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

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Abstract

Background. Herbivores play a critical role in structuring benthic communities on tropical coral dominated reefs because they remove macro and microalgae, which might otherwise overgrow adult corals or prevent successful recruitment of juveniles. Reducing herbivory has been implicated in promoting phase shifts from coral dominance to other ecosystem states following acute disturbances. Turbidity and sedimentation are key physical processes that also structure coral reef communities because they limit light penetration and may 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. Macroalgae, particularly *Sargassum* spp. are abundant on the reef flats, while adjacent reef slopes are dominated by diverse coral assemblages, yet nothing is known about the role of herbivory in structuring these heavily disturbed reefs.

Methods. To gain a better understanding of the role of herbivore biomass and potential herbivory in structuring these disturbed reefs, we quantified benthic cover of corals and macroalgae, fish biomasses 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. Using generalised linear mixed models we examine the relationship between herbivore abundances and benthic cover of corals and macroalgae.

Results. Average coral cover at 3-4 m depth was surprisingly high (~40%) compared to other Indo-Pacific reefs, considering decades of chronic anthropogenic impacts. In contrast, the average biomass of herbivorous fishes (~4 g m⁻²) was more typical of degraded and overfished reefs, while urchin abundances were within the range found at other Indo-Pacific sites. Herbivorous fish were not observed feeding on macroalgal assays during 29 h of filming, with all bites counted on EAM carried out primarily by territorial damselfish. There was a significant but weak relationship between coral cover and herbivore biomass but none for macroalgae or between urchin abundance and benthic cover.

Discussion. Relatively high coral cover and low macroalgal cover at 3-4 m depth has been maintained on these highly disturbed reefs, demonstrating possible resilience to coral-macroalgal phase shifts despite decades of chronic human disturbances. We suggest that 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 from outcompeting corals on turbid reefs such as those in the present study.
Introduction

The distribution of corals and algae on coral reefs is strongly influenced by biological processes and physical conditions including herbivory, sedimentation and light availability (Steneck 1988). 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/or inhibit 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 stressful 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, manifested as decreases in total coral cover and consequent deterioration of ecological function (Pandolfi et al. 2003). The effects of combined disturbances are not always additive and may in some cases be
antagonistic, resulting in the effect of one disturbance lessening the effect of another (Darling et al. 2010).

Declines in ecosystem 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). However, transitions to other ecosystem states also occur, with the type of transition influenced by local physical and biological conditions (Norström et al. 2009).

Most of the world’s reefs and the highest diversity of coral reef species occur within the biogeographic region including Malaysia, the Philippines, Indonesia and Papua New Guinea known as the ‘coral triangle’ (Hoeksema 2007). Many of the reefs in this region are close to high human population densities and have experienced the effects of extreme coastal development and overfishing (Burke et al. 2002). Singapore (on the edge of the coral triangle) 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. The population has risen from an estimated 150 people in 1819 (Hilton & Manning 1995) to >5.4 million at present (http://www.singstat.gov.sg/home). The majority of the southern coastline and islands, where Singapore’s coral reefs occur, have undergone reclamation and many of the intertidal flats of the fringing and patch reefs have been lost to make way for petrochemical plants, military and recreational areas (Lai et al. 2015).

Extensive coastal development in Singapore has resulted in sedimentation rates and levels of total suspended solids exceeding those considered optimal for
tropical reefs (Dikou, A. and van Woesik, R. 2006, Rogers, C. S. 1990, Todd, P. A. 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, L. M. 1996), and eutrophication has increased at least 30 fold in the last 60 years (Gin, K. Y. H. et al. 2000). Erect fleshy macroalgae, particularly *Sargassum* spp. have dominated shallow reef flats (~0-2 m depth) in Singapore since at least the 1970s (Chuang 1977), while adjacent upper reef slopes (~3-4 m depth) are dominated by diverse coral assemblages (>250 coral species) (Guest et al. 2005b; Huang et al. 2009).

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 (e.g., Chuang 1977; Dikou & van Woesik 2006; Guest et al. 2005a; Huang et al. 2009). In the present study we use a combination of surveys and *in situ* assays to quantify coral cover, algal cover, 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 several hypotheses about the role of herbivory and physical factors in the maintenance of coral cover on highly impacted reefs in Singapore.

**Methods and Materials**

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, EAM, other biota (e.g., sponges, zoantharians), crustose coralline algae (CCA), sand, silt, rock, recently dead coral, and unconsolidated rubble. 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: \( W = a \times L_T^b \), 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 epilithic algal matrix (EAM sensu Wilson et al. 2003a) 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 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. All macroalgae were collected from Pulau Tekukor. 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.

Data analysis

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 shallow sites used for the herbivory studies 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% (Fig. 3). 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).
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) with only ~16% of the biomass (4.4 SD ± 6.5 g m$^{-2}$) comprised of herbivorous fishes (Fig. 4a). Browsers within the family Siganidae 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 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 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 1). 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 1).

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 anthropogenic disturbances and changes in environmental conditions due to climate change (Bruno & Selig 2007). Singapore has lost much of its original reef area (an estimated 60%) to coastal reclamation (Lai et al. 2015). However, despite decades of anthropogenic impacts, Singapore’s remaining shallow reefs appear to have maintained relatively high levels of coral cover (~40%) compared to current levels found 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.

Mean macroalgal cover in Singapore (~8%) 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). EAM may form a stable and significant part
of the benthos on many reefs (Bellwood & Fulton 2008; Wilson et al. 2003b). Mean cover of EAM in Singapore was ~18% in November 2011 but dropped to <2% cover in May 2012. This may be due to seasonal variation in turf algal growth, although we have to be cautious about concluding this with only one year of surveys.

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 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 average cover at these sites has declined by ~15% since the surveys carried out in 1987. The precise cause of these declines not known, but we suggest that deterioration in water quality due to coastal development and dredging activities and two thermal bleaching episodes (in 1998 and 2010) (Guest et al. 2012) have made the greatest contribution.

Herbivory is critically important in the prevention of phase shifts from coral to algal dominance 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). In the present study, however, 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). 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).

The significant (albeit weak) relationship between coral cover and fish
herbivore biomass suggests 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). Nonetheless, the low rates of
herbivory found here strongly suggest that in addition to herbivory, other mechanisms
may be as 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 apparent resilience. Coral communities are dominated by stress
tolerant and generalist taxa that can withstand relatively high levels of sedimentation
and are relatively resistant to thermal stress (e.g., *Merulina* spp., *Platycladus* etc.)
(Bauman et al. 2015; Browne et al. 2015; Darling et al. 2013; Huang et al. 2009).
Following disturbances such as coral bleaching, surviving remnants colonies from
these taxa are capable of rapid regrowth. This may allow coral cover to recover
rapidly following bleaching disturbances, because recovery is not dependent on the
relatively slow process of larval recruitment (Bauman et al. 2015; Guest et al. 2016).
Physical factors (e.g., light and sedimentation) may also play 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* 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 and/or algal turfs 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).

Clearly, further studies are needed to understand the role of herbivores in structuring these heavily impacted reefs. It is likely, due to the relatively poor underwater visibility (typically ~2 m), that certain important herbivorous fish 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). 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. Furthermore, 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.

Degradation does not always occur gradually and phase shifts tend to occur when a system has reached a tipping point (Hughes et al. 2010). Despite declines in coral cover since surveys in the 1980s, the fact that many of Singapore’s shallow reef communities have remained in a coral dominated state for almost the last three decades does not mean that they will remain this way indefinitely. Furthermore,
despite relatively high coral cover and diversity, Singapore’s reefs may have lost much of their value in terms of ecological goods and services (e.g., diving tourism, commercial fishing). Therefore urbanized, turbid reefs, such as the ones studied here, may maintain high ecological value but low socio-economic value as they contribute little to the nation’s tourism industry and food security. Nonetheless, urbanised coral reefs form an important part of the country’s natural and ecological heritage and thus deserve effective management and protection.

Acknowledgements

We thank R. Bonaldo and D. Rasher for providing data on fish and urchin densities in IndoPacific reefs for comparative purposes.

References


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. Error bars are SE.
Fig. 5. Bite rates by different species (mean Log bites h⁻¹ + SE) on epilithic algal matrix (EAM) and on tethered macroalgal (MA) species during timed video assays.
Fig. 6. 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).
Table 1. 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) *Galaxaura filamentosa*, 7) *Chlorodesmis fastigiata*. EAM bite rates were estimated on 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.

<table>
<thead>
<tr>
<th>Location</th>
<th>Mean herbivorous fish biomass (g m$^{-2}$)</th>
<th>Mean abundance of herbivorous sea urchins (ind m$^{-2}$)</th>
<th>Total number of bites on macroalgae (bites h$^{-1}$)</th>
<th>Total number of bites on EAM (bites h$^{-1}$m$^{-2}$)</th>
<th>Reference</th>
</tr>
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<td>Singapore</td>
<td>4.3 (8.2)</td>
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<td>0</td>
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<td>Tioman, Malaysia</td>
<td>10.30 (14.85)</td>
<td>0.75 (0.12)</td>
<td>21.52</td>
<td>334.93</td>
<td>Vergés et al, unpublished data</td>
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<td>Keppel Islands, GBR Australia</td>
<td>13.80 (17.43)</td>
<td>No data</td>
<td>13.4</td>
<td></td>
<td>Vergés et al 2012</td>
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<tr>
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<td>186.53 (362.55)*</td>
<td></td>
<td>195.0*</td>
<td>67.78</td>
<td>Bennett et al. 2010</td>
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<tr>
<td>Viti Levu, Fiji</td>
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<td>3.64 (23.18)</td>
<td>997.41*</td>
<td>252.37*</td>
<td>Rasher et al. 2013</td>
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