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Scaling in the Aristotle's Lantern of *Lytechinus variegatus* (Echinodermata: Echinoidea)

C.M. Pomory
University of West Florida

M.T. Lares
University of Mary

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SHORT PAPERS AND NOTES

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SCALING IN THE ARISTOTLE'S LANTERN OF *LYTECHINUS VARIEGATUS* (ECHINODERMATA: ECHINOIDEA).—Size matters. This is a two-word conclusion supported by numerous investigations over many decades by biologists interested in how changes in organism size affect anatomical and physiological function (McMahon and Bonner, 1983; Reiss, 1989; Niklas, 1994; Calder, 1996; Brown and West, 2000). Two general relationships of isometry and allometry describe changes in body proportions or processes during growth (Huxley and Teissier, 1936). Isometric growth leads to relative proportions staying the same and is typically interpreted as merely the outcome of increases in size (Thompson, 1917; Huxley, 1932; Gould, 1966; Stern and Emlen, 1999; Gayon, 2000; Stevens, 2009). Allometric growth leads to a change in relative proportions and is often interpreted as functionally or evolutionarily important, with the implication that the more extreme the allometry the greater the functional significance (Thompson, 1917; Huxley, 1932; Gould, 1966; Stern and Emlen, 1999; Gayon, 2000; Stevens, 2009).

The Aristotle's lantern is a complex apparatus used for food acquisition in sea urchins that is composed of five primary elements called pyramids (Jackson, 1912; Märkel, 1975, 1979; Staurer, 1993). The lantern occupies the center area inside of the test (body of the sea urchin formed by the fusion of calcified plates) and its tip protrudes through the oral peristomial membrane, allowing it to contact food items. Muscles are able to move the lantern at various angles and open and close the five pyramids, resulting in the scraping/grasping of food items. The internal volume of the test must accommodate the presence of the digestive system, gonads, the lantern and muscles, and some room for the movement of the lantern. Since the test is typically rigid, the internal volume represents an ultimate limit to how large the internal structures can become.

Ebert (1980) suggested that the lantern may show a phenotypic response in size related to food availability, with the lantern increasing in size as food becomes more limited, potentially increasing feeding ability, although not all species respond the same way (Lawrence et al., 1996). Black et al. (1984) demonstrated that sea urchins, *Echinometra mathaei*, with larger lanterns

grazed more material than sea urchins with smaller lanterns. Any phenotypic response must take place within the scope of sizes determined by the growth pattern of the lantern as sea urchins grow from newly settled recruits to adults, the lantern's relation to other structures inside the test, and room available inside the test.

The time span from metamorphosis and recruitment (Doyle, 1975; Morse, 1990; Pawlik, 1992) through the early juvenile stages is one of vulnerability for many marine animals, including sea urchins (Hereu et al., 2005; Ebert, 2007). The early juvenile stage in most marine invertebrates is less well documented than the larval or adult stages. How the size of the feeding structure relates to the size of the body should be important in interpreting possible phenotypic responses and the ability to acquire food.

Lytechinus variegatus (Lamarck 1816), the variegated sea urchin, occurs in the Atlantic Ocean from North Carolina through southern Brazil (Moore et al., 1963; Hendler et al., 1995). It is typically found in seagrass beds where it feeds on a variety of animals and plants, including epibionts associated with seagrasses (Beddingfield and McClintock, 1998; Hill and Lawrence, 2003; Cobb and Lawrence, 2005; Watts et al., 2007). Populations of *L. variegatus* can undergo rapid increases in density that, although not as famous as sea urchin barren creation by *Strongylocentrotus* in kelp forests (Lawrence, 1975), can have dramatic impacts on seagrass beds in subtropical/tropical shallow-water marine areas (Camp et al., 1973; Drifmeyer, 1981; Maciá and Lirman, 1999; Rose et al., 1999; Maciá, 2000; Valentine et al., 2000).

In this study, we document the size of the pyramid of the Aristotle's lantern measured as both length and mass over a range of sizes of *L. variegatus* representing relatively new recruits to adults collected at the same time and location to establish a baseline against which phenotypic responses might be interpreted. We test the hypothesis that pyramid length and mass show an allometric response with body size.

Materials and methods.—Individual *L. variegatus* were collected (n = 167) in spring 2008 by hand from St. Joseph's Bay, FL (29°52.4'N 85°23.4'W), a location where sea urchins ranging from new recruits to adults can be consistently found in a well-described habitat (Beddingfield and McClintock, 2000). They were placed in 95% ethanol for 3 d for preservation. Spines were

removed from the test by scraping. The Aristotle's lantern was removed from each individual, soaked in household bleach (6% sodium hypochlorite) to remove organic tissue, rinsed with water, and air dried.

Test diameter at ambitus and test height were measured with SPI dial calipers (0.1 mm). Test volume was estimated using the formula for a dome or spherical cap: $V = [(\pi h)/6] \times (3r^2 + h^2)$ where V = test volume, π = mathematical constant pi, h = test height, and r = test radius at ambitus. A randomly selected pyramid from each individual was weighed on a Setra SI-410S electronic balance to obtain mass (1 mg). Pyramid length (Fig. 1) was measured with SPI dial calipers (0.1 mm). Original scale and ln-transformed data were examined using ordinary least squares (OLS) (Ryan, 1997) and geometric mean axis (GMA) (Ricker, 1984), also known as standardized major axis (Warton et al., 2006), regressions with pyramid mass or length as the dependent (Y) variable and test diameter, test height or test volume as the independent (X) variable. All combinations of test measures (diameter, height, volume) were examined using OLS and GMA regressions. Residuals from OLS regression were analyzed for normality, homogeneity of variance, and autocorrelation (Ryan, 1997). Normality was tested using skew, kurtosis, D'Agostino–Pearson, and Anderson–Darling tests (Anderson and Darling, 1954; D'Agostino et al., 1990; Pomory, 2006). Homogeneity of variance was tested using residual plots and the Brown–Forsythe test (Brown and Forsythe, 1974). Autocorrelation was tested using the Durbin–Watson test (Durbin and Watson, 1951).

Results.—OLS and GMA equations were very similar to one another, an expected outcome from the low degree of scatter in the X - Y plots, resulting in the same conclusions/interpretations for both types of regression (Figs. 2–4). Residual analysis revealed no assumption violations with the regressions.

The regression of test height vs test diameter was linear on both original scale (Fig. 2A) and ln-transform scale (Fig. 2B). The regression of test diameter vs test volume was curvilinear on the original scale (Fig. 2C) and linear on the ln-transform scale (Fig. 2D). The regression of test height vs test volume was curvilinear linear on the original scale (Fig. 2E) and linear on the ln-transform scale (Fig. 2F). The slopes of the ln-transform data indicate a slight allometric relation. Test height increases just a little faster than test diameter as size increases.

The regression of pyramid length vs test diameter was linear on both original scale



Fig. 1. Pyramid of *Lytechinus variegatus* showing length measurement points.

(Fig. 3A) and ln-transform scale (Fig. 3B). The regression of pyramid length vs test height was linear on both original scale (Fig. 3C) and ln-transform scale (Fig. 3D). The regression of pyramid length vs test volume was curvilinear on the original scale (Fig. 3E) and linear on the ln-transform scale (Fig. 3F). The slopes of the ln-transform data indicate an allometric relation.

The regression of pyramid mass vs test diameter was curvilinear on the original scale (Fig. 4A) and linear on ln-transform scale (Fig. 4B). The regression of pyramid mass vs test height was curvilinear on the original scale (Fig. 4C) and linear on ln-transform scale (Fig. 4D). The regression of pyramid mass vs test volume was curvilinear on the original scale (Fig. 4E) and linear on ln-transform scale (Fig. 4F). The slopes of the ln-transform data indicate an allometric relation. Pyramid mass increases faster than pyramid length relative to increases in test diameter, height, or volume. On the basis of the original-scale pyramid mass data (Fig. 4A), the curvilinear response indicates that a key transition in relative growth happens in the range of 25–30 mm test diameter.

Discussion.—In most sea urchins pyramid length is typically close to, or is, isometric in its relation to test diameter (e.g., Märkel, 1975, 1979; Ebert, 1980; Lawrence et al., 1995; current study). Fewer studies have measured pyramid mass, but mass is often more allometric than length (e.g., Lawrence et al., 1996; current study), with some exceptions (Lawrence et al., 1995). Pyramid length may be more constrained than mass by how the pyramid structurally fits with other components of the lantern and test. Different types of lantern (cidaroid, aulodont, stirodont, camarodont) may have different aspects of morphology that lead to different size-change

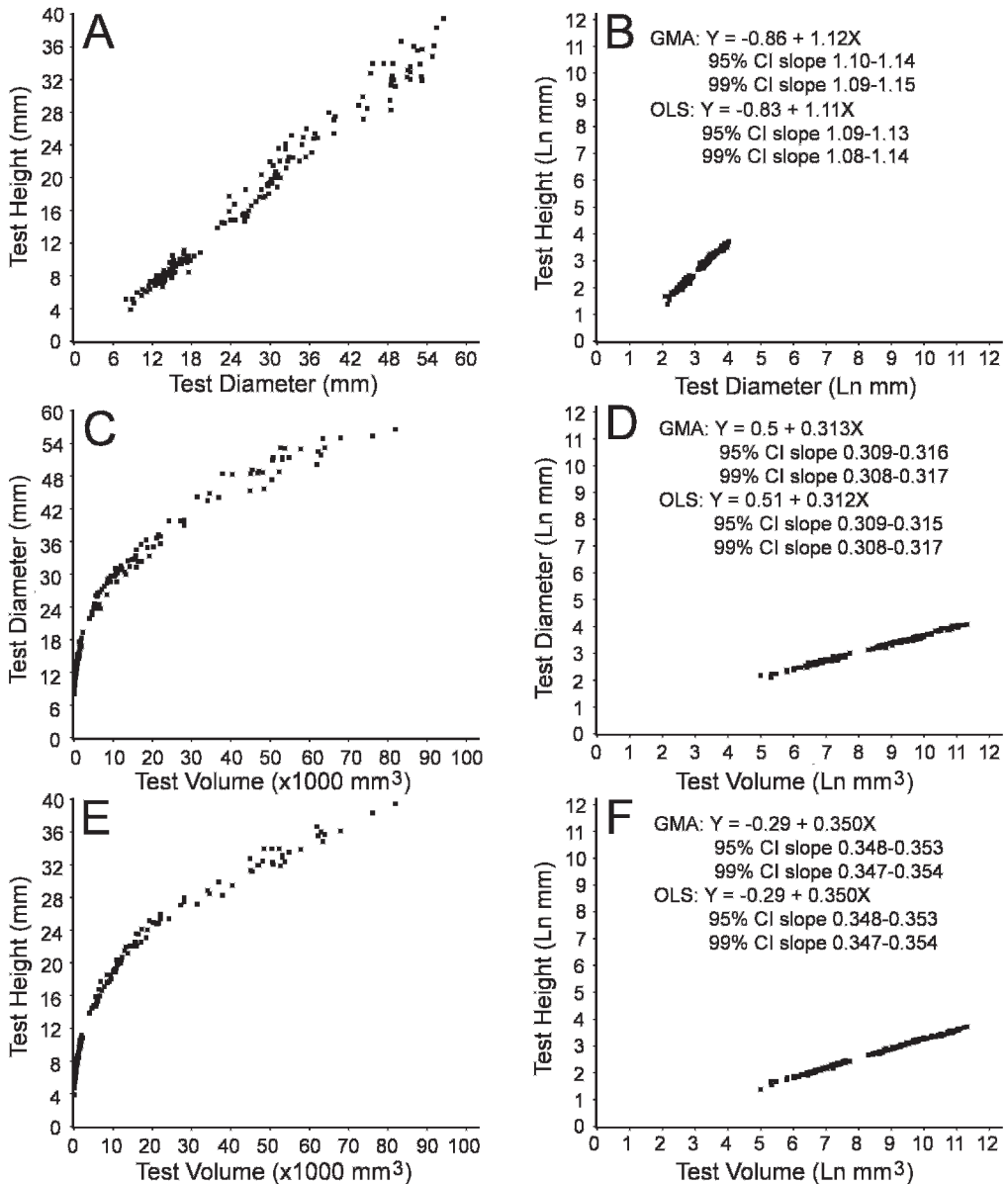


Fig. 2. Test measures for *Lytechinus variegatus*. (A) Original scale, and (B) Ln scale of test height and test diameter. (C) Original scale, and (D) Ln scale of test diameter and test volume. (E) Original scale, and (F) Ln scale of test height and test volume.

relationships (Märkel, 1979). If one accepts the premise that allometry equates with functional significance, then pyramid mass should be more important to lantern function than pyramid length. In *L. variegatus* mass increase of the lantern may reflect the diet, which includes animals as well as plants (Beddingfield and McClintock, 1998; Cobb and Lawrence, 2005). Increased pyramid mass may improve the ability to scrape a diversity of food material.

Although measuring phenotypic plasticity was not a purpose of this study, the outcome does relate in illustrating the size range of the pyramid onto which a phenotypic response will occur. On the basis of the curvilinear response in mass, we suggest that *L. variegatus* >25–30-mm size would be more likely to have a broader phenotypic response than smaller *L. variegatus*, and that pyramid mass may have a broader response than pyramid length.

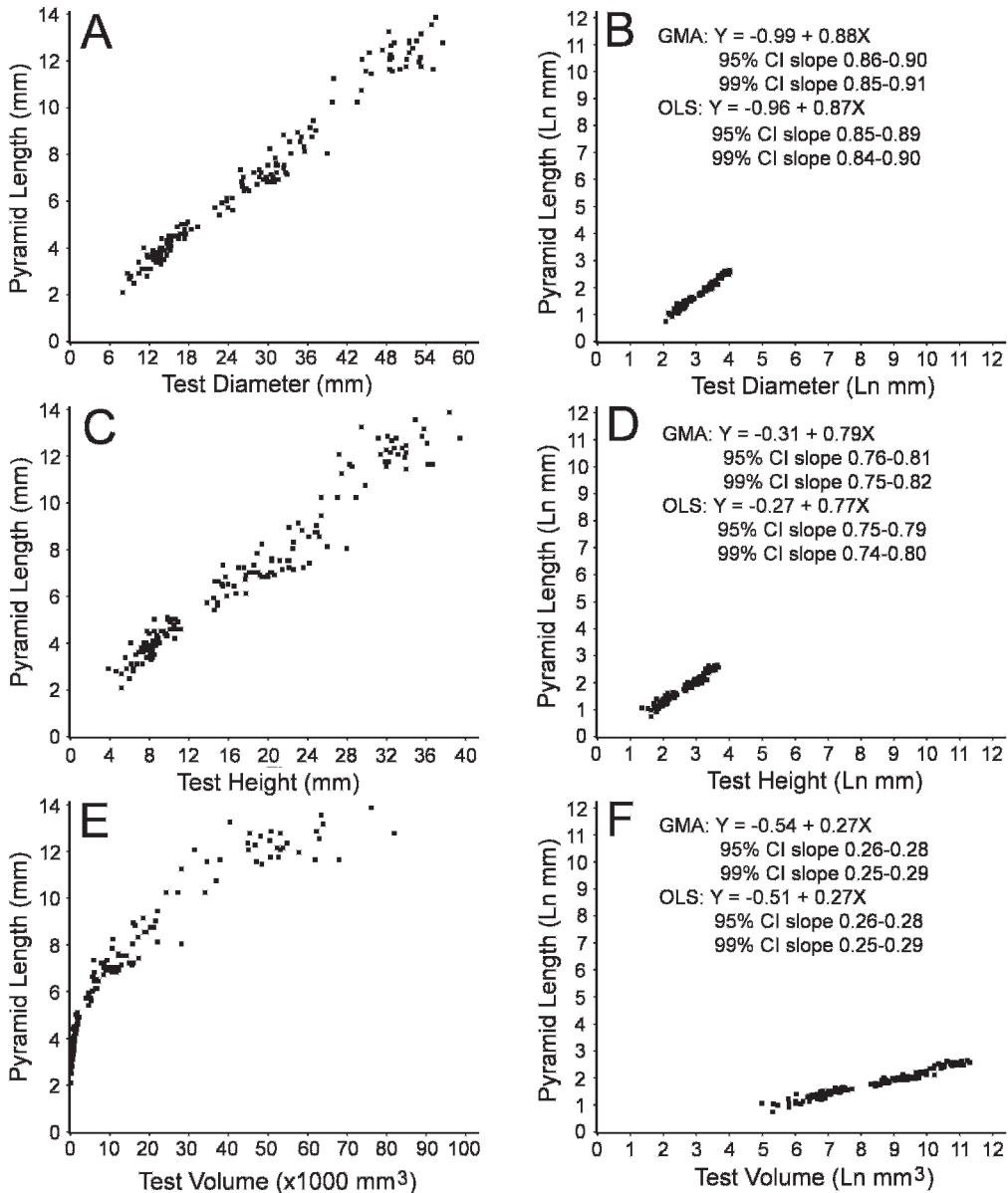


Fig. 3. Pyramid length vs test measures for *Lytechinus variegatus*. (A) Original scale, and (B) Ln scale of pyramid length and test diameter. (C) Original scale, and (D) Ln scale of pyramid length and test height. (E) Original scale, and (F) Ln scale of pyramid length and test volume.

In interpreting phenotypic plasticity in the lantern to food availability an important point to consider is what “relative increase” means. A relative increase in the lantern because the lantern increases and a relative increase in the lantern because the measure being indexed against (size of everything else) decreases are two different situations biologically. An increase in the lantern implies a phenotypic response in the lantern, making the lantern more robust,

possibly increasing feeding efficiency. A decrease in everything else is a phenotypic response in everything *except* the lantern, indicating that reserves are being used to supply energy under low food conditions. In the second case the lantern is not more robust after the “relative increase” than before. These two situations have not been made clear enough in discussions/interpretations on what phenotypic responses to food availability in sea urchins mean relative to

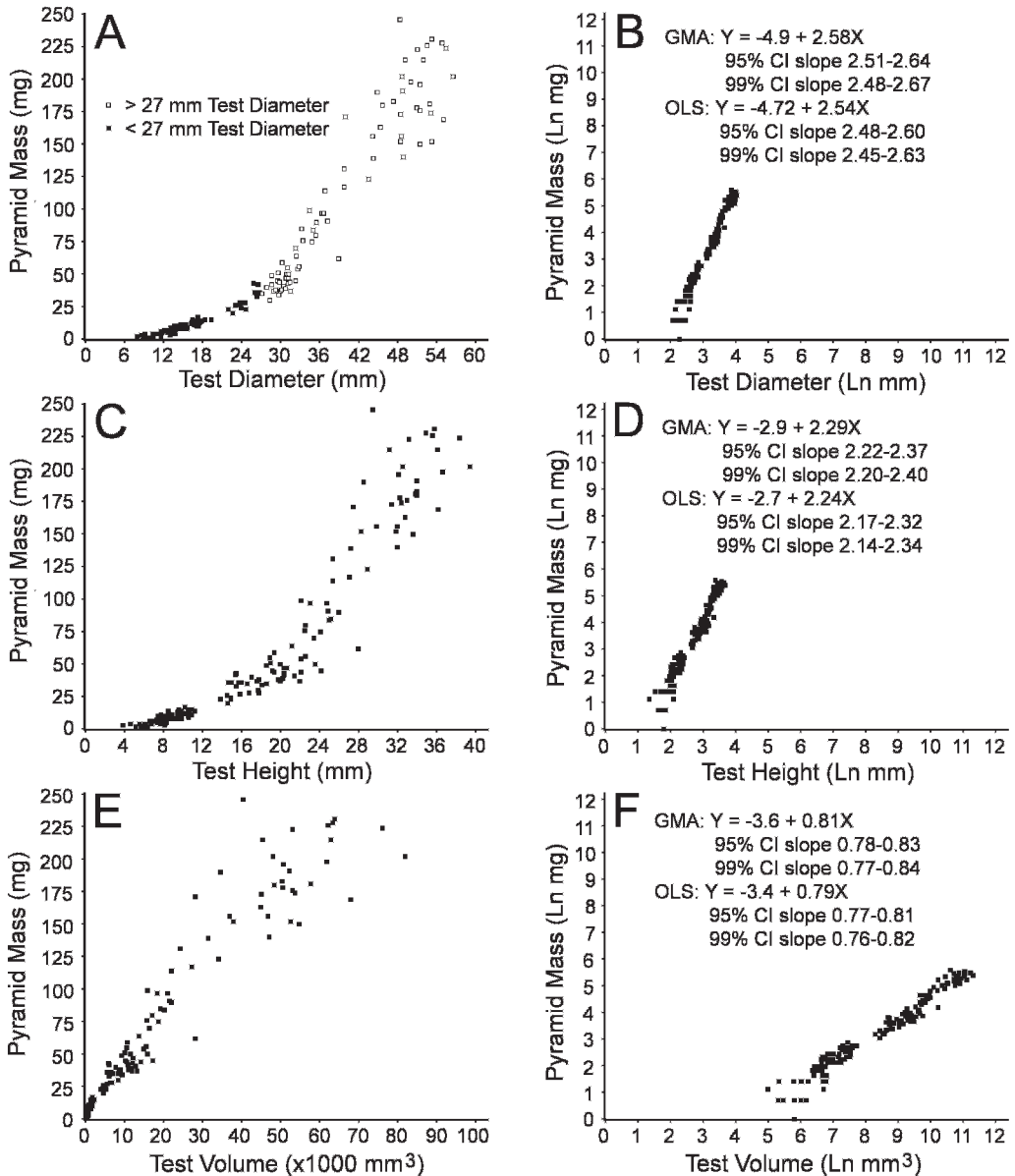


Fig. 4. Pyramid mass vs test measures for *Lytechinus variegatus*. (A) Original scale, and (B) Ln scale of pyramid mass and test diameter. (C) Original scale, and (D) Ln scale of pyramid mass and test height. (E) Original scale, and (F) Ln scale of pyramid mass and test volume.

energy allocation and feeding efficiency (e.g., Ebert, 1980; Black et al., 1984; Levitan, 1991) and in some cases may be partly due to measurement error (Ebert, 2004).

We offer two speculative implications on the importance of the allometric scaling demonstrated in this study. Sea urchins may have to reach a certain size before there is enough room in the test for phenotypic plasticity of the lantern to make a difference in the acquisition

of food. Put another way, test size constraints at small sizes may limit what sea urchins can feed on with the Aristotle's lantern as the lantern would not have room to change in size in response to variation in food resources (i.e., food type—algal vs animal vs detritus; food consistency—hard vs soft; food attachment—strong, crustose vs weak, upright; food amount—low vs high). That would have implications for survival of newly settled sea urchins

in the field because of possible food acquisition limitation, what is available relative to what can be physically consumed. The second implication deals with aquaculture of sea urchins through their entire life cycle and the use of prepared feeds. The feeds would have to have a small amount of variation around the right consistency to be handled by the lantern in small sea urchins compared with larger sea urchins. Food type affects survival and growth in *L. variegatus* (Beddingfield and McClintock, 1998). Allometric scaling of food capture structures suggests that the interaction between functional morphology and phenotypic response may change with a change in overall size.

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- C. M. POMORY AND M. T. LARES, *Department of Biology, University of West Florida, Pensacola, Florida 31514 (CMP) and Department of Biology, University of Mary, Bismarck, North Dakota 58504 (MTL).*