

Adaptive Value of Shell Variation in *Thais lamellosa*: Effect of Thick Shells on Vulnerability to and Preference by Crabs

by

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Abstract. Laboratory experiments with the predatory shallow-water crab *Cancer productus* revealed that thin-shelled individuals of the morphologically variable prosobranch gastropod *Thais lamellosa* (Gmelin, 1791) (= *Nucella lamellosa*; Muricacea; Thaididae) were significantly more likely to be eaten than thicker shelled individuals. Three of five crabs of different sizes (8.0-16.5 cm carapace width) were able to eat the largest thin-shelled snail offered (>45 mm shell length) over a period of 55 days. However, only the largest crab ate more than 10% of the thick-shelled snails offered over this same time period, and it was also able to eat the largest thick-shelled snail available (44.6 mm); hence, thick shells did not guarantee immunity from predation. Significantly, the few snails eaten from the "thick-shelled" population by the remaining four smaller crabs averaged nearly two standard deviations (mean = 1.99) lighter than the mean for animals of comparable length from that population, revealing that individuals further from the mean were selected against. The time sequence of consumption suggested that motivational state strongly influenced whether a crab attacked thick-shelled snails successfully: for all but one crab, thick-shelled snails were not consumed until more than 50% of the thin-shelled individuals had been eaten.

The adaptive value of thick shells appears to result from two factors: (1) a decrease in the range of sizes of crabs to which a snail of a given body size is ultimately vulnerable, and (2) a decrease in the desirability of snails to the larger crabs to which they are still vulnerable. Variation in shell thickness probably persists in *Thais lamellosa*, however, because thinner shells are favored in the absence of crabs: they are less expensive to produce and to transport, and they permit more rapid growth when food is abundant.

INTRODUCTION

THE SHELLS OF *Thais lamellosa* (= *Nucella lamellosa*) are among the most variable of those of prosobranch gastropods from the Pacific coast of North America; they vary extensively in color, banding, sculpture, thickness, and shape (ABBOTT, 1974; KINGAID, 1957; KITCHING, 1976; SPIGHT, 1973, 1976). The variation in shell sculpture and thickness is perhaps the most dramatic; it is often correlated with habitat, and the mean phenotype of populations can change dramatically over distances as short as a few hundred meters (Palmer, unpublished). The adaptive value of shell variation in this species, however, has not been addressed experimentally. Because increased shell thick-

ness in *T. lamellosa* is often associated with habitats in which crabs, in particular *Cancer productus*, are abundant, I examined the effectiveness of thick shells as deterrents to this shell-breaking predator (ZIPSER & VERMEIJ, 1978). In addition, because larger crabs generally are capable of eating larger gastropods (VERMEIJ, 1978), I examined the relationship between crab size and relative vulnerability of thin- versus thick-shelled snails.

METHODS

Thais lamellosa of two substantially different shell morphologies (comparable to illustrations 1905 and 1908 of ABBOTT, 1974) were collected in early February from two

Table 1

Offered sizes, eaten sizes, and "critical sizes" (defined in text) at the termination of the experiment, of thin- and thick-shelled *Thais lamellosa* for each of the five *Cancer productus* used in the experiments. Crab sizes are carapace widths. Twenty-one snails were offered initially in each group, eaten snails were not replaced. Question marks following critical sizes indicate unrepresentative values because many smaller snails were available but not eaten.

Crab size (cm)	Shell form	<i>Thais lamellosa</i> shell length (mm)				n	Final "critical size" (mm)
		Offered		Eaten			
		Small-est	Larg-est	Small-est	Larg-est		
8.0	Thin	23.5	46.9	23.5	39.3	18	42.9
	Thick	20.1	46.2	22.8	22.8	1	24.0?
9.1	Thin	21.0	45.5	21.0	45.5	21	>45.5
	Thick	21.4	42.4	29.4	29.4	1	29.5?
9.2	Thin	21.3	48.0	21.3	48.0	21	>48.0
	Thick	20.2	46.0	20.0	46.0	2	>46.0?
13.5	Thin	21.8	52.8	21.8	52.4	20	52.6
	Thick	19.5	50.7	—	—	0	<19.5
16.5	Thin	22.7	54.8	22.7	54.8	21	>54.8
	Thick	21.5	44.6	21.5	44.6	20	>44.6

different habitats on San Juan Island, Washington (USA). Thin-shelled, strongly sculptured individuals were collected at low tide from an isolated, offshore rock surrounded by deep water and swept by strong tidal currents (Turn Rock, 48°32'N, 122°58'W), and thick-shelled, smooth individuals were collected from rocky substrata in quiet water surrounded by a muddy bottom near the east shore inside the mouth of False Bay (48°29'N, 123°04'W). The snails were numbered individually (PALMER, 1980), and measured for shell length (apex to tip of siphonal canal) to 0.1 mm with vernier calipers. To estimate shell weight, live animals were immersed in seawater, and immersed weights were converted to shell dry weights using the regression: shell dry weight (g) = 1.572 immersed weight (g) + 0.0162 ($r^2 = 0.9998$; from PALMER, 1982). To measure the body size of the animals (excluding the shell), tissue wet weight was also estimated for a subsample from each population by subtracting estimated shell weight from the whole weight of the animals in air (PALMER, 1982).

Five specimens of *Cancer productus* of different sizes (8.0–16.5 cm carapace width) were collected, from False Bay, during nighttime low tides over several weeks prior to the experiments. Each specimen was placed individually into shallow concrete seawater trays (30 × 50 × 15 cm) supplied with running seawater at the Friday Harbor Laboratories, Friday Harbor, Washington (USA). These trays were adjacent to a south-facing window, and no

attempt was made to regulate lighting conditions. I did not attempt to standardize hunger levels of the crabs prior to the experiments, but over the duration of the experiments the only food available to the crabs was the introduced snails. Water temperatures ranged from 6.5 to 7.7°C.

The experiments were initiated by introducing simultaneously into each aquarium 21 snails of a comparable size range for each shell type (Table 1). The behavior of the crabs was observed closely over the first five and one-half hours to evaluate their initial responses to the snails; these observations were not continued on subsequent days because feeding activity was too unpredictable. Snails crawling up the sides of the aquaria were knocked back onto the bottom daily for the first two weeks, and every two to four days for the remainder of the experiment to ensure their availability to the crabs. Both dislodged and attached snails were equally likely to be attacked by a crab. The snails remaining in each aquarium were noted nine times over the next 55 days (Feb. 12–April 3). Following each enumeration, the bottoms of the aquaria were siphon-vacuumed to collect all shell fragments, and the fragments were examined for the presence of numbered tags to verify that missing snails had in fact been eaten. Of the 210 snails used in these experiments, only one disappeared without being eaten, and one died from other causes; these were not included in the analyses.

Regression lines were compared using analysis of covariance (ANCOVA), and differences among expected means were compared using the appropriate standard errors (SOKAL & ROHLF, 1981).

RESULTS

Differences in shell weight between the two populations of *Thais lamellosa* were highly significant: for animals of the same shell length, those from False Bay ranged from 50 to 100% heavier with increasing size (shell weight for the False Bay population was significantly higher for all positive shell lengths [$P < 0.001$, comparison of predicted mean weights from shell length for both populations]), and larger animals had proportionally heavier shells (the slope for the thick-shelled population was significantly higher than that for the thin-shelled one [$P < 0.001$, ANCOVA; Figure 1a]). For both populations, the slopes were significantly less than 3.0 ($P < 0.001$; Figure 1a), revealing a negative allometry in each. Rather curiously, in spite of the differences in shell weight, the tissue weights of animals of the same shell length did not differ between the two populations ($P > 0.45$; Figure 1b); hence, the body size of animals from both populations could be predicted from the same regression on shell length. Geometrically, this means that the shells of individuals from the thick-shelled population were wider for a given length.

Initial feeding activity varied rather markedly among crabs. During five and one-half hours of continuous observation on the first day of the experiment, two of the crabs (8.0 and 16.5 cm carapace width) did not even at-

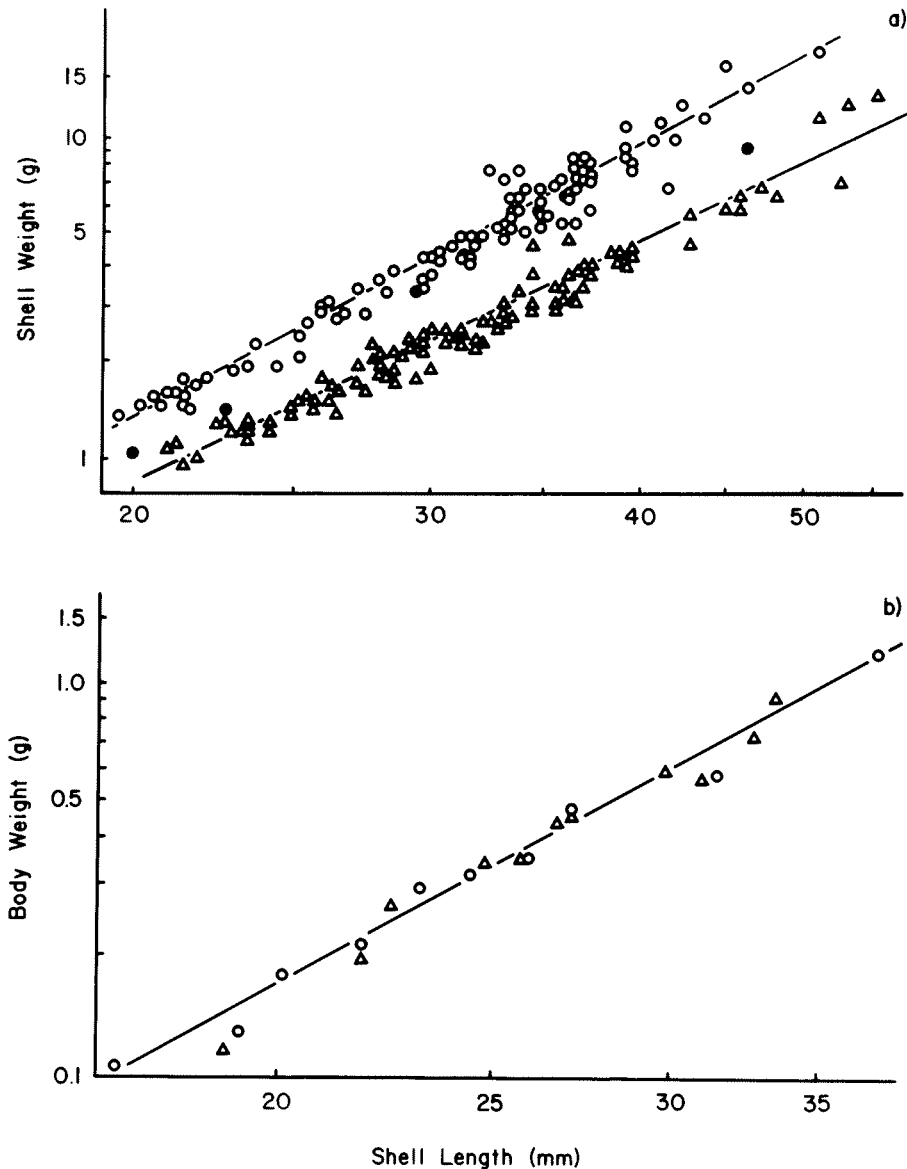


Figure 1

The relationships with shell length of shell weight (a) and body wet weight (b) for a thick- (circles) and a thin-shelled (triangles) population of *Thais lamellosa*. Solid circles in (a) indicate individuals eventually consumed by the smaller four crabs (see text). In (a), the regressions (\pm SE) of log shell weight (Y) on log shell length (X) for the two populations were: thick-shelled population, $Y = 2.787(\pm 0.060)X - 3.5030(\pm 0.006)$, $N = 106$, $r^2 = 0.953$; thin-shelled population, $Y = 2.450(\pm 0.050)X - 3.2588(\pm 0.005)$, $N = 106$, $r^2 = 0.958$. These slopes were significantly different ($P < 0.001$, ANCOVA). In (b) $\log(\text{body wet weight}) = 3.1904(\pm 0.105)\log(\text{shell length}) - 4.9279(\pm 0.009)$ (both populations combined; neither the slopes nor the adjusted means from ANCOVA were significantly different between populations [$P = 0.45$ and $P = 0.79$ respectively]).

tempt to eat any snails and one (13.5 cm) only investigated two thick-shelled snails but did not attempt to break their shells. A fourth crab (9.2 cm) attacked two thin- and three thick-shelled snails; it consumed one, and badly damaged the shell of the other thin-shelled individual, but it was unable to inflict any damage on the three thick-shelled

animals. In contrast, the fifth crab (9.1 cm) attacked and consumed five thin-shelled snails, and attacked two thick-shelled individuals unsuccessfully.

Differences in feeding behavior among crabs persisted for the first two weeks of the experiment (Figure 2). Within eight days of the start of the experiments, three of the five

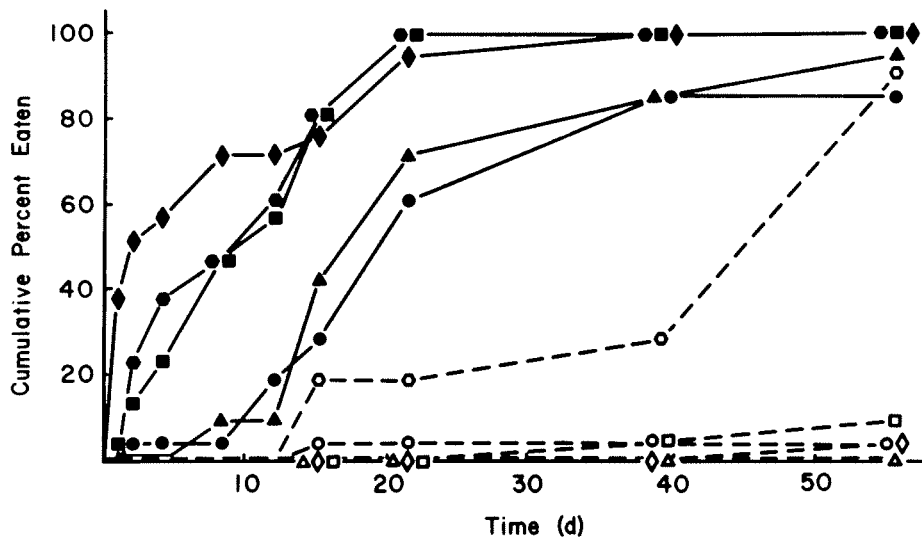


Figure 2

Cumulative percent of thick- and thin-shelled *Thais lamellosa* consumed as a function of time by each of five crabs. Solid symbols with solid lines: snails from the thin-shelled population. Open symbols with dashed lines: snails from the thick-shelled population. Different symbols correspond to crabs of different carapace widths: circles, 8.0 cm; diamonds, 9.1 cm; squares, 9.2 cm; triangles, 13.5 cm; hexagons, 16.5 cm.

specimens of *Cancer productus* had eaten nearly 50% of the thin-shelled *Thais lamellosa*. The remaining two did not consume that many of the thin-shelled form until after two weeks had elapsed.

In spite of the variation in feeding behavior among crabs,

snails of the two different shell types were consumed at significantly different rates (Figure 2; thin = 0.36 snails/day, thick = 0.09 snails/day; $P = 0.025$, Mann-Whitney U-test). Only the largest crab (16.5 cm carapace width) ate many of the thick-shelled form; after 55 days it had

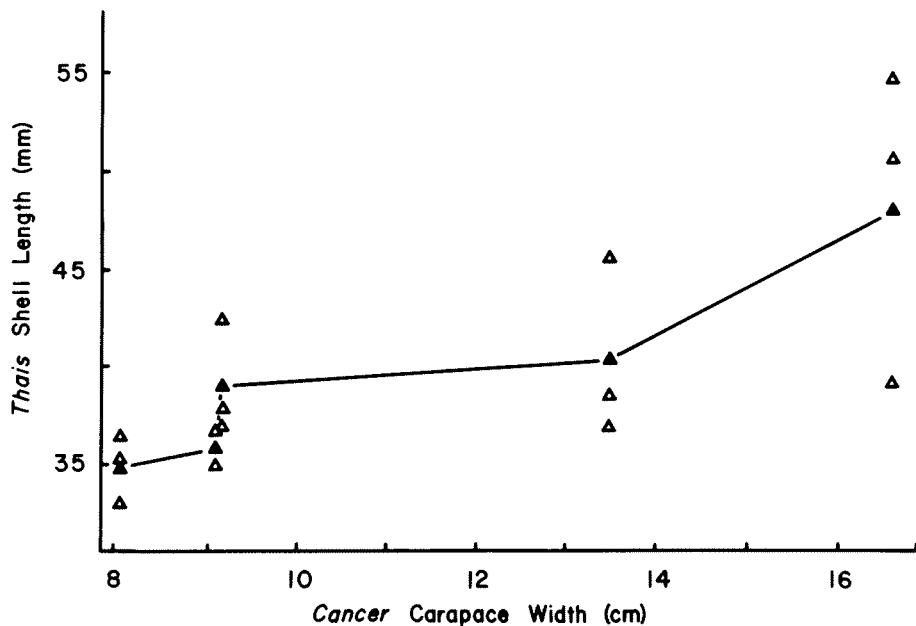


Figure 3

Shell lengths of the largest three thin-shelled *Thais lamellosa* eaten at LD 50 as a function of *Cancer productus* size (carapace width). Open symbols, individual snails; solid symbols, mean. $N = 15$, $r^2 = 0.609$, $P < 0.01$.

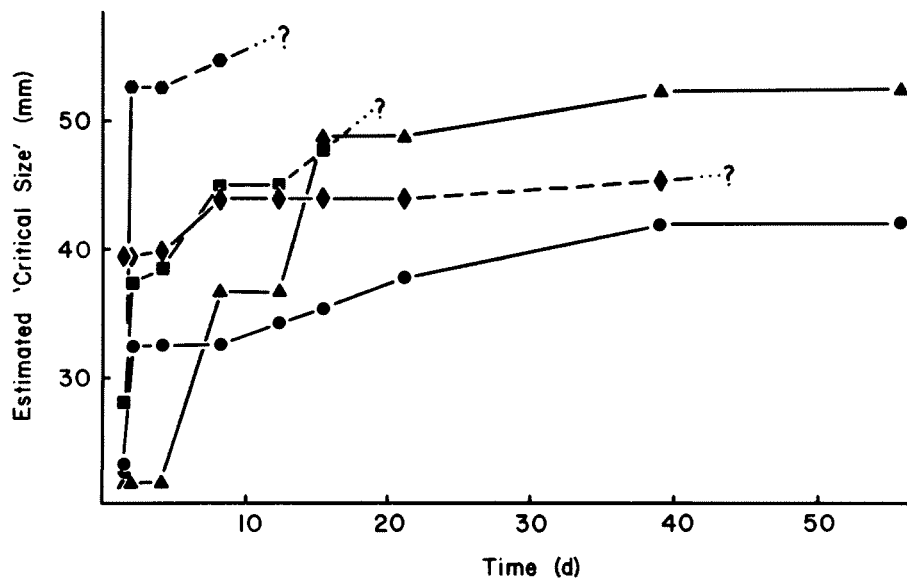


Figure 4

Change in the estimated "critical size" (mean shell length of the largest snail eaten and the next largest available; VERMEIJ, 1976) for each of the five crabs over the duration of the experiment. Dashed lines indicate that the largest available snail had been consumed during that interval; thus the estimated critical size would probably have continued to increase. Symbols for the crabs as in Figure 2.

consumed all but one of the initial 21 thick-shelled snails, in addition to all of the thin-shelled ones. The remaining four crabs ate at most only two of the 21 available thick-shelled snails even though three of them had eaten all, or all but one, of the thin-shelled snails. In addition, only one of these four crabs ate a thick-shelled snail before 50% of the thin-shelled snails had been eaten in its aquarium (Figure 2), and it was the only thick-shelled snail eaten by this crab. Thus, many thin-shelled snails were eaten before the crabs began attacking thick-shelled ones successfully.

Finally, the sizes of the largest thin-shelled snails eaten increased with crab size after 50% of those available had been consumed (Figure 3), even though, by the end of the experiment, three of the five crabs had eaten all of the thin-shelled snails available. Thus, smaller thin-shelled snails tended to be eaten before larger ones, particularly for the smaller crabs (see also Figure 4 below). For the two crabs that did not eat all of the thin-shelled snails, the final "critical size" (mean of shell length of the largest snail eaten and the next largest available; VERMEIJ, 1976) increased with crab size (Table 1). Final critical size was not related to crab size for the thick-shelled snails (Table 1), because the few snails eaten by the four smaller crabs were among the lightest of the thick-shelled animals offered, averaging 1.99 SD less than their expected values from regression (Figure 1a); thus, these values overestimate the actual critical sizes for the thick-shelled population.

DISCUSSION

Thaidid gastropods are notorious for their variation in shell appearance, variation that has been a frequent source of taxonomic confusion (ABBOTT, 1974; GRANT & GALE, 1931; KINCAID, 1957, 1964; VOKES, 1971; WELLINGTON & KURIS, 1983). The conspicuousness of this variation has resulted in many descriptive studies of geographic patterns within members of this family, including patterns in shell color (BERRY & CROTHERS, 1968, 1974; MOORE, 1936; SPIGHT, 1976) and in shell morphology (CROTHERS, 1982, and references therein; CURREY & HUGHES, 1982; KINCAID, 1957, 1964; KITCHING, 1976, 1977; PHILLIPS *et al.*, 1973; SEED, 1978; VERMEIJ & CURREY, 1980). A few studies have examined experimentally the potential adaptive value of morphological variation in these species (EBLING *et al.*, 1964; HUGHES & ELNER, 1979; KITCHING & LOCKWOOD, 1974; KITCHING *et al.*, 1966; WELLINGTON & KURIS, 1983), and they all have demonstrated, among other things, that thicker shelled individuals are more resistant to attack by shell-breaking crabs than thinner shelled ones. The results presented here support the conclusions of these experimental studies; however, they also demonstrate that thicker shells cannot guarantee immunity from predation by large crabs, and they reveal a probable additional advantage to thicker shells that relates to the motivational state of crabs.

The laboratory feeding experiments with *Cancer productus* yielded three results of significance. First, thicker

(=heavier) shelled individuals of *Thais lamellosa* were consumed at a much lower rate than thinner (=lighter) shelled ones by all sizes of crabs. Second, the largest *C. productus* was nonetheless capable of eventually consuming all sizes of the thicker shelled snails offered (up to 44.6 mm). Third, the successful attack of thicker shelled or larger snails was influenced by the availability of thinner shelled or smaller animals.

I use shell weight as interchangeable with shell thickness because of the convenience with which it can be measured and because I feel it is a more useful single measure of average thickness. Local increases in thickness associated with axial sculpture or apertural teeth make thickness measurements of a specific part of the shell arbitrary and sometimes difficult to interpret. Apertural teeth and axial sculpture may thicken the lip, reducing vulnerability to crabs that peel shells starting at the aperture, but such shells would still be vulnerable to crabs that crush (VERMEIJ, 1978). *Cancer productus* uses both techniques (ZIPSER & VERMEIJ, 1978); thus, shell weight provides a measure of average shell thickness that is more likely to reflect relative vulnerability of snails to this crab.

The adaptive value of thick shells appears to be a consequence of two factors. First, thicker shells decrease the size range of crabs to which snails of a given body size are ultimately vulnerable (see also REIMCHEN, 1982). The four smaller crabs in the experiments ate at most two of the available thicker shelled morph of *Thais lamellosa*, and all of these eaten snails had the thinnest shells of those available of comparable length (Figure 1a). Thus, sufficiently thick shells can render their bearers invulnerable to attack from all but very large crabs. This in turn reduces the total number of crabs to which the snails are potentially vulnerable and hence reduces their overall probability of mortality.

A second advantage to thicker shells results from the selective feeding behavior of crabs. When a diversity of prey is available, predators usually feed preferentially on the energetically more valuable prey (HUGHES, 1980; HUGHES & ELNER, 1979; PALMER, 1984). By increasing both the energy expended and the time required to break open a shell successfully, thicker shells will decrease the potential food value of snails to shell-breaking predators. This decrease in potential food value probably accounts for an aspect of the feeding behavior exhibited by all but one of the crabs that consumed one or more thick-shelled *Thais lamellosa*: the thick-shelled snails were not attacked successfully until more than 50% of the thin-shelled ones had been eaten (Figure 2). For the largest crab, which ate nearly all of the thick-shelled snails offered, 80% of the thick-shelled individuals were eaten only after *all* of the thin-shelled snails had been consumed (Figure 2). Had thinner shelled snails been replaced as they were eaten, the remaining 80% of the thick-shelled animals probably would not have been eaten. These results suggest strongly that thicker shelled snails were manipulated but rejected as undesirable by crabs earlier in the experiments.

Similarly, at 50% mortality of the thin-shelled snails, the mean size of the largest snails eaten increased with crab size ($r^2 = 0.61$; Figure 3), presumably reflecting an increase in the "preferred size" for the larger crabs when thin-shelled snails were initially abundant (ELNER & HUGHES, 1978). However, by the end of the experiments, the largest four crabs had eaten all, or all but one, of the thin-shelled *Thais lamellosa*. Hence, although larger snails were ultimately vulnerable, they were not consumed until most of the smaller ones had been eaten, again suggesting they were manipulated and rejected earlier in the experiment. Access to alternative prey of higher food value (energy/unit time, or potential for promoting growth; PALMER, 1983a) thus appears to influence substantially the probability of being eaten of more heavily defended or larger prey that are nonetheless still potentially vulnerable to crabs. A similar conclusion has been reached by BOULDING (1984) from experiments with *Cancer productus* feeding on infaunal bivalves.

In these experiments, the increase over time in the maximum size of snail eaten by individual crabs points to a methodological difficulty associated with measuring the "critical size" of different shell forms (maximum size of vulnerability to a given size and species of shell-breaking predator [VERMEIJ, 1976]—a larger critical size means snails are vulnerable to a larger size, *i.e.*, are more vulnerable). Clearly, the estimated critical size (mean size of the largest individual eaten and the next largest one available) depends upon the duration of the experiment (Figure 4). It will also depend upon the availability of alternative prey. When a number of prey are offered simultaneously to a predator, curves such as those of Figure 4 will increase confidence in the accuracy of the experimentally measured critical sizes (see also BOULDING, 1984), particularly for crabs, whose feeding activity in the lab is often erratic and unpredictable.

Finally, if thicker shells significantly reduce vulnerability to shell-breaking predators, why are not all populations of *Thais lamellosa* in particular, or all species of marine gastropods in general, thick-shelled? Presumably, the costs of a thicker shell outweigh the advantages in some cases. Shell material, or at least the organic matrix of shells, appears to be energetically expensive to produce (PALMER, 1983b, and references therein). Heavier shells are also more expensive to transport in surface-dwelling species; a two-fold increase in shell weight results in nearly a three-fold increase in the cost of locomotion in *T. lamellosa* (Palmer and LaBarbera, in preparation). In addition, the maximum rate of body growth in *T. lamellosa* is limited by the rate at which shell material can be produced rather than by the rate of ingestion or rate of tissue production (PALMER, 1981); thus, a thicker shelled individual would not be able to grow as rapidly as a thinner shelled one even when food is not limiting. All of these costs will counteract the selection for thicker shells as mortality due to shell-breaking predators decreases. The shell-thickness polymorphism in *Thais lamellosa* probably per-

sists because genetic fixation is prevented by some combination of (1) gene flow among adjacent populations subject to different intensities of predation, and (2) temporal fluctuations in crab abundance, which favor different phenotypes at different times at a given site.

Uncertainty exists over the degree of genetic control of intraspecific variation in shell morphology of thaidid gastropods. Because the variation among populations is usually greater than that within, it is often assumed to be genetic (CROTHERS, 1974, 1982; KINCAID, 1957; KITCHING & LOCKWOOD, 1974). However, the same pattern would result if this morphological variation were purely phenotypic. Growth in the laboratory of young individuals collected from populations of different adult morphology suggests that considerable phenotypic plasticity exists in the shell sculpture of *Nucella lapillus* (LARGEN, 1971) and shell shape of *Thais lamellosa* (SPIGHT, 1973). Breeding studies with *T. emarginata* have revealed that variation in spiral shell sculpture has both a genetic and an environmental basis (PALMER, 1985). Of the shell features that vary in both *T. emarginata* and *T. lamellosa*, shell thickness appears to be the most phenotypically labile (Palmer, unpublished), suggesting provocatively that these gastropods may be capable of producing predator-resistant shells in direct response to potential predation by crabs, as described for rotifers (GILBERT, 1966), bryozoans (YOSHIOKA, 1982; HARVELL, 1984), and cladocerans (GRANT & BAYLY, 1981) in response to their predators. Preliminary results (Appleton & Palmer, unpublished) have revealed that both thin- and thick-shelled *T. lamellosa* can be induced to produce thicker apertural lips in the presence of *Cancer productus* being fed conspecific snails.

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