

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

James R Guest^{1*}, Adriana Vergés^{1,2,3}, Andrew G Bauman⁴, Alexandra H Campbell^{1,2,3}, Loke Ming Chou⁵, David A Feary⁶, Jeffrey KY Low⁷, Ezequiel M Marzinelli^{1,2,3}, Karenne Tun⁷, Peter D Steinberg^{1,2,3}

¹Centre for Marine Bio-Innovation, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

²Evolution & Ecology Research Centre, School of Biological, Earth and Environmental Sciences, University of New South Wales, Sydney, NSW 2052, Australia

³Sydney Institute of Marine Science, 19 Chowder Bay Rd, Mosman, NSW 2088, Australia

⁴Experimental Marine Ecology Laboratory, Department of Biological Science, National University of Singapore, 117543 Singapore

⁵Tropical Marine Science Institute, National University of Singapore, S2S, 18 Kent Ridge Road, Singapore 119227

⁶School of Life Sciences, University of Nottingham, NG7 2UH, United Kingdom

⁷National Biodiversity Centre, National Parks Board, 1 Cluny Road, Singapore Botanic Gardens, Singapore 259569

*Corresponding author

Present address: SECORE International, 40 Jalan Anjung 5, Horizon Hills, Nusajaya 79100, Johor Malaysia

Email: jrguest@gmail.com, tel: +60126160712.

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.

1 Introduction

2

3 The distribution of corals and algae on coral reefs is strongly influenced by biological
4 processes and physical conditions including herbivory, sedimentation and light
5 availability (Steneck 1988). Herbivory is one of the key processes structuring shallow
6 tropical coral communities because it moderates coral-algal interactions through the
7 removal of fleshy macroalgae or algal turfs that can overgrow or injure adult corals,
8 and/or inhibit settlement and post-settlement survival of juvenile corals (Birrell et al.
9 2005; McCook et al. 2001; Rasher & Hay 2010). Sediments also have numerous
10 effects on coral reef benthic and community structure (McClanahan & Obura 1997).
11 Suspended sediments limit light penetration and particulates interfere with biological
12 processes, such as heterotrophy in corals, and may alter rates of herbivory by fish
13 (Bellwood & Fulton 2008; Rogers 1990). Generally, increased sedimentation is
14 considered detrimental for coral health; however sediments can also be a source of
15 food for corals and may provide a degree of protection from thermal stress by
16 reducing stressful levels of irradiance (Anthony & Fabricius 2000; Cacciapaglia &
17 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 (Erfteimeijer et al.
22 2012; Rogers 1990). These disturbances, among others, have been implicated in the
23 observed global decline in reef condition, manifested as decreases in total coral cover
24 and consequent deterioration of ecological function (Pandolfi et al. 2003). The effects
25 of combined disturbances are not always additive and may in some cases be

26 antagonistic, resulting in the effect of one disturbance lessening the effect of another
27 (Darling et al. 2010).

28 Declines in ecosystem condition occur gradually in many cases, but in others,
29 a combination of disturbances results in rapid transitions from one ecosystem state to
30 another. The most widely researched of these so called phase-shifts is from
31 dominance by hard corals to dominance by fleshy macro-algae (known as a coral to
32 macroalgal phase shift) (Bruno et al. 2009; Done 1992; Hughes 1994; Hughes et al.
33 2007; McManus & Polsenberg 2004). However, transitions to other ecosystem states
34 also occur, with the type of transition influenced by local physical and biological
35 conditions (Norström et al. 2009).

36 Most of the world's reefs and the highest diversity of coral reef species occur
37 within the biogeographic region including Malaysia, the Philippines, Indonesia and
38 Papua New Guinea known as the 'coral triangle' (Hoeksema 2007). Many of the reefs
39 in this region are close to high human population densities and have experienced the
40 effects of extreme coastal development and overfishing (Burke et al. 2002). Singapore
41 (on the edge of the coral triangle) has in the span of just under 200 years undergone a
42 transformation from a sparsely populated, forest-covered island to a highly urbanised
43 city-state. The population has risen from an estimated 150 people in 1819 (Hilton &
44 Manning 1995) to >5.4 million at present (<http://www.singstat.gov.sg/home>). The
45 majority of the southern coastline and islands, where Singapore's coral reefs occur,
46 have undergone reclamation and many of the intertidal flats of the fringing and patch
47 reefs have been lost to make way for petrochemical plants, military and recreational
48 areas (Lai et al. 2015).

49 Extensive coastal development in Singapore has resulted in sedimentation
50 rates and levels of total suspended solids exceeding those considered optimal for

51 tropical reefs (Dikou, A. and van Woesik, R. 2006, Rogers, C. S. 1990, Todd, P. A. et
52 al. 2004). Average underwater visibility, thought to have been about 10 m in the
53 1960's, has decreased to around 2 m at present (Chou, L. M. 1996), and
54 eutrophication has increased at least 30 fold in the last 60 years (Gin, K. Y. H. et al.
55 2000). Erect fleshy macroalgae, particularly *Sargassum* spp. have dominated shallow
56 reef flats (~0-2 m depth) in Singapore since at least the 1970s (Chuang 1977), while
57 adjacent upper reef slopes (~3-4 m depth) are dominated by diverse coral assemblages
58 (>250 coral species) (Guest et al. 2005b; Huang et al. 2009).

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

70

71 **Methods and Materials**

72

73 In November 2011 and May 2012, surveys of benthic cover, fish biomass and urchin
74 abundance were carried out at eight haphazardly selected shallow sites within the
75 southern islands group (Fig. 1) that are being examined as part of ongoing studies of

76 ecological processes on Singapore's reefs (Bauman et al. 2015; Guest et al. 2016).
77 The eight sites were Kusu Island, Pulau Hantu, Pulau Jong, Sisters Island, Semakau,
78 Raffles Lighthouse, Terumbu Pempang Tengah (TPT) and Terumbu Pempang Laut
79 (TPL) (Fig 1). The abundances of all reef fishes and urchins were quantified at each
80 site along eight belt transects (30×2 m for fishes, 30×1 m for urchins). Due to
81 logistical constraints, urchin surveys were only conducted in November 2011. Benthic
82 community structure was quantified along the same transects using the line point
83 count method with measurements taken every 50 cm. Categories used for the benthic
84 surveys were hard coral, macroalgae, EAM, other biota (e.g., sponges, zoantharians),
85 crustose coralline algae (CCA), sand, silt, rock, recently dead coral, and
86 unconsolidated rubble. All surveyed fish were categorized into 50 mm interval size
87 classes for later conversion to biomass using species-specific growth coefficients
88 (Froese & Pauly 2014). Length to weight conversions were calculated as follows: $W =$
89 $a * L_T^b$, where W is weight in grams, L_T is total length and parameters a and b are
90 constants obtained from the literature and Fishbase (Froese & Pauly 2014).

91 Rates of herbivory were estimated by videoing (GoPro® Hero2) feeding
92 assays to count bite rates on macroalgae and epilithic algal matrix (EAM *sensu*
93 Wilson et al. 2003a) in May 2012. Video assays took place at reef crests of three
94 shallow sites (Sisters Island, Kusu Island and TPT), haphazardly selected, from the
95 eight sites used for the surveys. For the macroalgal studies, four locally common
96 species were offered simultaneously *Sargassum ilicifolium*, *Lobophora variegata*,
97 *Padina australis* and *Halimeda tuna*. In the EAM assays, video cameras were placed
98 for 2-4 h in front of EAM patches (approx. 0.2 m^2) naturally clear of dominant
99 macrophytes and characterized by 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. All macroalgae
105 were collected from Pulau Tekukor. Quadrats of known area were placed in front of
106 each EAM camera at the beginning of filming for a few seconds to provide a spatial
107 scale, and so that bites could later be converted to bites cm^{-2} . To maximise
108 independence among replicates, we separated individual replicate assays by at least 5
109 m, and we positioned replicates in a different location every day within each site to
110 ensure independence among days. Video footage was analysed by counting the
111 number of bites per hour taken by individual fishes on either macroalgae or the EAM.
112 A video camera fault caused us to lose one replicate from the macroalgae assays on
113 one of the days. Total hours of footage viewed were 28.2 h and 36.5 h for macroalgae
114 and EAM assays, respectively.

115

116 *Data analysis*

117

118 The relationship between current coral and macroalgal benthic cover (as proportions);
119 and biomass of fish (g m^{-2} ; $\log[x+0.1]$ transformed) and abundance of urchins
120 (number of individuals m^{-2}) was examined among the eight shallow sites used for the
121 herbivory studies using Generalised Linear Mixed Models (GLMM) assuming a
122 binomial distribution, with sites as random effects (Zuur et al. 2009). Because fish
123 were surveyed twice (in Nov 2011 and May 2012), time was also fitted as a random
124 effect for analyses of relationships between coral/macroalgal cover and fish biomass.

125 Analyses were carried out using the glmmADMB package in R, with the betabinomial
126 family to account for overdispersion (Fournier et al. 2012; Skaug et al. 2012). To
127 determine spatial and temporal multivariate differences among the assemblages of
128 fishes feeding on the algal assays we used a two-way permutational analysis of
129 variance (PERMANOVA) with the following factors: Site (3 levels, random), and day
130 (2 levels, random, nested within site). We used Bray-Curtis distance as our metric in
131 these multivariate analyses. This was only done for the EAM assays as no fish were
132 observed to feed on macroalgae during our assays (see Results).

133

134 **Results**

135

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

150 The mean total biomass of fish across (all surveys pooled) was 26.6 g m^{-2} (SD
151 $\pm 42.4 \text{ g m}^{-2}$). Nearly 50% of the total fish biomass consisted of planktivores,
152 primarily fusiliers (f. Caesionidae) with only ~16% of the biomass ($4.4 \text{ SD} \pm 6.5 \text{ g m}^{-2}$)
153 comprised of herbivorous fishes (Fig.4a). Browsers within the family Siganidae
154 were the most dominant of the functional herbivore groups (~10% of fish biomass).
155 Scrapers (<1% of fish biomass) were rare, and no excavators were observed.
156 Parrotfish were rare (1% of the fish biomass) and no acanthurids were observed (Fig.
157 4b). Among sites and years, total fish biomass ranged from 2.7 g m^{-2} to 137.3 g m^{-2} ,
158 whereas biomass of fish herbivores ranged from 0.1 g m^{-2} to 20.8 g m^{-2} (Fig. 5).
159 Estimated fish herbivore biomass in Singapore is between ~2 and 43 times lower than
160 that at other Indo-Pacific reef sites with similarly high coral and low macroalgal
161 cover, but similar to that found on heavily overfished and degraded reef flats (e.g.,
162 Fiji) (Table 1). Average urchin abundance across all sites was $0.10 \text{ individuals m}^{-2}$
163 ($\text{SD} \pm 0.17 \text{ individuals m}^{-2}$), of which >99% were *Diadema setosum* (Fig. 5c). Urchin
164 abundances in Singapore are within the range found on comparable Indo-Pacific reefs
165 (Table 1).

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

175 Coral cover was positively related to herbivorous fish biomass (LRT Chi-
176 square = 4.35, $df = 1$, $p = 0.04$), however there was no relationship between the
177 percentage cover of macroalgae and herbivorous fish biomass (LRT Chi-square =
178 2.48, $df = 1$, $p = 0.12$). Sea-urchin densities were not related with cover of either
179 corals (LRT Chi-square = 1.80, $df = 1$, $p = 0.18$) or macroalgae (LRT Chi-square =
180 0.06, $df = 1$, $p = 0.81$)(Fig. 7).

181

182 Discussion

183

184 Coral cover has declined markedly on reefs worldwide in recent decades as a direct
185 result of increased anthropogenic disturbances and changes in environmental
186 conditions due to climate change (Bruno & Selig 2007). Singapore has lost much of
187 its original reef area (an estimated 60%) to coastal reclamation (Lai et al. 2015).
188 However, despite decades of anthropogenic impacts, Singapore's remaining shallow
189 reefs appear to have maintained relatively high levels of coral cover (~40%)
190 compared to current levels found in the broader Indo-Pacific region (Bruno & Selig
191 2007; De'ath et al. 2012). For example, average coral cover for the Great Barrier Reef
192 (GBR) (De'ath et al. 2012); 214 reefs surveyed over 27 y) and the wider Indo-Pacific
193 region (Bruno & Selig 2007); 390 reefs surveyed in 2003) is ~22 to 23% of the total
194 benthos.

195 Mean macroalgal cover in Singapore (~8%) was comparable to that reported
196 for reef crests and slopes of the Outer Central GBR but much lower than that on inner
197 central GBR reefs (Wismer et al. 2009). For example, average cover of macroalgae
198 ranges from 1.7 to 15.4% on the Outer Central GBR and 36.2 to 66.2% on inner
199 central GBR reefs (Wismer et al. 2009). EAM may form a stable and significant part

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

204 Surveys carried out at reef crests at 65 sites around Singapore's southern
205 island group between 1987 and 1991 found average coral cover to be similar to the
206 present study at 43.0% (SD \pm 19.1%)(Chua & Chou 1992). However, when we
207 compared data just from the eight sites used in the present study we found that
208 average cover at these sites has declined by ~15% since the surveys carried out in
209 1987. The precise cause of these declines not known, but we suggest that deterioration
210 in water quality due to coastal development and dredging activities and two thermal
211 bleaching episodes (in 1998 and 2010)(Guest et al. 2012) have made the greatest
212 contribution.

213 Herbivory is critically important in the prevention of phase shifts from coral to
214 algal dominance on reefs (Hughes et al. 2007). Estimates of herbivorous fish biomass
215 from underwater visual censuses can be strong predictors of grazing intensity on coral
216 reefs (Mumby 2006). In the present study, however, the estimated biomass of fish
217 herbivores ($\sim 4 \text{ g m}^{-2}$) in Singapore was seven times lower than the average for Indo-
218 Pacific reefs ($\sim 29 \text{ g m}^{-2}$) (Roff & Mumby 2012). Functionally important groups of
219 herbivorous fishes such as excavating parrotfishes were absent, while scraping
220 parrotfishes were present in very low numbers. Surgeonfishes (Family Acanthuridae),
221 one of the most diverse and abundant group of herbivorous fishes in coral reefs, were
222 not recorded during our surveys. No feeding by fish was observed on the macroalgal
223 assays in Singapore, while comparable studies outside of Singapore have found fish
224 bite rates ranging from ~13 to almost 1000 bites per hour on single or mixed species

225 algal assemblages (Vergés et al. 2012). Fish bite rates on EAM were, however, within
226 the range found for comparable Indo-Pacific sites (Bennett et al. 2010; Rasher et al.
227 2013) but most bites were taken by a single territorial damselfish species (*P.*
228 *littoralis*), whereas elsewhere, the majority of the fish recorded taking bites from
229 EAM are roving herbivores (e.g., *Scarus* spp., *Acanthurus* spp.)(Bennett et al. 2010;
230 Rasher et al. 2013).

231 The significant (albeit weak) relationship between coral cover and fish
232 herbivore biomass suggests either a functional role for fish in maintaining high cover
233 or for coral cover in maintaining high fish biomass at some sites, or that herbivorous
234 fishes are responding to some other factor (e.g., turbidity, sedimentation) that
235 is collinear with coral cover (Wismer et al. 2009). Nonetheless, the low rates of
236 herbivory found here strongly suggest that in addition to herbivory, other mechanisms
237 may be as important on these turbid reefs in preventing a shift away from coral
238 dominance and towards macroalgal dominance.

239 The composition of Singapore's coral communities has undoubtedly
240 contributed to their apparent resilience. Coral communities are dominated by stress
241 tolerant and generalist taxa that can withstand relatively high levels of sedimentation
242 and are relatively resistant to thermal stress (e.g., *Merulina* spp., *Platygyra* etc.)
243 (Bauman et al. 2015; Browne et al. 2015; Darling et al. 2013; Huang et al. 2009).
244 Following disturbances such as coral bleaching, surviving remnants colonies from
245 these taxa are capable of rapid regrowth. This may allow coral cover to recover
246 rapidly following bleaching disturbances, because recovery is not dependent on the
247 relatively slow process of larval recruitment (Bauman et al. 2015; Guest et al. 2016).

248 Physical factors (e.g., light and sedimentation) may also play an important role
249 in structuring the distribution of corals and algae on these reefs. Light attenuates

250 rapidly in Singapore's sediment-rich coastal waters, leading to an almost 50%
251 reduction in photosynthetic efficiency of *Sargassum* at the reef crest (Tun et al. 1994).
252 If algal growth is limited by light even at quite shallow depths, then relatively low
253 rates of herbivory may be sufficient to prevent macroalgae and/or algal turfs from
254 overgrowing coral dominated areas. If so, then this provides an example of an
255 "ecological surprise", where two negative impacts (increased turbidity and reduced
256 herbivory) interact antagonistically, resulting in stable shallow coral communities
257 (Paine et al. 1998).

258 Clearly, further studies are needed to understand the role of herbivores in
259 structuring these heavily impacted reefs. It is likely, due to the relatively poor
260 underwater visibility (typically ~2 m), that certain important herbivorous fish were
261 missed during surveys, indeed the importance of occasional roving herbivores are
262 known to be underestimated when using visual fish census methods (Hoey &
263 Bellwood 2010). Although we lack information about diel activity patterns of urchins
264 on Singapore's reefs, the dominant sea urchin in Singapore - *Diadema setosum* – is
265 known to be a nocturnal feeder (Muthiga et al. 2007). We cannot therefore rule out
266 the possibility that our video assays underestimated algal consumption rates by
267 urchins and other nocturnal herbivores. Furthermore, in the absence of historical data
268 on fish biomass we do not know if and when herbivores declined or whether certain
269 functional groups were more abundant in the past.

270 Degradation does not always occur gradually and phase shifts tend to occur
271 when a system has reached a tipping point (Hughes et al. 2010). Despite declines in
272 coral cover since surveys in the 1980s, the fact that many of Singapore's shallow reef
273 communities have remained in a coral dominated state for almost the last three
274 decades does not mean that they will remain this way indefinitely. Furthermore,

275 despite relatively high coral cover and diversity, Singapore's reefs may have lost
276 much of their value in terms of ecological goods and services (e.g., diving tourism,
277 commercial fishing). Therefore urbanized, turbid reefs, such as the ones studied here,
278 may maintain high ecological value but low socio-economic value as they contribute
279 little to the nation's tourism industry and food security. Nonetheless, urbanised coral
280 reefs form an important part of the country's natural and ecological heritage and thus
281 deserve effective management and protection.

282

283 **Acknowledgements**

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

286

287

288 **References**

289

290 Anthony KR, and Fabricius KE. 2000. Shifting roles of heterotrophy and autotrophy
291 in coral energetics under varying turbidity. *Journal of Experimental Marine*
292 *Biology and Ecology* 252:221-253.

293 Bauman AG, Guest JR, Dunshea G, Low J, Todd PA, and Steinberg PD. 2015. Coral
294 Settlement on a Highly Disturbed Equatorial Reef System. *PLOS ONE*
295 10:e0127874.

296 Bellwood DR, and Fulton CJ. 2008. Sediment-mediated suppression of herbivory on
297 coral reefs: Decreasing resilience to rising sea-levels and climate change?
298 *Limnology and Oceanography* 53:2695-2701.

299 Bennett S, Vergés A, and Bellwood D. 2010. Branching coral as a macroalgal refuge
300 in a marginal coral reef system. *Coral Reefs* 29:471-480.

301 Birrell CL, McCook LJ, and Willis BL. 2005. Effects of algal turfs and sediment on
302 coral settlement. *Marine Pollution Bulletin* 51:408-414.

303 Browne NK, Tay JK, Low J, Larson O, and Todd PA. 2015. Fluctuations in coral
304 health of four common inshore reef corals in response to seasonal and
305 anthropogenic changes in water quality. *Marine Environmental Research*
306 105:39-52.

307 Bruno JF, and Selig ER. 2007. Regional decline of coral cover in the Indo-Pacific:
308 timing, extent, and subregional comparisons. *PLOS ONE* 2:e711.

309 Bruno JF, Sweatman H, Precht WF, Selig ER, and Schutte VG. 2009. Assessing
310 evidence of phase shifts from coral to macroalgal dominance on coral reefs.
311 *Ecology* 90:1478-1484.

312 Burke L, Selig E, and Spalding M. 2002. *Reefs at Risk in Southeast Asia*: World
313 Resources Institute.

314 Cacciapaglia C, and Woesik R. 2015. Climate-change refugia: shading reef corals by
315 turbidity. *Global Change Biology*.

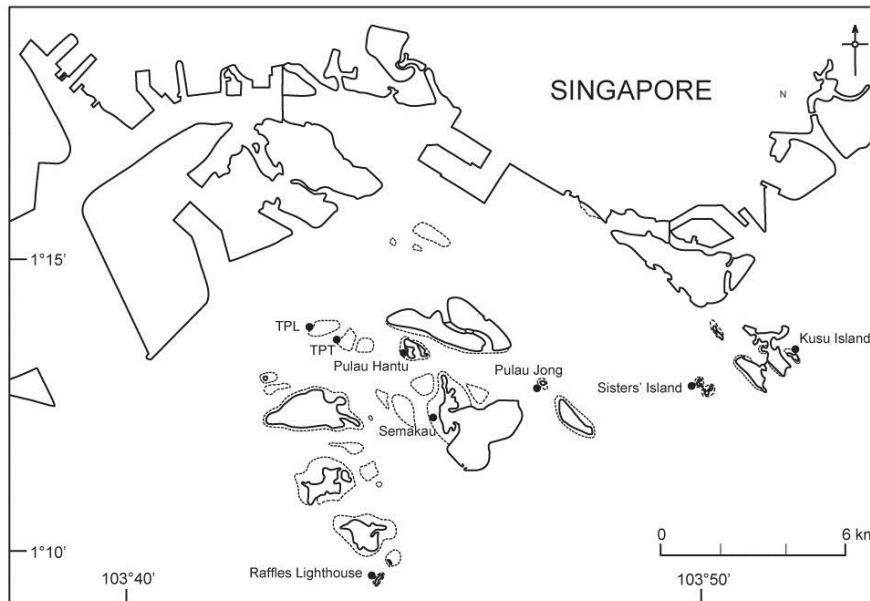
- 316 Chua CY, and Chou L. 1992. Coral reef conservation in Singapore-a case for
317 integrated coastal area management. Third ASEAN science and technology
318 week conference proceedings. p 437-445.
- 319 Chuang S-H. 1977. Ecology of Singapore and Malayan coral reefs-preliminary
320 classification. In: Taylor DL, editor. Proc Third Int Coral Reef Symp. Miami.
321 p 545-561.
- 322 Darling ES, McClanahan TR, and Côté IM. 2010. Combined effects of two stressors
323 on Kenyan coral reefs are additive or antagonistic, not synergistic.
324 *Conservation Letters* 3:122-130.
- 325 Darling ES, McClanahan TR, and Côté IM. 2013. Life histories predict coral
326 community disassembly under multiple stressors. *Global Change Biology*
327 19:1930-1940.
- 328 De'ath G, Fabricius KE, Sweatman H, and Puotinen M. 2012. The 27-year decline of
329 coral cover on the Great Barrier Reef and its causes. *Proceedings of the*
330 *National Academy of Sciences* 109:17995-17999.
- 331 Dikou A, and van Woesik R. 2006. Survival under chronic stress from sediment load:
332 Spatial patterns of hard coral communities in the southern islands of
333 Singapore. *Marine Pollution Bulletin* 52:7-21.
- 334 Done TJ. 1992. Phase shifts in coral reef communities and their ecological
335 significance. *The Ecology of Mangrove and Related Ecosystems*. Netherlands:
336 Springer, 121-132.
- 337 Edwards CB, Friedlander A, Green A, Hardt M, Sala E, Sweatman H, Williams I,
338 Zgliczynski B, Sandin S, and Smith J. 2014. Global assessment of the status of
339 coral reef herbivorous fishes: evidence for fishing effects. *Proceedings of the*
340 *Royal Society of London B: Biological Sciences* 281:20131835.
- 341 English SS, Wilkinson CC, and Baker VV. 1994. *Survey manual for tropical marine*
342 *resources*. Townsville, Australia: Australian Institute of Marine Science
343 (AIMS).
- 344 Erfteimeijer PL, Riegl B, Hoeksema BW, and Todd PA. 2012. Environmental impacts
345 of dredging and other sediment disturbances on corals: a review. *Marine*
346 *Pollution Bulletin* 64:1737-1765.
- 347 Fournier DA, Skaug HJ, Ancheta J, Ianelli J, Magnusson A, Maunder MN, Nielsen A,
348 and Sibert J. 2012. AD Model Builder: using automatic differentiation for
349 statistical inference of highly parameterized complex nonlinear models.
350 *Optimization Methods and Software* 27:233-249.
- 351 Froese R, and Pauly D. 2014. Fishbase. World Wide Web electronic publication.
352 www.fishbase.org, version (04/2014). Available at www.fishbase.org.
- 353 Guest J, Low J, Tun K, Wilson B, Ng C, Raingard D, Ulstrup K, Tanzil J, Todd P,
354 and Toh T. 2016. Coral community response to bleaching on a highly
355 disturbed reef. *Scientific Reports* 6.
- 356 Guest JR, Baird AH, Goh BPL, and Chou LM. 2005a. Reproductive seasonality in an
357 equatorial assemblage of scleractinian corals. *Coral Reefs* 24:112-116.
- 358 Guest JR, Baird AH, Goh BPL, and Chou LM. 2005b. Seasonal reproduction in
359 equatorial reef corals. *Invertebrate Reproduction and Development* 48:207-
360 218.
- 361 Guest JR, Baird AH, Maynard JA, Muttaqin E, Edwards AJ, Campbell SJ, Yewdall
362 K, Affendi YA, and Chou LM. 2012. Contrasting patterns of coral bleaching
363 susceptibility in 2010 suggest an adaptive response to thermal stress. *PLOS*
364 *ONE* 7:e33353.

- 365 Hilton MJ, and Manning SS. 1995. Conversion of coastal habitats in Singapore:
366 indications of unsustainable development. *Environmental Conservation*
367 22:307-322.
- 368 Hoeksema BW. 2007. Delineation of the Indo-Malayan centre of maximum marine
369 biodiversity: the Coral Triangle. *Biogeography, time, and place: distributions,*
370 *barriers, and islands.* Netherlands: Springer, 117-178.
- 371 Hoey AS, and Bellwood DR. 2010. Among-habitat variation in herbivory on
372 Sargassum spp. on a mid-shelf reef in the northern Great Barrier Reef. *Marine*
373 *Biology* 157:189-200.
- 374 Huang DW, Tun KPP, Chou LM, and Todd PA. 2009. An Inventory of zooxanthellate
375 scleractinian corals in Singapore including 33 new records. *THE RAFFLES*
376 *BULLETIN OF ZOOLOGY* Supp 22:69-80.
- 377 Hughes TP. 1994. Catastrophes, phase shifts and large-scale degradation of a
378 Caribbean coral reef. *Science* 265:1-23.
- 379 Hughes TP, Graham NA, Jackson JB, Mumby PJ, and Steneck RS. 2010. Rising to
380 the challenge of sustaining coral reef resilience. *Trends in Ecology &*
381 *Evolution* 25:633-642.
- 382 Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook
383 L, Moltschaniwskyj N, Pratchett MS, Steneck RS, and Willis B. 2007. Phase
384 shifts, herbivory, and the resilience of coral reefs to climate change. *Current*
385 *Biology* 17:360-365.
- 386 Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ,
387 Bradbury RH, Cooke R, Erlandson J, and Estes JA. 2001. Historical
388 overfishing and the recent collapse of coastal ecosystems. *Science* 293:629-
389 637.
- 390 Lai S, Loke LH, Hilton MJ, Bouma TJ, and Todd PA. 2015. The effects of
391 urbanisation on coastal habitats and the potential for ecological engineering: A
392 Singapore case study. *Ocean & Coastal Management* 103:78-85.
- 393 McClanahan T, and Obura D. 1997. Sedimentation effects on shallow coral
394 communities in Kenya. *Journal of Experimental Marine Biology and Ecology*
395 209:103-122.
- 396 McCook LJ, Jompa J, and Diaz-Pulido G. 2001. Competition between corals and
397 algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs*
398 19:400-417.
- 399 McManus JW, and Polsenberg JF. 2004. Coral-algal phase shifts on coral reefs:
400 ecological and environmental aspects. *Progress in Oceanography* 60:263-279.
- 401 Mumby PJ. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of
402 Caribbean coral reefs. *Ecological Applications* 16:747-769.
- 403 Muthiga N, McClanahan T, and Lawrence J. 2007. Ecology of Diadema. *Edible Sea*
404 *Urchins: Biology and Ecology*:205-225.
- 405 Norström AV, Nyström M, Lokrantz J, and Folke C. 2009. Alternative states on coral
406 reefs: beyond coral-macroalgal phase shifts. *Mar Ecol Prog Ser* 376:295-306.
- 407 Paine RT, Tegner MJ, and Johnson EA. 1998. Compounded perturbations yield
408 ecological surprises. *Ecosystems* 1:535-545.
- 409 Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle
410 D, McClenachan L, Newman MJH, Paredes G, Warner RR, and Jackson JBC.
411 2003. Global trajectories of the long-term decline of coral reef ecosystems.
412 *Science* 301:955-958.

- 413 Rasher DB, and Hay ME. 2010. Chemically rich seaweeds poison corals when not
414 controlled by herbivores. *Proceedings of the National Academy of Sciences*
415 107:9683-9688.
- 416 Rasher DB, Hoey AS, and Hay ME. 2013. Consumer diversity interacts with prey
417 defenses to drive ecosystem function. *Ecology* 94:1347-1358.
- 418 Roff G, and Mumby PJ. 2012. Global disparity in the resilience of coral reefs. *Trends*
419 *in Ecology & Evolution* 27:404-413.
- 420 Rogers CS. 1990. Responses of coral reefs and reef organisms to
421 sedimentation. *Marine Ecology Progress Series* 62:185-202.
- 422 Skaug H, Fournier D, Nielsen A, Magnusson A, and Bolker B. 2012. Package
423 glmmADMB: generalized linear mixed models using AD Model Builder. R
424 package version 0.7. 3. See ht tp. *r-forge r-project org/projects/glmmadmb*.
- 425 Steneck R. 1988. Herbivory on coral reefs: a synthesis. Proc 6th Int Coral Reef Symp.
426 p 37-49.
- 427 Tun K, Cheshire A, and Chou L. 1994. Photosynthetic production of the macroalgae
428 Sargassum and the seagrass Enhalus. In: Sudara S, Wilkinson CR, and Chou
429 LM, editors. Proceedings, Third ASEAN-Australia Symposium on Living
430 Coastal. Bangkok, Thailand: Chulalongkorn University. p 281-286.
- 431 Vergés A, Bennett S, and Bellwood DR. 2012. Diversity among macroalgae-
432 consuming fishes on coral reefs: a transcontinental comparison. *PLOS ONE*
433 7:e45543.
- 434 Wilson SK, Bellwood DR, Choat JH, and Furnas MJ. 2003a. Detritus in the epilithic
435 algal matrix and its use by coral reef fishes. In: Atkinson RJA, and Gibson
436 RN, eds. *Oceanography and Marine Biology, An Annual Review*. Oxford,
437 U.K.: Taylor & Francis, 279-309.
- 438 Wilson SK, Bellwood DR, Choat JH, and Furnas MJ. 2003b. Detritus in the epilithic
439 algal matrix and its use by coral reef fishes. *Oceanography and Marine*
440 *Biology* 41:279-310.
- 441 Wismer S, Hoey A, and Bellwood DR. 2009. Cross-shelf benthic community
442 structure on the Great Barrier Reef: relationships between macroalgal cover
443 and herbivore biomass. *Marine Ecology Progress Series* 376:45-54.
- 444 Zuur AF, Ieno EN, Walker NJ, Saveliev AA, and Smith GM. 2009. *Mixed effects*
445 *models and extensions in ecology with R*: Springer, New York.
- 446

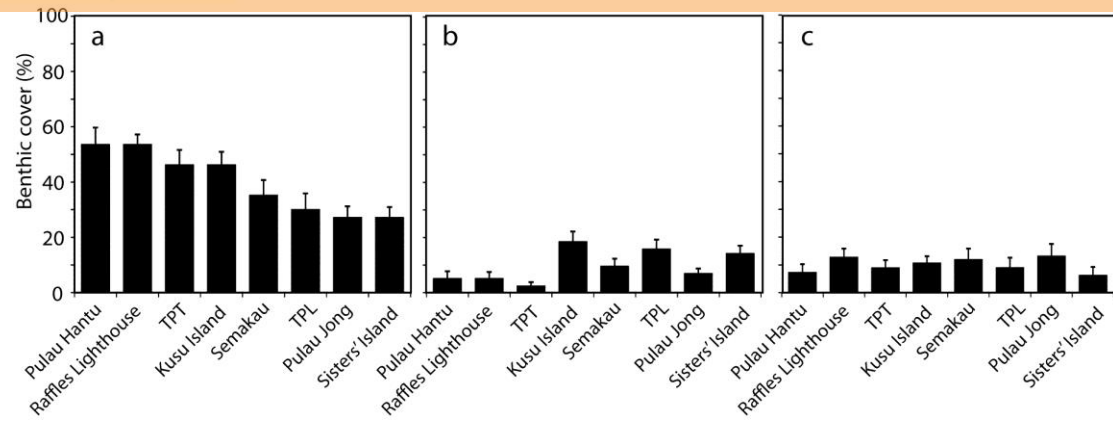
447

448



449

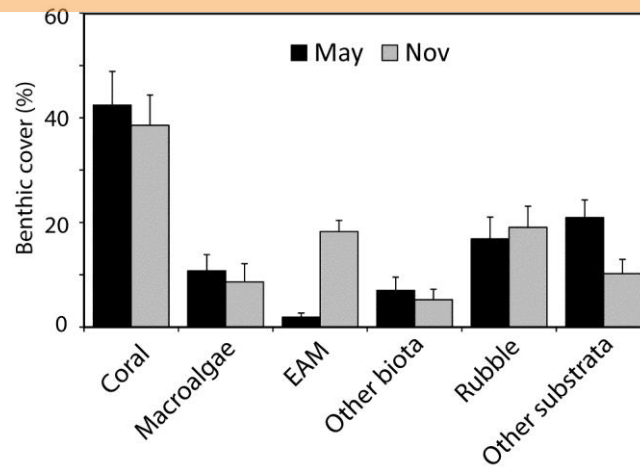
450 Fig. 1. Map of study sites in Singapore's southern island group.



451

452

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



456

457

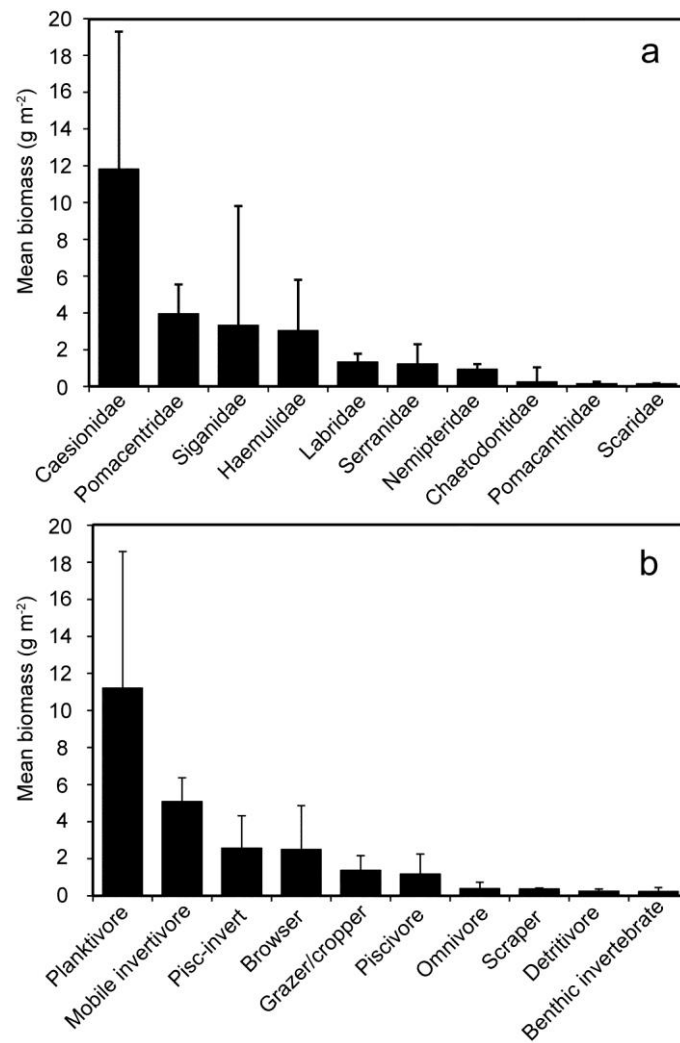
458 Fig. 3. Bar chart showing difference in mean benthic cover between sampling months

459 of coral, macroalgae, EAM, other biota, rubble and other substrata. Error bars are SE.

460

461

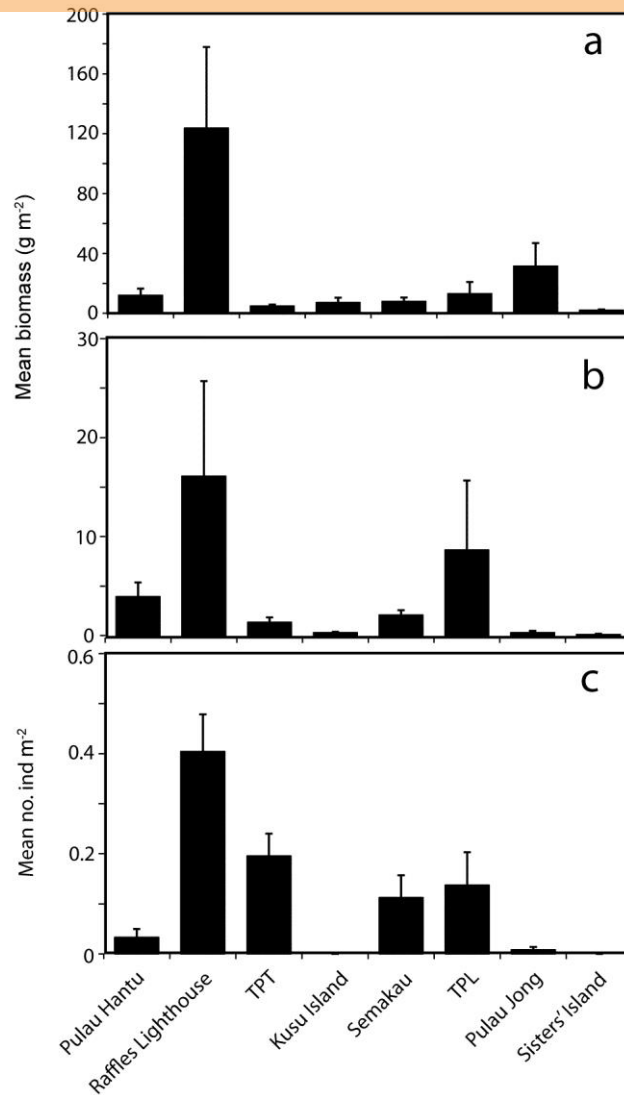
462



463

464

465 Fig. 4. Bar chart showing a) average biomass of fish families (g m⁻²) and b) fish
466 functional groups (g m⁻²) from all surveys pooled. Error bars are SE.



467

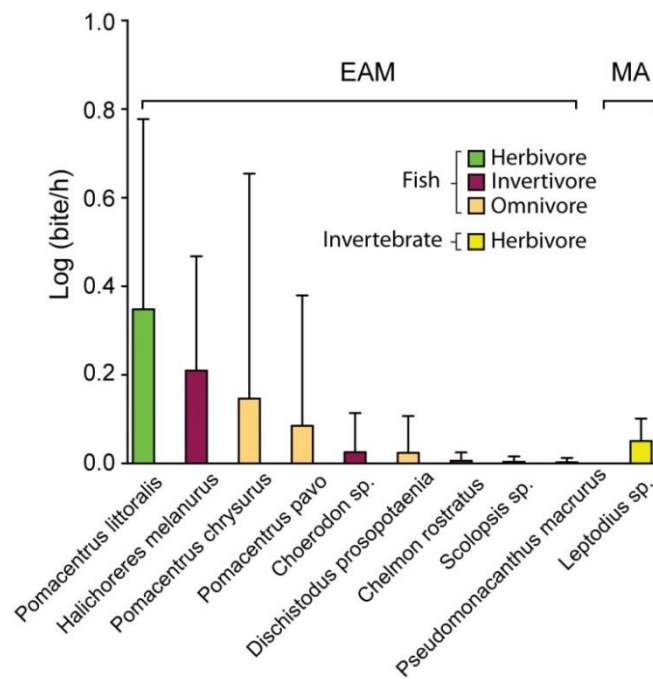
468 Fig. 5. Bar chart showing differences among sites in a) average biomass of all fish, b)

469 herbivorous fish (g m⁻²) and c) urchins (ind. m⁻²) from all surveys pooled. Error bars

470 are SE.

471

472



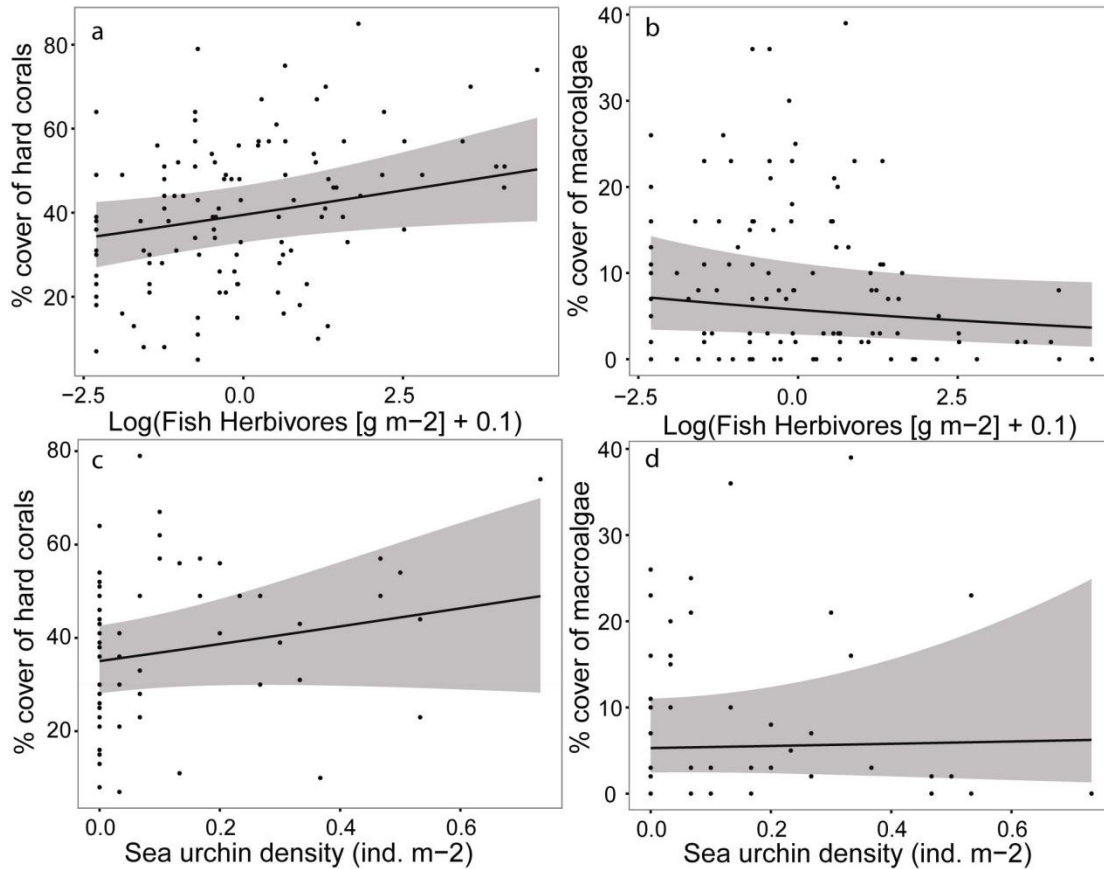
473

474

475 Fig. 5. Bite rates by different species (mean Log bites h^{-1} +SE) on epilithic algal matrix
 476 (EAM) and on tethered macroalgal (MA) species during timed video assays.

477

478



479

480

481 Fig. 6. The relationship between a) hard coral cover and fish herbivore abundance, b)
482 macroalgal cover and fish herbivore abundance, c) hard coral cover and urchin
483 density and d) macroalgal cover and urchin density among eight Singaporean reef
484 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 $\sim 0.2 \text{ m}^2$ in Singapore and 0.3 m^2 in Tioman. Average number of bites is shown as bites $\text{h}^{-1}\text{m}^{-2}$ for comparison across sites.

Location	Mean herbivorous fish biomass (g m^{-2})	Mean abundance of herbivorous sea urchins (ind m^{-2})	Total number of bites on macroalgae (bites h^{-1})	Total number of bites on EAM ($\text{bites h}^{-1}\text{m}^{-2}$)	Reference
Singapore	4.3 (8.2)	0.10 (0.13)	0	109.27	Present study
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	13.4		Vergés et al 2012
Australia				67.78	Bennett et al. 2010
Ningaloo, Western Australia	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)* 3.64 (23.18)		997.41*	252.37*	Rasher et al. 2013
		0.03 (0.02)* 0.02 (0.01)			Bonaldo, unpublished data

