

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.

1 Introduction

2

3 The distribution of corals and algae on coral reefs is strongly influenced by biological
4 processes and physical conditions including grazing, sedimentation and light
5 availability (Steneck 1988; Bak & Engel 1979; Loya 1976). Herbivory is one of the
6 key processes structuring shallow tropical coral communities because it moderates
7 coral-algal interactions through the removal of fleshy macroalgae or algal turfs that
8 can overgrow or injure adult corals and inhibits settlement and post-settlement
9 survival of juvenile corals (Birrell et al. 2005; McCook et al. 2001; Rasher & Hay
10 2010). Sediments also have numerous effects on coral reef benthic and community
11 structure (McClanahan & Obura 1997). Suspended sediments limit light penetration
12 and particulates interfere with biological processes, such as heterotrophy in corals,
13 and may alter rates of herbivory by fish (Bellwood & Fulton 2008; Rogers 1990).
14 Generally, increased sedimentation is considered detrimental for coral health;
15 however sediments can also be a source of food for corals and may provide a degree
16 of protection from thermal stress by reducing levels of irradiance (Anthony &
17 Fabricius 2000; Cacciapaglia & Woesik 2015).

18 Over fishing has led to both reductions in rates of herbivory and removal of
19 certain key herbivore species on many coral reefs (Edwards et al. 2014; Jackson et al.
20 2001). Coastal development, on the other hand, has led to decreases in water quality
21 (e.g., increased turbidity) and increased rates of sedimentation (Erftemeijer et al.
22 2012; Rogers 1990). These disturbances, among others, have been implicated in the
23 observed global decline in reef condition, decreases in total coral cover and
24 consequent deterioration of ecological function (Pandolfi et al. 2003). The effects of
25 combined disturbances are not always additive. Indeed, in some cases co-occurring

26 disturbances can interact antagonistically, resulting in the total impact of the
27 combined disturbances being less than the sum of individual impacts (Darling et al.
28 2010).

29 Declines in reef condition occur gradually in many cases, but in others, a
30 combination of disturbances results in rapid transitions from one ecosystem state to
31 another. The most widely researched of these so called phase-shifts is from
32 dominance by hard corals to dominance by fleshy macro-algae (known as a coral to
33 macroalgal phase shift) (Bruno et al. 2009; Done 1992; Hughes 1994; Hughes et al.
34 2007; McManus & Polsenberg 2004). Transitions to other ecosystem states also
35 occur, with the type of transition influenced by local physical and biological
36 conditions (Norström et al. 2009). It is generally accepted that reefs already
37 compromised by human disturbances (e.g., overfishing, reduced water quality) are
38 more prone to rapid phase shifts following acute disturbances.

39 Singapore has in the span of just under 200 years undergone a transformation
40 from a sparsely populated, forest-covered island to a highly urbanised city-state
41 (Hilton & Manning 1995). Extensive coastal development has resulted in
42 sedimentation rates and levels of total suspended solids exceeding those considered
43 optimal for tropical reefs (Dikou & van Woosik 2006; Rogers 1990; Todd et al.
44 2004). Average underwater visibility, thought to have been about 10 m in the 1960's,
45 has decreased to around 2 m at present (Chou 1996), and eutrophication has increased
46 at least 30 fold in the last 60 years (Gin et al. 2000). Erect fleshy macroalgae,
47 particularly *Sargassum* spp., dominate shallow reef flats (~0-2 m depth), particularly
48 during the north-east monsoon, when they bloom to form dense stands of individuals
49 measuring more than 2 m in length (Chuang 1977). Immediately adjacent to this,
50 upper reef slopes (~3-4 m depth) are dominated by diverse coral assemblages (>250

51 coral species) (Huang et al. 2009) with communities composed primarily of sediment
52 tolerant taxa (e.g., *Pectinia* spp., *Merulina* spp., *Pachyseris* spp., *Platygyra* spp. etc.)
53 and massive, sub-massive, foliose and encrusting growth forms (Bauman et al. 2015;
54 Browne et al. 2015).

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

66

67 **Methods and Materials**

68

69 All research carried out abided by local laws and was done with permission of the
70 Singapore National Parks Board (Permit no. NP/RP11-089). In November 2011 and
71 May 2012, surveys of benthic cover, fish biomass and urchin abundance were carried
72 out at eight haphazardly selected shallow sites within the southern islands group (Fig.
73 1) that are being examined as part of ongoing studies of ecological processes on
74 Singapore's reefs (Bauman et al. 2015; Guest et al. 2016). The eight sites were Kusu
75 Island, Pulau Hantu, Pulau Jong, Sisters Island, Semakau, Raffles Lighthouse,

76 Terumpu Pempang Tengah (TPT) and Terumpu Pempang Laut (TPL) (Fig 1). The
77 abundances of all reef fishes and urchins were quantified at each site along eight belt
78 transects (30 × 2 m for fishes, 30 × 1 m for urchins). Due to logistical constraints,
79 urchin surveys were only conducted in November 2011. Benthic community structure
80 was quantified along the same transects using the line point count method with
81 measurements taken every 50 cm. Categories used for the benthic surveys were hard
82 coral, macroalgae, epilithic algal matrix (EAM *sensu* Wilson et al. 2003), other biota
83 (e.g., sponges, zoantharians), crustose coralline algae (CCA), sand, silt, rock, recently
84 dead coral, and unconsolidated rubble. Coral community structure was also quantified
85 and data are presented in Bauman et al. (2015). All surveyed fish were categorized
86 into 50 mm interval size classes for later conversion to biomass using species-specific
87 growth coefficients (Froese & Pauly 2014). Length to weight conversions were
88 calculated as follows: $W = a * L_T^b$, where W is weight in grams, L_T is total length and
89 parameters a and b are constants obtained from the literature and Fishbase (Froese &
90 Pauly 2014).

91 Rates of herbivory were estimated by videoing (GoPro® Hero2) feeding
92 assays to count bite rates on macroalgae and EAM in May 2012. Video assays took
93 place at reef crests of three shallow sites (Sisters Island, Kusu Island and TPT),
94 haphazardly selected from the eight sites used for the benthic and herbivore surveys.
95 For the macroalgal studies, four locally common species were offered simultaneously
96 *Sargassum ilicifolium*, *Lobophora variegata*, *Padina australis* and *Halimeda tuna*. In
97 the EAM assays, video cameras were placed for 2-4 h in front of EAM patches
98 (approx. 0.2 m²) naturally clear of dominant macrophytes and characterized by
99 abundant EAM.

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

114 The relationship between current coral and macroalgal benthic cover (as
115 proportions); and biomass of fish (g m^{-2} ; $\log[x+0.1]$ transformed) and abundance of
116 urchins (number of individuals m^{-2}) was examined among the eight sites using
117 Generalised Linear Mixed Models (GLMM) assuming a binomial distribution, with
118 sites as random effects (Zuur et al. 2009). Because fish were surveyed twice (in Nov
119 2011 and May 2012), time was also fitted as a random effect for analyses of
120 relationships between coral/macroalgal cover and fish biomass. Analyses were carried
121 out using the glmmADMB package in R, with the betabinomial family to account for
122 overdispersion (Fournier et al. 2012; Skaug et al. 2012). To determine spatial and
123 temporal multivariate differences among the assemblages of fishes feeding on the
124 algal assays we used a two-way permutational analysis of variance (PERMANOVA)

125 with the following factors: Site (3 levels, random), and day (2 levels, random, nested
126 within site). We used Bray-Curtis distance as our metric in these multivariate
127 analyses. This was only done for the EAM assays as no fish were observed to feed on
128 macroalgae during our assays (see Results).

129

130 **Results**

131

132 Pooling all data from 2011 and 2012, average cover of coral across all eight shallow
133 sites was 40.5% (SD \pm 17.3%) and ranged from 27.2 to 53.6% among sites (Fig. 2a).
134 Average macroalgal cover was 8.2% (SD \pm 9.0%) and ranged from 1.1 to 16.9%
135 among sites (Fig. 2b) whereas average cover of EAM was 9.9% (SD \pm 9.4%) and
136 ranged from 13.1 to 6.2% among sites (Fig. 2c). Much of the remaining benthos was
137 composed of abiotic substrata including unconsolidated dead coral fragments (17.9 \pm
138 11.6%, mean \pm SD), rock (6.7% \pm 8.1%, mean \pm SD) and sand/silt (7.8% \pm 6.5%,
139 mean \pm SD) (Fig. 3). A relatively low proportion of the benthos (6.1% \pm 6.5%, mean
140 \pm SD) was covered by other fauna (e.g., sponges, soft corals, zoantharians) and
141 average cover of CCA was <1%. Between surveys in November and May there was a
142 marked difference in average benthic cover of EAM and abiotic substrata. Average
143 cover of EAM decreased from 18.3% (SD \pm 6.1%) in November to 1.9% (SD \pm
144 2.26%) in May, whereas average cover of abiotic substrata (i.e., rock, sand, silt, dead
145 coral) increased from 10.2% (SD \pm 19.4%) to 21.0% (SD \pm 11.4%) (Fig. 3).

146 Surveys carried out at reef crests at 65 sites around Singapore's southern
147 island group between 1987 and 1991 found average coral cover to be similar to that
148 found in the present study at 43.0% (SD \pm 19.1%)(Chua & Chou 1992). However,
149 when we compared data just from the eight sites used in the present study, we found

150 that cover has declined at six of the sites and mean coral cover has declined by ~15%
151 (Table 1).

152 The mean total biomass of fish across (all surveys pooled) was 26.6 g m^{-2} (SD
153 $\pm 42.4 \text{ g m}^{-2}$). Nearly 50% of the total fish biomass consisted of planktivores,
154 primarily fusiliers (f. Caesionidae) (Fig. 4b) with only ~16% of the biomass ($4.4 \text{ SD} \pm$
155 6.5 g m^{-2}) comprised of herbivorous fishes (Fig.4b). Browsers within the family
156 Siganidae (mostly *Siganus guttatus* and *S. virgatus*) were the most dominant of the
157 functional herbivore groups (~10% of fish biomass). Scrapers (<1% of fish biomass)
158 were rare, and no excavators were observed. Parrotfish were also rare (1% of the fish
159 biomass) and no acanthurids were observed (Fig. 4b).

160 Among sites and years, total fish biomass ranged from 2.7 g m^{-2} to 137.3 g m^{-2}
161 2 , whereas biomass of fish herbivores ranged from 0.1 g m^{-2} to 20.8 g m^{-2} (Fig. 5).
162 Estimated mean fish herbivore biomass in Singapore is between ~2 and 43 times
163 lower than that at other Indo-Pacific reef sites with similarly high coral and low
164 macroalgal cover, but similar to that found on heavily overfished and degraded reef
165 flats (e.g., Fiji) (Table 2). Average urchin abundance across all sites was 0.10
166 individuals m^{-2} (SD ± 0.17 individuals m^{-2}), of which >99% were *Diadema setosum*
167 (Fig. 5c). Urchin abundances in Singapore are within the range found on comparable
168 Indo-Pacific reefs (Table 2). Although we lack information about diel activity patterns
169 of urchins on Singapore's reefs, the dominant sea urchin in Singapore - *Diadema*
170 *setosum* – is known to be a nocturnal feeder (Muthiga et al. 2007). We cannot
171 therefore rule out the possibility that our video assays underestimated algal
172 consumption rates by urchins and other nocturnal herbivores.

173 No fish were recorded taking bites in the macroalgal assays during 28.2 hours
174 of filming, however a herbivorous crab (*Leptodius* sp) was recorded taking seven

175 bites (Fig. 6). A total of 741 bites ($20.3 \text{ bites h}^{-1}$) were recorded in the EAM assays.
176 Two damselfish species contributed *ca.* 80% of all bites to the EAM: *Pomacentrus*
177 *chrysurus* (~50 %) and *P. littoralis* (~30%). In addition, the wrasse *Halichoeres*
178 *melanurus* took a further 10% of all bites within the EAM (Fig. 6). There were no
179 significant differences among sites in the assemblage of fishes observed feeding on
180 the EAM assays (Pseudo- $F_{2,3} = 2.15$, $p = 0.07$) and no differences among days
181 (Pseudo- $F_{3,6} = 1.03$, $p = 0.45$).

182 Coral cover was positively related to herbivorous fish biomass (LRT Chi-
183 square = 4.35, $df = 1$, $p = 0.04$), however there was no relationship between the
184 percentage cover of macroalgae and herbivorous fish biomass (LRT Chi-square =
185 2.48, $df = 1$, $p = 0.12$). Sea-urchin densities were not related with cover of either
186 corals (LRT Chi-square = 1.80, $df = 1$, $p = 0.18$) or macroalgae (LRT Chi-square =
187 0.06, $df = 1$, $p = 0.81$)(Fig. 7).

188

189 Discussion

190

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

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

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

213 Mean macroalgal cover (~8%) on surveyed reefs, on the other hand, was
214 comparable to that reported for reef crests and slopes of the Outer Central GBR but
215 much lower than that on inner central GBR reefs (Wismer et al. 2009). For example,
216 average cover of macroalgae ranges from 1.7 to 15.4% on the Outer Central GBR and
217 36.2 to 66.2% on inner central GBR reefs (Wismer et al. 2009). Cover of EAM,
218 which often forms a stable and significant part of the benthos on many reefs
219 (Bellwood & Fulton 2008; Wilson et al. 2003b), varied markedly between surveys in
220 May and November. For example, average cover was ~18% in November 2011 but
221 dropped to <2% cover in May 2012. This apparent temporal variation in turf algal
222 abundance may be driven by seasonal environmental factors related to the change in
223 monsoons (e.g., Diaz-Pulido & Garzón-Ferreira 2002).

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

230 In the present study, the estimated biomass of fish herbivores ($\sim 4 \text{ g m}^{-2}$) in
231 Singapore was seven times lower than the average for Indo-Pacific reefs ($\sim 29 \text{ g m}^{-2}$)
232 (Roff & Mumby 2012). Fish herbivore biomass was up to 43 times lower than
233 relatively undisturbed reefs (e.g., Ningaloo), but similar to heavily degraded and
234 overfished reefs (e.g., Fiji) where similar studies have been conducted (Vergés et al.
235 2012; Rasher et al. 2013). The majority of herbivorous fish, in terms of biomass, were
236 macroalgal browsers, primarily from the family Siganidae. Functionally important
237 groups of herbivorous fishes such as excavating parrotfishes were absent, while
238 scraping parrotfishes were present in very low numbers. Surgeonfishes (Family
239 Acanthuridae), one of the most diverse and abundant group of herbivorous fishes in
240 coral reefs, were not recorded during our surveys.

241 No feeding by fish was observed on the macroalgal assays in Singapore, while
242 comparable studies outside of Singapore have found fish bite rates ranging from ~ 13
243 to almost 1000 bites per hour on single or mixed species algal assemblages (Vergés et
244 al. 2012). Fish bite rates on EAM were, however, within the range found for
245 comparable Indo-Pacific sites (Bennett et al. 2010; Rasher et al. 2013) but most bites
246 were taken by a single territorial damselfish species (*P. littoralis*), whereas elsewhere,
247 the majority of the fish recorded taking bites from EAM are roving herbivores
248 (e.g., *Scarus* spp., *Acanthurus* spp.)(Bennett et al. 2010; Rasher et al. 2013). In the

249 absence of historical data on fish biomass we do not know if and when herbivores
250 declined or whether certain functional groups were more abundant in the past.

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

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

270 The composition of Singapore's coral communities has undoubtedly
271 contributed to their ability to maintain relatively high levels of coral cover and resist
272 phase shifts towards macroalgal dominance. Coral communities are dominated by
273 stress tolerant and generalist taxa that can withstand high levels of sedimentation and

274 are relatively resistant to thermal stress (Guest et al. 2012; Browne et al. 2015;
275 Darling et al. 2013; Huang et al. 2009). For example, data from the present study
276 found the six most common coral genera to be *Pectinia*, *Merulina*, *Pachyseris*,
277 *Montipora*, *Echinopora* and *Platygyra* (presented in Bauman et al. 2015). Following
278 disturbances, such as coral bleaching, surviving remnant colonies from these taxa are
279 capable of rapid regrowth, allowing coral cover to return more rapidly following
280 bleaching disturbances, compared to the relatively slow process of larval recruitment
281 (Bauman et al. 2015; Guest et al. 2016). It is also possible that high coral cover in
282 Singapore has concentrated the efforts of herbivory to a relatively smaller area,
283 making lower rates of herbivory more effective at removing macroalgae (Williams et
284 al. 2001).

285 Physical factors (e.g., light and sedimentation) may also be playing an
286 important role in structuring the distribution of corals and algae on these reefs. Light
287 attenuates rapidly in Singapore's sediment-rich coastal waters, leading to an almost
288 50% reduction in photosynthetic efficiency of *Sargassum* spp. at the reef crest (Tun et
289 al. 1994). If algal growth is limited by light even at quite shallow depths, then
290 relatively low rates of herbivory may be sufficient to prevent macroalgae from
291 overgrowing coral dominated areas. If so, then this provides an example of an
292 "ecological surprise", where two negative impacts (increased turbidity and reduced
293 herbivory) interact antagonistically, resulting in stable shallow coral communities
294 (Paine et al. 1998). If this is the case, then management efforts to improve water
295 clarity may need to be combined with efforts to increase the biomass of key
296 functional herbivores.

297 Clearly, further studies are needed to determine the contribution that fish and
298 invertebrate herbivores play in structuring the distribution of corals and macroalgae

299 on Singapore's shallow reefs. Of particular importance are studies to identify
300 individual key functional fish species and to determine the precise role they play in
301 preventing transitions from coral to macroalgal dominance. Such information is of
302 critical importance to the future management of these highly disturbed, turbid, yet
303 remarkably diverse coral reefs.

304

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306

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309

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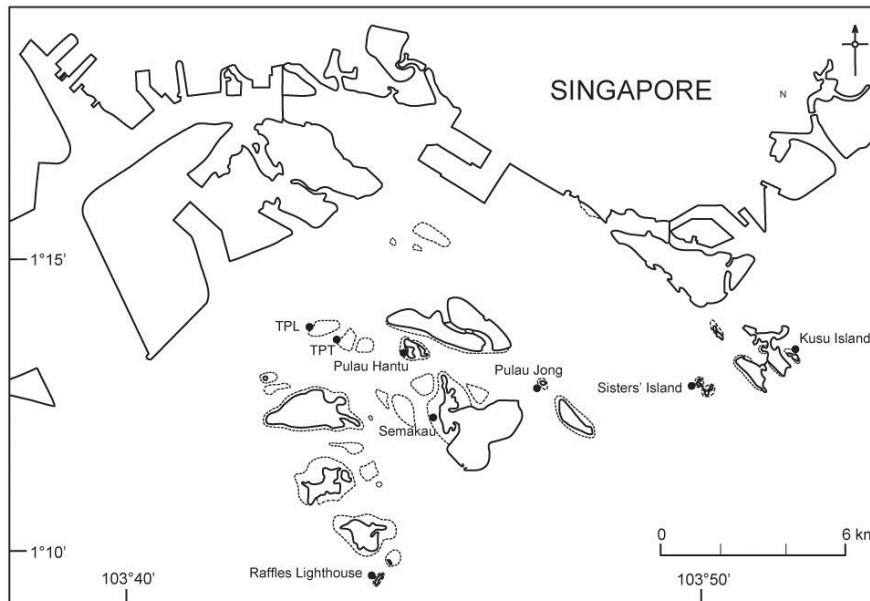
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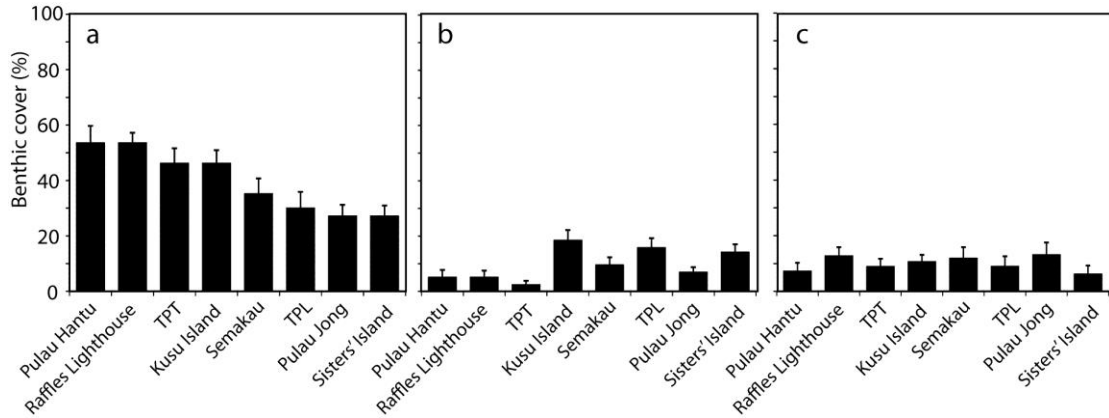
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484 Fig. 1. Map of study sites in Singapore's southern island group.

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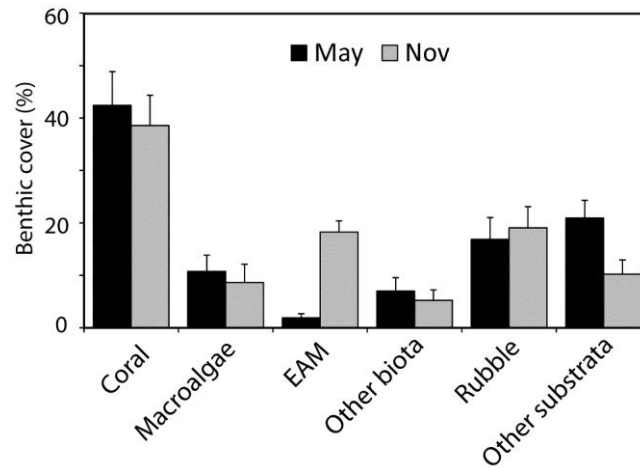


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488 Fig. 2. Bar chart showing a) mean cover of hard coral b) macroalgae and c) EAM by
489 sites (all surveys pooled). Sites are in order of decreasing mean coral cover from left
490 to right. Error bars SE.

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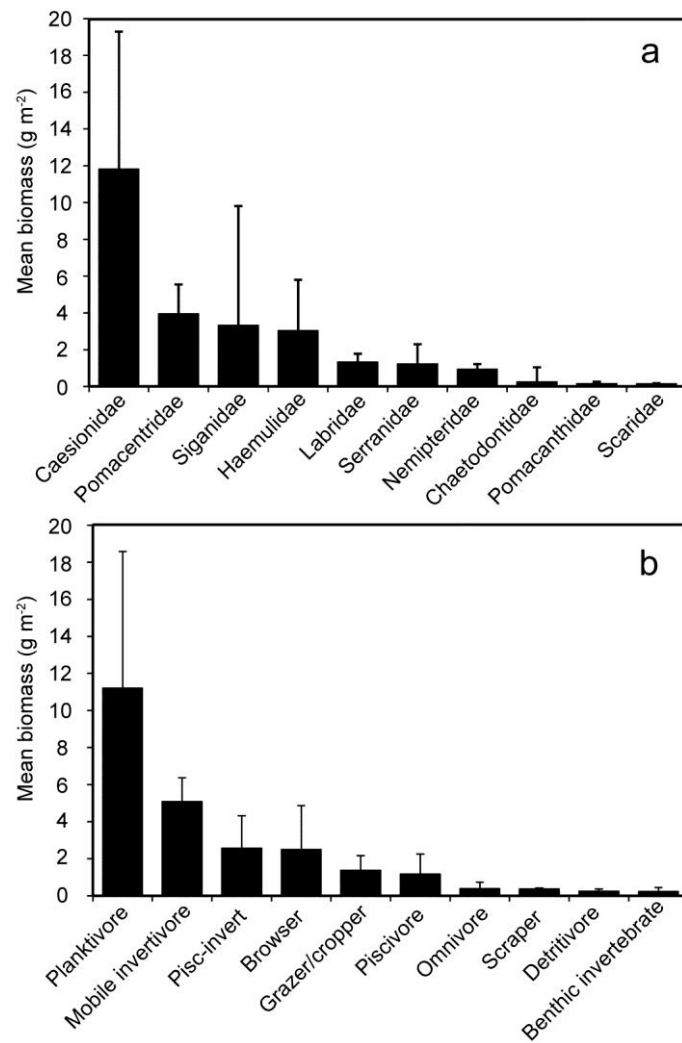
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494 Fig. 3. Bar chart showing difference in mean benthic cover between sampling months
495 of coral, macroalgae, EAM, other biota, rubble and other substrata. Error bars are SE.

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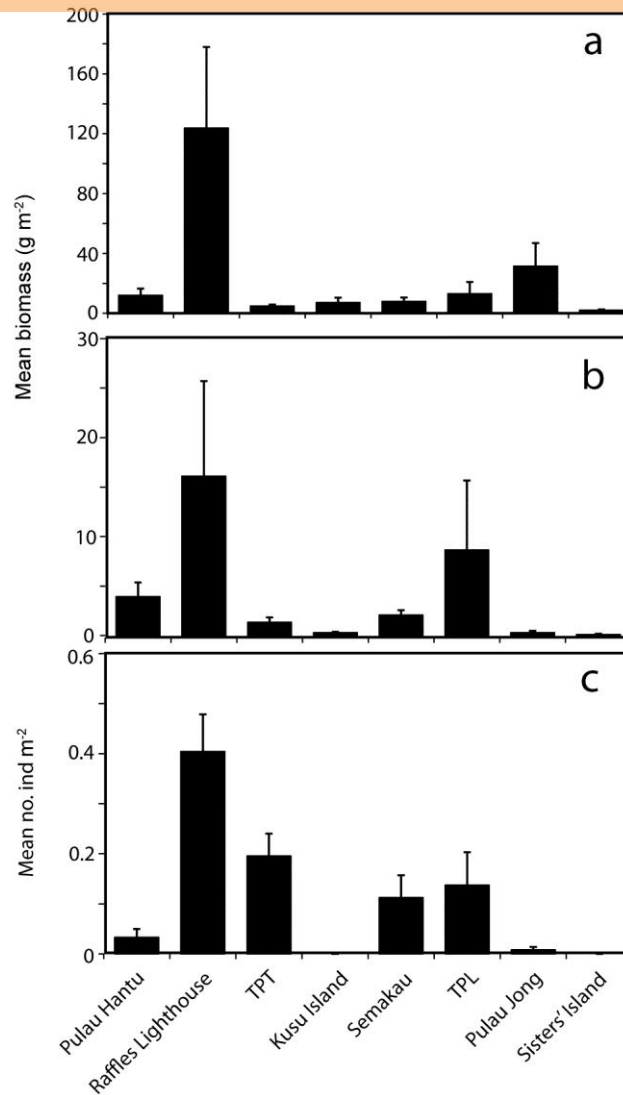
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501 Fig. 4. Bar chart showing a) average biomass of fish families (g m^{-2}) and b) fish
502 functional groups (g m^{-2}) from all surveys pooled. Error bars are SE.

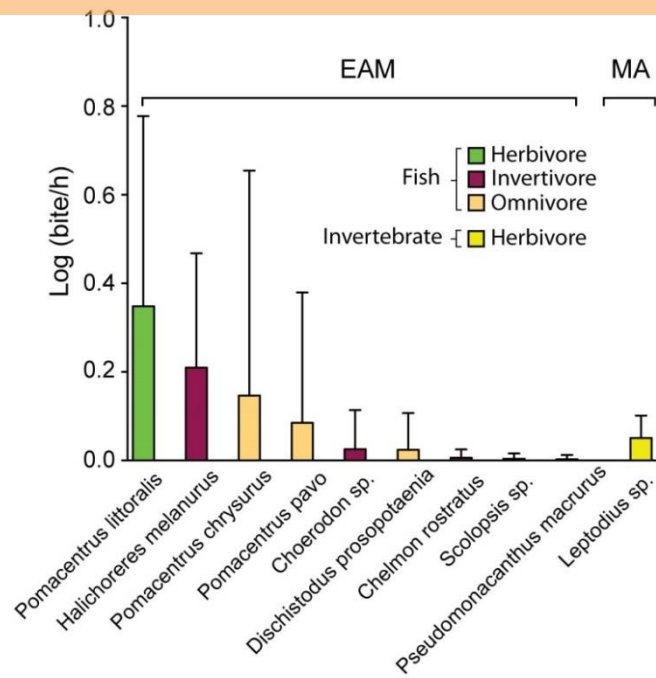


503

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

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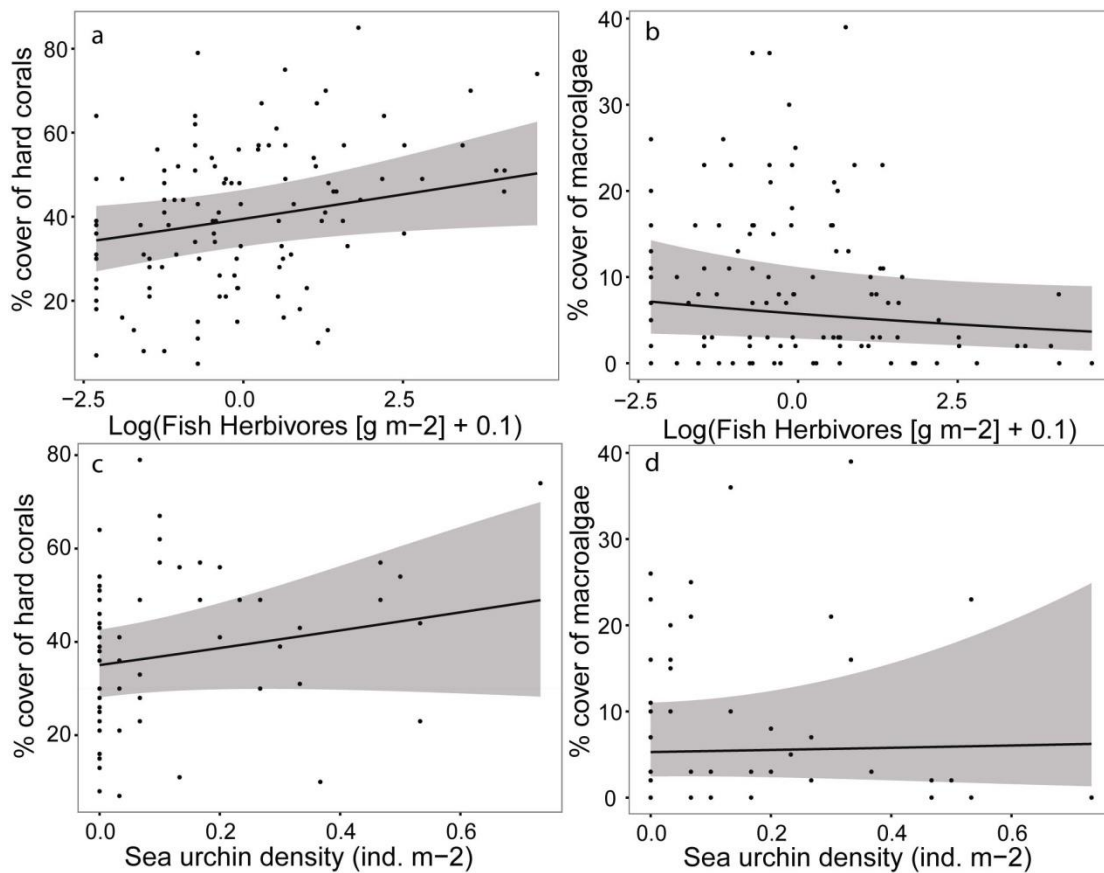
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512 Fig. 6. Bite rates by different species (mean Log bites h^{-1} +SE) on epilithic algal

513 matrix (EAM) and on tethered macroalgal (MA) species during timed video assays.

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

524 Table 1. A comparison of coral cover (%) at the upper reef slopes (3-4 m depth) of
525 eight sites in Singapore's southern islands group between surveys carried out during
526 1987-1991 and 2011-2012. Data from 1987-1991 are from Table 1 in (Chua & Chou
527 1992). The earlier surveys were carried out using the line intercept transect method on
528 a single 100 m transect at each site which differs from the method used in the present
529 study (8 × 30 m line point intercept transects). The precise location of the transects
530 were not the same between sampling periods, therefore some variation in coral cover
531 may be due to natural spatial heterogeneity.
532

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
<i>Mean</i>	<i>55.1</i>	<i>39.9</i>
<i>SD</i>	<i>15.0</i>	<i>11.3</i>

533

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 m² in Singapore and 0.3 m² in Tioman. Average number of bites is shown as bites h⁻¹m⁻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	186.53 (362.55)*	0.42 (0.41)	195.0*	67.78 No data	Bennett et al. 2010 Vergés et al 2012 Langdon 2012
Viti Levu, Fiji	39.61 (46.20)* 3.64 (23.18)	0.03 (0.02)* 0.02 (0.01)	997.41*	252.37*	Rasher et al. 2013 Bonaldo, unpublished data

