LIFE HISTORY VARIATION IN THE INTERTIDAL SNAIL *NUCELLA LAPILLUS* ACROSS A WAVE-EXPOSURE GRADIENT[1]

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Abstract. Demographic and life history characteristics of the intertidal whelk *Nucella lapillus* were measured across a wave-exposure gradient to quantify the variation in, and identify the ecological forces shaping, each trait. Growth rates, survivorship, size and age at maturity, fecundity, and per-offspring parental investment were estimated from marked snails during a 3-yr period. Growth rates as indicated by changes in shell length, total mass, shell mass, and body mass varied among populations from different exposure regimes. Relative to more protected sites, snails from exposed shores grew more slowly and terminated growth at a smaller size. Age at maturity did not differ between whelks from high- and low-wave-energy populations, but those on the exposed shore matured at a smaller size. Mortality rates increased with wave energy. Size-specific mortality rates indicated that the higher mortality on wave-swept shores reflected decreased survivorship of large (≥ 15 mm) adults relative to similar sized individuals on more protected shores. Exposed shore snails deposited twice as many egg capsules with twice as many hatchlings emerging from each capsule. Although the hatchlings were $\approx 25\%$ smaller, four times as many were produced, suggesting that reproductive effort was considerably greater on exposed coasts, offsetting the higher mortality rates. The ecological forces (energetic, physiological, abiotic, etc.) potentially responsible for the life history variation among populations from different wave-exposure regimes are discussed.

Key words: demography; growth rates; life history variation; Massachusetts coast; mortality rates; Nucella lapillus; *population dynamics; reproductive ecology; wave exposure.*

INTRODUCTION

The classical view of life history evolution was that of a suite of characters coadapted by natural selection to maximize reproductive success in a particular environment (reviewed by Stearns 1976). Recent work indicates that much of the intraspecific variation in life histories represents a plastic response to environmental heterogeneity and the interaction of these traits with developmental and physiological constraints (Stearns 1980, 1983, Brown 1983, Stearns and Koella 1986, Bosman and Hockey 1988, Brown and Quinn 1988). Stearns (1977) pointed out the importance of separating phenotypic from genetic variation in life histories, but it is equally important to understand the demographic, physiological, and developmental conditions under which specific life histories are favored. Only from this information will it be possible to identify the forces that shape life history characteristics. For instance, in a recent paper, Stearns and Koella (1986) demonstrated that variation in growth rates could lead to dramatic changes in other life history features because it shifted the organisms along their norm of reaction. Comparisons of conspecific populations under different demographic regimes should provide insights into the forces shaping life histories, whether the par-

ticular characters represent phenotypic modulation, developmental conversion, or genetic differentiation.

Demography often varies considerably along environmental gradients creating ideal conditions for studying the forces that influence life history traits. A dramatic environmental gradient exists intertidally among shores exposed to different levels of wave action. Few studies have considered the ecological and evolutionary consequences of wave-exposure gradients, although a burgeoning body of evidence indicates that wave action exerts a powerful and profound influence on the biology of intertidal and shallow subtidal marine organisms. The ecological effects of wave-generated forces can operate directly through the impact of waves and debris or through dislodgement, as well as indirectly by altering food availability, biotic interactions, and foraging efficiency. Several studies have demonstrated that differential exposure to wave action can affect or is correlated with changes in community composition (Dayton 1971, Menge 1976, Lubchenco and Menge 1978, McQuaid and Branch 1985), primary productivity (Leigh et al. 1987), predation intensity (Menge 1978*a, b*, 1983), competitive abilities (Menge 1974), growth rates (Hughes 1972, Osborne 1977, Janson 1982, Sebens 1984, Brown and Quinn 1988), mortality rates (Janson 1983*a*, Wethey 1985), morphologies (Struhsaker 1968, Crothers 1983, Janson 1983*b*, Etter 1988*a, b*), fecundity (Menge 1974), and size

TABLE 1. Measures of maximum wave forces at an exposed, intermediate, and protected shore ($n = 3$). Palumbi's (1984) wave-force dynamometers were used with force transducers made from empty plastic film cannisters.

Site	Wave force (kN/m²)	
	$\bar{X}$	SD
17 Jul–24 Jul 1985		
No Name Point (E1)	10.7	1.81
Pump House Cove (I3)	7.3	0.89
Mackerel Cove (P)	5.7	0.54
18 Nov–5 Dec 1985		
No Name Point (E1)	21.8	2.06
Canoe Beach Cove (I1)	17.8	1.96
Mackerel Cove (P)	5.6	1.17

(Menge 1974, Ebert 1982, Sebens 1984, Denny et al. 1985) of intertidal and shallow subtidal organisms. Organisms with distributions that span several exposure regimes may experience differences in foraging time, growth rates, reproductive success, competition, predation intensity, and mortality rates, all of which may impose important constraints on the suite of life history characteristics favored under local environmental conditions. Yet, virtually nothing is known about how the life history suites of single species vary across wave-exposure gradients.

In the present study, an integrated analysis of the demography and life history of the intertidal snail *Nucella lapillus* (L.) is contrasted among populations differentially exposed to wave action. This species has been extensively studied and exhibits considerable intraspecific genetic, morphological, physiological, and behavioral variation which appear to be associated with wave energies in a general way (reviewed in Crothers 1985).

Marked individuals in six populations along a wave-exposure gradient were followed for varying lengths of time between 1983 and 1985 to quantify differences in life history traits among populations. The results reveal that *N. lapillus* from different exposure regimes differed in growth rates, size at maturity, population size structure, mortality rates, reproductive effort, and the size and number of offspring produced.

STUDY SITES

Field data were collected from six sites along the Massachusetts coast that were chosen to represent a gradient in the degree of exposure to wave action (see Fig. 2). Mackerel Cove (P) is the most protected shore, Canoe Beach Cove (I1), Canoe Beach Point (I2), and Pump House Cove (I3) are intermediate in exposure, forming a continuum between relatively protected I1 to relatively exposed I3, while No Name Point Channel (E1) and No Name Point (E2) are the most exposed. Not all sites were used in each year. During 1983, as part of a preliminary study on life history variation, *N. lapillus* was monitored at five sites. Because each

of these sites received heavy wave action at some point during this field season, an extremely protected shore (P) was added to the monitored populations for 1984. In 1985, the number of sites was reduced to three (P, I1, E1). Populations at EP and IP were used exclusively for the analysis of size structure. The physical and biological characteristics of these study sites are described in detail elsewhere (Menge 1976, 1978*a, b*, Etter 1987, 1988*a*).

Wave action

The exposed sites 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, they are at the tip of a headland where wave energies tend to concentrate. E1 appears to experience slightly greater water velocities than does E2 because it is within a small narrow channel and waves accelerate as they move up the channel. The intermediate sites are all located within shallow coves which are partly sheltered from the direct impact of oceanic swells. Refraction of the waves entering the coves dissipates the energy over broad areas, thereby diminishing wave energies. The protected site 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.

Quantitative measures of maximum wave energies were collected on an exposed, intermediate, and protected shore using Palumbi's (1984) maximum wave-force dynamometers. The results confirmed my qualitative assessments (Table 1). Maximum wave energies were measured during a typical calm summer week and over a 2-wk period in November. The summer readings more accurately reflect the wave energies that *N. lapillus* experiences because most individuals move into deep crevices and become inactive during the relatively stormy months of the year (November–April). The two sets of measurements provided similar rankings of the study sites, but the November readings accentuated the differences between the protected shore and the exposed or intermediate sites. A storm that moved through in the latter part of October destroyed all wave-force dynamometers at Nahant. Measurements at the protected site averaged 5.31×10^3 N/m2.

METHODS

Marking snails

Between 200 and 500 *N. lapillus* ranging in shell length from 7 mm to the maximum size available in each population were collected at each site and returned to the laboratory. The shell surface was allowed to dry and then a small sander was used to sand a spot on the shell. A number was written on the spot using a rapidograph with white ink and, after drying, was waterproofed by covering the number with super glue.

The marked animals were returned to the field and numbers were checked and repaired at monthly intervals. Many of the markings persisted for >4 yr.

Growth

Growth rates were estimated by following monthly changes in (1) shell length, (2) total mass, (3) shell mass, and (4) body mass of marked individuals in each population during 5 mo of the spring–summer season (May–October) for the years 1983–1985. Four measures of growth were employed because shell length is often a poor indicator of growth and because I was interested in determining if shell growth differed from tissue growth. Growth was not followed during the winter months (November–April) because dog whelks become inactive and, for the most part, show little growth (R. Etter, *personal observation*). Moreover, *N. lapillus* is unable to reattach to the substrate when water temperatures drop below 5°C (Feare 1971), so disturbance during the winter months would cause high mortality in experimental populations.

Shell length was measured using vernier calipers (to ±0.1 mm) as the maximum distance from the shell apex to the tip of the siphonal canal. Total wet mass (shell + body mass) was obtained by weighing snails (to ±0.01 g) on a Mettler digital pan balance. Before weighing, snails were allowed to dry visibly and subsequently stimulated with an absorbant tissue (Kimwipe) until they retracted into their shell. This procedure forces snails to expel most extravisceral fluids which are absorbed by the tissue, improving the accuracy of mass determinations and reducing the error in estimating body mass (Palmer 1982). Shell mass and body mass were obtained using Palmer's (1982) nondestructive techniques.

To estimate shell mass, snails were weighed immersed in seawater. Because the body tissues of snails approximate the specific gravity of seawater, this technique eliminates most of the mass attributed to soft tissues. Regressions were developed for each population to convert immersed mass to actual shell mass. A complete range of snails from each population was collected, weighed immersed in seawater, and then placed in boiling water. Boiling permitted the removal of all body tissues without fracturing the shell. The empty shells were rinsed thoroughly in distilled water, dried at 40°, and reweighed (±0.01 g). Regressions of actual shell mass on immersed mass for each population were used to estimate shell mass from immersed mass. Regressions were highly significant with r^2 values ranging from 0.998 to 0.999. Wet body mass was obtained by subtracting shell mass from total wet mass. Body mass was the most variable of the growth characters because it incorporated three separate sources of error, (1) error in obtaining immersed masses, (2) error in converting immersed masses to shell masses, and (3) error in measuring total wet mass. An estimate of this error was obtained by comparing actual body masses to the masses predicted by the above procedure. Percentage error ranged from −7 to 181% and was greatest for small individuals. Mean percentage error was typically 20%. As a consequence, results involving body masses must be viewed with caution.

Since growth rates of snails are size dependent, a modification of a Ford-Walford plot was used to compare growth rates. Growth increment was plotted against initial size (e.g., shell length, total mass, shell mass, or body mass, whichever was appropriate) and a least-squares regression line fit to the data. All growth increments were corrected to 150 d to compensate for slight variation in the intervals between sampling the different populations. The data, for each estimate of growth (shell length, total mass, shell mass, and body mass), were tested against the Gompertz, power, and logistic growth curves to determine which curve best described growth (Kaufmann 1981). In each case, the logistic curve fit best and was used in all subsequent analyses. The elevation of the regression line represents the size-specific growth rate whereas the slope of the regression line represents the schedule of growth in the population (i.e., the rate at which the size-specific growth increment changes with size). The slope can also be viewed as the rate at which snails approach their asymptotic size.

Sainsbury (1980) showed that individual variation in the size at which growth stops (i.e., asymptotic size) creates an extensive distribution of large, nongrowing individuals. Inclusion of these individuals in regression analyses of growth increment on initial size produced biased estimates of growth rates. To alleviate this problem, snails that grew <0.5 mm in shell length, <0.05 g in total mass or shell mass, and <0.005 g in body mass over the summer growing season were excluded from their respective analyses.

Growth rates for each character were compared among sites to determine if exposure regime influenced growth. The data from the summers of 1984 and 1985 were used because they represented the most extensive data base. Growth rates were also compared among years (1983–1985) to elucidate annual cycles in growth. Only shell length was used for within-site comparisons of annual growth because the between-habitat analysis indicated that the other characters provided remarkably similar estimates of growth.

Statistical comparisons of growth rates were made with ANCOVA and a Tukey multiple comparisons test (Zar 1981). The ANCOVA was used to determine whether habitat type or year significantly affected the slope or elevation of the growth increment on initial size regression. If a significant effect was detected, the multiple comparisons test was employed to separate out which pairs of samples actually differed. Where slopes were found to be heterogeneous, a Johnson-Neyman test was employed to identify the region over which the elevation of the regression lines was not statistically different (Huitema 1980). The Johnson-

Neyman test employs simultaneous confidence limits of the regression to define the range of x values where the confidence bands of the regression lines overlap.

To determine how snails from different wave-exposure regimes apportion resources to protective (shell) and nonprotective (soft tissue) structures, the shell mass and wet body mass adjusted to a common shell length were compared among populations for 1984. Statistical procedures were similar to those used for growth (ANCOVA, Tukey multiple comparisons, Johnson-Neyman). The 1984 data were used in the analysis because they represent the most complete data set.

Population size structure

The size structure of populations of *N. lapillus* was assessed from shell length frequency distributions of the first 100 snails collected from one or two 0.64-m² quadrats blindly tossed into the intertidal zone at 0.6 m above mean low tide (MLT) in June 1984. Since age and size are not correlated over all size classes and cannot be equated among different habitats due to differences in growth rates, it is used here only to show the relative distribution of size classes among populations under different exposure regimes.

Mortality rates

Site-specific mortality rates were estimated by recording the loss of marked individuals from monthly samples in each population. Although estimating mortality from the loss of marked individuals includes snails that emigrate from the population, emigration should not be a major source of error in my estimates because I adjusted the search area to be twice as large as the furthest distance I found a marked snail from its release site.

The error in estimating mortality rates due to not finding marked individuals that were actually present at each site was calculated from the following equation:

$$E_m = \frac{1}{N} \sum \frac{M_i}{F_i + M_i}$$

where M_i = the number of snails missed in the ith month but found in subsequent months, F_i = the number of snails found in the ith month, and N = the number of months. To alleviate this error in estimating mortality rates, snails which were missed during monthly censuses, but found in subsequent months, were recorded as alive over the intervening months. This procedure mitigates the effect of intersite differences in the ability to find marked snails on calculating mortality rates, providing a better estimate.

The $\log_e$ number of individuals surviving at any particular census was regressed on the number of days since their initial release. The slope of this line was used as an estimate of daily mortality rates. The snails at each site were also divided into five shell length categories (5–<15 mm, 15–<20 mm, 20–<25 mm, 25–<30 mm, and >30 mm) and the size-specific mortality rates calculated for each size class in the same manner. The first size category lumped two 5-mm size classes because in several populations there were few snails <15 mm. Snails <7 mm were not used in the analysis because they could not be marked reliably. ANCOVA and a Tukey multiple comparisons test (Zar 1981) were used to compare daily mortality rates (slopes) among populations, years, size classes within sites and between sites for each size class to address the following questions. (1) Does mortality rate vary among populations from different exposure regimes? (2) If exposure regime influences mortality, are the differences consistent between years? (3) Does size influence mortality rates within populations? (4) Are the differences in mortality rates among populations consistent across all size classes?

Size at maturity

The shell length at which snails become sexually mature was investigated for an exposed (E1) and a protected (P) population to determine if size (and potentially age) at maturity differed between populations at the extremes of wave exposure. Approximately 500 snails spanning the available size range were collected at each site in March 1984. Collections were made in March because snails are reproductive at this time, making identification of sexually mature snails easier and more reliable. Snails ranging in size from 10 mm to the maximum size in each population (E1 = 27 mm, P = 35 mm) were examined for the onset of sexual maturity. Males were judged mature if they possessed a large sickle-shaped penis posterior to the right cephalic tentacle. A large majority of the females in each population also possessed a penis-like outgrowth posterior to the right cephalic tentacle, as in Blaber's (1970) observations, but this outgrowth was easily distinguished from the male penis because it was considerably smaller and was not sickle shaped. Unlike Blaber's (1970) findings though, the penis-like outgrowths were found on unspent females. Females were judged mature if they possessed a large white capsule gland. Once the range over which the transition from juvenile to sexually mature adult was established for each population, 20 snails in each 1-mm size category over this range were examined for sexual maturity and those sexually mature were recorded.

Reproductive characteristics

During 1984 several reproductive characteristics were measured for an exposed (E1), an intermediate (I1), and a protected (P) population. Egg capsules were collected intertidally from various aggregations at each site to minimize the chances of obtaining capsules of a single female. Egg capsules were maintained completely submerged in laboratory seawater tables continuously supplied with running seawater until embryonic development neared completion. The length (from
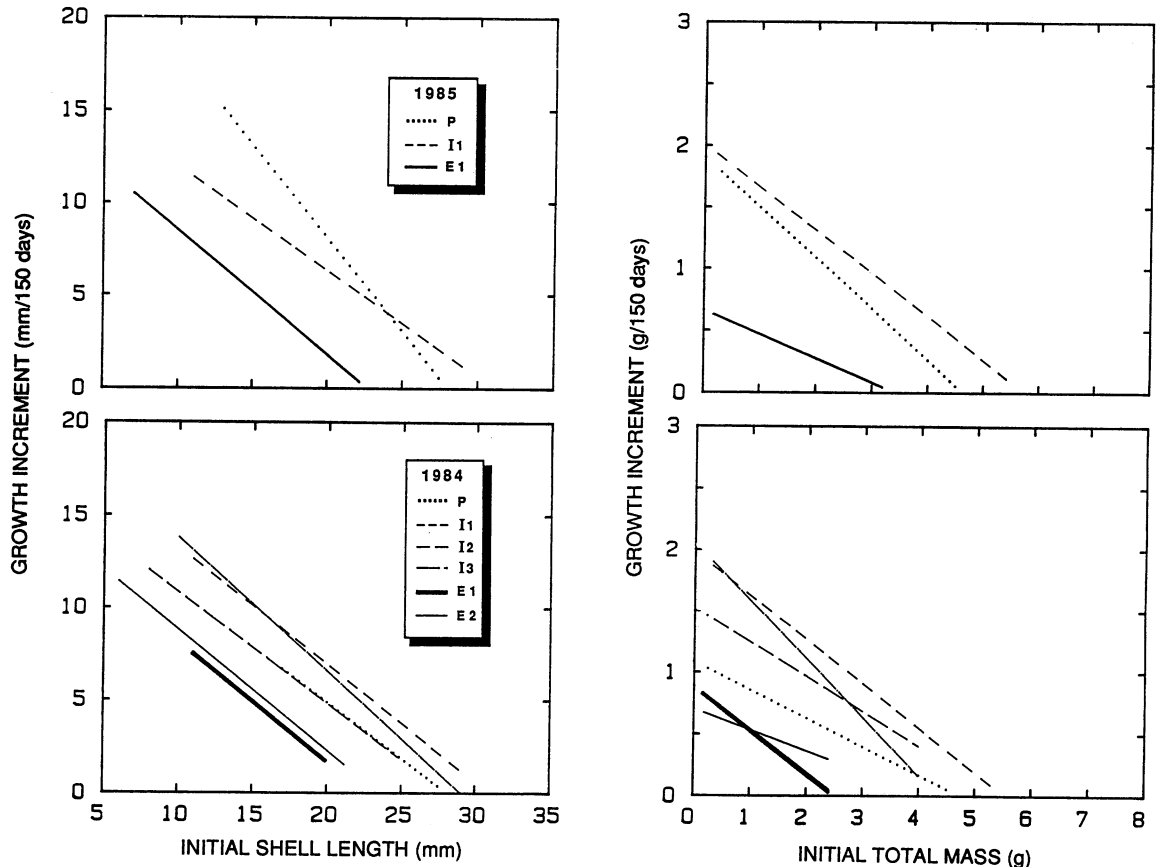
FIG. 1. Regression lines for growth in shell length (left) and total mass (right) of marked whelks from protected (P), intermediate (I), and exposed (E) shores over a 5-mo (May–Oct) period during the 1984 and 1985 growing season. See Table 2 for details of the regression equations.

the capsule–stalk junction to the edge of the capsule plug) and maximum width of each capsule were then measured (to ±0.08 mm). Capsules were placed individually into numbered petri dishes filled with seawater, and stored in a temperature-controlled room (10°). The seawater was changed every other day and any hatchlings that emerged were counted and their maximum shell length and shell width measured (to ±0.04 mm). All measurements were obtained using a dissecting microscope equipped with an ocular micrometer. Capsule dimensions were used to estimate the volume of egg capsules by assuming that their shapes approximate a prolate ellipsoid (Pechenik et al. 1984).

For 1985 similar data were collected, but in a slightly different manner. During the last week of March, before snails began to deposit egg capsules, ≈60 adult males and 60 adult females were collected from the exposed shore, E1, and from the protected shore, P. Five males and five females from E1 were placed in each of 12 replicate plastic cages (18 × 13.1 × 8.2 cm plastic containers with Nitex [≈1-mm mesh] windows in each panel) and supplied with mussels and barnacle-covered rocks. A similar set of 12 cages was prepared for snails from P. The size range of snails placed in

cages was 19–27 mm ($\bar{X}$ = 22.0 mm) for exposed- and 23–33 mm ($\bar{X}$ = 28.2 mm) for protected-shore adults, corresponding to a mean body mass of 0.552 and 0.793 g, respectively. All cages were maintained completely submerged in the laboratory seawater tables and supplied with a continuous flow of seawater. Cages were checked twice a month and any egg capsules that had been deposited were recorded and the food replenished if necessary. The average number of capsules deposited per female based on 12 replicate cages (and five females per cage) was calculated. When embryonic development neared completion, 10 capsules were removed from each cage and the length and width of each measured as described above. Capsules were maintained as described for 1984. Rather than measure all hatchlings from each capsule as was done in 1984, five hatchlings were measured at random to obtain a mean shell length for each capsule.

In 1984 an ANOVA was used to detect if reproductive characteristics varied among populations from different exposure regimes. If a significant effect was observed, a Tukey multiple comparisons test was used to identify which pairs of samples differed. In 1985 a simple *t* test was used.

TABLE 2. Regression lines for 150-d growth increments of shell length (y) on initial shell length (x) for protected, intermediate, and exposed populations of marked whelks during the 1984 and 1985 growing seasons, and the results of an ANCOVA and a Tukey multiple comparisons test comparing regressions among populations from different exposure regimes.

Site	Regression			ANCOVA			
	Equation	df	F		df	F	Multiple comparisons†
1984							
Shell length (mm)							
E1	$y = 14.7 - 0.647x$	57	39.555***	Slope	5,327	0.258	NS
E2	$y = 15.3 - 0.651x$	62	89.439***	Elevation	5,332	23.752***	E1, E2 < I1, I2, I3, P
I1	$y = 19.6 - 0.632x$	33	24.420***				I2 < I1, I3
I2	$y = 16.9 - 0.602x$	90	110.987***				
I3	$y = 21.0 - 0.724x$	62	33.186***				
P	$y = 16.8 - 0.599x$	35	18.763***				
Total mass (g)							
E1	$y = 0.89 - 0.349x$	114	26.787***	Slope	5,470	1.316	NS
E2	$y = 0.70 - 0.168x$	70	3.954	Elevation	5,475	29.059***	E1, E2 < P < I1, I2, I3
I1	$y = 1.98 - 0.358x$	63	28.575***				
I2	$y = 1.52 - 0.281x$	87	17.283***				
I3	$y = 1.99 - 0.447x$	70	14.264***				
P	$y = 1.08 - 0.229x$	78	15.638***				
1985							
Shell length (mm)							
E1	$y = 15.2 - 0.668x$	152	293.789***	Slope	2,262	11.911***	E1, I1 < P
I1	$y = 17.6 - 0.566x$	91	161.449***	Elevation	2,264	170.147***	E1 < I1, P
P	$y = 28.1 - 1.004x$	25	76.040***				
Total mass (g)							
E1	$y = 0.66 - 0.192x$	161	36.001***	Slope	2,300	3.645	NS
I1	$y = 1.94 - 0.357x$	102	48.288***	Elevation	2,302	106.574***	E1 < I1, P
P	$y = 1.90 - 0.411x$	43	24.933***				

*** $P < .001$.

† Those populations separated by an inequality sign were significantly different ($P \leq .05$) with the sign indicating the direction. Populations separated by a comma were not different and if a population was statistically similar to all others, it was not listed.

RESULTS

Growth

Variation in growth rates among populations from different exposure regimes as measured by shell length, total mass, body mass, and shell mass was quite similar so only the results for shell length and total mass will be presented. For the most part, the regressions were highly significant and indicated that growth rates decreased as a function of snail size (Table 2, Fig. 1). Growth schedules (regression slopes) were similar among populations from different exposure regimes for shell length and total mass during the 1984 growing season, indicating that snails from microhabitats that vary in wave energies approach their asymptotic size at comparable rates. Size-specific growth increments (regression elevations), in contrast, varied among populations. Multiple comparisons revealed that snails from intermediate shores generally exhibited the largest size-specific growth increments and reached a larger asymptotic size relative to those on exposed shores, which grew the least and terminated growth at much smaller sizes. Snails from the most protected shore grew at a moderate pace and reached an asymptotic size similar to snails from shores of intermediate wave action.

During the 1985 growing season, snails from the protected shore approached their asymptotic size more quickly than did those from the exposed or intermediate shore when growth was measured using shell length. Because the slopes were significantly different, a Johnson-Neyman test (Huitema 1980) was used to determine the range of initial shell lengths over which size-specific growth rates were similar. Size-specific growth rates were smaller for snails from the exposed shore relative to those from the protected site over the entire size range. Snails from the shore with intermediate wave energies grew more slowly than those at the protected shore until 21 mm in shell length, above which growth rates were similar. The regression slopes for the exposed and intermediate populations were not significantly different, but size-specific growth rates (= intercepts) were greater at shores with intermediate wave action. For most of the size range considered, therefore, size-specific growth rates measured by changes in shell length were inversely correlated with wave action (i.e., E1 < I1 < P); above 21 mm, growth rates did not differ between snails from the intermediate and protected shores (E1 < I1, P). Size-specific growth measured by changes in total mass was also lower on exposed shores. In summary, growth during 1984 and 1985 indicated that snails on exposed shores grew more slowly and attained much smaller adult sizes than did their counterparts on more protected shores.

TABLE 3. Regression lines for $\log_e$ body mass or shell mass on $\log_e$ shell length for snails from the exposed, intermediate, and protected shores during 1984, and the results of an ANCOVA, Tukey multiple comparisons, and Johnson-Neyman test comparing the slopes and elevations of regression lines.

	Regressions			ANCOVA		Multiple comparisons†			
Site	Equation	df	F	df	F	Contrast	Slope	Elevation	Johnson-Neyman test
				$\log_e$ body mass (y) on $\log_e$ shell length (x)					
E1	$y = -9.30 + 2.83x$	278	1052.98***	Slope 5,1184	71.409***	E1–E2	NS	NS	
E2	$y = -8.71 + 2.62x$	200	268.20***	Eleva- 5,1189	73.191***	E1–I1	NS	E1 > I1	
				tion					
I1	$y = -10.92 + 3.25x$	141	2635.46***			E1–I2	E1 < I2		22.7–26.8
I2	$y = -16.26 + 5.01x$	190	1688.90***			E1–I3	E1 < I3		25.9–36.3
I3	$y = -14.11 + 4.26x$	218	1111.20***			E1–P	NS	E1 > P	
P	$y = -11.47 + 3.40x$	157	683.64***			E2–I1	E2 < I1		22.7–26.5
						E2–I2	E2 < I2		21.1–27.1
						E2–I3	E2 < I3		23.2–35.5
						E2–P	NS	E2 > P	
						I1–I2	I1 < I2		18.5–22.6
						I1–I3	I1 < I3		20.5–27.4
						I1–P	NS	NS	
						I2–I3	I2 > I3		9.9–21.3
						I2–P	I2 > P		13.6–22.0
						I3–P	NS	NS	
				$\log_e$ shell mass (y) on $\log_e$ shell length (x)					
E1	$y = -10.39 + 3.41x$	278	3164.64***	Slope 5,1184	273.65***	E1–E2	NS	NS	
E2	$y = -11.05 + 3.57x$	200	3281.78***	Eleva- 5,1189	150.15***	E1–I1	E1 > I1		26.1–+++
				tion					
I1	$y = -9.34 + 3.11x$	141	3118.29***			E1–I2	E1 > I2		33.8–+++
I2	$y = -8.56 + 2.93x$	190	4101.52***			E1–I3	E1 > I3		35.1–+++
I3	$y = -8.95 + 3.04x$	218	5741.72***			E1–P	E1 > P		25.4–27.5
P	$y = -2.23 + 0.92x$	157	151.01***			E2–I1	E2 > I1		30.1–+++
						E2–I2	E2 > I2		36.1–+++
						E2–I3	E2 > I3		37.4–+++
						E2–P	E2 > P		26.3–29.3
						I1–I2	NS	I1 < I2	
						I1–I3	NS	I1 < I3	
						I1–P	I1 > P		24.6–26.4
						I2–I3	NS	NS	
						I2–P	I2 > P		22.2–24.1
						I3–P	I2 > P		22.9–24.3

*** $P < .001$.

† The direction of any significant difference ($P < .05$) in slope or elevation is indicated by the inequality sign for each contrast under the multiple comparisons column. Where slopes are significantly different, the Johnson-Neyman test indicates the range of shell lengths over which the elevations are not significantly different.

Site-specific growth rates were consistent between years with only two (P and E2) of the six sites exhibiting interannual variation. Size-specific growth increments were greater ($F = 5.549$, df = 1,57, $P < .05$) during the 1985 growing season relative to 1984 for snails at the protected shore. At the exposed shore E2, snails grew faster during 1983, both in terms of their approach to their asymptotic size ($F = 15.2$, df = 1,89, $P < .001$) and their size-specific growth rate ($F = 41.29$, df = 1,90, $P < .001$) when compared to 1984. The asymptotic size was quite similar among years at each site, even at those sites where growth rates differed between years.

The resources devoted to protective and nonprotective structures varied among populations (Table 3). Snails from exposed shores tended to have greater body mass and less shell mass than did similar sized individuals from more protected shores. Interestingly, the differences in wet body mass and shell mass among populations diminished in the larger size classes (>21 mm wet body mass and >25 mm shell mass) as evidenced by similar regression elevations (Johnson-Neyman test).

Population size structure

Differences in the size structure of populations closely paralleled exposure regime (Fig. 2). Mean shell length increased with a decrease in wave energies. Populations on exposed headlands (E1 and EP) were dominated by small adults ($\bar{X} = 17–19$ mm) and juveniles (<15 mm) with few snails exceeding 24 mm shell length. On shores with moderate exposure (IP, I3, and I1) populations tended to be dominated by much larger snails ($\bar{X} = 21–24$ mm) as well as a substantial number of juveniles (<20 mm). At the extremely protected shore P, large adults ($\bar{X} = 25.3$ mm) entirely dominated the popu-
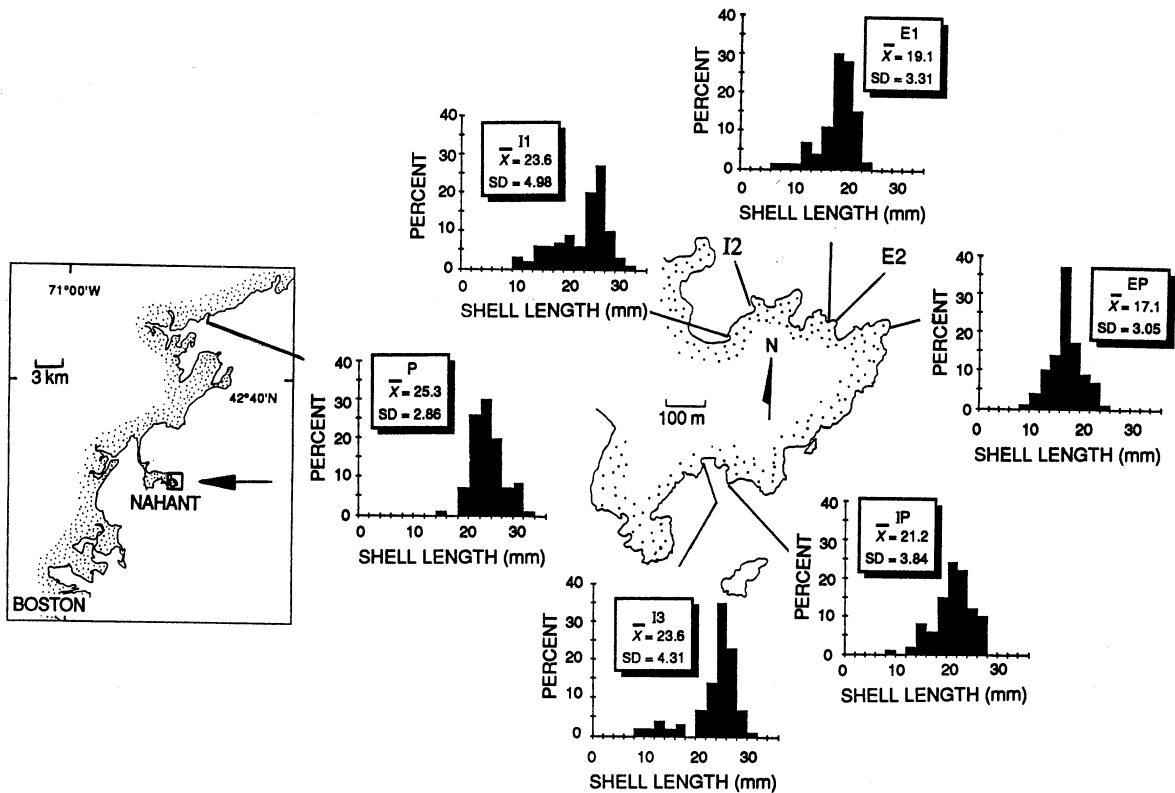
FIG. 2. The location of the exposed (E), intermediate (I), and protected (P) sites along the coast of Massachusetts. The eastern tip of Nahant enclosed in the small box has been enlarged. Histograms show shell length frequency distributions of the first 100 dogwhelks collected from one or two 6400-cm² quadrats. The mean and 1 SD are given within the legend for each population. EP = East point, the most exposed shore at Nahant. IP = a moderately exposed shore located at the tip of a headland within a shallow cove. Sites EP and IP were used exclusively for analyses of shell length frequency distributions. All other sites were used as described in Methods. The data were collected in June 1984.

lation, and juveniles (<20 mm) were virtually absent. The asymptotic size calculated from 1985 and 1984 growth equations also showed an inverse association with wave energies (E1 = 22.7mm, I3 = 29.1mm, I1 = 31.2mm, P = 27.5mm) with few individuals exceeding the asymptotic size.

Mortality rates

The greatest error in estimating mortality rates was at the protected shore where, at any sampling period, an average of 38% (E_m = 0.38) of the marked snails was missed even though they must have been present in the population. The difficulty in finding marked snails at this site was undoubtedly due to the presence of large boulders under which I was unable to sample. The inability to find snails (E_m) tended to decrease with an increase in wave energy (I1 = 0.279, I2 = 0.175, I3 = 0.283, E1 = 0.188, and E2 = 0.216).

Rates at which marked snails were lost from populations varied with the degree of wave exposure (Table 4). Two of the four 1983 regressions were not significant, so comparisons were not made among sites for 1983. During the 1984 growing season, P and I1 suffered the least mortality (≈0.4 and 0.7%/d, respectively) while all other sites suffered much greater mor-

tality rates ranging from 1.5 to 2.3%/d. I3 experienced unusually high mortality in 1984, losing ≈2.3%/d. The reasons for such a high mortality rate are unknown, but the much lower rates during 1983 and where snails were followed from 1983 through 1984 suggest the 1984 values may be unusually high. During the 1985 growing season, the snails at P and I1 suffered the least mortality again (≈1%/d) while those at E1 were lost about twice as fast (≈2%/d). Mortality rates differed between the 1984 and 1985 growing seasons for snails at the protected (df = 1,4; F = 74.23; P < .001) and intermediate sites (df = 1,4; F = 8.23; P < .05). At both sites, mortality rates were greater during 1985. Snails on exposed shores experienced about the same mortality rates during both growing seasons (df = 1,4; F = 1.04).

When mortality rates were followed through both years (1984–1985) for P, I1, and E1, the results showed clearly that snails at P and I1 suffered much less mortality than those at E (Table 4). Mortality rates based on 1–3 yr of data are considerably less than those restricted to the summer growing season because surprisingly little mortality occurs during the winter months when snails tend to be inactive and aggregate in crevices (Feare 1971, Menge 1976). These results

TABLE 4. Regression lines of daily mortality rates ($\log_e$ number surviving vs. time) for populations at protected, intermediate, and exposed shores, and the results of an ANCOVA and Tukey multiple comparisons test comparing daily mortality rates (slopes) among sites. See Table 2 for an explanation of the multiple comparisons column.

Site	Regression			ANCOVA		
	Equation	df	F	df	F	Multiple comparisons
			1984			
P	$y = 4.81 - 0.004x$	2	36.392*	5,12	22.632***	P, I1 < I2, I3, E1, E2
I1	$y = 4.97 - 0.007x$	2	359.630**			I2, E2 < I3
I2	$y = 5.32 - 0.015x$	2	59.121*			
I3	$y = 5.28 - 0.023x$	2	5067.635***			
E1	$y = 5.51 - 0.019x$	2	182.104**			
E2	$y = 4.85 - 0.015x$	2	41.334*			
			1985			
P	$y = 4.85 - 0.010x$	2	743.682**	2,6	19.943**	P, I1 < E1
I1	$y = 5.34 - 0.011x$	2	92.608*			
E1	$y = 5.89 - 0.021x$	2	108.615**			
			1983–1984			
I1	$y = 4.54 - 0.003x$	5	34.686**	3,20	13.294***	I1, I2, I3 < E2
I2	$y = 4.90 - 0.008x$	5	119.379***			I1 < I2
I3	$y = 4.53 - 0.006x$	6	32.821**			
E2	$y = 4.88 - 0.011x$	4	85.619***			
			1984–1985			
P	$y = 4.52 - 0.003x$	6	29.033**	2,17	21.05***	P, I1 < E1
I1	$y = 4.87 - 0.005x$	9	88.487***			
E1	$y = 4.99 - 0.011x$	5	57.560***			

* $P < .05$; ** $P < .01$; *** $P < .001$.

indicate survivorship decreases with increased wave action and suggest that the life-span of *N. lapillus* is much shorter on wave-swept shores.

Size-specific mortality rates

Mortality rates among size classes within sites were not significantly different during the 1984 and 1985 growing seasons suggesting that, above ≈10 mm in shell length, an increase in size does not confer increased survivorship (Fig. 3, Table 5). Only at the exposed shore E1 did size have a significant effect on mortality rates, but a Tukey multiple comparison test was unable to detect any specific differences among pairs of 5-mm size classes. The lack of difference between the smallest size class and the larger size classes may reflect the small number of snails <10 mm. There were few snails <10 mm at the exposed sites and none at the protected and intermediate shores.

When size-specific mortality rates were compared among sites, the results were more complicated (Table 6). Snails between 5 and 15 mm shell length during 1984 and 1985 suffered similar rates of mortality independent of exposure regime. Differences emerged among sites in each of the 5-mm size classes between 15 and 30 mm for 1984, and 15 and 25 mm for 1985. The differences among sites for each particular size class closely paralleled the results which included all size classes. In general, populations at P and I1 suffered much less mortality than those at the other sites, especially exposed shore populations. During 1985, snails >25 mm also suffered similar mortality rates at all three sites, but the sample size at the exposed site was
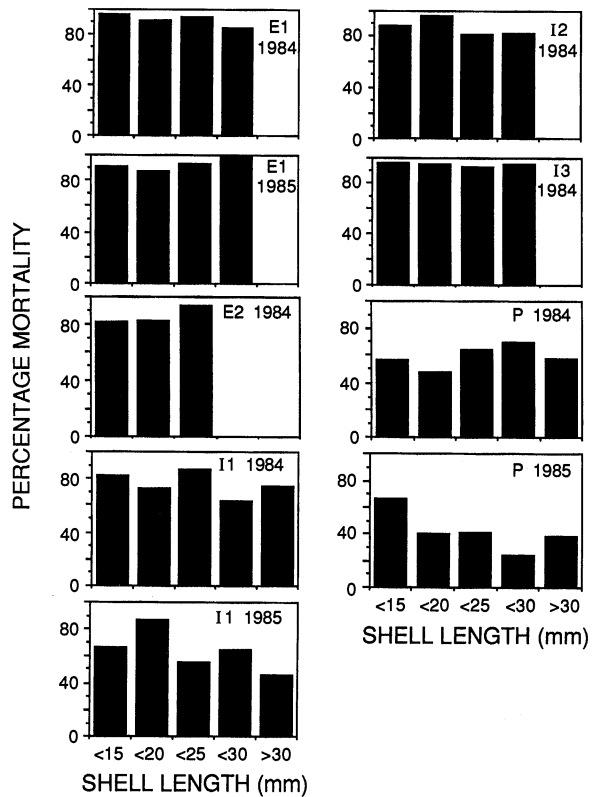

FIG. 3. The percentage mortality of snails in different shell length size classes. Each size class includes only those snails that are larger than the previous size class (e.g., <20 = all snails ≥15 mm but <20 mm).

TABLE 5. Regression lines of daily size-specific mortality rates (log$_e$ number surviving vs. day) for populations at protected, intermediate, and exposed shores, and the results of an ANCOVA comparing daily mortality rates (slopes) among size classes within sites.

		Regression			ANCOVA	
	Size	Equation	df	F	df	F
		1984				
P						
	5–<15	$y = 1.25 - 0.012x$	2	6.479	4,10	2.691
	15–<20	$y = 1.59 - 0.005x$	2	22.830*		
	20–<25	$y = 3.80 - 0.005x$	2	21.506*		
	25–<30	$y = 4.04 - 0.002x$	2	17.147		
	>30	$y = 2.55 - 0.004x$	2	23.302*		
I1						
	5–<15	$y = 1.90 - 0.008x$	2	3.351	4,10	1.922
	15–<20	$y = 2.77 - 0.014x$	2	14.352		
	20–<25	$y = 2.98 - 0.006x$	2	140.813**		
	25–<30	$y = 4.36 - 0.008x$	2	104.668**		
	>30	$y = 3.07 - 0.005x$	2	48.121*		
I2						
	5–<15	$y = 3.88 - 0.017x$	2	90.290*	3,8	3.543
	15–<20	$y = 3.67 - 0.026x$	2	21.808*		
	20–<25	$y = 4.59 - 0.013x$	2	29.847*		
	25–<30	$y = 3.39 - 0.014x$	2	133.588**		
I3						
	5–<15	$y = 2.66 - 0.025x$	2	12.551	3,8	0.111
	15–<20	$y = 2.76 - 0.023x$	2	107.854**		
	20–<25	$y = 4.79 - 0.022x$	2	479.742**		
	25–<30	$y = 3.68 - 0.022x$	2	33.801*		
E1						
	5–<15	$y = 2.38 - 0.020x$	2	111.254**	3,8	4.110*
	15–<20	$y = 4.74 - 0.016x$	2	707.250**		
	20–<25	$y = 4.72 - 0.022x$	2	157.328**		
	25–<30	$y = 1.88 - 0.097x$	2	6.425		
E2						
	5–<15	$y = 4.06 - 0.013x$	2	10.255	2,6	3.634
	15–<20	$y = 3.55 - 0.015x$	2	68.020*		
	20–<25	$y = 3.60 - 0.022x$	2	529.498**		
		1985				
P						
	5–<15	$y = 1.67 - 0.007x$	2	2.532	4,10	0.861
	15–<20	$y = 2.87 - 0.007x$	2	12.156		
	20–<25	$y = 3.68 - 0.010x$	2	141.992**		
	25–<30	$y = 3.98 - 0.012x$	2	74.162*		
	>30	$y = 2.44 - 0.008x$	2	55.947*		
I1						
	5–<15	$y = 3.38 - 0.012x$	2	8.869	4,10	1.188
	15–<20	$y = 3.47 - 0.009x$	2	35.910*		
	20–<25	$y = 4.31 - 0.015x$	2	30.762*		
	25–<30	$y = 4.07 - 0.008x$	2	68.097*		
	>30	$y = 2.63 - 0.011x$	2	26.252*		
E1						
	5–<15	$y = 3.81 - 0.024x$	2	47.589*	3,8	0.945
	15–<20	$y = 4.93 - 0.020x$	2	99.867**		
	20–<25	$y = 5.15 - 0.022x$	2	76.195*		
	25–<30	$y = 1.79 - 0.017x$	2	16.614		

* $P < .05$; ** $P < .01$.

extremely small because few individuals reached this size. The lack of a difference may therefore have reflected a small sample size at the exposed shore. The higher mortality on wave-swept shores appeared to reflect a decreased survivorship for large snails relative to similar sized individuals on more sheltered coasts.

Size at maturity

The shell length at which snails became sexually mature differed between the exposed and protected shore (Fig. 4). Snails on the exposed shore E1 began to mature at 15 mm and all were sexually mature by 20 mm. In contrast, snails from the protected shore P did not

TABLE 6. The results of an ANCOVA and a Tukey multiple comparisons test comparing daily mortality rates within size classes between sites for 1984 and 1985. See Table 2 for explanation of the multiple comparisons column.

Size (mm)	df	F	Multiple comparisons
		1984	
5–<15	5,12	2.007	NS
15–<20	5,12	5.048*	P < I2, I3
20–<25	5,12	31.683***	P, I1 < I2, I3, E1, E2
25–<30	4,10	4.995*	P, I1, I2, I3 < E1
		1985	
5–<15	2,6	4.472	NS
15–<20	2,6	14.602**	P, I1 < E1
20–<25	2,6	5.877*	P < E1
25–<30	2,6	3.468	NS
>30	1,4	1.012	NS

$* P < .05; ** P < .01; *** P < .001.$

begin to mature until 20 mm and at 25 mm a few individuals had yet to develop sexual characteristics. The wet body mass at maturity also indicated that maturation occurred at a slightly larger size on the protected shore, but the difference was not as pronounced. The difference in size at maturity primarily reflected the difference in growth rates between the two populations since most snails at both P and E1 reproduced for the first time in the spring of their 2nd yr.

Fecundity

Although the length, width, and volume of egg capsules were similar among populations during 1984, the number and size of hatchlings differed (Table 7). Egg capsules of *N. lapillus* collected from protected shores released fewer larger hatchlings than those collected from wave-swept shores. Results were consistent whether the comparisons employed shell length or shell width of hatchlings. Hatchlings from shores of moderate exposure generally exhibited intermediate shell dimensions differing from exposed populations in both shell length and shell width. The number and size of offspring produced by *N. lapillus* formed a cline across the wave-energy gradient.

Similar comparisons were made for data collected

in 1985, but as pointed out above, these data were collected from caged adults to enable the number of egg capsules deposited per female to be estimated (Table 8). Capsule length was similar, but snails from the exposed shore deposited wider capsules with larger internal volumes. As in 1984, relatively more and smaller hatchlings emerged from capsules deposited by snails from the wave-swept shore. The most interesting finding was that exposed-shore snails deposited about twice as many egg capsules as did those from the protected shores. Although hatchlings from the exposed shore were ≈20% smaller, snails from the exposed shore deposited twice as many egg capsules with twice as many hatchlings emerging from each, suggesting that reproductive effort was greater on wave-swept shores.

A comparison of the reproductive characteristics between years revealed that the width of capsules deposited in 1984 was similar to 1985, but capsules were shorter for both populations in 1985, resulting in capsules with smaller internal volumes. The mean number of hatchlings emerging from each capsule dropped and their mean size increased for both populations in 1985. As capsule volume decreased, the number of hatchlings deposited in those capsules decreased, demonstrating an interdependence between the number of hatchlings that can develop within a capsule and its internal volume.

Since a portion of the variance in the number of hatchlings emerging from capsules may reflect differences in capsule volume among sites, an ANCOVA and a Tukey multiple comparisons test were performed to determine if differences among populations in number of hatchlings per capsule remained after the confounding differences in capsule volume were removed. For both 1984 and 1985, the number of hatchlings emerging from exposed shore capsules was greater than the number emerging from protected shore capsules (Table 9) when capsule volume was held constant. In 1984 the regression line for capsules from a shore of moderate exposure (I1) fell directly between the exposed and protected lines (Fig. 5) and was not significantly different from either (Table 9). Although regres-
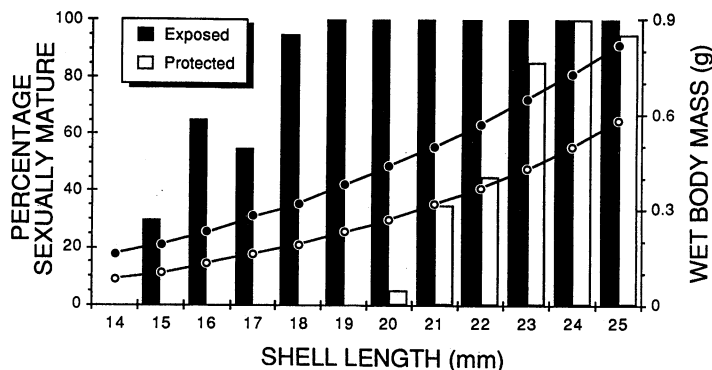

FIG. 4. The percent of 20 exposed and 20 protected individuals within each 1-mm size class between 14 and 25 mm that were sexually mature (bars). The wet body masses predicted from shell length for each size interval are also shown (circles).

TABLE 7. Values for various reproductive characteristics measured in an exposed, intermediate, and protected population during 1984, and the results of an ANOVA and Tukey multiple comparisons test comparing reproductive characters among populations are also given. For an explanation of the multiple comparisons column see Table 2.

Site	N	$\bar{X} \pm$ SE	ANOVA F (2,84)	Multiple comparisons
Capsule length (mm)				
E1	38	5.66 ± 0.085		
I1	27	5.73 ± 0.129	0.699	
P	20	5.60 ± 0.065		
Capsule width (mm)				
E1	38	2.77 ± 0.042		
I1	27	2.70 ± 0.058	1.261	
P	20	2.66 ± 0.042		
Capsule volume (mm³)				
E1	38	185.3 ± 7.36		
I1	27	180.1 ± 10.38	0.906	
P	20	167.5 ± 6.67		
No. hatchlings/capsule				
E1	38	21.3 ± 1.03		
I1	27	18.0 ± 1.91	7.885***	E1 > P
P	20	13.1 ± 1.24		
Hatchling shell length (mm)				
E1	38	1.02 ± 0.014		
I1	27	1.14 ± 0.024	21.196***	P, I1 > E1
P	20	1.19 ± 0.021		
Hatchling shell width (mm)				
E1	38	0.89 ± 0.012		
I1	27	0.97 ± 0.02	13.223***	P, I1 > E1
P	20	0.99 ± 0.021		

*** $P < .001$.

sion lines for exposed and protected shores differed in slope for the 1985 season, a Johnson-Neyman test indicated that elevations were significantly different over the entire range of capsule volumes considered. (The maximum volume considered was 250 mm³. Elevations were not significantly different between 250 and 11801 mm³.)

Variation in hatchling size among populations from different exposure regimes was in part a function of variation in the number of embryos developing within each capsule as evidenced by the strong dependence of hatchling size on the number of embryos within capsules (Table 10, Fig. 6). ANCOVA was used to determine if variation in hatchling size among populations across the wave-energy gradient remained when the number of embryos developing in each capsule was held constant. The least-squares regression lines did not differ in slope among populations for 1984 indicating that the rate at which mean hatchling size decreased as the number of capsulemates increased was similar for all populations. Elevations were significantly different and a Tukey multiple comparisons test revealed that capsules from the exposed shore released smaller hatchlings than did those from the protected or intermediate sites.

The results from 1985 were quite different. The slopes of the regression lines differed, indicating that, in this case, exposed and protected populations varied in the rate at which mean hatchling size decreased as a function of the number of capsulemates (Table 10). The dissimilar rates appear to reflect the fact that the two populations occupy quite different regions of the morphospace defined by those two variables (Fig. 6). A Johnson-Neyman test revealed that where the number of hatchlings per capsule overlapped between exposed and protected populations (8–17 hatchlings per capsule), hatchling size did not differ across a small portion of the overlap zone (11–15 hatchlings per capsule), in direct contrast to the 1984 results. The relationship between hatchling size and the number of hatchlings per capsule was similar for the exposed population between years ($F = 1.25$, $P > .05$), but the slope was steeper in 1985 at the protected site ($F = 13.941$, $P < .001$).

DISCUSSION

The demography and life history characteristics of N. lapillus varied across a wave-exposure gradient on the New England coast. Relative to dog whelks from a protected shore, those on exposed coasts grew more slowly, terminated growth at a smaller size, suffered greater mortality primarily in the larger size classes, became sexually mature at a smaller size, produced more egg capsules per female with many small offspring in each, and appeared to devote more energy to reproduction. The life history characteristics measured in populations from shores of intermediate exposure were typically intermediate between those from protected

TABLE 8. Results of t tests comparing various reproductive characteristics between an exposed and protected population during 1985. The number of egg capsules deposited per female is based on 60 snails divided among 12 cages.

Site	N	$\bar{X} \pm$ SE	t_s
Capsule length (mm)			
E1	120	5.22 ± 0.039	0.055
P	120	5.21 ± 0.063	
Capsule width (mm)			
E1	120	2.77 ± 0.02	5.293***
P	120	2.60 ± 0.024	
Capsule volume (mm³)			
E1	120	169.12 ± 3.18	3.721***
P	120	150.49 ± 3.94	
No. hatchlings/capsule			
E1	72	19.51 ± 0.742	10.437***
P	40	8.32 ± 0.53	
Hatchling shell length (mm)			
E1	74	1.05 ± 0.012	7.703***
P	40	1.27 ± 0.029	
No. egg capsules deposited/female			
E1	12 (60)	21.4 ± 1.61	3.334**
P	12 (60)	12.4 ± 2.17	

** $P < .01$; *** $P < .001$.

TABLE 9. Least-squares regression analysis on the number of hatchlings emerging from an egg capsule vs. capsule volume for a protected, intermediate, and exposed population in 1984 and 1985. Log-transformed regression lines are compared among shores with an ANCOVA and a Tukey multiple comparisons test. The multiple comparisons column is explained in Table 2.

Site	Regression			ANCOVA			
	Equation	df	F		df	F	Multiple comparisons
				1984			
P	$y = 0.429x^{0.652}$	18	1.177	Slope	2,79	0.576	
I1	$y = 0.106x^{0.969}$	25	13.281**	Elevation	2,81	8.428***	P < E1
E1	$y = 0.842x^{0.611}$	36	9.051**				
				1985			
P	$y = 0.004x^{1.478}$	37	11.713**	Slope	1,105	6.182*	
E1	$y = 1.734x^{0.462}$	68	6.361*	Elevation	1,106	114.207***	

* $P < .05$; ** $P < .01$; *** $P < .001$.

and exposed shores. These results are quite similar to variation in life histories of *Littorina* spp. from protected and exposed shores (Emson and Faller-Fritsch 1976, Raffaelli and Hughes 1978, Hughes and Roberts 1981, Hart and Begon 1982, Janson 1982, 1983a). For
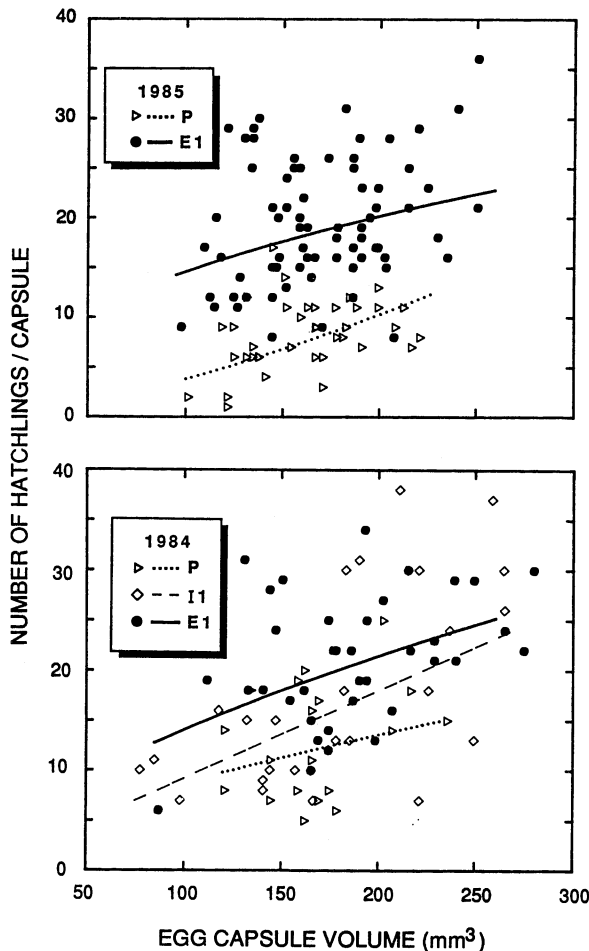

FIG. 5. The number of hatchlings emerging from egg capsules as a function of egg capsule volume for a protected, intermediate, and exposed population. The details of the regression lines are given in Table 9.

instance, *Littorina rudis* on exposed coasts grew more slowly, matured at a smaller size, and produced more offspring of smaller size than did those from protected shores (Atkinson and Newbury 1984). The fact that two distinct groups of snails with different life-styles possess quite similar variation in their life histories across wave-exposure gradients suggests that these "strategies" represent successful solutions to the environmental problems encountered by intertidal snails inhabiting shores that vary in wave energy.

The observed variation in life history traits is consistent with the accepted schemes predicted by classical theoretical models of life history evolution: low growth rates, early maturity, high reproductive effort with many small offspring vs. high growth rate, late maturity, low reproductive effort, and few large offspring (Stearns 1977). The conditions under which natural selection favors a particular suite of characters differ between the two basic models of life history evolution. In the more deterministic model (*r* and *K*-selection) density-independent mortality favors the former suite of characters and density-dependent mortality favors the latter (MacArthur and Wilson 1967). The stochastic model, in contrast, predicts the first suite of characters when adult mortality is high and the second suite when juvenile mortality is high (Stearns 1976). In addition to separating the genetic and phenotypic components of life history characteristics, it is important to identify the ecological and evolutionary forces that shape these characters. Several biotic and abiotic factors covary with wave exposure and each may proximally or ultimately affect the life histories of intertidal organizations.

Growth

Growth was found to vary among sites with the highest rates observed on the protected and intermediate shores. These results were consistent across years and independent of the particular character measured. Variation in growth among populations from different exposure regimes may reflect a multitude of factors. For instance, the first and most obvious is food avail-

TABLE 10. Least-squares regression analysis of mean size of hatchlings from a capsule vs. the number of hatchlings emerging from that capsule for a protected, intermediate, and exposed population in 1984 and 1985. Regression lines are compared among shores with an ANCOVA and a Tukey multiple comparisons test. The multiple comparisons column is explained in Table 2.

	Regression			ANCOVA			
Site	Equation	df	F		df	F	Multiple comparisons
				1984			
P	$y = 1.36 - 0.013x$	18	29.707***	Slope	2,79	0.747	
I1	$y = 1.31 - 0.010x$	25	33.368***	Elevation	2,81	13.166***	P, I1 > E1
E1	$y = 1.23 - 0.010x$	36	34.399***				
				1985			
P	$y = 1.60 - 0.040x$	37	15.795***	Slope	1,105	37.504***	
E1	$y = 1.19 - 0.007x$	68	42.228***	Elevation	1,106	7.535**	

** $P < .01$; *** $P < .001$.

ability. The food available to a particular organism is a function of prey density, predator density, and the time available for foraging. Menge's (1976, 1978a, b, 1983) work on intertidal community structure and predation intensity along exposure gradients, which involved several of the shores considered in this study, shows quite clearly that food availability is greater at exposed shores and decreases as shores become more sheltered. The only difference I observed from these published descriptions was that at the protected shore (P) barnacles covered >60% of the available primary space at all tidal levels, except the very lowest (below MLT) where mussels predominated. The small amount of unoccupied primary space and the high percent cover of barnacles indicate that food reserves were also quite abundant on protected shores. Growth rates of N. lapillus were unrelated to prey density in the present study; at exposed shores prey were abundant but growth was low whereas higher growth rates were observed on more protected shores even though food was less abundant. Shores of intermediate exposure supported the highest growth rates despite having the least amount of prey.

The direct and indirect effects of wave action on foraging time and efficiency may have a more pronounced effect on the growth of intertidal snails. Menge (1978a, b) proposed that high wave energies on exposed coasts limited the foraging time and efficiency of intertidal predators and demonstrated that N. lapillus from both exposed and protected shores consumed fewer mussels on exposed shores relative to protected shores. Brown and Quinn (1988) found that the growth rates of three intertidal gastropods, N. emarginata, Collisella digitalis, and Collisella scabra, were lower on an exposed shore relative to a more sheltered coast and, by reciprocally transplanting snails between sites, demonstrated that the reduced growth on the exposed shore was environmentally induced. They suggested growth was suppressed on exposed shores because the high wave energies reduced foraging time and thereby reduced energy available for growth. Growth rates of N. lapillus reciprocally transplanted

between exposed and protected shores were also lower on exposed shores and may, in part, reflect reduced foraging time and efficiency imposed by increased wave action (Etter 1987). Physiological stress from desiccation and heat load decreases with wave exposure (Etter 1988b) and has been shown to limit foraging time (Menge 1978a, b, Moran 1980, Spight 1981, 1982,
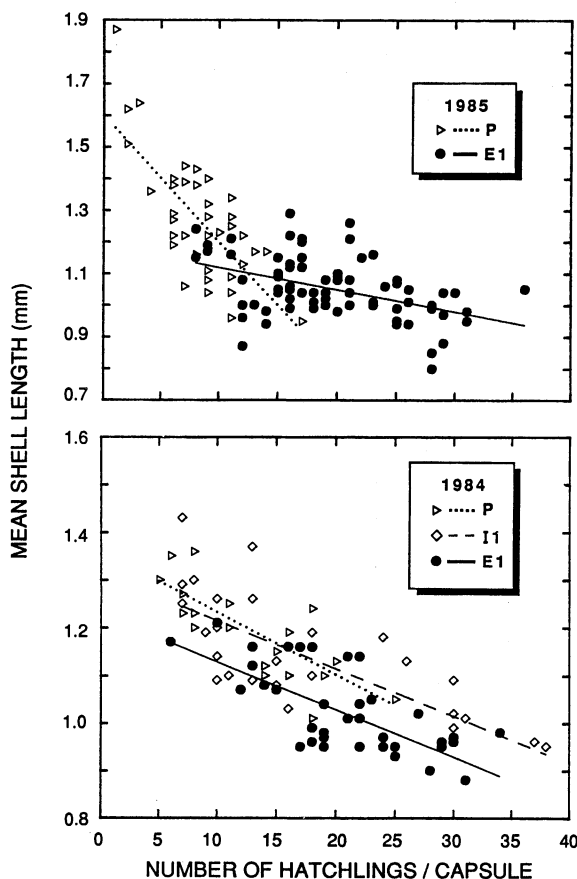

FIG. 6. The mean hatchling shell length as a function of the number of hatchlings emerging from each capsule for a protected, intermediate, and exposed population. The details of the regression lines are given in Table 10.

Garrity 1984), but because physiological stresses operate over a much shorter time of the potential foraging period (only during diurnal low tides) these constraints should be less important. This hypothesis may partially explain why snails on intermediate shores have growth rates as high or higher than snails on protected shores despite having less food available and experiencing greater wave action. Intermediate shores were covered by a blanket of erect macroalgae (Menge 1976, 1978*a*, *b*, R. Etter, *personal observation*) which would tend to reduce physiological stress during tidal emersion and may permit greater foraging time relative to protected shores.

Prey quality is known to affect growth rates in several marine invertebrates (Vadas 1977, Palmer 1983*a*, Moran et al. 1984). Mussels and barnacles are the primary prey of *N. lapillus* and their relative abundance varies across the exposure gradient (Menge 1976, Petraitis 1987*a*, R. Etter, *personal observation*). Mussels dominated at exposed shores whereas barnacles became relatively more abundant with decreased wave energy. Mussels support less growth than barnacles in closely related muricids (Palmer 1983*a*, Moran 1984), so the lower growth of snails on exposed shores may reflect a diet high in mussels.

Finally, the allocation of energy to reproduction may differ among populations. The reproductive biology of *N. lapillus* (discussed below) suggests that exposed populations devote more energy to reproduction. Since this would diminish energy available for growth, low growth rates may be a consequence of a greater reproductive effort. According to this hypothesis, growth rates of *N. lapillus* from exposed and protected shores should be similar before reaching sexual maturity (assuming maintenance costs are similar at exposed and protected shores) because before maturation all net energy is channeled into growth. Osborne (1977) found that snails below ≈13 mm grew at similar rates, independent of exposure, while above 13 mm exposed shore snails grew more slowly. Interestingly, exposed shore whelks begin to mature at this size, suggesting a trade-off between growth and reproduction. Because all of these forces are likely to be operating, future research efforts should experimentally identify the relative importance of each in altering growth rates among populations from different exposure regimes.

Asymptotic size and size at maturity

The size at which snails mature and asymptotic size are tightly linked because *N. lapillus* tends to cease growth at maturity. Asymptotic size varied among shores with snails on exposed coasts ceasing growth at smaller sizes. The asymptotic size for each population was remarkably consistent through the 3 yr (varying <2 mm) indicating that the forces governing maximum size exhibit little temporal variation or that asymptotic size is under tight genetic control.

Small adult size may be favored on exposed shores

because large snails are more vulnerable to dislodgement by wave action. That intertidal organisms tend to be smaller on wave-swept shores has frequently been observed (Lewis 1968, Harger 1970, Connell 1972), especially for snails (Emson and Faller-Fritsch 1976, Osborne 1977, Raffaelli and Hughes 1978, Crothers 1983, Brown and Quinn 1988). Denny et al. (1985) provided both theoretical and empirical evidence that wave energies can impose mechanical limits on the size of intertidal organisms, although their results for two closely related muricids suggested size limits were likely to be biological in nature. In the present analysis, large *N. lapillus* on wave-swept shores suffered greater mortality than similar sized individuals on more sheltered coasts, probably due to dislodgement by waves. Predation should be less important because exposed shores generally suffer less predation (Menge 1978*a*, *b*, 1983) and what predation exists, appears to be more intense on juveniles (Feare 1969). On the other hand, small adult size may be a simple consequence of the low growth rates and higher mortality rates on exposed shores, reducing the probability that any will survive long enough to become large. I have followed marked individuals at the protected shore P and the intermediate shore I1 for 4 yr, and several individuals were at least 2 yr old when marked. No snails have survived >2 yr at the exposed shores.

A larger asymptotic size may be favored on less exposed shores because *N. lapillus* suffers more intense predation (Kitching et al. 1966, Menge 1983), and larger individuals are less vulnerable to predation (Ebling et al. 1964, Kitching et al. 1966, Vermeij 1978, Hughes and Elner 1979, Lawton and Hughes 1985, Palmer 1985). In addition, small rocks and boulders were present at the intermediate and protected sites and a recent study by Shanks and Wright (1986) indicates that wave-borne rocks can dramatically increase mortality of intertidal organisms, especially small individuals. Although the size-specific mortality data in this study revealed no consistent pattern with size within sites, very few snails <10 mm were used and consequently the most vulnerable size classes were not analyzed. Increased predation and crushing by boulders may also select for the higher growth rates observed on more protected shores. Snails may channel more energy into growth to grow quickly out of those size classes that are at risk. The relatively heavier shell produced by snails from more sheltered coasts may also reflect the more intense predation and crushing by wave-borne rocks. The maximum difference in shell mass among populations from the exposed and protected shores was in the smaller size classes which is precisely where they would be most vulnerable to predation or crushing.

Size structure

A marked change in the size structure of *N. lapillus* populations paralleled wave exposure. Populations on exposed shores were dominated by small adults with

many juveniles. Intermediate- and protected-shore populations were dominated by large adults and all had a fair number of juveniles, except the protected population. The maximum size in each population undoubtedly reflects the factors influencing asymptotic size. The absence of juveniles at the protected shore is more enigmatic. The fact that juveniles grow rapidly and spend little time in smaller size classes, reducing the likelihood of being found, is insufficient as an explanation for their absence, since one would expect similar results at intermediate sites. Three other explanations are possible and are not mutually exclusive. (1) Protected populations produce fewer offspring, reducing the chances of finding juveniles. The data on fecundity indicate that protected-shore snails produce many fewer offspring. (2) Juvenile mortality is higher. At least for snails >10 mm, the mortality data do not support this notion. Mortality rates were similar among all size classes at the protected shore. However, as noted above, the sample sizes were small and more work with smaller individuals is necessary. (3) Juvenile behavior may reduce the probability of capture. The protected site was the only shore with large boulders under which I was unable to sample. If juveniles remained under boulders they would be missed during sampling. To test the importance of this idea for explaining the low number of juveniles, I turned over 20 large boulders in June 1985 and one or two juveniles were present under more than half (12). The absence of juveniles on the protected shore may be partially explained by this evidence that young snails hide under boulders, but it is insufficient to explain the low numbers fully.

Mortality rates

Rates of mortality and their size-specific schedules are important forces shaping life history characteristics. Gradients in both mortality rates and size-specific schedules were apparent among populations differentially exposed to wave action. *N. lapillus* on exposed shores experienced the highest mortality rates while those on protected shores suffered the least. Mortality rates on moderately exposed shores varied between those on exposed and protected shores. The difference in mortality rates among sites reflected differences in the survivorship of snails >15 mm. The size-specific mortality rates indicated that individuals >15 mm on exposed shores suffer greater mortality than similar sized individuals on intermediate and protected shores. Why should large snails experience lower survivorship on wave-swept shores? Predation, dislodgement resulting from wave generated forces, and immobilization by mussels probably represent the major sources of mortality for *N. lapillus*. Predators of *N. lapillus* include crabs (Ebling et al. 1964, Kitching et al. 1966, Hughes and Elner 1979, Lawton and Hughes 1985), fish (Connell 1961, Chao 1973), and birds (Connell 1961, Feare 1966*a, b,* 1970, 1971, Feare and Summers

1986), but the few studies which have attempted to assess the natural impact of these predators on *N. lapillus* have concluded that they are generally unimportant sources of mortality, especially on adults (Menge 1976, Osborne 1977, Lubchenco and Menge 1978, Bertness et al. 1981, Etter 1988*b*). Purple Sandpipers offer the only exception; they were responsible for 93% of the 89% mortality of *N. lapillus* yearlings on an exposed British shore (Feare 1969). But since the largest size taken was <10 mm shell width, this could not account for the increased mortality of large snails (>15 mm) at the exposed shores.

A more plausible explanation is that larger snails on exposed coasts are subjected to greater drag forces increasing the probability of dislodgement which may carry them into the subtidal zone and expose them to a more diverse predator guild. Two lines of evidence support this notion. (1) When a size range of 60 *N. lapillus* was tethered intertidally for >3 mo (September–December) at an exposed shore, virtually no mortality occurred (Etter 1988*b*), suggesting that predation rates were extremely low and few individuals were lost if snails were prevented from being washed off the shore. (2) When 200 small (<20 mm) and large (>20 mm) exposed shore snails were marked and released on an exposed shore, significantly more of the larger snails were found subtidally and fewer found intertidally (R. Etter, *personal observation*). Recovery rates for both groups were similar. Another problem large snails on exposed shores face is a decrease in the availability of crevices that can be exploited as refuges from wave action. Emson and Faller-Fritsch (1976) increased the mean shell length of populations of *L. rudis* by increasing the size of crevices. Raffaelli and Hughes (1978) observed a strong correlation between the size of intertidal crevices and the sizes of *L. rudis* and *L. neritoides* on an exposed shore, but no correlation on more protected shores. However, Atkinson and Newbury (1984) recently showed that larger *L. rudis* suffered mortality rates comparable to smaller individuals and thus outgrowing crevices did not appear to be an important problem.

A recent study by Petraitis (1987*b*) demonstrated that *N. lapillus* suffered high mortality rates when the mussel *Mytilus edulis* immobilized attacking individuals with byssus threads. Since the exposed shores are primarily covered by mussels, the higher mortality rates at these sites may also reflect immobilization by *M. edulis*. Larger individuals may be more at risk because they present a greater target area for the attachment of byssi. Invariably there were empty shells of *N. lapillus* entrapped by byssi on the exposed shores, but it was impossible to determine how many of these were alive when the byssi were attached.

Reproductive characteristics

The reproductive biology of *N. lapillus* varied considerably among populations from different exposure

regimes. Relative to snails from the protected shore, those from the exposed shore produced about twice as many capsules that contained nearly twice as many hatchlings, suggesting that whelks from the exposed shore produce four times as many offspring. This contrasts with the typical pattern for muricids where large snails deposit larger capsules with more offspring in each (Spight et al. 1974, Spight and Emlen 1976, Crothers 1985). The smaller adults at the exposed shore (in terms of body mass protected morphs were 40% [calculated from average adult size in each population] larger than exposed morphs), in this case, produced more rather than less offspring, and thus the relationship between fecundity and adult body size may only hold within populations. Although the size of hatchlings emerging from exposed shore capsules was 20–30% smaller, four times as many were produced, suggesting that individuals on exposed coasts allocate substantially more energy to reproduction. This, of course, assumes that the energy to produce an offspring of unit size is similar among shores. Numbers of hatchlings emerging from exposed shore capsules were quite similar to the number Feare (1970) obtained from an exposed shore population on the British Coast, but the number of capsules deposited per female differed considerably from estimates by Hughes (1972). This difference may be due to the technique Hughes employed in estimating number of capsules per female. Fretter and Graham (1985) give values similar to those found at Nahant.

The difference in the number of capsules deposited by snails from the exposed and protected populations in this study may be an artifact of maintaining snails in the laboratory. Although it is impossible to say definitively, there are several facts that argue directly against this notion. First, gametogenesis begins >1 yr before snails deposit egg capsules (Feare 1970) and because snails stop feeding during the winter, most of the energy used to produce gametes is obtained during the previous summer. Therefore, it is unlikely that laboratory conditions during a short interval before depositing capsules would have much of an effect on either population. Second, the differences in reproductive data between 1984 and 1985 (capsules were smaller and the number and size of hatchlings decreased in 1985) are opposite of what would be expected if maintaining snails continually immersed with an ample supply of food increased the energy available for reproduction. Finally, if maintaining the snails in the laboratory was stressful, the effects should be more pronounced on snails from exposed shores since laboratory conditions most closely approximate the protected environment. The snails from the exposed shore, however, deposited more capsules, just the opposite of what would be expected if they were stressed.

If egg capsules are energetically expensive to produce (Perron 1981), why do populations differ in the number of hatchlings deposited in a capsule of similar volume?

Even when the larger size of protected shore hatchlings is considered, capsules from exposed shores contain greater biomass. The answer to the above question is unknown, but the lower water velocity at the protected shore may have important consequences. As pointed out above, snails on protected shores will tend to suffer greater physiological stress and more intense predation. If capsules act as protective structures from physiological stress and/or predation (Spight 1975, 1977, Pechenik 1978, 1979, 1982, 1983, Perron 1981) and the protective quality depends on capsule wall thickness (Perron 1981, Pechenik 1982, 1983), then greater physiological stress or predation may select for thicker capsule walls. Although the thicker walls may act as a deterrent to rapid osmotic flux (Pechenik 1982), they may also slow the exchange of oxygen and waste material, and thereby place constraints on the number of embryos that can develop within the capsules (Perron and Corpuz 1982, Strathmann and Chaffee 1985). Thicker capsule walls would also reduce the internal volume.

In addition to differences in reproductive effort and the packaging of embryos, populations appeared to differ in the allocation of energy to offspring. The hatchling size data suggest that whelks on protected shores invest greater energy per offspring than do those on exposed coasts. This result rests on the assumption that hatchling size accurately reflects energy invested. Pechenik et al. (1984) compared the total mass (shell mass + tissue mass) and the tissue mass of *N. lapillus* hatchlings of different sizes. The analysis showed that increases in hatchling shell lengths greater than ≈ 1.02 mm (maximum size considered ≈ 1.20 mm) were accompanied by an increase in total mass but not tissue mass. These results suggest that many hatchlings with shell lengths >1.02 mm are adding shell material but not body tissues. The difference between populations may therefore reflect differences in shell calcification.

The size at which hatchlings emerge from an egg capsule is likely to influence their fitness. Spight (1976) proposed that hatchlings should be larger where environmental stresses are more severe because larger hatchlings (1) tolerate physiological (desiccation and high temperatures) stresses better, (2) are less susceptible to predation, (3) can survive longer periods of starvation, (4) can travel greater distances to find food, and (5) can choose from a wider array of prey. Since protected shores tend to suffer greater levels of predation (Kitching et al. 1966, Menge 1978*a*, *b*, 1983) and greater physiological stresses (Etter 1988*b*) relative to exposed shores, the emergence of larger hatchlings on protected shores is consistent with Spight's (1976) hypothesis, but the putative selective mechanisms favoring larger sized offspring require experimental verification. Rivest (1983) demonstrated that larger hatchlings of the rocky intertidal gastropod *Searlesia dira* were less likely to be preyed upon by hermit and small brachyuran crabs. Larger hatchlings of *N. lapillus* (>1

mm) were also less susceptible to predation by *Carcinus maenas* juveniles (carapace width < 5 mm) and survived longer periods of desiccation (R. Etter, *personal observation*). However, field experiments are still necessary to show that these are the forces operating in nature.

Knowledge of the conditions favoring particular life history traits is crucial for developing theories about life history evolution. Moreover, life history variation will have important ramifications for understanding population dynamics, biotic interactions (competition, predation, mutualism, etc.), and the role of particular species in structuring communities. The life history characteristics of *N. lapillus* vary considerably among populations distributed across a wave-energy gradient, indicating that wave action and its ecological correlates can have a profound influence on life histories. Although the variation fits accepted schemes of life history evolution, future research efforts need to separate the genetic and ecophenotypic components of this variation and experimentally identify the relative importance of the proposed ecological factors in shaping life histories.

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