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GC Trussell
Virginia Institute of Marine Science

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PHENOTYPIC CLINES, PLASTICITY, AND MORPHOLOGICAL TRADE-OFFS IN AN INTERTIDAL SNAIL

GEOFFREY C. TRUSSELL[1]
Department of Biological Sciences, School of Marine Science, College of William & Mary, Gloucester Point, Virginia 23062
Marine Science Center, Northeastern University, Nahant, Massachusetts 01908

Abstract.—Understanding the genetic and environmental bases of phenotypic variation and how they covary on local and broad geographic scales is an important goal of evolutionary ecology. Such information can shed light on how organisms adapt to different and changing environments and how life-history trade-offs arise. Surveys of phenotypic variation in 25 *Littorina obtusata* populations across an approximately 400-km latitudinal gradient in the Gulf of Maine revealed pronounced clines. The shells of snails from northern habitats weighed less and were thinner and weaker in compression than those of conspecifics from southern habitats. In contrast, body size (as measured by soft tissue mass) followed an opposite pattern; northern snails weighed more than southern snails.

A reciprocal transplant between a northern and southern habitat revealed substantial plasticity in shell form and body mass and their respective measures of growth. Southern snails transplanted to the northern habitat produced lighter, thinner shells and more body mass than controls raised in their native habitat. In contrast, northern snails transplanted to the southern site produced heavier, thicker shells and less body mass than controls raised in their native habitat. Patterns of final phenotypic variation for all traits were consistent with cogradient variation (i.e., a positive covariance between genetic and environmental influences). However, growth in shell traits followed a countergradient pattern (i.e., a negative covariance between genetic and environmental influences). Interestingly, body growth followed a cogradient pattern, which may reflect constraints imposed by cogradient variation in final shell size and thickness. This result suggests the existence of potential life-history trade-offs associated with increased shell production.

Differences in *L. obtusata* shell form, body mass, and their respective measures of growth are likely induced by geographic differences in both water temperature and the abundance of an invading crab predator (*Carcinus maenas*). Water temperatures averaged 6.8°C warmer during the transplant experiment and *C. maenas* abundance is greater in the southern Gulf of Maine. Because both increased water temperature and crab effluent affect shell form in the same way, future experiments are needed to determine the relative importance of each. Nevertheless, it is clear that phenotypic plasticity has an important role in producing geographic variation in *L. obtusata* shell form. Moreover, the evolution of phenotypic plasticity in *L. obtusata* and other marine gastropods may be driven by architectural constraints imposed by shell form on body mass and growth.

Key words.—*Carcinus maenas,* cogradient variation, countergradient variation, crab predation, growth, latitude, *Littorina obtusata,* natural selection, phenotypic plasticity, water temperature.

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Understanding the basis (genetic vs. ecophenotypic) of intraspecific variation across different environments has strongly influenced our views on adaptation, speciation, and geographic variation (Endler 1977; West-Eberhard 1989; Schlichting and Pigliucci 1998). Both narrow- and broad-scale patterns of phenotypic variation are often considered adaptive rather than ecophenotypic phenomena (Kitching et al. 1966; Endler 1977, 1986; Futuyma 1998). However, intraspecific variation also can reflect phenotypic plasticity; the within-generation response of a genotype to its environment (Via and Lande 1985; Stearns 1989; Schlichting and Pigliucci 1998).

Studies of the evolution of phenotypic plasticity often focus on genotype-by-environment (G × E) interactions (Via 1984; Via and Lande 1985), but this information alone aids little in understanding why micro- and macrogeographic patterns of phenotypic variation arise in the first place. Furthermore, genetic and environmental influences on phenotypes may act in concert or in opposition (Conover and Schultz 1995). With cogradient variation (CoGV), selection and plasticity act in the same direction (they covary positively). In this scenario (''synergistic selection'' of Falconer 1989), phenotypic differences are pronounced among native phenotypes (N_1 vs. N_2 in Fig. 1a), whereas phenotypes of transplanted organisms converge toward native phenotypes (T_1 vs. T_2 in Fig. 1a). In contrast, countergradient (CnGV) variation occurs when selection and plasticity act in opposition (they covary negatively). In this scenario (''antagonistic selection'' of Falconer 1989), little or no phenotypic differentiation occurs among native phenotypes (N_1 vs. N_2 in Fig. 1b), whereas the form of transplanted organisms diverges from native phenotypes (T_1 vs. T_2 in Fig. 1b). These covariance relationships determine whether clinal variation is observed (Levins 1968, 1969; Berven et al. 1979; Berven 1982a,b) and are essential for interpreting life-history trade-offs across environments (Conover and Schultz 1995).

Rocky intertidal snails exhibit dramatic morphological variation across environmental gradients on both small and large geographic scales (Kitching et al. 1966; Phillips et al. 1973; Vermeij 1978, 1987; Palmer 1985, 1990; Etter 1988; Trussell et al. 1993; Trussell 1996, 1997). Predation by shell-crushing predators is thought to be particularly important in producing geographic and historical variation in gastropod shell form (Vermeij 1978, 1987). For example, better-defended shell morphologies and higher frequencies of shell repair in post-Paleozoic fossil shells versus Paleozoic assemblages (Vermeij 1978, 1987; Vermeij et al. 1981; Signor and Brett 1984)

[1] Present address: Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912; E-mail: geoffrey_trussell@brown.edu.

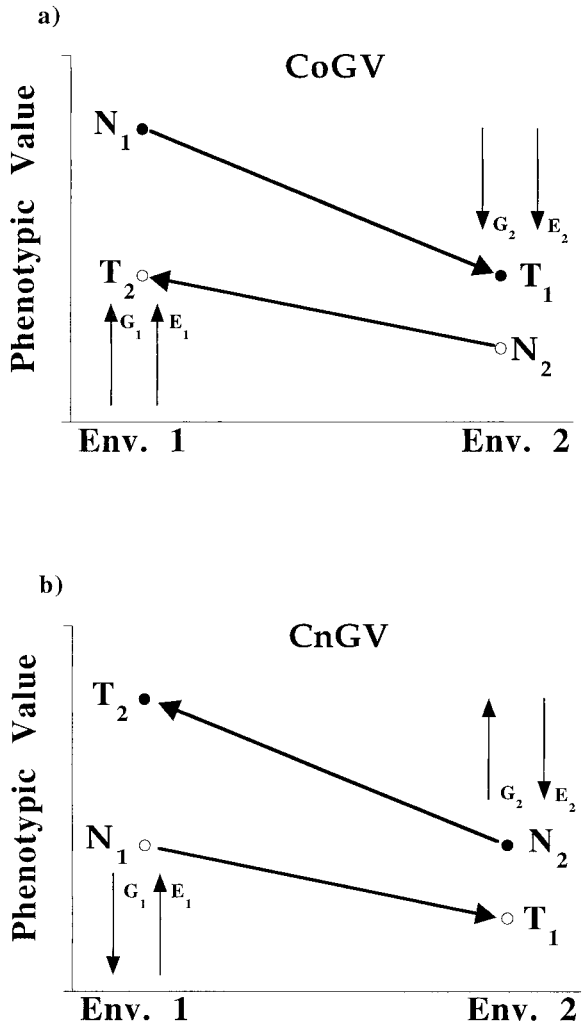

FIG. 1. (a) Phenotypic variation consistent with cogradient variation (CoGV). Note the large difference in phenotypic values of phenotypes in their native environments (N_1 and N_2) and the shift of their respective transplants (T_1 and T_2) towards the phenotypic values of native phenotypes. (b) Phenotypic variation consistent with countergradient variation (CnGV). Note the similarity in phenotypic values of phenotypes in their native environments (N_1 and N_2) and the divergence in the phenotypic values of their respective transplant phenotypes (T_1 and T_2). Arrows with G and E refer to the direction of genetic and environmental influences on phenotypes within their respective environments. See text for further explanation (adapted from Conover and Schultz 1995).

are thought to reflect the coincident diversification of shell-crushing predators in the Mesozoic (Vermeij 1977). Biogeographic evidence suggests that gastropod species have more robust shell morphologies in regions (tropical vs. temperate) where shell-crushing predators are more taxonomically diverse, capable of producing greater crushing forces, and there has been a longer time for coevolution between predator and prey (Vermeij 1978, 1987; Vermeij and Veil 1978).

The Carcinus maenas Range Expansion and Phenotypic Shifts in Littorina obtusata

Transitions in the shell form of two intertidal species (*Nucella lapillus* and *Littorina obtusata*) that occurred after the range expansion of the green crab (*Carcinus maenas*) into the Gulf of Maine also suggest the action of natural selection (see Vermeij 1982; Seeley 1986). Although the cause for this expansion is unknown, it may have been facilitated by increases in mean annual sea surface temperatures over the last 100 years in the Gulf of Maine (Welch 1968; Lazzari 1997). Beginning in 1900, the range of *C. maenas* in North America began to expand north of Cape Cod, Massachusetts. *Carcinus maenas* reached Portland, Maine, in the early 1900s; midcoastal Maine by the 1930s; and northern Maine and the Bay of Fundy by the 1950s (Scattergood 1952; Welch 1968). Consequently, snails in northern Maine have been cohabiting with *C. maenas* for approximately 50 years, whereas snails in Massachusetts have been cohabiting with *C. maenas* for approximately 100 years.

Museum specimens of *L. obtusata* collected in the Gulf of Maine before the *C. maenas* invasion in 1900 were thinner and higher spired than those collected from similar locations in the mid-1980s (Seeley 1986). Moreover, experiments demonstrated that thin-shelled, high-spired morphs from northern Maine were more vulnerable to *C. maenas* predation than thick-shelled, low-spired morphs collected elsewhere. Seeley (1986) concluded that the range expansion of *C. maenas* and coincident changes in *L. obtusata* shell form were an example of rapid microevolutionary change via natural selection.

Recent evidence of phenotypic plasticity in response to predator effluent has changed our thinking about the evolution of shell form (Appleton and Palmer 1988; Crowl and Covich 1990; Palmer 1990; Trussell 1996, in review). For example, Appleton and Palmer (1988) demonstrated that the scent of crabs and damaged conspecifics can induce the development of larger apertural teeth in *Nucella lamellosa*. Similarly, thicker shells in *L. obtusata* can be induced by raising snails in the presence of effluents associated with *C. maenas* feeding on conspecifics (Trussell 1996). Indeed, the taxonomic and geographic diversity of this response indicates that it is a general phenomenon (Appleton and Palmer 1988; Crowl and Covich 1990; Palmer 1990; Trussell 1996; Leonard et al. 1999).

The Environmental Effects of Water Temperature on Gastropod Shell Form

Water temperature also can influence both micro- and macroscopic properties of calcium carbonate ($CaCO_3$) based shells (Lowenstam 1954a,b; Dodd 1963, 1964; Kennedy et al. 1969; Graus 1974; Vermeij 1978, 1993). Both the deposition and maintenance of shells should be more difficult in colder versus warmer waters because $CaCO_3$ becomes less saturated and more soluble with decreasing water temperature (Malone and Dodd 1967; Graus 1974; Vermeij 1978, 1993; Clarke 1983). Although there are exceptions (Vermeij 1993), this view is supported by increased calcification indices (the ratio of shell mass to its internal volume) in tropical versus temperate molluscs (Nicol 1967; Graus 1974; Vermeij 1978) and by experimental evidence of increased calcification rates in *Mytilus edulis* at higher temperatures (Malone and Dodd 1967). In addition, Lowenstam (1954a,b) and Dodd (1963) found that calcite:aragonite ratios in *M. edulis* increased with latitudinal decreases in water temperature. Latitudinal chang-

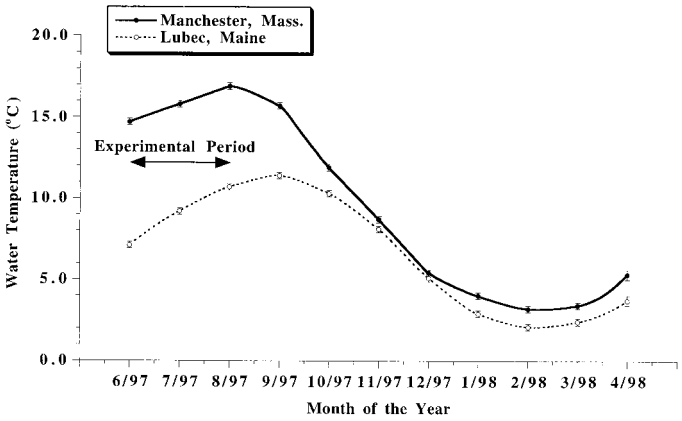

FIG. 2. Mean (± SE) water temperature at the two sites used in the reciprocal transplant experiment. ''Experimental period'' refers to 90 days during which the experiment was conducted.

es in shell mineralogy may reflect the higher solubility of aragonite (versus calcite) in colder waters (Pytkowicz 1969). In terms of shell strength, the relative amount of aragonite may be important because calcite is softer, less dense, and tends to break along well-defined cleavage planes (Carter 1980). For gastropods like *L. obtusata* that are distributed across a latitudinal temperature gradient in New England (Fig. 2), shells in colder waters are expected to be thinner, weaker, and thus more vulnerable to crushing predators than those in warmer waters.

Because both water temperature (Fig. 2) and *C. maenas* abundance are greater in the southern versus northern Gulf of Maine, one objective of this study was to determine whether latitudinal clines exist in shell traits and body mass (defined as soft tissue mass). In addition, a reciprocal transplant experiment was conducted in the field between a northern (Lubec, ME) and southern (Manchester, MA) population to examine genetic and environmental influences on shell form and body mass and their respective growth. By measuring variation in morphological traits and their respective growth rates, I examined the role of cogradient and countergradient phenomena in producing geographic patterns of phenotypic variation. Finally, data from both experiments were used to address whether there are costs associated with increased shell production.

MATERIALS AND METHODS

Phenotypic Clines in Shell Form, Body Size, and Shell Strength

To examine geographic variation in several traits across a latitudinal gradient, I sampled 25 populations along the New England coast from Manchester, Massachusetts, to Lubec, Maine (see Appendix 1 for locations). All collections were made between November and December (1995–1997) to minimize potential seasonal effects on the traits of interest. From each site, approximately 100 snails were sampled from 0.25-m^2 quadrats tossed haphazardly in the mid-intertidal zone. Fifty snails from each sample were randomly chosen from the available sample; however, I did attempt to maximize the size range of snails from each population. In the laboratory, I measured shell length and shell thickness with digital calipers (± 0.01 mm). The mean of two measures of shell thickness was used in statistical analyses (see Fig. 1 in Trussell 1996). After measurement of shells, I carefully cracked each shell with a C-clamp and separated shell fragments from soft tissue. Shell material and soft tissue were then oven dried at 60°C for 48 h before weighing on an analytical balance. Shell mass was measured (± 0.001 g) on a Mettler (Toledo, OH) PG503 and soft tissue mass, which served as my measure of body size, was measured (± 0.0001 g) on a Mettler AE100.

For seven sites in the Cape Ann region of Massachusetts and six sites in the Quoddy region of Maine, 50 additional snails were collected. These samples were used to measure the maximum force required to crush each snail's shell on an Instron (Canton, MA) Dynamic Testing machine (± 0.01 N; Model 4301). These tests were not meant to simulate crab predation, but to provide a relative measure of breaking force, which should influence vulnerability to crab predation (Vermeij and Currey 1980). Snails were kept submerged in seawater for 24 h prior to testing. I placed live snails aperture down between two steel platens and crushed the shell by lowering the top platen onto each shell at a rate of 10 mm/min. Shells were loaded until they were crushed; a loud ''cracking'' noise reliably indicated failure of the shell.

Nondestructive Estimates of Shell Mass and Body Mass

Because I wanted to document growth in shell and body mass of snails to be used in the reciprocal transplant experiment (described below), it was necessary to make non-destructive estimates of shell and body mass. Following the methods of Palmer (1982), I generated regressions between measurements of actual shell mass (Y) on measurements of shell mass while submerged in seawater (X; hereafter, submerged mass) for each population. To do so, 50 snails spanning the available size range were collected from the two protected shore populations used in the experiment: a northern site in Lubec, Maine (Quoddy Head), and a southern site in Manchester, Massachusetts (Lobster Cove). In the laboratory, shell length was measured with digital calipers (± 0.01 mm). Submerged mass was measured while snails were submerged in seawater (± 0.001 g). Snails were then allowed to dry on towels 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]). All mass measurements were made on a Mettler PG503 analytical balance. After total mass measurements, snails were carefully crushed and tissue separated from the shell. Both tissue and shell material was dried at 60°C for 48 h before weighing to determine the actual mass of each variable.

Regressions of actual shell mass on submerged mass for snails from each population yielded highly significant R^2-values (northern: $Y = 1.561X - 0.0018$, $R^2 = 0.9991$; southern: $Y = 1.582X + 0.0023$, $R^2 = 0.9999$), indicating that submerged mass is a reliable predictor of actual shell mass (Palmer 1982). By inserting measurements of initial submerged mass of snails collected for the reciprocal transplant experiment into the respective regression equations for each population, I was able to estimate initial actual shell mass

from initial submerged mass. To calculate initial body mass, I subtracted the estimate of actual shell mass from the total mass of snails when weighed in air (Palmer 1982).

Reciprocal Transplant between a Northern and Southern Population

I reciprocally transplanted snails between the northern and southern site to test the hypothesis that geographic differences in shell form and body mass (defined by tissue mass) have an ecophenotypic component. In mid-May 1997, I collected juvenile snails from both populations (Quoddy Head mean [±SE] shell length = 5.66 ± 0.03; Lobster Cove mean shell length = 5.46 ± 0.04), individually labeled them with waterproof markers (Trussell 1997), and measured for shell length and shell thickness as described above. Following the Palmer (1982) protocol, I also made measurements of submerged mass and total mass in air to obtain estimates of actual shell mass and wet body mass. Measurements of growth in terms of shell length, shell thickness, shell mass, and body mass were calculated by subtracting initial from final values.

After completion of measurements, I placed 10 snails from each population in 24 separate replicate cylindrical chambers (4 cm height × 15 cm diameter) that served as experimental units for statistical analyses. The top and bottom of each chamber were constructed from plastic mesh (3.75 mm × 2.90 mm) to permit water flow. There were six replicate chambers yielding a total of 60 snails for each transplant group: (1) north >> north (NN; control); (2) north >> south (NS; transplant); (3) south >> south (SS; control); and (4) south >> north (SN; transplant). In the mid-intertidal zone at each site (~1.5 mean low water [MLW]), I anchored chambers to bricks with cable ties. Chambers were haphazardly placed at each site within an area of approximately 50 m^2. Although snails were able to feed on the microflora that colonized each chamber during the course of the experiment, I also supplemented the food supply by placing 30 g (wet mass) of the alga *Ascophyllum nodosum* in each chamber. Any snails or egg masses on *A. nodosum* fronds were removed before placing the algae in the chambers. I replaced the algae in each chamber every 30 days. Chambers were recovered from the field after 90 days for final measurement of shell length, shell thickness, submerged mass, and total mass in air. Using the same protocol described above, 15–25 snails randomly sampled from each experimental group were sacrificed to generate new regressions to estimate final actual shell mass and final body mass (SS: $Y = 1.568X + 0.0028$, $R^2 = 0.9981$; SN: $Y = 1.582X + 0.0009$, $R^2 = 0.9980$; NS: $Y = 1.607X - 0.0031$, $R^2 = 0.9962$; NN: $Y = 1.548X - 0.0009$, $R^2 = 0.9955$). During the course of the experiment I lost one SN replicate, three SS replicates, and two NS replicates.

Water temperature was monitored at each transplant location with HoboTemp dataloggers (Onset Computer Corp., Pocasset, MA) anchored to bricks at each site among my experimental chambers. I programmed HoboTemps to record water temperature each hour for the duration of the experiment. These devices were not available for the first two weeks of the experiment (late May 1997 to early June 1997), but based on the trends in Figure 2, I suspect that differences in water temperature between the two regions were even greater than the 7.6°C average difference recorded for the latter part of June. Water temperatures at the same sites in 1998 averaged 6.1°C colder at the northern site for all of June (Trussell 1998).

Statistical Analyses

To examine latitudinal clines in shell traits and body mass, it was necessary to adjust for the potential effects of size on each response variable. Therefore, data for snails from each population were expressed as a deviation from a regression of: (1) log shell mass (Y) versus log shell length (X); (2) log shell thickness (Y) versus log shell length (X); or (3) log body mass (Y) versus log shell length (X) across all 25 populations (see Smith and Palmer 1994). Means for each population generated by ANOVA on the residuals produced by these regressions were then regressed against latitude. Means are shell thickness, shell mass, and body mass expressed as a percent deviation from the appropriate regression. Shell breaking force data were analyzed with a two-way nested analysis of covariance (ANCOVA) that treated geographic region as a fixed effect, sites within region as a random nested effect, and shell length as the covariate.

Data from the reciprocal transplant experiment were analyzed with a two-factor nested ANCOVA. Both transplant location and source population were treated as fixed effects and replicates as a random nested effect. Covariates depended on the analysis in question. The effects of shell size on the analysis of shell thickness and body mass were adjusted by using final shell length as the covariate. Final body mass could not be used as a covariate for the analysis of final shell mass because of insufficient overlap in final body mass among experimental groups. Therefore, to examine variation in final shell mass in relation to final body mass, I used the approach of Palmer (1990) to calculate mean shell mass at a standard body mass of 50 mg. These data were then analyzed with ANOVA, treating transplant location and source population as fixed effects and replicates as a random nested effect. For analyses of shell mass, shell length and body growth (the difference between final and initial measurements), initial values for the trait in question were used as the covariate. Shell thickness growth was analyzed with a ANOVA (as described above) because initial shell thickness had no significant effect on shell thickness growth when analyzed with ANCOVA. Slopes in all ANCOVAs on the transplant experiment were homogeneous and thus pooled before final analysis. All analyses were conducted using JMP statistical software (vers. 3.2.1 for the Macintosh, SAS Institute, Cary, NC). Because sample populations and nested replicates were declared random effects in all models, JMP used the Satterthwaite approximation to calculate mean squares, *F*-ratios, and their respective degrees of freedom. A priori post-hoc comparisons on least-squares adjusted means were conducted using the linear contrast feature in JMP.

RESULTS

Geographic Differences in Shell Form, Shell Strength, and Body Mass

Regression analyses revealed that both shell mass (Fig. 3a) and shell thickness (Fig. 3b) decreased with increasing lat-

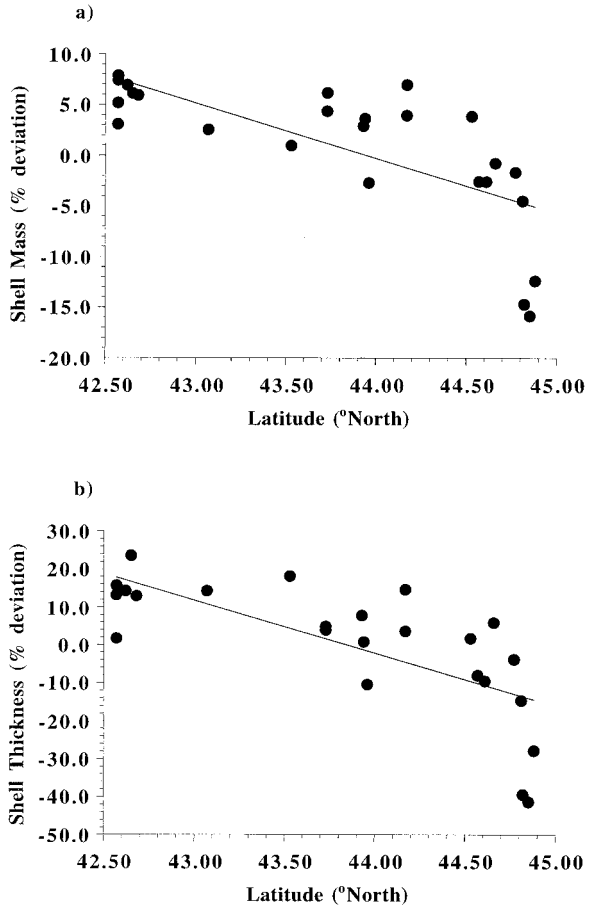

FIG. 3. (a) Shell mass (Y) and (b) shell thickness (Y) as a function of latitude (X) for 25 *Littorina obtusata* populations in the Gulf of Maine. Both shell mass ($Y = -5.410X + 237.771$, $R^2 = 0.49$, $P < 0.001$) and thickness ($Y = -13.89 + 608.87$, $R^2 = 0.51$, $P < 0.0001$) decrease with increasing latitude. Each point represents the mean percent deviation for each population from a common regression for each trait across all populations. $N = 50$ for each population. Error bars are smaller than symbols.

itude. Allometric analyses on shell thickness and shell mass revealed no clear relationship with latitude (Table 1, Appendix 1). These differences in shell form translated into geographic differences in shell breaking force; snails from the Cape Ann region of Massachusetts required significantly greater force to break than snails from the Quoddy region of Maine (ANCOVA: $F_{1,11} = 31.34$, $P < 0.001$; Fig. 4).

Regression analysis of body mass as a function of latitude revealed an opposite trend to that found for shell traits; body mass increased with increasing latitude (Fig. 5). Allometric analyses revealed no clear association with latitude (Table 1, Appendix 1). Costs to increased shell production in the form of reduced body mass were also suggested by regression analysis of body mass for all populations as a function of shell thickness and shell mass. For both comparisons, body mass decreased significantly with increasing shell mass (Fig. 6a) and increasing shell thickness (Fig. 6b).

Reciprocal Transplant Experiment

Final phenotypes: shell thickness, shell mass, and body size.—Geographic differences in shell mass and thickness persisted in control groups throughout the experiment; northern snails raised at their native site (NN) weighed less and were thinner than southern snails raised at their native site (SS; Tables 2a, 3a; Figs. 7a, c). However, transplanting between geographic locales had dramatic effects on the shell mass and thickness of each population. Northern snails transplanted to the southern site (NS) were significantly heavier and thicker than their controls (NN) raised at their native site. In contrast, southern snails transplanted to the northern site (SN) produced lighter and thinner shells than their controls (SS) raised at their native site. A significant population × location interaction (Tables 2a, 3a) indicated that populations responded differently to transplanting. NS snails showed a greater increase in shell mass (136%) and thickness (43%) over their controls than that shown for these traits by SN snails (44% for shell mass, 18% for thickness) relative to their controls. Thus, northern snails were more plastic in these traits than southern snails (Table 4).

Interestingly, NS snails and SN snails produced shells of nearly identical mass and thickness (Tables 2a, 3a; Figs. 7a, c). Despite large differences in shell mass and thickness of northern and southern snails at the beginning of the experiment, the differential thickening of NS snails and thinning of SN snails led to a convergence in the shell mass and thickness for these two groups.

Initial differences in body mass between geographic regions persisted in control groups with NN snails maintaining more soft tissue than SS snails (Table 5a; Fig. 8a). Transplanting snails between each location also significantly affected body mass, and northern snails were again more plastic (Table 4). Relative to their controls (NN), the body mass of NS snails was significantly lighter (25%) after the experiment, whereas the body mass of SN snails was significantly heavier (14%) than their controls (SS). Although plasticity in body mass occurred, in most cases it was not as dramatic as that for shell mass and thickness (Table 4), where percentage changes in these traits ranged from 44% to 136% and 18% to 43%, respectively. Like shell mass and shell thickness, there was a convergence in body mass for NS and SN snails.

Growth analyses: shell thickness, shell mass, shell length, and body mass.—Countergradient variation was found in shell mass growth, with no statistical difference between SS and NN snails (Table 2b; Fig. 7b). The significant population × location interaction indicated a difference in the shell mass growth rates of northern and southern snails (Table 4). Comparisons involving transplant groups revealed large differences. For shell mass, SS snails grew 33% more than SN snails, whereas NS snails grew 76% more than NN snails and 134% more than SN snails.

Countergradient variation in shell thickness growth also was found, even though SS snails grew 25% more than NN snails (Table 3b; Fig. 7d). However, the difference in growth between control groups was much smaller than that between transplant snails and their respective controls; SN snails grew 60% less than SS snails, whereas NS snails grew 88% more than NN snails. Direct comparison of transplant groups revealed that NS snails grew 140% more than SN snails. Smaller differences in growth among snails in their native habitats (i.e., NN vs. SS) relative to large differences produced by

TABLE 1. Summary of regression equations (all variables $\log_{10}$ transformed; slope and intercept [±SE]) for morphological traits of field transplants analyzed with ANCOVA. ANCOVA models were used only when the relevant covariate term was significant (see Materials and Methods). t_s, the value of a two-tailed *t*-test for allometry based on the observed slopes and that expected for isometry (1.0 or 3.0 depending on dimensionality). Degrees of freedom = $n - 2$. Because four tests were performed, a Bonferroni alpha of 0.0125 was used to evaluate significance. Also shown are the mean (± SE) and the minimum and maximum values of covariates (untransformed) for each experimental group. All linear measurements are in millimeters and all mass measurements are in grams.

Group	Regression	R^2	N	t_s	Covariate summary		
					Mean	Minimum	Maximum
Shell mass growth (Y) versus initial shell mass (X)							
NN	0.718 (± 0.154) + 0.056 (± 0.275)	0.27	57	−1.83	0.022 (± 0.001)	0.012	0.037
NS	0.563 (± 0.139) + 0.043 (± 0.231)	0.29	38	−3.14*	0.023 (± 0.001)	0.014	0.033
SN	0.618 (± 0.099) − 0.237 (± 0.142)	0.44	49	−3.86**	0.039 (± 0.001)	0.017	0.072
SS	0.630 (± 0.138) − 0.094 (± 0.195)	0.41	30	−2.68	0.040 (± 0.001)	0.018	0.061
Final shell thickness (Y) versus final shell length (X)							
NN	1.56 (± 0.20) − 1.56 (± 0.19)	0.51	57	2.80*	8.48 (± 0.07)	7.13	9.41
NS	0.95 (± 0.22) − 0.84 (± 0.20)	0.32	38	−0.23	8.31 (± 0.09)	6.90	9.40
SN	0.93 (± 0.11) − 0.82 (± 0.09)	0.62	49	−0.64	7.72 (± 0.08)	6.84	9.07
SS	0.86 (± 0.12) − 0.68 (± 0.10)	0.64	30	−1.16	7.60 (± 0.11)	6.46	8.62
Shell length growth (Y) versus initial shell length (X)							
NN	0.21 (± 0.31) + 0.30 (± 0.23)	−0.01	57	−2.55	5.64 (± 0.05)	4.96	6.24
NS	0.08 (± 0.39) + 0.36 (± 0.29)	−0.03	38	−2.36	5.67 (± 0.05)	4.97	6.25
SN	0.31 (± 0.22) + 0.13 (± 0.16)	0.02	49	−3.14*	5.44 (± 0.06)	4.34	6.18
SS	0.63 (± 0.43) − 0.14 (± 0.32)	0.04	30	−0.86	5.48 (± 0.06)	4.47	6.27
Final body mass (Y) versus final shell length (X)							
NN	2.566 (± 0.092) − 3.577 (± 0.085)	0.93	57	−4.72**	8.48 (± 0.07)	7.13	9.41
NS	3.147 (± 0.149) − 4.208 (± 0.137)	0.92	38	0.99	8.31 (± 0.09)	6.90	9.40
SN	2.675 (± 0.101) − 3.826 (± 0.090)	0.94	49	−3.22*	7.72 (± 0.08)	6.84	9.07
SS	2.900 (± 0.120) − 4.087 (± 0.105)	0.95	30	−0.83	7.60 (± 0.11)	6.46	8.62
Body mass growth (Y) versus initial body mass (X)							
NN	0.372 (± 0.186) − 0.808 (± 0.0301)	0.05	57	−3.38*	0.025 (± 0.004)	0.015	0.035
NS	0.472 (± 0.336) − 0.873 (± 0.543)	0.03	38	−1.57	0.025 (± 0.001)	0.015	0.033
SN	0.289 (± 0.073) − 1.105 (± 0.140)	0.23	49	−9.73**	0.013 (± 0.001)	0.005	0.022
SS	0.391 (± 0.164) − 1.027 (± 0.315)	0.14	30	−3.71**	0.013 (± 0.001)	0.005	0.019

* $P < 0.01$; ** $P < 0.001$.

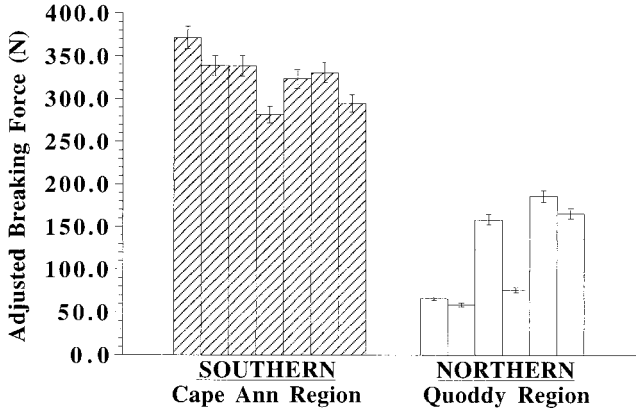

FIG. 4. Adjusted breaking force (± SE) at a shell length mean of 11.00 mm (± 1.72) for *Littorina obtusata* from seven southern and six northern populations in the Gulf of Maine. Snails from southern populations required significantly more force ($P < 0.001$) to break than snails from northern populations.

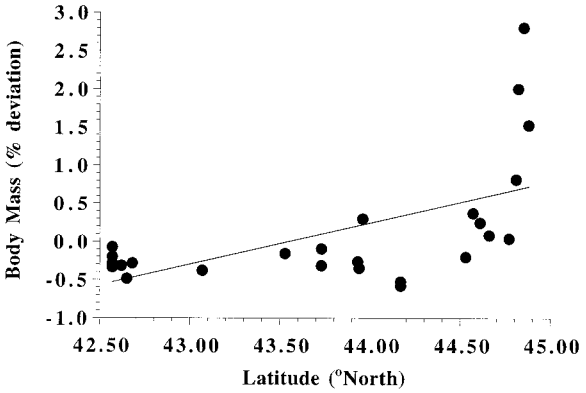

FIG. 5. Body mass (Y) as a function of latitude (X) for 25 *Littorina obtusata* populations in the Gulf of Maine. Body mass increases significantly with increasing latitude ($Y = 0.540X - 23.51$, $R^2 = 0.31$, $P < 0.005$). Each point represents the mean percent deviation for each population from a common regression across all populations. $N = 50$ for each population. Error bars are smaller than symbols.

transplanting (i.e., NS vs. SN) indicate a countergradient pattern in growth.

Variation in body growth followed a cogradient pattern (Table 5b; Fig. 8b) with large differences between snails raised in their native habitats; NN snails grew 84% more than SS snails. Although both northern and southern snails raised in their native habitats (NN and SS) exhibited significant differences in body growth relative to their respective transplant groups (NS and SN), growth rates of NS snails were identical to those of SS snails. Despite the 32% increase in growth of southern snails at the northern site and the 67% decrease in growth of northern snails at the southern site, the lack of a significant population × location interaction indicates that the effects of transplanting were statistically similar for northern and southern snails (Tables 4, 5b; Fig. 8b).

The cogradient variation found in shell length growth was opposite that for final shell mass and thickness (Table 3c; Fig. 9). There were significant differences in growth rates among snails in their native habitats (NN vs. SS) and between snails in their native habitats and their respective transplants. NN snails grew 10% more than NS snails, whereas SN snails grew 10% more than SS snails. The lack of a significant population × location interaction indicates that northern and southern snails responded similarly to transplanting.

DISCUSSION

Shell thickness, shell mass, and shell breaking force of New England populations of *L. obtusata* all decreased with increasing latitude (Figs. 3, 4). Phenotypic clines in molluscan shell form occur in numerous marine species on both microgeographic (Kitching et al. 1966; Palmer 1985; Trussell 1996, 1997) and macrogeographic scales (Nicol 1964, 1967; Phillips et al. 1973; Vermeij 1977, 1978, 1993; Palmer 1979). For example, *L. littorea* south of Cape Cod, Massachusetts, are thicker and stronger than conspecifics found north of Cape Cod (Dudley 1980), and shell strength is greater for tropical versus temperate species of Thaididae (Vermeij and Currey 1980). Although the presence of more taxonomically diverse and powerful shell-crushing predators may explain the oc-

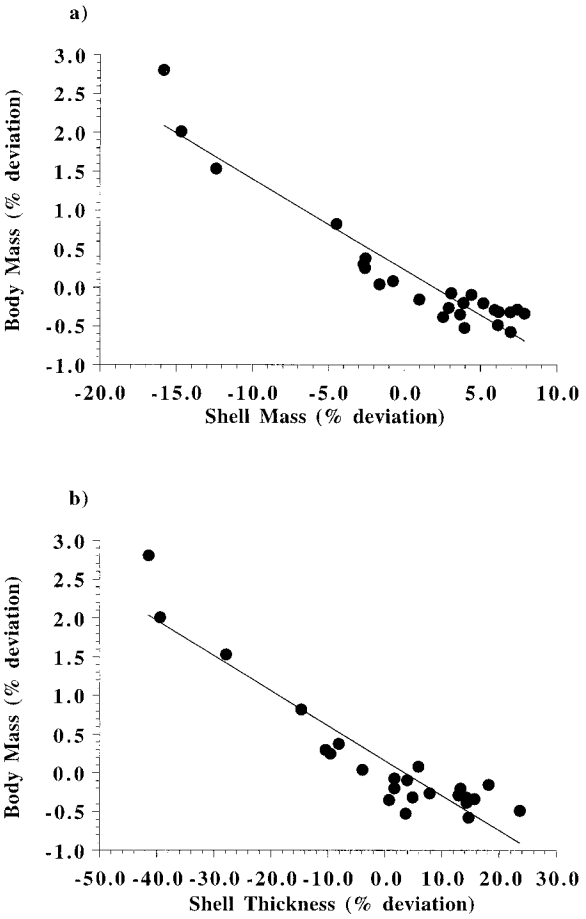

FIG. 6. Body mass (Y) as a function of (a) shell mass (X) and (b) shell thickness (X) for 25 *Littorina obtusata* populations in the Gulf of Maine. Body mass decreases with increasing shell mass ($Y = -0.117X + 0.231$, $R^2 = 0.89$, $P < 0.0001$) and thickness ($Y = 0.045X + 0.163$, $R^2 = 0.86$, $P < 0.0001$). Each point represents the mean percent deviation (± SE) for each population from a common regression for each trait across all populations. $N = 50$ for each population. Error bars are smaller than symbols.

TABLE 2. Results of (a) nested ANOVA on shell mass at a standard body mass of 50 mg (see Palmer 1990) and (b) nested ANCOVA on shell mass growth (Y) versus initial shell mass (X) for *Littorina obtusata* reciprocally transplanted between a northern and southern site. Inequality signs between group labels indicate the direction of significant differences in adjusted means (all $P \leq 0.01$).

(a) Source	df	*F*	*P*	Multiple comparison
Location (Loc)	1, 14	1296.83	< 0.0001	SS > SN = NS > NN
Population (Pop)	1, 14	1552.13	< 0.0001	
Pop × Loc	1, 14	161.48	< 0.0001	
Rep {Pop, Loc}	14, 156	0.89	0.57	
(b)				
Location (Loc)	1, 14	82.64	< 0.0001	NS > SS = NN > SN
Population (Pop)	1, 36	50.49	< 0.0001	
Pop × Loc	1, 14	8.75	< 0.05	
Rep {Pop, Loc}	14, 155	1.82	< 0.05	
Covariate	1, 155	88.02	< 0.0001	
Slope	1, 154	0.41	0.5245	

currence of more robust, defended prey species in the tropics (Vermeij 1978, 1987), environmentally induced variation in shell form in response to predator effluent (sensu Appleton and Palmer 1988; Palmer 1990; Trussell 1996; Trussell and Smith, in press) and water temperature (Lowenstam 1954 a,b; Graus 1974; Dudley 1980) also may be important.

Latitudinal Variation in Littorina obtusata Shell Form: The Role of Selection by Carcinus maenas

If selection by *C. maenas* produced the temporal shifts in *L. obtusata* shell form documented by Seeley (1986), then latitudinal differences in the intensity of selection by *C. maenas*, both presently and historically, also may yield latitudinal clines in shell form. Thus, the shells of southern snails weigh more, are thicker, and stronger because they have been exposed to natural selection by *C. maenas* for a longer time period (~100 years) than northern snails (~50 years). This argument assumes that, all else being equal, similar levels of genetic variation exist across latitudes. Consequently, genetic variation would not act to constrain shell form responses to selection in northern populations had they been subjected to *C. maenas* predation for the same amount of time. My data cannot rigorously address this hypothesis, but Boulding and Hay (1993) concluded that in *Littorina sitkana* sufficient additive genetic variance existed for shell form to respond to selection and suggested that their results support Seeley's (1986) interpretation of historical changes in *L. obtusata* shell form as evidence of microevolutionary change.

Latitudinal Variation in Littorina obtusata Shell Form: The Role of Phenotypic Plasticity

Although selection by *C. maenas* may partly explain latitudinal and historical variation in *L. obtusata* shell form, my reciprocal transplant experiment revealed substantial plasticity in shell form. Relative to their respective controls, shell

TABLE 3. Results of (a) nested ANCOVA on shell thickness (Y) versus shell length (X); (b) nested ANOVA on shell thickness growth; and (c) nested ANCOVA on shell length growth (Y) versus initial shell length (X) for *Littorina obtusata* reciprocally transplanted between a northern and southern site. Inequality signs between group labels indicate the direction of significant differences in adjusted means (all $P \leq 0.01$).

(a) Source	df	*F*	*P*	Multiple comparison
Location (Loc)	1, 14	277.75	< 0.0001	SS > SN = NS > NN
Population (Pop)	1, 23	287.46	< 0.0001	
Pop × Loc	1, 14	37.94	< 0.0001	
Rep {Pop, Loc}	14, 155	1.52	0.1102	
Covariate	1, 155	159.34	< 0.0001	
Slope	1, 154	2.90	0.0906	
(b)				
Location (Loc)	1, 14	133.91	< 0.0001	NS > SS > NN > SN
Population (Pop)	1, 14	45.38	< 0.0001	
Pop × Loc	1, 14	2.97	0.1072	
Rep {Pop, Loc}	14, 156	1.88	0.0318	
(c)				
Location (Loc)	1, 14	5.65	< 0.05	NN > NS > SN > SS
Population (Pop)	1, 15	36.77	< 0.0001	
Pop × Loc	1, 14	0.001	0.9785	
Rep {Pop, Loc}	14, 155	2.44	< 0.005	
Covariate	1, 155	4.24	< 0.05	
Slope	1, 154	0.26	0.6115	

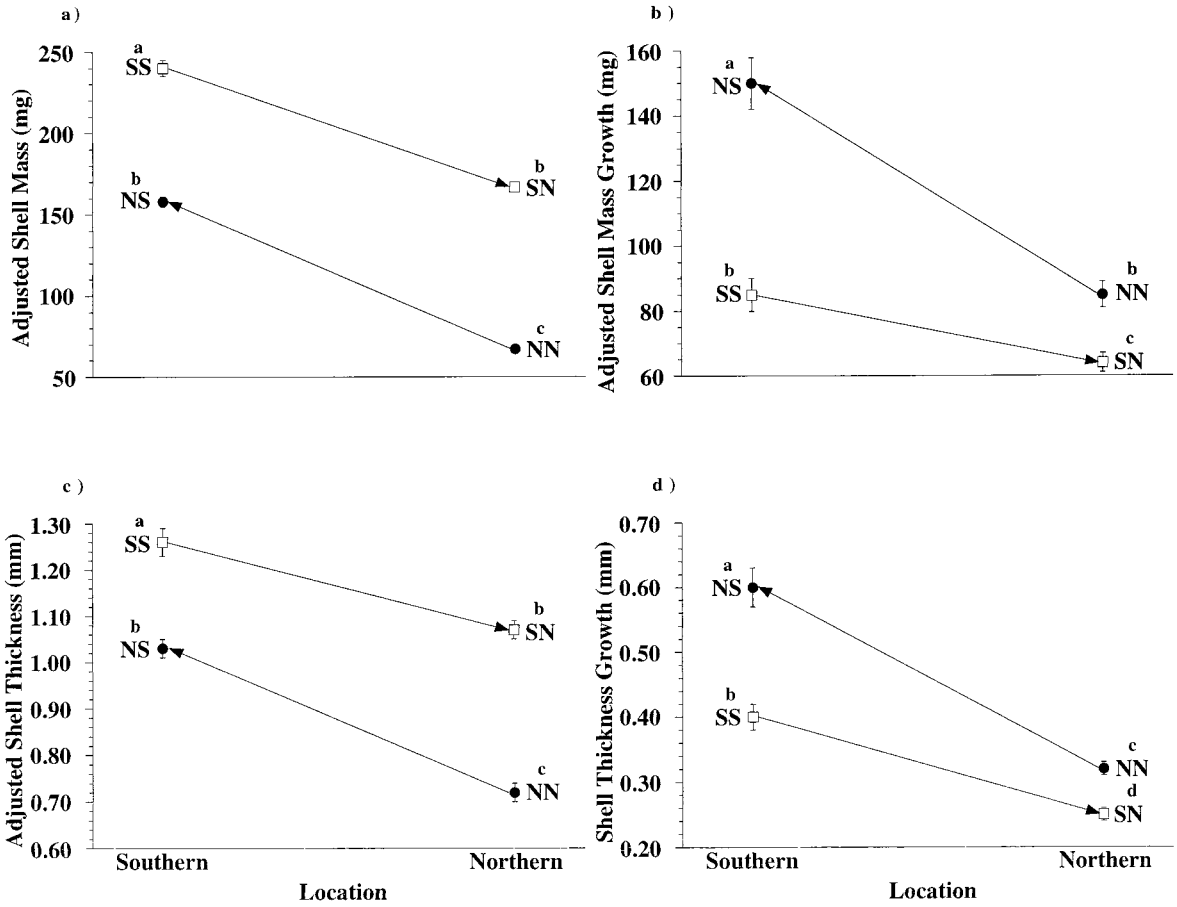

FIG. 7. (a) Shell mass (± SE) at a standard body mass of 50 mg; (b) adjusted shell mass growth (± SE) from ANCOVA at a covariate mean of 0.031 (± 0.001); (c) adjusted shell thickness (± SE) from ANCOVA at a covariate mean of 8.08 (± 0.05); and (d) shell thickness growth (± SE) for *Littorina obtusata* reciprocally transplanted between a northern and southern site in the Gulf of Maine for 90 days. NN, north to north; NS, north to south; SS, south to south; SN, south to north. Groups not sharing a common letter are significantly different (all $P < 0.01$). Error bars were sometimes smaller than data symbols. See Table 1 for allometric analyses and Tables 2 and 3 for results of ANCOVA and ANOVA.

mass and thickness decreased in southern snails after transplantation to the northern site (SN vs. SS), but increased for northern snails transplanted to the southern site (NS vs. NN). Moreover, plasticity in shell form was so pronounced that transplant groups (SN and NS) produced shells of nearly identical mass and thickness (Figs. 7a, c).

It is difficult to precisely determine the environmental stimuli inducing the plastic shifts in shell form because geographic differences in both present-day *C. maenas* abundance and water temperature could explain the observed responses either separately or synergistically. At the northern site, both reduced *C. maenas* abundance and colder water temperatures should promote the development of thinner shells, whereas increased *C. maenas* abundance and warmer water temperatures in the south should promote thicker shells.

Elsewhere (Trussell 1996; Trussell and Smith, in press), I have shown that *L. obtusata* from locally and broadly separated populations develop thicker, heavier shells in the presence of *C. maenas* than conspecifics raised in the absence of *C. maenas.* Clearly this response to *C. maenas* effluent is typical of New England *L. obtusata,* and similar occurrences in *N. lapillus* in the British Isles (Palmer 1990) and *Mytilus edulis* in the Gulf of Maine (Leonard et al. 1999), suggest that it is taxonomically and geographically widespread.

Although the development of heavier, thicker shells by NS snails and lighter, thinner shells by SN snails may reflect geographic differences in *C. maenas* effluent concentration, I suspect that geographic differences in water temperature are an important, if not dominating, factor (Lowenstam 1954 a,b; Graus 1974; Vermeij 1978, 1993). During the experiment water temperatures differed considerably between the two transplant sites, averaging 6.8°C colder at the northern site during the experiment. Moreover, the plastic shifts in shell form after 90 days (44–136% for shell mass and 18–43% for shell thickness; Table 4) were greater than those found in a laboratory study of *C. maenas* induced plasticity in snails from the two populations studied here (11–24% for shell mass, 13–17% for shell thickness after ~115 days; Trussell, in review). Laboratory responses to *C. maenas* effluent should be maximal because effluent concentrations in the laboratory were likely greater than those occurring under natural field conditions. However, such conditions can also lead to overstimulation, which may diminish differences among effluent treatments (Palmer 1990).

TABLE 4. Summary of percent differences in the means of morphological traits and growth of *Littorina obtusata* reciprocally transplanted between a northern and southern site. For each paired comparison, values were calculated as the percent increase required for the smaller mean of the two means to equal the larger of the two means. The direction of the difference (+ or −) is based on the first group relative to the second. For example, for shell mass SS snails were 158% heavier than NN snails, whereas NN snails were 136% lighter than NS snails. Also shown in parentheses are coefficients of variation for each pair of means. These values were calculated as 100 × SD/mean of the two means for each paired comparison. Values in bold refer to comparisons between control groups and comparisons between control groups and their respective transplant groups.

Comparison	Shell mass		Shell mass growth	
SS vs. NN	**+158%**	**(79%)**	**+0%**	**(0%)**
SS vs. SN	**+44%**	**(25%)**	**+33%**	**(20%)**
NN vs. NS	**−136%**	**(57%)**	**−76%**	**(39%)**
SS vs. NS	+52%	(29%)	−76%	(39%)
NN vs. SN	−149%	(61%)	+33%	(20%)
SN vs. NS	−6%	(4%)	−134%	(57%)

Comparison	Shell thickness		Thickness growth		Shell length growth	
SS vs. NN	**+75%**	**(38%)**	**+25%**	**(17%)**	**−35%**	**(21%)**
SS vs. SN	**+18%**	**(11%)**	**+60%**	**(33%)**	**−10%**	**(6%)**
NN vs. NS	**−43%**	**(25%)**	**−88%**	**(43%)**	**+10%**	**(7%)**
SS vs. NS	+22%	(14%)	−50%	(28%)	−23%	(15%)
NN vs. SN	−49%	(28%)	+28%	(17%)	+23%	(14%)
SN vs. NS	+4%	(3%)	−140%	(58%)	−12%	(8%)

Comparison	Body mass		Body mass growth	
SS vs. NN	**−57%**	**(31%)**	**−84%**	**(41%)**
SS vs. SN	**−14%**	**(11%)**	**−32%**	**(18%)**
NN vs. NS	**+25%**	**(16%)**	**+67%**	**(36%)**
SS vs. NS	−26%	(15%)	−11%	(5%)
NN vs. SN	+38%	(23%)	+40%	(23%)
SN vs. NS	−10%	(7%)	+19%	(13%)

Countergradient Variation in Shell Mass and Shell Thickness Growth

Because growth rate is often a function of temperature (Cossins and Bowler 1987; Atkinson 1994), intraspecific variation in growth rates should decrease with increasing altitude or latitude. However, several studies have found countergradient growth patterns in species having wide altitudinal (Levins 1968, 1969; Berven et al. 1979; Berven 1982a,b) or latitudinal (Dehnel 1955, 1956; Ament 1979; Parsons 1997) distributions; growth rates in colder environments typical of high altitudes and latitudes are often similar to, or may actually exceed, those of conspecifics in warmer environments (Conover and Schultz 1995). For some species this pattern may reflect metabolic compensation (sensu Levinton 1983), but this hypothesis does not explain the more rapid growth of some high latitude versus low latitude conspecifics when raised at warmer temperatures (see Conover and Present 1990; Conover and Schultz 1995).

Countergradient patterns in shell mass and thickness growth suggest that water temperature strongly influences variation in *L. obtusata* shell form. Northern and southern snails raised in their native locations showed similar rates of total shell deposition (shell mass) and thickness deposition (NN vs. SS; Figs. 7b, d). However, when raised in warmer southern waters, northern transplants showed the highest rates for both forms of growth, outgrowing southern snails in their native environment (NS vs. SS; Figs. 7b, d). In addition, relative to their controls, rates for both forms of deposition decreased for southern snails transplanted to the northern site (SN vs. SS; Figs. 7b, d).

In northern habitats, the critical issue may be shell maintenance rather than defense against crab predation because reduced water temperatures retard shell production by making calcification more difficult and increasing dissolution of deposited shell material. Selection should therefore favor increased deposition rates, especially if they are necessary to offset increased dissolution rates and a shorter growing season. Thus, the effects of genetic and environmental influences on shell growth in northern habitats act in opposition. Despite the negative impact of colder waters in northern habitats, genetic differences allow NN snails to maintain deposition rates similar to those of SS snails. Transplanting northern snails to warmer southern waters enhances this genetic potential with NS snails exhibiting dramatic increases in the rates of both forms of deposition.

In southern habitats, genetic and environmental influences on shell growth are expected to act in the same direction. In terms of plastic responses, both increased water temperature and crab abundance should induce increased deposition rates. Genetic controls for increased deposition rates also would be favored by selection imposed by *C. maenas.* In contrast, selection due to water temperature should be weak because the environment is more favorable (vs. northern habitats) to shell deposition and maintenance. Despite the presumed synergistic effects of selection and plasticity, SS snails still exhibited lower total and thickness deposition rates than NS snails, suggesting that they do not possess the genetic capacity for higher deposition rates. Given the adaptive value of better-defended shells in southern habitats, one would expect higher deposition rates to evolve. This inability may reflect the evo-

TABLE 5. Results of nested ANCOVA on (a) body mass (Y) versus shell length (X); and (b) body mass growth (Y) versus initial body mass (X) for *Littorina obtusata* reciprocally transplanted between a northern and southern site. Inequality signs between group labels indicate the direction of significant differences in adjusted means (all $P \leq 0.01$).

(a) Source	df	*F*	*P*	Multiple comparison
Location (Loc)	1, 14	396.95	< 0.0001	NN > NS > SN > SS
Population (Pop)	1, 26	780.94	< 0.0001	
Pop × Loc	1, 14	16.31	< 0.005	
Rep {Pop, Loc}	14, 155	1.17	0.3019	
Covariate	1, 155	2155.04	< 0.0001	
Slope	1, 154	0.39	0.5323	
(b)				
Location (Loc)	1, 14	39.81	< 0.0001	NN > SN > SS, NS
Population (Pop)	1, 38	6.59	< 0.05	
Pop × Loc	1, 14	3.72	0.0744	
Rep {Pop, Loc}	14, 155	2.58	< 0.005	
Covariate	1, 155	21.93	< 0.0001	
Slope	1, 154	0.25	0.6164	

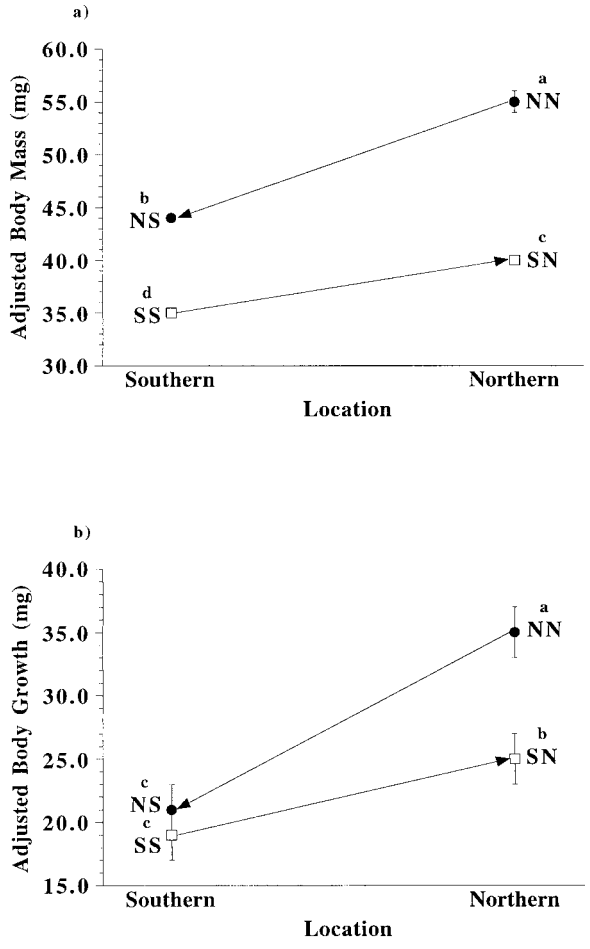

FIG. 8. (a) Adjusted body mass (± SE) at a covariate mean of 8.08 (± 0.05); and (b) adjusted body mass growth (± SE) at a covariate mean of 0.019 (± 0.001) from ANCOVA for *Littorina obtusata* reciprocally transplanted between a northern and southern site in the Gulf of Maine for 90 days. Symbols as in Figure 7. Error bars were sometimes smaller than data symbols. See Table 1 for allometric analyses and Table 5 for results of ANCOVA and ANOVA.

lution of an optimal deposition rate that is closely tied to life-history trade-offs in southern habitats (see Plasticity in Shell Form: Trade-offs). Alternatively, the growth of southern snails raised in their native habitat (SS) may simply reflect ontogenetic or architectural constraints arising from their different developmental history (compared to northern snails) before collection for the transplant experiment. In other words, more rapid shell deposition in SS snails may have been limited by the fact that they were already considerably thicker than northern snails at the beginning of the experiment.

Although countergradient growth in shell mass and thickness suggests that water temperature is an important factor driving shell form in *L. obtusata*, my data suggest that *C. maenas* effluents are also modulating shell form. Although SS and NN snails exhibited identical total deposition rates, SS snails allocated more of this material to the apertural lip by having thickness deposition rates that were 25% greater than those of NN snails (Table 4).

Parsons (1997) also detected countergradient variation in the shell growth of the latitudinally separated populations of

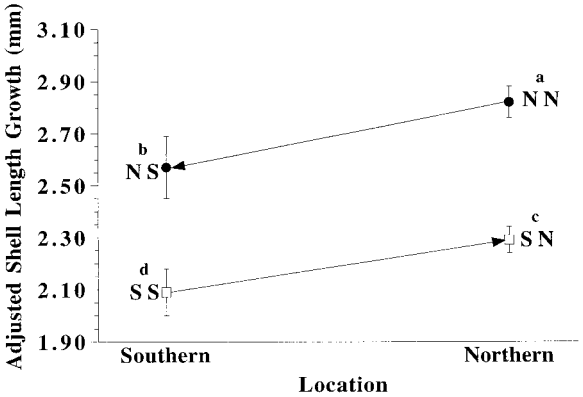

FIG. 9. Adjusted shell length growth (± SE) at a covariate mean of 5.56 (± 0.03) from ANCOVA for *Littorina obtusata* reciprocally transplanted between a northern and southern site in the Gulf of Maine for 90 days. Symbols as in Figure 7. See Table 1 for allometric analysis and Table 3 for results of ANCOVA and ANOVA.

the marine gastropod *Bebicium vittatum* and this pattern appears to be tied to latitudinal differences in water temperature. Like my results for shell mass and thickness, she found that countergradient variation in shell growth was accompanied by cogradient variation in shell morphology (shape). These results are consistent with the growing list of examples in which morphological traits across latitudinal gradients exhibit cogradient variation and life-history traits (such as growth) exhibit countergradient variation (see Conover and Schultz 1995). However, despite this consistency, the presence of cogradient variation in body growth and shell length growth in this study indicate that much remains to be learned about the factors shaping the presence and absence of latitudinal variation in form and growth.

Plasticity in Shell Form: Trade-Offs

Assessing the trade-offs associated with phenotypic plasticity is essential to fully understand its adaptive value in changing environments (Stearns 1989, 1992; Schlichting and Pigliucci 1998). Because gastropods must live within the shell they construct, they provide an ideal system for the study of potential trade-offs associated with induced changes in shell form. Several results suggest that there are costs associated with increased shell production. In field populations, latitudinal gradients in shell form were negatively correlated with gradients in body mass; shell mass and thickness decreased with increasing latitude while body mass increased (Figs. 3a–b, 5). Moreover, regression analyses across all populations of body mass against shell mass and thickness revealed strong negative correlations (Figs. 6a–b). In the reciprocal transplant experiment, both increases in shell mass and thickness and their respective growth rates were accompanied by large decreases in body mass and body growth in NS snails (Figs. 8a–b). In contrast, decreases in shell mass and thickness and their respective growth rates in SN snails were accompanied by increases in body mass and body growth (Figs. 8a–b).

Clearly there is a negative relationship between body mass and body growth and the production of more robust shell morphologies. Ultimately, reductions in either growth or body mass could have profound reproductive costs (Peters 1983). For example, in their study of plastic responses in *Physella virgata virgata*, Crowl and Covich (1990) found that snails raised in the presence of cues emanating from crayfish feeding on conspecifics were both older and larger at first reproduction than snails raised in the absence of these cues. These life-history shifts likely resulted because of the increased energetic investment required to produce, or the constraints associated with producing, a larger shell.

Palmer (1981) focused on two potential costs tied to the production of thicker shells. The first involved the energetic costs of shell deposition and maintenance. Although Palmer (1992) experimentally demonstrated an energetic cost to calcification, he concluded that in areas where surface seawater is saturated with $CaCO_3$, the cost is small relative to other metabolic functions and the production of the organic component of the shell. However, in colder waters, where $CaCO_3$ saturation is lower and dissolution rates are higher (Vermeij 1978, 1993), energetic costs may be significant. For example, rough calculations based on the relationship between the solubility product of $CaCO_3$ and water temperature (Sverdrup et al. 1942, p. 206) indicate that the $CaCO_3$ solubility product over the course of the reciprocal transplant was 9.5–13.9% greater at the northern study site.

Palmer (1981) concluded that geometric, rather than energetic, constraints (termed the ''skeleton-limitation'' hypothesis) best explained reduced body mass and growth in thick-shelled snails. Because tissue growth cannot proceed ahead of the protective shell, body mass and growth are limited by the linear rate of shell growth. Moreover, if more shell material is devoted to thickening the shell, less material will be available for advancing the shell margin because there is a maximum rate at which calcification can occur (Palmer 1992). Constraints on body mass are further compounded because snails with thick-walled shells have less internal habitable volume available for tissue growth than thin-walled morphs of similar size and shape. For example, Kemp and Bertness (1984) found that rapidly growing shells in the snail *Littorina littorea* were thinner and more globose and thus able to accommodate more tissue growth than slowly growing snails (see also Swan 1952; Goreau 1959).

Growth patterns detected in the reciprocal transplant were consistent with the skeleton-limitation hypothesis. Although NN and SS snails exhibited similar rates of total deposition, SS snails devoted more of this material to lip thickness, whereas NN snails channeled it into growth in terms of shell length (Fig. 9). Thus, the rapidly growing (in terms of shell length), thinner shells of NN snails have more internal volume available for body growth (Fig. 8a–b). This pattern is also evident when comparing snails raised in their native environments with their respective transplant groups (i.e., NN vs. NS and SS vs. SN). For example, slowly growing (in terms of shell length) NS snails versus rapidly growing NN snails (Fig. 9) exhibited increased total and thickness deposition rates but reduced body mass and reduced body growth (Figs. 7b, d, 8a–b).

Bergmann Variation in Body Mass: A Product of Constraints Imposed by Shell Form?

Both the causes and adaptive value of Bergmann clines (Ray 1960) in body size (increased body size with increasing latitude) are actively debated (McNab 1971; Geist 1987, 1988; Paterson 1988; Atkinson 1994; Atkinson and Sibly 1997; Mousseau 1997; Partridge and Coyne 1997; Van Voorhies 1997). Much of this debate has focused on the inadequacy of adaptive arguments based on surface-to-volume ratios (Geist 1987, 1988; Paterson 1988) and whether Bergmann clines reflect genetic or ecophenotypic phenomena. Evidence for ectotherms suggests that growth at reduced temperatures often leads to increased body size (Atkinson 1994) and that this phenomenon may reflect increases in cell size that are induced by reduced temperatures (Partridge et al. 1994; Partridge and French 1996; Van Voorhies 1996). However, several insect studies have shown geographic trends contrary to Bergmann's rule (Mousseau and Roff 1989; Mousseau 1997); insect size often decreases with mean annual temperature (Orr 1996) and high-altitude and -latitude

populations are often smaller than low-altitude and -latitude populations (Orr 1996; Mousseau 1997).

Although selection may contribute to the latitudinal increases in body mass I found for Gulf of Maine *L. obtusata*, ecophenotypic responses are also involved and these are likely due to geographic differences in water temperature. Snails from both populations raised in colder waters at the northern site (NN and SN) had more body mass and exhibited increased rates of body growth relative to individuals from both populations raised in warmer southern waters (NS and SS, respectively; Figs. 8a–b).

Although these results are consistent with the expected effects of reduced water temperature on growth (Atkinson 1994), they were inversely correlated with plastic changes in shell form. Those snails producing thicker, heavier shells tended to have reduced body mass and body growth (Figs. 7a, c, 8a–b). Given the constraints imposed by shell form on gastropod body mass and growth (Palmer 1981; Kemp and Bertness 1984), latitudinal variation in *L. obtusata* body mass may reflect latitudinal differences in shell form. Because latitudinal variation in shell form is likely influenced by water temperature (Graus 1974; Vermeij 1978), care must be exercised in identifying the reasons for latitudinal increases in the body size of shelled gastropods. Thus, Bergmann variation in *L. obtusata* body mass and in other gastropods may reflect their unique architectural constraints and the effects of reduced water temperature on shell form, rather than temperature dependent responses in cell number (James et al. 1995) and cell size (Van Voorhies 1996).

Geographic Variation in Plasticity

The presence of significant population × location interactions in most ANCOVA analyses indicate that northern and southern snails responded differently to the effects of transplanting. Because these interactions were accompanied by consistently greater changes in trait means for snails from the northern versus southern population, they suggest among-population genetic variation in plasticity (Table 4). Genetically based geographic variation in plasticity suggests that reaction norms for the traits measured have either: (1) evolved different trajectories in each region; or (2) that northern and southern snails occupy different regions of the same reaction norm.

By definition, adaptive phenotypic plasticity must have a genetic basis and there must be genetic variation in plasticity for it to evolve. There is debate, however, as to whether phenotypic plasticity is a target (Scheiner 1993) or by-product (Via 1993, 1994) of selection and a lack of consensus on the relative importance of each remains (Via et al. 1995; Schlichting and Pigliucci 1998). Assuming that selection by *C. maenas* is shaping reaction norms in *L. obtusata* shell form (i.e., plasticity is a target of selection), one would expect reduced plasticity to evolve in southern populations given their longer historical contact with *C. maenas* and the current predictability of the presence *C. maenas* in the southern Gulf of Maine. The evolution of reduced plasticity in southern populations may be especially rapid if there are genetically based limits and costs to plasticity (sensu DeWitt et al. 1998). Although snails from the southern population were often less plastic than northern snails, they still retain plasticity in shell form and body mass, suggesting that sufficient spatial and/or temporal variation in selection pressures remain to favor plastic responses.

In contrast, the increased plasticity exhibited by northern snails may reflect historically weak selection by *C. maenas* and the present unpredictability of *C. maenas* abundance. In addition, increased developmental sensitivity to differences in water temperature may have evolved in northern populations due to the comparably shorter growing season (Conover and Present 1990; Conover and Schultz 1995). If selection favors higher growth for snails at northern latitudes, then placing these snails in better growth conditions may also produce a greater plastic response, and these responses may override those tied to *C. maenas.* Future experiments that simultaneously address the role of plasticity induced by *C. maenas* effluent and water temperature may clarify the mechanisms underlying geographic variation in shell form and body mass as well as geographic variation in the magnitude of plastic responses.

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Corresponding Editor: T. Mousseau

Appendix 1

Location and regression equations (both variables log transformed; slope and intercept [± SE]) for field populations surveyed. For all regressions, shell length was used as the independent variable (mean [± SE] = 10.61 [0.05], minimum = 6.32, maximum = 14.88). t_s, the value of a two-tailed *t*-test for allometry based on the observed slopes and that expected for isometry (1.0 or 3.0 depending on dimensionality). Degrees of freedom for all *t*-tests were 48. Because 25 tests were performed, a Bonferroni alpha of 0.002 was used to evaluate significance. $N = 50$ for all populations. R^2, coefficient of determination.

Site	Lat., Long.	Shell thickness	R^2	t_s
Manchester Harbor, MA	(42°N 33.79′, 70°W 46.19′)	1.02 (± 0.06) − 0.86 (± 0.06)	0.86	0.33
Lobster Cove, MA	(42°N 33.80′, 70°W 46.20′)	0.88 (± 0.06) − 0.72 (± 0.06)	0.84	−2.00
Brandwood Cove, MA	(42°N 33.87′, 70°W 47.13′)	1.01 (± 0.07) − 0.89 (± 0.07)	0.83	0.14
Black Beach, MA	(42°N 34.74′, 70°W 43.82′)	0.97 (± 0.04) − 0.81 (± 0.04)	0.92	−0.75
Gloucester, MA	(42°N 35.41′, 70°W 39.83′)	0.94 (± 0.04) − 0.78 (± 0.05)	0.90	−1.50
Plum Cove, Rockport, MA	(42°N 37.32′, 70°W 37.43′)	0.98 (± 0.04) − 0.80 (± 0.04)	0.93	−0.50
Rockport Harbor, MA	(42°N 39.65′, 70°W 36.75′)	0.90 (± 0.07) − 0.74 (± 0.07)	0.76	−1.43
Newcastle, NH	(43°N 04.24′, 70°W 42.52′)	0.88 (± 0.05) − 0.72 (± 0.05)	0.86	−2.40
Prout's Neck, ME	(43°N 31.79′, 70°W 19.33′)	1.13 (± 0.05) − 0.97 (± 0.05)	0.91	2.60
Mackerel Cove, ME	(43°N 43.71′, 69°W 59.91′)	0.95 (± 0.06) − 0.82 (± 0.06)	0.84	−0.83
South Harpswell, ME	(43°N 43.96′, 70°W 01.53′)	0.80 (± 0.07) − 0.67 (± 0.07)	0.73	−2.86
Port Clyde, ME	(43°N 55.73′, 69°W 15.71′)	0.92 (± 0.05) − 0.78 (± 0.05)	0.87	−1.60

APPENDIX 1. Continued.

Site	Lat., Long.	Shell thickness	R^2	t_s
Mosquito Cove, ME	(43°N 56.48′, 69°W 13.80′)	0.92 (± 0.08) − 0.80 (± 0.08)	0.73	−1.00
Turkey Cove, ME	(43°N 57.49′, 69°W 16.06′)	0.84 (± 0.09) − 0.76 (± 0.09)	0.65	−1.78
Burnt Cove, ME	(44°N 09.96′, 68°W 41.77′)	0.93 (± 0.08) − 0.80 (± 0.08)	0.73	−0.88
Goose Cove, ME	(44°N 10.20′, 68°W 42.79′)	0.91 (± 0.05) − 0.75 (± 0.05)	0.87	−1.80
Jonesport, ME	(44°N 31.63′, 67°W 38.49′)	1.00 (± 0.05) − 0.88 (± 0.05)	0.89	0.00
Bar Island, ME	(44°N 34.03′, 67°W 34.13′)	0.95 (± 0.05) − 0.86 (± 0.06)	0.86	−1.00
Roque Bluffs, ME	(44°N 36.89′, 67°W 29.85′)	1.09 (± 0.07) − 1.00 (± 0.07)	0.82	1.29
Cutler, ME	(44°N 39.41′, 67°W 12.40′)	1.09 (± 0.06) − 0.96 (± 0.06)	0.86	1.50
Bailey's Mistake, ME	(44°N 46.03′, 67°W 03.79′)	0.98 (± 0.06) − 0.88 (± 0.06)	0.86	−0.33
Carrying Place Cove, ME	(44°N 48.57′, 66°W 58.74′)	0.89 (± 0.06) − 0.83 (± 0.06)	0.84	−1.83
Quoddy Head, ME	(44°N 49.21′, 66°W 57.97′)	1.26 (± 0.10) − 1.30 (± 0.10)	0.77	2.60
Johnson Bay, ME	(44°N 51.14′, 67°W 00.33′)	1.48 (± 0.11) − 1.55 (± 0.11)	0.79	4.36**
Major Island, ME	(44°N 52.59′, 67°W 00.79′)	0.93 (± 0.09) − 0.92 (± 0.09)	0.68	−0.78

Site	Shell mass	R^2	t_s
Manchester Harbor, MA	2.984 (± 0.059) − 3.430 (± 0.061)	0.98	−0.27
Lobster Cove, MA	2.857 (± 0.057) − 3.326 (± 0.060)	0.98	−0.30
Brandwood Cove, MA	2.981 (± 0.063) − 3.480 (± 0.064)	0.98	−2.02
Black Beach, MA	2.901 (± 0.049) − 3.349 (± 0.051)	0.99	−0.75
Gloucester, MA	2.943 (± 0.063) − 3.397 (± 0.064)	0.98	−0.90
Plum Cove, Rockport, MA	3.043 (± 0.059) − 3.506 (± 0.059)	0.98	0.73
Rockport Harbor, MA	3.037 (± 0.066) − 3.505 (± 0.067)	0.98	0.56
Newcastle, NH	2.937 (± 0.061) − 3.442 (± 0.061)	0.98	−1.03
Prout's Neck, ME	3.049 (± 0.055) − 3.575 (± 0.056)	0.98	0.89
Mackerel Cove, ME	3.159 (± 0.076) − 3.627 (± 0.078)	0.97	2.09
South Harpswell, ME	2.903 (± 0.059) − 3.385 (± 0.060)	0.98	−1.64
Port Clyde, ME	3.001 (± 0.057) − 3.503 (± 0.059)	0.98	0.02
Mosquito Cove, ME	2.960 (± 0.070) − 3.452 (± 0.072)	0.97	−0.57
Turkey Cove, ME	2.736 (± 0.121) − 3.309 (± 0.122)	0.91	−2.18
Burnt Cove, ME	3.030 (± 0.080) − 3.518 (± 0.079)	0.97	0.38
Goose Cove, ME	2.986 (± 0.049) − 3.441 (± 0.050)	0.99	−0.29
Jonesport, ME	3.111 (± 0.066) − 3.602 (± 0.067)	0.98	1.68
Bar Island, ME	3.060 (± 0.092) − 3.633 (± 0.093)	0.96	0.65
Roque Bluffs, ME	3.127 (± 0.103) − 3.701 (± 0.104)	0.95	1.23
Cutler, ME	3.331 (± 0.097) − 3.885 (± 0.100)	0.96	3.41*
Bailey's Mistake, ME	3.224 (± 0.079) − 3.782 (± 0.078)	0.97	2.84
Carrying Place Cove, ME	3.001 (± 0.078) − 3.602 (± 0.081)	0.97	0.01
Quoddy Head, ME	3.464 (± 0.102) − 4.268 (± 0.105)	0.96	4.55**
Johnson Bay, ME	3.606 (± 0.158) − 4.450 (± 0.165)	0.91	3.84**
Major Island, ME	2.862 (± 0.148) − 3.596 (± 0.156)	0.88	−0.93

Site	Body mass	R^2	t_s
Manchester Harbor, MA	2.899 (± 0.089) − 4.771 (± 0.092)	0.96	−1.13
Lobster Cove, MA	3.109 (± 0.094) − 4.976 (± 0.098)	0.96	1.16
Brandwood Cove, MA	2.790 (± 0.117) − 4.609 (± 0.120)	0.92	−1.79
Black Beach, MA	3.067 (± 0.101) − 4.922 (± 0.103)	0.95	0.66
Gloucester, MA	3.144 (± 0.102) − 5.012 (± 0.104)	0.95	1.41
Plum Cove, Rockport, MA	3.120 (± 0.071) − 5.024 (± 0.071)	0.98	1.69
Rockport Harbor, MA	2.893 (± 0.110) − 4.758 (± 0.113)	0.93	−0.97
Newcastle, NH	2.962 (± 0.079) − 4.864 (± 0.079)	0.97	−0.48
Prout's Neck, ME	2.920 (± 0.107) − 4.777 (± 0.109)	0.94	−0.75
Mackerel Cove, ME	3.039 (± 0.106) − 4.912 (± 0.109)	0.94	0.37
South Harpswell, ME	3.124 (± 0.098) − 4.948 (± 0.101)	0.95	1.27
Port Clyde, ME	3.264 (± 0.071) − 5.151 (± 0.073)	0.98	3.72**
Mosquito Cove, ME	3.152 (± 0.103) − 5.057 (± 0.106)	0.95	1.48
Turkey Cove, ME	2.990 (± 0.227) − 4.759 (± 0.229)	0.78	−0.04
Burnt Cove, ME	2.906 (± 0.150) − 4.830 (± 0.148)	0.88	−0.63
Goose Cove, ME	2.810 (± 0.070) − 4.749 (± 0.071)	0.97	−2.71
Jonesport, ME	3.149 (± 0.097) − 4.990 (± 0.098)	0.96	1.53
Bar Island, ME	3.367 (± 0.094) − 5.136 (± 0.096)	0.96	3.94**
Roque Bluffs, ME	3.111 (± 0.152) − 4.895 (± 0.153)	0.90	0.73
Cutler, ME	2.800 (± 0.093) − 4.610 (± 0.095)	0.95	−2.15
Bailey's Mistake, ME	3.162 (± 0.087) − 4.972 (± 0.087)	0.96	1.86
Carrying Place Cove, ME	2.930 (± 0.132) − 4.638 (± 0.087)	0.96	−0.53
Quoddy Head, ME	2.825 (± 0.131) − 4.493 (± 0.135)	0.90	−1.34
Johnson Bay, ME	2.562 (± 0.105) − 4.164 (± 0.109)	0.92	−4.17**
Major Island, ME	2.620 (± 0.115) − 4.321 (± 0.121)	0.91	−3.30*

* $P < 0.002$; ** $P < 0.001$.