Benefits of a replenishment zone revealed through trends in focal species at Glover's Atoll, Belize

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ABSTRACT: Marine protected areas or replenishment zones have become one of the more popular tools within an ecosystem-based management approach aimed at balancing environmental health with socio-economic needs. We examined changes in populations of an ecologically representative suite of focal species, including ones important to local small-scale fisheries, over a 7 yr period using both independent visual surveys and fisheries-dependent data. Most small-scale fisheries targets showed increases in density, biomass, or size within the replenishment zone and stable or increasing catch rates beyond replenishment zone boundaries. Lower trophic level, high recruiting species of more limited movement such as parrotfish, conch, and lobster appeared to respond most clearly to protection, while higher trophic level, late maturing, and more widely dispersing snappers and groupers generally displayed more limited recovery. Patterns of mid-trophic level hogfish and queen triggerfish appeared to be linked to the availability of appropriate prey, i.e. conch and urchins respectively, with increasing angelfish catch per unit effort appearing to replace large parrotfish since the ban on harvesting herbivorous fish in 2009. Patterns of triggerfish and angelfish may also be linked to benthic cover, given their preferences for urchins and sponges, respectively. These results address the core management objectives for Glover's Reef Marine Reserve, Belize, to ensure sustainability of its resources and enhance economic benefits from fisheries. Our study highlights the importance of using other fisheries conservation strategies (size limits, closed seasons) in conjunction with replenishment zones, as well as direct consultation with resource users in order to maximize benefits.

KEY WORDS: Coral reef fishes · Invertebrate fisheries · Small-scale fisheries · Marine protected area · Trophic structure

INTRODUCTION

Although some fisheries are sustainably managed, many populations worldwide are overexploited and continue to decline, particularly in countries that lack the resources for rigorous population assessment and enforcement of fisheries regulations (Melnychuk et al. 2017). Natural refuges may provide inaccessible areas that can protect some populations from exploitation (Karpov et al. 1998, Tyler et al. 2009). The refuge concept, often termed reserve or protected area, has given resource managers a valuable tool to potentially enhance fisheries in areas beyond reserves (Rowley 1994, McClanahan & Mangi 2000, Roberts et al. 2001). Marine reserves or marine protected areas (MPAs) are now common, have evoked considerable public interest, and have become one of the more popular tools within an ecosystem-based management approach aimed at balancing environmental health with socio-economic needs (Dugan & Davis

1993, McClanahan & Mangi 2000, Pinnegar et al. 2000, Agardy et al. 2003, Arkema et al. 2006, Edgar et al. 2014, Di Franco et al. 2016). Areas within MPAs where all extractive processes are prohibited are traditionally referred to as 'no-take areas' which may be imbedded within larger marine reserves that include areas for legal extraction of marine resources under broader fisheries conservation strategies such as minimum sizes and closed seasons (Moore 1999, Agardy et al. 2003, Dahlgren 2014). However, in Belize the term 'replenishment zone' (RZ) has recently been adopted instead of 'no-take zone' to emphasize the overall objective of enhancing benefits to small-scale fisheries (SSF) based livelihoods both within the RZ and in surrounding areas that are fished (Dahlgren 2014). The term 'replenishment zone' may also have a less negative connotation for resource users concerned about being restricted from operating in traditional fishing areas and will be a more universally accepted term for use by scientists, conservationists, resource managers, and fishers in promoting such a management tool (Dahlgren & Tewfik 2015).

A number of studies have described benefits that may be provided by RZs, including conservation of target species, improved fisheries yields, and protection of ecosystem structure, function, and integrity (Lester et al. 2009, Molloy et al. 2009, Babcock et al. 2010). The ecological basis for conveying benefits to target species from RZs begins with the development of a high density of large, mature, and highly fecund individuals (Bertelsen & Matthews 2001, Stoner et al. 2012, Hixon et al. 2014). Once such densities are persistent, the enhancement of fisheries yields, non-target species, and living habitat (e.g. corals) may occur through (1) the net export of larvae ('recruitment effect') and (2) the net emigration of post-settlement animals ('spillover effect') from the RZ (Stoner et al. 1998, Chapman & Kramer 1999, Lipcius et al. 2001, Tewfik & Bene 2003). While the recruitment effect largely depends on hydrodynamic processes of tides and currents, the spillover effect is driven by species and community-specific density-dependent needs for adequate habitat, which underlies the requirements of both food and shelter within the RZ (Dugan & Davis 1993, Rowley 1994, Russ & Alcala 1996, Davidson et al. 2002).

Empirical studies of RZ effects over time typically contrast the density, biomass, or individual size of target species within RZs to similar habitats outside and consider changes in these population parameters over time (Russ & Alcala 1996, Davidson et al. 2002, McClanahan et al. 2011, Dahlgren 2014). In addition, the comparison of catch rates or total catches before and after the establishment of the reserve or across a time series have also been used to reveal positive effects beyond the boundaries of RZs (Kerwath et al. 2013). The time required to detect increases in density, biomass, and size of target species within RZs, as well as the impact of the recruitment and spillover effects beyond, will depend on a variety of factors, including the status and life history of the targeted populations (e.g. growth rate, fecundity, planktonic larval duration, movement rates), characteristics of the RZ (e.g. habitats, oceanographic conditions, efficacy of enforcement, boundary porosity), the nature of the fishery operating around it, and interactions with non-target species (Rowley 1994, Pinnegar et al. 2000, Gell & Roberts 2003, Micheli et al. 2004, Lester et al. 2009, Molloy et al. 2009, Dahlgren & Tewfik 2015).

Here, we examined changes in populations of an ecologically representative suite of focal species (Zacharias & Roff 2001) including ones important to local SSF (Fig. 1). We define focal species as those whose abundance or population structure have the expectation of providing '… a means to understanding the composition, state and/or function of a more complex community' (Zacharias & Roff 2001, p. 59), in this case Glover's Reef Atoll, Belize, as well as the complex dynamics associated with enhancement of biodiversity and SSF from RZs. Specifically, we estimated overall density, biomass, and size of focal species on a series of patch reefs in the RZ (i.e. no-take) and the general use zone (GUZ) at Glover's Reef Marine Reserve (GRMR) across a 7 yr time series (2007–2013). These data were coupled with catch data collected over the same time series. Increases in density, biomass, and size of focal species within the RZ are likely to be the result of protection (i.e. no-take status), and such increases would augment, either stabilize or increase, catch per unit effort (CPUE) within the GUZ, thus supporting SSF livelihoods (Rowley 1994). The trophically diverse nature of the focal species suite examined will allow observations of interactions between species and the responses of species given different life history strategies under both protection (RZ) and extraction (GUZ) (Micheli et al. 2004). The focal species included invertebrates, i.e. queen conch *Lobatus gigas* (herbivore) and Caribbean spiny lobster *Panulirus argus* (invertivore), which are the basis of important SSF in Belize and throughout the region (Cochrane & Chakalall 2001, Theile 2001, Acosta 2006, Babcock et al. 2015a) (Fig. 1). A representative suite of commercially important fish species (black grouper *Mycteroperca bonaci*, Nassau grouper *Epinephelus striatus*, mutton snapper *Lutjanus analis*, hogfish *Lachnolaimus maximus*, and queen triggerfish
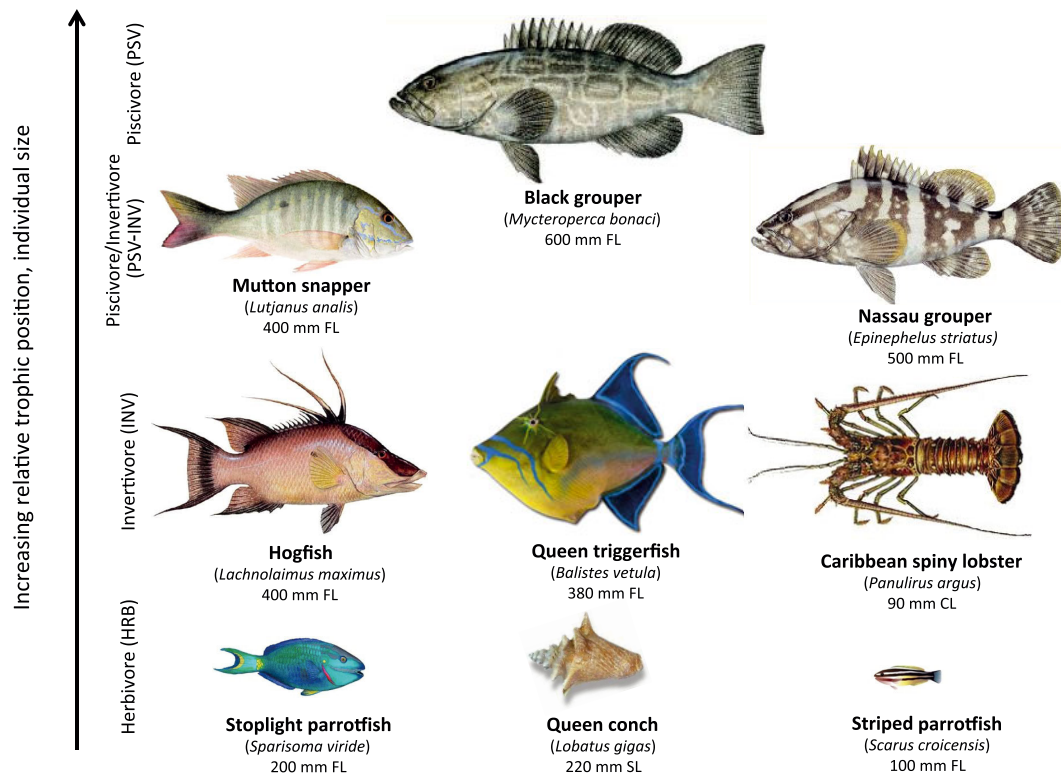
Fig. 1. Focal species targeted by the Long-term Atoll Monitoring Program (LAMP). Physical sizes are relative based on approximate maximum measures (mm; FL: fork length, CL: carapace length, SL: shell length) encountered on patch reef habitat between 2007 and 2013. Details of trophic classification for fish are given in Table 1. Herbivores (HRB) are further subdivided into large parrotfish (LHRB, 3 species, e.g. stoplight) and small parrotfish (SHRB, 3 species, e.g. striped; see Table 1). Queen conch depicted is a juvenile lacking the broad shell lip typically associated with adults

Balistes vetula; Babcock et al. 2013), as well as 6 common parrotfish (Scaridae) species (Vallès & Oxenford 2014) were also examined to provide an assessment of potential changes across a trophically diverse fish community that uses a range of habitats (Fig. 1). Two of the focal species included in our study (queen conch; Nassau grouper) have been identified as conservation targets within GRMR management plans given their dependence on a wide range of habitats and importance to SSF (Walker & Walker 2007, Gibson et al. 2011).

The purpose of this study was to test for changes in density, biomass, and size of the focal species in the RZ and in the GUZ, to infer the impact of the RZ on these populations. If any of these metrics are higher in the RZ than in the GUZ at the beginning of the study, that may indicate that the RZ has been effective, since the reserve had been in effect before our study began; however, differences in habitat quality may also lead to differences between zones. An increase over time in both zones may indicate that the RZ is improving population status in both zones through a buildup in the RZ followed by either spillover or recruitment into

the GUZ, or the increase may be caused by environmental changes or a change in fishing effort. The strongest evidence for an impact of the RZ would be an increase in the RZ combined with a decrease in the GUZ. Although the RZ has been in place since 1993, it would not be surprising to see continued divergence between zones over time, especially because enforcement of the RZ has been greatly improved since the establishment of the reserve. This has included the construction of an observation tower at the heart of the RZ on Middle Caye and the use of spotting scopes and radar as well as the deployment of a new patrol vessel, increased fuel allocation, use of night-vision goggles, and spot lights for night patrols leading to a declining rate of infractions (Gibson & Hoare 2006, Gibson et al. 2013). Also, because the effects of marine reserves often take decades to play out, particularly for long-lived species and due to delays of cascading trophic interactions (Micheli et al. 2004, Babcock et al. 2010), our study period may therefore provide the best evidence for the utility of monitoring focal species that represent trophic diversity, SSF targets (including invertebrates), and the effectiveness

of RZs in supporting fisheries-based livelihoods since the establishment of GRMR. The importance of using other fisheries conservation strategies (e.g. size limits, closed seasons) in conjunction with RZs is also highlighted.

MATERIALS AND METHODS

Study site

Glover's Reef Atoll (16° 44′ N, 87° 48′ W) lies approximately 42 km east of the Belizean mainland and 22 km to the east of the main Belize Barrier Reef. It is 1 of 7 protected areas that comprise the Belize Barrier Reef Reserve System, inscribed as a UNESCO World Heritage Site in 1996 (Fig. 2a). The atoll is approximately 33 km long and 14 km wide, with an area of approximately 350 km² defined by the 200 m depth contour. Water depth around the atoll ranges from 300 to 400 m to the north and west, while the east side drops to over 1000 m. Water depth in the inner lagoon, which is surrounded by a reef crest barrier, averages 6–8 m with depths up to 28 m. Three main channels connect the ocean, fore-reef, and lagoon habitats, with the lagoon containing more than 800 patch reefs. The entire Glover's Reef Atoll was established as a Marine Reserve in 1993 (Statutory Instrument 38 of 1993 under the Fisheries Act Chapter 210) and is managed by staff of the Belize Fisheries Department based at the Wildlife Conservation Society's Research Station on Middle Caye. The RZ (i.e. no-take area), which includes a wilderness zone and a spawning aggregation zone, is approximately 79.6 km² or 22.7 % of the entire reserve (Fig. 2). Specific management objectives for GRMR include: (1) 'to regulate use of the
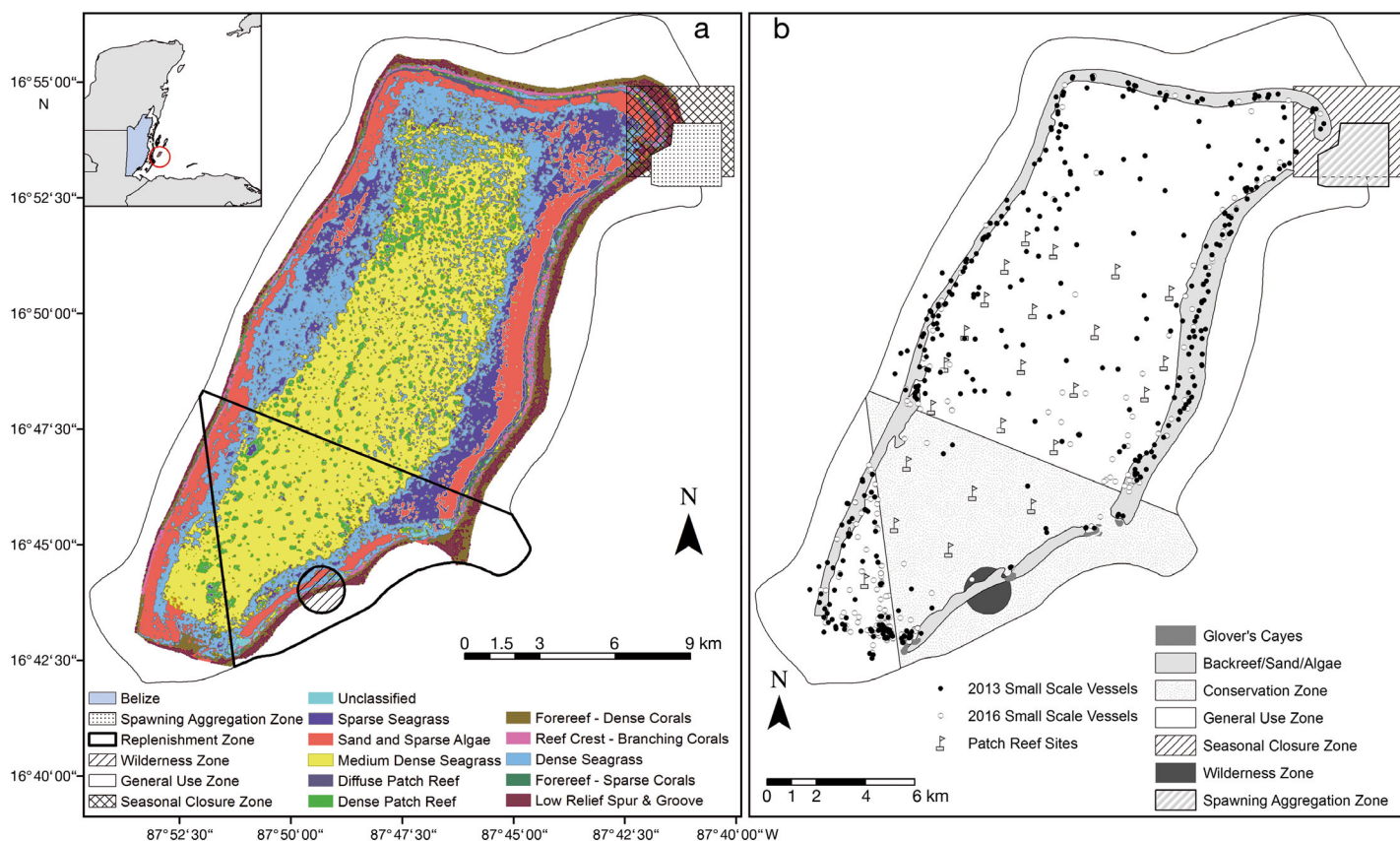

Fig. 2. (a) Glover's Reef Marine Reserve (GRMR), including management zones and principal benthic habitat types (Mumby & Harborne 1999). The wilderness zone and spawning zone are part of the replenishment zone permanently closed to fishing. The seasonal closure zone is closed to all fishing between 1 December and 31 March of the following year and implemented to protect the spawning activities of Nassau grouper *Epinephelus striatus*. The outer boundary of the reserve is approximated by the 200 m depth contour. Inset: location of Glover's Atoll (circled) off the coast of Belize. (b) Location of monitored patch reef sites at GRMR, position of enforcement encounters with small-scale fishing vessels, and distribution of management zones. Positions of small-scale vessels were collected by Belize Fisheries Department Enforcement Officers using tablets equipped with the 'Spatial Monitoring and Reporting Tool' (SMART, version 3.1, http://smartconservationtools.org/) software

area to ensure sustainability of its resources, resilience of its ecosystems, and maintenance of ecological processes'; (2) 'to encourage use of the atoll for applied scientific research by the national and international scientific community, and to feed the results of research into the marine reserve's management-decision process'; and (3) 'to enhance the social and economic benefits of the area by promoting uses compatible with conservation and sustainable development principles.' (Walker & Walker 2007, p. 95).

A number of fisheries regulations have been put in place across Belize to protected exploited species. These include: a ban on the use of SCUBA to collect any seafood; closed seasons for queen conch (1 July – 30 September), spiny lobster (15 February – 14 June), and Nassau grouper (1 December – 31 March); size limits for queen conch (>177 mm shell length, >85 g market meat mass), spiny lobster (>76 mm carapace length, >113 g tail mass), and Nassau grouper (50–76 cm total length, must be landed whole), as well as a complete ban on the harvest of scarids (parrotfish) and acanthurids (tang/surgeonfish/doctorfish). Permit *Trachinotus falcatus*, tarpon *Megalops atlanticus*, and bonefish *Albula vulpes* may not be landed but are important to recreational catch-and-release fishing associated livelihoods. Nurse sharks *Ginglymostoma cirratum* and whale sharks *Rhincodon typus* are completely protected. All other fish landed as fillet must include a skin patch (5 × 2.5 cm) for species identification in order to prevent circumvention of the whole Nassau grouper landing rule.

Field survey techniques

The Long-term Atoll Monitoring Protocol (LAMP) was introduced in 1996 to exclusively monitor spiny lobster and queen conch populations within the GRMR (Acosta 2003). In 2000, it was expanded to include the monitoring of 5 commercially important finfish species: black grouper, Nassau grouper, mutton snapper, hogfish, and queen triggerfish (Acosta 2003) (Fig. 1). In March 2006, 6 species of parrotfish were provisionally included in the monitoring program because of their importance as generalist grazers on reefs, as well as their increasing importance in the commercial catch at that time (McClanahan et al. 2011, Babcock et al. 2013). These 6 species are: stoplight *Sparisoma viride*; redtail *S. chrysopterum*; redfin (or yellowtail) *S. rubripinne*, redband *S. aurofrenatum*, princess *Scarus taeniopterus*; and striped *Scarus croicensis*. The 13 focal species were monitored together as of 2007 and represent a trophically diverse set of consumers (pisci-

vores, piscivore-invertivores, invertivores, herbivores) found across Glover's atoll habitats (Fig. 1, Table 1). The suite of focal species was monitored at a series of patch reefs inside and outside the RZ (Fig. 2b) between 2007 and 2013. The number of patch reefs monitored was expanded from 5 RZ and 6 GUZ sites (2007–2009) to include an additional 12 GUZ sites (2010–2013). Therefore, the LAMP data collected from 2007–2013 represent the best available information on the widest set of sites and species, including commercially and ecologically significant invertebrates (conch and lobster), since the inception of the reserve in 1993. Patch reef area ranged between 0.04 and 1.43 ha, determined from patch reef-specific polygons constructed using a series of on-site determined GPS waypoints. Each individual patch reef was sampled once per year during April, May, or June to avoid seasonal effects. Limited sample sizes for some of the higher trophic level species required the use of all individual length data collected during other months (February, November) between 2007 and 2009. The limited size and shallowness of the patch reefs did not permit the use of standardized transects (McClanahan et al. 2011). The entire area of each patch reef, mean depth of 1.6 ± 0.2 m including sloping sides, was examined by 3 snorkelers down to 3 m. The first snorkeler entered the water alone and recorded the abundance and estimated fork length (5 cm visual bins) of focal fish species in a systematic manner across all patches. Free-diving was very limited, with most observations of fish taken from the surface on these shallow patches. The second and third snorkelers entered the water after the fish surveyor had covered one side of a patch in an effort to minimize disturbance to the resident fish community. The second snorkeler recorded the abundance and size of spiny lobster (carapace length ± 5 mm using a marked fiberglass rod) and the third examined queen conch (shell length and lip thickness determined with Vernier calipers ± 1 mm).

Approximately 34 sailboats were engaged in fishing operations at Glover's Atoll during the study period, with no trend in numbers over time. Catch data were collected for 3 d monthly outside the RZ through haphazard encounters with individual fishers, operating from canoes, based on sailboats (i.e. mother vessels) with 4 to 7 fishers (i.e. crews). A total of 3 to 5 sailboats were encountered each month, and approximately 30% of the fleet was sampled each year. Individual fishers hand-collected (conch), hooked (lobster), or speared (fish) targets during multiple free-dives over the course of a day. The abundance and size of all individual targets, as well as the number of hours fished to obtain the assessed

Table 1. Focal species included in the Long-term Atoll Monitoring Program (LAMP) surveys (2007–2013). Length–weight (Len-Wt) conversion parameters obtained from Fishbase (accessed September 2014) to calculate mass (W, in g) from visually estimated fork lengths (FL, in cm) as $W = aFL^b$. Diet data (fish, arthropod, mollusk, echinoderm, cnidarian, porifera, algae, seagrass, other) are percent of stomach volumes from very large samples collected by spearfishing, mainly in Puerto Rico and the Virgin Islands (Randall 1967), and used for trophic groupings. PSV: piscivore (>75% fish), PSV-INV: piscivore-invertivore, INV: invertivore, HRB: herbivore, LHRB: large herbivore, SHRB: small herbivore. Angelfish (gray *Pomacanthus arcuatus*; French *P. paru*; queen *Holacanthus ciliaris*), which are not LAMP focal species, are classified as spongivores (SPV, >70% porifera, subcategory of INV; see Fig. 7). Parrotfish size classes are based on data from Vallès & Oxenford (2014). Queen conch market clean meat mass (W_{MC}, in g) is calculated from shell length (SL, in mm) and maturity ($m = 0$ for immature or 1 for mature) using the equation $\ln(W_{MC}) = -7.838 + 2.368 \ln(b) + 0.217m$ (Babcock et al. 2015b). Spiny lobster carapace length (CL, in mm) to mass (W, in g) is calculated as $W = aCL^b$ (Babcock et al. 2015a)

Common name	Family	Scientific name	Len-Wt parameters		Diet (%)					Trophic group
			a	b	Fish	Arthrop.	Mollusk	Echinod.	Other	
Black grouper	Serranidae	*Mycteroperca bonaci*	0.010	3.06	100	0	0	0	0	PSV
Nassau grouper	Serranidae	*Epinephelus striatus*	0.013	3.05	54	43	0	0	3	PSV-INV
Mutton snapper	Lutjanidae	*Lutjanus analis*	0.013	2.98	30	52	16	0	2	PSV-INV
Hogfish	Labridae	*Lachnolaimus maximus*	0.022	2.98	0	12	83	5	0	INV
Queen triggerfish	Balistidae	*Balistes vetula*	0.026	2.96	0	8	7	77	8	INV
					Algae	Seagrass	Cnidaria	Porifera	Other	
Stoplight	Scaridae	*Sparisoma viride*	0.013	3.05	96	3	0	1	0	LHRB
Redtail	Scaridae	*Sparisoma chrysopterum*	0.011	3.10	83	17	0	0	0	LHRB
Yellowtail/redfin	Scaridae	*Sparisoma rubripinne*	0.009	3.04	92	7	0	1	0	LHRB
Princess	Scaridae	*Scarus taeniopterus*	0.018	3.00	100	0	0	0	0	SHRB
Striped	Scaridae	*Scarus iseri*	0.011	3.01	100	0	0	0	0	SHRB
Redband	Scaridae	*Sparisoma aurofrenatum*	0.010	3.13	97	2	1	0	0	SHRB
Queen conch	Strombidae	*Lobatus gigas*	(see legend)							HRB
Spiny lobster	Palinuridae	*Panulirus argus*	0.0046	2.63						INV

catch, were recorded for each individual fisher during each encounter. Fish were measured for fork length (cm) and total un-gutted mass (g), conchs were assessed for individual market clean meat mass (g) (meats removed from the shell and trimmed of viscera), and lobsters were assessed for carapace length (mm) and total mass (g) or tail mass (g) if already removed from the cephalothorax (Babcock et al. 2013, 2015a,b).

As the LAMP protocol did not include habitat assessments during the time series examined (2007–2013), a set of patch reefs were surveyed in June of 2015 using the Mesoamerican Barrier Reef System (MBRS) Synoptic Monitoring protocol (Almada-Villela et al. 2003). Four GUZ and 7 RZ patch reefs were surveyed including many of the original patch reefs surveyed for LAMP. Five transects (30 m by 2 m), spaced at least 10 m apart, were placed from SW to NE across the entire patch reef into the predominant current within the lagoon. Benthic substrate category types were assessed at points every 0.25 m along the 30 m tape (N = 120 points transect^{-1}) for a total of 600 points in each patch reef. Substrate types were compiled to include hard corals (identified to species), sponges, gorgonians, fleshy algae, other algae (including calcareous, crustose), and non-living (sand, rubble, bare rock) components.

Data handling and statistical analyses

Benthic habitat

For the purposes of analysis, non-living substrate types were left out. Proportions of the living types (hard coral, gorgonian, sponge, fleshy algae, other algae) in each transect were calculated. After attempts to normalize the proportions data using several transformations, including the arcsine-square root transformation, failed, a permutational analysis of variance (PERMANOVA; Anderson 2001) was performed using a Bray-Curtis similarity matrix on the proportions of the living substrate types. The model was run using the adonis function in the R library vegan (Oksanen et al. 2016, R Development Core Team 2016).

LAMP density and size

All fish species were grouped into 5 trophic classifications (Table 1) based on their known trophic ecology (Randall 1967). The 6 parrotfish species were secondarily grouped as large and small herbivores (Vallès & Oxenford 2014). The species groups we evaluated were: (1a) mature queen conch (lip

thickness ≥5 mm) (Appeldoorn 1988), (1b) immature conch (lip thickness <5 mm); (2a) legal-sized Caribbean spiny lobster (carapace length ≥76 mm) (Babcock et al. 2015a); (2b) sublegal lobster (carapace length <76 mm); (3) black grouper; (4) Nassau grouper; (5) mutton snapper; (6) hogfish; (7) large herbivores (stoplight, yellowtail, and redtail parrotfish); and (8) small herbivores (princess, redband, and striped parrotfish). Analysis of parrotfish assemblages have been found to be useful alternative indicators of fishing effects over the conditions of most Caribbean shallow reefs (Vallès & Oxenford 2014). Queen triggerfish were not analyzed because only 5 individuals were observed. To evaluate whether there was a trend in time for each species group in each zone, the expected count $\mu_{i,j}$ of individual fish observed at each patch reef j in each sampling period i was modeled as:

$$\ln(\mu_{i,j}) = \beta_0 + \beta_1 Y_i + \beta_2 Z_j + \beta_3 Z_j Y_i + S_j + \text{offset}(\ln(A_j)) \quad (1)$$

where Y_i is the numerical year (1 to 7), Z_j is the zone (1 for GUZ, 0 for RZ), and the β values are regression coefficients, such that β_0 is the intercept, β_1 is the slope with year in the RZ, β_2 is the change in intercept for the GUZ, and β_3 is the change in slope for the GUZ. Because the survey involved repeated measures at the same patch reefs, patch reef was treated as a random effect in the model; the patch reef effects S_j were assumed to be normally distributed with a mean of 0. The natural log of the area of each patch reef A_j was included as an offset term, so that the predicted count in each patch reef would equal the predicted density times the area. For each species group, we also considered the null model and models without the interaction, with only the year effect, and with only the zone effect.

For all species groups, generalized linear mixed models (GLMMs) of the form shown in Eq. (1) were fitted using a negative binomial error structure. The negative binomial distribution is appropriate for modeling counts, similar to the Poisson distribution, except that, unlike the Poisson, the negative binomial may have a variance that is larger than the mean. The relationship of the variance to the mean may be modeled either as a linear ($\sigma^2 = k\mu$, called binomial 1), or quadratic ($\sigma^2 = \mu[1 + \mu/k]$, called binomial 2), where the dispersion parameter (k) is an estimated parameter in the model (Skaug et al. 2015). For each species group, Akaike's information criterion (AIC) was used to find the best model. The expected trend in density was calculated using only the fixed components of the AIC best model. For the full model, Eq. (1), the expected mean is:

$$\mu_{i,j} = \exp(\beta_0 + \beta_1 Y_i + \beta_2 Z_j + \beta_3 Z_j Y_i) \quad (2)$$

This corresponds to the expected trend in counts at a typical patch reef in each zone, with a unit area (offset = 0). To calculate the 50% confidence interval of the mean, 100 000 values of the regression coefficients were drawn from a multivariate normal distribution with means and variance-covariance matrix corresponding to those estimated by the GLMM models; Eq. (2) (or the equivalent for the AIC best model) was used to calculate the mean for each draw, and the 50% confidence intervals were calculated as the 0.25 and 0.75 quantiles (Peel et al. 2013).

In addition, similar models were fitted using total weight rather than count of each species group to calculate biomass. Weights were calculated using length–weight relationships from Fishbase and Babcock et al. (2015a,b) (Table 1). For fish or shellfish for which lengths were not recorded (0% of conch, 3% of lobsters, and 0.4% of finfish), weights of unmeasured animals were set equal to the median for that species. For lobsters, because lengths were used to assign individuals to the legal and sublegal categories, sample units (patch reefs on a particular day) were excluded from the analysis if there were any lobsters recorded without a carapace length. This reduced the sample size by 7% for lobsters.

Biomass was modeled as above, except that the error structure followed the Tweedie distribution rather than the negative binomial. The Tweedie distribution (Shono 2008, Zhang 2013) is a generalized distribution that includes the Poisson and gamma as special cases. The variance of the Tweedie distribution is a function of its mean ($\sigma^2 = \varphi\mu p$) where the dispersion parameter φ and the index parameter p can be estimated. If φ and p both equal 1, then the Tweedie reduces to the Poisson distribution; if p is 2, it is the gamma. Values between 1 and 2 imply a gamma distribution with an extra mass at 0. Thus, this model is useful for fitting continuous data with large numbers of zeroes.

Finally, a linear model was used to determine whether the lengths of fish in each species group were different between zones, or had a trend across years. Because the variance in lengths between patch reefs was small compared to the residual variance, patch reef was not included as a random effect. The model was:

$$L_{i,j} = \beta_0 + \beta_1 Y_i + \beta_2 Z_j + \beta_3 Z_j Y_i \quad (3)$$

where L_{ij} is the shell lip thickness for mature conch, shell length for immature conch, carapace length for lobster, or fork length for all finfish, Y_i is year (1 to 7), and Z_j is zone.

All analyses were conducted in R (R Development Core Team 2016), using the package glmmADMB (Skaug et al. 2015) for the negative binomial models, and cplm (Zhang 2013) for the Tweedie models.

CPUE

A similar analysis was conducted for the CPUE dataset for lobster, conch, and finfish. For the finfish, only data from speargun fishers (i.e. sailboat based) was used, because the intention was to focus on the predominantly shallow-water reef fish habitat (i.e. patch reefs) within the atoll's lagoon. Hook and line fishers who may have been fishing in deep waters outside the lagoon were excluded. Individual fishers were used as the sample unit. Fishers tend to arrive at Glover's Reef as crews in sailboats, but disperse in individual canoes to fish on a daily basis. Thus, fishers from the same sailboat on the same day may not be independent. Also, observations from the same sailboat may be more similar due to the crew's fishing methods or preferred fishing locations. To account for the possibility of a sailboat effect on catch rates, sailboat was included as a random effect (Maunder & Punt 2004, Ortiz & Arocha 2004, Babcock et al. 2015a). However, the sailboat effect was not estimated separately for each fishing day. Rather sailboats were assumed to have similar characteristics on each day they fished. The sailboat effects were assumed to be drawn from a normal distribution with a mean of 0 and an estimated variance.

The species considered in the analysis were queen conch, spiny lobster, hogfish, mutton snapper, Nassau grouper, black grouper, and angelfishes (gray *Pomacanthus arcuatus*; French *P. paru*; queen *Holacanthus ciliaris*). Parrotfishes were only captured in the first 2 yr of the dataset (2007–2008) due to the ban beginning in 2009, and queen triggerfish were not commonly caught. Lobsters and conchs were not classified by size or maturity, because whole animals are not often encountered (conch removed from shells, lobster separated from the cephalothorax), and maturity is then difficult to assess.

CPUE was calculated as mass caught per fisher-hour for each target species or group. For conch, market clean meat mass was recorded for most observations. Unprocessed or fillet mass for conch was converted to market clean meat mass using the equations from Babcock et al. (2015b). For lobster, tail mass was converted to whole mass using the equations from (Babcock et al. 2015a). Whole mass was available for all

finfish. The mean biomass of fish caught per fisher-day was modeled as:

$$\ln(\mu_{i,j}) = \beta_0 + \beta_1 Y_i + B_j + \text{offset}(\ln(h_j)) \qquad (4)$$

where Y_i is decimal year (= day since 1 January 2007 divided by 365), and B_j is the random effect of sailboat j. The offset was the log of the total number of hours fishing h_j for each fisher. For the conch data, in some cases, more than 1 fisher reported catch together, in which case their reported hours were multiplied by the number of fishers.

The Tweedie distribution was used, and the AIC value determined whether the random effect of sailboat was necessary in the model. The average CPUE in catch per fisher-hour was calculated as:

$$\mu_{i,j} = \exp(\beta_0 + \beta_1 Y_i) \qquad (5)$$

and confidence intervals were calculated as described above.

RESULTS

Benthic habitat

Living benthic cover on RZ and GUZ patch reefs, collected in 2015, was dominated by fleshy macroalgae (RZ: 58%, range 23–85%, GUZ: 64%, range 26–96%) including high proportions of *Turbinaria* spp. and *Lobophora* spp. followed by sponges and soft and hard corals. Hard coral cover was concentrated on the leeward edge (SW) of the patch reefs and dominated by massive starlet *Siderastrea siderea*, mustard hill *Porites astreoides*, boulder star *Orbicella annularis*, and finger coral *P. porites*, with similar levels of both fire coral (hydrozoans) and soft coral (gorgonians). The PERMANOVA results indicated that the proportion of benthic habitat types did not differ significantly between zones, although the patch reefs were different from each other within zones (Table 2).

LAMP density and size

The LAMP dataset included 125 sample units, across 23 patch reefs in 7 yr. A total of 14 287 individuals of the focal species were counted and measured: 3437 invertebrates, 846 predatory fish, and 10 004 parrotfish. The negative binomial model for density and the Tweedie model for biomass fit adequately. See the Supplement at www.int-res.com/articles/suppl/m580p037_supp.pdf for histograms of the den-

Table 2. PERMANOVA showing the significance of management zone and site within zone on the proportions of live benthic habitat types, using Bray-Curtis distance

	df	Sums of squares	Mean squares	F	R²	p(>F)
Zone	1	−0.023	−0.023	−0.367	−0.004	0.999
Patch reef in zone	9	2.941	0.327	5.132	0.514	0.000
Residuals	44	2.802	0.064		0.490	
Total	54	5.720			1.000	

sity data (Fig. S1), residuals of the negative binomial model for density (Fig. S2) and Tweedie model for biomass (Fig. S3), AIC values used to choose the best density model (Table S1), model parameters (Table S2) for the negative binomial density model, and AIC values (Table S3) and model parameters (Table S4) for the Tweedie biomass model. The linear models of the size over time also fit adequately (Table S5).

For mature queen conch, the AIC best model found increases over time in both density and biomass in the RZ where conchs are more abundant, but no significant trend in the GUZ (Fig. 3a,b, Table 3a,b). However, the average lip thickness of mature conch (lip thickness ≥5 mm) decreased over time in both

zones (Fig. 3c, Table 3c). Immature conch increased in density and biomass in both zones, and decreased in average shell length (Fig. 3d–f, Table 3a–c).

Legal-sized lobsters are currently more abundant, both in terms of density and biomass, in the RZ. They have increased in biomass over time in both zones, but density has only increased in the RZ (Fig. 4a,b, Table 3a). There was a linear decrease in size over time (Fig. 4c, Table 3c). Sub-legal lobsters were more abundant in the GUZ than the RZ at the beginning of the time series. However, they increased in density and biomass in the RZ while not changing in the GUZ (Fig. 4d,e, Table 3a,b). Individual size decreased in both zones (Fig. 4f, Table 3c).

For large herbivores, there was an increasing trend in density in the RZ and very wide confidence interval with no clear trend in the GUZ (Fig. 5a, Table 3a). The biomass and size of large herbivores increased over time in both zones, and were larger in the RZ (Fig. 5b,c, Table 3b,c). Small herbivores decreased consistently in density and biomass in both zones
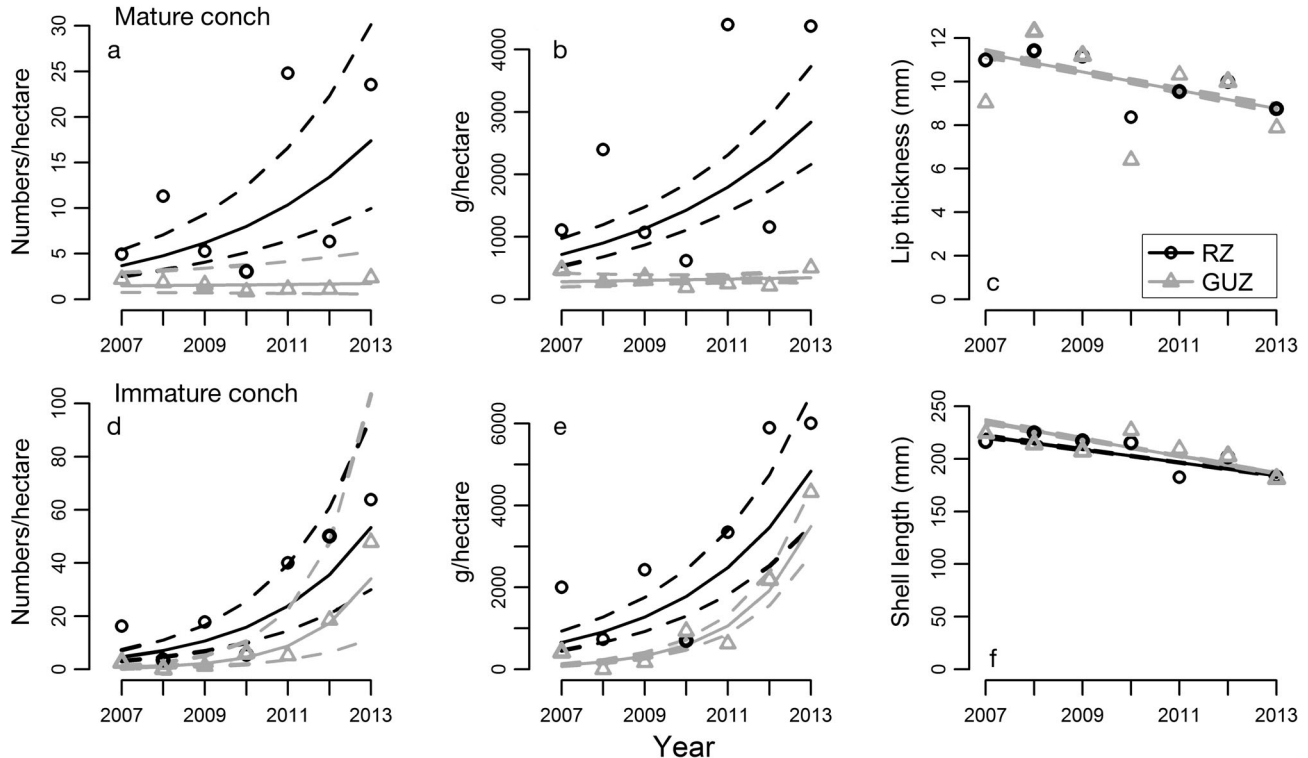

Fig. 3. Trends over time in (a,d) density, (b,e) biomass, and (c,f) size for mature (a–c) and immature (d–f) queen conch *Lobatus gigas*, from the AIC best models (solid lines are medians, dashed lines are 25 and 75% quantiles). Size is lip thickness for mature conchs, and shell length for immature conchs. Open symbols are unprocessed means in each year and zone. RZ: replenishment zone, GUZ: general use zone

Table 3. Fixed-effect coefficients (95% confidence interval) from the AIC best models. RZ: replenishment zone, GUZ: general use zone

(a) Density

Species	β_0 (intercept)	β_1 (year)	β_2 (zone)	β_3 (year × zone)	$\beta_1+\beta_3$ (year in GUZ)
Conch–mature	1.05 (–0.07 to 2.16)	0.26 (0.08 to 0.43)	–0.67 (–2.24 to 0.90)	–0.23 (–0.50 to 0.03)	0.02 (–0.34 to 0.39)
Conch–immature	1.15 (–0.09 to 2.4)	0.40 (0.22 to 0.58)	–2.39 (–4.10 to –0.69)	0.28 (0.02 to 0.54)	0.68 (0.33 to 1.04)
Lobster–legal	1.54 (0.56 to 2.53)	0.17 (0.05 to 0.30)	0.24 (–1.06 to 1.53)	–0.18 (–0.36 to 0.01)	0 (–0.25 to 0.25)
Lobster–sublegal	–0.30 (–1.6 to 1.01)	0.23 (0.04 to 0.41)	2.10 (0.52 to 3.67)	–0.22 (–0.46 to 0.01)	0 (–0.28 to 0.29)
Herbivore–large	2.79 (2.11 to 3.46)	0.11 (0.02 to 0.21)	0.64 (–0.21 to 1.5)	–0.15 (–0.27 to –0.02)	–0.03 (–0.2 to 0.14)
Herbivore–small	6.90 (6.27 to 7.54)	–0.52 (–0.64 to –0.40)			–0.52 (–0.64 to –0.4)
Hogfish	0.26 (–1.29 to 1.81)	0.20 (0.07 to 0.33)	–2.14 (–3.92 to –0.35)		0.2 (0.07 to 0.33)
Mutton snapper	1.67 (0.57 to 2.77)	–0.19 (–0.40 to 0.01)			–0.19 (–0.4 to 0.01)
Nassau grouper	0.93 (0.55 to 1.31)				
Black grouper	0.68 (–0.41 to 1.78)	–0.14 (–0.39 to 0.10)	–0.81 (–2.51 to 0.89)	0.04 (–0.31 to 0.40)	–0.1 (–0.6 to –0.4)

(b) Biomass

Species	β_0 (intercept)	β_1 (year in RZ)	β_2 (zone)	β_3 (year × zone)	$\beta_1+\beta_3$ (year in GUZ)
Conch–mature	6.34 (5.39 to 7.30)	0.23 (0.10 to 0.36)	–0.73 (–2.34 to 0.88)	–0.20 (–0.47 to 0.07)	0.03 (–0.2 to 0.27)
Conch–immature	6.15 (5.03 to 7.26)	0.33 (0.20 to 0.47)	–2.16 (–3.75 to –0.58)	0.26 (0.05 to 0.48)	0.6 (0.43 to 0.76)
Lobster–legal	8.97 (7.99 to 9.96)	0.11 (0.01 to 0.21)	–1.05 (–2.11 to 0.02)		0.11 (0.01 to 0.21)
Lobster–sublegal	4.66 (3.22 to 6.09)	0.29 (0.05 to 0.52)	2.49 (0.77 to 4.21)	–0.31 (–0.6 to –0.03)	–0.02 (–0.19 to 0.14)
Herbivore–large	8.25 (7.46 to 9.03)	0.11 (0.02 to 0.21)	–0.88 (–1.68 to –0.08)		0.11 (0.02 to 0.21)
Herbivore–small	9.94 (9.3 to 10.58)	–0.47 (–0.59 to –0.36)			–0.47 (–0.59 to –0.36)
Hogfish	6.54 (4.72 to 8.35)	0.19 (0.01 to 0.37)	–0.85 (–3.31 to 1.60)	–0.23 (–0.55 to 0.09)	–0.04 (–0.31 to 0.23)
Mutton snapper	6.84 (5.68 to 8.01)	–0.20 (–0.41 to 0.01)	0.54 (–1.0 to 2.08)		–0.2 (–0.41 to –0.01)
Nassau grouper	6.4 (5.31 to 7.49)	0.23 (0.01 to 0.45)	–1.50 (–2.76 to –0.23)	–0.37 (–0.67 to –0.06)	–0.13 (–0.35 to 0.08)
Black grouper	6.1 (5.11 to 7.09)				

(c) Size

Species	β_0 (intercept)	β_1 (year in RZ)	β_2 (zone)	β_3 (year × zone)	$\beta_1+\beta_3$ (year in GUZ)
Conch–mature	11.7 (11.03 to 12.38)	–0.42 (–0.58 to –0.26)	15.4 (6.65 to 24.15)		–0.42 (–0.58 to –0.26)
Conch–immature	227.0 (223.48 to 232.28)	–6.28 (–7.17 to –5.40)	–10.1 (–14.67 to –5.53)	–1.86 (–3.41 to –0.31)	–8.14 (–9.42 to –6.87)
Lobster–legal	122.8 (117.78 to 127.85)	–2.07 (–3.16 to –0.97)			–2.07 (–3.16 to –0.97)
Lobster–sublegal	59.7 (55.6 to 63.82)	–1.28 (–2.14 to –0.42)			–1.28 (–2.14 to –0.42)
Herbivore–large	17.9 (17.19 to 18.64)	0.67 (0.5 to 0.83)	–3.32 (–3.95 to –2.69)		0.67 (0.5 to 0.83)
Herbivore–small	9.8 (9.3 to 10.39)	0.66 (0.48 to 0.83)	–0.13 (–0.85 to 0.6)	–0.58 (–0.79 to –0.36)	0.08 (–0.05 to 0.21)
Hogfish	24.0 (20.78 to 27.24)	0.50 (–0.29 to 1.28)	9.01 (3.61 to 14.4)	–1.2 (–2.54 to 0.14)	–0.7 (–1.79 to 0.39)
Mutton snapper	33.0 (28.05 to 38.04)	–2.43 (–3.76 to –1.1)	–9.93 (–16.99 to –2.86)	2.24 (0.41 to 4.07)	–0.19 (–1.45 to 1.07)
Nassau grouper	22.1 (18.77 to 25.51)	0.80 (0.0 to 1.61)	2.5 (–2.05 to 7.06)	–1.28 (–2.36 to –0.2)	–0.48 (–1.2 to 0.24)
Black grouper	22.9 (16.58 to 29.29)	1.45 (–0.49 to 3.38)	10.55 (0.97 to 20.13)	–2.77 (–5.38 to –0.17)	–1.33 (–3.07 to 0.42)

(d) CPUE

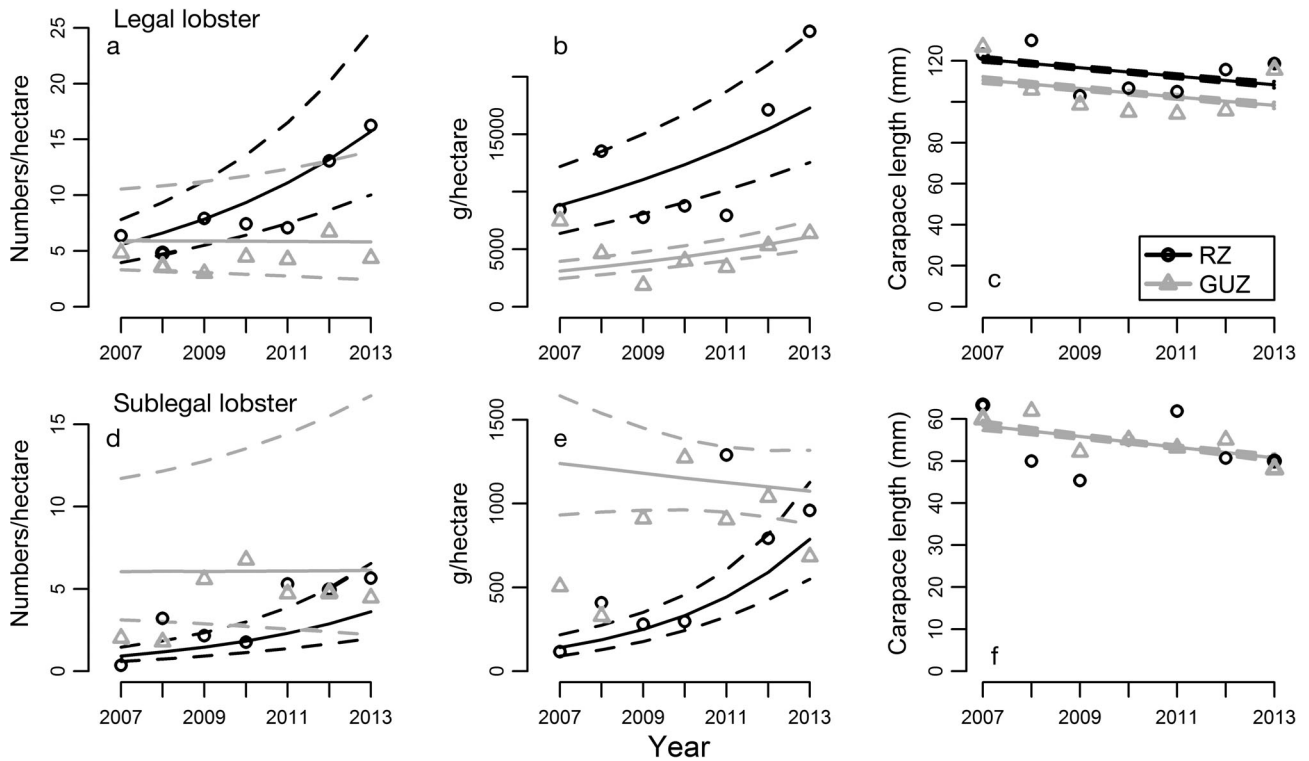| Species	β_0 (intercept)	β_1 (day)
Conch	6.59 (6.3 to 6.87)	0.03 (–0.01 to 0.06)
Lobster	6.92 (6.77 to 7.08)	0.05 (0.01 to 0.08)
Hogfish	6.15 (5.9 to 6.41)	
Mutton snapper	4.67 (4.42 to 4.92)	
Nassau grouper	2.13 (–0.02 to 4.29)	–0.57 (–0.93 to –0.22)
Black grouper	5.1 (4.6 to 5.61)	
Angelfish	1.57 (–0.11 to 3.24)	0.3 (0.07 to 0.52)

Fig. 4. Trends over time in (a,d) density, (b,e) biomass, and (c,f) size for legal sized (a–c) and sub-legal (d–f) spiny lobsters *Pan-ulirus argus* from the AIC best models (solid lines are medians, dashed lines are 25 and 75% quantiles). Open symbols are unprocessed means in each year and zone. RZ: replenishment zone, GUZ: general use zone
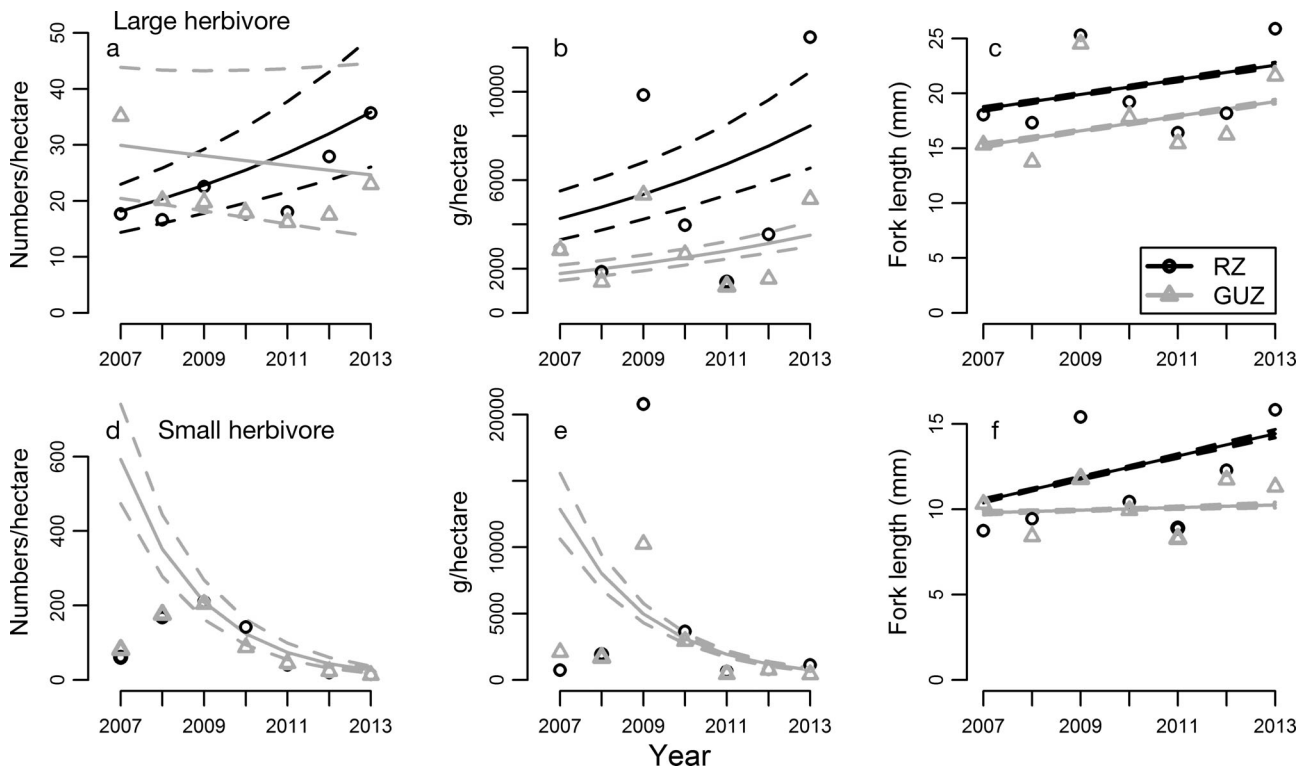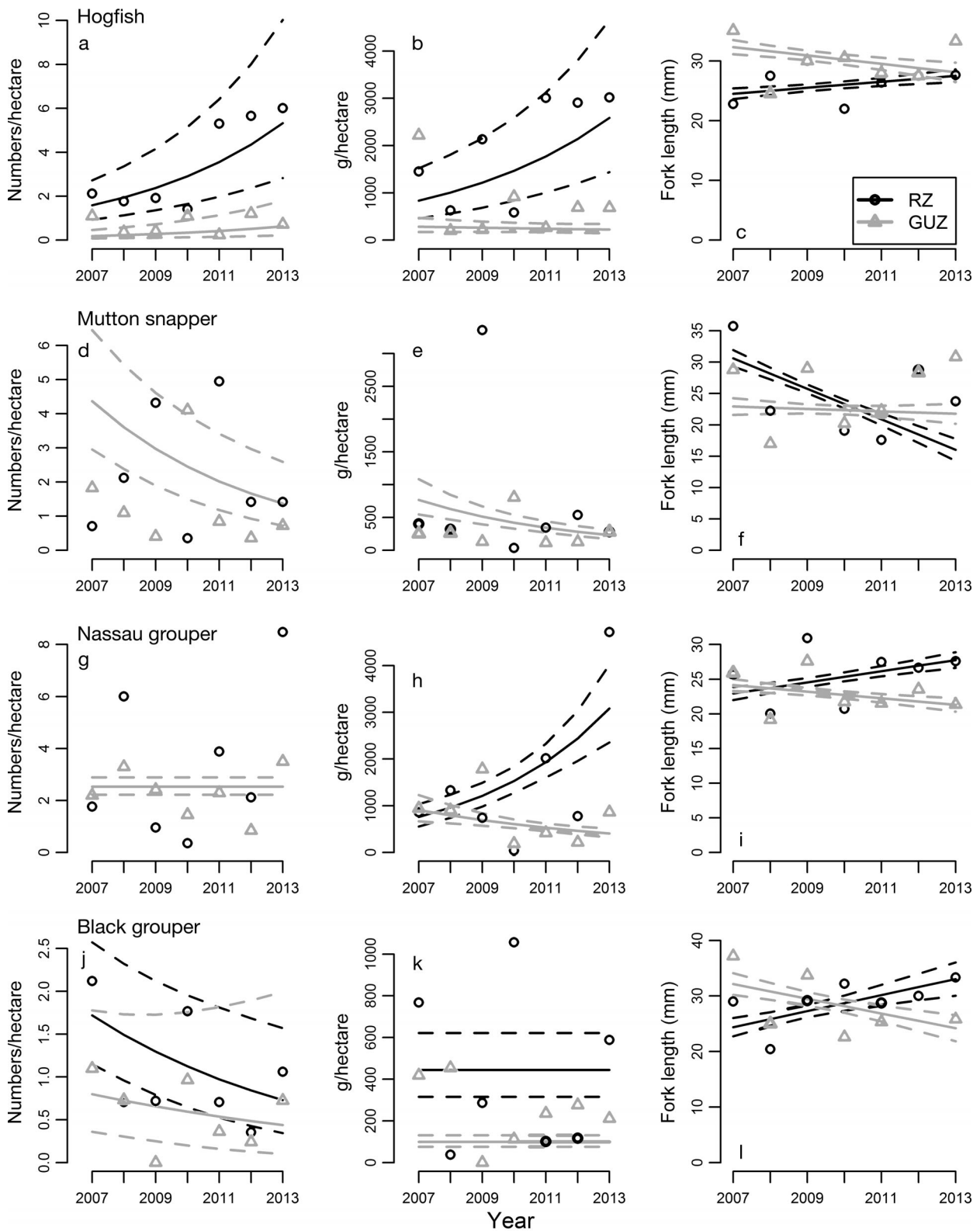

Fig. 5. Trends over time in (a,d) density, (b,e) biomass, and (c,f) size for large herbivores (a–c) and small herbivores (d–f) from the AIC best models (solid lines are medians, dashed lines are 25 and 75% quantiles). Open symbols are unprocessed means in each year and zone. RZ: replenishment zone, GUZ: general use zone

Fig. 6. Trends over time in (a,d,g,j) density, (b,e,h,k) biomass, and (c,f,i,l) size for hogfish (a–c), mutton snapper (d–f), Nassau grouper (g–i), and black grouper (j–l) from the AIC best models (solid lines are medians, dashed lines are 25 and 75% quantiles; see Table 1 for scientific names of species). Open symbols are unprocessed means in each year and zone. RZ: replenishment zone, GUZ: general use zone

(Fig. 5d,e, Table 3a,b). However, they increased in size in the RZ while remaining relatively constant in the GUZ (Fig. 5f, Table 3c).

The 4 predator species with sufficient data had very different trends. Hogfish increased in density and biomass in the RZ (Fig. 6a–c Table 3a,b) The year effect coefficient for the size included 0 in its confidence interval, implying that it was not significant, but the mean value was positive (Table 3c). They increased in density, but had no significant change in size and biomass in the GUZ (Table 3). Mutton snapper decreased in both density and biomass in both zones, and decreased in size in the RZ according to the AIC best model (Fig. 6d–f); however, only the size model had coefficients that did not include 0 (the boundary of the CI was 0.01 for both density and biomass; Table 3a–c). Nassau grouper showed no trend and no difference in density between zones (Fig. 6g, Table 2a). However, they increased in both biomass and size in the RZ, and appeared to decrease in size and biomass in the GUZ, but with confidence intervals that included zero (Fig. 6h,i, Table 3b,c). Black grouper appeared to increase in size in the RZ (Fig. 6l, Table 3c), which may explain why their biomass remained constant (Fig. 6k, Table 3b) despite the decrease in density in both zones (Fig. 6j, Table 3a). However, due to the high variability and low sample sizes for black grouper, the confidence intervals of all the trends include 0. No trend patterns were available for queen triggerfish given limited data.

CPUE

A total of 51 619 individual catch items were measured between 2007 and 2013: queen conch (N = 42 029, 81.4 %); Caribbean spiny lobster (N = 7522, 14.6 %), and fish (N = 2068, 4.0 %). The top 21 species (> 94 % of total abundance) of fish caught by sailboat fishers at Glover's Atoll included all 5 focal predators which span a wide trophic range (Fig. 7a). Catches of spongivores (e.g. angelfish) have increased

since parrotfish stopped being caught in 2009, while catches of piscivores and invertivores are highly variable between years (Fig. 7b). The CPUE data included 1012 fisher-days for conch, 871 fisher-days for lobster, and 306 fisher-days for fish. The samples were fairly evenly distributed across years (Table S6). Lobster had the highest mean CPUE (1229 g fisher-hour^{-1}), followed by conch (1105 g fisher-hour^{-1}), while the finfish species together had a mean CPUE of 1081 g fisher-hour^{-1} (hogfish 487, mutton snapper 104, Nassau grouper 58, black grouper 184,
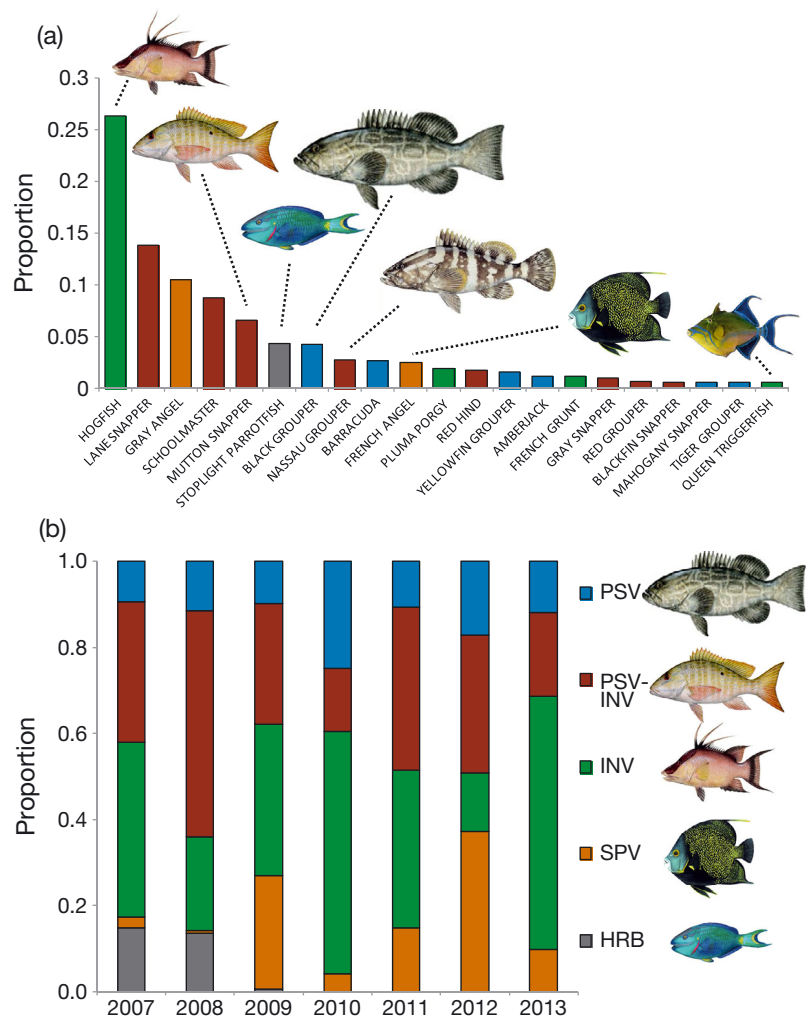

Fig. 7. Pattern of fish landings (sailboat only), representing 54 species (2068 individuals), during the study period (2007–2013). (a) Top 21 species (n = 1949, >94 % of total) highlighting focal species, as well as angelfish. Species ranked by decreasing proportions landed: hogfish *Lachnolaimus maximus* (0.263); mutton snapper *Lutjanus analis* (0.065); black grouper *Mycteroperca bonaci* (0.043); stoplight parrotfish *Sparisoma viride* (0.043); Nassau grouper *Epinephelus striatus* (0.028); French angelfish *Pomacanthus paru* (0.025); queen triggerfish *Balistes vetula* (0.005). (b) All species classified by trophic group (Randall 1967) (see Table 1) for each year. Trophic classifications: piscivore (PSV, >75 % fish); piscivore-invertivore (PSV-INV, mixed); invertivore (INV); spongivore (SPV, subcategory of INV); and herbivore (HRB)

and angelfish 248 g fisher-hour^{-1}).

The Tweedie models for CPUE fit adequately (Tables S7 & S8, Figs. S4 & S5 in the Supplement). The AIC best models for CPUE included a positive trend over time for conch (Fig. 8a), lobster (Fig. 8b), and angelfish (Fig. 8g), with confidence intervals that did not include 0 for lobster and angelfish (Table 2d), a negative trend for Nassau grouper (Fig. 8e), and no trend for hogfish, mutton snapper, or black grouper (Fig. 8c,d,f, Table 3d, also see Table S8). The sailboat effect was included in the best model for all species. The increasing trends in conch (Fig. 8a) and lobster (Fig. 8b) CPUE and flat or decreasing CPUE trends in most fish, Nassau grouper being an exception, are consistent with a density-dependent spillover effect from the RZ.

DISCUSSION

With the analysis of a small set of focal species representing a wide range of trophic groups, we were able to provide evidence of increasing density, biomass, or size for a number of SSF targets (invertebrates and fish) within a spatial closure and, perhaps more importantly, stable or increasing trends in catch beyond the boundaries of the refuge between 2007 and 2013. These results are based on annual fisheries-independent snorkel surveys of well-defined habitats (i.e. patch reefs) routinely accessed by fishers as well as monthly catch data collections from those same fishers. These results show that core objectives for the management of GRMR, including ensuring sustainability and enhancing economic benefits within a more general ecosystem-based approach to fisheries, were achieved (Rowley 1994, Walker & Walker 2007, Dahlgren & Tewfik 2015).

Our analysis of patch reef benthic habitats and previous results from Glover's patch reefs (McClanahan et al. 2011) highlight dominance by macroalgae and no differences in coral or fleshy macroalgae cover between management zones. The structural components of both *Acropora* spp. and *Orbicella* spp. have been in decline for some time across the region, with fleshy macroalgae colonizing dead coral surfaces and
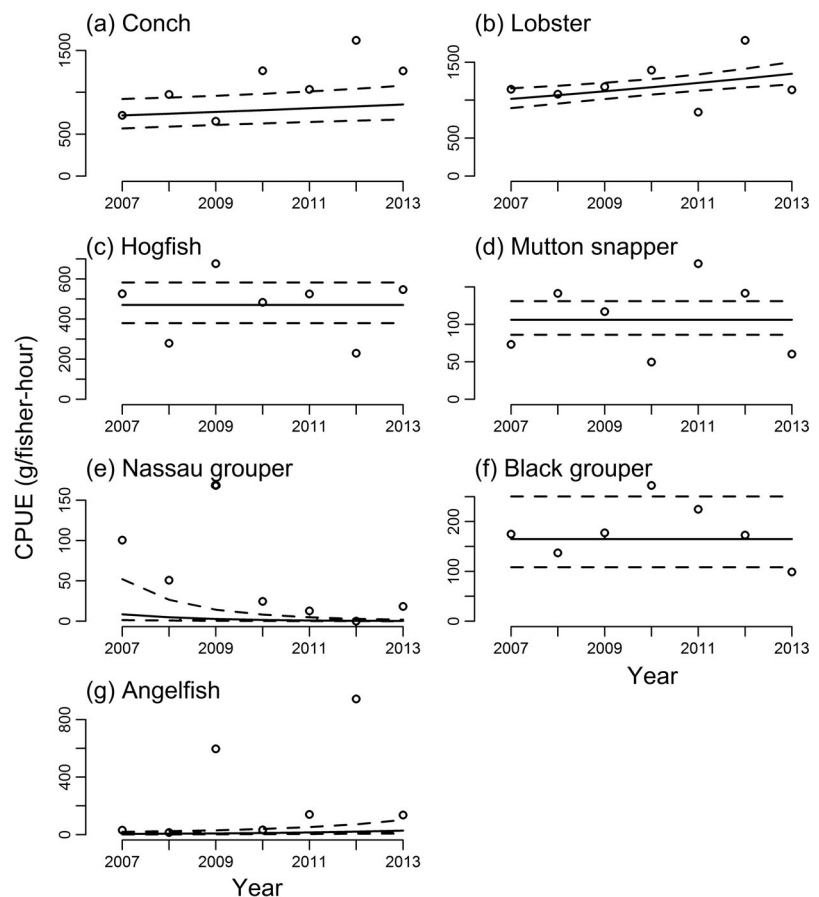

Fig. 8. Trends in catch per unit effort (CPUE; g fisher-hour^{-1}) with 50% confidence intervals, for (a) conch, (b) lobster, (c) hogfish, (d) mutton snapper, (e) Nassau grouper, (f) black grouper, and (g) angelfish from the AIC best models (see Table 1 and Fig. 7 for scientific names of species). Open symbols are unprocessed means in each year

herbivores unable to reverse the decline (Edmunds & Elahi 2007, Schutte et al. 2010). This may be associated with very low densities of the urchin *Diadema antillarum* and the inability of the sympatric and abundant urchin *Echinometra viridis* to reduce exposed fleshy macroalgae (McClanahan 1999, McClanahan et al. 2011). In addition, the potentially overwhelming impact of nutrient enrichment coming from poorly managed watersheds and coastal zones across the Mesoamerican region may substantively explain the high cover of fleshy macroalgae that has persisted for several decades rather than the lack of herbivory (Suchley et al. 2016, Arias-González et al. 2017). The differences in focal species density, biomass, and sizes are not due to habitat differences between the RZ and GUZ in our study (Miller & Russ 2014). It may be inferred that the benefits including stable or increasing CPUE conveyed by the RZ may be supported by broader fisheries conservation strategies

(size limits, closed seasons) directed specifically at queen conch, Caribbean spiny lobster, and Nassau grouper and a total ban on harvest of 'herbivorous' fish (acanthurids, scarids). These regulations are widely known to the fishing community and reinforced during the annual renewal period for fishing licenses. In addition, fisheries officers patrol and encounter SSF vessels regularly within the GRMR to maintain compliance with regulations (Fig. 2b), which has improved over the study period (Gibson et al. 2013). Finally, the Glover's Reef Advisory Committee (GRAC), formed in 2000, includes members representing (1) fisher associations from areas that fish at GRMR and (2) the principal fishing cooperatives, of which most fishers in Belize are members and to which they sell their product (Walker & Walker 2007). The GRAC is also the principal mechanism through which direct consultation with the fisher community on management strategies and effectiveness at Glover's Reef Atoll is conducted (Walker & Walker 2007, Gibson et al. 2011, 2013, Di Franco et al. 2016).

Despite the relatively small size of the RZ (22.7% of the total reserve area), we have observed positive results for a number of species (Cote et al. 2001, Edgar et al. 2014). Some of the most dramatic changes involved both small and previously harvested large parrotfish which have responded to conservation strategies that include spatial protection and a complete ban (2009) on the harvest of herbivorous fish in Belize. Trends for both queen conch and spiny lobster are very relevant given their ecological importance and status as the 2 most economically important species used by small-scale fishers at Glover's Atoll and throughout Belize (Acosta 2006, Babcock et al. 2015b). These invertebrate species are rarely included in broader, multi-species reef resource assessments within the region. The relatively small size of the RZ (<80 km^2) may be considered insufficient to cause significant changes for some larger and higher trophic level predators given their longer life history, use of habitats beyond our study (e.g. fore-reef), and propensity for long-range movements across management boundaries to reproductive aggregation sites (Halpern 2003, Sadovy & Domeier 2005, Starr et al. 2007, Edgar et al. 2014, Burns & Tewfik 2016). However, a number of positive trends have been observed for black and Nassau groupers which are also prime targets for SSF in Belize (Babcock et al. 2013). The remainder of this discussion will provide additional details on the patterns we have observed and will outline proposed improvements to our monitoring program.

Queen conch densities have increased in the RZ over the time series examined. These increases are consistent with recent analysis of conch densities in national surveys (Gongora 2012) as well as at the GRMR in particular (Acosta 2006, Babcock et al. 2015b). Variability in both density and biomass and declines in the mean lip thickness (i.e. age) for mature conch and may be attributed to the regular movement of adults out of the RZ and to deeper areas (lagoon floor, fore-reef), a known life history pattern (Tewfik & Bene 2003) beyond the scope of this study, as well as the harvesting of these mature individuals in the GUZ (Tewfik 2017). This may partially explain the slightly increasing CPUE observed in our study. At the same time, the decreasing shell length of immature conch could be related to increases of new recruits to the population, perhaps driven by the availability of ecological space in the heavily fished GUZ. The increasing juvenile conch densities may also be partially responsible for the overall increase in conch CPUE, as immature conch >177 mm shell length are permitted to be extracted in Belize. However, the large harvest of juvenile conch that we have observed may jeopardize the sustainability of the fishery both in terms of population dynamics and economics, because harvested juveniles have no opportunity to reproduce, and they yield small meat mass (Stoner et al. 2012, Babcock et al. 2015b). In addition, an adequate density of mature conch (lip ≥5 mm) and level of reproductive activity (copulation, spawning) must be maintained for the long-term integrity of the fishery (Stoner et al. 2012, Tewfik 2017).

There is evidence for increases in density and biomass of legal-sized spiny lobster within the RZ, which is likely responsible for the increase in CPUE observed in our study. This positive trend in CPUE reflects significant recruitment, which may be a result of large adults resident in fore-reef habitats of the atoll which are largely inaccessible to free-diving fishers due to depth and rough sea conditions (Karpov et al. 1998, Tewfik 2014, Babcock et al. 2015a). In addition, the location of the atoll outside the main Belize barrier reef may be conducive to receiving larvae from distant areas (Lipcius et al. 2001, Truelove et al. 2015). The decline in the size of legal-sized lobsters may be driven by selective harvest of the largest individuals in accessible shallow patch reef habitats. Although sub-legal lobster increased in density and biomass within the RZ, their density was stable or perhaps declining in the GUZ, which may indicate that fishing mortality rates in the GUZ are unsustainable. Finally, the minimum harvestable size of lobster presently used in Belize (76 mm carapace length)

allows a significant proportion of the population to be removed before they are able to engage in a single reproductive event; this may threaten the long-term viability of the fishery (Tewfik & Bene 2004).

The importance of herbivory by a number of taxa in the maintenance of coral reef systems has been highlighted (Mumby et al. 2007, Idjadi et al. 2010, Butler & Mojica 2012). Together with an adequate control of bottom-up impacts, most significantly nutrient enrichment (Lapointe 1997, 1999), herbivory may help control macroalgae which may otherwise out-compete hard coral species and thus impact the overall integrity of the coral reef ecosystem (Mumby et al. 2007). Here we examined a suite of common parrotfish which were grouped as large and small herbivores (Vallès & Oxenford 2014). Large parrotfish significantly increased in density in the RZ, with both biomass and size increasing in both zones. Importantly, all scarids (parrotfish) and acanthurids (tang/surgeonfish/doctorfish) were banned from exploitation in 2009, because large species (e.g. stoplight parrotfish *Sparisoma viride*) were being increasingly targeted by fishers in Belize (McClanahan et al. 2011). Catch of herbivores almost entirely ended by 2008, providing ideal conditions for the recovery of large parrotfish that we have observed. In contrast, small parrotfish have declined significantly in density (McClanahan et al. 2011) and biomass, displaying a strong compensatory indirect ecological decrease, likely due to the recovery of the competitively superior larger parrotfish (Micheli et al. 2004, Babcock et al. 2010). Despite the decreases in density and biomass of the smaller species of parrotfish, the remaining individuals of those species have increased in size in the RZ and remained stable in size in the GUZ, most likely due to a release from competition with conspecifics and other small parrotfish species which were formerly at high density. The opposing trends that we have observed for large and small parrotfish over a relatively short time series is likely related to a combination of conservation strategies (RZ and fisheries ban), as well as the shorter life histories and restricted movement of these species, and indicate that RZs can be effective in restoring a more natural community structure (Cote et al. 2001, Micheli et al. 2004, Karnauskas et al. 2011, Mumby et al. 2012). Despite these changes in the 'herbivorous' fish community, no changes in the level of fleshy macroalgae have been detected (Suchley et al. 2016, Arias-González et al. 2017).

Four of the suite of focal predatory fish species observed in our study responded very differently. Hogfish appeared to have increased in abundance,

biomass, and perhaps size in the RZ likely owing to strong site fidelity and limited home ranges (Lindholm et al. 2006). Positive metrics for hogfish within the RZ may also be influenced by increasing densities of newly recruited queen conch which are a major prey item for this molluscivorous species (Randall 1967). Despite limited increases in the density and biomass of hogfish in the GUZ, as well as stable or declining size, the steady CPUE observed is likely supported by significant production within the RZ and associated spillover. In contrast, mutton snapper appeared to decrease for all metrics in both management zones, although these results were uncertain in that the confidence intervals for the trends in density and biomass included 0. This possible effect could be associated with larger home ranges, as well as more distant ontogenetic and reproductive-associated movements for this species, which could make them more vulnerable to fishers (Farmer & Ault 2011, Kojis & Quinn 2011). However, this does not appear to have affected the CPUE for mutton snapper, which is somewhat surprising since mutton snapper are overfished in Belize (Graham et al. 2008, Babcock et al. 2013).

Although Nassau grouper did not appear to increase in density in either management zone, significant increases in both biomass and size were observed in the RZ. This pattern is likely related to a series of conservation strategies (closed season, size regulations, and closed spawning sites) put in place for this species in 2009 (Burns & Tewfik 2016). In addition, an informal agreement between the Fisheries Department and Glover's Reef fishers was reached in 2007 that Nassau grouper would not be caught in return for fishers being allowed to catch conch and lobster in the seasonal closed area associated with the principal Nassau grouper spawning site at NE Point. This may have also affected the pattern of declining CPUE that we have observed. However, the seasonal movements of Nassau grouper to the spawning aggregation site and the high desirability of this species have led to overfishing and poaching (Sala et al. 2001, Burns & Tewfik 2016). Such mortality could quickly reduce spawning biomass, recruitment, and population viability especially given the isolated nature of Glover's Reef Atoll (Sadovy & Domeier 2005, Starr et al. 2007, Babcock et al. 2013, Burns & Tewfik 2016). A similar, but more muted, pattern was observed for black grouper, with stable biomass and perhaps increasing size in the RZ. However, despite the large size of black grouper, they appear to have limited home ranges (Farmer & Ault 2011), which may include a series of nearby patch reefs. Thus, black grouper should be protected

at the core of even a moderately sized RZ, and its CPUE did remain constant. However, black grouper are also highly desirable targets and quite vulnerable to small-scale fishers as they leave individual territories in shallow waters within the lagoon and migrate out of the RZ to fore-reefs and mass spawning sites in the GUZ up to 4 times a year (Sadovy & Domeier 2005, Babcock et al. 2013).

The very low numbers of queen triggerfish *Balistes vetula* being recorded in our independent visual surveys and catch data (<2% of the total) may still be informative. Queen triggerfish prefer echinoids, including *E. viridis*, in their diet (72.8%) with a special affinity for *D. antillarum* (86% of urchins in gut samples; Randall 1967). However, extremely low density of *D. antillarum* and cryptic populations of *E. viridis* observed at Glover's patch reef habitats, which appear unable to control fleshy macroalgae production (McClanahan 1999, McClanahan et al. 2011), likely provide limited prey targets for queen triggerfish and may reflect the low density and catch we have observed. In an analogous Indian Ocean reef system, orange-lined triggerfish *Balistapus undulatus* had a strong positive association with hard coral and calcifier cover while its primary prey, the rock-boring sea urchin *E. mathaei*, had a strong negative association with coral cover and particularly calcifier cover (McClanahan & Muthiga 2016). Therefore, the patterns of individual triggerfish species at Glover's Reef (*B. vetula*) and on the Indian Ocean reefs (e.g. *B. undulatus*) highlight the utility of observations based around important focal species, which may well be associated with broader environmental conditions including benthic cover (McClanahan & Muthiga 2016).

Although angelfishes were not targeted in the LAMP data, previous visual survey work has indicated a significant increase in their abundance between 1997 and 2004 in both management zones followed by a drastic decline in the GUZ between 2008 and 2009 (McClanahan et al. 2011). This has been followed by a noticeable increase in the CPUE of angelfish which may be a response to the shift of fishers away from herbivores (i.e. large parrotfishes) due to the ban begun in 2009. According to an analysis of the sizes of fish caught in the fishery, French angelfish are probably not overfished, but gray angelfish may be (Babcock et al. 2013). The broader response of natural communities and fishers through a series of transitory states must be noted and adapted to with regards to monitoring and management of resources (Micheli et al. 2004, Mumby et al. 2012). More specifically, with the increasing catch of angelfish, primarily spongivores (Randall 1967), comes the

potential for significant changes in broader environmental conditions. Increases in faster-growing palatable sponges due to losses of spongivorous angelfishes may lead to further erosion of live hard coral cover (Loh & Pawlik 2014, Loh et al. 2015).

Our results indicate that the use of a suite of ecologically and socio-economically important focal species can provide evidence of the benefits of conservation strategies for biodiversity and fisheries enhancement. In particular, lower trophic level, high recruiting species of more limited movement such as parrotfish, conch, and lobster appeared to respond most clearly to protection, while higher trophic level, late maturing, and widely dispersing snappers and groupers generally displayed more limited recovery. Patterns of mid-trophic level hogfish and queen triggerfish appeared to be strongly linked to the availability of appropriate prey, i.e. conch and urchins respectively, even as increasing angelfish catches appear to be replacing large parrotfish since the ban in 2009. The increases we have observed in density, biomass, individual size, and CPUE for a number of species in the GUZ stem from a reasonably sized and configured RZ, which may likely have facilitated spillover and larval recruitment effects (Rowley 1994, Chapman & Kramer 1999, Davidson et al. 2002, Tewfik & Bene 2003). These benefits have also been supported by a broader set of fisheries conservation strategies (size limits, closed seasons, species ban) which are well known to fishers who also participate in management decisions, management effectiveness evaluations, and promotion of sustainable practices through representation and membership on the GRAC (Walker & Walker 2007, Gibson et al. 2011, 2013, Di Franco et al. 2016).

Despite some successes associated with the implementation of these conservation strategies, a number of modifications and additions are now being implemented to enhance the monitoring of conservation benefits at Glover's Atoll. A more holistic (LAMP II) assessment for patch reefs has now been implemented using the MBRS Synoptic Monitoring protocol allowing broader habitat, invertebrate, and fish community assessments to be made (Almada-Villela et al. 2003). This is critical given the shift in fisheries targets that is perhaps best reflected with the decreased use of large parrotfish and increased use of spongivorous angelfish amongst others. New investigations in deeper atoll habitats (lagoon floor, fore-reef, deep channels) are focused on locating high densities of large and mature individuals, which support internal recruitment and spillover to existing fisheries (Rowley 1994, Bertelsen & Matthews 2001,

Tewfik & Bene 2003, Stoner et al. 2012, Hixon et al. 2014, Tewfik 2017). These individuals are largely inaccessible to free-diving fishers in the GUZ due to depth, turbidity, and rough oceanic conditions for much of the year (Karpov et al. 1998, Tyler et al. 2009, Tewfik 2014). Despite fairly regular and rigorous enforcement activities conducted by Glover's atoll based fisheries officers as well as activities through GRAC over the time series examined, additional assets (Coast Guard) are now being implemented to strengthen general patrols and protect fish spawning aggregation sites, which are vulnerable to poaching by local and foreign line fishers. It is hoped that the continually evolving nature of conservation strategies being used will provide an appropriate balance between biodiversity and ecosystem services protection, including fisheries and tourism based livelihoods, for the foreseeable future of the GRMR with broader applicability across the Mesoamerican Barrier Reef System.

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