

Experiment mimics fishing on parrotfish: insights on coral reef recovery and alternative attractors

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ABSTRACT: Dominance shifts in ecosystems can occur rapidly, resulting in alternative stable states. While some coral reef ecosystems shift and recover relatively quickly, others recover slowly or not at all over periods of centuries. We explore the role of large (fishing-susceptible) parrotfish in triggering algal phase shifts as alternative attractors that may lock reefs into coral-depleted alternative stable states. We designed an experiment to modestly reduce herbivory only from large parrotfish in the immediate vicinity of experimental coral settlement nursery habitats. We used vertical pegs ('parrotfish deterrents' or PDs) around coral settlement plates on 2 Belizean forereefs. Time-lapse videos and a year's accumulation of bite-marks on plates confirmed that only herbivory from large parrotfish declined significantly due to PDs. Patches of macroalgae developed around PDs reducing coral recruitment in this treatment only. Two dominant reef-dwelling coral genera (*Porites* and *Agaricia*) recruited to our settlement plates. The fast-growing, high-light requiring, reef-building coral *Porites* was more negatively affected by phase shifts; this coral failed to recruit at and above mid-levels of algal abundance. We illustrate the direct roles ecological processes such as herbivory from large parrotfish play in regulating algal abundance, which in turn reduces the recruitment potential of reefs and thus the ecosystem's capacity to recover. Combining our empirical results with an individually-based ecological simulation model, we determined that these processes cascade to drive alternative states and create a 'hysteresis' effect delaying or preventing recovery of the coral reef ecosystem.

KEY WORDS: Alternative attractors · Alternative stable states · Coral recruitment · Herbivory · Hysteresis · Parrotfish · Phase shift · Reinforcing feedback

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INTRODUCTION

Coral reefs are complex and often highly diverse ecosystems that can rapidly flip between coral-dominated and alternative states. These systems can lock into alternative stable states (Knowlton 1992) or rapidly recover to their former structure (e.g. Golbuu et al. 2007). Contrasting ecosystem states on coral reefs are often called 'phase shifts' (Done 1992, Hughes 1994). Phase shifts were initially defined as a shift between a 'coral-dominated' and 'coral-depleted and/or algal dominated' state (Done 1992). When reef-corals die, dominance of the ecosystem shifts to other organisms (e.g. Norström et al. 2009) but most

commonly to benthic marine algae. Thus, anything that kills most corals on a reef, by definition, creates a phase shift. The conspicuous shift to foliose macroalgae is now synonymous with phase shifts on most Caribbean coral reefs (e.g. Hughes 1994).

Coral mortality has increased globally over the last several decades (Gardner et al. 2003, Bruno & Selig 2007) due to disease, predator out-breaks, climate-induced bleaching and hurricanes. Mortality events are often sudden and may involve thresholds such as well-known thermal thresholds that trigger coral bleaching and death (Lesser 2004). However, we know much more about what kills corals and drives phase shifts towards coral-depletion, than we do

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about what drives coral recruitment and the recovery phase of these ecosystems back to coral dominance. While some reef ecosystems recover rapidly (i.e. decade scale; Golbuu et al. 2007), others, especially Caribbean reef ecosystems, are notoriously slow to recover or have shown no signs of recovery from disturbances (Connell 1997). Invariably, massive (or near complete) coral mortality requires the recruitment of reef corals to initiate recovery. This is especially true for Caribbean reefs today after the mass mortality of primarily clonally-propagating acroporid corals shifted dominance to smaller, primarily recruiting poritid-corals (Pandolfi & Jackson 2006, Mumby & Steneck 2008).

Deficient coral recruitment and poor recovery of reef ecosystems may result from myriad sources. There may be too few reproductive corals to maintain high fertilization success and therefore too few larvae (i.e. Allee effects; Knowlton 1992). Too few larvae may arrive to nursery habitats from reproductive populations (i.e. connectivity effects; Jones et al. 2009). Arriving larvae may fail to find nursery habitats or detect necessary triggers for metamorphosis and settlement (facilitation effects; Harrington et al. 2004). Finally, it is possible that rates of post settlement mortality are too high for any coral to survive, negating all earlier events (Harrington et al. 2004, Arnold et al. 2010).

The existence of phase shifts does not necessarily imply that the contrasting states are stable or reinforced by feedbacks that slow recovery. While this topic remains hotly debated (e.g. Dudgeon et al. 2010), it has long been known that coral reefs are nonequilibrium systems (Connell 1978), so they do not necessarily lock into one state versus another indefinitely. However, many previous studies have suggested that ecological feedbacks could create a hysteresis lag that slows or seemingly stops ecosystem recovery (e.g. Mumby et al. 2013b). Accordingly, we explore what drives the trajectory of coral reef community composition. Specifically, we study how herbivory may drive contrasting states in a phase shift in ways that interfere with coral recruitment. If this happens, it can change the trajectory of ecosystem structure in what Scheffer & Carpenter (2003) call alternative attractors. Our understanding of phase shifts and the role of herbivores as a driver of ecosystem structure on coral reefs has focused on (1) small-scale herbivore exclusion experiments (Lewis 1986), (2) natural field experiments where fishing levels have manipulated herbivory (Dulvy et al. 2002), (3) large-scale correlations between herbivores and macroalgal cover (Williams & Polunin

2001), and (4) ecological models of processes (Mumby et al. 2007). Despite this broad range of studies, we lack experimental evidence of the mechanism by which depletion—but not exclusion—of herbivores leads to a loss of coral. In other words, how does the depletion of herbivory, mostly by fishing larger and most vulnerable parrotfish (Hawkins & Roberts 2004), foster an increase in algae and a depletion of coral? We designed a small-scale experiment to manipulate herbivory and quantify the impact on algal structure and the recruitment of corals. We then placed our results in an ecosystem-context by incorporating the manipulation in an ecological model. We found that our observed decline in coral recruitment under reduced herbivory is consistent with the mechanism predicted by ecological models to drive and lock reinforcing feedbacks on the shift from coral to algal dominance.

Specifically, our experiments used terra-cotta coral settlement plates to standardize recruitment habitat architecture, substrate composition and succession. We controlled for changes due to larval connectivity effects by clustering treatments and controls in the same small (i.e. 1 to 2 m diameter) footprint on coral reefs. We used stainless steel pegs to physically impede the largest herbivorous fish (i.e. parrotfishes) from the microhabitat surrounding coral nursery habitats. We excluded large fish because they are frequently most vulnerable to fishing pressure on coral reefs (Hawkins & Roberts 2004), and large herbivores may play a disproportionately large functional role in coral reef ecosystems (Mumby et al. 2006). Explicitly, we sought to determine if modest alterations at small-scales in the frequency and intensity of herbivore-induced disturbances could result in localized phase shifts to macroalgal abundance sufficient to affect the recruitment of corals and at larger scales to the recovery of coral reef ecosystems.

MATERIALS AND METHODS

All experiments were placed at 10 m water depth on wave-exposed fore reefs (i.e. facing eastward) at Glovers Reef and Carrie Bow Cay on the Belizean Barrier Reef (Fig. 1A). Physically the 2 sites are similar in terms of sea temperatures (27 to 29°C; Mumby et al. 2014) and water clarity (horizontal secchi disk distances exceed 20 m at both sites); however, wave exposure is greater at Glovers (log of wave exposure is 8 J m^{-3} versus 6 J m^{-3} at Carrie Bow; Chollett & Mumby 2012).

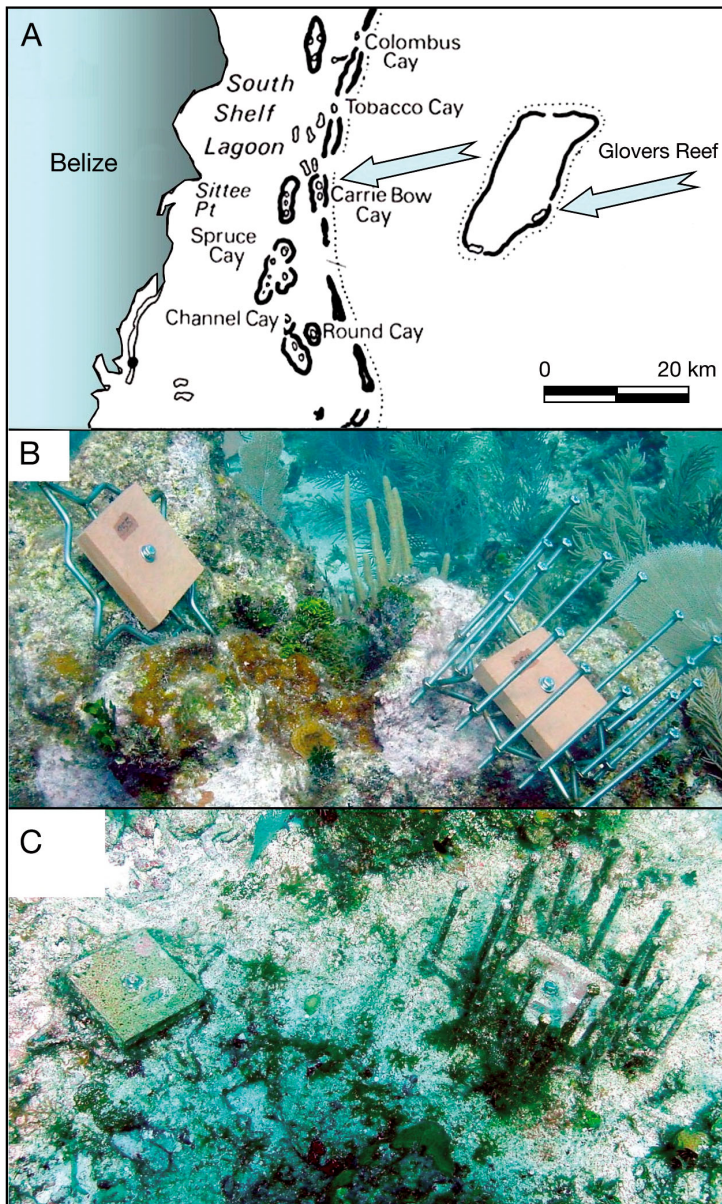


Fig. 1. (A) Belize: Glovers Reef and Carrie Bow Cay study sites. Arrows: average wind direction. Parrotfish deterrents (PDs) and PD-control (B) on deployment and (C) after 1 yr at Glovers Reef

Standardized coral settlement substrata and parrotfish deterrents

We used terra-cotta coral settlement plates to quantify coral recruitment in a standardized way (methods of Arnold et al. 2010). Specifically, unglazed terra-cotta ceramic tiles ($10 \times 10 \times 1$ cm) were affixed to the reef with sheetrock wall anchors. All settlement tiles were elevated above the reef surface by a 1 cm spacer. This method of quantifying coral

recruitment has been used throughout the world's coral reefs (reviewed in Ritson-Williams et al. 2009).

To determine the effect of macroalgae on coral recruitment, we designed a simple means of reducing herbivory in ways having least effect on light and water motion (2 key factors driving benthic algal productivity). To impede herbivory specifically from large bodied grazing fishes in the immediate vicinity of our coral settlement plates, we installed a 20 cm diameter stainless steel wire frame under the plates that was bent into an 8-point star with stainless steel nuts welded to each point and valley. Into each nut we screwed a 15.2 cm stainless steel bolt. These parrotfish deterrents (PDs) thus consisted of a 16-point crown of spikes with 4 cm gaps surrounding the elevated terra-cotta coral settlement plate (Fig. 1B). Control frames bent identically but without any stainless steel bolts represented the PD control (Fig. 1B). A second control of 'naked' settlement tiles (i.e. without PDs or PD control frames) was deployed in equal numbers.

In March 2007, PDs, PD controls and naked plates were deployed in 24 sets of the 3 setups (1 treatment and 2 controls for a total of 72 settlement tiles) at Glovers Reef, with an identical array of treatments and controls nearly 20 km to the west on the Belizean Barrier Reef adjacent to Carrie Bow Cay (Fig. 1A). The experiment was terminated 1 yr later in March 2008.

Quantifying herbivory

We used 2 independent methods to quantify herbivory on and around the 144 experimental coral settlement plates 1 yr after placement so succession of reef organisms would be complete and in order to minimize novelty effects. First, species-specific and size-specific rates of grazing were quantified using stationary video cameras, and second, the size and density of parrotfish bite marks on the settlement plates were quantified.

Rates of grazing by all fish were recorded from 37 videos of 1 to 2 h duration during March 2008. Cameras were placed in areas distant from diver activity, and often no humans were in the water for the dura-

tion of the video observations. Dominant fish groups were parrotfish (Scaridae), tangs (Acanthuridae) and damselfishes (Pomacentridae). Since only the former 2 families are known to create net reductions in algal biomass (Steneck 1988), we quantified all species and size-specific bite rates on them.

To estimate the frequency and intensity of parrotfish grazing, we measured the size (nearest mm) and number of bite marks on each edge of the terra-cotta tiles. For this, after plates had been analyzed for coral spat, substrate colonization and photographed, they were decalcified in hydrochloric acid to remove all calcified epibionts. The plates themselves were unaffected by the acid digestion. The bite mark method quantified the annually accrued frequency and intensity of grazing. This analysis was only applied at the Carrie Bow site because the Glovers Reef plates were unavailable.

Quantifying algal abundance

We quantified algal abundance within the 10 cm perimeter surrounding coral settlement plates. The perimeter, rather than the plate itself, was examined because nearly all settling corals are found on the distal portion of the underside of the tiles (e.g. Arnold et al. 2010; discussed further in 'Results'). Percent cover of fleshy macroalgae was visually assessed within 25 × 25 cm quadrats, and canopy heights were measured to the nearest mm. The product of these 2 measurements is a nondestructive proxy for algal biomass (Steneck & Dethier 1994, Mumby et al. 2013b).

To determine if the PD posts increase algal abundance by their mere presence (e.g. creating an algal friendly habitat) or by deterring herbivores, we measured macroalgal abundance around each post so the algal extent outside the PD crown can be compared to that growing inside the crown. If herbivores have no effect, the algal abundance should have an isodiametric pattern.

Quantifying coral recruitment and rates of growth

Coral spat recruit primarily to the underside of terra-cotta plates at 10 m (Arnold et al. 2010). A pilot study at the same location using the same settling plate method examined coral spat on all surfaces and found that over 80 % of the coral spat were on the distal portion of the underside of the plates (Arnold & Steneck 2011).

To quantify coral recruitment, plates were retrieved from the field by unbolting them from the reef surface and sliding the plates onto a threaded rod with 1 cm spacers placed between them to prevent abrasion and damage of organisms (including corals) living on them (methods of Arnold et al. 2010). In the laboratory, we examined the underside of each plate with a dissecting microscope. Each coral was identified to genus (if possible), and measured for size and distance from the outer edge of the plate. The abundance of all other colonizing organisms and their proximity to the coral spat were quantified, but these data were not used in this study. We used differences in the diameter of newly settled corals to estimate intraspecific differences in growth rates relative to where they settled on the underside of terra-cotta plates. Previous studies on identical settlement plates determined coral recruitment with distance from the edge of the plate does not change over the course of the year (Arnold 2011 and unpubl. data); therefore differences in size reflect differences in growth rates rather than simply older spat being larger.

Modeling PD effects to ecosystem scale resilience

To investigate the wider ecosystem-level impacts of the PD manipulation, we incorporated the observed effects of the PDs on parrotfish grazing into an existing model of a Caribbean reef system (Mumby et al. 2007). The model is a spatial simulation of ecological processes including the recruitment, growth, mortality, competition and disturbance of corals and algae on forereef environments. All parameters have an empirical justification and the model behavior has previously been tested (and found to follow) an independent 20 yr time series of reef dynamics in Jamaica (Mumby et al. 2007). The model makes no *a priori* assumptions about the existence of alternative stable states, yet these emerge from simulations. We estimated the impact of the PDs on grazing in 3 steps. First, we determined the instantaneous grazing intensity of the entire parrotfish community at the Glovers Reef site. Parrotfish community structure was surveyed at the beginning and end of the study using ten 30 × 4 m transects per sampling period. Data were pooled across census periods, and the grazing behavior of each fish was converted to a grazing intensity based on allometric scaling relationships between the species, body size, and life phase of a parrotfish and its grazing rate and bite area (Mumby 2006). This

resulted in the mean total grazing intensity (GIR) of the fish community (% of the reef h^{-1}). The second step disaggregated the total grazing intensity by each fish size class so that the direct bite rate observations on PDs, for which fish were placed into 4 size classes, could be related to the wider reef-scale GIR measurements derived from the fish census. This was done using Eq. (1),

$$\text{GI}_{\text{PD}} = \sum_{i=1}^C \left(\frac{\text{BR_PD}_i}{\text{BR_PC}_i} \right) \text{GIR}_i \quad (1)$$

where GI_{PD} is the grazing intensity on reefs whose herbivores have been depleted by the level simulated using PDs; BR_PD and BR_PC are the observed bite rates of parrotfishes on the PDs and PD controls respectively; GIR is the modeled grazing intensity from fish census on reefs without PDs, and i is the i th parrotfish size class (C), from 1 to 4 (i.e. <10, 11–15, 16–20, and >20 cm).

Lastly, the effect of PDs on the instantaneous grazing intensity of the fish community was scaled to a longer-term, 6-monthly measure of grazing used by the ecological model, PRG (Proportion of Reef Grazed). The PRG effectively represents the net outcome of algal production and the integrated action of fish grazing over a 6 mo period, which is the time interval of the model. Previous studies at Glovers Reef concluded that the entire parrotfish community was able to maintain ~0.30 of the reef in a grazed state over time (Mumby 2006). Eq. (2) was then used to adjust the PRG to that expected on a reef whose herbivores had been depleted by the level simulated by the PD manipulation. PRG_{PD} denotes the proportion of the reef grazed with depleted herbivores:

$$\text{PRG}_{\text{PD}} = 0.3 \left(\frac{\text{GI}_{\text{PD}}}{\text{GIR}} \right) \quad (2)$$

The ecosystem impact of a PD-like reduction in fish grazing was investigated by superimposing the change in reef state upon a plot of the system's state equilibria and thresholds. Coral cover at the sites was determined using 5 line intercept transects of 10 m length.

RESULTS

Herbivory

The frequency and intensity of herbivore-induced disturbance differed between the 2 study reefs. We recorded 293 grazing events among 7 species of herbivorous fishes in the 37 videos (1 h duration)

trained on PDs or PD controls (often both were in the same field of view) that had been in place for 1 yr on the 2 reefs. Parrotfishes (Scaridae) were the dominant herbivores comprising 92 and 69% of the grazing fish fauna on videos taken at Carrie Bow and Glovers reefs, respectively. Surgeonfishes, the Acanthuridae, accounted for the rest of the observed herbivory. Of surgeonfishes, 2 size classes grazed the areas of the PD and PD controls but showed no significant effect of site or treatment ($p > 0.37$); thus, they will not be considered further.

Grazing parrotfishes were larger (Fig. 2A) at Glovers than at Carrie Bow Cay. Striped and red-band parrotfishes (*Scarus iserti* and *Sparisoma aurofrenatum*, respectively) predominated, comprising 92% of grazing fish observed at Carrie Bow compared to 54% of the grazing at Glovers. Three other parrotfish species grazed around PDs at Glovers, including the large and powerful stoplight parrotfish, *Sparisoma viride*.

Observed fish bite rates were analyzed with generalized linear models (GLM) with quasipoisson errors (to allow for over-dispersion of the data). A separate model was created for each size class of fish (Fig. 2A) where each model attempted to predict number of bites per plate h^{-1} based on 2, potentially-interacting predictors: the site (Glovers versus Carrie Bow) and treatment (PDs versus PD control). We found site effects for body size with bite rates from small parrotfish (<10 cm) being greater at Carrie Bow than Glovers (Fig. 2A, $p = 0.01$). Parrotfishes >15 cm appeared to graze more at Glovers than at Carrie Bow (marginal significance, $p = 0.08$; Fig. 2A). However, significant treatment effects were only found in the largest size class of parrotfishes (>20 cm), such that grazing was significantly greater in PD controls ($p = 0.029$; see Fig. 2A) than PDs (e.g. PDs had no bites from large parrotfish at Carrie Bow yet a modest bite rate of 0.3 on PD controls).

The size and number of bite marks etched onto the terra-cotta plates during the year (Fig. 2B) effectively recorded the intensity (amount removed per bite) and frequency (number of bites per time) of parrotfish-induced disturbance, respectively. We subdivided measured bite marks on plates into small (≤ 5 mm) and large (> 5 mm) and examined effects for all treatments (Fig. 2B). While small and large bites looked suppressed in the PD treatments, only the decline of bite marks from large parrotfish was significant (quasipoisson GLM intercept based on naked plates: 2.09 with coefficient for PD at -0.87 and $p = 0.03$). PD effects on small bites were only marginally significant ($p = 0.07$).

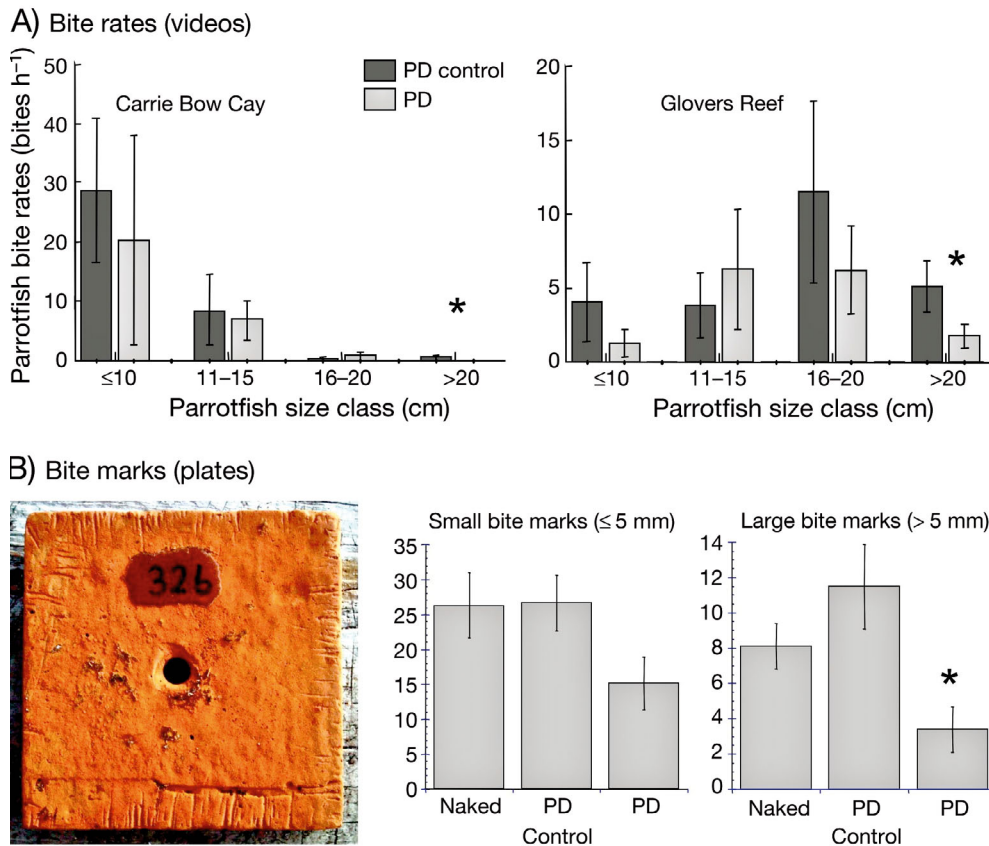


Fig. 2. (A) Parrotfish bite rates per size class at Glovers and Carrie Bow Cay reef sites recorded from videos. (B) Bite marks on terra-cotta settlement plate after 1 yr at Carrie Bow Cay reef (left), and bite rates (# marks yr⁻¹) for small and large scrapes for the parrotfish deterrents (PDs) treatment, PD control, and 'naked' settlement tiles control. *Significant reduction only exists for large parrotfish bites compared to controls (see text)

Algal abundance

At both sites, algal abundance increased in the perimeter space around the PD terra-cotta tiles (Fig. 3). These localized phase shifts to macroalgae were clearly visible and often in stark contrast with the lower algal abundance evident on the adjacent PD controls (photo in Fig. 1C). Erect fleshy macroalgae were dominated by brown algae of the genus *Dictyota*. Other macroalgae included the genera of *Padina*, *Liagora*, *Sargassum*, *Gelidium* and *Zonaria*. We quantified macroalgae abundance by spatial coverage (i.e. percent cover), canopy height and algal index (a product of percent cover and canopy height used as a proxy for algal biomass; Mumby et al. 2013b). All were significantly more abundant in the PD treatments compared to PD control and naked plates (Fig. 3, linear models of arc-sin transformed data with site and treatment as fixed effects found significant negative coefficients for the PD with $p = 0.004$ for macroalgal cover, 0.0016 for canopy height, and 0.0004 for the algal index).

To test for algal retention effects of the stainless steel posts in the PD, we measured the linear dis-

tance of macroalgae away from the posts towards the plate (inside the PD crown) versus away from the plate (outside the PD crown). If algae simply grow readily on stainless steel independently of herbivore effects, the algal growth should be radially equidistant. However, macroalgae consistently extended asymmetrically towards the inner portion of the PD (i.e. towards the coral settlement plate). The average contiguous extent of macroalgae away from the PD posts was 2.3 mm (± 0.61 SE) outside the PD crown and 10.69 (± 0.59 SE) towards the inside. This pattern is consistent with higher rates of herbivory outside the PD crown.

There was no consistent site effect across treatments; however, macroalgal cover was significantly greater on the PDs at Glovers compared to Carrie Bow (linear model intercept with naked plates at Carrie Bow = 28.1, PD coefficient = 10.2, $p = 0.004$, interaction between PD and Glovers coefficient = 11.7, $p = 0.01$; model $r^2 = 0.41$, $p < 0.0001$). Macroalgal canopy heights had a significant treatment effect ($p = 0.0016$) but no site effect. The algal index had a significant treatment effect for PDs ($p = 0.0004$) and marginally-significant differences in the PDs between Glovers and Carrie Bow ($p = 0.06$).

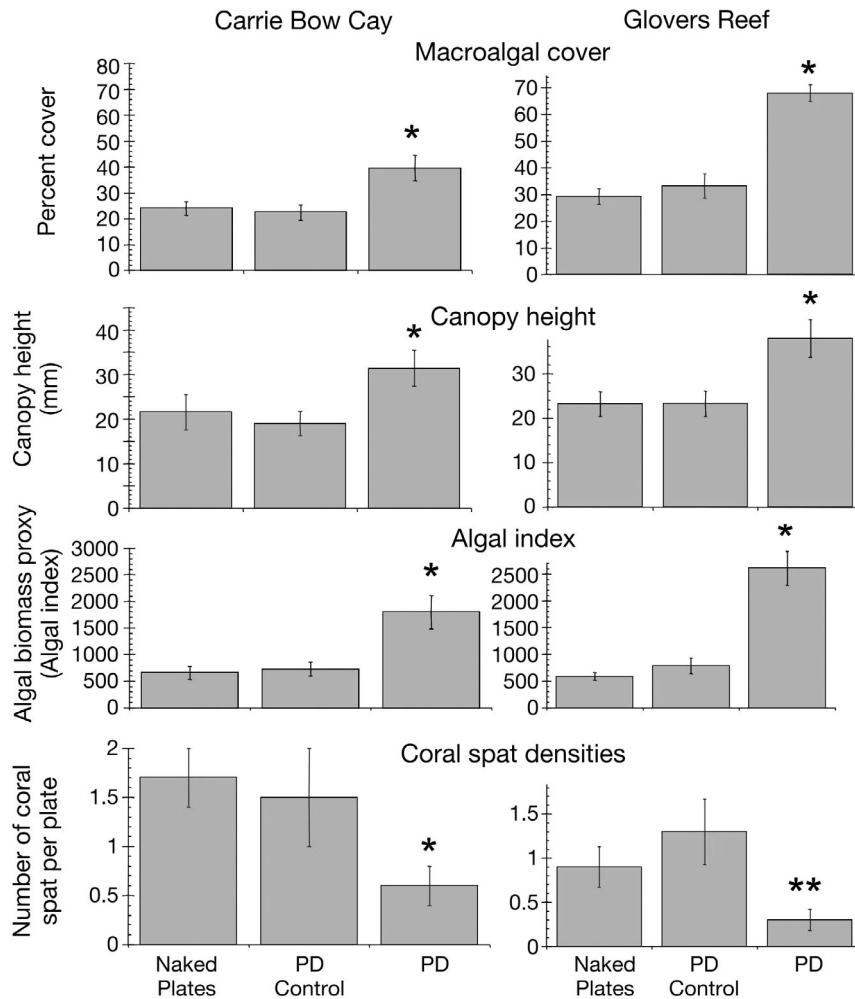


Fig. 3. Fleshy macroalgae abundance as percent cover, canopy height and biomass proxy 'algal index' (% cover \times canopy height in mm) on the benthos surrounding coral settlement plates. Coral recruitment densities on the underside of the terra-cotta settlement plates (pooling all taxa). * $p < 0.05$, ** $p < 0.01$ compared to naked plates and PD controls. See Fig. 2 for definitions

Coral recruitment and growth

Newly settled coral ('spat') were more abundant on the undersides of naked plates and PD controls than on the surface of PD plates surrounded by localized algal phase shifts at both study locations (Fig. 3, quasipoisson GLM with site and treatment as fixed effects, significant negative coefficient for PDs with $p = 0.008$).

The 2 coral genera comprising most of the spat identified on the terra-cotta tiles, *Agaricia* and *Porites*, differ ecologically and geologically, and they displayed different treatment effects. The most common *Agaricia* species to recruit to settlement plates (and found on the reef as juvenile corals) were *A. agaricites* and *A. humilis* but not *A. tenuifolia* (Arnold 2011). *Agaricia* spp. recruited to all treatments at all sites but its probability of occurrence was only significantly retarded on PDs at Glovers (Fig. 4; binomial test assigning its observed prevalence of 0.42 on both naked plates and PD controls to that of 0.16 on PDs, yielded a probability of 0.008). *Porites astreoides*, the most probable *Porites* species recruiting to the settlement plates, is a reef building coral (Pandolfi & Jackson 2006) that now dominates Caribbean reef frameworks (Pandolfi & Jackson 2006). Although species determinations are impossible among newly recruited corals, we confirmed the presence of *P. astreoides* on other longer-duration settlement plates placed at these sites. Importantly, *Porites* failed to recruit to any of the PD treatments (Fig. 4). The probability that *Porites* would fail to recruit to PDs by chance was less than 0.001 at each site (i.e. binomial test assigning the observed prevalence on either naked plates or PD controls to the observed prevalence on PDs).

On those treatments that *Porites* spat were able to settle, their distribution was confined to the outer edge of the underside of the settle-

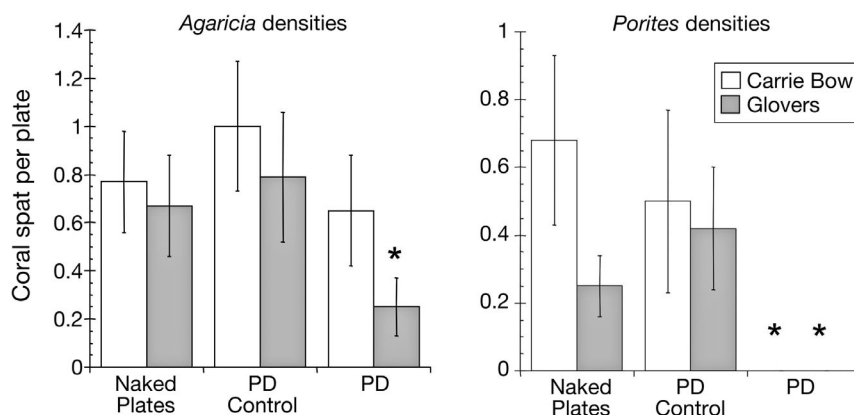


Fig. 4. Population density of newly settled corals for the 2 most abundant genera: *Agaricia* and *Porites* at both study reefs. *Significant differences compared to parrotfish deterrent (PD) control and 'naked' control

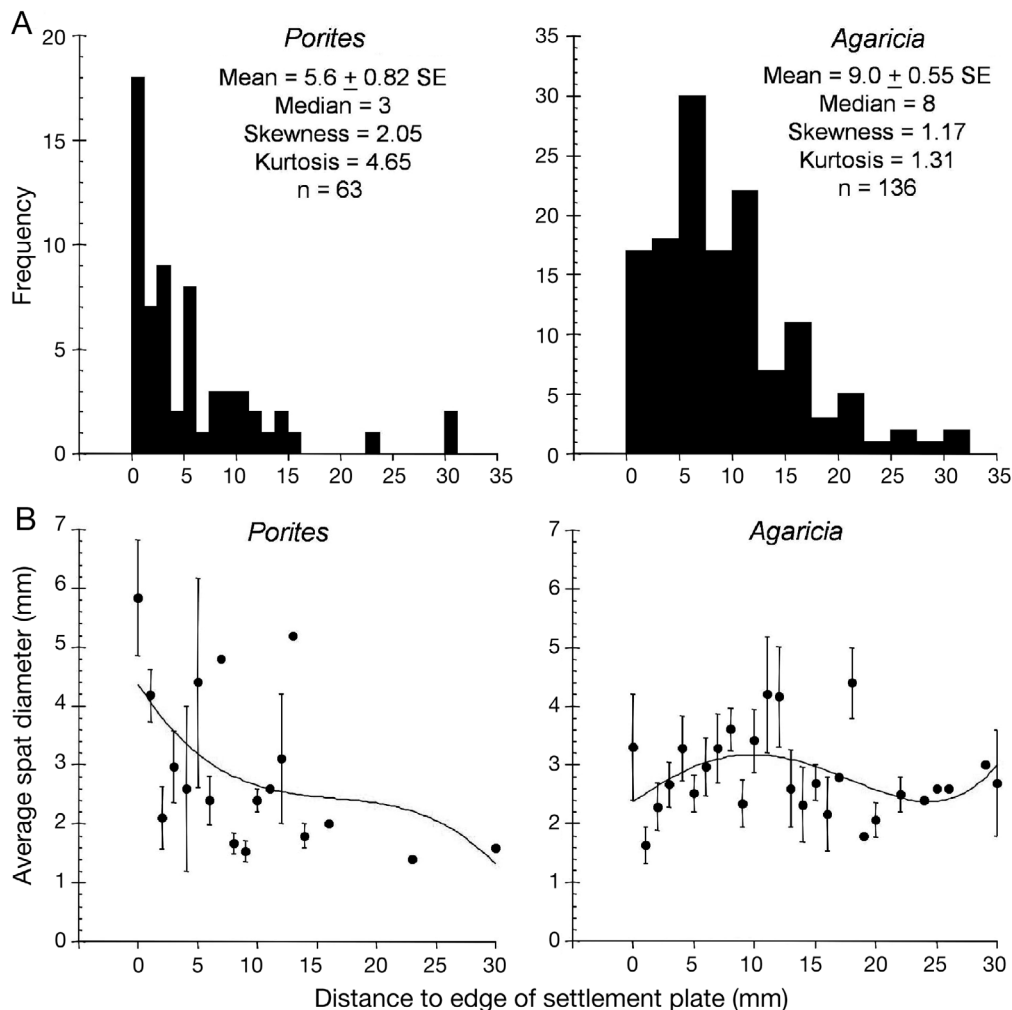


Fig. 5. (A) Frequency of coral spat with distance from the distal edge on the underside of settlement plates. *Porites* recruits significantly closer to the outer edge ($p < 0.01$; see text). (B) Average size per mm size class (\pm SE) (i.e. spat size rounded to nearest mm size class) of newly settled corals with distance to outer under-side edge

ment plates (Fig. 5A). The mean distance to the edge was 5.6 and 9.0 mm for *Porites* and *Agaricia*, respectively (Student's $t = 3.58$, $p = 0.0005$, $df = 125$). The distance-frequency for *Porites* settlement was strongly skewed to the left (mode of 0 mm from the edge of the settlement plate) as reflected in its higher degree of skewness and kurtosis relative to *Agaricia* (Fig. 5A). In our other studies of coral spat on terra-cotta plates at 10 m that were monitored every 2 to 4 mo from March 2004 through August 2005, we found *Porites* settlement was greatest in early summer (i.e. over 70% of *Porites* spat were observed during the month of June), and spat settled within the underside area from the edge to about 1.5 cm from the edge (average distance from the edge: >5 mm) (S. Arnold unpubl. data). The pattern of no preferential settlement near the edge of the plate did not change during periodic observations over the year. The spat that did settle early but away from the edge of the plate appeared not to have grown much over the course of the year. Thus

we interpret the differences in coral size with respect to the edge as relating to differences in coral growth rates.

The largest and thus most rapidly growing newly settled *Porites* were near the distal edge on the underside of settlement plates (Fig. 5B). *Agaricia* sizes and growth rates were relatively unchanged with distance from the plate edge (with a possible maximum 10 mm from plate's edge). The size of recently settled corals on settlement plates reflects both the timing of settlement and their subsequent rates of growth. We assumed that for any given settlement event there was no systematic temporal difference in habitat selection so intraspecific differences in size reflect differences in growth rates.

Coral recruitment densities declined with algal abundance surrounding settlement plates (Fig. 6). We pooled all treatments and observed that *Porites* declined more precipitously than *Agaricia* as a function of local macroalgal abundance.

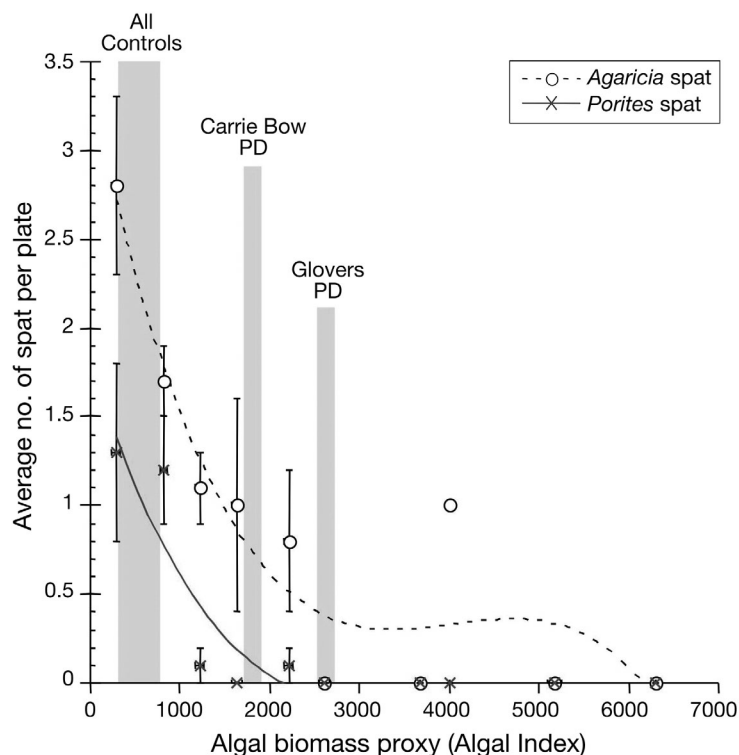


Fig. 6. Population density of newly recruited corals (\pm SE) as a function of algal biomass surrounding the settlement plates at Carrie Bow and Glovers. All treatments and sites are pooled but algal abundance recorded for parrotfish deterrents (PD) treatment and controls are represented by vertical gray bars. None of the macroalgae was physically in contact with coral spat growing on the underside of settlement plates. Best fit curves were 3rd order polynomial for both taxa; $R^2 = 0.53, 0.40$ for *Porites astreoides* and *Agaricia*, respectively

Scaling up parrotfish deterrent manipulation to ecosystem stability

When the bite rates upon PDs were scaled to a community-wide impact on total parrotfish grazing (Eq. 1), the total grazing intensity was predicted to fall by 52% from 1.14 to 0.55 h^{-1} . Converting this to a proportion of reef grazed, the PD manipulation was equivalent to a decline in grazing from 0.3 to ~0.15 (Eq. 2). Given a coral cover at the study sites of ~15% (mean ranging between 12 and 17%), the change in reef state was superimposed upon a plot of reef equilibria (Fig. 7A). It can be seen that a 52% fall in grazing at a coral cover of 15% is predicted to shift the system from one basin of community attraction to another. At the higher level of grazing, coral population dynamics tend towards the upper stable equilibrium and would therefore tend to exhibit a trajectory of recovery, with recruitment and growth exceeding mortality. In contrast, the reduction in grazing crosses an unstable equilibrium (threshold), resulting in the system

becoming driven towards a coral-depleted state, rich in macroalgae.

The proposed mechanism for development of a coral-depleted system state is a bottleneck in recruitment. The model can be used to illustrate this mechanism. A simulation of coral trajectories under the experimental PD manipulation versus full grazing reveals divergent pathways as expected from the location of reefs on either side of the unstable equilibrium (Fig. 7B). Censusing the size distribution of corals as they approach equilibrium (Fig. 7C) reveals that the low grazing system does not possess enough juvenile corals (sizes 14 to 60 cm^2) to sustain larger size classes. Under high grazing, cohorts move through size classes resulting in an accumulation of large adult corals (Fig. 7C). Note that higher settlement was found in the low grazing model because (1) the system was modeled conservatively as completely open and (2) because space occupied by macroalgae is more dynamic than that of adult corals (which dominate the high grazing treatment) and therefore allows for greater coral recruitment, albeit with high post-settlement mortality. Note also that the model differs slightly from the experiment in that it does not attempt to model pre-recruitment processes; corals enter the population at a diameter of 1 cm. However, despite this ontogenetic offset between the model and experiment, both found an algal-driven bottleneck in the population dynamics of corals associated with early ontogeny.

DISCUSSION

By locally and modestly impeding the grazing rates of large parrotfish (Fig. 2A,B), PDs created micro-phase shifts of elevated algal abundance (Figs. 1C & 3). These phase shifts depressed coral recruitment nonlinearly within the algal dominated footprint (Fig. 6). Algal domination was greatest inside the parrotfish deterrent crowns so herbivory was the most likely driver of algal abundance. All of this suggests that processes controlling algal abundance indirectly control the recruitment potential of coral reef ecosystems (sensu Steneck & Dethier 1994) for settling corals and create the reinforcing feedbacks necessary for alternative attractors.

Since coral mortality initiates reef phase-shifts from coral dominance to some other dominant(s), the struc-

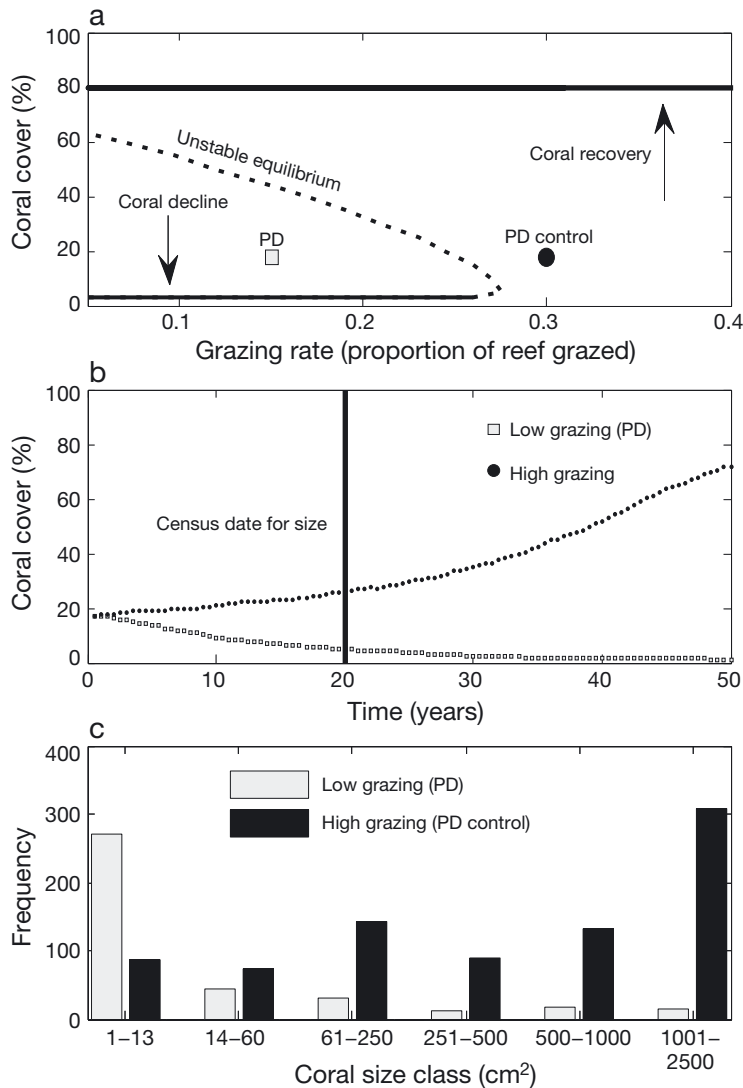


Fig. 7. Projected ecosystem effects of the experimental manipulation of grazing. (A) The system's stable (solid lines) and unstable equilibria (dotted line) in the absence of perturbation. (B) Projected long-term trajectories of coral assemblages under experimental grazing in the absence of external perturbation. (C) Predicted size distributions of corals under experimental grazing levels censused after 20 yr. PD: parrotfish deterrent

turing processes in place at that time will likely canalize succession in ways that can affect coral recruitment and the likelihood of coral reef ecosystems returning to coral dominance. Succession can result in myriad alternative states for coral reefs such as soft corals, other colonial cnidarians and sponges (Norström et al. 2009). However, despite those end results, virtually all coral reefs at first become colonized by algae following disturbances simply because they are ubiquitous and can respond most rapidly. Of all possible phase shifts, those to algal dominance are most common (Hughes 1994, McManus & Polsenberg 2004). However, depending upon herbivory, productivity,

and succession, algal community structure may stabilize at different end point functional groups ranging from encrusting coralline algae that can facilitate coral recruitment (Arnold et al. 2010), to diminutive to modest-canopy height filamentous algal turfs, and finally to taller-canopy macroalgae that can inhibit coral recruitment in their nursery microhabitats (Birkeland 1977, reviewed in Steneck 1988). In essence, as algal biomass and canopy height increase, coral reefs become more hostile to recruiting corals.

Of the 2 corals commonly recruiting in our experiment, *Porites astreoides* is a reef builder (Pandolfi & Jackson 2006), and it may be most susceptible to light effects from macroalgal phase shifts. As with most reef-building corals, it has small feeding polyps, may be more autotrophic (Porter 1976), and thus requires higher light for growth and survival. In contrast, the larger polyped *Agaricia* may be more heterotrophic, allowing it to occupy more habitats as an opportunistic or fugitive species. The requirement for microhabitats having a higher productivity potential may also explain the proclivity of *Porites* to settle and grow most rapidly in high light nursery microhabitats on the distal underside edge of settlement tiles (Fig. 5A,B). Subcryptic nursery habitats for newly settled corals are important for keeping this vulnerable stage relatively safe from predators and competitors so that with modest growth they will be under full sunlight. Other studies found that when *P. astreoides* larvae contact *Dictyota* spp. macroalgae, the larvae die or fail to recruit (Paul et al. 2011). Taken together, our results and those of other studies (Arnold et al. 2010) suggest that algal abundance regulates the process of coral recruitment by reducing or eliminating coral nursery

microhabitats, and thus is the proximate 'driver' of recovery in Caribbean coral reef ecosystems (Fig. 8).

Ecological cascades can be of several forms. Best known are trophic cascades (e.g. Paine 1980), but there are others including those involving ecosystem engineers (Jones et al. 1997). All require a functional—and often sequential—nexus with strong interactors and their associated processes. These create reinforcing feedbacks in the physical-biological system that self-organizes towards different alternative states (Rietkerk et al. 2004). Such ecological cascades and feedbacks transmitted from herbivory to algal development and finally to coral recruitment have

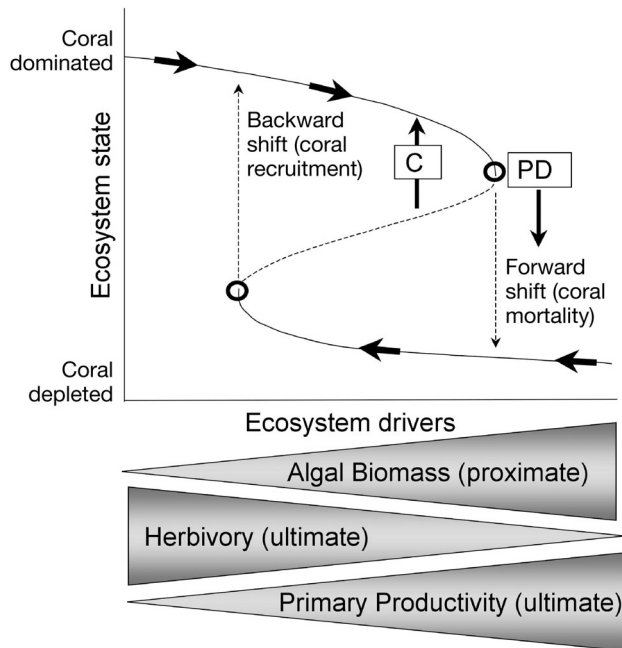


Fig. 8. Alternative attractors as traditionally illustrated (e.g. Scheffer & Carpenter 2003) with ecosystem state varying as a function of environmental conditions or parameters ('ecosystem drivers'). The strength of the driver is indicated by the width of the wedge. Circles represent bifurcation points. The right bifurcation forward shifts to a coral depleted state (down arrows). To the right of this point, coral recruitment and ecosystem recovery may be impossible. Left of this point towards the backward shift bifurcation (up arrows) reflects the hysteresis lag for recovery to a coral dominated state. Left of the backward shift bifurcation indicates ecosystem drivers without hysteresis for recovery. Solid curved lines denote stable states to the bifurcation points that have basins of attraction that will move the ecosystem towards those coral dominated (upper) or coral depleted (lower) states. Dotted curved line denotes an unstable state that will shift backwards to coral dominated if above, or forward to a coral depleted state if below that line. Solid upward arrow indicates perturbations that will move the ecosystem state towards recovery to the previous state; and solid downward arrow indicates perturbations that will move the system to the coral depleted state with little chance of rapid recovery. Note the relatively small difference between control (C) and parrotfish deterrent (PD) experiments resulting in a large difference in the capacity of the ecosystem to recover from perturbations

also been proposed for coral reefs (Mumby & Steneck 2008), but, as far as we know, never tested with experiments for only the role of large herbivores (but see Jayewardene 2009 for experiments demonstrating the proportionately greater reduction in algal abundance by large parrotfish).

Locally elevated algal abundance developed around PDs at both study regions. However, subtle differences in algal abundance between the regions could be important. Both reefs were qualitatively similar and PD treatment effects excluded the reef building coral

Porites at both. However, *Agaricia* recruitment declined significantly only at Glovers. The simplest explanation for this result is that the magnitude of the PD effect on algal biomass (i.e. cover, canopy height and hence the algal index) was greater at Glovers, both in absolute terms (algal index in the PD treatment was 1.6 times greater at Glovers than Carrie Bow) and in relative terms, with PDs causing a 4.3 fold rise in algal index at Glovers compared to only a 2.2 fold rise at Carrie Bow (Fig. 6). This regional difference may have only a modest effect on *Agaricia*, a low, light-tolerant (perhaps more heterotrophic) coral more suited to persisting under moderate algal growth at Carrie Bow than the larger algal bloom at Glovers (Figs. 4 & 6). Understanding what drives such subtle but potentially important geographic differences in algal abundance may help explain differences in rates of recovery following perturbations in these ecosystems.

The ecological processes of primary productivity and herbivory drive algal abundance, which causes declines in coral recruitment (Steneck & Dethier 1994; Fig. 8). Parrotfish deterrent results illustrate the importance of herbivory from large parrotfishes. Note that the Carrie Bow site had overall higher bite rates from parrotfishes, but they were primarily small fish (Fig. 2A). Thus the high frequency of low intensity herbivore-induced disturbance and relatively few large parrotfish maintained an overall lower algal abundance in PD treatments at Carrie Bow compared to Glovers reef (Figs. 2 & 3). This may be due to higher algal growth rates and productivity at Glovers. Elevated productivity potential of the environment could result from Glover's higher wave exposure and water flow that increases nutrient delivery and gas exchange due to its relatively long fetch and incident wave exposure (Mumby et al. 2014). Glovers' fetch is functionally unlimited (>100 km, see Ekeboom et al. 2003) whereas Carrie Bow is in the lee of Glovers 20 km up wind (Fig. 1A; see arrows indicating wind direction). Future studies will examine the impact of the PDs under a wider range of bottom-up and top-down forcing functions. Indeed, the position of thresholds (at or near bifurcation points) would be expected to change with shifts in the driving processes of productivity, herbivory or both (Fig. 8 bottom).

At some low level of algal biomass resulting from high rates of herbivory, low rates of productivity or both, the reef ecosystem will be unaffected by the negative effects of algae (left of the backward shift bifurcation point; Fig. 8). At that point, reefs recover without hysteresis lags. This condition has been described in concept as 'surplus herbivory' (Mumby & Steneck 2008). It represents the conditions where

even massive coral mortality does not result in a persistent phase shift to macroalgae. Under those conditions we would not expect to see micro-phase shifts resulting from parrotfish deterrents. We intend to test this prediction in future studies to compare results with what we found in Belize.

To scale up to an entire reef the consequences of the 52% reduction in parrotfish grazing resulting from PDs, we developed a field-tested ecosystem stability model for the Belize reef ecosystem. The model predicted that a shift in grazing of this magnitude would cause the ecosystem to flip from a coral-dominated basin of attraction to an alternative, algal-dominated basin. This switch in attractor occurs in the model because a rise in algal cover reduces the rate of coral recruitment until it can no longer sustain the population (Mumby et al. 2013c). Here, by experimentally manipulating herbivory, we show that the model behavior is borne out empirically; the micro phase shift of algae drastically reduces coral recruitment. The pivotal role of macroalgae on coral recruitment also helps interpret the hysteresis predicted by models of the ecosystem (Figs. 7 & 8). The unstable equilibria that distinguish alternative basins of attraction (diagonal curve in Fig. 7) reflect the interaction of coral cover (y-axis) and grazing rate (x-axis) on the intensity of grazing upon macroalgae, assuming no differences in rates of primary productivity. When coral cover is low, a high grazing rate (number of herbivores) is needed to exert sufficient constraints upon macroalgae that a bottleneck in coral recruitment is avoided (Fig. 7). However, increases in coral cover reduce the foraging area available to grazers and therefore intensify grazing. This increase in grazing intensity with rising coral cover has been demonstrated experimentally (Williams et al. 2001). When coral cover is high, fewer grazers are needed to generate sufficiently intense grazing that coral recruitment is maintained. Thus, unstable equilibria represent an isocline of grazing intensity from high-coral/low-grazing rate to low-coral/high-grazing rate. We also note that increases in macroalgae might exacerbate negative reinforcing feedbacks by further reducing grazing, poisoning or reducing reproductive output of corals (Hoey & Bellwood 2011, Rasher & Hay 2010, Foster et al. 2008, respectively).

We focused on the importance of cascading processes on system stability, beginning with how modest changes in the process of herbivory (i.e. reduction of disturbance intensity from large parrotfish) affect algal biomass. This in turn affected and even halted the process of coral recruitment for *Porites* species now known to dominate contemporary coral reef

frameworks in the Caribbean (Pandolfi & Jackson 2006). While coral recruitment is essential for the recovery of this ecosystem following a perturbation, the overall effect of cascading processes involving herbivory, algal productivity, and coral recruitment complicates and makes less predictable how this ecosystem behaves.

We are not arguing that our experiments prove the existence of alternative states. Rather, we provide mechanistic evidence from our experiment that a modest reduction in grazing is sufficient to shut down coral recruitment. We provided empirical support for the theoretical mechanisms and feedbacks that drive alternative attractors (sensu Scheffer & Carpenter 2003), which could lead to alternative stable states on coral reefs. While little mystery remains why coral dominance declines on reefs (i.e. from bleaching events or disease), few experimental studies have focused on what prevents them from recovering. Our experiments showed that modest reductions only in herbivory from large parrotfish allow macroalgae to bloom, which creates a bottleneck in the process of coral recruitment, thereby driving conditions at our 2 study regions towards a 'catastrophic bifurcation' (sensu Scheffer & Carpenter 2003; Fig. 8) from which recovery is stopped (e.g. for *Porites*) or greatly slowed. Our empirical study, together with mechanistic models, strongly support the supposition that Caribbean reefs exhibit nonlinear dynamics resulting in persistent algal-dominated states.

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