

# Recovery of *Diadema antillarum* reduces macroalgal cover and increases abundance of juvenile corals on a Caribbean reef

Peter J. Edmunds\*† and Robert C. Carpenter†

Department of Biology, California State University, Northridge, CA 91330-8303

Edited by Robert T. Paine, University of Washington, Seattle, WA, and approved February 6, 2001 (received for review November 2, 2000)

**The transition of many Caribbean reefs from coral to macroalgal dominance has been a prominent issue in coral reef ecology for more than 20 years. Alternative stable state theory predicts that these changes are reversible but, to date, there is little indication of this having occurred. Here we present evidence of the initiation of such a reversal in Jamaica, where shallow reefs at five sites along 8 km of coastline now are characterized by a sea urchin-grazed zone with a mean width of 60 m. In comparison to the seaward algal zone, macroalgae are rare in the urchin zone, where the density of *Diadema antillarum* is 10 times higher and the density of juvenile corals is up to 11 times higher. These densities are close to those recorded in the late 1970s and early 1980s and are in striking contrast to the decade-long recruitment failure for both *Diadema* and scleractinians. If these trends continue and expand spatially, reefs throughout the Caribbean may again become dominated by corals and algal turf.**

Many coral reefs throughout the Western Atlantic region have undergone dramatic changes in community structure over the past two decades. The best known examples of these changes are found in the Caribbean (1), where reefs that were formerly dominated by scleractinian corals and diminutive algal turfs have become overgrown by macroalgae. This transition is referred to often as a phase shift to an alternate state (1–4), where the alternative state (i.e., one dominated by macroalgae) is considered stable unless, or until, a reversal of one or more of the causative agents favors another change. However, there are few examples of multiple phase shifts on coral reefs (5) and none, to our knowledge, of a reversal from macroalgal to scleractinian dominance. Here we present evidence from the north coast of Jamaica suggesting that such a change has been initiated. On these reefs, there is localized recovery of populations of the sea urchin *Diadema antillarum*, a decrease in the abundance of macroalgae, and an increase in the abundance of juvenile corals. Although there are few comparable data spanning the last 30 years in Jamaica, there is evidence that the present densities of *Diadema* and juvenile corals have not been reported for more than a decade. If these patterns persist, the widespread recovery of *Diadema* populations alone may result in reefs dominated once again by scleractinian corals and algal turfs.

Phase shifts on Caribbean coral reefs can be caused by a variety of anthropogenic and natural factors (1, 6–8), and are integral features of communities that demonstrate multiple stable states (2, 3). However, their detection is a function of the spatiotemporal scale of investigation (2, 9), and evidence of phase shifts has come only from reefs such as those in Jamaica (1) and Hawaii (10), where decades of data are available. Even such long-term studies can provide only equivocal evidence of the underlying mechanisms of change; thus, there is still debate concerning the role of bottom-up [i.e., nutrification (7)] vs. top-down [i.e., herbivore (11, 12)] control in mediating macroalgal phase shifts. Regardless of the mechanism, the numerous reports of macroalgal phase shifts together with the absence of any documented reversals have contributed to the popular

opinion that reefs in the Caribbean now are in a highly degraded state (13).

The coral reefs along the north coast of Jamaica, particularly at Discovery Bay, provide the most familiar example of the collapse of Caribbean reefs. Discovery Bay has been studied extensively since the 1950s (1, 5, 14), arguably more than any other reef in the Caribbean, and has remained at the forefront of the reports of a macroalgal phase shift along the north coast of Jamaica. Virtually identical trends have been reported at multiple sites in Jamaica (1), but the majority of these sites have been monitored less frequently than those at Discovery Bay. In the 1950s, the reefs at Discovery Bay were characterized by small amounts of macroalgae, and scleractinian corals covered as much as 90% of the substratum (14). By the 1990s, after two major hurricanes, decades of overfishing, the near-complete loss of the keystone echinoid *Diadema* (8), increasing human population pressure, and possible nutrification, Jamaican reefs were dominated by macroalgae to a depth of 35 m, and coral cover was reduced to less than 5% (1). However, in 1992 there were small patches of *Diadema* on the forereef of Discovery Bay (15), and by 1995–96, *Diadema* had become locally abundant (e.g., 1.8 per m<sup>2</sup>, ref. 16) in shallow water (<6-m depth) and formed larger patches of macroalgal-free substratum (P.J.E., unpublished observations). Typically, these patches were scalloped-shaped, tens of meters in width, and contained locally dense populations of the herbivorous echinoids *Diadema* and *Tripneustes ventricosus* (12, 16). *Tripneustes* normally is rare or absent in forereef habitats (16), and its co-occurrence with *Diadema* in 1995–96 suggested that it might play a pivotal role in initiating the removal of macroalgae (12, 16). By January 2000, the expansion and coalescence of macroalgal-free areas formed contiguous zones hundreds of meters in length, suggestive of a reversal in community structure. This study was designed to quantify the sea urchin zones on a larger scale and test the prediction that recovery of *Diadema* populations both enhances coral recruitment and facilitates a return to coral dominance.

## Methods

**Study Sites.** Five sites were selected haphazardly along an 8-km section of the north coast of Jamaica (Fig. 1). At each site, the sea urchin and algal zones sampled were parallel to the shore and to one another and were between 4.5 and 8.5 m in depth. However, within a site, the sampled portions of the sea urchin and algal zones differed by 2 m or less in depth. At most sites, *Diadema* were found in depths as shallow as 1 m, and algal zones extended to >20 m in depth. Widths of the zone of highest

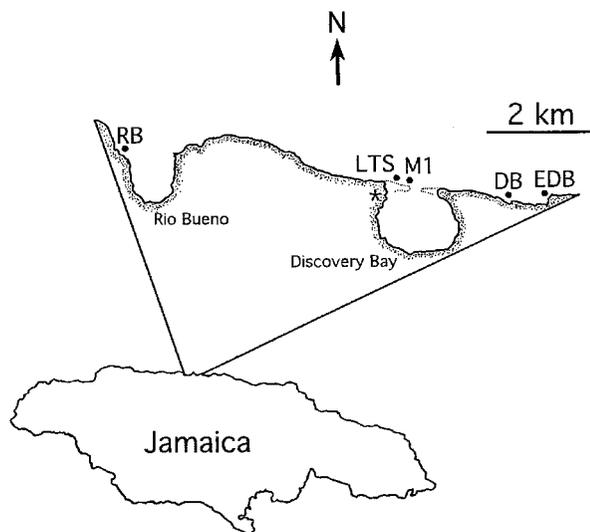
This paper was submitted directly (Track II) to the PNAS office.

See commentary on page 4822.

\*To whom reprint requests should be addressed. E-mail: peter.edmunds@csun.edu.

†P.J.E. and R.C.C. contributed equally to this work.

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.



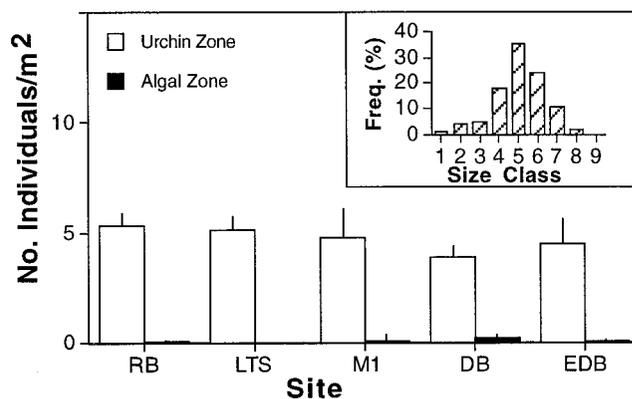
**Fig. 1.** Map of Jamaica showing the location of the study sites along the north coast. RB = Rio Bueno, LTS = Long Term Survey, M1 = Mooring 1, DB = Dairy Bull, EDB = East Dairy Bull ( $\approx 0.7$  km east of DB), and \* = Discovery Bay Marine Laboratory. Sites were selected to sample reefs that have been the subject of long-term studies [RB, LTS, M1 (refs. 1, 11, 15, and 18)] and recent surveys (DB; ref. 19), and to span the greatest scale accessible with small boats (e.g., EDB).

abundance of *Diadema* were measured perpendicularly from shore (EDB, DB) or from the reefcrest (M1, LTS, RB) to the point where benthic community structure changed abruptly from algal turf dominance (i.e., *Diadema*-grazed, ref. 17) to macroalgae (measurements at two randomly selected locations at each site). All surveys were completed during January 2000.

**Echinoid Abundances and Sizes.** Abundances of sea urchins were estimated in 1-m<sup>2</sup> quadrats ( $n = 20$  per zone) that were randomly located along a 40-m transect line. The transect was positioned haphazardly and parallel to the shore, and the same line was used for the census of juvenile corals and for the analysis of community structure (see below). Sea urchin size was defined as the maximum test diameter, and was measured to the nearest millimeter by using long-jawed calipers. The test diameters of the first 100 *Diadema* encountered in randomly located, 1-m<sup>2</sup> quadrats at each site were measured.

**Benthic Community Sampling.** Percent cover of major benthic components, such as algal turf (in the sense of Carpenter; see ref. 17), macroalgae, crustose coralline algae, and live coral, were estimated in randomly located 0.25-m<sup>2</sup> quadrats ( $n = 20$ ) in each zone. Quadrats were subdivided into 25 squares (each representing 4% of the quadrat), and the benthic component dominating each subdivision was recorded.

**Juvenile Coral Abundances and Sizes.** Juvenile corals were defined as colonies between  $\approx 2$  mm (1 polyp) and  $\leq 4$  cm in diameter (20), and were counted by using randomly located 1-m<sup>2</sup> quadrats ( $n = 10$  per zone). Juvenile corals (i.e., not spat) were located by carefully examining the substratum beneath the macroalgal canopy when necessary and by removing sediment; they were identified to species or to genus when they lacked features allowing congeners to be distinguished. *Siderastrea radians* and *Favia fragum* were omitted from all analyses because small colonies ( $\leq 4$  cm diameter) of these species are sexually mature (21); inclusion of these species did not alter the patterns described (data not shown). The sizes of juvenile corals were measured in each zone by using calipers ( $\pm 0.1$  mm), and size was



**Fig. 2.** Population densities of *Diadema antillarum* in sea urchin and algal zones at five sites along the north coast of Jamaica. (Bars = mean population densities; error bars = 1 SE; see Fig. 1 for site designations.) The size–frequency distribution of *Diadema* pooled across all sites (sea urchin zones only) is shown in the *Inset* graph with the percent occurrence of nine size classes based on the maximum test diameter. Size-class designations represent the following ranges of maximum test diameters: 1 < 20 mm, 2 = 20–29 mm, 3 = 30–39 mm, 4 = 40–49 mm, 5 = 50–59 mm, 6 = 60–69 mm, 7 = 70–79 mm, 8 = 80–89 mm, and 9 = 90–99 mm.

taken as the average of the two major diameters of the basal portion of each colony. The most common genera at each site/zone were measured (*Leptoseris*, *Porites*, *Siderastrea*, *Stephanocoenia*, and *Agaricia*), by using colonies ( $n = 50$ , except for *Agaricia* at DB, where  $n = 100$ ) that were selected haphazardly while swimming along the transect line used for counting juvenile corals and community structure.

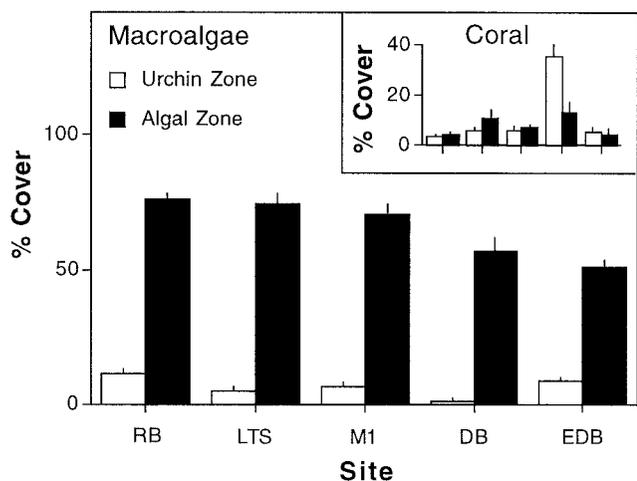
**Statistical Analyses.** Echinoid abundance, community structure (i.e., percentage cover), density of juvenile corals, and the number of genera of juvenile corals per quadrat were compared among sites and between zones with a two-way, Model III ANOVA (zone = fixed factor, site = random factor). Percentage data were arcsine transformed, the density of juvenile corals was square root-transformed, and all data were tested for the assumptions of ANOVA with graphical analyses of the residuals. Statistical analyses were completed by using SYSTAT 5.2.

## Results

Abundances of *Diadema* at each site were highest in a band extending seaward from the shore (or reef crest) to form a contiguous zone  $60 \pm 13$  m in width (mean  $\pm$  SE, pooled across sites). Mean population densities of *Diadema* were more than an order of magnitude higher within the urchin zone ( $\approx 5$  per m<sup>2</sup> with abundances reaching 12 per m<sup>2</sup> in some locations) than in the adjacent seaward algal zone at similar depths (Fig. 2), and differed among zones ( $F_{1,4} = 206.57$ ,  $P < 0.001$ ). *Diadema* densities did not vary significantly among sites, and the site–zone interaction was not significant. In the areas between the five study sites there were a few isolated pockets of *Diadema* that were surrounded by macroalgal-dominated substrata. Other species of echinoids were rare at all sites, and the highest mean abundances were 0.15 per m<sup>2</sup> for *Tripneustes ventricosus*, 2.3 per m<sup>2</sup> for *Echinometra viridis*, 0.24 per m<sup>2</sup> for *Lytechinus williamsi*, and 0.15 per m<sup>2</sup> for *Eucladaria tribuloides*.

The size–frequency distributions of *Diadema* in the sea urchin zones were similar at all sites (data not shown), although mean sizes differed among sites ( $F_{4,190} = 2.75$ ,  $P < 0.03$ ), with mean sizes varying  $< 0.5$  cm between sites. The size–frequency distribution of *Diadema* pooled across sites is shown in Fig. 2 *Inset*.

Benthic community structure differed greatly between the zones where *Diadema* was abundant (urchin zone) and adjacent

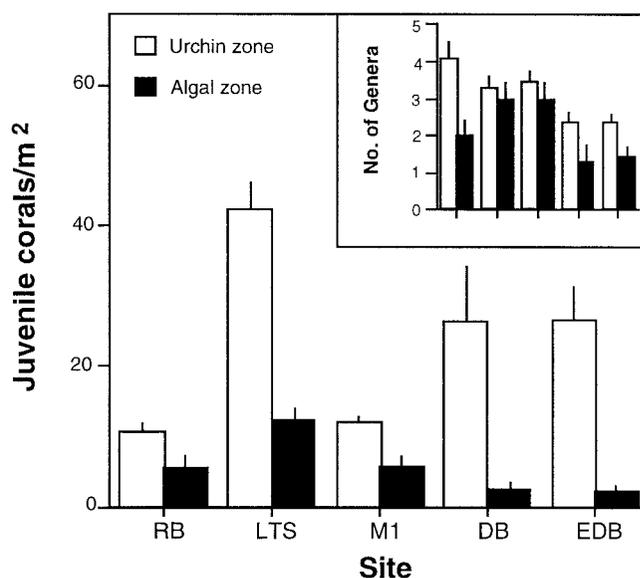


**Fig. 3.** Abundances of macroalgae and corals (*Inset*) in sea urchin and algal zones at five sites along the north coast of Jamaica. (Bars = mean percent cover; error bars = 1 SE.) See Fig. 1 for site designations; the order of sites in the *Inset* is the same as for the main graph.

areas where sea urchins were rare (algal zone). Percent cover of macroalgae was, on average, 10 times higher in areas where urchins were rare (Fig. 3), and differed significantly among zones ( $F_{1,4} = 139.83, P < 0.001$ ). The pattern of higher macroalgal abundance outside the urchin zone held across all sites, but was stronger at some sites than others, as demonstrated by the strong site-zone interaction ( $F_{4,190} = 6.58, P < 0.001$ ). The benthic community within the sea urchin zone was dominated by algal turfs ( $70 \pm 3\%$  cover, mean  $\pm$  SE) and crustose coralline algae ( $9 \pm 1\%$  cover, mean  $\pm$  SE). Abundances of algal turfs varied across zones ( $F_{1,4} = 50.04, P < 0.005$ ) but not between sites, and there was a significant site-zone interaction ( $F_{4,190} = 12.94, P < 0.001$ ). Percent cover of crustose coralline algae differed between sites ( $F_{4,190} = 14.76, P < 0.001$ ) but not between zones, and there was a significant site-zone interaction ( $F_{4,190} = 17.58, P < 0.001$ ). The percent cover of live coral was  $<10\%$  at four of five sites, and varied across sites ( $F_{4,190} = 19.76, P < 0.001$ ) but not between zones (Fig. 3), although a significant site-zone interaction ( $F_{4,190} = 5.92, P < 0.001$ ) resulted from the high coral coverage and large difference between zones at Dairy Bull. High coral cover has been reported previously at the Dairy Bull site (19).

In the sea urchin zone, juvenile corals were grazed around and over by *Diadema* and were conspicuous against the substratum. Juvenile coral density, pooled by taxon, was between 2- and 11-fold higher in the sea urchin zone compared with the algal zone at all sites (Fig. 4). Overall, the density of juvenile corals was significantly higher in the sea urchin zone compared with the algal zone at all sites ( $F_{1,4} = 21.82, P < 0.010$ ); the mean value in all five urchin zones was  $\approx 24$  per  $m^2$ , with 43 per  $m^2$  at one site. There was a significant site-zone interaction ( $F_{4,90} = 4.42, P < 0.010$ ) as a result of the among-site differences in the magnitude of the increase of juvenile-coral density in the sea urchin zone.

The juvenile corals at the five sites belonged to 14 genera and at least 17 species, and the number of genera per quadrat was up to 2.1 times higher in the sea urchin zone compared with the algal zone, although this difference was not significant ( $F_{1,4} = 10.20, P = >0.050$ , Fig. 4). The most common taxa of juvenile corals encountered were *Agaricia* spp. ( $n = 915$ ), *Porites* spp. ( $n = 167$ ), *Siderastrea siderea* ( $n = 323$ ), *Leptoseris cucullata* ( $n = 46$ ), and *Stephanocoenia michilini* ( $n = 40$ ); there were small numbers of several primary reef-framework-building corals, including *Acro-*



**Fig. 4.** Density and number of genera per quadrat (*Inset*) of juvenile corals in sea urchin and algal zones at five sites along the north coast of Jamaica (mean  $\pm$  SE;  $n = 10$  for each bar). See Fig. 1 for site designations; the order of sites in the *Inset* is the same as for the main graph.

*pora cervicornis* ( $n = 3$ ), *Acropora palmata* ( $n = 1$ ), *Montastraea annularis sensu lato* ( $n = 2$ ), *Montastraea cavernosa* ( $n = 2$ ), *Diploria* spp. ( $n = 11$ ), and *Colpophyllia natans* ( $n = 1$ ). Juvenile *A. cervicornis*, *A. palmata*, and *M. annularis* were found only in the urchin zones. The sizes of all juvenile corals (pooled by genus) were significantly different among sites ( $F_{4,859} = 6.08, P < 0.001$ ) but not between zones ( $F_{1,4} = 5.538, P > 0.050$ ), and the interaction was not significant. Mean sizes (pooled by genus and zone) varied from  $21.7 \pm 0.5$  mm ( $\pm$ SE,  $n = 180$ ) at DB to  $25.7 \pm 0.6$  mm ( $\pm$ SE,  $n = 180$ ) at LTS, with a grand mean size (pooled by genus, site, and zone) of  $23.1 \pm 0.4$  mm ( $\pm$ SE,  $n = 745$ ). Similarly, the sizes of juvenile *Porites* and *Agaricia* (the only two genera found at all five sites) varied significantly among sites ( $F_{4,220} = 5.20, P < 0.010$  and  $F_{4,286} = 3.30, P < 0.050$ , respectively) but not between zones, and there was no significant interaction. Thus, the size of juvenile corals was similar in urchin and algal zones, and there were significant but relatively small differences ( $\leq 5$  mm) among sites.

### Discussion

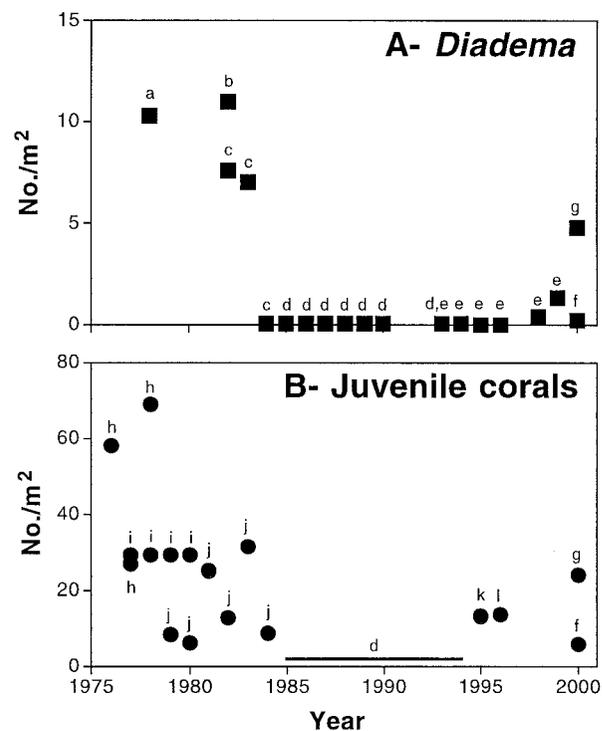
The results of our surveys demonstrate that increased densities of sea urchins are associated with a reduction in cover by macroalgae and elevated densities of juvenile corals (up to 11-fold). Together with a plethora of correlational and experimental studies of *Diadema* grazing (8, 17), as well as recent results based on 7 years of data at an adjacent site (12), our findings suggest that *Diadema* caused the decline in macroalgae and initiated a change in community structure at the spatial scale examined. Given the rarity of *Tripneustes* on the shallow fore-reefs of Jamaica, the hypothesized synergistic role of this sea urchin in initiating the removal of macroalgae (12, 16) is not supported by the present results. Instead, our findings demonstrate a putative phase reversal (from macroalgae) in the presence of high densities (up to 12 per  $m^2$ ) of *Diadema* and the near-complete absence of *Tripneustes* ( $<0.15$  per  $m^2$ ).

There are several mechanisms by which *Diadema* could have facilitated the changes underway in Jamaica. The most conspicuous result of *Diadema* grazing is the removal of macroalgae and its replacement by a low biomass, high-turnover algal community (algal turf) interspersed with crustose coralline algae (17).

Experimental manipulations have demonstrated more subtle effects, including the enhancement of recruitment and survivorship of juvenile corals at intermediate densities of *Diadema* (4 per m<sup>2</sup>). While settlement of coral spat is highest in the absence of *Diadema*, survivorship of juvenile corals is low due to algal overgrowth. At high sea-urchin densities, intense grazing damages juvenile corals, and coral survivorship is reduced (22). Additionally, increased cover of crustose coralline algae might enhance coral settlement (23). Decreased survivorship of juvenile corals in the absence of grazing likely is caused by a variety of factors including overgrowth, shading and/or abrasion by macroalgae (24), smothering by sediment that accumulates and is stabilized by higher algal biomass (25), or a combination of these effects. As a result, grazing by *Diadema* may increase the abundance of juvenile corals through enhanced coral settlement, and/or increased survivorship of juveniles. Manipulative experiments will be required to determine the relative importance of these processes.

Further support for the pivotal role of *Diadema* in the recent changes in Jamaica comes from the temporal coincidence of events. *Diadema* densities increased at the same time that macroalgal-free patches began to appear on the north coast of Jamaica (in 1995–96; P.J.E., unpublished observations; ref. 12); age estimates for *Diadema* and average-sized juvenile corals are consistent with their recruitment close to, or after, 1995. For *Diadema*, growth rates are rapid during their first year and slow considerably as individuals approach a maximum size of ≈100 mm (test diameter) after 3–4 years (26). Growth rates and test diameters also are affected by resource availability, often reflected by the inverse relationship between *Diadema* population density and mean individual size (27, 28). Given the abundant algae on the study reefs in Jamaica and the low probability that *Diadema* growth was limited by resources, test diameter consequently may allow estimation of age. For the range of maximum test diameters measured in this study (10–89 mm), and assuming size-specific growth rates (29), the individuals range from approximately 1 month to 4 years old. The overall mean individual size pooled over all sites is 56 mm with an estimated age of ≈2 years. For scleractinians, the relationship between age and size is determined by the time-integrated exposure to partial mortality and growth rates. Older colonies likely have experienced one or more partial mortality events and have a poor relationship between size and age (30). Juvenile colonies are less likely to have experienced partial mortality and, therefore, their size and age are related more closely. The published growth rates of juvenile corals are highly variable, ranging from ≈2 mm/y (20) to ≈36 mm/y (31), but many grow at ≈12 mm/y (31, 32). When 12 mm/y is used as a working growth-rate estimate, juvenile corals 23 mm in diameter (the mean size of all juveniles in this study) are ≈23 months old, or about the same age as the average-sized *Diadema*. Whereas such calculations demonstrate that the concordance of ages of *Diadema* and juvenile corals is consistent with a cause-and-effect hypothesis, such correlational evidence cannot prove that *Diadema* has resulted in increased abundances of juvenile corals. Nevertheless, the recovery of *Diadema* on the study reefs in Jamaica and its association with elevated densities of juvenile corals (and reduced macroalgal cover) suggest that there is a functional relationship between these events. Further studies are required to determine whether coral cover in Jamaica will increase after decades of decline, or whether the new state is stable. In January 2001, the sea urchin zones in Jamaica still contained  $4.0 \pm 0.9$  *Diadema* per m<sup>2</sup> and were  $60 \pm 2$  m in width (both mean  $\pm$  SE,  $n = 5$  sites), thereby demonstrating persistence over at least 1 year.

When the present results are placed in a historical context, comparing abundances of *Diadema* and juvenile corals in Jamaica over the last 20+ years, it seems that the present abundances are increasing after more than a decade of apparent



**Fig. 5.** (A) Population densities of *Diadema* at depths between 4 and 10 m along the north coast of Jamaica from 1977 to 2000. Reported abundances are averaged over sites and depths within a sampling period (year) for each study. (a) Discovery Bay (R.C.C., unpublished data), (b) Discovery Bay (36), (c) Discovery Bay and Rio Bueno (37), (d) 14 sites in Jamaica (1), (e) Discovery Bay (12), (f) algal zones at five sites (this study), (g) sea urchin zones at five sites (this study). (B) Densities of juvenile corals along the north coast of Jamaica between 1976 and 2000. There are no comparable data from the mid-1980s to the early 1990s (1), but it is likely that there was little or no coral recruitment over this period (1). Densities of juvenile corals from the present study (averaged across sites) for the algal and urchin zones (f and g, respectively). (h) The densities of juvenile corals ( $\leq 5$  cm diameter) on Discovery Bay (11-m depth) in 1976–1978 (34) calculated from ref. 38 (i) for foliaceous corals ( $\leq 50$  cm<sup>2</sup>) at Rio Bueno (10-m depth) between 1977 and 1980, and calculated from ref. 39 (j) by using the densities of new recruits ( $\leq 2.6$  cm diameter) of *Agaricia agaricites* and *Leptoseris cucullata* at 10-m and 20-m depths, assuming that they represented 75% of the coral recruits. (k) The average densities of juvenile corals ( $\leq 4$  cm diameter) at four sites (10-m depth) on, or close to, Discovery Bay (19). (l) Juvenile corals ( $\leq 4$  cm diameter) at Dairy Bull (10-m depth; P.J.E., unpublished data).

recruitment failure (Fig. 5). Significantly, the densities we report here for both *Diadema* and juvenile corals are approaching those recorded before the mass mortality of *Diadema* in 1983–84. In addition to the common genera of juvenile corals encountered (e.g., *Agaricia*, *Porites*, and *Siderastrea*), all of which typically are abundant recruits on Caribbean reefs (32), it also is ecologically significant that we found small numbers of recruits of *Acropora cervicornis*, *A. palmata*, and *Montastraea annularis* in the sea urchin zones, because these species are among the most important reef-framework-building corals in the Caribbean (33). Although the recruits of these species currently are found at low densities ( $<0.4$  per m<sup>2</sup>) along the north coast of Jamaica, this is routinely the case in studies of coral recruitment in the Caribbean (32). Moreover, the present-day densities are at least as high as those recorded 24 years ago at Discovery Bay (34), when adult colonies of *Acropora* and *Montastraea* were the dominant species on Jamaican reefs (6, 14, 35).

If the patterns documented here result in a reversal of the phase shift from macroalgae to corals and algal turf on shallow

reefs in Jamaica, it would indicate that macroalgal dominance of Caribbean reefs is not an inevitable and terminal consequence of natural and anthropogenic disturbances. Instead, our results reemphasize the disproportionate effects of a single species (*Diadema*) in mediating transitions between alternate states on present-day reefs, particularly those with reduced abundances of herbivorous fishes (8). The coral reefs of Jamaica have been at the forefront of reports of ecosystem collapse, and predictions of the future for most reefs remain gloomy (40, 41). Although our results should not be construed to mean that reef recovery is

inevitable throughout the western Atlantic, this study does provide good news about the recovery of highly degraded Caribbean coral reefs.

We thank S. Genovese for facilitating the collaboration that generated this research, M. Haley for graciously hosting our stay at the Discovery Bay Marine Laboratory, and R. Habeeb and C. Zilberberg for diving assistance. This work was supported by the East/West Marine Biology Program of Northeastern University and, in part, by a National Institutes of Health Grant Minority Biomedical Research Support GM48680 (to R.C.C.). This is Discovery Bay Marine Laboratory contribution number 631.

1. Hughes, T. P. (1994) *Science* **265**, 1547–1551.
2. Knowlton, N. (1992) *Am. Zool.* **32**, 674–682.
3. Done, T. (1992) *Hydrobiologia* **247**, 121–132.
4. Ostrander, G. K., Armstrong, K. M., Knobbe, E. T., Gerace, D. & Scully, E. P. (2000) *Proc. Natl. Acad. Sci. USA* **97**, 5297–5302. (First Published May 2, 2000; 10.1073/pnas.090104897)
5. Aronson, R. B. & Precht, W. F. (2001) in *Evolutionary Paleocology: The Ecological Context of Macroevolutionary Change*, eds. Allmon, W. D. & Bottjer, D. J. (Columbia Univ. Press, New York), 171–233.
6. Woodley, J. D., Chornesky, E. A., Clifford, P. A., Jackson, J. B. C., Kaufman, L. S., Knowlton, N., Lang, J. C., Pearson, M. P., Porter, J. W., Rooney, M. C., et al. (1981) *Science* **214**, 749–755.
7. Lapointe, B. E. (1997) *Limnol. Oceanogr.* **42**, 1119–1131.
8. Lessios, H. R. (1988) *Annu. Rev. Ecol. Syst.* **19**, 371–393.
9. Petraitis, P. S. & Laitham, R. E. (1999) *Ecology* **80**, 429–442.
10. Hunter, C. L. & Evans, C. W. (1995) *Bull. Mar. Sci.* **57**, 501–515.
11. Hughes, T. P., Szmant, A. M., Steneck, R. S., Carpenter, R. C. & Miller, S. L. (1999) *Limnol. Oceanogr.* **44**, 1583–1586.
12. Aronson, R. B. & Precht, W. F. (2000) *Limnol. Oceanogr.* **45**, 251–255.
13. Ginsburg, R. N., ed. (1997) *Proceedings of the Colloquium of Global Aspects of Coral Reefs: Health, Hazards and History* (Rosenstiel School of Marine and Atmospheric Science, University of Miami).
14. Goreau, T. F. (1959) *Ecology* **40**, 67–89.
15. Woodley, J. D. (1999) *Coral Reefs* **18**, 192.
16. Woodley, J. D., Gayle, P. M. H. & Judd, N. (1999) *Coral Reefs* **18**, 193.
17. Carpenter, R. C. (1986) *Ecol. Monogr.* **56**, 345–363.
18. Liddell, W. D. & Ohlhorst, S. L. (1987) *Bull. Mar. Sci.* **40**, 311–329.
19. Edmunds, P. J. & Bruno, J. F. (1996) *Mar. Ecol. Prog. Ser.* **143**, 165–171.
20. Edmunds, P. J. (2000) *Mar. Ecol. Prog. Ser.* **202**, 113–124.
21. Soong, K. (1993) *Coral Reefs* **12**, 77–83.
22. Sammarco, P. S. (1980) *J. Exp. Mar. Biol. Ecol.* **45**, 245–272.
23. Morse, D. E. N., Hooker, N., Morse, A. N. C. & Jensen, R. A. (1988) *J. Exp. Mar. Biol. Ecol.* **116**, 193–217.
24. Miller, M. W. & Hay, M. E. (1996) *Ecol. Monog.* **66**, 323–344.
25. Birkeland, C., Rowley, D. & Randall, R. H. (1981) *Proc. 4th Int. Coral Reef Symp.* **2**, 339–344.
26. Lewis, J. B. (1966) *Bull. Mar. Sci.* **16**, 151–158.
27. Carpenter, R. C. (1981) *J. Mar. Res.* **39**, 749–765.
28. Levitan, D. R. (1988) *Oecologia* **76**, 627–629.
29. Levitan, D. R. (1991) *Biol. Bull.* **181**, 261–268.
30. Hughes, T. P. & Jackson, J. B. C. (1980) *Science* **209**, 713–715.
31. VanMoorsel, G. W. M. N. (1988) *Mar. Ecol. Prog. Ser.* **50**, 127–135.
32. Bak, R. P. M. & Engel, E. H. (1979) *Mar. Biol.* **54**, 341–352.
33. Sheppard, C. R. C. (1982) *Mar. Ecol. Prog. Ser.* **7**, 83–115.
34. Rylaarsdam, K. W. (1983) *Mar. Ecol. Prog. Ser.* **13**, 249–260.
35. Liddell, W. D., Ohlhorst, S. L. & Boss, S. K. (1984) *Paleontol. Am.* **59**, 385–389.
36. Morrison, D. (1988) *Ecology* **69**, 1367–1382.
37. Hughes, T. P., Keller, B. D., Jackson, J. B. C. & Boyle, M. J. (1985) *Bull. Mar. Sci.* **36**, 377–384.
38. Hughes, T. P. & Jackson, J. B. C. (1985) *Ecol. Monog.* **55**, 141–166.
39. Hughes, T. P. (1985) *Proc. 5th Int. Coral Reef Symp.* **4**, 101–106.
40. Hoegh-Guldberg, O. (1999) *Mar. Freshwater Res.* **50**, 839–866.
41. Hughes, T. P. & Tanner, J. E. (2000) *Ecology* **81**, 2250–2263.