

Caribbean reef trajectories dominated by rapidly increasing macroalgal cover

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Long-term phase shifts from coral to macroalgal dominated reef systems are well-documented in the Caribbean. Although the impact of coral diseases, climate change and other factors is acknowledged, major herbivore loss through disease and overfishing is often assigned a primary role. However, direct evidence for the link between herbivore abundance, macroalgal and coral cover is sparse, particularly over broad spatial scales. In this study we use a database of coral reef surveys performed at 85 sites along the Mesoamerican Reef of Mexico, Belize, Guatemala and Honduras, to examine potential ecological links by tracking site trajectories over the period 2005-2014. We found increasing fleshy macroalgal cover to be pervasive. Herbivorous fish populations were not responsible for this trend: fleshy macroalgal cover change was not correlated with herbivorous fish biomass levels or change, and the majority of sites experienced increases in macroalgae browser biomass. This suggests the role of external factors such as terrestrial nutrient run-off in providing algae-favourable conditions. However, herbivorous fish, in addition to marine protection, had a positive impact on hard coral cover, which increased over the observation period, while coral cover trends were unrelated to macroalgal cover. This implicates the presence of alternative mechanisms such as reduced competitive pressure, disease prevalence, and physical damage benefiting coral communities.

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2 **macroalgal cover**

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15

16 Abstract

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18 documented in the Caribbean. Although the impact of coral diseases, climate change
19 and other factors is acknowledged, major herbivore loss through disease and
20 overfishing is often assigned a primary role. However, direct evidence for the link
21 between herbivore abundance, macroalgal and coral cover is sparse, particularly over
22 broad spatial scales. In this study we use a database of coral reef surveys performed at
23 85 sites along the Mesoamerican Reef of Mexico, Belize, Guatemala and Honduras, to
24 examine potential ecological links by tracking site trajectories over the period 2005-
25 2014. We found increasing fleshy macroalgal cover to be pervasive. Herbivorous fish
26 populations were not responsible for this trend: fleshy macroalgal cover change was not
27 correlated with herbivorous fish biomass levels or change, and the majority of sites
28 experienced increases in macroalgae browser biomass. This suggests the role of
29 external factors such as terrestrial nutrient run-off in providing algae-favourable
30 conditions. However, herbivorous fish, in addition to marine protection, had a positive
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33 alternative mechanisms such as reduced competitive pressure, disease prevalence,
34 and physical damage benefiting coral communities.

35

36 Introduction

37 Caribbean coral reefs have experienced major declines over recent decades, with
38 substantial reductions in live coral cover accompanied by concomitant losses in reef
39 accretion and structural complexity (Schutte, Selig & Bruno, 2010; Alvarez-Filip et al.,
40 2011; Perry et al., 2015). Although a wide array of factors have contributed to reef
41 deterioration including coral diseases, coastal development and climate change, the
42 loss of key herbivores is thought to be a leading driver of ecosystem transition towards
43 macroalgal domination at many reef sites in the region (Hughes, 1994; Jackson et al.,
44 2014). Macroalgae compete with corals, reducing coral fecundity, recruitment and
45 survival via various mechanisms including overgrowth, shading and allelopathy
46 (McCook, Jompa & Diaz-Pulido, 2001; Hughes et al., 2007; Bruno et al., 2009; Rasher
47 et al., 2011). Today, populations of key herbivore taxa are diminished on many
48 Caribbean reefs. *Diadema antillarum*, previously an important grazer in the Caribbean,
49 has shown only limited population recovery subsequent to the 1983/4 mass mortality
50 event (Lessios, Robertson & Cubit, 1984; Kramer, 2003; Hughes et al., 2010).
51 Furthermore, long-term overfishing has resulted in marked reductions in herbivorous
52 fish populations at many sites across the region (Jackson et al., 2001; Paddack et al.,
53 2009).

54 Given the pivotal role of herbivores in controlling macroalgal growth (Mumby et al.,
55 2006), it is widely accepted that restoring populations of key herbivores enhances reef
56 resilience by controlling algal communities and facilitating coral recovery by freeing
57 space for coral recruits (Nyström, Folke & Moberg, 2000; McCook, Jompa & Diaz-
58 Pulido, 2001; McManus & Polsenberg, 2004; Bruno et al., 2009). Consequently, coral

59 reefs with high herbivore abundance are expected to have lower macroalgal cover and
60 greater coral cover (Jackson et al., 2014; Kramer et al., 2015). This paradigm has
61 encouraged global awareness campaigns promoting conservation and fisheries
62 management strategies to protect and restore populations of key herbivorous fishes
63 (Jackson et al., 2014). In the Mesoamerican region, for example, Belize and Guatemala
64 have banned the capture and possession of herbivorous fishes (Kramer et al., 2015).

65 Direct evidence of herbivores' ability to facilitate the maintenance and recovery of
66 resilient coral reefs is limited and hindered by the presence of multiple feedback
67 mechanisms (Mumby & Steneck, 2008; Dixon, Abrego & Hay, 2014; Adam et al.,
68 2015a). Experimental herbivore exclusion studies demonstrate the action of *Diadema*
69 and herbivorous fish grazing on macroalgal cover, although evidence for the impact on
70 corals is limited by the short-term nature and restricted spatial extent of the experiments
71 (Lirman, 2001; Burkepile & Hay, 2006, 2009; Hughes et al., 2007). Observational
72 studies tend to focus on inter-site comparisons without an explicit temporal dimension,
73 rather than tracking long-term reef change trajectories to provide a more in-depth
74 understanding of drivers of ecosystem dynamics (Karr et al., 2015). Little consensus
75 exists between studies, which exhibit contrasting patterns between herbivorous fish
76 populations and macroalgal cover. In a Caribbean wide point-in-time study, Newman et
77 al. (2006) found a significant negative correlation between herbivorous fish biomass and
78 fleshy algal biomass, while for the Northern Mesoamerican Reef of Mexico; Bozec et al.
79 (2008) did not observe a relationship between these variables. In a long-term study
80 Ilves et al. (2011) observed increases in both herbivorous fish abundance and algal
81 cover in the Bahamas. Contrastingly, on the Northern Florida Reef Tract, Lirman &

82 Biber (2000) observed no correlation between algal biomass and cover and fish grazer
83 abundance and consumption rates. Jackson et al. (2014) found a significant negative
84 correlation between parrotfish biomass and macroalgal cover in 16 Caribbean locations,
85 however no such relationship was observed for a broader data set covering 46
86 locations. This pattern is evident for other regions: Carassou et al. (2013), for example,
87 found that macroalgal cover was not correlated with the biomass, density and diversity
88 of macroalgae feeders in the South Pacific.

89 To further understand the relationship between herbivory pressure and changes in
90 macroalgal cover we propose a simple conceptual framework (Fig. 1). Here, reefs may
91 experience one of four scenarios of temporal changes in fleshy macroalgal cover and
92 herbivorous fish biomass, a reliable proxy for herbivory levels (Graham et al., 2015).
93 Principal ecological drivers are presented for each idealised scenario, however in reality
94 a number of drivers act in conjunction to varying extents. Coral to algae domination
95 phase shift due to herbivore loss is represented by the scenario in the upper-left
96 quadrant. Here, decreasing herbivory leads to increasing macroalgal cover. Conversely,
97 in the bottom-right quadrant, *increases* in herbivorous fishes result in reduced
98 macroalgal cover. This quadrant represents the scenario sought by the creation of
99 Marine Protected Areas, prohibition of fishing within No Take Zones, and fisheries
100 regulations (Selig & Bruno, 2010; Guarderas, Hacker & Lubchenco, 2011). By limiting
101 extractive practices, especially of larger more fecund individuals, fish population
102 declines can be halted or reversed within marine reserves (Halpern, 2003; Lester et al.,
103 2009).

104 Alternatively, a *positive* relationship may exist between macroalgal cover and
105 herbivorous fish biomass, as represented by the scenarios of the upper-right and
106 bottom-left quadrants of Fig. 1. This may occur when herbivores are food limited, as
107 evidenced by increases in herbivore abundance and biomass following algal growth and
108 by resource competition between *Diadema* and herbivorous fishes (Hay & Taylor, 1985;
109 Carpenter, 1990; Adam et al., 2011). In these scenarios, predominantly external drivers
110 such as nutrient availability, temperature and solar irradiance determine macroalgal
111 cover and herbivorous fish biomass responds according to food availability (Burkepile &
112 Hay, 2006; Ferrari et al., 2012). Numerous experimental manipulation studies have
113 reported the significant positive impact of nutrient enhancement on primary producer
114 abundance, although herbivory has generally been found to play a greater role
115 (Burkepile & Hay, 2006). Contrastingly, few studies have addressed the importance of
116 macroalgal productivity potential relating to environmental factors such as light
117 availability and temperature (Steneck & Dethier, 1994; Ferrari et al., 2012).

118 Herbivore and algal community composition also play an important role in herbivore-
119 algal dynamics. Subsequent to the *Diadema* mass mortality event of the early 1980's,
120 herbivorous fishes of the Scaridae and Acanthuridae families are recognised as the
121 primary herbivores on many Caribbean reefs (Jackson et al., 2014; Adam et al., 2015a).
122 While common *Acanthurus* surgeonfishes have a broad diet feeding on a combination
123 of turf algae, macroalgae and detritus, *Sparisoma* and *Scarus* parrotfishes are more
124 selective (Burkepile & Hay, 2011; Adam et al., 2015a). *Sparisoma* parrotfishes, with the
125 exception of the excavating *S. viride*, are macroalgae browsers, while *Scarus* spp.
126 primarily graze algal turfs (Bonaldo, Hoey & Bellwood, 2014; Adam et al., 2015b).

127 Consequently, a suitable mix of herbivores are required in order to both graze turf algae
128 to facilitate coral recruitment and to crop down macroalgal stands to reduce competition
129 with adult coral colonies (McCook, Jompa & Diaz-Pulido, 2001; Hughes et al., 2007;
130 Burkepile & Hay, 2008). However, herbivores' ability to effectively moderate macroalgal
131 cover is mediated by macroalgal predation defences (Rasher, Hoey & Hay, 2013). Such
132 defences are species specific and include morphological, structural, mineral and
133 chemical traits that deter herbivores, with several genera (e.g. *Lobophora*, *Peyssonnelia*
134 and *Codium*) being unpalatable (Hay, 1997; Smith, Hunter & Smith, 2010). These
135 defences likely influence herbivore feeding preferences and conversely algal community
136 structure is often influenced by herbivore mix, resulting in a complex interaction
137 between the two communities (Adam et al., 2015a).

138 Here, by following individual site trajectories, we examine the prevalence of the four
139 herbivorous fish and macroalgae change scenarios across 85 sites surveyed over the 9-
140 year period 2005 to 2014 along the Mesoamerican Reef. We also consider herbivore
141 functional group composition and trajectories, and compare these with overall trends.
142 Subsequently, we evaluate the effect of herbivorous fish biomass, fleshy macroalgal
143 cover and other factors such as degree of protection, on changes in coral cover during
144 the same timeframe. Our hypothesis is that for sites where herbivory increased, fleshy
145 macroalgal cover decreased, and that herbivore biomass and the decline in macroalgal
146 cover are among the main factors explaining coral cover on today's reefs.

147

148 **Materials & Methods**

149 We used data produced by the Healthy Reefs Initiative (HRI) and the Atlantic and Gulf
150 Rapid Reef Assessment (AGRRA) programs, which include ecological censuses for 398
151 sites along the Mesoamerican Reef in Mexico, Belize, Guatemala and Honduras from
152 2005 to 2014. Site selection was based on benthic habitat maps produced by the
153 Millennium Reef Mapping Program, with 200 m × 200 m sites randomly selected
154 following stratification by geomorphological characteristics and depth (Andréfouët et al.,
155 2003; Kramer, 2003). The database contains 85 long-term monitoring sites that were
156 surveyed in 2005/2006 and 2013/2014 over a 7, 8 or 9-year period, a timeframe
157 sufficient to observe ecologically meaningful changes (Babcock et al., 2010). Of these
158 sites, 43 were repeatedly surveyed in four time periods (2005/2006, 2009/2010,
159 2011/2012 and 2013/2014). Sites were located primarily on the fore reef and reef crest
160 at a mean (\pm Standard Error s.e.m.) depth of 6.9 ± 0.2 m.

161 Benthic cover and reef fish surveys were performed according to AGRRA protocol, with
162 transects located haphazardly, parallel to the coast (Lang et al., 2010). The majority of
163 sites were surveyed at similar times during the summer year-on-year in order to
164 minimise seasonal effects. At each site an average of five to six 10 m-transects were
165 surveyed using point intercept methodology to determine benthic cover including hard
166 coral percentage cover and fleshy macroalgal percentage cover. The abundance and
167 total length (TL) of 81 key reef fish species, including herbivorous fishes of the Scaridae
168 and Acanthuridae families, was recorded in ten 30 m-long, 2 m-wide transects. Reef fish
169 abundance was subsequently converted to biomass density using standard allometric
170 length-weight conversions.

171 The data analyses focussed on the relation between three ecological indicators for each
 172 reef site: herbivorous fish (Scaridae and Acanthuridae) biomass, fleshy macroalgal
 173 cover and hard coral (scleractinians and *Millepora* spp.) cover. Very few *Diadema* spp.
 174 were observed and therefore we focussed on reef fishes as the principal herbivores. For
 175 all three ecological indicators, a number of metrics were calculated in order to evaluate
 176 and examine temporal trends: absolute annual change, annual relative rate of change
 177 and geometric rate of change. The metrics for each ecological indicator (I) were
 178 determined as follows:

$$179 \quad I_{\text{Absolute Annual Change}} = \frac{(I_{t_f} - I_{t_0})}{\Delta t} \quad (1)$$

$$180 \quad I_{\text{Annual Relative Rate of Change}} = \frac{(I_{t_f} - I_{t_0})}{I_{t_0} \times \Delta t} \quad (2)$$

$$181 \quad I_{\text{Annual Geometric Rate of Change}} = \left(\frac{I_{t_f}}{I_{t_0}} \right)^{\frac{1}{\Delta t}} - 1 \quad (3)$$

182 where I_{t_f} is the value of the ecological indicator at the end of the period, I_{t_0} is the initial
 183 value and Δt is the length of the period (in years). The former two metrics provide
 184 complementary information, for example: if an ecological indicator such as coral cover
 185 increases from 10 % to 15 %, the absolute change (equation (1)) is 5 %, while the
 186 relative rate of change (equation (2)) indicates that coral cover has increased by 50 %
 187 relative to its initial value. Geometric rate of change (equation (3)) was utilised in order
 188 to assess and compensate for non-linearity in the relative rate of change, while still
 189 providing an interpretable value (Côté et al., 2005).

190 Univariate comparison of ecological indicators was performed using ANOVA, t-tests or
191 non-parametric equivalents (Mann-Whitney U or Wilcoxon Signed Rank tests), based
192 on an assessment of normality and homogeneity of variance using Shapiro-Wilk and
193 Levene tests. To test our first hypothesis, herbivorous fish biomass was compared with
194 fleshy macroalgal cover using Spearman rank-order correlation due to non-normality.
195 Herbivorous fishes were further categorised according to feeding preferences as
196 macroalgae browsers (*Sparisoma* spp., with the exception of *S. viride*), turf grazers /
197 scrapers (*Scarus* spp. and *Acanthurus* spp.) or bioeroders (*Sparisoma viride*) (Bellwood
198 et al., 2004; Burkepile & Hay, 2011; Bonaldo, Hoey & Bellwood, 2014; Adam et al.,
199 2015a,b). Change in functional group biomass was compared with overall change in
200 herbivorous fish biomass using Spearman rank-order correlation. Furthermore, change
201 in macroalgal cover was compared with absolute levels of overall herbivorous fish and
202 macroalgae browser biomass both graphically by categorising sites by initial fish
203 biomass (based on deciles) and by using Spearman rank-order correlation.

204 To test our second hypothesis, change in absolute coral cover from 2005/6 to 2013/4 for
205 long-term monitoring sites was modelled using multiple linear regressions as model
206 assumptions were satisfied. To address the common problem of spatial autocorrelation
207 in multi-site studies we performed a Moran's I test on coral cover change by site
208 location which reported no spatial autocorrelation present (Moran's I = 0.070, P = 0.08).
209 The optimum regression model was selected based on Akaike Information Criterion
210 (AIC). Candidate independent variables were selected based on ecological relevance
211 and data availability (Table 1). Potential collinearity among predictor variables was

212 examined using Pearson correlations and variance inflation factors. All statistical
213 analyses were performed using R (R Core Team, 2014).

214

215 **Results**

216 85 long-term Mesoamerican Reef monitoring sites were surveyed in 2005/2006 and
217 2013/2014 over a 7, 8 or 9-year period. Of these, 43 sites were repeatedly surveyed in
218 four time periods (2005/2006, 2009/2010, 2011/2012 and 2013/2014). Here we present
219 herbivorous fish biomass and fleshy macroalgal cover average trends for repeatedly
220 surveyed sites and assess changes in these variables for long-term monitoring sites.
221 Subsequently we examine herbivorous fish feeding guilds and geographic trends for
222 long-term monitoring sites, and assess the effect of protection on site trajectories.
223 Finally we present the ecological drivers of long-term coral cover change.

224 *Herbivorous fish biomass and macroalgal cover trends*

225 In the time period 2005 to 2014 regional averages showed a clear trend of increasing
226 fleshy macroalgal cover on the Mesoamerican Reef, while herbivorous fish biomass
227 remained relatively constant. Across 43 sites surveyed repeatedly in four time periods
228 (Fig. 2), mean herbivorous fish biomass did not change significantly (Wilcoxon Signed
229 Rank, $Z = 0$, $P = 1$), while mean macroalgal cover doubled during the same period
230 (Wilcoxon Signed Rank, $Z = -5.02$, $P < 0.001$). Between 2005/2006 and 2009/2010
231 mean herbivorous fish biomass decreased and mean fleshy macroalgal cover increased
232 significantly (Wilcoxon Signed Rank, $Z = 3.36$, $P < 0.001$ and $Z = -3.86$, $P < 0.001$,

233 respectively). From 2009/10 to 2011/12 the trend appeared to be reversed, although the
234 changes were not significant for macroalgae (Wilcoxon Signed Rank, $Z = -2.95$, $P =$
235 0.003 and $Z = 0.59$, $P = 0.55$, respectively; Fig. 2). From 2011/2012 to 2013/2014
236 macroalgal cover increased significantly, while herbivorous fish biomass remained
237 unchanged (Wilcoxon Signed Rank, $Z = -3.81$, $P < 0.001$ and $Z = -0.35$, $P = 0.73$,
238 respectively; Fig. 2).

239 Tracking individual trajectories of the 85 long-term monitoring sites surveyed over a 7, 8
240 or 9-year period permitted a more detailed investigation of the relation between the
241 temporal changes in herbivorous fish biomass and fleshy macroalgal cover.
242 Herbivorous fish biomass ranged from approximately 50 to 14,000 g/100m² and fleshy
243 macroalgal cover ranged from 0 to 57.5 %. There was no correlation between the
244 changes in herbivorous fish biomass and fleshy macroalgal cover for long-term
245 monitoring sites (Spearman, $r_s = -0.11$, $P = 0.35$). Only 7 % of sites exhibited increased
246 herbivorous fish biomass and decreased macroalgal cover; 35 % of sites displayed
247 decreases in fish biomass and increases in macroalgal cover; almost half of the sites
248 (48 %) exhibited increases in both herbivorous fish biomass and macroalgal cover; and
249 10 % displayed decreased fish biomass and macroalgal cover (Fig. 3). Across all sites
250 macroalgal cover increased irrespective of initial conditions of herbivorous fish biomass
251 (Spearman, $r_s = -0.12$, $P = 0.3$; Fig. 4a) and macroalgae browser biomass (Spearman,
252 $r_s = -0.21$, $P = 0.3$; Fig. 4b).

253 Considering herbivorous fish feeding preferences, communities of the Mesoamerican
254 Reef present a mixture of guilds with 24.3 % macroalgae browsers by biomass in
255 2013/14 (19.4 % in 2005/6), 48.4 % (57.3 %) turf grazers / scrapers and 27.3 % (23.3

256 %) bioeroders. Herbivorous fish biomass and macroalgal cover change were broadly
257 similar between macroalgae browsers and overall results (Fig. 3). Macroalgae browser
258 biomass displayed a slightly greater tendency for increase than overall herbivorous fish
259 biomass, as observed for 61 % of sites compared with 55 %, and site-level changes in
260 these were correlated (Spearman, $r_s = 0.70$, $P < 0.001$).

261 Geographically, the principal trend was for increasing fleshy macroalgal cover and
262 herbivorous fish biomass in Mexico and northern Belize, including the atolls of Turneffe
263 and Lighthouse Reef, but for increasing fleshy macroalgal cover and decreasing
264 herbivorous fish biomass to the south in south-central and southern Belize, Glover's
265 Reef, Guatemala and Cayos Cochinos, Honduras (Fig. 3). However, the Bay Islands of
266 Honduras were exceptions to this broad north-to-south trend with Guanaja island
267 displaying the highest proportion of sites with increasing herbivorous fish biomass and
268 decreasing macroalgal cover. The only other three sites that experienced a similar trend
269 were located at Isla Mujeres and Puerto Morelos in Mexico, and San Pedro in Belize.

270 Of the 85 long-term monitoring sites, 12 sites were located within No Take Zones
271 (NTZs), 47 were within Marine Protected Areas but not NTZs (MPAs), and the
272 remaining 26 were unprotected. The level of protection was observed to affect the initial
273 levels of fleshy macroalgal cover and herbivorous fish biomass, in addition to changes
274 in these over time. In 2005/6, sites within NTZs exhibited similar herbivorous fish
275 biomass and fleshy macroalgal cover to sites located elsewhere within Marine Protected
276 Areas (Mann-Whitney, $U = 197$, $Z = -1.60$, $P = 0.11$; and $U = 297$, $Z = 0.28$, $P = 0.78$
277 respectively; Fig. 5). Protected sites (both MPAs and NTZs) displayed significantly
278 higher initial macroalgal cover than unprotected sites (Mann-Whitney, both $U \geq 247$, $Z \geq$

279 2.85, $P \leq 0.003$; Fig. 5), but only protected sites outside of NTZs exhibited significantly
280 higher initial herbivorous fish biomass than unprotected sites (Mann-Whitney, MPA vs
281 unprotected, $U = 819$, $Z = 2.40$, $P = 0.016$; NTZ vs unprotected, $U = 161$, $Z = 0.16$, $P =$
282 0.89 ; Fig. 5). Along the protection gradient (from unprotected, through MPA to no-take
283 protection), sites appeared to experience a greater increase in herbivorous fish biomass
284 and a lesser increase in macroalgal cover, although the differences were not statistically
285 significant (ANOVA, annual geometric rate of change in fish biomass, $F_{2,82} = 0.04$, $P =$
286 0.97 ; annual geometric rate of change in macroalgal cover, $F_{2,80} = 1.01$, $P = 0.37$).

287 *Predicting coral cover change*

288 Across all 85 long-term monitoring sites, mean (\pm s.e.m.) hard coral cover increased
289 significantly from 12.2 ± 0.8 % in 2005/6 to 15.0 ± 0.8 % in 2013/14 (Wilcoxon Signed
290 Rank, $Z = -3.81$, $P < 0.001$). Individual sites displayed varying trajectories with annual
291 changes in coral cover ranging from -3.1 % to $+2.7$ %. The optimum linear regression
292 model for the annual absolute change in hard coral cover displayed a modest but
293 significant fit (Adjusted $R^2 = 0.18$, $F_{7,74} = 3.57$, $P = 0.002$). The model included seven
294 predictor variables (Table 1), of which four were significant: MPA, Country (Honduras),
295 annual logarithmic change in herbivorous fish biomass and initial hard coral cover (Fig.
296 6). Interpreting these significant variables, sites within Marine Protected Areas
297 experienced greater increases in coral cover than unprotected sites; Honduran sites
298 experienced lesser increases in coral cover than other countries; and increases in
299 herbivorous fish biomass corresponded with increases in coral cover. Initial coral cover
300 was the most significant predictor of coral cover change and therefore in order to further
301 understand its impact, sites were categorised as low (<10 %), medium (10-20 %) or

302 high ($\geq 20\%$) initial coral cover. For the 12 long-term monitoring sites with high initial
303 coral cover, mean coral cover decreased over time (mean \pm s.e.m. annual change in
304 coral cover of $-0.6 \pm 0.4\%$), while coral cover increased for sites with lower levels of
305 initial cover (low initial coral cover, $+0.6 \pm 0.1\%$; medium initial coral cover, $+0.4 \pm 0.2$
306 %).

307 Despite not being selected in the optimum regression model, we further explored the
308 relationship between coral and macroalgal cover due to the long-term ecological shifts
309 reported on many Caribbean reefs. Across all 85 long-term monitoring sites, mean (\pm
310 s.e.m.) macroalgal cover increased significantly from $12.0 \pm 1.1\%$ in 2005/6 to $24.1 \pm$
311 1.5% in 2013/14 (Wilcoxon Signed Rank, $Z = -7.07$, $P < 0.001$). We observed little or
312 no relationship between coral and macroalgal cover since macroalgal cover consistently
313 increased irrespective of changes in coral cover (Supplementary Fig. S3 online). All
314 initial coral cover categories (low ($< 10\%$), medium (10-20%), and high ($\geq 20\%$))
315 experienced increases in fleshy macroalgal cover, and initial macroalgal cover, similarly
316 categorised, did not impact coral cover changes over time (ANOVA, $F_{2,82} = 1.10$, $P =$
317 0.34).

318

319 **Discussion**

320 Rapid changes in the ecological composition of the Mesoamerican Reef were evident in
321 a time span of only nine years. The principal trend is for increasing fleshy macroalgal
322 cover, as observed at 83% of long-term monitoring sites (Fig. 3). Mean fleshy
323 macroalgal cover increased (relatively) by approximately 125% in the region between

324 2005 and 2014 (Fig. 2). Mean herbivorous fish biomass remained relatively stable (Fig.
325 2), although displaying substantial site variation, with 55 % of sites showing an increase
326 in herbivorous fish biomass between 2005 and 2014 (Fig. 3). The scenario of both
327 increasing fleshy macroalgal cover and herbivorous fish biomass was experienced at 48
328 % of sites while the 'desirable' scenario of increasing herbivorous fish biomass and
329 decreasing macroalgal cover was the least frequent of all four scenarios (Fig. 3). Similar
330 trends were observed for the macroalgae browsing fish guild (Fig. 3), with site-level
331 macroalgae browser biomass change correlating with overall herbivorous fish biomass
332 change. This suggests that fish herbivory was not a major driver of fleshy macroalgal
333 cover change in the majority of surveyed sites across the Mesoamerican Reef (Fig. 3).

334 The clear pattern of increasing macroalgal cover and stable herbivorous fish biomass
335 on Mesoamerican reefs contrasts with the widely accepted coral reef phase shift
336 paradigm that suggests that increasing herbivory would lead to declines in fleshy
337 macroalgal cover (Nyström, Folke & Moberg, 2000; McCook, Jompa & Diaz-Pulido,
338 2001). However, long-term reduction in Caribbean reef fish populations and increases in
339 macroalgal cover from historical levels had already occurred prior to the onset of this
340 study (Jackson et al., 2001; McClenachan, 2009; Paddack et al., 2009). In a recent
341 study of four Philippine islands covering the multi-decadal (30 year) period associated
342 with reef phase shifts, Russ et al. (2015) observed that macroalgal cover was not
343 related to long-term parrotfish losses due to fishing, supporting our findings. Our
344 findings suggest that in the period 2005-2014 environmental factors such as nutrient
345 availability, temperature or solar irradiance may be responsible for increasing
346 macroalgal cover, rather than reduced herbivory (Burkepile & Hay, 2006; Ferrari et al.,

347 2012). In Mexico, other studies have observed no relationship between herbivore
348 biomass and macroalgal cover, relating reef structural change to coastal development
349 (Bozec et al., 2008) and associated nutrient discharges (Baker & Fogel, 2013;
350 Hernández-Terrones et al., 2015). In southern Belize and Honduras we suggest that
351 riverine discharge and escalating reef sediment and nutrient loads associated with
352 urban and agricultural run-off may have played a role (Burke & Sugg, 2006; Carilli et al.,
353 2009; Soto et al., 2009). This finding contrasts the results of herbivore exclusion
354 studies, which emphasize the relative importance of herbivory over nutrient availability,
355 although such studies tend to be conducted on restricted spatial and temporal scales
356 (McClanahan, Cokos & Sala, 2002; Burkepale & Hay, 2006, 2009; Sotka & Hay, 2009).
357 Observed increases in herbivorous fish populations may be due to a *positive*
358 relationship with macroalgal cover, driven by herbivore food-limitation, or independently
359 via conservation efforts (Carpenter, 1990; Lester et al., 2009; Adam et al., 2011).
360 Herbivores can be food limited even on reefs with high algal cover since macroalgae
361 often have physical and chemical defences (McClanahan et al., 2000). Algal defences
362 play an important role in reef herbivory dynamics and likely influence herbivore feeding
363 preferences (Hay, 1997; Erickson et al., 2006; Adam et al., 2015a). Increases in
364 macroalgal cover, potentially due to nutrient enrichment, may be related to changes in
365 algal community composition towards unpalatable species, concealing the underlying
366 influence of herbivory (Smith, Hunter & Smith, 2010). Consistent algal species
367 information was not available in the database used in this study and thus it was not
368 possible to evaluate the magnitude of this effect on the Mesoamerican Reef.

369 One alternative that could partially explain the rapid increases in fleshy macroalgae
370 across the Mesoamerican Reef is that reef ecosystems passed critical thresholds
371 beyond which herbivorous fish are unable to control macroalgae (Mumby, Hastings &
372 Edwards, 2007). However, this explanation is unlikely as regional average macroalgal
373 cover increased from 10 % in 2005/6 to 22 % in 2013/14 (Fig. 2), values that are likely
374 considerably below ecosystem thresholds for Caribbean reefs (Bruno et al., 2009). With
375 regards to herbivorous fish thresholds, an examination of macroalgal change by
376 absolute levels of herbivorous fish biomass revealed increasing fleshy macroalgal cover
377 even for those sites with the highest initial fish biomass (the uppermost deciles
378 possessed average overall herbivorous fish biomass and macroalgae browsing fish
379 biomass of 9,065 g/100m² and 1,762 g/100m² respectively; Fig. 4). Although there is
380 little consensus on Caribbean reef state thresholds, a global assessment of the status of
381 coral reef herbivorous fishes identified only 9 of 132 localities as having herbivorous fish
382 biomass greater than 9,000 g/100m², suggesting this to be a high benchmark (Mumby,
383 Hastings & Edwards, 2007; Edwards et al., 2014). Furthermore, a negative correlation
384 between Caribbean reef herbivorous fish biomass and fleshy algal biomass has been
385 previously observed with a site maximum of only 7,000 g/100m² approximately
386 (Newman et al., 2006).

387 The threshold hypothesis would be particularly relevant if the decline in average
388 herbivorous fish biomass between 2005/6 and 2009/10 resulted in changes in the
389 relative proportion of key functional groups, favouring non-macroalgae browsing species
390 (Adam et al., 2015b; Fig. 2). However, the relative proportions of the three main
391 herbivorous fish functional groups remained stable during the study period

392 (Supplementary Fig. S4 online). Additionally, a close examination of those sites that
393 suffered the greatest herbivorous fish biomass losses between 2005 and 2009 revealed
394 that these sites experienced similar macroalgae growth from 2009 to 2014 compared
395 with other sites (Supplementary Fig. S5 online). This evidence suggests that no
396 threshold effects were experienced and that the lack of relationship between fish
397 biomass and macroalgal cover change was indeed due to other factors.

398 In post phase-shift degraded reef systems coral and macroalgal cover are probably less
399 tightly coupled compared to reefs that experienced rapid losses of coral cover in the
400 recent past. At the onset of this study, hard corals were not the dominant benthic
401 component on the Mesoamerican Reef, with a mean cover of only 12.2 % at long-term
402 study sites. By 2013/14 mean coral cover had increased to 15.0 %, but was unrelated to
403 macroalgal cover which had increased considerably more (from 12.0 % in 2005/6 to
404 24.1 % in 2013/14). Our model showed that instead of changes in macroalgal cover,
405 increases in coral cover are related to initial coral cover, increasing biomass of
406 herbivorous fish, geographical location and MPA protection (Fig. 6). Initial coral cover
407 was the primary driver, with gains for sites with < 20 % coral cover initially and losses at
408 sites with ≥ 20 % initial cover (Supplementary Fig. S3 online). Although coral losses at
409 initially better preserved sites were not accompanied by concomitant increases in
410 macroalgal cover, it is likely that ongoing deterioration in environmental conditions, such
411 as rising temperatures and increased coral disease prevalence, continue to impact coral
412 communities (Harvell et al., 2007; Hoegh-Guldberg et al., 2007; Sokolow, 2009;
413 Kennedy et al., 2013).

414 Reef protection has a positive impact on herbivorous fish biomass and coral cover,
415 although fleshy macroalgal cover continued to increase at most sites. Herbivorous fish
416 populations were observed to generally increase to the North, in Mexico and northern
417 Belize, while decreasing to the South of the region (Fig. 3). Although protection
418 impacted herbivorous fish biomass and macroalgal cover trajectories (Fig. 5), initial
419 differences between protected and unprotected sites tend to persist, with unprotected
420 sites continuing to display lower macroalgal cover. This may be attributable to reserve
421 age, as protected sites were located within reserves designated in 2003 (± 1 year) on
422 average, and studies have shown that protection influence may be subject to a lag
423 effect (Selig & Bruno, 2010; Babcock et al., 2010). Additionally, local conditions and
424 reserve regulations often obfuscate protection impact due to variability of internal factors
425 such as reef community structure and enforcement level, and external impacts including
426 local stressors and global climate change (Mora et al., 2006; McClanahan et al., 2006;
427 Selig, Casey & Bruno, 2012). Indeed, the predominant trend of increasing macroalgal
428 cover for both protected and unprotected sites suggests that external factors such as
429 terrestrial nutrient import have a substantial impact on macroalgal proliferation.

430 Coral recovery was related to MPA protection level and increasing biomass of
431 herbivorous fish, but not via the expected mechanism of macroalgal declines through
432 fish herbivory. Alternative mechanisms for the effect of protection on reef corals are less
433 well studied, but may include reduced disease prevalence, and diminished physical reef
434 damage through regulation of fishing and recreational diving practices (Hasler & Ott,
435 2008; Lamb et al., 2015). Replenished fish communities inside marine reserves can
436 also drive coral recovery through ecological processes not necessarily linked with

437 herbivory. For example, trophically diverse fish communities inside marine reserves
438 have been shown to ameliorate coral disease prevalence, although the pathways
439 through which this takes place remain unclear (Raymundo et al., 2009). Also,
440 overfishing of spongivorous parrotfishes and angelfishes has been shown to have a
441 negative impact on reef-building corals through the alleviation of predation pressure on
442 sponges which exhibit competitive superiority over corals (Loh et al., 2015).
443 Consequently, the observed positive effects of herbivorous fishes on the coral
444 communities of the Mesoamerican Reef may be the result of a broad range of
445 mechanisms associated with reef protection. Our findings for coral cover contrast those
446 of Russ et al. (2015) who in a long-term study of four islands of the Philippines observed
447 a generally negative relationship between parrotfish density and hard coral cover. Russ
448 et al. (2015) report a positive relationship between dead coral cover and parrotfish
449 density and suggest that this may be due to the prevalence of turf, detritus and
450 sediment feeding guilds in the study area, since these are commonly associated with
451 dead substrata.

452 In conclusion, during the last decade increasing fleshy macroalgal cover was the
453 principal trend on the coral reefs of the Mesoamerican Reef. Herbivorous fish
454 populations were not responsible for this trend, contrasting the results of some studies
455 performed over smaller spatial scales, and implicating the role of external factors such
456 as terrestrial nutrient import in providing algae-favourable conditions. However,
457 herbivorous fish, in addition to marine protection, had a positive impact on hard coral
458 cover, which increased over the observation period. We suggest that these factors
459 benefited coral communities through alternative mechanisms such as lower disease

460 prevalence, diminished competition and reduced physical damage, despite increasing
461 fleshy macroalgal cover. Consequently, in addition to more concerted efforts regarding
462 watershed management and climate change mitigation, local marine protection efforts
463 are important tools for coral reef managers. Additionally, ongoing monitoring should be
464 employed to track reef environmental conditions, and further studies on the
465 mechanisms underlying protection impacts on coral communities would inform ongoing
466 reef management and protection planning.

467

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477

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Figure 1(on next page)

Relationship between changes in herbivorous fish biomass and benthic fleshy macroalgal cover.

Possible cause-and-effect scenarios with external drivers are postulated for each quadrant. Fish and algae graphics by Diana Kleine and Tracey Saxby (IAN Image Library, Integration and Application Network, University of Maryland Center for Environmental Science, <http://ian.umces.edu/imagelibrary>).

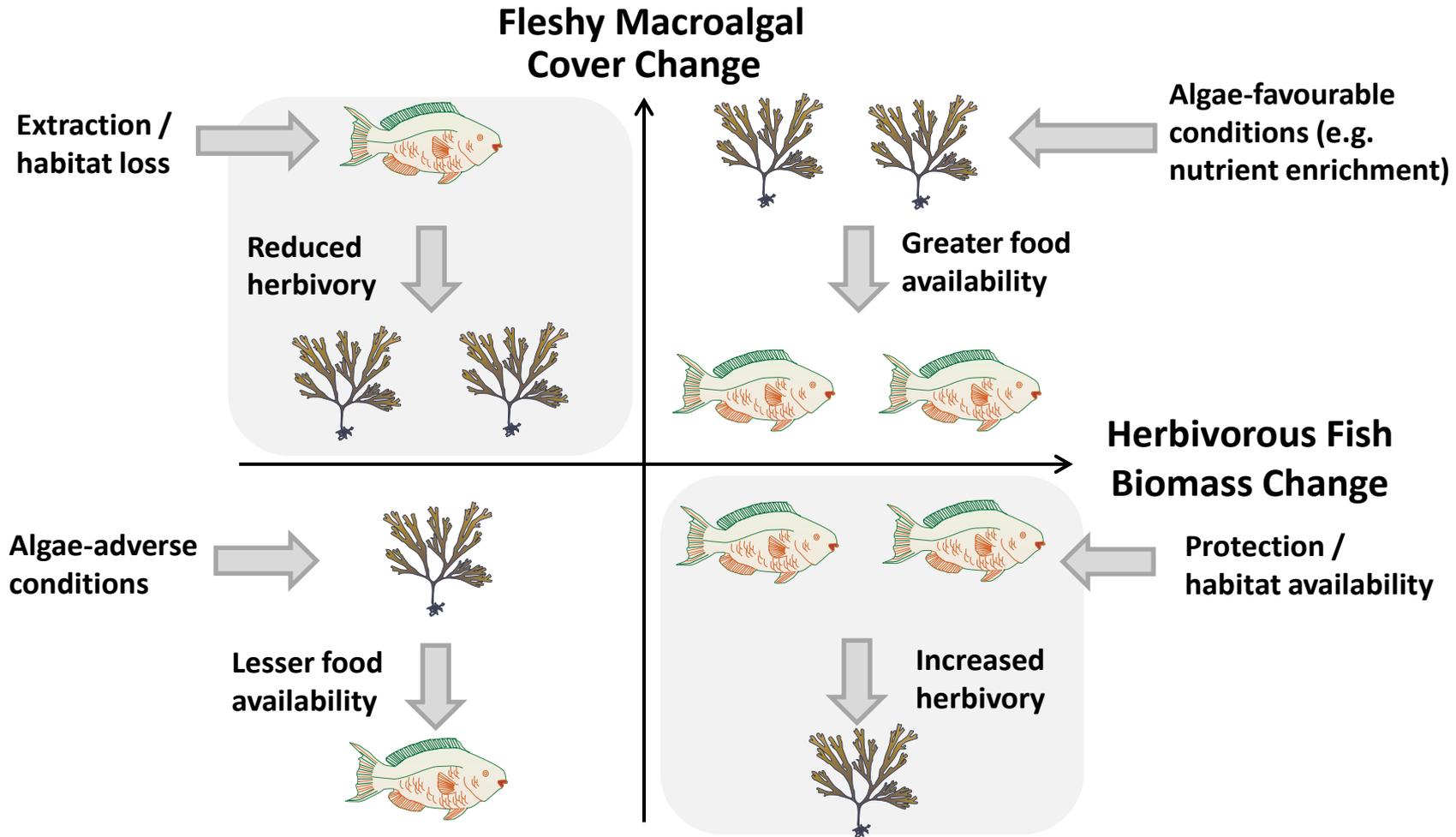


Figure 2 (on next page)

Temporal trend in mean herbivorous fish biomass and benthic fleshy macroalgal cover on the Mesoamerican Reef.

Mean (\pm s.e.m.) values are shown for all 43 sites surveyed repeatedly in each monitoring period (2005/2006, 2009/2010, 2011/2012 and 2013/2014). Similar trends were observed for all sites surveyed in consecutive monitoring periods (Supplementary Fig. S1 online).

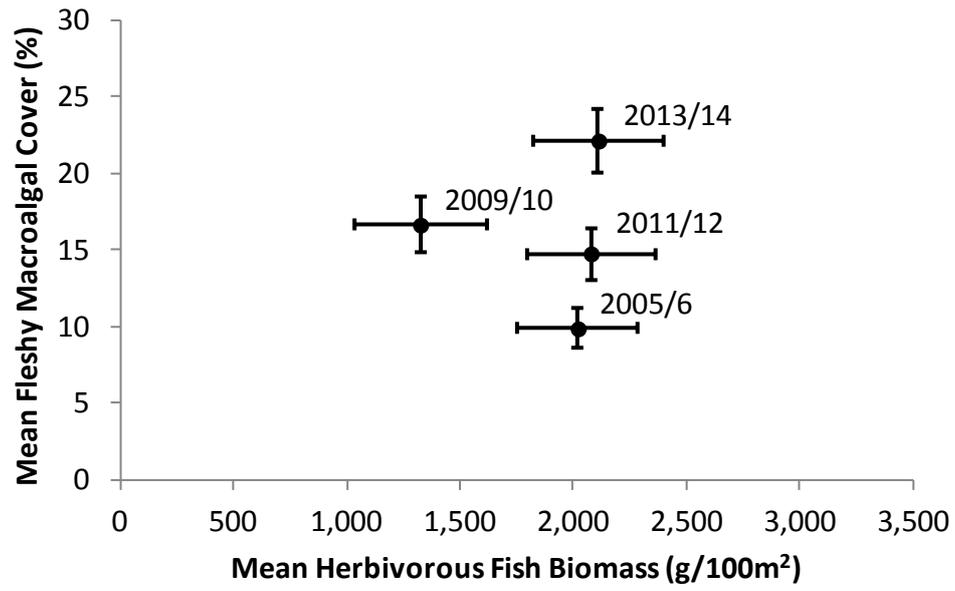


Figure 3(on next page)

Long-term herbivorous fish and benthic fleshy macroalgal cover trends on the Mesoamerican Reef.

Map and graphs indicating relationship between changes in overall and macroalgae browsing herbivorous fish biomass and fleshy macroalgal cover from first (2005 or 2006) to last (2013 or 2014) year for all (85) long-term monitoring sites with ≥ 7 years' history. Map indicates Healthy Reef Initiative regions within countries and locates sites by the relationship between changes in herbivorous fish biomass and fleshy macroalgal cover (Kramer et al., 2015). Inset graphs separately indicate relationship between changes in herbivorous fish biomass and fleshy macroalgal cover, and macroalgae browsing herbivorous fish biomass and fleshy macroalgal cover. For inset graphs, each circle represents the sites for that quadrant and circle position reflects mean site-level annual geometric rates of change. Circle area represents proportion of sites in that quadrant (also labelled). All (85) sites with ≥ 7 years' of history are plotted in order to provide long-term trends, although the equivalent analysis for sites with ≥ 8 years' of history produced similar results (Supplementary Fig. S2 online).

Legend

HRI Sites ≥ 7 years history

- ★ Algae Increasing + Fish Increasing
- ★ Algae Increasing + Fish Decreasing
- ★ Algae Decreasing + Fish Increasing
- ★ Algae Decreasing + Fish Decreasing

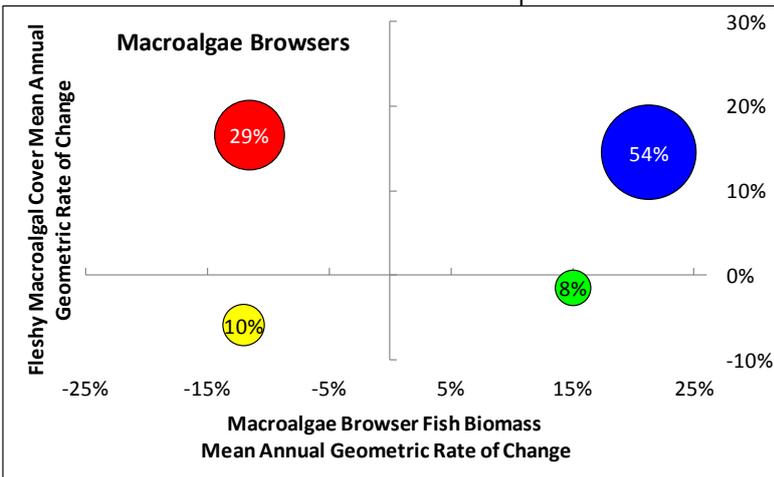
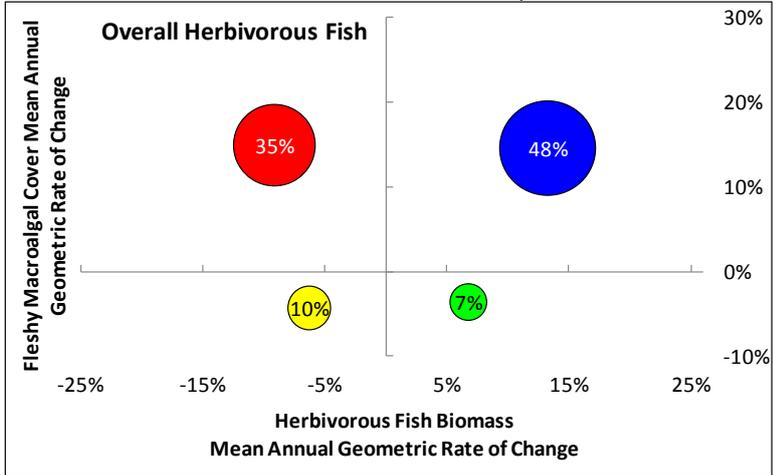
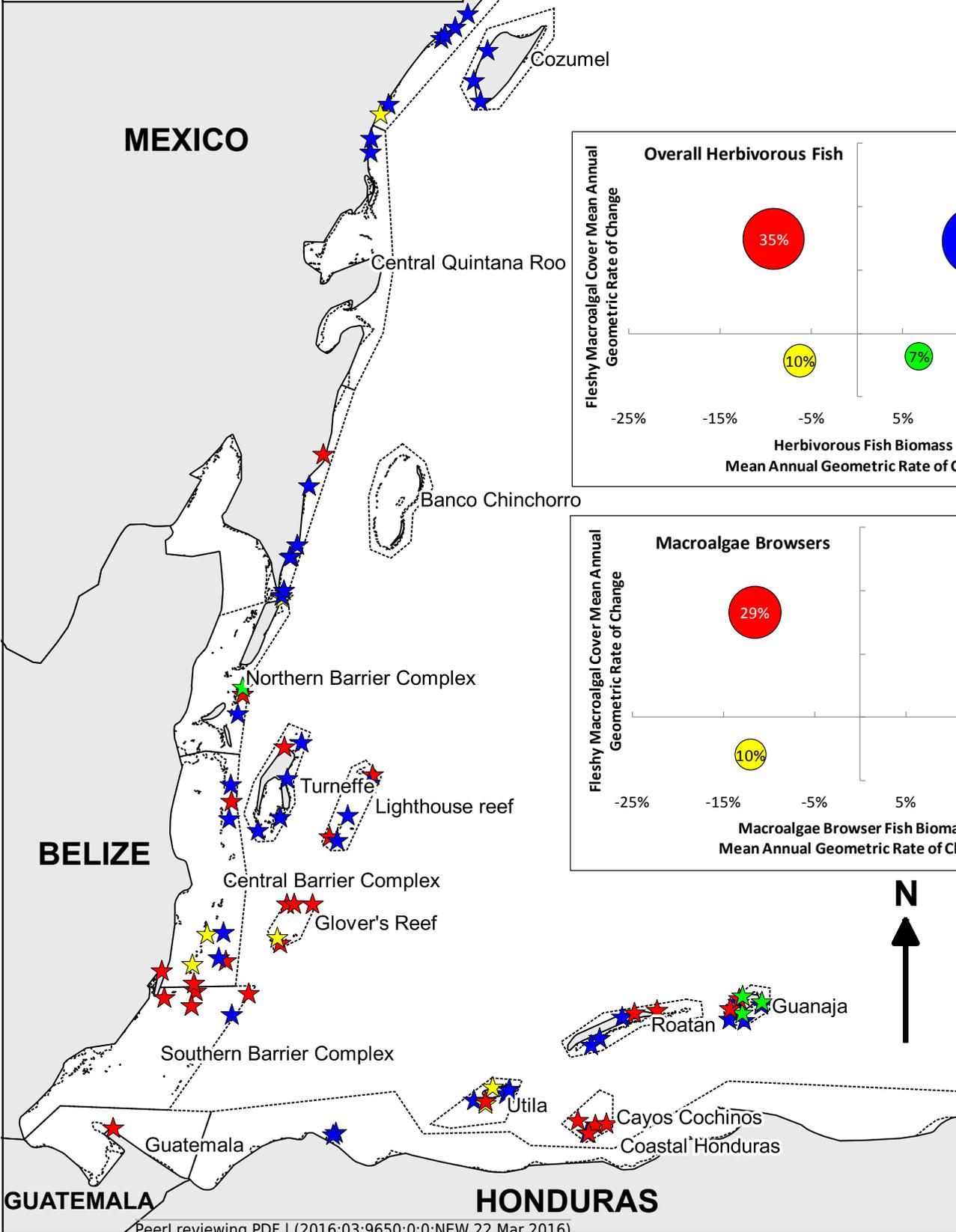


Figure 4(on next page)

Effect of initial herbivorous fish biomass on fleshy macroalgal cover on the Mesoamerican Reef.

a) Mean (\pm s.e.m.) benthic macroalgal cover in 2005/6 (green symbols) and 2013/14 (red symbols) by initial level of overall herbivorous fish biomass, for all (85) long-term monitoring sites. Sites divided into 10 categories based on initial overall herbivorous fish biomass deciles. b) Mean (\pm s.e.m.) benthic macroalgal cover in 2005/6 (green symbols) and 2013/14 (red symbols) by initial macroalgae browser biomass, for all (85) long-term monitoring sites. Sites divided into 10 categories based on initial macroalgae browser biomass deciles.

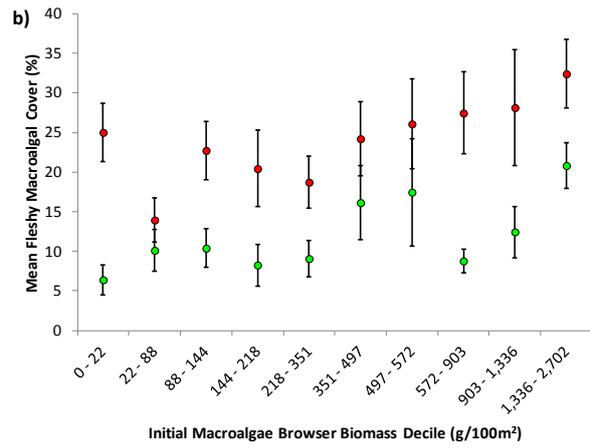
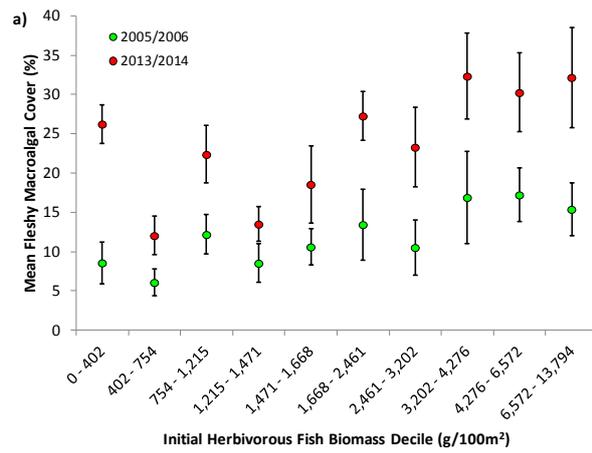


Figure 5 (on next page)

Effect of protection on herbivorous fish biomass and fleshy macroalgal cover on the Mesoamerican Reef.

Mean (\pm s.e.m.) herbivorous fish biomass and benthic macroalgal cover in 2005/6 (green symbols) and 2013/14 (red symbols) by level of protection, for all (85) long-term monitoring sites. Unprotected = sites outside Marine Protected Areas ($n = 26$), MPA = sites inside Marine Protected Areas but not within No Take Zones ($n = 47$), NTZ = sites within No Take Zones within Marine Protected Areas ($n = 12$).

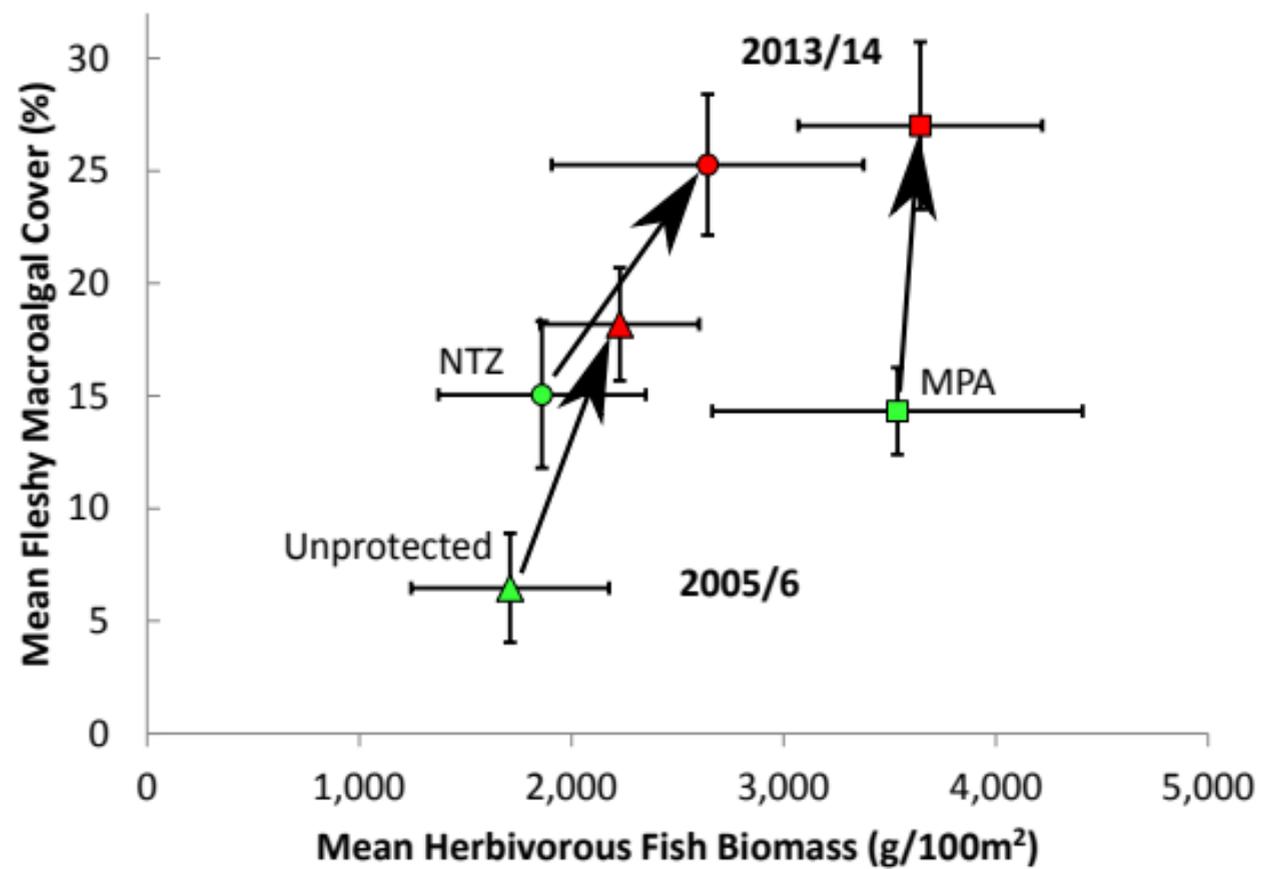


Figure 6(on next page)

Prediction of coral cover change on the Mesoamerican Reef.

Standardised regression coefficients for independent variables in AIC-selected optimum model of annual absolute change in hard coral cover from 2005/6 to 2013/14 for all (85) long-term monitoring sites. Coefficients reflect the number of standard deviations change in the dependent variable for a one standard deviation increase in each independent variable, while controlling for all other independent variables. Error bars are coefficient standard errors. Significant variables (in non-standardised regression) are highlighted (***) 0.001 level, * 0.05 level).

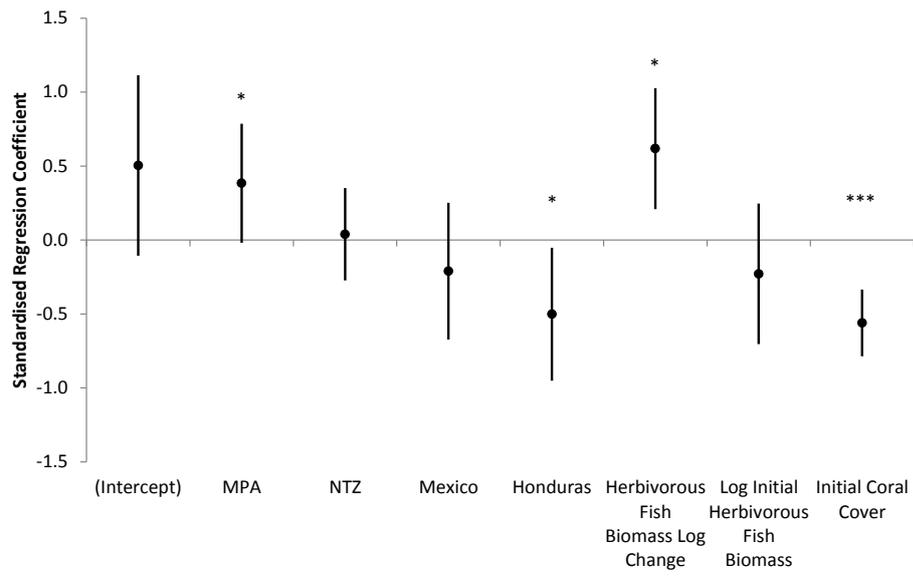


Table 1 (on next page)

Candidate predictor variables of coral cover change on the Mesoamerican Reef.

Site country classification was split into three binary variables. All sites in Northern Quintana Roo, Mexico are considered to have been impacted by hurricanes in 2005. Some sites were surveyed in August and September 2005 after Hurricane Emily (17/7/2005), although this was not considered to have a sizeable effect on the results as Wilma (21-24/10/2005) was the strongest hurricane registered in the Caribbean (Álvarez-Filip & Gil, 2006).

Variable	Type	Description
MEX	Binary	Binary indicator of location of site within Mexico
BEL	Binary	Binary indicator of location of site within Belize
HON	Binary	Binary indicator of location of site within Honduras
Island	Binary	Binary indicator of island or continental (mainland) site
Hurricane	Binary	Binary indicator of sites affected by 2005 hurricanes
Log ₁₀ (Fish_Initial)	Continuous	Logarithm of initial herbivorous fish biomass. Log values used to modify scale
Fish_Log_Diff	Continuous	Annual logarithmic change in herbivorous fish biomass
Algae_Initial	Continuous	Initial benthic cover by fleshy macroalgae. Decimal values from 0 to 1 representing 0 % to 100 %
Algae_Diff	Continuous	Absolute annual percentage change in fleshy macroalgal cover (decimal values)
Coral_Initial	Continuous	Initial benthic cover by hard coral. Decimal values from 0 to 1 representing 0 % to 100 %
NTZ	Binary	Binary indicator of location of site within a No Take Zone
MPA	Binary	Binary indicator of location of site within a Marine Protected Area