

# Calcification in marine molluscs: How costly is it?

(Gastropoda/Nucella/shells/energy budget/growth)

A. RICHARD PALMER

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

Communicated by R. T. Paine, November 18, 1991 (received for review August 1, 1991)

**ABSTRACT** Although crucial to our understanding of skeletal evolution in marine invertebrates, the cost of calcification has remained elusive for a simple reason:  $\text{CaCO}_3$  is an inorganic material. Its cost thus derives solely from the metabolic expenses of accumulating, transporting, and precipitating  $\text{CaCO}_3$  and cannot normally be separated from other metabolic costs. Traditionally, calcification cost has been ignored and total shell cost has been assumed to derive solely from skeletal organic matrix. The cost estimated here was permitted by the substantial natural variation in shell thickness in two rocky-shore gastropods (*Nucella lamellosa* and *Nucella lapillus*). In both the field and laboratory, data from three separate experiments revealed that groups of snails producing extra shell material under a particular set of experimental conditions also consumed extra food. The cost of calcification was estimated by computing the extra energy assimilated per unit extra shell produced at a common rate of tissue growth and then subtracting the cost of the organic matrix. At 1–2 J/mg of  $\text{CaCO}_3$ , the calcification cost reported here is roughly 5% of that for the predominantly proteinaceous organic fraction of molluscan shells on a per-gram basis. This may explain why calcareous microstructures high in organic content have become less common evolutionarily.

The benefits of calcified external skeletons are many and varied (1, 2). One of the most obvious is reduced vulnerability to predation. Heavier shells are both more difficult to penetrate via drilling (3, 4) and more difficult to break by durophagous predators, including crabs (5–7), lobsters (8), and fishes (9–11). Given such evident benefits, why are heavier shells not more widespread? Presumably, they entail greater costs.

Although the costs of calcified skeletons may seem apparent, their magnitudes are poorly known (12, 13). At least three have been identified: (i) the cost of production, including organic matrix and calcification, (ii) in mobile species, the cost of transport, and (iii) growth limitation. In marine molluscs, production costs have been computed solely on the organic component of the shell. The energy committed to organic matrix alone ranges from 10% to 60% of that for somatic growth and from 15% to 150% of that for gametes (14–18). If calcification costs were included, the total cost of shell production might increase dramatically. Skeletal transportation costs as a fraction of overall energy budget are unknown, but preliminary data for the marine gastropod *Nucella lamellosa* suggest that the cost of locomotion roughly triples with a doubling of shell weight (A.R.P. and M. LaBarbera, unpublished observations). Finally, in rapidly growing organisms, the rate of skeletal growth may limit the rate of body growth and thus impose a cost in terms of reduced potential for growth. Although documented in a marine gastropod (19), this cost may be relevant only at

near-maximal rates of growth. However, despite their level of mobility or rate of growth, all calcified invertebrates must pay the cost of calcification.

## PROCEDURES

In spite of its importance, the cost of calcification has eluded measurement because it appears only as energy expended in respiration and cannot readily be separated from other metabolic expenditures. I was able to overcome this obstacle by taking advantage of the extensive natural shell variation found in thaidine gastropods. Relative shell weight may vary substantially among nearby populations, with heavier shells generally occurring on quiet-water shores where predation by crabs is more likely (5, 7, 20). Some of this variation among populations may be induced by the scent of crabs or damaged conspecifics (21, 22).

The two previous studies of phenotypic plasticity (21, 22), and an earlier one on growth limitation (19), shared a common protocol: two or three replicate groups of juvenile snails, from each of two populations of differing shell thickness, were allowed to feed on barnacles under various experimental conditions in the field or laboratory. Rates of somatic growth, shell growth, and barnacle consumption were monitored for each group. Although experimental conditions produced large differences, discussed in detail in the original studies (19, 21, 22), small differences remained among replicates (Table 1). These residual differences among replicates permitted the estimate of calcification cost reported here.

## RESULTS AND DISCUSSION

**Calculating the Cost of Calcification.** The cost of calcification was derived from differences among replicate cages, rather than among treatments, to avoid the confounding effects of experimentally induced differences in rates of feeding (in excess of 2-fold in all three experiments, Table 1). For example, gross growth efficiency (energy in tissue growth/energy ingested) can either increase or decrease with rate of feeding depending upon (i) the extent to which metabolism during periods of inactivity renders energy unavailable for growth and (ii) the extent to which assimilation efficiency (energy assimilated/energy ingested) decreases with increased rate of ingestion (26). Presumably, residual differences among replicates arose from natural variation among snails in the rate of shell growth relative to body growth and from random differences among cages.

The cost of calcification was estimated via analysis of residuals among replicate cages (Table 1). In all three experiments, for a given rate of somatic growth, more energy was consumed in those cages where more shell was produced (regressions 5–7, Table 2), although this association only approached statistical significance in experiment 3. Since

The publication costs of this article were defrayed in part by page charge payment. This article must therefore be hereby marked "advertisement" in accordance with 18 U.S.C. §1734 solely to indicate this fact.

Abbreviations: OLS, ordinary least-squares regression; RMA, reduced major axis regression.

Table 1. Initial values, growth rates, and ingestion rates of two species of *Nucella* from three independent experiments used to estimate the cost of calcification

Sample analyzed		Initial value			Average change			Ingestion rate		Residual shell weight change	Residual energy ingested				
<i>Nucella</i>	Treatment condition	Rep	n	Shell length, mm	Body weight, mg	Shell weight, mg	Shell length, mm per snail	Body weight, mg per snail	Shell weight, mg per snail	Barnacles eaten, no. per snail	Energy ingested, J per snail	weight change, mg per snail	energy ingested, J per snail		
<i>Experiment 1</i>															
lm	a	Low	1.00	1	5	25.1 ± 1.01	72.2 ± 8.28	1365 ± 124.3	4.6 ± 1.32	45.7 ± 14.71	894 ± 225.8	35.8	3064	-103.45	-410.68
lm	a	Low	1.00	2	5	26.4 ± 0.34	82.1 ± 5.00	1396 ± 51.2	6.1 ± 0.16	49.1 ± 5.35	1146 ± 28.5	39.6	4021	103.45	410.68
lm	a	Mid	1.00	1	5	25.3 ± 0.91	79.2 ± 10.91	1297 ± 137.3	5.5 ± 0.50	42.8 ± 6.68	936 ± 121.4	26.2	2600	34.95	-128.35
lm	a	Mid	1.00	2	5	24.3 ± 0.77	63.4 ± 3.94	1197 ± 90.9	5.7 ± 0.47	44.5 ± 5.55	946 ± 100.5	31.6	2863	22.02	72.32
lm	a	Mid	1.00	3	5	25.3 ± 0.90	68.2 ± 6.43	1166 ± 141.9	5.5 ± 1.18	44.5 ± 13.01	867 ± 183.6	24.2	2847	-56.98	55.99
lm	b	Low	1.00	1	5	24.5 ± 0.90	65.3 ± 7.33	2046 ± 216.1	4.8 ± 0.73	38.0 ± 7.60	1022 ± 121.9	28.8	2577	-3.35	-136.81
lm	b	Low	1.00	2	5	24.8 ± 0.69	69.7 ± 6.05	2052 ± 167.9	4.9 ± 0.58	42.8 ± 10.42	1088 ± 120.0	31.0	3041	3.35	136.81
lm	b	Mid	1.00	1	4	24.9 ± 0.52	71.8 ± 3.80	2080 ± 160.3	3.2 ± 0.12	21.6 ± 2.48	846 ± 12.0	17.5	1673	107.12	-250.80
lm	b	Mid	1.00	2	5	23.8 ± 0.49	59.0 ± 5.80	1893 ± 129.9	3.2 ± 0.68	19.4 ± 4.75	633 ± 110.6	19.6	1754	-56.21	-87.60
lm	b	Mid	1.00	3	5	23.6 ± 0.86	58.7 ± 7.40	1809 ± 109.7	3.5 ± 0.60	23.6 ± 4.84	756 ± 136.8	27.0	2343	-29.49	338.40
<i>Experiment 2</i>															
lm	c	NC	0.33	1	10	17.6 ± 0.44	23.9 ± 1.62	430 ± 26.6	6.7 ± 0.64	33.5 ± 4.41	601 ± 59.6	20.5	1796	-9.00	-4.77
lm	c	NC	0.33	2	10	17.7 ± 0.55	25.6 ± 2.12	478 ± 45.0	8.2 ± 0.48	45.0 ± 3.37	785 ± 61.4	24.0	2255	9.00	4.77
lm	c	NC	0.67	1	10	17.5 ± 0.50	23.6 ± 2.05	429 ± 36.1	8.5 ± 0.61	53.6 ± 3.78	761 ± 54.2	34.7	3192	28.25	326.97
lm	c	NC	0.67	2	10	17.7 ± 0.57	24.1 ± 2.39	424 ± 42.3	8.8 ± 0.56	63.4 ± 6.05	805 ± 65.1	30.9	2918	-28.25	-326.97
lm	c	FC	0.33	1	10	17.6 ± 0.33	23.0 ± 1.40	419 ± 19.7	6.0 ± 0.59	29.2 ± 4.72	589 ± 69.7	20.8	1921	7.89	-130.49
lm	c	FC	0.33	2	10	17.7 ± 0.49	24.5 ± 2.23	426 ± 37.7	5.7 ± 0.51	29.0 ± 2.77	569 ± 56.0	23.8	2172	-7.89	130.49
lm	c	FC	0.67	1	10	17.7 ± 0.42	25.2 ± 1.85	467 ± 36.3	8.9 ± 0.50	53.3 ± 4.39	942 ± 69.3	29.4	2929	43.53	78.43
lm	c	FC	0.67	2	10	16.9 ± 0.47	20.9 ± 1.71	434 ± 42.9	8.9 ± 0.60	52.9 ± 3.98	850 ± 64.9	31.2	2758	-43.53	-78.43
lm	d	NC	0.33	1	9	17.3 ± 0.48	20.2 ± 1.91	860 ± 93.3	3.5 ± 0.70	22.1 ± 3.55	397 ± 71.6	19.8	1970	11.28	7.75
lm	d	NC	0.33	2	9	17.8 ± 0.45	21.6 ± 1.64	913 ± 81.8	3.0 ± 0.55	23.2 ± 2.36	394 ± 58.6	21.8	1993	-11.28	-7.75
lm	d	NC	0.67	1	9	17.2 ± 0.80	19.3 ± 2.66	832 ± 117.0	6.1 ± 0.50	44.1 ± 4.12	665 ± 56.7	27.6	2610	46.12	-195.48
lm	d	NC	0.67	2	10	17.6 ± 0.57	21.4 ± 2.12	912 ± 95.5	5.0 ± 0.52	38.9 ± 3.01	521 ± 40.1	31.9	2794	-41.51	195.48
lm	d	FC	0.33	1	10	17.8 ± 0.66	22.0 ± 2.09	948 ± 93.4	2.4 ± 0.37	15.1 ± 2.20	364 ± 43.9	15.5	1372	-21.65	-52.47
lm	d	FC	0.33	2	10	17.5 ± 0.52	20.7 ± 2.00	887 ± 73.0	2.7 ± 0.36	16.0 ± 1.28	431 ± 40.9	17.0	1517	21.65	52.47
lm	d	FC	0.67	1	10	17.2 ± 0.66	20.2 ± 1.96	835 ± 106.6	5.9 ± 0.61	35.8 ± 4.63	785 ± 75.1	23.6	2071	34.39	14.41
lm	d	FC	0.67	2	9	17.8 ± 0.61	21.6 ± 2.50	929 ± 103.8	5.1 ± 0.65	36.9 ± 4.32	730 ± 69.3	23.7	2090	-38.21	-14.41
<i>Experiment 3</i>															
lp	e	NC	1.00	1	10	14.8 ± 0.16	32.8 ± 1.33	317 ± 20.6	7.6 ± 0.41	79.0 ± 6.25	1332 ± 113.7	188.7	3646	-0.40	46.40
lp	e	NC	1.00	2	10	15.0 ± 0.16	33.7 ± 1.53	318 ± 15.4	6.6 ± 0.59	69.7 ± 7.87	1191 ± 120.5	188.0	3270	0.40	-46.40
lp	e	FC	1.00	1	9	14.9 ± 0.19	32.8 ± 1.57	333 ± 20.8	7.1 ± 0.59	54.7 ± 5.81	1444 ± 144.7	115.8	2063	-125.19	-52.60
lp	e	FC	1.00	2	10	15.1 ± 0.19	34.7 ± 1.66	333 ± 15.6	7.5 ± 0.40	56.9 ± 4.86	1714 ± 84.8	148.5	2233	112.67	52.55
lp	f	NC	1.00	1	10	21.3 ± 0.23	36.4 ± 1.85	1467 ± 68.6	1.8 ± 0.53	31.1 ± 6.44	529 ± 128.0	108.4	1713	-90.70	-347.74
lp	f	NC	1.00	2	8	21.2 ± 0.17	33.7 ± 1.31	1360 ± 87.9	2.7 ± 0.67	31.1 ± 8.33	735 ± 132.2	164.0	2411	113.38	347.74
lp	f	FC	1.00	1	9	21.2 ± 0.19	35.3 ± 1.35	1402 ± 81.4	1.2 ± 0.39	12.8 ± 3.69	482 ± 102.2	94.4	1303	-71.64	-66.50
lp	f	FC	1.00	2	8	20.8 ± 0.21	34.2 ± 0.99	1271 ± 46.9	2.6 ± 0.69	20.7 ± 5.78	846 ± 196.7	105.4	1677	80.60	66.50

For complete descriptions of procedures, see refs. 19, 21, and 22 for experiments 1–3, respectively. Abbreviations, codes, and derivations are as follows: Sp, species (lm, *Nucella lamellosa*; lp, *N. lapillus*). Po, population (a and b, Turn Rock and False Bay, respectively, San Juan Island, Puget Sound, U.S.A.; c and d, Ross Islets and Grappler Inlet, respectively, Barkley Sound, Vancouver Island, Canada; e and f, Trearddur Bay and Trwyn Y Penrhyn, respectively, Anglesey, Wales, U.K.). Treatment conditions [NC, no crab (laboratory control); FC, fish-crab (snails grown in the laboratory exposed to the scent of crabs fed frozen fish); 0.33, 0.67, and 1.0, snails offered barnacles 2 of 6 days, 4 of 6 days, or continuously; Low and Mid, snails held in cages in the field at 0.0 and +0.61 m tidal height (U.S. datum)]. Rep, replicate cage. n, Number of snails. Initial values, mean ± SE of shell and body traits [shell length, apex to tip of siphonal canal; body weight and shell weight, nondestructive estimates of body ash-free dry weight (AFDW) and shell dry weight using the technique of Palmer (23) and an average value of 0.18 g of AFDW per g of wet weight]. Average change, mean change ± SE in shell length, body AFDW, and shell dry weight per snail, as measured above. Barnacles eaten, total barnacles eaten per snail (experiments 1 and 2, *Balanus glandula*; experiment 3, *Semibalanus balanoides*). Energy ingested, barnacle flesh was converted to joules of energy via regression (see regressions 1 and 2 in Table 2) and assuming 13% ash for *S. balanoides* flesh (24), and a caloric value of barnacle flesh of 22.55 J/mg of AFDW (25) for both species, table entries represent total energy consumed per snail. Residual shell weight change, the amount of extra shell produced per snail relative to that expected for a given change in body weight [computation: for snails in all replicates for a given experimental condition (i.e., species × population × treatment; hence, n varied from 10 to 20), change in shell weight per snail was regressed against change in body wet weight per snail, and values were computed as the average deviation of snails within a replicate from this least-squares linear regression; equations for these 16 regressions are not presented]. Residual energy ingested, the amount of extra energy consumed per snail relative to that expected for a given change in body wet weight per snail [computation: for each species of snail, energy ingested in each replicate (column 13) was regressed against average change in body wet weight for that replicate (column 10; see regressions 3 and 4 in Table 2), and values were computed as the deviations of replicates from this least-squares linear regression where the intercept was determined separately for each experimental condition (i.e., species × population × treatment); because each cage contained multiple snails, individual differences in rates of feeding could not be determined directly; hence, residuals per snail were computed by dividing the cage residual by the number of snails per cage]. Note: data in columns 9–15 are all expressed as totals over the duration of each experiment (31, 76, and 94 days, respectively, for experiments 1–3).

slopes did not differ significantly among experiments ( $P = 0.88$ , analysis of covariance), data were pooled to yield a single relationship ( $P = 0.047$ , regression 8, Table 2; Fig. 1).

The fitting of linear relations to bivariate data must be done with care, particularly where conclusions depend upon the precise value for a single slope rather than upon statistical

Table 2. Regressions used to estimate the cost of calcification

Regression	Slope	Intercept	$r^2$	$n$	$N_r$	$P$
1	$3.206 \pm 0.1519$	$-1.418 \pm 0.0234$	0.943	119	—	<0.001
2	2.954	-1.199	0.870	39	—	<0.001
3	$7.015 \pm 0.9935$	$983.3 \pm 72.42$	0.675	26	—	<0.001
4	$5.405 \pm 1.1191$	$953.5 \pm 170.43$	0.795	8	—	0.002
5	$1.144 \pm 1.2582$		0.094	10	6	0.27
6	$0.725 \pm 1.3398$		0.021	16	8	0.37
7	$1.533 \pm 0.5655$		0.551	8	4	0.13
8	$1.300 \pm 0.5162$		0.165	34	18	0.047
9	$3.196 \pm 2.003, 5.098^*$					

Data are expressed as statistic  $\pm$  SE. Regressions 1–8 are least-squares linear regressions. Regression 1: log body ash-free dry weight ( $y$ , mg) vs. log opercular diameter ( $x$ , mm) for *B. glandula*; rostro-carinal opercular diameter was measured to the nearest 0.1 mm, and barnacle flesh was separated from the skeletal plates, dried to constant weight at 60°C, and ashed for 3 hr at 550°C. Regression 2: log body dry weight ( $y$ , mg) vs. log opercular diameter ( $x$ , mm) for *S. balanoides* [from Burrows and Hughes (27)]. Regressions 3 and 4: energy ingested ( $y$ , J) vs. mean change in body wet weight ( $x$ , mg) for *N. lamellosa* and *Nucella lapillus*, respectively (data from columns 10 and 13 of Table 1). Regressions 5–8: residual energy ingested ( $y$ , J) vs. change in residual shell weight ( $x$ , mg) for, respectively, experiments 1, 2, and 3 and all experiments pooled (data from columns 14 and 15 of Table 1). The intercepts from a residual analysis such as this are zero (e.g., see Fig. 1).  $n$ , Size of sample used to compute regression statistics (slope, intercept,  $r$ ).  $N_r$ , size of sample used to compute  $P$  values (i.e., corrected for degrees of freedom used to estimate residuals).  $P$ , probability values for one-tailed tests of the hypothesis that the slope is greater than zero.

\*Slope from reduced major axis regression based on the same data as regression 8 with lower and upper 95% confidence intervals computed according to McArdle (28).

differences among slopes or intercepts. Substantial controversies in the scaling literature, for example, have arisen purely because inappropriate regression techniques were used to describe coefficients of allometry (29). OLS assumes among other things that all error variation is parallel to the  $y$  axis (29). RMA, the most robust of model II regression procedures (28), acknowledges error variation in both the  $x$  and  $y$  variables. Unlike OLS, RMA regression also has the particularly desirable property that reversing the axes merely inverts the computed slope (i.e.,  $b_{y,x} = 1/b_{x,y}$ ) (30). RMA regression revealed that an extra 3.2 J of energy was ingested per extra mg of shell produced (regression 9, Table 2).

To obtain the cost of calcification, however, both the cost of the organic matrix and the efficiency with which ingested energy is assimilated must be incorporated. The cost of the organic matrix includes (a) the energetic content of the matrix (0.393 J for *Nucella*, Fig. 2), about 10% of the total shell-production cost, and (b) the metabolic cost of synthesizing the matrix. Although not known precisely, differences in this latter cost would have little effect on the estimated cost of calcification (<2%, Fig. 2). In contrast, the estimated cost of calcification is rather sensitive to assumptions about assimilation efficiency (Fig. 2). For logistical reasons, assimilation efficiencies could not be measured in these experiments. Based on the assimilation efficiency reported for *N.*

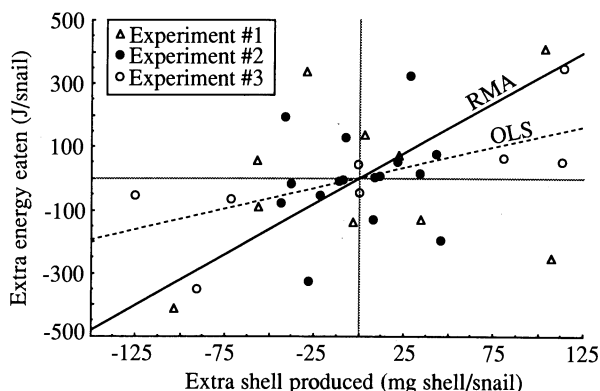


FIG. 1. Association of residual energy consumed as a function of residual shell produced (including the organic matrix) over the duration of each of three different experiments with two species of *Nucella*. Residuals were computed relative to the rate of wet tissue growth (data from columns 14 and 15 of Table 1). OLS, ordinary least-squares regression; RMA, reduced major axis regression.

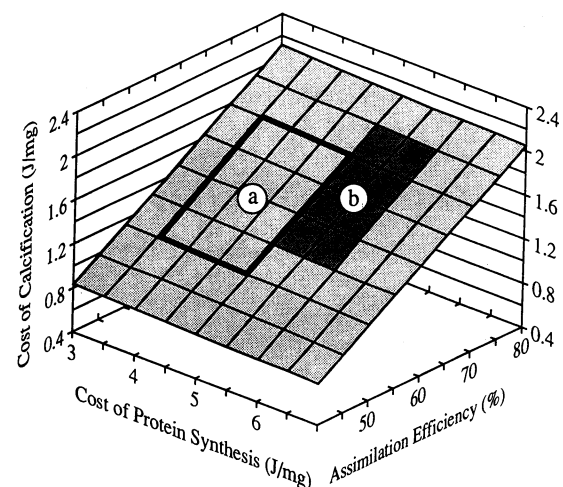


FIG. 2. Illustration of how sensitive the estimated cost of calcification is to assumptions I had to make about (a) assimilation efficiencies (energy assimilated/energy ingested) and (b) the metabolic cost of protein synthesis (J/mg of protein), neither of which is known precisely. The relationship describing the surface in the figure is  $C = (xI - yP - O)/(1 - P)$ , where  $C$  = cost of precipitating 1 mg of  $\text{CaCO}_3$  (J/mg),  $x$  = assimilation efficiency,  $y$  = cost of synthesizing 1 mg of organic matrix (J/mg),  $I$  = extra energy ingested per mg of shell produced (3.196 J/mg from regression 9, Table 2),  $P$  = mg of organic matrix per mg of shell [0.0166 from Palmer (31)], and  $O$  = energy content of organic matrix per mg of shell [0.393 J, assuming 1.66% organic matrix (31), and 23.66 J/mg of protein (32) since the organic matrix of molluscan shells is predominantly protein with a small fraction of amino sugars (33, 34)]. Region a bounds the cost of calcification based upon some less restrictive assumptions: assimilation efficiencies for carnivorous marine gastropods range from 50% to 70% (35) and estimates of the metabolic cost of protein synthesis range from 3.6 to 5.0 J/mg (36–38). Region b bounds the cost of calcification based upon more restrictive assumptions for *Nucella*. The average gross growth efficiency (energy in somatic growth/energy ingested) of  $38.8\% \pm 1.79\%$  [computed across all experiments from data in Table 1 using 24.47 J/mg of ash-free dry weight for *Nucella* tissue (24)] suggests that the estimated assimilation efficiency of  $65.8\% \pm 12.3\%$  for *Nucella* feeding on mussels (39) is reasonable, though perhaps a bit low. Waterlow (38) argues cogently that the estimated metabolic cost of protein synthesis of 3.6 J/mg, based on the cost of peptide bonds, is almost certainly too low. Allowing for costs of amino acid and protein transport, signal peptides, and maintenance of ribosomal machinery, a 50% increase in the cost of synthesis to 5.4 J/mg may be more reasonable.

*lapillus* feeding on mussels (66%) (39), which is well within the range of those reported for carnivorous gastropods (26, 35), and based on a reasonable approximation of the metabolic cost of protein synthesis, the best estimate of calcification cost would be 1–2 J/mg of CaCO<sub>3</sub> (Fig. 2).

**Ecological and Evolutionary Significance.** How biologically significant is this estimated cost of calcification? First, from the perspective of overall energy budgets, the cost of calcification would equal 6% of total respiratory losses but would be equivalent to 75% and 410% of the energy invested in somatic growth and reproduction, respectively, in the rocky shore archeogastropod *Tegula funebris* (14). Second, and perhaps of greater interest, the total cost of CaCO<sub>3</sub> (1–2 J/mg) is considerably less than the total cost of protein (29 J/mg, including the metabolic cost of synthesis), as suggested by a previous study (31). Consequently, although making up only a few percent of molluscan shells by weight (12, 40), the organic matrix would account for 22% of the cost for shell material having only 1.5% organic matrix but nearly 50% of the cost of shell material with 5% organic matrix. This disproportionately high cost of organic matrix may have contributed to the otherwise puzzling evolutionary decline of molluscan shell microstructures with superior mechanical properties but a higher percentage organic matrix (13, 41–45).

Given the apparent saturation of CaCO<sub>3</sub> in surface seawater at low and middle latitudes (40, 46), the low cost of calcification relative to other metabolic costs is not too surprising. The cost of calcification for freshwater and terrestrial molluscs, however, may be much higher.

I thank Jim Thompson for helpful discussions of the cost of protein synthesis and Lois Hammond, Roger Hughes, Tim Rawlings, and Gary Vermeij for critical comments on the manuscript. This research was supported by Natural Sciences and Engineering Research Council Operating Grant A7245.

- Vermeij, G. J. (1978) *Biogeography and Adaptation: Patterns of Marine Life* (Harvard Univ. Press, Cambridge, MA).
- Vermeij, G. J. (1987) *Evolution and Escalation: An Ecological History of Life* (Princeton Univ. Press, Princeton, NJ).
- Kitchell, J. A., Boggs, C. H., Kitchell, J. F. & Rice, J. A. (1981) *Paleobiology* **7**, 533–552.
- Palmer, A. R. (1982) *Paleobiology* **8**, 31–44.
- Kitching, J. A., Muntz, L. & Ebling, F. J. (1966) *J. Anim. Ecol.* **35**, 113–126.
- Boulding, E. G. (1984) *J. Exp. Mar. Biol. Ecol.* **76**, 201–223.
- Palmer, A. R. (1985) *Veliger* **27**, 349–356.
- Robles, C., Sweetnam, D. & Eminike, J. (1990) *Ecology* **71**, 1564–1577.
- Palmer, A. R. (1979) *Evolution* **33**, 697–713.
- Wainwright, P. C. (1987) *J. Zool. (London)* **213**, 283–297.
- Meyer, A. (1989) *Oecologia* **80**, 431–436.
- Wilbur, K. M. & Saleuddin, A. S. M. (1983) in *The Mollusca: Physiology*, eds. Saleuddin, A. S. M. & Wilbur, K. M. (Academic, New York), Part 1, pp. 235–287.
- Currey, J. D. (1988) in *The Mollusca: Form and Function*, eds. Trueman, E. R. & Clarke, M. R. (Academic, New York), pp. 183–210.
- Paine, R. T. (1971) *Limnol. Oceanogr.* **16**, 86–98.
- Dame, R. F. (1976) *Estuarine Coastal Mar. Sci.* **4**, 243–253.
- Hibbert, C. J. (1977) *Mar. Biol.* **44**, 71–76.
- Griffiths, C. L. & King, J. A. (1979) *Mar. Biol.* **53**, 217–222.
- Vahl, O. (1981) *J. Exp. Mar. Biol. Ecol.* **53**, 297–303.
- Palmer, A. R. (1981) *Nature (London)* **292**, 150–152.
- Kitching, J. A. & Lockwood, J. (1974) *Mar. Biol.* **28**, 131–144.
- Appleton, R. D. & Palmer, A. R. (1988) *Proc. Natl. Acad. Sci. USA* **85**, 4387–4391.
- Palmer, A. R. (1990) *Hydrobiologia* **193**, 155–182.
- Palmer, A. R. (1982) *Malacologia* **23**, 63–73.
- Paine, R. T. (1964) *Ecology* **45**, 384–387.
- Wu, R. S. S. & Levings, C. D. (1978) *Mar. Biol.* **45**, 225–235.
- Bayne, B. L. & Newell, R. C. (1983) in *The Mollusca: Physiology*, eds. Saleuddin, A. S. M. & Wilbur, K. M. (Academic, New York), Part 1, pp. 407–515.
- Burrows, M. T. & Hughes, R. N. (1990) *J. Anim. Ecol.* **59**, 723–742.
- McArdle, B. H. (1988) *Can. J. Zool.* **66**, 2329–2339.
- LaBarbera, M. L. (1989) *Annu. Rev. Ecol. Syst.* **20**, 97–117.
- Sokal, R. R. & Rohlf, F. J. (1981) *Biometry* (Freeman, San Francisco).
- Palmer, A. R. (1983) *Mar. Biol.* **75**, 287–292.
- Crisp, D. J. (1971) in *Methods for the Study of Marine Benthos*, IBP Handbook No. 16, eds. Holmes, N. A. & McIntyre, A. D. (Blackwell, Edinburgh), pp. 197–323.
- Degens, E. T., Spencer, D. W. & Parker, R. H. (1967) *Comp. Biochem. Physiol.* **20**, 553–579.
- Lowenstam, H. A. & Weiner, S. (1989) *On Biomineralization* (Oxford Univ. Press, Oxford).
- Hughes, R. N. (1986) *A Functional Biology of Marine Gastropods* (Johns Hopkins Univ. Press, Baltimore).
- Webster, A. J. F. (1976) in *Meat Animals: Growth and Productivity*, eds. Lister, D., Rhodes, D. N., Fowler, V. R. & Fuller, M. F. (Plenum, New York), pp. 89–102.
- Webster, A. J. F. (1981) *Proc. Nutr. Soc.* **40**, 121–128.
- Waterlow, J. C. (1984) *Q. J. Exp. Physiol.* **69**, 409–438.
- Bayne, B. L. & Scullard, C. (1978) *J. Exp. Mar. Biol. Ecol.* **32**, 113–128.
- Milliman, J. D. (1974) *Marine Carbonates* (Springer, New York).
- Taylor, J. D. & Layman, M. (1972) *Paleontology* **15**, 73–87.
- Taylor, J. D. (1973) *Paleontology* **16**, 519–534.
- Currey, J. D. (1974) *J. Zool. (London)* **173**, 395–406.
- Currey, J. D. (1977) *Proc. R. Soc. London Ser. B* **196**, 443–463.
- Vermeij, G. J. (1989) *Palaos* **4**, 585–589.
- Li, Y. H., Takahashi, T. & Broecker, W. S. (1969) *J. Geophys. Res.* **74**, 5507–5525.