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PHYSIOLOGICAL STRESS AND COLOR POLYMORPHISM IN THE INTERTIDAL SNAIL *NUCELLA LAPILLUS*

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Abstract.—The intertidal snail *Nucella lapillus* exhibits considerable variation in shell color both within and between populations differentially exposed to wave action. Populations from high-wave-energy shores tended to be highly polymorphic and were dominated by pigmented morphs (especially brown), while those at more sheltered locations exhibited less polymorphism and were predominantly white. Field and laboratory experiments were conducted to determine the role of physiological stress and selective predation in maintaining the observed distribution of color morphs.

The results demonstrated that 1) physiological stress from high temperature and desiccation during periods of tidal emersion was greater on protected shores, 2) under similar natural conditions, brown morphs heated up faster, attained higher temperatures, desiccated more rapidly, and suffered greater mortality than did white morphs, and 3) when pairs of brown and white morphs were tethered intertidally there was virtually no mortality of either morph on the exposed shore or in shaded microhabitats on the protected shore, but brown morphs suffered much greater mortality in sunny microhabitats on the protected shore. These findings demonstrate that the interpopulation variation in shell color of *N. lapillus* is in part a response to a selective gradient in physiological stress. Selection for crypsis by visually hunting predators did not appear to play a prominent role; however, only adults were considered, and the predation experiments were conducted in the fall before shorebirds that prey on whelks had arrived from their summer feeding grounds. Further experimentation to quantify the effects of visual predators such as birds and fish, particularly on juvenile snails, is necessary to assess adequately the importance of predation.

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Many intertidal gastropods are highly polymorphic for shell color but are unlike their terrestrial counterparts (Sheppard, 1951; Jones et al., 1977; Bantock and Ratsey, 1980; Cain, 1983) in that virtually nothing is known about the processes favoring this polymorphism. Variation in shell color often seems to parallel background coloration, leading investigators to invoke selection by visual predators as the mechanism maintaining the polymorphisms in several species (*Nerita forskalii* and *N. polita* [Safriel, 1969], *Thais lamellosa* [Spight, 1976], *Crepidula convexa* [Hoagland, 1977], and *Littorina* spp. [Heller, 1975; Smith, 1976; Reimchen, 1979; Hughes and Mather, 1986]). However, only two recent studies have actually tested this hypothesis (Reimchen, 1979; Hughes and Mather, 1986). Similarly, reflexive selection (Safriel, 1969) and apostatic selection (Smith, 1976; Atkinson and Warwick, 1983; Hughes and Mather, 1986) have been proposed as possible selective mechanisms, but these are unsupported by experimental evidence. Some studies have suggested that shell coloration may be of no selective importance (Fischer-Piette et al., 1963, 1964) or that selection may be operating on characters closely linked to shell color (Berry and Crothers, 1974; Raffaelli, 1979; Berry, 1983; Sergievskii and Berger, 1984). Our nescience concerning the processes involved in maintaining shell-color polymorphism in intertidal gastropods reflects a lack of experiments designed to falsify or identify the relative contribution of alternative explanations.

Nucella lapillus is a widely distributed intertidal snail that exhibits considerable variability in shell color (Berry and Crothers, 1974; Osborne, 1977). Several hypotheses have been proposed to explain this variation. Cooke (1895) and Colton (1916, 1922) noted a correspondence between shell color and substrate color and argued that variation in shell color might be related to selection for protective coloration. Burton (1932) and Berry (1983) found no correlation between shell and substrate color, indicating that if visual selection is operating its importance may vary spatially and/or temporally. Moore (1936) suggested that diet influenced shell color and reported that when pigmented morphs that had previously been eating mussels were fed a diet of barnacles they began to form unpigmented shells. More recent studies (Rowland, 1976; Osborne, 1977; Berry, 1983; Etter, unpubl.) have indicated that basic shell color is unaffected by diet, although intensity of pigmentation might be slightly altered. Breeding experiments have shown that shell color and banding in a closely related muricid, *Thais* (=*Nucella*) *emarginata,* is directly inherited (Palmer, 1984, 1985), and it is quite likely that shell color in *N. lapillus* is also genetically controlled. In other studies, a slight correlation between frequencies of pigmented morphs and wave exposure has been noted, suggesting that natural selection might be operating on physiological and/or morphological traits that are genetically correlated with shell color (Berry and Crothers, 1974; Osborne, 1977; Berry, 1983). Despite the numerous hypotheses invoked to explain variation in shell color within and between populations of *N. lapillus,* as well as in other prosobranchs, the paucity of experimental evidence has precluded an understanding of the importance of shell color or its polymorphism. Here, I describe the results of a series of field and laboratory experiments designed to determine the forces mediating shifts in shell color among populations of *N. lapillus.*

The frequencies of the basic color morphs (ignoring banding) of *N. lapillus* along a portion of the Massachusetts coast are depicted in Figure 1. Although the basic shell colors exhibit continuous gradation in intensity of pigmentation, the color morphs were easily distinguished, and each shell was assigned to one of six color categories. Morph frequencies and degree of polymorphism roughly parallel gradients in wave exposure. As one moves from exposed headlands to more sheltered bays and inlets, there is a reduction in polymorphism and a shift from populations dominated by pigmented morphs (particularly brown) to populations that are monomorphically white. This pattern is especially apparent around the eastern tip of Nahant, MA (see inset in Fig. 1). Populations at the most exposed shore (East Point) are highly polymorphic with a predominance of brown morphs, while at the relatively more sheltered sites (Canoe Beach Cove and Pump House Cove) there is a reduction in polymorphism and a shift to populations dominated by white morphs. At an extremely protected shore (Mackerel Cove) about 15 km north, there is a complete loss of pigmented morphs. The pattern is less obvious around the tip of Cape Ann (Gloucester). Although populations on relatively protected shores are again dominated by white morphs, those on more exposed headlands are not consistently dominated by brown morphs.

Hypotheses

The predation hypothesis simply suggests that predators remove those individuals that are not cryptic. White shell color should therefore be favored on protected shores, where barnacles cover most of the intertidal zone (Etter, 1988), and brown shell color should be favored on exposed shores, where the intertidal zone is dominated by mussels (Etter, 1988). Several types of visual predator may be involved in imposing this selection pressure, including crabs, fish, birds, and mammals. It is unclear whether crabs possess the spectral sensitivity to detect colors, but they may be selecting snails that contrast maximally with the substratum. Accordingly, crabs need not distinguish among the various color morphs but could simply select between pigmented and nonpigmented morphs on either light or dark substrata.

Snails on shores that are sheltered from high wave energies may experience more severe desiccation and thermal stress during periods of tidal emersion than do their counterparts on exposed shores (Dayton, 1971; Osborne, 1977). This difference may exist for two reasons: 1) snails on protected shores are splashed and sprayed less by breaking waves; and 2) sheltered shores in this study tend to be covered primarily by barnacles (pers. observ.), while mussels and small fucoids often occupy up to 100% of the space on exposed shores (Lewis, 1964; Menge, 1976). Mussel beds retain more water at low tide, and the evaporation of the water during periods of tidal emersion may reduce temperatures and increase humidity on exposed shores, especially close to the substrate surface, where snails live. An increase in the severity of physiological stress on protected shores may favor white shell color because it has a higher reflectance

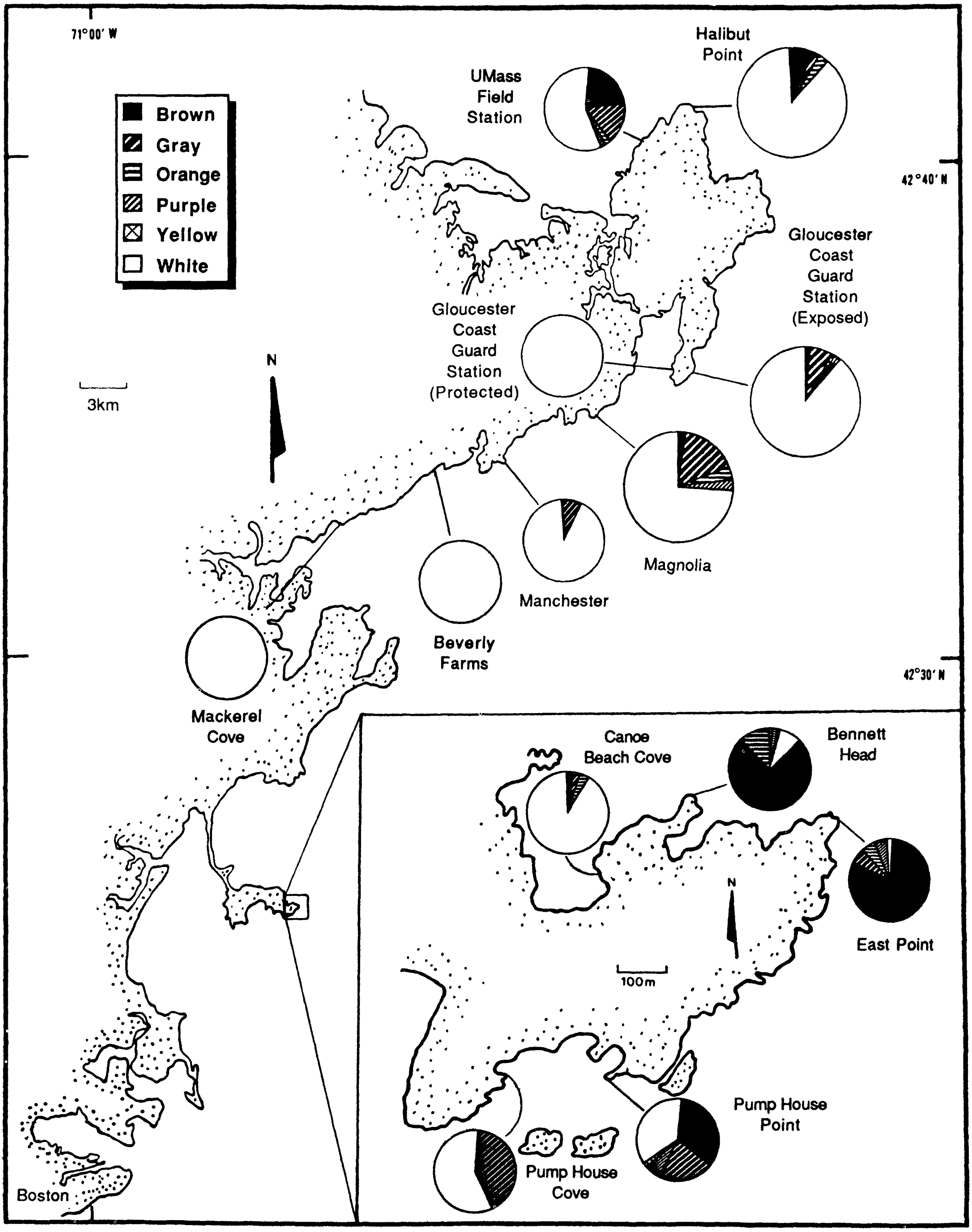

FIG. 1. The distribution of background shell color among populations of *N. lapillus* along the northern coast of Massachusetts. The circles show the proportion of the population with a particular shell color.

for incident visible solar radiation, which may act to reduce tissue temperatures, water loss, and/or mortality. The higher heat load on pigmented morphs due to solar radiation may restrict their foraging time or decrease foraging efficiency on protected shores or simply increase their mortality. Under this hypothesis shell color is free to vary on exposed shores, where there is no selection for or against any particular morph.

MATERIALS AND METHODS

Study Sites

The experimental field work was conducted primarily at three sites located on the northern coast of Massachusetts (Fig. 1): 1) East Point, Nahant, MA, 2) Bennett Head, Nahant, MA, and 3) Mackerel Cove, Beverly, MA. Study sites were chosen to represent the extremes in exposure to wave action typical of shores along the coast of New England. East Point and Bennett Head are shores that experience high wave energies, while Mackerel Cove is considerably more sheltered. More detailed descriptions of the physical and biological characteristics of these sites are given in Etter (1988).

The snails for the experiments were collected from one of the exposed shores (Bennett Head or East Point) or from the protected site (Mackerel Cove). The color morphs in the text will be referred to by the following abbreviations: Brown (B), Brown banded (Bb), Orange (O), White from an exposed shore (W_e), and White from a protected shore (W_p). Since the snails at Mackerel Cove are monomorphically white, all pigmented morphs were collected from exposed shores. White morphs were collected at both exposed and protected shores and are kept separate in the analysis because they differ in shell thickness and shell shape (Ebling et al., 1964; Kitching et al., 1966; Osborne, 1977) and often differ in the degree of shell surface erosion (the outer shell surface of many snails at Mackerel Cove were highly eroded and/or partially covered with a microfilamentous algae).

Laboratory Experiments

The first experiment was designed to investigate the potential for differential heating of the various color morphs by following the internal temperatures of empty shells. Five replicate snails of each of five color morphs (B, Bb, O, W_e, and W_p) with minimum differences in morphology (size, shape, sculpture, etc.) were collected, and the soft body parts were removed from the shell by boiling the snails in seawater and extracting the body tissues with a pair of forceps. The aperture of each shell was then sealed with silicone glue and filled with seawater. The seawater was added to approximate the thermal properties of living snails and because it damps rapid fluctuations in temperature, facilitating more accurate temperature measurements. A fine (0.4-mm) copper-constantan thermocouple was inserted through the silicone seal and connected to a portable chart recorder (model 142, Omega Engineering, Stamford, CT) through an ice-point reference. The shells were placed in direct sunlight, and the temperature of the internal seawater was recorded hourly over the day (7 June 1985). All thermocouples were shielded from solar radiation, including infrared.

A similar experiment was conducted with live snails to determine whether there were physiological mechanisms associated with thermal balance which might negate any differential heating observed in the internal temperature experiment described above. Five replicate snails of four color morphs (B, Bb, W_e, and W_p) with minimum differences in morphology, were collected from Bennett Head and Mackerel Cove and maintained completely submerged in flow-through seawater tables for 24 hours prior to the beginning of the experiment. This procedure reduces differences among snails in their extravisceral fluid and their tissue temperatures. Individuals were removed from the seawater tables and placed aperture-down in a systematic design on a large concrete platform just outside the laboratory on a cloudless summer day (26 July 1984). The platform had a southern aspect and received direct sunlight for most of the day (9:00 A.M.–5:00 P.M.). A thermocouple was inserted through the aperture of each snail until it made direct contact with the pedal tissues. Tissue temperatures of the snails were recorded at irregular intervals over 2.5 hours.

Desiccation rates of B and W_p morphs were examined to determine whether shell color influenced the amount or rate of water loss from snails during periods of aerial exposure. The extremes in shell pigmentation were used to estimate maximum difference in shell-color-dependent water loss. Thirty B morphs from Bennett Head and 30 W_p morphs from Mackerel Cove were collected and again maintained submerged for at least 24 hours in a seawater table. Snails were then removed from the seawater, gently patted dry with tissue paper, weighed (±0.01 g), and placed on a large sheet of plexiglas. The order in which the snails were weighed was haphazard, but B and W_p morphs were alternated. After the snails were positioned on the plexiglas sheet, it was placed outside in direct sunlight, and the amount of water lost from each snail was estimated from weight changes recorded at irregular intervals over five hours. The experiment was conducted on 25 July 1984, a clear sunny day, with temperature ranging between 26.1°C and 27.7°C and humidity ranging between 33% and 37%. The snails were resubmerged in seawater tables for 24 hours before the number of snails of each color morph that survived the experiment was determined by noting which individuals responded to a stimulus (poke from a dissecting probe) by contracting into the shell.

The desiccation experiment described above reveals differences in water loss and mortality between W_p morphs from a protected shore and B morphs from an exposed shore, but differences between these populations cannot be attributed solely to shell color. The reasons for this are twofold. First, snails from protected shores are likely to be acclimated to greater desiccation stresses and might be less sensitive to desiccation. Second, desiccation rates during tidal emersion are quite possibly a function of the surface area of the foot (Vermeij, 1971*a*, 1971*b*, 1973), and exposed shore snails have been shown to possess a larger pedal surface area than those from more sheltered shores (Kitching et al., 1966; Etter, 1988). As a consequence, differences in water loss and/or mortality between B and W_p morphs inhabiting contrasting exposure regimes may reflect differences in acclimation or pedal surface area rather than shell color.

To eliminate these confounding effects, survivorship curves were constructed during a second series of desiccation experiments using B and W_e morphs form an exposed shore (Bennett Head). Various color morphs from the same habitat show no consistent differences in pedal surface area (pers. observ.) and should be similarly acclimated to desiccation stress. The experimental design was similar to that described above, except that five B and five W_e snails were removed from the direct sunlight every 30 minutes and placed in separate cages (plastic freezer containers with nitex windows to permit water flow) submerged in a seawater table. Snail viability was determined for each time interval by applying a stimulus to the snails 24 hours later, as described above.

In order to verify that any differences in survivorship were due strictly to shell color, the experiment was repeated with snails that were placed in a drying oven maintained at 40°C instead of in direct sunlight. Because snails in the oven will experience the same temperature independent of shell color, this experiment eliminates the effects of solar heating and tests for any differences between B and W_e morphs in their sensitivity to thermal stress.

One additional experiment was conducted to separate the effects of desiccation from those of thermal stress. Thirty B and 30 W_e morphs from Bennett Head were placed in three desiccators (10 B and 10 W_e per desiccator) with silica gel in a temperature-controlled room (10°C), and survivorship was monitored every six hours until a few individuals showed no response and then every hour thereafter.

Field Experiments

Physiological Stress.—To investigate the influence of shell color on tissue temperatures of *N. lapillus* under natural conditions, temperatures of B and white morphs were measured (±0.1°C) in situ at an exposed and a protected shore using an Omega digital thermometer (model 873C) with an Alumel-Chromel thermocouple (0.5 mm diameter). The thermocouple was inserted under the ventral edge of the aperture of attached snails and gently pushed in until it made contact with the foot tissues. If a snail became dislodged during this process, it was immediately overturned, and the thermocouple was inserted between the inner aperture wall and the tissues of the head and foot region. Care was taken to avoid touching the snail during temperature recording to prevent handling artifacts. In each experience, only snails that were similar in size (20–25 mm) and color hue were used in the analysis.

Variability in tissue temperatures within a site was investigated by recording temperatures of snails occupying various microhabitats (crevice, mussel bed, barnacle, bare rock, etc.) at East Point. Tissue temperatures were also measured simultaneously at Mackerel Cove and East Point to determine whether snails from a protected shore experienced higher temperatures than those on exposed shores. Snails selected for measurement between sites were those occupying open microhabitats that were exposed to solar radiation. Only the temperature of W_p morphs could be recorded at the protected site (because the natural population is monomorphically white), but at the exposed shore temperatures of both B and W_e morphs were recorded. Each site was first surveyed to determine which snails best fit these criteria, and then temperature measurements were taken just before the breaking surf of the flood tide approached each snail. The time of measurement could then be used as an estimate of the vertical position of the snail in the intertidal zone.

Since most snails remain in crevices during low tide at exposed shores or hide under boulders at protected shores, few individuals that fit the criteria were found. As a consequence, it was necessary to pool the temperatures of snails over the low-tide period. This was not considered to be a serious problem in that 1) snails were measured within the same 45-minute window within which air temperatures remained stable, 2) results from the laboratory study on tissue temperatures indicated that snails rapidly (within the first ten minutes of aerial exposure) attain thermal equilibrium, and 3) there was no correlation between the time at which temperature was recorded and the temperature difference between B and W morphs ($r = 0.07$, $d.f. = 21$, $P = 0.757$).

Snails from protected shores differ morphologically (Osborne, 1977; Crothers, 1983) and probably physiologically from those at exposed shores. To eliminate this potentially confounding influence and to compare temperatures of B morphs between exposed and protected shores, a more controlled tissue-temperature experiment was conducted. The goal was to investigate the possibility that snails on shores sheltered from wave action experience higher temperatures than do those on protected shores. Both B and W_e snails were collected from East Point, and a small hole was drilled through the aperture wall of each snail's shell. Snails were maintained in the laboratory seawater tables for one week following drilling to verify that the drilling process did not have an adverse effect. Pairs of B and W_e morphs were then tethered in selected areas at both exposed and protected shores by attaching a monofilament line (8-lb test) to the hole drilled in the shell and anchoring the line to the substrate using underwater cement. Tethers were 15–30 cm long. Twenty pairs of B and W_e morphs were tethered at Mackerel Cove on top of barnacle-covered boulders (+0.6 m [all tidal heights will be referenced to mean low water]). At East Point, ten pairs were tethered in the barnacle zone (+0.9 m), and another ten pairs were tethered on the mussel bed (+0.6 m). Snails were allowed to acclimate for at least two complete tidal cycles (48 hr), before tissue temperatures of tethered snails at both the exposed and protected shore were measured simultaneously during low tide on a cloudless day.

Intensity of Crab Predation.—Crab foraging was observed with SCUBA or snorkeling during high tide to assess the level of crab predation on snails in the intertidal zone. Data were collected over a five-hour period (2.5 hr before–2.5 hr after high tide) on each day. During this time, I swam far enough off the bottom to avoid disturbing the crabs, yet low enough that most of the time I was able to identify their prey. In general, it was quite easy to determine what the crabs were eating. On those occasions when I could not easily identify the prey, I swam down and attempted to take whatever the crab had in its grasp. Often the crab would simply drop the item and scurry away. The data were recorded by writing a code for each prey item (e.g., mussel = m, barnacle = b, *Nucella* = n, etc.) on a slate under the column corresponding to *Carcinus maenas, Cancer irroratus,* or *Cancer borealis* (the three species of crab that are common in the shallow waters along the coast of New England). Since crabs are extremely abundant at Nahant and a large majority of them were feeding, it was not difficult to observe about 300 feeding crabs along a 600 m transect over a 5-hr period (≈60 crabs/hr). Only crabs that were actively feeding were included in the census. Observations were made over a period of three days around Nahant (Canoe Beach Cove–East Point) and over three days at Mackerel Cove.

Differential Mortality of Color Morphs.—Differential mortality of color morphs on the protected shore was investigated by following the survivorship of 75 B, O, and W_e morphs from East Point which were released at the protected shore Mackerel Cove. Pairs of B and W_e morphs were tethered at an exposed shore and at a protected shore to separate mortality induced by physiological stress from predation. When a tethered snail died, the shell often remained attached to the tether, and the cause of death could be inferred with some confidence. At Mackerel Cove, 30 pairs of B and W_e morphs were tethered to the top surface of barnacle-covered boulders (+0.6 m), where they would be exposed to direct sunlight, and another 15 pairs were tethered in shady (under boulders but still at +0.6 m tidal height) microhabitats. Snails under boulders should not experience direct solar radiation, but should remain susceptible to predators (except possibly birds). The snails tethered at East Point could not be used for long-term experiments, because the intense wave action continually tore tethered snails off the rocks. Hence, a less exposed site was selected for the survivorship experiments. Thirty pairs of B and W_e morphs were tethered in the mussel bed (+0.6 m), and another 30 pairs tethered in the barnacle zone (+0.9 m) at Bennett Head. After the first week, the survivorship of tethered snails was monitored every other day when possible and any dead snails were replaced. Snails were considered to be alive if they responded to a stimulus (a poke from a blunt dissecting probe). Only snails that were unresponsive and completely intact (both shell and body tissues) were considered to have succumbed to physiological stress.

RESULTS

Laboratory Experiments

The rate at which the internal temperature of shells increased when exposed to direct solar radiation and the maximum temperature attained were strongly influenced by shell pigmentation (Fig. 2). The initial temperature measurement was taken inside the laboratory, where snails were not exposed to direct solar radiation, and the final measurement was recorded after all shells had become shaded. Internal temperatures of brown (B and Bb) morphs increased more quickly and attained higher temperatures than did W_p, W_e, or O morphs. Unpigmented shells from exposed shores (W_e) exhibited the slowest rate of temperature increase and maintained the lowest temperatures, while unpigmented shells from protected shores (W_p) and orange morphs (O) exhibited intermediate values. Note that the greatest increase in temperature occurred at the beginning of the experiment, when shells were initially placed in sunlight, and thereafter exhibited a fairly regular pattern of temperature change, closely tracking that of ambient air. Figure 2 also shows that shade eliminates differences in temperature among color morphs. The internal temperatures of shaded shells were similar to those of air.

Temperature differences among the color morphs at each time interval were compared using an ANOVA and a Dunn-Sidak multiple-comparisons test (Sokal and Rohlf, 1981) after variances were shown to be homoscedastic ($F_{\max}$ test). The results indicate that shell color had a significant effect on internal temperature for each time interval except the first and last, when the shells were not in direct sunlight (Table 1). Multiple comparisons showed that white shells were always cooler than pigmented shells, but the temperature of eroded W_p shells (with reduced albedo) often approached the temperature of B shells and only differed from these initially. For the most part, O shells were slightly warmer than at least one of the brown shells and did not differ from the W_p shells. The brown shells (B and Bb) did not differ significantly throughout the experiment.

When this experiment was repeated on an overcast day (Table 1), W_e, W_p, and O shells still maintained cooler temperatures than B or Bb shells, although the absolute temperature differences were small. Therefore, a potential exists for heat load to differ

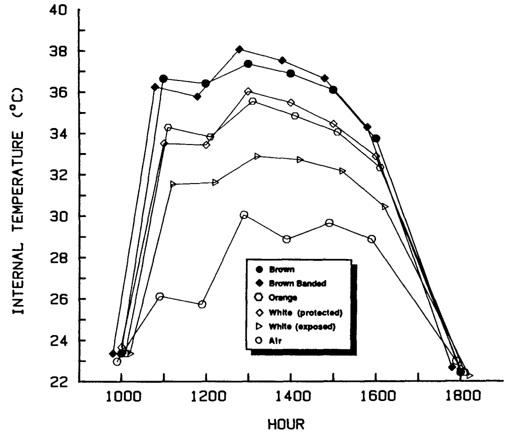

FIG. 2. The internal temperature of B, Bb, W_e, and W_p shells filled with sea water and placed in direct sunlight on a cloudless summer day (7 June 1985). Each point represents the mean of five replicate snails. Air temperature was recorded from a shaded thermocouple. The first recording was taken prior to placing shells in direct sunlight, and the last took place after the shells had become shaded.

among the color morphs even on cloudy days.

The effects of direct solar radiation on the tissue temperatures of various living color morphs and on internal temperatures of shells filled with sea water were quite similar (Fig. 3). Brown morphs experienced the greatest increase in temperature and maintained the highest temperature, W_p morphs had the lowest temperature, and W_e morphs were intermediate. Statistical comparison of temperatures among color morphs (ANOVA) indicated that, after the first 20 minutes, shell color consistently influenced tissue temperatures (Table 2), but a multiple-comparisons test did not detect differences among color morphs when pairs of means were compared. The W_p morphs had lower tissue temperatures than the B morphs at five minutes and lower temperatures than the Bb morphs at 140 minutes. The inability to detect temperature differences among the color morphs with a multiple-comparisons test probably reflects the small sample size used as well as the increased variability resulting from the movement of live snails during temperature measurements. Their movements affected both tissue-thermocouple contact and the orientation of the snails relative to the sun. Despite the lack of significant differences among pairs of means, the color morphs maintained their rank order with respect to tissue temperatures over the duration of the experiment. However, the rank order of W_e and W_p morphs switched, suggesting that W_p morphs somehow mitigate the higher heat load they experience due to incident solar radiation.

TABLE 1. Results of ANOVA and Dunn-Sidak multiple-comparisons test for the internal temperatures of B, Bb, O, W_e, and W_p shells filled with sea water at each recording time in Figure 2 (clear day) and on an overcast day (14 May 1985). The multiple-comparisons column indicates those morphs that had significantly ($P < 0.05$) lower internal temperatures than other morphs (e.g., W_e < B, Bb, O implies that W_e was significantly cooler than B, Bb, and O morphs).

Time	$F_{[4, 20]}$	Multiple comparisons
Clear day:		
10:00 A.M.	1.13	ns
11:00	23.595***	W_e < B, Bb, O W_p < B, Bb O < B
12:00	14.769***	W_e < B, Bb, O W_p < B O < B
1:00 P.M.	13.263***	W_e < B, Bb, O O < Bb
2:00	13.186***	W_e < B, Bb O < Bb
3:00	15.407***	W_e < B, Bb O < Bb
4:00	7.753***	W_e < B, Bb
6:00	1.520	ns
Cloudy day:		
10:00 A.M.	1.0	ns
1:00 P.M.	18.554***	W_e < B, Bb W_p < B, Bb O < B, Bb
3:30	9.351***	W_e < B, Bb W_p < B, Bb

*** $P < 0.001$.

The most valuable result to emerge from this experiment is that maximum temperature change occurred shortly after snails were removed from seawater and exposed to direct solar radiation. All snails started at ambient seawater temperature (12.2°C) and gained approximately 10°–12°C after one minute and another 8°C after five minutes; there were relatively small changes in tissue temperatures thereafter. This result indicates that within the first few moments of tidal emersion tissue temperatures of *N. lapillus* equilibrate and begin to track air

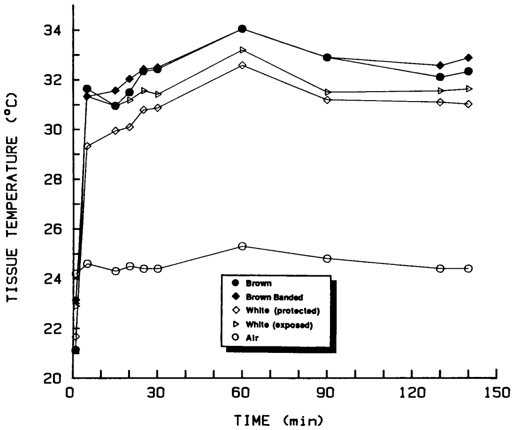

FIG. 3. The tissue temperatures of B, Bb, W_p, and W_e morphs in direct sunlight on a cloudless summer day (26 July 1984). Each point represents the mean of five replicate snails. Air temperature was recorded from a shaded thermocouple.

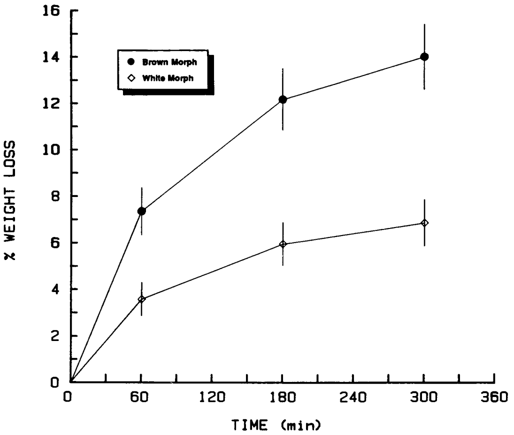

FIG. 4. Desiccation rates of B and W_p morphs estimated from percentage weight loss after placement in direct sunlight on 25 July 1984. Each point represents the mean of 30 morphs. Error bars show 95% confidence intervals.

temperature, remaining 6°–10°C higher, depending on the absorbence spectrum of the shell pigmentation. Note that temperatures measured in this manner reflect tissue temperatures at the animal-environment interface. Body core temperature may be substantially cooler.

The rate and overall amount of water loss when snails were exposed to direct solar radiation were strongly affected by shell pigmentation. In addition to heating up faster, B snails desiccated much more quickly than did W_p snails (Fig. 4). The maximum rate of water loss by both B and W_e morphs occurred during the first hour of emersion, with an attenuation thereafter. Although this method of representing the results is sufficient to illustrate desiccation rates, it can be misleading with respect to the overall amount of water lost, because B snails tend to be smaller and to weigh less per unit size (exposed shore snails are much smaller and have much thinner shells [Crothers, 1973, 1974, 1981, 1983; Kitching et al., 1966; Etter, 1987]) than W_p morphs. Therefore, even if both B and W_p morphs lost similar quantities of water, a plot similar to Figure 4 may depict them as quite different.

TABLE 2. Results of ANOVA and a Dunn-Sidak multiple-comparisons tests for the tissue temperatures of B, Bb, W_e, and W_p morphs at each recording time in Figure 3. The multiple-comparisons column indicates those morphs that had significantly ($P < 0.05$) lower internal temperatures than other morphs.

Time (min)	$F_{[3, 16]}$	Multiple comparisons
1	1.785	ns
5	3.817*	$W_p < B$
15	2.529	ns
20	4.330**	ns
25	4.673**	ns
30	4.406*	ns
60	3.392*	ns
90	3.639*	ns
130	3.645*	ns
140	4.953**	$W_P < Bb$

* $P < 0.05$.
** $P < 0.025$.

In order to alleviate this problem and to incorporate differences in weight at the beginning of the experiment, a Ford-Walford plot (Walford, 1946) was used to compare water loss among color morphs (Fig. 5). Ford-Walford plots have been widely applied in growth studies (Ebert, 1982; Sebens, 1984) to examine growth rates that vary with size (and/or age). Final weight is plotted against initial weight, and a least-squares regression line is fit to the data. The change in growth rate with weight is described by the slope of the regression line, while the displacement (elevation) of the regression line from the zero-growth curve represents the weight-specific growth. These growth parameters can then easily be compared among treatments or populations with ANCOVA. In this case, the Ford-Walford plot

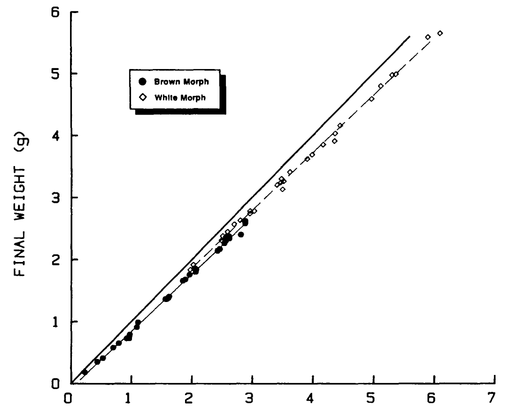

FIG. 5. Ford-Walford plot depicting the initial and final weights of B and W_p morphs from Figure 4. The thick solid line at a 45° angle represents the line of zero weight change over the experimental period. The regression lines fit to the data for each morph are: $B_f = 0.921B_i - 0.078$ and $W_f = 0.928W_i + 0.009$ where the f and i subscripts denote the final and initial weights (*B* and *W*) of B and W_p morphs.

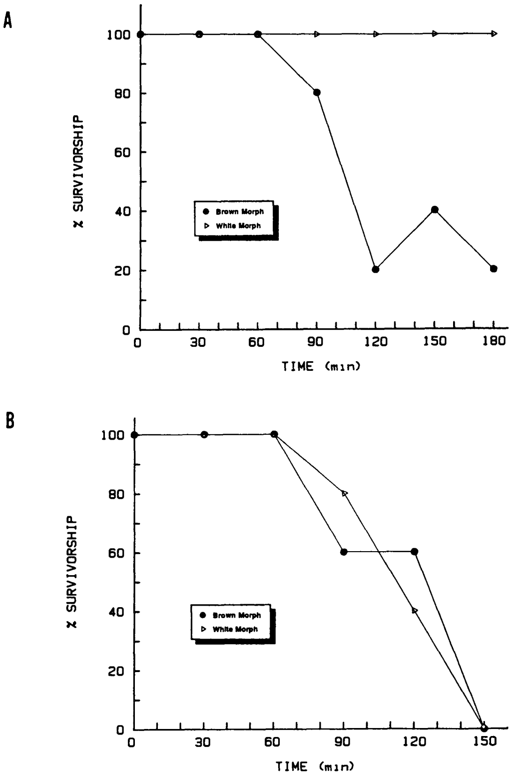

FIG. 6. Survivorship curves of B and W_e morphs after being placed A) in direct sunlight or B) in a 40°C drying oven.

is used to compare water loss by B and W_p morphs by measuring weight loss during five hours of aerial exposure to direct solar radiation. The greater the negative displacement of the regression line from the zero-growth line, the greater the water loss.

An ANCOVA on the regression lines fit to the initial and final weight data of Figure 4 showed no difference in slopes ($t = 0.0845$, $d.f. = 56$, $P > 0.05$), indicating that the rate at which water loss changed as a function of weight was similar in B and W_p morphs. In contrast, the elevations were quite different ($t = 6.208$, $d.f. = 56$, $P < 0.001$), with the regression line for the B morph displaced further from the zero-growth line, indicating that B morphs lost significantly more water than W_p morphs.

The difference in the amount of water lost by B and W_p morphs had a profound effect on their subsequent survival. When these snails were returned to the seawater table, only two of 30 B morphs survived, whereas all 30 W_p morphs survived. Surviving snails were monitored for one week, during which time none died.

Because the B morphs originated from an exposed shore while the W_p snails came from a protected shore, the differences in survivorship may reflect differences in acclimation to desiccation stress or pedal surface area, as described above. To eliminate these confounding factors, survivorship curves were constructed for B and W_e morphs from the exposed shore, Bennett Head. When they were placed in direct sunlight, W_e morphs exhibited no signs of stress, even after three hours, while B morphs began to succumb after 90 minutes and most did not survive three hours (Fig. 6A). When snails were instead placed in a drying oven at 40°C, the survivorship curves of B and W_e morphs were quite similar (Fig. 6B). Both morphs began to succumb after 90 minutes, and none survived 2.5 hours at 40°C, suggesting that shell color was not associated with thermal sensitivity. Susceptibility to desiccation, as indicated by LD 50's (time required to kill 50%) of snails placed in desiccators at 10°C, did not differ between B and W_e morphs ($t = 1.0$, $d.f. = 4$, $P = 0.374$). These findings suggest that survivorship differences be-

TABLE 3. A) Means ($N = 5$) and standard deviations (SD) of tissue temperatures and B) the results of a two-way ANOVA for B and W_e morphs that were crawling on different substrata at the exposed shore (East Point) on 21 August 1985.

A.

Shell color	Temperature Mean	Temperature SD
Mussel substrate:		
Brown	27.8	0.84
White	23.4	1.79
Barnacle substrate:		
Brown	29.8	1.35
White	28.8	1.69

B.

Source of variation	$F_{[1,16]}$	P
Shell color	35.932	<0.001
Substrate	19.134	<0.001
Color × substrate	8.130	<0.025

tween B and W_e morphs exposed to direct sunlight result from differential heating and its effect on osmotic stress.

The results of the laboratory experiments clearly demonstrate the potential of shell color in mitigating the physiological stresses commonly experienced by snails during periods of aerial exposure, but what remains to be established is that exposed and protected shores differ with respect to these stresses and that these differences result in differential fitness or mortality of the color morphs.

TABLE 4. Mean tissue temperatures, standard deviations (SD), and the results of paired t tests comparing tissue temperatures of B and W_e morphs tethered in specific microhabitats at exposed and protected shores on 19 September 1985.

Color	N	Temperature Mean	Temperature SD	t	P
Exposed mussel bed:					
Brown	5	17.8	1.13	3.067	<0.05
White	5	16.3	0.53		
Exposed barnacle zone:					
Brown	11	21.6	2.04	1.705	>0.1
White	11	20.7	1.74		
Protected barnacle zone:					
Brown	22	28.0	1.97	6.177	<0.001
White	22	26.4	2.22		

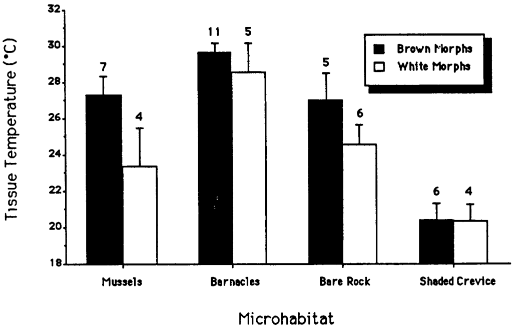

FIG. 7. Mean tissue temperatures of B and W_e morphs in various microhabitats at the exposed shore (Bennett Head) on 21 August 1985. The numbers above the confidence intervals are sample sizes, and the vertical lines extend to the upper 95% confidence limit.

Field Experiments

Both shell color and the substrate that snails were crawling over influenced tissue temperatures in natural field populations (Table 3). B morphs experienced higher temperatures than W morphs independent of substrate type and, on average, were 3°C warmer. Snails crawling on barnacles tended to heat up more than those on mussels, with mean temperature differences between microhabitats of approximately 4°C. Snails may remain cooler on mussels because evaporation of the residual water retained by mussel beds during periods of tidal emersion cools the air close to the substrate. The interaction between shell color and substrate indicates that actual temperature differences between color morphs depend on the substrate the snails are crawling over. The smaller temperature differences between color morphs attached to barnacles may reflect an increase in the importance of conductivity, relative to radiation, in determining tissue temperatures on such a hot and dry substrate. Heat load due to conductive exchange would be indifferent to shell color, and as conductivity became relatively more important, temperature differences between color morphs would decline.

Temperature differences between color morphs in several microhabitats at the exposed shore are shown in Figure 7. B morphs were consistently warmer than W_e morphs, except in shaded crevices, where differential solar heating would not be effective. Snails crawling on barnacles experienced the high-

TABLE 5. Mean tissue temperatures, standard deviations (SD), and the results of ANOVAs for tissue temperatures of resident and tethered snails at protected and exposed shores on 28 August 1985 (natural population) and 19 September 1985 (tethered snails).

Site	*N*	Temperature		*F*	*P*
		Mean	SD		
		Natural population			
White morph:					
Protected	20	27.9	1.78	13.128	<0.001
Exposed	27	26.1	1.63		
		Tethered snails			
Brown morph:					
Protected	23	28.0	1.95	77.695	<0.0001
Exposed	11	21.6	2.04		
White morph:					
Protected	24	26.4	2.19	56.119	<0.0001
Exposed	11	20.7	1.74		

est temperatures, while those in crevices experienced the lowest.

Tissue temperatures of B and W_e morphs tethered in specific microhabitats also differed (Table 4). B morphs on barnacle-covered boulders at the protected shore and in the mussel bed at an exposed site experienced tissue temperatures on average 1.5°C higher than nearby W_e morphs. Temperature differences between B and W_e morphs in the exposed barnacle zone did not differ significantly. Tissue temperatures of B morphs were about 1°C higher, on average. The B morph was actually cooler than the W_e morph in three of the 11 paired comparisons. Two of these anomalies were due to the B morph being shaded from direct sunlight.

Between-site comparisons of tissue temperatures measured simultaneously indicated that snails on shores protected from wave action experienced higher temperatures than did those on more wave swept shores (Table 5). In situ comparisons of resident populations between an exposed and sheltered shore involved only white morphs since the protected population is monomorphically white. For populations occurring naturally across across a wide variety of microhabitats (bare rock, barnacles, mussels, crevices, vertical walls, horizontal walls, etc.), white snails at the protected site were nearly 2°C warmer than those on exposed shores. When pairs of tethered snails that occupied similar microhabitats were compared, both B and W_e morphs experienced tissue temperatures about 6°C higher on protected shores, indicating that snails on protected shores experience greater thermal stress.

The potential for desiccation stress at both sites was measured by the volume of water evaporated over a 120 minute period from a series of 60-ml jars with mouths 5 cm in diameter. More water evaporated from six jars placed intertidally at Mackerel Cove (mean = 6.5 ml) than from those on the more exposed shore, Pump House Point (mean = 5.3 ml; t [one tailed] = 2.02, *d.f.* = 5, $P < 0.05$), indicating that desiccation stress is higher at more protected shores.

Crab Predation.—The results of field observations on crab foraging over three days indicate that crabs are not important consumers of *N. lapillus* (Table 6). Along a transect extending from a shore of moderate exposure to an exposed shore (Canoe Beach Cove–East Point), crabs were primarily feeding on mussels (*Mytilus edulis*), with a small fraction preying on other invertebrates. Although *N. lapillus* densities ranged from 62 to 247 per m^2, only in one of the 650 observations of feeding by *Carcinus maenas* was *N. lapillus* attacked, and it was unsuccessful (wave surge disturbed the crab, forcing it to drop the snail). *Nucella lapillus* comprised about 2% (5/279) of the diet of *Cancer irroratus*, and *Cancer borealis* was not observed feeding on *N. lapillus*. The densities of crabs were much lower at Mack-

TABLE 6. A summary of field observations on crab foraging over three days during high tide. Only actively feeding crabs were included in the analysis.

Prey item	*Cs. maenas*	*C. irroratus*	*C. borealis*
Canoe Beach Cove–East Point:			
Mussel	634	269	56
Barnacle	7	3	0
Sea Urchin	4	0	2
Crab	0	1	2
Littorina	1	0	1
Nucella	1	5	0
Bryozoan	3	1	0
Total	650	279	61
Mackerel Cove:			
Mussel	62	6	1
Barnacle	224	4	1
Total	286	10	2

erel Cove, and crabs were not observed feeding on *N. lapillus. Carcinus maenas* was the most abundant crab species, preying primarily on barnacles, while *Cancer irroratus* and *C. borealis* were uncommon, remaining mostly on the sand flats just seaward of the rocky outcropping.

Differential Mortality.—The recapture rate of 75 B, O, and W_e morphs (25 of each) released at Mackerel Cove and collected two months later was quite unexpected. Recapture rates for B and W_e morphs were the same (40%), while that for the O morphs was much higher (60%). This result initially appears to be inconsistent with a selection hypothesis operating against pigmented morphs at the protected site, whether it involves physiological stress or predation. However, if the snails are exploiting microhabitats that reduce physiological stress or predation, these results may support one or both of the hypotheses. All snails recovered were found either under boulders or on vertical surfaces, where both temperature and desiccation stress tend to be less extreme (Johnson, 1975; Garrity, 1984). Snails on vertical surfaces should be vulnerable to predation by birds and fish, and crabs were frequently observed foraging on vertical surfaces during high tide and under boulders at all times; thus, these microhabitats are unlikely to provide a refuge from predation. The fact that O morphs were recaptured at a higher rate probably reflects the extremely conspicuous appearance of the O shell.

Mortality rates of snails tethered at an exposed and a protected shore were considerably different (Table 7). Pairs of B and W morphs at the exposed site (Bennett Head), survived the three-month experiment quite well regardless of tidal height or substrate type, whereas only those pairs tethered in shady microhabitats at the protected shore (Mackerel Cove) survived well. B morphs were clearly selected against in sunny microhabitats at Mackerel Cove; 30 B morphs died during the three-month period, while only three white morphs died. Of the 30 B morphs that died, only about half (13) of the deaths could be attributed directly to physiological stress. That is, only 13 snails were found completely intact but unresponsive. For the remaining 17 B morphs, it was not possible to distinguish individuals preyed on while alive from those that had died and were subsequently attacked.

DISCUSSION

Physiological-Stress Hypothesis

Physiological stresses imposed by aerial exposure during periods of tidal emersion profoundly affect the biology of intertidal organisms. High temperature, desiccation, and concomitant osmotic stress are widely recognized as the principle physical stresses marine organisms must endure to persist intertidally (Newell, 1979). The intensity of environmental stress varies directly with height on the shore and has led to physiological, morphological, and/or behavioral adaptations (reviewed by Newell [1979]).

In addition to the widely recognized and well studied vertical gradient in the intensity of environmental stress, a second gradient exists horizontally but has received little attention. Physiological stress should be negatively correlated with exposure to wave action (Dayton, 1971; Connell, 1972; Menge, 1978*a*, 1978*b*). Shores sheltered from high wave energies will be splashed less than those at exposed sites, perhaps promoting more severe thermal and desiccation stress on low-wave-energy shores. In addition, where exposed shores are dominated by mussels, the immense quantity of water retained in mussel beds during low

TABLE 7. Mortality of pairs of B and W_e morphs tethered in various microhabitats at an exposed shore (Bennett Head) and a protected shore (Mackerel Cove). Survivorship of the tethered morphs was followed from 31 August through 15 December 1985. Snails that died during the experiment were immediately replaced to maintain the complement of snails at the initial number.

Site	Microhabitat	Number tethered		Mortality
		B	W	
Bennett Head	Mid-intertidal mussel bed	30	30	0
	High-intertidal barnacle zone	30	30	1B
Mackerel Cove	Barnacle zone, sunny	30	30	30B, 3W
	Barnacle zone, shady	15	15	0

tide may function to reduce stress through evaporative cooling, which would reduce the temperature and increase humidity.

Despite its potential importance to the distribution of intertidal organisms, few studies have considered the effects of this horizontal gradient. Dayton (1971) noted that various intertidal algal species, which are sensitive indicators of physiological stress, were abundant on outer coasts but were absent from more protected shores. Dayton (1971) attributed this shift in algal cover to increased desiccation stress in sheltered areas. He also experimentally demonstrated that the absence of *Anthopleura elagantissima* from convex surfaces on protected shores resulted from an intolerance of desiccation during diurnal tidal emersions. In a series of manipulative field experiments, Menge (1978*a*, 1978*b*) showed that the predation intensity imposed by *N. lapillus* was coupled to wave exposure in a complex nonlinear fashion. Both the high wave energies at the exposed shore and the greater desiccation stress at protected shores were shown to affect predation rates. Differential exposure to wave action and its effects on desiccation stress were similarly found to influence the predatory behavior of another intertidal whelk, *Morula marginalba* (Moran, 1980, 1985; Underwood, 1986).

The shift in shell color among populations of *N. lapillus* across a wave-exposure gradient may in part reflect a response to this horizontal gradient. B morphs heat up faster, attain higher temperatures, lose more water at a faster rate, and experience higher mortality rates than do W morphs when both are exposed to solar radiation. The combined effects of these differences dramatically increase the risk of mortality to B morphs during tidal emersion. The higher temperatures and greater desiccation potential experienced by snails when they are emersed on protected shores reduces the fitness of B morphs by imposing ecological constraints or increasing mortality relative to W morphs.

Although physiological stress can be inferred with a fair degree of confidence, the actual cause of death for B morphs in the field is unknown. The temperatures recorded from the tissues of snails in nature did not exceed lethal temperatures (36°C) reported by Sandison (1967) for *N. lapillus* from British shores, and only B morphs at the protected shore approached temperatures that would lead to heat coma (30°C). However, lethal temperatures for snails in this study may be quite different from those reported in the literature, because lethal temperatures are known to vary with relative humidity (Gibson, 1970) among populations occupying different shores (Sandison, 1967) and may even vary among individuals that occupy different tidal heights within populations (Davies, 1969; Wallace, 1972; Bertness and Schneider, 1976). A more serious problem with extrapolating laboratory results to natural systems is that most laboratory studies ignore the simultaneous effects of several environmental factors (e.g., O_2 tension, air temperature, water temperature, relative humidity, air velocity, immersion and emersion time, recovery time, incident solar radiation, absorbence spectrum, etc.) that critically affect the multidimensional zone of physiological tolerance (Alderdice, 1972). Nevertheless, it is quite likely that B morphs experience temperatures approaching those reported to be lethal by Sandison (1967). First, temperature recordings of snails were taken on warm (but not exceptionally hot) days. Second, B morphs typically experience tissue temperatures 5°–10°C higher than ambient air temperatures and air temperatures on the coast of Massachusetts during the summer often exceed 30°C. More importantly though, B morphs began to die after one hour in direct sunlight, when the air temperature was only 21°C and relative humidity was 64%, whereas white morphs showed no signs of stress. The lethality of air temperatures as low as 21°C probably represents the effects of the multiple environmental factors mentioned above and supports the notion that the mortality experienced by B morphs at the protected shore was due to physiological stress.

Still, differential mortality of color morphs is an unlikely outcome of increased physiological stress in nature, because snails can effectively avoid stress by moving to shaded, cool, and moist microhabitats. The increased risk of physiological stress on protected shores may instead impose important ecological constraints on B morphs reducing their fitness relative to W morphs. *N. lapillus* forages primarily when submerged but will often continue feeding when emersed, if it has not completely consumed a prey item (Menge, 1976; pers. observ.). The time required to consume a mussel has been shown to vary between 33 and 200 hours (Hughes and Dunkin, 1984), while for a barnacle it varies between four and 26 hours (Dunkin and Hughes, 1984), both depending on experience with the particular prey item and prey size. This presents an important dilemma for snails that risk lethal physiological stress during daytime tidal emersions. As the diurnal ebb tide nears, snails must either continue foraging and feeding (and risk the potentially lethal effects of aerial exposure) or return to protected microhabitats (which normally are devoid of prey). The particular strategy employed will undoubtedly vary with the severity of the risks, but B morphs clearly suffer a greater risk from physiological stress, which may force them to limit the area over which they forage and/or the time available for foraging. As a consequence, B morphs (and probably any pigmented morphs) would spend more time hiding and would tend to be disfavored by natural selection on protected shores.

It is quite apparent that the risk of physiological stress during tidal emersion can impose ecological constraints on intertidal snails. For instance, feeding rates of *N. lapillus* from both exposed and protected shores were lower in August than in September, and this difference was attributed to foraging constraints imposed by increased desiccation stress during August (Menge, 1976). Three species of whelk, *Thais canaliculata, Thais emarginata,* and *Thais lamellosa,* from the north Pacific coast of the United States foraged more when risks due to physiological stresses were less severe (Spight, 1981, 1982). Moran (1980; Underwood, 1986), in his studies of the intertidal predatory whelk *Morula marginalba*, found that the proportion of snails foraging away from crevices increased as a function of increasing wave action and suggested that this pattern resulted from decreased desiccation stress at more exposed shores, due to increased splash and spray from breaking waves. In addition, a remarkably close association was observed between the proportion of snails in crevices and the time of daytime low tide on the previous day. The proportion of snails in crevices was high during midday low tides, when physiological stresses would be greatest, but during early morning or late afternoon low tides, when stresses would tend to be less severe, most snails were out foraging. Garrity (1984) showed that the foraging patterns of several tropical intertidal gastropods were tightly coupled to tidal cycles. During daytime low tides, snails were restricted to refuge microhabitats, such as under rocks or in crevices, where desiccation and thermal stress would be less severe. If snails were removed from these refugia during a low tide, most died before resubmergence by the flood tide.

Although I have no quantitative evidence, observations on *N. lapillus* during frequent visits to the protected site indicated that the behavior of resident W morphs was quite similar to that described for snails under physiological stress in other intertidal habitats (Moran, 1980, 1985; Spight, 1981, 1982; Garrity, 1984). Snails at the protected site returned to crevices or under boulders during summer (June–September) daytime ebb tides and were extremely rare away from cool microhabitats. Those few that failed to return to cool refugia tended to occupy vertical surfaces that were shaded from direct solar radiation. This was particularly obvious when I attempted to measure tissue temperatures of natural field populations at the protected site. After searching over 500 m of shore line, I only found about 20 snails exposed to direct sunlight. In contrast, during nocturnal ebb tides or on cool overcast days, snails remained on the vertical and horizontal surfaces of large boulders and did not return to protected microhabitats. As temperatures and concomitant physiological stress decreased during the fall (September–December), *N. lapillus* occurred more commonly on rock surfaces during daytime low tides. These observations suggest that the risk of physiological stress during diurnal tidal emersion exerts an important influence on the behavior of W morphs at the protected site. Since B morphs suffer a greater risk of mortality from aerial exposure, they should experience more severe ecological constraints.

Differential heat load of color morphs has also been shown to be important in the biology of terrestrial pulmonates (reviewed in Jones et al. [1977] and Cain [1983]) and *Littoraria pallescens,* a marine prosobranch (Cook, 1986*a,* 1986*b*; Cook and Freeman, 1986). More heavily pigmented morphs suffer higher heat loads when they are exposed to direct solar radiation (Heath, 1975; Cook and Freeman, 1986), and this has been shown to affect activity patterns (Jones, 1973), metabolic rate (Steigen, 1979), reproductive success (Wolda, 1967), microhabitat partitioning (Cook, 1986*b*; Cook and Freeman, 1986), and survivorship (Jones, 1973, 1980; Bantock, 1980; Heller, 1981). In addition, several studies have demonstrated a correlation between the geographic distribution of color morphs and climate (Jones, 1973; Bantock, 1980; Heller, 1981). Typically, dark morphs are more prevalent in cool habitats, while light-colored snails predominate in warmer locations. These findings are consistent with those presented here.

Several lines of indirect evidence also support the physiological-stress hypothesis. First, the mortality of B morphs tethered on the protected shore consistently followed periods of warm dry weather during afternoon spring low tides when desiccation and thermal stresses would be maximal. Similar instances of high mortality during afternoon spring low tides have been noted in several high intertidal limpets (Frank, 1965; Sutherland, 1970; Branch, 1975). Second, as predicted by the physiological-stress hypothesis, pigmented morphs begin to decrease in frequency in the populations along the southern coast of Cape Ann (see Fig. 1) from Gloucester to Mackerel Cove, which represents a gradient of decreasing wave action. Moreover, around the tip of Cape Ann, from the University of Massachusetts field station to Magnolia (see Fig. 1), the shores are predominately covered by mussels (pers. observ.), yet the most abundant color morph in each population is W. This finding is inconsistent with the predation hypothesis, but not with the physiological-stress hypothesis. Finally, a corollary to the physiological-stress hypothesis would predict that, towards the southern extension of the range of this species, where even at exposed sites the physiological stresses may exceed the tolerances of *N. lapillus,* only white morphs would persist, because they minimize heat gain. Osborne (1977) found that all populations south of Cape Cod had predominately W morphs, and very few pigmented morphs were found in any of the populations, independent of exposure regime.

A weakness with the physiological-stress hypothesis is that it fails to explain the presence of B morphs on exposed shores, especially when they are the dominant morph. If physiological stress were the principal selective force operating on shell color, then selection for any particular shell color would be relaxed at exposed shores, because stresses tend to be ameliorated from the splash and spray of breaking waves, and hence, shell color would be free to vary. Support for this notion is derived from the results of the tethering experiment. Of the 120 B and W morphs tethered at the exposed shore at Bennett Head, only one B morph died over the three-month experimental period. In addition, none of the 40 B and W morphs tethered at the extremely exposed East Point died, although a number were missing (always just after heavy wave action and probably due to the breaking of tethers by storm-generated surge).

If selection is not operating, then the presence of B morphs as well as the color polymorphism (including background color and banding) at exposed shores may simply reflect mutation pressure and genetic drift. This is an untestable hypothesis without temporal replicates of morph frequencies for each population over many years. Yet if valid, it would explain three additional observations. 1) Not all exposed shores are dominated by B morphs despite being covered primarily by mussels (pers. observ; Fig. 1). 2) The degree of color and banding polymorphism appears to vary randomly among populations on exposed shores (Fig. 1). 3) Populations of *N. lapillus* from the British Isles exhibited a low but significant correlation between wave exposure and shell color or banding frequencies (Berry and Crothers, 1974; Berry, 1983). The low correlation would be more easily understood if selection were operating most strongly at protected shores, since frequencies at exposed shores would tend to vary randomly. However, a pattern similar to that observed would emerge if predation varied temporally and spatially in an unpredictable manner, such as has been observed for shorebird foraging (O'Connor and Brown, 1977; Marsh, 1986*a,* 1986*b*) and fish predation (Garrity et al., 1986). Because *N. lapillus* has several visually cued predators, it seems unlikely that shell color is selectively neutral, and thus, a more plausible explanation for the pattern at exposed shores is that predation intensity varies spatially and temporally.

Predation Hypothesis.—The predation hypothesis suggests that shifts in shell color among populations of *N. lapillus* result from selective predation on noncryptic morphs. Osborne (1977) observed no significant pattern of color selection by *Cancer borealis* or *Carcinus maenas* in a set of laboratory experiments. Whether crabs possess the necessary spectral sensitivity to differentiate various shell colors remains unresolved (Horridge, 1967; Goldsmith and Bruno, 1973; Hyatt, 1975; Bursey, 1984). However, as pointed out earlier, crabs may only need to distinguish morphs that maximally contrast the background shade of the environment.

Independent of their visual spectrum, crabs along the Massachusetts coast do not appear to be major predators of *N. lapillus*; field observations indicate that their diet consists primarily of mussels and barnacles, with an extremely small percentage feeding on other invertebrates. The remarkably small fraction of tethered snails preyed upon during the three-month experimental period (September–December), regardless of how cryptic snails appeared and despite a large number of crabs foraging, also supports this notion. Moreover, it was impossible to differentiate crab-induced mortality from crab necrophagy when snails were attacked, and hence, the observed mortality may result from the scavenging nature of crabs rather than selective predation. Several laboratory experiments (Hughes and Elner, 1979; Lawton and Hughes, 1985) and field experiments (Ebling et al., 1964; Kitching et al., 1966) in which crabs were caged with snails unequivocally demonstrated the efficacy of crabs in crushing *N. lapillus.* These experiments have been marshalled as evidence that crabs are important predators of *N. lapillus,* but none of these studies actually measured the incidence of crab-induced mortality in the field. The only other direct assessment of predation pressure in nature is provided by Bertness et al. (1981), who observed no predation on 120 shells of *N. lapillus* that were glued to the intertidal rock substrate at Nahant for over 24 hours. Long-term field experiments on the community ecology of the rocky intertidal on the New England coast, (Menge, 1976; Lubchenco and Menge, 1978) also indicated that crabs, fish, and birds were unimportant predators of *N. lapillus,* although this was not tested directly. If crabs are involved in altering morph frequencies among populations, the effect is likely to be minor.

Predators that rely to a greater extent on visual cues for locating prey, such as birds and fish, are more likely to select differentially against noncryptic morphs. In a series of field experiments, Mercurio et al. (1985) demonstrated that birds and fish both preyed on noncryptic acmaeid limpets; the light colored *Collisella digitalis* experienced higher mortality on mussels than barnacles, while the converse was true for the dark shelled *Collisella pelta.* Hughes and Mather (1986) observed a decrease in the frequency of the cryptic yellow morph of *Littorina* spp. (*scabra*?) living on the Gray mangrove *Avicennia marina* when predation by birds and fish was restricted by cages. Selective predation on noncryptic morphs by the intertidal fish *Blennius pholis* was implicated through a series of laboratory experiments as the mechanism favoring shell color polymorphism in *Littorina mariae* (Reimchen, 1979), but no direct field experiments were performed.

Several species of fish that forage intertidally along the New England coast, including blenny, cunner, sculpin, pollack, gunnel, and cod (Collette, 1986) as well as juvenile flounder (pers. observ. at Mackerel Cove) may impose selection for crypsis on *N. lapillus.* Connell (1961) found dogwhelks in the stomachs of cod and cunner while Chao (1972, 1973) reported small *N. lapillus* and *Littorina* spp. in the gut contents of 10 of 37 cunners examined. In a recent study of cunner feeding, Sanderson (unpubl.) discovered only one of 36 with *N. lapillus,* shell fragments in the stomach. The lack of predation on B and W morphs tethered intertidally, however, suggests that selective fish predation on adults is not responsible for the variation in shell color among populations. Yet, the hypothesis that fish mediate selection for crypsis by removing noncryptic juvenile morphs of *N. lapillus* needs to be examined experimentally.

Both terrestrial and shore birds forage intertidally on rocky shores (Feare and Summers, 1986) and may play a major role in selection for crypsis. Crows have been observed feeding on *N. lapillus* on Cape Ann (Dexter, 1947) and are frequent visitors to the intertidal at Mackerel Cove (pers. observ.). Several studies have reported predation on *N. lapillus* by gulls, both in Europe and at Nahant (Connell, 1961; Harris, 1965; Osborne, 1977), but Kadlec and Drury (1968) and Osborne (1977) argue that this occurs infrequently. In a comprehensive series of papers, Feare showed that oystercatchers preyed on adult *N. lapillus* (Feare, 1971), while purple sandpipers and rock pipets preyed on juveniles (Feare, 1966*a*, 1966*b*, 1970). In fact, Feare (1970) found that the diet of purple sandpipers between January and May consisted almost entirely of juvenile *N. lapillus,* and he calculated that 93% of the 89% mortality of *N. lapillus* yearlings on British shores could be attributed to purple sandpipers (Feare, 1969). Connell (1961) found 28 spires of small (1–9 mm) *N. lapillus* in the fecal pellets of purple sandpipers feeding intertidally at Millport in January. I have also observed a large number of fractured shells of juvenile *N. lapillus* in the fecal pellets of purple sandpipers feeding on rocky shores near Nahant, but it was not possible to establish whether they were taking noncryptic morphs. The hypothesis that birds are imposing selection for crypsis in *N. lapillus,* especially early in the life history of this snail, also remains to be tested experimentally.

Recent studies on color polymorphism in gastropods clearly demonstrate that shell color results from the interplay of several, often opposing, selective pressures (reviewed by Cain [1983]). It is likely that both physiological stress and predation are operating, but their relative importance varies temporally, with wave exposure and with size or age of the snails. In this context, it is important to note that the experiments conducted thus far have only treated selection on adults (>10 mm), while selection may operate at much earlier stages of the life cycle (yearlings or immatures). This is particularly interesting in that hatchlings emerging from egg capsules at Mackerel Cove, where the adults are monomorphically white, were highly polymorphic and predominately brown but immediately after emergence began to secrete white shell material. The fact that this result was independent of the habitat the hatchlings were reared in (exposed shore, protected shore, or laboratory) suggests that the color shift is genetic and not environmentally induced. More importantly, whatever the selective mechanisms are that favor white morphs at Mackerel Cove, they operate early in the life history of *N. lapillus.* Of course, this does not minimize the importance of desiccation and thermal stress demonstrated here, since small snails tend to be more vulnerable to physiological stress than are adults (Davies, 1969; Branch, 1975; Garrity, 1984), but it does underscore the importance of considering selection on the early life-history stages of this intertidal snail.

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