Evaluation of Biogeographic Classification Schemes for Conservation Planning: Application to New Zealand's Coastal Marine Environment

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Abstract:

For many regions worldwide multiple and often contrasting biogeographic classifications exist that are based on a variety of taxa and techniques. This presents a major challenge for managers who must choose appropriate large-scale spatial frameworks for systematic conservation planning (SCP). We demonstrate how systematically collected community data can be used to evaluate existing biogeographic classifications, identify the most appropriate metric for biogeographic patterns seen in other taxonomic groups, and develop an independent biogeographic classification scheme for SCP. We evaluated six existing biogeographic classifications for New Zealand's nearshore marine environment using community similarity metrics based on abundance and presence-absence data for macroalgae (107 species) and mobile macroinvertebrates (44 species). The concordance between community metrics and the previous classifications was high, as indicated by a high multivariate classification success (CS) (74.3-98.3%). Subsequently we carried out an independent classification analysis on each community metric to identify biogeographic units within a hierarchical spatial framework. The classification based on macroalgal presence-absence data achieved the highest CS and is proposed as a meso-scale classification scheme where 11 regional groupings (4 northern and 7 southern), termed *bioregions* (CS=73.8-84.8%), are nested within northern and southern biogeographic provinces (CS=90.3-98.7%). We illustrate how these techniques can be used for SCP in informing the design of representative and comprehensive networks of marine protected areas by evaluating the current coverage of marine reserves in each bioregion. Currently 0.22% of the territorial sea around mainland New Zealand is protected in no-take MPA's, with between 0 and 1.5% of each bioregion represented.

Introduction

The scale of current global change in natural systems means that biogeography has moved from the status of scholarly pursuit to an urgent requirement for Systematic Conservation Planning (SCP) (Lourie & Vincent 2004; Whittaker et al. 2005). One of the primary aims of SCP is to protect the full variety of biodiversity present in a planning region (Margules & Pressey 2000). This requires an understanding of patterns of biodiversity and a hierarchical classification scheme that represents the nested nature of biological patterns across a range of spatial scales (MacNally et al. 2002; Lourie & Vincent 2004; Higgins et al. 2005). At high levels in the classification hierarchy, biogeographic data can be used to develop biologically meaningful planning units at spatial scales of 100s to 1000s of kilometers (Lourie & Vincent 2004; Whittaker et al. 2005). Such units are a prerequisite for achieving a representative system of protected areas as it provides a large-scale biogeographic framework within which finer-scale classification and modeling studies can support the selection of priority or representative areas for protection (e.g., Moritz et al. 2001; Sala et al. 2002; Airame et al. 2003; Higgins et al. 2005). For example, under the International Convention on Biological Diversity the New Zealand government have a stated goal to protect 10% of the marine environment in a network of representative marine protected areas (MPAs) based on an agreed bioregional classification system by 2010 (Anonymous 2000).

Given that biodiversity encompasses multiple levels of biological organisation, from genes to regional landscape attributes (Noss 1990) there can be numerous classifications for a single geographic region that differ in spatial extent and resolution, depending on the sampling techniques used, and the taxa or biological measures of diversity (e.g., the South African coast, Emanuel et al. 1992; Bustamante & Branch 1996; Turpie et al. 2000; Primo & Vazquez 2004). This has potential to confuse or even paralyse the decision making process because managers are faced with choosing from a set of "competing" classifications to determine the most appropriate spatial framework for SCP. Since no single study can be expected to incorporate all scales, all taxa and all levels of organisation, some confusion is perhaps inevitable. This is particularly acute in marine systems, where biogeographic boundaries are inherently diffuse and dynamic (Gaylord & Gaines 2000), there are large differences in the life-history attributes and ecology of focal organisms (Kinlan & Gaines 2003), and comparatively less is known about the appropriate methodologies or spatial scales for discerning biogeographic patterns (Lourie & Vincent 2004). While the urgent need to protect biodiversity means that the management of natural systems should be based on the best available information (Margules & Pressey 2000), approaches are needed to evaluate competing classification schemes and assess how these represent overall patterns of biodiversity.

The development of indicator or surrogate measures of diversity has been seen as a means to forward SCP in the absence of better information on biodiversity patterns (Noss 1990). Although such approaches are typically applied to SCP for the purposes of selecting priority areas for protection (Howard et al. 1998; Moritz et al. 2001), how surrogates can be used to represent different biogeographic patterns and develop biogeographic classification schemes has not been fully explored. Metrics of community similarity are often promoted as surrogates for conservation area prioritization as these are likely to maximize the overall representation of biodiversity in a region (Steinitz et al. 2005; Pawar et al. 2007). Such metrics may also be useful for developing biogeographic classifications that reflect biogeographic patterns across multiple groups of taxa. Systematically collected community data across geographic regions provide an opportunity to evaluate existing biogeographic schemes, but also to compare how different community metrics reflect biogeographic variation seen in other groups of taxa. Developing and evaluating independent classifications based on metrics that show high concordance with previous studies can provide a robust and transparent approach to choosing a large-scale spatial framework for SCP.

In the island nation of New Zealand (hereafter NZ), complexities in the near-shore marine environment (e.g. numerous offshore islands, extensive shelves, canyons, rivers, and associated variations in oceanographic processes) have created difficulties in defining clear biogeographic provinces in the region (Dell 1962). To date, several studies have divided mainland NZ into between two and four macro-scale biogeographic units (e.g., Moore 1949, Knox 1975, Walls 1995, Nelson 1994, Francis 1996, Apte & Gardner 2002; Fig. 1a). The boundaries and number of biogeographic units proposed by these authors differ depending on the spatial scale, taxonomic group(s) and techniques used (e.g., genetic analyses, records from museum collections, Delphic summaries and quantitative data). In most cases the classification methods used do not allow quantitative comparisons of the degree of biological similarity among units or demonstrate how well a given classification represents biological patterns for other taxonomic groups. Furthermore, the focus of these studies on the description of macro-scale biogeographic units (i.e. 1000s of km) is of limited value for conservation planning purposes, particularly when conservation management and decision making is carried out within smaller administrative boundaries. For example, the NZ Department of Conservation, which has the legislative obligation for the implementation, management, and monitoring of no-take marine reserves, is divided into 13 management units (termed Conservancies)(Fig. 1b).

We used data from an independent systematic survey of subtidal macroalgae and macroinvertebrates from subtidal rocky reefs throughout New Zealand's three main islands ("mainland NZ"; Fig. 1) to derive several community similarity metrics and determine their congruence with a variety of published biogeographic classification (Table 1). The different attributes of the previous classifications examined provided a means to empirically evaluate how community similarity metrics, based on two phylogenetically distinct shallow water taxa, reflected the biogeographic variation seen in other taxa and therefore assess the value of these metrics as general surrogates for coastal biogeography. We then carried out an independent classification analysis based on each community metric to both inform the evaluation of existing classifications and identify meso-scale planning units within a hierarchical framework. Subsequent classifications were evaluated to determine which classification scheme based on the available data best represents overall patterns of coastal biogeography for mainland NZ. To illustrate the utility of this approach for SCP and guide decisions required to achieve stated management goals, the optimal classification was then used to evaluate the current no-take MPA network of mainland NZ.

Methods

Biological Sampling. We used data from a broad-scale survey of 237 shallow subtidal reef sites throughout mainland NZ, where 2-15 replicate sites were sampled within 42 locations (Fig. 2, Shears & Babcock In press). Sites were selected to provide representative examples of subtidal reefs within each location; however, actual sampling sites were constrained by sea conditions and reef accessibility, resulting in large distances between sampling locations for some areas of the coast. The majority of site surveys were carried out over austral summer months between 1999 and 2002 (i.e. 194 sites), with 12 additional sites sampled on the South Island west coast in December 2003 and 31 sites around Stewart Island in February 2005. Sites were mostly located on open coasts (except at Long Island, Paterson Inlet, Port Adventure and the Fiordland locations) and were characterised by contiguous moderate sloping reefs, where depths from 0 to 12 m could be sampled within 150 m of intertidal reef. At each site, biological assemblages were sampled in five haphazardly placed 1 m^2 quadrats at four fixed depth strata (0-2, 4-6, 7-9 and 10-12 m below mean low water). For all macroalgal species (> 5 cm) the numerical abundance and size (large brown algal species), or percent cover (foliose and turfing species), was quantified in each quadrat. In addition, the abundance of all conspicuous mobile macroinvertebrates (>1 cm) was counted in each quadrat.

Data Analysis. To account for the differing field measurements for macroalgal taxa (percent cover and counts), we converted data to biomass with equations provided in Shears and Babcock (In press). Analyses were carried out on a data set for macroalgae based on total biomass and a data set for mobile macroinvertebrates based on numerical abundance. Site level information on biomass/abundance was pooled across depths as a means to integrate variations in vertical zonation and characterise the community composition at individual sites.

Two measures of community composition were used to evaluate different elements of biogeographic patterns for both macroalgae and macroinvertebrates. Community composition based on presence-absence data was used as a metric likely to reveal changes in the distributional ranges of species, while biomass or abundance data were used to represent community structure where finer-scale environmental factors are more likely to have an influence on local-scale pattern (e.g. Bustamante & Branch 1996; Shears & Babcock In press). Detection of systematic trends in biomass/abundance of species would therefore reflect biogeographical processes that do not result in the establishment or elimination of a species from a given locality, but influence its growth, fecundity, and survivorship (reflected in overall biomass/abundance).

Bray-Curtis dissimilarity was calculated for biomass/abundance and presence-absence data to represent community composition for each group of taxa, resulting in four community metrics. Calculations were based on 107 species of macroalgae and 44 species of mobile macroinvertebrates (see Shears & Babcock In press for species list). These matrices excluded species found only at one site to reduce the potential effects of unequal sampling effort among locations (Clarke & Warwick 1994). Species that could not be identified to the species level (e.g., *Ulva* spp., coralline algae) were excluded, as higher order taxonomic groupings may mask important biogeographic patterns or variation among the species within that group. Biomass/abundance data were fourth-root transformed prior to dissimilarity calculations to down-weight the relative contribution of dominant species.

Evaluation of Previous Biogeographic Classifications.

We evaluated six published biogeographic classification schemes for the coastal region of mainland NZ (Table 1, Fig. 1a). These schemes were largely based on reef-associated species (Moore 1949; Nelson 1994; Francis 1996; Apte & Gardner 2002), although the classifications of Walls (1995) and Knox (1975) included a variety of taxonomic groups (including molluscs and crustaceans) from inshore habitats. The concordance between each biogeographic classification and the four community metrics was tested with unconstrained analysis of similarity (ANOSIM, PRIMER version 6, Clarke & Warwick 1994) and constrained canonical analysis of principal coordinates (Anderson & Willis 2003). In both tests, study sites were grouped according to the biogeographic units proposed in previous studies and differences between groups tested. Canonical analysis of principal coordinates (CAP) performs a constrained ordination with reference to an a priori hypothesis (i.e. no difference in sites among groups) and carries out a permutation test for differences among groups. The CAP procedure also provides misclassification errors by carrying out a "leave-one-out" allocation of observations (sites) into groups, whereby each observation is removed from the analysis and then classified according to the nearest group centroid in canonical space (Anderson & Willis 2003). This provides a measure of the classification success (CS) of the groupings (i.e. the percentage of sites allocated to the correct group) and therefore gives an indication of how well site data for each community metric conform to the biogeographic units of previous schemes.

Hierarchical Classification based on Community Similarity Metrics. To independently investigate biogeographic patterns among the 43 sampling locations for each community metric we used principal coordinates analysis [PCOORD program, \Anderson, 2003 #235] and unweighted group-average hierarchical cluster analysis (PRIMER software, version 6). We then used similarity profile permutation tests (SIMPROF, PRIMER version 6) to identify significant groupings of locations at the 99% significance level. This resulted in a classification scheme for each metric that we evaluated with site-level data (employing ANOSIM and CAP as above), where individual sites were assigned to each location grouping and the CS tested with the leave-one-out procedure. Although some circularity is evident in this process we considered that the high-degree of variability among sites within locations provided a powerful test of the location groupings, which were based on pooled site-level data.

Results

Concordance Between Community Metrics and Previous Biogeographic Classifications. A high level of variation was evident in macroalgal and macroinvertebrate species composition among sites within each of the previously described biogeographic units (Fig. 2 – only presence-absence metrics presented). However, both unconstrained and constrained analyses revealed statistically significant differences between biogeographic units for all classification schemes for each metric (ANOSIM, significance level = 0.1% for all tests; CAP, p=0.0002 for all tests). The mean classification success (CS) of the previous classification schemes, when evaluated against each of the community metrics, ranged from 81.0 to 95.1% (Table 2a). Community metrics of macroalgal data generally achieved a higher CS than those based on macroinvertebrates, reflected in clearer regional groupings and less overlap of sites (Table 2a, Fig. 2). There were no consistent differences in the CS of metrics based on presence-absence versus those based on abundance (or biomass) data (Table 2a).

The biogeographic schemes of Nelson (1994) and Apte and Gardner (2002) achieved the highest mean CS across all metrics (Table 2a). These studies propose a northern and southern biogeographic unit (Fig. 1), and there was a high CS with little overlap among sites despite differences in their proposed boundaries (Table 2a, Fig. 2). Classifications that divided the country into more than two biogeographic units tended to achieve a lower CS, with schemes proposing four generally being the lowest. There was a particularly high level of variation among sites in Central (or Cookian) regions and a low CS. Unconstrained pair-wise tests revealed no significant difference between sites in Moore's Intermediate and Central grouping (ANOSIM, significance level >5%) for each metric except invertebrate abundance. Similarly, there was no difference between Walls' North Cape region and her Northeastern and Central regions for each metric. However, only 2 sites were sampled in the North Cape region, which was also reflected by the low mean CS for this region (Table 2a).

Regional Variation and Classification of Community Metrics. For each of the community metrics there was a general north-south spread of locations along PC1, with North Island locations on the left of ordinations and South Island locations on the right (Fig. 3). There was also some division between east and west coast locations for metrics based on macroalgal data, with several west coast locations generally grouping out on the lower portion of the ordinations (Fig. 3a and 3b). This east-west division was not evident for invertebrate data and there appeared to be greater variability among sites within each location (Fig. 3c and 3d) than seen for macroalgae.

Hierarchical cluster analysis revealed a macro-scale division between northern and southern locations based on both macroalgal community metrics (Fig. 3a and 3b). For macroalgal presence-absence all North Island locations (excluding Wellington) and locations on the northern coast of the South Island were separated from the remaining South Island locations and Wellington at the 25% dissimilarity level (Fig. 3a). A similar north-south division was evident based on macroalgal biomass data at the 15% dissimilarity level, although Banks Peninsula locations were grouped with northern locations (Fig. 3b). There was no clear macro-scale division of locations based on invertebrate assemblages (Fig. 3c and 3d).

Between 5 and 12 smaller-scale groupings were identified by SIMPROF analysis based on the four community metrics (Fig. 3). The macroalgal presence-absence metric resulted in 12 groups of locations that were spatially delineated into regional clusters within the larger northern and southern groupings (Fig. 3a). Macroalgal biomass revealed 8 groups of locations (Fig. 3b); all North Island locations (excluding Wellington) formed one group but there was discontinuity in the spatial delineation of South Island locations. Similarly, the groupings of locations based on both macroinvertebrate metrics were not spatially delineated among regions (Fig. 3c and 3d), e.g., based on abundance the northern-most location (Cape Reinga) was grouped with one of the southern-most locations (Preservation Inlet).

Significant differences were found among the location groupings identified for each of the metrics (ANOSIM, significance level = 0.1% for all tests; CAP, p=0.0002 for all tests). There was considerable variation in the CS of each location grouping when evaluated against each metric (Table 2b), but on average the macroalgal presence-absence grouping which proposed 12 groups achieved the highest mean classification success (78.8%). Interestingly, this grouping exhibited greater concordance with macroalgal biomass (85.7%) and invertebrate abundance (79.8%), than the metric upon which it was derived (macroalgal presence-absence, 76.8%), demonstrating little effect of circularity in the analytical procedure. On average groupings based on macroalgal biomass and invertebrate abundance also scored highly (76.2 and 78.2%), but these proposed fewer groups (8 and 5).

A Biogeographic Classification based on Macroalgal Presence-Absence. The high concordance of the macroalgal presence-absence community metric with previous classifications (Table 2a), the clear regional delineation of the location groupings based on this metric (Fig. 3a), and high overall CS (Table 2b), supports its use as the basis for a single biogeographic classification for mainland NZ. The 12 location groups based on algal presence-absence were divided between a northern and southern group (Fig. 3a) suggesting a macro-scale biogeographic division between a Northern and Southern province at about Cook Strait (Fig. 4). Both ANOSIM and CAP tests showed significant differences (significance level = 0.1% for all tests; CAP, p=0.0002 for all tests) between these two provinces when evaluated against all metrics, with the classification success ranging between 90.3 and 98.7% (Table 2c).

The location groupings within these larger provinces represented regionally delineated groups of locations typically at the meso-scale (100s of km). One exception was the Green Islets location, which formed its own group (Fig. 3a). However, this location was most similar to the group including Stewart Island locations, and ANOSIM carried out on site level data revealed no significant difference between these two groups, supporting the inclusion of the Green Islets with the Stewart Island grouping. Subsequently, we propose that the remaining 11 groups represent discrete meso-scale biogeographic units or "bioregions" (sensu Commonwealth-of-Australia 2006). We have named these according to the region of coast where locations are situated and approximated the boundaries between each bioregion based on boundaries proposed in previous studies (Fig. 4). The overall CS of sites into the bioregions ranged from 73.8-94.1% for the metrics and the average CS for each bioregion ranged from 66.7-94.9% (Table 2c). The Raglan and Buller bioregions generally scored the lowest, however, in many cases sites from these bioregions were misclassified as being in spatially segregated bioregions, e.g., based on macroalgal presence-absence sites from Raglan on the west coast were misclassified as Portland, which occurs at similar latitudes on the east coast.

Discussion

Evaluation of Previous Biogeographic Classification Systems

The analytical techniques we used provide an explicit approach to compare the classification success (CS) between biogeographic studies and the biogeographic units proposed. Existing classification schemes with high CS can inform conservation planning by providing confidence in their biological distinctiveness across different taxonomic groups and levels of biological organisation. Analyses showed that for all of the published biogeographic classification schemes evaluated there was high concordance with community metrics based on rocky reef macroalgae and mobile macroinvertebrate species (Table 1a). Biogeographic classifications with fewer provinces achieved the highest CS (e.g., Nelson 1994; Apte & Gardner 2002). While this could be expected due to chance, principal components analysis revealed little overlap of sites between the proposed northern and southern groups (Fig. 2) suggesting distinct attributes between northern and southern assemblages. In contrast, classifications that proposed an additional central (or Cookian) province were characterised by a lower CS and had a high degree of overlap with Northern and Southern groups. This central province, which includes Cook Strait, has generally been regarded as a region of overlap between northern warm-water species and southern cold-water species, with few species having ranges restricted to its borders (Dell 1962; Knox 1975; Adams 1994; Francis 1996). Although the analysis carried out provides strong support for distinct northern and southern groupings, the boundary between these groups differed among the studies examined highlighting the problems associated with NZ's complex nearshore marine environments and the general north-south gradient in species composition (Fig. 3).

The ability to compare a variety of existing classifications with systematically collected data from different species groups (macroalgae and macroinvertebrates) also provides a means to solve the common problem of deciding which taxa should be used for developing a biogeographic classification (e.g., Turpie et al. 2000). The overall high CS for the schemes evaluated suggests that the metrics based on subtidal rocky reef assemblage data may serve as surrogates for other species or taxonomic groups, as well as represent genetic variation associated with biogeographic provinces. Although four of the schemes evaluated were based on reef associated species, there was also high concordance with schemes based on a variety of coastal taxa (Knox 1975; Walls 1995) suggesting they may also serve as more general surrogates for coastal biogeography. We are unaware of any classifications based on taxa from other coastal habitats (e.g., soft sediment invertebrates) to further test this generality.

Differences in the congruence between existing classification schemes and the metrics used in such analyses also provide insights into the ecological processes underlying observed patterns. Community metrics based on macroalgal data tended to achieve a higher CS than those based on macroinvertebrate data and exhibited clearer regional groupings of sites (Fig. 3a). This may be due to greater potential dispersal distances and broader geographic ranges of macroinvertebrates relative to macroalgae (Kinlan & Gaines 2003). Similar results have been found in terrestrial systems where diverse taxonomic groups with limited dispersal exhibit the greatest biogeographic disjunction (Pawar et al. 2007). In addition, macroalgae are a dominant feature of subtidal reefs in temperate regions worldwide and have the ability to form complex habitats for other organisms which may explain the relatively high level of congruence with classifications based on other reef-associated taxa. Vegetation has also been recognised as a good biodiversity surrogate at broad spatial scales in terrestrial systems (MacNally et al. 2002), but at smaller spatial scales (e.g., 10s of km) vegetation appears less reliable as a surrogate of biodiversity (Ward et al. 1999; Kati et al. 2004).

The different measures of community similarity (i.e. based on presence-absence or abundance/biomass) had little influence on the levels of congruency with previous classifications, which is consistent with Mac Nally et al. (2002). However, independent classification of locations yielded contrasting results for the two macroalgal metrics. The presence-absence metric grouped locations into spatially delineated regions, while spatially disjunct locations were often grouped together based on the biomass metric. Similar patterns have been documented in terrestrial systems where presence-absence data better represent geographic variation and abundance (or biomass) data best reflect local environmental conditions (Steinitz et al. 2005). For this reason, analyses based on presence-absence data appear to be advantageous for developing broad-scale biogeographic classification schemes, whereas abundance data may be useful for better understanding ecological processes and discerning finer-scale classification or habitat units within biogeographic regions.

Development of a Hierarchical Biogeographic Classification

Once previous classifications are able to be evaluated a number of questions remain regarding which biogeographic classification to use as a spatial framework for SCP. Given that planning units should encompass the appropriate scales of biodiversity within a hierarchical framework, macro-scale biogeographic provinces alone are of limited value for conservation planning. The quantitative and consistent methodology we used provided a basis to objectively identify biogeographic groupings of sampling locations at different levels of organisation in a classification hierarchy and statistically evaluate the relative strength of these groupings for each metric. We found that the classification based on macroalgal presence-absence achieved the highest average CS when evaluated against other community metrics supporting its use as a biogeographic classification for SCP. At high levels in this classification we identified a division around Cook Strait reflecting a break between two mainland biogeographic provinces (Fig. 4). This division contrasted with previous studies in that the northern coast of the South Island was included in the Northern Province, and the south coast of the North Island lay in the Southern province. Furthermore, nested within these two provinces were eleven smaller-scale biogeographic units (termed "bioregions", sensu Commonwealth-of-Australia 2006). Such meso-scale divisions in a classification hierarchy provide ecologically meaningful planning regions at scales relevant to SCP (Lourie & Vincent 2004).

Our approach, whereby biogeographic differences among groups of locations (bioregions) were identified, meant that boundaries between bioregions could only be approximated. In such cases the spatial distribution and number of sampling locations is likely to influence the number of groupings in a proposed bioregional framework and the position of proposed boundaries. Furthermore, in some instances large distances between sampling locations in adjacent bioregions was unavoidable due to logistical constraints and the distribution of suitable habitat. While additional sampling could help better resolve boundaries or even result in a different grouping of locations, the high concordance between boundaries identified in previous studies (Fig. 1a) with those proposed based on algal species composition (Fig. 4) provides support that this classification represents biogeographic patterns seen in other taxa. As nationally consistent quantitative datasets become available from other coastal habitat types throughout NZ these will provide a further opportunity to evaluate and refine the classification presented here. However, given the complexity of island nations such as NZ and evidence suggesting that biogeographic boundaries are inherently diffuse and dynamic in marine systems (Gaylord & Gaines 2000) our approach provides a way forward in making decisions on the spatial framework for SCP.

Application to Systematic Conservation Planning

To illustrate how these techniques can be applied to SCP an analysis of the present coverage of no-take MPAs across the proposed mainland NZ bioregions is given in Fig. 4. It is clear that the cumulative area and proportional cover of reserves is at a particularly low level (308 km^2 or 0.22% of mainland territorial waters, i.e. within 12 nautical miles) and some bioregions are currently unrepresented. However, the analysis also demonstrates the uneven representation of bioregions within jurisdictions of administrative regions of the NZ Department of Conservation (conservancies). For example, some conservancies have multiple bioregions in their jurisdiction (e.g., Southland (SOU)), while some bioregions span multiple conservancies (e.g., the Northeastern bioregion). This imbalance is likely to have operational consequences for individual conservancies and means that achieving biogeographic representation in the 10% protection target across mainland NZ is going to require coordinated planning among conservancies.

The proportional area protected within each bioregion only provides us with a crude indication of the proportion of biodiversity protected as the extent and variety of marine habitats are likely to vary across bioregions. However, more importantly the proposed bioregions provide a meso-scale biogeographic framework within which one can carry out finer-scale planning and classifications to ensure that the full variety of biodiversity is represented. Although biogeographic data (species distribution and composition) have proven valuable at delimiting planning units at scales of 100s to 1000s of km, abundance data and physical proxies are likely to be more valuable in developing classification systems to encompass the variety of community types and functional ecosystem or habitat units at smaller spatial scales (1-10s of km) (e.g., Hume & Herdendorf 1988; Ward et al. 1999; Zacharias et al. 1999).

The *ad hoc* creation of reserves in New Zealand has resulted in a paucity in the number of reserves and poor representation of individual bioregions, therefore compromising the principles of SCP (Pressey et al. 1993). Although this presents a considerable challenge for managers (in terms of the size and urgency of the task), it can also be seen as an opportunity for New Zealand to show international leadership in applying SCP to marine conservation. The application of analyses such as the one we have presented here provides a defensible basis for such planning with biogeographic classifications at spatial scales relevant to management units. We have described a statistically robust approach to evaluating existing biogeographic classifications and developing a hierarchical classification based on the metric that best explains biogeographic variation observed across competing classifications. Such tools provide integrated and transparent approaches to SCP essential to aid managers and planners to achieve stated goals of representativeness and comprehensiveness in reserve network design for terrestrial, aquatic and marine ecosystems.

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Table 1. Existing marine biogeographic classifications schemes for New Zealand's nearshore marine environment evaluated in this study (see Fig. 1a for boundaries).

Classification scheme	Area[a]	Units	Method	No. of species	Groups of organisms
Qualitative classifications					
Moore (1949)	NZ archipelago [a]	7 Marine algal provinces (4 mainland)	Species distribution lists from museum collections – identified groups of species with similar range limits	200	Macroalgae
Knox (1975) [b]	NZ archipelago [a]	6 Biogeographic provinces (3 mainland)	Review of previous qualitative studies, generally based on field observations and museum collections	-	Multiple taxa from inshore and shelf habitats – macroalgae, echinoderms, scleractinia corals, gammarid amphipods, brachyura
Walls (1995)	NZ archipelago [a]	8 Biogeographic regions (4 mainland)	Delphic approach – expert workshop identified regions based on available biotic, oceanographic and geological information	-	Fish, molluscs, echinoderms, bryozoans, sponges, ascidians, antipatharians, foraminifera, brachiopods and algae
Quantitative classifications					
Nelson (1994)	NZ archipelago [a]	8 groupings [c] (2 mainland) of predefined geographical regions	Twinspan analysis of presence-absence data based on museum collections	98	Large brown macroalgae
Francis (1996)	NZ archipelago [a] (also Lord Howe and Norfolk Island)	8 groupings [c] (3 mainland) of predefined geographical regions	Principal components analysis of presence-absence data based on literature, diving observations, museum records and research trawls	375	Reef fish
Apte and Gardner (2002)	Mainland NZ	2 groups	Phylogeographic analysis of mitochondrial DNA of mussels collected throughout NZ. Divided into groups based on differences in haplotype frequencies	1	Greenshell mussel *Perna canaliculus*

[a] The New Zealand (NZ) archipelago includes the subtropical Kermadec Islands, the Chatham Islands (c.800 km to the east of New Zealand), and the group of subantarctic islands to the south.

[b] Knox's classification was also used in King et al. (1985).

[c] Groupings not specified as biogeographic regions or provinces.

Table 2. Percent classification success (CS) based on each community metric for previous marine biogeographic classifications schemes (a), groupings of locations from SIMPROF for each metric (b), and the proposed classification units (provinces and bioregions, Fig. 5) based on macroalgal species presence-absence data (c). For each scheme, excluding the SIMPROF groupings (b), the classification success for each of the proposed classification units is given (numbers in parentheses indicate the number of sites sampled within each)

	Community metric				
Classification scheme/grouping	Macroalgae PA	Macroalgae biomass	Invertebrate PA	Invertebrate Abundance	*Mean*
a					
Moore 1949	**82.3**	**84.8**	**74.3**	**82.7**	***81.0***
Auckland (76)	94.7	85.5	72.4	82.9	*83.9*
Intermediate (18)	72.2	100.0	38.9	61.1	*68.1*
Central (78)	62.8	74.4	83.3	91.0	*77.9*
Forsterian (65)	93.9	92.3	75.4	78.5	*85.0*
Knox 1975	**91.1**	**90.7**	**82.3**	**87.8**	***88.0***
Auporian (82)	96.3	96.3	91.5	95.1	*94.8*
Cookian (90)	86.7	85.6	77.8	87.8	*84.5*
Forsterian (65)	90.8	90.8	76.9	78.5	*84.3*
Nelson 1994	**97.1**	**93.3**	**94.5**	**95.4**	***95.1***
Northern (76)	98.7	96.1	96.1	98.7	*97.4*
Southern (161)	96.3	91.9	93.8	93.8	*94.0*
Walls 1995	**77.6**	**84.0**	**78.9**	**85.7**	***81.6***
North Cape (2)	50.0	100.0	50.0	0.0	*50.0*
Northeastern (69)	91.3	97.1	82.6	97.1	*92.0*
Central (89)	51.7	75.3	71.9	77.5	*69.1*
Forsterian (77)	96.1	81.8	84.4	87.0	*87.3*
Francis 1996	**94.5**	**92.4**	**82.7**	**83.5**	***88.3***
Northeastern (71)	91.6	97.2	93.0	97.2	*94.8*
Central (60)	95.0	91.7	68.3	73.3	*82.1*
Forsterian (106)	96.2	89.6	84.0	80.2	*87.5*
Apte and Gardner 2002	**98.3**	**94.5**	**88.2**	**87.3**	***92.1***
Northern (131)	100.0	100.0	87.8	87.8	*93.9*
Southern (106)	96.2	87.7	88.7	86.8	*89.9*
Community metric mean	***90.2***	***89.9***	***83.5***	***87.1***	
b					
Macroalgae PA (12 groups)	**76.8**	**85.7**	**73.0**	**79.8**	***78.8***
Macroalgae biomass (8 groups)	**83.1**	**88.6**	**65.8**	**67.1**	***76.2***
Invertebrate PA (9 groups)	**79.8**	**77.6**	**55.7**	**72.2**	***71.3***
Invertebrate abundance (5 groups)	**76.4**	**78.5**	**73.0**	**84.8**	***78.2***
c					
Provinces	**98.7**	**94.9**	**91.1**	**90.3**	***93.8***
Northern (125)	98.4	100.0	92.0	93.6	*96.0*
Southern (112)	99.1	89.3	90.2	86.6	*91.3*
Bioregions	**77.2**	**84.8**	**73.8**	**80.6**	***79.1***
Northeastern (71)	80.3	94.4	76.1	95.8	*86.7*
Portland (6)	100.0	100.0	83.3	100.0	*95.8*
Raglan (11)	63.6	72.7	72.7	45.5	*63.6*
Abel (37)	70.3	75.7	86.5	81.1	*78.4*
Cook (12)	100.0	91.7	50.0	58.3	*75.0*
Banks (8)	87.5	75.0	87.5	75.0	*81.3*
Buller (7)	71.4	42.9	71.4	71.4	*64.3*
Westland (20)	80.0	90.0	75.0	80.0	*81.3*
Fiordland (17)	94.1	88.2	52.9	52.9	*72.0*
Stewart Island (42)	59.5	78.6	71.4	83.3	*73.2*
Chalmers (6)	83.3	100.0	66.7	66.7	*79.2*

Figure 1. New Zealand marine biogeographic classification schemes evaluated in this study (a) (Dashed lines indicate proposed biogeographic boundaries, see Table 1 for details) and locations where reef communities were sampled around New Zealand (b) in the present study (see Shears & Babcock In press for site positions within each location). Locations: Cape Reinga (CR), Cape Karikari (CK), Poor Knights Island's (PKI), Mokohinau Island's (Mok), Leigh (Lei), Tawharanui (Taw), Hahei (Hah), Tuhua (Tuh), Gisborne (Gis), Mahia (Mah), Raglan (Rag), Gannet Rock (Gan), New Plymouth (New), Kapiti Island (Kap), Wellington (Wel), Long Island (Lon), Nelson (Nel), Abel Tasman (Abe), Karamea (Kar), Cape Foulwind (CFo), Kaikoura (Kai), Banks Peninsula north (Ban), Flea Bay (Fle), Moeraki (Moe), Open Bay Island (OBI), Jackson Head (JaH), Cascades (Cas), Barn Island's (Bar), Big Bay (Big), Bligh Sound (Bli), Charles Sound (Cha), Doubtful Sound (Dou), Preservation Inlet (Pre), Green Islets (GrI), Bluff (Blu), Codfish Island (Cod), Ruapuke Island (Rua), Titi Island's (Tit), Paterson Inlet (Pat), Port Adventure (Por), Otago Peninsula (Ota) and Catlins (Cat). The administrative boundaries for the Department of Conservation's management areas on land (termed *Conservancies*) are also given in (b) (see www.doc.govt.nz for Conservancy names).

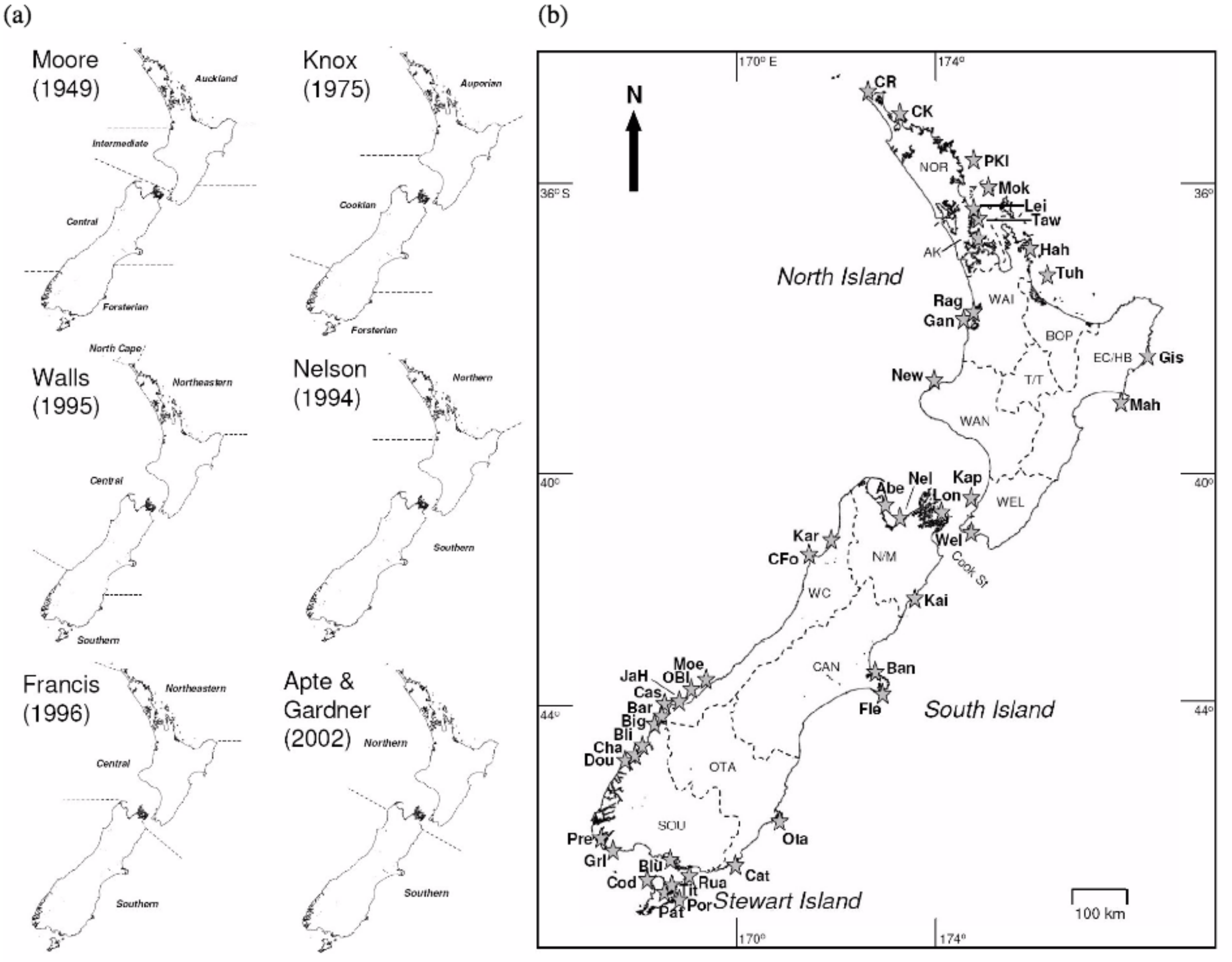

Figure 2. Concordance between macroalgae (a) and mobile macroinvertebrate (b) species composition (presence-absence) and existing biogeographic classification schemes (Figure 1a, Table 1) based on principal coordinates analysis. The ordinations are repeated for each of the six schemes and the symbols indicate the proposed biogeographic unit in which each site is located.

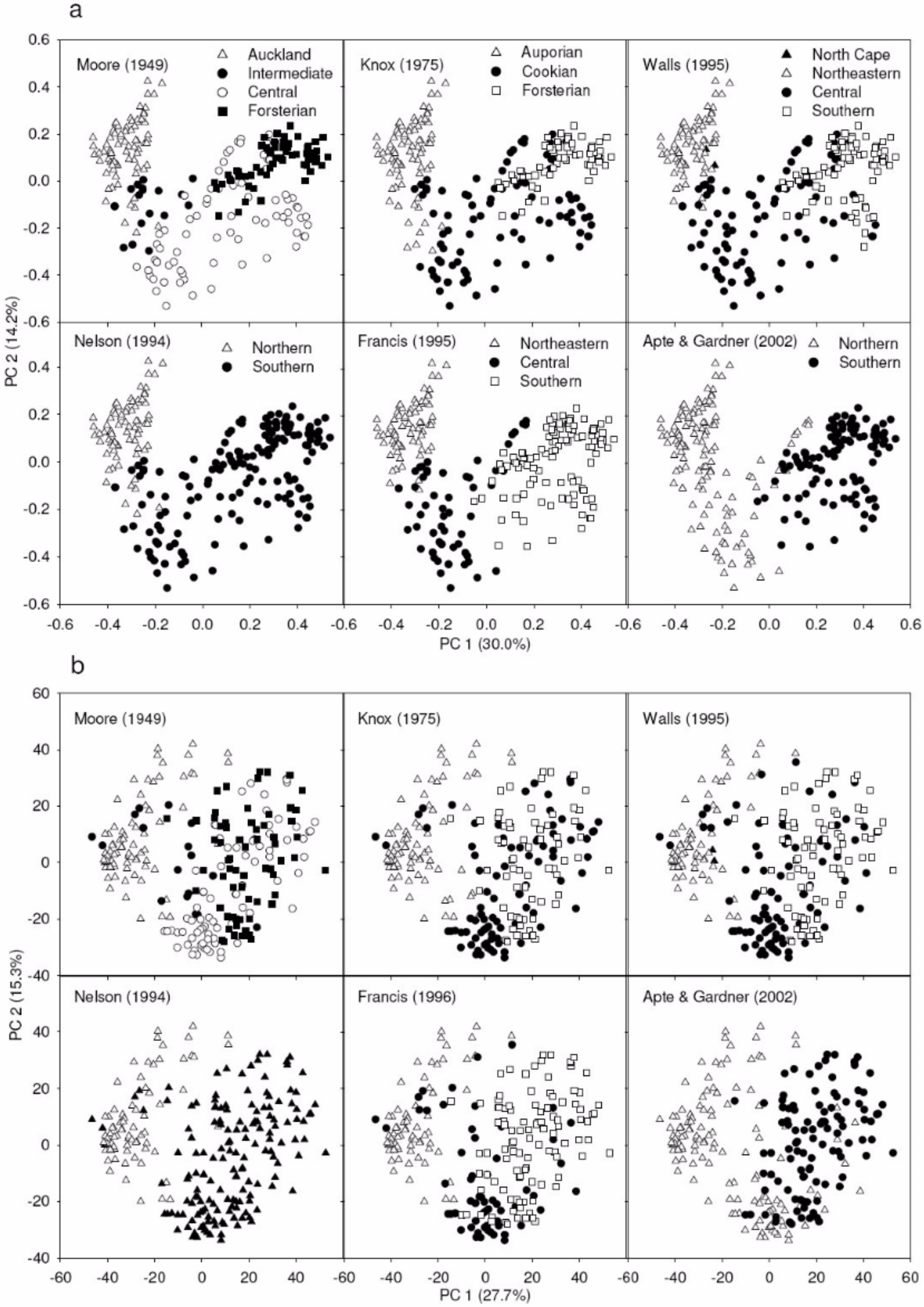

Figure 3. Principal coordinates analysis of locations based on macroalgal presence-absence (a) and biomass (b), and macroinvertebrate presence-absence (c) and abundance (d). Location symbols represent groupings identified by SIMPROF analysis, which are overlayed on the NZ coast on the right of the ordinations. Centroids are given for each location with error bars indicating variation (1 SE) among sites. Dashed line in (a) and (b) indicate a higher-order division between northern and southern locations at the 25% and 15% dissimilarity level, respectively, identified from hierarchical cluster analysis.

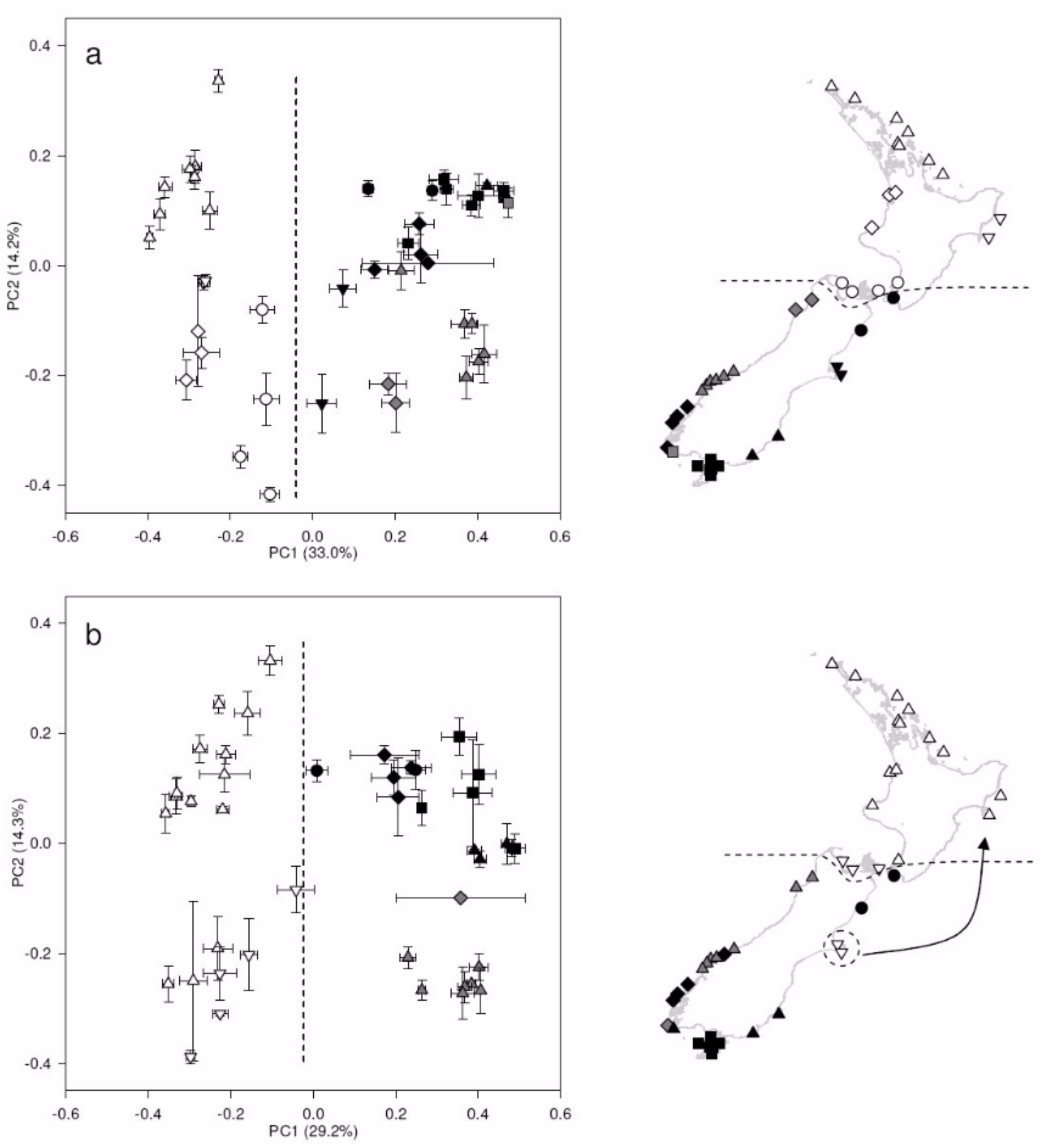

Fig. 3 Continued

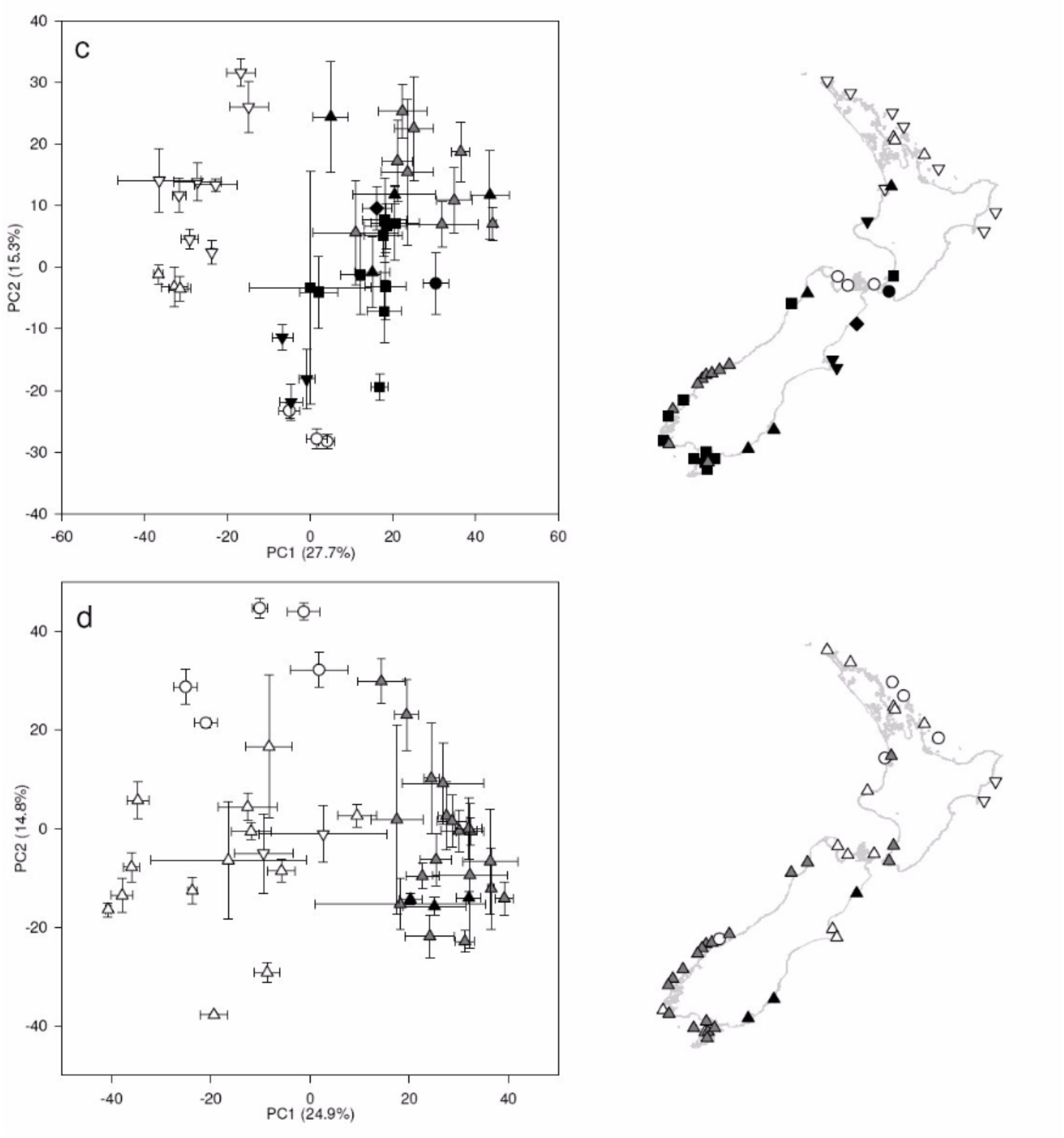

Figure 4. Proposed biogeographic provinces (Northern and Southern) and bioregions for mainland New Zealand based on groupings of locations using macroalgal species presence-absence as a surrogate (Fig. 3a and 4a). Dashed black line indicates a proposed biogeographic province break, and dashed grey bars indicate proposed boundaries between bioregions (Note: positions of boundaries between bioregions are approximated based on previous studies especially where sampling density from this study was sparse. Numbers in brackets indicate the number of existing no-take marine reserves and the percentage of the mainland territorial sea (nearshore marine environment out to 12 nautical miles) currently protected in no-take MPA's within each bioregion (calculations based on the area of the 29 mainland marine reserves administered by the Department of Conservation (see www.doc.govt.nz) and 2 other no-take MPAs: Sugarloaf Islands Conservation Area and Tawharanui Marine Park). Note: the Three Kings Islands were excluded from calculations of the mainland territorial sea.