Caribbean reef trajectories dominated by rapidly increasing macroalgal cover

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Abstract

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

Comment [JB1]: End of Abstract could be edited for clarity. And a stronger final sentenc or two, more directly related to the findings would be good.

Comment [JB2]: Im tempted to suggest editing this to “making environmental conditio more favourable for algae” or “increasing primary production”.

Comment [JB3]: Edit this sentence for clari

Comment [JB4]: Im sceptical herbivores benefited coral cover, esp. since there was n macroalgal effect (of herbivores on macroalga or macroalgae on corals). What would the mechanism be? I suspect if anything, fish we attracted to live coral. In fact Fig 6 suggest th as initial herbivore biomass was unrelated an herbivores and corals increased together temporally.

Comment [JB5]: ? What does this refer to?

Comment [JB6]: Yes, via coral mortality

Comment [JB7]: I don’t understand what th sentence is getting at.

Introduction

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

Given the pivotal role of herbivores in controlling macroalgal growth (Mumby et al., 2006), it is widely accepted that restoring populations of key herbivores enhances reef resilience by controlling algal communities and facilitating coral recovery by freeing space for coral recruits (Nyström, Folke & Moberg, 2000; McCook, Jompa & Diaz-Pulido, 2001; McManus & Polsenberg, 2004; Bruno et al., 2009). Consequently, coral reefs with high herbivore abundance are expected to have lower macroalgal cover and greater coral cover (Jackson et al., 2014; Kramer et al., 2015). This paradigm has encouraged global awareness campaigns promoting conservation and fisheries management strategies to protect and restore populations of key herbivorous fishes, particularly parrotfishes (Jackson et al., 2014). In the Mesoamerican region, for example, Belize and Guatemala have banned the capture and possession of herbivorous fishes (Kramer et al., 2015).

Direct evidence of herbivores' ability to facilitate the maintenance and recovery of resilient coral reefs is limited and hindered by the presence of multiple feedback mechanisms (Mumby & Steneck, 2008; Dixson, Abrego & Hay, 2014; Adam et al., 2015a). Experimental herbivore exclusion studies demonstrate the action of *Diadema* and herbivorous fish grazing on macroalgal cover, although evidence for the impact on corals is limited by the short-term nature and restricted spatial extent of the experiments (Lirman, 2001; Burkepile & Hay, 2006, 2009; Hughes et al., 2007). Observational studies tend to focus on inter-site comparisons without an explicit temporal dimension, rather than tracking long-term reef change trajectories to provide a more in-depth understanding of drivers of ecosystem dynamics (Karr et al., 2015). Little consensus exists between studies, which exhibit contrasting patterns between herbivorous fish populations and macroalgal cover. In a Caribbean wide point-in-time study, Newman et al. (2006) found a significant negative correlation between herbivorous fish biomass and fleshy algal biomass, while for the Northern Mesoamerican Reef of Mexico; Bozec et al. (2008) did not observe a relationship between these variables. In a long-term study Ilves et al. (2011) observed increases in both herbivorous fish abundance and algal cover in the Bahamas. ~~Contrastingly~~In contrast, on the Northern Florida Reef Tract, Lirman & Biber (2000) observed no correlation between algal biomass and cover and fish grazer abundance and

Comment [JB8]: Point unclear. What is hindered? The ability of herbivores? The acquisition of evidence? What feedback mechanisms? Please clarify here and in response letter to the editor.

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

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

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

Herbivore and algal community composition also play an important role in herbivore-algal dynamics. Subsequent to the *Diadema* mass mortality event of the early 1980's, herbivorous fishes of the Scaridae and Acanthuridae families are recognised as the primary herbivores on many Caribbean reefs (Jackson et al., 2014; Adam et al., 2015a). While common *Acanthurus* surgeonfishes have a broad diet feeding on a combination of turf algae, macroalgae and detritus, *Sparisoma* and *Scarus* parrotfishes are more selective (Burkepile & Hay, 2011; Adam et al., 2015a). *Sparisoma* parrotfishes, with the exception of the excavating *S. viride*, are macroalgae browsers, while *Scarus* spp. primarily graze algal turfs (Bonaldo, Hoey & Bellwood, 2014; Adam et al., 2015b). Consequently, a suitable mix of herbivores are required in order to both graze turf algae to facilitate coral recruitment and to crop down macroalgal stands to reduce competition with adult coral colonies (McCook, Jompa & Diaz-Pulido, 2001; Hughes et al., 2007; Burkepile & Hay, 2008). However, herbivores' ability to effectively moderate macroalgal cover is mediated by macroalgal predation defences (Rasher, Hoey & Hay, 2013). Such defences are species specific and include morphological, structural, mineral and chemical traits that deter herbivores, with several genera (e.g. *Lobophora*, *Peyssonnelia* and *Codium*) being unpalatable (Hay, 1997; Smith, Hunter & Smith, 2010). These defences likely influence herbivore feeding preferences and conversely algal community structure is often influenced by herbivore mix, resulting in a complex interaction between the two communities (Adam et al., 2015a).

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

Materials & Methods

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

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

The data analyses focussed on the relation between three ecological indicators for each reef site: herbivorous fish (Scaridae and Acanthuridae) biomass, fleshy macroalgal cover and hard coral (scleractinians and *Millepora* spp.) cover. Very few *Diadema* spp. were observed and therefore we focussed on reef fishes as the principal herbivores. For all three ecological indicators, a number of metrics were

Comment [JB9]: Might need to define - eg does this include Halimeda? And presumably not turf algae.

calculated ~~in order~~ to evaluate and examine temporal trends: absolute annual change, annual relative rate of change and geometric rate of change. The metrics for each ecological indicator (*I*) were determined as follows:

$$I_{\text{AbsoluteAnnualChange}} = \frac{\left(I_{t_f} - I_{t_0}\right)}{\Delta t} \quad (1)$$

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

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

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

Univariate comparison of ecological indicators was performed using ANOVA, t-tests or non-parametric equivalents (Mann-Whitney U or Wilcoxon Signed Rank tests), based on an assessment of normality and homogeneity of variance using Shapiro-Wilk and Levene tests. To test our first hypothesis, herbivorous fish biomass was compared with fleshy macroalgal cover using Spearman rank-order correlation due to non-normality. Herbivorous fishes were further categorised according to feeding preferences as macroalgae browsers (*Sparisoma* spp., with the exception of *S.*

viride), turf grazers / scrapers (*Scarus* spp. and *Acanthurus* spp.) or bioeroders (*Sparisoma viride*) (Bellwood et al., 2004; Burkepile & Hay, 2011; Bonaldo, Hoey & Bellwood, 2014; Adam et al., 2015a,b). Change in functional group biomass was compared with overall change in herbivorous fish biomass using Spearman rank-order correlation. Furthermore, change in macroalgal cover was compared with absolute levels of overall herbivorous fish and macroalgae browser biomass both graphically by categorising sites by initial fish biomass (based on deciles) and by using Spearman rank-order correlation.

To test our second hypothesis, change in absolute coral cover from 2005/6 to 2013/4 for long-term monitoring sites was modelled using multiple linear regressions as model assumptions were satisfied. To address the common problem of spatial autocorrelation in multi-site studies we performed a Moran's I test on coral cover change by site location which reported no spatial autocorrelation present (Moran's I = 0.070, P = 0.08). The optimum regression model was selected based on Akaike Information Criterion (AIC). Candidate independent variables were selected based on ecological relevance and data availability (Table 1). Potential collinearity among predictor variables was examined using Pearson correlations and variance inflation factors. All statistical analyses were performed using R (R Core Team, 2014).

Results

85 long-term Mesoamerican Reef monitoring sites were surveyed in 2005/2006 and 2013/2014 over a 7, 8 or 9-year period. Of these, 43 sites were repeatedly surveyed in four time periods (2005/2006, 2009/2010, 2011/2012 and 2013/2014). Here we present herbivorous fish biomass and fleshy macroalgal cover average trends for

Comment [JB10]: Not sure this belongs in t
Results section. Maybe move to Methods.

repeatedly surveyed sites and assess changes in these variables for long-term monitoring sites. Subsequently we examine herbivorous fish feeding guilds and geographic trends for long-term monitoring sites, and assess the effect of protection on site trajectories. Finally we present the ecological drivers of long-term coral cover change.

Herbivorous fish biomass and macroalgal cover trends

~~In~~ During the time period 2005 to 2014, regional averages showed a clear trend of increasing fleshy macroalgal cover on the Mesoamerican Reef, while herbivorous fish biomass remained relatively constant. Across 43 sites surveyed repeatedly in four time periods (Fig. 2), mean herbivorous fish biomass did not change significantly (Wilcoxon Signed Rank, Z = 0, P = 1), while mean macroalgal cover doubled during the same period (Wilcoxon Signed Rank, Z = -5.02, P < 0.001). Between 2005/2006 and 2009/2010 mean herbivorous fish biomass decreased and mean fleshy macroalgal cover increased significantly (Wilcoxon Signed Rank, Z = 3.36, P < 0.001 and Z = -3.86, P < 0.001, respectively). From 2009/10 to 2011/12 the trend appeared to be reversed, although the changes were not significant for macroalgae (Wilcoxon Signed Rank, Z = -2.95, P = 0.003 and Z = 0.59, P = 0.55, respectively; Fig. 2). From 2011/2012 to 2013/2014 macroalgal cover increased significantly, while herbivorous fish biomass remained unchanged (Wilcoxon Signed Rank, Z = -3.81, P < 0.001 and Z = -0.35, P = 0.73, respectively; Fig. 2).

Comment [JB11]: Wow.

Tracking individual trajectories of the 85 long-term monitoring sites surveyed over a 7, 8 or 9-year period permitted a more detailed investigation of the relation between the temporal changes in herbivorous fish biomass and fleshy macroalgal cover. Herbivorous fish biomass ranged from approximately 50 to 14,000 g/100m^2 and fleshy macroalgal cover ranged from 0 to 57.5 %. There was no correlation between the changes in herbivorous fish biomass and fleshy macroalgal cover for long-term monitoring sites (Spearman, r_s = -0.11, P = 0.35). Only 7 % of sites exhibited increased herbivorous fish biomass and decreased macroalgal cover; 35 % of sites displayed decreases in fish biomass and increases in macroalgal cover; almost half of the sites (48 %) exhibited increases in both herbivorous fish biomass and macroalgal cover; and 10 % displayed decreased fish biomass and macroalgal cover (Fig. 3). Across all sites macroalgal cover increased irrespective of initial conditions of herbivorous fish biomass (Spearman, r_s = -0.12, P = 0.3; Fig. 4a) and macroalgae browser biomass (Spearman, r_s = -0.21, P = 0.3; Fig. 4b).

Comment [JB12]: Amazing result.

Considering herbivorous fish feeding preferences, communities of the Mesoamerican Reef present a mixture of guilds with 24.3 % macroalgae browsers by biomass in 2013/14 (19.4 % in 2005/6), 48.4 % (57.3 %) turf grazers / scrapers and 27.3 % (23.3 %) bioeroders. Herbivorous fish biomass and macroalgal cover change were broadly similar between macroalgae browsers and overall results (Fig. 3). Macroalgae browser biomass displayed a slightly greater tendency for increase than overall herbivorous fish biomass, as observed for 61 % of sites compared with 55 %, and site-level changes in these were correlated (Spearman, r_s = 0.70, P < 0.001).

Comment [JB13]: Might add citation, “base on ….”

Geographically, the principal trend was for increasing fleshy macroalgal cover and herbivorous fish biomass in Mexico and northern Belize, including the atolls of Turneffe and Lighthouse Reef, but for increasing fleshy macroalgal cover and decreasing herbivorous fish biomass to the south in south-central and southern Belize, Glover’s Reef, Guatemala and Cayos Cochinos, Honduras (Fig. 3). However, the Bay Islands of Honduras were exceptions to this broad north-to-south trend with Guanaja island displaying the highest proportion of sites with increasing herbivorous

Comment [JB14]: Totally agree-our monitoring data is suggestive of the same pattern.

fish biomass and decreasing macroalgal cover. The only other three sites that experienced a similar trend were located at Isla Mujeres and Puerto Morelos in Mexico, and San Pedro in Belize.

Of the 85 long-term monitoring sites, 12 sites were located within No Take Zones (NTZs), 47 were within Marine Protected Areas but not NTZs (MPAs), and the remaining 26 were unprotected. The level of protection was observed to affect the initial levels of fleshy macroalgal cover and herbivorous fish biomass, in addition to changes in these over time. In 2005/6, sites within NTZs exhibited similar herbivorous fish biomass and fleshy macroalgal cover to sites located elsewhere within Marine Protected Areas (Mann-Whitney, $U = 197$, $Z = -1.60$, $P = 0.11$; and $U = 297$, $Z = 0.28$, $P = 0.78$ respectively; Fig. 5). Protected sites (both MPAs and NTZs) displayed significantly higher initial macroalgal cover than unprotected sites (Mann-Whitney, both $U \geq 247$, $Z \geq 2.85$, $P \leq 0.003$; Fig. 5), but only protected sites outside of NTZs exhibited significantly higher initial herbivorous fish biomass than unprotected sites (Mann-Whitney, MPA vs unprotected, $U = 819$, $Z = 2.40$, $P = 0.016$; NTZ vs unprotected, $U = 161$, $Z = 0.16$, $P = 0.89$; Fig. 5). Along the protection gradient (from unprotected, through MPA to no-take protection), sites appeared to experience a greater increase in herbivorous fish biomass and a lesser increase in macroalgal cover, although the differences were not statistically significant (ANOVA, annual geometric rate of change in fish biomass, $F_{2,82} = 0.04$, $P = 0.97$; annual geometric rate of change in macroalgal cover, $F_{2,80} = 1.01$, $P = 0.37$).

Predicting coral cover change

Across all 85 long-term monitoring sites, mean (± s.e.m.) hard coral cover increased significantly from 12.2 ± 0.8 % in 2005/6 to 15.0 ± 0.8 % in 2013/14 (Wilcoxon

Signed Rank, Z = -3.81, P < 0.001). Individual sites displayed varying trajectories with annual changes in coral cover ranging from -3.1 % to +2.7 %. The optimum linear regression model for the annual absolute change in hard coral cover displayed a modest but significant fit (Adjusted $R^2 = 0.18$, $F_{7,74} = 3.57$, P = 0.002). The model included seven predictor variables (Table 1), of which four were significant: MPA, Country (Honduras), annual logarithmic change in herbivorous fish biomass and initial hard coral cover (Fig. 6). Interpreting these significant variables, sites within Marine Protected Areas experienced greater increases in coral cover than unprotected sites; Honduran sites experienced lesser increases in coral cover than other countries; and increases in herbivorous fish biomass corresponded with increases in coral cover. Initial coral cover was the most significant predictor of coral cover change and therefore in order to further understand its impact, sites were categorised as low (<10 %), medium (10-20 %) or high (≥ 20%) initial coral cover. For the 12 long-term monitoring sites with high initial coral cover, mean coral cover decreased over time (mean ± s.e.m. annual change in coral cover of -0.6 ± 0.4 %), while coral cover increased for sites with lower levels of initial cover (low initial coral cover, +0.6 ± 0.1 %; medium initial coral cover, +0.4 ± 0.2 %).

Despite not being selected in the optimum regression model, we further explored the relationship between coral and macroalgal cover due to the long-term ecological shifts reported on many Caribbean reefs. Across all 85 long-term monitoring sites, mean (± s.e.m.) macroalgal cover increased significantly from 12.0 ± 1.1 % in 2005/6 to 24.1 ± 1.5 % in 2013/14 (Wilcoxon Signed Rank, Z = -7.07, P < 0.001). We observed little or no relationship between coral and macroalgal cover since macroalgal cover consistently increased irrespective of changes in coral cover (Supplementary Fig. S3 online). All initial coral cover categories (low (< 10 %),

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Comment [JB15]: I was assuming coral los played a role in facilitating algal increase, but perhaps not.

medium (10-20 %), and high (≥ 20 %)) experienced increases in fleshy macroalgal cover, and initial macroalgal cover, similarly categorised, did not impact coral cover changes over time (ANOVA, $F_{2,82} = 1.10$, $P = 0.34$).

Discussion

~~Rapid~~ Substantial changes in the ecological composition of the Mesoamerican Reef were evident in a time span of only nine years. The principal trend is for increasing fleshy macroalgal cover, as observed at 83 % of long-term monitoring sites (Fig. 3). Mean absolute cover of fleshy macroalgal ~~cover~~ increased ~~(relatively)~~ by approximately 125 % in the region between 2005 and 2014 (Fig. 2). Mean herbivorous fish biomass remained relatively stable (Fig. 2), although displaying substantial site variation, with 55 % of sites showing an increase in herbivorous fish biomass between 2005 and 2014 (Fig. 3). The scenario of both increasing fleshy macroalgal cover and herbivorous fish biomass was ~~experienced~~ observed at 48 % of the xx sites while the 'desirable' scenario of increasing herbivorous fish biomass and decreasing macroalgal cover was the least frequent of all four scenarios (Fig. 3). Similar trends were observed for the macroalgae browsing fish guild (Fig. 3), with site-level macroalgae browser biomass change correlating with overall herbivorous fish biomass change. This suggests that fish herbivory was not a major driver of fleshy macroalgal cover change ~~in~~ on the majority of surveyed sites across the Mesoamerican Reef (Fig. 3).

Comment [JB16]: Report absolute change, not relative change.

The clear pattern of increasing macroalgal cover and stable herbivorous fish biomass on Mesoamerican reefs contrasts with the widely accepted coral reef phase shift paradigm and management recommendations that suggests that increasing herbivory would lead to declines in fleshy macroalgal cover (Nyström, Folke & Moberg, 2000; McCook, Jompa & Diaz-Pulido, 2001). However, long-term reduction in Caribbean reef fish populations and increases in macroalgal cover from historical levels had already occurred prior to the onset of this study (Jackson et al., 2001; McClenachan, 2009; Paddack et al., 2009). In a recent study of four Philippine islands covering the multi-decadal (30 year) period associated with reef phase shifts, Russ et al. (2015) observed that macroalgal cover was not related to long-term parrotfish losses due to fishing, supporting our findings. Our findings suggest that in the period 2005-2014 environmental factors such as nutrient availability, temperature or solar irradiance may be responsible for increasing macroalgal cover, rather than reduced herbivory (Burkepile & Hay, 2006; Ferrari et al., 2012). In Mexico, other studies have observed no relationship between herbivore biomass and macroalgal cover, ~~relating~~ suggesting that benthic compositional ~~reef structural~~ change was due largely to coastal development (Bozec et al., 2008) and associated nutrient discharges (Baker & Fogel, 2013; Hernández-Terrones et al., 2015). In southern Belize and Honduras we suggest that riverine discharge and escalating reef sediment and nutrient loads associated with urban and agricultural run-off may have played a role (Burke & Sugg, 2006; Carilli et al., 2009; Soto et al., 2009). This finding contrasts the results of herbivore exclusion studies, which emphasize the relative importance of herbivory over nutrient availability, although such studies tend to be conducted on restricted spatial and temporal scales (McClanahan, Cokos & Sala, 2002; Burkepile & Hay, 2006, 2009; Sotka & Hay, 2009). Observed increases in herbivorous fish populations may be due to a *positive* relationship with macroalgal cover, driven by herbivore food-limitation, or independently via conservation efforts (Carpenter, 1990; Lester et al., 2009; Adam et al., 2011). Herbivores can be food

Comment [JB17]: Probably should address the role of coral cover somewhere; since change in macroalgal cover was unrelated to coral cover, and since coral cover is so low everwhere, we suspect the observed increase macroalgal cover was not caused by coral losses. (probably need to break that up into a few sentences.

Comment [JB18]: And

limited even on reefs with high algal cover since macroalgae often have physical and chemical defences (McClanahan et al., 2000). Algal defences play an important role in reef herbivory dynamics and likely influence herbivore feeding preferences (Hay, 1997; Erickson et al., 2006; Adam et al., 2015a). Increases in macroalgal cover, potentially due to nutrient enrichment, may be related to changes in algal community composition towards unpalatable species, concealing the underlying influence of herbivory (Smith, Hunter & Smith, 2010). Consistent algal species information was not available in the database used in this study and thus it was not possible to evaluate the magnitude of this effect on the Mesoamerican Reef.

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

Comment [JB19]: I don't understand exact what the threshold might be – too much production?

Comment [JB20]: Good point. Note Smith al 2016 Proc Roy Soc B reported macroalgal cover of 12% on isolated central Pacific reefs

Comment [JB21]: Still somewhat vague – I assume we are talking about algal production and grazing biomass, but more clarity would help.

Caribbean reef herbivorous fish biomass and fleshy algal biomass has been previously observed with a site maximum of only 7,000 g/100m^2 approximately (Newman et al., 2006).

Comment [JB22]: Yeah - I agree this is a werid result Ive often wondered about.

The threshold hypothesis would be particularly relevant if the decline in average herbivorous fish biomass between 2005/6 and 2009/10 resulted in changes in the relative proportion of key functional groups, favouring non-macroalgae browsing species (Adam et al., 2015b; Fig. 2). However, the relative proportions of the three main herbivorous fish functional groups remained stable during the study period (Supplementary Fig. S4 online). Additionally, a close examination of those sites that suffered the greatest herbivorous fish biomass losses between 2005 and 2009 revealed that these sites experienced similar macroalgae growth from 2009 to 2014 compared with other sites (Supplementary Fig. S5 online). This ~~evidence~~ suggests that ~~no~~ the observed patterns are not due to ecological thresholds.~~ effects were experienced and that the lack of relationship between fish biomass and macroalgal cover change was indeed due to other factors~~.

Comment [JB23]: Again, more clarity abou what is being alluded to here.

In post phase-shift degraded reef systems coral and macroalgal cover are probably less tightly coupled compared to reefs that experienced rapid losses of coral cover in the recent past. At the onset of this study, hard corals were not the dominant benthic component on the Mesoamerican Reef, with a mean cover of only 12.2 % at long-term study sites. By 2013/14 mean coral cover had increased to 15.0 %, but was unrelated to macroalgal cover which had increased considerably more (from 12.0 % in 2005/6 to 24.1 % in 2013/14). Our model showed that instead of changes in macroalgal cover, increases in coral cover are related to initial coral cover, increasing biomass of herbivorous fish, geographical location and MPA protection

Comment [JB24]: I doubt this is real – it is below the precision of the method and it certainly isn't ecologically meaningful.

(Fig. 6). Initial coral cover was the primary driver, with gains for sites with < 20 % coral cover initially and losses at sites with ≥ 20 % initial cover (Supplementary Fig. S3 online). Although coral losses at initially better preserved sites were not accompanied by concomitant increases in macroalgal cover, it is likely that ongoing deterioration in environmental conditions, such as rising temperatures and increased coral disease prevalence, continue to impact coral communities (Harvell et al., 2007; Hoegh-Guldberg et al., 2007; Sokolow, 2009; Kennedy et al., 2013).

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

Coral recovery was related to MPA protection level and increasing biomass of herbivorous fish, but not via the expected mechanism of macroalgal declines through fish herbivory. Alternative mechanisms for the effect of protection on reef corals are less well studied, but may include reduced disease prevalence, and diminished physical reef damage through regulation of fishing and recreational diving practices (Hasler & Ott, 2008; Lamb et al., 2015). Replenished fish communities inside marine reserves can also drive coral recovery through ecological processes not necessarily linked with herbivory. For example, trophically diverse fish communities inside marine reserves have been shown to ameliorate coral disease prevalence, although the pathways through which this takes place remain unclear (Raymundo et al., 2009). Also, overfishing of spongivorous parrotfishes and angelfishes has been shown to have a negative impact on reef-building corals through the alleviation of predation pressure on sponges which exhibit competitive superiority over corals (Loh et al., 2015). Consequently, the observed positive ~~effects~~ association of herbivorous fishe biomass and coral covers on ~~the coral communities of~~ the Mesoamerican Reef may be the result of a broad range of mechanisms associated with reef protection. Our findings for coral cover contrast those of Russ et al. (2015) who in a long-term study of four islands of the Philippines observed a generally negative relationship between parrotfish density and hard coral cover. Russ et al. (2015) report a positive relationship between dead coral cover and parrotfish density and suggest that this may be due to the prevalence of turf, detritus and sediment feeding guilds in the study area, since these are commonly associated with dead substrata.

Comment [JB25]: Exactly – which makes m
think it's the parrotfishes responding to
increased live coral or just covariance or cora
and fishes to local protection.

In conclusion, during the last decade increasing fleshy macroalgal cover was the principal trend on the coral reefs of the Mesoamerican Reef. Herbivorous fish populations were not responsible for this trend, contrasting the results of some studies performed over smaller spatial scales, and implicating the role of external factors such as terrestrial nutrient import in providing algae-favourable conditions. However, herbivorous fish, in addition to marine protection, had a positive impact on hard coral cover, which increased over the observation period. We suggest that these factors benefited coral communities through alternative mechanisms such as lower disease prevalence, diminished competition and reduced physical damage, despite increasing fleshy macroalgal cover. Consequently, in addition to more concerted efforts regarding watershed management and climate change mitigation, local marine protection efforts are important tools for coral reef managers. Additionally, ongoing monitoring should be employed to track reef environmental conditions, and further studies on the mechanisms underlying protection impacts on coral communities would inform ongoing reef management and protection planning.

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Acknowledgments

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