Density-dependent size regulation and negative growth in the sea urchin *Diadema antillarum* Philippi

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Summary. This study documents size- and density-dependent growth (positive and negative), in the sea urchin *Diadema antillarum*. In the summer of 1983, an inverse relationship was found between *Diadema* test diameter and population density at seven sites in Lameshur Bay, St. John, United States Virgin Islands. The regression of this relationship improved when test diameter was plotted against density per unit grazing area. A field experiment demonstrated that 1) *Diadema* has the ability to reduce skeletal body size, and 2) direction (growth or shrinkage) and rate of growth can be predicted accurately based on the urchin's body size and population density. The ability to adjust body size as density fluctuates may allow *Diadema* to persist when density increases, by shrinking and reducing metabolic costs, and to take advantage of decreases in density, by increasing in size and fecundity.

Key words: Body size – Density-dependent – *Diadema antillarum* – Indeterminate growth – Size-dependent

The ability to reduce body size when food is limiting is documented in several phyla (Sebens 1981; Reynoldson 1968; Ebert 1967; Feder 1970). This ability to regulate size is generally associated with resource fluctuations; as the availability of resources diminishes so does the body size that can be supported (Sebens 1982). Size regulation is qualitatively different from size stunting or starvation. Size stunting (Worthington 1949; Le Cren 1958) implies that individuals have not reached maximum size because of resource limitation; this does not suggest negative growth. Starvation implies a loss of nutrient reserves and/or a disproportionate reduction of gonad size. Size regulation refers to a proportional size adjustment (positive or negative). This includes skeletal elements and other body tissues, as well as nutrient reserves.

Although size regulation has been documented in laboratory and field situations (reviewed in Sebens 1987; Lawrence and Lane 1982) there is no direct evidence that size regulation occurs in response to changes in population density. A likely place to find density-dependent size regulation would be in situations where population density and body size are inversely related. Such patterns are commonly found (reviewed in Lawrence and Lane 1982) and may reflect size constraints caused by decreased per capita food

availability. An inverse relationship between size and density is not sufficient evidence for size regulation since, this pattern can be a result of size stunting or variation in recruitment and longevity (Dix 1972; Sebens 1983). Growth rate data on individual organisms at various densities are needed to establish whether size regulation can be density-dependent. If size regulation is density-dependent, then organisms would tend to grow or shrink towards some critical size that decreases as density increases.

Methods

During the summer of 1983, the sea urchin *Diadema antillarum* was studied at seven sites in Lameshur Bay, St. John, United States Virgin Islands. Size frequency data were collected by gathering every urchin from a randomly selected area until approximately 150 (range 100–227) urchins had been collected. Urchin test diameters were measured into 5 mm size classes. Population density was measured in 5 (1 m^2) contiguous quadrats in each of 3 transects (total of 15 quadrats per site). Transects followed depth contours at 2, 3, and 4 m. The frame placed over the quadrats had intersecting monofilament lines, producing a grid with 100 regularly placed points (a total of 1500 points per site). The substrate under these points were recorded to estimate percent cover of sessile invertebrate and algal species. Percent cover data were used as an estimate of algal food resource per unit area. Carpenter (1981) has shown a preference of *Diadema* for algae rather than encrusting invertebrates. Estimating algal percent cover allowed the calculation of urchin population density per unit algal cover or "grazing area".

A field experiment was conducted to determine if *Diadema* exhibits density-dependent and size-dependent variation in growth (positive and negative). During the summer of 1984, sixteen 0.25 m^2 cages, constructed of 1/4″ mesh hardware cloth, were placed at randomly selected locations in 2–3 m of water on the fringing reef of Greater Lameshur Bay. Each cage held urchins of all three size classes (15–20 mm, 30–35 mm, 45–50 mm test diameter) at one of three densities (12/m^2, 24/m^2, 48/m^2). Eight cages at low density had one urchin per size class, four cages at medium density had two urchins per size class, and two cages at high density had four urchins per size class. Urchin test diameter (measured with vernier calipers), was monitored every week.
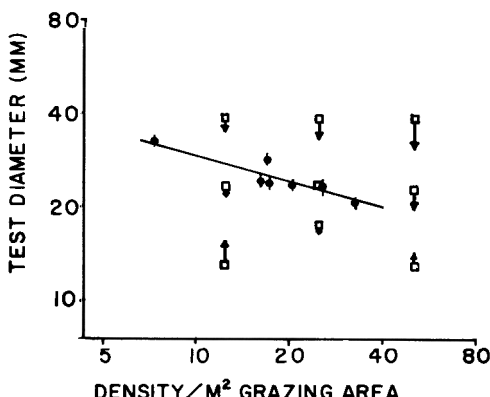
Fig. 1. *Diadema antillarum*. Mean (solid circles) and standard error of test diameter versus population density per unit grazing area (log scale). Data are from Lameshur Bay, St. John, USVI. Equation of line is: log mean size (mm) = (− 0.28)log density (/m² grazing area) + 1.87, F = 19.2, P < 0.005. Open squares are the initial conditions of the caging experiment. Arrows indicate direction of growth and final size of urchins in each treatment group
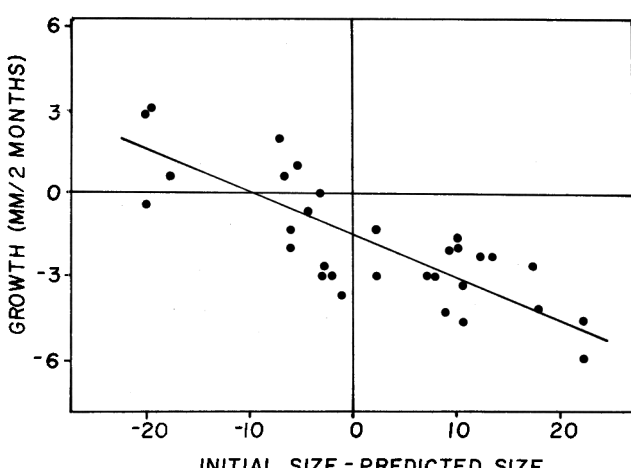

Fig. 2. *Diadema antillarum*. Plot of urchin growth rate as a function of the deviation of the urchins initial size from the size predicted by the survey data (Fig. 1). For details see text

Results

Diadema mean test diameter was inversely related to population density ($R^2 = 0.70$, F = 19.2, P < 0.025). A similar inverse relationship between *Diadema* mean test diameter and population density was reported in St. Croix (Carpenter 1981) and in Barbados (Hunte et al. 1986). For the Lameshur Bay data, this relationship improved when mean test diameter was plotted against density per unit grazing area ($R^2 = 0.79$, F = 19.2, P < 0.005, Fig. 1). Grazing area was characterized by dead coral and rock encrusted with a thin veneer of filamentous algae. Percent cover of grazing area in this study ranged from 70.0 to 96.2%.

In the field experiment, two cages at medium density were lost due to wave action, and only 8 urchins in the small size class survived to 9 weeks (4 small urchins survived at low density, 1 at medium density, and 3 at high density). There was no mortality of medium or large urchins. The growth of urchins within the cages appear to be related to the relationship between test diameter and population density found in the survey data (Fig. 1); urchins smaller

than the predicted mean size grew, and urchins larger than predicted mean size shrank. To test the hypothesis that the growth of urchins in the cages was related to the survey data, a linear regression was calculated. Growth rate (mm/ 2 mo.) was tested against the deviation of the treatments initial mean size, from that predicted by the survey data (data was mean growth rate of each size class, in each cage, $n = 31$, Fig. 2). The regression of this relationship is significant (P < 0.001 of the slope = 0, $R^2 = 0.65$), and the intercept goes near the origin (intercept = − 1.5 mm, s.e. 0.2). This latter point is important since it predicts zero growth of urchins when they are near the size predicted by the survey data.

Discussion

The size-density distribution found in the field indicates a significant inverse relationship between mean body size and population density. This type of relation is consistent with a hypothesis that *Diadema's* body size is regulated by food availability. This hypothesis is supported by the following evidence: 1) The regression between size and density improved when grazing area was taken into account. 2) The growth rate experiment indicates that when *Diadema* are manipulated such that their body size and population density deviate from the predicted value (from the survey data), they grow toward the predicted value (Fig. 2). If the relationship between size and density represents the mean body size that the environment can support at a particular density, then manipulating the density of urchins results in either positive or negative growth towards that critical mean size.

Large urchins were shrinking in the same cages in which small urchins were growing (Fig. 1). This might be evidence for scramble rather than contest competition. Energy intake is related to how much algae can be gathered during an urchins movement while grazing. The intensity of competition may be determined by the frequency of grazing of an area by several conspecifics (consumptive competition, Yodzis 1986). If there is no agonistic behavior between individuals, then large body size would not confer a competitive advantage (Persson 1985). Gregarious behavior is generally acknowledged for *Diadema* (Randall et al. 1984; Levitan 1988a). When food limited, smaller size associated with a smaller energy requirement, would confer an advantage of higher surplus energy available for reproduction (Sebens 1982).

The loss of small urchins in the caging experiment was probably due to cannibalism by larger urchins (personal observation of cannibalism of living *Diadema* in cage and laboratory conditions). The loss of urchins due to starvation is unlikely since only urchins from the small size class died. This size class had the only positive growth rates (mean percent increase of 6.32% test diameter for all densities at this size). Both the medium and large size classes exhibited negative growth and no mortality was recorded in either of these two size classes.

A prediction can be made for how *Diadema* might respond to the mass-mortality event which was Caribbean-wide and resulted in a one hundred-fold decrease in population densities (Lessios et al. 1984). Growth rates and body size should increase because of increased algal abundance due to decreased urchin abundance (Levitan 1988b). Data for Lameshur Bay indicate that as of June 1987 mean body

size has increased to 60 mm test diameter (the mean size prior to the mass-mortality was 34 mm), and has been growing at a rate of 11.3 mm/year since the population crash (Levitan 1988b). This growth rate should continue until the population reaches the predicted mean body size for current population densities (i.e., at Lameshur Bay during July 1986 densities were 0.25–0.75/m^2 and predicted mean body sizes were 80–110 mm).

The data presented here indicate that *Diadema* exhibits an inverse relation between size and density and that this organism has the ability to adjust it's skeletal body size towards this relationship. This adaptation may buffer the adverse effects of increases in population density and allows for exploitation of resources during decreases in population density.

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