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SIZE-SPECIFIC EMERGENCE OF THE MARSH SNAIL, *LITTORINA IRRORATA*: EFFECT OF PREDATION BY BLUE CRABS IN A VIRGINIA SALT MARSH

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ABSTRACT Marsh periwinkles of 5 to 7 mm in shell height were eaten regularly by blue crabs. Fractures marking unsuccessful crab attacks were present in about 25% of medium-sized (10–16 mm) snails and over 60% of larger snails (over 16 mm). Medium-sized snails, subject to predation, leave the water more frequently than larger snails, but only about a quarter of the snail population leaves the water during high tide. We found no evidence that the snails leave the water because they sense blue crabs in the water.

INTRODUCTION

The marsh periwinkle *littorina irrorata* (Say) is a grayish gibbous, intertidal snail common in salt marshes from New York to Texas. It is believed to be a grazer, feeding largely on plant detritus and epipelic algae (Odum and Smalley 1959; Stiven and Kuenzler 1979). According to Bingham (1972) and Hamilton (1976, 1978), periwinkles are effectively supratidal; they avoid submergence by crawling upward out of the water when innundated. Bingham (1972) attributed the absence of snails in barren areas to "reluctance of the species to remain submerged." Bleil and Gunn (1978) demonstrated that this response is not caused by threat of drowning; the snails can survive long periods under water. Hamilton (1976) attributed the avoidance of submergence to predation by the blue crab *Callinectes sapidus* Rathbun, which enters the marsh with the flood tide and preys on periwinkles. Crist (1979) found that a size gradient exists in periwinkles; larger individuals occur more frequently than smaller snails at lower elevations in the marsh. He attributed this in part to differential predation on smaller snails by blue crabs, which are more abundant at lower elevations.

Preliminary observations on a study site at Wallops Island, Virginia, indicated that a substantial majority of specimens of *L. irrorata* remained under water at high tide, despite an abundance of emergent vegetation. That observation was an obvious contradiction to the behavior of *L. irrorata* in an aquarium—all snails crawl out of the water immediately (Bingham 1972).

We noticed also that smaller snails tended to be more abundant out of water on stalks of vegetation than in the water. We reasoned that there may be a size-specific difference in the response of snails to submergence because of differential predation on smaller snails relative to larger ones.

The purpose of this paper is to quantify the size-specific proportions of snails which emerge from the water at high tide in the field, and to test the hypothesis that blue crab predation may influence those proportions.

MATERIALS AND METHODS

The study site was a juvenile sloping foreshore marsh located on Cow Gut Flat at the north end of Wallops Island, near Chincoteague, Virginia. Drainage at low tide is nearly complete, and freshwater input is limited to rainfall and groundwater discharge. No tidal creeks or primary pans are present. Tall and medium vigor *Spartina alterniflora* (Loisel) predominate. *Salicornia* spp. is abundant at some higher elevations; the highest elevations are dominated by marsh elder, *Iva frutescens* (Linnaeus) (Reidenbaugh and Banta 1980).

Tidal wrack, consisting primarily of dead stalks of *S. alterniflora*, formed dense mats, which were rafted into the site during abnormally high tides (Reidenbaugh and Banta 1980). Vegetation compressed beneath stranded mats often is partly or completely killed, and in the most severe cases, secondary bare areas formed.

Field experiments were conducted within a 17,000-m^2 study site marked by wooden stakes placed at 10-m intervals from below mean low water to above mean high water. The study site has been named the Intensive Biometric Intertidal Survey (IBIS) marsh (Reidenbaugh and Banta 1980).

To determine the size distribution of *Littorina irrorata* in the IBIS marsh survey grid, 30 sampling points were located relative to stakes, using computer-generated random numbers. Elevations at each collecting site were determined by linear interpolation among the four surrounding stakes. Stake elevations were determined by transit relative to Bench Mark IBIS, +1.427 m National Geodetic Vertical Datum (NGVD). A 1-m^2 quadrat was centered at each of the sampling points at or near the time of low tide between 16 and 18 July, 1979. The weather during this time was uniformly sunny and warm, with temperature maxima near 30°C. All marsh periwinkles were collected, counted, measured to the nearest 1 mm shell height, and returned to the same quadrat.

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The proportion of emergent snails was determined by returning to the same 30 quadrats at high tide. Predicted high tides at Chincoteague Point, 1 km away, were used. United Stated Geodetic Survey tide tables predict tides at the IBIS marsh site within less than 2 mm (Reidenbaugh 1978). A 1-m² wood frame was floated on the surface of the water, and emergent snails on stems and blades of emergent vegetation were counted and measured. Water depth and average height of the highest stalks were estimated using a meterstick; height of emergent vegetation was estimated as the difference between those two values. Variation in plant density among sites was relatively constant (Reidenbaugh 1978).

To study crab predation on snails, blue crabs of various sizes were netted near the IBIS marsh and starved about 24 hours in separate 85-liter aquaria with filter beds of crushed oyster shell; crabs were then offered snails of various sizes. Observations and photographs were made of the crabs' behavior, and damage to the snails was noted.

For studying fractures in shells, 330 snails were removed at low tide from five randomly selected quadrats at various elevations in the study site between 0.173 and 0.434 NGVD. Individuals were measured and examined for repaired fractures in the shell, and for evidence of severe shell erosion which might obliterate visible marks.

To determine if the presence of crabs in the marsh had an effect on the behavior of the periwinkles, three crabs were placed in a plastic mesh bag. Five such bags were staked in the center of five of the 30 sampling quadrats on an incoming tide. At high tide emergent snails were measured and counted.

RESULTS AND DISCUSSION

Figure 1 illustrates the proportion of snails emergent at low tide at 30 randomly selected quadrats. Of the 1,722 snails present in all quadrats at low tide, 491 (29%) were emergent at high tide. No significant correlation was found between the proportions of snails emergent at high tide and the absolute elevation of the marsh surface ($n=30$, $r=0$, $p[t]=0.977$). This finding confirmed our visual observations that snails tended to be scattered fairly evenly along vegetation stalks and that they were fairly indifferent to submergence.

Large snails (19 mm and greater in height) were about twice as likely to be submerged as smaller snails (12–18 mm) (Fig. 2). Snails less than 12 mm in height were present in relatively low numbers (fewer than 20) and were not considered further.

We attempted to determine if the relative submergence of *L. irrorata* might vary geographically. We reasoned that predation of crabs might be heavier farther south, selecting for an adaptive cline in water avoidance—that is, more southerly snails might be more subject to predation and therefore be selected to spend more time out of water than their more northerly conspecifics.

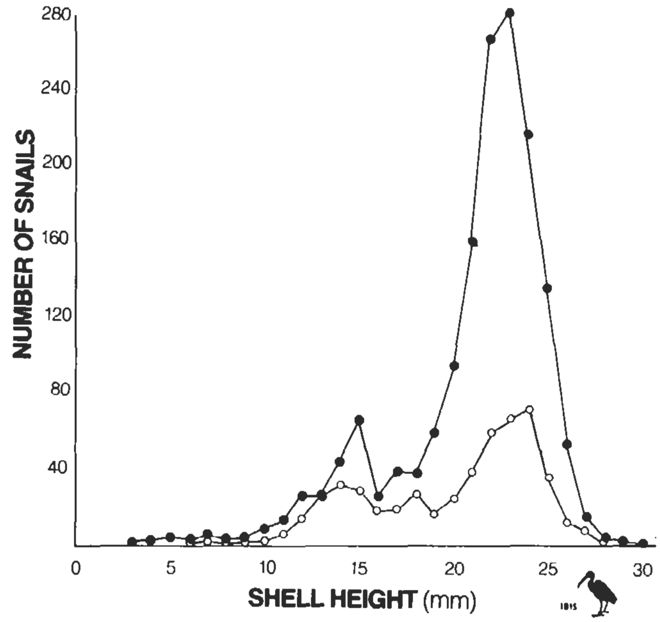

Figure 1. Size-frequency distribution of snails from randomly selected 1-m² quadrats. Closed dots represent all snails counted at low tide; open circles indicate snails emergent at high tide.

We made a cursory inspection of a *Juncus* marsh in which *L. irrorata* was abundant, at Ocean Springs, Mississippi, during March 1979. More snails appeared to be under water than out of it. In a study of a marsh in Georgia, four quadrats were selected, each at a different elevation. Eighty snails were counted when the tide was out; 36 (45%) were counted out of the water on the stalks when the tide was in. We conclude that individuals of *L. irrorata* spend a

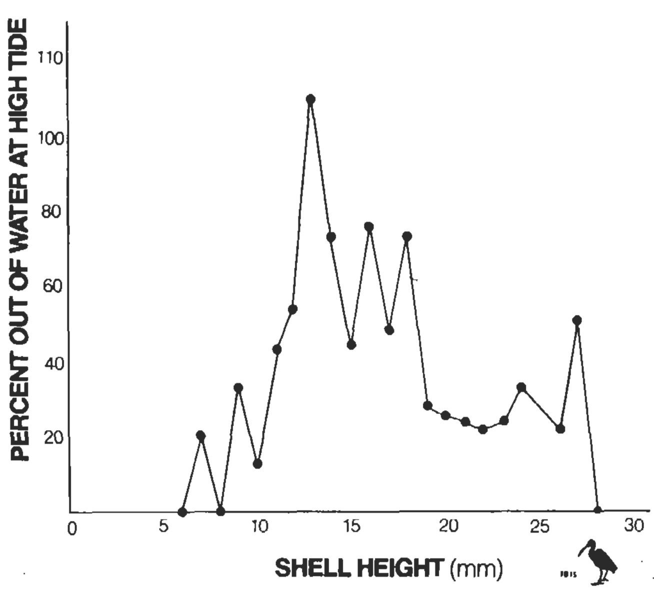

Figure 2. Percentage of snails out of the water on vegetation stalks at high tide plotted against shell length. Conventions as in Figure 1.

substantial part of their lives under water, at least through most of the animal's range.

Blue crabs attacked specimens of *L. irrorata* by breaking away bits of the outer body whorl. This process was described in detail by Hamilton (1976). Crabs did not attack snails with a shell height less than about 5 mm, presumably because the snails were too small to be noticed or too small to trouble with. If an attack on a snail succeeded, i.e., if the crab ingested significant meat from the shell, the entire snail was usually eaten and the shell reduced to small fragments.

Our data suggests that crabs may learn to eat periwinkles. One large crab (carapace width, 15 cm) refused periwinkles of all sizes until we drilled two small holes in the shell near the aperture of a 20 mm snail. The holes allowed the crab to grasp the shell securely and eventually to break it to pieces. Thereafter, the crab was an active predator on *Littorina*, regularly eating snails up to 16 mm long.

The largest undamaged snail we observed being crushed by any crab was 17 mm, almost the same size (16 mm) reported by Hamilton (1976).

Occasionally, crabs in aquaria abandoned their attempts to open periwinkle shells after they had only chipped the aperture. We observed similar fracture marks on live snails in the field; those fractures were usually preserved as growth discontinuities some distance from the aperture.

The proportion of snails whose shells were marked by fractures varied with size (Fig. 3). No snails with a shell length of less than 10 mm had fractures. Relatively low proportions (about 25% of medium-sized snails, 12–16 mm) contained fractures. We attribute the low proportion of fracture marks among small snails to the way that blue crabs eat periwinkles. Snails too small for blue crab predation (under about 5 mm), obviously will be free of fracture marks. Snails between 5 mm and about 10 mm were eaten almost each time they were attacked by blue crabs. In these cases the shells are reduced to small, unrecognizable shell fragments. The proportion of snails with fracture marks on their shells increased dramatically to about 60% in snails 17 to 20 mm in height, then dropped steadily among snails over 22 mm in height. The largest snails examined (26–27 mm) showed no signs of fractures. The decline in proportion of fractured shells among the largest snails is probably due to shell erosion; the proportion of the shell which was badly eroded correlated strongly with size (Fig. 3).

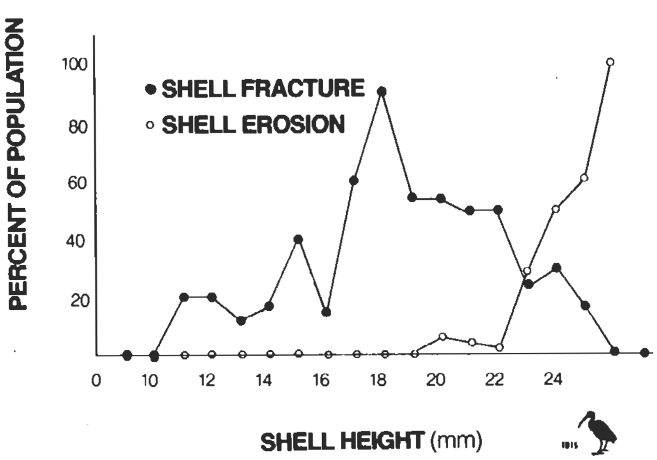

Figure 3. Percentage of the *L. irrorata* population showing evidence of predation as healed fractures in the shell, plotted against shell length. Also shown is the frequency of obvious shell erosion. The two data points at 27 mm are based on the same single specimen. Other data points are based on numerous individuals.

We found no evidence to indicate that *L. irrorata* sense blue crabs in the water during high tide. A t-test showed no significant difference in snails out of water between control trials and trials in which blue crabs were restrained in the experimental quadrats ($n=5$, $t=0.463$, $p[t]=0.492$).

SUMMARY AND CONCLUSIONS

1. On the average, marsh periwinkles at our study site in Virginia were distributed on the marsh floor or along vegetation stalks. We found no significant correlation between the absolute elevation of the marsh surface and the proportion of snails out of water at high tide. Most snails appeared to be relatively indifferent to submergence by the tide. Preliminary evidence suggests that the same is true for *L. irrorata* in Georgia and Mississippi.

2. Snails of about 12 to 18 mm in shell height spend proportionally more time out of the water than larger snails (19 mm and over). The change in behavior that occurred when snails reached about 18 to 19 mm in height may be an adaptation to crab predation, because smaller snails, less than about 17 mm, can be crushed and eaten by blue crabs, whereas larger snails were relatively safe.

3. Blue crabs were almost always successful in attacking snails of 5 to 15 mm in height; the shells were reduced to small fragments. Unsuccessful attacks, recorded as fractures in shells, were common on individuals over 10 mm in height. Over 60% of larger snails were probably attacked unsuccessfully.

4. We found no evidence to indicate that **L. irrorata** leaves the water in response to the presence of blue crabs nearby.

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