

# Rocky intertidal community structure in oceanic islands: scales of spatial variability

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**ABSTRACT:** There is a clear bias in the literature on island ecology towards terrestrial rather than marine systems, which have remained comparatively poorly studied. Marine populations are typically open, and local production may have little impact on local recruitment, such that long-distance dispersal is an important determinant of population ecology. Since oceanic islands form discrete patches of habitat surrounded by a structurally different environment, we tested the general hypothesis that processes operating at the scale of islands have a greater influence on these populations than the processes operating at smaller, intra-island scales. A hierarchical design examined the patterns of abundance and distribution of conspicuous taxa at 3 tidal heights at a range of spatial scales, ranging from a few meters to hundreds of kilometres apart in the rocky intertidal of the Azores. Both uni- and multivariate analyses showed that at the largest scale (islands), significant variation was detected in the lower and mid-shore communities, but not on the upper shore. Along the vertical gradient of immersion there was a trend for increasing small-scale patchiness towards the top of the shore. The potential role of local environmental stress gradients and broad-scale oceanographic patterns of recruitment in structuring these assemblages is discussed. This study corroborates the suitability of the analytical tools used here to examine patterns of distribution over a range of spatial scales and its applicability in the field of island marine ecology.

**KEY WORDS:** Hierarchical analysis · Variance component · Spatial scale · Community structure · Rocky intertidal · Fragmented habitats · Oceanic island · Azores · Assemblage biogeography

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## INTRODUCTION

Ecological systems are naturally complex and inherently variable, and there is an increasing appreciation that more knowledge about this variability is crucial to understanding the ecological processes structuring these systems. Because different ecological processes generate variability at different scales, examination of patterns across a range of spatial scales is a fundamental step before explanatory models for these patterns can be proposed (Underwood & Chapman 1996, Hewitt et al. 2007). The development of analytical approaches, such as hierarchical designs and estimates of

variance components, allow variability to be examined at a range of spatial scales, from very small variability at the scale of the sampling unit, to large geographic comparisons (Underwood 1997).

Rocky intertidal communities have been extensively studied and have proved to be tractable systems for experimental ecology, contributing much to our general understanding of population and community ecology. There is an extensive literature on most aspects of assemblage structure, including manipulative experiments to test models of competition (e.g. Connell 1961), predation or herbivory (e.g. Paine 1974, Coleman et al. 2006). More complex designs have tested

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models on the interplay between physical and biological factors (e.g. Thompson et al. 2004). Furthermore, there has been considerable analysis of spatial and temporal scales of variability of intertidal populations over the last decade (Underwood & Chapman 1996, Benedetti-Cecchi 2001, see Fraschetti et al. 2005 for review).

Habitat loss and fragmentation are among the principal factors leading to biodiversity loss (Pimm & Raven 2000), prompting considerable research on the study of habitat patchiness. Archipelagos form highly fragmented habitats surrounded by a structurally different system and are useful to test ecological hypotheses that can be of relevance to a range of other patchy habitats, including marine protected areas, seamounts, and freshwater lakes. In recent years, island ecology has been dominated by island biogeography theory based on MacArthur & Wilson (1967), which posits that the number of species on islands results from the balance between immigration and extinctions—the former influenced by the distance from the mainland and the latter by the effect of island area acting on population size. Thus, a common approach has been to count the number of species on islands of differing sizes and relate these patterns of species richness to the geographical or physical attributes of islands (Báldi & McCollin 2003). However, the model of island biogeography has been fraught with difficulties owing to the accumulation of contradictory results and the study of island ecology has more recently embraced a meta-population approach (Lomolino 2000, Báldi & McCollin 2003). Although the importance of carrying out work over a greater range of spatial scales in the study of islands has been stressed (e.g. Whittaker 2000), such studies have remained scarce; the literature on marine island ecology has lagged behind that on terrestrial ecosystems (but see Tuya & Haroun 2006, Cornell et al. 2007).

A suite of analytical procedures is now available to ecologists that allows us to examine patterns of distribution at a range of spatial (or temporal) scales not previously possible. The few studies that have applied these methodologies to marine island ecology (e.g. Ramírez et al. 2005, Tuya & Haroun 2006) have provided valuable insights into the processes shaping these populations. Hence one of the principal objectives of this study was to identify the relevant scales of variation in order to help focus our attention on the physical and biological factors that most probably influence these systems.

In addition, oceanic islands form patches of habitat surrounded by a struc-

turally different oceanic environment. In such open systems larval retention is probably low and local production may have little impact on local recruitment (Hughes et al. 1999, Swearer et al. 1999). Since the majority of intertidal animals and plants have at least a short planktonic phase during their life-cycle, and because the capability to disperse over long distances is a strong determinant of the biogeography of sessile marine organisms which vary noticeably among species (Johnson et al. 2001), it has been suggested that the processes operating at larger scales may play a key factor in the population biology and in structuring marine island communities. Thus, as a second objective of this study, we examined the proposition that regional-scale processes are central in structuring marine island communities and that this will be detected by greater inter-island variability (i.e. among different islands) rather than intra-island variability (i.e. at the scale of shores or sites; see 'Materials and methods').

## MATERIALS AND METHODS

**Study site and community.** The present study was done in the Azorean archipelago, which comprises 9 volcanic islands and several small islets organised into 3 separate groups (eastern, central and western), and is located between 37 to 40°N and 25 to 31°W (Fig. 1). The islands are surrounded by deep water (~1000 m) and the coastline presents a convoluted topography with high and steep cliffs alternating with rocky beaches (Morton et al. 1998). Shores are exposed to medium and high levels of wave action with sheltered areas restricted to harbours.

Tidal range in the archipelago never exceeds 2 m above Chart Datum (CD) although some intertidal organisms such as chthamalid barnacles and littorinids

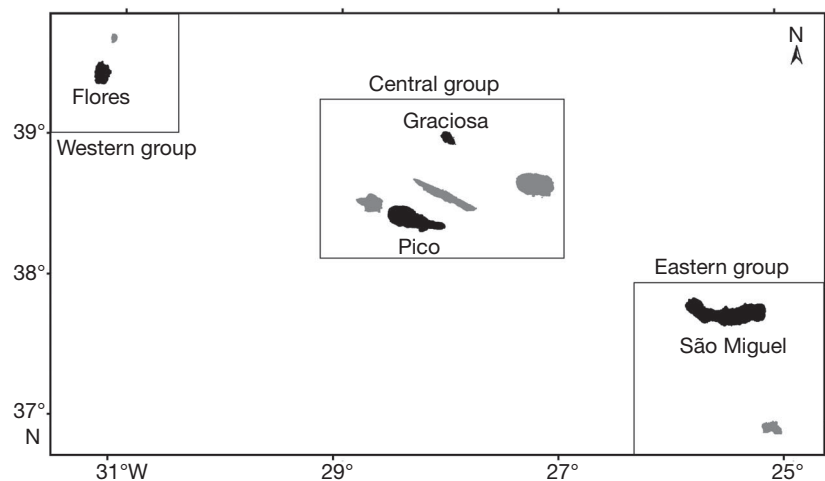


Fig. 1. Azores archipelago; 4 surveyed islands shown in black

can extend their vertical distribution far above this level due to frequent swell and wave splash. The present study was carried out at 3 shore heights corresponding to distinct communities: low shore algal-dominated levels ( $1.20 \pm 0.10$  m above CD), mid shore levels ( $1.90 \pm 0.10$  m above CD) at the boundary between the turf-forming algae and barnacle/rock cover, and upper-shore animal-dominated levels ( $2.50 \pm 0.10$  m above CD) towards the upper limit of limpets and barnacles. Heights were determined in relation to low water using levelling poles. The most abundant organisms throughout the archipelago were turf-forming algae lower on the shore and the chthamaliid barnacle *Chthamalus stellatus* higher up. Among patellid limpets, *Patella candei* was the most common grazer at mid-shore levels, whereas *P. aspera* was also present on the low shore. *Fucus spiralis* formed scattered clumps at mid-shore levels, while *Sargassum* spp. and *Cystoseira* spp. were commonly found in rock pools. Upper-shore grazers included the littorinids *Littorina striata* and *Melarhapha neritoides*. Mussels, a dominant space occupier on most temperate rocky shores, were absent, while canopy algae, which are an important habitat modifier on many shores worldwide, were rare.

**Sampling design.** A hierarchical design was adopted to examine patterns of species distribution at 4 islands separated by 120 to 515 km. Islands were randomly selected but stratified to encompass at least one island per group (western, central and eastern) and hence cover the whole archipelago (Fig. 1).

Within each island, we selected 3 exposed locations (located several kilometres apart) at random. Within each location, 3 sites (at least 20 m apart) comprising a stretch of coast of 20 m were randomly selected and 5 replicate quadrats (a few metres apart) of  $25 \times 25$  cm randomly placed on well-drained rock were used at each tidal level at each site. Digital photography was used to rapidly assess assemblage structure and hence allow for a high level of geographical coverage and replication. Photographs were analysed by overlaying 50 random points and recording the organisms beneath. The lack of abundant erect algae allowed this approach to accurately determine percentage cover of major space occupiers. The abundance of coralline turf (e.g. *Corallina elongata*, *Jania* spp.), coarsely branched algae (e.g. *Gelidium* spp., *Callithamnion* spp., *Osmundea* spp.), foliose algae *Ulva* spp., canopy-forming algae *Fucus spiralis* and the barnacle *Chthamalus stellatus* were expressed as percentage cover. Mobile invertebrates such as gastropods were counted and expressed as number per quadrat. Organisms that were scarce at the levels examined (e.g. encrusting and erect corallines *Melarhapha neritoides*) or difficult to identify against a black basaltic background (e.g. the encrusting alga *Ralfsia* spp.) were not analysed.

**Data analysis. Univariate analysis:** To examine patterns of spatial variation we used a 3-way fully nested ANOVA for each tidal height. Factors were island (random, 4 levels), shore (random, 3 levels) and site (random, 3 levels) with 5 replicates. Cochran's test was used to check homogeneity of variances and transformations applied where necessary (Underwood 1997). Occasionally, heterogeneity of variances persisted after transformation. In these cases, analysis was done on untransformed data, since ANOVA is robust to departures from this assumption where replication is high (Underwood 1997). However, a more conservative p-value ( $<0.01$ ) was used.

MS estimates were used to assess the variation associated with each scale. This was done by dividing the difference between the MS of the term of interest and the MS of the term hierarchically below by the product of the levels of all terms below that of interest. Negative estimates of variation were removed from the analysis and all the other values were recalculated following the procedure described by Fletcher & Underwood (2002). Estimates of spatial variation were reported as actual variances to guarantee independence and allow comparisons with other habitats, but also as percentages to ascertain the magnitude of each scale's contribution to patterns of distribution.

**Multivariate analysis:** To examine patterns of assemblage structure at different spatial scales, the same general procedure as described for the univariate analysis was applied, but using a distance-based multivariable analysis of variance (PERMANOVA, Anderson 2001). The multivariate pseudo-variance components can be considered as analogues to the univariate ANOVA estimators (M. J. Anderson pers. comm.) and these were used to calculate the components of variation associated with each term in a similar way as described for the univariate analysis. Graphical representation of the centroids for sites used non-metric dimensional scaling (MDS). All multivariate analyses were performed on untransformed data, using Bray-Curtis dissimilarity measures and 999 permutations.

## RESULTS

### Univariate analysis

#### Low shore community

The lower-shore community was dominated by algal turf assemblages mainly composed of coralline (e.g. *Corallina* spp.) and coarsely branched (e.g. *Gelidium* spp.) algae. Macroinvertebrates were scarce and restricted to a few individuals of *Patella aspera*. Three morphological groups of algae were considered for

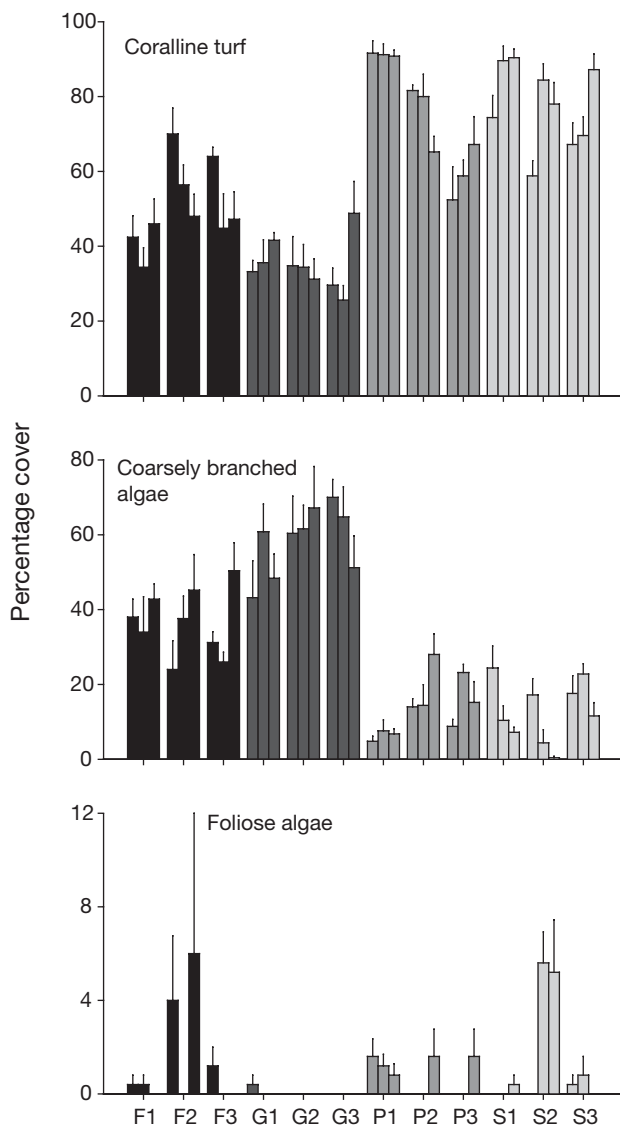


Fig. 2. Low shore mean ( $\pm$ SE) algal cover. Each bar represents one site on each shore. Flores — F1: Fajã grande; F2: Lajedo; F3: Fajãzinha. Graciosa — G1: Porto Afonso; G2: Santa Cruz; G3: Carapacho. Pico — P1: Prainha; P2: Lajes; P3: Santa Cruz. São Miguel — S1: Lagoa; S2: Caloura; S3: Mosteiros

analysis. These differed significantly in their patterns of spatial variability (Fig. 2, Table 1). Coralline turfs and coarsely branched algae showed significant variation at both small and large spatial scales, but for both, the processes generating inter-island variation was responsible for most of the overall variability (Table 2). Mean percentage cover varied among islands from 35 to 78% and from 13 to 59% in coralline turfs and coarsely branched algae, respectively (Fig. 2). In contrast, foliose algae showed no variation at this spatial scale (Table 1) but had high variability at the smaller scale of quadrats (Table 2).

### Mid-shore community

The mid-shore community structure was a mixture of both algae and animals (Figs. 3 & 4). These formed a mosaic structure consisting of algal patches, mainly composed of coarsely branched algae and in few locations of *Fucus spiralis*, interspersed among patches of barnacles and bare space. Limpets were the main grazing gastropods and were found in algal-free patches. Among the algae, 3 morphological groups were relatively abundant but differed significantly in their patterns of distribution (Fig. 3, Table 3). Coarsely branched algae showed no significant variation at either the scale of island or site (Table 3) and most variability was present at the scale of quadrats (Table 2). In contrast, foliose algae and *F. spiralis* showed significant variation at the scale of islands, ranging in cover between 1 and 8%, and 0 and 7%, respectively (Fig. 3, Table 3), but for both, the scales associated with most variation differed. Whilst for foliose algae most of the variation was similarly associated with both the larger (38%) and smaller (45%) spatial scales, for *F. spiralis* the processes operating at the smaller scale of quadrats had much greater influence (86%) on the patterns of distribution (Table 2).

Patterns of spatial distribution differed substantially among invertebrates (Fig. 4). The barnacle *Chthamalus stellatus* showed significant inter-island variation,

Table 1. Three-way fully-nested ANOVA comparing the abundance of lower shore taxa at a hierarchy of spatial scales

Source	df	MS	F	p	MS	F	p	MS	F	p
		Coralline turf			Coarsely branched			Foliose algae		
Island	3	19063.08	13.80	<0.01	21330.63	49.05	<0.001	22.43	0.71	>0.57
Shore (Island)	8	1381.07	3.45	<0.01	434.89	1.31	>0.28	31.71	3.33	<0.02
Site (Island $\times$ Shore)	24	399.76	2.68	<0.001	232.87	1.93	<0.01	9.53	1.08	>0.37
Residual	144	149.04			172.60			8.87		
Transformation		None			None			None		
Cochran's test		C = 0.079 ns			C = 0.098 ns			C = 0.564 p < 0.01		

Table 2. Univariate estimates of variance associated with each scale and respective percentage contribution. Bold values denote contributions >50% of overall variability

	Island		Shore		Site		Quadrat	
<b>Low shore</b>								
Coralline turf	392.93	<b>60</b>	65.42	10	50.14	8	149.04	23
Coarsely branched	464.35	<b>69</b>	6.80	1	32.05	5	172.60	26
Foliose algae	0.00 <sup>a</sup>	0	1.31	13	0.13	1	8.87	<b>86</b>
<b>Mid shore</b>								
Coarsely branched	42.03	7	107.46	18	24.61	4	430.02	<b>71</b>
Foliose algae	11.57	38	4.55	15	0.61	2	13.84	45
<i>Fucus spiralis</i>	9.46	9	0.00 <sup>a</sup>	0	5.94	5	95.40	<b>86</b>
<i>Chthamalus stellatus</i>	55.50	18	20.66	7	38.65	12	199.28	<b>63</b>
<i>Patella aspera</i>	0.01	0	0.00 <sup>a</sup>	0	0.00 <sup>a</sup>	0	1.41	<b>100</b>
<i>Patella candei</i>	2.55	21	1.96	16	0.34	3	7.17	<b>60</b>
<i>Littorina striata</i>	1.71	2	1.61	2	3.37	4	71.67	<b>91</b>
<b>Upper shore</b>								
<i>Chthamalus stellatus</i>	0.00 <sup>a</sup>	0	65.07	22	71.79	24	164.83	<b>55</b>
<i>Littorina striata</i>	10.13	2	63.19	14	85.77	20	277.45	<b>64</b>

<sup>a</sup>Negative values were set to zero following Fletcher & Underwood (2002)

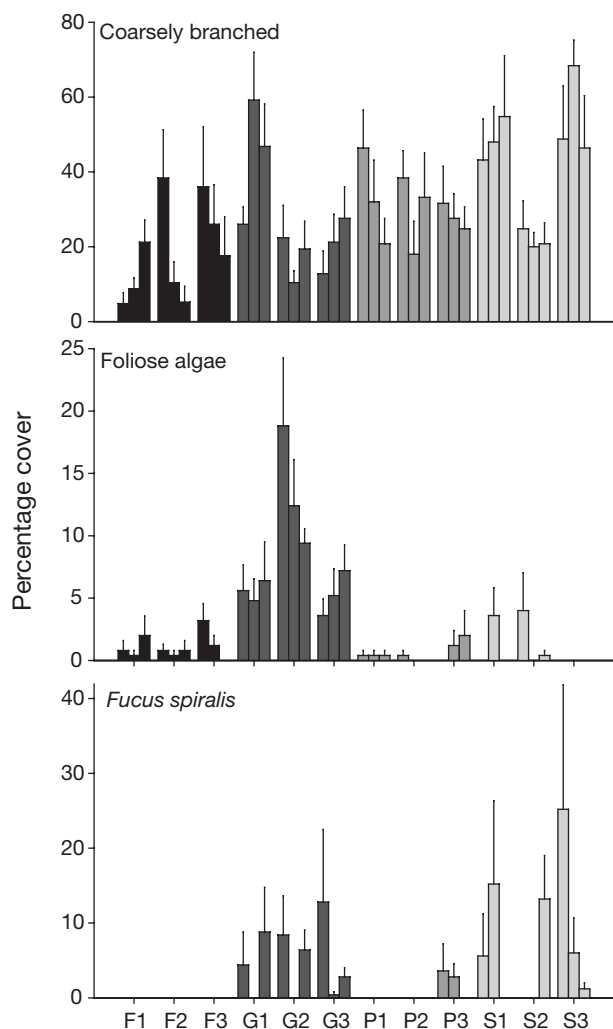


Fig. 3. Mid-shore mean (+SE) algal cover. Legend as in Fig. 2

ranging in mean cover between 16% (São Miguel) and 36% (Flores) (Fig. 4, Table 3). Significant intra-island variation was also detected at the scale of sites. Heterogeneity of variances meant that at a more conservative p-value, there was no significant variation associated with any scale for *Patella aspera* (Table 3). However, patterns of distribution of the conspecific *P. candei* differed among shores (Fig. 4, Table 3). For all mid-shore invertebrates the greatest proportion of spatial variation was associated with the smallest scale of quadrats (Table 2).

#### Upper-shore community

On the animal-dominated upper-shore, erect algae were reduced to a few plants of *Ulva rigida*, but these were mostly restricted to pits or crevices. *Patella candei* was the only limpet found at this tidal height but its abundance was low. We limited our analysis to the 2 most abundant species: *Chthamalus stellatus* and *Littorina striata* (Fig. 5). Both species showed similar patterns of spatial distribution with significant intra-island variation at the scales of shore and site, but not at the scale of islands (Table 4). For both species, a greater proportion of variability was associated with the smaller scale of quadrats, whilst intermediate levels of variation were found at the scales of shore and site (Table 2).

#### Multivariate analysis

Significant variation in the assemblage structure was detected at all spatial scales both on the lower- and mid-shore tidal heights (Fig. 6, Table 5). In contrast, the structure of upper-shore assemblages was similar among the 4 islands examined, although there was significant intra-island variation. Inter-island variability was high lower on the shore but decreased with increasing shore height (Table 6). Residual variation, however, was low at the bottom of the shore and high at both the mid- and upper-shore assemblages.

#### DISCUSSION

The structure of rocky intertidal communities in temperate oceanic islands has received far less attention than that of mainland coastlines. Characterization of spatial (or temporal) scales of variation is a preliminary

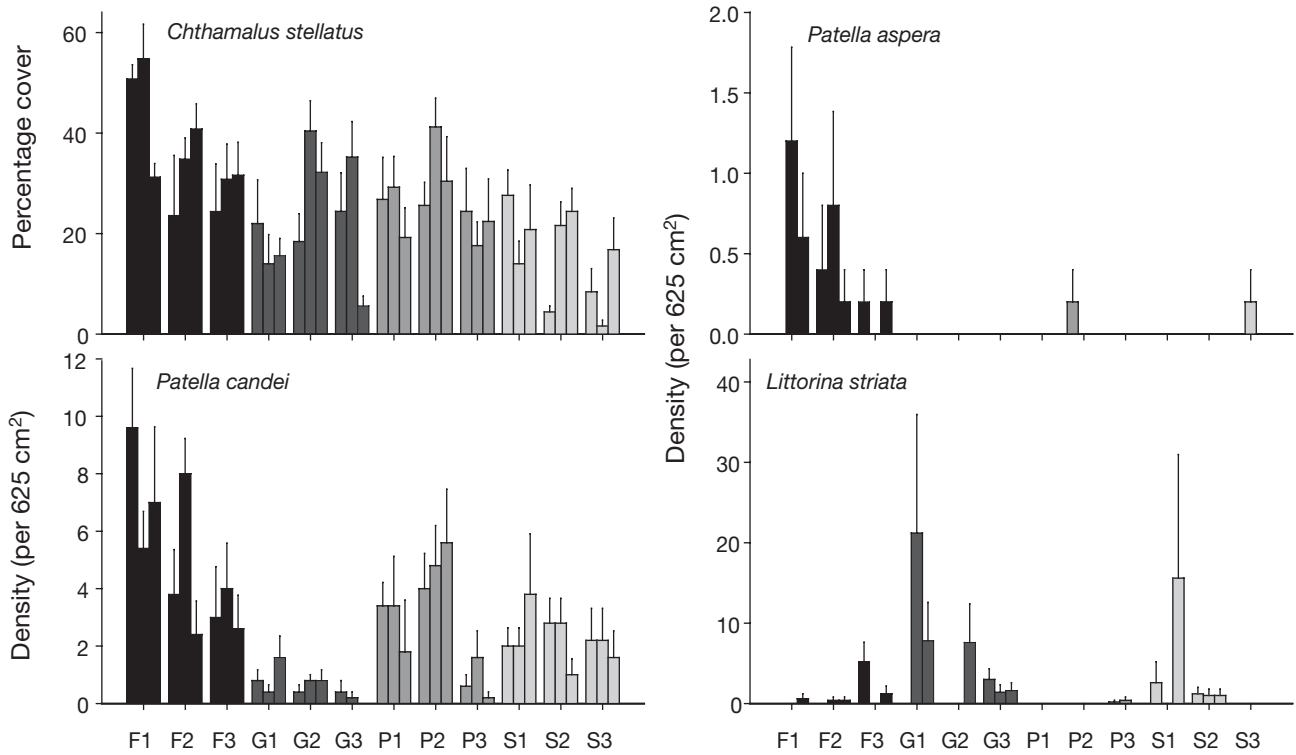


Fig. 4. Mid-shore mean (+SE) animal abundance. Legend as in Fig. 2

Table 3. Three-way fully-nested ANOVA comparing the abundance of mid shore taxa at hierarchy of spatial scales

Source	df	MS	F	p	MS	F	p	MS	F	p	
Coarsely branched											
Island	3	4056.27	1.87	>0.21	27.65	12.88	<0.01	9.53	14.34	<0.01	
Shore (Island)	8	2165.01	3.91	<0.05	2.15	4.09	<0.01	0.66	0.34	>0.94	
Site (Island × Shore)	24	553.07	1.29	>0.18	0.52	1.03	>0.43	1.96	2.39	<0.001	
Residual	144	430.02			0.51			0.82			
Transformation		None				sq rt				ln(x+1)	
Cochran's test		C = 0.085 ns				C = 0.121 ns				C = 0.118 ns	
<i>Chthamalus stellatus</i>											
Island	3	3200.15	4.56	<0.05	1.67	7.35	<0.02	153.07	3.99	>0.05	
Shore (Island)	8	702.45	1.79	>0.12	0.23	1.11	>0.39	38.33	4.33	<0.01	
Site (Island × Shore)	24	392.51	1.97	<0.01	0.21	1.23	>0.22	8.86	1.23	>0.22	
Residual	144	199.28			0.17			7.17			
Transformation		None				None				None	
Cochran's test		C = 0.099 ns				C = 0.283 p < 0.01				C = 0.134 ns	
<i>Patella aspera</i>											
Island	3	189.53	1.68	>0.24							
Shore (Island)	8	112.62	1.27	>0.30							
Site (Island × Shore)	24	88.53	1.23	>0.22							
Residual	144	71.97									
Transformation		None				None				None	
Cochran's test		C = 0.455 p < 0.01				C = 0.455 p < 0.01				C = 0.455 p < 0.01	
<i>Patella candei</i>											
Island	3	189.53	1.68	>0.24							
Shore (Island)	8	112.62	1.27	>0.30							
Site (Island × Shore)	24	88.53	1.23	>0.22							
Residual	144	71.97									
Transformation		None				None				None	
Cochran's test		C = 0.455 p < 0.01				C = 0.455 p < 0.01				C = 0.455 p < 0.01	
<i>Littorina striata</i>											
Island	3	189.53	1.68	>0.24							
Shore (Island)	8	112.62	1.27	>0.30							
Site (Island × Shore)	24	88.53	1.23	>0.22							
Residual	144	71.97									
Transformation		None				None				None	
Cochran's test		C = 0.455 p < 0.01				C = 0.455 p < 0.01				C = 0.455 p < 0.01	

step to experimental testing of hypotheses. Identification of appropriate scales can centre our attention on the most relevant processes (Benedetti-Cecchi 2001), while integrative studies, including manipulative ex-

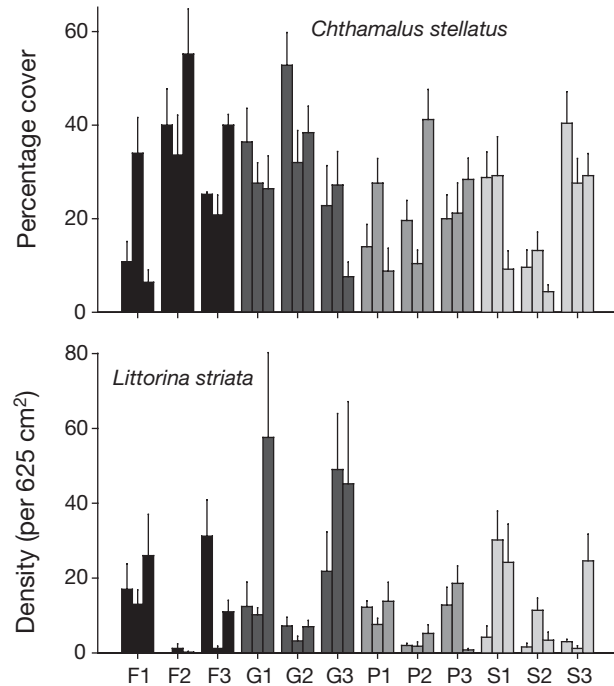


Fig. 5. Upper shore mean (+SE) animal abundance. Legend as in Fig. 2

Table 4. Three-way fully-nested ANOVA comparing the abundance of taxa on the upper shore at a hierarchy of spatial scales

Source	df	MS	F	p	MS	F	p
		<i>Chthamalus stellatus</i>			<i>Littorina striata</i>		
Island	3	1106.19	0.67	>0.59	5.96	0.58	>0.64
Shore (Island)	8	1647.47	3.15	<0.05	10.22	2.97	<0.05
Site (Island × Shore)	24	523.76	3.18	<0.001	3.44	3.77	<0.001
Residual	144	164.83			0.91		
Transformation		None			ln(x+1)		
Cochran's test		C = 0.078 ns			C = 0.114 ns		

Table 5. Three-way fully-nested PERMANOVA comparing the assemblage structure at a hierarchy of spatial scales on each tidal height

Source	df	MS	F	p	MS	F	p	MS	F	p
		Low shore			Mid shore			Upper shore		
Island	3	22805.27	21.48	<0.01	14705.35	4.11	<0.01	4163.49	0.57	>0.77
Shore (Island)	8	1061.77	2.22	<0.05	3576.32	2.03	<0.05	7352.65	2.90	<0.01
Site (Island × Shore)	24	479.12	2.29	<0.01	1766.01	1.69	<0.01	2537.91	2.65	<0.01
Residual	144	209.68			1044.14			959.11		

periments across identified significant scales of variation, are an important means of scaling up from local manipulative experiments (Hewitt et al. 2007). Moreover, partitioning natural variability across a range of spatial scales is useful for comparisons with other studies and habitats, provided that similar scales are used.

Much experimental work has provided evidence of the small-scale processes influencing rocky intertidal populations. For instance, small-scale variation may result from spatial differences in pre-recruitment processes, such as the dispersal of larvae or propagules (Bobadilla & Santelices 2005), from recruitment itself (Coleman 2003), or from post-recruitment processes, such as grazing (Benedetti-Cecchi et al. 2001), competition (Steneck et al. 1991), or mortality (Jenkins et al. 2001) and physical stress mediated by small-scale spatial differences in topographic features of the substratum (Underwood 2004) and disturbances (Sousa 1979). A high level of small-scale variation seems to be an intrinsic feature of most marine habitats, including soft-sediment habitats (Ysebaert & Herman 2002), rock pools (Metaxas & Scheibling 1993), coral reefs (Hughes et al. 1999) or seagrass beds (Piazzi et al. 2004). Whilst many studies on marine systems provide evidence of the pervasive nature of small-scale spatial variability (see Fraschetti et al. 2005 and references therein), few have examined naturally fragmented and isolated habitats such as islands.

Oceanic islands typically form discrete patches of habitat. In such open systems, larvae produced by benthic adults and released to the water column are dispersed away through physical transport and local larval retention may be minimal (Hughes et al. 1999, Swearer et al. 1999). Since recruitment is a key process in structuring marine populations (reviewed by Caley et al. 1996), we suggest that patterns of oceanic current transport will be a key process in structuring island populations. Although the experimental manipulation of large-scale processes is fraught with difficulties, their influence on population dynamics can

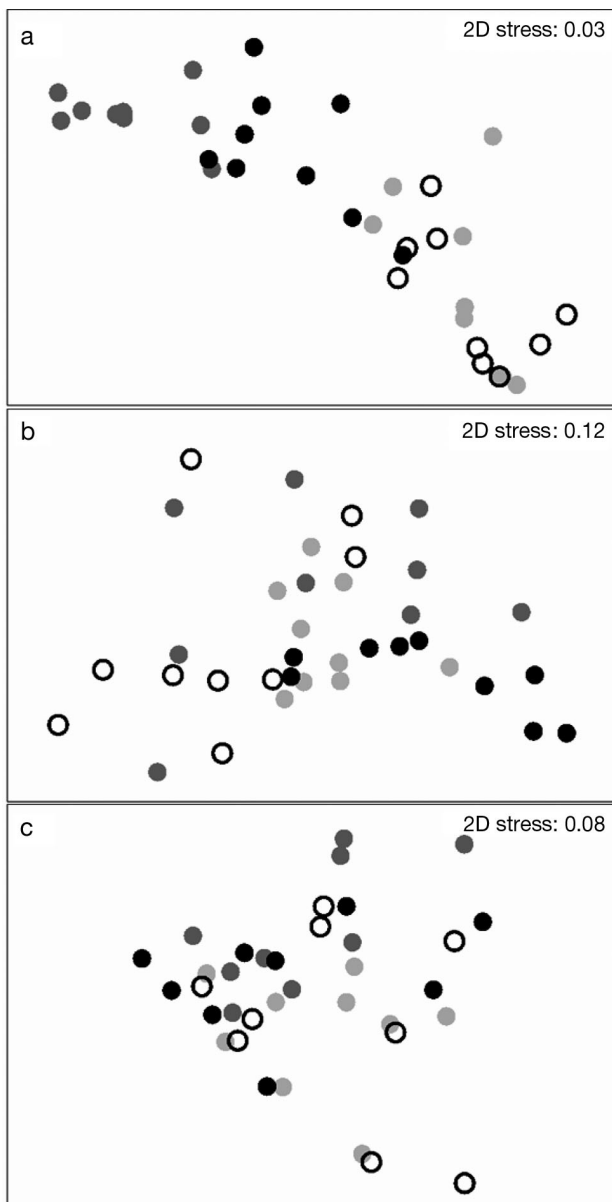


Fig. 6. MDS ordination representing the community structure on the (a) low-, (b) mid-, and (c) upper-shore tidal heights. Each circle represents the centroid for that site. Black: Flores; dark grey: Graciosa; light grey: Pico; white: São Miguel

Table 6. Multivariate estimates of pseudo variance associated with each scale and respective percentage contribution. Bold values denote contributions >50% of overall variability

	Island		Shore		Site		Quadrat	
Low shore	483.19	<b>62</b>	38.84	5	53.89	7	209.68	27
Mid shore	247.31	16	120.69	8	144.37	9	1044.14	<b>67</b>
Upper shore	0.00 <sup>a</sup>	0	262.99	17	315.76	21	959.11	<b>62</b>

<sup>a</sup>Negative values were set to zero following Fletcher & Underwood (2002)

be ascertained by examining the scale at which most variability is associated. For instance, work in the Canary Islands has detected significant inter-island variation in the abundance of several taxa (Ramírez et al. 2005, Tuya & Haroun 2006); this variation has been linked to regional-scale differences in the productivity of coastal waters. This has also been shown in fragmented terrestrial systems, where an important proportion of variation is also commonly detected at the scale of landscapes (Saab 1999).

In this study, there was significant inter-island variation for most taxa in the lower and mid shore but not higher on the shore. Lower-shore algal-dominated communities were mostly influenced by processes operating at the scale of islands. At mid-shore heights, however, despite significant inter-island variation, there was a greater proportion of variability at the scale of the sampling unit, except for foliose algae, which showed similar levels of variability associated with both the smallest and largest scales. Both univariate and multivariate analyses concurred with these patterns, suggesting that along the vertical gradient of emersion, there is a trend for a decreasing influence of larger-scale processes with increasing shore height. This may be the result of differences in the dispersal ability between the lower-shore, algal-dominated assemblages (Bobadilla & Santelices 2005) and the higher-shore, animal-dominated communities (Johnson et al. 2001). However, higher-shore assemblages were notably dominated by the barnacle *Chthamalus stellatus* and the grazing mollusc *Littorina striata*. Both species have planktonic larvae and hence can disperse over large spatial scales. In fact, genetic evidence indicates that, at least for *L. striata*, there is larval exchange among islands (De Wolf et al. 2000). This highlights the potential influence that large-scale processes (e.g. currents) may have on the distribution of these animals and it is, therefore, odd that inter-island variation was not detected in the present study. A more likely explanation could be that the influence of large-scale factors on upper-shore populations was masked by an interaction between the increased

environmental harshness towards the top of the shore, which tends to lead to greater patchiness (Underwood & Chapman 2000), and the reduced time during which these populations are influenced by the marine environment. This pattern was clear in populations of *C. stellatus*, which showed a broad vertical distribution. At the lower limit of its distribution, there was significant variation at the largest and smallest spatial scales. However,



toward the upper limit of distribution, variation significantly increased at the smaller spatial scale.

The rocky intertidal of the Azores is characterised by hard basaltic shores exposed to high wave action with sheltered areas restricted to harbours. Any nutrients that run off from the land are quickly lost in the vastness of the sea and the islands' isolation limits any such influence from the nearest land mass (Morton et al. 1998). In addition, the islands have little latitudinal variation, with similar climate among islands. Thus, the rocky intertidal of the Azores forms a rather uniform habitat with few obvious gradients in the physical environment. Hence, the sources for the large-scale variation in the distribution and numbers of rocky intertidal animals and plants are probably related to the seasonal variation in the intensity and direction of currents, the time that larvae can spend in the water column and their ability to find suitable substratum for colonisation. Examination of the temporal and spatial patterns of settlement and recruitment could greatly benefit our understanding regarding the dynamics of these populations. However, the possibility that other processes could also produce significant variation in the structure of intertidal populations at the larger scale of islands must not be discarded. For instance, there is evidence suggesting that the influence of anthropogenic activities (e.g. fishing) can change the abundance of exploited species among islands (Tuya et al. 2006). In the present study, this could well be the case for patellid limpets, which are known to be harvested at dissimilar levels on different islands (Hawkins et al. 2000).

## CONCLUSIONS

It is clear that variability is an intrinsic feature of oceanic islands. Significant variation was detected at all spatial scales examined, indicating the complexity of insular intertidal systems. As hypothesised, the processes operating at the larger scale of islands played an important role in structuring these populations. This was, however, most pronounced on the lower, algal-dominated communities, suggesting an interaction between the processes affecting the horizontal (e.g. currents, coastal productivity) and vertical (e.g. environmental harshness) patterns of distribution. The pervasive nature of small-scale variability was also confirmed in this study, but this was more pronounced higher in the shore as a result of increased physical stress. This study emphasises the need to use complex analyses to realistically describe patterns of variability. This can be achieved by using an integrative approach involving uni- and multivariate analyses of hierarchical spatial (or temporal) scales of variation and analysis

of associated variance components, and should be applied in a range of ecological studies relevant to the field of island ecology.

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