Phenotypic selection in an intertidal snail: effects of a catastrophic storm

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ABSTRACT: *Littorina obtusata* exhibits clear morphological variation (e.g. shell height, shell length, and aperture area) among shores differentially exposed to wave energies. Selection imposed by the hydrodynamic environment is often invoked to explain the correlation between morphology and wave exposure in intertidal organisms, but rarely is this hypothesis tested. I examined the effects of a catastrophic storm on the shell length and relative shell height and aperture area of *L. obtusata* populations on 2 protected and 1 wave-exposed shore in New England (USA) to test this hypothesis. Snails sampled after the storm had relatively squatter shells than those sampled before the storm, which is consistent with the pattern in shell height found in natural populations. The rapid shift supports the hypothesis that shell morphology on wave-exposed shores reflects, in part, selection imposed by hydrodynamic stress. Compared to morphological differences found between natural populations, shifts in relative shell height after the storm were small. Hence, despite its magnitude, the impact of this storm may be limited by available variation in relative shell height, especially if selection pressures operating during 'typical' conditions have depleted variation in this trait. There were 2 surprising results. First, relative aperture area decreased after the storm. This result is counter-intuitive because one would expect a shift to larger apertures, which can accomodate a larger adhesive foot. Second, a decrease in shell length after the storm was found only at the wave-exposed site, suggesting that the effects of the storm were more pronounced on this population. Because a shift in relative shell height and aperture area occurred at all 3 sites, these traits appear to be more sensitive to large storms than is shell length. The shifts in both relative shell height and aperture area may reflect differences in the hydrodynamic properties of shells collected before and after the storm, but I suggest that the shifts were mediated by the ability of snails to avoid free-stream flows by hiding in sheltered crevices. Both reduced shell height and aperture area may be advantageous when trying to fit into sheltered microhabitats during periods of increased hydrodynamic stress. In particular, the shift in aperture area may reflect the premium on successful crevice use over conventional adhesion during periods of extreme wave energies. Finally, while recent work on intertidal snails has emphasized the importance of phenotypic plasticity to morphological differentiation among populations, my results suggest that selection can assume a more prominent role during unusual events like this storm.

KEY WORDS: Catastrophic storm · Hydrodynamic forces · *Littorina obtusata* · Morphological variation · Phenotypic and natural selection · Wave energies

INTRODUCTION

Wave energy on intertidal shores varies considerably in both space and time and is thought to exert a strong influence on morphological variation in intertidal spe-

cies (Kitching et al. 1966, Palumbi 1984, 1986, Denny et al. 1985, Etter 1988a, Trussell et al. 1993). One consequence of increased wave energy is the increased risk of dislodgement for organisms living in the intertidal zone. The risk of dislodgement may interfere with various aspects of a wave-swept existence (Menge 1974, Menge 1978a, b, Denny et al. 1985, Brown & Quinn 1988, Etter 1989), and may be lethal if individuals are removed from their typical environment (Etter 1988a) or if wave forces exceed the individual's structural

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strength (Denny 1988). The magnitude of hydrody-namic forces (drag, lift, and acceleration reaction) is expected to be greatest on wave-exposed shores because mean and maximum water velocities and accelerations are greater (Denny 1985, 1988, Denny et al. 1985, Denny & Gaines 1990). On wave-exposed shores natural selection is expected to favor traits that reduce the risk of dislodgement.

The risk of dislodgement for intertidal snails is dependent on a number of factors, including flow velocity and acceleration, shell shape and size, and the adhesive strength of the foot (Etter 1988a, Trussell et al. 1993, Trussell 1997). For snails to resist dislodge-ment, their adhesive ability, which is a function of foot size (Trussell et al. 1993, Trussell 1997), must exceed the magnitude of the hydrodynamic forces acting on the snail. Wave-imparted hydrodynamic forces act directly on the snail's shell so shell shape and size can reduce the risk of dislodgement in 2 ways. Changes in shell shape and size may (1) directly alter the magni-tude of hydrodynamic forces acting on the shell, and (2) influence a snail's ability to hide from free-stream flows in sheltered cracks or crevices.

Morphological variation in intertidal snails is often correlated with differences in wave energies (Kitching et al. 1966, Kitching 1976, Kitching & Lockwood 1974, Raffaelli 1978, Crothers 1983, Johannesson 1986, Etter 1988a, Trussell et al. 1993, Trussell 1996, 1997). In gen-eral, predation by crab predators on protected shores and dislodgement by wave forces on wave-exposed shores are believed to be the major forces driving habi-tat-specific differences in shell morphology (Kitching et al. 1966, Reimchen 1982, Palmer 1985, Trussell 1997). Typically, the shells of snails on wave-exposed shores are thinner, squatter relative to shell length, smaller-sized, and larger-apertured than those of pro-tected conspecifics. In addition, wave-exposed snails typically have a larger adhesive foot than similarly-sized protected conspecifics and are therefore able to resist greater dislodgement forces. Hence, the above traits are expected to reduce the risk of dislodgement for snails on wave-exposed shores.

It is clear that wave energies, particularly on wave-exposed shores or during large storms, are an impor-tant agent of disturbance in intertidal communities (Suchanek 1978, 1981, Sousa 1979, 1984, Paine & Levin 1981). Disturbances are discrete events that can displace or kill individuals or populations, and are often defined by their intensity of impact and fre-quency of occurrence (Sousa 1984). Here, I examine the impact of a catastrophic storm on the shell mor-phology of the intertidal snail Littorina obtusata. This storm was classified as a '50-year storm' and is one of the largest on record for the Gulf of Maine (Davis & Dolan 1992) The storm lasted for 144 h and had wave

heights reaching ~11 m (Davis & Dolan 1992); wave heights of 10 m were observed at the Canoe Beach Cove study site (G. Trussell & J. Witman pers. obs.).

I evaluated the effects of the storm on Littorina obtusata shell morphology by collecting pre- and post-storm samples from a wave-exposed and 2 protected shores. In considering shell shape, I focused on shell height relative to shell length because previous work (Trussell et al. 1993, Trussell 1997) on several popula-tions found obvious differences in relative shell height that were associated with wave-exposure. I also made measurements of aperture length and width to calcu-late aperture area, which can serve as a predictor of snail adhesive ability (Palmer 1992). Finally, I evalu-ated the storm's effect on snail size by using shell length as my size criterion.

MATERIALS AND METHODS

I made pre-storm measurements of shell height, shell length, aperture length and width to character-ize shell traits and tenacity of a wave-exposed [Pemaquid Point, Maine (43° 50' N, 69° 39' 12" W)] and 2 protected [South Harpswell, Maine (43° 43' 54" N, 70° 02' W); Canoe Beach Cove, Nahant, Massachu-setts (42° 25' 42" N, 70° 55' 48" W)] populations of Lit-torina obtusata in New England. Detailed descriptions of these sites are provided elsewhere (Trussell et al. 1993, Trussell 1997). Shell height was measured as the maximum distance perpendicular to the plane of the aperture and the highest point of the shell and shell length as the maximum dimension of the shell parallel to the plane of the aperture (see Fig 1 in Trussell et al. 1993). Aperture width (AW) was mea-sured as the maximum dimension of the aperture run-ning perpendicular to the axis of shell length. Aper-ture length (AL) was measured as the maximum dimension of the aperture along the same axis as the shell length measurement. Aperture area was calcu-lated from these measurements assuming an elliptical shape using the formula 0.25π (AW × AL) (Miller 1974, Lowell 1986). Measurements were made with digital calipers to the nearest 0.01 mm. Snails were sampled (Table 1) from 0.25 m^2 quadrats blindly tossed on each shore at the same tidal height [~1.5 to 2 m mean low water (MLW)].

Soon after this sampling a catastrophic storm occurred from October 28 to 31, 1991. In addition to direct observation of wave heights near 10 m at the Canoe Beach Cove site, I obtained wind speed data recorded during the storm and the latter half of 1991 (Fig. 1) Wind speeds, in addition to fetch and the duration that the wind blows, can be used to estimate wave heights and wave forces experienced by inter-
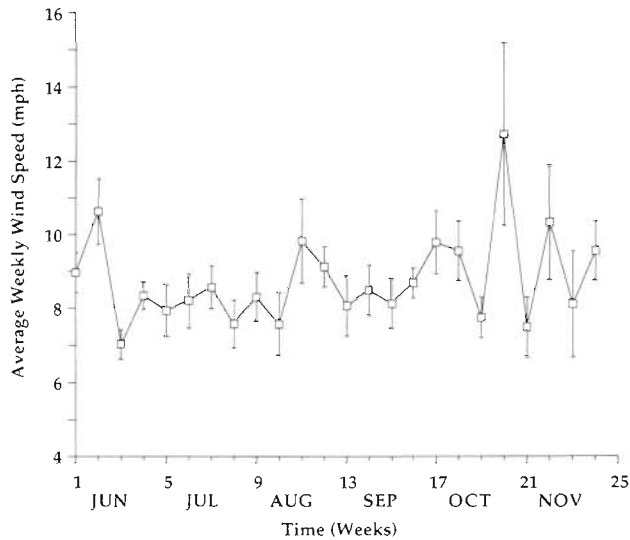
Fig. 1. Average weekly wind speeds (±SE) for the latter half of 1991. Maximum wind speeds of 80 mph (129 km h^{-1}) and wave heights of ~10 m were recorded at Nahant, Massachusetts (where the Canoe Beach Cove site is located). Data were recorded at the Portland, Maine International Jetport and obtained from the National Oceanic and Atmospheric Administration, Asheville, North Carolina

tidal organisms (Denny 1988). Due to the magnitude of this storm, storm surges elevated water velocities and accelerations far above their typical levels on each shore. Because wave-imparted forces are directly proportional to water velocity and acceleration (Denny et al. 1985), snails must have experienced greater hydrodynamic forces during this storm than during conditions of normal wave energy. Hence, the probability of snail dislodgement was increased on each shore.

To test the effect of increased wave energies on shell morphology, I repeated measurements of shell height, shell length and aperture length and width using the methods described above on post-storm samples of snails from each population. Post-storm samples were collected 1 to 3 wk after the storm from each population at the same tidal height and location as pre-storm samples (Table 1).

Statistical analyses. I conducted analyses of covariance (ANCOVA) to determine (1) pre-storm differences in relative shell height and aperture area between the 3 study sites, and (2) differences in relative shell height and aperture area between pre- and post-storm samples for each population. In all ANCOVAs I used shell length as the covariate to adjust for size effects on shell height and aperture area. For those ANCOVAs involving aperture area, both shell length and aperture area were $\log_{10}$ transformed. Otherwise, analyses were performed on untransformed data using Type III sums of squares (Wilkinson 1989). I also used ANOVA on shell length data to examine size differences between populations and before and after the storm.

RESULTS

Pre-storm comparisons

The ANCOVA on pre-storm samples from the 3 sites indicated homogeneity of slopes ($F_{(2,139)}$ = 1.95; p > 0.05) and that snails from both protected sites (Canoe Beach Cove and South Harpswell) had significantly taller shells in terms of relative shell height than wave-exposed (Pemaquid Point) conspecifics ($F_{(2,141)}$ = 150.27; p < 0.00001; Fig. 2, Table 2). ANOVA on shell length found that protected snails fom both sites were longer than those from the wave-exposed site ($F_{(2,142)}$ = 18.21; p < 0.00001).

Pre-storm comparison of aperture area relative to shell length revealed homogeneous slopes ($F_{(2,139)}$ = 1.83; p > 0.05) and that snails from both protected sites had smaller apertures than conspecifics from the wave-exposed site ($F_{(2,141)}$ = 37.06; p < 0.00001; Fig 3, Table 2).

Table 1. Dates of sample collection for 3 populations of *Littorina obtusata* before and after the storm event. For populations having multiple sample dates for both before and after the storm (i.e. Canoe Beach Cove and South Harpswell) samples for each period were pooled

Before storm	After storm	Time after storm (d)	Overall time difference (d)
Pemaquid Point, Maine (wave-exposed)			
Oct 24, 1991 (N = 50)	Nov 22, 1991 (N = 46)	22	29
Canoe Beach Cove, Massachusetts (protected)			
Sep 20, 1991 (N = 20)	Nov 8, 1991 (N = 45)	8	49
Oct 10, 1991 (N = 25)	Nov 9, 1991 (N = 45)	9	30
South Harpswell, Maine (protected)			
Oct 16, 1991 (N = 25)	Nov 11, 1991 (N = 83)	18	33
Oct 24, 1991 (N = 25)			25

Table 2. *Littorina obtusata*. Summary of least-squares regression statistics and range of shell lengths of snails in samples collected before (BS) and after (AS) the storm. Linear measurements are in mm and area measurements in mm^2

	Regression	R^2	N	Range of shell lengths in sample
Shell height (Y) vs shell length (X):				
Canoe Beach Cove				
BS	$Y = 0.51X + 1.42$	0.94	45	7.77–14.64
AS	$Y = 0.51X + 1.31$	0.94	90	6.61–13.80
South Harpswell				
BS	$Y = 0.55X + 1.07$	0.97	50	6.88–14.19
AS	$Y = 0.56X + 0.86$	0.98	88	4.72–14.23
Pemaquid Point				
BS	$Y = 0.52X + 0.70$	0.95	50	6.72–10.78
AS	$Y = 0.52X + 0.57$	0.93	46	6.40–10.66
Aperture area (Y) vs shell length (X):				
Canoe Beach Cove				
BS	$Y = 4.78X - 21.91$	0.95	45	Same as above
AS	$Y = 4.52X - 19.94$	0.94	90	Same as above
South Harpswell				
BS	$Y = 4.75X - 21.12$	0.94	50	Same as above
AS[a]	$Y = 4.89X - 24.28$	0.94	45	6.61–14.01
Pemaquid Point				
BS	$Y = 5.03X - 21.12$	0.95	50	Same as above
AS	$Y = 4.45X - 18.15$	0.95	46	Same as above

[a]Aperture area measurements were not made for all snails collected after the storm at South Harpswell

Fig. 3. *Littorina obtusata*. Adjusted mean log aperture area (±SE) from ANCOVA for snails sampled before the storm from a wave-exposed and 2 protected shores in New England, USA. See Table 1 for sampling dates and Table 2 for regression statistics and sample sizes

Fig. 4. *Littorina obtusata*. Adjusted mean shell height (±SE) from ANCOVA for snails sampled before and after the storm at each study site. See Table 1 for sampling dates and Table 2 for regression statistics and sample sizes
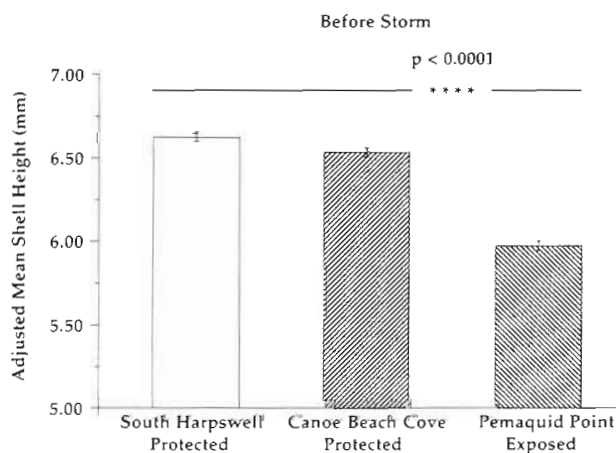

Fig. 2. *Littorina obtusata*. Adjusted mean shell height (±SE) from ANCOVA for snails sampled before the storm from a wave-exposed and 2 protected shores in New England, USA. See Table 1 for sampling dates and Table 2 for regression statistics and sample sizes

Pre-storm versus post-storm comparisons

ANCOVAs on pre- and post-storm measurements of shell height as a function of shell length for each site found that slopes in all cases were homogeneous (all
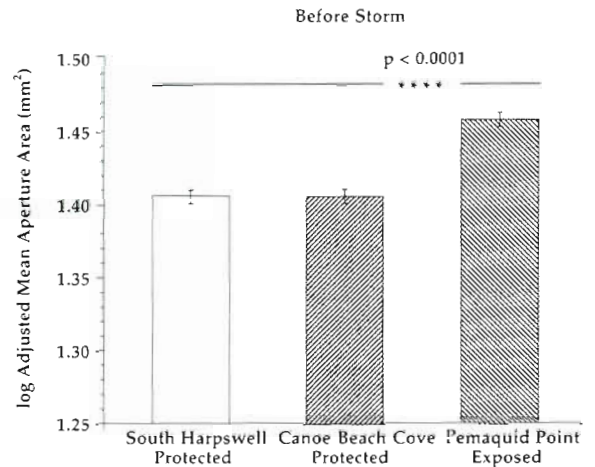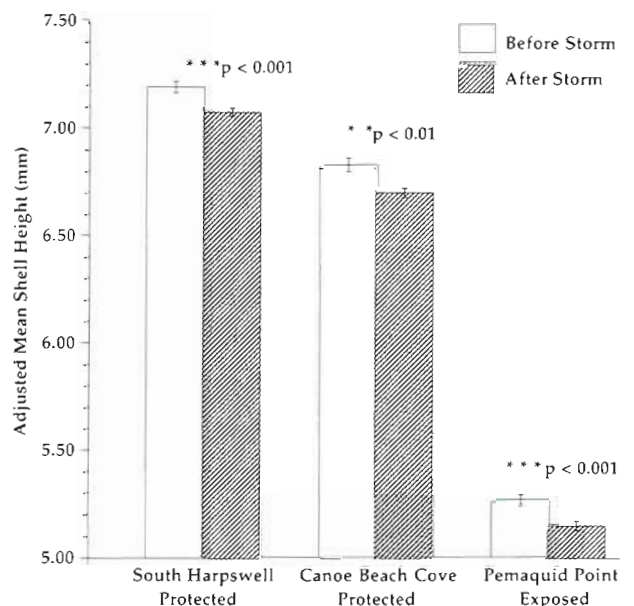
$p \geq 0.55$). Snails measured before the storm from Canoe Beach Cove ($F_{(1, 132)} = 9.42$; $p < 0.005$; Fig. 4), South Harpswell ($F_{(1, 135)} = 12.33$; $p < 0.001$; Fig. 4), and Pemaquid Point ($F_{(1, 101)} = 13.06$; $p < 0.001$; Fig. 4) all had taller shells relative to shell length than conspecifics measured from each site after the storm.

ANCOVAs on aperture area as a function of shell length found that the apertures of post-storm samples were smaller than those of pre-storm samples collected
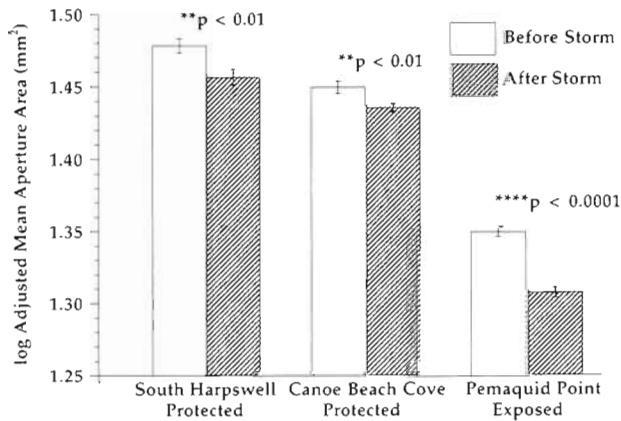
Fig. 5. *Littorina obtusata*. Adjusted mean log aperture area (±SE) from ANCOVA for snails sampled before and after the storm at each study site. See Table 1 for sampling dates and Table 2 for regression statistics and sample sizes

from Canoe Beach Cove ($F_{(1,132)}$ = 8.85; p < 0.01; Fig. 5), South Harpswell ($F_{(1,92)}$ = 8.47; p < 0.01; Fig. 5), and Pemaquid Point ($F_{1,93}$ = 71.66; p < 0.00001; Fig. 5). In all cases slopes were homogeneous (all p at least ≥ 0.20).

ANOVA on shell length for samples collected before and after the storm detected a shift to smaller-sized shells at the wave-exposed site (Pemaquid Point: $F_{(1,94)}$= 6.92; p < 0.01). However, no differences in pre- versus post-storm shell length was detected at both protected sites (Canoe Beach Cove: $F_{(1,133)}$ = 0.04; p > 0.05; South Harpswell: $F_{(1,136)}$ = 3.01; p > 0.05).

DISCUSSION

Wave energy is believed to be an important selective force on many intertidal snail attributes. Although snail growth rates (Janson 1982, Brown & Quinn 1988), reproductive output (Etter 1988b), and physiological stress (Etter 1989) are known to vary with gradients in wave-exposure, substantial emphasis has considered the influence of wave energy on snail shell form (Kitching et al. 1966, Kitching & Lockwood 1974, Palmer 1985, Johannesson 1986, Trussell et al. 1993, Trussell 1996, 1997).

I found that the shells of protected snails were taller and smaller apertured relative to shell length than wave-exposed conspecifics (Figs. 2 & 3). For relative shell height, the dramatic increase in water velocity and acceleration during the storm reinforced the pattern of relatively squatter shells as wave exposure increased. Snails measured from each population after the storm had significantly squatter shells relative to shell length than those measured before the storm

(Fig. 4). Hence, the natural experiment supports the hypothesis that among population variation in relative shell height is partly due to differences in wave energy among the 3 study sites. Compared to the morphological differences found between natural populations, shifts in relative shell height after the storm were small. Despite the magnitude of the storm recorded in this study, its impact on natural populations may have been limited by the available variation in relative shell height, especially if selection pressures operating during 'typical' conditions have depleted variation in this trait.

Selection against relatively taller shells by increased hydrodynamic forces may reflect 2 factors. First, a decrease in relative shell height may reduce the shell's coefficients of lift and/or drag; theoretically a reduction in either of these coefficients could reduce the magnitude of hydrodynamic forces acting on the snail's shell and thus the risk of dislodgement. For example, Dudley (1985) found that limpets from highly wave-exposed environments had shells that experienced lower relative drag than those of limpets from sheltered environments (see also Branch & Marsh 1978). Denny (1989) also reported a limpet shell shape that reduced drag but concluded that the conditions favoring streamlining, such as predictable flow direction and the absence of upstream objects (Vogel 1981), are unlikely to occur in the field. In addition, since both studies were conducted in laboratory flumes with orientation of shells into flow controlled, their relevance to field conditions is difficult to determine.

A second and perhaps more likely scenario is that relatively squatter shells will increase the availability of sheltered microhabitats for snails during periods of intense wave energy. Exclusion from sheltered cracks and crevices may force taller-shelled snails to bear the full brunt of storm surge. Crevice use in intertidal snails is common and the size structure of some snail populations is coupled with microhabitat size and availability. For example, Emson & Faller-Fritsch (1976) increased the size structure of *Littorina rudis* populations by increasing crevice size, and Rafaelli & Hughes (1978) found a tight relationship between the sizes of *L. rudis* and *L. neritoides* and the size of available crevices. Interestingly, the relationship documented by Rafaelli & Hughes (1978) held for wave-exposed shores but not protected shores suggesting that crevice size and availability are more important on wave-exposed shores in reducing the effects of wave-imparted forces. *L. obtusata* on wave-exposed shores, especially after periods of increased wave action, are typically found in or near cracks and crevices, while protected-shore snails are typically found on the intertidal alga *Ascophyllum nodosum* (author's pers. obs.). If size-related exclusion from sheltered microhabitats

is the mechanism accounting for my results, then crevice size and availability may be important on both wave-exposed and protected shores during unusually intense storms.

The crevice use hypothesis also explains the peculiar shift to smaller apertures after the storm in each population (Fig. 5). Intuitively, since aperture area is a reliable predictor of tenacity, one would expect a shift to larger apertures in response to increased hydrodynamic stress. This logic has been used to account for the typically larger apertures of wave-exposed snails, which are presumably capable of accomodating a larger adhesive foot. However, during unusually large storms the ability to exploit sheltered microhabitats is probably paramount in reducing the risk of dislodgement because it is unlikely that snails are able to withstand such intense free-stream flows via adhesion. The shift to both relatively squatter shells and smaller apertures probably reflects the premium on successful exploitation of sheltered crevices during larger storms. Despite this discussion, much remains to be learned about how and why the shift in aperture area occurred.

As expected, a shift to shorter shells after the storm occurred at the wave-exposed study site. Shorter shells could directly reduce the magnitude of hydrodynamic forces (Denny et al. 1985) and, like relatively squatter shells and smaller apertures, may improve the ability to hide in sheltered microhabitats. However, this shift did not occur at the protected sites. These results imply that the effects of the storm were only pronounced enough at the wave-exposed site to elicit a shift to shorter shells. If so, then it appears that relative shell height and aperture area are more sensitive to the effects of large storms than shell length because the shift in both traits occurred at all 3 study sites.

Although the correlation between the change in relative shell height and aperture area and the storm suggests that selection occurred, the lack of direct evidence of storm-induced mortality requires that my results be viewed with caution. However, if snails were able to survive being swept to the subtidal, I think the amount of time that samples were taken after the storm (Table 1) was probably sufficient for survivors to return to the intertidal zone.

While both pre- and post-storm samples were taken at the same tidal height and location on each shore, other factors such as storm or seasonally-induced migration downshore out of my sampling areas could also explain the morphological shifts I detected. For example, harsh weather conditions are known to restrict foraging behavior in *Nucella lapillus* (Burrows & Hughes 1989). I think it unlikely, however, that snails would migrate large distances downshore during unusually intense storms. Instead, I would expect snails to seek the nearest available crevice and remain stationary until conditions improve, especially since Miller (1974) showed that the ability of snails to remain attached to the substratum (tenacity) is reduced when crawling. Hence, the risk of dislodgement for migrating snails during intense storms would be greater than that for snails remaining in crevices. Fletcher (1990) detected no seasonal effects on the vertical zonation of *Littorina obtusata* suggesting that pronounced seasonal migrations do not occur. Despite my arguments, these and other snail behaviors may be involved and more research is needed to determine their potential influence on the morphological changes I observed.

In summary, the precise mechanism responsible for the morphological shifts I observed remains unclear. However, I suggest that both relative shell height and aperture area, or factors related to them (Endler 1986), have an important role in reducing the wave-imparted hydrodynamic forces acting on snails during large storms. Moreover, the shift in relative shell height is consistent with differences observed among natural populations experiencing different wave energies. This result suggests that increased water velocities and accelerations may, directly or indirectly, serve as potent selective forces on shell morphology that contribute to variation in gastropod shell form on shores differentially exposed to wave action. Although phenotypic plasticity in snail traits such as foot size (Etter 1988a, Trussell 1997) and shell thickness (Appleton & Palmer 1988, Palmer 1990, Trussell 1996) have demonstrated that selection is not the sole factor responsible for morphological differences among populations, my results suggest that selection can assume a more prominent role during unusual events like this storm (Bumpus 1899, Boag & Grant 1981, Endler 1986).

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