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Evaluation of the New Zealand Marine Environment Classifications using Ocean Survey 20/20 data from Chatham Rise and Challenger Plateau.

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Environmental classifications are potentially useful tools for summarising broad-scale spatial patterns in ecological and environmental gradients, particularly when biological data are limited in availability. Such classifications can be tuned with respect to specific faunal groups, but their usefulness depends on the validity of the assumption that biological distributions are correlated with gradients in the biophysical environment. Two marine environment classifications with relevance to benthic invertebrate distributions have been developed for New Zealand's Exclusive Economic Zone (EEZ): the Marine Environment Classification (MEC) and the Benthic Optimised Marine Environment Classification (BOMEC). Until now, however, the ability of the MEC and the BOMEC to map benthic habitats and fauna has not been evaluated against independent sample data.

We used benthic invertebrate faunal data from video and epibenthic sled samples collected during Ocean Survey 20/20 (OS 20/20) surveys of Chatham Rise and Challenger Plateau to assess whether the MEC and BOMEC provide a reliable means of mapping benthic habitats and faunal assemblage composition. We also generated a new environmental classification ("Chat/Chall"), tuned solely to the OS 20/20 sample data, to assess the effect of sampling of this type on classification performance.

First, we compared the three environmental classifications (MEC, BOMEC, and Chat/Chall) with the OS 20/20 sample sites assigned to a set of 12 biotic habitats which were derived independently by clustering of the faunal data alone. Comparisons were made both visually and using chi-squared tests of goodness-of-fit. Second, using the full multivariate detail of the OS 20/20 faunal data, we used ANOSIM R and homogeneity statistics to assess how well each classification grouped the OS 20/20 sites at all classification levels up to 60 classes. Third, we compared how well each of the environmental classifications grouped the OS 20/20 sample sites in relation to a set of univariate biodiversity metrics calculated for each site from the sample data.

None of the three environmental classifications discriminated well between biotic habitats at the site level, but visual comparisons showed consistent patterns which broadly matched distributions of the biotic habitats at larger spatial scales (100–1000 km) in all classifications except the MEC at the 20-class level. These patterns included differentiation between Chatham Rise and Challenger Plateau, and between the north and south flanks of Chatham Rise. ANOSIM R and homogeneity statistic values were low for all three classifications at all class levels, indicating poor ability to map benthic distributions at the spatial scale and taxonomic resolution of the OS 20/20 samples. The classifications also showed poor ability to discriminate the OS 20/20 sites on the basis of biodiversity metrics. The BOMEC and Chat/Chall classifications were generally similar in performance and both were better than the MEC.

Our main conclusions from these results are: (1) the BOMEC is an improvement over the MEC for mapping benthic distributions; (2) neither the BOMEC nor the MEC provide reliable information at the spatial scale of individual OS 20/20 sample sites; (3) at larger spatial scales (ca. over 100s km) both MEC and BOMEC classifications produced patterns that were broadly consistent with sampled benthic distributions, suggesting that they might have applications in regional-scale assessment of benthic habitats; (4) to be useful in management or planning applications, objective criteria for determining appropriate, ecologically relevant, classification levels and spatial scales are needed, and (5) further OS 20/20-style surveys could be effective for expanding the scope and generality of existing marine environment classifications.

INTRODUCTION

The size of New Zealand's Exclusive Economic Zone (EEZ), about 4.2 million km^2 and the lack of ecological data across it (Gordon et al. 2010) provide a challenge for understanding ecosystem processes and management of marine resources. Environmental classifications are a potentially useful tool for summarising broad-scale spatial patterns in ecosystem character, particularly when biological data are limited in availability (Pressey et al. 2000, Leathwick et al. 2011), and a number of initiatives have been taken to define biologically relevant marine environmental classifications for New Zealand. Such classifications map the distributions of biota or habitats on the assumption that these distributions are correlated with gradients in environmental variables such as depth, temperature, and salinity. Classifications can be tuned with respect to specific taxonomic groups (e.g., Leathwick et al. 2006a, Snelder et al. 2007a), and are generally represented as discrete classes because these are more practical for management than are representations of continuous gradients. The actual number of classes used (the 'class level'), however, can vary depending on the specific application and the spatial scale at which the classification is applied (Leathwick et al. 2009). Although environmental classifications have been successful in the terrestrial realm (Pressey et al. 2000, Ferrier et al. 2002/2004, Snelder & Hughey 2005, Leathwick et al. 2011), to date, they have not been widely used in marine environments. Reasons for this include the difficulty of obtaining representative samples of the fauna, and the relatively recent availability of suitably detailed broad-scale environmental layers (Antonov et al. 2005, Locarnini et al. 2005).

In New Zealand, the first marine classification initiative was the Marine Environment Classification (MEC, Snelder et al. 2007b). The MEC was defined based on the weighting and transformation of gridded environmental variables that best correlated with the distribution of demersal fish assemblages, surface chlorophyll-*a* concentrations, and a limited set of benthic invertebrate data (Snelder et al. 2007b). Thus, it described environmental patterns influencing both benthic and pelagic faunal distributions. Leathwick et al. (2006a) also developed an environmental classification tuned specifically in relation to demersal fish, using detailed and extensive biological data from research trawl records. This performed better than the MEC in terms of how well environmental classes matched sampled fish distributions. However, this was primarily because of the high sampling density and broad spatial coverage of the fish data, which contrast strongly with the situation for benthic invertebrates for which data are both sparse and patchy. These authors also compared this environmental classification with a biologically-defined classification based directly on distribution models for individual fish species and concluded that, where detailed biological data are available, a biologically defined classification will be superior to an environmental classification (Leathwick et al. 2006a/2006b). Where detailed data are not available, however, environmentally based classifications remain the most promising approach.

Most recently, a classification tuned specifically with respect to benthic invertebrate distributions has been defined: the benthic optimised marine environment classification (BOMEC) (Leathwick et al. 2009). Compared to the MEC, the BOMEC used more detailed data on benthic faunal distributions, together with additional seabed environmental layers, (e.g., temperature at the seabed, sediment type, and seabed relief). The BOMEC also used generalised dissimilarity modelling (GDM, Ferrier et al. 2007) which is a more refined statistical approach to weighting and transforming environmental variables with respect to community composition. The overall aim of both the MEC and BOMEC classifications was to classify New Zealand's marine environments for resource and conservation management (Snelder et al. 2007b, Leathwick et al. 2009). However, neither the MEC nor the BOMEC have yet been evaluated by reference to independent sample data.

In this study, we used benthic invertebrate faunal data from video and epibenthic sled samples collected during extensive Ocean Survey 20/20 (OS 20/20) surveys of Chatham Rise and Challenger Plateau (Nodder 2008, Bowden 2011) to examine the extent to which the MEC and BOMEC provide a reliable means of mapping benthic habitats and faunal assemblage composition. We also generated a new environmental classification ("Chat/Chall") tuned solely by reference to the OS 20/20 sample data in order to assess the effect of planned benthic surveys on classification performance. The analyses were in three parts. First, we compared the three environmental classifications (MEC, BOMEC, and Chat/Chall) with the OS 20/20 sample sites assigned to a set of 12 biotic habitats which were derived independently by clustering of the OS 20/20 faunal data alone (Hewitt et al. in press). Comparisons were made both visually and using chi-squared goodness-of-fit tests. Second, using the full detail of the OS 20/20 faunal data, we used ANOSIM R and homogeneity statistics to assess how well each classification grouped the OS 20/20 sites into discrete classes at all classification levels up to 60 classes. Third, we compared how well each of the environmental classifications grouped the OS 20/20 sample sites in relation to a set of biodiversity metrics calculated for each site (NIWA unpublished data).

The overall objective of this research was to determine if environmental classification schemes based on remote-sensed and modelled data can be used to predict seabed community composition, function, and diversity. Specifically, we aimed to assess the extent to which the 2005 Marine Environment Classification and subsequent variants can provide cost-effective, reliable, means of assessing biodiversity at the scale of the Ocean Survey 20/20 surveys.

METHODS

1.1 Benthic invertebrate sample data

Research voyages in April and June 2007 collected samples of benthic invertebrate fauna at 100 sites on Chatham Rise and 49 sites on Challenger Plateau as part of the New Zealand's Ocean Survey 20/20 initiative (Nodder et al. 2007, Bowden 2011). Several sampling methods were used but the minimum sampling effort at each site was one seabed video transect using NIWA's Deep Towed Imaging System (DTIS, ca. 1500 m^2 swept area per transect), and one epibenthic sled sample using NIWA's 'Seamounts sled' (SEL, 25 mm mesh, ca. 1000 m^2 swept area per transect). These methods both sample primarily larger epifauna (over 50 mm body size for video, over 25 mm for sled samples), with some shallow infaunal taxa also caught in sled samples. All benthic invertebrate fauna in all samples were identified to the finest achievable taxonomic level and counted. For sled samples, most specimens were identified to species level, whereas for video samples this was often not possible, resulting in a range of taxonomic levels in the final data set. Data from the video were more reliably quantitative than those from the sled, for which sampling efficiency cannot be ascertained. Full details of all data sets from the Chatham-Challenger OS 20/20 voyages are given in Bowden (2011). For comparisons with environmental classifications in the present project, we used only the video and sled data from the OS 20/20 surveys because they have the greatest sample density across the Chatham-Challenger area, coupled with the finest taxonomic resolution and most consistent identifications. These data sets were collected over a three month period using standardised methods of collection and analysis across the entire area, and therefore have a high degree of internal consistency. Thus, they are particularly useful for description of spatial patterns in benthic assemblage composition, and for evaluation of predictions arising from existing environmental classifications.

1.2 Classification methods

1.2.1 Marine Environment Classification

The MEC was defined using 15 environmental variables (Table 1) which were tuned with respect to three biological datasets (demersal fish, surface chlorophyll-*a*, and limited benthic invertebrate data). Mantel tests (Mantel 1967) were used to identify the best weightings and transformations of the environmental variables to improve correlation with the biological data (Snelder et al. 2007a). The Gower metric was used as a measure of inter-site environmental distance, and Bray-Curtis dissimilarities were used to measure biological distances between sites. Groupings of the transformed and weighted environmental variables were made using a two-stage clustering analysis; initially a non-hierarchical clustering procedure (ALOC, Belbin 1995 in Snelder et al. 2007a), followed by hierarchical clustering (flexible UPGMA, Lance & Williams 1967 in Snelder et al. 2007a). In total, 290 hierarchical class levels were defined and the classification was made available to end users across the full range of class levels (i.e., from 2 to 290 classes).

1.2.2 Benthic Optimised Marine Environment Classification

The BOMEC was defined using 12 environmental variables (Table 1) and 8 taxonomic groups: asteroids; bryozoans; foraminiferans; fish; octocorals; polychaetes; scleractinians, and sponges. Data for each of these groups were compiled from museum records, research surveys, and taxonomic experts, and species present at fewer than five sites were removed from the analysis. GDM was used for the classification.

GDM uses matrix regression techniques that accommodate the curvilinear relationship between environmental and biological distances to model the rate of species turnover along an environmental gradient and to identify the main gradients along which species composition changes (Ferrier et al. 2007). Based on these modelled responses, GDM then transforms and weights the environmental gradients so that they are maximally correlated with the observed biological data. The transformed environmental space is then clustered. The clustering procedure provides a means of subdividing the transformed environmental space into discrete classes. Classes are organised hierarchically such that higher levels of classification divide the overall area into progressively more classes.

Biological distances were defined as Bray-Curtis dissimilarities based on presence absence data. Transforms from the GDM for each of the eight taxonomic groups were then applied separately to the raw environmental data, and values were averaged for the eight transformed matrices (Leathwick et al. 2009). The resulting matrix of transformed environmental variables was then clustered using a two-stage procedure because of the large size of the dataset. In the first stage, a non-hierarchical medoid clustering procedure (*clara*, in the R cluster library) identified 300 groups, using the Manhattan metric as a distance measure. The second stage of the clustering was performed on the average values of these 300 groups using flexible UPGMA, as implemented in PATN (Belbin 1991 in Leathwick et al. 2009). On completion, the results were imported into a geographic information system (GIS) for display (ArcGIS 9.3). The GDM analysis identified depth as the most important variable contributing to compositional turnover, followed by temperature and salinity (Figure 1).

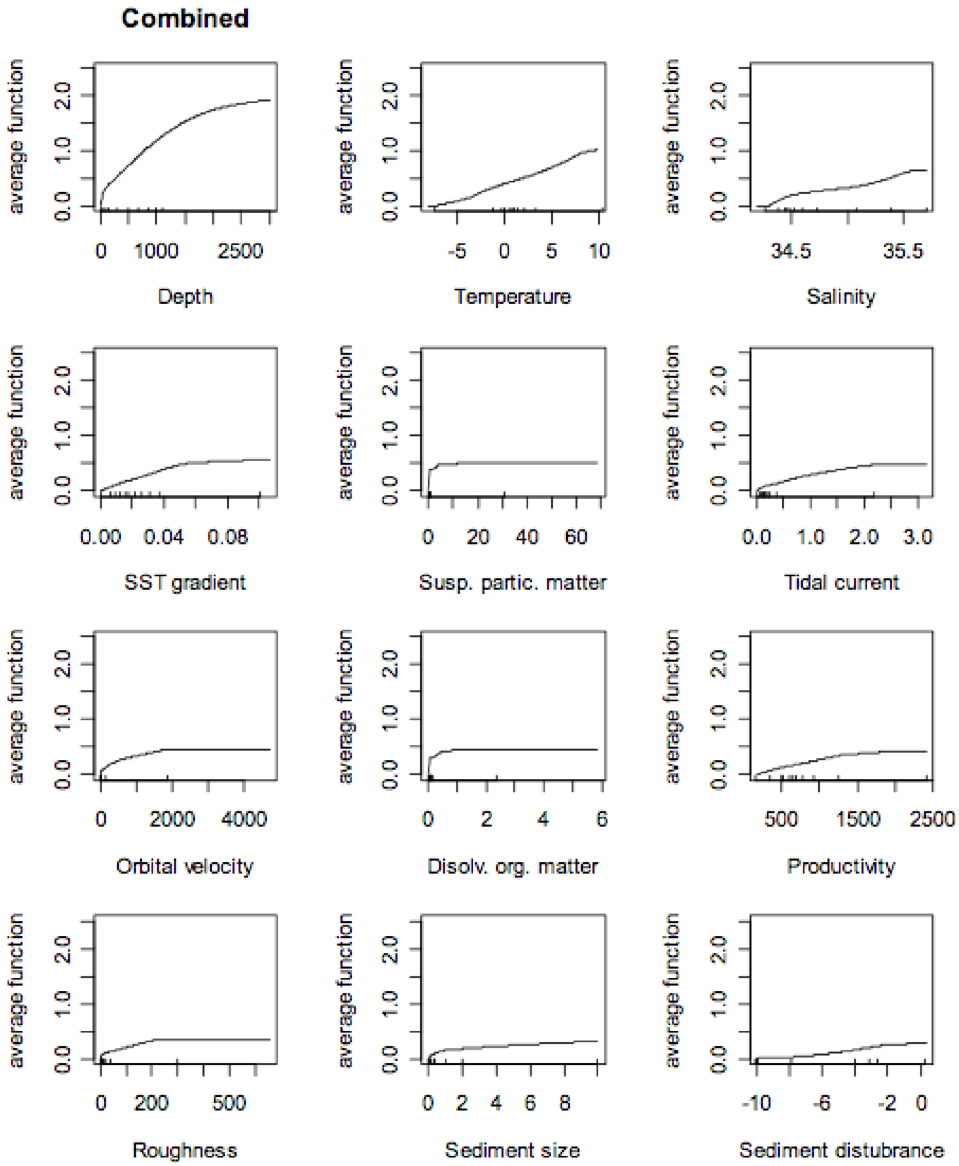

Figure 1: BOMEC classification: the relative influence of environmental variables explaining benthic invertebrate assemblage composition is shown by the height of the response curves. These are the average functions (across 8 taxonomic groups for each variable) that describe the relationship between species turnover and environment (figure taken from Leathwick et al. 2009). See Table 1 for a description of variables and abbreviations.

1.2.3 Chatham Challenger classification

The Chatham Challenger classification (Chat/Chall) was defined for this analysis using benthic invertebrate data from the OS 20/20 video and epibenthic sled samples, which were combined for this analysis. The same GDM and clustering procedures as described above for the BOMEC were used, except that five environmental variables (orbital velocity; suspended particular matter; dissolved organic matter; sediment size and sediment disturbance) were dropped from the analysis because they either did not show a strong response, or were strongly correlated with other environmental variables. The fitted response of the explanatory variables (Figure. 2) did not change significantly after removal of these variables and depth was, again, the most important variable. To define the Chat/Chall classification, half of the OS 20/20 sites were sampled at random and modelled with respect to the environmental variables using GDM. The fitted functions from the GDM were used to transform the environmental variable values in each grid cell, and these were then clustered to make 300 hierarchical classes across the EEZ. Although the Chat/Chall classification was extended over the entire EEZ, and thus well beyond the sampled domain of the OS 20/20 data, which is unlikely to produce ecologically realistic results, this did not affect comparisons with the other classifications because all classifications were assessed only by reference to the OS 20/20 sites. Data from the OS 20/20 sites that were not included in development of the Chat/Chall classification were used to test classification performance.

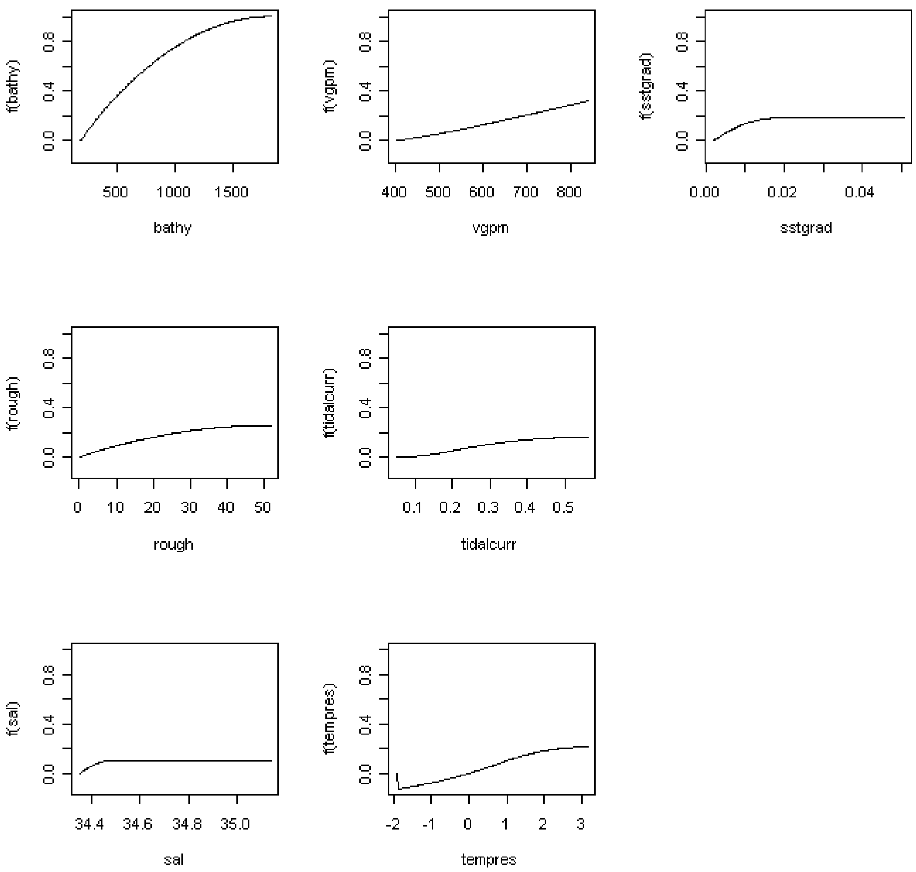

Figure 2: Chatham-Challenger classification: the relative influence of environmental variables explaining benthic invertebrate assemblage composition is shown by the height of the response curves. See Table 1 for a description of the variables and abbreviations (note, some abbreviations used in this model differ from those used in the BOMEC, see Table 1).

Table 1: Environmental variables used in the three classifications evaluated here: MEC, BOMEC, and Chat/Chall.

Abbreviation	Variable	MEC	BOMEC	Chat/Chall
bathy *or* depth	Depth/bathymetry	✓	✓	✓
Rad_mean	Mean solar radiation	✓		
Rad_wint	Winter solar radiation	✓		
SSTwint	Winter sea surface temperature	✓		
SSTanamp	Annual amplitude of sea surface temperature	✓		
SSTanom	Summer time sea surface temperature anomaly	✓		
Orb_v_95	Extreme orbital velocity	✓		
Sed (MEC)	Sediment type	✓		
Bed_prof	Rate of change of slope	✓		
Bed_curv	Seabed curvature	✓		
Bed_plan	Seabed planform curvature	✓		
FW	Freshwater fraction	✓		
Temperature *or* tempres	Depth corrected bed temperature		✓	✓
Salinity *or* sal	Salinity at seafloor		✓	✓
Roughness *or* rough	Roughness or rugosity at the sea bed		✓	✓
Orbital velocity	Mean orbital velocity	✓	✓	
Dissolv org matter	Dissolved organic matter		✓	
Sst gradient *or* sstgrad	Spatial gradient annual mean sea surface temperature	✓	✓	✓
Productivity *or* vgpm	Surface water productivity as estimated by a vertically generalised productivity model		✓	✓
Suspended partic matter	Suspended particular matter		✓	
Tidal current *or* tidalcurr	Tidal current	✓	✓	✓
Sediment size	Sediment grain size		✓	
Sediment disturbance	Resuspension of sediment		✓	

1.3 Classification testing

1.3.1 Comparisons with OS 20/20 biotic habitats

An independent analysis of the OS 20/20 benthic invertebrate faunal data (Hewitt et al. in press) classified the OS 20/20 sampling sites into 19 biotic habitats. Briefly, this was done by clustering faunal abundance data from the OS 20/20 seabed video transects. Data were log-transformed and faunal assemblage dissimilarity between sites was calculated as Modified Gower distances (Anderson et al. 2006). Sites were then classified into the 19 biotic habitats using group-average clustering. The ecological validity of the groupings was assessed using a range of criteria including expectations that (1) neighbouring sites would be in the same biotic habitat, and (2) that where this was not the case, changes would coincide with changes in environmental gradients (Hewitt et al. in press). There were pronounced differences in the distributions of biotic habitat between Chatham Rise and Challenger Plateau, and between the north and south flanks of Chatham Rise (Table 2). Less pronounced patterns included differences between east and west ends of Chatham Rise, and generally greater levels of shared habitats between Chatham Rise and Challenger Plateau with increasing depth (Hewitt et al. in press).

Table 2: Distribution of biotic habitats (B1, B2, … , m19) , as defined by Hewitt et al. (Hewitt et al. in press) across Chatham Rise and Challenger Plateau. Values are the numbers of OS 20/20 sampling sites in each biotic habitat.

Biotic habitat	Chatham Rise		Challenger Plateau
	North	South	
B1		6	1
B2	12		
B3			18
B4	6	9	
B5	4	23	
B6	2	4	
B7	7	1	7
B8	7	1	9
B9	13	1	3
m10	3		
m11		2	
m12			1
m13		2	
m14		1	
m15	1		
m16	1		
m17			1
m18	1		
m19	1		

First, we made visual comparisons between these biotic habitats and the three environmental classifications (MEC, BOMEC, and Chat/Chall) at three classification levels: 20, 50, and 150 classes. Maps were produced for each of the three classifications at each class level, and the OS 20/20 sampling sites labelled with their biotic habitats were then overlaid on them. This enabled visual evaluation of the correspondence between classes defined by the classifications and assemblage groupings from the OS 20/20 sample data.

We then statistically tested the match between the biotic habitats and classes defined by the three classifications. For these tests, we first selected the class level of each classification that divided the

OS 20/20 Chatham Rise and Challenger Plateau survey area in to about 12 groups; this being the number of the biotic habitats that contained more than one OS 20/20 sampling site (Table 2). It was not possible to find hierarchical class levels that produced exactly 12 groups across the Challenger/Chatham area for each of classification methods. For the MEC, BOMEC, and Chat/Chall classifications, hierarchical class levels of 70, 30, and 19, respectively, resulted in 10, 10, and 13 classes, respectively, within the Chatham Rise Challenger Plateau OS 20/20 sample region. We then used χ^2 goodness-of-fit tests to determine how consistently each of the three classifications placed sites in the same biotic habitats into one environmental class. Thus, the expected value in each test is that all sites belonging to the same biotic habitat will fall in a single environmental class. By comparing this value with the actual value, a test statistic (χ^2) is generated and compared to its known distribution at the appropriate number of degrees of freedom.

1.3.2 Comparisons with full community composition data

To assess the ability of the three classifications to discriminate the full detail of benthic community data in the OS 20/20 test data (as opposed to the biotic habitat groups used above), the classes within each hierarchical class level from each of the three classifications were linked to the full-detail OS 20/20 faunal data in ArcMap 9.3 using the "Intersect Point Tool" in Hawth's Tools (www.spatialecology.com). Two different measures of classification strength were then used to compare how well each classification grouped the faunal data into discrete classes: the homogeneity statistic and the ANOSIM R statistic.

The homogeneity statistic is a measure of the difference between the average biological distance between all pairs of sites within an environmental class and the average biological distance between all sites (Bedward et al. 1992). It is computed as:

$$\text{Homogeneity statistic} = 1 - D_{\text{class av}}/D_{\text{av}},$$

where D_{av} is the average distance between all sites (no classes) and $D_{\text{class av}}$ is the average distance between sites within the same environmental class. The homogeneity statistic ranges between 0 and 1, where 0 indicates that there is no difference between within-class and overall average distances, and values tending towards 1 indicate that within-class distances are distinct from the overall average distances. Thus, for an environmental classification, higher values indicate greater separation of sample data within environmental classes.

Analysis of similarities (ANOSIM, Clarke 1993) uses a test statistic, R, which can be used as a measure of relative dissimilarity between groups of sites in different classes. The statistic is calculated as the difference in average ranked biological dissimilarities arising from all pairwise comparisons between all sites (r_B), and all pairwise comparisons between sites within the same class (r_W), adjusted by the total number of sites:

$$R = (r_B - r_W)/(n\ (n-1)/4)$$

where n is the total number of sites. R is scaled to range between -1 and 1. A value of 0 occurs when there is no difference in average dissimilarities between sites inside and outside classes, and a value of 1 occurs when all sites within classes are more similar to each other than to sites in other classes. A value of -1 would result from the improbable scenario where all sites within a class were more similar to sites outside of their class than to others within it (Chapman & Underwood 1999).

All biological distances were calculated as the presence-absence Bray-Curtis measure of compositional dissimilarity. Because the test data had few species in common across all sites (i.e., there were many joint absences) we extended the dissimilarities using an iterative flexible shortest path adjustment (FSPA) (following De'Ath 1999). FSPA uses the matrix of dissimilarities produced for all pairs of sites with species in common to estimate dissimilarities for sites with no species in common. Using a pair of sites with no species in common, FSPA finds an intermediate site, which shares a species with each member of the pair and also has the shortest ecological distance to the pair with no shared species, and then sums the dissimilarities of all three sites (De'Ath 1999). To reduce bias, we excluded environmental classes which contained fewer than five test sites.

To evaluate the ability of the MEC and BOMEC to discriminate the OS 20/20 faunal assemblage data, we first calculated homogeneity and ANOSIM R statistics for each of these two classifications up to 60 class level using faunal data from the full set of OS 20/20 sampling sites. To evaluate the differences in performance between the three environment classifications (i.e., including Chat/Chall), we recalculated homogeneity and ANOSIM R statistics for each using the half of the OS 20/20 faunal data that was not used to generate the Chat/Chall classification. Confidence intervals were calculated using a resampling procedure similar to bootstrap estimation. Bootstrapping, which normally involves taking repeated samples with replacement, is not effective when used with distance matrices because the distance between a sample and itself is zero. Instead, we made 150 subsets of the test data by randomly selecting 90% of the data, without replacement, and calculating the test statistic for each subset (Goslee & Urban 2007). The 5^{th} and 95^{th} confidence intervals were then estimated from the distribution of the test statistics. The conservative assumption is that significant differences in classification performance exist when the confidence intervals do not overlap.

Although we compare similar hierarchical class levels between the three classifications, the number of classes represented within the Chatham-Challenger area at each hierarchical classification level will differ because we are examining only a sub-area of an entire EEZ classification. For instance, within the Chatham-Challenger OS 20/20 sampling area there might be 26 classes in the 50 class-level of the MEC and 35 classes in the 50 class-level of the BOMEC. The difference in the number classes at each hierarchical class level means that the comparison of interest is between the maximum values of the test statistics achieved at any class level for each classification, rather than direct comparisons at individual class levels.

Because the BOMEC was defined using the EEZ boundary, OS 20/20 sites outside the EEZ (i.e., the northwestern section of the Challenger Plateau) were excluded from these tests. All analyses were performed in R (R Development Core Team 2008) using *gdm* (Ferrier et al. 2007), the EnvClass 1.3 Library and the *vegan* package (Oksanen et al. 2010).

1.3.3 Comparisons with diversity metrics

We compared how well each of the environmental classifications (MEC, BOMEC, and Chat/Chall) divided the Chatham Rise and Challenger Plateau OS 20/20 sample sites in relation to a suite of five biodiversity metrics calculated from the OS 20/20 video faunal data at each sampling site. The biodiversity metrics used were: taxon richness (S), Margalef's evenness (J'), Simpson's index ($1-\lambda'$), the proportion of taxa rare in abundance (S_{RA}), and the number of infrequently occurring taxa (S_{RF}). In addition to the three environmental classifications, we included the *biotic habitat* groups described above as a reference classification, with the expectation that these would best match the diversity metrics because they are derived directly from the same sample data. In much the same way as the comparisons of community composition above, a global test statistic was used to quantify the difference between within- and between-class similarities for each diversity index. Initially we intended to use the global F-statistic from a general linear model for this, but neither S nor S_{RF} met the test assumptions. For this reason, the statistic used was the model deviance divided by the error deviance computed from one-way Generalised Linear Models, using the appropriate error structures.

RESULTS

1.4 Comparisons with OS 20/20 biotic habitats

1.4.1 Visual comparisons

At larger spatial scales (over about 100 km), there was correspondence between the distribution of biotic habitats and the environmental classes defined by each of the three classifications. At the 50 and 150 class levels, all three classifications differentiated between the Chatham Rise and the Challenger Plateau, while at the 20 class level, only the MEC did not make this distinction. Similarly, all three classifications defined more environmental classes across Chatham Rise than Challenger Plateau, corresponding with broad patterns in the distribution of biotic habitats (Table 2). They also showed that while the Chatham Rise and Challenger Plateau have different environments at shallow depths, they are likely to share similar communities in deeper waters. Within the Chatham Rise, further correspondence with biotic habitats was apparent in that the BOMEC and Chat/Chall classifications differentiated between the north and south flanks of the rise. For the MEC, this distinction was apparent only at the 150 class level. At finer spatial scales, however, there was little evidence of correspondence between individual biotic habitats and environmental classes from any of the classifications at any of the three class levels.

In these comparisons, it was apparent that higher class levels of the MEC were more similar to lower class levels of the BOMEC and Chat/Chall classifications. For instance, the MEC at 150 classes had more similarities with the BOMEC at 20 classes than did the MEC at 20 classes (Figures 3 and 5). This is related to the spatial scale at which each classification was originally formulated, and to the spatial resolution of sample data used to tune them. The MEC encompasses the largest area (from 25° S to 57° S and from 158° E to 168° W), whereas the BOMEC is restricted to the EEZ boundary, and sample data for the Chat/Chall classification are at finer spatial resolution and come only from the Chatham-Challenger region. These factors result in different numbers of environmental classes being defined within the Chatham Rise and Challenger Plateau OS 20/20 survey area for each classification at any given overall class level. At the 20 class level (Figure 3) there are: 13 classes of the Chat/Chall classification, 8 classes of the BOMEC, and 5 classes of the MEC. At the 50 class level (Figure 4), there are 23 classes of the Chat/Chall classification; 12 classes of the BOMEC, and 8 classes of the MEC. At the 150 class level (Figure 5) there are: 44 classes of the Chat/Chall classification; 34 classes of the BOMEC, and 16 classes of the MEC.

At higher class levels (Figure 5), the BOMEC and Chat/Chall classifications were increasingly defined by depth gradients; depth being the variable with the biggest contribution in the GDM models (Figures 1 and 2). Although GDM-based environment classifications subdivide environmental space and increase the discrimination of community composition by organising the classes hierarchically, there is a point at which increased classification detail exceeds the capacity of the data to differentiate ecologically meaningful community composition changes. Previous studies suggest that this can occur above about 60 hierarchical class levels (Snelder et al. 2009), and based on this result we restricted further examinations of the three environmental classifications to class levels of under 60 classes.

1.4.2 Statistical comparisons

In statistical tests of goodness-of-fit, none of the environmental classification schemes discriminated well between the biotic habitats at the spatial scale of individual OS 20/20 sample sites. With few exceptions, OS 20/20 sample sites belonging to a single biotic habitat were not assigned to a single classification group in any of the environmental classifications (Table 3, χ^2 = 11.8, 19.3 and 17.8 respectively for MEC, BOMEC and Chat/Chall, critical value $\chi^2_{11,\,0.05} = 4.57$).

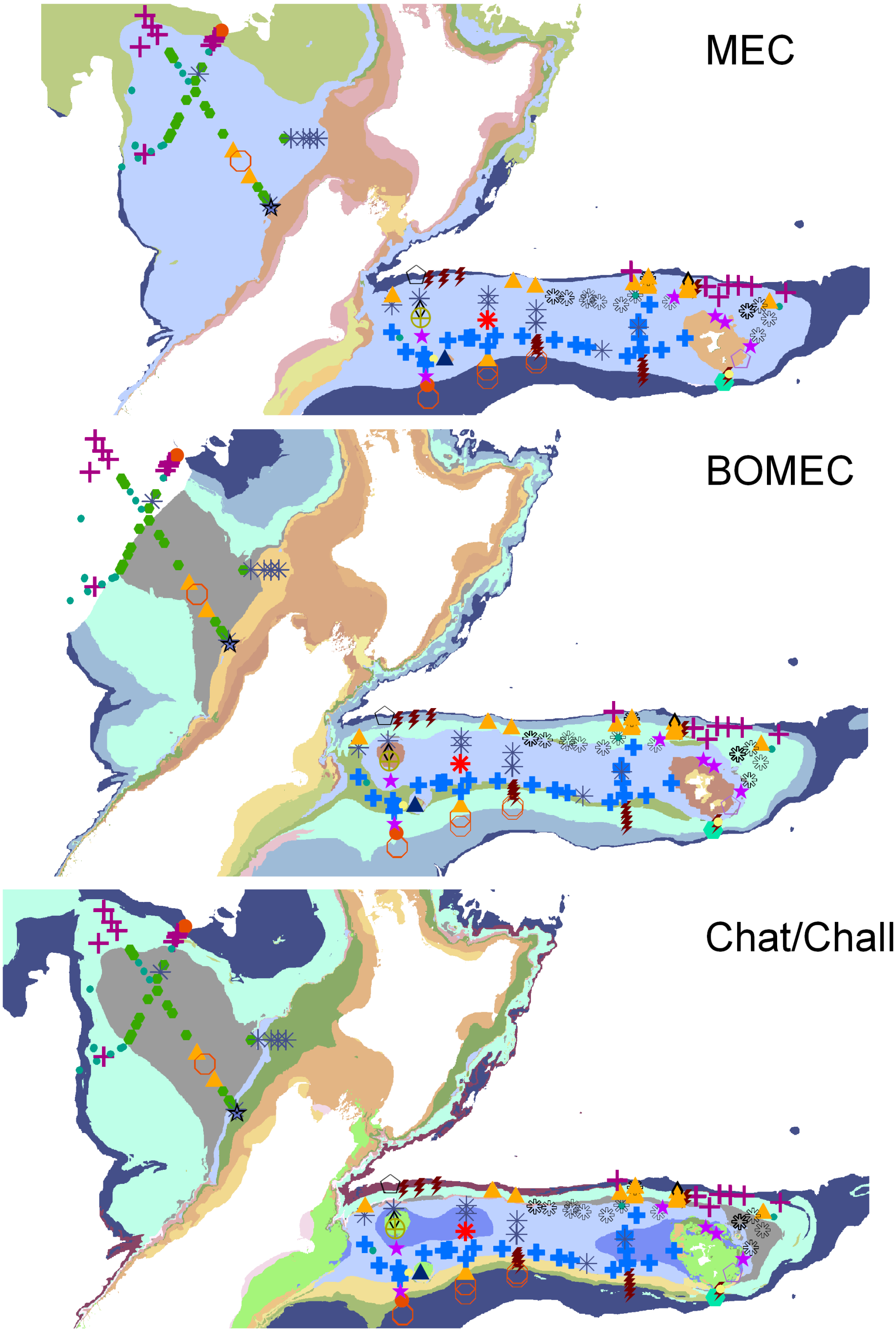

Figure 3: A comparison at the 20 class level of the three environmental classifications (MEC, Marine Environment Classification; BOMEC, Benthic Optimised Marine Environment Classification; Chat/Chall, Chatham-Challenger classification) with biotic habitat groupings (coloured symbols) which were derived independently by clustering of the OS 20/20 sample data; see section 2.3.1 for details.

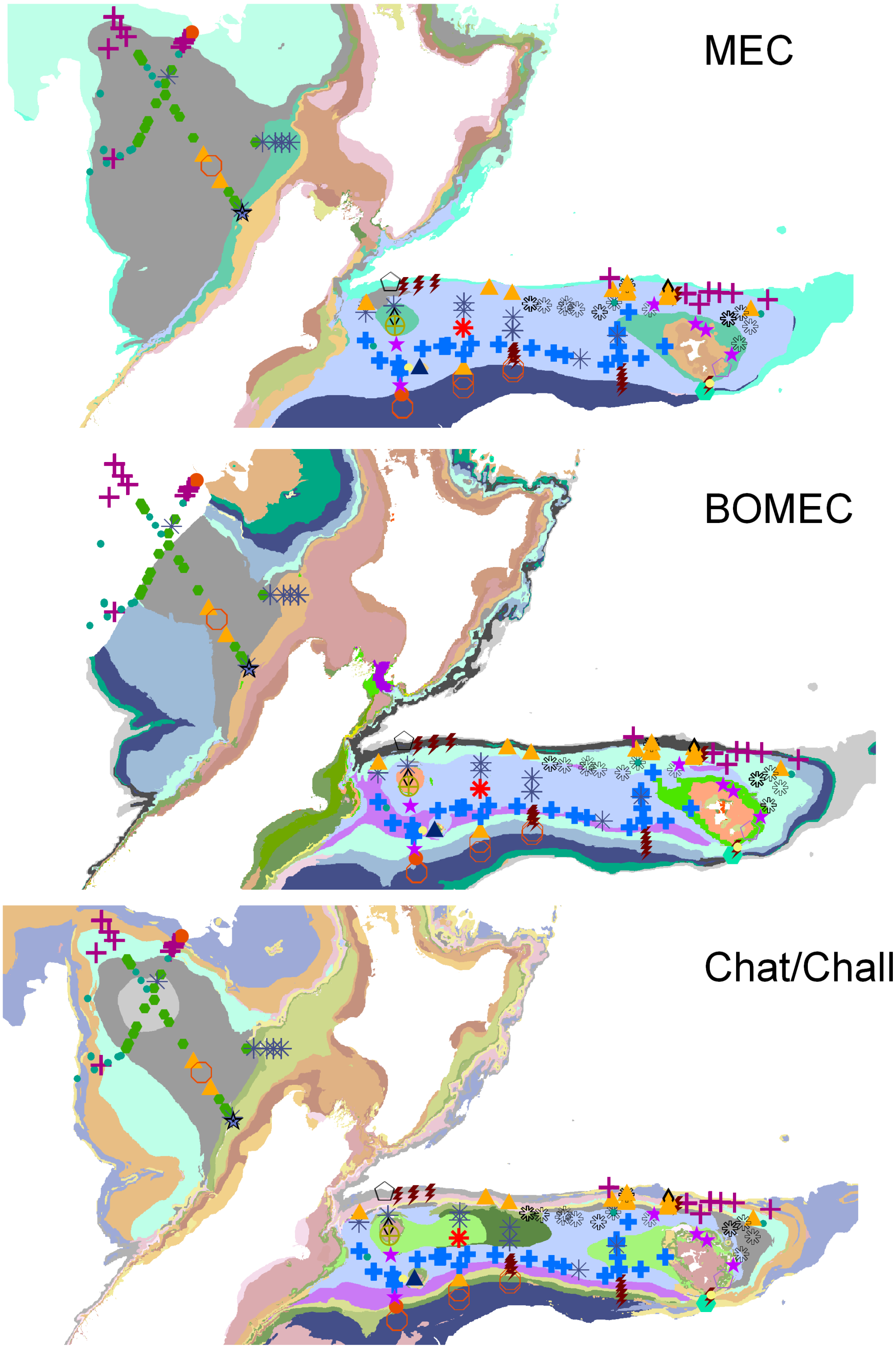

Figure 4: A comparison at the 50 class level of the three environmental classifications (MEC, Marine Environment Classification; BOMEC, Benthic Optimised Marine Environment Classification; Chat/Chall, Chatham-Challenger classification) with biotic habitat groupings (coloured symbols) which were derived independently by clustering of the OS 20/20 sample data; see section 2.3.1 for details.

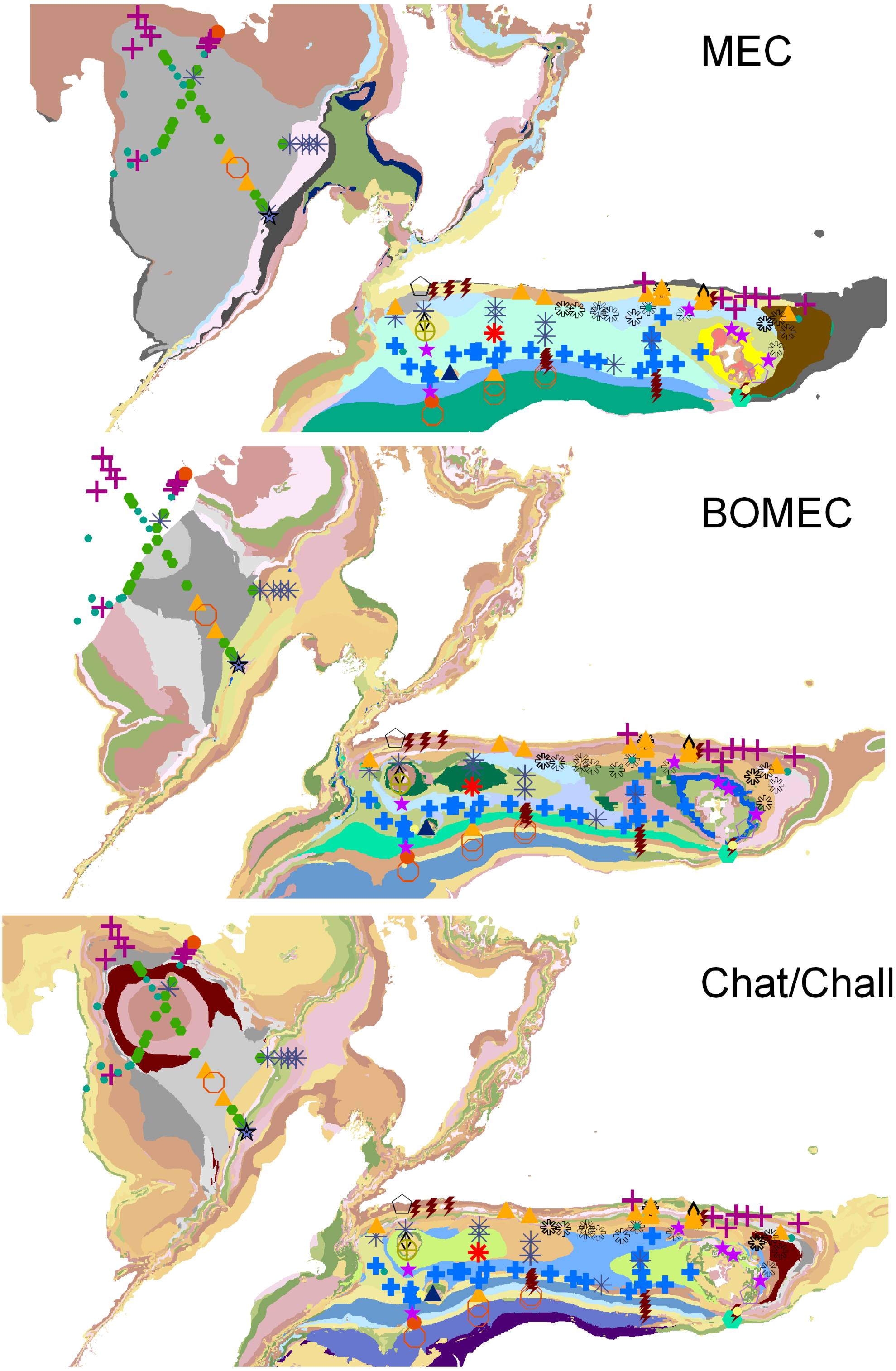

Figure 5: A comparison at the 150 class level of the three environmental classifications (MEC, Marine Environment Classification; BOMEC, Benthic Optimised Marine Environment Classification; Chat/Chall, Chatham-Challenger classification) with biotic habitat groupings (coloured symbols) which were derived independently by clustering of the OS 20/20 sample data; see section 2.3.1 for details.

Table 3: **Numbers of sites found in different OS 20/20 *biotic habitats* compared with their classification by the three environmental classifications: (a) Chat/Chall; (b) BOMEC; (c) MEC. Column labels (G prefix) are the environmental classes, row labels (B or m prefix) are the biotic habitats. Values are the number of OS 20/20 sample sites within each environmental class for each biotic habitat. Thus, in (a), of seven OS 20/20 sites in biotic habitat B1, six were in environmental class G1 and one was in G3. (Goodness-of-fit: χ^2 = 11.8, 19.3 and 17.8 respectively for MEC, BOMEC and Chat/Chall, critical value $\chi^2_{11,\,0.05} = 4.57$)**

(a) Chat/Chall classification

	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10	G11	G12	G13
B1	6		1										
B2			3					8	1				
B3			11					1					
B4	3			6	3		1				1		
B5								21		1			4
B6					1			1	1				3
B7								6	5		1		2
B8	2			4		1					1		
B9	1		3	12		1							
m10				2								1	
m11								1				2	
m13	1											1	

(b) BOMEC

	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10
B1	1	1		1						
B2		5				5				
B3	11									
B4		7			3	1				
B5		1				11	10			
B6		2				4				
B7	1	1	4			6				
B8		2		1	4					
B9	2	10			4					
m10					2				1	
m11							1		1	
m13		1						1		

(c) MEC

	G1	G2	G3	G4	G5	G6	G7	G8	G9	G10
B1		1					5			
B2					6	2			2	
B3		11								
B4					8	1	2			
B5						20		1		
B6					2	2		1	1	
B7		1	5		1	5				
B8	2				5					
B9		3			13					
m10			1		2					
m11						1		1		
m13				1			1			

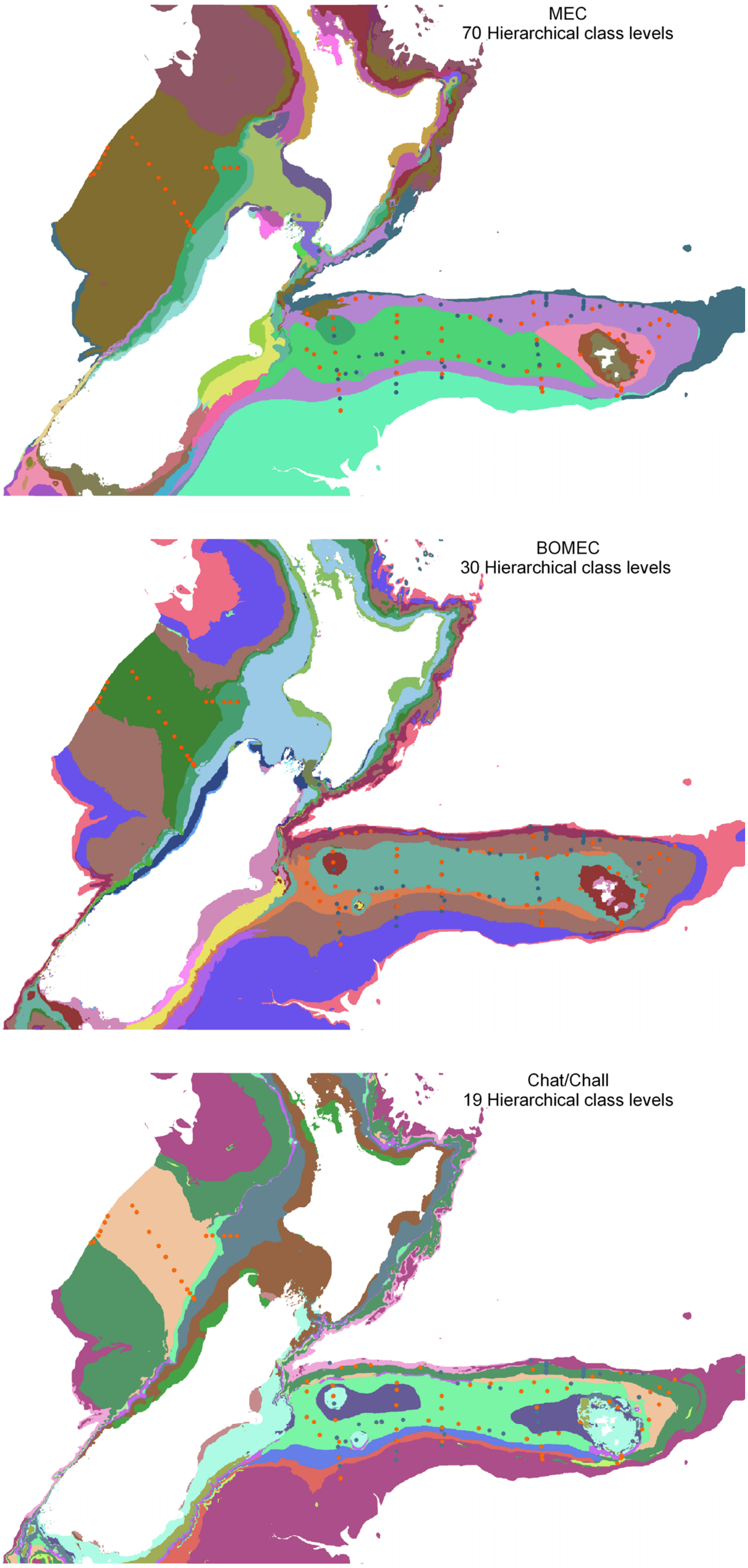

Figure 6: Three environmental classifications (MEC, BOMEC, and Chat/Chall) at overall class levels selected to result in ~12 classes being defined within the Chatham Rise and Challenger Plateau OS 20/20 sampling region (coloured dots show OS 20/20 sampling sites). Within the OS 20/20 region, the MEC at 70 class level has 10 classes; the BOMEC at 30 class level has 10 classes, and the Chat/Chall classification at 19 class level has 13 classes.

1.5 Comparisons with full community composition data

Values of the homogeneity statistic for the MEC and BOMEC calculated using the full OS 20/20 data were low (mean values under 0.04), indicating poor discrimination of community composition, but mean values were higher for the BOMEC than for the MEC at all class levels up to 60 (Figure 7, top). Homogeneity for the BOMEC increased steadily to about 25 class level and thereafter the rate of increase declined. For the MEC, the greatest increases in homogeneity came at about 33 and about 53 class levels, with uniformly low values below about 30 class level. In comparisons of all three classifications calculated using only half of the OS 20/20 sample data (to enable inclusion of the Chat/Chall classification), all homogeneity statistic values were again low (mean values under 0.04) and had greater variability around the mean values than when using the full sample data (Figure 7, bottom). The MEC classification had the lowest average performance but again improved beyond the about 53 hierarchical class level. Of the three classifications, the BOMEC had on average the highest performance, followed closely by the Chat/Chall classification, the two classifications having very similar performance at about 30–40 class levels. Although differences were apparent in the mean values for the three environment classifications, they were not significantly different from each other as indicated by the large 95% confidence intervals for each environment classification.

Values of ANOSIM R for the MEC and BOMEC calculated using the full OS 20/20 data were also low (mean values under 0.06, Figure 8) but, again, mean values were higher for the BOMEC than for the MEC at all class levels greater than six (Figure 7, top). ANOSIM R values for all three classifications, tested using only a subset of the OS 20/20 test data, were also low (mean R under 0.10) and were highly variable, indicating poor discrimination of benthic community composition (Figure 8). Although the R values were low, the BOMEC classification showed a significantly better performance than the MEC and Chat/Chall classifications at hierarchical class levels over 32 (i.e., non-overlapping confidence intervals with the MEC and Chat/Chall). The MEC was no better than random at most class levels below about 53 but above this level values were similar to those from the Chat/Chall classification.

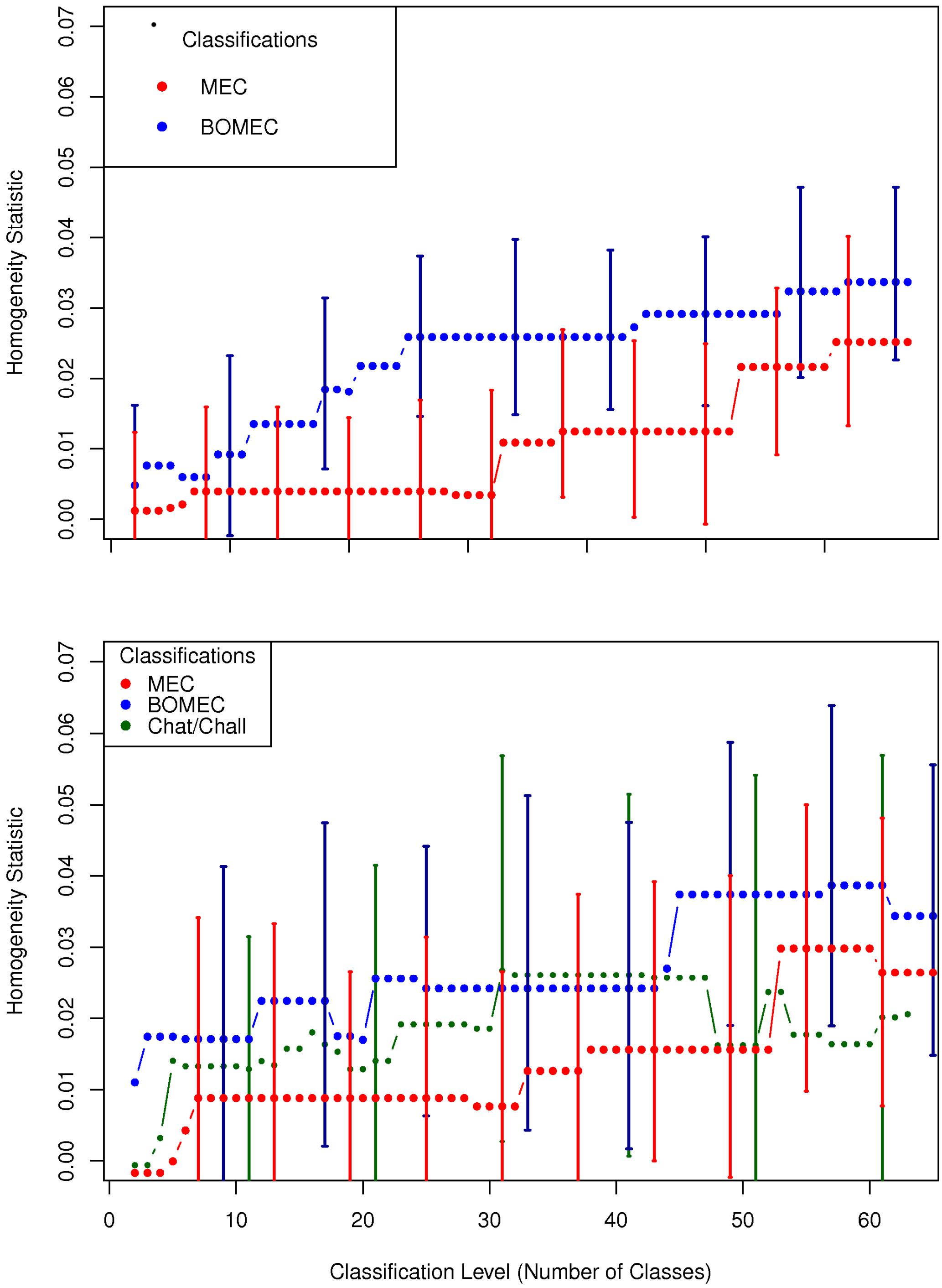

Figure 7: The homogeneity statistic for (top panel) the Marine Environment Classification (MEC) and Benthic Optimised Classification (BOMEC) calculated using the full OS 20/20 biological data set, and (bottom panel) for the three marine environmental classifications (MEC, BOMEC and Chat/Chall) calculated using the half of the OS 20/20 data not used to generate the Chat/Chall classification. Higher values indicate greater within-class similarity, and thus better matching of environmental classes with sampled benthic assemblage composition. The 95% confidence intervals from the bootstrapping procedure are shown.

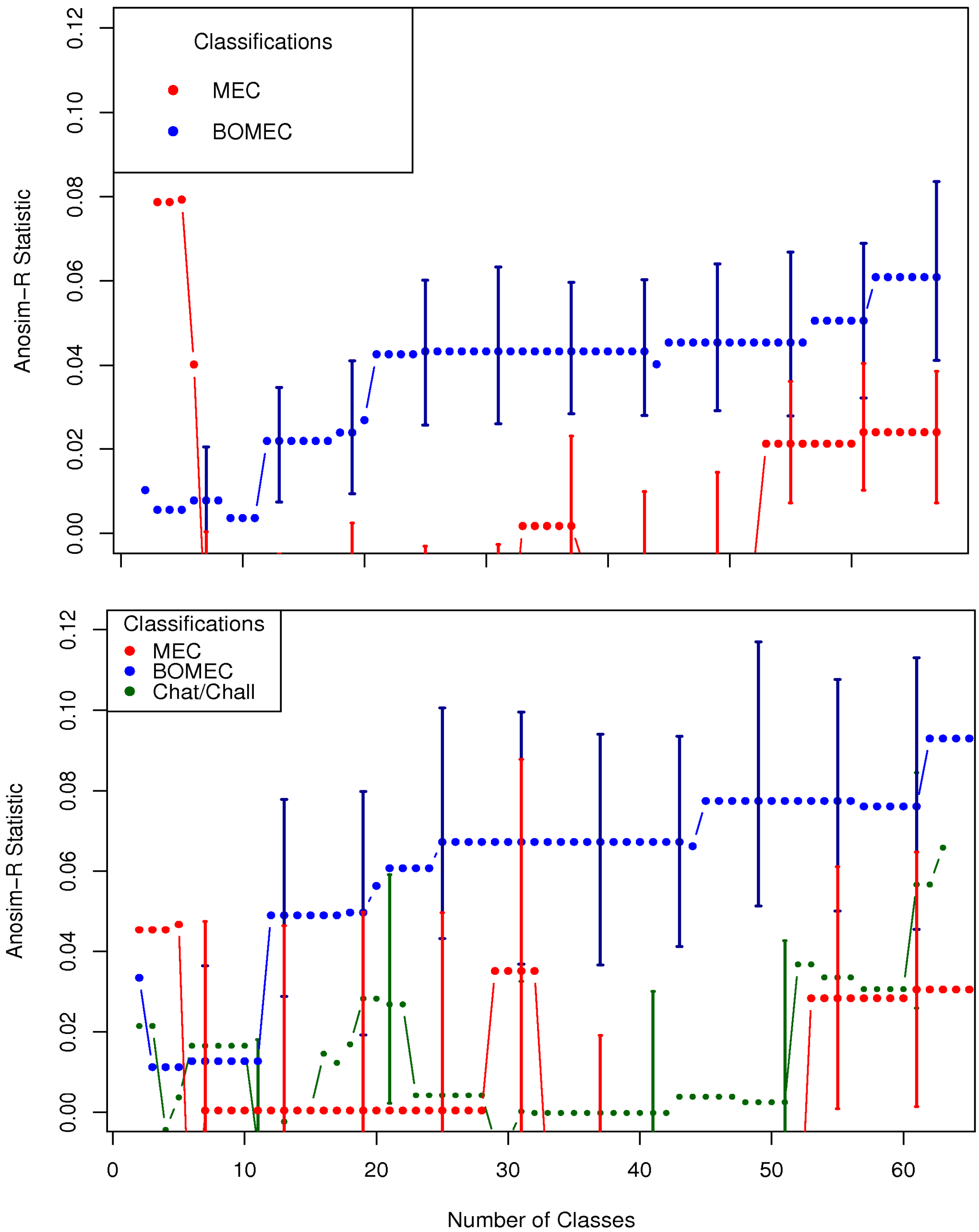

Figure 8: The ANOSIM R statistic for (top panel) the Marine Environment Classification (MEC) and Benthic Optimised Classification (BOMEC) calculated using the full OS 20/20 biological data set, and (bottom panel) for the three marine environmental classifications (MEC, BOMEC and Chat/Chall) calculated using the half of the OS 20/20 data not used to generate the Chat/Chall classification. Higher values of R indicate greater within-class similarity, and thus better matching of environmental classes with sampled benthic assemblage composition. The 95% confidence intervals from the bootstrapping procedure are shown

1.6 Comparisons with diversity metrics

As expected, the biotic habitats derived from the OS 20/20 sample data were most effective for predicting differences in all five of the biodiversity metrics, with model-to-error deviance ratios ranging from 0.35 for S_{RF}, to 0.97 for 1-λ' (higher values indicating better agreement, Table 4). Of the three environmental classifications, the Chat/Chall classification performed best, but the BOMEC had very similar performance. Ratios for all biodiversity metrics for these two classifications were substantially lower than those for biotic habitats, ranging from 0.12 (S_{RF}, both classifications) to 0.39 (1-λ', BOMEC). The MEC had the lowest overall performance, with ratios ranging from 0.01 (S) to 0.35 (1-λ').

Table 4: Ratio of model-to-error deviance from generalised linear models of differences between environmental classifications (MEC, BOMEC, and Chat/Chall) and five biodiversity metrics (S, J', 1-λ', S_{RA}, S_{RF}) calculated for each OS 20/20 site from the OS 20/20 video sample data. Ratios for the biotic habitats (BH) categories, which were developed directly from the OS 20/20 sample data, are included as reference values.

	BH	MEC	BOMEC	Chat/Chall
Taxon richness (S)	0.43	0.01	0.25	0.25
Margalef's evenness (J')	0.85	0.35	0.33	0.35
Simpson's index (1-λ')	0.97	0.35	0.39	0.35
Proportion of taxa rare in abundance (S_{RA})	0.48	0.26	0.25	0.28
Number of infrequently occurring taxa (S_{RF})	0.35	0.09	0.12	0.12

DISCUSSION

We employed several methods to evaluate the ability of the Marine Environment Classification (MEC) and the Benthic Optimised Marine Environment Classification (BOMEC) to discriminate patterns in the distribution of benthic invertebrate assemblages across Chatham Rise and Challenger Plateau. The classifications were evaluated against benthic invertebrate sample data from the extensive Chatham-Challenger OS 20/20 surveys of the region. We also used the Chatham-Challenger OS 20/20 benthic invertebrate sample data to define a new "Chat/Chall" classification which we compared with the MEC and BOMEC. Our results point to two different evaluations of the environmental classifications depending on the spatial scale at which comparisons were made.

Broad-scale visual comparisons of the environmental classifications with the distribution of biotic habitats (which effectively reduce the full taxonomic detail of the OS 20/20 sample data to a set of categories) showed that all three classifications indicated similar spatial patterns in benthic assemblages at scales of 100s–1000s km (Figures 3–5). For instance, at all class levels the BOMEC and Chat/Chall classifications showed that Chatham Rise and Challenger Plateau are different environments at shallow depths, but that they are likely to share similar communities in deeper waters, and that the north and south flanks of Chatham Rise contain different sets of habitats. Both classifications also identified the Chatham Rise as being a more environmentally diverse area than the Challenger Plateau. Although the MEC was less detailed than the other two classifications, particularly at low class levels (less than 50), it also identified these broad scale distinctions.

In contrast with this, χ^2 tests indicated only poor correspondence between environmental classes and the biotic habitats derived from the OS 20/20 sample data (Section 2.3.1), suggesting that neither the

MEC, the BOMEC, nor the Chat/Chall classifications, are useful for discriminating changes in benthic fauna or habitats at spatial scales less than about 100 km. This conclusion was strengthened by the results of subsequent comparisons of the environmental classes against both the full taxonomic detail of the OS 20/20 video faunal sample data (Section 2.3.2), and biodiversity metrics derived from these data (Section 2.3.3), both of which indicated little correspondence between the classifications and the OS 20/20 sample sites.

There are several potential reasons for the poor predictive abilities of the classifications at smaller spatial scales. Most obviously, distributions of marine organisms in space and time are partially stochastic, rather than being entirely dependent on environmental characteristics, i.e., biota may be present in one place and absent from another purely because of chance. There are also likely to be mismatches between the resolution of environmental layers used in the classifications and environmental factors that influence the distributions of benthic fauna at local scales. For instance, the environmental layers used in the classifications have a maximum resolution of 1 km^2 (Snelder et al. 2007b, Leathwick et al. 2009), but substrate heterogeneity, turbulence, biological interactions, and other ecologically important factors will all vary at scales considerably less than this, creating local and landscape-scale patchiness in distributions (Levin 1992). Thus the spatial resolution of the environmental data used in these classifications may be too coarse to discriminate factors that influence benthic assemblage composition at the scale of individual OS 20/20 sites. However, this would not explain the lack of concordance with the biotic habitats, which operate at scales of about 50–100 km (Hewitt et al. in press), suggesting that the situation is more complex. Relationships between organisms and environmental variables are driven by the magnitude of changes in the environmental variables (Huston 1999, Menge et al. 2002). Such environmental changes are likely to be pronounced at large spatial scales (i.e., sites further apart are likely to be less similar than those closer together) but this is not always the case. In marine environments, strong environmental gradients, often associated with depth or frontal mixing, can occur at relatively small spatial scales and have major influences on faunal distributions (Genin 2004). We would expect environmental classifications to identify the effects of these steep gradients because faunal changes will be strongly associated with the strong environmental changes. When environmental gradients are weaker, however, a number of different benthic communities with overlapping ecological tolerances and shared species might coexist. Thus, environmental classifications are likely to work best where there are pronounced differences in environment, which can occur at both large and small spatial scales, and worst where environmental gradients are slack.

There are also potential reasons for the poor ability of the environmental classifications to predict biology which are unrelated to spatial scale. First, there is likely to be uncertainty associated with some of the environmental layers used, whether through measurement errors, compilation of data from sources with inconsistent units, or assumptions used in generating modelled variables. Second, the temporal scales at which some environmental variables are measured might not be well matched to the life-history characteristics of benthic fauna. For example, successful recruitment of some benthic species might depend on currents or temperatures that occur only for short periods of the year, or during intermittent upwelling events (Hughes et al. 2002, Witman & Smith 2003). Third, if widespread anthropogenic disturbance such as trawling affects benthic distributions but is not included as a predictor variable in environmental classifications, spatial and temporal variations in the intensity of the disturbance will decrease concordance between the classifications and sampled biological distributions.

Finally, there are shortcomings associated with the modelling and classification techniques currently in use (Araujo & Guisan 2006, Barry & Elith 2006). The BOMEC and Chat/Chall classifications were both defined using GDM. GDM-based environment classifications subdivide environmental space and increase the discrimination of community composition by organising the environmental classes hierarchically, but there is a point beyond which increased classification detail does not yield a corresponding increase in the ability to describe community composition. Snelder et al. (2009) have shown that at high classification levels (over about 50 classes), GDM-based approaches do not improve ecological and environmental discrimination; rather, they only further subdivide those environmental variables that fit the observed biological patterns at the scale of the entire model domain. As might be expected for marine benthic environments, depth is the main gradient driving the classifications compared here (see Figures 1 and 2) and the effect of increasing classification levels beyond limits useful for ecological interpretation can be seen in the Chat/Chall and BOMEC classifications at 150 class level, where classes are subdivided primarily by depth (see Figure 3).

An additional shortcoming of GDM and other methods is that they do not cope well with the high levels of faunal dissimilarity between sites that are characteristic of marine benthic faunal data. For the Chatham Rise and Challenger Plateau OS 20/20 faunal data used here, for instance, overall median Bray-Curtis dissimilarity between all pairs of sites was over 90%, reflecting differences in regional species-pools between the two study areas and relatively high proportions of rare taxa within each area. Aggregation of the OS 20/20 faunal data to coarser levels of taxonomic resolution might be considered as a pragmatic way to overcome these limitations (by increasing the overall similarity between sites). However, because we found similar results when using *biotic habitat* categories and the biodiversity metrics, both of which also have the effect of increasing overall similarity between sites, as we did with the full detail data, taxon aggregation is unlikely to be useful.

The MEC and BOMEC were developed with the aim of providing broad-scale guides to the distributions of marine assemblages generally (MEC) and benthic assemblages specifically (BOMEC) that would inform decision-making in the management of marine living resources at the scale of the EEZ (Snelder et al. 2007b, Leathwick et al. 2009). It is important for interpretation of the present results, therefore, that the performance of these classifications should be evaluated at spatial scales appropriate to their intended use. In this context, there is a strong case for concluding that the BOMEC in particular does, indeed, provide useful information on the distribution of benthic habitats in the Chatham-Challenger region at the larger spatial scales examined. However, for any practical application, a significant problem associated with this conclusion is that the spatial scales (equivalent to the class levels) at which we can have confidence in any of these environmental classifications have not been defined. Both the MEC and the BOMEC were defined at a wide range of class levels but, to date, the levels at which they have been most widely discussed appear to have been selected on an arbitrary basis related more to the number of discrete classes that can readily be displayed on a page, than to any ecologically relevant criteria. For instance, the MEC is most often cited at the 20 class level, yet results here and in the original formulation of the MEC (Snelder et al. 2007b) suggest that it matches observed biological distributions better at higher class levels; more than about 53 classes (this study), or more than about 70 classes (see Snelder et al. 2007b, figure 6). If these classifications are to be useful in resource management, conservation, or research planning, objective criteria will be needed to define which class level, and thus which spatial scale, is appropriate for use in a given application. Such criteria have yet to be developed for any of the marine classifications.

The BOMEC and the Chat/Chall classifications were similar to each other in most comparisons, and both performed better than the MEC. Thus, although the OS 20/20 survey data are more internally consistent with respect to sampling methods and taxonomic identifications than the compiled fauna datasets used in the BOMEC, this did not translate into a noticeable difference between the Chat/Chall and BOMEC classifications in their ability to discriminate benthic assemblage structure in the Chatham-Challenger region. Although this result was initially surprising, examination of the data showed that Chatham Rise has the highest density of historical benthic sampling of any deepwater region in the EEZ (see figures 1a and 1b in Leathwick et al. 2009). Thus, for the main area of our study, the faunal data used to define the BOMEC had a substantially higher sample density than was realised in the OS 20/20 sampling. If data from a single sampling programme such as the Chatham-Challenger OS 20/20 surveys can generate a benthic environmental classification (Chat/Chall) that performs as well as the BOMEC does in its best-informed area, it seems likely that further OS 20/20-style sampling in other parts of the EEZ could be effective in expanding the scope and generality of the existing BOMEC.

CONCLUSIONS

Our results suggest that, while the BOMEC is an improvement over the MEC for mapping benthic distributions, neither classification provides reliable information at the spatial scale and taxonomic resolution of the OS 20/20 sampling. However, at larger spatial scales (over about 100 km), both MEC and BOMEC classifications produced patterns that were broadly consistent with sampled benthic distributions, suggesting that they might have applications in regional-scale assessment of benthic faunal and habitat distributions. Before they can be used with any confidence in practical management or planning applications, however, objective criteria will be needed to determine appropriate, ecologically relevant, classification levels to be used. That the Chat/Chall classification was similar to the BOMEC in all comparisons indicates that a single planned OS 20/20 sampling programme can provide the same level of spatial discrimination as the compiled historical data used in the BOMEC. As the Chatham Rise has by the far highest density of historical sampling of any part of the EEZ, this suggests that further OS 20/20-style sampling in other parts of the EEZ could be effective for expanding the scope and generality of existing marine environment classifications.

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