

# Spatial patterns of diverse macrofaunal assemblages in coralline turf and their associations with environmental variables

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Mats of articulated coralline algal turf are common on many rocky intertidal shores. The dense fronds provide a habitat for extremely diverse and abundant macrofaunal assemblages. Despite a large contribution to faunal biodiversity of rocky shores, little has been published about these assemblages. This study describes patterns of distribution and abundance of macrofauna in coralline turf on rocky shores around Sydney. In addition, the potential of environmental variables (sediment, epiphytes, length and density of coralline fronds) for determining these patterns was also investigated. Relatively consistent differences were found between macrofauna in low- and mid-shore areas at all times of sampling and on all shores. Although there was some variation among shores, there was generally significant variation in macrofauna between sites separated by tens of metres. Generally, a relatively small number of taxa were responsible for the great majority of dissimilarity between assemblages. Apart for the small bivalve *Lasaea australis*, however, these taxa varied between heights on the shore, among times of sampling and among shores. These data illustrate the important contribution that coralline turf has for biodiversity of faunal assemblages on rocky shores around Sydney. They also provide a basis for investigating biological processes and physical factors responsible for structuring patterns of biodiversity of macrofaunal assemblage in coralline turf.

## INTRODUCTION

The quantitative description of patterns of distribution and abundance is the basis of understanding processes that structure assemblages of organisms (Andrew & Mapstone, 1987; Underwood et al., 2000). There has been a long history of description of patterns of distribution and abundance of organisms on rocky intertidal shores (see Southward, 1958; Connell, 1972, for reviews). In the past, much of this research focused on variation in assemblages of organisms along obvious environmental gradients, such as among different heights on the shore (e.g. Connell, 1961; Dayton, 1971; Paine, 1974) or among shores with different exposure to waves (e.g. Crisp & Southward, 1958; Lewis, 1964) and often small-scale variation was overlooked (but see Connell, 1972). More recently, it has been shown that a considerable amount of variability in abundances of organisms on rocky shores occurs at scales of tens of metres or less (Lohse, 1993; Chapman, 1994; Underwood & Chapman, 1996). Consequently, a greater emphasis is being placed on describing and explaining variation in the diversity and abundance of organisms at a range of different spatial scales (Morrissey et al., 1992; Thompson et al., 1996; Underwood & Chapman, 1996, 1998).

The spatial scales of variability of many organisms on rocky shores of south-eastern Australia have been well-described (Underwood & Chapman, 1996). In many cases, the major processes responsible for these patterns

have been determined experimentally (Denley & Underwood, 1979; Underwood et al., 1983; Fairweather, 1985; Chapman & Underwood, 1994). The majority of this research has focused on large and conspicuous animals and algae. Rocky shores, however, have many complex mat-like habitats with extremely diverse assemblages of small and cryptic invertebrates (Hicks, 1971; Myers & Southgate, 1980; Seed, 1996). In contrast to the more conspicuous organisms on rocky shores, published studies on these cryptic macrofaunal assemblages are relatively scarce (Underwood & Petraitis, 1993; Menge, 1995). Common forms of mat-like habitats on rocky shores include mussel beds (Tsuchiya & Nishihira, 1985; Peake & Quinn, 1993; Seed, 1996), ascidians (Fielding et al., 1994; Otway, 1994), algal turf (Hicks, 1980; Myers & Southgate, 1980; Dean & Connell, 1987a,b) and lichens (Seed & O'Connor, 1980; Healy, 1996).

Environmental variables relating to the habitat are generally considered to have a strong influence on macrofaunal assemblages in mat-like habitats (Hicks, 1980; Dean & Connell, 1987a; Johnson & Scheibling, 1987; Gibbons, 1988; Gee & Warwick, 1994). For example, the amount of sediment within a mat-like habitat often increases the diversity and abundance of associated macrofauna (Wigham, 1975; Hicks, 1980; Gibbons, 1988, 1991; Whorff et al., 1995). It has been postulated that this is because sediment creates a more heterogeneous habitat for infaunal and epifaunal species (Hicks, 1985; Gibbons, 1991) and

retains moisture when the habitat is emersed (Gibbons, 1988). Similarly, the amount of epiphytic algae attached to a mat-like habitat increases the diversity of the associated faunal assemblage by providing food and shelter (Johnson & Scheibling, 1987; Duffy, 1990; Martin-Smith, 1993). In addition, the amount and complexity of physical structure of mat-like habitats may increase the diversity of associated organisms by providing greater available surface area (Connor & McCoy, 1979; McGuinness & Underwood, 1986), providing a better refuge from predation (Russ, 1980; Coull & Wells, 1983; Dean & Connell, 1987b), reducing environmental harshness (e.g. increase relative humidity; Nixon et al., 1971) or reducing the impact of disturbances (e.g. reduce effects of wave action; Dommasnes, 1968; Whorff et al., 1995).

Articulated coralline algae often form mat-like habitats and are a major component of algal assemblages on many rocky shores (Stewart, 1982; Grahame & Hanna, 1989; Dye, 1993; Benedetti-Cecchi & Cinelli, 1994). They are extremely abundant in low-shore areas and relatively abundant in mid-shore areas of wave-exposed and sheltered rocky shores in New South Wales, Australia (Underwood, 1981; Underwood & Chapman, 1998). The dense fronds provide a habitat for extremely diverse macrofaunal assemblages (Hicks, 1971; Akioka et al., 1999) and may contain in excess of 200,000 individuals  $m^{-2}$  (Brown & Taylor, 1999). Given the abundance of coralline algal turf and diversity of the associated macrofaunal assemblage, it is clear that turfs generally support a large component of faunal biodiversity of many rocky shores. Despite this, there has only been one published study investigating macrofaunal assemblages associated with coralline turf in Australia (Davenport et al., 1999, South Australia) and only a handful world-wide (Dommasnes, 1968, 1969; Hicks, 1971; Ballesteros, 1988; Grahame & Hanna, 1989; Hull, 1997; Lopez & Stolz, 1997; Akioka et

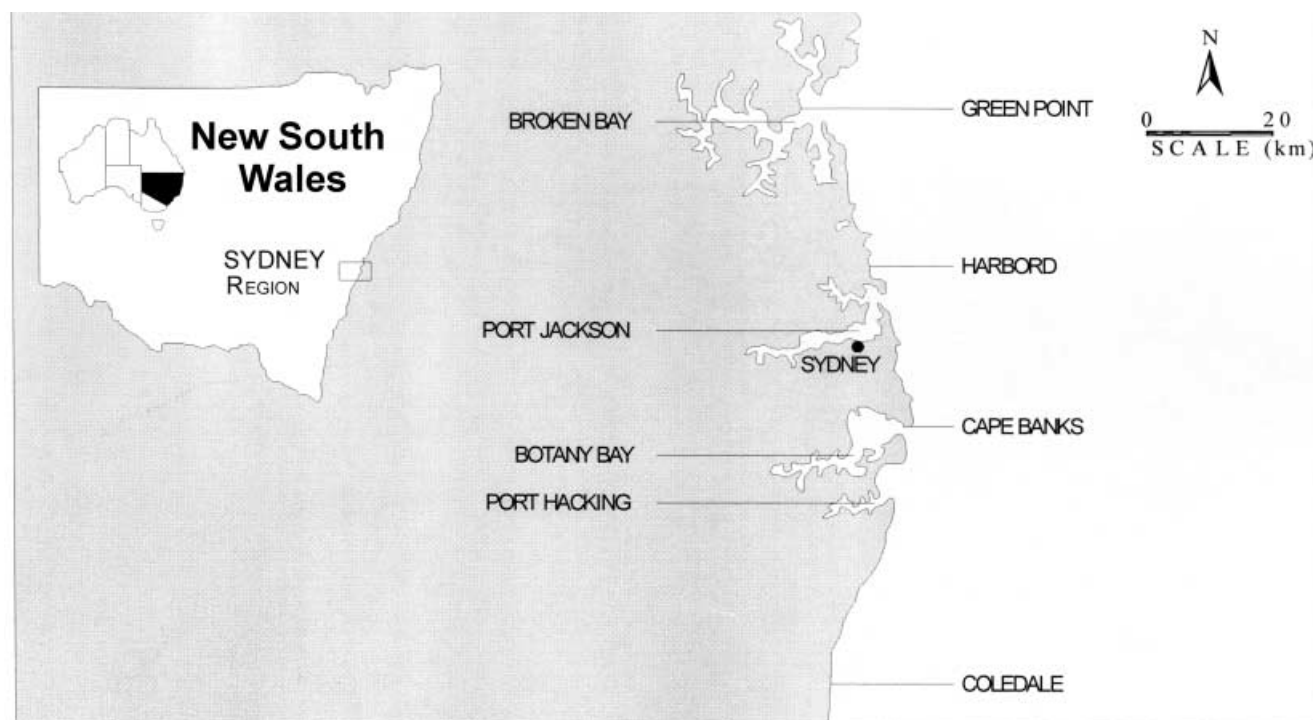
al., 1999; Brown & Taylor, 1999). Of these studies, some are limited to only one day of sampling (e.g. Davenport et al., 1999) or a single site (e.g. Hull, 1997; Davenport et al., 1999) or use very broad taxonomic groups (e.g. Grahame & Hanna, 1989; Brown & Taylor, 1999). Detailed quantitative information on the spatial patterns at a range of scales of diverse assemblages associated with coralline turf is therefore conspicuously lacking.

The present study describes tests of the hypotheses that macrofaunal assemblages in coralline turf: (i) differ between low- and mid-shore areas; and (ii) differ at scales of tens of metres at each height on the shore. This study also investigated the potential for environmental variables to explain the patterns by testing the hypothesis that the amount of sediment and epiphytes associated with the turf and the structural complexity of the coralline turf will show similar patterns of spatial variation as does the macrofaunal assemblage. In addition, it was hypothesized that each of these environmental variables will be positively associated with the diversity of macrofauna. Finally, it has been shown that supposed general patterns of distribution of organisms can vary among times of sampling and shores (Foster, 1990; Underwood & Chapman, 1998). In this study, the generality of spatial patterns of macrofaunal assemblages in coralline turf was evaluated by re-testing hypotheses about spatial variability three times at one shore near Sydney, Australia and then at three other shores in the Sydney region.

## MATERIALS AND METHODS

### *Study sites and characterization of coralline turf*

This study was mostly done at Cape Banks Scientific Marine Research Area (hereafter called Cape Banks), located on the northern headland of the entrance to



**Figure 1.** Shores sampled around Sydney, New South Wales, Australia.

Botany Bay (34°00'S 151°15'E; Figure 1). On this shore, exposure to waves, slope and aspect of platforms vary from place to place (Underwood et al., 1983; Fairweather & Underwood, 1991). All the sites used in this shore had medium to heavy exposure to waves. Three other rock platforms were also sampled. From north to south, these were Green Point (33°33'S 151°18'E), Harbord (33°47'S 151°18'E) and Coledale (34°11'S 150°57'E; Figure 1). Harbord and Coledale are fully exposed to waves and Green Point has an increasing gradient of wave exposure from south to north (Underwood, 1981). On this shore, sites were selected in areas exposed to wave-action.

All shores had large patches of coralline turf in low- and mid-shore areas. This turf was almost entirely *Corallina officinalis* Linnaeus. Nevertheless, at different places and different times, *Haliptilon roseum* (Lamarck) Garbary and Johansen, *Jania* spp. Lamouroux and *Amphiroa* spp. Lamouroux, were found in the turfing matrix. Often, non-coralline algae occupied small amounts of primary space amongst the turf (e.g. *Sargassum* spp. C. Agardh, *Hormosira banksii* (Turner) Decaisne). The coralline turf was associated with a diverse epiphytic assemblage. The most obvious and abundant epiphytic species were *Ulva lactuca* Linnaeus, *Endarachne binghamiae* J. Agardh, *Colpomenia sinuosa* (Mertens ex Roth) Derbes and Solier and *Enteromorpha* spp. Linnaeus. Many other species of filamentous and foliose algae were found in small abundances, but were extremely variable in space and time.

#### Sampling methods

At Cape Banks, patches of turf were sampled in May 1997, September 1997 and January 1998. At each time of sampling, two sites (2×4 m patches of coralline turf) not previously sampled were haphazardly selected in low- and mid-shore areas. At each height, sites were approximately 50–70 m apart. The top of mid-shore areas was defined by the uppermost patches of coralline turf in any

given area. The heights of mid-shore sites varied between 0.58 and 0.82 m above ILWS (Indian Low Water Springs at Fort Denison, Sydney). Low-shore sites were defined as the lowest patches of coralline turf that could be safely sampled on a calm day with a low tide less than 0.30 m above ILWS. Heights of low-shore sites varied between 0.21 and 0.42 m above ILWS. All sampling was done on days with low swell, calm seas and a low tide less than 0.3 m above ILWS because it was not possible to sample low-shore areas with the same care as mid-shore areas on days with smaller tides or rough conditions.

The macrofauna in natural coralline turf was sampled using a sharpened metal corer, which had an internal diameter of 8 cm (~50 cm<sup>2</sup>). This size of core was the most appropriate compromise between the precision of estimates of diversity and abundance and time required to sort each core (Kelaher, 2000). In each site, four randomly-placed replicate cores were collected. For each replicate, the corer was pushed into the coralline turf and the algae and sediment inside the corer were scraped off at the level of the rock, placed in a plastic bag and taken to the laboratory. Because other species of algae were sometimes found amongst the coralline turf, only areas with greater than 95% primary cover of *Corallina officinalis* were sampled. All replicates were preserved in a 7% formalin solution.

In the laboratory, each replicate core was washed thoroughly in a 500-µm sieve. The fauna remaining in the sieve was identified and counted using a binocular microscope (×16 magnification). Sessile animals that were permanently attached to the fronds or substrata were commonly found in the turf (e.g. sponges, bryozoans, serpulid and spirorbid polychaetes, barnacles, etc.). These organisms were not included in this study because the methods used were not appropriate to quantify these animals accurately. In total, 71,776 individual animals were counted and identified into 147 different taxa (Table 1). Taxonomic resolution of macrofauna varied

**Table 1.** Summary of the 147 macrofaunal taxa found in coralline turf during this study.

| Phylum          | Class          | No. of taxa and resolution |
|-----------------|----------------|----------------------------|
| Cnidaria        | Anthozoa       | 1 Taxon                    |
| Platyhelminthes | Turbellaria    | 1 Taxon                    |
| Nematoda        | —              | 1 Taxon                    |
| Nemertea        | —              | 1 Taxon                    |
| Annelida        | Oligochaeta    | 1 Taxon                    |
|                 | Polychaeta     | 19 Families                |
| Sipuncula       | —              | 1 Taxon                    |
| Arthropoda      | Insecta        | 3 Species                  |
|                 | Pycnogonida    | 1 Taxon                    |
|                 | Arachnida      | 1 Taxon                    |
|                 | Ostracoda      | 1 Taxon                    |
|                 | Copepoda       | 1 Taxon                    |
|                 | Malacostraca   | 29 Families*               |
| Mollusca        | Polyplacophora | 6 Species                  |
|                 | Gastropoda     | 65 Species                 |
|                 | Bivalvia       | 11 Species                 |
| Echinodermata   | Asteroidea     | 2 Species                  |
|                 | Ophiuroidea    | 1 Taxon                    |
|                 | Echinoidea     | 1 Species                  |

\*, 17 of the 29 families of malacostraceans were in the order Amphipoda.

among taxa because many of the species have not been described in Australia and many of the animals were juveniles and could not be reliably identified to species using taxonomic keys (when keys were available).

To test the hypothesis that spatial patterns of macrofauna in coralline turf at Cape Banks are general to rocky shores in the Sydney Region, the four shores described above (including Cape Banks) were sampled in summer, on 27 and 28 January 1998. Each shore was sampled using similar methods to those described for Cape Banks, except five cores were taken from each site to increase the power and resolution of analyses.

To test hypotheses about environmental variables, the dry weight of sediment and epiphytes and the average length and density of fronds were measured for each core sampled at each of the four shores in January 1998. For each core, the dry weight of epiphytes was measured by carefully removing epiphytes from the coralline fronds. The epiphytes were dried for 48 h at 60°C, cooled in a desiccator for four hours and weighed. Occasionally, non-coralline algal species occupied primary space. It was not possible to separate these from epiphytic algae in the laboratory. Therefore, all non-coralline algae in each core were defined as epiphytes. For each core, the sediment particles greater than 63 µm were collected, dried in an oven for 48 h at 80°C, cooled in a desiccator for four hours and weighed. Because the sediment was relatively

coarse, the component of sediment less than 63 µm only had a small contribution to the total weight (less than 2%) and was therefore not quantified (see also Gibbons, 1988).

The average length and density of fronds were used to quantify characteristics of the physical structure of coralline turf. The average length of fronds for each core was determined from measurements of length of four randomly-selected fronds. Each frond measured had an intact holdfast and was not broken. For each core, the density of coralline turf ( $\text{g cm}^{-3}$ ) was determined by dividing the dry weight of coralline fronds per  $\text{cm}^2$  by the average length. To measure the dry weight of coralline fronds, the epiphytes and animals on each frond were carefully removed. The coralline fronds were then dried and weighed using similar methods to those used for epiphytes.

#### Analyses of data

Specific hypotheses were tested for entire macrofaunal assemblages and the number of taxa of polychaetes, amphipods and gastropods. Gastropods, polychaetes and amphipods were analysed separately because they were the most diverse and dominant faunal groups (Table 1).

Non-parametric multivariate analyses of variance (NP-MANOVA) were used to test hypotheses about

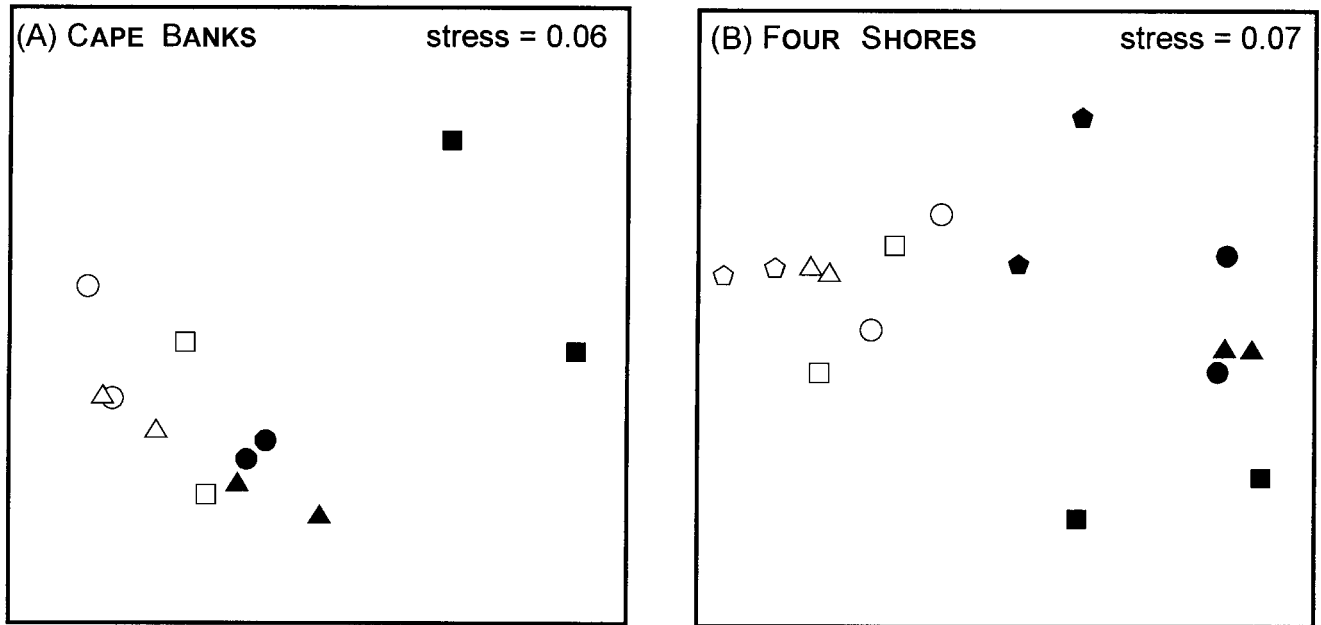
**Table 2.** Results of NP-MANOVA analyses for macrofaunal assemblages sampled (A) at Cape Banks and (B) at the four shores sampled in January 1998. Analyses were done (i) comparing heights at each time or shore, or (ii) comparing times or shores at each height. 'he' is the fixed comparison between mid- and low-shore areas; 'ti' is the comparison among randomly-chosen times; 'sh' is the comparison among randomly-chosen shores; 'si' is the comparison of sites nested in height, times or shores.

| A. <i>Cape Banks</i> .       |          |          |     |         |                   |           |
|------------------------------|----------|----------|-----|---------|-------------------|-----------|
|                              | Analyses |          |     |         | Post-hoc tests    |           |
| (i) Analyses at each time    | si(he)   | df       | he  | df      | mid-shore         | low-shore |
| May 1997 (T1)                | ***      | 2, 12 df | **  | 1, 2 df | S1 ≠ S2           | S1 = S2   |
| September 1997 (T2)          | ***      | 2, 12 df | **  | 1, 2 df | S1 = S2           | S1 ≠ S2   |
| January 1998 (T3)            | ***      | 2, 12 df | *   | 1, 2 df | S1 ≠ S2           | S1 ≠ S2   |
| (ii) Analyses at each height | si(ti)   | df       | ti  | df      | times             |           |
| mid-shore                    | ***      | 2, 12 df | Ns  | 2, 3 df | T1 = T2 = T3      |           |
| low-shore                    | ***      | 2, 12 df | **  | 2, 3 df | T1 = T2 ≠ T3      |           |
| B. <i>Four shores</i> .      |          |          |     |         |                   |           |
|                              | Analyses |          |     |         | Post-hoc tests    |           |
| (i) Analyses at each shore   | si(he)   | df       | He  | df      | mid-shore         | low-shore |
| Green Point (GP)             | ***      | 2, 16 df | **  | 1, 2 df | S1 ≠ S2           | S1 ≠ S2   |
| Harbord (HA)                 | ns       | 2, 16 df | *** | 1, 2 df | —                 | —         |
| Cape Banks (CB)              | ***      | 2, 16 df | *   | 1, 2 df | S1 ≠ S2           | S1 ≠ S2   |
| Coledale (CD)                | ***      | 2, 16 df | *** | 1, 2 df | S1 ≠ S2           | S1 ≠ S2   |
| (ii) Analyses at each height | si(sh)   | df       | Sh  | df      | shores            |           |
| mid-shore                    | ***      | 4, 32 df | *** | 3, 4 df | GP = HA = CB ≠ CD |           |
| low-shore                    | ***      | 4, 32 df | *** | 3, 4 df | GP = HA = CB ≠ CD |           |

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ns, not significant. Post-hoc comparisons are presented for sites, times and locations. For post-hoc comparisons: <sup>1</sup>,  $P < 0.05$ ; =, not significant.

multivariate differences among macrofaunal assemblages (Anderson, 2001). The NP-MANOVAs were followed by a posteriori pair-wise comparisons on appropriate terms in the model found to be significant at  $P \leq 0.05$ . For these tests, only probability values are presented because the multivariate  $F$ -statistics and  $T$ -statistics were generated by permutations. For some comparisons, tests were done by permuting the residuals of the full model to obtain a significance level with  $P \leq 0.05$  (described by Ter Braak,

1992; Anderson & Legendre, 1999). Because NP-MANOVA can only analyse one or two factors at one time, temporal and spatial differences in macrofaunal assemblages at Cape Banks were tested in two ways. First, two-way nested analyses were done to test for differences between 'heights' (two levels, orthogonal and fixed) and 'sites' (two levels, nested within heights) at each time. Second, two-way nested analyses were done to test for differences among 'times' (three levels, orthogonal and



**Figure 2.** Two-dimensional nMDS ordinations comparing macrofaunal assemblages from mid- (unfilled) and low-shore (filled) areas. Data are averaged among replicates within sites. (A) Assemblages sampled at Cape Banks in May 1997 (circles), September 1997 (triangles) and January 1998 (squares); (B) assemblages sampled at Green Point (circles), Harbord (triangles), Cape Banks (squares) and Coledale (pentagons) in January 1998.

**Table 3.** Percentage contributions of individual taxa to dissimilarity between sites (i) in mid-shore, (ii) in low-shore areas and (iii) mean of comparisons among every replicate in low-shore sites with each replicate in mid-shore sites. Dissimilarities are from the (a) three times of sampling at Cape Banks and (b) at the four shores sampled in January 1998. The ten taxa selected contributed more than 60% of the total dissimilarity for all comparisons and each taxon made a relatively large contribution to the total dissimilarity compared to other taxa found in coralline turf.

| Taxa                           | A. Cape Banks |    |    |                |    |    |                  |    |    | B. Four shores |    |    |    |                |    |    |    |                  |    |    |    |
|--------------------------------|---------------|----|----|----------------|----|----|------------------|----|----|----------------|----|----|----|----------------|----|----|----|------------------|----|----|----|
|                                | (i) mid-shore |    |    | (ii) low-shore |    |    | (iii) mid vs low |    |    | (i) mid-shore  |    |    |    | (ii) low-shore |    |    |    | (iii) mid vs low |    |    |    |
|                                | T1            | T2 | T3 | T1             | T2 | T3 | T1               | T2 | T3 | GP             | HA | CB | CD | GP             | HA | CB | CD | GP               | HA | CB | CD |
| Nematodes                      | 0             | 1  | 5  | 3              | 24 | 1  | 1                | 8  | 2  | 2              | 4  | 4  | 3  | 1              | 1  | 1  | 4  | 1                | 1  | 2  | 2  |
| Syllid polychaetes             | 2             | 2  | 2  | 6              | 2  | 4  | 2                | 1  | 4  | 16             | 10 | 2  | 5  | 6              | 3  | 4  | 9  | 12               | 2  | 5  | 2  |
| Orbinid polychaetes            | 2             | 0  | 0  | 15             | 9  | 11 | 4                | 5  | 6  | 0              | 0  | 0  | 0  | 0              | 0  | 10 | 0  | 0                | 0  | 5  | 0  |
| <i>Limonia marina</i>          | 1             | 3  | 3  | 0              | 1  | 0  | 1                | 2  | 2  | 7              | 6  | 4  | 5  | 0              | 0  | 0  | 0  | 8                | 5  | 2  | 4  |
| Janirid isopods                | 10            | 14 | 1  | 1              | 3  | 1  | 4                | 5  | 1  | 0              | 1  | 1  | 0  | 0              | 1  | 1  | 1  | 0                | 0  | 1  | 0  |
| Tanaids                        | 7             | 1  | 33 | 0              | 1  | 5  | 5                | 0  | 9  | 0              | 0  | 33 | 0  | 5              | 3  | 5  | 0  | 2                | 2  | 10 | 0  |
| Melitid amphipods              | 0             | 0  | 0  | 1              | 2  | 23 | 0                | 1  | 12 | 0              | 0  | 0  | 0  | 6              | 12 | 22 | 7  | 7                | 8  | 10 | 1  |
| Isherosid amphipods            | 0             | 0  | 0  | 0              | 0  | 5  | 0                | 0  | 5  | 0              | 0  | 0  | 0  | 36             | 32 | 5  | 3  | 10               | 13 | 4  | 1  |
| <i>Eatoneilla atropurpurea</i> | 3             | 0  | 6  | 6              | 4  | 10 | 3                | 3  | 6  | 14             | 6  | 6  | 3  | 1              | 1  | 10 | 6  | 6                | 1  | 6  | 1  |
| <i>Lasaea australis</i>        | 41            | 53 | 19 | 32             | 26 | 4  | 52               | 54 | 27 | 31             | 53 | 20 | 54 | 12             | 11 | 5  | 27 | 22               | 48 | 27 | 68 |
| Total dissimilarity            | 66            | 74 | 69 | 64             | 72 | 64 | 72               | 79 | 74 | 70             | 80 | 70 | 70 | 67             | 64 | 63 | 57 | 70               | 81 | 71 | 79 |

T1, May 1997; T2, September 1997; T3, January 1998; GP, Green Point; HA, Harbord; CB, Cape Banks; CD, Coledale.

random) and 'sites' (two levels, nested within times) for each height separately. A similar approach was used to test the generality of the spatial patterns at Cape Banks, except in these analyses the factor 'shores' (four levels, orthogonal and random) replaced the factor 'time'.

Non-metric multidimensional scaling (nMDS, Field et al., 1982; Clarke, 1993) was used to produce two-dimensional ordination plots to show relationships among macrofaunal assemblages. Similarity percentage analysis (SIMPER) (Clarke, 1993) was used to determine the taxa contributing most to the dissimilarity between groups. All multivariate analyses were done using the Bray–Curtis similarity coefficient (Bray & Curtis, 1957; Clarke & Green, 1988; Clarke, 1993) and the data were untransformed. Analysis of variance was used to test hypotheses about differences in the number of taxa of the main faunal groups. These analyses were preceded by Cochran's test for homogeneity of variances (Winer et al., 1991; Underwood, 1997). Where variances showed significant heterogeneity, the data were transformed using  $(x+1)^{0.5}$  or  $\ln(x+1)$  transformations where appropriate (Underwood, 1997). For univariate comparisons, all three factors were included in analyses.

BIO-ENV (Clarke & Ainsworth, 1993) was used to investigate the relationships between macrofaunal assemblages and environmental variables. For these analyses, a weighted Spearman's rank coefficient was used (recommended by Clarke & Ainsworth, 1993). For univariate comparisons, patterns of association were tested using Pearson's  $r$  correlation coefficient (Winer et al., 1991). To decrease the probability of excessive Type I errors, multiple comparisons were only considered significant if  $P < 0.01$ . Because of large differences between macrofaunal assemblages at different heights on the shore (see Results), analyses investigating relationships between environmental variables and macrofauna were done separately in low- and in mid-shore areas.

## RESULTS

### *Patterns of macrofaunal assemblages at Cape Banks*

At each time of sampling at Cape Banks, there were significant differences between assemblages from low- and from mid-shore areas (Table 2A; Figure 2A). There were also significant differences between sites at each height,

**Table 4.** Analyses of number of taxa of the three main taxonomic groups from (A) the three times of sampling at Cape Banks and (B) the four shores sampled in January 1998. 'ti' is the comparison among three times of sampling at Cape Banks. 'sh' is the comparison among the four randomly-chosen shores; 'he' is the fixed comparison between mid- and low-shore areas; 'si' is the comparison of sites nested in 'ti' and 'he' or 'sh' and 'he'.

| A. Cape Banks.  |    | (N=4)                                                                |         |                         |          |                       |          |
|-----------------|----|----------------------------------------------------------------------|---------|-------------------------|----------|-----------------------|----------|
|                 |    | Species of Gastropods                                                |         | Families of Polychaetes |          | Families of Amphipods |          |
| Transform       |    | none                                                                 |         | none                    |          | none                  |          |
|                 | df | MS                                                                   | F       | MS                      | F        | MS                    | F        |
| ti              | 2  | 103.14                                                               | 9.24 –  | 12.33                   | 0.74 ns  | 38.58                 | 3.62 ns  |
| he              | 1  | 161.33                                                               | 2.02 –  | 54.18                   | 13.55 ns | 72.52                 | 1.98 ns  |
| ti×he           | 2  | 77.77                                                                | 7.14*   | 4.00                    | 0.24 ns  | 36.58                 | 3.44 ns  |
| site(ti×he)     | 6  | 11.16                                                                | 1.34 ns | 16.56                   | 7.87***  | 10.64                 | 8.38***  |
| residual        | 36 | 8.32                                                                 |         | 2.10                    |          | 1.27                  |          |
| SNK             |    | T1: NS T2: NS T3: M < L<br>M: T1=T2=T3 L: T1=T2 < T3                 |         |                         |          |                       |          |
| B. Four shores. |    | (N=5)                                                                |         |                         |          |                       |          |
|                 |    | Species of Gastropods                                                |         | Families of Polychaetes |          | Families of Amphipods |          |
| Transform       |    | none                                                                 |         | $\ln(x+1)$              |          | $\ln(x+1)$            |          |
|                 | df | MS                                                                   | F       | MS                      | F        | MS                    | F        |
| sh              | 3  | 83.01                                                                | 5.82 –  | 8.51                    | 0.44 ns  | 30.13                 | 3.93 ns  |
| he              | 1  | 180.00                                                               | 2.14 –  | 10.51                   | 0.76 ns  | 396.05                | 47.62**  |
| sh×he           | 3  | 84.10                                                                | 5.89*   | 13.84                   | 0.72 ns  | 8.31                  | 1.08 ns  |
| site(sh×he)     | 8  | 14.27                                                                | 3.10**  | 19.33                   | 8.29***  | 7.67                  | 17.30*** |
| residual        | 64 | 4.60                                                                 |         | 3.86                    |          | 0.44                  |          |
| SNK             |    | GP: NS HA: NS CB: M < L CD: M < L<br>M: GP=HA=CB=CD L: GP=HA=CD < CB |         |                         |          |                       |          |

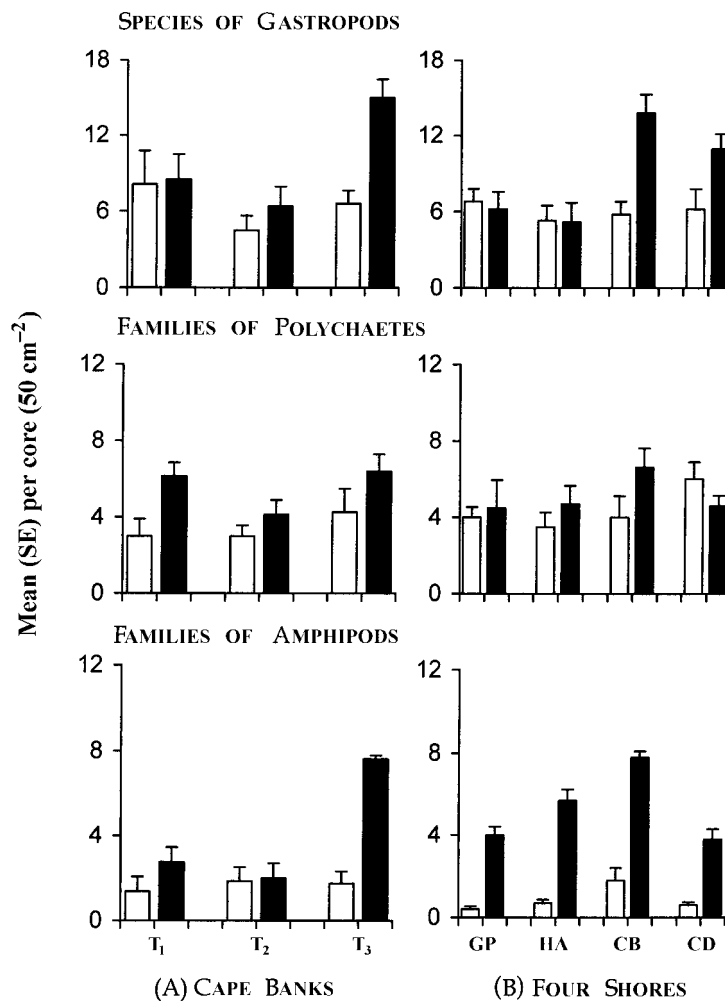
\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ns, not significant; –, no test possible because of significant interaction. For Student–Newman–Keuls (SNK) comparisons: T1, May 1997; T2, September 1997; T3, January 1998; GP, Green Point; HA, Harbord; CB, Cape Banks; CD, Coledale; M, mid-shore areas; L, low-shore areas; <,  $P > 0.05$ ; =, not significant.

but these differences varied from time to time. There were no significant temporal differences among assemblages in mid-shore areas, but in low-shore areas, assemblages in January 1998 were significantly different from those at the other two times of sampling (Table 2A; Figure 2A). The magnitude of temporal change between the first two times of sampling was similar between assemblages in low- or mid-shore, but differed greatly at the third time of sampling (Figure 2A).

The small and abundant bivalve, *Lasaea australis* (Lamarck), made large contributions to the dissimilarity between sites in low- and mid-shore areas and between mid- and low-shore areas at all times of sampling at Cape Banks, except low-shore areas in January 1998 (Table 3A). Janirid isopods (mostly *Ianiropsis* sp.) made large contributions to the dissimilarities among sites in mid-shore areas in May and September 1997, but not in January 1998. In contrast, tanaids made relatively small contributions to the dissimilarity among mid-shore sites at the first two times of sampling, compared with their contribution in January 1998. Orbinid polychaetes and the small gastropod, *Eatoniella atropurpurea* (Fauenfeld), made consistently large contributions to the dissimilarity between sites in low-shore areas at all times of sampling. Nematodes made a

large contribution to the dissimilarity between sites in low-shore areas in September 1997 and melitid amphipods (mostly *Elasmopus* sp.) were major contributors in January 1998. At the first two times of sampling, *L. australis* contributed more than 50% of the difference between assemblages in low- and mid-shore levels. In contrast, a range of species contributed to the dissimilarity at the third time of sampling (*L. australis* contributing only 27%; see Table 3).

There were no significant differences in the number of families of polychaetes or amphipods between low- and mid-shore areas (Table 4A; Figure 3). There were significantly more species of gastropods in low- than in mid-shore areas in January 1998, but not at other times of sampling (Table 4A; Figure 3). There were also significantly more species of gastropods in January 1998 than at other times of sampling. Although not significantly different, at each time of sampling, there were more families of polychaetes and amphipods and more species of gastropods in low- than in mid-shore areas (Figure 3). There was also significant variability in the number of families of amphipods and polychaetes between sites, but not in the number of species of gastropods (Table 4A).



**Figure 3.** Mean (SE) number of taxa of the three main faunal groups for (A) the three times of sampling at Cape Banks (T1, May 1997; T2, September, 1997 and T3, January, 1998); and (B) the four shores (GP, Green Point; HA, Harbord; CB, Coledale and CD, Coledale) sampled in January 1998. Data are from mid- (unfilled) and low-shore areas (filled) and are averaged across sites.

*Generality of patterns of macrofaunal assemblages*

At each shore, there were significant differences between assemblages from low- and mid-shore areas (Table 2B; Figure 2B) and the magnitude of these differences were relatively similar (Figure 2B). Nevertheless, the assemblages in low- and in mid-shore areas at Coledale were significantly different from those at other shores (Table 2B). There were also significant differences between sites in low- and mid-shore areas at all shores, except Harbord (Table 2B).

Syllid polychaetes, the insect larvae, *Limonia marina* Skuse, the small gastropod, *E. atropurpurea*, and the small bivalve, *Lasaea australis*, made relatively large contributions to the dissimilarity between sites in mid-shore areas (Table 3B). Syllid polychaetes, melitid amphipods, ischyrocerid amphipods and the small bivalve, *Lasaea australis*, made a relatively large contribution to the dissimilarity between sites in low-shore areas. *Lasaea australis* made an extremely large contribution to dissimilarity between low- and mid-shore areas at all locations sampled. Melitid and ischyrocerid amphipods were relatively large contributors between low- and mid-shore areas at all locations, except Coledale. Syllid polychaetes and the insect larvae, *Limonia marina*, made relatively large contributions to dissimilarity at all locations.

There were no significant differences in the number of families of polychaetes between low- and mid-shore areas (Table 4B; Figure 3). There were, however, significantly more families of amphipods in low- than in mid-shore

areas (Table 4B; Figure 3). There were also significantly more species of gastropods in low- than in mid-shore areas at Cape Banks and Coledale, but not at the other shores (Table 4B; Figure 3). There was significant variability in the number of taxa of amphipods, polychaetes and gastropods among sites within shores (Table 4B).

*Environmental variables and their relationship with macrofaunal assemblages*

Except for epiphytes, all environmental variables differed significantly between sites in low- and in mid-shore areas (Table 5). In addition, the length of fronds and amount of epiphytes were significantly greater in low- than in mid-shore areas at all locations (Table 5; Figure 4). There were no overall significant differences in the amount of sediments or density of fronds between low- and mid-shore areas (Table 5; Figure 4). All environmental variables varied significantly among shores, although the length of fronds only varied among shores in low-shore areas (Table 5; Figure 4).

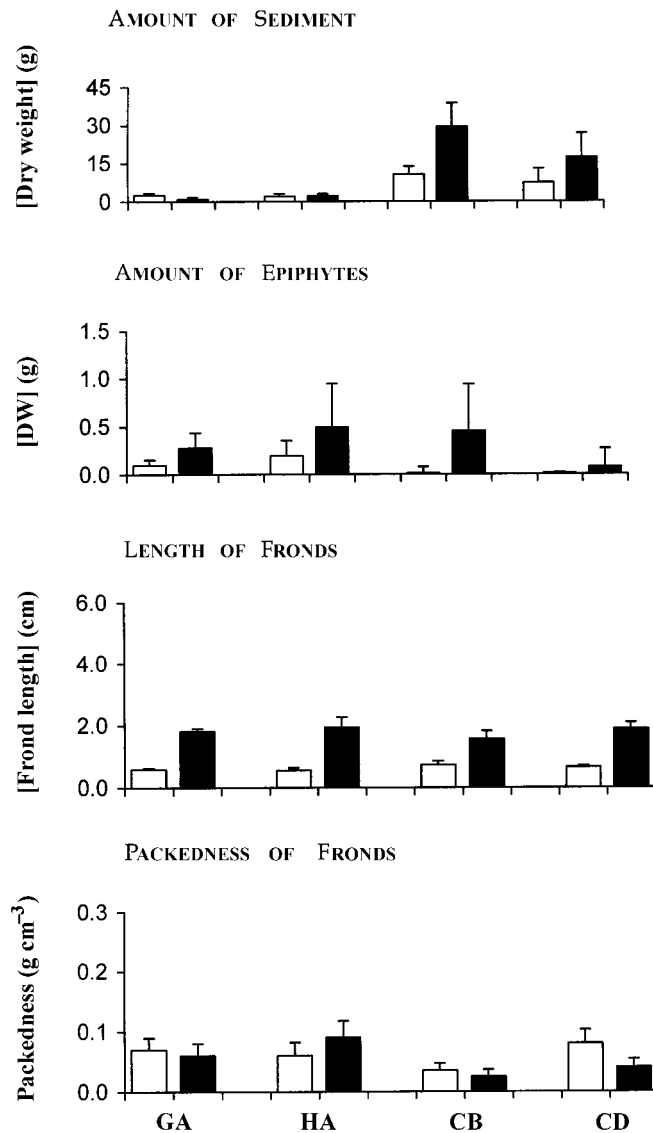
Of all the environmental variables, sediment showed the strongest relationship with the macrofaunal assemblage in either low- or mid-shore areas (Table 6). In mid-shore areas, the strength of the relationship between sediment and macrofauna became greater as architectural characteristics of turf (length and density of fronds) were also incorporated. In low-shore area, the relationship between sediment and macrofauna became weaker as extra environment variables were included in analyses.

**Table 5.** Analyses of environmental variables at the four shores sampled in January 1998. 'sh' is the random comparison among the four shores; 'he' is the fixed comparison between mid- and low-shore areas; 'si' is the random comparison of sites nested in 'sh' and 'he'.

| Transform  | Sediment |        |                                         | Epiphytes |               |
|------------|----------|--------|-----------------------------------------|-----------|---------------|
|            | none     |        |                                         | sq(x + 1) |               |
|            | df       | MS     | F                                       | MS        | F             |
| Sh         | 3        | 16.49  | 8.09***                                 | 0.17      | 5.39*         |
| He         | 1        | 0.03   | 0.03 ns                                 | 0.61      | 26.14*        |
| sh×he      | 3        | 1.18   | 0.58 ns                                 | 0.02      | 0.75 ns       |
| si(sh×he)  | 8        | 2.04   | 16.29***                                | 0.03      | 1.37 ns       |
| Residual   | 64       | 0.12   |                                         | 0.02      |               |
| SNK height |          |        |                                         |           | M < L         |
| Location   |          |        | GP=HA < CB=CD                           |           | GP=HA=CB=CD   |
| Transform  | Length   |        |                                         | Density   |               |
|            | none     |        |                                         | none      |               |
|            | df       | MS     | F                                       | MS        | F             |
| Sh         | 3        | 0.32   | 1.97 –                                  | 59.45     | 5.07*         |
| He         | 1        | 108.44 | 57.42 –                                 | 13.89     | 0.45 ns       |
| sh×he      | 3        | 1.88   | 11.67**                                 | 30.68     | 2.67 ns       |
| si(sh×he)  | 8        | 0.16   | 2.03*                                   | 11.74     | 4.73***       |
| Residual   | 64       | 0.08   |                                         | 2.48      |               |
| SNK height |          |        | GP: M < L HA: M < L CB: M < L CD: M < L |           |               |
|            |          |        | M: GP=HA=CB=CD L: GP=CD=CB < HA         |           | CD < GP=HA=CD |

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ns, not significant. For Student–Newman–Keuls (SNK) tests: GP, Green Point; HA, Harbord; CB, Cape Banks; CD, Coledale; L, low-shore areas; M, mid-shore areas; <,  $P > 0.05$ ; =, not significant.





**Figure 4.** Mean (SE) measures of environmental variables in each core from the four shores (GP, Green Point; HA, Harbord; CB, Coledale; and CD, Coledale) sampled in January 1998. Data are from mid- (unfilled) and low-shore areas (filled) and are averaged across sites.

**Table 6.** Correlation coefficients ( $N=40$ ) for comparisons between the macrofaunal assemblage and combinations of environmental variables from BIO-ENV analyses. Values indicate the strength of relationships relative to other comparisons at each height on the shore. Bold values indicate the strongest relationships for comparisons involving either one, two or three variables.

|                           | Mid-shore sites | Low-shore sites |
|---------------------------|-----------------|-----------------|
| sediment (se)             | <b>0.19</b>     | <b>0.42</b>     |
| epiphytes (ep)            | 0.15            | 0.10            |
| length (le)               | 0.06            | 0.02            |
| packedness (density) (pa) | -0.12           | 0.02            |
| se + ep                   | 0.16            | 0.26            |
| se + le                   | <b>0.21</b>     | <b>0.32</b>     |
| se + pa                   | 0.17            | <b>0.32</b>     |
| ep + le                   | 0.09            | 0.06            |
| ep + pa                   | 0.06            | 0.08            |
| le + pa                   | 0.18            | 0.13            |
| se + ep + le              | 0.18            | 0.27            |
| se + ep + pa              | 0.18            | 0.26            |
| se + le + pa              | <b>0.22</b>     | <b>0.34</b>     |
| ep + le + pa              | 0.13            | 0.11            |
| se + ep + le + pa         | 0.20            | 0.28            |

**Table 7.** Summary of correlations between environmental variables and the number of taxa in the three main faunal groups. Correlations are divided into (i) mid- and (ii) low-shore areas.

|                            | Sediment<br><i>r</i> | Epiphytes<br><i>r</i> | Length<br><i>r</i> | Density<br><i>r</i> |
|----------------------------|----------------------|-----------------------|--------------------|---------------------|
| <i>A. Mid-shore areas.</i> |                      |                       |                    |                     |
| Families of Amphipods      | −0.15                | 0.57**                | 0.53**             | −0.25               |
| Families of Polychaetes    | 0.51**               | −0.54**               | −0.26              | 0.28                |
| Species of Gastropods      | 0.04                 | 0.02                  | −0.04              | 0.09                |
| <i>B. Low-shore areas.</i> |                      |                       |                    |                     |
| Families of Amphipods      | 0.38                 | 0.31                  | −0.33              | −0.20               |
| Families of Polychaetes    | 0.43**               | 0.13                  | −0.14              | −0.14               |
| Species of Gastropods      | 0.65**               | −0.05                 | −0.46**            | −0.54**             |

*r*, Pearson's correlation coefficient; \*\*,  $P < 0.01$ ;  $N = 40$ .

In mid-shore areas, there was a significant positive correlation between the number of families of polychaetes and the amount of sediment, between the number of families of amphipods and the amount of epiphytes and length of fronds (Table 7A) and there was a significant negative correlation between the number of families of polychaetes and the amount of epiphytes (Table 7A). In low-shore areas, there was a significant positive correlation between the number of families of polychaetes and number of species of gastropods and the amount of sediment (Table 7A). In addition, there was a significant negative correlation between number of species of gastropods and the length and density of fronds in low-shore areas (Table 7A).

## DISCUSSION

Prior to this study, little was known about the biodiversity of macrofauna in coralline turf on rocky shores around Sydney. In this study, 147 taxa of mobile macrofauna were identified and densities of macrofauna often exceeded  $250,000 \text{ m}^{-2}$  (Table 1; Kelaher, 2000). Given the great abundance of coralline turf on rocky shores of New South Wales (Underwood, 1981; Underwood & Chapman, 1998), it is clear that this assemblage makes an extremely large contribution to biodiversity of these habitats. Even considering differences in methods of sampling, the macrofauna in coralline turf on the shores investigated in this study appears to be relatively rich compared with shores in other countries (Japan: 91 taxa (Akioka et al., 1999); Chile: 36 taxa (Lopez & Stolz, 1997); Norway: 72 taxa (Dommasnes, 1969); New Zealand: 106 using similar taxonomic resolution of the phyla in Table 1 (Hicks, 1971); Ireland: 92 taxa using the same taxonomic resolution as here, B.P.K., unpublished data).

At each time of sampling at Cape Banks and at the other shores, there were differences between assemblages in low- and mid-shore areas. These results were not unexpected because this pattern is generally found for other assemblages of organisms on rocky intertidal shores (Lewis, 1964; Dayton, 1971; Menge, 1976; Lubchenco et al., 1984; Underwood & Chapman, 1998). Despite a large body of literature documenting the patterns of vertical distribution of algae and animals, the generality of these patterns has rarely been tested. In the few cases where generality has

been tested, it has been found that patterns may vary from shore to shore (Foster, 1990; Underwood & Chapman, 1998). In this study, assemblages at Coledale were significantly different from those at other shores. Despite this, however, the differences between low- and mid-shore areas appeared to be relatively consistent among shores.

There was a trend for greater numbers of taxa of gastropods, amphipods and polychaetes in low- than in mid-shore areas at each time of sampling at Cape Banks, although these differences were not always significant. In contrast to the multivariate results, however, when the patterns of richness of gastropods and polychaetes were tested, there was no generality among shores. For example, there were more families of polychaetes in mid- than in low-shore areas at Coledale and more species of gastropods in mid- than low-shore areas at Green Point. This lack of generality indicates that no common process is responsible for structuring patterns of richness of gastropods and polychaetes between low- and mid-shore areas over the region studied (120 km) and that local processes are extremely important for structuring some aspects of the macrofaunal assemblage. In contrast to gastropods and polychaetes, there were more families of amphipods in coralline turf in low- than in mid-shore areas at each shore sampled. Similar results have been reported in other studies (Tararam et al., 1986; Underwood & Verstegen, 1987; Lintas & Seed, 1994), indicating the possibility of general biological processes or environmental factors being responsible for the vertical distribution of amphipods on rocky shores.

At every time of sampling at Cape Banks and at the other shores, except Harbord, there were significant differences among macrofaunal assemblages and the richness of polychaetes, amphipods and gastropods in sites separated by tens of metres. In previous studies investigating macrofaunal assemblages in mat-like habitats on rocky shores, replication at the scales of tens of metres has rarely been considered (e.g. Dommasnes, 1968; Lintas & Seed, 1994). This is probably because sorting and identifying macrofauna from these habitats is extremely time-consuming (Hicks, 1977) and replication is usually minimized. Nevertheless, this study showed that macrofauna in mat-like habitats can vary at the scales of tens of metres, as do other intertidal assemblages on rocky shores

(Caffey, 1985; Archambault & Bourget, 1996; Underwood & Chapman, 1998). These results with those of other studies emphasize the need for within-shore or within-height replication before different shores or different heights on the shore can be compared (see Hurlbert, 1984; Underwood, 1994).

Much of the variation in assemblages between low- and mid-shore areas and between sites in each height on the shore can be attributed to relatively few taxa. Of these taxa, the small bivalve, *Lasaea australis*, made an extremely large contribution to dissimilarity among assemblages at nearly all times of sampling and shores. This is not unexpected because *L. australis* often reached densities of more than 100,000 m<sup>-2</sup>, was spatially variable and was more abundant in mid- than in low-shore areas (Kelaher, 2000). Other studies have shown a similar dominance of *Lasaea* spp. in macrofaunal assemblages in other mat-like habitats on rocky shores (Ong Che & Morton, 1992; Peake & Quinn, 1993). Other than *L. australis*, the taxa most contributing to spatial variation tended to vary from shore to shore and from time to time. For example, Ischerid amphipods were relatively large contributor to dissimilarity between sites in low-shore areas and between low- and mid-shore areas at Green Point and Harbord, but not at Cape Banks or Coledale. Nevertheless, this taxon rarely contributed to differences between sites in mid-shore areas at any time of sampling. In contrast, tanaids made an extremely large contribution to dissimilarity among sites in mid-shore areas in January 1998 at Cape Banks, but not at other shores or at other times. At any one time of sampling or shore, there was generally a relatively small group of taxa responsible for most of the dissimilarity between assemblages. Apart from *L. australis*, it is difficult to identify specific taxa that were consistently responsible for large amount of dissimilarity among assemblages at all times of sampling and shores.

Environmental variables, such as the amount of sediment, epiphytes or the amount or type of physical structure of the habitat, are generally considered important for structuring macrofaunal assemblages in algal turf (Hicks, 1980; Dean & Connell, 1987a; Johnson & Scheibling, 1987; Gibbons, 1988; Gee & Warwick, 1994). In this study, it is obviously not possible to determine the effects of environmental variables on the spatial variability of macrofaunal assemblages in coralline turf because the data are descriptive. Nevertheless, the patterns of spatial variability of environmental variables and correlations between environmental variables and macrofauna may provide indications of their relative importance and guide future research. For example, the average length of fronds and the amount of epiphytes were greater in low- and in mid-shore areas. Coralline turf with long fronds may have a greater surface area available for colonization and reduce the effects of waves more effectively than turf with short fronds (Dommasnes, 1968; Whorff et al., 1995). In addition, epiphytes provide both food and shelter for associated assemblages of organisms (Johnson & Scheibling, 1987; Duffy, 1990; Schneider & Mann, 1991a,b; Martin-Smith, 1993). Therefore, each of these variables may contribute to differences between the macrofaunal assemblages in low- and mid-shore areas. Nevertheless, because the amount of sediment and density of coralline fronds did

not vary between different heights on the shore, these variables probably explain little of the variation between assemblages in low- and mid-shore areas.

Like the macrofaunal assemblages in coralline turf, all environmental variables, except epiphytes, varied at scales of tens of metres. Moreover, all environmental variables were significantly correlated with some aspect of the assemblage in either low- or mid-shore areas. Nevertheless, except for the positive association between richness of polychaetes and the amount of sediment, the relationships between macrofauna and the environmental variables were much more complicated than the simple positive relationships found in other studies (e.g. Dean & Connell, 1987a; Gibbons, 1988; Gee & Warwick, 1994). For example, the length of coralline fronds was negatively associated with the number of families of amphipods in low-shore areas, but positively associated in mid-shore areas. In addition, the directions of correlations were strongly dependent on the type of organisms being investigated, e.g. the amount of epiphytes in mid-shore areas was positively correlated with the richness of amphipods and negatively correlated with the richness of polychaetes. Although the results suggest that variation in environmental variables may explain some of the spatial variability in the richness of macrofauna in coralline turf, they also show that direction of the effects depends on the height on the shore and the taxa being investigated.

Of the four environmental variables measured, sediment had the strongest and most consistent associations with the macrofauna. It has been postulated that sediment creates a more heterogeneous habitat for infaunal and epifaunal species and thereby increases opportunities for different types of macrofauna (Hicks, 1980, 1985; Gibbons, 1991). This cannot explain the lack of positive associations between the amount of sediment and the richness of amphipods and gastropods in mid-shore areas. Gibbons (1988) argued that sediment enhances the diversity of macrofauna in mat-like habitats in intertidal areas because it retains moisture when the habitat is exposed during low tide. It is possible that the positive associations between sediment and the richness of amphipods and gastropods existed in low- but not mid-shore areas, because the water-retaining properties of sediment in low-shore areas allowed species more commonly found in sub-tidal areas (e.g. dexamimid amphipods or the small opisthobranch, *Runcina australis*) to remain in low-shore intertidal areas.

In this study, the length and density of fronds provided measures of the amount and complexity of physical structure of the habitat. It has usually been shown that as the amount and complexity of structure increases, the richness of the associated assemblage of organisms also increases (MacArthur & MacArthur, 1961; Kohn & Leviten, 1976; Heck & Weststone, 1977; Stoner, 1980; Dean & Connell, 1987a; Beck, 2000). Nevertheless, apart from the positive association between richness of amphipods and the length of fronds, the majority of associations between length and density of fronds were negative. The results found here therefore directly contrast with the positive relationships shown by other similar studies (e.g. Dean & Connell, 1987a; Gibbons, 1988). It is difficult to explain these results, except that they imply that there are other biological processes or environmental variables that are

strongly interacting with the physical characteristics of the coralline turf (see Stoner, 1982; Gibbons, 1988). These results do provide, however, initial evidence that generalizations about positive relationships between the physical structure of habitat and the diversity of the associated assemblage of organisms may not be valid in all situations. Careful manipulative experiments that separate the effects of the physical structure of coralline turf on associated macrofauna from other factors are needed before more concrete conclusions can be reached.

It is clear from this study that coralline algal turf make a large contribution to patterns of variation of invertebrates on rocky intertidal shores around Sydney. Despite some temporal variation and some differences among shores, much of the variability of these assemblages was at small spatial scales (between low and mid-shore areas and between sites separated by tens of metres). Therefore, understanding the processes or environmental variables that create and maintain the structure of these assemblages will be best achieved by initially testing hypotheses about processes that affect small-scale spatial variability, rather than focusing on larger-scale variation among shores.

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## REFERENCES

- Akioka, H., Baba, M., Masaki, T. & Johansen, W., 1999. Rocky shore turfs dominated by *Corallina* (Corallinales, Rhodophyta) in northern Japan. *Phycological Research*, **47**, 199–206.
- Anderson, M.J., 2001. A new method for non-parametric multivariate analysis of variance. *Austral Ecology*, **26**, 32–46.
- Anderson, M.J. & Legendre, P., 1999. An empirical comparison of permutation methods for tests of partial regression coefficients in a linear model. *Journal of Statistical Computation and Simulation*, **62**, 271–303.
- 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.
- Ballesteros, E., 1988. Composición y estructura de la comunidad infralitoral de *Corallina elongata* Ellis and Solander, 1786 de la Costa Brava (Mediterráneo occidental). *Investigaciones Pesqueras. Barcelona*, **52**, 135–151.
- Beck, M.W., 2000. Separating the elements of habitat structure: independent effects of habitat complexity and structural components on rocky intertidal gastropods. *Journal of Experimental Marine Biology and Ecology*, **249**, 29–49.
- Benedetti-Cecchi, L. & Cinelli, F., 1994. Recovery of patches in an assemblage of geniculate coralline algae: variability at different successional stages. *Marine Ecology Progress Series*, **110**, 9–18.
- Bray, J.R. & Curtis, J.T., 1957. An ordination of the upland forest communities of southern Wisconsin. *Ecological Monographs*, **27**, 325–349.
- Brown, P.J. & Taylor, R.B., 1999. Effects of trampling by humans on animals inhabiting coralline algal turf in the rocky intertidal. *Journal of Experimental Marine Biology and Ecology*, **235**, 45–53.
- Caffey, H.M., 1985. Spatial and temporal variation in settlement and recruitment of intertidal barnacles. *Ecological Monographs*, **55**, 313–332.
- Chapman, M.G., 1994. Small- and broad-scale patterns of distribution of the upper-shore littorinid *Nodilittorina pyramidalis* in New South Wales. *Australian Journal of Ecology*, **19**, 83–95.
- Chapman, M.G. & Underwood, A.J., 1994. Dispersal of the intertidal snail, *Nodilittorina pyramidalis*, in response to topographic complexity of the substratum. *Journal of Experimental Marine Biology and Ecology*, **179**, 145–169.
- Clarke, K.R., 1993. Non-parametric analyses of changes in community structure. *Australian Journal of Ecology*, **18**, 117–143.
- Clarke, K.R. & Ainsworth, M., 1993. A method of linking multivariate community structure to environmental variables. *Marine Ecology Progress Series*, **92**, 205–219.
- Clarke, K.R. & Green, R.H., 1988. Statistical design and analysis for a 'biological effects' study. *Marine Ecology Progress Series*, **46**, 213–226.
- Connell, J.H., 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. *Ecology*, **42**, 710–723.
- Connell, J.H., 1972. Community interactions on marine rocky intertidal shores. *Annual Review of Ecology and Systematics*, **3**, 169–192.
- Connor, E.F. & McCoy, E.D., 1979. The statistics and biology of the species–area relationship. *American Naturalist*, **113**, 791–833.
- Coull, B.C. & Wells, J.B., 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology*, **64**, 1590–1609.
- Crisp, D.J. & Southward, A.J., 1958. The distribution of intertidal organisms along the coasts of the English Channel. *Journal of the Marine Biological Association of the United Kingdom*, **37**, 157–208.
- Davenport, J., Butler, A. & Cheshire, A., 1999. Epifaunal composition and fractal dimensions of marine plants in relation to emersion. *Journal of the Marine Biological Association of the United Kingdom*, **79**, 351–355.
- Dayton, P.K., 1971. Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. *Ecological Monographs*, **41**, 352–389.
- Dean, R.L. & Connell, J.H., 1987a. Marine invertebrates in algal succession. II. Tests of hypotheses to explain diversity with succession. *Journal of Experimental Marine Biology and Ecology*, **109**, 217–247.
- Dean, R.L. & Connell, J.H., 1987b. Marine invertebrates in algal succession. III. Mechanisms linking habitat complexity with diversity. *Journal of Experimental Marine Biology and Ecology*, **107**, 249–273.
- Denley, E.J. & Underwood, A.J., 1979. Experiments on factors influencing settlement, survival and growth of two species of barnacles in New South Wales. *Journal of Experimental Marine Biology and Ecology*, **36**, 269–293.
- Dommasnes, A., 1968. Variations in the meiofauna of *Corallina officinalis* L. with wave exposure. *Sarsia*, **34**, 117–124.
- Dommasnes, A., 1969. On the fauna of *Corallina officinalis* L. in western Norway. *Sarsia*, **38**, 71–86.
- Duffy, J.E., 1990. Amphipods on seaweeds: partners of pests? *Oecologia*, **83**, 267–276.
- Dye, A.H., 1993. Recolonization of intertidal macroalgae in relation to gap size and molluscan herbivory on a rocky shore on the east coast of southern Africa. *Marine Ecology Progress Series*, **95**, 263–271.
- Fairweather, P.G., 1985. Differential predation on alternative prey and the survival of rocky intertidal organisms in New South Wales. *Journal of Experimental Marine Biology and Ecology*, **109**, 135–156.

- Fairweather, P.G. & Underwood, A.J., 1991. Experimental removals of a rocky intertidal predator: variations within two habitats in the effects on prey. *Journal of Experimental Marine Biology and Ecology*, **154**, 29–75.
- Field, J.G., Clarke, K.R. & Warwick, R.M., 1982. A practical strategy for analysing multispecies distribution patterns. *Marine Ecology Progress Series*, **8**, 37–52.
- Fielding, P.J., Weerts, K.A. & Forbes, A.T., 1994. Macroinvertebrate community associated with intertidal and subtidal beds of *Pyura stolonifera* (Heller) (Tunicata: Ascidacea) on the Natal coast. *South African Journal of Zoology*, **29**, 46–53.
- Foster, M.S., 1990. Organization of macroalgal assemblages in the northeast Pacific: the assumption of homogeneity and the illusion of generality. *Hydrobiologia*, **192**, 21–33.
- Gee, J.M. & Warwick, R.M., 1994. Metazoan community structure in relation to the fractal dimensions of marine macroalgae. *Marine Ecology Progress Series*, **103**, 141–150.
- Gibbons, M.J., 1988. The impact of sediment accumulations, relative habitat complexity and elevation on rocky shore meiofauna. *Journal of Experimental Marine Biology and Ecology*, **122**, 225–241.
- Gibbons, M.J., 1991. Rocky shore meiofauna: a brief overview. *Transactions of the Royal Society of South Africa*, **47**, 595–603.
- Grahame, J. & Hanna, F.S., 1989. Factors affecting the distribution of the epiphytic fauna of *Corallina officinalis* (L.) on an exposed rocky shore. *Ophelia*, **30**, 113–129.
- Healy, B., 1996. The distribution of Oligochaeta on an exposed rocky shore in southeast Ireland. *Hydrobiologia*, **334**, 51–62.
- Heck, K.L. & Wetstone, G.S., 1977. Habitat complexity and invertebrate species richness and abundance in tropical seagrass meadows. *Journal of Biogeography*, **4**, 135–142.
- Hicks, G.R.F., 1971. Check list and ecological notes on the fauna associated with some littoral coralline algae. *Bulletin of Natural Sciences*, **2**, 47–58.
- Hicks, G.R.F., 1977. Species association and seasonal population densities of marine phytal harpacticoid copepods from Cook Strait. *New Zealand Journal of Marine and Freshwater Research*, **11**, 621–643.
- Hicks, G.R.F., 1980. Structure of phytal harpacticoid copepod assemblages and the influence of habitat complexity and turbidity. *Journal of Experimental Marine Biology and Ecology*, **44**, 157–192.
- Hicks, G.R.F., 1985. Meiofauna associated with rocky shores algae. In *The ecology of rocky coasts* (ed. P.G. Moore and R. Seed), pp. 36–56. London: Hodder and Stoughton.
- Hull, S.L., 1997. Seasonal changes in diversity and abundance of ostracods on four species of intertidal algae with differing structural complexity. *Marine Ecology Progress Series*, **161**, 71–82.
- Hurlbert, S.H., 1984. Pseudoreplication and the design of ecological field experiments. *Ecological Monographs*, **54**, 187–211.
- Johnson, S.C. & Scheibling, R.E., 1987. Structure and dynamics of epifaunal assemblages on intertidal macroalgae *Ascophyllum nodosum* and *Fucus vesiculosus* in Nova Scotia, Canada. *Marine Ecology Progress Series*, **37**, 209–227.
- Kelaher, B., 2000. *Biodiversity of macrofaunal assemblages in coralline algal turf*. PhD thesis, University of Sydney, Sydney, Australia.
- Kohn, A.J. & Leviten, P.J., 1976. Effect of habitat complexity on population density and species richness in tropical intertidal predatory gastropod assemblages. *Oecologia*, **25**, 199–210.
- Lewis, J.R., 1964. *The ecology of rocky shores*. London: English University Press.
- Lintas, C. & Seed, R., 1994. Spatial variation in the fauna associated with *Mytilus edulis* on a wave-exposed rocky shore. *Journal of Molluscan Studies*, **60**, 165–174.
- Lohse, D.P., 1993. The importance of secondary substratum in a rocky intertidal community. *Journal of Experimental Marine Biology and Ecology*, **166**, 1–17.
- Lopez, C.A. & Stolz, W.B., 1997. Description of the fauna associated to *Corallina officinalis* L. in the intertidal of the rocky shore of 'Palo Colorado' (Los Vilos, IV-Region, Chile). *Revista de Biología Marina y Oceanografía*, **32**, 17–35.
- Lubchenco, J. et al., 1984. Structure, persistence, and role of consumers in a tropical rocky intertidal community (Taboguilla Island, Bay of Panama). *Journal of Experimental Marine Biology and Ecology*, **78**, 23–74.
- MacArthur, R.H. & MacArthur, J.W., 1961. On bird species diversity. *Ecology*, **42**, 594–598.
- Martin-Smith, K.M., 1993. Abundance of mobile epifauna: the role of habitat complexity and predation by fishes. *Journal of Experimental Marine Biology and Ecology*, **174**, 261–275.
- McGuinness, K.A. & Underwood, A.J., 1986. Habitat structure and the nature of communities on intertidal boulders. *Journal of Experimental Marine Biology and Ecology*, **104**, 97–123.
- Menge, B.A., 1976. Organization of the New England rocky intertidal community: role of predation, competition and environmental heterogeneity. *Ecological Monographs*, **46**, 335–393.
- Menge, B.A., 1995. Indirect effects in marine rocky intertidal interaction webs: patterns and importance. *Ecological Monographs*, **65**, 21–74.
- 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.
- Myers, A.A. & Southgate, T., 1980. Artificial substrates as a means of monitoring rocky shore cryptofauna. *Journal of the Marine Biological Association of the United Kingdom*, **60**, 963–975.
- Nixon, S.W., Oviatt, C.A., Rodgers, C. & Taylor, R.K., 1971. Mass and metabolism of a mussel bed. *Oecologia*, **8**, 21–30.
- Ong Che, R.G. & Morton, B., 1992. Structure and seasonal variations in the abundance of the macroinvertebrate community associated with *Septifer virgatus* (Bivalvia: Mytilidae) at Cape d'Aguilar, Hong Kong. *Asian Marine Biology*, **9**, 217–233.
- Otway, N.M., 1994. Population ecology of the low-shore chitons *Onithochiton quercinus* and *Plaxiphora albida*. *Marine Biology*, **121**, 105–116.
- Paine, R.T., 1974. Intertidal community structure: experimental studies on the relationship between a dominant competitor and its principal predator. *Oecologia*, **15**, 93–120.
- Peake, A.J. & Quinn, G.P., 1993. Temporal variation in species–area curves for invertebrates in clumps of an intertidal mussel. *Ecography*, **16**, 269–277.
- Russ, G.R., 1980. Effects of predation by fishes, competition, and the structural complexity of the substratum on the establishment of a marine epifaunal community. *Journal of Experimental Marine Biology and Ecology*, **42**, 55–69.
- Schneider, F.I. & Mann, K.H., 1991a. Species specific relationships of invertebrates to vegetation in a seagrass bed. I. Correlational studies. *Journal of Experimental Marine Biology and Ecology*, **145**, 101–117.
- Schneider, F.I. & Mann, K.H., 1991b. Species specific relationships of invertebrates to vegetation in a seagrass bed. II. Experiments on the importance of macrophyte shape epiphyte cover and predation. *Journal of Experimental Marine Biology and Ecology*, **145**, 119–139.
- Seed, R., 1996. Patterns of biodiversity in the macro-invertebrate fauna associated with mussel patches on rocky shores. *Journal of the Marine Biological Association of the United Kingdom*, **76**, 203–210.
- Seed, R. & O'Connor, R.J., 1980. Shell shape and seasonal changes in population structure in *Lasaea rubra* (Bivalvia: Erycinidae). *Journal of Molluscan Studies*, **46**, 66–73.
- Southward, A.J., 1958. The zonation of plants and animals on rocky sea shores. *Biological Reviews*, **33**, 137–177.

- Stewart, J.G., 1982. Anchor species and epiphytes in intertidal algal turf. *Pacific Science*, **36**, 45–59.
- Stoner, A.W., 1980. The role of seagrass biomass in the organization of benthic macrofaunal assemblages. *Bulletin of Marine Science*, **30**, 537–551.
- Stoner, A.W., 1982. The influence of benthic macrophytes on the foraging behaviour of pinfish, *Lagodon rhomboides* (Linnaeus). *Journal of Experimental Marine Biology and Ecology*, **8**, 271–284.
- Tararam, A., Wakabara, Y. & Leite, F.P., 1986. Vertical distribution of amphipods living on algae of a Brazilian intertidal rocky shore. *Crustaceana*, **51**, 183–187.
- Ter Braak, C.J., 1992. Permutation versus bootstrap significance tests in multiple regression and ANOVA. In *Boot strapping and related techniques* (ed. K.H. Jockel et al.), pp. 79–86. Berlin: Springer-Verlag.
- Thompson, R.C., Wilson, B.J., Tobin, M.L., Hill, A.S. & Hawkins, S.J., 1996. Biologically generated habitat provision and diversity of rocky shore organisms at a hierarchy of spatial scales. *Journal of Experimental Marine Biology and Ecology*, **202**, 73–84.
- Tsuchiya, M. & Nishihira, M., 1985. Islands of *Mytilus edulis* as a habitat for small intertidal animals: effect of island size on community structure. *Marine Ecology Progress Series*, **25**, 71–81.
- Underwood, A.J., 1981. Structure of a rocky intertidal community in New South Wales: patterns of vertical distribution and seasonal changes. *Journal of Experimental Marine Biology and Ecology*, **51**, 57–85.
- Underwood, A.J., 1994. Things environmental scientists (and statisticians) need to know to receive (and give) better statistical advice. In *Statistics in ecology and environmental monitoring* (ed. D. Fletcher and B.F.J. Manly), pp. 33–61. Dunedin: University of Otago Press.
- Underwood, A.J., 1997. *Experiments in ecology: their logical design and interpretation using analysis of variance*. Cambridge: Cambridge University Press.
- 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., 1998. Spatial analyses of intertidal assemblages on sheltered rocky shores. *Australian Journal of Ecology*, **23**, 138–157.
- Underwood, A.J., Chapman, M.G. & Connell, S.D., 2000. Observation 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. & Moran, M.J., 1983. Experimental analyses of the structure and dynamics of mid-shore rocky intertidal communities in New South Wales. *Oecologia*, **56**, 202–219.
- Underwood, A.J. & Petraitis, P.S., 1993. Structure of intertidal assemblages in different locations: how can local processes be compared? In *Species diversity in ecological communities: historical and geographical perspectives* (ed. R.E. Ricklefs and D. Schluter), pp. 38–51. Chicago: University of Chicago Press.
- Underwood, A.J. & Verstegen, P.H., 1987. Experiments on the association between the intertidal amphipod *Hyale media* Dana and the limpet *Cellana tramoserica* (Sowerby). *Journal of Experimental Marine Biology and Ecology*, **119**, 83–98.
- Whorff, J.S., Whorff, L.L. & Sweet, M.H., 1995. Spatial variation in an algal turf community with respect to substratum slope and wave height. *Journal of the Marine Biological Association of the United Kingdom*, **75**, 429–444.
- Wigham, G.D., 1975. The biology and ecology of *Rissoa parva* (Da Costa) [Gastropoda: Prosobranchia]. *Journal of the Marine Biological Association of the United Kingdom*, **55**, 45–67.
- Winer, B.J., Brown, D.R. & Michels, K.M., 1991. *Statistical principles in experimental design*. New York: McGraw-Hill.

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