

Current Biology

Herbivorous Crabs Reverse the Seaweed Dilemma on Coral Reefs

Highlights

- Coral reefs worldwide are undergoing a phase shift from coral to seaweed dominance
- Separate field experiments tested whether grazing by native crabs reverses the shift
- Crab grazing reduced seaweed cover, resulting in more corals and fishes on reefs
- Results have major implications for coral reef restoration in the Caribbean

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In Brief

Spadaro and Butler demonstrate in two separate field experiments that enhancing the density of native, herbivorous Caribbean king crabs on coral patch reefs overgrown by seaweeds reversed an ecological phase shift and shifted reef communities toward recovery by reducing seaweed cover and increasing the abundance and diversity of corals and fishes.



Report

Herbivorous Crabs Reverse the Seaweed Dilemma on Coral Reefs

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SUMMARY

Coral reefs are on a steep trajectory of decline, with natural recovery in many areas unlikely.^{1–3} Eutrophication, overfishing, climate change, and disease have fueled the supremacy of seaweeds on reefs,^{4,5} particularly in the Caribbean, where many reefs have undergone an ecological phase shift so that seaweeds now dominate previously coral-rich reefs.^{6–8} Discovery of the powerful grazing capability of the Caribbean's largest herbivorous crab (*Maguimithrax spinosissimus*)⁹ led us to test the effectiveness of their grazing on seaweed removal and coral reef recovery in two experiments conducted sequentially at separate locations 15 km apart in the Florida Keys (USA). In those experiments, we transplanted crabs onto several patch reefs, leaving others as controls (n = 24 reefs total; each 10–20 m² in area) and then monitored benthic cover, coral recruitment, and fish community structure on each patch reef for a year. We also compared the effectiveness of crab herbivory to scrubbing reefs by hand to remove algae. Crabs reduced the cover of seaweeds by 50%–80%, resulting in a commensurate 3–5-fold increase in coral recruitment and reef fish community abundance and diversity. Although laborious hand scrubbing of reefs also reduced algal cover, that effect was transitory unless maintained by the addition of herbivorous crabs. With the persistence of Caribbean coral reefs in the balance, our findings demonstrate that large-scale restoration that includes enhancement of invertebrate herbivores can reverse the ecological phase shift on coral reefs away from seaweed dominance.

RESULTS AND DISCUSSION

No marine ecosystem is more iconic, nor more imperiled, than the world's coral reefs.^{1–3} For more than a century, coral reefs that once supported >25% of global marine biodiversity have declined precipitously, fueled by the synergistic effects of climate change, eutrophication, overfishing, and disease.^{3–5} Typically, this degradation is manifested by a dramatic shift in benthic community dominance from corals to fleshy seaweeds, representing a phase shift to an alternative ecological state^{6–8} that negatively influences the growth, reproduction, recruitment, and survival of corals.^{10–12} Evidence of the long-standing competition between seaweeds and corals is exemplified by the coevolution of coral-fish symbiotic relationships in which corals damaged by seaweeds release chemicals to signal the aid of herbivorous fish.¹³ Overgrowth of seaweeds may also promote the proliferation of reef sponges in a “vicious circle” of nutrient cycling between seaweeds and sponges to the detriment of corals.^{8,14}

On Caribbean coral reefs, the explosion of seaweeds is caused by coastal eutrophication and the loss of grazers,¹⁵ the most dramatic example being the near extirpation of the long-spined sea urchin (*Diadema antillarum*) in the early 1980s, a catastrophe caused by an unknown pathogen.¹⁶ Overfishing of herbivorous reef fishes and the die-off of shelter-providing

branching corals^{17,18} has also resulted in a loss in fish grazing on reefs despite regulations to reduce their overfishing.^{18,19} In at least one instance, the void in the grazing niche space once held by fishes has been filled by small invertebrate herbivores released from competition and predation by fish.²⁰ In many places, reefs have likely degraded beyond a threshold whereby natural recovery of corals is possible. This prospect has sparked numerous restoration efforts in which corals are transplanted from nurseries onto degraded reefs in an attempt to bolster coral biomass and sexual reproduction of corals. Thus far, this approach has not returned reefs to their former state,²¹ and some argue that unless the underlying reef habitat is unencumbered by the overgrowth of seaweeds, reefs will remain largely depauperate of live coral and suffer degraded ecosystem function.^{10,21,22}

We discovered a potential solution to this “seaweed dilemma” based on our previous research with the Caribbean king crab (*Maguimithrax spinosissimus*), a large, cryptic, and primarily herbivorous crab native to the Caribbean and western Atlantic Ocean. This species consumes seaweeds at rates that exceed nearly all other fish or invertebrate grazers in the Caribbean;^{9,23,24} they even eat chemically and physically defended algae (e.g., *Halimeda* spp.) that other grazers avoid.⁹ However, their natural density on Caribbean coral reefs is low^{9,20,23,24} (<0.04 crabs/m²), probably a consequence of high predation



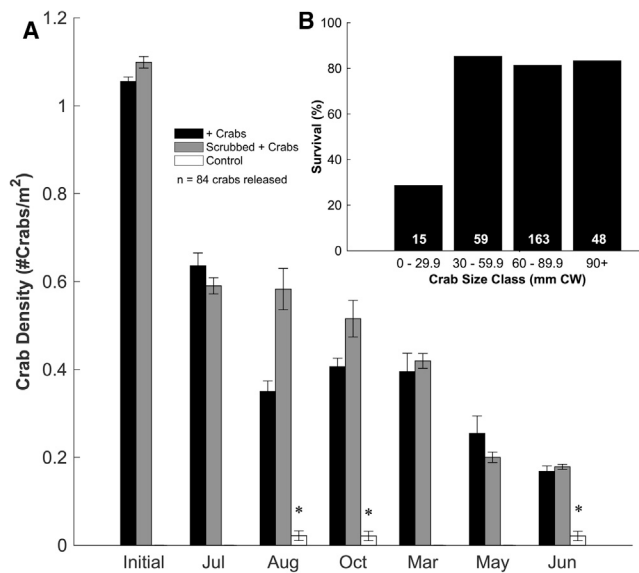


Figure 1. Site Fidelity and Survival of Stocked Caribbean King Crabs on Coral Reefs

(A) Change in total recaptures of tagged Caribbean king crabs (*Maguimithrax spinosissimus*) for one year after the release of 84 individuals onto four coral patch reefs, demonstrating the site fidelity and persistence of crabs on reefs after transplantation. Data are expressed as the mean ($\pm$ SE) density of tagged crabs per m² of patch reef.

(B) Survival (%) of crabs of four different size classes when tethered for 24 h on coral reefs; sample sizes for each size class are indicated for each histogram. All crabs >30 mm carapace width (CW) had high survival.

on juvenile crabs,²³ so their effect on reef seaweeds is muted.^{9,20,23,24} This was confirmed in experiments in which we tested size-specific predation on tethered crabs and found that, when large enough (>30 mm carapace width [CW]), *M. spinosissimus* reach a size refuge that lowers their predatory mortality (Figure 1B). We therefore hypothesized that if higher densities of large crabs could be established on degraded coral reefs, their grazing effects would reverse the shift from seaweed dominance and help restore balance to coral reef communities. We tested this in two separate experiments.

Our first test of the grazing effects of crabs on degraded coral reef communities was conducted from 2014 to 2015 on 12 isolated coral patch reefs (each ~3 m diameter) in the middle Florida Keys (Florida, USA), wherein each reef was assigned to one of three experimental treatments (n = 4 replicate reefs/treatment): unmanipulated control reefs, reefs stocked with crabs (+ crabs), and reefs on which divers first manually removed (i.e., scrubbed) seaweeds and then stocked reefs with crabs (scrubbed + crabs). Diver surveys during the experiment confirmed that nearly half of the 84 tagged crabs released onto reefs were still present a year later (Figure 1A); none had moved among experimental reefs, and therefore crab abundance remained higher on the crab-stocked reefs throughout the study. At the start of the experiment, seaweeds covered 85% ($\pm$ 7 SE) of the surface area of the reefs, and coverage remained high on unmanipulated control reefs throughout the year-long study (Figure 2A). In contrast, the effect of crab stocking on seaweed cover was rapid and dramatic. On reefs where we increased crab densities (1 crab

m⁻²) to mirror historic densities of *Diadema*, the crabs reduced and maintained seaweed cover at <50% of that on unmanipulated control reefs (Figure 2A). In the treatment where divers initially scrubbed the reefs free of seaweeds and then added crabs to reefs, seaweed cover was even lower: ~80% lower than on control reefs.

To assess the generality of these striking results, we repeated the study for another year from 2016 to 2017 at 12 additional patch reefs ~13 km away from the first study location. We also added a fourth treatment (i.e., scrubbed reefs with no crabs added) to yield a fully orthogonal design (n = 3 replicate reefs/treatment). The initial seaweed coverage on the second set of reefs was somewhat lower (mean = 65% $\pm$ 10 SE) than in the first study (85%; Figure 2B), but the experiment yielded nearly identical results—demonstrating the repeatability of our findings. Seaweed cover was again reduced by ~50% on reefs stocked with crabs and further reduced by ~70% where seaweeds were first removed and crabs added to maintain grazing pressure. In the new treatment with no crabs, but where reefs were scrubbed free of seaweeds, seaweeds eventually regrew to levels nearly as high as they had been initially and at levels similar to those of unmanipulated coral reefs.

Seaweeds smother, shade, and are allelopathic to coral larvae and juveniles,¹⁰ so we also conducted diver surveys to quantify the abundance of juvenile corals on each experimental reef in the two studies. These surveys were conducted two years after each experiment was initiated to allow time for coral recruitment and growth to a size that could be effectively censused by divers. Each patch reef was painstakingly and completely searched by divers who counted and identified all juvenile corals²⁵ (i.e., those <4 cm in their longest dimension), even those beneath the seaweed canopy on control reefs. We observed a total of 131 living juvenile corals (7 species) on the patch reefs used in the first experiment and 830 juvenile corals (15 species) on reefs included in the second experiment (see Supplemental Information). The density of juvenile corals was more than twice as high on scrubbed reefs and almost four times greater on reefs to which crabs were added (Figure 2C) as compared to unmanipulated control reefs.

Seaweeds also release chemicals that larval reef fishes avoid, causing large changes in the composition of reef fish communities.²⁶ Therefore, we hypothesized that the removal of seaweeds by grazing crabs would also have a positive, cascading effect on reef fish community composition, a metric that we monitored using time-lapse photography and diver surveys on each experimental patch reef. Again, crab grazing and reef scrubbing resulted in a 2–3-fold increase in species richness and a 3–5-fold increase in the abundance of coral reef fishes on reefs to which crabs were added, seaweed was removed, or both as compared to unmanipulated controls (Figures 2D and 2E).

The results of our two field experiments conducted in different years at different locations demonstrate that the consumption of seaweeds by grazing crabs was dramatic and persistent, and resulted in positive indirect effects on coral and fish communities. Seaweed cover on crab-stocked patch reefs was cut in half and remained so for both year-long experiments, while the abundance and diversity of juvenile corals and fishes rose two to five times higher on reefs with herbivorous crabs than on unmanipulated control reefs. Scrubbing reefs clean of seaweeds had

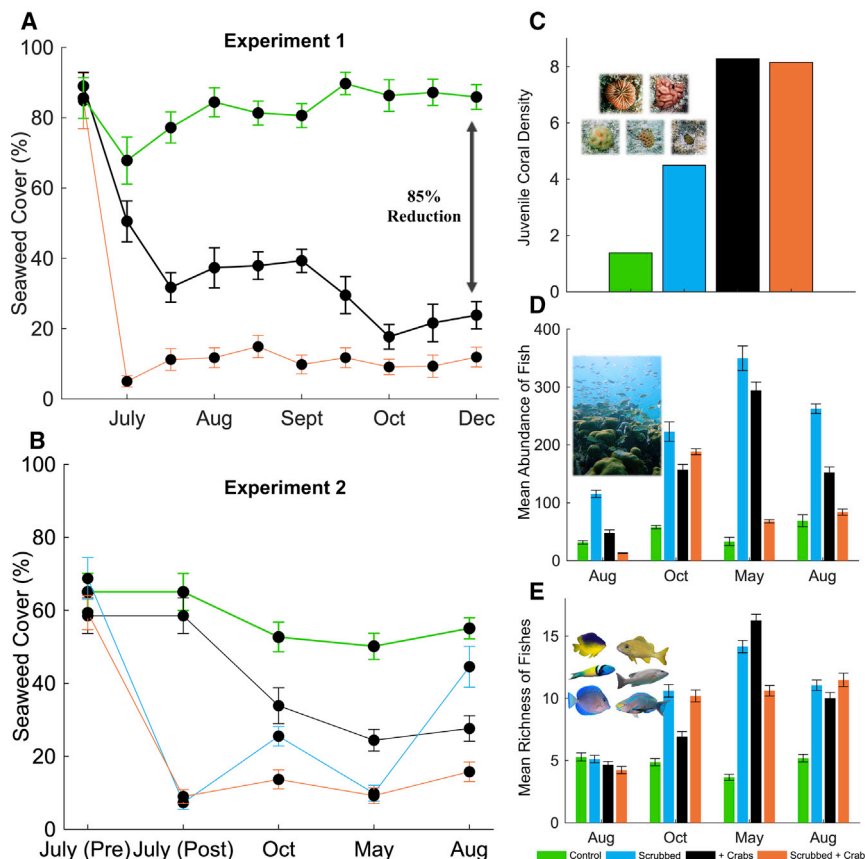


Figure 2. Changes in Coral Reef Community Structure in Response to Grazing by Caribbean King Crabs

(A) Change in cover (%) of seaweeds (means $\pm$ SE) on coral patch reefs over time in three experimental treatments (unmanipulated control, + crabs, scrubbed + crabs) for the first field experiment.

(B) Change in cover (%) of seaweeds (means $\pm$ SE) on coral patch reefs over time in four experimental treatments (unmanipulated control, + crabs, scrubbed, scrubbed + crabs) for the second field experiment. Both experiments demonstrate the clear negative effect that crabs and reef scrubbing have on seaweeds.

(C) Abundance (mean $\pm$ SE) of juvenile corals counted by divers on coral reefs subject to four treatments at the conclusion of the second field experiment.

(D) Abundance of coral reef fishes (mean $\pm$ SE) obtained from time lapse images on coral reefs subject to four treatments during the second field experiment.

(E) Richness of coral reef fishes (mean $\pm$ SE) obtained from time lapse images on coral reefs subject to four treatments during the second field experiment.

See also Table S1.

similar initial effects but were not as long lasting as the introduction of herbivorous crabs. The effectiveness of *M. spinosissimus* in reducing and maintaining low seaweed cover is particularly noteworthy given that our experiments were conducted on reefs in shallow, nearshore waters where seaweed growth is high and dominated by calcareous green algae (*Halimeda* spp.) that are both chemically and physically defended and thus avoided by most grazers, but not by the crabs (Figure 3).

We did not census the recruitment of newly settled corals in our study. Instead, we exhaustively surveyed each reef for juvenile corals 2 years after the start of each experiment. While doing so, we searched beneath fleshy seaweeds on control reefs so as not to miss corals that might be obscured. Our in-depth surveys, the long time that elapsed between the imposition of treatments and juvenile coral counts, and the magnitude of the difference in juvenile corals among treatments leads us to conclude that the removal of seaweeds by grazing crabs resulted in higher coral recruitment or juvenile coral survival on those patch reefs. Such results are difficult to explain otherwise and are consistent with those of other studies that detail how seaweeds repel coral larvae and overgrow fragile coral recruits.^{10,26}

One might expect that the response of corals to experimental reef restoration might be limited to “weedy” species whose rate of recruitment is typically higher and more consistent. Our juvenile coral counts included fifteen species of coral, half of which are framework builders in the Florida Keys, including *Colpophyllia natans*, *Diploria labyrinthiformis*, *Montastrea cavernosa*, *Orbicella faveolata*, *Pseudodiploria strigosa*, *Siderastrea siderea*, and

Stephanocoenia intersepta. The majority of juveniles of both the framework building corals (six of eight species) and weedy corals (five of seven species) increased in mean density with similar magnitudes: 60% ($\pm$ 40% SD) for framework species and 62% ($\pm$ 32% SD) for weedy species. We suspect that the strong response observed even for framework building corals is due to the fact that inshore patch reefs in the Florida Keys currently harbor greater coral cover²⁷, hence recruitment potential, than the offshore barrier reef that has experienced a greater decline in coral cover due to climate change and disease.^{27–30}

With respect to the strong positive effect of crab herbivory on reef fish communities including dominant fish taxa (Figure 4), we postulate that not only were seaweed odors diminished that otherwise may have deterred settlement of larval fishes,²⁶ but that fishes may also have been attracted to reefs relieved of seaweed overgrowth that obscured shelter-providing holes and crevices. Coral bleaching, disease, hurricanes, and stress-related reductions in rates of reef accretion all contribute to the “flattening” of coral reefs, and that loss of architectural complexity is reflected in less diverse and abundant reef fish communities.^{17,18} We propose that the architectural complexity of coral reefs is also diminished when overgrown by seaweeds, especially unpalatable calcareous green seaweeds (e.g., *Halimeda* spp.) that fill in or obscure the numerous crevices and voids within reefs that provide shelter to small fishes. In turn, larger, more mobile fishes may then be attracted to these prey-rich reefs, further increasing fish community structure. Indeed, the rugosity of our experimental coral reefs (a

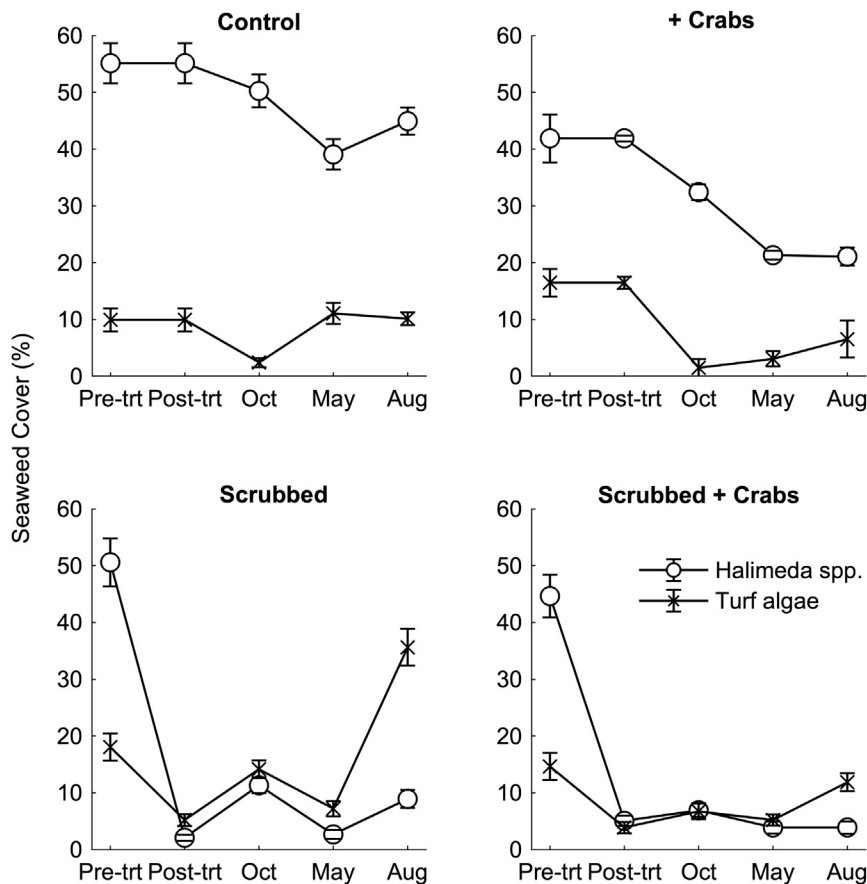


Figure 3. Changes in the Cover of Two Prominent Types of Seaweed on Coral Reefs during the Second Field Experiment

Summary of major seaweed taxa (*Halimeda* spp. and turf) presence (mean % cover $\pm$ SE) on experimental patch reefs during experiment 2 at Cheeca Rocks. *Halimeda* spp. and turf dominated the seaweed communities on these reefs, and although other types of seaweeds were present (e.g., *Dictyota* spp., *Wrangelia* spp.), they rarely, if ever, were present in photo quadrat surveys.

In contrast, *M. spinosissimus* is not a bio-eroder, and its short planktonic larval duration (4–6 days), herbivorous/omnivorous diet, and rapid growth make the crabs amenable for mariculture.⁴¹ But as with any large-scale restoration approach that relies on restocking (e.g., corals, mangroves, or fish), if *M. spinosissimus* is to be added to reefs on scales appropriate for coral reef restoration, it will be necessary to develop new mariculture programs that produce and grow sufficient numbers of crabs to a size (>30 mm CW) large enough to overcome their low natural abundance and high rates of juvenile mortality.

In summary, our experiments provide compelling evidence of the positive ecological effects that *Maguimithrax*

measure of reef physical complexity) increased by 30% ($\pm$ 6 SE) once seaweeds were removed and the rocky reef buried beneath seaweeds was revealed. This explanation of the effect of seaweed overgrowth on coral reef fish community structure (i.e., competition for space between seaweeds and small fishes) remains to be tested.

Because the problems that seaweeds pose for coral reefs are so well documented, the problem has prompted management actions of two kinds: herbivore protection and enhancement. Protection of grazing fish populations through legislation and the establishment of Marine Protected Areas^{15,19,31} stems from the results of many studies reporting the positive associations between fish grazing and coral recruitment or juvenile coral density.^{32–34} However, the effectiveness of grazing fishes in removing seaweeds is complex and depends on many factors, including enforcement of fishing regulations, ample recruitment of fishes, grazer traits, season, and the local condition of the reef community, among other things.^{15,35–37}

Another widely considered solution to the seaweed dilemma has been the reintroduction or enhancement of herbivorous *Diadema* onto seaweed-covered coral reefs, but those efforts have met with mixed success.^{24,38} Moreover, paleontological records of *Diadema* and coral co-abundance cast doubt on the historical importance of *Diadema* for corals,³⁹ and the complicated larval life history of urchins has thwarted their large-scale mariculture. Much like parrotfish (Scaridae), *Diadema* are also bioeroders of coral reefs and can be a source of mortality for coral recruits.⁴⁰

can have on coral reefs overgrown by seaweeds, and demonstrate their utility as a driver of recovery by shifting reefs away from their current seaweed-dominated state. The generality of our results was validated by nearly identical results in two separate field experiments conducted at different locations and in different years. Despite pleas from the scientific community for important results to be demonstrably repeatable,⁴² studies such as ours that include repeatable results remain rare in the ecological literature. Yet, verifying ways to resuscitate coral reefs has never been more important because many coral reefs are at an ecological crossroad, teetering on the brink of collapse. For example, the composition of coral reefs in the Florida Keys has been remarkably stable over the last 8,000 years, but coral cover along the world's third longest coral reef now stands at <2%, a fraction of what it was just a few decades ago⁴³—it has become a coral reef without corals. Plans to coalesce reef restoration programs into large-scale rescue programs in places like the Florida Keys are emerging,⁴⁴ but still nascent. Given the magnitude of the “seaweed dilemma” as part of the problem, our results provide a compelling argument that enhancement of *M. spinosissimus* density is an integral component of those restoration efforts. Still, given the complexity of the problems facing modern coral reefs, it is overly simplistic to think that transplantation of corals and herbivores alone will stem the worldwide decline of coral reefs. Doing so also depends on reversing the overarching threats posed by ocean

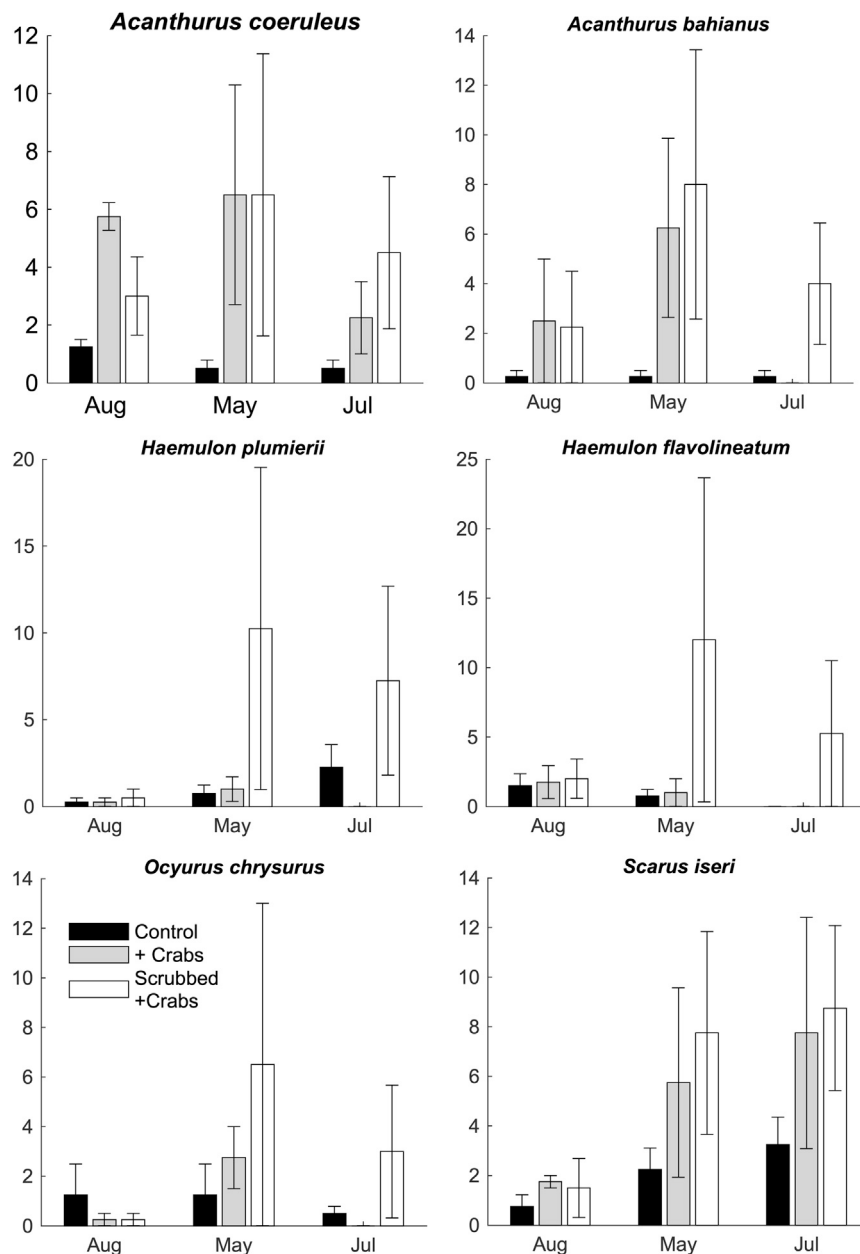


Figure 4. Changes in the Mean Abundance of the Dominant Fish Species during the Second Field Experiment

Mean abundance of each of the six fish species whose mean abundance showed the greatest response to treatments through time. Error bars are standard error of the mean.

warming and acidification, coral diseases, and the adverse impacts of coastal pollution and overexploitation of coral reef fisheries.

STAR★METHODS

Detailed methods are provided in the online version of this paper and include the following:

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SUPPLEMENTAL INFORMATION

Supplemental Information can be found online at <https://doi.org/10.1016/j.cub.2020.10.097>.

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AUTHOR CONTRIBUTIONS

A.J.S. and M.J.B. were both engaged in the conceptualization of the study, acquisition of funding, conduct of the study, and writing of the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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STAR★METHODS

KEY RESOURCES TABLE

REAGENT or RESOURCE	SOURCE	IDENTIFIER
Deposited Data		
Datasets required for running the analyses and figures	This paper; Mendeley Data	https://doi.org/10.17632/jphnt7r22p.1
Software and Algorithms		
MATLAB software R2020a	Mathworks	https://www.mathworks.com/
Fathom toolbox for MATLAB software	[48]	https://www.usf.edu/marine-science/research/matlab-resources/fathom-toolbox-for-matlab.aspx

RESOURCE AVAILABILITY

Lead Contact

Further information and requests for resources and reagents should be directed to and will be fulfilled by the Lead Contact, Mark Butler (mbutleri@fiu.edu), Institute of Environment, Department of Biological Sciences, Florida International University, Miami, FL 33181 USA.

Materials Availability

*Materials Availability Statement: This study did not generate new unique materials or reagents

Data and Code Availability

*Data and Code Availability Statement: Original datasets generated during this study are available at Mendeley Data (<https://doi.org/10.17632/jphnt7r22p.1>)

EXPERIMENTAL MODEL AND SUBJECT DETAILS

Study Location and Design

We conducted our field studies in the Florida Keys (Florida, USA), a 212 km-long island archipelago offshore of which lies the world's third longest barrier reef system. Our first field experiment was conducted between July 2013 and August 2015 on 12 shallow (1.5 - 7 m depth) patch reefs (mean surface area: 10 m²) situated ~1.5 km offshore of Lower Matecumbe Key. The second set of field experiments were conducted between July 2015 and August 2017 on a separate set of 12 shallow (5 - 7 m) patch reefs (mean surface area: 21.35 m²) situated ~2.3 km offshore of Upper Matecumbe Key approximately 13 km from the first site. Crabs for our experiments were collected by divers from various habitats throughout the Middle Florida Keys.

We began by conducting two field experiments to test the suitability of *M. spinosissimus* for our *in situ* density manipulation. The first allowed us to estimate size- and sex-specific predation rates in the patch reef environment, whereas the second experiment was designed to test the site fidelity of crabs. Those studies were followed by the main experiment testing the effects of enhanced crab density on coral reef recovery, which we repeated at two locations and times.

METHOD DETAILS

Predation on crabs

Size- and sex-specific predation of crabs was tested in a tethering study conducted on patch reefs in the first study area. Crabs were sorted by sex (M,F) and into four size classes (0-29.9, 30-59.9, 60-89.9, 90+ mm CW) and fitted with a monofilament harness (9 kg-test for crabs < 50 mm CW; 23 kg-test for crabs > 50 mm CW) with a snap swivel affixed dorsally to the carapace by a knot and cyanoacrylate adhesive. Divers deployed tethered crabs onto patch reefs where the crabs were attached by a 1 m long 23 kg test monofilament line to a concrete block shelter, around which the nocturnal crabs could forage. Replicate crabs were deployed a minimum of 5 m apart on each patch reef to ensure independence. The status of tethered crabs was assessed by divers after 24 h. Crabs were considered victims of predation based on the condition of the tether and on visible evidence of the event (i.e., pieces of carapace and/or limbs remaining).

Crab Retention on Reefs

We stocked tagged crabs on eight coral patches within the first study area at a density of 1 crab m⁻² of surface area and monitored their presence on those patch reefs and on nearby patch reefs periodically for 12 months. Only crabs > 30 mm CW were stocked due to high mortality of smaller crabs. Each crab was fitted with a unique color-coded external tag on the last walking leg and with a

colored Visible Implant Elastomer cohort tag (VIE; Northwest Marine Technology, Inc., Shaw Island, WA, USA) in the soft tissue at the insertion of the right cheliped. The VIE tags are best viewed with ultraviolet light under which the VIE tags fluoresce. External tags allowed us to track individual crabs in experiments until the crab molted and the tag was lost, whereas VIE tags allowed us to track crabs through successive molts, and thus for the duration of the 12-month crab density manipulation study.

The crabs are nocturnal, therefore surveys of *M. spinosissimus* were conducted at night by divers after 1 wk, 3 wks, 3 mos, 8 mos, and 12 mos after the release of crabs onto experimental patch reefs. Crabs were not collected during these surveys but when possible the tag ID, sex, and size of crabs were recorded. Divers searched not only the patch reefs onto which the crabs were stocked, but also nearby patch reefs.

Experiments testing increased *M. spinosissimus* density on coral patch reef communities

We tested the effect of *M. spinosissimus* density on seaweed cover in two separate locations and conducted one year apart. For the first experiment, three treatment groups were randomly assigned to 12 patch reefs by manipulating crab density via stocking and initial seaweed cover by manual removal of seaweed from the reefs. Those treatments were: (1) control (natural seaweed cover and no crabs added), (2) + crabs (crabs added but no seaweed removed), and (3) scrubbed + crabs (crabs added and seaweed removed). After establishment of the treatments, divers monitored crab abundance and seaweed cover approximately monthly for a year. This non-orthogonal design prevented a statistical assessment of the interaction between crab addition and manual seaweed reduction (i.e., reef scrubbing) or an independent assessment of the effectiveness of seaweed reduction alone. However, neither of those was of central interest to this study, and others had already shown the effect of seaweeds on the abundance of corals.

We replicated the first field experiment described above at a different location starting in July 2015, but this time 12 independent patch reefs were assigned to one of four treatment groups ($n = 3$) in a two-factor crossed (orthogonal) design: crab density (two levels: Crabs Added (1 crab m^{-2}) or No Crabs Added) $\times$ initial seaweed cover (two levels: Seaweed Removed (seaweed manually removed from reef) or No Seaweed Removed (unmanipulated)). Divers again monitored crab abundance and seaweed cover on each experimental reef, this time quarterly instead of monthly. We measured four ecosystem responses to crab manipulation as follows.

Effects of Crabs on Seaweeds

Prior to and immediately following the application of treatments, divers took ten 1 m^2 photo quadrats at haphazardly selected locations on each experimental reef. Each reef was resampled in the same manner approximately monthly for one year during the first experiment and quarterly for one year in the second experiment. Each digital image was processed using the default point intercept method in the Coral Point Count with Excel extensions (CPCe) software package.⁴⁵

Effect of Crabs on Coral Recruitment

Two years after the start of each crab stocking experiment (July 2015 and 2017), divers conducted a visual census of each of the two sets of experimental patch reefs to quantify patterns in the density of living juvenile corals. We defined “juvenile coral” as any living Scleractinian coral colony with < 25 distinct coralites or < 40 mm in its longest dimension, similar to the method described by Carpenter and Edmunds (25). These data, along with an estimate of the surface area of the patch reefs, were used to calculate the mean number of juvenile coral colonies per m^2 in each treatment group (Table S1: Table summarizing the juvenile coral density and size data by treatment on patch reefs surveyed by divers during both experiments. Related to Figure 2).

Effect of Crabs on Reef Fish Community Composition

We quantified reef fish communities on each experimental patch reef in the first and second experiments prior to experimental manipulations of crabs and seaweeds, and then quarterly thereafter. Preliminary estimates of fish abundance and diversity conducted with both stationary diver surveys and time-lapse photography on the same sites yielded comparable results, so here we only present the photo-based survey results. On each patch reef, a diver mounted a small submersible digital camera (GoPro Hero 2) to a concrete block situated 2 m from the experimental reef and set to record an image every 30 s.

Effect of seaweed on reef structural complexity

To test what effect that dense, late-successional stands of benthic seaweed (particularly *Halimeda* spp.) have on the structural complexity of the reef matrix, we measured reef rugosity (i.e., topography) along 14 1-m long line transects on each experimental patch reef before and after the removal of seaweeds. Reef rugosity was quantified using the standard chain method wherein a rugosity index of 1.0 represents a completely flat surface and values greater than 1.0 represent increasingly complex structures. We measured reef rugosity before (D_i) and after (D_f) seaweed removal and the difference between those values ($\Delta D = D_f - D_i$) was then calculated to determine the effect that seaweed removal, like that caused by crab herbivory, had on fine-scale reef surface rugosity.

QUANTIFICATION AND STATISTICAL ANALYSIS

Predation on Crabs

We analyzed data from the tethering study in a three-way log-linear contingency analysis to determine the effects of size class and sex on crab mortality. For this experiment, the experimental unit (n) was defined as an individual tethered crab specimen.

Crab Retention on Reefs

The effect of experimental treatment through time was analyzed as a model I repeated-measures general linear model (GLM). These data did not satisfy assumptions of homogeneity, so were rank transformed prior to the analysis. Tukey's test was used to determine

differences in crab retention among treatment groups. For this experiment, the experimental unit (n) was defined as an individual experimental patch reef.

Experiments testing increased *M. spinosissimus* density on coral patch reef communities

For each of the following experiments involving crab density manipulation, the experimental unit (n) was defined as an individual experimental patch reef. Each patch reef was a discrete structure composed of both living and dead Scleractinian corals surrounded by relatively flat sandy bottom.

Effects of Crabs on Seaweeds

The data were reciprocal transformed to improve their fit to a gamma distribution and analyzed in a generalized linear mixed effects model in MATLAB (using the *fitglm* function with a gamma distribution) and a log likelihood link function to model the change in seaweed cover on experimental reefs (random effect) with respect to manipulations of crab density and initial seaweed cover treatments (predictor variables) through time (repeated-measure).

Effect of Crabs on Coral Recruitment

We tested the effect of treatment group on juvenile coral density with a general linear mixed-effects model (*fitglm* function in MATLAB with a gamma distribution and a log likelihood link function) where both crab treatment (2 levels) and seaweed treatment (2 levels) were fixed effects ; reef size (surface area) was included as a random effect.

Effect of Crabs on Reef Fish Community Composition

For each survey, the first and last 30 frames (15 min.) were discarded to minimize bias in the sample during times when divers were present. Individual fish in 25 randomly selected images were then counted and identified to the lowest possible taxonomic level and ontogenetic phase. The sample size of 25 frames was determined using a Scree plot of Menhinick's richness index. The data matrices were then analyzed in a non-parametric (permutation based) MANOVA (Fathom toolbox for MATLAB).

Effect of seaweed on reef structural complexity

To determine the effect of seaweed removal on the rugosity of experimental reefs, we used a paired-samples t test to compare rugosity index measurements prior to and after seaweed removal. In this experiment, the experimental unit (n) was defined as an individual 1 m transect