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Dispersion of the Salt-Marsh Periwinkle *Littoraria irrorata*: Effects of Water Level, Size, and Season

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ABSTRACT: This paper documents horizontal and vertical dispersion patterns of a Texas population of the salt-marsh periwinkle, *Littoraria irrorata*, over a 15-month period. The study was conducted within a tidal marsh on the Anahuac National Wildlife Refuge in Galveston Bay. Two mark-recapture experiments demonstrated that *L. irrorata* rarely move more than 2 m from their release point over long periods of time and do not home to individual *Spartina* plants. Adult *L. irrorata* forage farther away from the base of *Spartina* stalks at low tide than do juvenile snails. Remaining near the plant base may decrease both temperature and desiccation stress on juveniles. During warm months, *L. irrorata* climb grass stalks with tidal inundation and forage on the substratum at low tide. Snails are inactive and aggregate in detrital debris at the base of *Spartina* clumps during the winter.

Introduction

Zonation and migratory patterns of rocky intertidal littorinids are well known (Newell 1970; Underwood 1979) and correlated with environmental stresses such as temperature, desiccation, and salinity (Mayes 1962; Vermeij 1971; Garrity 1984; Ohgaki 1985, 1989). Dispersion of littorinids in the vegetated intertidal has received comparatively little attention (Kohlmeyer and Bebout 1986; Lasik and Dye 1986). *Littoraria irrorata* (Say) (= *Littorina irrorata*, Reid 1986) (Gastropoda: Prosobranchia), the salt marsh periwinkle, is a common inhabitant of intertidal marshes along the southern Atlantic and Gulf coasts of the United States where it is associated with emergent vegetation, typically smooth cordgrass, *Spartina alterniflora* (Loisel) (Bequaert 1943; Daiber 1982). The snails are well known for their circumtidal migratory behavior on *Spartina* stems. They feed on the marsh substratum at low tide and climb grass stalks with tidal inundation (Bingham 1969, 1972a). Several recent studies have investigated the ecological benefits of this climbing behavior (Hamilton 1976; Warren 1985; West and Williams 1986; Vaughn and Fisher 1988; McBride et al. 1989). However, despite the

common occurrence of this climbing behavior, little is known about within-population variation or the effects of season on vertical migration, and no one has examined age or size variation in climbing. The present paper documents size-specific vertical migration patterns of a Texas population of *L. irrorata* over a 15-month period. We also examine horizontal dispersion patterns and compare these to existing information on eastern populations.

Methods

STUDY SITE

The study site was a tidal marsh on the north shore of East Bay, the eastern lobe of the Galveston Bay estuary of the upper Texas coast. This marsh is contained within the Anahuac National Wildlife Refuge. East Bay is brackish, and both salinity and water levels are dependent on prevailing winds and the amount of freshwater inflow produced by local precipitation. Salinity at the study site ranged from 5‰ to 15‰. Annual precipitation is approximately 132 cm, and varies from 66 cm yr⁻¹ to 249 cm yr⁻¹. Air temperature ranges from 5°C to 36°C, with an annual mean of 20°C. Prevailing winds are from the south and southeast.

HORIZONTAL MOVEMENT

Two mark-recapture experiments were conducted to determine the horizontal movement patterns of the snails. Experiment 1 was conducted to determine the horizontal distance covered by snails over a long period of time. On May 16, 1987 we marked and released 160 *L. irrorata* which were captured at random from the study site. Snails were tagged in the field by numbering the dorsal surface of the shell with permanent black ink and painting over the number with Superglue (Alexander et al. 1985). Snails were released at four locations in the *S. alterniflora* zone: one location each in the low and high marsh, and two locations in the mid-marsh. The low marsh area was almost always submerged. The mid-marsh areas were covered and uncovered at least once daily by the tide. The high marsh area was where *S. alterniflora* begins to be replaced by *S. patens*. This area was only inundated during high spring tides. The locations of marked *L. irrorata* which happened to be recaptured as part of a regular monthly population census (Vaughn and Fisher 1988, and see below) during June, July, and August 1987 were recorded relative to their release point.

In experiment 2 we tagged individual snails and *Spartina* plants to determine if snails returned to a "home" plant after foraging. "Homing" was defined as a snail being recaptured on the same *Spartina* stalk from which it was originally captured, marked, and released. On August 3, 1987 we randomly selected 50 *L. irrorata* which were attached to *S. alterniflora* stems located along a zigzag transect across the intertidal marsh mid-zone. Each plant was marked with a numbered plastic flag anchored in the marsh substratum. A snail on each numbered plant was tagged with a matching number without removing the snail from the plant, using the marking technique described. The location of marked snails relative to their "home" plant was monitored weekly for 3 wk.

FORAGING DISTANCE

While working in the marsh during low tide, we noticed that small snails stayed close to the *Spartina* stalks whereas larger snails foraged further out onto the substratum. To quantify this behavior we ran transects through the marsh and recorded the distance of snails from their "nearest neighbor" plant. On June 25 and July 28, 1987 a 50-m transect was sampled in the mid-marsh zone. Every snail within 2 cm on either side of the transect line was counted. The distance of each snail from the nearest *S. alterniflora* stem and the total shell length of each snail were measured. A total of 291 snails were counted. In addition, on July 28 a YSI telether-

ometer was used to measure the temperature of the substratum directly adjacent to each snail and the temperature inside the snail shell directly behind the operculum. The second measurement was assumed to be an approximate indication of snail tissue temperature.

VERTICAL LOCATION

The *L. irrorata* population was censused monthly from June 1986 through August 1987 (with the exception of November 1986) as part of a larger study (Vaughn and Fisher 1988). Samples consisted of 314 cm² circular quadrats. Each month five transect lines were randomly laid out in the *S. alterniflora* zone. We randomly sampled ten quadrats within 2 m of each transect line in June 1986, and five quadrats per transect line per month thereafter. The following data were collected for each quadrat sample at the time of collection: *L. irrorata* density, the vertical location of each individual of *L. irrorata* (see below), shell length of each snail, and water depth. The total shell length of each snail was measured with dial calipers.

The vertical location of a snail on a plant stem was determined by measuring the distance between the snail and either the substratum or the water, whichever was closer. For graphical purposes, snail vertical locations were grouped into 10-cm frequency classes by water level. For data analysis purposes, water depths 10 cm and greater were assigned to a "marsh covered" category and water depths less than 10 cm were called "marsh uncovered." December through February were considered cold season months, and March through October were considered warm season months. Snails were assigned to the following size classes based on length: <12 mm, >12–17 mm, >17–22 mm, and >22 mm (Vaughn and Fisher 1988). Snail vertical location data for each month were pooled by water depth category, season, and snail size class. Means of the pooled data were analyzed with a two-way ANOVA for the effects of water level, season, and size class on snail vertical position (Sokal and Rohlf 1981) (Table 1).

Results

HORIZONTAL MOVEMENT PATTERN

Mark-Recapture Experiments

Fifty-two of the 160 snails which were marked and released in experiment 1 were recaptured, and three snails were recaptured twice. Of these, 73% were 1 m or closer to their release point when recaptured (Fig. 1). Only 11% were greater than 2 m from their release point.

In experiment 2, no snails were recaptured on their original release plants, but the majority re-

TABLE 1. Results of analysis of variance for effects of season and snail size class on snail vertical location. F-values are given in the table with degrees of freedom in parentheses. Levels of significance are * = $p < 0.01$.

	Season	Size Class
Marsh uncovered	3.87 (1,7)	0.10 (3,7)
Marsh inundated	33.73 (1,7)*	0.84 (3,7)

mained close to the plant to which they were originally attached. Snails were usually a maximum of 2 m from their release point even after four months (Fig. 2).

Foraging Distance

Measurements of the distances of snails from their "nearest neighbor" plant showed that the majority (61%) of small (<12 mm) snails were less than 1 cm away from the plant base or attached to the plant base at low tide (Fig. 3). Larger snails were more evenly spread out. We found significant correlations between substratum temperature and the distance from a plant that the temperature was measured ($r = 0.79, p < 0.01$), and between substratum temperature and the temperature inside the snail shell ($r = 0.34, p < 0.01$). The correlation between distance from a plant and snail temperature was nonsignificant ($r = 0.14$).

VERTICAL LOCATION

The population of *L. irrorata* exhibited a seasonal circumtidal vertical migration pattern on *Spartina* stalks. During warm weather, most snails were found on the marsh substratum when the marsh was uncovered. With tidal inundation they would climb grass stalks and remain 10 cm to 30 cm above the water line (Fig. 4).

Winter high tides at the Anahuac Marsh often did not cover the marsh for weeks at a time. Consequently, all of our winter sampling data are for

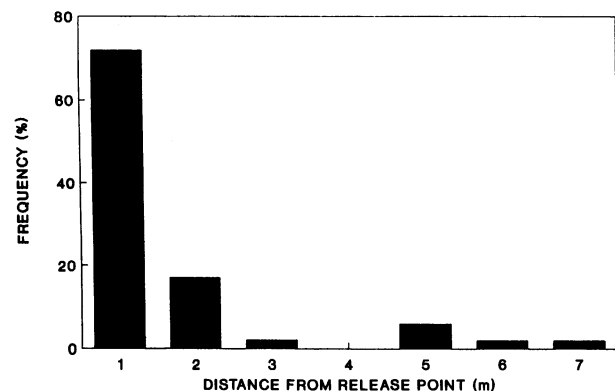


Fig. 1. Distance of marked snails from their release point in mark-recapture experiment 1.

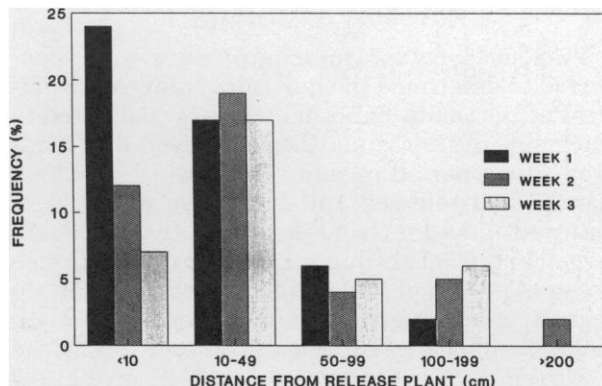


Fig. 2. Distance of marked snails from the plant on which they were originally located in mark-recapture experiment 2.

water depths of <10 cm. However, *L. irrorata* at our study site were inactive during cold weather. Snails did not migrate on the grass stalks (Fig. 4). Most snails were found clustered under clumps of *Spartina* containing large amounts of detrital debris. Snails in the debris were withdrawn into the shell and inactive. Some of the population were passively attached to grass stalks with mucous holdfasts (Bingham 1972b).

A two-way ANOVA showed significant differences in snail vertical locations at high tide (when the marsh was covered) during warm versus cold months (Table 1). There were no significant seasonal differences in snail vertical locations at low tide (when the marsh was uncovered). There were no significant differences in vertical locations of different size classes of snails regardless of water depth or season (Table 1).

Discussion

Horizontal movement patterns of our Texas salt marsh *L. irrorata* population were similar to those reported by Hamilton (1978a, b) for a Florida bar-

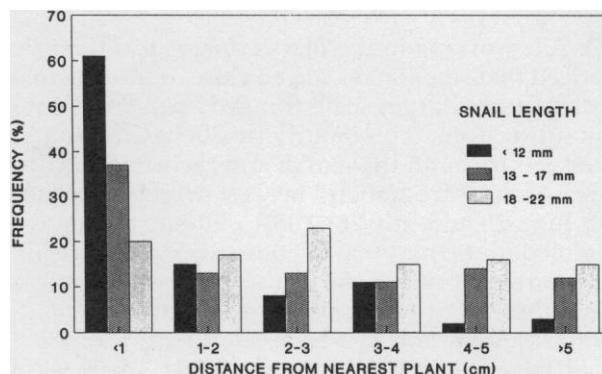


Fig. 3. Distance of snails from their "nearest neighbor" plant.

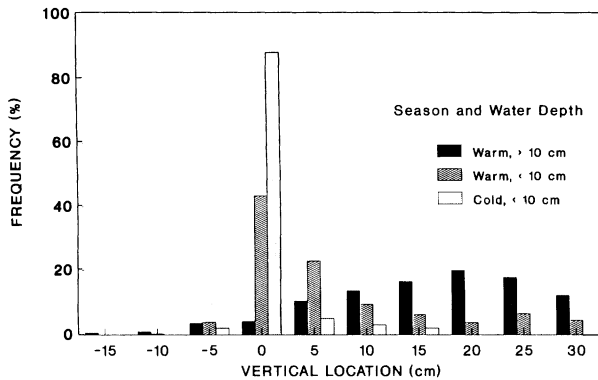


Fig. 4. Frequencies of snail vertical locations (in 5-cm increments, see Methods) by water level and season. Data are pooled for the entire 15-month study period (June 1986 through August 1987).

rier beach *L. irrorata* population. Hamilton found that *L. irrorata* had the ability to travel an average resultant distance of 20 cm per activity period, but stayed within 2 m to 4 m of their release point over an 11-month study period. The majority of our tagged *L. irrorata* stayed within 1 m of their release point over a 4-month period. Some gastropods exhibit little or no resultant movement over long periods of time because they possess "home sites" (Thomas 1973). *L. irrorata* might remain near individual *Spartina* clumps because they have better vision than most gastropods (Hamilton and Winter 1982; Hamilton et al. 1983), locate individual plants visually prior to climbing stalks at high tide (Hamilton 1977, 1978b), and often follow conspecific mucous trails while foraging (Hall 1973; Stirling and Hamilton 1986; Tankersley 1989, 1990). However, we found that although snails remained near the original plant from which they were captured, they did not return to a specific plant.

When *L. irrorata* foraged on the substratum at low tide, smaller snails stayed closer to the bases of *Spartina* stalks than larger snails. Baxter (1983) also observed that small snails rarely foraged more than one cm away from a plant base, and often actually remained on the plant. Staying close to the plant or on the plant stem may offer the small snail a greater benefit than the additional food it could gather by foraging farther away from the plant. Possible benefits include avoidance of predators, heat stress, and desiccation.

Most predators on *L. irrorata* feed at high tide while the snails are attached to the marsh grass (Vaughn and Fisher 1988); however, clapper rails and other marsh-inhabiting birds occasionally eat *L. irrorata* (Heard 1982). These birds may feed on *L. irrorata* at low tide (although we never observed this behavior). If smaller snails are the "preferred prey," then they may be safer closer to the plant.

Other potential low-tide predators would include infaunal forms such as nematodes (Kneib 1984).

Bingham (1969) examined body temperatures of *L. irrorata* during July in a Florida marsh. Snails on the substratum had an average body temperature 2°C higher than snails attached to grass. Baxter (1983) reported that the highest, nonpredation-related mortalities of *L. irrorata* in a North Carolina marsh were in the area of the marsh that had the highest mean and maximum summer sediment temperatures. The distribution of intertidal dwellers is limited by desiccation intolerance in young members of the population (Underwood 1979). The mangrove whelk, *Telescopium*, aggregates under mangrove trees during long periods of aerial exposure to avoid both desiccation and heat stress (Lasiak and Dye 1986). Whelks not allowed to aggregate lose control of their foot musculature and are unable to sustain retraction of soft tissues. The resultant higher heat stress and water loss leads to high mortality rates for these snails. Large *Nodilittorina unifasciata* in Tasmania are more tolerant of high temperatures and desiccation than are smaller, younger snails (Chen and Richardson 1987). Staying close to the base of *Spartina* clumps likely works to decrease both heat stress and desiccation in young *L. irrorata*.

This is the first study to quantitatively document seasonal differences in *L. irrorata* climbing behavior. Observations of grass-stalk climbing in *L. irrorata* are frequent enough that it is assumed to be a standard component of the animal's behavioral repertoire (Daiber 1982). However, most studies reporting circumtidal migration of *L. irrorata* have been conducted during warm weather (Bingham 1972a; Hamilton 1977; Baxter 1983; Warren 1985) and have linked climbing to predator avoidance (Hamilton 1976; Vaughn and Fisher 1988). Recently, McBride et al. (1989) experimentally demonstrated a positive relationship between substratum temperature and *L. irrorata* climbing frequency that was not correlated with tidal levels; snails would climb grass stems at low tide if the substratum was warm enough. They concluded that *L. irrorata* climb to thermoregulate, and that predator avoidance is a secondary benefit. The relative importance of avoidance of physiological stress versus avoidance of predators as an underlying cause of climbing behavior cannot be determined from our data. In Texas marshes, high substratum temperatures and frequent high tides that carry natant predators to the marsh both occur during warm months, and this is when snails climb grass stems. In addition, in this study the majority of snails foraged on the substratum and did not climb grass stalks at low tide during warm months. During winter months snails at our study site, and at a similar site in Lou-

isiana studied by Alexander (1979), were inactive. This inactivity is most likely a direct effect of lower air temperatures. Factors underlying climbing behavior (high substratum temperatures and predators) are also absent at this time of year.

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LITERATURE CITED

- ALEXANDER, J. E., T. E. AUDESIRK, AND G. J. AUDESIRK. 1985. Classical conditioning in the pond snail *Lymnaea stagnalis*. *American Biology Teacher* 47:295-298.
- ALEXANDER, S. K. 1979. Diet of the periwinkle *Littorina irrorata* in a Louisiana salt marsh. *Gulf Research Reports* 93:295.
- BAXTER, D. L. 1983. The influence of habitat heterogeneity on the population ecology of *Littorina irrorata* Say, the salt marsh periwinkle. Ph.D. Dissertation, Duke University, Durham, North Carolina. 99 p.
- BEQUAERT, J. C. 1943. The genus *Littorina* in the western Atlantic. *Johnsonia* 1:1-27.
- BINGHAM, F. O. 1969. The influence of environmental stimuli on the direction of movement of the supralittoral gastropod *Littorina irrorata*, with notes on additional biological aspects of the species. M.S. Thesis, Florida State University, Tallahassee, Florida. 65 p.
- BINGHAM, F. O. 1972a. The influence of environmental stimuli on the direction of movement of the supralittoral gastropod *Littorina irrorata*. *Bulletin of Marine Science* 22:309-335.
- BINGHAM, F. O. 1972b. The mucus holdfast of *Littorina irrorata* and its relationship to relative humidity and salinity. *Veliger* 15:48-50.
- CHEN, Y. S. AND A. M. M. RICHARDSON. 1987. Factors affecting the size structure of two populations of the intertidal periwinkle, *Nodilittorina unifasciata* (Gray, 1839), in the Derwent River, Tasmania. *Journal of Molluscan Studies* 53:69-78.
- DAIBER, F. C. 1982. Animals of the Tidal Marsh. Van Nostrand Reinhold Co., New York. 422 p.
- GARRITY, S. D. 1984. Some adaptations of gastropods to physical stress on a tropical rocky shore. *Ecology* 65:559-574.
- HALL, J. R. 1973. Intraspecific trail-following in the marsh periwinkle *Littorina irrorata* Say. *Veliger* 16:72-75.
- HAMILTON, P. V. 1976. Predation on *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea; Portunidae). *Bulletin of Marine Science* 26:403-409.
- HAMILTON, P. V. 1977. Daily movements and visual location of plant stems by *Littorina irrorata* (Mollusca: Gastropoda). *Marine Behaviour and Physiology* 4:293-304.
- HAMILTON, P. V. 1978a. Intertidal distribution and long-term movements of *Littorina irrorata* (Mollusca: Gastropoda). *Marine Biology* 46:49-58.
- HAMILTON, P. V. 1978b. Adaptive visually-mediated movements of *Littorina irrorata* (Mollusca: Gastropoda) when displaced from their natural habitat. *Marine Behaviour and Physiology* 5:255-271.
- HAMILTON, P. V., S. C. ARDIZZONI, AND J. S. PENN. 1983. Eye structure and optics in the intertidal snail, *Littorina irrorata*. *Journal of Comparative Physiology* 152:435-455.
- HAMILTON, P. V. AND M. A. WINTER. 1982. Behavioral responses to visual stimuli by the snail *Littorina irrorata*. *Animal Behavior* 30:752-760.
- HEARD, R. W. 1982. Observations on the food and food habits of clapper rails, *Rallus longirostris* (Boddaert), from tidal marshes along the East and Gulf coasts of the United States. *Gulf Research Reports* 7:125-135.
- KNEIB, R. T. 1984. Patterns of invertebrate distribution and abundance in the intertidal salt marsh: Causes and questions. *Estuaries* 7:392-412.
- KOHLMEYER, J. AND B. BEBOUT. 1986. On the occurrence of marine fungi in the diet of *Littorina angulifera* and observations on the behavior of the periwinkle. *Marine Ecology* 7:333-343.
- LASIAK, T. AND A. H. DYE. 1986. Behavioral adaptations of the mangrove whelk *Telescopium* (L.) to life in a semi-terrestrial environment. *Journal of Molluscan Studies* 52:174-179.
- MAYES, P. A. 1962. Comparative investigations of the euryhaline character of *Littorina* and the possible relationship to intertidal zonation. *Nature* 195:1269-1270.
- MCBRIDE, C. J., A. H. WILLIAMS, AND R. P. HENRY. 1989. Effects of temperature on climbing behavior of *Littorina irrorata*: On avoiding a hot foot. *Marine Behaviour and Physiology* 14:93-100.
- NEWELL, R. C. 1970. Biology of Intertidal Animals. Logos Press, London.
- OHGAKI, S. 1985. Field observations on the rhythmic up-and-down movement of *Nodilittorina exigua* (Gastropoda: Littorinidae). *Journal of Ethology* 3:49-58.
- OHGAKI, S. 1989. Vertical movement of the littoral fringe periwinkle *Nodilittorina exigua* in relation to wave height. *Marine Biology* 100:443-448.
- REID, D. G. 1986. The Littorinid Molluscs of Mangrove Forests in the Indo-Pacific Region. The Genus *Littorina*. British Museum of Natural History, London. 73 p.
- SOKAL, R. R. AND F. J. ROHLF. 1981. Biometry (second ed.), W.H. Freeman and Co., San Francisco. 859 p.
- STIRLING, D. AND P. V. HAMILTON. 1986. Observations on the mechanisms of detecting mucous trail polarity in the snail *Littorina irrorata*. *Veliger* 29:31-37.
- TANKERSLEY, R. A. 1989. The effect of trail-following on the locomotion of the marsh periwinkle, *Littorina irrorata* (Meso-gastropoda: Littorinidae). *Marine Behaviour and Physiology* 15:89-100.
- TANKERSLEY, R. A. 1990. Trail following in *Littorina irrorata*: The influence of visual stimuli and the possible role of tracking in orientation. *Veliger* 33:116-123.
- THOMAS, R. F. 1973. Homing behavior and movement patterns in the pulmonate limpet, *Siphonaria pectinata* Linnaeus. *Proceedings of the Malacological Society of London* 40:303-311.
- UNDERWOOD, A. J. 1979. The ecology of intertidal gastropods. *Advances in Marine Biology* 16:111-120.
- VAUGHN, C. C. AND F. M. FISHER. 1988. Vertical migration as a refuge from predation in intertidal marsh snails: A field test. *Journal of Experimental Marine Biology and Ecology* 123:163-176.
- VERMEIJ, G. J. 1971. Temperature relationships of some tropical Pacific intertidal gastropods. *Marine Biology* 10:308-314.
- WARREN, J. H. 1985. Climbing as an avoidance behavior in the salt marsh periwinkle, *Littorina irrorata* (Say). *Journal of Experimental Marine Biology and Ecology* 89:11-28.
- WEST, D. L. AND A. H. WILLIAMS. 1986. Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. *Journal of Experimental Marine Biology and Ecology* 100:75-95.

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