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# Distribution and Morphology of *Littoraria irrorata* in Mesohaline Tidal Marshes Dominated by *Juncus roemerianus*

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## Abstract

Marsh periwinkle snails (*Littoraria irrorata*) are common in salt marshes of the Atlantic and Gulf of Mexico coast and often occupy important ecological roles. Much of the published research examining the abundance and role of this species has been conducted in marshes dominated by smooth cordgrass (*Spartina alterniflora*). We investigated the distribution and morphology of *L. irrorata* in marshes dominated by black needlerush (*Juncus roemerianus*) an important marsh species that commonly forms monotypic conditions in more mesohaline conditions. Eight marshes along the coastal border of Alabama and west Florida, USA, were sampled for *L. irrorata* and other environmental data (plant density and biomass) at four different proximities to the marsh-bay edge. We also examined *L. irrorata* abundance, shell size, and biomass across a salinity gradient (quantified using a salinity regime index). We found that (1) abundance of *L. irrorata* in *J. roemerianus*-dominated marshes ($1.0 \pm 1.0$ to $25.3 \pm 12.6$ snails $m^{-2}$) were within the lower range of snail densities reported for *S. alterniflora*-dominated marshes elsewhere, (2) most *L. irrorata* were detected along the 10-m waterward edge of the marsh, and (3) considering snails at the waterward edge, a positive relationship ($r^2 = 0.53$, $p = 0.04$) was detected between marsh salinity and snail density along with a negative relationship ($r^2 = 0.86$, $p < 0.01$) between marsh salinity and mean snail shell length. Mechanisms associated with *L. irrorata* abundance and morphology are unclear but likely relate to various aspects of salinity and tidal connectivity. These results suggest that mesohaline *J. roemerianus* marshes may be marginal in terms of *L. irrorata* habitat; however, further research is encouraged.

**Keywords** *Littoraria irrorata* · Marsh periwinkle · Black needlerush · *Juncus roemerianus* · Mesohaline · Tidal marshes

## Introduction

The salt marsh periwinkle snail (*Littoraria irrorata*) is an omnivorous snail found in salt marshes along the Atlantic and Gulf of Mexico coasts of North America. As one of the most abundant macroinvertebrates in salt marshes (Schalles et al. 2013), they play important roles in these ecosystems (Kemp et al. 1990; Sullivan and Moncreiff 1990; Graça et al. 2000; Silliman and Bertness 2002). For example, *L. irrorata* was found to exert top-down control on primary production in *Spartina alterniflora* (smooth cordgrass) dominated marshes (Silliman and Zieman 2001). This effect may be circumstantial and other studies have found a positive correlation or lack of relationships between *L. irrorata* and *S. alterniflora* densities suggesting snails may not typically exert top-down control when snail density is more moderate (West and Williams 1986; Hutchens and Walters 2006; Kiehn and Morris 2009). *Littoraria irrorata* are also important prey for several coastal species including fishery species such as the blue crab (*Callinectes sapidus*) (Lewis and Eby 2002) and the diamondback terrapin (*Malaclemys terrapin*), an important species for conservation (Butler et al. 2012).

The majority of marsh studies focused on *L. irrorata* have been conducted in marshes dominated by *S. alterniflora*. There is less research focusing on *L. irrorata* found in marshes dominated by other species although interest is increasing. For example, Failon et al. (2020) recently documented that *L. irrorata* were found in marshes dominated by *Spartina cynosuroides* (big cordgrass), a salt marsh species typically occurring in less saline conditions. Their estimates

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showed that *L. irrorata* densities were comparable to other marsh studies. *Juncus roemerianus* (black needlerush) is another common salt marsh species known to support *L. irrorata* (Bingham 1972; Hamilton 1976; Hamilton and Winter 1982; Schalles et al. 2013). *Juncus roemerianus* covers approximately 320,000 ha of salt marsh in North America with 170,000 ha found along the Gulf of Mexico coast (Eleuterius 1976). It commonly forms monotypic cover in marshes along with coastal west Florida, Alabama, and Mississippi where it is the dominant intertidal marsh form. *Juncus roemerianus* marshes commonly occur in more mesohaline conditions along the gulf and frequently dominate intertidal zones along bayous, tidal creeks, and bays (de la Cruz and Gabriel 1974; Stout 1984). Previous studies have shown that *L. irrorata* can be sensitive to lower salinities (Bingham 1972; Crist and Banta 1983); however, they are known to occur across a range of tidal conditions. Intramarsh distribution patterns have shown that *L. irrorata* are more abundant closer to the marsh-water edge (West and Williams 1986; Hutchens and Walters 2006) but again, this work has been largely applied to marshes dominated by *S. alterniflora*. Determining the importance of *J. roemerianus* as a habitat for *L. irrorata* is needed to better understand the ecosystem value of these regionally important wetlands.

The goal of this study was to evaluate the abundance and morphology of *L. irrorata* in *J. roemerianus*-dominated salt marshes. We sought to compare our results to patterns detected elsewhere for *L. irrorata* in *S. alterniflora*-dominated marshes. Using eight *J. roemerianus* marshes representing a mesohaline-salinity gradient on the Alabama-Florida, USA border, we evaluated the distribution patterns of *L. irrorata* within and among these marshes. We predicted (1) *L. irrorata* density, size, biomass, and intra-marsh distribution will be comparable to those reported in *S. alterniflora* marshes, and (2) snail density will vary between marshes with those marshes more proximate to the Gulf of Mexico having the highest densities and biomass.

## Methods

### Site Selection

Eight salt marshes along Alabama and west Florida coasts were sampled June–July 2019 (Fig. 1). Each marsh was classified as estuarine, emergent, intertidal, and persistent by the U.S. Fish & Wildlife Service National Wetland Inventory (https://www.fws.gov/wetlands/). All marshes fringed local bays that varied in size and proximity to the gulf (Table 1). Upon inspection, all sites had a near monotypic cover by *J. roemerianus* with secondary species at some sites including *Cladium jamaicense* (saw grass), *Distichlis spicata* (saltgrass), *S. alterniflora*, *Spartina patens* (saltmeadow cordgrass), and *Sagittaria latifolia* (broad-leaf arrowhead).

### Snail, Vegetation, and Water Surveys

To capture variable conditions within each marsh, snails were sampled along two parallel transects (50 m apart) that extended perpendicular from the marsh-bay edge to the upland border. Because *Juncus* marshes in this region are relatively flat and microtidal (Stout 1984), transitions between low and high marsh can be subtle and less perceptible in the field. Therefore, sampling of each site consisted of a total of four plots located along each transect: (1) marsh-bay edge (edge), (2) 10-m from the marsh-bay

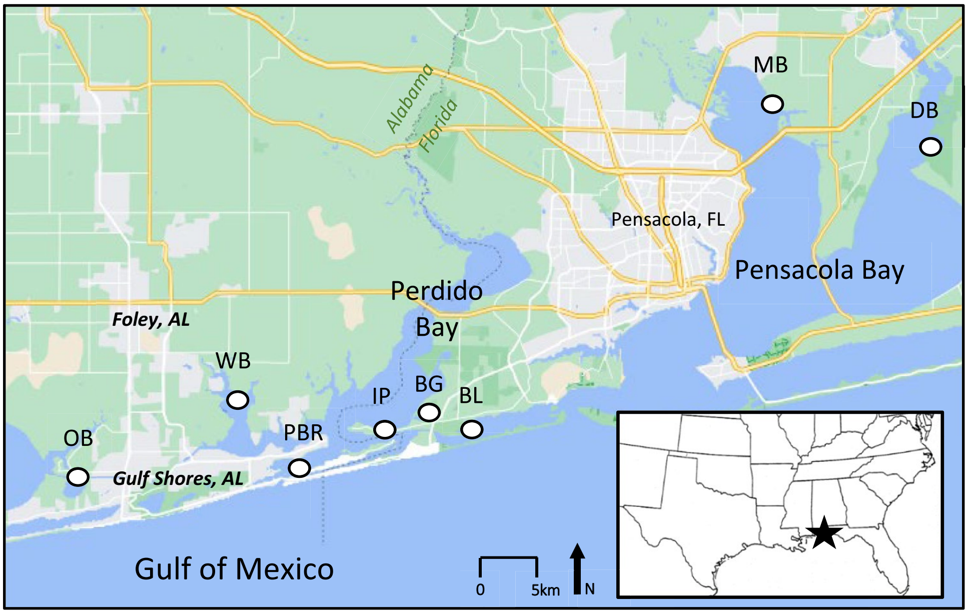


**Fig. 1** Study wetlands in the Pensacola-Perdido Bay region of Alabama and West Florida (see Table 1 for site names) (modified map source: Map Data ©2021 Google, INGEI, USA)

**Table 1** Site name, location, mean (± SE) *J. roemerianus* biomass/culm density, seasonal median salinity (ppt), and salinity regime index (SRI). High and low seasonal salinity based on NOAA Estuary Zones per NOAA Gulf of Mexico Data Atlas

| Location (Site) | Lat | Long | Approx. transect length (m) | Mean Juncus biomass (g/m$^2$) | Mean Juncus stem density (#/m$^2$) | NOAA Estuary Zone (median salinity ppt) | | SRI |
|---|---|---|---|---|---|---|---|---|
| | | | | | | High salinity season | Low salinity season | |
| Wolf Bay (WB) | 30.338560 | −87.589321 | 120 | 623 (128) | 417 (40) | III (10) | III (10) | 10.0 |
| Doghole Basin (DB) | 30.520316 | −87.009920 | 140 | 418 (60) | 360 (68) | III (10) | III (10) | 10.0 |
| Mulat Bayou (MB) | 30.550388 | −87.129906 | 102 | 703 (107) | 480 (63) | IV (20) | II (2.5) | 11.3 |
| Bayou Garcon (BG) | 30.321196 | −87.427757 | 47 | 648 (156) | 451 (85) | IV (20) | III (10) | 15.0 |
| Oyster Bay (OB) | 30.279665 | −87.725443 | 184 | 683 (209) | 584 (149) | IV (20) | III (10) | 15.0 |
| Kees Bayou (IP) | 30.313701 | −87.474201 | 44 | 1043 (225) | 646 (125) | IV (20) | IV (20) | 20.0 |
| Big Lagoon (BL) | 30.307823 | −87.406547 | 51 | 887 (205) | 489 (110) | IV (20) | IV (20) | 20.0 |
| Cotton Bayou (PBR) | 30.277663 | −87.562308 | 110 | 1025 (191) | 706 (111) | V (25) | V (25) | 25.0 |

edge (10-m), (3) halfway between the marsh-bay edge and upland (mid), and (4) at the marsh-upland edge (upland). Surveying each marsh in proximity to the marsh-bay edge was also designed to be comparable to other studies (Hutchens and Walters 2006; Rietl et al. 2018) that have detected snail preferences for certain portions of the salt marsh. At each plot, two subplots were established 5 m perpendicular from the transect. For each subplot, a 0.25-m$^2$ quadrat was carefully placed at or near the marsh surface and all *L. irrorata* specimens found on plant stems or the unflooded ground were collected. Specimens were not detected below water as *L. irrorata* are known to climb plant stems during tidal flooding to avoid predation (Hamilton 1976; Warren 1985). All snails in the plot were collected, placed in freezer bags (per plot), labeled, and transported in an iced cooler. Specimens were returned to the laboratory for counting, size measurements, and biomass calculation (see below).

Measures of vegetation and water salinity were also collected at each wetland. At each transect plot (in between snail subplots), vegetation was sampled using a 0.25-m$^2$ quadrat placed at or near the marsh surface and all vegetation in the quadrat was clipped at the marsh surface if unflooded or at the water surface if flooded. Harvesting vegetation below the water surface was difficult so an alternate approach to estimating this biomass was devised (see below). Plants were bagged and then returned to the laboratory. Surveys were conducted throughout the tidal cycle; however, most plots were shallowly flooded (typically 10–25 cm). Where standing water was present in the plot, the depth was recorded in the center of the quadrat. In between parallel transects at the marsh-bay edge, surface water temperature and salinity were measured using a YSI 30 (Yellow Springs, OH, USA) environmental meter just beyond the marsh in the subtidal zone.

## Snail Abundance and Morphology

In the laboratory, snails were stored in a walk-in cooler (5° C) until processed (within 1 week of collection). Snails were counted per plot and abundance calculated as number of snails per square meter. Shell length (mm) measurements of each snail were taken using a caliper along the vertical axis of the shell. Snail ash-free dry mass (AFDM) was estimated for each individual using a power law equation produced by Hutchens and Walters (2006). Individual snail mass was calculated and then averaged for all snails per plot.

$$\text{Snail AFDM (mg)} = 0.008 * \text{Snail shell length (mm)}^\wedge 3.1157 \qquad (r^2 = 0.93)$$

## Vegetation Stem Density and Biomass

In the laboratory, vegetation was stored in a walk-in cooler (5° C) until being processed (within 3 weeks). For each plot, the number of live (> 75% green) and senescent *J. roemerianus* culms were counted and separated per plot. Other non-*Juncus* specimens were also identified and separated. All vegetation groups were bagged separately, dried to constant mass in an oven at 60° C, and weighed. Total plot biomass was calculated as the sum of live *Juncus* and other non-*Juncus* specimens. A portion of oven-dried live *Juncus* culms ($n = 10$) were selected and individually measured for length and weight. Culms of different sizes were selected to approximate the proportion of sizes collected in the field. A length to dry-weight relationship was calculated using linear regression:

$$\textit{Juncus}\text{ culm-biomass (g)} = 0.021 * \textit{Juncus}\text{ culm-length (cm)}+0.0102 \qquad (r^2 = 0.73)$$

This equation was used to approximate the biomass of live *J. roemerianus* culms below water per plot by determining the total culm length below water (i.e., number of live *Juncus* culms * depth of water). This biomass was then added to the total live *Juncus* biomass calculated per plot.

## Marsh Salinity Regime

To evaluate the potential role of long-term marsh salinity, tidal connectivity, and overall proximity to the Gulf of Mexico, we developed a salinity regime index (SRI) based on spatial data available in the Salinity Zones-Estuarine option within the NOAA Gulf of Mexico Data Atlas (https://www.ncei.noaa.gov/maps/gulf-data-atlas/atlas.htm?plate=Salinity-Zones). In this option, estuaries along the Gulf of Mexico have been delineated into one of five salinity zones based on historical data and multivariate analyses (Bulger et al. 1993; Orlando et al. 1993; Christensen et al. 1997; Fig. 2). Delineation of zones is provided for both high and low salinity seasons (typically lasting 3–4 months per year) based on seasonal fluctuations caused by local variations in freshwater inflows (Nelson 2015). Highest and lowest seasonal inflows for this region are typically January-April and September-December, respectively. For our index, we determined the mapped zone location for each marsh site and calculated the corresponding median salinity for that zone (25 ppt was used for Zone V: > 25 ppt, see Table 1). This process was conducted for both low and high salinity season (Fig. 2) and then averaged between seasons to provide an SRI score for each site. Calculated salinity regime scores corresponded well with measured salinity at each site (Pearson correlation analysis: $r=0.87$, $p<0.05$). Salinity zones and corresponding SRI scores for each site are provided in Table 1.

## Statistical Analysis

Using plot-level data, Friedman's non-parametric test was used to evaluate differences in *L. irrorata* density based on plot location (i.e., upland, mid, 10 m, and edge) with marsh site as a categorical block variable. Based on these results, pairwise comparisons between plot locations were made using Wilcoxon signed-rank test. Analyses were conducted to evaluate the potential relationships between *L. irrorata* density and shell length with marsh SRI. For these analyses, snail density and shell length were averaged across all plots and for waterward plots only (edge and 10 m) per marsh. These averages were then examined with wetland SRI (independent variable) using linear regression. Linear regression was also used to detect relationships between *L. irrorata* density and biomass with *J. roemerianus* biomass. All statistical analyses were conducted using Minitab Version 21.1 (Minitab, LLC, State College, Pennsylvania).

## Results

The density and size of *L. irrorata* varied significantly within and among wetlands. The highest density of snails was detected at wetland BL which yielded an average of 58.5 ± 10.7 snails $m^{-2}$ across all plots. The lowest average snail density was detected at WB (1.0 ± 1.0 snails $m^{-2}$). There were notable differences between wetlands in the presence and absence of snails across transect plots. Only three wetlands had snails detected in the mid and upland plots (BL, IP, and PBR, Fig. 3). The remaining wetlands only had snails detected at the edge and/or 10-m plots across the transect. Consequently, mean snail density and biomass were higher in the waterward plots (edge and 10-m) than means across wetlands (except for wetland BL, Table 2). Differences in density between plot locations was supported by Friedman's test (df = 3, chi-square = 12.67, $p=0.005$). Post hoc analyses based on Wilcoxon signed-rank test indicated differences ($p<0.001$) in density when waterward plots (edge and 10 m) were paired with interior plots (mid and upland).

Similar to density, there was considerable variation in snail size within and between wetlands. On average, sites with snails only detected at the waterward plots (edge and 10-m plots) had a larger range of average shell lengths (range: 21.5 ± 0.3 to 23.0 ± 0.9 mm) than sites with snails in all plots (BL, IP, and PBR) (range: 18.1 ± 1.4 to 20.1 ± 0.2 mm). Sites BL, IP, and PBR also had greater SRI scores compared to the other sites (Table 1). It was noted that sites with SRIs < 15 were only occupied by larger adult snails (> 13-mm shell length) while sites with SRI > 15 also contained sub-adults (6–13-mm shell length), although no juveniles (< 6-mm shell length) were detected (size classes per Zengel et al. 2016). Based on shell lengths, estimated AFDM biomass across all plots yielded mean snail biomass that ranged between 0.14 ± 0.14 to 6.04 ± 1.06 g-AFDM $m^{-2}$ (Table 2) with all but one site (BL) averaging < 2.0 g-AFDM $m^{-2}$.

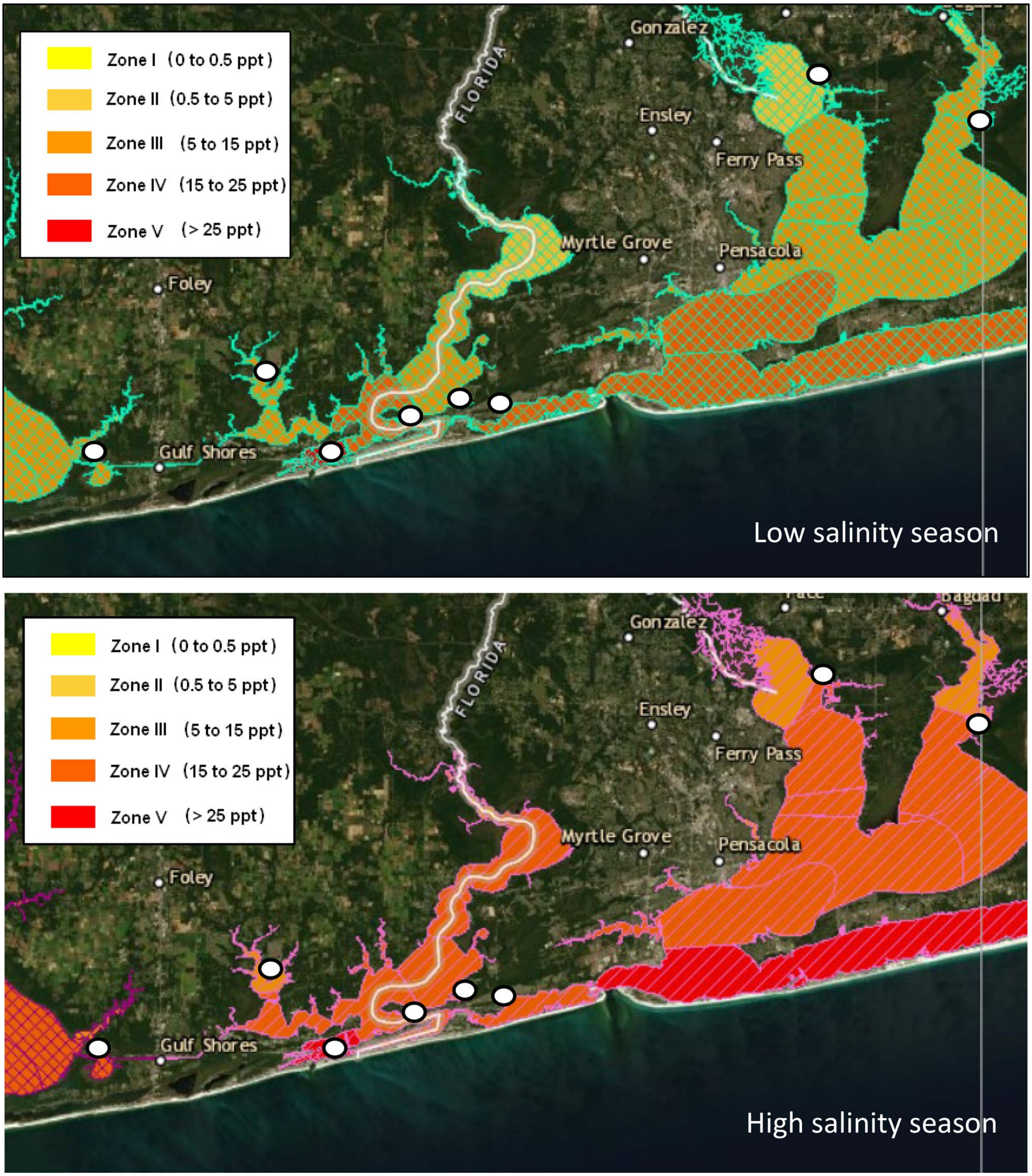


**Fig. 2** Salinity zone-estuarine maps produced from the NOAA Gulf of Mexico Data Atlas for the Pensacola-Perdido Bay region and study sites for both the low and high salinity season. Wetland site identification labels are provided in Fig. 1

Analysis of site-level mean snail density and other measures had notable relationships with SRI. When examining snail density and shell length averaged using the two waterward plots (edge and 10-m), we found a positive relationship between SRI and snail density ($r^2 = 0.53$, $p = 0.04$) and a negative relationship with mean shell length ($r^2 = 0.86$, $p < 0.01$). These relationships weakened somewhat when considering site snail averages across all plots (Fig. 4);

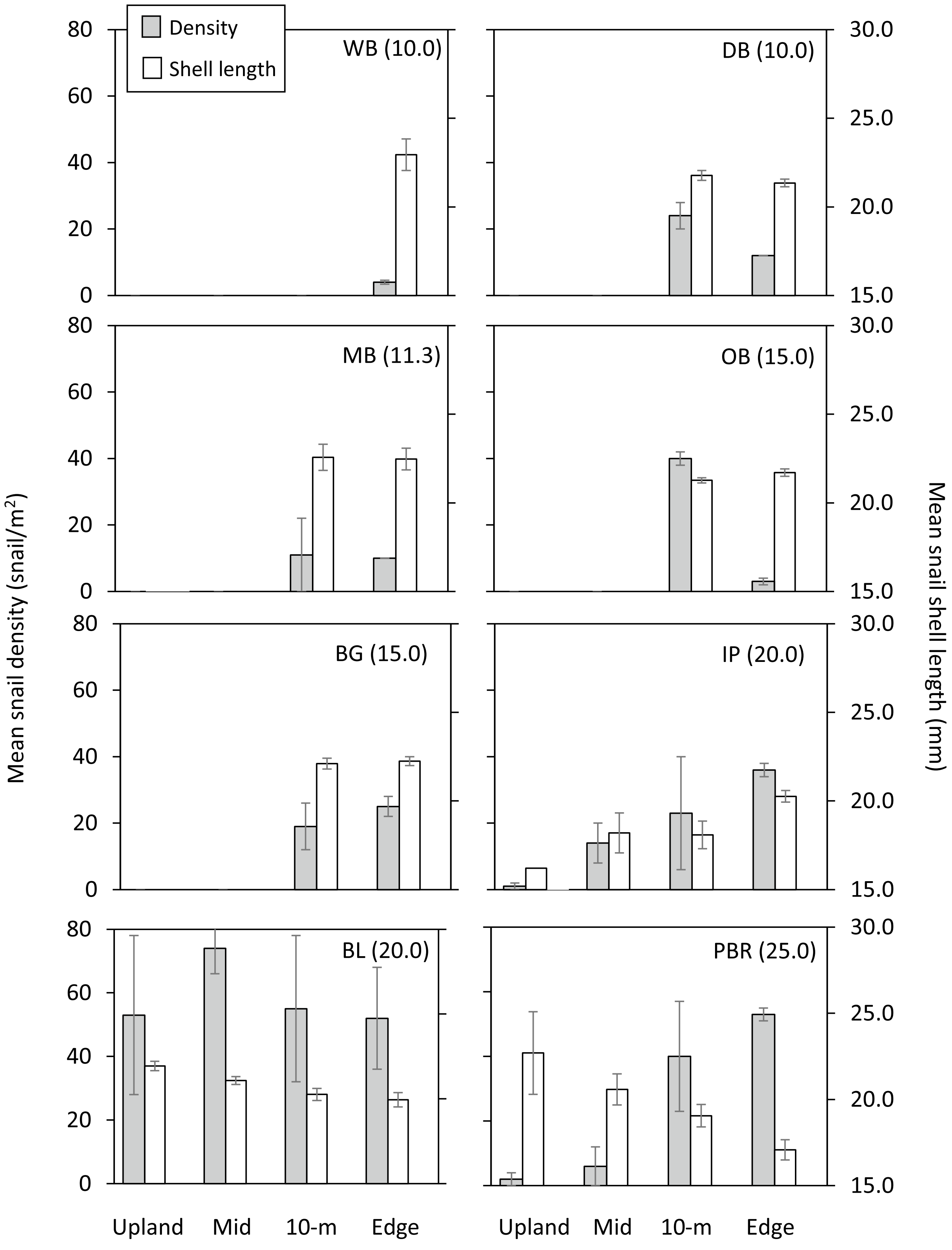


**Fig. 3** Mean (± SE) snail density and shell length per plot. Wetland SRI is provided in parentheses

**Table 2** Mean (± SE) snail density, shell length, and biomass across all plots and waterward plots (Edge and 10 m only)

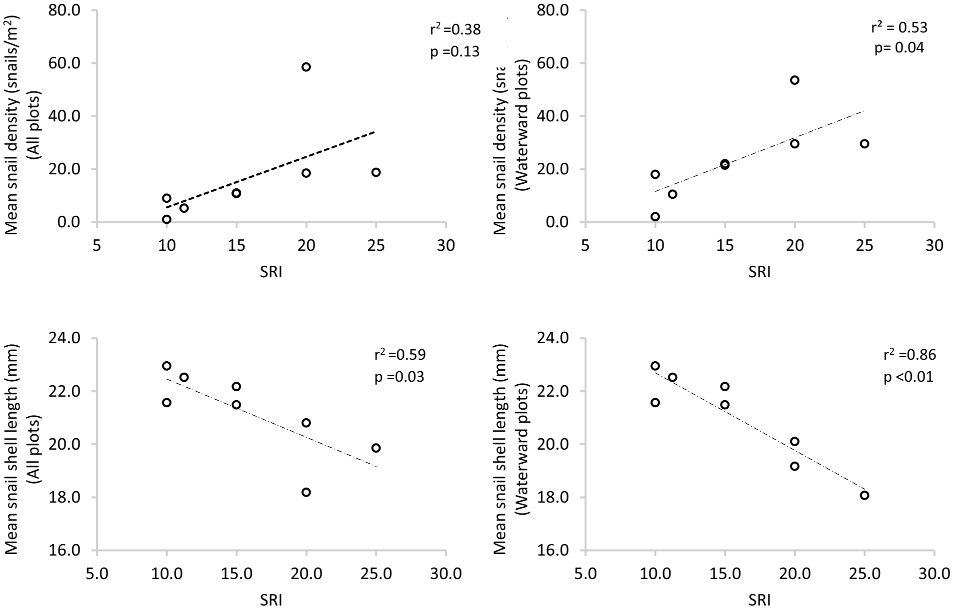
| Location (site) | All plots (edge, 10-m, mid, and upland) | | | Waterward plots (edge and 10-m) | | |
|---|---|---|---|---|---|---|
| | Snail density (#/m$^2$) | Shell length (mm) | Snail biomass (g/m$^2$) | Snail density (#/m$^2$) | Shell length (mm) | Snail biomass (g/m$^2$) |
| Wolf Bay (WB) | 1.0 (1.0) | 23.0 (0.9) | 0.14 (0.14) | 2.0 (2.8) | 23.0 (0.9) | 0.28 (0.39) |
| Doghole Basin (DB) | 9.0 (3.8) | 21.6 (0.3) | 1.04 (0.67) | 18.0 (8.5) | 21.6 (0.3) | 2.08 (1.06) |
| Mulat Bayou (MB) | 5.3 (2.9) | 22.5 (0.1) | 0.69 (0.40) | 10.5 (0.7) | 22.5 (0.1) | 1.38 (0.11) |
| Big Lagoon (BL) | 58.5 (10.7) | 20.8 (0.3) | 6.04 (0.72) | 53.5 (2.1) | 20.1 (0.2) | 4.93 (0.36) |
| Oyster Bay (OB) | 10.8 (6.4) | 21.5 (0.3) | 1.18 (1.07) | 21.5 (26.2) | 21.5 (0.3) | 2.37 (2.85) |
| Kees Bayou (IP) | 18.5 (5.9) | 18.2 (0.8) | 1.48 (0.71) | 29.5 (9.2) | 19.2 (1.5) | 2.46 (1.32) |
| Bayou Garcon (BG) | 11.0 (4.5) | 22.2 (0.1) | 1.38 (0.81) | 22.0 (4.2) | 22.2 (0.1) | 2.75 (0.57) |
| Cotton Bayou (PBR) | 21.0 (9.1) | 19.9 (1.1) | 1.49 (0.66) | 38.0 (9.2) | 18.1 (1.4) | 2.55 (0.79) |

however, the lack of a significant relationship between snail density and SRI occurred only because of the unusually high number of snails detected at BL. While not specifically the focus of this study, SRI was also positively correlated with mean *J. roemerianus* biomass ($r^2 = 0.80$, $p < 0.01$) and culm density ($r^2 = 0.71$, $p < 0.01$), although it should be noted that a post hoc regression ran between plot-level measures of *J. roemerianus* (density and biomass) and snail density did not result in a detectable relationship.

## Discussion

Results from our eight sites showed both intra- and inter-marsh trends in the spatial distribution of *L. irrorata*. One goal of this study was to determine if *L. irrorata* densities found in *J. roemerianus* marshes would be comparable to numbers detected in more common *S. alterniflora* studies. Comparing our results to others published (i.e., those tabulated by Hutchens and Walters 2006; Rietl et al. 2018), *L. irrorata* densities were within the range published for *S. alterniflora* marshes; however, most sites were low in comparison. If we consider the average *L. irrorata* density in all plots per site (Table 2), five sites (62%) had < 18 snails m$^{-2}$. In contrast, published snail densities tabulated in Rietl et al. (2018) for various studies in the southeast U.S. (both Atlantic and Gulf of Mexico coasts) showed only four of 27 study sites (15%) reported snail density < 18 snails m$^{-2}$. Even if we consider averages from the waterward plots where snails were most detected, the average density was still < 26 snails m$^{-2}$ for all but one site (PBR). The vast majority (74%) of studies tabulated by Rietl et al. (2018) reported snail

**Fig. 4** Wetland mean and linear regression results for snail density (top panels) and mean snail shell length (bottom panels) in relation to wetland SRI. Snail results are averaged for all plots (left panels) and only waterward plots (10 m and Edge) (right panels)



densities > 30 snails m$^{-2}$, although these studies represent varied sampling locations within marshes. These comparisons suggest that many *J. roemerianus* marshes along the Gulf coast may represent marginal habitat for *L. irrorata*. The low abundance of *L irrorata* across most of our study sites also contributed to estimates of overall low areal biomass of snails when compared to ranges reported from other studies in the southeast U.S. (0.5–57 g m$^{-2}$, Rietl et al. 2018).

Examining the variation of snail abundance across transects, we found that all but one marsh (BL) had the highest density of snails detected at the edge and 10-m plots. In over half the cases (BG, DB, MB, WB and OB), these waterward plots were the only plots where snails were detected. Indications that *L. irrorata* are more abundant (and in some cases only present) near the marsh-bay edge are consistent with patterns from other studies. At a *S. alterniflora* marsh in nearby Dauphin Island, West and Williams (1986) detected peak snail density approximately 40-m inland from mean low water. In South Carolina, Hutchens and Walters (2006) found *L. irrorata* density was significantly higher in the low and mid-marsh portions and Rietl et al. (2018) found a maximum abundance 10 m from the marsh-water edge of Louisiana marshes.

We also found variations in snail size across transects. Only three sites in our study had *L. irrorata* detected in all plots along the transect and, interestingly, all three showed a pattern of increasing or decreasing shell length across the transect. Two sites (PBR and BL) showed shell length declining as transects reached the marsh-bay edge while IP showed a mean shell length increase (Fig. 3). Higher blue crab (*C. sapidus*) predation on smaller snails (< 18-mm shell length, West and Williams 1986) near the water edge has been used to explain the seaward increase of mean snail shell size documented elsewhere (Crist and Banta 1983). However, others have suggested the opposite trend (seaward decrease in mean shell length) because larger snails are more resistant to desiccation and therefore increasingly occur in the high marshes (Vermeij 1972). Our results showed mixed results, similar to Hutchens and Walters (2006) who found two marshes with increasing snail shell length as transects extended from the low to high marsh, while a third marsh showed no pattern. We cannot comment on the amount of predator pressure on *L. irrorata* by *C. sapidus* or other predators; however, tidal inundation can be an important regulator of intra-marsh predator pressure. When present, *C. sapidus* predation is most intense along the water edge (Lewis and Eby 2002); but, like *L. irrorata*, *C. sapidus* abundance and distribution tend to decline in more mesohaline environments (< 20 ppt) (Childress and Permenter 2012).

Site-level snail density varied considerably between marshes and corresponded closely with salinity regimes and proximity to the gulf. The relationships detected between marsh-level snail density and our SRI were unexpected. Although marsh salinity is likely important for the habitat suitability of these snails, it is important to note that this index represents other potential gradients that may be contributing to these patterns such as tidal connectivity and proximity to the Gulf of Mexico. Snails were more abundant in sites located closest to the gulf and may represent more frequent colonization. Sites located in the lower salinity zones are influenced greater by freshwater inputs which can be an important habitat factor that may impact snail abundance. Crist and Banta (1983) experimentally examined the impact that freshwater exposure had on the survivorship and activity of *L. irrorata*. They found that most snails > 21-mm shell length died after 6 days of 5 ppt exposure and that all snails became less active after exposure to < 10 ppt. Collectively, there appear to be important thresholds related to snail suitability that may limit them from many *J. roemerianus* marshes. Sampling five marshes along the Louisiana coast, Rietl et al. (2018) found that average snail density decreased with increasing marsh proximity to either the Atchafalaya or Mississippi River. As a possible contributing factor, they noted that sites closer to rivers also had lower N content in *S. alterniflora*. Bingham (1972) attributed a steep decline in *L. irrorata* abundance at the transition to the high marsh where salinity was < 15 ppt. Furthermore, it was demonstrated experimentally that *L. irrorata* eggs developed better as salinity increased incrementally from 5 to 25 ppt.

In addition to snail abundance, there were differences in size classes and other measures related to SRI. Sites with SRIs < 15 were only occupied by larger adult snails while sites with SRI > 15 also contained sub-adults. This contributed to the declining average snail size with increasing SRI. Because snails can live for several years, missing size classes may indicate that recruitment events are infrequent. Perhaps at low salinity sites, snails only recruit and establish during drier years when salinities are somewhat elevated. Adults are probably more resistant of low salinities than juveniles and so could persist and grow large even when recruitment fails. It is uncertain why smaller size classes were absent from many sites occupying lower salinities; however, it is further evidence that more suitable habitat for *L. irrorata* occurs in more saline conditions. The distribution of snail size classes based on shell length in marshes with SRI > 15 was similar to distributions reported for five Louisiana salt marshes (Rietl et al. 2018). Interestingly, at the site level, there was a similar relationship detected for *J. roemerianus* (culm density and standing biomass) and SRI. The role of stem density and marsh productivity has been reported extensively (Lewis and Eby 2002; Silliman et al. 2005; Hutchens and Walters 2006; Kiehn and Morris 2009), especially in relation to potential top-down effects that *L irrorata* may have on *S. alterniflora* (Silliman and Zieman 2001). Although site averaged *L. irrorata* and *J. roemerianus* density were both correlated with SRI, we found no relationship between plot-level averages of *J. roemerianus* (culm density or biomass) and measures of *L. irrorata* (density or biomass).

## Summary

To date, little information is available regarding their occurrence in black needlerush (*J. roemerianus*) marshes, a regionally important ecotype that often occupies more mesohaline conditions. For this study, eight marshes dominated by *J. roemerianus* were surveyed to evaluate the abundance, morphology, and spatial distribution of *L. irrorata*. Our results indicated that the abundance of *L. irrorata* in *Juncus*-dominated marshes was within the lower range of snail densities reported for *Spartina*-dominated marshes elsewhere. Using a long-term salinity regime index (SRI), we also detected a strong positive relationship between marsh salinity and snail density and a strong negative relationship between marsh salinity and mean snail shell length. These results suggest that the lower salinities occupied by many *J. roemerianus* marshes likely represent a marginal habitat for *L. irrorata*. Our results indicate that salinity or factors related to tidal connectivity play an important role in the distribution of this species. Although *L. irrorata* densities are low in *Juncus* marshes compared to *Spartina* marshes, the regional abundance of *Juncus* marshes on the Gulf of Mexico indicates that they may be an important secondary habitat. Moreover, the ecological role that *L. irrorata* plays in *Juncus* marshes as consumers and as prey for higher trophic levels remains to be determined and deserves further investigation.

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