Gulf and Caribbean Research

Volume 7 | Issue 3

January 1983

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Recommended Citation

Crist, R. and W. C. Banta. 1983. Distribution of the Marsh Periwinkle *Littorina irrorata* (Say) in a Virginia Salt Marsh. Gulf Research Reports 7 (3): 225-235.
Retrieved from https://aquila.usm.edu/gcr/vol7/iss3/4
DOI: https://doi.org/10.18785/grr.0703.04

Gulf Research Reports, Vol. 7, No. 3, 225–235, 1983

DISTRIBUTION OF THE MARSH PERIWINKLE *LITTORINA IRRORATA* (SAY) IN A VIRGINIA SALT MARSH

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ABSTRACT *Littorina irrorata* varies over its geographic range in maximum size, preferred elevations relative to tidal datum planes, and in the type of vegetation it inhabits. On Wallops Island, Virginia, postlarvae of *Littorina irrorata* with shell lengths <5 mm long live almost exclusively in dead, curled-up leaves of *Spartina alterniflora* at elevations near mean tide level, below elevations occupied by larger conspecifics. Snails longer than 5 mm in length increase in average size with decreasing elevation. This distribution is opposite to that found by Hamilton (1978) in a marsh in Florida. No difference was found in our study area in growth rate of marked snails at two different elevations, so the size-elevation gradient probably is not caused by differences in growth rate. Snails 15 to 19 mm long are more active when exposed to reduced salinities than snails >21 mm long. The lowest salinities recorded in the marsh occurred at the highest elevations. This salinity effect, together with mortality from known size-selective predators, may account, at least in part, for the seaward increase in mean shell size.

INTRODUCTION

Many species of intertidal gastropods segregate by size on shore. The size segregation pattern exhibited by a species probably reflects size-specific responses to environmental gradients related to elevation and time of tidal innundation and exposure (Edwards 1969, Vermeij 1972). Vermeij (1972) described two types of size distributions among intertidal gastropods. In type-1, shell length increases upshore; this probably results from higher mortality among small individuals at higher elevations caused by physical extremes such as temperature, drying, or salinity extremes. Snails with a type-2 distribution increase in size downshore, probably because of higher mortality among small individuals at lower elevations, resulting from biological interactions such as predation or interspecific competition. The type-1 distribution is most frequent in species occupying high intertidal zones; type-2 is more common at lower intertidal levels.

Littorina irrorata (Say), the salt marsh periwinkle, is found in salt marshes bordering the Atlantic and Gulf coasts of the United States from New York to Texas (Bequaert 1943). *L. irrorata* feeds largely on *Spartina* detritus (Alexander 1976, Stiven and Kuenzler 1979). The snails occupy elevations between mean tide level and mean high water, but part of the population may actively maintain a supralittoral distribution by crawling up stalks of rooted vegetation after being wetted by the incoming tide (Bingham 1972a, Hamilton 1976, Stanhope et al. 1982).

Smalley (1959), working in Georgia, found highest *L. irrorata* densities in short-form *Spartina alterniflora* Loisel; he found few periwinkles in levee and middle-marsh zones. Hamilton (1978) studied *L. irrorata* on the Gulf coast of Florida. He found that snails <13 mm in length occurred throughout the *S. alterniflora* zone, but larger snails were found mostly in the upper half of the zone. According to Hamilton's data, *L. irrorata* appears to fit Vermeij's (1972) type-1 distribution, with mean shell size increasing upshore.

The purpose of this study was to determine the distribution limits of *L. irrorata* and the patterns of its size-class segregation with respect to elevation and tidal datum planes in a salt marsh on Wallops Island, Virginia. Tolerances of snails to a range of reduced salinities were determined experimentally for comparison with snail distribution patterns and with salinities measured in the field.

METHODS

The study site is a juvenile sloping foreshore marsh (Redfield 1972) located on Cow Gut Flat at the north end of Wallops Island, near Chincoteague, Virginia (Reidenbaugh and Banta 1980). Drainage at low tide is nearly complete, and freshwater input is limited to rainfall and minor groundwater discharge. No tidal creeks or primary pans are present. Tall and medium vigor *Spartina alterniflora* predominates. *Salicornia* spp. are abundant at some higher elevations; the highest elevations are dominated by saltbush, *Iva frutescens* Linnaeus (Reidenbaugh 1978, Reidenbaugh and Banta 1980). The study site has been named the IBIS (Intensive Biometric Intertidal Survey) Marsh (Reidenbaugh and Banta 1980).

Tidal wrack, consisting primarily of dead stalks of *S. alterniflora*, forms mats which are rafted into the site during extreme high tides (Reidenbaugh and Banta 1980). Vegetation compressed beneath stranded mats is often partially or completely killed. In the most severe cases, bare mud areas form (Figure 1).

Field work was conducted within a 17,000-m^2 study site marked by wooden stakes placed in a rectangular grid at 10-m^2 intervals from below mean low water to above mean high water. The elevations of all sampling sites, located in

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Manuscript received August 24, 1982; accepted November 29, 1982.

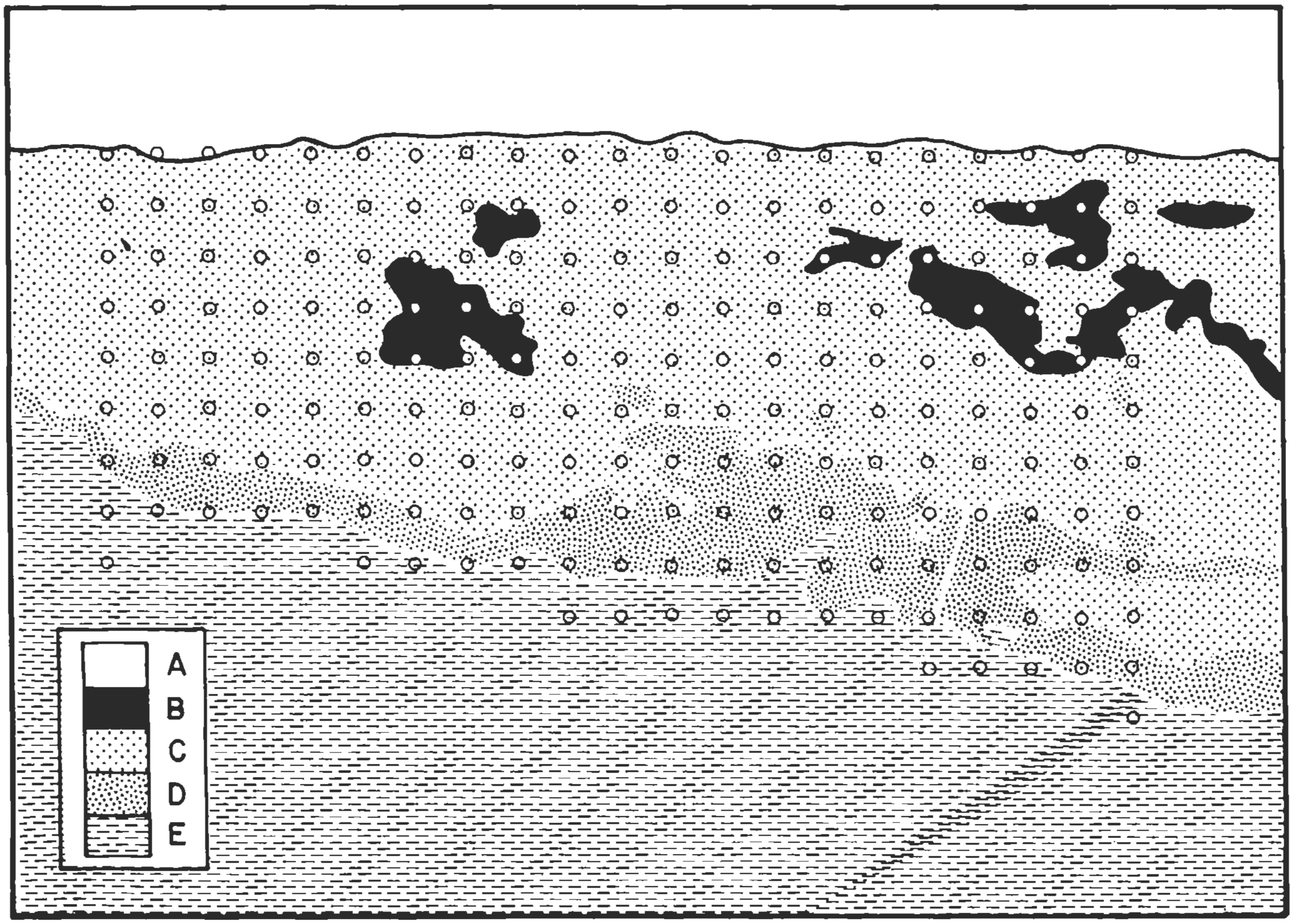

Figure 1. Vegetation map of the IBIS study site made from aerial photographs taken during 1975. Stakes marking sampling locations are represented by circles 10 m apart. Cover types: (A) tidal wrack, (B) bare soil, (C) middle marsh, (D) tall and levee *Spartina alterniflora*, (E) water. Redrawn from Reidenbaugh (1978).

the same relative position 1 m from each stake, were determined by surveying to the nearest stake. Stake elevations were determined relative to a local bench mark; its elevation was in turn determined relative to a U.S. Coast and Geodetic Survey (USGS) bench mark 1 km from the site (Reidenbaugh et al. in press). Tidal datum planes were calculated using estimates from the U.S. National Ocean Survey for Chincoteague, Virginia. The mean tidal range is about 0.8 m. Details are available in Reidenbaugh (1978).

The population density of *L. irrorata* was determined within quadrats at each sampling site three times during the summer of 1975 on 23–25 May, 2–5 July, and 3–10 September. Counts were made in 0.25-m^2, 0.50-m^2, or in 1-m^2 areas, depending on the density and types of vegetation present in each quadrat. The same areas were searched at each site on each sampling date. During two additional censuses made during 23–30 June and 17–30 September, shell length measurements were made with calipers of all periwinkles $>$ 5 mm long in 1-m^2 quadrats along three of the 20 transects in the sampling grid. Snails $<$ 5.0 mm in length were counted in 0.125-m^2 parts of each quadrat along three transects of the grid.

To determine growth rates of snails at different elevations, 167 individuals from two quadrats were marked, measured, and released to the same quadrats on 8 August, 1975. The quadrats selected were at elevations of 0.15 and 0.20 m. Marked snails were recaptured and measured 50 days later. To mark the snails, they were dried with paper towels, and a small tag of red fingernail polish was applied. After the polish dried, they were uniquely numbered in black India ink and coated with polyurethane.

About 200 salinity measurements were made on an almost daily basis from May to September using a hand refractometer, calibrated against ten dilutions of standard sea water and read to 0.5 ppt. Salinity readings of tidal water were taken midway between the surface and the bottom. Interstitial salinities were measured by placing a core sample from 2 to 3 cm below the surface into a 50-ml plastic syringe and extruding water through a filter onto a refractometer. Salinity measurements were made from cores taken from six transects sampled between June and September. Additional salinity measurements were made from other sampling locations, such as bare areas and depressions, where topographic and vegetational differences suggested variations in drainage.

The method used to determine salinity tolerance was similar to that used by Arnold (1972). Snails were collected adjacent to the sampling grid in an area where they were most abundant. The snails were divided into two size classes, 15–19 mm and 22–25 mm. Five snails from each size class were placed in a 250-ml Erlenmeyer flask containing sea water dilutions of 0, 5, 8, 10, 15, 20, or 30 ppt made from commercial sea salts (Instant Ocean®) and distilled water. Each flask was stoppered with a 2-hole rubber stopper to keep the snails submerged; the water was aerated using glass tubing extending to the bottom of the flask. Activity of each snail was scored between 11:00 A.M. and 2:00 P.M. daily, and the mean was recorded. All salinities were run simultaneously to eliminate possible systematic variations among snails caused by tidal rhythms. The activity scores used were: 0, dead; 1, inactive, retracted inside the shell, and not attached to the flask; 2, retracted inside the shell and attached to the side of the flask by a mucous holdfast; 3, attached to the side of the flask with the foot extended; 4, actively crawling with the head and foot extended. Snails were considered dead if they did not respond to probing of their foot or operculum within 1 hour after removal from the water.

RESULTS

Distribution of snails less than 5 mm long

The smallest snails, those with a shell length < 5 mm, generally were distributed quite differently from larger snails. The smallest snails were of two types. By far the largest numbers were found inside the curl of dead leaves of *Spartina alterniflora,* just distal to the ligule. They were usually arranged in tandem, like peas in a pod, with as many as 13 in a single leaf. These snails were found in a relatively narrow range of elevations, peaking near 0 m National Geodetic Vertical Datum (NGVD) near mean tide level (MTL). These snails reached very high densities, averaging over 300/m^2 near 0 m. A much smaller number of snails < 5 mm long, was found at the base of rooted vegetation or on the mud surface high in the marsh from about 0.3 to 0.4 m (about mean high water neap tide, MHWN, to mean high water, MHW) (Figure 2).

Snails greater than 5 mm in length

When periwinkles reach a shell length over about 5 mm, they graze on the marsh floor or attach to the surface of emergent vegetation.

The density-elevation distribution of snails > 5 mm remained fairly constant from June to September (Figure 3). Densities peaked sharply from about halfway between MTL and MHW, with a mean density of 48/m^2 (Figure 3). The maximum density recorded from a single quadrat was 140/m^2. About 85% of the population was found between -0.05 and 0.35 m NGVD. Population density decreased sharply above MHWN. Only 2% of the population occurred above

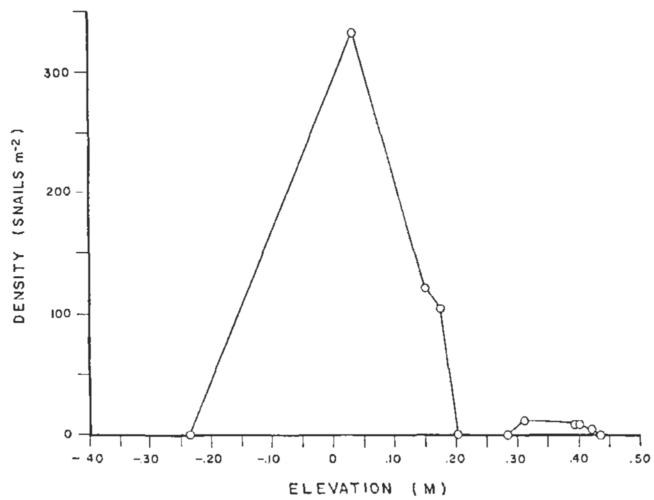

Figure 2. Density distribution of *Littorina irrorata* < 5 mm long plotted against elevation in m NGVD. Zero meters NGVD at this site is very near Mean Sea Level. Data from July 1975. No quadrats were sampled from elevations between -0.23 and 0.03 m.

mean high water spring tide (MHWS), and virtually all of those snails were found beneath tidal wrack; a high proportion of them were dead. Those snails accounted for a slight tail on the distribution curves above MHWS (Figure 3), and probably represent individuals rafted above their normal range by clinging to wrack.

Snails > 5 mm long achieved peak densities in medium growth form of *Spartina alterniflora,* but also were abundant in tall and levee *Spartina* (Reidenbaugh 1978). Few snails were found at any elevation in areas devoid of standing vegetation, or in areas covered by thick mats of *Spartina* wrack. With these exceptions, no coincidence was found between sudden changes in snail density and changes in vegetation type. For example, no snails were found below -0.15 m, even though *Spartina* occurs well below this, to about -0.30 m (Reidenbaugh et al. 1982). Low densities of *L. irrorata* occurred in areas where *Salicornia* spp. were abundant, mixed with *S. alterniflora* (elevations about 0.4 to 0.6 m) (Reidenbaugh 1978). However, *L. irrorata* also occurred at about the same densities at the same elevations in regions where *S. alterniflora* dominated and *Salicornia* was uncommon.

Snail density varied considerably within elevation intervals. Calculation of chi-square, using variance to mean ratios (Elliot 1971), demonstrated that the population is clumped ("contagious", $p < 0.05$) within all but the two elevation intervals about MHWS. These exceptions occurred where the snail population was small and apparently distributed at random.

The total population of snails > 5 mm long declined early in the summer, then increased to a maximum in early fall; there was a 14% increase between May and July and a 23% increase between July and September (Table 1; Figure 3). Relative densities within elevational categories, however,

Table 1.

Density distribution of *Littorina irrorata* >5 mm long.

		May				July				September			
Elevation interval (m)	Quadrats Sample	No. Snails	Mean m^{-2}	Std. Dev.	%	No. Snails	Mean m^{-2}	Std. Dev.	%	No. Snails	Mean m^{-2}	Std. Dev.	%
.700 to .749	3	0	0.0	–	–	0	0.0	–	–	0	0.0	–	–
.650 to .699	3	0	0.0	–	–	0	0.0	–	–	0	0.0	–	–
.600 to .649	7	2	0.3	0.5	0.1	1	0.1	0.4	0.1	2	0.3	0.5	0.1
.550 to .599	3	2	0.7	0.6	0.2	2	0.7	1.2	0.3	3	1.0	0.0	0.3
.500 to .549	12	21	1.8	3.3	0.6	3	0.2	0.8	0.1	35	2.9	4.3	1.0
.450 to .499	10	25	2.5	4.3	0.9	19	1.9	2.5	0.7	22	2.2	2.4	0.7
.400 to .449	20	136	6.8	6.3	2.4	136	6.8	7.4	2.7	183	9.2	7.7	3.1
.350 to .399	13	173	13.3	25.9	4.7	116	8.9	11.7	3.5	158	12.2	13.5	4.1
.300 to .349	14	438	31.3	43.0	11.1	381	27.2	23.6	10.8	430	30.7	32.4	10.3
.250 to .299	15	476	31.7	33.5	11.2	305	20.3	19.1	8.0	457	30.5	28.6	10.2
.200 to .249	25	656	26.2	22.2	9.3	552	22.1	14.1	8.7	747	29.9	25.2	10.0
.150 to .199	12	600	50.0	26.6	17.7	497	41.4	23.0	16.3	634	52.8	22.9	17.7
.100 to .149	7	223	31.9	19.0	11.3	189	27.0	29.6	10.6	160	22.9	20.4	7.7
.050 to .099	8	220	27.5	24.1	9.7	263	32.9	31.6	12.9	259	32.4	32.4	10.8
.000 to .049	6	142	23.7	36.6	8.4	149	24.8	22.2	9.7	151	25.2	21.7	8.4
-.050 to -.001	5	69	13.8	11.3	4.9	138	27.6	19.3	10.8	135	27.0	20.6	9.0
-.100 to -.051	3	52	17.3	18.0	6.1	30	10.0	10.0	3.9	59	19.7	20.0	6.6
-.150 to -.101	3	11	3.7	4.0	1.3	7	2.3	4.0	0.9	0	0.0	–	–
-.200 to -.151	1	0	0.0	–	–	0	0.0	–	–	0	0.0	–	–
-.250 to -.201	4	0	0.0	–	–	0	0.0	–	–	0	0.0	–	–
-.300 to -.251	3	0	0.0	–	–	0	0.0	–	–	0	0.0	–	–
Total	177	3245	282.1		99.9	2788	254.2		99.9	3435	298.9		100.0

changed little and the density distribution remained fairly constant (Table 1). In other words, net changes in relative population density appeared to be relatively independent of elevation. Stiven and Kuenzler (1979) estimated mortality of *L. irrorata* in several experimental pens in North Carolina. They recorded much higher mortalities, up to 90% within a few weeks. However, these results were based on pooled data from experimental cages with sizable artificial alterations in density, experimental changes in initial size-frequency distributions, and variations in the amount of decaying vegetation that was added to each sampling site. Elevations were not measured. No direct comparisons seem possible.

Size-frequency distributions for June and September are shown in Figure 4. The curve for June was weakly bimodal and negatively skewed. Larger snails were most abundant, with a peak at 24 mm shell length; a second peak occurred at a shell length of 19 mm. In September the distribution was similar, but a new peak appeared at 11 mm. The overall population increase (23%) during the interval between samplings was evident, but a decrease in the numbers of snails > 25 mm long suggests some mortality among snails in that size class. Frequency generally increased with size; that is, larger snails were most abundant, suggesting that large snails are relatively long-lived.

The mean length of snails > 5 mm decreased with increasing elevation ($p < 0.01$) (Figure 5). Size-frequency distributions for snails from each of five elevation intervals are shown in Figure 6. The three peaks seen in Figure 4 are evident, with small, medium, and large snails in some or all of the elevation intervals. Each of the three size classes appear to be distributed differently along the elevation gradient. In June, the smaller snails (5–14 mm) showed peak densities between 0.2 and 0.4 m (near MHWN), but occurred in numbers throughout the marsh. The same was true in September, but peak densities were shifted to lower elevations, between 0.1 and 0.3 m (about midway between MTL and MHWN). Medium-sized snails (15–21 mm) reached peak densities between 0.2 and 0.4 m in both June and September; they dominated the population between 0.3 and 0.4 m (about MHWN to MHW), but medium-sized snails were almost excluded from lower elevations. The largest snails (> 21 mm) are most abundant between 0.0 and 0.2 m (just above MTL) and are uncommon above 0.3 m (near MHWN). The smallest snails (< 5 mm) peaked sharply at about 0.18 m (Figure 2).

Results of marked snail recapture experiments are summarized in Figure 7. No significant difference in growth rate was observed between the two elevations compared.

Marsh salinity

The results of about 200 measurements of salinity of tidal and interstitial water are shown in Figure 8. The salinity of tidal water varied little, ranging from 30.0 to 32.5 ppt;

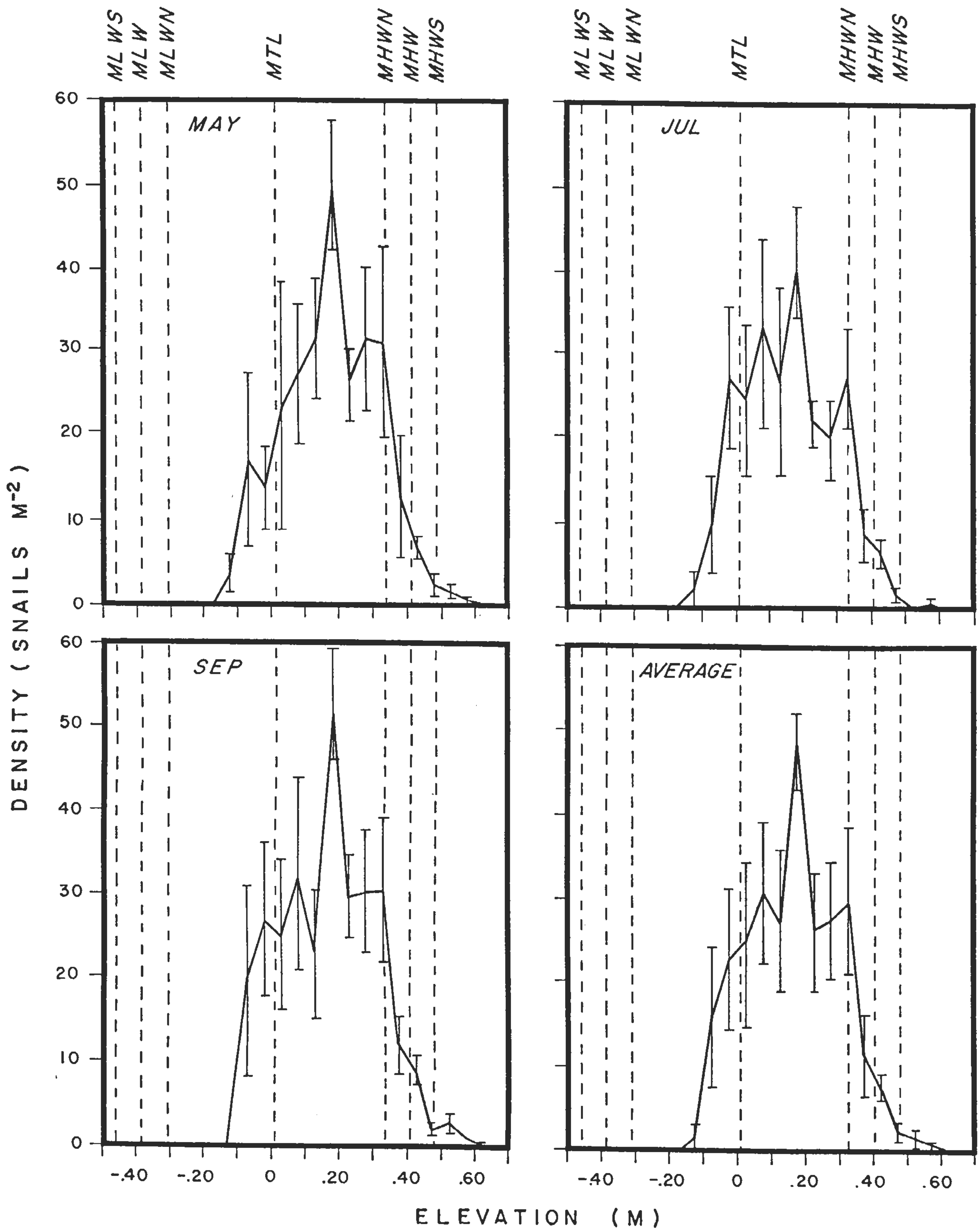

Figure 3. Density of *Littorina irrorata* >5 mm in length plotted against elevation; data from May, June, and September 1975, and averaged for the three sampling periods. The combined counts for each elevation interval were normalized to the number of snails/m^2. Vertical bars represent plus and minus one standard deviation. Tidal data are shown as dashed lines.

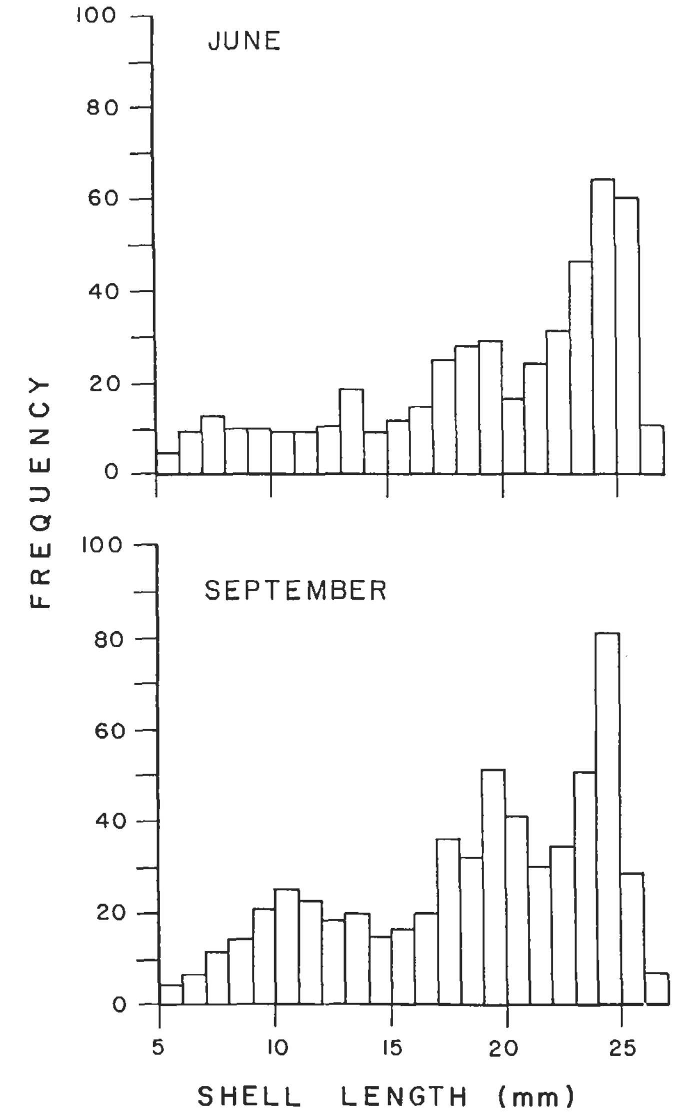

Figure 4. Size density distribution of all *Littorina irrorata* collected during June and September 1975.

the mode was 30.5 ppt. Interstitial salinities were generally less than those measured from tidal water, averaging 27.4 ppt (n=76, SD=6.7). Interstitial salinity dropped dramatically during rainfall, but returned to near normal levels immediately after innundation by a high tide. Interstitial salinities below about 20 ppt were uncommon in the marsh, and were not recorded at all below MTL, although they probably do occur briefly at low tide during rains. Extremely low salinities of 15 ppt or less were rare, but occurred throughout most of the upper part of the snails' range during or after precipitation (Figure 8).

Tolerance to reduced salinity

Activity levels and percent survival of *L. irrorata* submerged in waters of various salinities are shown in Figure 9. All medium-sized snails (15–19 mm) survived 10 days of exposure in waters of all salinities tested above that of fresh water, and all survived 5 days or more in fresh water. Larger snails (> 21 mm) were less tolerant; they began to die after 6 days exposure at 5 ppt, and none survived 7 days exposure to fresh water.

Mean activity levels also showed differences between large- and medium-sized snails throughout the salinity range studied (Figures 9 and 10). At all salinities below 30 ppt, activity of large snails was less than that of medium-sized snails.

DISCUSSION

Littorina irrorata appears to vary in maximum size among different marshes. The largest snails reported from the Gulf coast of Florida are 20.5 mm long (Bingham 1972a) and 22 mm (Hamilton 1978). An anonymous reviewer of this manuscript, however, states that he or she "encountered Gulf coast *L. irrorata* to at least 27 mm." Smalley (1959)

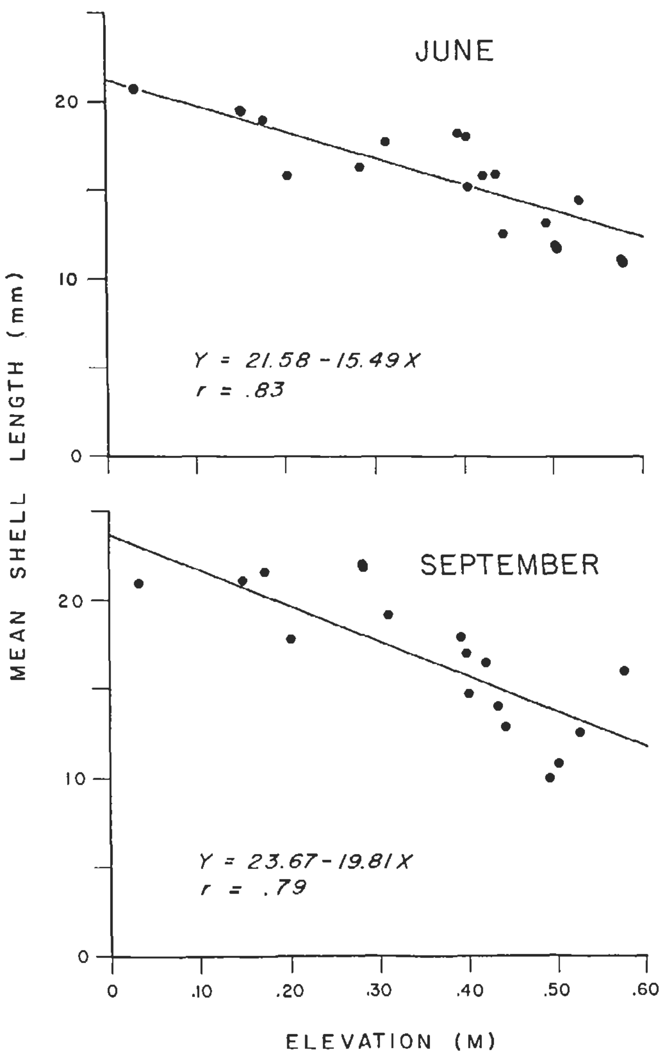

Figure 5. Regression of mean shell length at each sampling site plotted against elevation; data for June and September 1975.

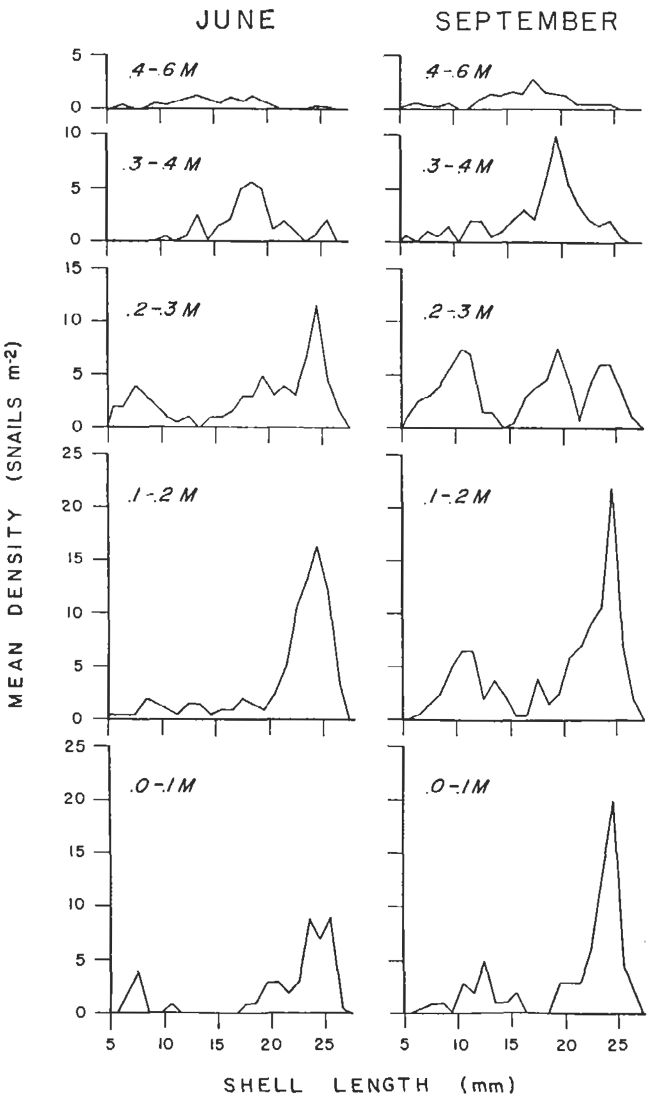

Figure 6. Size-frequency distributions of *Littorina irrorata* for June and September 1975, at five elevation intervals. Frequency was normalized to number of snails/m^2. Note: graph at top combines data from a 0.2-m interval (0.4–0.6 m). All others are 0.1-m intervals.

found no snails over 21 mm long at Sapelo Island, Georgia. Values calculated from Stiven and Hunter (1976) and Stiven and Kuenzler (1979) using length/width equations from Bingham (1972b) yield maximum lengths near 29 mm from North Carolina. The largest snail found during this study in Virginia was 28 mm long, but individuals up to 29 mm are occasionally encountered in the IBIS Marsh (M. Temkin, Department of Biology, The American University, personal communication).

Mean size of *L. irrorata* is more difficult to compare because of variation in size-frequency distributions with elevation. No other simultaneous measurements of size-frequency and elevation are available, and we know of no previous size-frequency distributions taken on *L. irrorata* collected randomly from all elevations in any marsh. However, the increase in maximum size with increasing latitude suggests that the same thing may be true of mean size.

Throughout its range, *Littorina irrorata* varies in its distribution relative to tide height and vegetation type. Hamilton (1978) found *L. irrorata* ranging from near MTL to elevations above MHW in marshes dominated by *Spartina alterniflora* and *Juncus roemarianus.* Bingham (1972a) found peak densities in needle rush (*J. roemarianus*) about halfway between MTL and MHW, and indicated that snails > 5 mm long were not common near the marsh-water edge. Smalley (1959) found peak densities of all size classes in short *S. alterniflora* near MHW. He reported that snails > 5 m long were nearly absent near creeks and in levee and middle marsh, although the smallest snails (< 5 mm) were fairly abundant there in leaves of *S. alterniflora.* In the IBIS Marsh, snails occurred in highest densities in medium-height *S. alterniflora* about halfway between MTL and MHW, and were abundant at elevations down to about the middle of the tall *S. alterniflora* zone (Figure 3).

Maximum density of the smallest snails (< 5 mm) occurred near MTL, well below that of any other size class. Most of those snails were distributed in a very narrow tidal range. Smalley (1959) found that the smallest snails were abundant throughout the marsh. He attributed the small numbers of larger snails at low elevations to higher mortality rates among snails at low elevations compared to those at higher elevations. In the IBIS Marsh, members of the next larger size class (5–14 mm) occur throughout the marsh (Figure 6),

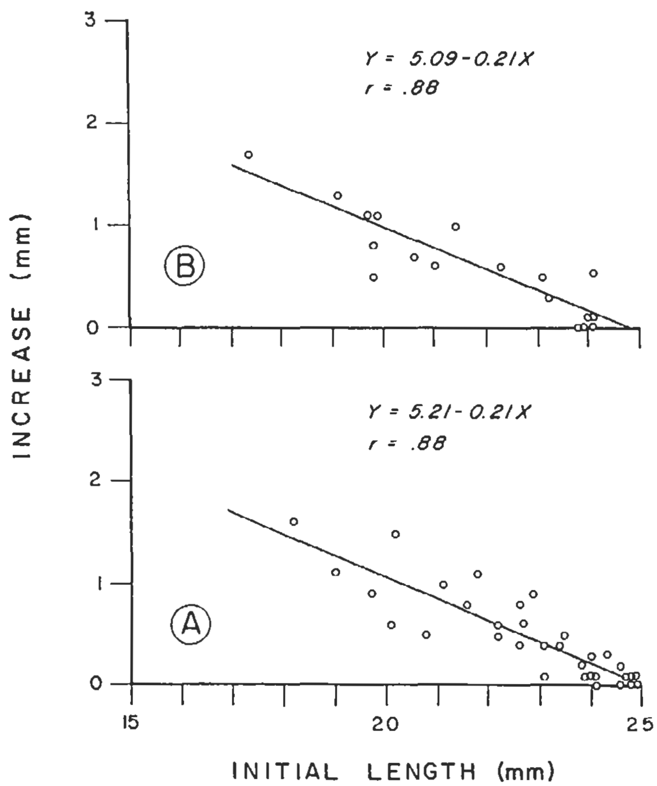

Figure 7. Growth of *Littorina irrorata* during 50 days at elevations 0.15 m (A) and 0.20 m (B).

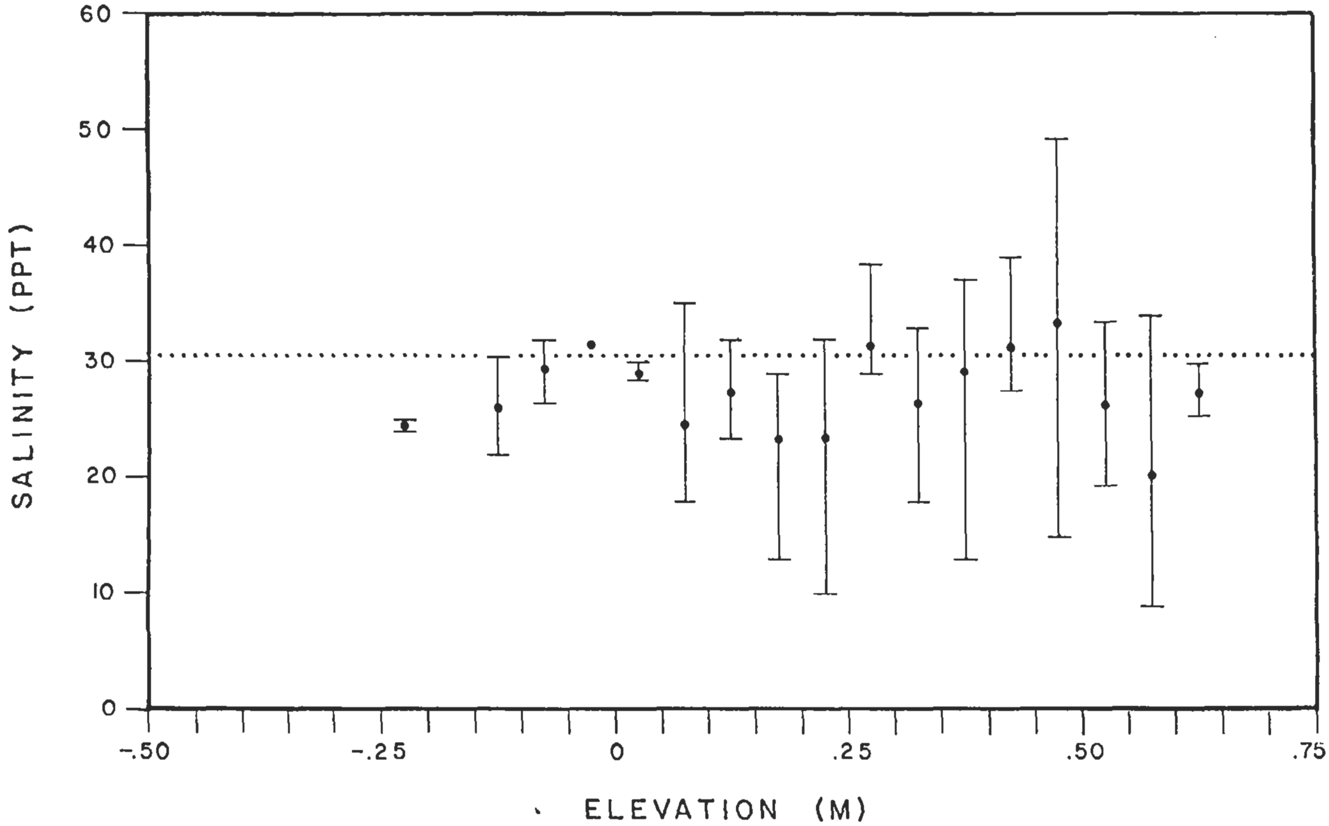

Figure 8. Salinity of water extracted from sediment samples collected within 0.05-m intervals. Average salinities are represented by dots. Vertical bars show the range of salinities measured within each interval. Salinity of tidal water flooding the study site is shown as a dotted line.

although they are most abundant at middle elevations, 0.1 to 0.3 m (Figure 6). These data suggest that the young snail population becomes dispersed in the marsh shortly after they leave dead *S. alterniflora* leaves. The observed distribution pattern of 5–14 mm snails (Figure 6; compare Figure 2) can be explained either by increased mortality at higher elevations or by differential movement of snails upshore to middle elevations (0.1 to 0.3 m). The great difference in numbers of snails between the < 5 mm and the 5–14-mm size classes suggests high mortality among the smallest snails.

The mean length of snails over 5 mm in length decreased with increasing elevation in the IBIS Marsh. *Littorina irrorata,* therefore, seems to have a distribution corresponding to the "type 2" gastropods of Vermeij (1972), in which larger individuals occur lower in the intertidal zone than smaller ones. Vermeij pointed out that such a size distribution is characteristic of species living at lower intertidal levels. He attributed that distribution to predation or other biological interactions which are most intense at lower tide levels. He proposed that the opposite type of distribution, that is, larger snails at higher elevations, arises from physical stresses which are most intense at higher elevations, causing higher mortality among smaller individuals, which are less able to withstand physical stresses.

If snails < 5 mm long were included in the size-elevation calculations, their large numbers and their population peak at low elevations would indicate that *L. irrorata* fits into Vermeij's "type 1" gastropod category. That is, average size would increase with decreasing elevation, opposite to the distribution of snails more than 5 mm long. On the other hand, the smallest snails occupy a different environment in the marsh than 5–14-mm snails, because the former live in curled-up leaves of *S. alterniflora,* whereas snails > 5 mm live exposed on the marsh surface or on the surface of emergent vegetation. For this reason, combining the smallest snails with those > 5 mm in calculating size-elevation distributions is probably not a meaningful exercise.

Hamilton (1978) found *L. irrorata* distributed opposite to that described here; that is, he reported that mean size increased in an upshore direction. The snail, therefore, apparently responds differently to elevation in different parts of its range.

Stiven and Kuenzler (1979) gave size-frequency data for *L. irrorata* based on 159 individuals. Their data for the Calico Marsh (see their Figure 2) most closely resembles our data for quadrats low in the IBIS Marsh, about -0.1 to +0.1 m; their data from the Causeway Marsh and Tar Landing resemble our size-frequency distributions for elevations higher in the IBIS Marsh (+0.2 to +0.3 m). Furthermore, their density estimates for populations of *L. irrorata* at the Calico Marsh ($42/m^2$) are much higher than at the Causeway ($0.8/m^2$) or Tar Landing ($18/m^2$). (For this example, we

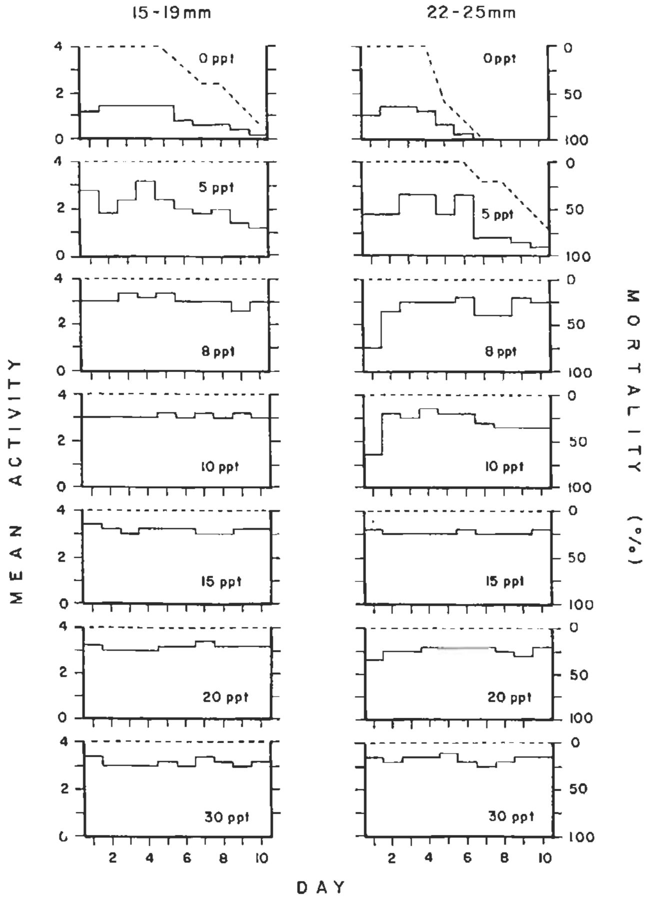

Figure 9. Activity (solid line) and mortality (dashed line) of *Littorina irrorata* in size classes 15–19 mm and 22–25 mm at salinities from 0 to 30 ppt.

arbitrarily used their October data; data for other months are comparable.) Above about 0.15 m in the IBIS Marsh, population densities decreased rapidly with increasing elevation. At least some of the differences among *L. irrorata* populations in the various marshes studied by Stiven and his coworkers may be due to unmeasured differences in elevations among those sites.

At the Calico Marsh, where size-frequency distributions for *L. irrorata* resembled those from the IBIS Marsh from elevations near 0.15 m, Stiven and Kuenzler (1979) speculated that "the relatively low abundance of the smallest size classes. . .may reflect sparse or sporadic settlement." However, in the IBIS Marsh, settlement of postlarvae of *L. irrorata* is quite heavy (Figure 2). Furthermore, data from summers of 1975, 1976, and 1978 (Banta, unpublished) indicated that settlement was consistently high and that size-frequency distributions remained stable from year to year.

We could measure no difference in growth rates at two different elevations with populations differing markedly in their size-frequency distributions. This would seem to eliminate the possibility that the elevation-dependence of mean size results from differences in growth rate. There are many

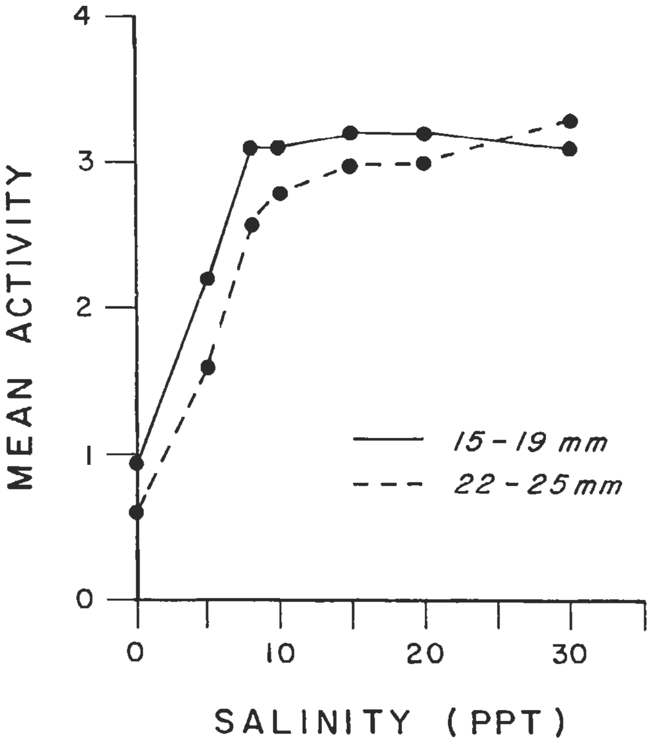

Figure 10. Activity scores averaged from 10 days of observation at salinities from 0 to 30 ppt.

other possible selective pressures which might account for the downshore increase in mean size of *L. irrorata* in the IBIS Marsh; we suggest two factors which might contribute: predation and salinity tolerance.

Relatively few predators are known for *Littorina irrorata*. Fish, including the mummichog *Fundulus heteroclitus* (Linnaeus), eat the smallest snails (< 5 mm) (Cherr 1974). Blue crabs *Callinectes sapidus* Rathbun (Hamilton 1976), and apparently clapper rails *Rallus longirostris* Gmelin (Oney 1951) eat snails > 5 mm long. Blue crabs are probably the most abundant and important predators on *L. irrorata* once the snails leave dead *S. alterniflora* leaves. Blue crabs are size-selective predators of *L. irrorata* and cannot eat snails over about 16 mm long (Hamilton 1976, Stanhope et al. 1982). Presumably, predation pressure from blue crabs increases with decreasing elevation because the crabs seldom leave the water. It seems possible, therefore, that blue crab predation may contribute substantially to the downshore increase in average size of *L. irrorata*.

On the other hand, the smaller snails (5–14 mm) are most subject to crab predation, not those over 14 mm (Stanhope et al. 1982). Thus, there is no obvious predation-related reason for the relative scarcity of medium-sized snails (14–21 mm) at low elevations. Perhaps medium-sized snails are crowded out by competition from larger ones, or perhaps there is an unknown predator which enters the marsh with tidal waters and selectively attacks medium-sized snails.

Extreme salinities in the IBIS Marsh did not persist long (seldom for more than one tidal cycle). Because the salinity of tidal waters varies little within the IBIS Marsh, the probability of a snail experiencing extreme salinities must increase with increasing elevations, and the mean duration of salinity extremes also must increase with elevation. No negative effect was observed on snails exposed to salinities higher than normal, but extremely low salinities (5 ppt) began to kill larger snails (> 21 mm) after 6 days. Fresh water killed large and medium-sized snails (14–21 mm) after 5 days. It seems unlikely that the snails would ever be exposed to those extremely low salinities long enough to kill them. Not only were salinity extremes much shorter lived than 5 days, but snails normally can climb out of the water, whereas our experimental animals were restrained below the surface.

Activity of snails, on the other hand, was depressed at salinities below about 8 ppt. Large snails (> 21 mm) were considerably less active than medium-sized snails (14–21 mm) at any salinity below that of the measured salinity of tidal water in the IBIS Marsh. Assuming that decrease in activity is deleterious, then one would expect to find the observed decrease in mean size with increasing elevation, because the probability of lowered salinity increases with increasing elevation.

SUMMARY AND CONCLUSIONS

1. *Littorina irrorata* varies from marsh to marsh in the type of vegetation with which it is associated, its maximum size, and its size-distribution patterns.

2. At our study site, periwinkles with a shell length < 5 mm were found almost exclusively inside curled-up leaves of *Spartina alterniflora,* and achieved peak densities of more than 300/m^2 near MTL.

3. Periwinkles > 5 mm in shell length were most abundant halfway between MTL and MHW, with mean peak densities of 48/m^2.

4. The mean size of snails > 5 mm in length decreased with increasing elevation. Within elevation intervals, the snails displayed a contagious (clumped) distribution.

5. Small snails 5–14 mm long were found predominantly at elevations slightly below MHWN. Medium-sized snails 15–21 mm long dominated the population between MHWN and MHW. Snails > 21 mm predominated from MTL to below MHWN.

6. We could detect no difference in growth rates between snails living at 0.15 and 0.20 m, even though the same elevation categories showed markedly different size-frequency distributions.

7. Extremes of interstitial salinities were more common at higher elevations than at lower ones. Snails between 15 and 19 mm in length are more active at all salinities below 30 ppt than are snails > 20 mm. Snails 15–19 mm long survived longer when submerged in fresh water and sea water at 5 ppt than did larger snails.

8. The main predator of *L. irrorata* in the IBIS Marsh is probably the blue crab *Callinectes sapidus,* which preys selectively on smaller snails. This predation may account in part for the seaward increase in mean size of *L. irrorata.*

9. The observed size-elevation distribution of *L. irrorata* in the IBIS Marsh may have been caused in part by the decrease in average salinity with increasing elevation. Large snails showed a greater decrease in activity with decrease in salinity than did smaller snails, and the frequency of lowered salinities increased upshore.

ACKNOWLEDGMENTS

We thank Dr. Joseph Rosewater, Marsha J. Loeb, and Michael A. Champ for their helpful reviews of the manuscript, and J. Lockwood Chamberlin and Talbot Murray for helpful discussions on *Littorina.* An anonymous reviewer made many helpful suggestions.

This manuscript is Contribution 14 of the IBIS (Intensive Biometric Intertidal Survey) project, a long-term ecological study of a marsh on Wallops Island, Virginia, W.C. Banta, Director. Student investigators Anna Hoffman, Doug Hornbeck, Donna Krivach, Richard Sigman, Daxel Tarner, and Karen Tarner provided much needed help in the field. We especially thank Thomas G. Reidenbaugh for his friendship and dedication; this paper never would have been written without him.

This research was supported in part by grants from the National Science Foundation, the Griffis Foundation, and the Helminge Fellowship (Department of Biology, The American University). Portions of this work were submitted to the Graduate Faculty of the American University in partial fulfillment of the requirements for the degree of Master of Science (Crist 1979).

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