**Biogeosciences
Discussions**

# Multi-scale interactions between local hydrography, seabed topography, and community assembly on cold-water coral reefs

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## Abstract

We investigated how the interactive effects of hydrography, topography and intrinsic community dynamics influence the assembly of species and functional traits across multiple spatial scales of a cold-water coral reef seascape. In a novel approach for these ecosystems, we use a spatially resolved complex three-dimensional flow model of hydrography to help explain assembly patterns. Forward selection of distance-based Moran's eigenvector mapping (dbMEM) variables identified two submodels of spatial scales at which communities are structured: broad-scale (across reef) and fine-scale (within reef). Canonical variance partitioning revealed broad-scale structures created mainly by variability in bathymetry and hydrography across reefs, which manifest as relatively narrow environmental niches for predators and scavenging detritivores. Fine-scale assembly was related more to processes that create spatially autocorrelated patches of fauna within a reef due to restricted dispersal in sessile fauna but social mating interactions and food supply in more mobile organisms. Our study implies that perturbations such as habitat fragmentation and altered hydrodynamic regimes have the potential to induce significant changes in the structure and function of cold-water coral reef ecosystems at spatial scales that span the entire seascape.

## 1 Introduction

Fundamental differences in species' functional ecology have important implications for the distribution of whole ecosystems and their functioning. Species' traits such as dispersal, feeding mode and growth rate govern the ways in which organisms use environmental resources such as space, light, and nutrients and interact with other organisms. Therefore natural or human-induced changes to the compositional structure of communities (their "assembly") can potentially affect biophysical and geochemical processes such as nutrient cycling, metabolism and respiration, depending on the spatial scale at which these traits are important in an ecosystem (De Bello et al., 2010).

Ultimately, variability in species and trait distribution affects the delivery of ecosystem goods and services (Lavorel et al., 2011) and the distribution of whole ecosystems (Reu et al., 2011), making the preservation of species traits and ecosystem multifunctionality paramount to mitigate global declines in biodiversity (Cadotte et al., 2011; Mouillot et al., 2011).

Predictions about ecosystem functioning confronted with critical issues such as species loss, habitat fragmentation and climate change are hampered by community assembly models dominated by single-scale, and taxonomically narrow species-based approaches. This narrows our perception of when processes are important because even distantly-related taxa may be functionally equivalent. Therefore these approaches cannot answer ecologically compelling questions about the importance of environmental versus stochastic processes across functionally different taxa or spatial scales (Weiher et al., 2011).

This potential for functional equivalence is especially true for coral reef communities, which can exhibit high species niche overlap and competition for resources between unrelated taxa. For example, interactions between seabed topography and hydrography on coral reefs are important to the spatial structuring of sessile organisms (Vroom et al., 2005; Becking et al., 2006); this sessile "guild" however is comprised of a phylogenetically diverse set of taxa, e.g. macroalgae, sponges, corals, crinoids, bivalves, and some polychaetes. In contrast to sessile fauna, the distribution of highly mobile scavengers and predators with more complex behaviours may be more be more closely linked to intrinsic dynamics that result in mating or feeding aggregations (Krafft et al., 2012). Furthermore, the spatial scale at which these relationships emerge may depend on species ecology. Sessile reef organisms with restricted dispersal of larval propagules may be spatially autocorrelated at smaller scales (Blanquer et al., 2009), while their broader scale distribution across an area governed more by environmental variability (Becking et al., 2006; de Voogd et al., 2006).

The use of spatial eigenfunctions is an emerging tool for ecologists to dissect the spatial structure in biological communities. Distance-based Moran's eigenvector

mapping (dbMEM, formerly called principal coordinates of neighbour matrices, PCNM) is one particular method of eigenfunction analysis. It is based simply on geographical co-ordinates, their pairwise distances and the minimum distance between sites that preserves their overall spatial connectivity (Borcard and Legendre, 2002). When only positive eigenfunctions are retained from this type of analysis, these values maximise Moran's index of spatial autocorrelation with respect to an initial spatial matrix of distances (Dray et al., 2006). Therefore these eigenfunctions can be used in canonical regression analyses to partition the variation in species composition between the roles of spatial autocorrelation alongside environmental filtering (Borcard et al., 2004).

The present study seeks to overcome the limitations of single-scale, taxonomically narrow studies. Our study tests pragmatic a priori hypotheses developed from realistic scenarios of a biologically diverse cold-water coral reef ecosystem formed by the coral *Lophelia pertusa* (Scleractinia) at the Mingulay reef complex off Western Scotland. In a novel interdisciplinary approach, we combine the power of dbMEM with predictive habitat models of seabed bathymetry and hydrography to develop a multi-scale model of how the distribution of species and their functional traits varies in relation to environmental filtering versus intrinsic spatial dynamics.

Detailed, spatially contiguous high-resolution maps of seabed bathymetry have been derived from multibeam remote sensing surveys of the *Lophelia* reefs at Mingulay (Roberts et al., 2005a, 2009). Bathymetric variability structures much of the biodiversity at Mingulay (Henry et al., 2010), but the effects of hydrography on the reef fauna have not been quantified. Local hydrographic regimes affect particle encounter rates and thus food supply to *Lophelia* reefs (Thiem et al., 2006); thus, hydrographic variability has the potential to affect the distribution of organisms that depend on currents for their food such as sessile filter and suspension feeders. At larger spatial scales, carbon flux can also limit body size across a broader range of functionally different organisms inhabiting the deep marine realm (McClain et al., 2012). In situ lander-based measurements revealed tidally-driven downwelling of surface waters and advection of turbid bottom waters at Mingulay, which are the likely key food-delivery mechanisms

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for these communities (Davies et al., 2009; Duineveld et al., 2012). But discrete in situ measurements of local hydrography required modelling and interpolation techniques to extrapolate estimates that would span the length of the reef complex and across depths.

5    Further synthesis into the effects of hydrography was prevented until a new spatially resolved hydrographic model of the reef complex was developed (Moreno Navas et al., 2012). Data generated by 3DMOHID (Modelo Hidrodinamico), a dynamic mathematical three-dimensional model of hydrography at the reef complex, are an innovative tool to predict hydrography. Complex flow models in 3DMOHID are programmed using
10   ANSI FORTRAN 95 with typical applications in coastal circulation, nutrient loads, water exchange and aquaculture environmental problems in coastal and estuarine ecosystems (Moreno Navas et al., 2011). Exploring the wealth of relationships between local hydrography, bathymetry and community assembly across multiple spatial scales provides an interdisciplinary framework that can vastly improve our appreciation of how
15   human activities and climate change may impact the functioning of marine ecosystems.

## 2   Methods

### 2.1   Study area

The Mingulay reef complex is a seascape of aphotic coral reefs formed by the azoox-
20   anthellate hard coral *Lophelia pertusa* (Linnaeus, 1758) in the Sea of the Hebrides off Western Scotland in waters 120–190 m deep (Fig. 1; Roberts et al., 2009). Individual reefs form mounds up to five metres high (Roberts et al., 2005a), with strong currents downwelling and impinging on the rough topography of the seabed and supplying food to reef fauna (Duineveld et al., 2012). Together, bathymetric variability and hydrography
25   appear to closely modulate the biodiversity of sessile organisms at the reef complex (Henry et al., 2010).

Two reefs were examined in this study (Fig. 2), Mingulay Area 1 (MRC1) and Mingulay Area 5 North (MRC5N). The former is a 4 km long ridge oriented east to west. The north-facing aspect of this ridge slopes gently and supports well-developed coral mounds near a gap in the ridge in contrast to the south-facing side that slopes steeply down to depths greater than 250 m (Roberts et al., 2005a). MRC5N is another ridge about 2 km long, oriented SW–NE. It slopes gently down from 109 to 240 m depth. Seabed sediments adjacent to the reefs are predominantly muddy, with extensive grounds of crinoids (Roberts et al., 2005a).

## 2.2 Seabed habitat mapping and benthic sampling

### 2.2.1 Seabed bathymetry

A remote-sensing multibeam sonar survey of MRC1 and MRC5N was conducted on board the R/V *Pelagia* in June 2006 using a hull-mounted 30 kHz Kongsberg EM300 multibeam echosounder (Maier, 2006; Roberts et al., 2009). Several seabed terrain variables were derived for each of the 14 sites from the multibeam data (Table 1) using ArcGIS 9.2 with ESRI spatial analysis and benthic terrain modeler extensions (Wright et al., 2005). Variables included depth, slope (degrees of inclination), aspect (orientation into the currents, measured in radians), rugosity (a non-metric measure of topographic unevenness) and the bathymetric position index (BPI; a non-metric measure of whether the area is on a topographic "hill" or low "depression" relative to the surrounding area). The mean of each variable in a 10 m diameter buffer around each station was estimated as rate change between cells in a 3 × 3 neighbourhood (Table 1, Fig. 2). Rugosity was positively correlated with slope ($R^2$ = 0.97, $p < 0.0001$), therefore only the latter was used in subsequent analyses.

### 2.2.2 Local hydrography

The hydrodynamic model 3DMOHID solves the equations of a three-dimensional flow for incompressible fluids and an equation of state relating density to salinity and temperature (Santos, 1995; Martins et al., 1998, 2001). The nested system consists of two sub-components: a coarse-resolution outer model covering part of the Sea of the Hebrides with a fine-scale resolution inner model covering the Mingulay reef complex with a horizontal resolution of roughly 100 m. The model ran for specific dates, seven days covering the same measurement time for hydrographic lander stations described in Davies et al. (2009). Average current speed ($C_{AVE}$), maximum current speed ($C_{MAX}$) and current speed standard deviation ($C_{SD}$) were calculated and exported as *.txt files to be integrated in a 3-D Geographic Information System. $C_{AVE}$, $C_{MAX}$ and $C_{SD}$ were extracted from the spatially resolved model for each station and used as predictor variables for subsequent analyses (Table 1, Fig. 2).

### 2.2.3 Benthos

Benthic fauna were collected on board the MY *Esperanza* in May 2005 using a day grab sampling an area of approximately 1 m$^2$ (Roberts et al., 2005b). A total of 14 grabs were analyses for this study (Table 1, Fig. 2). Grab contents were washed and sieved on-board at 1 mm, stored in 4 % borax-buffered seawater and transferred to 70 % industrial methylated spirit. These were identified to the lowest possible taxonomic level, producing a list of 172 species across the 14 sites (excluding sponges, which were excluded due to a lack of taxonomic resolution).

### 2.3 Statistical analyses

Species data were transformed to presence-absence data, followed by Hellinger distance transformation to give low weights to rare species and preserve linear relationships between species and environmental gradients (Legendre and Gallagher, 2001).

The development of spatial eigenfunctions first required the pairwise Euclidean distances between all 14 sites ($d_{ij}$) to be computed based on their universal transverse mercator geographic coordinates to generate a distance matrix $D$. Second, a threshold value $t$ was selected that truncated $D$ to a new matrix $^*D$ according to the rules provided by Eq. (1):

$$D^* = d_{ij} \quad \text{if} \quad d_{ij} \le t, \quad \text{and} \quad 4t \quad \text{if} \quad d_{ij} > t \tag{1}$$

A $t$ value of 993.62 m was chosen as this was the greatest distance between neighbouring sites and thus the minimum distance that would keep all 14 sites connected. Pairwise distances $> 993.62$ m were therefore changed to a value of $4 \times 993.62$ m = 3974.48 m. Principal coordinate analysis of the truncated matrix $D^*$ followed by a restriction to only positive eigenvalues estimated eight spatial scales (eigenfunctions) of autocorrelation in the study area (Table 2).

To avoid overfitting any models and inflating type I error, a parsimonious set of eigenfunctions was selected from the wider set using a stepwise forward selection procedure (Blanchet et al., 2008) to maximise the adjusted amount of explained variance while balancing type I error rates. Forward selection of variables in this way identified spatial "submodels" relating to the scale of ecological responses they are associated with (broad- to fine-scale).

Canonical variance partitioning was used to decompose the total variation in community assembly into variation explained by the environment, space, spatially structured environment and residual (unexplained) mechanisms. Redundancy analysis (RDA) for each submodel was performed first with the full suite of forward selected variables, then followed by partial redundancy analyses (pRDA) controlling for the effects of either spatial or environmental covariables (Borcard et al., 2004).

# 3   Results

## 3.1   Reduction in the number of explanatory variables

The dbMEM analysis identified 13 eigenvalues, the first eight of which had positive values and which were therefore retained as variables that represented positive spatial autocorrelation. These were ordered in decreasing order of the spatial scales they represented as eigenfunctions (Table 2).

The full suite of eigenfunctions explained 61 % of the variation in community assembly. Forward selection identified a reduced set of five (Eig2, 3, 4, 5 and 7; Table 2), the combination of which explained 45 % of the variation in community assembly. This reduced set of variables represented two types of spatial submodels: broad-scale (inter-reef and across reef distances of hundreds of metres to several kilometers) and fine-scale (within reef distances of tens to a few hundreds of metres).

The full suite of environmental variables explained a total of 56 % of the variation in assembly. Forward selection of environmental variables reduced this set of variables to two topographic (aspect and BPI) and two hydrographic ($C_{MAX}$ and $C_{SD}$) variables, which explained nearly as much variation, with 40 % of changes in community composition attributed to gradients in these key variables.

## 3.2   Drivers of broad-scale community assembly

The full broad-scale RDA model (a combination of $C_{MAX}$, current speed variability $C_{SD}$, aspect, BPI, and the eigenfunctions 2, 3 and 4) explained 65 % ($p = 0.04$) of the variation in reef species assembly (Table 3).

When the effects of space were excluded by partialling out their effects in the redundancy analysis (Table 3), species assembly was significantly related to environmental heterogeneity ($p = 0.048$). The first two axes were closely correlated with topography and hydrography, respectively (Fig. 3). In contrast, the pure effects of space (controlling

for environmental variability) were not statistically significant at broad spatial scales ($p = 0.146$).

Filter and suspension feeders displayed large variations in their distribution across environmental gradients (Fig. 4). Some species appear to inhabit topographically raised seabed areas, with some taxa preferring to face directly into current regimes that are both temporally dynamic and with very fast currents of up to $64\,\mathrm{cm\,s^{-1}}$. Predators and scavenging detritivores displayed some variability in composition across the bathymetric gradient (Fig. 4). Some exhibited more clear preferences for facing into the current on topographic highs, while others inhabited local seabed depressions with slower currents. Generally, predators and scavenging detritivores were more narrowly distributed across the hydrography axis. This reflected a more restricted preference for slower and less variable current speeds. Few species were correlated with faster, more variable currents, but even these were not as strongly related to these environments as some sessile fauna (Fig. 4).

## 3.3 Drivers of fine-scale community assembly

The full fine-scale RDA model (maximum current speed, current speed variability, aspect, BPI, eigenfunctions 5 and 7) explained 58.9 % of the variation in species assembly ($p = 0.034$; Table 3). The first and second axes were closely related to eigenfunctions 5 and 7, respectively. Pure effects of bathymetry did not explain a statistically significant amount of variation in the fine-scale structure of reef communities ($p = 0.096$), whereas pure effects of space accounted for a significant proportion of the variation ($p = 0.036$).

A subset of species was simultaneously related to eigenfunctions 5 and 7. Sessile species that most strongly exhibited this trend included serpulid polychaete worms, hydroids, bryozoans and anomiid bivalve molluscs. Species-specific life history information indicated a predominance of larval dispersal strategies that produce clumps of recruits, e.g. philopatry, or high mobility to look or defending resources both produce spatial autocorrelation.

## 4  Discussion

Our multi-scale analyses identified a common set of community assembly drivers across a phylogenetically and functionally diverse range of taxa. However mechanisms underlying the environmental and spatial control of assembly were dependent on species' ecology and life histories. This underscores the relevance of having highly resolved taxonomic data and information on the basic natural history of species at hand for a post-phylogenetic and trait-based era of community assembly paradigms.

### 4.1  Broad-scale environmental control of community assembly

The net effect of environmental variability across a marine landscape can induce spatial variability in the distribution of functional traits (Hewitt et al., 2008). Our study demonstrated that environmental gradients were very important to the broad-scale (hundreds of metres to several kilometres) spatial structure of species and functional assembly at the Mingulay reef complex. Topographic variations in BPI and aspect alongside hydrographic variability across many hundreds of metres to several kilometres were particularly important in creating different seabed environments, which in turn supported distinct faunal and functional communities.

### 4.1.1  Interactive effects of topography and hydrography on sessile fauna

Filter and suspension feeders were widely distributed across the reef complex, but species composition differed across topographic and hydrographic gradients. Current speeds affect particle capture rates among passive suspension feeders in a species-specific way (Shimeta, 2009) that affect population dynamics of sessile suspension feeders (Arkema, 2009). The distribution of sessile fauna such as sponges in particular is controlled by fine-scale microenvironmental processes such as competition and allelopathy. These influence sponge settlement and survival, and explain why

environmental variation and not spatial autocorrelation can explain large scale trends in assembly (Becking et al., 2006; de Voogd et al., 2006).

Few of the suspension-feeding fauna at Mingulay were observed facing directly into prevailing, fast-flowing currents. Those most strongly associated with this environmental setting had a low-lying encrusting morphology that adapts an organism to high flow regimes by maximising particle capture efficiency. At Mingulay, this encrusting fauna included the barnacle (*Verruca stroemi*), bryozoans *Diplosolen obelia* and *Schizomavella hastata*, and the anomiid bivalves *Heteranomia squamula* and *Monia patelliformis*.

### 4.1.2 Energetic and behavioural constraints on mobile fauna assembly

Significant faunal turnover at spatial scales of tens to hundreds of metres has been attributed to changes in topographic and hydrographic steering of food on continental shelf and deep-sea canyon ecosystems (Schneider et al., 1987; McClain et al., 2010). Hydrographic variation also seemed to drive assembly at the Mingulay reef complex, with a striking lack of predators and scavengers in fast dynamic flow regimes. These patters may reflect energetic balances between obtaining food, mates and social interactions and having to expend resources to move in a fast, variable flow regime. Slower less dynamic currents provide a temporally stable flux of detritus to the seabed, while pulsed episodes of food particle delivery can elicit a rapid but temporary aggregating response in mobile deep-sea fauna (Bett et al., 2001). Fast dynamic currents may also dilute and mix chemical cues used by crabs and shrimps to detect prey (Power and Kittinger, 2002), which may explain the association of predators such as the polychaetes *Glycera lapidum* and *Eunice norvegica*, the crabs *Xantho incisus* and *Munida sarsi*, and the spongivore limpet *Emarginula fissura* with slower currents. This might be particularly important for predators such as *Munida sarsi* that ambush prey from burrows (Hudson and Wigham, 2003).

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## 4.2 Fine-scale assembly and spatial autocorrelation

Environmental control of sessile suspension feeders at Mingulay was previously detected at broad spatial scales (Henry et al., 2010). However significant and relatively more important effects of spatial autocorrelation were detected at finer spatial scales only by using the multi-scale dbMEM approach. This "environmental decoupling" at smaller spatial scales is consistent with other patterns detected by dbMEM in lotic gastropod assemblages (Hauffe et al., 2011) and spatially autocorrelated patches of megafauna inhabiting fjords at the same spatial scale from tens to a few hundreds of metres (Gonzalez-Mirelis et al., 2009). Spatial autocorrelation created highly aggregated communities across the phylogenetically and functionally diverse range of reef taxa considered in this study. But like understanding how broad-scale changes in the environment can structure communities, dissecting the mechanisms that create fine-scale spatial structure requires knowledge of species autoecology and natural history. Sessile fauna that tended to be spatially aggregated were those that exhibit strong levels of limited dispersal arising through philopatry or gregarious larval settlement. Spatially aggregated mobile fauna tended to be crabs and shrimp that may have been aggregating for social interaction.

### 4.2.1 Dispersal limitation in sessile reef organisms

Sessile fauna at Mingulay that exhibited the strongest degree of spatial autocorrelation at fine scales tended to exhibit life history strategies that promote the retention of larvae and recruits near the adult. The serpulid polychaetes *Hydroides norvegicus* and *Serpula vermicularis* were closely related to the spatial eigenfunctions Eig5 and 7, and both are known to exhibit gregarious larval settlement (Bosence, 1979; Keough, 1983). The hydroid *Eudendrium* sp. also exhibited strong patterns of spatial autocorrelation, which may be due to the tendency for eudendriids to exhibit philopatric larval settlement (Sommer, 1992; Oliveira and Marques, 2005).

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### 4.2.2 Social mediation of decapod aggregations

Spatial autocorrelation of "local" communities is expected to be less prevalent in highly mobile fauna (Weiher et al., 2011): individuals are assumed free to forage and socialise across large home ranges, their mobility effectively erasing barriers to dispersal. But the
5 assembly of mobile organisms is often spatially aggregated in marine ecosystems (see Schneider et al., 1987; Becking et al., 2006), a phenomenon that requires explanations beyond dispersal capabilities.

Spatial autocorrelation of krill swarms are largely unrelated to hydrography or topography: instead, these are spatially autocorrelated because they aggregate by active
10 locomotion (Krafft et al., 2012). Active swimming and aggregations of crustaceans may relate to social foraging (Laidre, 2012) or mating behaviours. Notably, mating pairs of some brachyuran crabs are known to form aggregations at the same spatial scales as Mingulay, from tens to a hundred metres (Sainte Marie et al., 1999). Many of the crabs and shrimp collected during our surveys were gravid including *Munida sarsi*, *Pagurus*
15 *forbesii*, and *Pandalina brevirostris*, and juveniles were frequently encountered, which could indicate recent or on-going mating events in these species. Aggregations of predators may also be related to fine-scale patches in prey recruitment (White, 2007), which in turn may depend on levels of predation that selects for restricted prey dispersal (Barraquand and Murrell, 2012). These local community dynamics highlight the
20 importance of disentangling the interactive effects of density-dependence on spatial structure in marine communities (Hewitt et al., 2008).

### 5 Conclusions

There is an urgent need to assess the cumulative impacts of human activities and unprecedented rates of climate change on the deep seafloor environment (Nellemann
25 et al., 2008). Critical to this assessment is an understanding of the spatial scales at which these impacts alter the environment, the scales of environmental control on

biological communities and scales of assembly determined by intrinsic species dynamics such as larval dispersal and social gregariousness.

Multi-scale analyses help avoid spatial mis-matches in making these assessments, which can occur when studies are conducted at smaller or larger spatial scales than those at which environmental controls or intrinsic processes operate (Gallucci et al., 2009). Marine spatial planning for the Mingulay reef complex therefore requires cumulative impact studies that appropriately consider all scales of human impacts (cf Foley et al., 2010), from offshore renewable energy that modifies broad-scale hydrography, to the effects of bottom fishing that can fragment populations that our study shows are already limited by dispersal.

# References

Arkema, K. K.: Flow-mediated feeding in the field: consequences for the performance and abundance of a sessile marine invertebrate, Mar. Ecol.-Prog. Ser., 388, 207–220, 2009.

Barraquand, F. and Murrell, D. J.: Intense or spatially heterogeneous predation can select against prey dispersal, PLOS One, 7, e2892, doi:10.1371/journal.pone.0028924, 2012.

Becking, L. E., Cleary, D. F. R., de Voogd, N. J., Renema, W., de Beer, M., van Soest, R. W. M., and Hoeksema, B. W.: Beta diversity of tropical marine benthic assemblages in the Spermonde Archipelago, Indonesia. Mar. Ecol.-P.S.N.Z.I., 27, 76–88, 2006.

Bett, B. J., Malzone, B. E., Narayanaswamy, B. E., and Wigham, B. D.: Temporal variability in phytodetritus and megabenthic activity at the seabed in the deep Northeast Atlantic, Prog. Oceanogr., 50, 349–368, 2001.

Blanchet, F. G., Legendre, P., and Borcard, D.: Forward selection of explanatory variables, Ecology, 89, 2623–2632, 2008.

Blanquer, A., Uriz, M.-J., and Caujapé, J.: Small-scale spatial genetic structure in *Scopalina lophyropoda*, an encrusting sponge with philopatric larval dispersal and frequent fission and fusion events, Mar. Ecol. Prog.-Ser., 380, 95–102, 2009.

Borcard, D. and Legendre, P.: All-scale spatial analysis of ecological data by means of principal coordinates of neighbour matrices, Ecol. Model., 153, 51–68, 2002.

Borcard, D., Legendre, P., Avois-Jacquet, C., and Tuomisto, H.: Dissecting the spatial structure of ecological data at multiple scales, Ecology, 85, 1826–1832, 2004.

Bosence, D. W. J.: The factors leading to aggregation and reef formation in *Serpula vermicularis* L, in: Proceedings of an International Symposium Held at the University of Durham, April 1976, Biology and Systematics of Colonial Organisms, edited by: Larwood, G. and Rosen, B. R., Academic Press, London, 299–318, 1979.

Cadotte, M. W., Carscadden, K., and Mirotchnick, N.: Beyond species: functional diversity and the maintenance of ecological processes and services, J. Appl. Ecol., 48, 1079–1087, 2011.

Davies, A. J., Duineveld, G., Lavaleye, M., Bergman, M. J., van Haren, H., and Roberts, J. M.: Downwelling and deep-water bottom currents as food supply mechanisms to the coldwater *Lophelia pertusa* (Scleractinia) at the Mingulay reef complex, Limnol. Oceanogr., 54, 620–629, 2009.

De Bello, F., Lavorel, S., Díaz, S., Harrington, R., Bardgett, R., Berg, M., Cipriotti, P., Cornelissen, H., Feld, C., Hering, D., Martins da Silva, P., Potts, S., Sandin, L., Sousa, J. P., Storkey, J., and Wardle, D.: Functional traits underlie the delivery of ecosystem services across different trophic levels, Biodivers. Conserv., 143, 2873–2893, 2010.

de Voogd, N., Cleary, D. F. R., Hoeksema, B. W., Noor, A., and van Soest, R. W. M.: Sponge beta diversity in the Spermonde Archipelago, SW Sulawesi, Indonesia, Mar. Ecol.-Prog. Ser., 309, 131–142, 2006.

Duineveld, G. C. A., Jeffreys, R. M., Lavaleye, M. S. S., Davies, A. J., Bergman, M. J. N., Watmough, T., and Witbaard, R.: Spatial and tidal variation in food supply to shallow cold-water coral reefs on the Mingulay reef complex (Outer Hebrides, Scotland), Mar. Ecol.-Prog. Ser. 444, 97–115, 2012.

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Dray S., Legendre, P., and Peres-Neto, P. R.: Spatial modelling: a comprehensive framework for principal coordinate analysis of neighbour matrices (PCNM), Ecol. Model., 196, 483–493, 2006.

Foley, M. M., Halpern, B. S., Micheli, F., Armsby, M. H., Caldwell, M. R., Crain, C. M., Prahler, E., Rohr, N., Sivas, D., Beck, M. W., Carr, M. H., Crowder, L. B., Duffy, J. E., Hacker, S. D., McLeod, K. L., Palumbi, S. R., Peterson, C. H., Regan, H. M., Ruckelshaus, M. H., Sandifer, P. A., and Steneck, R. S.: Guiding ecological principles for marine spatial planning, Mar. Policy, 34, 955–966, 2010.

Gallucci, F., Moens, T., and Fonesca, G.: Small-scale patterns of meibenthos in the Arctic deep sea, Mar. Biodivers., 39, 9–25, 2009.

Gonzalez-Mirelis, G., Bergström, P., Lundälv, T., Jonsson, J., and Lindegarth, M.: Mapping the benthos: spatial patterns of seabed-dwelling megafauna in a Swedish fjord, as derived from opportunistic video data, Mar. Biodivers., 39, 291–302, 2009.

Hauffe, T., Albrecht, C., Schreiber, K., Birkhofer, K., Trajanovski, S., and Wilke, T.: Spatially explicit analysis of gastropod biodiversity in ancient Lake Ohrid, Biogeosciences, 8, 175–188, doi:10.5194/bg-8-175-2011, 2011.

Henry, L.-A., Davies, A. J., and Roberts, J. M.: Beta diversity of cold-water coral reef communities off Western Scotland, Coral Reefs, 29, 427–436, 2010.

Hewitt, J. E., Thrush, S. F., and Dayton, P. D.: Habitat variation, species diversity and ecological functioning in a marine system, J. Exp. Mar. Biol. Ecol., 366, 116–122, 2008.

Hudson, I. R. and Wigham, B. D.: In situ observations of predatory feeding behaviour of the galatheid squat lobster *Munida sarsi* using a remotely operated vehicle, J. Mar. Biol. Assoc. UK, 83, 463–463, 2003.

Keough, M. J.: Patterns of recruitment of sessile invertebrates in two subtidal habitats, J. Exp. Mar. Biol. Ecol., 66, 213–245, 1983.

Krafft, B. A., Skaret, G., Knutsen, T., Melle, W., Klevjer, T., and Søiland, H.: Antarctic krill swarm characteristics in the Southeast Atlantic sector of the Southern Ocean, Mar. Ecol.-Prog. Ser., 465, 69–83, 2012.

Laidre, M. E.: Foraging across ecosystems: diet diversity and social foraging spanning aquatic and terrestrial ecosystems by an invertebrate, Mar. Ecol., doi:10.1111/j.1439-0485.2012.00527.x, 2012.

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Lavorel, S., Grigulis, K., Lamarque, P., Colace, M.-P., Garden, D., Girel, J., Pellet, G., and Douzet, R.: Using plant functional traits to understand the landscape distribution of multiple ecosystem services, J. Ecol., 99, 135–147, 2011.

Legendre, P. D. and Gallagher, E. D.: Ecologically meaningful transformations for ordination of species data, Oecologia, 129, 271–280, 2001.

Maier, C.: Biology and ecosystem functioning of cold water coral bioherms at Mingulay (Hebrides), NE Atlantic, Cruise Report, BIOSYS 2006 Cruise 64PE250 on R/V Pelagia, Oban-Oban, 7–23 July 2006, Royal Netherlands Institute for Sea Research, Texel, 2006.

Martins, F., Leitao, P. C., Silva, A., and Neves, R. J.: 3D modelling in the Sado estuary using a new generic vertical discretization approach, Oceanol. Acta, 24, 51–62, 2001.

Martins, F. A., Neves, R. J., and Leitão P. C.: A three-dimensional hydrodynamic model with generic vertical coordinate, in: Proceedings of Hidroinformatics, 98, 2, edited by: Babovic, V. and Larsen, L. C., Balkerna/Rotterdam, Copenhague, Denmark, August 1998, 1403–1410, 1998.

McClain, C. R. and Barry, J. P.: Habitat heterogeneity, disturbance, and productivity work in concert to regulate biodiversity in deep submarine canyons, Ecology, 91, 964–976, 2010.

McClain, C. R., Allen, A. P., Tittensor, D. P., and Rex, M. A.: Energetics of life on the deep seafloor, P. Natl. Acad. Sci. USA, doi:/10.1073/pnas.1208976109, 2012.

Moreno Navas, J., Telfer, T. C., and Ross, L. G.: Application of a 3D hydrodynamic and particle tracking models for better environmental management of finfish culture, Cont. Shelf Res, 31, 675–684, 2011.

Mouillot, D., Villéger, S., Scherer-Lorenzen, M., and Mason, N. W. H.: Functional structure of biological communities predicts ecosystem multifunctionality, PLOS One, 6, e17476, doi:10.1371/journal.pome.0017476, 2011.

Nellemann, C., Hain, S., and Alder, J. (Eds): In Dead Water – Merging of Climate Change with Pollution, Over-Harvest, and Infestations in the World's Fishing Grounds, United Nations Environment Programme, GRID-Arendal, Norway, 2008.

Oliveira, O. M. P. and Marques, A. C.: Population biology of *Eudendrium caraiuru* (Cnidaria, Anthoathecata, Eudendriidae) from São Sebastião Channel, Southeastern Brazil, Iheringa Ser. Zool., 95, 241–246, 2005.

Reu, B., Zaehle, S., Proulx, R., Bohn, K., Kleidon, A., Pavlick, R., and Schmidtlein, S.: The role of plant functional trade-offs for biodiversity changes and biome shifts under scenarios of global climatic change, Biogeosciences, 8, 1255–1266, doi:10.5194/bg-8-1255-2011, 2011.

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Roberts, J. M., Brown, C. J., Long, D., and Bates, C. R.: Acoustic mapping using a multibeam echosounder reveals coldwater coral reefs and surrounding habitats, Coral Reefs, 24, 654–669, 2005a.

Roberts, J. M., Davies, A. J., Dodds, L. A., and Santillo, D.: Report of the MY *Esperanza* cold-water coral research cruise to the Mingulay reef complex, 11–20 May 2005, Cruise Report for the Scottish Association for Marine Science and Greenpeace, 2005b.

Roberts, J. M., Davies, A. J., Henry, L.-A., Dodds, L. A., Duineveld, G. C. A., Lavaleye, M. S. S., Maier, C., van Soest, R. W. M., Bergman, M. I. N., Hühnerbach, V., Huvenne, V. A. I., Sinclair, D. J., Watmough, T., Long, D., Green, S. L., and van Haren, H.: The Mingulay reef complex, Northeast Atlantic: an interdisciplinary study of cold-water coral habitat, hydrography and biodiversity, Mar. Ecol.-Prog. Ser., 397, 139–151, 2009.

Sainte Marie, B., Urbani, N., Sévigny, J.-M., Hazel, F., and Kuhnlein, U.: Multiple choice criteria and the dynamics of assortative mating during the breeding season of female snow crab *Chionoecetes opilio* (Brachyura, Majidae), Mar. Ecol.-Prog. Ser., 181, 141–153, 1999.

Santos, A. P.: Modelo hidrodinámico de circulacáo oceaánica e estuarina (in Portuguese), PhD Thesis, IST, Lisbon, 1995.

Schneider, D. C., Gagnon, J.-M., and Gilkinson, K. D.: Patchiness of epibenthic megafauna on the outer Grand Banks of Newfoundland, Mar. Ecol.-Prog. Ser., 39, 1–13, 1987.

Shimeta, J.: Influence of flow speed on the functional response of a passive suspension feeder, the spionid polychaete *Polydora cornuta*, Mar. Biol., 156, 2451–2460, 2009.

Sommer, C.: Larval biology and dispersal of *Eudendrium racemosum* (Hydrozoa, Eudendriidae), Sci. Mar., 56, 205–211, 1992.

Thiem, Ø., Ravagnan, E., Fosså, J. H., and Berntsen, J.: Food supply mechanisms for cold-water corals along a continental shelf edge, J. Mar. Syst., 60, 207–219, 2006.

Vroom, P. S., Page, K. N., Peyton, K. A., and Kukea-Schulz, J. K.: Spatial heterogeneity of benthic communities with an emphasis on reef algae at French Frigate Shoals, Northwestern Hawai'ian Islands, Coral Reefs, 24, 574–581, 2005.

Weiher, E., Freund, D., Bunton, T., Stefanski, A., Lee, T., and Bentivenga, S.: Advances, challenges and a developing synthesis of ecological community assembly theory, Philos. T. R. Soc. B, 366, 2403–2413, 2011.

White, J. W.: Spatially correlated recruitment of a marine predator and its prey shapes the large-scale pattern of density-dependent prey mortality, Ecol. Lett., 10, 1054–1065, 2007.

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Wright, D. J., Lundblad, E. R., Larkin, E. M., Rinehart, R. W., Murphy, J., Cary-Kothera, L., and Draganov, K.: ArcGIS Benthic Terrain Modeler, Corvallis, Oregon, Oregon State University, Davey Jones Locker Seafloor Mapping/Marine GIS Laboratory and NOAA Coastal Services Center, http://csc.noaa.gov/digitalcoast/tools/btm/index.html, last access: November 2012, 2005.

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**Table 1.** Topographic and hydrographic variables for each of the 14 sites at the reef complex.

| Site | Latitude (dec deg) | Longitude (dec deg) | $C_{AVE}$ $\mathrm{m\,s}^{-1}$ | $C_{MAX}$ $\mathrm{m\,s}^{-1}$ | $C_{SD}$ $\mathrm{m\,s}^{-1}$ | BPI | Aspect (deg rad) | Rugosity | Slope (°) | Depth (m) |
|---|---|---|---|---|---|---|---|---|---|---|
| 1156 | 56.78733 | −7.4165 | 0.330 | 0.549 | 0.116 | 123 | 0.5 | 1.0663 | 15.2 | 140 |
| 1157 | 56.7875 | −7.4075 | 0.256 | 0.428 | 0.071 | 94 | 97.8 | 1.1705 | 26.6 | 122 |
| 1163 | 56.8175 | −7.40783 | 0.336 | 0.637 | 0.157 | −25 | 122.8 | 1.1124 | 19.3 | 125 |
| 1151 | 56.81896 | −7.39345 | 0.277 | 0.387 | 0.065 | −6 | 239.7 | 1.0181 | 8.4 | 121 |
| 1168 | 56.819816 | −7.411883 | 0.336 | 0.637 | 0.157 | −17 | 201.7 | 1.0123 | 7.2 | 125 |
| 1159 | 56.81983 | −7.397 | 0.324 | 0.575 | 0.135 | −6 | 239.7 | 1.0181 | 8.4 | 155 |
| 1169 | 56.820666 | −7.40955 | 0.344 | 0.604 | 0.135 | −17 | 201.7 | 1.0123 | 7.2 | 128 |
| 1153 | 56.82083 | −7.386 | 0.339 | 0.559 | 0.123 | −16 | 138.0 | 1.0078 | 4.1 | 126 |
| 1164 | 56.821166 | −7.402166 | 0.282 | 0.463 | 0.091 | 42 | 89.7 | 1.0402 | 11.6 | 128 |
| 1162 | 56.823016 | −7.3942 | 0.321 | 0.599 | 0.142 | 34 | 275.3 | 1.0363 | 10.4 | 129 |
| 1154 | 56.8233 | −7.391166 | 0.335 | 0.616 | 0.150 | −12 | 5.7 | 1.0112 | 6.1 | 146 |
| 1158 | 56.82383 | −7.39433 | 0.336 | 0.637 | 0.157 | 34 | 275.3 | 1.0363 | 10.4 | 138 |
| 1165 | 56.82685 | −7.397633 | 0.314 | 0.523 | 0.115 | 1 | 334.8 | 1.0061 | 4.6 | 174 |
| 1167 | 56.8288166 | −7.39463 | 0.297 | 0.450 | 0.077 | 1 | 334.8 | 1.0061 | 4.6 | 187 |

**Table 2.** Spatial eigenfunctions representing scales of positive autocorrelation detected in communities across the reef complex. A reduced set of five eigenfunctions (* broad-scale, ** fine-scale) explained much of the variation in assembly.

| Eig1 | *Eig2 | *Eig3 | *Eig4 | **Eig5 | Eig6 | **Eig7 | Eig8 |
|---|---|---|---|---|---|---|---|
| 846.67 | −531.18 | 1586.73 | −731.95 | 163.25 | −81.06 | −0.04 | −5.91 |
| 1310.68 | 101.78 | 1281.41 | 273.37 | −983.02 | −61.53 | 0.04 | −9.87 |
| 1569.61 | 467.60 | −24.62 | −544.51 | −279.71 | −192.27 | 0.06 | 21.69 |
| −1858.46 | 2385.39 | 564.64 | 322.74 | 247.16 | −0.01 | −275.12 | 0.06 |
| −1858.46 | 2385.39 | 564.63 | 322.75 | 247.16 | 0.11 | 275.12 | 0.06 |
| 1192.36 | −93.24 | −573.72 | 817.75 | −158.78 | −5.36 | −0.03 | 25.27 |
| 451.43 | −1121.20 | 1035.84 | 652.95 | 304.02 | 152.41 | $-8.57 \times 10^{-5}$ | 15.78 |
| 1191.50 | −101.67 | −555.26 | 829.36 | −160.62 | −75.18 | −0.01 | −31.02 |
| −1928.13 | −1746.72 | 539.40 | −1002.66 | 755.76 | −4.48 | $1.92 \times 10^{-3}$ | 0.18 |
| 629.37 | −782.68 | −257.74 | −129.53 | 1019.70 | −71.81 | 0.04 | −9.85 |
| 1541.34 | 490.23 | −131.74 | −580.84 | −202.78 | 349.43 | −0.06 | −6.37 |
| 884.45 | 1043.04 | −2274.69 | −795.91 | 465.29 | −14.78 | $2.30 \times 10^{-3}$ | 0.04 |
| −2410.64 | −865.24 | −788.05 | −812.64 | −1477.41 | 4.06 | $-1.17 \times 10^{-3}$ | −0.09 |
| −1561.71 | −1631.51 | −966.83 | 1379.12 | 59.98 | 0.49 | $-1.09 \times 10^{-3}$ | 0.04 |

**Table 3.** Redundancy and partial redundancy analyses that quantified the amount (%) of community assembly variability explained by pure environmental (env), spatial (space), and spatially structured environmental variables ($env_{space}$), alongside the statistical significance of the model (set at $p < 0.05$, indicated by *), which for $env_{space}$ cannot be estimated using any method (Bocard et al., 2004) thus was not applicable (NA).

| Spatial model | variability explained (%) | $p$ |
|---|---|---|
| Broad-scale | | |
| env + space + $env_{space}$ | 65.0 | 0.040* |
| pure env | 36.6 | 0.048* |
| pure space | 23.9 | 0.146 |
| pure $env_{space}$ | 4.5 | NA |
| unexplained variance | 35.0 | NA |
| Fine-scale | | |
| env + space + $env_{space}$ | 58.9 | 0.034* |
| pure env | 37.0 | 0.096 |
| pure space | 17.8 | 0.036* |
| pure $env_{space}$ | 4.0 | NA |
| unexplained variance | 41.1 | NA |
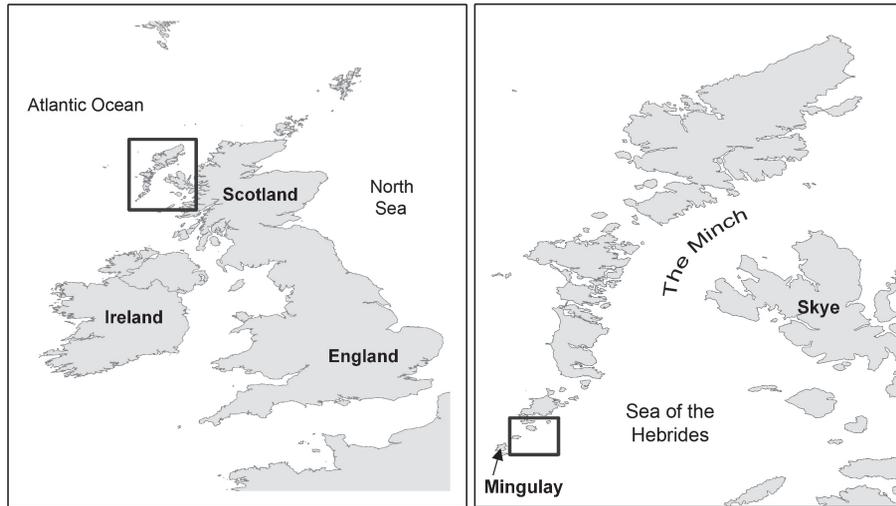
**Fig. 1.** Regional setting of the Mingulay reef complex in the Sea of the Hebrides, Northwest Scotland.

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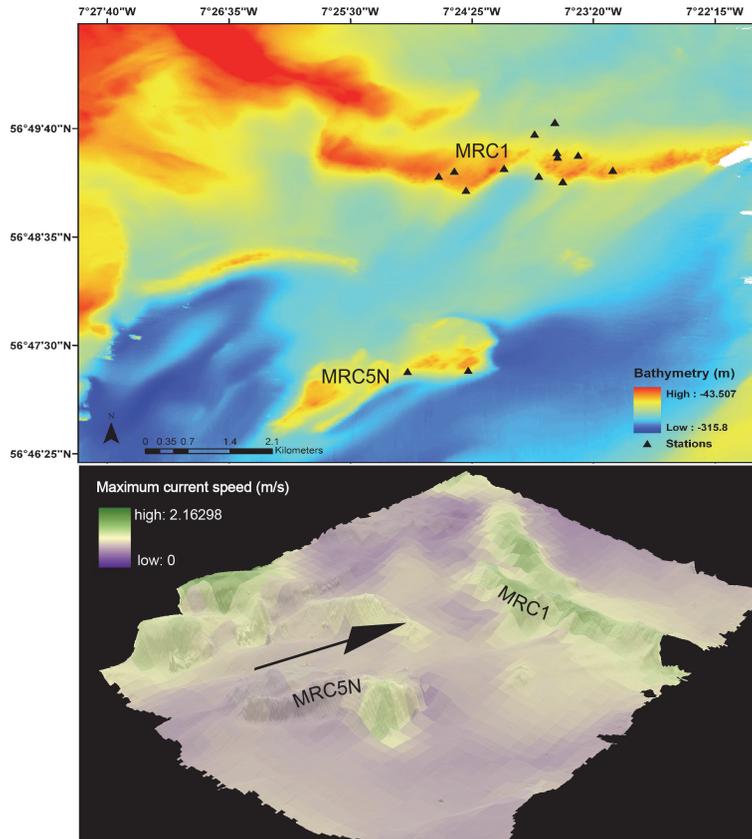
**Fig. 2.** Grab sampling stations on the reef complex in May 2005 (*n* = 14) in relation to multibeam bathymetry (top) and hydrography (bottom). The prevailing SSW to NNE currents are indicated by a black arrow in the bottom image of hydrography. Mingulay Area 1 = MRC1, Mingulay 5 North = MRC5N.

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**Fig. 3.** Environmental control of assembly at broad (across reef) spatial scales determined by topographic variation in BPI and aspect (near horizontal shaded ellipse) and hydrographic variability in $C_{MAX}$ and $C_{SD}$ (near vertical shaded ellipse). Line length reflects the strength of a variable with respect to community assembly. Sites are also indicated to demonstrate the wide range of environmental set.

**Fig. 4.** Environmental control of functional assembly at broad spatial scales. Mobile scavenging detritivore (*D*) and predator (*P*) species are distributed across more narrow environmental niches (dark grey shaded area) than sessile filter and suspension feeders (*S*), which are found across all sets of topographic and hydrographic conditions (light grey shaded area). Mobile fauna inhabit sites with slower, less dynamic currents, while sessile fauna colonise every type of habitat at the reef.

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**Fig. 5.** Gravid decapod crustaceans on the reef complex. Top: the galatheid crab *Munida sarsi*. Middle: the hermit crab (without shell) *Pagurus forbesii*. Bottom: the pandalid shrimp *Pandalina brevirostris*.