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# Examining the relationship between fish herbivore biomass, coral and macroalgal cover on Singapore's heavily disturbed reefs

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## Abstract

Herbivores play a critical role in structuring benthic communities on tropical coral dominated reefs by removing macroalgae. Reducing herbivory has been implicated in promoting phase shifts from coral dominance to other ecosystem states following disturbances. Turbidity and sedimentation are key physical processes that also structure coral reef communities because they limit light penetration and interfere with biological processes such as heterotrophy. Singapore's coral reefs have been heavily impacted by human activities for decades and experience very high levels of sedimentation and turbidity. As a result, coral and algal growth is restricted to shallow reef flats and upper reef slopes. While macroalgae, particularly *Sargassum* spp., are abundant on the reef flats (0-2 m depth), adjacent upper reef slopes (3-4 m depth) are dominated by diverse hard coral assemblages composed primarily of sediment tolerant taxa. To gain a better understanding of the role of herbivore biomass and herbivory rates in structuring these disturbed reefs, we examined the relationship between cover of corals, macroalgae, fish herbivore biomass and urchin abundance at eight representative sites among Singapore's southern islands during two seasons. In addition we filmed herbivory assays on replicate experimental macroalgal stands (4 separate macroalgal species) and natural EAM patches at three of these sites to estimate species-specific rates of herbivory. Average coral cover at 3-4 m depth was surprisingly high (~40%), compared to current levels found on other Indo-Pacific reefs, although comparisons with historical data from these sites suggests ~15% decline in cover over the last three decades. The average biomass of herbivorous fishes (~4 g m$^{-2}$), on the other hand, was more typical of degraded and heavily overfished reefs, while urchin abundances were within the range found at other Indo-Pacific sites. Herbivorous fish were not observed feeding on macroalgal assays, while fish bites recorded on EAM were mostly made by territorial damselfish. There was a

significant but weak relationship between coral cover and fish herbivore biomass but none for macroalgae or between urchin abundance and benthic cover of corals and macroalgae. A possible explanation for the relatively low cover of macroalgae and low biomass of fish herbivores is that a disproportionate amount of the grazing is being carried out by one or a few fish species not captured by visual survey methods. In addition, the composition of the coral community, which is dominated by sediment tolerant taxa that are relatively resistant to thermal stress, has undoubtedly contributed to the ability of these shallow turbid reefs to persist in a coral dominated state. Furthermore, a combination of limited space for algal growth and low light levels at 3-4 m depth may limit algal growth rates so that only low levels of herbivory are necessary to prevent seaweeds outcompeting corals on these disturbed reefs.

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## Introduction

The distribution of corals and algae on coral reefs is strongly influenced by biological processes and physical conditions including grazing, sedimentation and light availability (Steneck 1988; Bak & Engel 1979; Loya 1976). Herbivory is one of the key processes structuring shallow tropical coral communities because it moderates coral-algal interactions through the removal of fleshy macroalgae or algal turfs that can overgrow or injure adult corals and inhibits settlement and post-settlement survival of juvenile corals (Birrell et al. 2005; McCook et al. 2001; Rasher & Hay 2010). Sediments also have numerous effects on coral reef benthic and community structure (McClanahan & Obura 1997). Suspended sediments limit light penetration and particulates interfere with biological processes, such as heterotrophy in corals, and may alter rates of herbivory by fish (Bellwood & Fulton 2008; Rogers 1990). Generally, increased sedimentation is considered detrimental for coral health; however sediments can also be a source of food for corals and may provide a degree of protection from thermal stress by reducing levels of irradiance (Anthony & Fabricius 2000; Cacciapaglia & Woesik 2015).

Over fishing has led to both reductions in rates of herbivory and removal of certain key herbivore species on many coral reefs (Edwards et al. 2014; Jackson et al. 2001). Coastal development, on the other hand, has led to decreases in water quality (e.g., increased turbidity) and increased rates of sedimentation (Erftemeijer et al. 2012; Rogers 1990). These disturbances, among others, have been implicated in the observed global decline in reef condition, decreases in total coral cover and consequent deterioration of ecological function (Pandolfi et al. 2003). The effects of combined disturbances are not always additive. Indeed, in some cases co-occurring disturbances can interact antagonistically, resulting in the total impact of the combined disturbances being less than the sum of individual impacts (Darling et al. 2010).

Declines in reef condition occur gradually in many cases, but in others, a combination of disturbances results in rapid transitions from one ecosystem state to another. The most widely researched of these so called phase-shifts is from dominance by hard corals to dominance by fleshy macro-algae (known as a coral to macroalgal phase shift) (Bruno et al. 2009; Done 1992; Hughes 1994; Hughes et al. 2007; McManus & Polsenberg 2004). Transitions to other ecosystem states also occur, with the type of transition influenced by local physical and biological conditions (Norström et al. 2009). It is generally accepted that reefs already compromised by human disturbances (e.g., overfishing, reduced water quality) are more prone to rapid phase shifts following acute disturbances.

Singapore has in the span of just under 200 years undergone a transformation from a sparsely populated, forest-covered island to a highly urbanised city-state (Hilton & Manning 1995). Extensive coastal development has resulted in sedimentation rates and levels of total suspended solids exceeding those considered optimal for tropical reefs (Dikou & van Woesik 2006; Rogers 1990; Todd et al. 2004). Average underwater visibility, thought to have been about 10 m in the 1960's, has decreased to around 2 m at present (Chou 1996), and eutrophication has increased at least 30 fold in the last 60 years (Gin et al. 2000). Erect fleshy macroalgae, particularly *Sargassum* spp., dominate shallow reef flats (~0-2 m depth), particularly during the north-east monsoon, when they bloom to form dense stands of individuals measuring more than 2 m in length (Chuang 1977). Immediately adjacent to this, upper reef slopes (~3-4 m depth) are dominated by diverse coral assemblages (>250 coral species) (Huang et al. 2009) with communities composed primarily of sediment tolerant taxa (e.g., *Pectinia* spp., *Merulina* spp., *Pachyseris* spp., *Platygyra* spp. etc.) and massive, sub-massive, foliose and encrusting growth forms (Bauman et al. 2015; Browne et al. 2015).

Despite several decades of study on the ecology of Singapore's reefs, nothing is known about herbivore abundance, rates of fish herbivory or the role that herbivores play in structuring coral and algal distribution on these highly disturbed, turbid reefs (e.g., Chuang 1977; Dikou & van Woesik 2006; Guest et al. 2005; Huang et al. 2009). In the present study we use a combination of surveys and *in situ* assays to quantify benthic community structure, herbivore biomass and herbivory rates and use these data to examine the relationship between coral and algal cover and herbivores at representative sites in Singapore's southern islands. We also compare coral cover to historical values to look for evidence of decline over the last three decades and develop hypotheses about the role of herbivory and physical factors in the maintenance of coral cover on highly disturbed turbid reefs.

## Methods and Materials

All research carried out abided by local laws and was done with permission of the Singapore National Parks Board (Permit no. NP/RP11-089). In November 2011 and May 2012, surveys of benthic cover, fish biomass and urchin abundance were carried out at eight haphazardly selected shallow sites within the southern islands group (Fig. 1) that are being examined as part of ongoing studies of ecological processes on Singapore's reefs (Bauman et al. 2015; Guest et al. 2016). The eight sites were Kusu Island, Pulau Hantu, Pulau Jong, Sisters Island, Semakau, Raffles Lighthouse, Terumpu Pempang Tengah (TPT) and Terumpu Pempang Laut (TPL) (Fig 1). The abundances of all reef fishes and urchins were quantified at each site along eight belt transects (30 × 2 m for fishes, 30 × 1 m for urchins). Due to logistical constraints, urchin surveys were only conducted in November 2011. Benthic community structure was quantified along the same transects using the line point count method with measurements taken every 50 cm. Categories used for the benthic surveys were hard coral, macroalgae, epilithic algal matrix (EAM *sensu* Wilson et al. 2003), other biota (e.g., sponges, zoantharians), crustose coralline algae (CCA), sand, silt, rock, recently dead coral, and unconsolidated rubble. Coral community structure was also quantified and data are presented in Bauman et al. (2015). All surveyed fish were categorized into 50 mm interval size classes for later conversion to biomass using species-specific growth coefficients (Froese & Pauly 2014). Length to weight conversions were calculated as follows: $W = a * L_T^b$, where W is weight in grams, $L_T$ is total length and parameters a and b are constants obtained from the literature and Fishbase (Froese & Pauly 2014).

Rates of herbivory were estimated by videoing (GoPro® Hero2) feeding assays to count bite rates on macroalgae and EAM in May 2012. Video assays took place at reef crests of three shallow sites (Sisters Island, Kusu Island and TPT), haphazardly selected from the eight sites used for the benthic and herbivore surveys. For the macroalgal studies, four locally common species were offered simultaneously *Sargassum ilicifolium*, *Lobophora variegata*, *Padina australis* and *Halimeda tuna*. In the EAM assays, video cameras were placed for 2-4 h in front of EAM patches (approx. 0.2 $m^{-2}$) naturally clear of dominant macrophytes and characterized by abundant EAM.

Video assays were done on two separate days per site with two replicates deployed per food type (macroalgae and EAM). In the macroalgae assays, we placed video cameras approximately 1 m in front of an experimental rope to which we tied individual whole thalli from the four algal macroalgal species. In each replicate the four algae specimens were selected to be as similar in size as possible. Quadrats of known area were placed in front of each EAM camera at the beginning of filming for a few seconds to provide a spatial scale, and so that bites could later be converted to bites cm$^{-2}$. To maximise independence among replicates, we separated individual replicate assays by at least 5 m, and we positioned replicates in a different location every day within each site to ensure independence among days. Video footage was analysed by counting the number of bites per hour taken by individual fishes on either macroalgae or the EAM. A video camera fault caused us to lose one replicate from the macroalgae assays on one of the days. Total hours of footage viewed were 28.2 h and 36.5 h for macroalgae and EAM assays, respectively.

The relationship between current coral and macroalgal benthic cover (as proportions); and biomass of fish (g m$^{-2}$; log[x+0.1] transformed) and abundance of urchins (number of individuals m$^{-2}$) was examined among the eight sites using Generalised Linear Mixed Models (GLMM) assuming a binomial distribution, with sites as random effects (Zuur et al. 2009). Because fish were surveyed twice (in Nov 2011 and May 2012), time was also fitted as a random effect for analyses of relationships between coral/macroalgal cover and fish biomass. Analyses were carried out using the glmmADMB package in R, with the betabinomial family to account for overdispersion (Fournier et al. 2012; Skaug et al. 2012). To determine spatial and temporal multivariate differences among the assemblages of fishes feeding on the algal assays we used a two-way permutational analysis of variance (PERMANOVA) with the following factors: Site (3 levels, random), and day (2 levels, random, nested within site). We used Bray-Curtis distance as our metric in these multivariate analyses. This was only done for the EAM assays as no fish were observed to feed on macroalgae during our assays (see Results).

## Results

Pooling all data from 2011 and 2012, average cover of coral across all eight shallow sites was 40.5% (SD ± 17.3%) and ranged from 27.2 to 53.6% among sites (Fig. 2a). Average macroalgal cover was 8.2% (SD ± 9.0%) and ranged from 1.1 to 16.9% among sites (Fig. 2b) whereas average cover of EAM was 9.9% (SD ± 9.4%) and ranged from 13.1 to 6.2% among sites (Fig. 2c). Much of the remaining benthos was composed of abiotic substrata including unconsolidated dead coral fragments (17.9 ± 11.6%, mean ± SD), rock (6.7% ± 8.1%, mean ± SD) and sand/silt (7.8% ± 6.5%, mean ± SD) (Fig. 3). A relatively low proportion of the benthos (6.1% ± 6.5%, mean ± SD) was covered by other fauna (e.g., sponges, soft corals, zoantharians) and average cover of CCA was <1%. Between surveys in November and May there was a marked difference in average benthic cover of EAM and abiotic substrata. Average cover of EAM decreased from 18.3% (SD ± 6.1%) in November to 1.9% (SD ± 2.26%) in May, whereas average cover of abiotic substrata (i.e., rock, sand, silt, dead coral) increased from 10.2% (SD ± 19.4%) to 21.0% (SD ± 11.4%) (Fig. 3).

Surveys carried out at reef crests at 65 sites around Singapore's southern island group between 1987 and 1991 found average coral cover to be similar to that found in the present study at 43.0% (SD ± 19.1%)(Chua & Chou 1992). However, when we compared data just from the eight sites used in the present study, we found that cover has declined at six of the sites and mean coral cover has declined by ~15% (Table 1).

The mean total biomass of fish across (all surveys pooled) was 26.6 g $m^{-2}$ (SD ± 42.4 g $m^{-2}$). Nearly 50% of the total fish biomass consisted of planktivores, primarily fusiliers (f. Caesionidae) (Fig. 4b) with only ~16% of the biomass (4.4 SD ± 6.5 g $m^{-2}$) comprised of herbivorous fishes (Fig.4b). Browsers within the family Siganidae (mostly *Siganus guttatus* and *S. virgatus*) were the most dominant of the functional herbivore groups (~10% of fish biomass). Scrapers (<1% of fish biomass) were rare, and no excavators were observed. Parrotfish were also rare (1% of the fish biomass) and no acanthurids were observed (Fig. 4b).

Among sites and years, total fish biomass ranged from 2.7 g $m^{-2}$ to 137.3 g $m^{-2}$, whereas biomass of fish herbivores ranged from 0.1 g $m^{-2}$ to 20.8 g $m^{-2}$ (Fig. 5). Estimated mean fish herbivore biomass in Singapore is between ~2 and 43 times lower than that at other Indo-Pacific reef sites with similarly high coral and low macroalgal cover, but similar to that found on heavily overfished and degraded reef flats (e.g., Fiji) (Table 2). Average urchin abundance across all sites was 0.10 individuals $m^{-2}$ (SD ± 0.17 individuals $m^{-2}$), of which >99% were *Diadema setosum* (Fig. 5c). Urchin abundances in Singapore are within the range found on comparable Indo-Pacific reefs (Table 2). Although we lack information about diel activity patterns of urchins on Singapore's reefs, the dominant sea urchin in Singapore - *Diadema setosum* – is known to be a nocturnal feeder (Muthiga et al. 2007). We cannot therefore rule out the possibility that our video assays underestimated algal consumption rates by urchins and other nocturnal herbivores.

No fish were recorded taking bites in the macroalgal assays during 28.2 hours of filming, however a herbivorous crab (*Leptodius* sp) was recorded taking seven bites (Fig. 6). A total of 741 bites (20.3 bites $h^{-1}$) were recorded in the EAM assays. Two damselfish species contributed *ca*. 80% of all bites to the EAM: *Pomacentrus chrysurus* (~50 %) and *P. littoralis* (~30%). In addition, the wrasse *Halichoeres melanurus* took a further 10% of all bites within the EAM (Fig. 6). There were no significant differences among sites in the assemblage of fishes observed feeding on the EAM assays (Pseudo-$F_{2,3}$ = 2.15, p = 0.07) and no differences among days (Pseudo-$F_{3,6}$ = 1.03, p = 0.45).

Coral cover was positively related to herbivorous fish biomass (LRT Chi-square = 4.35, df = 1, $p$ = 0.04), however there was no relationship between the percentage cover of macroalgae and herbivorous fish biomass (LRT Chi-square = 2.48, df = 1, $p$ = 0.12). Sea-urchin densities were not related with cover of either corals (LRT Chi-square = 1.80, df = 1, $p$ = 0.18) or macroalgae (LRT Chi-square = 0.06, df = 1, $p$ = 0.81)(Fig. 7).

## Discussion

Coral cover has declined markedly on reefs worldwide in recent decades as a direct result of increased human driven disturbances and changes in environmental conditions due to climate change (Bruno & Selig 2007). Singapore has lost much of its original reef area to coastal reclamation (Lai et al. 2015). Evidence from the present study suggests that coral cover on shallow reefs has also declined, on average, by around 15% over the last three decades. Surveys from the two survey periods are not from permanent transects, so some of this decline may be due to natural spatial heterogeneity. Furthermore, surveys during 2011-2012 were carried out just one to two years after a major thermal bleaching event in Singapore (Guest et al. 2016).

Nonetheless, we suggest that deterioration in water quality as a result of coastal development and dredging activities (Chou 2006; Gin et al. 2000) and other localised direct impacts such as boat groundings have led to an overall decline in coral cover on Singapore's shallow reefs since 1987.

Despite decades of anthropogenic impacts, however, Singapore's remaining shallow reefs appear to have maintained levels of coral cover (~40%) comparable to or higher than many reefs in the broader Indo-Pacific region (Bruno & Selig 2007; De'ath et al. 2012). For example, average coral cover for the Great Barrier Reef (GBR) (De'ath et al. 2012; 214 reefs surveyed over 27 y) and the wider Indo-Pacific region (Bruno & Selig 2007; 390 reefs surveyed in 2003) is ~22 to 23% of the total benthos. While coral cover alone should not be used as a measure of reef health, our data suggest a surprising resilience for these shallow reefs considering decades of human disturbances and close proximity to a highly populated urban center.

Mean macroalgal cover (~8%) on surveyed reefs, on the other hand, was comparable to that reported for reef crests and slopes of the Outer Central GBR but much lower than that on inner central GBR reefs (Wismer et al. 2009). For example, average cover of macroalgae ranges from 1.7 to 15.4% on the Outer Central GBR and 36.2 to 66.2% on inner central GBR reefs (Wismer et al. 2009). Cover of EAM, which often forms a stable and significant part of the benthos on many reefs (Bellwood & Fulton 2008; Wilson et al. 2003b), varied markedly between surveys in May and November. For example, average cover was ~18% in November 2011 but dropped to <2% cover in May 2012. This apparent temporal variation in turf algal abundance may be driven by seasonal environmental factors related to the change in monsoons (e.g., Diaz-Pulido & Garzón-Ferreira 2002).

Herbivory is critically important in mediating transitions between coral to algal dominance following disturbances on reefs (Hughes et al. 2007). Estimates of herbivorous fish biomass from underwater visual censuses can be strong predictors of grazing intensity on coral reefs (Mumby 2006) and both herbivore biomass and the dominant type of herbivores (e.g, scrapers, grazers etc.) are strong predictors of reef state (Jouffray, 2015).

In the present study, the estimated biomass of fish herbivores (~4 g $m^{-2}$) in Singapore was seven times lower than the average for Indo-Pacific reefs (~29 g $m^{-2}$) (Roff & Mumby 2012). Fish herbivore biomass was up to 43 times lower than relatively undisturbed reefs (e.g., Ningaloo), but similar to heavily degraded and overfished reefs (e.g., Fiji) where similar studies have been conducted (Vergés et al. 2012; Rasher et al. 2013). The majority of herbivorous fish, in terms of biomass, were macroalgal browsers, primarily from the family Siganidae. Functionally important groups of herbivorous fishes such as excavating parrotfishes were absent, while scraping parrotfishes were present in very low numbers. Surgeonfishes (Family Acanthuridae), one of the most diverse and abundant group of herbivorous fishes in coral reefs, were not recorded during our surveys.

No feeding by fish was observed on the macroalgal assays in Singapore, while comparable studies outside of Singapore have found fish bite rates ranging from ~13 to almost 1000 bites per hour on single or mixed species algal assemblages (Vergés et al. 2012). Fish bite rates on EAM were, however, within the range found for comparable Indo-Pacific sites (Bennett et al. 2010; Rasher et al. 2013) but most bites were taken by a single territorial damselfish species (*P. littoralis*), whereas elsewhere, the majority of the fish recorded taking bites from EAM are roving herbivores (e.g., *Scarus* spp., *Acanthurus* spp.)(Bennett et al. 2010; Rasher et al. 2013). In the absence of historical data on fish biomass we do not know if and when herbivores declined or whether certain functional groups were more abundant in the past.

There was a significant (albeit weak) relationship between coral cover and fish herbivore biomass, suggesting either a functional role for fish in maintaining high cover or for coral cover in maintaining high fish biomass at some sites, or that herbivorous fishes are responding to some other factor (e.g., turbidity, sedimentation) that is collinear with coral cover (Wismer et al. 2009). The relatively low cover of fleshy macroalgae at study reefs, however, is surprising considering the overall low fish herbivore biomass, recorded low rates of herbivory and the lack of any significant relationship between macrolagal cover and fish biomass among sites.

One possible explanation is that a single functionally important fish species is responsible for a disproportionate amount of grazing in Singapore. It is possible, due to the relatively poor underwater visibility (typically ~2 m), that certain key species were missed during surveys, indeed the importance of occasional roving herbivores are known to be underestimated when using visual fish census methods (Hoey & Bellwood 2010). Such functional redundancy has been reported elsewhere, for example, a single fish species (*Naso unicornis*) was found to be responsible for ~90% of bites taken on *Sargassum* sp. in a range of reef habitats on the GBR (Hoey & Bellwood 2009). Furthermore, in addition to herbivory, other processes may be equally important on these turbid reefs in preventing a shift away from coral dominance and towards macroalgal dominance.

The composition of Singapore's coral communities has undoubtedly contributed to their ability to maintain relatively high levels of coral cover and resist phase shifts towards macroalgal dominance. Coral communities are dominated by stress tolerant and generalist taxa that can withstand high levels of sedimentation and are relatively resistant to thermal stress (Guest et al. 2012; Browne et al. 2015; Darling et al. 2013; Huang et al. 2009). For example, data from the present study found the six most common coral genera to be *Pectinia*, *Merulina*, *Pachyseris*, *Montipora*, *Echinopora* and *Platygyra* (presented in Bauman et al. 2015). Following disturbances, such as coral bleaching, surviving remnant colonies from these taxa are capable of rapid regrowth, allowing coral cover to return more rapidly following bleaching disturbances, compared to the relatively slow process of larval recruitment (Bauman et al. 2015; Guest et al. 2016). It is also possible that high coral cover in Singapore has concentrated the efforts of herbivory to a relatively smaller area, making lower rates of herbivory more effective at removing macroalgae (Williams et al. 2001).

Physical factors (e.g., light and sedimentation) may also be playing an important role in structuring the distribution of corals and algae on these reefs. Light attenuates rapidly in Singapore's sediment-rich coastal waters, leading to an almost 50% reduction in photosynthetic efficiency of *Sargassum* spp. at the reef crest (Tun et al. 1994). If algal growth is limited by light even at quite shallow depths, then relatively low rates of herbivory may be sufficient to prevent macroalgae from overgrowing coral dominated areas. If so, then this provides an example of an "ecological surprise", where two negative impacts (increased turbidity and reduced herbivory) interact antagonistically, resulting in stable shallow coral communities (Paine et al. 1998). If this is the case, then management efforts to improve water clarity may need to be combined with efforts to increase the biomass of key functional herbivores.

Clearly, further studies are needed to determine the contribution that fish and invertebrate herbivores play in structuring the distribution of corals and macroalgae on Singapore's shallow reefs. Of particular importance are studies to identify individual key functional fish species and to determine the precise role they play in preventing transitions from coral to macroalgal dominance. Such information is of critical importance to the future management of these highly disturbed, turbid, yet remarkably diverse coral reefs.

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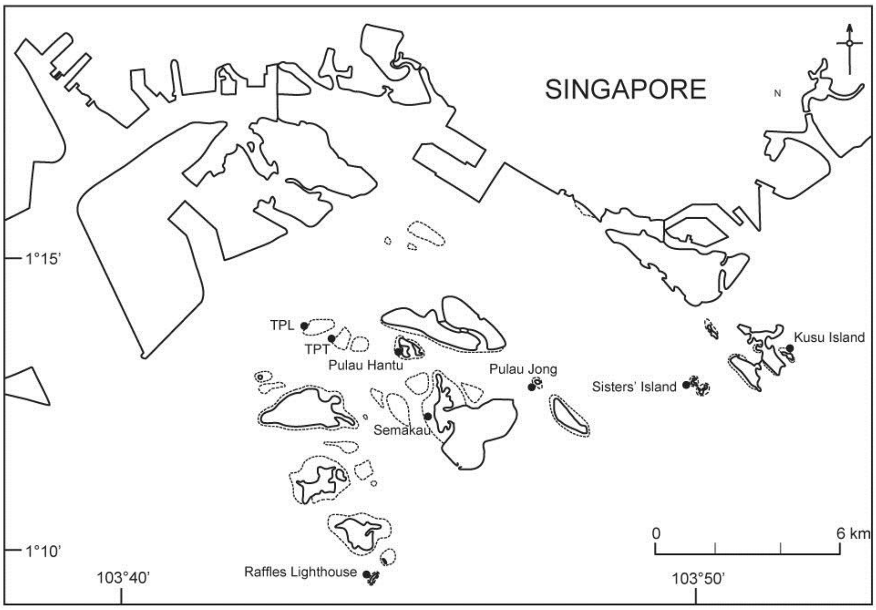


Fig. 1. Map of study sites in Singapore's southern island group.

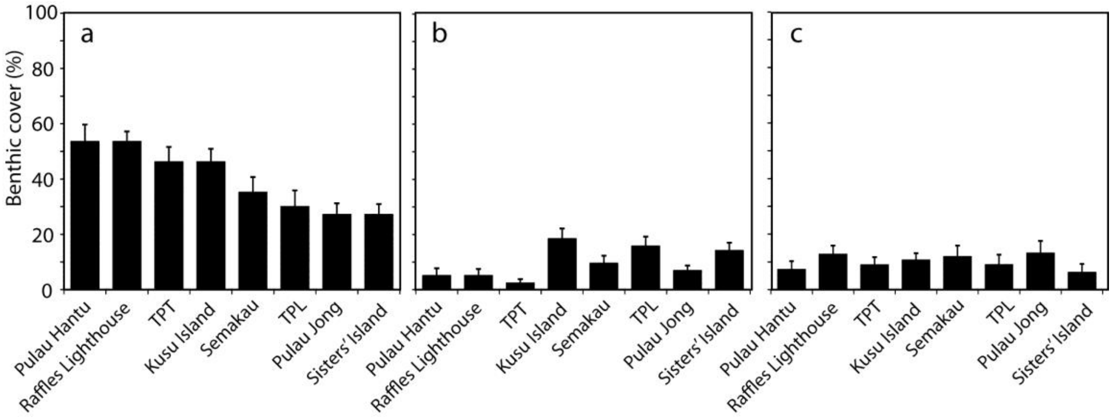


Fig. 2. Bar chart showing a) mean cover of hard coral b) macroalgae and c) EAM by sites (all surveys pooled). Sites are in order of decreasing mean coral cover from left to right. Error bars SE.

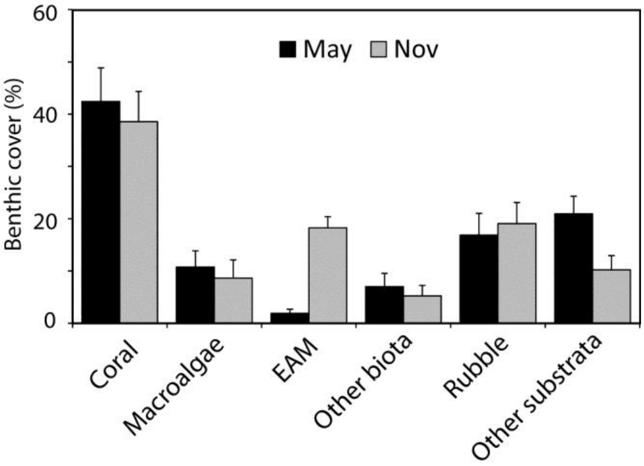


Fig. 3. Bar chart showing difference in mean benthic cover between sampling months of coral, macroalgae, EAM, other biota, rubble and other substrata. Error bars are SE.

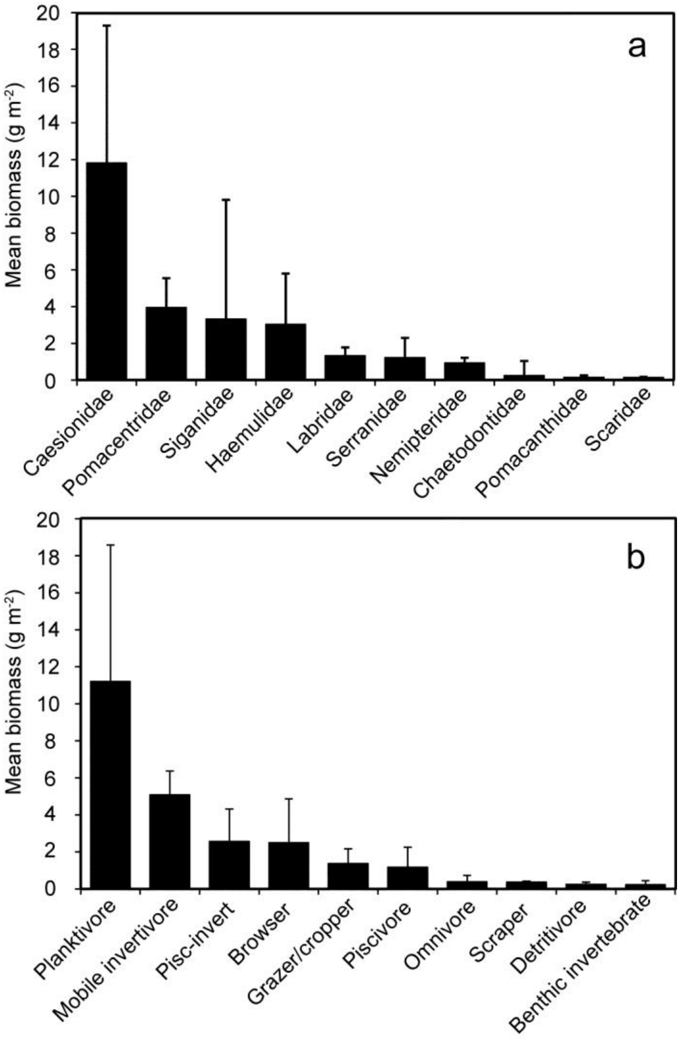


Fig. 4. Bar chart showing a) average biomass of fish families (g m$^{-2}$) and b) fish functional groups (g m$^{-2}$) from all surveys pooled. Error bars are SE.

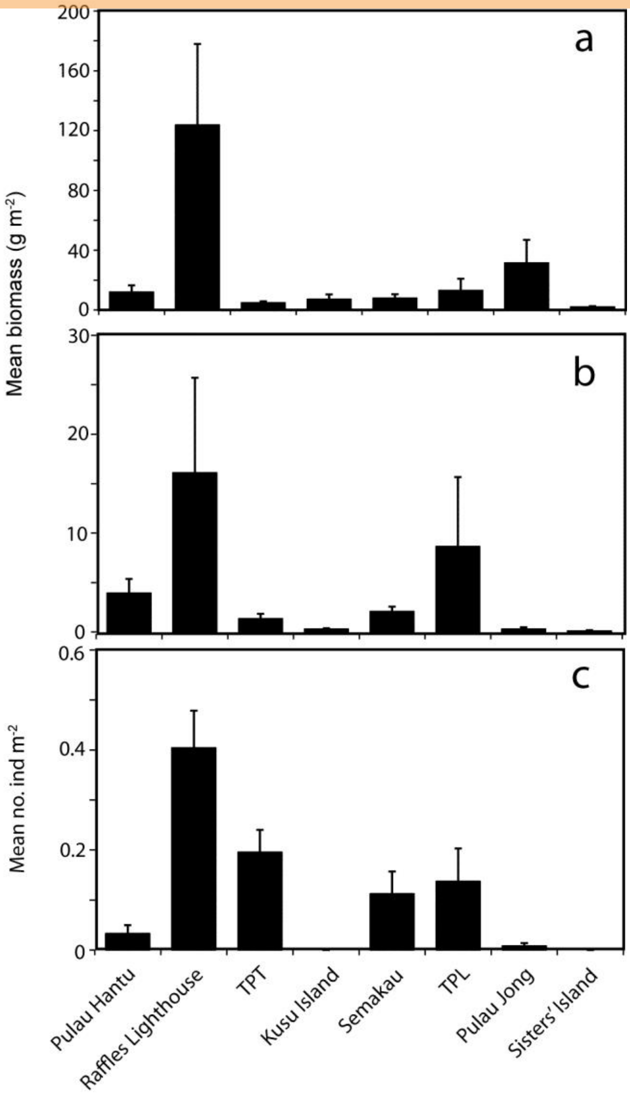
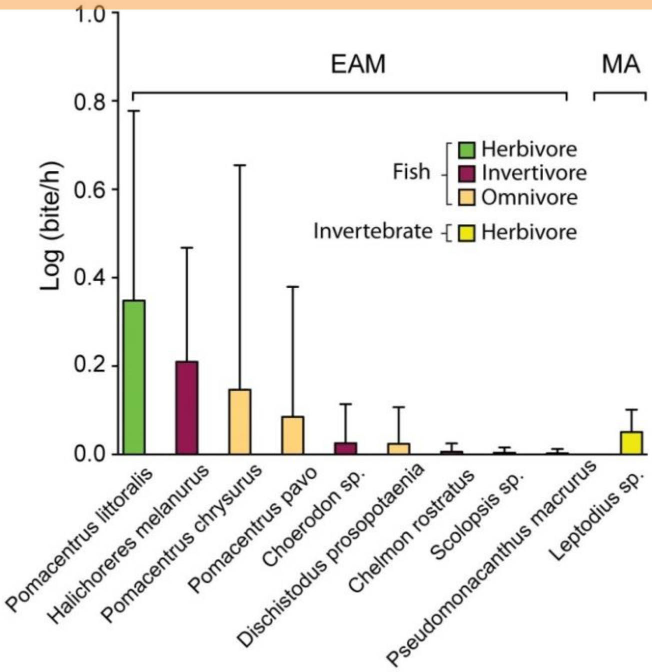


Fig. 5. Bar chart showing differences among sites in a) average biomass of all fish, b) herbivorous fish (g $m^{-2}$) and c) urchins (ind. $m^{-2}$) from all surveys pooled. Sites are in the same order as Fig. 2 with decreasing mean coral cover from left to right. Error bars are SE.



510
511
512 Fig. 6. Bite rates by different species (mean Log bites $h^{-1}$ +SE) on epilithic algal
513 matrix (EAM) and on tethered macroalgal (MA) species during timed video assays.

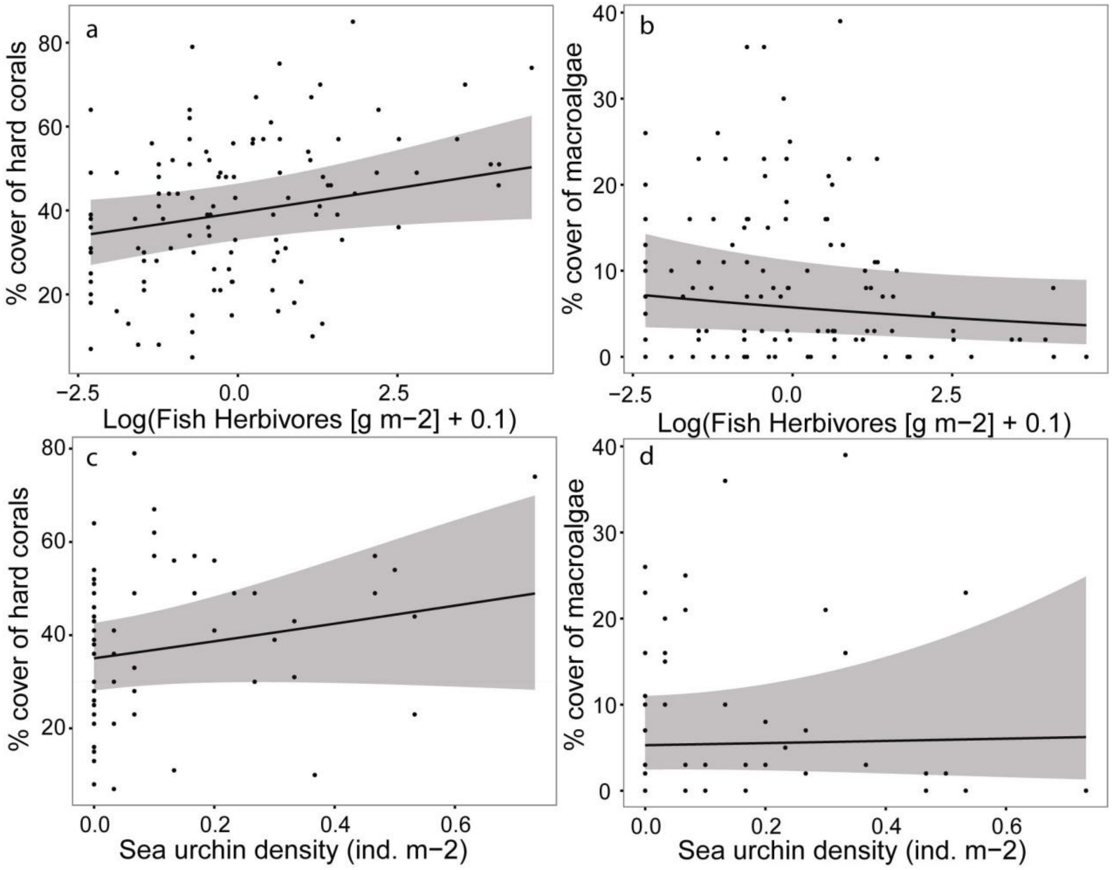


Fig. 7. The relationship between a) hard coral cover and fish herbivore abundance, b) macroalgal cover and fish herbivore abundance, c) hard coral cover and urchin density and d) macroalgal cover and urchin density among eight Singaporean reef sites surveyed in Nov 2011 (fish and urchins) and May 2012 (fish). The fitted line is the predicted cover based on the GLMM and shaded areas are 95% confidence intervals.

Table 1. A comparison of coral cover (%) at the upper reef slopes (3-4 m depth) of eight sites in Singapore's southern islands group between surveys carried out during 1987-1991 and 2011-2012. Data from 1987-1991 are from Table 1 in (Chua & Chou 1992). The earlier surveys were carried out using the line intersept transect method on a single 100 m transect at each site which differs from the method used in the present study (8 × 30 m line point intercept transects). The precise location of the transects were not the same between sampling periods, therefore some variation in coral cover may be due to natural spatial heterogeneity.

| **Sites** | **1987-1991** | **2011-2012** |
|---|---|---|
| Raffles Lighthouse | 73.3 | 53.6 |
| Pulau Hantu | 43.8 | 53.6 |
| Sisters Island | 65.7 | 27.2 |
| Pulau Jong | 43.2 | 27.2 |
| TPT | 73.9 | 46.2 |
| TPL | 57.0 | 30.0 |
| Kusu Island | 33.1 | 46.2 |
| Semakau | 51.0 | 35.2 |
| *Mean* | *55.1* | *39.9* |
| *SD* | *15.0* | *11.3* |

Table 2. Comparison of herbivores and herbivory on Indo-Pacific reefs. Numbers in parentheses are SD. * denotes that data came from inside sanctuary zones. For the comparison of macroalgal bite rate assays, different species assemblages were used in each study as follows: Singapore & Tioman, Malaysia = 1) *Sargassum ilicifolium*, 2) *Lobophora variegata*,3) *Padina australis and* 4) *Halimeda tuna*; Keppel Islands & Ningaloo = 1) *S. myriocystum*; Viti Levu, Fiji = 1) *Sargassum polycystum*, 2) *Turbinaria conoides*, 3) *Padina boryana*, 4) *Dictyota bartayresiana*, 5) *Amphiroa crassa*, 6) *Galaxuraura filamentosa*, 7) *Chlorodesmis fastigiata*. EAM bite rates were estimated for benthic patch sizes of ~0.2 $m^2$ in Singapore and 0.3 $m^2$ in Tioman. Average number of bites is shown as bites $h^{-1}m^{-2}$ for comparison across sites.

| **Location** | **Mean herbivorous fish biomass (g $m^{-2}$)** | **Mean abundance of herbivorous sea urchins (ind $m^{-2}$)** | **Total number of fish bites on macroalgae (bites $h^{-1}$)** | **Total number of bites on EAM (bites $h^{-1}m^{-2}$)** | **Reference** |
|---|---|---|---|---|---|
| Singapore | 4.30 (8.2) | 0.10 (0.13) | 0.00 | 109.27 | Present study |
| Pulau Tioman, Malaysia | 10.30 (14.85) | 0.75 (0.12) | 21.52 | 334.93 | Vergés et al, unpublished data |
| Keppel Islands, GBR | 13.80 (17.43) | No data | 13.40 | | Vergés et al 2012 |
| Ningaloo, Western Australia | | | | 67.78 | Bennett et al. 2010 |
| | 186.53 (362.55)* | | 195.0* | No data | Vergés et al 2012 |
| | | 0.42 (0.41) | | | Langdon 2012 |
| Viti Levu, Fiji | 39.61 (46.20)*<br>3.64 (23.18) | | 997.41* | 252.37* | Rasher et al. 2013 |
| | | 0.03 (0.02)*<br>0.02 (0.01) | | | Bonaldo, unpublished data |

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