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THE RESPONSE OF CARIBBEAN CORAL REEF COMMUNITIES TO THE RESTORATION OF *ACROPORA* CORALS

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THE RESPONSE OF CARIBBEAN CORAL REEF COMMUNITIES TO THE RESTORATION OF *ACROPORA* CORALS.

BY

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ABSTRACT

Coral reef ecosystems are biologically diverse and ecologically important communities that provide valuable ecosystem services to coastal communities, such as coastal protection, food, and tourism. In response to the progressive worldwide decline in coral cover, the active rehabilitation of coral populations by outplanting has become an increasingly common conservation strategy. In the Caribbean, however, assessments of restoration projects have been limited to the outplanted species (mostly *Acropora* spp). We, therefore, evaluated changes in non-restored species and ecosystem functions post-restoration. We compared six locations across the Caribbean that had been outplanted with *Acropora spp*. to nearby unrestored controls. *Acropora* densities were higher at restored locations than controls, indicating successful restoration of the focal species. Overall, there were few significant responses in species composition, species richness or functional diversity across treatments. Nonetheless, *Acropora* restoration triggered recovery of some herbivores (macroalgal browsers and excavators) and fish species known to use *Acropora* for shelter, while appearing to reduce recruitment of most other coral species and the percent cover of a few benthic taxa (*Millepora spp*. and *Porites spp*.). Ecosystem responses may thus take longer than a decade (plots were 1-11 years post-restoration), require greater restoration effort, or new restoration approaches.

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PREFACE

The following thesis has been submitted in manuscript format following the formatting guidelines of the journal *Restoration Ecology*.

TABLE OF CONTENTS

LIST OF TABLES

TABLE PAGE

LIST OF FIGURES

CHAPTER 1

The response of Caribbean coral reef communities to the restoration of *Acropora* corals

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AUTHOR CONTRIBUTIONS

SS and GF formulated the research questions and constructed the experimental design; SS, GF and KN carried out the field research and data collection; SS, KN and GF analyzed the data; SS wrote the manuscript; GF and KN edited the manuscript. Those who did not contribute to the creation of the manuscript but collaborated in the field are listed in the acknowledgements.

ABSTRACT

Coral reef ecosystems are biologically diverse and ecologically important communities that provide valuable ecosystem services to coastal communities, such as coastal protection, food, and tourism. In response to the progressive worldwide decline in coral cover, the active rehabilitation of coral populations by outplanting has become an increasingly common conservation strategy. In the Caribbean, however, assessments of restoration projects have been limited to the outplanted species (mostly *Acropora* spp). We, therefore, evaluated changes in non-restored species and ecosystem functions post-restoration. We compared six locations across the Caribbean that had been outplanted with *Acropora spp*. to nearby unrestored controls. *Acropora* densities were higher at restored locations than controls, indicating successful restoration of the focal species. Overall, there were few significant responses in species composition, species richness or functional diversity across treatments. Nonetheless, *Acropora* restoration triggered recovery of some herbivores (macroalgal browsers and excavators) and fish species known to use *Acropora* for shelter, while appearing to reduce recruitment of most other coral species and the percent cover of a few benthic taxa (Millepora spp. and *Porites*

spp.). Ecosystem recovery may thus take longer than a decade (plots were 1-11 years post-restoration), require greater restoration effort, or new restoration approaches.

IMPLICATIONS FOR PRACTICE

- We confirmed that *Acropora* populations were successfully restored by outplanting.
- Although we detected some signs of recovery in other species, practitioners are cautioned that community responses may take a decade or more to be detectable.
- Baseline monitoring data for non-restored species is lacking and, where possible, should be collected before and after restoration.
- Adoption of standardized protocols for monitoring and simple data sharing practices will allow systematic assessment of current restoration practices.

INTRODUCTION

Ecological restoration has developed in response to anthropogenic pressures that have caused many ecosystems to decline in biodiversity, habitat structure, and functionality (Jordan et al. 2011). Restoration projects establish a suite of general goals that involve the recovery of rare species, enhancement of biodiversity, and the return of ecosystem functioning and services (Hallett et al. 2013). Common strategies used to achieve these goals include native species re-introduction, restoration of foundation species, removal of invasive species, and modification of physical conditions (Benayas et al. 2009) .

Restoration commonly involves restoring a single species, which is selected using several criteria, including risk of extinction, practicality of restoration, and ecosystem importance (references). Often, ecosystem engineers (*sensu* Jones et al. 1994) are

selected because they provide habitat architecture and facilitate recruitment of numerous other species, thus increasing biodiversity. Sometimes, species meet more than one criterion, for example ecosystem engineers can be at risk of extinction (Lotze et al., 2006). Single-species restoration of seagrasses, which are ecosystem engineers and have often become rare, has been shown to promote a broad community recovery, resembling that of natural meadows (Yap 2000; Paling et al. 2009; McSkimming et al. 2016). These species interact and create positive feedbacks that stabilize the community and restore ecosystem dynamics (Maxwell 2016). Similarly, the single-species restoration of the red mangrove rapidly increases tree biomass and the recovery of important functional groups (Ferreira et al. 2015; Gorman & Turra 2016).

Caribbean corals have severely declined over the past 40 years following human and natural disturbances (Gardner et al. 2003; Jackson et al. 2014). *Acropora cervicornis* and *Acropora palmata* have suffered the most serve declines, and were the first Caribbean corals listed under the US Endangered Species Act (NMFS 2006, 2014) and the IUCN red list (IUCN 2016). The severity of their decline is one key reason why most coral restoration in the Caribbean has focused on these species (Young et al. 2012). Caribbean reef communities, however, have undergone additional widespread changes. Coinciding with coral decline was a shift to macroalgal dominance of the benthos, plus declines of key predators (fish), herbivores (fish and urchins), and scavengers (lobsters) (Hughes 1989; Jackson 1997; Precht et al. 2002; Pandolfi et al. 2003; Jackson et al. 2014). Reef communities have thus undergone broad changes in functional composition that may have compromised their provision of ecosystem services (Micheli et al. 2014).

Much of the literature on coral restoration has focused on the coral species restored, rather than the response of the coral reef community to restoration (Rinkevich 2005; 2014). This focus was necessary to understand how best to create viable populations of restored corals. Athough not always clearly stated, an implied goal for *Acropora* restoration in the Caribbean is also to recreate habitat and thus increase biodiversity (Young et al. 2012; Lirman and Schopmeyer 2016). Limited funding and resources may, however, have limited opportunities to evaluate change in species other than those directly restored. Because there has been limited study of how other species respond to *Acropora* restoration, we assessed recovery of other adult and juvenile coral species, fish, and benthic composition post-restoration and quantify biodiversity and functional recovery in the Caribbean.

METHODS

Study system

Acroporid corals are major reef builders, they create calcium carbonate three-dimensional structures that provide habitat for other species. *Acropora palmata* formerly created large thickets on the reef crest often being exposed to air during low tides or in-between crashing waves (Vaughan 1916; Goreau 1959; Almy & Carrion-Torres 1963; Goreau & Wells 1967). Their thick and flattened branches allowed them to offer coastal protection by dissipating strong wave action and acted as refuge for big herbivorous fish. *Acropora cervicornis*, on the other hand, was found deeper in the fore reef zone, mostly in thickets but occasionally as individuals between other coral species. Their branches offered refuge to smaller prey fish (Vaughan 1916; Goreau 1959; Almy & Carrion-Torres 1963; Goreau & Wells 1967). They are known to be the first colonizers of sandy bottoms

because after strong storms and hurricanes, loose fragments can take anchor in the bottom and continue to grow (Tunnicliffe 1981a). Both species are highly competitive with the potential of creating large monospecific reefs and excluding other coral species. They colonize locally by fragmentation and between distant reefs by larvae that prefer to settle in substrates covered in crustose coralline algae (Connell, 1973, Connell et al. 1997).

Study design

To isolate the effect of restoration, we compared restored reefs (RES) to adjacent unrestored reefs (UNR), which served as spatial controls. The design assumes no systematic differences between RES and UNR plots at the time of restoration. We surveyed six restoration projects in different Caribbean locations from May-August 2016 (Table 1). Five locations had been restored with *A. cervicornis*, and two (Guana Island and Belize) with a mix of *A. cervicornis* and *A. palmata*. Projects differed in the size of plots restored, the timing of restoration, the specific outplanting protocols used, and the number of corals outplanted (Table 1). At each location, we compared multiple restored plots (n = 2-12 per location) and control plots (n = 1-5 per location) (Table 1). Control plots were close to restored plots (15-100 m) and selected to be similar to restored plots in wave exposure, depth, distance to shore and human visitation. All plots surveyed were in shallow water (1-15 m) and were popular destinations for snorkeling, swimming, and diving, except for those in Jamaica, which were regularly visited by fishermen.

Surveying the benthic community

We used the point intercept method to quantify benthic taxa. We placed 30 m tapes at haphazard locations within plots, and noted the taxa underlying the tape every 20 cm (n = 150 points per tape). Benthic taxa were classified into 12 categories:

scleractinian corals, soft coral (gorgonians), macroalgae, fire coral (*Millepora spp*.), crustose coralline algae, algal turf, coral rubble, sand, seagrass, sponges, *Palythoa caribaeorum* (zoanthid), and other sessile invertebrates (anemones, featherdusters, and tunicates). The percent cover of each taxon was estimated as the percentage of points intercepted by that taxon.

Surveying scleractinian corals

We used the Strong Method (following Strong, 1966 in Bakus et al, 2002) to estimate the colony density of larger corals (> 10 cm in colony diameter). We identified each coral colony intersecting the 30m transect line to species, and measured the maximum width of the colony orthogonal to the line (M). The density (colonies per m^2) of each species was estimated as density = $\Sigma(1/M)$(unit area/total transect length).

We used quadrats (50 x 50 cm, area = 0.25m^2) to count the density of smaller corals (< 10 cm in colony diameter). Quadrats were placed every 3 m along the 30 m transect line, on alternating sides. Coral recruits were identified to species and categorized by size (colony diameter = 0-2 cm, 2-4 cm and 4-10 cm).

Surveying fish and other mobile consumers

We quantified fish densities within belt transects (30 x 1.5 m, area = 45 m^2). A diver swam slowly along the transect line counting and identifying fish to species. We counted all small-medium sized taxa that are day-active, except for some small benthic taxa that are often hidden and difficult to count visually (e.g., some gobies and blennies). For some taxa (e.g. larger wrasses and parrotfishes) that have home ranges larger than the study plots, counts are indices of visitation and use of the habitat rather than population density. We also counted two mobile invertebrates, long-spined urchins (*Diadema*

antillarum) and spiny lobsters (*Panulirus argus*), because of their ecological and economic significance respectively (references). Urchins were counted within the belt transects (30 x 1.5 m), whereas lobsters were counted within the entire plot.

Surveying the structural complexity of reefs

We quantified reef structure (rugosity) using two methods. First, we used the chain-and tape-method, in which rugosity is calculated as the ratio of the length of the stretched tape and the length of chain moulded to the reef surface (Alvarez-filip 2009). We used a 3 m chain, placed at 5 m intervals along the 30 m tape. Second, rugosity was estimated using the consecutive height difference method. For this method, the height of the tape off the bottom was measured every 50 cm and rugosity calculated as the square root of the sum of the squared differences between successive height measurements (McCormick 1994).

Calculating functional diversity

We calculated functional diversity separately for scleractinian corals and fishes. Each coral species was classified by both life strategy (competitive, weedy, stress-tolerant, generalist, and not placed) and morphology (branching-open, encrusting, branching-closed, massive, columnar, digitate, laminar) (Veron 2000, 2002). Each fish species was classified by both size (<25 cm, 25-50 cm, 50-100 cm, and >100 cm) and trophic groups (Macrocarnivores, Piscivores, Mobile Benthic Invertivores, Sand Invertivores, Coral/Colonial Invertivores, Spongivores, Diurnal Planktivores, Nocturnal Planktivores, Territorial Gardeners, Turf Grazers, Scrapers, Excavator/Eroders, Macroalgae Grazers, General Omnivores) (Halpern and Floeter, 2008). We used the functional groups to calculate functional diversity using the Shannon-Weiner Index

formula. Functional diversity = - Σ [(number of individuals in all functional groups/ number of functional groups) x ln (number of individuals in all functional groups/ number of functional groups)].

Statistical analysis

Plot means were used as replicates in analyses. We used two-factor analysis of variance (ANOVA) models to test the effect of restoration (restored vs. controls), with a term for location to account for differences among restoration projects (using SPSS version 24). Our intent was to also model the influence of location (e.g. reserve status, fishing activity) or plot-level (e.g. time since restoration, coral outplant density, and plot area) covariates that might be expected to affect the outcome of restoration but these data were not available for all sites, leaving too few degrees of freedom to estimate the linear models. The simple two-factor model thus provides a simple qualitative test for the effect of restoration, and the effects of other factors are subsumed into either location or error terms. In the results, we present marginal means for restored and control plots, which are adjusted for differences among locations. Prior to analysis, data were checked for normality using Normal Q-Q plots, skewness, curtosis and the Shapiro Wilks test, and assessed for homoscedasticity using Levene's Test.

For specific groups of taxa, we also tested for consistency in the directionality of response (increase or decrease in abundance) across species using a simple binomial test.

RESULTS

Coral populations

Large (> 10 cm) *Acropora* colonies were effectively absent at control plots, indicating no natural recovery of the species in the area. In contrast, *Acropora* were at

reasonably high densities at all restored plots ($p < 0.01$), indicating that the target species was successfully reestablished by the restoration projects (Fig. 1). Small *Acropora* colonies (≤ 10 cm) were close to absent at all plots (Fig. 1), indicating a general lack of recruitment.

Of the 27 corals species encountered as adults (> 10 cm), there was no systematic tendency for species to increase (17 species) or decrease (10 species) in density at restored sites (binomial test, H_0 increases ≠ decreases, df = 16, p = 0.12). When species were tested individually, adult colony densities were indistinguishable between control and restored plots for all species except for *Porites porites*, whose adult density was reduced in restored plots (Fig. 2; p = 0.037).

For juvenile (≤ 10 cm) corals, mean densities were lower in restored plots than in control plots for 16 of the 22 species encountered (Fig. 2). Declines were thus observed more often than expected by chance (binomial test, H_0 increases ≠ decreases, df = 21, p = 0.026). Densities of all species were, however, relatively low and, when species were tested separately, we detected no significant differences between treatments in density (Fig. 2; means ± SE for all species pooled: RES= 7.37 ± 1.676 and UNR = 11.707 ± 2.29, p = 0.136).

Other benthic taxa and reef structural complexity

Most major benthic taxa and substratum categories appeared uninfluenced by restoration (Fig. 3). The one clear exception was fire coral, whose percent cover was reduced from 3.4% at control plots to 1.1% at the restored plots ($p < 0.0001$). Although not statistically significant (p = 0.12), we also note that mean macroalgal cover was 9% lower at restored plots than at controls (reduced from 33% to 23%; Fig. 3).

Neither of the two estimates of rugosity (chain-and-tape and consecutive height difference) differed between restored and unrestored plots ($p = 0.383$ and $p = 0.394$ respectively), indicating that restoring *Acropora* populations did not increase architectural complexity of the reef.

Fish and other consumers

The first of the important macroinvertebrates we monitored, the herbivorous sea urchin *Diadema antillarum*, had colonized restored reefs but was effectively absent at control plots (Fig. 4; $p < 0.0001$). The second species, the commercially harvested lobster *Panulirus argus*, did not differ in density between treatments (Fig. 4., $p = 0.338$).

For fishes, total adult and juvenile densities did not differ significantly between restored and control plots (Fig. 5; means ± SE: RES= 83.29 ± 8.47, UNR= 90.305 ± 8.95, $p<0.776$ and RES= 79.31 ± 11.04, UNR= 73.171 ± 11.67, $p<0.25$ respectively).

Fish species reported in the literature to use *Acropora* as habitat did, however tend to increase in density at restored sites. The 10 damselfish and grunt species encountered were classified as either associating with Acropora (5 species) or not (5 species). The density of none of the 10 species was affected significantly by *Acropora* restoration when tested individually (Fig. 6). Nonetheless, all species reported in the literature to associate with *Acropora* (5 of 5) had higher densities at restored plots (a pattern unlikely to have occurred by chance; binomial test, H_0 increases ≠ decreases, $df = 4$, $p = 0.03$), whereas there was no obvious pattern in the density of species with no reported association (2 of 5 were at higher density in control plots; binomial test, H_0 increases ≠ decreases, $df = 4$, $p = 0.5$) (Fig. 6).

Species richness and functional diversity

When corals and fishes were classified by functional group, few groups were affected by *Acropora* restoration. Of the coral groups, only the Branching-open/Competitive was affected by restoration, simply because *A. cervicornis* was the only representative of this group at our plots ($p < 0.0001$). For fish and macroinvertebrates, which were grouped into trophic categories, just 2 of the 12 groups were affected significantly by restoration. Densities of Macroalgal browsers, of which the most abundant was *D. antillarum*, were at six-fold higher densities in restored areas than in controls (Fig. 5). Excavators, which comprised stoplight and rainbow parrotfish, showed a threefold increase at restored plots relative to controls (Fig. 5) (RES= 2.07 ± 0.407, UNR= 0.700 ± 0.530, $p<0.047$ and RES= 9.140 ± 1.73, UNR= 1.396 ± 2.26, $p<0.0009$ respectively).

When fish and coral groups were pooled to calculate functional diversity, neither group differed between treatments (Fig. 6). Similarly, overall species richness of both corals and fish did not differ across plots (Fig. 6).

DISCUSSION

Restoration was successful in establishing populations of the target *Acropora* species at all six locations. However, the almost complete absence of recruits, is discouraging. Sexual recruits may be inhibited by the lack of preferred substrata for larval recruitment due to high macroalgal cover and rarity of crustose coralline algae (Ritson-Williams et al. 2010). Moreover, it has been described that sexual reproduction in Pacific and Atlantic Acroporids is reduced as an adaptive response to hostile environments (Wallace, 1985; Lirman, 2000; Baums, 2006). Although we saw no evidence that

restoration encourages settlement by larvae, our visit to Belize in the aftermath of a hurricane revealed numerous asexual fragments broken from outplanted *Acropora*. Research prior to its population decline showed that *A. cervicornis* can persist and spread via fragmentation following hurricane disturbances as a natural part of its life-history (Tunnicliffe 1981b, 1982; Pearson 1981), thus restoration may facilitate this mechanism of population growth (Bowden-Kerby 2001; Williams & Miller 2010; Guest et al. 2011).

Acropora restoration elicited a few statistcally significant responses that may suggest community composition recovery. *Porites porites* and *Millepora spp*. were more abundant in the control plots, possibly inhibited by the presence of *Acropora* at the experimental plots which has been previously supported in Pacific studies reporting Poritids suppressed by *Acropora* restoration (Yap, 2009). Opportunistic weedy corals like Poritids are often displaced by competitive and massive individuals such as *Acropora spp*. and *Orbicella spp* (McCook et al. 2001). Weedy and laminar coral types have shown higher resilience to climate change in nature than competitive genera, so restoration may eventually shift coral composition away from bleaching resistant taxa (Jackson 2001, Gardner, 2003).

Two key herbivore functional groups increased with restoration, which included two large excavating parrotfish and the macroalgal browsing urchin, *Diadema antillarum.* The reduction in herbivory that followed declines of both groups, was a major contributor to the shift from coral-dominated to algal-dominated reefs in the 1970s and 1980s (Lessios et al. 1984; Hughes et al. 1987; Jackson 1997). Increased coral cover and herbivores on a macro-algae dominated reefs is predicted to trigger a regime shift to a coral dominated ecosystem as macroalgae is suppressed (Done 1992; Knowlton 1992;

Dudgeon et al. 2010; Fung et al. 2011). The increase in macroalgal herbivores following *Acropora* restoration is thus encouraging, but, although macroalgal cover was lower in restored plots this decrease was not statistically significant.

For the most part, we saw no evidence of increases in species richness or functional diversity as a response to single-species restoration of Acropora. Short-term monitoring of Acroporid outplanting in the Pacific triggered increases in fish and benthic taxa (Yap, 2009). However, the limited community-wide response to restoration in the Caribbean may be due to coral-dominated habitats needing more time to recover. A practical reason for choosing *Acroporas* for restoration is their rapid growth rate, but many other coral species can take decades to recover after disturbance. Furthermore, to track responses that take years to manifest, we need to apply standardized quantitative methodology that can be shared and compared among coral practitioners. Our research represents the first Caribbean-wide restoration effect assessment and highlights the urgency for coral restoration practitioners to monitor and validate appropriate protocols to maximize restoration efficiency (Precht & Robbart 2006).

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TABLE LEGENDS

Table 1. Caribbean Coral Restoration Project Locations

Table 2. Fish functional group abundance on controlled and restored plots

Table 3. Adult coral functional group abundance on controlled and restored plots

Table 4. Juvenile coral functional group abundance on controlled and restored plots

TABLES

Table 1.

Location	# R	# C	Mean Depth (ft)	Time Post-Restoration (years)	Mean Fragments Outplanted	Mean area (m^2)	Restoration Effort (fragments/m^2)	Recreational Activities allowed
Guana	5	1	8.3	1-11	183.5	186.26	0.95	Snorkeling Boating
St. Croix	9	2	30.6	0-4	160	100	1.6	Snorkeling Diving Boating Fishing
Dominican Republic	12	2	22.4	0-5	97	Not available	Could not be calculated	Snorkeling Diving Boating Fishing
Bahamas	3	3	40.5	0-2	Not available	400	Could not be calculated	Snorkeling Diving Boating Fishing
Jamaica	2	2	32.3	2	4175	4000	1.04	Snorkeling Diving Boating Fishing
Belize	7	5	5	2-6	685	627.21	4.06	Snorkeling Diving Boating

Table 2.

Fish functional group	Mean abundance (± SE)	
	Restored	Control
THER	38.160 (±4.821)	33.228 (±6.286)
DPLA	73.813 (±8.729)	62.736 (±11.380)
OMNI	0.736 (±0.507)	1.650 (±0.661)
MINV	27.707 (±6.616)	30.125 (±8.625)
SCRP	13.145 (±2.983)	16.142 (±3.890)
EXCV	**2.067 (±0.407)**	0.700 (±0.530)
SINV	3.867 (±0.875)	2.656 (±1.141)
SPON	0.068 (±0.058)	0.056 (±0.075)
TURF	0.768 (±0.555)	1.939 (±0.723)
MCAR	1.198 (±0.245)	0.949 (±0.319)
PISC	1.956 (±0.561)	0.132 (±0.732)
MALG	**9.140 (±1.738)**	1.396 (±2.265)
SAND	3.50E-18 (±0.030)	0.033 (±0.039)

Table 3.

Adult Coral Functional Group	Mean abundance (± SE)	
	Restored	Control
Stress Tolerant/Encrusting	0.55 (± 0.275)	0.957 (± 0.377)
Weedy/Laminar	5.362 (± 1.537)	6.767 (± 2.10)
Weedy/Branching-Closed	1.498 (± 0.67)	3.109 (± 0.917)
Weedy/Massive	5.029 (± 0.903)	4.205 (± 1.236)
Weedy/digitate	0.321 (± 0.193)	0.355 (± 0.264)
Generalist/Massive	0.799 (± 0.214)	0.798 (± 0.294)
Competitive/Branching-open	**3.981 (± 0.467)**	**-4.44E-16 (± 0.64)**
Stress/Massive	2.637 (± 0.447)	2.351 (± 0.612)

Table 4.

Juvenile Coral functional group	Mean abundance (± SE)	
	Restored	Control
Stress Tolerant/Encrusting	1.138 (± 0.222)	1.207 (± 0.293)
Weedy/Laminar	2.449 (± 0.774)	3.233 (± 1.025)
Weedy/Branching-Closed	1.008 (± 0.312)	1.451 (± 0.043)
Weedy/Massive	0.064 (± 0.045)	0.133 (± 0.059)
Weedy/digitate	0.117 (±0.104)	0.267 (± 0.137)
Competitive/Branching	0.153 (± 0.08)	0.1 (± 0.106)
Generalist/Massive	0.075 (± 0.046)	0.178 (± 0.061)

FIGURE LEGENDS

Fig 1. *Acropora cervicornis* marginal mean density (#/m²) in restored and control. Error bars represent standard error values. *p<0.05

Fig 2. The marginal mean density of each size class (0-2cm, 2-4cm, 4-10cm, and >10cm) for total coral excluding *Acropora spp*. and the 4 of the most common coral species on restored and control plots. Error bars represent standard error around the mean

Fig 3. The marginal mean percent cover (%) of all benthic groups on restored and control plots. Error bars represent standard error around the mean values. *p<0.05

Fig 4. The marginal mean density (#/m²) of *Diadema* and lobsters on restored (above x-axis) and control (below x-axis) plots. Error bars represent standard deviation values around the mean. * p≤0.05

Fig 5. The marginal mean abundance of Damselfish and Grunt species on restored and control plots. Abundance values are fish per transect (45m²). Error bars represent standard deviation values around the mean.

Fig 6A. Functional diversity of fish, coral, and juvenile coral species on restored (above x-axis) and control (below x-axis) plots. Functional diversity was calculated using the Shannon-Weiner diversity index formula. Error bars represent standard deviation values around the mean. B. Total fish, coral, and juvenile coral species richness on restored (above x-axis) and control (below x-axis) plots. Error bars represent standard error around the mean values.

FIGURES

Figure 1.

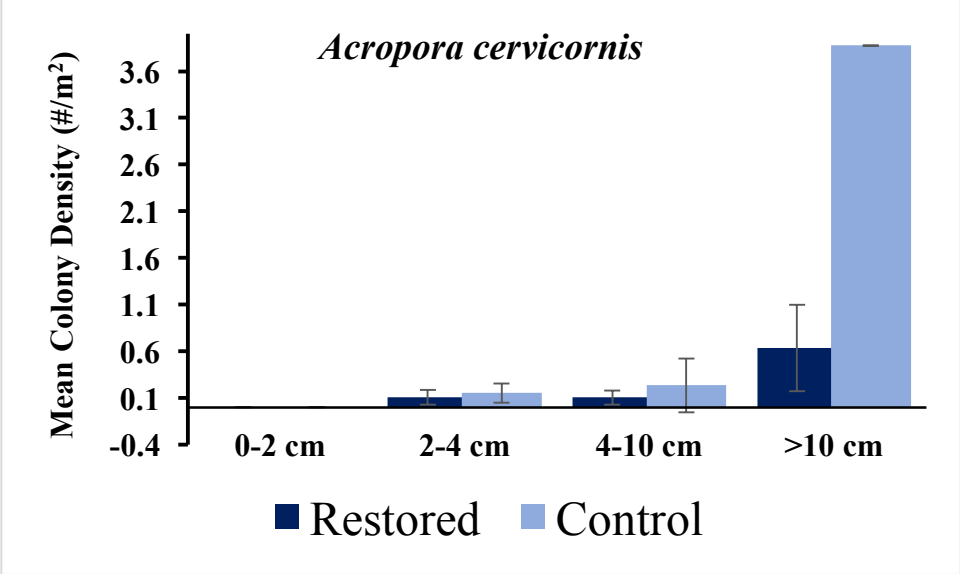


Figure 2.

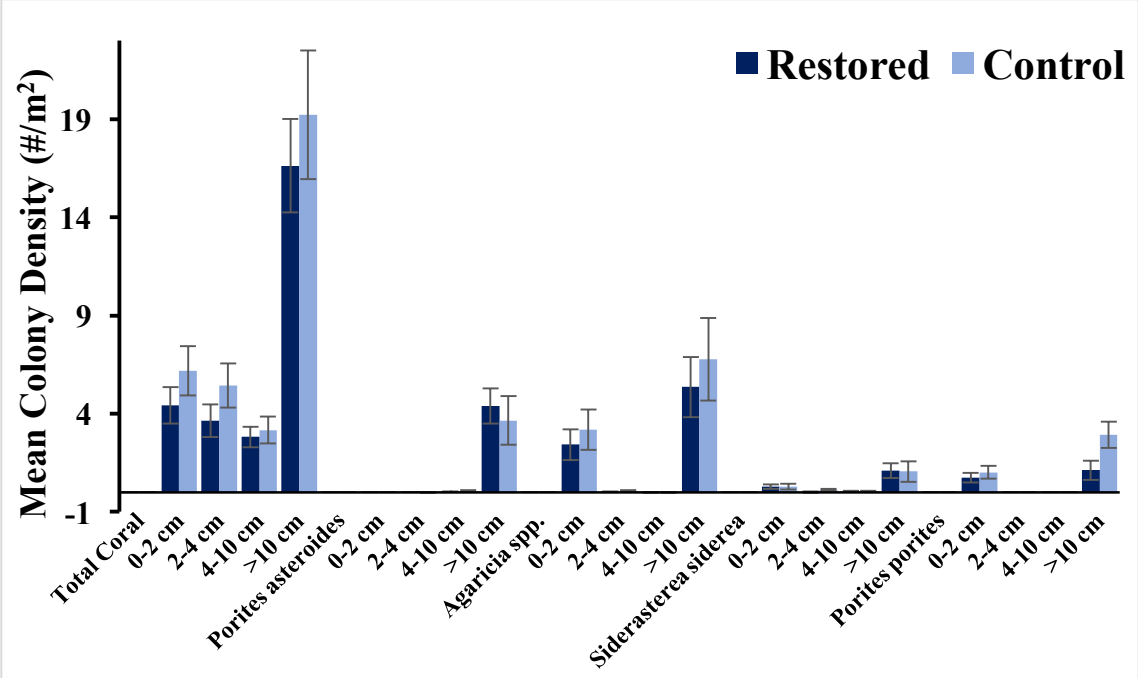

Restored
Control
Mean Colony Density (#/m²)
19
14
9
4
-1
Total Coral
0-2 cm
2-4 cm
4-10 cm
>10 cm
Porites asteroides
0-2 cm
2-4 cm
4-10 cm
>10 cm
Agaricia spp.
0-2 cm
2-4 cm
4-10 cm
>10 cm
Siderasterea siderea
0-2 cm
2-4 cm
4-10 cm
>10 cm
Porites porites
0-2 cm
2-4 cm
4-10 cm
>10 cm

Figure 3.

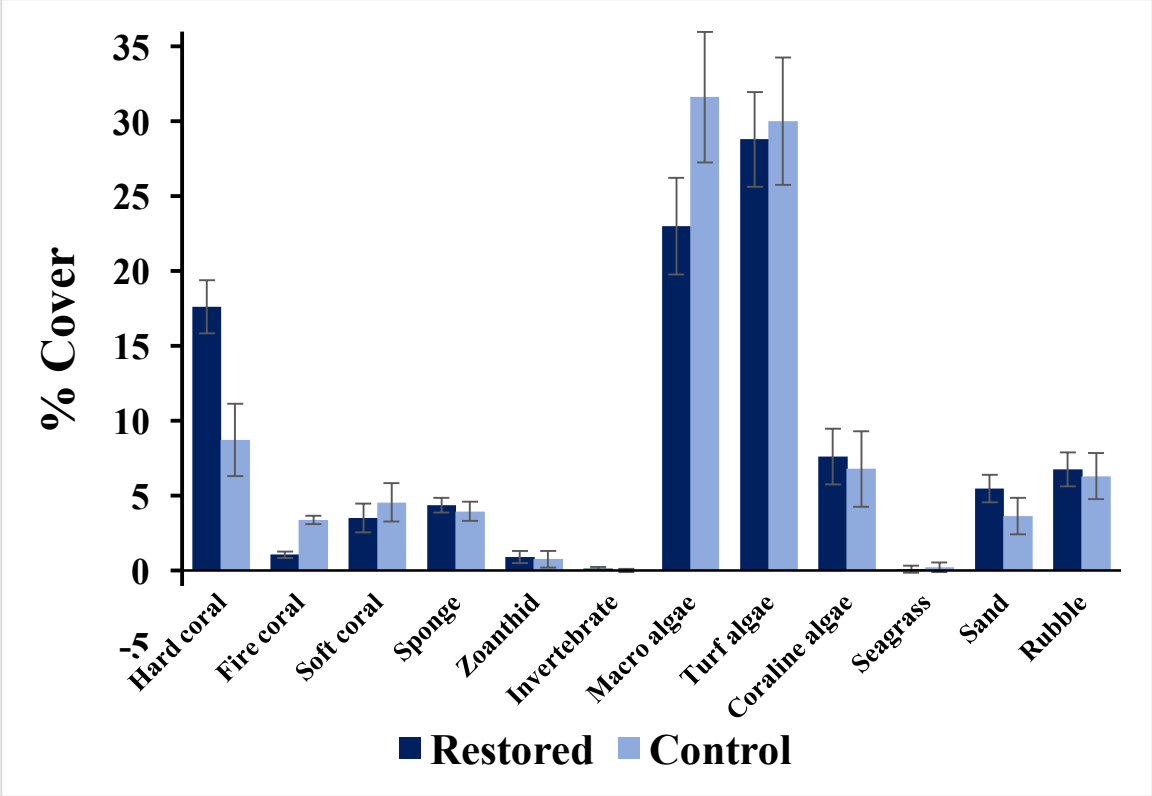

% Cover
35
30
25
20
15
10
5
0
-5
Hard coral
Fire coral
Soft coral
Sponge
Zoanthid
Invertebrate
Macro algae
Turf algae
Coraline algae
Seagrass
Sand
Rubble
Restored
Control

Figure 4.

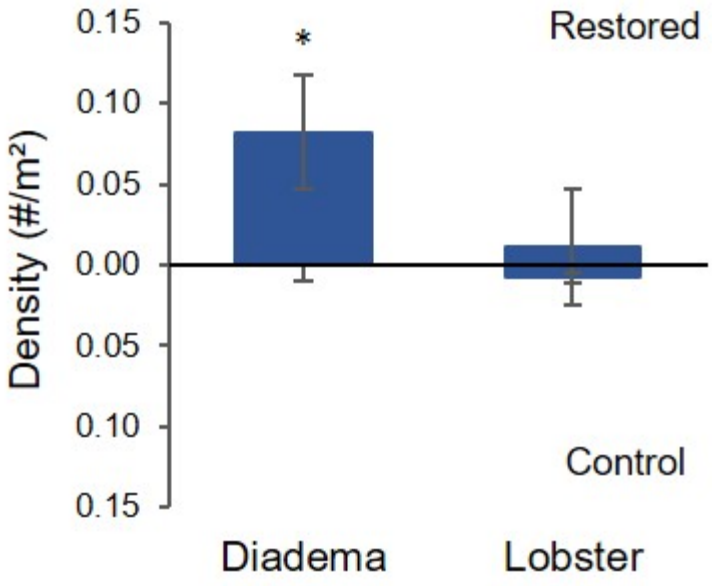

0.15
0.10
0.05
0.00
0.05
0.10
0.15
Density (#/m²)
*
Restored
Control
Diadema
Lobster

Figure 5.

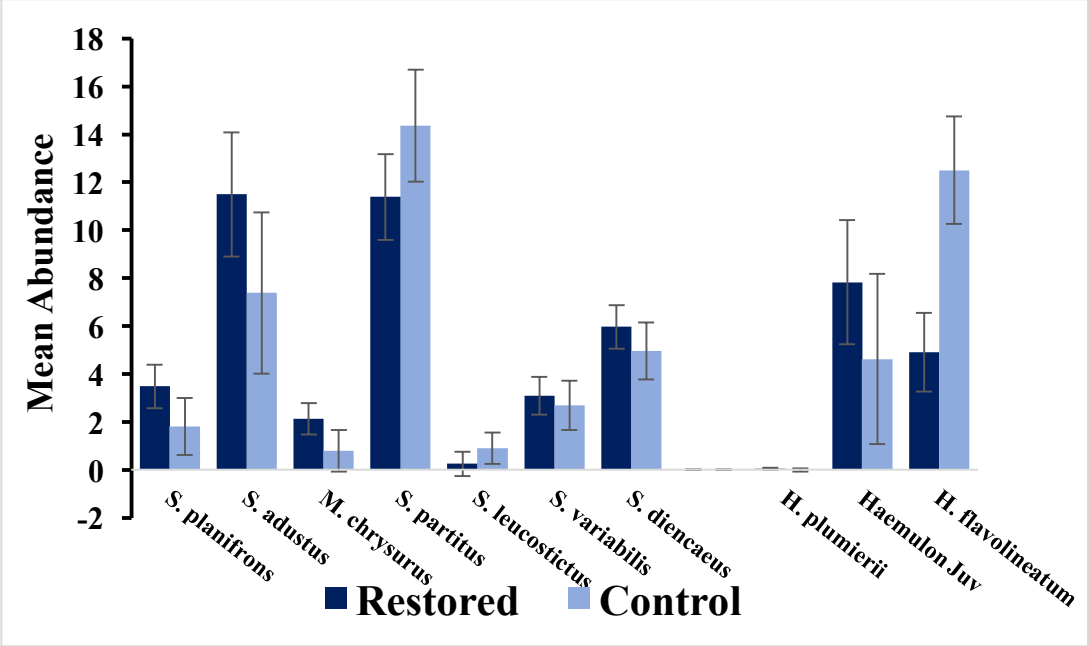
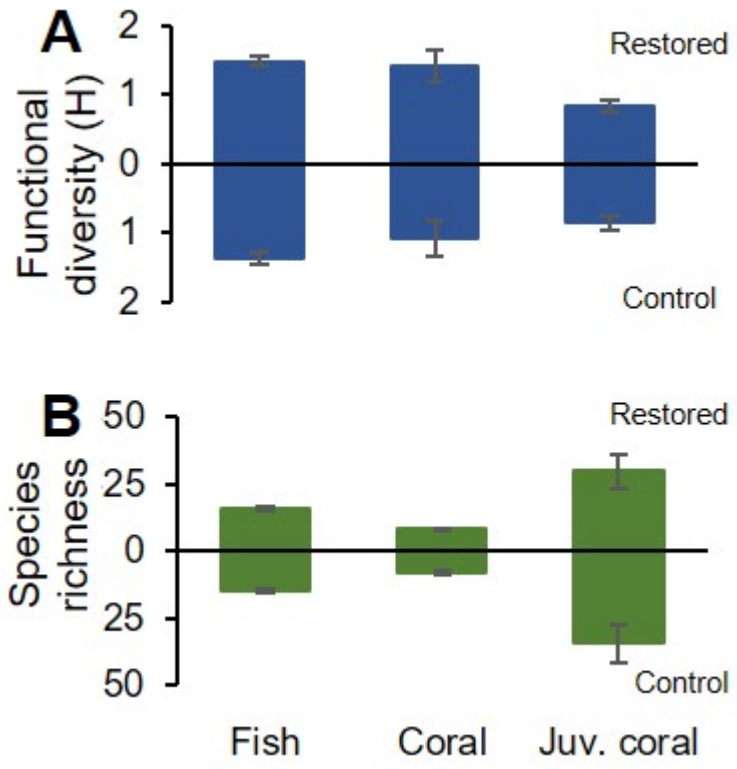

Mean Abundance
18
16
14
12
10
8
6
4
2
0
-2
S. planifrons
S. adustus
M. chrysurus
S. partitus
S. leucostictus
S. variabilis
S. dienecaeus
H. plumierii
Haemulon Juv
H. flavolineatum
Restored
Control

Figure 6.


A
Functional diversity (H)
2
1
0
1
2
Restored
Control
B
Species richness
50
25
0
25
50
Restored
Control
Fish
Coral
Juv. coral