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Succession of seawall algal communities on artificial substrates

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Abstract. Increasing coastal urbanisation has resulted in the extensive conversion of natural habitats with man-made hard structures, such as seawalls, which tend to support communities with low biodiversity. While seawalls are often colonised by species that can be found on natural rocky shores, some studies have shown that their community structure and dynamics are markedly different. However, relative to rocky shores, ecological research on seawalls is limited, and this is especially so in the tropics. To our knowledge, no research to date has examined, in the context of artificial coastal defences, the ecological succession of communities on substrates of varying complexity near the equator. Hence, the aim of the present study is to quantify the patterns of algal succession on 'simple' and 'complex' concrete tiles and granite controls mounted onto seawalls at two offshore sites in Singapore (Pulau Hantu and Kusu Island). Our results revealed the development of an algal assemblage that is typical of many tropical rocky shores; i.e., ephemeral green turfs succeeded by high cover of a grazer-resistant mat of erect and encrusting algae with the foliose macroalgal functional group poorly represented. All treatments developed macroalgal cover by the first month. Final mollusc assemblage structure after one year was also quantified, as molluscs are important consumers in structuring algal assemblages. While the succession trajectories were similar at both sites, the rates of succession differed. The transitions from ephemeral green turfs to the mixture of red and brown macroalgal assemblages, as well as the development of encrusting coralline and non-coralline algae, occurred two months later at Pulau Hantu (the more sheltered site). Granite controls did not support foliose or articulated calcareous algal functional groups within the sampling period, probably due to material and structural/topographical differences. Documenting such small-scale spatial patterns of algal distribution represents the first step towards a better understanding of the processes occurring in artificial habitats—and this should ultimately aid their reconciliation.

Key words. Algae, equatorial tropics, seawalls, ecological succession, Singapore

INTRODUCTION

Coastal regions around the world are increasingly becoming urbanised (Moschella et al., 2005; Chapman & Underwood, 2011). More than 67% of the global population is concentrated on or near coastlines (Hammond, 1992; Atilla et al., 2003; Bulleri et al., 2005) a figure that is expected to double within the next two decades (Norse, 1995; Gray, 1997). Urbanisation has resulted in the extensive replacement of natural shorelines with artificial coastal defences such as seawalls, groynes, and breakwaters (Airoldi et al., 2005; Bulleri & Chapman, 2010). Seawalls are often constructed to protect shorelines from land subsidence, erosion and flooding—events which are becoming more frequent due to human influence on coastal processes (such as off-shore dredging and land reclamation), rising sea levels, and more intense storms associated with climate change (Airoldi et al., 2005; Moschella et al., 2005).

Presently, there is a "strong scientific consensus" behind the current best estimate of global sea level rise of 0.4–0.6 m by 2100 (French & Spencer, 2001; Nicholls & Cazenave, 2010). While the mean may seem small, inter-annual variability and acceleration is less predictable (and requires at least 10 to 20 years to detect) (French & Spencer, 2001). Even the most conservative sea level rise prediction is still sufficient to exacerbate existing problems of erosion, habitat loss, and flood risk to coastal property, and the construction of seawalls is rapidly becoming a primary means of mitigating such threats. As a habitat, seawalls differ from natural shores fundamentally in material type, slope and structural complexity (Chapman & Bulleri, 2003; Chapman, 2006), which together alter community composition and dynamics, diversity, and relative abundance of littoral species (Chapman, 2003; Bulleri & Chapman, 2004; Bulleri et al., 2004). Despite the proliferation of coastal defences, which directly reduces biodiversity and results in habitat loss and fragmentation, only recently have studies documented the assemblages inhabiting them or examined their ecological impacts (e.g., Chapman & Bulleri, 2003; Firth et al., 2013). The lack of understanding in the way in which assemblages develop and

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are maintained (especially in the tropics) has therefore limited the ability of coastal engineers and managers to predict the community responses to these novel habitats. In particular, a better understanding of dynamics of algal succession on artificial structures is needed. As an assemblage, algae can significantly alter the complexity of the substrate as well as levels of shading and moisture (habitat conditions), directly facilitating the colonisation of other species (Bruno et al. 2003).

Ecological succession, i.e., the sequence of colonisation and replacement of species after a disturbance (Connell & Slatyer, 1977), on rocky intertidal shores is relatively well studied, especially in temperate regions with several models and mechanisms of succession have been proposed (Farrell, 1991; Sousa, 2001; Petraitis & Dudgeon, 2005). For instance, in early views of succession, community development on rocky shores was thought to be a highly deterministic process resulting in a "climax stable state" maintained by strong competitive interactions and the colonists' influence on habitat structure (Odum, 1969; Connell & Slatyer, 1977). Later, however, the idea that different assemblages might represent alternative stable states gained momentum; i.e., the rates and trajectories of succession may be altered by various factors and processes such as the scale of perturbation and local consumer effects (Petraitis & Latham, 1999). Nevertheless, it cannot be assumed, that the same mechanisms and models of succession of rocky shores will apply to artificial coastal structures. While some basic research on the succession of species has been carried out on temperate seawalls, to our knowledge, no similar studies have been conducted in the equatorial tropics.

As an island city-state, Singapore is a quintessential example of the many issues associated with near-shore urbanisation; for instance, except for a 300 m stretch of beach at Labrador Park, coastal modifications have destroyed all of the natural shoreline along the southern coast of the main island, a distance of over 60 km (Todd & Chou, 2005; Huang et al., 2006). Most of this modification is a direct result of land reclamation, which has increased Singapore's land area by ~25%, with another 100 km^2 predicted to be reclaimed by 2030 (Hilton & Manning, 1995; Chou et al., 1998). Land reclamation methods in Singapore usually require seawalls to guard against erosion and stabilise the fill material (Tan, 1976; Wong, 1992). To date, the total length of seawalls is 319 km, constituting 63.3% of the coastline, and it is expected to exceed 600 km by 2030 with seawalls accounting for most of this increase (Lai et al., 2015). With rising sea levels, more seawalls are expected to be built to defend the country's 505 km coastline (Lai et al., 2015). Despite their pervasiveness, knowledge of seawall ecology is in Singapore is extremely limited, as is the case for tropical SE Asia in general. However, intertidal assemblages on seawalls around Singapore's mainland and Southern Islands have been recently documented and compared by Lee et al. (2009a) and Lee & Sin (2009) and several new species records of marine algae found (Lee et al., 2009b).

As the construction of seawalls will inevitably continue, understanding their environmental, biological and ecological impact is critical. This knowledge can be integrated into engineering practices (Bergen et al., 2001; Airoldi et al., 2005), which should aid the enhancement and conservation of urban shore biodiversity (Savard et al., 2000; Chapman & Underwood, 2011). Hence, the aim of the present study is to quantify the patterns of succession on tiles mounted onto seawalls at two offshore sites (Pulau Hantu and Kusu Island, Singapore) over a period of 12 months. To our knowledge, this represents the first study quantifying the successional trajectory of algae on artificial coastal defense structures in the tropics. Final mollusc assemblage structure after one year was also quantified, as consumers are fundamental in structuring algal assemblages.

MATERIAL AND METHODS

Study sites. Singapore is located 1°15' north of the equator at the southern tip of the Malay Peninsular in Southeast Asia. It is hot and wet all year round with relatively uniform temperatures. Tides are semi-diurnal and natural wave energy is generally low (Hilton & Chou 1999). Many near-shore habitats have been replaced by coastal defences (Lai et al., 2015). The study was conducted along granite rip-rap seawalls at two island sites: Pulau Hantu (1°13'34" N, 103°45'0" E) and Kusu Island (1°13'22" N, 103°51'40" E) (Fig. 1).

Pulau Hantu (13.0 ha) is located 7 km from Singapore Island (Wong, 1988). In 1974, most of its reef flats were reclaimed and granite seawalls were erected around the island's perimeter. Kusu Island (7.6 ha) is located 5.6 km from Singapore Island's southern shore but is more exposed to wave action (Wong, 1988). Similar to Pulau Hantu, it was reclaimed in 1974.

Tile fabrication and experimental design. As part of a larger experimental study aimed at testing whether topographically complex concrete tiles attached to seawalls can enhance their biodiversity, concrete tiles (400 × 400 × 32 mm^3,

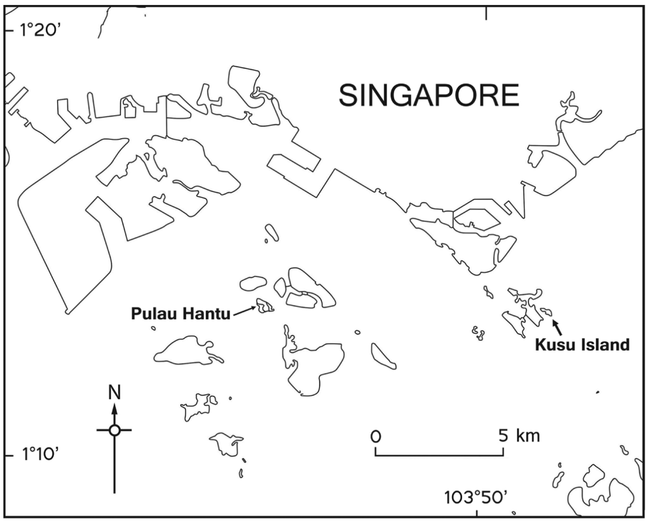

Fig. 1. Location of the two study sites in relation to Singapore's southern coastline.

Table 1. Algal functional categories used in this study and their main components.

Functional Group	Dominant Component Taxa
Microalgae/biofilm	Unidentified cyanobacteria and diatoms
Ephemeral green turf algae	*Ulva* spp. (formerly known as *Enteromorpha* spp.)
Red/brown algal assemblage	*Parviphycus antipae*, *Gelidiopsis variabilis*, *Dictyota* spp. and Ceramiales
Encrusting algae	Ralfsiaceae and/or Neoralfsiaceae, and crustose coralline algae
Articulated calcareous algae	*Jania* spp.
Foliose algae	*Padina* spp. only

width × length × depth) representing two levels ('simple' and 'complex') of complexity, and two different structural designs ('pits' and 'grooves'), plus a granite control, were designed with the aid of the software CASU (Loke et al., 2014) and fabricated. Five replicates of each tile type were attached randomly onto granite seawalls (~0.5 m above Chart Datum) at the two islands (Fig. 1), creating a two-way ANOVA design with 'Site' and 'Tile type' as factors.

Field sampling, data extraction and analyses: Algal succession. Tiles were monitored (i.e., photographed) monthly for 12 months from July 2011 to June 2012, before they were collected in the final month. Algal cover was quantified using CPCe image analysis software (Kohler & Gill, 2006), with percentage cover tabulated from 40 random point intercepts per tile. The algae were identified to functional groups listed in Table 1; *Padina* spp. was the only visually dominant species of foliose macroalgae. A margin of 10 mm around each tile was not examined (i.e., only an area of 390 × 390 mm^2 was considered) to avoid edge effects.

Field sampling, data extraction and analyses: Final molluscan assemblage structure. All epibiotic animals were sampled by scraping and picking the specimens off each tile for 10 minutes and then quickly placing them into self-sealing plastic bags. These were frozen in a −20°C freezer until they could be sorted, identified and quantified. Only molluscs were analysed in this study; these were identified and counted using a dissecting or compound microscope. Individuals were identified to species or morphospecies level.

Variation in the community composition across both sites was examined using non-metric multidimensional scaling (MDS) in PRIMER v6 (Clarke & Gorley, 2006). MDS ordination was based on Bray-Curtis similarities calculated on log(X+1) transformed abundance data (Clarke & Warwick, 2001). Differences in community composition between the sites were assessed using a one-way analysis of similarities (ANOSIM). To identify the percentage contribution that each species made to the measures of dissimilarity among sites, and within each site, a 'similarity percentages' routine (SIMPER) was performed.

RESULTS

Succession on bare concrete and granite surfaces was rapid in all treatments, with biofilm and ephemeral green turfs developing by the first month (Figs. 2, 3), and consisting of 89% of the tile surface on average. The shift from biofilm and ephemeral green turfs (dominated by *Ulva* spp.), to the more diverse mix of red/brown algal assemblage (consisting mainly of *Parviphycus antipae*, *Gelidiopsis variabilis*, *Dictyota* spp. and Ceramiales), differed between sites. This shift, however, occurred only on concrete tiles and was similar between simple and complex tiles; that is, the transition never took place on the granite tiles (Figs. 2, 3). Quantification of algal cover revealed that the pattern of transition occurred on concrete tiles placed at Kusu Island between the 4^{th} to 5^{th} months whereas the same pattern only occurred at Pulau Hantu between the 6^{th} to 7^{th} months (i.e., two months later).

Encrusting algae (consisting mainly of the leathery crustose brown alga under the family Ralfsiaceae and/or Neoralfsiaceae, and crustose coralline algae), developed 1−2 months after deployment at Kusu Island, while at Pulau Hantu, they were seen only 3−4 months after deployment (Fig. 3). Granite tiles did not support *Padina* spp. or articulated calcareous algal functional groups (e.g., *Jania* sp.) within the sampling period. These minor functional groups were however present on the concrete tiles but at very low abundances and always with the presence of the later dominant red/brown algal assemblage. Ephemeral green turfs, which dominated initially, later recurred only in small patches. There was no apparent difference in the visual cover of algal functional groups between complex and simple tiles as well as between the 'pits' and 'groove' designs throughout the study period (Fig. 2).

Molluscs comprised ≈78% of the animal epibiota found on the tiles. Mean (±SD) and maximum densities of abundant mollusc species at each study site were calculated (Table 2). Community composition between sites also differed significantly between sites (Fig. 4; ANOSIM, global $R = 0.454$, $p = 0.001$). SIMPER analysis revealed that 13.44% of the total dissimilarity between the two sites was associated with the carnivorous drill, *Drupella margariticola* (formerly known as *Cronia margariticola*) (Table 3). This species was also the largest contributor to the average similarities within both site groups (Table 4). The species that contributed more than 5% to the similarities within each site and dissimilarities between the sites are presented in Tables 3 and 4.

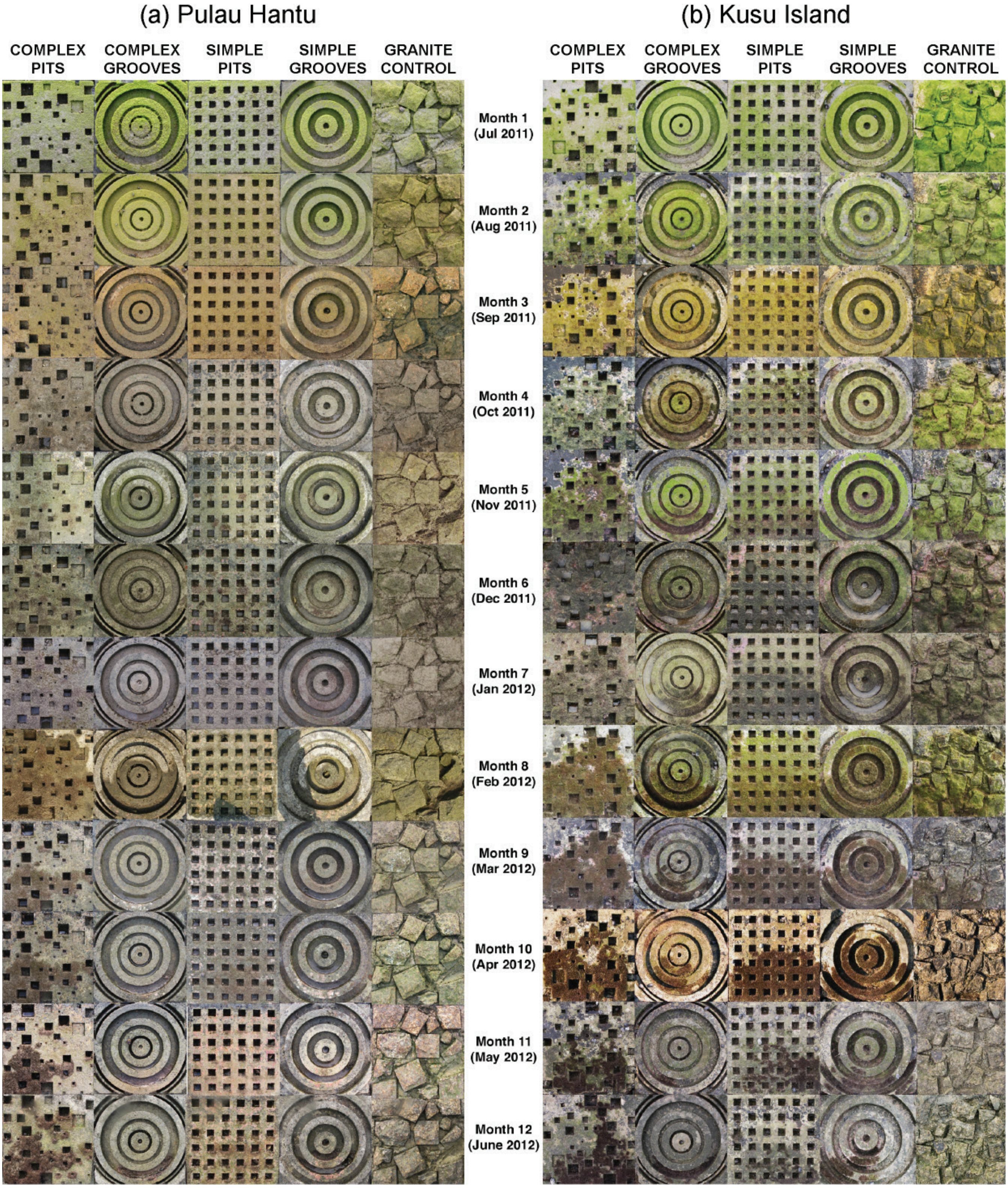

Fig. 2. Visual representation of the monthly change in algal composition on each tile type at (a) Pulau Hantu and (b) Kusu Island.

Table 2. Mean (±SD) and maximum densities of abundant mollusc species at each study site: (a) Pulau Hantu and (b) Kusu Island (n=5). 'NA' (Non Applicable) is used when only single counts were recorded and hence SD could not be calculated.

Species	Density (per tile)					
	(a) Pulau Hantu			(b) Kusu Island		
	Mean	SD	Maximum	Mean	SD	Maximum
Nerita chamaeleon	2.47	2.45	9	0.04	NA	1
Nerita undata	–	–	–	3.80	3.19	11
Drupella margariticola	7.74	6.12	26	8.52	5.45	20
Morula musiva	1.50	1	3	0.08	NA	1
Pictocollumbella ocellata	1.60	1.34	4	2.54	2.15	7
Nassarius livescens	4.50	4.51	11	1.67	1.16	3
Nassarius crenoliratus	1.75	0.89	3	–	–	–
Patelloida saccharinoides	–	–	–	1.67	1.16	3
Clypeomorus batillariaeformis	3.00	2.30	8	–	–	–
Cerithium zonatum	2.44	1.92	7	–	–	–
Euplica scripta	1.67	0.82	3	–	–	–
Pardalina testudinaria	1.63	1.06	4	–	–	–
Arca navicularis	1.67	0.58	2	–	–	–
Acanthopleura gemmata	1.00	NA	1	9.40	8.08	19
Pinctada sp.	1.29	0.49	2	2.50	2.12	4
Siphonaria atra	–	–	–	2.30	0.82	3
Siphonaria guamensis	–	–	–	2.25	1.42	5
Cellana radiata	1.60	0.89	3	0.08	NA	1
Isognomon legumen	1.20	0.45	2	4.82	5.04	23
Modiolus sp.	6.63	12.09	36	2.13	1.36	5
Tellinid (*Semele* sp.)	2.00	1.73	4	–	–	–
Nassarius pauper	1.50	0.71	2	–	–	–
Littoraria sp.	3.50	2.12	5	–	–	–
Total	18.56	17.53	81	21.48	16.32	64

Table 3. Species discriminating community differences between Kusu Island and Pulau Hantu. 'Average contribution' refers to the mean contribution of the species to the average similarity within the site; 'ratio' was calculated by dividing the 'average contribution' by the standard deviation.

Species	Mean Abundance		Average Contribution	Ratio	% Contribution
	Kusu Island	Pulau Hantu			
Drupella margariticola	1.2	1.0	10.2	1.2	13.4
Clypeomorus batillariaeformis	0.0	0.5	6.1	0.9	8.0
Nerita undata	0.5	0.0	5.9	1.2	7.8
Cerithium zonatum	0.0	0.4	4.7	0.7	6.2
Isognomon legumen	0.4	0.0	4.5	1.0	5.9
Siphonaria atra	0.3	0.0	4.1	0.7	5.4
Pictocollumbella ocellata	0.3	0.1	4.1	0.9	5.4
Siphonaria guamensis	0.3	0.0	4.0	0.8	5.3
Nerita chamaeleon	0.0	0.3	3.9	0.8	5.1

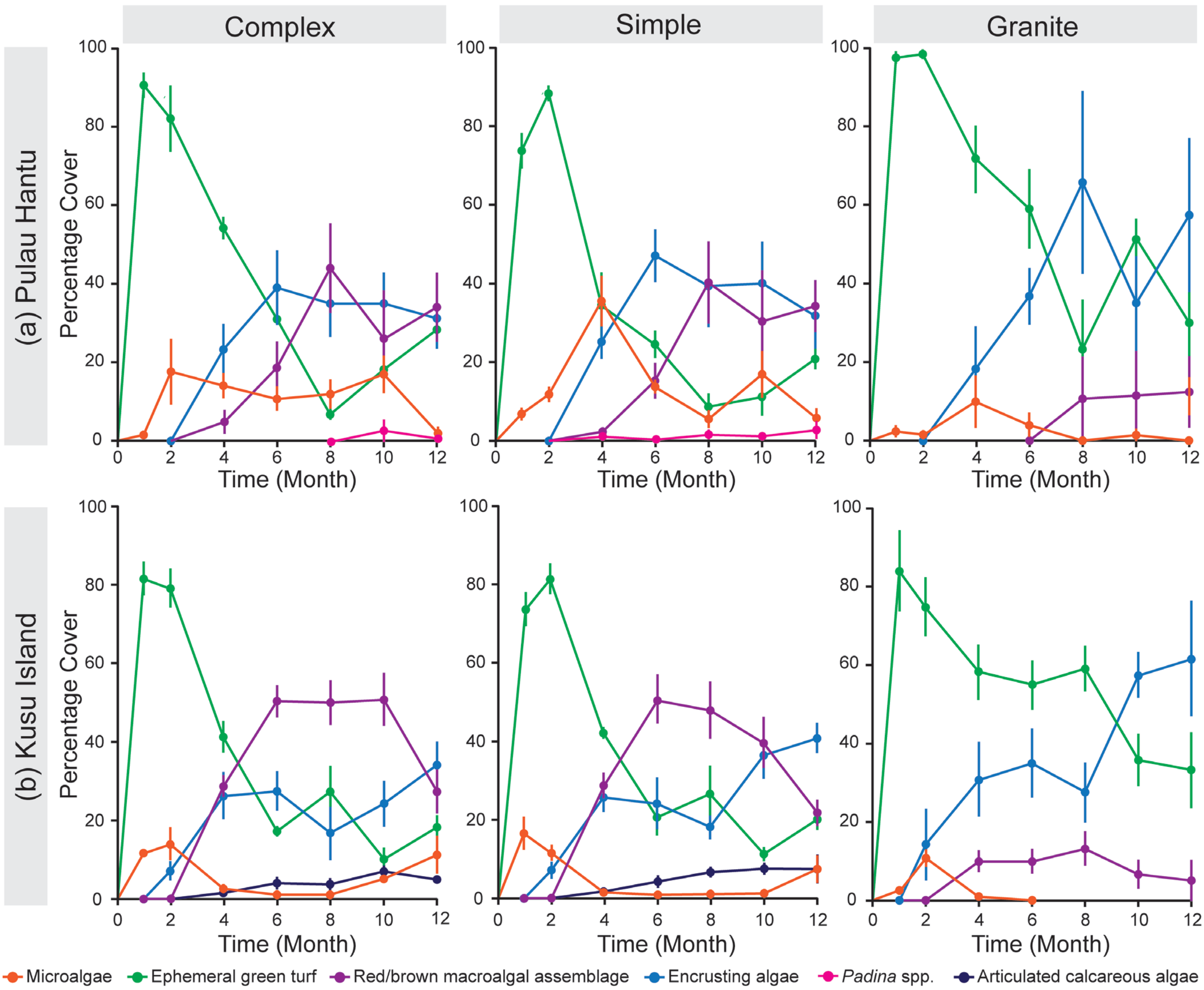

Fig. 3. Variation in mean percentage cover (±1SE; n=3) of visible macroalgae and biofilm for each tile type (complex, simple, granite), at (a) Pulau Hantu and (b) Kusu Island, with time.

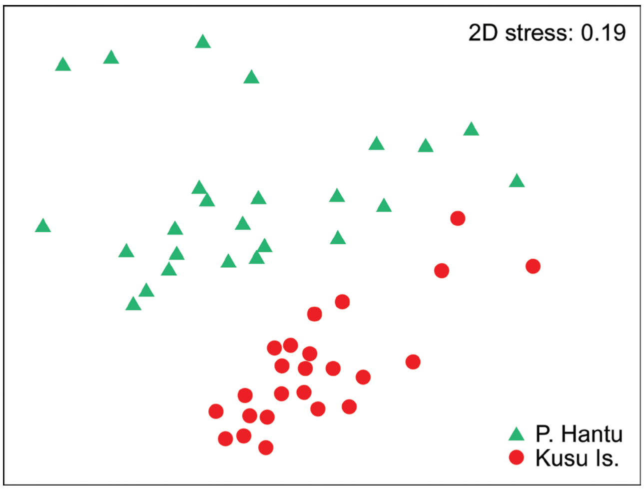

Fig. 4. Non-metric multidimensional scaling (MDS) ordination of the mollusc assemblage at each site (Pulau Hantu and Kusu Island).

DISCUSSION

While seawalls are often colonised by species that can be found on natural rocky shores (Chapman & Bulleri, 2003; Pister, 2009), their community structure, dynamics and abundances are markedly different—at least in the temperate systems that have been studied to date (Bulleri & Chapman, 2004; Bulleri et al., 2005). For example, artificial structures often host a lower number of species compared to natural rocky shores with no species unique to them (Firth et al., 2013; Lai, 2013). In the tropics, ecological research on seawalls is limited and no previous studies have examined the ecological succession of communities on artificial substrates near the equator. Our results revealed the development of an algal assemblage that is typical of many tropical rocky shores; i.e., ephemeral green turfs succeeded by a high cover of grazer-resistant mat of erect and encrusting algae with the foliose macroalgal functional group poorly represented (Kaehler & Williams, 1998; Williams et al., 2000).

While the succession trajectories were similar at both sites, the rates of succession differed. The transitions from ephemeral

Table 4. Characteristic species within sites: (a) Kusu Island and (b) Pulau Hantu. 'Average contribution' refers to the mean contribution of the species to the average similarity within the site; 'ratio' was calculated by dividing the 'average contribution' by the standard deviation.

Species	Mean Abundance	Average Contribution	Ratio	% Contribution	Cumulative %
(a) Kusu Island					
Drupella margariticola	1.2	25.7	2.3	60.0	60.0
Nerita undata	0.5	5.3	1.1	12.5	72.5
Isognomon legumen	0.4	3.6	0.8	8.4	80.1
Siphonaria guamensis	0.3	2.4	0.5	5.5	86.4
Pictocollumbella ocellata	0.3	2.3	0.5	5.4	91.7
(b) Pulau Hantu					
Drupella margariticola	1.0	15.8	1.5	51.7	51.7
Clypeomorus batillariaeformis	0.5	5.3	0.7	17.4	69.1
Nerita chamaeleon	0.3	2.9	0.6	9.5	78.6
Cerithium zonatum	0.4	2.7	0.5	8.7	87.2

green turfs to the mixture of red and brown macroalgal assemblage, as well as the development of encrusting coralline and non-coralline algae, occurred two months later at Pulau Hantu. As the two sites differed mainly in their exposure it is possible that water energy could have played an important role, since disturbance induced by hydrodynamic forces are known to influence and control the distribution and abundance of intertidal organisms (Denny, 1985; Denny, 2006). Adjacent shores can be characterised by very different habitat types and ecological communities depending on local flow conditions (Bertness et al. 2002); for instance, shores with greater exposure to wave-forces and high flow tend to have greater densities of grazer and predator populations as well as enhanced recruitment (Leonard et al., 1998; Davis, 2002). The site at Pulau Hantu was protected by a nearby patch reef and therefore particularly sheltered (Todd et al., 2004), whereas Kusu Island was much more exposed to shipping traffic and associated ship-wakes (pers. obs.).

Grazing is known to exert a great influence on the distribution, species diversity and abundance of algae on intertidal shores of varying environmental conditions (Hawkins & Hartnoll, 1983; Williams et al., 2013). Grazing itself is mediated by factors such as refuge availability and predation intensity (Williams et al., 2000). As molluscs were the principal grazers on the seawalls at both Pulau Hantu and Kusu Island, the significant difference in their communities could explain the contrasting rates of algal succession between sites. SIMPER results also showed that the mollusc species typifying the assemblage at Kusu Island were more functionally diverse (i.e., they included grazers, predators as well as scavengers) whereas those that at Pulau Hantu were more generally characterised by grazers. Since benthic consumers often have large effects on their food sources, the differences in the two mollusc communities may have contributed to the differences in algal development between the sites as well (Steneck & Watling, 1982; Heck & Valentine, 2007).

Variation in the sizes of living space provided by the complex tiles relative to simple concrete tiles did not have an observable effect on the succession of algae. At the design and fabrication stages, the complexity of the tiles was manipulated at the scale of 8 to 56 mm and this probably had little influence on the algal communities, which tend to be affected by topography at scales of 10 µm and smaller (Fletcher & Callow, 1992; Schumacher et al., 2007). This would explain the similar algal percentage cover between the simple and complex tiles of both designs. The type of structural component (i.e., 'pits' and 'grooves'), manipulated at the same scale, was likely to be most relevant to organisms such as molluscs seeking refuge from desiccation or predators (McGuinness & Underwood, 1986; Fairweather, 1988; Loke & Todd, in press). Protection from harsh intertidal conditions by topographic features, such as crevices, grooves and pits, represents a critical resource for the survival of most mollusc species (Moran, 1985; Fairweather, 1988; Moschella et al., 2005; Loke et al. 2015).

The succession trajectories between concrete and granite control tiles were very different; the red and brown algal assemblage that later dominated concrete tiles was not abundant on granite tiles even after a year of colonisation. Further, there was an absence of minor algal functional groups on granite tiles. The material used could potentially have affected settlement due to differences in physical and/or chemical properties (Chapman & Bulleri, 2003; Bulleri, 2005). For instance, a study by Connell and Glasby (1999) comparing various artificial surfaces (i.e., concrete, wood and sandstone) found that they harboured different assemblages. Burt et al. (2009), on the other hand, reported no significant difference between colonising assemblages on granite and concrete tiles attached to breakwaters in Dubai. The differences in structural complexity between the tile types tested in the present study make it difficult to disentangle the effects of habitat structure and substrate material. Possible differences in hydrodynamics (due to their various topographies) over the concrete and granite tiles could also have contributed to their diversity and community composition. Many laboratory and field studies have demonstrated the importance of hydrodynamic processes in structuring benthic communities at small spatial scales (e.g., Eckman, 1983; Butman, 1987; Butman et al., 1988;

Butman, 1989). For example, the drag across the surface of the concrete tiles (which had more topographical features) may have been higher, resulting in a longer time available for larval settlement (Meadows & Campbell, 1972; Hedvall et al., 1998).

Lai (2013) hypothesised that the lower diversity and abundance of algae on seawalls compared to natural rocky shores could have restricted the ability of the system to support higher trophic levels and biodiversity. Our study showed that, relative to concrete tiles, granite tiles (constructed to mimic natural seawalls) supported a lower diversity of algal functional groups and had a different successional trajectory, i.e., one that was dominated by encrusting algae that may not be as palatable to grazers as the red/brown algal assemblage. Conversely, the diverse algal assemblage on concrete tiles could have facilitated the establishment of other species (Bruno et al. 2003). Whether the assemblage would change given a longer period of colonisation, or if the red/brown algal assemblage represents a "climax state", remains unknown; however, based on observations of the surrounding granite seawalls, further succession at the same tidal height seems unlikely. Given these observations, future applied studies could consider enhancing complexity on seawalls by introducing structural components at relevant scales and testing different materials of construction. Nevertheless, more basic research is required and the model and mechanisms of succession on tropical seawalls should be more thoroughly investigated. Very little is known regarding how seawall assemblages develop and are maintained and this has limited the ability of coastal engineers and managers to predict the community responses to artificial coastal defences. Determining such small-scale spatial patterns of distribution represents the first step towards a better understanding of the processes occurring on seawalls—and this should ultimately aid the reconciliation of these novel habitats.

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