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ASYMMETRICAL DEVELOPMENTAL PLASTICITY IN AN INTERTIDAL SNAIL

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Abstract.—Field and laboratory experiments were used to investigate the variation and phenotypic plasticity in the adhesive abilities of the intertidal snail *Nucella lapillus* between high- and low-wave-energy environments. Whelks from an exposed coast produced a larger pedal surface area and were more resistant to dislodgement than were similar-sized individuals from a protected shore. Tenacity (g/cm^2) was similar between individuals from exposed and protected shores, indicating that variation in resisting dislodgement was solely a function of pedal surface area.

Whelks from exposed and protected shores did not differ in pedal surface area as they emerged from egg capsules or when reared in the laboratory under uniform conditions, suggesting that variation between populations does not represent genetic differentiation. Individuals from high- and low-wave-energy environments reared intertidally produced a larger pedal surface area than did those reared in the laboratory. The extent to which pedal surface area increased corresponded to the intensity of wave action. These findings suggest that pedal surface area is a highly plastic character modulated or induced by the water turbulence accompanying breaking waves. A reciprocal-transplant experiment confirmed this notion but revealed an asymmetry in the plasticity. Snails from the protected site transplanted to an exposed shore formed a much larger pedal surface area than did controls reared on the protected shore. In contrast, whelks from a wave-swept shore transplanted to a protected shore differed little from their controls reared on the exposed shore. The asymmetric response parallels a possible asymmetry in the risks of acclimating to a temporally unpredictable environmental cue, such as wave action.

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A fundamental question facing ecological and evolutionary biologists is how organisms cope with spatially and temporally varying environments. Organisms mitigate the effects of environmental variability through a variety of physiological, morphological, and/or behavioral modifications. Natural selection has favored four basic responses for adjusting phenotypes to environmental heterogeneity (Mayr, 1963; Levins, 1968): individuals may 1) form a constant phenotype independent of the environment (homeostasis or canalization), 2) produce a flexible phenotype modulated by selected features of the environment (plasticity), 3) have genetically based, environmentally induced developmental switches (developmental conversion), or 4) differ genetically with respect to a particular trait (genetic polymorphism). The specific strategy favored by natural selection depends on the character involved and the nature and scale of environmental heterogeneity (Levins, 1968; Roughgarden, 1979).

The boreal intertidal zone represents an extremely heterogeneous environment, exhibiting considerable spatial and temporal variability (reviewed in Lewis [1964] and Newell [1979]). Variation in wave action among shores and through time is one of the most obvious aspects of environmental heterogeneity in the intertidal zone and has been shown to exert a profound influence on the biotic and abiotic conditions under which organisms must live (Dayton, 1971; Menge, 1974, 1978*a,* 1978*b*; Lubchenco and Menge, 1978; Ebert, 1982; Palumbi, 1984*a,* 1984*b,* 1986; Denny et al., 1985; McQuaid and Branch, 1985; Wethey, 1985; Leigh et al., 1987). Breaking waves can impart tremendous forces on intertidal organisms. Waves range in force from slight trickles to raging torrents in which water velocities reach 20 m/sec with accelerations of 500 m/sec^2 (Denny, 1984). Drag components of such velocities would be tantamount to wind velocities in excess of 460 m/sec (1,000 mph) in an analogous terrestrial situation (Vogel, 1981). It is not surprising, therefore, that many intertidal organisms exhibit morphological variation that parallels gradients in wave exposure. For instance, several prosobranch gastropods differ in shape or sculpture among shores differentially exposed to wave action (Struhsaker, 1968; Emson and Faller-Fritsch, 1976; Raffaelli and Hughes, 1978; Hart and Begon, 1982; Crothers, 1983; Janson, 1983; Atkinson and Newbury, 1984), limpets from exposed habitats incorporate drag reducing features into their shell structure (Branch and Marsh, 1978; Dudley, 1985), sponges produce stiffer tissues with smaller conducting elements under high wave energies relative to those produced under low wave energies (Palumbi, 1984*b,* 1986), and shallow-water corals often have branching morphologies that depend on exposure regime (Chamberlin and Graus, 1975; Graus et al., 1977). However, the question of which of the above four strategies is best suited for adjusting phenotypes to such a temporally and spatially varying environment is poorly understood.

The intention of the work presented here was to explore how the intertidal snail *Nucella lapillus* L. alters its adhesive ability between shores of high and low wave energy. To persist in the intertidal zone, organisms must circumvent the tendencies of wave action to dislodge them by seeking sheltered microhabitats, reducing drag and/or increasing adhesion. Intertidal snails adhere to the substrate with a single muscular foot that functions simultaneously in adhesion and locomotion. Previous work has indicated that the pedal surface area (PSA) of several intertidal prosobranchs (Miller, 1974), including *N. lapillus* (Kitching et al., 1966), varies among shores differentially exposed to wave action. However, whether this variation represents genetic differentiation or phenotypic plasticity has not been addressed. In this study, the variation in pedal surface area, dislodgement force, and tenacity between whelks from exposed and protected shores was quantified. Field and laboratory experiments were also conducted to separate the genetic and environmental components of variation. Pedal surface area and the ability of snails to resist dislodgement varied with wave exposure and appeared to be plastic. However, the plasticity in high- and low-wave-energy environments was not symmetrical.

Natural History

Nucella lapillus is a predatory gastropod (Prosobranchia: Neogastropoda) with an extensive geographic distribution that encompasses both sides of the North Atlantic. In the eastern North Atlantic it extends from Cape St. Vincent, Portugal (37°N) northward to Novaya Zemlya, U.S.S.R. (73°N), while in the western North Atlantic it is found from Long Island Sound, NY, U.S.A. (41°N) to Notre Dame Bay, Newfoundland, Canada (50°N) and across to the southwest shores of Greenland (60°N) and Iceland (70°N) (Cooke, 1915; Thorson, 1941). Vertically it ranges from mean high-water neap tides to near low-water spring tides. *N. lapillus* feeds primarily on mussels (*Mytilus edulis*) and barnacles (*Semibalanus balanoides*). The sexes are separate and fertilization is internal. Mature females deposit egg capsules on the undersides of rocks and in crevices, and the young emerge as metamorphosed juveniles, which immediately begin a benthic existence.

Study Sites

Wave Action.—The experimental field work was conducted primarily at three sites located on the northern coast of Massachusetts. Study sites were chosen to represent the extremes in exposure to wave action typical of shores along the coast of New England. Figure 1 shows the location of the three sites: 1) No Name Point, Nahant (exposed), 2) Bennett Head, Nahant (exposed), and 3) Mackerel Cove, Beverly (protected).

The most wave-exposed sites (No Name Point and Bennett Head) are located at the eastern tip of Nahant which protrudes into Massachusetts Bay and receives the direct impact of oceanic swells and storm-generated surge. Furthermore, both exposed sites are at the tip of a headland where wave energies tend to concentrate. The protected site (Mackerel Cove) is located in Beverly harbor and is completely sheltered from the direct forces of oceanic swells. In addition, a sand bar located 10–30 m seaward of this site acts as a barrier to any waves generated within the harbor. Wave heights over a five-year period rarely exceeded 0.5 m (pers. observ.).

Quantitative measures of maximum wave energies were collected using Palumbi's (1984*a*) wave-force dynamometers. Measurements were taken on No Name Point and at Mackerel Cove. Although the wave energies were not measured at Bennett Head, its proximity to No Name Point suggests

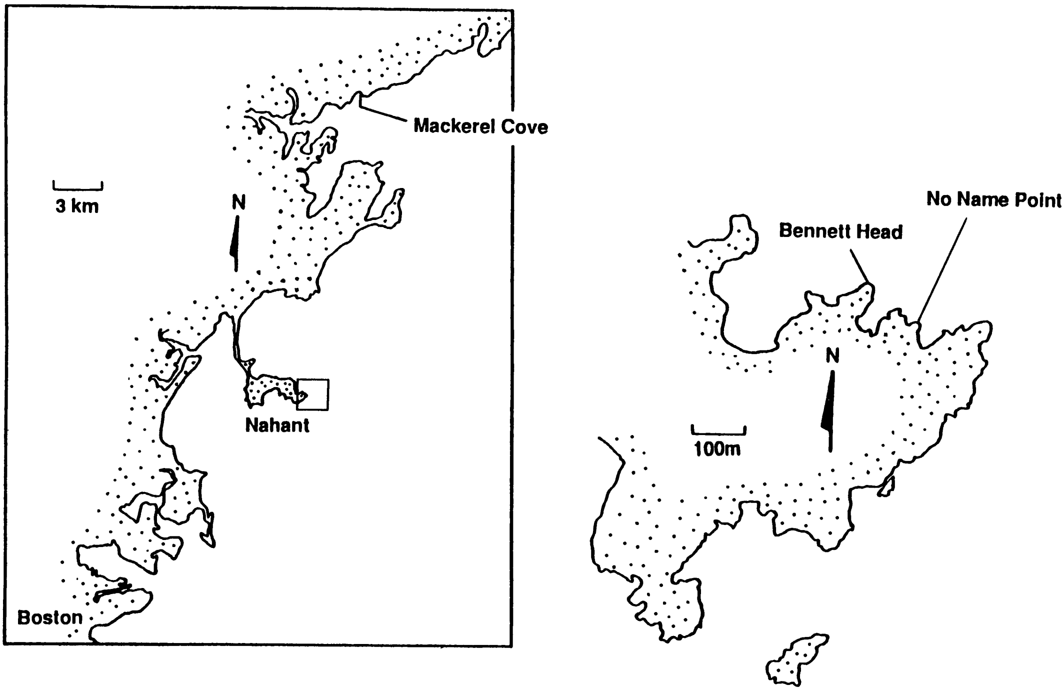

FIG. 1. The location of the study sites along the northern coast of Massachusetts. The eastern tip of Nahant (small box) has been enlarged. See text for a description of the study sites.

that the sites experience similar exposure regimes. The results of the quantitative measurements confirmed the qualitative assessments (Table 1). An initial series of measurements were collected over a typical calm summer week (17–24 July 1985). These readings more accurately reflect the wave action that *N. lapillus* experiences, because most individuals move into deep crevices and become inactive during the relatively stormy months of the year (November–April). Nevertheless, measures of wave action over a two-week period in November (18 November–5 December 1985) gave similar results but accentuated the differences between sites. Attempted measures during a storm which moved through in the latter part of October resulted in the destruction of all wave-force dynamometers at No Name Point; those at Mackerel Cove averaged 5.31 × 10^3 N/m^2.

Physical and Biological Characteristics.— The exposed shores at Nahant consist of lightly metamorphosed basalt, limestone or shale in the form of vertical faces and large horizontal shelves. The intertidal zone has a very gradual slope, whereas the subtidal drops off steeply to depths of 10–20 m. The high intertidal zones at No Name Point and Bennett Head exhibit a dense cover of barnacles (*Semibalanus balanoides*). The mid and low intertidal zones are populated by a combination of mussels (*Mytilus edulis*), barnacles, fucoids (*Fucus distichus* and *Fucus vesiculosus*) and ephemeral algae (*Ulva* spp. and *Enteromorpha* spp.) with up to 50%

TABLE 1. Measures of maximum wave forces at an exposed and protected shore during a one-week period in the summer and two-week period during the fall. The mean (N = 3) and standard deviations are given in kN/m^2. Palumbi's (1984*a*) wave force dynamometers were used with force transducers made from empty plastic film cannisters.

Site	$\bar{x}$	SD
17 July 1985–24 July 1985:		
No Name Point	10.7	1.81
Mackerel Cove	5.7	0.54
18 Nov. 1985–5 Dec. 1985:		
No Name Point	21.8	2.06
Mackerel Cove	5.6	1.17

unoccupied primary space (Menge, 1978*a*). In contrast to the exposed sites, Mackerel Cove is a granitic rock outcropping comprised of large irregular shaped boulders extending out over a shallow sandy bay. The bottom slopes off very gently from the high intertidal to a depth of about 5–10 m, with an extensive sand bar located about 10–30 m offshore. The organization of the community here is quite different from that of the exposed sites. Boulders are densely covered by barnacles regardless of their height in the intertidal zone. A few of the boulders also exhibit a very dense cover of a small erect macroalgae, *F. vesiculosus,* which forms a shallow canopy on the upper surfaces. Extensive mussel beds completely cover the sandy substrate among the boulders and extend to just below mean low water.

MATERIALS AND METHODS

Adhesive Properties.—In order to determine whether exposure regime influences the adhesive ability of *N. lapillus* and whether variation in adhesion reflects morphological variation in the surface area of the foot, dislodgement force and tenacity were measured for whelks from high- and low-wave-energy environments. Tenacity is defined here as the shearing force per unit area of the foot necessary to dislodge attached snails (g/cm^2).

Snails for the analysis were collected during October 1985 from three 0.64-m^2 quadrats haphazardly tossed in the mid intertidal zone at No Name Point and Mackerel Cove. Because a range of sizes was desired for the analysis and small whelks are rare at Mackerel Cove (Etter, 1987), a few small individuals were collected outside the quadrats at the protected site. All snails were brought to the laboratory and numbered. A small hole was drilled through the outer aperture shell wall of snails larger than 10 mm, and a fine monofilament loop was tied to the shell through this hole. To ensure that the tagging and drilling procedures did not adversely affect the snails, they were submerged in seawater tables for 48 hours and subsequently assayed for responsiveness by gently prodding each with a blunt dissecting probe. Individuals that failed to respond or responded slowly were not used in the analysis. Only three of over 100 snails were excluded using this criterion.

Snails were then placed in a five-gallon aquarium partially filled with sea water and were allowed to attach to the glass panels for at least 30 minutes. Water was drained from the aquarium to mimic intertidal conditions and to obtain a more accurate and consistent measure for the surface area of the foot and its tenacity. As the water was drained, snails became stationary and withdrew their propodia, with each snail forming its foot into an ellipse directly beneath the aperture. This stance maximizes tenacity in spite of the smaller surface area in contact with the substratum (Miller, 1974). Tenacity is greater because the columellar muscle forms short, straight connections between the shell and foot, and the foot becomes more rigid, which enhances adhesion (Miller, 1974; Branch and Marsh, 1978; Grenon and Walker, 1981). Once snails became stationary, pedal surface area was measured by tracing the outline of the foot onto a piece of cellophane tape placed against the aquarium panel. For snails smaller than 10 mm, a separate technique employing a camera lucida (described below) was used. The outline was transferred to paper, and the area was computed with a digitizer connected to an Apple IIe microcomputer. To obtain an estimate of the error in measuring PSA, three hatchlings, juveniles, and adults were measured three times and the mean percentage of error was calculated for each size class from the maximum difference among the three measures for each individual.

Resistance to dislodgement was measured immediately after tracing the surface area of each foot. Prior to testing, each snail was lightly tapped to induce it to clamp down tightly. The hook of a strain gage was inserted through the monofilament loop tied to the shell and a gradually increasing force ($\approx$25 g/sec) was applied parallel to the substrate to mimic shearing forces imparted by breaking waves. The shearing force was directed to the left of the snail, and the force required to dislodge each snail was recorded. Vernier calipers were used to measure shell length as the maximum distance between the shell apex and the tip of the siphonal canal.

Genetic and Plastic Components to Variation.—Juveniles (defined ad hoc as those snails between 2 and 20 mm long) from the exposed and protected shores were reared between May and October 1985 under similar conditions in the laboratory to identify the genetic component of variation in pedal surface area (PSA). They were maintained completely submerged in water tables supplied with a continuous flow of seawater. Each week, snails were provided with mussels and barnacles of a size range typical of that found naturally in their habitats. Any differences in PSA that developed in the laboratory were assumed to reflect an underlying genetic difference because the environmental stimulants were similar. In October, the shell length and PSA of each snail were measured as described above.

To identify the stage of growth and development during which the PSA of whelks from exposed and protected shores begin to diverge, PSA's of hatchlings were measured as they emerged from egg capsules. The egg capsules were collected from several aggregations at each shore to minimize the chances of collecting capsules deposited by a single female. Capsules were placed within plastic containers with sealed lids and nitex screened windows (mesh size $\approx$ 300 μ) to permit water flow. The containers were maintained completely submerged in water tables supplied with a continuous flow of seawater. Due to the small size of hatchlings ($<$1.5 mm), shell length was measured with a binocular dissecting microscope fit with an ocular micrometer. Pedal surface area was obtained by placing hatchlings in a small petri dish filled with seawater and allowing them to attach to the bottom panel. The water was then drained, and the petri dish inverted and examined under the dissecting microscope. A camera lucida was used to trace the perimeter of the foot onto paper, and the digitizer was then used to calculate surface area as described above.

A reciprocal-transplant experiment was employed to estimate the genetic and plastic components of variation in PSA between populations from high- and low-wave-energy environments. Juvenile whelks were collected from an exposed headland at No Name Point and from Mackerel Cove in May 1985, brought to the laboratory, and tagged. Each snail was tagged by writing a small number on the shell with white drawing ink, placing a small dot at the apex of the shell, and covering both areas with Super Glue®. Of the whelks collected on the protected shore, 110 were released on an exposed shore at Bennett Head (see Fig. 1), and 83 were released on a separate protected shore at Mackerel Cove. For those collected from the exposed shore, 144 were released at Mackerel Cove and 87 were released at Bennett Head. Tagged whelks were recollected from both shores in October 1985, and the shell length and pedal surface area were measured as described above.

Statistical Procedures.—The relationships between PSA and shell length, between dislodgement force and shell length, and between dislodgement force and PSA were tested using linear, exponential, and geometric least-squares regressions. The best-fit model was employed in subsequent analyses, and appropriate transformations ($\log_e$) were performed where necessary to linearize the relationships in order to use ANCOVA to compare PSA or tenacity between exposed and protected populations. When more than two populations were involved, an SNK multiple-comparisons test (Zar, 1974) was used to determine which pairs of samples differed. When slopes were found to be heterogeneous, a Johnson-Neyman analysis (Huitema, 1980) was conducted to compute the region over which the elevations of the regression lines were not significantly different.

RESULTS

An estimate of the error in measuring PSA indicated that repeated measures varied by about ten percent for hatchlings and juveniles, and four percent in adults. For snails from either a high- or low-wave-energy shore, PSA increased geometrically with shell length, but whelks from the exposed shore produced a relatively larger foot (Table 2, Fig. 2A). The shearing force necessary to dislodge stationary whelks also increased geometrically with shell length, and, compared to those from the sheltered shore, similar sized snails from the exposed habitat required a relatively greater force to be dislodged (Table 2, Fig. 2B). Tenacity can be altered by changing any one of three vari-

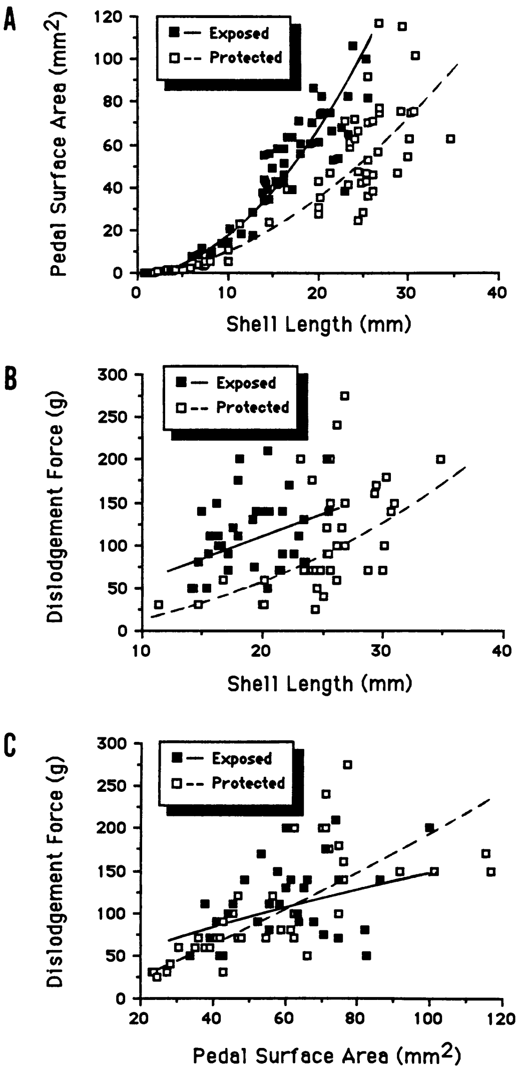

FIG. 2. The relationship between A) pedal surface area and shell length, B) dislodgement force and shell length, and C) dislodgement force and pedal surface area for whelks from exposed and protected shores. Details of the regression lines for snails with shell length >10 mm are given in Table 2.

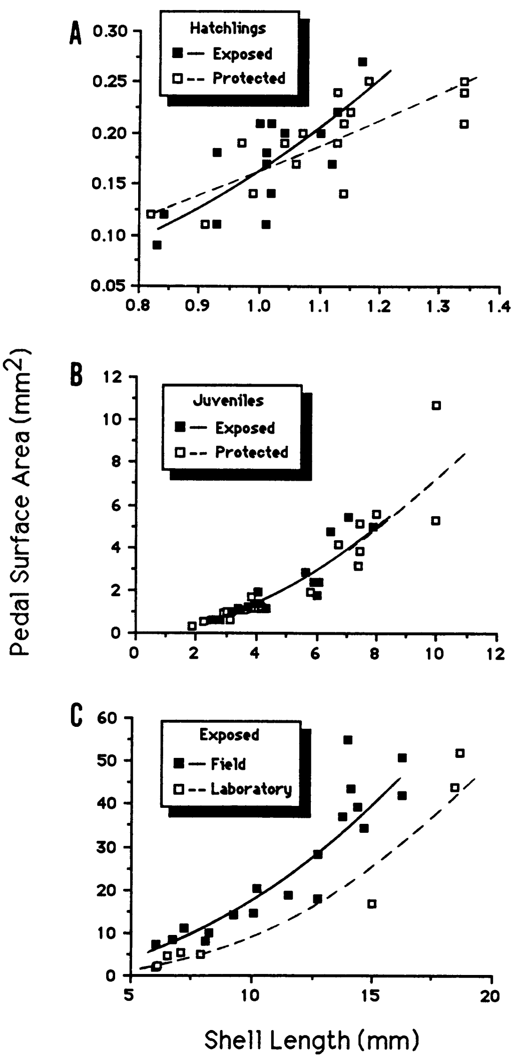

FIG. 3. The relationship between pedal surface area and shell length for A) hatchlings from the exposed and protected shore, B) juveniles from the exposed and protected shore reared in the laboratory, and C) exposed juveniles reared in the laboratory or intertidally at the exposed shore. Details of the regression analysis are given in Table 3.

ables: PSA, viscoelastic properties of the pedal mucus, or the thickness of the pedal mucus. The force required to dislodge individuals was similar between whelks from exposed and protected shores when the data were normalized by the surface area of the foot in contact with the substrate (Table 2, Fig. 2C), indicating that interpopulation variation in resisting dislodgement derives entirely from differences in pedal surface area. The mean (±SE) tenacities for whelks from exposed and protected sites were 188.6 ± 11.2 g/cm^2 and 178.8 ± 10.5 g/cm^2 respectively.

The pedal surface area of hatchlings emerging from egg capsules collected from shores differentially exposed to wave action were statistically indistinguishable (Table 3, Fig. 3A), and the PSA's of juveniles from exposed and protected shores reared in the

TABLE 2. Regression lines describing the relationships between pedal surface area and shell length, between dislodgement force and shell length, and between dislodgement force and pedal surface area for whelks (>10 mm shell length) from exposed (E) and protected (P) populations. Results of an ANCOVA comparing regression lines between populations.

	Regression			ANCOVA		
Population	Equation	N	r		$d.f.$	F
Pedal surface area (Y) vs. shell length (X):						
E	$Y = 2.645X^{1.063}$	34	0.662***	slope:	1, 71	0.566
P	$Y = 0.754X^{1.326}$	41	0.651***	elevation:	1, 72	34.201***
Dislodgement force (Y) vs. shell length (X):						
E	$Y = 6.877X^{0.932}$	34	0.404*	slope:	1, 71	3.095
P	$Y = 0.194X^{1.913}$	41	0.628***	elevation:	1, 72	21.990***
Dislodgement force (Y) vs. pedal surface area (X):						
E	$Y = 7.085X^{0.661}$	34	0.460**	slope:	1, 71	0.145
P	$Y = 0.657X^{1.237}$	41	0.828***	elevation:	1, 72	0.250

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

laboratory were practically identical (Table 3, Fig. 3B). The lack of differentiation in hatchlings and in whelks reared in the laboratory under uniform conditions suggests that variation in pedal surface area between whelks from exposed and protected shores is environmentally induced. This notion is further supported by comparing PSA between laboratory-reared whelks and their counterparts from nature.

Figure 3C illustrates the difference in foot dimensions between exposed snails reared in the laboratory and those reared intertidally. Regardless of whether whelks from exposed or protected populations were used, PSA was significantly greater for individuals that developed in the intertidal zone (Table 3). Although the ANCOVA indicated heterogeneity of the slopes for the experimental groups from the protected shore, a Johnson-

TABLE 3. Regression analysis of the relationship between pedal surface area (Y) and shell length (X) for exposed (E) and protected (P) whelks reared in the field (subscript F) or in the laboratory (subscript L). Different-sized juveniles were used in each of the analyses to maximize the overlap between experimental groups. Results of an ANCOVA comparing regression lines between experimental groups are also shown.

	Regression			ANCOVA		
Experimental group	Equation	N	r		$d.f$	F
Hatchlings:						
E_L	$Y = 0.162X^{2.385}$	15	0.764***	slope:	1, 27	2.157
P_L	$Y = 0.162X^{1.482}$	16	0.785***	elevation:	1, 28	0.236
Juveniles (size = 2–10 mm):						
E_L	$Y = 0.104X^{1.853}$	16	0.937***	slope:	1, 31	0.056
P_L	$Y = 0.112X^{1.803}$	19	0.970***	elevation:	1, 32	0.002
Juveniles (size = 6–20 mm):						
E_F	$Y = 0.145X^{2.075}$	19	0.946***	slope:	1, 23	2.023
E_L	$Y = 0.031X^{2.467}$	8	0.971***	elevation:	1, 24	29.511***
Juveniles (size = 2–22 mm):						
P_F	$Y = 2.970X^{0.832}$	8	0.688*	slope:	1, 23	5.776*
P_L	$Y = 0.112X^{1.803}$	19	0.970***	elevation:	1, 24	9.911**
Juveniles (size = 10–22 mm):						
E_F	$Y = 0.808X^{1.481}$	30	0.808***	slope:	1, 34	2.908
P_F	$Y = 2.970X^{0.832}$	8	0.688*	elevation:	1, 35	53.692***

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

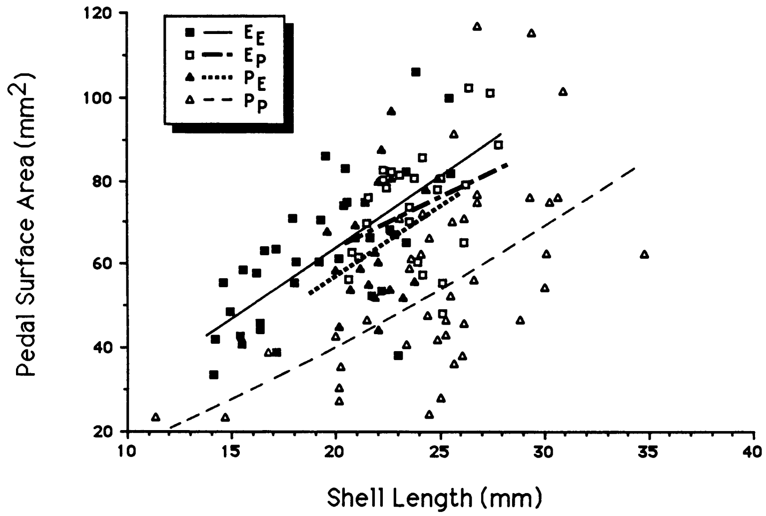

FIG. 4. The relationship between pedal surface area and shell length for whelks from exposed and protected shores reciprocally transplanted between shores. Subscripts refer to the shore at which snails were reared (E = exposed, P = protected). Details of the regression analysis are given in Table 4.

Neyman analysis showed that the shell lengths over which the laboratory and field groups did not differ significantly in elevation of the regression line were greater than 19 mm. Since the analysis was concerned with juveniles (2–20 mm), those reared intertidally at the protected shore also had larger PSA's for the size range of interest. Moreover, whelks from the exposed shore reared intertidally had larger PSA's than did protected snails, despite possessing a foot of comparable surface area at hatching (Table 3).

The reciprocal-transplant experiment indicated that pedal surface area is a highly plastic character, molded by the particular environment, but it also revealed an asymmetry in the plasticity. Juveniles from the protected shore reared on an exposed shore (P_E) formed larger PSA's than did controls reared in a sheltered cove (P_P; Table 4, Fig. 4). An SNK multiple-comparison test performed on the elevations of the regression lines for each experimental population showed that pedal surface area was similar in P_E and both populations originally from the exposed shore (E_E and E_P). In contrast, whelks from a high-wave-energy environment reared on the protected shore (E_P) did not form smaller PSA's than did the controls (E_E). After five months of growth on a sheltered shore, they maintained PSA's that were substantially larger than those of similar sized individuals from the protected

TABLE 4. Regression lines describing the relationship between pedal surface area (*Y*) and shell length (*X*), for exposed (E) and protected (P) morphs reared on exposed (subscript E) or protected (subscript P) shores. Results of an ANCOVA and an SNK multiple-comparison test comparing regression lines between experimental groups. The inequality sign in the multiple-comparison column (MC) separates experimental groups that differed significantly ($P < 0.05$) and indicates the direction of the difference. Treatments separated by commas were statistically indistinguishable.

Experimental group	Regression			ANCOVA			
	Equation	*N*	*r*		*d.f.*	*F*	MC
E_E	$Y = 2.645X^{1.063}$	34	0.662***	slope:	3, 115	0.435	—
E_P	$Y = 6.661X^{0.756}$	26	0.342	elevation:	3, 118	19.347***	E_E, E_P, P_E > P_P
P_E	$Y = 1.189X^{1.890}$	22	0.331				
P_P	$Y = 0.754X^{1.326}$	41	0.651***				

*** $P < 0.001$.

shore. The plastic response of *N. lapillus* to the environment was asymmetrical; under the harsh conditions of the exposed coast, snails from the protected shore formed larger PSA's while the more benign protected shore failed to induce a reciprocal shift in the PSA's of whelks from the wave-swept habitat.

The percentages of the transplanted whelks recovered were similar in populations originally from the high- and low-wave-energy shores (26/144 = 18% and 22/110 = 20%, respectively). Recovery rates were greater for resident populations and differed slightly between exposure regimes. About 49% (41/83) of the resident whelks at the protected shore were recovered, while only 39% (34/87) were recovered at the exposed shore.

DISCUSSION

Widely distributed inhabitants of the intertidal zone experience considerable variability in wave energies. The results presented here indicate that the ability of *N. lapillus* to resist the hydromechanical forces of the pounding surf corresponds to the intensity of the prevailing wave energies. Whelks from the exposed shore had larger pedal surface areas and required greater shearing forces to be dislodged than did similar-sized individuals from a protected shore. Tenacity is defined as the force necessary to dislodge an organism from a surface per unit area attached to the surface. Contrary to earlier arguments involving suction, recent studies indicate that tenacity in gastropods is a function of the viscoelastic properties of the pedal mucus (Branch and Marsh, 1978; Grenon and Walker, 1981; Denny, 1984). Adhesion develops between two surfaces (foot and substrate) separated by a thin layer of fluid (pedal mucus) according to the equation

$$F = \frac{2AS}{d}$$

where F is the adhesive force, A is the area of contact between two surfaces, S is the surface tension (i.e., viscoelastic properties) of the liquid, and d is the thickness of the liquid (Cottrell, 1964; cited in Branch and Marsh [1978]). Assuming that *N. lapillus* employs a similar mechanism for attachment, the similarity in tenacity between populations implies that the biomechanical properties of the pedal mucus and its thickness are also similar.

Intraspecific variation in pedal surface area paralleling exposure gradients has been described elsewhere. Miller (1974) reported that pedal surface area was larger in high-wave-energy environments for both *Nucella emarginata* (Deshayes) and *Acmaea pelta* (Eschscholtz). *Nucella lapillus* from exposed coasts on the British Isles also produce a larger foot than do those from a more protected shore (Kitching et al., 1966). Differences in tenacity among snails from shores differentially exposed to wave action have been less clearly documented. Branch and Marsh (1978) found that tenacity of six species of patellid limpets from the South African coast increased in a manner corresponding to the wave energies they might experience in nature. Grenon and Walker (1981) failed to discover intraspecific differences in tenacity between *Patella vulgata* (Linnaeus) from exposed and protected shores and argued that the differences observed by Kitching et al. (1966) for *N. lapillus* reflected deficiencies in their experimental methods. However, Kitching et al. (1966) did not measure tenacity; they simply showed that pedal surface area was larger for exposed snails and that exposed snails were less vulnerable to dislodgement by wave-generated forces. The present analysis demonstrates quite clearly that tenacity is similar between snails from exposed and protected habitats, but individuals from the exposed shore are better able to resist dislodgement because they have larger PSA's. From the data reported by Grenon and Walker (1981) and by Branch and Marsh (1978) it was not possible to determine whether the pedal surface area varied among exposed and protected populations of limpets. Future studies on the adhesive powers of intertidal snails should draw a clear distinction between the force necessary to dislodge snails and their tenacities (i.e., adhesive force/unit foot area).

Phenotypic Plasticity.—As evidenced by the laboratory and the reciprocal-transplant experiments, PSA in *N. lapillus* is a highly plastic character, which appears to be influence by the intensity of wave action. Whelks from both exposed and protected shores reared intertidally had larger PSA's than did laboratory-reared snails, indicating that even a small increase in water turbulence induced the formation of a larger foot. Furthermore, the extent to which PSA increased was directly proportional to the intensity of wave action; exposed whelks had significantly larger PSA's than did individuals of similar size from the protected shore. To my knowledge, this is the first demonstration that PSA is plastic and that wave action and its accompanying hydromechanical forces may induce or modulate shifts in pedal surface area. This does not imply that other ecological factors such as temperature, desiccation (Vermeij, 1971*a*, 1971*b*, 1973) and predation (Menge, 1978*a*, 1978*b*; Lowell, 1985, 1986) are unimportant in determining foot morphology. It is likely that all are involved, but the work presented here was concerned primarily with the influence of wave energies.

The plasticity of the foot was asymmetrical; juveniles from the protected shore reared on an exposed coast showed a dramatic increase in pedal surface area, while very little change occurred for exposed morphs transplanted to a protected shore. The asymmetric response parallels a possible asymmetry in the risks associated with acclimating incorrectly to a temporally unpredictable environmental cue. Survival of intertidal snails depends in part on their ability to resist dislodgement, which in turn is a function of pedal surface area. As shown above, PSA was highly plastic and was probably influenced by wave action. A reduction in PSA by snails at exposed shores during extended calm periods would likely result in high mortality as wave energies returned to normal levels. Individuals with reduced PSA's would be more vulnerable to dislodgement which may result in their being carried into the subtidal zone, where they would be exposed to a more diverse predator guild. In contrast, producing a larger PSA in response to high wave energies on protected shores during extended periods of stormy weather is less likely to reduce survivorship. Therefore, acclimation towards the wave-tolerant morphology is less risky than acclimation towards the wave-intolerant form.

An asymmetric plastic response to a harsh versus benign environment was also reported by Palumbi (1984*b*). He reciprocally transplanted genetically identical fragments of the demosponge *Halichondria panicea* between wave-exposed and wave-protected habitats and followed changes in structural properties of new tissues. Soft sponges from low-energy environments transplanted to a high-energy shore began producing stiffer tissues within four weeks, but stiff colony fragments transplanted from a high-energy habitat to a low-energy habitat delayed producing weaker tissues for about ten weeks. Palumbi interpreted the slower transition away from a stress-tolerant morphology as a response to a temporally unpredictable environment. He concluded that the control of acclimatory responses was coupled to environmental predictability and the risks of error in environmentally cued acclimation.

Because pedal surface area did not decrease when snails from the exposed shore were reared on the protected shore in the present study, two alternative explanations of the asymmetry exist. First, for *N. lapillus,* the shift to the wave-stressed form may reflect a developmental conversion (sensu Smith-Gill, 1983), an environmentally induced genetic switch that activates a separate developmental program. Developmental conversion usually involves a single environmental cue that typically induces the formation of the stress-tolerant form (Lively, 1986*a*, 1986*b*). Which developmental program is activated depends on the nature of the environment an organism inhabits. Under benign conditions, the stress-tolerant program is inactive, and an intolerant morphology is produced. Harsh conditions activate the genetic switch and the stress-tolerant form develops. In the case of *N. lapillus,* the cue may be high wave energies, and, thus, a decrease in wave action would not elicit a reduction in pedal surface area. Although this possibility cannot presently be ruled out, it seems unlikely, because developmental conversions are typified by all-or-nothing responses (Kruegar and Dodson, 1981; Harvell, 1984; Lively, 1986*b*), while the shift in PSA was a more continuous response; snails from both exposed and pro-

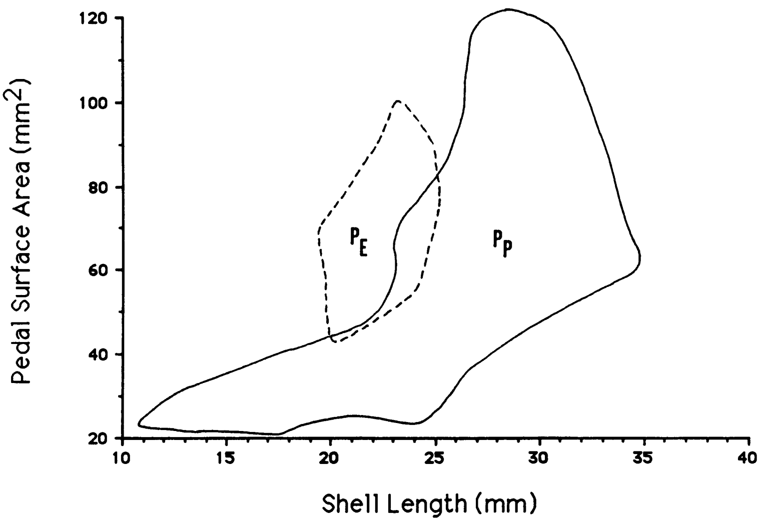

FIG. 5. The minimum area envelopes for the relationship between pedal surface area and shell length for whelks from the protected shore reared on an exposed or protected shore. Subscripts refer to the shore at which snails were reared (E = exposed, P = protected).

tected shores produced pedal surface areas larger than those of snails reared in the laboratory, but the difference between laboratory and intertidally reared juveniles was much greater for those from high-wave-energy environments. Phenotypic variation of this genre is more typical of phenotypic modulation (Smith-Gill, 1983).

The second possible explanation is that the mechanical forces imparted by breaking waves on exposed coasts simply select against individuals from the protected shore with a small foot, while wave action on the protected shore caused little direct mortality. Again, this hypothesis can not be entirely ruled out, but two points argue directly against it. First, according to the selection argument, snails from sheltered shores reared on the exposed shore (P_E) should exhibit higher PSA than their controls (P_P), but there should be considerable phenotypic overlap between the two populations. At the start of the experiment, snails were randomly divided into transplant and resident populations, so phenotypic variation initially should have been quite similar between experimental groups. Since selection can act only on the available phenotypic pool, overlap should be high, because there is little or no selection on foot morphology at the protected shore (as evinced by the reciprocal transplant experiment) and the high wave energies at the exposed shore are simply imposing selection favoring those individuals from the protected population with a relatively large PSA. A comparison of the minimum area envelopes of the two populations shows that there is little overlap between P_P and P_E, suggesting that there has been a change in the phenotypic pool (Fig. 5). Second, there is virtually no overlap between exposed-shore snails reared intertidally and those reared in the laboratory (Fig. 3C). According to the selection argument, there should again be significant overlap. Undoubtedly, selection is operating, but selection alone cannot account for the above results.

The asymmetric plastic response of *N. lapillus* to wave-stressed versus wave-benign environments appears to reflect an asymmetry in the risk associated with acclimating to a temporally unpredictable environmental cue. These results may also represent an example of a more general phenomenon. If natural selection favors a plastic response to environmental heterogeneity that is cued to a temporally unpredictable environmental component, then natural selection should also favor a more rapid response to the stress-tolerant form than to the stress-intolerant form.

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