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Development of an Ecologic Marine Classification in the New Zealand Region

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ABSTRACT / We describe here the development of an ecosystem classification designed to underpin the conservation management of marine environments in the New Zealand region. The classification was defined using multi-variate classification using explicit environmental layers

chosen for their role in driving spatial variation in biologic patterns: depth, mean annual solar radiation, winter sea surface temperature, annual amplitude of sea surface temperature, spatial gradient of sea surface temperature, summer sea surface temperature anomaly, mean wave-induced orbital velocity at the seabed, tidal current velocity, and seabed slope. All variables were derived as gridded data layers at a resolution of 1 km. Variables were selected by assessing their degree of correlation with biologic distributions using separate data sets for demersal fish, benthic invertebrates, and chlorophyll-*a*. We developed a tuning procedure based on the Mantel test to refine the classification's discrimination of variation in biologic character. This was achieved by increasing the weighting of variables that play a dominant role and/or by transforming variables where this increased their correlation with biologic differences. We assessed the classification's ability to discriminate biologic variation using analysis of similarity. This indicated that the discrimination of biologic differences generally increased with increasing classification detail and varied for different taxonomic groups. Advantages of using a numeric approach compared with geographic-based (regionalisation) approaches include better representation of spatial patterns of variation and the ability to apply the classification at widely varying levels of detail. We expect this classification to provide a useful framework for a range of management applications, including providing frameworks for environmental monitoring and reporting and identifying representative areas for conservation.

Ecologic classifications provide fundamental tools for ecosystem-based environmental and conservation management by characterizing and mapping ecologic (i.e., abiotic and biotic) heterogeneity (Carpenter and others 1999; Grossman and others 1999; Bourgeron and others 2001). Ecologic classifications summarise spatial variation in abiotic and biotic characteristics, thereby allowing more specific quantification of responses of patterns and processes to human use and quantitative assessment

of conservation efforts (Detenbeck and others 2000; Bourgeron and others 2001). Classifications also permit the collation, unification, and synthesis of data collected for environmental and ecologic monitoring by providing an objective basis for stratification and aggregation. In New Zealand, ecologic classifications of rivers and terrestrial environments have been developed and used for conservation and environmental management (e.g., Snelder and Biggs 2002; Leathwick and others 2003). In 2001, several government agencies with responsibility for marine management determined that an ecologic classification of marine environments of the New Zealand region (Fig. 1) was required.

International attempts to classify marine ecosystems have been less advanced than those for terrestrial environments. This difference probably reflects the relative

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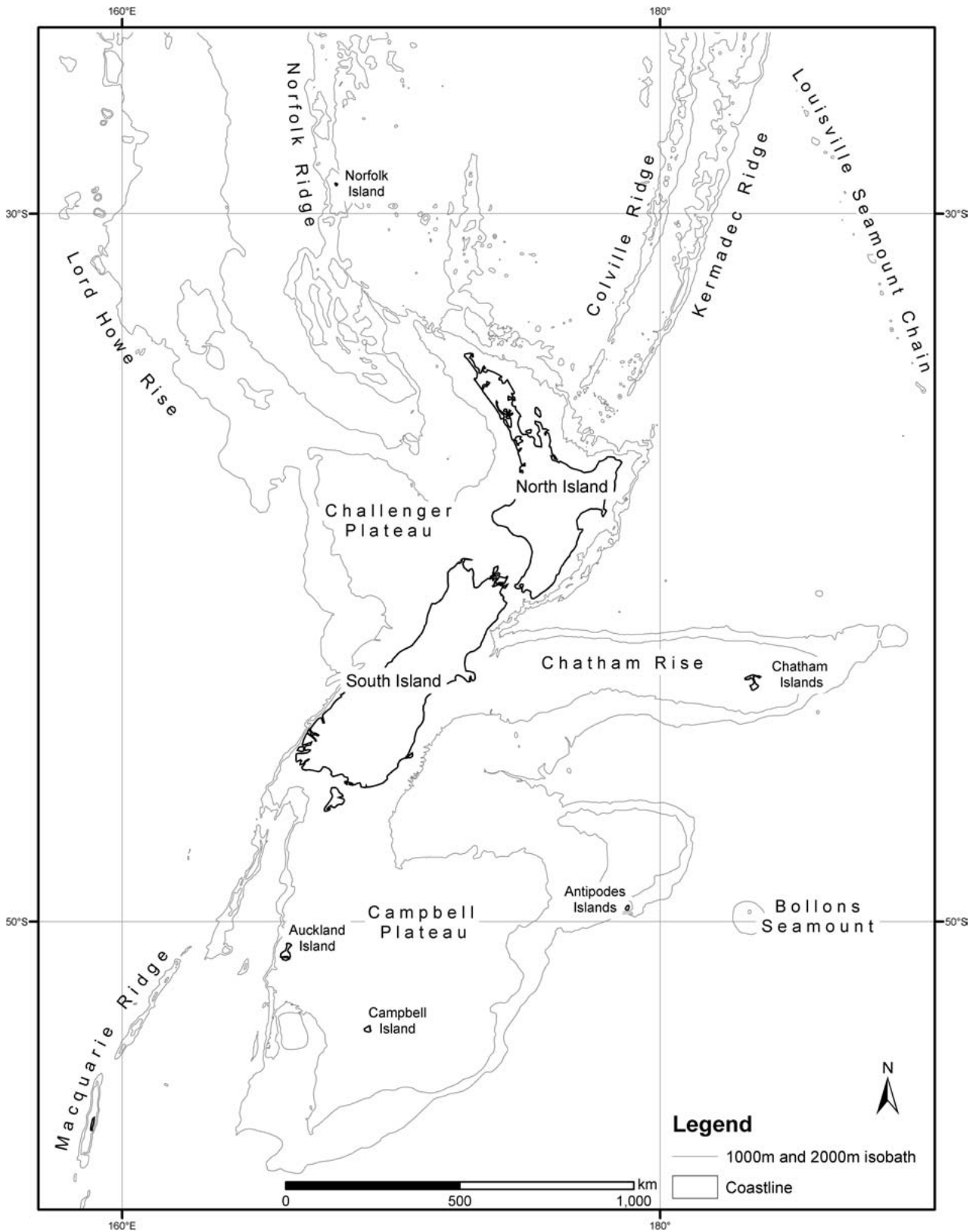


Figure 1. The classified region showing New Zealand, the outlying islands, and some of the important regional bathymetric features.

inaccessibility of most marine systems, the slower transition to ecosystem-based management of marine compared with terrestrial environments, and the relative complexity of dynamic and three-dimensional marine environments. Existing global-scale marine classifications are based mostly on qualitative interpretation of descriptors of broad physical process (e.g., Hayden and others 1984; Bailey 1998) and/or the distributions of planktonic biomass and community composition (e.g., Longhurst 1998). These global-scale classifications lack the detail necessary for management at a regional level. For example, Bailey (1998) subdivided the entire New Zealand region into only three domains, whereas Longhurst's (1998) scheme produced five divisions. A small number of more detailed regional classifications, including the British Columbia marine ecosystem classification (Zacharias and others 1998) and a geophysical classification of the Scotian Shelf (Roff and others 2003), have been developed. These classifications have combined thematic layers—such as wave exposure, tidal currents, seafloor composition and slope—that differentiate ecologic variation at regional scales.

Here we outline the process used to develop a classification of the marine environments of the New Zealand region (Fig. 1). The objective of this article is to summarise this complex 5-year project, which has been comprehensively described in project reports by Snelder and others (2005) and the references within. The aim of the New Zealand Marine Environment Classification (MEC) was to provide a broad-scale ecologic classification of this 8.8 million-km² area based on environmental (abiotic) factors that discriminates biotic variation (including that for phytoplankton, fish, and benthic invertebrates) primarily for conservation-management purposes (Snelder and others 2005). Our approach differs from other regional marine classifications, which have defined units by subjective subdivision of individual thematic layers. The MEC has been defined numerically using a statistical procedure. Numeric classifications are objective and offer some particular advantages over more traditional subjective approaches, including continuous stratification of variation and homogeneous within-class variation (Belbin 1993; Leathwick and others 2003; Múcher and others 2003; Hargrove and Hoffman 2005). In this article, we first describe a number of conceptual issues and then detail the definition of the classification and the subsequent assessment of its performance.

Approach to Classification

Our objective was to produce a single classification of the marine environments in the New Zealand

region. Given the highly diverse range of environments and organisms that occur in any large region, a single classification would not provide optimal discrimination of any individual ecosystem component, and there could be more than one plausible solution. Therefore, it was necessary to reach agreement among both (1) the research team (the present investigators, i.e., researchers with theoretical and practical experience of the environmental and biologic character of the region and classification procedures, who would define the classification) and (2) an advisory group representing the stakeholders (principally science and policy staff from the Ministry for the Environment, Ministry of Fisheries, the Seafood Industry Advisory Council and Department of Conservation, i.e., those who would use the classification) on how the classification would be performed. We used an iterative and adaptive process described by Holling (1980) and Walters (1986) to integrate the research disciplines, expertise, and user requirements and to attempt to decrease, or better understand, the uncertainties associated with the final classification. We used a series of workshops and meetings with groups of researchers and stakeholders to develop a conceptual framework and the procedure used to define the classification.

Ideally, an ecologically relevant marine classification should be based on a comprehensive description of geographic variation in ecosystem character throughout the study region and would delineate units having similar biologic attributes. However, given the paucity of data describing the distributions of many taxonomic groups for the New Zealand region (see review by Nelson and Gordon 1997), we had little choice but to take an abiotic or “environment-based” approach, focusing on environmental variables that were thought to be drivers of biologic patterns. This approach is more practical given that most of the required environmental variables can be relatively easily defined at a resolution that is suitable for regional scale management purposes over the entire spatial domain.

Our next choice concerned the procedure that would be used to define the classification. Whereas most other classifications of marine ecosystems have been defined qualitatively, typically by subjectively categorising and combining individual thematic layers, we decided that the MEC should be defined quantitatively using multivariate statistical procedures. Although these techniques have been little used for marine classifications, they have been applied in the development of terrestrial classifications (e.g., Belbin 1993; Leathwick and others 2003; Múcher and others 2003; Hargrove and Hoffman 2005).

Having adopted an environment-based numeric approach, the distinction between geographic and environmental space (in the sense of Austin and Smith 1989) brought clarity to a number of practical issues. This distinction has important implications in the context of the development of classification frameworks (Leathwick and others 2003). For example, so-called bioregional and ecoregional classifications are generally based on subdivisions in geographic space, with units encompassing areas of broadly similar biotic or ecologic (i.e., biotic and abiotic) character (e.g., Bailey 1998; Olsen and others 2001). However, because boundaries are defined in geographic space, usually at a predetermined scale, local anomalies or distinctive local communities are often subsumed into surrounding units, and units often vary widely in their degree of within-unit biologic or environmental variability.

By contrast, when classifications are defined in environmental space, geographic locations (e.g., points on a grid) are classified based on measured or modeled attributes of the physical environment. The classification is then mapped back into geographic space by assigning each geographic location to an environmental group. In this approach, areas of similar environment are identified regardless of their size or geographic location, and this allows inherent spatial patterns of environmental variability to be more realistically portrayed. This approach assumes that species distributions are determined by aspects of the physical environment rather than by processes operating in geographic space (e.g., dispersal, predation, recruitment). Although a mix of environmental and geographic factors will determine actual distributions, environment is likely to explain a large amount of variation occurring within a region (Zajac and others 2000).

Another important conceptual distinction of environment-based approaches is that between indirect and direct environmental gradients (e.g., Austin and Smith 1989; Grossman and others 1999). Indirect gradients are factors such as depth or latitude, which, although easily measured, are important mostly because of the physical changes (e.g., pressure, light, temperature, salinity) associated with them and that have a more proximate effect on the distributions of organisms. The problem with using indirect gradients, such as depth, is that their correlations with more causal factors are often location specific. We therefore attempted to develop a set of "candidate" environmental variables that were likely to have a direct effect on biologic variation and then tested the utility of these variables as predictors of biologic distributions across the entire region using available biologic data sets.

Then, having established which of the variables could be used as a surrogate for the (incompletely known) biologic variation, we classified all locations based on their environmental attributes.

Four major steps were used in defining the classification: the assembly of relevant environmental and biologic data; the analysis of relations between biota and environment to identify the best predictors of biologic patterns from the environmental data and their optimal weighting and transformations; the definition of groups using a two-stage multivariate classification procedure; and evaluation of the ability of the resulting classification to summarise variation in the biologic data. These steps are discussed below.

Environmental and Biologic Data Sets

Candidate Environmental Variables

Fifteen candidate environmental variable "layers" were derived, each consisting of estimates at points on a 1-km² grid extending from 25° to 58°S and from 158°E to 172°W. We derived environmental data at the maximum possible resolution and interpolated these to grids whose resolution was determined by the resolution of bathymetric data, which in turn determined the resolution of a number of modeled variables. The rationale for the consideration of each variable, and a brief description of how the data sets were produced, is as follows.

Depth is correlated with many direct drivers of biologic distribution, including light, temperature, pressure, and salinity (Thistle 2003). Although more direct measures of these variables are described in the CARS data set (Ridgway and others 2001), this does not currently extend across the entire study area and so could not be used for our classification. Depth was interpolated from a large quantity of depth data of variable quality and resolution (CANZ 1997). The resulting depth layer was then used to derive estimates of seabed slope, as a measure of seabed relief, using standard routines available in the geographic information system ArcGis (ESRI 1992). To some extent, seabed relief can influence directly and/or indirectly the distribution of pelagic and benthic biotic assemblages (e.g., Genin 2004).

Solar radiation directly controls primary production and shows considerable spatial variation over the New Zealand region. Annual mean surface solar radiation was estimated by first calculating clear-sky solar irradiance from the instantaneous solar elevation using the method of Davies and others (1975), with allowances for atmospheric water vapor and dust appropriate for clean oceanic air at 40°S. Daily mean clear-sky solar

irradiance was then calculated by numeric integration of solar irradiance for noontime solar elevation calculated for the mid-date of each month. The clear-sky estimates were then modified with monthly mean cloud cover data from the International Satellite Cloud Climatology Project D2 data set of global cloud parameters monthly means from July 1983 through December 1995 (Rossow and Schiffer 1999). Winter surface solar radiation estimates were calculated as for annual mean surface solar radiation for the shortest day of the year (late June) and combined with cloud-cover data for June. Values for the winter surface solar radiation showed a much steeper decrease with increasing latitude than the annual solar radiation estimates, reflecting the combined effects of both lower sun angles and shorter day lengths at higher latitudes during winter.

Caddy and Bakun (1994) noted that the global distribution of fisheries resources corresponds with areas of high productivity and based their classification on the major drivers that act to mitigate nutrient constraints. We acknowledged the importance of nutrient concentration, as well as variation in water temperature and salinity, and used four remotely sensed sea-surface temperature (SST) variables to discriminate variation in water masses, seasonal stratification, vertical mixing, upwelling, and frontal systems. These parameters can influence the composition of pelagic and benthic assemblages (see Longhurst 1998). The SST variables were calculated from a climatology data set developed from advanced very high-resolution radiometer satellite data and procedures for collecting, detecting cloud and retrieving SST as described by Uddstrom and Oien (1999). A climatology was prepared by compositing data for each of the 96 months in the years 1993 to 2000 on a grid with approximately 9-km resolution. The climatologies were later interpolated onto the 1-km² classification grid. This interpolation was considered reasonable because of the relatively smooth and slowly changing character of most of the climatologic SST variables.

Wintertime SST was chosen as a proxy for regional variation in water mass, which is related to differences in both temperature and chemical characteristics of the water, including nutrient availability (Longhurst 1998). Wintertime SST distinguished subtropical from sub-Antarctic water masses, which differ markedly in temperature, salinity, and nutrient availability. Wintertime SST was evaluated by spatial smoothing of temperature at the time of typically lowest SST (day 250 in early September). The annual amplitude of SST variable was included in an attempt to describe variation in seasonal stratification across the region. Seasonal

stratification by surface heating, followed by destratification and mixing caused by cooling and wind, drives spatial and temporal variation in light received in the upper ocean by phytoplankton, temperature, and nutrients (Parsons and others 1984). Annual amplitude of SST was generated by spatially smoothing the annual harmonic. The spatial gradient of annual mean SST was used to define fronts in oceanic water masses that are expected to correlate with variation in primary productivity (Parsons and others 1984). This variable was produced by smoothing the annual mean SST grid and then evaluating the magnitude of the spatial gradient (in °C km⁻¹) for each cell by centered differencing. The summer SST anomaly was included in an attempt to differentiate areas with distinctive water column character, particularly in nutrient concentration, that occur as a consequence of hydrodynamic forcing, including upwelling and mixing caused by eddies, which bring nutrient rich waters to the surface (Parsons and others 1984). Summer SST anomaly was derived from SST measured in late February (day 50), the time of year when SST is typically highest, by band-pass filtering at scales between 20 and 450 km.

Mean and extreme orbital velocity describe swell-wave-induced velocity at the seabed. Orbital velocities cause bed stress and resuspension of bed material, which plays a role in structuring benthic communities (e.g., Warwick and Uncles 1980) and in determining local water-column characteristics (Parsons and others 1984). We used mean orbital velocity to represent average conditions and extreme orbital velocity (represented by the 95th percentile orbital velocity) to discriminate locations with similar average conditions but differing exposure to extreme wave events. The orbital-velocity variables were based on a wave climatology derived from a 20-year hindcast (1979 through 1998) of swell-wave conditions in the New Zealand region (Gorman and others 2003). The wave climatology was used to interpolate the mean and 95th percentile values of significant wave height and mean values of wave peak period onto the 1-km bathymetry grid. The wave height, period, and depth were then used to estimate mean and 95th percentile bed orbital velocities. An important limitation of this method was that wave refraction and sheltering by land was not taken into account. This limitation resulted in some unreasonably high values in sheltered coastal environments.

Maximum depth-averaged tidal current velocity was estimated by interpolating outputs from the New Zealand region tide model (Walters and others 2001). Tidal current velocity was chosen because it influences benthic communities (Rees and others 1999) and,

coupled with depth, influences mixing of the water column (Parsons and others 1984).

Finally, we unsuccessfully attempted to develop two additional variables describing variation in sea-floor sediments and freshwater inputs into coastal waters. Variation in the nature of sea-floor sediments influences the composition of benthic communities (e.g., Van Hoey and others 2004), but existing maps for the New Zealand region (Mitchell and others 1989) provide only broad categorical descriptions at low spatial resolution (scale 1: 6,000,000). Although data from this map were successfully included in exploratory statistical models relating the distributions of benthic organisms to environment, we were concerned with their low spatial resolution and reliability. In addition, the categorical nature of these data made them difficult to include in the numeric classification process.

Although development of a variable describing the freshwater inputs into New Zealand's coastal waters is desirable (because localised decreases in salinity influence the distribution of nearshore biota, e.g., Giberto and others 2004) and technically feasible, we were unable to successfully develop and validate such a variable within the required time frame for the development of the classification. Research currently underway aims to develop such data from remotely sensed ocean color imagery, and a freshwater input variable may be incorporated into the classification when it becomes available.

Biologic Data

Although our overall approach to defining a classification was environment based, we used biologic data to help decide which environmental variables to include in the classification and to determine their optimal transformation and weighting. Ideally, we would have used samples describing a comprehensive range of marine taxa that had been systematically collected throughout the New Zealand region. In reality, because the available data were collected for widely varying purposes, and because of the practical difficulties associated with sampling at depths greater than approximately 1500 m, samples were unevenly distributed with respect to both environment and geography (Nelson and Gordon 1997). For example, only a limited number of samples had been taken from depths >1500 m despite these deeper waters making up >60% of the total extent of New Zealand's exclusive economic zone and an even higher percentage of the region classified. Three main sources of biologic data eventually used were as follows.

Fish Data Set. The fish data set comprised data from a large collection of research trawls taken during the period from 1961 to 1997 (Francis and others 2002) and mostly describes the distributions of demersal fish. The data set contained records for 19,232 sites falling within our study area and for 123 species (after excluding those that occurred in <1% of the trawls). Because sampling efficiency varied due to differences in nets (types and sizes) and vessels (towing power), abundance data contained in this data set were decreased to presence-or-absence form for our analyses.

Benthic Invertebrate Data Sets. The benthic invertebrate data sets were extracted from a large database describing the distributions of benthic macroinvertebrate species collected at approximately 10,000 sites across the region since the 1950s (Gordon 2000). Limitations with the taxonomic resolution and reliability of these data restricted their species-level use to presence-or-absence records of 176 and 154 species in the echinoderm orders Asterozoa (1,565 sites) and Ophiurozoa (1,197 sites), respectively (Clark and McKnight 2000; McKnight 2000; Clark and McKnight 2001). However, for 274 sites sampled during a continental shelf survey, reliable data were available for 145 taxa across a number of macroinvertebrate taxonomic groups (McKnight 1969). However, even with these data, the quality of the identifications of some species limited our analyses to the taxonomic level of families, which we considered sufficient to identify broad trends in distributional patterns (Olsgard and Somerfield 2000). For the analyses, data from the three invertebrate data sets were pooled at the resolution of the 1-km² grid cell.

*Chlorophyll-*a* Data Set.* The chlorophyll-*a* concentration data set was derived from remotely sensed ocean color data in six visible wavebands, which is an accepted proxy for phytoplankton biomass (O'Reilly and others 1998). Atmospherically corrected green and blue water leaving radiances collected between September 1997 and July 2001 by the Sea-Viewing Wide-Field-of-View Sensor (SeaWiFS; McClain and others 1998) was converted to estimated surface chlorophyll-*a* using an empirical algorithm (OC4v4; O'Reilly and others 1998). Observations from individual satellite orbits were remapped and composited to monthly standard mapped image format (Campbell and others 1995) with a spatial resolution of approximately 9 km. The chlorophyll-*a* data set was produced by randomly subsampling this coverage at approximately 10,000 points across the region. Remotely sensed chlorophyll-*a* data are generally related to the relative occurrence of phytoplankton in surface waters and given reasonable assumptions are proxies for phytoplankton biomass in the ocean (Martin 2004). The

amount (and quality) of phytoplankton associated with surface water is likely to influence the composition of pelagic and subsequently benthic faunal assemblages (e.g., Karakassis and Eleftheriou 1997).

Before any analyses were performed, we used histograms to examine the degree to which the sites from the biologic data collectively represented the full range in the environmental variables occurring across the region. The complete spatial coverage of the chlorophyll-*a* data set resulted in it providing comprehensive sampling of environmental variation. However, both the demersal fish and benthic invertebrate data sets were strongly biased in their distributions, with very few samples from depths either < 10 m or > 1500 m or from sites with steeply sloping bottom topography, strong tidal currents, or high orbital velocities. These limitations affected our ability to identify the best predictors of biologic patterns and to tune the classification, ultimately meaning that some classification decisions were subjective.

Defining the Classification

Selection of Environmental Variables

Before defining the classification, we performed a number of analyses to establish the strength of relations between the individual environmental variables and the distributions of demersal fish, benthic invertebrates, and chlorophyll-*a*. We then used the results of these analyses to decide which environmental variables should be included in the classification.

We used multiple statistical methods and sought general agreement among methods to provide confidence in the final choice of environmental variables. For the fish and benthic invertebrate data sets, we used (1) multivariate classification to group samples of similar species composition, followed by use of analysis of variance to test the magnitude of environmental differences among these groups; (2) canonical correspondence analysis (CCA) (ter Braak 1986); and (3) analysis of correlations between matrices of biologic and environmental distances (Clarke and Warwick 2001). For the chlorophyll-*a* data set, we tested the relationship between chlorophyll-*a* concentrations and environmental variables using generalised additive models (Hastie and Tibshirani 1987). Finally, classification and regression trees (De'ath and Fabricius 2002) were applied to all three biologic data sets using class membership derived by multivariate clustering of the fish with benthic invertebrate data sets and chlorophyll concentration as independent variables.

Although we found differences in the strength of relations between environmental variables and the

different biologic data sets, there were also some striking similarities, particularly for the demersal fish and benthic invertebrate data sets. For these, depth was the most consistently chosen variable and generally had the strongest relationship with variation in biologic composition. For example, the CCA model of the demersal fish explained 18.3% of the total variation in species composition, and its first dimension, which accounted for approximately half (50.9%) of the model variance, was highly correlated with depth ($r = 0.99$). Although the amount of variance explained by the CCA was low, it is a considerable improvement over the 13.1% explained for the same fish data set by Francis and others (2002) using a CCA model with the explanatory variables depth, latitude, and longitude. The CCA models of Asteroidea and Ophiuroidea species explained between 11% and 18% of the compositional variation, depending on whether a threshold for occurrence of rare species of 1% or 2.5% of sites was applied. In both cases, the first CCA dimension was most strongly correlated with depth. Mean annual solar radiation and wintertime SST, followed by depth, made the largest and most consistent contribution to the GAM and CART models of chlorophyll-*a*.

The results of each of the validation analyses were used to rank the variables in order of their explanatory power (e.g., variables were ranked by F ratio, and contribution to deviance explained for the ANOVA and CART analyses, respectively). An overall ranking was then defined by calculating the average rank across all statistical methods. A subjective decision was then made to define the point in the ranking at which variables added little explanatory power or were inconsistent across methods. This resulted in 8 of the 15 original candidate variables being identified as useful predictors, ranked in the following decreasing order of importance: depth, wintertime SST, mean annual solar radiation, annual amplitude of SST, spatial gradient annual mean SST, mean orbital velocity, tidal current, and slope.

Classification Procedure

Although the procedures used to perform a multivariate classification are objective in the sense that they are repeatable, subjective choices are still required at several stages, and these can affect the classification outcome. For example, the relationship of objects to one another is sensitive to the choice of distance measure (Sneath and Sokal 1973). We used the Gower metric as a measure of environmental distances among locations because the range standardisation that is inherent in this Manhattan-type distance measure accommodates variables that are measured on different scales (Sneath and Sokal 1973). In practical

terms, our choice of a classification strategy was strongly constrained by the large amount of data. This prevented the direct use of hierarchical clustering procedures, for which processing requirements increase rapidly with increasing data set size. The clustering was therefore performed in two stages. In the first stage, a nonhierarchical clustering procedure (ALOC; Belbin 1995) was used with a computationally manageable 25% sample of the data points. The procedure defined approximately 300 groups, which was considered to be the maximum number of classes that would be needed for application of the classification. This procedure carries out an initial allocation of grid cells to groups based on their environmental distances from each other. It then performs an iterative testing phase during which each point is removed from its allocated group; the distance between it and all groups is recalculated; and it is allocated to the group to which it is closest. This procedure is repeated until only a small number of reallocations of points to groups can be made.

In the second phase, a more conventional agglomerative clustering procedure (flexible UPGMA; Lance and Williams 1967) was used to define relations among the groups created by the initial nonhierarchical clustering. This procedure was performed with slight space dilation ($\beta = -0.1$) to discourage chaining (i.e., the production of clusters with few individuals) (Lance and Williams 1967). All grid cells were then individually assigned to the non-hierarchically defined classification groups to which they were most closely located in the multivariate environmental space using the Gower metric. Results from this process were written to a GIS grid layer that was then coupled with results from the hierarchical classification. This allowed the non-hierarchically defined groups to be successively fused from approximately 300 to 2 classes so that the classification could be displayed at varying levels of detail.

Tuning the Classification

Initial trial classifications using the procedure previously described made it clear that classification outcomes were sensitive to the set of input variables used. This in turn affected the ability of the classes to discriminate variation in biologic composition, and we realised that classification performance (i.e., its ability to discriminate biologic variation) could probably be manipulated by varying the weighting and transformation of the input variables. In large measure this reflects our choice of distance measure. First, the range standardization inherent in the Gower metric results in all variables having an equal contribution, but in many ecosystems environmental drivers differ markedly in

their contribution to biologic variation. Second, the Gower metric is an interval-type measure, i.e., the same relative difference with respect to a variable measured at two sites contributes the same amount to the final distance measure regardless of the value at which that difference occurs. Although this implies that biologic variation occurs at similar rates along environmental gradients, changes in biologic composition are frequently nonlinear. For example, our analyses suggested that change in demersal-fish community composition with depth occurs rapidly at shallow depths but becomes more muted in deep water.

Given these considerations, we developed a procedure to optimise the classification by providing a rigorous basis for selecting, weighting, and transforming variables. This was based on use of the Mantel test (Mantel 1967), which measures the correlation between two matrices containing environmental and biologic distances for a common set of biologic sample locations. We used the Gower metric to calculate intersite environmental distances because this was our choice for defining the environmental space. We used the Bray-Curtis distance measure to calculate biologic distances for the fish and shelf-survey benthic invertebrate data sets because it is unaffected by “joint absences” (Clarke and Warwick 2001), which is an important consideration when biologic samples are being compared from sites that cover a wide range of environmental conditions. Because the chlorophyll-*a* data set was univariate, we used simple differences as the measure of biologic distance.

Two main options were explored for increasing the correspondence between environmental and biologic distances. First, we explored the effects of including biologically important variables more than once to increase their contribution to the environmental distances. Second, we explored the ability of transformations of environmental variables to improve the correlation between environmental and biologic distances. As the transformation selectively compresses or expands values in some part of the variable range, this could be expected to increase correlations where the rate of biologic turnover varies along an environmental gradient (i.e., is nonlinear). For example, a transformation such as square root or log transformation, which compresses higher values, could be expected to increase the correlation between environmental and biologic distances if biologic turnover is slower at high values of the environmental variable. We therefore calculated Mantel *r* values using varying combinations of environmental variables, and with varying transformations and weightings, while holding the biologic distance matrix constant. This procedure enabled us to

identify an optimal set of variables, along with their weightings and transformations. We also used bootstrapping procedures to ensure that the observed differences in the Mantel r values were significant. All calculations were carried out in MATLAB using the statistical procedures available in the FATHOM package (Jones 2003).

Results from this testing on all biologic data sets were considered collectively to decide on a final definition of environmental space. Testing confirmed that the mix of eight variables identified during the initial validation stage gave the strongest correlation between environmental and biologic distances. We found that some transformations or weightings improved the correspondence between the environmental and biologic data sets. However, practical considerations were also important. For example, results from the Mantel tests using various transformations of depth, averaged over all the biologic data sets, indicated that a fourth root transformation gave the largest increase in correlation. However, when this transformation was given a trial run in the classification, it produced groups that provided very little discrimination of environmental variability in depths >1500 m where few biologic data was available for testing. After experimenting with various alternatives, we made a subjective decision to use a less-severe square root transformation of depth. Similarly we found that weighting depth by greater than three times improved correlations for the fish data set but decreased correlation for chlorophyll data (Fig. 2). We therefore applied a final weighting of two to depth.

Finally, we applied a \log_{10} transformation to mean orbital velocity, a cube root transformation to tidal current, and a square transformation to slope, all of which were based on qualitative assessment of trial classification results. All three of these variables had highly skewed distributions, which resulted in only their extreme values making a significant contribution to overall environmental distances when left untransformed. Compressing the extreme values of the mean orbital velocity and tidal current variables allowed a greater proportion of the range of the variable to contribute to the definition of environmental distance. This transformation meant that instead of identifying a small number of classes that were distinctive because of extreme values of these variables, classes were defined that more evenly subdivided the total range in variation. We considered that a degree of species turnover along the entire gradient for these variables was more likely than a lack of species variation until values became very large, which was implied by the untransformed variables. In contrast, we inflated the extreme

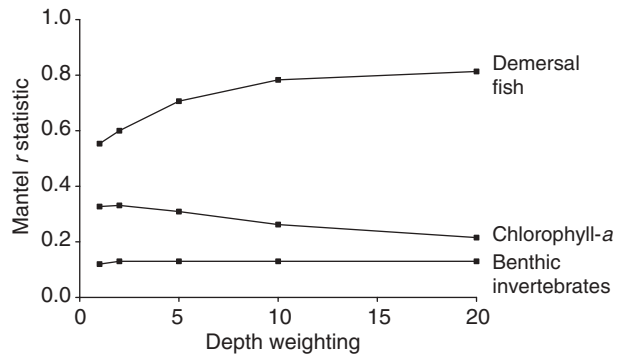


Figure 2. Mantel test results showing the change in correlation (Mantel r) for various weightings of depth for chlorophyll- a , demersal fish, and benthic invertebrates.

values of the slope variable to decrease its contribution at low values. This transformation had the effect of defining classes that were distinctive due to steep seabed, while avoiding finely subdividing variation in low values of Slope. Areas of relatively steep seabed slope, such as the continental slope, canyons, ridges and seamounts have distinct environmental characteristics thought responsible for the presence of particular biotic assemblages (e.g., seamounts, see Rogers 1994). Although more rigorous assessment of the effect of these transformations would have been desirable, biologic data were lacking from sites with extreme values for all three of these variables.

The Resulting Classification

At the end of the tuning process, we defined a final classification, using the variables, weightings, and transformations, as described in the preceding section, that contained 290 classes. Relations between the uppermost 20 classes are easily appreciated, interpreted, and understood and are summarised in the dendrogram shown in Figure 3, and the mean values of the eight contributing variables are shown in Table 1. At the higher levels of classification, differences between classes mostly reflected variation in depth, water temperature, and solar radiation. For example, at the 2-class level (Fig. 4) (thick line in Table 1), there was a broad division between coastal environments (class no. 12) and deeper oceanic environments (class no. 219). Within this latter class, further divisions at the 4-class level were associated with differences in mean annual solar radiation and wintertime SST (thin solid lines in Table 1). These subdivisions approximately defined subtropical waters, the plateaus and subtropical front, and the sub-Antarctic waters, respectively. Subtropical waters were further subdivided at the 9-class level into bathyal (i.e., approximately 200 to 2000 m) (class

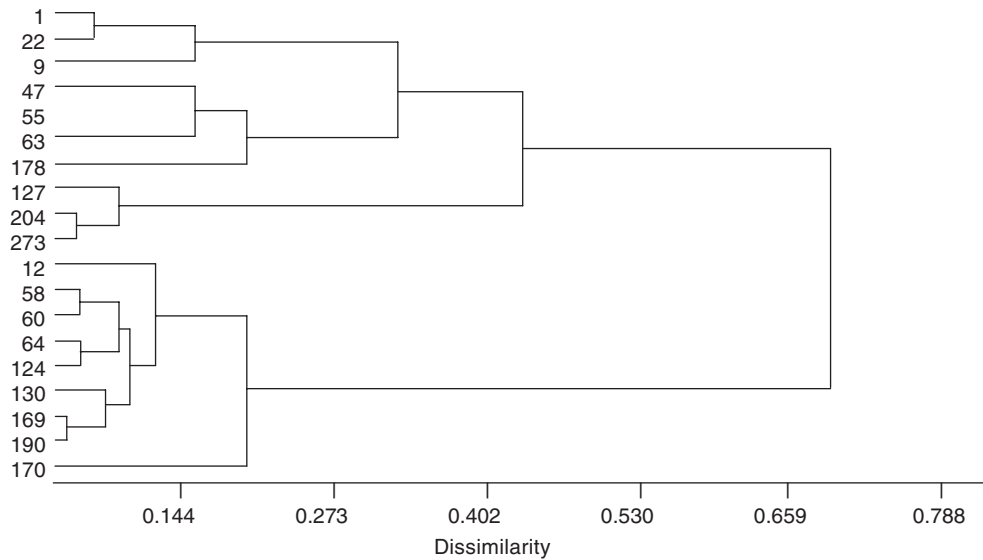


Figure 3. Dendrogram showing the relationship between classes at the 20-class level of classification. The dissimilarity measure is the Gower metric. The class numbers were assigned automatically during initial nonhierarchical sorting stage of the classification procedure and should be regarded as labels only.

no. 1) and abyssal environments (i.e., approximately 2000 to 6000 m) (class no. 9) and the plateaus and subtropical front waters into bathyal subtropical front (class no. 47), central continental shelf (class no. 55), and southern continental shelf environments (class no. 178) (dotted lines in Table 1). Similarly, the coastal environment was subdivided into three classes at the 9-class level: northern (class no. 12), central (class no. 58), and southern (class no. 170) areas (dotted lines in Table 1). These classes were principally distinguished by differences in mean annual solar radiation and wintertime SST. The 20-class level further defined environmental groups that are mostly differentiated by variation in depth, with its strong influence reflecting its double weighting.

A key advantage of a numeric approach is the ability to quantify differences between classes. To illustrate this we generated a continuously varying colour scheme for the most detailed level of the classification (290 classes) (Fig. 5) using the method described by (Mackey and others 1988). Using the mean environmental values for each of the 290 classes, we defined a 3-dimensional ordination using principal components analysis (PCA), which summarises environmental relations between groups. The positions of each class on the ordination axes were then used to specify its colour, with the PCA axis scores defining the levels of red, green, and blue components of the resulting map. Hence, the greater the similarity between any 2 classes, the more similar their colours appear. The first PCA axis scores were used to define the blue component

because it was positively correlated with depth and negatively correlated with tidal current and mean orbital velocity. Thus, intense blue areas are associated with deeper waters and with lower tidal current and mean orbital velocity. Scores on the second PCA axis were used to control the red component and were positively correlated with wintertime SST and annual mean surface solar radiation. Scores on the third PCA axis controlled the level of green and was most correlated with slope and SST gradient and moderately correlated with tidal current.

Assessing Classification Strength

Having defined the classification, we then assessed its effectiveness using the biologic data used for variable tuning. Although this was somewhat circular, our aim was not its ability to predict (which would have required an independent data set) but rather (1) assess the classification's ability to discriminate areas having different biologic character and (2) assess how this discrimination varied across classification levels.

Classification strength was assessed at a range of hierarchical levels using (ANOSIM) (Clarke and Green 1988). ANOSIM can be used to calculate either the global average difference in compositional similarity across all classes (global R) or the average difference in compositional similarity between pairs of classes (R). The global R statistic was calculated as the difference in ranked biologic similarities arising from all pairs of replicate sites *between* different classes, and the average of all rank similarities *within* classes, adjusted by the

Table 1. Average values for each of the eight defining environmental variables in each class of the 20-class level of the Marine Environment Classification. See Figure 4 for location of the classes. The horizontal divisions within the table show how environmental variation is differentiated at the 2, 4 and 9-class levels (SST = Sea Surface Temperature)

Class	Area (km ²)	Depth (m)	Seabed Slope (cm m ⁻¹)	Orbital Velocity (ms ⁻¹)	Mean Annual Solar Radiation (W m ⁻²)	SST Amplitude (°C)	SST Gradient (°C km ⁻¹)	Wintertime SST (°C)	Tidal Current (ms ⁻¹)	2-class level	4-class level	9-class level
1	88503	3001	1.4	0	17.5	2.3	0.01	19.5	0.06		Subtropical	Bathyal
22	53368	1879	1.5	0	15.4	2.4	0.01	16.3	0.11			
9	64306	5345	1.4	0	14.8	2.6	0.01	16.1	0.03			Abyssal
47	60053	2998	1.0	0	12.1	2.4	0.01	11.6	0.07	Oceanic	Plateaus and sub tropical front	
55	2213	334	1.6	0	15.5	2.4	0.02	15.1	0.20			Central
63	26626	754	0.9	0	12.8	2.4	0.02	12.1	0.18			
178	39360	750	0.4	0	9.5	1.3	0.01	7.6	0.15			Southern
127	60884	4830	0.5	0	10.7	1.7	0.01	10.0	0.05			
204	18277	2044	3.0	0	9.2	0.9	0.01	8.0	0.08		Sub-Antarctic	
273	805	2550	9.1	0	8.4	1.4	0.03	4.4	0.05			
219	93982	4779	0.6	0	8.9	1.0	0.01	6.7	0.04			
12	149	94	0.9	0.10	17.8	2.3	0.01	19.3	0.30			Northern
58	394	117	0.7	0.06	14.7	2.2	0.03	13.0	1.09	Coastal		
60	4084	112	0.3	0.02	14.4	2.5	0.02	13.2	0.26			
64	2689	38	0.3	0.27	14.2	2.9	0.02	12.6	0.19			
124	68	8	0.4	0.84	13.4	2.3	0.02	12.7	0.00			Central
130	14	10	0.4	0.35	14.1	2.4	0.09	11.9	0.21			
169	932	66	0.2	0.11	12.4	2.7	0.04	9.9	0.21			
190	339	321	1.9	0.00	12.3	2.3	0.06	9.4	0.10			
170	5208	129	0.3	0.01	10.2	1.3	0.02	9.3	0.55			Southern

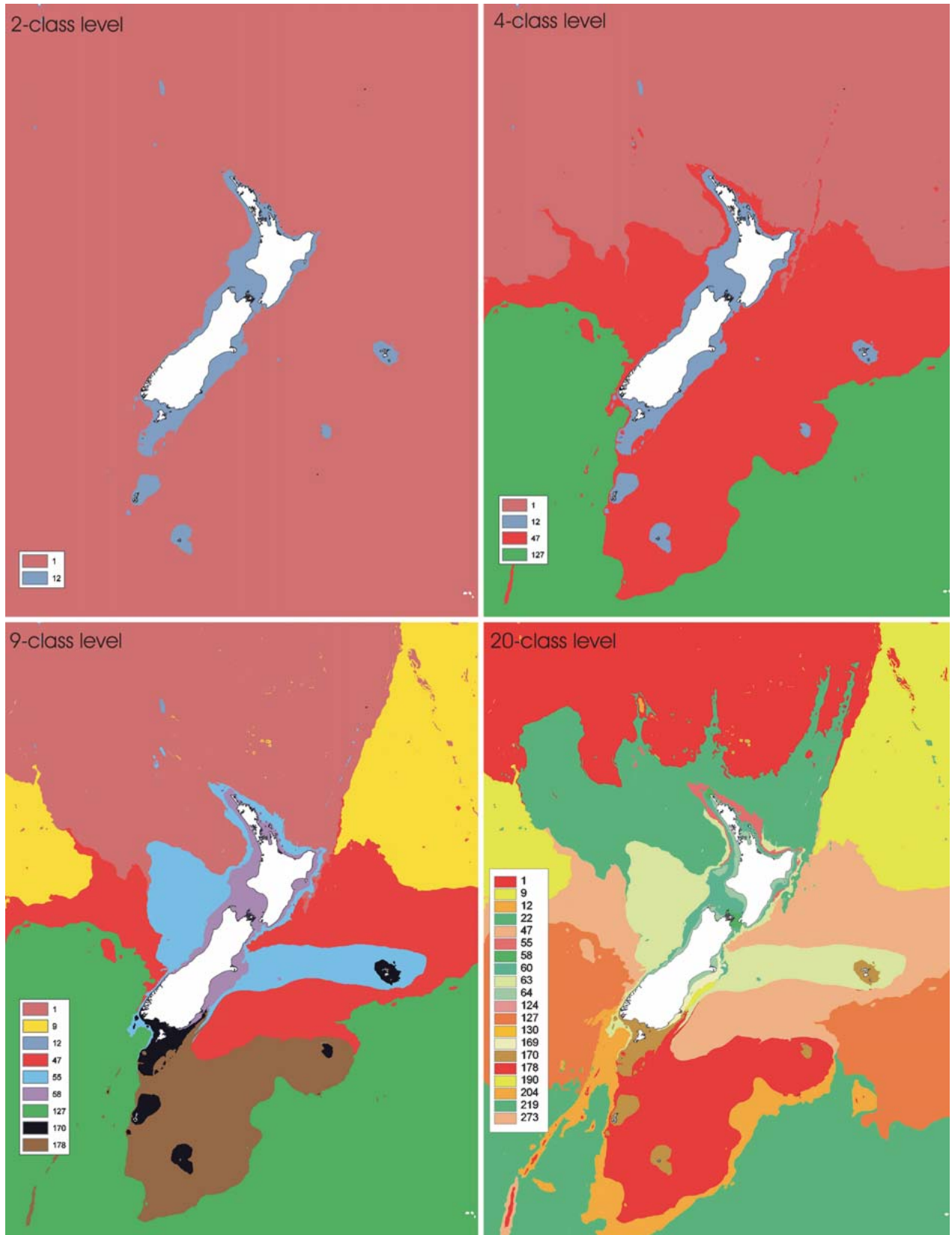


Figure 4. The MEC for the New Zealand region showing the location of classes at the 2-, 4-, 9-, and 20-class levels. The class numbers were assigned automatically during initial nonhierarchical sorting stage of the classification procedure and should be regarded as labels only.

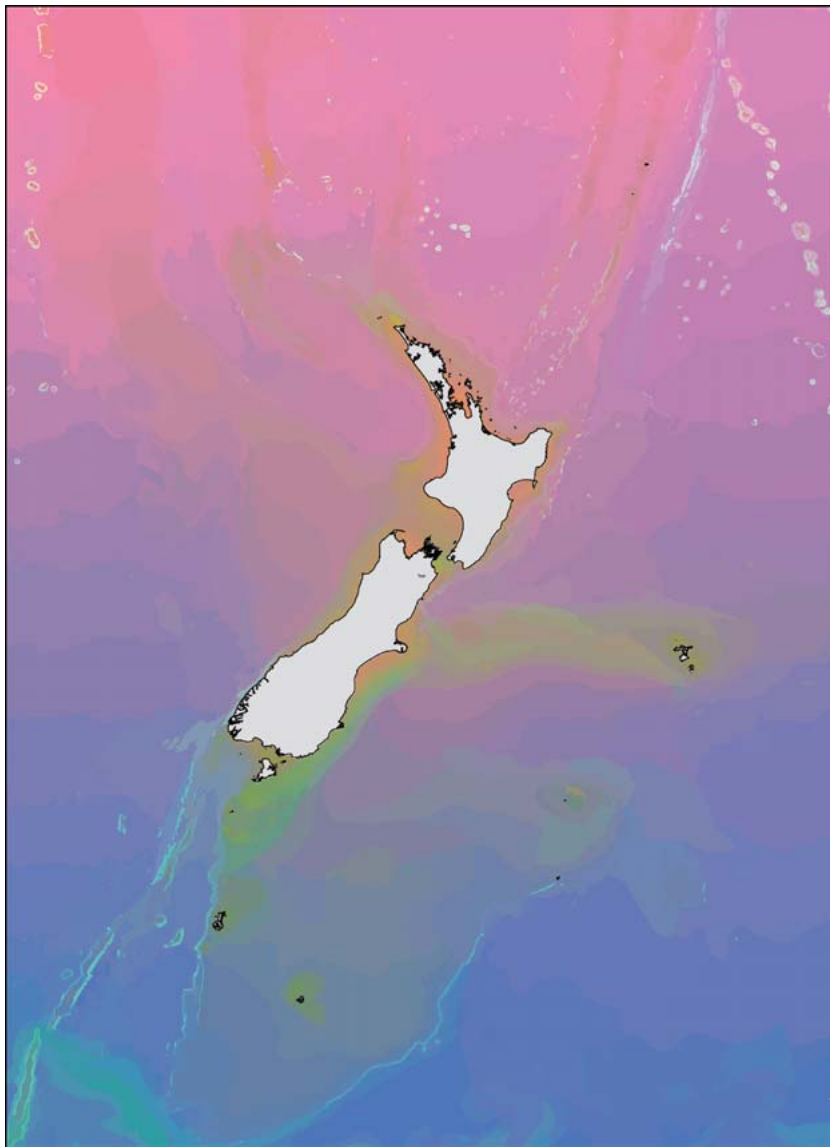


Figure 5. Map of the most detailed level (290 classes) of the MEC for the New Zealand region using a continuous color scheme. Blue shades represent areas that are deeper and have lower tidal current and lower mean orbital velocity. Red shades indicate areas having high values of wintertime SST and annual mean surface solar radiation. Green shades indicate areas with higher seabed slopes, areas of high SST gradient, and to a lesser extent, strong tidal currents. Gray lines = 1000- and 2000-meter isobaths.

total number of sites. Global R is equal to 1 if all replicates within classes are more similar to each other than any replicates from different classes and is approximately 0 if there is no class structure. The R statistic was also calculated for individual pairs of classes as the between-class similarities minus within-class similarities for all pairs of sites. The significance of the ANOSIM statistics were tested with a randomisation procedure based on the null hypothesis of no class structure (Manly 1986). The ANOSIM tests were carried out in MATLAB using the statistical procedures available in the FATHOM package (Jones 2003).

The ANOSIM analysis was complicated by both the continuous nature of the classification, which could define groups at any level of detail from 1 to 290

classes, and the limited biologic data, i.e., the latter were unevenly distributed across the environmental classes. Consequently, a large proportion of classes at any particular classification level had either few biologic sites or lacked them altogether. We therefore commenced our analysis by determining the number of classes with adequate biologic data (≥ 5 sites) at each level of the classification (Table 2). Table 2 shows that although chlorophyll and fish data were available for approximately 75% and 55% of classes at the 20-class level of the classification, adequate benthic invertebrate data were only available for 45% of the classes. We assessed the global R statistic for all classes with adequate data for a range of classification levels between 2 and 290 classes (Fig. 6). We also assessed the signifi-

Table 2. Results of the pair-wise ANOSIM analysis for the three biological datasets at varying levels of classification detail

	Level of classification detail (number of classes)	Proportion of classes contributing to test	Proportion of significant inter-class differences	Average significant ANOSIM <i>R</i> -statistic
Chlorophyll- <i>a</i>	20	0.75	0.90	0.48
	50	0.70	0.93	0.60
	100	0.57	0.96	0.63
	160	0.43	0.97	0.66
Demersal fish	20	0.55	1.00	0.59
	50	0.45	0.98	0.63
	100	0.36	0.99	0.67
	160	0.30	0.99	0.70
Benthic invertebrates	20	0.45	0.56	0.23
	50	0.32	0.62	0.39
	100	0.18	0.59	0.38
	160	0.16	0.62	0.41

cance of biologic differences for all possible pair-wise combinations of classes for the 20-, 50-, 100- and 160-class levels of the classification (Table 2).

All of the global ANOSIM *R* values were significant at the 1% level except for the benthic invertebrate data set, the values for which were nonsignificant for classification levels with < 15 classes (Fig. 6). The global *R* values generally increased for all data sets as the classification detail was increased, indicating that finer levels of classification detail defined more biologically distinctive environments (Fig. 6). The ANOSIM *R* values were higher for the fish and chlorophyll-*a* data than for the benthic invertebrates. The increase in the classification strength became more gradual for all data sets once the number of classes exceeded approximately 75.

The individual pairwise comparisons of the fish and chlorophyll-*a* data indicated that $\geq 90\%$ of the potential contrasts were significantly different in their biologic composition ($P < 0.01$, Table 2). For the benthic invertebrates the proportion of significantly different pairwise contrasts was fewer at approximately 60%. In addition, the pairwise ANOSIM *R* statistic was consistently lower for the benthic invertebrate samples than for the other two biologic data sets. Thus, the strength of the classification at any given level is lower for benthic invertebrates than for fish and chlorophyll-*a*.

Discussion

The MEC project aimed to classify New Zealand's marine environments for resource and conservation management. Although not all of the challenges that we encountered were resolved, we are confident that the final classification provides a reasonable broad-scale stratification of ecologic variation within the region. We also consider that progress has been made

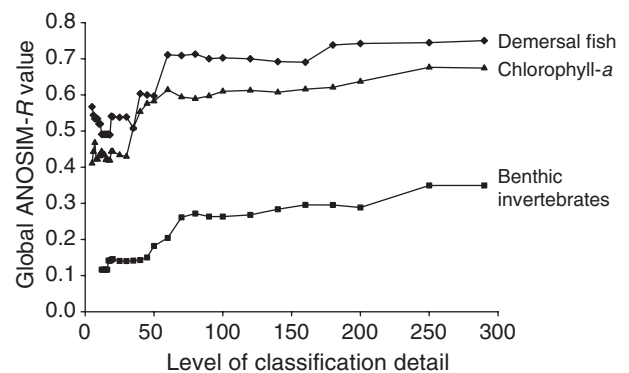


Figure 6. Results of global ANOSIM analysis for the three biologic data sets at varying levels of classification detail. All global *R* values were significant at a 1% level except for the benthic data set, for which *R* values were not significant > 15 classes. The proportion of the total classes that had adequate data to be tested at each level of the classification is shown in Table 1.

with the analytic assessment of how to combine, transform, and weight variables in a multivariate classification. Clarifying the overall conceptual framework (i.e., a classification based on environmental space) and defining clear objectives was fundamental to this process.

In large measure, development of the classification was facilitated by our ability to derive spatially explicit data layers describing variation in a number of biologically important physical variables at moderate resolution over the entire region. This reflected the diverse range of information describing New Zealand's marine environments that was already available, much of which was collected in ongoing fundamental research into the functioning of marine ecosystems.

Despite this depth of existing knowledge, many of these variables were not direct drivers of biologic variation. For example, the SST variables and depth are correlates of various water column properties that directly impact or are proxies for ecologic processes. We also lacked useful data describing some important drivers of biotic pattern. For example, freshwater input is likely to be an important cause of variation in coastal locations, and variation sea-floor sediments is likely to strongly influence benthic invertebrate community patterns. In addition, the accuracy of many variables, including depth, is variable close to shore. Future gains in classification performance are likely with the development of more direct and accurate descriptors of ecosystem drivers.

The environmental variables were moderately successful as predictors of biologic pattern. For example, the variables gave results that were a clear improvement over earlier analysis of demersal-fish distributions based on fewer and less direct environmental variables (Francis and others 2002). Similarly, the GAM and CART models of average chlorophyll-*a* explained >85% of the total variation. However, analysis of environment–biology relations was frustrated by the uneven distribution of biologic samples. Some environments had been sampled very intensively, whereas others had either inadequate samples or lacked samples entirely. For example, sampling methods such as trawling are rarely used in waters with depths >1600 m and, even in shallow waters, are rarely used on sites where the sea-floor is steeply sloping. Information from these environments could increase our confidence in the classification, which is important because future environmental concerns will no doubt increase as fishing pressure increases and the potential deep-sea mining of mineral crusts is explored (Glover and Smith 2003).

In most published classifications using multivariate methods, decisions on what variables to include as well as their weighting and transformation have been totally subjective (e.g., Belbin 1993; Leathwick and others 2003; Múcher and others 2003; Hargrove and Hoffman 2005). For this study we developed novel methods to test the effect of transformation and weighting on the strength of the classification. This enabled us to identify a set of environmental variables and their transformations and weightings that improved the correlation between biologic and environmental differences calculated between sample locations. We assumed that this definition of environmental space would produce a final classification with approximately maximum ability to discriminate or summarize variation in ecologic character. The main factor constraining our use of this approach was the uneven spread of

biologic data with respect to environmental variation. However, it was this lack of comprehensive biologic data that constrained us at the outset to implementing an environment-based classification.

Our subsequent evaluation of classification performance using the ANOSIM tests showed that the environmentally defined classes are capable of discriminating variation in biologic pattern. The relationship between the global *R* values and the level of classification detail varied by biologic data set and was lowest for the benthic invertebrates, probably reflecting both the lower taxonomic resolution of the shelf-survey data set and the lack of reliable descriptions of sea-floor sediments, which precluded the use of a substrate variable in the classification. In addition, the rate of increase in the global *R* statistic decreased with increasing classification detail, particularly for the fish and chlorophyll-*a* data sets. Our assumption was that a single hierarchical classification could represent all biotic variation and that pelagic and benthic patterns would be nested such that coarser scales of classification detail would discriminate pelagic variation and benthic variation would be discriminated at finer levels of the classification. Coarse levels of classification detail provided broad-scale stratification of the benthic data, but the global *R* statistic reached a plateau at the 80-class level, which was similar to the plateau for the fish and chlorophyll data sets but with a relatively lower *R* value. This suggests that different classification scales are relevant to different biologic patterns but did not confirm our assumption that patterns would be nested.

At least two possible reasons exist that finer-scale causes of biologic variation may not be well represented by the classification. First, because of shortcomings with existing data, we were unable to include variables describing sea-floor sediments and freshwater inputs. This omission is likely to have decreased the effectiveness of the classification at finer levels of detail likely to be important for benthic invertebrates, particularly in coastal waters where sediments and freshwater inputs may be heterogeneous on small scales (e.g., Zajac and others 2000). Second, use of the Gower distance measure assumes that the relationship between biologic and environmental variation is linear, i.e., occurs at a constant rate throughout the environmental space, but this may not be realistic (Ferrier and others 2002). Although our use of transformations increased the correspondence between environmental and biologic distances for some variables, this approach is relatively simplistic given its reliance on a limited range of parametric transformations. The generalised dissimilarity modeling approach of Ferrier and others (2002)

provides an alternative approach that may have greater flexibility.

Finally, the difference in the performance of the classification with different taxonomic groups suggests the possibility of tailoring individual classifications to discriminate different ecosystem components, e.g., demersal fish and benthic invertebrates. Although this is feasible using the methods developed here, we believe that a single integrated classification provides the best starting point for encouraging ecosystem-based management of marine resources. We suggest that development of more focused classifications should be discouraged unless this integrated classification is shown to be inadequate for particular applications.

Our classification of the New Zealand region demonstrates the feasibility of numeric environment-based methods for marine classification. In practical terms, this approach has three distinct advantages over more conventional geographic-based approaches (regionalization). First, the classification is geographically independent, meaning that it identifies groups of locations that are environmentally similar irrespective of their geographic location, and distinctive environments will be identified even if they are of small extent or occur in many scattered locations. We argue that these properties mean that our classification is more able to define the inherent patterns of variation in ecologic character than geographic approaches. Second, the numeric procedure produces classes that exhibit a high degree of within-class homogeneity, and this increases the likelihood of a consistent response to management actions within a class. This within-class homogeneity is also important where a classification is used as a framework within which to assess the representativeness of conservation reserves (e.g., Margules and Pressey 2000; Trakhtenbrot and Kadmon 2005) or as strata for sampling (e.g., Bunce and others 1996). Third, the level of similarity among all classes is quantified, allowing them to be aggregated and disaggregated for use at different levels of classification detail. This allows users to choose a level of classification detail that is most suitable for particular applications and is consistent with the view that management must occur at different levels of detail depending on the activities being considered (e.g., Christensen and others 1996). Finally, we emphasize that the classification is a “hypothesis” about biologic pattern and the utility of the broad-scale discrimination of pattern that it achieves is untested. Complete testing of such a classification is unlikely, and this means that pragmatically the classification will become part of the models and assumptions that underlie future management actions

and must be tested by monitoring (e.g., Christensen and others 1996).

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