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Vertical migration as a refuge from predation in intertidal marsh snails: a field test

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Abstract: Marsh periwinkles *Littorina irrorata* Say are common gastropod inhabitants of tidal marshes along the East and Gulf coasts of the U.S.A. These snails migrate up cordgrass *Spartina alterniflora* Loisel stems with tidal inundation. We conducted a field experiment in a Texas coastal marsh to determine if climbing grass stalks provides a refuge from predation for *L. irrorata* from blue crabs *Callinectes sapidus* Rathbun and other predators which enter and feed in the marsh at high tide. Treatments consisted of cages with short or tall grass heights from which predators were either excluded (closed cage) or allowed to enter and leave with the tides (open cage). A folded aluminum edging prevented most *L. irrorata* emigration from open treatments. Our results show that snails not allowed to climb grass stalks suffered significantly higher predation-related mortality than climbing snails indicating that vertical migration does provide a refuge from predation. Analysis of population size structure data from this and other studies show that juvenile *L. irrorata* are less abundant than larger conspecifics during the summer reproductive peak when abundances should be high. We attribute this to size selective predation by spring-recruited blue crabs and other predators.

Key words: Caging experiment; *Callinectes sapidus*; Intertidal marsh; *Littorina irrorata*; Prey refuge; *Spartina alterniflora*

INTRODUCTION

Many molluscs are able to exist in the presence of their predators with a reduced risk of mortality. This may be accomplished by the development of heavy shell sculpture (Vermeij, 1978), by growing to a size above which predator success is limited (Dayton, 1971; Paine, 1976) or by existing in a habitat that is inaccessible to predators (Connell, 1970; Menge, 1976; Virnstein, 1977). Crab predation has been a major selective agent in the evolution of gastropod shells (Vermeij, 1978) and behavior patterns (Hughes, 1986). Gastropod antipredator defenses can be viewed as either passive or active (Ansell, 1969). Shell characteristics, such as shell strength and morphology (Vermeij, 1978), the use of refugia (Covich & Knezevic, 1978; Vermeij & Covich, 1978; Covich, 1981) camouflage, and warning coloration (Ansell, 1969; Fishlyn & Phillips, 1980), are considered primarily passive defenses. Passive defenses protect the prey by reducing the

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chance that they will be detected by a predator and/or by decreasing the possibility that they will be killed by shell-crushing predators.

Prey refugia may be spatial or temporal. Spatial refugia work by placing the prey out of reach of the potential predator and have been observed in rocky-intertidal (Connell, 1970; Menge, 1976) and soft-bottom (Virnstein, 1977; Blundon & Kennedy, 1982a, 1982b) marine communities. Temporal refugia are often manifested as differences in activity pattern between predator and prey (Endler, 1985). Submerged vegetation is commonly used as a spatial prey refuge in both marine (Heck & Orth, 1980; Morgan, 1980; Heck & Thoman, 1981; Leber, 1985; Young & Young, 1978) and freshwater (Covich & Knezevic, 1978) environments.

Marsh periwinkles *Littorina irrorata* (Say) (Gastropoda: Prosobranchia) are abundant residents of tidal marshes along the southern Atlantic and Gulf coasts. They are usually found on emergent vegetation, typically the stems of the cordgrass *Spartina alterniflora* Loisel. On *S. alterniflora*, these snails perform a rhythmic vertical migration that is correlated with the tides. When the tide is low, the snails descend the grass and feed on algae and detritus on the lower parts of stems and on the marsh surface. With tidal inundation (Wehking, 1967; Bingham, 1972a), snails climb back up the grass stalks. Snails typically remain at least 15 cm above the waterline (Bingham, 1972a; Hamilton, 1976; Vaughn & Fisher, in review).

Natant predators, such as blue crabs *Callinectes sapidus* Rathbun and cyprinodontid fishes, reside in tidal creeks during low tides, then enter and feed over the tidal marsh surface with the high tide (Kneib, 1984). Avoidance of natant predators has been proposed as a selective pressure maintaining the vertical migration patterns of *L. irrorata* (Hamilton, 1976; Warren, 1985). If climbing *Spartina* stems provides a refuge from predation for *L. irrorata*, then snails denied this refuge should suffer heavier predation mortality. This paper documents field experiments performed to test the above hypothesis. The results are combined with demographic data in order to discuss predation effects on population structure.

METHODS

This study was conducted in a brackish tidal marsh on the north shore of East Galveston Bay, the eastern lobe of the Galveston Bay estuary of the upper Texas coast. This marsh is irregularly flooded with an average tidal range of only 0.3 m (Borey *et al.*, 1983; Hall & Fisher, 1985). The bayward edge of the marsh is fringed with regularly flooded stands of *S. alterniflora*. Our study site was a stand of *S. alterniflora* inside the Anahuac National Wildlife Refuge which harbored a large population of *L. irrorata* and was known to be frequented by *C. sapidus*.

POPULATION STRUCTURE

The *L. irrorata* population was censused on a monthly basis from June 1986 through August 1987 in conjunction with a larger demographic study (Vaughn & Fisher, in review). Samples consisted of 314-cm² circular quadrats which were laid out randomly in transects perpendicular to the shoreline in the low-marsh *S. alterniflora* zone (Daiber, 1982). Fifty quadrats were sampled in June 1986 and 25 · month⁻¹ thereafter. The number of snails in each quadrat were counted and the total length of each snail was measured with dial calipers. Snails were assigned to the following size classes based on length: (1) <or = 12 mm; (2) > 12 – 17 mm; (3) > 17 – 22 mm; and (4) > 22 mm (Vaughn & Fisher, in review). The number of shell-fracture scars were also recorded for each snail (Blundon & Vermeij, 1983).

FIELD EXPERIMENTS

Cages were constructed of wooden frames 100 cm high and 50 cm wide. Closed cages were totally enclosed with 1.5 mm mesh fiberglass screening. Open cages had no mesh on the tidal side to allow entry of aquatic predators. Open cages had an edging of aluminum roof flashing surrounding the side open to the tide. In preliminary laboratory and field observations, we found that the $\approx 15^\circ$ angle of this edging made it difficult for *L. irrorata* to manipulate its foot and escape the cage. The edging effectively prevented most *L. irrorata* emigration and immigration (see Results) during the time frame of these experiments. The edging did not appear to effect either the temperature regime or plant growth inside the cages. Cages were held in place by driving 30 cm long angle iron stakes into the marsh substratum at each cage corner. Sections of aluminum roof flashing 50 cm wide and 20 cm tall were driven 15 cm into the substratum on each cage side to prevent burrowing in and out of the cages. Preliminary observations indicated that *C. sapidus* would enter the open cages and feed on *L. irrorata*.

Clapper rails and other marsh-inhabiting birds are known to occasionally eat *L. irrorata* (Heard, 1982). Although clapper rails are abundant at our study site, they were never observed near the cages or eating *L. irrorata*. Herons were twice observed roosting on the cages, but no birds were ever seen inside the cages. This study does not address bird predation.

Treatments consisted of closed cages with tall grass ($n = 2$), closed cages with short grass ($n = 2$), open cages with tall grass ($n = 2$), and open cages with short grass ($n = 2$) (Table I). Tall grass was clipped to 90 cm, if necessary, to allow air circulation between the grass and the top of the cage. Short-grass treatments were uniformly clipped to 20 cm in height. Cages were placed along a transect line parallel to the shore and 3 m from the shoreline. We determined that within this transect our stand of *S. alterniflora* was uniform with respect to substratum elevation and *S. alterniflora* stem height, spacing, and robustness (Baxter, 1983). Cages were placed 50 cm apart and treatment sequence by cage was altered for each experimental trial (Table I) to ensure adequate treatment interspersion (Hurlburt, 1984).

At the beginning of a trial, all *L. irrorata* and other visible macrofauna were removed from each cage. Then, 40 marked snails ranging from 15 to 20 mm in length were placed in each cage. This number corresponds to the average density of 160 *L. irrorata* · m⁻²

TABLE I

Cage-placement sequence and treatments for each experimental period. $n = 40$ snails for each cage. CL, closed cage; OP, open cage; TL, tall grass; SH, short grass.

Cage	Trail			
	1	2	3	4
1	CL-TL	OP-SH	CL-SH	OP-TL
2	OP-TL	CL-SH	CL-TL	OP-SH
3	CL-SH	OP-TL	OP-SH	CL-TL
4	OP-SH	CL-TL	OP-TL	CL-SH
5	CL-TL	OP-SH	CL-SH	OP-TL
6	OP-TL	CL-SH	CL-TL	OP-SH
7	CL-SH	OP-TL	OP-SH	CL-TL
8	OP-SH	CL-TL	OP-TL	CL-SH

in the study area (Vaughn & Fisher, in review). Snails were captured and marked in the field within several hours of the beginning of each trial. Marking consisted of numbering the snails on the dorsal surface of the shell with permanent black ink and painting over the number with Superglue (Alexander *et al.*, 1985). After 10 days, each cage was censused and snails were assigned to status categories. Live snails were those inside the cage which were marked. Dead marked snails found inside the cages were called dead-not consumed. Immigrant snails were unmarked snails found inside the cages.

In conjunction with cage censusing, a 5-m radius around the cages was searched for marked snails. Concurrent with these caging experiments, we conducted two separate mark-recapture experiments with uncaged snails. These experiments are described in detail in Vaughn & Fisher (in review). Our mark-recapture observations showed that uncaged snails rarely stray > 1 or 2 m from their release point even after 4 months (and see Hamilton, 1978). Therefore, a 5-m search area was liberal and allowed us to locate any marked snails which had escaped the cages. These snails were designated as emigrants. Any marked snails that were not located, either inside or outside of the cages, were designated as missing and were presumed to have been consumed by predators.

The experiment was conducted four times during the summer of 1987 (Table I), once in June and July, and twice in August. All statistical analyses were run on an IBM PC microcomputer using the BIOM-PC package of statistical programs (Rohlf, 1983). To test for any effects due to cage-placement sequence or trial date, each treatment type was compared across trials using the Kruskal-Wallis test (Sokal & Rohlf, 1981). Data from all four trials were then pooled. To ensure that data met the assumptions for ANOVA, we (1) tested for homogeneity of variances using the F_{\max} test and (2) calculated the Kolmogorov-Smirnov statistic to determine if the data adhered to a normal

distribution (Sokal & Rohlf, 1981). Treatment effects within each snail-status category were determined using Model I single classification ANOVA on untransformed data (Sokal & Rohlf, 1981).

RESULTS AND DISCUSSION

TREATMENT EFFECTS

We found no significant differences within treatment types due to the effects of cage-placement sequence or date of experiment (Table II). We therefore pooled the data

TABLE II

Results of Kruskal–Wallis tests for differences due to cage-placement sequence or date of experiment within treatment types. Values given are H values and all are nonsignificant when compared with $X^2_{.05}(3) = 7.815$.

Snail status	Treatment type			
	Closed–Short	Closed–Tall	Open–Short	Open–Tall
Live	5.10	3.50	5.50	0.69
Consumed			5.10	3.50
Dead-not consumed	5.10	3.50	2.47	2.21
Immigrants			1.03	0.95
Emigrants			2.74	3.36

from all four trials before further analysis. A Kruskal–Wallis test showed that there were significant differences between the mean number of live snails among the four treatment types (Fig. 1; $H = 23.91$, $P > 0.001$). Data in snail-status categories consumed, dead-not consumed, emigrants, and immigrants met the assumptions for single-classification ANOVA: all had homogenous variances with the F_{\max} test, and the Kolmogorov–Smirnov statistic, D , was within the limits of normality at $\alpha = 0.15$. Highly significant differences existed between the number of snails consumed in short-grass as opposed to tall-grass treatments (Table III). When other sources of mortality were compared over all four treatment types, no significant differences were found. There were also no significant differences between the number of snails immigrating into or emigrating out of short-grass as opposed to tall-grass treatments.

These results support the predator-avoidance hypothesis for vertical migration in *L. irrorata* as first suggested by Hamilton (1976). In a Florida study, he observed that blue crabs would swim to the surface in the intertidal during high tide and remove *L. irrorata* adhering to *S. alterniflora* stems near to and above the waterline. In general, crabs could not reach snails at least 15 cm above the waterline. We have found that *L. irrorata* in our study area prefer to be between 20 and 30 cm above the waterline at high tide (Vaughn & Fisher, in review). In Hamilton's study, a boring snail, the crown conch *Melongena corona*, also commonly preyed upon *L. irrorata*. They captured

L. irrorata which fell into the water or which were attached to short stems at high tide. Hamilton suggested that the movement of *L. irrorata* up plant stems on an advancing tide serves as a defense against predation by *C. sapidus*, *M. corona*, and possibly other predators such as fish.

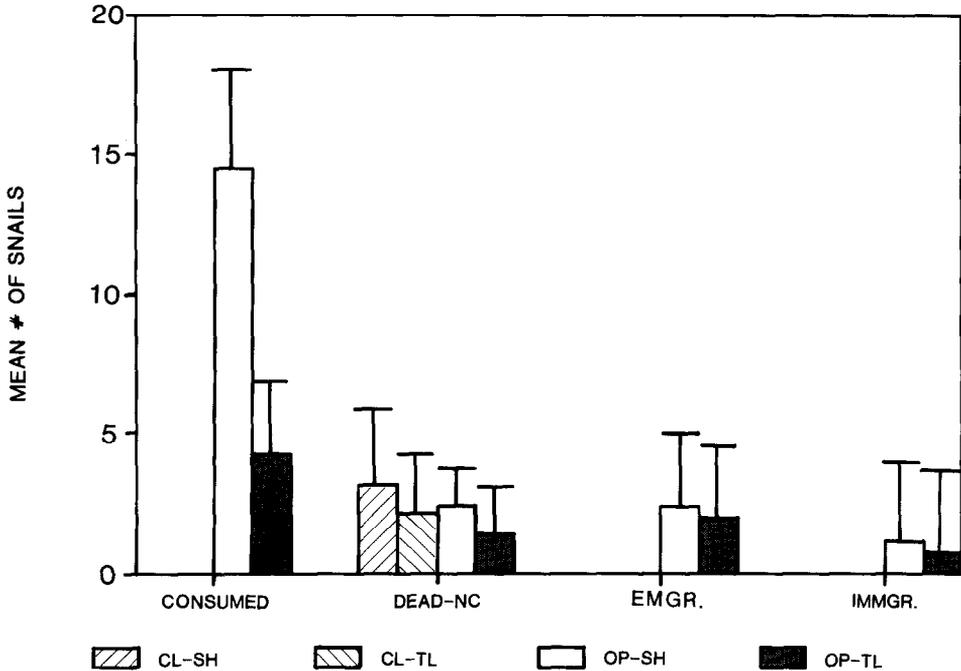


Fig. 1. Mean frequencies \pm 1 SD of consumed, dead-not consumed, emigrant, and immigrant *L. irrorata* by treatment type for field experiment. Data are pooled for all four experimental trials. Treatment types are described in text.

Warren (1985) performed relatively long-term (45 days) field experiments in a Florida marsh examining the effects of blue crab and crown conch predation on *L. irrorata* mortality. Warren tethered snails to *S. alterniflora* stalks either near to or well above the substratum in caged, open, and roofed treatments. She found that mortality rates were much higher in open treatments where snails were tethered near the substratum than in open treatments where snails were tethered above the reach of conch and crab predators. These results agree with our data which show that the number of snails consumed by natant predators are significantly higher in short-grass open cages than in tall-grass open cages (Fig. 1; Table III). However, in Warren's study, mortalities of snails from sources other than predation are higher in caged snails tethered near the substratum than in caged snails tethered above the waterline. We found no such differences in nonpredation-related mortality among treatments (Table III).

Warren suggested that climbing decreases mortality from sources other than predation. In particular, she suggested that vertical migration is an evolutionary response to osmotic stress brought about by influxes of freshwater during heavy rains. This explanation runs counter to prevailing ideas about osmotic regulation in estuarine gastropods

TABLE III

Single-classification ANOVA results for effects of grass height (short, tall) and cage treatments (open, closed) within each snail-status category.

Source of variation	SS	df	MS	F	Significance
Consumed snails					
Grass height	420.25	1	420.25	38.83	$P > 0.001$
Error	151.50	14	10.82		$F_{.001}(1,14) = 17.1$
Dead-not consumed					
Grass height					
X cage treatment	12.50	3	4.17	1.20	NS
Error	97.50	28	3.48		
Grass height	8.00	1	8.00	2.35	NS
Error	102.00	30	3.40		
Cage treatment	4.50	1	4.50	1.28	NS
Error	105.50	30	3.52		
Immigrants					
Grass height	0.56	1	0.56	0.64	NS
Error	12.37	14	0.88		
Emigrants					
Grass height	0.56	1	0.56	0.40	NS
Error	19.87	14	1.42		

in general and what is known about *L. irrorata* in particular. Most estuarine gastropods are commonly exposed to wide cyclical or intermittent salinity fluctuations to which they can osmoconform accordingly (Hughes, 1986). *L. irrorata* commonly withdraws into its shell and closes its operculum when exposed to low salinities (pers. obs.; Wehking, 1967) and can remain submerged for long periods of time with a reduced respiratory rate (Bleil & Gunn, 1978). This phenomenon has also been observed in rocky intertidal populations of *Littorina littorea* which withdraw into their shells when exposed to low salinities with a concomitant decrease or cessation of oxygen consumption (Shumway, 1978). We feel that avoidance of osmotic stress is an unlikely ultimate selection factor for climbing behavior in *L. irrorata*.

We suggest that a more plausible explanation for Warren's high mortalities in snails tethered near the substratum but protected from predators may be the effects of intraspecific competition or stress resulting from overcrowding in her experimental

cages. Her experimental densities of $450 \text{ snails} \cdot \text{m}^{-2}$ are at the high end of the range of densities she reports for her study area ($0\text{--}600 \text{ snails} \cdot \text{m}^{-2}$) (Warren, 1985) and 2 – 10 times as high as natural densities reported for East coast (Stiven & Hunter, 1976; Baxter, 1983) and Gulf coast (Alexander, 1979; West & Williams, 1986; Vaughn & Fisher, in review) populations. In addition, Warren did not remove resident *L. irrorata* from her treatment plots before introducing experimental snails, so actual total densities of *L. irrorata* in her cages may be twice as high as reported. Intraspecific competition for both space and food was shown to affect both growth and mortality of three separate populations of *L. irrorata* in North Carolina (Stiven & Hunter, 1976). High mortalities were not found in Warren's caged snails which were tethered above the waterline, but should not be expected. These snails were not allowed to descend and ascend the grass stalks in their natural manner, and, thus, were denied access to both their food source and water for 45 days. Under these stressful conditions, the snails would have been in a quiescent state and would not be affected by overcrowding. *L. irrorata* withdraw into their shell and secrete a mucus holdfast when exposed to relative humidities of $< 75\%$ (Bingham, 1972b) and/or when denied submergence for $> 24 \text{ h}$ (personal observation). Snails in this condition slow their metabolism by an order of magnitude (Bleil & Gunn, 1978).

POPULATION STRUCTURE

Snails are abundant in the marsh year-round and summer and winter total densities do not vary much. Population-size structure does, however, vary throughout the year (Fig. 2). Juvenile snails $< 12 \text{ mm}$ in length are present only during the warmer months and peak in mid-summer. Snails $> 12 \text{ mm}$ and $< 22 \text{ mm}$ are present in fairly high densities year-round, but snails $12\text{--}17 \text{ mm}$ are always less abundant than those $18\text{--}22 \text{ mm}$ in length. Very large snails ($> 22 \text{ mm}$) are always rare.

The absence of juvenile snails during the winter is not surprising. *L. irrorata* reproduce only during the warm months (Bingham, 1972c; Vaughn & Fisher, in review) and grow quite rapidly (Bingham, 1972d). Snails recruited during the summer would have grown into Size Class 2 ($12\text{--}17 \text{ mm}$) by fall (Vaughn & Fisher, in review). However, the low numbers of juveniles and Size Class 2 snails in comparison to Size Class 3 snails during the warmer months is not what would be expected if sources of mortality were equal for all sizes of snail. We suggest that lower densities of smaller snails may reflect size-selective predation on these snails by blue crabs and other natant predators. Blue crabs are known to control the size distribution of the mussel *Geukensia demissa* in tidal marshes (Seed, 1980; Hughes & Seed, 1981; Duobinus-Gray & Hackney, 1982).

In a series of short-term (between-tides) field predator-inclusion experiments utilizing *C. sapidus*, *L. irrorata*, the minnow *Fundulus heteroclitus*, and an infaunal bivalve, West & Williams (1986) found increased mortality in $14\text{--}18\text{-mm}$ snails over larger snails. They also found lower densities in the $14\text{--}18\text{-mm}$ size class at their study site and attributed this to size-selective predation by blue crabs. In a Virginia marsh studied by Stanhope

et al. (1982), medium snails were less abundant than larger snails, and medium snails were preferred over large snails in laboratory experiments. They also attributed this to size-selective predation. However, in laboratory experiments performed by Baxter

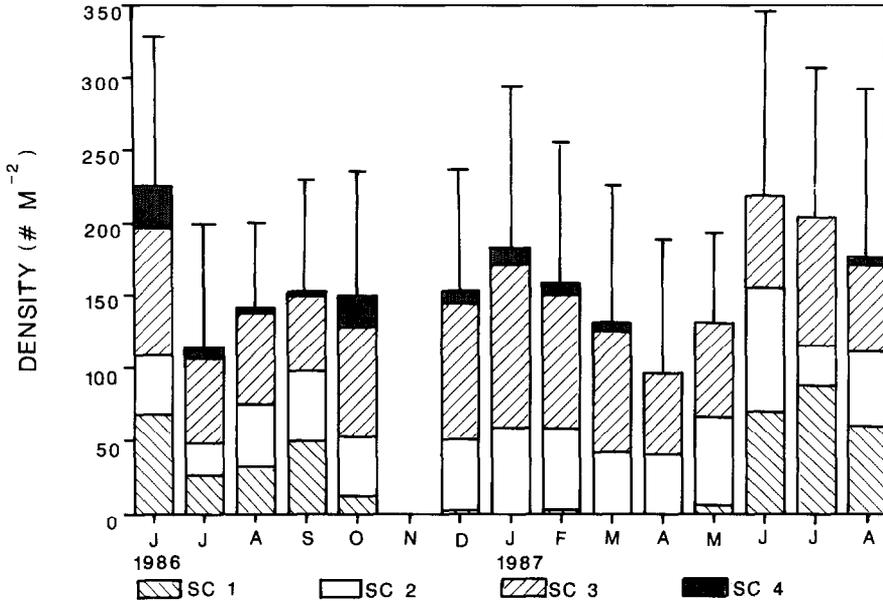


Fig. 2. Population size structure of *L. irrorata* at the Anahuac National Wildlife Refuge from June 1986 to August 1987. Size classes are defined in text.

(1983), there was no apparent size refuge for *L. irrorata* from predation by blue crabs. These differences can be explained by the fact that the size of snail a blue crab is able to consume depends on the size of that crab. While blue crabs do not have to crush the strongest part of the shell to feed on *L. irrorata*, they must be able to peel back the shell along existing sutures or crack the apex and larger crabs have greater chelae strength (Blundon & Kennedy, 1982a; Blundon & Vermeij, 1983). In Hamilton's (1976) study, blue crabs which ate *L. irrorata*, were either immature females or small, mostly male adults. The average length of *L. irrorata* preyed upon was 15 mm. The crabs in West & William's study were also smaller spring-recruit crabs. In contrast, the blue crabs that Baxter observed were large. Densities of smaller spring-recruit crabs reach their peak in tidal marshes during the summer. Since these crabs would be restricted to feeding on smaller snails, they may well be contributing towards controlling the size structure of the *L. irrorata* population. In addition, since handling time of *L. irrorata* prey increases with shell size (Hamilton, 1976), and the time available to blue crabs for foraging is limited to periods of tidal inundation, crabs would be expected to maximize their energy intake by selecting smaller prey (Kneib, 1984). Stiven & Hunter (1976) found that the density of small *L. irrorata* increased with distance from the shore and

attributed this to decreased predation pressure by natant predators as a result of decreased inundation and, thus, foraging time.

Other natant predators may also be feeding on *L. irrorata* in a size-selective manner. Cherr (1974) found that small *L. irrorata* were numerous in the stomachs of *Fundulus* minnows in an East coast tidal marsh. The gape size of these fish would restrict them to feeding on smaller *L. irrorata*. These minnows are common in our study marsh and may be feeding on smaller *L. irrorata*, although this behavior was never observed. Summer is the time of heaviest recruitment of *Fundulus* into salt marshes (Kneib & Stiven, 1978), so effects of predation would be expected to be greatest then.

CRAB EXPERIENCE AND PATCH USE

Blue crabs have been reported to feed on a wide variety of prey, from detritus to fish, but concentrate mainly on mollusks, fish, and crustaceans (Darnell, 1958; Tagatz, 1968; Laughlin, 1982). Data indicate that blue crabs must learn to feed on *L. irrorata*. Hamilton (1976) observed that some crabs were heavily involved in predation on *L. irrorata* while others were not at all. Six of eight crabs that Warren (1985) presented with snails, were unable to crush the shells or manipulated them in an awkward manner. Prior experience of the crab is correlated with the ability and amount of time necessary to crush a snail (Warren, 1985).

Stanhope *et al.* (1982) found that a blue crab in their laboratory would not eat snails until they drilled holes in the shell. While they suggested that this enabled the crab to better grasp and manipulate the shell, we suggest that it may also have stimulated the crab into a feeding mode. Crabs held in our laboratory would not eat *L. irrorata* until stimulated with another food type (chicken), but rapidly became voracious and efficient snail consumers with experience. Blundon & Vermeij (1983) have indicated that chemicals released by shell cracking of bivalve prey attract other nearby blue crabs and stimulate feeding. Similarly, the cracking of *L. irrorata* in a clump of *S. alterniflora* may attract other nearby crabs to that clump.

Indirect evidence that crabs must learn to crush *L. irrorata* shells comes from shell-fracture data. These fracture scars remain visible as the snail grows and leave a record of past unsuccessful predation attempts. Frequency of shell-fracture scars by snail size class are shown in Fig. 3. < 6% of Size Class 1 snails had one fracture scar, and the presence of two scars was extremely rare. These snails would be easily crushed and consumed, thus scars should be rare. 16–19% of snails in Size Class 2 and 3 had at least one scar, and 2–5% had two fracture scars. More than two fracture scars were observed only in larger snails. Stanhope *et al.* (1982) found that fractures were present in $\approx 25\%$ of medium-sized and 60% of larger snails in a Virginia marsh. Baxter found fracture scars in 65% of the *L. irrorata* population in a North Carolina marsh.

Various studies report differences in the intensity of blue crab predation on bivalve and fish prey (Seed, 1980; Duobinus-Gray & Hackney, 1982; Kneib, 1982). West & Williams (1986) found that blue crabs preferred *L. irrorata* over bivalves and minnows

in their study site. They attributed this to the fact that the infaunal bivalves were harder to find and the fish harder to catch than *L. irrorata*. In contrast, both Hamilton (1976) and Warren (1985) found predation by *L. irrorata* to be patchy. Alexander (1986) found that the diet of blue crabs on Galveston Island, Texas, was a reflection of crab body

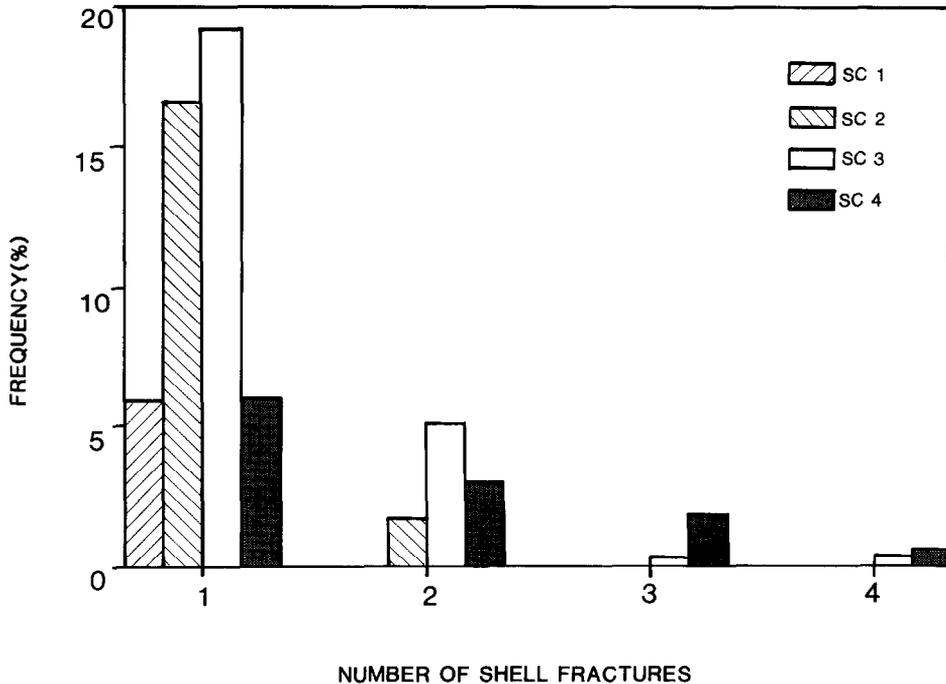


Fig. 3. Frequency of shell-fracture scars by size class for *L. irrorata* collected from Anahuac National Wildlife Refuge. Data are pooled for October 1986 to August 1987. Size classes are defined in text.

size and food availability. Larger crabs utilized mollusks, crustaceans, and fish more frequently than smaller crabs which relied on detritus and vegetation, but the actual food selected depended on the particular patch the crab happened to be in. Differences in the intensity of blue crab predation on *L. irrorata* populations are probably a reflection of both crab age and experience as well as patchiness of prey distribution.

In conclusion, the vertical migration pattern displayed by *L. irrorata* is strikingly different from that typical of rocky-intertidal *Littorina* species which withdraw into their shells at low tide, and forage below the water surface at high tide (Hughes, 1986). In moving above the waterline, *L. irrorata* expose themselves to potentially stressful environmental conditions such as desiccation and insolation. During high tide, it would seem more advantageous for these snails to attach to the base of plant stems and remain close to their food source, the marsh detritus, and periphyton. Submergence per se appears to be unimportant since *L. irrorata* can withstand continued submergence in

the laboratory for as long as 24 days while remaining in the active unretracted position (Bingham, 1972a; Bleil & Gunn, 1978). While questions remain about both the underlying proximal and ultimate causes of this behavior (Wehking, 1967; Bingham, 1972a; Warren, 1985; McBride, 1986), our results show that at least one benefit is refuge from predation.

Analysis of population-size structure data from this and other studies shows that juvenile *L. irrorata* are less abundant than larger conspecifics during the summer reproductive peak when abundances should be high. This is likely due to size-selective predation by spring-recruited blue crabs and perhaps fish predators on small *L. irrorata*.

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