# Rapidly increasing macroalgal cover not related to herbivorous fishes on Mesoamerican reefs

Adam Suchley, Melanie D McField, Lorenzo Alvarez-Filip

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  **Rapidly increasing macroalgal cover not related to herbivorous fishes**

2  **on Mesoamerican reefs**

4  Adam Suchley[1,2], Melanie D. McField[3] & Lorenzo Alvarez-Filip[2]

5  [1]Posgrado en Ciencias del Mar y Limnología, Instituto de Ciencias del Mar y Limnología, Universidad

6  Nacional Autónoma de México, Mexico City, Mexico

7  [2]Unidad Académica de Sistemas Arrecifales, Instituto de Ciencias del Mar y Limnología, Universidad

8  Nacional Autónoma de México, Puerto Morelos, Quintana Roo, Mexico

9  [3]Healthy Reefs for Healthy People Initiative, Smithsonian Institution, Ft Lauderdale, Florida, USA

11  Corresponding Author:

12  Lorenzo Alvarez-Filip[2]

13  Unidad Académica de Sistemas Arrecifales, Puerto Morelos, ICML, UNAM, Prol. Av. Niños Héroes S/N,

14  Domicilio conocido, C.P. 77580, Puerto Morelos, Quintana Roo, Mexico

15  Email address: lorenzo@cmarl.unam.mx

17  **Abstract**

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

19  documented in the Caribbean. Although the impact of coral diseases, climate change

20  and other factors is acknowledged, major herbivore loss through disease and

21  overfishing is often assigned a primary role. However, direct evidence for the link

22  between herbivore abundance, macroalgal and coral cover is sparse, particularly over

23  broad spatial scales. In this study we use a database of coral reef surveys performed at

24  85 sites along the Mesoamerican Reef of Mexico, Belize, Guatemala and Honduras, to

25  examine potential ecological links by tracking site trajectories over the period 2005-

26  2014. Despite the long-term reduction of herbivory capacity reported across the

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

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

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

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

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

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

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

34  Increasing macroalgal cover typically suppresses ecosystem services and leads to

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

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

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

## Introduction

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

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

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

43  2011; Perry et al., 2015). Although a wide array of factors have contributed to reef

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

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

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

47  2014). Macroalgae compete with corals, reducing coral fecundity, recruitment and

48  survival via various mechanisms including overgrowth, shading and allelopathy

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

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

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

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

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

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

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

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

57  Paddack et al., 2009).

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

59  2006), it is widely accepted that restoring populations of key herbivores enhances reef

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

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

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

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

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

65    encouraged global awareness campaigns promoting conservation and fisheries

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

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

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

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

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

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

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

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

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

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

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

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

78    consensus exists between studies, which exhibit contrasting patterns between

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

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

81    herbivorous fish biomass and fleshy algal biomass, whereas Loh et al. (2015) observed

82    that overfished Caribbean sites had lower macroalgal cover than protected sites. For

83    the Northern Mesoamerican Reef of Mexico, Bozec et al. (2008) did not observe a

84    relationship between herbivore biomass and macroalgal cover. In a long-term study,

85   Ilves et al. (2011) observed increases in both herbivorous fish abundance and algal

86   cover in the Bahamas. On the Northern Florida Reef Tract, Lirman & Biber (2000)

87   observed no correlation between algal biomass and cover and fish grazer abundance

88   and consumption rates. Jackson et al. (2014) found a significant negative correlation

89   between parrotfish biomass and macroalgal cover in 16 Caribbean locations, however

90   no such relationship was observed for a broader data set covering 46 locations. The

91   lack of relationship between herbivorous fish and macroalgal cover is evident for other

92   regions: Carassou et al. (2013), for example, found that macroalgal cover was not

93   correlated with the biomass, density and diversity of macroalgae feeders in the South

94   Pacific.

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

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

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

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

99   2015). Principal ecological drivers are presented for each idealised scenario, although

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

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

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

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

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

105  management measures and fisheries regulations restricting extraction, particularly of

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

107  Hacker & Lubchenco, 2011).

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

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

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

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

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

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

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

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

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

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

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

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

120    macroalgal productivity potential relating to environmental factors such as light

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

139 defences likely influence herbivore feeding preferences and conversely algal community

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

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

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

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

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

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

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

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

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

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

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

151

152 **Materials & Methods**

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

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

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

156   2005 to 2014. Site selection was based on benthic habitat maps produced by the

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

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

159   2003; Kramer, 2003). The database contains 85 long-term monitoring sites that were

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

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

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

163   2011/2012 and 2013/2014). Sites were located primarily on the fore reef and reef crest

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

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

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

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

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

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

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

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

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

173   abundance was subsequently converted to biomass density using standard allometric

174   length-weight conversions.

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

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

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

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

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

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

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

182    each ecological indicator ($I$) were determined as follows:

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

199    Herbivorous fishes were further categorised according to feeding preferences as

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

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

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

203    2015a,b). Change in functional group biomass was compared with overall change in

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

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

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

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

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

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

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

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

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

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

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

215    and data availability (Table S1). Potential collinearity among predictor variables was

216    examined using Pearson correlations and variance inflation factors, and outliers were

217    removed on the basis of Cook's D. All statistical analyses were performed using R (R

218    Core Team, 2014).

219

220    **Results**

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

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

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

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

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

226    change.

227    *Herbivorous fish biomass and macroalgal cover trends*

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

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

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

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

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

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

234    2009/2010 mean herbivorous fish biomass decreased and mean fleshy macroalgal

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

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

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

238    2.95, P = 0.003 and Z = 0.59, P = 0.55, respectively; Fig. 2). From 2011/2012 to

239    2013/2014 macroalgal cover increased significantly, while herbivorous fish biomass

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

241    0.73, respectively; Fig. 2).

242    Tracking individual trajectories of the 85 long-term monitoring sites surveyed over a 7, 8

243    or 9-year period permitted a more detailed investigation of the relation between the

244    temporal changes in herbivorous fish biomass and fleshy macroalgal cover.

245    Herbivorous fish biomass ranged from approximately 50 to 14,000 g/100m$^2$ and fleshy

246    macroalgal cover ranged from 0 to 57.5 %. There was no correlation between the

247    changes in herbivorous fish biomass and fleshy macroalgal cover for long-term

248    monitoring sites (Spearman, $r_s$ = -0.11, P = 0.35). Only 7 % of sites exhibited increased

249    herbivorous fish biomass and decreased macroalgal cover; 35 % of sites displayed

250    decreases in fish biomass and increases in macroalgal cover; almost half of the sites

251    (48 %) exhibited increases in both herbivorous fish biomass and macroalgal cover; and

252    10 % displayed decreased fish biomass and macroalgal cover (Fig. 3). Across all sites

253    macroalgal cover increased irrespective of initial conditions of herbivorous fish biomass

254    (Spearman, $r_s$ = -0.12, P = 0.3; Fig. 4A) and macroalgae browser biomass (Spearman,

255    $r_s$ = -0.21, P = 0.3; Fig. 4B).

256    Considering herbivorous fish feeding preferences based on Bellwood et al. (2004),

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

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

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

260    macroalgal cover change were broadly similar between macroalgae browsers and

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

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

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

264    $r_s$ = 0.70, P < 0.001).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

285    (Mann-Whitney, both U ≥ 247, Z ≥ 2.85, P ≤ 0.003; Fig. 5), but only protected sites

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

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

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

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

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

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

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

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

294    *Predicting coral cover change*

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

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

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

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

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

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

301    predictor variables (Table S1), of which four were significant: MPA, country (Honduras),

302    annual logarithmic change in herbivorous fish biomass and initial hard coral cover (Fig.

303    6). Interpreting these significant variables, sites within Marine Protected Areas

304    experienced greater increases in coral cover than unprotected sites; Honduran sites

305    experienced lesser increases in coral cover than other countries; and increases in

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

307   was the most significant predictor of coral cover change and therefore in order to further

308   understand its impact, sites were categorised as low (<10 %), medium (10-20 %) or

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

310   coral cover, mean coral cover decreased over time (mean ± s.e.m. annual change in

311   coral cover of -0.6 ± 0.4 %), while coral cover increased for sites with lower levels of

312   initial cover (low initial coral cover, +0.6 ± 0.1 %; medium initial coral cover, +0.4 ± 0.2

313   %).

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

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

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

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

318   1.5 % in 2013/14 (Wilcoxon Signed Rank, Z = -7.07, P < 0.001). We observed little or

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

320   increased irrespective of changes in coral cover (Fig. S3). All initial coral cover

321   categories (low (< 10 %), medium (10-20 %), and high (≥ 20 %)) experienced increases

322   in fleshy macroalgal cover, and initial macroalgal cover, similarly categorised, did not

323   impact coral cover changes over time (ANOVA, $F_{2,82}$ = 1.10, P = 0.34).

324

325   **Discussion**

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

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

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

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

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

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

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

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

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

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

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

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

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

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

340    Mesoamerican Reef (Fig. 3).

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

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

343    herbivore control paradigm and management recommendations that advocate

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

345    2000; McCook, Jompa & Diaz-Pulido, 2001). This result is consistent with a multi-

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

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

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

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

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

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

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

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

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

355 2015) and the subsequent degradation of reef systems (Bozec et al., 2008). In southern

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

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

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

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

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

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

362 2006, 2009; Sotka & Hay, 2009). However, contrary to the present study, such

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

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

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

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

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

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

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

370 2007). This is particularly relevant given that Caribbean reefs may suffer from

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

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

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

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

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

376  2005/6 to 22 % in 2013/14 (Fig. 2), values that are likely considerably below ecosystem

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

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

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

380  uppermost deciles possessed average overall herbivorous fish biomass and

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

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

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

384  132 localities as having herbivorous fish biomass greater than 9,000 g/100m$^2$,

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

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

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

388  only 7,000 g/100m$^2$ approximately (Newman et al., 2006).

389  The threshold hypothesis would be particularly relevant if the decline in average

390  herbivorous fish biomass between 2005/6 and 2009/10 resulted in changes in the

391  relative proportion of key functional groups, favouring non-macroalgae-browsing

392  species (Adam et al., 2015b; Fig. 2). However, the relative proportions of the three main

393  herbivorous fish functional groups remained stable during the study period (Fig. S4).

394  Additionally, a close examination of those sites that suffered the greatest herbivorous

395  fish biomass losses between 2005 and 2009 revealed that these sites experienced

396  similar macroalgal growth from 2009 to 2014 compared with other sites (Fig. S5). This

397  suggests that the observed rapid increases in fleshy macroalgae are not due to

398    Mesoamerican reefs passing critical thresholds of excessive algal production and/or

399    insufficient herbivory.

400    Fish populations may impact benthic communities indirectly through mediation of

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

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

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

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

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

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

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

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

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

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

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

412    al 2010).

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

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

444    reduction and consequently elevated macroalgal growth inside marine reserves.

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

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

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

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

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

450

451    **Conclusions**

452    Despite the long-term reduction of herbivory capacity reported across the Caribbean,

453    the Mesoamerican Reef displayed relatively low macroalgal cover at the onset of this

454    study. Subsequently, during the last decade, fleshy macroalgal cover increased rapidly

455    on Mesoamerican reefs. Herbivorous fish populations were not responsible for this

456    trend, contrasting the coral reef top-down herbivore control paradigm and implicating

457    the role of external factors in making environmental conditions more favourable for

458    algae. Increasing macroalgal cover typically suppresses ecosystem services and leads

459    to degraded reef systems. Consequently, policy makers and local managers should

460    consider complementary protection measures such as watershed management, in

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

462

463    **Acknowledgments**

464 The authors recognize the invaluable efforts of Healthy Reefs Initiative (HRI) partner

465 organizations and individual field researchers who collaborated over the years in

466 collecting the data. Data contributors are listed in HRI Report Cards and supplemental

467 reports, available at www.healthyreefs.org. In particular Ian Drysdale, Marisol Rueda,

468 Ana Giro and Roberto Pott are recognised for coordinating field surveys, training and

469 data entry. The HRI database is processed and managed in conjunction with Ken Marks

470 and Judith Lang. Our manuscript was significantly improved by insightful comments

471 from R. Iglesias-Prieto, J. Bruno and one anonymous reviewer.

472

## 473 References

474 Adam TC., Schmitt RJ., Holbrook SJ., Brooks AJ., Edmunds PJ., Carpenter RC., Bernardi G. 2011. Herbivory,
475     connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS One*
476     6:e23717.

477 Adam TC., Burkepile DE., Ruttenberg BI., Paddack MJ. 2015a. Herbivory and the resilience of Caribbean coral reefs:
478     knowledge gaps and implications for management. *Marine Ecology Progress Series* 520:1–20.

479 Adam TC., Kelley M., Ruttenberg BI., Burkepile DE. 2015b. Resource partitioning along multiple niche axes drives
480     functional diversity in parrotfishes on Caribbean coral reefs. *Oecologia* 179:1173–1185.

481 Alvarez-Filip L., Dulvy NK., Côté IM., Watkinson AR., Gill JA. 2011. Coral identity underpins architectural complexity
482     on Caribbean reefs. *Ecological Applications* 21:2223–2231.

483 Álvarez-Filip L., Gil I. 2006. Effects of Hurricanes Emily and Wilma on coral reefs in Cozumel, Mexico. *Coral Reefs*
484     25:583.

485 Alvarez-Filip L., Gill JA., Dulvy NK. 2011. Complex reef architecture supports more small-bodied fishes and longer
486     food chains on Caribbean reefs. *Ecosphere* 2:118.

487 Andréfouët S., Kramer P., Torres-Pulliza D., Joyce KE., Hochberg EJ., Garza-Pérez R., Mumby PJ., Riegl B.,
488     Yamano H., White WH., Zubia M., Brock JC., Phinn SR., Naseer A., Hatcher BG., Muller-Karger FE. 2003.
489     Multi-site evaluation of IKONOS data for classification of tropical coral reef environments. *Remote Sensing of*
490     *Environment* 88:128–143.

491 Babcock RC., Shears NT., Alcala AC., Barrett NS., Edgar GJ., Lafferty KD., McClanahan TR., Russ GR. 2010.
492     Decadal trends in marine reserves reveal differential rates of change in direct and indirect effects. *Proceedings*
493     *of the National Academy of Sciences of the United States of America* 107:18256–18261.

494 Baker DM., Rodríguez-Martínez RE., Fogel ML. 2013. Tourism's nitrogen footprint on a Mesoamerican coral reef.
495     *Coral Reefs* 32:691–699.

496 Bellwood DR., Hughes TP., Folke C., Nyström M. 2004. Confronting the coral reef crisis. *Nature* 429:827–833.

497 Bonaldo RM., Hoey AS., Bellwood DR. 2014. The ecosystem roles of parrotfishes on tropical reefs. *Oceanography*
498     *and Marine Biology: An Annual Review* 52:81–132.

499  Bozec YM., Acosta-González G., Núñez-Lara E., Arias-González JE. 2008. Impacts of coastal development on
500      ecosystem structure and function of Yucatan coral reefs, Mexico. *Proceedings of the 11th International Coral*
501      *Reef Symposium*:691–695.

502  Bruno JF., Sweatman H., Precht WF., Selig ER., Schutte VGW. 2009. Assessing evidence of phase shifts from coral
503      to macroalgal dominance on coral reefs. *Ecology* 90:1478–1484.

504  Burke L., Sugg Z. 2006. *Hydrologic Modeling of Watersheds Discharging Adjacent to the Mesoamerican Reef*.
505      Washington, D.C.

506  Burkepile DE., Hay ME. 2006. Herbivore vs. nutrient control of marine primary producers: context-dependent effects.
507      *Ecology* 87:3128–3139.

508  Burkepile DE., Hay ME. 2008. Herbivore species richness and feeding complementarity affect community structure
509      and function on a coral reef. *Proceedings of the National Academy of Sciences of the United States of America*
510      105:16201–16206.

511  Burkepile DE., Hay ME. 2009. Nutrient versus herbivore control of macroalgal community development and coral
512      growth on a Caribbean reef. *Marine Ecology Progress Series* 389:71–84.

513  Burkepile DE., Hay ME. 2011. Feeding complementarity versus redundancy among herbivorous fishes on a
514      Caribbean reef. *Coral Reefs* 30:351–362.

515  Carassou L., Léopold M., Guillemot N., Wantiez L., Kulbicki M. 2013. Does herbivorous fish protection really improve
516      coral reef resilience? A case study from New Caledonia (South Pacific). *PLoS One* 8:e60564.

517  Carilli JE., Prouty NG., Hughen KA., Norris RD. 2009. Century-scale records of land-based activities recorded in
518      Mesoamerican coral cores. *Marine Pollution Bulletin* 58:1835–1842.

519  Carpenter RC. 1990. Mass mortality of *Diadema antillarum*. II. Effects on population densities and grazing intensity of
520      parrotfishes and surgeonfishes. *Marine Biology* 104:79–86.

521  Côté IM., Gill JA., Gardner TA., Watkinson AR. 2005. Measuring coral reef decline through meta-analyses.
522      *Philosophical Transactions of the Royal Society of London B* 360:385–395.

523  Edwards CB., Friedlander AM., Green AG., Hardt MJ., Sala E., Sweatman HP., Williams ID., Zgliczynski B., Sandin
524      SA., Smith JE. 2014. Global assessment of the status of coral reef herbivorous fishes: evidence for fishing
525      effects. *Proceedings of The Royal Society of London B* 281:20131835.

526  Estes JA., Terborgh J., Brashares JS., Power ME., Berger J., Bond WJ., Carpenter SR., Essington TE., Holt RD.,
527      Jackson JBC., Marquis RJ., Oksanen L., Oksanen T., Paine RT., Pikitch EK., Ripple WJ., Sandin SA., Scheffer
528      M., Schoener TW., Shurin JB., Sinclair ARE., Soulé ME., Virtanen R., Wardle DA. 2011. Trophic downgrading
529      of planet Earth. *Science* 333:301–306.

530  Ferrari R., Gonzalez-Rivero M., Ortiz JC., Mumby PJ. 2012. Interaction of herbivory and seasonality on the dynamics
531      of Caribbean macroalgae. *Coral Reefs* 31:683–692.

532  Graham NAJ., Jennings S., MacNeil MA., Mouillot D., Wilson SK. 2015. Predicting climate-driven regime shifts versus
533      rebound potential in coral reefs. *Nature* 518:94–97.

534  Guarderas AP., Hacker SD., Lubchenco J. 2011. Ecological effects of marine reserves in Latin America and the
535      Caribbean. *Marine Ecology Progress Series* 429:219–225.

536  Halpern BS. 2003. The impact of marine reserves: do reserves work and does reserve size matter? *Ecological*
537      *Applications* 13:S117–S137.

538  Hasler H., Ott JA. 2008. Diving down the reefs? Intensive diving tourism threatens the reefs of the northern Red Sea.
539      *Marine Pollution Bulletin* 56:1788–1794.

540  Hay ME. 1997. The ecology and evolution of seaweed-herbivore interactions on coral reefs. *Coral Reefs* 16:S67–
541      S76.

542  Hay ME., Taylor PR. 1985. Competition between herbivourous fishes and urchins on Caribbean reefs. *Oecologia*
543      65:591–598.

544  Hernández-Terrones LM., Null KA., Ortega-Camacho D., Paytan A. 2015. Water quality assessment in the Mexican
545      Caribbean: impacts on the coastal ecosystem. *Continental Shelf Research* 102:62–72.

546  Houk P., Musburger C. 2013. Trophic interactions and ecological stability across coral reefs in the Marshall Islands.

547    *Marine Ecology Progress Series* 488:23–34.

548    Hughes TP. 1994. Catastrophes, phase shifts and large-scale degradation of a Caribbean coral reef. *Science*
549        265:1547–1551.

550    Hughes TP., Rodrigues MJ., Bellwood DR., Ceccarelli D., Hoegh-Guldberg O., McCook L., Moltschaniwskyj N.,
551        Pratchett MS., Steneck RS., Willis B. 2007. Phase shifts, herbivory, and the resilience of coral reefs to climate
552        change. *Current Biology* 17:360–365.

553    Hughes TP., Graham NAJ., Jackson JBC., Mumby PJ., Steneck RS. 2010. Rising to the challenge of sustaining coral
554        reef resilience. *Trends in Ecology and Evolution* 25:633–642.

555    Ilves KL., Kellogg LL., Quattrini AM., Chaplin GW., Hertler H., Lundberg JG. 2011. Assessing 50-year change in
556        Bahamian reef fish assemblages: evidence for community response to recent disturbance? *Bulletin of Marine*
557        *Science* 87:567–588.

558    Jackson JB., Kirby MX., Berger WH., Bjorndal KA., Botsford LW., Bourque BJ., Bradbury RH., Cooke R., Erlandson
559        J., Estes J a., Hughes TP., Kidwell S., Lange CB., Lenihan HS., Pandolfi JM., Peterson CH., Steneck RS.,
560        Tegner MJ., Warner RR. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science*
561        293:629–637.

562    Jackson JBC., Donovan MK., Cramer KL., Lam V. 2014. *Status and Trends of Caribbean Coral Reefs: 1970-2012*.
563        Gland, Switzerland: Global Coral Reef Monitoring Network, IUCN.

564    Karr KA., Fujita R., Halpern BS., Kappel C V., Crowder L., Selkoe KA., Alcolado PM., Rader D. 2015. Thresholds in
565        Caribbean coral reefs: implications for ecosystem-based fishery management. *Journal of Applied Ecology*
566        52:402–412.

567    Kramer PA. 2003. Synthesis of coral reef health indicators for the western Atlantic: results of the AGRRA program
568        (1997-2000). *Atoll Research Bulletin* 496:1–58.

569    Kramer P., McField M., Álvarez Filip L., Drysdale I., Rueda Flores M., Giró A., Pott R. 2015. *2015 Report Card for the*
570        *Mesoamerican Reef*. Healthy Reefs Initiative. *Available at http://www.healthyreefs.org*.

571    Lamb JB., Williamson DH., Russ GR., Willis BL. 2015. Protected areas mitigate diseases of reef-building corals by
572        reducing damage from fishing. *Ecology* 96:2555–2567.

573    Lang JC., Marks KW., Kramer PA., Kramer PR., Ginsburg RN. 2010. *AGRRA Protocols Version 5.4*. The Atlantic and
574        Gulf Rapid Reef Assessment (AGRRA) Program.

575    Lessios HA., Robertson DR., Cubit JD. 1984. Spread of *Diadema* mass mortality through the Caribbean. *Science*
576        226:335–337.

577    Lester SE., Halpern BS., Grorud-Colvert K., Lubchenco J., Ruttenberg BI., Gaines SD., Airamé S., Warner RR. 2009.
578        Biological effects within no-take marine reserves: a global synthesis. *Marine Ecology Progress Series* 384:33–
579        46.

580    Lirman D. 2001. Competition between macroalgae and corals: effects of herbivore exclusion and increased algal
581        biomass on coral survivorship and growth. *Coral Reefs* 19:392–399.

582    Lirman D., Biber P. 2000. Seasonal dynamics of macroalgal communities of the Northern Florida Reef Tract.
583        *Botanica Marina* 43:305–314.

584    Loh T-L., McMurray SE., Henkel TP., Vicente J., Pawlik JR. 2015. Indirect effects of overfishing on Caribbean reefs:
585        sponges overgrow reef-building corals. *PeerJ* 3:e901.

586    Loh T-L., Pawlik JR. 2014. Chemical defenses and resource trade-offs structure sponge communities on Caribbean
587        coral reefs. *Proceedings of the National Academy of Sciences of the United States of America* 111:4151–4156.

588    McClanahan TR., Marnane MJ., Cinner JE., Kiene WE. 2006. A comparison of marine protected areas and
589        alternative approaches to coral-reef management. *Current Biology* 16:1408–1413.

590    McClenachan L. 2009. Historical declines of goliath grouper populations in South Florida, USA. *Endangered Species*
591        *Research* 7:175–181.

592    McCook LJ., Jompa J., Diaz-Pulido G. 2001. Competition between corals and algae on coral reefs: a review of
593        evidence and mechanisms. *Coral Reefs* 19:400–417.

594    McManus JW., Polsenberg JF. 2004. Coral-algal phase shifts on coral reefs: ecological and environmental aspects.

595      *Progress in Oceanography* 60:263–279.

596      Mora C., Andrèfouët S., Costello MJ., Kranenburg C., Rollo A., Veron J., Gaston KJ., Myers RA. 2006. Coral reefs
597      and the global network of Marine Protected Areas. *Science* 312:1750–1751.

598      Mumby PJ., Dahlgren CP., Harborne AR., Kappel C V., Micheli F., Brumbaugh DR., Holmes KE., Mendes JM., Broad
599      K., Sanchirico JN., Buch K., Box S., Stoffle RW., Gill AB. 2006. Fishing, trophic cascades, and the process of
600      grazing on coral reefs. *Science* 311:98–101.

601      Mumby PJ., Hastings A., Edwards HJ. 2007. Thresholds and the resilience of Caribbean coral reefs. *Nature* 450:98–
602      101.

603      Newman MJH., Paredes GA., Sala E., Jackson JBC. 2006. Structure of Caribbean coral reef communities across a
604      large gradient of fish biomass. *Ecology Letters* 9:1216–1227.

605      Nyström M., Folke C., Moberg F. 2000. Coral reef disturbance and resilience in a human-dominated environment.
606      *Trends in Ecology & Evolution* 15:413–417.

607      Paddack MJ., Reynolds JD., Aguilar C., Appeldoorn RS., Beets J., Burkett EW., Chittaro PM., Clarke K., Esteves R.,
608      Fonseca AC., Forrester GE., Friedlander AM., García-Sais J., González-Sansón G., Jordan LKB., McClellan
609      DB., Miller MW., Molloy PP., Mumby PJ., Nagelkerken I., Nemeth M., Navas-Camacho R., Pitt J., Polunin
610      NVC., Reyes-Nivia MC., Robertson DR., Rodríguez-Ramírez A., Salas E., Smith SR., Spieler RE., Steele MA.,
611      Williams ID., Wormald CL., Watkinson AR., Côté IM. 2009. Recent region-wide declines in Caribbean reef fish
612      abundance. *Current Biology* 19:590–595.

613      Perry CT., Steneck RS., Murphy GN., Kench PS., Edinger EN., Smithers SG., Mumby PJ. 2015. Regional-scale
614      dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef
615      growth. *Global Change Biology* 21:1153–1164.

616      Porter JW., Targett NM. 1988. Allelochemical interactions between sponges and corals. *Biological Bulletin* 175:230–
617      239.

618      R Core Team. 2014.R: A language and environment for statistical computing. *Available at http://www.r-project.org*.

619      Rasher DB., Stout EP., Engel S., Kubanek J., Hay ME. 2011. Macroalgal terpenes function as allelopathic agents
620      against reef corals. *Proceedings of the National Academy of Sciences of the United States of America*
621      108:17726–17731.

622      Rasher DB., Hoey AS., Hay ME. 2013. Consumer diversity interacts with prey defenses to drive ecosystem function.
623      *Ecology* 94:1347–1358.

624      Raymundo LJ., Halford AR., Maypa AP., Kerr AM. 2009. Functionally diverse reef-fish communities ameliorate coral
625      disease. *Proceedings of the National Academy of Sciences of the United States of America* 106:17067–17070.

626      Rizzari JR., Bergseth BJ., Frisch AJ. 2015. Impact of conservation areas on trophic interactions between apex
627      predators and herbivores on coral reefs. *Conservation Biology* 29:418–429.

628      Russ GR., Questel S-LA., Rizzari JR., Alcala AC. 2015. The parrotfish–coral relationship: refuting the ubiquity of a
629      prevailing paradigm. *Marine Biology* 162:2029–2045.

630      Schutte VGW., Selig ER., Bruno JF. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic
631      communities. *Marine Ecology Progress Series* 402:115–122.

632      Selig ER., Bruno JF. 2010. A global analysis of the effectiveness of Marine Protected Areas in preventing coral loss.
633      *PLoS One* 5:e9278.

634      Selig ER., Casey KS., Bruno JF. 2012. Temperature-driven coral decline: the role of marine protected areas. *Global
635      Change Biology* 18:1561–1570.

636      Smith JE., Hunter CL., Smith CM. 2010. The effects of top-down versus bottom-up control on benthic coral reef
637      community structure. *Oecologia* 163:497–507.

638      Soto I., Andréfouët S., Hu C., Muller-Karger FE., Wall CC., Sheng J., Hatcher BG. 2009. Physical connectivity in the
639      Mesoamerican Barrier Reef System inferred from 9 years of ocean color observations. *Coral Reefs* 28:415–
640      425.

641      Steneck RS., Dethier MN. 1994. A functional group approach to the structure of algal-dominated communities. *Oikos*
642      69:476–498.

643

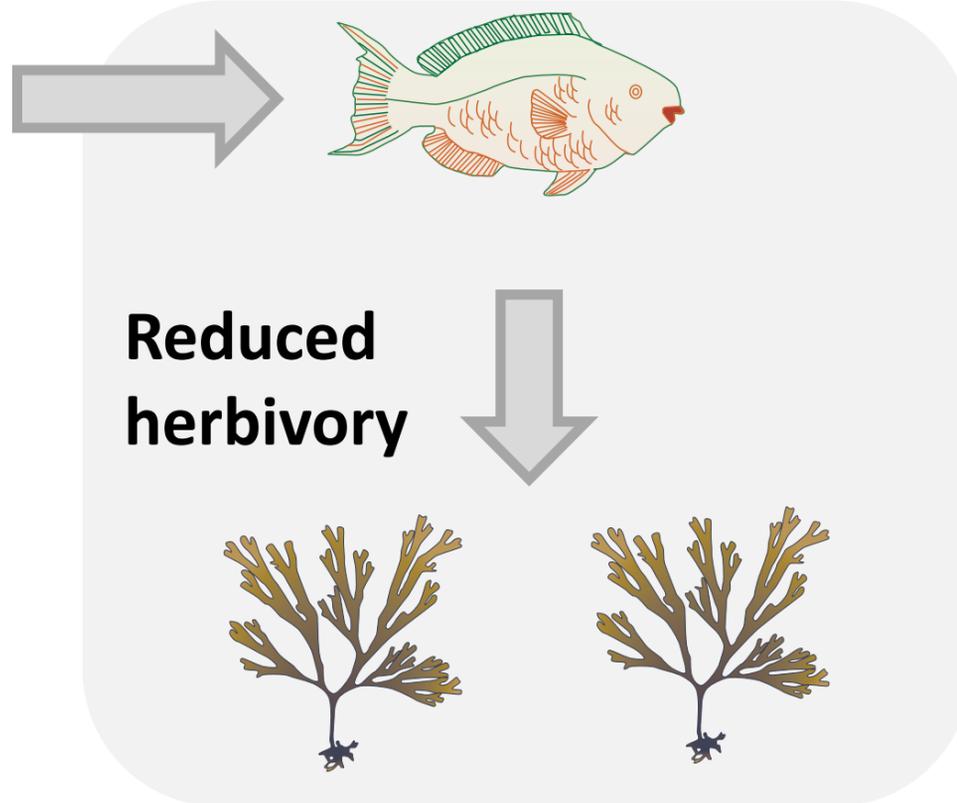
Relationship between changes in herbivorous fish biomass and benthic fleshy macroalgal cover.

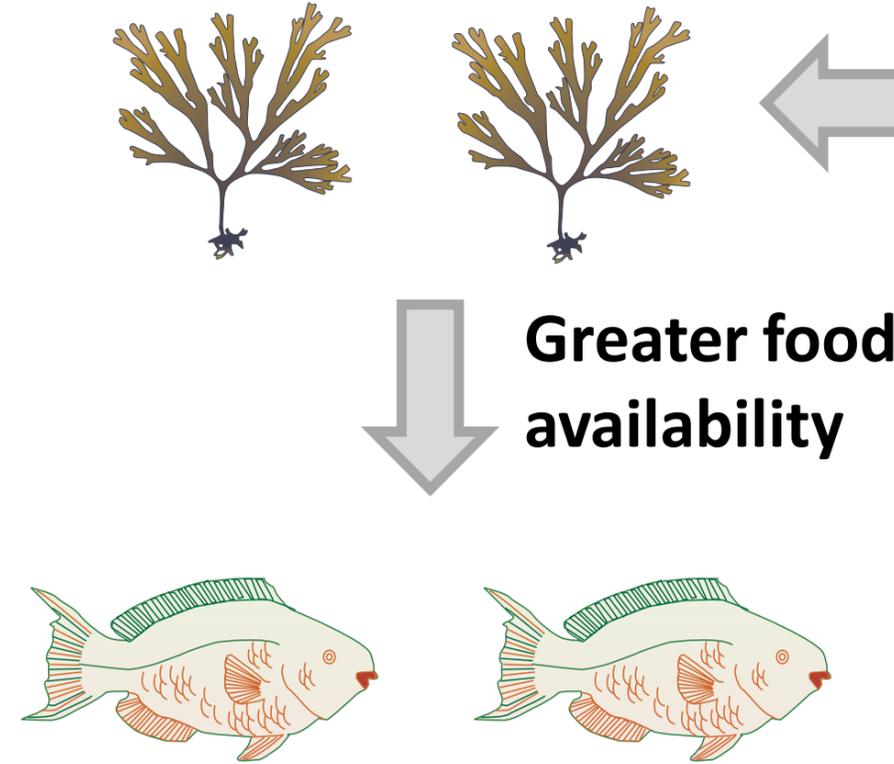
Possible cause-and-effect scenarios with external drivers are postulated for each quadrant. Fish and algae graphics by Diana Kleine and Tracey Saxby (IAN Image Library, Integration and Application Network, University of Maryland Center for Environmental Science, http://ian.umces.edu/imagelibrary).

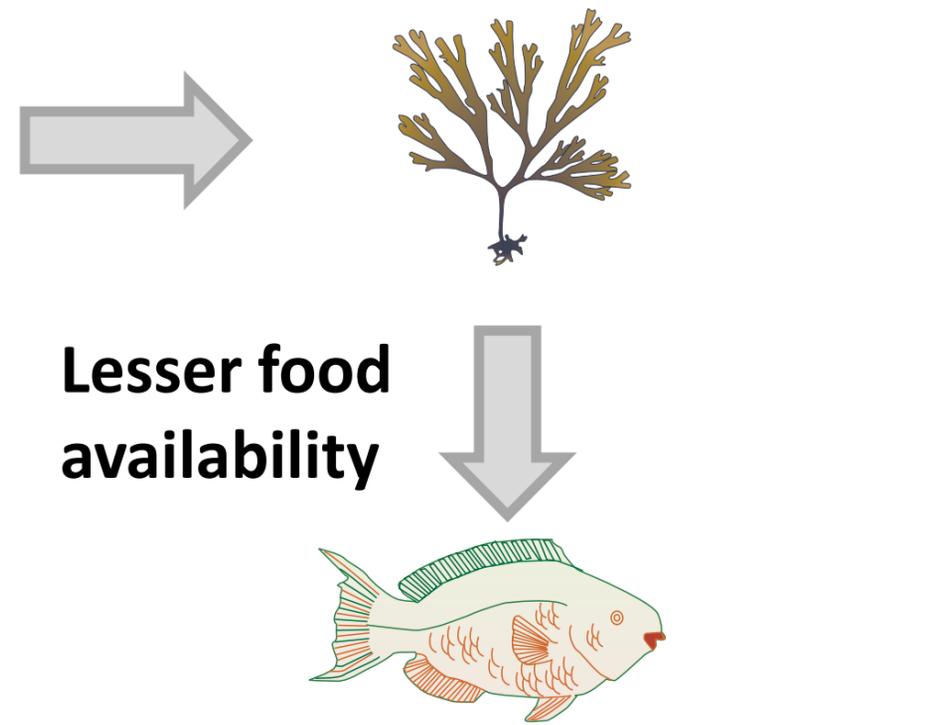
**Fleshy Macroalgal Cover Change**

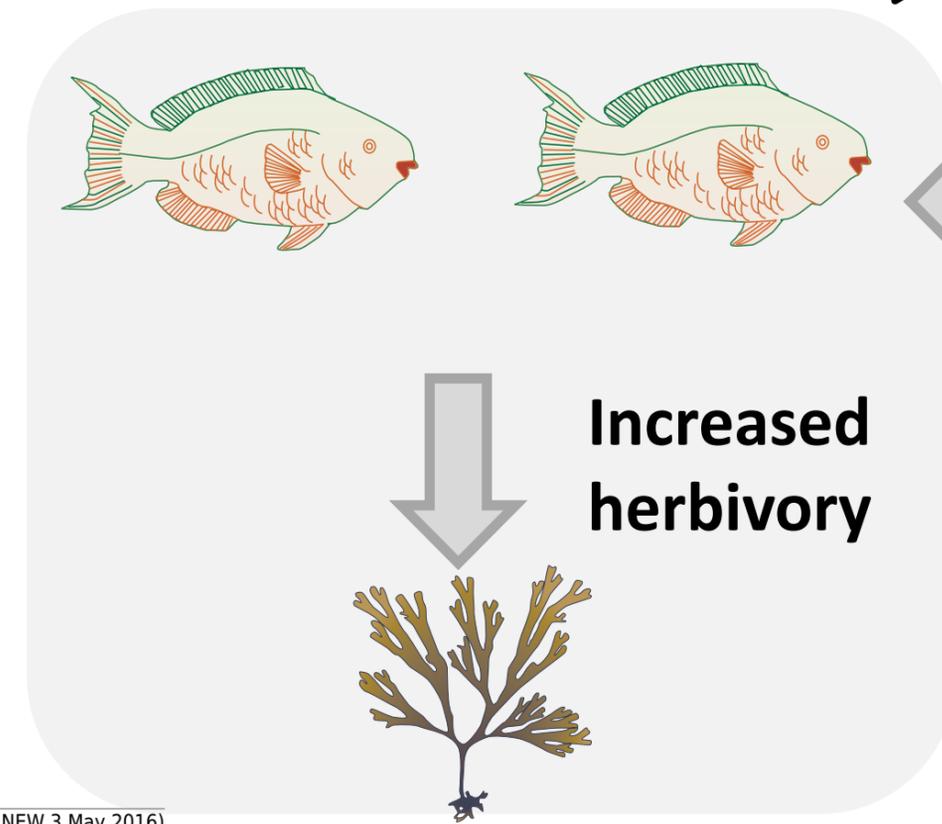
**Herbivorous Fish Biomass Change**

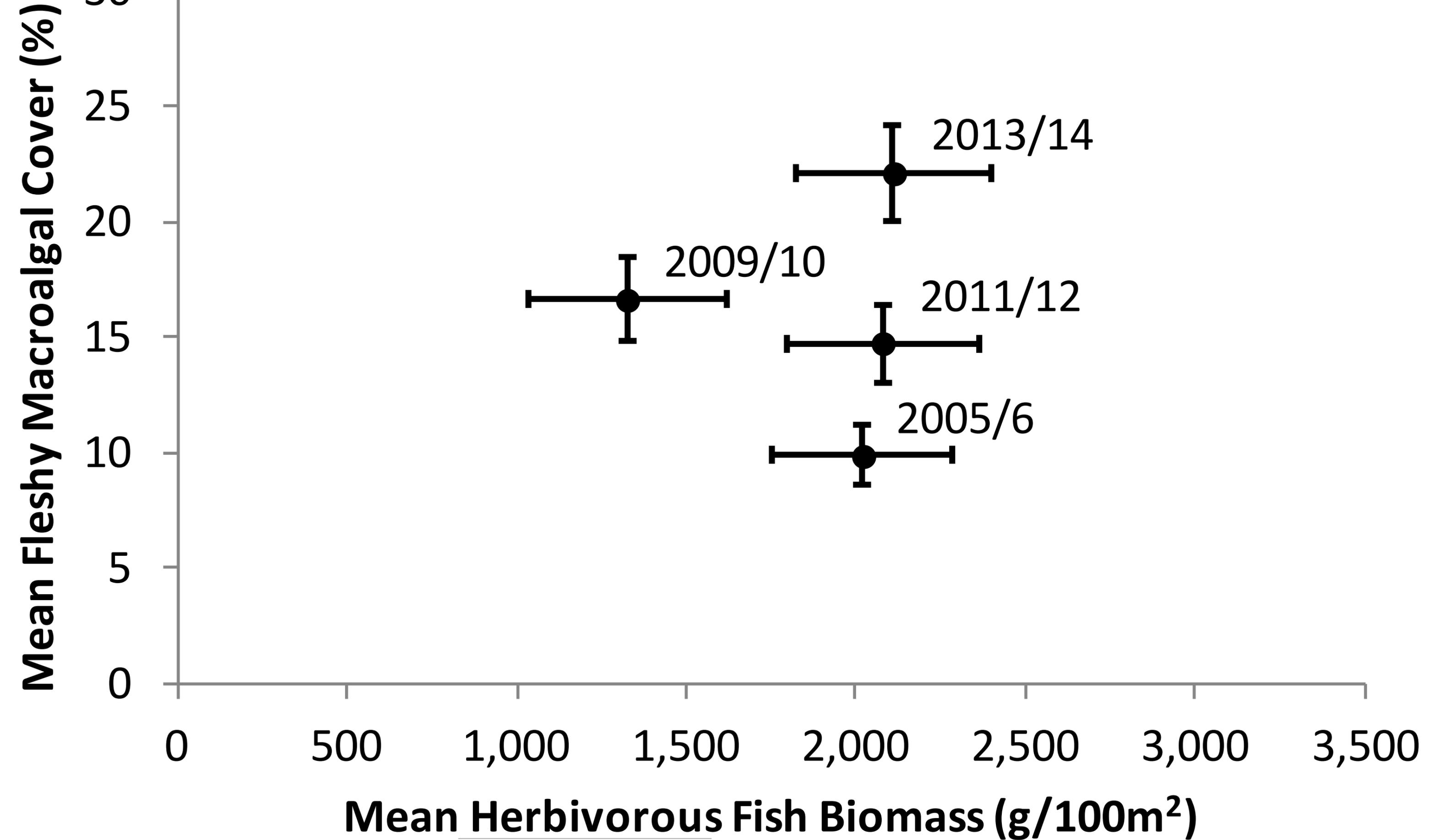
Extraction / habitat loss

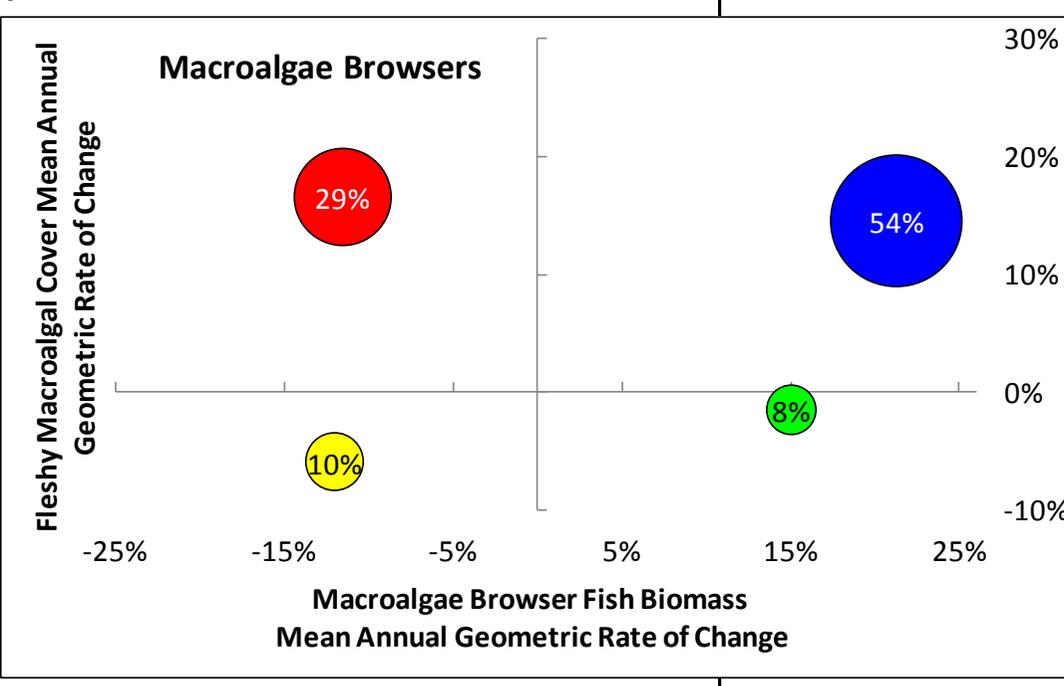
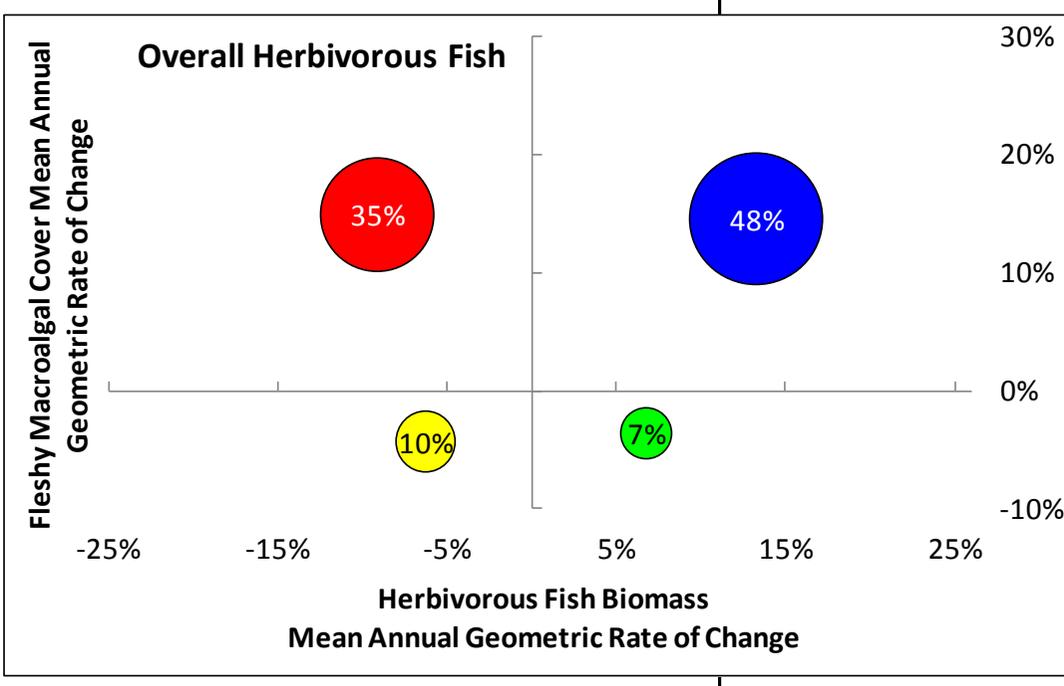
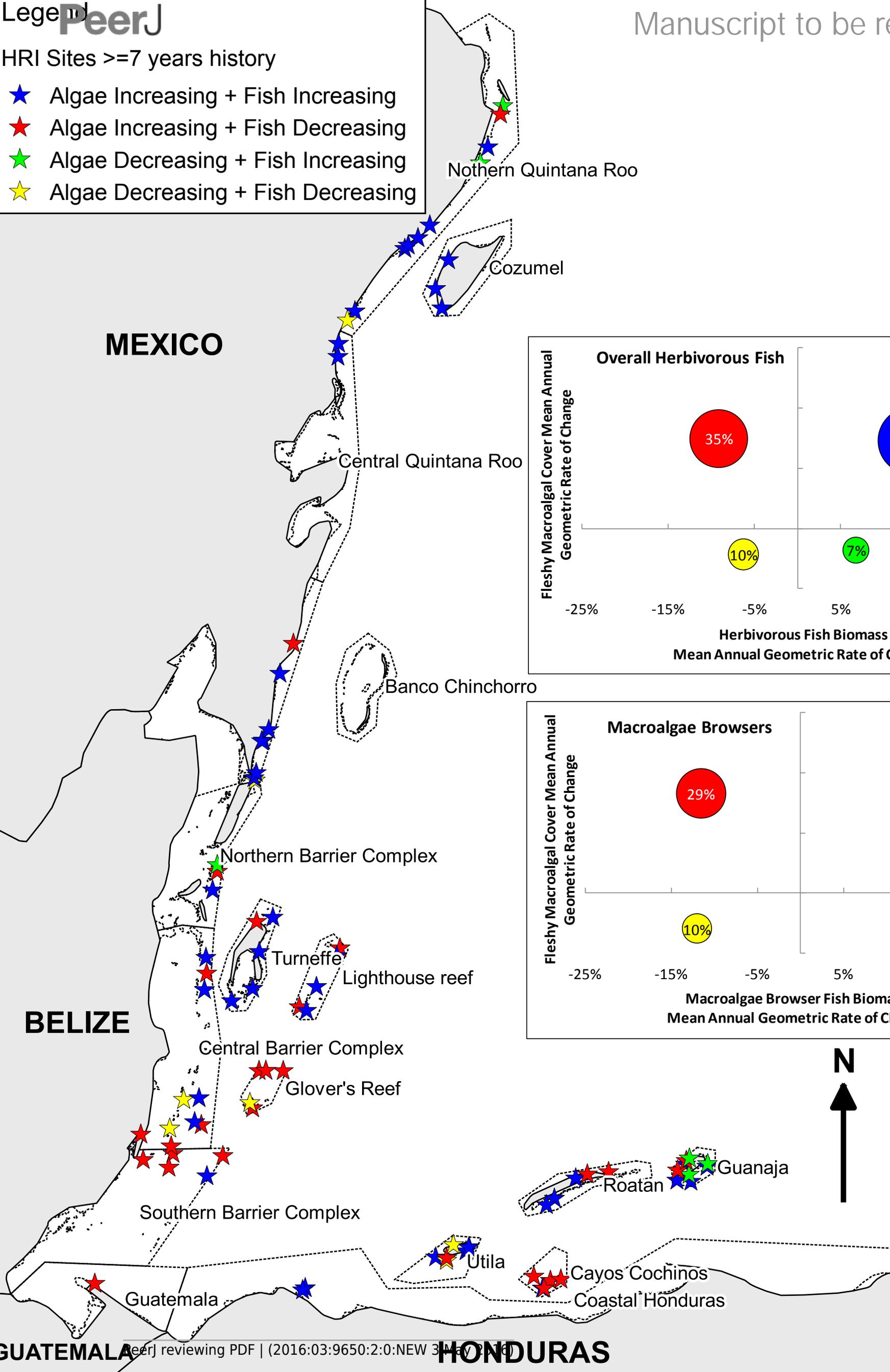
Reduced herbivory

Algae-favourable conditions (e.g. nutrient enrichment)

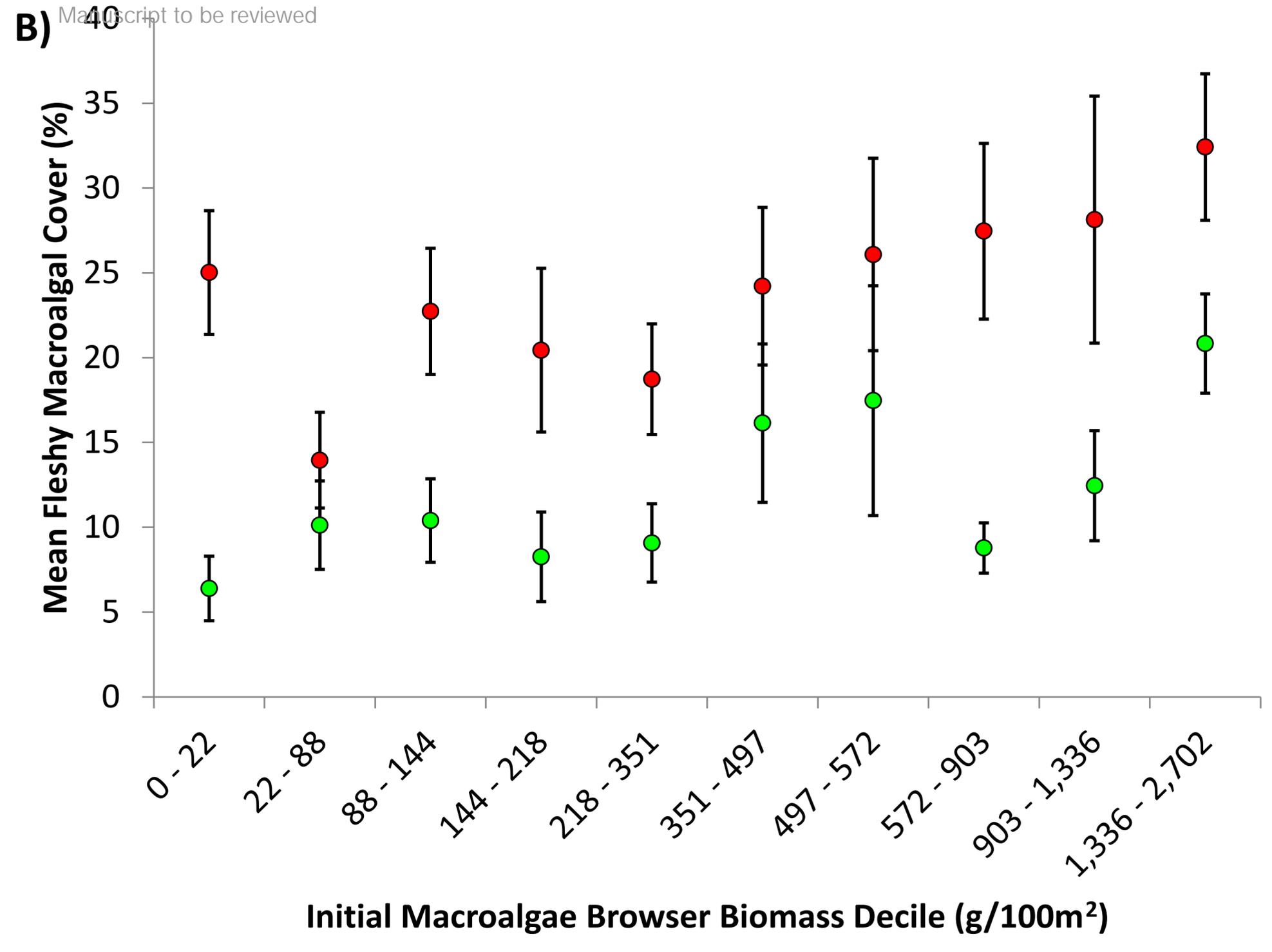
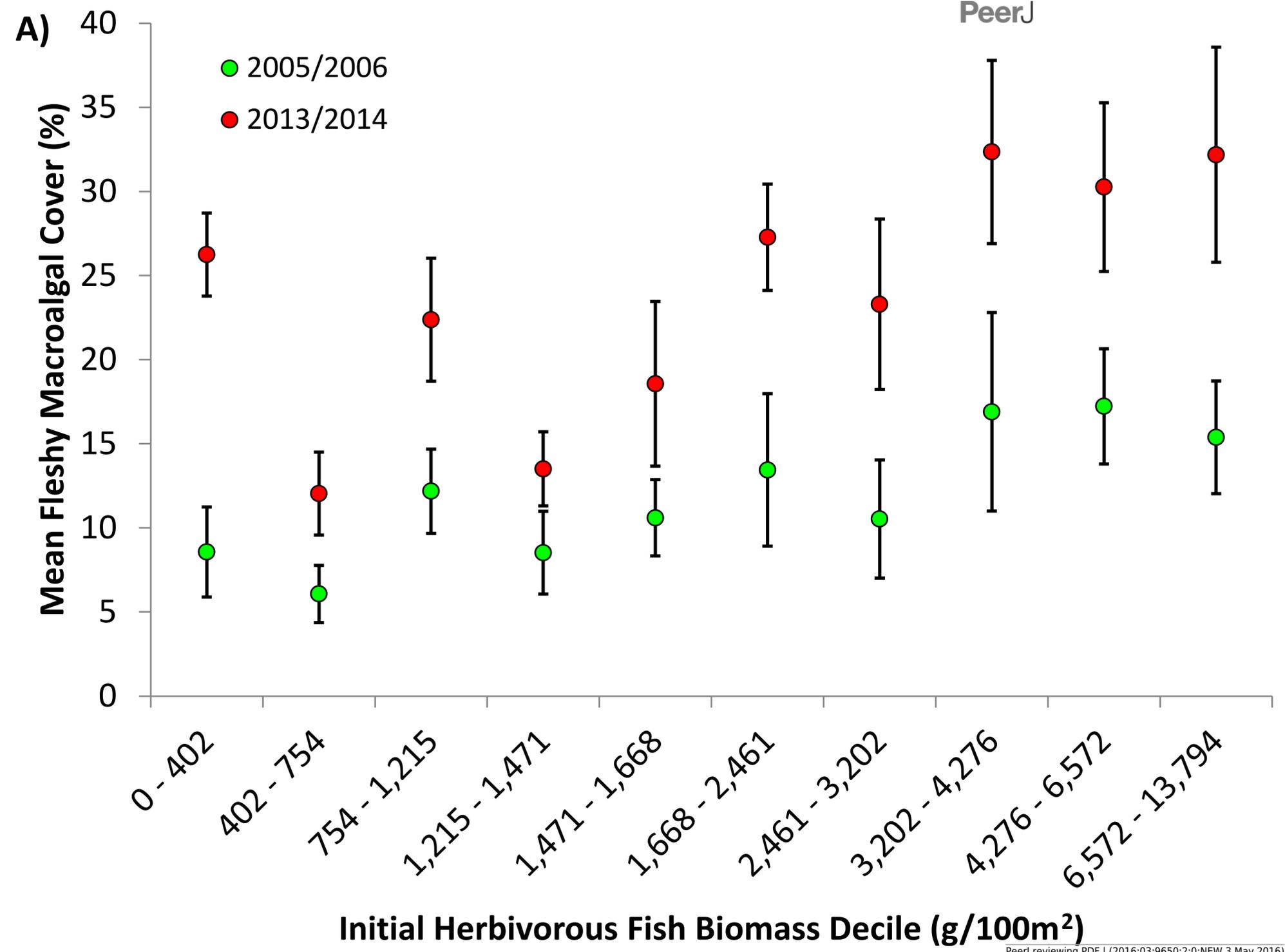
Greater food availability

Algae-adverse conditions

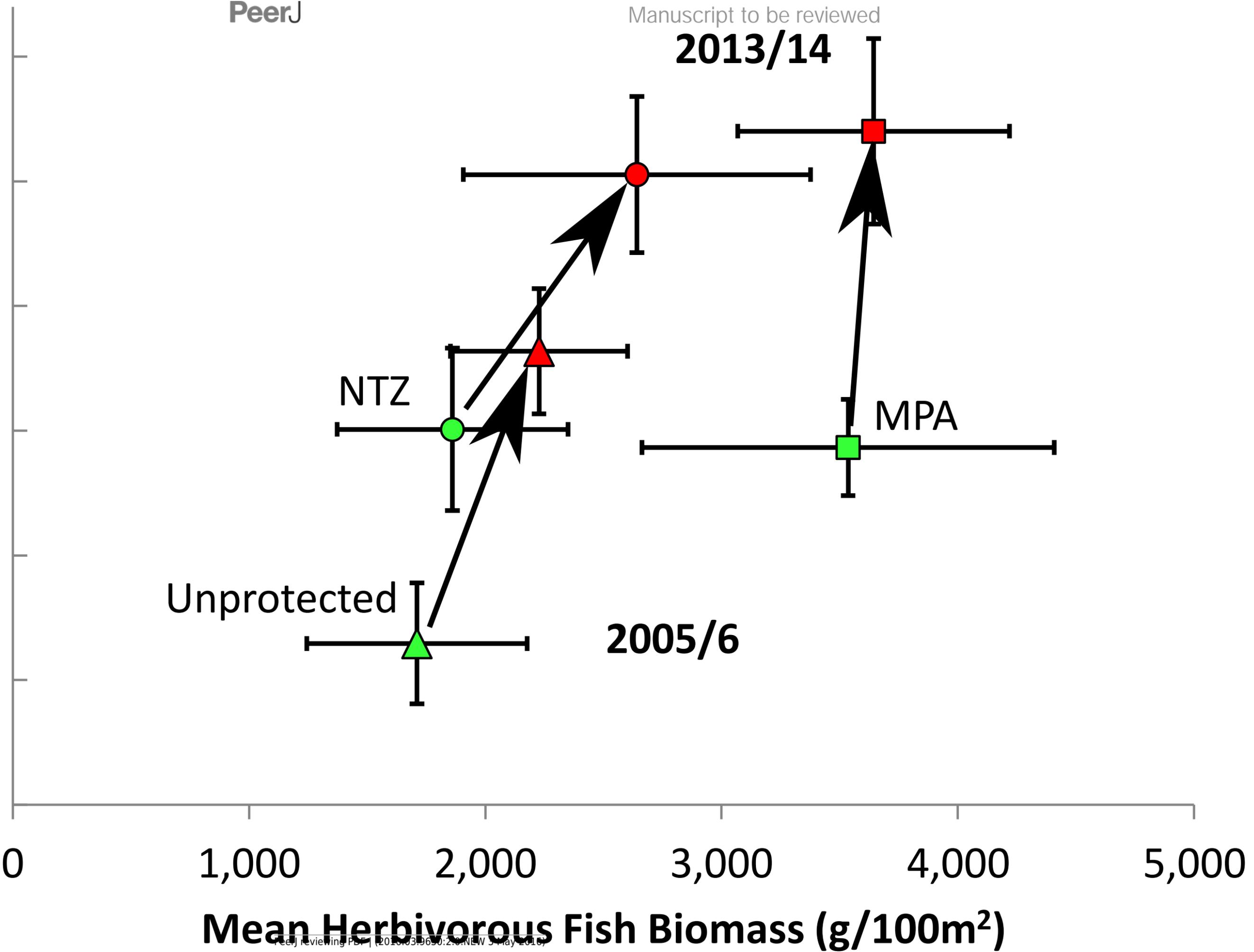
Lesser food availability

Protection / habitat availability

Increased herbivory

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 (Fig. S1).

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 the 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 (Fig. S2).

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.

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).

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).