Hydrobiologia **193**: 155–182, 1990.
K. Johannesson, D. G. Raffaelli and C. J. Hannaford Ellis (eds), Progress in Littorinid and Muricid Biology.

Effect of crab effluent and scent of damaged conspecifics on feeding, growth, and shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.)

A. Richard Palmer
Department of Zoology, University of Alberta, Edmonton, Alberta T6G 2E9 and Bamfield Marine Station, Bamfield, British Columbia VOR 1BO, Canada

Key words: gastropod, *Cancer*, phenotypic variation, plasticity, laboratory experiment, allometry, alarm response, norm of reaction, adaptation

Abstract

Juvenile *Nucella lapillus* of two different shell phenotypes, exposed shore and protected shore, were maintained in running seawater under each of three experimental conditions for 94 d: a) laboratory control, b) exposed to the effluent of crabs (*Cancer pagurus*) fed frozen fish ('fish-crab'), and c) exposed to the effluent of crabs fed live conspecific snails ('snail-crab'). Rates of barnacle consumption and rates of body weight change varied significantly between phenotypes and among experimental conditions. Individuals from the protected-shore consumed consistently fewer barnacles and grew consistently less than those from the exposed shore. Body weight increases in the fish-crab treatments were from 25 to 50% less than those in the controls and body weights in the snail-crab treatment either did not change or actually decreased. The perceived risk of predation thus appears to have a dramatic effect on the rates of feeding and growth of *N. lapillus*.

At the end of the experiment, size-adjusted final shell weights for both phenotypes were consistently higher than controls (no crab) in both the fish-crab and snail-crab treatments. In addition, apertural tooth height, thickness of the lip, and retractability (i.e. the extent to which a snail could withdraw into its shell), with few exceptions all varied in an adaptive manner in response to the various risk treatments. Similar changes in the shell form of starved snails exposed to the same stimuli suggest very strongly that the morphological responses of both phenotypes were not just due to differences in rates of growth. These differences, at least in part, represented a direct cueing of the shell form of *Nucella lapillus* to differences in the perceived risk of predation. Somewhat surprisingly, the extent of phenotypic plasticity appeared to differ between the populations examined. Both field and laboratory evidence suggest that the exposed-shore population was much more labile morphologically than the protected-shore population.

In many instances, particularly among starved snails, the development of antipredatory shell traits was greater in the fish-crab treatment than in the snail-crab treatment. Because the scent of crabs was present in both treatments, these results suggest a) that, at the frequency/concentration used in the experiments, the scent of damaged conspecifics may have been a supernormal stimulus and b) that the morphological response in these treatments might have been greater if the stimulus had been provided at a lower level.

Introduction

The shells of dogwhelks (Thaidinae) can vary enormously among populations within a single species. This variability is a conspicuous feature of species from rocky shores of the northeastern Pacific (*Nucella canaliculata*, *N. emarginata*, *N. lamellosa* and *N. lima*; Kincaid, 1957, 1964; Kitching, 1976; Spight, 1973), Australia (*Dicathais aegrota*; Phillips *et al.*, 1973), New Zealand (*Lepsiella albomarginata*, *L. scobina*; Kitching & Lockwood, 1974), the North Atlantic (*Nucella lapillus*; Colton, 1916, 1922; Crothers, 1985) and South Africa (*Nucella dubia*; Kilburn & Rippey, 1982) and includes variability in shell thickness, shape and sculpture. In *Nucella lapillus*, this variation has persisted at least since the Late Pliocene (Cambridge & Kitching, 1982; Moore, 1985).

Much of the intraspecific variation in the shells of dogwhelks appears to be adaptive. Thicker shells, or those with smaller apertures, are less vulnerable to predation by shell-breaking crabs (Hughes & Elner, 1979; Kitching *et al.*, 1966; Kitching & Lockwood, 1974; Palmer, 1985a). Thinner shells, on the other hand, are less expensive to produce energetically and less likely to limit the maximum rate of growth (Palmer, 1981). Larger apertures are associated with proportionally larger feet which reduce the probability of dislodgement by breaking waves (Etter, 1988; Kitching *et al.*, 1966). Compared to smooth shells, spiral sculpture increases the force required to crush entire shells and may reduce the vulnerability of snails to attack by shell-crushing fish (Palmer, unpublished observations).

Although some of this morphological variation has a genetic basis (Largen, 1971; Palmer, 1985b), a sizeable fraction may also be ecophenotypic (Etter, 1988; Palmer, 1985b; Spight, 1973). *Nucella lamellosa* of the northeastern Pacific exhibit a rather striking range of shell forms in response to environmental cues. In this species, the scents of crabs and of damaged conspecifics both induce the development of larger apertural teeth (Appleton & Palmer, 1988) and heavier shells (Palmer, unpublished observations) compared to controls. Rates of feeding and growth also declined substantially with increasing apparent risk (Appleton & Palmer, 1988). To determine the generality of these responses in dogwhelks I initiated a similar experiment examining the effect of these environmental stimuli on the feeding, growth and shell morphology of the North Atlantic dogwhelk, *Nucella lapillus* (L.).

Materials and methods

Collection and measurement

Dogwhelks were collected from two sites on the shores of Anglesey, North Wales, UK. Because of different wave-exposure regimes these two sites harbored different shell phenotypes. One site was an exposed headland at the southwestern edge of Trearddur Bay facing directly west into the Irish Sea ('exposed'; 53° 16′ 00″ N, 4° 37′ 10″ W, Ordnance Survey grid reference SH250779) and the other a boulder and cobble beach towards the north end of the Menai Straits, Trwyn Y Penrhyn ('protected'; 53° 17′ 45″ N, 4° 03′ 10″, O.S. grid reference SH631798).

Small preliminary samples were collected initially on July 10, 1986 to determine the relationship between shell length and wet body weight for each site. Based on this relationship, large numbers of dogwhelks of approximately the same wet body weight were collected from each site on July 20 and taken to the University College of North Wales Marine Science Laboratory at Menai Bridge where they were held immersed in running seawater. Snails were identified individually by writing a number on their shell with a fine-tipped permanent marker and covering it with a clear, cyanoacrylate glue to prevent abrasion.

Prior to the experiment, shells were measured for total length, aperture length and width, body whorl diameter, and thickness of the apertural lip (Fig. 1) to the nearest 0.05 mm using Vernier calipers. Lip thickness was measured either between apertural teeth, if present, or at the location on the lip where the teeth would have devel-

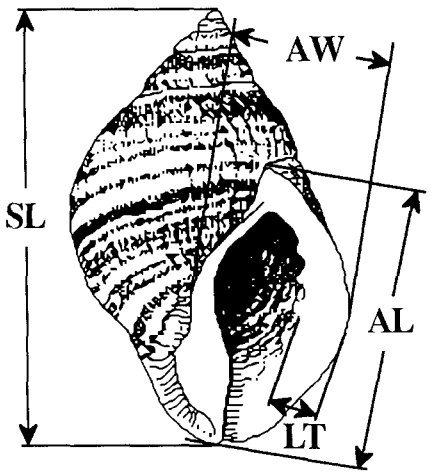

Fig. 1. Dimensions measured on the shells of *Nucella lapillus* (mm). SL – shell length, AL – aperture length, AW – aperture width, LT – thickness of the apertural lip. Diameter of the body whorl was measured by aligning the axis of coiling with the jaws of Vernier calipers, placing the aperture of the shell flush against the lower jaw and bringing the upper jaw in contact with the dorsal-most surface of the body whorl.

oped. At the end of the experiment these traits were remeasured and apertural tooth height was also measured. Apertural tooth height was measured as the difference between two measurements of lip thickness at the middle of the apertural lip, one from the tip of an apertural tooth to the outside of the lip, and perpendicular to it, and the other from the adjacent inter-tooth space to the same point on the outside of the lip. Because the snails were small and actively growing, no apertural teeth were present on any of them at the beginning of the experiment.

Initial shell weights and wet body weights were estimated following the procedure of Palmer (1982). Snails were first weighed while suspended in seawater (immersed weight) to estimate shell dry weight using a previously determined regression of destructively sampled shell dry weight (Y, mg) upon immersed weight (X, mg) for each shell phenotype: Exposed – $Y = 1.5707 \pm 0.0048X - 6.75$ ($r^2 = 0.9998$, $N = 28$), Protected – $Y = 1.6036 \pm 0.0021X - 4.68$ ($r^2 = 0.9999$, $N = 29$). Snails were then weighed in air (whole weight) after gently pressing out as much of the extravisceral water as possible and allowing the shells to dry. Subtracting estimated shell dry weight from whole weight yielded a non-destructive estimate of wet body weight. Test correlations between estimated wet body weight and destructively sampled wet body weight were high for both phenotypes (Exposed–$r^2 = 0.997$, $N = 28$; Protected–$r^2 = 0.990$, $N = 29$). Immersed weight was measured twice, 24 h apart, for each snail prior to initiation of the experiment.

The unoccupied volume of a shell was measured to compare the body size of a snail to the habitable volume of its shell and hence provide a measure of retractability. Unoccupied volume was measured by placing a live snail aperture up on a small supporting ring on the tray of the balance. The shell was orientated carefully so that the plane of the aperture was as close to horizontal as possible. After orientating the shell, the balance was tared and distilled water was introduced into the aperture with a Pasteur pipette until the water was flush with the lip and the columella. The weight of water added was then recorded as volume of shell unoccupied (1 g = 1 ml). Prior to this procedure, the snail had been pressed gently back into the shell with absorbent tissue, to remove as much of the extravisceral water as possible, and the shell was allowed to dry. Repeat estimates of unoccupied volume on the same individual, accomplished by refilling the aperture a second time while still on the balance, varied by less than 5% [mean difference = 2.1 ± 1.38% (mean ± SD); $N = 21$].

Barnacles (*Semibalanus balanoides*), collected on small stones from the protected site, were provided as food for dogwhelks. Barnacle size was measured to the nearest mm as opercular diameter between the inside margins of the rostral and carinal plates. Crabs (*Cancer pagurus*) were collected by divers from the Menai Straits and their size was measured as maximum carapace width.

Experimental design

The basic unit of the experiment consisted of a 20-liter plastic aquarium provided with a continuous supply of running seawater at ambient

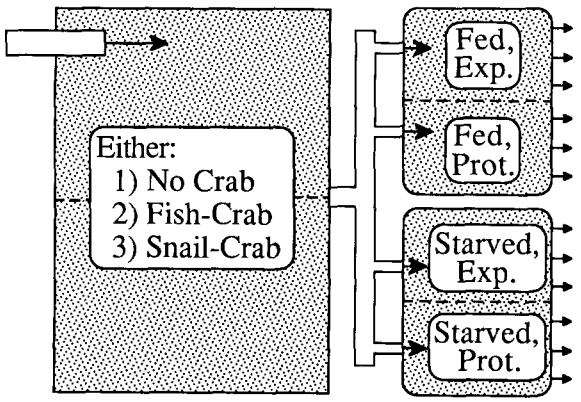

Fig. 2. Patterns of water circulation through experimental cages. Exp. – compartment containing snails from the exposed-shore population, Prot. – compartment containing snails from the protected-shore population. Dashed lines indicate permeable partitions between adjacent compartments.

temperature (Fig. 2). To this aquarium was added either a) nothing ('no crab' = laboratory control) or b) two crabs, one male and one female, which were fed frozen fish (= 'fish-crab') or c) two crabs, one male and one female, fed live, intact *N. lapillus* (15–20 mm shell length) from the exposed site (= 'snail-crab'). Each of these three risk treatments was replicated twice. The four aquaria containing crabs were subdivided with rigid, but perforated partitions to keep the two crabs separate and to allow seawater to circulate between compartments. They were also kept covered with black plastic to minimize disturbance to the crabs. The *C. pagurus* were size-matched as much as possible among replicates (Table 1), however, some crabs moulted or died over the course of the experiment. These were replaced within 24 h.

From each experimental aquarium, seawater flowed by gravity into two cages made from plastic freezer containers (20 × 16 × 7 cm) from which the center of the lids had been removed and replaced with 7 mm plastic mesh. Each cage was further subdivided into two compartments by a plastic mesh partition (Fig. 2). The cages were tilted slightly so that seawater flowed in one side and out the other. Each compartment contained 10 *N. lapillus* from one of the source populations, and the adjoining compartment contained 10 snails from the other. Both compartments of a given cage were either loaded with stones covered with barnacles ('fed') or with bare stones ('starved'). In this manner, snails in the 'starved' treatments were unable to sense food available in the 'fed' treatments. Before placing them in the cage, the stones covered with barnacles were inspected carefully and dead barnacles (i.e. those missing opercular plates) were removed. Upon subsequent examination, all dead barnacles were then assumed to have been eaten.

Table 1. Carapace widths and final wet weights of the crabs (*Cancer pagurus*) used over the course of the experiments (July 24–Oct. 26, 1986). Crabs that escaped, moulted or died were replaced as noted. Dashes indicate crabs that survived for the entire experiment. Total snails eaten refers to the total number of *N. lapillus* eaten by both crabs in a particular replicate. Repl. – replicate, m – male, f – female.

Treatment	Repl.	Initial			Replacement			Final wet weight (g)	Total snails eaten
		Carapace width (mm)	Sex	Dates (mo/d)	Carapace width (mm)	Sex	Dates (mo/d)		
Fish-crab	1	107	m	7/24–9/16	104	m	9/16–10/26	167.3	
		79	f	7/24–9/3	100	f	9/3–10/26	172.7	
	2	101	m	7/24–8/26	125	m	8/26–10/26	285.5	
		110	f	7/24–10/26	–	–	–	215.0	
Snail-crab	1	76	m	7/24–10/26	–	–	–	72.3	544
		84	f	7/24–10/13	111	f	10/13–10/26	154.9	
	2	82	f	7/24–8/16	105	f	8/16–10/26	171.0	703
		98	m	7/24–10/26	–	–	–	153.7	

Execution of the experiment

From the time of collection until initiation of the experiment (4 d), snails were held continuously immersed in cages without food in fresh running seawater which, at least after entering the laboratory seawater system, had no prior contact with crabs. On July 24, following tagging and measurement, all snails were loaded into their respective cages and then the cages were connected to aquaria containing the experimental stimuli.

Snails from the starved and fed treatments were monitored differently. To determine the effect of risk treatments on the short-term rates of shell deposition of starved snails, immersed weight was measured 24 h after initiation of the experiment, at 48 h intervals for the next six days, at 72 h intervals for the subsequent six days, and with declining frequency for the remainder of the experiment. These weighings were conducted as quickly as possible to minimize disturbance. Snails of both phenotypes were removed from an individual cage, held immersed in seawater in a plastic container, weighed and then returned to running seawater in their respective cage within 15 min. At the end of the experiment (October 26), snails were removed from their cages and measured for shell length, lip thickness, apertural tooth height, immersed weight and whole weight.

Snails in the fed treatment were not monitored as frequently to avoid disturbing them. At 10 to 30 d intervals they were measured for shell length and immersed weight. Whole weight was not measured because it disrupted activity of the snails for the subsequent 24–48 h. Barnacles were replaced with fresh ones every 20–30 d. Both eaten and uneaten barnacles removed from the cages were counted and the opercular diameters of eaten barnacles measured.

Flow rates through the aquaria were measured every two to four days and adjusted if necessary to a rate close to 1.7 liters min^{-1} (0.85 l m^{-1} $cage^{-1}$). In addition, the aquaria were inspected daily to insure that the flow of seawater had not been interrupted. Water temperature was also measured daily and ranged from 16 °C at the beginning to 13 °C at the end of the experiment. At least once a day, the number of snails eaten by crabs in the snail-crab treatments were recorded, and replacement snails were added to bring the total up to five per crab. Over the 94 day duration of the experiment, more than 250 snails were eaten per crab (Table 1). Crabs in the fish-crab treatment were fed roughly 2–4 g of frozen fish (haddock or cod) every third or fourth day, and any uneaten fish was removed at the end of the day.

Statistical analyses

Statistical analyses were conducted using the microcomputer statistical package Statview 512 + ™ (Abacas Concepts, Berkeley, CA). Because of the design of the experiment, F-values from analysis of variance (ANOVA) were computed according to the procedure suggested by Hartley (1962) and Sokal & Rohlf (1981; p. 395–396) as follows. Sums of squares (SS) were computed via a three-way fully factorial ANOVA (A = risk treatment × B = source population × C = replicate). Because replicates were nested within the main effects, and because the question to be answered was whether the variation among main effects exceeded that between replicate cages rather than that among snails within cages, the mean squares (MS) for main effects (A or B) and their interaction (AB) were tested over the MS for replicates. The appropriate MS for replicates was computed by summing the SS for three terms: a) the dummy main effect 'replicate' (C), b) the two two-way interactions which included this dummy effect (AC and BC), and c) the three-way interaction term (ABC). This sum was then divided by the sum of the degrees of freedom for these terms. This MS for replicates was then tested over the error MS.

Because rates of growth varied among risk treatments, so did the final sizes of snails. Hence to compare morphological traits among groups of different average size the effect of size had to be scaled out. Analysis of covariance (ANCOVA) could not be conducted with confidence on these data for two reasons. First, because the final size

ranges of some experimental groups did not overlap, adjusted means would have to have been extrapolated outside the range for which I had data. Second, because the size range within experimental groups was not very large slopes within groups could not be determined with much confidence. To circumvent these difficulties, reference samples of 100 snails each were collected near the end of the experiment (October 16, 17). Both phenotypes were collected from the same sites as those that had yielded the experimental snails. These samples included roughly equal numbers of all sizes of snails from 10 mm shell length up through fully mature adults and were used to define the size-dependence of the traits of interest for each population.

To compare traits of experimental snails at the end of the experiment, the size of the trait in question for a given snail was transformed to that of a standard-sized snail as follows:

$$\log V_i = (\log O_i - \log E_i) + \log V_s$$

where V_i = value of a trait for snail i scaled to that of a standard-sized snail, O_i = original observed value of the trait for snail i, E_i = the expected value of that trait for a snail of the same size as i determined from the regression obtained from the appropriate reference sample (see Table 2), and V_s = the average expected value of that trait for the standard-sized snail, also determined from the reference sample regression. For example, the observed final shell weight of 1580 mg for a snail of the protected phenotype of 270 mg wet body weight was transformed to that for a snail of 350 mg wet body weight as follows: O_i = log(1580), E_i = 0.921 (log(270)) + 1.013 (from regression 6b, Table 2), and V_s = 0.921 (log(350)) + 1.013. Hence V_i = 2007 mg. This transformation assumes that both the variance and the effects of the risk treatments were proportional to size. Although means and standard errors of these size-scaled values were graphed in untransformed units, statistical analyses [i.e. t-tests comparing adjusted means ($V_i \pm$ SE) vs. expected means ($V_s \pm$ SE), and the relevant P values of Figs. 12 and 13] were conducted on the log-transformed variates.

Results

Morphological variation within and between populations

Field-collected snails of both phenotypes differed substantially in most traits examined. For shells of a given length, the aperture was significantly longer and significantly wider for the exposed-shore phenotype (Figs. 3a, b; Regressions 1a, b, and 2a, b in Table 2). Mature snails of both phenotypes had equally thick lips (Fig. 3c) but because of their lower spires, lip thickness at a given length was greater for the exposed-shore

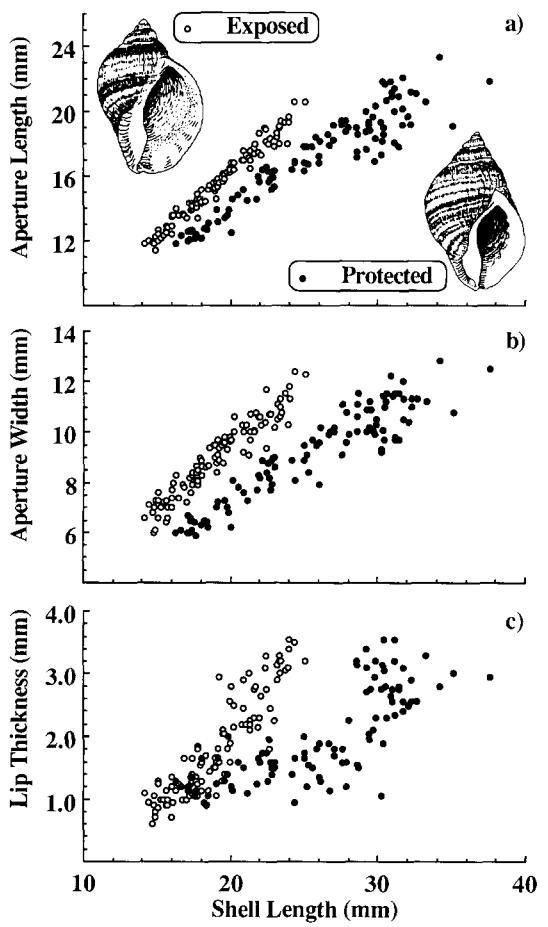

Fig. 3. Variation in aperture length, aperture width and lip thickness as a function of shell length for two populations of *Nucella lapillus* from shores of different wave exposure. See Table 2 for regression equations (of log-transformed values) and statistics.

Table 2. Regression equations (both variables log-transformed; slope and intercept ± SE) describing morphological differences between the exposed- and protected-shore populations of *Nucella lapillus* used in the experiments. See Figs. 3–5 for scatterplots of these data[§].

X	Y	Source	Regression	r^2	Comparison of slopes			
					Allometry		a) vs b) or c) vs d)	
					T_s	P	T_s	P
1) Shell length	Aperture length	a) ExpII	$Y = 0.991(\pm 0.017)X - 0.078(\pm 0.001)$	0.972	0.53	0.60	6.58	<0.001
		b) ProtII	$Y = 0.792(\pm 0.025)X + 0.120(\pm 0.002)$	0.910	8.32	<0.001		
2) Shell length	Aperture width	a) ExpII	$Y = 1.070(\pm 0.035)X - 0.416(\pm 0.002)$	0.905	2.00	0.048	3.14	0.002
		b) ProtII	$Y = 0.921(\pm 0.032)X - 0.337(\pm 0.003)$	0.895	2.47	0.015		
3) Shell length	Body whorl diameter	a) ExpII	$Y = 1.014(\pm 0.022)X - 0.309(\pm 0.001)$	0.957	0.64	0.53	0.03	0.97
		b) ProtII	$Y = 1.013(\pm 0.020)X - 0.345(\pm 0.002)$	0.962	0.65	0.52		
4) Shell length	Lip thickness	a) ExpII	$Y = 2.677(\pm 0.126)X - 3.191(\pm 0.008)$	0.821	13.31	<0.001	7.94	<0.001
		b) ProtII*	$Y = 1.343(\pm 0.111)X - 1.619(\pm 0.010)$	0.601	3.09	0.003		
		b′) ProtII**	$Y = 0.635(\pm 0.144)X - 0.695(\pm 0.010)$	0.254	2.53	0.014		
5) Shell length	Body wet wt.	a) ExpII	$Y = 2.948(\pm 0.075)X - 1.227(\pm 0.005)$	0.941	0.69	0.49	5.38	<0.001
		b) ProtII	$Y = 3.468(\pm 0.061)X - 2.291(\pm 0.006)$	0.971	7.67	<0.001		
		c) ExpI	$Y = 2.891(\pm 0.174)X - 1.153(\pm 0.010)$	0.911	0.63	0.53	0.09	0.93
		d) ProtI	$Y = 2.911(\pm 0.144)X - 1.587(\pm 0.008)$	0.938	0.62	0.54		
6) Body wet wt.	Shell wt.	a) ExpII	$Y = 1.275(\pm 0.042)X - 0.216(\pm 0.008)$	0.903	6.54	<0.001	7.61	<0.001
		b) ProtII	$Y = 0.921(\pm 0.020)X - 1.013(\pm 0.007)$	0.955	3.95	<0.001		
		c) ExpI	$Y = 1.134(\pm 0.083)X - 0.002(\pm 0.015)$	0.879	1.61	0.118	1.39	0.17
		d) ProtI	$Y = 0.979(\pm 0.075)X - 0.899(\pm 0.013)$	0.864	0.28	0.78		
7) Shell length	Shell wt.	a) ExpII	$Y = 3.974(\pm 0.092)X - 2.056(\pm 0.006)$	0.950	10.58	<0.001	6.34	<0.001
		b) ProtII	$Y = 3.245(\pm 0.069)X - 1.169(\pm 0.006)$	0.958	3.55	<0.001		
		c) ExpI	$Y = 3.512(\pm 0.175)X - 1.588(\pm 0.011)$	0.939	2.92	0.007	1.93	0.059
		d) ProtI	$Y = 3.050(\pm 0.163)X - 0.916(\pm 0.010)$	0.928	0.31	0.76		
8) Body wet wt.	Unocc. volume	a) ExpII†	$Y = 0.710(\pm 0.040)X - 2.427(\pm 0.008)$	0.769	7.25	<0.001	0.75	0.45
		b) ProtII	$Y = 0.745(\pm 0.026)X - 2.317(\pm 0.009)$	0.892	9.77	<0.001		
9) Shell length	Unocc. volume	a) ExpII†	$Y = 2.251(\pm 0.100)X - 3.499(\pm 0.007)$	0.839	7.49	<0.001	4.21	<0.001
		b) ProtII	$Y = 2.643(\pm 0.086)X - 4.108(\pm 0.008)$	0.907	4.15	<0.001		

§ Linear dimensions are in mm, weights in mg and volume in ml. All regression equations are for log-transformed values, even though some scatterplots are on linear axes. The SEs tabulated for intercepts actually correspond to the SE of the expected Y at the average X for the sample. $N = 100$ for both populations except for ExpI and ProtI where $N = 28$. T_s – either the value from a T-test for allometry, computed as the difference between observed slopes and those expected theoretically for isometry (1.0 or 3.0 depending on dimensionality), or the value from a T-test comparing the slopes of the two populations sampled [a) vs b) or c) vs. d)], r^2 – coefficient of determination, P = exact probability, Source - source population, Exp – exposed-shore phenotype, Prot – protected-shore phenotype. ExpI and Prot I were collected July 10, 1986, ExpII and ProtII were collected from the field near the end of the experiment (Oct. 16/17; see methods).

* Relationship not linear even on log-log plot (see Fig. 3c).

** Regression for linear region of scatter: snails ≤ 28 mm shell length ($N = 59$); used to estimate adjusted lip thickness in Fig. 13.

† One outlier removed prior to computing regression (see Fig. 5).

snails. In addition to aperture size, the body weight of the animal occupying a shell of a given length was significantly greater for the exposed-shore phenotype (Fig. 4a, Regressions 5a–d). Related to this latter difference, the weight of shell for a given weight of animal was substantially higher for the protected-shore phenotype (Fig. 4b, Regressions 6a–d). Ironically, because of the difference in shape, the shell weights of the two phenotypes overlapped broadly for a given shell length (Fig. 4c, Regressions 7a–d). The two phenotypes did, however, differ in another interesting way: the volume of unoccupied shell, a measure of retractability, was proportionally larger for the protected- than the exposed-shore phenotype (Fig. 5; Regressions 8a, b). This assumes that the visceral mass extends equally far up the apex of both phenotypes, an assumption which seems justified based upon an examination of animals removed from fractured shells. Curiously, the diameter of the body whorl did not differ between populations for shells of the same length (Regressions 3a, b).

Several traits exhibited significant allometry within populations, and the coefficients of allometry themselves often differed between populations. Aperture length, for example, became proportionally smaller with increasing shell length for the protected- but not the exposed-shore population (Regressions 1a, b, Table 2). Aperture width, on the other hand, became proportionally larger with increasing length in the exposed population but proportionally smaller in the protected one (Regressions 2a, b). In the protected but not the exposed population, body weight increased disproportionally with increasing shell length (Regressions 5a, b), whereas shell weight increased disproportionally with length in both populations (Regressions 7a, b). In contrast, shell

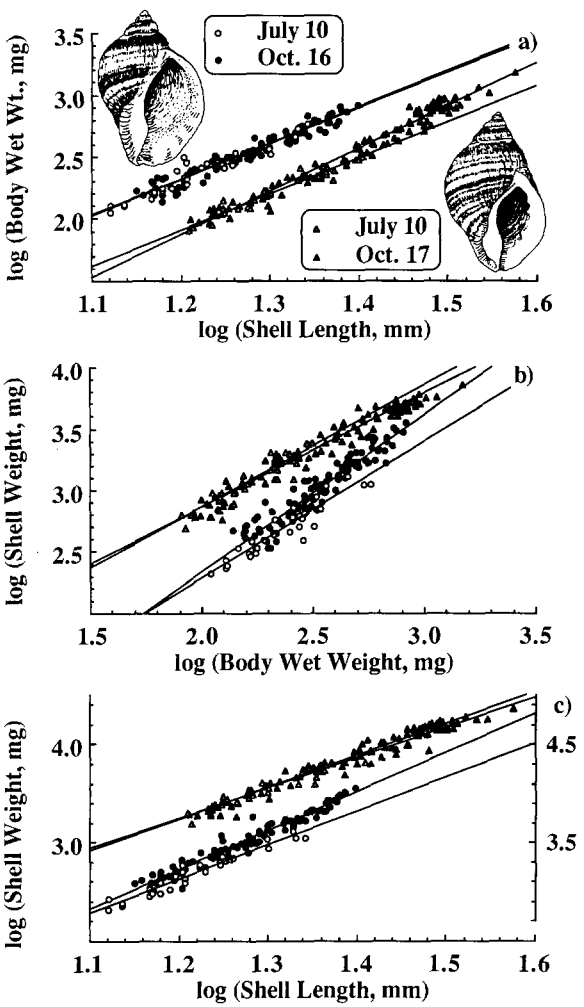

Fig. 4. Relationships between log transformed shell length, wet body weight and shell weight for two populations of *Nucella lapillus* from shores of different wave exposure. The samples were collected on two different dates in 1986. See Table 2 for regression equations and statistics. Triangles – protected-shore population, circles – exposed-shore population. Note that points for the protected-shore population have been shifted up 0.5 log units in Fig. 4c to avoid overplotting those of the exposed-shore population and should thus be compared against the axis to the right of figure.

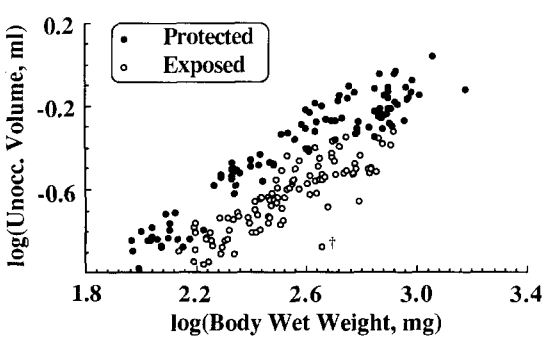

Fig. 5. The relation between unoccupied volume of the shell and wet body weight for two populations of *Nucella lapillus* from shores of different wave exposure. See Table 2 for regression equations and statistics. † – this point was eliminated as an outlier prior to computing Regression 8a (Table 2).

weight increased disproportionally with respect to body weight only for the exposed population, while it decreased with respect to body weight in the protected population (Regressions 6a, b). These last two patterns were qualitatively the same for the smaller preliminary samples collected from the same sites three months earlier (Regressions 6c, d and 7c, d), but were less dramatic probably because of smaller sample sizes and narrower size ranges. Finally, the volume of unoccupied shell decreased in proportion to body weight in both populations as size increased (Regressions 8a, b, 9a, b).

The thickness of the apertural lip exhibited the most complicated variation with size (Fig. 3c). In both populations, lip thickness increased disproportionally with increasing shell length (Regressions 4a, b, Table 2), but even log-transformed values varied nonlinearly (most notable for protected-shore snails; data not shown). For both populations, as snails approached maturity, lip thickness increased at a much more rapid rate (Fig. 3c).

Temporal change within natural populations

Rather unexpectedly, the field collections of exposed-shore *N. lapillus* on two different dates (July 10 and Oct. 16) differed in relative shell weight. Snails collected in October had significantly heavier shells than those collected in July for a given wet body weight (Fig. 4b) and also for a given shell length (Fig. 4c). Body weight for a given shell length, however, did not differ between dates (Fig. 4a) hence the variable that changed was shell weight (compare Regressions 5a vs. 5c, 6a vs. 6c and 7a vs. 7c, Table 2).

Of interest, no significant differences were observed for these traits between dates in snails from the protected shore (Figs. 4a–c; compare Regressions 5b vs. 5d, 6b vs. 6d and 7b vs. 7d).

Variation among initial groups

Because of the many morphological differences outlined above, some attribute had to be used by which animals of comparable size from the two populations studied could be selected for the experimental groups. I chose wet body weight for this purpose because it seemed the least biased measure of overall animal size (see size scaling in discussion for an expanded consideration of this problem). Snails from both populations were sorted by shell length and then individuals were chosen to be close to 195 mg wet weight based on Regressions 5a, b (Table 2). No significant differences in wet body weight were present among risk treatments or between source populations at the beginning of the experiment for either starved or fed snails (Tables 3, 4). Unfortunately, by chance, a significant difference did materialize among replicates in the starved treatments ($P = 0.02$), but this did not occur in the fed treatments. Among the remaining traits (shell length, shell weight and lip thickness) no significant differences existed among risk treatments or replicates for either fed or starved snails, even though, as expected, differences between source populations were highly significant (Tables 3, 4).

Short-term rates of shell deposition in starved snails

In the 24 h immediately prior to the experiment, the daily rate of shell deposition ranged from 5 to 8 mg snail^{-1} d^{-1} among groups in the starved series (Fig. 6). Although significant differences existed between the two source populations ($P = 0.016$), none appeared among risk treatments ($P = 0.16$, Table 5). In the first 24 h of the experiment, however, some interesting differences arose among risk treatments (Fig. 6). Compared to baseline values, the daily rate of deposition declined dramatically in the snail-crab treatments: -26 and -46% for the exposed- and protected-shore phenotypes respectively. This decline was less dramatic in the fish-crab treatments (-13 and -27% respectively). In the no-crab treatments the rate of shell deposition either continued to increase ($+19\%$) or declined slightly (-14%) for the exposed- and protected-shore phenotypes respectively. These differences among risk treatments were highly significant ($P = 0.008$, Table 5).

Table 3. Initial and final values of four traits of *Nucella lapillus* held under various experimental conditions in the laboratory for 94 d. SE – standard error.

Source population	Treatment	Replicate	N	Shell length (mm)				Body wet wt. (mg)				Shell weight (mg)				Lip thickness (mm)			
				Initial		Final		Initial		Final		Initial		Final		Initial		Final	
				Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
Starved																			
Exposed	No crab	1	9	15.6	0.20	16.1	0.16	218	7.6	155	6.9	388	25.1	512	33.2	0.75	0.037	1.13	0.082
		2	10	15.1	0.16	15.5	0.18	188	9.1	132	7.2	337	23.4	432	31.9	0.75	0.043	0.97	0.054
	Fish-crab	1	9	15.3	0.17	15.8	0.22	202	11.2	146	9.5	341	18.6	475	33.9	0.71	0.020	1.17	0.073
		2	10	15.0	0.17	15.3	0.22	185	7.0	127	5.2	296	11.2	413	23.7	0.71	0.015	1.15	0.083
	Snail-crab	1	10	15.0	0.15	15.1	0.18	185	7.0	127	6.1	346	20.4	394	26.2	0.75	0.042	0.91	0.063
		2	10	15.1	0.12	15.2	0.17	195	7.8	139	5.6	323	10.5	393	18.1	0.71	0.022	0.89	0.040
Protected	No crab	1	10	21.3	0.20	21.1	0.20	181	9.3	139	6.9	1402	74.9	1434	78.6	1.42	0.062	1.54	0.071
		2	8	21.3	0.25	21.2	0.23	196	7.3	164	9.6	1328	46.0	1359	44.5	1.31	0.054	1.34	0.069
	Fish-crab	1	10	21.6	0.26	21.4	0.25	227	11.0	172	8.9	1459	104.7	1517	100.2	1.32	0.101	1.52	0.092
		2	8	21.2	0.35	21.1	0.35	191	13.4	144	10.0	1347	64.9	1392	54.5	1.42	0.096	1.56	0.091
	Snail-crab	1	10	21.5	0.30	21.4	0.28	208	9.6	159	7.7	1477	76.2	1516	72.7	1.45	0.055	1.52	0.061
		2	9	21.2	0.22	21.0	0.23	202	8.6	154	10.8	1267	61.5	1316	62.0	1.29	0.073	1.46	0.073
Fed																			
Exposed	No crab	1	10	14.8	0.16	22.5	0.40	182	7.4	621	38.0	317	20.6	1648	113.8	0.65	0.028	1.80	0.153
		2	10	15.0	0.19	21.6	0.56	187	8.5	574	37.1	318	15.4	1510	115.8	0.67	0.033	1.78	0.142
	Fish-crab	1	9	14.9	0.19	22.1	0.64	182	8.7	485	34.4	333	20.8	1777	145.6	0.74	0.059	2.13	0.201
		2	10	15.1	0.19	22.5	0.41	193	9.2	509	28.7	333	15.6	2047	85.5	0.72	0.023	2.66	0.091
	Snail-crab	1	10	15.3	0.20	15.7	0.17	209	14.6	179	10.8	372	19.0	496	23.4	0.78	0.032	1.10	0.080
		2	9	14.7	0.16	16.5	0.22	174	5.9	204	4.5	304	14.5	590	39.5	0.64	0.024	1.12	0.092
Protected	No crab	1	10	21.3	0.23	23.1	0.60	202	10.3	375	38.1	1467	68.6	1997	140.7	1.44	0.087	1.43	0.082
		2	8	21.2	0.17	23.9	0.58	187	7.3	360	44.9	1360	87.9	2095	109.6	1.39	0.079	1.48	0.104
	Fish-crab	1	9	21.2	0.19	22.5	0.43	196	7.5	265	19.4	1402	81.4	1875	134.7	1.29	0.067	1.74	0.084
		2	8	20.8	0.21	23.3	0.78	190	5.5	305	34.6	1271	46.9	2117	195.7	1.29	0.062	1.82	0.081
	Snail-crab	1	10	21.5	0.16	21.2	0.17	206	6.3	175	6.1	1457	59.1	1511	53.4	1.42	0.090	1.59	0.090
		2	10	21.6	0.26	21.3	0.27	213	11.9	184	9.8	1589	106.4	1690	114.9	1.57	0.078	1.83	0.083

Table 4. Results from ANOVA on initial traits of *Nucella lapillus* used in the experiments. See Table 3 for trait means. Treatments – No crab, Fish-crab, Snail-crab. Source populations – exposed, protected. df – degrees of freedom, MS – mean squares, P – exact probability. $MS_{replicates}$ was tested over MS_{error}, all other MS were tested over $MS_{replicates}$ (see methods for computation of $MS_{replicates}$ and F values).

Source of variation	df	Shell length		Body wet wt.		Shell weight		Lip thickness	
		MS	P	MS	P	MS	P	MS	P
Starved snails									
Main effects									
Treatment	2	0.18	0.73	292	0.88	1046	0.98	0.0018	0.95
Source pop.	1	1071.54	<0.001	858	0.55	3043×10^4	<0.001	11.5067	<0.001
Interaction	2	0.33	0.58	2668	0.36	15657	0.75	0.0049	0.88
Replicates	6	0.55	0.99	2166	0.02	52667	0.09	0.0384	0.29
Error	101	0.445		797		27900		0.0308	
Fed snails									
Main effects									
Treatment	2	0.77	0.29	1497	0.39	91077	0.19	0.0854	0.16
Source pop.	1	1113.24	<0.001	3549	0.16	3393×10^4	<0.001	13.8481	<0.001
Interaction	2	0.61	0.36	358	0.78	77410	0.23	0.1438	0.07
Replicates	6	0.50	0.24	1363	0.13	40586	0.24	0.0344	0.43
Error	102	0.371		801		30084		0.0344	

Except for a brief increase following day three, the rates of shell deposition declined roughly exponentially over the remainder of the experiment (Fig. 6). Following the measurements of day three, bare stones were added to otherwise empty cages to provide a more natural substratum for the starved snails. This appeared to result in an

Table 5. Results from ANOVA on rates of shell deposition of starved *Nucella lapillus* held under various conditions in the laboratory (Fig. 6). Baseline – rate of deposition over 24 h immediately prior to the experiment. % Change in rate – percent change in the rate of deposition from baseline to that of the first 24 h of the experiment. Abbreviations and analyses as in Table 4.

Source of variation	df	Baseline		% Change in rate	
		MS	P	MS	P
Main effects					
Treatment	2	14.113	0.16	14077	0.008
Source pop.	1	62.085	0.016	13797	0.013
Interaction	2	0.029	0.99	820	0.53
Replicates	6	5.609	0.63	1148	0.65
Error	101	7.679		1649	

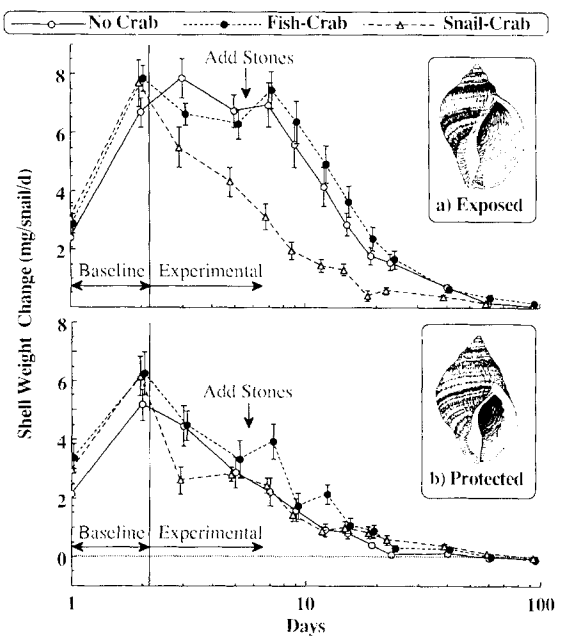

Fig. 6. Changes in the rate of shell deposition (mean ± SE) as a function of time for *Nucella lapillus* from shores of different wave exposure. Snails were held without food under three different experimental conditions in the laboratory. Note that time is plotted on a logarithmic scale. Add stones – bare stones added to cages. See Table 1 for sample sizes.

Table 6. Results from ANOVA on final values and total change for traits of starved *Nucella lapillus* held under different conditions in the laboratory (Fig. 7). Abbreviations and analyses as in Table 4.

Source of variation	df	Body weight change		Shell weight change		Final tooth ht.		Lip thickness change	
		MS	P	MS	P	MS	P	MS	P
Main effects									
Treatment	2	348	0.18	12785	0.016	0.04812	0.044	0.2660	0.022
Source pop.	1	4018	0.002	82530	<0.001	0.03733	0.085	0.9351	0.002
Interaction	2	704	0.061	11976	0.019	0.02781	0.11	0.1295	0.086
Replicates	6	153	0.32	1451	0.50	0.00868	0.062	0.0343	0.26
Error	101	128		1627		0.00417		0.0261	

increase in the rate of shell deposition for both phenotypes in the fish-crab treatments as well as for the exposed phenotype in the no-crab treatment (Fig. 6).

Differences in final shell morphology among starved snails

Snails of the exposed-shore phenotype lost significantly more body weight over the 94 d of the experiment than those of the protected-shore phenotype (Fig. 7a, Table 6). Risk treatment had no overall effect on body weight loss, although the interaction between source population and risk treatment was nearly significant ($P = 0.061$, Table 6). Shell weight gain, however, not only varied significantly among risk treatment groups ($P = 0.016$) and between source populations ($P < 0.001$), but the interaction between these main effects was also significant ($P = 0.019$; Fig. 7b, Table 6). For both populations, the total

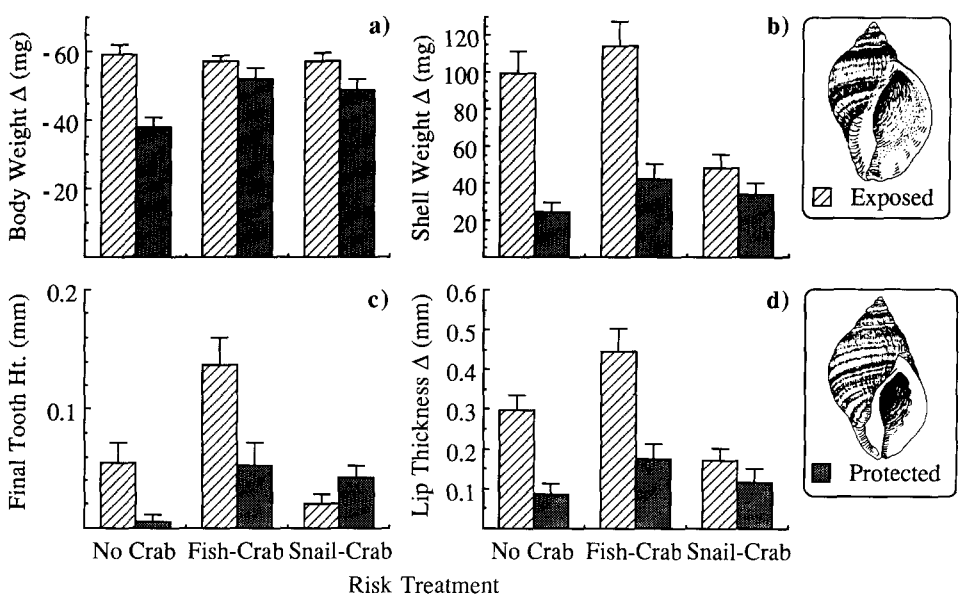

Fig. 7. Total change (Δ) in wet body weight, shell weight, apertural tooth height, and lip thickness of *Nucella lapillus* from shores of different wave exposure (mean ± SE). Snails were held without food under three different experimental conditions in the laboratory for 94 d. All snails lacked apertural teeth at the beginning of the experiment, thus final tooth height is synonymous with the change in tooth height. See Table 3 for sample sizes and initial and final values.

shell added was highest in the fish-crab treatments. Exposed-shore snails, however, added consistently more shell than those from the protected shore.

The rank order of final apertural tooth height and change in lip thickness of starved snails paralleled that for total shell weight change among risk treatments (Fig. 7c, d). For both traits, risk treatment had a statistically significant effect, and source population had a significant or nearly significant effect (Table 6). As observed for shell weight gain, the increase in tooth height and lip thickness was the greatest in the fish-crab treatments. Note, however, that the teeth which developed in these immature snails were not very large for either population in any treatment.

Differences in feeding and growth

Rates of barnacle consumption differed significantly between source populations and also varied substantially among risk treatments (Fig. 8, Table 7). In all risk treatments fewer barnacles were consumed by the protected- than the exposed-shore snails. Among risk treatments, the rate of barnacle consumption was highest in the no-crab treatment: 2.09 and 1.48 barnacles snail^{-1} d^{-1} for the exposed- and protected-shore phenotypes respectively. The feeding rate declined by more than 25% in the fish-crab treatment (to 1.48 and 1.11 barnacles snail^{-1} d^{-1} respectively) and by more than 75% in the snail-crab treatment (to 0.50 and 0.24 barnacles snail^{-1} d^{-1}).

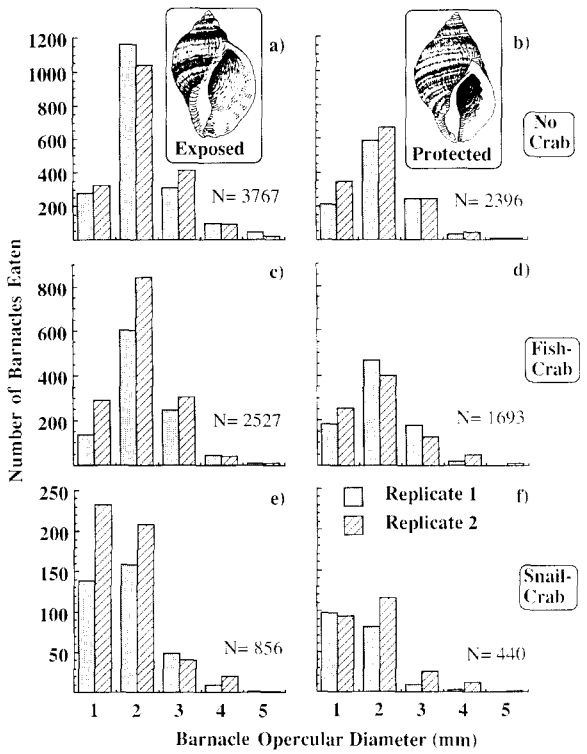

Fig. 8. Size-frequency distributions of barnacles eaten by *Nucella lapillus* from shores of different wave exposure. Snails were held under three different experimental conditions in the laboratory for 94 d. See Table 3 for the number of snails in each cage. Note the different scales of the vertical axes among risk treatments. N – total barnacles eaten of all sizes.

Not surprisingly, differences in the rates of

Table 7. Results from ANOVA on numbers of barnacles consumed by and % change in wet body weight of fed *Nucella lapillus* held under various conditions in the laboratory (see Figs. 8, 9; see Table 3 for final body weights). Abbreviations and analyses as in Table 4. – not applicable.

Source of variation	Total # barnacles eaten			% Change in body weight		
	df	MS	P	df	MS	P
Main effects						
Treatment	2	1500530	<0.001	2	279702	<0.001
Source pop.	1	572470	0.002	1	235675	<0.001
Interaction	2	57297	0.16	2	42118	0.001
Replicates	6	22800		6	1737	0.65
Error	–	–	–	101	2693	

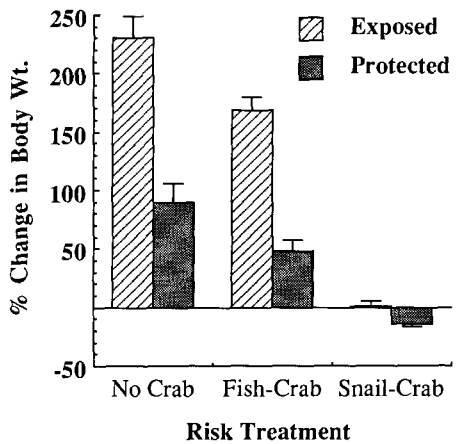

Fig. 9. Percent change in wet body weight of *Nucella lapillus* from shores of different wave exposure (mean ± SE). Snails were held with food (barnacles) under three different experimental conditions in the laboratory for 94 d. See Table 3 for sample sizes and initial and final values.

body growth paralleled those of feeding rate (Fig. 9). For both phenotypes, total body weight change declined in the order: no crab → fish-crab → snail crab ($P < 0.001$, Table 7). Snails from the protected-shore population, however, gained less than half as much in body weight as those from the exposed shore in the no-crab and fish-crab treatments and actually lost weight in the snail-crab treatment. The greater range of rates of body growth among exposed- compared to protected-shore snails was also reflected in a significant interaction between risk treatment and source population ($P < 0.001$, Table 7).

In contrast to the differences in total body weight change, changes in shell length over time were effectively the same for the no-crab and fish-crab treatments for both shell phenotypes (Figs. 10a, c, Table 8). In the snail-crab treatment, however, shell length either increased only slightly for the exposed phenotype or decreased slightly (presumably due to dissolution and abrasion of the apex while handling the shells) for the protected phenotype.

Rates of shell deposition also differed somewhat from rates of body weight gain (Figs. 10b, d, Table 8). Even though they gained less in body weight, snails in the fish-crab treatments added either more shell material than (exposed) or the same amount as (protected) those in the no-crab treatment. Shell weight gains in snails from the snail-crab treatment were slight for both phenotypes.

Differences in final shell morphology among fed snails

Final apertural tooth height of fed snails not only varied among risk treatments, but the pattern of variation differed between source populations (Fig. 11). Apertural tooth height was highest in the fish-crab treatment for the exposed phenotype but highest in the snail-crab treatment for the protected phenotype. Because of the magnitude of this interaction ($P = 0.037$, Table 8), neither of the main effects was significant statistically when both source populations were analyzed together (Table 8), even though the effect of risk treatment was highly significant for both source populations

Table 8. Results from ANOVA on final shell length (Fig. 10a, c), final shell weight (Fig. 10b, d) and final apertural tooth height (Fig. 11) of fed *Nucella lapillus* held under various conditions in the laboratory. Abbreviations and analyses as in Table 4.

Source of variation	df	Final shell length		Final shell weight		Final tooth ht.	
		MS	P	MS	P	MS	P
Main effects							
Treatment	2	206.87	<0.001	8517938	<0.001	0.0312	0.13
Source pop.	1	165.52	<0.001	8068268	<0.001	0.0255	0.17
Interaction	2	55.49	0.002	2257363	0.005	0.0631	0.037
Replicates	6	2.41	0.31	155493	0.26	0.0104	0.13
Error	101	2.01		119502		0.0061	

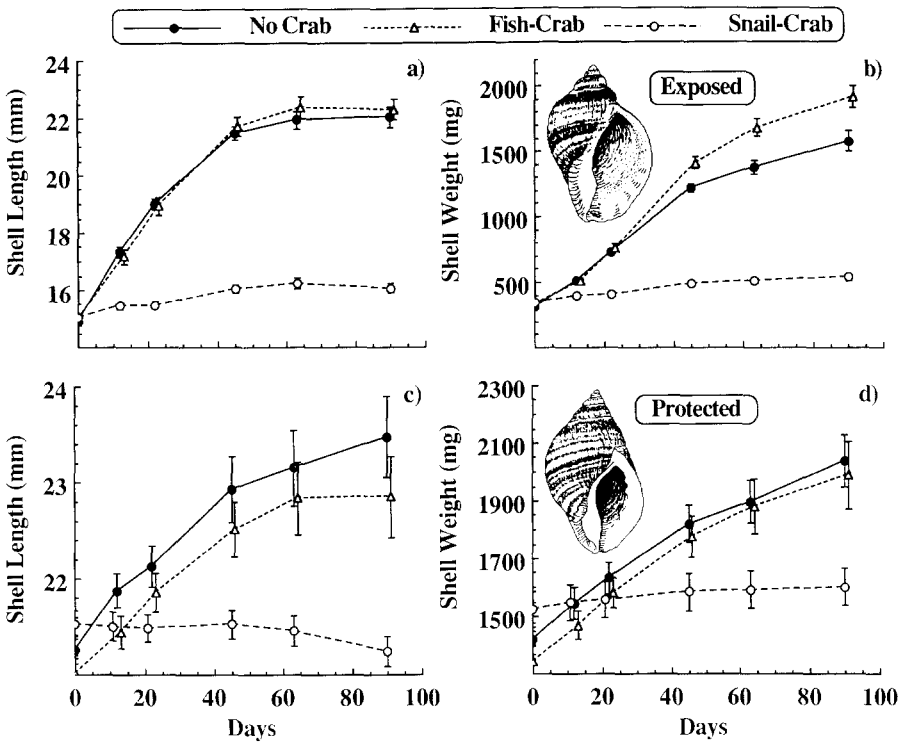

Fig. 10. Changes in shell length and shell weight as a function of time by *Nucella lapillus* from shores of different wave exposure. Snails were held with food (barnacles) under three different experimental conditions in the laboratory for 94 d. See Table 3 for sample sizes and initial and final values. Note that some points have been shifted slightly right or left to avoid overplotting. The actual dates on which the measurements were taken lie underneath the points for the no-crab treatment (solid circles). Each point represents a mean ± SE. Where error bars are not present they are less than the diameter of the symbol.

when each was analyzed separately ($P = 0.003$ and $P < 0.001$ for exposed and protected respectively from 1-way ANOVA).

Both relative shell weight and retractability varied consistently (with one exception) among risk treatments for both shell phenotypes (Fig. 12). Relative shell weight and retractability were lowest in the no-crab, intermediate in the fish-crab and highest in the snail-crab treatments. The only exception to this pattern occurred in exposed-shore snails: retractability in the snail-crab treatment did not differ from controls (no crab).

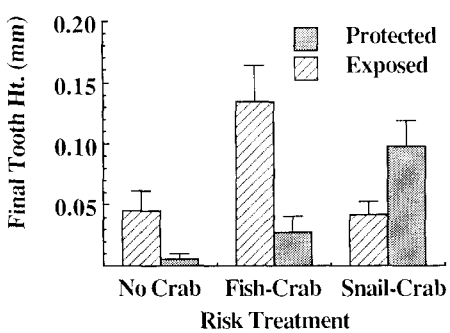

Fig. 11. Final apertural tooth height (mean ± SE) of *Nucella lapillus* from shores of different wave exposure. Snails were held with food (barnacles) under three different experimental conditions in the laboratory for 94 d. See Table 3 for sample sizes.

The precise pattern of variation, and the degree of change relative to references shells collected from the field at the beginning of the experiment, however, depended upon the metric used to standardize 'size'. For shells of a standard length for both phenotypes, shell weight increased significantly (or nearly so) in all groups relative to the reference samples (Fig. 12a). This increase in relative shell weight was highest in the snail-crab treatment, slightly less in the fish-crab treatment and lowest in the no-crab treatment. For snails of

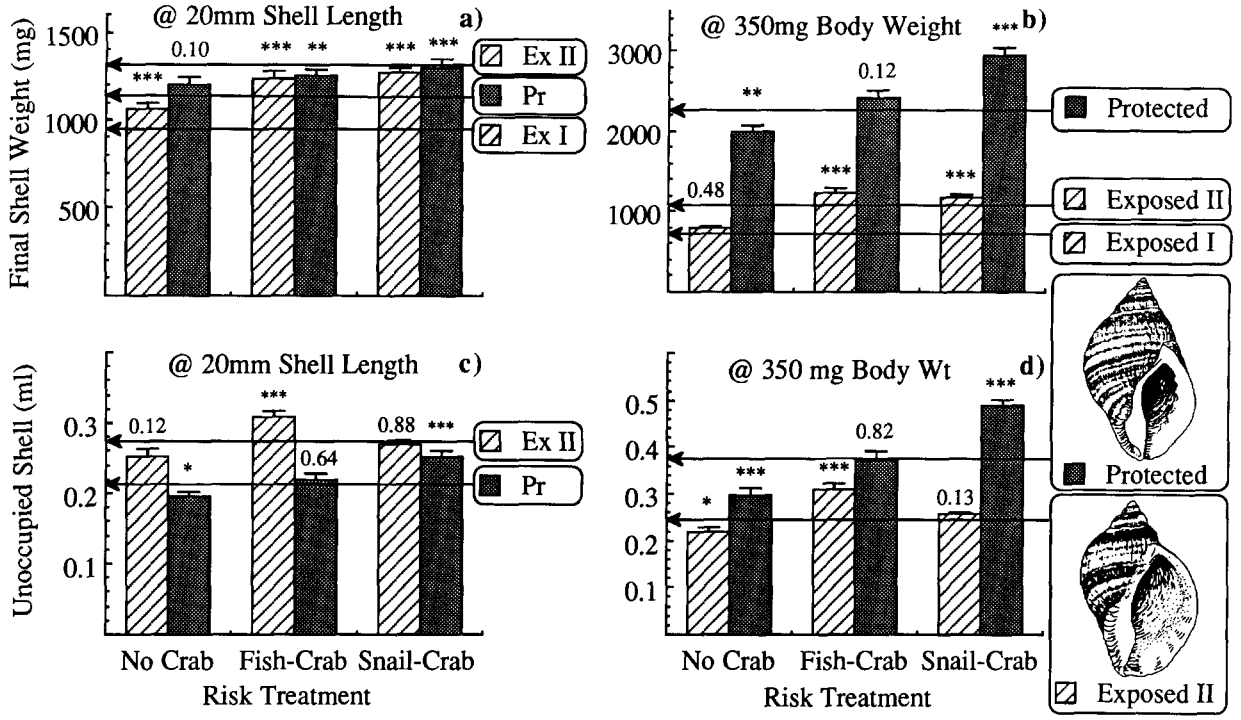

Fig. 12. Final shell weights (a,b), and unoccupied volume of shells (c,d) for *Nucella lapillus* from shores of different wave exposure (mean ± SE). Snails were held with food (barnacles) under three different experimental conditions in the laboratory for 94 d. For each trait, the final values have been expressed for a standard-sized snail. The two figures for each trait show the results of using different size metrics (shell length or body weight) to standardize size. See Table 3 for sample sizes, and initial and final values, and see methods for the procedure used to transform these values to those for a standard-sized snail. Arrows indicate the values of these traits for reference shells collected from the field. Exposed I – exposed-shore snails collected in mid July, Exposed II – exposed-shore snails collected from the field in mid October, Protected – protected-shore snails collected in mid October (see methods). Asterisks above bars indicate the significance level of the difference between the experimental group and reference shells (Exposed I, or Protected) from T-tests (* – <0.05, ** – <0.01, *** – <0.001), otherwise exact P values are given. Although means and SE are displayed on a linear scale, P values were computed from log-transformed values.

a standard wet body weight, however, although the rank order of response among risk treatments was the same as that observed for snails of a standard shell length, the departures of relative shell weight from that of the references shells were different (Fig. 12b). Relative shell weight was again significantly higher than that of the reference shells in the snail-crab treatment. In the fish-crab treatment, relative shell weight also increased, but only significantly so for the exposed-shore phenotype. In contrast, relative shell weight in the no-crab treatment either did not change compared to reference shells (exposed-shore phenotype) or actually decreased (protected-shore phenotype).

Because the shell weight of exposed-shore snails collected from the field increased between the time the experiment was started (mid July) and the time it ended (end of October; compare solid vs. open circles Figs. 4b, c), the interpretation of change depended upon which field-collected sample was used as the frame of reference. When compared to shells collected at the end of the experiment (Exposed II), relative shell weight did not change very much in the fish-crab and snail-crab treatments (Figs. 12a, b) whereas it was significantly lower in the no-crab treatment. Hence, although the increase relative to initial shell weight was rather dramatic in the fish-crab and no-crab treatments, this change was within the natural range of temporal variation in the exposed-shore population.

The effect of risk treatment on retractability (unoccupied volume of the shell) was rather insensitive to the method used to standard size (Fig. 12c, d). The main consequence of using different metrics to standardize size was a change in the ranking of the field reference values for the two populations (retractability relative to length was higher for exposed-shore snails whereas retractability relative to body weight was lower). For snails of the exposed-shore phenotype, retractability increased significantly in the fish-crab treatment, remained the same in the snail-crab treatment and decreased slightly in the no-crab treatment. In contrast, retractability of the protected-shore phenotype increased substantially in the snail-crab treatment, whereas it did not change in the fish-crab treatment and actually decreased significantly in the no-crab treatment.

Adjusted final lip thickness also varied rather substantially among groups (Fig. 13). Compared to the no-crab treatment, the lip thickness of both phenotypes increased significantly in both the fish-crab and snail-crab treatments. For the exposed-shore phenotype, this increase was greater in the snail-crab than the first-crab treatment whereas for the protected-shore phenotype the increase was about the same in these two treatments.

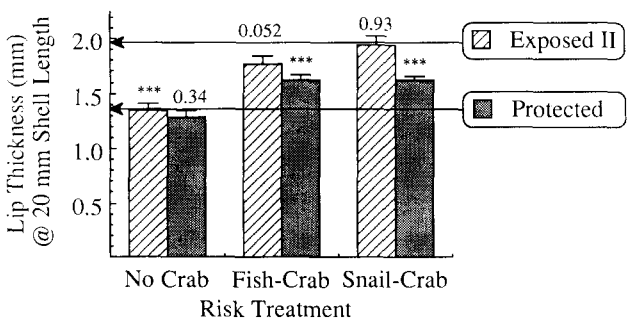

Fig. 13. Final thickness (mean ± SE) of the apertural lip of shells of *Nucella lapillus* from shores of different wave exposure. Snails were held with food (barnacles) under three different experimental conditions in the laboratory for 94 d. The final values have been expressed for a standard-sized snail. See Table 3 for sample sizes and initial and final values. See methods for the procedure used to transform these values to those for a standard-sized snail, and Fig. 12 for an explanation of symbols and abbreviations.

Trajectories of shell form over time

Because shell weights and shell lengths were measured repeatedly, the change in these traits relative to each other could be examined over time. The exposed-shore groups exhibited the most interesting morphological trajectories (Fig. 14a). Individuals in the snail-crab treatment increased only slightly in shell length, but their shell weight relative to length increased steadily over the duration of the experiment and it was consistently higher than at the beginning. Of some interest, among snails in both the fish-crab and no-crab treatments, shell weight relative to length

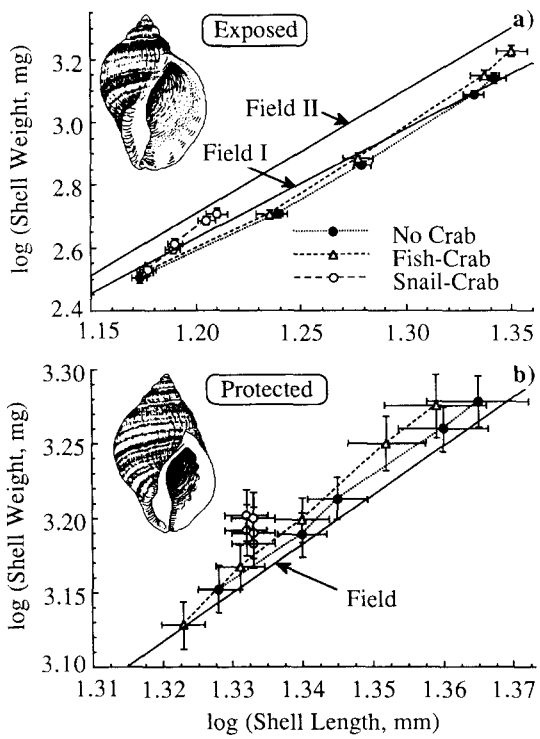

Fig. 14. Trajectories of shell weight vs. shell length for *Nucella lapillus* from shores of different wave exposure. Snails were held with food under three different experimental conditions in the laboratory. See Table 3 for sample sizes and initial and final values. Each point corresponds to the average shell length (± SE) and average shell weight (± SE) on a particular date, starting with those at the initiation of the experiment. Solid lines describe the static relationship between these variables for samples of reference shells collected from the field. Field I – snails collected in mid July, Field & Field II – snails collected from the field in mid October.

actually decreased in the early portion of the experiment and then increased towards the end so that the final shell weights relative to shell length were either not significantly different from (no crab) or were significantly higher than (fish-crab) those initially. Curiously, compared to the heavier-shelled snails collected from the field at the end of the experiment (e.g. see Fig. 4c), the shell weights from all risk treatments were lower.

Snails of the protected-shore phenotype grew considerably less than those of the exposed-shore and consequently the within-group variation was large relative to the total change (Fig. 14b). The shell weight of snails from all three risk treatments increased relative to shell length over the duration of the experiment. This increase was greatest in the snail-crab and fish-crab treatments and least in the no-crab treatment. Unlike the exposed-shore population, the shell form of field-collected snails from the protected shore did not change between the beginning and end of the experiment, hence these experimental snails were only compared to a single reference sample.

Discussion

Morphological differences between field populations

The observation that the shells of *Nucella lapillus* vary with wave exposure is not new; this phenomenon is widespread and well documented (see Crothers, 1985 for a review). The differences in shell shape and thickness between the two populations reported above are consistent with those described by others (e.g. see Seed, 1978). *N. lapillus* from more wave-exposed shores have wider apertures, lower spires and relatively thinner shells than those from protected shores. This variation appears to be maintained by the opposing selection pressures of wave action on exposed shores and crab predation on protected shores (Kitching *et al.*, 1966).

Three aspects of the shell variation observed in these natural populations seem worthy of note. First, because the wet body weight for a given shell length was much lower for snails from the protected shore (Fig. 4a), shell length will not be a reliable predictor of body size when comparing *N. lapillus* populations of different shell morphology (see size scaling below). Second, the unoccupied volume of the shell was larger by more than 50% for snails of the same body weight from the protected shore. This difference seems likely to be adaptive since animals from the protected shore would thus be able to retract substantially further into their shell than those from the exposed shore. For both populations, however, the capacity to retract into the shell declined allometrically with increasing size (Regressions 8a, b, Table 2). This allometric shift may reflect an ontogenetic increase in the amount of visceral mass relative to foot as animals approach and then reach maturity.

Third, a number of traits exhibited interesting allometric variation within populations. For example, relative aperture width increased with increasing size in the exposed-shore population, and both relative aperture width and length declined with increasing size in the protected-shore population (Regressions 1 and 2, Table 2). Hence, within each population, allometric changes amplified the differences observed between populations which are known to be adaptive (Etter, 1988; Kitching *et al.*, 1966). These data suggest that patterns of allometry themselves may be adaptive, although they do not reveal whether this allometric variation is genetically or environmentally determined. In addition, the significant positive allometry of shell weight relative to length exhibited by both populations could be adaptive, or it could reflect a tradeoff between growth rate and shell thickness. Heavier shells may be more advantageous to mature animals if they are long-lived. On the other hand, because the rate of shell production may limit the maximum rate of body growth (Palmer, 1981), juveniles may have to sacrifice some of the added defense a heavier shell might provide to enable them to grow more rapidly. The initial decline in shell weight relative to length during the period of rapid growth, followed by the increase in shell weight relative to length in the same individuals as growth slowed towards the end of the experiment

(exposed-shore phenotype in both the no-crab and fish-crab treatments; compare Figs. 10a and 14a) illustrates nicely the dependence of relative shell weight upon growth rate.

Short-term rates of shell deposition

The high initial rates at which starved, intermediate-sized *N. lapillus* deposited shell material (5–8 mg d^{-1}; Fig. 6) permitted a detailed view of short-term patterns of temporal change. The two- to three-fold increase in the rate of deposition between the first and second day of the baseline period prior to the experiment, most likely reflected a recovery from the trauma associated with obtaining estimates of wet body weight non-destructively (see methods). Although this pattern does suggest that the animals were disturbed by this procedure, it also reveals that this disturbance did not last much more than 24 h (e.g. compare day three to day two for the no-crab treatments Figs. 6a, b).

In addition, the temporary increase in the rate of deposition observed in three of the six groups following the introduction of bare stones into otherwise empty experimental cages suggests that rather subtle changes in the environment of *N. lapillus* can influence their rate of shell deposition. One interpretation of this response is that the stones somehow improved the 'quality of the habitat' as perceived by the snails. The ability to measure such changes on a daily basis would appear to provide a sensitive technique for assessing the impact of a variety of environmental stimuli on rates of shell deposition.

Effect of perceived risk on shell form of starved snails

The exposure of *N. lapillus* to various risk stimuli in the absence of food might seem like a curious experiment to conduct because these conditions would be rather unlikely to occur in the field. These starved treatments, however, were necessary to distinguish between those morphological differences that were a byproduct of differences in rates of growth and those that reflected a direct morphological response to risk stimuli. If I had used only fed snails in these experiments, I would not have been able to separate these effects and consequently would not have been able to determine if morphological differences in antipredatory traits resulted from different levels of feeding activity and growth rate, or from an amplification of these antipredatory traits via a direct cueing on the scents released by predatory crabs or damaged conspecific snails. The net result and hence the adaptive significance is the same, of course, whether a snail produces a thicker shell directly in response to the scent of crabs or indirectly by growing less rapidly in response to the same stimulus. By using starving snails, however, I was able to distinguish between these pathways of transduction.

The morphological responses of starved *N. lapillus* to the two risk treatments were not a straightforward function of perceived risk. Compared to controls, the scent of crabs alone resulted in significantly larger apertural teeth (Fig. 7c), a significantly thicker apertural lip (Fig. 7d) and heavier shells overall, although this last difference was not significant statistically (Fig. 7b, Table 6). Hence this form of perceived risk, which would signal predators in the vicinity but not feeding on snails, clearly resulted in adaptive morphological responses. These results parallel rather closely those reported by Appleton & Palmer (1988) for the northeastern Pacific *Nucella lamellosa* [= *Thais lamellosa*]. They also provide convincing evidence that, although starvation alone may lead to the production of apertural teeth (Crothers, 1971), the scent of crabs clearly amplifies this response. Hence the induction of apertural teeth is at least in part a direct response to the scent of crabs.

The responses of *N. lapillus* to the scent of conspecifics being eaten by crabs, which would signal predators in the vicinity that were also consuming conspecific snails, were notably different, however. Although these stimuli should have indicated a higher immediate risk of predation, the rate of shell deposition of both shell phenotypes dropped dramatically in the 24 h following ini-

tiation of the experiment, compared both to controls and to the fish-crab treatment (Figs. 6a, b; Table 5). Similarly, both the total change in shell weight and lip thickness were either not significantly different from (protected-shore), or were significantly less than (exposed-shore), those of the no-crab treatment (Figs. 7b, d; Table 6). Only the protected-shore phenotype exhibited a significant increase in the height of apertural teeth compared to the no-crab treatment. Hence, the scent of damaged conspecifics being eaten by crabs did not appear to elicit a morphological response which would reduce the risk of predation. On the contrary, these stimuli together appeared to have a more profound effect on the level of physiological or behavioral activity (see supernormal stimulus below). The lack of response to bare stones introduced into the otherwise empty cages on day three of the experiment suggests that, in contrast to nearly all of the remaining treatments, snails in this treatment did not perceive the stones to improve the 'quality' of their living conditions.

The reduced morphological response of starved *N. lapillus* in the snail-crab treatment, compared to controls (no crab) and compared to the fish-crab treatment, is difficult to explain with the present data, although it may reflect unrealistically high stimulus concentrations (see supernormal stimulus below). If, as suggested by Appleton & Palmer (1988), the scent of conspecifics being eaten somehow induced a heightened metabolic rate which burned up the energy reserves of these starving snails more quickly and hence resulted in less shell being produced, then snails in the snail-crab treatment should have lost more body weight over the course of the experiment than those in the fish-crab treatment. No differences in body weight loss were apparent, however, between these treatments for either of the two shell phenotypes examined (Fig. 7a). Because of the duration of the experiment (94 d), the lack of differences in weight loss may be somewhat of an artifact. For example, snails in the different risk treatments may have lost weight at different rates over the early part of the experiment, but ultimately declined asymptotically to roughly the same final body weight at the end of the experiment. I cannot address this possibility with the present data.

Effect of perceived risk on rates of feeding and growth

Perceived risk had a dramatic effect on rates of feeding and growth in *N. lapillus* from both source populations (Figs. 8–10). The decline in feeding rate with increased risk parallels observations reported for mosquito larvae in the presence of predatory notonectid water bugs (Sih, 1980, 1984), and for sticklebacks in the presence of a simulated avian predator (Milinski & Heller, 1978). Rather remarkably, the suppression of feeding by *N. lapillus* in the snail-crab treatment was so great (Fig. 8) that they either did not gain any body weight at all (exposed-shore) or actually lost weight (protected-shore) over the 94 days of the experiment (Fig. 9) even though barnacles were available *ad libitum*.

Three observations suggest that the dramatically reduced rates of feeding by *N. lapillus* in the snail-crab treatments were a direct result of a predator-induced avoidance behavior as opposed to a generalized reduction in activity. First, when these cages were inspected or cleaned, snails of both phenotypes were almost always found about the lower margins or undersides of the barnacle-covered stones. Second, a substantial majority of the barnacles eaten in these cages was restricted to these same regions of the stones. Hence, although the snails may have been less active overall, they also appeared to restrict their movements to the regions of stones where they would have been least likely to encounter a foraging crab. Third, the size distribution of barnacles eaten was shifted towards smaller barnacles for snails of both phenotypes compared to the no-crab and fish-crab treatments (compare Figs. 8e, f to 8a–d) This patterns suggests that *N. lapillus* in the snail-crab treatment preferentially consumed prey with shorter handling times, another behavior which would reduce their exposure to foraging crabs. Because no data were recorded on the sizes of barnacles on different surfaces of the stones,

however, the apparent preferential consumption of smaller barnacles may have been a product of the reduced foraging ambit of the snails. Barnacles on the lower margins and undersides of stones may have been smaller than those on the upper surfaces.

Rather curiously, although feeding activity was lower in the fish-crab treatments compared to controls (Fig. 8c, d), the distribution of barnacle mortality about the surface of stones did not suggest an obvious reduction in foraging ambit by *N. lapillus* of either shell phenotype. In addition, no differences were observed in the size distributions of barnacles eaten compared to the no-crab treatment. Needless to say, a closer examination of the behavior of these snails when exposed to such risk-related stimuli would be very illuminating.

Effect of perceived risk on shell morphology of fed snails: comparisons among laboratory treatments

The effects of perceived risk on the shell morphology of *Nucella lapillus* in these experiments are most readily interpreted by comparing the final shell form of snails in the fish-crab and snail-crab treatments to that of snails in the no-crab treatment which served as a control for laboratory conditions. This comparison provides a measure of the effects of each treatment relative to each other. As I will discuss below, however, the shell form of snails in the laboratory controls (no-crab treatment) did differ in some cases from those of reference shells collected from the field. Because these changes in shell form were in the opposite direction in some cases from those in the two crab treatments, laboratory conditions may have heightened the differences observed among experimental groups. Nonetheless, with one exception (lip thickness of the exposed-shore phenotype), the greatest departure of shell form from that of reference snails collected from the field occurred in one of the two risk treatments (fish-crab or snail-crab).

The scent of crabs alone clearly influences shell form in an adaptive manner in *N. lapillus*. Compared to controls (no crab), snails of both phenotypes in the fish-crab treatment exhibited a significantly greater expression of shell traits that would reduce vulnerability to shell-breaking crabs (Hughes & Elner, 1979; Palmer, 1985a; Seed, 1978; Vermeij, 1978): apertural tooth height ($+200\%$, $+370\%$ for exposed- and protected-shore phenotypes respectively; Fig. 11), shell weight relative to length [$+16\%$ and $+4\%$ (not significant for protected); Figs. 12a], shell weight relative to body weight ($+54\%$ and $+21\%$; Figs. 12b), and relative lip thickness ($+31\%$ and $+26\%$; Fig. 13). The response of exposed-shore snails provided the most convincing evidence for this. These snails grew substantially in both the no-crab and fish-crab treatments. The increase in length of more than 50% (Fig. 10a) and the approximate tripling in wet body weight (Fig. 9) transformed them from immature juveniles to the size of mature adults over the course of the experiment. Hence the differences in final shell form reflected to a very large extent differences in new shell added. In other words, these differences were not diminished very much by the similarity of original juvenile shells at the beginning of the experiment. By the same reasoning, however, the differences between the no-crab and fish-crab treatments almost certainly lead to an underestimate of the potential morphological response of the protected-shore snails. A much greater fraction of their shell at the end of the experiment was already present at the beginning because they did not grow nearly as much (Figs. 9, 10a, b).

Because of their reduced growth, the morphological differences observed between the snail-crab and no-crab treatments must also be interpreted with some caution. Even though provided with food *ad libitum*, the body weight of snails either did not change (exposed-shore) or actually decreased (protected-shore; Fig. 9), and not much new shell material was added (Fig. 10a, b). As a consequence, for example, the increased shell weight for a given wet body weight in protected-shore snails in the snail-crab treatment (Fig. 12b) was partly an artifact because they lost body weight (Fig. 9). This nearly 30% increase in relative shell weight, however, exceeded the 14%

loss in body weight experienced by these snails and even when scaled by shell length they exhibited an increase in shell weight and lip thickness relative to controls (Figs. 12a, 13). Here again, even though antipredatory traits of both phenotypes in this treatment developed to the same or greater extent than in the fish-crab treatment (except for apertural tooth height of exposed-shore snails, see supernormal stimulus below), these increases probably also underestimate the full impact of the scent of damaged conspecifics on shell morphology.

Effect of perceived risk on shell morphology of fed snails: direction of change from field samples

Although the final shell form of snails in both the fish-crab and snail-crab treatments differed from that of the controls (no crab), these differences could have resulted from either a) an amplification of antipredatory traits in the experimental groups or b) a reduced expression of antipredatory traits in the controls. For example, if the control groups produced much less well defended shells, as a product of holding these intertidal snails continuously immersed in the laboratory with superabundant food, then the greater development of antipredatory traits in the experimental groups would be an illusion. Thus, to assess the direction of change, the shells of laboratory raised snails must be compared to those collected directly from the field. Alternatively, when measuring phenotypic plasticity (see plasticity below), the range of phenotypes expressed under a particular range of conditions is the variable of interest, not the direction of change.

The shells of protected-shore snails did not change significantly when held under control conditions in the laboratory (no crab). At the end of the experiment, neither apertural teeth (Fig. 11), shell weight at a given length (Fig. 12a), nor lip thickness (Fig. 13) differed from field-collected reference shells [the decrease in shell weight at a given body weight (Fig. 12b) resulted from an increase in the size of the snail relative to the habitable volume of the shell (see retractability below)]. Both laboratory crab treatments thus resulted in shells that were more well defended than those of protected-shore snails from the field.

In contrast, the shells of exposed-shore snails did change when held under control conditions in the laboratory. Furthermore, the direction of morphological change depended upon which reference shells were used for comparison, those collected at the beginning of the experiment (Exposed I) or those collected at the end (Exposed II). Relative to shells collected at the beginning of the experiment (Exposed I), those produced by snails in the no-crab treatment had larger apertural teeth [Fig. 11; most likely because they had nearly reached maturity by the end of the experiment (see Fig. 10a)] and were considerably thinner at the lip (Fig. 13). The shells were also heavier for a given length (Fig. 12a), although relative to body weight they did not differ from those initial reference shells (Fig. 12b). Hence, with the exception of lip thickness, both laboratory crab treatments also appeared to result in shells that were more well defended than those of exposed-shore snails from the field. Note, however, that these changes were of the same magnitude that occurred naturally at the exposed-shore site over the duration of the experiment (compare Exposed I to Exposed II reference values, Figs. 12a, b). Unfortunately, I cannot be sure whether lip thickness increased or decreased relative to initial values for two reasons: a) lip thickness was not measured for the initial reference sample (Exposed I) and the shells were subsequently destroyed while developing shell weight and body weight calibrations, and b) the initial snails used in the experiments did not span a large enough size range to allow me to extrapolate with any confidence to shells of larger size.

In conclusion, the amplification of antipredatory traits in both crab treatments do appear to represent changes in an adaptive direction; they were not an artifact of reduced expression of antipredatory traits in control snails.

Effect of perceived risk on retractability

The changes observed in unoccupied volume of the shell, a measure of the degree to which a snail may retract into its shell, were rather intriguing and suggest another way in which snails may reduce their vulnerability to predation by crabs. Considering only snails which exhibited significant growth over the duration of the experiment (no-crab and fish-crab treatments), the fraction of the internal volume of the shell actually occupied by body tissue appeared to vary in an adaptive manner. For example, the unoccupied volume of the shell of protected-shore *N. lapillus* decreased in the absence of crabs but did not change in their presence (fish-crab, Fig. 12c, d) even though both groups grew (Fig. 9). In contrast, the unoccupied volume of the shell of exposed-shore snails decreased in the absence of crabs but increased significantly in their presence (fish-crab, Fig. 12c, d). Hence, even though body weight increased more than 150% in this latter group (Fig. 9), the snails expanded the internal volume of their shell much more than required to accommodate the increase in body size. As a consequence, they would have been able to retract further into their shell to avoid apertural probing by predatory crabs.

Of interest, these changes paralleled those observed between field-collected snails of both phenotypes. Dogwhelks from the protected shore, where the risk of crab predation was presumably higher, were able to withdraw further into their shells than those from the exposed shore (Fig. 5).

Apertural tooth development in Nucella lapillus *compared to* N. lamellosa

The development of apertural teeth in fed *N. lapillus* differed in only one notable respect from that of starved snails. When provided with food, snails of the protected-shore phenotype in the snail-crab treatment developed the largest teeth by more than a factor of two compared to the fish-crab treatment (Fig. 11). When starved, no difference was observed between these two treatments. Even though snails of the protected-shore phenotype lost weight (Fig. 9), these data suggest that the availability of at least some food was essential to the development of moderate-sized apertural teeth. Note that snails in this treatment developed teeth that were at least twice as large as the largest teeth produced by any other group for this phenotype whether provided with food or not (compare Fig. 11 with Fig. 7c). Rather curiously, for the exposed-shore population, the pattern of development of apertural teeth by fed snails did not differ from that of starved snails either qualitatively or quantitatively (fish-crab > no crab $\approx$ snail-crab; Figs. 9, 11). Hence, the availability of food appeared to have no effect on the capacity of exposed-shore snails to produce teeth.

The development of apertural teeth in both starved and fed *N. lapillus* paralleled rather closely that observed for *N. lamellosa* under similar experimental conditions (Appleton & Palmer, 1988). Among starved snails of both phenotypes the largest teeth were developed in the fish-crab treatment, whereas among fed snails the largest teeth were developed in the snail-crab treatment. The one notable difference between these species occurred in fed, exposed-shore snails in the snail crab treatment. *N. lamellosa* under these conditions produced the largest apertural teeth whereas the teeth produced by *N. lapillus* under these conditions did not differ from those in the fed controls (Fig. 11).

Several observations suggest that some of the morphological responses of exposed-shore *N. lapillus* were anomalous. For example, the qualitative responses of both phenotypes in the fish-crab treatment were very similar (Table 9). In addition, in the snail-crab treatment the responses of the protected-shore phenotype was qualitatively similar to those of both phenotypes in the fish-crab treatment. Hence, where snails in the remaining three groups exhibited increases in the development of antipredatory traits compared to controls, exposed-shore snails in the snail-crab treatment exhibited no change or decreases. With the present data, however, I am not sure how to account for the seemingly anomalous response of

Table 9. Qualitative summary of the effects of three risk treatments on various aspects of the biology of *Nucella lapillus*. Retractability – ability of snail to withdraw into the shell (measured as the unoccupied volume of shell). Entries in each column indicate the magnitude of the change compared to controls (no crab): (0) < 10% difference compared to controls, (−) 10–25% less than controls, (− −) 25–50% less, (− − −) > 50% less, (+) 10–25% greater than controls, (+ +) 25–50% greater (+ + +) > 50% greater.

Variable exhibiting response	Fish-crab		Snail-crab	
	Exposed	Protected	Exposed	Protected
Starved snails				
Initial daily rate of shell deposition (Fig. 6)	−	−	− −	− − −
Total body weight loss (Fig. 7a)	0	+ +	0	+ +
Total shell weight gain (Fig. 7b)	+	+ +	− − −	+
Apertural tooth development Fig. 7c)	+ + +	+ + +[†]	− − −	+ + +[†]
Change in lip thickness (Fig. 7d)	+ + +	+ + +	− −	+
Fed snails				
Rate of feeding (Fig. 8)	− −	− −	− − −	− − −
Rate of body growth (Fig. 9)	− −	− −	− − −	− − −
Apertural tooth development (Fig. 11)	+ + +	+ + +[†]	0	+ + +[†]
Relative shell weight (Fig. 12a)	+	0	+	0
Relative retractability (Fig. 12c)	+	+	0	+ +[§]
Relative lip thickness (Fig. 13)	+ +	+ +	+ +	+ +

[†] Teeth in no-crab treatment not significantly different from zero.
[§] Snails lost weight.

this group. Perhaps, because the snails fed to crabs in the snail-crab treatment were collected from the exposed-shore site, experimental snails from this site were more sensitive to the stimuli than those from the protected-shore site.

Phenotypic plasticity in Nucella lapillus *compared to* N. lamellosa

In the experiments with both *N. lamellosa* and *N. lapillus*, populations exhibiting two quite different shell forms were examined for phenotypic plasticity. The patterns of variation exhibited by these species suggests that the relative plasticities of the two phenotypes differ between species. For *N. lamellosa*, the range of development of apertural teeth among experimental groups was similar for both phenotypes (Appleton & Palmer, 1988), although the range in relative shell weight among these groups was greater in snails from the protected shore (Palmer, unpublished). In *N. lapillus*, on the other hand, exposed-shore snails exhibited a broader range of final shell form than those from the protected-shore for nearly all traits examined, regardless of whether snails were starved or fed. In addition, the protected-shore population was the only one to exhibit changes in shell form over time in the field (Figs. 4b, c). Hence, although reasons exist for believing that morphological change in one direction may be more likely than in another (Palumbi, 1984; Etter, 1988), the evidence from dogwhelks suggests no simple generalization will emerge about which populations retain a greater capacity to modify their shells ecophenotypically.

Apparent differences in phenotypic plasticity between the populations of these two species must be interpreted with caution because the experiments were started with individuals that had already spent one or more years in the field. The shells that they developed while in the field may thus have limited their ability to respond in the laboratory. To be sure that genetically based

differences in phenotypic plasticity exist among populations, snails with a common history would have to be compared.

Temporal morphological change in natural populations

The increase in relative shell weight observed between July 10 and Oct. 14 in exposed-shore *N. lapillus* collected from the field (Fig. 4, Table 2) was unexpected. Without additional data, little can be said with confidence about the reasons for this variation. Two points, however, do seem worth mentioning. First, this temporal variation was unlikely to have been due to bias during collection: a) the snails were collected from the identical location on both occasions, and b) many of the data points for the July collection lie well outside the scatter of those for October (e.g. Fig. 4c). Second, no change of average shell weight was observed for the protected-shore population over this same time interval (Fig. 4, Table 2). Furthermore the difference in the degree of variation over time in the two field populations was consistent with their response to experimental conditions in the laboratory: exposed-shore snails appeared to be more phenotypically plastic than those from the protected shore (e.g. Figs. 11, 14). I suspect that the increase in average shell weight at the exposed-shore site may be a normal seasonal occurrence associated with a decline in the rate of growth over the course of the summer and into the fall, because shell weight tends to increase with decreasing rate of growth (Wellington & Kuris, 1983; Vermeij, 1980).

Scaling out size differences in gastropod morphometrics

Because of the substantial variation in shape, and the partial ability of body size to change independent of the shell, the procedures used to scale out differences in 'size' in species of gastropods whose shell varies extensively are problematical, although they are hardly unique to the morphometrics of gastropod shells. Shell length is probably the most commonly used index of size because of its convenience. Shell length, however, is a very poor predictor of wet body weight for *N. lapillus* with shells of different shape (e.g. see Fig. 4a). Snails from protected shores have a relatively longer apex than those from exposed shores, hence shell length substantially underestimates body weight. This contrasts with observations on *N. lamellosa* of the northeastern Pacific for which shell length can be an accurate predictor of body weight for populations having shells of different thickness (Palmer, 1985a). In addition, because of their different shapes, shells of protected- and exposed-shore *N. lapillus* have nearly the same weight for a given length (Fig. 4c). Hence, although one might argue that shell length is therefore a more accurate predictor of shell weight, this gives a very misleading impression about the amount of shell material committed to defense, and also about the ability of the shell to resist predation by shell breaking crabs (Currey & Hughes, 1982; Hughes & Elner, 1979), since the amount of shell per unit body weight is substantially different between these populations (Fig. 4b). When comparing differences in the commitment of resources to defense, body weight would seem to be a more relevant variable for scaling size than shell length.

For other comparisons, however, body weight may yield a misleading impression about differences in shell form. For example, body weight may either increase or decrease without any change in shell weight or dimensions. More invidiously, the fraction of the habitable volume of the shell actually occupied by animal tissue may itself vary in an adaptive manner (see retractability above). Given the potentially confounding effects of independent variation in body weight, shell length would seem to be a better measure of size for shells of similar shape.

Perhaps the search for an idealized descriptor of 'size' is unwarranted. After all, normally one is interested in the variation of one trait compared to that in another. Hence the choice of the trait by which to scale size will depend upon the question being asked. Where the energetics of defensive

morphologies or the relation of defensive morphologies to life history are concerned, body weight may be the most relevant basis for comparison. On the other hand, if one is interested in the geometric distribution of shell material shell length may be a more relevant descriptor of size. Perhaps the safest tactic is to explore the variation in the trait of interest with respect to more than one descriptor of size. In this manner, potential biases associated with any single descriptor should become apparent.

Was the scent of damaged conspecifics a supernormal stimulus?

The dramatic inhibition of feeding and growth observed in the snail-crab treatment (Figs. 9, 10), and the concomitant effects of reduced growth on shell morphology and on estimates of phenotypic plasticity, deserve some additional comment. In the experiments described above, and in those done previously with *N. lamellosa* (Appleton & Palmer, 1988), no attempt was made to control the experimental stimuli quantitatively. The experimental groups were exposed to stimuli of arbitrary intensity to examine the presence/absence of morphological responses. If the stimulus I provided in the laboratory far exceeded any that these snails would normally encounter, this could account for two observations: a) the responses of starved dogwhelks in the snail-crab treatment were often less than in the fish-crab treatment (Fig. 7), and b) dogwhelks in the snail-crab treatment either did not grow or actually lost weight even in the presence of abundant food (Fig. 9). The number of snails eaten by crabs in the experimental aquaria, for example, were 2.9 and 3.7 snails $crab^{-1}$ day^{-1} (5.8 and 7.5 snails $treatment^{-1}$ day^{-1}). I think it rather unlikely that individual *N. lapillus* in the field are ever exposed to the scent of conspecifics being eaten continuously at this rate by crabs for this long a period of time.

A priori, I would have expected the scent of conspecifics being eaten by crabs, which should be a more reliable predictor of increased risk to predation, to have elicited a greater morphological response than the scent of crabs alone, since the scent of crabs in the vicinity but not feeding on snails would seem to pose a lessor risk. At the very least, because both contained the same level of crab stimulus, the behavioral and morphological responses of snails in the snail-crab treatment should have been the same as those in the fish-crab treatment. Compared to the fish-crab treatments, several aspects suggest that the stimulus level in the snail-crab treatments was unnaturally high: a) among starved snails, the reduced development of apertural teeth, the smaller change in shell weight and the smaller increase in lip thickness (Fig. 7b–d), and b) among snails provided with abundant food, the lack of body growth or actual loss in body weight (Fig. 9). To verify this conjecture, snails would have to be held in the presence of crabs being fed conspecific snails at different rates.

Adaptive behavioral and morphological variation in Nucella lapillus

Despite the complexities of some of the patterns, two important conclusions may be drawn from the above experiments. First, both the scent of crabs and the scent of damaged conspecifics dramatically reduce the rates of feeding and growth of *N. lapillus*. Second, these stimuli can also amplify the development of several different antipredatory traits. Hence the effects of risk-related chemical cues in the environment must be considered when interpreting variation in behavior and shell morphology among natural populations of gastropods.

Although numerous gastropods flee from slow-moving predators such as starfish and other predatory gastropods (Snyder & Snyder, 1971; Vermeij, 1978, 1987), examples of escape responses to more rapidly moving predators such as crabs and fishes are rare. Nonetheless, the fact that such behaviors do occur (Geller, 1982) indicates that gastropods are capable of detecting chemical cues even from highly mobile predators. The reduced rates of feeding and growth in the

fish-crab compared to the no-crab treatment reveal that, as observed for *N. lamellosa* from the northeastern Pacific (Appleton & Palmer, 1988), *N. lapillus* can also recognize and respond adaptively to the scent of predatory crabs.

The greater suppression of feeding activity of dogwhelks in the snail-crab compared to the fish-crab treatments indicates that *N. lapillus* also have an alarm response. Other marine and freshwater gastropods exhibit alarm responses to the scent of damaged conspecifics (Snyder, 1967; Atema & Stenzler, 1977; Stenzler & Atema, 1977) and these responses appear to be adaptive (Ashkenas & Atema, 1978; Hadlock, 1980). Both the reduced rates of feeding, and the tendency for snails to remain about the lower margins and undersides of stones in the snail-crab treatments, would reduce the probability that individual *N. lapillus* were encountered by foraging crabs. Hence the alarm response in *N. lapillus* also appears to be adaptive.

Perhaps the most surprising aspect of this study, and that of Appleton & Palmer (1988), is that gastropods can also respond morphologically to chemical cues released by predators and damaged conspecific snails. Such morphological responses are rare among solitary organisms (Harvell, 1986, but see Liveley, 1986). Furthermore, the morphological responses are in an adaptive direction – in the presence of these stimuli, *N. lapillus* produced heavier shells with thicker lips and more well-developed apertural teeth. All of these traits reduce the vulnerability to attack by shell-breaking crabs (Kitching *et al.*, 1966; Hughes & Elner, 1979; Palmer, 1985a; Vermeij, 1987). Because these environmental stimuli can have a significant effect on shell morphology, interpretations of morphological differences observed among natural populations must be done with caution. Such differences may result from either genetic or environmental effects, or some combination of the two (e.g. Janson, 1982; Palmer, 1985b). Thus, for example, the changes in shell morphology observed in *Littorina obtusata* (Seeley, 1986) and *N. lapillus* (Vermeij, 1982) following the introduction of *Carcinus maenas* may not reflect microevolutionary change, since such changes could equally likely have been an ecophenotypic response to the scent of crabs.

Acknowledgements

I thank Roger Hughes for generously agreeing to host my sabbatical visit to Wales and both he and John Davenport for assistance in numerous ways during my stay. Gary Vermeij and Lois Hammond offered useful comments on various drafts of the manuscript. This research was supported by a Natural Sciences and Engineering Research Council of Canada travel grant T7684, and by operating grant A7245 whose sustained funding I acknowledge with gratitude.

References

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

Ashkenas, L. & J. Atema, 1978. A salt marsh predator-prey relationship: attack behavior of *Carcinus maenas* (L.) and defenses of *Ilyanassa obsoletus* (Say). Biol. Bull. 155: 426.

Atema, J. & D. Stenzler, 1977. Alarm substance of the marine mud snail, *Nassarius obsoletus*: biological characterization and possible evolution. J. chem. Ecol. 3: 173–187.

Cambridge, P. G. & J. A. Kitching, 1982. Shell shape in living and fossil (Norwich Crab) *Nucella lapillus* (L.) in relation to habitat. J. Conch. Lond. 31: 31–38.

Colton, H. S., 1916. On some varieties of *Thais lapillus* in the Mount Desert Island region. A study of individual ecology Proc. Acad. nat. Sci., Philad. 68: 440–454.

Colton, H. S., 1922. Variation in the dog whelk, *Thais lapillus*. Ecology 3: 146–157.

Crothers, J. H., 1971. Further observations on the occurrence of 'teeth' in the dog-whelk *Nucella lapillus*. J. mar. biol. Ass. UK. 51: 623–639.

Crothers, J. H., 1985. Dog-whelks: An introduction to the biology of *Nucella lapillus* (L.). Field Studies 6: 291–360.

Currey, J. D. & R. N. Hughes, 1982. Strength of the dog-whelk *Nucella lapillus* and the winkle *Littorina littorea* from different habitats. J. anim. Ecol. 51: 47–56.

Etter, R. J., 1988. Asymmetrical developmental plasticity in an intertidal snail. Evolution 42: 322–334.

Geller, J. B., 1982. Chemically mediated avoidance response of a gastropod, *Tegula funebralis* (A. Adams); to a predatory crab, *Cancer antennarius* (Stimpson). J. exp. mar. Biol. Ecol. 65: 19–27.

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.

Hartley, O., 1962. Analysis of variance. In: Mathematical Methods for Digital Computers, Vol. 1. Ralston, A. & H. S. Wilf (eds). Wiley, New York. pp. 221–230.

Harvell, C. D., 1986. The ecology and evolution of inducible defenses in a marine bryozoan: cues, costs, and consequences. Am. Nat. 128: 810–823.

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

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

Kilburn, R. & E. Rippey, 1982. Sea Shells of Southern Africa. Macmillan South Africa, Johannesburg, 249 pp.

Kincaid, T., 1957. Local races and clines in the marine gastropod *Thais lamellosa*, a population study. Calliostoma Co., Seattle, 75 pp, 65 Plates.

Kincaid, T., 1964. Notes on *Thais* (*Nucella*) *lima* (Gmelin), a marine gastropod inhabiting areas in the North Pacific Ocean. Calliostoma Co., Seattle.

Kitching, J. A., 1976. Distribution and changes in shell form of *Thais* spp. (Gastropoda) near Bamfield, B.C. J. exp. mar. Biol. Ecol. 23: 109–126.

Kitching, J. A. & J. Lockwood, 1974. Observations on shell form and its ecological significance in Thaisid gastropods of the genus *Lepsiella* in New Zealand. Mar. Biol. 28: 131–144.

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

Largen, M. J., 1971. Genetic and environmental influences upon the expression of shell sculpture in the dog whelk (*Nucella lapillus*). Proc. malac. Soc. Lond. 39: 383–388.

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

Milinski, M. & R. Heller, 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks (*Gasterosteus aculeatus* L.). Nature 275: 642–644.

Moore, P. G., 1985. Shell shape in living and fossil ('25ft' beach) dog-whelks, *Nucella lapillus* (L.), from the Isle of Cumbrae, Scotland. Glasg. Nat. 21: 81–91.

Palmer, A. R., 1981. De carbonate skeletons limit the rate of body growth? Nature 292: 150–152.

Palmer, A. R., 1982. Growth in marine gastropods: a non-destructive technique for independently measuring shell and body weight. Malacologia 23: 63–73.

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

Palmer, A. R., 1985b. Quantum changes in gastropod shell morphology need not reflect speciation. Evolution 39: 699–705.

Palumbi, S. R., 1984. Tactics of acclimation: morphological changes of sponges in an unpredictable environment. Science 225: 1478–1480.

Phillips, B. F., N. A. Campbell & B. R. Wilson,, 1973. A multivariate study of geographic variation in the whelk *Dicathais*. J. exp. mar. Biol. Ecol. 11: 27–69.

Seed, R., 1978. Observations on the significance of shell shape and body form in the dogwhelk (*Nucella lapillus* (L.)) from North Wales. Nature in Wales 16: 111–122.

Seeley, R. H., 1986. Intense natural selection caused a rapid morphological transition in a living marine snail. Proc. nat. Acad. Sci., USA 83: 6897–6901.

Sih, A., 1980. Optimal behavior: Can foragers balance two conflicting demands? Science 210: 1041–1043.

Sih, A., 1984. The behavioral response race between predator and prey. Am. Nat. 123: 143–150.

Snyder, N. F. R., 1967. An alarm of aquatic gastropods to intraspecific extract. New York Agric. Experiment Sta., Ithaca, Mem. 403: 1–122.

Snyder, N. F. R. & H. A. Snyder, 1971. Defenses of the Florida apple snail, *Pomacea paludosa*. Behaviour 40: 175–215.

Sokal, R. R. & F. J. Rohlf, 1981. Biometry, W. H. Freemen and Co., San Francisco.

Spight, T. M., 1973. Ontogeny, environment, and shape of a marine snail, *Thais lamellosa* (Gmelin). J. exp. mar. Biol. Ecol. 13: 215–228.

Stenzler, D. & J. Atema, 1977. Alarm response of the marine mud snail, *Nassarius obsoletus*: specificity and behavioral priority. J. chem. Ecol. 3: 159–171.

Vermeij, G. J., 1978. Biogeography and Adaptation. Patterns of Marine Life. Harvard University Press, Cambridge. 332 pp.

Vermeij, G. J., 1980. Gastropod shell growth rate, allometry and adult size: environmental implications. In: Rhoads, D. C. & R. A. Lutz, (eds.) Skeletal Growth of Aquatic Organisms. Plenum Press, New York: 379–394.

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

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

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