Do carbonate skeletons limit the rate of body growth?

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Many marine invertebrates produce mineralized skeletons whose form suggests an economical construction. Porous as opposed to solid skeletal components are produced by scleractinian corals[1,2], balanoid and coronuloid barnacles[3], ostreid and hippuritid bivalves[4], and almost all modern echinoderm classes[5,6]. They were also produced by rudist bivalves which were widely successful in Cretaceous tropical seas[7]. Marine prosobranch gastropods produce a stout external shell sculpture in place of a uniformly thick, ultimately stronger shell[8,9]. The costs implied by these patterns of economical skeleton construction, however, are unknown[10–12]. The term 'cost' refers to an evolutionary cost measured in terms of reduced fitness. Note that not all such costs are energetic; non-energetic constraints may also influence fitness. I present here evidence that both thick- and thin-shelled morphs of *Thais* (=*Nucella*) *lamellosa* (Gastropoda, Prosobranchia) produce shell material at a remarkably similar rate during maximal growth. Thick-shelled animals, however, exhibit a significantly slower rate of body growth. These results suggest that rates of skeletal growth can limit the rate of body growth and that this limitation represents a potentially important evolutionary cost.

Costs associated with carbonate skeletons can be subdivided into at least three categories: (1) an energetic, depositional cost including organic matrix production and mineralization; (2) an energetic, post-depositional cost, limited primarily to organisms that must expend energy transporting a skeleton; and (3) a non-energetic, growth-rate-limitation cost where the rate of maximal body growth may be set not by the energy available for growth but rather by the maximum rate at which skeleton may be produced. This latter cost is important to recognize because different patterns of energy consumption and growth will be exhibited with increasing availability of energy than would be expected if skeleton costs were strictly energetic.

Figure 1 illustrates the relationship between body growth and increasing energy (food) availability for three alternative hypotheses about factors which potentially limit body growth rate. Predictions about the relative rates of shell growth and rates of energy consumption for each hypothesis are included in Fig. 1 legend. The first hypothesis (Fig. 1*a*) predicts that if a physiologically determined upper limit to the rate of tissue production (dotted line) is reached before some upper limit to the rate of ingestion or assimilation (dashed line), rates of body growth in organisms with thick and thin skeletons will be identical when energy availability is high. Given an energetic cost to shell material, however, organisms with a thick or dense skeleton will require more energy to achieve the same rate of body growth because of additional energy expended in producing more skeletal material. The second hypothesis (Fig. 1*b*) predicts that if an ingestion (or assimilation) limit (dashed line) is reached before a tissue production limit (dotted line), then organisms with thick or dense skeletons will exhibit a lower maximal rate of body growth than those with thin or porous skeletons. Here, organisms with thick and thin skeletons should ingest (assimilate) equal amounts of energy at high energy availability, but because of energy invested in shell, thick-shelled animals should have a slower rate of body growth.

The third hypothesis (Fig. 1*c*) predicts that if a shell production limit is reached before either an ingestion or a tissue production limit, organisms with thick skeletons will again show slower rates of body growth at high energy availability, as with hypothesis *b*. However, because body growth cannot proceed in advance of skeleton growth, organisms with thick or dense skeletons should consume less energy (food) than those with thin or porous skeletons.

To test these hypotheses, pre-reproductive individuals of similar body weight (Table 1) were selected from a thick- and a thin-shelled population of the morphologically variable, intertidal gastropod, *Thais lamellosa*. Although having similar body weights, thick-shelled individuals had almost 50% heavier shells (Table 1). Growth experiments (Tables 1, 2) demonstrated that both thick- and thin-shelled animals added significantly less shell (mean, 22.6% less) and less tissue (mean, 25.2% less) at the upper than the lower tidal level. At both tidal levels, however, thick-shelled animals consumed fewer barnacles (Table 3) and also gained less body weight (mean, 32.5% less). Of particular interest is the fact that thick- and thin-shelled animals of the same initial body size produced almost equal weights of shell material at both tidal heights. These patterns of growth and prey consumption are inconsistent with the first two hypotheses (Fig. 1*a*, *b*), and support the skeleton-limitation hypothesis (Fig. 1*c*)

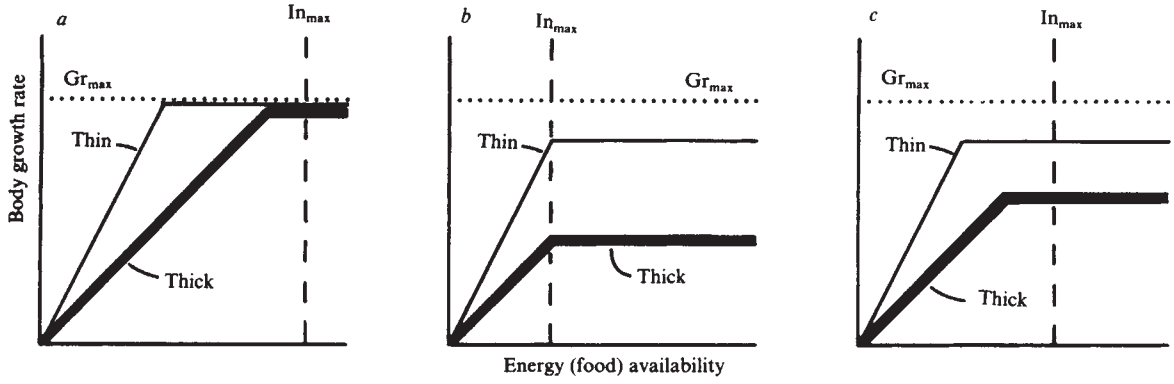

Fig. 1 Graphical illustration of hypothetical growth patterns with increasing rate of energy (food) supply for thick- and thin-shelled organisms subject to different growth constraints. *a*, Maximum rate of body growth limited by maximum rate of tissue production. *b*, Maximum rate of body growth determined by maximum rate of ingestion (or assimilation). *c*, Maximum rate of body growth determined by maximum rate of shell production. Predicted differences in rates of shell production at maximum body growth rate are: *a*, *b*, thick > thin; *c*, thick = thin. Expected energy (food) intakes at maximum body growth rate are: *a*, thick > thin; *b*, thick = thin; *c*, thick < thin. These differences will only be true when animals are growing at a maximum rate. In_{max}, potential maximum rate of ingestion (assimilation). Gr_{max}, potential maximum rate of body growth. Thin-lined curve, organism with low-density skeleton or thin shell; thick-lined curve, organism with high-density skeleton or thick shell.
Note for hypothesis *c* that the inflection points of the two curves need not coincide on either axis, in contrast to hypotheses *a* and *b*.

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Table 1 Size and growth parameters for thick- and thin-shelled *T. lamellosa*

Tidal height (ft)	Morph	n	Initial			Total weight change	
			Shell length (mm)	Shell weight (g)	Body weight (g)	Shell weight (g)	Body weight (g)
0.0	Thick	10	21.9 (1.08)	1.68 (0.370)	0.23 (0.052)	1.43 (0.309)	0.37 (0.133)
	Thin	9	22.2 (1.26)	1.06 (0.169)	0.24 (0.042)	1.49 (0.177)	0.50 (0.092)
+2.0	Thick	14	21.6 (0.95)	1.59 (0.208)	0.22 (0.039)	1.06 (0.260)	0.25 (0.074)
	Thin	15	21.5 (1.67)	0.95 (0.216)	0.23 (0.045)	1.19 (0.329)	0.41 (0.138)

Values are means and standard deviations of size and growth parameters for thick- and thin-shelled *T. lamellosa* pooled from replicates at two tidal heights. Thick-shelled animals were collected from False Bay and thin-shelled animals from Turn Rock, both located on San Juan Island, Washington, USA. Shell and body weights were measured non-destructively by methods described elsewhere[40]. Replicate groups of individually marked, measured and weighed animals of each shell type were placed in plastic screen cages mounted on pilings at two tidal heights (0.0 and +2.0 ft above MLLW[41]) at the Friday Harbor Laboratories, Friday Harbor, Washington, USA. Throughout the experiment the *Thais* were supplied freely with their preferred prey, *Balanus glandula*, on small stones[41]. Prey were made available at all times in high densities so that searching times were negligible. Snails were supplied with barnacles from 13 August to 5 September and 14 September to 14 October, and final body weights (wet) were measured on 13 November, 1978. *n*, Total number of individuals in each treatment. Numbers in parentheses are pooled standard deviations. There were two replicate cages for each treatment at the lower, and three for each treatment at the upper tidal level.

Table 2 Analysis of variance on initial values and two growth parameters of thick- and thin-shelled *T. lamellosa* at two tidal heights

Source of variation	d.f.	Initial				Growth parameter			
		Shell weight		Body weight		Shell weight change		Body weight change	
		MS	*P*	MS	*P*	MS	*P*	MS	*P*
Main effects									
Shell morph	1	5.101	0.001*	0.0002	0.737	0.118	0.244	0.283	0.001*
Tidal height	1	0.056	0.339	0.0013	0.419	0.880	0.002*	0.103	0.008*
Interaction	1	0.009	0.701	0.0001	0.844	0.014	0.686	0.001	0.857
Residual	44	0.063		0.0020		0.088		0.014	
Total	47	0.170		0.0021		0.112		0.022	

d.f., Degrees of freedom; MS, mean square; *P*, exact probability of *F* values obtained by dividing the component mean squares by the residual mean square. Data are from Table 1.
* Significant *F* ratios.

Table 3 Consumption rates of barnacles, *Balanus glandula*, by thick- and thin-shelled *T. lamellosa* at two tidal heights

Consumption rates			Two-way analysis of variance on consumption rates			
	Shell morph					
Tidal height (ft)	Thick	Thin	Source of variation	d.f.	MS	*P*
0.0	0.93	1.15	Main effects			
	1.01	1.28				
			Shell morph	1	0.120	0.029*
	0.56	0.85	Tidal height	1	0.231	0.007*
+2.0	0.63	1.02				
	0.85	0.78	Interaction	1	0.002	0.725
			Error	6	0.015	
			Total	9	0.049	

Consumption rates were measured as barnacles eaten per snail per day from 14 September to 14 October, 1978. Each value represents an average for five snails (individual consumption rates are not known as five snails were contained in each cage). An analysis of variance was performed on these average values: d.f., degrees of freedom; MS, mean square; *P*, exact probability.
* Significant *F* ratios.

that rate of shell production limits the maximum rate of body growth. However, these data cannot rule out the possibility that animals from the thick-shelled population consumed barnacles more slowly for other reasons and that the production of equal weights of shell material was coincidental. That this occurred at both tidal heights due to chance alone seems unlikely.

Two otherwise enigmatic patterns of invertebrate growth may be explained by the skeleton-limitation hypothesis. First, shell production continues in the absence of feeding in species of barnacles[13], meso-[14] and neogastropods (A.R.P., unpublished results), and both pteriomorphian[15,16] and heterodont[17] bivalves. Although difficult to explain energetically, this may reflect either an increase in a shell's habitable volume in anticipation of future body growth or a reinforcement of thinner shell produced during periods of more rapid growth[18]. Second, scleractinian corals frequently show seasonal changes in the density of skeletal material produced[19]. Higher density bands are generally believed to form during periods of slower growth (refs 19–22). In both examples, energetic considerations would predict a decrease in skeleton production when tissue growth decreases or stops, yet calcification continues. Both examples would thus seem to be more readily explained as a response to skeleton-limited rates of body growth, rather than as a result of a high energetic cost to skeletal material.

A third growth pattern may also be explained by the skeleton-limitation hypothesis: rapidly growing organisms frequently produce less skeleton per unit body weight (for example, species of ramose scleractinian corals[20,23], pteriomorphian[24] and heterodont[25] bivalves, echinoids[26] and echinoderms in general[27]). In addition, a number of organisms exhibit ontogenetic

changes in skeletal growth. Juveniles, for whom maximal growth may be critical[9,28], exhibit more porous or, in some cases, significantly less massive skeletons than adults (for example, species of balanoid and coronuloid barnacles[29,30], strombid and cypraeid gastropods[31,32] and some extinct armoured heterostracan fishes[33]). Although juveniles are more vulnerable than adults to most predators[9], a heavier skeleton could limit the rate of body growth, increasing the time spent at smaller, more vulnerable sizes[8]. When mature and slow growing, skeletal reinforcement would no longer restrict potential growth. Where there is a refuge in size from predation[9], trade-offs between rate of growth and extent of morphological defence may represent an important compromise.

Step(s) which limit the rate of skeleton production are unknown. Neither rates of ion transfer across epithelia[34] nor availability of dissolved calcium carbonate in surface seawater (<100 m; refs 35–37) are likely to limit the rate of skeletal growth. A probable limiting step is the rate at which crystals can grow from a biologically maintainable precipitating medium. If this is the case, during rapid growth crystal growth limitations would favour shell microstructures with many small crystals because of the increased surface for precipitation. Limited data reveal such a pattern in comparisons of seasonally rapid and slow growth increments in two bivalve species[38]. Furthermore, both bivalved[4,39] and shelled gastropod[39] molluscs exhibit an evolutionary loss of nacre, a shell microstructure composed of large crystal elements. Thus both ecological and evolutionary patterns in skeletal architecture may be explained by the skeleton-limitation hypothesis.

The above evidence indicates that a potentially important non-energetic 'cost' exists due to growth constraints imposed by carbonate skeletons, both for marine gastropods and possibly for other marine invertebrates. The prevailing attempt to explain morphological adaptations purely in terms of energetic costs and benefits may be too narrow a perspective.

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Segment-specific organization of leg motoneurones is transformed in bithorax mutants of *Drosophila*

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In *Drosophila*, genes controlling segmentation in the thorax and abdomen are clustered in one region of the genome known as the bithorax complex. Studies of the genetics of this complex suggest that loss of activity of a gene causes transformation of a particular segment to a more anterior one, mesothorax representing the ultimate transformation[1]. This transformation is well described for the epidermis, but it is not clear whether other segmentally arranged tissues are also transformed. The segmental ganglia are fused in *Drosophila* into a single compact mass termed the thoracic ganglion but the segmental organization of the nervous system is still apparent. There are discrete regions of neuropil, termed neuromeres, corresponding to the three thoracic segments: prothorax, mesothorax and metathorax. A small terminal neuromere corresponds to the abdominal segments. Evidence is presented here that the leg motoneurones of each of the three thoracic segments are arranged in a segment-specific pattern in the thoracic ganglion. In mutant flies which have the metathoracic cuticle transformed to mesothoracic, the arrangement of the metathoracic leg motoneurones can be altered to resemble that of the mesothoracic leg motoneurones.

Horseradish peroxidase (HRP) filling of cells was used to study the innervation of the leg. This enzyme is applied to a cut made in the tarsus and is transported through those sensory axons that have been cut. It is also taken up by motoneurone terminals and transported in a retrograde fashion to fill the entire cell. The HRP-filled cells can be visualized by any one of several methods[2,3]. Figure 1 is a composite drawing showing leg motoneurones in each neuromere. The arrangement of the leg motoneurones is different in the three neuromeres: in the prothoracic (anterior) neuromere, the cell bodies are in a region of the cortex anterior to the neuropil. The axons project back into the neuropil, into which they branch, collect into a loose bundle and course laterally and ventrally to leave the ganglion in the prothoracic leg nerve. In the mesothoracic (middle) neuromere, the cell bodies are in the cortex anterior and ventral to the neuropil. The axons project posteriorly to exit through the mesothoracic leg nerve. Branches are directed dorsally into the lateral neuropil, segregated from sensory neurone arborizations which are in the medial region. In the metathoracic (posterior) neuromere, the motoneurone cell bodies lie laterally and somewhat posteriorly to the neuropil. Their axons project anteriorly from the cell bodies, then loop back and run posteriorly to the nerve. All the axons loop back at the same point although the cell bodies are spread through a region 30–60 μm posterior to the loop. As in the mesothoracic neuromere, the arborizations of the motoneurones are laterally placed in the neuromere, not overlapping the medially placed arborizations of the sensory neurones. In each neuromere a single motoneuron sends a branch contralaterally. These cross in

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