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Predation induced changes in behavior and growth rate in three populations of the intertidal snail, *Littorina sitkana* (Philippi)[1]

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Abstract

We investigated the sublethal effects of a predatory crab, *Cancer productus* (Randall), on the behavior and growth of its snail prey, *Littorina sitkana*, by setting up controlled rearing and prey-size selection experiments. *L. sitkana* were collected from three sites on San Juan Island, WA, USA. These sites varied in snail size, abundance, and vertical distribution, and in the abundance of the crab predator *C. productus*. Snails from all three populations were raised for 34 days under the following treatments: no-crab control, a non-feeding *C. productus* encased in mesh box, and an encased *C. productus* feeding on *L. sitkana*. The non-feeding crab treatment did not affect snail foraging behavior or growth rate in comparison with the no-crab control. In contrast, the presence of a feeding crab elicited escape behavior in the snails, halted grazing, and consequently reduced growth rates. A population difference in escape behavior was observed: upward migration in snails from rocky shores and hiding in crevices in snails from a mud flat. It thus appears that chemicals leaching from crushed conspecific snails, rather than the presence of the crab predator, act as the ''alarm substance'' to which *L. sitkana* react. The magnitude of the growth depression in the presence of feeding crabs was 85%, with no difference among the three populations. Once the feeding crab stimulus was removed, snails in all populations resumed normal growth, suggesting that this response to feeding predators is reversible with changing environmental conditions. Laboratory experiments were set up to determine if all size classes of *L. sitkana* are equally susceptible to *C. productus* predation. *C. productus* consistently selected the largest of three size classes of *L. sitkana*. These results suggest that slow growth rate and small size in *L. sitkana* may actually be an adaptation for coexisting with high *C. productus* abundance, rather than simply a cost of escape behavior.

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[1]This manuscript is dedicated to the memory of Mamie L. Markham, a longtime supporter of marine biological research.

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1. Introduction

The effects of predators on their prey varies from direct lethal to subtle non-lethal. While direct predation affects the distribution, abundance, size structure, and genetic make-up of prey populations (Kettlewell, 1959; Paine, 1976; Robles, 1987; Gotelli, 1993), the mere presence of a predator can also have important effects on prey populations by inducing alterations in prey life history, behavior, and morphology (Havel, 1987; Sih, 1987). For example, the presence of a predator can trigger bryozoans, cladocerans and rotifers to grow spines, whelks to produce thicker shells, barnacles to develop a bent-over morphology, and pond snails to grow faster [Harvell, 1984; Havel and Dodson, 1984; Palmer, 1990; Lively, 1986; Sternberger and Gilbert, 1987; Appleton and Palmer, 1988; Crowl and Covich, 1990, reviewed by Harvell (1990)]. In each case, the phenotypic alteration was triggered by a water-borne ''alarm substance'' (Hadlock, 1980), or chemical cue released by the predator or the damaged prey, and resulted in reduced vulnerability to the predator. Predator-induced defenses appear to be a widespread phenomenon, especially in shallow marine systems (Vermeij, 1987; Harvell, 1990). The advantage of an inducible defense over a purely genetic one is its flexibility. A purely genetic adaptation to a specific predatory regime at one time and place could be maladaptive in the next. Inducible defenses would thus be favored in cases where predation pressure varies in space and time, and cues are reliable (Havel, 1987; Harvell, 1990).

To address the question of whether inducible defenses vary among populations subject to different predation pressures, we studied responses of three populations of the grazing snail, *Littorina sitkana*, to a crab predator, *Cancer productus*. Previous studies with these spatially separated populations of *L. sitkana* on San Juan Island, WA, USA suggest that the life history of this snail is affected by *C. productus* (Behrens Yamada, 1989; Behrens Yamada and Boulding, 1996). *L. sitkana* lay gelatinous egg masses on rocks, in crevices, or on algae, and young hatch as juvenile snails (Behrens, 1972; Behrens Yamada, 1989, 1992). Since no free larval stages are involved, and adult snails disperse little (Boulding and Van Alstyne, 1993), each population can adapt to the unique environmental conditions of its habitat, such as desiccation, wave action, and predation intensity (Behrens, 1972; Behrens Yamada, 1977, 1989; Janson, 1983; Behrens Yamada and Boulding, 1996). In a reciprocal transplant experiment with three distinct populations of *L. sitkana* from San Juan Island, individuals from Roche Harbor (a rocky shore on the north end of the island) grew less at all sites than those from False Bay, (a mud flat 18 km from Roche Harbor on the west side of the island) (Table 1; Behrens Yamada, 1989). In addition to having the lowest intrinsic individual growth rates, individuals at the Roche Harbor site had the smallest mean and maximum sizes, lowest densities, highest intertidal distribution and lowest recovery rate of marked and released *L. sitkana*,

Table 1
Characteristics of three populations of *Littorina sitkana* from San Juan Island, WA, USA

	Population characteristics		
Source population	Maximum shell height (mm)	Population density (No./m^2)	Individual growth rate in common site for snails of 8.9 mm initial shell height (mm/year)
False Bay	20	$>300/m^2$	5.9
Cantilever Pier	14	$>300/m^2$	5.5
Roche Harbor	12	$<20/m^2$	4.5
	Site characteristics		
Site	Recovery rate of marked *L. sitkana* (%)	Predation rate on tethered *L. sitkana* (%/day)	*Cancer productus* abundance (catch/h)
False Bay	33	0	0
Cantilever Pier	21	8	2
Roche Harbor	14	40	12

C. productus abundance is negatively correlated with maximum shell height, density, growth rate, and recovery rate of marked and released snails ($N>1000$), and positively correlated with predation rate of tethered snails. (See Behrens Yamada, 1989; Behrens Yamada and Boulding, 1996).

while individuals at False Bay, had the largest sizes, highest densities and highest recovery rate (Table 1; Behrens Yamada, 1989; Behrens Yamada and Boulding, 1996). Subsequent experiments with tethered *L. sitkana*, direct observations, and test fishing with crab rings identified the red rock crab, *C. productus*, as the most important predator of *L. sitkana*, accounting for a mortality rate on tethered snails at Roche Harbor of up to 40% per day (Table 1; Walker and Behrens Yamada, 1993; Behrens Yamada and Boulding, 1996). Hungry *C. productus* (50–100 mm carapace width) inside plastic boxes are capable of eating 70 *L. sitkana* (5–10 mm shell length) per day (see below). This predator is absent at the False Bay site (Table 1).

The objectives of our research were: (1) to determine if snails change their behavior and growth responses to the presence of feeding or non-feeding crab predators, and (2) to determine if these responses can be adaptive, reducing predation by *C. productus*. Controlled rearing experiments in which individuals from the three populations of *L. sitkana* were grown in the presence and absence of feeding or non-feeding crabs allowed us to evaluate behavioral and growth rate changes in snails and to determine if these changes were reversible after the stimulus was removed. Prey size preference experiments with adult *C. productus* and previous prey tethering experiments, allowed us to test the hypothesis that smaller *L. sitkana* are less susceptible to *C. productus* predation than larger ones.

2. Methods

2.1. Role of alarm substance on behavior and growth rate

For the controlled rearing experiments, seawater tanks at the Oregon State University Hatfield Marine Science Center in Newport, OR, USA were set for depths of 25 cm and flow-rates of 6 l/min. Water temperature during the experiment remained at 13°C, and salinity, at 32 ppt. Nine large tanks (318 × 118 × 30 cm) were randomly assigned to three treatments: (a) no-crab controls, (b) non-feeding crabs, and (c) feeding crabs. Both the intake and outflow pipes were located near the center of the tanks. Three tanks served as no-crab controls, while the other six tanks received one medium size *C. productus* (50–100 mm carapace width) housed in the center of the tank inside plastic boxes (25 cm × 25 cm × 11 cm) with 2 mm mesh sides to allow for water circulation. In three feeding crab treatment tanks each crab received 100 *L. sitkana* (6–9 mm shell height) two times a week; in the non-feeding crab treatment the crabs received no food. Each week crabs were rotated: from the feeding crab treatment to a holding tank without food; from the holding tank to the non-feeding crab treatment; and from the non-feeding crab treatment to the feeding crab treatment. Thus crabs did not starve, crab feces did not interfere with the non-feeding treatment, and a high and similar level of hunger and predatory activity was maintained in the feeding treatment.

On October 5, 1992 *L. sitkana* (shell height = 6–9 mm) were collected from three sites on San Juan Island, WA, USA: False Bay, Cantilever Pier and Roche Harbor (see Behrens Yamada (1989) for site description). The main differences among sites in terms of *L. sitkana* sizes and growth rates and *C. productus* abundance are summarized in Table 1. Snails were transported to the Oregon State University Hatfield Marine Science Center at Newport, OR, USA. Snails were air-dried, stuck aperture down to double-sided carpet tape on sheets of cardboard and sprayed with a different color of model paint for each population.

On October 10, 1992, 30 painted snails were added to plastic mesh cages (2 mm mesh opening) with oblong bottoms (30 × 20 cm) and 35 cm tall sides that extended about 3 cm above the water level. A Velcro® strip at the top of the sides allowed the cages to be easily opened and closed. Each cage contained a building brick (6 cm × 19.5 cm × 39 cm), perforated at the sides with three 2 cm wide ''tunnels''. Fronds of the green alga *Ulva* sp. were anchored by inserting their holdfasts into one of the tunnels to provide abundant food for the snails. Six cages containing snails, two representing each population, were placed in each of the nine tanks. Once a week the tanks were cleaned, algal food in the snail cages was replaced, snails were placed on top of bricks, and the flow-rate, temperature and salinity were checked. The position of the snail cages with respect to the center of the tank was switched once a week to minimize position effects.

We noticed that between the weekly monitoring that the snails in the crab treatment cages had a tendency to move to the top of cages or hide within the brick tunnels. On November 13, 1992 we quantified this tendency by scoring the position of the snails using the following categories: ''top of cage''—snails were at the top of the cage, above the water level; ''brick tunnel''—inside the brick tunnels; and ''grazing''—on grazing

surfaces such as the algae, or on diatom covered bricks and cage walls. *G*-tests were used to determine if treatment and source population affected the snail's behavior (Sokal and Rohlf, 1981).

On November 13, after 34 days of treatment, snails were measured using digital calipers. Growth was apparent as bands of unpainted shell and was measured by subtracting the initial length from the final length. For those snails that grew < 0.05 mm in length, length increment was estimated by measuring the width of the unpainted band and dividing it by 3.57 [see details in Behrens Yamada (1989)]. We tested for the effects of source population and treatment on shell growth rate using a split-plot analysis of variance (ANOVA) (Mead, 1988; Kuehl, 1994), in which the crab treatments were applied as the main-plot level (tanks) and populations to the sub-plot level (snail cages). Growth increments were log-transformed and assumptions of variance homogeneity and normality were checked by Cochrans' *C* test (Sokal and Rohlf, 1981), Shapiro Wilks' test, and visual inspection of residual plots.

To determine if the treatment effects were irreversible, affecting subsequent growth of snails after the stimulus was removed, another growth experiment was set up immediately following the first. This time, six tanks were randomly assigned to two ''History'' treatments: (a) previously under the no-crab control, and (b) previously under the feeding crab treatment. The non-feeding crab treatment was not included because no significant difference was observed between this and no-crab controls (see Section 3). The apertural edges of shells of a subset of snails from each of the three populations previously assigned to the control and feeding crab treatments were painted with model paint, and the snails placed in clean cages. One snail cage per population, with 30 snails each, was placed into each tank. No crabs were kept in any of the tanks. The subsequent growth of snails was measured after 26 days on December 10. Log-transformed growth increments were analyzed using a split-plot ANOVA (see details above).

2.2. Size selective predation

To determine if adult *C. productus* are size selective predators, we set up prey size selection experiments at Friday Harbor Laboratories on June 27, 1990 and August 19, 1991. Two large water tables (107 cm $\times$ 107 cm) with a water height of 15 cm and flow-rate adjusted to 3 l/min. served as the experimental arenas. A building block ($6 \times 19.5 \times 39$ cm) covered with the green alga *Ulva* sp. and diatoms was positioned in the center of each tank. Fifty large (13–17 mm shell length), fifty medium (9–13 mm) and fifty small (6–9 mm) *L. sitkana* were collected from False Bay and placed on the top of each block. To allow crushed shells to be assigned to the correct size class, the apices of the shells were color-coded with model paint. Once snails started to graze, three large *C. productus* (carapace width of 115–140 mm) were introduced into each water table. Water tables were enclosed in black plastic sheets to prevent visual cues from distracting the foraging crabs and to maintain independence between tanks. After 24 h the fate of the snails in each size category was noted. The hypothesis that there was no difference in the proportion of snails killed in each size category was tested using χ^2 tests. Separate analyses were conducted for each of the four trials.

3. Results

3.1. Effect of alarm substance on behavior

Analysis of the snail position data yielded significant interactions of treatment on behavior ($G = 543$, df = 4, $p < 0.001$) and of source population on behavior ($G = 54.93$, df = 4, $p < 0.001$). These significant interactions were due to snails in the crab feeding treatment behaving differently than in the other two treatments, and to False Bay snails responding differently to feeding crabs than the other two populations (Fig. 1). In the control and the non-feeding crab treatment greater than 57% of the snails from each population were found on ''grazing'' surfaces while less than 21% were hiding in

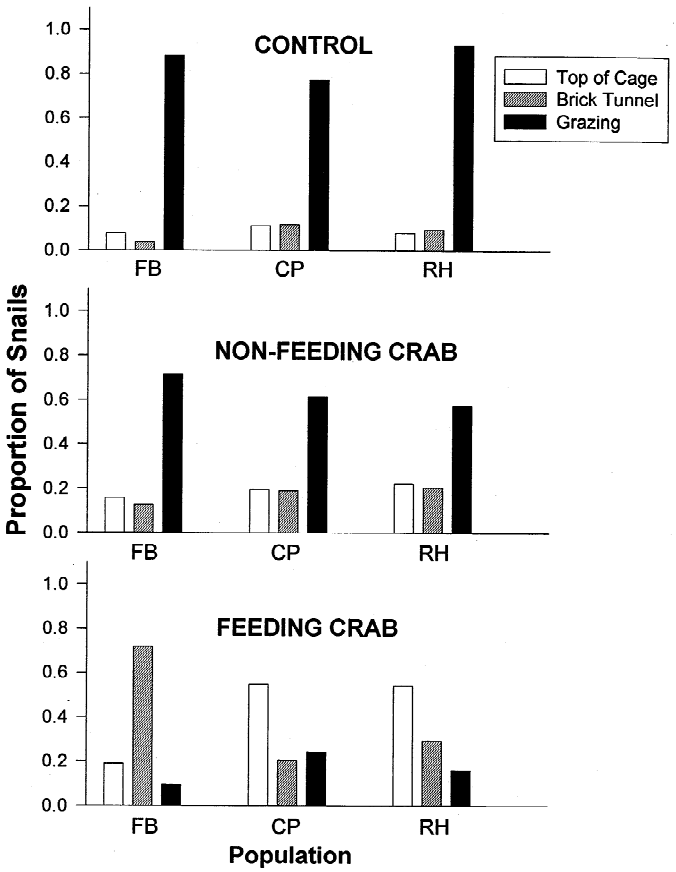

Fig. 1. Position of *Littorina sitkana* from three source populations exposed to three laboratory treatments: (a) no-crab control; (b) non-feeding crab; (c) feeding crab. Snails were scored as being on the ''top of cages'', inside ''brick tunnels'' or on ''grazing'' surfaces such as the algae, the top surface of diatom covered bricks, or the cage walls. FB = False Bay, CP = Cantilever Pier, RH = Roche Harbor. Snails in the crab feeding treatment behaved differently than in the other two treatments ($G = 543$; df = 4; $p < 0.001$), and False Bay snails responded differently to feeding crabs than the other two populations ($G = 54.93$; df = 4; $p < 0.01$).

tunnels and less than 25% had crawled to the top of cages (Fig. 1a,b). In contrast, less than 25% of the snails in the crab-feeding treatment were found on grazing surfaces, and most were found in tunnels and tops of cages (Fig. 1c). Furthermore, the False Bay snails behaved different from the other two populations. Seventy two percent of the False Bay snails were hiding in tunnels, whereas 55% of the Roche Harbor and Cantilever Pier snails had crawled to the top of the cages (Fig. 1c).

3.2. Effect of alarm substance on growth rate

L. sitkana grew between 0.6–1.4 mm/month under the no-crab and non-feeding crab treatments, but only 0.2 mm/month or less in the presence of crabs feeding on conspecific snails (Fig. 2, Table 2). The phenotypic response elicited by feeding crabs [''reaction norm'' sensu Stearns (1989)] was similar in snails from the three tested populations: mean growth in the feeding crab treatment was only 15% that of the no-crab controls for each of the three populations (Fig. 2; Table 2, no significant Population × Treatment interaction on log-transformed growth data). A Tukey multiple comparison test (Sokal and Rohlf, 1981) on main effects showed no significant difference between the no-crab controls and the non-feeding crab treatments.

Snails from Cantilever Pier grew significantly more than those from the other two sites (Fig. 2), in contrast with previous field results in which the False Bay snails

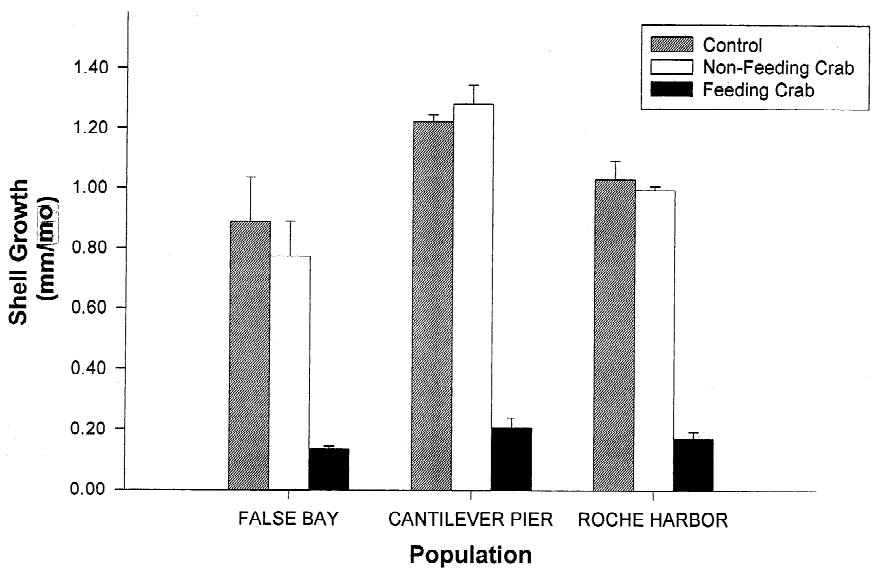

Fig. 2. Shell growth response of *Littorina sitkana* from three source populations to the presence of feeding and non-feeding *Cancer productus* and a no-crab control. The presence of feeding crabs significantly depressed growth rates of *L. sitkana*, while non-feeding crabs had no effect, in comparison to the no-crab control. Snails from Cantilever Pier exhibited a significantly higher growth rate than those from the other two sites. The experiment ran for 34 days, from October 10 to November 13, 1992. Error bars represent one standard error of the mean.

Table 2
Split-plot analysis of variance of shell growth increments (log-transformed) for the three *Littorina sitkana* populations (False Bay, Cantilever Pier, Roche Harbor) under three treatments (''Treatment'' = no-crab control, non-feeding crab, feeding crab)

Source	df	MS	*F*	*P*
Treatment	2	0.251853	87.93	0.0001
Tank (error 1)	6	0.002931	3.79	0.0235
Population	2	0.017602	22.80	0.0001
Population × Treatment	4	0.002412	3.12	0.0561
Population × Tank (error 2)	12	0.000772	1.10	0.3961
Residual error	27	0.000699		

The error 1 is used to test for the significance of ''Treatment'' and the error 2 to test for differences among populations within tanks. The residual error is due to cages inside each tank.

exhibited the greatest annual growth rates (Table 1, Behrens Yamada, 1989). This apparent discrepancy can be explained by population differences in seasonal reproductive patterns in which the False Bay populations grows less following its reproductive peak in early fall (Behrens Yamada, 1989).

Significant differences among experimental tanks were also observed (Table 2). Despite our efforts to standardize conditions by using only hungry crabs, we could not control the number of snails each crab attacked. Thus, the tank effect on growth rate might have been produced by small variations in the concentration of alarm substance between tanks.

Prior exposure to the alarm substance did not result in permanent depression of growth rate. Once the source of the alarm substance was removed, *L. sitkana* previously under the feeding crab treatment grew at the same rate as control snails (Fig. 3; Table 3).

3.3. Size selective predation

In all four trials, adult *C. productus* exhibited a significant preference for large *L. sitkana* (Fig. 3; $\chi^2 > 6.8$, df = 2, $p < 0.05$). From 24 to 44 large *L. sitkana* were crushed and eaten per day, compared to only 2 to 21 small *L. sitkana* (Fig. 4).

4. Discussion

The mere presence of the crab, *C. productus*, did not alter the behavior or reduce the growth rate of the prey, *L. sitkana*. The crabs had to be actively feeding on conspecific snails to produce the altered behavior and growth inhibition in *L. sitkana*. Exposure of *L. sitkana* to crushed conspecific snails resulted in the same escape behavior in laboratory and field trials (Needham, in prep.). It thus appears that chemicals leaching from the tissues of damaged *L. sitkana* act as the chemical messenger, or ''alarm substance'' to which the snails react (Hadlock, 1980).

Our observations suggest that the mechanism by which this ''alarm substance'' results in growth inhibition involves at least two steps. First, snails perceive the ''alarm

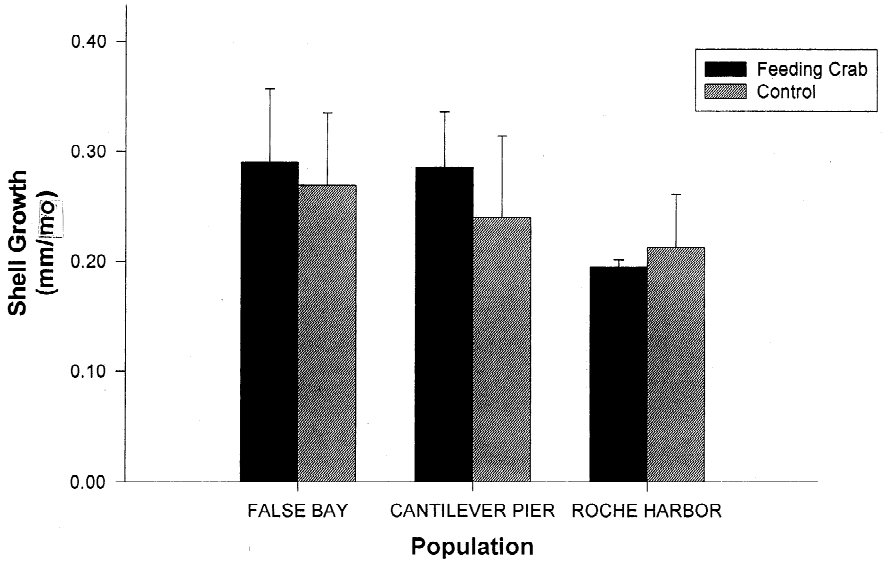

Fig. 3. The role of prior exposure to feeding crabs on shell growth of *Littorina sitkana* from three source populations. Prior exposure to feeding crabs had no effect on subsequent shell growth, nor was there a significant difference in growth rate among populations. The experiment ran for 26 days, from November 14, to December 10, 1992. Error bars represent one standard error of the mean.

substance'' in the ambient water and respond by changing their behavior by either climbing to the top of the cages and aggregating along the Velcro® closures, or by hiding in the tunnels of the bricks. These behaviors appear to be ''escape responses'' to the presence of feeding predators. Second, the altered behavior results in reduced foraging activity, and consequently a depressed growth rate. Over 57% of *L. sitkana* in no-crab control and non-feeding crab treatments were found on grazing surfaces such as on *Ulva* and on the diatom-covered bricks and cage sides. The reverse was true in the feeding crab treatment. Most of the snails (75%–91%) either had climbed to the top of the cages, or were hiding in the brick tunnels. Both of these ''escape'' behaviors appear to have survival advantage in the field. Warren (1985) showed that *Littorina irrorata*'s behavior of climbing up the stalks of marsh grass with the incoming tide, reduces the risk of predation from crabs and conchs. When marked *L. sitkana* were released at the 2.7 m tidal level at Roche Harbor, those snails that stayed at this level experienced much

Table 3
Split-plot analysis of variance of shell growth for the three *Littorina sitkana* populations previously under the feeding crab and no crab control treatments (''History'', see Table 2 for details)

Source	df	MS	*F*	*P*
History	1	0.001527	0.10	0.7666
Tank (error 1)	4	0.015093	1.29	0.3504
Population	2	0.012560	1.07	0.3862
Population × History	2	0.002049	0.18	0.8424
Population × Tank (error 2)	8	0.011689		

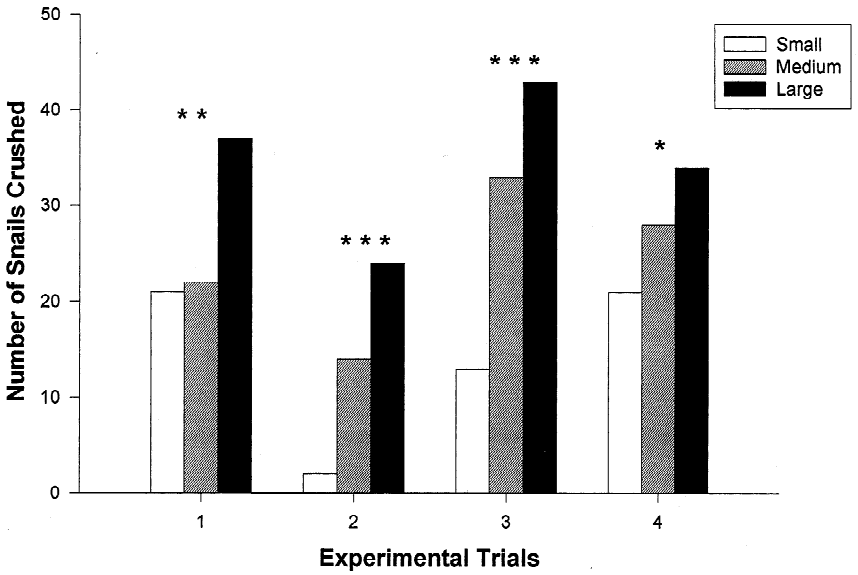

Fig. 4. Prey size selection by adult *Cancer productus*. In each trial, 50 large (13–17 mm), 50 medium (9–13 mm) and 50 small (6–9 mm) *Littorina sitkana* were offered to three adult *C. productus* (115–140 mm carapace width) and the number of snails crushed in each size category in a 24 h period noted. Significantly more large snails than medium or small snails were crushed than expected by chance alone. Asterisks indicate the significance level of χ^2 tests with 2 df: * $p < 0.05$, ** $p < 0.01$, and *** $p < 0.001$.

higher crab mortality than those that crawled higher up the shore (Needham, in prep.). Changes in behavior in response to an ''alarm substance'' seem common in snails. For instance, Hadlock (1980), working with the crab, *Carcinus maenas*, and the snail, *Littorina littorea*, found that once the ''alarm substance'' (a crushed *L. littorea*) was added to a tide pool, resident snails increased their locomotory activity and within 10 min took shelter in crevices and at the bases of algal holdfasts. She concluded that snail juice was an effective alarm substance because once one snail was attacked by a crab, the remaining snails had enough time to seek shelter before the crab finished consuming the first snail and started searching for another. Similarly, chemical and acoustical cues from the stone crab, *Menippe adina*, and chemical cues from *Cancer productus* resulted in decreased foraging activity and growth rates of the snails *Stramonita haemastoma* and *Nucella lamellosa*, respectively (Appleton and Palmer, 1988; Richardson and Brown, 1992). Because snails in the crab feeding treatment spent less time feeding, they grew less than snails in the other two treatments. Reduced growth rate in response to predators was also observed in protozoans (Wicklow, 1988) bryozoans (Yoshioka, 1982; Harvell, 1992) barnacles (Lively, 1986) frog larvae (Werner and Anholt, 1996) and juvenile fish (Diehl and Eklöv, 1995).

The environmental modulation of genetic variation into phenotypic variation can itself be under genetic control, and thus subject to selection (Woltereck, 1909). If phenotypic plasticity has a genetic component, then different genotypes might exhibit different norms of reaction to the same environmental conditions. In our case, we might expect

the snails from the three non-interbreeding populations to differ in their responses to the same concentration of alarm substance because they are naturally exposed to different abundances of crab predators in the field. If we use behavior as the index of response, this prediction holds true because we did detect significant population differences in escape behavior: snails from False Bay tended to hide in crevices, while snails from the other two populations tended to crawl to the top of the cage. Upward migration appears to be adaptive for rocky shores such as Roche Harbor and Cantilever Pier, and hiding, for mud flats such as False Bay (Needham, in prep.). While we observed population differences in the type of escape behavior, the consequence of these behaviors was the same. All three populations of snails exhibited a similar reduction in foraging activity and an 85% depression in growth rate in the presence of feeding crabs. One explanation for this observation is that the alarm substance produced by crushed conspecifics is such a strong environmental cue, that the response it produces overrides any subtle heritable variation in the reaction norm between the populations. While a strong signal produced by up to 100 crushed *L. sitkana* could occur in nature, it is very unlikely that such a strong signal would persist for 34 days. Further experimentation with intermediate levels of chemical cues might reveal differences in the intensity of the reaction norm among populations. Another explanation for the similar foraging and growth depression is that escape behavior and its consequential reduction in foraging activity, has such a strong selective value that it is a constant response for all populations of a species, regardless of the predation pressure that population has experienced.

The experimental treatments did not result in increased snail mortality nor in a permanent growth depression. Once the feeding crab was removed, snails from the crab feeding treatment resumed normal grazing behavior, and consequently grew at the same rate as the controls. This flexibility in the predator avoidance response appears to be an adaptation to temporal variability in predation pressure. When the risk of predation is reduced, normal foraging can resume. These observed results, in which the response to an alarm substance varies directly with predation risk and indirectly with cost, is a characteristic shared with many other predator–prey systems in both aquatic and terrestrial systems (Havel, 1987).

Slow growth rate and small size in the Roche Harbor population of *L. sitkana* may actually be an adaptation for coexisting with high densities of *C. productus*, rather than simply a cost of escape behavior. Large size in littorinid snails is positively correlated with increased fecundity (Hughes and Answer, 1982), and may be selected for in sites, like False Bay, where large mobile crab predators are rare. Small size of *L. sitkana* at Roche Harbor could be a reflection of three factors working alone or together: growth inhibition by alarm substance, size selective predation, and natural selection for slow growth. Field studies in which *L. sitkana* behavior was studied with and without the addition of alarm substance at both False Bay and Roche Harbor, suggest that high residual levels of alarm substance are present at Roche Harbor, the site with high *C. productus* abundance and high predation rates (Needham, in prep.). If this is true, then growth inhibition, the consequence of chronic exposure to alarm substance, could contribute to the small size and slow growth rate of snails from Roche Harbor. Our laboratory trials indicate that small *L. sitkana* are significantly less vulnerable to the voracious, size selective predator *C. productus* (of carapace width 115–140 mm) than

larger snails. Similar results were observed in the field when two size classes of *L. sitkana* were tethered to lead lines at four sites on San Juan Island (Behrens Yamada and Boulding, 1996). At each site, large adult *C. productus* selected the larger *L. sitkana*. If large snails are selected against on beaches with high *C. productus* abundance, then slower growing individuals may be favored. We have shown that growth inhibition by feeding crabs and size selective predation could generate the observed negative correlation between *L. sitkana* size and *C. productus* abundance. If growth rate has a genetic component, as Janson (1982) has shown for *Littorina saxatilis*, then *C. productus* could also select for genetically slower growing *L. sitkana*.

In summary, the escape behavior and associated decrease in foraging and growth in *L. sitkana* exhibit all the characteristics of a classical inducible defense (Harvell, 1990): (1) the environmental cue (crushed conspecific snails) is directly correlated with the unpredictable appearance of the selective agent, (*C. productus*); (2) escape behavior increases the survival of its bearer; and (3) the benefit of escape behavior has a measurable cost, namely reduced growth. We believe that this cost may not be as large as it appears because small size is beneficial in the presence of the selective agent.

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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. 85, 4387–4391.

Behrens, S., 1972. The role of wave impact and desiccation on the distribution of *Littorina sitkana* (Philippi, 1845). Veliger 15, 129–132.

Behrens Yamada, S., 1977. Geographic range limitation of the intertidal gastropods *Littorina sitkana* and *L. planaxis*. Mar. Biol. 39, 61–65.

Behrens Yamada, S., 1989. Are direct developers more locally adapted than planktonic developers? Mar. Biol. 103, 403–411.

Behrens Yamada, S., 1992. Niche relationships in Northeastern Pacific littorines. In: Grahame, J., Mill, P.J., Reid, D.G. (Eds.), Proceedings of the Third International Symposium on Littorinid Biology. The Malacol. Society of London, UK, pp. 281–291.

Behrens Yamada, S., Boulding, E.G., 1996. Highly mobile predatory crabs and the intertidal zonation of their gastropod prey. J. Exp. Mar. Biol. Ecol. 204, 59–83.

Boulding, E.G., Van Alstyne, K., 1993. Mechanisms resulting in differential survival and growth of two species of *Littorina* on wave-exposed and on protected shores. J. Exp. Mar. Biol. Ecol. 169, 139–166.

Crowl, T.A., Covich, A.P., 1990. Predator-induced life-history shifts in a freshwater snail. Science 247, 949–951.

Diehl, S., Eklöv, P., 1995. Effects of piscivore-mediated habitat use on resources, diet, and growth of perch. Ecology 76, 1712–1726.

Gotelli, J.N., 1993. Ant lion zones: causes of high density predator aggregations. Ecology 74, 226–237.

Hadlock, R.P., 1980. Alarm response of the intertidal snail *Littorina littorea* (L.) to predation by the crab *Carcinus maenas* (L.). Biol. Bull. 159, 269–279.

Harvell, C.D., 1984. Predator-induced defense in a marine bryozoan. Science 224, 1357–1359.

Harvell, C.D., 1990. The ecology and evolution of inducible defenses. Q. Rev. Biol. 65, 323–340.

Harvell, C.D., 1992. Inducible defenses and allocation shifts in a marine bryozoan. Ecology 73, 1567–1576.

Havel, J.E., 1987. Predator-induced defenses: a review. In: Kerfoot, W.C., Sih, A. et al. (Eds.), Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover/London, pp. 263–278.

Havel, J.E., Dodson, S.I., 1984. *Chaoborus* predation on typical and spined morphs of *Daphnia pulex*. Limnol. Oceanogr. 29, 487–494.

Hughes, R.N., Answer, P., 1982. Growth, spawning and trematode infection of *Littorina littorea* (L) from an exposed shore on north Whales. J. Moll. Stud. 48, 321–330.

Janson, K., 1982. Genetic and environmental effects on the growth rate of *Littorina saxatilis*. Mar. Biol. 69, 73–78.

Janson, K., 1983. Selection and migration in two distinct phenotypes of *Littorina saxatilis* in Sweden. Oecol (Berlin) 59, 58–61.

Kettlewell, H.B.D., 1959. Darwin's missing evidence. Sci. Am. 3, 200–253.

Kuehl, R.O., 1994. Statistical Principles of Research Design and Analysis. Duxbury Press, Belmont, CA, USA.

Lively, C.M., 1986. Predator-induced shell dimorphism in the acorn barnacle *Chthamalus anisopoma*. Evolution 40, 232–242.

Mead, R., 1988. The Design of Experiments: Statistical Principles for Practical Applications. Cambridge University Press, Cambridge, UK.

Paine, R.T., 1976. Size-limited predation: an observational and experimental approach with the *Mytilus–Pisaster* interaction. Ecology 57, 858–873.

Palmer, A.R., 1990. Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). Hydrobiolgia 193, 155–182.

Richardson, T.D., Brown, K.M., 1992. Predation risk and feeding in an intertidal predatory snail. J. Exp. Mar. Biol. Ecol. 163, 169–182.

Robles, C., 1987. Predator foraging characteristics and prey population structure on a sheltered shore. Ecology 68, 1502–1514.

Sih, A., 1987. Predators and prey lifestyles: an evolutionary and ecological overview. In: Kerfoot, W.C., Sih, A. (Eds.), Predation: Direct and Indirect Impacts on Aquatic Communities. University Press of New England, Hanover/London, pp. 203–224.

Sokal, R.R., Rohlf, F.H., 1981. Biometry, second ed. Freeman, New York.

Stearns, S.C., 1989. The evolutionary significance of phenotypic plasticity. Biol. Sci. 39 (7), 436–445.

Sternberger, R.S., Gilbert, J.J., 1987. Multiple-species induction of morphological defense in the rotifer *Keratella testudo*. Ecology 68, 370–378.

Vermeij, G.J., 1987. Evolution and Escalation: an Ecological History of Life. Princeton University Press, Princeton.

Walker, S.E., Behrens Yamada, S., 1993. Mistaken predation by crabs on empty mollusc shells. Palaeontology 36, 735–741.

Warren, J.H., 1985. Climbing as an avoidance behaviour in the salt marsh periwinkle, *Littorina irrorata* (Say). J. Exp. Mar. Biol. Ecol. 89, 11–18.

Werner, E.E., Anholt, B.R., 1996. Predator-induced behavioral indirect effects: consequences to competitive interactions in anuran larvae. Ecology 77, 157–169.

Wicklow, B.J., 1988. Developmental polymorphism induced by intraspecific predation in the ciliated protozoan *Onychodromus quadricornutus*. J. Protozool. 35, 137–141.

Woltereck, R., 1909. Weitere experimentelle Untersuchungen über Artveränderung, speziell über das Wesen quantitativer Artunterschiede bei Daphniden. Verh. D. Tsch. Zool. Ges. 1909, 110–172.

Yoshioka, T.M., 1982. Predator-induced polymorphism in the bryozoan *Membranipora membranacea* (L.). J. Exp. Mar. Bio. Ecol. 61, 233–242.