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Predator-induced plasticity and morphological trade-offs in latitudinally separated populations of *Littorina obtusata*

Geoffrey C. Trussell*

Department of Biological Sciences, School of Marine Science, College of William & Mary, Gloucester Point, VA 23062 and Marine Science Center, Northeastern University, Nahant, MA 01908, USA

ABSTRACT

Predation by shell-crushing predators is thought to be a principal force driving the evolution of gastropod shell form. However, recent evidence suggests that phenotypic plasticity in response to risk stimuli associated with predators may also be important. Thus, morphological co-evolution between predators and their gastropod prey may be driven by natural selection on reaction norms rather than genetically fixed phenotypes. In this study, I examined whether geographic variation in morphology and its plasticity in the intertidal snail (*Littorina obtusata*) were associated with both historical and present-day differences in the abundance of one its principal crab predators (*Carcinus maenas*). *C. maenas* has been well established in the southern Gulf of Maine for about 100 years, but has been present in the northern Gulf of Maine for at most 50 years. The shells of snails from the northern Gulf were thinner, weighed less and were weaker in compression than those of southern Gulf conspecifics. These geographic patterns in shell form may reflect, in part, either selection on genetically fixed phenotypes or environmentally induced phenotypes in response to geographic differences in *C. maenas* effluent concentrations.

A laboratory experiment raising snails from the same field populations in the presence and absence of *C. maenas* effluent was conducted to test whether differences in the duration of contact with *C. maenas* influences plasticity in shell form. When raised in the presence of crabs, snails from all populations produced significantly thicker and heavier shells than conspecifics raised without crabs. These results support the hypothesis that geographic differences in shell form may partly reflect geographic differences in the abundance of *C. maenas* and, thus, the concentration of effluent indicating a risk of predation. In other words, the thinner shells of northern snails may reflect non-induced phenotypes, whereas the thicker shells of southern snails are an induced defence in response to *C. maenas*. Interestingly, despite their different periods of contact with *C. maenas*, both northern and southern snails showed similar shell thickness plasticity in the laboratory, suggesting that reaction norms in each region have evolved similar slopes. However, laboratory data coupled with comparisons of field populations suggest that there has been an evolutionary shift in reaction norm intercept; southern snails, regardless of treatment, consistently produced thicker shells and showed less plasticity relative to their counterparts in the field. Predator-induced increases in shell thickness were accompanied by significant reductions in body mass (defined by soft tissue mass) and body growth.

* Adddress all correspondence to Geoffrey C. Trussell, Department of Ecology and Evolutionary Biology, Box G-W, Brown University, Providence, RI 02912, USA. e-mail: geoffrey_trussell@brown.edu
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These trade-offs probably reflect geometric constraints imposed by shell form on body mass and may explain the existence of micro- and macro-geographic variation and the evolution of inducible defences in marine gastropod shell form.

Keywords: *Carcinus maenas*, geographic variation, Gulf of Maine, *Littorina obtusata*, natural selection, phenotypic plasticity, trade-offs.

INTRODUCTION

Natural selection via predation by crushing predators is thought to be a principal force driving the evolution of gastropod shell form in ecological and geological time (Vermeij, 1976, 1977, 1978, 1987; Palmer, 1979; Vermeij *et al*., 1981; West and Cohen, 1996). For example, higher frequencies of shell repair (Vermeij *et al*., 1981) and transitions to more defended shell forms (e.g. low spires, thick shell walls and apertural lips, narrow apertures) in the fossil record coincide with the diversification of shell-crushing predators in the Mesozoic (Vermeij, 1978, 1987; Signor and Brett, 1984). On broad geographic scales, more robust shell forms are found in regions where shell-crushing predators are more taxonomically diverse and powerful and there has been a longer period of contact between predator and prey (Vermeij, 1978, 1987; Vermeij and Veil, 1978). Hence, tropical gastropod shells are more robust than those of temperate snails (Vermeij, 1978; Vermeij and Currey, 1980); Indo-West Pacific snails are better defended than Caribbean congeners (Vermeij, 1976); and freshwater snails from ancient African rift valley lakes are stronger than snails from nearby, but younger lakes (West *et al*., 1991). These historical and geographic patterns are thought to reflect co-evolution between predators and prey (Vermeij, 1978, 1987).

Rapid and recent (within the last 100 years) morphological transitions to thicker shells in two intertidal gastropods after the range expansion of the green crab, *Carcinus maenas*, are thought to represent powerful evidence of natural selection by crab predators on shell form (see Vermeij, 1982; Seeley, 1986). Native to the northeastern Atlantic, *C. maenas* was introduced to the US Mid-Atlantic in the early 1800s from Europe (Cohen *et al.*, 1995). Around 1900, *C. maenas* spread north of Cape Cod, Massachusetts into the Gulf of Maine. Increased water temperatures are thought to have facilitated this range expansion (Welch, 1968; Lazzari, 1997). *C. maenas* continued moving north, reaching Portland, Maine in the early 1900s, mid-coastal Maine by the 1930s, and northern Maine and the Bay of Fundy by the 1950s (Scattergood, 1952; Welch, 1968; see Fig. 1). The northern extent of *C. maenas* in the northwest Atlantic is apparently limited by cold water; following a decline in water temperatures in the late 1950s, *C. maenas* populations in the Bay of Fundy decreased (Welch, 1968). Presently, *C. maenas* is abundant at some sheltered sites in the northern Gulf of Maine, but populations in this region are generally small or ephemeral compared with well-established and dense populations on sheltered shores in the southern Gulf of Maine (Seeley, 1985; G. Trussell, personal observation).

Shifts to more defended shells in *Littorina obtusata* that coincided with the *Carcinus maenas* range expansion in the 1900s have been argued to reflect evidence of natural selection driven by *C. maenas* (Seeley, 1986). Museum specimens collected in New England before 1900 were high-spired and thin-shelled. Comparison of these snails with collections from the same three regions in the mid-1980s revealed that pre-1900 snails were thinner and higher-spired than recent specimens. In addition, experiments with thin-shelled, high-spired

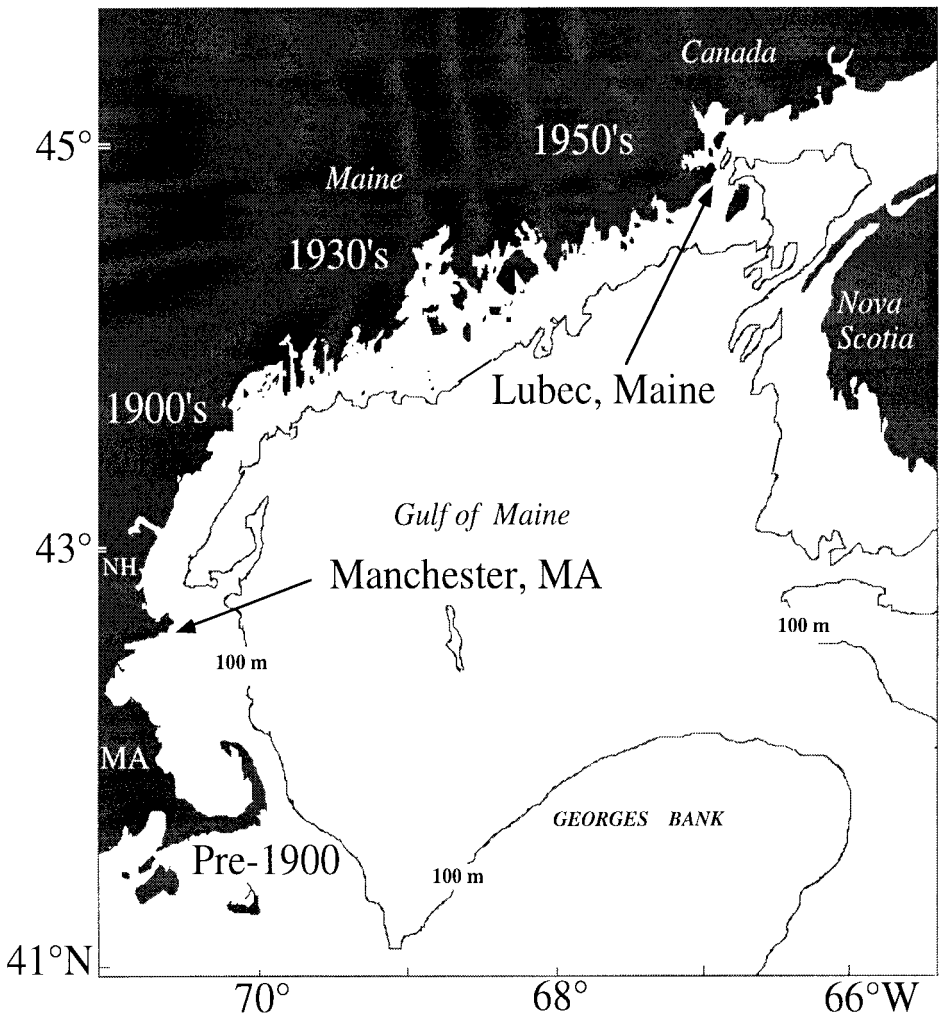

Fig. 1. Map of the Gulf of Maine showing the northward progress of the *Carcinus maenas* biogeographic range expansion from 1900 to the present day (based on Scattergood, 1952; Vermeij, 1978). Also shown are the locations of the two study areas in the southern (Manchester, Massachusetts) and northern (Lubec, Maine) Gulf of Maine.

morphs from northern Maine revealed that these morphs were more vulnerable to predation than thick-shelled, low-spired morphs.

Recent evidence suggests that phenotypic plasticity in response to cues emanating from predators is also important to driving evolutionary and geographic patterns in shell form (Appleton and Palmer, 1988; Crowl and Covich, 1990; Palmer, 1990; Trussell, 1996). For example, Trussell (1996) found that Gulf of Maine *Littorina obtusata* develop thicker shells when raised with effluent emanating from *Carcinus maenas* feeding on conspecific snails and suggested that the morphological transitions documented by Seeley (1986) may reflect plasticity rather than rapid selection. Predator-induced defences in gastropods

appear to be taxonomically and geographically ubiquitous – for example, marine gastropod *Nucella lamellosa* in the northeast Pacific (Appleton and Palmer, 1988), marine gastropod *Nucella lapillus* in the British Isles (Palmer, 1990), marine gastropod *L. obtusata* and marine mussel *Mytilus edulis* in the Gulf of Maine (Trussell, 1996; Leonard *et al*., 1999) and freshwater gastropod *Physella virgata virgata* (Crowl and Covich, 1990) – and their discovery has invited reinterpretation of views that recent or fossil transitions in gastropod shell form are unequivocal evidence of rapid Darwinian selection (Vermeij, 1982; Seeley, 1986) or speciation (Williamson, 1981; Palmer, 1985).

The ubiquity of predator-induced defences in gastropod shell form suggests that natural selection may act on developmental reaction norms (*sensu* Schlichting and Pigliucci, 1998) rather than on genotypes encoding for different levels of constitutive defence. The evolution of inducible defences is expected to occur when the impact of predators is highly variable or unpredictable, whereas constitutive defences should evolve when predator impacts are predictable or more uniform (Van Tienderen, 1991; Tollrian and Harvel, 1999).

In the southern Gulf of Maine, *Littorina obtusata* has been in contact with *Carcinus maenas* for longer (80–100 years) than populations near the Maine–Canadian border (at most 50 years). Given the geographic difference in the historical contact between *L. obtusata* and *C. maenas* in the Gulf of Maine, two scenarios may arise regarding reaction norms for snail shell form. First, reaction norms may evolve different slopes (i.e. degrees of plasticity), which, in turn, produce geographic differences in shell form. The more consistent abundance of *C. maenas* in the southern Gulf should favour the evolution of reduced plasticity in snail shell form (i.e. towards a constitutive defence) compared with snails in the northern Gulf where *C. maenas* has been less abundant over the last 100 years (Welch, 1968; Welch and Churchill, 1983). To address this hypothesis, I raised snails from two northern Maine and two Massachusetts populations in the laboratory with and without *C. maenas* effluent.

Second, assuming that reaction norms have evolved similar slopes in each region, snails from each region may either occupy different regions of the same reaction norm or have reaction norms with different intercepts. These scenarios may arise if the position occupied on a reaction norm is determined by predator cue availability or if genetic differentiation in shell form exists. In other words, geographic differences in the shell form of southern and northern snails may reflect different degrees of induction or genetic differentiation. For example, southern snails are expected to have thicker shells than northern snails because exposure to *C. maenas* cues in the field is more likely to occur given the greater present-day abundance of *C. maenas* in the southern Gulf of Maine. Previous work (Trussell, 2000; Trussell and Smith, 2000) suggests that geographic differences in the presence of *C. maenas* cues may partly contribute to geographic differences in snail shell form. After 90 days in the field, northern *Littorina obtusata* transplanted to a southern site produced thicker shells, whereas southern snails transplanted to the northern site produced thinner shells. Here, I examine whether there are geographic differences in the shell thickness and breaking force of snails from the same four populations used in the laboratory effluent experiment.

Finally, costs or trade-offs in other morphological or life-history traits are expected to accompany inducible defences; otherwise, organisms should produce constitutive rather than conditional defences. I address the potential life-history trade-offs associated with the production of thicker shells by examining whether (1) there are geographic differences in body mass and (2) predator-induced increases in shell thickness are accompanied by reductions in body mass and growth.

MATERIALS AND METHODS

Geographic differences in shell thickness and mass, shell breaking force and body mass

Geographic differences in shell thickness were examined by collecting 100–150 snails from 0.25 m^2 quadrats tossed haphazardly in the mid-intertidal zone at each study site (Fig. 1). Because wave energy can influence snail shell form (Trussell *et al.*, 1993; Trussell, 1997a,b), snails were collected at two sheltered sites in Lubec, Maine (Johnson Bay and Quoddy Head) and two sheltered sites in Manchester, Massachusetts (Lobster Cove and Manchester Harbor). From each sample, 50 snails were chosen for measurement of shell thickness, shell mass, shell breaking force and body mass. An attempt was made to maximize the size range for each sample.

Measurements of shell thickness and shell length were made as described in Trussell (1996) with digital callipers (± 0.01 mm). After shell measurements, I determined the maximum force required to crush each snail's shell with an Instron Dynamic Testing Machine (± 0.1 N; Model 4301). These tests were not meant to simulate crab predation but to provide a relative measure of shell breaking force, which should influence vulnerability to crab predation (Vermeij and Currey, 1980). Before testing, live snails were kept submerged in running seawater for 24 h. Snails were then placed aperture down on a stationary platen and their shells crushed by lowering the top platen onto the shell at a rate of 10 $mm \cdot min^{-1}$. Shells were loaded until they were crushed; a loud 'cracking' noise reliably indicated failure of the shell. After testing, soft tissue was separated from shell fragments and both were dried at 60°C for 48 h before weighing on an analytical balance.

Non-destructive estimates of shell mass and body mass

Because I wanted to examine variation in body mass (defined by tissue mass) and body growth of snails raised in the presence and absence of *Carcinus maenas*, it was necessary to make non-destructive estimates of shell and body mass. To do so, I first generated destructive regressions for each population. Fifty snails spanning the available size range were collected from the four populations described above. Live snails were then weighed while submerged in seawater (hereafter, submerged mass, ± 0.001 g). Snails were then allowed to dry on towelling for approximately 30 min. To remove extravisceral water trapped inside the shell, snails were forced into their shell with absorbent tissue before weighing in air (hereafter, total mass, ± 0.001 g). After total mass measurements, snails were carefully crushed and tissue separated from the shell. Shell material was then dried at 60°C for 48 h before weighing to determine actual shell mass.

Because the specific gravity of snail soft tissue is similar to that of seawater, the weighing of snails while submerged in seawater (i.e. submerged mass) provides a reliable estimate of shell mass. The destructive regressions of actual shell mass (y) on submerged mass (x) described above for snails from each population yielded highly significant R^2 values (Quoddy Head: $y = 1.561x - 0.002$, $R^2 = 0.9991$; Johnson Bay: $y = 1.545x - 0.001$, $R^2 = 0.9952$; Lobster Cove: $y = 1.582x + 0.002$, $R^2 = 0.9999$; Manchester Harbor: $y = 1.589x + 0.002$, $R^2 = 0.9999$), indicating that submerged mass is indeed a reliable indicator of actual shell mass. By using the regressions of actual shell mass (y) on submerged mass (x) obtained destructively for each population, I calculated population-specific estimates of actual shell mass from submerged mass measurements (Palmer, 1982) made on snails

for the laboratory effluent experiment (see below). These estimates of actual shell mass were then subtracted from total mass measurements made in air to estimate body mass (Palmer, 1982).

Experimental test of predator-induced phenotypic plasticity

I made additional collections of approximately 250 juvenile snails from each northern and southern population for a laboratory experiment that assessed the effect of crab effluent on shell morphology and growth. All snails were individually labelled with waterproof markers (Trussell, 1997a) and measured for shell length, shell thickness, submerged mass and total mass. Measurements of body mass and shell mass growth were calculated by subtracting initial from final values.

Once initial measurements were completed, 30 snails (hereafter, 'experimental snails') from each population were randomly assigned to 6 of 24 replicate rectangular chambers ($32 \times 24 \times 15$ cm). Hence, each chamber contained 30 snails from a single population and there were a total of six chambers for each of the four populations. Water was delivered individually to each chamber through 24 adjustable valves and each chamber was aerated with its own airstone. Plastic mesh panels on the top and bottom of each chamber permitted water to exit each chamber. Fifty-five grams wet mass of the brown alga *Ascophyllum nodosum* was placed within each chamber to serve as food for the experimental snails. One chamber for each population was then randomly assigned to each of six large seatables. Hence, each seatable contained four chambers, one for each of the four field populations. Three seatables were used for the 'crab' treatment; the remaining three were used as a control ('no-crab'). The 'crab' treatment was created by placing a small perforated plastic tub (diameter = 13.5 cm, height = 5.5 cm) containing a single crab (*Carcinus maenas*) and 20 conspecific snails (hereafter, 'stimulus snails') on top of each of the four chambers housing experimental snails. For the control ('no-crab'), I placed identical perforated tubs containing only stimulus snails on top of each of the four chambers housing experimental snails. This design contained three replicates for each population nested within each treatment (4 populations $\times$ 3 replicates $\times$ 2 treatments = 24 chambers).

Every 2 weeks, I added a new set of 20 stimulus snails to the perforated tubs in each treatment and replaced the food supply for experimental snails with fresh *Ascophyllum nodosum*. This experiment was conducted for ~ 115 days from early May until late August 1997 when final measurements of shell length and thickness and estimates of shell mass and body mass were made as described above.

Non-destructive estimates of final body and shell mass were calculated as described above except that these estimates were based on new destructive regressions of final actual shell mass (y) as a function of final submerged mass (x) generated for each experimental group. I generated these new regressions because the relationship between final submerged mass and final actual shell mass may have changed after exposure to the experimental treatments. Hence, final regressions were generated with 25–30 snails randomly sampled from each experimental group by crushing the shell with a C-clamp and separating soft tissue and shell material. Shell material was then dried in an oven at 60°C for 48 h before weighing. These new regressions were then used to estimate actual final shell mass from final submerged mass. Final body mass was then calculated as described above. Like the initial regressions, these final regressions indicated that final submerged mass was a reliable indicator of final actual shell mass (all $R^2 \geq 0.9990$).

Statistical analyses

A two-factor analysis of covariance (ANCOVA) with populations (random) nested within each geographic region (fixed) was conducted to test for geographic differences in shell thickness and mass, shell breaking force and body mass. Shell length was used as the covariate to adjust for the effects of shell size on shell thickness, shell mass and shell breaking force. Because I was interested in the potential energetic consequences of increased shell mass on body mass, analysis of among-population differences in body mass used shell mass as the covariate. To analyse final trait values from the predator-induced plasticity experiment, I conducted a three-factor ANCOVA, with treatment ('crab' and 'no-crab') and geographic location (Maine and Massachusetts) as fixed effects, source population (Johnson Bay, Quoddy Head, Lobster Cove, Manchester Harbor) as a random effect nested within each geographic location, and replicate chambers as a random nested effect. Analyses of final shell thickness, shell mass and body mass used the same covariates as described above. For analysis of body growth, initial body mass was used as the covariate. Because all analyses employed ANCOVA techniques to adjust for the potential effects of either final or initial size on response variables, discussion regarding statistical differences due to experimental treatments, geographic location or source population is based on least squares adjusted means generated by ANCOVA. Slopes in all analyses were homogeneous ($P > 0.05$).

The above analyses were conducted on $\log_{(10)}$ transformed data using JMP software (Version 3.2.1, SAS Institute Inc., Cary, NC) for the Macintosh. Because both source population and replicates were declared random nested effects in all models, JMP used the Satterthwaite approximation to calculate mean squares and their respective degrees of freedom.

I also compared the final mean shell thickness of snails from the laboratory experiment to mean shell thickness from each field population. This comparison was made to determine how the shell thickness of snails raised in the laboratory treatments differed from that of snails that had lived in the field. Because field samples encompassed a much wider size range than laboratory samples, I used the approach of Palmer (1990, p. 160) to calculate final shell thickness for a standard sized snail for both laboratory treatments and field samples. Regression equations for both experimental laboratory treatments and field populations were used to transform the observed final shell thickness to that expected for a standard sized snail. I used the mean shell length from each effluent treatment × source population combination as the standard size. These standardized values were then analysed with a one-way analysis of variance (ANOVA). Standardization of final shell thickness and the analysis comparing laboratory groups and field populations was performed with $\log_{(10)}$ transformed data on JMP software.

RESULTS

Geographic differences in shell thickness and mass, shell breaking force and body mass

Analysis of covariance revealed that the shells of snails from both southern populations were thicker (Fig. 2a) and heavier (Fig. 2b) than those of snails from both northern populations (Table 1). These differences in shell form translated into differences in shell-breaking force; southern snails required significantly greater forces to crush than northern snails

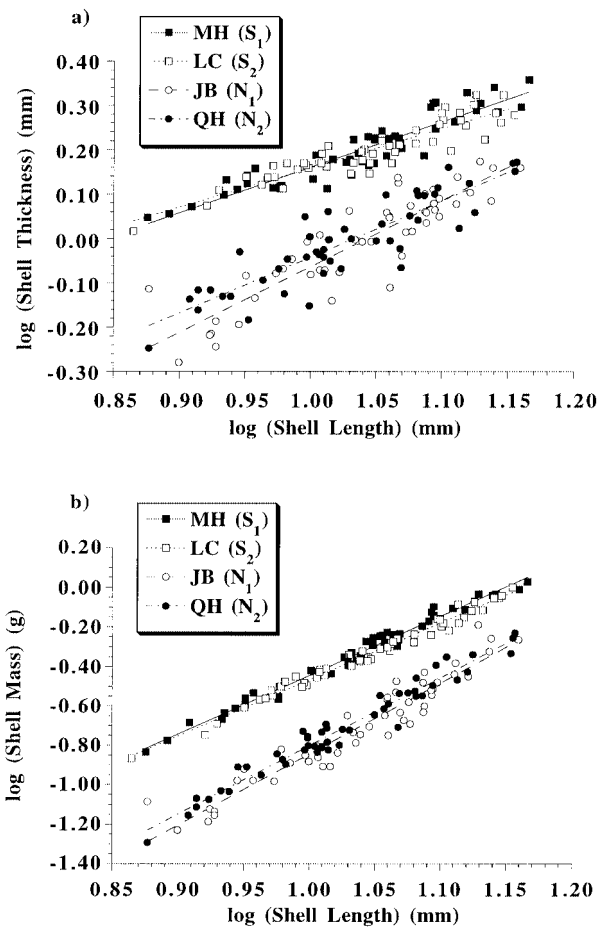

Fig. 2. (a) log(shell thickness) (y) as a function of log(shell length) (x) for *Littorina obtusata* collected from two southern (S; Manchester, Massachusetts) and two northern (N; Lubec, Maine) populations in the Gulf of Maine. MH = Manchester Harbor ($y = 1.02x - 0.86$, $R^2 = 0.86$; $P < 0.001$); LC = Lobster Cove ($y = 0.88x - 0.72$, $R^2 = 0.84$; $P < 0.001$); JB = Johnson Bay ($y = 1.48x - 1.55$, $R^2 = 0.80$; $P < 0.001$); QH = Quoddy Head ($y = 1.26x - 1.30$, $R^2 = 0.77$; $P < 0.001$). (b) log(shell mass) (y) as a function of log(shell length) (x) for *Littorina obtusata* collected from the same populations. MH = Manchester Harbor ($y = 2.98x - 3.43$, $R^2 = 0.98$; $P < 0.001$); LC = Lobster Cove ($y = 2.86x - 3.33$, $R^2 = 0.98$; $P < 0.001$); JB = Johnson Bay ($y = 3.61x - 4.45$, $R^2 = 0.92$; $P < 0.001$); QH = Quoddy Head ($y = 3.46x - 4.27$, $R^2 = 0.96$; $P < 0.001$).

(Table 1; Fig. 3). Geographic differences in body mass followed a trend different from that for shell traits; northern snails had significantly more body mass than southern snails (Table 1; Fig. 4).

Phenotypic plasticity in shell thickness and mass, body mass and body growth

Analysis of covariance revealed that snails from both populations from each geographic location produced thicker shells when raised in the presence of *Carcinus maenas* feeding on

Table 1. Nested ANCOVA for *Littorina obtusata* from two 'northern' (Lubec, Maine) and two 'southern' (Manchester, Massachusetts) populations

Source	d.f.	*F*	*P*
Comparison: log(shell thickness) (*y*) *vs* log(shell length) (*x*): Fig. 2a			
Location	1,2	643.58	0.0015
Population{Location}	2,195	1.62	0.2005
Slope	2,193	1.98	0.1402
Comparison: log(shell mass) (*y*) *vs* log(shell length) (*x*): Fig. 2b			
Location	1,2	242.02	0.0041
Population{Location}	2,195	8.49	0.0003
Slope	2,193	0.61	0.5409
Comparison: log(breaking force) (*y*) *vs* log(shell length) (*x*): Fig. 3			
Location	1,2	570.06	0.0017
Population{Location}	2,195	4.10	0.0180
Slope	2,193	1.92	0.1500
Comparison: log(body mass) (*y*) *vs* log(shell mass) (*x*): Fig. 4			
Location	1,2	110.70	0.0069
Population{Location}	2,195	17.74	<0.0001
Slope	2,193	2.90	0.0573

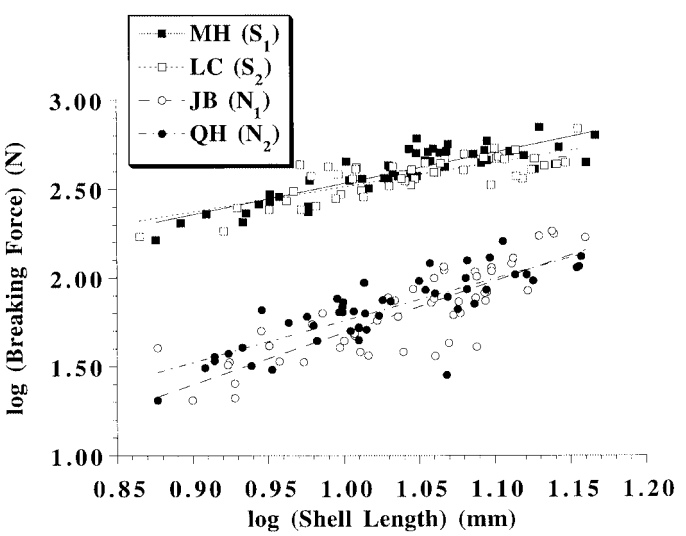

Fig. 3. log(breaking force) (*y*) *vs* log(shell length) (*x*) for *Littorina obtusata* collected from two southern (S; Manchester, Massachusetts) and two northern (N; Lubec, Maine) populations in the Gulf of Maine. MH = Manchester Harbor ($y = 1.75x + 0.79$, $R^2 = 0.73$; $P < 0.001$); LC = Lobster Cove ($y = 1.39x + 1.12$, $R^2 = 0.63$; $P < 0.001$); JB = Johnson Bay ($y = 2.92x - 1.23$, $R^2 = 0.69$; $P < 0.001$); QH = Quoddy Head ($y = 2.37x - 0.61$, $R^2 = 0.66$; $P < 0.001$). See Table 1 for results of ANCOVA.

Table 2. Nested ANCOVA testing the effect of risk stimuli ('crab' *vs* 'no-crab'), geographic location and source population on (a) shell thickness and (b) shell mass of *Littorina obtusata* from two 'northern' (Lubec, Maine) and two 'southern' (Manchester, Massachusetts) populations

Source	d.f.	*F*	*P*
(a) Comparison: shell thickness (*y*) *vs* shell length (*x*): Fig. 5a			
Treatment (Treat)	1,16	124.91	<0.0001
Location (Loc)	1,2	113.13	0.0090
Population{Loc}	2,16	3.19	0.0675
Treat × Loc	1,16	1.42	0.2510
Treat × Population{Loc}	2,656	2.91	0.0553
Replicate	16,646	2.84	0.0002
Slope	2,646	2.95	0.0532
(b) Comparison: log(shell mass) (*y*) *vs* log(shell length) (*x*): Fig. 5b			
Treatment (Treat)	1,16	100.26	<0.0001
Location (Loc)	1,2	150.34	0.0068
Population{Loc}	2,16	4.52	0.0272
Treat × Loc	1,16	6.18	0.0242
Treat × Population{Loc}	2,654	2.14	0.1187
Replicate	16,646	2.42	0.0015
Slope	2,646	2.30	0.1009

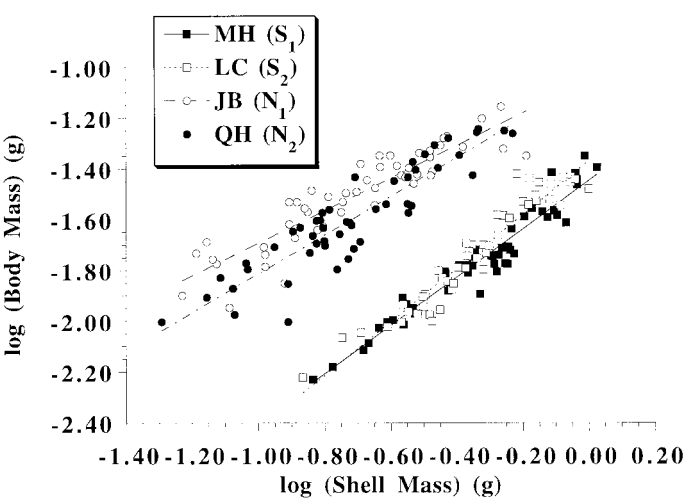

Fig. 4. (a) log(body mass) (*y*) as a function of log(shell mass) (*x*) for *Littorina obtusata* collected from two southern (S; Manchester, Massachusetts) and two northern (N; Lubec, Maine) populations in the Gulf of Maine. MH = Manchester Harbor ($y = 0.951x - 1.446$, $R^2 = 0.93$; $P < 0.001$); LC = Lobster Cove ($y = 1.055x - 1.368$, $R^2 = 0.92$; $P < 0.001$); JB = Johnson Bay ($y = 0.642x - 1.052$, $R^2 = 0.82$; $P < 0.001$); QH = Quoddy Head ($y = 0.766x - 1.048$, $R^2 = 0.83$; $P < 0.001$). See Table 1 for results of ANCOVA.

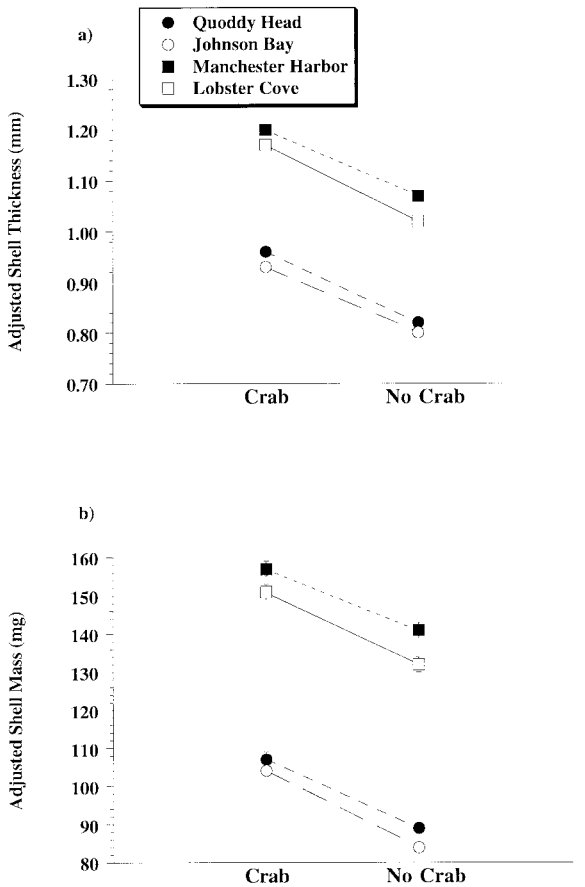

Fig. 5. Adjusted mean (± standard error) (a) shell thickness and (b) mass at a covariate mean of 7.92 ± 0.04 for *Littorina obtusata* from two southern (Manchester, Massachusetts) and two northern (Lubec, Maine) populations in the Gulf of Maine that were raised in the presence and absence of *Carcinus maenas* for 115 days. See Table 2 for results of ANCOVA.

conspecifics (Table 2a; Fig. 5a). The treatment × location interaction term was not significant, indicating that snails responded similarly to experimental treatments regardless of their geographical origin. Southern snails raised with crabs produced shells that were 12.1–14.7% thicker than southern snails raised without crabs, while northern snails raised with crabs produced shells that were 16.2–17.1% thicker than northern snails raised without crabs.

Predator-induced increases in shell thickness resulted in heavier shells for snails raised with *Carcinus maenas* (Table 2b; Fig. 5b). In contrast to shell thickness, a significant treatment × location interaction indicated that crab-induced responses in shell mass differed for northern and southern snails. Southern snails raised with crabs produced shells that were 11.3–14.4% heavier than southern snails raised without crabs, while northern snails raised with crabs produced shells that were 20.2–23.8% heavier than northern snails raised without crabs.

Significant reductions in body mass were also induced by *Carcinus maenas* effluent. Snails from both southern populations raised with crabs produced 21.4–23.8% less body mass relative to their controls, while snails from both northern populations raised with crabs produced 20.8–29.8% less body mass relative to their controls (Table 3a; Fig. 6a). Reductions in body mass were statistically similar for northern and southern snails as indicated by a non-significant treatment × location interaction.

Differences in final body mass appear to reflect differential body growth. Southern snails raised with *Carcinus maenas* grew 46.7–58.8% less than their controls raised without crabs, while northern snails raised with crabs grew 16.7–25.0% less than their controls raised without crabs (Table 3b; Fig. 6b). Despite the two-fold differences in growth among northern and southern snails, high variability prevented the detection of a significant treatment × location interaction.

Comparisons between field populations and laboratory snails

The one-way ANOVA on laboratory-raised snails and field populations detected significant differences among groups (i.e. 'crab', 'no-crab', 'field') for each population in final shell thickness (ANOVA: $F_{1,11} = 373.81$, $P < 0.0001$). *A priori* linear contrasts (see Fig. 7) revealed that northern snails raised with *Carcinus maenas* had significantly thicker shells than snails raised without crabs, and snails raised without crabs were significantly thicker than field snails (both $P < 0.0001$; Fig. 7). The patterns revealed by *a priori* linear contrasts between laboratory-raised and field snails for snails from southern sites depended on source population. For Manchester Harbor, the shells of snails raised with crabs were significantly thicker

Table 3. Nested ANCOVA testing the effect of risk stimuli ('crab' *vs* 'no-crab'), geographic location and source population on body mass and body growth of *Littorina obtusata* from two 'northern' (Lubec, Maine) and two 'southern' (Manchester, Massachusetts) populations

Source	d.f.	*F*	*P*
(a) Comparison: log(body mass) (*y*) *vs* log(shell mass) (*x*): Fig. 6a			
Treatment (Treat)	1,16	113.52	<0.0001
Location (Loc)	1,2	164.05	0.0055
Population{Loc}	2,16	4.31	0.0315
Treat × Loc	1,16	1.18	0.2928
Treat × Population{Loc}	2,470	1.88	0.1532
Replicate	16,646	3.76	<0.0001
Slope	2,646	1.57	0.2086
(b) Comparison: body mass growth (*y*) *vs* initial body mass (*x*): Fig. 6b			
Treatment (Treat)	1,16	7.75	0.0132
Location (Loc)	1,2	0.74	0.4797
Population{Loc}	2,16	2.87	0.0859
Treat × Loc	1,16	1.41	0.2524
Treat × Population{Loc}	2,654	0.39	0.6755
Replicate	16,646	6.94	<0.0001
Slope	2,646	0.38	0.6851

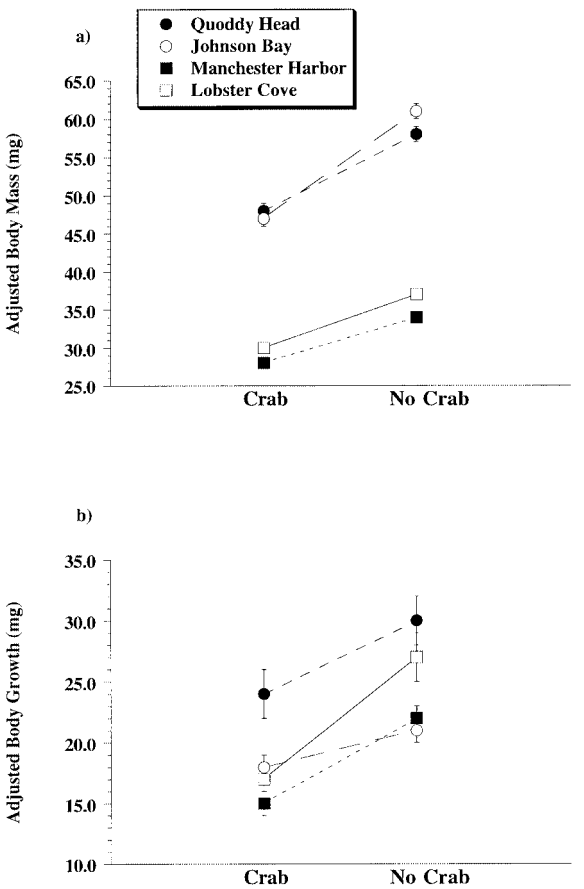

Fig. 6. (a) Adjusted mean (± standard error) (a) body mass at a covariate mean of 0.131 ± 0.002 and (b) body growth at a covariate mean of 0.019 ± 0.0002 for *Littorina obtusata* from two southern (Manchester, Massachusetts) and two northern (Lubec, Maine) populations in the Gulf of Maine that were raised in the presence and absence of *Carcinus maenas* for 115 days. See Table 3 for results of ANCOVA.

than those of field snails ($P < 0.005$), and field snails had significantly thicker shells than snails raised without crabs ($P < 0.005$; Fig. 7). In contrast, Lobster Cove snails raised with crabs and those from the field had shells of similar thickness, and the shells of these two groups were significantly thicker compared to snails raised without crabs ($P < 0.0001$; Fig. 7).

DISCUSSION

Inducible defences should be favoured over constitutive defences when (1) predators are temporally or spatially variable, (2) the production of a defensive trait confers some benefit to the organism, such as improved survival, growth or reproduction, (3) there is the presence of a reliable cue that induces the defence, and (4) the cost of producing a constitutive

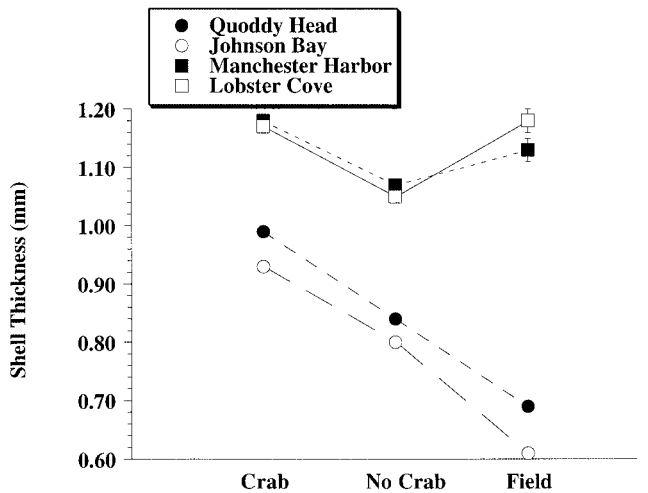

Fig. 7. Comparison of mean shell thickness at a standard size (shell lengths: Manchester Harbor = 7.85 mm, Lobster Cove = 7.97 mm, Quoddy Head = 8.01 mm, Johnson Bay = 7.86 mm) for *Littorina obtusata* raised with and without *Carcinus maenas* in the laboratory with snails from their respective populations in the field. For both northern populations, the rank order of significant differences in shell thickness is 'crab' > 'no crab' > 'field' (all $P < 0.0001$). For Manchester Harbor, the rank order of significant differences in shell thickness is 'crab' > 'field' > 'no crab' (all $P < 0.005$) and for Lobster Cove it is 'crab' = 'field' > 'no crab' (all $P < 0.0001$).

defence is greater against the local environmental background (Levins, 1968; Lively, 1986a; Stearns, 1989; DeWitt *et al*., 1998; Tollrian and Harvell, 1999). Predator-induced defences are known among diverse taxa and include spine formation in bryozoans (Harvell, 1984, 1991), crest enlargement in cladocerans (Dodson, 1989), shell size and shape change in freshwater snails and marine barnacles (Crowl and Covich, 1990; Lively, 1986b; DeWitt, 1998), body deepening in fish (Brönmark and Miner, 1992, Brönmark *et al*., 1999) and shell thickening in marine gastropods (Appleton and Palmer, 1988; Palmer, 1990; Trussell, 1996). Despite the taxonomic diversity of this phenomenon, all of the examples cited above involve within or among (on a very localized scale) population responses. However, predator-induced defences may also contribute to broad-scale patterns of morphological differentiation. Understanding the role of phenotypic plasticity in producing geographic variation may yield further insights into its role in adaptation, as well as less understood processes such as speciation (West Eberhard, 1989).

This study revealed geographic differences in shell form and breaking force that are correlated with the historical and present abundance of *Carcinus maenas* in the Gulf of Maine. In northern Maine, where *C. maenas* has been present for about 50 years, the shells of *Littorina obtusata* are thinner, weigh less and are weaker than those of conspecifics in Massachusetts where *C. maenas* has been present for about 100 years (Figs 2–4). According to the selection hypothesis (*sensu* Seeley, 1986), southern snails are thicker, weigh more and are stronger because selection by *C. maenas* on traits having a fixed genetic basis has been acting on southern populations for a longer time. Hence, geographic differences in shell form simply reflect geographic differentiation in genetic controls on shell form.

Although selection by *Carcinus maenas* is surely involved, the critical issue is determining whether selection is acting on genetically fixed traits or on genetically based reaction norms. In the laboratory, the presence of *C. maenas* induced the production of thicker and heavier shells in snails from all four populations (Figs 5a,b), suggesting that reaction norms shaped by selection are contributing to broad-scale differentiation in *Littorina obtusata* shell form. Thus, the thicker shells of southern snails may reflect responses to increased *C. maenas* effluent concentrations, while the thinner shells of northern snails may reflect the relative absence of *C. maenas* effluent.

Interestingly, the increases in shell thickness (Fig. 5a) induced by *Carcinus maenas* were statistically similar for northern and southern snails, suggesting that these reaction norms have evolved similar slopes within each geographic region. However, the results also suggest that there has been an evolutionary shift in reaction norm intercept. Regardless of experimental treatment, southern snails consistently exhibited thicker shells than northern snails (Fig. 5a). Moreover, while northern snails raised in the laboratory with crabs produced considerably thicker shells than their counterparts in the field, southern snails raised in the laboratory with crabs and their counterparts in the field produced shells of similar thickness (Fig. 7). Hence, when compared with field snails, southern snails exhibited less plasticity than northern snails. Although such differences may partly reflect geographic differences in exposure to *C. maenas* effluent in the field before snails were collected for the experiment, they also suggest the evolution of different reaction norms.

Littorina obtusata has direct development, which should restrict gene flow among such widely separated populations and enhance population differentiation. One might expect this condition, coupled with the geographic differences in the variability of *Carcinus maenas* abundance over the last 100 years, to promote the evolution of different reaction norms. In particular, one would expect reduced plasticity or even a constitutive defence to evolve in southern populations given the presumed predictability of *C. maenas* abundance in this region. That southern snails possess predator-induced plasticity in shell form suggests three things, which are not mutually exclusive. First, present-day *C. maenas* abundance in the southern Gulf is sufficiently variable to favour the retention of inducible defences. Second, the evolution of reaction norms in *L. obtusata* may be sensitive to time-scales greater than that considered here. This scenario may apply if the recent *C. maenas* invasion during this century is just one of similar events in the past. Hence, if *C. maenas* has experienced multiple expansions and contractions of its geographic range, then the retention of inducible defences may be favoured. Finally, the evolution of constitutive defences once inducible defences are in place may occur slowly, especially if strong life-history trade-offs accompany constitutive defences.

In contrast to shell thickness, exposure to *Carcinus maenas* effluent induced greater plasticity in the shell mass of northern than southern snails (Fig. 5b). This result is consistent with theory because greater variability in contact between predator and prey like that expected in northern habitats should favour the evolution of increased plasticity. The inconsistencies in trait-specific plasticity indicate that much remains to be learned about the forces shaping reaction norms for *Littorina obtusata* shell form. However, my results provide further support of the hypothesis (Trussell, 2000; Trussell and Smith, 2000) that phenotypic plasticity may contribute significantly to both macro-scale geographic variation and historical transitions in gastropod shell form (*sensu* Vermeij, 1982; Seeley, 1986).

Comparison of the laboratory-raised snails and field populations also support the hypothesis that geographic differences in *Littorina obtusata* shell thickness may partly

reflect geographic differences in the presence of *Carcinus maenas* effluent. For example, while southern field snails were 78% thicker than northern field snails, northern snails raised with crabs were only 21% thinner than southern field snails and 23% thinner than southern snails raised with crabs. The convergence of northern snail shell thickness towards that of southern snails after exposure to crab effluent suggests that the thin shells of northern field snails are representative of either non-induced, or partially induced, phenotypes. In contrast, southern field snails and those raised with *C. maenas* produced shells of comparable thickness, which suggests that effluent concentrations in the laboratory were similar to (Lobster Cove) or slightly greater than (Manchester Harbor) those found in the field. This scenario, in addition to differential thinning in the laboratory in the absence of crabs, may explain why southern snails raised without crabs produced phenotypes of intermediate shell thickness (Fig. 7).

Interestingly, northern snails raised without *Carcinus maenas* had thicker shells than their counterparts in the field (Fig. 7), suggesting that other factors are modulating shell form. Recent work (Trussell, 2000; Trussell and Smith, 2000) suggests that geographic differences in water temperature, by altering rates of calcium carbonate deposition and dissolution (Vermeij, 1978, 1993), may contribute to this pattern. For example, reciprocal transplant experiments between northern and southern *Littorina obtusata* populations revealed that northern snails produced thicker shells when transplanted to a southern site and southern snails produced thinner shells when transplanted to a northern site (Trussell, 2000). Hence, because the laboratory effluent experiment was conducted in Massachusetts, where water temperatures average ~ 6°C warmer than in northern Maine (Trussell, 2000; Trussell and Smith, 2000), northern individuals raised without crabs may have increased shell deposition in response to warmer water temperatures. This scenario is thought to reflect countergradient variation in shell thickness growth (Trussell, 2000). Although water temperature is surely operating here, other work (Trussell and Smith, 2000) suggests that the effects of water temperature and *C. maenas* effluent on shell thickness are similar in magnitude.

Trade-offs associated with induced increases in shell thickness

A thorough understanding of both the adaptive value of inducible defences and the constraints on their evolution requires an assessment of accompanying costs or trade-offs (Stearns, 1989, 1992; DeWitt *et al*., 1998). The evolution of inducible over permanent defences implies that defensive structures are costly to produce; otherwise, the same phenotypes would be produced across different environments. The nature of these costs may fall into two broad categories (see DeWitt *et al*., 1998): (1) 'true' or 'pure' costs of plasticity (e.g. production costs, maintenance of plasticity machinery, developmental instability) and (2) limits to the benefits of plasticity (e.g. lagged response times, unreliable assessment of the local environment, limited developmental ranges, morphological trade-offs). Costs and limits to plasticity are probably subject to natural selection and instrumental in determining both the adaptive benefits and evolutionary potential of phenotypic plasticity (Schlichting and Pigliucci, 1998).

In the case of predator-induced defences, there has been an emphasis on the direct costs associated with the production of defensive structures (Harvell, 1986; Lively, 1986c; Tollrian, 1995). However, these costs are not necessarily indicative of costs of plasticity (DeWitt *et al*., 1998). For example, in the case of shell thickness, the direct costs associated

with producing a thicker shell should be the same for a fixed and plastic genotype. Only those trait production costs for plastic genotypes *in excess* of those for fixed genotypes could be considered a true cost of plasticity (DeWitt *et al.*, 1998). Hence, it is possible that trade-offs (e.g. reduced body mass and body growth) accompanying the production of thicker shells reflect costs derived from producing more shell material rather than costs tied to the ability to exhibit plasticity in shell thickness *per se*.

Previous studies of predator-induced changes to better defended shell morphologies have documented life-history trade-offs in growth (Appleton and Palmer, 1988), size at maturity (Crowl and Covich, 1990) and fecundity (Lively, 1986c). Although the production of more shell material by marine gastropods is expected to be energetically costly (Palmer, 1981), the cost of increased calcification is probably small relative to other metabolic costs, especially in areas where surface seawater is saturated with calcium carbonate (Palmer, 1992). Palmer (1981) concluded that a second, non-energetic cost best explains reduced body mass and body growth in thick-shelled snails. This hypothesis ('skeleton limitation' hypothesis) emphasizes the unique geometric constraints that shell form imposes on the snail living inside. Because there is a maximum rate at which calcification can occur (Palmer, 1992), the more material that is devoted to thickening the shell, the less that is available for advancing the shell margin. Hence, because tissue growth cannot proceed ahead of the protective shell, body mass and growth will be constrained by the reduced rates of linear shell growth accompanying increased thickness deposition. In addition to constraining linear shell growth (i.e. increasing shell size), thicker shells can limit body mass because thick-walled shells have less internal volume available for tissue growth than thin-walled shells of similar size and shape. Kemp and Bertness (1984) documented these patterns in the field. They found that rapidly growing shells in the snail *Littorina littorea* were thinner, more globose and thus able to accommodate more tissue growth than more slowly growing shells (see also Swan, 1952; Goreau, 1959; Trussell, 2000).

The results of this study indicate that trade-offs due to architectural constraints exist between shell form and body mass. First, geographic patterns in body mass and shell thickness were inversely related – while southern snails had thicker shells, they also had reduced body mass relative to northern conspecifics (Fig. 4; see also Trussell, 2000). Second, predator-induced increases in shell thickness and mass for snails from all populations were accompanied by reduced body mass and body growth (Figs 6a,b). Hence, the thicker-walled shells of snails raised with crabs probably limited the internal space available for body growth. Because gastropod fecundity is often a positive function of body size (Spight and Emlen, 1976; Palmer, 1983), predator-induced trade-offs in body mass and growth may have important implications for snail life history (Peters, 1983; Stearns, 1992). These trade-offs may partly explain the existence of micro- and macro-geographic variation in shell form and body mass as well as the evolution of inducible defences in marine gastropod shell form.

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