Density-Dependent Size Regulation in Diadema Antillarum: Effects on Fecundity and Survivorship

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DENSITY-DEPENDENT SIZE REGULATION IN *DIADEMA ANTILLARUM*: EFFECTS ON FECUNDITY AND SURVIVORSHIP[1]

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Abstract. Food limitation can often result in reduced fecundity or death. However, a reduction in body size can minimize these negative effects. This study demonstrates that the sea urchin *Diadema antillarum* has the ability to adjust body size quickly (by positive or negative growth) to a resource- or density-dependent level. In a field experiment, small (27.5 mm test diameter) and large (37.5 mm) urchins were placed in cages at low (12 individuals/m^2) and high (24 individuals/m^2) densities. After 26 wk, body size in the high density treatment had converged at 30 mm, and body size in the low density treatment had converged at 36 mm test diameter. Mortality was not size or density dependent. After 32 wk, the effects of initial size on mass, gonad volume, and gamete production could not be detected. *Diadema* adjusted body size to a density-dependent level predicted by the inverse relationship between mean size and density seen in field populations. In a laboratory experiment, urchins were placed in groups of one or three, and fed one of four rations of food. After 23 wk, the urchins had adjusted test diameter, mass, and gonad volume to a level determined by per capital food availability and not crowding. Gonad volume was not significantly different from that predicted by body size (compared to field populations), regardless of whether the urchins had grown or shrunk. Among the fed urchins, mortality was not resource dependent, even though the urchins in the low-food group exhibited significant negative growth. Size regulation thus increases survivorship and reproductive output under rapidly changing conditions of population density and resource availability. A consequence of this life history strategy is that populations tend to track carrying capacity closely.

Key words: body size; density dependent; Diadema antillarum; *echinoid; history; indeterminate growth; population regulation; size regulation; Virgin Islands.*

INTRODUCTION

When food is limiting, the relationship between population density and body size is an important consideration. Body size can be limited by available resources for both plants (Harper 1967, 1977, Pitelka 1984) and animals (Sutherland 1970, Menge 1972, Paine 1976, Sebens 1982*a*). Organisms growing during favorable climatic regimes or at low population densities can increase to a size too large to be supported when conditions change (Sebens 1981, 1983). When this occurs, animals disperse (Taylor and Taylor 1979, Hurd and Eisenberg 1984), have reduced fecundity (Eisenberg 1966, Spight and Emlen 1976, Keller 1983), or die (Frank et al. 1957, Keller 1983). However, reducing body size can be an important alternative for many organisms with indeterminate growth (Sebens 1982*b*, 1987, Levitan 1988*a*).

The ability to regulate body size by growth and negative growth can be important under unstable environmental conditions (Sebens 1982*b*, Levitan 1988*a*, *b*). Food may be scarce either seasonally or unpredictably due to a changing food resource (Benayahu and Loya 1977), an increase in population density (Eisenberg 1966), or the presence of another species (Menge 1972). During times of food limitation, a decrease in body size is favorable; smaller organisms require less food than larger conspecifics (Zeuthen 1953) and during negative growth somatic tissue can be converted into energy for metabolism (Zeuthen 1948, Lawrence and Lane 1982). Conversely, during pulses of increased food availability an increase in body size is favorable; there may be a size-dependent aspect to predator resistance (Paine 1976) or competitive ability (Sebens 1982*c*), an increase in gamete production due to increased size (Bagenal 1966), or storage of somatic tissue for times of food limitation (Florant and Greenwood 1986). Size plasticity may increase fitness by allowing individuals to maximize surplus energy for reproduction under rapidly changing conditions (Sebens 1982*a*).

Although size plasticity has been documented in many groups (cnidarians, flatworms, annelids, mollusks, echinoderms, and urochordates; reviewed in Sebens 1987), it is often unclear to what extent organisms can adjust body size and how size plasticity affects reproductive output. Theoretical models predict how organisms might respond to changing conditions by

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adjusting body size; however, clear experimental evidence is lacking. Typical evidence provides data on negative growth, or fitting observational data to growth models (reviewed in Sebens 1987). From this, predictions have been made that organisms can reduce their size to a level that can be supported by available resources and still allocate energy for reproduction. These predictions are untested, as are the costs and lingering historic effects of size reduction.

Diadema antillarum Philippi is a good experimental organism for studying size regulation. *Diadema* has fast growth rates compared to other sea urchins (Ebert 1982), thus expediting experimental work. Reproduction occurs on a lunar cycle (Iliffe and Pearse 1982, Levitan 1988*c*), so reproductive output can be periodically monitored. *Diadema* commonly exhibits an inverse relationship between body size and population density (Carpenter 1981, Hunte et al. 1986, Levitan 1988*a, b*), suggesting that food is often limited. Finally, previous research has demonstrated that echinoids can reduce in size (Ebert 1967, 1968) and that *Diadema* does so in a density-dependent manner (Levitan 1988*a*).

MATERIALS AND METHODS

Field experiment

A field experiment was conducted to determine the effect of population density on body size and fecundity in *Diadema antillarum.* On 19 January 1986, 32 cages were placed in 4 m of water, on hard substrate, off the fringing reef of Lameshur Bay, St. John, United States Virgin Islands. Cages were constructed of 1.27-cm mesh hardware cloth and each enclosed a 0.25 m^2 area. Once a week the wire mesh was scrubbed inside and out to remove newly settled algae.

On 23 January, 144 *Diadema antillarum* from two sizes classes (35–40 and 25–30 mm) were collected from the south side of St. John. This size range (25–40 mm) encompassed 67% of the size range of field populations in 1983 (the mean body size of the field population was 34 mm, Levitan 1988*a*). Each size class was placed separately in cages at two densities (3 or 6 per cage; 12 or 24 individuals/m^2). The design was stratified and balanced with four treatment groups and eight replicates per treatment. If an urchin died, another urchin, differing in size by 5 mm from the other experimental urchins, was added to the cage. This size difference allowed me to distinguish it from the original experimental urchins. The added urchins were not used for data (as in Andrew and Choat 1985). Urchins were weighed at the start of the experiment and then at weeks 18 and 32, when the experiment was terminated. Live masses were measured (to the nearest 0.1 g) in the laboratory and averaged for a single datum per cage. Test diameters were measured along three diameters per urchin using vernier calipers (to the nearest 0.1 mm). The mean size of urchins per cage was used as a datum. Sizes were measured in situ every 2 wk. In addition to test diameter, percent cover of algae and bare space were monitored. This was done by blindly tossing a 5 × 5 cm piece of 1.27-cm mesh hardware cloth four times per cage and recording the presence or absence of algae under the 25 wire intersections of the quadrat. In addition to the 32 cage enclosures, 2 cage controls (lacking urchins) and 2 uncaged controls (to monitor effect of cages on algal growth) were monitored for algal percent cover.

The experiment was terminated on the day of the new moon, one lunar cycle after body sizes had converged at a density-dependent level for all treatments. This allowed urchins to feed and reallocate energy for reproduction, after size adjustments had been made. At the end of the experiment all urchins were measured, weighed, and injected with 0.5 mL of 0.5 mol/L KCl to stimulate spawning (Palmer 1937). Repeated injections of KCl did not stimulate any additional spawning in these experimental urchins. Thompson (1983) recommends this technique to determine gamete production in urchins. All released gametes were collected with a pipette and volume measured (to the nearest 0.01 mL). Urchins were then immediately dissected, and remaining gonad volumes estimated (to the nearest 0.01 mL) by water displacement. Estimates of gonad volume are based on the sum of the gametes and gonad volumes measured. Gonad volume data were recorded in addition to gamete data, since spawning is poorly synchronized in *Diadema antillarum.* Spawning is spread over 3 wk of the lunar cycle. On the new moon (the peak day of spawning activity), only 10–15% are ready to spawn (Levitan 1988*c*).

Laboratory experiment

On 29 January 1986, a laboratory experiment was started to discriminate the effects of crowding and per capita food availability on body size and fecundity in *Diadema antillarum.* Urchins (40–45 mm test diameter) were placed in groups of one or three, within sectioned-off areas of a wet table supplied with flowing sea water. Each urchin (regardless of level of crowding) received one of four levels of food (4, 2, 1 or 0 g wet mass of the green alga *Ulva,* every 4 d). This produced a design with four levels of food and two levels of crowding (2 × 4 with eight replicates). *Ulva* was attached with a tie-wrap to a small (≈5 cm diameter) piece of coral rubble. In the sections with three urchins, food was distributed evenly among three pieces of rubble. In the treatments receiving no food, alga-free rubble was added. Fecal pellets and any other debris were removed daily by siphoning. Once a week the wet table and rubble were scrubbed to remove any newly settled algae. Every 2 wk urchins were weighed and measured as in the field experiment (the mean of each section used as the datum). The experiment was monitored daily for any mortality. Mortality was attributed to

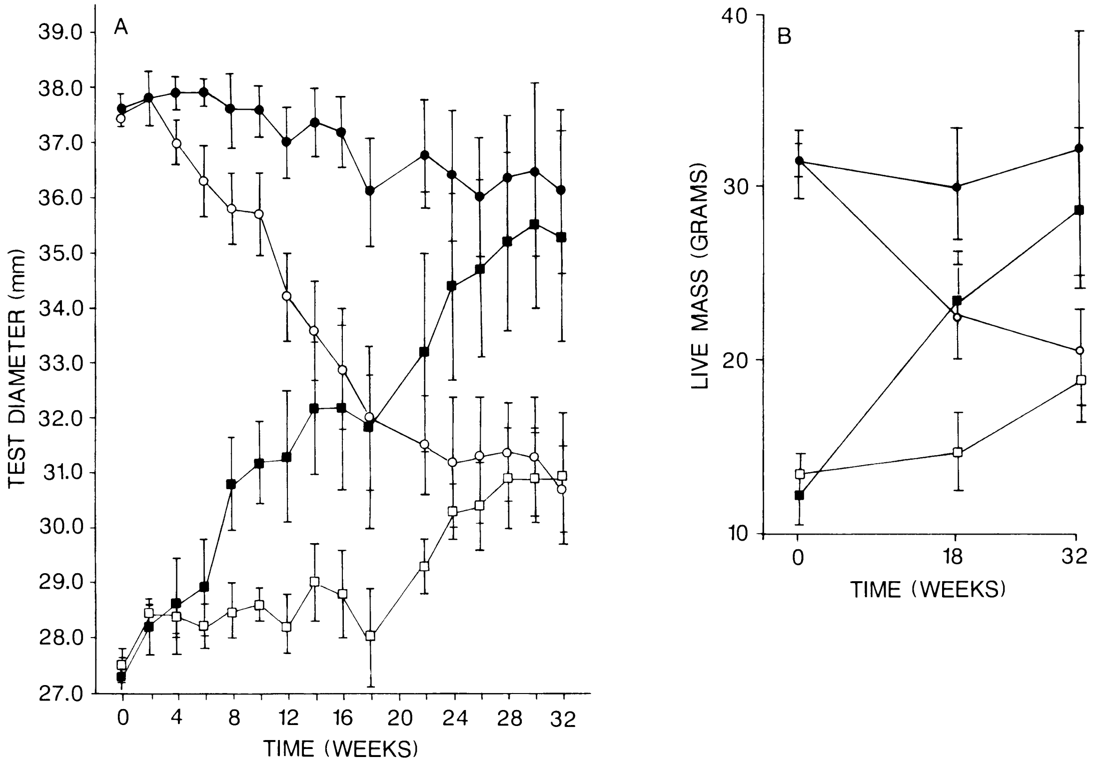

FIG. 1. A field experiment examining the effects of population density and initial body size over time on body size in *Diadema antillarum*. (A) Test diameter. (B) Live mass. Data are means ± 1 SE. Symbols: circles (initially large urchins), squares (initially small urchins), solid symbols (low density), open symbols (high density).

either cannibalism or other sources. An urchin was considered killed by cannibalism only if the urchin was still active with healthy erect spines and with a hole grazed in the test. This was used to distinguish cannibalism from the ingestion of dead or dying urchins. When an urchin died, its remains and food supply were removed. The experiment was terminated on the day of the new moon 6 mo later. Gamete production and gonad volume were measured in the same manner as described for the field experiment.

Field sample

Field samples were collected on the days of the new moon on 18 January 1985 ($n = 41$), 15 August 1985 ($n = 21$), and 6 August 1986 ($n = 39$). The size, mass, gonad, and gamete measures were taken in the same manner as above. Because an analysis of covariance indicated no significant differences between sample dates (gonad volume adjusted by size: MS = 0.18, MSE = 0.31, $F = 0.58$, with 2,6 df), all three samples were pooled. Gonor (1972) cautions against using gonadal indices to make comparisons among sizes, because somatic and gonadal tissue do not increase linearly. More importantly, for comparisons of reproductive output, it is inappropriate to equate different size animals with the same gonadal index, since the larger animal is producing more gametes. For these reasons only gonad and gamete estimates are used. These values are compared among and between treatments and against similar size urchins from the field.

TABLE 1. *Diadema antillarum* field experiment; two-way ANOVA testing the effects of initial size and population density against the variables: test diameter at week 26 (T.D. 26), final test diameter (T.D. 32), final urchin mass, final gonad volume (G.V.), and final urchin biomass per cage (Biomass).†

Source of variation	df	T.D. 26		T.D. 32		Final mass		G.V.		Biomass	
		MS	*F*	MS	*F*	MS	*F*	MS	*F*	MS	*F*
Size	1	5.66	NS	0.14	NS	36.64	NS	0.07	NS	783.88	NS
Density	1	150.64	***	171.59	***	827.22	***	0.73	*	5499.08	**
Interaction	1	0.04	NS	1.61	NS	0.19	NS	0.01	NS	0.63	NS
Error	25	1.75		2.63		24.66		0.14		302.17	

*** $P < .001$, ** $P < .01$, * $P < .05$, NS = not significant.

† Three cages were lost during the course of the experiment, one from each treatment except small urchins at high density.

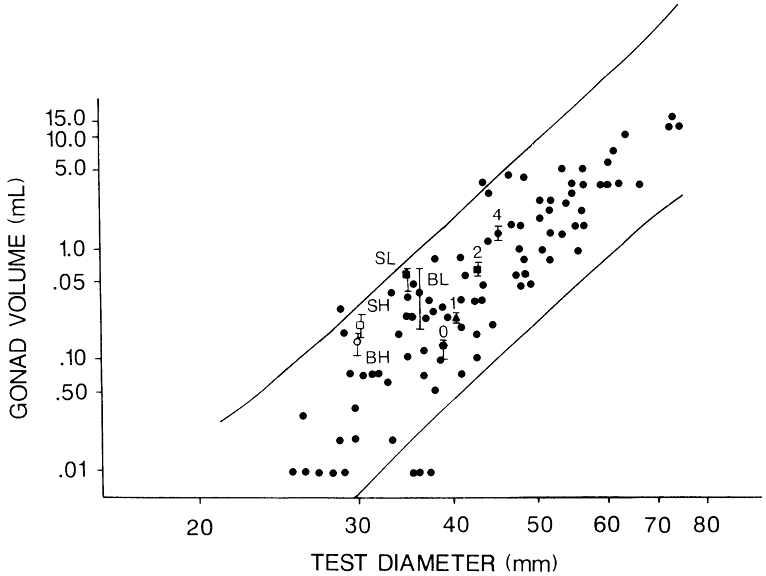

FIG. 2. The gonad volume of field and experimental *Diadema antillarum* plotted as a function of test diameter. Data points are from the field sample with the 95% CI on the predicted value. Means ± 1 SE are plotted from the field (BL = large urchin at low density, BH = large urchins at high density, SL = small urchins at low density, and SH = small urchins at high density) and laboratory experiment (pooled by food level 4, 2, 1, and 0 g of *Ulva* per capita every 4 d). Regression equation and R^2: log gonad volume = 6.88 log size − 11.59, where gonad volume is in millilitres and test size is in millimetres; $R^2 = 0.77$; $n = 101$.

RESULTS

Field experiment

After 26 wk, urchin sizes converged to density-dependent levels. Large (37.5 mm) and small (27.5 mm) urchins at 12 individuals/m^2 converged at 36 mm test diameter. Large and small urchins at 24 individuals/m^2 converged at 30 mm test diameter (Fig. 1). A two-way ANOVA revealed a significant effect of population density on test diameter; initial body size had no significant effect (Table 1). After 32 wk the experiment was terminated. Two-way ANOVAs were conducted testing the effect of population density and initial body size with the variables of interest being test diameter (millimetres), live mass (grams), and gonad volume (millilitres). For all variables only the effect of population density was significant (Table 1).

TABLE 2. *Diadema antillarum* field experiment; survivorship of urchins, number of urchins spawning, and volume of gametes released when injected with 0.5 mL of 0.5 mol/L KCl.

Treatment*	Surviving		Spawning		Mean gamete volume
	No.	(%)	No.	(%)	(mL)
BH	22	(45)	2	(9)	0.01
BL	13	(54)	0	(0)	···
SH	30	(62)	1	(3)	0.03
SL	14	(58)	3	(21)	0.03

Fisher's Exact Tests:

Spawning vs. nonspawning	Living vs. dying
B vs. S NS ($P = .69$)	NS ($P = .18$)
H vs. L NS ($P = .41$)	NS ($P = .86$)

* B = large initial size (37.5 mm), S = small initial size (27.5 mm), H = high population density (24/m^2), L = low population density (12/m^2).

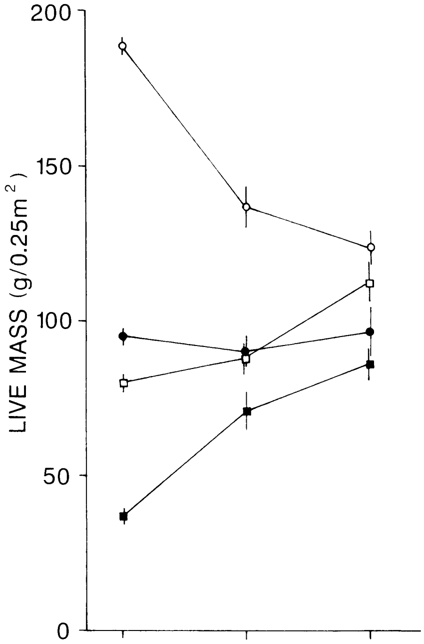

FIG. 3. A field experiment examining the effects of population density and initial body size over time on *Diadema antillarum* biomass per unit area. Data are means ± 1 SE. Symbols as in Fig. 1.

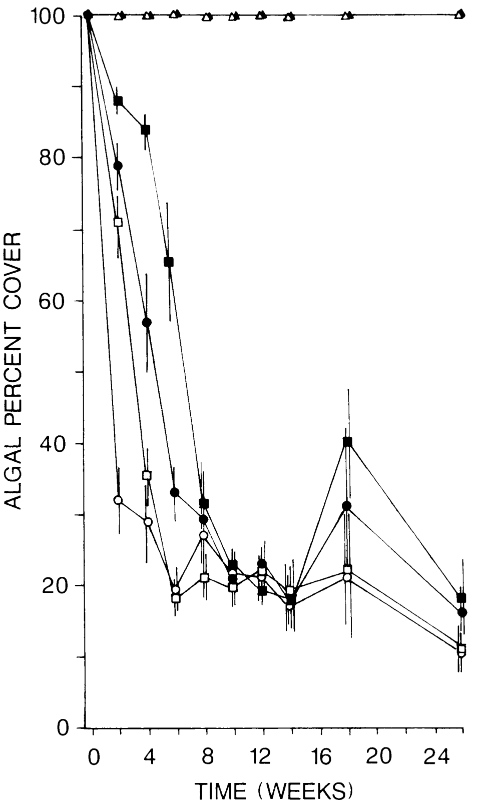

FIG. 4. A field experiment examining the effects of population density and initial body size of *Diadema antillarum* over time on percent cover of algae. Data are means ± 1 SE and were calculated using arcsine-transformed values. Open and solid triangles are caged and uncaged controls, the remaining symbols as in Fig. 1.

Gonad volumes determined from the caging experiment were compared to the field sample. The field sample was analyzed with a linear regression of log test diameter vs. log gonad volume ($R^2 = 0.77$, $n = 101$). The experimental gonad volumes from the caging experiment lie within the 95% confidence interval of the field sample for animals of the same size (Fig. 2).

On average, 8% of the urchins released gametes when injected with KCl (Table 2). Spawning frequency was not size or density dependent (Table 2). In addition to the induced spawning, there were two occasions when urchins were seen to spawn spontaneously during the experiment (large urchins at high density on 15 May 1986 and small urchins at high density on 29 May 1986). The mean (±SD) volume of gametes released when injected with KCl, were 0.02 ± 0.01 mL, $n = 3$ and 0.03 ± 0.03 mL, $n = 3$ for high and low density treatments, respectively. The frequency and volume of gametes spawned are within the normal range seen in urchins of similar size from the field (for details of urchin spawning, see Levitan 1988*c*).

Survivorship of caged urchins was not size or density dependent (Table 2). The mean survivorship was 54% across all treatments. Sources of mortality might have included cannibalism (presence of a hole in the test) or disease (spine loss noted inside, as well as outside, the cages in the field population at weeks 8–12). Mortality due to starvation was unlikely, since mortality levels were not significantly different between treatments with positive and negative growth.

Urchin biomass per unit area was calculated by totalling the mass of individuals per cage. This was done at weeks 0, 18, and 32. The results indicated a convergence of urchin biomass of all treatment groups (Fig. 3). This convergence was not complete. At the end of the experiment a two-way ANOVA indicated a significant effect of population density on urchin biomass; the effect of initial size was not significant (Table 1).

The rate at which algae were consumed was directly proportional to urchin biomass. The treatment with the lowest initial urchin biomass reduced algal abundance slowest and the treatment with the highest initial urchin biomass reduced algal abundance fastest. Percent cover of algae converged for all treatments at 20%. Caged and uncaged controls remained at 100% cover throughout the experiment (Fig. 4). Percent cover of algae is only a rough estimate of algal biomass and does not estimate algal productivity. Algal biomass appeared to be much lower towards the end of the experiment.

Laboratory experiment

All treatment groups initially had a mean size of 43.5 mm (range 43.1–44.1 mm). At the end of the experiment the mean sizes of the urchins were 45.4, 42.5, 40.3, and 37.8 mm test diameter for the 4, 2, 1, and 0 g treatment groups, respectively (Fig. 5). Two-way ANOVAs were conducted testing the effects of per cap-

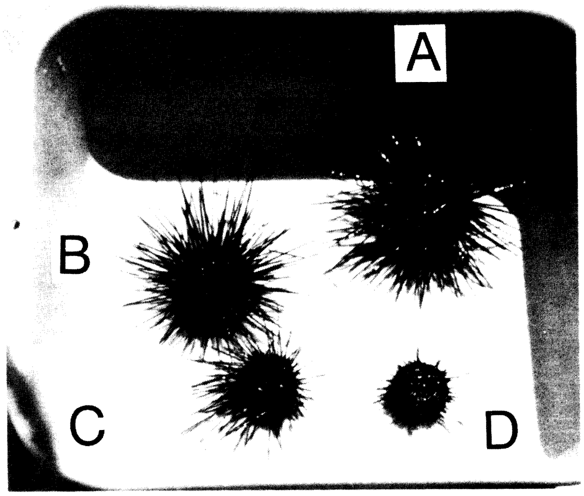

FIG. 5. Mean size individuals at the termination of the laboratory experiment examining the effects of per capita food availability and crowding on body size in *Diadema antillarum*. (A) 4 g treatment, (B) 2 g treatment, (C) 1 g treatment, (D) 0 g treatment. All individuals started out at 43.5 mm (size of B urchin).

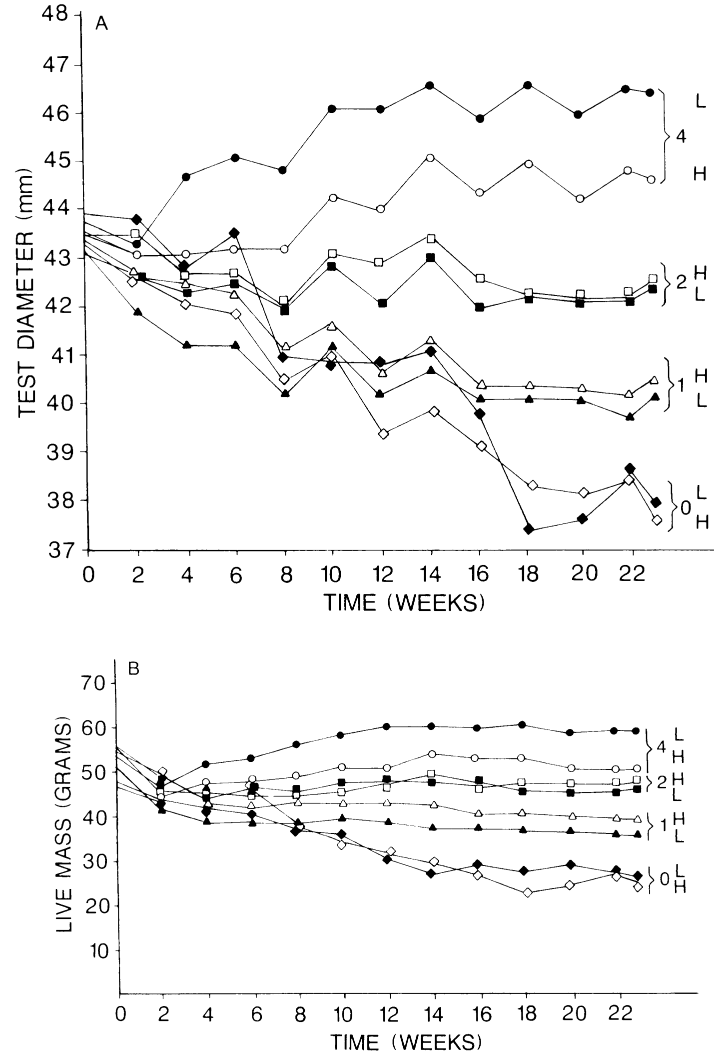

FIG. 6. A laboratory experiment examining the effects of per capita food availability and crowding on body size in *Diadema antillarum.* (A) Mean test diameter. Student-Newman-Keuls test for multiple comparisons of food level: minimum difference 1.93 mm ($P < .05$, df = 45, MSE = 2.32). SE not plotted for clarity (range of 1 SE at final time was 0.34–0.78 mm). (B) Mean live body mass. Student-Newman-Keuls test for multiple comparisons of food level: minimum difference 10.65 g (df = 18, MSE = 19.8) and 8.87 g (df = 23, MSE = 29.0) for the single and triple treatments, respectively. Range of 1 SE was 0.85–2.54 g. Symbols: solid symbols are single urchin treatments (L), open symbols are triple urchin treatments (H). Circles, squares, triangles, and diamonds are the 4, 2, 1, and 0 g food treatments, respectively (mass of *Ulva* every 4 d).

TABLE 3. *Diadema antillarum* laboratory experiment; two-way ANOVA testing the effects of per capita food and level of crowding against the variables: final test diameter (T.D.), final mass, and final gonad volume (G.V.).†

		T.D.		Mass		G.V.	
SV	df	MS	*F*	MS	*F*	MS	*F*
Food	3	88.91	***	1113.85	···	5.02	***
Crowding	1	0.33	NS	10.96	···	0.16	NS
Interaction	3	3.44	NS	107.98	**	0.45	NS
Error	41	2.27		24.97		0.25	

*** $P < .001$, ** $P < .01$, NS = not significant.

† Type III sums of squares were used since mortality caused the cells to be unbalanced (GLM SAS statistical package). Since the mass variable had a significant interaction an ANOVA was calculated for each of the two levels of crowding. For both levels, there was a significant ($P < .001$) food effect (MS/MSE = 718/20, df 3,18 and 572/29, df 3,23 for single and triple levels of crowding, respectively).
]

TABLE 4. *Diadema antillarum* laboratory experiment; mortality data and R × C tests of independence with *G* statistic.

Fate Food level (g/4d)	4		2		1		0		
Crowding (urchins/0.25 × m²)	1	3	1	3	1	3	1	3	Total
Mortality cannibalism	...	5	...	9	...	14	...	6	34
Mortality other sources	2	1	0	5	1	0	7	14	30
Survived	6	18	8	10	7	10	1	4	64
Total	8	24	8	24	8	24	8	24	128

R × C tests of independence

Test	*G*
Total mortality (pooled by crowding level)	
All treatments	25.62***
Food treatments	3.91^{NS}
Food vs. non-food	21.71***

*** $P < .001$, NS = not significant.

ita food level and crowding with the variables of interest being test diameter (millimetres), live mass (grams), and gonad volume (millilitres). For size and gonad volume, the effect of food level was significant, crowding was not (Table 3). A Student-Newman-Keuls test indicated that all pairwise comparisons of food level were significantly different for the size data (Fig. 6). For the mass data, there was a significant interaction of food level and crowding. A separate ANOVA on each level of crowding indicated that food was significant for both levels. Pairwise comparisons (Student-Newman-Keuls) indicated that all levels of food were different except for the 4 and 2 g treatments at the high level of crowding (Table 3 and Fig. 6). The estimates of gonad volumes were within the 95% confidence interval of similar size urchins from the field (Fig. 2).

In the laboratory experiment, 8% of the urchins spawned when injected with KCl. The mean (±SD) volume of gametes released was 0.54 ± 0.44 mL (n = 5). There were eight occasions when urchins spontaneously spawned during the experiment. At least one individual spawned in each group that was fed. No urchins from the starvation treatment spawned spontaneously during the experiment or when injected with KCl.

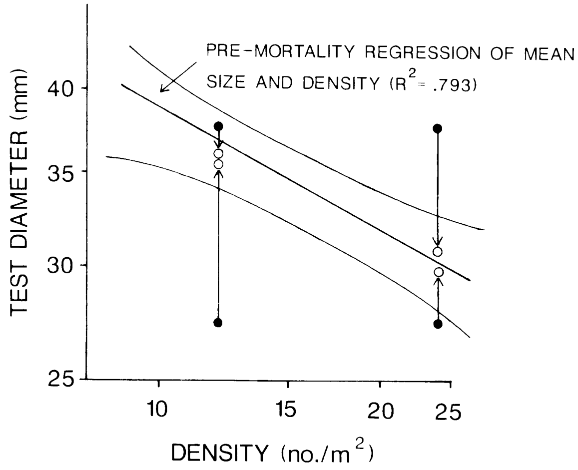

FIG. 7. Comparison of results of field experiment and the inverse relationship between mean test diameter and population density reported for Lameshur Bay previous to the mass mortality of *Diadema* (from Levitan 1988*a*). ● initial sizes, ○ final sizes. Regression (R^2 = 0.79) and 95% CI values on the mean.

There were mortality differences between treatments in the laboratory experiment (Table 4). Urchins without food had significantly higher mortality (0 g treatment: 84%) than urchins with food (4, 2, 1 g treatments: 39%). Among the fed urchins, there were no significant differences in mortality between treatments. Cannibalism was responsible for 63% of the mortality in the treatments with three urchins. Except in the starvation group, cannibalism was inversely related to food level. There were no significant differences in noncannibalistic mortality between the levels of crowding (data paired by food level, Student's t = 0.95, NS).

Differential mortality might have caused the observed changes in body size. A paired t test was used to compare the size of an individual when it died to the mean size of surviving urchins within its treatment. For all food levels (levels of crowding were pooled), there were no significant differences (Student's t = 0.96, 0.33, 0.11, and 0.45 for the 4, 2, 1, and 0 g food groups, respectively). This indicates that the observed size and mass differences were due to differential growth rates rather than mortality.

DISCUSSION

In 1983, there was an inverse relationship between *Diadema* population density and mean body size (Fig. 7) at the St. John study site (Levitan 1988*a*) and other areas in the Caribbean (St. Croix [Carpenter 1981] and Barbados [Hunte et al. 1986]). This pattern is found in several diverse groups of organisms and is often associated with resource limitation caused by intraspecific competition (Sutherland 1970, Branch 1975, Paine 1976, Harper 1977, Scheibling 1980, Pitelka 1984).

The notion that intraspecific competition resulted in food limitation and reduced body size in natural populations of *Diadema* is supported by the effects of the mass mortality. In December 1983, 99% of the *Diadema* at St. John died during the 1983–1984 mortality event which affected the entire Caribbean (Lessios et al. 1984). Following this event, algal biomass increased 30-fold within the first 6 mo. Despite the fact that population density increased only fourfold during the next 3 yr, *Diadema* median mass increased 10-fold. This resulted in a 40-fold increase in urchin biomass per unit area. This increase is consistent with the hypothesis that *Diadema* responded to a release from food limitation by increasing body size (Levitan 1988*b*).

In the present study, urchins from two size classes (27.5 and 37.5 mm test diameter) were taken from a field population at low density (≈ 0.25 individuals/m^2) and placed in cages at 12 individuals/m^2 and 24 individuals/m^2. After 26 wk, the urchins had converged in body size to density-dependent levels. Final mean body sizes were compared with the mean sizes predicted by the 1983 field pattern (Fig. 7). There were no significant differences between predicted mean sizes and the final mean sizes in the caged manipulation (experimental values are within the 95% confidence interval of the field regression). This provides strong evidence that the inverse relationship between body size and density found in the field was a result of individual urchins regulating body size.

Urchins growing or shrinking to a density-dependent body size had the same test diameter, mass, gonad volume, and survivorship regardless of their previous body size. The laboratory study indicated that these size adjustments were based on food availability rather than crowding effects on behavior. Test diameter, mass, and gonad volume were not significantly different from that expected from similar size urchins found in the field, whether the laboratory urchin grew or shrank to that size. This indicates that *Diadema antillarum* adjusted skeletal test material, body mass, and gonadal tissue proportionally.

Somatic and gonadal tissue were produced and resorbed as a function of body size (determined by recent food availability) not history. This distinguishes size regulation from starvation. Starvation implies that energy demands exceed energy intake. Size regulation implies that an adjustment can be made so that energy costs are reduced, and surplus energy can still be allocated for reproduction at a level expected for that size, regardless of historic size and conditions.

This result is different from that found by Peterson and Black (1988). They found that history had a major effect on the survivorship of bivalves. The design constraints of shelled mollusks may prevent size regulation. Although mollusks have been reported to reduce up to 40% of their biomass when starved, shell size does not change (reviewed in Sebens 1987). This disproportionate loss of tissue may place an excessive burden on the organism, thus increasing the likelihood of mortality (N. Andrew, *personal communication*). The effects of history may be most important in groups of organisms that cannot regulate body size.

Diadema antillarum has the ability to survive and reproduce under drastic population fluctuations. In the cage manipulation, urchins were taken from a field density of 0.25 individuals/m^2 and placed at densities as high as 24 individuals/m^2. This density shock, which caused a 34% reduction in body mass, is probably much more intense than any individual would experience in the field. Yet, after only 32 wk, gonad volume and gamete production were at a level expected for the urchins' current size (compared to field populations). Even under a severe environmental press (sensu Bender et al. 1984), *Diadema* can reproduce successfully. Under less drastic and more typical fluctuations in food availability, *Diadema* probably makes rapid, small size changes, thus maximizing the energy available for reproduction every lunar cycle.

An iteroparous organism that is capable of successful reproduction through large changes in resource availability will have a greater chance of replacing itself, compared to an organism that reproduces sporadically, dependent on environmental conditions. This is especially important for organisms with high (Gadgil and Bossert 1970) or variable (Murphy 1968) juvenile mortality. When recruitment is a rare and unpredictable event, as is common with long distance planktotrophic larvae, reproductive success may hinge on the organisms' ability to reproduce often, and under all environmental conditions.

The response to a resource-limited condition depends on the type of intraspecific competition that organisms experience. Organisms that can use an advantage of larger size to maintain space or to rob resources from smaller conspecifics (contest competition) will respond differently than organisms that gather resources without physically inhibiting conspecifics (scramble or consumptive competition; Persson 1985). Contest competition is exemplified by plants that self-thin (Yoda et al. 1963, Harper 1977). In this case, larger plants continue to grow while "suppressed weaklings" are thinned out. The increase in individual size is balanced by increased mortality of smaller individuals unable to obtain resources. Consumptive competition is exemplified in the present study. As density increases, all individuals experience competition. However, the ability to reduce body size and its associated metabolic costs allows these organisms to survive and allocate the appropriate amount of energy for reproduction at that food level. In a previous experiment (Levitan 1988*a*), small *Diadema* grew in the same cages in which large urchins shrank. This provides evidence that large size can be costly when food is limited, and that smaller individuals in the same environment can still have surplus energy available for growth. Consumptive competition is also observed in sessile organisms that experience environmental fluctuations in food availability (Sebens 1982*a*). In this case, larger body size would not confer an advantage since the reduction in resource availability is experienced by all conspecifics. Organisms that cannot regulate body size will be at a disadvantage in such situations. These organisms will be too large to be supported by the available resources; reproductive output will be diminished or absent, and under extreme conditions they will die.

Population regulation

Carrying capacity is generally defined in terms of the numbers of organisms an environment can support (McNaughton and Wolf 1979, Ricklefs 1979). This definition is not satisfactory in situations where population density is inversely related to body size. In such cases, food may be limiting along a continuum of population densities. For this reason, it might be prudent to estimate carrying capacity by comparing the relative biomass of the population and the biomass of its resources (Grant 1986, Levitan 1988*b*).

Regulation of populations is often discussed with respect to numerical oscillations around a carrying capacity (May 1981). In the absence of migration, this involves a time delay as the affected reproductive output of one generation determines the population density of the next. This time lag can be even greater if resource depletion causes a population crash (Nicholson 1958). Since individual *Diadema antillarum* can adjust body size quickly when conditions change, population biomass regulation occurs rapidly and within the same generation. Thus, one of the consequences of size plasticity is that populations tend to track resource variation closely (Scheibling 1980). It should be emphasized that the individual advantage to size plasticity is to avoid starvation and maximize reproductive output under changing environmental conditions. Population biomass regulation is simply an outcome of this life history strategy.

In populations with highly dispersed larvae, recruits can continue to arrive after food becomes limiting, regardless of the reproductive output of the local population. As population numbers continue to increase past the threshold of food availability, the resource deficit may be compensated for by body size regulation. How far past this resource threshold an organism can function is limited by its ability to regulate body size. At extreme densities, other factors such as increased mortality or dispersal are likely to be important.

Since food limitation may not determine numerical abundance of *Diadema*, what if anything regulates population density? Predation, habitat availability, and recruitment are all likely to have a major influence on numerical abundance. However, the most dramatic fluctuation in *Diadema* densities was caused by the Caribbean-wide mass mortality of this species in 1983 (Lessios et al. 1984). Previous to the mass mortality, *Diadema* was extremely abundant (up to 72 individuals/m^2 in Jamaica; Sammarco 1980). It is possible that high population density facilitated the spread of the pathogen. The role of infectious disease has generally been underestimated as a mechanism of population regulation (Smith 1941, Rasmussen 1977, Anderson and May 1978). Echinoderms are commonly known to have high local abundance (Birkeland and Chia 1971, Keegan and Konnecker 1979, Sammarco 1980, Aronson and Harms 1985), to exhibit an inverse relation between size and density (Smith 1940, Paine 1976, Lawrence 1980, Scheibling 1980, Carpenter 1981, Hunte et al. 1986, Levitan 1988*a*), to grow indeterminately (Ebert 1967, 1968, Feder 1970, Menge 1972, Levitan 1988*a*), and to experience mass mortalities (Pearse and Hines 1979, Miller and Colodey 1983, Lessios et al. 1984, Scheibling 1984, Scheibling and Stephenson 1984). A consequence of size regulation may be unchecked population growth. This might lead to disease, possibly the single most important mechanism regulating population numbers in echinoderms (Scheibling 1984).

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