

## ECOLOGY

# Attenuating effects of ecosystem management on coral reefs

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Managing diverse ecosystems is challenging because structuring drivers are often processes having diffuse impacts that attenuate from the people who were “managed” to the expected ecosystem-wide outcome. Coral reef fishes targeted for management only indirectly link to the ecosystem’s foundation (reef corals). Three successively weakening interaction tiers separate management of fishing from coral abundance. We studied 12 islands along the 700-km eastern Caribbean archipelago, comparing fished and unfished coral reefs. Fishing reduced biomass of carnivorous (snappers and groupers) and herbivorous (parrotfish and surgeonfish) fishes. We document attenuating but important effects of managing fishing, which explained 37% of variance in parrotfish abundance, 20% of variance in harmful algal abundance, and 17% of variance in juvenile coral abundance. The explained variance increased when we quantified herbivory using area-specific bite rates. Local fisheries management resulted in a 62% increase in the archipelago’s juvenile coral density, improving the ecosystem’s recovery potential from major disturbances.

## INTRODUCTION

Many of the world’s resource management agencies are legally mandated to use an ecosystem-based management (EBM) approach (1). EBM approaches might simply limit the impact of an activity on the wider ecosystem (2) or take a more proactive approach to generate beneficial conservation outcomes (3). Regardless of the intent, it is important to understand the link between human activity, which typically involves harvesting, and the ecosystem response. Cause-and-effect relationships of these interactions are well established in some less diverse ecosystems. Classic examples include “trophic downgrading,” in which the loss of large apex consumers affects the structure and functioning of large ecosystems (4). Among the best-known examples are keystone predators, such as the sea otter of Alaska’s Aleutian Islands (5), whose exploitation allows urchin populations to expand and graze kelp beds into barrens. In that case, a trophic cascade (that is, impacts evident over at least three trophic levels) involves a limited number of key species that interact strongly (killer whales, otters, urchins, and kelp) and drive the ecosystem’s structure and function (5). However, more diverse ecosystems tend to have more diffuse interactions involving many species (6). Understanding the links between human actions and ecosystem responses is more challenging under these circumstances, and evidence in support of management, especially at the scale of ecosystems, is more likely to be equivocal and controversial. However, an absence of clear causal evidence of human impacts in complex ecosystems can arise for multiple reasons and should not necessarily be taken as evidence of no human effect.

In marine ecosystems exploited by humans, evidence of impacts can be strongly influenced by several factors. First, the number of ecological interactions between a human activity and the ecosystem’s structure is important. This can lead to successive attenuation of management impacts with each ecological step. A resulting attenuation of the “management signal” may occur because each ecological step (or level) adds variance from other ecological processes that could collectively obscure

the intended impact of management (Fig. 1). Few studies have explicitly considered this attenuation of management signals, yet this phenomenon might explain apparent discrepancies between controlled small-scale experimental and larger observational studies of ecosystem dynamics.

Other challenges in measuring human impacts on ecosystems include selecting and quantifying appropriate response variables. This task is particularly difficult for studies of ecological cascades because the causative mechanisms act through ecological processes that can be difficult to measure directly and may have confounding effects that increase variance with each ecological step. An additional problem is the common practice of substituting easily measured state variables such as “population density” or “biomass” of consumers as surrogates of ecological processes such as predation or herbivory. This state variable grouping might be a poor proxy of an ecosystem process when it ignores species-specific differences in rates among consumer species such as parrotfishes.

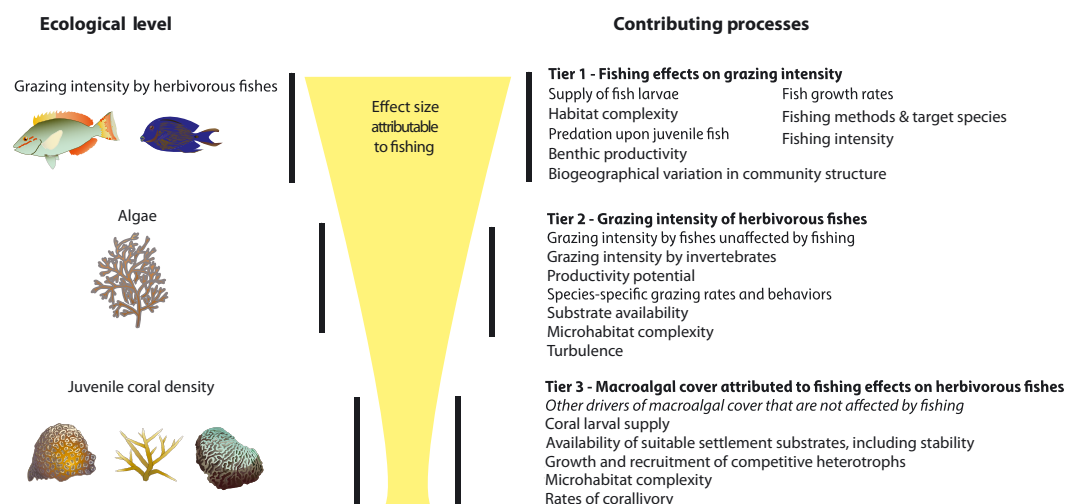
Here, we study the attenuation of fisheries management impacts across multiple ecological levels in a complex Caribbean coral reef ecosystem. We used a large-scale but hierarchical study design to determine whether limiting fishing pressure (via fisheries closures or “reserves” where fishing is heavily managed or completely prohibited) can foster diffuse but sufficiently strong ecological cascades to affect coral recruitment and thus the resilience of coral reef ecosystems. Specifically, fisheries-induced declines of herbivorous fishes can allow seaweeds to proliferate, which then reduces the recruitment of corals through competition or by disrupting connectivity (7, 8). Experimental studies of the candidate processes are well established; fishing can reduce herbivore populations (9), herbivores can influence seaweed (macroalgae) abundance (10–12), and seaweeds can suppress coral recruitment (8, 12). However, large-scale empirical demonstrations of an overarching relationship between fishing and coral recruitment have mostly been extrapolated from relatively small experimental scales (10–15). Moreover, recent larger-scale studies found no significant relationships between local human impacts and either algal abundance or coral recruitment (16, 17). Therefore, this ecological cascade is ripe for study at large scales, particularly through the lens of attenuating drivers, which might mask detection of significant positive management effects.

We stratified our sampling design to minimize confounding effects of the environment by sampling along the eastern Caribbean

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**Fig. 1. Factors contributing to the attenuation of effect size attributable to fishing on coral reef ecosystems.** Each tier has sources of variability that can reduce the signal-to-noise transmission of fishing effects to lower ecological levels such as fostering juvenile corals.

archipelago on low islands that experience relatively little runoff, have no upstream source of eutrophication, are physically separated by strong ocean currents, and thus have only modest or no interisland connectivity (18). We asked whether the local “management signal” from restricted fishing remains evident despite attenuation across successive trophic levels or “tiers,” from humans to fish (importantly including herbivorous fishes; first tier), to seaweeds or “algae” (second tier), to juvenile corals (third tier; Fig. 1). We also illustrate the degree to which the signals from widely used proxies of ecological processes may degrade with each tier of interaction (that is, Fig. 1) and asked whether the use of more accurate grazing metrics may decrease management signal attenuation through these tiers. Our study used identical methods to quantify and compare results by first using a simple proxy of herbivory (total biomass of herbivorous fishes) and then one in which we included key components of the driving process of herbivory such as effects of species composition, body size, habitat complexity, and the area available for feeding. The latter approach was designed to be a more explicit measure of grazing pressure on reef substrata occupied by algae and juvenile corals. We point out that the use of more accurate—but time-consuming—grazing metrics is not, in itself, novel (19–21), but their ability to clarify an ecological relationship of management significance has not previously been measured.

## RESULTS

### Tiered effects of fishing

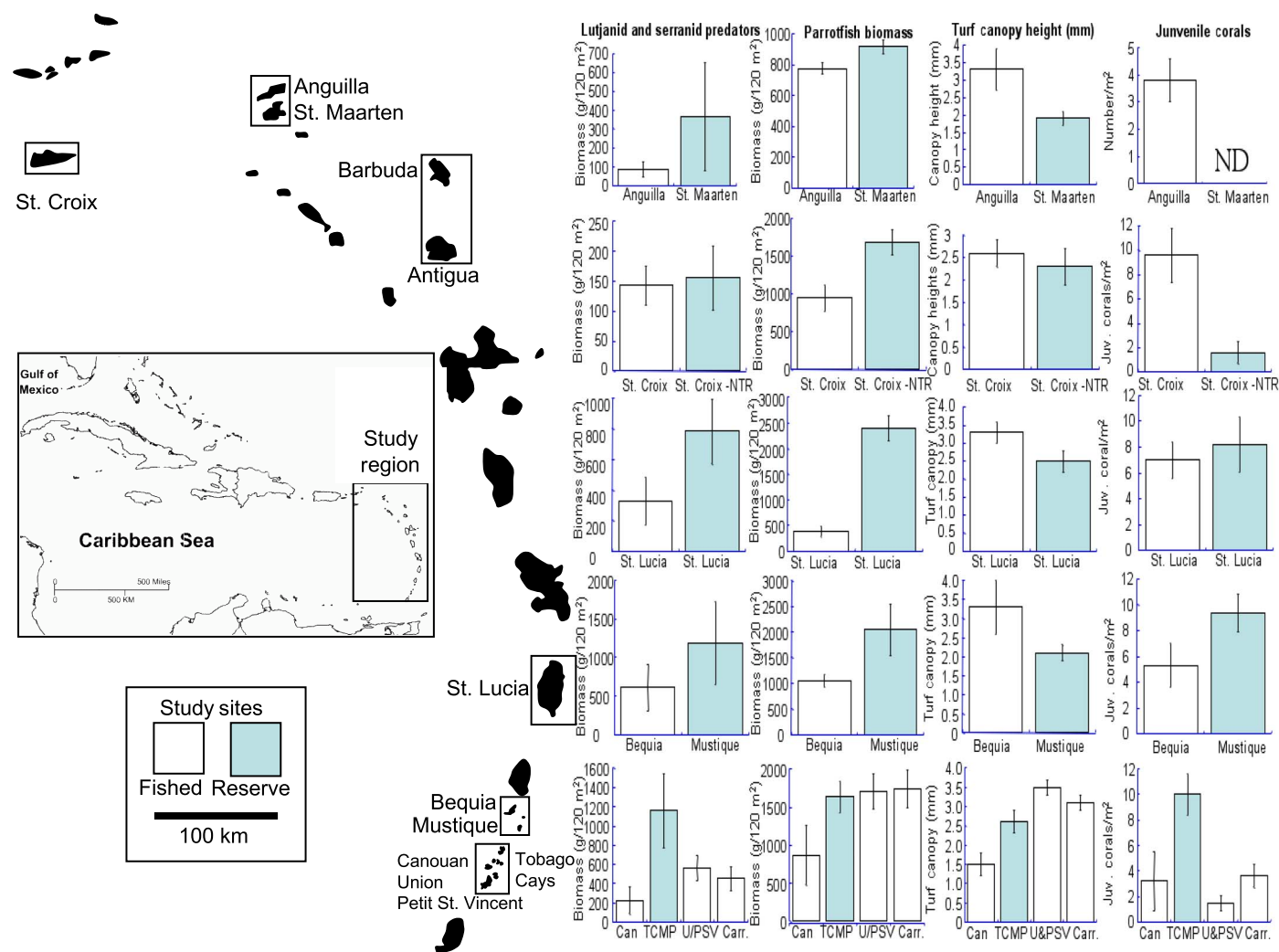
In the first tier of management impacts, fishing reduced the overall biomass of targeted reef fish. The average biomass for targeted predatory fishes (serranids and lutjanids) was 290 and 728 g/120 m<sup>2</sup> for fished and no-take reserves, respectively ( $n = 443$  transects; table S1). Similarly, parrotfish abundances were 944 and 1736 g/120 m<sup>2</sup> for fished and no-take reserves, respectively (table S1). Thus, the no-take reserves were largely effective, being associated with significantly higher fish biomass. However, to capture the regional context, we also compared geographically paired treatments (Fig. 2).

Regional island comparisons between fished and no-take reserves showed increased biomass among targeted predatory and herbivorous fishes (Fig. 2). The percent variance explained by those variables at this first tier of fishing impact ranged from a high of 37% for

parrotfish to a low of 12% for surgeonfish (Fig. 3). Highly targeted fish, such as groupers and snappers, also showed consistently negative effects of fishing (25 and 22% of the variance of fish biomass loss were explained).

The second tier of impacts, or those once removed from human fishing effects, focused on the impacts of reserves on algal abundance given that higher abundances of herbivores may reduce algal abundance. The only significant result from this analysis was a reduction in the canopy height of filamentous algal turfs (Figs. 2 and 3) such that canopies were 2.26 mm in reserves ( $\pm 0.13$  SE) and 3.06 mm ( $\pm 0.24$  SE) in fished areas ( $P = 0.007$ ). This difference was reflected in all among island comparisons (Fig. 3), and fishing pressure explained 20% of the variance in turf canopy height (Fig. 3). When we looked specifically at the direct relationship between herbivore biomass and metrics of algal volume using hierarchical models, we found no relationship ( $P \geq 0.36$ ). One of the reasons for this was high interisland variation, as evidenced by random effects explaining up to 98% of variation and the existence of weak underlying negative Pearson correlations between parrotfish biomass and both turf canopy height ( $r = -0.21$ ,  $P = 0.003$ ) and macroalgal cover ( $r = -0.25$ ,  $P < 0.001$ ). We mention these correlations, indicated by dashed lines in Fig. 3, only to highlight the potential for meaningful ecological interactions. The biomass of surgeonfish exhibited no relationship with any aspect of algal assemblage structure (for example,  $P = 0.79$  and  $P = 0.77$  for macroalgal cover and turf canopy height, respectively, in hierarchical models). Moreover, neither algal metric was correlated to surgeonfish biomass ( $r = 0.18$ ,  $P = 0.22$  for macroalgal cover;  $r = 0.04$ ,  $P = 0.78$  for turf canopy height) because they were with parrotfish biomass.

The percent cover of algae, in general, and algal turfs, in particular, is not very informative because they vary inversely as a function of the cover of live coral and other space-occupying organisms on hard substrate. If corals die, turf algal cover invariably increases, but because that pattern is correlated with the abundance of other space occupiers on reefs, it conveys no new information. In contrast, with thick (high canopy) algal turfs being lethal to settling corals (8), low canopy height in turf algae is both a good indication of strong herbivory and improved conditions for coral recruitment [for example, see the studies of Arnold *et al.* (8) and Jorissen *et al.* (22)]. An accounting of the major space occupiers is shown in table S1.



**Fig. 2. Study sites and organism abundances along the eastern Caribbean archipelago.** Study regions and setting (left) with mean abundance data for predatory fishes, parrotfishes, turf algal canopy heights, and juvenile corals (right). Variance is expressed as SEM. ND, no data; NTR, no-take reserve; Can, Canouan; TCMP, Tobago Cays Marine Park; U/PSV, Union and Petit St. Vincent; Carr, Carriacou.

The sea urchin, *Diadema antillarum*, is an important herbivore when its population density exceeds “functional population densities” of  $1/\text{m}^2$  (23). In our study, *Diadema* rarely approached functional densities in any region. High densities were patchy and sufficiently minor to suggest that they do not have an effect at the scale of our study (that is, only 3 of 178 transects had functional densities).

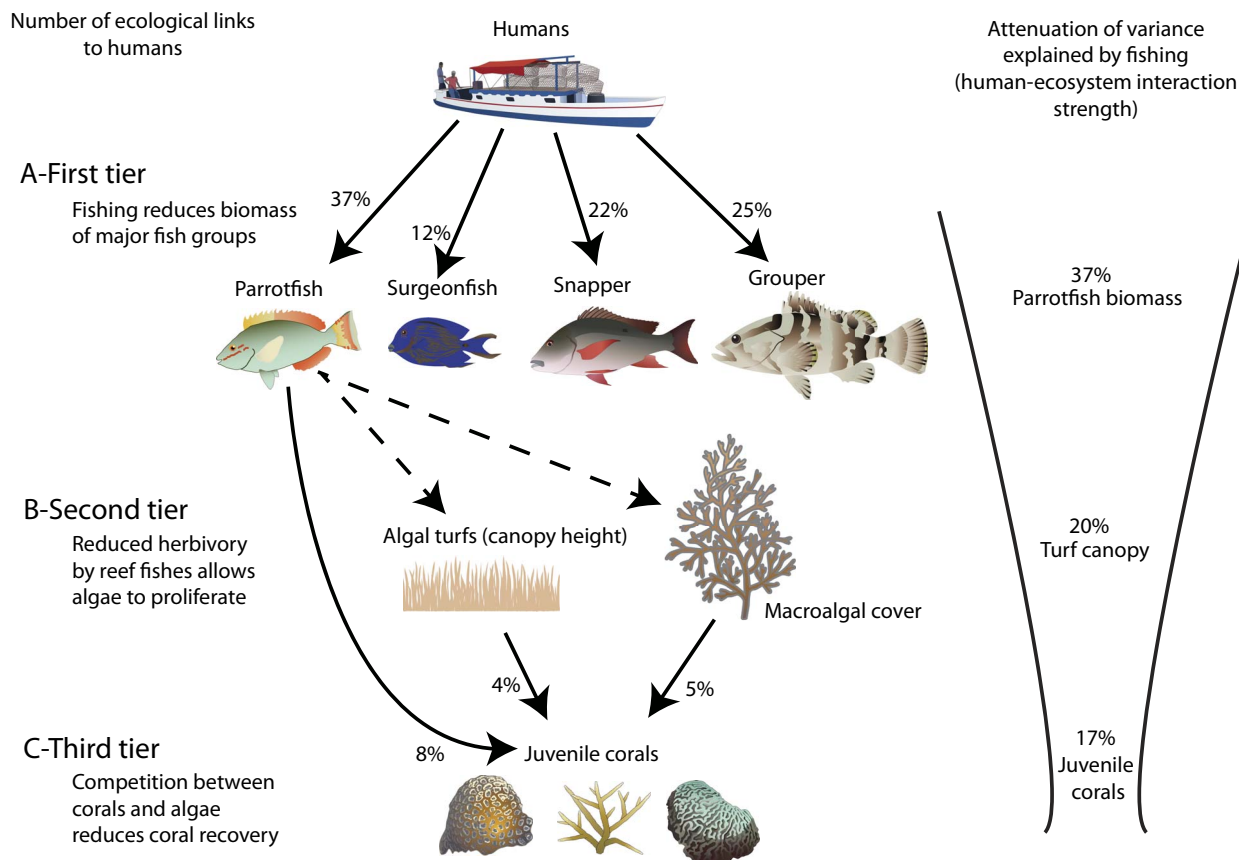
The third tier links fishing management impacts indirectly to the abundance of juvenile corals (that is, corals  $\geq 40$  mm in diameter). The dominant species of juvenile corals found throughout our study were the same species we found dominating the coral reefs (fig. S1). Overall, fishing management explained only 17% of the variance in juvenile coral density ( $P = 0.003$ ; Fig. 3). Juvenile corals were more abundant at our southern sites compared to our northern sites (Fig. 2). At this large scale, there was a weak but significant negative impact of turf canopy height (4% of variance) and macroalgal cover (5% of variance) on juvenile coral density. Parrotfish biomass alone only explained 8% of variation in the density of juvenile corals, with a positive impact (Fig. 3). The overall pattern suggests that the effects of key drivers (fishing pressure and region) attenuate from explaining a maximum of 37% of

variance in parrotfish biomass to 20% of variation in turf algal cover to a low of 17% of variance in juvenile coral density (that is, right side of Fig. 3).

### Scaling drivers to coral reefs

Large-scale abstractions of ecosystem processes on coral reefs are often oversimplifications. Parrotfish grazing pressure varies according to body size (that is, grazing intensity) and species-specific bite rates (that is, grazing frequency; Fig. 4, A and B), relative to the area upon which they can graze (Fig. 4C). We quantified and integrated these factors into what we call the “parrotfish grazing pressure” metric (see Materials and Methods).

When we applied the approach of integrating intrinsic differences among parrotfishes (Fig. 4, A and B) relative to grazable reef surface area (that is, parrotfish grazing pressure; Fig. 4C), a much higher proportion of variance in both algal assemblage metrics was explained (Fig. 5A); our more precise parrotfish grazing pressure metric significantly explained 18 and 27% of the variance in turf canopy height ( $P = 0.04$ ) and macroalgal cover ( $P = 0.03$ ), respectively (Fig. 5, B and C). A similar



**Fig. 3. Three tiers of measured effects from human fishing activities to juvenile corals.** **Left:** Ecological processes expected that result from managing fishing pressure (that is, “first tier”). **Middle:** Solid lines indicate statistically significant results with the proportion of variance explained between each tier. Dashed lines indicate significant correlations across the data set, but the clarity of these relationships was swamped by interregional variation in hierarchical models. **Right:** Aggregate attenuation of variance explained by fishing to juvenile corals.

phenomenon occurred when linking herbivory with coral recruitment. The simple parrotfish biomass metric explained only 8% of juvenile coral density, whereas the more precise metric of parrotfish grazing pressure explained 23% of variance.

Moreover, juvenile corals showed a clear positive relationship with the frequency of parrotfish grazing (Fig. 5D). The relationship between algae and juvenile coral density was revisited through a more mechanistic lens based on earlier work, which suggests that algae can act as a gatekeeper to coral recruitment. Specifically, when inhibitory algae (from a coral perspective) are scarce, then a range of processes will affect recruitment, including larval supply. Thus, one would expect highly variable juvenile densities, but the potential exists for high levels. However, recruitment can be constrained once algae become sufficiently abundant or large enough to inhibit either the settlement or postsettlement survivorship of corals. Thus, a relationship would be expected between metrics of algal abundance and the maximum coral recruitment attained (for example, see Fig. 5E), as has been reported in both the Caribbean and tropical Pacific (8, 15, 24).

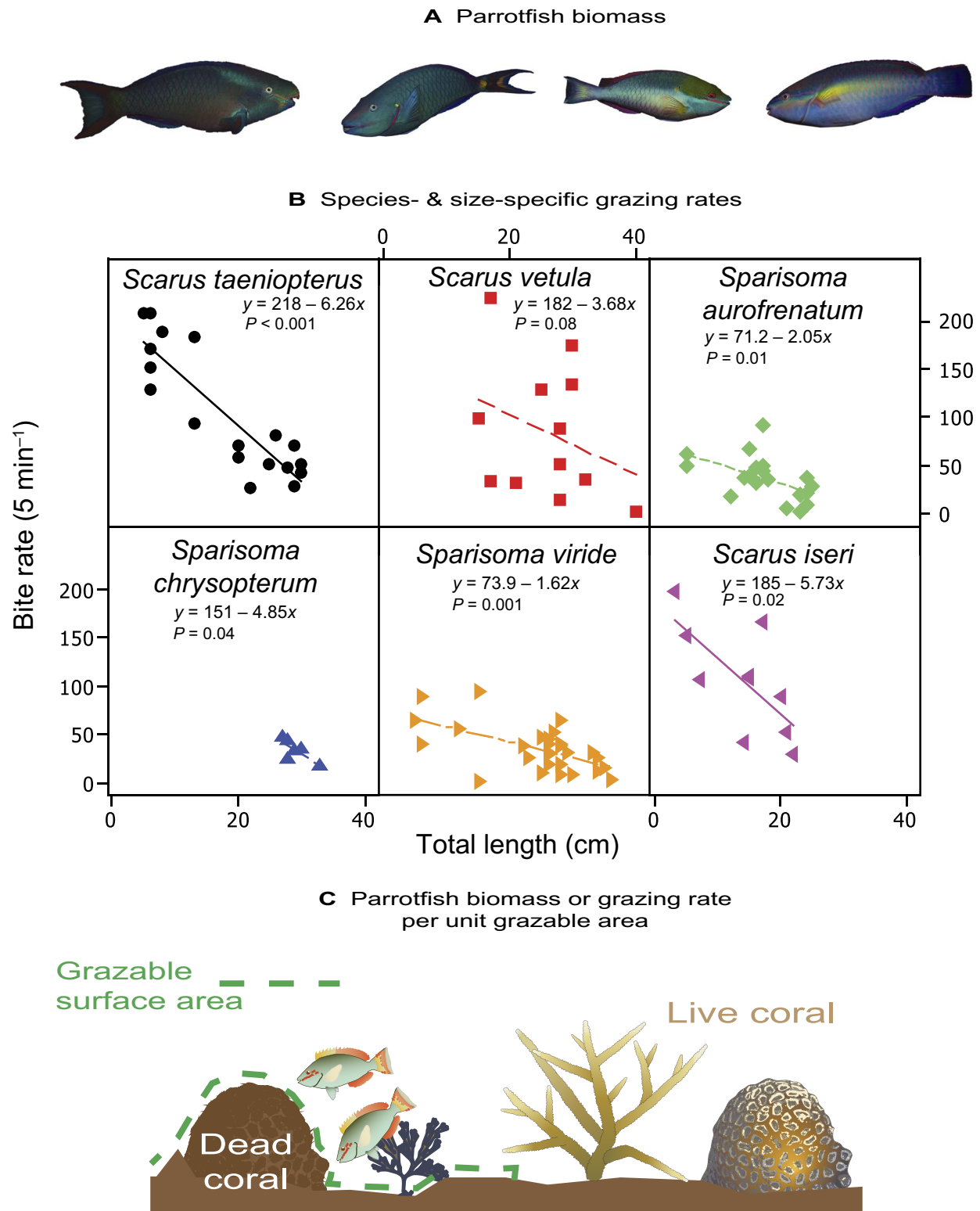
We used the maximum juvenile coral density per site as the response variable and considered several algal metrics including the mean and maximum values of turf canopy height, macroalgal cover, and macroalgal index (volume of macroalgae). We first ascertained which algal predictors were most appropriate using distance-based linear models (PRIMER) with the Akaike information criteria (AIC). This analysis

found that the best model used two predictors: mean turf canopy height and maximum macroalgal cover. When entered into a hierarchical mixed-effects model, both algal metrics contributed to explaining maximum densities of juvenile corals. Mean turf canopy height explained 23% of recruit variance ( $P = 0.004$ ), whereas maximum macroalgal cover explained a further 11% of variance ( $P = 0.048$ ; Fig. 5A). Region only explained 1%, and the remaining 65% of variance was unexplained. Note that mean algal turf canopy height and maximum macroalgal cover were uncorrelated (Pearson  $r = -0.3$ ,  $P = 0.12$ ). Often, differences on reefs were obvious when herbivorous fish or suitable substrates were rare (Fig. 5F, left and right, respectively).

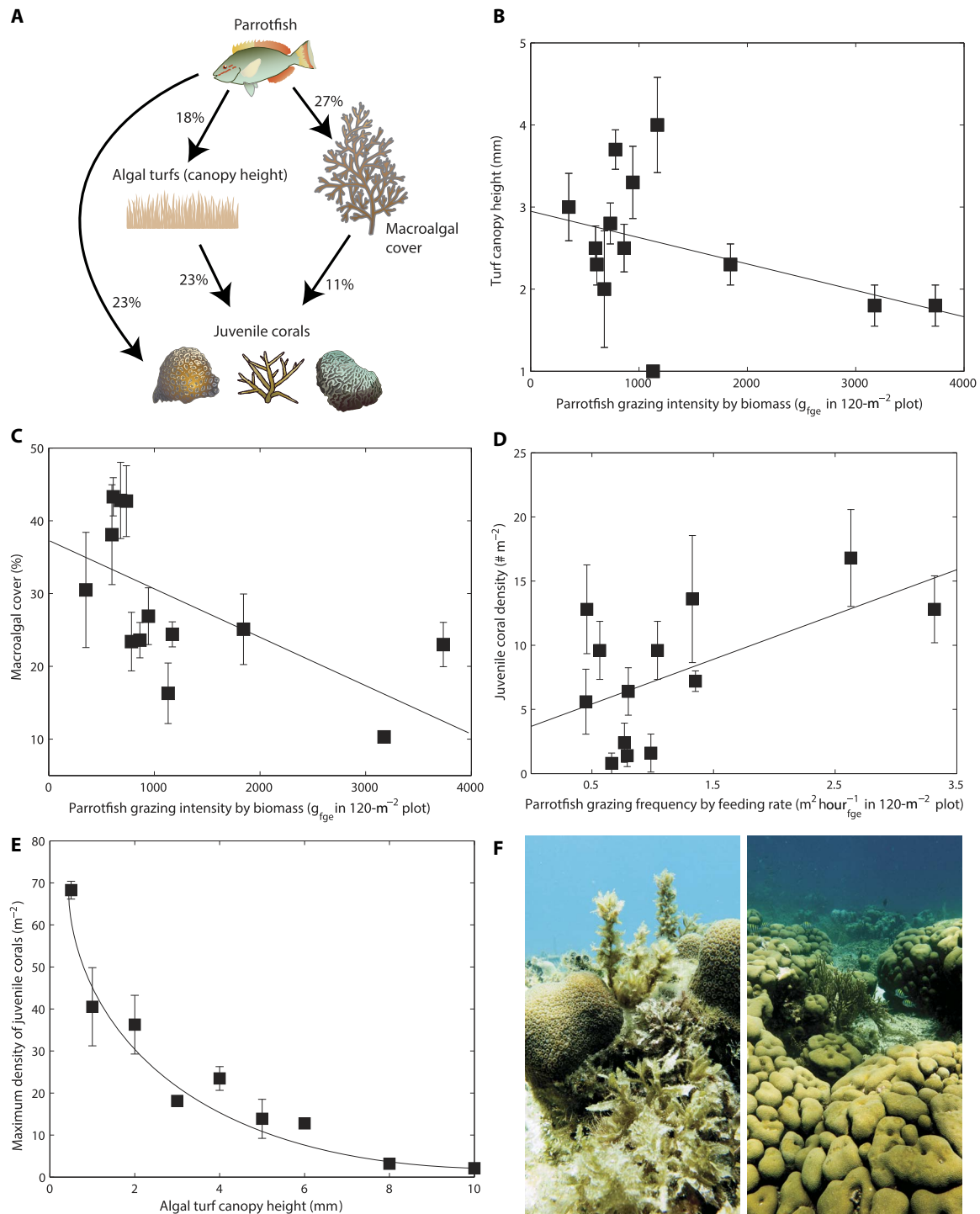
## DISCUSSION

We found that, in multiple independent island reefs, management actions improved the resilience of coral reef ecosystems. No-take reserves (as a proxy for managed fishing pressure) in the eastern Caribbean explained 37% of the variance in parrotfish biomass, but that translated to only 20% of the variance in algal cover explained and an even lower proportion (17%) of explained variance in the abundance of juvenile corals (Fig. 3). For coral reef managers, the coral response is most important. Thus, this attenuation of a fisheries management effect could erode stakeholder confidence for these management measures.





**Fig. 4. Species- and size-specific grazing pressure from parrotfish.** Illustration of relative grazing area. (A to C) Differences in parrotfish biomass (A) relative to species-specific bite rates (B) were applied to the “grazable” surface of the reef (C).



**Fig. 5. Mechanistic relationships between herbivory and coral recruitment.** (A) Proportion of variance explained by parrotfish grazing pressure for algal cover and juvenile coral density. Solid lines indicate statistical significance ( $\alpha = 0.05$ ), and the numbers represent the proportion of variance explained by each link. (B) Turf algal canopy height as a function of parrotfish grazing intensity (biomass). (C) Macroalgal cover as a function of grazing intensity. (D) Juvenile coral density as a function of parrotfish grazing frequency (bite rate). (E) Mean maximum juvenile coral density as a function of canopy height of algal turfs. (F) Photo illustrating reefs with low grazing pressure and high grazing pressure due to the scarcity of grazable (that is, noncoral) substrates (left and right, respectively). Variance is expressed as SEM. Photo credit: Peter Mumby.

There is no management panacea for any ecosystem and especially not for coral reefs. Certainly, stresses on reef corals from climate and atmospheric changes are serious and create real problems for this ecosystem (25). However, we suggest that local management measures can positively affect the trajectory of recovery of coral reefs and eventually their overall condition. We suggest that there is not a uniform blanket of death settling over coral reefs but neither are positive signs uniform among the best managed coral reefs. For example, St. Croix's no-take reserve around Buck Island had an excellent enforcement record after 2003 yet showed only modest increases in predatory fishes and declines in algal abundance (Fig. 2). This result may be because of a recovery lag, which can last decades after establishing marine reserves before targeted fisheries species and their function reach preharvest levels (26, 27).

### Measuring EBM effects through the fog of attenuating drivers

Coral reefs are complex ecosystems, in part, because they contain myriad species, any of which may be influenced by several ecological processes. This creates a challenge for managers using EBM. Characterizing the patterns of distribution and abundance of reef-dwelling organisms is easier than determining which processes "drive" those observed patterns. Nevertheless, there is consensus about a few key drivers for coral reef ecosystems. For example, it is well known that the accumulation of algal biomass reduces or halts the recruitment of reef corals [for example, see the studies of Birkeland (28) and Ritson-Williams *et al.* (29)]. Also, it is well known that virtually every study that caged out herbivores from a section of a coral reef resulted in increased algal biomass [for example, see the studies of Lewis (10) and Hughes *et al.* (12)]. Therefore, management regulating herbivory should affect algae, which is instrumental to the recovery phase of coral reefs. Although there are good small-scale experimental studies in support of this hypothesis, to date, it has rarely been demonstrated at larger scales relevant to the management of coral reef ecosystems (30).

However, less understood is how even small changes in turf canopies can affect juvenile coral abundance and how even modest changes in juvenile corals can translate to higher abundances of adult corals. For example, after other factors such as connectivity and larval supply are accounted for (that is, enumerated in Fig. 1), the canopy height of algal turfs become the final limitation for coral recruitment. Pooling all of our data, we found that, at low turf canopy heights (that is, 0.5 mm), the average maximum juvenile coral density was 70/m<sup>2</sup>, but among turfs with a 1-mm canopy, coral densities drop to 40/m<sup>2</sup> (a 43% decline). Thicker turfs drive the maximum density of coral recruits to zero (Fig. 5E). A similar pattern exists for macroalgae abundance (cover), so in our final hierarchical analysis (Fig. 5A), a considerably higher proportion of the variance explained by parrotfish grazing pressure translating to juvenile coral densities was observed (Fig. 5D). Other published studies found that a small shift from 2- to 4-mm turf canopy height resulted in a decline of 75% in coral recruitment (8).

Similarly, it is a fair question to ask whether a 17% increase in variance explained in juvenile coral density in no-take reserves (that is, from 4.5 to 7.3 juvenile corals per square meter) is significant (Fig. 3). Although this represents a 62% increase, the juvenile densities are low. Nevertheless, similar small changes in juvenile coral densities in fished versus no-take reserve sites in other published studies (30) have been shown to result in significantly greater future coral cover. Specifically, low juvenile coral densities in a fished region of the Bahamas were similar to what we report (that is, five individuals per square meter), and densities in an adjacent Bahamian reserve were only slightly higher than

those in our study (that is, 9 to 13 individuals per square meter). Nevertheless, a repeated analysis 2 years later found that coral cover had increased by 28% in the reserve site (31). Given the geographic scale and diversity of reserve locations in our present study, it is unsurprising that the average reserve effect size is just over half of that observed in a single, well-enforced Bahamian reserve.

Today's Caribbean coral reefs are dominated by what some describe as weedy coral species, in that they readily recruit and grow relatively rapidly. Pandolfi and Jackson (32) contrasted species composition of Caribbean coral reefs from the Pleistocene with those of today and found that modern reefs are dominated, in rank order by the following species: *Porites astreoides*, *Porites porites*, *Siderastrea* sp., *Agaricia* (now *Undaria*) *agaricites*. *P. astreoides* and *P. porites* were the two most abundant adult corals found in all our surveys. The four most abundant species identified by Pandolfi and Jackson (32) were among the top five species in our juvenile coral surveys. Of these species, *P. astreoides* dominated both juvenile and adult coral abundance (see fig. S1). It is a known contributor to coral reef bioherms. Whereas this shift of Caribbean reef corals to weedier *Porites* species reduces habitat architecture (33), it also concentrates and increases herbivory (34), thereby improving conditions for recruiting corals and the recovery potential of the reef.

Our study illustrated the value of managing fish stocks for the process of herbivory as an indirect driver of coral recruitment and thus the resilience of coral reef ecosystems (Fig. 3). When comparing the effectiveness of no-take reserves with adjacent reefs facing unconstrained fishing pressure (Fig. 2), we found that fishing reduced the abundance of large fishes (including functionally important parrotfishes) and limited algal cover and algal canopy height, resulting in increased abundance of juvenile corals. We note that the increase in total fish biomass in reserves compared to fished sites exceeded the target threshold advanced by McClanahan *et al.* (35). We also found that the biomass of herbivores in no-take reserves was comparable to other studies in well-grazed coral reef ecosystems (36). However, biomass is not the best metric to use. Herbivory is better characterized when specific factors, such as parrotfish species identity, body size, and mouth size, were integrated with metrics of grazable surface area on each reef (Fig. 4) because all these traits are central to the process of herbivory. We further broke down herbivore-induced disturbance into grazing intensity (which scales with herbivore body size) and frequency (which scales with herbivore bite rate; Fig. 5).

Many studies have focused on the patterns of abundance (that is, biomass) of herbivores rather than changes to the process of herbivory. Certainly, the two are linked as was evident following the mass mortality of the abundant herbivorous sea urchin, *D. antillarum* in the early 1980s. Algae increased significantly throughout the Caribbean basin following that mortality event (37–39). Less appreciated are the changes in herbivory that result without any change in herbivore distribution, abundance, or biomass. For example, immediately following large-scale coral mortality (from bleaching or disease), phase shifts to abundant algae often occur (40). This results from algae rapidly colonizing recently dead coral surfaces, thereby reducing the per-area bite rates from local grazers and thus effectively reducing the process of herbivory (34, 41).

Algal abundance on coral reefs reflects a dynamic balance between per-area rates of algal productivity and consumption (42). Because these two rates vary independently, they become increasingly variable at larger spatial scales. Local studies effectively control for regional productivity effects, invariably demonstrating that, when herbivory is either eliminated

or impeded, algal abundance increases, and recruitment of reef corals declines (10, 12). However, when identical herbivore deterrent experiments were deployed on coral reefs that differ in their productivity potential, they resulted in different patterns of algal growth and coral recruitment after 1 year [for example, Belize with abundant algae versus Moorea in French Polynesia with little to no difference in algal abundance; see the studies of Steneck *et al.* (15) and Mumby *et al.* (24), respectively]. This illustrates the necessity to stratify and standardize the sampling design to address questions at larger spatial scales applicable to ecosystems. It is also important to know how herbivory was quantified and under what habitats or conditions (for example, wave exposure, productivity, or eutrophication) it was measured. Different investigators apply different methods in different habitats, thereby reducing the signal-to-noise ratio in assessments for any given management action. As a result, it might be tempting, but misleading, to conclude that failure to find statistically significant effects of management implies that its ecological benefits are not particularly important.

Similarly, our proxy for managed fish stocks required relatively effective no-take reserves. This is why we evaluated the efficacy of stakeholder compliance for each reserve before treating it as one. This is critical because it is well known that “paper-parks” (that is, parks that only exist on paper) far outnumber enforced and functional no-take reserves on tropical coral reefs (43–46). We do not imply that the reserves we studied were 100% effective, but they were sufficient to have significantly reduced fisheries impacts.

All of the above concerns are embedded in the larger regional setting where reefs developed. To stratify sampling, we specifically focused on exposed forereef habitats on low-relief islands of the eastern Caribbean that are isolated from each other by the North Equatorial Current to avoid confounding factors from runoff, sedimentation (47), or connectivity from adjacent regions (18). We also focused on coral reefs where their bioherms were known to have developed over the past several millennia (48). As a result, we excluded other tropical marine habitats that are not, and perhaps never were, bioherms created by coral reef ecosystems. Thus, we avoided pavements, hard bottom, or gorgonian plains, which naturally have low structural complexity, typically few fish, and low covers of both corals and macroalgae (49). Studies have found that strong physical scouring and sediment resuspension prevent algae from becoming established (47–49). Therefore, it is not surprising that when relatively featureless habitats are combined with true coral reefs where biological processes such as herbivory are more important, that considerable variance from confounding drivers occurs (17, 50). It follows that variance will increase with inadequate stratification and thus be compounded when pooled at larger scales.

### Resilience in diverse ecosystems having diffuse drivers

To be clear, our study was not intended to be a test of coral reef resilience per se. What we show is that relatively small changes can nudge this ecosystem toward one that can maintain and sustain itself. Factors that limit algal abundance improve the capacity of coral reefs to remain coral dominated (14). Here and in smaller studies in which no-take reserves improved conditions for herbivores, these measures reduced algal abundance and improved conditions for juvenile and ultimately adult coral reefs (Figs. 3 and 5) (30). By contrast, in Jamaica, when herbivorous sea urchins suffered a mass mortality in 1983, algae rapidly colonized the reef (37, 38) and in the decades since algae, not coral, have remained the dominant space occupiers in the ecosystem. We suggest that even modest improvement in the conditions necessary for recruiting corals is progress toward resilience.

Above, we argued that diverse ecosystems can be structured by relatively few ecological processes that are collectively driven by numerous species but create demographically important interactions. In contrast, in low diversity ecosystems, single species can control the structure and function of the ecosystem. They are often labeled a “keystone species” (51, 52). Although no keystone species has ever been described for a diverse terrestrial or aquatic ecosystem, there is strong evidence that when an entire trophic level is sufficiently depleted to be dysfunctional, the larger ecosystem consequences can be profound. It is possible that the considerably lower species diversity naturally occurring in Caribbean coral reefs compared to the diverse reefs of the Indo-Pacific makes the former more vulnerable to ecological dysfunction. Studies concluded that the striking increase in algae on Caribbean coral reefs following *Diadema* mass mortality were set up by the earlier extirpation of most of the important herbivorous fishes (38).

It is tempting to assume that strong ecosystem drivers will be evident no matter the scale at which they are measured. However, this ignores the specific nature of the interactions that construct the ecosystem. For example, scleractinian corals are the foundation species that define coral reef ecosystems. Although adult corals can live for thousands of years, epizootic disturbances such as thermally triggered bleaching or disease kills vast areas of reefs (25, 53). As a result, ecosystem resilience often depends on the coral’s ability to recruit and survive. The scale of interactions that regulate the mortality or growth of juvenile coral is very local (8, 54). Detailed experiments have shown that, under identical reef conditions only meters apart, an increase in turf canopy height from 2 to 4 mm can result in a 75% reduction in coral recruitment (8). Because demographic changes such as this occur at the scale of millimeters or centimeters, it is necessary to study and model key interactions at that scale.

EBM will be more successful if processes driving the structure and function of the ecosystem are known and managed. However, if the ecosystem state is several steps removed from the management action, the resulting attenuation of the management effect can erode the social feedback necessary to foster a conservation ethic among stakeholders. This is a perennial problem for diverse ecosystems such as coral reefs, and as a result, it may require much more of a bottom-up (socially driven) approach to create a durable path for future marine conservation and EBM (55, 56).

## MATERIALS AND METHODS

### Stratified design

To determine whether local management has measurable effects on the structure and functioning of coral reefs, we conducted quantitative surveys on commensurable reefs having significant protection from fishing compared to those in the region without protection (Fig. 2). Protected areas required that fishing was locally prohibited by law, properly demarcated, regularly patrolled, and confirmed by our interviews with reef managers and our scuba observations (that is, the absence of fish traps and nets or evidence of early morning or evening fishing). The latter was easy to observe because we were living at the reef sites for a month or more in some cases. None of the sites were perfectly protected nor they needed be. Our goal was to find areas having sustained efforts to curtail fishing and the political will and funding for enforcement. When possible, we selected nearby areas where fishing was unconstrained. St. Lucia and St. Croix have fished and unfished areas that exist at the same island. Several other sites were paired for fished and unfished areas in close proximity (Fig. 2).



## Site selection criteria

The islands we studied (Fig. 2) had significant Holocene reef bioherms evident as recently as over the past half century (48). Field sites were accessed via a 10.4-m sailboat (S/V *Alaria*) equipped with a scuba compressor, scuba tanks, solar and wind electrical power for computers, and lights. The research team lived on the sailboat for the duration of the project. On the islands of St. Maarten, Barbuda, St. Lucia, Mustique, Tobago Cays Marine Park, Petit St. Vincent, and St. Croix managers or officers who enforced local marine regulations provided field transportation to the study sites we had selected (table S1). For all other sites, we used an inflatable boat for our diving operations. Reef studies began early in November 2013 and ended late in April 2014.

We stratified our design for determining the strength of hypothesized drivers of resilience in coral reef ecosystems (26) by conducting identical empirical surveys within forereef habitats at a specific (10 m) depth. Specifically, we quantified the abundance of reef coral species, benthic algae, and important reef fish species (quantified by size, population density, and biomass). We studied low islands of the Caribbean (that is, less than 300 m in elevation), many of which had no freshwater rivers, to minimize land-based (bottom-up) effects to their adjacent coral reef ecosystem. To determine local management plans and practices, we obtained local regulations, interviewed managers (when possible), made observations of fishing practices, and recorded fishing evident during our dives (for example, gill nets, traps, and fishing line on the reef) over 1 to 2 months of our stay at each study island (see table S1). Although none of the reefs were “pristine,” those with protective laws and regular patrols had significantly reduced fishing pressure. It is against that gradient in fishing pressure that we studied the structure, functioning, and resilience of the coral reef ecosystem of the eastern Caribbean. At a subset of sites, we conducted higher-resolution studies to quantify area-specific herbivory by quantifying the rugosity of the grazable surfaces of reefs and the specific behaviors of foraging by parrotfish species (the dominant herbivore group in our study domain) using in situ behavioral observations in replicate 5-min periods ( $n > 5$ ). To minimize observer and protocol differences, all data on benthic organisms (including coral and algae) and fishes were collected by the same three people and in identical fashion at each site.

Both islands of the country Antigua and Barbuda were fished without enforced limitations, so we had no locally unfished areas for contrast. The significantly lower human population density on Barbuda (that is, 10.2 people/km<sup>2</sup> versus 289 people/km<sup>2</sup> in Antigua) corresponded to higher abundances of targeted predatory fishes (119 g/120 m<sup>2</sup> versus 84.5 g/120 m<sup>2</sup> for Barbuda versus Antigua, respectively) and parrotfish (672 g/120 m<sup>2</sup> versus 339 g/120 m<sup>2</sup>). However, because those two islands could not meet our criteria to test for fisheries management effects, we excluded them from the remaining analyses.

## Surveys

We used a modified Atlantic and Gulf Rapid Reef Assessment (AGRRA) protocol (57) to quantify sessile benthic community structure at each site. At each site, replicate 10-m transect lead lines were placed on the reef ( $n = 4$  per reef). The number of centimeters on each transect intercepted by live coral (measured for each coral species), sponges, gorgonians, and benthic algae [measured by functional group such as algal turfs, encrusting coralline (Corallinales) and noncoralline (peyssonnelid) crusts, and macroalgae] was recorded. Benthic macroalgae were further subdivided into erect corticated macrophytes [sensu Steneck and colleagues (58, 59)] and the genera *Lobophora* and *Halimeda* because of their damaging effects on reef corals (14, 54). Canopy heights were

measured to the nearest millimeter for all nonencrusting algae. The percent cover of each benthic organism (per transect) was determined by summing the centimeters intercepted by the organism and then dividing that total by the length of the transect. Macroalgal biomass was inferred by quantifying the volume [the product of percent cover and canopy height, called “algal index” (59)].

Juvenile corals were quantified by deploying 25 cm × 25 cm quadrats at five locations (0-, 2.5-, 5-, 7.5-, and 10-m marks) on each benthic transect. Quadrats were placed on the reef substrata largely devoid of adult corals (that is, <25% cover of live corals). Operationally, we defined juvenile corals as those less than 40 mm in maximum diameter. Each juvenile coral was identified to species and measured to the nearest millimeter.

*D. antillarum* were enumerated by surveying belt transects (1 m × 10 m) on either side of the transect used for quantifying sessile benthic organisms. Thus, within each belt transect, we surveyed a 20-m<sup>2</sup> area. We measured the test size of each urchin encountered to the nearest millimeter.

Fish population density and body sizes were quantified for all large fishes (that is, excluding small planktivores such as *Chromis* and all blennies and gobies) using replicate 30 m × 4 m belt transects (60). This involved attaching a spool with 30 m of line to dead coral and swimming slowly recording all large vagile species including most predatory and herbivorous fishes. On the return swim, smaller less vagile species such as territorial damselfishes were recorded. The biomass of each species (per transect) was determined using published length-weight relationships.

## Higher-resolution research

A series of islands were selected for a detailed study following the initial surveys. The islands included Bequia, Mustique, Tobago Cays, Union, Petit St. Vincent, and St. Croix. In all cases, there were equal numbers of fished and unfished reefs adjacent to one another.

**Measuring rugosity** – We quantified the structural characteristics of the reef by measuring the length of reef surface under each linear meter along a 10-m transect [that is, as spatial index (SI) or “rugosity” values (33); see the study of Wilson *et al.* (61) for validation of means of measuring habitat complexity]. In addition to the simple rugosity measurements, we specifically recorded the length from low portions of the meter transects to the highest location (that is, “sides”), and we also measured the length and substrate composition (coral, turf, and macroalgae) of upper and lower surfaces. These data were used to quantify herbivory over the entire reef surface in our study area.

**Quantifying herbivory** – Detailed studies of parrotfish grazing rates required divers to follow individuals of an estimated size and record their grazing rates during 5-min periods [see methods of Bruggemann *et al.* (20);  $n > 5$  per individual]. We recorded the species, life phase, size, and bite rates of the parrotfishes on grazable substrates. The number of individuals studied per species is as follows: *Scarus taeniopterus*,  $n = 18$ ; *Scarus vetula*,  $n = 12$ ; *Scarus iseri*,  $n = 9$ ; *Sparisoma aurofrenatum*,  $n = 18$ ; *Sp. chrysopteron*,  $n = 6$ ; and *Sp. viride*,  $n = 12$ . This approach helped account for the disparate feeding behaviors among parrotfish species—particularly between genera—and as such helped to provide a more accurate measure of grazing pressure among sites. However, it must be borne in mind that many aspects of herbivore nutrition are poorly understood, particularly in the Caribbean. For example, although *Scarus spp.* feed predominantly from the epilithic algal matrix, they may derive much of their nutrition from microorganisms and detritus (62). Members of the genus *Sparisoma* took a considerable portion of their bites from fleshy macroalgae (20), and although they are able to

assimilate various phaeophytes (63), their overall nutritional biology has received less study than that of *Scarus* species.

Because most herbivorous reef fishes avoid feeding on live coral, it follows that where coral cover is high, herbivory is concentrated on the remaining grazable substrata. To determine more realistic grazing rates, we quantified bite rates per species on grazable reef surfaces including its three-dimensional rugosity (measured as described above). Reef rugosity measurements allowed us to quantify the grazable substrates for each linear meter to the nearest centimeter. Grazable substrates excluded live coral, sponges, and other substrates rarely targeted by herbivorous fishes (64). The first of two metrics of parrotfish grazing pressure was derived from these data in three steps: (i) Multiply the observed bite rates per species and body size with genus-specific relationships of bite area against body size (65), giving total area grazed ( $\text{m}^2$ ) per hour per transect ( $120 \text{ m}^2$ ) for the entire fish assemblage; (ii) calculate three-dimensional grazable area as the product of the reef complexity index and proportional cover of grazable substrates; and (iii) divide (i) by (ii) to give a total parrotfish grazing frequency by feeding rate adjusted for the three-dimensional area of grazable substratum ( $\text{m}^2 \text{ hour}^{-1} \text{ fge}$  in a  $120\text{-m}^2$  plot where fge denotes fish grazing equivalent). The second metric was slightly simpler in substituting parrotfish biomass for (i), yielding parrotfish grazing intensity by biomass ( $\text{g}_{\text{fge}}$  in a  $120\text{-m}^2$  plot).

## Analyses

Our rationale was to use the most powerful analytical approach while allowing for most appropriate covariates. Thus, because interpretation of fish data requires site-level measurements of the SI (also called rugosity; see the study of Wilson *et al.* (61)), analyses were carried out at a site level, whereas analyses of corals and algae—which do not require site-level covariates of SI—were carried out using transect level hierarchical mixed models. To determine reserve effects on first, second, and third tier ecosystem processes (fish abundance, algal cover and turf canopy height, and juvenile coral density, respectively), we used mixed-effects permutational multivariate analysis of variance (PERMANOVA) based on Euclidean distance matrices with fished/no-take reserve as a fixed effect along with a coarse measure of structural complexity and geographic region as random effects. Sample sizes and all categories of information quantified are in shown Results and table S1. When examining revised metrics that potentially offer greater mechanistic insight into ecological processes, we added an additional processing step when multiple metrics were available. Specifically, in assessing the relationship between juvenile corals and algal assemblages, we used distance-based linear models (DistLM) (66) with AIC to identify the best subset of algal predictors (from the means and maximum values of algal turf cover, canopy height, macroalgal cover, macroalgal canopy height, and macroalgal index/volume). Because DistLM does not consider random effects, we then incorporated the best predictors within the standard mixed-effects models used elsewhere.

## SUPPLEMENTARY MATERIALS

Supplementary material for this article is available at <http://advances.sciencemag.org/cgi/content/full/4/5/eaao5493/DC1>

fig. S1. Abundance of adult and juvenile coral species from entire study.

table S1. Summary data averages pooled by family for fish and most benthic components at a 10-m depth (that is, Fig. 2).

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**Acknowledgments:** We had help from long-haul sailors A. Sawyer, P. Calder, C. Smith, L. Incze, and E. James. N. Rincón Díaz helped with algal taxonomy and fish grazing measures. Regional assistance came from E. Babau (Petit St. Vincent); H. Balmar (Bequia); T. Bervoets (St. Maarten); J. Compton (St. Lucia); R. Camacho, R. Camacho, and B. Cooper (Antigua); Z. Hillis-Star (St. Croix); S. Humphery (Mustique); A. Johnson (Barbados); O. Joseph (Union Island, St. John); K. A. Lewis (The Nature Conservancy (TNC), St. Croix); and A. Lockhart (St. Vincent). TNC’s R. Blyther and J. Jobe helped us make connections throughout the eastern Caribbean. Video documentation was performed by D. Conover (Compass Light Productions). To all we are grateful. **Funding:** Funding for this project came from a National Geographic Society grant to R.S.S. (9362-13). Additional funds were from an Australian Research Council Laureate Fellowship and the Centre of Excellence for Reef Studies to P.J.M. **Competing interests:** The authors declare that they have no competing interests. **Author contributions:** Designed research: R.S.S. and P.J.M. Collected and processed data: R.S.S., P.J.M., C.M., D.B.R., and G.S. Analyzed data: P.J.M. and R.S.S. Wrote the paper: R.S.S. and P.J.M. Reviewed and revised the paper: All authors. **Data and materials availability:** All data needed to evaluate the conclusions in the paper are present in the paper and/or the Supplementary Materials. Additional data related to this paper may be requested from R.S.S.

Submitted 2 August 2017

Accepted 20 March 2018

Published 9 May 2018

10.1126/sciadv.aao5493

**Citation:** R. S. Steneck, P. J. Mumby, C. MacDonald, D. B. Rasher, G. Stoyile, Attenuating effects of ecosystem management on coral reefs. *Sci. Adv.* **4**, eaao5493 (2018).

## Attenuating effects of ecosystem management on coral reefs

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*Sci Adv* 4 (5), eaao5493.

DOI: 10.1126/sciadv.aao5493

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