

# Relationships between taxonomic resolution and spatial scales of multivariate variation

MARTI J. ANDERSON\*, SEAN D. CONNELL†, BRONWYN M. GILLANDERS‡, CAROL E. DIEBEL‡<sup>1</sup>, WILMA M. BLOM§, JUSTINE E. SAUNDERS¶ and TODD J. LANDERS§

\*Department of Statistics, Tamaki Campus, University of Auckland, Private Bag 92019, Auckland, New Zealand;

†Southern Seas Ecology Laboratories, DP418, School of Earth and Environmental Sciences, The University of Adelaide, Adelaide, South Australia 5005; ‡Curator of Marine Biology Collections, Auckland War Memorial Museum, Private Bag 92018, Auckland, New Zealand; §Auckland War Memorial Museum, Marine Biology Collections, Private Bag 92018, Auckland, New Zealand; and ¶Leigh Marine Laboratory, University of Auckland, PO Box 349, Warkworth, New Zealand

†Southern Seas Ecology Laboratories, DP418, School of Earth and Environmental Sciences, The University of Adelaide, Adelaide, South Australia 5005; ‡Curator of Marine Biology Collections, Auckland War Memorial Museum, Private Bag 92018, Auckland, New Zealand; §Auckland War Memorial Museum, Marine Biology Collections, Private Bag 92018, Auckland, New Zealand; and ¶Leigh Marine Laboratory, University of Auckland, PO Box 349, Warkworth, New Zealand

## Summary

1. We investigated the effects of changes in taxonomic resolution on analyses of patterns of multivariate variation at different spatial scales for the highly diverse fauna inhabiting holdfasts of the kelp *Ecklonia radiata*.

2. Multivariate analyses were performed using several transformations to examine differences in spatial patterns of variation from metres up to hundreds of kilometres for composition vs. relative abundance in assemblages.

3. The greatest variability in assemblages occurred at the smallest spatial scale, from plant to plant, pointing to the existence of important small-scale processes. The proportional amount of variation at the smallest spatial scale decreased with decreasing taxonomic resolution (i.e. from species through to phyla). For composition, the next-greatest source of variation was at the largest spatial scale (hundreds of kilometres), while for relative abundance, the next-greatest source of variation was at the level of sites (hundreds of metres to kilometres).

4. For abundance data, location-level variation became less important and site-level variation became more important with decreasing taxonomic resolution, while for compositional data, the opposite pattern occurred. This suggests that variation in the presence of species or taxa at a particular location along the coast is driven by large-scale processes, while variation in relative abundances within locations is driven by medium-scale processes.

5. The lack of significant variation in the proportional abundances of phyla at large spatial scales suggests that some consistency of pattern may emerge at larger scales (spatial and/or taxonomic), even in the presence of high small-scale variability. These findings strengthen the idea that substantial local variation need not preclude the existence of broad-scale organization in ecological patterns and biodiversity.

*Key-words:* biodiversity, kelp holdfast assemblages, marine invertebrates, multi-scale patterns, New Zealand.

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Correspondence: M. J. Anderson, Department of Statistics, Tamaki Campus, University of Auckland, Private Bag 92019, Auckland, New Zealand. Tel: 64 9 373 7599 ext. 85052; Fax: 64 9 373 7000; E-mail: mja@stat.auckland.ac.nz

<sup>1</sup>Present address: Director of Natural Environment, Te Papa Tongarewa – National Museum of New Zealand, 169 Tory Street, Wellington, New Zealand.

## Introduction

Understanding spatial patterns of variation in ecological systems is essential in order to develop and test hypotheses about processes (Dutilleul 1993; Underwood, Chapman & Connell 2000). Our understanding of spatial patterns of variation, in turn, depends on the scale at which we

choose to observe them (Andrew & Mapstone 1987; Wiens 1989; Levin 1992); yet there are constraints on general inferences imposed by arbitrary local scales of observation. Attempts to generalize often involve comparisons of independent small-scale studies that employed different sampling protocols. Such comparisons usually highlight the inconsistency of patterns, reinforcing the idea that few generalities are possible in ecology, with measures of variation often being greatest at local scales (Levin 1992; Underwood & Chapman 1996). The result is a potential bias against the development of ecological generality (Fowler-Walker & Connell 2002). There is an increasing need, therefore, to test the existence of general patterns using coherent sampling protocols that span the range of regions of interest.

A useful way of thinking about and measuring different ecological scales centres on a hierarchical approach, where smaller-scaled phenomena (or sampling structures) are nested within larger-scaled ones (Allen & Starr 1982; Kotliar & Wiens 1990). Structured hierarchical sampling designs have been used successfully to investigate and explicitly quantify spatial scales of variability in marine populations and assemblages on rocky intertidal shores (Archambault & Bourget 1996; Underwood & Chapman 1996; Benedetti-Cecchi 2001) subtidal hard surfaces (Glasby 1998; Fraschetti *et al.* 2001), in benthic soft-sediment systems (Morrisey *et al.* 1992; Kendall & Widdicombe 1999; Stark, Riddle & Simpson 2003) and in mangrove forests (Chapman 1998a). Despite numerous studies of the incredibly diverse marine fauna inhabiting kelp holdfasts from many parts of the world, often sampled from several sites over large spatial areas (Jones 1971; Moore 1974; Edwards 1980; Sheppard, Bellamy & Sheppard 1980; Ojeda & Santelices 1984; Smith, Simpson & Cairns 1996; Smith & Simpson 1998), to our knowledge there has not been an explicit quantitative study of natural spatial scales of variation in such assemblages.

We provide here a quantitative study of spatial scales of variation for faunal assemblages inhabiting holdfasts of the kelp, *Ecklonia radiata* (C. Agardh) J. Agardh, in north-eastern New Zealand. Although there are many ways in which scaling issues can be manifested in ecological phenomena and studies of them (e.g. Dungan *et al.* 2002), our focus here is on three specific aspects of 'scale' and their interaction: (1) the relative importance of spatial scales of variation (from metres up to hundreds of kilometres); (2) the effects of taxonomic scales of resolution (from species to phyla) on analyses of these spatial patterns; and (3) the effects of different transformations (from raw abundances to simple presence/absence) on such analyses. The latter two may be thought of as simplifications of complex systems which may either clarify important features of the data or result in a loss of information (Levin 1992).

Transformations are known to affect analyses of multivariate patterns (Clarke & Green 1988; Olsford, Somerfield & Carr 1998; Legendre & Gallagher 2001; Stark *et al.* 2003). They can be used to shift the emphasis

of the analysis onto different components of the biota along a continuum from the most abundant and dominant species or taxa (for untransformed data) through to the rare taxa (for presence/absence data) (e.g. Clarke 1993; Goodsell & Connell 2002). Moore (1974) suggested that reducing abundance data down to presence/absence may lead to an increase in efficiency, despite a loss of information, and proposed that ecological patterns would still be clear from reduced data if the number of species was ~30 or more (Frontier & Ibanez 1974; Moore 1974).

We expected that the use of different transformations would have significant effects on our perceptions of spatial patterns in kelp holdfast assemblages. Specifically, we were interested in the qualitative ecological difference in emphasis between changes in composition vs. changes in relative abundance. When analysing presence/absence data, the variability being measured is explicitly the variation in the presence or absence of particular species (or taxa) in different holdfasts at different places: thus compositional change is the essential (and only) feature. This can be contrasted against analyses based on other transformations (or untransformed data) for which variation in relative abundance plays a more important, or even a dominant, role in the analysis.

Previous studies of the effects of reducing taxonomic resolution have generally focused on whether or not the loss of information results in a loss of our ability to detect significant effects, particularly environmental impacts (Warwick 1988; Somerfield & Clarke 1995; Olsford *et al.* 1998; Olsford & Somerfield 2000; Stark *et al.* 2003) or changes in biodiversity (Williams & Gaston 1994; Gaston & Blackburn 1995; Balmford, Jayasuriya & Green 1996). Using higher taxa rather than species can lead to greater efficiency, as enumerating abundances of all organisms down to a fine level of taxonomic resolution takes considerable resources and expertise that could be redirected to more replication and better sampling designs.

Our interest in taxonomic resolution is not to see whether or not patterns seen in species data can be recovered using lower levels of resolution, such as families or phyla. Rather, we postulated that different 'scales' of taxonomic resolution are like different scales of spatial or temporal resolution: different processes drive variation in the system at different levels. We expect that spatial processes of biogeography, climate and history will create variation at large scales for higher taxonomic levels, whereas processes at smaller scales, such as competition, settlement and behaviour, will create additional local variation for species. Combinations and balances in these forces should be seen through the analysis of different levels of taxonomic resolution at different spatial scales. Species should be affected by large-scale and small-scale processes, whereas higher-level taxa should only be affected by large-scale processes. Specifically, we hypothesized that:

1. There will be high and significant variability detected at small and at large spatial scales for data analysed at the species level.

2. The relative importance of variability at small spatial scales will decrease with decreases in taxonomic resolution.
3. At low levels of taxonomic resolution (e.g. whole phyla), we expect to see very little variation at small scales, but significant variation at large spatial scales should remain.

## Methods

### COLLECTION OF HOLDFASTS

Kelp holdfasts of the species *E. radiata* were collected according to a structured hierarchical experimental design. The largest spatial scale examined was locations (four levels, separated by hundreds of kilometres), which were approximately equally spaced along a large stretch of the north-eastern coast of New Zealand (Fig. 1) and included Berghan Point (34°55'78"S, 173°32'72"E), Home Point (35°19'38"S, 174°21'38"E), Leigh (36°17'43"S, 174°48'82"E) and Hahei (36°50'86"S, 175°49'32"E). Within each location, there were two sites (separated by hundreds of metres to kilometres), and within each site, there were two areas (separated by tens of metres and measuring approximately 10 m × 10 m). Within each area,  $n = 5$  replicate holdfasts, separated by several metres, were taken haphazardly from the kelp forest. The depth at each site was kept fairly uniform (median = 12 m, interquartile range = 11.0 m–14.5 m) and sites had similar exposures to the north-east (Fig. 1). The median for each location from 18 values of fetch calculated at 20-degree intervals ranged from 927 m to 1301 m.

Holdfasts were collected by cutting off the stipe of the plant at its base, covering the holdfast with a plastic bag, and prying the holdfast away from the substratum into the bag, which was then sealed with a plastic zip tie. At the surface, holdfasts were immersed in a 10% solution of magnesium chloride (Epsom salts) for a period of approximately 1 h to relax the organisms. Holdfasts were then fixed and stored in a solution of

5–7% formalin buffered in seawater. All collections were completed within a period of 1 month during the austral summer, from 7 January to 5 February 2002.

In the laboratory, individual holdfasts and the contents in each bag were rinsed onto a 0.5 mm sieve. All organisms retained on the sieve, or remaining attached to the holdfast, were identified down to the finest level of taxonomic resolution possible or practicable. This differed for different groups. For example, molluscs and bryozoans were generally identified to species, several polychaetes and crustaceans were identified only to family level, while nemerteans, sipunculids and flatworms were counted at the phylum level. We shall refer to the individual taxa identified to the lowest practical level possible as 'species'. Individuals of each species were counted, but for organisms that were encrusting or colonial (e.g. sponges, ascidians, bryozoans, etc.), an ordinal semiquantitative score from 0 to 3 was given according to the relative coverage of the organism on the holdfast. This corresponds to a scaling which would be comparable to that of very abundant taxa (numbering in the hundreds or thousands) after transformation to a fourth-root or log scale. No data were obtained for algae; only fauna were enumerated. In addition, the volume of each holdfast was measured using water displacement.

### STATISTICAL ANALYSES

Multivariate data consisted of counts from a total of 80 holdfasts for each of 351 taxa ('species'). The data were analysed according to the three-factor hierarchical experimental design using permutational multivariate analysis of variance (PERMANOVA, Anderson 2001a; McArdle & Anderson 2001). This approach partitions the variability in the original dissimilarity matrix according to the full multifactorial design, with tests of individual terms obtained using permutations. For all analyses, the volume of the holdfast was included as a covariate, because the diversity and abundance of assemblages in holdfasts vary significantly with holdfast volume (e.g. Sheppard *et al.* 1980; Ojeda & Santelices 1984; Smith *et al.* 1996). Measures of multivariate variability at different spatial scales were calculated from the mean squares of the PERMANOVA, using a direct multivariate analogue to the usual ANOVA estimators of variance components (e.g. Searle, Casella & McCulloch 1992). We refer to these as measures of 'pseudo' multivariate variation because, unlike a traditional multivariate variance-covariance matrix, they contain no information regarding covariances among variables (Mardia, Kent & Bibby 1979). The statistical significance of each pseudo multivariate variance component was tested using a random subset of 4999 permutations of residuals under a reduced model (Anderson 2001b), with appropriate units being permuted for each term in the design (Anderson & ter Braak 2003).

For graphical presentation and comparisons, the variability at each spatial scale is expressed as a proportion of the total variation (after removing the effect of the

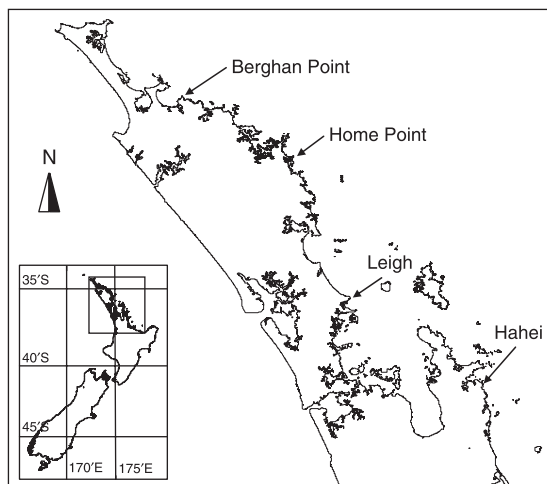


Fig. 1. Map of the locations from which kelp holdfasts were sampled.

covariate). That is, for the additive variance components, we have:  $\hat{\sigma}_T^2 = \hat{\sigma}_L^2 + \hat{\sigma}_S^2 + \hat{\sigma}_A^2 + \hat{\sigma}_R^2$ , where subscripts indicate total (*T*), location (*L*), site (*S*), area (*A*) and residual (*R*) or error variability. Then, for example, a value in a graph showing proportional variability for locations is given as  $\hat{\sigma}_L^2/\hat{\sigma}_T^2$ . This was also performed so that analyses based on different numbers of variables and/or different transformations could be compared. Comparisons of proportions of variation explained by individual variance components between different data sets may be difficult, particularly if the data sets differ in their proportion of residual variation or in their sampling design (Underwood & Petraitis 1993). This does not pose a problem in the present investigation, however, because the same data set was being examined, just using different analytical treatments (i.e. different taxonomic resolutions, transformations, etc.).

Separate analyses were performed on data sets constructed for each of the following levels of taxonomic resolution: species (351 variables), genus (296 variables), family (213 variables), order (72 variables), class (26 variables) and phylum (15 variables). For each of these taxonomic levels, separate analyses were also performed using the Bray–Curtis measure on different transformations: presence/absence, square-root, fourth-root or untransformed data. Data were also analysed using Euclidean distance on data standardized by the total number of organisms in the holdfast (i.e. proportions). The latter is useful because it concentrates only on differences in relative proportional abundances, a tangible quality of assemblage structure that is not addressed directly by the Bray–Curtis measure on untransformed data. Non-metric multidimensional scaling ordinations (NMDS) and second-stage NMDS plots (Sommerfield & Clarke 1995) were performed to visualize and compare results from analyses based on different transformations and taxonomic resolutions, using the PRIMER version 5 computer program (Clarke & Gorley 2001).

## Results

The analysis at the taxonomic level of species, using the Euclidean distance on proportions, showed a significant relationship of the assemblage with volume of the holdfast (which occurred in all analyses) and significant variability at small and medium spatial scales (areas and sites), but not at the scale of locations (Table 1). The

greatest component of variation occurred at the smallest spatial scale (the residual, 55%), followed by site-to-site variation (33.6%), with areas and locations contributing very little (at 6.6% and 4.7%, respectively, Table 1).

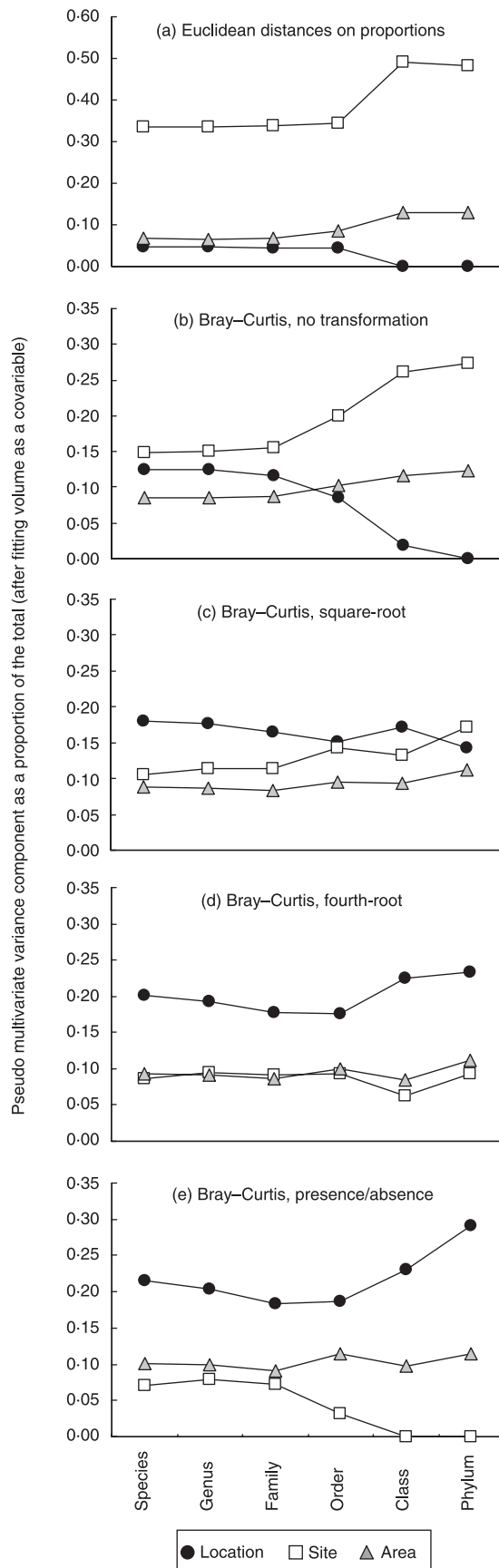
With decreases in taxonomic resolution, the relative importance of site-to-site variability increased, at the expense of location-to-location variability (Fig. 2a). In fact, components of variation from location to location were estimated at zero for class-level and phylum-level analyses (Fig. 2a). Although variation due to locations was never detected to be statistically significant using Euclidean distances on proportions (Table 2), the estimated size of the component due to locations did decrease with decreases in taxonomic resolution (Fig. 2a).

**Table 2.** *P*-values for tests of significant variability at different spatial scales for different levels of taxonomic resolution and using different transformations. Results that are not significant at the 0.05 level are given in bold type. Note that the smallest possible *P*-value with 4999 permutations is 0.0002; note also that no corrections have been made for multiple tests

	Euc	BC p/a	BC 4th-root	BC sqrt	BC nt
Species					
Loc	<b>0.1506</b>	0.0004	0.0002	0.0004	0.0002
Site	0.0006	0.0030	0.0004	0.0002	0.0006
Area	0.0022	0.0002	0.0002	0.0002	0.0002
Genus					
Loc	<b>0.1518</b>	0.0010	0.0002	0.0002	0.0002
Site	0.0002	0.0020	0.0002	0.0002	0.0004
Area	0.0020	0.0002	0.0002	0.0002	0.0002
Family					
Loc	<b>0.1734</b>	0.0002	0.0004	0.0006	0.0002
Site	0.0002	0.0034	0.0006	0.0004	0.0002
Area	0.0018	0.0002	0.0002	0.0002	0.0002
Order					
Loc	<b>0.2098</b>	0.0004	0.0002	0.0004	0.0076
Site	0.0002	<b>0.1650</b>	0.0006	0.0002	0.0002
Area	0.0010	0.0002	0.0002	0.0002	0.0002
Class					
Loc	<b>0.7680</b>	0.0010	0.0002	0.0002	<b>0.3026</b>
Site	0.0026	<b>0.5916</b>	<b>0.0648</b>	0.0058	0.0020
Area	0.0004	0.0136	0.0010	0.0010	0.0016
Phylum					
Loc	<b>0.7432</b>	0.0030	0.0002	0.0176	<b>0.4060</b>
Site	0.0012	<b>0.5824</b>	0.0312	0.0060	0.0054
Area	0.0004	0.0264	0.0014	0.0006	0.0014

**Table 1.** PERMANOVA based on Euclidean distances calculated on proportional abundances of individual species per holdfast (351 variables) with volume as a covariate, including estimates of pseudo multivariate variation at each spatial scale and expressed as a proportion of the total (ignoring the covariate)

Source	d.f.	SS	MS	<i>F</i>	<i>P</i>	Variation	Proportion
Volume = covariate	1	0.1109	0.1109	5.734	0.0004		
Location	3	0.5448	0.1816	1.220	0.1506	0.00164	0.047
Site (Location)	4	0.5954	0.1488	4.818	0.0006	0.01179	0.336
Area (site (Location))	8	0.2472	0.0309	1.598	0.0022	0.00232	0.066
Residual	63	1.2181	0.0193			0.01930	0.551
Total	79	2.7163				0.03505	



**Fig. 2.** Proportion of variability accounted for by individual pseudo multivariate variance components of location, site and area, for each of several kinds of analysis, as indicated (a–e). Proportions have been calculated from PERMANOVA mean squares after fitting volume as a covariate.

**Table 3.** Proportions of the variability accounted for by the pseudo multivariate variance component for the residual, after fitting volume as a covariate and all other spatial scales in the full model

	Species	Genus	Family	Order	Class	Phylum
Euc	0.551	0.551	0.550	0.524	0.379	0.388
BC, nt	0.642	0.640	0.642	0.614	0.603	0.604
BC, sqrt	0.626	0.625	0.638	0.610	0.603	0.574
BC, 4th-rt	0.620	0.622	0.645	0.632	0.628	0.563
BC, p/a	0.615	0.620	0.653	0.666	0.687	0.611

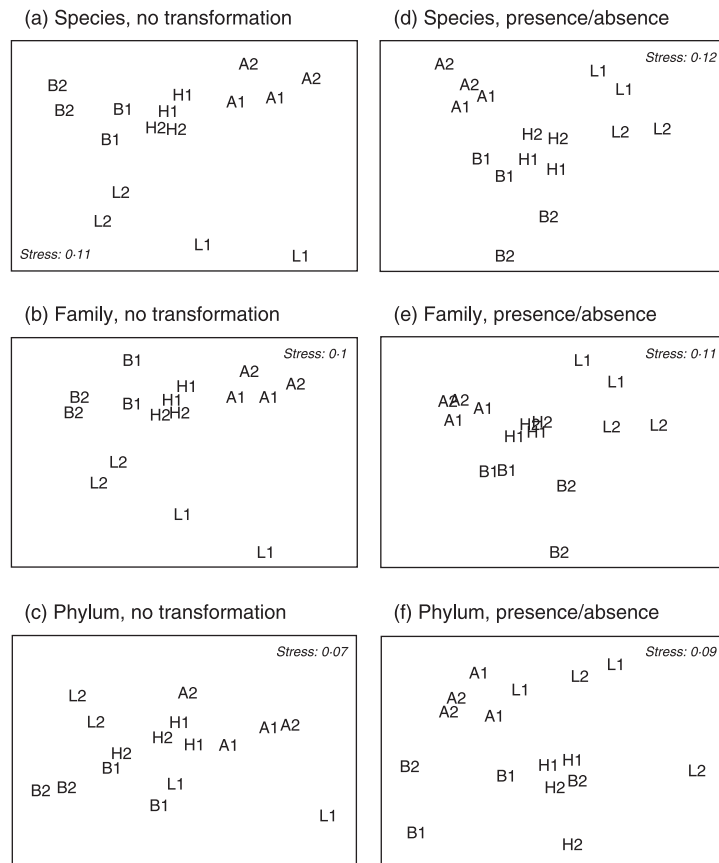
In addition, the variability from one holdfast to the next (residual) was also reduced with decreases in taxonomic resolution (Table 3).

Similar patterns were seen for the analysis of assemblages based on Bray–Curtis dissimilarities of untransformed abundance data (Fig. 2b). Although the variation from location to location was detected as statistically significant for analyses at the species, genus, family and order levels, it was not statistically significant at the level of class or phylum using Bray–Curtis on untransformed data (Table 2). This result can be seen visually in NMDS plots, where individual sites and locations remain distinct for analyses on untransformed data using either species or families, but location-level differences are no greater than site-level differences for the analysis of phyla (see the left-hand side of Fig. 3a–c). For this and for other analyses using the Bray–Curtis measure, there was not, however, an obvious decrease in the relative proportion of residual variation with decreases in taxonomic resolution (Table 3).

These results (using either Bray–Curtis on untransformed data or Euclidean distances on proportions) imply that variability in either the proportions or raw abundances of the most abundant taxa is greatest from site to site (scales of hundreds of metres to kilometres), with very little additional variation seen from one location to the next (scales of hundreds of kilometres along the coast). Locations did not differ significantly in assemblage structure in terms of proportional or raw abundances of major phyla for holdfasts of a given volume.

With increases in the severity of the transformation, moving toward an emphasis on the less abundant taxa and more on composition, there is an important concomitant shift in the pattern of relative importance of different spatial scales. For analyses based on the Bray–Curtis measure, as we move from untransformed to square-root transformed, then on to fourth-root transformed and finally to data transformed to presence/absence, we see a gradual swap in relative importance of variability at different scales: initially, sites > locations, but with increasing severity of transformation, locations > sites (cf. Fig. 2b–e). This occurs with very little change in either the relative importance of variability due to areas (Fig. 2b–e) or in the residual variation (Table 3).

Analyses using presence/absence data (Fig. 2e) emphasize changes in composition only and showed increases



**Fig. 3.** Non-metric MDS plots of assemblages in kelp holdfasts at each of two sites (indicated by 1 or 2) in each of four locations (B = Berghan Point, H = Home Point, A = Hahei and L = Leigh), generated for three different taxonomic resolutions (species, family or phylum) and Bray–Curtis dissimilarities from either untransformed or presence/absence data. Each point represents the centroid from  $n = 5$  replicate holdfasts within an area, with two areas per site.

in variation among locations with decreases in taxonomic resolution, at the expense of variability due to sites. In fact, they showed no significant variability among sites at the level of order, class or phylum (Table 2). These patterns are seen visually in NMDS plots where the variability among sites and locations is clear using either species or family-level resolution (Fig. 3d,e). At the level of phylum, however, site-level differences are not as clear, although locations remained fairly distinct (Fig. 3f).

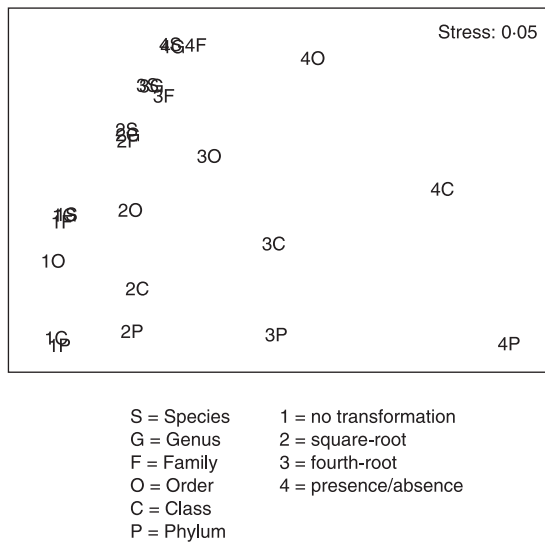
The results suggest that the presence of a particular species, family or phylum in a particular holdfast is largely driven by processes at large spatial scales (hundreds of kilometres), while relative or proportional abundances are driven by processes at the site level (hundreds of metres). In addition, variation in occurrences or relative abundances of species was always greatest at the smallest spatial scale, from one holdfast to another. This indicates that rapid turnover and change in these assemblages occurs at fine scales and fine taxonomic resolutions. Another result which was fairly consistent regardless of which taxonomic resolution or transformation was used: the area-to-area variation remained relatively constant and statistically significant, although small in size, ranging from 6.6 to 13.0% of the total variation (Fig. 2).

Further insights were obtained from a second-stage NMDS plot. For each of the transformations, there was very little difference between analyses based on species, genus or family, with the S, G and F symbols virtually superimposed on top of one another (Fig. 4). This is reflected in the similar-looking NMDS plots for the species and family-level analyses shown in Fig. 3. Analyses using different transformations appear to differ in similar ways, regardless of taxonomic resolution: symbols 1, 2, 3 and 4 move progressively from the left to the right of the diagram. Analyses on the basis of order, class or phylum then radiate downwards in a 'fan'-shaped pattern, from top to bottom (as in Olsgard *et al.* 1998). Thus, differences at different taxonomic resolutions are more marked for presence/absence data, and less marked for untransformed data.

## Discussion

### SPATIAL SCALES OF VARIATION

There was generally significant variation in kelp holdfast assemblages at all spatial scales, but the relative importance of different spatial scales in the hierarchy varied with different taxonomic resolutions and with different



**Fig. 4.** Second-stage NMDS plot showing the relationships among Bray–Curtis dissimilarity matrices among kelp holdfasts with changes in taxonomic resolution and choice of transformation. Each dissimilarity matrix is indicated by two symbols. For example, 3C indicates the analysis based on fourth-root transformed abundance data at the taxonomic level of class.

choices of transformation. One of the most salient and consistent results was that the largest proportion of variation occurred at the smallest spatial scale: from one kelp holdfast to the next at a scale of just metres. For analyses based on Bray–Curtis dissimilarities, the proportion of multivariate variation at the smallest spatial scale (residual or error variation) ranged from 56.3% to 68.7%. Such large variation at small spatial scales (from tens of centimetres up to several metres) has been found by many other studies of marine invertebrate communities: in soft-sediment systems (Morrissey *et al.* 1992; Stark *et al.* 2003), on subtidal hard surfaces (Glasby 1998; Frascchetti *et al.* 2001; Fowler-Walker & Connell 2002) and on rocky intertidal shores (Archambault & Bourget 1996; Underwood & Chapman 1996; Benedetti-Cecchi 2001). Small-scale spatial variation may well be a common feature of invertebrate communities. There are many different possible mechanisms that may explain patchiness at these small scales, including behavioural aggregation (Chapman 1998b), small-scale heterogeneity of habitat (Archambault & Bourget 1996), competitive interactions (Connell 1961), differential settlement cues (LeTourneux & Bourget 1988) or patchy disturbance and succession (Sousa 1979; Thrush *et al.* 1996).

The use of the kelp holdfast itself as a natural ‘sampling package’ (*sensu* Kitching, Daiqin & Stork 2001) obviates the need for an arbitrary decision to be made about an appropriate scale to use at the lowest level, i.e. the size and shape of sampling unit (Andrew & Mapstone 1987; Bellehumeur, Legendre & Marcotte 1997). Individual plants correspond to a natural unit of experience (scale-wise) for the organisms sampled. Mechanisms that can

produce small-scale patchiness in kelp holdfast assemblages may include aggregation of certain components of the biota relative to individual plants (Thiel & Vásquez 2000), diversity in the density or diversity of forest stands and the spatial arrangement of neighbouring plants (Goodsell & Connell 2002; Goodsell *et al.* 2004), mobility of fauna among plants (Norderhaug, Christie & Rinde 2002) and variation in the health of plants (Cole & Syms 1999).

#### RELATIONSHIP WITH TAXONOMIC RESOLUTION

The proportional amount of variation at the level of individual kelp plants (residual variation) did decrease with decreases in taxonomic resolution, in accordance with our hypothesis. This suggests that small-scale processes are of less importance for higher taxonomic groups, such as whole families or phyla. Some care is required in interpreting this result, however, because two important aspects of reducing taxonomic resolution are a reduction in the number of variables and a reduction in the number of zeros in the data set (Vanderklift, Ward & Jacoby 1996). These effects are complex and were not distinguished in the present study.

Variation in composition was greatest at large spatial scales: locations separated by hundreds of kilometres along the coast (that is, over and above the high residual variation from plant to plant, as already described). We therefore propose that the processes which determine the presence or absence of particular species, genera, families and even phyla are largely those governed by large spatial scales, such as oceanographic dispersal and transport mechanisms, biogeography, history, climate and latitudinal gradients in environmental variables, such as temperature, sunlight, type of substratum, turbidity or nutrients. These processes may be acting on the biotic structure of kelp holdfast assemblages directly, or indirectly through their actions on the demography of kelp forests (Schiel & Foster 1986; Schiel 1990).

In contrast, the greatest variation in raw or proportional abundances of individual species (or families or phyla) over and above the residual occurred at spatial scales of sites (hundreds of metres), not locations. In fact, variation among locations was so small as to be estimated at zero in the case of phyla or classes when proportional abundances were analysed. Thus, we postulate that the mechanisms driving differences in the abundances of the most prevalent species (or higher taxa) occur at medium scales – from site to site within particular locations along the coast.

One possible mechanism that could generate variation in relative abundances at the scale of sites is variation in the dispersal of larvae and recruitment (Underwood & Denley 1984; Gaines & Roughgarden 1985; Gaines, Brown & Roughgarden 1985; Underwood & Chapman 1996). Other possible mechanisms include medium-scale variation in topography, currents or exposure.

In addition, kelp periodically experience dieback at the scale of whole forests at a site, which may be followed by dispersal-mediated recovery processes in developing forests (Cole & Syms 1999; Schiel 1990; Reed *et al.* 2000).

Some other studies provide evidence to support the notion that variability at larger scales is compositional, while smaller-scale variation is driven more by changes in relative abundance, particularly by numerically dominant taxa. Chapman (1998a) investigated the effect of a reduction from 93 taxa down to nine major groups on spatial patterns of differences in assemblages of mangrove forests. She found strong correlations in the Bray–Curtis dissimilarities among sampling units, using either coarse or fine resolution. Nevertheless, transformations to fourth-root altered patterns observed within sites (separated by tens of metres), although patterns of differences between sites remained (Chapman 1998a), suggesting differences among quadrats (metres apart) within sites were mostly determined by changes in relative abundances of individual taxa within the major groups, rather than compositional change. Archambault & Bourget (1996), in a study of intertidal assemblages of the St Lawrence Estuary, Canada, found that species richness was best explained at the scale of kilometres, while variation in abundance was best explained by small scales (less than 20 cm).

#### EFFECTS OF TRANSFORMATIONS

In our study, effects of changes in taxonomic resolution varied, depending on the transformation used. However, results obtained using species, genera or families were highly comparable for a given transformation. This is consistent with results obtained in previous studies (Vanderklift *et al.* 1996; Olsgard *et al.* 1998; Stark *et al.* 2003) and suggests that family-level identifications are sufficient for distinguishing natural spatial patterns of variability in these kelp holdfast assemblages. It is unlikely that organisms which were identified only at the family level dominated the species-level analyses. There was a substantial reduction in the total number of variables from analyses based on species (351) to those based on families (213).

The effect of decreasing taxonomic resolution beyond orders to classes or phyla did, however, result in important changes in perceived patterns of spatial variation. These differences were more pronounced for presence/absence data and progressively less important for square-root, fourth-root and raw abundance data. For presence/absence data, decreases in taxonomic resolution to class or phylum resulted in increases in the proportional importance of location-level effects and the virtual disappearance of site-level effects. In contrast, for raw abundance data, decreases in taxonomic resolution resulted in increases in the proportional importance of site-level effects and the virtual disappearance of location-level effects. For intermediate transformations (fourth-root and square-root), information on relative abundances and composition are both included in

balance and, as a consequence, significant spatial variation was detected at all spatial scales even at low taxonomic resolutions.

#### PREDICTIONS FROM LOCAL TO REGIONAL SCALES

Our prediction that location-level effects would be maintained at higher levels of taxonomic resolution was incorrect. In fact, differences in the proportional abundances of higher-level taxa were not statistically significant across locations, given site-to-site variability. That is, the proportional abundances of annelids, arthropods, molluscs, echinoderms, etc. within holdfasts did not differ significantly among locations. It is not possible to know whether this apparent lack of difference in the proportions of phyla at large spatial scales was caused simply by our inability to detect it over and above the large site-to-site variation, which apparently increased with decreasing taxonomic resolution, or whether it was caused by a genuine decrease in location-to-location variation. However, location-level variation was estimated to be zero for these analyses (Fig. 2a), suggesting that there is consistency in relative proportions of classes or phyla at large spatial scales.

The potential for apparent structure at large scales to arise out of chaos or stochasticity at small scales was discussed by Chesson (1996). He provided models showing how non-linear dynamics of populations (such as density dependence) combined with spatial heterogeneity occurring at small spatial scales may average out to produce stability in populations or communities at large spatial scales (Chesson 1996). Kitching (1987), in studies of food webs for animals inhabiting water-filled tree holes, contrasted ‘local’ webs, shaped largely by stochastic events and short- and mid-term environmental heterogeneity vs. ‘regional’ webs, for which plausible deterministic explanations were available. Sale & Guy (1992) suggested that supposed ‘emergent properties’ at higher taxonomic levels (such as families or guilds) for coral reef fishes also may be explained by simple processes of random averaging. Chesson’s models were intended to be applied to single populations at increasing spatial scales. It is possible, however, that apparent stability in assemblages at large scales may be produced in a similar fashion simply through the ‘lumping’ procedure of decreasing taxonomic resolution.

The approach we used measured multivariate variability in the structure of assemblages at different spatial scales directly. This contrasts with many previous studies in biodiversity that have inferred the relative importance of local vs. regional processes purely on the basis of the nature of the relationship between local and regional richness (e.g. Cornell & Lawton 1992; Cornell & Karlson 1996). Potential problems with this approach have been discussed (Srivastava 1999; Crawley & Harral 2001), and Cornell & Lawton’s (1992) original idea has also been extended to include measures of beta-diversity in addition to alpha-diversity (e.g. Rivadeneira,

Fernández & Navarrete 2002). In contrast, here we considered variance to be the real currency of ecological relevance for investigation. Multivariate measures, by including information on identities of taxa, have greater sensitivity and information content than do univariate summary statistics such as richness (e.g. Clarke 1993). The partitioning of dissimilarity matrices according to the hierarchical design using PERMANOVA gave multivariate measures of variation in assemblage structure, providing an informative basis for directly analysing and comparing community variation at different spatial scales.

We have made observations based only on one time of sampling, which limits the inferential scope of our results. Nevertheless, we propose that the most important spatial scales of variation in kelp holdfast assemblages on temperate reefs in north-eastern New Zealand depend on which aspect of the assemblage is of interest. For compositional variation, the smallest spatial scale (i.e. from plant to plant) and the largest spatial scale of locations (hundreds of kilometres) are most important. For variation in relative abundances, the smallest spatial scale and the intermediate scale of sites (hundreds of metres) were most important. These individual natural 'packages' of intense diversity, which are discrete, phylogenetically complex, widespread and replicated, provide a remarkable insight into patterns of scaling in marine communities. We suggest that the relationships we found between taxonomic resolution and spatial scales of variation will be found in other speciose assemblages in marine or other ecological systems with open populations. We hypothesize that while large-scale processes will drive compositional variation, intermediate-scale processes will drive variation in relative abundance. This conjecture remains to be tested.

In conclusion, these results suggest that researchers are generally working at scales where complexity and variation are often greatest (i.e. at local or small scales). However, the relative consistency of patterns in biodiversity across large scales at high taxonomic levels is encouraging. It suggests that large-scale patterns can emerge from complexity at local scales and provide predictive capacity to new situations and localities with different taxonomic composition (i.e. at biogeographical scales). This realization not only suggests that there are opportunities to uncover general patterns in ecology, but that such generalities may also have predictive power for new insights across biogeographical regions that remain unexplored.

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### References

- Allen, T.F.H. & Starr, T.B. (1982) *Hierarchy: Perspectives for Ecological Complexities*. University of Chicago Press, Chicago.
- Anderson, M.J. (2001a) A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.
- Anderson, M.J. (2001b) Permutation tests for univariate or multivariate analysis of variance and regression. *Canadian Journal of Fisheries and Aquatic Sciences*, **58**, 626–639.
- Anderson, M.J. & ter Braak, C.J.F. (2003) Permutation tests for multi-factorial analysis of variance. *Journal of Statistical Computation and Simulation*, **73**, 85–113.
- Andrew, N.L. & Mapstone, B.D. (1987) Sampling and the description of spatial pattern in marine ecology. *Oceanography and Marine Biology: Annual Review*, **25**, 39–90.
- Archambault, P. & Bourget, E. (1996) Scales of coastal heterogeneity and benthic intertidal species richness, diversity and abundance. *Marine Ecology Progress Series*, **136**, 111–121.
- Balmford, A., Jayasuriya, A.H.M. & Green, M.J.B. (1996) Using higher-taxon richness as a surrogate for species richness. II. Local applications. *Proceedings of the Royal Society of London, Series B*, **263**, 1571–1575.
- Bellehumeur, C., Legendre, P. & Marcotte, D. (1997) Variance and spatial scales in tropical rain forest: changing the size of sampling units. *Plant Ecology*, **130**, 89–98.
- Benedetti-Cecchi, L. (2001) Variability in abundance of algae and invertebrates at different spatial scales on rocky sea shores. *Marine Ecology Progress Series*, **215**, 79–92.
- Chapman, M.G. (1998a) Relationships between spatial patterns of benthic assemblages in a mangrove forest using different levels of taxonomic resolution. *Marine Ecology Progress Series*, **162**, 71–78.
- Chapman, M.G. (1998b) Variability in trail-following and aggregation in *Littorina unifasciata* Gray. *Journal of Experimental Marine Biology and Ecology*, **224**, 49–71.
- Chesson, P. (1996) Matters of scale in the dynamics of populations and communities. *Frontiers of Population Ecology* (eds R.B. Floyd, A.W. Sheppard & P.J. De Barro), pp. 353–368. CSIRO Publishing, Melbourne.
- Clarke, K.R. (1993) Non-parametric multivariate analysis of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.
- Clarke, K.R. & Gorley, R.N. (2001) *PRIMER v5: User Manual Tutorial*. Primer-e, Plymouth, UK.
- Clarke, K.R. & Green, R.H. (1988) Statistical design and analysis for a biological effects study. *Marine Ecology Progress Series*, **46**, 213–226.
- Cole, R.G. & Syms, C. (1999) Using spatial pattern analysis to distinguish causes of mortality: an example from kelp in north-eastern New Zealand. *Journal of Ecology*, **87**, 963–972.
- Connell, J.H. (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, **42**, 710–723.

- Cornell, H.V. & Karlson, R.H. (1996) Species richness of reef-building corals determined by local and regional processes. *Journal of Animal Ecology*, **65**, 233–241.
- Cornell, H.V. & Lawton, J.H. (1992) Species interactions, local and regional processes, and limits to the richness of ecological communities: a theoretical perspective. *Journal of Animal Ecology*, **61**, 1–12.
- Crawley, M.J. & Harral, J.E. (2001) Scale dependency in plant biodiversity. *Science*, **291**, 864–868.
- Dungan, J.L., Perry, J.N., Dale, M.R.T., Legendre, P., Citron-Pousty, S., Fortin, M.-J., Jakomulska, A., Miriti, M. & Rosenberg, M.S. (2002) A balanced view of scale in spatial statistical analysis. *Ecography*, **25**, 626–640.
- Dutilleul, P. (1993) Spatial heterogeneity and the design of ecological field experiments. *Ecology*, **74**, 1646–1658.
- Edwards, A. (1980) Ecological studies of the kelp, *Laminaria hyperborea*, and its associated fauna in south-west Ireland. *Ophelia*, **19**, 47–60.
- Fowler-Walker, M.J. & Connell, S.D. (2002) Opposing states of subtidal habitat across temperate Australia: consistency and predictability in kelp canopy–benthic associations. *Marine Ecology Progress Series*, **240**, 49–56.
- Fraschetti, S., Bianchi, C.N., Terlizzi, A., Fanelli, G., Morri, C. & Boero, F. (2001) Spatial variability and human disturbance in shallow subtidal hard substrate assemblages: a regional approach. *Marine Ecology Progress Series*, **212**, 1–12.
- Frontier, S. & Ibanez, F. (1974) Utilisation d'une cotation d'abondance fondée sur une progression géométrique, pour l'analyse des composantes principales en écologie planctonique. *Journal of Experimental Marine Biology and Ecology*, **14**, 217–224.
- Gaines, S., Brown, S. & Roughgarden, J. (1985) Spatial variation in larval concentrations as a cause of spatial variation in settlement for the barnacle, *Balanus glandula*. *Oecologia*, **67**, 267–272.
- Gaines, S. & Roughgarden, J. (1985) Larval settlement rate: a leading determinant of structure in an ecological community of the marine intertidal zone. *Proceedings of the National Academy of Sciences USA*, **82**, 3707–3711.
- Gaston, K.J. & Blackburn, T.M. (1995) Mapping biodiversity using surrogates for species richness: macro-scales and New World birds. *Proceedings of the Royal Society of London, Series B*, **262**, 335–341.
- Glasby, T.M. (1998) Estimating spatial variability in developing assemblages of epibiota on subtidal hard substrata. *Marine and Freshwater Research*, **49**, 429–437.
- Goodsell, P.J. & Connell, S.D. (2002) Can habitat loss be treated independently of habitat configuration? Implications for rare and common taxa in fragmented landscapes. *Marine Ecology Progress Series*, **239**, 37–44.
- Goodsell, P.J., Fowler-Walker, M.J., Gillanders, B.M. & Connell, S.D. (2004) Variations in the configuration of algae in subtidal forests: implications for invertebrate assemblages. *Austral Ecology*, **29**, 350–357.
- Jones, D.J. (1971) Ecological studies on macroinvertebrate populations associated with polluted kelp forests in the North Sea. *Helgoländer wiss. Meeresunters*, **22**, 417–441.
- Kendall, M.A. & Widdicombe, S. (1999) Small scale patterns in the structure of macrofaunal assemblages of shallow soft sediments. *Journal of Experimental Marine Biology and Ecology*, **237**, 127–140.
- Kitching, R.L. (1987) Spatial and temporal variation in food webs in water-filled treeholes. *Oikos*, **48**, 280–288.
- Kitching, R.L., Daiqin, L. & Stork, N.E. (2001) Assessing biodiversity 'sampling packages': how similar are arthropod assemblages in different tropical rainforests? *Biodiversity and Conservation*, **10**, 793–813.
- Kotliar, N.B. & Wiens, J.A. (1990) Multiple scales of patchiness and patch structure: a hierarchical framework for the study of heterogeneity. *Oikos*, **59**, 253–260.
- Legendre, P. & Gallagher, E.D. (2001) Ecologically meaningful transformations for ordination of species data. *Oecologia*, **129**, 271–280.
- LeTourneux, F. & Bourget, E. (1988) Importance of physical and biological settlement cues used at different spatial scales by the larvae of *Semibalanus balanoides*. *Marine Biology*, **97**, 57–66.
- Levin, S.A. (1992) The problem of pattern and scale in ecology. *Ecology*, **73**, 1943–1967.
- Mardia, K.V., Kent, J.T. & Bibby, J.M. (1979) *Multivariate Analysis*. Academic Press, London, UK.
- McArdle, B.H. & Anderson, M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, **82**, 290–297.
- Moore, P.G. (1974) The kelp fauna of northeast Britain. III. Qualitative and quantitative ordinations, and the utility of a multivariate approach. *Journal of Experimental Marine Biology and Ecology*, **16**, 257–300.
- Morrisey, D.J., Howitt, L., Underwood, A.J. & Stark, J.S. (1992) Spatial variation in soft-sediment benthos. *Marine Ecology Progress Series*, **81**, 197–204.
- Norderhaug, K.M., Christie, H. & Rinde, E. (2002) Colonisation of kelp imitations by epiphyte and holdfast fauna; a study of mobility patterns. *Marine Biology*, **141**, 965–973.
- Ojeda, F.P. & Santelices, B. (1984) Invertebrate communities in holdfasts of the kelp *Macrocystis pyrifera* from southern Chile. *Marine Ecology Progress Series*, **16**, 65–73.
- Olsgard, F. & Somerfield, P.J. (2000) Surrogates in marine benthic investigations – which taxonomic unit to target? *Journal of Aquatic Ecosystem Stress and Recovery*, **7**, 25–42.
- Olsgard, F., Somerfield, P.J. & Carr, M.R. (1998) Relationships between taxonomic resolution, macrobenthic community patterns and disturbance. *Marine Ecology Progress Series*, **172**, 25–36.
- Reed, D.C., Raimondi, P.T., Carr, M.H. & Goldwasser, L. (2000) The role of dispersal and disturbance in determining spatial heterogeneity in sedentary organisms. *Ecology*, **81**, 2011–2026.
- Rivadeneira, M.M., Fernández, M. & Navarrete, S.A. (2002) Latitudinal trends in rocky intertidal herbivore assemblages: spatial scale and the relationship between local and regional species richness. *Marine Ecology Progress Series*, **245**, 123–131.
- Sale, P.F. & Guy, J.A. (1992) Persistence of community structure: what happens when you change taxonomic scale? *Coral Reefs*, **11**, 147–154.
- Schiel, D.R. (1990) Macroalgal assemblages in New Zealand: structure, interactions and demography. *Hydrobiologia*, **192**, 59–76.
- Schiel, D.R. & Foster, M.S. (1986) The structure of subtidal algal stands in temperate waters. *Oceanography and Marine Biology: Annual Review*, **24**, 265–307.
- Searle, S.R., Casella, G. & McCulloch, C.E. (1992) *Variance Components*. John Wiley and Sons, Toronto.
- Sheppard, C.R.C., Bellamy, D.J. & Sheppard, L.S. (1980) Study of the fauna inhabiting the holdfasts of *Laminaria hyperborea* (Gunn.) Fosl. along some environmental and geographical gradients. *Marine Environmental Research*, **4**, 25–51.
- Smith, S.D.A. & Simpson, R.D. (1998) Recovery of benthic communities at Macquarie Island (sub-Antarctic) following a small oil spill. *Marine Biology*, **131**, 567–581.
- Smith, S.D.A., Simpson, R.D. & Cairns, S.C. (1996) The macrofaunal community of *Ecklonia radiata* holdfasts: description of the faunal assemblage and variation associated with differences in holdfast Volume. *Australian Journal of Ecology*, **21**, 81–95.
- Somerfield, P.J. & Clarke, K.R. (1995) Taxonomic levels in marine community studies, revisited. *Marine Ecology Progress Series*, **127**, 113–119.

- Sousa, W.P. (1979) Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. *Ecology*, **60**, 1225–1239.
- Srivastava, D.S. (1999) Using local-regional richness plots to test for species saturation: pitfalls and potentials. *Journal of Animal Ecology*, **68**, 1–16.
- Stark, J.S., Riddle, M.J. & Simpson, R.D. (2003) Human impacts in soft-sediment assemblages at Casey Station, East Antarctica: spatial variation, taxonomic resolution and data transformation. *Austral Ecology*, **28**, 287–304.
- Thiel, M. & Vásquez, J.A. (2000) Are kelp holdfasts islands on the ocean floor? – indication for temporarily closed aggregations of peracarid crustaceans. *Hydrobiologia*, **440**, 45–54.
- Thrush, S.F., Whitlatch, R.B., Pridmore, R.D., Hewitt, J.E., Cummings, V.J. & Wilkinson, M.R. (1996) Scale-dependent recolonization: the role of sediment stability in a dynamic sand-flat habitat. *Ecology*, **77**, 2472–2487.
- Underwood, A.J. & Chapman, M.G. (1996) Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia*, **107**, 212–224.
- Underwood, A.J., Chapman, M.G. & Connell, S.D. (2000) Observations in ecology: you can't make progress on processes without understanding the patterns. *Journal of Experimental Marine Biology and Ecology*, **250**, 97–115.
- Underwood, A.J. & Denley, E.J. (1984) Paradigms, explanations, and generalizations in models for the structure of intertidal communities on rocky shores. *Ecological Communities: Conceptual Issues and the Evidence* (eds D.R. Strong, D.S. Simberloff, L.G. Abele & A.B. Thistle), pp. 151–180. Princeton University Press, Princeton, NJ.
- Underwood, A.J. & Petraitis, P.S. (1993) Structure of intertidal assemblages in different locations: how can local processes be compared? *Species Diversity in Ecological Communities* (eds R. Ricklefs & D. Schuler), pp. 39–51. University of Chicago Press, Chicago, IL.
- Vanderklift, M.A., Ward, T.J. & Jacoby, C.A. (1996) Effect of reducing taxonomic resolution on ordinations to detect pollution-induced gradients in macrobenthic infaunal assemblages. *Marine Ecology Progress Series*, **136**, 137–145.
- Warwick, R.M. (1988) The level of taxonomic discrimination required to detect pollution effects on marine benthic communities. *Marine Pollution Bulletin*, **19**, 259–268.
- Wiens, J.A. (1989) Spatial scaling in ecology. *Functional Ecology*, **3**, 385–397.
- Williams, P.H. & Gaston, K.J. (1994) Measuring more of biodiversity: can higher-taxon richness predict wholesale species richness? *Biological Conservation*, **67**, 211–217.

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