Intercontinental test of generality for spatial patterns among diverse molluscan assemblages in coralline algal turf

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ABSTRACT: The potential generality of local processes in determining spatial patterns of molluscan assemblages in turfs of *Corallina officinalis* is evaluated by testing hypotheses about consistency in ecological pattern on shores in Australia, Ireland and Chile. Identical sampling protocols on 2 shores in each country were used to test 2 specific hypotheses: (1) that molluscan assemblages vary significantly among patches of turf separated by tens of meters, and (2) that these assemblages differ significantly between low- and mid-shore areas. In total, 58, 24 and 27 species of molluscs were found in samples from Australia, Ireland and Chile, respectively. There was a remarkable degree of congruence in the proportion of species that were represented in broad taxonomic groups, with prosobranch gastropods accounting for 52 to 79% of the total diversity at each locality. As predicted, there was significant variation in diversity and abundance of molluscs among patches of turf separated by tens of meters on each of the shores sampled. There was, however, little consistency in the structure of molluscan assemblages at different tidal heights, with significant differences on Australian shores, weak differences on Irish shores and no clear pattern on Chilean shores. Moreover, while the richness of species and abundance of prosobranchs was significantly greater in low-shore areas in Australia and Chile, the opposite trend was found in Ireland. Overall, the results show the potential for generality of factors that have previously been demonstrated to cause patchiness in molluscan assemblages in coralline turf at scales of tens of meters. It is proposed that testing for consistency in ecological patterns can be a useful and cost-effective first step in establishing the general importance of ecological processes.

KEY WORDS: Generality · Molluscs · Coralline turf · Spatial patterns · Rocky shore

INTRODUCTION

A major criticism of ecological science has been its apparent failure to find valid general theories (Peters 1991, Shrader-Frechette & McCoy 1993). The apparent lack of generality has been enhanced by the premature acceptance of ecological theory on insufficient evidence, only to see that theory fail in different systems, places or times (see Beck 1997a for review). In response to this, several authors have stressed the necessity for generality to be incorporated into the study of ecology (e.g. Shrader-Frechette & McCoy 1993, Underwood & Petraitis 1993, Dunham & Beaupre 1998). Despite this, pragmatic considerations of time and resources have usually limited experimental field ecology to relatively small spatial and temporal scales.

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However, several studies have extended beyond the usual pragmatic boundaries to address ecological generality in space (e.g. Gee & Warwick 1996, Chapman & Underwood 1998, Benedetti-Cecchi 2000, Jenkins et al. 2001), time (e.g. Berlow 1997, Berlow & Navarrete 1997) and across systems (e.g. Connell 1983, Schoener 1983, Gurevitch et al. 1992, 2000).

Various methods have been used to generalize the findings of small-scale field manipulations. One approach is to combine the results of many studies via a simple scoring system or meta-analysis (Connell 1983, Gurevitch et al. 1992, 2000). There is no real evidence, however, to suggest that the accumulation of small-scale experimental studies with different methodologies can provide true generality (Underwood & Petraitis 1993, Petraitis 1998), especially given a tendency toward publishing results that support current theory (Underwood 1999). More rigorous approaches have included (1) focusing on repeatability—by redoing experiments several times at the same location (e.g. Berlow 1997, Berlow & Navarrete 1997), or (2) increasing the geographic range of small-scale studies—by repeating experiments at randomly chosen locations (e.g. Beck 1997b, Chapman & Underwood 1998, Benedetti-Cecchi 2000). To date, these experimental approaches remain the most effective, although they are also by far the most resource-intensive.

Rather than experiments, Foster (1990) tested hypotheses about the generality of keystone predation on the rocky shores of northern California by measuring the ecological pattern as an indicator of the strong underlying processes. While studies of ecological pattern cannot demonstrate causality (Weins 1983, Underwood 1990), in many cases, testing hypotheses about the generality of patterns is a cost-effective first step in establishing the potential generality of local processes, because it demonstrates what further manipulations might be useful.

A big hurdle for valid tests of ecological generality is commensurability of response variables, spatial scales, sample units, and sample sizes (Underwood & Petraitis 1993, Gee & Warwick 1996, Beck 1997a). Comparisons among biogeographical provinces are particularly problematic because similar habitats in different provinces are generally associated with different suites of species. For such comparisons, it is necessary to test hypotheses using species-independent variables, such as species richness, broad taxonomic groups and functional guilds (see Underwood & Petraitis 1993 for review of benefits and limitations of such an approach). Sensible quantitative tests among biogeographical provinces also require that similar methodologies are used. Careful attention must be paid to the size of sample units, the number of replicates, and the

spatial scales used, as each of these can strongly influence interpretations of results (Andrew & Mapstone 1987, Underwood 1997).

In this study, we focus on coralline algal turf, which is common on rocky intertidal shores around the world (e.g. Lewis 1964, Stephenson & Stephenson 1972, Stewart 1982, Dye 1993, Benedetti-Cecchi & Cinelli 1994, Underwood & Chapman 1998, Akioka et al. 1999, Coleman 2002). This habitat is associated with extremely rich macrofaunal assemblages, which encompass hundreds of species in densities of up to $250\,000$ ind. m^{-2} (see Kelaher et al. 2001 for review). Until recently, the study of these faunal assemblages was limited to a few descriptive papers (e.g. Dommasnes 1968, 1969, Hicks 1971, Grahame & Hanna 1989). In the last 3 yr, however, a series of published studies have detailed the patterns of spatial variation of gastropod assemblages associated with coralline turf, and have experimentally determined some of the major processes responsible for these patterns at Cape Banks Scientific Marine Research Area, Sydney, Australia. Specifically, this work has shown that (1) colonization processes and environmental variables can strongly influence the variation in gastropod assemblages in coralline turf at different tidal heights (Kelaher 2001, Kelaher in press, Kelaher et al. 2003), and (2) habitat architecture (e.g. density and length of fronds), amount of sediment, behavior of the component species, and patterns of adult and juvenile colonization are responsible for much of the variation at scales of tens of meters, which is so prevalent in these assemblages (Kelaher 2001, 2003a,b, in press, Olabarria 2002, Olabarria et al. 2002).

The time-consuming nature of manipulative experiments has unfortunately limited the progress on process-orientated investigations to gastropod assemblages at a single locality near Sydney. The general importance of these processes for a broader assemblage of organisms, a wider geographical area near Sydney, or rocky shores with coralline turf in other parts of the world, remains unknown. We have followed the approach advocated by Foster (1990), in which the potential generality of local processes was evaluated by testing hypotheses about consistency in ecological patterns. To do this, we sampled turfs of *Corallina officinalis* on shores in Australia, Ireland and Chile using identical procedures (i.e. similar spatial scales and experimental design) to test 2 specific hypotheses: (1) that molluscan assemblages vary significantly among patches of turf separated by tens of meters, and (2) that these assemblages in the low-shore differ significantly from those in the mid-shore, with greater species richness occurring in low-shore patches.
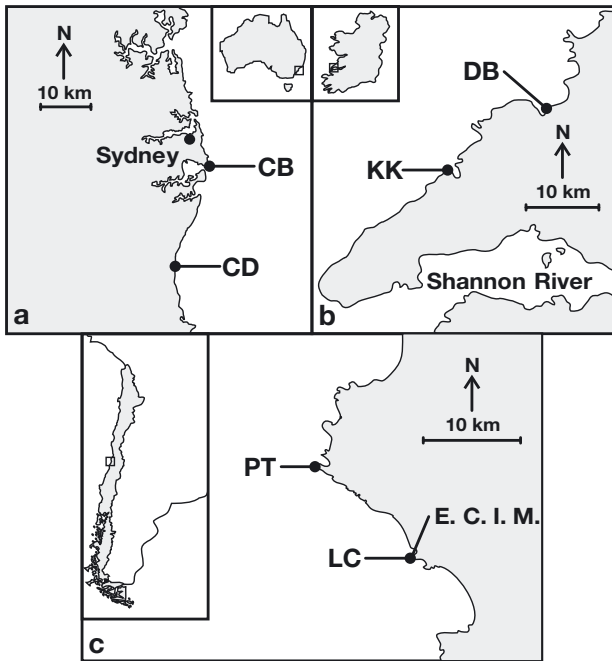
Fig. 1. Location of shores at the 3 sampling localities: (a) east coast of Australia, (b) west coast of Ireland, and (c) central coast of Chile. CB, Cape Banks; CD, Coledale; DB, Doonbeg; KK, Kilkee; PT, Punta Tralca; LC, Las Cruces

MATERIALS AND METHODS

Description of locations. This study was undertaken on wave-exposed rocky shores on the east coast of Australia, the west coast of Ireland, and the central coast of Chile (Fig. 1). The Australian shores, Cape Banks and Coledale, were located near Sydney and were separated by 19 km (Fig. 1a). The tidal range for these shores was 1.5 to 2 m, and the intertidal communities were dominated by turfs of *Corallina officinalis* (Underwood 1975, 1981). The Irish shores, Kilkee and Doonbeg, were located in County Clare and were separated by approximately 11 km (Fig. 1b). The 3.5 to 5 m tidal range of these shores was substantially larger than those for the other localities. Here, the intertidal communities were dominated by patches of mussels (*Mytilus edulis* and *M. galloprovincialis*), mats of *C. officinalis* and other species of turf-forming algae. The Chilean shores at Las Cruces and Punta Tralca were separated by 12 km and had a tidal range of 1 to 1.5 m (Fig. 1c). The area sampled at Las Cruces was just north of Estación Costera de Investigaciones Marinas, which is a well-known marine protected area (Duran & Castilla 1989, Castilla 1999). The structure of intertidal communities at Las Cruces and Punta Tralca were similar to those described for central Chile, in that they were dominated by beds of the mussel *Perumytilus*

purpuratus in mid-shore areas, and mats of mixed algal turf and the large macroalga *Lessonia nigrescens* lower on the shore (Castilla 1981, Broitman et al. 2001). Turfs of *C. officinalis* were also common, but less so than at the other localities. The physical structure of coralline turfs (length and density of fronds) appeared similar at all geographic localities.

Sampling methods. Turfs of *Corallina officinalis* were sampled on the 2 shores in each of the 3 geographical localities using similar methods. The Australian, Irish and Chilean shores were sampled in January 1998, June 1999 and April 2003, respectively. Each locality was therefore sampled during summer/ early autumn, thereby reducing seasonal influences. All sampling was carried out during periods of spring tides and calm conditions.

On each shore, 2 sites (each 2 × 4 m) containing patches of coralline turf were haphazardly selected in low- and mid-shore areas. To ensure commensurability among shores with different tidal ranges, low-shore sites were selected at mean low water of neap tides, and mid-shore sites were at mid-tide level. Mid-shore sites were, therefore, just below the upper limit of dense mats of coralline turf, and the low sites were located within low-shore assemblages. At each tidal height, sites were 50 to 70 m apart. At each site, 5 randomly placed replicate cores of coralline turf were collected using a sharpened metal corer, which had an internal diameter of 80 mm (0.005 m²). Cores were only sampled in areas that were not permanently covered by water. This size of core provides relatively precise estimates of the richness and abundance of macrofauna in coralline turf (Kelaher 2001). For each replicate, the corer was pushed firmly into the coralline turf and the algae and sediment contained within the corer scraped off at the level of the rock, placed in a plastic bag and taken to the laboratory. Only areas with 100% primary cover of algae, of which at least 95% was *Corallina officinalis*, were sampled. All replicates were washed in a 500 µm sieve and preserved in 7% formalin solution. Any molluscs retained on the sieve were sorted using a binocular microscope (12× magnification) and identified to species.

Data analysis. Because all sites were sampled using identical methods, it was possible to directly compare the assemblages from the 3 geographical localities. Logistical constraints inevitably meant there were differences in the dates that each locality (2 shores sampled within each country) could be sampled, and sampling could not be temporally replicated. It is unlikely, however, that the year of sampling is particularly important because each locality will have a unique ecological history. Nevertheless, some caution is needed when interpreting differences among localities because there was no estimate of temporal variation in

Table 1. Mean proportion of species in each of the 6 broad taxonomic groups

	Australia	Ireland	Chile
Total number of species	58	24	27
Taxonomic groups (%)			
Chitons	10.3	4.2	18.5
Prosobranch gastropods	74.1	66.7	51.9
Mussels	5.2	16.7	14.8
Other bivalves	5.2	8.3	11.1
Opisthobranch gastropods	3.4	4.2	0.0
Pulmonate gastropods	1.7	0.0	3.7

the Ireland and Chile samples. Previous work, however, has shown that the spatial patterns of the molluscan assemblages being tested are relatively consistent through time at the Cape Banks Scientific Marine Research Area (Kelaher 2001, 2003a).

For each locality, pooled species richness was estimated by rarefying data with Coleman's rarefaction index[1]. These sample-based rarefactions were plotted against the number of individuals to account for variation in abundance (Gotelli & Colwell 2001). Hypotheses about differences among localities were only tested with identity-free measures of assemblage structure (i.e. species richness, total abundance and evenness J', Pielou 1975). In addition, molluscan assemblages were divided into 6 broad taxonomic groups for analysis (Table 1).

ANOVA was used to test hypotheses about univariate measures of assemblage structure and broad taxonomic groups. These analyses had 4 factors: locality (3 levels and random), height on the shores (2 levels and fixed), shores nested within each locality (2 levels and random) and sites nested in each locality, shore and height (2 levels and random). Further ANOVAs were also done using shores, heights and sites within each locality to test the generality of significant variation at the scale of tens of meters. Student-Newman-Keuls (SNK) tests were used for *a posteriori* comparisons among means. The distributions of raw data for most variables were skewed and variances were heterogeneous (Cochran's C-test, p < 0.05). To satisfy the assumptions of ANOVA, data were transformed to $\ln(x+1)$ prior to analysis (Underwood 1997). Evenness (J') was not transformed because it was neither skewed nor heterogeneous (Cochran's C-test, p > 0.05). Abundances of opisthobranchs and pulmonates were not statistically analyzed because they were far too rare for sensible interpretation.

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[1]Colwell RK (1997) EstimateS: statistical estimation of species richness and shared species from samples. Available at http://viceroy.eeb.uconn.edu/EstimateS

Non-parametric multivariate analysis of variance (NP-MANOVA) was used to test hypotheses about spatial patterns in molluscan assemblages within each locality (Anderson 2001, McArdle & Anderson 2001). These analyses test for overall multivariate changes in community structure, which may include differences in composition, richness and/or abundances of individual species. Non-metric multidimensional scaling (nMDS, Field et al. 1982) was used to produce 2D ordination plots that show relationships among molluscan assemblages. All multivariate analyses were carried out using untransformed data and Bray-Curtis similarity coefficients (Bray & Curtis 1957).

RESULTS

Comparisons of richness patterns among localities

In total, 58, 24 and 27 species of molluscs were found in the samples from Australia, Ireland and Chile, respectively (Table 1). As species-individuals curves from Australia and Chile were not asymptotic after rarefaction, accurate comparison of pooled species richness among localities was problematic (Fig. 2). Despite this, it was abundantly clear that the richness of species and total abundance of individuals was greater on the Australian shores than the other localities (Fig. 2). At the termination of the curve with the least number of individuals (Irish shores), the rarefaction curves showed 42 species in samples from Australian shores and 24 species in both the Irish and Chilean samples. Given more cores, however, it is likely that the actual richness of the Chilean shores is greater because spe-
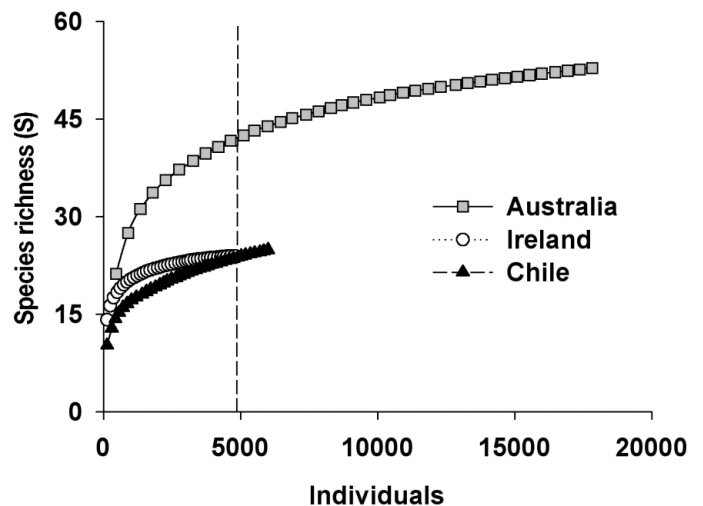

Fig. 2. Coleman rarefaction curves generated using pooled replicate cores from the 3 localities sampled
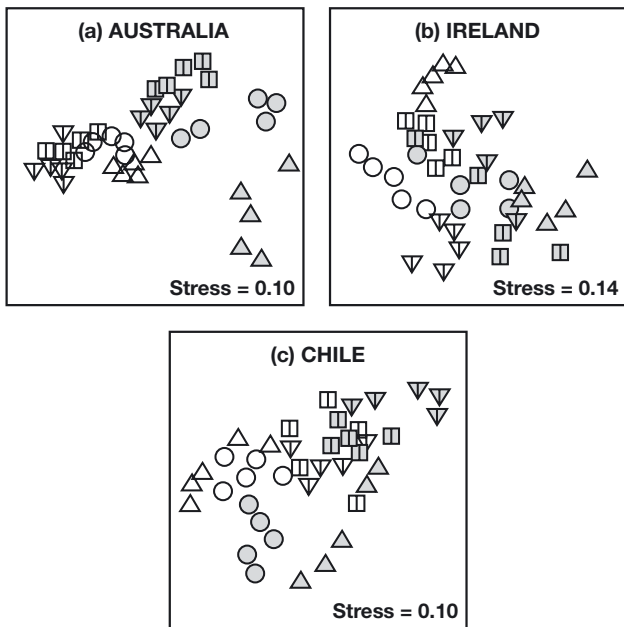
Fig. 3. 2D non-metric multidimensional scaling (nMDS) ordination comparing molluscan assemblages in mid- (clear symbols) and low-shore (gray symbols) areas of each locality. Undashed and dashed symbols represent different shores. Symbols of different shapes represent sites nested at each level of height and shore

cies were still accumulating in the Chilean samples after the Irish curve had clearly become asymptotic.

Despite differences in pooled species richness, the mean proportion of species in each of the 6 broad taxonomic groups did not vary significantly among localities (Table 1, $\chi^2 = 9.71$, df = 10, p = 0.47). Overall, the species compositions of these assemblages were dominated by prosobranch gastropods, with other gastropod taxa (opisthobranchs and pulmonates) having only minor contributions (Table 1). Approximately, similar numbers of mussel species were found at each locality, but these represented a higher proportion of the total

number of species in Chile and Ireland. The richness of chitons on the shores in Australia (6 species) and Chile (5 species) were substantially greater than on Irish shores (1 species).

Assemblage-level spatial variation within each locality

The structure of molluscan assemblages in coralline turf on the Australian shores differed significantly between low- and mid-shore areas (post-hoc test, p < 0.01, see significant Sh × He interaction in Table 2a). This pattern is evident in Fig. 3a, which shows 2 distinct groups of replicate cores from different tidal heights. There was, however, a strong trend of differences between shores that was only significant in low-shore areas (post-hoc test, p < 0.05).

In contrast to the Australian shores, there were no significant differences between the molluscan assemblages at different tidal heights on the Chilean or Irish shores (Table 2b,c). Nevertheless, Fig. 3b does reveal a trend toward differences between low- and mid-shore areas on Irish shores, but clearly not as distinct as that from the Australian shores. For Chilean shores, the structures of molluscan assemblages massively overlap between low- and mid-shore areas (Fig. 3c). For this locality, however, there were significant differences between molluscan assemblages at Punta Tralca and Las Cruces (Table 2). For all localities, there was significant variation among sites nested in shores and tidal heights (Table 2).

Univariate comparisons of molluscan assemblages among and within localities

The relationship between species richness (per core) and tidal height varied significantly among localities (see significant interaction Lo × He in Table 3a). On the Australian and Chilean shores there were significantly

Table 2. NP-MANOVAs comparing molluscan assemblages within each locality (n = 5 replicate cores). Sh: comparison between randomly chosen shores; He: fixed comparison between mid- and low-shore areas; Si: comparison between sites nested in each level of shore and height

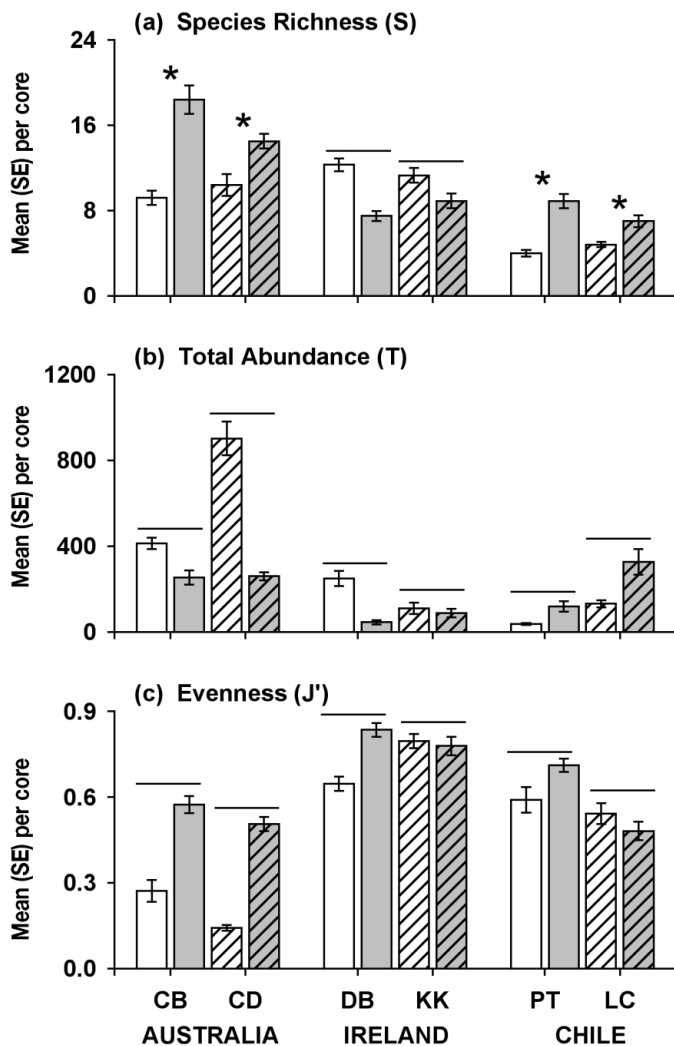|	df	Permutable units	(a) Australia			(b) Ireland			(c) Chile		
			MS	F	p	MS	F	p	MS	F	p
Sh	1	8 site units	8383.99	2.60	0.07	5882.15	0.70	0.64	18554.84	4.02	0.03
He	1	4 interaction units	28661.52	2.70	0.18	14703.23	2.16	0.17	10437.94	2.57	0.19
Sh × He	1	8 site units	10633.11	3.30	0.04	6800.99	0.81	0.55	4055.55	0.88	0.38
Si (Sh × He)	4	40 replicate units	3225.35	6.77	<0.01	8392.80	7.88	<0.01	4613.73	5.58	<0.01
Residual	32		476.39			1064.52			826.20		

Fig. 4. Mean (±SE, n = 2 sites) values of univariate measures of molluscan assemblages in mid- (clear bars) and low-shore (gray bars) areas at the 3 localities. Lines (Student-Newman-Keuls, SNK, p > 0.05) or * (SNK, p < 0.05) above bars indicate the significance of differences between low- and mid-shore areas. See Fig. 1 for locations and abbreviations

more molluscan species in low- than mid-shore areas (Fig. 4a). In contrast, there was a non-significant trend to greater richness of molluscs in mid-shore areas of Irish shores (Fig. 4a). Despite Australian turf containing substantially more species than Irish turf, the average species richness per core in mid-shore areas of Irish shores was significantly greater than in other localities (SNK, p < 0.05). In low-shore areas, however, there were significantly more species in Australia than in the other localities (SNK, p < 0.05).

The total abundance of molluscs in coralline turf did not vary significantly among tidal heights in any locality. It did, however, vary significantly among shores nested in localities (Table 3b, Fig. 4b). These differences were mostly caused by significant variation among the Chilean shores (SNK, p < 0.05), as there were no significant differences at the other localities (SNK, p > 0.05). The evenness of molluscan assemblages varied significantly among localities and shores nested within localities (Table 3c). There was also a non-significant trend towards greater evenness in low-shore areas compared to mid-shore areas of Australian shores, although not at the other localities (Fig. 4c).

Chitons were most abundant in the Australian turf, followed by Chilean and then Irish turfs (SNK, p < 0.05, Table 4a, Fig. 5a). The abundance of prosobranch gastropods was also greater in Australia than in the other localities in low-shore areas (SNK, p < 0.05). In mid-shore areas, however, they were most abundant in coralline turf on Irish shores (SNK, p < 0.05, see Lo × He interaction in Table 4b, Fig. 5b). Prososbranchs were also more abundant in low- than in mid-shore turf in Australia and Chile (SNK, p < 0.05), although the opposite trend was found for Irish shores (Fig. 5b). The abundance of mussels varied significantly among localities (Table 4c). Although SNK tests were not sufficiently powerful to discern any patterns, the average abundances of mussels in coralline turf on Chilean shores was much greater than those on Australian shores (Fig. 5c). Other bivalves, by contrast, were most

Table 3. ANOVAs comparing univariate measures of molluscan assemblages (n = 5 replicate cores). Lo: comparison among the 3 localities; He: fixed comparison between mid- and low-shore areas; Sh: comparison between shores nested in each locality; Si: comparison between sites nested at each level of shore, height and locality. Evenness data are not transformed to ln(x + 1)

	df	(a) Species richness (S)			(b) Total abundance (T)			(c) Evenness (J')		
		MS	F	p	MS	F	p	MS	F	p
Lo	2	4.71	291.81	<0.01	26.44	5.06	0.11	1.53	14.72	0.03
He	1	1.36	0.60	0.52	2.77	0.23	0.68	0.67	2.59	0.25
Sh(Lo)	3	0.02	0.16	0.92	5.22	4.55	0.02	0.10	4.58	0.02
Lo × He	2	2.28	9.71	0.05	12.04	5.28	0.10	0.26	3.92	0.15
He × Sh(Lo)	3	0.23	2.25	0.13	2.28	1.99	0.17	0.07	2.90	0.08
Si (Sh[Lo] × He)	12	0.10	3.00	<0.01	1.15	6.26	<0.01	0.02	3.06	<0.01
Residual	96	0.03	0.18	0.01						

Table 4. ANOVAs comparing broad molluscan taxa (n = 5 replicate cores). Lo: comparison among the 3 localities. He: fixed comparison between mid- and low-shore areas; Sh: comparison between shores nested in each locality; Si: comparison between sites nested at each level of shore, height and locality

	df	(a) Chitons			(b) Prosobranchs		
		MS	F	p	MS	F	p
Lo	2	25.06	223.63	<0.01	70.99	27.50	0.01
He	1	0.05	0.13	0.76	18.12	0.98	0.43
Sh(Lo)	3	0.11	0.14	0.93	2.58	1.16	0.36
Lo × He	2	0.40	4.82	0.12	18.42	23.63	0.01
He × Sh(Lo)	3	0.08	0.11	0.96	0.78	0.35	0.79
Si (Sh[Lo] × He)	12	0.79	3.78	<0.01	2.22	6.55	<0.01
Residual	96	0.21		0.34			
	df	(c) Mussels			(d) Other bivalves		
		MS	F	p	MS	F	p
Lo	2	93.04	11.90	0.04	264.05	59.21	<0.01
He	1	0.81	0.11	0.77	22.48	1.25	0.38
Sh(Lo)	3	7.82	2.02	0.16	4.46	2.08	0.16
Lo × He	2	7.44	2.90	0.20	18.01	1.76	0.31
He × Sh(Lo)	3	2.57	0.66	0.59	10.26	4.78	0.02
Si (Sh[Lo] × He)	12	3.87	14.31	<0.01	2.15	9.65	<0.01
Residual	96	0.27		0.22			

abundant on Australian shores, followed by Irish and then Chilean shores (SNK, p < 0.05, see Lo × He interaction in Table 4b, Fig. 5b). These bivalves were also more abundant in mid- than in low-shore areas on the Australian shores and at Doonbeg in Ireland (Fig. 5d). At all localities, small bivalves in the genus *Lasaea* accounted for more than 95% of the total abundance of this grouping. Opisthobranch and pulmonate gastropods were always extremely rare relative to other taxa (Fig. 5e,f).

For all univariate analyses of assemblage structure and broad taxonomic groups there was significant variation in sites separated by 50 to 70 m, even though there were only 2 sites at each tidal height on each shore (Tables 3 & 4). When comparisons were divided among localities, significant among-site variation was also detected for nearly every variable tested (Table 5). The only exceptions were the total abundance of macrofauna and prosobranchs in Australia and the evenness of assemblages in Chile (Table 5). Each of these Australian variables has been shown to vary significantly among sites at other places and times (Kelaher et al. 2001).

DISCUSSION

Given the extremely large distances separating localities, it was no surprise to find that there were major differences in the composition, diversity and abundance of molluscs associated with coralline turf on the shores in Australia, Ireland and Chile. Overall, molluscs on the Australian shores were ca. 40% more diverse and abundant than at the other localities. By contrast, the diverse Australian assemblages were on average much less even (J') than at the other localities, especially in mid-shore areas. The unusual relationship between richness, abundance and evenness in the molluscan assemblages on Australian shores was mostly caused by the small bivalve *Lasaea australis*, which dominates the macrofaunal abundances in coralline turf near Sydney (Tong 1990, Kelaher 2001, in press).

Table 5. *F*-tests (4, 32 df, n = 5 replicate cores) comparing sites nested within the interaction of shores and heights at each of the 3 localities. No test (NT) was possible for chitons at the Irish locality because only 1 individual was found

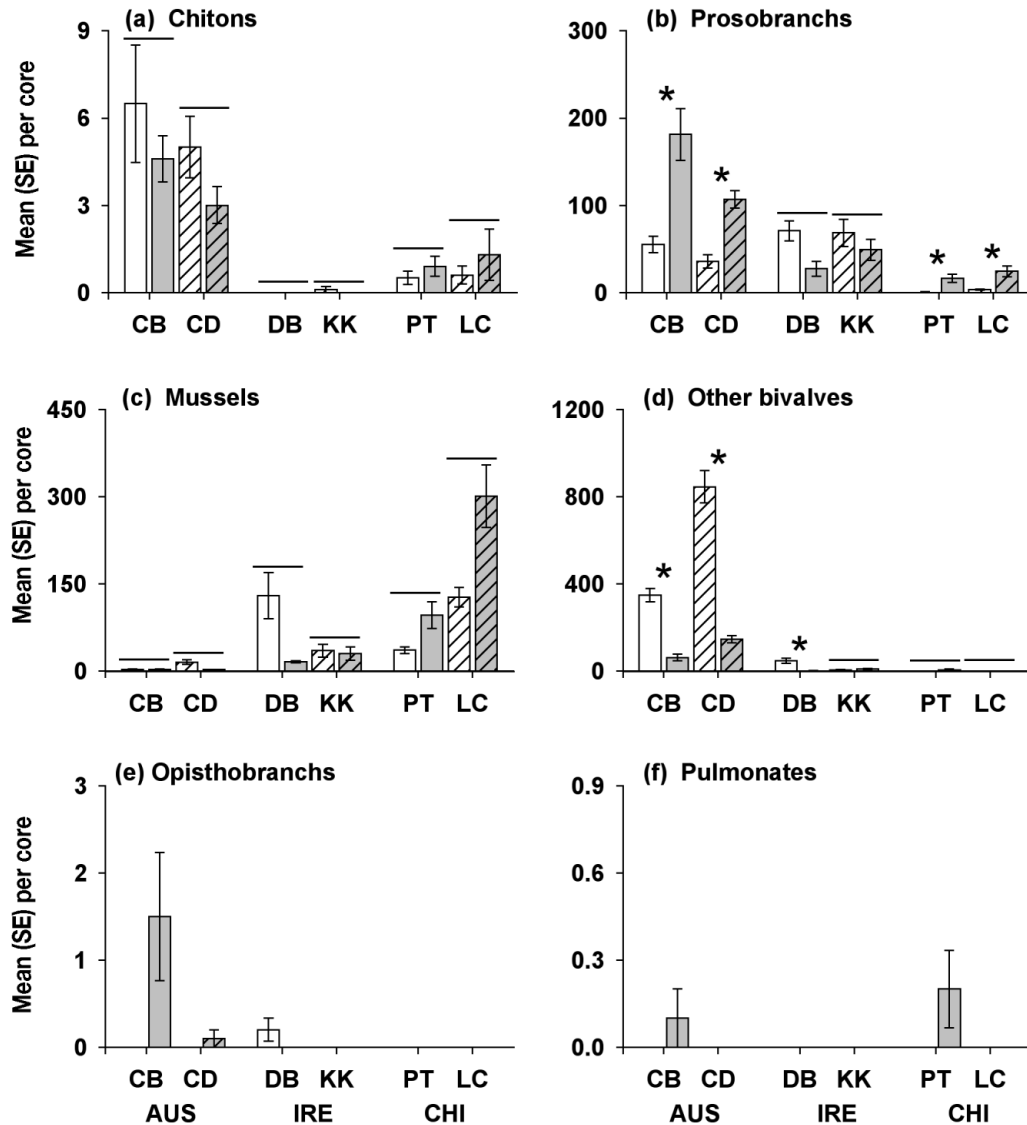|	(a) Australia		(b) Ireland		(c) Chile	
	F	p	F	p	F	p
Species richness	3.09	0.03	4.84	<0.01	3.29	0.02
Total abundance	2.52	0.06	9.07	<0.01	5.64	<0.01
Evenness	3.51	0.02	2.62	0.05	1.72	0.17
Chitons	5.91	<0.01	NT	NT	3.07	0.03
Prosobranchs	1.34	0.27	5.85	<0.01	14.06	<0.01
Mussels	6.91	<0.01	26.94	<0.01	5.08	<0.01
Other bivalves	5.00	<0.01	8.65	<0.01	16.62	<0.01

Fig. 5. Mean (±SE, n = 2 sites) abundance of molluscan taxonomic groups in mid- (clear bars) and low-shore (gray bars) areas at the 3 localities. Lines (Student-Newman-Keuls, SNK, p > 0.05) or * (SNK, p < 0.05) above bars indicate the significance of differences between low- and mid-shore areas. AUS, Australia; IRE, Ireland; CHI, Chile. See Fig. 1 for more specific locations and abbreviations

Despite major differences in molluscan diversity among localities, 2 striking generalities in ecological pattern emerge from this study. The first of these was the similarity in the proportion of species that were represented in each broad taxonomic group. The richness at each locality was dominated by prosobranchs (52 to 79%), with bivalves (mussels and others) and chitons being the next most important groups. Bell-wood & Hughes (2001) reported similar taxonomic consistency for coral and fish assemblages over equally large spatial scales, but using many more locations. They argued that the congruence in diversity patterns was the product of regional-scale assembly rules. It is

difficult to conceive, however, of an overriding set of general ecological processes that could be responsible for the guild proportionality of molluscan assemblages in coralline turf. It is more probable that the congruence is a function of evolutionary history, although regional-scale assembly rules cannot be overlooked until more work is done.

The second striking generality was the consistent differences in the diversity and abundance of molluscs among sites, despite the fact that there were only 2 sites at each height on each shore. The large variation at this scale is similar to that described for gastropod assemblages at Cape Banks Scientific Marine

Research Area (Kelaher 2001, 2003a, Olabarria & Chapman 2001), allowing for the possibility of generality in the dominant processes that create such variation. At Cape Banks, variation at scales of tens of meters is mostly caused by differences in the physical structure of the habitat, amount of sediment, and rates of colonization and recruitment (Kelaher 2001, 2003a,b, in press, Olabarria 2002). These factors have also been highlighted as major determinants in structuring faunal assemblages in other algal turfs on rocky shores (e.g. Hicks 1980, Dean & Connell 1987, Gibbons 1988, Gee & Warwick 1994, Whorff et al. 1995, Hull 1997, Davenport et al. 1999). Although not quantified, it appeared that the amount of sediment, and the density and length of coralline fronds varied substantially among sites on shores in Chile and Ireland. Therefore, repeating the Cape Bank's manipulative experiments at a variety of randomly chosen localities has the potential to elucidate generally important ecological and environmental factors structuring molluscan assemblages in coralline turf on rocky shores around the world. The strategy required to design such experiments is described by Underwood & Petraitis (1993) and Beck (1997a).

Apart from the 2 general patterns outlined above, there were no other obvious consistencies in the spatial patterns of molluscan assemblages among the different localities. This is best demonstrated by the inconsistencies in molluscan assemblage structure between tidal heights, which is perhaps the most predictable and well-studied environmental gradient in intertidal marine ecology (Lewis 1964, Underwood 1994, Raffaelli & Hawkins 1996). At the assemblage level, there were strong differences between mid- and low-shore areas on Australian shores, weak differences on Irish shores, and no clear pattern on Chilean shores. Moreover, whilst there were significantly more species of molluscs and more prosobranch gastropods associated with coralline turf in low- than in mid-shore areas on Australian and Chilean shores, the opposite trend prevailed on Irish shores. Although there was some similarity in these variables between Australian and Chilean shores, these patterns are swamped at the assemblage level by mussels and other bivalves. On Australian shores, the small and extremely abundant bivalve *Lasaea australis* made a substantial contribution to multivariate differences between tidal heights because it was substantially more abundant in mid- than in low-shore areas. On Chilean shores, however, by far the most abundant molluscs were the mussels *Brachidontes granulata*, *Perumytilus purpuratus*, and *Semimytilus algosus*. As their abundances did not vary between low- and mid-shore areas, they strongly contributed to the lack of assemblage-level variation at the different tidal heights on the Chilean shores.

At Cape Banks Scientific Marine Research Area, the clear differences between gastropod assemblages at different tidal heights are caused by variation in biological processes (e.g. competition or predation) mediated by environmental conditions, environmental stress (e.g. exposure at low-tide), and differential colonization and recruitment (Kelaher et al. 2003, unpubl.). The similarity in the patterns exhibited by the molluscan assemblages on the shores near Sydney demonstrates the potential for such factors to be generally important at this particular locality. It is unlikely, however, that the same factors are acting in the same way or with the same intensity on Irish or Chilean shores, because the assemblage level patterns are so markedly different. Nevertheless, despite inconsistencies in spatial patterns among localities, the direction and magnitude of differences between tidal heights in the richness and abundance of molluscs within each locality was remarkably consistent. Therefore, whilst it appears that the dominant factors structuring molluscan assemblages at different tidal heights are unique to each locality, there is still potential for these unique factors to be generally important on shores within each locality.

Overall, evaluating the generality of spatial patterns of molluscan assemblages in coralline turf has been extremely informative for assessing the potential generality of dominant local processes and for highlighting directions for future research. Because careful attention was paid to commensurability, it was possible to compare directly the small-scale spatial patterns of molluscan assemblages in coralline turf in very different parts of the world. The conclusions from this work are therefore substantially more robust than a qualitative or a quantitative coalition of published studies, because the results do not suffer from differences in experimental methodologies, statistical inconsistencies or biases in published results. While this mensurative approach is not as rigorous as the experimental methods suggested by Underwood & Petraitis (1993) and Beck (1997a), it does provide a useful guide for further experimental studies because it highlights areas where such generality could exist. For the above reasons, we propose that testing the generality of spatial patterns should be considered as a useful and cost-effective first step in establishing the general importance of ecological processes.

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