INTERTIDAL ASSEMBLAGES ON COASTAL DEFENCE STRUCTURES IN SINGAPORE II. CONTRASTS BETWEEN ISLANDS AND THE MAINLAND

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ABSTRACT. **–** In Singapore, breakwaters have replaced natural rocky shores as the predominant hard-substratum intertidal coastal habitat on both the main island as well as the smaller islands to the south. These form isolated and non-contiguous areas of relatively homogenous rock (granite), separated by sandy shore or water. Insular assemblages of species at island locations are expected to be more stochastic in organisation than those on the mainland, due in part to variable patterns of colonisation and extinction. As such, there should be differences between the mainland and islands in terms of assemblage composition, structure and in the variability of abundances of taxa at a range of spatial scales. This study examines the structure of assemblages on seawall habitats located on the Singapore mainland and its southern islands. Analyses revealed differences between island and the mainland in the structure, but not the composition of intertidal assemblages, and also in the magnitude of variation in abundances of individual taxa at the spatial scales examined. Differences were more pronounced in assemblages lower on the shore than in high shore and supralittoral assemblages. In addition, assemblages tended to be more similar within locations, but there was no tendency for variability in the mean abundances of any taxa to be consistently higher at any habitat or spatial scale. On the whole, the results do not support the model of higher stochasticity of assemblages on artificial intertidal rocky habitats on islands. Instead, it revealed that high spatial variability at mainland locations could be linked to highly localised environmental conditions. Community organisation on these seemingly homogenous structures is shown to be complex and idiosyncratic. Factors and mechanisms influencing assemblage structure in natural rocky intertidal habitats are likely to operate differently on these artificial habitats, and should be examined critically prior to management decisions assuming or relying on the surrogacy of these structures as alternative marine habitats.

KEY WORDS. – spatial distribution, variability, intertidal, community structure, artificial habitats, island vs. mainland.

INTRODUCTION

The rapid urbanisation of coastal areas is predicted to accelerate with global population growth, with an increasing proportion of the population living in proximity to coastlines (Hammond, 1992; Norse, 1993). This urbanisation is coupled with considerable change to the ecology of coastal habitats as natural coastal habitats are modified, either by the addition of or replacement with urban structures such as seawalls, jetty pilings and pontoons (Glasby & Connell, 1999; Chapman & Bulleri, 2003; Bacchiochi & Airoldi, 2003). These structures provide habitat for a variety of epibenthic and associated organisms (Connell & Glasby, 1999; Davis et al., 2002; Bacchiocchi & Airoldi, 2003; Chapman & Bulleri, 2003; Bulleri & Chapman, 2004), although community structure has been shown to differ strongly from nearby natural equivalents, particularly for hard substrata (e.g., Anderson & Underwood, 1994; Connell & Glasby, 1999; Connell, 2000, 2001; Chapman, 2003; Chapman & Bulleri, 2003; Bulleri & Chapman, 2004). A particular quirk of artificial habitats is that non-indigenous species survival seems to be enhanced relative to equivalent natural habitats (Holloway & Keough, 2002; Lambert & Lambert, 2003; Thornber et al., 2004; Bulleri & Airoldi, 2005).

Management and planning rely on ecological theory developed for natural marine systems, but the generality of this when extended to artificial habitats has not been examined (Bulleri, 2006). The suitability of directly applying ecological theories developed from terrestrial ecosystems to marine systems has previously been called into question (Underwood & Denley, 1984); ecological theories developed for natural systems may be even less applicable to artificial systems. Urban habitats differ from natural ones in several ways, including the novelty of habitat and disturbance history (Rebele, 1994). As such, theories developed from natural marine ecosystems may not be wholly appropriate to these artificial environments.

In this study, we compared assemblages inhabiting breakwaters on the mainland and at small nearshore islands off the southern coast of Singapore. The concept that assemblages on islands and mainland differ was originally developed for terrestrial organisms (MacArthur & Wilson, 1967) and successfully adapted to marine coastal ecosystems (e.g. Dayton, 1975; Benedetti-Cecchi et al., 2000; 2001; 2003). The uniqueness of insular assemblages is thought to arise from unpredictability; patterns of colonisation/extinction are dependent on distance from other sources of colonists and island size. Also, environmental heterogeneity on islands may be increased by differences in physical processes, biotic interactions, and disturbance regimes (see review by Brown & Lomolino, 2000). These characteristics are likely to result in assemblages that can differ from those on the mainland in composition, structure, and in the scales of temporal and spatial variability of organisms (Benedetti-Cecchi et al., 2003).

Whether these patterns are retained in artificial rocky habitats is still unknown. Disparity in the spatial scaling of variability between artificial and natural habitats (Bulleri & Chapman, 2004) suggests that assemblage organisation is likely to operate differently. Due to construction design and material, coastal defence structures are, as a whole, physically more similar than natural coastal habitats. This may potentially alter the processes that operate on small- and meso- spatial scales in natural rocky habitats. However, the basic elements of island biogeography, including but not limited to stochasticity in composition due to differential larval delivery, relative insularity from anthropogenic disturbances etc. should remain as viable factors in community organisation. The primary objectives of this study were to a) identify differences in assemblages between artificial structures on the mainland and on islands (i.e., shore type) and b) contrast spatial variation in the abundance of taxa between island and mainland seawalls.

MATERIAL AND METHODS

Sampling Methodology. – Assemblages were sampled at each of six locations along the coast of mainland Singapore and six locations on nearshore islands to the south between April 2002 and February 2003 (Fig. 1). Detailed descriptions of the seawalls have been provided in Lee et al. (2009). At each location, sampling was conducted at two sites, approximately 50 m to 200 m apart. Within each site, assemblages were sampled at four shore heights: Supralittoral (SP), > 1.1 m above mean sea level (MSL), High Shore (HS, 0.5–1.1 m above MSL), Upper Midshore (UM, from -0.5 to 0.5 m with respect to MSL) and Lower Midshore (LM, between 0.5 and 1.2 m with respect to MSL). Assemblages at each shore height were sampled using 20 random quadrats of 30×10 cm. Data consisted of visual estimates of percent cover for colonial organisms (algae and invertebrates) and numbers of individuals within each quadrat for motile animals. Fast-moving organisms such as crabs (mainly Grapsidae) and *Ligia* were excluded from the data as they exhibited a pronounced response to quadrat placement and were consistently under-sampled. Where possible, organisms were identified to species level; else they were grouped into taxa/functional groups (for details, see Lee et al., 2009) and treated as taxa in subsequent analyses.

Analyses. – For each shore height, separate multivariate analyses were used to compare assemblages on islands with those of the mainland. An average sample for each site was first obtained by averaging data across quadrats. Bray-Curtis similarity matrices were calculated for each pair of these "average sites" using square-root transformed data. This transformation has been previously advocated for similar data as it causes abundance and percentage cover to be within similar ranges and at the same time reduces dominant effects of very abundant species in the analyses (Underwood & Chapman, 1998). Two-way nested PERMANOVA with Shore (fixed) and Location (nested in Shore) was used to test for differences between islands and mainland and among locations using sites as replicates. Non-metric Multi-dimensional scaling (nMDS) was used as an ordination technique to present the spatial structure of the assemblages within two spatial dimensions while maintaining as much of the relative distances among replicate units as possible (Clarke, 1993). SIMPER (Clarke, 1993) was then used to examine the percentage similarity within and percentage dissimilarity among all sites, and to identify taxa that were important to either characterizing a shore type or distinguishing between shore types. All these procedures were conducted using procedures in PRIMER v6.1.12 & PERMANOVA+ v1.0.2 (PRIMER-E, 2009).

Variance components were estimated for untransformed abundance data for individual species based on a fully hierarchical 2-factor ANOVA design with Location (random, six levels) and Sites (two levels, nested in Location) as main factors. This was done separately for each shore type using the Variance Components module in STATISTICA 6 (STATSOFT, 2001). Negative estimates were assumed as underestimates of zero variances (Underwood, 1996) and were not included in the comparisons. One-tailed F tests were used to compare the magnitudes of non-negative variation at each spatial scale between mainland and island locations.
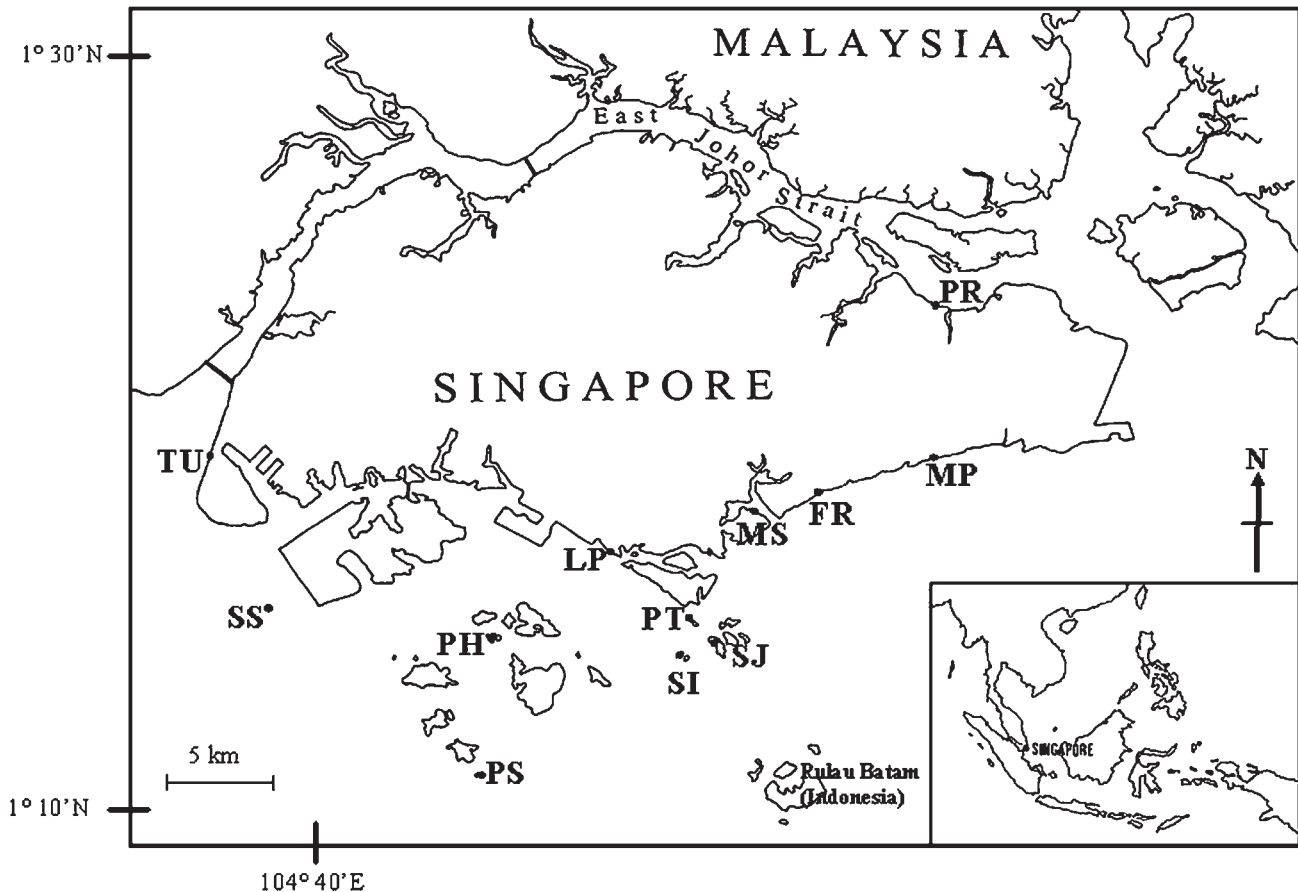
Fig. 1. Locations of sampling sites in Singapore. Abbreviations used: PR, Pasir Ris; MP, Marine Parade; FR, Fort Road; MS, Marina South; LP, Labrador Park; TU, Tuas and island; SJ, St John's Island; PT, Pulau Tekukor; SI, Sister's Islands; PH, Pulau Hantu; PS, Pulau Satumu, SS, Sultan Shoal; sites around Singapore.

RESULTS

Spatial patterns in assemblages. – PERMANOVA results showed that the assemblages on islands and mainland were significantly different at highshore, upper midshore and lower midshore, but not at the supralittoral (Table 1). The nMDS ordination plots distinguished between shore types at most heights, although assemblages varied significantly among locations within shore type (Fig. 2, Table 1). Assemblages at islands were generally more similar than assemblages on the mainland with less dispersion among locations and sites in the MDS ordination plots (Fig. 2). Within shore type, assemblages were progressively more similar from highshore to lower midshore levels (Fig. 2 and Table 2). Assemblages on mainland and island breakwaters were least dissimilar at the supralittoral and lower midshore (Fig. 2a, d Table 2 and most distinct at highshore habitats (Fig. 2b, Table 2). The MDS plots showed that lower midshore assemblages were the second least distinguishable between shore types (Fig. 2d) although similarity within shore types was the highest observed (Table 2). There were some differences in assemblage composition between islands and the mainland (Table 3), with a greater number of taxa unique to mainland rather than island breakwaters (Table 3). Of these, several were recorded only from single

locations and this was particularly true of island biota (Table 3). As such, none were found to be important in either characterising or discriminating between islands and the mainland (Table 4). Assemblage structure was therefore more important than composition in discriminating between islands and the mainland. Dissimilarity measures between islands and mainland were always greater when calculated on abundance rather than presence/absence data (Table 1). Results of SIMPER analyses further support this; species that contributed at least 10% to dissimilarity between shore types were frequently also important in characterising both habitats (Table 4). One major exception to this pattern is filamentous cyanobacteria, which contributed 11.27% to average dissimilarity at the supralittoral but characterised neither shore at that height (Table 4).
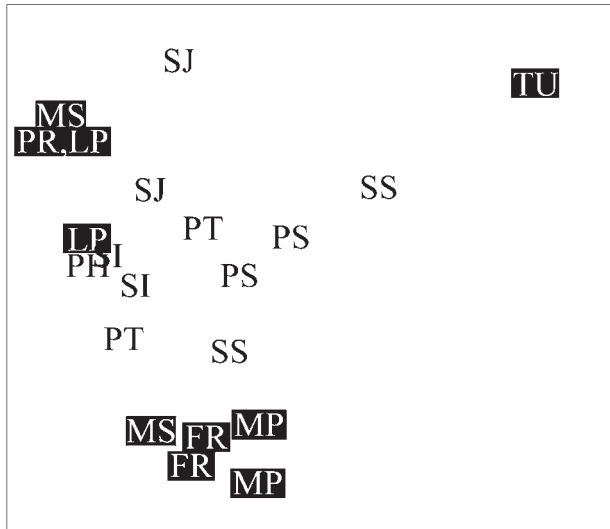
Just seven of the 91 taxa (see Lee et al., this volume) sampled and analysed were found to be important in either characterising ($\geq$ 10% average similarity) or distinguishing ($\geq$ 10% average dissimilarity) between mainland and island assemblages (Table 4). All taxa that were important in discriminating between shore types at any given height continued to contribute at least 5% to average dissimilarity at other heights (Table 4). Of these, balanid barnacles, *Echinolittorina malaccana* and *Siphonaria guamensis*,

filamentous cyanobacteria and algal turfs were consistently more abundant (Figs. 3–6) at and consequently characterised mainland locations (Table 4), though the gastropods and algal turfs could also characterise islands at some heights (Table 4). For example *E. malaccana* characterised supralittoral assemblages, *S. guamensis* high shore and algal turfs lower midshore assemblages on islands (Table 4). At those heights, abundances of *E. malaccana*, *S. guamensis* and algal turfs on islands were less than on the mainland, but variation among locations and between sites were relatively lower (Figs. 3, 4 and 6). *Littoraria*, encrusting cyanobacteria and *Lobophora variegata*, which characterized island assemblages (Table 2) were consistently more abundant at islands (Figs. 3–6). Only chthamalid barnacles were not consistently more abundant at either mainland or islands; these were more abundant on the mainland at supralittoral habitats but occurred in greater numbers at highshore habitats on islands (Figs. 3, 4).

*Scales of spatial variation.* – Among the invertebrates,

spatial variation was greater on islands than the mainland for *Littoraria*, and *Siphonaria atra* at the scale of quadrat (Table 5). At larger scales, only Chthamalid barnacles fluctuated more among islands than at mainland locations (Table 5). All of these taxa occurred in greater abundance at islands than on the mainland (Figs. 3–6). Barnacles and the remaining gastropods were more variable at the mainland than on islands at the scale of quadrat (Table 5). However, at larger scales, variation was significantly greater at mainland only for *S. guamensis* (Site), *P. saccharina* at the scales of site and location (Table 5). Variation in balanid abundances was also large at the scale of site (Figs. 5, 6) on the mainland but significance could not be tested (Table 5). The abundances of these were generally greater at mainland locations than at islands, but differences among sampling sites were often considerable, exceeding observed differences between shore types (Figs. 4–6).

Encrusting cyanobacteria, *Lobophora variegata* and
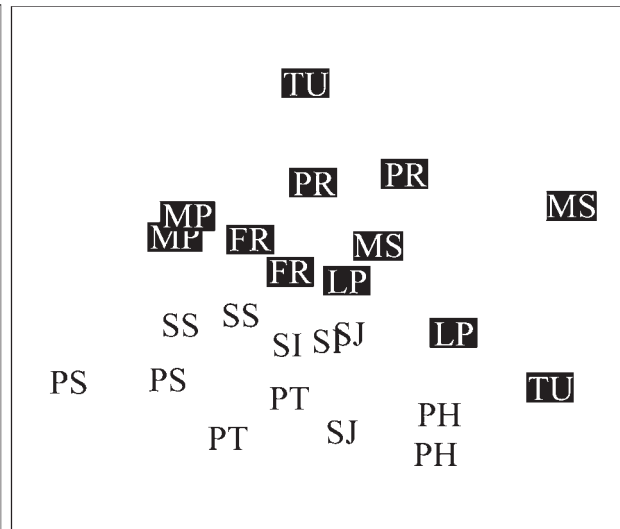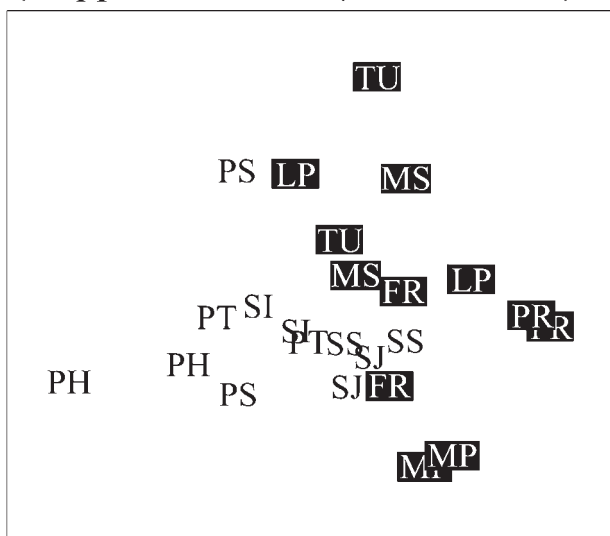
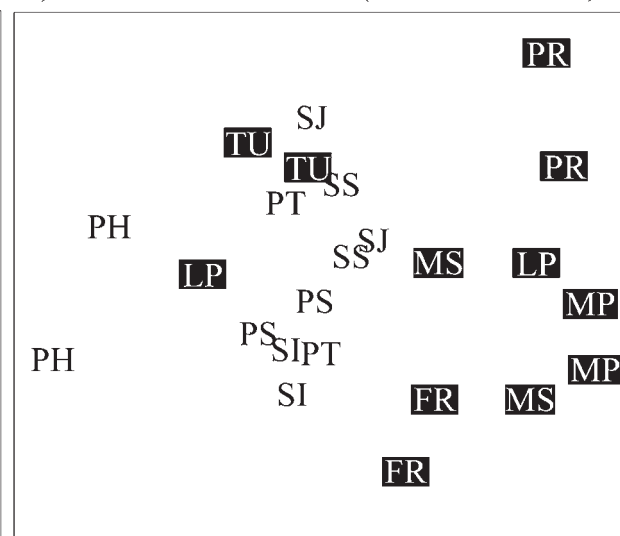
Fig. 2. Two-dimensional MDS plot of centroids of the replicate sites in: a, supralittoral (SP); b, high shore (HS); c, upper midshore (UM); d, lower midshore (LM) assemblages. Closed symbols = mainland sites, Open symbols = island sites
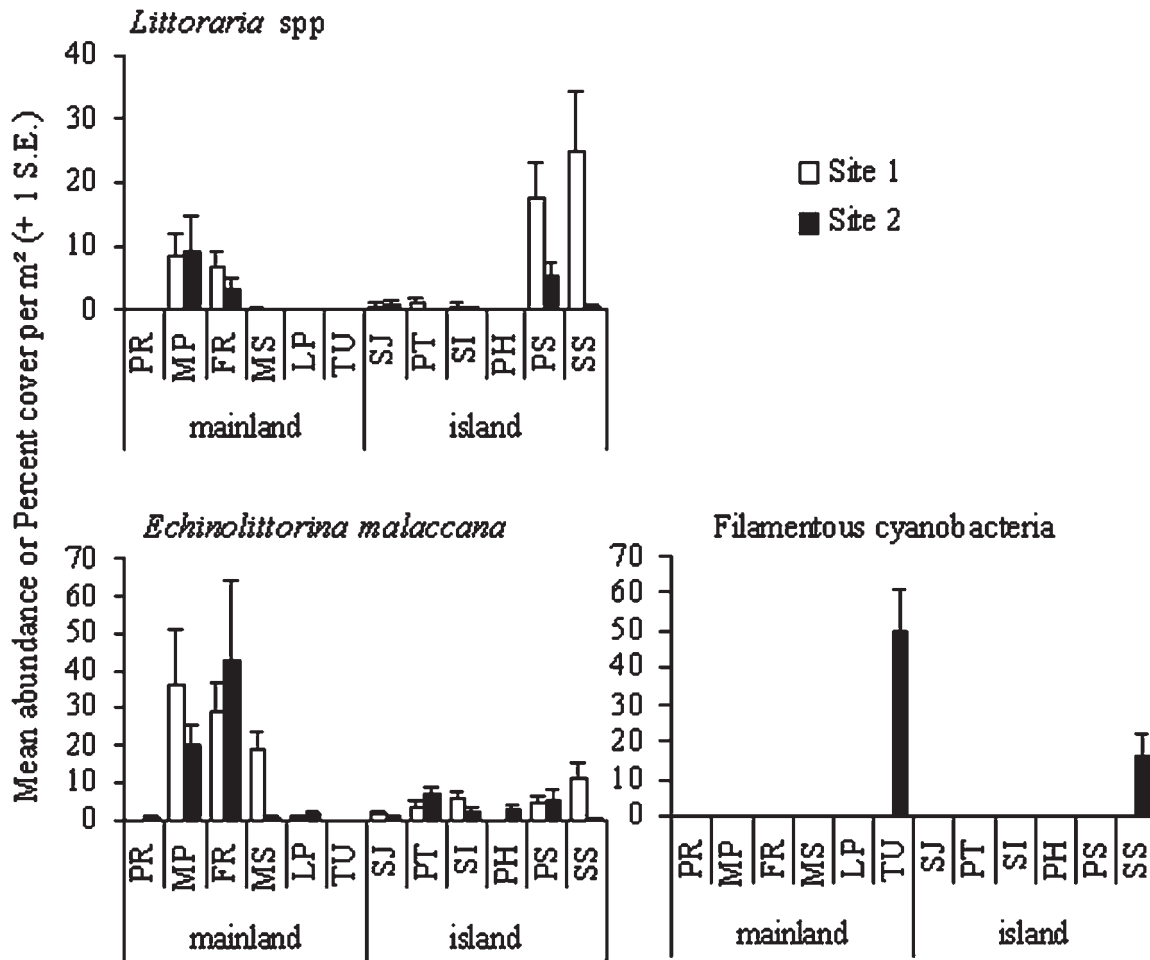
Fig. 3. Mean abundance (± 1 S.E.) of invertebrates and macroalgae in supralittoral shore heights. Data presented as mean numbers per m² for each site in each location.

Lithothamnion also appeared more variable at islands at the quadrat scale (Table 5). This appeared consistent for some at larger spatial scales; abundances of *L. variegata* were significantly more variable among islands than mainland locations (but not between sites) and cover of *Lithothamnion* fluctuated more on islands at the scales of site and location, although the latter could not be tested (Table 5). Filamentous algae (cyanobacteria and *Enteromorpha*) were more variable on the mainland at the scales of quadrat and site (Table 5). Variation in the cover of filamentous cyanobacteria among mainland locations was also very large (Table 5). The cover of turfing algae was more variable on the mainland than islands at the smallest and largest spatial scales, but variability was similar between the two shore types at the scale of site (Table 5). *Peysonnelia* abundances were more variable at islands at the kilometre scale (location) but greater at mainland at smaller spatial scales (Table 5).

DISCUSSION

This study revealed differences between islands and mainland Singapore in assemblage structure and in patterns of spatial variation in abundances of individual taxa occupying hard coastal defence structures. Assemblages were generally less similar among mainland locations than among islands. This is contrary to our expectations, and also disagrees with other authors that demonstrated higher variability (in terms of dissimilarity) at island locations (Benedetti-Cecchi et al., 2003). Although there were compositional differences in mainland and island assemblages, differences between assemblages were due primarily to structure rather than composition. None of the taxa unique to either shore type were distributed at all islands or mainland locations. In fact, many were restricted to single locations, and this was more pronounced at islands than on the mainland. The composition of insular assemblages are expected to differ considerably from those on the mainland because they are affected more by unpredictable patterns of colonisation, growth and extinction that depend greatly on distance from larval sources and size of islands (MacArthur & Wilson, 1967), and in local oceanography (Alexander & Roughgarden, 1996). These are expected to make large contributions towards differences between island and mainland habitats, as well as idiosyncratic differences among island habitats.

In addition, large-scale differences in environmental

Fig. 4. Mean abundance (± 1 S.E.) of invertebrates and macroalgae in highshore assemblages. Data presented as mean numbers per m² for each site in each location.

Fig. 5. Mean abundance (± 1 S.E.) of invertebrates and macroalgae in upper midshore. Data presented as mean percent cover per m² for each site in each location.
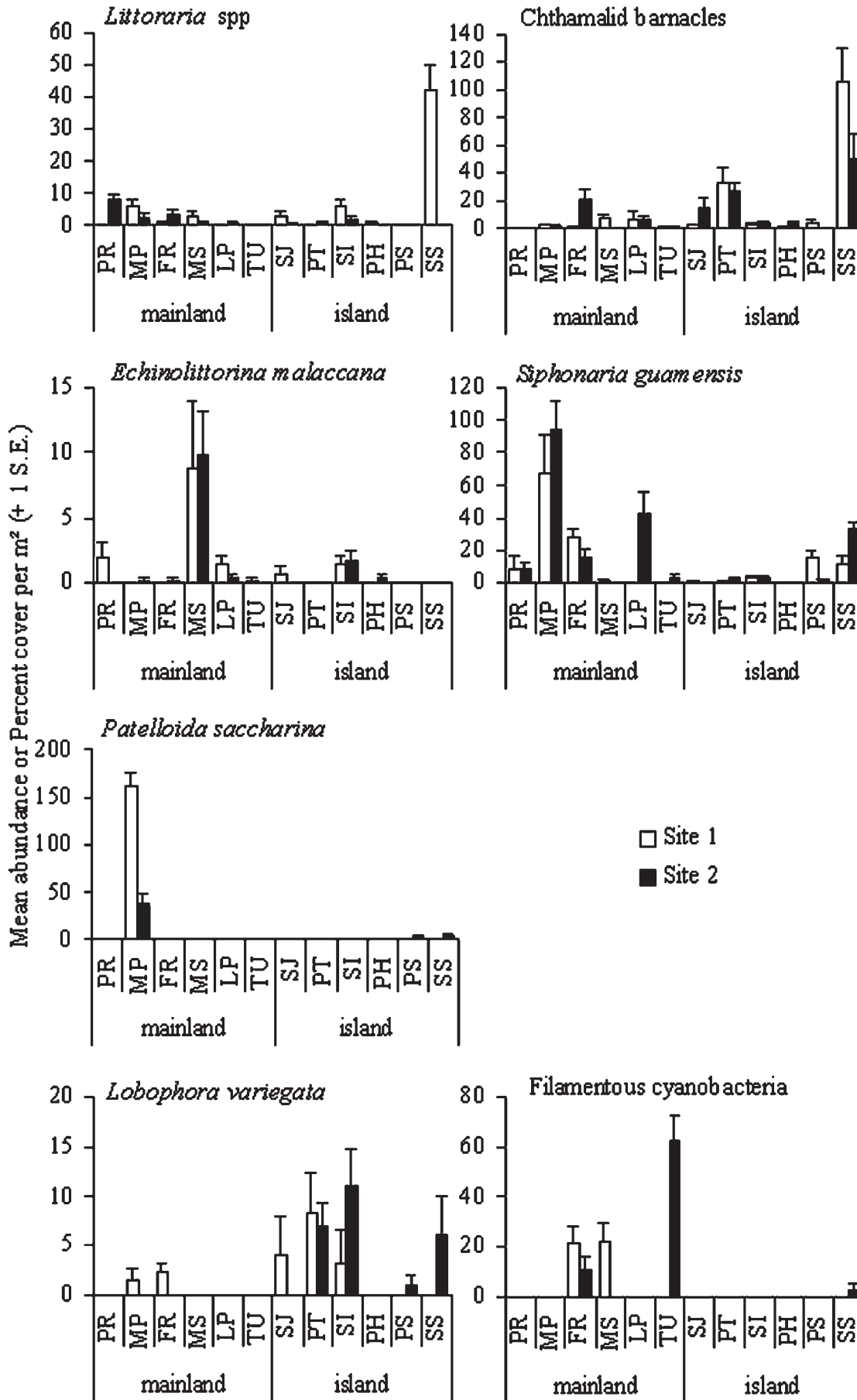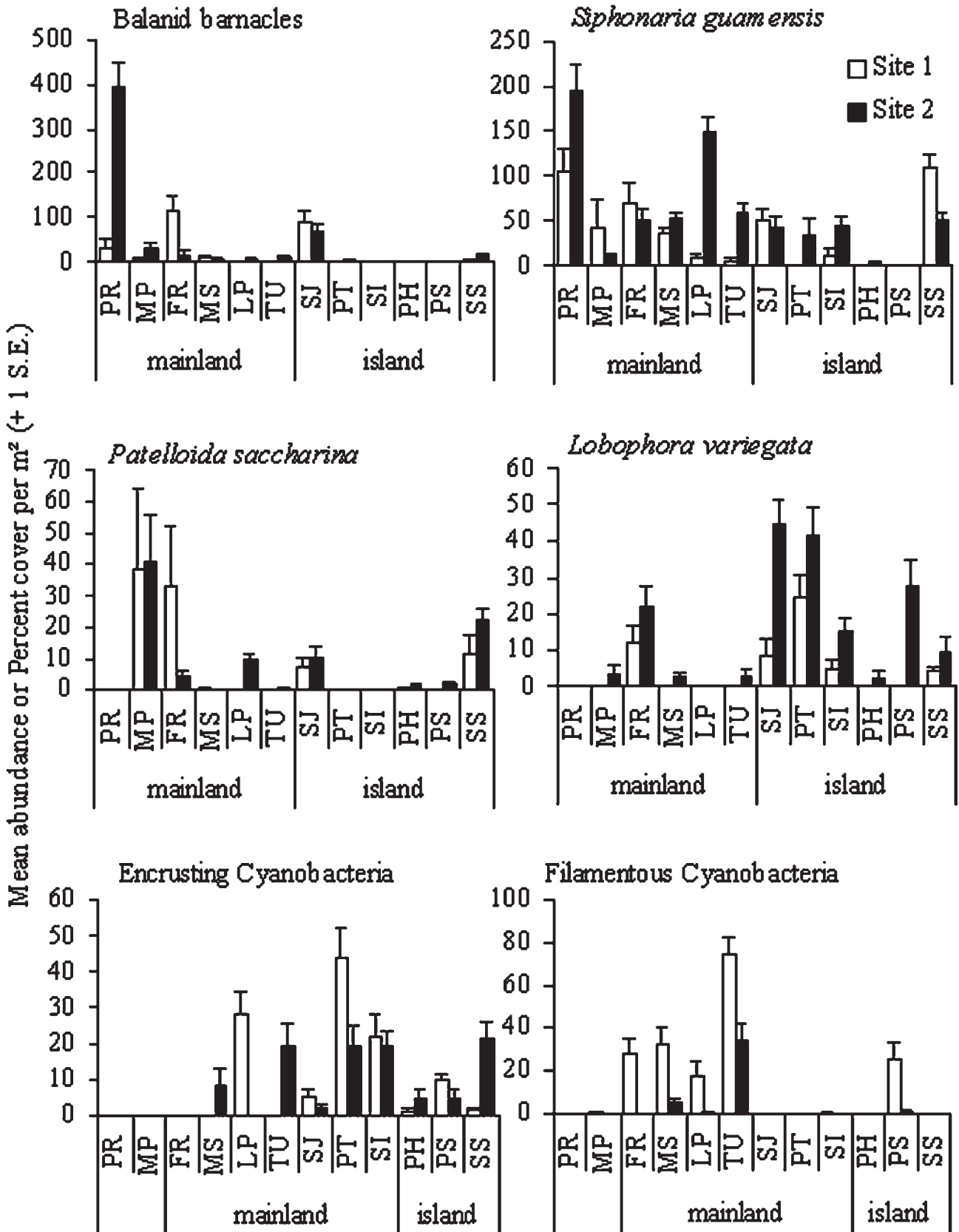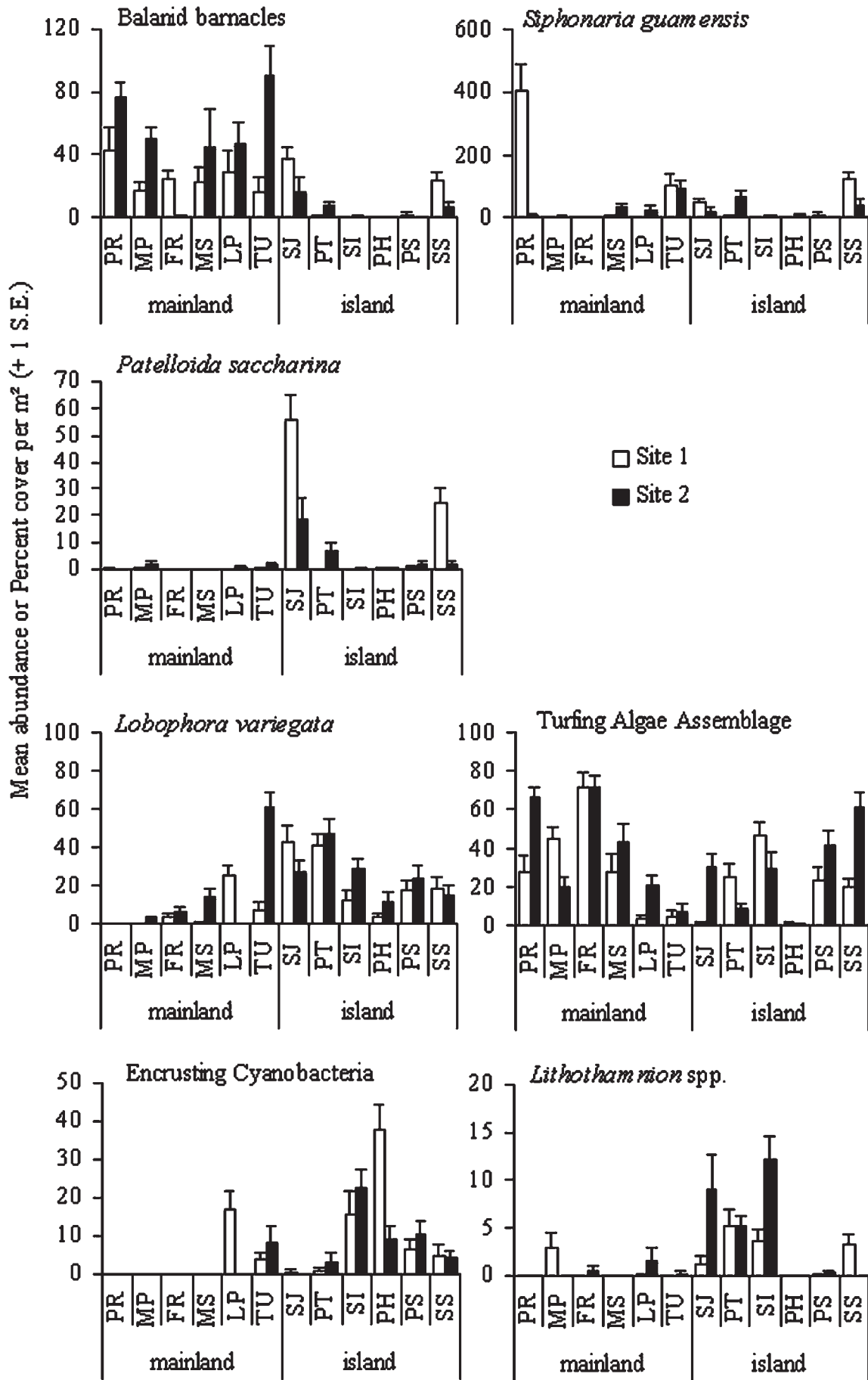
Fig. 6. Mean abundance (± 1 S.E.) of invertebrates and macroalgae in lower midshore. Data presented as mean numbers per m² for each site in each location.

Table 1. PERMANOVA results for the analyses of differences between Shore (fixed, two levels) and Location (nested in Shore, six levels) on square-root transformed abundances of organisms at each shore height (SP = Superlittoral, HS = Highshore, UM = Upper midshore, LM = Lower midshore). * $P < 0.05$, ** $P < 0.01$.

Source	df	SP		HS		LM		UM	
		MS	F	MS	F	MS	F	MS	F
Shore	1	3365.1	0.99	7819.7	2.10*	9949	2.82**	7549.2	3.12**
Location (Sh)	10	3574	2.89**	3720.4	2.10**	3345.3	3.28**	2421	2.38**
Res	9	1234.8		1768.9		1020.3			

Table 2. Comparison between average similarities at individual heights on shore and pooled (SP = Superlittoral, HS = Highshore, UM = Upper midshore, LM = Lower midshore) within shore types and dissimilarity between shore types based on square root-transformed abundance data versus presence absence data.

Shore ht	Abundance			Presence/absence		
	Mainland Similarity	Island Similarity	Between Dissimilarity	Mainland Similarity	Island Similarity	Between Dissimilarity
Pooled	20.59	25.82	81.64	29.14	33.13	73.15
SP	29.99	38.64	69.19	36.67	49.97	56.69
HS	26.53	31.40	77.54	42.19	45.40	62.39
UM	34.93	40.12	71.48	40.53	47.66	64.26
LM	38.62	48.97	64.31	39.77	53.22	62.08

Table 3. Numbers of species (or taxa – see details in text) in each location on each shore type and those species/taxa unique to one shore type. The number of locations at which each taxon was recorded is given in brackets, or the location code if only found at a single location. For location codes see Fig. 1.

Group	Numbers of species/taxa		Unique taxa	
	Mainland	Island	Mainland	Island
Encrusting algae	5	5		
Foliose algae	17	17	*Asparagopsis taxiformis* (MS)	*Dictyosphaeria* (PH)
			Acetabularia (LP)	*Neomeris* (3)
Filamentous algae	6	6		
Sessile animals	18	17	*Ostrea.* (2)	*Tetraclitella* (SS)
			Septifer excisus (MP)	Spirorbidae (PT)
			Trapezium (PR)	*Musculista senhausia* (SI)
			Xenostrobus (2)	*Dendropoma* (SS)
			Perna viridis (2)	*Favia* (SS)
			Ascidiacea (2)	*Platygyra* (PS)
			Porifera (MS)	
Mobile animals	37	31	*Gyrineum natator* (MP)	Diogenidae (SI)
			Nerita lineata (TU)	*Haminoea* (PS)
			Pictocollumbella duclosiana (PR)	*Nerita squamulata* (PH)
			P. scripta (FR)	*Thais echinata* (2)
			Thais clavigera (3)	*T. squamosa* (PS)
			T. jubilea (2)	
			T. rugosa (MS)	
			T. rufotincta (2)	
			T. gradata (PR)	
			Onchidiidae (2)	
			Chiton (4)	

Table 4. Species or taxa contributing ≥ 5% to within shore (mainland or island locations) average similarity or to between shore average dissimilarity for each shore height. Contributions greater than 10% are in bold.

	Supralittoral			Highshore		
	Similarity		Dissimilarity	Similarity		Dissimilarity
	Mainland	Island	Main.vs Island	Mainland	Island	Main.vs Island
Chthamalid barnacles	1.51	5.71	9.88	**18.85**	**33.78**	**12.24**
Echinolittorina malaccana	**84.87**	**64.92**	**24.97**	**13.95**	1.82	5.18
Littoraria spp.	7.73	**16.67**	**14.95**	**10.47**	7.44	6.22
Siphonaria guamensis	0.94	0.81	5.44	**35.09**	**10.74**	**12.75**
Filamentous cyanobacteria	0.00	0.00	**11.27**	**12.71**	0	**12.31**
Lobophora variegata	0.00	1.03	5.26	0.46	**18.73**	**10.78**
Encrusting cyanobacteria	0.00	0.55	3.46	0.00	7.75	9.91

	Upper midshore			Lower midshore		
	Similarity		Dissimilarity	Similarity		Dissimilarity
	Mainland	Island	Main.vs Islandd	Mainland	Island	Main.vs Island
Balanid barnacles	**16.23**	2.67	9.30	**23.77**	2.58	7.05
Siphonaria guamensis	**38.60**	**13.96**	9.84	9.19	7.64	7.74
Filamentous cyanobacteria	**15.68**	0.42	**11.05**	2.66	0.34	4.43
Lobophora variegata	3.14	**23.94**	**10.04**	8.61	**29.95**	9.52
Encrusting cyanobacteria	2.40	**29.85**	**10.38**	1.11	**13.36**	7.38
Turfing algal assemblage	6.74	6.14	8.06	**40.82**	**21.90**	8.80

Table 5. Estimates of variance components and one-tailed *F*-ratios comparing patterns of spatial variation between mainland and island locations. * P < 0.05; ** P < 0.01; NS = Not significant.

	Location (df 5,5)			Site(L) (df 6,6)			Quadrat (S(L)) (df 228,228)		
	Mainland	Island	Test	Mainland	Island	Test	Mainland	Island	Test
Balanids	3.539	9.509	NS	80.260	-0.000200	–	487.640	66.720	M > I**
Chthamalids	2.573	13.020	I > M*	3.603	13.530	NS	157.590	89.670	M > I**
Littoraria	0.131	-0.176	–	-0.0370	2.358	–	3.859	9.863	I > M**
E. malaccana	1.149	-0.0150	–	-0.119	0.0530	–	38.150	1.818	M > I**
P. saccharina	15.040	1.859	M > I*	6.533	0.4080	M > I**	95.460	15.850	M > I**
S. guamensis	35.790	18.980	NS	55.430	11.160	M > I*	885.530	141.400	M > I**
Encrusting cyanobacteria	-1.363	-6.652	–	13.140	37.260	NS	75.780	306.800	I > M**
Filamentous cyanobacteria	133.600	-0.096	–	31.760	3.828	M > I*	472.000	68.760	M > I**
Enteromorpha	-1.012	0.100	–	26.430	0.151	M > I**	101.700	15.850	M > I**
L. variegata	0.181	34.840	I > M**	19.950	10.480	NS	169.100	469.600	I > M**
Lithothamnion	-0.00800	0.404	–	0.0330	0.700	I > M**	2.180	16.090	I > M**
Peysonnelia	0.00100	0.667	I > M**	6.327	0.450	M > I**	40.840	29.530	M > I*
Turfing algae	59.670	8.916	M > I*	13.680	30.690	NS	615.800	365.600	M > I**

conditions may structure assemblages between islands and mainlands, as well as among locations. Distinct differences were observed in mainland vs. island assemblage composition among congeners, as well as within functional groups. Predatory thaids were more diverse at mainland, with 6 species unique to that shore type. *Thais echinata* and *T. squamosa,* which appear confined to clear waters (Tan, 1995) were observed only from offshore locations. Taxa richness and densities of filter feeders were higher on mainland than at islands, where seston availability is usually lower. The occurrence of *Perna viridis* at Pasir Ris and Marina South, *Xenostrobus* sp. at Pasir Ris and Marine Parade, and *Nerita lineata* at Tuas are may be related to the estuarine conditions at those locations.

Assemblages from different mainland and islands were found to differ primarily in relative abundance of a very small subset of the species sampled. Discrimination between shore types was greater in highshore and upper midshore assemblages than in supralittoral and lower midshore assemblages. The poor discrimination between shore types in supralittoral assemblages may be attributable to a very small species pool (consisting primarily of littorinid gastropods and chthamalid barnacles) that can persist in the relatively harsh conditions. Overall, very few taxa in each assemblage made important contributions to Bray-Curtis measures of similarity within shore types, and even fewer to dissimilarity between shore types. As a result, although shore types could be characterised by several taxa, very few taxa were useful in discriminating between shore types at any shore height. Balanid barnacles and filamentous cyanobacteria characterised midshore assemblages only on the mainland, while encrusting cyanobacteria and *L. variegata* characterised islands, but only *L. variegata* consistently discriminated between shore types at these heights.

Although the differences between islands and the mainland primarily arose from differences in relative abundances of taxa, the effect of shore type was only significant for few taxa. Significant effects of shore type were detected on the abundances of *L. variegata* and *Lithothamnion* spp. and encrusting cyanobacteria, with other species of encrusting algae occurring in greater abundances on islands. With the exception of *Sargassum* spp., which are reef-associated, greater abundances of foliose algae were recorded from the mainland. Algal effects between shore types may be related to nutrient and grazing pressures. Meta-analyses of nutrient enrichment and herbivore exclusion experiments demonstrated very strong response of tropical algae to herbivore removal (Burkepile & Hay, 2006). Herbivore exclusion had significant positive effects on upright macroalgae, but strongly decreased abundance of crustose algae under either nutrient regime (Burkepile & Hay, 2006). Grazing pressure from greater abundances of *Echinolittorina* and *Siphonaria* on the mainland is likely to also contribute to lower cover of encrusting cyanobacteria in the upper intertidal.

Abiotic interactions also likely to also be important -

survival of algae in high-energy intertidal is related to the size and strength of the alga and the nature of the substratum (Black & Peterson, 1987; Carrington, 1990), with a general decrease in frond size and increase in attachment strength as hydrodynamic forces increase (Gaylord et al., 1994; Denny, 1999). Large, but non-significant effects of shore were detected for balanid barnacles and *E. malaccana* on mainland. The higher abundances of balanid barnacles on mainland rather than island locations run contrary to higher barnacle densities recorded at exposed compared to sheltered tropical shores (Coates, 1998). This is unlikely due solely to smaller scale processes such as type and texture of the substratum (see Raimondi, 1988), but a likely a combination of oceanographic processes and local features of the environment (Hutchinson & Williams, 2001).

One major finding of this study was the magnitude of variability that occurred over relatively small spatial scales. Among-location differences in the abundance of taxa were often large and significant in both shore types, even along the same coastline (viz Marine Parade, Fort Road and Marina South). There were also considerable differences between sites. Large inter-site variation within a location (or shore) has previously been documented in California by Foster (1990), on exposed and sheltered rocky shores in Sydney (Underwood, 1981; Underwood & Chapman, 1998) and Canada (Archambault & Bourget, 1996), but this is demonstrated for the first time on breakwaters in the Indo-Pacific. The similarity in design and relatively homogenous (mainly granite) substratum provided by breakwaters should have reduced sources of habitat variability. Underwood (1981) excluded gradients in wave action as a causal factor on exposed rocky shores, and while causality was not specifically examined by Archambault & Bourget (1996), they noted that differences in rates of response to localised disturbances could contribute to spatial differences within a shore. On sheltered shores, consistent differences (in space and time) in recruitment intensities have been recorded between sites (Underwood & Chapman, 1998). Pronounced inter-site differences in the recruitment intensities of species such as *S. guamensis* have also been recorded at our study locations (unpublished data), but whether this is temporally consistent, and the extent to which these differences translate to differences among assemblages is still undetermined.

Further differences between mainland and island assemblages were revealed by comparison of spatial variances. Algal turfs, *Siphonaria guamensis* and balanids were more abundant at mainland, where variation was greater at the scale of quadrat, but often non-significant at larger spatial scales. Conversely, Chthamalids and *Peysonnelia* were more abundant at islands frequently exhibited greater variation at islands at larger spatial scales, variation was significantly greater at smaller scales on the mainland. Again, causality is unclear and likely to involve complex interactions among abiotic as biotic processes. The spatial variations in patterns of assemblages described here are complex and inconsistent. It would have been ideal if natural rocky shores were included in the sampling design for comparisons, but with extensive coastal re-design in

Singapore there were insufficient natural contiguous rocky shores for an equivalent study.

Urban coastal structures not only provide an alternative habitat for marine organisms, but in themselves have the potential to alter communities in adjacent natural habitats (e.g. Connell & Glasby, 1999). Research has demonstrated a higher proportion of successful establishment of introduced species in artificial habitats, perhaps due to the imbalance in species turnover rates (Rebele, 1994). It has been reiterated by many authors that understanding how assemblages occupying urban habitats are structured is critical sustainable management of increasingly urbanised coastlines, but as yet these processes remain unclear. Historically, marine ecology has borrowed heavily from models developed in terrestrial environments. Under scrutiny, the validity of this practice has often been shown to be inappropriate (Underwood & Denley, 1984). The application of ecological theory developed in relatively undisturbed marine environments to urban contexts is a current and emerging challenge (Bulleri, 2006). Urban communities are often in a state of disequilibrium due to a combination of disturbance regime and novelty of habitat (Rebele, 1994), and theories based on communities in equilibrium may be highly inappropriate for urban ecosystems. Collectively, the findings of this study do not support established models for greater stochasticity on islands than mainland with regard to colonisation, assemblage composition or spatial variability.

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