



Urban coral reefs: Degradation and resilience of hard coral assemblages in coastal cities of East and Southeast Asia

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ARTICLE INFO

Keywords:

Pollution
Reef compression
Reef restoration
Urban ecology
Urbanization

ABSTRACT

Given predicted increases in urbanization in tropical and subtropical regions, understanding the processes shaping urban coral reefs may be essential for anticipating future conservation challenges. We used a case study approach to identify unifying patterns of urban coral reefs and clarify the effects of urbanization on hard coral assemblages. Data were compiled from 11 cities throughout East and Southeast Asia, with particular focus on Singapore, Jakarta, Hong Kong, and Naha (Okinawa). Our review highlights several key characteristics of urban coral reefs, including “reef compression” (a decline in bathymetric range with increasing turbidity and decreasing water clarity over time and relative to shore), dominance by domed coral growth forms and low reef complexity, variable city-specific inshore-offshore gradients, early declines in coral cover with recent fluctuating periods of acute impacts and rapid recovery, and colonization of urban infrastructure by hard corals. We present hypotheses for urban reef community dynamics and discuss potential of ecological engineering for corals in urban areas.

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1. Introduction

Globally, coastal zones are undergoing unprecedented rates of urbanization and population growth (Small and Nicholls, 2003; Hugo, 2011; Dsikowitzky et al., 2016). Changes to the marine environment associated with urbanization, such as increased sediment delivery, nutrients, and pollutants (Carpenter et al., 1998; Airoidi, 2003), are particularly detrimental to reef-building corals (Roberts, 1993) and a major threat to coral reef ecosystems (Bridge et al., 2013). Despite this, hard corals and coral reefs are found in urban waterways of many tropical and subtropical cities (Grigg, 1995; Banks et al., 2007; Martinez et al., 2017). Many of these urban coral reef ecosystems have been studied in isolation (e.g., Becking et al., 2006; Hongo and Yamano, 2013; Cleary et al., 2014, 2016; Polónia et al., 2015; Baum et al., 2016a; Duprey et al., 2016; Guest et al., 2016), however, efforts to collate these works and look for unifying patterns across coastal cities in the tropics have thus far been lacking. Since urban coral reefs have been subject to a multitude of anthropogenic stressors that likely reflect future conditions for corals across much of their range as coastal urbanization proliferates, understanding the characteristics of urban coral reef ecosystems is important for anticipating future trends in what is currently an understudied areas of coral reef ecology and conservation.

Urban coral reefs may differ in composition, physical characteristics, and ecosystem dynamics from coral reefs in more remote locations (Hodgson, 1999; Mora, 2008) due to the unusual combination of relatively extreme abiotic conditions that characterize urban marine environments (McClelland et al., 1997; Bulleri and Chapman, 2010; Dafforn et al., 2015; Mayer-Pinto et al., 2015). Sediment pollution, which is often extremely high in urban waterways, limits photosynthetic activity of zooxanthellae, is energetically demanding for corals to remove sediments, and impacts reproductive cycles of some coral species (Erfteimeijer et al., 2012; Jones et al., 2015); this may select for sediment-tolerant hard corals and symbionts, alter interspecific interactions, and lead to depth distribution patterns that defy expectation based on traditional paradigms from more pristine reef environments (Rogers, 1990; Darling et al., 2012). Nutrient influx from a multitude of urban sources (runoff, wastewater systems, and industrial activities) may create favourable conditions for macroalgae that compete with corals for space and for coral bleaching and disease (Pastorok and Bilyard, 1985; Bruno et al., 2003; Rådecker et al., 2015; Shidqi et al., 2018). Early removal of essential grazers and other ecologically important groups, which likely preceded overfishing in more remote areas (Kirby, 2004; Van Houtan and Kittinger, 2014), may have compounded impacts from nutrient loading, helping shape the evolutionary trajectory of coral assemblages in urban areas. This trajectory may have been further influenced by high concentrations of

dissolved copper and other contaminants (Howard and Brown, 1984; Rinawati et al., 2012; Sindern et al., 2016), the abundance of novel habitat provided by urban infrastructure (Bulleri and Chapman, 2015), and altered ecological connectivity associated with ocean sprawl (Bishop et al., 2017; Heery et al., 2017). Yet, the community traits and ecological processes that define urban coral reefs, and their adaptation and resilience to such stressors have not been clearly characterized.

In this review, we compile available information on the urban coral reefs of East and Southeast Asia with the aim of identifying unifying patterns and characteristics of urban coral reefs. Although many past reviews have presented anthropogenic factors that negatively impact corals and coral reefs broadly (i.e., Wilkinson, 1999; Hughes et al., 2003; Fabricius, 2005; Knowlton and Jackson, 2008; Erfteimeijer et al., 2012), we focus on impacts from urbanization specifically and look for patterns across multiple cities. Although resource use and extraction had major impacts on coral reefs near cities historically (Butcher, 2004; Hoeksema and Koh, 2009; van der Meij et al., 2010), they have become less extensive in recent decades (Rachello-Dolmen and Cleary, 2007), and thus are covered only to the extent necessary to understand past and current trajectories of urbanized reefs. We define urban coral reefs as hard-coral-dominated habitats that are located in urban waterways, urban watersheds, or areas where there are clear urban gradients in one or more of the abiotic conditions especially relevant for hard corals, as dominant reef builders (Table 1; for basic definitions of ‘urban’ and ‘urbanization’, see McIntyre et al., 2000; Wu, 2014). Evidence of carbonate deposition is not a criterion under this definition; this is to include recently or currently forming coral reefs, as well as coral-dominated habitats near the latitudinal limits of reef-building corals. Additionally, while we use the distance from urban centres as a proxy for urban-related environmental conditions, our definition of urban coral reefs intentionally excludes more specific spatial metrics, as the footprint or coastline extent of urbanization is expected to differ considerably from one coastal city to the next, and between stressors caused by urban development.

We focus on East and Southeast Asia because of the large number of rapidly growing, densely populated coastal cities in this region that overlap with historically coral-dominated reef systems. Asia is a global hotspot for coral biodiversity (especially the South China Sea and the Coral Triangle), supporting > 500 species of coral, and hundreds to thousands of other invertebrates, algae, and reef fish (Bellwood and Hughes, 2001; Roberts et al., 2002; Hoeksema, 2007; Huang et al., 2015). At the same time, Asia has been experiencing the most rapid coastal population growth globally for several decades (Jiang et al., 2001), and has a larger population and higher population densities in coastal zones than any other continent (McGranahan et al., 2007). Additionally, Southeast Asia has more people living within 30 km of a

Table 1
Urban-related changes in coastal waters that are particularly relevant for hard corals.

Urban-related changes	Potential or known effect(s)	Selected references
Pollution		
Terrigenous and Marine sediments	Reduced light availability; more rapid light attenuation; reduced photosynthetic capacity of zooxanthellae; smothering of coral polyps	Fabricius (2005) Pollock et al. (2014, 2016)
Nitrogen and phosphorus	Elevated plankton productivity and shading; risk of eutrophication and hypoxia	Pastorok and Bilyard (1985)
Heavy metals	Toxicity for metazoans	Howard and Brown (1984)
Organic contaminants	Integration into coral tissues; potential effects on invertebrate larvae	Thomas and Li (2000)
Plastic litter	Uptake of microplastics by plankton; integration into coral tissue	Hall et al. (2015)
Marine debris	Abrasion of coral colonies; some types may serve as novel settling substrate	Gall and Thompson (2015)
Light pollution	Potential to impede natural cues for mass spawning	Kaniewska et al. (2015)
Noise pollution	Potential to impede detection of acoustic cues for free-swimming coral larvae	Vermeij et al. (2010)
Artificial substrates	Plastic nets and floating debris	Hoeksema and Hermanto (2018)
Artificial rocky habitat	Potential to serve as artificial habitat for corals; placement loss if constructed on existing reefs; altered hydrodynamic conditions with potential impacts on larval transport and connectivity	Burt et al. (2009a, 2009b) Bulleri and Chapman (2010)
Floating structures		Bishop et al. (2017)
Piers and pilings		Gilbert et al. (2015)
Scoria deposits		Lai et al. (2015)
Artificial islands	Decreased reef area through placement loss; potential increase in intertidal environments	

coral reef and greater participation in marine fisheries relative to population size compared with other regions, which has resulted in many coral reefs near major population centres becoming overexploited and degraded (Burke et al., 2002, 2011). East and Southeast Asia is thus the ideal region in which to examine cross-city patterns in urban coral reefs.

The review consists of three parts: (1) Case studies of urban coral reefs in several major East and Southeast Asian coastal cities, (2) an evaluation of the unifying patterns and characteristics that emerge from published literature across these case study cities, and (3) remaining research needs and current mitigation efforts for urban coastlines. Although there were many candidate cities in the region, we focused our review on four main case studies for which temporally and spatially comprehensive coral survey data were available: Singapore, Jakarta (Indonesia), Hong Kong (PR China), and Naha (Okinawa, southern Japan). These four in-depth case studies are accompanied by shorter synopses of urban coral reefs in Pattaya (Thailand), Nha Trang (Vietnam), Davao City (southern Mindanao, Philippines), Kota Kinabalu (northwest Sabah, Malaysia), Bandar Seri Begawan (Brunei Darussalam), Padang (West Sumatra, western Indonesia), and Makassar

(South Sulawesi, eastern Indonesia) (Fig. 1). Ultimately, the patterns detailed in this review form the basis for future hypothesis testing and field experimentation that mechanistically elucidates the major drivers of urban coral reef ecosystem structure and function. Such advancement in our knowledge of urban reef ecosystems is crucial as rapid population growth in coastal regions threatens to urbanize vast swaths of nearshore habitats.

2. Urban reefs: case studies

2.1. Singapore

Singapore is situated 1° north of the equator, at the southern tip of Peninsular Malaysia (Fig. 1; Table 2). It comprises a heavily developed main island and numerous offshore islands to the south (Fig. 2; Chou, 2006). Extensive land reclamation has transformed the coastline over the last century (Corlett, 1992; Lai et al., 2015), expanding Singapore's total land area by > 50% (Tan et al., 2016) but also increasing turbidity and sedimentation in surrounding marine habitats (Hilton and Manning, 1995). Sediment inputs from land reclamation and coastal



Fig. 1. Map of East and Southeast Asia with all case study cities are labelled. The four main case study cities (Singapore, Jakarta, Hong Kong, and Naha) are shown in larger font.

Table 2
Comparison of demographic, biophysical, and coral reef characteristics of Singapore, Jakarta, Hong Kong, and Naha.

	Singapore	Jakarta	Hong Kong	Naha
Latitude	1° 17' N	6° 7' S	22° 17' N	26° 12' N
Climate	Tropical	Tropical	Subtropical	Subtropical
Population (millions) ^[1]	5.6	10.3–28.9	7.3	0.3–1.2
Annual rate of population change (%) ^[2]	2.39	1.08–3.7	0.87	0.4
City GDP per capita (USD)	\$66,864 ^[3]	\$9984 ^[3]	\$57,244 ^[3]	\$28,893 ^[4]
Gini coefficient ^a	0.46 ^[5]	0.43 ^[2]	0.54 ^[2]	0.31 ^[6]
Unemployment (%) ^[2]	2.8	11.3	4.4	5.4
Port volume (millions of TEU ^b /year)	30.9 ^[7]	5.2 ^[8]	20.1 ^[9]	0.5 ^[10]
Land area (km ²)	719 ^[5]	664–2784 ^[11,12]	1106 ^[13]	39–478 ^[14]
% reclaimed land	33.5 ^[15]	Unknown	5 ^[16]	16.72 ^[17]
Coastline length (km)	505 ^[18]	35 ^[12]	800 ^[19]	33 ^c
Sea surface temperature (°C)	27–31 ^[20]	27–30 ^[21]	13–30 ^[22]	21–28 ^[23]
Annual average precipitation (mm)	2329 ^[24]	2000 ^[25]	2399 ^[26]	2037 ^[27]
Minimum salinity (PSU)	28 ^[28]	32 ^[29]	22 ^[18]	25 ^[30]
Turbidity (NTU)	4.8–6.6 ^[31]	0.4–1.5 ^[32]	2.6–5.6 ^[33]	4.2–12.1 ^[34]
Visibility (m)	2 ^[35]	3 ^[11]	1–3 ^[18]	< 5 ^[36]
Chl <i>a</i> (µg/L)	1.7–3.2 ^[28]	0.9–15.7 ^[32]	1.8–2.5 ^[33]	0.13–0.25 ^[37]
NO ₃ + NO ₂ (µM/L)	0.04–0.15 ^[28]	0.26–1.29 ^[32]	0.02–0.04 ^[33]	0.03–0.52 ^[34]
NH ₄ (µM/L)	0.02–0.09 ^[28]	0.46–11.64 ^[32]	0.03–0.07 ^[33]	0.01–0.59 ^[34]
PO ₄ (µM/L)	0.01–0.04 ^[28]	0.05–4.09 ^[32]	0.01–0.02 ^[33]	0.14–0.22 ^[34]
Contaminants				
Heavy metals in water samples exceeding recommended limits ^d	Cu ^[38]	Pb, Hg, Cd, Cu, As, Cr, Co ^[39]	NA ^[40]	Pb ^[41]
Organic contaminants of greatest concern	PAHs, PCBs, pesticides ^[42]	PAHs, LASs, PCBs, LABs, DPN ^[43]	PAHs, PCBs, DDT, PBDEs ^[40,44]	PAHs, PCBs, pesticides ^[45]
Faecal coliforms (cfu/100 mL)	120–39,726 ^[46]	Up to 16,000 ^{[25]e}	24–2643 ^[18]	4–31 ^[47]
<i>Escherichia coli</i> (cfu/100 mL)	10–5794 ^[46]	Up to 1100 ^{[25]e}	2–1150 ^[18]	Unk
Maximum reef depth (m)	8 ^[48]	10 ^[29]	5 ^[49]	30 ^[50]
No. of hard coral species (historically)	255 ^[51]	158 ^[52]	92 ^[53]	340 ^[54]
Typical hard coral percent cover	13 to 49% ^[55]	0 to 72% ^[56]	< 10 to > 50% ^[53]	0 to 50% ^[57]
Typical macroalgal percent cover	< 20% ^[55]	< 35% ^[58]	< 20% ^[18]	< 10% ^[50]
No. of reef fish species (historically)	> 200 ^[59]	216 ^[60]	> 325 ^[61]	87 ^[62]

[1] UN Population Division (2014). World Urbanization Prospects. Available online at: <https://esa.un.org/unpd/wup/CD-ROM/>; [2] UN Habitat (2016). UN World Cities Report 2016. Available online at: <https://unhabitat.org/books/world-cities-report/>; [3] Citie (2017). City Initiatives for Technology, Innovation and Entrepreneurship. Available online at: <http://citie.org/cities/>; [4] OECD (2016). Organization for Economic Co-operation and Development. Available online at: <http://stats.oecd.org/Index.aspx?QueryId=51329#>; [5] Dept of Statistics Singapore (2016). Key Household Income Trends, 2016. Available online at: https://www.singstat.gov.sg/docs/default-source/default-document-library/publications/publications_and_papers/household_income_and_expenditure/pp-s23.pdf; [6] Katayama et al. (2013); [7] PSA (2016). Port of Singapore Authority. Available online at: <https://www.singaporepsa.com/about-us/>; [8] IPC (2016). Port of Tanjung Priok. Available online at: <http://www.priokport.co.id/>; [9] Marine Department (2016). Government of Hong Kong Special Administrative Region Marine Department. Available online at: www.mardep.gov.hk; [10] NPA (2016). Naha Port Authority. Available online at: <http://www.nahaport.jp/promotion/English/4.html>; [11] Cleary et al. (2014); [12] Tan et al. (2015); [13] Lands Department (2005). Government of Hong Kong Special Administrative Region Lands Department. Available online at: <http://www.landsd.gov.hk/mapping/en/publications/total.htm>; [14] UN (2008) Demographic Yearbook 2008. Available online at: <https://unstats.un.org/unsd/demographic/products/dyb/>; [15] Thiagarajah et al. (2015); [16] Glaser et al. (1991); [17] Japan Ministry of the Environment (2004) Available at: <https://www.env.go.jp/nature/biodic/coralreefs/reference/mokuji/0204j.pdf>; [18] Lai et al. (2015); [19] Fabricius and McCorry (2006); [20] Hilton and Manning (1995); [21] Scoffin et al. (1989); [22] Yeung et al. (2014); [23] Hongo and Yamano (2013); [24] Meteorological Service Singapore (2017). Available online at: <http://www.weather.gov.sg/climate-climate-of-singapore/>; [25] Phanuwat et al. (2006); [26] GovHK (2017). Hong Kong - The Facts. Available online at: <https://www.gov.hk/en/about/abouthk/facts.htm>; [27] Tsuchiya et al. (2004); [28] Gin et al. (2000); [29] Baum et al. (2015); [30] Kawahata et al. (2004); [31] Loh et al. (2006); [32] Baum et al. (2016a); [33] Yung et al. (2001); [34] Reimer et al. (2015); [35] Chou (1996); [36] Shimabukuro and Reimer pers. obs. Unpublished BSc thesis.; [37] Soliman et al. (2016); [38] Browne et al. (2015); [39] Siregar et al. (2016); [40] Liu and Kueh (2005); [41] Ramos et al. (2004); [42] Sin et al. (2016); [43] Breckwoldt et al. (2016); [44] Deng et al. (2015); [45] Iino et al. (2008); [46] Goh et al. (2017); [47] Okinawa Prefecture (2017). Available online at: http://www.pref.okinawa.jp/site/kankyo/hozen/mizu_tsuchi/water/20140603suiyokujo.html; [48] Bauman et al. (2015); [49] Morton (1994); [50] Reimer (2017) pers. obs.; [51] Huang et al. (2009); [52] Cleary et al. (2006); [53] Duprey et al. (2016); [54] Nishihira and Veron (1995); [55] Guest et al. (2016); [56] Cleary et al. (2016); [57] Shilla et al. (2013); [58] Draisma et al. (2018); [59] Low et al. (1997); [60] Madduppa et al. (2012); [61] Sadovy and Cornish (2000); [62] Lecchini et al. (2003).

^a A measure of dispersion in incomes commonly used to represent wealth distribution of a city's residents. Values closer to 0 reflect greater income equality; values closer to 1 reflect greater income inequality.

^b TEU: twenty-foot equivalent unit (metric used to quantify a cargo ship's volumetric capacity; 1 TEU = volume of 1 standard 20' shipping container (20 ft. L × 8 ft H)). Values provided are from 2015, as compiled by the World Shipping Council (<http://www.worldshipping.org/about-the-industry/global-trade/top-50-world-container-ports>).

^c Estimated from maps.

^d ANZECC (2000). In: Strategy, NWQM (Ed), Australian and New Zealand Guidelines for Fresh and Marine Water Quality, p. 314. NA indicates that all metals detected in water samples were within recommended limits.

^e Value represents geometric mean concentration measured in Ciliwung River discharge, as values from marine waters in Jakarta were unavailable.

construction far outweigh those from fluvial sources (van Maren et al., 2014) and are estimated to have reduced average visibility from 10 m to 2 m distance since 1960 (Chou, 1996). Additionally, Singapore's port is among the busiest in the world (Chou, 2006), as the port of call for over 500 large commercial vessels every month (Lim et al., 2017) and

with a throughput of nearly 30 million shipping containers every year (Yap and Lam, 2013). Dredging to maintain shipping channels and port terminals is another driver of high sediment loads in Singapore's waters (Chou, 2006).

Corals reefs in Singapore's territorial waters include shallow patch



Fig. 2. Map of Singapore, including the main and surrounding islands. Numbers represent survey sites where coral cover data shown in Fig. 3 were collected by Guest et al. (2016) and those in Fig. 10 by J.S.Y. Wong et al. (2018).

and fringing reefs that are extremely compact, as well as extensive intertidal reef flats (Hilton and Chou, 1999). Most coral cover in Singapore is limited to a relatively narrow strip between the reef crest and upper reef slope from 3 to 6 m depth (Huang et al., 2009; Guest et al., 2016). This depth restriction is due to the upper reef flats (0–2 m) being dominated by the canopy-forming macroalgae *Sargassum* for most of the year (Low, 2015) and extreme light attenuation with increasing depth (> 6 m) from chronic high sediment deposition and suspended particles (Todd et al., 2010). Dikou and van Woesik (2006) note that coral genera normally found in deeper zones, such as *Leptoseris* and *Oxypora*, occur at relatively shallow depths in Singapore. At the same time, shallow-water taxa that are typical of the region, such as *Acropora*, are not abundant (Guest et al., 2016). The most common hard corals include a variety of sediment-tolerant genera, such as *Montipora*, *Pectinia*, and *Porites* (Dikou and van Woesik, 2006). Even for sediment-tolerant taxa, high sediment loads and light limitation in Singapore waters can alter calice morphology, reduce growth rates, and limit other aspects of coral condition (Ow and Todd, 2010; Browne et al., 2015).

Total reef area in Singapore has declined considerably during the 20th century (Chou, 1996). Using historical maps, Hilton and Manning (1995) estimated that the total area of intertidal reefs in Singapore decreased from 32.2 km² in 1922 to 30.5 km² in 1953. A subsequent analysis by Lai et al. (2015) indicated further decreases to 17 km² in 1993 and 9.5 km² in 2011. There have also been widespread losses in the subtidal reef zone as large areas of subtidal reef have been covered by sediments and artificial structures as a result of dredging and land reclamation (Low and Chou, 1994; Chou, 1996). This has coincided with considerable decreases in coral cover at reef sites that remain, particularly for deeper habitats. Guest et al. (2016), for instance, found a decrease in coral cover of nearly 30% at deep sites (6–7 m) between

1986 and 2012. During the same period, mean coral cover at shallow sites (3–4 m depth) decreased by approximately 12% (Guest et al., 2016).

Time series data suggest that coral reefs in Singapore may rebound rapidly following thermal bleaching events. For instance, at shallow sites surveyed by Guest et al. (2016), coral cover returned to pre-bleaching levels in < 10 years following El Niño-associated bleaching in 1998. The 2010 thermal anomaly also caused a decline in coral cover of > 20% but it had recovered about a quarter of that lost cover by 2012 (Guest et al., 2016), and fully by early 2016 (J.S.Y. Wong et al., 2018). This rapid recovery is unlikely to be driven by new recruitment, as settlement of coral larvae in Singapore is limited (Bauman et al., 2015). Rather, taxa that dominate Singapore's coral reefs, such as *Merulina*, are particularly adept at regrowth following partial to near-complete colony death, and may rapidly increase coral cover levels via horizontal expansion (Guest et al., 2016). Despite this general, mostly anecdotal pattern, predicting coral susceptibility and recovery in response to thermal stress in Singapore remains complex (Chou et al., 2016).

Given chronic sedimentation throughout much of Singapore's territorial waters, hard coral species richness is surprisingly high. Historically, 255 species of hard coral have been documented in Singapore (Huang et al., 2009), but only a subset of these have been recorded in recent years. For instance, Huang et al. (2009) observed 161 species in 2006–2007, a level of diversity on par with surveys at more remote locations within the surrounding region (Harborne et al., 2000; Affendi et al., 2005; Huang et al., 2015). Macroalgal competitors of coral include the genera *Bryopsis* and *Sargassum* (Lee et al., 2012) but cover on the reef crest is generally low at ≤ 20% (Guest et al., 2016), though this varies considerably between sites, as well as in relation to

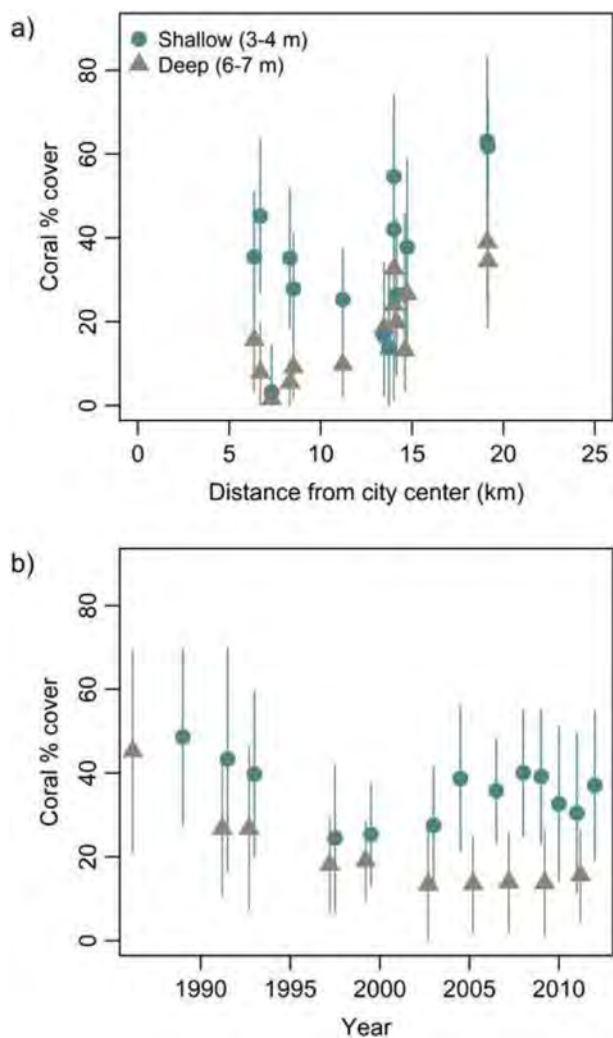


Fig. 3. Percent cover of hard corals with increasing distance from the Singapore's city centre (a) and over time (b). Points represent mean values and bars show the maximum standard deviation across years (a) or sites (b). Data are shown for two depths: shallow (circles: 3–4 m, gray) and deep (triangles: 6–7 m, black). Source: Guest et al. (2016).

abundances of the urchin, *Diadema setosum* (Goh and Lim, 2015). Guest et al. (2016) found no evidence of phase shifts between coral and macroalgal dominated states over time. Rather, sedimentation and light availability may be limiting to corals and macroalgae alike (Low et al., 1997), and is generally considered to be among the most essential drivers of community structure locally.

Coral reefs in Singapore are highly variable across small spatial scales (hundreds of meters), but some broader spatial patterns are evident with increasing distance from Singapore's main island. Dikou and van Woessik (2006) found inshore reefs comprised more encrusting and massive growth forms compared with offshore reefs, which had more foliose corals. At inshore sites, coral cover tends to be low, but varies considerably from one site to the next (Fig. 3; Dikou and van Woessik, 2006; Guest et al., 2016). These patterns do not necessarily carry over to coral diversity, as Huang et al. (2009) found no evidence of inshore-offshore gradations in coral species richness. However, richness is consistently highest at Raffles Lighthouse, the site farthest from Singapore's main island (Guest et al., 2016).

2.2. Jakarta, Indonesia

Jakarta is situated on the northwestern side of the Indonesian island of Java (Fig. 4). It is one of the world's largest cities. Population estimates range from 10 million to 30 million depending on the boundaries used to define the greater metropolitan area (Forstall et al., 2009; Baum et al., 2016b). The city is bounded to the north by Jakarta Bay, a 500 km² open embayment, which is part of the semi-enclosed Java Sea. Three major rivers deliver freshwater inside or just outside the bay: the Ciliwung, Cisadane, and Citarum (Poerbandono et al., 2014; van der Wulp et al., 2016a, 2016b). Sewage discharge, runoff, and contamination from heavy metals and organic and inorganic pollutants are chronic problems, with wastewater plumes extending tens of kilometers into surrounding marine areas (Hosono et al., 2011; Breckwoldt et al., 2016; Dsikowitzky et al., 2017). Water quality is also impacted by coastal construction and land reclamation (Verstappen, 1988), although current estimates of total reclaimed land area were found to be lacking in our review (however see illustration by Takagi et al., 2017). Additional future plans to reclaim > 50% of Jakarta Bay, adjoining either the 5-m or the 10-m isobath (Han et al., 2013; Priyambodho et al., 2015; van der Wulp et al., 2016a, 2016b), would support high-end housing, tourism, shipping, and economic growth, and help to mitigate land subsidence and coastal flooding, but would have negative impacts on those in the lowest socio-economic brackets and on fishermen (Colven, 2017).

Historically, Jakarta and surrounding areas contained extensive and diverse coral reefs (Moll and Suharsono, 1986) that were essential for local subsistence and small-scale fisheries (Padawangi, 2012; Baum et al., 2016b). Reconstruction of historical data suggest Jakarta Bay hosted diverse coral assemblages as recently as 1920, with > 70 acroporids, > 30 faviids (now classified as merulinids), > 20 poritids, and numerous other families of hard coral (van der Meij et al., 2010). Jakarta Bay was also rich in other benthic and demersal organisms, including 11 species of macroalgae (Draisma et al., 2018), 36 benthic forams (Hofker, 1968), 171 species of molluscs (van der Meij et al., 2009), a diversity of sponges and other invertebrates (Cleary et al., 2008; de Voogd and Cleary, 2008), and various commercially valuable fish species (Baum et al., 2016b).

Today, Jakarta's coral reefs are considerably less diverse (van der Meij et al., 2009, 2010; Draisma et al., 2018), are limited to shallow depths < 10 m (de Voogd and Cleary, 2008; Baum et al., 2015) and exhibit pronounced patterns along an inshore-offshore gradient (Cleary et al., 2008, 2016; Baum et al., 2015). Reefs within approximately 20 km of Jakarta have lower coral cover and diversity than reefs further away (Fig. 5; Cleary et al., 2008, 2016). The diversity of macroalgae, sponges, molluscs, echinoderms, ascidians, and fishes is also reduced in inshore areas (Cleary et al., 2008, 2016; de Voogd and Cleary, 2008; Madduppa et al., 2013; Draisma et al., 2018). Gradations in species diversity are closely tied with water quality, as inshore sites have higher turbidity, mean temperature, pH, dissolved oxygen, and chlorophyll-*a* concentrations, as well as lower salinity, compared with offshore sites (Cleary et al., 2008, 2016).

Given spatial complexities in the decline of Jakarta's coral reefs over time (van der Meij et al., 2010; Cleary et al., 2014), temporal trends are perhaps best considered within distinct spatial strata. The Jakarta Bay-Thousand Island reef complex is commonly divided into three zones (Cleary et al., 2006): Zone 1, < 18 km (the area south of -5.97° latitude); Zone 2, ~18 to 40 km (between -5.97° and -5.77° latitude); and Zone 3, > 40 km from Jakarta (north of -5.77° latitude) (Fig. 4; Cleary et al., 2016). Coral reefs in Zone 1 declined rapidly and early, and had low diversity and percent cover, as well as relatively small colony size, by the 1980s (Moll and Suharsono, 1986; Cleary et al., 2014). Cleary et al. (2014) subsequently observed further declines in inshore coral cover from 10% in 1985 to < 5% by 1995. By 2005, acroporids and milleporids were not recorded on reefs in Zone 1 (van der Meij et al., 2010). Although corals in the families Merulinidae (taxa



Fig. 4. Map of Jakarta's shoreline and neighboring islands. Numbers represent survey sites where coral cover data shown in Fig. 5 were collected.

previously included in Faviidae; sensu Huang et al., 2011), Poritidae, Fungiidae, and others persisted (van der Meij et al., 2010), overall coral cover remained low in 2005 (Cleary et al., 2014). More recent surveys in 2011 and 2012 show little change in coral cover (Baum et al., 2015, 2016a) and continued low diversity of other taxa (Cleary et al., 2016) in Zone 1.

Further offshore, coral reefs have also declined, partly due to bleaching (Brown and Suharsono, 1990; Hoeksema, 1991), but their

trajectory has been variable among sites. Overall, coral cover decreased from 50 to 30% in Zone 2 and from 74 to < 20% in Zone 3 between 1985 and 1995 (Cleary et al., 2014). In Zone 2, these decreases were driven most by losses in submassive corals. In Zone 3, losses of both massive and submassive coral growth forms, and particularly of the genus *Porites*, were widespread, as were declines in the branching corals, *Seriatopora* and *Acropora* (Cleary et al., 2014). In the decades that followed, coral cover throughout Zone 3 and at some sites in Zone

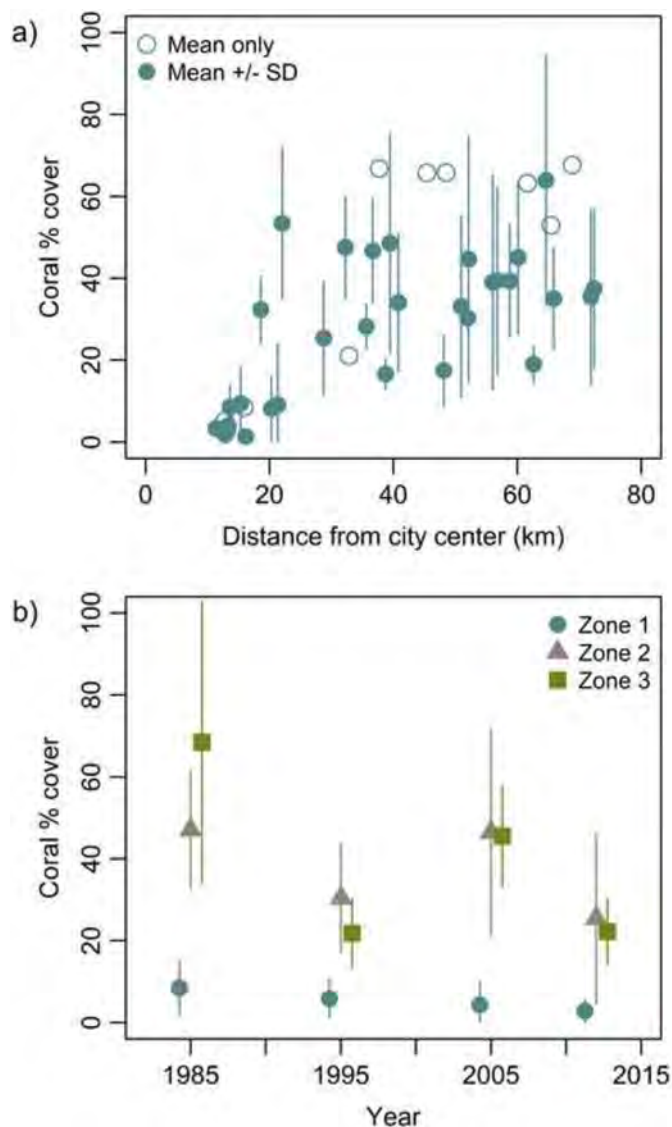


Fig. 5. Percent cover of hard corals with increasing distance from the Jakarta city centre (a) and over time (b). Points represent mean values averaged across sites. Bars show the maximum standard deviation across years (a) or sites (b). In (a), circles represent sites for which only mean coral cover data were available and solid circles represent sites with variance estimates. In (b), coral cover over time is summarized separately for three spatial zones: Zone 1 (circles: closest to Jakarta, south of -5.97° latitude), Zone 2 (triangles: midshore zone between -5.97° and -5.77° latitude) and Zone 3 (squares: farthest from Jakarta, north of -5.77° latitude).

Sources: Cleary et al. (2006, 2008, 2016) and Baum et al. (2016a).

2 fluctuated, rebounding by 2005 and then decreasing again by 2011, following the 2010 thermal bleaching event. Recent temporal fluctuations in Zone 3 have been associated primarily with changes in non-*Acropora* branching and submassive corals. During this same period, Cleary et al. (2014) noted a gradual increase in *Acropora* to $> 10\%$ in Zone 3 by 2011.

2.3. Hong Kong

Hong Kong is a city of 7.3 million, located at 22° N latitude, with a collective land area of 1106 km^2 comprising several land masses, including Hong Kong Island, the New Territories and Kowloon, and 236 islands and islets (Fig. 6). Similar to Jakarta and Singapore, Hong Kong is a major shipping and commercial centre with a long history of marine

contamination, nutrient enrichment, and elevated sedimentation rates, which are likely perpetuated by ongoing land reclamation and dredging activities (Goodkin et al., 2011). Benthic communities in the area are also strongly influenced by freshwater inputs from the Pearl (Zhujiang) River, 80 km west of Hong Kong. Surface salinities can drop below 22 PSU and sea surface temperature can fall below 15°C during periods of high riverine flow. Southwest to northeast gradations in salinity and temperature are also evident throughout the year due to fluvial inputs (Fabricius and McCorry, 2006).

Despite sub-optimal temperature and salinity conditions, over 90 species of hard coral have been documented in Hong Kong (Duprey et al., 2016). Hard coral colonies are primarily limited to depths $< 5 \text{ m}$ (Morton, 1994). Many of the taxa present are slow growing and long-lived (Goodkin et al., 2011). Although there is little evidence of long-term accretion of reefs (both historically and presently), hard corals are a major component of sessile subtidal assemblages in the Hong Kong area (Goodkin et al., 2011). In some locations, particularly on the northeast side of the city where freshwater input from the Pearl River is limited, coral cover commonly exceeded 75% as recently as the 1980s (Scott, 1990). This cover declined over subsequent decades (Fig. 7), and particularly during a series of coral mortality events in the early 1990s. Coral cover exceeding 50% has not been uncommon in more recent surveys in the 2000s and 2010s (Duprey et al., 2016), but there has been a gradual shift in coral composition. Morton (1994) noted a reduction in branching and plate-like acroporids in the 1980s, while massive growth form corals such as merulinids have persisted (Collinson, 1997; Lam et al., 2007).

Temporal and spatial gradients in Hong Kong's coral assemblages are heavily influenced by eutrophication and water quality (Morton, 1989; Scott, 1990). Data from multiple surveys conducted between 1998 and 2006 indicate that chlorophyll-*a* and inorganic nutrients are strong predictors of hard coral assemblages. Coral cover and richness tend to be greatest where chlorophyll-*a* is $< 2 \mu\text{g/L}$, dissolved inorganic nitrogen is $< 2 \mu\text{M}$, and dissolved inorganic phosphorus is $< 0.1 \mu\text{M}$, and is also weakly negatively correlated with suspended particulate matter (Duprey et al., 2016). These water quality parameters vary considerably over small spatial scales due to numerous input sources throughout Hong Kong. The city's shoreline is also highly complex (Fig. 6) and coral cover data available for this review were available from a relatively limited range of distances from the city centre (Fig. 7). For these reasons, no conclusions can be made regarding urban-related inshore-offshore gradients in Hong Kong. However, as in other case study cities, coral genera such as *Acropora* have been particularly negatively affected by urban-related abiotic conditions and are rare on Hong Kong reefs (Duprey et al., 2016).

2.4. Naha, Japan

Naha, the capital city of Okinawa Prefecture (Japan), is positioned at the mouth of the Kokuba River (Fig. 8), on the west coast of Okinawa Main Island. It has the highest latitude of the case study cities considered in this review (26°N latitude). Waters surrounding Naha are warmed by the Kuroshio Current, which travels northward from the equator as the eastern boundary current of the North Pacific Gyre. With a human population of 0.3 to 1.2 million, depending on the geographic boundaries used, Naha is relatively small compared with the case study cities discussed thus far. Okinawa Main Island has a total land area of 1208 km^2 and is inhabited by nearly 1.5 million people. Population density is greatest on the southern half of the island, where Naha is located; urbanization throughout the island likely influences the health of adjacent reefs. In particular, rivers in southern Okinawa deliver high concentrations of nutrients and pollutants such as endocrine disruptors and bisphenol A (BPA) to coastal waters (Shilla et al., 2013).

The coastline of Naha is almost completely artificial, with extensive land reclamation of shallow fringing reefs since the reversion of Okinawa to Japanese control from the United States in 1972

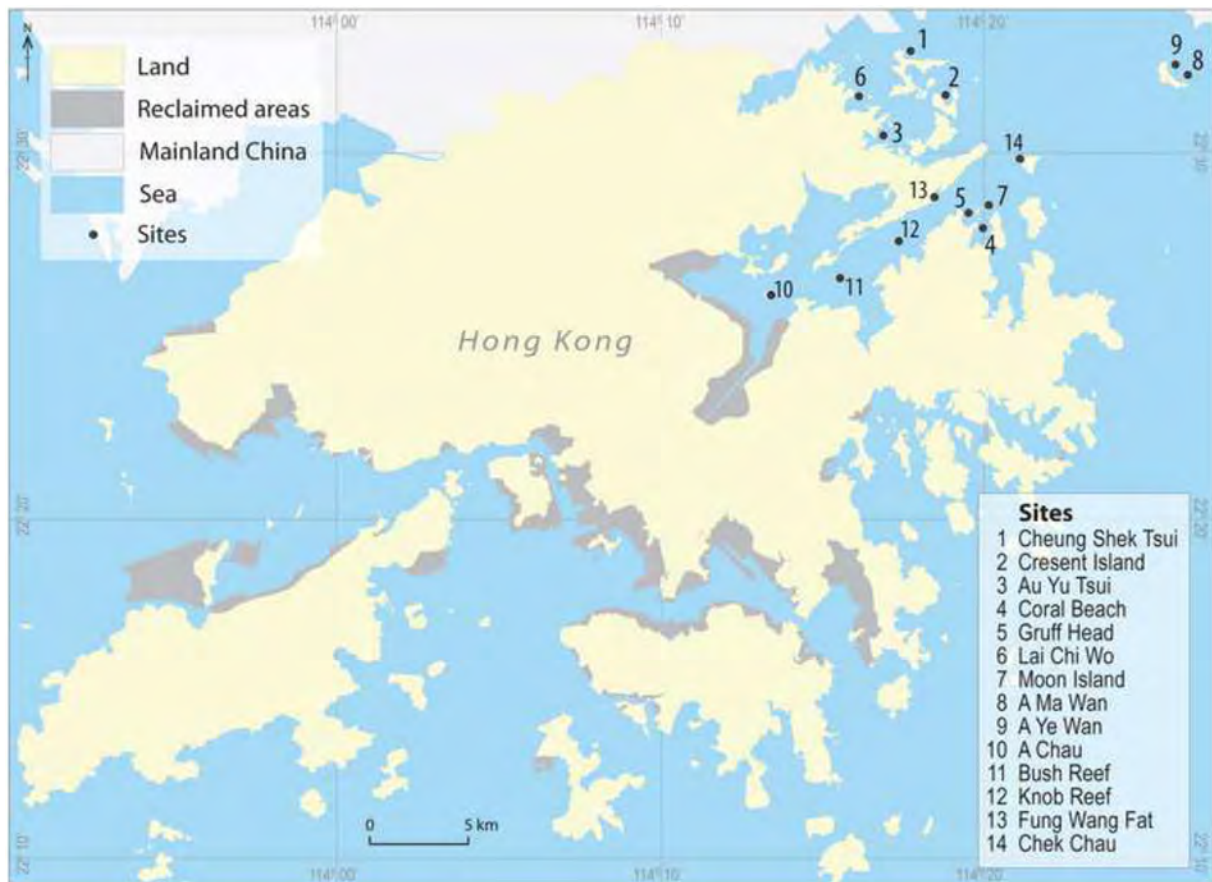


Fig. 6. Map of Hong Kong. Numbers represent survey sites where coral cover data shown in Fig. 7 were collected.

(Kuwahara, 2012; Reimer et al., 2015). Environmental assessment and protection laws remain generally weak in Japan (e.g. “coral friendly port construction”, Maekouchi et al., 2008), and loss of fringing coral reefs due to land reclamation has been controversial, with statements requesting greater protection having been released publicly by numerous academic and scientific societies. Despite this, reclamation is still ongoing with the expansion of Naha Airport, and at numerous other locations within Okinawa Main Island (Reimer et al., 2015).

Fringing and patch reefs form throughout Okinawa, including in urban waters immediately adjacent to Naha (Shilla et al., 2013). A total of 340 species of hard coral have been documented in the Okinawa Islands (Nishihira and Veron, 1995; Tsuchiya et al., 2004; Hongo and Yamano, 2013). This level of hard coral species richness is very high compared with that at similar latitudes on the Great Barrier Reef (Tsuchiya et al., 2004). However, percent cover of hard corals varies widely on Okinawa Main Island (Fig. 9), and tends to be particularly low (< 20%) near river outputs (Hongo and Yamano, 2013; Shilla et al., 2013). Unfortunately, there have been few studies documenting spatial patterns in coral cover with increasing distance from Okinawa Island or from Naha. To some extent, this is due to Okinawa reefs primarily occurring close to shore. Data from the Japanese Ministry of Environment showed little difference in hard coral cover on reefs surrounding Naha and those in the nearby uninhabited Chibishi Islands (~8 km to the west; Fig. 9). While data across the Ryukyu Island chain (see Lecchini et al., 2003), which extends hundreds of kilometers to the south (as well as to the north), may thus constitute the best available proxy of coral cover relative to urbanization, they are confounded by a natural thermal gradient across the archipelago, and were thus excluded from this review.

Percent cover of hard corals in Okinawa is thought to have declined considerably over the latter part of the 20th century (Fig. 9; Hongo and

Yamano, 2013). Crown-of-thorns sea stars, *Acanthaster* sp., have played a major role in this decline, with particularly dramatic predation events occurring in the 1970s and 1980s (Tsuchiya et al., 2004). Most authors refer to *Acanthaster planci*, which is an Indian Ocean species, whereas the name of the Pacific species still needs to be established (Vogler et al., 2008; Haszprunar et al., 2017). Coral cover also decreased as a result of thermal bleaching events in the 1980s, 1998, and 2001 (Yamazato, 1999; Loya et al., 2001), as well as in 2016–2017 (Kayanne et al., 2017; Ministry of the Environment of Japan, 2017). Temporal declines have been particularly pronounced among branching and tabular hard coral taxa, with *Acropora* decreasing dramatically by the late 2000s. Stress-tolerant genera such as *Porites*, *Dipsastraea*, *Favites*, and *Leptastrea* have persisted over recent decades and now have the greatest relative abundance surrounding Okinawa Main Island (Hongo and Yamano, 2013).

Water quality is thought to be an important factor dictating both spatial and temporal patterns in coral cover on Okinawa reefs (Ramos et al., 2004; Imo et al., 2007, 2008; Shilla et al., 2013; Reimer et al., 2015), although in general water quality is good, possibly due to Naha's position next to oceanic waters. Terrestrial soil from Okinawa is iron-rich and red in color, and altered runoff patterns combined with increasing nutrient influx from terrestrial sources has been highlighted as a major driver of reef decline (Shilla et al., 2013). Okinawa Prefecture has taken steps to reduce runoff in recent years (Okinawa Prefecture, 2016). Whether related to these mitigation measures or other factors, coral cover in the Naha area appeared to increase from 2004 to 2009 according to surveys from the Japanese Ministry of Environment (Fig. 9). This recovery pattern was not detected by Hongo and Yamano (2013); their study included sites on both the west and east coasts of Okinawa Main Island, yet included few locations near central Naha (Hongo and Yamano, 2013).

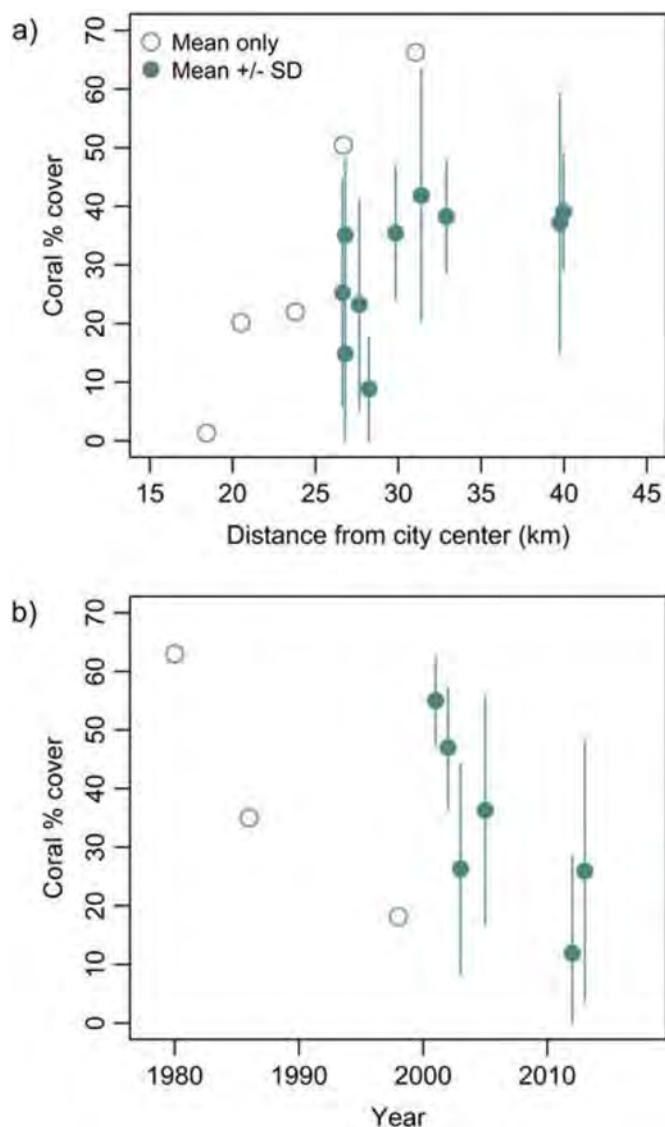


Fig. 7. Percent cover of hard corals with increasing distance from the Hong Kong's city centre (a) and over time (b). Points represent mean values and bars show the maximum standard deviation across years (a) or sites (b); data points for which only mean coral cover data were available are shown with open circles.

Source: K.T. Wong et al. (2018).

2.5. Other examples

In addition to the four major cities discussed above, we compiled information on coral reefs and the factors shaping reef health from seven additional coastal cities: Pattaya (near Bangkok, Thailand), Nha Trang (Vietnam), Davao City (southern Mindanao, Philippines), Kota Kinabalu (northwest Sabah, Malaysia), Bandar Seri Begawan (Brunei Darussalam), Padang (West Sumatra, western Indonesia), and Makassar (South Sulawesi, eastern Indonesia) (Fig. 1). All seven cities are located in the tropics. The cities in Brunei, Malaysia, eastern Indonesia, and the Philippines are situated in the Coral Triangle, which is the centre of maximum marine biodiversity, depending on how its boundaries are defined (Hoeksema, 2007; Huang et al., 2015; Veron et al., 2015; Asaad et al., 2018).

Table 3 summarizes geographical and social-economic aspects, coastal and reef morphology, river discharge and pollution, potentially harmful human activities, other factors causing reef degradation, coral and fish diversity, and reef mitigation for each city. Sedimentation

through river discharge, pollution, and unsustainable fisheries were the most common and severe factors impacting the health of the reefs.

2.5.1. Pattaya (near Bangkok, Thailand)

Pattaya is situated at the northeastern side of a shallow, semi-enclosed bay, recognized as Inner Bay of Bangkok, where water circulation is limited (Fig. 1; Tanaka et al., 2013). The reefs off Pattaya are 50 km from Bangkok and even closer to Thailand's largest industrial harbor, which is 13 km north of Pattaya (Table 3). Although commercial fisheries do not occur in the vicinity of Pattaya's reefs, most litter on local reefs consists of lost nets (Table 3). Sewage and water discharge from large rivers are the main sources of high sediment and nutrient loads (Table 3). The major degrading impacts of urbanization on Pattaya's reefs consist of sedimentation from coastal development, water pollution, and mass tourism (Table 3). Bleaching, ocean acidification, and flooding associated with extreme climate variability are also important stressors (Pongsakun et al., 2012).

2.5.2. Nha Trang (Vietnam)

Nha Trang is positioned in southeast Vietnam and the western part of the South China Sea (Fig. 1), where the continental shelf is narrow and subjected to summer upwelling, which results in low summer temperatures (Binh et al., 2015). Fringing reefs occur along the mainland and around large islands in Nha Trang Bay (Nguyen et al., 2013) and have been subjected to pollution and sedimentation from river discharge and port dredging (Table 3). Nha Trang Bay is part of the most diverse region within the western South China Sea (Huang et al., 2016). Since the upwelling helps prevent thermal stress and bleaching, the reefs in Nha Trang Bay are considered regional refugia for reef replenishment (Vo et al., in press). The major impacts of urbanization on Nha Trang Bay reefs consist of dredging, land filling and construction works, resulting in increased sedimentation during the rainy season (Table 3).

2.5.3. Davao City (South Mindanao, Philippines)

Davao City is located deep inside Davao Gulf at the southern Philippine island of Mindanao (Fig. 1). It is the third most populous metropolitan area of the Philippines (Feldman, 1975). There are two major ports, Davao City and Panabo City. Corals live on fringing reefs along the main coast and around two large islands in front of the city. The seafloor here is much shallower than the southern part of the bay (Bos et al., 2008). The reefs of Davao Gulf are exposed to sediment discharge from rivers and creeks (Table 3). Major degrading effects of urbanization on nearby reefs are caused by nearshore pollution from gold mining, cement production, domestic litter, and agrochemicals, as well as ongoing eutrophication, sedimentation, coastal development, harbor construction, tourism, and unsustainable fisheries (Table 3).

2.5.4. Kota Kinabalu (Sabah, Malaysia)

Kota Kinabalu, the capital of Sabah, is positioned near the north-eastern tip of Borneo (Fig. 1). Corals can be found on fringing reefs around five islands in front of the city and on some offshore patch reefs (Table 3). The five islands form the Tunku Abdul Rahman Park, which is a popular tourist attraction for marine recreational activities. Reefs in the north and west of the islands are exposed to waves and sea swells forming rocky outcrops, while reefs in the south and east that are facing the mainland have sheltered conditions (Wood, 1979). There are two major industrial harbors, one in the city and one in nearby Sapangar Bay. Commercial fishing is prohibited in inshore waters (Shah and Selamat, 2016). Degrading effects of urbanization on nearby reefs are predominantly caused by sewage, pollution from industry, tourism, and sedimentation resulting from land clearing, dredging, and reclamation works (Table 3).

2.5.5. Bandar Seri Begawan (Brunei Darussalam)

Bandar Seri Begawan is the capital of Brunei Darussalam, which is



Fig. 8. Map of Okinawa Main Island and surrounding islands, with Naha labelled. Numbers represent survey sites where coral cover data shown in Fig. 9 were collected. Points 6 through 11 surround the Chibishi Islands.

located on the northern Borneo coast (Fig. 1). Together with satellite urban developments, it forms the largest population centre in Brunei. Port activities are concentrated in the shallow, sheltered, and muddy Brunei Bay known as Inner Brunei Bay (Chua et al., 1987). There are no fringing reefs but some coastal coral communities occur nearby. Off-shore coral reefs are mainly submerged shoals with high species richness and live coral cover values, indicating minimal effects of urbanization, although water visibility is poor inshore (Table 3). Rocky outcrops in the turbid nearshore zone are dominated by gorgonian whip corals and sea fans (Lane, pers. obs), while some muddy, nearshore shoals are inhabited by other benthic fauna (Reimer et al., 2012). Reefs close to oil and gas platforms are difficult to access (McManus, 2017) but may become covered by slurry and scrap metal (Hoeksema and Lane, pers. obs.). Most of Brunei's reefs are considered potential thermal refugia during periods of elevated sea surface temperature (Lane, 2011) and could become important sources of coral recruits to re-seed neighbouring reefs.

2.5.6. Padang (West Sumatra, western Indonesia)

Padang, the capital of West Sumatra, is situated on the west coast of Sumatra (Fig. 1). It is served by two sea ports. Most reefs off Padang are patch reefs arranged in two rows along a relatively steeply sloping deep shelf that is semi-enclosed by large continental islands (Table 3). Nearshore reefs are exposed to sedimentation from rivers, especially after heavy rainfall (Efendi, 1995). They are also affected by coastal development and increasing tourism. The rivers and port are sources for agrochemicals and industrial pollutants (Table 3). Large-scale coral death, which has occurred around most of the offshore patch reefs down to 20 m depth, started around 1994–1995 and was attributed to coral bleaching, which was succeeded by red tides in 1997 (Table 3).

2.5.7. Makassar (South Sulawesi, eastern Indonesia)

Makassar (named Ujung Pandang from 1971 to 1999) is the capital of South Sulawesi and the largest city and port in eastern Indonesia, with a well-documented reputation for fisheries (Table 3). It is located in the southern part of Makassar Strait (Fig. 1) and is considered the maritime gateway for eastern Indonesia. Its reef system is known as the Spermonde Archipelago and consists of many patch reefs, which are either cay-crowned or submerged and arranged in lines parallel to the coast, with clear nearshore-offshore gradients (Table 3). Most of the reef cays are densely inhabited (Anri et al., 2017). The coastal area and islands of Makassar have received much research attention (Table 3), perhaps more than reef systems near other cities in Indonesia.

2.5.8. Common patterns

The seven urban areas differ in population size and reef damage, ranging from Bandar Seri Begawan with smallest number of people and the least affected reefs, as opposed to Davao City and Makassar. Their reefs are exposed to terrigenous run-off as primary source for sediments, mostly through river discharge. All cities have harbors, which need dredging (Erftemeijer et al., 2012), which together with shipping activities in shallow water will cause sediment resuspension. The cities have many other different kinds of pollution in common, which are related to sewage, litter, industrial activities, and more. All are directly or indirectly related to population size. Unsustainable fisheries is a common factor but perhaps less obviously related to urban reefs, because fishermen usually do not live in cities and the proximity of cities would facilitate management and inspections. On the other hand, demand for seafood is larger near cities. The common occurrence of environmental gradients with increasing distance away from cities is not surprising. There is no clear relation with bleaching, coral diseases and

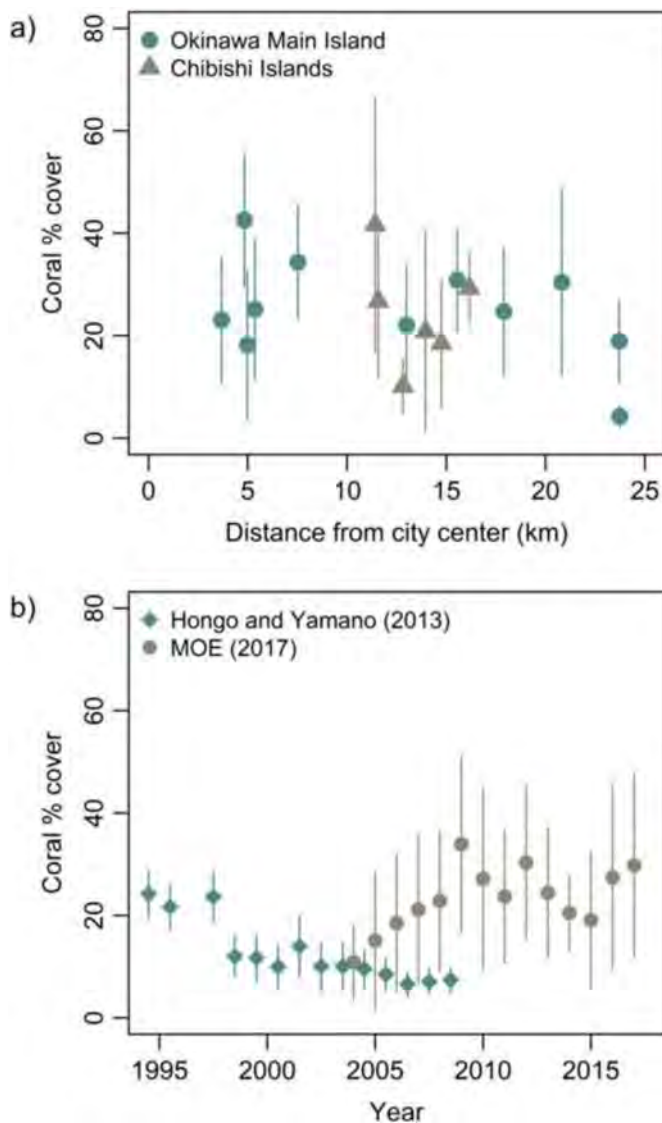


Fig. 9. Percent cover of hard corals with increasing distance from Naha's city centre (a) and over time (b). Points represent mean values while bars represent maximum standard deviations across years or sites. For spatially distributed data (a), circles represent sites on Okinawa Main Island while triangles represent sites in the nearby uninhabited Chibishi Islands. Temporally distributed data were available from two separate sources (shown as diamonds or circles in (b)), which included different sites and covered different time periods. Sources: (a) Ministry of the Environment of Japan (2017); (b) Hongo and Yamano (2013) and Ministry of Environment of Japan, MOA (2017).

coral predation, which are not all well monitored perhaps. Important developments are land reclamation on top of reefs or in close proximity and the construction of seawalls. The latter may not be detrimental as long as seawalls and concrete structures do not facilitate the settlement of non-native species (Glasby et al., 2007; Chapman and Underwood, 2011) or enhance the dominance of certain native species, such as *Tubastraea* spp. (Ho et al., 2017).

3. Effects of urbanization on coral reefs

Urbanization results in a variety of environmental changes that impact hard corals (Table 1). Coral reefs in urban areas have been subjected to and shaped by these changes over many decades, and in some cases over multiple centuries. The cities considered in this review indicate that urban coral reefs share several key characteristics, which

we discuss below.

3.1. Domed growth forms and low reef complexity

Like other degraded reefs, urban coral reefs were dominated by stress-resistant, “domed” growth form (massive, submassive, and encrusting) species that generate reefs of moderate to low structural complexity (or ‘architectural complexity’, sensu Tews et al., 2004; Harris et al., 2018). Particularly well represented were massive, submassive, and encrusting species of merulinids, *Porites*, and *Montipora* (Table 4). Of the most common taxa for which life-strategy designations (sensu Darling et al., 2012) were available, nearly all were considered “stress-tolerant” or “generalists”. Branching, competitive taxa, such as *Acropora* spp., were uncommon in heavily urbanized areas (within 20 km for the main case study cities). Domed coral growth forms tend to be favoured under high sedimentation, low light conditions because they optimize sediment shedding while maximizing photosynthesis (Ertfemeijer et al., 2012). Although other growth-forms can also be successful, particularly where aided by alternative adaptations to sediment and low light. Mushroom corals, which are free-living and rid themselves of settling particles through pulsed inflation and ciliary action in addition to a convex upper surface (Hoeksema and Moka, 1989; Bongaerts et al., 2012). They were found in dense multi-species assemblages on nearshore reefs (< 5 km) in Singapore, Makassar, and Nha Trang, (Hoeksema and Koh, 2009; Hoeksema, 2012a, pers. obs.).

Shifts in three-dimensional structure of reefs have important implications for ecosystem functioning (Done et al., 1996). Refugia tend to be limited on low-complexity reefs. This can increase predation risk, reduce grazing activity, and coincide with reduced species richness and abundance of reef fishes and invertebrates (Almany, 2004; Idjadi and Edmunds, 2006; Wilson et al., 2007). Structural complexity also tends to be negatively correlated with algal cover and urchin densities (Graham and Nash, 2013), and low-complexity reefs may be less likely to recover from disturbance events, particularly in the presence of high nutrient loads and other stressors (Graham et al., 2015). Structurally complex reefs additionally provide a variety of ecosystem services to coastal populations, including slowing water flow rates and serving as natural breakwaters that reduce shoreline erosion and inundation during storms (Moberg and Folke, 1999), as well as a suite of other services relating tourism (Graham and Nash, 2013) and exploitable resources.

Similarities in the taxa that were prominent in heavily urbanized areas suggest that the selective pressure hard corals face as a result of urbanization is similar regardless of the city where they are located. While urbanization (in combination with meso-scale processes) may functionally eliminate certain coral taxa (e.g. *Acropora*), it likely leads to more nuanced ecological and evolutionary trajectories for other coral species. Only a small minority of coral taxa, such as *Oulastrea crispata* (Cleary et al., 2016), appear to respond opportunistically to urban-related environmental changes (Sawall et al., 2011). For the remainder of taxa that occur in urbanized environments, stress-tolerance (Madin et al., 2016), ecological versatility (Graham, 2007), and phenotypic and trophic plasticity (Todd et al., 2004; Todd, 2008; Seemann et al., 2013; Sawall et al., 2014) are likely essential. The ability to capitalize on reduced interspecific competition associated with urban-related abiotic conditions is probably advantageous. Understanding the ecological and evolutionary trajectories of urban coral reefs may be key for developing ecological engineering and mitigation strategies that maintain ecosystem functions and services that city populations value.

3.2. Spatio-temporal characteristics

3.2.1. Temporal decline followed by fluctuations associated with acute impacts and rapid recovery

Decreases in coral cover and species richness over time have been widely documented throughout the region (Pandolfi et al., 2003;

Table 3

Comparison of coastal waters and coral reef characteristics of seven additional case study cities. All additional case study cities are located in tropical areas within Asia (Fig. 1).

City	Pattaya	Nha Trang	Davao City	Kota Kinabalu	Bandar Seri Begawan	Padang	Makassar
Coordinates	12°55'N 100°52'E	12°15'N 109°11'E	07°04'N 125°36'E	05°58'N 116°04'E	04°55'N 114°55'E	00°57'S 100°21'E	05°08'S 119°25'E
Population in 2018 ($\times 10^6$) ^[1]	0.1	0.28	1.21 ^[34]	0.46	0.06 ^[65]	0.84	1.32
Harbor/shipping activities nearby (Y/N)	Y ^[2]	Y ^[20]	Y	Y	Y	Y ^[76]	Y ^[88]
Fringing reefs (F), patch reefs (P), or both (FP)	F	FP	F	FP	p ^[66]	PF	p ^[89]
River discharge on reefs (Y/N)	Y ^[3]	Y ^[21]	Y ^[35]	Y ^[46]	Y ^[67]	Y ^[77]	Y ^[91]
Sewage discharge nearby (Y/N)	Y ^[3]	Y ^[21]	Y	Y ^[47]	N ^[68,69]	Y ^[77]	Y ^[90,91]
High nutrient levels (Y/N)	Y ^[4]	N ^[22]	Y ^[35]	Y ^[48]	N ^[69]	Y ^[77]	Y ^[92]
Elevated chl-a concentrations (Y/N)	Y ^[5]	N ^[22]	–	Y ^[49]	Y ^[70]	Y ^[78]	Y ^[91]
High heavy metal concentrations	Cd Cu Hg Pb ^[6]	Cd Hg Pb ^[23]	Hg ^[36]	Cd Cr Cu Pb Zn ^[50]	– ^[69]	–	Cd Cr Cu Pb Zn ^[93]
Industrial pollution (Y/N)	Y ^[2]	–	Y ^[35,36]	Y ^[51]	N ^[68]	Y ^[79]	–
High sedimentation (Y/N)	Y ^[3,7]	Y ^[21]	Y ^[35]	Y ^[52]	Y ^[67]	Y ^[77]	Y ^[89]
Observations on litter (Y/N) ^[8]	Y ^[9]	Y ^[24]	Y ^[37]	Y ^[53]	Y	Y ^[77]	Y ^[94]
Effects from fisheries and mariculture (Y/N)	Y ^[9]	Y ^[21]	Y ^[38]	Y ^[54]	Y ^[67]	Y ^[80]	Y ^[95]
Damage from marine tourism (Y/N)	Y ^[10]	Y ^[25]	Y	Y ^[55]	N	Y ^[79]	N ^[96]
Harvesting for curio and aquarium trade (Y/N)	N	Y ^[26]	Y ^[39]	Y ^[46,56]	N	Y ^[79]	Y ^[97]
Environmental gradients in impact (Y/N)	Y ^[11]	Y ^[27]	Y ^[40]	Y ^[57]	Y ^[67]	Y ^[81]	Y ^[98]
Estimated impact radius city on reefs (km)	10–15	1–5	1–30	1–10	1–4	1–5	1–36
Reef degradation (Y/N)	Y ^[12]	Y ^[22]	Y ^[40]	Y ^[52]	Y ^[24,67]	Y ^[76–81,85]	Y ^[95]
Land reclamation present/planned (Y/N)	N	Y ^[24]	–	Y ^[58]	Y	N	Y ^[99]
Coral bleaching (Y/N)	Y ^[13]	Y ^[28]	Y	Y ^[59]	Y ^[71]	Y ^[77,80,82]	Y ^[100]
Coral diseases (Y/N)	Y ^[14]	Y ^[29]	–	–	–	–	Y ^[101]
Harmful algal blooms (Y/N)	Y ^[15]	Y ^[30]	Y ^[41]	Y ^[46]	Y ^[70]	Y ^[82]	N ^[102]
Coral predation and bioerosion (Y/N)	Y ^[16]	Y ^[28]	Y ^[42]	Y ^[60]	Y ^[72]	Y ^[83]	Y ^[83,103]
Estimated coral species richness	50 ^[17]	350 ^[31]	> 100 ^[43]	203 ^[61]	400 ^[73]	164 ^[76,84]	270 ^[104]
Estimated reef fish species richness	83 ^[18]	528 ^[32]	> 1000 ^[44]	573 ^[62]	713 ^[74]	362 ^[85]	> 400 ^[105]
Seawalls as artificial substrate (Y/N)	Y	Y	–	Y ^[63]	Y ^[67]	Y ^[76]	N
Coral reef restoration (Y/N)	Y ^[19]	Y	Y	Y	Y	Y ^[86]	N
Marine park (Y/N)	N	Y ^[33]	Y ^[45]	Y ^[64]	N ^[75]	Y ^[87]	N ^[106]

[1] <http://worldpopulationreview.com>; [2] Senarak (2016), Vongvisessomjai (2017); [3] Nakano et al. (2009), Sutthacheep et al. (2009, 2017), Sangmanee et al. (2012), Sangaroon et al. (2016); [4] Cheevaporn and Menasveta (2003), Musika et al. (2014); [5] Buranapratheprat et al. (2008, 2009), Doydee et al. (2010); [6] Hungspreugs and Yuangthong (1983), Cheevaporn et al. (1995), Thongra-ar and Parkpian (2002), Thongra-ar et al. (2008), Tanaka et al. (2013), Musika et al. (2014), Kornkanitnan et al. (2015), Qiao et al. (2015), PCD (2016); [7] Sudara et al. (1991), Cheevaporn and Menasveta (2003), Srisuksawad et al. (2013); [8] origin: industrial, household, and fisheries; [9] lost fishing gear on reefs (Suebpaala et al., 2017; Sutthacheep et al., 2017); [10] poor waste management for mass tourism (Phillips, 2015); [11] Pengsakun and Yeemin (2011), Samsuvan et al. (2015); [12] unpublished or unofficial data; [13] Yeemin et al. (2009), Pengsakun and Yeemin (2011), Pengsakun et al. (2012), Sutthacheep et al. (2012); [14] Saengsawang and Yeemin (2009), Samsuvan et al. (2015); [15] Cheevaporn and Menasveta (2003), Lirdwitayaprasit et al. (2006), Musika et al. (2014); [16] Ruengsawang and Yeemin (1998), Sangmanee et al. (2012, 2015), Thummasan et al. (2015); [17] Sakai et al. (1986), Chou et al. (1991), Putschim et al. (2002), Hoeksema and Yeemin (2011); [18] Manthachitraa and Sudara (2002), Suantha and Yeemin (2011), Yucharoen et al. (2012); [19] Yeemin et al. (2006), Kanchanopas-Barnette et al. (2012); [20] there is a port for fishing boats. Nha Trang port was used for commercial transportation but is now serving tourism and ferries; [21] Vo (2011), Latypov (2006), Nguyen et al. (2013), Hoang et al. (2015), Tkachenko (2015); [22] Tkachenko (2015), Thu et al. (2016), Tkachenko et al. (2016); [23] Nghia et al. (2009); [24] local newspapers; [25] untrained recreational snorkelers; [26] Vo (2002), Nguyen and Phan (2008); [27] Vo et al., 2004; [28] Long and Vo (2014); [29] Beleneva et al. (2005); [30] Tang et al. (2004); [31] Vo et al. (2004), Dautova et al. (2007), Hoeksema et al. (2010), Latypov (2011); [32] Long (2009); [33] Hon Mun Island Marine Park or Nha Trang Protected Area (Kaida and Dang, 2016); [34] population size of the Davao Gulf conurbation is much larger; [35] Alcalá et al. (2003), Villanoy (2009), Fraser et al. (2014); [36] Appleton et al. (1999), Drasch et al. (2001), Abarquez (2015); [37] Villanoy (2009), Abreo et al. (2016); [38] Nañola and Ingles (2003), Armada (2004), Mamaug (2004), Rosario (2006), Subaldo (2011); [39] Ochavillo et al. (2004); [40] Gumanao (2009), Magdaong et al. (2014); [41] A.R. Bos. (pers. obs.); [42] *Acanthaster* (Bos et al., 2013) and *Drupella* (Gumanao, pers. obs.); [43] a conservative estimate based on the presence of 56 scleractinian genera and 35 mushroom coral species (Gumanao, 2009; Bos and Hoeksema, 2017); [44] Nañola and Ingles (2003), Bos (2012, 2014), Bos and Gumanao (2012, 2013), Bos and Smits (2013), Bos and Hoeksema (2015, 2017), Gumanao et al. (2016), Bos et al. (2018); [45] Mancao et al. (2008), Horigue et al. (2012), Cabral et al. (2014); [46] Wood (1977, 1979); [47] Aripin et al. (2002); [48] Spait (2001), Jakobsen et al. (2007); [49] Abdul-Hadi et al. (2013), Gallagher et al. (2016); [50] Ali et al. (2014); [51] Ali et al. (2015); [52] Mathias and Langham (1978), Pilcher and Cabanban (2000), Spait (2001), Theng et al. (2003), Waheed et al. (2007); [53] Adnan et al. (2015), Mobilik et al. (2016); [54] Woodman et al. (2004), Reef Check Malaysia (2010); [55] Cabanban and Nais (2003); [56] Phillips (1979); [57] Waheed and Hoeksema (2014); [58] Spait (2001); [59] in 2012 and 2016 (Aw and Syed Hussein, 2012; Waheed pers. obs.); [60] Syed Hussein and Nooramli (2016); [61] Nyanti and Johnston (1992), Waheed et al. (2011), Huang et al. (2015), Waheed and Hoeksema (2014); [62] Townsend (2015); [63] Pang et al. (2016); [64] Tunkul Abdul Rahman Park (Nyanti and Johnston, 1992); [65] the population of the Brunei-Muara District conglomerate is much larger; [66] Chou et al. (1987), DeVantier and Turak (2009), Turak and DeVantier (2009); [67] Turak and DeVantier (2009), Lane and Lim (2013); [68] De Silva (1987); [69] Yong et al. (2006), most reports are about Brunei Bay and not about the offshore reefs (e.g. Adiana et al., 2017; [70] Subramaniam et al. (1994), Alkhadher et al. (2015); [71] Lane (2011); [72] *Acanthaster* and *Drupella* (Turak and DeVantier, 2009; Lane, 2011, 2012); [73] Turak and DeVantier (2011), Benzoni et al. (2014), Hoeksema and Lane (2014), Huang et al. (2015, 2016), Lane and Hoeksema (2016); [74] Allen (2009), Tornabene et al. (2016); [75] three offshore marine protected areas (MPAs) to be legally gazetted; [76] Kunzmann and Samsuardi (2017); [77] Kunzmann and Efendi (1994), Efendi (1995), Kunzmann (2002); [78] Praseno et al. (1999); [79] Efendi and Syarif (1995); [80] Kunzmann (1997, 2002) [81] Johan et al. (2016); [82] Abram et al.

(2003), Hoeksema and Cleary (2004), Johan et al. (2016); [83] *Acanthaster* was observed in 2007 to the south of Padang (Baird et al., 2013); [84] Jonker and Johan (1999), Hoeksema (2009); [85] Kunzmann et al. (1999), [86] Quinn and Johan (2015); [87] Darmawan et al. (2012); [88] Idris et al. (2017), Nagel (2017); [89] Wijisman-Best et al. (1981), Hoeksema (2012a), Polónia et al. (2015); [90] Edinger et al. (1998), Kegler et al. (2017); [91] Sawall et al. (2011, 2013), Polónia et al. (2015), Teichberg et al. (2018); [92] Erftemeijer and Herman (1994), Nasir et al. (2015); [93] Ambo-Rappe (2014), Rukminasari (2015), Najamuddin et al. (2017); [94] Tahir et al. (2017); [95] Pet-Soede and Erdmann (1998), Pet-Soede et al. (2001), Ferse et al. (2012, 2014), Sawall et al. (2013), Glaser et al. (2015), Schwerdtner Máñez and Ferse (2010), Navarrete Forero et al. (2017), Glaeser et al. (2018); [96] moderately developed tourism in the city without much damage to reefs (Erham and Hamzah, 2014; Arief et al., 2017; Hoeksema pers. obs.); [97] Bruckner (2002), Knittweis and Wolff (2010), Ferse et al. (2012), Madduppa et al. (2014, 2018), Hoeksema (pers. obs.); [98] Cleary et al. (2005), Becking et al. (2006), Hoeksema (2012b), Polónia et al. (2015), Timm et al. (2017); [99] Saleh et al. (2016), Yurnita et al. (2017); [100] Yusuf and Jompa (2012); [101] Muller et al. (2012); [102] Mujib et al. (2015); [103] *Acanthaster* (Plass-Johnson et al., 2015b); [104] Best et al. (1989), Hoeksema and Best (1991), Hoeksema (2012a); [105] Erftemeijer and Allen (1993), Iwatsuki et al. (2000), Sudirman et al. (2009), Burhanuddin and Iwatsuki (2010, 2012), Pogoreutz et al. (2012), Burhanuddin and Erviani (2016), Plass-Johnson et al. (2018); [106] discussed but not implemented (Glaser et al., 2010).

Table 4

Hard coral species that were among the ten most dominant corals in the four main case study cities with respect to percent cover (PC) and frequency of occurrence (Occ). The table presents the family, maximum depth, growth form, and life strategy (Darling et al., 2012) where available. Rankings of each species in terms of percent cover and frequency of occurrence are shown as numbers following abbreviations for each city (SG: Singapore, JK: Jakarta, HK: Hong Kong, NH: Naha).

Species	Family	PC	Occ	Max depth (m) ^a	Growth form	Life-strategy (Darling et al., 2012)
<i>Coelosera mayeri</i>	Agariciidae	JK8		5	Massive	na
<i>Cyphastrea serailia</i>	Merulinidae		HK3	20–50	Massive	Stress-tolerant
<i>Diploastrea heliopora</i>	Diploastreidae	SG8		30	Massive	Stress-tolerant
<i>Dipsastraea favus</i>	Merulinidae		SG10	30–50	Massive	Stress-tolerant
<i>Dipsastraea speciosa</i>	Merulinidae		SG4/HK10	20–45	Massive	na
<i>Dipsastraea veroni</i>	Merulinidae		JK4	25	Massive	na
<i>Favites abdita</i>	Merulinidae		HK7	10–50	Massive	Stress-tolerant
<i>Favites chinensis</i>	Merulinidae		HK5	20	Massive	Stress-tolerant
<i>Favites halicora</i>	Merulinidae		JK5	55	Massive	Stress-tolerant
<i>Favites pentagona</i>	Merulinidae		HK1/SG5	40–50	Submassive	Stress-tolerant
<i>Favites rotundata</i>	Merulinidae		JK3	20	Massive	na
<i>Favites valenciennesi</i>	Merulinidae		SG9	30	Submassive	Stress-tolerant
<i>Goniastrea pectinata</i>	Merulinidae	SG5	SG6	20–40	Submassive	na
<i>Goniastrea retiformis</i>	Merulinidae		JK7	2–20	Massive	Stress-tolerant
<i>Goniopora columna</i>	Merulinidae	SG6/JK10	JK6	15	Columnar	na
<i>Leptastrea purpurea</i>	Incertae sedis	NH9		2–40	Encrusting	Weedy
<i>Leptastrea transversa</i>	Incertae sedis	JK7	JK8	20–50	Encrusting	na
<i>Merulina ampliata</i>	Merulinidae	SG3	SG3	20–50	Laminar	Generalist
<i>Montipora digitata</i>	Acroporidae	JK4	NH9	5	Branching	Competitive
<i>Montipora informis</i>	Acroporidae	JK3	JK9	10–20	Massive	na
<i>Montipora peltiformis</i>	Acroporidae		HK8	30	Submassive	na
<i>Mycedium elephantotus</i>	Merulinidae	SG7	SG7	20–70	Laminar	Generalist
<i>Oulastrea crispata</i>	Incertae sedis	JK1	JK1	10	Encrusting	na
<i>Oulophyllia crispa</i>	Merulinidae	NH6		40	Massive	Stress-tolerant
<i>Pachyseris speciosa</i>	Incertae sedis	SG1	SG2	30–88	Laminar	Generalist
<i>Pavona decussata</i>	Agariciidae	JK9		2–20	Digitate	Generalist
<i>Pectinia paeonia</i>	Merulinidae	SG2	SG10	20–25	Laminar	na
<i>Platygyra acuta</i>	Merulinidae		HK4	20	Massive	na
<i>Platygyra lamellina</i>	Merulinidae		JK10	30	Massive	Stress-tolerant
<i>Platygyra sinensis</i>	Merulinidae	SG9	SG8	30	Massive	Stress-tolerant
<i>Plesiastrea versipora</i>	Incertae sedis		HK6	20–40	Massive	Stress-tolerant
<i>Podabacia crustacea</i>	Fungiidae	SG4		20–50	Laminar	na
<i>Porites lobata</i>	Poritidae	JK5		30–67	Massive	Stress-tolerant
<i>Porites lutea</i>	Poritidae	JK2	JK2/HK9	20–70	Massive	Stress-tolerant
<i>Porites rus</i>	Poritidae	JK6		20	Digitate	Weedy
<i>Psammocora profundacella</i>	Psammocoridae	NH8	HK2	20–50	Submassive	na
<i>Turbinaria peltata</i>	Dendrophylliidae	SG10		20–40	Laminar	na

^a Max depth represents the range of maximum values recorded across the species' range and is not limited to urban areas.

Hoegh-Guldberg et al., 2007), and urban areas are no exception. It is unclear whether the trajectory of temporal declines is comparable in urban versus more remote settings. Presumably, localized drivers of coral reef degradation arose in population centres first. Certainly fishing pressure and resource extraction were major drivers in the early development of cities like Jakarta (van der Meij et al., 2010), and may have been more intensive near settlements than in other areas during this period (Kirby, 2004; Van Houtan and Kittinger, 2014). However, the absence of time series data in most coastal cities makes it difficult to assess precisely when declines began and how rapidly they progressed (van der Meij et al., 2010). Some insight into historical patterns may be gained from museum specimens (Hoeksema and Koh, 2009; Hoeksema, 2015) and by examining historical social and economic activities that likely impacted coral reef health (Neo and Todd, 2012), but studies that directly compare long-term growth patterns of hard corals in heavily

versus minimally urbanized locations are lacking.

In case study cities we reviewed, declines in urban coral reefs throughout the 20th Century were followed by fluctuations in coral cover in the 2000s and 2010s (Figs. 3, 5, 7, and 9). These fluctuations may simply be a function of asymptotic population dynamics, wherein urban coral reefs – having “collapsed” (sensu Jackson et al., 2001) into a heavily degraded state – fluctuate stochastically as this state is more or less maintained. Under this hypothesis, it is important to note how different this heavily degraded state looks across the case study cities; in Jakarta, the decimation of reefs within 20 km of the city centre manifest in extremely depauperate coral assemblages, while in Singapore, inshore reefs had comparably higher species richness (Fig. 10). Alternatively, recent fluctuations could be due to the combination of eco-evolutionary trajectories and major pulse disturbances. Corals that persisted in case study cities by the early 1990s were presumably the

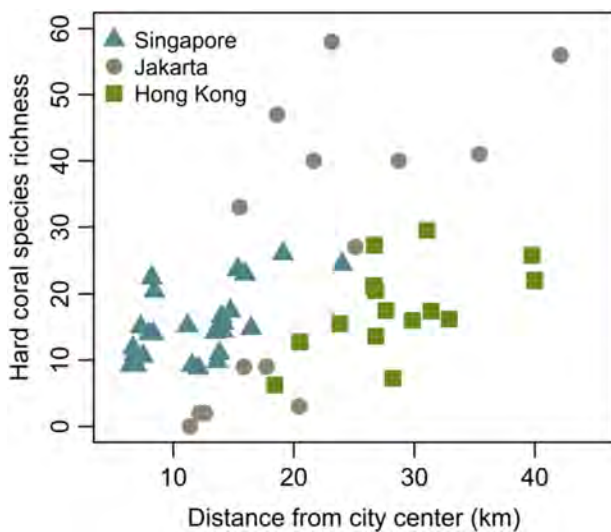


Fig. 10. Hard coral species richness with increasing distance from the city centre in Singapore (triangles), Jakarta (circles), and Hong Kong (squares). We were unable to comparable data across an inshore-offshore gradient for Naha. Sources: Singapore: J.S.Y. Wong et al. (2018); Jakarta: Cleary et al. (2016); Hong Kong: K.T. Wong et al. (2018).

product of decades of selective pressure from urban-related abiotic factors, and might have been expected to proliferate into high-cover, low-diversity reefs over subsequent decades if regional conditions had remained relatively constant (we specify constant “regional conditions” here, as we found no evidence in the literature of recent fluctuations in localized urban-related abiotic conditions coinciding with observed variation in coral survey data). Yet, regional conditions have not remained constant. Inter-annual spikes in sea surface temperature led to multiple regional bleaching events in the 1980s, 1990s, 2000s, and 2010s. These events may have been extreme even for hard coral species that had survived the selective pressures of urban life over prior decades. Recent fluctuations under this hypothesis are thus the result of acute response and recovery among highly stress-adapted corals given repeated pulse disturbance events.

One noteworthy trait of recent fluctuations in Singapore specifically was the pace at which they occurred. Coral cover time series data from Singapore showed relatively rapid recovery following thermal bleaching events. In 1998, for instance, mean coral cover declined to < 20% across multiple urban reef sites due to elevated sea surface temperature (Guest et al., 2016). The 1998 El Niño impacted corals in more remote settings in the region as well (Goreau et al., 2000). Unlike their more remote counterparts, however, urban coral reefs in Singapore had rebounded to exceed pre-bleaching levels of total cover within as little as 5–7 years (Guest et al., 2016). This does not take away from their more depauperate status (Huang et al., 2009; though there was a coinciding change in community structure, driven primarily by *Montipora* and *Plerogyra*, as described by Guest et al., 2016); indeed the lower total richness of hard corals in Singapore may have been among the characteristics that contributed to rapid recovery rates, along with pre-selected physiological and morphological traits, altered competitive dynamics, and other urban-specific ecosystem properties that are yet to be understood. Whatever the mechanism(s), the rapid recovery of Singapore's reefs following climate-related disturbances suggests that unique population dynamics may be at play.

3.2.2. Inshore-offshore gradients

Inshore-offshore gradients are a feature of many coral reef systems, both urban and non-urban. In urban areas, coral species richness generally tends to increase with increasing distance from city centres (Fig. 10). However, our review suggests that the scale and strength of

inshore-offshore gradients varies considerably across cities. Of the four main case study cities in our analysis, Jakarta had the most extreme inshore-offshore gradient along a string of reefs arranged perpendicularly to the shoreline away from the city. Mean coral cover within 20 km of the Jakarta's centre was consistently low (< 10%; Fig. 5). Conversely, coral cover was commonly > 20% in waters immediately adjacent to Naha, a city less than a tenth the size of Jakarta, and which showed little evidence of inshore-offshore patterns (Fig. 9). Makassar offers another suitable example of a clear inshore-offshore gradient, but with reefs arranged in rows parallel to the shoreline starting close to the city across the shelf from east to west with highest coral species diversity around mid-shelf reefs (Moll, 1983; Hoeksema, 2012a). Although human population density is likely to be positively correlated with (and a good proxy for) the spatial extent of urbanization's effect, variation in inshore-offshore gradients in small and moderately sized cities suggests other aspects of coastal development and urban land-use are also important. For instance, in Singapore, although sites farthest from the city centre had consistently high coral cover, there was considerable variation in coral cover closer to the city's main island (Fig. 3). One possible explanation is highly localized sedimentation and pollution due to active land reclamation projects, petrochemical facilities, and other industrial activities. Natural drivers may also be at play. Small-scale spatial variability in Singapore and other study city, as well as differences across cities in the strength and spatial extent of inshore-offshore gradients underscore the importance of city-specific, localized drivers.

3.2.3. Reef compression

One of the key themes emerging across case-study cities was reef compression, which is defined here as a decline in bathymetric range with increasing turbidity and decreasing water clarity. This decline presumably occurs over time, as has been noted in Singapore over the latter half of the 20th Century (Chou, 1996), and with decreasing distance from urban centres. Although we were unable to find papers clearly documenting inshore-offshore gradients in reef depth, the shallow maximum depth of urban reefs in this review are indicative of reef compression (Tables 2 and 3). Coral reefs in the Indo-Pacific typically extend well below 30 m depth (Bridge et al., 2013; Loya et al., 2016), while maximum reef depth within 20 km of the primary case study cities was < 10 m (Table 2). This was supported by some of the cities listed in Table 3 as well, such as Pattaya, Kota Kinabalu, and Makassar, which had limited depth ranges of nearshore reefs.

Reef compression may be difficult to discern from naturally occurring variation in reef depth that is determined by the bathymetry of the seafloor around shelf-based reefs near the mouths of rivers (Kleypas et al., 1999; Hoeksema, 2012b). In some cases (away from major estuaries), naturally occurring reef compression may be patchier than that in urban areas, with greater small-scale spatial variation in reef depth due to highly localized differences in turbidity (Larcombe et al., 1995; Anthony and Larcombe, 2000; Cooper et al., 2007; Browne et al., 2013; Tarya et al., 2018). Conversely, elevated sediment loads in urban areas frequently extend over tens of kilometers (Baum et al., 2015), and may reduce the depth of reefs more ubiquitously across this range. Reef compression associated with small-scale shoreline development is often relatively limited in spatial extent (Hoitink and Hoekstra, 2003), with reduced reef depth evident only within a few kilometers of the source of suspended sediments (Brakel, 1979; Macdonald and Perry, 2003). Further work is needed to understand the factors that determine the geographic extent of urban reef compression, including location-specific seasonal and temporal variation in turbidity (Wolanski and Spagnol, 2000).

3.3. Coral colonization of novel habitats

In addition to the coral reefs that persist with urbanization, we found multiple records of hard corals colonizing artificial structures,

which are particularly extensive in urban settings (Bulleri and Chapman, 2010; Dafforn et al., 2015). Corals recruit to a wide variety of urban substrate types, including concrete, steel, various types of quarried boulders, scoria deposits, and, to a lesser extent, marine debris such as car tires (Fitzhardinge and Bailey-Brock, 1989; Baine, 2001; Lam, 2003; Creed and De Paula, 2007; Burt et al., 2009a; Gilbert et al., 2015). Established coral colonies (≥ 10 cm) have been documented on granite seawalls (Tan et al., 2012; J.S.Y. Wong et al., 2018), cement, granite, and gabbro breakwaters (Wen et al., 2007; Burt et al., 2009b; Vijayakarn et al., 2009; Ho et al., 2017), concrete “tetrapod” jacks and other types of interlocking shoreline construction units (Burt et al., 2009b; Giraudel et al., 2014), and fiberglass and concrete structures in urban areas (Loh et al., 2006; Dupont, 2008).

Direct comparisons of coral assemblages on urban artificial structures versus natural reefs are rare. Burt et al. (2009b) conducted one of the few such studies available, comparing coral communities on breakwaters and natural coral patches in Dubai. They found higher coral cover but lower species richness on artificial breakwaters. The composition of coral assemblages also differed significantly between habitat types; breakwaters were strongly dominated by *Cyphastrea microphthalma*, *Platygyra daedalea*, and *Porites lutea*, while species composition in natural habitats was more variable (Burt et al., 2009b). It is unclear whether these patterns extend to other cities and other artificial structure types. Seawalls in Singapore, for instance, appear to support an impressive diversity of corals (Tan et al., 2012), yet may include taxa not found on surrounding reefs (J.S.Y. Wong et al., 2018). In another study, Gilbert et al. (2015) report on the settlement of a rare mushroom coral endemic, *Cantharellus noumeae*, on a deposit of scoria in the main harbor of Nouméa, the capital of New Caledonia. This scoria is a waste product of metal mining and in this case serves as an artificial substrate that may help to support the occurrence of the coral population in a sediment-rich and metal-contaminated environment, although it shows higher abundances on natural substrate in close proximity.

Urban artificial substrates may additionally be important in the dispersal of both native and non-native species (Bishop et al., 2017). Floating marine debris, much of which originates in cities, is readily colonized by corals, as was recently illustrated on discarded plastic nets near the harbor of Bitung, Indonesia (Hoeksema and Hermanto, 2018). Plastic, glass, and metal flotsam can transport coral recruits over vast distances and potentially facilitate invasions of invasives such as *Tubastraea* corals (Jokiel, 1992; Hoeksema et al., 2012, 2018; Santos and Reimer, 2018). Biofouling corals are also transported between urban centres by ships and other mobile or towed structures such as oil rigs, and these structures may become part of a larger network of artificial-substrate “stepping stones” for species invasions (Bertelsen and Ussing, 1936; Wanless et al., 2010; Yeo et al., 2010; Farrapeira et al., 2011; Miranda et al., 2016; Brito et al., 2017).

More research is needed to characterize the coral assemblages that form on man-made structures in tropical coastal cities. This work should elucidate both the link between substrate material type and the resulting composition of coral assemblages, as well as between coral composition and demersal fish communities that then establish on artificial structures. Understanding these linkages and the mechanisms behind them would help facilitate the development of ecological engineering strategies that enhance the value and extent of ecosystem services provided by corals to urban populations.

3.4. Are urban coral reefs distinct ecosystems?

While most of the respective abiotic changes we have discussed (Table 1) are not exclusive to urban areas, they tend to be extreme and occur concurrently, often with compounding effects, in urban marine environments. Some impacts are particularly prevalent in urban areas, such as land reclamation, noise and light pollution, boat traffic, and various water-borne pollutants (Fig. 11). Furthermore, urban coral reefs may be distinct from other degraded reef ecosystems if there are

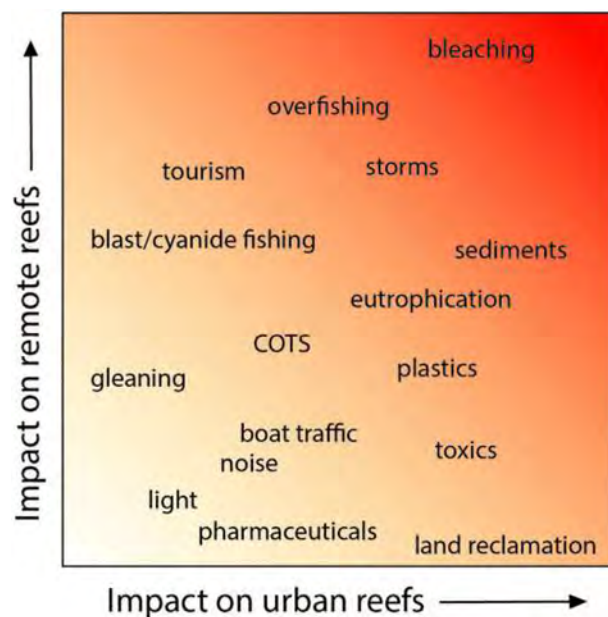


Fig. 11. Conceptual diagram showing the relative severity of various stressors on urban reefs (x-axis) compared with remote reefs (y-axis). Stressors listed in the lower righthand quadrant of the figure are likely to be of particular importance for hard corals in urban settings.

interactive effects between the multiple abiotic parameters that are characteristic of urban areas on coral community composition, species interactions, and ecosystem dynamics. There is considerable need for studies evaluating coral community response to multiple urban-related stressors. For instance, do certain corals species prefer seawall habitats and if so, will the proliferation of urban seawalls enhance the localized larval supply of those species? Do common urban coral species respond differently to heavy metal contaminants and if so, which life stage is most impacted (Scott, 1990; Goh, 1991; Esslemont, 2000; Negri and Heyward, 2001; Reichelt-Brushett and Harrison, 2005; Gilbert et al., 2015)? And what is the net effect of these combined factors on coral species composition on contaminated, armoured shorelines? Furthermore, potential responses to multiple abiotic processes such as these must be considered concurrently with important biotic interactions. For instance, differential effects of elevated sediment loads and light limitation could alter the strength of competitive interactions between hard corals and macroalgae, which are important drivers of ecosystem dynamics (McCook et al., 2001). Similarly, greater overlap in the niche space of deep and shallow corals caused by surface-ward shifts in deep-water coral species such as *Leptoseris* and *Oxypora*, as has been documented in Singapore (Dikou and van Woesik, 2006), could facilitate novel species interactions and interaction networks that influence the trajectory of coral communities in urban areas.

Presently, these ideas remain conjectures and hypotheses that have yet to be tested in the field. Although data collated for this review likely constitute the most comprehensive source of information on urban coral reefs currently available, they are far from ideal. We primarily present percent cover data, which may be informative with respect to broader ecosystem patterns (Hughes et al., 2010). The data we present are also too sparse to support rigorous statistical analyses or meta-analysis, and we provide limited information on other important reef associated organisms, such as reef fish, as it is not readily available. Information in this review thus can only be considered in a qualitative manner, and cannot be used as evidence or grounds for strong and formal conclusions about the nature of urban coral reefs more broadly.

Limited data on urban coral reefs beyond these cities currently make it impossible to discern whether coral reefs in urban areas constitute a unique ecosystem type, or whether they are structurally and

functionally comparable to other degraded reefs subject to multiple anthropogenic stressors. A similar question has challenged terrestrial ecologists since the establishment of urban ecology as a distinct sub-discipline (McDonnell, 2011) and remains a source of debate (Pickett and Cadenasso, 2017) despite extensive recent development of urban terrestrial ecology's core principles and theoretical basis (Forman, 2016). For urban marine environments, it is a question that cannot begin to be addressed until the necessary data are available and relevant hypotheses have been experimentally evaluated in the field; dwelling on it prematurely is unproductive. We know that urban coral reefs have for decades been subject to a convergence of anthropogenic stressors that likely reflect the stressors which await coral reefs across a much greater spatial scale in the decades to come as urbanization and coastal development accelerates, particularly throughout Asia (Yeung, 2001; Neumann et al., 2015). Thus, regardless of definitions, expanded research and improved understanding of the structure and function of coral reef ecosystems in coastal cities may be essential to proactively meet future nearshore management and conservation needs.

4. Planning for the future

4.1. Data and research needs

As the footprint of urbanization grows, expanded data collection on coral reefs in urban areas is sorely needed. Most coastal cities lack baseline information on the condition of pre-industrial coral reefs (though some early records exist for Jakarta, Makassar, Padang, and Singapore; see Sections 2.1, 2.2, 2.5.6, and 2.5.7). However, even information on present-day spatial and community patterns from additional cities would help to determine the extent to which patterns described here are generalizable. Examples of other Asian cities with reefs in their proximity can be found in Cambodia (Sihanoukville), China (Sanya, southern Hainan), Indonesia (Ambon, Bandar Lampung, Bitung, Manado, Sibolga), Malaysia (Miri, Penang, Semporna), Taiwan (Hengchun), Thailand (Phuket), the Philippines (Bolinao, Cebu City, Puerto Galera, Puerto Princessa), and Vietnam (Da Nang, Qui Nhon) (UNEP/IUCN, 1988a, 1988b; Spalding et al., 2001). These cities vary in population size and in the types and degrees of urban stressors likely affect local coral reefs. Manado (North Sulawesi), for example, is well known for its diving tourism but it has also undergone extensive land reclamation for its waterfront development plan that has impacted coral reefs (Lagarese, 2013). Semporna (NE Sabah) is a small city that is economically dependent on the diving industry and surrounded by a high concentration of reefs with high species diversity of corals and fishes (Kassem et al., 2012; Waheed and Hoeksema, 2013). Despite this, reefs close to the city are subject to elevated sedimentation and domestic litter, discarded fish nets are common (Kassem et al., 2012; Waheed and Hoeksema, pers. obs.), and, like elsewhere in Southeast Asia, illegal blast fishing has frequently been observed, particularly at offshore reefs (Kunzmann, 1997; Edinger et al., 1998; Pet-Soede and Erdmann, 1998; Fox et al., 2005; Sawall et al., 2013). Reef surveys near cities such as these at both urban and more remote sites would allow for expanded cross-city comparisons that further elucidate potential interactive effects of different urban stressors, as well as critical thresholds in these stressors that shape coral reef response to urbanization and global drivers over time.

Furthermore, in order to develop a mechanistic understanding of urban coral reef communities, experimental studies in the field and laboratory are needed to systematically evaluate the hypotheses we have proposed and additional hypotheses that arise as observational data become available from more cities. In this review, we focused principally on hard corals and the effects of urban environmental variables on species richness and percent cover, yet more complex processes that are not captured by these data are likely at play. The dynamics of hard coral assemblages are interlinked with those of primary producers, and can shift toward the latter in response to

disturbance (McCook, 1999; McCook et al., 2001). While a diverse assemblage of herbivorous fishes could hinder such a process (Burkepile and Hay, 2008), the functional diversity and capacity of consumers to remove macroalgae tends to decrease near developed coastlines, as has been demonstrated in Makassar (Plass-Johnson et al., 2015a, 2016). In Singapore, a single species of fish has been shown to be responsible for the majority of macroalgae removal (Bauman et al., 2017). This lack of functional redundancy in macroalgal browsing is alarming (Hoey and Bellwood, 2009) and an important area for research moving forward. Diversity and abundance data on corals, fish, and macroalgae from more coastal cities could help to elucidate the major biotic interactions that influence hard coral assemblages. Recent evidence suggests that coral-associated microbial assemblages may also be distinct in urban areas (Ziegler et al., 2016), and data on microbial composition across tropical coastal cities could be informative. Ultimately, a mechanistic understanding of how different functional groups are linked and how they each respond to urban stressors is required to begin characterizing the dynamics of urban coral reefs (Madin et al., 2016; Harborne et al., 2017).

4.2. Mitigation and restoration

Coastal urbanization brings about a permanent to semi-permanent changes in the marine environment, which we have illustrated via the case studies in this review. Concrete, quarried rock, and man-made materials dominate urban coasts and demarcate new coastlines formed after shore reclamation has obliterated natural coastal habitats, as demonstrated in Jakarta, Kota Kinabalu, Makassar, and Singapore (Sections 2.1, 2.2, 2.5.4, 2.5.7). Land-based sediment pollution and elevated resource exploitation, particularly early in a city's history, lead to dramatic losses in diversity and ecologically important species (Edinger et al., 1998; Erfteimeijer et al., 2012). Also, litter from urban sources enters the system in large quantities (Evans et al., 1995; Uneputty and Evans, 1997a, 1997b; Leite et al., 2014), potentially compounding the effects of urbanization on coral reefs (de Carvalho-Souza et al., 2018; Lamb et al., 2018). Although urban coral reefs can never be returned to their pre-urbanization state, mitigation and restoration efforts may redirect their current trajectory. Environmental regulation and enforcement is gradually improving environmental conditions in many coastal cities (Hosono et al., 2011). Concurrently, existing urbanized coasts can be transformed into novel habitats to support coral growth and development through restoration and rehabilitation.

Over the past several decades, coral restoration and rehabilitation programs have been a crucial component of maintaining hard coral species diversity and countering negative effects from anthropogenic pressure on coral reefs (Rinkevich, 2005). Many techniques have been developed and attempted (Edwards, 2010), and restoration efforts have a relatively long history in several urban locations, such as Singapore (Bongiorni et al., 2011; Ng et al., 2016; Chou et al., 2017). Coral restoration by passive or active means is possible and can be facilitated by ecological engineering of coastal defence structures and design strategies that reduce the intensity of environmental stressors. Such designs should be informed through experimentation and careful study of existing structures that interact with corals and coral reefs. For instance, reefs incorporated into breakwaters in Makassar were found to have elevated densities and diversity of mushroom corals compared with unarmoured sites, as the orientation of breakwaters reduced sediment flux across the reef flat (Hoeksema, 2012a). While coral restoration and ecological engineering cannot reproduce a reef community equivalent to that of a natural reef (Rinkevich, 2014), artificial structures remain a novel habitat in which coral communities can develop under new environmental conditions to provide some level of ecosystem services. In such situations, some prefer to use the term 'rehabilitation', as it denotes the shifting back of a degraded ecosystem toward one of 'greater value' in terms of structure and function, but not necessarily back to

some historic or pre-disturbed state (Edwards and Gomez, 2010).

There are still gaps in understanding of the interaction between artificial substrates and coral restoration (Spieler et al., 2001). Many of the materials used in coral restoration are based on local availability and cost. For instance, in Southeast Asia, PVC pipes and giant clam shells are used (Chou et al., 2009), while in Komodo, Indonesia, rocks are piled in heaps on the seafloor (Fox et al., 2005). For the more permanent artificial structures, substrate materials are considered for long-term durability and suitability as a substrate for the attachment of corals and reef-associated organisms either through natural recruitment or translocation. Concrete is the most commonly used material, likely due to its low cost, material properties (e.g. durability and high characteristic, compressive and tensile strength) and because it can be cast in a variety of configurations and size. The added advantage is that many concrete construction items can be purchased off the shelf and used immediately as they come in different shapes and sizes that can be readily positioned in various configurations on site. However, more work is needed to develop materials for urban infrastructure that improve recruitment and translocation success and promote intertidal biodiversity (Browne and Chapman, 2011; Firth et al., 2014). For corals, artificial shores could incorporate tidal pools so that restoration or recruitment need not be confined to the subtidal zone.

Although urban habitat enhancement does not generate surrogates for natural reefs, it is a pragmatic response to heavy urbanization where environmental transformation is permanent and irreversible. Integrating reef restoration into the design of coastal defences and planning based on around local hydrodynamic conditions and societal needs could improve effectiveness at and multifunctionality of defence structures (Reguero et al., 2018). Ecological engineering of artificial structures can also provide the opportunity of testing the tolerance limits of coral species to conditions expected from climate change (Rinkevich, 2015). The cost of ecological engineering of coastal structures and active restoration of corals will certainly be high (Firth et al., 2014). However, such costs can be offset by the benefits of ecosystem services. Some have also suggested that costs of transplanting corals onto coastal structures can be saved entirely by involving trained volunteers (Toh et al., 2017), although this approach might be limited to smaller scales.

4.3. Urban planning and ecological engineering

Although much remains to be determined regarding the ecology of urban coral reefs, they are ultimately ecosystems of our making. Urban coral reefs have been shaped by human modification of coastal habitats that suit human needs and interests over short to intermediate time scales. These modifications may not be in our interest over longer time scales, particularly given the myriad of ecological goods and services that healthy coral reefs provide. However, it is possible to choose how we modify urban habitats of the future. As more data become available and urban marine ecology advances as a field, novel approaches to ecologically-informed urban planning choices and novel strategies for ecological engineering could help to ensure that future urban coral reefs provide enhanced ecosystem services and support broader conservation goals.

Arguably, current knowledge of the negative effects of sediment pollution on hard corals is sufficient to justify several major urban planning changes in coastal cities, such as stronger regulatory requirements for major sources of sediment pollution, improved containment of sediments during coastal construction, and environmental planning standards for shoreline development that incorporate ecological engineering strategies. Cities vary considerably with respect to governance structure, planning and environmental policy challenges, and general commitment to sustainable practices, as is evident in past reviews and social science literature from cities we used as case studies (Chou, 2008; Yoo et al., 2014; Baum et al., 2016b; Lai et al., 2016). In all cases, policy and planning changes are complicated by the vast array

of stakeholders and human interests present in urban centres. They also require cooperation and efficient communication between multiple governmental organizations, as well as with the private sector. Recently-developed approaches such as Integrated Coastal Management (ICM) and related decision support systems (Chang et al., 2008) may help to lessen these challenges. For instance, the ICM governance framework is currently used to manage ~12% of China's coastline and has been shown (using a mix of qualitative and quantitative data) to be effective in promoting 'coral sustainability' in China's coastal cities (Ye et al., 2015).

Urban planning and coastal engineering informed by science has the potential to redirect the trajectory of and help rebuild urban coral reefs. Although it requires considerable investment on the part of city governments and private industry, the potential of environmentally-oriented shoreline development and ecological engineering to deliver improved ecosystem services to coastal populations should not be understated. As urban population density surges in coastal cities over the coming decades, urban coral reefs have the potential to supplement the availability of protein and enhance food security, mitigate flood risk and reduce storm surge, and provide recreational opportunities and access to natural environments that are increasingly recognized as important for human well-being in cities (Fuller et al., 2007; Panagopoulos et al., 2016). Because of the risks posed by sea level rise and inundation, major investment in coastal infrastructure and shoreline construction may be inevitable for many coastal cities over the next decade. These projects will likely be the largest of their kind for the foreseeable future if they are to effectively meet the threats detailed in current climate projections. As such, they serve as an opportunity and a potential crossroads for coastal habitats, with the potential to redirect the future of urban coral reefs if innovative urban planning and effective ecological engineering strategies are incorporated. Caution should be taken to ensure mitigation via ecological engineering is not used as an excuse to green light further environmental destruction.

5. Conclusions

This review highlights several characteristics of urban coral reefs based on case study cities throughout East and Southeast Asia. Reef compression, whereby reefs occur over a relatively narrow vertical range with a shallow maximum depth, and colonization of urban infrastructures were common in urban areas. Urban coral reefs tended to be dominated by domed growth form corals with relatively low architectural complexity, which may have important implications for ecosystem dynamics of coral reefs in cities. The strength of inshore-offshore gradients in urban areas and the total footprint of urbanization's effect on coral reefs, though loosely proportional to city population size, varied considerably between case studies and is likely influenced by small-scale variation in urban-related abiotic variables and by urban planning choices of individual cities. A shortage of research in urban areas has limited our understanding of how far the influence of urban centres extends, to what extent urban-related impacts interact with non-anthropogenic stressors (Baum et al., 2015), and whether urbanization affects ecosystem function. We expect that the temporal and spatial patterns exhibited by urban coral reefs and described in this review are shaped by a complex combination of interacting abiotic and biotic processes. However, considerable expansion of research will be required to elucidate these processes and understand the mechanisms by which they influence coral reef ecosystem dynamics in urban areas.

In addition to advancing the field of urban marine ecology, which is in its infancy, an expanded study of urban coral reefs would provide important contributions to coral reef ecology and conservation more broadly. Across the world, the increasing human ecological footprint from growing coastal populations and urbanization is profoundly changing coral reef ecosystems (Jackson et al., 2001; Hughes et al., 2003; Mora et al., 2011). Impacts from multiple anthropogenic stressors and the superimposed effects of climate change are leading to

widespread losses of biodiversity on coral reefs—causing declines in ecosystem functions and resilience, and the loss of key ecosystem services. One of the main challenges for coral reef scientists and managers is to identify and maintain the ecosystem functions that are crucial for sustaining coral reefs (Hughes et al., 2017) despite rapid and ongoing anthropogenic change. Urban coral reefs have been shaped for decades by both regional and multiple, severe, localized anthropogenic impacts. An improved, mechanistic understanding of coral community responses to abiotic and biotic processes in urban areas could thus provide valuable insights for coral reef conservation and management. Further, innovative ecological engineering strategies that are developed in cities in a manner consistent with broader conservation goals could be essential for future mitigation and restoration efforts as tropical and subtropical nearshore environments globally become increasingly urbanized.

Acknowledgements

This review was supported by the National Research Foundation, Prime Minister's Office, Singapore under its Marine Science Research and Development Programme (Award No. MSRDP-05). Research by Bert Hoeksema was financed by the Netherlands Foundation for the Advancement of Tropical Research (WOTRO, grants W77-96, W84-354). We are grateful to Tomofumi Nagata (Okinawa Environment Science Center Foundation Inc) and Japanese Ministry of Environment (2004-2017) Monitoring Site 1000 for coral reefs for providing data for this review. We want to thank the anonymous reviewer for his very constructive comments, which helped us to improve the ms. This paper is part of a special volume dedicated to Dr. Charles Sheppard, previous editor-in-chief of Marine Pollution Bulletin. By being very productive as outstanding researcher and editor, he has contributed much to our understanding of coral reefs, ranging from natural history to human impacts.

Declarations of interest

None.

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