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Evolution

Intense natural selection caused a rapid morphological transition in a living marine snail

(predation/morphological variation/evolution)

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ABSTRACT **Shell shape and shell thickness of the intertidal snail *Littorina obtusata* changed markedly between 1871 and 1984 in northern New England. Shells collected prior to 1900 were high-spired with thin walls, whereas shells collected in 1982–84 were low-spired with thick walls. An intertidal crab (*Carcinus maenas*) which preys on *L. obtusata* expanded its range into northern New England around 1900. This suggests that the change in snail shell form was a response to predation by *Carcinus*. Field and laboratory experiments demonstrated that the high-spired form of *L. obtusata*, which can still be found in some Maine localities, is more vulnerable to predation by *Carcinus* than is the low-spired form of *L. obtusata*. Electrophoretic comparisons of high- and low-spired populations of *L. obtusata* confirmed that these populations represent different morphological forms of *L. obtusata* rather than different species [Nei's *D* (unbiased measure of genetic distance) = 0.003]. These data demonstrate that classical Darwinian selection can produce a rapid morphological transition without speciation.**

A pattern of punctuated morphological evolution in the fossil record may be widespread (1), but there is strong disagreement among evolutionary biologists over the mechanisms producing this pattern (2, 3). The main debate focuses on whether or not the punctuated equilibrium pattern (including both long-term morphological stasis and rapid morphological change) can be explained by classical neo-Darwinian mechanisms (3). Some evolutionary biologists conclude that morphological breaks observed in fossil lineages represent speciation events and suggest that natural selection plays a minor role in these rapid transitions (4–7). Other biologists maintain that natural selection may cause rapid transitions as well as slow and gradual change and that no new mechanisms need be invoked to explain punctuated morphological evolution (8–10). Many have challenged the claim that rapid transitions documented in fossil lineages represent speciation events (11–16). Recent theoretical models (17–19) analyzing the response of populations experiencing classical neo-Darwinian processes of selection and random genetic change have shown that morphological evolution in these populations may be rapid and result in a pattern like that of the punctuated equilibrium model.

Testing the power of natural selection to produce a rapid morphological transition in real organisms has been difficult for both ecologists and paleontologists: rapid transitions are rarely witnessed by ecologists, and the selective processes which might drive such a transition are not visible in the fossil record. I report here that a rapid morphological transition occurred in the intertidal snail *Littorina obtusata* (L.) between 1871 and 1984 in northern New England (USA) in response to intense natural selection by the crab *Carcinus maenas* (L.). This intertidal predator did not occur north of Cape Cod, Massachusetts, before 1900 (20); after 1900 *Carcinus* moved north of Cape Cod into northern New England. At present it is found as far north as northern Nova Scotia (21). Snail shells collected prior to 1900 in northern New England are high-spired with thin walls, but shells from *L. obtusata* populations in most areas of northern New England today are low-spired with thick walls. However, populations of *L. obtusata* with high-spired shells can still be found at some Maine localities (22) (Fig. 1). Geographic variation among living *L. obtusata* populations makes it possible to compare the vulnerability of high- and low-spired shells to crab predation and, thus, test whether directional selection by *Carcinus* is likely to have caused the rapid change in snail shell morphology.

Field and laboratory studies demonstrated that high-spired shells of *L. obtusata* are more vulnerable to *Carcinus* than are low-spired shells. Furthermore, genetic analyses indicated that living populations of high- and low-spired snails are not reproductively isolated. These data support the view that morphological transitions that appear abrupt in the fossil record may be a product of classical Darwinian selection and should not be assumed to represent speciation. This confirms a key prediction of Kirkpatrick's recent theoretical model (17): that morphological transitions resulting from adaptive shifts of populations can be both large and abrupt.

METHODS

L. obtusata shells collected before 1900 [some of which were labeled *Littorina palliata* (Say)] were found from Nahant, Massachusetts (42° 25.5′ N, 70° 55.0′ W), at the Museum of Comparative Zoology, Harvard University (1898, MCZ 2000); from Appledore Island, Maine (42° 57′ N, 70° 35′ W; 1871, deposited in Yale Peabody Museum, YPM 19351); and from Isle au Haut, Maine (44° 04.3′ N, 68° 38.3′ W; 1893, MCZ 13972). A sample from Nahant collected in 1915 (YPM 19079) was also measured. To compare shells collected prior to 1900 with shells of living populations of *L. obtusata*, snails from four different sites at each of the three above-named localities were collected (YPM 19345–19349, 19352–19358). In addition, snails from two living populations of *L. obtusata* from Perry, Maine (Sipp Bay, YPM 19359; Gleason Point, YPM 19360), which appeared to represent a high- and low-spired shell form, respectively, were collected.

The shell form of a *L. obtusata* population was assessed by measuring four shell characters (spire height, shell thickness, shell width, and shell height, all in mm). Spire height was defined as the height of the shell above the body whorl; shell thickness, as the width of the outer lip of the aperture; shell width, as the width of the body whorl; and shell height, as the length of the shell from apex to the base of the outer lip (22). The first two characters were measured with an ocular

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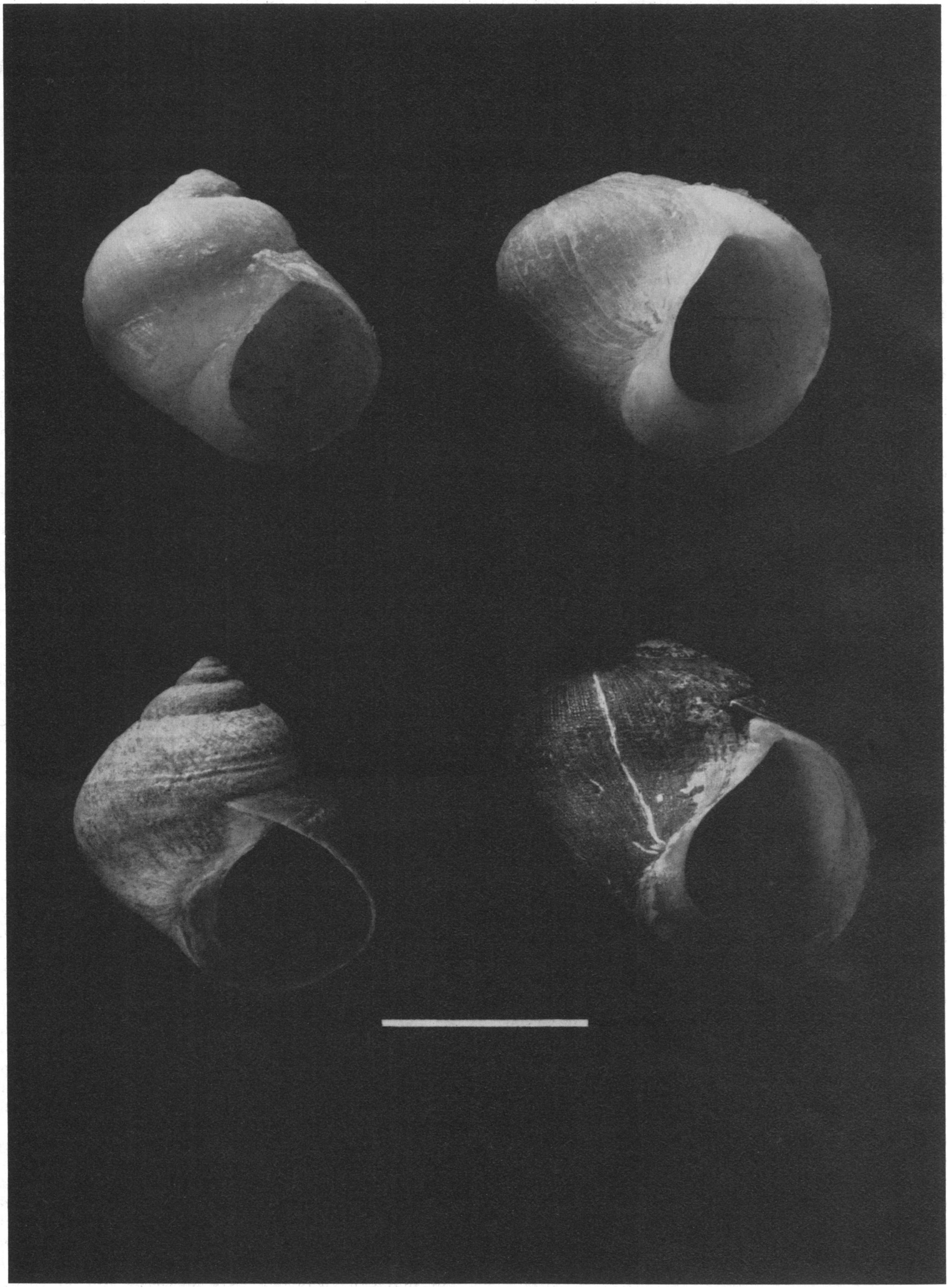

FIG. 1. Historical and geographic variation in *L. obtusata* (L.) from Maine (USA). (*Upper Left*) Appledore Island, 1871 (YPM 19351). (*Upper Right*) Appledore Island, 1982 (YPM 19349). (*Lower Left*) Sipp Bay, Perry, 1984 (YPM 19359). (*Lower Right*) Gleason Point, Perry, 1984 (YPM 19360). (Bar = 5 mm.)

micrometer at ×10 magnification; the latter two were measured with calipers. Shell shape was defined as relative spire height: $\log_e$ spire height/$\log_e$ shell width. Relative shell thickness was calculated as $\log_e$ shell thickness/$\log_e$ shell width.

For snail populations within each of four localities (Nahant, Appledore Island, Isle au Haut, and Perry), shell shape and relative thickness of medium-sized (4- to 8-mm shell height) snails were compared with a Kruskal–Wallis test. Kruskal–Wallis tests were also used to check the assumption that shell width did not differ between the populations being compared.

Relative spire height was distributed normally for all three (1898, 1915, 1982–84) Nahant populations. To quantify the amount of change in shell shape over time, means and standard deviations were calculated for relative spire height in these populations.

Tests of the vulnerability of the high- and low-spired snail shell forms to *Carcinus* were conducted both in the field and in the laboratory. Field experiments were set up at three Maine sites that differed in abundance of *Carcinus*. Crab abundance was assessed by summing the number of individuals of *Carcinus* found in two 60-min searches (in September and October 1984) in the intertidal zone. Crabs were abundant at Gleason Point, Perry ($n = 97$); much less abundant at Sipp Bay, Perry ($n = 4$), and extremely rare at Timber Cove, Trescott ($n = 0$). At each of these sites 15 pairs of large (8- to 10-mm shell height) snails (a higher-spired shell paired with a lower-spired shell) were tethered to fucoid algae in the mid-intertidal zone. At both Gleason Point and Sipp Bay, snails collected from Sipp Bay (a higher-spired population) and Gleason Point (a lower-spired population) were tethered. At Timber Cove snails from Timber Cove (higher-spired) and snails from Strawberry Creek, Brunswick (Maine) (lower-spired) were tethered (precise localities are recorded in ref. 22).

Each snail was attached to a 10-cm-long piece of 8-lb (4.03 kg) test nylon monofilament tied through a <1-mm-diameter hole drilled near the base of the snail shell. The other end of the tether was tied around a frond of fucoid algae. On day 16 of the experiment, I calculated the percentage survival of each population representing either shell form as (the number of snails alive with an intact shell)/(the number of snails alive with an intact shell + the number of snails dead with a crushed shell). The significance of the difference in survival between two populations was tested with the test for equality of two percentages (23). A small number of snails in these experiments were lost from their tether (3%) or died inside an intact shell (17%); these data were omitted from calculations of survivorship.

Laboratory tests took place at the Shoals Marine Laboratory, Appledore Island, Maine. Individual crabs (size range, 35.1- to 45.9-mm carapace width; $n = 16$, mean ± SD = 40.6 ± 3.6 mm) were offered a high-spired ($n = 8$ from Eastport, Maine) or low-spired ($n = 8$ from Appledore Island) snail between 6- and 8-mm shell height. Crabs were randomly chosen, tested only once, and observed for up to 8.25 min (or until the crab rejected the snail by pushing the shell away with its claw) to determine whether or not they were able to crush the shell. Snails whose shells were fatally crushed required only 42 ± 17 sec (mean ± SD) of handling by crabs.

Horizontal starch gel electrophoresis was conducted on individuals from Sipp Bay (high-spired) and Gleason Point (low-spired) populations to determine whether the two shell forms are likely to represent two species. Snails were collected in November 1984 and immediately frozen in tissue buffer at −80°C (22). Wicks of Whatman no. 1 filter paper were applied to a snail homogenate and inserted into a gel made with one of five buffers [TEB 9.1, TEB 8, and TC 6, (24); Poulik (22); and PC 7, (25)]. Conditions under which gels were run are provided in ref. 22. Gels were sliced, stained, and scored for 13 loci. Stain recipes for aspartate aminotransferase, phosphoglucomutase, phosphoglucoisomerase, leucine aminopeptidase, xanthine dehydrogenase, glucose-6-phosphate dehydrogenase, and mannose phosphate isomerase are provided in ref. 24; recipes for esterase and sorbitol dehydrogenase are provided in ref. 22. Allele frequencies were analyzed with the BIOSYS package of programs (26). Genetic distance was calculated using Nei's (27) unbiased measure of genetic distance (D).

RESULTS

Snail shells collected at Nahant, Appledore Island, or Isle au Haut prior to 1900 were significantly taller in spire and thinner in shell wall than were snail shells collected at these localities in 1982–84 (Figs. 1 and 2*A*, and Table 1). At Nahant, relative spire height decreased from a mean of 0.34 in 1898 (SD, 0.07) to a mean of −0.04 in 1915 and to −0.35 in 1982–84. This is a change of 5.4 standard deviations in at most 17 generations (1898–1915) and a change of 9.9 standard deviations in at most 86 generations (1898–1984). Shells of *L. obtusata* individuals collected from Sipp Bay in 1984 were higher-spired and thinner than shells collected from Gleason Point in 1984 (Figs. 1 and 2*B* and Table 1).

High-spired individuals of *L. obtusata* are more vulnerable to crab predation than are low-spired individuals. At Gleason Point, where crabs are abundant, survival of the low-spired population was 57%, but in the high-spired population, it was only 14% ($P < 0.01$, $n = 28$). At Sipp Bay, where crabs are less abundant, survival of the low-spired population was 89% but only 33% in the high-spired population ($P < 0.01$, $n = 21$). However, at Timber Cove, where crabs are rare, survival of both high-spired and low-spired populations was 100% ($n = 20$) (Fig. 3). In laboratory experiments, only 12% of the low-spired snails but 100% of the high-spired snails were successfully attacked by *Carcinus* ($P < 0.001$, $n = 16$).

Living snail populations differing markedly in shell form (Gleason Point and Sipp Bay, Figs. 1 and 2*B*) are very similar in frequencies of alleles detectable by starch gel electrophoresis (Nei's $D = 0.003$).

DISCUSSION

Results of field observations and experiments reported here demonstrate that intraspecific variation in shell spire height and thickness in *L. obtusata* is likely a product of varying intensities of crab predation. Low-spired shells are better defended against crab attack because of increased whorl overlap in these shells (Fig. 1). Because shell thickness increases with each successive whorl, increased overlap causes the thin shell whorls of the juvenile snail to be enclosed in the thicker whorls of the adult. In high-spired shells, these thin (and thus more vulnerable) whorls are exposed to crushing predators. The studies of the effects of *Carcinus* predation on living *L. obtusata* populations differing in shell form strongly support the hypothesis that the rapid morphological transition which took place during the last century in *L. obtusata* was a response to intense directional selection by *Carcinus*.

The claim for gradual, adaptive evolution of the low-spired form of *L. obtusata* is subject to the objection that current utility of the low-spired shell as a successful defense against crabs does not demonstrate that the low-spired form evolved in response to crab predation. However, the observation that the shift in shell form occurred during the same period of time that crabs were introduced, and the existence of a strongly positive correlation between "low-spired-ness" of the shell of living snail populations and abundance of *Carcinus* (22)

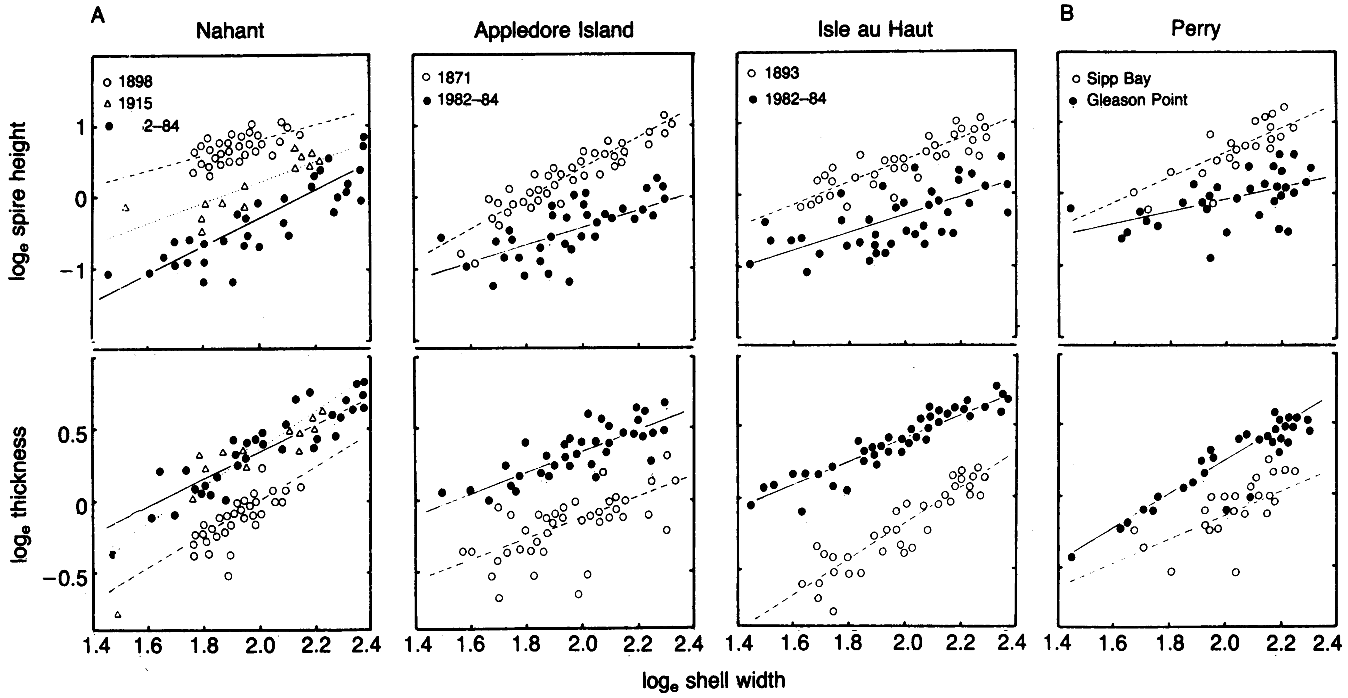

FIG. 2. Historical and geographic variation in shell morphology (spire height and shell thickness) between populations of *L. obtusata* (see *Methods* for museum lot numbers). The locality of each collection represented is shown over each pair of plots. Lines drawn in each plot represent least-squares regressions. (*A*) Historical variation between pre-1900 (○) and 1982–84 (●) shell collections from three localities in northern New England. (*B*) Geographic variation between two populations in eastern Maine (Fig. 1) in 1984.

strongly supports the claim for an adaptive morphological transition in *L. obtusata*.

A second potential objection to the claim for adaptive evolution of shell form within a species is that the pattern of rapid change in shell form is compatible with a process of extinction (of a high-spired species) and range expansion (of a low-spired species) as well as with a process of *in situ* evolution of a single snail species. Two findings indicate that evolution of populations within a single species is the correct interpretation of this pattern. First, two populations from eastern Maine (Sipp Bay and Gleason Point) differing in shell shape and thickness (Figs. 1 and 2*B*) are genetically as similar as are conspecific populations of other *Littorina* species (28). Second, snail populations at localities with moderately high numbers of crabs are intermediate in shell form to more extreme high- or low-spired populations (22) found at localities where crab abundance is low and high, respectively. Data revealing that shells collected from Nahant in 1915 are also intermediate in spire height further support the interpretation of this morphological transition as a gradual, within-species response to a new selective pressure.

The pattern of rapid morphological change observed in *L. obtusata* matches the pattern of change predicted by Kirkpatrick (17) for a population moving rapidly from one fitness peak to another as a result of a changed environment. Kirkpatrick's (17) theoretical model predicts that a rapid transition driven by natural selection would be likely to appear discontinuous in the fossil record because of the brevity of the transitional period relative to sampling interval. Analysis of the morphological transition in *L. obtusata* indicates that it took place in approximately 100 years (≤ 100 generations). The intermediate shell shape of the 1915 Nahant collection (Fig. 2*A* and Table 1) suggests that at this locality, transitional forms were present only 17 years (≤ 17 generations) after high-spired snails had been collected. This supports the conclusion of the Kirkpatrick (17) model that morphological transitions driven by selection in a changing environment can occur rapidly. As Palmer (29) has pointed

Table 1. Comparison of shell shape (relative spire height) and thickness of *L. obtusata* populations collected at different times from one locality or from different sites within a locality in 1984

	Populations from one locality at different times							Populations from different Perry sites in 1984	
	Nahant			Appledore Island		Isle au Haut			
Parameter	1898 (44)	1915 (8)	1982–84 (39)	1871 (46)	1982–84 (50)	1893 (23)	1982–84 (47)	Sipp Bay (15)	Gleason Point (16)
Relative spire height									
Median	0.34	−0.06	−0.34	0.15	−0.23	0.14	−0.29	0.15	−0.10
Minimum	0.19	−0.29	−1.03	−0.58	−0.73	−0.10	−0.64	−0.36	−0.47
Maximum	0.52	0.27	0.08	0.36	0.16	0.32	0.20	0.45	0.10
$P <$	0.0001	0.003		0.0001		0.0001		0.03	
Relative shell thickness									
Median	−0.06	0.15	0.13	−0.06	0.17	−0.19	0.18	−0.13	0.03
Minimum	−0.26	−0.54	−0.25	−0.41	−0.25	−0.46	−0.07	−0.52	−0.30
Maximum	0.13	0.22	0.34	0.09	0.28	−0.03	0.26	0.00	0.20
$P <$	0.001	0.93		0.0001		0.0001		0.003	

Numbers of observations are shown in parentheses. Significance levels are shown for results of Kruskal–Wallis tests.

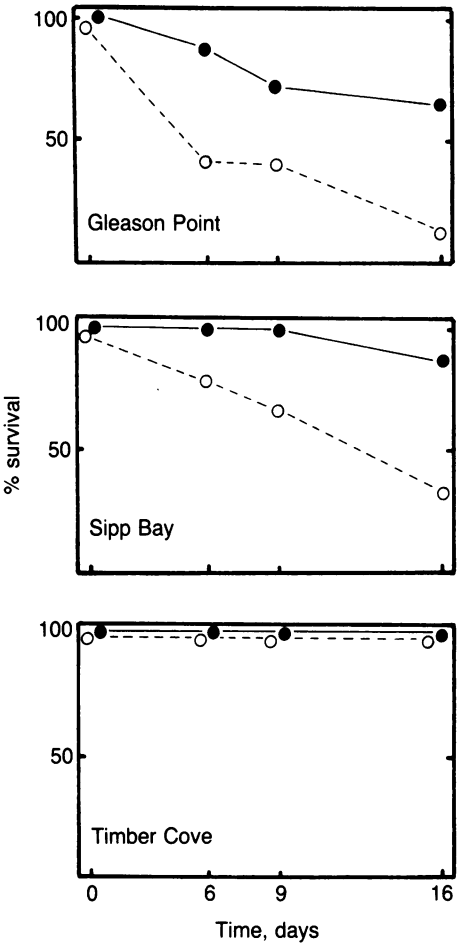

FIG. 3. Differences in survival of populations representing high- and low-spired shell forms of *L. obtusata* at three Maine sites differing in crab (*Carcinus*) abundance. Crabs were very abundant at Gleason Point, much less abundant at Sipp Bay, and extremely rare at Timber Cove (see text). ○, High-spired populations; ●, low-spired populations.

out, quantum changes in the shell morphology of fossil gastropods could result from changes at few gene loci and need not represent a speciation event, as suggested by Williamson (7, 30–31) for Turkana Basin gastropods.

Finally, study of the relationship between crabs and *L. obtusata* shell morphology indicates that the potential importance of classical Darwinian selection on individual organisms as a mechanism underlying morphological discontinuities in fossil lineages should not be underestimated. The rate and degree of morphological response to selection will differ among taxa according to population structure, ecological conditions, and the degree to which change in a character is developmentally constrained. This is underscored by Vermeij's initial discovery that two other gastropod species showed no significant morphological change [*Littorina littorea* (L.); ref. 32] or a minor change in shell form [*Nucella lapillus* (L.); ref. 33] in response to the range expansion of *Carcinus*. *L. obtusata*, in contrast, apparently responded to this significant ecological event with a major change in shell morphology.

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