J. Exp. Mar. Biol. Ecol., 1983, Vol. 73, pp. 95–124
Elsevier

JEM 176

GROWTH RATE AS A MEASURE OF FOOD VALUE IN THAIDID GASTROPODS: ASSUMPTIONS AND IMPLICATIONS FOR PREY MORPHOLOGY AND DISTRIBUTION

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Abstract: Rates of body growth were measured for three species of rocky intertidal gastropods: *Thais* (or *Nucella*) *lamellosa* (Gmelin), *T.* (or *N.*) *canaliculata* (Duclos), and *T.* (or *N.*) *emarginata* (Deshayes). Three size classes of each predator species were grown experimentally in cages at two tidal heights on four size classes of each prey species: *Semibalanus cariosus* (Pallas), *Balanus glandula* Darwin, and *Mytilus edulis* L. Growth was also assessed for *Thais canaliculata* feeding on *Mytilus californianus* Conrad, and *Thais emarginata* feeding on *Chthamalus dalli* Pilsbry.

Rates of body growth varied as a function of predator size, prey size and prey species. With one exception (large *Thais canaliculata*) intermediate sized *Balanus glandula* promoted the most rapid growth for all sizes of all three species of *Thais*; thus these potentially competing predator species have the same highest ranked prey. Among prey promoting slower growth, those encountered commonly in the normal habitats of the predator promoted more rapid growth than those encountered rarely, suggesting that past evolutionary experience has influenced present food value (= growth potential) of prey. For some predators, the ranking of prey species changed with predator size; *Chthamalus dalli* and similar sized *Balanus glandula* promoted comparable growth in small *Thais emarginata* but *Chthamalus dalli* promoted much slower growth than similar sized *Balanus glandula* in larger *Thais emarginata*. Rank differences based on prey size in *Balanus glandula* became more pronounced and in some instances changed with increasing predator size; larger *B. glandula* promoted relatively faster growth for large snails than for small snails in all *Thais* species. Finally, growth rates were correlated with two important attributes of fitness in *T. canaliculata* and *T. emarginata*; in general, prey promoting more rapid growth also resulted in an earlier age of first reproduction for initially immature snails and higher rate of egg capsule production for mature individuals. Thus, these growth rates provide a basis from which to examine quantitatively patterns of prey selection from an energy- or growth-maximization perspective.

These patterns of predator growth also permit inferences about the possible influence of predation on the evolution of prey morphology, life-history, and microhabitat distribution. Size refuges from *Thais* predation were confirmed for both *Semibalanus cariosus* and *Mytilus californianus*. Both *Balanus glandula* and *Mytilus edulis*, on the other hand, were vulnerable to predation by all sizes of *Thais* examined (> 10 mm) regardless of prey size; thus, neither of these species achieves a size refuge. In addition, on rocky shores, vertical distributions of the prey species reflect general preference patterns of their predators: higher value prey species, i.e. those with less well developed defensive morphologies (*Balanus glandula*, *Mytilus edulis*), generally occur higher on the shore. This pattern would be expected if preferred prey are consumed first lower on the shore where they are more available.

INTRODUCTION

Muricacean gastropods are common predators of barnacles and mussels on rocky shores worldwide (Stephenson & Stephenson, 1972; Taylor *et al.*, 1980 and references

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therein). They have been an important source of mortality for molluscan prey since the Upper Cretaceous (Sohl, 1969; Vermeij, 1977; Taylor *et al.*, 1980). They also exert a dramatic influence on present-day rocky-shore distributions of barnacles (Connell, 1961a,b, 1970; Dayton, 1971; Menge, 1978a,b) and mussels (Suchanek, 1978), and may have been responsible for the long term evolutionary trend towards reduction in the number of parietal (lateral wall) plates observed in nearly all lineages of balanomorph barnacles since the Cretaceous (Palmer, 1982a). Although aspects of *Thais* (or *Nucella*) feeding behavior have been examined by a number of authors (Fischer-Piette, 1935; Moore, 1938; Chapmann, 1955; Connell, 1961a,b, 1970; Emlen, 1966; Paine, 1966a,b; Murdoch, 1969; Dayton, 1971; Morgan, 1972a,b; Menge, 1974; Spight, 1974; Carefoot, 1977; Menge, 1978a,b; Bayliss, 1982), no attempt has been made to quantify the value of different prey to these predators. Such a quantification is fundamental to understanding patterns of prey selection by *Thais* as well as to predicting their potential impact on prey populations in both ecological and evolutionary time.

Thaidid gastropods, like muricid gastropods, consume hard-shelled invertebrate prey by drilling through the shell, using both the accessory boring organ and the radula (Carriker & Van Zandt, 1972). Total handling time (drilling plus ingestion) can be upwards of 60 h for bivalve prey (Carriker & Van Zandt, 1972; Carefoot, 1977; Palmer, 1980). For some prey species, initial penetration is followed by the injection of a toxic saliva (Huang, 1971, 1972) that relaxes the prey and facilitates tissue ingestion. While this toxin may reduce the handling time for barnacles (Palmer, 1982a) it does not appear to be used when consuming mussels (Palmer, 1980).

The three *Thais* (or *Nucella*) species examined in this study are all common on rocky shores of the Pacific Northwest: *T. lamellosa*, *T. canaliculata* and *T. emarginata* (Ricketts *et al.*, 1968; Kozloff, 1974; Carefoot, 1977). Growth rates are presented for various predator size–prey size combinations for five prey species: three barnacles, *Balanus glandula* Darwin, *Semibalanus cariosus* (Pallas), and *Chthamalus dalli* Pilsbry (*Thais emarginata* only) and two mussels, *Mytilus californianus* Conrad (*Thais canaliculata* only) and *Mytilus edulis* L. Growth rates of snails for all predator–prey combinations (except for *Chthamalus dalli* and *Mytilus californianus*) were measured in cages deployed at two tidal heights, to assess the impact of tidal exposure.

Because growth will occur only when all costs associated with consuming a prey have been paid, it provides a practical, biologically meaningful assessment of net food value, even though the costs themselves are unknown, as long as the animals are still growing and are not expending energy in reproduction. With growth as a measure of food value and consequently of prey preference (Palmer, unpubl.), it is possible to examine potentially adaptive patterns of prey morphologies, life-history attributes, and microhabitat distributions as well as to test quantitatively predictions of prey-selection models (Palmer, unpubl.). To justify further the use of growth as a measure of food value, I examine and provide some supporting evidence for the assumptions implicit to such an approach.

METHODS

MEASUREMENT OF PREDATOR GROWTH

To monitor growth rates, 12 wooden frame cages bounded by 3 mm plastic mesh (VEXAR, DuPont) were constructed. Each cage contained 12 individual units ($\approx 10 \times 10 \times 10$ cm) all of which were accessible easily via closeable flaps (Fig. 1).

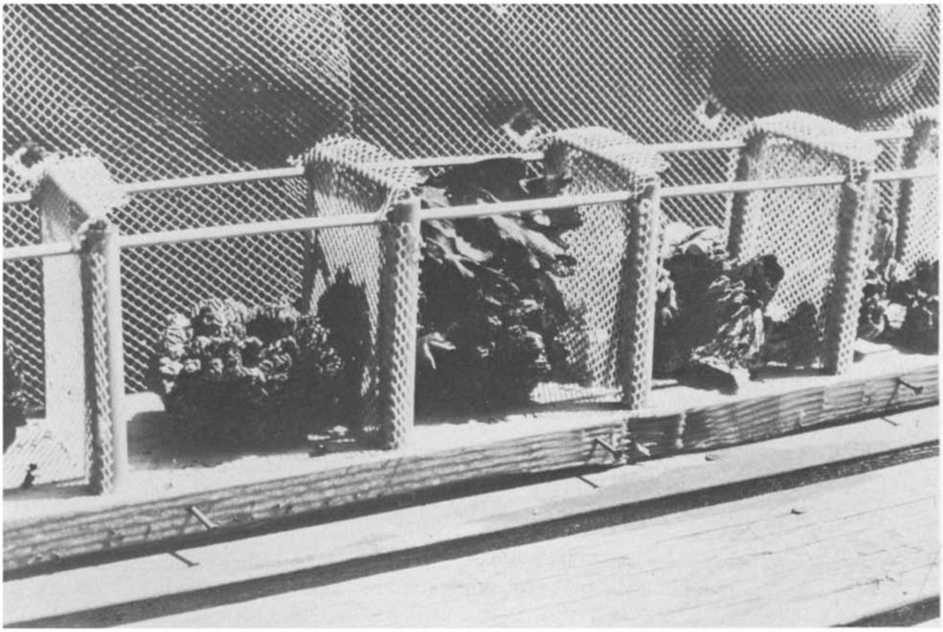

Fig. 1. A close-up photograph of individual growth-rate cage units with small barnacle-covered stones: a tuft of *Fucus distichus* is present in the middle cage unit.

Plastic screen was bonded to wood using a high-temperature adhesive (Hot-Melt Glue, USM Corporation, Reading, PA, U.S.A.) that effectively bonds most plastics to each other, releases no synthetic compounds, is water resistant and remains flexible when cooled. Four cages were deployed at each of three tidal heights on pilings adjacent to the Friday Harbor Laboratories, Friday Harbor, WA (U.S.A.) (48°33′N : 123°01′W; Fig. 2). A floating breakwater was constructed to protect the cages from driftwood and floating debris (Fig. 2). *Thais lamellosa* (Gmelin) and *T. canaliculata* (Duclos) were collected from Turn Rock and *T. emarginata* (Deshayes) from Low Island, both in the San Juan Islands, WA (U.S.A.) (Palmer, 1980). Snails of all sizes showing evidence of moderate, recent shell growth were selected over those showing little or no growth, to obtain animals of similar age and growth condition, since molluscs of the same shell size may not necessarily be the same age (Walne, 1958; Yamaguchi, 1958; Richards & Merrit, 1965). Animals were returned to the laboratory and sorted into size classes

(5-mm classes for *T. lamellosa* and 2.5-mm classes for *T. canaliculata* and *T. emarginata*). While awaiting placement in a cage, snails were held continuously immersed without food in running sea-water aquaria for a period not exceeding 2 wk.

Fig. 2. The complete array of experimental cages with the accompanying floating breakwater at the Friday Harbor Laboratories, Friday Harbor, Washington.

Experimental snails were tagged individually by writing numbers in India ink on smooth spots ground on the shell with a small electric grinder and coating them with a clear glue (Dekophane, Rona Pearl Corp., Bayonne, NJ, U.S.A.). Shell length (apex to tip of siphonal canal) was measured to 0.1 mm with Vernier calipers. Shell weight and body weight were estimated nondestructively within 24 h of the beginning and the end of each growth interval. Shell weight was estimated by weighing live animals in sea water. Because tissue contributes $<5\%$ of this weight it provided a very accurate measure of shell weight ($r^2 > 0.9995$ for all three *Thais*; Palmer, 1982b). Whole weight in air, after most of the extravisceral water was removed, provided a measure of shell weight plus body wet weight. Estimated shell weight was then subtracted from the whole weight to obtain an estimate of body wet weight. This measure of body weight provided a reliable estimate of actual body ash-free dry weight ($r^2 = 0.805$, $N = 27$ for *T. lamellosa*; $r^2 = 0.912$, $N = 21$, for *T. canaliculata*; and $r^2 = 0.985$, $N = 19$ for *T. emarginata*; Palmer, 1982b). These regressions were used to estimate initial and final body weights of all experimental animals.

Growth was assessed for a single *Thais* species at a time in separate experiments lasting approximately one month (28, 31, and 30 days respectively for *T. lamellosa*, *T. canaliculata*, and *T. emarginata*; actual dates in figure legends). Three predator size classes were established that spanned the size range of each species (actual sizes in figure headings). Four individual snails from each size class were caged in a single cage unit along with a single size class of a single prey species (see below) and provided with a small tuft of *Fucus vesiculosus* for cover (Fig. 1). Except for *Chthamalus dalli*, there were four size classes of each prey species. Growth rates were measured simultaneously for groups of animals at two tidal heights: + 0.5 ft and + 2.5 ft above MLLW (0.15 and 0.80 m) for *Thais lamellosa* and *T. canaliculata*, + 2.5 ft and + 4.5 ft (0.80 and 1.45 m) for *T. emarginata*. Results are also presented from laboratory growth experiments with *T. canaliculata* on *Mytilus edulis* and *M. californianus* collected from Tatoosh Island (48°24′N : 124°44′W).

ESTABLISHING DISCRETE SIZE CLASSES OF PREY

Discrete size classes were obtained differently for mussels and barnacles. *M. edulis* were collected from pilings of the Friday Harbor Laboratories dock and sorted individually into 5-mm size classes based on shell length. Any barnacles present on their valves were removed. Appropriately sized mussels were counted into cages and the cages deployed intertidally 1 wk prior to introducing snails, to allow the mussels to attach fully. This procedure reduced the likelihood that snails would become trapped by byssus threads. Mussel sizes were measured as shell length (maximum dimension parallel to the long, ventral margin of the shell).

Barnacles of both species were collected from sites where fairly narrow size ranges could be obtained on small stones. Where barnacles of an inappropriate size occurred among those in the desired range, these were removed individually with a pair of point-nosed pliers. Small *Balanus glandula* were collected on the shores of Sinclair Inlet, WA (U.S.A.), in May as recently metamorphosed barnacles on *Mytilus edulis* valves. These barnacles were all probably < 1 month old when collected and were held in running sea-water aquaria to retard growth until used (Blake, 1960). They were prepared by splitting open the mussels with a knife, separating the valves and removing the flesh. A continuous cover of mussel valves with barnacles was then lashed to screens of 1 cm mesh galvanized hardware cloth with 10 lb test monofilament line and the screens were suspended from the Friday Harbor Laboratories dock for 1 wk prior to use to allow the barnacles to feed. Barnacle sizes are reported throughout as opercular diameters (rostro-carinal diameter inside the aperture).

One size class of *Semibalanus cariosus* required special handling. Medium-small *S. cariosus*, collected from Crane Rock (Palmer, 1980), developed from a heavy set of barnacles that had metamorphosed on the sides of much larger *S. cariosus* (15 to 25 mm opercular diameter) the previous summer. The larger, substratum-forming barnacles were killed enough in advance of the experiments so that any residual flesh degraded. The smaller two *S. cariosus* size classes were not as discrete as those for *Balanus glandula*, and in some cases overlapped broadly (Palmer, 1980).

CAGE MONITORING AND DATA ANALYSIS

In all experiments cages were inspected and prey replenished where necessary at 10-day intervals; snails were never allowed to consume all the prey in their cage unit. During inspections cages were scrubbed to remove accumulated diatoms and other algae. For barnacle cages, if more than half the originally supplied barnacles on a stone had been eaten, the stone was removed and replaced with a fresh one. Drilled mussel valves with no flesh remaining were removed and more mussels added when necessary. Snails that were in the process of feeding during cage checks were left in place on their prey when possible. These periodic checks were conducted during times of low water so the cages could be returned to their position before or shortly after they would have been immersed by the rising tide, thus minimizing disturbance to the snails. All eaten and uneaten prey were measured; the data on consumption rates and growth efficiencies, however, will be presented elsewhere (Palmer, in prep.).

With one exception (*Thais canaliculata* growing on *Mytilus edulis* and *M. californianus*) growth rates are presented below as mean percent change in body weight of four snails per cage over the growth interval. However, in a few cages, individual snails died, apparently due to trauma from handling, some escaped and were lost, and some adults were noted laying egg capsules during the inspections (primarily adult *Thais emarginata*). The mean growth rates in these treatments were computed only for the remaining snails. In addition, when one snail grew substantially slower than the remaining three in a cage, the following elimination criteria were used. A suspected deviant snail first had to differ from the remaining snails in a cage by an amount greater than the cumulative maximum error of the tissue weight estimates for each species (20% for *T. lamellosa*, 10% for *T. canaliculata*, and 10% for *T. emarginata*; Palmer, 1982b). If this criterion was satisfied, the suspected deviant was subject to an outlier test (Sokal & Rohlf, 1969); snails different from those remaining at the 5% level were not included when computing treatment means. The total number of animals so eliminated was six for *T. lamellosa*, one for *T. canaliculata* and six for *T. emarginata* out of > 150 animals used for each species. Treatments where individuals were eliminated statistically are noted by a + adjacent to the point in the figures.

In the figures, growth is plotted against prey size for the four size classes established for each prey species. Because prey size classes are arbitrary and because they are not directly comparable in an absolute sense, except perhaps as percent of maximum adult size, some care must be exercised when comparing growth rates on different prey species. This convention was adopted because biomass differences among the prey species (e.g. *Balanus glandula* versus *M. edulis*) were so great that comparisons on a single figure would have been difficult.

Data from the main growth experiments were analyzed statistically as follows. A nested analysis of variance, BMDP2V (Dixon & Brown, 1979), with two levels (prey sizes within prey species) was conducted for each size class of each predator species at each tidal height, because absolute values of percent body weight change among different sizes of snails are not directly comparable. The mean rates of body growth for each predator size class at each tidal height were then compared using the SNK test for a posteriori multiple comparisons among means (Zar, 1974). Means not significantly different from each other at a 5% experiment-wise error level are indicated by vertical bars adjacent to each figure.

RESULTS

THAIS LAMELLOSA

For all but the large size class of *Thais lamellosa*, there were significant treatment effects due to prey species and prey size (Table I). The significance among prey species is due largely to the consistently higher rate of *T. lamellosa* growth on *Balanus glandula*. Small *Thais lamellosa* (mean length 23.0 mm) grew significantly more rapidly on all sizes of *Balanus glandula* than on any other prey at both tidal heights (except for the small class at the low level; $P < 0.05$, SNK test; Fig. 3). *Semibalanus cariosus* > 6.0 mm opercular diameter were beyond the size that these small *Thais lamellosa* could consume as none were eaten (e.g. see Table V; Palmer, 1980). Of prey types that could be consumed successfully (all *Balanus glandula*, smaller two size classes of *Semibalanus cariosus*), *Mytilus edulis* was of significantly lower value for small *Thais lamellosa* in five of eight cases. A replicate series conducted in August and September 1978 along with the *T. emarginata* experiments (open circles, Fig. 3a) supports this interpretation.

TABLE I

F values from a two-level nested analysis of variance (prey sizes within prey species) for *Thais lamellosa*: each predator size class was analyzed separately for each tidal height; predator size abbreviations: s, small; m, medium; l, large (see Figs. 2–8 and 10–12 for actual predator sizes); tidal height (Ht) abbreviations: l, low (+0.5 ft, 0.15 m); m, mid (+2.5 ft, 0.8 m); groups, prey species (*Balanus glandula, Mytilus edulis, Semibalanus cariosus*); subgroups, prey size classes; Sig, significance of *F* values (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$); degrees of freedom: MS (within) = 36, among all subgroups = 11, groups = 2, subgroups within groups = 9.

			F value					
Predator size	Ht	MS within subgr.	Among all subgr.	Sig.	Among groups	Sig.	Subgr. within groups	Sig.
s	m	373.97	8.57	***	16.51	***	2.24	*
s	l	193.86	20.19	***	11.08	**	7.13	***
m	m	80.09	7.54	***	4.91	*	4.44	***
m	l	78.86	13.56	***	4.93	*	7.92	***
l	m	37.91	1.16		0.37		1.31	
l	l	82.58	1.60		8.75	**	0.66	

Patterns of growth for medium- (mean length 37.1 mm, Fig. 4) and large-sized (mean 47.8 mm, Fig. 5) *T. lamellosa* are difficult to interpret because of their smaller differences in growth rates on different prey. The overall patterns appeared qualitatively similar to those observed for the small size class: intermediate- and large-sized *Balanus glandula* were the highest value, small *B. glandula*, smaller *Semibalanus cariosus* and *Mytilus edulis* were of intermediate value, and large *Semibalanus cariosus* were the lowest value

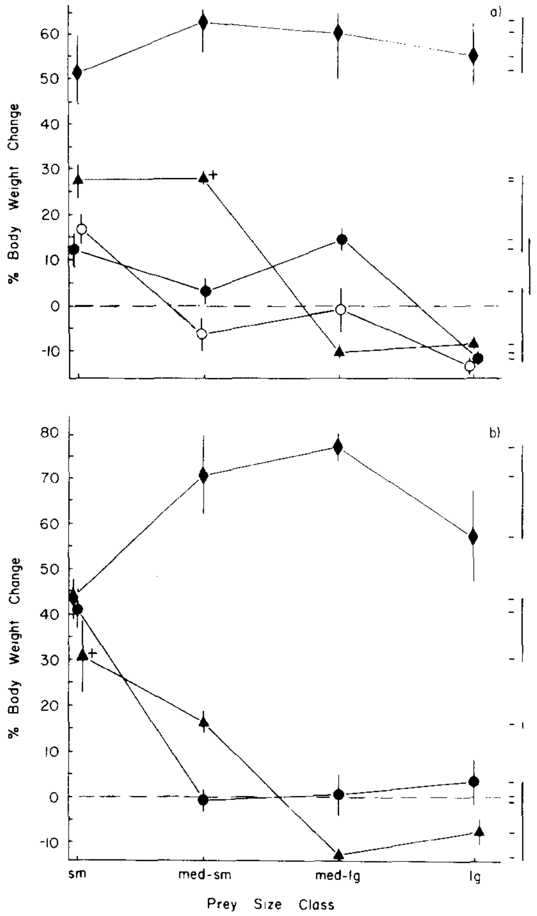

Fig. 3. Percent body weight change over 28 days (6 June to 5 July, 1977) of small (23.0 ± 0.81 mm) *Thais lamellosa* as a function of prey size-class at two tidal heights: a, mid (+2.5 ft, +0.8 m); b, low (+0.5 ft, +0.15 m); ◆, *Balanus glandula*; ●, *Mytilus edulis*; ▲, *Semibalanus cariosus*; each point corresponds to the mean for four snails; error bars are ±1 SE; ○, replicate series conducted for 30 days from 26 August to 25 September, 1978; + adjacent to a point indicates that an individual has been statistically removed (see text); the actual prey sizes for each prey species are, from smallest to largest: *Balanus glandula*, 1.7 mm, 3.5 mm, 5.5 mm, 9.0 mm; *S. cariosus*, 4.0 mm, 5.0 mm, 7.0 mm, 11.0 mm; *Mytilus edulis*, 20.0 mm, 32.5 mm, 42.5 mm, 52.5 mm; barnacle sizes are opercular diameters, *Mytilus* sizes are shell lengths; vertical bars to the right of each figure indicate means (denoted by dashes) among which there are no significant differences ($P < 0.05$, SNK multiple comparisons test; Zar, 1974).

prey. Individual replicates from other control cages (separate open symbols) tended to confirm this (open symbols, Fig. 4).

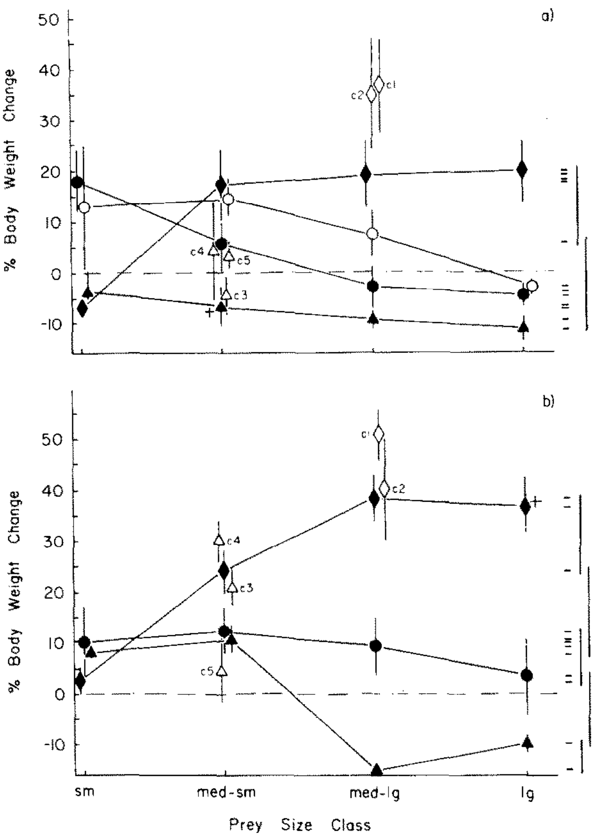

Fig. 4. Percent body weight change over 28 days (6 June to 5 July, 1977) of medium (37.0 ± 0.58 mm) *Thais lamellosa* as a function of prey size-class at two tidal heights: a, mid (+ 2.5 ft, + 0.8 m); and b, low (+ 0.5 ft, + 0.15 m); ◆,◇, *Balanus glandula*; ●,○, *Mytilus edulis*; ▲,△, *Semibalanus cariosus*; the curve of open circles is a replicate series conducted for 30 days from 26 August to 25 September, 1978; individual open symbols are for cages from other experiments; the c series represents controls for prey collected from different sites (Palmer 1980): c1, medium-large *B. glandula* from Wescott Bay; c2, replicate cage of medium-large *B. glandula* from Argyle Creek; c3, medium-small *S. cariosus* from Argyle Creek; c4, replicate cage of medium-small *S. cariosus* from Crane Rock; c5, medium-small *S. cariosus* from Turn Rock; other symbols and notations as in legend of Fig. 3.

Recurrent "negative" growth in large *Thais lamellosa* was probably due to differences in handling procedure between the initial and final weighings; repeatable removal of extravisceral water is considerably more difficult for larger snails (Palmer, 1982b) and more extravisceral water may have been removed during the terminal weighings. Such errors affect only comparisons of absolute rates of growth among predator size classes, not among prey within a predator size class.

Two trends with tidal height were noteworthy for *T. lamellosa*. First, rates of growth on the three larger size classes of *Balanus glandula* tended to diminish with increasing tidal height (Figs. 3–5), probably reflecting decreased feeding time. Secondly, there were some shifts in prey ranking for small *Thais lamellosa* (Fig. 3), including: (1) a change in the relative values of small *Mytilus edulis* and small *Balanus glandula* (barnacles significantly better at +2.5 ft, +0.8 m; not different from mussels at +0.5 ft, +0.15 m); and (2) a possible reversal in the values of small *Semibalanus cariosus* and small *Mytilus edulis* (barnacles better at +2.5 ft, +0.8 m, mussels better at +0.5 ft, +0.15 m).

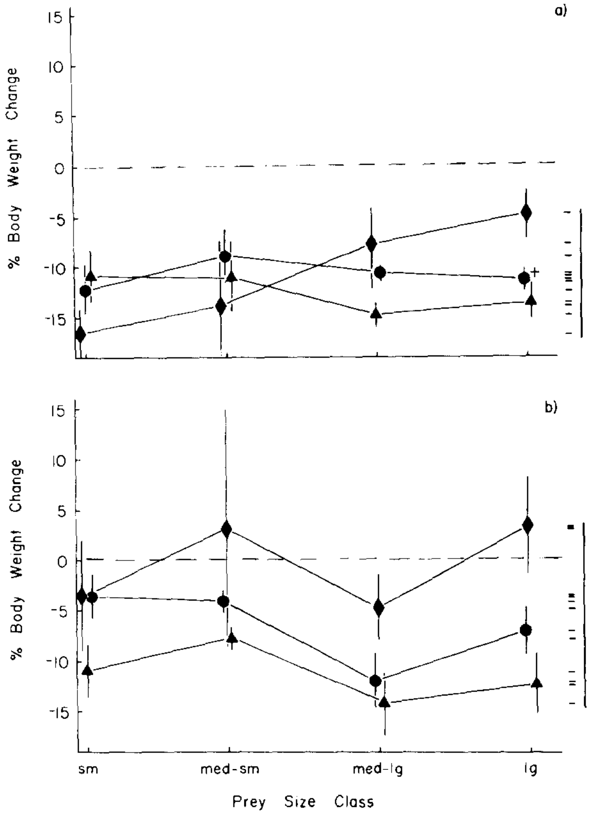

Fig. 5. Percent body weight change over 28 days (6 June to 5 July, 1977) of large (47.8 ± 0.89 mm) *Thais lamellosa* as a function of prey size-class at two tidal heights: a, mid (+2.5 ft, +0.8 m); b, low (+0.5 ft, +0.15 m); ◆, *Balanus glandula*; ●, *Mytilus edulis*; ▲, *Semibalanus cariosus*; other symbols and notations as in legend of Fig. 3.

THAIS CANALICULATA

For all sizes of *T. canaliculata* there were highly significant differences ($P < 0.001$) in rates of growth on different size classes of prey within prey species (Table II).

TABLE II

F values from a two-level nested analysis of variance (prey sizes within prey species) for *Thais canaliculata*: notations, groupings and degrees of freedom as in Table I.

			F value					
Predator size	Ht	MS within subgr.	Among all subgr.	Sig.	Among groups	Sig.	Subgr. within groups	Sig.
s	m	332.57	30.85	***	2.73		23.48	***
s	l	814.04	21.76	***	4.78	*	12.89	***
m	m	184.51	30.37	***	3.97		19.73	***
m	l	572.07	12.04	***	2.58		9.35	***
l	m	67.50	17.06	***	2.05		14.32	***
l	l	133.81	20.40	***	1.10		20.05	***

However, because of the complexity of the patterns of growth on different sizes of each prey species, there were significant differences among prey species in only one of six cases (small *T. canaliculata*, low). As with *T. lamellosa*, intermediate-sized *Balanus glandula* promoted the most rapid growth for small *Thais canaliculata* (mean length 16.3 mm), though significantly so in only one case (Fig. 6). Small *Balanus glandula*, mussels of all sizes and smaller *Semibalanus cariosus* were of intermediate value, and the larger-size classes of *S. cariosus* were of significantly lower value than all other prey.

The growth rates of medium-sized *Thais canaliculata* (mean length 23.8 mm) were nearly the same as for small ones, except that small *Balanus glandula* were of significantly lower value than *Mytilus edulis* (seven of eight cases) and growth on medium-large *Semibalanus cariosus* was significantly > 0 at the low level (Fig. 7).

Growth rates of large *Thais canaliculata* (mean length 32.6 mm) differed from those of the smaller two size classes in two interesting ways (Fig. 8). For all but one case, average growth when feeding on the three larger size classes of *Balanus glandula* was not significantly different from that on the two intermediate sizes of *Mytilus edulis* and medium-small *Semibalanus cariosus*. In addition, medium-small *S. cariosus* were significantly better than either the smallest or the two larger size classes.

Growth data for *Thais canaliculata* fed *Mytilus californianus*, the dominant exposed coast mussel (Suchanek, 1978), were obtained in laboratory experiments conducted in growth-rate cages in running sea-water aquaria at the Friday Harbor Laboratories (Palmer, 1980). Comparable sizes of *M. californianus* collected from Tatoosh Island, WA (U.S.A.) (mean length = 22.6 mm, SD ± 4.84 mm), *M. edulis* from Tatoosh (mean length = 23.3 mm, SD ± 5.73 mm) and *M. edulis* collected from pilings off the Friday

Harbor Laboratories' dock (mean length = 24.8 mm, SD ± 5.49 mm) were offered to similar size ranges of *Thais canaliculata*, also collected at Tatoosh. Snails were measured for whole weight (shell plus body weight, Palmer, 1982b) at the beginning and the end

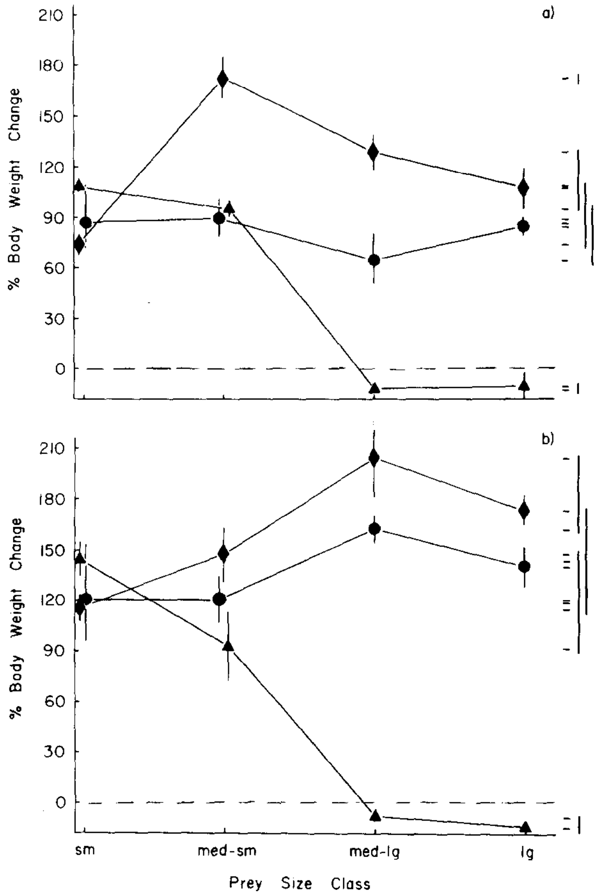

Fig. 6. Percent body weight change over 31 days (17 July to 17 August, 1977) of small (16.3 ± 0.33 mm) *Thais canaliculata* as a function of prey size-class at two tidal heights: a, mid (+ 2.5 ft, + 0.8 m);and b, low (+ 0.5 ft, + 0.15 m); ◆, *Balanus glandula*; ●, *Mytilus edulis*; ▲, *Semibalanus cariosus*; other symbols and notations as in legend of Fig. 3.

of a 2-month feeding interval. Even at this relatively small size, *Mytilus californianus* promoted substantially poorer growth than *M. edulis* (Fig. 9). In addition, there was no detectable difference in the ability of these snails to grow on *M. edulis* collected from the two different sites. These experiments were conducted with an artificial, 12-h tidal cycle in the laboratory with no other environmental cues; however, the magnitude of the difference in growth rates on these two mussel species suggests strongly that a real difference exists in their relative value as prey.

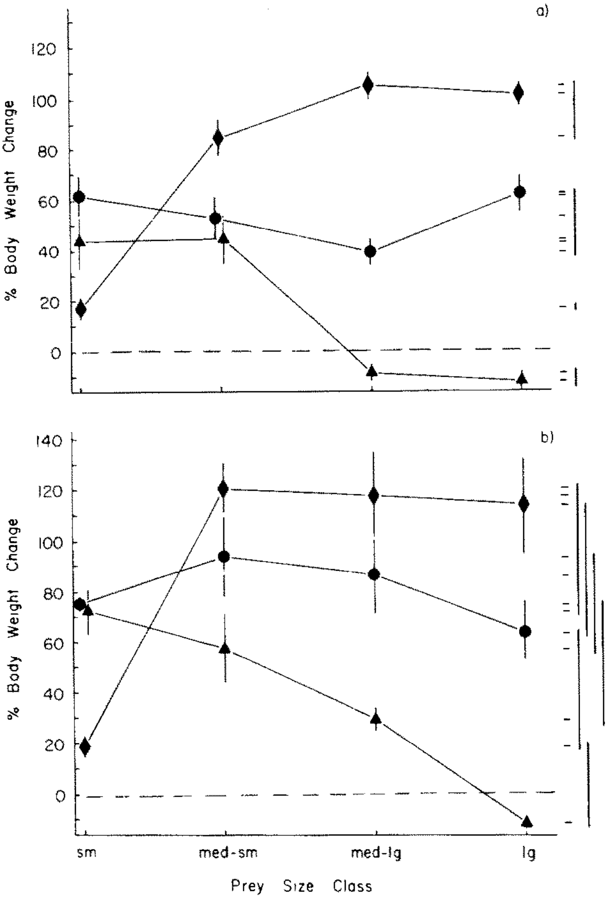

Fig. 7. Percent body weight change over 31 days (17 July to 17 August, 1977) of medium (23.8 ± 0.49 mm) *Thais canaliculata* as a function of prey size-class at two tidal heights: a, mid (+2.5 ft, +0.8 m); b, low (+0.5 ft, +0.15 m); ◆, *Balanus glandula*; ●, *Mytilus edulis*; ▲, *Semibalanus cariosus*; other symbols and notations as in legend of Fig. 3.

THAIS EMARGINATA

In addition to growth rates on the three principal prey species, growth of *T. emarginata* was also measured on *Chthamalus dalli*. Because *Chthamalus* is such a small barnacle (average adult opercular diameter ≈2–3 mm) no attempt was made to establish separate size classes. It is placed towards the center of the figures as this would represent the "average size" of each prey species. Due to cage space restrictions the two replicates with *Chthamalus* were limited to the higher level (+4.5 ft, +1.4 m).

Highly significant differences in rates of growth among prey species were observed for all sizes of *Thais emarginata* (Table III), largely because of the consistently slow growth on all sizes of *Semibalanus cariosus* (Fig. 10–12). However, with one exception,

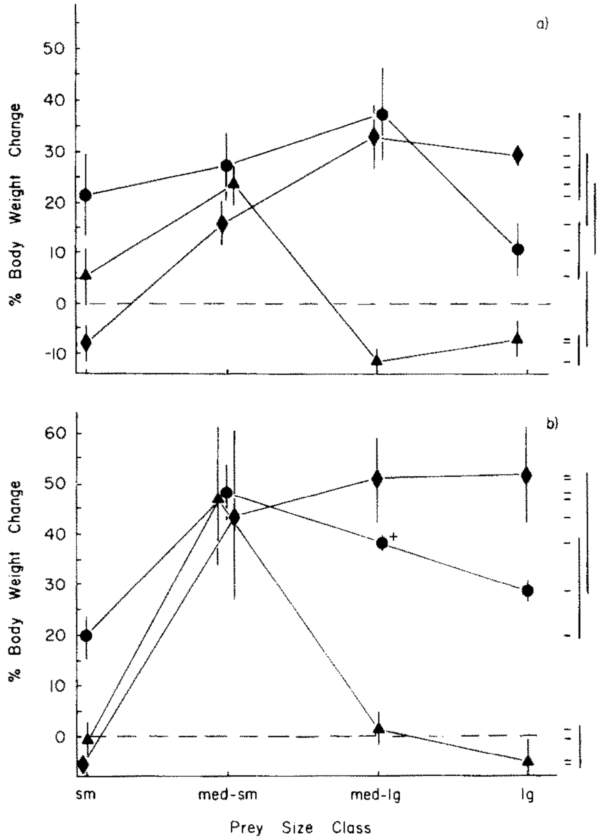

Fig. 8. Percent body weight change over 31 days (17 July to 17 August, 1977) of large (32.6 ± 0.66 mm) *Thais canaliculata* as a function of prey size-class at two tidal heights: a, mid (+ 2.5 ft, + 0.8 m); b, low (+ 0.5 ft, + 0.15 m); ◆, *Balanus glandula*; ●, *Mytilus edulis*; ▲, *Semibalanus cariosus*; other symbols and notations as in legend of Fig. 3.

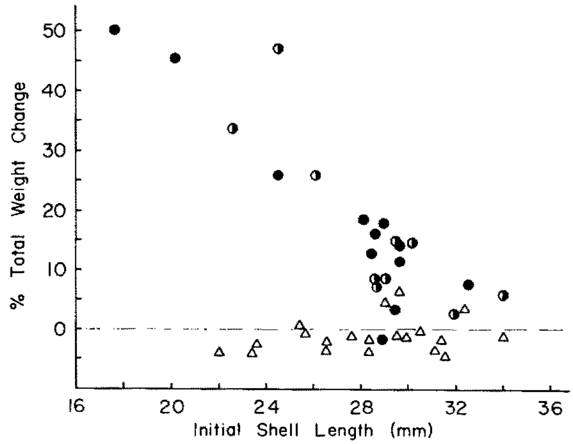

Fig. 9. Percent total weight change of Tatoosh Island *Thais canaliculata* as a function of initial shell length, when grown on *Mytilus californianus* (△), and *Mytilus edulis* from two sites: Tatoosh Island (◑) and the Friday Harbor Laboratories dock (●); each point represents an individual snail.

TABLE III

F values from a two-level nested analysis of variance (prey sizes within prey species) for *Thais emarginata*: tidal height abbreviations: m, mid (+ 2.5 ft, 0.8 m); h, high (+ 4.5 ft, 1.4 m); notations, groupings and degrees of freedom as in Table I.

			F value					
Predator size	Ht	MS within subgr.	Among all subgr.	Sig.	Among groups	Sig.	Subgr. within groups	Sig.
s	h	428.33	25.77	***	86.24	***	1.56	
s	m	408.10	24.22	***	29.86	***	3.88	**
m	h	423.58	14.11	***	65.36	***	1.11	
m	m	378.02	9.23	***	17.08	***	3.89	**
l	h	148.57	15.60	***	32.47	***	2.32	*
l	m	188.17	11.23	***	12.99	**	3.53	**

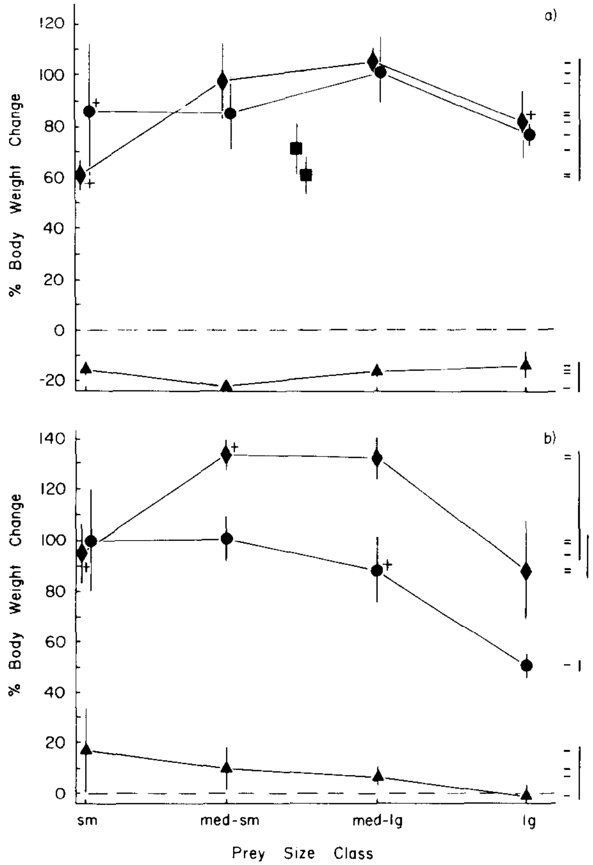

Fig. 10. Percent body weight change over 30 days (26 August to 25 September, 1977) of small (13.6 ± 0.32 mm) *Thais emarginata* as a function of prey size-class at two tidal heights: a, high (+ 4.5 ft, + 1.4 m); b, mid (+ 2.5 ft, + 0.8 m); ◆, *Balanus glandula*; ●, *Mytilus edulis*; ▲, *Semibalanus cariosus*; ■, *Chthamalus dalli*; *C. dalli* were available in all sizes, up to 2.5 mm opercular diameter; other symbols and notations as in legend of Fig. 3.

differences among size classes within prey species were pronounced only at the lower of the two tidal levels.

Except when feeding on *Chthamalus*, patterns of growth were similar for both small- (mean length 13.6 mm) and medium-sized (mean length 18.6 mm) *Thais emarginata* (Figs. 10 and 11). Growth on all sizes of *Balanus glandula* and *Mytilus edulis* were not significantly different from each other at the upper level (Fig. 10a and 11a); intermediate-sized *Balanus glandula* tended to promote more rapid growth than *Mytilus edulis* at the lower level, but significantly so compared only to the largest *M. edulis* (Figs. 10b and 11b). Two pairs of replicates with medium-sized snails were conducted concurrently with the main experiments, and both showed remarkable agreement with the main treatments (open symbols, Fig. 11a). All sizes of *Semibalanus cariosus* promoted significantly lower growth than all but one of 32 remaining prey types (Fig.

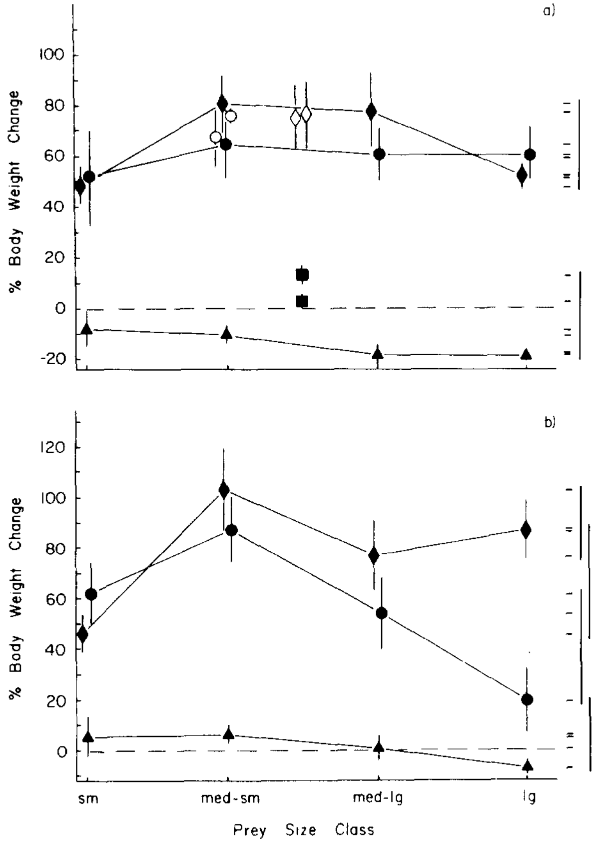

Fig. 11. Percent body weight change over 30 days (26 August to 25 September, 1977) of medium (18.6 ± 0.35 mm) *Thais emarginata* as a function of prey size-class at two tidal heights: a, high (+ 4.5 ft, + 1.4 m); b, mid (+ 2.5 ft, + 0.8 m); ◆, *Balanus glandula*; ●, *Mytilus edulis*; ▲, *Semibalanus cariosus*; ■, *Chthamalus dalli*; open symbols are from individual replicate cages (4 snails/cage) over the same time interval; other symbols and notations as in legend of Fig. 3.

10 and 11). For small *Thais emarginata*, both *Chthamalus* replicates yielded the same or slightly higher growth compared to the small size class of *Balanus glandula* (Fig. 10a). This suggests that for small snails very small barnacles all may be of comparable value (note that the smallest size class of *Semibalanus cariosus*, 4 mm opercular diameter, was closer in size to the medium-small class, 3.5 mm, than to the small class of *Balanus glandula* at 1.7 mm; Fig. 3). In contrast, medium- and large-sized *Thais emarginata* grew significantly more slowly on *Chthamalus* than on small *Balanus glandula* (Figs. 11a and 12a). I am not certain whether these differences also would have been true lower in the intertidal.

Large *Thais emarginata* exhibited rather substantial differences in patterns of growth between the mid (+ 2.5 ft, + 0.8 m) and high (+ 4.5 ft, + 1.4 m) levels (Fig. 12a,b). At

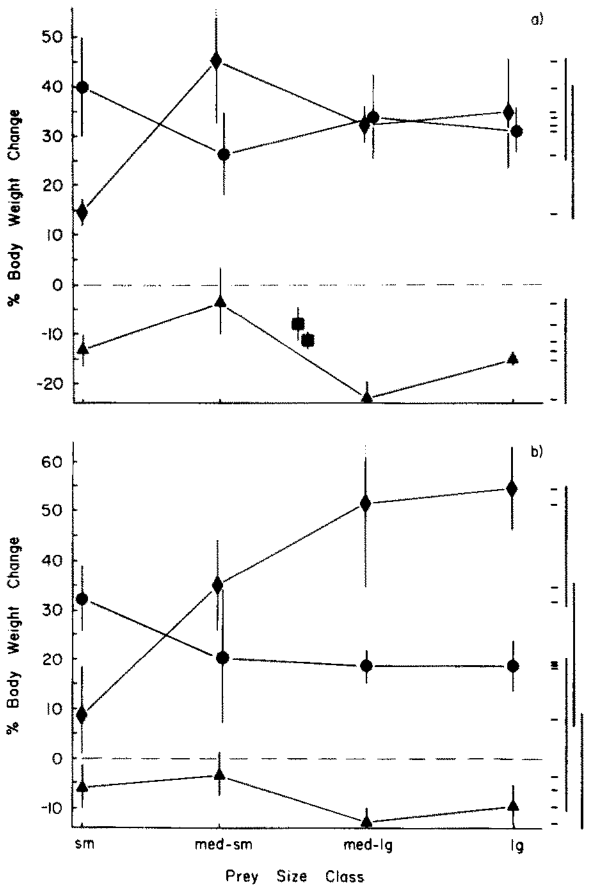

Fig. 12. Percent body weight change over 30 days (26 August to 25 September, 1977) of large (23.3 ± 0.41 mm) *Thais emarginata* as a function of prey size-class at two tidal heights: a, high (+ 4.5 ft, + 1.4 m); b, mid (+ 2.5 ft, + 0.8 m); ◆, *Balanus glandula*; ●, *Mytilus edulis*; ▲, *Semibalanus cariosus*; ■, *Chthamalus dalli*; other symbols and notations as in legend of Fig. 3.

the mid level, the larger two sizes of *Balanus glandula* promoted significantly more rapid growth than all other prey except small *Mytilus edulis* and medium-small *Balanus glandula*. Mussels and smaller *B. glandula* were of intermediate value and all sizes of *Semibalanus cariosus* were of low value. Larger *Balanus glandula* were increasingly more valuable than smaller ones with the reverse being true of *Mytilus edulis*. At the high level, though, there was no clear relation between value and size for these two prey species, and in addition all four size classes of *M. edulis* were not significantly different in value from the three larger size classes of *Balanus glandula*. Prey rankings thus appear to change with tidal height for large *Thais emarginata*. Finally, *Chthamalus dalli* was of significantly lower value than all sizes of *Balanus glandula* and *Mytilus edulis* to large *Thais emarginata*.

DISCUSSION

GROWTH RATE AS A MEASURE OF FOOD VALUE

Short-term rate of growth is perhaps the most biologically relevant measure of net food value to a consumer (subject to certain qualifications presented below) and has been used to assess food quality for a variety of marine organisms including: bryozoa (Jebram, 1974), prosobranch gastropods (Moore, 1938; Engle, 1942; Ino, 1952; Hanks, 1960; Leighton & Boolootian, 1963; Phillips *et al.*, 1973; Hatfield, 1979; Uki & Kikuchi, 1979), opisthobranch gastropods (Carefoot, 1967; Jensen, 1975), marine isopods (Carefoot, 1973), asteroids (Feder, 1970; Menge, 1970, 1972; Yamaguchi, 1974), echinoids (Vadas, 1977, and references therein), and fishes (Paloheimo & Dickie, 1966; LeBrasseur, 1969). The value of food items is otherwise difficult to assess in units meaningful to the consumer because they may vary in both the length of time to be consumed and their total potentially usable energy. Processing costs will also vary among food types, and may include: (1) wear and tear on the consumer's feeding apparatus (Kitting, 1980); (2) metabolic conversion of food calories to calories in a form usable by the consumer; and (3) disposal of waste products. Consequently, indirect measures of food value such as size of an item or caloric content (Paine & Vadas, 1969) may not reflect its value to the consumer accurately in terms of growth or reproduction.

The appeal of growth rate as a measure of food value is that, when no energy is being committed to reproduction, it provides a direct measure of the energy remaining after all costs associated with consuming a prey have been paid. In addition, it requires no knowledge of what these costs actually are. It also may be related directly to various fitness attributes (see below). However, growth rates may vary among individuals or among populations for reasons other than food quality or availability; in particular, invertebrates with heavier skeletons often exhibit slower rates or maximal growth (Palmer, 1980, 1981). Throughout the following discussion "value" or "quality" of prey refer to potential for promoting growth in the consumer.

Several assumptions underly the use of growth rates to assess food value. First, and perhaps most fundamental, is the assumption that rates of growth, when food is supplied ad libitum under experimental conditions, actually reflect inherent food value (per item capacity to promote growth) and are not some measure of desirability (differential consumption rate due to factors not related to growth potential). Thus I have assumed that the rates of growth observed in the experimental cages represented the maximum possible rates for a particular predator on a particular size and species of prey. While most snails were observed feeding during the periodic cage inspections and thus could safely be assumed to have been feeding continuously, snails in some cages consumed few if any prey (Palmer, 1980). Obviously this would occur where available prey were too large to have been consumed and no feeding attempts were made. However, snails caged with medium-large or large mussels often consumed only one or two mussels per snail over a period of 30 days, suggesting that feeding was not continuous. I have assumed that such low consumption rates are associated with feeding constraints due to large prey size, such as digestive pauses (Bayne & Scullard, 1978) or radular replacement, and that although feeding was not continuous, it occurred at the maximum possible rate for that particular prey type.

A second assumption is that prey yielding more rapid growth also yield a relatively higher fitness. This is also an assumption of foraging models in general (Schoener, 1971; Pulliam, 1974; Charnov, 1976; Hughes, 1979). Many studies have documented a positive relation between growth rate and fitness attributes (Moore, 1938; Otte, 1975; Oosterhoff, 1977; Vadas, 1977; Seed & Brown, 1978; see also reviews by Stearns, 1976; Rapport & Turner, 1977). Two fitness attributes may correlate with food value when fed pure diets: (1) age or size at first reproduction, and (2) total reproductive output.

The relationship between growth rate and fitness attributes was examined directly in a separate set of preliminary growth experiments with *Thais emarginata* and *T. canaliculata*, where prey species was restricted but prey size was not. Snails of four non-overlapping size ranges were caged separately with complete size ranges of either *Balanus glandula*, *Semibalanus cariosus*, or *Mytilus edulis* and allowed to feed for 91 days during the summer of 1975. The animals were grown in cages under the same conditions as described in the methods and were interrupted once after 42 days to replenish prey and measure growth.

Growth rate correlated with fitness attributes in both *Thais emarginata* and *T. canaliculata*. In *T. emarginata*, more rapid growth on *Balanus glandula* resulted in an earlier age of first reproduction for initially immature animals (14.2 mm shell length, Table IV). In addition, growth potential of prey (Figs. 11 and 12) was positively related to snail egg capsule production for nearly all sizes of snails (Table IV; but see Skoog, 1978, who found that egg production in freshwater gastropods may not correlate with the growth potential of food). The relation between growth rate and fitness was similar but less clear for *Thais canaliculata* (Table IV). In initially immature snails (20.6 mm shell length), more rapid growth resulted in both an earlier age of first reproduction, when fed *Balanus glandula* and *Mytilus edulis* compared with *Semibalanus cariosus*, and a higher rate of egg-capsule production, when fed *Balanus glandula* compared to *Mytilus edulis*. However, egg capsule production among initially mature animals (> 25 mm) was exceedingly erratic among cages, probably because *Thais canaliculata* have the capacity to produce egg capsules for 3 to 6 wk following removal of food (pers. obs.) and hence rate of capsule production may not respond rapidly to short-term changes in energy intake. Finally, Spight & Emlen (1976) found that larger females of *T. lamellosa* produced more egg capsules than smaller ones. Since *T. lamellosa* spawn only once a year (Spight, 1974), larger size at maturity is a likely consequence of more rapid growth when immature. Thus, fitness appears to correlate positively with growth rate in all three species of *Thais*.

TABLE IV

Total number of egg capsules produced by *Thais canaliculata* and *T. emarginata* during 91 days of feeding (28 June to 27 Sept., 1975) at three tidal heights on three different prey species: 12 snails were present in each size category (± SD); numbers in parentheses include: (1) average size of prey eaten (mm), and (2) average food value of that size of prey, interpolated for predator and prey size from data in Figs. 6–8 and 10–12; rank order: * highest value prey resulted in more egg capsules than lowest value prey; ** rank order of food value for all three prey the same as the rank order of egg capsules produced; ?, no capsules produced.

Initial shell length	*Balanus glandula*	*Mytilus edulis*	*Semibalanus eariosus*	Rank order
		Thais canaliculata		
32.1 ± 3.18 mm	472 (5.1, 27.8)	250 (37.7, 32.6)	431 (9.0, −7.0)	
26.5 ± 2.15	23 (4.8, 74.7)	0 (39.6, 39.8)	15 (8.1, −9.6)	*
20.6 ± 1.85	61 (4.5, 119)	35 (37.8, 51.0)	0 (7.0, −8.1)	**
14.2 ± 2.20	0 (4.6, 152)	0 (36.7, 82.4)	0 (5.4, 74.2)	?
		Thais emarginata		
25.6 ± 2.22 mm	274 (4.8, 46.0)	288 (34.8, 20.2)	431 (7.6, 12.8)	*
21.0 ± 3.57	197 (4.6, 65.9)	98 (34.4, 41.4)	18 (5.1, −0.1)	**
18.6 ± 1.33	63 (4.5, 89.4)	20 (37.2, 53.3)	0 (7.5, 1.3)	**
14.2 ± 2.28	23 (4.3, 129)	0 (34.7, 88.4)	0 (5.7, 8.3)	*

Rapid growth, however, need not result necessarily in a higher fitness. Experiments with *T. lamellosa* have demonstrated that the rate of shell production may limit the maximum rate of body growth (Palmer, 1981). Thus, more rapid body growth could result in thinner shells that would increase the probability of being eaten by crabs (Kitching *et al.*, 1966; Palmer, unpubl.). On the other hand, smaller snails are more vulnerable to crabs of a given size than larger snails (Vermeij, 1978), so a compromise exists between decreasing vulnerability and decreasing the amount of time spent as a small-sized individual (Palmer, 1979, 1981). In such situations, maximal growth may not be advantageous.

A third assumption about the use of growth on pure diets as a measure of food value, is that growth rate on a single prey type will not be enhanced by the consumption of another type (Grime *et al.*, 1970; Westoby, 1974; Pulliam, 1975; Rapport, 1980).

However, complementarity is likely to be less important for carnivores than for herbivores or omnivores because animal flesh is more nutritionally complete. Thus for *Thais*, the assumption of little or no nutrient complementarity among prey species seems safe.

A fourth assumption is that growth is distributed uniformly throughout the body, or more specifically, that, regardless of reproductive condition, the ratio of body weight gain to assimilated energy is constant. Mature individuals may store energy in gonads and exhibit less body weight gain than individuals using energy for tissue growth. Consequently rates of growth of mature animals are not necessarily comparable to those of immature ones. Growth of immature animals should provide the most valid measure of food value. Another difficulty with using growth rates of mature individuals is that metabolic requirements for growth and reproduction may be different. Thus while growth rates of immatures will influence age or size at first reproduction, the rate of body-weight gain on different diets may be less correlated with fitness in animals storing energy for or expending energy in reproduction. In the main experiments of 1977, immature snails were allowed to grow for only one month and none produced egg capsules; thus differences in rate of growth should not reflect differential partitioning of energy to growth and reproduction.

ECOLOGICAL IMPLICATIONS

RESOURCE PARTITIONING AMONG *THAIS* SPECIES

Despite some similarities, trends in growth rates varied among the three species of *Thais* examined, reflecting or perhaps being partly responsible for differences in habitat use (Ricketts *et al.*, 1968; Kitching, 1977; Bertness, 1977; Palmer, 1980). Based on the results for small- and intermediate-sized snails, *T. lamellosa*, the lower shore species from more protected coasts, grows consistently more rapidly (11 of 12 cases) on intermediate- to large-sized *Balanus glandula* (significantly so in 8 of 12 cases), and appears to grow the least well on intermediate- to large sized *Mytilus edulis* of all three *Thais* (not significantly different from 0 in 20 of 24 cases; Figs. 3 and 4). *T. emarginata*, on the other hand, the high shore species from regions of intermediate to high wave exposure, grows most rapidly on all sizes of *Balanus glandula* and *Mytilus edulis* (significantly greater than all sizes of *Semibalanus cariosus* in 43 of 48 cases; Figs. 10–12) both of which are more likely to occupy the upper intertidal. It grows consistently more slowly on *S. cariosus* (16 of 16 cases, the lower intertidal barnacle with which it has less frequent contact. Finally *Thais canaliculata*, the mid-intertidal species most restricted to current-swept or wave-exposed shores (Palmer, 1980), grows rapidly on *all* species of prey; the only prey promoting growth that was not significantly different from 0 were the larger two size classes of *Semibalanus cariosus* (11 of 12 cases), small *Balanus glandula* (3 of 6 cases), and small *Semibalanus cariosus* (2 of 6 cases); (Fig. 6 to 8). Furthermore, it is the only species to show a significant positive growth on the medium-large size class of *S. cariosus* (Fig. 7b), and is also the only species for which *Mytilus edulis* may surpass *Balanus glandula* in value (Fig. 8). The three species of *Thais*, by experiencing different availabilities of prey species correlated with differences in predator habitat, appear to have evolved different abilities to grow on these different prey species.

Since the growth rate differences described here fairly accurately predict prey preferences exhibited by all three *Thais* when a choice of prey is available (Palmer, unpubl.), they may reflect food resource partitioning among these potentially competing predators. The prey rankings described above also suggest that partitioning of lower value prey types may be more important ecologically than partitioning of high value prey. High value prey always may be eaten opportunistically while low value prey may be potentially important sources of food during times of shortage. The three *Thais* species thus exhibit differences in both habitat use and prey rankings. The data presented here do not permit an evaluation of which resource dimension is more important in permitting coexistence, but both appear to reduce the degree of overlap of shared resources.

PREY RANKING DIFFERENCES AMONG *THAIS* SIZE CLASSES

Two trends with predator size were apparent (Table V): (1) medium-small and medium-large *Semibalanus cariosus* and large *Balanus glandula* were of relatively higher value prey for larger *Thais* of all three species while smaller barnacles were of lower

TABLE V

Cumulative change in rank position of prey (from Figs. 3–8 and 10–12) from the small to the large size class of predator, summed for both tidal levels: actual prey sizes listed in legend of Fig. 3; N.O., not offered.

Prey		Predator species		
Species	Size	*Thais lamellosa*	*Thais canaliculata*	*Thais emarginata*
Balanus glandula	Sm	-7	-3	-2
	MS	-7	-7	0
	ML	-5	-1	-4
	Lg	+4	+2	+8
Mytilus edulis	Sm	+3	0	+2
	MS	+11	+7	-4
	ML	+2	+6	-1
	Lg	+1	0	+3
Semibalanus cariosus	Sm	-2	-11	-2
	MS	-2	+6	+4[a]
	ML	0[a]	+2[a]	–[b]
	Lg	–[b]	–[b]	–[b]
Chthamalus dalli		N.O.	N.O.	-4[c]

[a] Prey not eaten by smallest snail size class.

[b] Prey not eaten by any snail size class.

[c] Value doubled from rank at one tidal height to be comparable with all other tabled values.

value for larger predators; and (2) with the exception of *Thais emarginata*, *Mytilus edulis* of all sizes tended to increase in relative value with increasing snail size. In addition, for *Thais emarginata*, the rank value of *Chthamalus dalli* was substantially lower for larger snails. The rank decrease for *C. dalli* was greater than that for comparable sized *Balanus glandula* (small size class, Table V) suggesting that this rank change was not due solely to the small size of *Chthamalus dalli.* Prey rankings thus change with snail size, both within and among prey species. Small barnacles may be valuable prey for small snails but not for large ones of the same species. On the other hand, within the size range that barnacles are vulnerable to snails, larger barnacles are of higher value to larger snails. Such rank shifts underscore the need to define prey types in units relevant to the predator. Prey species may not always be a relevant unit.

Although different prey rankings may be evidence for resource partitioning among *Thais* species, ranking shifts with predator size seem unlikely to reflect intraspecific resource partitioning; the size-related ranking shifts are due more likely to mechanical limitations imposed by the size of the radula or accessory boring organ (Radwin & Wells, 1968), to limitations to the rate at which tissue may be consumed, or possibly to sensory limitations. When drilling barnacles, all three *Thais* attack preferentially at sutures between skeletal plates, either between parietal plates (*T. canaliculata* and *T. lamellosa*) or between opercular plates (*T. emarginata*) (Palmer, 1982a). Large snails may have difficulty locating sutures on small barnacles, whereas small snails may be unable to consume all the flesh of large barnacles before it begins to decompose. Thus size-related rank shifts are probably a consequence of nonadaptive size constraints rather than a result of selection for resource partitioning among predator size classes.

POSSIBLE EFFECTS OF *THAIS* PREFERENCES ON PREY DISTRIBUTION

One consequence of preferential consumption of higher value prey by *Thais* is that, to avoid being eaten, natural selection should favor the ability of these higher value prey to survive higher on the shore. Because risk to *Thais* from temperature or desiccation stress at low tide increases in an upshore direction (Bertness, 1977), snails are less likely to forage, and thus prey are less likely to be consumed, higher on the shore. However, evidence from other species suggests that predators will expose themselves to increased risk if the potential rewards are higher (Milinski & Heller, 1978; Sih, 1980). Predatory intertidal gastropods appear able to assess the risk of dislodgement by waves associated with consuming particular prey and to modify their choices accordingly (Menge, 1974). Hence, if *Thais* can evaluate the trade-offs between risk and reward, as suggested elsewhere (Emlen, 1966; Menge, 1978a,b; Palmer, unpubl.), the upper shore limit to which they should be willing to feed on particular prey species should be related positively to the food value of that prey species.

The parallel between the food value rankings and the vertical distributions of prey in the field suggests that relative food value to *Thais* has been an important component of the selective environment influencing the evolution of these prey species. When the

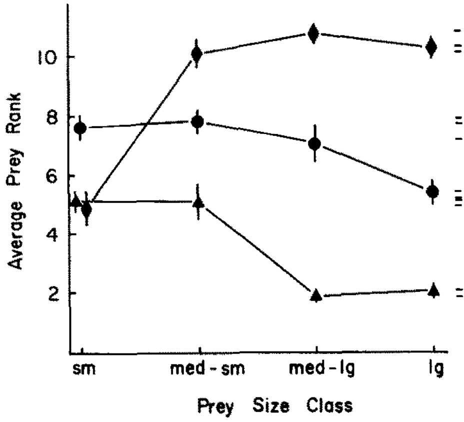

Fig. 13. Mean prey rank, pooled for all sizes and species of *Thais* and all tidal heights, as a function of prey size class: each point corresponds to a mean of 18 rank values; ◆, *Balanus glandula*; ●, *Mytilus edulis*; ▲, *Semibalanus cariosus*; error bars are ± 1 SE; actual prey sizes in Fig. 3; vertical bars to the right of the figure indicate means among which there are no significant differences ($P < 0.05$, SNK multiple comparisons test; Zar, 1974).

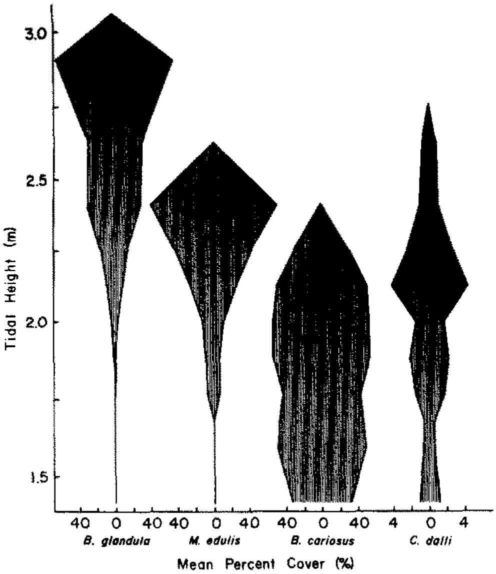

Fig. 14. Vertical distributions of *Thais* prey species in Torch Bay, Alaska (58°20'N: 136°48'W) in July 1980: the width of a figure at a given tidal height represents the mean percent cover of the species based on six replicate 0.1 m^2 quadrats; note the different scale used for *Chthamalus dalli*; tidal heights are in meters above MLLW (US DATUM).

rank values of all prey types are pooled for the three *Thais*, highly significant differences among prey species result: except for the smallest size class of *Balanus glandula* and the largest of *Mytilus edulis*, *Balanus glandula* is of significantly higher rank than *M. edulis* which is of significantly higher rank than *Semibalanus cariosus* (Fig. 13). Distributional surveys have shown that the upper limits of these species have the same rank order: *Balanus glandula* > *Mytilus edulis* > *Semibalanus cariosus* (Dayton, 1971; Kitching, 1977; Bertness, 1977). This pattern also applies to the heights of maximum prey abundance and is particularly apparent on shores of intermediate exposure on the coast of SE Alaska (Fig. 14) where *Thais* densities can be very high (>300 individuals/m^2, Palmer, 1980). On the outer coast of Washington, *M. edulis* is generally restricted to higher shore levels than *Mytilus californianus* except when it temporarily invades patches cleared of *M. californianus* lower on the shore (Suchanek, 1978). This vertical distribution agrees with the food value ranking of these two prey species for *Thais canaliculata* (Fig. 9), the exposed coast specialist (Kitching, 1977; Palmer, 1980). Thus, not only can the presence of a predator influence the distribution of its prey, but the relative food value of the prey can determine the extent of this influence.

POSSIBLE EFFECTS OF *THAIS* PREDATION ON THE EVOLUTION OF PREY MORPHOLOGY AND LIFE HISTORY PATTERNS

Regional differences in the intensity of predation may influence the degree of development of antipredatory morphologies in both ecological and evolutionary time (Vermeij, 1977, 1978; Palmer, 1979, 1982a). Also, in marine systems larger predators commonly are capable of consuming larger prey (Dayton, 1971; Paine, 1976; Black, 1978; Palmer, unpubl.). These two patterns receive additional support from the present study. Although any sized *Balanus glandula* and *Mytilus edulis* may be consumed by almost any sized *Thais* larger than 10 mm, both *Semibalanus cariosus* and *Mytilus californianus* reach sizes at which they are invulnerable to attack (Table V, Fig. 9). Thus these two species are able to persist lower on the shore in the face of *Thais* predation, presumably because both possess heavier skeletons than their congeneric counterparts (Emlen, 1966; Harger, 1972). *Semibalanus cariosus* also possesses strongly sculptured parietal plates that may reduce the ability of *Thais* to recognize sutures between plates (Palmer, 1982a). Finally, small adult size in *Chthamalus dalli* may have been selected because it reduces the potential value of this barnacle as food to most sizes of *Thais* (Fig. 11 and 12). *Chthamalus dalli* may persist in the rocky intertidal due to its escape from predation at the small end of the size spectrum as suggested by Paine (1981), rather than at the large end, in contrast to normally observed size refuges. This assumes, of course, that other barnacle predators, such as nemerteans or starfish, and disturbance agents such as bulldozing limpets (Dayton, 1971), are not as harmful proportionately to small barnacles.

FOOD VALUE, PREDATOR FITNESS AND THE STRENGTH OF SELECTION

To assess the adaptive value of traits or behaviors requires that presumed benefits somehow be related to differences in fitness. Because it is difficult to measure fitness directly, indirect measures are usually used. I have proposed here that growth rates on single species diets provide a biologically meaningful measure of food value to prereproductive, carnivorous predators. One important assumption implicit to such a proposition appears to be justified for *Thais*: age at first reproduction is earlier and egg capsule production greater on diets promoting more rapid growth. A connection thus exists between prey value, in terms of growth potential, and fitness.

Thais growth rates vary among prey species, among sizes of prey within species, and with predator size and tidal height. The complexity of these patterns emphasizes the importance of assessing food value or rank in terms relevant to the predator. These patterns also highlight how measures of food value relate to attributes of the prey (adult size, shell thickness, skeletal morphology) and also how prey preferences may determine the degree of impact a predator has on prey distributions.

The evolutionary pressure exerted by a particular predator will depend on its relative contribution to the total mortality experienced by a prey species. At a given tidal height, prey of higher value will be more likely to be consumed than prey of lower value (Palmer, unpubl.). Natural selection thus should favor the evolution of traits that either: (1) reduce the value of prey to the predator, or (2) reduce the accessibility of prey to the predator. In the system described here, those prey that have remained more accessible (lower in the intertidal) have evolved defensive morphologies or life-history attributes that act to reduce their value to *Thais*: heavier skeletons (*Semibalanus cariosus*, *Mytilus californianus*), strong external sculpture (*S. cariosus*), large adult size (*S. cariosus*, *Mytilus californianus*), or very small adult size (*Chthamalus dalli*). Those prey that have less effective morphological or life-history defenses have evolved distribution patterns that reduce their accessibility: both *Balanus glandula* and *Mytilus edulis* extend higher in the intertidal than their co-occurring congeners thus increasing the potential risk experienced by snails attempting to consume them.

The above conclusions depend upon on a biologically meaningful evaluation of prey value and emphasize the power of such an approach. The prey rankings obtained from the growth experiments thus not only provide a foundation from which to evaluate *Thais* foraging behavior quantitatively (Palmer, unpubl.) but also provide some insights into the potentially strong selective pressures exerted by *Thais* on the evolution of their prey. Clearly, many other factors are also likely to have influenced the evolution of morphology and distribution in these prey species. However, since predation by *Thais* can virtually eliminate preferred prey from lower on the shore (Connell 1961a, 1970; Menge, 1978b; Suchanek, 1978; Palmer, 1980), it seems likely to be and to have been an important agent of natural selection.

ACKNOWLEDGEMENTS

This paper derives in part from a dissertation submitted in partial fulfillment of the requirements of a Ph.D. at the University of Washington, Seattle (U.S.A.). I thank my reading committee (Drs. R. T. Paine, T. W. Schoener, and R. R. Strathmann) and P. W. Frank, J. C. Holmes, R. B. Lowell, L. Stinson, and C. M. Young for helpful comments. This research was funded in large part from NSF grants to R. T. Paine. The Director and staff of the Friday Harbor Laboratories are gratefully acknowledged for their assistance during this study.

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