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Notes:

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Reduced fishing pressure and weak predator-prey interactions within marine reserves can create trophic cascades that increase the number of grazing fishes and reduce the coverage of macroalgae on coral reefs. Here, we show that the impacts of reserves extend beyond trophic cascades and enhance the process of coral recruitment. Increased fish grazing, primarily driven by reduced fishing, was strongly negatively correlated with macroalgal cover and resulted in a 2-fold increase in the density of coral recruits within a Bahamian reef system. Our conclusions are robust because four alternative hypotheses that may generate a spurious correlation between grazing and coral recruitment were tested and rejected. Grazing appears to influence the density and community structure of coral recruits, but no detectable influence was found on the overall size-frequency distribution, community structure, or cover of corals. We interpret this absence of pattern in the adult coral community as symptomatic of the impact of a recent disturbance event that masks the recovery trajectories of individual reefs. Marine reserves are not a panacea for conservation but can facilitate the recovery of corals from disturbance and may help sustain the biodiversity of organisms that depend on a complex three-dimensional coral habitat.

biodiversity | coral reef | grazing | predation

Marine reserves have become one of the most widely adopted tools for managing commercially important fishes and protecting marine biodiversity (1). Several direct effects of reserves are relatively straightforward to anticipate: Reduced fishing mortality usually increases the biomass of target and bycatch species of fishes (2, 3), and reserve status may help prevent acute anthropogenic disturbance such as destructive fishing practices that damage benthic communities (4). However, by enhancing the abundance of fishery species, reserves may also exert indirect impacts on other nonfishery species that naturally interact with fishery species through processes of predation and competition (5).

Because the indirect effects of reserves on biodiversity arise from species interactions and trophic cascades (6), they are generally complex and may have surprising outcomes (7, 8). We reported such complex outcomes in a study of The Bahamas' Exuma Cays Land and Sea Park (ECLSP), which, at 442 km², is one of the largest and most successful marine reserves in the Caribbean. The ECLSP is a rare example in which sustained fisheries exclusion has resulted in a high biomass of predatory fishes (2 kg per 100 m²). Our *a priori* hypothesis was that high levels of piscivorous fishes such as the Nassau grouper (*Epinephelus striatus*) would exert top-down predatory impacts on grazing fishes (a prey item) and, by reducing the biomass of grazers, promote increases in the cover of macroalgae. However, the hypothesis was not supported because large-bodied species of grazer (parrotfish) were found to experience a size-escape

from predation, and therefore the expected negative effects of trophic cascades on grazers were unexpectedly weak (9). In addition, these large-bodied parrotfishes such as *Sparisoma viride* benefited numerically from a reduction of fishing pressure in the reserve. Because large-bodied individuals are responsible for the majority of algal grazing, the net outcome of the reserve was a doubling of grazing and a 4-fold reduction in macroalgal cover (9).

Our study of the ECLSP contributes to a growing body of literature that documents conservation-driven trophic cascades within ecosystems, often with fishing pressure at the apex (10, 11). Here, we move beyond trophic cascades and reveal further ecological consequences of reserve implementation. Specifically, because trophic cascades within the ECLSP resulted in an increase in grazing and reduction of macroalgae, we explore the consequences of this shift in benthic community structure on another ecosystem process: the recruitment of corals. Coral recruitment is clearly an essential demographic process for the persistence of coral populations (12). Such processes have received renewed attention because of the great vulnerability of corals to climate change (13).

Corals and macroalgae compete for space on reefs and interact through several mechanisms (14). Coral planulae cannot settle on macroalgae, and therefore the space occupied by macroalgae reduces the availability of suitable settlement space for corals (15). Algae can trap sediment that smothers coral recruits (16) and direct contact with macroalgae reduces coral growth rates (17) and may even result in direct overgrowth and coral mortality (18). It is also feasible that macroalgae can negatively influence corals through allelochemicals (19), triggering disease (20) and enhancing microbial activity driven by algal-derived dissolved organic carbon (21). Therefore, any management intervention that reduces macroalgal cover may enhance the recovery of coral populations and resilience of the system (22). We test the hypothesis that increased grazing, largely driven by implementation of marine reserves, can increase the recruitment of corals.

Results

Main Hypothesis: Grazing Determines Macroalgal Cover, Which in Turn Influences Coral Recruitment. Parrotfish grazing intensity was strongly negatively correlated to macroalgal cover (Fig. 1 and

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The authors declare no conflict of interest.

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Table 2. Alternative hypotheses that may account either partially or fully for the observed correlation between grazing (g) and coral recruitment (r)

Alternative hypothesis	Tests	Result
(i) Because recruitment in the Caribbean is dominated by brooding species whose larvae have short planktonic phases (50), recruitment density may be driven by the local cover of brooding corals. A positive correlation between grazing intensity and recruitment could then be observed because, coincidentally, grazing intensity is also correlated to the adult cover of brooders (and spawners) because such areas have higher rugosity and availability of shelter.	$r(r,c) = 0.07, P = 0.84, 1 - \beta = 0.07, n = 9$ $r(c,g) = 0.31, P = 0.37, 1 - \beta = 0.26, n = 9$	Reject
(ii) Corals recruit in cryptic areas and recruitment density is positively correlated to rugosity. This is particularly true of settling corals, although the degree to which it holds for larger recruits that have survived early postsettlement processes is unclear. Coincidentally, grazing is also correlated to rugosity of the habitat.	$r(r,rg) = 0.21, P = 0.59, 1 - \beta = 0.54, n = 9$ $r(rg,g) = 0.4, P = 0.28, 1 - \beta = 0.18, n = 9$	Reject
(iii) Increased levels of predation in reserves reduce the biomass and density of territorial damselfish (Pomacentridae). Reduced numbers of damselfish allow enhanced survival of coral recruits because there are fewer territories (56) and/or reduce the amount of macroalgae in territories. In this scenario, the correlation between parrotfish grazing and either coral recruitment or macroalgal cover arises because parrotfish grazing responds to the reserve in the same way as predator abundance, yet it is the latter that influences recruitment and macroalgal cover because of predator impacts on damselfishes.	$r(g,d) = 0.31^*, P = 0.43, 1 - \beta = 0.33, n = 9$ $r(r,d) = -0.06^*, P = 0.89, 1 - \beta = 0.07, n = 9$	Reject
Overall test of hypotheses <i>i-iii</i> seeking evidence for conditional dependence of main effect $r(r,g)$ on other factors $r_p(r,g,c,d,rg) = 0.98, P = 0.0002, n = 9$. Reject spurious correlation. Also, because strongest nonsignificant relationship is $r(rg,g), r_p(r,g,rg) = 0.87, P = 0.0054$. Reject.		
(iv) Elevated coral recruitment in no-take marine reserve (where fish grazing is greater) is due to exceptionally high larval supply. Although this would not disprove the main hypothesis, because elevated grazing and larval supply could enhance recruitment together, it could constitute an alternative explanation if larval supply were the only factor involved in determining recruitment. Tested using Lagrangian simulation model of larval dispersal.	GLM no. coral larvae $P_{time} < 0.001, P_{site} = 0.12$ DP = 3.9	Reject

Other variables are denoted c (coral cover), rg (rugosity), and d (pomacentrid biomass). r , Pearson correlation coefficient; r_p , partial correlation coefficient with conditional variables separated by ; P , probability that coefficient = 0; $1 - \beta$, power; GLM, generalized linear model with time (serial autocorrelation, measured by using ACF (empirical autocorrelation function), removed using 5-day aggregate) and site as fixed factors, quasipoisson errors, and a log link (55); DP, dispersion parameter for quasipoisson family.

*Similar result using density of adult damselfishes.

fish grazing on coral recruitment had not previously been documented. We infer that parrotfishes are the primary grazer responsible for this pattern because biomass of the main alternative fish group, Acanthuridae, exhibited a vanishingly weak ($r = -0.05$), nonsignificant ($P = 0.89$) correlation with recruitment. These results have an important implication for coral reef management: Maintaining high levels of grazing reef fishes can, in principle, enhance the recovery of Caribbean coral populations from disturbance, as predicted by ecological models (29). Therefore, the results provide empirical support for the notion of managing grazers as part of a strategy to mitigate disturbance on coral reefs and enhance resilience (22). Unfortunately, parrotfishes are rarely protected by fisheries' regulations, and therefore no-take reserves remain the most common instrument to manage their biomass (29).

The management of grazers is not a panacea for conservation (30). Coral population dynamics are the outcome of processes of colonization and mortality. Grazing may enhance colonization rates, but its impact on coral mortality is unknown. Possible negative effects of grazing include the predation of parrotfishes on corals (31), whereas possible positive effects include reducing the frequency and duration of coral-algal interactions, which may in turn reduce the incidence of disease and physiological demands on corals for immune response. Indeed, the processes governing the community structure of corals are complex and strongly influenced by the history of disturbance in addition to

changes in colonization rate (32). Such complexity probably explains the absence of a detectable influence of grazing on coral cover, size-frequency distribution, or overall community structure. First, the coral community is dominated by adult colonies whose composition differs dramatically from that of the juvenile community (the former being dominated by spawners and the latter by brooders; see SI). Second, adult corals in the study area experienced extensive mortality from coral bleaching in 1998 (33), and the persistent impact of this event masks differences in the recovery trajectories of reefs. Future studies need to quantify the degree to which grazer-mediated increases in coral recruitment can buffer elevated levels of disturbance.

Our results reveal local-scale impacts of grazing on coral recruitment along a continuous reef system. However, further studies are needed to illuminate the importance of candidate mechanisms such as space occupation by macroalgae and coral-algal competition. Furthermore, additional processes may affect the outcome of grazing on recruitment at larger spatial scales. Harrington *et al.* (34) described the importance of specific coralline algal species in facilitating the settlement and subsequent early survival of corals. Future studies will need to quantify the availability of such facilitators at various scales and quantify their overall importance in determining large-scale patterns of coral recruitment.

Reserve-driven trophic cascades were found to facilitate the recruitment of corals, which should, in theory, enhance the

study. Parrotfish biomass has limited efficacy as a proxy for grazing because of variation in bite size and rate among fish species and life phases (29). Therefore, the observed size-frequency distributions of individual parrotfishes were converted to an overall measure of grazing intensity by using a model that has been tested elsewhere (9, 29). The model uses species-level data on bite rate and genus-level data on the allometric scaling between fish length, sexual phase, and bite size to determine the total area bitten by the parrotfish community. This is then expressed as the maximum percentage of horizontal reef area grazed per hour. The biomass of individual surgeonfish species (Acanthuridae) was sampled simultaneously with that of parrotfishes. The urchin *Diadema antillarum*, a historically important grazer on Caribbean reefs, was not observed in the ECLSP, and its density outside the park never reached functionally important levels (0.04 m^{-2}).

Modeled Larval Supply Between Reserve and Nonreserve Sites. Coupled biophysical models rich in mechanistic details have become the most efficient tools in larval transport studies (45). A spatially explicit 3D individual-based model developed by Paris *et al.* (46, 47) and adapted for the wider Caribbean (26) was used to model spatial patterns of larval supply for a typical genus of brooding coral (*Agaricia*) and the dominant parrotfish species, *S. viride*. An ocean circulation module uses daily outputs of the high-resolution (6–7 km) Atlantic HYbrid Coordinates Ocean Model forced by real daily winds to represent present-day oceanographic conditions. Vertical resolution is prescribed by the larval vertical behavior and set to 20-m layers (48). The model domain for this extends to the wider Caribbean. The habitat layer of the model was created by satellite remote sensing of the Exuma Cays region. Individual reefs were buffered by a 5-km sensory zone and divided into ≈ 10 -km segments (i.e., into ≈ 50 -km² polygons). Initial conditions (i.e., spawning time and frequency) and parameterization (i.e., larval swimming behavior and pelagic larval duration) of the biological module used the larval traits of *S. viride* and *Agaricia* spp. Ontogenetic vertical migration was simulated for *S. viride*, which has a precompetent period of 47 days and a maximum competency or pelagic larval duration of 80 days (49). Planulae of *Agaricia* stay in the surface layer (0–20 m), their precompetent period is 48 h, and pelagic larval duration is 42 days (50). Cohorts of 100 virtual larvae (particles) were released simultaneously into the velocity field at all individual reef sites (93 sites around the Exuma Sound). To simulate reproductive behavior, releases occurred monthly and year round for *S. viride* but only during summer months for *Agaricia* spp. A total of 27,900 and 111,600 particles were released for the coral and parrotfish species, respectively. Field

study sites corresponded to five of the model polygons (two north of the park, two within the park, and one south of the park), so recruitment was recorded daily in each of the five relevant model polygons. Further details of the model appear in SI.

Statistical Analyses and Alternative Hypotheses. The relationship between grazing intensity and recruit density (standardized and raw data) was quantified by using Pearson product-moment correlation. Inferences on the strength of correlation and determination of power followed Cohen (51). Further insight was gained by repeating the analyses separately for those genera that brood their larvae and those that undertake mass spawning. Spatial patterns in the community structure of (i) coral recruits (by density of species or genus) and (ii) the entire coral community (by percentage cover of each species or genus) were explored by using nonmetric multidimensional scaling with the Bray–Curtis dissimilarity measure (23). All data were double square-root-transformed to allow less common species to influence the analysis. A formal test of the relationship between community structure and grazing was undertaken by using the procedure RELATE (52), which correlates the dissimilarity matrices of recruit data (Bray–Curtis dissimilarity among sites) and grazing intensity (Euclidean distance in grazing among sites) by using nonparametric Spearman rank correlation (note, the power of nonsignificant nonparametric tests is usually not reported). To guard against making type I error with a total of 13 statistical tests, α was reduced conservatively to 0.0038 by using the Dunn–Šidák method (53).

We conducted an exploratory analysis of the impact of grazing on the size-frequency distribution of both brooding and spawning corals. Grazing intensity was correlated with the skewness, kurtosis (53), and half the mean of successive squared differences among size categories. The latter measure is an indicator of heterogeneity among size classes. Size-frequency distributions comprised all individual corals at a site but excluded fragments. All size data were transformed by using natural logarithms before the computation of size-frequency distributions (*sensu* ref. 54).

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