

Structure and dynamics of sponge-dominated assemblages on exposed and sheltered temperate reefs

D. E. Roberts^{1,2,3,*}, S. P. Cummins³, A. R. Davis², M. G. Chapman³

¹BIO-ANALYSIS: Marine, Estuarine & Freshwater Ecology, 7 Berrys Head Road, Narara, New South Wales 2250, Australia

²Institute for Conservation Biology, School of Biological Sciences, University of Wollongong, Wollongong, New South Wales 2522, Australia

³Centre for Research on Ecological Impacts of Coastal Cities, Marine Ecology Laboratories A11, University of Sydney, Sydney, New South Wales 2006, Australia

ABSTRACT: There have been few studies on the structure and dynamics of sponge-dominated assemblages, despite the fact that such assemblages are vulnerable to environmental impacts from many anthropogenic disturbances. Sponges are generally slow to recruit, slow growing and long lived; hence, they may be very vulnerable to anthropogenic and natural disturbances. In order to understand how such assemblages may respond to disturbance, it is essential to measure natural patterns of spatial differences and temporal changes, so that any future impact assessments can be identified. This study quantified and contrasted patterns of abundance in sponge-dominated assemblages on deep reefs (18 to 20 m) exposed to direct oceanic swell with reefs in the more protected entrances to large embayments. We examined the hypothesis that erect sponges would dominate the reefs within embayments, while encrusting species would be more prevalent on the wave-exposed reefs. We also predicted that wave-exposed reefs would show greater temporal and spatial variability. Four reefs within embayments and 4 open coastal reefs, each with 3 nested sites, were sampled with randomly placed photo-quadrats. Sponges dominated the reefs we examined, accounting for around 25 % of the cover of the substratum on exposed reefs and usually >40 % on sheltered reefs. A total of 82 species of sponge were identified. As predicted, erect sponges accounted for the majority of the species richness and cover of sponges on sheltered reefs, whereas encrusting species predominated on the exposed reefs. The contribution of other sessile invertebrates to the cover and species richness on these reefs was small. nMDS plots revealed striking and consistent differences in the assemblages between the exposed and sheltered reefs, although PERMANOVA failed to detect significant differences. ANOVA revealed significant fluctuations in the cover and richness of taxa at various spatial and temporal scales. Examination of the components of variation of selected taxa showed that most of the variability was found at the smallest spatial scale, i.e. within the residual, and this variability was generally greatest for taxa on exposed reefs compared with sheltered reefs. These results have important implications for monitoring programmes designed to detect environmental impacts on sponge-dominated assemblages.

KEY WORDS: Porifera · Marine assemblages · Ecological patterns · Wave exposure · Sessile invertebrates · Scales of variation

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INTRODUCTION

Scales of patchiness and variation in assemblages, either in time or space, have become an important focus of many marine ecological studies (Underwood & Chapman 1998a). They have 2 key foci. First, studies that determine the spatial and temporal scales at

which species and assemblages show most variability, allow one to identify the scales at which important ecological processes are likely to be operating (e.g. Archambault & Bourget 1996, Thompson et al. 1996, Underwood & Chapman 1998b, Hewitt et al. 2002) and the scales at which disturbance and recovery of assemblages are likely to be shown (Warwick & Clarke 1993,

*Email: dan@bioanalysis.com.au

Bishop et al. 2002). The second key focus relates to the scales that must be incorporated into sampling strategies needed to identify natural or anthropogenically induced changes to assemblages (Underwood 2000, Stewart-Oaten & Bence 2001).

Previous studies show that many marine assemblages vary at a hierarchy of scales, from centimetres to 100s of kilometres and from days to years (Coleman 2002, Hewitt et al. 2002, Davis et al. 2003). Most of these types of studies have, however, been done in the intertidal or in relatively shallow water, and, consequently, our understanding of the spatial and temporal scales of variability in invertebrate assemblages in deep water is scant and cannot be readily predicted from previous work.

Deeper subtidal reefs in temperate waters, such as those below 18 m on the east coast of Australia, are generally dominated by sessile invertebrates, comprised predominantly of sponges, but also ascidians, bryozoans and cnidarians (Roberts & Davis 1996, Hooper & Kennedy 2002). Sponges are renowned for their morphological plasticity (Hill & Hill 2002), particularly in relation to wave action or flow (Palumbi 1986, Barthel 1991, Ginn et al. 2000, McDonald et al. 2003). Encrusting or prostrate forms closely adhere to the substratum and are considered to be better suited to high-energy environments, such as those found on shallow subtidal reefs (Roberts & Davis 1996, McDonald et al. 2002). In contrast, erect or massive forms possessing a relatively small basal area relative to volume do poorly in such environments (Wulff 1995, Bell & Barnes 2000), while they often dominate deeper temperate reefs (e.g. Roberts & Davis 1996). Given their prevalence on deep reefs and their longevity, sponges are excellent organisms with which to explore predictions about the size and scale of disturbances.

The structures of invertebrate assemblages on shallow temperate reefs are modified by physical and biological disturbances (Ayling 1981, Underwood et al. 1991), and it appears that these processes occur at relatively small scales (<10 m; Davis et al. 2003). Deeper, subtidal reefs also routinely experience significant exposure to water movement from storms and ocean waves (Short & Trenaman 1992), which may play an important structuring role at larger spatial scales. It has been argued that natural physical processes (e.g. storms) may account for a large proportion of the variation in assemblages observed between habitats on exposed coastlines (Underwood et al. 1991, Wulff 1995, Posey et al. 1996, Underwood 1998, 1999), whereas, in more sheltered locations, e.g. the subtidal reefs at the entrances to estuaries and embayments, the frequency and severity of the physical effects of exposure will be greatly reduced. In these habitats, strong tidal currents or episodic pulses

of freshwater after heavy and prolonged rainfall may play a significant role in some of the processes determining the structure and dynamics of sponge-dominated assemblages (Hummel et al. 1988).

Here, we examine the spatial and temporal variability of sponge-dominated assemblages on exposed and sheltered reefs at depths of 18 to 20 m, in temperate New South Wales, Australia. Much of our understanding of these assemblages stems from studies on artificial substrata or natural reefs in shallow water (e.g. Ayling 1981, Kay & Butler 1983, Chapman et al. 1995, Butler & Connolly 1996). Predictions from such studies may not hold on natural surfaces in deeper (>18 m depth) water. Importantly, because of large differences in physical conditions between sheltered and exposed reefs, e.g. water movement (Palumbi 1986, Barthel 1991, Graham et al. 1997), siltation (Bell & Barnes 2000), potential differences in recruitment (Maldonado & Young 1996, Maldonado & Uriz 1998), competition and predation (Wright et al. 1997), one can propose that patchiness in these assemblages, at scales of metres to 10s or 100s of metres, may differ between sponge-dominated assemblages on sheltered and those on exposed reefs. Quantification of such differences would therefore focus attention on the scales at which processes may differ between these habitats. These are important considerations given that wave-exposed reefs are targeted for the disposal of sewage (Roberts et al. 1998), while sheltered reefs are often subject to urbanisation and the development of port facilities (Carballo et al. 1996).

Specifically, we tested the hypothesis that spatial and temporal patterns of variability in sponge-dominated assemblages would be different on exposed reefs compared with those on sheltered reefs at the same depth. We believe that storm-related physical disturbance will lead to elevated dynamism and variability in wave-exposed assemblages by releasing space for settlement and recruitment. We predicted that: (1) assemblages on wave-exposed reefs would show spatial and temporal variation at larger scales, but possess lower sponge cover than assemblages on sheltered reefs; (2) sheltered reefs would have more species and cover of erect sponges compared with sponges on exposed reefs; (3) exposed reefs would have more species and cover of encrusting sponges relative to sheltered reefs.

MATERIALS AND METHODS

Study locations and sampling. Spatial and temporal patterns in subtidal, sponge-dominated assemblages were determined by sampling exposed and sheltered reefs, between Botany Bay and Broken Bay, New

South Wales, Australia (Fig. 1); 4 exposed and 4 sheltered estuarine reef locations were sampled at depths of approximately 18 to 20 m. Some of these reefs have been described previously (see Underwood et al. 1991, Chapman et al. 1995, Roberts & Davis 1996), but no previous study has incorporated the spatial and temporal scales of the present study to quantify the relative scales of variability for the suite of sponges in these habitats.

The assemblages on these reefs were sampled using a diver-operated camera rig that supported a 35 mm Sea & Sea Motor Marine-2 underwater camera and strobe. The assemblages at each location were sampled on 7 random occasions from April 1993 to September 1995. Within-location variability in the assemblages was determined by haphazardly photographing 5 replicate quadrats (photo-quadrat dimensions: 0.8 m × 0.56 m, total area 0.45 m²) at each of 3 randomly nested sites (approximately 50 m in diameter and 50 m apart) within each location.

Within each location, different sites were sampled at each time.

The photo-quadrats were analysed using a Bell and Howell 'black box' projector. An overlay plastic grid of 100 regularly spaced points was placed on the screen, and estimates of the percentage cover and number of species were recorded from the photo-quadrat. Many of the crustose coralline and foliose macroalgae could not be identified to species. They were grouped into morpho-taxa and termed foliose macroalgae and crustose coralline algae. To help differentiate the taxa recorded in photo-quadrats, specimens were collected at all locations. An *in situ*, close-up, 35 mm colour photograph was taken of each specimen prior to collection, as a permanent record of the habit of the organism. Many invertebrates (especially sponges) lose colour and shape once out of the water, so another photograph was taken on the surface and the samples were labelled and immediately frozen for later identification. This voucher collection is lodged with the Queensland Museum, Australia.

Queensland Museum, Australia.

Data analysis. Differences in the assemblages between exposed and sheltered locations were tested using a nested design (locations nested in exposure and sites nested in locations) using PERMANOVA (=NPMANOVA; Anderson 2001) on Bray-Curtis dissimilarities calculated from untransformed data. Analyses were done for each time separately, to provide 7 independent estimates of variability for each spatial scale. These analyses identified whether there was significant variation among sites and locations, as an estimate of relative variability at different scales, although pairwise tests were not done to examine this further, as sites and locations are random factors, selected to represent spatial scales at which one might expect these assemblages to vary. Non-metric multi-dimensional scaling (nMDS) ordinations were used to graphically illustrate patterns in the assemblages.

To test the hypotheses that the amount of small-scale variability in these assemblages at the scale of metres (among replicates within a site) and 10s of metres (among replicates between sites) was consistent among locations and consistently different between sheltered and exposed conditions, Bray-Curtis dissimilarities were calculated between randomly paired

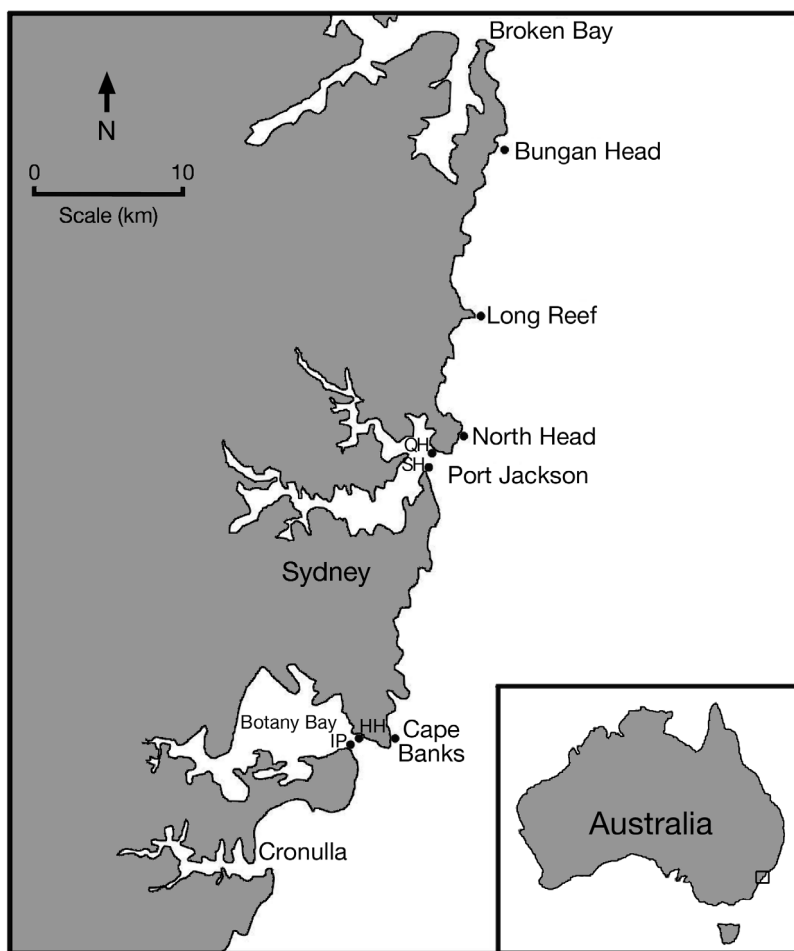


Fig. 1. Locations of the reefs in exposed (Bungun Head, Long Reef, North Head, Cape Banks) and sheltered (IP: Inscription Point; HH: Henry Head; QH: Quarantine Head; SH: South Head) habitats along the Sydney coastline

replicates within or between sites at each time of sampling. These measures can be used in an analysis of variance framework, because each replicate measure is an independent estimate of variability (Underwood & Chapman 1998a). These data do not test whether variability in the assemblage increases as spatial scale increases (as per PERMANOVA and ANOVA for multivariate and univariate measures, respectively), but specifically test the hypothesis that the magnitude of small-scale variability is consistent at larger scales. This will indicate whether small-scale variability is simply ecological 'noise', or whether there are small-scale processes that consistently act over larger scales. These measures were compared between exposures and among locations (and sites for measures of within-site variability) using analyses of variance, with times (random), exposure (fixed), locations and sites (random and nested).

To measure spatial variation within sites, 2 pairs of replicates per site were paired, to provide 2 independent Bray-Curtis dissimilarities per site. To measure variation at the scale of 100s of metres, replicates were paired between sites (2 replicates in Site 1 with 2 in Site 2, 2 in Site 1 with 2 in Site 3 and 2 in Site 2 with 2 in Site 3), giving 6 independent Bray-Curtis dissimilarity measures per location per time.

Temporal variation in the assemblage was measured for each site by calculating the average Bray-Curtis dissimilarities among times using the site centroids. These were then similarly compared between exposure and among locations, using the temporal variation within each site as a replicate measure.

Prior to ANOVA, data for selected taxa were examined for homogeneity of variances using Cochran's test (Winer 1971). Where variances were heterogeneous, data were $\ln(x + 1)$ transformed for number of taxa and arcsine transformed for percentage cover (Winer 1971). Where transformations did not result in homogeneous variances, analyses were done on the untransformed data (Underwood 1997). If variances could not be stabilised at $p = 0.05$, but could be stabilised at $p = 0.01$, ANOVA was interpreted using the $p = 0.01$ probability level (Underwood 1997).

In addition, the spatial scales at which most variation could be explained were examined for the cover of selected taxa. The relative contribution of each scale to the total variation was calculated from the components of variation. These were estimated from mean squares using the untransformed data in the ANOVA (Underwood 1997). When negative estimates of components of variation were found, that source of variation was removed from the model and all components recalculated using the method described by Fletcher & Underwood (2002). Two-tailed F -tests were used to compare the residual variation between exposed and sheltered

reefs (Underwood 1997). Comparisons of variance components for sites and locations using 2-tailed F -tests are not valid, and these results were interpreted qualitatively.

RESULTS

Sponges were the most diverse and abundant taxon encountered on sheltered and on exposed reefs. A total of 82 species of sponges were identified. Of the other major phyla, 14 ascidians, 12 bryozoans and 12 cnidarians were also identified. The most abundant algae were crustose Corallinacea and a mixture of macroscopic foliose species. A matrix of silt, consisting of a mixture of micro-flora and fauna, silt and micro-organisms, was the dominant primary cover on exposed reefs and, at some times, the dominant cover on sheltered reefs.

Patterns in assemblage structure

PERMANOVA showed a significant difference among replicate sites on 4 of 7 occasions and among locations on all occasions. Therefore, data could not be pooled across sites or locations to increase the power of the test for the main effect of exposure. A significant difference was only determined between exposures in April 1993 ($F_{1,6} = 3.02$, $p < 0.05$). Nevertheless, nMDS ordinations clearly plotted assemblages on exposed reefs as separate from those on sheltered reefs in April 1993, April 1994, January 1995 and April 1995, indicating that these 2 conditions do support distinctly different assemblages (Fig. 2). In August 1993 and January 1994, only locations at North Head overlapped with those in the sheltered locations, whereas, in September 1995, assemblages were much more similar.

When the data for all exposed or sheltered locations were averaged and plotted for all times, there was a consistent separation between assemblages in sheltered and exposed locations across all times (Fig. 2).

Because environmental conditions can affect patchiness at multiple spatial scales, Bray-Curtis dissimilarities estimating variation at the scale of metres (within sites) and 100s of metres (between sites) were calculated for independent pairs of quadrats. Maintaining their independence allows one to test the hypotheses that these levels of variation are themselves inconsistent among location and exposure using standard ANOVA (Underwood & Chapman 1998a).

There was a significant interaction between times and locations ($F_{36,112} = 1.91$, $p < 0.01$) for analyses of the Bray-Curtis dissimilarities between replicates within sites (i.e. measuring variation at the scale of metres),

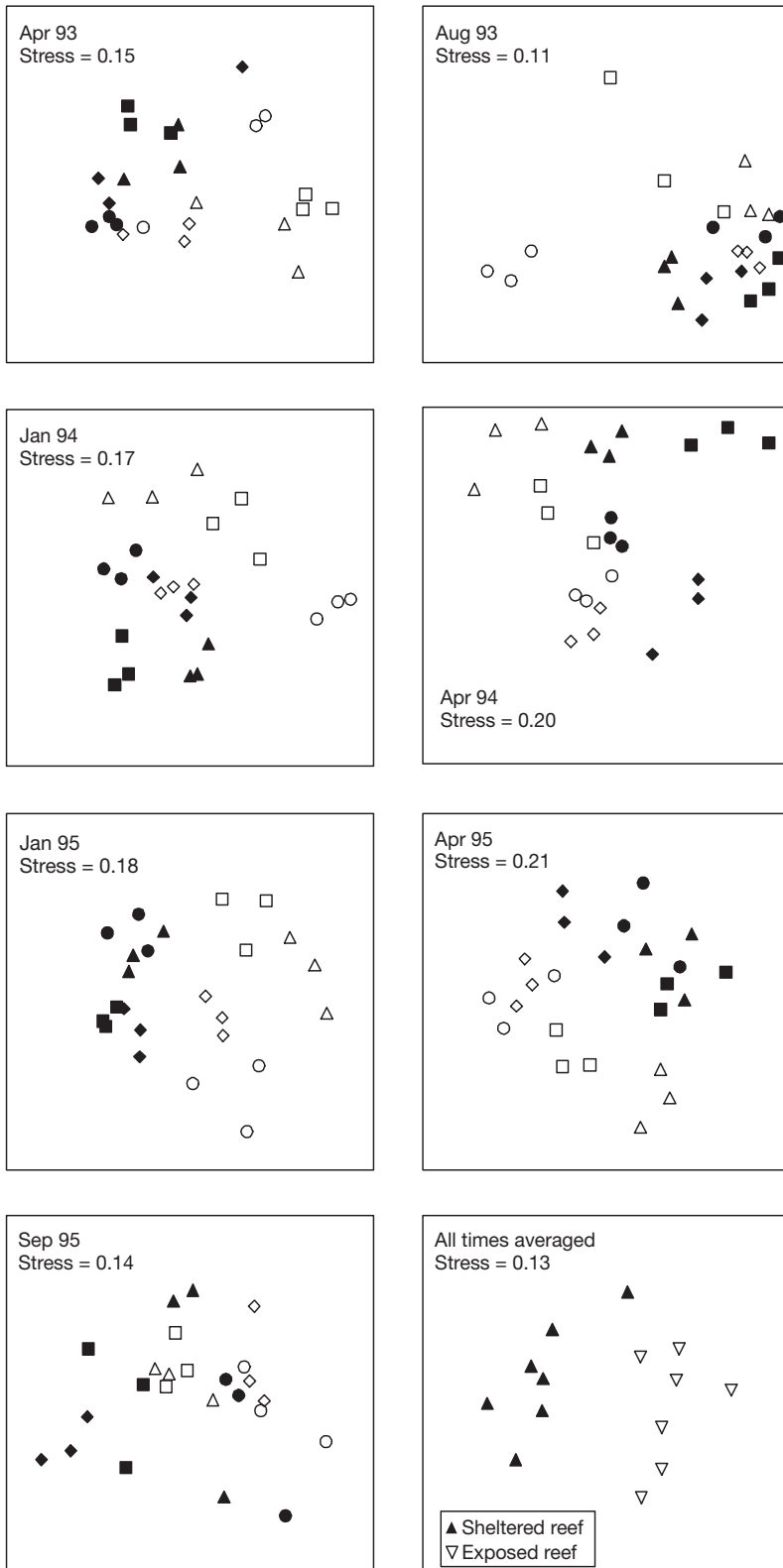


Fig. 2. Non-metric multidimensional scaling plots for each time of sampling. (Exposed: (O) Bungan Head, (Δ) Long Reef, (◇) North Head, (□) Cape Banks. Sheltered: (●) Quarantine Head, (▲) South Head, (◆) Henry Head, (■) Inscription Point)

but there was no effect of exposure (determined after pooling terms in the analysis with $p > 0.25$; mean for exposed locations = 49% dissimilarity, mean for sheltered locations = 47% dissimilarity). Variation at this scale was also tested using the average Bray-Curtis dissimilarity per site and the sites as replicates, and similar results were obtained (a significant interaction between times and locations; $F_{36,112} = 1.82, p < 0.01$).

The Bray-Curtis dissimilarities measured between sites, i.e. variation in the assemblage at the scale of 100s of metres, similarly gave a significant interaction between times and locations ($F_{36,280} = 1.82, p < 0.01$) and no general effect of exposure after pooling (mean for exposed locations = 52% dissimilarity, mean for sheltered locations = 50% dissimilarity).

Patterns in richness and cover

The cover of algae was generally greatest on the exposed reefs, although the number of species and their covers fluctuated at various spatial and temporal scales (Fig. 3a to c, Table 1). The cover of the silt matrix also fluctuated at various spatial and temporal scales, although it was not as variable through time on the sheltered reefs as on the exposed reefs (Fig. 3d, Table 1). The total number of species and cover of all the fauna combined fluctuated significantly at the smallest scale examined (Table 1), although both the number of species and the cover of fauna were generally greater on the sheltered reefs (Fig. 3e,f).

There were significant spatial and temporal fluctuations in the total number of species of sponge and cover of sponges (Fig. 4a,b, Table 2). Generally, greater richness and cover of sponges were recorded on the sheltered reefs, compared with the exposed reefs (Fig. 4a,b). The richness and cover of encrusting and erect sponges also fluctuated through time (Fig. 4c to f, Table 2). There were generally fewer differences in the richness of encrusting sponges between the 2 different

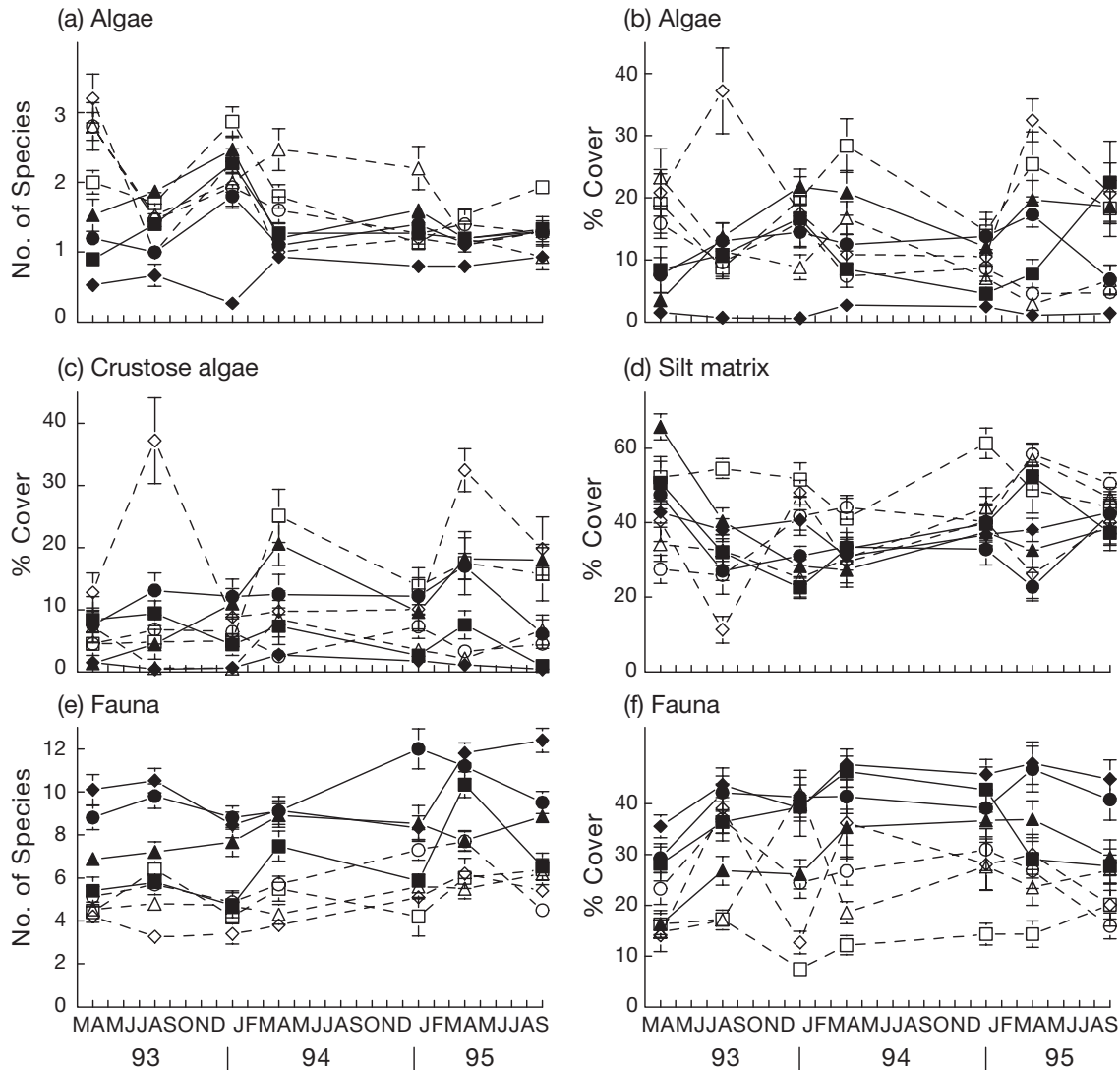


Fig. 3. Mean (\pm SE): (a) number of species of algae, (b) total cover of algae, (c) cover of crustose algae, (d) cover of silt matrix, (e) number of species of fauna and (f) total cover of fauna on the reefs at: (O) Bungan Head, (Δ) Long Reef, (\diamond) North Head, (\square) Cape Banks, (\bullet) Quarantine Head, (\blacktriangle) South Head, (\blacklozenge) Henry Head and (\blacksquare) Inscription Point. Total $n = 15$

Table 1. Summaries of F -ratios from analyses comparing spatial and temporal variation in the species richness and cover of algae, silt matrix and total fauna at locations in habitats on exposed and sheltered reefs in New South Wales, Australia (Ti: time; Ha: habitat; Lo: location; None: no transformation required; n.s.: not significant [$p > 0.05$]; significant * $p < 0.05$, ** $p < 0.01$)

Source	df	Algal richness		Algal cover		Crustose algae		Silt matrix		Faunal richness		Faunal cover	
		MS	F	MS	F	MS	F	MS	F	MS	F	MS	F
Time	6	11.4		256.1		658.7		2927.8		80.6		1875.2	
Habitat	1	54.0		5181.8		960.8		2458.3		2506.4		43935.3	
Location (Habitat)	6	8.6		3922.6		4279.8		2878.0		163.3		3496.7	
Site (Ti \times Ha \times Lo)	112	0.6	1.5**	123.3	1.4**	142.9	1.8**	363.3	1.4**	5.2	1.3*	224.0	1.3*
Ti \times Ha	6	8.7		686.8		229.1		2332.5		3.9		350.2	
Ti \times Lo (Ha)	36	2.3	4.1**	426.5	3.5**	527.4	3.7**	1188.9	3.3**	16.9	3.3**	663.1	2.9**
Residual	672	0.4		85.9		78.1		252.4		3.9		169.2	
Cochran's test			0.058**		0.037, n.s.		0.036, n.s.		0.032, n.s.		0.029, n.s.		0.026, n.s.
Transformation			None		None		Arcsine		None		None		None

habitats (Fig. 4c), whilst on some occasions, there were greater covers of encrusting sponges on the exposed reefs (Fig. 4d). The erect sponges were generally more diverse and had greater covers on the sheltered reefs compared with those on the exposed reefs (Fig. 4e,f).

The cover and richness of ascidians, bryozoans and cnidarians fluctuated at various spatial and temporal scales (Fig. 5a to f, Table 3). Their contribution to primary cover was very small in both habitats when compared with the sponges. There were generally no patterns in their species richness or cover between the exposed or sheltered reefs, with the exception that, at times, there were greater numbers of ascidian species in some sheltered reef locations (Fig. 5a).

Examination of the components of variation for each of the derived variables on exposed and sheltered reefs indicated that most of the variation was at the smallest scale, i.e. within the residual mean squares (Table 4). Relatively little variation was at the scale of site or location, and there were many negative estimates at each of these scales (Table 4). Significant differences in the components of variation were found in the residual (i.e. among replicates) using the 2-tailed *F*-tests (Table 4). Generally, there was significantly greater variability on exposed reefs than on sheltered reefs for the cover of silt, algae and encrusting sponges (Table 4). There was generally significantly greater variability for the cover of erect sponges on sheltered reefs (Table 4).

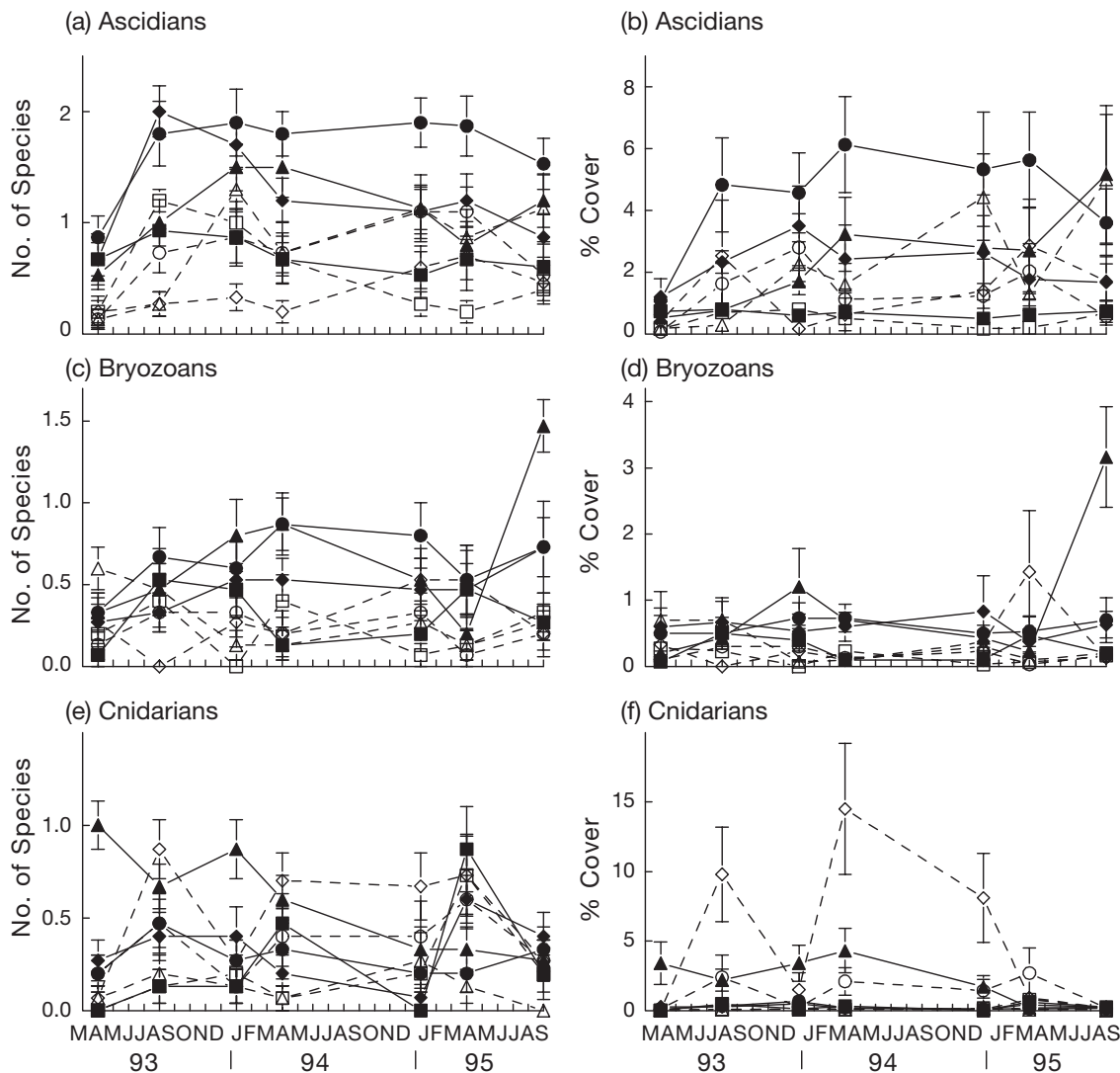


Fig. 5. Mean (\pm SE): (a) number of species of ascidians, (b) total cover of ascidians, (c) number of species of bryozoans, (d) cover of bryozoans, (e) number of species of cnidarians and (f) cover of cnidarians on the reefs at: (○) Bungan Head, (△) Long Reef, (◇) North Head, (□) Cape Banks, (●) Quarantine Head, (▲) South Head, (◆) Henry Head, and (■) Inscription Point ($n = 15$)

Table 3. Summaries of *F*-ratios from analyses comparing spatial and temporal variation in the species richness and cover of ascidians, bryozoans and cnidarians at locations in habitats on exposed and sheltered reefs in New South Wales, Australia (Ti: time; Ha: habitat; Lo: location; None: no transformation required; n.s.: not significant [$p > 0.05$]; significant * $p < 0.05$, ** $p < 0.01$)

Source	df	Ascidian				Bryozoan				Cnidarian			
		richness		cover		richness		cover		richness		cover	
		MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>	MS	<i>F</i>
Time	6	6.6		191.8		0.8		1.6		1.4		97.9	
Habitat	1	65.2		1472.1		15.2		24.7		0.8		167.9	
Location (Habitat)	6	10.1		489.8		1.6		4.3		2.7		332.4	
Site (Ti × Ha × Lo)	112	0.9	1.4**	35.7	1.2, n.s.	0.3	0.9, n.s.	0.9	0.9, n.s.	0.3	1.5**	27.1	1.8**
Ti × Ha	6	0.8		21.7		1.1		3.9		0.9		69.9	
Ti × Lo (Ha)	36	1.3	1.5*	55.6	1.6*	0.6	1.9**	2.9	3.1**	0.6	1.8**	65.7	2.4**
Residual	672	0.6		29.7		0.3		1.0		0.2		15.2	
Cochran's test		0.028, n.s.		0.035, n.s.		0.029, n.s.		0.213**		0.031, n.s.		0.212**	
Transformation		None		Arcsine		None		None		None		None	

DISCUSSION

Sponges were the dominant faunal group (greatest richness and cover) on both exposed and sheltered reefs, whilst ascidians were the next in importance. In terms of the cover of primary space, foliose and crustose macroalgae and a silt matrix were also important in contributing to the structure of the assemblages. The silt matrix was generally responsible for the greatest primary cover on the exposed reefs, whilst sponges had the greatest cover on sheltered reefs. The cover of macroalgae (foliose and crustose) was generally greatest on exposed reefs, whereas the covers of the other fauna (ascidians, bryozoans and cnidarians) were generally similar in terms of the amount of space they occupied in both habitats.

The greater richness and cover of sponges on sheltered reefs was primarily due to the presence of more massive or erect forms, e.g. *Spirastrella* sp., *Desmapsamma kirki* Bowerbank and *Mycale* spp. Whilst these species were also found on the exposed reefs, their morphology or form of growth tended to be more prostrate. Patterns of increased cover and richness of prostrate sponges with decreasing depth have been described for temperate (Roberts & Davis 1996, Bell & Barnes 2000) and tropical reefs (Wilkinson & Evans 1989). Energy generally decreases with depth, which may partly explain these types of patterns. In general, those species with small basal area to volume ratios do poorly in high-energy environments (Wulff 1995, Bell & Barnes 2000). Greater richness and cover of encrusting sponges were found on the exposed reefs, where there was generally more water turbulence. Depth-related patterns associated with turbulence have also been described for other types of subtidal assemblages (Schmahl 1990, Clarke et al. 1993, Bell & Barnes 2000).

Increased sedimentation, light and water turbulence

associated with depth gradients have all been identified as important factors in structuring the distribution and abundance of subtidal assemblages of sponges in temperate (Underwood et al. 1991, Zea 1993, Roberts & Davis 1996, Bell & Barnes 2000, Hooper & Kennedy 2002), tropical (Liddell & Ohlhorst 1987, Wilkinson & Evans 1989) and polar (Barthel 1991) regions. In the present study we can exclude patterns of distribution and abundance of sponges being related to depth gradients, because consistently different community structures were found between the 2 habitat types, at the same depth. Underwood et al. (1991) described a mosaic of subtidal habitat types along the coastline of New South Wales, Australia, with the distribution of assemblages related to depth, wave exposure and herbivory, although their study did not extend into the habitats below 15 m.

Habitat-related differences have also been described at smaller spatial scales (Wright et al. 1997), where differences in the structure of sponge assemblages between 2 adjacent habitats at the same depth were related to the ability of some sponges to withstand predation by using chemical defences. In shallow subtidal habitats, grazing sea urchins and molluscs have been found to effectively maintain the structure of coralline algal crusts in barren ground habitats (Davis et al. 2003). At this stage, however, the processes that interact to determine the structure of subtidal assemblages on reefs at depths >18 to 20 m are largely unknown (Underwood et al. 1991).

In general, the analyses of components of variation supported the hypothesis of increased variability for the assemblages on the exposed reefs. Warwick & Clarke (1993) identified increased variability in meiobenthic, macrobenthic, coral reef and fish assemblages associated with different types of disturbance in natural habitats, and concluded that this variability

Table 4. Estimates of components of variation derived from the analyses of variance between exposed and sheltered reefs for cover of selected taxa at each time (n.s.: not significant [$p > 0.05$]; significant [$p < 0.05$]; Exp: exposed; She: sheltered; Re: residual; Si: site; Lo: location)

Taxa	Treatment	Time 1			Time 2			Time 3			Time 4			Time 5			Time 6			Time 7			
		Re	Si	Lo	Re	Si	Lo	Re	Si	Lo	Re	Si	Lo	Re	Si	Lo	Re	Si	Lo	Re	Si	Lo	
Silt matrix	Exp	337.3	3.5	2.9	208.9	3.7	11.6	314.9	-	31.3	226.9	11.5	-	412.3	7.6	-	409.5	-	51.9	284.1	-	-	-
	She	232.7	3.7	2.7	152.7	0.2	0.9	123.1	-	13.2	166.1	1.5	-	238.0	0.2	-	230.9	-	36.8	206.4	-	-	-
	F-test	1.5*			1.4*			2.6*			1.4*			1.7*			1.8*			1.4*			
Total algae	Exp	228.5	0.9	-	213.5	0.99	6.7	154.4	-	3.3	85.5	7.5	2.1	102.0	-	1.0	154.1	-	56.0	193.9	-	13.8	
	She	84.9	0.8	-	63.8	0.06	1.3	71.4	-	20.6	98.1	3.5	1.6	64.6	-	7.0	69.9	-	18.7	207.6	-	22.4	
	F-test	2.7*			3.4*			2.2*			1.2*			1.6*			2.2*			1.0, n.s.			
Total fauna	Exp	109.0	-	2.9	129.8	-	13.4	131.1	1.4	8.6	245.6	-	24.7	257.1	-	10.1	176.2	-	9.2	145.6	1.0	2.3	
	She	105.2	-	15.4	180.4	-	35.5	156.4	6.9	0.6	157.9	-	5.6	176.3	-	1.1	239.8	-	17.3	169.4	4.9	0.3	
	F-test	1.0, n.s.			1.4*			1.2*			1.6*			1.5*			1.4*			1.2*			
Total sponges	Exp	106.1	-	3.5	152.7	-	15.0	136.6	0.6	8.1	132.3	-	5.2	219.6	-	5.8	182.1	-	3.4	143.7	0.3	-	
	She	106.2	-	18.5	115.5	-	11.9	142.7	7.9	1.3	200.4	-	16.5	162.5	-	5.6	264.3	-	12.2	172.6	8.1	-	
	F-test	1.0, n.s.			1.3*			1.0, n.s.			1.5*			1.4*			1.5*			1.2*			
Encrust. sponges	Exp	38.2	-	5.3	98.1	-	32.9	135.6	-	20.9	170.9	-	8.5	109.5	1.2	0.5	163.4	-	2.3	102.6	-	2.7	
	She	41.2	-	2.2	48.1	-	2.9	56.1	-	1.3	69.9	-	5.5	43.5	0.5	0.2	11.5	-	0.8	19.5	-	0.2	
	F-test	1.1*			2.0*			2.4*			2.4*			2.5*			14.2*			5.3*			
Erect sponges	Exp	99.8	-	0.2	78.7	-	10.5	67.3	0.05	1.2	46.6	-	0.9	186.2	0.8	-	70.1	0.6	0.12	80.4	-	2.6	
	She	96.8	-	6.7	48.1	-	2.9	197.8	4.8	1.2	174.5	-	3.3	154.9	0.04	-	254.6	3.8	1.12	188.9	-	23.2	
	F-test	1.0, n.s.			1.6*			2.9*			3.7*			1.2*			3.6*			2.4*			

may be a symptom of stress (but see Chapman et al. 1995). Wave energy and storms are considered to be natural physical disturbances in temperate subtidal reefs within embayments, estuaries and on exposed coastlines (Kennelly 1989, Underwood 1999). The greatest changes in assemblages will occur where the disturbance is not one that the assemblage normally experiences and will depend on its type and magnitude, the pre-disturbance structure of the community (Roberts et al. 1998) and the morphological and physiological adaptations of its members (Schratzberger & Warwick 1999).

There were significant interactions at small spatial scales for many of the variables we examined. These interactions are ecologically important and show how assemblages experience patchiness in their distributions at different spatial scales. The incorporation of a hierarchy of spatial scales into sampling programmes, as well as the need for appropriate spatial scales required to detect the effects of anthropogenic disturbance, was highlighted by Underwood (2000). Significant variability was found at all the spatial scales we examined, although the variability among replicate quadrats consistently contributed to the greatest proportion of the total variation. This reinforces the model that patchiness at small spatial scales, which is caused by local processes, is important in structuring assemblages rather than processes that operate at larger scales. Local processes and small-scale heterogeneity within a site may cause increased variability that is far greater than what may be caused by processes at larger scales. From a managerial perspective, if small scales are not included in sampling programmes that measure environmental disturbances, then impacts may go undetected (Underwood et al. 2003).

If we ignore for the moment that assemblages of subtidal marine organisms living on coastal reefs close to large cities may be affected by various forms of anthropogenic disturbance, then natural physical processes, such as storms, may account for a large proportion of the variation in differences between habitats (Underwood et al. 1991). Physical, chemical and biological factors, which could potentially determine the structure and dynamics of assemblages on these subtidal reefs, would need to be tested using appropriate manipulative experiments. The potential physical distinctions between the habitats studied here include increased wave energy (Short & Trenaman 1992) and light penetration on exposed reefs (Rendell & Pritchard 1996), with stronger tidal currents and increased siltation on the sheltered estuarine reefs (Middleton et al. 1996). There would also be greater loads of nutrients and fluctuations in salinity on the reefs in the estuarine locations (Middleton et al. 1996, Rendell & Pritchard 1996). Differences related to predation (Ayling 1981),

recruitment (Butler 1986) and competition for space (Ayling 1983) cannot be discounted as potentially important determinants of the structure and dynamics of assemblages within these 2 types of habitat. As Underwood (2000) noted and Hill & Hill (2002) demonstrated, hypotheses derived from models such as those outlined above must be tested by manipulation of the regime of disturbances.

Presenting these results was an important, logical, first-step in developing an understanding of the ecology of sponge-dominated assemblages on subtidal reefs at depths of 18 to 20 m. Research into the ecology of subtidal assemblages living on hard substrata has unfortunately been 'depth limited', with most effort spent on those shallow-water assemblages, which are easily sampled using SCUBA techniques (Underwood et al. 1991, Davis & Ward 1999) or by examining assemblages on artificial structures (Kay & Butler 1983, Glasby 1999). In recent years, marine ecologists have rightfully focussed on experimental tests of hypotheses about processes to explain patterns of variability; nevertheless, descriptive quantitative tests of mensurative models are still a necessary pre-cursor to experimental manipulative analyses (Underwood et al. 2000). For sponge-dominated assemblages on deeper temperate reefs, experimental tests of hypotheses about the processes producing their structure and dynamics were considered to be premature, until spatial and temporal variability has been quantified at appropriate scales.

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