

Snail shape and growth rates: Evidence for plastic shell allometry in *Littorina littorea*

(morphology/food availability/phenotypic variation)

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ABSTRACT The periwinkle *Littorina littorea* exhibits morphological variation among southern New England populations that appear to be genetically continuous. In dense populations, individuals have relatively elongate shells in comparison to individuals in sparse populations, which have rounder, globose shells. We experimentally demonstrate that this shell variation is a function of snail growth rate. Rapidly growing snails develop thin, globose shells that accommodate more body mass than thicker, more elongate shells. The implications of these results are discussed in relation to interpreting morphological variation in extant gastropods and in the molluscan fossil record.

Morphological variation among populations or in the lineage of a species may be attributed either to genetic differences or to environmental influences acting on the phenotypic expression of a genotype. In shell-secreting organisms, such as gastropods, Gould (1) has suggested that shell shape is governed by genetically set allometric relationships. This assumption of constant shell allometry has led to the interpretation of interpopulation and historical differences in gastropod shell morphology as representing genetic differences and evolutionary change (2-5) (but see refs. 6 and 7). Although environmental influences on shell allometry have been suggested (8), this idea has not been examined explicitly. Here we document variation in shell shape among populations of a common marine snail and test the hypothesis that much of the variation can be explained by differences in the growth rates of snails from different populations.

The herbivorous snail *Littorina littorea* is a habitat generalist found abundantly in littoral habitats along the northeastern coast of North America. It has a relatively long-lived (4-6 wk; ref. 9) planktonic larval stage, which has been suggested to buffer it from adapting defensive shell morphology in response to local variations in predation pressure (10, 11). Nonetheless, shell morphology varies markedly among *L. littorea* populations on southern New England beaches (Fig. 1A, Table 1). Snails from dense populations tend to have elongate, cone-shaped shells (shell length greatly exceeds shell width), whereas *L. littorea* from low-density populations have a more globose shell morphology (shell width approaches shell length). The globose morph has a larger internal shell volume (Fig. 1B) and is thinner-shelled (see below) than the coned morph. Snail density may affect food availability, so the apparently negative relationship between shell globosity and snail density led us to hypothesize that fast-growing snails develop rounded shells to accommodate a larger body mass within a given amount of shell material.

To test the above hypothesis, we experimentally manipulated the density of *L. littorea* on a beach with a dense snail population (Haffenreffer Beach, Table 1). Under reduced snail density conditions, snails grew significantly faster ($P <$

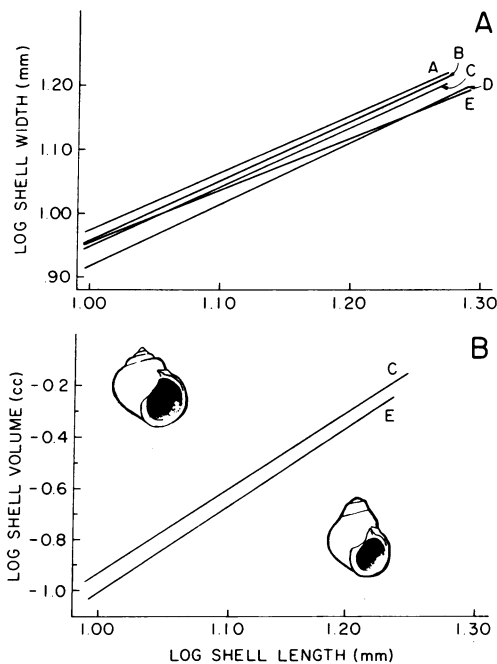


FIG. 1. (A) Shell length/width regressions of *L. littorea* collections made in July 1982. See Table 1 for snail densities and regression equations for each site. There is a significant difference ($P < 0.001$, ANCOVA) among populations, with all individual regressions significantly different from each other ($P < 0.01$, Schaffe test), with the exception of populations B and C. (B) Shell length/internal volume regressions for snails from the Haffenreffer Beach (site E in Table 1; $\log V = 3.36 \log L - 4.40$, $r^2 = 0.74$, $n = 25$) and Guilford (site C in Table 1; $\log V = 3.09 \log L - 4.04$, $r^2 = 0.95$, $n = 15$) populations. ($P < 0.001$, ANCOVA). Sketches of individuals of similar length (≈ 15 mm) from each population are shown adjacent to each line. Shell volumes were determined by measuring the water holding volume of a size range of shells from each population.

0.001, t test, lip expansion) and after the experiment were significantly larger ($P < 0.001$, t test, shell length and width) than snails at natural densities (Table 2). After only 12 weeks, individuals from the reduced density area were thinner-shelled ($P < 0.001$, t test; Table 2), had rounder apertures ($P < 0.001$, t test; Table 2), and had more ($P < 0.001$, t test) internal shell volume than control snails.

To compare shell allometry between fast growing and slow growing snails, we calculated allometric curves for all marked individuals by regressing monthly measurements of shell length and width. The slope of this regression is the allometric constant K for each individual snail (1). Individuals from the area with low snail densities had higher ($P < 0.05$, Wilcoxon rank test) allometric constants than did the slower growing snails in control areas (Table 2). This indicates that in faster growing snails, shell width was increasing faster, relative to shell length, than in the control snails—i.e., fast growing snails were becoming more globose. These

Table 1. Sites and line equations for regressions in Fig. 1A

Site	<i>L. littorea</i> density, no. per m ²	<i>n</i>	Regression equation	r ²
A. Rumstick Cove, Barrington, RI	<25	36	W = 0.876L + 0.101	0.971
B. One Hundred Acre Cove, Barrington, RI	<25	22	W = 0.924L + 0.028	0.985
C. Yale Marine Station, Guilford, CT	50–200	80	W = 0.910L + 0.049	0.986
D. Nantucket Harbor, Nantucket, MA	250–350	54	W = 0.954L + 0.035	0.965
E. Haffenreffer Beach, Bristol, RI	600–800	200	W = 0.814L + 0.143	0.895

W, log shell width; L, log shell length; r², correlation coefficient.

results provide evidence for environmentally mediated morphological plasticity in *L. littorea* and suggest that much of the morphological variation among *L. littorea* populations (Fig. 1A) is the result of differences in food supply and individual growth rates among populations. We suggest the following explanation for these results.

If calcium carbonate deposition is carried out at a relatively constant rate (13) that can limit body growth (14), a globose shell may allow an increase in growth rate that would not be possible without a change in shell morphology. A globose shell has a larger internal volume and, thus, maximizes shell volume available for body growth while minimizing the amount of shell material required to accommodate a given body mass. We suggest that globose shells allow increased body mass given a limiting rate of calcium carbonate deposition. The notion that calcium carbonate deposition is carried out at a relatively constant rate (13, 14) is reflected in our data in two ways. First, fast-growing snails have thinner shells than do slower-growing snails (Table 2). Second, the shell composition of fast- and slow-growing snails differed. Shells of fast-growing snails had significantly more ($P < 0.01$, *t* test) organic matrix ($\bar{x} = 2.32 \pm 0.09\%$, $n = 5$) than did slow-growing control snails ($\bar{x} = 1.88 \pm 0.11\%$, $n = 10$) from the same initial population (see ref. 15 for methods). An increased proportion of organic material in the shells of fast-growing snails may allow these individuals to cover a larger area with shell material with a given amount of calcium carbonate. Interpopulation differences in shell composition also support this idea. The globose snails from the natural low-density *L. littorea* population at Guilford (Fig. 1A, Table 1) have a relatively high ($2.12 \pm 0.195\%$, $n = 10$) organic matrix content.

Our results show that rapid growth in *L. littorea* results in a thin-shelled, globose shell morph composed of a reduced proportion of calcium carbonate, in comparison to slower growing snails. We interpret these differences as results of a relatively fixed maximum rate of calcium carbonate secre-

tion in gastropods. In the past, a genetic basis has been assumed for most morphological variation in gastropods (2, 3, 16–20). Examination of the literature, however, suggests that environmentally mediated plasticity in shell shape is common in molluscs (21–37) and has been documented several times (21, 29, 30, 38, 39). In most of these studies, documented morphological variation is consistent with our interpretation (for an exception, see ref. 40). Such morphological plasticity may be the prevalent explanation for shape variation in molluscs with planktonic larva or living in restricted bodies of water where panmixia is probable. In addition, if snails have only limited control over the maximum rate of calcium carbonate deposition, as our results imply, adaptive development of thick and axial sculpturing may entail selection pressure for reduced growth rates (14, 27, 41–45).

Our results also have important implications for interpretation of patterns in the fossil record of calcium carbonate-secreting organisms. Our findings warn that changes in skeletal morphology over time may reflect environmental changes that influence growth rates. In a recent, widely cited paper (5), repeated and synchronous episodes of variation in the intensity of shell globing have been suggested to illustrate rapid speciation events. Interestingly, most of the rapid changes observed, occurred simultaneously in all lineages and were manifested in similar shell shape changes (see also refs. 46 and 47). Three of the four gastropod lineages examined (5) were epifaunal deposit feeders and showed synchronous episodes of reduced shell globosity coinciding with the temporary disappearance of the original globose morph. The fourth lineage, an infaunal deposit feeder, increased shell globosity when the epifaunal lineages were decreasing shell globosity. Three of the four initial morphs in these lineages have survived to the present time in the lake basin in spite of their absence during episodes of shell change, while none of the rapidly evolved "species" have survived. In light of our results, we feel that this data (5) may simply reflect a history of changing conditions in the lake basin that has influenced

Table 2. Results of *L. littorea* density manipulations

Date	Density	Variables, $\bar{x} \pm SD$					
		Shell			Lip expansion, mm	Allometric constant <i>K</i>	Aperture index
Length, mm	Width, mm	Thickness, mm					
June 1982	Normal	13.25 ± 2.02	11.57 ± 1.65	0.38 ± 0.07	—	—	—
	Reduced	13.25 ± 1.95	11.51 ± 1.65	0.39 ± 0.08	—	—	—
September 1982	Normal	15.44 ± 1.15	13.35 ± 0.89	0.42 ± 0.05	11.87 ± 5.14	0.85 ± 0.30	—
	Reduced	17.43 ± 1.31	14.83 ± 1.00	0.37 ± 0.06	20.55 ± 5.85	0.90 ± 0.14	0.80 ± 0.05
	Normal (unmarked)	17.04 ± 2.46	13.99 ± 1.66	0.51 ± 0.10	—	—	0.73 ± 0.05

Two groups of 250 *L. littorea* from a local population (Haffenreffer Beach; site E in Fig. 1A) were measured and marked. Length, columella length; width, maximum dimension perpendicular to the columella; thickness, shell thickness 1 mm from the shell lip at the furthest point on the aperture from the columella. All measurements were made to ±0.01 mm. Snails were individually numbered, and apertures were notched (12). Each group was then introduced into one of two 3 × 3 m pens constructed in the middle intertidal zone of the beach. All *L. littorea* had been removed from one of these pens (reduced snail density), and the other was left as a control (normal snail density). Marked snails were placed in the pens on June 20, 1982, and were collected, remeasured, and remarked (if necessary) on a monthly basis. Unmarked snails were continuously removed from the removal pen during the course of the experiment. All snails were collected and sacrificed on September 14, 1982, (removal $n = 186$, control $n = 167$). Because there was a disparity in size between the removal and control groups on September 14, a second group of control snails of comparable length to the experimental snails was randomly collected on September 20, 1982. This group ($n = 200$) was used to compare volume and aperture differences between reduced-density snails and snails of similar length from the normal population. Aperture index is defined as maximum aperture dimension/minimum aperture dimension and is used as a measure of aperture roundness (1).

snail growth rates. We suggest that a better understanding of the determinants of morphological variation may allow real and apparent pattern in the fossil record to be distinguished, thus improving the resolution and message of the fossil record.

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