

Journal of Experimental Marine Biology and Ecology 282 (2003) 23-41



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# Experimental transplantations of coralline algal turf to demonstrate causes of differences in macrofauna at different tidal heights

# B.P. Kelaher\*, A.J. Underwood, M.G. Chapman

Centre for Research on Ecological Impacts of Coastal Cities, Marine Ecology Laboratories A11, University of Sydney, Sydney, New South Wales 2006, Australia

Received 3 May 2002; received in revised form 2 September 2002; accepted 12 September 2002

#### Abstract

On rocky intertidal shores, dense fronds of coralline algal turf provide habitat for diverse assemblages of macrofauna. There are large differences in these assemblages and in the physical structure of coralline turf between low- and mid-shore areas. Using reciprocal experimental transplantations of coralline turf on a rocky shore near Sydney, Australia, hypotheses were tested to differentiate among three models: (i) algal-specific properties, (ii) height-specific factors and (iii) their interaction, which may explain variation in macrofaunal assemblages at different heights on the shore. Similar hypotheses were also tested for eight common species, with patterns of abundance correlated with tidal height. Results showed that algal-specific properties had little influence on differences between macrofauna in low- and mid-shore areas. Height-specific factors must be responsible for these differences. The amount of sediment among the fronds also influenced spatial patterns of abundance of some animals. Most work on macrofaunal assemblages associated with algal turf has focussed on effects of physical and biological characteristics of the habitats. Shifting attention to focus on the effects of biological processes mediated by local environmental conditions (e.g. competition or predation) will therefore be a major step forward in understanding the ecology of these diverse faunal assemblages.

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Keywords: Rocky shore; Macrofauna; Coralline turf; Transplantation

<sup>\*</sup> Corresponding author. Present address: Department of Ecology and Evolution, Life Sciences Building, State University of New York, Stony Brook, NY 11974-5245, USA. Tel.: +1-631-632-8601; fax: +1-631-632-7626.

E-mail address: bkelaher@life.bio.sunysb.edu (B.P. Kelaher).

# 1. Introduction

One widely documented pattern on rocky intertidal shores is differences among assemblages of organisms at various tidal heights (e.g. Dayton, 1971; Underwood, 1981). Many processes, such as competition (Connell, 1961; Branch, 1984), disturbance (Dayton, 1971; Paine and Levin, 1981), grazing (Underwood, 1980; Lubchenco and Gaines, 1981), predation (Paine, 1966; Menge, 1978), recruitment (Underwood and Denley, 1984; Gaines and Roughgarden, 1985) and physiological tolerance (Wolcott, 1973) are responsible for these patterns. Generally, it has been argued that the relative strengths of these physical and biological processes change with local environmental conditions and that these differences structure local assemblages at any given tidal height (Dayton, 1971; Underwood, 1985; Menge and Sutherland, 1987).

Organisms that form mat-like structures, such as algal turf, mussels, ascidians and lichens, are common on rocky intertidal shores. Generally, these organisms make major contributions to local faunal diversity by providing habitat for diverse macrofaunal assemblages, which can reach abundances of more than 250,000 animals per m<sup>2</sup> (Fielding et al., 1994; Whorff et al., 1995; Seed, 1996; Kelaher et al., 2001). As in other rocky shore assemblages, there are, however, large differences in macrofauna associated with these habitats at different tidal heights (Lintas and Seed, 1994; Kelaher et al., 2001). Unlike many other assemblages, little is known about processes that cause these differences (Seed, 1996; Kelaher et al., 2001).

Most studies on macrofauna in mat-like habitats have focussed on physical and biological characteristics of these habitats as determinants of diversity and abundance of associated fauna, rather than the influence of more traditionally studied processes (such as those listed above). The physical structure of these habitats generally has a major influence on these assemblages by trapping sediment and organic material (Tsuchiya and Nishihira, 1985; Gibbons, 1988) and by providing a refuge from desiccation (Nixon et al., 1971; Gibbons, 1988), predation by fish (Coull and Wells, 1983; Dean and Connell, 1987a) and wave-action (Dommasnes, 1968; Whorff et al., 1995). Similarly, biological characteristics of living organisms that form mats also influence associated macrofaunal assemblages by providing food and detritus for some animals (Tsuchiya and Nishihira, 1985; Brawley, 1992), consuming larvae (Woodin, 1976) or producing chemicals, which may attract or repel settling larvae (see Underwood, 1979; Young, 1990 for reviews) or influence herbivory (Hay, 1996). While physical and biological characteristics of mat-like habitats can have important influences on associated assemblages, few studies have investigated experimentally the role of these characteristics in determining differences in the diversity and abundance of organisms at different tidal heights.

Articulated coralline algae are a major component of algal assemblages on many rocky shores and generally form mat-like habitats (Stewart, 1982; Dye, 1993). Coralline turf is 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; Chapman and Underwood, 1998). Previous studies have shown large and consistent differences in diverse macrofaunal assemblages between coralline turf in low- and in mid-shore areas (Akioka et al., 1999; Kelaher et al., 2001). More specifically, in New South Wales, there are generally similar numbers of taxa in low- and mid-shore areas, but large

differences in the composition of taxa and abundances of individual species at different heights on the shore (Kelaher et al., 2001). In addition to differences in associated macrofauna, the physical structure of coralline turf and the composition of coralline algal species in the turf can also vary with height on the shore (Kelaher et al., 2001). Furthermore, it is possible that important biological characteristics which have been shown to vary in other algal species, such as the chemical composition or amount of secondary compounds (Matlock et al., 1999), may also vary in articulated coralline algae at different tidal heights.

Because the characteristics of coralline algal turf and the associated assemblages vary with tidal height, it is possible that differences in macrofaunal assemblages between coralline turf in low- and in mid-shore areas are caused by algal-specific properties. Alternatively, biological or physical processes correlated with tidal height may cause the differences in macrofauna at different heights on the shore, or the differences may be caused by a combination of algal- and height-specific factors. The present paper describes the results of reciprocal transplantation of coralline turf between different tidal heights to test hypotheses that distinguish among these three models (explicit models and hypotheses are presented in Table 1). In addition to hypotheses about assemblages, specific hypotheses were tested about abundances of eight individual species that are extremely common in coralline turf and had previously shown consistent differences in abundance between low- and mid-shore levels (Kelaher, 2000). Four of these species, the insect larvae, Limonia marina (Skuse, 1890), and Clunio sp., the small bivalve, Lasaea australis (Lammarck, 1819) and juveniles of the common snail, Austrocochlea porcata (Adams, 1851), are usually more abundant in mid-shore areas. The remaining four, the small snail, Amphithalamus incidatus (Fruenfeld, 1867), the melitid amphipod, Elasmopus warra (Kelaher and Lowry, 2002), the tanaid, Paratanais sp. and the orbinid polychaete, *Proscoloplos* sp. are more abundant in low-shore areas. Because the morphology of algae has been shown to vary with vertical height on the shore (Hodgson, 1980; Schonbeck and Norton, 1980), the coralline turf itself may also respond to transplantation. Therefore, hypotheses about changes in morphology of coralline turf transplanted to a different height on the shore were also tested.

#### 2. Methods

#### 2.1. Experimental materials and methods

Experiments were done at the Cape Banks Scientific Marine Research Area, on the northern headland of the entrance to Botany Bay, Sydney, Australia (34°00'S, 151°15'E; see Underwood, 1975 for description). Relative to experiments where individual organisms are transplanted, published studies where habitat has been transplanted (e.g. Gunnill, 1982; Kelaher et al., 1998) are rare. Moreover, these types of experiments have not been done for mat-like habitats on rocky shores because of the technical difficulties associated with removing these delicate complex structures then reattaching them to rock platforms. This study used methods described by Kelaher (2002), in which cores of rock with intact coralline turf are drilled out of the platform, defaunated and cemented back into position.

Table 1				
Summary	of logical	structure	of experimental	transplantations

Explanatory models	(a) Hypotheses relating to upshore transplantations	(b) Hypotheses relating to downshore transplantations
<i>Model 1</i> is that assemblages are controlled by characteristics of the algal turf, which differ among heights.	Hypothesis 1a is that when turf is transplanted from low- to mid-shore areas, faunal assemblages will develop similarly to those in low-shore areas (because the turf is the same) and different from those in mid-shore areas (where the turf is different).	<i>Hypothesis 1b</i> is that faunal assemblages in turf transplanted downshore will develop similarly to those in mid-shore areas and different from those in low-shore areas
<i>Model 2</i> is that assemblages are controlled by components of the local environment that differ from one height to another, regardless of features of the turf.	<i>Hypothesis 2a</i> is that turf transplanted from low- to mid-shore areas will develop assemblages similar to those in mid-shore areas and different from those in low-shore areas because of local environmental variables.	<i>Hypothesis 2b</i> is that turf transplanted downshore will develop assemblages similar to those in low-shore areas and different from those in mid-shore areas.
<i>Model 3</i> is that the structures of faunal assemblages are generated by features of the turf and the local environment, operating interactively.	<i>Hypothesis 3a</i> is that turf transplanted from low- to mid-shore levels will develop differently from those at low- and mid-shore levels because transplanted turf has the wrong combination of characteristics and local environ- ment for normal assemblages to develop.	<i>Hypothesis 3b</i> is turf transplanted downshore will develop assemblages different from those in low- and mid-shore areas.

Hypotheses come from explanatory models of the same number. Hypotheses denoted with same number and a or b are reciprocal.

After 4 months, macrofaunal assemblages in defaunated turf were not significantly different from those in natural coralline turf (Kelaher, 2002), indicating that there are few long-term artefacts associated with these methods.

For the present experiment, two large patches of coralline algal turf (at least  $5 \times 2$  m) were selected in each of low- (0.30 and 0.40 m above I.L.W.S) and mid-shore (0.50 and 0.60 m above I.L.W.S) areas. The four patches of turf were evenly distributed along 150 m of shore and were randomly allocated into two sites, with each site having one patch in low- and one patch in mid-shore areas (Fig. 1). The coralline algal turf was comprised predominantly of *Corallina officinalis* Linnaeus, although *Jania* spp. Lamouroux and *Amphiroa* spp. Lamouroux were occasionally found, especially in low-shore areas.



Fig. 1. Diagram of the design of the experimental transplantations. Comparisons are divided into two types of analyses: (i) comparison with turf originally from low-shore areas and moved to mid-shore areas (site 1 is treatments A, B, C, D; site 2 is treatments E, F, G, H); (ii) comparisons with turf originally in mid-shore areas that is moved to low-shore areas (site 1 is treatments I, J, C, D; site 2 is treatments K, L, G, H). In each type of analysis, there are comparisons among treatments (four levels—orthogonal fixed; low-shore control, transplantation treatment, translocation treatment and mid-shore control) and between sites (2 levels—orthogonal and random).

The experiment had four manipulated treatments and untouched controls in low- and in mid-shore areas (Fig. 1). For one half of the experiment, coralline turf was transplanted from low- to mid-shore areas. The other half of the experiment was based around the reciprocal transplantation of turf from mid- to low-shore areas (Fig. 1). Because it is possible that any differences between treatments are caused by the experimental methods used to move turf (Chapman, 1986), treatments were also included in which coralline turf was translocated on rock cores between patches at each height on the shore. In each manipulated treatment, four rock cores (10 cm in diameter) with intact coralline turf were drilled from the rock platform in each patch using a diamond-tipped corer. To reduce any effects of the existing assemblages on colonising animals, the cores were defaunated by vigorously rinsing the algae with running freshwater and carefully picking through with forceps for any remaining animals (see Kelaher, 2002 for further details of methods). Along with the animals, much of the sediment trapped by the coralline fronds is also removed by these defaunating procedures. Sediment has a strong influence on faunal assemblages in mat-like habitats on rocky shores (Hicks, 1980; Gibbons, 1988; Whorff et al., 1995). To determine the extent to which the amount of sediment accumulated on the rock cores was affected by these methods, sediment in the turf was weighed at the end of the experiment (see below). The cores were cemented back into holes in the rock platform using quick setting cement (Flashcrete<sup>®</sup>). Cores in the transplanted treatments were cemented into holes in a patch of turf in the same site, but at a different height on the shore. Cores in the translocated treatments were cemented into holes in a different site, but at the same height on the shore (Fig. 1).

After 5 months, macrofauna in the centre of each rock core and in untouched coralline turf were sampled using an 8 cm diameter (50  $\text{cm}^2$ ) corer. This size of core was used because it provides reasonably precise estimates of numbers and abundances of macrofaunal species (Kelaher, 2000). Centres of cores were sampled to reduce potential edgeeffects caused by drilling and concreting cores. For each replicate, the coralline turf and sediment inside the corer were scraped off at the level of the rock and washed thoroughly in a 63-µm sieve. In each replicate, the sediment was carefully separated from turf and dried for 48 h at 80 °C, cooled in a desiccator for 4 h and weighed. To test hypotheses that the physical structure of coralline turf changes in response to transplantation, the length and density of C. officinalis fronds were measured for each core. The average length of fronds was determined from measurements of length of four randomly selected fronds in each core. Each frond measured was complete, with an intact holdfast. For each core, the density of fronds (kg  $m^{-3}$ ) was estimated indirectly by dividing the dry weight of coralline fronds per cm<sup>2</sup> by the average length of fronds. This surrogate measure was shown to be a reasonable representation of the number of fronds per unit area and was used because it was difficult to measure accurately the density of fronds directly. To measure the dry weight of coralline fronds, the epibiota on each frond were carefully removed. The fronds were then dried for 48 h at 60 °C, cooled in a desiccator for 4 h and weighed.

Macrofauna were washed in a 500- $\mu$ m sieve; animals were identified and counted using a binocular microscope (× 16 magnification). Although sessile animals permanently attached to the fronds or substrata (e.g. sponges, bryozoans, serpulid and spirorbid polychaetes, barnacles, etc.) were commonly found in the turf, these animals were not included in the study because the methods used were not appropriate. In total, 13,631 individual animals were counted and identified into 96 different taxa (Table 2). The taxonomic resolution of macrofauna varied among groups because many of the animals were juveniles and could not be reliably identified to species using taxonomic keys (when keys were available) and many of the species have not been described.

# 2.2. Statistical methods

Analyses were centred on the place where the transplanted turf originated and were therefore separated into comparisons using turf from low- or from mid-shore areas. For these analyses, there were comparisons among four treatments (a fixed factor, Fig. 1) and between two sites (an orthogonal random factor, Fig. 1) and predictions were subsequently tested with post hoc tests.

Nonparametric multivariate analyses of variance (NP-MANOVA) were used to test hypotheses about differences among macrofaunal assemblages (Anderson, 2001). NP-MANOVAs were followed by a posteriori pair-wise comparisons on appropriate terms in the model found to be significant at P < 0.05. For these tests, only probability values are presented because the multivariate *F*-statistics and *t*-statistics are generated by permutations. Nonmetric multidimensional scaling (nMDS, Field et al., 1982) was used to produce two-dimensional ordinations to show relationships among samples of macrofaunal assemblages. All multivariate analyses were done using Bray–Curtis similarity coefficients (Bray and Curtis, 1957). Analyses of variance were used to test hypotheses about individual variables. Variances were homogenous for all environmental variables (Cochran's tests, P > 0.05). For analyses of abundances, distributions were often skewed

Table 2 Summary of the 96 macrofaunal taxa found in coralline turf during this study

	6 1	
Phylum	Class	Number of taxa and resolution
Cnidaria	Anthozoa	1 Taxon
Platyhelminthes	Turbellaria	1 Taxon
Nematoda	_	1 Taxon
Nemertea	_	1 Taxon
Annelida	Oligochaeta	1 Taxon
	Polychaeta	15 Families
Sipuncula	_	1 Taxon
Arthropoda	Insecta	3 Species
-	Pycnogonida	1 Taxon
	Ostracoda	1 Taxon
	Copepoda	1 Taxon
	Malacostraca	19 Families
Mollusca	Polyplacophora	4 Species
	Gastropoda	38 Species
	Bivalvia	5 Species
Echinodermata	Asteroidea	2 Species
	Ophiuroidea	1 Taxon

and variances were mostly heterogeneous (Cochran's tests, P < 0.05). Abundances were therefore transformed to  $\ln(x+1)$  (Underwood, 1997).

## 3. Results

#### 3.1. Effects of transplantation on structure of habitat and sediment

Although there were no significant differences in the length of fronds in three out of four analyses, there were consistent trends in the patterns among means (Table 3a). For turf transplanted from low- to mid-shore areas, coralline fronds became shorter (Fig. 2a). For turf transplanted from mid- to low-shore sites, the fronds on average became longer. For the only site where there were significant differences, fronds transplanted from mid- to low-shore areas increased in length, but did not become as long as those in low-shore areas (Fig. 2a).

For analyses of turf transplanted between low- and mid-shore areas, the density of coralline fronds differed among treatments (Table 3b), but SNK tests were not powerful enough to detect patterns among the treatments (Fig. 2b). There was, however, a trend for a greater density of fronds in natural coralline turf in mid- than in low-shore areas. The tendency for the density of fronds to increase in turf transplanted from low- to mid-shore sites (Fig. 2b) was not significant. For algae taken from low- to mid-shore areas, there was

	df	(i) Low to mid tranplantation		(ii) Mid to low tranplantation			
		MS	F	Р	MS	F	Р
(a) Length o	f fronds						
Т	3	147.3	5.6	0.10	113.7	4.7	0.11
S	1	1.7	0.2	0.68	3.8	0.5	0.48
$\mathbf{T} \times \mathbf{S}$	3	26.5	2.8	0.06	24.2	3.2	0.04
Residual	24	9.5			7.6		
(b) Density of	of fronds						
Т	3	3800.1	11.6	0.04	3345.9	2.5	0.23
S	1	192.0	0.4	0.55	1696.4	2.6	0.12
$T \times S$	3	328.4	0.6	0.61	1332.1	2.0	0.13
Residual	24	532.4			652.5		
(c) Amount of	of sediment						
Т	3	18.8	2.5	0.24	12.0	1.3	0.41
S	1	15.4	7.6	0.01	0.1	0.0	0.91
$T \times S$	3	7.5	3.7	0.02	9.0	5.6	< 0.01
Residual	24	2.0			1.6		

Table 3 Analyses of variance of variables associated with algal turf (n=4 replicate cores)

'T' is the fixed comparison between four treatments; 'S' is the comparison among randomly located sites. See Fig. 2 for interpretation of SNK tests.



Fig. 2. Comparisons of mean (S.E., n = 4) variables associated with algal turf within each site. (i) Turf transplanted from low- to mid-shore areas  $\square$ , natural coralline turf in mid-shore areas  $\square$ , turf translocated between sites in low-shore areas  $\square$ , turf translocated between sites in low-shore areas  $\square$ , turf translocated between sites in mid-shore areas  $\square$ , turf translocated between sites in mid-shore areas  $\square$  and natural coralline turf in low-shore areas  $\square$  and natural coralline turf in low-shore areas  $\square$  and natural coralline turf in low-areas  $\square$  areas (see above for symbols). Letters above bars indicate results of SNK tests. In each site, treatments with different letters are significantly different (P < 0.05) and treatments with the same letters are not significantly different (P > 0.05).

an apparent (nonsignificant) artefact of translocation on the density of fronds in site 1, but no tendency for change in site 2.

For all analyses, the amount of sediment in the turf varied significantly among treatments and sites (Table 3c). Some replicate patches of turf had much greater amounts of sediments than others, but there were no consistent or interpretable patterns among treatments and sites (Fig. 2c).

# 3.2. Effects on fauna of transplantation from low- to mid-shore areas

For turf transplanted from low- to mid-shore sites, macrofaunal assemblages in treatments varied from site to site (NP-MANOVA, treatment × site interaction, df=3,24,

P < 0.001). Despite this, in each site, there were significant differences in macrofaunal assemblages among all treatments (P < 0.05), except that the transplantation treatment did not differ from the mid-shore control (P > 0.05). The interaction was caused by variation in the directions and magnitudes of differences among treatments, which is clearly illustrated in Fig. 3(i). This figure also shows that the assemblages that developed in transplanted cores resembled those in mid-shore areas and were as different from the low-shore controls as were the mid-shore controls. These data strongly support the second model (height-specific factors), rather than properties of the turf or an interaction of height- and algal-specific factors (models 1 and 3).

Another way of illustrating this is by examining the Bray–Curtis dissimilarities in Table 4(i). First, the dissimilarity between faunal assemblages in transplanted cores and those in the low-shore controls (TP vs LC) was always greater than the dissimilarity between assemblages in the transplanted cores and those in the mid-shore controls (TP vs MC). So, faunal assemblages in transplanted cores were more similar to natural assemblages in mid-shore areas, than to those in low-shore areas.

Second, the dissimilarity between faunal assemblages in transplanted cores and those in the low-shore controls (TP vs LC) was approximately the same as the dissimilarity between the macrofaunal assemblages in natural controls in mid- and in low-shore areas (LC vs MC). So, the magnitude of change between assemblages in transplanted cores and the low-shore controls was similar to natural differences in assemblages at the different tidal heights.

Finally, the dissimilarity between macrofaunal assemblages in transplanted cores and those in the low-shore control (TP vs LC) was always greater than the dissimilarity between macrofaunal assemblages in the translocated cores and those in the



Fig. 3. Two-dimensional nMDS ordination comparing macrofaunal assemblages among treatments for (i) turf transplanted from low- to mid-shore areas and (ii) for turf transplanted from mid- to low-shore areas (n=4). Assemblages are from natural coralline turf from site 1  $\oplus$  and site 2  $\bigcirc$  in low-shore areas and from site 1  $\oplus$  and site 2  $\bigcirc$  in mid-shore areas; turf transplanted from low- to mid-shore areas in site 1  $\oplus$  and site 2  $\triangle$ ; turf transplanted from mid- to low-shore areas in site 1  $\oplus$  and site 2  $\triangle$ ; turf transplanted from mid- to low-shore areas  $\square$  and turf transplanted from site 2 to site 1 in low-shore areas  $\square$  and in mid-shore areas  $\blacksquare$ .

Table 4

		(i) Low to mid	(ii) Mid to low
(a) LC vs MC	S1	55	55
	S2	63	63
(b) TP vs LC	S1	55	49
	S2	64	34
(c) TP vs MC	S1	30	67
	S2	35	60
(d) TL vs LC	S1	49	_
	S2	54	_
(e) TL vs MC	S1	_	38
	S2	_	35

Total average Bray-Curtis dissimilarities for comparisons among treatments (i) for turf transplanted from low- to mid-shore areas and (ii) for turf transpanted from mid- to low-shore areas

TP, turf transplanted to a different height on the shore; TL, turf translocated to a new site at the same height on the shore; MC, natural coralline turf in mid-shore areas; LC, natural coralline turf in low-shore areas.

low-shore controls (TL vs LC). Moving low-shore cores to mid-shore areas generates a different faunal assemblage, but moving cores to another low-shore site does not.

# 3.3. Effects on fauna of transplantation from mid- to low-shore areas

For turf transplanted from mid- to low-shore sites, the pattern among macrofaunal assemblages in treatments also varied from site to site (NP-MANOVA, treatment × site interaction, df= 3,24, P < 0.001). In site 1, there were significant differences among faunal assemblages in all treatments (P<0.05), except that the translocated cores did not differ from mid-shore controls (P>0.05). In site 2, there were significant differences among macrofaunal assemblages in all treatments (P<0.05), except that assemblages in turf transplanted from mid- to low-shore areas were not different from those that occurred naturally in low-shore areas (P>0.05). Fig. 3(ii) clearly illustrates that assemblages that developed in transplanted cores were similar to those in low-shore controls (apart from a small deviation in site 2), but as different from mid-shore controls as were the natural assemblages in low-shore areas. These data, therefore, once again demonstrate the importance of height-specific factors (model 2), rather than the alternative explanations (models 1 and 3).

Similar to analyses of cores transplanted from low- to mid-shore areas, patterns in the Bray–Curtis measures of dissimilarities among treatments provide further support for model 2 (Table 4(ii)). First, the dissimilarity between faunal assemblages in transplanted cores and those in the mid-shore controls (TP vs MC) was always greater than the dissimilarity between assemblages in the transplanted cores and those in the low-shore controls (TP vs LC).

Second, the dissimilarity between natural assemblages in mid- and in low-shore areas (LC vs MC) was similar to the dissimilarity between faunal assemblages in transplanted cores and those in mid-shore controls (TP vs MC).

Finally, the dissimilarity between faunal assemblages in transplanted cores and those in mid-shore controls (TP vs MC) was always greater than the dissimilarity between assemblages in the translocated cores and those in the mid-shore controls (TL vs MC).

# 3.4. Effects of transplantation on species more abundant in mid-shore areas

The four species that are typically more abundant at mid-shore levels accounted for 53% and 38% of the total dissimilarity between low- and mid-shore areas in site 1 and site 2, respectively. These species also showed strong and consistent patterns among treatments. For nearly all analyses, there were significantly greater abundances in natural controls in mid- than in low-shore areas (Table 5; Fig. 4). The abundance of each species in the transplanted treatments became similar to that in the controls at the height on the shore to which they were transplanted. The abundances of the species in translocated cores did not differ from controls at the same height on the shore (Fig. 4). These results, therefore, show that height-specific factors (model 2) determine abundances of these species at different tidal heights, rather than characteristics of the algal turf or the interaction between factors (models 1 and 3).

Table 5

Analyses of variance of abundances of animals more abundant in mid-shore areas (n=4 replicate cores)

	df	(i) Low to mid tranplantation		(ii) Mid to low tranplantation			
		MS	F	Р	MS	F	Р
(a) Clunio s	р.						
Т	3	14.48	4.61	0.12	15.27	4.67	0.12
S	1	2.49	4.81	0.04	0.28	0.57	0.46
$T \times S$	3	3.14	6.08	< 0.01	3.27	6.62	< 0.01
Residual	24	0.52			0.49		
(b) Lasaea d	australis						
Т	3	3.44	37.24	< 0.01	0.69	5.14	0.03
S	1	0.01	0.04	0.85	1.69	3.10	0.19
$T \times S$	3	0.09	0.46	0.71	0.55	4.05	0.02
Residual	24	0.20			0.14		
(c) Limonia	marinia						
Т	3	9.49	177.06	< 0.01	11.08	73.87	< 0.01
S	1	0.22	0.80	0.38	0.01	0.02	0.90
$T \times S$	3	0.05	0.20	0.90	0.15	1.86	0.16
Residual	24	0.27			0.08		
(d) Austroco	ochlea porc	cata					
Т	3	20.81	167.48	< 0.01	18.08	73.62	< 0.01
S	1	0.28	1.55	0.23	0.07	0.03	0.59
$T \times S$	3	0.12	0.68	0.57	0.25	1.08	0.38
Residual	24	0.18			0.23		

'T' is the fixed comparison between four treatments; 'S' is the comparison among randomly located sites. See Fig. 4 for interpretation of SNK tests.



Fig. 4. Comparisons of mean (S.E., n = 4) abundance of mid-shore species. (i) Turf transplanted from low- to midshore areas  $\square$ , natural coralline turf in mid-shore areas  $\square$ , turf transplanted from mid- to low-shore areas  $\square$ , turf transplanted from mid- to low-shore areas  $\square$ , turf transplanted from mid- to low-shore areas  $\square$ , turf transplanted between sites in mid-shore areas  $\square$  and natural coralline turf in low-shore areas  $\square$  and natural coralline turf in low-shore areas  $\square$  areas and natural coralline turf in low-shore areas  $\square$  areas and natural coralline turf in low-shore areas  $\square$  areas a natural coralline turf in low-shore areas  $\square$  areas areas are as a natural coralline turf in low-shore areas (see above for symbols). Letters above bars indicate results of SNK tests. In each site, treatments with different letters are significantly different (P < 0.05) and treatments with the same letters are not significantly different (P > 0.05).

There were, however, two deviations from these relatively general results. First, there was a decreased abundance of *Clunio* sp. in the translocated treatment from those in the natural control in one mid-shore area (site 1; Fig. 4a). Second, the abundance of the small bivalve, *L. australis*, was increased by moving turf between site 1 and site 2 in mid-shore areas (Fig. 4b).

#### 3.5. Effects of transplantation on species more abundant in low-shore areas

The four species that are typically more abundant in low-shore areas had much smaller contribution to the total dissimilarity in assemblages between low- and mid-shore areas (11% and 13% for site 1 and site 2, respectively) than did species more abundant in mid-shore levels. For low-shore species, the patterns among treatments were also less consistent and more site-specific. Abundances of the amphipod, *E. warra*, and the polychaete, *Proscoploplos* sp., were greater in controls in low- than in mid-shore areas (Table 6a,b; Fig. 5a,b). The abundances of each species in the transplanted cores were not significantly different from those in the natural controls at the height on the shore to which they were transplanted. The abundance of each species in translocated cores did not generally differ from natural controls at the same height on the shore, although there were some exceptions (Fig. 5a,b). These results also demonstrate that height-specific processes (model 2) determine greater abundances of these species in low-shore areas.

For *A. incidatus*, results were contradictory and difficult to interpret because, in site 1, there were actually more *A. incidatus* in mid- than in low-shore areas, the opposite of

	df	(i) Low to mid tranplantation		(ii) Mid to low tranplantation			
		MS	F	Р	MS	F	Р
(a) Elasmop	us warra						
Т	3	15.82	15.30	0.03	16.99	26.2	0.01
S	1	0.09	0.36	0.56	2.64	23.5	< 0.01
$T \times S$	3	1.03	4.08	0.02	0.65	5.8	< 0.01
Residual	24	0.25			0.11		
(b) Proscolo	plos sp.						
Т	3	10.65	6.55	0.08	9.09	8.0	0.06
S	1	0.01	0.07	0.79	2.43	13.2	< 0.01
$T \times S$	3	1.62	8.84	< 0.01	1.13	6.2	< 0.01
Residual	24	0.18			0.18		
(c) Amphith	alamus inc	idatus					
Т	3	0.44	0.12	0.81	0.38	0.1	0.97
S	1	0.24	0.63	0.94	0.51	1.7	0.21
$T \times S$	3	3.67	9.75	< 0.01	4.96	16.6	< 0.01
Residual	24	0.38			0.30		
(d) Paratana	ais sp.						
Т	3	4.29	0.80	0.57	4.41	1.5	0.38
S	1	0.01	0.01	0.96	10.25	22.3	< 0.01
$T \times S$	3	5.37	12.31	< 0.01	2.97	6.5	< 0.01
Residual	24	0.44			0.46		

Analyses of variance of abundances of animals more abundant in low-shore areas (n=4 replicate cores)

'T' is the fixed comparison between four treatments; 'S' is the comparison among randomly located sites. See Fig. 5 for interpretation of SNK tests.

Table 6



Fig. 5. Comparisons of mean (S.E., n = 4) abundance of low-shore species. (i) Turf transplanted from low- to midshore areas  $\mathbf{N}$ , natural coralline turf in mid-shore areas  $\mathbf{N}$ , turf translocated between sites in low-shore areas  $\mathbf{N}$ , turf translocated between sites in low-shore areas  $\mathbf{N}$ , turf translocated between sites in mid-shore areas  $\mathbf{N}$ , (ii) Turf transplanted from mid- to low-shore areas  $\mathbf{N}$ , turf translocated between sites in mid-shore areas  $\mathbf{N}$  and natural coralline turf in low- and mid-shore areas (see above for symbols). Letters above bars indicate results of SNK tests. In each site, treatments with different letters are significantly different (P < 0.05) and treatments with the same letters are not significantly different (P > 0.05).

what had been found in previous studies and found here in site 2 (Fig. 5c). There was some evidence that the abundances of *Paratanais* sp. were determined by height-specific factors (Table 6d). Since *Paratanais* sp. were absent from site 1, it is difficult to draw robust conclusions for this species (Fig. 5b).

# 4. Discussion

Patterns among Bray-Curtis dissimilarity measures and nMDS plots indicated that height-specific factors, rather than algal-specific properties, determine differences between associated macrofauna in low- and mid-shore areas. Interpretations of the multivariate statistical tests were, however, more complicated because there were significant differences between assemblages in translocated turf compared to assemblages in the site from where the turf originated. While this suggests experimental artefacts for one site in mid-shore areas, site-to-site variation can explain most of these differences. The nMDS plots clearly showed that assemblages in turf translocated between low-shore sites became similar to those in the place to which they were moved, which was significantly different from the place where they originated. The variation between low-shore sites also explains some of the small anomalies in abundances of common species (e.g. E. warra, Proscoloplos sp. and Paratanais sp.). Although there may be many factors responsible for this site-to-site variation, it is likely that the threefold difference in sediment between sites in low-shore areas had a major contribution. Sediment trapped by algal turf generally has a strong influence on associated faunal assemblages (Hicks, 1980; Gibbons, 1988; Whorff et al., 1995) and, like the macrofauna, the amount of sediment in translocated turf became similar to the site to which cores were transplanted and different from where it originated.

Because there are no differences in total number of macrofaunal taxa in coralline turf at different tidal heights, differences in assemblages mostly arise from changes in abundances of individual species and species composition (Kelaher et al., 2001). Two very common species, A. porcata and Proscoloplos sp., were only found in treatments at one tidal height and therefore provide examples of taxa contributing to differences in species composition. All the other common species were present at each level on shore, but, as predicted, showed large variations in abundance with tidal height. Similar to the multivariate results, the patterns of abundance for all but two of these species, Amphithalamus incidatus and Paratanais sp., demonstrated the importance of local physical and biological processes, rather than algal-specific factors or their interaction, for determining differences in abundances between low- and mid-shore areas. The small crustacean, Paratanais sp., showed patterns among treatments indicating the importance of the local environment at one site, but they were found in such small abundances in the other site that it is difficult to reach sensible conclusions. In contrast to the other species, the patterns among treatments of the small snail, A. incidatus, were extremely complex. For one site, there were greater abundances of A. incidatus in mid- than in low-shore areas. This was opposite to patterns found in the other site and to that found previously (Kelaher, 2000).

These complex effects may, however, be explained by variation in sediment, which is an important component of the habitat for *A. incidatus* (Olabarria and Chapman, 2001a,b). Across all treatments, there was a significant positive relationship between the abundance of *A. incidatus* and the amount of sediment (Pearson r=0.32, df=46, P<0.05). It is therefore possible that amount of sediment determines the abundance of *A. incidatus* in coralline turf, regardless of height on the shore. Similar positive associations have been reported for other small rissoid gastropods in red-algal turf (Wigham, 1975; Southgate, 1982).

Many studies have shown strong relationships between the physical structure of algae and the diversity and abundance of associated faunal assemblages (e.g. Hicks, 1980; Dean and Connell, 1987b; Gee and Warwick, 1994). In the present study, although some aspects of the structure and sediments in transplanted algae changed towards those in the height to which they were transplanted (e.g. length of fronds at both heights, density of algae taken from low- to mid-shore areas), none of these changes was significant. Differences in algal structure and amount of sediment are inadequate to explain the differences and experimental changes in macrofaunal assemblages. Although the physical structure of algae may influence faunal assemblages for a particular set of environmental conditions (Hicks, 1980; Dean and Connell, 1987b), from the present study, there is little evidence to suggest that these effects operate over strong environmental gradients, such as tidal height on rocky shores. Consequently, other biological and physical processes associated with different heights of the shore must be more important in causing differences in faunal assemblages in coralline turf at different tidal height.

Similar to other mat-like habitats on rocky shores (Seed, 1996; Dean and Connell, 1987b; Whorff et al., 1995), coralline turf greatly increases local faunal diversity (Kelaher et al., 2001). Most of the work on faunal assemblages in these habitats has focused on the effects of biological and physical characteristics of the habitat (Hicks, 1980; Gee and Warwick, 1994) and their impact on large external predators (Coull and Wells, 1983; Dean and Connell, 1987a) or rates of colonisation (Myers and Southgate, 1980; Edgar, 1991). This study has demonstrated that other biological processes mediated by the local environment (e.g. competition, predation, recruitment or disturbance) must be responsible for differences in faunal assemblages in coralline turf at different tidal heights. Although there is a long history of experimental investigations of such processes on rocky intertidal shores (e.g. Connell, 1961; Dayton, 1971; Underwood, 1985), little is known about these basic ecological interactions among macrofauna within mat-like habitats. Because the small cryptic animals in these habitats contribute so much to local faunal diversity, elucidating the effects of biological processes on these assemblages in addition to habitat-related effects will be a major step forward in understanding biological diversity on rocky intertidal shores.

## Acknowledgements

This study was part of a PhD supported by an Australian Post-Graduate Award and by funds from the Australian Research Council through the Centre for Research on Ecological Impacts of Coastal Cities. We would like to thank Melinda Coleman, Nathan Knott and Maria Punales for help with fieldwork and anonymous referees for improvements to the paper. **[RW]** 

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