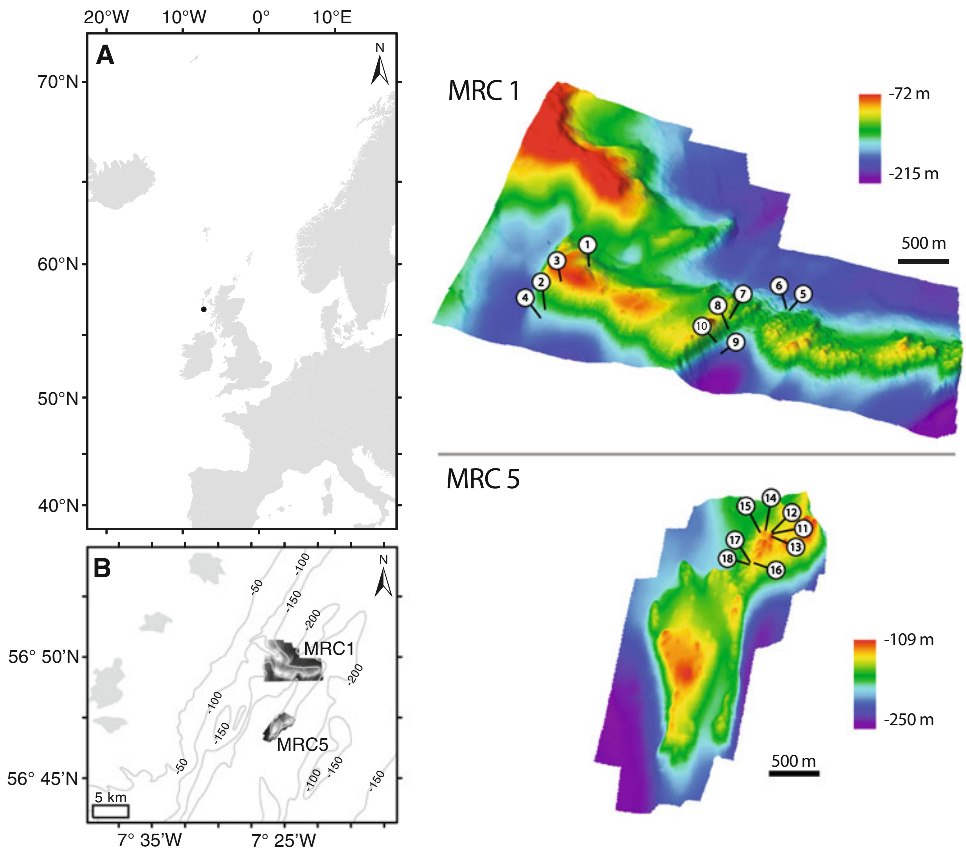

Fig. 1 Regional context of the MRC (**a**) with study area (see inset **b**) indicated by a *black dot*. Detailed multibeam bathymetry map (**b**) of MRC1 and MRC5 showing locations of grab samples

sand). Samples were washed through a 1-mm sieve, fixed in 4% borax-buffered solution of formalin and seawater, and stored in alcohol. Roberts et al. (2005a) enumerated subsampled fauna from these grabs: in the present study, the full sample of grab taxa was sorted and identified to the lowest possible taxonomic level. A total of 223 species were identified but analyses were restricted to the 77 species of attached epibenthic sponges, cnidarians, bryozoans and tunicates that represented a functionally equivalent "ecological community" (Hubbell 2005) of sessile suspension feeders. Every taxonomically distinct species was recorded as either present or absent in each grab (Electronic Supplemental Material; ESM, Appendix 1).

Digital terrain analysis

Supplementing the processed depth values from the multibeam data, several topographic variables were derived within a geographical information system (ArcGIS 9.2, ESRI Software). A buffer of 10 m diameter around each grab location was used, and the mean was calculated for each of the following derived variables within the buffer distance (ESM, Appendix 2). Calculations were performed using the Benthic Terrain Modeler (BTM) extension for ArcGIS 9.2 using routines from Jenness (2002). "Aspect" is the direction of slope measured in degrees from north ranging from zero to 359.9 ("general aspect") but only aspects measured in continuous radians ranging from -1 to 1 ("easterly" and "northerly aspect") were used in the statistical analyses. Each aspect was calculated using a 3×3 cell neighbourhood to determine the rate of change from each cell to its neighbours. "Slope" is the maximum change from each cell using a 3×3 neighbourhood. Slope values range from zero (flat surface) to 90° (vertical surface). "Rugosity" is the ratio of surface area to planar area and provides an index of how variable the surrounding area is within a 3×3 neighbourhood (Jenness 2002). Using this method, flat areas had a value close to one, while high relief areas had higher values of rugosity. "Bathymetric position index" (BPI) is derived from the topographic position index and provides a measure for a location relative to the other locations surrounding it, which can be part of a positive (e.g., living reef) or negative (e.g., depression) feature of the terrain surface. Values near zero represent flat areas or areas of constant slope. The BPI was calculated using the BTM extension with a 3×3 cell inner neighbourhood, and an outer neighbourhood of 5×5 that focused the analysis on fine-scale rather than broad-scale terrain features to correspond with the small spatial scale from which the reef communities were sampled. Geo-referenced environmental data for each grab sample are reported in ESM, Appendix 2.

Statistical analysis

Community characterisation and explanatory variable correlations

PRIMER v6 (Clarke and Gorley 2006) was used to ordinate Sørensen indices into a non-metric multidimensional scaling (nMDS) plot, and the similarity of percentages analysis (SIMPER) was used to identify species that contributed up to approximately 50% of the similarity within groups of grab samples. The Pearson correlation coefficient rho (ρ) and its statistical significance at $\alpha = 0.05$ were measured between all spatial and environmental variables (including the number of species or "species richness", but excluding the categorical variable macrohabitat) using XLSTAT-2008® Addinsoft SARL.

Beta diversity

A raw-data canonical approach was used to explain beta diversity in relation to environmental and spatial variables. Canonical correspondence analysis (CCA, described by Ter Braak 1986) partitions the variance in community composition due to constrained variables of interest and unconstrained residual inertia. This constrained variance can be further partitioned into three fractions of pure environmental, spatial and spatially structured environmental effects (Borcard et al. 1992; Legendre 2008). In the present study, these fractions were estimated by measuring the variance explained by the matrix of environmental variables, the matrix of the spatial variables, the environmental matrix (with co-varying spatial variables) and the spatial matrix (with spatial variables co-varying): the latter two are partial analyses or pCCA, described by Borcard et al. (1992), each of which generates the contribution of purely environmental (or geospatial and thus spatially autocorrelated) effects uncoupled from geospatial (or environmental) effects.

The response variables were species presence–absence data. Species that occurred in only one grab were excluded from the CCA and pCCA analyses, as these disproportionately inflate the effects of rare species on canonical ordinations (Legendre and Gallagher 2001).

The explanatory variables included both spatial and environmental data (including species richness). Any redundant environmental variable, i.e., one that was significantly correlated to another environmental variable already in the model, was excluded. This reduced any effects of multicollinearity that otherwise makes variable coefficients unstable, and thus their degree to which they "explain" variance in community composition.

Results

Community characterisation and explanatory variable correlations

Three community types (grabs 1–5, grabs 6–10 and grabs 10–18) were visible in the nMDS (Fig. 2): grabs 1–5 were characterised by the bryozoans *Pyripora catenularia*, *Disporella hispida*, Cheilostomata sp. 5 and *Diplosolen obelia*, and the hydroids *Clytia hemisphaerica* and *Modeeria rotunda*; grabs 6–10 were characterised only by the zoanthid *Parazoanthus anguicomus*; grabs 11–18 were characterised by *P. anguicomus*, the bryozoan *Chartella barleei* and the hydroid *Halecium muricatum*.

UTM northing and BPI ($\rho = -0.559$), UTM easting and richness ($\rho = -0.811$), rugosity and slope ($\rho = 0.973$), BPI and depth ($\rho = -0.599$) were all significantly correlated.

Beta diversity

Slope and depth were excluded from the model due to their significant correlations with rugosity and BPI, respectively. Linear combinations of northing, easting, rugosity, northerly aspect, easterly aspect, BPI, macrohabitat and species richness explained 68.1% of the variation in community composition, and this was statistically significant (Fig. 3; $P = 0.003$). Partial CCA determined that pure environmental effects explained 51.1% of the variation, but this was not statistically significant, at least at a type I error rate of 0.05 ($P = 0.106$). Pure spatial effects only accounted for 5.1% of the variance, and this was also not statistically significant ($P = 0.983$). Pure effects of spatially structured environmental effects explained an additional 11.9% of the variation; however, their statistical significance cannot be measured (Borcard et al. 1992), leaving 31.9% of the total variation unexplained.

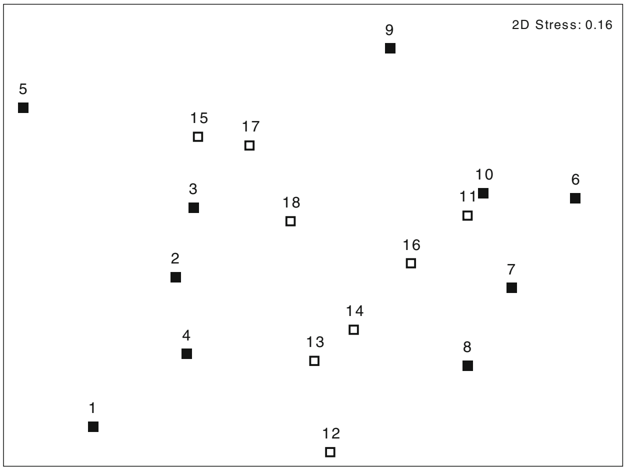

Fig. 2 Non-metric MDS ordination of grab samples. *Closed squares* = MRC1, *open squares* = MRC5. High stress (0.16) and overlap of samples from MRC1 and MRC5 indicate high similarity of the two reef communities

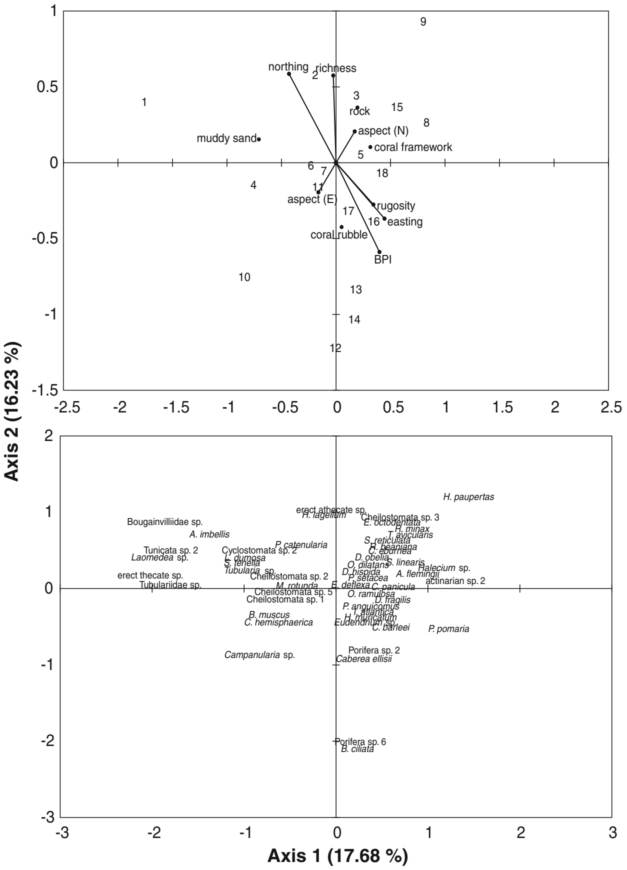

Fig. 3 Two-dimensional canonical biplots of constrained inertia with ordination of sites and then species along the first two canonical axes (percentage of constrained variance explained given in parentheses). *Path length* indicates the correlation between a predictor variable and a canonical axis. The correlation between a categorical variable and a canonical axis is given as a single point. Species are abbreviated as follows: *P. anguicomus* = *Parazoanthus anguicomus*; *B. muscus* = *Bougainvillia muscus*; *C. hemisphaerica* = *Clytia hemisphaerica*; *L. dumosa* = *Lafoea dumosa*; *C. panicula* = *Campanulina panicula*; *P. setacea* = *Plumularia setacea*; *H. muricatum* = *Halecium muricatum*; *M. rotunda* = *Modeeria rotunda*; *S. tenella* = *Sertularella tenella*; *C. eburnea* = *Crisia eburnea*; *O. dilatans* = *Oncousoecia dilatans*; *I. atlantica* = *Idmidronea atlantica*; *B. ciliata* = *Bicellaria ciliata; D. obelia* = *Diplosolen obelia*; *E. deflexa* = *Entalophoroecia deflexa*; *D. hispida* = *Disporella hispida*; *P. catenularia* = *Pyripora catenularia*; *C. barleei* = *Chartella barleei*; *A. imbellis* = *Alderina imbellis*; *A. flemingii* = *Amphiblestrum flemingii*; *R. minax* = *Ramphonotus minax*; *C. ellisii* = *Caberea ellisii*; *H. flagellum* = *Hippothoa flagellum*; *E. octodentata* = *Escharella octodentata*; *S. reticulata* = *Smittoidea reticulata*; *S. linearis* = *Schizomavella linearis*; *T. avicularis* = *Turbicellepora avicularis*; *O. ramulosa* = *Omalosecosa ramulosa*; *R. beaniana* = *Reteporella beaniana*; *D. fragilis* = *Dysidea fragilis*; *H. paupertas* = *Hymedesmia paupertas*; *P. pomaria* = *Polycarpa pomaria*

The first two canonical axes contributed 33.9% of the constrained inertia (explained variance) and 23.1% of the total inertia. Spatially structured environments on the MRC were evident from the gradients that characterised these axes. Axis 1 was largely characterised by gradients in seabed topography (rugosity, BPI) and macrohabitat that were themselves spatially structured across a longitudinal gradient. Axis 2 was also largely characterised by spatially structured gradients but these were due to changes in aspect, richness and macrohabitat (Fig. 3) that varied along a latitudinal gradient. The encrusting sponge *Hymedesmia paupertas* was positively associated with both axes, being found only at northeastern sites (grabs 8 and 9) on rocky and coral framework macrohabitats that were also among the more species-rich communities, in highly rugose and variable topographical areas with northwesterly aspects (Fig. 3). A group of small (mostly < 5 mm) epizoic hydroids (Bougainvilliidae sp., *Laomedea* sp., erect thecate sp. and Tubulariidae sp.) were strongly associated with northwestern locations that were also the most speciose communities, from muddy sand macrohabitat and relatively homogenous areas of surrounding seafloor. Another group of small epizoic hydroids (*Bougainvillia muscus*, *Clytia hemisphaerica* and *Campanularia* sp.) were also found in relatively homogenous areas of seafloor, but on less speciose coral rubble macrohabitats with more southeasterly aspects. The tunicate *Polycarpa pomaria* and the lobate bryozoans *Chartella barleei* and *Caberea ellisii* were found at the easternmost locations, on species-poor coral rubble macrohabitats distributed in highly rugose areas of varied surrounding topography (Fig. 3).

Discussion

Bathymetry-mediated control of community composition

The present study demonstrated predominantly bathymetry-mediated control of beta diversity patterns on the MRC, which is consistent with studies from shallow warm-water coral reefs. Seabed properties that directly relate to a sessile suspension feeder's hydrographical niche seem to play especially important roles and are all spatially structured on the MRC.

Variation in community composition due to changes in aspect strongly relates to how species respond to differences in water flow (Best 1988; Glasby 2000; Glasby and Connell 2001). On the MRC, differences in flow arise through variations in the orientation of communities into the prevailing currents. Since biological functioning of suspension feeders such as feeding efficiency can vary between upstream and downstream flow (Holland et al. 1987), aspect creates beta diversity in coral reef communities (Cleary and de Voogd 2007). On the MRC, currents are tidally driven and flow in an approximately south to north direction (Davies et al. 2009). Differences in aspect polarise northward-facing sites from those with more southward-facing orientations because the former are oriented downstream away from the prevailing currents and are thus more sheltered, while the latter are oriented upstream into the current and are thus more exposed. In the present study, the encrusting sponge *Hymedesmia paupertas* only occurred in grabs 8 and 9, which were northward-facing and thus less exposed sites. The present study not only demonstrates the concept of current-mediated control on this species' distribution, but also is supported by the habitat distribution of *H. paupertas* in British waters (Picton and Morrow 2007).

Varied slope, rugosity and bathymetric position also create beta diversity on cold-water coral reefs. The slope or inclination of a substratum produces differential larval recruitment and feeding ability in sessile suspension-feeding fauna. Like the variable "aspect", these differences arise due to species-specific niches related to water flow, and result in increasingly dissimilar communities as slope and its variance increase between sites, for example, in subtidal algal/invertebrate assemblages (Balata et al. 2007) and sponges from bathyal shelf and canyon ecosystems (Schlacher et al. 2007). Seabed rugosity also has profound implications for benthic biodiversity or marine ecosystems from rocky shores (Beck 2000) to coral reefs (Alvarez-Filip et al. 2009), and as a proxy for hard-bottom marine habitats in general, is vital for models of regional marine biodiversity (Dunn and Halpin 2009). Varied bathymetric position creates beta diversity by increasing seabed heterogeneity between sites with positive versus negative relief features and is known to affect benthic species' distribution and community structure on offshore banks (Buhl-Mortensen et al. 2009). *Lophelia* itself thrives on topographic highs and irregularities associated with positive relief seafloor features such as ridges (Frederiksen et al. 1992; Mortensen et al. 2001; Thiem et al. 2006; Davies et al. 2008; Guinan et al. 2009). In the present study, live *Lophelia* was only collected from grab 8 from a moderately rugose and sloped site (ESM, Appendix 1 and 2). Similarly, *Hymedesmia paupertas* was only collected from grabs 8 and 9 from areas of deeper waters and moderately rugose and sloped sites (Appendix 1 and 2), which corresponds to its known habitat in British waters including the MRC (Maier and party 2006). Although the larval ecology and natural history of many species from the MRC are unknown, the occurrence of the bryozoan *Plagioecia patina* at a steeply sloped site with high BPI (Appendix 1 and 2) is supported by evidence for enriched larval settlement patterns in cryptic or downwardly concave or lateral surfaces (McKinney and McKinney 2002).

Water depth was related to changes in sponge community composition on bathyal *Lophelia* reefs off southwest Ireland (van Soest et al. 2007). The present study's depth range of 76 m was also large enough to elicit significant changes in community composition, which are related to species' habitat requirements. Several species found at the deeper sites on the MRC are typically deep-water and even bathyal species, also occurring on other deeper *Lophelia* reefs including *Axinella infundibuliformis*, *Hymedesmia paupertas*, *Plagioecia patina* and *Smittina crystallina*. But depth was excluded from the canonical model in preference for BPI (see Materials and methods) because the former is actually a composite variable: water temperature, salinity, nutrient input or the water masses themselves could all vary with depth on the MRC. Current speeds and turbidity are known to decrease with depth and are spatially structured on the MRC as a consequence of the interplay between reef topography and local hydrography (Davies et al. 2009); such gradients surely pose niche consequences for suspension-feeding reef fauna as they seem to, for example, in the local deep-water bryozoan fauna (Hughes 2001). Depth-related changes in sediment oxygenation and food availability are also invoked to explain bathymetric shifts in benthic community structure in marine ecosystems ranging from coastal to slope ecosystems, and even across a basin-wide scale (Blake and Grassle 1994; Vanaverbeke et al. 1997a, b; Bonsdorff et al. 2003; Danovaro et al. 2008). Long-term in situ monitoring of near-seabed environments on the MRC and other *Lophelia* reefs using e.g., benthic landers (Roberts et al. 2005b; Linke et al. 2006; Davies et al. 2009) will be critical for identifying important variables encompassed by the depth factor.

The present study confirms that spatial heterogeneity in the distribution of *Lophelia* reef macrohabitats creates significant beta diversity in the sessile fauna inhabiting these niches. Substratum heterogeneity creates beta diversity in all marine ecosystems because many species have specific habitat requirements. Consequently, much of the beta diversity observed in marine ecosystems can be explained by heterogeneity in seabed types, including those that are inhabited by cold-water corals (Serrano et al. 2006; 2009). The present study also points to the importance of species richness, which for the macrofauna, is generally highest in macrohabitats with less live coral cover (Mortensen and Fosså 2006; van Soest et al. 2007; Roberts et al. 2008) and is spatially structured on the MRC (Fig. 3). The most speciose communities were found in grabs 2, 3 and 4 (rock and coral rubble macrohabitats), all of which were located in the westernmost portion of the study area (Fig. 1; ESM, Appendix 1). The significant decline in richness with easting may have created beta diversity simply because there were fewer species in the easternmost reaches of the MRC, and thus communities vary along this longitudinal gradient. Alternatively, another unmeasured environmental variable that closely correlates with species richness (e.g., disturbance) actually controls community composition on the MRC and is also longitudinally structured.

The role of unmeasured environmental and historical variables

Variance partitioning demonstrated a very minor role of spatial autocorrelation in creating beta diversity on the MRC. Furthermore, despite over half of the variance in community composition being explained by purely environmental variables, beta diversity was not significantly controlled by the measured variables. This leaves one to consider the significance of spatially structured environmental variables. But perhaps more important are the effects of the unmeasured environmental variables that may too be spatially structured. For example, current speeds are known to be reduced in the easternmost reaches of MRC1 (Davies et al. 2009). This variable likely represents an important unmeasured but spatially structured environmental variable that induced spatial dependence in the sessile suspension-feeding communities, as it was for sponges in shallow water coral reefs (Cleary and de Voogd 2007). There may be spatial gradients in other unmeasured variables e.g., the distribution of food resources that create biodiversity in marine ecosystems (Hewitt et al. 2005), which also vary beta diversity itself between areas with patchy versus continuous resources (Harrison 1997). Statistical methods that can integrate directional forces in environmental variables such as current regimes using, for example, an asymmetric eigenvector map method (Blanchet et al. 2008) will be integral for future work given the spatially structured nature of hydrodynamics across the MRC (Davies et al. 2009), but this invokes the fundamental need for further in situ deployment of instrumentation on the reefs themselves to measure these environmental variables.

Beta diversity was best explained by multibeam bathymetry data estimated at a small buffer size. This suggests that beta diversity of *Lophelia* reef communities on the MRC is created by local scale environmental heterogeneity. However, regional processes can still exert control over local community biodiversity (Gage 2004; Leibold et al. 2004; Harrison et al. 2006), and this may be the case for *Lophelia* reefs as well in both an environmental and historical context. Regional environmental factors on these reefs include large-scale hydrographical variables such as tidal regimes, water masses and currents. Forces that are temporally variable over palaeoecological time scales can also influence beta diversity of marine communities, particularly if these forces themselves varied across between regions (Danovaro et al. 2008). The importance of spatial autocorrelation may be more pronounced in historically dispersal-limited species (Baselga and Jiménez-Valverde 2007; Wang et al. 2008); contemporary *Lophelia* reefs are colonised by a range of species that vary in their dispersal potentials and those with highly finite dispersal ranges would have been more unlikely to overcome historical dispersal barriers created by, e.g., glacial periods that impoverished reef fauna and significantly reduced suitable habitats. Thus, a function of both regional (hydrography, distribution of *Lophelia* reefs) and local (species-determined traits) processes has produced extant local communities derived from a common regional species pool wherein species associations are overwhelmingly facultative (Henry and Roberts 2007). Basin-wide analysis of the fauna on *Lophelia* reefs across long temporal scales will better illuminate the roles of such historical and regional processes, bearing in mind that methodologies must advance to study in situ dispersal and recruitment limitation on cold-water coral reefs across multiple spatial scales.

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