SPATIAL VARIATION IN MOLLUSCAN ASSEMBLAGES FROM CORALLINE TURFS OF ARGENTINEAN PATAGONIA

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ABSTRACT

Patterns of spatial variation of molluscan communities associated with coralline algal turfs were evaluated over 1,000 km of the coast of Argentinean Patagonia. A hierarchically-nested experimental design was used to determine the relative importance of molluscan assemblage variation at three different spatial scales (shores, sites and cores). Hypotheses were also tested about the potential role of habitat variables (frond density, frond length, sediment and epiphytes) for determining molluscan community structure. In total, 38 molluscan species were found comprising 16, 18 and 4 species of bivalves, gastropods and polyplacophorans, respectively. Densities of molluscs in coralline turfs reached *ca* 77,000 individuals per m^2 and were dominated by mussels, especially *Perumytilus purpuratus*. Multivariate and univariate analyses of assemblage structure consistently showed that variation at scales of metres and hundreds of kilometres dominated, with sites 20–50 m apart always contributing less than 24% of the total. Significant associations between molluscan community structure and both frond density and frond length demonstrated the potential importance of habitat structure in determining community structure at local scales. Variation in molluscan assemblages at the scale of shores, however, did not appear to correlate with latitudinal, temperature or wave exposure gradients, indicating that other processes must be operating. The compositions of molluscan assemblages in coralline turfs on the coast of Argentina were similar to those reported for central Chile. Comparisons of the richness of these South American assemblages to other parts of the world revealed some striking biogeographical patterns that warrant further investigation. Overall, this work highlights the general importance of small-scale variation in molluscan assemblages on rocky shores and the consistent influence of habitat complexity in determining the structure of diverse molluscan communities associated with mat-like habitats.

INTRODUCTION

Many living species in marine environments provide habitat for diverse molluscan communities (e.g. mussels, corals or seagrass, Seed, 1996; Bruno & Bertness, 2001; Kelaher, Chapman & Underwood, 2001). These habitat-forming species improve local environmental conditions for molluscs by reducing the impact of physical disturbance, providing refuge from environmental stress, altering predation pressures and competitive interactions and increasing local resources, such as food or space (Thompson *et al*., 1996; Kelaher *et al*., 2001). The presence of habitat-forming species in a community strongly influences local biodiversity and ecosystem performance (Jones, Lawton & Shachak, 1994, 1997).

On rocky intertidal shores, organisms that form mat-like structures, such as algal turfs (Davenport, Butler & Cheshire, 1999; Kelaher, Castilla & Seed, 2004), ascidians (Cerda & Castilla, 2001; Monteiro, Chapman & Underwood, 2002) and mussel beds (Suchanek, 1985; Seed, 1996; Prado & Castilla, 2006), provide habitats for extremely diverse assemblages of micromolluscs and juvenile stages of larger species, many of which are of socio-economic importance (Dye, 1992; Castilla & Defeo, 2001). The quality of habitat provided by mat-forming species is extremely variable and depends on habitat structural complexity and heterogeneity, as well as the biological characteristics of the species in question (Davenport *et al*., 1999; Kelaher, 2003). For example, changes in the length and density of fronds in algal turf influences the physical complexity of the habitat provided, which in turn influences the area available for molluscan colonization (Kelaher *et al*., 2001) and effectiveness of larger predators (Coull & Wells, 1983). Similarly, sediment and organic material trapped by algal turfs increase habitat heterogeneity, providing opportunity for infaunal molluscs as well as frond-dwelling species (Gibbons, 1988). The fronds themselves and their associated epiphytes (attached algae) may also provide a nutritional source for grazing snails (Hay, Duffy & Pfister, 1987) or chemicals given off by the fronds may attract or repel molluscan larvae (Young, 1990).

Mat-like habitats have been a focus of ecological study because they greatly promote local molluscan biodiversity (Seed, 1996; Bruno & Bertness, 2001; Kelaher *et al*., 2001). An initial step for understanding factors that create and maintain diversity in these habitats has been determining important spatial scales over which communities vary (Underwood & Chapman, 1996). For prominent molluscs on rocky shores, important variation has been demonstrated at multiple spatial scales, from centimetres all the way up to thousands of kilometres (Olabarria & Chapman, 2001; Fraschetti, Terlizzi & Benedetti-Cecchi, 2005). The most substantial variation seems to occur (1) at the scale of metres, which correlated with the distances over which adult molluscs show behavioural preferences, compete

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and interact (Kelaher *et al.*, 2001; Fraschetti *et al.*, 2005), and (2) at the scales of tens to hundreds of metres, which is thought to reflect variation in recruitment and mortality (Underwood & Chapman, 1996; Kelaher *et al.*, 2004). On the coast of central and northern Chile, substantial variation in populations of molluscs has also been demonstrated at scales of hundreds of kilometres, which has been attributed to variation in ocean upwelling and other mesoscale oceanographic features (Broitman *et al.*, 2001).

Despite the crucial role that mat-like habitats play in facilitating local molluscan biodiversity on rocky shores, the time consuming nature of processing samples has limited ecological investigations of these habitats to relatively local scales, reducing ecological understanding of these important systems (but see Thiel & Ullrich, 2002). We directly addressed this issue, by sampling molluscan communities associated with coralline algal turf over *ca* 1,000 km of the rarely studied Patagonian coast of Argentina. Along with mussel beds, mats of coralline turf dominate the low- to mid-shore areas of this coastline. The densely packed coralline fronds provide habitat for a diverse range of molluscan taxa with densities of up to 77,000 individuals per m^2. Here, we describe for the first time the composition of species, patterns of abundance and spatial structure of these molluscan communities and then evaluate the potential importance of habitat characteristics for determining these patterns.

MATERIAL AND METHODS

Description of shores

Eight rocky intertidal shores, ranging from Punta Mejillón (41°00′52″S, 64°10′05″W) to Cabo Blanco (47°12′21″S, 65°44′28″W) (Fig. 1), were sampled along *ca* 1,000 km of the Patagonian coast of Argentina. Water temperature along this coastline varies from 4 to 8°C in winter and from 14 to 22°C in summer (Hoffman, Nunez & Piccolo, 1997), and there is a large tidal range (between 4 and 9 m). Wave exposure of these shores varied from sheltered (Piedras Coloradas, Punta Mejillón and Punta Ameghino), medium exposure (Puerto Lobos and Bahía Camarones) to relatively exposed (Punta Ninfas, Comodoro Rivadavia, Cabo Blanco). There was also variation in rock type, which included sedimentary rocks (agglomerates: Punta Mejillón; sandstones: Punta Ameghino, Punta Ninfas and Comodoro Rivadavia), volcanic rocks (Bahía Camarones, Piedras Coloradas and Cabo Blanco) and consolidated deposits of volcanic rocks (Puerto Lobos). The mid- to low-shore areas of these rocky shores were dominated by either patches of coralline turfing algae, *Corallina officinalis*, or beds of the mussel, *Perumytilus purpuratus*. The densely packed coralline fronds formed expansive turfs that had average frond length of 31.4 (SD = 7.7, $n = 960$) mm.

Sampling methods

Molluscan assemblages in coralline turfs were sampled at each of the eight shores between the 25 and 31 of December 2004 using methods described by Kelaher & Castilla (2005). Four sites (each 2 × 2 m) at each shore containing patches of coralline turf were haphazardly selected at approximately mean low water of neap tides. Each site was separated from its nearest neighbour by 20–50 m and was sampled with three randomly-placed replicate cores (80 mm in diameter, 0.005 m^2). This size of core provides relatively precise estimates of the richness and abundance of macrofauna in coralline turfs (Kelaher *et al.*, 2001). For each replicate, the algae, sediment and molluscs within the corer were scraped off at the level of the rock and preserved in 7% formalin solution. Only areas with 100% primary cover of algae, of which at least 95% was *C. officinalis*, were sampled. In the laboratory, each core was washed in a 500 μm sieve stacked on top of a 63 μm sieve. All molluscs retained on the 500 μm sieve were sorted and identified using a binocular microscope (×12 magnification). Although there are other taxa associated with these mat-like habitats, molluscan assemblages were the main focus because they are numerically-dominant, encompass important functional groups and are well described.

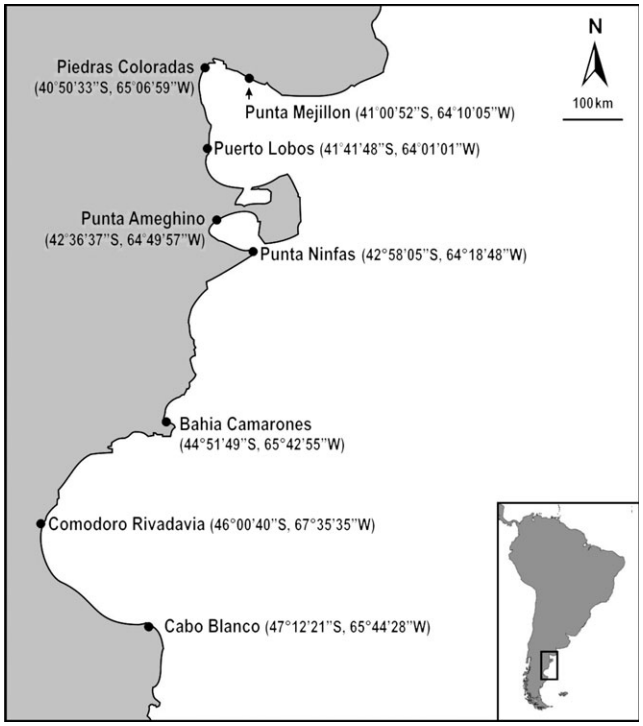


Figure 1. Shores sampled over *ca* 1,000 km of the Argentinean coast (40–47°S).

Habitat characteristics that have previously been shown to influence molluscan community structure, such as frond density, frond length and the amount of associated sediment and epiphytes, were also quantified. For each core, sediment particles greater than 63 μm were dried in an oven for 48 h at 80°C and weighed. Because the sediment was relatively coarse, grains less than 63 μm only made a small contribution to the total weight (less than 2%) and were therefore not quantified (Kelaher *et al.*, 2001). The average length of *C. officinalis* fronds was determined for each core from the measurement of five randomly selected fronds. Each frond measured was complete, with an intact holdfast. Because of the difficulties involved in accurately measuring the density of fronds directly, a surrogate measure was determined by dividing the dry weight of coralline fronds per m^2 by the average frond length (units = $kg{\cdot}m^{-3}$). This surrogate is a relatively good representation of the number of fronds per unit area (Kelaher & Castilla, 2005). To measure the dry weight of coralline fronds and epiphytes, the *Corallina* was carefully scraped clean of epibiota (all attached organisms). The separated coralline fronds and epiphytic algae were then dried for 48 h at 80°C and weighed.

Data analysis

The experimental design had eight randomly chosen shores, four sites nested in each shore and three replicate cores within each site. This hierarchically-nested design allows variation to be independently partitioned into three spatial scales (shores, sites and cores) and for hypotheses to be tested about significant

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variation at each spatial scale (Underwood & Chapman, 1996). To evaluate multivariate patterns of variation in molluscan assemblages, nonparametric multivariate analyses of variance (per-MAVOVA) were used (Anderson, 2001). These analyses allow for comparisons of overall multivariate changes in community structure, which may include differences in composition, richness and/or individual species abundances. The test statistic (*pseudo-F*) is a multivariate analogue of Fisher's *F*-ratio and is calculated from a symmetric dissimilarity matrix (Anderson, 2001). Unlike MANOVA, these nonparametric tests are robust to data from the highly variable assemblages found in coralline turfs (Kelaher, 2003). To visualize graphically multivariate patterns in benthic assemblages, nonmetric multidimensional scaling (nMDS) (Field, Clarke & Warwick, 1982) was used to generate two-dimensional ordination plots. All multivariate analyses used untransformed data (Clarke, 1993) and the Bray–Curtis similarity coefficient (Bray & Curtis, 1957). Hypotheses about differences in species richness, evenness of assemblages J' (Pielou, 1975), and abundances of major molluscan groups were tested with nested analyses of variance (ANOVA). Except for evenness, all univariate molluscan assemblage variables were transformed with $\ln(X+1)$ prior to analysis to ensure assumptions of general linear models were met.

Variance components were used to estimate the percentage of variation contained at each spatial scale (shores, sites and cores). For multivariate measures of molluscan assemblages, estimated mean squares of per-MANOVA analyses were used to calculate multivariate variance components using standard methods (Kelaher & Levinton, 2003). For univariate measures of molluscan assemblages, components of variation were estimated using the Residual Maximum Likelihood Method (Robinson, 1987).

To test the potential importance of habitat variables for explaining variation in molluscan community structure, the BIO-ENV procedure was used (Clarke & Ainsworth, 1993). This technique correlates multivariate community data with predictor variables to determine which variable or which combination of variables best explains community structure. For these analyses, a weighted Spearman's rank coefficient was used and the significance levels of the most important variables were tested with a Mantel's test (Mantel, 1967). Partial correlation coefficients were used to determine the unique contribution of variance explained in molluscan assemblages by each habitat variable over and above the effects of the other habitat variables in the model. For instance, using these methods we were able to determine whether frond density was capable of explaining significant variation in molluscan species richness, independent of frond length, sediment or epiphytes. After transformation (see above) data satisfied assumptions of multiple regression and tolerances, variation inflation factors and eigenvalues indicated that colinearity among predictor variables did not influence results (Quinn & Keough, 2002). Because data were used multiple times in these analyses (Neter *et al*., 1996) and in other places, significance levels were adjusted using a sequential Bonferroni correction method (Holm, 1979) whenever multiple comparisons were used.

Table 1. List of molluscs associated with turfs of *Corallina officinalis* in Argentinean Patagonia.

Bivalvia
Perumytilus purpuratus (Lamarck, 1819)
Aulacomya atra (Molina, 1782)
Mytilus edulis Linnaeus, 1758
Brachidontes blakeanus Melvill & Standen, 1914
Brachidontes granulata (Hanley, 1843)
Lasaea adansoni (Gmelin, 1791)
Lasaea petitiana (Récluz, 1827)
Kellia sp.
Nucula sp.
Diplodonta patagonica (d'Orbigny, 1842)
Carditella tegulata (Reeve, 1843)
Astarte longirostris d'Orbigny 1846
Hiatella sp.
Lithophaga patagonica (d'Orbigny, 1846)
Musculus viator (d'Orbigny, 1846)
Mytilus edulis platensis d'Orbigny, 1846
Gastropoda
Epitonium sp.
Carditella tegulata (Reeve, 1843)
Eatoniella sp.
Tegula patogonica (d'Orbigny, 1840)
Siphonaria lessoni (Blainville, 1824)
Crepidula dilatata (Lamarck, 1822)
Onoba sp.
Turbonilla smithi Pfeiffer,1906
Cerithiopsis sp.
Fissurella sp.
Trophon geversianus (Pallas, 1769)
Balcis sp.
Mathilda magellanica Fischer, 1883
Anachis isabellei (d'Orbigny, 1841)
Odostomia sp.
Omalogya sp.
Sinezona sp.
Littorinidae sp.
Polyplacophora
Acanthopluera granulata (Gmelin, 1791)
Polyplacophora sp. 1
Polyplacophora sp. 2
Polyplacophora sp. 3

RESULTS

Spatial variation in structure of molluscan assemblages

In total, 38 species of molluscs were found on the Argentinean shores (Table 1), of which one gastropod species, *Sinezona* sp. has never previously been reported from this coastline. There were substantially more gastropod species (18 species) and bivalve (16 species) than species of polyplacophorans (4 species), and the taxonomic compositions of these groups were fairly representative of those found in coralline turfs from other parts of South America (Kelaher *et al*., 2004). Assemblages were mostly made up of micromolluscs (e.g. *Eatoniella* sp. and *Lasaea adamsoni*) and juveniles of larger species (e.g. *Acanthopleura granulata* and *Aulacomya atra*).

Molluscan assemblages differed significantly among shores ($pseudo\text{-}F = 7.28$, 7,24 df, $P < 0.002$) and among sites nested within shores ($pseudo\text{-}F = 2.12$, 24, 65 df, $P < 0.002$). At the scale of shores, molluscan assemblages fell out into three main groups (Fig. 2). However, obvious environmental variables, such as latitude, wave exposure, rock type and platform shape, did not appear to correlate with any differences among groups. For example, there were no significant differences between molluscan turf assemblages on the sheltered sandstone shore at Punta Ameghino and the exposed volcanic rocky shore at Bahía Camarones, which is *ca* 300 km further south. In contrast, there were significant differences between molluscan turf assemblages at Punta Ninfas and Comodoro Rivadavia, despite these

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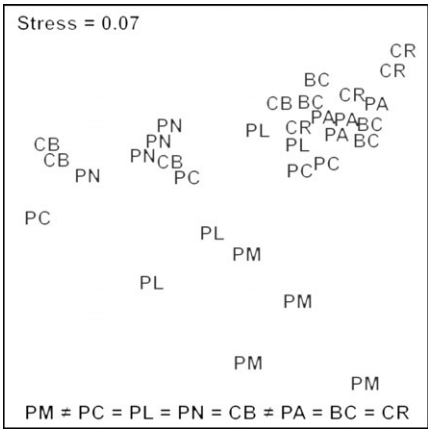


Figure 2. Two-dimensional nMDS ordination ($n = 4$ sites) comparing molluscan assemblages in coralline turf at Punta Mejillón (PM), Piedras Coloradas (PC), Puerto Lobos (PL), Punta Ameghino (PA), Punta Ninfas (PN), Bahía Camarones (BC), Comodoro Rivadavia (CR), Cabo Blanco (CB). Results of NP-MANOVA pair-wise comparisons are indicated with '$=$'($P > 0.05$) and '$\neq$'($P < 0.05$).

shores having similar rock-type and wave exposure. Variance components demonstrated substantial variation in molluscan assemblages at the scales of shores (47%) and replicate cores (39%), with sites only accounting for 14%. On average, mussels accounted for 85% of the total dissimilarity among shores, with *Perumytilus purpuratus* alone being responsible for 57% of the total. Gastropods only accounted for 4% of the among shore dissimilarity, despite being almost three times as diverse as mussels. Although there was substantially less variation in molluscan assemblages at the scale of sites relative to shores, mussels once again accounted for 84% of the total among-site variation on average, with gastropods making up less than 5%.

Molluscan species richness, total abundance, assemblage evenness and the abundances of major taxonomic groups varied significantly among shores (Table 2, Fig. 3). Despite powerful tests ($N = 32$ sites), significant differences among sites were not detected in gastropod species richness or in the abundances of gastropods and bivalves other than mussels. Like the multivariate results, in most cases there were no obvious environmental variables that explained variation in univariate assemblage measures among locations. The average abundance of gastropods, however, doubled on the two most southern shores, although they were still an order of magnitude less than gastropods in coralline turf from other part of the world (Kelaher *et al*., 2004). Similar to multivariate analyses, variance components consistently highlighted shores and replicates as the spatial scales encompassing most variation in molluscan assemblages (Table 2). For every analysis, sites were the least important scale, accounting for only 0–23% of total variation.

Relationship between molluscan assemblages and habitat characteristics

The physical structure of coralline turf had a strong influence on molluscan communities, as there were significant multivariate correlations between molluscan assemblages and frond density and length (Table 3). The addition of extra habitat variables, only marginally improved the strength of the best correlation ($R = 0.25$ for frond density and $R = 0.26$ for frond density plus epiphytes). Frond density did not influence the richness of molluscs, but did affect the total abundance and evenness of assemblages (Table 4). As the coralline turf became more complex, the relative numerical dominance of small mussels, especially *P. purpuratus*, increased dramatically. This resulted in significant negative correlation between frond density and the evenness of molluscan assemblages and a strong positive correlation between frond density and total abundance of molluscs (Table 4). Similarly, increases in frond length positively affected the abundances of mollusc's, whereas epiphytes had the exact opposite influence (Table 4). Finally, sediment did not explain significant amount of variation in either multivariate or univariate measures of the structure of molluscan assemblages.

DISCUSSION

Through documenting the spatial scales at which there is significant variation in community structure, we are able to identify the relative importance of different ecological processes and environmental factors which may be responsible for such variation (Underwood & Chapman, 1996). Variation in molluscan assemblages in coralline turf from Argentina was most pronounced at the scale of replicate cores (metres) and at the scale of shores (100 s of km). At the scale of a few metres, the most likely cause of variation was differences in microhabitat, which influences a variety of biotic interactions (Underwood & Chapman, 1996). For example, the density of fronds is effectively a measure of habitat complexity (i.e. the number of units per m^2, McCoy & Bell, 1991; Kelaher, 2003) and appeared

Table 2. Nested-ANOVAs comparing molluscan assemblages (n=3 replicate cores) and abundances of broad taxonomic groups among shores and among sites nested in shores.

	df	(a) Species richness				(b) Total abundance				(c) Evenness†			
		MS	*F*	*P*	VC (%)	MS	*F*	*P*	VC (%)	MS	*F*	*P*	VC (%)
Shores	7	0.41	8.04	<0.001	29.73	5.04	8.19	<0.001	39.23	0.26	7.21	<0.001	44.67
Sites (Shores)	24	0.05	0.89	0.62	0.90	0.62	2.75	<0.001	21.90	0.04	2.16	<0.01	15.48
Residual	64	0.06			69.37	0.22			38.87	0.02			39.86
	df	(d) Gastropods				(e) Mussels				(f) Other bivalues			
		MS	*F*	*P*	VC (%)	MS	*F*	*P*	VC (%)	MS	*F*	*P*	VC (%)
Shores	7	1.59	4.30	<0.01	13.10	0.26	7.21	<0.001	38.16	5.51	5.59	<0.001	25.80
Sites (Shores)	24	0.37	0.71	0.83	0.00	0.04	2.16	<0.05	23.11	0.99	1.56	0.08	0.00
Residual	64	0.52			86.90	0.02			38.74	0.63			74.20

VC(%) is the variance component expressed as a percentage of the total variance. †Data not transformed.

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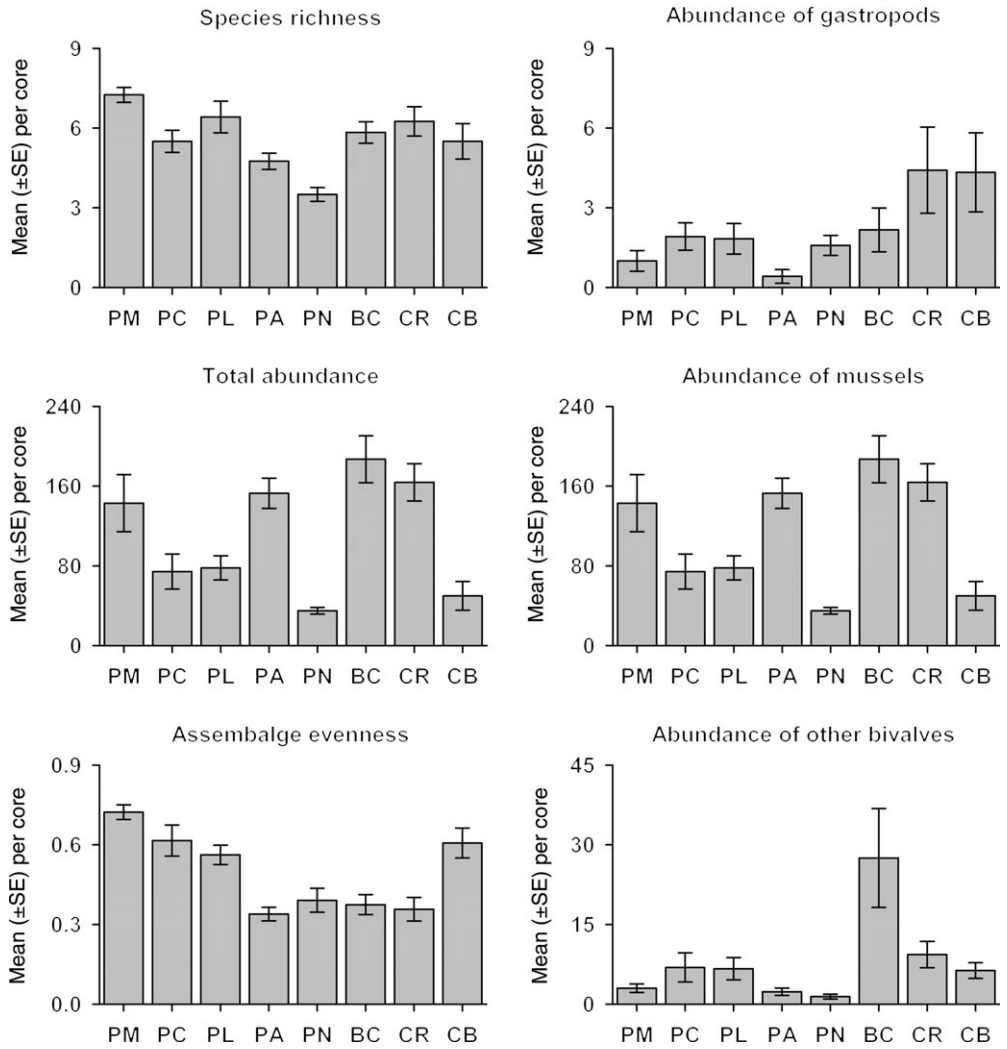


Figure 3. Mean (SE, $n = 12$ sites) value of univariate assemblage measures and large taxonomic groups comparing molluscs in coralline turf at Punta Mejillón (PM), Piedras Coloradas (PC), Puerto Lobos (PL), Punta Ameghino (PA), Punta Ninfas (PN), Bahía Camarones (BC), Comodoro Rivadavia (CR), Cabo Blanco (CB).

to influence the structure of molluscan assemblages. While frond density had no influence on molluscan species richness, it had a strong positive association with the abundance of mussels, especially *Perumytilus purpuratus*, which in turn resulted in reduced assemblage evenness. Densely-packed fronds might confer several advantages to recruitment and survival of small mussels compared to loosely packed fronds. Firstly, more fronds per unit area increases the amount of surface area of habitat available for mussel attachment (Grahame & Hanna, 1989; Kelaher, 2003). Perhaps more importantly, more complex habitats significantly reduce the effectiveness of predators (Coull & Wells, 1983; Dean & Connell, 1987). It is probable that physical changes in the habitat associated with frond length also contributed to greater surface area for attachment, as well as influencing predation pressure (Kelaher & Levinton, 2003).

The amount of sediment among algal turf fronds and other mat-like habitats has been shown to be a strong determinant of molluscan community structure (Gibbons, 1988; Kelaher *et al.*, 2001). Sediment increases habitat heterogeneity in this system by providing opportunities for infaunal species, which added to the frond dwelling species substantially increases overall diversity and abundance (Gibbons, 1988). Contrary to past work, sediment appeared to have little influence on molluscan community structure in coralline turf from Argentina. One possible explanation for the lack of a sediment effect was the small abundances of microgastropods relative to mussels. Compared to small snails, mussels have reduced ability to select

Table 3. Correlation coefficients from BIO-ENV analyses to test for relationships between the molluscan assemblages and habitat variables ($n = 96$ replicate cores).

	R	*P*
Single variables		
Front Density (FD)	0.25	**< 0.001**
Frond Length (FL)	0.12	**0.004**
Epiphytes (EP)	0.03	>0.200
Sediment (SM)	−0.04	>0.200
Best combinations	4	
FD+EP	0.26	**< 0.001**
FD+EP+FL	0.26	**< 0.001**
FD+EP+FL+SM	0.24	**< 0.001**

For brevity, only the best combinations are presented for any given number of variables. The significance of each coefficient is tested with Mantel's test and those that are significant after correction for multiple comparisons are indicated in bold.

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Table 4. Partial correlation coefficients from multiple regressions to test for relationships between the molluscan assemblages and habitat variables ($n = 96$ replicate cores).

	(a) Species richness		(b) Total abundance		(c) Evenness	
	r_p	P	r_p	P	r_p	P
Frond density	−0.06	0.550	0.27	0.009	−0.36	**< 0.001**
Frond length	0.19	0.064	0.30	**0.003**	0.03	0.793
Sediment	−0.21	0.046	−0.23	0.025	−0.18	0.078
Epiphytes	−0.03	0.741	−0.28	**0.005**	0.20	0.058

Tests that are significant after correction for multiple comparisons are indicated in bold.

their microhabitat after settlement. Rather than moving to a preferred habitat with either small or large amounts of sediment, these dominant species must simply persist in coralline turf irrespective of local sediment dynamics. In contrast, microgastropods in coralline turf on Australian shores number tens of thousands per square-metre with relatively small abundance of mussels (Kelaher, 2003). Numerically-dominant microgastropods in Australian coralline turf respond quickly to changes in sediment availability by selecting the most preferable microhabitat, thereby quickly altering molluscan community structure (Olabarria, Underwood & Chapman, 2002).

Relative to other scales, variance components demonstrated that there was little variability in the diversity and abundance of molluscs in coralline turf at the scales of tens of metres. This contrasts with molluscan communities living in algal turf on rocky shores from other parts of the world that consistently show significant variation at this scale (Kelaher *et al*., 2004; Fraschetti *et al*., 2005). Although several processes can cause variation at scales of tens of metres, differences in recruitment, colonization, water flow and sedimentation have all been considered extremely important determinants of interpatch differences in turf assemblages separated by tens of metres (Davenport *et al*., 1999; Kelaher *et al*., 2001). The lack of variation in Argentinean molluscan assemblages indicate either the reduced role of these processes in determining molluscan turf communities or that these processes act fairly consistently within each shore.

Multivariate and univariate analyses highlighted significant variation in molluscan assemblage structure at the scale of shores separated by hundreds of kilometres. There are several environmental variables that may cause these patterns, such as latitudinal gradients in temperature, coastal topography, rock type, wave exposure or oceanographic conditions. However, there was no evidence for strong latitudinal gradients and difference in molluscan assemblages among shores did not seem to correspond to either coastal topography, rock type or wave exposure. Because mussels were major contributors to variation of scale, mesoscale recruitment patterns may play an important role in the development of molluscan assemblages. Mesoscale oceanographic features have a major influence on mussel recruitment at the scales of hundreds of kilometres on the coast of Chile (Broitman *et al*., 2001). It is possible that similar mechanisms may be driving community dynamics on the Argentinean coast.

The composition and diversity of molluscan assemblages in coralline turfs from the coast of Argentinean Patagonia were remarkably similar to those reported by Kelaher, Castilla & Prado (in press) for Central Chile and the mean number of species per core along the two coasts was identical (Table 5). Molluscan assemblages in turf from each coast were dominated by mussels, especially *P. purpuratus*, and the total diversity and abundance of gastropods was relatively low. Although the total numbers of species found was slightly higher in Argentina (38) compared to central Chile (30), this difference is almost certainly a function of fewer shores and cores sampled from Chile. In general, there appears to be a trends of greater molluscan richness in coralline turfs in countries sharing a Gondwanan heritage (Argentina, Chile, Australia and New Zealand, Table 5), relative to those previously sampled in the northern hemisphere, although some consideration needs to be given to different sampling methodologies. Recent work has, however, uncovered high molluscan diversity in coralline turf in Southern California (Tonya Huff, personal communication.) In terms of the molluscan taxa found in coralline turf of Gondwanan countries, there were many similarities at the genus level. The major difference between the Australasian countries and those of South America was the diversity of microgastropods, which was substantially higher in Australia and New Zealand. There are several suspected reasons for the hub of microgastropod diversity in Australia relative to other coasts with Gondwanan origins. Firstly, the Australian continent was isolated for a significant period after separation from the Antarctic plate *ca* 40 Mya, allowing speciation of gastropod species with Gondwanan heritage. After this separation, the Australian continent began a northward drift through *ca* 20° of latitude (Schmidt & Clark, 2000), which provided significant environmental change and potentially a strong natural selective force for speciation. The eventual collision of Australia and the island arcs *ca* 15 Mya (Müller, Gaina & Clark, 2000) then provided the opportunity for invasions of tropical species into the molluscan fauna. The global distribution of coralline turf and the emerging biogeographical patterns provides an excellent future research direction for an

Table 5. Comparison of molluscan species richness in coralline turf on shores in different parts of the world.

	Shores sampled	Total richness*	Mean richness per core†	Standard error	Number of cores	Reference
Argentina (Southern)	8	37	5.63	0.19	96	Results section
Australia (South-Eastern)	4	85	11.38	0.48	80	Kelaher *et al*., 2001
Chile (Central)	2	30	5.63	0.29	30	Kelaher *et al*., in press
Chile (Northern)	7	34	5.79	0.29	84	Kelaher & Castilla, 2005
Japan	1	22	nd	nd	nd	Akioka *et al*.1999
Ireland (West Coast)	2	24	10.00	0.43	40	Kelaher *et al*., 2004
New Zealand	1	51	nd	nd	nd	Hicks, 1971
Norway	3	27	nd	nd	nd	Dommasnes, 1969
Wales	2	30	nd	nd	nd	Bussell *et al*., in press

nd: no data available because a different sized sample unit used.

*Separation among shores varies substantially from hundreds of kilometres to tens of kilometres.

†To ensure comparability, data presented for means and SE's all come from cores that were 80 mm in diameter (0.005 m^2).

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improved understanding of processes that create and maintain large scale patterns of molluscan biodiversity in marine systems.

Overall, this study supports the growing paradigm about the general importance of processes that generate small scale variation in molluscan communities on rocky shores around the world (Kelaher *et al*., 2004; Fraschetti *et al*., 2005). Although several processes may cause local scale variation, the influence of habitat complexity is consistently shown to be a strong determinant of molluscan community structure in mat-like habitats. While there is generally substantial variation at scales of metres, this work highlights inconsistencies in the relative importance of larger-scale variation in molluscan assemblages in coralline turf on shores from Argentina, Chile, Australia and Ireland. Such unpredictability is likely to be a function of relative differences in the importance of processes operating at meso- and regional scales combined with small differences in effects of local processes magnified over large areas. Resolving the relative contribution of local versus regional scale processes may be the key to understanding patterns of molluscan biodiversity on rocky shores.

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REFERENCES

ANDERSON, M.J. 2001. A new method for non-parametric multivariate analysis of variance in ecology. *Austral Ecology*, **26**: 32–46.

AKIOKA, H., BABA, H., MASAKI, T. & JOHANSEN, W. 1999. Rocky shore turfs dominated by *Corallina* (Corallinales, Rhodophyta) in northern Japan. *Phycological Research*, **47**: 199–206.

BRAY, J.R. & CURTIS, J.T. 1957. An ordination of the upland forest communities of Southern Wisconsin. *Ecological Monographs*, **27**: 325–349.

BROITMAN, B.R., NAVARRETE, S.A., SMITH, F. & GAINES, S.D. 2001. Geographic variation of southeastern Pacific intertidal communities. *Marine Ecology Progress Series*, **224**: 21–34.

BRUNO, J.F. & BERTNESS, M.D. 2001. Habitat modification and facilitation in benthic marine communities. In: *Marine community ecology* (M.E. Hay, ed.), 201–218. Sinauer Associates Inc., Massachussetts.

BUSSELL, J., LUCAS, I. & SEED, R. 2007. Patterns in the invertebrate assemblage associated with *Corallina officinalis* in tide pools. *Journal of the Marine Biological Association of the United Kingdom*, **87**: 383–388.

CASTILLA, J.C. & DEFEO, O. 2001. Latin American benthic shellfisheries: emphasis on co-management and experimental practices. *Reviews in Fish Biology and Fisheries*, **11**: 1–30.

CERDA, M. & CASTILLA, J.C. 2001. Diversity and biomass of macroinvertebrates in intertidal matrices of the tunicate *Pyura praeputialis* (Heller, 1878) in the Bay of Antofagasta, Chile. *Revista Chilena de Historia Natural*, **74**: 841–853.

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.

COULL, B.C. & WELLS, J.B. 1983. Refuges from fish predation: experiments with phytal meiofauna from the New Zealand rocky intertidal. *Ecology*, **64**: 1599–1609.

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.

DEAN, R.L. & CONNELL, J.H. 1987. Marine invertebrates in an algal succession. III. Mechanisms linking habitat complexity with diversity. *Journal of Experimental Marine Biology and Ecology*, **107**: 249–273.

DOMMASNES, A. 1969. On the fauna of *Corallina officinalis* L. in western Norway. *Sarsia*, **38**: 71–86.

DYE, A.H. 1992. Experimental studies of succession and stability in rocky intertidal communities subject to artisanal shellfish gathering. *Netherlands Journal of Sea Research*, **30**: 209–217.

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.

FRASCHETTI, S., TERLIZZI, A. & BENEDETTI-CECCHI, L. 2005. Patterns of distribution of marine assemblages from rocky shores: evidence of relevant scales of variation. *Marine Ecology Progress Series*, **296**: 13–29.

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.

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.

HAY, M.E., DUFFY, J.E. & PFISTER, C.A. 1987. Chemical defense against different marine herbivores: are amphipods insect equivalents. *Ecology*, **68**: 1567–1580.

HICKS, G. 1971. Check list and ecological notes on the fauna associated with some littoral corallinacean algae. *Bulletin of Natural Sciences*, **2**: 47–58.

HOFFMAN, J.A.J., NUNEZ, M.N. & PICCOLO, M.C. 1997. Características climáticas del Océano Atlántico Sudoccidental. In: *El mar argentino y sus recursos pesqueros*, Vol. 1 (E. Boschi, ed.), **1**: 163–193. Instituto Nacional de Investigación y Desarrollo Pesquero (INIDEP), Mar del Plata, Argentina.

HOLM, S. 1979. A simple sequentially rejective multiple test proceedure. *Scandinavian Journal of Statistics*, **6**: 65–70.

JONES, C.G., LAWTON, J.H. & SHACHAK, M. 1994. Organisms as ecosystem engineers. *Oikos*, **69**: 373–386.

JONES, C.G., LAWTON, J.H. & SHACHAK, M. 1997. Positive and negative effects of organisms as physical ecosystem engineers. *Ecology*, **78**: 1946–1957.

KELAHER, B.P. 2003. Changes in habitat complexity negatively affect diverse gastropod assemblages in coralline algal turf. *Oecologia*, **135**: 431–441.

KELAHER, B.P. & CASTILLA, J.C. 2005. Habitat characteristics influence macrofaunal communities in coralline turf more than mesoscale coastal upwelling on the coast of Northern Chile. *Estuarine Coastal and Shelf Science*, **63**: 155–165.

KELAHER, B., CASTILLA, J. & PRADO, L. 2007. In there redundancy in bioengineering for molluscan assemblages on the rocky shores of Central Chile? *Revista Chilena de Historia Natural*, (in press).

KELAHER, B.P., CASTILLA, J.C. & SEED, R.S. 2004. Intercontinental test of generality for spatial patterns among diverse molluscan assemblages in coralline algal turf. *Marine Ecology Progress Series*, **271**: 221–231.

KELAHER, B.P., CHAPMAN, M.G. & UNDERWOOD, A.J. 2001. Spatial patterns of diverse macrofaunal assemblages in coralline turf and their associations with environmental variables. *Journal of the Marine Biological Association of the United Kingdom*, **81**: 917–930.

KELAHER, B.P. & LEVINTON, J.S. 2003. Variation in detrital enrichment causes spatio-temporal variation in soft-sediment assemblages. *Marine Ecology Progress Series*, **261**: 85–97.

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McCOY, E.D. & BELL, S.S. 1991. Habitat structure: the evolution and diversification of a complex topic. In: *Habitat structure: the physical arrangement of objects in space* (H.R. Mushinsky, ed.), 1–27. Chapman and Hall, London.

MANTEL, N. 1967. The detection of disease clustering and a generalized regression approach. *Cancer Research*, **27**: 209–220.

MONTEIRO, S.M., CHAPMAN, M.G. & UNDERWOOD, A.J. 2002. Patches of the ascidian *Pyura stolonifera* (Heller, 1878): structure of habitat and associated intertidal assemblages. *Journal of Experimental Marine Biology and Ecology*, **270**: 171–189.

MÜLLER, R.D., GAINA, C. & CLARK, S. 2000. Seafloor spreading around Australia. In: *Billion-year history of Australia and its neighbours in Gondwanaland* (J.J. Veevers, ed.), 18–28. Geomoc Press, Sydney.

NETER, J., KUTNER, M.H., NACHTSHEIM, C.J. & WASSERMAN, W. 1996. *Applied linear statistical models*. McGraw-Hill/Irwin, Chicago.

OLABARRIA, C. & CHAPMAN, M.G. 2001. Comparison of patterns of spatial variation of microgastropods between two contrasting intertidal habitats. *Marine Ecology Progress Series*, **220**: 201–211.

OLABARRIA, C., UNDERWOOD, A.J. & CHAPMAN, M.G. 2002. Appropriate experimental design to evaluate preferences for micro-habitat: an example of preferences by species of microgastropods. *Oecologia*, **132**: 159–166.

PIELOU, E.C. 1975. *Ecological diversity*. Wiley, New York.

PRADO, L. & CASTILLA, J.C. 2006. The bioengineer *Perumytilus purpuratus* (Mollusca: Bivalvia) in central Chile: biodiversity, habitat structural complexity and environmental heterogeneity. *Journal Marine Biological Association of the United Kingdom*, **86**: 417–421.

QUINN, G.P. & KEOUGH, M.J. 2002. *Experimental design and analysis for biologists*. Cambridge University Press, Cambridge.

ROBINSON, D.L. 1987. Estimation and use of variance components. *Statistician*, **36**: 3–14.

SCHMIDT, P.W. & CLARK, D.A. 2000. Paleomagnetism, apparent polar-wander path, and paleolatitude. In: *Billion-year history of Australia and its neighbours in Gondwanaland* (J.J. Veevers, ed.), 12–17. Geomoc Press, Sydney.

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.

SUCHANEK, T.H. 1985. Mussels and their role in structuring rocky shore communities. In: *The ecology of rocky coasts* (R. Seed, ed.), 70–96. Hodder and Stoughton, London.

THIEL, M. & ULLRICH, N. 2002. Hard rock versus soft bottom: the fauna associated with intertidal mussel beds on hard bottoms along the coast of Chile, and considerations on the functional role of mussel beds. *Helgoland Marine Research*, **56**: 21–30.

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.

UNDERWOOD, A.J. & CHAPMAN, M.G. 1996. Scales of spatial patterns of distribution of intertidal invertebrates. *Oecologia*, **107**: 212–224.

YOUNG, C.M. 1990. Larval ecology of marine invertebrates: a sesquicentennial history. *Ophelia*, **32**: 1–48.

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