



# Numbers and density of species as measures of biodiversity on rocky shores along the coast of New South Wales

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## ABSTRACT

Numbers of species at mid-shore levels on rocky shores were sampled across 415 km to test hypotheses about patterns along the coast of New South Wales, Australia. In two different years, sampling in winter revealed increased numbers of species sampled over shores with increasing distance from north to south. There was no such trend during summer. The latitudinal increase in species was due to sessile fauna and to a lesser extent, to mobile fauna. Encrusting and foliose algae did not contribute to the pattern. The seasonal difference was mostly due to changing numbers of species between seasons. The numbers of species per sample-unit (i.e. species-density) always increased with distance from north to south in both seasons and both years when grain-size of sampling was quadrats (scattered <1 m apart) or sites on the shore (20–30 m apart). Species-density was unreliable as an estimate of diversity along the coast, because it revealed spurious trends in summer when there was no increased number of species from north to south. Analyses of densities, dispersions, frequencies of occurrences and multivariate dissimilarities of the organisms did not explain why species' densities showed a trend along the coast. Comparisons of diversity where species are not censused, but must be sampled, are made difficult by the dispersions of individual taxa across sample-units.

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## 1. Introduction

Patterns of biodiversity or variation in abundances of species along large stretches of coastlines have been studied worldwide (e.g. Canada, Archambault and Bourget, 1996; South Africa, Bustamante and Branch, 1996; Xavier et al., 2007; Japan, Nakaoka et al., 2006; Europe, Jenkins et al., 2005; Cole and Chapman, 2007; USA, Foster, 1990; Blanchette et al., 2006; Sagarin and Gaines, 2006; South America, Rivadeneira et al., 2002; Kelaher et al., 2007). Differences in numbers of species across large areas of the same habitat are generally thought to be determined by processes that operate at large scales. Consequently, many studies have investigated biological variation across large areas with respect to physical gradients of environmental variation (McQuaid et al., 2000; Benedetti-Cecchi et al., 2001; Denny et al., 2004), including upwelling (Menge et al., 2004) and temperature (Crisp, 1964).

Quantifying patterns in abundances of plants and animals over large scales is also important for reliable measures of ecological variables in order to test for generality of local ecological processes across large scales (e.g. Foster, 1990; Chapman and Underwood, 1998) and to provide baseline data for accurate assessment of large-scale impacts. Biodiversity on the coast is under threat from increasing anthropogenic use of coastal areas, although it has received relatively little attention (Gray,

1997). To understand the loss of species in response to these threats and potential consequent changes to assemblages and their effects on ecological functions, patterns in numbers of species must first be quantitatively documented and understood.

The need to quantify biodiversity requires a definition of what to measure and how it is to be measured. Biodiversity (a shortened form of biological diversity; Wilson and Peter, 1988) has many different operational meanings, although the most commonly used and simplest for ecologists is the number of species in a given area (Gray, 1997). Different methods have been used to measure the number of species and the meanings of such measures have been confused in the literature (Hurlbert, 1971). For example, the number of species in a sampling unit (i.e. species-density) is not the same as the number of species recorded over a defined habitat or area, such as an island (Gray, 2001a). This is entirely analogous to the difference between abundance of some population in an area and the density of that population per sample-unit as an estimate of abundance. The mean number of species per sampling unit is an average measure of species-density, not a measure of “species richness”, although it is often considered as such. Different methods of counting species affect estimates of diversity (Gotelli and Colwell, 2001) and thus conclusions about variation in diversity across different scales. Gray (2001a,b) clearly indicated the need to distinguish between whether numbers of species are measured per sample-unit, per area, habitat, region, assemblage, etc., before attempting to draw conclusions about patterns in diversity across large spatial scales. Many of the studies of

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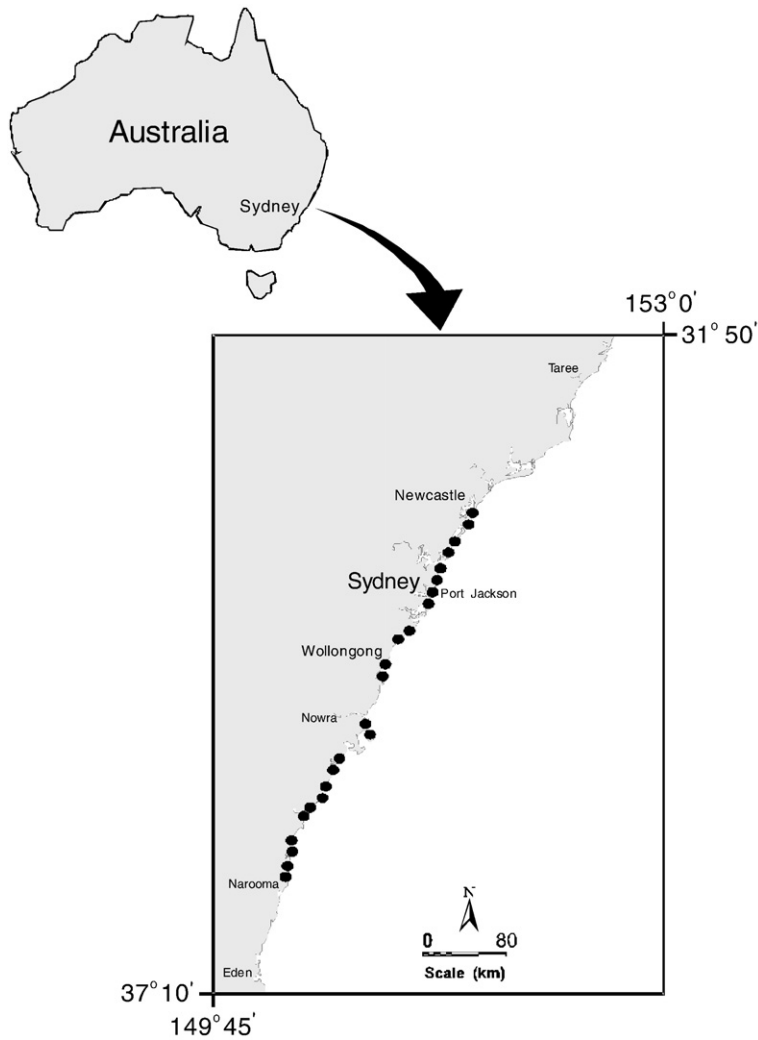


Fig. 1. Coast of New South Wales, Australia, showing locations of study sites.

biodiversity in marine habitats (although not always explicitly stated) use “species-density” (i.e. the number of species per unit area sampled, e.g. Archambault and Bourget, 1996; Davidson et al., 2004).

The scale of a study clearly influences results obtained and thus estimates of diversity (Levin, 1992; Whittaker et al., 2001). Scale is a complex issue that has received a lot of attention in recent years (Menge and Olson, 1990; Morrisey et al., 1992; Levin, 1992; Underwood and Chapman, 1996; Hewitt et al., 2007). The scale must be relevant to the hypotheses of interest and to the ecology of the organism(s) under investigation (Underwood and Petraitis, 1993). Increasing size of an area is generally associated with increased number of species, but, when habitats are sampled, rather than fully censused, the grain and extent of sampling will affect the patterns in diversity used. Grain is determined by the size of individual sampling units (e.g. quadrats, cores) and will clearly affect the species that can be sampled; if the grain is too small, many taxa cannot be sampled, if it is too large, abundances of many taxa are too large to count. The extent is the overall area encompassed by the study (Wiens, 1989); as this increases, there is usually a trade-off between the number of replicate samples per site and the number of sites that can be sampled because of limited resources. This may lead to very poor estimates of diversity in any one place (Gray, 2001b). The focus of the study is the scale at which grain is aggregated (or averaged) and thus represents the scale which the “point (or sample) data” are meant to represent (Scheiner, 2003). Studies over large spatial scales generally keep the size of the sampling unit (the grain) constant, but broaden the focus by collecting

data from similar sampling units over larger areas (Ellingsen and Gray, 2002).

There is a clear link between abundance (numbers of individuals) and occupancy (the number of sites occupied, each of which influences the likelihood of a species being present in any sample-unit (Gaston, 1994). Thus, abundant species are more likely to be sampled than are sparse species and estimates of diversity using small numbers of sampling units will underestimate diversity, by under-sampling rare species. This is likely to be particularly severe in estimating diversity of marine invertebrates, which include large numbers of very rare species. The degree of aggregation also influences the probability of getting species in samples, especially where only few replicates are used to estimate numbers of species; more widely scattered species are more likely to be sampled where few replicates have been used. Thus, densities and dispersion of the individual species influence estimates of diversity.

Mensurative studies, using space or time as the variable of interest are often confounded due to sampling over smaller scales than those implicit in the hypothesis (Hurlbert, 1984). Thus, many studies draw conclusions about seasonal changes when sampling has been done once per season, rather than by sampling independent replicates of each season (see Underwood, 1994 for review). In many large-scale, spatial studies, information about number of species over a large area is the result of combinations of datasets collected over a range of different seasons and over many years (Gaston 1994). Alternatively, different areas are sampled in different seasons or years (Ellingsen and

Gray, 2002), thus potentially confounding spatial patterns of diversity with temporal patterns. This will be very likely if season influences patterns of abundance or distribution of individual species.

Assemblages on intertidal rocky shores are diverse and have been useful in increasing understanding of general ecological phenomena (Underwood, 2000), especially issues of scale (Levin, 1994; Archambault and Bourget, 1996; Underwood and Chapman, 1996). Latitudinal patterns in diversity are not, however, always clear-cut and may be more strongly affected by local processes, rather than broad-scale environmental variables (e.g. Chapman and Underwood, 1998; Kelaher et al., 2007). Many studies examining local patterns of diversity have been replicated to provide reasonably accurate estimates of diversity, but large-scale studies usually sacrifice local replication for large-scale extent (e.g. Kelaher et al., 2007), thus decreasing confidence in any local estimate of diversity (see also Gray, 2001b for critique of extrapolation of large-scale patterns of subtidal benthos from either unquantitative or minimal quantitative sampling). There has been a call for more studies at intermediate scales

(Gray, 2001a), where replication is not sacrificed, but large spatial scales are incorporated into studies.

This research measured changes in diversity (number of species) of midshore intertidal organisms (algae and animals) on 24 shores along 415 km of the coastline of NSW, using large numbers of replicates per shore. By examining diversity at the scales of sampling units, site and shores, the effects of changing grain on patterns of diversity across the same extent (415 km) was examined. The assemblages were sampled four times, in two summer-autumn and two winter periods, to test for temporal changes in these spatial patterns. Sampling only once in each season would preclude attributing differences between times of sampling to seasonal differences, which requires appropriate replication. Although here there are only two replicated summers and winters, the differences between these times of sampling are considered in this study to be seasonal differences. The effects of differences in density and/or dispersion of species on the patterns of diversity were also examined. This study thus addresses the need raised by Gray (2001a), among others, for more studies of diversity for

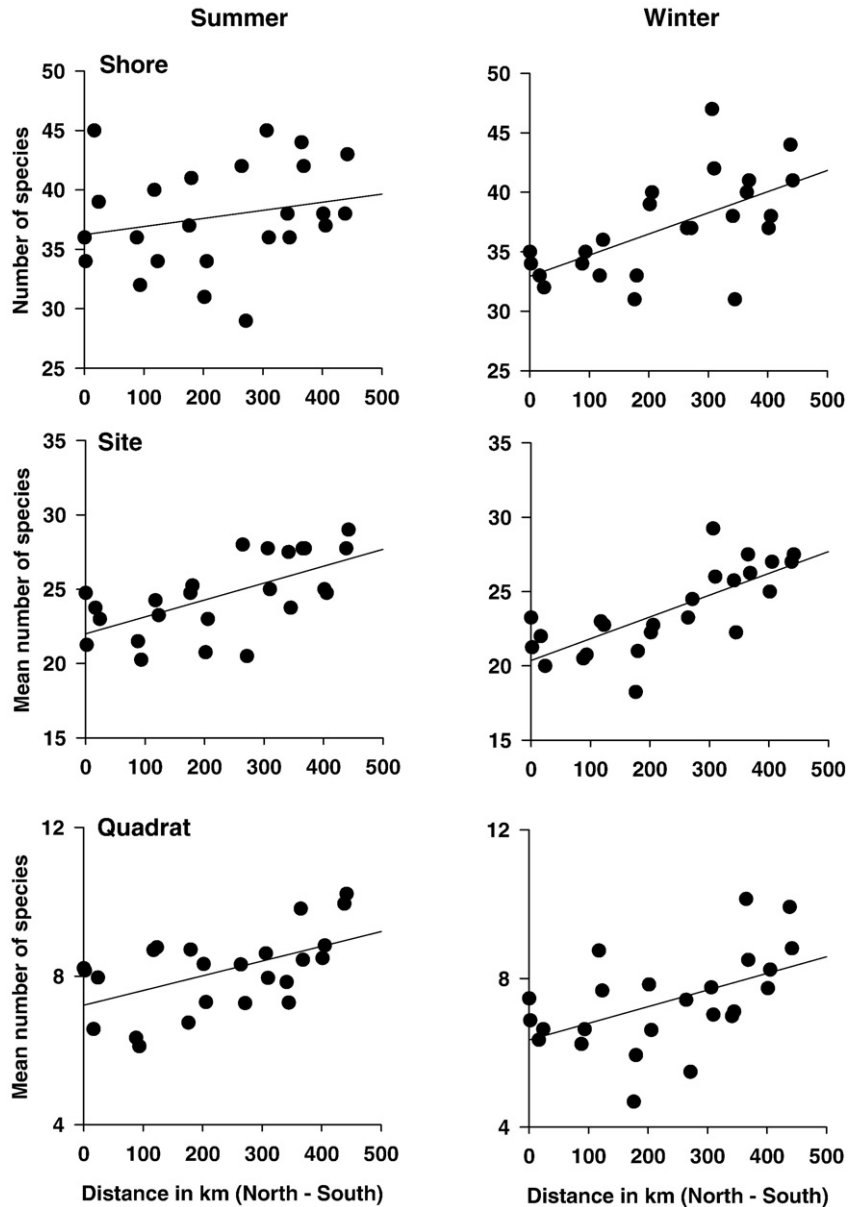


Fig. 2. Mean number of species per shore for 24 shores from counts per quadrat ( $n=80$ ), per site ( $n=4$ ) and per shore ( $n=1$ ) for one summer period (S1) and one winter period (W1).

many different types of assemblages at scales large enough to include environmental variability, but without loss of replication.

## 2. Methods

The sampling design included (for the purposes of other studies to be described elsewhere) a nested pair of shores about 1–2 km apart at each of 12 positions along 415 km of the coast of New South Wales (Australia), from the north of Newcastle (Bogie Hole) to the north of Narooma (Kianga Point) on the south coast (Fig. 1). The two (nested) shores were chosen, at random, from those available within a few km or so for each position; they all had moderate wave-exposure and were characterized by the same assemblages, typical of shores with this sort of wave-action. As far as practicable, shores were chosen to have similar slopes in their midshore regions. On each shore, 4 sites (each generally 4 m × 4 m, but varying according to the topography of the shore) and separated by 20–30 m, were sampled with 20 randomly placed quadrats (0.3 m × 0.3 m). Mid-shore assemblages (i.e. above the primarily algal-dominated lower shore and below areas characterised by few species other than littorinid snails; Underwood, 1981) were sampled independently because they have a diverse mix of species of plants and animals. The heights sampled varied a little from shore to shore, but this is irrelevant because the hypotheses being tested required that the same general assemblage was sampled on each shore. The same sites were sampled with new randomly-placed quadrats during two summer/autumn periods (February–March 2000 (S1) and February–April 2001 (S2)) and twice during winter/spring (July–September 2000 (W1) and July–September 2001 (W2)).

In each quadrat, point-covers of each sessile species were estimated and mobile species counted. Data were analysed at 3 scales of increasing grain-size. First, the average number of species per quadrat for each of the 24 shores was obtained from all ( $n=80$ ) quadrats per shore (“Quadrats”). This is equivalent to “Point Richness” ( $SR_p$  as defined by Gray, 2001a). Next, the data from all quadrats in each site were combined to provide 4 replicate estimates (“Site”) of number of species per site (each from  $n=20$  quadrats), which were then averaged to give the mean number of species per shore (“Shore”). Grain thus increased from areas of  $<1$  m<sup>2</sup> (each quadrat) to 16 m<sup>2</sup> (each site, although species were not counted throughout the latter, but estimated from the 20 replicate quadrats). Third, grain was increased further, by combining all data from a shore to estimate the number of species in all 80 quadrats combined. In all cases, the focus (the area sampled, i.e. the individual shores) and the extent of the study (415 km coastline) were kept constant.

Although sampling pairs of shores was not relevant to these hypotheses, there was concern that there may have been an artefact associated with treating the data as 24 individual shores, when the design consisted of pairs of shores very close together and separated from the adjacent pair of shores. Thus, patterns were also examined for the number of species for each of 12 pairs of shores (with  $n=160$ ), rather than 24 individual shores.

## 3. Results

### 3.1. Correlations of numbers of species and distance along the coast

During summer, there was no relationship between number of species per shore (calculated from the sum of all 80 quadrats) and location along the coast (Pearson's  $r$ ; S1,  $r=0.29$ ; S2, 0.01,  $P>0.05$ ; illustrated for S1 in Fig. 2). There was, however, an increase from north to south when data were averaged as mean number of species per quadrat (although this was not significant at S2; S1, 0.63,  $P<0.05$ ; S2, 0.33,  $P>0.05$ ), or as mean number per site (S1, 0.54,  $P<0.05$ ; S2, 0.41,  $P<0.05$ ). During each winter (illustrated for W1 in Fig. 2), there was a significant positive increase in diversity from north to south for

numbers of species at each grain-size (W1,  $r=0.62$ , 0.75, 0.51; W2, -0.46, 0.62, 0.44,  $P<0.05$ , for shore, site and quadrat, respectively). The number of species per pair of shores (in 160 quadrats) showed the same north-south trend as the number of species per shore, i.e. positive, but only significantly so in winter (S1,  $r=0.30$ ; S2, 0.49,  $P>0.05$ ; W1, 0.81, W2, 0.64,  $P<0.05$ , each 11 df).

To test hypotheses that similar large-scale patterns are found for different components of the intertidal assemblage (Gray, 2001a), or different levels of functional diversity (Peterson et al., 1998), species were grouped into encrusting algae, foliose algae, sessile animals or mobile animals and the correlations between mean number of species of each functional group per quadrat, site and total numbers on each shore examined with location along the coast. There were no significant relationships for encrusting or foliose algae, except for the mean number of encrusting species per quadrat for one time in summer, which gave a significant negative relationship, opposite to that shown for the entire assemblage; Table 1). Sessile animals, in contrast, showed the same patterns as the entire assemblage for all times and spatial scales (Table 1). Patterns of mobile species were less consistent, although there was always a significant positive trend in accordance with those shown by the entire assemblage at the scale of sites (Table 1).

### 3.2. Seasonal changes in total numbers of species

The increase in number of species down the coast at the scale of shores in winter and not in summer, may be due to an increase in the number of species on the southern shores from summer to winter and/or a decrease in the number of species on the northern shores from winter to summer. Such patterns should only be found at the largest scale of shores.

This was examined by averaging the numbers of species per quadrat, site and shore for the 6 southernmost and 6 northernmost shores (Table 2). There was no general increase or decrease in numbers of species per quadrat nor per site between summer and winter, for either the northern nor southern shores. In the north, there was, however, a clear decrease in number of species per shore between summer and winter (Table 2). In the south, numbers per shore did not vary significantly between summer and winter. Therefore, the trend was due to a decrease in diversity in the northerly (more towards the tropics) shores during the colder time of the year.

### 3.3. Alternative models to explain the observed pattern

The patterns described above indicate a general increase in diversity from north to south in winter, whether species were

**Table 1**  
Correlation coefficients ( $r$ ) between number of species per shore, site or quadrat for each of 4 functional groups and distance along the coast

Time	S1	S2	W1	W2
<b>Encrusting algae</b>				
Shore	0.13	-0.27	-0.08	-0.19
Site	0.17	-0.22	-0.12	-0.14
Quadrat	-0.16	<b>-0.45</b>	-0.28	-0.39
<b>Foliose algae</b>				
Shore	-0.07	-0.32	0.26	-0.20
Site	0.09	-0.30	0.04	-0.14
Quadrat	0.02	-0.37	-0.19	-0.38
<b>Sessile animals</b>				
Shore	0.07	0.29	<b>0.54</b>	<b>0.54</b>
Site	<b>0.67</b>	<b>0.67</b>	<b>0.77</b>	<b>0.72</b>
Quadrat	<b>0.70</b>	<b>0.60</b>	<b>0.82</b>	<b>0.71</b>
<b>Mobile animals</b>				
Shore	<b>0.46</b>	0.32	0.39	<b>0.60</b>
Site	<b>0.63</b>	<b>0.64</b>	<b>0.69</b>	<b>0.70</b>
Quadrat	0.38	<b>0.51</b>	<b>0.54</b>	0.42

Values in bold indicate correlations are significant at  $P<0.05$  (22 df).

**Table 2**

Mean (SE) number of species per shore for the northern and southern region of the study at each time of sampling ( $n=6$  shores per region)

Region	Time	Shore	Site	Quadrat
North	S1	37.0 (1.9)	22.4 (0.7)	7.2 (0.4)
	S2	37.3 (2.0)	21.5 (1.3)	6.3 (0.4)
	W1	33.7 (0.6)	21.1 (0.5)	6.7 (0.2)
	W2	34.8 (2.5)	20.8 (0.8)	7.0 (0.2)
South	S1	40.2 (1.1)	27.0 (0.7)	9.3 (0.3)
	S2	38.7 (1.7)	25.9 (1.0)	8.3 (0.5)
	W1	39.8 (1.1)	26.6 (0.4)	8.9 (0.4)
	W2	40.5 (2.4)	27.2 (1.0)	8.8 (0.5)

averaged in quadrats, in sites (as the number of distinct species in 20 quadrats per site) or totalled over the entire shore (the number of distinct species over the 80 quadrats from a shore), each a measure of species-density. In summer, however, a similar increase was only found at the two smallest grain-sizes.

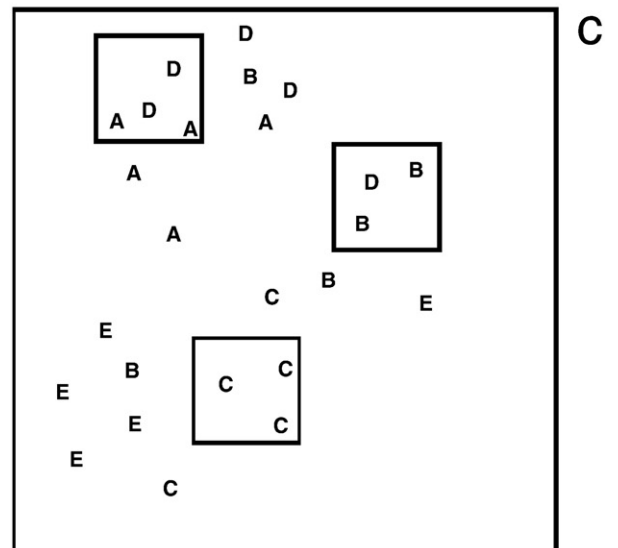
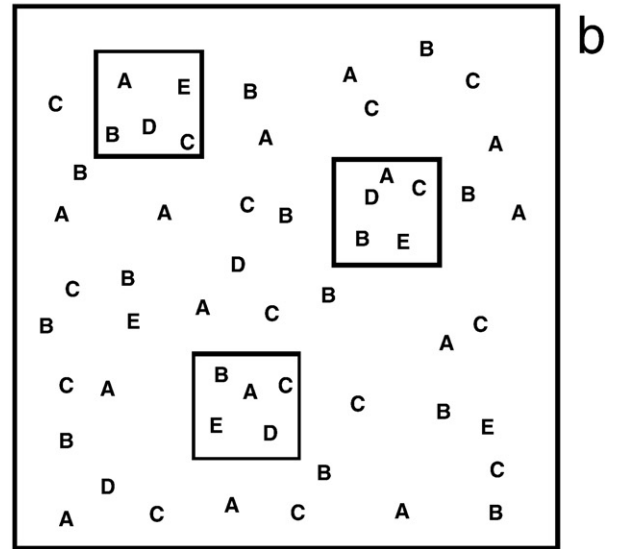
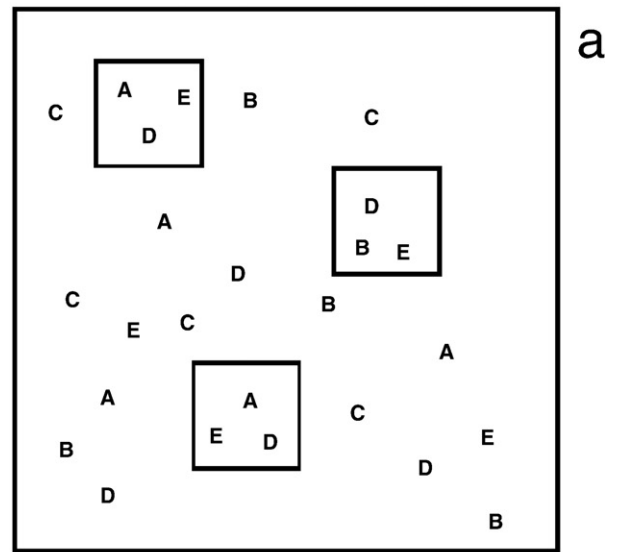
A number of models might explain how changes in diversity alongshore in summer vary according to the grain-size at which diversity was measured, i.e. how the lack of a pattern at the scale of the whole shore might result in a significant trend when species are averaged among samples at a smaller grain-size. For example, changes in density or dispersion of individual species could affect the number of species recorded in sampling units, without a change in true number of species in an area. Hypotheses from such models were therefore tested in an attempt to understand characteristics of the assemblages that may have caused the interaction between the alongshore pattern in summer and the scale at which numbers of species were measured.

3.3.1. Densities or percentage covers

An increase in densities (or amounts of cover) of individual species from the northern to southern shores in summer could create a pattern of increasing numbers of species down the coast when species are averaged across replicated small sample-units, with no differences in real number of species per shore, because of a greater probability of getting individuals in sampling units when they are at larger densities/cover (Fig. 3a, b).

From this model, it was predicted that there would be an increase in mean cover or in densities of animals from north to south in summer, but not in winter, or a greater increase in summer than in winter. This hypothesis was tested using the most abundant fauna found throughout the range of the study. They included percentage covers of a tube-forming polychaete (*Galeolaria caespitosa*) and 5 species of barnacles, plus counts of a predatory whelk (*Morula marginalba*), a neritid snail (*Nerita atramentosa*), a littorinid (*Littorina unifasciata*) and 5 species of limpets (Table 3).

Twenty of the 26 correlations in summer were positive, although only 2 were significant at  $P < 0.05$  (the barnacles *Catomerus polymerus* and *Tetraclitella purpurascens*) and then only in one of the two summer periods (Table 3). Nevertheless, these barnacles, plus *G. caespitosa*, *N. atramentosa* and *P. latistrigata* showed quite strong positive (albeit non-significant) trends in each summer period. In winter, however, 18 of the correlations were also positive, with *C. polymerus*, *Siphonaria denticulata* and *P. latistrigata* at each period (Table 3). Thus, the increase in diversity down the coast when measured at small grain-sizes could have been influenced by changes in densities of some species, but this cannot account for the change in the large-scale (whole shore) differences between summer and winter.



**Fig. 3.** Illustration of effects on mean count of species per sample-unit ( $\bar{s}$ ) due to differences in means or variances of individuals. (a) – (c) each has 5 species (A – E);  $n=3$  quadrats sampled. (a) each species has a total abundance of 5,  $\bar{s}=3.0$ ; (b) as in (a), but abundances of species A – C are 15,  $\bar{s}=5.0$ ; (c) as in (a), but aggregation of individuals (and variances of numbers per quadrat of each species) are greater,  $\bar{s}=1.7$ .

### 3.3.2. Patterns of dispersion

More species could be detected on southern compared to northern shores at small scales of sampling in summer even if the same number of species occur in the same densities along the coast, if individuals are more widely scattered in the south (Fig. 3a,c). This would result in them being sampled in more quadrats, increasing the average number of species per quadrat (and possibly per site). This would not happen when the numbers of species are derived from the combination of all quadrats on a shore.

This model makes a number of predictions regarding patterns of dispersion. First, it predicts that individual species should occur in more quadrats on the southern compared to the northern shores in summer, but not in winter. This was tested using the same species listed in Table 3, correlating the number of quadrats containing each species with distance along the coast (Table 4).

Again, 20 of the 26 correlations between frequency of occurrence and distance down the coast were positive in summer, although only 4 of these were significant and no species showed a significant pattern in each of the summer periods (Table 4). There was also a similar pattern in winter; 18/26 correlations were significant, with *G. caespitosa* and *C. tramoserica* showing a significant pattern in each of the winter periods. Thus, increased frequency with which species occurred in quadrats on the southern shores cannot explain the observed changes to diversity with grain-size between summer and winter, although increased occurrences might have inflated counts of species in quadrats or sites on the southern shores in all seasons.

If species are more scattered in the south than the north, one can also predict larger variances for individual species (among measures of cover or abundance per quadrat) in the north (where they are less evenly scattered) compared to the south in summer, but not in winter. This is illustrated in Fig. 3. Here, only just over half of the 26 correlations between variances and distances along the coast in summer were positive, with only 2 significant (Table 5) and no species showed a significant relationship in each summer period. In winter, patterns were similarly variable, although there were more significant increases in variance down the coast and the barnacle, *C. polymerus*, showed a consistent pattern in both winter periods. Thus, the increase in numbers of species per quadrat down the coast was not strongly influenced by the degree of clustering on the shore of the individual species.

Overdispersion also affects the shape of the frequency distributions of numbers per quadrat (skewness). Where species are more scattered, there should be fewer quadrats with counts of zero or very large counts, compared to where individuals are more clumped or aggregated (Fig. 3). Therefore, if the patterns of increased diversity down the coast in summer at the scales of quadrats and sites, but not shores, is due to overdispersion affecting numbers of species per quadrat, skewness should decrease towards the south in summer and there should be no such trends in winter.

**Table 3**

Correlation coefficients (*r*) between the mean percentage covers of 4 sessile organisms and densities of 8 mobile organisms and distance along the coast

Time	S1	S2	W1	W2
<b>Sessile invertebrates</b>				
<i>Catomerus polymerus</i>	<b>0.60</b>	0.27	<b>0.64</b>	<b>0.47</b>
<i>Galeolaria caespitosa</i>	0.36	0.33	0.52	0.28
<i>Tesseropora rosea</i>	0.01	-0.20	-0.27	-0.41
<i>Tetraclitella purpurascens</i>	<b>0.59</b>	0.33	<b>0.48</b>	0.12
<b>Mobile invertebrates</b>				
<i>Cellana tramoserica</i>	-0.23	-0.19	-0.19	-0.18
<i>Littorina unifasciata</i>	-0.18	-0.17	-0.05	-0.23
<i>Montfortula rugosa</i>	-0.02	0.18	0.28	0.05
<i>Morula marginalba</i>	0.03	0.11	0.02	0.02
<i>Nerita atramentosa</i>	0.26	0.39	0.12	0.21
<i>Patelloida latistrigata</i>	0.27	0.34	<b>0.59</b>	<b>0.47</b>
<i>Siphonaria denticulata</i>	0.06	0.13	0.20	-0.17
<i>Siphonaria virgulata</i>	0.17	0.35	<b>0.69</b>	<b>0.46</b>

Values in bold indicate correlations are significant at  $P < 0.05$  (22 df).

**Table 4**

Correlation coefficients (*r*) between the number of quadrats containing each of 12 species and distance along the coast

Time	S1	S2	W1	W2
<b>Sessile invertebrates</b>				
<i>Catomerus polymerus</i>	<b>0.42</b>	0.16	-0.03	<b>0.62</b>
<i>Galeolaria caespitosa</i>	<b>0.53</b>	0.16	<b>0.69</b>	<b>0.43</b>
<i>Tesseropora rosea</i>	0.24	0.31	0.39	0.09
<i>Tetraclitella purpurascens</i>	0.08	0.02	0.12	0.09
<b>Mobile invertebrates</b>				
<i>Cellana tramoserica</i>	0.01	<b>0.64</b>	<b>0.66</b>	<b>0.56</b>
<i>Littorina unifasciata</i>	-0.08	-0.12	-0.12	-0.28
<i>Montfortula rugosa</i>	0.25	0.20	-0.02	0.03
<i>Morula marginalba</i>	-0.16	0.24	0.23	0.04
<i>Nerita atramentosa</i>	-0.26	-0.20	-0.36	-0.18
<i>Patelloida latistrigata</i>	0.21	-0.30	-0.13	0.07
<i>Siphonaria denticulata</i>	0.05	0.23	<b>0.48</b>	0.13
<i>Siphonaria virgulata</i>	0.33	0.21	0.36	0.33

Values in bold indicate correlations are significant at  $P < 0.05$  (22 df).

Skewness was measured from the frequency distributions of number of species per quadrat for all 80 quadrats on a shore for each time of sampling. In summer, in accordance with this prediction, skewness tended to decrease towards the south, although only significantly so for one time of sampling (S1,  $r = -0.33$ ,  $P > 0.05$ ; S2, 0.42,  $P < 0.05$ ). At S1, one shore appeared to be an outlier and at S2, 2 shores appeared as outliers, so these shores were removed and the analyses rerun; they produced essentially the same results (S1,  $r = -0.11$ ,  $P > 0.05$ ; S2, 0.47,  $P < 0.05$ , 20 df). In winter, there was no significant trend along the coast (W1,  $r = -0.06$ ; W2, 0.07,  $P > 0.05$ ).

More scattering among species within or among sites on shores towards the south of the range should also create assemblages that are more similar to each other at small spatial scales within sites. Dissimilarity among quadrats would, therefore, be predicted to be greater towards the north than the south. Average dissimilarity for each shore was estimated from Bray-Curtis dissimilarities among all pairs of quadrats per shore, using presence/absence data. There was no significant trend in dissimilarity of assemblages from north to south at any time (S1,  $r = 0.09$ ; S2, -0.04, W1, 0.23; W2, -0.05,  $P > 0.05$ ).

## 4. Discussion

This study showed a clear trend in numbers of species per shore in a midshore intertidal assemblage along a >400 km stretch of coastline in south-east Australia. Interestingly, the trend was increasing numbers of species from north to south. This is in contrast to the generally described pattern of more species towards the equator. This study was not designed to consider patterns of numbers of species over a large range of latitude. There is, however, a previous example of intertidal organisms in the southern hemisphere showing increased numbers of species towards the south, i.e. algae (Santelices, 1980). The apparent simplicity of this pattern was complicated by a number of factors, including different patterns among different functional groups in the assemblage, differences in the observed patterns according to the grain of sampling, which was itself confounded with the season in which the assemblage was sampled and the potential influence of differences in densities of some species. There is no reason to expect large-scale patterns to be simple, nor to be primarily affected by single (or a few) environmental variables that might vary across the extent of the study. Yet many studies of assemblages across much larger scales than incorporated into this study, have not considered seasonal changes, have not examined effects of the grain of sampling on the resultant patterns, any effects of densities, or numerous other factors that can affect counts of numbers of species in sampling units (reviewed by He and Legendre, 2002; but see Rivadeneira et al., 2002). This manuscript is a response to the need for more studies of patterns of diversity across intermediate spatial scales, which are large enough to encompass different environmental conditions, but small enough to incorporate a

**Table 5**

Correlation coefficients (*r*) between the variance of percentage covers of sessile animals and densities of mobile animals among replicate quadrats on each shore and distance along the coast

Time	S1	S2	W1	W2
<b>Sessile invertebrates</b>				
<i>Catomerus polymerus</i>	<b>0.46</b>	0.32	<b>0.49</b>	<b>0.44</b>
<i>Galeolaria caespitosa</i>	0.25	0.28	0.38	0.00
<i>Tesseropora rosea</i>	0.07	-0.25	-0.17	<b>-0.43</b>
<i>Tetraclitella purpurascens</i>	0.29	<b>0.40</b>	<b>0.48</b>	-0.02
<b>Mobile invertebrates</b>				
<i>Cellana tramoserica</i>	-0.16	-0.08	0.08	-0.11
<i>Littorina unifasciata</i>	-0.23	-0.25	-0.16	-0.29
<i>Montfortula rugosa</i>	0.15	0.09	0.25	0.02
<i>Morula marginalba</i>	-0.06	0.11	-0.15	-0.02
<i>Nerita atramentosa</i>	0.29	0.38	-0.00	0.13
<i>Patelloida latistrigata</i>	-0.15	0.26	<b>0.62</b>	0.38
<i>Siphonaria denticulata</i>	-0.08	-0.05	0.34	-0.22
<i>Siphonaria virgulata</i>	0.34	-0.10	<b>0.60</b>	0.03

Values in bold indicate correlations are significant at  $P < 0.05$  (22 df).

rigorous sampling regime to ensure that conclusions are based data of good quality (Gray, 2001a,b).

Large-scale patterns in diversity are generally either based on quantitative data from sampling within multiple sites, or from records of species' occurrences. There are many problems with the latter, which are often only qualitative (or semi-quantitative), but these are not considered further here. In the first case, the number of species is only actually known for the samples themselves, even though these estimates are extrapolated to much larger areas (e.g. Gray, 2002; Ugland et al., 2005; Mingoti and Meeden, 1992). Unless one can extrapolate up from the area that is actually sampled to the area of interest (for which there are many different procedures, each with their own set of assumptions and problems as summarized by Colwell and Coddington, 1994; Ugland et al., 2003, amongst others), one must keep in mind that what one is describing is species-density (i.e. the number of species per unit of habitat), not the true number of species. Nevertheless, it is common to refer to numbers of species derived from samples as measures of species richness (e.g. Archambault and Bourget, 1996; Boulinier et al., 1998; Lennon et al., 2004), even though these are not the same thing (e.g. Hurlbert, 1971; Gray, 2001a).

Many studies of differences in numbers of species across large areas have focussed on particular taxocoenes (e.g. birds, Blackburn and Gaston, 1996; fish, Guidetti, 2002; plants, Quinn et al., 1994; bryozoans, Clarke and Lidgard, 2000). Marine studies, perhaps more than terrestrial studies, have tended to look for patterns in mixed assemblages of animals and plants, sometimes comparing patterns among different groups of taxa within an assemblage. For example, Bustamante and Branch (1996) showed greater diversity of autotrophs, predators and filter-feeders between the western and eastern coast of Southern Africa, which appeared to be strongly influenced by wave-action. This pattern was not, however, shown by other groups in the assemblage.

In the assemblage studied here, different functional groups showed different alongshore patterns. Thus, sessile animals reflected the pattern of the entire assemblage, both with respect to the longshore trend and the change in this trend between summer and winter at the largest grain-size of sampling. The mobile animals, in contrast, showed a similar change in numbers of species along the coast, but no seasonal change. The algae showed no longshore trend nor seasonal change, even though, in New South Wales, some algae show changes in abundance or position on the shore between summer and winter (Underwood, 1981; Underwood and Jernakoff, 1984). Mobile animals can change position on the shore (e.g. Gendron, 1977; Lambert and Farley, 1968), or move into different habitats (Feare, 1971) at different times of the year, potentially removing themselves temporarily from the assemblage being censused. It is therefore interesting that neither the mobile animals nor the algae

showed any changes according to season in this study. The sessile animals, which did show seasonal patterns, can only change their abundances by processes such as recruitment or mortality. The seasonal change in the pattern down the coast appeared to be due primarily to the loss of species in the more tropical northern sites in winter and increases in summer, although the cause of this is not known.

Because of the logistics involved in large-scale studies, data are typically collected only once in each site (e.g. Archambault and Bourget, 1996; Bustamante and Branch, 1996). Sampling a large region may take many months or years (e.g. Rivadeneira et al., 2002), thus potentially confounding spatial and temporal variation (although these authors tested for temporal change on a subset of shores by resampling once a year later). Rivadeneira et al. (2002) suggested that "snapshot sampling" may be adequate to measure large-scale spatial patterns because there was little interannual variation in the patterns they observed. They did, however, sample all the sites in the same season. This study also showed that the patterns of diversity along the coast were consistent for two different years of sampling, but it was seasonal, rather than annual variation, that changed spatial patterns of diversity. Yet, when large-scale patterns of diversity are described, they are not usually described as changes in numbers of species "in summer" or "in winter", but as a general pattern. It is important to consider effects that seasonal changes may have on spatial patterns of diversity, especially when sampling is spread over a long period. Better still, is to attempt to test whether there are temporal changes that might confound spatial patterns (Rivadeneira et al., 2002).

Of greater interest here was the finding that seasonal patterns interacted with the scale at which numbers of species were measured and were only detectable at the largest of the three grain-sizes examined. Thus, at the scales of species-density per quadrat (30 cm × 30 cm) and sites (4 m × 4 m, with species number obtained from counts in 20 quadrats, i.e. over 1.8 m<sup>2</sup> of rock-surface within each site), there was no seasonal change in alongshore pattern. When species were enumerated for the entire shore (from counts in 20 quadrats in 4 different sites on a shore, 7.2 m<sup>2</sup>), the alongshore pattern did change between summer and winter. There is generally little consideration of the grain of sampling (which is determined by the size of the sampling unit). Most studies on this topic that are based on (semi-)quantitative field data use a single grain-size (e.g. quadrat, transect, etc.), or timed searches of a fixed time (which is equivalent).

As pointed out by Hurlbert (1971), Gotelli and Colwell (2001), Gray (2002) and others, estimates of numbers of species from samples are not true measures of species richness. These measures are influenced by the densities and dispersions of different species (each of which affects the number of species found per number of individuals sampled and the number of species found per unit of habitat sampled). Many techniques that have been developed to compare numbers of species across areas that have been sampled with different intensity have associated problems, e.g. rarefaction depends on individuals being randomly sampled, which is unlikely in any species that have aggregated populations (i.e. most species; Gray, 2002). Estimating total species numbers from species-accumulation curves do not have this problem, but have numerous other problems, often severely over- or under-estimating numbers of species, according to the model used (Colwell and Coddington, 1994), especially where there is considerable variability in habitat over the area being sampled (Ugland et al., 2003). This study showed that there was an increase in densities of the more common species down the coast, along with an increase in numbers of species, in both summer and winter. Abundances of rarer species were not specifically examined, due to the typically poor estimates of densities of very sparsely distributed species (Gaston, 1994; Gaston and McArdle, 1993). Thus, the alongshore pattern could, at least in part, be due to increased densities, resulting in more species per sampling unit when the grain size was small. This cannot, however, account for the seasonal change in the pattern at the larger grain size because there was no change in patterns of density from summer to winter.

The frequency with which species were sampled in quadrats also varied alongshore with density and numbers of species. Although this could theoretically have been due to changes in density and/or dispersion, the latter seems unlikely because other measures of dispersion (i.e. variances in abundances, skewness in numbers of occupied quadrats) did not vary along the coast. It is, nevertheless, important to realise that many factors affect the density and dispersion of species. On rocky shores, these include availability of habitats (e.g. Yamada, 1977), local environmental conditions (reviewed by Connell, 1975), interactions with other species (reviewed by Underwood, 1985), etc., all of which are local phenomena. Analysing patterns of differences or changes in numbers of species simply by use of numbers of species, so that there is no information on species' identities, precludes much more sophisticated and revealing analyses of ecological patterns (Warwick and Clarke, 1995). When numbers of species are analysed without information about their abundances and frequencies of occurrence, it is impossible to identify how much of any changes or difference among samples is due to a loss (or gain) of species from one sample to another, or due to greater probability of sampling species that are present everywhere, but at varying densities or in different patterns of dispersion (see He and Legendre, 2002 for review of the effect of these factors on estimates of species richness). It would therefore be extremely useful if future studies at least recorded which species were present in each sample and incorporated relevant measures of abundances and variances within sites to assist in interpretation of patterns across sites.

Information on the distributions and abundances of organisms is an important basis for decisions made in ecology and management and understanding natural variability is essential to develop management plans (Landres et al., 1999). Intertidal rocky shores are under increasing pressure from recreational activities of humans, particularly for harvesting of bait and food (Agardy, 1994; Castilla, 1999) and there is an increasing need to select areas for protection (Roberts et al., 2003; Rothley, 1999). Recently, Oliver et al. (2007) surveyed a panel of environmental managers in Australia to design a protocol to determine benchmarks to assess impacts on biodiversity, but, as pointed out by Gray (2002), signing protocols to produce inventories of biodiversity, or protect it, have no meaning if we do not yet know how to measure it. In most protocols, scale of sampling and season are not mentioned as important variables that need to be incorporated in the design of assessments of biodiversity.

As shown here, sampling – even with reasonably large sizes of samples – produces estimates of numbers of species that are affected by numerous variables associated with the densities, dispersions, frequencies of occurrence and other ecological properties of the individual species. Comparisons of lists of species from one area or time to another, or assessments of trends in numbers of species across gradients or between disturbed and reference areas are compromised when the numbers of species are not unambiguously estimated. Such estimation is rarely achievable where species are counted in sample-units rather than being completely censused. Of course, different hypotheses require different information to be collected. The point is that interpretations of patterns in numbers of species must take into account the compromising influences of the fact that different species are being sampled with different precisions and accuracies.

Attempts to discriminate amongst different possible causes of trends along a coast and how these changed seasonally were complex. They required data about densities, dispersions, frequencies, etc., which are not always available. Furthermore, changing the grain-size of sampling produced different patterns in the trends along the coast. All of these issues must be much more fully explored than is usually the case where data on the presence/absence of species are all that is available to underpin comparisons among areas or times.

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