Fishing disturbance and marine biodiversity: role of habitat structure in simple soft-sediment systems

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ABSTRACT: Broad-scale anthropogenic disturbances that reduce the density of epifauna and homogenise surficial sediments can have important consequences for seafloor biodiversity. We investigated the habitat structure and macrofaunal diversity of relatively simple soft-sediment habitats over a number of spatial scales (cm to km) to identify the role of habitat structure in influencing macrobenthic diversity and to assess the validity of using habitat structure as a surrogate measure for biodiversity. We sampled 10 locations with differences in habitat structure using a sampling design that nested macrobenthic core samples within videoed transects of the seafloor. This allowed us to determine relationships between observable habitat structure and macrobenthic diversity at a number of spatial scales. We characterised elements of habitat structure based on direct counts of surficial sediment characteristics and the presence of other immobile features, many of which were biogenic in origin. We also used multivariate measures (the relative multivariate dispersion, the mean and range of the Bray-Curtis dissimilarity along the transects) to characterise habitat structure at the transect scale. We developed regression models based on measures of habitat structure that explained 74 to 86% of the variance in macrobenthic diversity. This result suggests that removal of habitat structure in relatively low-structure soft-sediment systems will significantly decrease their biodiversity, and consequently that of the wider marine ecosystem.

KEY WORDS: Biodiversity · Soft-sediments · Habitat structure · Habitat heterogeneity · Habitat complexity · Habitat disturbance · Fishing impacts · Nested multi-resolution sampling · Kawau Bay · New Zealand

INTRODUCTION

Habitat disturbance by trawling and dredging is probably one of the most significant threats to marine benthic biodiversity (Hammer & Jansson 1993, Norse 1993, Dayton et al. 1995, 1998, Jennings & Kaiser 1998, Thrush et al. 1998, Auster & Langton 1999). While some fisheries are targeted in areas of highly structured habitat (e.g., Cranfield et al. 1999, Koenig et al. 2000), most of the seafloor is soft-sediment habitat. These soft-sediment habitats are not generally considered highly structured habitats, although they can support high diversity (Etter & Grassle 1992, Coleman et al. 1997, Gray et al. 1997, Snelgrove 1999). Given the intrinsic and extrinsic value of marine biodiversity (e.g., Bengtsson et al. 1997, Costanza et al. 1997, Freckman et al. 1997, Gray 1997, Schlapfer & Schmid 1999), there is an increasing need for resource managers to sustain, maintain or enhance biodiversity under national or international laws or agreements (e.g., United Nations Environment Programme 1992, Fisheries Act 1996). There are a number of habitat management options aimed at reducing the threat to marine biodiversity, ranging from the creation of marine protected areas through the spatial and tempo-

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ral management of areas of the seafloor, to gear limitation or modification. These options have common elements of reducing habitat disturbance and actively managing the seafloor. Justifying the need for and testing the efficacy of habitat management will require the collection of data to rigorously define the biodiversity of a habitat and assess responses to disturbance. This presents 3 problems: (1) methods of sampling potentially large areas of the seabed cost-effectively to directly or indirectly estimate biodiversity need to be developed; (2) traditional macrobenthic sampling techniques (e.g., cores or grabs) are not always appropriate for collecting the information on biogenic and physical structures needed to define benthic habitats; (3) aspects of the seafloor habitat most related to biodiversity need defining. To reach general conclusions about the relationship between habitat structure and biodiversity, we need to assess relationships across sampling scales and define operational measures that treat habitat structure as landscape elements characterised by variations in patch density, size and spatial arrangement.

Biodiversity is often considered to be positively associated with habitat complexity or heterogeneity (Tokeshi 1999). There are problems with the definition of these terms (see Kolasa & Rollo 1991, McCoy & Bell 1991). For example, McCoy & Bell (1991) define habitat heterogeneity as the variation in relative abundance of different structural components, while complexity is defined as the absolute abundance of individual components. However, other terminology and definitions are common (Bell et al. 1991). In this paper, we use sampling and analytical procedures that combine elements of both heterogeneity and complexity as defined by McCoy & Bell (1991), and we refer to habitat structure as a term encompassing the variety, abundance and spatial arrangement of a variety of physical and biological processes.

Soft-sediment habitats are often considered to have low topographic structure. Perception of habitat structure is of course scale-dependent, but complex seafloor habitats are generally thought of as distinct features such as reefs, kelp forests or seagrass beds, despite the fact that organisms that modify the 3-dimensional structure above and below the sediment surface are widely distributed and can affect benthic community structure (e.g., Rhoads et al. 1977, Reise 1981, van Blaricom 1982, Woodin 1983, Luckenbach 1987, Dame 1993, Graf & Rosenberg 1997, Green et al. 1998).

Studies that merely contrast simple and highly structured habitats are of limited value in defining general relationships between habitat structure and diversity. Firstly, the importance of these processes will be dependent on the spatial and temporal scales of observation or sampling (Dayton & Tegner 1984, Schneider

et al. 1987, Thrush et al. 1997b). For example, Blanchard & Bourget (1999) related various aspects of physical heterogeneity of a rocky-shore coastline measured at multiple spatial scales to aspects of benthic community structure (including diversity) and showed that processes operating over different spatial scales best explained different aspects of community structure. Macrobenthic diversity was best explained at intermediate scales (100s of metres), although effects cascaded across scales. Secondly, operational measures of habitat heterogeneity, complexity and structure are needed that include the quantification of a variety of different elements. Many studies categorise habitats into 'simple' or 'structured' based on the presence of a single feature rather than treating them as landscape elements (for examples of the latter see Robbins & Bell 1994, Irlandi et al. 1995, Thrush et al. 1997a). The problem of over-generalizing results is especially relevant to any general consideration of biodiversity (Huston 1997). Thus to reach general conclusions on the influence of habitat structure on biodiversity, it is important to assess the role of a variety of features, not just variation in a single element of habitat structure.

In this study, our goal was to estimate the relationship between habitat structure and macrobenthic diversity in a coastal environment contrasting a variety of soft-sediment habitats. We employed a novel, nested sampling design that links macrobenthic core samples to video transects. This allowed us to sample at multiple spatial scales, detecting locally important elements of habitat structure while also extending the generality of the survey by encompassing a variety of habitats. Our sampling strategy was not designed to fully characterise macrobenthic diversity within a site, but rather to enable us, with minimal cost and effort, to make comparisons between sites while still including high levels of variation in habitat structure within sites. We tested the prediction that across sites there would be a positive relationship between habitat structure and macrobenthic diversity, and that this relationship resulted from different aspects of habitat structure occurring at different scales. This sampling design also enabled us to assess the utility of using seafloor video images as a surrogate measure for macrobenthic diversity.

METHODS

Site description and sampling. Sites were located in the vicinity of Kawau Bay (36° 24' S, 174° 48' E) a large, 10 to 20 m deep, embayment on the north-east coast of North Island, New Zealand (Fig. 1). Kawau Bay is composed mainly of soft-sediment habitats that vary in both sediment characteristics and biogenic structure.

Sites were chosen to reflect this habitat variation and to encompass a range of geographic locations around the bay. In total, 10 sites were sampled between 18 and 25 February 1999.

Sampling involved the collection of variable numbers of core samples at each site following the sampling design of Hewitt et al. (unpubl. data). When sampling to assess diversity, it is desirable to encompass as much variation as possible by sampling many different sites and taking multiple samples to assess variation within sites. Inevitably the need to collect many samples at many locations must be balanced against cost/effort constraints. The sampling strategy developed by Hewitt et al. (unpubl. data) maximises the variability encompassed along a transect while minimising the number of core samples collected. It involves nesting core samples within videoed transects of the seafloor, thus allowing analysis of relationships between observed habitat structure and macrobenthic diversity at a number of spatial scales.

Fig. 1. Location of the 10 sampling sites in Kawau Bay, North Island, New Zealand

Within each site, 2 locations were haphazardly chosen. At each location a pair of 20 m transects were deployed. The 2 transects were laid on the seafloor at right angles to each other. One transect in each pair was always aligned with the tidal flow (typically north-south). As each transect rope was laid out, the diver observed variations in habitat features. Habitat structural elements included the presence of large bivalves, sponges, hydroids, and surficial sediment characteristics (e.g., shell hash, sand, mud). Corers (10 cm diameter, 12 cm deep) were then positioned along the transect to record the apparent variation in habitat structure at the 20 m scale. A maximum of 5 cores were collected along each transect, depending on the habitat variability observed: where the sediment structure appeared homogeneous down the length of the transect, 1 core was taken at the start and end of a transect. We focused on sampling in and out of large patches (<4 m diameter) or near and away from individual features (e.g., sponges) down the transect. The sampling programme was not intended to provide detailed information on small-scale density variation that would be encompassed by contiguous sampling. After corers had been inserted into the sediment, the transect was videoed using a digital video camera with the lens held perpendicular to the seafloor at 0.7 m above the seabed
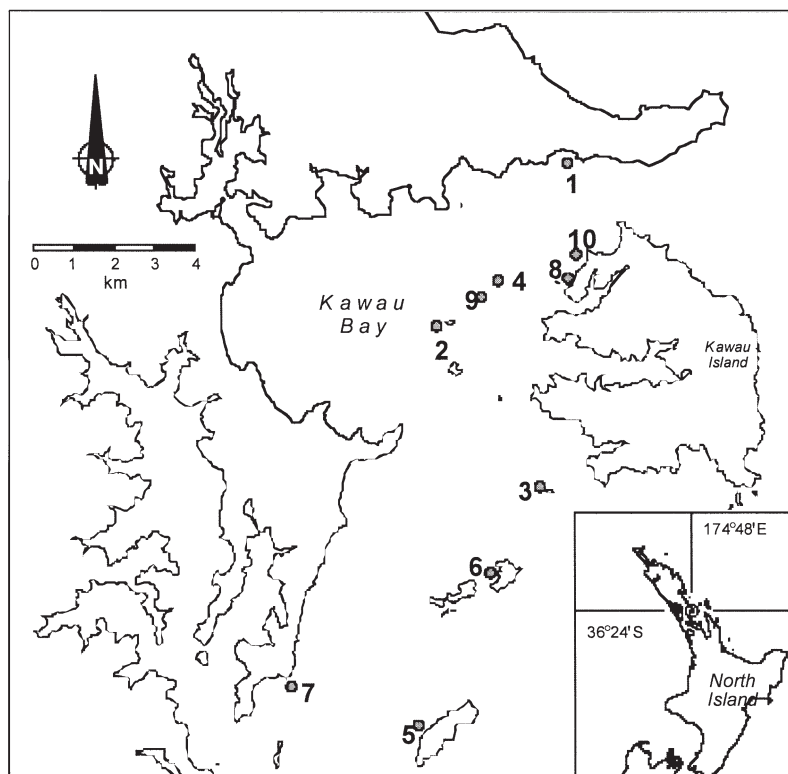
(width of video transect = 80 cm). Corers were premarked so that they could be individually identified on the videotape. After the corers and transect had been videoed, core samples were collected and taken to the surface.

Core samples were sieved (500 μm mesh), and then preserved in 70% isopropanol and 0.1% Rose Bengal in seawater. In the laboratory, macrofauna were sorted, and identified to the genus level (with the exception of syllid polychaetes which were identified as either Syllinae and Exogoninae).

Visual classification of video images. For visual classification, a composite strip 100 cm long centred on each corer was assembled from 2 to 4 individual video frames, using a frame grabber (Sony DVBK 2000E Version 1.00). Pixel resolution was 1.7 mm. Grids of 30 × 30, 30 × 60, and 30 × 100 cm were overlaid on the grabbed strip (again centred on the core) to provide a measure of the number of different habitat features represented at each spatial scale. Habitat features were counted where they intersected with nodes of the grid (5 cm line spacing) and were assigned to 1 of 4 different categories of habitat structure (see Table 1). Habitat structure measures (based on the number of different habitat features observed) were then calculated for each of the 3 spatial sam-

pling grains (i.e., 30 × 30, 30 × 60, and 30 × 100 cm) surrounding each core.

Statistical analysis. A number of diversity indices were calculated using the PRIMER software package (Clarke 1993). We used the number of genera per core, Margalef's richness (d = number of genera – 1)/ log number of individuals; Shannon-Wiener diversity $H' = -\Sigma(P_i \times \log (P_i))$, where P_i = the proportion of the total sample belonging to the ith genus; and Pielou's evenness ($J' = H'$/log number of genus). These indices are common measures of diversity (Hill 1973, Peet 1975, Pielou 1975, Krebs 1989) and, by using a number of indices, we included a variety of information about diversity beyond merely the number of taxa. Gray (2000) pointed out the substantive confusion in the application of various measures of species diversity and the scales at which they are applied. In this paper we describe sample (within-site) diversity and determine the strength of relationships between these indices and measures of habitat structure at this scale.

Preliminary analysis indicated interactions between the different elements of habitat structure and the sampling grains over which they were influencing macrobenthic diversity. Thus, we determined the relationship between habitat structure reflected by visual counts from video images for each of the 3 spatial grains (i.e., 30 × 30, 30 × 60, and 30 × 100 cm).

We used direct counts of the habitat features categorised in Table 1. Mobile biological features were not included in our analysis, because we could not be sure how long those elements were resident over the sediments sampled. The basic measures of variation in habitat structure in the vicinity of macrofaunal core samples provided an incomplete picture of variation in habitat structure, as the habitat features can change along the length of the transect (e.g., a shift from sponges to shell hash). To overcome this problem, we also used multivariate approaches to define the average and range of variation in habitat structure along transects within each site. The multivariate measures were the relative multivariate dispersion, the mean Bray-Curtis dissimilarity between habitat structure variables, and the range of Bray-Curtis dissimilarities. These variables were calculated using PRIMER. High relative multivariate dispersion values indicate a high number of different habitat elements within a site (see Warwick & Clarke [1993] for discussion of relative multivariate dispersion). High mean Bray-Curtis dissimilarity reflects a site containing a number of dissimilar habitats.

Kruskal-Wallis tests were used to test for overall differences between sites in both macrobenthic diversity and habitat structure. When tests were significant (p = ≤ 0.05), Tukey's rank-sum multiple-comparison test was used to identify sites or groups of sites that were significantly different from the others (Zar 1984).

Exploring relationships between habitat structure and macrobenthic diversity. Mean values of the different measures of macrobenthic diversity were calculated for each site and regressed (Model 1) against all the measures of habitat structure and water depth averaged across transects at each site. To develop regression models we used backwards variable selection with an exit level of p = 0.15. Variables were dropped from the model only if their removal did not markedly affect the adjusted r^2 (McCullagh & Nelder 1989, Crawley 1993). The first variables removed were the different sample grains used to characterise habitat structure. Regression models were constrained to only

Table 1. Elements of habitat structure assigned to different categories

Immobile biological features	Mobile biological features	Sediment characteristics	Miscellaneous
Ascidians	Drift weed	Boulder (256 to 4096 mm)	Sand ripples
Coralline algae	Gastropod: *Cominella* sp.	Cobble (64 to 256 mm)	Ray pits
Chaetopterid tubes	Hermit crabs: *Paguristies* sp.	Gravel (2 to 4 mm)	Shells
Diatom mat	Pseudofaeces	Sand	Shell hash
Horse mussels (live *Atrina zelandica*)	Starfish: *Asteropecten* sp., *Cosinasteris* sp., *Asterina* sp.	Sandy mud	Horse mussel shells lying flat
Holes/burrows	Sea cucumbers: *Stichopus mollis*	Muddy sand	Horse mussels upright and dead
Hydroids	Ophiuroids	Mud	Scallop shells
Mounds			Dead sponge
Scallops (*Pecten novaezelandiae*)			
Sponges			
Seaweed			
Spionid worm tube mat			

maximally include 1 sample grain for each variable. After finding the most parsimonious model, a number of different orders of dropping variables were tried to determine if the sample grains chosen produced the best and most consistent model.

To investigate how well the multivariate pattern exhibited by the macrobenthic core data reflected the multivariate pattern of habitat structure elements derived from the video data, we used the RELATE routine within PRIMER (Clarke & Warwick 1994). This is a Procrustes-type analysis (see Gower 1987, Legendre & Legendre 1998) except that whereas Procrustes analysis depends on dimensionality, here the fundamental constructs are the similarity matrices and they are compared by the Spearman rank-correlation coefficient. Comparison of multivariate data structure was based on genus-level presence/absence core data and Euclidean distance matrix of the presence/absence of all habitat structure elements (except mobile biological features) found in video data at the largest grain sampled (30×100 cm). Due to software limitations, the data set was split in half, and the 2 transect directions (north-south and east-west) were tested separately.

RESULTS

Variation in habitat structure and macrobenthic diversity measures between sites

Macrobenthic diversity and habitat structure varied significantly between sites (Fig. 2, Table 2). Kruskal-Wallis and associated multiple-comparison tests revealed variation in the rank order of sites for each diversity measure. However, sites grouped as either highest or lowest diversity were similar. Univariate measures of habitat structure based on immobile biological features, sediment particle characteristics and miscellaneous features all showed differences amongst sites. The order of sites varied for the different habitat structure elements, indicating different combinations of habitat features across sites (Fig. 2). Although 3 different sample grains were initially used in the analysis, Table 2 presents results only for those grains finally selected for use in the regression modelling. We included this multi-scale aspect in the analysis as we expected habitat structure to vary with scale and potentially reflect differences in the strength and
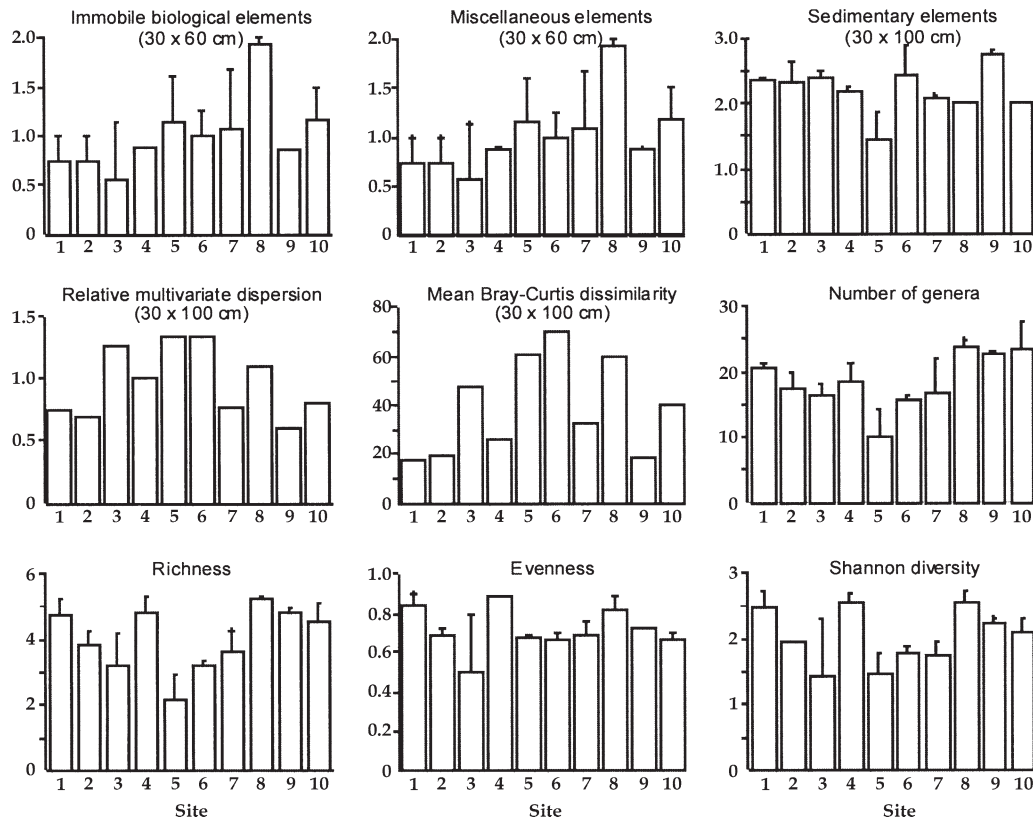
Fig. 2. Variation in habitat structure elements and macrobenthic diversity between sites. For habitat structure elements the sample grain is presented in parentheses. Only the sampling grain finally selected for use in the regression modelling is presented. Results for 30×30 cm are not presented as this was not the most important grain. All values are mean (+SE), except for the multivariate measures (relative multivariate dispersion and mean Bray-Curtis dissimilarity), which are simply value per site

Table 2. Site differences in macrobenthic diversity and habitat structure. p values derived from Kruskal-Wallis tests; sites connected by lines are not significantly different from each other (Tukey's test). Sites are ordered (left-to-right) from highest to lowest mean values. Site average minimum and maximum values are also presented for each variable. Data are presented only for those size categories selected for regression modelling

——— Macrobenthic diversity ———			——————— Habitat structure ———————				
p	Site order	Min. – max.		Sample grain (cm)	p	Site order	Min. – max.
Number of genera 0.0001	8 10 9 1 4 2 7 3 6 5	10.1 – 23.7	Immobile biological	30 × 60	0.0108	8 10 5 6 9 7 4 1 2 3	0.62 – 1.9
Shannon-Wiener 0.0001	8 4 1 9 10 2 7 6 3 5	1.4 – 2.6	Sediments	30 × 100	0.0001	9 6 2 1 3 4 7 8 10 5	1.5 – 2.8
Evenness 0.0001	4 1 8 7 9 2 10 5 6 3	0.5 – 0.9	Miscellaneous	30 × 60	0.0108	8 10 5 6 9 7 4 1 2 3	0.6 – 1.2
Richness 0.0001	8 9 1 4 10 2 7 3 6 5	2.2 – 5.3					

direction of ecological relationships. Observations of habitat structure for these variables sampled at different spatial grains showed the same general pattern between sites, although differences in the p values for the tests for different grain of the same variable provided some evidence that habitat structure varied with scale of sampling. Not surprisingly, the multivariate measures of habitat structure revealed the strongest differences between sites; these variables best accounted for habitat structure at the site scale based on the largest grain sampled (30 × 100 cm).

Relationships between habitat structure and macrobenthic diversity

We developed regression models, based on measures of habitat structure, that explained 74 to 86% of the variance in macrobenthic diversity (Table 3). Water depth, averaged across transects at a site, was not important in explaining differences in macrobenthic diversity between sites. However, for each diversity index, both univariate and multivariate measures of habitat structure were important. The relative multivariate dispersion, was important for all indices of macrobenthic diversity, except number of genera. Slope estimates indicate that this factor was positively related to diversity. The mean Bray-Curtis dissimilarity was important for all diversity measures, but was negatively related to diversity. These 2 multivariate measures of within-site variation in habitat structure generally work in combination, with the mean Bray-Curtis dissimilarity restricting over-estimation of diversity by the relative multivariate dispersion at more complex sites. This suggests the possibility of a threshold effect

of a threshold effect where biodiversity no longer increases with increasing habitat structure.

For all measures of biodiversity, sites with high average numbers of different habitat structural elements had high diversity. The type of habitat features that were important depended on the diversity index. All measures of diversity, except evenness, were related to number of different sedimentary features. However, all the measures of diversity were also related to either the number of different immobile biological features or the number of different miscellaneous features. The different elements of habitat structure had effects on diversity at different sample grains, although the most important sample grain for each element was consistent. Thus, the number of different sedimentary features was always important at a grain of 30 × 100 cm. Interestingly, the grain at which the number of different sedimentary features was most important was larger than that at which the number of different immobile biological features was most important. Nevertheless, the presence of habitat structure elements always had a positive effect on the 4 macrobenthic diversity indices.

The RELATE procedure demonstrated significant agreement in the pattern within the multivariate matrices describing the macrobenthic and habitat structure data (global Spearman's ρ = 0.212 and 0.189 with p = 0.003 and 0.039 for the east-west and north-south directions, respectively). The stronger concordance running in the east-west direction indicated stronger effects across tidal flows. Overall, both data sets described complementary patterns, and thus measures of habitat structure derived from video analysis appear to be a good surrogate for estimating macrobenthic diversity.

Table 3. Regression models based on habitat structure developed to explain variation in macrobenthic diversity between the 10 site samples in Kawau Bay. Grain of sampling used in the video counts is given

Macrobenthic diversity	r^2	Factor	Parameter estimate	p
Evenness	0.7510	Intercept	0.678903	0.0007
		ln(immobile biological, 30 × 60 cm)	0.435387	0.0081
		Relative multivariate dispersion, 30 × 100 cm	0.561242	0.0504
		Mean Bray-Curtis dissimilarity, 30 × 100 cm	−0.012562	0.0148
Shannon-Wiener	0.8265	Intercept	0.734187	0.3902
		ln(miscellaneous, 30 × 60 cm)	1.873924	0.0081
		ln(sediment characteristics, 30 × 100 cm)	1.423658	0.0785
		Relative multivariate dispersion, 30 × 100 cm	2.049470	0.0624
		Mean Bray-Curtis dissimilarity, 30 × 100 cm	−0.044275	0.0203
Richness	0.8626	Intercept	1.242798	0.4529
		ln(miscellaneous, 30 × 60 cm)	3.659516	0.0082
		ln(sediment characteristics, 30 × 100 cm)	3.852469	0.0284
		Relative multivariate dispersion, 30 × 100 cm	2.907110	0.1437
		Mean Bray-Curtis dissimilarity, 30 × 100 cm	−0.074547	0.0344
ln(number of genera)	0.7372	Intercept	2.358474	0.0005
		ln(immobile biological, 30 × 60 cm)	0.609790	0.0196
		ln(sediment characteristics, 30 × 100 cm)	1.000411	0.0339
		Mean Bray-Curtis dissimilarity, 30 × 100 cm	−0.005818	0.1102

DISCUSSION

The results support our prediction that there is a positive relationship between habitat structure and macrobenthic diversity in coastal soft-sediment habitats. Our sites spanned a range of habitats that differed both in sediment characteristics and the presence of a variety of epifauna. Our analysis implies that relatively low-density features creating small-scale structure on the seafloor (e.g., sponges <2; hydroids <1; horse mussels <17 individuals per 0.3 m^2) can significantly influence macrobenthic diversity on the 100 to 1000s of metres scale. Although there was variability in the strength and the exact parameters of relationships derived for the different diversity indices, our conclusions are consistent regardless of the index used.

The relative importance of physical and biological elements of habitat structure varied with spatial scale. We constrained our statistical models to include 1 sampling grain for each factor to prevent very strong co-variation amongst variables affecting the consistency of our results. Our measures of habitat structure were divided into sedimentary, immobile biological and miscellaneous aspects. Across different measures of macrobenthic diversity, our results consistently suggest that small-scale macrofaunal biodiversity is affected directly or indirectly by immobile epifauna within an area of 0.18 m^2, while the influence of sediment characteristics accumulates over 0.3 m^2. The miscellaneous aspects were a combination of factors representing small-scale disturbance (e.g., ripples, mounds, feeding pits) and dead bivalve shells. Thus, this category also represents biogenic features. Sedimentary aspects were important for most measures of diversity, although not for evenness. Habitat structure immediately surrounding the macrofauna (i.e. within 30 × 30 cm) was never the most closely related factor. We were also able to include estimates of habitat structure calculated over larger scales by investigating within-site variability using multivariate analysis. The relative multivariate dispersion and mean Bray-Curtis dissimilarity encapsulated changes in the elements defining habitat structure down each transect. These measures of within-site variability in habitat structure were always important in explaining the relationship between macrobenthic diversity and habitat structure, although their relative importance changed between diversity indices. Consistency in their relative importance was observed for all but number of genera. While the relative multivariate dispersion of habitat structure elements was always positively related to diversity, the estimate of mean within-site variability (represented by mean percent dissimilarity) always had negative slope parameter estimates. This restricted over-estimation of diversity by the relative multivariate dispersion at more structured sites and suggests the possibility of a threshold in the relationship between biodiversity and habitat structure.

Using the regression estimates for the different diversity indices, we determined how habitat structure

affected macrofaunal diversity at individual sites. We demonstrated this with reference to evenness and richness. For example, Sites 4 and 8 both have moderate variability in within-site structure; thus our regression would predict medium evenness. They also both have medium to high numbers of different types of immobile biological features, which should increase the evenness values. However, Site 8 has higher mean within-site dissimilarity and thus has a lower evenness. Similarly, Sites 8 and 9 exhibit the highest richness, even though Site 9 has a much lower variability of within-site structure and fewer types of immobile biological features. However, Site 9 also has more types of sedimentary features and a lower mean within-site dissimilarity (both of which increase richness).

To best define the relationship between habitat structure, as measured by video, and macrofaunal diversity, we stratified our sampling to include as many samples from different habitats as possible. This was done at 2 different scales. Firstly, sites were chosen to reflect different levels of habitat structure generated by different features. For example, bare substratum could be mud or sand, but both represent a low level of structure. A higher level of structure would result from an area of horse mussel shells protruding from the sediment or from a mix of sand, diatom mats and sponges. Secondly, within-transect differences in habitat type were identified and samples were taken within each type. This second scale of sampling allowed us to investigate the importance of local variation in habitat structure (measured within 1 m of the core) in accounting for variation in macrobenthic diversity measured across sites (km scale). Small-scale heterogeneity is often important in accounting for variations in density, biomass and diversity in marine benthic assemblages (e.g., Thrush 1991, Blanchard & Bourget 1999). By including small-scale habitat structure, our sampling method increased the gradient of effect, and allowed the detection of a relationship with a minimum of samples at a variety of sites distributed over scales of kilometres.

The integration of small-scale variation into broader patterns is important because we might expect threshold effects and non-linearities in multi-species biotic and environmental processes that create biodiversity. For example, differences in density and species amongst a functionally similar group of bioturbators had different effects on biodiversity (Widdicombe & Austen 1999). Cummings et al. (2001) demonstrate the potential for different responses of macrobenthic assemblages to the presence of a large epifaunal bivalve under a number of different physical regimes and local species pools. Regardless of the potential complexity of underlying processes, we found strong relationships between diversity and habitat structure

using relatively simple measures of structure. Rather than emphasising the need to improve our understanding of small-scale variability to resolve the nature of factors affecting benthic community structure and function (i.e., biodiversity), we tried to scale-up and identify general patterns. We did this by summarising within-site patterns to avoid noise and be able to assess emergent patterns while still retaining information at the fine-scale resolution (Hewitt et al. 1998).

Our results also enabled us to assess the utility of using seafloor video images as a surrogate for direct estimates of macrobenthic diversity. The regression models relating macrobenthic diversity to habitat structure provide evidence that the video images were a good surrogate. However, we also carried out a direct comparison between the macrofaunal communities observed in each core with observations of the seafloor around the core samples. Unlike the habitat structure analyses, this analysis included abundances of the different features and also mobile features such as epibenthic predators and grazers. The 2 multivariate datasets were significantly related, indicating that seafloor video imagery could be used as a surrogate for direct measures of macrobenthic diversity. This has real value for developing rapid assessment strategies for soft-sediment habitats, particularly as video imagery of the seafloor can be carried out over large distances and at great depth. Recently, effort has been put into finding surrogates to increase our ability to rapidly assess large areas. Ward et al. (1999) found that habitat-level surrogates were useful for initial identification of marine reserves, while plant assemblages were poor surrogates for overall species richness. This is consistent with our results that emphasise elements of both biotic and physical heterogeneity and complexity. Being able to rapidly assess diversity at relatively fine resolutions would minimise the possibility of missing important diversity hot-spots in the landscape when mapping-unit resolution is too coarse (Stohlgren et al. 1997).

Our results have important implications for assessing the consequences to marine biodiversity of broad-scale disturbance events that remove epifauna and homogenise sediment characteristics. We found local variation in surficial sediment characteristics and the presence of other immobile features, many of which are biogenic, to be strongly related to diversity. As macrobenthic diversity makes a significant contribution to marine biodiversity (Gray 1997, Snelgrove 1999), our results suggest that relatively sparse elements of habitat structure can have important implications for resource management and conservation. Many types of broad-scale disturbance modify these features of soft-sediment habitat structure (Ellis et al. 2000). In particular, the disturbance and removal of epifauna

and homogenisation of small-scale variability in sediment characteristics has been reported from studies of trawling and dredging (Mayer et al. 1991, Dayton et al. 1995, Jennings & Kaiser 1998, Thrush et al. 1998, Auster & Langton 1999). Removal of habitat structure can, therefore, be anticipated to not only decrease macrobenthic diversity but also the more general biodiversity of the marine system. Given the spatial extent of marine soft-sediment habitats and the extent to which these habitats are subject to intensive bottom-fishing (FAO 1997), creating marine protected areas is unlikely to be sufficient to maintain and enhance biodiversity. Integrated and spatially explicit schemes that actively manage marine habitats are necessary (Ray 1996, Gray 1997, Auster & Langton 1999).

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