

Testing for top-down control: can post-disturbance fisheries closures reverse algal dominance?

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ABSTRACT

1. The response of fish, sea urchins, benthic cover, herbivory, and predation on sea urchins were studied over a 14-year period in and out of a recently established fully closed and fished atoll reef lagoon of the remote Glover's Reef, Belize.

2. Closure from fishing was predicted to result in the recovery of predatory fish and herbivores, herbivory rates, and subsequently reduce erect algae and lead to the recovery of herbivore resistant and calcifying taxa such as hard corals and calcifying algae. Recovery of predatory fishes was the largest response to closure and the herbivore response was weak and no corals and calcifying algae changed in the predicted direction.

3. Hard corals declined where they were most abundant and all sites appear to have reached a stable point of ~15% cover by the end of the study. Generalized and possibly opportunistic carnivores, such as jacks, barracuda, groupers, snappers, grunts, and sparids showed the greatest increases and there was a trend towards more small-bodied herbivores such sea urchins and damselfish in the open and a slight gain in large herbivores in the closed area, but this had little effect in increasing total herbivory.

4. Factors that may have influenced this unexpected response include: (1) a complex food web that did not produce a simple cascade response; (2) attenuation of the cascade effect towards the lower trophic levels; (3) insufficient compliance, closure time, and space; (4) a post- rather than pre-disturbance establishment of the closure; (5) habitat or site specificity; and (6) overriding environmental disturbances, such as oceanographic oscillations and a warming climate.

5. The results suggest a need to further evaluate fisheries management systems, contingencies, and interventions that will promote coral reef resilience to climate change and ecosystem sustainability.

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KEY WORDS: ecosystem approach; fishing; climate change; marine protected areas; macrophytes; sea urchins; resilience

INTRODUCTION

Coral reefs in the Caribbean have experienced an unprecedented ecological change in the past three decades (Aronson *et al.*, 2003, 2005) that has seen an 80% decline in the cover of hard coral and associated reef complexity (Gardner *et al.*, 2003; Alvarez-Filip *et al.*, 2009; Schutte *et al.*, 2010). Non-erect turf algae have colonized some exposed surfaces of some reefs (Bruno *et al.*, 2009), while others have exhibited an increase in erect algae (Levitan, 1988; Carpenter, 1990; Shulman and Robertson, 1996; McClanahan and Muthiga, 1998). Some investigators have described this change as an ecological phase shift or an alternative stable state (Hughes, 1994; Dudgeon *et al.*, 2010), attributable to a top-down trophic cascade resulting from a

reduction in the rate of herbivory (Petraitis and Dudgeon, 2004; Mumby *et al.*, 2006a). Many investigators attribute this shift to the loss of herbivores, both fish and sea urchins, and consider fishing restrictions and closures as a primary way to manage and possibly reverse this change (Jackson *et al.*, 2001; Hughes *et al.*, 2003; Pandolfi *et al.*, 2003; Bellwood *et al.*, 2004; Mumby *et al.*, 2006a, 2007a, 2007b; Cinner *et al.*, 2009). Some investigators see reef degradation in the Caribbean as the long-term failure of local-level fisheries management and the inability of reef scientists to agree on the major causes and suggest local-level management solutions (Pandolfi *et al.*, 2005) while others see it as a result of the massive decline and poor recovery of the sea urchin *Diadema antillarum* or recent climatic shift that is only partially manageable at the local level (Aronson and Precht, 2006; Dudgeon *et al.*, 2010).

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The death of corals is often associated with diseases, warm water, and hurricanes (Mumby, 1999; Aronson *et al.*, 2003, 2005; Schutte *et al.*, 2010) while other studies suggest that corals lose the competition with erect algae when nutrient loads increase (Lapointe *et al.*, 2004). The issue is hard to resolve because of the difficulty of separating the effects of nutrients and heavy fishing pressure from possible climatic change that would affect both onshore and offshore ecosystems (Sotka and Hay, 2009). The observed changes are not, however, just limited to areas close to shore or those associated with large human populations, in some cases nearshore areas appear to be less affected than offshore areas (Lirman and Fong, 2007). Coral mortality and dominance of erect algae is also common on remote coral reefs (McClanahan and Muthiga, 1998; Ostrander *et al.*, 2000; Gardner *et al.*, 2003; Kramer, 2003; Bruno *et al.*, 2009) and the high erect algal abundance cannot always be explained by the lack of abundance of reef herbivores (Williams and Polunin, 2001). Changes appear to be persistent such that, with few exceptions (Edmunds and Carpenter, 2000; Idjadi *et al.*, 2006), stony coral populations, particularly in the Caribbean, show little sign of recovery after disturbances and the establishment of erect algae (Connell, 1997; Baker *et al.*, 2008; Schutte *et al.*, 2010).

The potential to shift reef ecology back to coral dominance has only recently been explored through short-term algal reduction experiments, but these restoration methods have largely been unsuccessful over the period of one year when herbivore numbers were low (McClanahan *et al.*, 2001). Attempts have also been undertaken to manipulate coral and algal cover, and nutrients on relatively small scales (Miller *et al.*, 1999; McClanahan *et al.*, 1999; Thacker *et al.*, 2001; Williams and Polunin, 2001; Williams *et al.*, 2001; Sotka and Hay, 2009). Experiments to manipulate herbivory on the small scale have also been popular, mostly using small to moderate herbivore exclusion cages (Carpenter, 1986; Lewis, 1986; Miller *et al.*, 1999; Smith *et al.*, 2001; Thacker *et al.*, 2001; Diaz-Pullido and McCook, 2003; Jompa and McCook, 2003) or the local redistribution of the algal-feeding sea urchin *Diadema antillarum* (Macia *et al.*, 2007), which is associated with coral recovery in a few places where their numbers have recovered (Dudgeon *et al.*, 2010; Hughes *et al.*, 2010).

These small-scale experiments suggested that there is potential to reduce algae through manipulation of herbivores, and results promoted the call for more marine protected areas (MPAs) after the loss and poor recovery of the herbivorous sea urchin, *D. antillarum*, in 1983 (Hughes, 1994; Lessios *et al.*, 2001; Mumby *et al.*, 2006a). Increased herbivory and coral recruitment in the Bahamas MPAs with high parrotfish abundance further supported this management intervention (Mumby *et al.*, 2006a; Mumby, 2009a; Mumby and Harborne, 2010). MPAs and fisheries closures are seen by many as the main way to mitigate the effects of climate change and to enhance recovery of corals often believed to be lost due to competition with algae or unable to recover after algae dominated the benthic substratum (Hughes *et al.*, 2003, 2007; West and Salm, 2003; Bellwood *et al.*, 2004; Mumby *et al.*, 2006a).

An unresolved issue, however, is to what extent high herbivory has to be present before the time of the disturbance, or if an increase after the disturbance can quickly and successfully reverse a phase shift (Idjadi *et al.*, 2006; McClanahan, 2008; Dudgeon *et al.*, 2010). A meta-analysis of coral cover change in MPAs and unprotected reefs found that

it was largely the oldest fisheries closures that were able to resist the effects of climatic disturbances and, in the Caribbean, coral cover declined up to 14 years after the establishment of the MPA (Selig and Bruno, 2010). Similarly, it can be decades or more before herbivorous fish populations increase inside fisheries closures (McClanahan *et al.*, 2007a). Additionally, even when herbivore numbers increase, coral cover does not necessarily increase (Newman *et al.*, 2006). Consequently, the efficacy of post-disturbance management in promoting the recovery of coral reefs remains an area of applied coral reef science that is promoted based on reasonable ecological theory, some experimental, case studies, and assumptions. Nevertheless, the possibility of stabilizing feedbacks, ecological hysteresis, and overriding alternative disturbances has not been well explored with empirical field studies at the scale of the management application.

The extrapolation of small-scale and short-term studies to large-scale managed phase-shift reversals is likely to be fraught with scaling problems that are associated with the complexity of ecosystems, the time and spatial scale of ecological processes, and the continual change in the biophysical environment. In addition, the alternative explanation or hypothesis that changes are not a top-down phase shift driven by small but critical changes in key processes, such as herbivory, but rather a gradual or punctuated change to a resilient alternative state driven by physico-chemical environmental changes (Petraitis and Dudgeon, 2004; McClanahan *et al.*, 2007b) has only been tested from recent geological records (Aronson *et al.*, 2005) and discussion on the interpretation of the recent geological record is ongoing (Aronson *et al.*, 2003; Pandolfi *et al.*, 2003).

There is no reliable way to test the above hypothesis on a convincing scale apart from through the establishment and long-term monitoring of full-closure MPAs that are larger than a few square kilometres and far enough from shore and human population density to minimize the stronger water quality effects. This is because environmental disturbances that can control corals and override herbivory effects are likely to occur on time scales such as the El Niño Southern Oscillation (ENSO), of four years or longer (Huppert and Stone, 1998). The creation of MPAs is likely to result in complex species responses that will not just increase herbivore numbers but result in complex ecological interactions and responses. For instance, a recent study of coral recovery in the MPAs of Kenya after the 1998 ENSO found that many of the large parrot and triggerfishes in MPAs fed on or were destructive to corals and ENSO disturbance resulted in a shift towards predator-tolerant coral taxa (McClanahan *et al.*, 2005; McClanahan, 2008). Caribbean studies have also found heavy predation on corals by parrotfish (Littler *et al.*, 1989; Rotjan *et al.*, 2006). Consequently, the rates of corallivory and herbivory and the abundance of the coral and algal taxa could determine the long-term outcomes of the coral–algal dynamic (Rotjan and Lewis, 2008). Mumby (2009a) reviewed this subject for the Caribbean and concluded that parrotfish herbivory and corallivory generally had a net benefit for corals and that the protection of parrotfish could assist the recovery of corals from climate change disturbances (Mumby and Harborne, 2010).

Another important factor to consider when evaluating hypotheses is the time and spatial scale of recovery of tropical MPAs. Meta-analysis of closures of different ages have suggested the changes are 'rapid and long lasting' (Halpern

and Warner, 2002), but a number of more site-specific studies in the Indo-Pacific suggest that the recovery time of some key factors, such as fish biomass, is ~25 years (Russ and Alcala, 2004; Russ *et al.*, 2005; McClanahan *et al.*, 2007a) and dependent on issues such as MPA size and management compliance (McClanahan *et al.*, 2009; Pollnac *et al.*, 2010). The only published study of recovery of coral reef herbivorous fish from the beginning of a fishing closure, suggests recovery is slow, possibly slower than the recovery times of many carnivores with full recovery times >40 years of closure (McClanahan *et al.*, 2007a). In contrast, a recent long-term study in the Caribbean found that one reef herbivore, the ocean surgeonfish, had life-history characteristics that prevented it from being greatly affected by fishing (Robertson *et al.*, 2005) and this species can play an important role in controlling herbivory and coral condition (Burkpile and Hay, 2010). Nevertheless, herbivore numbers have declined annually at ~4% between 1996 and 2007 throughout the Caribbean (Paddack *et al.*, 2009).

Meta-analysis type spatial comparisons of ecosystems and closures in space have shown patterns consistent with the top-down cascade hypothesis (Newman *et al.*, 2006; Mora, 2008), but spatial comparisons are troubled by site selection issues, their initial conditions, and are not nearly as powerful as comparison over time in different management treatments (MacNeil, 2008; Stewart-Oaten, 2008; Huntington *et al.*, 2010). Conclusions are strongest when experimental or management manipulations are studied over long enough periods to determine the interactions between climate, trophic ecology, and closed area management. Top-down reasoning has often assumed that all consumers benefit from reduced fishing but the potentially top-down role that piscivores may have on herbivorous fish and their release from fishing is unclear, not supported by simple food-chain theories (De Feo and Rinaldi, 1997; Hairston and Hairston, 1997), and may depend greatly on the herbivores ability to quickly achieve a size that allows them to escape their predators (Baskett, 2006; Mumby *et al.*, 2006a). Consequently, there is enough complexity in responses that simple cascade models, where all fish consumers benefit from closure management, will require more study of reefs and long-term and large-scale case studies (Huntington *et al.*, 2010; Solomon *et al.*, 2010). Given these theories and concerns, an area fully closed to fishing was studied and data collected from the inception of this management and across the 1998 ENSO disturbance was used to contrast climate versus fishing control hypotheses. Results are presented in a top-down format where ecological control is expected to cascade down from fishing to consumers and finally influence primary producers.

The objectives were, therefore, to evaluate the following hypotheses where herbivores, climate, and other ecological interactions were considered and it is predicted that (1) closures would increase herbivore numbers and herbivory and lead to declines in leathery macrophytes and erect algae and increases in calcifying corals and algae (Hughes *et al.*, 2003, 2007; Mumby *et al.*, 2006a; McClanahan, 2008; Mumby and Harborne, 2010), and (2) that the climatic disturbance, here represented by the 1998 ENSO disturbance, was the major cause of ecological change and that local management through closures would have little effect on the recovery. These hypotheses are not mutually exclusive and could interact through interactive, synergistic or opposing influences.

METHODS

Study area

Glover's Reef Atoll is an area of 260 km² dominated by coral and seagrass and located approximately 40 km off of the Belizean coastline (Figure 1). The atoll lagoon patch reefs in Glover's Reef have undergone an ecological change since Wallace (1975) first described them in 1970–1971. McClanahan and Muthiga (1998) repeated his surveys in 1996–1997 and found that coral cover had declined from 80% to 20%. Fleishy macroalgae occupied most (75%) of the available space and biotic homogenization had largely eliminated some of the original ecological zones. Recognition that the ecology of this atoll had been degraded led to the legal gazettement of the southern half of the reef as a no-fishing reserve in 1993, which slowly came into effect after 1995 and covers 70.8 km² or approximately one quarter of the atoll. This study focused on the patch reef environment in the lagoon of this atoll in the Conservation zone, which is designated as a fisheries closure, and the General Use zone where fishing is regulated by the Belize Fisheries Department. The patch reefs chosen in this study were the high complexity (McClanahan, 1999) and high patch reef neighbourhood density (Type II reefs) ones described by Huntington *et al.* (2010), which showed the greatest response to closure.

The atoll is far from many human land-based sources of pollution but pulsed and intermittent river influences may influence water quality (Andréfouët *et al.*, 2002; Cherubin *et al.*, 2008). Migrant fishers from the Belizean mainland use spears and hook-and-line to capture reef fishes and also seasonally collect lobster and conch (Acosta, 1999; Sala *et al.*, 2001).

Field methods

Field data collection occurred over a 14-year period on eight patch reefs, divided equally between the two management zones that were repeatedly but episodically sampled across years with sampling always undertaken between May and July. Benthic substratum measurements were completed 10 times while sea urchin and fish densities and predation and herbivory assays were undertaken 8 to 10 times between 1996 and 2009.

Physico-chemical measurements

Water temperature, water flow, and water quality measurements (nutrients concentrations) were taken during the middle of the survey to test for possible differences between the two management zones. Automated temperature gauges (Hobo temperature gauges – Onset Corporation, Pocasset, MA, USA – accuracy 0.35 °C at 25 °C) were deployed in shallow water (<1 m at low tide) and cemented under dead corals hidden from direct sunlight. Differences in the battery lives of the gauges and other logistic difficulties resulted in non-continuous comparisons for some of the temperature data, so we present and compare only those 383 days between July 2003 and December 2004 when there were comparable data. Average daily temperature when the times directly overlapped between the two management zones are presented and differences between means were tested with a *t*-test.

Water flow was estimated using the 'clods' or calcium sulfate dissolution method (Doty, 1971). Three weighed clods were deployed on each of the eight patch reefs at haphazard times in 2002 and 2004, clods were collected after ~24 h, dried, and weighed again. The weight losses were converted to average

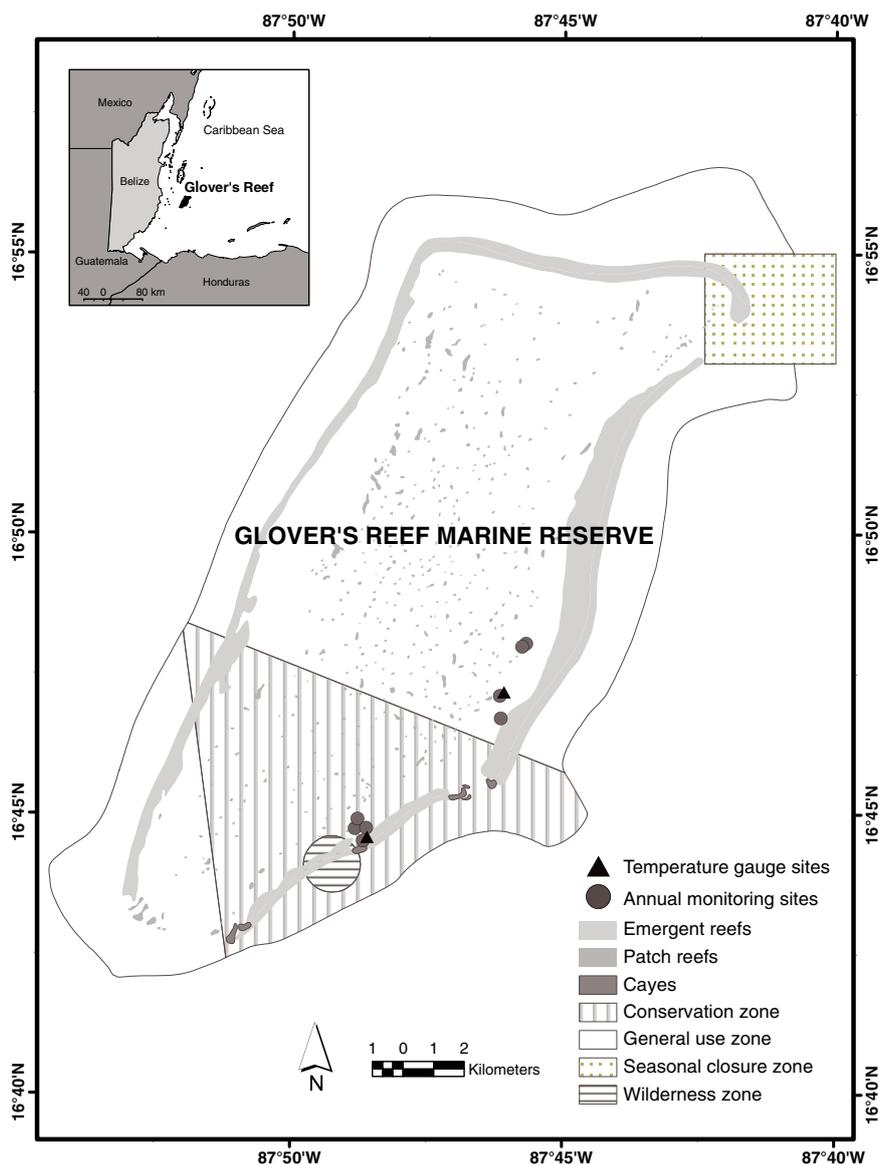


Figure 1. Map of Glover's reef atoll showing the two management zones. The Conservation zone is managed as a closed area and the General Use zone is open to fishing.

current flow speed ($V_w = \text{cm s}^{-1}$) using the equation $V_w = (\text{Clod change in weight} - 0.932)/2.357$, which was obtained by studies of clod dissolution in a flume with controlled water flow (Anzai, 2001). Differences between years and management zones were tested with a *t*-test.

Water samples were collected on the patch reefs haphazardly in the summer during the mid-period of this study (2002–2004) to test for differences in nutrient concentrations and turbidity between the two management zones of the atoll. Water samples were collected 5–10 cm above the patch reef substratum in acid-washed 1 L bottles and analysed for nitrite, nitrate, ammonium, soluble phosphates, and turbidity on the day of collection. A Hach DR/2500 spectrophotometer using the cadmium reduction for nitrate and ascorbic acid methods for phosphorus and a 2.5 cm cell length was used for the analyses. This method has a detection limit of 0.02 mg L^{-1} for phosphorus and a limit of 0.2 mg L^{-1} for nitrate and 0.002 mg L^{-1} for nitrite. The sum of the nitrogen measurements was presented as total nitrogen. Statistically significant relationships were found with known concentrations

when testing the spectrophotometer accuracy, but scatter in the data was high ($\text{COV} = 50\%$) at low nutrient concentrations. Consequently, sampling variance at low concentrations could override differences in treatments but there was no prior reason to expect differences in nutrient concentrations between the management zones. A repeated-measures ANOVA was used to test for differences in time and management for phosphorus, total nitrogen, and turbidity.

Fisheries catch

Fisheries catch data from the Glover's reef atoll were compiled from a monitoring programme designed to determine trends in landings and fishing pressure at the atoll. Most fishers originated from Sarteneja, Belize and operated long-distance sailboats for trips of over a week and largely rely on Hawaiian slings or spearguns and, to a lesser extent, traditional hand lines. Fishing for conch and lobster is seasonal, due to seasonal closures, and largely drives the seasonal migrations. Each sailboat berthed

approximately six to eight fishers who used their individual 'dories' or canoes from which to fish during the day.

On each sampling trip, approximately three boats were sampled with five or more fishers on each sailboat. Sampling was done on three consecutive days per month depending on the presence of Sarteneja sailboats. Catch data were collected usually when fishers returned to the sailboat at midday. For each fisher's catch, the name of the fisher, family of catch, fork or tail length size (cm), weight (g), fishing gear, and total fishing effort (hours fished) were recorded. Fish identification was done to gross groups or common names; for example the catch group parrotfish largely comprised two species (*Scarus viride* and *Scarus aurofrenatum*) (Appendix 1). Catch per unit effort (CPUE) by weight of finfish per hour is presented.

Fish population estimates

Fish were sampled to determine the changes in the species richness and main families and functional groups over time. Visual counts of fish were carried out using the discrete group sampling (DGS) method where a limited number of species were sampled during a single sampling period (Greene and Alevizon, 1989). The shallowness and small size of patch reefs did not permit the use of standard belt transects or point counts and, therefore, a 5 min search interval was used to sample fish. During the total 35 min sampling period the investigator swam haphazardly over each patch reef and recorded the number of species and individuals in each of seven groups for a 5 min interval species (Humann, 1993). Individual fish less than 3 cm were not counted and fish sizes and biomass were not recorded. Species were separated into discrete groups based on their taxonomy and position in the reef or water column. Each of the following seven discrete groups were sampled separately: Group 1 Chaetodontidae (butterflyfishes) and Pomacanthidae (angelfishes); Group 2 Acanthuridae (surgeonfishes); Group 3 Haemulidae (grunts), Sparidae (porgies) and Lutjanidae (snappers); Group 4 Scaridae (parrotfishes); Group 5 Labridae (wrasses); Group 6 Sphyraenidae (barracuda), Balistidae (triggerfish), Aulostomidae (trumpetfish), Carangidae (jacks), Serranidae (groupers) and *Chromis* sp.; and Group 7 benthic Pomacentridae (damselfishes). Species were pooled into families and trophic categories, based on their feeding and size characteristics (Randall, 1967; Appendix 1) for some of the presentation and statistical analyses. Body size was used to distinguish the herbivorous fish, as this was expected to influence their susceptibility to fishing. Consequently, large herbivores, included surgeonfish and all parrotfish except the striped parrotfish, and small herbivores, included the brown damselfish and striped parrotfish.

Sea urchin density and predation experiments

Sea urchins were studied to determine the potential impacts of fisheries management on their populations and herbivory rates. All sea urchins were counted in nine, 10 m² circular plots per patch reef distributed haphazardly by the toss of a weighted line from the edge to centre of the reef. *Echinometra viridis* were the only species found in abundance (>1 ind per 10 m²) and the presentation of results is therefore, restricted to this species. Predation was estimated by tethering experiments where individual *E. viridis* were pierced with a hypodermic needle, threaded with monofilament line, and tied to loops at ~2 m intervals on three lines (10 urchins per line) distributed from the

edge to centre of each patch reef (McClanahan, 1999). The tethered individuals were inspected after ~24 h to determine the number of individuals that died over each daily interval and classified by the condition of the carcass (McClanahan and Muthiga, 1989). A predation index was calculated where the Predation Index = 1 - S/1 where S is the survival if either a 0 (if dead) or a 1 (if alive) individual was found.

Herbivory assays

Herbivory was studied nine times between 1997 and 2009 in the two management zones using assays of the seagrass *Thalassia testudinum*, which has a moderate palatability and shape that makes it a useful generic assay (Hay, 1981). Seagrass blade tips were collected and visually inspected to avoid pre-bitten or epiphyte-covered samples. Seagrass blades were cut to a standard 10 cm length, clippings were held by weighted clothespins, and attached to a line fastened on the reef at ~2 m intervals (McClanahan *et al.*, 1994). Three lines were haphazardly placed from edge to centre positions on the patch reefs and ten clippings were positioned on each line. Assays were left for 24 h before inspection. Divers recorded whether or not the samples had been bitten, the amount of seagrass bitten (to the closest 0.5 cm), and based on bite scar characteristics the type of herbivores responsible for the bites, fish or sea urchin (Hay, 1981; McClanahan *et al.*, 1994). This herbivory assay method is biased towards macrophyte-feeding species and underestimates herbivory by some groups that do not feed on macrophytes, including some grazing surgeonfish. This method when combined with counts of herbivores provides an additional perspective on herbivory (McClanahan *et al.*, 1994; Fox and Bellwood, 2008).

Benthic cover and algal biomass

Benthic cover on each patch reef was assessed by the line intercept method. Three 10 m lines were laid haphazardly but parallel to the patch reef's windward north-east edge. One transect was laid in three positions: on the edge (the transition from the sand to patch reef), shoulder (shallow windward edge), and centre. Canopy cover under a draped transect line of the benthic groups >3 cm was measured to the nearest centimetre and taxa were identified to the species for stony corals (Humann, 1993), the genus for fleshy and calcareous algae (Littler and Littler, 2000), and by gross functional groups for encrusting coralline algae, turf, seagrass, sand, sponge, soft coral, and zoanthids. Percentage cover for each group was estimated as the sum of each cover category divided by the sum of all categories.

Data analyses

Data were frequently presented as time series and two-factor ANOVA tests of significance of time, management, and their interaction applied when data fit the assumptions (Sala *et al.*, 2001). Detrended correspondence analyses (DCA) were also presented on the multi-taxa groups of fish trophic levels and fish family groups to evaluate changes in fish community structure over time and management. Data pooled at the fish family and trophic groups were seldom normally distributed and, therefore, non-parametric Wilcoxon tests were undertaken to compare differences between the management zones. Numbers of fish species were, however, normally distributed and ANOVA tests

of time, management, and their interaction were undertaken to test for differences over time and treatment. Fisheries catch data were presented as the caught weight CPUE for each finfish group.

RESULTS

Physico-chemical measurements

Average daily water temperatures ranged from 21°C in December/January to 31°C in September/October and did not differ significantly between the two management zones although temperature varied more in the Conservation than in the General Use zone (Figure 2). Current speed was slow and varied from 3.9 to 4.8 cm s⁻¹, with statistical but no consistent differences between the management zones or the years sampled (Table 1). For example, current speed was higher in the General Use zone than in the Conservation zone in 2002, but the opposite occurred in 2004. Moreover, sites within the Conservation zone showed no statistical differences between years while the sites within the General Use zone had significantly higher current speeds in 2002 than 2004. Nutrient concentrations and turbidity were also low and showed no statistical differences between the management zones (Table 2).

Fisheries catch

Fisheries catch data were collected for a total of 74 days and a total of 110 Sarteneja fishers were sampled, ranging from 21 fishers in 2005 to 45 fishers in 2008. A total of 54 finfish species and 1202 individuals were recorded during the period 2005 to 2008. Parrotfish CPUE was ~2.5 times higher than the other

Table 1. Summary and *t*-test comparisons of water flow (cm s⁻¹) between the Conservation and General Use zones within each year and between years within each zone

	Conservation zone		General Use zone		Comparison	
Year	Mean	SEM	Mean	SEM	<i>t</i> =	<i>P</i> <
2002	3.96	0.23	4.79	0.20	2.67	0.01
2004	4.64	0.19	3.90	0.18	-2.43	0.05
Comparison between years						
	<i>t</i> =	1.69		-2.82		
	<i>P</i> <	NS		<i>P</i> <0.01		

NS = not statistically significant.

Table 2. Concentrations (mean ± SD) of phosphorus (PO₄), total N, and turbidity in the Conservation and General Use zones. Repeated-measure MANOVA tests found no differences for comparisons between management zones

Parameter	Management	Mean	SD	Sample size
Phosphorus, mg L ⁻¹	Conservation zone	0.03	0.01	48
	General Use zone	0.03	0.01	48
Total nitrogen, mg L ⁻¹	Conservation zone	0.06	0.01	40
	General Use zone	0.06	0.01	40
Turbidity, mg L ⁻¹	Conservation zone	1.50	0.71	48
	General Use zone	1.38	0.53	48

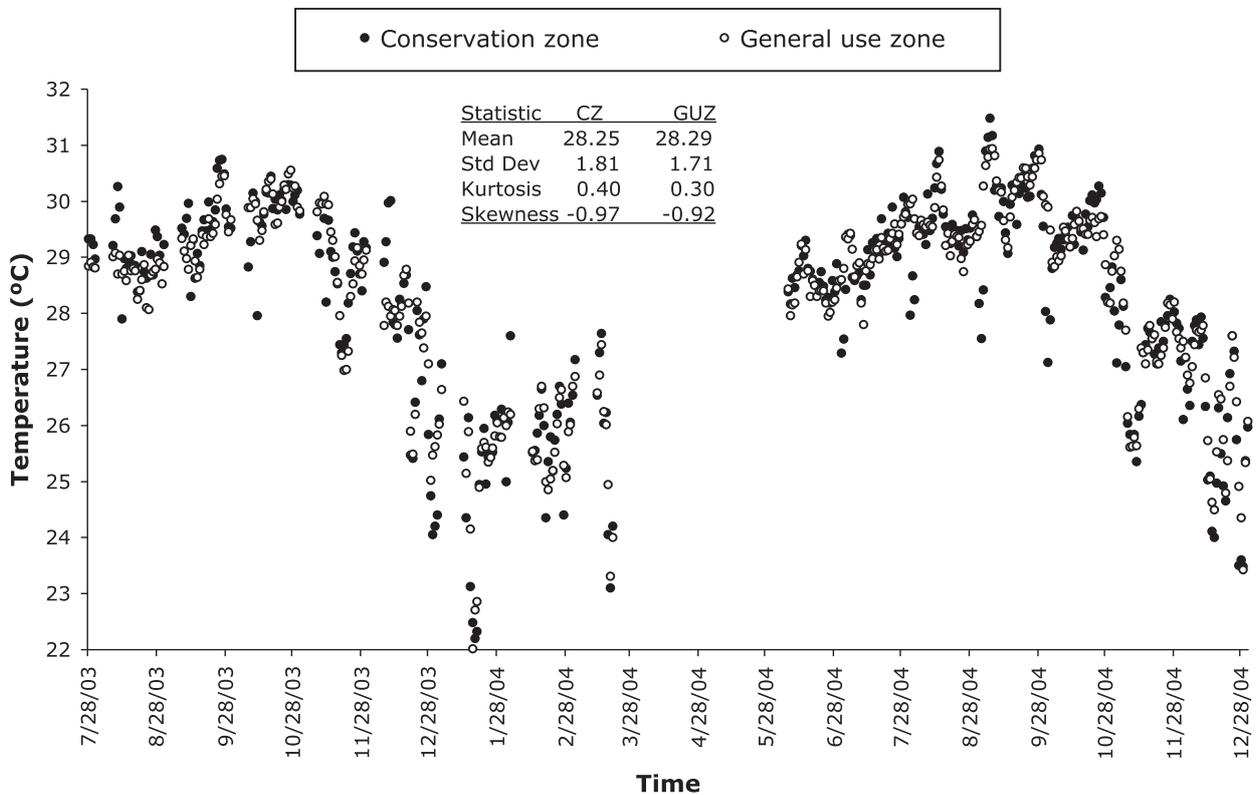


Figure 2. Time-series and summary statistics of temperature variations in the Conservation and General Use zones.

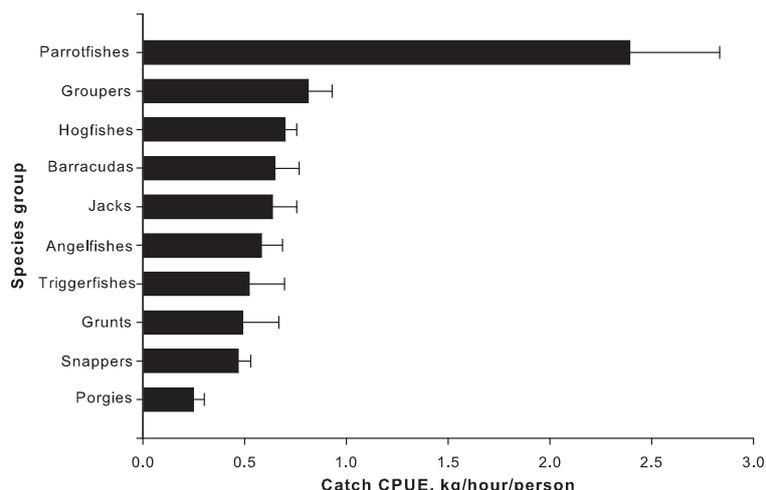


Figure 3. Catch per unit effort (CPUE mean \pm SEM) of fish caught at Glover's reef General Use zone between 2005 and 2008.

target groups at 2.39 ± 2.34 (\pm SD) $\text{kg h}^{-1} \text{ person}^{-1}$ (Figure 3). The rest of the catch was composed of carnivores and each catch group varied from ~ 0.25 to $0.80 \text{ kg h}^{-1} \text{ person}^{-1}$ and total catch averaged $5.1 \pm 0.56 \text{ kg h}^{-1} \text{ person}^{-1}$.

Coral reef fish abundance

The overall abundances of finfish depended on the trophic groups (Appendix 1), the family and the species of fish. In general, the larger-bodied carnivorous species including piscivores (jacks, barracuda, groupers, and trumpetfish), and sea urchin predators (mostly porgies and hogfish) showed significantly higher abundances in the Conservation than the General Use zone (Table 3) and increased significantly over the sampling period (Figure 4). The abundance of large herbivores including surgeonfishes and parrotfish was also on average higher in the Conservation zone than the General Use zone (Table 3) and had increased significantly ($\sim 28\%$) by 2008 with a small decline in both zones in 2009.

Total herbivore numbers were not different between zones, and small herbivores showed a general decline over time in both zones and were more abundant in the General Use zone. Although fish that feed on sponges did not show significant differences between the management zones, abundances increased in both management zones from <1 to 3 ind per 5 min count until 2008 but, in 2009, no sponge-eaters were encountered on patch reefs in the General Use zone. Detrended correspondence analyses (DCA) showed that both zones had mainly herbivores at the start of sampling with a move towards higher trophic levels (piscivores and micro- and

macro-invertebrates) in the Conservation zone while showing no significant changes in trophic groups in the General Use zone (Figure 5)

Comparisons of the fish families showed that, in general, the wrasses, grunts, damselfish, and parrotfish were the most abundant fish families ranging from 50 to 135 ind per 5 min count (in order of increasing numbers), while the butterflyfish, groupers, goatfish, jacks, angelfish and porgies occurred in very low abundances <2 ind per 5 min count (Table 4). Large parrotfish occurred in much lower abundances (~ 20 ind per 5 min count) than small parrotfishes (~ 100 ind per 5 min count). In general, the total number of species showed a significantly larger increase in the Conservation zone (19 to 27) than in the General Use zone (17 to 20) over the study period (Figure 6).

Changes in abundances of fish families over time depended on the taxa (Figure 7). Snappers showed the largest increases (13–72 ind per 5 min count) within the Conservation zone while remaining at ~ 7 ind per 5 min count in the General Use zone. Grunts and surgeonfish increased in the Conservation zone and showed lower numbers but no consistent trends in the General Use zone. Angelfish on the other hand increased in both zones and although the overall numbers were generally low they were significantly higher in the Conservation zone by 2009. There were no significant changes in time or between the different management zones in either the butterflyfish or wrasse numbers but the parrotfish showed a 60% decrease in both management zones, which was largely attributable to a decrease in the small parrotfishes. Damselfish were the only group that showed a significant increase in numbers in the General Use zone (58%) and a small increase in the Conservation zone (17%) after 1999,

Table 3. Average abundance of fish (mean \pm SEM ind per 5 min) categorized by trophic group between the Conservation and General Use zones. Classification of species by trophic groups described in Appendix 1

Trophic categories	Conservation zone		General Use zone		Statistical comparison	
	Mean	SEM	Mean	SEM	Wilcoxon Z-statistic	P-value
All herbivores	283.64	33.22	298.00	27.36	1.23	NS
Piscivores	16.46	3.52	4.10	1.76	-6.04	<0.0001
Macroinverteviores	2.18	1.33	0.95	0.78	-3.36	<0.001
Microinverteviores	158.86	20.37	125.80	13.43	-4.75	<0.0001
Sponge eaters	0.96	0.80	0.82	0.66	-1.62	NS
Small herbivores	179.13	24.81	209.25	19.29	3.44	<0.001
Large herbivores	104.52	14.35	88.75	12.87	-2.23	<0.05

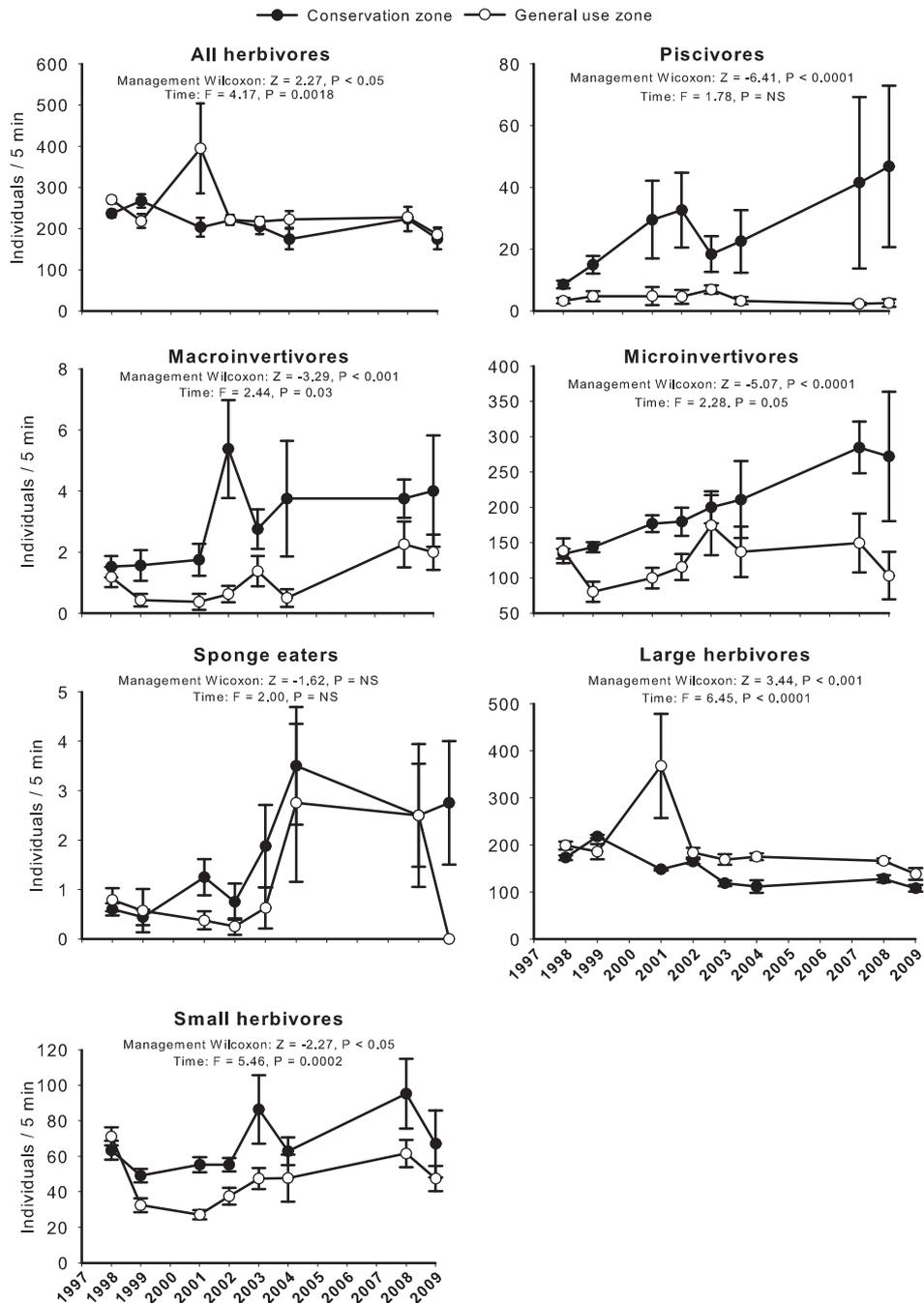


Figure 4. Changes in the number of individuals (mean \pm SEM ind per 5 min) in different trophic categories of the fish groups in the Conservation and General Use zones from 1998 to 2009.

which was attributable to an increase in the damselfishes *Stegastes* spp. The DCA of the fish families (Figure 8) also showed changes away from parrotfish and butterflyfish at the beginning of the period in both zones and towards more groupers, porgies, goatfish, and snappers in the Conservation zone and towards more damselfish in the General Use zone.

Sea urchins and predation

Echinometra viridis was the dominant sea urchin species comprising 99.2% of the 20 291 urchins censused followed by *E. lucunter* (0.76%), while *Diadema antillarum*, *Tripeustes*

ventricosus and *Eucidaris* sp. were very rare (0.07%). Urchin abundances changed in both management zones from 1996 showing an increase in the General Use zone (~15 to 70 ind per 10 m²) and a decrease in the Conservation zone (~30 to 15 ind per 10 m²) from 1996 to 2008 and then a rise in 2009. Both time and management were statistically significant with management being the stronger of the two variables (Figure 9(a)).

Within each patch reef, rates of predation on tethered *E. viridis* were generally low (<35% eaten) but significantly higher along the deeper (Predation index = 0.26 and 0.39 for General Use and Conservation zones, respectively) than shallower transects (Predation index = 0.14 and 0.23 for

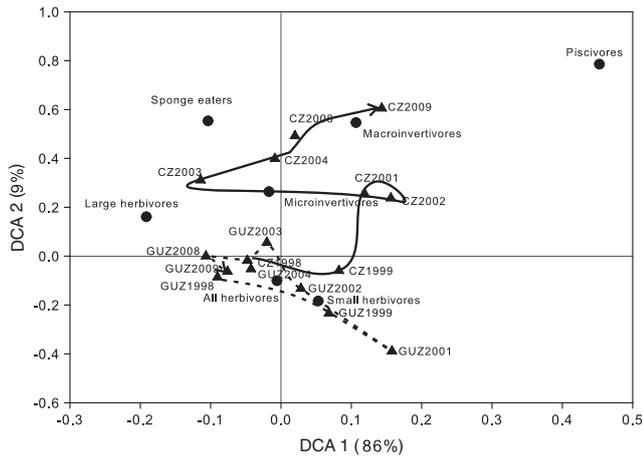


Figure 5. Changes in the numbers of fish pooled into trophic groups in the Conservation (CZ) and General Use zones (GUZ) from 1998 and 2009 based on a detrended correspondence Analysis (DCA). Solid and dashed lines show temporal change of the General Use and Conservation zones, respectively.

General Use and Conservation zones, respectively). Predation rates increased quickly in the Conservation zone after 1996 then slowly decreased between 1998 and 2004 and increased again until 2009, such that the total rate approximately doubled from ~0.15 to 0.30 over the 14-year period. The Predation index steadily declined in the General Use zone, from ~0.32 to 0.10 over the 14-year period (Figure 9(b)).

Herbivory

Herbivory rates on assays of *Thalassia testudinum* blades indicate a generally low level of herbivory with < 35% of the assays being bitten per day (Figure 10(a)). The two management zones had similar levels of herbivory during the initial part of the study (~20%) and appeared to track each other over time. The amount of the assay eaten declined for a few years and increased after 2001 until 2004 and then remained largely constant until 2009. Total herbivory was slightly higher in the

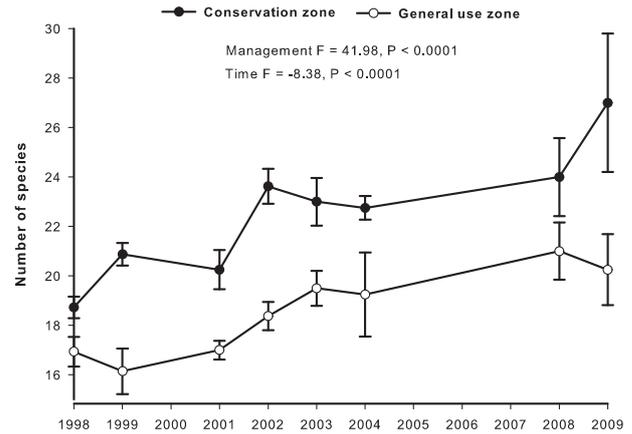


Figure 6. Changes (mean ± SEM) in the number of species of fish in the Conservation and General Use zones from 1998 to 2009.

Conservation zone after the first few years and the differences were weakly significant for time and management (Figure 10(a)).

There were also differences in the amount of the assays eaten by sea urchins and by fish, with greater losses attributed to sea urchins in the Conservation zone at the beginning of the study period, which declined from ~20 to 10% over time (Figure 10 (b)). Bites attributed to sea urchins increased from ~0 to 15% in the General Use zone by 2004 and then declined to ~5% in 2009. Bites attributed to fish in the Conservation zone increased from 20% peaking at 45% in 2004 and subsequently declined to ~30% in 2009. Herbivory attributed to fish in the General Use zone declined from 20% to ~10% between 1996 and 1999 and remained relatively constant at this level up to 2009.

Benthic substratum

Erect fleshy algae (~46%) dominated the benthic cover followed by hard coral (~17%), turf algae, red coralline, and green calcareous algae (9%, 8%, 5% respectively) while sand, sponge, and seagrass were < 6% of the substratum cover (Figure 11). Fleshy algae showed some fluctuations, increasing after 1998 and declining slightly after 2002 with no significant difference between the

Table 4. Average fish densities (mean ± SEM ind per 5 min) of the main fish families within the Conservation and General Use zones between 1998 and 2009

Family category	Conservation zone		General Use zone		Statistical comparison	
	Mean	SEM	Mean	SEM	Wilcoxon Z-ratio	P-value
Chaetodontidae	3.57	0.25	3.32	0.28	-0.83	NS
Pomacanthidae	0.96	0.15	0.82	0.17	-1.62	NS
Lutjanidae	21.76	2.21	8.15	0.91	-5.14	< 0.0001
Sparidae	1.33	0.21	0.70	0.15	-2.09	< 0.05
Haemulidae	71.02	4.98	60.23	9.01	-3.78	< 0.001
Large parrotfishes	20.86	1.20	20.39	1.47	-0.99	NS
Small parrotfishes	100.80	5.49	115.46	13.17	0.28	NS
Scaridae (all)	121.66	5.78	135.85	13.21	0.29	NS
Acanthuridae	20.82	1.42	15.99	1.05	-2.34	< 0.05
Labridae	49.82	2.27	49.47	2.37	0.18	NS
Pomacentridae	78.33	2.87	93.80	3.58	3.08	< 0.01
Carangidae	2.72	0.50	1.81	0.51	-2.60	< 0.01
Kyphosidae	0.16	0.05	0.00	0.00	-	-
Sphyraenidae	1.62	0.38	0.16	0.07	-5.28	< 0.0001
Gerreidae	0.86	0.32	0.00	0.00	-	-
Mullidae	1.02	0.20	0.90	0.16	0.62	NS
Serranidae	1.11	0.12	0.70	0.11	-2.97	< 0.01

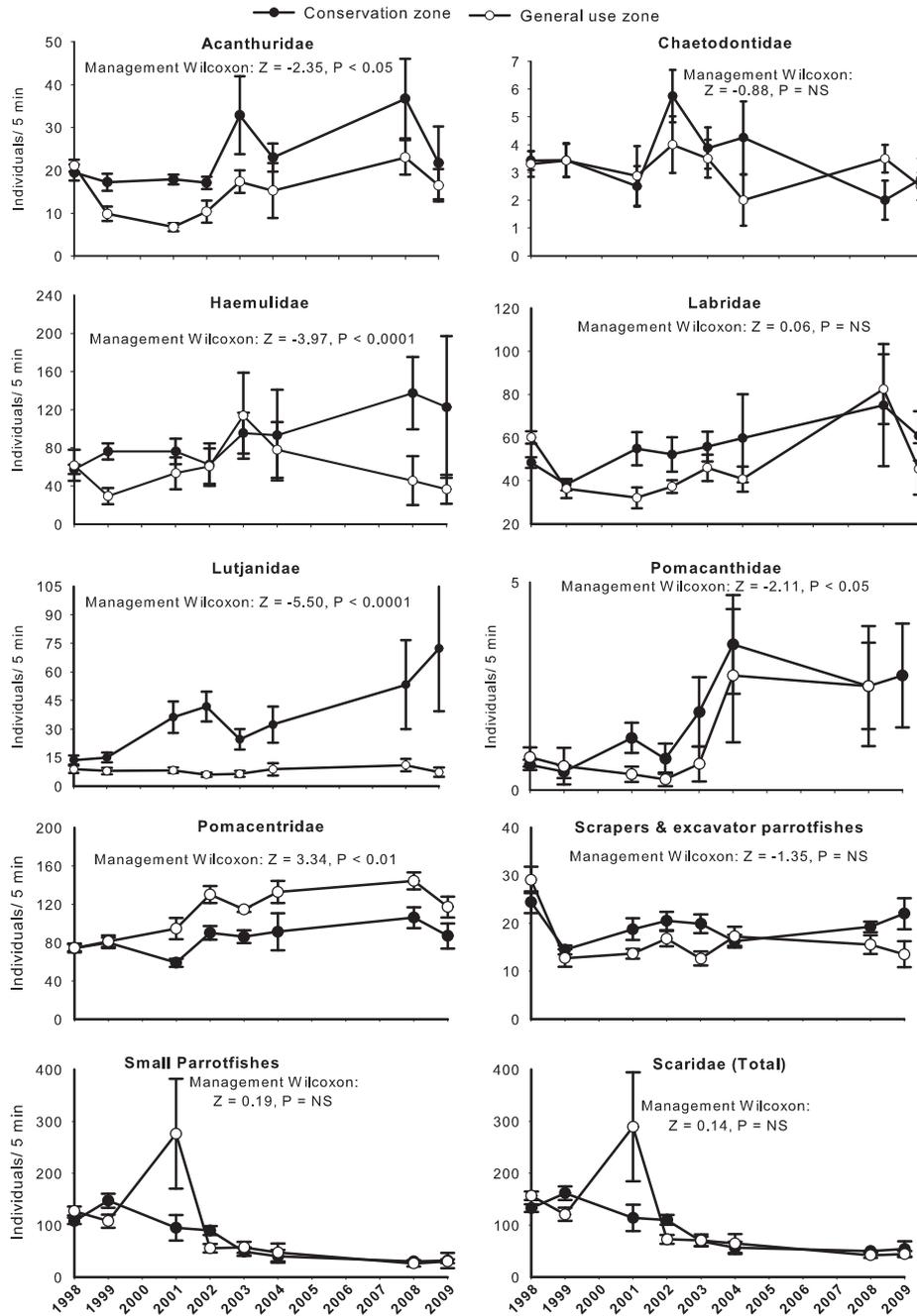


Figure 7. Changes in number of individuals (mean \pm SEM) of some of the dominant fish groups in the Conservation and General Use zones from 1998 to 2008. Scaridae are pooled into total, small and the large species.

management zones and the time-management interaction (Figure 11). Hard coral cover on the other hand showed a weakly significant decline in the Conservation zone; most of this occurred between 1998 and 2001 (~26% at the time of closure to 10%) and a slight recovery to ~15% by 2009. Hard coral cover remained relatively stable at ~15–20% in the General Use zone and there was a weak difference between management zones. Calcifying algae (both green and red) showed significant time and management interactions but the differences in time and management were not consistent between the green and red calcifying algae – green increasing and staying only slightly more abundant in the Conservation zone over time, but changes in red corallines were not consistent with management and not different

at the end of the study. The same inconsistent patterns with management were also observed for seagrass cover.

DISCUSSION

The development of areas closed to fishing is likely to be one of the primary management tools that can potentially reverse or rehabilitate reefs that have undergone the reported ecological change in the Caribbean and elsewhere (Mumby *et al.*, 2006a, 2007a, 2007b; Hughes *et al.*, 2007; Selig and Bruno, 2010). The trophic cascade and herbivore-control model could help local management of what are, at a minimum, regional-, but largely,

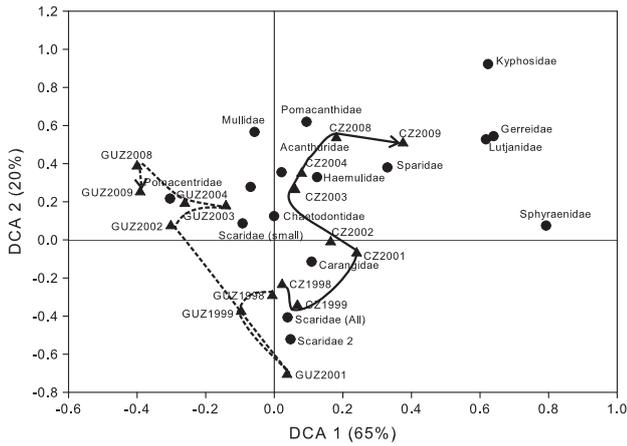


Figure 8. Changes in fish families in the Conservation and General Use zones from 1998 and 2009 based on a detrended correspondence analysis (DCA). Solid and dashed lines show temporal change of the General Use (GUZ) and Conservation zones (CZ), respectively.

global-level changes associated with some combination of warming sea water, increased disease, declining consumers and herbivores, and strong oceanographic oscillations (McClanahan, 2002; Schutte *et al.*, 2010). Fisheries closures have the potential for improved management and resilience to climate disturbances but empirical tests at the appropriate scale and against

alternative hypotheses are needed before the recommendation can be broadly supported (Mumby and Harborne, 2010).

The results presented here are only weakly supportive of some links in the trophic cascade hypothesis and not supportive of others, at this 14-year time and 70 km² closure scale of study. The closure, for example, does produce an increase in the numbers of some groups of fish reduced by fishing and this weakly increases some of the ecological processes of predation on sea urchins and herbivory, based on the assay results. The effect on the benthos is, however, not evident and the hard coral cover declines in the Conservation zone were largely driven by the 1998 ENSO warm water, bleaching, and coral mortality. Despite somewhat higher predation on the seagrass assay in the Conservation zone, there was also a notably small increase in large herbivores. The larger effect was a switching of herbivore dominance over time in the two management areas, where the General Use zone experienced an increase in sea urchins and damselfish and the Conservation zone had slightly more large herbivorous surgeonfish (and possibly chub and damselfish) over time. Overall, differences were not large, there was no evidence of a continuous increase, and many abundance patterns were unchanged over many years. The main responses to the closures were among the piscivores (jacks, barracuda, and groupers) and generalized consumers of invertebrates and carnivores (snappers, grunts, and porgies). The further down the food web from these top consumers, the less the response.

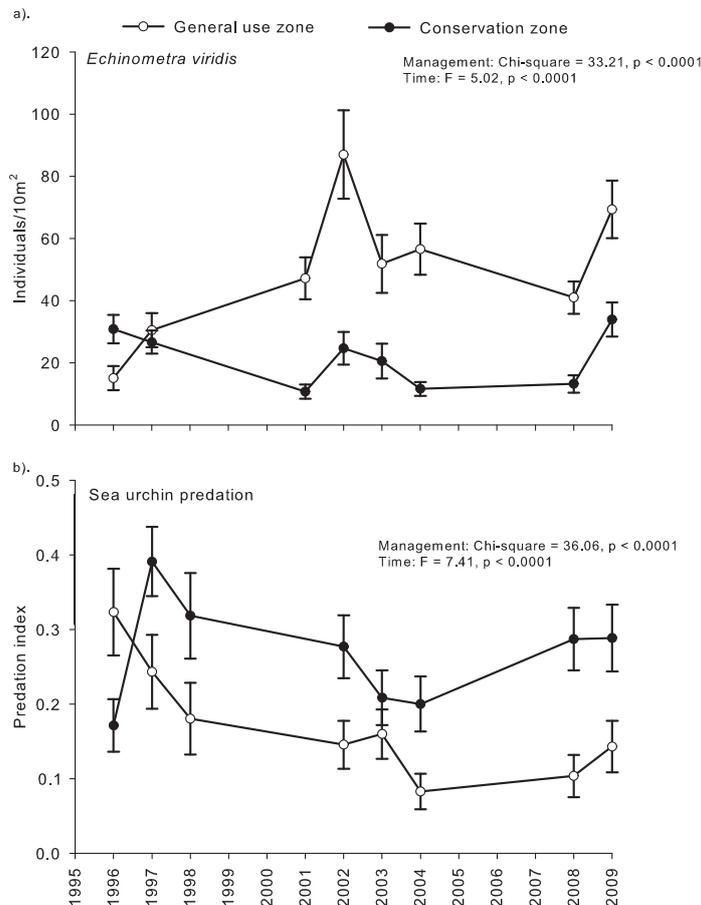


Figure 9. Changes (mean ± SEM) in (a) the abundance and (b) predation rates on the sea urchin *Echinometra viridis* in the Conservation and General Use zones between 1996 and 2009.

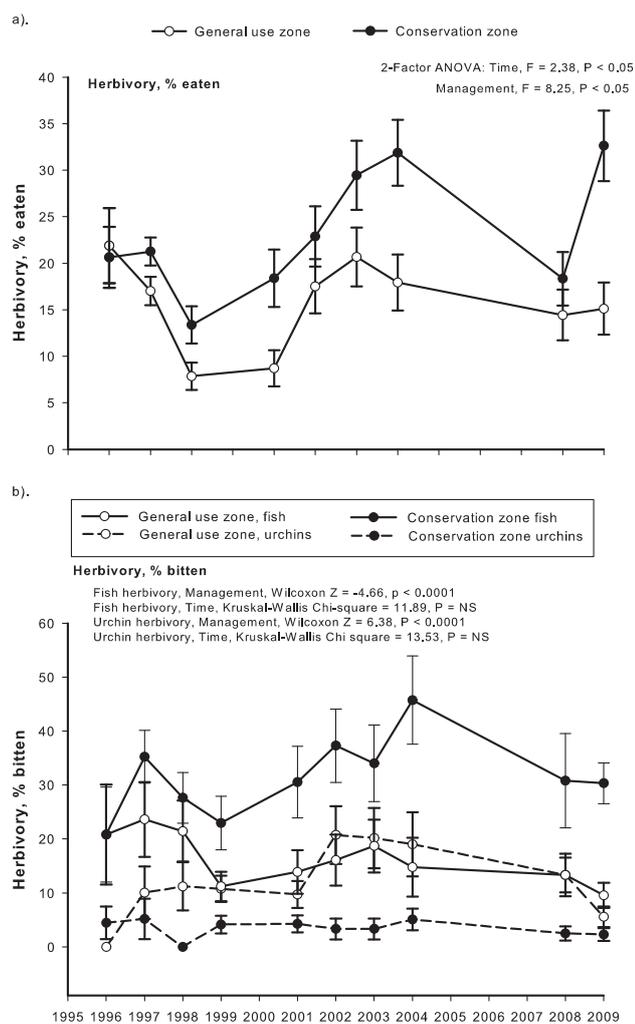


Figure 10. Patterns of herbivory (mean \pm SEM) on *Thalassia testudinum* assays soaked for 24 h in the patch reefs of the Conservation and General Use zones between 1997 and 2009. (a) The proportion of seagrass eaten and (b) percentage of bites attributable to sea urchins or fish based on bite scar characteristics.

The lack of support for the management hypothesis can be attributed to a number of issues: these include: (1) a poor or overly simplified view of fishing effects, the food web, and cascade response; (2) attenuation of the cascade effect towards the lower trophic levels due to food web complexity; (3) insufficient compliance, closure time, and space; (4) an ecological hysteresis or irreversibility effect caused by the establishment of the closure after rather than before critical levels of the fishing and environmental disturbances; (5) patch reef habitat or Glover's Atoll site specificity; and (6) overriding environmental disturbances, such as oceanographic oscillations and a warming climate. It is likely that all of these factors contributed to the weak support for the cascade model, as the hypotheses are not mutually exclusive, can interact, and fully represent the ecological complexity that influences ecosystems and any large-scale management experiments. These factors and the evidence for and against these alternatives are briefly discussed below.

The expectation that closures should increase herbivores is reasonable given that parrotfish are the major take in the open-access fishery of the north end of the atoll and there is

generally a positive relationship between the response of fish to closures and their exploitation rates (Guarderas *et al.*, 2011). Parrotfish response to closure was, however, difficult to detect and the larger recovery responses were among the groups with lower CPUE, including various piscivores and micro- and macro-invertivores. The largest relative response was among the piscivores, their numbers approximately quadrupling, most notably the barracuda and snappers. This observation raises the possibility that increases in piscivores are suppressing the recovery of herbivores and that these large herbivores may have intrinsically low population growth rates that respond very slowly to closures, particularly in the presence of barracuda and other predators. Evidence for control by piscivory was weak but could include the increase in damselfish in the General Use zone over time that might indicate their release from predators. Yet, there was also a smaller increase in damselfish numbers in the Conservation zone and careful studies of their populations find they are most affected by coral microhabitats (Precht *et al.*, 2010). Nevertheless, small parrotfish declined in all zones over time suggesting some larger-scale pattern influencing their numbers rather than piscivory. Consequently, piscivore control remains a viable alternative explanation but difficult to validate and tease apart from other explanations, such as reduced reproduction and recruitment, with the existing data.

The complexity of the food web and the existence of omnivory, parasitism, and braided feeding pathways may attenuate the full strength of the trophic cascade (Polis and Strong, 1996). There are, however, a number of examples of trophic cascades in marine ecosystems and coral reefs (Pinnegar *et al.*, 2000). Nevertheless, the multiple pathways and different susceptibilities to fishing and predation seldom produce cascades that predictably influence gross trophic levels determined by the number of levels in the food chain (Hairston and Hairston, 1997; Solomon *et al.*, 2010). Greater complexity in coral reef food webs is likely to cause the switches in dominance observed here, such that processes such as herbivory are potentially compensated for by other species or functional groups when one is reduced by fishing or predation. This has been shown, for example in East African reefs, where sea urchins play a key role in maintaining herbivory when their predators and herbivorous fishes are reduced through fishing (McClanahan *et al.*, 1999). A similar effect was observed here where damselfish and the sea urchin, *Echinometra viridis*, increased when their predator numbers were low and were partially able to compensate for the decline in the larger parrotfish.

Our measurements and biases in the herbivory assay do not allow us to quantify the potential compensation in herbivory by the different herbivore groups. Regardless, a key finding is that erect frondose and other algae did not change in the predicted direction in either of the management areas over the full length of this study. Therefore, it would seem that the potential top-down cascade was attenuated at the level of herbivores for at least 14 years. Changes, such as these, can however, have different quantitative and qualitative effects because, for example, low functional redundancy (Bellwood *et al.*, 2003) and the specific influences created by the compensating species can produce changes in community structure and associated processes, such as productivity and calcification (O'Leary and McClanahan, 2010). The species studied here are widespread and abundant in the Caribbean and, therefore, the patterns observed here are potentially common responses to fishing and closure management in the region. Site specificity and poor

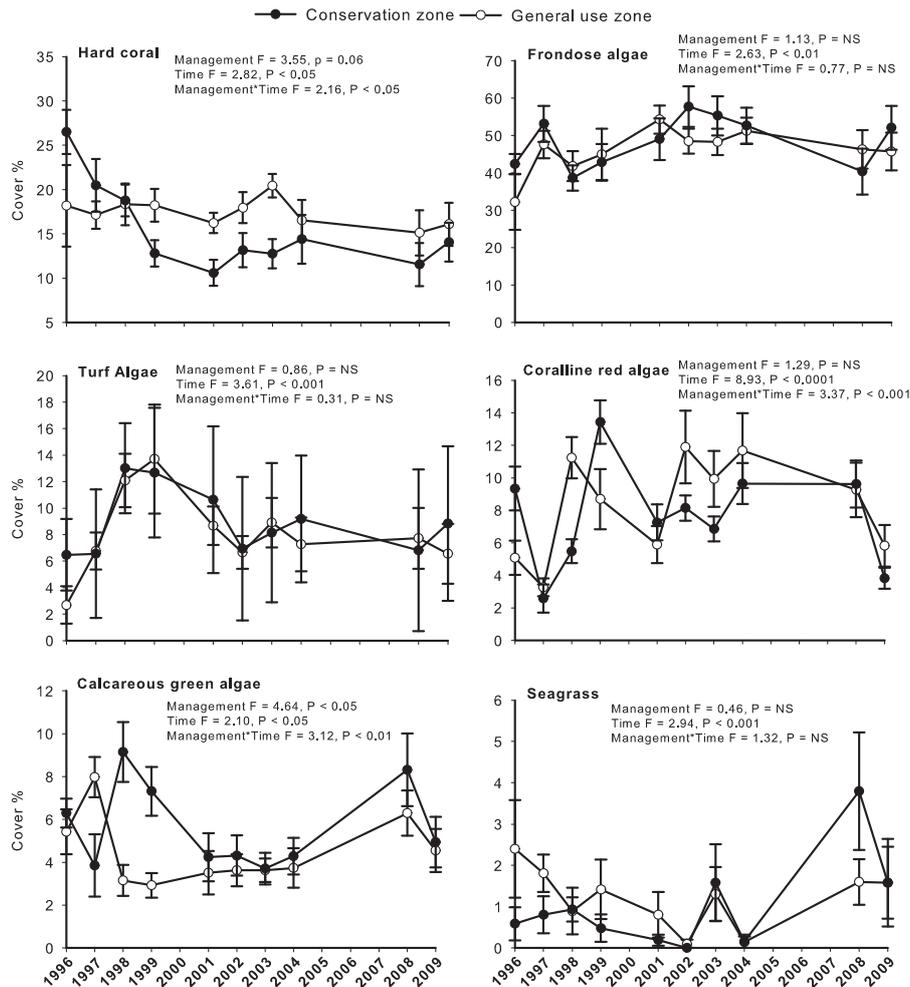


Figure 11. Gross benthic cover functional group changes (mean \pm SEM) in the Conservation and General Use zones between 1996 and 2009.

management compliance are, however, a common criticism of any case study that does not find support for a widely supported management intervention. Compliance is likely to have been reasonable as the fisheries department and conservation NGO that manage the closure are located on an island in the atoll. Perhaps, either movement of fish or fishers across boundaries may have influenced the poor response, but this is difficult to confirm. The isolated and offshore nature of this atoll, the single closure, and the evaluation of just the patch reef habitat can potentially increase the chances that results are site specific and reduce the generality of these findings. Nevertheless, despite some evidence for trophic cascades in Caribbean marine reserves (Guarderas *et al.*, 2011), there are a number of examples of fisheries closures and habitats in the Caribbean that have not behaved as predicted by the cascade model (Williams and Polunin, 2001; Aronson and Precht, 2006; Newman *et al.*, 2006; Coelho and Manfrino, 2007; Huntington *et al.*, 2010).

The age of the closures may be important if ecological hysteresis is a factor influencing recovery. The low numbers of older Caribbean closures make it difficult to be confident whether the proliferation of closures after the major disturbances in the Caribbean will have effects similar to older closures, or if the reported recovery is specific to a few unusual sites recognized for their conservation value many decades ago.

For example, Selig and Bruno (2010) found that the positive MPA effects in the Caribbean were found for closures with >14 years of protection. Further, one of the best and most successful old closures, Exuma Cays Land and Sea Park in the central Bahamas, found <2% increase in absolute coral cover over a 2.5 year period when macroalgal cover was <6%, while coral cover did not increase in any sites where macroalgal cover >6% (Mumby and Harborne, 2010). Given that the mean macroalgal cover in the Caribbean between 1996 and 2006 was reported as 23.6 ± 0.8 (SE, $n = 530$) (Bruno *et al.*, 2009) around 65% of Caribbean reefs would have macroalgal cover greater than this possible 6% threshold, a small number of these would be in closures, and an even smaller number in old closures. Further, this very small increase in coral cover occurred over a period after the 1998 ENSO (2004–2007), a period when no major climatic disturbances were reported at this site. Consequently, the evidence that fisheries closures promote recovery and resilience of corals to climate change in the Caribbean may be contingent on a number of factors, such as low initial macroalgal cover, closures established before disturbances, abundant parrotfish, and infrequent climate disturbances. Few of these factors are likely to simultaneously coincide or be widespread, which, if contingent on age, habitat, and initial benthic conditions (Huntington *et al.*, 2010), greatly reduces the generality and predictive strength of this management intervention.

Might the scale of disturbance from fishing, diseases, and coral bleaching in the Caribbean be so large that moderate sized and isolated closures lack the potential to recover? Perhaps even remote atolls, such as Glover's reef, cannot simulate the ecological conditions of large undisturbed seascapes that preceded the changes initiated after 1981 without decades of closure? The fact that sea surface temperatures in portions of the Caribbean were equally warm in the mid-20th century compared with the past decade (Barton and Casey, 2005) and large-scale ecological change was not reported until after 1981 (Schutte *et al.*, 2010) can be cited as evidence that large-scale water quality and resource use interact with rising temperature to degrade coral reef ecosystems (Jackson *et al.*, 2001; Pandolfi *et al.*, 2003; Carilli *et al.*, 2010). A series of diseases and the loss of fish consumers are likely to have been proximate causes of this transformation (Lessios *et al.*, 1984; Schutte *et al.*, 2010), but mass-mortality from diseases often reflects environmental conditions and, therefore, ultimate causes still remain unclear. Further, declines in the common moderate trophic level fishes, many of them un-fished, seemed to have followed rather than preceded the change (Paddock *et al.*, 2009). The loss of the apex predators, such as sharks may be important forces in promoting trophic cascades that encourage parrotfish through their reduction of groupers and other piscivores (Bascompte *et al.*, 2005; Chapman *et al.*, 2006) but this study was not a convincing case for a cascade effect from sharks to corals. Shark numbers have remained more widespread, abundant, and stable in Glover's reef than most Caribbean reefs (Chapman *et al.*, 2005; Pikitch *et al.*, unpublished data), grouper numbers have declined in Glover's reef associated with heavy fishing of their spawning site (Sala *et al.*, 2001), but groupers can also increase in the presence of sharks (Mumby *et al.*, 2006b).

Small and isolated closures and particularly patch reefs that are further isolated may be among the reef types least likely to recover quickly from closure management. In patch reefs, communities are often less uniform and less influenced by density-dependent ecological processes and possibly more influenced by topographic complexity, larval recruitment, stochasticity, and associated time lags (Ault and Johnson, 1998; McClanahan and Arthur, 2001; Huntington *et al.*, 2010). The fast recovery of generalist species, such as snappers and grunts, in this study indicates that these vagile and opportunistic species were the main beneficiaries under these conditions. They may, however, have a limited capacity to drive some of the key ecological processes that transform the benthic community. One result of our study that might forebode future change was the continual rise in numbers of species over this period, particularly in the Conservation zone, and the potential for more gains and possibly the ecological impacts of these recruiting species in the future.

Priority effects, hysteresis, and irreversibility are increasingly being recognized as important processes in ecology with implications for early detection, policy formation, and management needs (Beisner *et al.*, 2003; Biggs *et al.*, 2009). There is recognition of multiple stable states in coral reefs (McClanahan *et al.*, 2002; Nystrom *et al.*, 2008; Mumby, 2009b; Hughes *et al.*, 2010) but the reversibility or irreversibility of these states has only recently been explored (Dudgeon *et al.*, 2010). Early evaluations suggest that reversing states is not a simple process and may depend on both successfully reducing the causative stressors and having functional groups that play key roles in reversing the change (McClanahan *et al.*, 1996; Bellwood

et al., 2006). For example, it has been determined that despite the considerable diversity of herbivorous coral reef fish, many will not eat late-succession algae and reverse a shift back to corals (McClanahan *et al.*, 1999, 2001; Bellwood *et al.*, 2006). Thus, many species may be responsible for preventing the shift to erect algal dominance, but few can reverse the condition (Bellwood *et al.*, 2006; Hoey and Bellwood, 2009). This has important implications for the management of fisheries closures in that encouraging key species is required to promote reversibility and not just the reduction of the fishing stress. These key regime-shift reversing species have not been identified in the Caribbean but might include chubs, for example, or possibly species of parrotfish that are dependent on mangroves, which were not abundant at Glover's reef (Mumby *et al.*, 2004). Clearly, this is a key area for future investigation with application to reef restoration.

Physico-chemical environmental controls observed after the warm water generated by 1998 ENSO promoted bleaching and subsequent coral diseases and death in Belize (McField, 2002) and other Caribbean reefs (Baker *et al.*, 2008). This had the largest net impact on the Conservation zone in the present study, which started with higher and ended with coral cover similar to the General Use zone over the course of this study. There were not large or noticeable differences in the physico-chemical environments in the two management systems and the Conservation zone may have originally contained more *Montastraea* and the General Use zone more *Acropora* coral cover, with both zones having ~90% hard coral cover in the early 1970s (Wallace, 1975). *Acropora* cover probably declined in the 1980s along with most of the Caribbean *Acropora* (Schutte *et al.*, 2010) while the observed decline in the *Montastraea* zone was probably the tail end of a slower decline of this more robust genus (Edmunds and Elahi, 2007). The decline in corals after 1998 and the lack of recovery in the Conservation zone suggest physico-chemical climate forces and past histories of diseases were the strongest factors influencing hard corals in this study. Erect algae colonized the dead surfaces and herbivores have not been able to reverse the decline of hard coral (Aronson and Precht, 2006).

This study addressed the highly visible issues of the interaction between climate, fishing, and fisheries closures through a 14 year case study in a remote but fished coral reef of the large Central American Barrier Reef System (West and Salm, 2003; Bellwood *et al.*, 2004; Hughes *et al.*, 2010). The ability of fisheries closures to increase herbivory and reverse the degradation of patch reefs on appropriately large temporal and spatial scales was tested in a remote offshore area. The impact of fishing parrotfish was present, and confounding human influences, such as anthropogenic eutrophication, were minimal. The support for the fishing control of parrotfish and cascading effect on erect algae was weak and more suggestive of piscivore control or repulsion of parrotfish by unpalatable algae, but all of these forces may have influenced the response. Larger and longer studies may find support for the hypothesis, but the changes were slow and some variables lacked any detectable inter-annual changes towards the predicted outcome. These results are unexpected and suggest a need for evaluating more management systems, more contingencies, and to reevaluate the fisheries management objectives and actions that will promote coral reef resilience to climate change and ecosystem sustainability. This study indicates the complexity of closures and the limits of their ability to resist climate change. Management that focuses on the broad scale

restrictions of species important for resisting or reversing phase shifts, such as the 2009 Belizean law to outlaw the take of parrotfish, may have more efficacy than closures alone.

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REFERENCES

- Acosta CA. 1999. Benthic dispersal of Caribbean spiny lobsters among insular habitats: implication for the conservation of exploited marine species. *Conservation Biology* **13**: 603–612.
- Alvarez-Filip L, Dulvy NK, Gill JA, Cote IM, Watkinson AR. 2009. Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proceedings of the Royal Society of London B* **276**: 3019–3025.
- Andréfouët S, Mumby PJ, McField M, Hu C, Muller-Karger FE. 2002. Revisiting coral reef connectivity. *Coral Reefs* **21**: 43–48.
- Anzai R. 2001. The effects of coral morphology and water flow rates on coral growth and passive diffusion. MSc thesis, University of Ryukyus, Japan.
- Aronson RB, Bruno JF, Precht WF, Glynn PW, Harvell CD, Kaufman L, Rogers CS, Shinn EA, Valentine JF. 2003. Causes of coral reef degradation. *Science* **302**: 1502–1503.
- Aronson RB, Macintyre IG, Lewis SA, Hilbun NL. 2005. Emergent zonation and geographic convergence of coral reefs. *Ecology* **86**: 2586–2600.
- Aronson RB, Precht WF. 2006. Conservation, precaution, and Caribbean reefs. *Coral Reefs* **25**: 441–450.
- Ault TR, Johnson CR. 1998. Spatially and temporally predictable fish communities on coral reefs. *Ecological Monographs* **68**: 25–50.
- Baker AC, Glynn PW, Riegl B. 2008. Climate change and coral reef bleaching: an ecological assessment of long-term impacts, recovery trends and future outlook. *Estuarine Coastal and Shelf Science* **80**: 435–471.
- Barton AD, Casey KS. 2005. Climatological context for large-scale coral bleaching. *Coral Reefs* **24**: 536–554.
- Bascompte J, Melian C, Sala E. 2005. Interaction strength combinations and the overfishing of a marine food web. *Proceedings of the National Academy of Sciences USA* **102**: 5443–5447.
- Baskett ML. 2006. Prey size refugia and trophic cascades in marine reserves. *Marine Ecology Progress Series* **328**: 285–293.
- Beisner BE, Haydon DT, Cuddington K. 2003. Alternative stable states in ecology. *Frontiers in Ecology and the Environment* **1**: 376–382.
- Bellwood D, Hoey S, Choat JH. 2003. Limited functional redundancy in high diversity systems: resilience and ecosystem function on coral reefs. *Ecology Letters* **6**: 281–285.
- Bellwood DR, Hughes TP, Folke C, Nystrom M. 2004. Confronting the coral reef crisis. *Nature* **429**: 827–832.
- Bellwood DR, Hughes RH, Hoey AS. 2006. Sleeping functional group drives coral-reef recovery. *Current Biology* **16**: 2434–2439.
- Biggs R, Carpenter SR, Brock WA. 2009. Turning back from the brink: detecting an impending regime shift in time to avert it. *Proceedings of the National Academy of Sciences USA* **106**: 826–831.
- Bruno JF, Sweatman H, Precht WF, Selig ER, Schutte GW. 2009. Assessing evidence of phase shifts from coral to macroalgal dominance on coral reefs. *Ecology* **90**: 1478–1484.
- Burkpile DE, Hay ME. 2010. Impact of herbivore identity on algal succession and coral growth on a Caribbean reef. *PLoS One* **5**(1):e8963. doi:10.1371/journal.pone.0008963.
- Carilli JE, Norris RD, Black B, Walsh SM, McField M. 2010. Century-scale records of coral growth rates indicate that local stressors reduce coral thermal tolerance threshold. *Global Change Biology* **16**: 1247–1257.
- Carpenter RC. 1986. Partitioning herbivory and its effects on coral reef algal communities. *Ecological Monographs* **56**: 345–363.
- Carpenter RC. 1990. Mass mortality of *Diadema antillarum* I. Long-term effects on sea urchin population-dynamics and coral reef algal communities. *Marine Biology* **104**: 67–77.
- Chapman DD, Pikitch EK, Babcock E, Shiyji MS. 2005. Marine reserve design and evaluation using automated acoustic telemetry: a case-study involving coral reef-associated sharks in the Mesoamerican Caribbean. *Marine Technology Society Journal* **39**: 42–55.
- Chapman DDF, Pikitch EK, Babcock EA. 2006. Marine parks need sharks? *Science* **312**: 526–527.
- Cherubin LM, Kuchinke CP, Paris CB. 2008. Ocean circulation and terrestrial runoff dynamics in the Mesoamerican region from spectral optimization of SeaWiFS data and a high resolution simulation. *Coral Reefs* **27**: 503–519.
- Cinner JE, McClanahan TR, Graham NAJ, Pratchett MS, Wilson S. 2009. Gear-based fisheries management as a potential adaptive response to coral bleaching. *Journal of Applied Ecology* **46**: 724–732.
- Coelho V, Manfrino C. 2007. Coral community decline at a remote Caribbean island: marine no-take reserves are not enough. *Aquatic Conservation: Marine and Freshwater Ecosystems* **17**: 666–685.
- Connell JH. 1997. Disturbance and recovery of coral assemblages. *Coral Reefs* **16**: S101–S113.
- De Feo O, Rinaldi S. 1997. Yield and dynamics of tritrophic food chains. *The American Naturalist* **150**: 328–345.
- Diaz-Pulido G, McCook LJ. 2003. Relative roles of herbivory and nutrients in the recruitment of coral-reef seaweeds. *Ecology* **84**: 2026–2033.
- Doty MS. 1971. Measurement of water movement in reference to benthic algal growth. *Botanica Marina* **14**: 32–35.
- Dudgeon SR, Aronson RB, Bruno JF, Precht WF. 2010. Phase shifts and stable states on coral reefs. *Marine Ecology Progress Series* **413**: 201–206.
- Edmunds PJ, Carpenter RC. 2000. Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef. *Proceedings of the National Academy of Sciences USA* **98**: 5067–5071.
- Edmunds PJ, Elahi R. 2007. The demographics of a 15-year decline in cover of the Caribbean reef coral *Montastrea annularis*. *Ecological Monographs* **77**: 3–18.
- Fox RJ, Bellwood DR. 2008. Remote video bioassays reveal the potential feeding impact of rabbitfish *Siganus canaliculatus* (f. Siganidae) on an inner-shelf reef of the Great Barrier Reef. *Coral Reefs* **27**: 605–615.
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR. 2003. Long-term region-wide declines in Caribbean corals. *Science* **301**: 958–960.
- Greene LE, Alevizon WS. 1989. Comparative accuracies of visual assessment methods for coral reef fishes. *Bulletin of Marine Science* **44**: 899–912.

- Guarderas AP, Hacker SD, Lubchenco J. 2011. Ecological effects of marine reserves in Latin America and the Caribbean. *Marine Ecology Progress Series* **429**: 219–225.
- Hairston NG Jr, Hairston NG Sr. 1997. Does food web complexity eliminate trophic-level dynamics? *The American Naturalist* **149**: 1001–1007.
- Halpern BS, Warner RR. 2002. Marine reserves have rapid and lasting effects. *Ecology Letters* **5**: 361–366.
- Hay ME. 1981. Spatial patterns of grazing intensity on a Caribbean barrier reef: herbivory and algal distribution. *Aquatic Botany* **11**: 97–109.
- Hoey AS, Bellwood DR. 2009. Limited functional redundancy in a high diversity system: single species dominates key ecological process on coral reefs. *Ecosystems* **12**: 1316–1328.
- Hughes TP. 1994. Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* **265**: 1547–1551.
- Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JBC, Kleypas J, et al. 2003. Climate change, human impacts, and the resilience of coral reefs. *Science* **301**: 929–933.
- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltschanowsky N, Pratchett MS, Steneck RS, Willis B. 2007. Phase shifts, herbivory, and resilience of coral reefs to climate change. *Current Biology* **17**: 360–365.
- Hughes TP, Graham NAJ, Jackson JBC, Mumby PJ, Steneck RS. 2010. Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology & Evolution* **25**: 633–642.
- Humann P. 1993. *Reef Coral Identification: Florida, Caribbean and Bahamas*. New World Publications, INC: Jacksonville, FL.
- Huntington BE, Karnauskas M, Babcock EA, Lirman D. 2010. Untangling natural seascape variation from reserve effects using a landscape approach. *PLoS One* **5**: e12327. doi:10.1371/journal.pone.0012327.
- Huppert A, Stone L. 1998. Chaos in the Pacific's coral reef bleaching cycle. *The American Naturalist* **152**: 447–459.
- Idjadi JA, Lee SC, Bruno JF, Precht WF, Allen-Requa L, Edmunds PJ. 2006. Rapid phase shift reversal on a Jamaican coral reef. *Coral Reefs* **25**: 209–211.
- Jackson JBC, Kirby MX, Berger WA, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlanson J, Estes JA, et al. 2001. Historical overfishing and the recent collapse of coastal ecosystems. *Science* **293**: 629–638.
- Jompa J, McCook LJ. 2003. Coral-algal competition: macroalgae with different properties have different effects on corals. *Marine Ecology Progress Series* **258**: 87–95.
- Kramer PA. 2003. Synthesis of coral reef health indicators for the western Atlantic: results of the AGGRA program (1997–2000). *Atoll Research Bulletin* **496**: 1–58.
- Lapointe BE, Barile PJ, Yentsch CS, Littler MM, Littler DS, Kakuk B. 2004. The relative importance of nutrient enrichment and herbivory on macroalgal communities near Norman's Pond Cay, Exumas Cays, Bahamas: a 'natural' enrichment experiment. *Journal of Experimental Marine Biology and Ecology* **298**: 275–301.
- Lessios HA, Garrido MJ, Kessing BD. 2001. Demographic history of *Diadema antillarum*, a keystone herbivore on Caribbean reefs. *Proceedings of the Royal Society of London B* **268**: 1–7.
- Lessios HA, Robertson DR, Cubit J. 1984. Spread of *Diadema* mass mortality through the Caribbean. *Science* **226**: 335–337.
- Leviton DR. 1988. Algal-urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, U.S. Virgin Islands. *Journal of Experimental Marine Biology and Ecology* **119**: 167–178.
- Lewis SA. 1986. The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* **56**: 183–200.
- Lirman A, Fong P. 2007. Is proximity to land-based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. *Marine Pollution Bulletin* **54**: 779–791.
- Littler DS, Littler MM. 2000. *Caribbean Reef Plants*. Offshore Graphics, Inc: Washington D.C.
- Littler MM, Taylor PR, Littler DS. 1989. Complex interactions in the control of coral zonation on a Caribbean reef flat. *Oecologia* **80**: 331–340.
- Macia S, Robinson MP, Nalevanko A. 2007. Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a coral reef. *Marine Ecology Progress Series* **348**: 173–182.
- MacNeil MA. 2008. Making empirical progress in observational ecology. *Environmental Conservation* **35**: 193–196.
- McClanahan T, Polunin N, Done T. 2002. Ecological states and the resilience of coral reefs. *Conservation Ecology* **6**: 18. <http://www.consecol.org/vol6/iss2/art18/>
- McClanahan TR. 1999. Predation and the control of the sea urchin *Echinometra viridis* and fleshy algae in the patch reefs of Glovers Reef, Belize. *Ecosystems* **2**: 511–523.
- McClanahan TR. 2002. The near future of coral reefs. *Environmental Conservation* **29**: 460–483.
- McClanahan TR. 2008. Response of the coral reef benthos and herbivory to fishery closure management and the 1998 ENSO disturbance. *Oecologia* **155**: 169–177.
- McClanahan TR, Arthur R. 2001. The effect of marine reserves and habitat on populations of East African coral reef fishes. *Ecological Applications* **11**: 559–569.
- McClanahan TR, Muthiga NA. 1989. Patterns of predation on a sea urchin, *Echinometra mathaei* (de Blainville), on Kenyan coral reefs. *Journal of Experimental Marine Biology and Ecology* **126**: 77–94.
- McClanahan TR, Muthiga NA. 1998. An ecological shift in a remote coral atoll of Belize over 25 years. *Environmental Conservation* **25**: 122–130.
- McClanahan TR, Nugues M, Mwachireya S. 1994. Fish and sea urchin herbivory and competition in Kenyan coral reef lagoons: the role of reef management. *Journal of Experimental Marine Biology and Ecology* **184**: 237–254.
- McClanahan TR, Kamukuru AT, Muthiga NA, Yebio MG, Obura D. 1996. Effect of sea urchin reductions on algae, coral, and fish populations. *Conservation Biology* **10**: 136–154.
- McClanahan TR, Hendrick V, Rodrigues MJ, Polunin NVC. 1999. Varying responses of herbivorous and invertebrate-feeding fishes to macroalgal reduction on a coral reef. *Coral Reefs* **18**: 195–203.
- McClanahan TR, McField M, Huitric M, Bergman K, Sala E, Nystrom M, Nordemar I, Elfving T, Muthiga NA. 2001. Responses of algae, corals and fish to the reduction of macroalgae in fished and unfished patch reefs of Glovers Reef Atoll, Belize. *Coral Reefs* **19**: 367–379.
- McClanahan TR, Maina J, Starger CJ, Herron-Perez P, Dusek E. 2005. Detriments to post-bleaching recovery of corals. *Coral Reefs* **24**(2): 230–246.
- McClanahan TR, Graham NAJ, Calnan JM, MacNeil MA. 2007a. Toward pristine biomass: reef fish recovery in coral reef marine protected areas in Kenya. *Ecological Applications* **17**: 1055–1067.
- McClanahan TR, Ateweberhan M, Sebastian CR, Graham NAJ, Wilson SK, Guillaume MMM, Bruggemann JH. 2007b. Western Indian Ocean coral communities: bleaching responses and susceptibility to extinction. *Marine Ecology Progress Series* **337**: 1–13.
- McClanahan TR, Graham NAJ, Wilson SK, Letourneur Y, Fisher R. 2009. Effects of fisheries closure size, age, and history of compliance on coral reef fish communities in the western Indian Ocean. *Marine Ecology Progress Series* **396**: 99–109.
- McField MD. 2002. Influence of disturbance on coral reef community structure in Belize. *Proceedings of the Ninth International Coral Reef Symposium*, Bali. **1**: 63–68.

- Miller MW, Hay ME, Miller SL, Malone D, Sotka EE, Szmant AM. 1999. Effects of nutrients versus herbivores on reef algae: a new method for manipulating nutrients on coral reefs. *Limnology and Oceanography* **44**: 1847–1861.
- Mora C. 2008. A clear human footprint in the coral reefs of the Caribbean. *Proceedings of the Royal Society of London B* **275**: 767–773.
- Mumby PJ. 1999. Bleaching and hurricane disturbances to populations of coral recruits in Belize. *Marine Ecology Progress Series* **190**: 27–35.
- Mumby PJ. 2009a. Herbivory versus corallivory: are parrotfish good or bad for Caribbean coral reefs? *Coral Reefs* **28**: 683–690.
- Mumby PJ. 2009b. Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* **28**: 761–773.
- Mumby PJ, Harborne AR. 2010. Marine reserves enhance the recovery of corals on Caribbean reefs. *PloS One* **5**: 1–7.
- Mumby PJ, Edwards AJ, Arias-Gonzalez JE, Lindeman KC, Blackwell PG, Gall A, Gorczynska MI, Harborne AR, Pescod CL, Renken H, et al. 2004. Mangroves enhance the biomass of coral reef fish communities in the Caribbean. *Nature* **427**: 533–536.
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes J, Broad K, Sanchirico JN, et al. 2006a. Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* **311**: 98–101.
- Mumby PJ, Micheli F, Dahlgren CP, Litvin SY, Gill AB, Brumbaugh DR, Broad K, Sanchirico JN, Kappel CV, Harborne AR, Holmes KE. 2006b. Response [4]. *Science* **312**: 527–528.
- Mumby PJ, Harborne AR, Williams J, Kappel CV, Brumbaugh DR, Micheli F, Holmes KE, Dahlgren CP, Paris CB, Blackwell PG. 2007a. Trophic cascade facilitates coral recruitment in a marine reserve. *Proceedings of the National Academy of Sciences USA* **104**: 8362–8367.
- Mumby PJ, Hastings A, Edwards HJ. 2007b. Thresholds and the resilience of Caribbean coral reefs. *Nature* **450**: 98–101.
- Newman MJH, Paredes GA, Sala E, Jackson JBC. 2006. Structure of Caribbean coral reef communities across large gradient of fish biomass. *Ecology Letters* **9**: 1216–1227.
- Nystrom M, Graham NAJ, Lokrantz J, Norstrom AV. 2008. Capturing the cornerstones of coral reef resilience: linking theory to practice. *Coral Reefs* **27**: 795–809.
- O'Leary JK, McClanahan TR. 2010. Trophic cascades result in large-scale coralline algal loss through differential grazer effects. *Ecology* **91**: 3584–3597.
- Ostrander GK, Armstrong KM, Knobbe ET, Gerace D, Scully EP. 2000. Rapid transition in the structure of a coral reef community: the effects of coral bleaching and physical disturbance. *Ecology* **97**: 5297–5302.
- Paddack MJ, Reynolds JD, Aguilar C, Appeldoorn RS, Beets J, Burkett EW, Chittaro PM, Clarke K, Esteves R, Fonseca AC, et al. 2009. Recent region-wide declines in Caribbean reef fish abundance. *Current Biology* **19**: 590–595.
- Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJH, Paredes G, et al. 2003. Global trajectories of the long-term decline of coral reef ecosystems. *Science* **301**: 955–958.
- Pandolfi JM, Jackson JBC, Baron N, Bradbury RH, Guzman HM, Hughes TP, Kappel CV, Micheli F, Ogden JC, Possingham HP, Sala E. 2005. Are U.S. coral reefs on the slippery slope to slime? *Science* **307**: 1725–1726.
- Petraitis PS, Dudgeon SR. 2004. Detection of alternative stable states in marine communities. *Journal of Experimental Marine Biology and Ecology* **300**: 343–371.
- Pinnegar JK, Polunin NVC, Francour P, Badalamenti F, Chemello R, Harmelin-vivien ML, Hereu B, Milazzo M, Zabala M, D'anna G, Pipitone C. 2000. Trophic cascades in benthic marine ecosystems: lessons for fisheries and protected-area management. *Environmental Conservation* **27**: 179–200.
- Polis GA, Strong DR. 1996. Food web complexity and community dynamics. *The American Naturalist* **147**: 813–846.
- Pollnac R, Christie P, Cinner JE, Dalton T, Daw TM, Forrester GE, Graham NAJ, McClanahan TR. 2010. Marine reserves as linked social-ecological systems. *Proceedings of the National Academy of Sciences USA* **107**: 18262–18265.
- Precht WF, Aronson RB, Moody RM, Kaufman L. 2010. Changing patterns of microhabitat utilization by the three spot damselfish, *Stegastes planifrons*, on Caribbean reefs. *PloS One* **5**(5): e10835. doi:10.1371/journal.pone.0010835
- Randall JE. 1967. Food habits of reef fishes of the West Indies. *Studies in Tropical Oceanography* **5**: 665–847.
- Robertson DR, Choat JH, Posada JM, Pitt J, Ackerman JL. 2005. Ocean surgeonfish *Acanthurus bahianus*. II. Fishing effects on longevity, size and abundance? *Marine Ecology Progress Series* **295**: 245–256.
- Rotjan RD, Dimond JL, Thornhill DJ, Leichter JJ, Helmuth B, Kemp DW, Lewis SM. 2006. Chronic parrotfish grazing impedes coral recovery after bleaching. *Coral Reefs* **25**: 361–368.
- Rotjan RD, Lewis SM. 2008. Impact of coral predators on tropical reefs. *Marine Ecology Progress Series* **367**: 73–91.
- Russ GR, Alcala AC. 2004. Marine reserves: long-term protection is required for full recover of predatory fish populations. *Oecologia* **138**: 622–627.
- Russ GR, Stockwell B, Alcala AC. 2005. Inferring versus measuring rates of recovery in no-take marine reserves. *Marine Ecology Progress Series* **292**: 1–12.
- Sala E, Ballesteros E, Starr RM. 2001. Rapid decline of Nassau Grouper spawning aggregations in Belize: fishery management and conservation needs. *Fisheries* **26**: 23–30.
- Schutte V, Selig E, Bruno J. 2010. Regional spatio-temporal trends in Caribbean coral reef benthic communities. *Marine Ecology Progress Series* **402**: 115–122.
- Selig ER, Bruno JF. 2010. A global analysis of the effectiveness of marine protected areas in preventing coral loss. *PloS One* **5**: e9278.
- Shulman MJ, Robertson DR. 1996. Changes in the coral reef of San Blas, Caribbean Panama: 1983 to 1990. *Coral Reefs* **15**: 231–236.
- Smith JE, Smith CE, Hunter CL. 2001. An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* **19**: 332–342.
- Solomon AK, Gaichas SK, Shears NT, Smith JE, Madin EMP, Gaines SD. 2010. Key features and context-dependence of fishery-induced trophic cascades. *Conservation Biology* **24**: 382–394.
- Sotka EE, Hay ME. 2009. Effects of herbivores, nutrient enrichment, and their interactions on macroalgal proliferation and coral growth. *Coral Reefs* **28**: 555–568.
- Stewart-Oaten A. 2008. Chance and randomness in design versus model-based approaches to impact assessment: comments on Bulleri et al. (2007). *Environmental Conservation* **35**: 8–10.
- Thacker RW, Ginsburg DW, Paul VJ. 2001. Effects of herbivore exclusion and nutrient enrichment on coral reef macroalgae and cyanobacteria. *Coral Reefs* **19**: 318–329.
- Wallace RJ. 1975. A reconnaissance of the sedimentology and ecology of Glovers Reef Atoll, Belize (British Honduras). PhD thesis, Princeton, NJ, USA.
- West JM, Salm RV. 2003. Resistance and resilience to coral bleaching: implications for coral reef conservation and management. *Conservation Biology* **17**: 956–967.
- Williams ID, Polunin NVC. 2001. Large-scale associations between macroalgal cover and grazer biomass on mid-depth reefs in the Caribbean. *Coral Reefs* **19**: 358–366.
- Williams ID, Polunin VC, Hendrick VJ. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* **222**: 187–196.

**APPENDIX: GLOVER'S FISH SPECIES
TAXONOMICAL AND TROPHIC
GROUP CLASSIFICATIONS**

Family	Species	Trophic category	Common name
Acanthuridae	<i>Acanthurus bahianus</i>	Large herbivores	Ocean surgeonfish
	<i>Acanthurus chirurgus</i>	Large herbivores	Doctorfish
	<i>Acanthurus coeruleus</i>	Large herbivores	Blue tang
Aulostomidae	<i>Aulostomus maculatus</i>	Piscivores	Trumpetfish
Balistidae	<i>Balistes vetula</i>	Macroinverteviores	Queen triggerfish
	<i>Canthidermis sufflamen</i>	Macroinverteviores	Ocean triggerfish
Carangidae	<i>Caranx</i>	Piscivores	Yellow jack
	<i>bartholomaei</i>		
	<i>Caranx ruber</i>	Piscivores	Bar jack
Chaetodontidae	<i>Chaetodon capistratus</i>	Microinverteviores	Foureye butterflyfish
	<i>Chaetodon ocellatus</i>	Microinverteviores	Spotfin butterflyfish
	<i>Chetodon striatus</i>	Microinverteviores	Banded butterflyfish
Diodontidae	<i>Diodon hystrix</i>	Macroinverteviores	Porcupinefish
Fistularidae	<i>Fistularia tabacaria</i>	Piscivores	Blue-spotted cornetfish
Gerreidae	<i>Gerrus</i> spp	Microinverteviores	Mojarra
Haemulidae	<i>Haemulon album</i>	Microinverteviores	White margate
	<i>Haemulon aurolineatum</i>	Microinverteviores	Tomtate
	<i>Haemulon flavolineatum</i>	Microinverteviores	French grunt
	<i>Haemulon plumieri</i>	Microinverteviores	White grunt
	<i>Haemulon sciurus</i>	Microinverteviores	Blue-striped grunt
	Juv. grunts	Microinverteviores	Juvenile grunts
Kyphosidae	<i>Kyphosus sectatrix</i>	Large herbivores	Chub
Labridae	<i>Bodianus rufus</i>	Macroinverteviores	Spanish hogfish
	<i>Clepticus parrae</i>	Microinverteviores	Creole wrasse
	<i>Halichoeres bivittatus</i>	Microinverteviores	Slippery dick
	<i>Halichoeres garnoti</i>	Microinverteviores	Yellowhead wrasse
	<i>Halichoeres pictus</i>	Microinverteviores	Rainbow wrasse
	<i>Halichoeres radiatus</i>	Macroinverteviores	Puddingwife
	<i>Lachnolaimus maximus</i>	Macroinverteviores	Hogfish

(Continues)

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Family	Species	Trophic category	Common name
	<i>Thalassoma bifasciatum</i>	Microinverteviores	Bluehead wrasse
Lutjanidae	<i>Lutjanus analis</i>	Microinverteviores	Mutton snapper
	<i>Lutjanus apodus</i>	Microinverteviores	Schoolmaster
	<i>Lutjanus griseus</i>	Microinverteviores	Grey snapper
	<i>Lutjanus synagris</i>	Microinverteviores	Lane snapper
Lutjanidae	<i>Ocyurus chrysurus</i>	Microinverteviores/ piscivores	Yellowtail snapper
Mullidae	<i>Mulloidichthys martinicus</i>	Microinverteviores	Yellow goatfish
	<i>Pseudupeneus maculatus</i>	Microinverteviores	Spotted goatfish
Pomacanthidae	<i>Holocanthus ciliaris</i>	Sponge eaters	Queen angelfish
	<i>Holocanthus tricolor</i>	Sponge eaters	Rock beauty
	<i>Pomacanthus arcuatus</i>	Sponge eaters	Gray angelfish
	<i>Pomacanthus paru</i>	Sponge eaters	French angelfish
Pomacentridae	<i>Chromis cyanea</i>	Microinverteviores	Blue chromis
	<i>Stegastes</i> spp.	Small herbivores	Brown Dames/ Damsel fish
Scaridae	<i>Scarus coelestinus</i>	Large herbivores	Midnight parrotfish
	<i>Scarus croicensis</i>	Small herbivores	Striped parrotfish
	<i>Sparisoma aurofrenatum</i>	Large herbivores	Redband parrotfish
	<i>Sparisoma rubripinne</i>	Large herbivores	Redfin parrot
	<i>Sparisoma viride</i>	Large herbivores	Spotlight parrotfish
Serranidae	<i>Epinephelus cruentatus</i>	Piscivores	Graysby
	<i>Epinephelus fulvus</i>	Piscivores	Coney
	<i>Epinephelus striatus</i>	Piscivores	Nassau grouper
	<i>Mycteroperca bonaci</i>	Piscivores	Black grouper
	<i>Mycteroperca interstitialis</i>	Piscivores	Yellowmouth grouper
Sparidae	<i>Calamus bajorado</i>	Macroinverteviores	Jolthead porgy
Sphyracnidae	<i>Sphyracna barracuda</i>	Piscivores	Great barracuda
Synodontidae	<i>Synodus intermedius</i>	Piscivores	Sand diver