Functional significance of shell sculpture in gastropod molluscs: test of a predator-deterrent hypothesis in *Ceratostoma foliatum* (Gmelin)

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Abstract

A predator-deterrence function for the varices of the muricid gastropod *Ceratostoma foliatum* was tested. In the first set of experiments, snails of five treatment groups were presented over a 10-week period to one of three predators: sunflower stars (*Pycnopodia helianthoides* Brandt), red rock crabs (*Cancer productus* Randall), and kelp-greenling fish (*Hexagrammus decagrammus* Pallas). The five treatment groups were: snails with all varices removed, snails with one only of the right, middle, or left varix removed, and snails with all varices intact. The kelp-greenling fish ate no snails and were discarded from subsequent experiments. Seastars consumed significantly more snails with all varices removed than any of the other treatment groups. Crabs ate significantly more snails with all varices- and right varix-removed compared with the other three groups. Thus, snails with all varices intact were less likely to be eaten by either crab or seastar predators. Scoring the shells of *Ceratostoma*, but leaving the varices intact had no effect on consumption rates by either seastars or crabs. In a second set of experiments, the smooth-shelled *Nucella lamellosa* (Gmelin) was presented as a food item along with *Ceratostoma* with all varices removed and *Ceratostoma* with all varices intact for an 8-week period. Seastars clearly preferred the smooth-shelled *Nucella* over the other two groups. In contrast, crabs ate *Ceratostoma* with all varices removed at a greater rate than control *Ceratostoma* and *Nucella.* Energy content of dry flesh of the two snail species was almost identical, suggesting that other factors were involved in governing selection of one prey species over the other. In both sets of experiments, ingestive conditioning learning was not apparent for either the seastars or the crabs. Crabs were videotaped while feeding on *Ceratostoma* with all, one only, or no varices removed. The videotapes revealed that a combination of chipping the shell around the aperture with the chelipeds, then snapping it in half, was the method most often used to gain access to the soft parts of the shell. However, snails with all varices removed were more often snapped in two without any preliminary chipping, presumably because the lack of varices made them easier to break apart. There was no relationship

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between snail treatment and the time it took to break into the shell. © 1999 Elsevier Science B.V. All rights reserved.

1. Introduction

Muricid gastropods are characterized by elaborately sculptured shells, but little is known about the function of these ornamentations. Indeed, little is known about the behaviors generally of muricid gastropods, save for that relating to feeding and reproduction (Spight et al., 1974; Spight and Lyons, 1974; Radwin and D'Attilio, 1976; Kent, 1981). Suggestions for varix function fall into four general categories relating to: (1) stabilizing the shell in currents, waves, or shifting substrata, (2) affecting falling and subsequent landing orientations, (3) aiding in feeding or sensory input, and (4) protecting through camouflage or shell-strengthening (references in Carefoot and Donovan, 1995). Of these, only the second has received any specific attention, although the fourth, shell-strengthening, is inferred from numerous studies on the relationship between shell thickness and predation of thaidid gastropods by crabs and fish (Ebling et al., 1964; Kitching et al., 1966; Hughes and Elner, 1979; Palmer, 1979, 1985; Vermeij, 1982; Wellington and Kuris, 1983; Lawton and Hughes, 1985).

Tests on falling and landing orientation in *Ceratostoma foliatum*, a muricid species characterized by three large wing-like varices on the main body whorl (Fig. 1), have shown that the middle varix acts to destabilize the animal's orientation during long falls through the water column (greater than 20 body lengths; Palmer, 1977), while the right
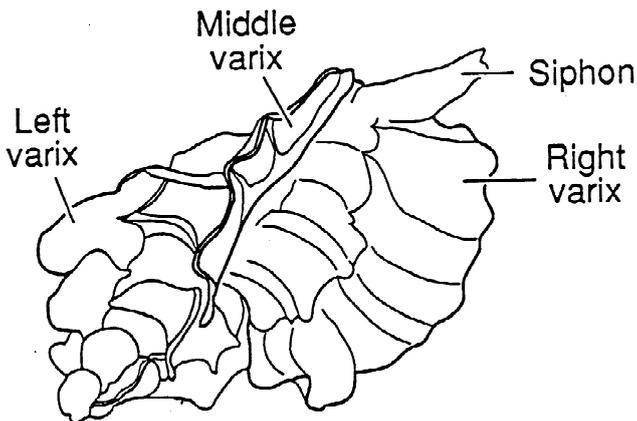

Fig. 1. Oblique view of *Ceratostoma foliatum* to show the three varices.

varix acts to destabilize during short falls (less than five body lengths; Carefoot and Donovan, 1995). After long falls, landing in the aperture-down orientation predominates while, after short falls, if not in the aperture-down position, landing is more on the left and middle varix-pair at the expense of that on the right and middle pair. The importance to the animal of this bias in landing is that righting from a left-side orientation is much faster and four times less energetically costly than righting from the right-side orientation (Carefoot and Donovan, 1995). The broad implication evident from both studies is that a quick return to the stable, aperture-down, foot-attached position after falling is favored, presumably as protection against predators.

But what animals prey on *Ceratostoma*? Palmer (1977) suggests that kelp-greenling fish (*Hexagrammus decagrammus*) prey upon *C. foliatum* by dislodging the snails and consuming the exposed soft parts during righting, but direct evidence for this is lacking (see Carefoot and Donovan, 1995). Pile perch (*Rhacochilus vacca*) or spinynose sculpins (*Asemichthys taylori*) could possibly feed on juvenile *C. foliatum* of a size similar to that of their normal gastropod and mussel prey, but this has not been reported (McCormack, 1981; Norton, 1988). Cancrid crabs such as the red rock crab *Cancer productus* occupy the same rock-strewn habitat as *C. foliatum*, as do a variety of seastars including the large, fast-moving sunflower star *Pycnopodia helianthoides*. Although neither predator is known specifically to eat *C. foliatum*, both have the capability to capture, subdue, and ingest marine gastropods (Morris et al., 1980). In the case of *Cancer* spp., the snail is crushed by the chelipeds and the flesh extracted (Zipser and Vermeij, 1978; Lawton and Hughes, 1985). Commonly, the shell is peeled back in pieces from the aperture, as demonstrated by *Cancer pagurus* eating the thaidid *Nucella lapillus* (Lawton and Hughes, 1985). Refuge from crab and fish predation for *Nucella* and *Thais* is gained through possession of a thicker shell (Kitching et al., 1966; Palmer, 1979), longer spines (Palmer, 1979), and growth of larger apertural teeth resulting in a narrower aperture (Hughes and Elner, 1979; Appleton and Palmer, 1988). Death of snails from seastar predators is through no failure of shell structure; rather, size is presumably the determinant of whether or not a captured snail can be subdued by ingestion or digested in situ. The wing-like varices on *C. foliatum* could act as strengthening buttresses, thereby reducing crab predation, or could function to increase the overall size of the snail, thereby reducing both crab and seastar predation.

The purpose of the present study was to test the hypothesis that varices protect *Ceratostoma foliatum* from predators. In the first set of experiments, we predicted that intact specimens of *C. foliatum* would be less susceptible to predation than specimens with varices removed, either singly or all three absent. In the second set of experiments, we predicted that a species without varices, *Nucella lamellosa*, would be preferentially preyed upon rather than *C. foliatum*. Potential predators tested for these two sets of experiments included kelp-greenling fish *Hexagrammus decagrammus*, red rock crabs *Cancer productus*, and the sunflower star *Pycnopodia helianthoides*. As well as recording the final number of each prey consumed, cumulative weekly numbers of ingested prey were recorded to determine if predator learning occurred. Finally, we videotaped crabs as they attacked and consumed intact and devarixed *C. foliatum* in an attempt to disclose behavioral patterns in the crab to explain their preference for devarixed snails.

2. Materials and methods

Specimens were collected in Barkley Sound, British Columbia, in the vicinity of the Bamfield Marine Station, and transported to the Vancouver Aquarium where the experiments were conducted. Individual predators were contained in a pair of mesh baskets joined at their tops (50 cm diameter × 75 cm depth) with openings small enough to prevent the escape of the snails, but large enough to ensure adequate water circulation. The baskets were floated in a 1000-l capacity fiberglass tank through which fresh sea water was circulated at 100 l min^{-1} (27‰, 12–13°C). The close confines of the basket ensured that each predator had ready access to all prey, yet still provided freedom of movement. Prior to being used in an experiment, prey were held in baskets identical to those housing the predators and floated in the same fiberglass tank. They were kept with an abundant supply of mussels (*Mytilus trossulus*) as food. Varix removal (described below) of *Ceratostoma foliatum* was performed before the start of the experiment to minimize disruption to the snails during experimentation.

2.1. Feeding preferences on treated C. foliatum

The first set of experiments were designed to test whether *Ceratostoma* with varices removed would be preferentially preyed upon over intact *Ceratostoma*. Five kelp-greenling fish (25–30 cm in length), five seastars (19–28 cm diameter), and six crabs (8–15 cm carapace width) were individually caged with 15 *C. foliatum* (20–80 mm range in length). The predators were of average adult size, but not as large as the maximum for the respective species. The snail prey were divided into five treatment groups, with three representatives for each. The treatment groups were: (1) snails with all varices removed, (2–4) snails with one only of right, middle, and left varices removed, respectively, and (5) snails with all varices intact. Varices were removed with a rotary grinder, taking care not to heat the animals through friction or to weaken the shell at the shell–varix junction by over-grinding. To minimize this last risk, a small ridge of thickened shell representing the varix base was intentionally left. Since it was impossible to supply all predators with prey of identical size, a size range was used (noted above) which was similar for each treatment group. In order to replace consumed snails, the baskets containing predator and prey were removed from the water and the predator transferred to empty baskets. Prey that were eaten were identified as to size and treatment group, and replaced with comparable size and treated live snails. The length of each snail was measured prior to being placed in the predator's cage. A few minutes were allowed for the snails to attach to the cage before the predator was reintroduced. Replacement occurred every 2 days, thus the original size and treatment complement of 15 snails was re-established every 2 days. A single cage of 15 snails representing the five treatment groups, but without a predator, was maintained as a control. The experiment lasted 10 weeks.

Cumulative weekly totals of consumed prey were recorded to determine if predator learning occurred. In this case, if one treatment-type was preferred over other treatments, we would expect the number of preferred individuals consumed per week to increase as the experiment proceeded and a plot of cumulative number versus time would show an

accelerating rise. Conversely, numbers of non-preferred individuals consumed per week would decrease and the curve would show a decelerating fall.

In order to determine whether it was the result of grinding the shell, rather than actual removal of varices that was attracting predators, three treatments of *C. foliatum* were provided to seastar and crab predators (kelp greenling were discarded as predators in this and all subsequent experiments since no snails were consumed by these fish in the first experiment). Our hypothesis here was that grinding the varices could expose substances attractive to predators such that devarixed snails would be preferentially preyed upon because of the grinding rather than the lack of varices. The treatments were: (1) snails whose shells had been scored with a grinder such that fresh shell was exposed parallel with and along the length of each varix but no varices removed, (2) snails with all varices removed, and (3) snails with all varices intact. Thus, in the experimental baskets nine snails (29–81 mm length) were available to each seastar ($n = 6$; 19–28 cm overall diameter) and crab ($n = 6$; 12–18 cm carapace width), with the consumed snails being replaced every two days as described above. The experiment lasted 8 weeks.

2.2. Feeding preferences on different species of snails

The second set of experiments were designed to test whether a smooth-shelled snail *Nucella lamellosa* (28–48 mm range in length) would be preferentially preyed upon by seastars and crabs over comparably sized *C. foliatum* (represented by two treatment groups: ones with all varices removed and ones with all varices intact; both 28–48 mm range in length). Here, shell length was standardized so apparent size of the intact *C. foliatum* was considerably greater than *N. lamellosa* owing to the extended varices of the former. The de-varixed treatment group of *C. foliatum* was intended to mimic the *Nucella* group. Each treatment group included three individuals. Thus, in the experimental baskets, nine snails were available to each seastar ($n = 7$; 17–33 cm overall diameter) and crab ($n = 5$; 12–17 cm carapace width), with the eaten snails being replaced every two days as described for the first experiment. The experiment lasted 8 weeks and cumulative weekly totals of consumed prey were recorded as described in the first experiment. A similar control cage of snails without predators was maintained as described above.

To determine if differences in feeding rates on the different species of snails could be due to energy content of the snails, the J Unit mass^{-1} of each snail species was determined. The flesh from a size range of individuals of each species (31–66 mm length for *C. foliatum* and 19–65 mm length for *N. lamellosa*) was extracted from the shells, dried to constant weight at 90°C, pulverized, and combusted individually in a Phillipson micro-bomb calorimeter.

2.3. Videotaped feeding behaviors of crabs

In the final experiment, crabs were videotaped as they attacked and consumed intact and devarixed *C. foliatum* in an attempt to disclose behavioral patterns in the crab to explain their preference for devarixed snails. Crabs ($n = 4$) were placed individually in aquaria supplied with fresh seawater (4 l min^{-1}) and shrouded in black plastic to

minimize disturbance. Five equal-sized snails (one each of the five treatment types described in the first feeding experiment) were placed in each aquarium. Each crab was videotaped overnight and the tanks were examined the next morning for signs of feeding. Consumed snails were identified as to their treatment type and shell fragments from these snails were collected. The videotapes were analyzed for information on which treatment type was picked up and eaten directly, and which type was discarded for another. For the first category, the following data were obtained: (1) treatment type, (2) how long manipulated before being eaten, and (3) method of death (shell chipped away, shell snapped in two, or a combination of both). For the second category, where one snail was put down for one or more others before one was eaten, the following was noted in addition to the three above: (1) the treatment types picked up and manipulated prior to the one ultimately eaten.

2.4. Statistical analyses

There is considerable controversy over the correct statistical tests for analysis of feeding preference data, because the selection of one food item will affect subsequent selection of others (Peterson and Renaud, 1989; Roa, 1992; Manly, 1993). Specifically, since three or more prey items were presented simultaneously to individual predators, the consumption of one prey type was not independent of the consumption of the other types. After initial statistical analysis showed that the data from several of our experiments were not normally distributed and since autogenic change (Peterson and Renaud, 1989; Roa, 1992) was not an issue due to the length of the experiments, we chose to use the Quade test (Conover, 1981; Roa, 1992) to analyze differences in feeding rates of predators on the different snail treatments. Using this test, null hypotheses of no differences in the consumption of different prey items were rejected if the test statistic, T_1, was greater than the F distribution at the $\propto = 0.05$ level for the appropriate degrees of freedom. A multiple comparison test for use with the Quade test (Conover, 1981; Roa, 1992) was used if a significant difference between groups was found.

Analysis of the learning curves (plots of cumulative numbers of ingested prey versus time) was also confounded by lack of independence of the data. Thus, we have limited our discussion of these data to general comments based on shapes of the curves with no formal statistical analysis.

An ANOVA followed by Newman–Keuls' multiple comparison test was applied to some data on sizes of snails eaten by the predators.

3. Results

3.1. Feeding preferences on treated C. foliatum

No snails were consumed by the kelp-greenling fish during the first experiment, and the fish were subsequently dropped as a potential predator from the rest of the experiments. The fish were placed together in a larger tank with a supply of snails for a

subsequent 20-week period, but no *C. foliatum* were consumed. No snails died in the control groups in any of the feeding experiments, indicating that all mortalities were due to crab or seastar predators.

The seastar *Pycnopodia helianthoides* ate the five treatment types of *C. foliatum* at significantly different rates (Fig. 2a and b; $T_1 = 3.2$, $p < 0.05$, Quade Test), with the completely devarixed group differing significantly from all other groups ($p < 0.05$, multiple comparison test). Daily observations on the activity of the predators showed that all snails were killed by being ingested; none was killed through stomach extrusion and external digestion. In addition to the 53 snails eaten in total by the seastars, six others were ingested but not digested. These were later regurgitated in apparently good health after residing in the gut for periods ranging from 1–3 days. There was no effect of predator size on prey size eaten (snail length eaten (mm) = 26.3 + 0.77 seastar size (cm), $r^2 = 0.57$, $t = 1.99$, $p = 0.14$. Note: underestimations of slopes in this regression and in ones to be presented later were compensated for by application of reliability ratios k: see Carefoot and Donovan, 1995). The smallest seastar at 19 cm diameter ate snails ranging in length from 28–58 mm, while the largest seastar at 28 cm diameter ate snails of 29–61 mm.

The crab *Cancer productus* also ate the five treatment groups of *C. foliatum* at significantly different rates (Fig. 3a and b; $T_1 = 5.4$, $p < 0.01$, Quade test). The groups differed significantly with the all varix- and right varix-removed groups being eaten most and the left varix-removed, middle varix-removed, and intact groups being eaten least ($p < 0.05$, multiple comparison test). However, there was statistical overlap between these groups. As with the seastars, there was no significant effect of crab size on prey size eaten (snail length eaten (mm) = 42.7 + 0.75 crab width (cm), $r^2 = 0.43$, $t = 1.73$, $p = 0.16$), and the smallest of the six crabs at 80 mm carapace width was able to eat the same size range of snails as did the largest crab at 148 mm carapace width.

Mock varix removal had no effect on consumption of *C. foliatum* by either the seastars or crabs. Seastars consumed snails with all varices removed at a greater rate than either intact or mock-treated snails (Fig. 4a; $T_1 = 8.7$, $p < 0.01$, Quade test; $p < 0.05$, multiple comparison test). Likewise, crabs consumed snails with all varices intact at nearly the same rate as mock-treated snails, while snails with all varices removed were consumed at a significantly greater rate (Fig. 4b; $T_1 = 8.4$, $p < 0.01$, Quade test; $p < 0.05$, multiple comparison test).

3.2. Feeding preferences on different species of snails

In the second set of experiments, which compared predation on normal and all-devarixed *C. foliatum*, and on the smooth-shelled morph of *Nucella lamellosa*, seastars consumed *Nucella* almost exclusively (Fig. 5a). When the data were size-corrected, seastars ate significantly more *Nucella* than intact *Ceratostoma* or all-devarixed *Ceratostoma* (Fig. 5b; $T_1 = 11.6$, $p < 0.01$, Quade test; $p < 0.05$, multiple comparison test).

In comparison, crabs consumed all-devarixed *Ceratostoma* at the greatest rate, followed by intact *Ceratostoma* and *Nucella*, respectively (Fig. 6a). The size-corrected rates of consumption for the groups differed significantly ($T_1 = 14.7$, $p < 0.01$, Quade
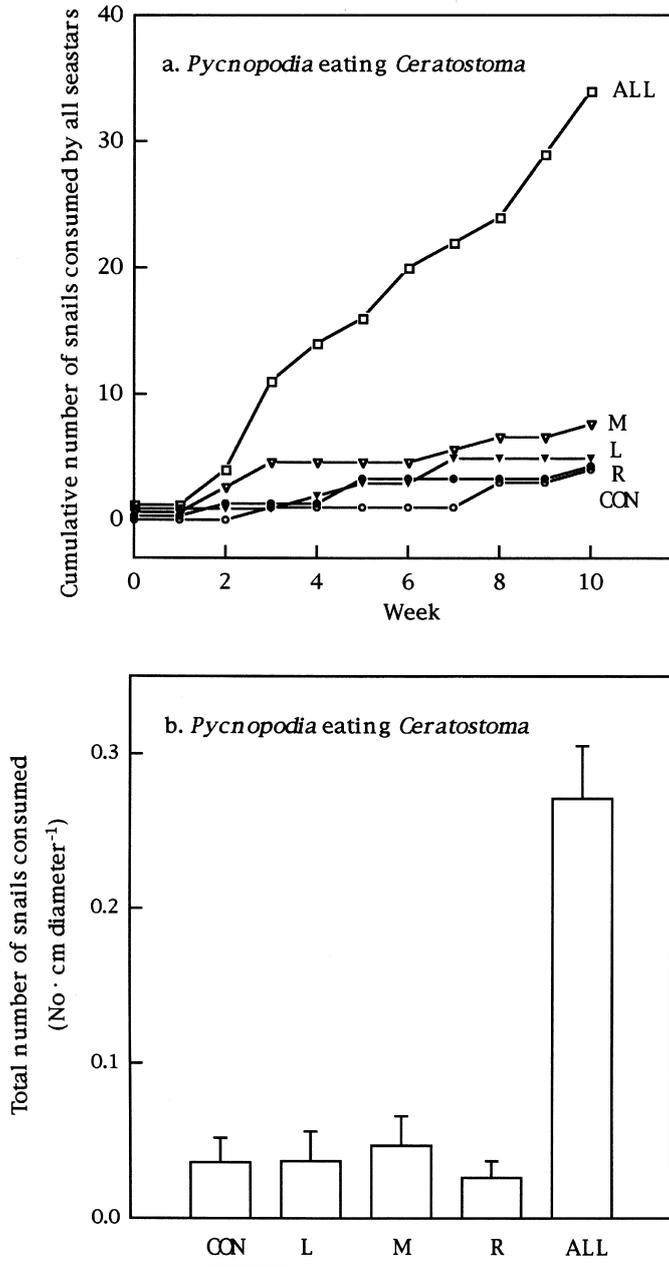
Fig. 2. Consumption data for the seastar *Pycnopodia helianthoides* eating the snail *Ceratostoma foliatum* over a 10-week period. (a) Cumulative number of snails eaten by five seastars. (b) Total number of snails eaten, corrected for size of seastar. Vertical bars in (b) represent S.E. and solid lines below the *x*-axis show statistically homogenous groupings ($p < 0.05$, multiple comparison test). Treatment groups of snails were: CON: all varices intact; L, M, R: either the left, middle, or right varix removed, respectively; ALL: all varices removed.
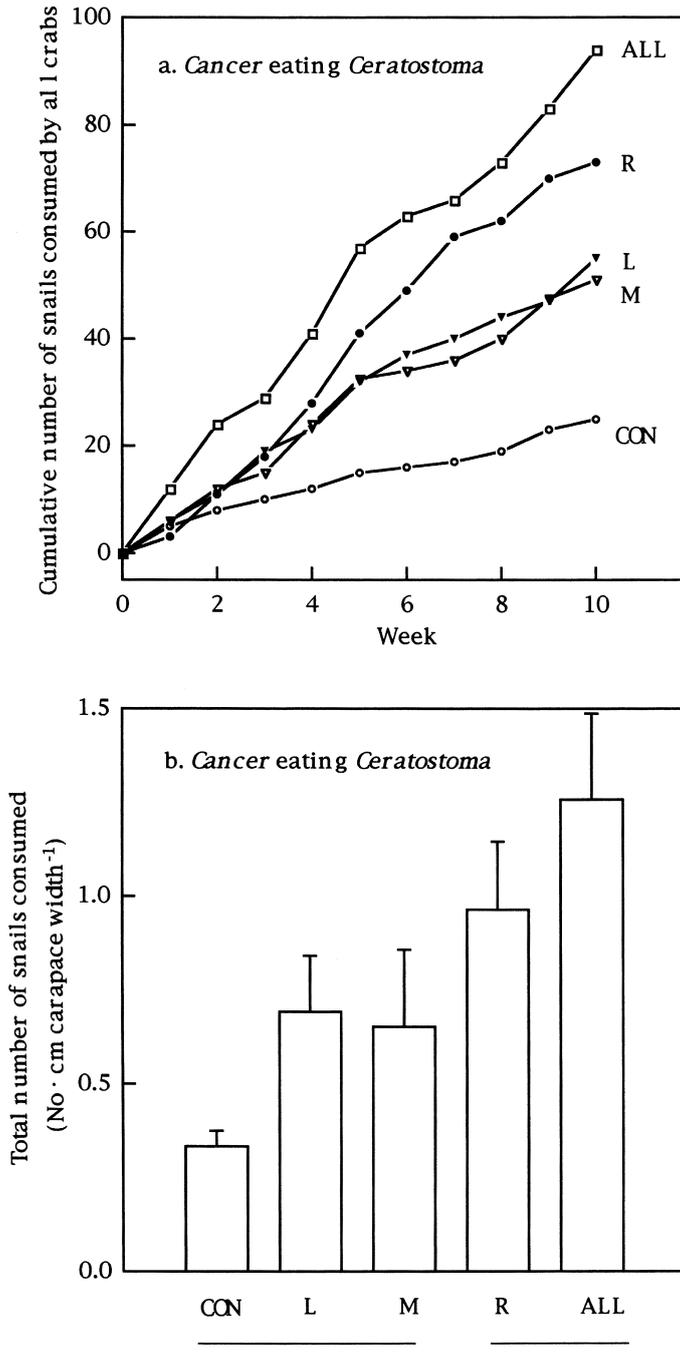
Fig. 3. Consumption data for the crab *Cancer productus* eating the snail *Ceratostoma foliatum* over a 10-week period. Details same as Fig. 2.
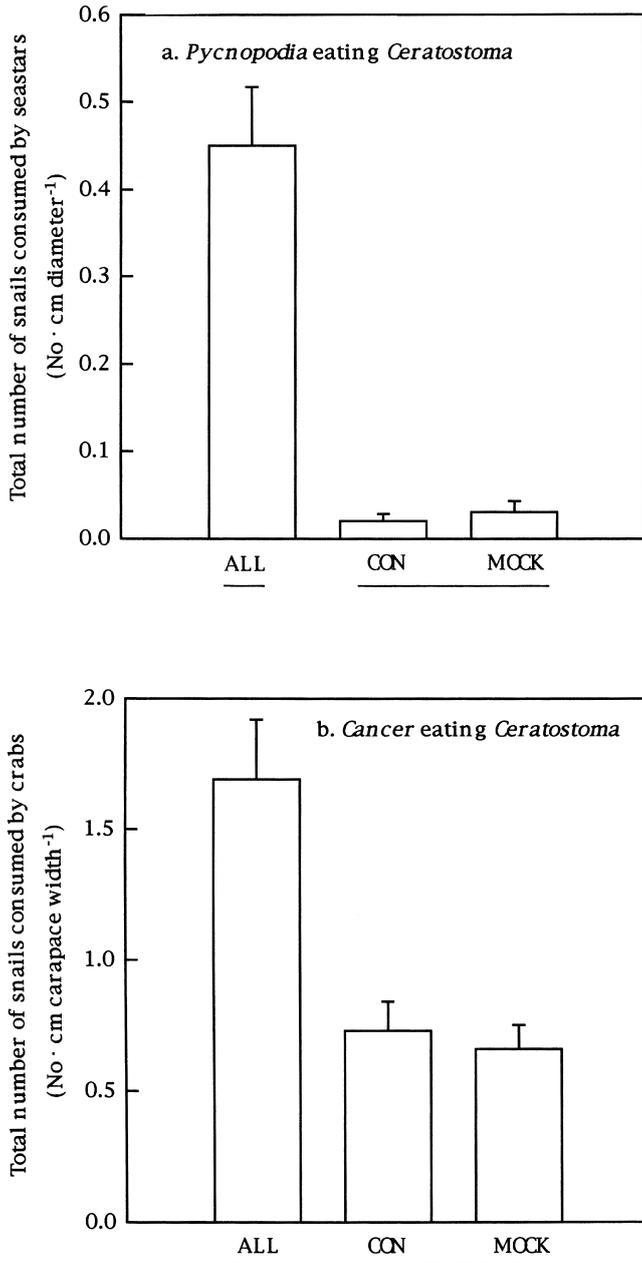
Fig. 4. Consumption data for (a) the seastar *Pycnopodia helianthoides* and (b) the crab *Cancer productus* eating different treatment groups of the snail *Ceratostoma foliatum*. Vertical bars in (b) represent S.E. and solid lines below the *x*-axis show statistically homogenous groupings ($p < 0.05$, multiple comparison test). Treatment groups of snails were: CON: all varices intact, ALL: all varices removed; MOCK: shells scored with a grinder, but varices left intact.
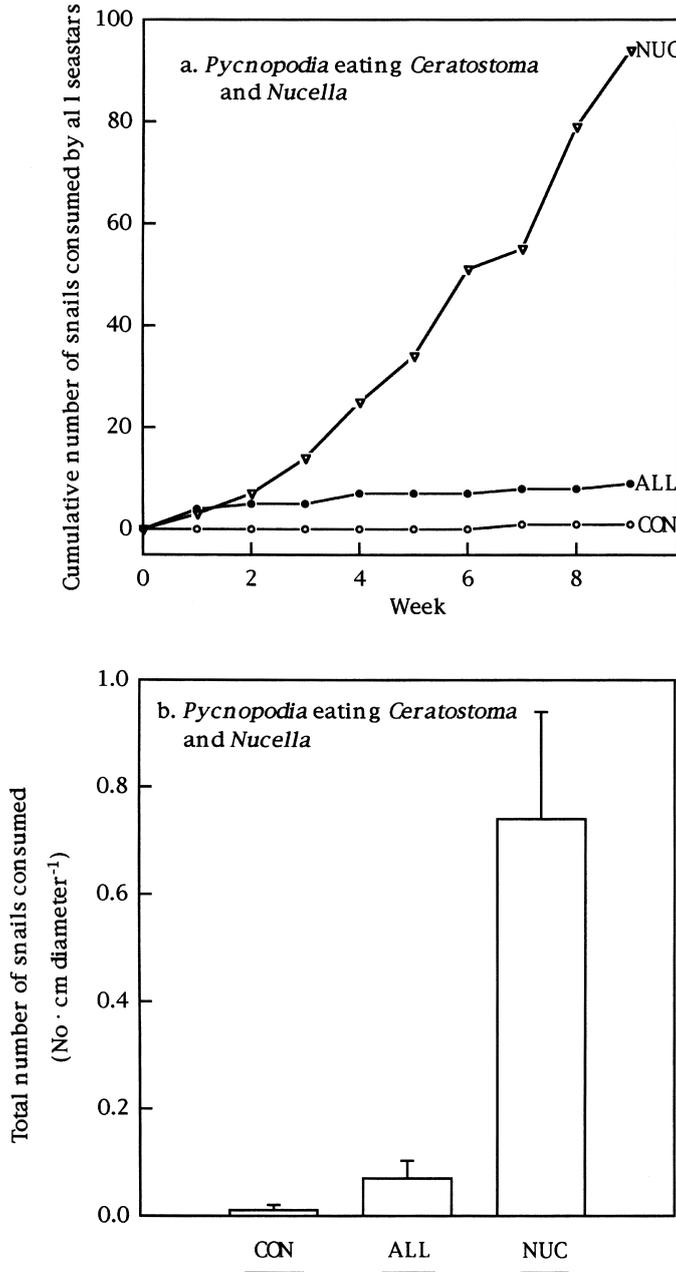
Fig. 5. Consumption data for the seastar *Pycnopodia helianthoides* eating the snails *Ceratostoma foliatum* and *Nucella lamellosa* over an 8-week period. (a) Cumulative number of snails eaten by seven seastars. (b) Total number of snails eaten, corrected for size of seastar. Vertical bars in (b) represent S.E. and solid lines below the *x*-axis show statistically homogenous groupings ($p < 0.05$, multiple comparison test). Treatment groups of snails were: CON: *Ceratostoma* with all varices intact; ALL: *Ceratostoma* with all varices removed; NUC: *Nucella*.
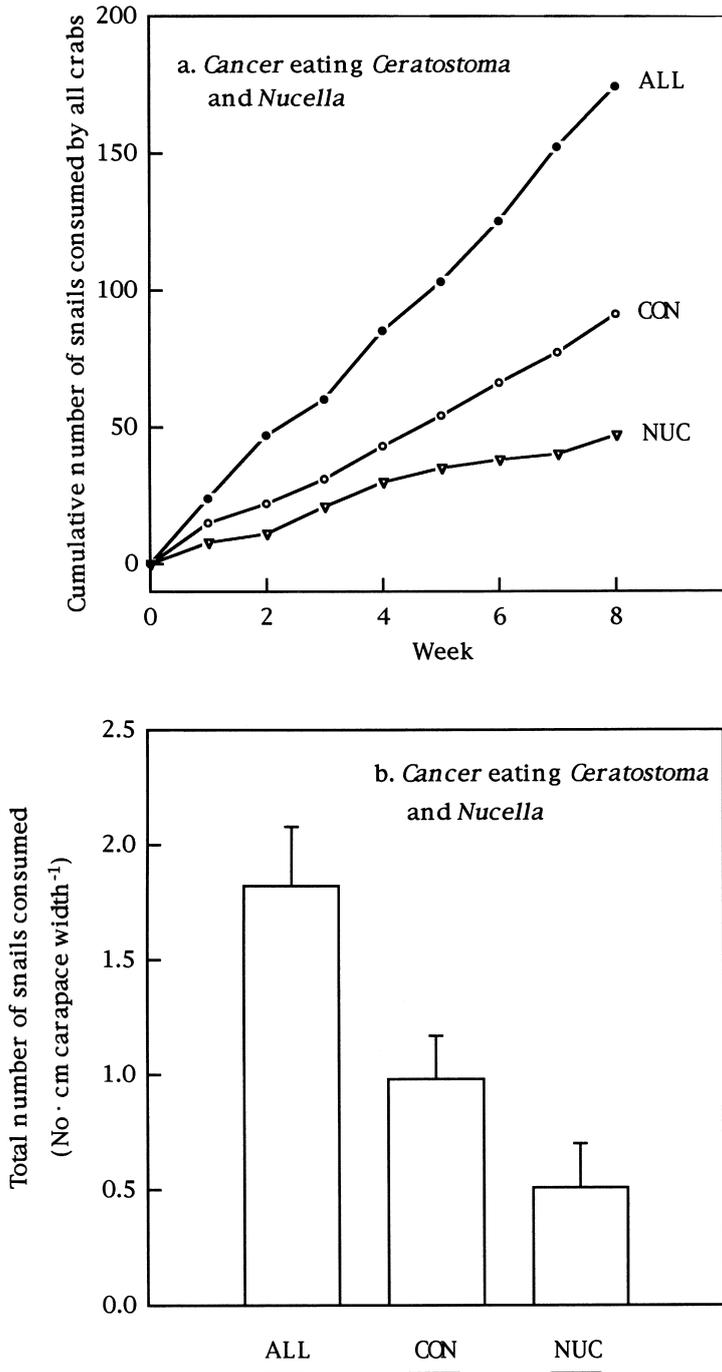
Fig. 6. Consumption data for the crab *Cancer productus* eating the snails *Ceratostoma foliatum* and *Nucella lamellosa* over an 8-week period. Details same as Fig. 5.

test), with all varix-removed snails, intact *Ceratostoma*, and *Nucella* separating into three statistically homogenous subgroups ($p < 0.05$, multiple comparison test) (Fig. 6b).

Energy content of dry flesh of *C. foliatum* was almost identical with that of *Nucella lamellosa* (19.4 kJ dry g^{-1}±0.5 S.E. and 19.0 kJ dry g^{-1}±0.7, respectively). Therefore, energy content was unlikely to have been a factor in governing selection of one prey species over another. Likewise, there was no significant effect of size on energy content for either species (*Ceratostoma*: kJ = 18.0 + 0.303 g dry weight, $n = 10$, $r^2 = 0.059$, $t = 0.71$, $p = 0.50$; *Nucella*: kJ = 21.9 − 0.687 g dry weight, $n = 10$, $r^2 = 0.278$, $t = 1.64$, $p = 0.15$).

3.3. Videotaped feeding behaviors of crabs

During the videotaping sessions, a total of 49 snails were eaten by the four crabs. Of these 49 snails, the five treatment types were consumed in similar proportions as compared with the first experiment (intact: 0.16 vs 0.08 in the first experiment, left varix-removed: 0.16 vs 0.18, middle varix-removed: 0.10 vs 0.17, right varix-removed: 0.25 vs 0.24, and all varix-removed: 0.33 vs 0.32). Of the 49 snails eaten, 24 yielded unobstructed records (that is, where the crab's body did not obstruct the camera's view) which could be analyzed for feeding behaviors and these records are summarized in Table 1. Most often, the crabs consumed the first snail they picked up (18 of 24). Manipulations prior to eating involved: (1) moving the snails with chelipeds and walking legs into a favorable position for subsequent shell-breaking, (2) chipping away the shell from around the aperture, (3) snapping the shell in two with the chelipeds, or (4) some combination of chipping and snapping. Average handling times, from when the snail was first picked up until it was chipped or snapped and the crab began feeding, ranged from 21 min for intact snails to 42 min for left varix-removed snails (Table 1), but with no obvious relationship between time and treatment. This was surprising as we expected that snails with all varices removed, or those with the large right varix removed, would be easier, and therefore faster, for the crabs to break into. A

Table 1
Summary of 24 unobstructed videotapes of feeding by *Cancer pagurus* exposed to a selection of five *Ceratostoma foliatum* representing one each of five treatment types

Snail type	No. consumed	Percent consumed	Average total handling time before eating (min, mean±S.E.)	Killing method		
				Chip	Snap	Combination
CON	3	12	21±7	2	0	1
L	5	21	42±15	2	1	2
M	2	8	36±18	0	0	2
R	5	21	35±10	0	0	5
ALL	9	38	27±7	1	6	2
Totals	24	100		5	7	12

Treatments were: CON = snails with all varices intact; L, M, and R = snails with left, middle, and right varices removed, respectively; and ALL = snails with all varices removed.

combination of chipping the shell from around the aperture, then snapping it in half, was most often used to obtain access to the soft parts of the snail, although snails with all varices removed were more likely to be simply snapped in two (Table 1). There was no relationship between size of snail and method of killing (chipping: 66 mm$\pm$2 S.E.; snapping: 70 mm$\pm$2 S.E.; combination of chipping and snapping: 68$\pm$1; $F = 1.32$, $p = 0.29$, ANOVA), and even the largest snails could be killed by being snapped in two. The remaining six snails (of the 24 with unobstructed visual records) were consumed after one or more other snails had been manipulated for a time. The six comprised three with all varices removed, two with intact varices, and one with left varix removed (thus representing three 'easy' and three 'hard' prey). The crabs never consumed a 'harder' snail after an 'easier' one had been manipulated (i.e. consumed an intact, left varix- or middle varix-removed after manipulating an all varix- or right varix-removed), but they did put down two 'harder' snails (left varix- and middle varix-removed) for two 'easier' snails (two all varix-removed).

4. Discussion

It is clear from our study that the varices on *C. foliatum* provide protection from both crab and seastar predators. The seastar *Pycnopodia helianthoides* seemed to prefer smoother-shelled prey since, in the first experiment, *C. foliatum* without varices were eaten at a much greater rate than snails with intact varices and, in the second experiment, smooth-shelled *Nucella lamellosa* were eaten almost to the exclusion of normal and devarixed *C. foliatum*. Clearly the varices are perceived in some way by the seastar and avoided. Whether the tube feet or other soft tissues are adversely stimulated by the varices, or whether the arms prefer to wrap around a smooth surface, is not known. In this regard, *P. helianthoides* is more successful at eating short-spined over long-spined sea urchins when presented with both (Moitoza and Phillips, 1979), so it seems likely that textural differences are important in governing prey selection by this species.

Crabs most preferred all varix- and right varix-removed *Ceratostoma* compared with intact, left varix- and middle varix-removed snails. This is probably a function of the methods employed by crabs to gain access to and remove the flesh from the shell of a snail. Our videotape records showed the following general pattern: a potential prey was selected and manipulated by the chelipeds for a time. This was followed by exploratory chipping, usually commencing at the edges of the large right varix or, in its absence, at the thin right edge of the aperture. At this point the crab sometimes snapped the snail in two or proceeded to chip, can-opener style, along the main body whorl until the flesh of the snail was encountered. The absence of all varices favored the snapping-in-half mode, while the absence of the right varix favored a combination of chipping and snapping. Presumably, the crab chips away at the shell until enough material has been removed to allow for a quick snapping. In this case, the absence of all varices made chipping unnecessary. Similar behaviors for *Cancer* spp. have been observed by Zipser and Vermeij (1978), and Lawton and Hughes (1985). These authors noted that small gastropod prey were most frequently crushed, while large ones were attacked at the

aperture. We found no such size distinction and even the largest *Ceratostoma* were killed by the snapping method.

The crabs in this study also preferred completely devarixed *Ceratostoma* to equal-sized *Nucella* and intact *Ceratostoma*. It may be that shell thickness is a deterrent of predation along with varices, since *Nucella* have much thicker shells than do *Ceratostoma*. Shell thickness has been shown by Hughes and Elner (1979) to increase in areas where *Nucella* spp. coexist with crabs, suggesting a protective function, and it is known that *C. productus* preys preferentially on thin-shelled as compared with thick-shelled *N. lamellosa* (Palmer, 1985). A smoother shell, such as that of *Nucella*, may also be protective since the chelipeds cannot get a firm hold on the snail (Lawton and Hughes, 1985). In comparison, we surmise that the rough shell of *Ceratostoma* would offer better purchase for attack by the crab.

We are inclined to think that no learning occurred with either the seastars or the crabs. Habituation and associative learning are known for both crustaceans and echinoderms (Wells, 1965; Krasne, 1973; Willows et al., 1973; Valentincic, 1983; Carew and Sahley, 1986), but presence of ingestive conditioning learning of a type expected here seems to be known only for echinoderms. For example, in a learning experiment on the seastars *Pisaster* spp., Landenberger (1968) found that animals given only snails (*Tegula funebralis*) to eat for 3 months showed an increased preference for these snails over chitons (*Nuttalina californica*) and their normally preferred mussel prey (*Mytilus* spp.). In our experiments none of the curves displayed a typical learning curve shape (such as an accelerating rise for a learned-preference, or a decelerating fall for a learned-avoidance: see Fig. 2a, Fig. 3a, Fig. 5a, Fig. 6a). There also appeared to be no learned selection of smaller prey by either predator. Additionally, as devarixed snails might appear to crabs to be smaller in size than normal snails, we anticipated that crabs might select a size range of completely devarixed snails which was larger than that selected of snails with all varices intact, while snails lacking a single varix, regardless of which varix, would be intermediate. The data, however, showed that no treatment group was favored in size over another. Nonetheless, it does appear that crabs choose their prey at least partly by sight since, during the videotaping, 18 of 24 snails ingested were the first snails to be seized and manipulated, and this selection was strongly biased to right varix- and all varix-removed prey.

In the case of *Ceratostoma*, it appears that lack of varices, rather than shell damage caused by grinding, was responsible for the preferential predation. Crabs were shown by Pearson et al. (1979) to be attracted to minute quantities of snail flesh released into the surrounding medium, but in our study it appears that crabs and seastars were unresponsive to any chemicals that might have been released from grinding the shell.

It is possible that replacing only the consumed snails caused biases in our results in the event that these snails were preferentially preyed upon because of their 'newness'. However, even is this was a factor, we do not think this was the main criteria by which predators selected prey for the following reasons. First, all of the predators of a given type (*Ceratostoma* or *Pycnopodia*) showed the same preferences for snail treatments. This would not have occurred if 'newness' was the main criteria for selection since all of the snails were newly introduced at the beginning of the experiment and would have had an equal chance of being consumed first, thus leading to differences in which snails were

replaced and subsequently consumed. Second, if the newly introduced snails were more appealing, we would expect to see changes in feeding rates over the course of the study. At the beginning of the experiment, when all the snails were new, a preference would be established based only on shell type but, after some types were replaced more often and 'newness' became a factor, those types would be preferentially eaten because of both shell type and 'newness', leading to an increase in feeding rate. Inspection of Fig. 3a and Fig. 6a indicates that this did not occur for *Cancer*, but it is a possibility for *Pycnopodia* based on Fig. 2a and Fig. 5a. However, the differences between the number of snails of one type consumed and those of the other types are so large that there is clearly a preference based on shell type when seastars are the predators.

Our study indicates a defensive role for varices in *C. foliatum*. More significant than this, we believe, is the multiplicity of function that has been demonstrated for the varices of this muricid species. These include the influence of destabilization during both long and short vertical falls through the water column on landing orientation, and now defense. Other functions, such as making the snail appear larger to visual predators, camouflage, and perhaps increased stability in currents, are also possible.

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References

Appleton, R.D., Palmer, A.R., 1988. Water-borne stimuli released by predatory crabs and damaged prey induce more predator-resistant shells in a marine gastropod. Proc. Natl. Acad. Sci. USA 85, 4387–4391.

Carefoot, T.H., Donovan, D.A., 1995. Functional significance of varices in the muricid gastropod *Ceratostoma foliatum*. Biol. Bull. 189, 59–68.

Carew, T.J., Sahley, C.L., 1986. Invertebrate learning and memory: from behavior to molecules. Annu. Rev. Neurosci. 9, 435–487.

Conover, W.J., 1981. Practical Nonparametric Statistics. Wiley, New York.

Ebling, F.J., Kitching, J.A., Muntz, L., Taylor, C.M., 1964. The ecology of Lough Ine. XIII. Experimental observations of the destruction of *Mytilus edulis* and *Nucella lapillus* by crabs. J. Anim. Ecol. 33, 73–82.

Hughes, R.N., Elner, R.W., 1979. Tactics of a predator, *Carcinus maenas*, and morphological responses of the prey, *Nucella lapillus*. J. Anim. Ecol. 48, 65–78.

Kent, B.W., 1981. Feeding and food preferences of the muricid gastropod *Ceratostoma foliatum*. Nautilus 95, 38–42.

Kitching, J.A., Muntz, L., Ebling, F.J., 1966. The ecology of Lough Ine. XV. The ecological significance of shell and body forms in *Nucella*. J. Anim. Ecol. 35, 113–126.

Krasne, F.B., 1973. Learning in Crustacea. In: Corning, W.C., Dyal, J.A., Willows, A.O.D. (Eds.), Invertebrate Learning, vol. 2, Arthropods and Gastropod Mollusks. Plenum Press, New York, pp. 49–130.

Landenberger, D.E., 1968. Studies in selective feeding in the Pacific starfish *Pisaster giganteus* in Southern California. Ecology 49, 1062–1075.

Lawton, P., Hughes, R.N., 1985. Foraging behaviour of the crab *Cancer pagurus* feeding on the gastropods *Nucella lapillus* and *Littorina littorea*: comparisons with an optimal foraging theory. Mar. Ecol. Prog. Ser. 27, 143–154.

Manly, B.F.J., 1993. Comments on design and analysis of multiple-choice feeding-preference experiments. Oecologia 93, 149–152.

McCormack, S.M.D., 1981. The maintenance of shore-level size gradients in an intertidal snail (*Littorina sitkana*). MSc thesis, University of British Columbia, 90 pp.

Moitoza, D.J., Phillips, D.W., 1979. Prey defense, predator preference, and nonrandom diet: the interactions between *Pycnopodia helianthoides* and two species of sea urchins. Mar. Biol. 53, 299–304.

Morris, R.H., Abbott, D.P., Haderlie, E.C., 1980. *Ceratostoma foliatum*. In: Intertidal Invertebrates of California, Stanford University Press, Palo Alto, CA, pp. 275–276

Norton, S.F., 1988. Role of the gastropod shell and operculum in inhibiting predation by fishes. Science 241, 92–94.

Palmer, A.R., 1977. Function of shell sculpture in marine gastropods: hydrodynamic destabilization in *Ceratostoma foliatum*. Science 197, 1293–1295.

Palmer, A.R., 1979. Fish predation and the evolution of gastropod shell sculpture: experimental and geographic evidence. Evolution 33, 697–713.

Palmer, A.R., 1985. Adaptive value of shell variation in *Thais lamellosa*: effect of thick shells on vulnerability to and preference by crabs. Veliger 27, 349–356.

Pearson, W.H., Sugarman, P.C., Woodruff, D.L., Olla, B.L., 1979. Thresholds for detection of feeding behavior in the Dungeness crab, *Cancer magister*. J. Exp. Mar. Biol. Ecol. 39, 65–78.

Peterson, C.H., Renaud, P.E., 1989. Analysis of feeding preference experiments. Oecologia 80, 82–86.

Radwin, G.E., D'Attilio, A., 1976. Murex Shells of the World. Stanford University Press, Palo Alto, CA, 284 pp.

Roa, R., 1992. Design and analysis of multiple-choice feeding-preference experiments. Oecologia 89, 509–515.

Spight, T.M., Lyons, A., 1974. Development and functions of the shell sculpture of the marine snail *Ceratostoma foliatum*. Mar. Biol. 24, 77–83.

Spight, T.M., Birkeland, C., Lyons, A., 1974. Life histories of large and small murexes (Prosobranchia: Muricidae). Mar. Biol. 24, 229–242.

Valentincic, T., 1983. Innate and learned responses to external stimuli in asteroids. In: Jangoux, M., Lawrence, J.M. (Eds.) Echinoderm Studies, vol. 1, pp. 111–138.

Vermeij, G.J., 1982. Phenotypic evolution in a poorly dispersing snail after arrival of a predator. Nature 299, 349–350.

Wellington, G.M., Kuris, A.M., 1983. Growth and shell variation in the tropical eastern Pacific intertidal gastropod genus *Purpura*: ecological and evolutionary implications. Biol. Bull. 164, 518–535.

Wells, M.J., 1965. Learning in marine invertebrates. Adv. Mar. Biol. 3, 1–62.

Willows, A.O.D., Dyal, J.A., Corning, W.C., 1973. The Echinoderms. In: Corning, W.C., Dyal, J.A., Willows, A.O.D. (Eds.), Invertebrate Learning, vol. 3. Plenum Press, New York, pp. 103–134.

Zipser, E., Vermeij, G.J., 1978. Crushing behavior of tropical and temperate crabs. J. Exp. Mar. Biol. Ecol. 31, 155–172.