Algal–urchin biomass responses following mass mortality of *Diadema antillarum* Philippi at Saint John, U.S. Virgin Islands

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Abstract: A mass mortality occurred in 1983, killing 95–99% of the *Diadema antillarum* Philippi in the Caribbean. This study, conducted in Lameshur Bay, Saint John, U.S. Virgin Islands, reports the impact of the mass mortality on *Diadema* population density, algal biomass, and *Diadema* body size. Census dates were 6 months before and 6, 12, 18, 26, 30, and 42 months after the mass mortality. There was an initial 100-fold decrease in population density after the mortality. During the first 12 months after the mortality, there was a slight increase in density. During the next 30 months, however, population density remained constant. There was a 30-fold increase in algal biomass 6 months after the mortality. During the next 36 months, however, algal biomass decreased to only 5-fold premortality levels. After the mass mortality, mean and maximum urchin test diameter increased 2- and 1.5-fold, respectively. Median *Diadema* weight increased 10-fold from 1984 to 1987. During the same time period, *Diadema* biomass per unit area increased 42-fold. Although postmortality densities may not return to premortality levels for several decades, the increase in body size of *Diadema* may return urchin and algal biomass to premortality levels much sooner.

Key words: Body size; *Diadema antillarum*; Indeterminate growth; Mass mortality; Plant–herbivore interaction

INTRODUCTION

In January 1983, mass mortalities of the sea urchin *Diadema antillarum* were reported in Panama (Lessios *et al.*, 1983). By 1984, an unknown agent had reduced population density to 1–5% of former levels throughout the Caribbean (Lessios *et al.*, 1984b). Since that time, algal biomass has increased dramatically in several locations (Saint Croix: Carpenter, 1985, 1988; Jamaica: *Hughes et al.*, 1985, 1987; Curaçao: Ruyter van Steveninck & Bak, 1986). These authors have suggested that the increase in algal abundance was due to a release from herbivory by *Diadema*. This suggestion follows from earlier experimental work which demonstrated that grazing by *Diadema* has a major influence on benthic algal abundance (Sammarco *et al.*, 1974; Carpenter, 1981, 1986; Sammarco, 1982).

Previous to the mass mortality, *Diadema* body size was inversely related to population density (Saint Croix: Carpenter, 1981; Barbados: Hunte *et al.*, 1986; Saint John: Levitan, in press a). In other systems, this relationship has been used as evidence of food limitation; at high population density, body size is suppressed (Ebert, 1968; Sutherland, 1970; Branch, 1975). If this hypothesis is correct, following the mass mortality, the surviving urchins and new recruits should grow to a level exceeding the premortality maximum size. This study provides evidence that indeterminate growth allows *Diadema* to exploit increases in food availability (caused by reduction in population density) by increasing body size.

Previous reports have documented the extent of the die-off and initial conditions of *Diadema* population structure following the mass mortality (Bak *et al.*, 1984; Lessios *et al.*, 1984a,b; Hughes *et al.*, 1985; Hunte *et al.*, 1986). In this paper, I describe changes in the size and structure of *Diadema* populations from 6 months prior to 42 months after the mass mortality. Concurrent changes in algal abundance are also reported. The results of these observations emphasize the importance of body size regulation to the population ecology and grazing potential of *D. antillarum* Philippi.

MATERIALS AND METHODS

During the summer of 1983 (6 months prior to the mortality event), five sites were chosen in Greater and Little Lameshur Bay, Saint John, U.S. Virgin Islands (Fig. 1),
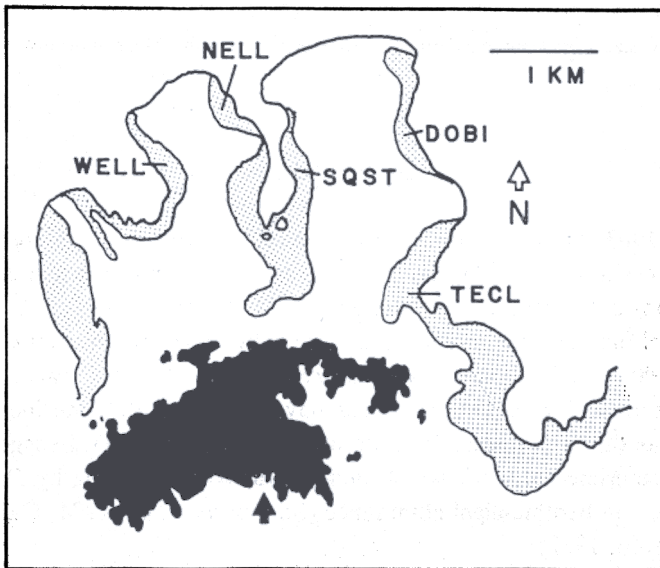

Fig. 1. Map of Saint John, U.S. Virgin Islands (in black). Inset is of Lameshur Bay (location on Saint John indicated by black arrow). Stippled area indicates fringing reef. Center of bay is occupied by seagrass beds. Study sites are indicated by abbreviations: WELL, West Little Lameshur; NELL, Northeast Little Lameshur; SQST, Squid Site; DOBI, Donkey Bight; TECL, Tektite Cliffs.

to investigate the relationship between body size and population density. Each site was monitored for *Diadema* population density, size structure, and the composition of algal and sessile invertebrate species on the substratum. After the mass mortality (December 1983 for Saint John: Lessios *et al.*, 1984b; P. Ross, pers. comm.), these sites were monitored at months 6, 12, 18, 26, 30, and 42. Population density and test diameter were assessed in each site along two belt transects (total of 1000 $m^2 \cdot$ site^{-1}) on either side of the 3-m depth contour line (previous to the mortality, 15 m^2 was used because of the abundance of urchins). All the urchins within the transects were collected. Urchins were then counted and measured (horizontal test diameter to 0.1 mm) with needle-nose vernier calipers and placed in suitable crevices within the transect. Urchin biomass per unit area was estimated by calculating the weight of urchins per m^2 (size to weight regression: log live weight (g) = 2.99 × log size (mm test diameter) − 3.20, $r^2 = 0.99$, $n = 182$).

Percent cover of algal and invertebrate species was monitored, at all sites, in five 1-m^2 quadrats per transect, along three transects, following the 2-, 3-, and 4-m depth contours. A 1-m^2 frame was placed over the quadrats. The frame had intersecting monofilament lines, producing a grid with 100 regularly placed points (a total of 1500 points $\cdot$ site^{-1}). The organisms under these points were recorded to estimate percent cover of sessile invertebrate and algal species. Percent cover was monitored in the summer of 1983, 1984, and January 1985.

Algal biomass was monitored yearly, in 10 × 10-cm quadrats on algal covered bottom. During the first 3 yr, biomass was estimated at 10 random locations $\cdot$ transect^{-1}, along three parallel transects, in Lameshur Bay. During the last 2 yr, biomass estimates were expanded to three transects per site, for all five sites. In each quadrat, algae were scraped off the substratum and sucked into an airlift. Since the substratum was primarily smooth volcanic rock rather than limestone, the algae could be collected free of limestone debris. In the laboratory, the algae were rinsed in freshwater, and the sediment was removed. The samples were then oven-dried (24 h at 60 °C), and the dry weights were recorded. Algal biomass per unit area was then calculated as dry weight (g) $\cdot$ m^{-2} × the proportion of percent cover occupied by algae.

RESULTS

DIADEMA POPULATION DENSITY

In the summer of 1983, the mean *Diadema* population density was 14.38 $\cdot$ m^{-2} (Table I). During December 1983, mass mortality of *Diadema* occurred in Saint John, killing >99% of this species (transects by P. Ross, pers. comm.). In the summer of 1984, the mean population density was 0.079 $\cdot$ m^{-2} (SD = 0.047, n = five sites), <1% of premortality levels. During the first 12 months following the mortality, density increased to 0.169 $\cdot$ m^{-2}. After the summer of 1985, however, population density did

not change significantly (two-way ANOVA of sites by time $P < 0.001$, Duncan's multiple range test $P < 0.05$ for pair-wise comparisons, Table I).

TABLE I

D. antillarum population density. Mean density ($\cdot m^{-2}$) of five sites (n), SE, and total area sampled (m^2) at each survey date. Lower section is ANOVA table of density tested over time and site. Premortality time period is not included in ANOVA. Critical range of Duncan's multiple range test ($P < 0.05$) = 0.119.

Time			SE	Area	
Jun–Aug	1983	14.380	2.440	75	5
Jun–Aug	1984	0.079	0.021	5000	5
Jan	1985	0.169	0.062	5000	5
Jun–Aug	1985	0.269	0.112	5000	5
Feb–Mar	1986	0.281	0.106	5000	5
Jun–Aug	1986	0.255	0.084	5000	5
Jun	1987	0.312	0.094	5000	5

ANOVA summary table

SV	df	SS	MS	F
Time	5	0.190	0.038	6.33**
Site	4	0.749	0.187	31.17***
Error	20	0.129	0.006	
Total	29	1.068		

*** $P < 0.001$, ** $P < 0.01$

TABLE II

Changes in algal dry weight ($g \cdot 100\ cm^{-2}$) in Lameshur Bay previous to and following mass mortality. Mean value, SD, and number of 10×10-cm quadrats are reported. Lower section is ANOVA summary table of log-transformed data, tested over time.

Time			SD	
Aug	1983	0.101	0.06	36
Aug	1984	3.037	1.32	46
Aug	1985	1.289	0.66	21
Apr	1986	0.496	0.82	225
Jun	1987	0.666	0.80	150

ANOVA summary table

SV	df	SS	MS	F
Time	4	60.51	15.13	42.03***
Error	449	162.74	0.36	
Total	453	223.25		

*** $P < 0.001$.

ALGAL ABUNDANCE

The mean algal percent cover was 68.8% in the summer of 1983. Mean algal percent cover ranged from 61.6 to 75.9% in the two summers following the mass mortality. Algal percent cover did not change significantly after the mass mortality (two-way ANOVA of sites by time with angular transformed data was not significant. F ratio for a time effect = 1.87 with 2 and 8 df, residual MS = 53.47, $P > 0.05$).

There were significant differences in algal dry weights between years (values and log-transformed ANOVA $P > 0.001$, Table II). Algal dry weights first increased significantly 3000% and then decreased significantly 84% during the 2nd and 3rd yr. Algal weights did not change significantly in the 4th yr (Tukey's studentized range tests, $\alpha = 0.05$). Following the mass mortality, the thin layer of filamentous algae was replaced by large fleshy macroalgae (predominantly *Dictyota* and *Padina*) and several species of 2–5 cm long filamentous green algae. This macroalgae decreased after a peak abundance 6 months after the mortality event. One possible source of error in these measurements is that algal biomass was only monitored once a year. To compensate for this problem, samples were taken during the same season, and never after a storm (which can redistribute drift algae – Hay & Taylor, 1985).

DIADEMA BODY SIZE

The *Diadema* population 6 months after the mass mortality contained survivors of the die-off and new recruits (Fig. 2). One year after the die-off, the size-frequency distribution was bimodal with a large new pulse of recruits and continued growth of the adult cohort. By the summer of 1985, 18 months after the die-off, the previous January's juvenile cohort had grown and blended into the adult cohort. After the summer of 1985, the adult cohort increased in size with little recruitment of juveniles into the population.

In Lameshur Bay, 6 months after the mass mortality, mean test diameter was 8.1 mm less than premortality mean size (from 34.5 to 26.4 mm). After this initial decrease, mean size increased significantly (two-way ANOVA of sites by time, $P < 0.001$, Table III, Fig. 3). In the summer of 1987, mean test diameter was 25.9 mm larger than premortality size (from 34.5 to 60.4 mm), and had increased at a rate of $11.3 \text{ mm} \cdot \text{yr}^{-1}$.

TABLE III

D. antillarum body size (mm test diameter) before and after mass mortality. ANOVA summary table testing mean size over time and site.

	df	SS	MS	F
Time	5	4904.55	980.91	71.49***
Site	4	192.26	48.06	3.50*
Error	20	274.45	13.72	
Total	29	5371.26		

*** $P < 0.001$, * $P < 0.05$.

In the same summer, maximum test diameter was 32.6 mm larger than premortality size (from 55.3 to 87.9 mm), and had increased at a rate of 13.7 mm · yr⁻¹. Maximum size was calculated as the mean of the largest individual measured per site. From 1983 to 1987, median individual weight had increased from 20 to 200 g.
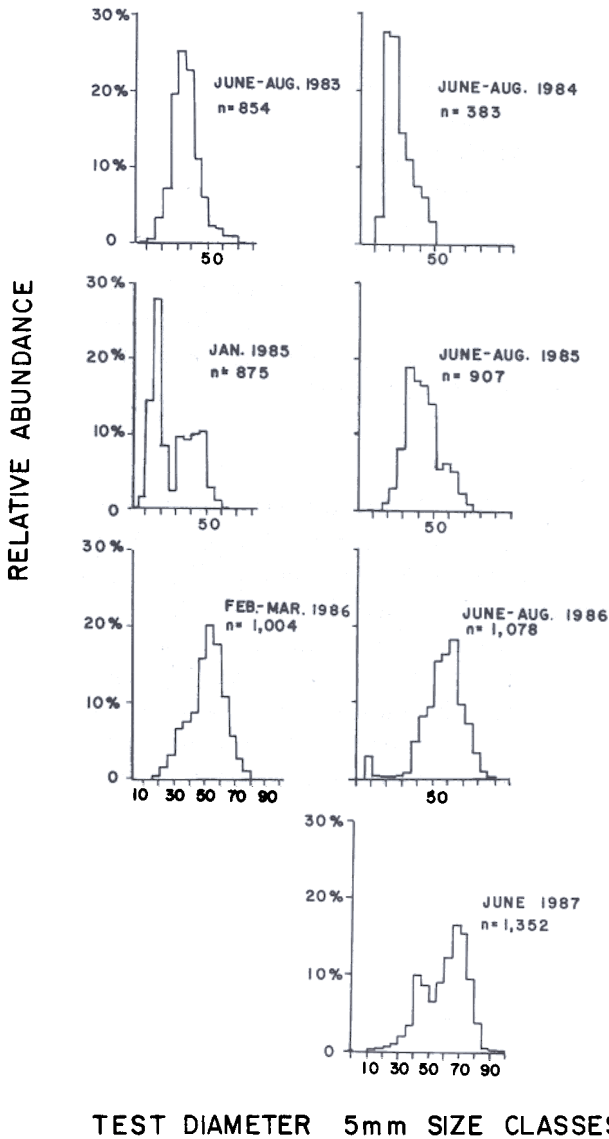

TEST DIAMETER   5mm SIZE CLASSES)

Fig. 2. *D. antillarum*. Histograms of relative size frequency distributions following mass mortality. Summer of 1983 is before mortality event. Histograms are cumulative values for all sites.

URCHIN AND ALGAL BIOMASS

Urchin biomass per unit area increased significantly during the time following the mass mortality (values and log-transformed two-way ANOVA of sites by time,
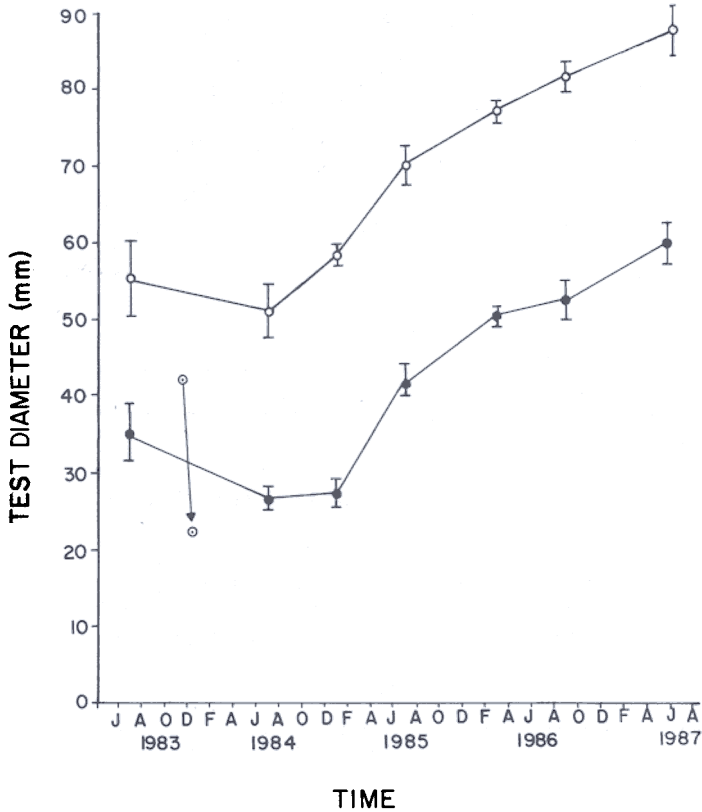

Fig. 3. *D. antillarum*. Mean (closed circles) and maximum (open circles) test diameter (mm) following mass mortality. Summer of 1983 is before mortality event. Means and SE of five sites are plotted. Large open circles, separated by arrow, represent change in mean size reported during mortality event in Panama (from Lessios *et al.*, 1984b).

$P < 0.001$, Table IV). Previous to the mortality, urchin biomass was $390.1 \text{ g} \cdot \text{m}^{-2}$. Urchin biomass dropped to $1.0 \text{ g} \cdot \text{m}^{-2}$, 6 months after the die-off. Urchin biomass in the summer of 1987 was $42.0 \text{ g} \cdot \text{m}^{-2}$.

To determine the relationship between urchin grazing and the algal resource, algal biomass (g dry weight $\cdot \text{m}^{-2}$) was plotted against urchin biomass (g live weight $\cdot \text{m}^{-2}$). This yielded a significant inverse relationship (Fig. 4). Urchin biomass dropped immediately after the mortality. Within 6 months, algal biomass had increased to a peak abundance level. During the next 3 yr, algal biomass decreased as urchin biomass increased.
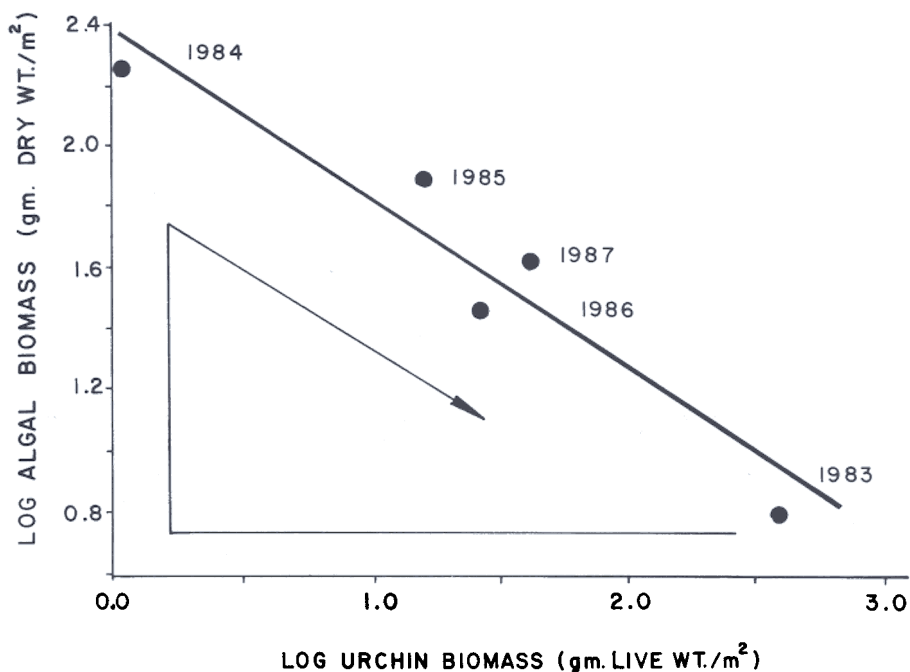
Fig. 4. Plot of mean urchin biomass (log g live weight · m^{-2}) vs. mean algal biomass (log g dry weight · m^{-2}). Regression equation, associated r^2, and F test on slope are as follows: log algal biomass = -0.57 (log urchin biomass) + 2.39, $r^2 = 0.92$, $P < 0.01$, $n = 5$. Each datum is mean value for all five sites. Arrow indicates time sequence. Sample dates are indicated next to data points.

TABLE IV

D. antillarum biomass (g live weight · m^{-2}) before and after mass mortality. Mean biomass, SD, and number of sites are reported. Lower section is ANOVA summary table testing log-transformed urchin biomass over time and site.

Time			SD	
Jun–Aug	1983	390.12	111.33	5
Jun–Aug	1984	1.02	0.45	5
Jun–Aug	1985	16.00	16.30	5
Feb–Mar	1986	26.27	24.06	5
Jun	1987	41.99	31.73	5

ANOVA summary table

SV	df	SS	MS	F
Time	4	17.52	4.38	146.00***
Site	4	0.98	0.24	8.00***
Error	16	0.52	0.03	
Total	24	19.02		

*** $P < 0.001$.

Discussion

CHANGES IN POPULATION DENSITY

As a result of the mass mortality, *D. antillarum* densities in Saint John were reduced by 99%. This value seems consistent with density reductions reported in other areas of the Caribbean (Panama: 95–99%, Lessios et al., 1984a; Curaçao: 98–100%, Bak et al., 1984; Jamaica: 98–100%, Hughes et al., 1985; Barbados: 87–100%, Hunte et al., 1986).

In Lameshur Bay, population density increased significantly in the first 12 months following the die-off. After this period, population density remained stable. The increase in density was probably due to recruitment of new individuals, rather than migration of adults, since a large cohort of small individuals accounts for density differences (Fig. 2). No new large pulse of recruits were seen after January 1985 (12 months after the mass mortality). Bak (1985) noted that recruitment of *Diadema* stopped abruptly 5 months after the mass mortality on Curaçao. Growth of small *D. antillarum* (2–30 mm) is estimated to be 3–4 mm · month^{-1} (Randall et al., 1964; Bauer, 1976; Bak, 1985). This provides an approximate time of 4–6 months to attain the median size of the juvenile cohort (17.5 mm) found in January 1985. It is possible that the large influx of juveniles seen in January 1985 was produced by premortality populations from down-current islands.

The poor recruitment seen after the mass mortality could be caused by low population density. Since echinoderms are dioecious external spawners, the comparatively low population density following the mass mortality might lead to poor fertilization success (Levitan, in press b). Even if urchins are reproducing at the same individual rate as before the mortality, total recruitment would be poor. Lessios (in press) supports this suggestion. His data indicated that poor recruitment, after the mortality event, is due to a lack of larvae rather that any biological interactions influencing recruitment and early juvenile survivorship.

INCREASES IN ALGAL BIOMASS

The 3000% increase in algal biomass 6 months after the mass mortality is indicative of the importance of *Diadema* as a herbivore in this coral reef community. This particular study had no experimental controls to determine if increased algal abundance was directly due to decreased *Diadema* density. However, increased algal abundance following the mass mortality has been well documented in several areas of the Caribbean (Saint Croix: Carpenter, 1985, 1988; Jamaica: Hughes et al., 1985, 1987; Curaçao: Ruyter van Steveninck & Bak, 1986). In addition, many experimental studies have documented that removal of *Diadema* results in increased algal abundance (Sammarco et al., 1974; Carpenter, 1981, 1986; Sammarco, 1982, Hay & Taylor, 1985; Levitan, unpubl. data).

Ruyter van Steveninck & Bak (1986) suggested that, because of poor *Diadema*

recruitment, algal abundance will remain high for quite some time. The following two sections provide evidence that the grazing potential of *Diadema* is rapidly returning. This is due to increases in urchin biomass, caused by increases in algal abundance, following the mass mortality. Individual growth has partially compensated for the loss of urchin numbers.

INCREASES IN URCHIN BODY SIZE

Size-frequency distributions have changed rapidly since the summer of 1983. Size-frequency distributions of *Diadema* from Panama (Lessios *et al.*, 1984a) immediately following the mass mortality indicated higher survivorship of small rather than large urchins. This resulted in a decrease of mean test diameter of 20 mm over a period of 1 month. In Lameshur Bay, 6 months after the die-off, mean test diameter had decreased by 8.1 mm. In the months that followed, mean test diameter increased at a rate of $11.3 \text{ mm} \cdot \text{yr}^{-1}$.

It may be argued that the increase in mean size was due to the lack of recruitment. The presence of new recruits would tend to reduce the estimate of mean size. However, mean size also increased owing to the continued growth of the adult cohort to a size not seen in premortality populations (Fig. 2). This is evinced by the increased maximum size of *Diadema*. Maximum size in 1987 was 32.6 mm larger than seen in 1983. The flow of new recruits might affect the estimate of mean size, but not the estimate of maximum size of individuals in the population. Maximum size is often used as an indication of size constraints based on food availability (reviewed in Lawrence & Lane, 1982).

Assuming *Diadema* continues to grow to a mean size of 108 mm test diameter, urchin biomass per unit area will have returned to premortality levels (for present densities of $0.25 \text{ urchins} \cdot \text{m}^{-2}$). With the present growth rates, this should occur within the next 5 yr. Most likely growth rates will slow down as body size asymptotically increases to a resource limited state or some currently unrecognized size constraints. Even so, the return of urchin biomass to former levels will occur at a much faster rate than the return to former urchin densities.

DECREASES IN ALGAL BIOMASS

Decreases in algal biomass could be due, in part, to both a slight increase in *Diadema* population density and a large increase in mean test size. Field experiments indicate that body size and feeding rate are directly proportional (Hawkins & Lewis, 1982; Levitan, unpubl. data). Comparisons of urchin and algal biomass estimates indicate their dependence. From the summer of 1984 to 1987 algal biomass decreased from 3.0 to $0.5 \text{ g (dry weight)} \cdot \text{m}^{-2}$, a decrease of 84%. This has coincided with an increased urchin biomass from 1.0 to $42.0 \text{ g (live weight)} \cdot \text{m}^{-2}$, an increase of 4200%.

Although other factors might be important in reducing algal abundance (increased herbivory by fish – Carpenter, 1985, 1988, increased herbivory by other echinoids – A. H. Williams, pers. comm.), the present study provides data that 92% of the variation

in log algal abundance can be explained by changes in log urchin biomass (Fig. 4). This is strong circumstantial evidence that *Diadema* biomass regulates algal abundance. The decrease in urchin density caused by the mass mortality has been partially compensated for by an increase in urchin size.

As mentioned, herbivory by fish can have a substantial impact on algal abundance (Hay, 1984; Carpenter, 1985, 1986; Hay & Taylor, 1985; Lewis, 1986). *Diadema* and fish abundance vary, sometimes inversely, on different reefs (Hay, 1984). For this reason, conclusions drawn from one location should not be generalized to all areas in the Caribbean. Herbivory by fish was not estimated in the present study, and could have partially been responsible for changes in algal biomass. However, at nearby islands (Saint Thomas and Saint Croix, U.S. Virgin Islands), Hay & Taylor (1985) found that when *Diadema* was experimentally removed, herbivorous fish were unable to graze algae to preremoval conditions. In Saint Croix, Carpenter (1986) experimentally partitioned herbivory, and found that *Diadema*-grazed treatments were similar to treatments where all herbivores grazed. Fish-grazed treatments had two to four times the algal biomass as *Diadema*-grazed treatments. He also noted that algal biomass did not change when fish abundance varied seasonally. It appears that for the Virgin Islands, *Diadema* has the most impact of any grazer.

The occurrence of the mass mortality has temporarily removed the resource limitation on *Diadema* body size. This is indicated by the explosion of algal biomass, followed by an increase in urchin body size and urchin biomass per unit area. Although premortality densities may not be reached (if indeed they ever return) for several decades, the ability of *Diadema* to grow indeterminately will cause urchin biomass and *Diadema*'s grazing potential to be restored much sooner.

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