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Relative cost of producing skeletal organic matrix versus calcification: evidence from marine gastropods

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Abstract

Rates of shell regeneration in 15 species from all three suborders of prosobranch gastropods were related inversely to percent organic matrix of the shell. Since the gastropods in these experiments were not fed and therefore forced to rely upon stored energy reserves while regenerating, this inverse relationship suggests that the production of skeletal organic matrix is more demanding metabolically than the crystallization of calcium carbonate. Such a relationship between the organic and inorganic components of carbonate skeletons may help explain the evolutionary loss of skeletal microstructures with a high percent organic matrix in several major invertebrate groups.

Introduction

Skeletal growth in aquatic invertebrates is usually thought to occur at the expense of tissue growth and reproduction, hence the presumed advantage to skeletons of economical design (Taylor, 1973; Currey and Taylor, 1974; Vermeij, 1978; Highsmith 1979; Palmer, 1979, 1981). The evolutionary significance of such a trade-off, however, clearly depends upon the magnitude of the cost of skeleton production. This cost remains to be measured in its entirety (Taylor and Layman, 1972; Simkiss, 1976; Rachootin, 1979; Vincent, 1982).

Skeletons of marine invertebrates, with the possible exception of echinoderms (Raup, 1966; O'Neill, 1981), are composed of two structural elements: inorganic crystals, usually of calcium carbonate, and an organic matrix within and between crystals (Watabe and Wilbur, 1976; Rhoads and Lutz, 1980; Nakahara *et al.*, 1981; Wheeler *et al.*, 1981). Numerous estimates have been made of the fraction of the energy budget devoted to skeletal organic matrix in marine invertebrates including: serpulid polychaetes (Dixon, 1980), balanomorph barnacles (Wu and Levings, 1978), mytiloid (Kuenzler, 1961; Dame, 1972; Bernard, 1973; Griffiths and King, 1979; Rodhouse, 1979; Vahl, 1981), unionoid (Cameron *et al.*, 1979) and veneroid (Hughes, 1970; Mohlenberg and Kiorboe, 1981) bivalves, and prosobranch gastropods (Paine, 1971a). The energetic cost associated with calcium carbonate precipitation, however, has remained a persistent unknown. I report here evidence obtained from 15 species of marine prosobranch gastropods, that suggests that organic matrix is the metabolically more demanding component of shell material to produce: species with a higher fraction of skeletal organic matrix regenerated less shell material per day in the absence of feeding than those with a lower fraction. A comparatively high cost of the organic matrix component may have been an important factor influencing the evolutionary loss of crystal microstructures with a high fraction of organic material in several groups of marine invertebrates: the Brachiopoda (Williams and Rowell, 1965), and both the Gastropoda and the Bivalvia (Hare and Abelson, 1965; Taylor and Layman, 1972; Taylor, 1973; Carter, 1980; Rosenberg, 1980).

Material and methods

Gastropods of 15 species (Table 1) were collected from the vicinity of Bamfield Marine Station, on the west coast of Vancouver Island, (Bamfield, British Columbia, Canada, Lat. 48°50′N, Long. 125°08′W) and returned to the laboratory where they were numbered individually using Brady Wire Markers (W. H. Brady Co., Rexdale, Ontario, Canada) coated with a clear cement (Dekophane, Rona Pearl Corp, Bayonne, NJ, USA). Shell length was measured from the apex to the anterior-most edge of the aperture except for archeogastropods; limpet shell length

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was measured from the anterior to the posterior edge of the aperture, trochid and turbinid shell sizes were measured as maximum body whorl diameter across the axis of coiling starting at the lip of the aperture (all measurements to 0.1 mm with Vernier calipers). Live gastropods were weighed with a Mettler PK300 balance to the nearest mg while suspended in seawater to estimate shell weight; weight suspended in seawater, with the appropriate regressions, provides a very accurate estimate of shell dry weight ($r^2 > 0.999$; Palmer, 1982).

To measure relative rates of regeneration, collections of each species examined were divided into two treatment groups. In the first group, a portion of the aperture of each gastropod (approximately ¼ to ⅓ of the body whorl) was broken away with point-nosed pliers to simulate shell damage. Individuals in the second group were treated identically to those in the first, but they were not damaged and therefore served as a control. Within 12 h of damage, all individuals of both damaged and undamaged groups were weighed underwater to provide initial estimates of shell weight (Palmer, 1982). They then were held continuously immersed without food in plastic freezer containers with plastic mesh sides in running seawater aquaria for the duration of the experiments. All individuals were reweighed underwater at the end of the experiments to estimate the amount of new shell material produced. The

Table 1. Mean shell sizes, shell weights, amount of shell removed and regenerated, and percent organic matrix for 15 species of prosobranch gastropods. Values in parentheses are standard errors except for % organic matrix which are standard errors followed by the number of samples ashed. Treatment = experimental treatment (u = undamaged, d = damaged). n = sample size. Shell lengths were measured before damage. Undamaged immersed weight refers to the weight of live individuals suspended in seawater prior to any shell alteration. Percent new shell produced was calculated as the cumulative increase in immersed weight after damage divided by the initial, undamaged immersed weight × 100. Days = total days over which each species was allowed to produce new shell material. The percent shell regenerated per day was calculated by subtracting the percent shell produced by undamaged individuals from that produced by damaged ones and dividing the remainder by the number of days over which regeneration took place. For *Diodora aspera,* since none were examined, I have assumed that the percent new shell produced was 0 for undamaged individuals (average for the remaining archeogastropods was actually 0.15) to calculate the percent shell regenerated per day

Species	Treatment	n	Shell length (mm)	Undamaged immersed weight (g)	% shell removed	% new shell produced	Days	% Shell regen. per day	% organic matrix
Archeogastropoda									
Collisella digitalis	u	2	17.0 (0.65)	0.29 (0.062)	–	−0.72 (0.153)	39	0.071	2.89 (0.460,4)
	d	4	17.3 (0.81)	0.26 (0.032)	22.8 (2.00)	2.03 (0.576)			
Diodora aspera	u	0	–	–	–	–	39	0.064	2.58 (0.110,3)
	d	2	33.1 (3.55)	1.45 (0.565)	21.2 (0.37)	2.48 (0.447)			
Homolapoma luridum	u	4	8.3 (0.15)	0.13 (0.008)	–	1.01 (1.008)	39	−0.033	4.42 (0.342,4)
	d	8	8.3 (0.18)	0.14 (0.010)	21.8 (1.93)	−0.27 (0.350)			
Tegula funebralis	u	5	16.9 (2.08)	1.34 (1.509)	–	−0.06 (0.429)	35	0.035	4.43 (0.275,2)
	d	16	13.9 (0.46)	0.63 (0.062)	20.3 (1.40)	1.15 (0.318)			
T. pulligo	u	5	17.9 (0.60)	1.06 (0.048)	–	0.35 (0.470)	29	−0.030	4.10 (0.451,3)
	d	12	17.7 (0.31)	1.14 (0.045)	15.3 (1.00)	−0.52 (0.217)			
Mesogastropoda									
Littorina scutulata	u	4	12.9 (0.39)	0.22 (0.032)	–	−1.07 (0.252)	39	0.024	3.08 (0.508,3)
	d	13	13.2 (0.45)	0.26 (0.031)	13.6 (1.22)	−0.14 (0.275)			
L. sitkana	u	3	15.1 (1.76)	0.45 (0.131)	–	0.47 (0.328)	39	0.059	2.68 (0.402,5)
	d	11	14.3 (0.78)	0.35 (0.045)	20.5 (1.17)	2.78 (0.789)			
Opalia chacei	u	1	18.4 (–)	0.21 (–)	–	0.48 (–)	39	0.193	2.53 (0.475,2)
	d	4	18.3 (1.34)	0.22 (0.037)	21.6 (2.26)	8.02 (2.025)			
Neogastropoda									
Amphissa columbiana	u	3	16.1 (0.98)	0.21 (0.045)	–	8.05 (3.557)	39	0.158	2.54 (0.188,6)
	d	7	17.3 (0.68)	0.22 (0.037)	25.4 (3.08)	14.21 (2.787)			
Ceratostoma foliatum	u	2	40.1 (3.30)	2.95 (0.607)	–	−0.37 (0.280)	29	0.057	2.14 (0.486,4)
	d	4	39.7 (2.94)	2.93 (0.656)	33.5 (1.54)	1.27 (0.350)			
Ocenebra interfossa	u	1	17.0 (–)	0.37 (–)	–	−0.27 (–)	39	0.048	2.86 (0.421,4)
	d	4	16.6 (2.38)	0.33 (0.124)	22.6 (3.16)	1.62 (0.944)			
O. lurida	u	2	15.8 (1.20)	0.24 (0.052)	–	1.89 (0.842)	39	0.132	3.16 (0.601,4)
	d	8	16.5 (0.70)	0.29 (0.033)	19.1 (1.51)	7.05 (1.498)			
Searlesia dira	u	10	26.3 (1.03)	1.20 (0.196)	–	5.30 (0.515)	53	0.018	2.09 (0.058,3)
	d	40	25.1 (0.56)	1.01 (0.081)	14.4 (0.78)	6.24 (0.275)			
Thais emarginata	u	5	17.3 (0.67)	0.25 (0.037)	–	7.90 (3.320)	35	0.369	1.66 (0.106,4)
	d	17	16.7 (0.28)	0.23 (0.015)	26.6 (1.08)	20.82 (2.537)			
T. lamellosa	u	8	31.0 (2.45)	2.84 (0.607)	–	2.37 (0.953)	35	0.126	1.56 (0.052,3)
	d	29	30.3 (1.33)	2.57 (0.273)	20.5 (0.95)	6.78 (0.974)			

experiments were conducted during June, July and August of 1980 and 1981 at the Bamfield Marine Station, during which time seawater temperatures ranged from 12.5° to 14.3 °C.

Percent organic matrix was measured as the weight loss of dried shell after ashing (Vinogradov, 1953; Paine, 1971b). At the termination of the experiment, gastropods were killed by freezing, allowed to decompose partially in tap water, and removed from the shell. After decomposition of any residual tissue was complete (1 to 3 wk), the shells were rinsed for 30 to 60 s in a 5% sodium hypochlorite solution to try to remove any adsorbed organic film, rinsed again in tap water, and then dried at room temperature (ca 21 °C). Prior to ashing, shells were ground to a fine powder with a mortar and pestle, placed in preroasted, pre-weighed aluminum trays, and oven-dried to constant weight at 60° to 70 °C. For species with small shells, the entire shell was pulverized; for larger species only the first ½ to ⅔ of the body whorl was powdered to avoid introducing errors associated with weathering, or fungal or algal infection of older shell (Rasmussen, 1973). Weight losses after ashing of samples of older shell material taken from the same individuals exhibited considerable variation within and among species: older shell material sometimes lost more weight than more recent shell, but sometimes less. When more than one ash sample was taken from a single shell, only the result for the most recently produced shell was used. Before and after ashing, trays and their contents were weighed to the nearest 0.05 mg with a Mettler B6 analytical balance. The trays were then placed in a muffle furnace at room temperature (ca 21 °C) which was subsequently set at 550 °C, and turned on. Ash weights were measured two hours after the furnace had reached equilibrium temperature (60 min after switching on). Preliminary tests indicated that two hours (plus the 1 h warmup) was the optimum time to achieve maximal combustion of organic material with minimal conversion of $CaCO_3$ to CaO (Palmer, unpublished data).

Results

Individuals of nearly all species continued to produce shell material whether damaged or not, even though they were not feeding (Table 1). In addition, for most species, individuals with damaged shells produced more shell material than individuals with undamaged shells, a pattern noted in other invertebrates including scleractinian corals (Loya, 1976), ostreid bivalves (Loosanoff and Nomejko, 1955) and pulmonate gastropods (Wilbur, 1973). Of particular interest, the amount of additional shell material produced by regenerating gastropods decreased significantly with increasing skeletal organic matrix content ($r=0.62$, $P=0.015$; Fig. 1). Decreased regeneration with higher percent of organic matrix was also apparent within each prosobranch suborder although sample sizes were too small to demonstrate significance (Fig. 1). There was no

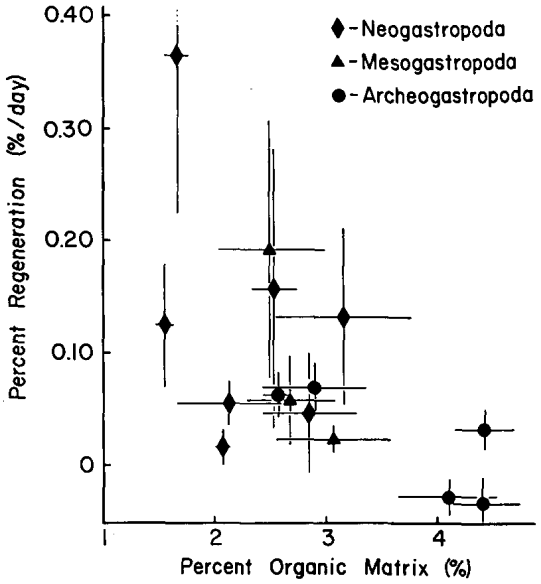

Fig. 1. Relation between mean percent of shell material regenerated per day by damaged individuals and mean percent skeletal organic matrix (actual values and sample sizes in Table 1). Error bars correspond to ± one standard error; when not present they are less than the distance across the symbol

significant association among species between the percent of additional shell regenerated by damaged gastropods and (a) initial shell weight ($r=0.15$, $P=0.59$), (b) relative shell weight (log shell wt/shell length; $r=0.38$, $P=0.17$), or (c) percent shell removed ($r=0.41$, $P=0.13$); thus differences in initial size, relative shell weight or degree of damage inflicted were not responsible for the above pattern. Minor weight losses by some species (≦ 1%) probably reflect a combination of minor shell erosion, and tissue weight loss since tissue weight represents a small but measurable portion of immersed weight (< 5%; Palmer, 1982).

Discussion

The energetics of skeleton production in marine invertebrates has proven to be a vexing problem. The primary difficulty is that while direct measurements can be made of the caloric content of the organic matrix (Kuenzler, 1961; Hughes, 1970; Paine, 1971a; Dame, 1972; Bernard, 1973; Wu and Levings, 1978; Cameron *et al.*, 1979; Griffiths and King, 1979; Rodhouse, 1979; Dixon, 1980; Mohlenberg and Kiorboe, 1981; Vahl, 1981), the mineralized portion of the skeleton has no caloric value. To estimate the total cost of skeleton production, it is thus necessary to measure not only the caloric content of the organic matrix but also the energy expended metabolically in both synthesis of the matrix and precipitation of the mineralized component. This latter component, the metabolic energy expended in skeleton formation, has eluded measurement.

Starving gastropods were used in the regeneration experiments to estimate this metabolic expenditure, since they would have been forced to draw to a large extent

upon reserves to produce new shell. These reserves would have been consumed both as a source of materials (amino acids and amino sugars; Degens *et al.*, 1967) and as a source of metabolic energy for protein synthesis and calcification. By subtracting new shell material produced by undamaged individuals from that produced by damaged individuals (Table 1, Fig. 1), differences among species in rates of shell production due to (a) possible differences in physiological condition at the beginning of the experiment, or (b) possible differences in ability to utilize dissolved organic material (Manahan *et al.*, 1982) or surface microflora, could be scaled out. Both damaged and undamaged individuals of each species should have been able to take advantage of any such supplemental energy sources equally.

Since there is probably a strong selective advantage to replacing lost skeletal material rapidly (Loosanoff and Nomejko, 1955; Wilbur 1973; Loya, 1976) and regaining lost living space, all species should have regenerated as much of the lost shell as possible. However, species whose shells contained a lower fraction of organic material regenerated significantly more shell than those with a high fraction (Fig. 1). This relationship suggests that the two structural components of molluscan shells, organic matrix and crystals of calcium carbonate, are not equally demanding to produce metabolically.

Three interpretations of this relationship are possible. First, shell regeneration may have required organic compounds (amino acids or amino sugars; Degens *et al.*, 1967) in limited supply during the experiment because the gastropods were not being fed. Starving gastropods appear to rely in part on protein catabolysis for metabolic energy (Stickle and Duerr, 1970; Stickle and Bayne, 1982), thus amino acids may have been required for other metabolic needs. However, even fed gastropods would experience a demand for amino acids for tissue growth and reproduction, thus from the standpoint of fitness amino acids are probably always in short supply. Unfortunately, the possibility that particular amino acids necessary for synthesizing organic matrix were in disproportionately short supply cannot be ruled out entirely with the present data. Second, there may have been a limit to the *rate* at which the organic matrix could be produced, thus species with a higher percent organic matrix could not have regenerated shell as rapidly. Elsewhere, I have demonstrated the existence of an upper limit to the rate of shell growth that may limit the maximum rate of body growth (Palmer, 1981), but the actual cause of this upper limit, either the rate of synthesis of organic matrix or the rate of growth of crystals of calcium carbonate, remains to be determined experimentally. More important to the present argument, however, absolute rates of shell production during regeneration were less than the maximum rates of shell production observed in fed individuals (Palmer, unpublished data), thus it seems unlikely that the rate of protein synthesis would have been limiting. Third, the energetic cost of protein synthesis may have been higher than the energetic cost of mineralization, thus gastropods with a higher percent organic matrix may have regenerated less total shell while starving because of the greater drain on energy reserves. Preliminary, direct measurements of the cost of calcification support this third interpretation: the cost of calcification appears to be less than $1/7$ to $1/30$ that of protein synthesis (Palmer, unpublished).

An important assumption implicit to the above experimental approach is that regenerated shell material is comparable in organic matrix composition to normal shell material. Regenerated shell in some species of marine invertebrates, although exhibiting similar general organization, differs from normal shell in microstructural detail [*e.g.* nautiloid cephalopods (Meenakshi *et al.*, 1974), pteriomorph (Meenakshi *et al.*, 1973) and paleoheterodont (Tsujii, 1976) bivalves]. However, these studies examined regeneration well back from the normal growing edge of the shell, and differences in regenerated shell were very likely a reflection of changes in the generative capacity of medial compared to marginal mantle tissue, rather than a direct result of regeneration *per se*. Studies of marginal shell repair in prosobranch gastropods (Andrews, 1935; Geller, 1982) have revealed little if any difference between normal and regenerated shell except for a brief disruption of the continuity of shell layers at the point of breakage. Even if some differences do exist between normal and regenerated shell produced at the margin of the aperture, the qualitative conclusion about the relative metabolic importance of skeletal organic matrix in prosobranch gastropods is justified if a less stringent assumption is valid. If the differences among species in the percent organic matrix of regenerated shell parallel the differences in the percent organic matrix of normal shell, the same result would obtain.

If confirmed for other invertebrate groups, the relatively high cost of organic matrix may be one reason for the independent, evolutionary loss of crystal microstructures with a high percent of organix matrix. A well known evolutionary trend in the Brachiopoda is the disappearance in the lower Paleozoic of many groups having chitinophosphatic skeletons (Williams and Rowell, 1965). The chitinophosphatic skeletons of modern species of brachiopods have a much higher proportion of organic material than the calcareous skeletons of their contemporaries. In both the Gastropoda and the Bivalvia, there is a repeated evolutionary tendency to lose nacre and prismatic microstructures from the shell (Hare and Abelson, 1965; Taylor and Layman, 1972; Taylor, 1973; Carter, 1980; Rosenberg, 1980). Both these microstructures have a higher percent organic matrix than other common microstructures in molluscan shells (Taylor and Layman, 1972). This evolutionary trend was considered enigmatic because of nacre's superior mechanical properties (Currey and Taylor, 1974; Currey, 1977), but is less surprising if the organic matrix is disproportionately expensive to produce.

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