

Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a coral reef

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ABSTRACT: The 1983 mass mortality of the sea urchin *Diadema antillarum* greatly decreased grazing intensity on Caribbean reefs, contributing to widespread increases in algal abundance and exacerbating decreases in coral cover. Urchin populations have been recovering in some areas, most notably the reefs of Jamaica's north coast. We manipulated the density of *D. antillarum* in the buttress zone of a previously unstudied Jamaican reef where the recovering urchins have a clumped distribution. Some buttresses have a large number of urchins while others nearby have none. We transplanted half of the urchins from high urchin density donor buttresses to low urchin density recipient buttresses. Transplantation significantly decreased the percent cover of macroalgae and increased the amount of bare space. These changes occurred despite a generally low retention of transferred urchins on recipient buttresses. Those urchins remaining on the recipient buttresses aggregated at rugose locations around which algae-free barrens appeared. Transplantation of urchins decreased their local density while maintaining overall density on the reef. The increase in algal consumption after transplantation implies that aggregated urchins compete for algae. Whereas aggregated *D. antillarum* tend to graze within the same area and have only a localized effect on algae, dispersed urchins compete less and eat more. Increased bare space could enhance recruitment of corals, further improving reef health. Our methods could potentially be used as an inexpensive reef restoration tool. Such restoration projects would be most effective if recipient sites with natural or artificially increased rugosity are used.

KEY WORDS: *Diadema antillarum* · Coral reef · Grazing · Competition · Macroalgae · Reef restoration · Rugosity · Buttress zone

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INTRODUCTION

In the past few decades, many coral reefs throughout the Caribbean have experienced a phase shift from coral-dominated to algal-dominated ecosystems (Gardner et al. 2003). Various factors have contributed to this phase shift, including overfishing (Hay 1984, Pandolfi et al. 2003, Hawkins & Roberts 2004), anthropogenic nutrient inputs (Lapointe 1997), widespread coral disease (Gladfelter 1982, Harvell et al. 1999, Aronson & Precht 2006), and hurricanes (Hughes et al. 1987). The 1983–84 Caribbean-wide mass mortality of the sea urchin *Diadema antillarum* (Lessios et al. 1984),

a major grazer of macroalgae on coral reefs, contributed directly to the increase in macroalgae and also exacerbated the declines in coral cover caused by the other disturbances (Bak et al. 1984, Carpenter 1988, Lessios 1988, Levitan 1988, Aronson & Precht 2006). In Jamaica, where the mortality rates of *D. antillarum* were 93–100%, macroalgal cover increased by as much as an order of magnitude over pre-die-off levels (Hughes et al. 1985). Coral cover on some Jamaican reefs, which had already undergone a significant decline following Hurricane Allen in 1980, was further reduced to almost zero by algal overgrowth (Hughes et al. 1987).

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Populations of *Diadema antillarum* on several reefs on the north coast of Jamaica have recently begun to recover (Aronson & Precht 2000, Carpenter & Edmunds 2006). On Lee Reef, St. Ann's Bay (see Maciá & Robinson 2005 for map), we observed highly patchy recovery of urchins. Before the die-off, the density of *D. antillarum* was 5.9 urchins m^{-2} at a site 2 km west of Lee Reef (Hughes et al. 1985). In 2003, we observed a maximum mean urchin density of 1.4 m^{-2} on Lee Reef, approximately 24 % of pre-die-off levels of the nearby reef (Hughes et al. 1985). *D. antillarum* occur primarily in the buttress zone, where steep-walled spurs of reef are separated from each other by channels of sand. Some buttresses on Lee Reef have relatively high populations of urchins (1.4 urchins m^{-2}), while others have few, if any (0.02 urchins m^{-2}) and noticeably more algae than buttresses with urchins.

In addition to the obvious buttress-scale aggregation, the urchins were also clumped at a scale of approximately 1 m^2 (unpubl. data). We hypothesized that this clumping increased localized competition for algae, causing the urchins to eat less algae than they would if evenly distributed. Such competition could potentially slow the recovery of reefs by decreasing the amount of bare substrate available for coral growth or recruitment. We tested our hypothesis by maintaining the average urchin density on the reef as a whole while distributing the urchins over a larger area (thereby decreasing small-scale population density). This was accomplished by removing half of the urchins from high urchin density buttresses and placing them on similarly sized buttresses with low urchin densities.

We predicted that if the urchins were competing, the decrease in population density on the buttresses would reduce overall competition on the reef. Although the amount of algae on the donor buttresses was expected to increase, we predicted that the corresponding decrease in algae on the recipient buttresses would be greater. Therefore, dispersal of the urchins would lead to a decrease in the total amount of algae on the reef, indicating competition among clumped urchins. Urchin transplantation may also prove to be a simple and inexpensive way to decrease algal abundance and improve the status of stressed Caribbean reefs.

MATERIALS AND METHODS

Baseline data. Our study was conducted on the fore-reef buttress zone of Lee Reef, in St. Ann's Bay, Jamaica. We collected baseline data on 24 buttresses between 21 May and 2 June 2003. Twelve initially had high urchin densities (hereafter referred to as 'high-urchin buttresses') and 12 had low urchin densities (hereafter referred to as 'low-urchin buttresses'). Each

buttress was located between 4.5 and 8 m depth. We measured the length of each buttress and the width at 3 points along that length: at the shallow end, deep end, and halfway between these 2 points. For the 8 buttresses longer than 20 m, the sampling area was limited to 20 m from the shallower end. There were no obvious differences between the sampled and unsampled portions on these 8 long buttresses. We calculated buttress area by multiplying the length by the average of the 3 width measurements. In addition, we counted all *Diadema antillarum* on each buttress.

On each buttress we randomly placed six 1 m^2 quadrats and quantified bottom cover with the point-intercept method by identifying the bottom type located directly below each of 16 intercept points. We measured rugosity 5 times at each buttress by randomly placing a 4 m chain (link size of 35 mm) along the reef and measuring the actual linear distance covered. The rugosity index was calculated as the ratio of the chain length (4 m) to the actual linear distance covered (Miller & Gerstner 2002); thus, higher values indicate greater rugosity. A value of 1 indicates a completely flat surface. The 5 values per buttress were averaged, and this mean was used in further analyses.

Urchin transplantation and resampling. After the initial surveys, we grouped the buttresses into sets of 4. Every set had 1 of each of the following treatments: high-urchin control, low-urchin control, donor (initially a high-urchin buttress), and recipient (initially a low-urchin buttress). We allocated buttresses to a set by first pairing high-urchin buttresses based on similar urchin density and area. We then added 2 low-urchin buttresses with areas similar to the first 2 buttresses. Experimental (donor/recipient) and control treatments were assigned randomly to 1 buttress within each high-urchin and each low-urchin pair.

Between 4 and 8 June 2003, we randomly selected half of the urchins from each donor buttress and transplanted them to its recipient, where we placed the urchins approximately 1 m from each other. Urchins were transported in cages (65 × 55 × 30 cm) made of stiff plastic netting with a mesh size of 3.2 cm and were either swum or taken by boat to the recipient buttress. The collection, transfer, and distribution of urchins on the recipient buttress took approximately 30 to 45 min for each donor-recipient pair. Urchins that had to be transported by boat were out of the water for less than 2 min. To control for handling effects, we randomly selected half of the urchins on each high-urchin control buttress and treated them in the same manner as the transplanted urchins except that they were returned to their original buttress. At each buttress we used long-jawed calipers to measure the test diameter (TD) of 25 urchins randomly selected from the individuals that were transplanted. We also measured TD of 25 random

urchins from the individuals not removed from the donor buttresses.

We resampled the buttresses 6 wk (12 to 17 July 2003) and 28 wk (14 to 20 December 2003) after transplantation. We used the same methods described above to count urchins and to measure bottom cover. On some recipient buttresses, urchins removed algae from large areas (barrens), and we made additional rugosity measurements at these barrens. We measured rugosity between 1 and 3 times (2.0 ± 0.36 , mean \pm SE) within each barren depending on its size and made the same number of measurements immediately outside each barren. We then calculated an average index for rugosity within and outside of each barren for further comparison.

Between 19 and 25 July 2003, we compared the spatial distribution of *Diadema antillarum* during the day and at night on all buttresses with at least 14 urchins (total of 17 buttresses). Starting with a haphazardly selected individual urchin, we measured the distance between it and its nearest neighbor. We then measured the distance between the second individual and its next nearest neighbor. This process was repeated until ca. 20 distance measurements were collected for each buttress or until all urchins were sampled if fewer than 20 were present. Daytime sampling was conducted between 07:00 and 09:00 h. Nighttime sampling was conducted between 20:30 and 22:30 h, at least 90 min after sunset (18:47 h) and 1 h after complete darkness fell.

Statistical analyses. Because of the multivariate nature of the benthic assemblages, we initially analyzed them with the PRIMER statistical package (Clarke & Gorley 2001). We summed the intercept points from all 6 quadrats (16 points for each quadrat) across each buttress for a total of 96 points for each buttress replicate (i.e. 6 replicates per treatment). We constructed a Bray-Curtis similarity index for square root-transformed counts of intercept points. We determined how dissimilar the assemblages of the treatments were by using a 2-way analysis of similarity (ANOSIM) followed by a 1-way ANOSIM. Although a 2-way ANOSIM tests for effects within single factors while holding variation in the other factor constant, it does not allow testing for interactions as does traditional analysis of variance (ANOVA). Therefore, we used a 1-way ANOSIM to perform a post hoc analysis on the week-buttress combinations and test for changes in treatment types over time. The significance of these tests was determined with randomization tests with up to 5000 permutations. We used the SIMPER procedure of PRIMER to determine the benthic types that explained most of the variation among all samples. SIMPER is a step-wise procedure that finds a model to explain the variation in the complete data set. We

followed these multivariate analyses with a 2-way randomization ANOVA on the average bare cover and on the average total algal cover. We used a randomization procedure analogous to Tukey's post hoc analyses to search for differences in means.

In addition to a comparison of the 4 treatment types, we tested the 'overall success' of the *Diadema antillarum* transplantation by examining changes in the benthic assemblages within the 4 buttress sets. We combined the 2 experimental buttresses (donor and recipient) and the 2 control buttresses (low and high urchin density) within each set by adding all of their intercept points. These data were then subjected to PRIMER analyses as before. We also performed a 2-way randomization ANOVA on the average bare cover and on the average total algal cover for the experimental-control combinations.

RESULTS

Mean (\pm SE) area of the 24 buttresses was 162.4 ± 12.8 m². The 12 high-urchin buttresses averaged 1.40 ± 0.18 urchins m⁻², whereas the 12 low-urchin buttresses averaged 0.02 ± 0.01 urchins m⁻². High-urchin buttresses had a significantly greater mean rugosity index (1.41 ± 0.02) than low-urchin buttresses (1.23 ± 0.05 ; $t = 6.67$, $df = 22$, $p < 0.0001$).

Prior to the urchin transplantation, 68.1% of the bottom was occupied by algae, 21.5% by bare rock, 9.6% by corals, and <1% by other organisms. Although we observed a total of 21 species of macroalgae, the benthic community was dominated by 2 macroalgae: *Dictyota dichotoma* and *Halimeda* spp. (over 98% of *Halimeda* biomass was *H. opuntia*; unpubl. data). *D. dichotoma* was present in 80% of all quadrats and covered 36.1% of the bottom. The calcareous alga *H. opuntia* was present in 84% of all quadrats and covered 13.6% of the bottom. *Porites* was the most common genus of coral, at 7.1% bottom cover.

We used non-metric multidimensional scaling (NMDS) to represent graphically the variation among the samples caused by the different substratum types (Fig. 1). Overall, the 2 factors of treatment type (2-way ANOSIM: global $R = 0.510$, $p < 0.01$) and week (2-way ANOSIM: global $R = 0.437$, $p < 0.01$) were significant. To compare all combinations of weeks and treatments, we ran a 1-way ANOSIM with each week-treatment combination as a sample. This 1-way analysis was significant overall (global $R = 0.607$, $p < 0.01$). Although the low-urchin control and recipient buttresses appeared distinct during the initial surveys in Week 0 (Fig. 1), pairwise tests revealed no significant difference between them ($R = -0.146$, $p > 0.5$). Donor buttresses, however, differed significantly from high-

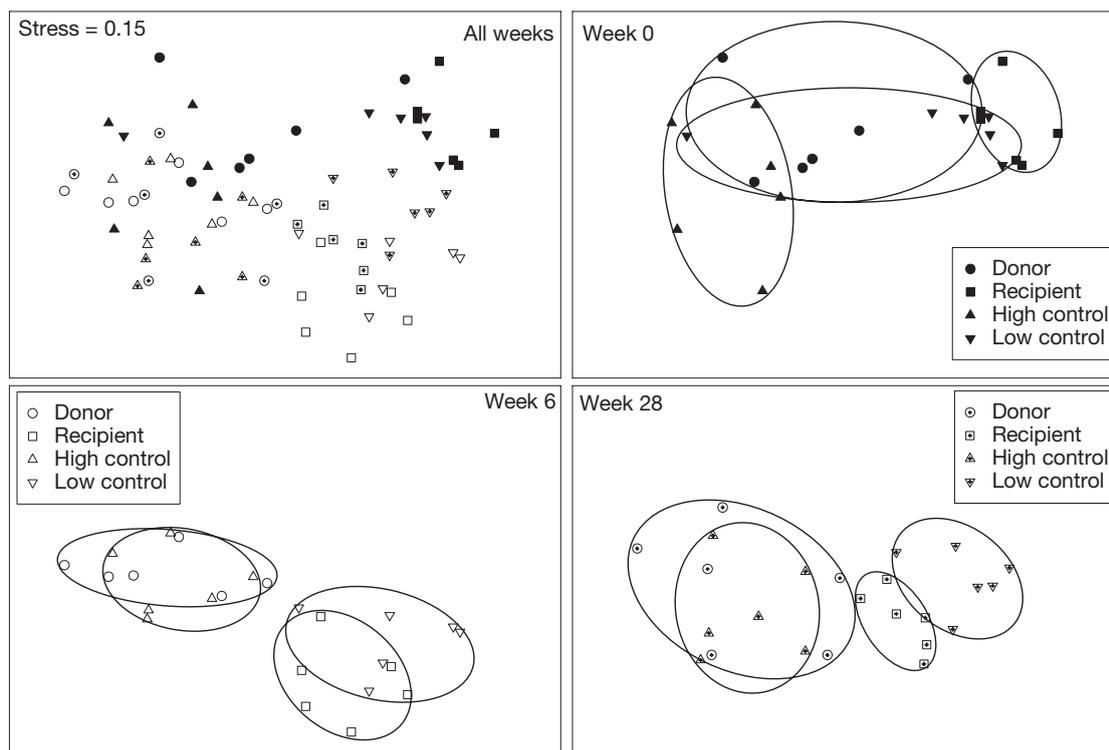


Fig. 1. Two-dimensional NMDS ordinations of square-root transformed benthic cover data. Stress value for overall analysis is 0.15. Upper left panel includes all butresses for every week. Symbols are the same throughout all 4 panels. To more easily compare treatment effects, 3 panels include only those butresses from the given week. Ellipses enclose all 6 butresses of a single treatment for the given week. Axes were held constant throughout the 4 panels so that each symbol has the same relative position

urchin control butresses at Week 0 ($R = 0.196$, $p = 0.030$). This difference was largely the result of greater abundances of *Dictyota dichotoma* and *Millepora* on donor butresses and of *Porites*, *Agaricia*, and bare substratum on high-urchin control butresses. *D. dichotoma* and bare substratum contributed rather inconsistently to these differences, however, as indicated by their relatively low scores for dissimilarity/SD (Table 1).

Post hoc analyses revealed a significant difference between recipient and low-urchin control butresses by Week 6 ($R = 0.257$, $p = 0.030$), and this difference increased by Week 28 ($R = 0.341$, $p = 0.020$). The initial difference observed between high-urchin control and donor butresses had disappeared by Week 6 ($R = -0.102$, $p > 0.5$) and was not apparent at Week 28 ($R = -0.015$, $p = 0.489$).

Relative to the low-urchin controls, recipient butresses at Week 0 tended to have less bare substratum, less cover by *Porites*, and more cover by *Dictyota dichotoma* and *Halimeda* spp. (Table 2), but there was no significant difference between the 2 treatments. At Week 6 there was a significant difference, attributable primarily to more bare substratum and lower *D.*

dichotoma cover on the recipient butresses (Table 2). Several other species contributed to this dissimilarity, although none nearly as much as bare space and *D. dichotoma* (i.e. all other dissimilarity/SD values < 1.45). *Halimeda* spp. made a moderate contribution to the difference between these 2 treatments, but it was much less important than at Week 0. At Week 28, the 2 most important contributors to the significant dissimilarity were again bare substratum and *D. dichotoma* (Table 2). As in Week 6, recipient butresses had more bare substratum and less *D. dichotoma* than their controls. These 2 substratum types combined for nearly 30% of the dissimilarity between the 2 treatments. Other benthic types that had discriminating power nearly as high or higher than bare substratum included crustose coralline algae, turf algae, and *Halimeda* spp.

Time had a significant effect on benthic cover. With one exception, each treatment type differed significantly from one sampling interval to the next (all $p < 0.010$). The one exception was no significant difference between donor butresses at Weeks 6 and 28 ($R = 0.022$, $p = 0.372$).

The 2-way randomization ANOVA revealed that algal cover was significantly affected by both the treat-

ment ($F_{3,60} = 43.844$, $p < 0.001$) and the time \times treatment interaction ($F_{6,60} = 2.302$, $p = 0.035$) but not time alone ($F_{2,60} = 2.372$, $p = 0.102$). Post-hoc comparisons within each week (Fig. 2) demonstrated significantly less macroalgal cover on the recipient buttresses than the low-urchin control buttresses at Week 28 ($p = 0.041$). A similar test on bare substratum cover (Fig. 2) found a significant difference for treatment only ($F_{3,60} =$

20.555 , $p < 0.001$), but not time ($F_{2,60} = 0.092$, $p > 0.5$) or their interaction ($F_{6,60} = 1.268$, $p = 0.277$). At Week 28, recipient buttresses had significantly more bare space than low-urchin control buttresses ($p = 0.002$) and did not differ from the high-urchin control or donor buttresses. At Week 28, there were no significant differences in algal or bare space cover between the high-urchin controls and the donor buttresses.

Table 1. Organisms contributing the most to differences between donor and high urchin-control buttresses at Week 0. Important species determined using SIMPER analysis in PRIMER. Mean abundances of each bottom type in the 2 treatments are included. Mean contribution of each benthic type to the dissimilarity between the 2 treatments and this mean value divided by its SD are also reported. The latter represents the consistency with which each benthic type contributes to overall dissimilarity (i.e. how good it is as a discriminator). Percent contribution of each benthic type to the dissimilarity and its cumulative contribution are also included (only those benthic types that contributed to the first 50% of total dissimilarity). Average dissimilarity between buttress types was 33.20. CCA: crustose coralline algae

Benthic type	Mean abundance		Mean contribution to dissimilarity	Dissimilarity/SD	% contribution	Cumulative %
	Donors	High-urchin controls				
<i>Dictyota</i>	25.17	8.00	3.98	1.08	11.99	11.99
Bare	30.83	38.50	2.72	0.94	8.19	20.18
<i>Porites</i>	7.00	14.00	2.51	1.74	7.57	27.75
<i>Millepora</i>	4.17	1.17	2.33	1.54	7.01	34.76
<i>Agaricia</i>	1.00	3.50	2.27	1.52	6.83	41.59
CCA	8.17	11.50	1.89	1.24	5.70	47.30
<i>Halimeda</i>	13.50	10.00	1.62	1.17	4.87	52.16

Table 2. Organisms contributing the most to differences between recipient and low urchin-control buttresses grouped by sampling date. Data presented as in Table 1. Given its importance to the local benthic community, we have included *Halimeda* whether or not it contributed to the first 50% of total dissimilarity. CCA: crustose coralline algae

Benthic type	Mean abundance		Mean contribution to dissimilarity	Dissimilarity/SD	% contribution	Cumulative %
	Recipient	Low-urchin controls				
Week 0; avg. dissimilarity = 28.43						
Bare	2.33	10.83	3.78	0.98	13.30	13.30
<i>Porites</i>	0.83	5.50	3.09	1.01	10.88	24.18
<i>Dictyota</i>	57.00	48.67	2.81	0.82	9.87	34.06
<i>Halimeda</i>	15.50	13.17	2.26	1.28	7.95	42.01
Turf algae	1.17	1.17	1.98	1.12	6.97	48.98
CCA	13.00	12.33	1.85	1.35	6.52	55.49
Week 6; avg. dissimilarity = 28.54						
Bare	10.17	5.50	3.63	2.46	12.72	12.72
<i>Dictyota</i>	6.00	14.83	2.80	1.79	9.83	22.55
<i>Galaxaura</i>	4.33	1.83	2.29	1.31	8.03	30.58
<i>Porites</i>	1.67	1.83	1.86	1.32	6.50	37.08
<i>Amphiroa</i>	1.67	0.17	1.75	1.30	6.13	43.21
<i>Lobophora</i>	2.33	0.67	1.75	1.37	6.12	49.33
Turf algae	4.83	3.83	1.65	1.17	5.78	55.11
<i>Halimeda</i>	35.17	31.17	1.39	1.36	4.87	64.94
Week 28; avg. dissimilarity = 28.52						
Bare	14.33	2.50	4.36	1.43	15.27	15.27
<i>Dictyota</i>	12.83	32.67	4.03	2.20	14.15	29.42
<i>Jania</i>	8.83	5.50	2.15	1.04	7.55	36.97
<i>Sargassum</i>	3.50	5.17	2.14	1.19	7.51	44.48
CCA	22.50	15.67	1.73	1.42	6.05	50.53
<i>Halimeda</i>	24.50	23.33	1.42	1.45	4.98	66.88

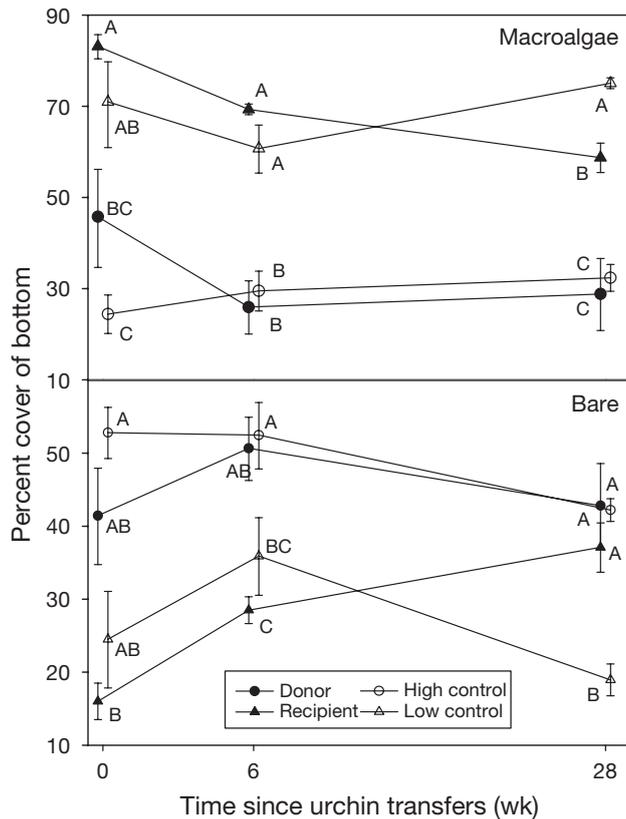


Fig. 2. Percent cover of macroalgae and bare space for 4 different buttress treatments at 3 different sampling intervals. Urchins were transferred from donor to recipient buttresses following Week 0. Means (\pm SE) have been back-transformed from arcsine transformations. Shared letters indicate means within each week that are not statistically different based on post hoc analyses from a randomization ANOVA ($\alpha = 0.05$). High and low control buttresses are controls with high and low densities of urchins, respectively. Note the different scales on the y-axes

Overall effect of urchin transplantation: experimental vs. control buttresses

Although the benthic assemblages of the combined experimental and combined control buttresses had a large overlap initially, the separation between them increased through time and was quite strong by Week 28 (Fig. 3). A 2-way ANOSIM was significant for both treatment (global $R = 0.185$, $p = 0.006$) and time (global $R = 0.662$, $p < 0.001$). A 1-way ANOSIM found no differences between the control and experimental buttresses at Week 0 ($R = 0.135$, $p = 0.052$) or at Week 6 ($R = 0.157$, $p = 0.117$), but the 2 groups differed significantly at Week 28 ($R = 0.261$, $p = 0.030$). This difference at Week 28 was largely a result of less *Dictyota dichotoma* cover and more bare substratum on experimental buttresses (Table 3). These 2 benthic types contributed

more than 37 % of the total dissimilarity between the 2 buttress types.

These multivariate analyses were supported by 2-way randomization ANOVA on the percentage of total algal cover and of bare cover. The only significant effect for algal cover was the time \times treatment interaction ($F_{2,30} = 6.553$, $p = 0.003$). Post hoc analyses indicated that the only within-week difference between experimental and control buttresses was at Week 0 when there was significantly more algal cover on the experimental buttresses ($63.2 \pm 4.3\%$) than the controls ($46.4 \pm 5.7\%$; $p = 0.008$). Bare cover was significantly affected by time ($F_{2,30} = 4.438$, $p = 0.018$) and the time \times treatment interaction ($F_{2,30} = 5.665$, $p = 0.006$). Post hoc analyses indicated that relative to the control buttresses, the experimentals had significantly less bare space ($28.5 \pm 3.4\%$ vs. $38.4 \pm 3.2\%$; $p = 0.043$) at Week 0 but more at Week 28 ($38.8 \pm 3.8\%$ vs. $26.7 \pm 1.4\%$; $p = 0.038$). There was no difference at Week 6 ($p = 0.395$).

Experimental transplant and urchin behavior

The mean TD of transplanted urchins (65.8 ± 0.7 mm) did not differ significantly (ANOVA with original buttress as blocking factor: $F_{1,301} = 3.032$, $p = 0.082$) from the mean TD of urchins that were not removed from the donor buttresses (67.4 ± 0.7 mm). Most recipient buttresses had low retention of transplanted urchins. Half of the recipient buttresses retained at least 35 % of the transplanted urchins after 6 wk, but only 2 buttresses retained that many urchins after 28 wk

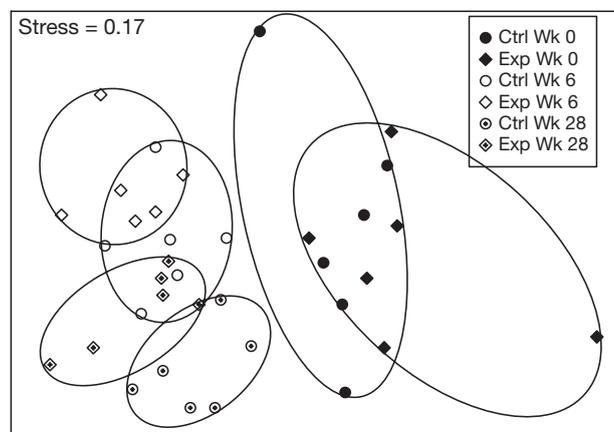


Fig. 3. Two-dimensional NMDS ordinations of square-root transformed benthic cover data representing combined cover data from control buttresses (low- and high-urchin density) and experimental buttresses (donors and recipients) within a buttress set. Each data point represents 2 buttresses (total of 192 point intercepts) during a single week. Stress value for the analysis is 0.17. Ellipses enclose all 6 groups of a single treatment for a given week

Table 3. Organisms contributing the most to differences between experimental (donor and recipient combined) and control (low-urchin and high-urchin combined) buttresses at Week 28. Data presented as in Table 1. CCA: crustose coralline algae

Benthic type	Mean abundance		Mean contr. to dissimilarity	Dissimilarity/SD	% contribution	Cumulative %
	Controls	Experimentals				
<i>Dictyota</i>	37.33	17.67	5.12	1.89	20.23	20.23
Bare	26.67	38.83	4.30	1.84	16.97	37.20
<i>Halimeda</i>	36.50	37.83	3.04	1.25	12.00	49.20
<i>Porites</i>	19.17	18.00	1.97	1.43	7.77	56.97
CCA	32.00	38.67	1.87	1.37	7.37	64.34
Turf algae	10.50	6.33	1.48	1.19	5.83	70.17
<i>Millepora</i>	3.83	7.33	1.42	1.49	5.60	75.77
<i>Jania</i>	8.00	10.33	1.27	0.94	5.03	80.80
<i>Sargassum</i>	6.17	4.00	1.06	0.92	4.17	84.97
<i>Agaricia</i>	2.50	4.33	0.77	1.28	3.03	88.00
Filamentous	2.00	2.67	0.58	1.33	2.29	90.29

(Table 4). Retention of the non-transplanted urchins on the donor buttresses was never lower than 82% at either 6 or 28 wk and was significantly greater than on recipient buttresses for both periods (2 Wilcoxon matched pair signed ranks tests [WMPSR], both: $T_s = 0$, $n = 6$, $p = 0.031$). Retention on donor buttresses did not differ from the high-urchin controls (where urchins were subjected to handling) at Week 6 and Week 28 (minimum 71% retention for both; 2 Mann-Whitney U -tests, both: $U < 27$, $n_1 = n_2 = 6$, $p > 0.20$).

Within a few days of transplantation, urchins were noticeably clumped on recipient buttresses. These aggregations were always at elevated or highly rugose locations around which the urchins created conspicuous areas with little or no algal cover, in stark contrast to the highly dense algae surrounding them. Six barrens were located on 5 separate recipient buttresses. The 2 barrens on the same buttress were distinctly separate and created by 2 independent aggregations of urchins. The rugosity index was always higher inside these barrens than in the area immediately surrounding them (Fig. 4; WMPSR: $n = 6$, $T_s = 0$, $p = 0.031$).

Table 4. *Diadema antillarum*. Retention of urchins transplanted from donor to recipient buttresses. Number of urchins added was half of the total population of the donor buttress

Recipient buttress	No. urchins added	After 6 wk		After 28 wk	
		No. urchins present	% urchins present	No. urchins present	% urchins present
1	50	43	86.0	38	76.0
2	173	130	75.1	72	41.6
3	93	35	37.6	13	14.0
4	35	6	17.1	4	11.4
5	105	16	15.2	9	8.6
6	42	4	9.5	2	4.8

Nocturnal and diurnal distribution of urchins

To compare the nocturnal and diurnal urchin distributions, we calculated the median distance between urchins for each buttress at night and during the day. The mean of those medians was significantly smaller during the day (16.4 ± 2.2 cm) than at night (23.8 ± 2.9 cm; WMPSR: $T_s = 34$, $n = 17$, $p = 0.044$).

DISCUSSION

The sea urchin *Diadema antillarum* was once a common and important grazer on Caribbean reefs (Lessios et al. 2001). Relative to pre-die-off levels, the currently recovering populations of *D. antillarum* are small and scattered (Aronson & Precht 2000, Miller et al. 2003), and individuals within these populations can occur in a clumped distribution (Carpenter & Edmunds 2006, Lee 2006, this study).

We transplanted *D. antillarum* from areas where they were relatively common to nearby areas where they were virtually absent. Our transplantation protocol involved both the removal and addition of urchins (from donor and to recipient buttresses, respectively). Multivariate analyses revealed significant differences in benthic cover between the recipient and low-urchin control buttress 6 and 28 wk post-transfer. These differences resulted largely from increases in bare space and decreases in the macroalga *Dictyota dichotoma* on the recipient buttresses. After 28 wk, recipient buttresses had a significantly lower percent cover of macroalgae and significantly more bare space relative to

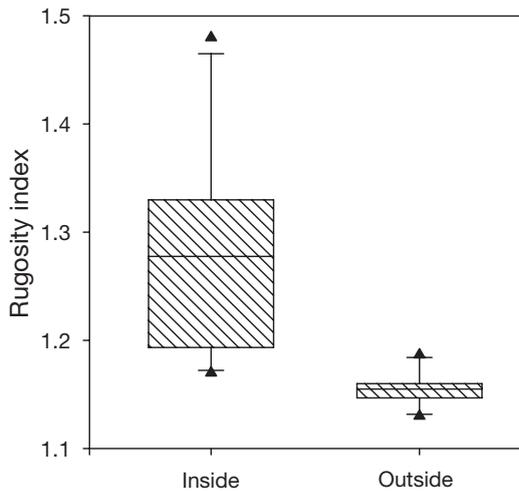


Fig. 4. Box plots of reef rugosity inside and immediately outside algal barrens on recipient buttresses 28 wk after urchin transplantation. Higher rugosity index values indicate more rugose surfaces. Box plots constructed as follows: middle horizontal line: median; boxes encompass the central 50% of data (25% above and 25% below the median); error bars: 90% confidence limits; ▲: data points beyond these limits

their low-urchin control buttresses. In addition, at 28 wk biomass of *D. dichotoma* was significantly lower on recipient buttresses than on low-urchin controls (unpubl. data).

To infer that the transplantation improved the overall health of the reef, however, requires that the total amount of algae on the experimental buttresses (i.e. recipients and donors combined) be less than on the controls. Transplantation of urchins did decrease the amount of algae on the experimental buttress pairs relative to the controls. Prior to the urchin transfer, algal percent cover was higher on the experimental buttresses than on the control buttresses. By the end of the experiment, however, algal cover on experimental buttresses had decreased such that there was no difference from the controls. ANOSIM analyses also indicated that the benthic community was significantly different between the experimental and control buttresses, primarily as a result of lower cover of *Dictyota dichotoma* (less than half as much, Table 3) and the greater amount of bare space on the experimental buttresses. Finally, at the end of the experiment, the biomass of *D. dichotoma* was significantly lower on experimental buttresses than on controls (unpubl. data).

By dispersing *Diadema antillarum*, we decreased the local (buttress-scale) densities of the urchins while maintaining their overall (reef-scale) population density. This dispersal led to a decrease in macroalgae and increase in bare space relative to initial conditions. In other words, the per capita grazing rate increased under dispersed conditions, implying that intraspecific competition is occurring in the recovering urchin pop-

ulation. Such competition is likely caused by the tendency of these urchins to aggregate. Clumped urchins tend to graze within the same relatively small area, creating the localized barrens we observed around aggregations of urchins. During their nocturnal foraging activities, *D. antillarum* spread out over a greater area. Such nocturnal dispersal suggests that the area immediately surrounding the urchin aggregations does not contain enough food for all of the urchins, and hence, intraspecific competition is probably occurring.

Our results imply that although the populations of *D. antillarum* are recovering, the recovery of Caribbean coral reefs is progressing more slowly than possible. After being experimentally spread out, urchins forage less in previously grazed areas and encounter and consume larger amounts of algae. Although early studies demonstrated intraspecific competition among *D. antillarum* prior to or shortly after the die-off (Bak & van Eys 1975, Levitan 1988, 1989), ours is the first study to suggest that even at the relatively low densities of recently recovered populations, such competition continues to be an important factor.

Retention of transplanted urchins

The effects of transplanting *Diadema antillarum* would probably have been even greater than we observed had the retention of urchins been higher on the recipient buttresses. Only 2 recipient buttresses retained more than 35% of their transplanted urchins. It appears that the urchins did not die but rather migrated away from recipient buttresses. Firstly, retention on high-urchin control buttresses, where urchins were subjected to handling controls, was high and did not differ from the donor buttresses. Secondly, we spent a significant amount of time observing these buttresses during the first 8 wk of the experiment, and we never saw any *D. antillarum* that appeared unhealthy or any remains of deceased urchins. Finally, because of overfishing, St. Ann's Bay lacks large fishes and other potential urchin predators (pers. obs.).

Reef rugosity was probably the most important factor in urchin retention. Although previous work has indicated that higher urchin abundances occur in more rugose coral reef areas (van den Hoek et al. 1978, Hunte & Younglao 1988, Miller et al. 2003, Lee 2006), only one of these studies actually quantified rugosity (Lee 2006). At our study site, high-urchin buttresses had a significantly higher rugosity index than low-urchin buttresses. Furthermore, the areas on donor buttresses where transplanted urchins aggregated had significantly higher rugosity than the immediately surrounding areas. *Diadema antillarum* are proficient bioeroders of coral reefs (Bak 1994). It is possible that the

greater rugosity on high-urchin buttresses was at least partially caused by bioerosion from the urchins themselves, but the rapid (within a few days) aggregation of transplanted urchins on rugose areas indicates an active preference for topographically complex substratum.

Implications for recovery of Caribbean reefs

Our experiment has implications for the recovery of Caribbean coral reefs and associated reef restoration projects. Although some areas have not shown any recovery (Chiappone et al. 2002, Lessios 2005), *Diadema antillarum* populations in many areas of the Caribbean have rebounded (Aronson & Precht 2000, Chiappone et al. 2001, Miller et al. 2003, Carpenter & Edmunds 2006). Many of these recovering populations have patchy distributions similar to our site (Carpenter & Edmunds 2006) and could be promising candidates for dispersal. By dispersing recovering populations of urchins, overall macroalgal abundance on the reef may be reduced and bare space increased, without a concomitant increase in algae on the donor buttresses. If the urchins can maintain low levels of algal cover for an extended amount of time, coral cover may eventually increase as observed on other Jamaican reefs (Carpenter & Edmunds 2006) and predicted by simulation models (Mumby et al. 2006).

The reefs of Jamaica are highly overfished, and predation on *Diadema antillarum* at our study site is lower than on pristine reefs. It is possible that our methods would have limited success at sites where abundant fish predators may prey on recently transplanted urchins, but given the extent of overfishing throughout the Caribbean (Hay 1981, Alvarado et al. 2004, Debrot & Nagelkerken 2006, Newman et al. 2006) there are many areas where fish predation should not affect transplanted urchins. Furthermore, our methods require sites with a recovering population of *D. antillarum*. At such candidate sites, the very presence of urchins would indicate that predators are not capable of completely removing the urchin population.

Increased rugosity is directly linked to urchin-induced decreases in macroalgal cover (Lee 2006). In our study, urchin retention was greater in more rugose areas. Therefore, practical applications of our transplant procedure would be most effective on recipient sites with high rugosity. Rugosity could be artificially increased with the addition of 3-dimensionally complex structures (e.g. cinder blocks or dead coral fragments) that can be secured to the reef. Alternatively, using recipient locations where *Diadema antillarum* cannot easily leave, such as patch reefs, could also improve retention.

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