Skeletal changes in the test and jaws of the sea urchin *Diadema antillarum* in response to food limitation

D. R. Levitan *

Bamfield Marine Station, Bamfield, British Columbia V0R 1B0, Canada, and Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9, Canada

Abstract. When food-limited, *Diadema antillarum* increases the relative size of Aristotle's lantern compared to the size of the test. This is accomplished primarily by decreasing the size of the test: the demipyramid grows at a reduced rate as the test shrinks. These results suggest that an altered relationship between demipyramid and test size can provide evidence for food-limitation in field populations. The sizes of the lantern and test of museum and fossil specimens can be investigated for the presence of food limitation and biotic interactions in recent and past times.

Introduction

Food limitation in echinoids results in an increase in the relative size of Aristotle's lantern compared to the size of the test (Ebert 1980, Black et al. 1982, 1984, Edwards and Ebert 1991). Ebert proposed the "plastic resource allocation" hypothesis when he noted this relationship in two species (*Strongylocentrotus purpuratus* and *Diadema setosum*). He suggested that food-limited echinoids increased the size of the jaw apparatus (measured by the length of the demipyramid) which increased their capacity to graze. Black et al. (1982) noted a similar relationship between demipyramid and test size dependent on population density in the echinoid *Echinometra mathaei*; as population density increased so did the relative size of the jaws. Black et al. (1984) suggested that a relatively larger Aristotle's lantern was associated with increased grazing ability. However, since these studies did not provided information on initial sizes (Ebert 1980, Black et al. 1984) or did not follow single individuals over time (Edwards and Ebert 1991), it is unknown whether this relationship is a result of an increase in demipyramid size and/or a decrease in the size of the test. The altered relationship between the size of the test and demipyramid under food-

limited conditions appears to be a general phenomenon. The present study elucidates the morphometric changes in the skeleton and provides evidence of these changes under experimental manipulations of population density and resource availability.

Materials and methods

Two experiments were conducted to determine how population density and food availability affect the growth of *Diadema antillarum* (for details, see Levitan 1989). The first was an 8-mo field experiment in which individuals from two size classes (25.0 to 30.0 and 35.0 to 40.0 mm test diameter) were placed in subtidal cages (0.25 m² in area) at two densities (12 and 24/m²). Each treatment group had eight replicate cages (total of 144 individuals). The second was a 6-mo laboratory experiment in which individuals from one size class (40.0 to 45.0 mm) were given one of four levels of food (4, 2, 1, and 0 g wet weight of the green alga *Ulva lactuca*, every 4 d). The laboratory experiment had two levels of crowding (one and three individuals per container), with both levels receiving the same per capita food level. Each treatment group had eight replicates (total of 128 individuals). Crowding did not affect growth (Levitan 1989), and for the present study these data were pooled by food level. In both these experiments, test diameter and the length of the demipyramid were measured for each individual. Test diameter was measured by picking up the echinoid with tongs, turning it oral side up, and placing the tips of needle-nose vernier calipers between the spines from one interambulacral region across the mouth to the opposite ambulacral region. Each individual was measured on three different diameters to 0.1 mm and the mean diameter was used as the datum (the mean standard error of the three measurements was 0.18 mm). Each individual was measured at the start of the experiment and every 2 wk thereafter for a total of 32 wk in the field experiment and 23 wk in the laboratory experiment. In the laboratory experiment, each echinoid was individually identified, and only those echinoids that survived to Week 22 were included in the analysis (those echinoids which died in the last week were kept and their skeletal measurements recorded). In the field experiment, individuals could not be identified within a cage, and thus differential mortality might have influenced measurements of changes in size. However, in this latter experiment, mortality rate was not significantly different between treatments, and in three out of four treatments the final sizes were outside the initial size range (Levitan 1989). In analyses where initial sizes were needed, only data from the laboratory experiment were used.

* Present address: Department of Zoology, University of California at Davis, Davis, California 95616-8755, USA
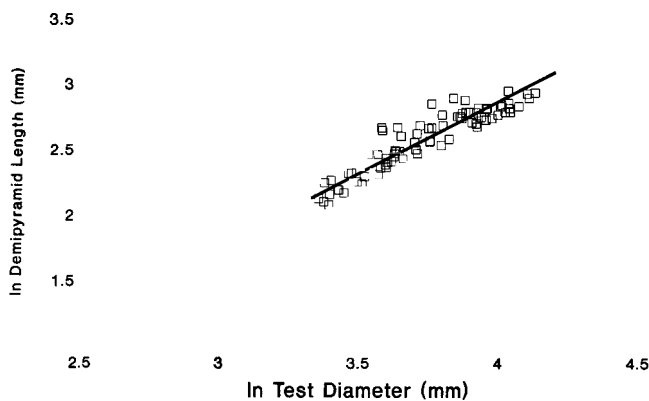
Fig. 1. *Diadema antillarum*. Demipyramid length vs test diameter for field-collected sea urchins. (Regression equation at end of "Materials and methods")

Fig. 2. *Diadema antillarum*. Demipyramid length vs test diameter in experimental treatment. □: Final sea urchin sizes in field experiment (B: initially large sea urchins; S: initially small sea urchins; (L: low density; H: high density); o: laboratory experiment (numbers indicate grams wet wt *Ulva lactuca* fed every 4 d) and regression of field-collected sea urchins. Data points show means ± standard errors; only half error bars plotted for field experiment and only lower half of 95% confidence interval (dotted line) plotted for regression of field-collected sea urchins for clarity. Arrows indicate size change from initial conditions

The length of the demipyramid was measured, with vernier calipers to 0.05 mm, from oral tip to the epiphysis junction at the aboral end (as in Ebert 1980) at the termination of the experiment. A mean of five demipyramids per individual was used as the datum (the mean standard error of the five measurements was 0.03 mm).

The demipyramids and tests of field-collected individuals were measured for comparative purposes. These field-collected individuals were in a food-abundant environment and grew rapidly (Levitan 1988a).

Initial demipyramid length in the laboratory experiment was estimated from the initial test diameter and the regression of demipyramid length and test diameter calculated from the field data [l_n demipyramid length (mm) = $1.101 \times l_n$ test diameter (mm) − 1.547, $R^2 = 0.92$, N = 92, Fig. 1].

Results

In the field experiment, *Diadema antillarum* changed test diameter in a density-dependent manner, by growth or shrinkage (Levitan 1989). A two-way ANOVA examining differences in test diameter as a function of population density and initial size class indicated a highly significant effect of density, but not of size (Levitan 1989). A similar ANOVA examining differences in demipyramid length indicated that both population density and initial size were significant factors (Table 1).

The laboratory echinoids changed test diameter (also by growth or shrinkage) as a function of food availability (Levitan 1989, and present Table 2). An ANOVA examining differences in demipyramid length indicated a significant effect of food level (Table 3).

Fig. 2 shows the relationship between demipyramid length and test diameter for the individuals in the field experiment, the laboratory experiment, and the field collection. The food-limited individuals in the field experiment increased demipyramid size relative to test size. The increases in relative demipyramid size, measured as the deviation of the demipyramid length from the length predicted by the field sample (for its test size), suggest an inverse relationship between growth rate and relative demipyramid length. Changes in test diameter were 7.3, 3.1, −1.7, and −6.7 mm for deviations of predicted demipyramid lengths of 0.85, 0.94, 1.31, and 1.61 mm, respectively (for the initially small individuals at low and
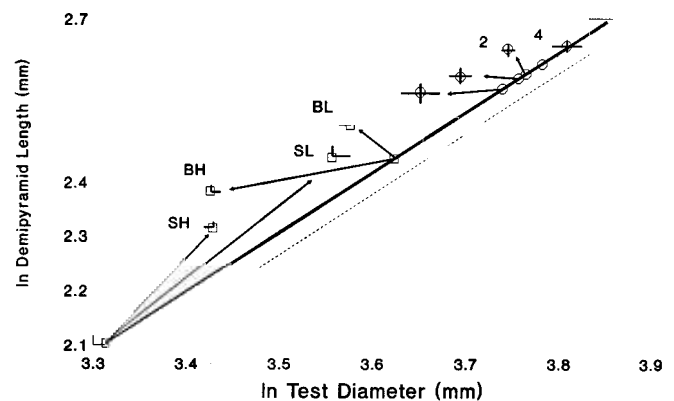
Table 1. *Diadema antillarum*. Analysis of variance of demipyramid length as a function of population density and initial size in field experiment. Data are mean values for each cage (3 of 32 cages missing due to mortality). SS: sum of squares; MS: mean square

Source of variation	df	SS	MS	F
Density		16.626	16.616	44.549***
Size		3.336	3.336	8.944**
Interaction	1	0.056	0.056	0.152 NS
Error	25	9.324	0.373	
Total	28	28.858		

*** $P < 0.001$, ** $P < 0.01$, NS $P > 0.05$

high density and the initially large individuals at low and high density, respectively; data are weighted means: Fig. 2). The positive deviation of demipyramid length in treatments with positive test growth is expected, since the growth rate of field-collected echinoids was higher than that of experimental echinoids [30 to 35 mm/yr (Levitan 1988a) and 12 mm/yr (Levitan 1989), respectively].

An inverse relationship between food level and relative demipyramid size was apparent in the laboratory study, which revealed demipyramid length deviations of 0.06, 0.94, 0.95, 1.14 mm for the 4, 2, 1, and 0 food group, respectively (data are weighted means: Fig. 2). An ANOVA testing the deviation in demipyramid length indicated highly significant differences among the four treatments (Table 4). The laboratory individuals fed the maximum ration had a demipyramid : test ratio similar to that of the field-collected individuals (the deviation of the demipyramid length is within the 95% confidence intervals of the field regression line: Fig. 2).

To examine whether the changes in the demipyramid and test were due to an increase in demipyramid length or a decrease in test diameter (or to some combination of the
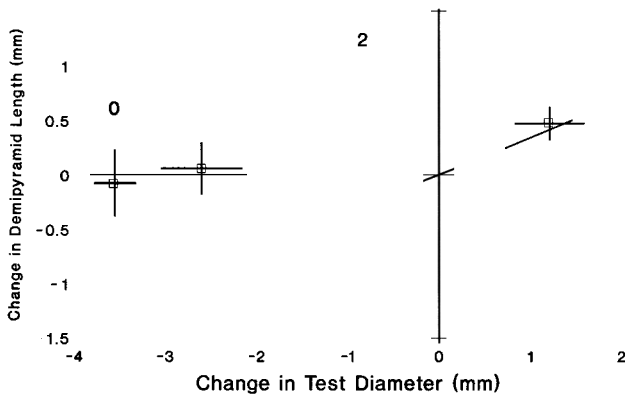
Fig. 3. *Diadema antillarum.* Change in demipyramid length vs change in test diameter for laboratory experiment. Data points show means ± standard errors; numbers indicate grams wet wt *Ulva lactuca* fed every 4 d. Line shows predicted ratio of ln test diameter and ln demipyramid length from slope of the field-collected sea urchins

Discussion

These results on *Diadema antillarum* are consistent with those reported by Ebert (1980), Black et al. (1982, 1984) and Edwards and Ebert (1991) in that the relative size of the demipyramid increased when echinoids were food-limited. High plasticity in Aristotle's lantern has been noted in several species of sea urchins (Ebert 1988). The present study documents that, for *D. antillarum*, this relationship primarily is due to a decrease in the size of the test. When food is limiting, more growth occurs in the demipyramids compared to the test, but demipyramid growth diminishes on an absolute scale (also noted by Edwards and Ebert 1991). This suggests that proportionately more energy is being allocated to jaw growth as the total amount of available energy diminishes. The changed demipyramid:test ratio induced by shifting energy allocation is greatly enhanced by the shrinking test.

The decrease in the size of the test of echinoids when food is limited has been known for some time (Ebert 1967, Cocanour 1969, Dix 1972, Moss and Lawrence 1972, Levitan 1988 b, 1989). In addition, a small amount of calcite resorption takes place in the plates of the test during normal growth (Lovén 1892, Deutler 1926, Gordon 1926, Mortensen 1927, Cutress 1965, Régis 1979, Märkel 1981). Märkel's study, using tetracycline growth lines and SEM, suggest clear zones of resorption in the interambulacral plates of both *Eucidaris tribuloides* and *Diadema antillarum* during growth. Calcite is resorbed in both echinoid spines (Märkel and Röser 1983) and parts of Aristotle's lantern (Märkel 1979).

Feeding and starvation studies of urchins injected with tetracycline give equivocal evidence of skeletal reworking and perhaps of calcite resorption. In Ebert's (1980) study, a clear tetracycline growth line was found in the jaws of *Diadema setosum* that were fed, but not in those that were starved. The starved echinoids had relatively larger jaws compared to the fed individuals. The lack of tetracycline lines on the jaws of starved echinoids suggest that these individuals either reworked calcite (as suggested by Ebert) and/or that the jaws did not grow and the test

shrank around them (as suggested by the present study). Since the jaws of the starved echinoids became relatively larger, but showed no indication of growth, negative test growth seems to be the most parsimonious explanation. Ebert also noted clear tetracycline lines in the coronal plates of some fed individuals, and faint lines in the starved individuals. The presence of faint tetracycline lines in the starved echinoids, suggesting some calcite addition in these individuals, presents an unresolved problem and underscores our ignorance of the mechanisms of calcite deposition and resorption in echinoids.

Pearse and Pearse (1975) found no evidence of resorption in two tetracycline studies of starved and fed *Strongylocentrotus purpuratus*. However, in their 3-mo-long study, the eight individuals in the starvation treatment had a slight weight gain (6%). This was attributed to nutrients from ingested wood and other debris found in the gut. In their 2-yr experiment, two individuals fed discontinuously (over four, 3- to 4-wk starvation periods) lost weight in only one starvation period. Perhaps the periods of stress were not long enough to cause resorption of skeletal elements.

Lewis et al. (1990) found no evidence of resorption of [45]calcium from the test of starved *Strongylocentrotus purpuratus* and its transfer and deposition in the still growing teeth. They suggested that resorption may take longer than the 4-wk starvation period of their study.

Märkel (1979, 1981) found differences in the patterns of calcification and resorption in cidaroid and non-cidaroid echinoids. Pearse and Pearse (1975) and Lewis et al. (1990) found no evidence of skeletal reworking in *Strongylocentrotus purpuratus*. The differences in the rates or patterns of calcite deposition and resorption between *Diadema* and *Strongylocentrotus* species may be taxonomic and perhaps related to the faster growth and thinner test of *Diadema* spp. [see Ebert (1982) for comparative growth data]. Investigations of taxonomic differences in skeletal plasticity should compensate for differences in growth rate by an appropriate scaling of the experimental time frame.

The ecological significance of plasticity in body components is that individuals can maximize reproductive output under rapidly changing conditions of food availability and population density. This is accomplished by an increase in the relative size of Aristotle's lantern, thus increasing energy intake (Ebert 1980, Black et al. 1984), and a decrease in the size of the body, thus decreasing the energetic costs of maintenance (Ebert 1968, Sebens 1982, Levitan 1988 b, 1989).

The ratio between the demipyramid and test can be used to ascertain the nutritional status of echinoids. Once the relationship between test and jaw size is established in a population of well-fed individuals, the degree of deviation from this ratio can be used as an index of food limitation for that species. This can be done at one sampling period, and may be preferable to monitoring long-term growth experiments which necessitate repeated measures of tagged individuals. This technique could be important for studies investigating intra- and interspecific competition. It may also be important for studies investigating whether small size is due to age or food

availability. Individuals which are size-stunted, due to food limitation, would have larger jaws compared to young well-fed individuals.

The paleobiological implications of this phenomenon include a record of biotic interactions in an echinoid's skeleton. Many biotic interactions influence per capita food availability. These interactions include intra- or interspecific competition for food, changes in predation pressure affecting that competition, and factors influencing the productivity of the algal resource. Present-day examples are known of temporal and spatial shifts in the abundance of competing species (Hay 1984), predators (Estes and Palmisano 1974) and conspecifics (Pearse and Hines 1979, Miller and Colodey 1983, Lessios et al. 1984, Scheibling 1984, Scheibling and Stephenson 1984, Levitan 1988a). Analysis of relative demipyramid size of museum collections and fossil specimens of extant species in combination with present-day experiments can provide evidence of changes in food availability and community structure in times past (Levitan in preparation).

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