# Herbivorous fish unable to prevent rapidly increasing macroalgal cover on Mesoamerican reefs

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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. Despite the long-term reduction of herbivory capacity reported across the Caribbean, the Mesoamerican reef region displayed relatively low macroalgal cover at the onset of the study. Subsequently, increasing fleshy macroalgal cover was pervasive. Herbivorous fish populations were not responsible for this trend as fleshy macroalgal cover change was not correlated with initial herbivorous fish biomass or change, and the majority of sites experienced increases in macroalgae browser biomass. This contrasts the coral reef top-down herbivore control paradigm and suggests the role of external factors in making environmental conditions more favourable for algae. Increasing macroalgal cover typically suppresses ecosystem services and leads to degraded reef systems. Consequently, policy makers and local coral reef managers should reassess the focus on herbivorous fish protection and consider complimentary measures such as watershed management in order to arrest this trend.

1    **Herbivorous fish unable to prevent rapidly increasing macroalgal**

2    **cover on Mesoamerican reefs**

3

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15

16 **Abstract**

17 Long-term phase shifts from coral to macroalgal dominated reef systems are well-

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. Despite the long-term reduction of herbivory capacity reported across the

26 Caribbean, the Mesoamerican reef region displayed relatively low macroalgal cover at

27 the onset of the study. Subsequently, increasing fleshy macroalgal cover was pervasive.

28 Herbivorous fish populations were not responsible for this trend as fleshy macroalgal

29 cover change was not correlated with initial herbivorous fish biomass or change, and

30 the majority of sites experienced increases in macroalgae browser biomass. This

31 contrasts the coral reef top-down herbivore control paradigm and suggests the role of

32 external factors in making environmental conditions more favourable for algae.

33 Increasing macroalgal cover typically suppresses ecosystem services and leads to

34 degraded reef systems. Consequently, policy makers and local coral reef managers

35 should reassess the focus on herbivorous fish protection and consider complimentary

36 measures such as watershed management in order to arrest this trend.

37

38   **Introduction**

39   Caribbean coral reefs have experienced major declines over recent decades, with

40   substantial reductions in live coral cover accompanied by concomitant losses in reef

41   accretion and structural complexity (Schutte, Selig & Bruno, 2010; Alvarez-Filip et al.,

42   2011; Perry et al., 2015). Although a wide array of factors have contributed to reef

43   deterioration including coral diseases, coastal development and climate change, the

44   loss of key herbivores is thought to be a leading driver of ecosystem transition towards

45   macroalgal domination at many reef sites in the region (Hughes, 1994; Jackson et al.,

46   2014). Macroalgae compete with corals, reducing coral fecundity, recruitment and

47   survival via various mechanisms including overgrowth, shading and allelopathy

48   (McCook, Jompa & Diaz-Pulido, 2001; Hughes et al., 2007; Bruno et al., 2009; Rasher

49   et al., 2011). Today, populations of key herbivore taxa are diminished on many

50   Caribbean reefs. The sea urchin *Diadema antillarum* was previously an important grazer

51   in the Caribbean (Jackson et al., 2001). In 1983/4 *Diadema* suffered mass mortality

52   across the Caribbean due to putative disease and populations have subsequently

53   shown only limited recovery (Lessios, Robertson & Cubit, 1984; Kramer, 2003; Hughes

54   et al., 2010). Furthermore, long-term overfishing has resulted in marked reductions in

55   herbivorous fish populations at many sites across the region (Jackson et al., 2001;

56   Paddack et al., 2009).

57   Given the pivotal role of herbivores in controlling macroalgal growth (Mumby et al.,

58   2006), it is widely accepted that restoring populations of key herbivores enhances reef

59   resilience by controlling algal communities and facilitating coral recovery by freeing

60   space for coral recruits (Nyström, Folke & Moberg, 2000; McCook, Jompa & Diaz-

61  Pulido, 2001; McManus & Polsenberg, 2004; Bruno et al., 2009). Consequently, coral

62  reefs with high herbivore abundance are expected to have lower macroalgal cover and

63  greater coral cover (Jackson et al., 2014; Kramer et al., 2015). This paradigm has

64  encouraged global awareness campaigns promoting conservation and fisheries

65  management strategies to protect and restore populations of key herbivorous fishes,

66  particularly parrotfishes (Jackson et al., 2014). In the Mesoamerican region, for

67  example, Belize and Guatemala have banned the capture and possession of

68  herbivorous fishes (Kramer et al., 2015).

69  Direct evidence of herbivores' ability to facilitate the maintenance and recovery of

70  resilient coral reefs is limited. Experimental herbivore exclusion studies demonstrate the

71  action of *Diadema* and herbivorous fish grazing on macroalgal cover, although evidence

72  for the impact on corals is limited by the short-term nature and restricted spatial extent

73  of the experiments (Lirman, 2001; Burkepile & Hay, 2006, 2009; Hughes et al., 2007).

74  Observational studies tend to focus on inter-site comparisons without an explicit

75  temporal dimension, rather than tracking long-term reef change trajectories to provide a

76  more in-depth understanding of drivers of ecosystem dynamics (Karr et al., 2015). Little

77  consensus exists between studies, which exhibit contrasting patterns between

78  herbivorous fish populations and macroalgal cover. In a Caribbean-wide point-in-time

79  study, Newman et al. (2006) found a significant negative correlation between

80  herbivorous fish biomass and fleshy algal biomass; while for the Northern

81  Mesoamerican Reef of Mexico, Bozec et al. (2008) did not observe a relationship

82  between these variables. In a long-term study Ilves et al. (2011) observed increases in

83  both herbivorous fish abundance and algal cover in the Bahamas. On the Northern

84 Florida Reef Tract, Lirman & Biber (2000) observed no correlation between algal

85 biomass and cover and fish grazer abundance and consumption rates. Jackson et al.

86 (2014) found a significant negative correlation between parrotfish biomass and

87 macroalgal cover in 16 Caribbean locations, however no such relationship was

88 observed for a broader data set covering 46 locations. The lack of relationship between

89 herbivorous fish and macroalgal cover is evident for other regions: Carassou et al.

90 (2013), for example, found that macroalgal cover was not correlated with the biomass,

91 density and diversity of macroalgae feeders in the South Pacific.

92 To further understand the relationship between herbivory pressure and changes in

93 macroalgal cover we propose a simple conceptual framework (Fig. 1). Here, reefs may

94 experience one of four scenarios of temporal changes in fleshy macroalgal cover and

95 herbivorous fish biomass, a widely used proxy for herbivory intensity (Graham et al.,

96 2015). Principal ecological drivers are presented for each idealised scenario, although

97 in reality a number of drivers act in conjunction to varying extents. A phase shift from

98 coral to algae domination due to herbivore loss is represented by the scenario in the

99 upper-left quadrant. Here, decreasing herbivory leads to increasing macroalgal cover.

100 Conversely, in the bottom-right quadrant, *increases* in herbivorous fishes result in

101 reduced macroalgal cover. This quadrant represents the scenario sought by

102 management measures and fisheries regulations restricting extraction, particularly of

103 herbivorous fishes (Halpern, 2003; Lester et al., 2009; Selig & Bruno, 2010; Guarderas,

104 Hacker & Lubchenco, 2011).

105 Alternatively, a *positive* relationship may exist between macroalgal cover and

106 herbivorous fish biomass, as represented by the scenarios of the upper-right and

107    bottom-left quadrants of Fig. 1. This may occur when herbivores are food limited, as

108    evidenced by increases in herbivore abundance and biomass following algal growth and

109    by resource competition between *Diadema* and herbivorous fishes (Hay & Taylor, 1985;

110    Carpenter, 1990; Adam et al., 2011). In these scenarios, predominantly external drivers

111    such as nutrient availability, temperature and solar irradiance determine macroalgal

112    cover and herbivorous fish biomass responds according to food availability (Burkepile &

113    Hay, 2006; Ferrari et al., 2012). Numerous experimental manipulation studies have

114    reported the significant positive impact of nutrient enhancement on primary producer

115    abundance, although herbivory has generally been found to play a greater role

116    (Burkepile & Hay, 2006). Contrastingly, few studies have addressed the importance of

117    macroalgal productivity potential relating to environmental factors such as light

118    availability and temperature (Steneck & Dethier, 1994; Ferrari et al., 2012).

119    Herbivore and algal community composition also play an important role in herbivore-

120    algal dynamics. Subsequent to the *Diadema* mass mortality event of the early 1980's,

121    herbivorous fishes of the Scaridae and Acanthuridae families are recognised as the

122    primary herbivores on many Caribbean reefs (Jackson et al., 2014; Adam et al., 2015a).

123    While common *Acanthurus* surgeonfishes have a broad diet feeding on a combination

124    of turf algae, macroalgae and detritus, *Sparisoma* and *Scarus* parrotfishes are more

125    selective (Burkepile & Hay, 2011; Adam et al., 2015a). *Sparisoma* parrotfishes, with the

126    exception of the excavating *S. viride*, are macroalgae browsers, while *Scarus* spp.

127    primarily graze algal turfs (Bonaldo, Hoey & Bellwood, 2014; Adam et al., 2015b).

128    Consequently, a suitable mix of herbivores are required in order to both graze turf algae

129    to facilitate coral recruitment and to crop down macroalgal stands to reduce competition

130    with adult coral colonies (McCook, Jompa & Diaz-Pulido, 2001; Hughes et al., 2007;

131    Burkepile & Hay, 2008). However, herbivores' ability to effectively moderate macroalgal

132    cover is mediated by macroalgal predation defences (Rasher, Hoey & Hay, 2013). Such

133    defences are species specific and include morphological, structural, mineral and

134    chemical traits that deter herbivores, with several genera (e.g. *Lobophora*, *Peyssonnelia*

135    and *Codium*) being unpalatable (Hay, 1997; Smith, Hunter & Smith, 2010). These

136    defences likely influence herbivore feeding preferences and conversely algal community

137    structure is often influenced by herbivore mix, resulting in a complex interaction

138    between the two communities (Adam et al., 2015a).

139    Here, by following individual site trajectories, we examine the prevalence of the four

140    herbivorous fish and macroalgae change scenarios across 85 sites surveyed from 2005

141    to 2014 along the Mesoamerican Reef. We also consider herbivore functional group

142    composition and trajectories, and compare these with overall trends. Subsequently, we

143    evaluate the potential effects of herbivorous fish biomass, fleshy macroalgal cover and

144    other factors such as degree of protection, on changes in coral cover during the same

145    timeframe. Our hypothesis is that for sites where herbivory increased, fleshy macroalgal

146    cover decreased, and that herbivore biomass and the decline in macroalgal cover are

147    among the main factors explaining coral cover on today's reefs.

148

149    **Materials & Methods**

150    We used data produced by the Healthy Reefs Initiative (HRI) and the Atlantic and Gulf

151    Rapid Reef Assessment (AGRRA) programs, which include ecological censuses for 398

152    sites along the Mesoamerican Reef in Mexico, Belize, Guatemala and Honduras from

153    2005 to 2014. Site selection was based on benthic habitat maps produced by the

154    Millennium Reef Mapping Program, with 200 m × 200 m sites randomly selected

155    following stratification by geomorphological characteristics and depth (Andréfouët et al.,

156    2003; Kramer, 2003). The database contains 85 long-term monitoring sites that were

157    surveyed in 2005/2006 and 2013/2014 over a 7, 8 or 9-year period, a timeframe

158    sufficient to observe ecologically meaningful changes (Babcock et al., 2010). Of these

159    sites, 43 were repeatedly surveyed in four time periods (2005/2006, 2009/2010,

160    2011/2012 and 2013/2014). Sites were located primarily on the fore reef and reef crest

161    at a mean (± Standard Error s.e.m.) depth of 6.9 ± 0.2 m.

162    Benthic cover and reef fish surveys were performed according to AGRRA protocol, with

163    transects located haphazardly, parallel to the coast (Lang et al., 2010). The majority of

164    sites were surveyed at similar times during the summer year-on-year in order to

165    minimise seasonal effects. At each site an average of five to six 10 m-transects were

166    surveyed using point intercept methodology to determine benthic cover including hard

167    coral percentage cover and fleshy macroalgal percentage cover. The abundance and

168    total length (TL) of 81 key reef fish species, including herbivorous fishes of the Scaridae

169    and Acanthuridae families, was recorded in ten 30 m-long, 2 m-wide transects. Reef fish

170    abundance was subsequently converted to biomass density using standard allometric

171    length-weight conversions.

172    The data analyses focussed on the relation between three ecological indicators for each

173    reef site: herbivorous fish (Scaridae and Acanthuridae) biomass, fleshy macroalgal

174    cover (excluding turf and calcareous algae) and hard coral (scleractinians and *Millepora*

175    spp.) cover. Very few *Diadema* spp. were observed and therefore we focussed on reef

176    fishes as the principal herbivores. For all three ecological indicators, a number of

177    metrics were calculated to evaluate and examine temporal trends: absolute annual

178    change, annual relative rate of change and geometric rate of change. The metrics for

179    each ecological indicator (*I*) were determined as follows:

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

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

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

183    where $I_{t_f}$ is the value of the ecological indicator at the end of the period, $I_{t_0}$ is the initial

184    value and $\Delta t$ is the length of the period (in years). The former two metrics provide

185    complementary information, for example: if an ecological indicator such as coral cover

186    increases from 10 % to 15 %, the absolute change (equation (1)) is 5 %, while the

187    relative rate of change (equation (2)) indicates that coral cover has increased by 50 %

188    relative to its initial value. Geometric rate of change (equation (3)) was utilised in order

189    to assess and compensate for non-linearity in the relative rate of change, while still

190    providing an interpretable value (Côté et al., 2005).

191    Univariate comparison of ecological indicators was performed using ANOVA, t-tests or

192    non-parametric equivalents (Mann-Whitney U or Wilcoxon Signed Rank tests), based

193    on an assessment of normality and homogeneity of variance using Shapiro-Wilk and

194   Levene tests. To test our first hypothesis, herbivorous fish biomass was compared with

195   fleshy macroalgal cover using Spearman rank-order correlation due to non-normality.

196   Herbivorous fishes were further categorised according to feeding preferences as

197   macroalgae browsers (*Sparisoma* spp., with the exception of *S. viride*), turf grazers /

198   scrapers (*Scarus* spp. and *Acanthurus* spp.) or bioeroders (*Sparisoma viride*) (Bellwood

199   et al., 2004; Burkepile & Hay, 2011; Bonaldo, Hoey & Bellwood, 2014; Adam et al.,

200   2015a,b). Change in functional group biomass was compared with overall change in

201   herbivorous fish biomass using Spearman rank-order correlation. Furthermore, change

202   in macroalgal cover was compared with absolute levels of overall herbivorous fish and

203   macroalgae browser biomass both graphically by categorising sites by initial fish

204   biomass (based on deciles) and by using Spearman rank-order correlation.

205   To test our second hypothesis, change in absolute coral cover from 2005/6 to 2013/4 for

206   long-term monitoring sites was modelled using multiple linear regressions as model

207   assumptions were satisfied. To address the common problem of spatial autocorrelation

208   in multi-site studies we performed a Moran's I test on coral cover change by site

209   location which reported no spatial autocorrelation present (Moran's I = 0.070, P = 0.08).

210   The optimum regression model was selected based on Akaike Information Criterion

211   (AIC). Candidate independent variables were selected based on ecological relevance

212   and data availability (Supplementary Table 1 online). Potential collinearity among

213   predictor variables was examined using Pearson correlations and variance inflation

214   factors, and outliers were removed on the basis of Cook's D. All statistical analyses

215   were performed using R (R Core Team, 2014).

216

217 **Results**

218 Here we present herbivorous fish biomass and fleshy macroalgal cover average trends

219 for repeatedly surveyed sites and assess changes in these variables for long-term

220 monitoring sites. Subsequently we examine herbivorous fish feeding guilds and

221 geographic trends for long-term monitoring sites, and assess the effect of protection on

222 site trajectories. Finally we present the ecological drivers of long-term coral cover

223 change.

224 *Herbivorous fish biomass and macroalgal cover trends*

225 During the time period 2005 to 2014, regional averages showed a clear trend of

226 increasing fleshy macroalgal cover on the Mesoamerican Reef, while herbivorous fish

227 biomass remained relatively constant. Across 43 sites surveyed repeatedly in four time

228 periods (Fig. 2), mean herbivorous fish biomass did not change significantly (Wilcoxon

229 Signed Rank, $Z = 0$, $P = 1$), while mean macroalgal cover doubled during the same

230 period (Wilcoxon Signed Rank, $Z = -5.02$, $P < 0.001$). Between 2005/2006 and

231 2009/2010 mean herbivorous fish biomass decreased and mean fleshy macroalgal

232 cover increased significantly (Wilcoxon Signed Rank, $Z = 3.36$, $P < 0.001$ and $Z = -3.86$,

233 $P < 0.001$, respectively). From 2009/10 to 2011/12 the trend appeared to be reversed,

234 although the changes were not significant for macroalgae (Wilcoxon Signed Rank, $Z = -$

235 $2.95$, $P = 0.003$ and $Z = 0.59$, $P = 0.55$, respectively; Fig. 2). From 2011/2012 to

236 2013/2014 macroalgal cover increased significantly, while herbivorous fish biomass

237 remained unchanged (Wilcoxon Signed Rank, $Z = -3.81$, $P < 0.001$ and $Z = -0.35$, $P =$

238 $0.73$, 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 $g/100m^2$ 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 based on Bellwood et al. (2004),

254　communities of the Mesoamerican Reef present a mixture of guilds with 24.3 %

255　macroalgae browsers by biomass in 2013/14 (19.4 % in 2005/6), 48.4 % (57.3 %) turf

256　grazers / scrapers and 27.3 % (23.3 %) bioeroders. Herbivorous fish biomass and

257　macroalgal cover change were broadly similar between macroalgae browsers and

258　overall results (Fig. 3). Macroalgae browser biomass displayed a slightly greater

259　tendency for increase than overall herbivorous fish biomass, as observed for 61 % of

260　sites compared with 55 %, and site-level changes in these were correlated (Spearman,

261　$r_s$ = 0.70, P < 0.001).

262   Geographically, the principal trend was for increasing fleshy macroalgal cover and

263   herbivorous fish biomass in Mexico and northern Belize, including the atolls of Turneffe

264   and Lighthouse Reef, but for increasing fleshy macroalgal cover and decreasing

265   herbivorous fish biomass to the south in south-central and southern Belize, Glover's

266   Reef, Guatemala and Cayos Cochinos, Honduras (Fig. 3). However, the Bay Islands of

267   Honduras were exceptions to this broad north-to-south trend with Guanaja island

268   displaying the highest proportion of sites with increasing herbivorous fish biomass and

269   decreasing macroalgal cover. The only other three sites that experienced increasing

270   herbivorous fish biomass and decreasing macroalgal cover were located at Isla Mujeres

271   and Puerto Morelos in Mexico, and San Pedro in Belize.

272   Of the 85 long-term monitoring sites, 12 sites were located within No Take Zones

273   (NTZs) where all extractive practices are prohibited, 47 were within Marine Protected

274   Areas but not NTZs (MPAs) where reefs benefit from regulation but some extractive

275   practices are permitted, and the remaining 26 were unprotected. The level of protection

276   was observed to affect the initial levels of fleshy macroalgal cover and herbivorous fish

277   biomass, in addition to changes in these over time. In 2005/6, sites within NTZs

278   exhibited similar herbivorous fish biomass and fleshy macroalgal cover to sites located

279   elsewhere within Marine Protected Areas (Mann-Whitney, $U = 197$, $Z = -1.60$, $P = 0.11$;

280   and $U = 297$, $Z = 0.28$, $P = 0.78$ respectively; Fig. 5). Protected sites (both MPAs and

281   NTZs) displayed significantly higher initial macroalgal cover than unprotected sites

282   (Mann-Whitney, both $U \geq 247$, $Z \geq 2.85$, $P \leq 0.003$; Fig. 5), but only protected sites

283   outside of NTZs exhibited significantly higher initial herbivorous fish biomass than

284   unprotected sites (Mann-Whitney, MPA vs unprotected, $U = 819$, $Z = 2.40$, $P = 0.016$;

285     NTZ vs unprotected, U = 161, Z = 0.16, P = 0.89; Fig. 5). Along the protection gradient

286     (from unprotected, through MPA to no-take protection), sites appeared to experience a

287     greater increase in herbivorous fish biomass and a lesser increase in macroalgal cover,

288     although the differences were not statistically significant (ANOVA, annual geometric rate

289     of change in fish biomass, $F_{2,82}$ = 0.04, P = 0.97; annual geometric rate of change in

290     macroalgal cover, $F_{2,80}$ = 1.01, P = 0.37).

291     *Predicting coral cover change*

292     Across all 85 long-term monitoring sites, mean (± s.e.m.) hard coral cover increased

293     significantly from 12.2 ± 0.8 % in 2005/6 to 15.0 ± 0.8 % in 2013/14 (Wilcoxon Signed

294     Rank, Z = -3.81, P < 0.001). Individual sites displayed varying trajectories with annual

295     changes in coral cover ranging from -3.1 % to +2.7 %. The optimum linear regression

296     model for the annual absolute change in hard coral cover displayed a modest but

297     significant fit (Adjusted $R^2$ = 0.18, $F_{7,74}$ = 3.57, P = 0.002). The model included seven

298     predictor variables (Supplementary Table 1 online), of which four were significant: MPA,

299     country (Honduras), annual logarithmic change in herbivorous fish biomass and initial

300     hard coral cover (Fig. 6). Interpreting these significant variables, sites within Marine

301     Protected Areas experienced greater increases in coral cover than unprotected sites;

302     Honduran sites experienced lesser increases in coral cover than other countries; and

303     increases in herbivorous fish biomass corresponded with increases in coral cover. Initial

304     coral cover was the most significant predictor of coral cover change and therefore in

305     order to further understand its impact, sites were categorised as low (<10 %), medium

306     (10-20 %) or high (≥ 20%) initial coral cover. For the 12 long-term monitoring sites with

307     high initial coral cover, mean coral cover decreased over time (mean ± s.e.m. annual

308    change in coral cover of -0.6 ± 0.4 %), while coral cover increased for sites with lower

309    levels of initial cover (low initial coral cover, +0.6 ± 0.1 %; medium initial coral cover,

310    +0.4 ± 0.2 %).

311    Despite not being selected in the optimum regression model, we further explored the

312    relationship between coral and macroalgal cover due to the long-term ecological shifts

313    reported on many Caribbean reefs. Across all 85 long-term monitoring sites, mean (±

314    s.e.m.) macroalgal cover increased significantly from 12.0 ± 1.1 % in 2005/6 to 24.1 ±

315    1.5 % in 2013/14 (Wilcoxon Signed Rank, Z = -7.07, P < 0.001). We observed little or

316    no relationship between coral and macroalgal cover since macroalgal cover consistently

317    increased irrespective of changes in coral cover (Supplementary Fig. S3 online). All

318    initial coral cover categories (low (< 10 %), medium (10-20 %), and high (≥ 20 %))

319    experienced increases in fleshy macroalgal cover, and initial macroalgal cover, similarly

320    categorised, did not impact coral cover changes over time (ANOVA, $F_{2,82}$ = 1.10, P =

321    0.34).

322

323    **Discussion**

324    Substantial changes in the ecological composition of the Mesoamerican Reef were

325    evident in a time span of only nine years. The principal trend is for increasing fleshy

326    macroalgal cover, as observed at 83 % of long-term monitoring sites (Fig. 3). Mean

327    absolute cover of fleshy macroalgal cover increased by approximately 12 % in the

328    region between 2005 and 2014 (Fig. 2). Mean herbivorous fish biomass remained

329    relatively stable (Fig. 2), although displaying substantial site variation, with 55 % of sites

330   showing an increase in herbivorous fish biomass between 2005 and 2014 (Fig. 3). The

331   scenario of both increasing fleshy macroalgal cover and herbivorous fish biomass was

332   observed at 48 % of the 85 sites while the 'desirable' scenario of increasing herbivorous

333   fish biomass and decreasing macroalgal cover was the least frequent of all four

334   scenarios (Fig. 3). Similar trends were observed for the macroalgae-browsing fish guild

335   (Fig. 3), with site-level macroalgae browser biomass change correlating with overall

336   herbivorous fish biomass change. This suggests that fish herbivory was not a major

337   driver of fleshy macroalgal cover change on the majority of surveyed sites across the

338   Mesoamerican Reef (Fig. 3).

339   The clear pattern of increasing macroalgal cover and stable herbivorous fish biomass

340   on Mesoamerican reefs contrasts with the widely accepted coral reef top-down

341   herbivore control paradigm and management recommendations that advocate

342   increasing herbivory to control fleshy macroalgal cover (Nyström, Folke & Moberg,

343   2000; McCook, Jompa & Diaz-Pulido, 2001). This result is consistent with a multi-

344   decadal study reporting that macroalgal cover was not related to long-term parrotfish

345   losses due to fishing in the Philippines (Russ et al., 2015). Furthermore, we found that

346   coral cover on the Mesoamerican Reef was low and unrelated to macroalgal cover.

347   Since both coral cover and reduced herbivory were not responsible for increasing

348   macroalgal cover, external factors may have played a role. For the Mesoamerican Reef

349   region a growing body of evidence shows that rising nutrient levels is a worsening

350   problem that may be accelerating macroalgal increase. In the Mexican Caribbean

351   previous studies have observed elevated nutrient input to coral reefs due to coastal

352   development (Baker, Rodríguez-Martínez & Fogel, 2013; Hernández-Terrones et al.,

353    2015) and the subsequent degradation of reef systems (Bozec et al., 2008). In southern

354    Belize and Honduras riverine discharge and escalating reef sediment and nutrient loads

355    associated with urban and agricultural run-off may have played a role in increasing

356    macroalgal cover (Burke & Sugg, 2006; Carilli et al., 2009; Soto et al., 2009). Our

357    finding that fish herbivory is not responsible for macroalgal cover trends contrasts the

358    results of herbivore exclusion studies, which emphasize the relative importance of

359    herbivory over nutrient availability (McClanahan, Cokos & Sala, 2002; Burkepile & Hay,

360    2006, 2009; Sotka & Hay, 2009). However, contrary to the present study, such

361    experiments tend to be conducted on restricted spatial and temporal scales.

362    Unfortunately, site nutrient data are not widely available for the Mesoamerican Reef,

363    impeding a quantitative exploration of this effect in our analyses.

364    One alternative that could partially explain the rapid increases in fleshy macroalgae

365    across the Mesoamerican Reef is that reef ecosystems passed critical thresholds

366    beyond which herbivorous fishes are unable to control macroalgae due to either

367    excessive algal production and/or insufficient herbivory (Mumby, Hastings & Edwards,

368    2007). This is particularly relevant given that Caribbean reefs may suffer from

369    insufficient herbivory due to both the limited population recovery of *Diadema antillarum*

370    subsequent to previous mass mortality and the inability of herbivorous fish to

371    adequately compensate for this loss (McClenachan, 2009; Paddack et al., 2009;

372    Hughes et al., 2010). However, excessive algal production is unlikely on the

373    Mesoamerican Reef as regional average macroalgal cover increased from only 10 % in

374    2005/6 to 22 % in 2013/14 (Fig. 2), values that are likely considerably below ecosystem

375    thresholds for Caribbean reefs (Bruno et al., 2009). Furthermore, an examination of

376    macroalgal change by absolute levels of herbivorous fish biomass revealed increasing

377    fleshy macroalgal cover even for those sites with the highest initial fish biomass (the

378    uppermost deciles possessed average overall herbivorous fish biomass and

379    macroalgae-browsing fish biomass of 9,065 g/100m$^2$ and 1,762 g/100m$^2$ respectively;

380    Fig. 4). Although there is little consensus on Caribbean reef herbivorous fish thresholds,

381    a global assessment of the status of coral reef herbivorous fishes identified only 9 of

382    132 localities as having herbivorous fish biomass greater than 9,000 g/100m$^2$,

383    suggesting this to be a high benchmark (Mumby, Hastings & Edwards, 2007; Edwards

384    et al., 2014). In addition, a negative correlation between Caribbean reef herbivorous fish

385    biomass and fleshy algal biomass has been previously observed with a site maximum of

386    only 7,000 g/100m$^2$ approximately (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

390    species (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 macroalgal growth from 2009 to 2014 compared

395    with other sites (Supplementary Fig. S5 online). This suggests that the observed rapid

396    increases in fleshy macroalgae are not due to Mesoamerican reefs passing critical

397    thresholds of excessive algal production and/or insufficient herbivory.

398    Fish populations may impact benthic communities indirectly through mediation of

399    benthic competition. Sponges are a major component of Caribbean coral reef benthos

400    that compete for space with corals and macroalgae (Loh et al., 2015). Sponges'

401    competitive superiority over corals is well documented and likely due to a number of

402    mechanisms including shading, smothering and allelopathy (Porter & Targett, 1988; Loh

403    et al., 2015). Overfishing of spongivorous parrotfishes and angelfishes has been shown

404    to alter ecosystem dynamics through the alleviation of predation pressure on sponges

405    (Loh & Pawlik, 2014; Loh et al., 2015). Therefore, it is likely that at sites with high

406    parrotfish biomass, spongivory will control benthic sponge cover, indirectly benefiting

407    macroalgal and coral communities via reduced benthic competition. Unfortunately we

408    could not further explore the role of sponges in shaping benthic interactions as the

409    survey protocol does not focus on producing reliable sponge cover information (Lang et

410    al 2010).

411    Coral recovery on the Mesoamerican Reef was related to MPA protection and

412    increasing biomass of herbivorous fish, but not via the expected mechanism of

413    macroalgal declines through fish herbivory. Alternative mechanisms for the effect of

414    protection on reef corals are less well studied, but may include reduced disease

415    prevalence, and diminished physical reef damage through regulation of fishing and

416    recreational diving practices (Hasler & Ott, 2008; Lamb et al., 2015). Replenished fish

417    communities inside marine reserves can also drive coral recovery through ecological

418    processes not necessarily linked with herbivory. For example, trophically diverse fish

419    communities inside marine reserves have been shown to ameliorate coral disease

420    prevalence, although the pathways through which this takes place remain unclear

421 (Raymundo et al., 2009). Alternatively, coral cover and complexity may influence

422 herbivorous fish populations, rather than vice-versa, or the relationship may be purely

423 correlative with both indicators being driven by marine protection (Halpern, 2003; Selig

424 & Bruno, 2010; Alvarez-Filip, Gill & Dulvy, 2011).

425 Reef protection has a positive impact on herbivorous fish biomass and coral cover,

426 although fleshy macroalgal cover continued to increase at most sites. Although

427 protection impacted herbivorous fish biomass and macroalgal cover trajectories (Fig. 5),

428 initial differences between protected and unprotected sites tend to persist, with

429 unprotected sites continuing to display lower macroalgal cover. This may be attributable

430 to reserve age, as protected sites were located within reserves designated in 2003 (± 1

431 year) on average, and studies have shown that protection influence may be subject to a

432 lag effect (Selig & Bruno, 2010; Babcock et al., 2010). Furthermore, the use of

433 protection categories (No Take Zones (NTZs), Marine Protected Areas but not NTZs,

434 and unprotected) is a coarse measure of the actual range of protection and fishing

435 pressure experienced at sites. Additionally, local conditions and reserve regulations

436 often obfuscate protection impact due to variability of internal factors such as reef

437 community structure and enforcement level, and external impacts including local

438 stressors and global climate change (Mora et al., 2006; McClanahan et al., 2006; Selig,

439 Casey & Bruno, 2012). Finally, trophic effects may play a role since trophic cascades

440 are expected when populations of large predators are enhanced due to protection

441 (Estes et al., 2011). The protection of piscivores, for example, may result in herbivore

442 reduction and consequently elevated macroalgal growth inside marine reserves.

443 However, studies that explored this question have found that changes in predator

444    populations do not discernibly influence, or are even positively correlated with the

445    density, size, and biomass of herbivorous fishes, suggesting that top-down forces may

446    not play a strong role in regulating large-bodied herbivorous fish on coral reefs (Mumby

447    et al., 2006; Houk & Musburger, 2013; Rizzari, Bergseth & Frisch, 2015).

448    In conclusion, despite the long-term reduction of herbivory capacity reported across the

449    Caribbean, the Mesoamerican Reef displayed relatively low macroalgal cover at the

450    onset of this study. Subsequently, during the last decade, fleshy macroalgal cover

451    increased rapidly on Mesoamerican reefs. Herbivorous fish populations were not

452    responsible for this trend, contrasting the coral reef top-down herbivore control

453    paradigm and implicating the role of external factors in making environmental conditions

454    more favourable for algae. Increasing macroalgal cover typically suppresses ecosystem

455    services and leads to degraded reef systems. Consequently, policy makers and local

456    managers should consider complementary protection measures such as watershed

457    management, in addition to herbivorous fish protection, in order to arrest this trend.

458

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469

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637

**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).
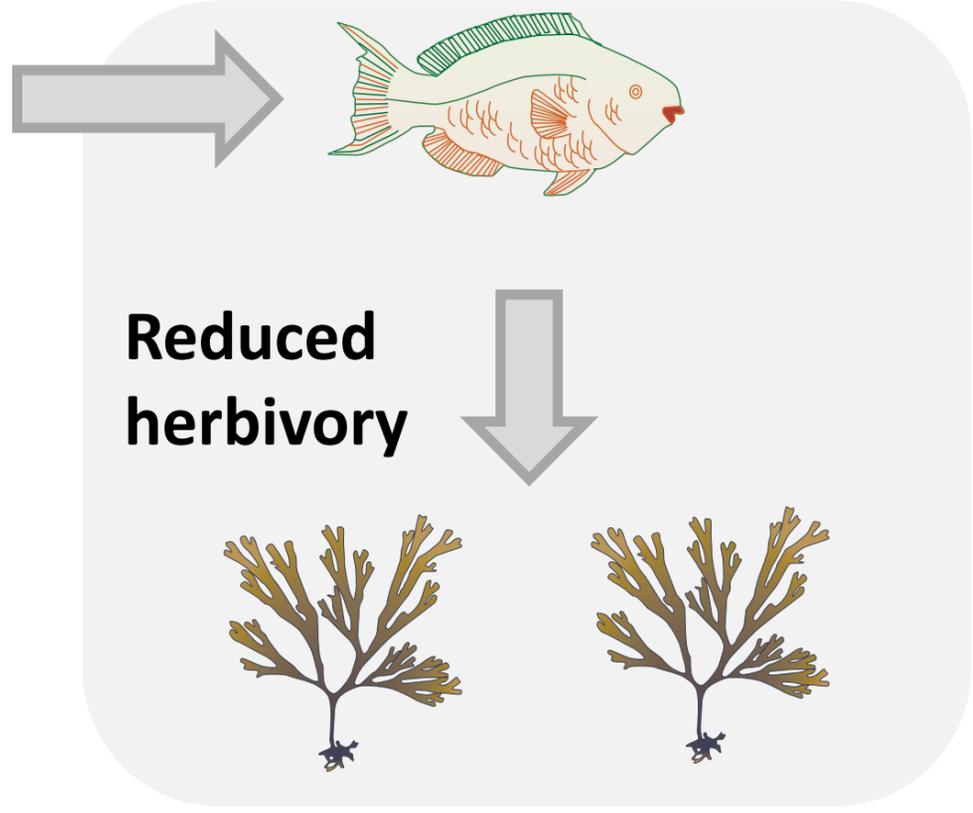
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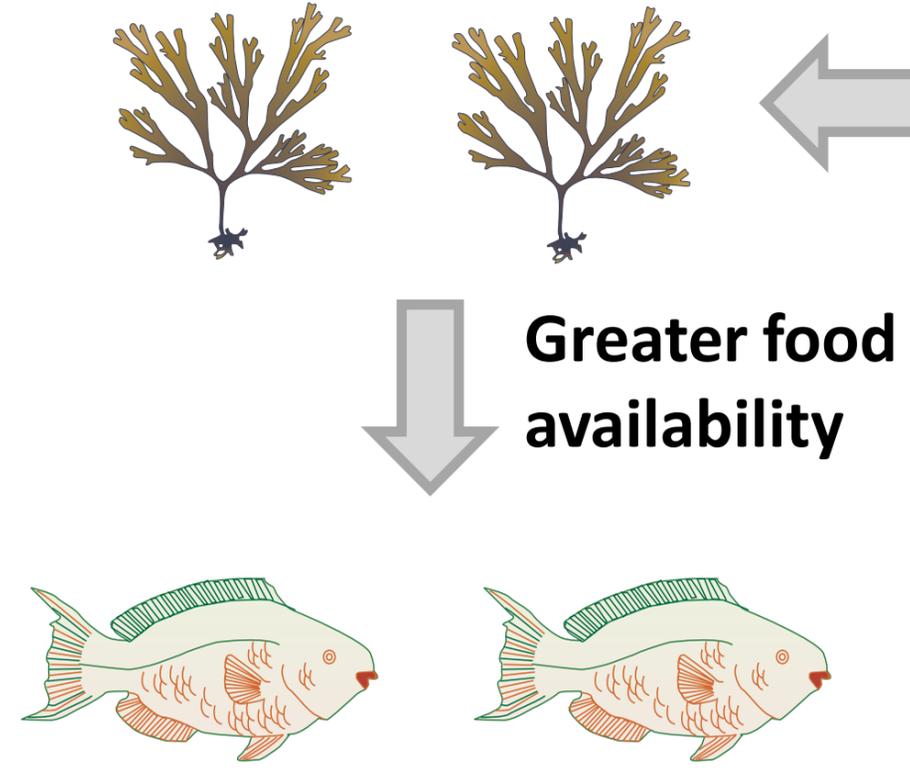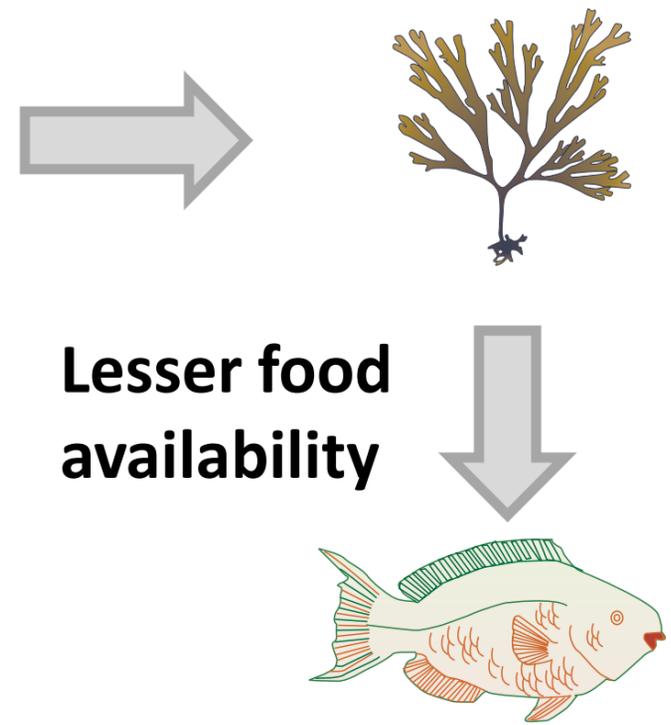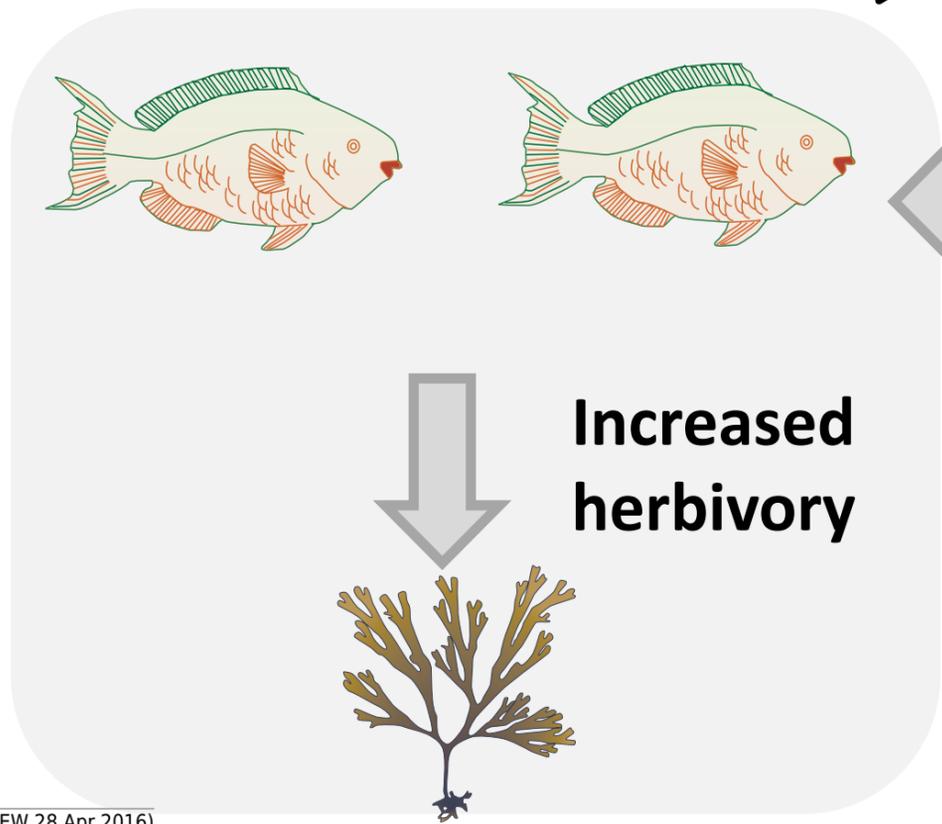
**Figure 2**(on next page)

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

Mean (± 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).
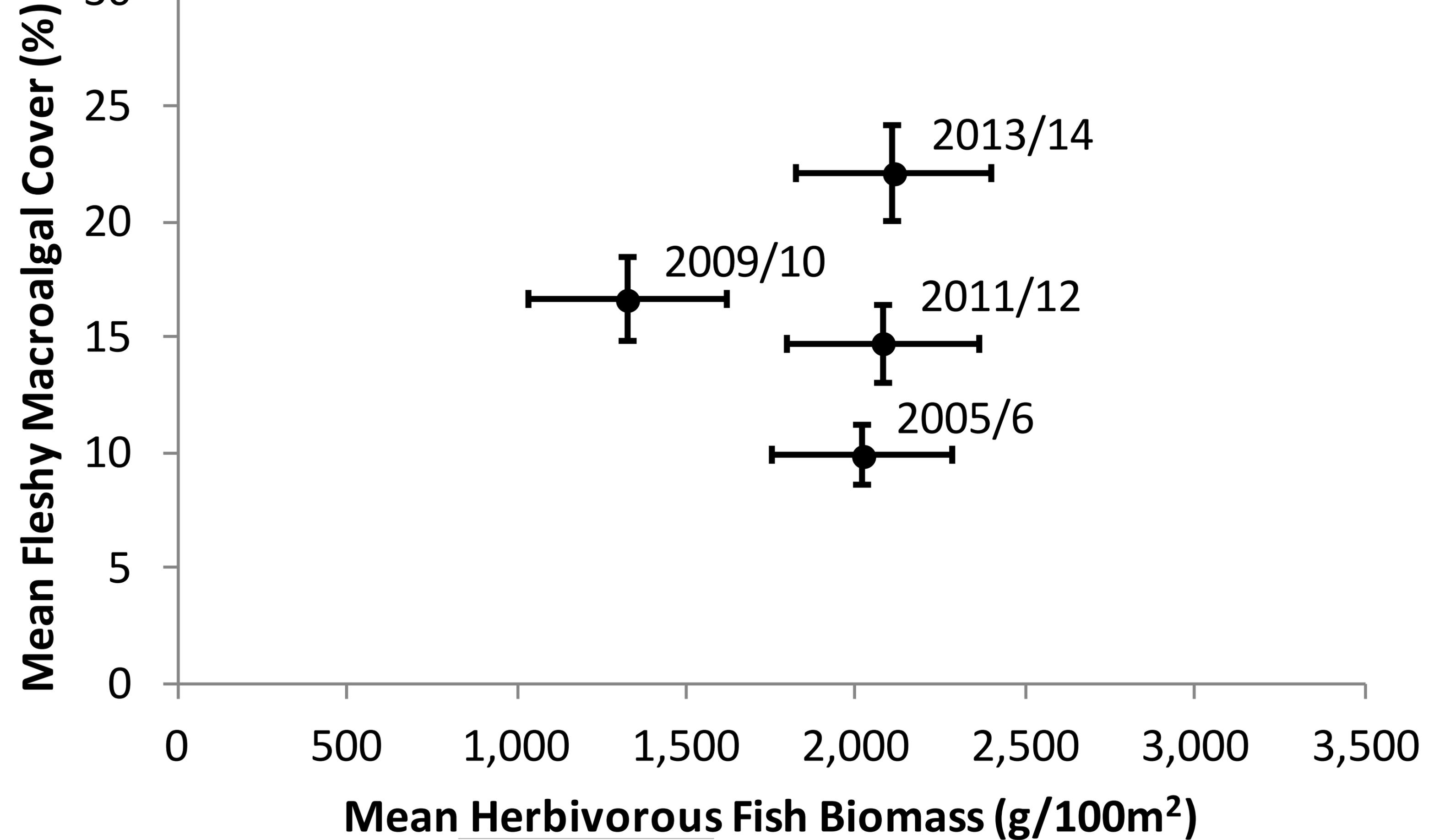
# Figure 3 (on next page)

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).
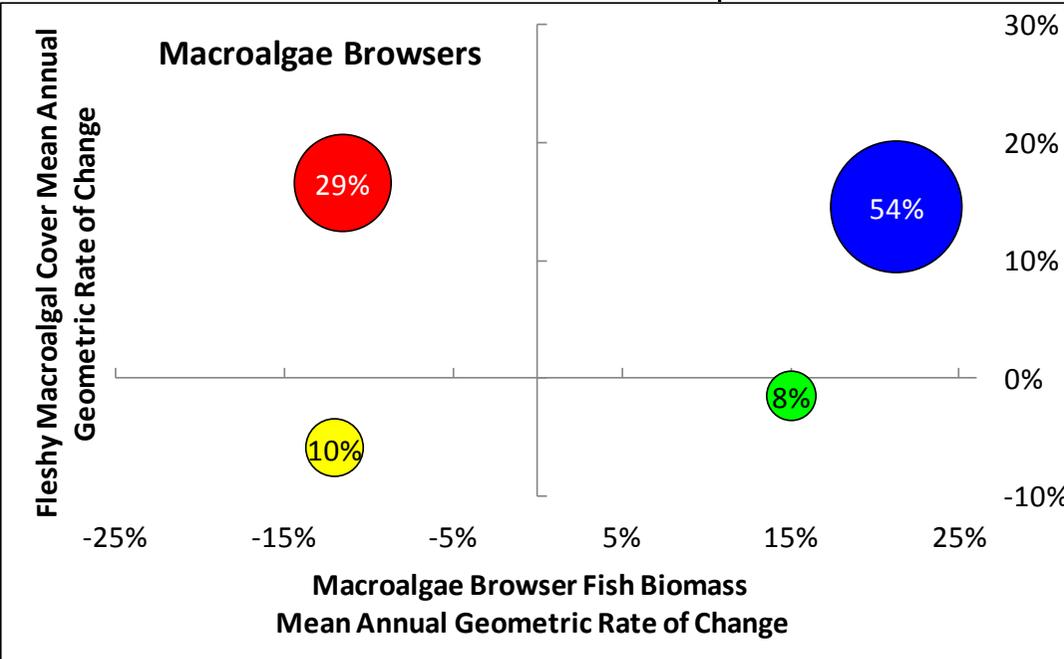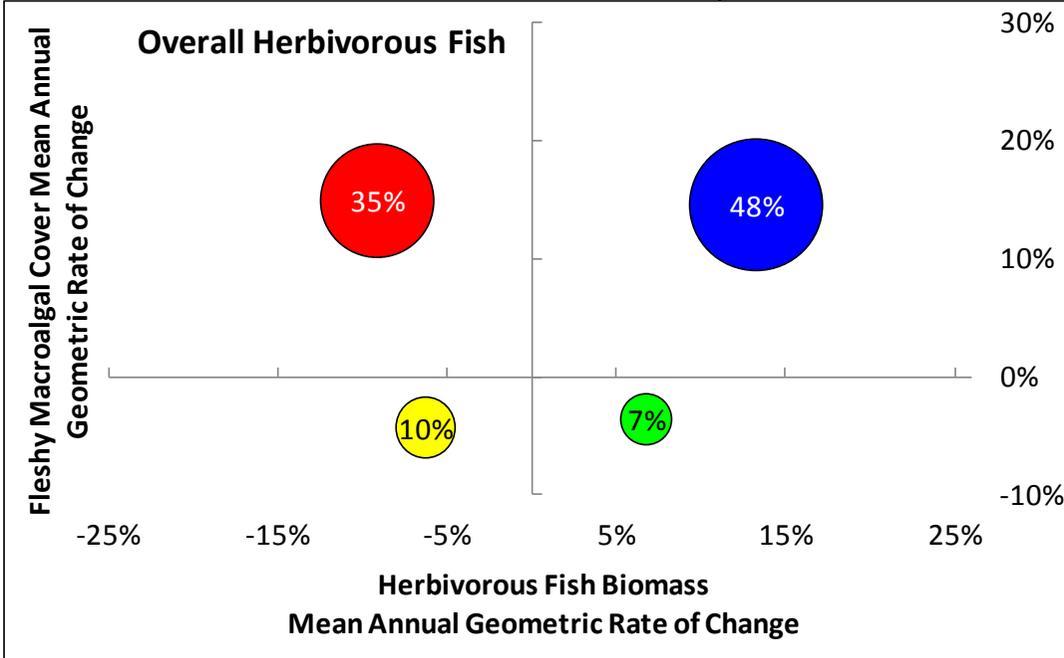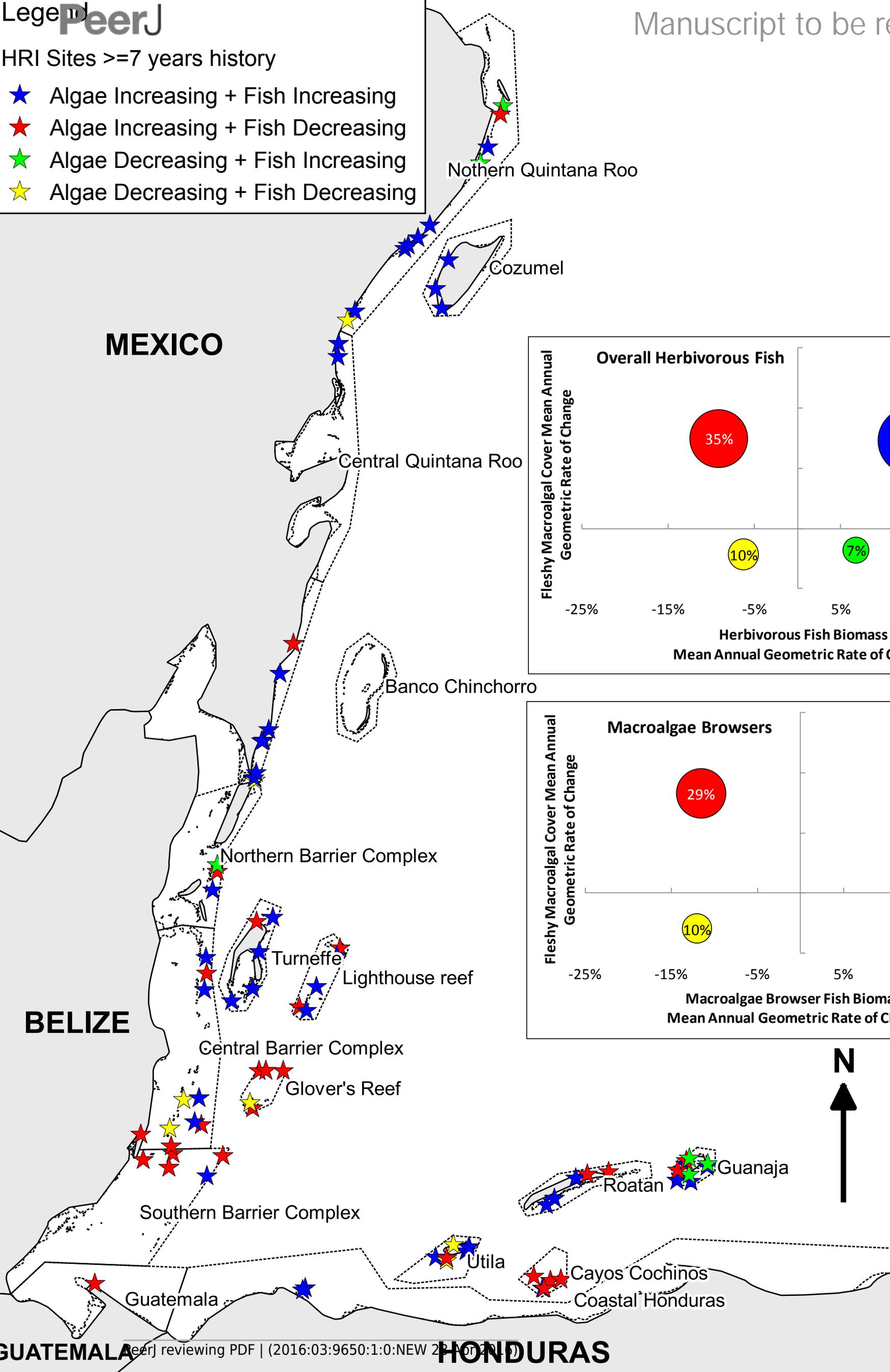
**Figure 4**(on next page)

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

A) Mean (± 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 (± 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.

**A)**

Mean Fleshy Macroalgal Cover (%)

- ● 2005/2006
- ● 2013/2014

Initial Herbivorous Fish Biomass Decile (g/100m²)

**B)**

Mean Fleshy Macroalgal Cover (%)

Initial Macroalgae Browser Biomass Decile (g/100m²)
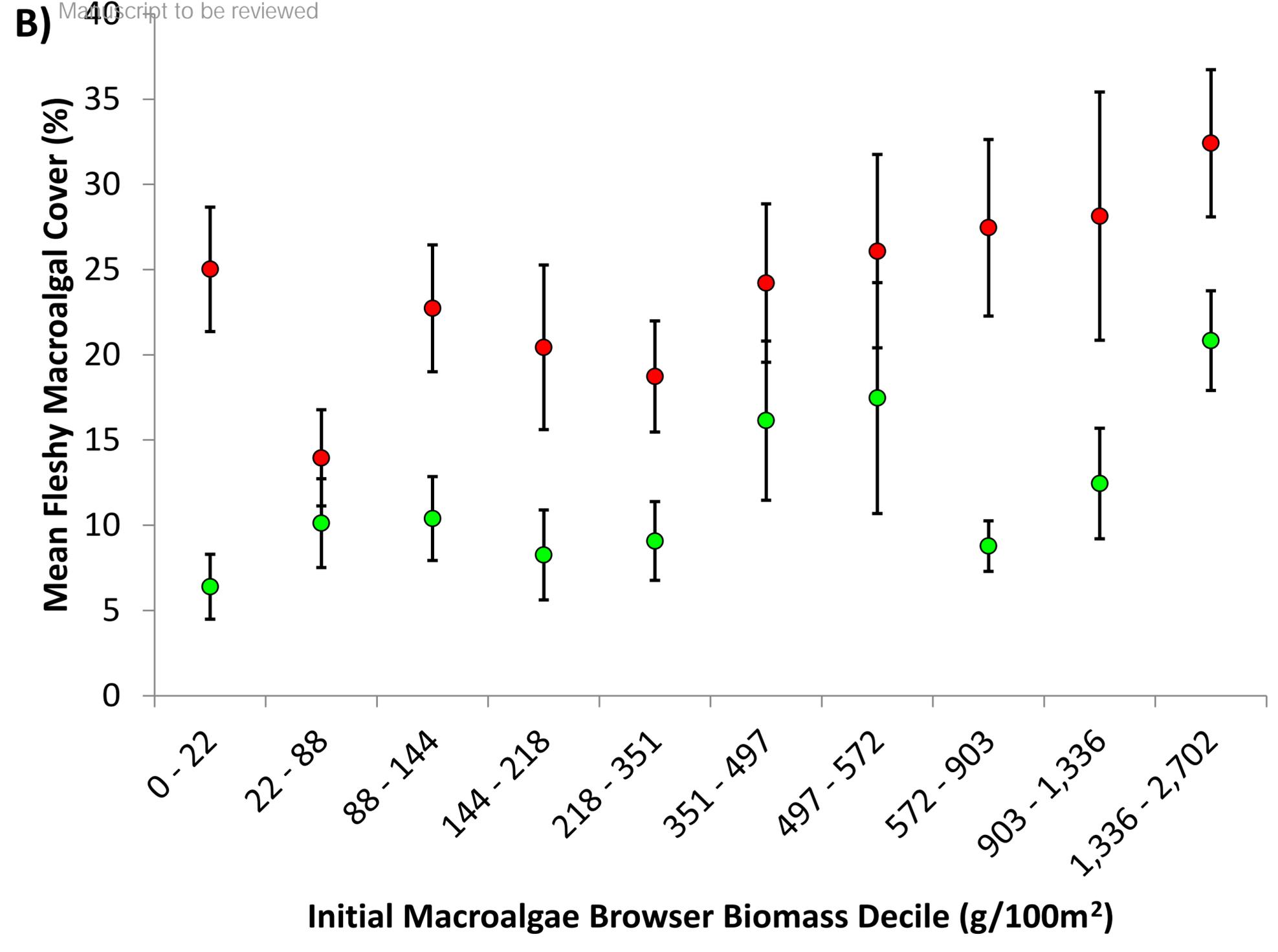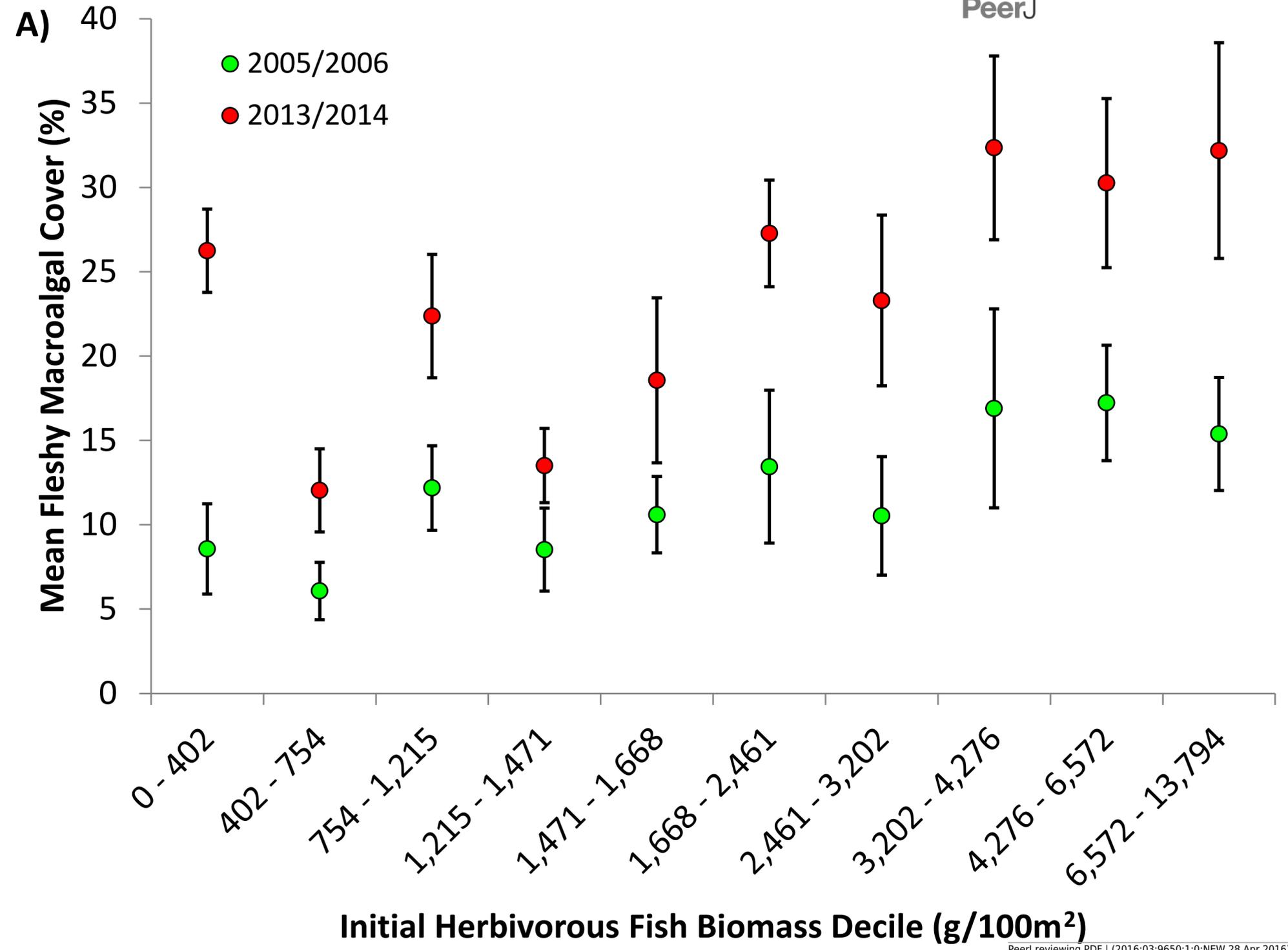
**Figure 5**(on next page)

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

Mean (± 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).
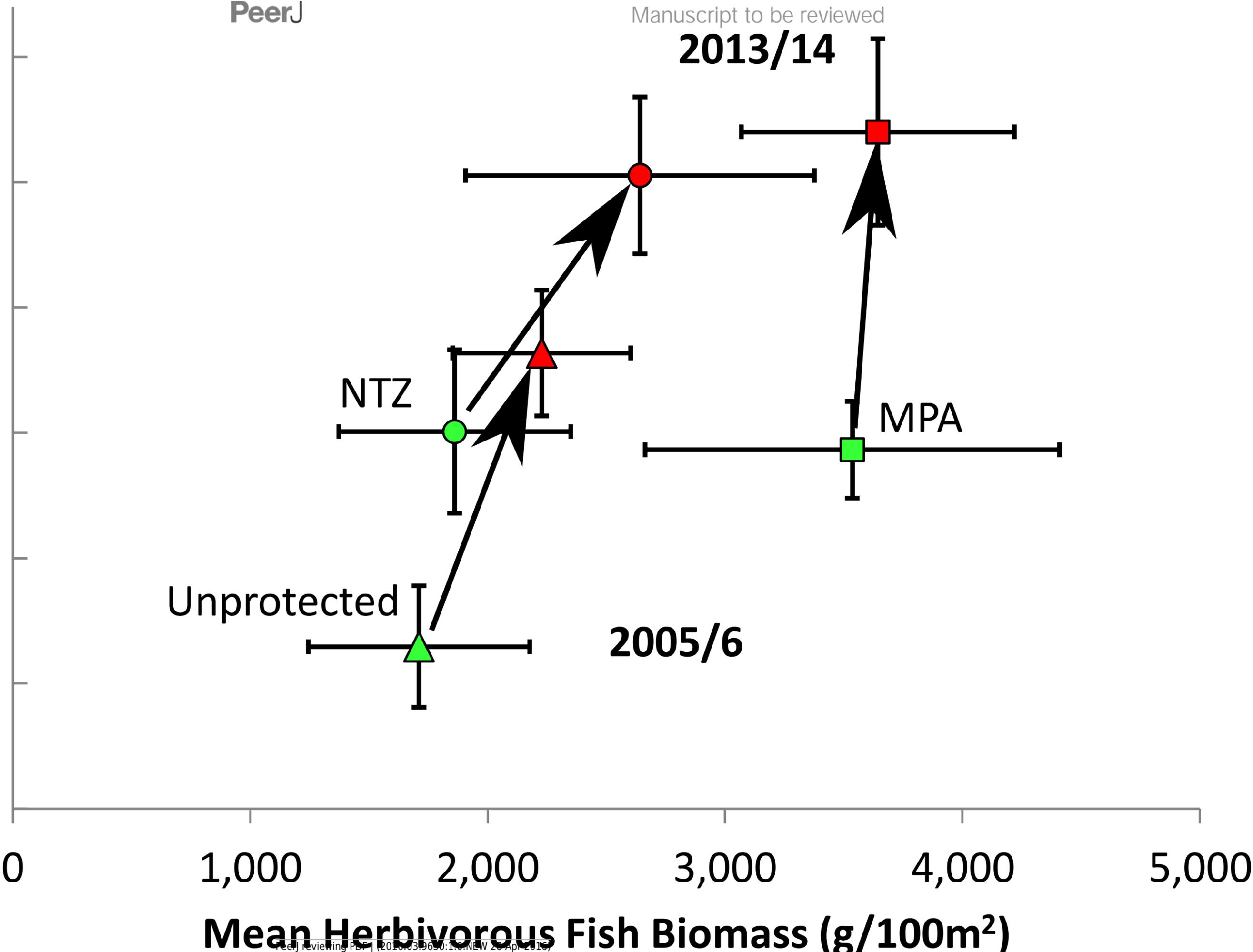
**Figure 6**(on next page)

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 long-term monitoring sites. MPA and NTZ are binary indicators of the location of sites within a Marine Protected Area or No Take Zone, respectively. Mexico and Honduras are binary indicators of the location of sites within those countries. 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).