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Evidence for positive density-dependent effects in recovering *Diadema antillarum* populations

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Abstract

Recovering populations may experience positive density-dependent feedbacks that contribute to population increases. *Diadema antillarum*, a keystone herbivore on Caribbean coral reefs, suffered a well-documented mass mortality in 1983–84. High densities of adults of this long-spined urchin could provide effective refuge from predation for juveniles under a spine canopy, as has been suggested for other urchin species. We evaluated the effect of adult density on juvenile persistence of *D. antillarum* experimentally, and examined size-frequency distributions of recovering local populations for evidence of positively density-dependent juvenile persistence at St. Croix, U.S. Virgin Islands. Juvenile persistence was significantly higher in high adult density treatments, and bimodal population size distributions also suggest potential positive effects of adult density on juveniles. This positive feedback could accelerate the recovery of this important coral reef grazer.

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1. Introduction

Ecological communities and single-species populations are often viewed as patch mosaics, with the patches in varying stages of recovery from disturbance (Sousa, 2001). Recovery from disturbance may be mediated by consumer pressure, and establishment of adult populations may initially depend on small-scale refuges [e.g., cracks and crevices (Bertness et al., 2002)] until the population reaches a critical level that promotes

persistence through positive feedbacks (Bertness et al., 2002). For example, beds of adult mussels protect juvenile mussels from predation and physical stresses (Witman, 1985; Bertness and Grosholz, 1985; Denny et al., 1985; Bertness and Leonard, 1997). Although most examples have focused on sessile species, similar processes appear to occur in populations of mobile animals. Caribbean spiny lobster, *Panulirus argus*, gain protection from predators through gregarious behavior, which increases with population size, leading Eggleston and Lipcius (1992) to describe conspecifics as a limiting resource for this species. Larvae of the sand dollar *Dendraster excentricus* settle preferentially in adult sand dollar beds, where tanaid crustaceans, important post-settlement predators, are excluded due to bioturbation of

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surface sediments by the adults (Highsmith, 1982). Similarly, juvenile purple sea urchins, *Strongylocentrotus franciscanus*, find refuge from predation by the lobster *Panulirus interruptus* under the spine canopy of adults (Tegner and Levin, 1983). Such positive density-dependent effects may be more prevalent than commonly acknowledged (Bruno et al., 2003).

Sea urchins are often important grazers of shallow subtidal benthos (e.g. Lawrence, 1975; Vance and Schmitt, 1979; McClanahan and Mutere, 1994). Their populations and the magnitudes of their impact may be controlled by predation (Duggins, 1980; Tegner and Dayton, 1981; Tegner and Levin, 1983; McClanahan and Muthiga, 1989; Sala and Zabala, 1996; Shears and Babcock, 2003), as well as other factors such as recruitment (Ebert, 1982; Balch and Scheibling, 2000), wave exposure (Ebert, 1982; Siddon and Witman, 2003), and disease (Scheibling, 1984; Azzolina, 1987; Dayton et al., 1992). Mass mortality of *Diadema antillarum*, the long-spined sea urchin, throughout the Caribbean in 1983–84 released macroalgae from what was their most important grazer on many reefs (Lessios, 1988a), particularly on overexploited reefs with few herbivorous fishes (Hay, 1984; Hay and Taylor, 1985). The disappearance of this important grazer, combined with coral mortality due to disease, bleaching, pollution, natural disturbance, and other stressors, has led to a widespread shift in community state from dense live coral to algal beds throughout much of the Caribbean (Lessios, 1988a; Hughes, 1989; Carpenter, 1990; Andres and Witman, 1995; Shulman and Robertson, 1996; Hughes and Connell, 1999; Edmunds and Carpenter, 2001).

Very low recruitment due to rarity of adults was probably the reason for lack of significant recovery of *D. antillarum* populations during the 20 years following the mass mortality (Lessios, 1988b, 1995, 2005; Carpenter, 1990; Karlson and Levitan, 1990). Low recruitment may have been exacerbated by low densities of adults, possibly causing Allee effects, inhibiting recruitment (Bak, 1985), and lowering recruit survivorship (Hunte and Younglao, 1988). Randall et al. (1964) identified 15 fish species and three invertebrates that prey on *D. antillarum*. Many urchin predators prey selectively on juveniles, which often depend on structural refuges like crevices and rock or coral rubble for concealment (Sala and Zabala, 1996; Hunt and Scheibling, 1997; Shears and Babcock, 2003), or on the spine canopies of adults for protection from predators (Tegner and Levin, 1983). Juvenile *D. antillarum* typically hide under coral rubble (Randall et al., 1964; Forcucci, 1982; this study), and have been found to

preferentially aggregate with adults (Hunte and Younglao, 1988); both behaviors may reduce predation mortality. Prior to the dieoff, predator exclusion was shown to increase sea urchin recruitment in a seagrass bed (Keller, 1982).

Recovery of *D. antillarum* has begun in some areas of the Caribbean in the past 5–10 years (Aronson and Precht, 2000; Edmunds and Carpenter, 2001; Miller et al., 2003). With increased recruitment, post-settlement mortality may take a larger role in regulating *D. antillarum* populations. In this study we evaluated experimentally the potential positive role of increased adult densities in post-settlement persistence of *D. antillarum*. Size-frequency distributions of current *D. antillarum* populations in St. Croix, U.S. Virgin Islands were also examined for evidence of positive density-dependent juvenile survival. Such a positive feedback effect would tend to enhance the recovery of this important coral reef grazer.

2. Materials and methods

2.1. Experiments

We conducted experiments designed to determine whether persistence of juvenile *D. antillarum* is positively related to adult density. These experiments were conducted in October 2004 near Rod Bay backreef (2–3 m depth), using twelve 1 m² artificial reefs constructed of concrete block rubble in 1999. The artificial reefs lie 3–5 m apart in a rough line that zig-zags across a sand bottom with sparse scattered seagrass (*Thalassia testudinum* and *Syringodium filiforme*) and macroalgae. All artificial reefs are at least 5 m from natural calcium carbonate structures that might harbor urchins, very few *D. antillarum* were present on the Rod Bay reef as a whole (Fig. 4), and no *Diadema* were found during a search of the area prior to the experiment. Prior to the experiment, all reefs were dismantled and carefully searched for juvenile *D. antillarum*, and the single juvenile found was removed. Adult urchin density was set at low (1/m²) or high (12/m²), with six reefs assigned randomly to each treatment. The high density was based on the similar pre-dieoff (Miller et al., 2003) and present-day aggregation densities (unpublished data) of *D. antillarum* in St. Croix. Adults (>50 mm test diameter) were collected in shallow water (<1 m depth) at Grassy Point (Fig. 1), an adjacent site with very high *D. antillarum* densities, and carefully moved to the artificial reefs in laundry baskets. Juveniles [test diameter ≤20 mm, estimated to be <6 months old (Karlson and Levitan, 1990)] were also

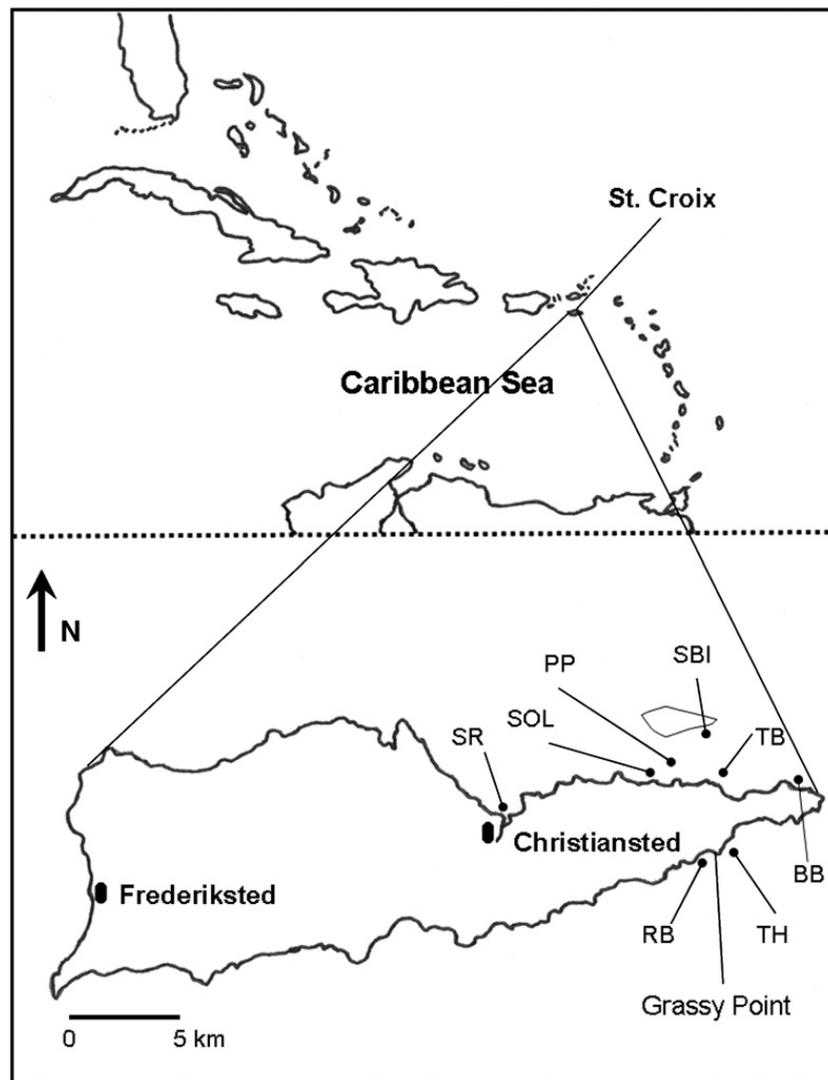


Fig. 1. Study locations on St. Croix, U.S. Virgin Islands: South Buck Island (SBI); Boiler Bay (BB); Tague Bay (TB); Solitude (SOL); Pow Point (PP); Salt River (SR); Rod Bay (RB); Turner Hole (TH). Forereef and backreef sites contiguous to the reef crest were surveyed at each location, so each location has a pair of sites. Grassy Point was the location of *Diadema antillarum* collections for the density experiment.

collected at Grassy Point. Five randomly selected juveniles were carefully transferred to the center of each reef after adult densities were set, making sure that they were secure in the reef and had adhered with their tube feet. After 5 days, we returned and counted all adults and juveniles on each reef, dismantling the reefs and searching the surrounding area to ensure that no urchins were missed. Missing adults and juveniles were replaced, and the experiment was run three times in consecutive 5 day periods.

2.2. Population structure

In October 2004 we measured size frequencies of *D. antillarum* on forereef and backreef habitats at eight

locations, for a total of 16 sites around St. Croix (map Fig. 1). At each site *D. antillarum* were counted and test diameters measured to the nearest mm, using long-jawed calipers, within 10 haphazardly located 10×1 m transects. All moveable rubble was lifted and examined, and crevices inspected as much as possible, to maximize accuracy of juvenile counts.

2.3. Data analysis

Experimental results were analyzed using mixed-model ANOVA, with factors experimental run (random, 3 levels: 1st, 2nd, 3rd) and adult density (fixed, 2 levels: low and high). The proportion of surviving juveniles on each reef at the end of each experiment, log-transformed

Table 1
Results of ANOVA on *Diadema antillarum* juvenile mortality with manipulation of adult density on artificial reefs

Source	df	SS	F	p
Adult density	1	26.856	869.33	0.001
Experimental run	2	0.121	1.96	0.34
Density × run	2	0.062	0.009	0.99
Residual	27	91.119		

Adult densities were low (1/m²) vs. high (12/m²), and the response variable was log-transformed proportional mortality.

to correct for non-normality, was the response variable. Due to logistic constraints, the experimental runs were conducted in three consecutive time intervals, which cannot be considered a random sample of times, and the results should not be interpreted as general across all times. Run was considered a random factor in the analysis, however, since the three times were not chosen for any particular reason (Underwood, 1997).

To determine whether positive density-dependent juvenile survival could be operating in natural populations, we applied least-squares regression to our survey data to test for positive association of numbers of juveniles ≤ 20 mm per transect with numbers of adults ≥ 49 mm (corresponds to average size of 1-year-old urchins, Karlson and Levitan, 1990). Juvenile and adult abundances were log-transformed to improve distribution of residuals (Ramsey and Schafer, 2001). Statistical analyses were performed using JMP software (v. 5.1 for the Macintosh, SAS Institute, Cary, NC, USA). Size-frequency histograms and quantile–quantile plots were inspected for evidence of bimodality, which has been

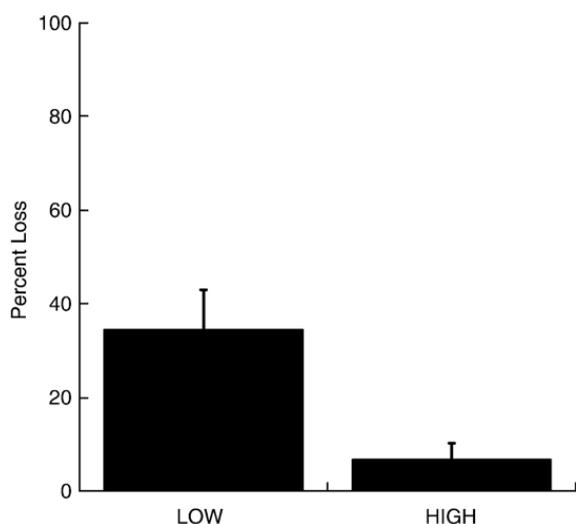


Fig. 2. Mean percentage juvenile *Diadema antillarum* mortality, per experimental reef, by adult density treatment. Error bars are one standard error.

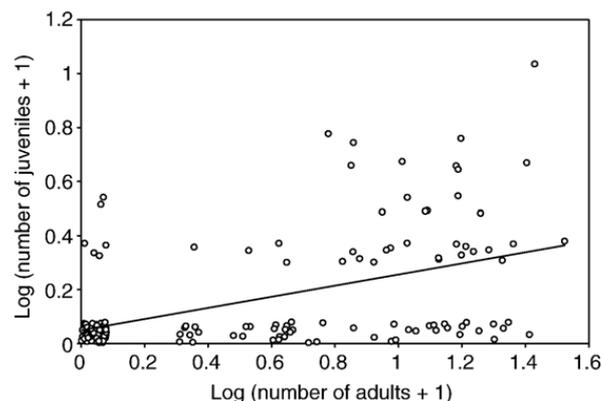


Fig. 3. Least-squares linear regression of log-transformed number of *Diadema antillarum* juveniles <20 mm vs number of adults >49 mm in 10 × 1 m transects at all sites. Positive slope is significant: $\text{Log}(\text{number of juveniles} + 1) = 0.03 + 0.23 * \text{log}(\text{number of adults} + 1)$; $r^2 = 0.29$, $df = 151$, $p < 0.0001$. Point coordinates have been jittered to eliminate over-plotting.

interpreted as evidence of a juvenile refuge effect in urchins (Tegner and Levin, 1983).

3. Results

3.1. Experiments

All adult urchins left one high-density artificial reef, which was intermittently occupied by a small (~10cm) spiny lobster (*P. argus*) and an octopus, before the end of each trial. The three replicates involving this reef were omitted from the analysis, though including these replicates did not change the overall results.

Table 2
Mean *Diadema antillarum* densities (number/m²) at the 16 study sites, based on ten 10 m² (10 × 1 m) transects per site

Site	Mean density	s.e.
South Buck Island backreef	0.04	0.04
South Buck Island forereef	1.29	0.2
Boiler Bay backreef	0.02	0.01
Boiler Bay forereef	0.02	0.01
Tague Bay backreef	0.02	0.01
Tague Bay forereef	2.86	0.6
Solitude backreef	0.34	0.2
Solitude forereef	0.88	0.3
Pow Point backreef	3.17	0.8
Pow Point forereef	1.71	0.2
Salt River backreef	1.26	0.4
Salt River forereef	0.32	0.1
Rod Bay backreef	0.08	0.1
Rod Bay forereef	0.03	0.05
Turner Hole backreef	0.88	0.3
Turner Hole forereef	0.1	0.1

See Fig. 1 for site locations.

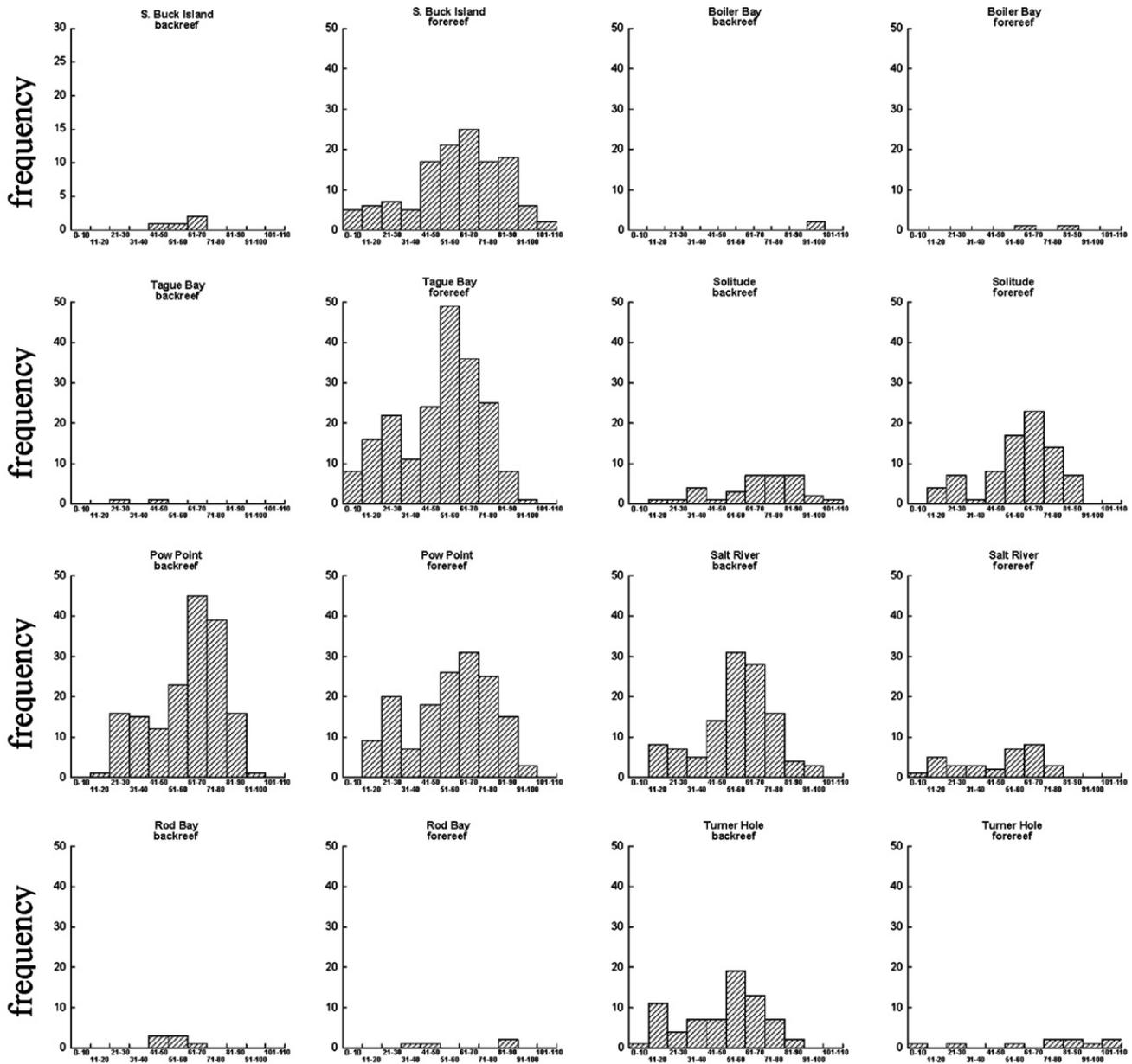


Fig. 4. Test diameter frequency histograms of *Diadema antillarum* for the 16 study sites. See Fig. 1 for site locations.

Retention of adults in the high-density reefs averaged 97.8% (s.e. 1.0%), while in the low-density reefs retention averaged 11.1% (s.e. 7.6%). The single adult placed on low-density reefs left by the end of the 5-day trial in 16 out of 18 cases. Many of these adults may have moved to neighboring high-density reefs, as in 7 out of 15 potential cases, the number of adult *Diadema* on high-density reefs actually increased. Adults were also sometimes found off the artificial reefs.

Loss of juveniles was significantly lower in reefs with high adult densities (6.7% versus 34%; ANOVA, $p=0.001$; Table 1, Fig. 2), with 5× as many juveniles disappearing from reefs relative to reefs with low adult densities. In contrast with adults, the number of juve-

niles on an artificial reef never increased over the course of a trial, and only one juvenile was ever found off the artificial reefs. There was no evidence of an experimental run effect, or of an interactive effect between run and treatment (Table 1).

3.2. Population structure

The number of adults ≥ 49 mm and juveniles ≤ 20 mm in transects was positively correlated, with adult abundance explaining 29% of the variation in juvenile abundance ($r^2=0.29$, $df=151$, $p<0.0001$; Fig. 3). 97% of transects where juvenile abundance exceeded 1 had adult abundances $>5/m^2$.

Mean population densities at the sites ranged from $0.02/\text{m}^2$ to $3.17/\text{m}^2$ (Table 2). Seven of the 16 sites had densities high enough to identify patterns in their size distributions (Table 2). Five of these seven sites show similar size distribution patterns: bimodality due to low occurrence in the 31–40 mm size class (South Buck Island forereef, Tague Bay forereef, Solitude forereef, Pow Point forereef, Salt River backreef; Fig. 4). The two remaining sites are different: Pow Pt. backreef shows a more unimodal distribution, while Turner Hole backreef shows a dip in the 21–30 mm size class.

4. Discussion

Density of adult *D. antillarum* appears to be important for persistence of juveniles. Loss of juveniles (≤ 20 mm) was lower on experimental reefs with high adult density (Fig. 1, Table 1). Karlson and Levitan (1990) estimated that *D. antillarum* grow 4 mm/month; at this rate it would take ~ 2.5 months for juveniles to grow through the 10–20 mm size class used for the experiments. The rates of loss we observed, therefore, translate to 60% (relative to initial abundance; 33% s.e.) loss for this size class in high adult density patches, and 306% (77% s.e.) loss in low adult density patches. These high loss rates generally correspond with mortality rates estimated for some other tropical urchin species (Ebert, 1982). Ebert (1982) also estimated mortality rates of 130–140%/year for *D. antillarum* (all size classes pooled) based on pre-dieoff data, although he noted that these rates may have been too high.

Adult *D. antillarum* left most of the low-density reefs, as might be expected of this typically aggregative species (Levitan, 1988). Could emigration also account for the missing juveniles? Most losses of adults from artificial reefs were accounted for by increases of adults on neighboring artificial reefs, with a few in nearby seagrass beds or rubble. Extra juveniles, however, were never found on the artificial reefs; only one juvenile was found outside the reefs after 5 days, and it was < 1 m from its reef. Fragments of juvenile spines and tests were observed in many experimental reefs, indicating predation, although predation was never observed directly. What organisms were responsible for the observed predation on juvenile urchins? Virtually all the 15 fish species that Randall et al. (1964) found to have *D. antillarum* in their guts had selected juvenile urchins (J.E. Randall, pers. comm.). However, none of these species were common in our study area except *Diodon hystrix* — we observed several porcupinefish on nearby backreef rubble habitat. Grunts (Haemulidae), several species of which consume *D. antillarum*

(Randall et al., 1964), were not common as adults in the lagoon, but they could have accessed the experimental reefs at night from the bank-barrier reef nearby (McFarland et al., 1979). Lessios (1988b) observed that adult wrasses such as *Thalassoma bifasciatum* and *Halichoeres bivittatus* were important predators of *D. antillarum* juveniles, and both were common around the experimental reefs, although we did not observe any predation on healthy juvenile *D. antillarum* by these species. Among known invertebrate predators, a few small (< 20 cm) spiny lobsters, *P. argus*, were present in the study area, and other small potential predators, such as crabs, shrimps, stomatopods, and polychaetes, were abundant in the reefs. The impact of such “micropredators” on newly-settled echinoderms is probably important, but has seldom been documented (see Highsmith, 1982, for an exception).

Studies in other marine communities have shown that the spines of adult sea urchins can reduce predation rates for conspecific juveniles. Experiments have shown that survival of juvenile urchins (Tegner and Levin, 1983) and juvenile abalone (Rogers-Bennett and Pearse, 2001) is greater under the spine canopy of adult *S. franciscanus*. *D. antillarum* have much longer spines than *S. franciscanus*, and numerous organisms shelter in them, including the juveniles of many reef fishes (Randall et al., 1964) and juvenile spiny lobster *P. argus* (authors' unpublished observations). Thus it seems likely that this refuge was responsible for the higher juvenile persistence in experimental reefs with high adult *D. antillarum* densities.

The positive association of adult and juvenile abundance that we observed (Fig. 3) is consistent with the experimental results indicating higher juvenile persistence with high adult density. However, this association could be caused by other factors, such as differential recruitment among sites due to oceanographic features or site selection at settlement, adults acting as a settlement cue (Lessios, 1988b), or facilitation of settlement by adult grazing (Bak, 1985). One study attempted to test whether the presence of adults facilitated settlement (Lessios, 1988b); no increase in *D. antillarum* settlement in patch reefs where adult density had been elevated experimentally was observed, but this was attributed to the extremely low abundance of larvae at the time. Prior research indicating spine-sheltering in other urchins inclines us to think that the high loss of juvenile *Diadema* in low-density treatments resulted directly from the lack of sheltering spines of neighboring conspecifics, but it could have been a secondary effect of low adult density. Vulnerable juveniles may have fallen to predators as they, like the less vulnerable

adults, attempted to reach centers of higher adult density — though our observations suggest that juveniles are much more reluctant to leave shelter than adults are. Another possibility, not involving positively density-dependant mortality, that could account for the correlation of juvenile and adult abundances is positive effects of adult grazing on juvenile habitat.

Bimodal size-frequency distributions can indicate high predation (Barry and Tegner, 1990) or episodic recruitment (Ebert, 1982). Stable bimodal size-frequency distributions were interpreted by Tegner and Levin (1983) as evidence of size-selective predation on urchins (*S. franciscanus*) that had outgrown an adult spine-canopy refuge, but were not large enough to escape predation through size. Theoretical analysis, however, suggests that such stable bimodal distributions could be maintained whenever mortality decreases faster than growth rate with increasing size (Barry and Tegner, 1990).

The bimodal size distributions we found at the majority of sites with high *D. antillarum* densities (Fig. 4) were not evident in St. Croix populations measured before the dieoff (Carpenter, 1990), and the size distribution from St. Croix sites in 2000 was unimodal, with no evidence of the gap at the 31–40 mm size class seen in this study (Miller et al., 2003). The bimodal distributions shown here will not be stable if they were caused by pulsed high recruitment combined with rapid juvenile growth, followed by declining growth rate with increasing size (Ebert, 1982). Rapid growth of *D. antillarum* during the first year after settlement was evident in a Florida population (Bauer, 1976), but populations in St. John, U.S.V.I., showed no evidence of higher growth of juveniles compared to adults (Karlson and Levitan, 1990). Sampling size distributions at the same sites over time (Karlson and Levitan, 1990) enable estimation and comparison of recruitment and mortality rates among sites. Continued monitoring of size distributions of recovering *D. antillarum* populations throughout the Caribbean could help determine whether these populations are still mainly recruitment limited, as they were during the 10 years immediately following the mass mortality event (Karlson and Levitan, 1990; Lessios, 1995).

Our experiments show positive density-dependent persistence of juvenile *D. antillarum*, a positive feedback effect that may be crucial to continued recovery of *D. antillarum* populations in the Caribbean. Positive density-dependence will also lead to increased patchiness in the spatial distribution of *Diadema*. Recovering populations of *Diadema*, indeed, have been very patchy, with grazed substrate clearly visible around clumps of the urchins (Edmunds and Carpenter, 2001; Miller et al., 2003; Carpenter and Edmunds, 2006). Considering the

important role of *Diadema* grazing in shaping reef communities (e.g. Sammarco, 1980; Carpenter, 1990), the interaction of this patchiness in *Diadema* populations with coral demography will affect coral abundance and species composition on Caribbean reefs. A wide-scale survey in the Caribbean has already shown increased recruitment of certain coral taxa in areas of high *Diadema* densities (Carpenter and Edmunds, 2006).

A small-scale attempt at restoration of *D. antillarum* in the Florida Keys was thwarted by high mortality of cultured juveniles placed on the reef (The Nature Conservancy, 2003). If further such efforts are judged appropriate and feasible, the results shown here indicate a possible benefit of placing juveniles in patches of high adult density to reduce such losses.

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