

Establishment of marine protected areas alone does not restore coral reef communities in Belize

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ABSTRACT: A variety of factors have caused the loss of corals and fishes on coral reefs, resulting in ecological, social, and economic consequences for reef ecosystems and the people who depend on them. A widely employed management action to restore reef communities is the implementation of marine protected areas (MPAs). We measured the effectiveness of the MPA network in Belize in promoting increases in fish and coral populations and identified key ecological and environmental factors that influence reef community structure and potentially protection success. From 2009 to 2013, we annually surveyed 16 reefs in Belize, including 8 MPA sites (where extractive fishing is limited or prohibited) and 8 unprotected sites. At each site, we quantified the biomass of reef fishes, coral and macroalgal cover, and several biotic and abiotic variables that are known to affect reef inhabitants. High predatory reef fish and parrotfish biomass values were associated with high reef structural complexity and low wave exposure. Mean macroalgal cover was negatively associated with parrotfish biomass in 1 protected zone. However, mean macroalgal cover remained above 40% across all sites, and no change in coral cover was observed during the study. Our results indicate that fisheries restrictions alone do not lead to increases in coral cover even when successful for fishes. We speculate that both illegal and legal fishing may be compromising Belize's MPA network goals. Furthermore, we suggest that species composition as well as local environmental conditions play key roles in coral reef recovery and should be considered when evaluating management strategies.

KEY WORDS: Coral reef · Belize · Coral recruitment · Trophic cascades · Parrotfish · MPAs

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INTRODUCTION

Caribbean coral reef ecosystems have experienced >3 decades of coral mortality and habitat degradation (Hughes 1994, Jones et al. 2004, Bellwood et al. 2004), with coral cover declining from ~50% in the 1970s to ~15% at present (Gardner et al. 2003, Schutte et al. 2010, Jackson et al. 2014). The proximate causes of coral loss in the greater Caribbean include ocean warming due to greenhouse gas emissions and subsequent disease outbreaks and coral bleaching, hurricanes, and poor land-use practices that lead to increased sedimentation and nutrient

pollution (Hughes 1994, Eakin et al. 2010, Randall & van Woesik 2015). Declines in coral cover and subsequent loss of structural complexity (Alvarez-Filip et al. 2011) can negatively affect reef fish abundance and diversity, as many species rely on the presence of living coral assemblages for habitat (Bell & Galzin 1984, Jones et al. 2004).

In some regions of the Caribbean, coral cover decline was followed by an increase in benthic macroalgae resulting from a combination of inter-related factors including (1) increased availability of habitable substrate via coral mortality (Aronson & Precht 2001), (2) a regional decrease in grazing

pressure caused by a decline of the herbivorous urchin *Diadema antillarum* (Hughes 1994, Woodley 1999, Lessios 2016), and (3) overfishing of herbivorous/detritivorous reef fishes, including parrotfish (scarids) and surgeonfish (acanthurids) (Hughes 1994). Large amounts of macroalgae on a reef can suppress coral recruitment through several mechanisms such as shading, abrasion, production of allelochemicals, and limiting suitable settlement substrate for new coral recruits, thus inhibiting coral population recovery (River & Edmunds 2001, Box & Mumby 2007, Rasher & Hay 2010). These changes in coral reef community structure continue to have negative and far-reaching effects on coastal communities that depend on coral reefs for fisheries production, tourism, protection from storms, and other ecosystem services (Costanza et al. 1997, Brander & van Beukering 2013).

Restoring herbivorous reef fish populations to control macroalgal growth and enhance the potential for coral population recovery has become a key goal of coral reef management (Mumby & Steneck 2008, Jackson et al. 2014). The establishment of marine protected areas (MPAs) is the principal strategy for restoring fish communities by reducing fishing pressure and subsequently increasing biomass and diversity (World Bank 2006, Lester et al. 2009). Although the ecological role of herbivorous fishes has been well documented (Carpenter 1986, Lewis 1986, Williams & Polunin 2001, Mumby et al. 2007), it is still unclear whether MPAs can restore grazing pressure to a level that facilitates coral recruitment and coral population recovery at a large scale. For this reason, long-term and large-scale monitoring efforts inside and outside of MPAs are critical for tracking changes in reef community structure and assessing overall effectiveness of the MPAs.

The purpose of our study was to test the effectiveness of Belize's national MPA network in protecting and restoring reef coral and fish populations and to identify key environmental and ecological factors contributing to reef health and the performance of Belize's MPA network. Our study utilizes recent advancements in MPA efficacy studies by comparing reef community structure across multiple protected areas over 5 yr, while controlling for seascape heterogeneity. We also tested the effects of several abiotic and biotic variables on fish biomass and benthic structure that could influence coral reef community structure and potentially protection success (Huntington et al. 2010).

The Belize Barrier Reef has one of the most extensive MPA networks in the Caribbean, consist-

ing of 18 MPAs that cover approximately 20% of territorial waters, but with only 3% fully protected from fishing (Healthy Reefs Initiative 2014). If these protected areas were effective prior to and during the study period, we hypothesize that lower fishing pressure within MPAs will increase both predatory and herbivorous fish biomass, decrease macroalgal cover as herbivorous fish biomass (and grazer pressure) increases, and increase percent cover for weedy coral species such as *Agaricia* sp. and *Porites* sp. as macroalgal cover decreases. We did not expect to observe significant changes in reef building corals such as *Orbicella* sp. over a 5 yr period as they need a longer period of time to increase in cover due to slow growth rates (Gladfelter et al. 1978, Knowlton 2001). Increases in predatory fish biomass may decrease prey fish biomass, including herbivorous fishes, leading to increased macroalgal cover and a decrease in coral cover. We tested this hypothesis; however, these types of trophic interactions between predators and herbivorous fishes are not common on coral reefs (Rizzari et al. 2015, Roff et al. 2016). The effect of herbivorous fish biomass on macroalgal cover is also influenced by species composition as diet preferences of herbivores vary by species (Randall 1967, Dromard et al. 2015). Macroalgae is not preferentially grazed by all parrotfishes with some species selectively feeding on turf algae (Randall 1967, Bruggemann et al. 1994, Adam et al. 2015, Dromard et al. 2015). Therefore, the overall effect of MPAs on the cascade from herbivores to algae will not only depend on reduced fishing pressure but also on species composition of both herbivorous fishes and algal species.

Most studies that evaluate MPA effects use control-impact comparisons, in which reef community structure inside and outside a protected area are compared (Osenberg et al. 2011). This type of comparison does not account for temporal changes in community structure or seascape heterogeneity that often occurs among sites or for trajectories of reef community parameters over time. For instance, Huntington et al. (2010) detected MPA effects at 1 protected area in Belize only after controlling for potential confounding effects of seascape heterogeneity. Rather than employing a traditional MPA–Control pairing approach, we compare reef communities within 8 MPAs (4 fully protected from fishing and 4 that allowed minimal fishing) to those within 8 control sites (essentially comparing 3 populations of sites, rather than making pairwise comparisons based on spatial proximity as is typically done).

MATERIALS AND METHODS

Study locations

We monitored reef communities at 16 fore reef sites (15–18 m depth) along the Belize Barrier Reef during the summer months of May and June in 2009, 2010, 2012, and 2013 (Table 1, see Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m563p065_supp.pdf). Experienced and trained divers performed all surveys. Sites were selected to maximize spatial coverage along the fore reef, include a range of protection zones, and to coincide with sites monitored in previous years by local collaborators (McField 2000, McField et al. 2001, Bood 2006). To minimize habitat variability of survey sites, we only surveyed spur-and-groove reef formations at each site and focused on habitats historically dominated by *Orbicella* spp. Survey sites included (1) 4 fully-protected management zones where only non-extractive activities were permitted (fully protected); (2) 4 general use zones where special restrictions were in place that include limited fishing licenses and banned use of traps, nets, and long-lines (general use); and (3) 8 unprotected reefs where finfish fishing was unrestricted except for herbivorous fishes and Nassau grouper (see Belize National Statutory Instrument No. 49 of 2009) (Table 1, Fig. S1). A ban on herbivorous fish harvesting was established for all Belizean waters in 2009.

Seasonal and size restrictions are currently in place for Nassau grouper in all waters. Information regarding zoning of protected areas is available from the Belize Fisheries Department (http://protectedareas.gov.bz/management_plans/) and the Healthy Reefs Initiative 2014 EcoAudit (www.healthyreefs.org/cms/belize/).

We classified level of enforcement at each MPA site according to rankings (i.e. good, moderate, and inadequate) published in the Healthy Reefs 2011 and 2014 EcoAudit for Belize (Healthy Reefs Initiative 2011, 2014). Sites with good enforcement had regular patrols and overall satisfactory compliance with regulations. Sites with moderate enforcement had regular patrols but limited poaching and insufficient legal outcomes. Protected sites with inadequate enforcement had irregular patrols, greater poaching, insufficient legal outcomes, and a high level of concern from the local community. These rankings were determined in a workshop setting and validated among all the participating MPA managers and Belizean NGO partners in the Healthy Reefs Initiative. We used the estimate of enforcement level from the 2011 EcoAudit for our 2009 and 2010 data and the estimate of enforcement level from the 2013 EcoAudit for our 2012 and 2013 data. These enforcement levels were not necessarily consistent over the duration of protection. Management plans and enforcement were not initiated at the time of MPA designation in all protected areas. For instance, active management within

Table 1. Monitoring site details. FP: fully protected zone; GU: general use zone; na: not applicable

Site	Latitude (°N)	Longitude (°W)	Reserve ID	Year established	Year managed	Size (km ²)	Protection status	Enforcement level
Calabash	17.2614	87.8197	Turneffe Atoll Marine Reserve	2012	2013	1115.8	None/GU ^a	na/Inadequate ^a
Half moon	17.2056	87.5467	Half Moon Caye National Monument	1982	1999	39.2	FP	Moderate
Middle Caye	16.7370	87.8053	Glover's Reef Marine Reserve	1993	1994	350.7	GU	Moderate/Good ^a
South of Middle Caye	16.7287	87.8286	Glover's Reef Marine Reserve	1993	1994	350.7	GU	Moderate/Good ^a
Tobacco Caye	16.9191	88.0475	No status	na	na	na	None	None
South Water Caye	16.8134	88.0775	South Water Caye Marine Reserve	1996	2010	476.7	GU/FP ^a	Inadequate/Moderate ^a
Alligator Caye	17.1966	88.0511	No status	na	na	na	None	None
Tackle Box	17.9105	87.9508	No status	na	na	na	None	None
Hol Chan	17.8634	87.9723	Hol Chan Marine Reserve	1987	1988	4.2	FP	Good
Mexico Rocks	17.9878	87.9038	No status	na	na	na	None	None
Bacalar Chico	18.1628	87.8222	Bacalar Chico Marine Reserve	1996		9.2	FP	Moderate
Gallows	17.4959	88.0425	No status	na	na	na	None	None
Pampion Caye	16.3731	88.0891	No status	na	na	na	None	None
Ranguana Caye	16.2850	88.1503	No status	na	na	na	None	None
Nicholas Caye	16.1123	88.2558	Sapodilla Cayes Marine Reserve	1996	2010	6.7	FP	Inadequate
Southwest Caye	16.7108	87.8461	Glover's Reef Marine Reserve	1993	1995	350.7	GU	Moderate/Good ^a

^aThe protection or enforcement level changed from the 2011 to 2013 EcoAudit assessments

the Sapodilla Cayes Marine Reserve and South Water Caye Marine Reserve was not introduced until 10 years after MPA designation (Table 1). Therefore, we also evaluate the effect of the duration of management within MPAs.

Fish surveys

We performed visual fish censuses to estimate reef fish species composition and density. Divers were trained by estimating fish sizes in the water against artificial fish models of known size and comparing these sizes to those estimated by a diver experienced in fish surveys. At each site, we counted and identified fishes within 2×30 m belt transects for individuals <40 cm in length, within 10×50 m belt transects for individuals >40 cm in length, and within 15×1 m belt transects for smaller fish (<5 cm). We deployed 6 to 8 belt transects per site at least 10 m apart and conducted surveys during daylight from 08:00 to 16:00 h. Fish species were identified and counted, and sizes were estimated in 10 cm intervals (McClanahan et al. 2011). Total lengths were recorded for species with rounded or truncated caudal fins, while fork lengths were recorded for all other species. Fish biomass was calculated through the allometric weight–length relationship, $W = aTL^b$, where W is the weight of each individual (in grams), TL is the length of each fish (in cm) estimated from visual surveys, and the parameters a and b are species-specific (Froese & Pauly 2011). When these variables were not available, we used the values of congeneric species of similar size and morphology. We used the mid-point of the 10 cm interval to calculate biomass.

Benthic surveys

Benthic cover was estimated using a point-intercept method (Lang et al. 2010, www.agrra.org). At each site, six 10 m lead-core transect lines were laid on the substrate along the spur and groove formation (15–18 m deep) spaced approximately 10 m apart. Benthic groups were identified at every 10 cm interval along the 10 m transect line. We broadly categorized the benthos as hard corals, macroalgae, crustose coralline algae, turf algae, zoanthids, sponges, gorgonians, rubble, sand, pavement, and other live categories that included bryozoans, anemones, and corallimorpharians. Hard corals and macroalgae were identified up to species and genus, respectively. Benthic transects occurred along the first 10 m of the fish transects.

Covariates

To assess the effectiveness of the Belize Barrier Reef MPA network, we examined 4 reef community parameters (predatory reef fish and parrotfish biomass, coral and macroalgae cover) that are commonly used as indicators of reef performance and health (McField & Kramer 2007, McField et al. 2011). We tested the effects of protection status, enforcement level, and duration of management on these 4 response variables as well as the effect of 8 additional biotic and abiotic variables that could influence coral reef community structure and potentially compromise management efforts. These additional explanatory variables included sea surface temperature anomalies, average oceanic net primary productivity (2002–2012), wave exposure, human population density, reef structural complexity, mangrove perimeter within 5 km, reef area within 5 km, and year of survey (Table S1 in the Supplement). The 4 response variables were also used as explanatory variables when appropriate. All variables were collected or calculated at the same 16 sites over the study period. For detailed descriptions, measurements, and justifications for each covariate, refer to the Supplement.

Data analysis

We used linear mixed effects models to test the effect of Belize's MPAs on parrotfish biomass and macroalgal cover and generalized linear mixed effect models to test MPA effects on coral and predatory fish biomass to account for a non-normal distribution. Predatory fish biomass and coral were modeled with a Gamma distribution with log link. We generated global models for all analyses that included all 16 sites with protection status, enforcement level, and a subset of the 8 covariates that could influence fish biomass or benthic community structure coded as fixed effects and with sites coded as random effects. Year was coded as a continuous variable in the linear mixed effects models when evaluating overall trends and as a discrete variable when evaluating differences between years. We detected evidence of temporal autocorrelation for parrotfish biomass and therefore included an autoregressive correlation structure (corAR1) in this model, which successfully accounted for this autocorrelation. To evaluate collinearity among all explanatory variables and generate models without correlated variables, we calculated the variance inflation factors (VIF) and sequentially removed

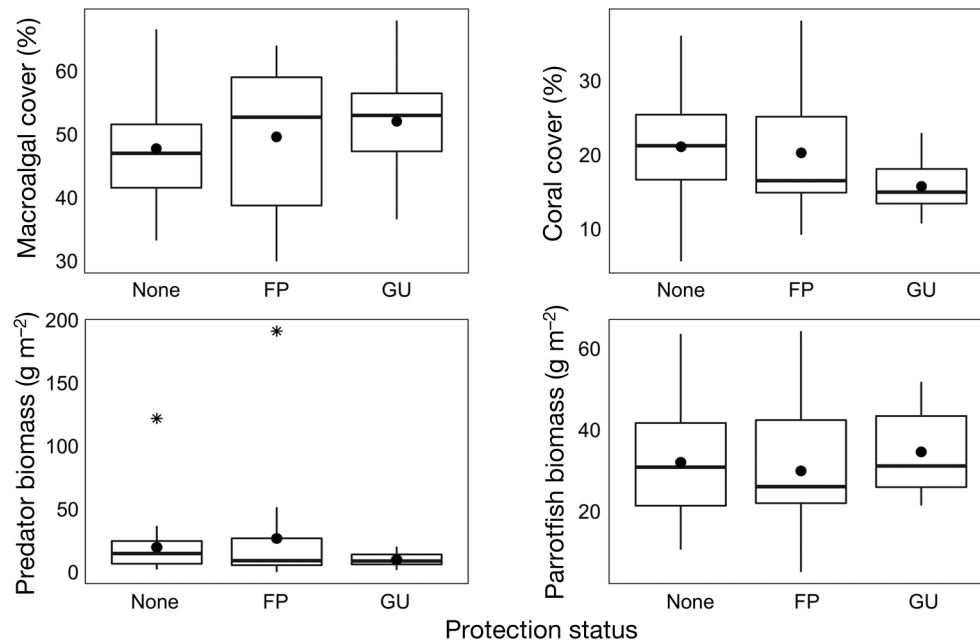


Fig. 1. Comparison of macroalgal cover, coral cover, predatory reef fish biomass, and parrotfish biomass by protection status including sites open to fishing (None), fully protected zones (FP), and partially protected general use zones (GU). Horizontal lines: medians; dots: means; boxes: 25th–75th percentiles (interquartile range, IQR); Lower/upper whiskers: extend to min./max. values within $1.5 \times$ IQR above/below 25th/75th percentile; asterisks: outliers

each covariate for which the VIF value was >2 (Graham 2003). Among the covariates, wave exposure, protection status, and enforcement level were sufficiently correlated to compromise interpretation when modeled together (Spearman rank correlation $r_s > 0.50$). Coral cover and macroalgal cover and coral cover and reef complexity were also sufficiently correlated. Therefore, we used 3 models for each response variable to account for correlated explanatory variables (Graham 2003). Table S1 provides the explanatory variables used in each model. Numerical covariates were standardized and centered (mean of zero and standard deviation of 1) to aid in model comparisons. Meaningful interactions and quadratic terms were included in exploratory models. To evaluate the effect of duration of protection, we generated a global model that included the 8 protected sites with the number of years managed and a subset of 8 covariates coded as fixed effects and sites coded as random effects.

Based on the global model, we ran all possible combinations of co-variables fitted by maximum likelihood to identify the top models that best explain the response indicators. Final models (those with a $\Delta AIC_c < 2$) were then run and averaged fitted by restricted maximum likelihood (Burnham & Anderson 2002). We calculated a marginal R^2 (R_m^2), which describes the proportion of variance explained by the fixed fac-

tor(s) alone, and a conditional R^2 (R_c^2), which describes the proportion of variance explained by both the fixed and random factors, using the package *piecewiseSEM* v1.1 (Lefcheck 2016).

Homogeneous and normal distribution errors of final top models were confirmed in the plot of residuals against predicted values and by using the normal scores of standardized residuals deviance, respectively (Zuur et al. 2009). Spline spatial correlograms were plotted to corroborate that the final model residuals were not spatially autocorrelated (Zuur et al. 2009). All analyses were performed in R v.2.15.2 (R Core Team 2013) using the package *nlme* v.3.1-113 for the linear mixed-effect models, *lme4* v1.1-7 for the generalized linear mixed-effects models, and *MuMin* v. 1.9.13 for the model averaging.

RESULTS

We found no detectable management effects on the mean biomass of predatory reef fishes and parrotfishes or on mean macroalgal and coral cover across the Belize coral reef system during the study period (Figs. 1 & 2, Table 2; see Fig. S2 in the Supplement). In contrast, based on the best-fit linear mixed effects models, we identified several ecological and environmental factors that influence these 4 reef community

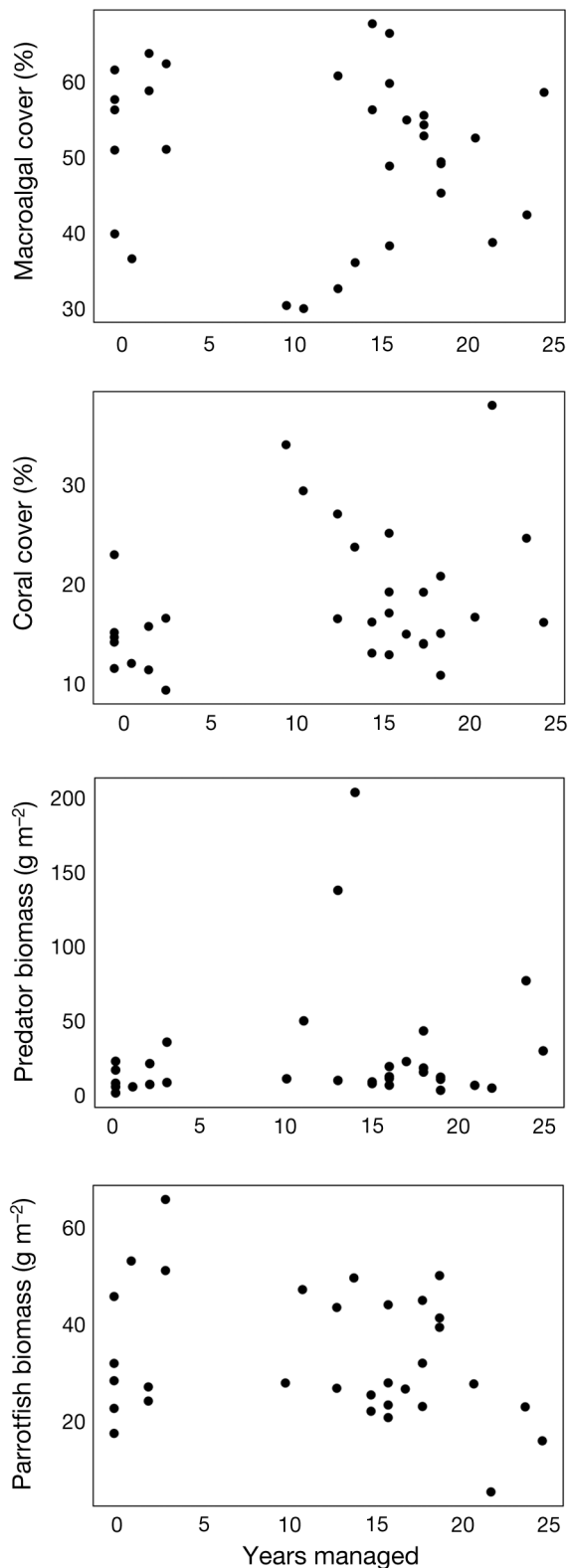


Fig. 2. Relationship between response variables and the number of years that the associated protected area was managed at the time of data collection. Points are response variable values across all protected sites and years

Table 2. Annual mean value across all sites and standard error (SE) of each response variable by protection status and enforcement level and results of the mixed effects models. N: number of sites across all years

Response variable	N	Mean	SE	p
Coral cover (%)				
<i>Protection status</i>				
Fully Protected	17	20.3	2.0	0.29
General Use	15	17.5	0.9	0.04
None	28	21.1	1.3	–
<i>Enforcement level</i>				
Good	10	21.0	4.8	0.51
Moderate	14	15.0	1.5	0.57
Inadequate	7	19.2	1.6	0.54
None	28	20.3	1.1	–
Macroalgal cover (%)				
<i>Protection status</i>				
Fully Protected	17	49.6	2.9	0.27
General Use	15	52.1	2.4	0.10
None	28	47.7	1.5	–
<i>Enforcement level</i>				
Good	10	52.3	5.5	0.76
Moderate	14	58.3	2.8	0.77
Inadequate	7	51.3	3.2	0.24
None	28	50.3	1.7	–
Predatory fish biomass (g m⁻²)				
<i>Protection status</i>				
Fully Protected	17	34.4	12.5	0.34
General Use	15	12.0	2.3	0.76
None	28	23.9	5.5	–
<i>Enforcement level</i>				
Good	10	17.2	8.0	0.67
Moderate	14	24.2	10.3	0.49
Inadequate	7	8.4	2.1	0.12
None	28	19.7	4.1	–
Parrotfish biomass (g m⁻²)				
<i>Protection status</i>				
Fully Protected	17	29.1	4.0	0.27
General Use	15	34.0	4.2	0.91
None	28	32.2	2.2	–
<i>Enforcement level</i>				
Good	10	17.4	4.7	0.007
Moderate	14	33.3	2.4	0.19
Inadequate	7	36.3	5.5	0.03
None	28	32.0	2.4	–

parameters and potentially the success of protection (Fig. 3; see Fig. S3, Table S1). Our findings may not translate to shallower reef habitats because we focused on deeper fore-reef habitat (15 to 18 m).

We did not observe higher predatory and herbivorous fish biomass inside Belize's MPAs than in fished areas (Fig. 3). However, we found that mean (site level) predatory reef fish biomass increased by approximately 300% from 2009 to 2013 ($p = 0.002$) in fully protected zones and on unprotected reefs (Fig. 3). In the fully protected zones, we observed

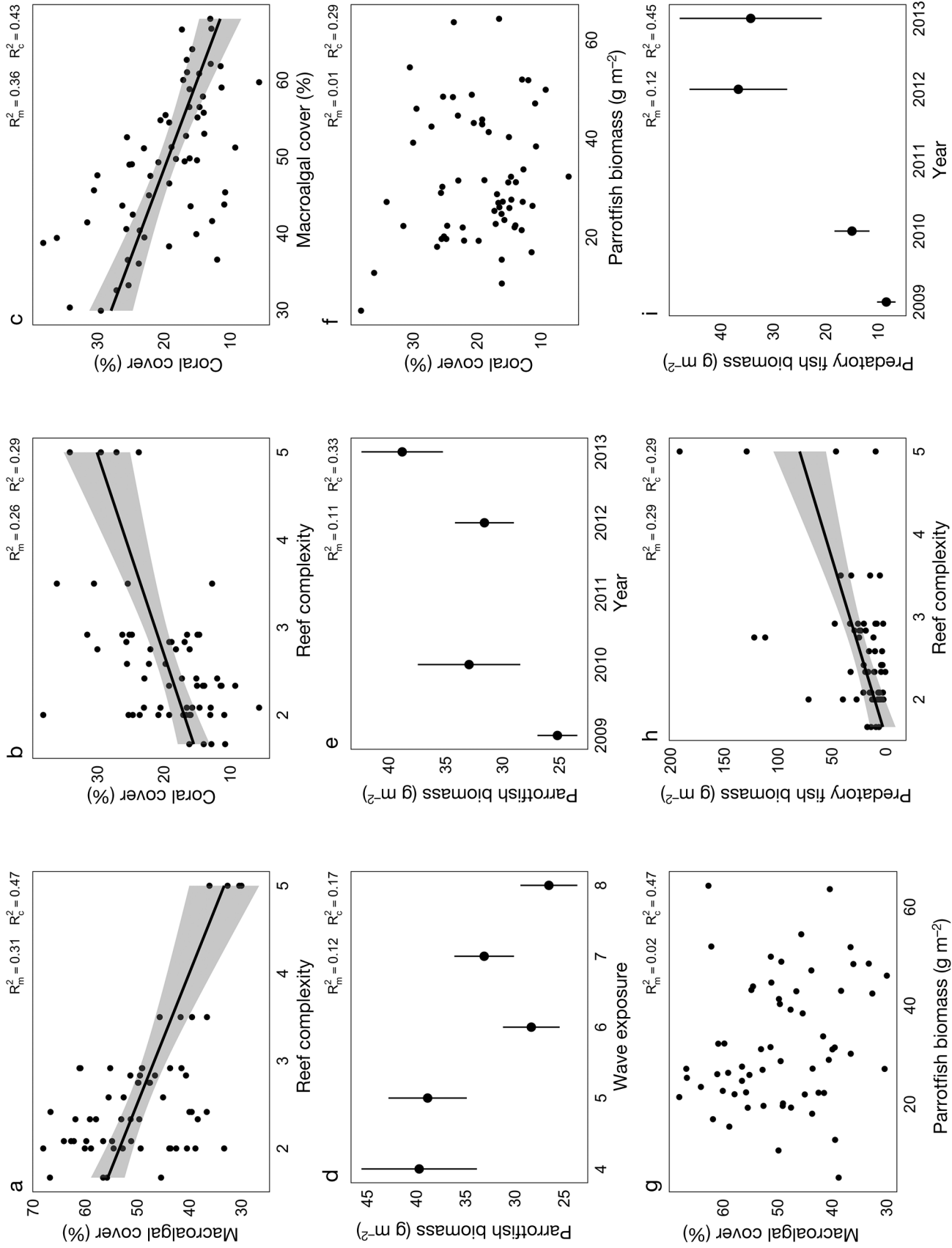


Fig. 3. Relationships between response variables and environmental or ecological covariates. Points are means by site for panels a-c and f-h. Solid points are means \pm standard error across all sites for panels d, e, and i. Black line is the mean ($\pm 95\%$ confidence interval in grey shading) of the predicted response variable as a function of a given covariate. R_m^2 is the proportion of variance explained by the fixed factor(s) alone, and R_c^2 is the proportion of variance explained by both the fixed and random factors. Refer to Fig. S3 in the Supplement for plots of the relationships between the remaining response and explanatory variables

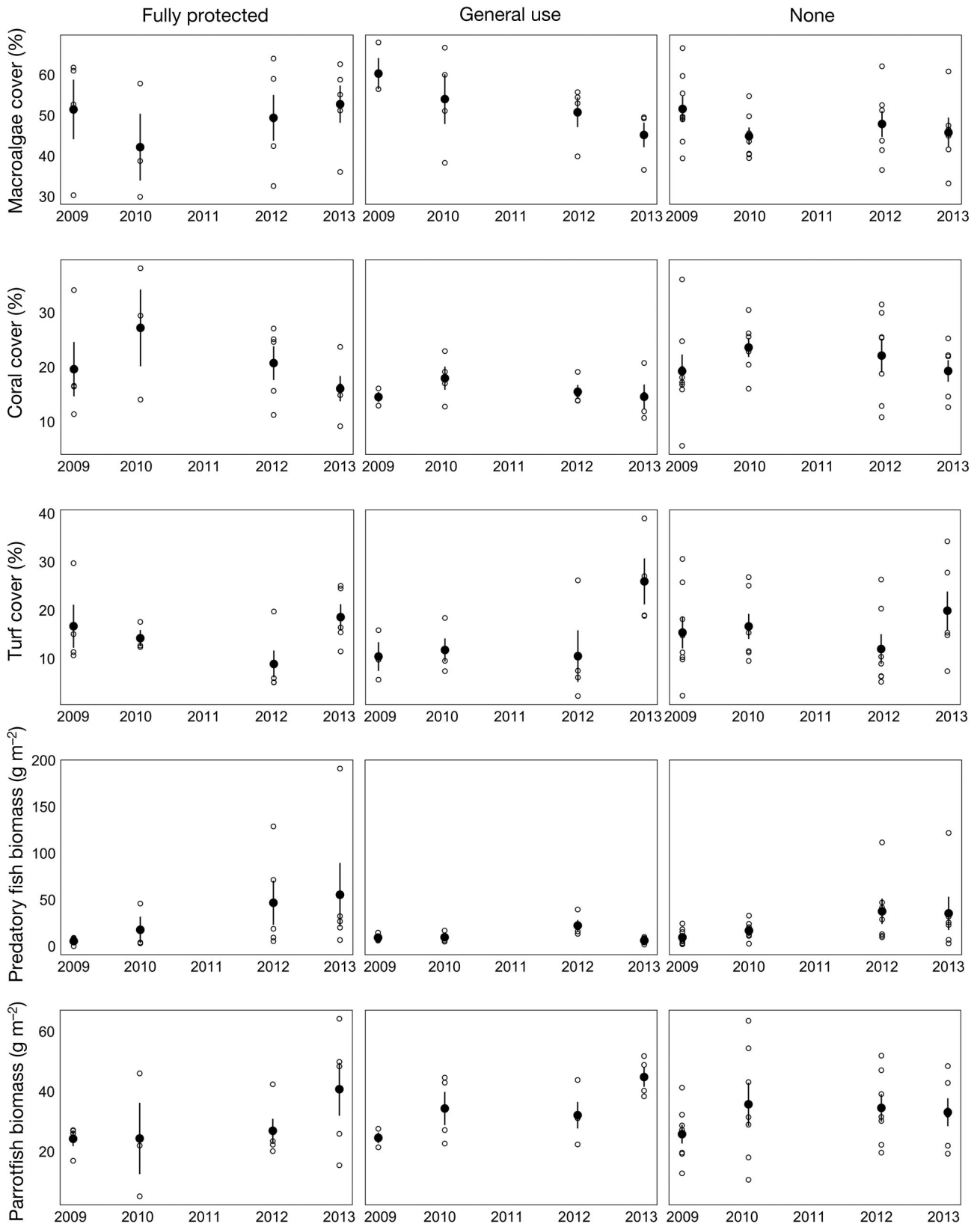


Fig. 4. Changes in parrotfish biomass, predator biomass, macroalgal cover, turf cover, and coral cover over time by protection status. Solid points are annual means \pm standard error. Open points are site means

Table 3. Mean value and standard error (SE) of (a) parrotfish and predatory fish biomass (g m^{-2}), and (b) benthic cover (%) by protection zone. *Comparisons between protection zones: * $p < 0.01$; ** $p < 0.05$

Taxon	Fully protected		General use		None	
	Mean	SE	Mean	SE	Mean	SE
(a) Fish biomass						
<i>S. viride</i>	12.8	1.2	12.1	2.9	12.2	1.2
<i>S. aurofrenatum</i>	5.8	1.0	7.4	1.3	7.3	0.4
<i>S. chrysopterus</i>	0.9	0.3	3.4*	0.8	1.7	0.4
<i>S. rubripinne</i>	1.6	1.1	3.6	0.8	2.5	1.0
<i>Scarus iserti</i>	5.9	0.7	5.9	0.6	6.2	0.5
<i>Scarus taeniopterus</i>	1.4	0.4	1.4	0.7	1.7	0.9
Total parrotfish	29.1	4.0	34.0	4.2	32.2	2.2
Total grouper	8.0	3.9	4.3	0.8	4.9	2.5
Total snapper	6.9	1.5	3.1	1.0	10.5	2.0
Total jack	9.5	3.4	3.1	1.7	11.8	5.1
<i>C. perezii</i>	7.6**	4.8	0.0	0.0	0.0	0.0
<i>Ginglymostoma cirratum</i>	1.4	0.9	0.0	0.0	2.1	1.5
<i>Sphyaena barracuda</i>	0.5	0.3	0.4	0.3	0.2	0.1
Total predatory fish	33.8	13.1	10.9	2.7	29.6	4.7
(b) Benthic cover						
Macroalgae	48.5	3.7	48.9	2.5	45.3	1.9
<i>Lobophora</i>	27.3	3.1	19.8	1.2	23.5	1.2
<i>Dictyota</i>	12.7	1.7	19.1	3.4	10.5	0.6
<i>Halimeda</i>	7.4	1.2	6.3	1.0	7.6	1.5
<i>Sargassum</i>	3.7	1.3	2.1	0.9	1.6	0.3
Coral	16.6	2.3	16.2	0.5	20.5	1.9
<i>Agaricia</i>	5.0	0.8	5.7	0.4	6.5	0.5
<i>Porites</i>	3.7	0.6	4.2	0.3	4.0	0.5
<i>Orbicella</i>	3.9	0.7	2.6	0.6	4.9	0.5
<i>Sideastrea</i>	1.8	0.2	2.0	0.4	2.4	0.3
<i>Diploria</i>	1.6	0.2	2.3	0.4	2.5	0.4
Turf	9.1	2.0	13.3	1.7	11.4	2.0
Crustose coralline algae	4.8	1.0	3.6	0.4	3.4	1.2
Sponge	4.7	2.1	2.2	0.8	3.8	0.6
Gorgonians	3.4	0.6	3.4	1.4	3.0	0.3

Protected areas within the Florida Keys showed higher abundances of large predatory and adult herbivorous fishes in MPAs after >2 decades of protection, yet juvenile parrotfish were more abundant in fished areas (Kramer & Heck 2007). Relatively high herbivorous fish biomass did translate into reductions of macroalgal cover, but coral cover has not recovered (Toth et al. 2014). Furthermore, coral recruitment was not positively associated with parrotfish abundance or adult coral recovery (van Woelk et al. 2014). Many of the reefs in the Florida Keys are now dominated by octocorals that may also preclude stony coral recovery (Ruzicka et al. 2013). Parrotfish biomass within the Exuma Cays Land and Sea Park (ECLSP) reserve in the Bahamas was 2-fold higher than in fished areas along the same reef tract (Mumby et al. 2006). As in the Florida Keys, the increase in grazing pressure led to a reduction of fleshy macroalgae (Mumby et al. 2007), but in contrast, protection also led to an in-

crease in coral recruits and coral cover for some weedy coral species (Mumby & Harborne 2010). Marine reserves on Kenyan reefs increased fish biomass, but coral bleaching has been the dominant driver of coral loss, and protection has not safeguarded coral from climate change (Darling et al. 2010).

It is clear that commercially targeted fish and invertebrate populations can respond to reductions in fishing, resulting in increased density and biomass (Polunin & Roberts 1993, Côté et al. 2001, Halpern 2003). However, maximum benefits are often not realized for some species because many MPA networks do not link larval supply and settlement areas or because they lack adequate enforcement (McClanahan et al. 2001, Gaines et al. 2010, Huntington et al. 2011). For instance, after >10 yr of reserve designation and management, Glover's Reef Marine Reserve in Belize has had a very weak effect on herbivorous fish abundance and no effect on macroalgal cover or coral cover (Huntington et al. 2011, McClanahan et al. 2011). Our results broaden the scale of previous findings in Belize and elsewhere and demonstrate that Belize's national MPA network (14 % of which is fully protected) has not yet consistently influenced predatory or herbivorous fish biomass and macroalgal or coral cover.

It is possible that MPAs in Belize do not have the combination of size and effective enforcement to increase fish biomass across the network. The ECLSP is a 456 km^2 no-take area that has been enforced since 1986 (Mumby et al. 2006). In Belize, Glover's Reserve is 350 km^2 and reports good enforcement but is not fully protected. The remaining MPAs in Belize are either large with inadequate enforcement or small with good to moderate enforcement, which may limit protection success (Edgar et al. 2014) (Table 1).

Predatory and herbivorous fish biomass

As expected, predatory fish biomass increased in the fully protected zone ($p = 0.006$; Fig. 4). Interestingly, predatory fish biomass also increased on the unprotected reefs ($p = 0.02$; Fig. 4). However, predatory fish biomass was highly variable among sites

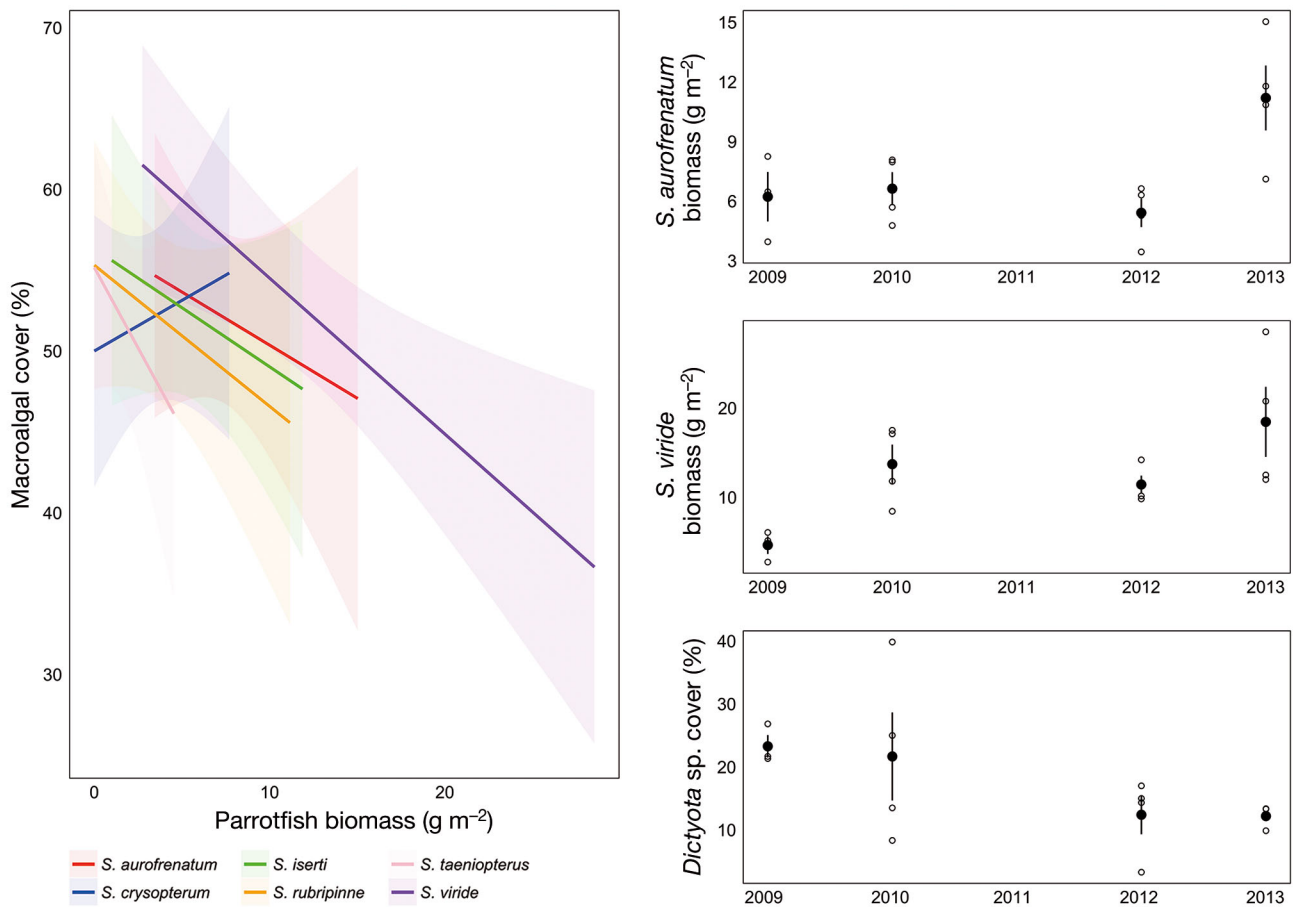


Fig. 5. (a) Relationships between parrotfish biomass and macroalgal cover by species within the general use zone. Points are means by site across all years. Corresponding colored line is the mean ($\pm 95\%$ confidence interval) of the macroalgal cover as a function of parrotfish biomass. (b–d) Significant changes in (b) *S. aurofrenatum* biomass, (c) *S. viride* biomass, and (d) *Dictyota* sp. cover over time within the general use zone. Solid points are annual means \pm standard error. Open points are site means

(see Fig. S5 in the Supplement). Only 2 sites (Tackle Box [none] and Half Moon [fully protected]) exhibited substantially higher predatory fish biomass in 2012 and 2013 compared to other sites, driving the overall increase in mean predatory fish biomass (Figs. S5 & S6). Mean parrotfish biomass increased over time, possibly due to compliance with a national ban on herbivorous fish harvesting implemented in 2009 (Cox et al. 2013). The mean parrotfish biomass increase was restricted to the general use zone (Fig. 4). However, mean parrotfish biomass in the fully protected zone masks the significant increase recorded within Half Moon Caye due to the lack of change within Bacalar Chico and Hol Chan (Fig. S7). Higher budgets, more supporting staff, and the close proximity of the fully protected zone to the reserve headquarters potentially make consistent vigilance and enforcement more successful at Half Moon Caye

leading to the observed increases in both predatory fish and parrotfish biomass. These results suggest that improved enforcement may be necessary to restore fish communities in some areas (Mumby & Steeneck 2008). Alternatively, larval export and emigration of adults and juveniles from MPAs to fished areas (spillover) may be masking the positive effects of the protected areas by spreading these benefits into the adjacent fished areas as is expected or planned for a successful network (Abesamis & Russ 2005, Stamoulis & Friedlander 2013).

Grazer composition and benthic community structure

Our study suggests that current parrotfish herbivory in Belize is not controlling overall macroalgal

cover. Across the Caribbean, current *Diadema* populations densities are approximately 12% of those before the mass die-off in the early 1980s (Lessios 2016). In 2004, *Diadema* abundance across sites in Belize ranged from <1 to approximately 4 ind. m⁻² at shallow depths of <6 m (Carpenter & Edmunds 2006). During our study, we did not observe *Diadema* along any transect at deeper (15–18 m) fore reef habitats. *Diadema* venture out on the reef at night to feed and return to shelter during the day; therefore, it is possible that some individuals were hidden in crevices (Carpenter 1984) and were undetected during our surveys. Without higher parrotfish biomass and in the absence of *Diadema*, it is not surprising that we did not observe lower macroalgal cover within MPAs as observed in the ECLSP, Bahamas (Mumby & Harborne 2010, Mumby et al. 2007), and the Florida Keys (Toth et al. 2014). However, we also found no relationship between mean macroalgal cover and mean parrotfish biomass across all sites and years (Fig. 3f). Suchley et al. (2016) also found no relationship between coral and macroalgal cover across the Mesoamerican region and suggest that fish herbivory was not a major driver of change in macroalgal cover, but that environmental conditions including rising nutrient levels play an important role in macroalgal growth. Nutrient enrichment can have strong effects on algal growth, particularly in the absence of sufficient herbivores or by overriding herbivory effects, potentially contributing to the severe phase-shift in Belize (Burkepile & Hay 2006). Similarly, there was no evidence that parrotfish density affected macroalgal or coral cover in no-take reserves in the Philippines (Russ et al. 2015). In this case, parrotfish populations were regulated by disturbance when coral mortality enabled increased macroalgae cover and primary productivity (Russ et al. 2015).

Mean macroalgal cover across the Caribbean is approximately 23%, and only 10% of 530 reef sites assessed in a 2009 study exhibited macroalgal cover > 50% (Bruno et al. 2009, Jackson et al. 2014). In our study, all sites had >30% macroalgal cover with parrotfish biomass ranging from 5 g m⁻² to 64 g m⁻² (Fig. 3). A previous study across 19 sites within 7 Caribbean locations showed that reefs with >30% macroalgal cover are associated with <10 g m⁻² of parrotfish biomass (Williams & Polunin 2001). This suggests that the amount of macroalgae on Belizean reefs may simply be greater than the consumption capacity of herbivorous fishes in the absence of *Diadema* (Adam et al. 2015). This in turn could preclude a potential cascading effect of herbivores on macroalgal abundance.

Furthermore, the parrotfish species assemblages present on the reefs in our study area may not be grazing on the dominant algal species due to dietary preferences (Burkepile & Hay 2008, 2010, Fricke et al. 2011). For example, despite a reduction in the cover of *Dictyota* spp., total mean macroalgal cover remained high (>40%) in 2013 mainly due to high *Lobophora* spp. cover (Fig. 5, Table 3, see Fig. S8). A lack of grazing was most likely a major contributor to the sustained levels of *Lobophora* spp. cover (Slattery & Lesser 2014). These findings highlight the importance of species composition in macroalgal reduction and control (Burkepile & Hay 2008, 2010, Fricke et al. 2011).

We expected to see increases in coral cover for weedy coral species (*Agaricia* and *Porites*) as macroalgal cover decreased. Despite a decrease in mean macroalgal cover in the general use zone, there was no change in coral cover, suggesting that a more severe coral to macroalgal phase-shift has occurred in this area in comparison with elsewhere in the Caribbean (Fig. 4).

Abiotic and biotic effects on reef community structure

Our study suggests that reef structural complexity and wave exposure can directly influence fish and benthic communities. Higher structural reef complexity has been shown to be a strong correlate of fish biomass (Wilson et al. 2007, Alvarez-Filip et al. 2011). Among our study sites, Half Moon Caye exhibits the highest structural reef complexity, and as our models predicted, this site supported high predatory fish biomass. Higher structural complexity may have led to relatively lower macroalgal cover compared to the other sites in our study (Fig. S4). However, parrotfish biomass was not associated with reef complexity across all sites (Fig. S3). Furthermore, macroalgae cover did not respond to parrotfish biomass, suggesting that the lower macroalgal cover at Half Moon Caye is a result of other grazers, potentially cryptic *Diadema*. Increased densities of *Diadema* have been associated with complex reef habitats, potentially explaining the lower macroalgal cover observed at Half Moon Caye (Lee 2006). Our results indicated that structural complexity is of vital importance to the health of this reef providing refuge from predators and potentially attracting *Diadema* and other marine organisms (Lee 2006).

Wave exposure has been a good predictor of spatial variation in reef building corals such as *Orbicella* sp.

(Chollett & Mumby 2012) and can partially explain beta diversity patterns of benthic communities (Harborne et al. 2006). Wave exposure may also directly affect the biomass and diversity of tropical reef fish (Friedlander et al. 2003) and the distribution and abundance of temperate reef fish by compromising swimming abilities (Fulton & Bellwood 2004). Alternatively, by modifying the distribution of foundation species such as corals, wave exposure could affect fish species that depend on them. Our findings are consistent with previous studies and highlight the importance of protecting sites protected from wave exposure to restore and sustain high parrotfish biomass.

CONCLUSION

As anthropogenic and natural pressures continue to intensify, effective marine protected areas are increasingly critical not only for conserving the species and ecosystems that they contain but also sustaining the human populations that rely on these ecosystems (Watson et al. 2014). Our results suggest that local managers should focus their enforcement efforts on those reefs with higher structural complexity that naturally support high predatory fish biomass and lower macroalgal cover and on those reefs protected from wave exposure that support higher parrotfish biomass. In addition, broader fisheries management strategies that are not limited to MPAs, such as the recent ban on herbivorous fish harvesting in all national waters in Belize, may be necessary to promote parrotfish population recovery independent of MPA designation or enforcement. Strengthening enforcement, limiting poaching within MPA boundaries, and implementing fisheries policies that cross MPA boundaries could promote faster recovery of fish communities. However, it is possible that restoring parrotfish populations in locations with high macroalgal cover such as Belize may be not be enough to reverse the shift from coral to macroalgal dominance. *Diadema* restoration efforts may be warranted in order to increase herbivory to functional thresholds. Furthermore, improving water quality by managing terrestrial runoff and sources of nutrients (particularly sewage treatment) may also be an important step toward reducing macroalgae and restoring coral reef communities. We suggest that community composition and local environmental conditions play key roles in coral reef recovery and should be considered when evaluating and designing reef management strategies.

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