

Coral community composition and carbonate production in an urbanized seascape

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Abstract

Coastal urbanization causes environmental modifications that directly and indirectly influence the distribution and functioning of coral reefs. However, the capacity of urban infrastructure to support corals and vertically accrete is less understood. Here, we investigated if coral communities on reefs and seawalls in Singapore are distinct, and examined the environmental variables influencing coral carbonate production. Surveys at 22 sites yielded 134 coral species, with richness significantly higher on reefs. Coral cover and Shannon index did not differ between habitat types. Community composition was distinct between habitat types, with seawalls supporting a higher proportion of massive and thick-plating species. ‘Distance from mainland’ was the single most important variable influencing normalized carbonate production rates (a function of species-specific linear extension rate and skeletal bulk density and site coral cover), which were higher further from the mainland where human activity and development pressures were greater. Our results indicate that environmental filtering strongly shapes coral communities and may influence ecosystem functioning in Singapore’s urbanized reef system. The findings will guide the management of reefs on increasingly urbanized coastlines.

Keywords: Coastal urbanization, ecosystem functioning, environmental filtering, reef accretion, Scleractinia, species traits, Southeast Asia

1. Introduction

Recent decades have seen burgeoning rates of urban growth across the globe and their concomitant effects on coastal and marine ecosystems (Yeung 2001; Wolanski 2006; Burt 2014). Increased establishment of urban infrastructure for residential, commercial and recreational purposes results in marked alterations to the environment, such as reduced water quality or substrate erosion stemming from changes in local hydrodynamics (Griggs et al. 1994; Rivero et al. 2013; Devlin et al. 2015), inevitably modifying the population dynamics of numerous marine species (Bulleri and Chapman, 2010; Firth et al. 2016). For example, soft-bottom macrobenthic communities can be affected by the accumulation of organic compounds or contaminants in the sediment, or simply by physical displacement upon the installation of artificial structures such as

pilings (Sim et al. 2015; Heery et al. 2017). Similarly, structures such as breakwaters, boat moorings and marinas can influence the abundance and behavior of fishes differently from coral reefs or seagrass beds due to variations in local conditions and differing capacities of resource provision (Clynick et al. 2008; Burt et al. 2013; Lanham et al. 2018). Additionally, some structures are barriers to movement while others may be conduits improving connectivity between distant populations (Bishop et al. 2017), although the latter could also inadvertently act as platforms for the recruitment and spread of non-indigenous species (Bulleri and Airoidi 2005; Duarte et al. 2013).

Tropical coral reefs are of particular concern as stressors generated from human activities and urbanization can directly and indirectly impact hard corals (Lamb and Willis 2011; Smith et al. 2016), compromising the provision of essential ecosystem goods and services (Moberg and Folke 1999). Reefs that are nearer to cities – the centers of greatest human disturbance – typically have lower coral cover and diversity than those that are further away (Cleary et al. 2006; Herrán et al. 2017; Heery et al. 2018). This is due to the effects of increased turbidity, sedimentation and nutrient inputs associated with terrestrial runoff, which hamper physiological processes such as growth and heighten the susceptibility of corals to other stressors (Fabricius 2005; Erftemeijer et al. 2012; D’Angelo and Wiedenmann 2014; Aeby et al. 2020). In addition, hard bottom habitats such as seawalls can have elevated temperature profiles (Zhao et al. 2019), which could potentially influence the thermal landscape of adjacent coastal waters (Perkins et al. 2015), reducing calcification rates and disease resilience in corals (Foster et al. 2014; Maynard et al. 2015). Changes in local hydrodynamics due to the presence of such artificial structures can also modify sedimentation regimes, which decrease recruitment and growth, and increase mortality in corals (Burt et al. 2010). Because of the extreme abiotic factors that manifest on an inshore to offshore gradient, these ‘urban coral reefs’ typically have a compact reef zone, reduced structural complexity, and are dominated by corals bearing massive growth forms (Burt et al. 2012; Heery et al. 2018). Local species extinctions have even occurred as a result of extensive coastal urbanization (Hoeksema and Koh 2009; Poquita-Du et al. 2019). Despite these impacts, there is growing evidence that reef-building corals can recruit and establish on coastal defenses or other human-made infrastructure within these urbanized systems (e.g. Wen et al. 2007; Burt et al. 2009a; Viyakarn et al. 2009; Toh et al. 2017). These observations indicate that

artificial substrates could play unique roles in the maintenance and resilience of urban coral reef systems.

In recent decades, knowledge on the ecology of urban infrastructure in temperate coastal zones has grown rapidly; yet, although corals are a major habitat-forming group, urban reef ecology remains a nascent field in the tropics (Todd et al. 2019). Relatively little has been reported in the literature on how coral assemblages and ecosystem functioning compare between natural reefs and urban infrastructure. Trends appear to be variable geographically. Coral diversity on nearly decade-old breakwaters in Thailand was comparable with that of surrounding reefs (Viyakarn et al. 2009). Mature breakwaters in Taiwan had similar coral cover as natural reefs in the shallow zone, although the former habitat supported more foliose corals and *Acropora* spp. (Wen et al. 2013). In Dubai, coral cover on mature breakwaters was significantly higher and comprised more massive and encrusting species than natural reefs, but the latter habitat supported greater species diversity (Burt et al. 2009b; Burt et al. 2011). While coral establishment on human-made structures has led to habitat provision for other coral-dependent biota (e.g. Toh et al. 2016; Taira et al. 2018) and contribution of genetic material during mass spawning events (Viyakarn et al. 2009), urbanization-driven changes to the community could result in other wide-ranging effects on overall ecosystem functioning (Lizée et al. 2011; Mayer-Pinto et al. 2018; Pyles et al. 2020). Given the dramatic scales at which natural coastlines – especially those in the tropics – are modified by human activity, both species composition and reef functionality across urbanized seascapes should therefore be explicitly characterized to understand these impacts and reduce uncertainties in the management of these systems.

One key ecosystem function is reef accretion, which hinges on the balance between the production and removal of calcium carbonate. As the dominant reef-building taxon, stony corals (Cnidaria: Anthozoa: Scleractinia) contribute a substantial amount of calcium carbonate to the biogenic structural framework (Hart and Kench 2007; van Woesik and Cacciapaglia 2018). Defined as the amount of calcium carbonate deposited by a stony coral per unit area per year, early estimates of coral carbonate production have ranged from 1 to 10 g cm⁻² y⁻¹ (Chave et al. 1972). For more accurate determination of coral carbonate production, data on calcification rates (derived as a product of two traits: linear extension rate and skeletal density) and coral cover at the species level (e.g. Norzagaray-López et al. 2015) are required. Abiotic factors that are

detrimental to coral skeletal development – including atypical sea surface temperatures, turbidity and sediment levels – would therefore depress calcification and carbonate production (Browne 2012; Tanzil et al. 2013; Foster et al. 2014; Howells et al. 2018; Courtney et al., 2020; Razak et al. 2020). Indeed, net coral carbonate production rates have been shown to decrease toward city centers due to the prevalence of various local pressures (Herrán et al. 2017), or be spatially patchy due to localized anthropogenic disturbances (de Bakker et al. 2019). Because coral carbonate production can vary widely over disturbance gradients, it has been recommended that assessments of coral diversity and functioning be carried out at high spatial resolution so that risk management strategies targeting specific anthropogenic impacts can be more focused (de Bakker et al. 2019).

Published trait data pertaining to reef accretion for many coral species are scant. Measurements of linear extension rates and skeletal density are each only available for approximately 10% of all reef-building species (Madin et al. 2016a), and species with data available for both traits constitute a mere 3% (Madin et al. 2016b). This has necessitated estimates of carbonate production to be made from averaging datasets over higher taxonomic levels, similar growth forms, or within sites. For example, Shi et al. (2008) averaged values across members of the same coral family to calculate the skeletal density of genera for which data were unavailable; Mallela and Perry (2007), on the other hand, used site-level skeletal density values as data for species that were not sampled. Acknowledging the difficulties of coral species identification in the extremely species-rich Indo-Pacific region, Perry et al. (2018) resorted to using averaged rates at the genus level or growth form. This knowledge gap is particularly stark for the biodiverse reefs of Southeast Asia, a region that has seen rapid urbanization and degradation of its coastal environment within a span of a few decades (Wolanski 2006), but for which effective management may be hampered by limited fine-scale resolution spatial and temporal assessments of its coral carbonate stock.

These observations underscore the need for a mechanistic understanding of the ecology of urbanized reef environments, such as how multiple stressors may interact and culminate in environmental filtering processes that dictate the functioning of reefal and human-made habitats. Integrating across a combination of methods involving field surveys, trait characterization and remote sensing, we examined how natural reefs and human-made areas within an urbanized reef

system may differ in ecology and function. Specifically, we were interested in 1) whether coral species composition differed between reef and seawall sites, and 2) how urban pressures influenced coral carbonate production in an equatorial urbanized reef system. Our findings are expected to enhance coastal management strategies, especially along rapidly urbanizing shorelines, where information is urgently needed with regard to baseline coral carbonate production across habitat types, as well as the degree of geo-ecological functionality that could potentially be lost, or reinstated by restoration initiatives (Perry and Alvarez-Filip 2018).

2. Materials and methods

2.1 Study sites

Our study was conducted in Singapore, a highly urbanized island-state in the central Indo-Pacific that has undergone extensive coastal development, land reclamation and seabed dredging for over five decades (Chou et al. 2019). Reclaimed land comprises more than 30% of the existing land area, and approximately two-thirds of the country's coasts are lined with seawalls (Lai et al. 2015; Tan et al. 2016). Among the offshore sites, considerable variations in turbidity, sedimentation and light levels exist that are likely related to the intensity of urbanization and marine resource usage (Chou et al. 2017). Sea surface temperatures are reported to vary temporally according to monsoonal patterns but not spatially (Sin et al. 2016; Chou et al. 2017). A nearshore to offshore gradient of increasing water quality has been observed (Tun 2012). While considerable loss and degradation of natural reefs have occurred, coral richness and diversity of the remaining reefs have remained considerably high (Huang et al. 2009; Wong et al. 2018; Chow et al. 2019). Colonization of reef corals on urban infrastructure such as seawalls have also been reported over the last decade (e.g. Ng et al. 2012; Chou et al. 2015; Kikuzawa et al. 2020; Lim et al. 2020). A total of 22 sites south of the Singapore mainland were selected, consisting of a mix of 16 natural reef and six seawall sites (Fig. 1).

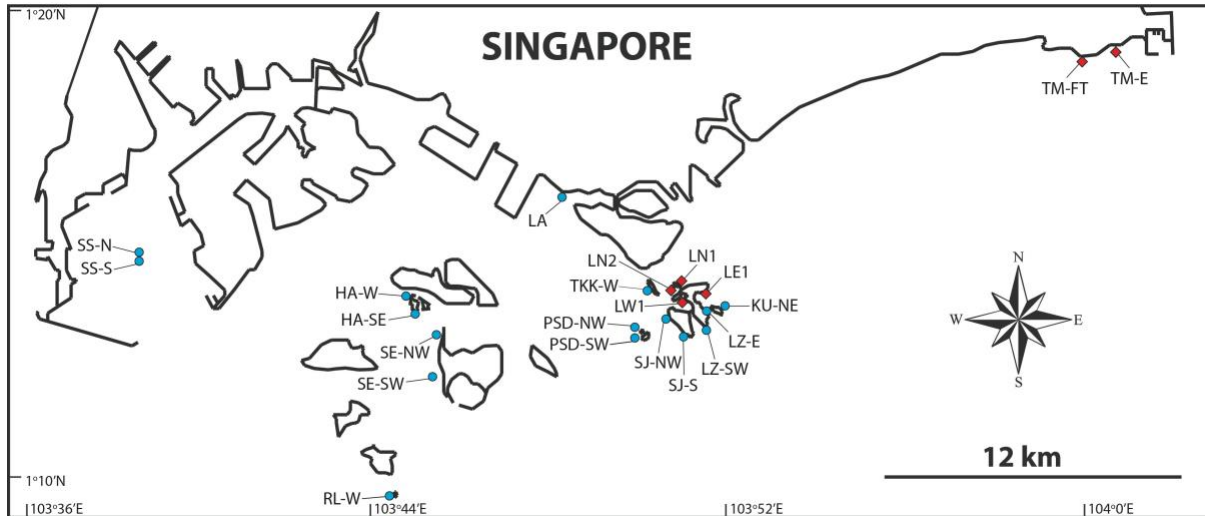


Fig. 1 Map of Singapore with study sites indicated. Reef (SS-N: Sultan Shoal North; SS-S: Sultan Shoal South; RL-W: Raffles Lighthouse West; HA-W: Hantu West; HA-SE: Hantu Southeast; SE-SW: Semakau Southwest; SE-NW: Semakau Northwest; LA: Labrador; PSD-NW: Pulau Subar Darat Northwest; PSD-SW: Pulau Subar Darat Southwest; TKK-W: Tekukor West; SJ-NW: St John’s Northwest; SJ-S: St John’s South; LZ-SW: Lazarus Southwest; LZ-E: Lazarus East; KU-NE: Kusu Northeast) and seawall sites (LN2: Lazarus North 2; LN1: Lazarus North 1; LW1: Lazarus West 1; LE1: Lazarus East 1; TM-FT: Tanah Merah Ferry Terminal; TM-E: Tanah Merah East) are indicated in blue and red respectively.

2.2 Species composition

Field surveys were carried out between July 2016 and October 2017, after the 2016 mass coral bleaching event and also when corals were visibly healthy. At each site, five 20-m line intercept transects (3–5 m between transects) were conducted at ~3 m below chart datum, the zone with the highest abundance and richness of reef corals in Singapore (Chou 2006). All corals were identified to species based on updated taxonomy (see references in Wong et al. 2018 ESM Table S2), and their abundances (as length) were recorded as a percentage of the total transect length at each site to provide a measure of live coral cover. While other benthos comprising both living (e.g. soft corals, zoanthids, sponges, algae) and non-living (e.g. rubble, rock, silt, sand) components along the transects were documented, we here focused our analyses on scleractinians given that they were the main habitat-forming group across sites (25% cover on average). *Porites lutea*, *P. lobata* and *P. australiensis* could not be conclusively distinguished in the field, and thus were collectively pooled as ‘massive *Porites* spp.’.

Comparisons of percent coral cover, species richness and Shannon diversity were made between reef and seawall sites using a Kruskal-Wallis test as these metrics did not fulfill the assumptions

of normality and homogeneity of variance. To compare variations in coral community between habitat types (i.e. reef and seawall sites), the data (as proportional coral cover, with transects analyzed as independent replicates) were first arcsine square-root transformed (square-root transformation yielded the same result) and a Bray-Curtis similarity matrix was constructed. Analyses were carried out using PERMANOVA+ in PRIMER (Anderson et al. 2008). The coral communities of reef and seawall sites were compared using PERMANOVA to test if the habitats differed (sites nested within habitat types), and the differences were visualized with principal coordinates analysis. Using SIMPER, which analyzes similarity percentages based on the decomposition of the Bray-Curtis similarity matrix (Clarke 1993), species which contributed most to the similarity between sites and dissimilarity between habitat types were identified.

2.3 Environmental parameters

Environmental factors known to influence coral calcification were identified and derived using remote sensing and ArcGIS (ESRI 2019):

- 1) Mean turbidity (i.e. ‘TSS’, or total suspended sediment, in mg l^{-1}) for the years 2016 and 2017 (method adopted from Lee et al. (2002)), as a proxy for stressors such as reduced light levels (Bessell-Browne et al. 2017).
- 2) Linear distance of each study site to the nearest shore on mainland Singapore (i.e. ‘distance from mainland’), as a proxy of urban-related environmental stressors such as land-based pollutants or nutrient inputs from runoff. These stressors are known to impact coral carbonate production by promoting competition with other taxa or via bioerosion processes (Birkeland 1987; Mutti and Hallock, 2003), but are difficult to deduce from remote sensing methods due to the high turbidity of Singapore’s shallow coastal waters (Sin et al. 2016).
- 3) Monthly composite data on sea surface temperature (SST) and maximum SST anomalies for the year 2017 (NOAA Coral Reef Watch 2018 v3.1). From these, the mean monthly values for SST (i.e. ‘mean monthly SST’) and SST anomalies (i.e. ‘maximum SST anomaly’) were calculated for each study site. Data from 2016 were not included as there were periods of anomalous SSTs that resulted in a mass coral bleaching event in Singapore that year (Toh et al. 2018; Ng et al. 2020).

Detailed technical descriptions of these parameters are provided in Supplementary Data 1.

2.4 Community coral carbonate production

Data on mean skeletal density (D) (see Supplementary Table S2) were obtained empirically for 84 species following the buoyant weight method described by Ng et al. (2019). Some of these species were not recorded from our current surveys. Consolidating empirical data here and published information from Ng et al. (2019) and the Coral Trait Database (Madin et al. 2016b), we generated a global list of 141 species with skeletal density data. While the number of replicates for each species was not consistent, the mean and range of skeletal density values were listed where available (Supplementary Table S2). Subsequently, we adopted a phylogeny-based approach to infill data for 46 species documented from the current surveys for which we lacked information on skeletal density. The use of phylogenetic imputation—as opposed to data removal—has been recommended when dealing with missing trait data, as it reduces biases and the subsequent risk of misinterpreting functional diversity patterns (Kim et al. 2018; see also McWilliam et al. 2018). Imputation was performed using the most recent completely-sampled scleractinian phylogeny ($n = 1547$) represented by 1000 Bayesian posterior trees (Huang and Roy 2015; Huang et al. 2018). Estimation of trait values for unobserved species was carried out with ancestral state reconstruction (via phylogenetically independent contrasts) of each tree, which had been rerooted at the most recent common ancestor of the focal species and all other species (Garland et al. 1992; Garland Jr and Ives 2000; see also Kembel et al. 2012; Madin et al. 2016a).

Data on mean linear extension rates (E) (see Supplementary Table S2) were first obtained empirically via a reef restoration project in Singapore, wherein the growth of 27 species of coral transplants were monitored for up to four years (Chou LM, unpublished data). Although small colonies or fragments are commonly used in reef restoration efforts (e.g. Chou et al. 2017), and growth rates may vary with fragment size (e.g. Pausch et al. 2018; Ishida-Castañeda et al. 2020), we do not expect the data to be overly skewed or our estimates to be confounded. Rather, growth rate is a phylogenetically conserved trait (Madin et al. 2016b), for which key spatial and temporal gaps can be filled via restoration projects, where coral growth is typically monitored as a success metric. We also consolidated published linear extension rate data for all other species

from studies that were previously conducted in Singapore (see Supplementary Table S2), as well as from the Coral Trait Database (Madin et al. 2016b), to capture a spectrum of growth data across colony sizes. Values were averaged for species with data from multiple sources, so as to obtain a mean linear extension rate per species, and ranges of linear extension rates were similarly provided where available (Supplementary Table S2). We generated a final list of 164 species, including those found in Singapore and elsewhere, with available linear extension rate data. Phylogenetic imputation was performed as above to infill data for 68 species recorded from our surveys for which published data were unavailable.

Adapting methods from Hart and Kench (2012), Norzagaray-López et al (2015), and Cabral-Tena et al (2018), site-specific coral carbonate production rates (P) were estimated with the following equation:

$$P = \sum_{i=1}^n (C_i D_i E_i A F_i) \times 10$$

where: C is the percent cover of species i at a site; D and E refer to the skeletal bulk density (g cm^{-3}) and linear extension rate (cm y^{-1}) of species i respectively; and ‘10’ is included as a coefficient to adjust the units from $\text{g CaCO}_3 \text{ cm}^{-2} \text{ y}^{-1}$ to $\text{kg CaCO}_3 \text{ m}^{-2} \text{ y}^{-1}$. We also accounted for coral growth forms with the adjustment factor AF as some do not exhibit uniform skeletal growth rates across their living surfaces, such as those with branching morphologies wherein the ‘effective cover’ is a fraction of the measured coral cover (Vecsei 2001). Growth forms of each species were recorded by first following the higher resolution classifications in McWilliam et al (2018) and then translating these to their equivalent categories based on Hart and Kench (2007) (see Supplementary Table S2).

Coral carbonate production rate (P) was first normalized by dividing it by the proportion of live coral cover along each transect to facilitate comparisons among sites. Although coral cover may account for a substantial amount of variation in census-based coral carbonate production (e.g. Guest et al. 2018), here we were interested in isolating the effect of community compositional differences on carbonate productivity. Additionally, while one of the transects at a particular site (LE1; see below) registered zero carbonate production, we included it in the analyses as it did not deviate from the otherwise very low productivity of that site. To assess the influence of the

fixed factors ‘distance from mainland’, ‘TSS’ and ‘habitat type’ (i.e. reef or seawall) on normalized coral carbonate production rates, we constructed a maximal linear mixed-effects model up to all two-way variable interactions and ‘site’ as a random effect to account for other site-level variations that were not measured (package ‘nlme’; Pinheiro et al. 2018). ‘Mean monthly SST’ and ‘maximum SST anomaly’ were not modeled as the variabilities among sites were minute (ranges of 0.09°C and 0.04°C respectively; see Supplementary Data 2) and thus not considered to be biologically significant in affecting coral carbonate production at such spatial scales (see Pratchett et al. 2015). We removed collinear variables (if their vif scores were > 3 ; package ‘car’; Fox and Weisberg 2011) and simplified the models in a stepwise manner based on the Akaike Information Criterion (AIC). Model assumptions were also checked for the final model. Analyses were carried out with R version 3.5.3 (R Core Team 2019).

3. Results

3.1 Species composition

A total of 134 species from 15 families were recorded from the surveys (Supplementary Table S1; Supplementary Table S2; Supplementary Data 2). Species richness was significantly higher in reef (mean $14.1 \pm \text{SD } 6.8$ species) than seawall sites (mean $11.3 \pm \text{SD } 6.9$) ($\chi^2 = 4.315$, $p = 0.038$) (Fig. 2a). However, habitat types did not differ significantly in terms of coral cover (reef: $24.4 \pm 15.5\%$; seawall: $25.2 \pm 19.6\%$) and Shannon diversity (reef H' : 2.11 ± 0.61 ; seawall H' : 1.87 ± 0.69) (Figs. 2b, c).

Coral communities at reef and seawall sites were significantly different from each other (Pseudo-F = 6.2668, $p = 0.0001$; Fig. 2d). Seven species made up almost half of the community at all reef sites: *Pectinia paeonia* (15.7%), *Pachyseris speciosa* (11.8%) *Merulina ampliata* (7.8%), massive *Porites* spp. (comprising *P. lutea*, *P. lobata* and *P. australiensis*; 7.5%), and *Favites pentagona* (7.1%). In comparison, five species – massive *Porites* spp. (comprising *P. lutea*, *P. lobata* and *P. australiensis*; 28.0%), *Podabacia crustacea* (12.5%), *Turbinaria mesenterina* (12.0%) – contributed to slightly more than half of the coral community at seawall sites. These species also contributed most to the dissimilarity between reef and seawall sites.

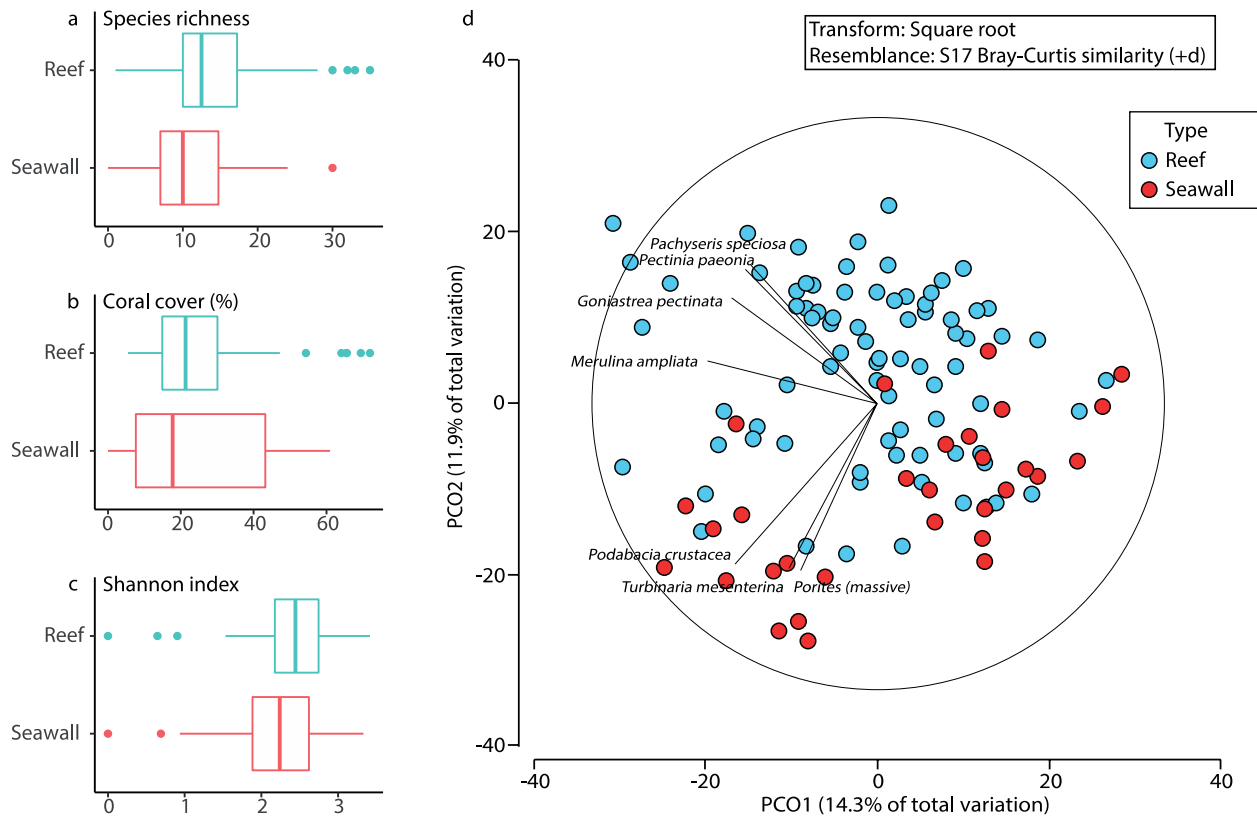


Fig. 2 Comparisons of scleractinian biodiversity at reef and seawall sites in Singapore, including: a) species richness, b) coral cover, c) Shannon index, and d) principal coordinates analyses of coral communities at both habitat types. The two principal coordinates account for 26.2% of the total variation. Factors shown within the circle correlate with PCO1 or PCO2 with a factor of at least 0.6

3.2 Environmental parameters

While natural reefs were generally further away from the mainland than seawall sites, mean turbidity levels did not differ significantly between both habitats (Fig. 3; Supplementary Data 2).

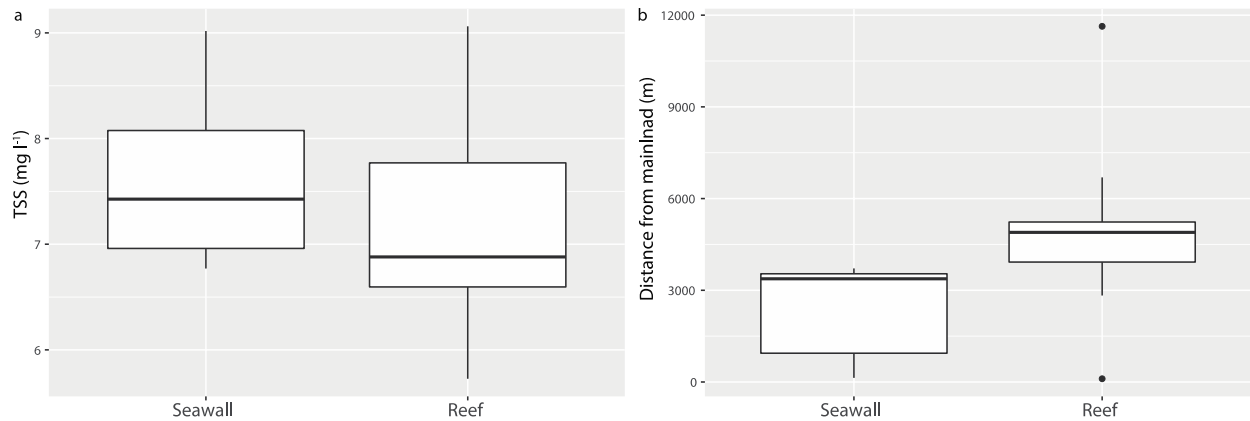


Fig. 3 Comparison of (a) Total suspended solids (TSS), (b) Distance from mainland at reef and seawall sites.

3.3 Community coral carbonate production

Pachyseris speciosa (11.3%), *Merulina ampliata* (8.9%), *Podabacia crustacea* (6.2%), massive *Porites* spp. (4.4%) and *Turbinaria mesenterina* (4.0%) accounted for approximately one-third of the total coral carbonate production in Singapore, while the remaining 127 species each contributed 3.9% or less. Coral carbonate production rates ranged widely with the highest at Raffles (16.12 kg CaCO₃ m⁻² y⁻¹), and lowest at Lazarus East (0.63 kg CaCO₃ m⁻² y⁻¹) (Fig. 4).

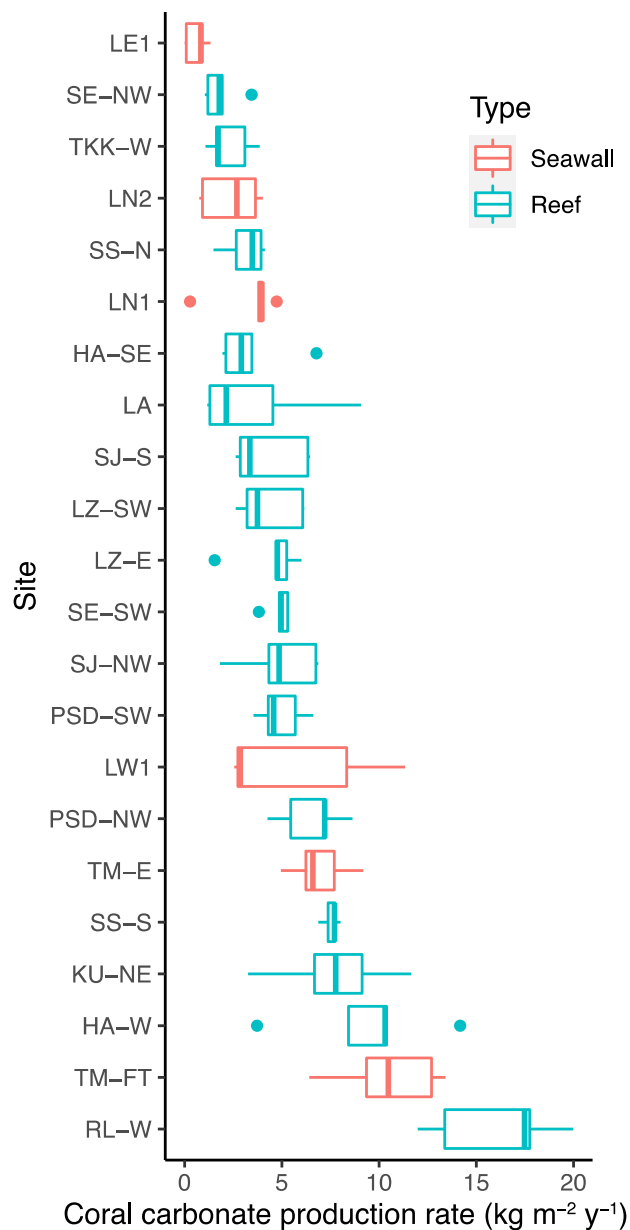


Fig. 4 Coral carbonate production rates across study sites. Full names of study sites are provided in Fig. 1.

Mean (\pm SD) coral carbonate production rates for reef and seawall sites were not significantly different at 5.60 ± 3.46 kg CaCO₃ m⁻² y⁻¹ and 4.89 ± 3.53 kg CaCO₃ m⁻² y⁻¹, respectively ($p = 0.4$). Nine species contributed nearly 50% of the coral carbonate at the reef sites: *P. speciosa* (14.0%), *M. ampliata* (7.8%), *Montipora monasteriata* (5.2%), *Goniopora columna* (5.1%), *Pectinia paeonia* (4.2%), *P. crustacea* (3.7%), *Psammocora haimiana* (3.5%), *Echinopora lamellosa* (3.3%), and *Mycedium elephantotus* (2.9%). At seawall sites, six species accounted for a similar percentage of coral carbonate: *P. crustacea* (13.9%), *M. ampliata* (12.5%), massive

Porites spp. (comprising *P. lutea*, *P. lobata* and *P. australiensis*; 10.7%), and *Turbinaria mesenterina* (8.7%).

After accounting for coral cover, the model that included only the main effect of ‘distance from mainland’ (with ‘site’ as a random effect) was selected as it was the most parsimonious (Table 1). Across sites, normalized coral carbonate production rates were higher with increasing distance from the Singapore mainland (0.000076 ± 0.00003556 , $p = 0.0442$) (Fig. 5; see Supplementary Fig. 1).

Table 1. Performance of candidate models accounting for normalized coral carbonate production in Singapore’s urban reef environment. Best model is in bold.

Model	AIC	R2
(Distance + Type + TSS)^2, random = (1 Site)	251.403	0.155
Distance + Type + TSS + Distance:Type + Type:TSS, random = (1 Site)	249.676	0.156
Distance + Type + TSS + Type:TSS, random = (1 Site)	248.159	0.160
Distance + Type + TSS, random = (1 Site)	249.487	0.181
Distance + Type, random = (1 Site)	248.095	0.185
Distance, random = (1 Site)	248.097	0.196
1, random = (1 Site)	250.660	0.218

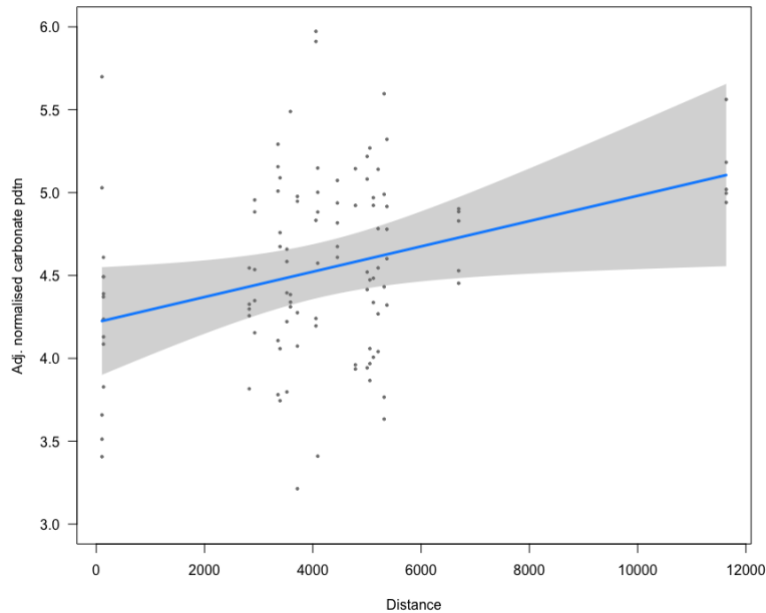


Fig. 5 Partial residual plot, visualized with the package ‘visreg’ (Breheny and Burnett 2017), depicting the influence of the distance of a study site from mainland Singapore on normalized coral carbonate production.

4. Discussion

Accelerating coastal urbanization can have far-reaching consequences on biodiversity and ecosystem functioning (Schermer et al. 2013; Firth et al. 2016). A more thorough understanding of the ecological trajectories of these habitats is necessary to improve their management, especially for human-made areas which may have important roles in biodiversity conservation and resource utilization (Todd et al. 2019). The island-state of Singapore supports an appreciable diversity of coral reef biota in spite of the extensive coastal zone development along its limited territorial waters (Chou et al. 2019), and thus represents an interesting case study for examining the effects of urbanization on its coastal and marine ecosystems. Here, we determined that coral community patterns differed between the reefal and seawall areas in Singapore, and that increasing distance from mainland-based stressors enhanced the reef-building functions of both habitat types.

While recent work has shown that reefs (e.g. Wong et al. 2018; Chow et al. 2019) and seawalls (e.g. Ng et al. 2012; Chou et al. 2015) in Singapore contain considerable coral diversity, we have

here provided a direct comparison of coral assemblages in both habitat types. Despite the reduced species richness, seawall sites supported comparable coral cover and diversity as natural reefs, consistent with observations from other locations in the central Indo-Pacific (e.g. Thailand, Viyakarn et al. 2009; Taiwan, Wen et al. 2013). Interestingly, there was a higher proportion of massive (*Porites* spp.) and thick-plating species (*Podabacia crustacea*, *Turbinaria mesenterina*) at seawall sites, which contrasted with the reef sites that comprised more thin-plating species (*Pectinia paeonia*, *Pachyseris speciosa*, *Merulina ampliata*). This difference in community composition between habitat types in the current study was more analogous to that in the western Indian Ocean, where Dubai breakwaters were also dominated by massive corals (e.g. *Platygyra daedalea*, *Cyphastrea microphthalma*, *Siderastrea savignyana*) and the reefs instead supported more branching species (e.g. *Acropora* spp., *Porites harrisoni*) (Burt et al. 2009b). That the seawall environment favors the establishment of more corals with a stress-tolerant life-history strategy than a generalist or a competitive one (Darling et al. 2019) suggests that conditions in such areas are generally more disturbed than reefs. Yet, this is unlikely to be driven solely by present-day mainland-based stressors or turbid water conditions, as our study sites were fairly spread out in the Strait of Singapore, and our findings had indicated that the levels of total suspended solids at both habitat types did not differ significantly. These community differences could be associated with habitat characteristics (e.g. structural complexity, steepness, material type) or species traits (e.g. feeding modes, competitive ability, susceptibility to stressors, larval settlement preferences) that were not studied here (Anthony and Fabricius 2000; Houlbrèque and Ferrier-Pagès 2009; Hata et al. 2017; Loke et al. 2019; Kikuzawa et al. 2020; Ng et al. 2020). Nevertheless, our findings corroborate earlier observations by Heery et al. (2018) that species compositional variations are a consequence of localized anthropogenic impacts, and strongly indicate that the assembly of coral communities across reefal and seawall areas has been shaped by past and present urbanization. For Singapore, the coastal modifications that are proposed for the coming decades will provide ample opportunity to test, at greater spatial scales, the extent to which such compositional variations (and relatedly, ecosystem functioning) hold for both natural and human-made habitats.

The dearth of species calcification rates in the scientific literature is striking, but we have attempted to fill this gap by contributing and consolidating information for a total of 165 species,

including 33 species not documented from our surveys (see Supplementary Table S2). Our derived linear extension rates and skeletal densities may originate from numerous sources and therefore vary across environments, but in the presence of such large gaps in trait datasets, they represent the best source of available data for Singapore's reef corals, and serve as stepping stones for advancing reef-scale carbonate production analyses. Spatial differences in species calcification rates are evident, such as in the case of *Cyphastrea microphthalma*, a common species in Abu Dhabi that calcified at $0.83 \text{ g cm}^{-2} \text{ y}^{-1}$ compared to $1.13 \text{ g cm}^{-2} \text{ y}^{-1}$ in our study (Howells et al. 2018). Highly common on Indo-Pacific reefs, *Porites lobata* registered rates of $0.65\text{--}0.72 \text{ g cm}^{-2} \text{ yr}^{-1}$ in the Mexican Pacific (Medellin-Maldonado et al. 2016; Tortolero-Langarica et al. 2016), $1.38 \text{ g cm}^{-2} \text{ yr}^{-1}$ in the Maldives (Morgan and Kench 2012), and $1.51\text{--}2.19 \text{ g cm}^{-2} \text{ y}^{-1}$ in Indonesia; whereas here we documented rates of $0.99 \text{ g cm}^{-2} \text{ y}^{-1}$. In addition, calcification rates of major reef-building species such as *Acropora gemmifera*, *A. digitifera*, and *A. nasuta* were $1.42\text{--}2.96 \text{ g cm}^{-2} \text{ yr}^{-1}$ in the Maldives (Morgan and Kench 2012), but $0.88\text{--}1.47 \text{ g cm}^{-2} \text{ yr}^{-1}$ in Singapore. These differences likely arise from the variations in local environmental conditions, which have considerable influence on skeletal density and linear extension rates over wide geographical scales (Scoffin et al. 1992; Edinger et al. 2000; Ng et al. 2019). This intraspecific variability in traits is critical for understanding the potential ranges of calcification rates across space and time, especially in light of the paucity in coral trait data, as well as for explaining the persistence of corals in reef environments which have been modified by disturbances (Bolnick et al. 2011). However, this also suggests that an over-reliance on trait data from other regions could result in the formulation of unsuitable management strategies. This therefore highlights the importance of empirical measurements to refine projections of reef futures for local or regional contexts.

Information on calcification is highly relevant for understanding how fast tropical reef frameworks are built via the relative contributions of individual species or functional groups (Hart and Kench 2007; Perry et al. 2015). One of the common approaches that quantifies reef growth involves subtracting the rates of carbonate removal (by bioeroders such as urchins, sponges and parrotfishes) from the rates of carbonate production (by calcifiers such as corals and coralline algae) (Perry et al. 2018; van Woesik and Cacciapaglia 2019). While erosional rates were not assessed, our study represents a first comprehensive step towards quantifying contemporary reef-scale growth from different habitat types in Singapore's urbanized marine

environment, complementing ongoing assessments of historical reef accretion (Ang et al. 2018). Relatedly, the wide range of coral carbonate production rates at both reef (1.88 kg m⁻² y⁻¹ at SE-NW to 16.12 kg m⁻² y⁻¹ at RL-W) and seawall (0.63 kg m⁻² y⁻¹ at LE1 to 10.47 kg m⁻² y⁻¹ at TMFT) sites, in comparison to values reported from a recent assessment (0.96–4.82 kg m⁻² y⁻¹; Januchowski-Hartley et al. 2020), suggest that generalizing carbonate production across species and space could lead to underestimation of reefs' functional breadth (see Schmidt-Kloiber & Nijboer 2004; Jansen et al. 2018).

At 5.41 kg m⁻² y⁻¹, the mean carbonate production rate in Singapore is comparable to that of fore-reef sites in the Indian Ocean and the Great Barrier Reef (5–6.7 kg m⁻² y⁻¹), which are characterized by low cover of branching corals, but lower than that of the Pacific Ocean islands (9.2–16.4 kg m⁻² y⁻¹) where branching corals are abundant (Vecsei 2001). Reefs in Singapore are known to be dominated by encrusting, massive and foliose corals due to the high levels of sediment and turbidity (Tun 2012; Dikou and van Woosik 2006; Guest et al. 2016; Wong et al. 2018), but there is hitherto little indication of how they accrete via the contributions of various species in such an environment. With just three species (*P. speciosa*, *M. ampliata* and *P. crustacea*) contributing to more than a quarter of the coral carbonate produced in Singapore, our study has demonstrated that foliose species bear outsized influence on the ecosystem functioning of turbid, urbanized reefs. This differs from that generally observed for Indo-Pacific reefs, wherein branching corals are often the major carbonate contributors at shallow depths, followed by massive and then foliose growth forms at depths below 10 m (Vecsei 2001). Additionally, compared to other areas where few species account for a disproportionate amount of carbonate produced, such as Micronesia where 80% of carbonate was contributed by five species (equivalent to <10% of local richness) (van Woosik and Cacciapaglia 2019), an equivalent proportion of coral carbonate was produced by 30 of 134 species in Singapore (i.e. 22.4% of total species richness). This disparity suggests that there is a greater degree of functional redundancy with regard to carbonate production in Singapore, in spite of the urbanization impacts that have chronically affected reef health. This redundancy also appears to apply across habitat types as there were equivalent contributions of carbonate by both reef and seawall sites, despite the latter supporting a smaller suite of species and growth forms.

Although urban reef systems may be spatially and environmentally heterogeneous, the environmental stressors generally decrease with growing distance from city centers; consequently, this is associated with concomitant increases in coral cover and species richness (Heery et al. 2018). These, by extension, could modify various aspects of reef functioning (Carlson et al. 2019). Our results are in line with those of Herrán et al. (2017), where local anthropogenic stressors nearer the city were associated with low coral cover and carbonate production. Even after accounting for coral cover, coral carbonate production was significantly influenced only by the proximity of a site to the mainland. Further tests indicate that the observed patterns were not driven entirely by Raffles (RL-W), though this site supported the greatest coral cover and highest carbonate production rate. Sites such as Kusu (KU-NE) and Raffles (RL-W) most likely benefited from adequate flushing and better water quality that characterizes offshore sites far south of the mainland (see Tun 2012; Chou et al. 2017), thus producing more carbonate per unit area of reef compared to those stressed by ongoing coastal development and land use activities nearer the southwestern coasts of the mainland, such as Sultan Shoal North (SS-N) and Labrador (LA). The impact of anthropogenic activities on ecosystem functioning is also evident at sites nearest the mainland. Despite registering the second and sixth highest coral carbonate production rates out of 22 study sites (see Fig. 4), Tanah Merah Ferry Terminal (TMFT) and Tanah Merah East (TM-E) ranked 15th and 19th, respectively, when normalized carbonate production rates were considered (see Supplementary Fig. 1). These findings highlight how carbonate productivity is mediated by community compositional differences, which are in turn driven by a coastal urbanization gradient.

Taken together, our results suggest that environmental filtering shapes coral community composition and may influence ecosystem functioning of urbanized reefs. Even though coral carbonate production rates were comparable between reefs and seawall sites, corals at the latter habitat type appeared to be more resistant toward urban stressors. This pattern highlights their importance as potential reservoirs of reef biodiversity in the Anthropocene. Our findings also have implications for coastal management, as different approaches may have to be applied to deal with the functional consequences of coastal urbanization. For example, biodiversity and habitat enhancement strategies that involve sourcing of coral material from donor sites far offshore for transplantation at recipient sites nearer the mainland may have to account for potential differences in reef functioning to optimize resource usage and outcomes. Given that

calcification trajectories may be species-specific (McCulloch et al. 2012; Razak et al. 2020), efforts to quantify carbonate production thresholds and carbonate stock across locations spanning different habitats will become increasingly important.

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