marine ecology

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Effects of coastal orientation and depth on the distribution of subtidal benthic assemblages

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Abstract

A better understanding of biological systems can only be gained if we understand what processes are important and how they operate to determine the distribution of organisms. Coastal orientation and depth can influence environmental conditions, including the degree of water motion and availability of light, which in turn may influence the horizontal and vertical patterns of organism distribution. Here, we used a mixed-model design to examine the effects of coastal orientation and depth on the structure of benthic assemblages by comparing the abundance and distribution of macroalgae and invertebrates in shallow and deep waters on the opposing coasts of São Miguel. Generally, coastal orientation had little influence on the distribution of most taxa. In contrast, significant differences were generally associated with depth, although patterns were spatially variable at the scale of locations. This study suggests that depth, and processes operating at the scale of location, but not at the scale of the coast, have an important influence on these assemblages, and that failure to recognise such a scale of variability may hamper our ability to better understand the processes that structure these communities.

Introduction

Spatial (or temporal) patterns of organism distribution are naturally heterogeneous (e.g. Underwood 1981; Underwood & Chapman 1996; Menconi et al. 1999) and are the result of complex interactions between biological and environmental processes (e.g. Lubchenco & Menge 1978; Benedetti-Cecchi et al. 2000; Jonsson et al. 2006). Understanding how different processes interact and influence the structure of assemblages is thus a fundamental goal of ecology with both a theoretical and applied interest.

Coastal orientation can determine a number of environmental conditions, which in turn may influence the distribution of organisms. For instance, coastal orientation can determine the degree of exposure to predominant winds and oceanic swells (e.g. leeward versus windward coasts of islands). Wave-action has profound effects on nearly all aspects of an organism's life (Denny 1988), such as recruitment and dislodgment of organisms (e.g. Vadas et al. 1990; Blanchette 1997), supply of food

and nutrients (e.g. McQuaid & Lindsay 2007) and foraging activities of consumers (e.g. Vergés et al. 2009; Taylor & Schiel 2010). A well known example is that presented by Lubchenco & Menge (1978) from along the coast of New England, where wave-action indirectly determines mussel dominance by directly regulating the abundance of its main predators (star-fish and whelks). It is thus not surprising that differences in community structure have been found between the leeward and windward coasts of islands (e.g. Hassett & Boehlert 1999; Tuya & Haroun 2006; Wernberg & Connell 2008).

Differences in community structure between coasts exposed to similar conditions of wave exposure can also arise due to differences in patterns of oceanographic conditions between coasts. For instance, Menge et al. (1999, 2003) showed consistent differences in community structure between coasts in New Zealand and attributed these to differences in species interactions as mediated by the influence of oceanographic conditions (e.g. formation of eddies, upwelling).

Another key factor in subtidal marine ecosystems is depth, which influences the vertical distribution of a number of environmental conditions. For instance, light intensity and water motion decline with increasing depth, affecting the photosynthetic rate and nutrient uptake by macroalgae (see Hurd 2000 for review). Different light compensation points among macroalgae were suggested to influence patterns of vertical distribution of algae and were generally associated with a decreasing complexity in algal structure (canopy, foliose, encrusting) with depth (Markager & Sand-Jensen 1992).

In addition, the amount of light can affect the dominance of algae and invertebrates. Experimental work has shown that sessile invertebrates generally dominate shaded conditions, whereas macroalgae and mobile invertebrates dominate well lit areas (e.g. Glasby 1999; Blockley & Chapman 2006). Thus, it is predicted that macroalgae will dominate shallow-water levels, whereas sessile invertebrates will increase in abundance with increasing depth. In addition, by affecting organism fitness and dominance (e.g. Lin & Carpenter 1997; Muller & Woesik 2009) light intensity can have indirect community-level cascading effects (e.g. Whitcraft & Levin 2007). Thus, there is a vertical gradient in the physical environment that influences the distribution of coastal benthic assemblages (Kautsky & Kautsky 1989; Underwood et al. 1991; Garrabou et al. 2002; Tuya et al. 2007).

However, environmental conditions, such as wave action or depth, cannot fully explain patterns of distribution in marine ecosystems on their own (e.g. Terlizzi et al. 2007) and different processes often interact in structuring biological communities (Benedetti-Cecchi et al. 2000; McQuaid et al. 2000; Saunders & Connell 2001; Ortega-Borges et al. 2009). Here we investigate the spatial distribution of subtidal benthic assemblages of macroalgae and invertebrates by comparing the assemblage structure on six locations distributed along the north and south coasts of São Miguel island. Furthermore, in each location, sampling was done at shallow and deep water levels so that the potential interactive effects of coast and depth can be examined.

Materials and methods

Study sites and community

The study was carried out on subtidal rocky basaltic substrata, where coastal benthic communities in the Azores are dominated by macroalgae. Shallow waters (~5 m) are dominated by encrusting coralline algae, articulated corallines, Dictyota spp. and Halopteris spp. whereas at deeper levels (~30 m), communities are domi-

nated by Zonaria tournefortii and encrusting coralline algae (Wallenstein et al. 2008a,b). At intermediate depths (10–20 m), communities are a mixture of both shallow and deeper water communities (Wallenstein et al. 2008a, b). Invertebrates, although common, rarely occur at high densities. Conspicuous species include sea-urchins (e.g. Arbacia lixula and Sphaerechinus granularis), star-fish (e.g. Marthasterias glacialis, Ophidiaster ophidianus), sessile polychaetes (e.g. Sabella spallanzani), mobile polychaetes (Hermodice carunculata), decapods (e.g. Calcinus tubularis, Percnon gibbesi) and gastropods (e.g. Stramonita haemastoma, Charonia lampas) (Martins et al. 2005).

São Miguel is a relatively long (west–east) but narrow (north–south) island (see Fig. 1A). The entire coast around São Miguel is exposed to oceanic swell and surge, with the few sheltered locations generally restricted to areas within harbours. However, the frequency of winds on the northern coast (windward) is at least twice that on the southern coast (leeward) (Fig. 1). In addition, according to the Global Atlas of Ocean Waves (http://www.sail.msk.ru/atlas/index.htm), oceanic swell and significant wave height is generally greater in areas north of the Azores. Around the Azores, swell direction is predominantly from N/NW, suggesting that locations on the south coast are protected by the landmass experiencing a reduced level of exposure to oceanic swells. The Azores are located in the northern region of the North Atlantic Subtropical Gyre and are influenced by the cold southern branch of the North Atlantic Current to the north and the warm Azores Current to the south (Morton et al. 1998; Bashmachnikov et al. 2004). However, an understanding of the interactions between these oceanic currents and coastal morphology around the Azorean islands is still in its infancy and it is difficult to predict whether these factors result in consistent differences that vary with coastal orientation.

Variation in fetch among sampled locations (Fig. 1B, estimated using the model described by Burrows et al. 2008), which is also known to affect the degree of exposure to wave-action (e.g. Burrows et al. 2008), did not differ between the lee and windward coasts (t-test, P > 0.05, Fig. 1B).

Water clarity, as measured by Secchi disk, varies seasonally, ranging between 11 and 27 m with a mean 15.8 m (SE = 0.5 m, n = 48) (Neto A.I., Brotas V., Azevedo J.M.N., Patarra R.F., Álvaro N.M.V., Gameiro C., Prestes A.C.L., Nogueira E.M. unpublished data).

Sampling design

Three locations were respectively selected both on the north and south coasts of São Miguel (Fig. 1A). All locations were similar in terms of substratum and were
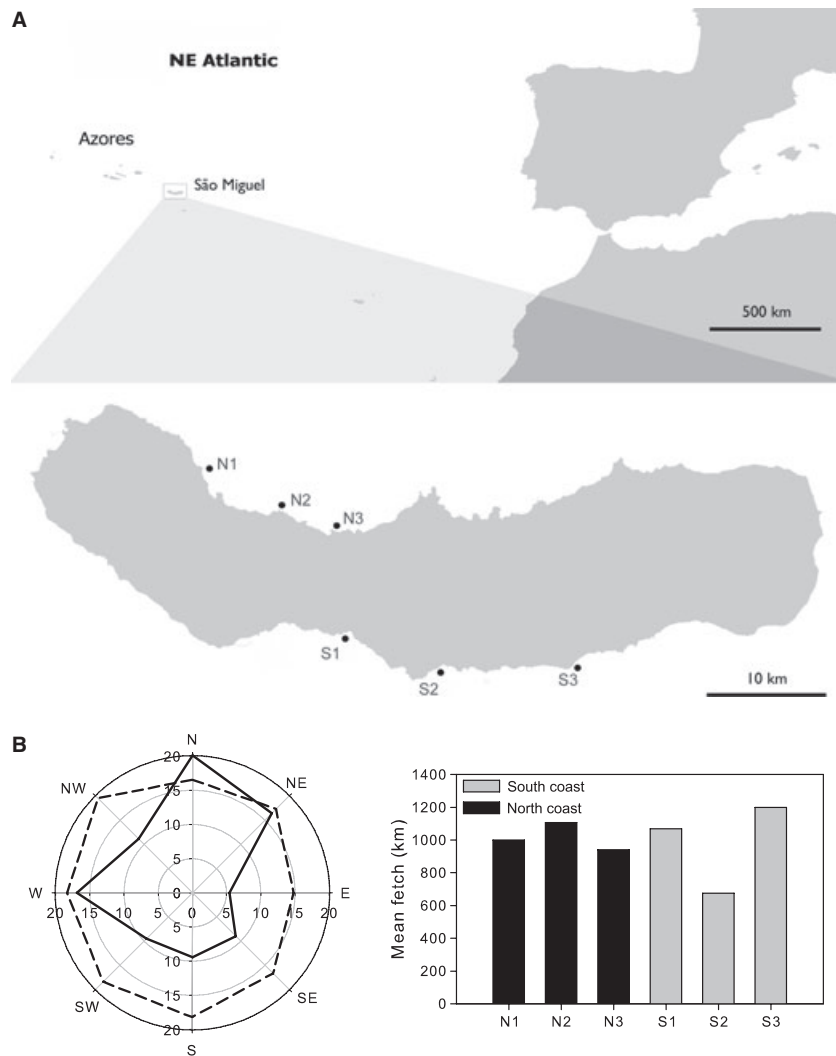
Fig. 1. (A) Map of São Miguel island (Azores) and sampling locations: N1 – Santo Antonio, N2 – Fenais da Luz, N3 – Rabo de Peixe, S1 – Lagoa, S2 – Água d'Alto, S3 – Ponta Garça, and (B) wind frequency (continuous line) and intensity (dashed line) based on data from 1961–1990 (Instituto Metereológico) (on the left) and fetch for each location based on the model of Burrows *et al.* (2008) (on the right).

composed of basalt *sensu latum* with a relative high topographic complexity (convoluted reefs). Sampling was done within areas of gentle sloping substrata (<45°) and avoided large substratum irregularities. At each location, sampling was done at 5 and 25 m depth. Maximum depth was set considering the time necessary for sampling within safety conditions.

At each location and depth, assemblages of animals and plants were identified *in situ* by SCUBA diving. The cover of macroalgae was estimated non-destructively in nine 50 × 50 cm quadrats (0.25 m^2) following the point-intersection method with a grid of 36 points per quadrat. Quadrats were randomly laid in horizontal substrata at least a few meters apart. Algae were identified to the lowest possible taxonomic resolution in the field. Unidentified algae were classified into morphological groups (e.g. filamentous red algae). Final values for each taxon were expressed as percentages.

The abundance of macroinvertebrates was estimated non-destructively in three 15 × 1 m transects (15 m^2). Transects were visually inspected and all conspicuous (>2 –3 cm) invertebrates were counted. The abundance of sessile colonial animals (e.g. sponges) was estimated as the number of colonies. Final values for each taxon were expressed as density (per 15 m^2). Sampling of macroalgae and invertebrates was done separately using quadrats and transects respectively because these have been shown previously to adequately represent these assemblages (Neto 1997; Martins *et al.* 2005).

Data analysis

Hypotheses were tested using univariate and multivariate procedures. For the former, macroalgae were grouped into four morpho-functional groups according to the literature (e.g. Steneck & Dethier 1994; Fowler-Walker &

Table 1. Three-way mixed model ANOVA testing for the effects of coastal orientation (n = north; S = south), depth (De) and location (Lo) on the abundance of macroalgae.

Source	df	Turf		Bush-like		Art. corall.		Encrusting	
		F	P	F	P	F	P	F	P
Depth = De	1	13.45	*	1.75	n.s.	2.67	n.s.	0.90	n.s.
Coast = Co	1	9.23	*	0.92	n.s.	0.06	n.s.	1.60	n.s.
Location(Co) = Lo(Co)	4	8.24	***	38.14	***	16.84	***	51.85	***
De × Co	1	4.41	*	0.00	n.s.	4.14	n.s.	0.79	n.s.
De × Lo(Co)	4	1.07	n.s.[†]	10.47	***	6.16	***	84.32	***
Residual	96								
Transformation		none		none		none		none	
Cochran's		$C = 0.32$	**	$C = 0.32$	**	$C = 0.34$	**	$C = 0.29$	**
SNK		Turf							
		N: 5 m = 25 m							
		S: 5 m > 25 m							
		5 m: N < S							
		25 m: N < S							

[†]Pooled term (P > 0.25, Underwood 1997).
*P < 0.05.
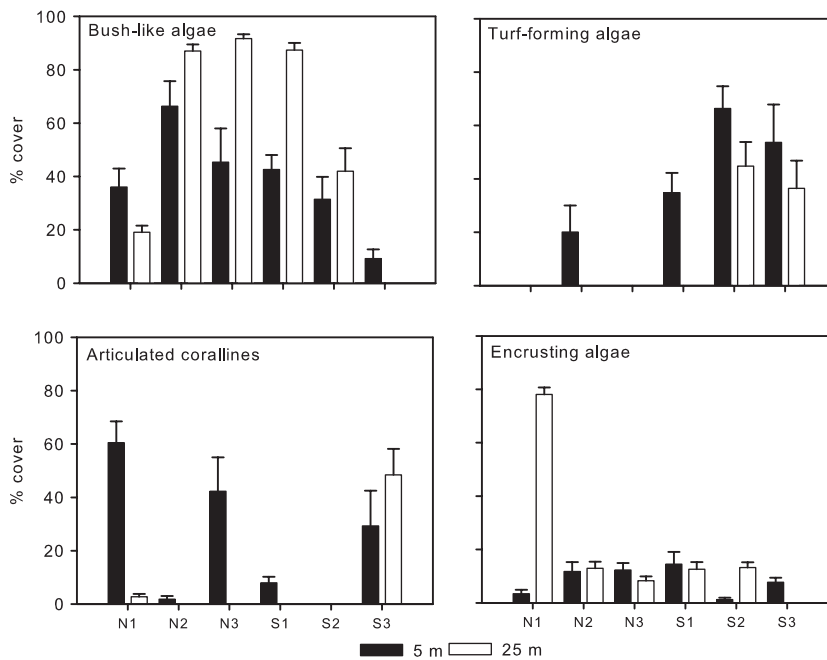**P < 0.01.
***P < 0.001.

Fig. 2. Mean (+SE, n = 9) abundance of macroalgae in relation to coastal orientation and depth. In the *x*-axis, N or S indicates north or south coasts, respectively, whereas the numbers stand for each location.

Connell 2002), especially macroalgae from similar habitats within Macaronesia (Tuya & Haroun 2006). Thus, macroalgae were classified as: turf-forming algae consisting of small cushion-shaped and filamentous algae, generally <5 cm height (e.g. *Codium* spp., *Colpomenia sinuosa*, *Polysiphonia* spp.), bush-like algae consisting of sheet-shaped and thick leathery species with >5 cm height (e.g. *Asparagopsis* spp., *Dictyota* spp., *Halopteris* spp., *Zonaria tournefortii*), articulated coralline algae con-

sisting of erect calcareous algae (e.g. *Corallina elongata*, *Jania* spp.) and encrusting algae (e.g. calcareous and non-calcareous encrusting algae). Invertebrates were also grouped into large morpho-functional groups such as sea-urchins, star-fish, sessile polychaetes and decapods. Because the hypothesis considers patterns of dominant species, univariate analyses of taxa occurring in <10% (e.g. corticated and canopy-forming algae such as *Sargassum* spp.) of the samples were not analysed. For

multivariate analysis, taxa were examined individually (not grouped).

A three-way mixed model analysis of variance (ANOVA) was used with coast (two levels, fixed), depth (two levels, fixed and orthogonal to orientation) and location (three levels, random and nested within north *versus* south). Prior to analysis, data were checked for heteroscedasticity (Cochran's test) and transformations were done where appropriate (Underwood 1997). In some situations, heteroscedasticity persisted after transformations. For these, analyses were performed on untransformed data, as ANOVA is relatively robust to departures from this assumption where replication is high (Underwood 1997). Post-comparisons within significant terms were analysed using the Student–Newman–Keuls (SNK) test.

The response of the assemblage as a whole was examined using multivariate procedures with the same three-way mixed model as described for the ANOVA. Analyses were done using permutational multivariate analysis of variance (PERMANOVA, Anderson 2001) and ordination techniques (non-metric multidimensional scaling, Clarke & Warwick 1994), based on the square root-transformed data and Bray–Curtis dissimilarities.

Results

Univariate analysis

For the macroalgae, a significant interaction between coastal orientation and depth was only found for the turf-forming algae (Table 1). SNK analyses showed that the abundance of turf-forming algae was greater in the leeward coast, where it was more abundant at shallow depths. However, in the windward coast its abundance did not vary with depth (Fig. 2, Table 1). For the remaining algal groups (bush-like, articulated and encrusting algae), there was no difference in abundance

Table 2. Three-way mixed model ANOVA testing for the effects of coastal orientation (N = north; S = south), depth (De) and location (Lo) on the abundance of invertebrates.

Source	df	Ascideans F	P	Decapods F	P	Gastropods F	P	Holothurians F	P	Mob. Polych. F	P
De	1	0.20	n.s.	0.76	n.s.	0.44	n.s.	3.38	n.s.	35.59	**
Co	1	11.86	*	1.39	n.s.	0.44	n.s.	0.01	n.s.	12.81	*
Lo(Co)	4	0.84	n.s.	14.91	***	10.88	***	5.16	**	1.80	n.s.
De × Co	1	0.20	n.s.	0.65	n.s.	1.56	n.s.	2.95	n.s.	12.81	*
De × Lo(Co)	4	3.09	*	5.28	**	10.88	***	3.43	*	1.80	n.s.
Residual	24										
Transformation		$x^{0.1}$		arcsin		none		$x^{0.1}$		none	
Cochran's		$C = 0.25$	n.s.	$C = 0.36$	n.s.	$C = 0.76$	**	$C = 0.29$	n.s.	$C = 0.31$	n.s.
SNK										Mob. Polych	
										N: 5 m = 25 m	
										S: 5 m < 25 m	
										5 m: N = S	
										25 m: N < S	

Source	df	Porifera F	P	Sess. Polych. F	P	Starfish F	P	Urchins F	P
De	1	0.91	n.s.	2.29	n.s.	2.56	n.s.	0.65	n.s.
Co	1	0.05	n.s.	0.16	n.s.	0.30	n.s.	1.02	n.s.
Lo(Co)	4	10.11	***	8.34	***	7.44	***	7.27	***
De × Co	1	0.38	n.s.	1.42	n.s.	0.16	n.s.	1.00	n.s.
De × Lo(Co)	4	7.07	***	10.49	***	1.56	n.s.	10.15	***
Residual	24								
Transformation		arcsin		$\sqrt{(x+1)}$		none		$\sqrt{(x+1)}$	
Cochran's		$C = 0.37$	n.s.	$C = 0.35$	n.s.	$C = 0.25$	n.s.	$C = 0.29$	n.s.

[*]$P < 0.05$.
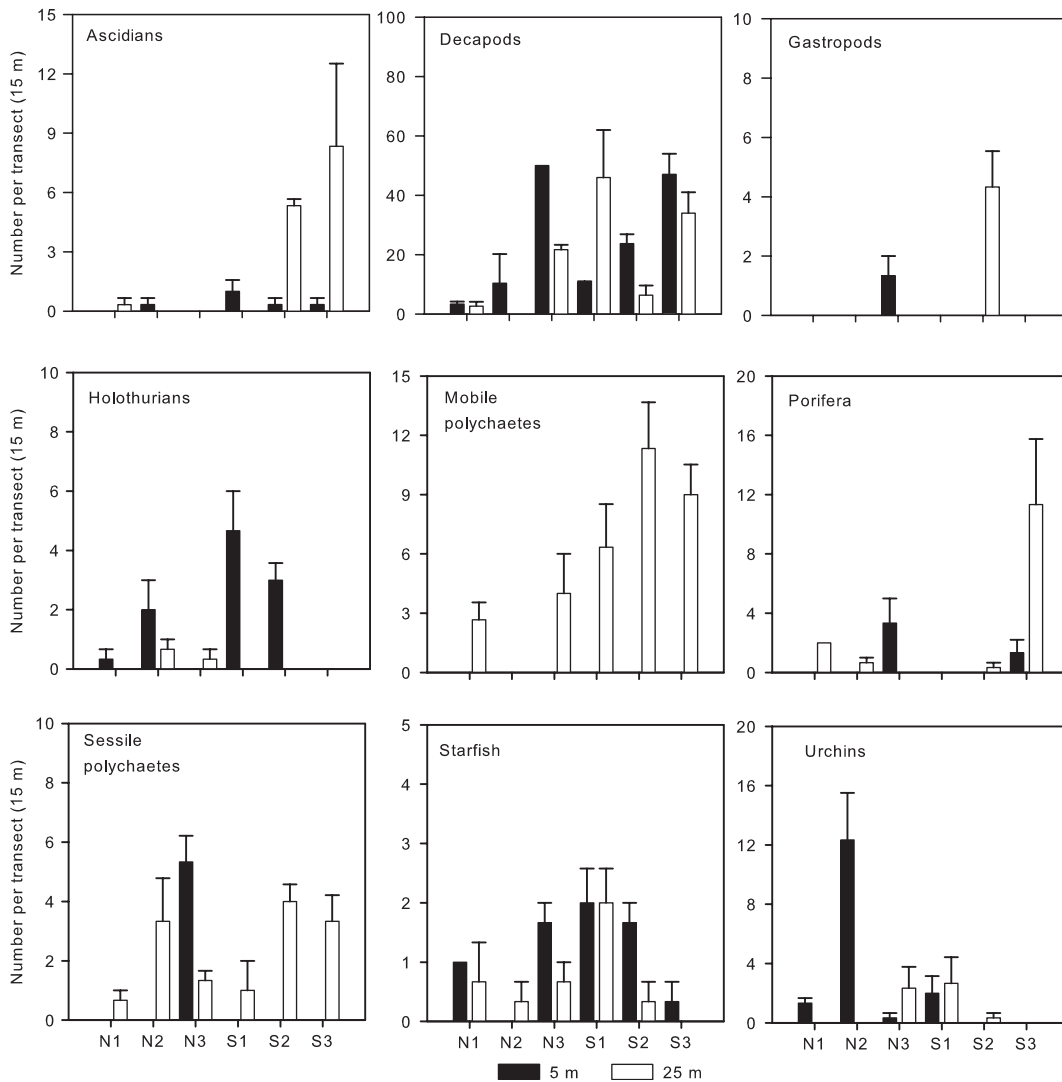[**]$P < 0.01$.
[***]$P < 0.001$.

Fig. 3. Mean (+SE, n = 9) abundance of invertebrates in relation to coastal orientation and depth. Legend as in Fig. 2. Note the different scales of the *y* axes.

between the lee and windward coasts (Fig. 2, Table 1) but there were generally differences in abundance between depths, although these were highly variable among locations (Table 1).

For the invertebrates, a significant interaction between depth and coastal orientation was only found for mobile polychaetes (Table 2). SNK tests showed that the abundance of mobile polychaetes was similar in the lee and windward coasts at shallow waters but greater on the leeward coast of the island at deeper water levels (Fig. 3, Table 2). Ascidia responded consistently to coastal orientation, being significantly more abundant on the leeward coast at shallow and deep levels. For the remaining and large majority of the taxa examined, there were no differences in their numbers in relation to coastal orientation but there were generally differences between depths,

although patterns were, again, not consistent among locations (Fig. 3, Table 2).

Multivariate analysis

For macroalgae, differences in multivariate assemblage structure between island coasts were consistent between depths (De × Co, P > 0.05), although variability from location to location affected differences between depths [De × Lo (Co), P < 0.001] (Fig. 4, Table 3). Inspection of pair-wise comparisons showed that despite variability among locations, there were consistent differences in the structure of assemblages at shallow and deeper levels.

Patterns of assemblage structure for invertebrates were similar to that of macroalgae (Fig. 4, Table 3). Hence, the effects of coastal orientation were consistent
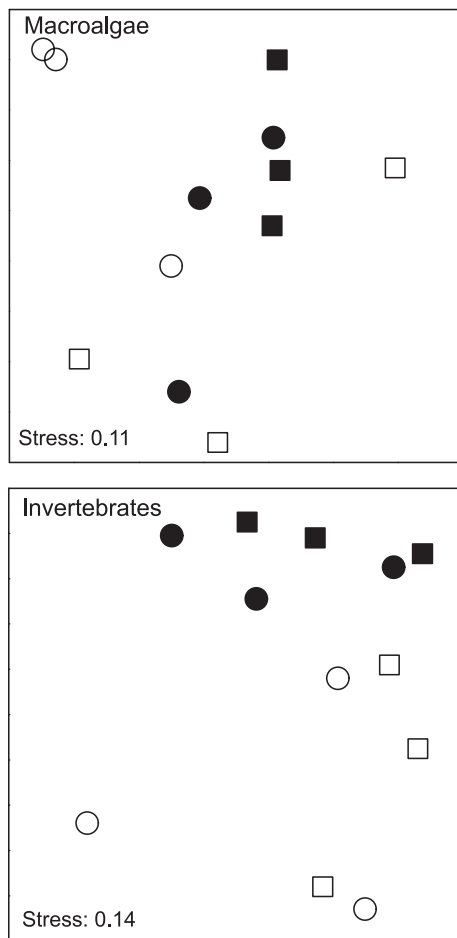
Fig. 4. Non-metrical multidimensional scaling (MDS) representing the assemblage structure of macroalgae (upper plot) and invertebrates (lower plot) according to coastal orientation and depth. For clarity, only the centroids for each location are shown. Open symbols, 25 m; filled symbols, 5 m; squares, southern locations; circles, northern locations.

Table 3. Three-way mixed model multivariate PERMANOVA testing for the effects of coastal orientation (N = north; S = south), depth (De) and locations (Lo) over the structure of macroalgal and invertebrate assemblages. Analyses were done on the square-root transformed data and using Bray–Curtis dissimilarity.

Source	df	Macroalgae F	P	df	Invertebrates F	P	F-ratio
De	1	2.75	n.s.	1	2.63	n.s.	De × Lo (N *vs.* S)
Co	1	1.54	n.s.	1	1.13	n.s.	Lo(N *vs.* S)
Lo(Co)	4	29.91	***	4	10.69	***	Residual
De × Co	1	1.44	n.s.	1	0.64	n.s.	De × Lo (N *vs.* S)
De × Lo(Co)	4	20.33	***	4	8.72	***	Residual
Residual	96			24			

***P < 0.001.

influence on these assemblages. This refutes the anecdotal perception that the northern coast is relatively more exposed to rough sea conditions (well known structuring processes of benthic assemblage; e.g. Lubchenco & Menge 1978; Blockley & Chapman 2006). Such general absence of differences in the distribution of organisms between different coasts of islands is also in contrast to the work done in other insular regions (Menge *et al.* 1999, 2003; Tuya & Haroun 2006). Unlike the Canary Islands, which are influenced by the trade winds, the Azores are located in the transition between the temperate and sub-tropical regions and experience very unstable meteorological conditions. Although winds in São Miguel blow predominantly from the north, it is clear that wind intensity is similar from all directions (see Fig. 1). This may mean that benthic communities in the south are already exposed to high levels of wave action so that the greater frequency of rough seas found in the north is not relevant. These results also suggest that variable patterns of oceanographic conditions (e.g. eddies, upwelling) such as the ones described for other regions (e.g. Menge *et al.* 1999, 2003) do not exist at the scale of the coast.

As expected, and unlike coastal orientation, there were generally differences in the structure of benthic assemblages associated with depth, as had been previously described for the region (Wallenstein *et al.* 2008a,b). However, in 10 of the 13 taxa examined, such differences were highly variable among locations. Variation at this spatial scale is common and has been found in previous studies both intertidally in the Azores (Martins *et al.* 2008) and elsewhere (e.g. Underwood & Chapman 1996; Fraschetti *et al.* 2005). It indicates that processes operating at the scale of the location (kilometers) are important and interact with depth in structuring these assemblages. This was also noted by Terlizzi *et al.* (2007) in the Medi-

among depths (De × Co, P > 0.05), but there was significant spatial variation among depths (De × Lo(Co), P < 0.001) with an overall effect of depth (pair-wise comparisons) affecting the structure of assemblages of invertebrates.

Discussion

Contrary to our predictions of variability associated with coastal orientation, there was generally no interactive effect between coastal orientation and depth. Moreover, most taxa did not respond to differences in coastal orientation at all. In contrast, taxa did generally respond to differences in depth, although patterns were spatially inconsistent. These results indicate that processes operating at the scale of the coast do not play a prominent

terranean; they found that, although there were generally characteristic differences in community structure among different depths, there was also high variability at all the spatial (and temporal) scales examined.

The results highlight that an understanding of the relevant scales of variation is key if we are to design experiments that realistically capture the spatial (and temporal) variation in community structure. Here, in spite of depth, processes operating at the scale of the locations, but not at the scale of the coast, play an important role in structuring subtidal benthic communities. Potentially important differences among locations include the fetch, which determines the degree of protection from coastal wave action (see Fig. 1B). Winds and currents are also deformed by terrestrial masses and the topography of the ocean floor generating small-scale complex patterns in near-shore hydrographic conditions (e.g. Hernández-León 1988; Narváez *et al.* 2004), which can influence the settlement and recruitment of key marine organisms among locations (e.g. Lagos *et al.* 2005, 2008).

An understanding of the scales at which variation in community structure occurs is a key step before explanatory models for these patterns can be made (Underwood & Chapman 1996; Hewitt *et al.* 2007). Further progress in the study of these communities may be hampered by neglecting the intrinsic and pervasive variability in community structure found at the scale of locations.

Acknowledgements

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