



# Change in fish and benthic communities in Belizean patch reefs in and outside of a marine reserve, across a parrotfish capture ban

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**ABSTRACT:** The role of a marine reserve and fisheries regulations in restoring fish populations on reefs disturbed by climate impacts was evaluated. Eight patch reefs, divided equally between no-fishing and fished zones in the remote Glover's Reef atoll lagoon, were studied for 22 yr: 13 yr before and 9 yr after a ban on parrotfish capture. Findings indicate that the main effect of the fisheries closure was the recovery of targeted carnivorous species, notably snappers, jacks, and groupers. Recovery continued for most of the time series, including the later period when parrotfish capture was banned. Parrotfish abundance slowly declined in both management zones and across the ban period. The loss occurred for both small non-fished species, such as the striped parrotfish *Scarus iserti*, and for larger fished species, such as the stoplight *Sparisoma viride* and red-band parrotfish *Sparisoma aurofrenatum*. Consequently, parrotfish abundance appeared to be controlled by the ecology of these patch reefs rather than fishing mortality. We suggest that the high and persistent cover of late-successional algae reduces the renewal rates of algae, which had negative consequences for all studied parrotfish populations. Low ocean currents and physical energy in the lagoon appeared to promote algal persistence. Thus, parrotfish bans may be more effective in promoting reef recovery in environments that promote rapid algal turnover. Fisheries regulations are unlikely to rapidly restore hard corals on these patch reefs, which have slowly transitioned to algal dominance since first described in 1970.

**KEY WORDS:** Herbivory · Marine reserves · Species restrictions · BACI design · Climate change · Caribbean

## 1. INTRODUCTION

Reef ecosystems in the Caribbean are experiencing multiple human and natural disturbances that are causing major basin-wide changes in their ecology and threatening their existence (Muñiz-Castillo et al. 2019, Siegel et al. 2019). Many Caribbean reefs are now dominated by fleshy or frondose brown algae that is causing reductions in hard coral and declines in calcium carbonate deposition (Roff & Mumby 2012, Bruno et al. 2014, Perry et al. 2015, Suchley et al. 2016, Preeht et al. 2019). These gross changes are also associated with changing community composition, as taxa with competitive life histories are replaced by opportunistic and stress resistant taxa

(Edmunds et al. 2014, Darling et al. 2019). These changes pose a major threat to coral reef health and persistence. Causes of the changes are controversial but include factors such as disease, bleaching, the loss of fish and sea urchin grazers, increased nutrients and sediments, and warm-water disturbances (W. F. Preeht et al. unpubl.). A major question for reef ecology and fisheries management is how changes differ within no-fishing and fishing zones over time (Newman et al. 2006, McClanahan et al. 2011a,b, Toth et al. 2014, Cox et al. 2017, Tewfik et al. 2017, Suchley & Alvarez-Filip 2018) and the subsequent effects on target species, their prey and ecological processes (Mumby 2009, Babcock et al. 2013, Steeneck et al. 2018).

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Various disturbances including thermal stress, disease, and human coastal development are killing hard corals (Eakin et al. 2010, Suchley & Alvarez-Filip 2018). The space opened by their death is subsequently colonized by various algae and soft corals, which are modified by predation and nutrification (McClanahan et al. 2002, Rasher et al. 2012, Pawlik et al. 2016). Some of these colonizing algae may be non-preferred or unpalatable and therefore repel some herbivorous fishes (McClanahan et al. 2000, Adam et al. 2018, Smith et al. 2018). The consequences of the change to algal-dominated reefs include reduced recruitment of corals, reduced abundance of herbivorous fishes and a reduction in their rates of herbivory, reduced abundance of coral-eating fishes, and variable responses among predators of invertebrates (Adam et al. 2015). Changes appear to be persistent, such that many stony coral populations show limited recovery after disturbance (Cox et al. 2017). Some investigators attribute this lack of recovery to chronic local disturbances, with little abatement; others suggest basin-wide thermal and nutrient problems have accelerated beyond a mitigating threshold, thus tilting the coral–algae imbalance in favor of various algae (Pawlik et al. 2016, De Bakker et al. 2017). This shift to algal dominance is widespread and jeopardizes the healthy functioning and growth of Caribbean reefs (Perry et al. 2015).

Fisheries investigators and managers in Belize have been actively addressing these problems through the establishment of monitoring and management via marine reserves and fisheries regulations intended to abate the decline (Cox et al. 2013, 2017). In the face of reef health decline, and dominance of algae, a ban on parrotfish capture was initiated by law and in practice by the Belize Fisheries Department in 2009 (Government of Belize 2009). Thus, our small-scale monitoring system of patch reefs in and outside of Glover's Reef Marine Reserve can evaluate the outcome of these restrictions (McClanahan et al. 2011a). Monitoring began in 1996, shortly after the establishment of the no-take marine reserve. This study, therefore, investigates ecological responses to the dual and interactive role of no-take marine reserves and the 2009 ban on parrotfish capture.

Banning the capture of parrotfish could promote herbivory, lower algal abundance, and increase hard coral, particularly outside of marine reserves (Bozec et al. 2016, Steneck et al. 2018). However, some empirical studies suggest that coral–algal changes in Belizean and Mesoamerican marine reserves have been small or undetectable and not clearly driven by herbivory (McClanahan et al. 2011a, Cox et al. 2017,

Suchley et al. 2016, Suchley & Alvarez-Filip 2018). For example, reefs dominated by *Acropora* spp. in the 1970s but subsequently impacted by disease and bleaching turned into coral rubble colonized by algae and small colonies of *Porites* spp. with no measurable effects on fish abundance (McClanahan & Muthiga 1998, Huntington et al. 2010). Conversely, a number of targeted fish populations increased in higher complexity patch reefs dominated by *Orbicella* spp. (McClanahan et al. 2011a). Thus, management outcomes are likely to vary with reef habitat.

Our study is restricted to repeat surveys of 8 *Orbicella* spp.-dominated patch reefs divided equally between a well-enforced, nationally-designated no-take marine reserve and a restricted-fishing zone. Our study is an effort to determine the effects of the parrotfish ban by examining the outcomes in a Before-After-Control-Impact (BACI) design where surveys were undertaken in the 13 yr before and the 9 yr after the ban. We asked if the trophic cascade model of reduced fishing mortality and recovery of parrotfish would increase herbivory, turf and calcifying algae, and hard coral, while decreasing erect frondose algae (Bellwood et al. 2004). The specific hypotheses tested were whether the fisheries closure and the ban on parrotfish capture promoted (1) an increase in parrotfish, (2) an increase in rates of herbivory, (3) an increase in calcifying and turf algae, and hard coral accompanied by a decrease in erect frondose algae, and (4) a change in fishing effort that decreases the abundance of less targeted fish species. These responses were predicted to occur shortly after the 2009 parrotfish ban and to be greater in fished than unfished reefs.

## 2. MATERIALS AND METHODS

### 2.1. Study sites

Glover's Reef (16°44'N, 87°48'W) is the most southerly of 3 Belizean atolls and is located offshore approximately 15 km east of the barrier reef (Fig. 1). The atoll covers 13 200 ha and has 6 sandy cays linked by an emergent windward reef crest. The reef crest is broken by 3 windward tidal channels, where water flows between the lagoon and open sea. The lagoon contains ~850 patch reefs of variable sizes and the study was undertaken in similarly sized reefs (~1000 m<sup>2</sup>), with shallow tops (1–2 m) that have been monitored since 1996 (McClanahan et al. 2001, 2011a). The outer edge of the atoll drops to >500 m in depth less than a kilometer from the crest, while the central lagoon

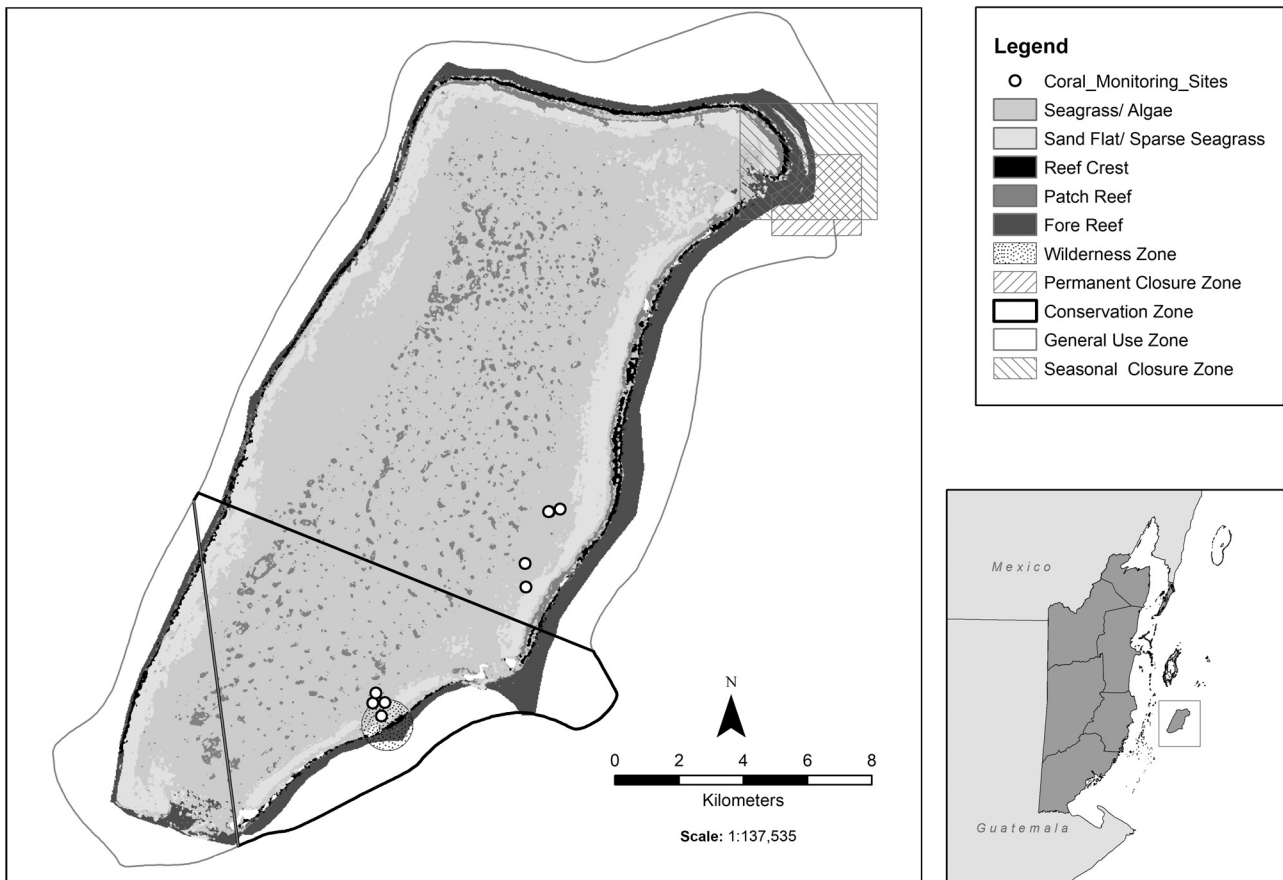


Fig. 1. Study sites in Glover's Reef atoll lagoon, Belize

depth seldom exceeds 20 m. The currents in the atoll are relatively weak and controlled by local wind and tidal forces (~0.18 m spring tidal range) especially in the southern portion of the atoll (McClanahan & Karnauskas 2011). Sea surface temperatures and nutrients measured in previous studies showed no significant differences between managed areas (McClanahan et al. 2011a). A number of seasonal thermal stresses, resultant coral bleaching, and also diseases occurred during the 1996–2018 study period, with notable thermal anomalies in 2005, 2010, and 2016 (Muñiz-Castillo et al. 2019). Despite the thermal stresses, fish populations increased and other ecological processes changed in the studied patch reefs inside the marine reserve, while fewer changes were observed outside (McClanahan et al. 2011a).

The southern end of the atoll was legally gazetted as a no-take marine reserve of 70.8 km<sup>2</sup> in 1993 and enforcement was initiated by 1995 when a field station was built on Middle Cay island, shortly before the first data in this study were collected. The southern quarter of the atoll is legally referred to as the Conservation Zone (CZ), where fishing is prohibited,

and the northern  $\frac{3}{4}$  is the General Use Zone (GUZ), where spear fishing is the dominant form of fishing (McClanahan et al. 2011a). Management rules are enforced by the Belize Fisheries Department patrol unit permanently based at Middle Cay adjacent to the CZ. Eight patch reefs were sampled during each sampling period, of which half were inside and half outside the CZ (Fig. 1).

## 2.2. Benthic cover and algal biomass

Benthic cover on each patch reef was assessed by the line intercept method for three 10 m line transects per reef. Transects were laid parallel to the patch reef's windward northeast edge at 3 locations: on the edge (the transition from the sand to patch reef), at the shoulder (shallow windward edge), and at the center. Substrate cover was recorded by species for stony corals, by genus for fleshy and calcareous algae, and by gross functional groups for encrusting coralline algae, branching coralline algae, algal turf, seagrass, sand, sponge, soft coral, zooanthids, and

microalgae (cyanobacteria and diatoms). All benthic organisms 3 cm or larger directly under the draped line were measured and recorded.

### 2.3. Fish population estimates

Visual counts were carried out using the Discrete Group Sampling (DGS) method, where a limited number of species are sampled during a single sampling period. The shallowness and small size of patch reefs did not permit the use of standard belt transects; therefore, 5 min search intervals or roving methods were used to sample fish. Roving methods have been shown to be efficient and increase the detection of species relative to belt transects (Beck et al. 2014). During the 35 min sampling periods, the investigator swam haphazardly around each patch reef, and recorded the number of species and individuals in each group over a 5 min interval per group, recorded with stopwatch. Individuals less than 3 cm were not counted.

Species were separated into discrete groups based on their taxonomy and position in the reef or water column. Each of the following 7 discrete family/functional groups were assessed separately: Group 1: Chaetodontidae (butterflyfishes) and Pomacanthidae (angelfishes); Group 2: Acanthuridae (surgeonfishes); Group 3: Haemulidae (grunts), Sparidae (porgies), and Lutjanidae (snappers); Group 4: Scarinae (parrotfishes); Group 5: Labridae (wrasses); Group 6: Sphyraenidae (barracuda), Balistidae (triggerfish), Aulostomidae (trumpetfish), Carangidae (jacks), and *Chromis* spp.; Group 7: Serranidae (groupers) and territorial benthic-attached pomacentrids (damselfishes). For some analyses, groupers, barracuda, and jacks were further pooled into a piscivores group. Parrotfish were counted in 2 groups: a small parrotfish group, composed mostly of the striped parrotfish *Scarus iserti* and juveniles of other species <15 cm, and a large parrotfish group composed of all species with body sizes >15 cm.

### 2.4. Herbivory assays

Herbivory rates on patch reefs were studied using a seagrass *Thalassia testudinum* assay. Seagrass blade tips were collected and visually inspected to avoid pre-bitten or epiphyte-covered samples. Seagrass blades were cut to a standard length of 9 cm and clippings held by weighted clothespins attached at ~2 m intervals to thin nylon lines. Nine clippings

were positioned in each zone (edge, shoulder, and center), for a total of 27 clippings per reef. Assays were left for 24 h before being recovered to determine the number of bites, the amount of seagrass bitten (to the closest 0.5 cm), and, based on bite scar characteristics, whether fish or sea urchin were responsible for the bites, (Hay 1984, McClanahan et al. 1994). This herbivory assay method is biased towards greater herbivory by macro-algae feeding species; it underestimates herbivory by some groups such as damselfish, excavating parrotfish, and sea urchins, and does not measure herbivory for some sucking and scraping species such as surgeonfish.

### 2.5. Data analyses

The study is based on a BACI design where the periods before and after the 2009 parrotfish capture ban were compared, as well as the fishing (GUZ) and no-fishing (CZ) management zones. Prior to choosing statistical tests, data were evaluated for the assumptions of normality and equal variance with raw data and square-root and logit transformations. Some data passed these tests, but most did not, depending on the measurement and pooling of data. For example, numbers of fish species and benthic cover groups were normally distributed and therefore a 2-way ANOVA with interactions was applied. Fish evaluated at the family/functional and species level were not normally distributed. Therefore, Kruskal-Wallis tests were used to test for differences between time periods and management zones. To evaluate the overall changes in the fish communities at the species and family/functional group levels, a principal component analysis (PCA) was performed, separating the sites and times by period and management zone. PCA ordination was used because the community data was unconstrained and had a short gradient with few zeroes (Legendre & Gallagher 2001).

Recruitment of fish was evaluated to determine its potential influence on the observed temporal patterns and if there was synchrony among species that might reflect environmental forcing. Recruitment was defined as a positive >2 SD deviation from the mean in abundance. Changes in the abundance of the dominant 25 species (92% of observations) were evaluated as variation from the species' full 25 yr time series mean. To more easily compare species, we standardized abundance to a range of  $\pm 3$  SD. The species' standardized annual mean was subtracted from the overall mean and plotted against time.

Changes in coral cover and species composition were evaluated by comparing the 3 sampling dates prior to and 3 dates after the parrotfish ban in 2009. The earlier part of the time series was strongly affected by the 1998 ENSO and therefore we restricted our evaluation to after 2004. There were also less severe thermal stress periods in 2010 and 2016 that could potentially affect corals, but most of the decline in *Acropora* spp. due to disease and bleaching occurred prior to 2004 (McClanahan et al. 2011a).

### 3. RESULTS

#### 3.1. Fish populations

The total number of parrotfish was higher in the GUZ than the CZ and declined in both locations over time (Table 1). These differences were largely

due to small parrotfish, including striped parrotfish and juveniles of other species (Table 1). The number of large parrotfish was, however, not different between the CZ and the GUZ, and declined over time and after the capture ban. There were no differences between management zones in the total densities of fish, wrasses, butterflyfish, or angelfish; however, damselfish were more abundant in the GUZ than the CZ. Increases over time were evident for many functional/family groups targeted by fishers, but not parrotfish (Figs. 2 & 3a). The total density of fish, as well as the number of snappers, piscivores, and angelfish increased in the CZ before and after the parrotfish capture ban. Angelfish numbers also increased in the GUZ after the ban but were still about half the densities found in the CZ. Number of fish species increased in the CZ and GUZ over time but most of this change occurred prior to the 2009 ban (Fig. 4).

Table 1. Mean  $\pm$  SE of numbers of fish, grouped by family/functional groups, observed per 5 min before and after the parrotfish capture ban in the Conservation and General Use Zones on Glover's Reef. Results of Kruskal-Wallis tests comparing periods and management zones are presented, as well as the 2-way ANOVA analysis for management, period and their interaction (management  $\times$  period)

Management	Fish group	Pre-ban	Post-ban	— Period — $\chi^2$ $p > \chi^2$		Average (both periods)	Management $\chi^2$ $p > \chi^2$	
Conservation	Total parrotfish	125.56 $\pm$ 5.44	102.7 $\pm$ 10.97	3.28	NS	121.48 $\pm$ 4.93	0.02	NS
General use	Total parrotfish	140.9 $\pm$ 12.95	93.3 $\pm$ 9.17	5.98	0.01	131.28 $\pm$ 10.65		
Conservation	Small parrotfish	58.73 $\pm$ 2.73	48.55 $\pm$ 5.43	2.86	NS	56.91 $\pm$ 2.46	0.06	NS
General use	Small parrotfish	67.87 $\pm$ 6.5	44.55 $\pm$ 4.57	5.94	0.01	63.16 $\pm$ 5.34		
Conservation	Large parrotfish	20.86 $\pm$ 1.19	15.25 $\pm$ 1.59	4.51	0.03	19.86 $\pm$ 1.04	2.09	NS
General use	Large parrotfish	20.39 $\pm$ 1.47	12.95 $\pm$ 1.12	5.95	0.01	18.89 $\pm$ 1.23		
Conservation	Grunts	71.02 $\pm$ 4.96	230.3 $\pm$ 92.56	1.45	NS	99.46 $\pm$ 17.66	17.74	<0.0001
General use	Grunts	60.23 $\pm$ 8.96	52.55 $\pm$ 8.39	1.55	NS	58.68 $\pm$ 7.34		
Conservation	Damselfish	67.8 $\pm$ 2.47	60 $\pm$ 4.98	1.05	NS	66.41 $\pm$ 2.23	31.85	<0.0001
General use	Damselfish	90.73 $\pm$ 3.46	87.55 $\pm$ 6.33	0.28	NS	90.09 $\pm$ 3.03		
Conservation	Wrasses	49.82 $\pm$ 2.27	84.75 $\pm$ 22.09	0.39	NS	56.06 $\pm$ 4.47	0.003	NS
General use	Wrasses	49.47 $\pm$ 2.36	53.4 $\pm$ 6.17	0.16	NS	50.26 $\pm$ 2.25		
Conservation	Snappers	21.76 $\pm$ 2.21	57.15 $\pm$ 12.01	15.47	<0.0001	28.08 $\pm$ 3.06	44.46	<0.0001
General use	Snappers	8.15 $\pm$ 0.92	7.9 $\pm$ 0.83	1.20	NS	8.1 $\pm$ 0.75		
Conservation	Surgeonfish	20.82 $\pm$ 1.41	21.7 $\pm$ 3.5	0.001	NS	20.98 $\pm$ 1.31	6.26	0.01
General use	Surgeonfish	15.99 $\pm$ 1.04	16.5 $\pm$ 1.53	0.36	NS	16.09 $\pm$ 0.88		
Conservation	Piscivores	10.6 $\pm$ 0.96	23.75 $\pm$ 6.16	11.46	0.001	12.95 $\pm$ 1.42	28.89	<0.0001
General use	Piscivores	7.03 $\pm$ 0.93	3.65 $\pm$ 0.44	1.30	NS	6.34 $\pm$ 0.76		
Conservation	Butterflyfish	3.57 $\pm$ 0.25	3.65 $\pm$ 0.42	0.34	NS	3.58 $\pm$ 0.21	1.22	NS
General use	Butterflyfish	3.32 $\pm$ 0.27	3.2 $\pm$ 0.39	0.03	NS	3.29 $\pm$ 0.23		
Conservation	Angelfish	0.96 $\pm$ 0.15	2.9 $\pm$ 0.58	13.54	0.0002	1.31 $\pm$ 0.17	2.83	NS
General use	Angelfish	0.82 $\pm$ 0.17	1.5 $\pm$ 0.27	8.65	0.003	0.96 $\pm$ 0.15		
Conservation	Total	451.51 $\pm$ 9.44	650.7 $\pm$ 98.77	4.04	0.04	487.08 $\pm$ 20.26	3.15	NS
General use	Total	464.9 $\pm$ 21.15	377.05 $\pm$ 16.16	7.07	0.008	447.15 $\pm$ 17.52		
Number of fish species, Term				Estimate $\pm$ SE		<i>t</i> ratio	Prob > [ <i>t</i> ]	
Intercept				21.71 $\pm$ 0.28		76.72	<0.0001	
Period[Post-ban]				2.64 $\pm$ 0.28		9.32	<0.0001	
Management[General use]				-1.90 $\pm$ 0.28		-6.70	<0.0001	
Management[General use] * Period[Post-ban]				-0.45 $\pm$ 0.28		-1.60	NS	



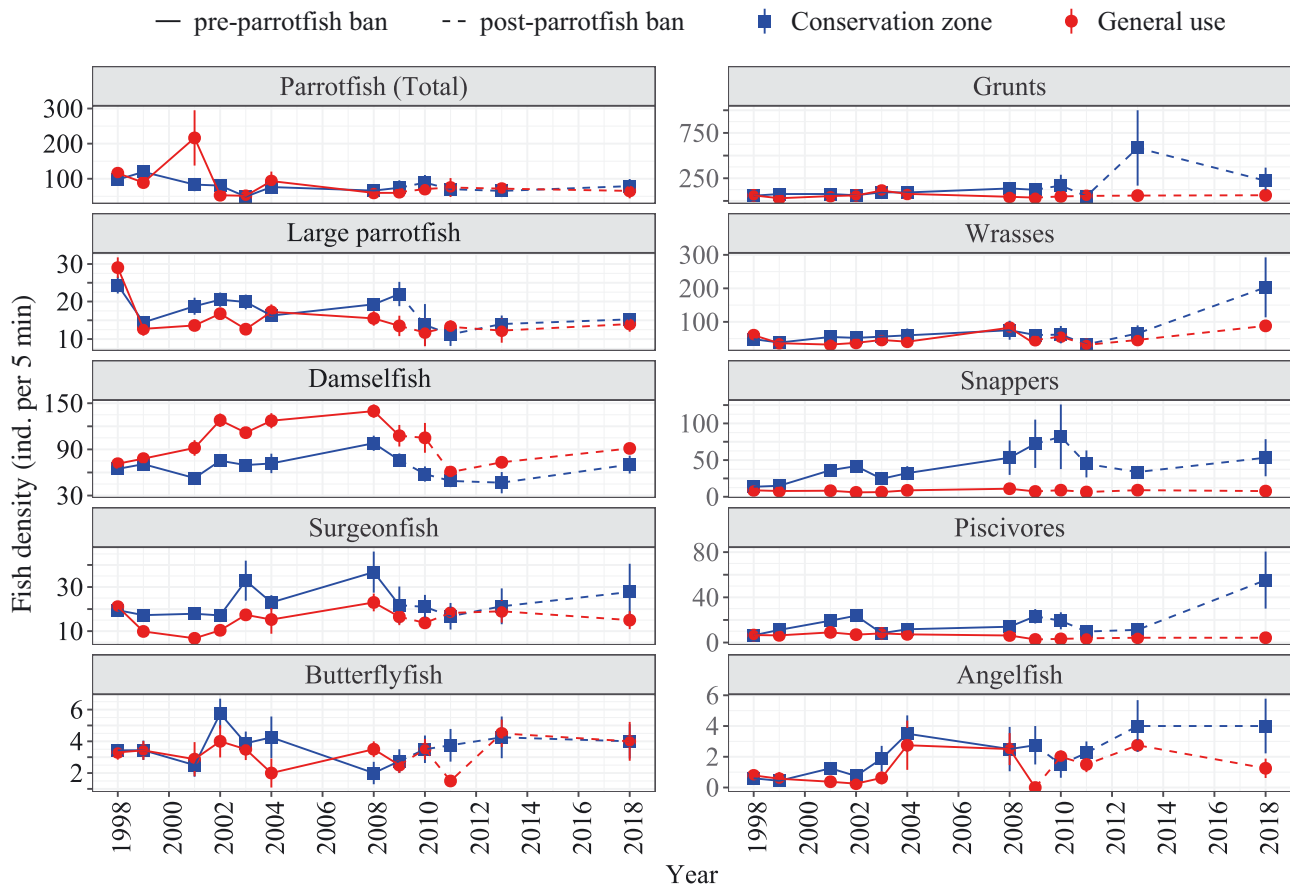


Fig. 2. Changes in the density of fish family/functional groups over the study period

The reserve management increased the abundance of targeted fished species, including blue-striped grunts *Haemulon sciurus*, blue tangs *Acanthurus coeruleus*, grey snapper *Lutjanus griseus*, yellowtail snapper *Ocyurus chrysurus*, lane snapper *Lutjanus synagris*, bar jacks *Caranx ruber*, schoolmaster *Lutjanus apodus*, jolthead porgy *Calamus bajonado*, great barracuda *Sphyraena barracuda*, queen angelfish *Holocanthus ciliaris*, mutton snapper *Lutjanus analis*, Nassau grouper *Epinephelus striatus*, hogfish *Lachnolaimus maximus*, black grouper *Mycteroperca bonaci*, and midnight parrotfish *Scarus coelestinus* (Table 2, Fig. 3b). Some unfished species that increased in the CZ were blue chromis *Chromis cyanea* and banded butterflyfish *Chaetodon striatus*. Grey angelfish *Pomacanthus arcuatus* were marginally more abundant in the GUZ than CZ.

After the ban, redband parrotfish *Sparisoma aurofrenatum* numbers declined in both the CZ and GUZ, while stoplight parrotfish *Sparisoma viride* declined in the CZ but not the GUZ. Redfin parrotfish *Sparisoma rubripinne* were not abundant; however, their

densities increased in the CZ over the ban period but not in the GUZ. Small striped parrotfish densities did not change across the ban period. A number of non-parrotfish fished species increased in the CZ after the ban, including the yellowtail snapper, schoolmaster, mutton snapper, Nassau grouper, graysby *Cephalopholis cruentata*, and grey, queen, and French *Pomacanthus paru* angelfishes. Several targeted fished species decreased in the GUZ after the ban, including grey snapper, doctorfish *Acanthurus chirurgus*, jolthead porgy, queen angelfish, chub *Kyphosus sectatrix*, and ocean triggerfish *Canthidermis sufflamen*. Coney were not abundant but increased after the ban in the GUZ. Some unexpected changes occurred in unfished species in the GUZ, such as declines in yellowhead wrasse but increases in blue chromis, rainbow wrasse, rocky beauty, and the banded butterflyfish. Recruitment of 25 dominant fish species showed variable patterns (Fig. 5). The 3 parrotfish species recruited only before 2002. Other species, such as various species of wrasse, snapper, and grunt, all had recruitment periods after 2002 but with little evidence for synchrony among the taxa.

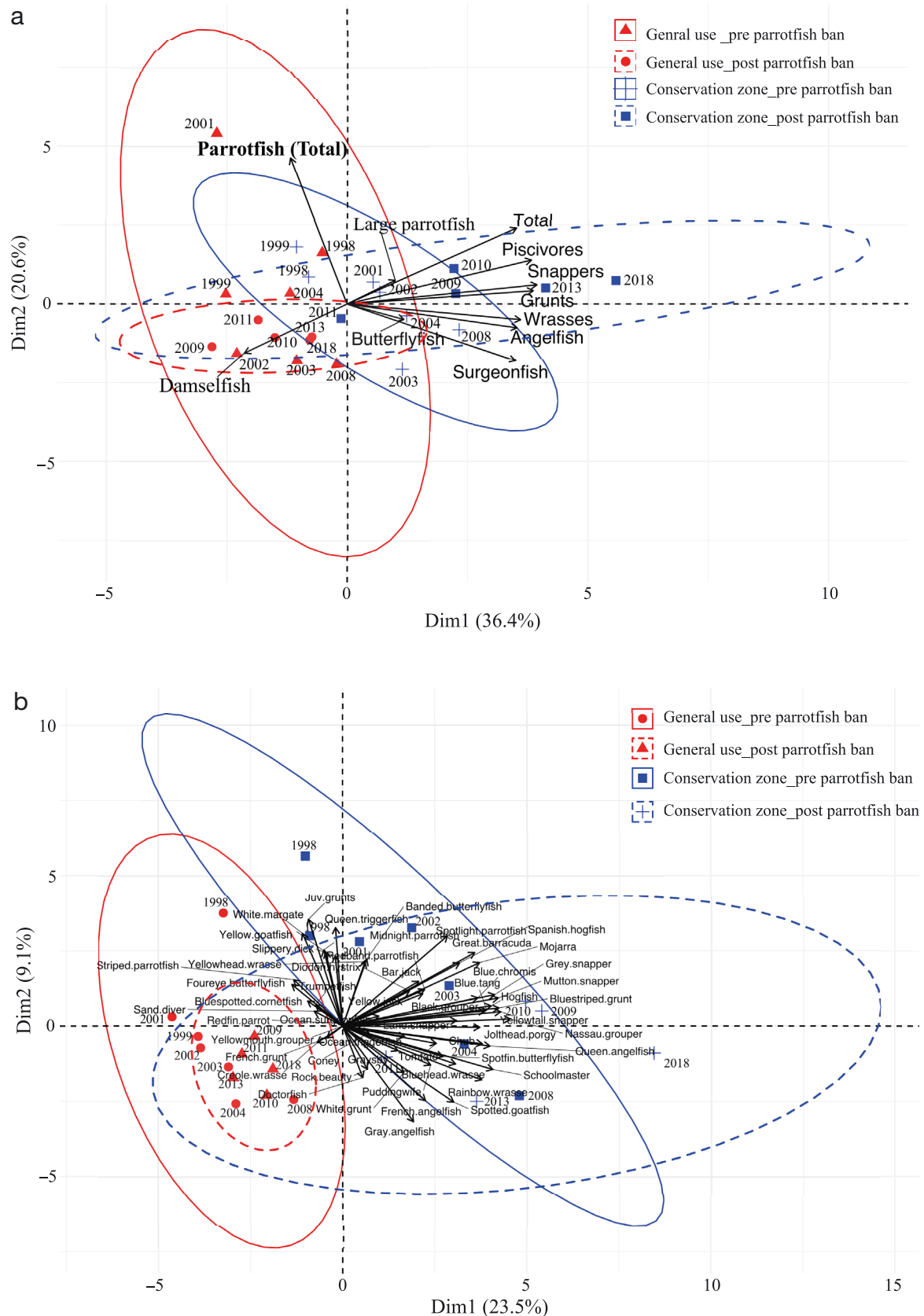


Fig. 3. Multivariate PCA analysis of fish grouped by (a) family/functional groups, and (b) genus/species

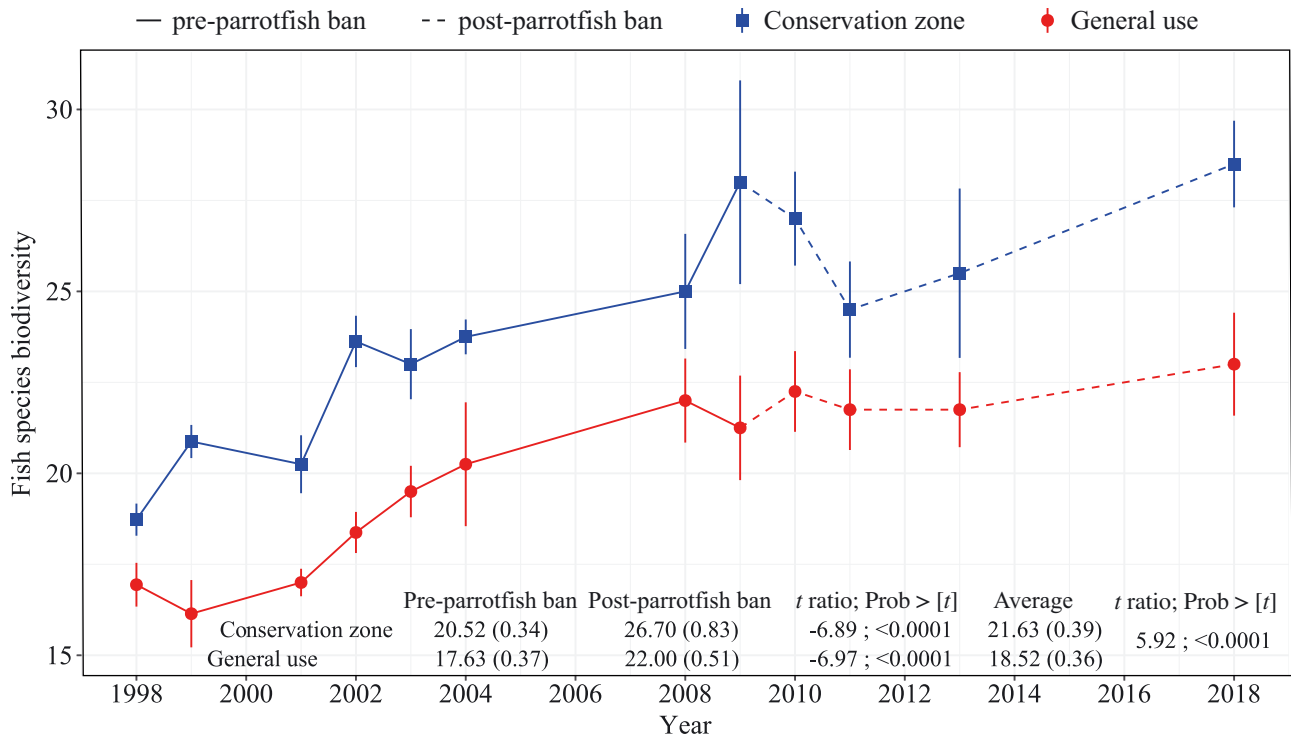


Fig. 4. Changes in total number of fish species observed over the 1998 to 2018 study period, including results of  $t$ -tests of differences between pre- and post-parrotfish capture ban in 2009, and Conservation and General Use Zones

### 3.2. Herbivory

Total herbivory, measured as total bite rates on assays, was not different between management zones (Table 3). There were, however, differences in bites attributable to fish and sea urchins, with higher herbivory by fish and lower herbivory by sea urchins in the CZ. Regardless, there were no differences in any bite rate metrics before and after the parrotfish ban. Time series plots indicate that herbivory by fish differed between the CZ and GUZ after 1999, when herbivory remained at ~40% per day in the CZ but declined in the GUZ to ~10–20% (Fig. 6). However, during the final sampling period in 2018, fish herbivory in the CZ declined considerably to ~15% of the deployed assays. Sea urchin bite rates in the CZ remained low at ~5% over the full time series. In the GUZ, however, sea urchin bite rates rose after 1996 and stayed between 10 to 20% of the assays until 2018.

### 3.3. Benthic cover

The main benthic cover functional groups displayed some changes in cover between management zones and periods (Table 4). Erect algae declined by

about 9% after the ban in both the CZ and GUZ but hard coral cover remained unchanged. Turf and calcareous green algae were (<2%) higher in the CZ than GUZ but did not change over time. Seagrass cover increased by 1.5% in the CZ after the ban but there were no differences between GUZ and CZ. Time-series plots indicate that the greatest increase in turf and erect algae occurred after 1998 when hard coral cover declined (Fig. 7). Turf algae responded first and increased before the erect algae, but turf algae eventually declined until 2009. Thereafter, turf algae increased and although erect algae fluctuated, it declined over time.

Hard coral cover dropped from 27 to 10% between 1996 and 2000 in the CZ but increased to 17% by 2018 (Fig. 7). The change in the coral cover in the GUZ was, however, less variable over time. A total of 24 genera were recorded and *Orbicella annularis*, *Agaricia agaricites*, *Porites porites*, *Siderastrea siderea* and *P. asteroides* contributed 87% of the coral cover. Comparison of the hard coral before and after the ban indicate increases of 33 and 23% in total cover in the CZ and GUZ, respectively. There was a mixture of increases and decreases at the species level (Table 5). In general, the dominant species increased while subdominant species decreased in both zones.



Table 2. Mean and SE of fish identified to species before and after the parrotfish capture ban and for both time periods pooled in the Conservation and General Use Zones on Glover's Reef. The numbers of fish species and Kruskal-Wallis tests of significance are presented for the 3 sets of comparisons

Fish species	Total no. of fish counted	Conservation zone			General use			Management		
		Pre-ban	Post-ban	$\chi^2$	p > $\chi^2$	Pre-ban	Post-ban	$\chi^2$	p > $\chi^2$	Conservation zone
Striped parrotfish	9881	45.97 ± 2.54	38.9 ± 5.82	1.97	NS	52.63 ± 6.5	35.8 ± 4.57	1.91	NS	44.71 ± 2.34
Bluehead wrasse	7419	32.14 ± 1.92	62 ± 19.37	0.0001	NS	30.58 ± 2.09	40.3 ± 6.01	2.67	NS	37.48 ± 3.89
French grunt	6560	27.32 ± 2.82	36.7 ± 14.72	0.98	NS	34.57 ± 6.16	29.1 ± 5.87	0.47	NS	28.99 ± 3.48
Bluestriped grunt	4293	24.01 ± 3.21	54 ± 18.71	0.07	NS	11.66 ± 2.65	4.15 ± 0.85	0.76	NS	29.37 ± 4.34
Tomtate	3093	6.07 ± 1.77	12.5 ± 93.68	0.06	NS	0.38 ± 0.11	0.25 ± 0.12	0.05	NS	27.3 ± 17
Yellowhead wrasse	3091	14.37 ± 1.06	12.45 ± 0.99	0.06	NS	17.09 ± 0.97	8.5 ± 1	20.59	<0.0001	14.02 ± 0.89
White grunt	2983	13.5 ± 1.84	14.6 ± 2.95	0.72	NS	13.52 ± 1.89	19.05 ± 4.61	3.17	NS	13.7 ± 1.6
Blue tang	2969	16.01 ± 1.08	16.75 ± 2.86	0.001	NS	11.81 ± 0.89	11.4 ± 1.55	0.00	NS	16.15 ± 1.02
Redband parrotfish	2746	12.76 ± 1.14	9.65 ± 1.21	0.57	NS	15.24 ± 1.35	8.75 ± 0.93	5.85	0.02	12.21 ± 0.96
Blue chromis	1563	10.53 ± 0.95	10.45 ± 2.25	0.03	NS	3.06 ± 0.38	7.2 ± 1.06	14.80	0.0001	10.51 ± 0.87
Spotlight parrotfish	1331	8.07 ± 0.35	5.35 ± 0.58	12.27	0.0005	5.08 ± 0.34	4.05 ± 0.53	1.28	NS	7.58 ± 0.32
Yellowtail snapper	1131	5.06 ± 0.7	14.8 ± 5.11	7.10	0.008	4.25 ± 0.71	1.65 ± 0.31	3.25	NS	6.8 ± 1.12
Lane snapper	810	4.31 ± 0.81	10.8 ± 3.06	9.95	0.002	1.89 ± 0.41	2.45 ± 0.44	6.93	0.008	5.47 ± 0.89
Ocean surgeonfish	627	3.12 ± 0.34	2.9 ± 0.79	0.54	NS	2.91 ± 0.36	2.6 ± 0.47	0.02	NS	3.08 ± 0.31
Foureye butterflyfish	550	2.69 ± 0.21	2.05 ± 0.37	1.66	NS	2.72 ± 0.27	2.35 ± 0.31	0.01	NS	2.57 ± 0.18
Bar jack	468	2.53 ± 0.47	3.95 ± 1.6	2.89	NS	1.8 ± 0.5	0.7 ± 0.25	0.06	NS	2.79 ± 0.48
Schoolmaster	446	2.28 ± 0.24	4.9 ± 0.81	11.19	0.0008	1.29 ± 0.17	1.85 ± 0.34	2.75	NS	1.4 ± 0.15
Doctorfish	346	1.69 ± 0.31	2.05 ± 0.49	1.79	NS	1.27 ± 0.17	2.5 ± 0.49	8.37	0.004	1.75 ± 0.27
Slippery dick	312	1.79 ± 0.36	0.95 ± 0.27	0.06	NS	1.16 ± 0.22	1.8 ± 0.63	0.78	NS	1.64 ± 0.3
Rainbow wrasse	299	0.75 ± 0.4	8.2 ± 2.84	26.56	<0.0001	0.25 ± 0.19	2.3 ± 1.14	20.44	<0.0001	2.08 ± 0.66
Jolthead porgy	247	1.33 ± 0.21	2.1 ± 0.5	3.76	NS	0.7 ± 0.15	1.4 ± 0.31	8.11	0.004	1.47 ± 0.2
Great barracuda	204	1.62 ± 0.38	1.95 ± 0.73	0.86	NS	0.16 ± 0.07	0.15 ± 0.08	0.17	NS	1.68 ± 0.34
Graysby	166	0.8 ± 0.11	1.25 ± 0.2	5.56	0.02	0.67 ± 0.11	0.75 ± 0.19	0.56	NS	0.88 ± 0.1
Spotfin butterflyfish	154	0.68 ± 0.12	1.5 ± 0.43	2.93	NS	0.59 ± 0.12	0.75 ± 0.27	0.30	NS	0.82 ± 0.13
Yellow goatfish	114	0.7 ± 0.16	0.35 ± 0.18	0.40	NS	0.46 ± 0.14	0.3 ± 0.16	0.0002	NS	0.64 ± 0.13
Gray angelfish	112	0.28 ± 0.09	1.2 ± 0.3	16.95	<0.0001	0.61 ± 0.13	0.7 ± 0.16	2.42	NS	0.45 ± 0.09
Spotted goatfish	104	0.32 ± 0.14	1.7 ± 0.64	26.04	<0.0001	0.44 ± 0.09	0.3 ± 0.13	0.17	NS	0.56 ± 0.17
Mojarra	96	0.86 ± 0.32	0.85 ± 0.42	2.77	NS	0 ± 0	0 ± 0	0.00	NS	0.86 ± 0.27
Queen angelfish	74	0.44 ± 0.07	1 ± 0.26	6.07	0.01	0.06 ± 0.03	0.45 ± 0.11	19.46	<0.0001	0.54 ± 0.08
Mutton snapper	67	0.32 ± 0.08	1.4 ± 0.41	11.02	0.0009	0.09 ± 0.05	0.15 ± 0.08	2.28	NS	0.51 ± 0.1
Spanish hogfish	64	0.5 ± 0.13	0.35 ± 0.11	0.71	NS	0.11 ± 0.05	0.1 ± 0.07	0.24	NS	0.47 ± 0.11
Nassau grouper	40	0.24 ± 0.05	0.85 ± 0.17	17.25	<0.0001	0.01 ± 0.01	0 ± 0	0.25	NS	0.35 ± 0.06
Hogfish	34	0.22 ± 0.06	0.45 ± 0.15	3.94	0.047	0.05 ± 0.02	0.05 ± 0.05	0.0001	NS	0.26 ± 0.06
French angelfish	31	0.09 ± 0.05	0.55 ± 0.23	12.87	0.0003	0.11 ± 0.04	0.15 ± 0.08	0.58	NS	0.17 ± 0.06
Chub	27	0.16 ± 0.05	0.45 ± 0.11	9.88	0.002	0.0 ± 0.0	0.15 ± 0.11	7.98	0.005	0.21 ± 0.04
Yellow jack	27	0.18 ± 0.09	0.4 ± 0.3	2.14	NS	0.01 ± 0.01	0.05 ± 0.05	1.11	NS	0.22 ± 0.09
Rock beauty	24	0.15 ± 0.04	0.15 ± 0.08	0.04	NS	0.04 ± 0.02	0.20 ± 0.09	6.31	0.01	0.15 ± 0.04
Creole wrasse	23	0.03 ± 0.03	0.10 ± 0.07	4.84	0.03	0.15 ± 0.08	0.30 ± 0.25	0.68	NS	0.04 ± 0.03
Banded butterflyfish	22	0.2 ± 0.06	0.10 ± 0.07	0.29	NS	0.0 ± 0.0	0.10 ± 0.10	3.95	0.047	0.18 ± 0.05
Black grouper	18	0.08 ± 0.03	0.45 ± 0.14	15.06	0.0001	0.01 ± 0.01	0.05 ± 0.05	1.11	NS	0.14 ± 0.04
Juvenile grunts	15	0.11 ± 0.11	0 ± 0	0.22	NS	0.06 ± 0.06	0.0 ± 0.0	0.25	NS	0.09 ± 0.09
Puddingwife	13	0.02 ± 0.02	0.25 ± 0.16	6.39	0.01	0.06 ± 0.04	0.05 ± 0.05	0.05	NS	0.06 ± 0.03
Redfin parrotfish	12	0.01 ± 0.01	0.1 ± 0.07	4.96	0.03	0.08 ± 0.04	0.15 ± 0.11	0.68	NS	0.03 ± 0.02
Ocean triggerfish	11	0.03 ± 0.02	0.3 ± 0.18	4.67	0.03	0.0 ± 0.0	0.1 ± 0.07	7.98	0.005	0.08 ± 0.04
Trumpetfish	11	0.04 ± 0.02	0.0 ± 0.0	0.89	NS	0.06 ± 0.04	0.1 ± 0.07	1.22	NS	0.04 ± 0.02
Ballonfish	8	0.04 ± 0.02	0.1 ± 0.1	0.03	NS	0.03 ± 0.02	0.0 ± 0.0	0.51	NS	0.05 ± 0.02
Sand diver	7	0.02 ± 0.02	0.05 ± 0.05	0.50	NS	0.03 ± 0.02	0.1 ± 0.07	2.27	NS	0.03 ± 0.02
Midnight parrotfish	5	0.02 ± 0.02	0.15 ± 0.08	6.28	0.01	0.0 ± 0.0	0.0 ± 0.0	0.00	NS	0.04 ± 0.02
Bluespotted cornetfish	4	0.02 ± 0.02	0.0 ± 0.0	0.22	NS	0.01 ± 0.01	0.05 ± 0.05	1.11	NS	0.02 ± 0.02
Queen triggerfish	4	0.04 ± 0.02	0.0 ± 0.0	0.89	NS	0.0 ± 0.0	0.0 ± 0.0	0.00	NS	0.04 ± 0.02
White margate	4	0.01 ± 0.01	0 ± 0	0.22	NS	0.04 ± 0.02	0 ± 0	0.78	NS	0.01 ± 0.01
Coney	2	0.0 ± 0.0	0.05 ± 0.05	4.60	0.03	0.0 ± 0.0	0.05 ± 0.05	3.95	0.047	0.01 ± 0.01

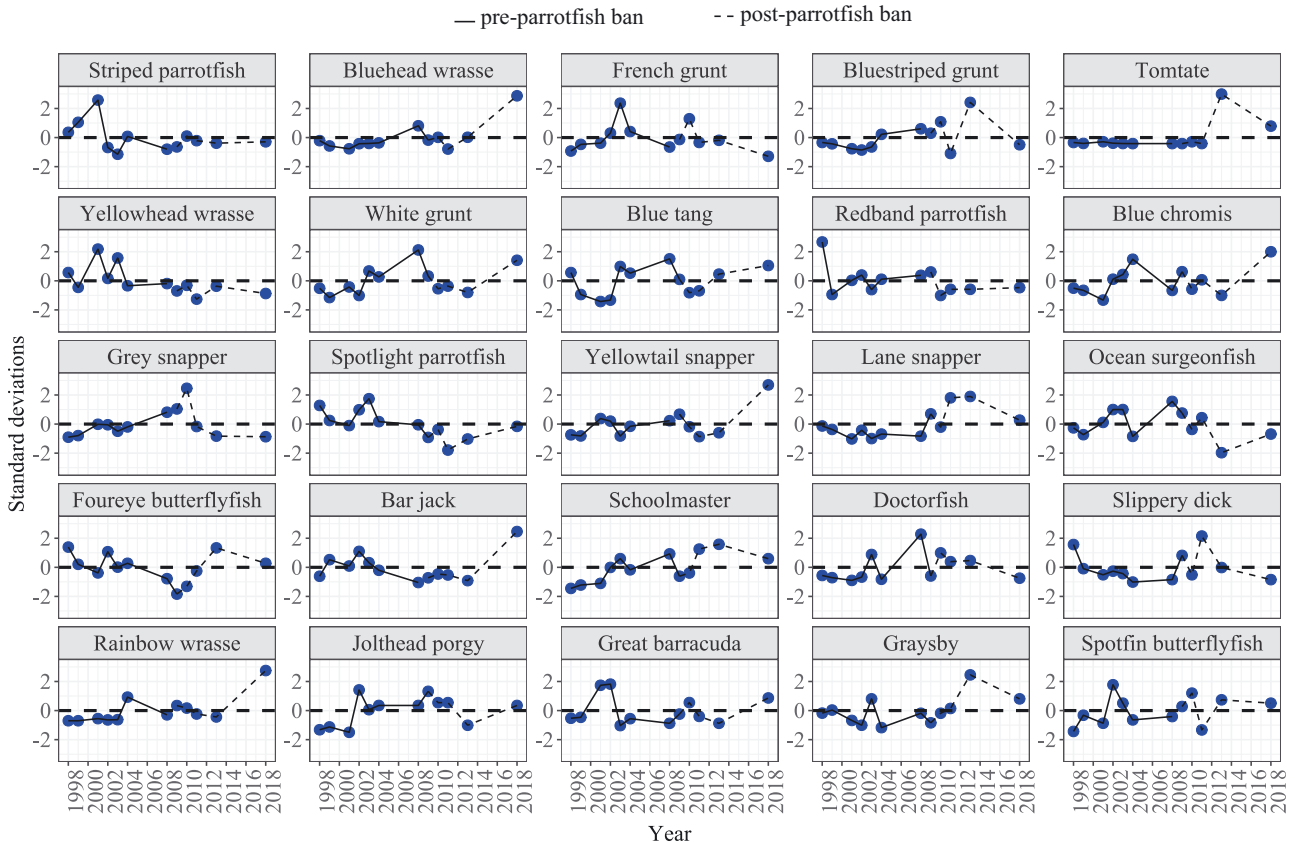


Fig. 5. Recruitment of dominant fish species in Glover's Reef atoll patch reefs ( $n = 8$ ) over the study period, presented as variation (normalized standard deviations) from the full time series means

#### 4. DISCUSSION

The 22 yr time series indicates complex ecological responses to climate disturbances and fishing in these patch reefs. Nevertheless, the patch reefs were persistently dominated by algae, which increased particularly after the thermal stress and associated coral mortality events of 1998 and 2010. After the major 1998 disturbance, there was a rapid succession from turf to erect algae, with a slight decline in turf algae after erect algae increased, followed by another

increase after 2010. Frondose erect algae maintained cover  $>30\%$  but also declined slightly after 1998 and more so after 2010. The CZ showed the greatest variability in hard coral cover, with a rapid decline in the early part of the time series and partial recovery after 2008. Thus, hard coral cover was most affected by the 1998 thermal stress and less by subsequent thermal stresses, largely due to the loss of *Acropora* spp. in 1998 and lack of recovery thereafter. Some of the dominant corals, such as *O. annularis*, *A. agaricites*, and *P. porites*, appeared to be increasing towards the

Table 3. Overall, fish, and sea urchin herbivory before and after the parrotfish capture ban period in the Conservation and General Use Zones of Glover's Reef. Data are mean  $\pm$  SE, and the results of Kruskal-Wallis tests comparing pre- and post-capture ban periods and management zones

Management	Herbivory type	Pre-ban	Post-ban	— Period — $\chi^2$	$p > \chi^2$	Average (both periods)	Management $\chi^2$	$p > \chi^2$
Conservation zone	Total	39.1 $\pm$ 2.12	38.31 $\pm$ 3.63	0.23	NS	38.89 $\pm$ 1.82	1.96	NS
General use	Total	34.25 $\pm$ 1.86	32.98 $\pm$ 2.86	0.48	NS	33.9 $\pm$ 1.56		
Conservation zone	Fish	34.88 $\pm$ 2.11	33.19 $\pm$ 3.63	0.44	NS	34.43 $\pm$ 1.82	29.44	$<0.0001$
General use	Fish	21.49 $\pm$ 1.82	18.15 $\pm$ 2.67	2.07	NS	20.56 $\pm$ 1.51		
Conservation zone	Sea urchin	4.6 $\pm$ 0.61	5.47 $\pm$ 1.04	0.41	NS	4.84 $\pm$ 0.52	55.20	$<0.0001$
General use	Sea urchin	13.64 $\pm$ 1.27	15.16 $\pm$ 1.84	0.76	NS	14.06 $\pm$ 1.05		

Table 4. Percentage cover (mean  $\pm$  SE) of each functional group substrate type before and after the parrotfish capture ban in the Conservation and General Use Zones of Glover's Reef. The results of Kruskal-Wallis tests comparing pre- and post-capture ban periods and management zones are presented

Management	Substrate type	Pre-ban	Post-ban	Period $\chi^2$	$p > \chi^2$	Average (both periods)	Management $\chi^2$	$p > \chi^2$
Conservation	Erect frondose algae	46.86 $\pm$ 1.65	37.08 $\pm$ 2.81	8.04	0.005	44.11 $\pm$ 1.46	0.10	NS
General use	Erect frondose algae	46.69 $\pm$ 1.54	38.11 $\pm$ 2.54	7.24	0.007	44.2 $\pm$ 1.35		
Conservation	Hard coral	16.05 $\pm$ 0.83	16.88 $\pm$ 1.23	0.43	NS	16.28 $\pm$ 0.69	3.42	NS
General use	Hard coral	17.48 $\pm$ 0.7	17.85 $\pm$ 1.17	0.04	NS	17.59 $\pm$ 0.6		
Conservation	Turf algae	9.43 $\pm$ 0.6	12.2 $\pm$ 1.28	2.60	NS	10.21 $\pm$ 0.57	8.01	0.005
General use	Turf algae	8.08 $\pm$ 0.68	8.97 $\pm$ 1.08	0.47	NS	8.34 $\pm$ 0.58		
Conservation	Coralline red algae	7.73 $\pm$ 0.43	7.68 $\pm$ 0.69	0.07	NS	7.71 $\pm$ 0.36	0.009	NS
General use	Coralline red algae	7.96 $\pm$ 0.56	8.4 $\pm$ 0.75	0.91	NS	8.09 $\pm$ 0.45		
Conservation	Calcareous green algae	6.13 $\pm$ 0.47	4.97 $\pm$ 0.58	1.77	NS	5.81 $\pm$ 0.37	4.70	0.03
General use	Calcareous green algae	4.94 $\pm$ 0.36	4.06 $\pm$ 0.48	1.94	NS	4.68 $\pm$ 0.29		
Conservation	Seagrass	0.95 $\pm$ 0.21	2.49 $\pm$ 0.49	8.16	0.004	1.38 $\pm$ 0.21	0.17	NS
General use	Seagrass	1.21 $\pm$ 0.2	1.38 $\pm$ 0.33	0.62	NS	1.26 $\pm$ 0.17		

end of the study but with simultaneous losses of *Montastraea carvernosa*, *Diploria* spp., and other rarer taxa. Calcifying red and green algae varied over time, showing some rises after coral mortality events but otherwise no clear relationship with disturbances and management. Thus, while erect algae declined after the parrotfish capture ban in 2009, this appeared to be part of a trend that began prior to the ban, as early as 2002. Moreover, while there was a

modest rise in hard coral cover after the ban, this was not clearly attributable to the fisheries closure, the ban, or increases in parrotfish numbers. It is more likely a slow shift in the coral community was provoked by repeated thermal stresses.

The implementation of marine reserve in 1995 clearly increased populations of many fished species, but largely generalist carnivores and piscivores and not parrotfish. Snappers, in particular, showed a

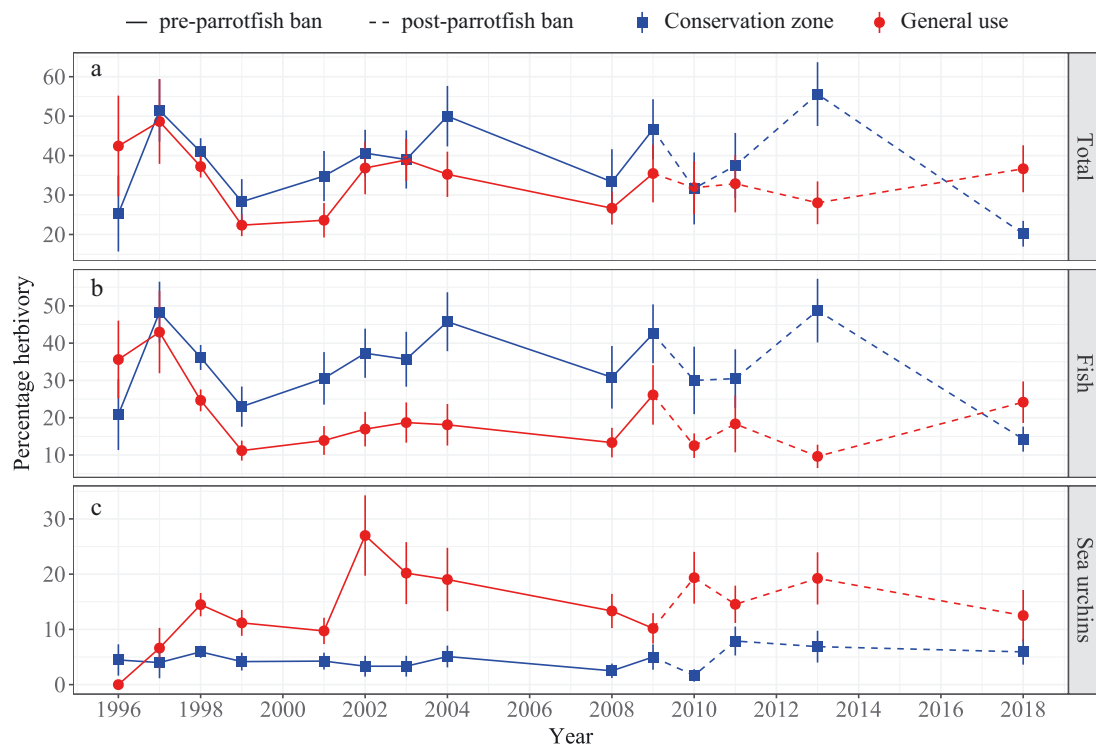


Fig. 6. Changes in (a) total herbivory, (b) herbivory attributable to fish, and (c) herbivory attributable to sea urchins in studied patch reefs over the study period. Herbivory is based on bites on a seagrass assay (see Section 2.4)

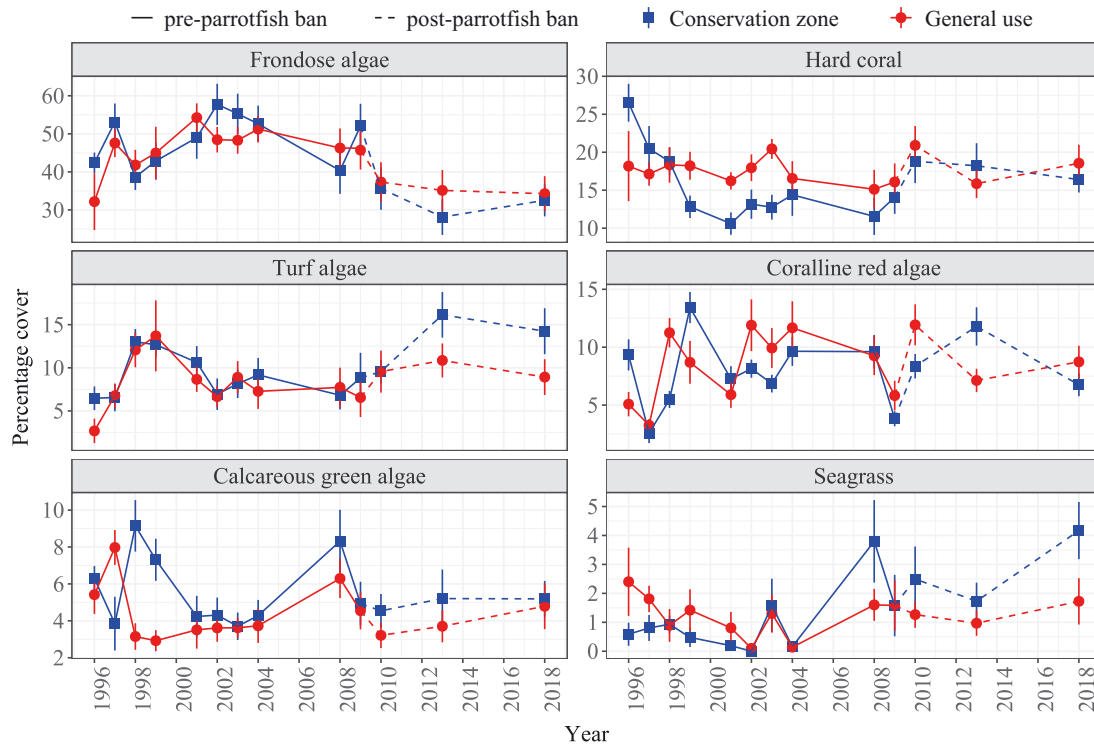


Fig. 7. Changes in benthic cover of the gross functional groups on the studied patch reefs over the study period

steady and consistent rise in numbers in the CZ that would be expected as a response to lower fishing mortality. Some increases in numbers, notably in black and Nassau groupers, continued past the first 10 yr of closure. This explains the greater changes in the CZ after the parrotfish capture ban, rather than some potential indirect or immigration effect from the ban. Parrotfish numbers, on the other hand, appeared to decline slowly over time with no evidence for an effect of the capture ban on their numbers. This decline occurred for small as well as large parrotfish, suggesting some shared ecological rather than fishing effect. The decline appeared to be a slow process that was not reversed by the single high recruitment peak of parrotfish observed in 2001. The failure of parrotfish recruitment after 2002 was not observed in other species and therefore unlikely to be driven by environmental factors shared by all species.

Bite rates on the seagrass assay indicate an early rise and stabilization of herbivory in the CZ, while a steady decline was observed in the GUZ associated with continued fishing. Bite rate maintenance in the CZ was, however, not evident at the end of the study, 9 yr after the ban. Patterns of herbivory are more likely to be explained by the sizes of the parrotfish, rather than their numbers. Parrotfish in the CZ, while not increasing in numbers, did maintain their sizes or grow larger over time, while body sizes declined in

the GUZ (T. R. McClanahan pers. obs.). The early rise in bite rates in the CZ is likely due to this increase in the size of targeted parrotfish rather than numbers. Fishing pressure is a better predictor of body size differences than population densities, as consistently reported for Caribbean parrotfish (Vallès & Oxenford 2014, Vallès et al. 2015). The lack of recruitment of parrotfish in the CZ over the full study period is likely what failed to produce the expected rise. At the end of the study, fish bite rates declined and this may be due to the long-term lack of net recruitment and consequent loss of larger parrotfish over the 22 yr period. Consequently, the evidence indicates that parrotfish populations and their expected impacts on algae and corals were controlled by factors other than fishing. One consistent trend in herbivory was a rise and levelling in bite rates by sea urchins within the GUZ. All of these changes occurred within the context of an early rise and levelling in the number of fish species in both the CZ and GUZs during the first decade of the closure.

The trophic model of fishing impacts on herbivory and subsequent control of coral–algal relationships was not consistently supported. The findings here suggest that other ecological processes influence these patch reefs, which limits the model's ability to predict outcomes of management interventions, as reported in other large-scale studies (Russ et al. 2015,

Table 5. Percent cover (mean  $\pm$  SE) and the percentage change for individual coral species and overall before (2004–2009) and after (2010–2018) the parrotfish capture ban in the Conservation and General Use Zones of Glover's Reef. Taxa are arranged in descending order of percent cover in the Conservation Zone before the parrotfish capture ban period

Coral taxa	— Conservation zone coral cover (%) —			— General use coral cover (%) —		
	2004–2009	2010–2018	Percentage change	2004–2009	2010–2018	Percentage change
<i>Orbicella annularis</i>	3.81 $\pm$ 0.00	4.32 $\pm$ 0.00	11.85	5.86 $\pm$ 0.00	6.66 $\pm$ 0.00	12.13
<i>Agaricia agaricities</i>	2.72 $\pm$ 0.42	3.61 $\pm$ 0.64	24.58	2.34 $\pm$ 0.44	3.02 $\pm$ 0.63	22.72
<i>Porites porites</i>	1.96 $\pm$ 0.40	3.85 $\pm$ 0.62	49.12	2.69 $\pm$ 0.47	3.65 $\pm$ 0.57	26.39
<i>Siderastrea siderea</i>	1.80 $\pm$ 0.47	1.33 $\pm$ 0.31	–36.08	1.95 $\pm$ 0.49	2.83 $\pm$ 0.58	31.27
<i>Porites asteroides</i>	1.18 $\pm$ 0.24	1.51 $\pm$ 0.21	22.13	0.91 $\pm$ 0.21	1.63 $\pm$ 0.27	44.32
<i>Diploria strigosa</i>	0.60 $\pm$ 0.28	0.76 $\pm$ 0.30	20.58	0.39 $\pm$ 0.17	0.59 $\pm$ 0.27	34.22
<i>Millepora complanata</i>	0.40 $\pm$ 0.12	0.60 $\pm$ 0.28	32.86	0.11 $\pm$ 0.07	0.21 $\pm$ 0.12	47.14
<i>Millepora alcicornis</i>	0.28 $\pm$ 0.11	1.60 $\pm$ 0.36	82.47	0.69 $\pm$ 0.20	0.58 $\pm$ 0.17	–19.44
<i>Montastraea cavernosa</i>	0.23 $\pm$ 0.17	0.00 $\pm$ 0.00	–100	0.14 $\pm$ 0.12	0.10 $\pm$ 0.08	–36.02
<i>Diploria clivosa</i>	0.15 $\pm$ 0.15	0.09 $\pm$ 0.06	–71.76	0.20 $\pm$ 0.09	0.07 $\pm$ 0.07	–175.42
<i>Diploria labyrinth</i>	0.08 $\pm$ 0.05	0.00 $\pm$ 0.00	–100	0.12 $\pm$ 0.09	0.03 $\pm$ 0.03	–346.29
<i>Dichocoenia stokesi</i>	0.05 $\pm$ 0.05	0.00 $\pm$ 0.00	–100	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00
<i>Mussa angulosa</i>	0.03 $\pm$ 0.03	0.05 $\pm$ 0.05	31.42	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00
<i>Eusmilia fastigiata</i>	0.02 $\pm$ 0.02	0.05 $\pm$ 0.03	48.08	0.00 $\pm$ 0.00	0.05 $\pm$ 0.05	100
<i>Acropora palmata</i>	0.02 $\pm$ 0.02	0.00 $\pm$ 0.00	–100	0.00 $\pm$ 0.00	0.09 $\pm$ 0.09	100
<i>Colpophyllia natans</i>	0.02 $\pm$ 0.02	0.00 $\pm$ 0.00	–100	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00
<i>Favia fragum</i>	0.01 $\pm$ 0.01	0.00 $\pm$ 0.00	–100	0.06 $\pm$ 0.02	0.00 $\pm$ 0.00	–100
<i>Manicina areolata</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00	0.04 $\pm$ 0.03	0.00 $\pm$ 0.00	–100
<i>Scolymia</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00	0.01 $\pm$ 0.01	0.00 $\pm$ 0.00	–100
<i>Acropora cervicornis</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00	0.23 $\pm$ 0.16	0.00 $\pm$ 0.00	–100
<i>Porites colonensis</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00
<i>Agaricia tenuifolia</i>	0.00 $\pm$ 0.00	0.02 $\pm$ 0.02	100	0.00 $\pm$ 0.00	0.09 $\pm$ 0.07	100
<i>Porites branneri</i>	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00	0.00 $\pm$ 0.00	0.00 $\pm$ 0.00	0.00
<i>Stephanocoenia michelini</i>	0.00 $\pm$ 0.00	0.03 $\pm$ 0.03	100	0.00 $\pm$ 0.00	0.02 $\pm$ 0.02	100
Total	13.36 $\pm$ 1.13	17.77 $\pm$ 1.59	33.01	15.74 $\pm$ 1.60	19.62 $\pm$ 1.94	23.13

McClanahan & Muthiga 2016, Bruno et al. 2019). Specifically, coral cover and sensitive taxa appeared to be more influenced by thermal stress and background environmental conditions and secondarily by interactions with algae (Williams et al. 2001, McClanahan et al. 2011b). Similarly, parrotfish numbers appeared to be more influenced by environmental or ecological forces rather than by fishing mortality. Fishing impacts are more likely to influence fish sizes and biomass and have short-term effects while fish densities may have long-term effects, especially when net recruitment fails (Skinner et al. 2019). The influence of recruitment failure and abundance was shown for both small and large parrotfish, where small parrotfish acted as a control for fishing mortality for the larger species. Given that a number of ecological factors are not well understood, the outcomes of parrotfish capture bans are potentially difficult to predict. Better understanding the environmental and habitat factors that limit and interact with parrotfish populations will therefore be critical to understanding the outcomes of managing parrotfish.

Parrotfish biomass has been shown to respond to reduced fishing mortality either through fisheries clo-

sures or changes in fishing effort and gear (McClanahan et al. 2007, Vallès & Oxenford 2014, O'Farrell et al. 2015). The rates of response can vary considerably and possibly be influenced by the variable or slow life history characteristics of some of the species (McClanahan & Humphries 2012, Taylor et al. 2014). In the case of a ban in Bermuda, the biomass of parrotfish recovered but without an increase in juvenile recruitment (O'Farrell et al. 2015). Thus, recruitment failures over time could result in long-term biomass declines, as we observed here. We observed high recruitment prior to 2002, which was followed by recruitment failures that suggest poor environmental conditions for parrotfish recovery. We also found that small striped parrotfish declined along with the larger-bodied stoplight and red-band parrotfish, suggesting that the species' maximum lengths and life histories were not a major influence. Nevertheless, the larger-bodied midnight, rainbow *Scarus guacamaia*, and blue parrotfish *Scarus coeruleus* were seldom or never observed in this habitat, suggesting some species-specific associations with the patch reef habitats and associated limitations determined by life history-environment interactions (Mumby et al. 2004).



Ecological and environmental conditions were more likely than fishing to have played a role in limiting these parrotfish species. The conditions in this lagoon are calm, and the weak physical current and wave forces (current speeds  $<10 \text{ cm s}^{-1}$ ) are likely to be structuring these communities (McClanahan & Karnauskas 2011, McClanahan et al. 2011b). This may be one reason why erect algae is so persistent, as algal succession is seldom arrested or reversed by strong waves, currents, and storms that periodically or seasonally impact reefs and remove late-successional algae (Vuki & Price 1994, Clifton 1995). In fact, coral growth in the southern end of the atoll has been shown to be more limited by water flow than the presence of erect algae (McClanahan et al. 2011b). Therefore, one explanation for the declines in parrotfish is that the environment is increasingly antagonistic for their recovery.

Striped parrotfish feeding, growth, and reproduction studies in Panamanian reefs found a positive association between the renewal rates of algae and parrotfish growth and reproduction rates (Clifton 1995). In the Florida Keys, parrotfish preference for turf algae increased with turf cover and, therefore, fleshy algae was not controlled by parrotfish biomass (Smith et al. 2018). Experimental reductions of algae in Glover's Reef patch reefs increased herbivorous fish numbers and feeding rates, mostly for the blue tang, but also the stoplight parrotfish (McClanahan et al. 2000). Thus, these lines of evidence suggest that slow renewal rates of algae could influence parrotfish feeding choices and impede feeding rates and population growth. Low current and wave energy and associated disturbances in the patch reefs are likely to produce low algal renewal rates, particularly in the southern portion of the atoll where currents are slow (McClanahan & Karnauskas 2011). Thermal stress and coral bleaching conditions are particularly stressful in these reef lagoons and therefore caused changes and losses of some rare and sensitive coral species over time (McClanahan & Muthiga 1998). If so, declining current strength would reduce algal renewal rates and promote declining parrotfish growth, reproduction, and recruitment, as well as their subsequent ability to control algae. The proposed algal renewal hypothesis could provide an important area of study to better understand limits on parrotfish populations.

Controlling reef algae is increasingly being understood as an interaction between the diversity of herbivore life histories, feeding rates, habitat requirements, and temporal and spatial patterns of animal movements and feeding (Mumby et al. 2004, Bonaldo et al. 2012, Thibaut et al. 2012, Humphries et al. 2014, Lef-

check et al. 2019, Ruttenberg et al. 2019). Thus, our patch reefs are likely to be an environment that fails to provide the conditions for effective herbivory and associated ecological stability. These reefs cannot, therefore, maintain the early successional or heavily grazed states that promote coral recruitment and recovery (O'Leary et al. 2012). Consequently, banning the capture of parrotfish is unlikely to reverse ongoing ecological changes that impede parrotfish recovery. Outside of hurricane affected reefs, low algal renewal environments may be increasing in the Caribbean and therefore promoting the dominance of late-succession algae. Interestingly, the number of species of fish increased after the CZ was established, while parrotfish diversity remained low. Low parrotfish diversity in these patch reefs is possibly associated with the lack of extensive mangrove forests on Glover's Reef atoll. This critical habitat can limit recruitment of some parrotfish species, notably those species not observed on patch reefs (Mumby et al. 2004).

Banning the capture of parrotfish was not clearly associated with increased mortality of other fish species or, at least, not detectable at our sites using our methods. Rather, there was some stability in angelfish and increases in chub abundances that might not be expected from the ban. It was clear that the reserve was protecting species and that the sizes of targeted species, such as angelfish, were smaller where they were fished. However, after 9 yr, it was not clear whether the ban had reduced the recruitment of alternative less-preferred target species whose capture might be promoted by the parrotfish ban. In contrast, there is some evidence that the reserve is supporting fisheries yields and preventing further and faster declines of targeted species where fishing occurs (Acosta 2002, Bond et al. 2012, Tewfik et al. 2017).

Banning the capture of parrotfish, either through marine reserves or fisheries regulations, is one of the few options for fisheries managers. Given the increasingly hostile conditions for hard corals and beneficial conditions for algae, it is advisable to maintain these management options. The outcomes of parrotfish bans are, however, likely to vary with the ecological forces and habitats of the reefs. Environments that promote algal renewal and habitat diversity (i.e. mangroves) are likely to promote herbivore populations and diversity in the absence of fishing mortality. Consequently, our study does not suggest a widespread failure of the ban but rather adds to the variety of potential responses, such as habitat-specific impacts. Therefore, management via banning is not a panacea for restoration of populations independent of other controlling factors (Bozec et al. 2016). The

marine reserve has been effective in preventing the decline and supporting the recovery of species that require long recovery periods (Acosta 2002, Bond et al. 2012, Babcock et al. 2013, Tewfik et al. 2017). However, some taxa, such as parrotfish, will require approaches that better consider habitats and other factors that are not always considered important in their distributions (Roff et al. 2019). The marine reserve is located at the southern end of the atoll and most of the fishing closure areas are located where current speeds are lowest. One would expect higher algal renewal rates elsewhere—in tidal channels, reef crests and slopes, and the northern portions of the atoll (McClanahan & Karnauskas 2011). If recovery and protection of parrotfish is a priority, then these are better habitats for promoting their recovery.

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