Vol. 243: 123–131, 2002 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published November 13

Evidence of countergradient variation in the growth of an intertidal snail in response to water velocity

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ABSTRACT: Growth rates in rocky intertidal snails can vary considerably across wave exposure gradients, and have both plastic and genetic bases. However, little is known regarding whether genetic and environmental influences on variation in growth act in the same (cogradient) or in an opposing (countergradient) direction. Determining how genetic and environmental influences on growth covary with one another may improve our understanding of how habitat-specific variation in growth emerges. This study utilized laboratory flumes to examine the effects of high and low water velocities on the growth of intertidal snails *Littorina obtusata* from a wave-exposed and a sheltered shore. Both flow velocity and source population significantly influenced all measures of growth (shell length, shell thickness, shell mass and tissue mass). Snails from both populations exhibited greater growth in low versus high flow velocity. In addition, snails from the wave-exposed population grew more than snails from the sheltered population regardless of flow treatment. This result yielded a pattern of countergradient variation in growth and suggests that genetic differentiation between the 2 populations was responsible for the more rapid growth of wave-exposed snails. This greater growth potential of wave-exposed snails was particularly evident when they were raised in an environment conducive to rapid growth (i.e. low flow velocity). Most examples of countergradient variation in the growth of intertidal gastropods have involved temperature effects on latitudinally separated populations. This study provides evidence that countergradient variation in growth can occur on localized spatial scales in response to environmental cues other than temperature. On rocky intertidal shores, countergradient variation in growth may reflect selection for fast-growing genotypes to offset limitations on foraging time imposed by increased hydrodynamic stress on wave-exposed shores.

KEY WORDS: Cogradient variation · Countergradient variation · Foraging · Growth · Natural selection · *Littorina obtusata* · Plasticity · Predation · Wave energy

INTRODUCTION

Identifying the genetic and environmental basis of phenotypic variation has greatly improved our understanding of adaptation and the evolution of geographic variation. However, our knowledge of how genetic and environmental influences interact to produce patterns of phenotypic variation across environmental gradients remains limited. Recently, Conover & Schultz (1995) suggested that attention to the covariance relationship between genetic and environmental influences, and subsequent effects on phenotypic expression, may provide a better understanding of how patterns of geographic variation emerge (see also Trussell & Etter 2001). Reciprocal transplant or common garden experiments with individuals from populations occurring across the environmental gradient of interest (e.g. changing latitude) provide a powerful means of addressing this issue.

When there are both genetic and plastic influences on phenotypic expression in organisms distributed across an environmental gradient, 2 patterns are likely

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to emerge: cogradient and countergradient variation. Cogradient variation is more familiar to ecologists and arises when genetic and environmental influences have the same effects on phenotypic expression. Hence, cogradient variation often causes observable phenotypic variation across environmental gradients because environmental effects intensify the genetic influences on phenotypes (i.e. a positive covariance). Cogradient variation revealed by a reciprocal transplant experiment will show differentiation among phenotypes raised in their native environments. In addition, the phenotypes of transplanted individuals converge towards native phenotypes.

In contrast, countergradient variation typically causes little or no observable phenotypic variation across the environmental gradient because genetic and environmental effects on phenotypes oppose one another (i.e. a negative covariance). In addition, the phenotypes of transplanted organisms diverge from those of native phenotypes. Importantly, if countergradient patterns occur, then considerable genetic differentiation may exist among geographically separated populations despite the absence of phenotypic differentiation across the environmental gradient (Conover & Schultz 1995). Hence, the presence of countergradient variation questions the assumption that the absence of clinal variation simply reflects genetic similarities among populations.

Cogradient variation is typically limited to morphological traits whereas countergradient variation is often found in physiologically based or life history traits (Conover & Schultz 1995). Most examples of countergradient variation involve growth of organisms having wide altitudinal (Levins 1969, Berven et al. 1979, Berven 1982a,b) or latitudinal distributions (Dehnel 1955, 1956, Ament 1979, Conover & Present 1990, Conover & Schultz 1995, Parsons 1997, Trussell 2000, Craig & Foote 2001), where dramatic temperature gradients are present. That temperature differences affect growth is not surprising (Cossins & Bowler 1987); in general, reduced temperatures are expected to suppress growth (Clarke 1983, Atkinson 1994). However, these studies have yielded the intriguing result that organisms from higher altitudes or latitudes (colder temperatures) exhibit growth rates that are comparable to those of conspecifics at lower altitudes and latitudes (warmer temperatures).

Levinton (1983) proposed the latitudinal compensation hypothesis to explain the comparable growth rates between high- and low-latitude organisms. Within a species, individuals from high-latitude populations have evolved the ability to grow more rapidly than low-latitude individuals at reduced temperatures; whereas low-latitude individuals grow more rapidly than high-latitude individuals at increased temperatures. This model has empirical support (Levinton 1983, Levinton & Monahan 1983, Lonsdale & Levinton 1985), but it cannot explain the more rapid growth of high-latitude versus low-latitude individuals at temperatures typical of low-latitude environments (Conover & Present 1990, Conover & Schultz 1995). Consequently, we have yet to arrive at a satisfactory explanation of why countergradient variation exists in natural populations, but it may arise due to trade-offs across different environments or different selection pressures among environments acting on the same trait (Conover & Schultz 1995).

Intertidal snails exhibit remarkable morphological variation on both local and broad geographic scales (Kitching et al. 1966, Vermeij 1978, Vermeij & Currey 1980, Trussell et al. 1993, Trussell 1997a,b, Boulding 1990, Boulding & Van Alstyne 1993, Boulding et al. 1999). Considerable evidence indicates that these patterns can reflect both genetic differentiation (Kitching et al. 1966, Struthsaker 1968) and phenotypic plasticity (Appleton & Palmer 1988, Etter 1988, Trussell 1996, 1997a, 2000, Trussell & Nicklin 2002). Although not always recognized as such, there are examples of countergradient variation in the growth of latitudinally separated molluscan populations (Dehnel 1955, Ament 1979, Parsons 1997, Trussell 2000). As with other taxa, results of these studies appear to be tied to latitudinal differences in temperature. However, the presence of countergradient variation on more localized scales in response to environmental characteristics other than temperature has received little attention.

This study examined variation in the growth of the intertidal gastropod *Littorina obtusata* raised under different water velocities (hereafter, flow velocity) in the laboratory. I chose flow velocity because it is known to influence a number of snail life history traits (Brown & Quinn 1988, Etter 1989, 1996). I found that countergradient variation in growth occurs across high and low flow velocity environments, thus providing evidence that it can evolve on micro-geographic spatial scales in response to environmental factors other than temperature.

MATERIALS AND METHODS

Laboratory flume experiment with *Littorina obtusata*. To examine the effects of source population and flow velocity on growth variation in *Littorina obtusata*, juvenile snails from a wave-exposed (East Point, Nahant, Massachusetts, 42° 25.18′ N, 70° 54.14′ W) and a sheltered (Lobster Cove, Manchester, Massachusetts, 42° 33.79′ N, 70° 46.19′ W) shore were raised under high and low flow velocities in experimental flumes (see Fig. 1 in Trussell 1997a). In early June 1998, juve-

nile snails were collected from each shore and individually marked with indelible ink (Trussell 1997a). Initial shell length for each snail was measured as the maximum dimension of the shell parallel to the plane of the aperture (Trussell 1997a) and shell thickness was estimated as the mean of 2 measures made on the apertural lip of the shell (Trussell 1996). To determine initial shell mass and initial body mass (defined by wet tissue mass) of juvenile snails, I followed the nondestructive protocol of Palmer (1982). Using a Mettler (PG503) analytical balance, I measured the mass (±0.001 g) of each snail while submerged in seawater (submerged mass) and then, after 30 min of drying in air, the total mass (±0.001 g) of each snail in air. Actual shell mass (Y) can be accurately predicted from submerged mass (X) using regressions generated by a destructive sampling of snails from each population (East Point: $Y = 1.563X - 0.003$, $R^2 = 0.9992$; Lobster Cove: $Y = 1.582X + 0.0023$, $R^2 = 0.9999$). To calculate body mass, I subtracted the estimate of actual shell mass from the total mass of snails when weighed in air.

Twenty snails from each shore (Wave-exposed = E; Sheltered = S) were placed in 4 replicate high flow velocity (H) and 4 replicate low flow velocity (L) flumes constructed from acrylic tubes (0.81 m length × 58.5 mm in diameter). Flumes were connected to seawater reservoirs (400 l) with PVC pipe (58.5 mm in diameter) and water flow through flumes was gravity driven (Trussell 1997a). To generate different flow velocities, the height of reservoirs above flumes was different for each treatment: high flow velocity reservoirs were 1.45 m above their flumes and low flow velocity reservoirs were 0.35 m above their flumes. An electronic timer that was programmed to open and close motorized solenoid ball valves every 2 min regulated wave events through flumes. This was the minimum interval possible without overheating the valves. Hence, during wave periods, snails in flumes were exposed to a wave event every 2 min. When the motorized ball valves opened, a turbulent bore of water from each reservoir pulsed through their respective flumes for approximately 10 s. Overall, during the 90 d of the experiment, snails in high and low velocity flumes were exposed to approximately 32 000 wave events.

Feeding snails during the experiment required periods of reduced flow velocities, particularly in the high velocity treatment, because high flow prevented placement of food within the flumes. Hence, the experiment had feeding periods and wave periods that were alternated every 5 to 6 d. Of the 90 d of the experiment, approximately $^1/_2$ were devoted to feeding periods and $^1/_2$ to wave periods. During feeding periods for both flow velocity treatments, 200 g wet mass of the alga *Ascophyllum nodosum* were placed in each flume and water was allowed to trickle at low velocities (~1 to 5 cm s^{-1}) rather than pulse through the flumes as a turbulent bore.

Periods of high and low tide also were manipulated throughout the experiment by changing the fitting on the end of each flume. During high tide, an inverted PVC trap prevented flumes from draining. Removal of this trap during low tides allowed flumes to completely drain after each wave event. For logistical reasons, snails were exposed to only 1 low tide (6 to 8 h in duration) d^{-1}. Because water within flumes during high tide slowed down the velocity of pulsing waves, there were differences in flow velocity between high and low tides. In high-velocity flumes flow velocity was 1.9 m s^{-1} during low tide and 1.7 m s^{-1} during high tide. In low-velocity flumes, flow velocity was 30 cm s^{-1} during low tide and ~10 cm s^{-1} during high tide. Flow velocities were calculated as described in Trussell (1997a).

After 90 d, snails were removed from the flumes and re-measured for shell length, shell thickness, shell mass and tissue mass using the methods described above. Growth increments were calculated by subtracting initial from final values.

Statistical analyses. Data from the flume experiment were analyzed with a 3-factor, nested analysis of covariance (ANCOVA) using JMP software for the Macintosh (Version 3.2.1, SAS 1995). Flow velocity treatment (high vs low) and source populations (wave-exposed vs sheltered) were considered fixed effects. My response variable in all analyses was growth increment, and my covariates were the initial values of the particular trait being analyzed. Growth was determined for each snail within each flume. Because multiple snails within each flume are not independent, individual flumes were the experimental unit and were declared a random effect nested within flow treatment. This nested term was used by JMP to construct error mean squares, *F*-ratios and their respective degrees of freedom for main effects and their interaction. Slopes in all ANCOVA analyses were homogeneous (all $p > 0.25$).

RESULTS

For all measures of growth, *Littorina obtusata* exhibited countergradient variation across the 2 flow velocity treatments. Both wave-exposed and sheltered snails grew significantly more when raised under low flow velocity compared to those raised under high flow velocity (Table 1, Figs. 1 to 4). Source population also had a consistent significant effect on growth (Table 1). For shell length, shell thickness and shell mass growth, wave-exposed snails always grew more than sheltered

Table 1. Results of ANCOVA on 4 measures of growth for wave-exposed (East Point, Nahant, MA) and sheltered (Lobster Cove, Manchester, MA) shore *Littorina obtusata* raised under high and low water velocities in laboratory flumes. $^{*}p < 0.05$, $^{**}p < 0.01$, $^{***}p < 0.001$

Source	df	MS	*F*	Interpretation
Shell length growth (Fig. 1)				
Flow (F)	1,6	1.68	21.28**	Low > High
Population (P)	1,288	6.40	209.30***	Exposed > Sheltered
F × P	1,288	0.002	0.08	
Replicate{Flow}	6,288	0.08	2.72*	
Slope	1,288	0.01	0.24	
Shell thickness growth (Fig. 2)				
Flow (F)	1,6	21.13×10^{-2}	6.25*	Low > High
Population (P)	1,288	3.04×10^{-2}	20.26***	Exposed > Sheltered
F × P	1,288	8.00×10^{-4}	0.53	
Replicate{Flow}	6,288	3.64×10^{-3}	2.43*	
Slope	1,288	4.60×10^{-4}	0.31	
Shell mass growth (Fig. 3)				
Flow (F)	1,6	3.00×10^{-4}	12.04**	Low > High
Population (P)	1,288	9.60×10^{-4}	68.90***	Exposed > Sheltered
F × P	1,288	1.83×10^{-6}	0.13	
Replicate{Flow}	6,288	4.00×10^{-5}	3.00**	
Slope	1,288	3.43×10^{-6}	0.25	
Body mass growth (Fig. 4)				
Flow (F)	1,6	2.90×10^{-4}	8.92*	Low > High
Population (P)	1,288	5.00×10^{-5}	5.79*	Exposed > Sheltered
F × P	1,288	2.00×10^{-5}	1.83	
Replicate{Flow}	6,288	4.00×10^{-5}	3.93***	
Slope	1,288	1.00×10^{-5}	1.26	

snails, regardless of the flow velocity treatment (Figs. 1 to 3). However, a slightly different pattern emerged for tissue growth (Fig. 4) because the tissue growth of wave-exposed snails was not uniformly greater across the 2 flow treatments. For example, although wave-exposed snails grew more than sheltered snails within each flow treatment, the tissue growth of sheltered snails raised in low flow velocity was greater than that of wave-exposed snails raised in high flow velocity.

For all growth analyses, I did not detect a significant population × flow treatment. Hence, changes in snail growth in response to both flow treatments were similar for snails from both populations.

DISCUSSION

Intraspecific variation in growth can have profound consequences to other life history traits such as the age and size of maturity (Stearns & Koella 1986, Stearns 1992). Clearly variation in growth can have both genetic and environmental components, but knowledge of whether these components act in concert with or in opposition to one another across different environments may improve our understanding of how intraspecific differences in life histories evolve. For rocky intertidal snails, spatial variation in wave energies is thought to be particularly important in driving intraspecific variation in both morphological (Kitching et al. 1966, Etter 1988, Trussell et al. 1993,

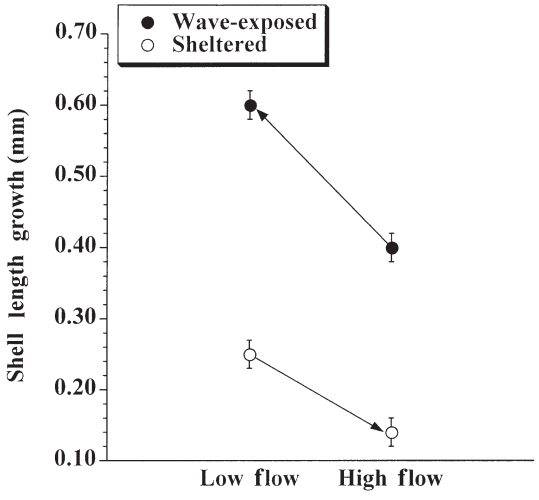

Fig. 1. *Littorina obtusata*. Least-squares adjusted means (±SE) from ANCOVA for shell length growth of wave-exposed (E) and sheltered (S) individuals raised under high- and low-flow velocities in experimental flumes. See Table 1 for results of ANCOVA

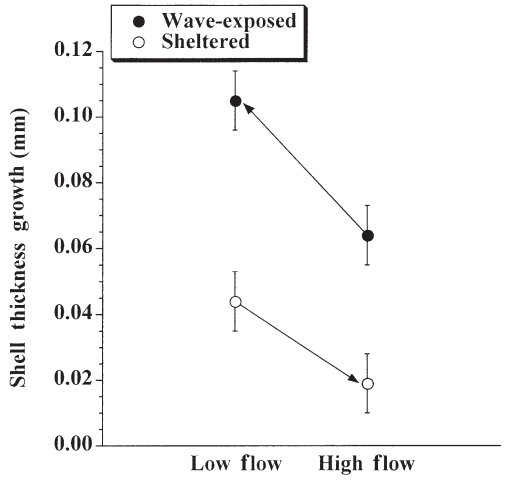

Fig. 2. *Littorina obtusata*. Least-squares adjusted means (±SE) from ANCOVA for shell thickness growth of wave-exposed (E) and sheltered (S) individuals raised under high- and low-flow velocities in experimental flumes. See Table 1 for results of ANCOVA

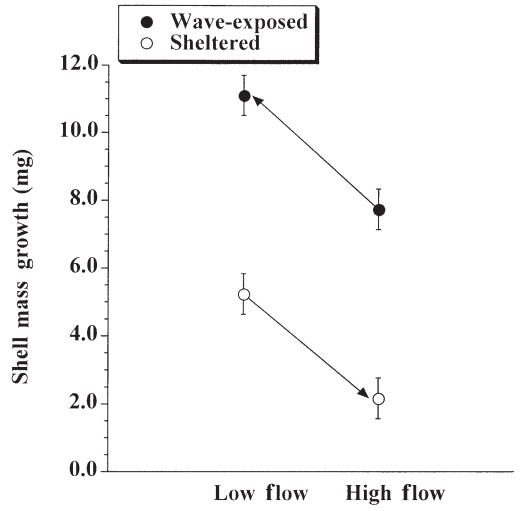

Fig. 3. *Littorina obtusata.* Least-squares adjusted means (±SE) from ANCOVA for shell mass growth of wave-exposed (E) and sheltered (S) individuals raised under high- and low-flow velocities in experimental flumes. See Table 1 for results of ANCOVA

Trussell 1996, 1997a,b) and life history traits such as growth (Janson 1982, Brown & Quinn 1988, Etter 1996), fecundity, and size at maturity (Etter 1989). In addition, morphological and life history variation across wave energy gradients appears to have both genetic and plastic bases (Janson 1982, Brown & Quinn 1988, Etter 1988, 1996, Trussell 1996, 1997a). However, there has been little, if any, research explicitly addressing how both factors interact to produce these patterns. This issue is important because the consequences of environmentally induced (plastic) variation in growth to other life history traits may be partly determined by whether plasticity in growth is reinforced (cogradient) or opposed (countergradient) by the prevailing selection regime (Fig. 5).

The influence of hydrodynamic forces accompanying breaking waves on intertidal snail morphology and life history is very likely mediated by differences in the risk of dislodgment on wave-exposed versus sheltered shores (Denny et al. 1985, Etter 1988, Trussell 1997a,b, Trussell et al. 1993). This risk should be greater on wave-exposed shores because the water velocities and accelerations accompanying breaking waves are much

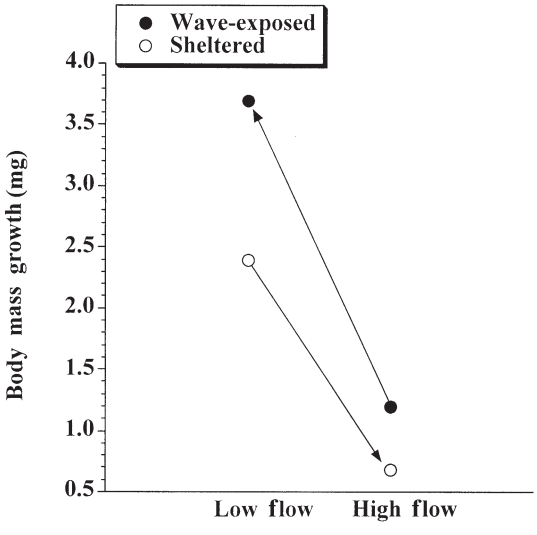

Fig. 4. *Littorina obtusata.* Least-squares adjusted means (±SE) from ANCOVA for tissue mass growth of wave-exposed (E) and sheltered (S) individuals raised under high- and low-flow velocities in experimental flumes. See Table 1 for results of ANCOVA. Error bars are smaller than symbols

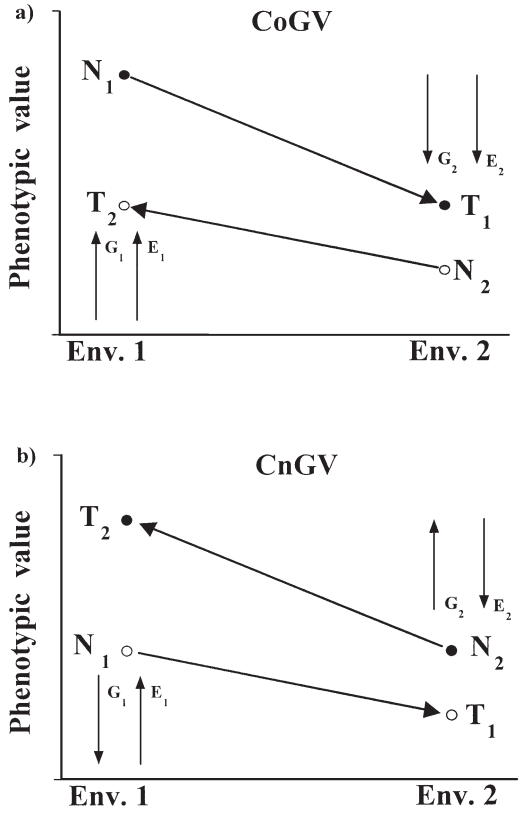

Fig. 5. *Littorina obtusata.* (a) Cogradient phenotypic variation. Note the large difference in phenotypic values of phenotypes in their native environments (N_1 and N_2) and the shift of their respective transplants (T_1 and T_2) towards the phenotypic values of native phenotypes. (b) Countergradient phenotypic variation. Note the similarity in phenotypic values of phenotypes in their native environments (N_1 and N_2) and the divergences 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 'Introduction' for further explanation (adapted from Conover & Schultz 1995)

greater compared to those typical of sheltered shores (Denny 1985, 1988, Denny et al. 1985, Denny & Gaines 1990). Reducing this risk is thus paramount on wave-exposed shores because dislodgment can reduce foraging time (Denny et al. 1985, Judge 1988), increase energy expenditures, or sweep snails into atypical habitats (e.g. the subtidal zone) with more diverse and efficient predator assemblages (Sebens 1981, Etter 1988). Consequently, snails on wave-exposed shores must restrict their foraging activity to periods when it is mechanically safe to do so, which results in reduced foraging time relative to conspecifics inhabiting sheltered shores. That snails remain stationary during periods of increased hydrodynamic stress is very likely tied to the reduction in tenacity that occurs when crawling (Miller 1974).

I found a countergradient pattern in all 4 measures of *Littorina obtusata* growth between the high- and low-flow velocity treatments (Figs. 1 to 4). Regardless of source population, snails always grew more in the low-flow velocity treatment compared to the high-flow velocity treatment, suggesting that low-flow environments were conducive to more rapid growth. The countergradient pattern in snail growth emerged because wave-exposed snails consistently grew more than sheltered snails, even in the low-flow velocity treatment. This result suggests that genetic variation for more rapid growth in wave-exposed snails has been favored by natural selection compared to that favored for sheltered snails. This genetic capacity for increased growth in wave-exposed snails may have evolved to offset environmental constraints on feeding time imposed by increased hyrodynamic stress on wave-exposed shores. By raising wave-exposed snails in an environment more favorable to growth (i.e. reduced flow velocities and accelerations) this genetic potential can be fully expressed; for all measures of growth, wave-exposed snails raised in low-flow velocities grew the most of the 4 experimental groups.

Knowing how snails allocate deposited shell material is essential to a better understanding of how patterns in body growth may arise. Because snails must live within the shell they construct, shell size and thickness can constraint the amount of body mass capable of fitting inside the shell. Such architectural constraints are thought to be the primary reason for the reductions in body mass that accompany predator-induced increases in snail shell thickness (Appleton & Palmer 1988, Palmer 1990, Trussell 1996, Trussell & Smith 2000, Trussell & Nicklin 2002). These architectural constraints arise because of a maximum limit to the rate of calcification (Palmer 1981, 1992); snails devoting more shell material to shell thickness do so at the expense of linear translation of the shell. In other words, thick-shelled snails generally grow less in terms of shell length than thin-shelled snails of similar shape (Kemp & Bertness 1984, Trussell & Nicklin 2002). Moreover, thick-shelled snails have less internal volume available for body growth than thin-shelled snails of similar size and shape.

Given these constraints, it may seem surprising that wave-exposed snails, compared to sheltered snails, consistently exhibited higher body mass growth despite their greater growth rate of shell thickness growth. However, one explanation for this result is that because shell thickness is positively correlated with shell length, the greater thickness growth of wave-exposed snails may simply be a byproduct of their equally rapid growth in terms of shell length. Indeed, on average wave-exposed snails compared to sheltered snails grew 166% more in terms of shell thickness, 166% more in terms of shell length and 154% more in terms of shell mass. The close correspondence between these values supports the argument that the greater shell thickness and shell mass growth of wave-exposed snails was a correlated response with shell length growth. These results also suggest that wave-exposed snails were able to achieve more body growth despite their greater shell thickness growth because of the increases in internal shell volume afforded by increased shell length growth.

The faster growth in the shell mass of wave-exposed snails suggests that these snails are either more efficient at calcification than sheltered snails or that sheltered snails were not depositing shell material at a maximal rate. This result is counterintuitive because one would expect more intense crab predation, which is typical of sheltered shores (Boulding 1990, Boulding & Van Alstyne 1993, Boulding et al. 1999), to favor greater calcification rates in sheltered snails. Presumably, selection would favor more rapid calcification rates in sheltered snails, allowing them to develop thicker shells quickly and reduce their risk of crab predation. However, I suspect that the lower overall shell deposition of sheltered snails may partly reflect the fact that they were significantly thicker than wave-exposed snails at both the beginning (ANCOVA: $F_{1,6} = 4318.06$; $p < 0.0001$) and end of the experiment (ANCOVA: $F_{1,6} = 3704.52$; $p < 0.0001$). These population-specific differences in shell thickness may have constrained plasticity in the thickness growth of sheltered snails. Alternatively, sheltered snails may have been devoting more effort to body mass to compensate for the constraints imposed by their thicker shells. This scenario may be especially likely because there were no predator cues in the flumes that would have induced the continued production of thicker shells (Trussell 1996, 2000, Trussell & Smith 2000, Trussell & Nicklin 2002).

I should note that the pattern of countergradient variation found here differs from typical examples (Conover & Schultz 1995), because there were differences in growth between wave-exposed and sheltered snails raised in flow treatments which were meant to simulate the flow environments they may experience in the field (EH vs SL, respectively). Typically, with countergradient variation, one would expect to observe no differences in the growth between wave-exposed snails raised in high water velocities (EH) and sheltered snails raised in low water velocities (SL). However, although differences in water velocities within the experimental flumes induced plastic differences in growth, 'high' water velocities in the lab may have been perceived as low by wave-exposed snails compared to what they typically experience in the field (5 to 10 m s^{-1} or greater; Denny et al. 1985). Hence, the genetic capacity of wave-exposed snails for increased growth also may have been emerging in the high water velocity treatment and caused the observed differences in growth between EH and SL snails. Nevertheless, I observed countergradient variation in this study because the divergence in growth rate of snails raised in water velocities different than they typically experience was greater (EL and SH) compared to the growth rate of snails raised in their 'native' environments (EH and SL).

Although not recognized as such, a reciprocal transplant experiment with 3 gastropod species between a wave-exposed and a sheltered shore in the California Pacific also yielded evidence of countergradient variation in growth (see Brown & Quinn 1988). In this study, differences in growth between conspecifics raised on their native shores were considerably less than those revealed after transplanting. This pattern was most striking for *Nucella emarginata*, but qualitatively similar results also were found for *Collisella digitalis* and *C. scabra*. Like several other studies (Menge 1978, Roberts & Hughes 1980, Hughes & Drewett 1985, Burrows & Hughes 1989), Brown & Quinn (1988) argued that reduced growth on wave-exposed shores may reflect restrictions on feeding time imposed by breaking waves. The argument that reductions in foraging time translate into reduced growth assumes that energy expenditures, assimilation efficiencies, and food quality and availability are similar among wave-exposed and sheltered environments. Although more work in this area is needed, Etter (1996) found that experimental inhibition of feeding in *Nucella lapillus* resulted in reduced growth rates, thus supporting the hypothesis that reduced growth rates on wave-exposed shores may partly reflect restricted feeding time imposed by increased hydrodynamic stress.

Because experimental feeding periods in both flow velocity treatments provided similar amounts of food, for the same amount of time, and relatively similar flow velocities, it would appear that actual feeding times were not different between the 2 flow velocity treatments. However, during the experiment, flumes in both treatments were quickly colonized by microflora (algae and diatoms) creating a natural food supply in addition to that provided experimentally. During wave periods, when *Ascophyllum nodosum* was not present in the flumes, there were obvious differences in snail behavior between flow velocity treatments. Snails in high flow velocities remained stationary and firmly attached to the flume walls. In contrast, snails in low flow velocities were able to move about the flumes, their rasping radula visibly indicating that they were feeding on microalgae and diatoms. Consequently, snails in low flow velocities had more actual feeding time than snails in high flow velocities. These observations are consistent with the hypothesis that differences in growth between the 2 flow velocity treatments arose because of flow-mediated differences in feeding time.

Although most examples of countergradient variation in marine gastropods have involved the effects of temperature on growth in latitudinally separated populations, my results suggest that this pattern can occur on localized spatial scales and in response to other environmental factors. However, the contrasting results of this study and others documenting both countergradient (Brown & Quinn 1988) and cogradient (Janson 1982, Etter 1996) variation in growth preclude generalities regarding how genetic and environmental influences may shape variation in growth across different flow environments. Clearly attention to factors other than those that physically characterize the intertidal environment, such as behavior, may improve our understanding of the processes shaping habitat-specific differences in the growth of gastropods on intertidal shores.

Acknowledgements. I thank M. Bertness, E. Duffy, R. Etter, J. Milliman and M. Patterson for providing many helpful comments on previous drafts and J. Ayers at the Marine Science Center in Nahant for providing laboratory space. Special thanks to Ken Heck for his patience during revision of the manuscript. This work was supported by a National Science Foundation Dissertation Improvement Grant (Division of Environmental Biology), Sigma Xi, the Lerner-Gray Fund of the American Museum of Natural History, the Hawaiian Malacological Society, and Minor Research Grants from the Virginia Institute of Marine Science. Support during writing was provided by a Mellon Foundation Postdoctoral Fellowship and a grant from the National Science Foundation (Integrative Biology and Neurophysiology).

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Editorial responsibility: Kenneth Heck (Contributing Editor), Dauphin Island, Alabama, USA

Submitted: October 23, 2000; Accepted: July 18, 2002
Proofs received from author(s): October 16, 2002