

Spatial distribution and morphological responses to predation in the salt marsh periwinkle

ANTHONY J. RIETL,^{1,†} MADELYN G. SORRENTINO,² AND BRIAN J. ROBERTS³ 

¹College of William and Mary, Virginia Institute of Marine Science, P.O. Box 1346, Gloucester Point, Virginia 23062 USA

²Rubenstein School of Environment and Natural Resources, University of Vermont, Burlington, Vermont 05405 USA

³Louisiana Universities Marine Consortium, Chauvin, Louisiana 70344 USA

Citation: Rietl, A. J., M. G. Sorrentino, and B. J. Roberts. 2018. Spatial distribution and morphological responses to predation in the salt marsh periwinkle. *Ecosphere* 9(6):e02316. 10.1002/ecs2.2316

Abstract. The salt marsh periwinkle (*Littoraria irrorata*) is a common and often abundant mollusk in marshes of the Gulf and Atlantic coasts of the United States. Several studies have focused on the effects of periwinkles on *Spartina alterniflora* production and the effects of oil on periwinkle survivability, yet the general ecology of the snail has been underreported. In this study, we measured spatial distributions, biomass, shell repair frequency, and a suite of morphological characteristics of *L. irrorata* at three sites in each of five regions spanning the southeastern Louisiana Coast between the Atchafalaya and Mississippi rivers. Sampling was conducted along 50 m edge-to-interior transects in *S. alterniflora*-dominated marshes. We found that *L. irrorata* density, individual biomass, and total areal biomass significantly varied by region. Each also significantly varied with distance from the marsh edge, with the exception of total periwinkle areal biomass. We saw a general trend across most regions where periwinkle density tended to be greatest 10 m from the marsh edge and biomass tended to be greatest 20–30 m from the marsh edge; however, neither periwinkle density nor biomass was related to *S. alterniflora* density or stem height. The allometric relationship between shell length and biomass varied significantly between all regions, indicating that this species has differing regional growth patterns. A possible driver of these regional patterns in allometry is differences in predation pressures, with increased predation scaring at Port Fourchon sites corresponding to snails with larger shells yet less internal biomass per length compared to other regions. This study provides the first large-scale description of the spatial ecology and regional morphometry of the salt marsh periwinkle, an important organism in structuring salt marsh ecosystems, and suggests that the pressures exerted by *L. irrorata* on plant production found in other studies likely varies by geography and spatial location within a marsh.

Key words: Gulf Coast; *Littoraria irrorata*; salt marsh periwinkle; snail ecology; *Spartina alterniflora*.

Received 15 May 2018; accepted 23 May 2018. Corresponding Editor: Hunter S. Lenihan.

Copyright: © 2018 The Authors. This is an open access article under the terms of the Creative Commons Attribution License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited.

† **E-mail:** AJRietl@Vims.edu

INTRODUCTION

The salt marsh periwinkle (*Littoraria irrorata*) inhabits salt marshes of the Atlantic and Gulf coasts of the United States where it is associated with emergent vegetation, most commonly *Spartina alterniflora*. The periwinkle displays the conspicuous behavior of climbing plant stems at high tide likely to avoid predation (Warren 1985),

but also linked to thermoregulation (Williams and Appel 1989, Henry et al. 1993). The periwinkle also plays many diverse roles in salt marsh ecosystems (Sullivan and Moncreiff 1990, Newell 1993, Newell and Barlocher 1993, Graça et al. 2000). *Littoraria irrorata* has been extensively studied in terms of the organisms effect on *S. alterniflora* productivity (Silliman and Ziemann 2001, Kiehn and Morris 2009) and on the effects of the Deepwater

Horizon oil spill on survivability (Zengel et al. 2016a, b); however, distributions (regionally and spatially within regions), areal biomass estimates, and morphological characteristics of this species are currently underreported across the species range, making extrapolations regarding this species effects on salt marsh ecosystems difficult.

Along the Atlantic Coast, densities of *L. irrorata* have ranged from 1.4 to 558 individuals/m² reported from marshes termed healthy and up to 2634 individuals/m² in marshes experiencing die-off in Georgia (Silliman et al. 2005). Similar ranges in density (4–700 individuals/m²) have been reported for other marsh sites along the Atlantic Coast (Newell et al. 1989, Silliman and Zieman 2001, Hutchens and Walter 2006). Densities along the Gulf Coast have been reported to be between 24 and 200 individuals/m² (Alexander 1979, McFarlin et al. 2015, Zengel et al. 2016a, b, Rietl et al. 2017). However, in each of these studies with the exception of Hutchens and Walter (2006), the variation in density and spatial distribution was not the focus of the work and density estimates were limited by low replication and a lack of assessment of within marsh spatial distribution and variation.

Likewise, even less is known about patterns in *L. irrorata* biomass on an individual or areal basis. Areal biomass values measured as ash-free dry mass (AFDM) ranged from approximately < 0.5 to 10 g/m² in North and South Carolina (Cammen et al. 1980, Hutchens and Walter 2006) to 57 g/m² in Louisiana (Tong et al. 2013). Very few studies have looked at within marsh spatial variability in biomass; however, Hutchens and Walter (2006) found significant biomass differences between low, mid, and high marsh plots, but only reported a maximum areal biomass of ~9 g/m². Similarly, low biomass estimates have been reported from salt marshes in Georgia and Louisiana in the range of 5–10 g/m² (as reported in Alexander 1979). The scarcity of reported biomass values for this species leaves us unable to assess the accuracy of these estimates and further emphasizes the high degree of variation in what is known about marsh periwinkle ecology. A better understanding of the basic ecology of this species could help put other marsh periwinkle studies into a broader and more applicable context. For example, top-down control of *S. alterniflora* production by marsh

periwinkles (Silliman and Zieman 2001) and energy flow through marshes (Cammen et al. 1980) are wholly dependent upon densities and spatial organization of local communities; thus, the effects of periwinkles on marsh processes may exhibit high spatial heterogeneity.

Littoraria irrorata shell morphology and predation has received considerably more attention in the literature relative to distributions and biomass estimates (Moody and Aronson 2007, 2012, Dietl and Alexander 2009) as well as the effects of the Deepwater Horizon oil spill on snail growth (Zengel et al. 2016a, b). Marsh periwinkle maximum size is known to vary between different marshes (Crist and Banta 1983), and shell length has been shown to increase with elevation in South Carolina and Florida (Hamilton 1978, Hutchens and Walter 2006), but decrease with elevation in Virginia (Crist and Banta 1983). Mean shell lengths (\pm SE) as reported by Zengel et al. (2016a) were between 17.3 ± 1.6 and 20.6 ± 0.6 mm in Louisiana and 14 mm in South Carolina (Kiehn and Morris 2009). Periwinkle size is important in predator–prey relationships with blue crabs (*Callinectes sapidus*), as these crabs are more effective at feeding on smaller periwinkles (greater crab width:snail length ratios) than on larger periwinkles (lower crab width:snail length ratios).

Snails often survive predation attempts leaving behind damaged shells (Schindler et al. 1994). Many studies have utilized shell scarring as a measure of predation, termed shell repair frequency (Dietl and Alexander 2009, Moody and Aronson 2012, Stafford et al. 2014). This predation measure has been linked to increased aperture ridge thickness, both in the field and in the laboratory experiments (Dietl and Alexander 2009, Moody and Aronson 2012). This is thought to better protect the periwinkle from predation by making the aperture opening smaller, thereby making it harder for predators to extract the snail from its shell. This is important as *C. sapidus* (blue crab) is known to progressively chip away at the aperture lip when attempting to feed on larger periwinkles (Schindler et al. 1994).

The goal of this study was to identify drivers of spatial and morphological variations in *L. irrorata* at two spatial scales (within marsh and regional). We hypothesized that (1) periwinkle density and biomass will be lower near the marsh edge where

predation pressures from blue crabs are likely highest (Schindler et al. 1994), as well as in the marsh interior due to less inundation and higher probabilities of desiccation (Williams and Appel 1989, Henry et al. 1993), that these within marsh patterns will differ among regions, and that areal biomass will closely track density patterns; (2) allometric relationships will vary among regions in concert with *S. alterniflora* nitrogen content and with marsh position; (3) periwinkle density will increase with *S. alterniflora* stem density due to reported controls over *S. alterniflora* production (Silliman and Zieman 2001, Kiehn and Morris 2009); and (4) shell repair frequency will decrease with distance from the marsh edge and exhibit thicker aperture ridges in regions with higher shell scarring frequencies (Moody and Aronson 2012).

METHODS

Sampling regions and design

Five study regions spanning the southeastern Louisiana Coast between the Atchafalaya and

Mississippi rivers were sampled between June and September of 2016 (Fig. 1). From west to east, we sampled Old Oyster Bayou (OB) near Fourleague Bay in September, Cocodrie (CO) near the Louisiana Universities Marine Consortium (LUMCON) DeFelice Marine Center facility in June, the Bay LaFleur/Lake Barre region of Terrebonne Bay (TB) in June, Port Fourchon (PF) north of the LUMCON laboratory in August, and the Bay Batiste/Bay Sansbois region in the east of Barataria Bay (EB) in August (Table 1). *Spartina alterniflora* is the dominant vegetation in all regions, but *Juncus roemerianus*, *Distichlis spicata*, and *Spartina patens* are also often present. *Spartina alterniflora* is preferred by the periwinkle, but it can be found on all four vegetation types (Alexander 1979). Two other snail species, eastern melampus (*Melampus bidentatus*), and *Neritina usnea* are found at much lower densities in our study regions.

Within in each region, 50 m marsh edge-to-interior transects were established at three sites where only *S. alterniflora* would be sampled and

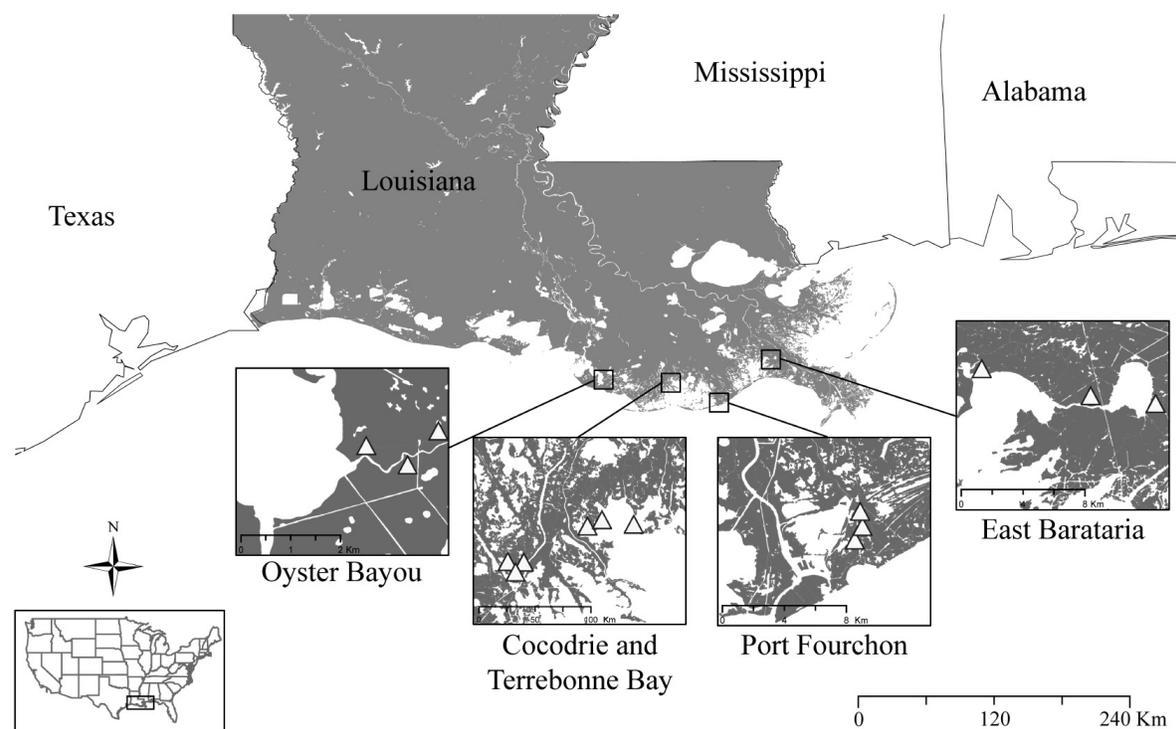


Fig. 1. Locations of the regions and sites within regions that were sampled in southeastern Louisiana. Site coordinates given in Table 2.

Table 1. Site coordinates and environmental variables measured at each region and distance from edge transect ($n = 2$ at each distance from edge point for water depth and *S. alterniflora* stem density; $n = 20$ for each distance from edge point for *S. alterniflora* height).

Region	Site	Latitude	Longitude	Water depth (cm)	<i>S. alterniflora</i> stems		<i>S. alterniflora</i> leaves	
					Height (cm)	Density (m^{-2})	C (%)	N (%)
Oyster Bayou	1	29°15'21.45" N	91°6'42.21" W	3.7 ± 1.1	76.7 ± 2.0	23.0 ± 0.8	43.8 ± 0.3	0.8 ± 0.1
	2	29°15'37.19" N	91°6'14.97" W	5.3 ± 1.2	80.2 ± 3.9	21.4 ± 2.1	44.8 ± 0.3	1.2 ± 0.1
	3	29°15'46.73" N	91°5'42.27" W	5.8 ± 1.0	81.6 ± 3.5	23.4 ± 3.2	45.3 ± 0.5	0.8 ± 0.1
	Mean			4.9 ± 0.9	79.5 ± 1.8	22.6 ± 1.3	44.6 ± 0.3	1.0 ± 0.1
Cocodrie	1	29°15'19.13" N	90°39'52.99" W	15.3 ± 1.6	83.2 ± 2.8	21.8 ± 2.5	44.6 ± 0.2	1.2 ± 0.1
	2	29°15'21.38" N	90°40'5.02" W	17.4 ± 1.2	84.2 ± 3.1	20.4 ± 2.4	44.2 ± 0.4	1.3 ± 0.03
	3	29°15'28.92" N	90°39'41.22" W	17.9 ± 3.1	79.8 ± 2.7	24.0 ± 2.2	44.0 ± 0.4	1.4 ± 0.1
	Mean			16.9 ± 0.9	82.4 ± 1.6	22.1 ± 1.3	44.2 ± 0.2	1.3 ± 0.04
Terrebonne Bay	1	29°17'35.17" N	90°36'17.29" W	20.3 ± 2.5	77.3 ± 1.8	21.8 ± 2.7	44.4 ± 0.4	1.6 ± 0.1
	2	29°17'29.27" N	90°36'10.89" W	30.2 ± 3.0	70.5 ± 2.9	16.5 ± 1.4	45.2 ± 0.2	1.6 ± 0.1
	3	29°17'47.02" N	90°33'0.01" W	16.6 ± 4.5	73.4 ± 3.4	22.5 ± 0.8	43.8 ± 0.4	1.4 ± 0.03
	Mean			22.4 ± 1.7	73.7 ± 1.6	20.3 ± 1.1	44.5 ± 0.3	1.6 ± 0.04
Port Fourchon	1	29°8'15.13" N	90°10'37.31" W	22.7 ± 1.6	74.3 ± 1.3	21.3 ± 1.9	44.3 ± 0.3	1.1 ± 0.1
	2	29°8'27.23" N	90°10'30.56" W	24.9 ± 1.2	84.1 ± 2.1	19.8 ± 1.2	44.1 ± 0.2	1.1 ± 0.1
	3	29°8'55.68" N	90°10'28.04" W	21.8 ± 2.0	82.3 ± 1.5	23.0 ± 1.6	44.7 ± 0.3	1.1 ± 0.1
	Mean			23.1 ± 0.7	80.2 ± 1.2	21.4 ± 0.9	44.4 ± 0.2	1.1 ± 0.1
East Barataria	1	29°28'31.65" N	89°51'17.16" W	16.2 ± 2.5	72.2 ± 2.8	16.5 ± 1.4	43.8 ± 0.5	0.8 ± 0.2
	2	29°27'23.75" N	89°47'34.63" W	28.7 ± 2.2	88.7 ± 3.2	18.1 ± 1.3	43.8 ± 0.5	0.7 ± 0.1
	3	29°27'19.90" N	89°45'31.34" W	0	86.1 ± 1.8	20.5 ± 1.4	44.9 ± 0.2	0.8 ± 0.1
	Mean			22.4 ± 1.8	82.4 ± 2.0	18.4 ± 0.8	44.2 ± 0.3	0.8 ± 0.1

Note: Values for water depth, *S. alterniflora* height, and stem density are means ± SE.

the marsh interior sampling point was at least 50 m from major waterbodies on all sides. Along each transect, all snails regardless of species were collected at 1, 10, 20, 30, and 50 m from the marsh edge within two replicate 0.25 × 0.25 m quadrats, kept on ice during transport, and stored at 4°C to await processing, which was completed within 80 h of collection. Within each quadrat, the total number of *S. alterniflora* stems was recorded along with the heights of ten representative stems, mean water depth from five points within the plot, and the third leaf from the top was collected from three *S. alterniflora* plants to determine C and N content. Salinity data were gathered from the Coastwide Reference Monitoring System (CRMS; <https://www.lacoast.gov/crms2/home.aspx>), sites 0326, 0369, 0355, 0164, and 4529, and were averaged for the growing season.

Sample processing

In the laboratory, all snails were rinsed clean and counted, and a series of morphological measurements as illustrated and described by Moody and Aronson (2012; Fig. 1) were made on *Littoraria irrorata* using digital calipers. Briefly, four size

metrics (shell length and width, and aperture length and width) were made along with three measurements of ridge thickness (anterior, central, and posterior) which were averaged into a single ridge thickness value. For ridge thickness measurements, only periwinkles ≥17 mm in shell length were used, as the labial ridge is only produced late in ontogeny and previous research shows that Gulf of Mexico populations show a threshold for ridge formation at approximately 15 mm in shell length (Moody and Aronson 2012).

Periwinkles were classified based on shell length as either juvenile (<6 mm), sub-adults (6–13 mm), or adults (>13 mm) as in Zengel et al. (2016a). The number of shell repair scars on each snail was also counted as an estimation of predation pressure (Dietl and Alexander 2009). The total number of scars was divided by the number of snails in a given quadrat to yield shell repair frequency. From each quadrat, ten periwinkles representative of all snail sizes within the quadrat were individually wrapped in aluminum foil and dried to constant mass at 80°C and were then ashed in a muffle furnace at 500°C for 4 h to determine AFDM. The remaining periwinkles from the quadrat were

dried and ashed in bulk, and these values were added to the subsample of ten periwinkles to obtain total areal biomass. *Melampus bidentatus* and *N. usnea* snails were dried and ashed in bulk by species per quadrat to obtain areal biomass estimates for each species. Leaves collected from *S. alterniflora* were wrapped in aluminum foil and dried to a constant mass at 80°C, ground to a fine powder, and passed through a 425-micron sieve, and 5 mg of the powder was analyzed for total organic C and total N using a Flash 1112 series elemental analyzer (CE Elantech, Lakewood, New Jersey, USA). We ran concurrent standards (National Institute of Standards and Technology, Buffalo River Sediment, 2704), which yielded C recoveries of $100.3 \pm 0.4\%$.

Statistical analysis

All data analyses were performed in R version 3.3.1 (<https://cran.r-project.org>). Linear regression and ANOVA were used to examine relationships between snail density, biomass, and morphology, and the relationship between these variables and the measured environmental variables (water depth, seasonal salinity from CRMS sites, and *S. alterniflora* parameters [stem height, density, and leaf C:N content]). All variables were checked for meeting the assumptions of normality when appropriate by visual inspection of qq-plots and Shapiro-Wilks tests on residuals, and data were transformed as necessary using either square root or natural log transformations. For instances in which data could not be transformed to meet the assumptions of normality, permutation tests were used, using the package *lmPerm*. The allometric relationship between snail shell length and biomass was modeled using the power law equation $y = kx^a$, where y was equal to individual periwinkle AFDM and x was equal to shell length. To test for differences in allometric relationships between regions, variances of residuals were assessed via Levene's test and inspecting boxplots, and comparisons between regions were made following Herberich et al. (2010) using the *glht* function within the package *multcomp*.

RESULTS

Site characteristics and environmental variables

Mean regional salinities of surface water during June–September 2016 for OB, CO, TB, PF, and EB

were 4.11 ± 0.16 , 2.60 ± 0.09 , 11.69 ± 0.15 , 15.69 ± 0.20 , and 5.78 ± 0.12 psu, respectively (CRMS; <https://www.lacoast.gov/crms2/home.aspx>), sites 0326, 0369, 0355, 0164, and 4529, respectively). Water depth significantly varied by region ($P < 0.001$, $n = 75$), with OB having the lowest water depths (4.9 ± 0.5 cm compared to 21.1 ± 0.7 cm for other regions), but did not vary by distance from edge on the dates of sampling. *Spartina alterniflora* stem density did not differ by region or distance from edge, with a mean (\pm SE) of 334.9 ± 9.2 stems/m². *Spartina alterniflora* height significantly varied by region ($P = 0.036$, $n = 75$) with TB having the shortest stems (72.8 ± 2.5 cm compared to 81.1 ± 0.8 cm across other regions), but did not vary by distance from edge. The percentage C in *S. alterniflora* leaf tissue was not different between regions or distance from marsh edge; however, percentage N significantly varied by region ($P < 0.001$; $n = 75$; Fig. 2) with TB having the highest N content.

Shell repair frequency did not vary by distance from marsh edge, but did vary by region with PF having a mean shell repair frequency ~ 2.5 –5 times higher than other regions (0.36 ± 0.03 compared to 0.07 ± 0.02 , 0.07 ± 0.02 , 0.14 ± 0.03 , and 0.12 ± 0.03 for OB, CO, TB, and EB, respectively). Shell repair frequency was only related to water depth regardless of region ($P < 0.001$, $n = 75$) where repair frequencies increased in deeper waters. A positive relationship between shell repair frequency and % N in *S. alterniflora* leaves was only observed at PF ($r^2 = 0.18$, $P = 0.065$, $n = 15$).

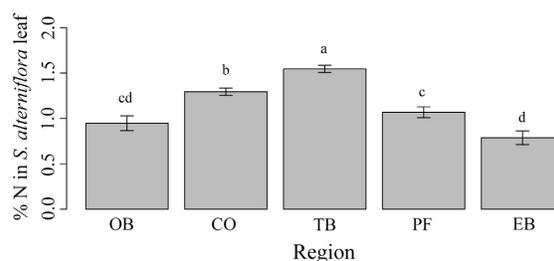


Fig. 2. Percent nitrogen (N) in *Spartina alterniflora* leaf tissue across five regions in southeastern Louisiana, Oyster Bayou (OB), Cocodrie (CO), Terrebonne Bay (TB), Port Fourchon (PF), and East Barataria Bay (EB). Values are means \pm SE, and lowercase letters represent significant differences based on post hoc pairwise comparisons.

Periwinkle distribution

We measured 1614 snails collected from five regions in southeastern Louisiana including 20 juvenile, 107 sub-adult, and 1487 adult snails. Mean (\pm SE) *Littoraria irrorata* density across all regions and marsh distance transects was 172.2 ± 10.4 individuals/m² with a maximum density of 520 individuals/m² recorded 10 m from the marsh edge at TB site 2 and a minimum density of 0 individuals/m² recorded 50 m from the marsh edge at OB site 3. *Littoraria irrorata* density significantly ($P < 0.001$, $n = 75$) varied by region and distance from marsh edge (Fig. 3). Mean densities at OB, CO, TB, PF, and EB were 115.2 ± 17.6 , 172.8 ± 18.4 , 276.3 ± 29.0 , 97.1 ± 13.1 , and 199.5 ± 20.7 individuals/m², respectively, and mean densities across all sites at 1, 10, 20, 30, and 50 m from the marsh edge were 135.5 ± 22.4 , 273.6 ± 25.0 , 185.1 ± 20.3 , 166.9 ± 21.3 , and 99.7 ± 14.8 individuals/m², respectively (Fig. 3). Snail density at TB was significantly ($P < 0.05$) higher than all regions except EB, and density 10 m from the marsh edge was significantly ($P < 0.001$) higher than all other distances (Fig. 3). The pattern of highest snail density at 10 m from the marsh edge was true for all regions

individually except for EB and PF, where densities at 10 m were not different from densities at 20 or 30 m for EB or 20 m at PF.

Periwinkle morphology, biomass, and allometry

Overall mean (\pm SE) individual shell length across all regions and marsh distance transects was 20.5 ± 0.1 mm. The largest snail recorded had a shell length and width of 28.63 and 20.42 mm, respectively, and was collected 20 m from the marsh edge at CO site 3. The smallest snail (4.14 mm in length and 3.18 mm in width) was collected 1 m from the marsh edge at TB site 3. Shell length and width were positively related ($r^2 = 0.93$, $P < 0.001$, $n = 1614$), as were aperture length and width ($r^2 = 0.82$, $P < 0.001$, $n = 1565$). Ridge thickness significantly ($P = 0.003$, $n = 74$) increased with shell repair frequency; however, only ~12% of the variation in ridge thickness was explained by shell repair frequency ($r^2 = 0.12$). Shell lengths and aperture lengths were significantly ($P < 0.001$) different between regions and distance from marsh edge, where TB had the smallest snails and PF the largest, and both shell and aperture lengths were the smallest at 1 m from the marsh edge, with all other distances

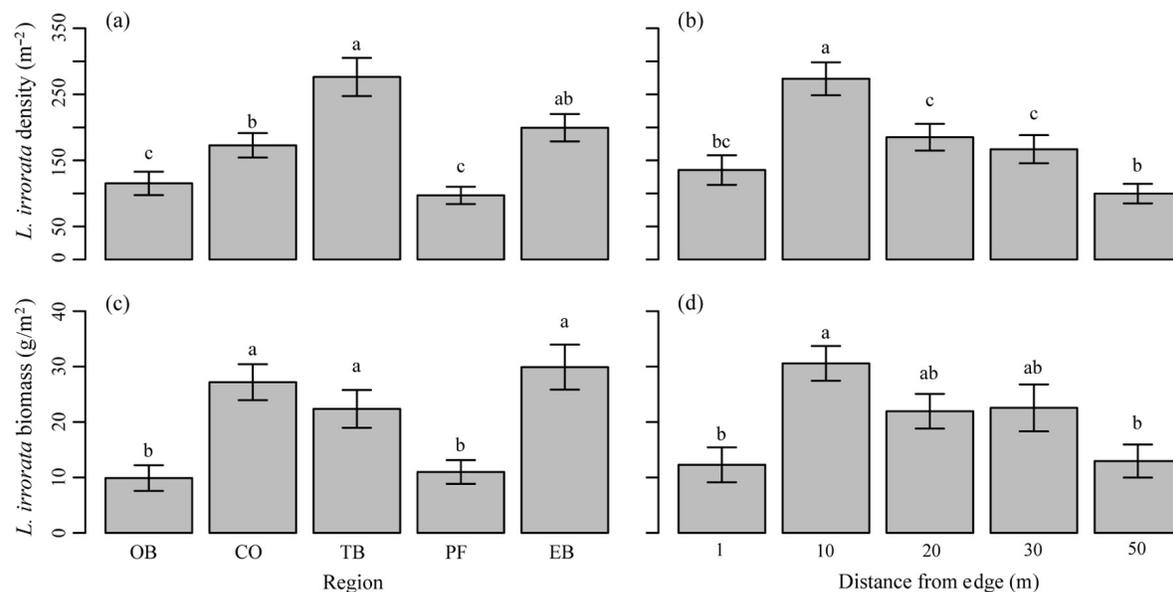


Fig. 3. *Littoraria irrorata* (a) density (m⁻²) and areal biomass (c) across five regions in southeastern Louisiana, Oyster Bayou (OB), Cocodrie (CO), Terrebonne Bay (TB), Port Fourchon (PF), and East Barataria Bay (EB). *Littoraria irrorata* (b) density (m⁻²) and (d) areal biomass across marsh transects with increasing distance (m) from the marsh edge. Values are means \pm SE, and lowercase letters represent significant differences.

from the edge being similar. Aperture ridge thickness differed only by region ($P < 0.001$; Table 2), with the same pattern of TB having the thinnest and PF the thickest aperture ridges. Terrebonne Bay was the only region in which juvenile snails were found (<7 mm shell length, $n = 20$; Fig. 4, Table 2). Similarly, TB had 79% of snails classified as sub-adult (7–13 mm shell length, $n = 85$; Fig. 4) and 28% of adult (>13 mm shell length, $n = 413$; Fig. 4) across the regions (Fig. 3, Table 2). Shell length was not related to percentage N in *S. alterniflora* leaves when all regions were combined, but when analyzed separately, we observed a negative relationship between shell length and percentage N in *S. alterniflora* leaves at PF ($r^2 = 0.48$, $P < 0.001$, $n = 15$).

The maximum individual snail biomass recorded (623 mg) was 20 m from the marsh edge at PF site 2, and the lightest (2 mg) was found at 50 and 1 m from the marsh edge at TB sites 2 and 3, respectively. Oyster Bayou (80 ± 0.002 mg) and TB (70 ± 0.003 mg) had the lowest mean individual biomasses and CO (162 ± 0.002 mg) and EB (132 ± 0.004 mg) had the highest (Fig. 5). We observed a significant ($P = 0.01$) interaction

between region and distance from marsh edge with respect to individual snail biomass ($r^2 = 0.33$, $n = 1080$; Fig. 5). Individual snail biomass was lowest at 1 m, but reached a maximum at different points along the transects in each region (Fig. 5). The relationship between shell length and biomass was significantly different between regions ($P \leq 0.037$, $n = 1082$). Thus, for a given shell length, periwinkle biomass differed by region with CO snails having more biomass and PF snails having less biomass for a given shell length (Fig. 6).

Overall mean (\pm SE) areal biomass was 20.1 ± 1.7 g/m² across all regions and marsh distance transects and varied significantly ($P < 0.001$) by region and distance from marsh edge (Fig. 3). EB and CO had the highest areal biomass (29.9 ± 4.1 and 27.2 ± 3.2 g/m², respectively) and OB and PF the lowest (9.9 ± 2.3 and 11.0 ± 2.1 g/m², respectively). Across all regions, areal biomass was significantly ($P < 0.01$) higher at 10 m, but did not differ from 20 or 30 m from the marsh edge (Fig. 3), a pattern which is also apparent within each region individually.

Littoraria irrorata density and areal biomass were significantly ($P < 0.001$) positively related

Table 2. Body size metrics for *Littoraria irrorata* by region and site.

		<i>Littoraria irrorata</i> shell metrics (mm)						
Region	Site	Shell length	Shell width	Aperture length	Aperture width	Posterior ridge thickness	Central ridge thickness	Anterior ridge thickness
Cocodrie	1	22.04 \pm 0.22	16.16 \pm 0.15	7.42 \pm 0.07	5.40 \pm 0.09	1.86 \pm 0.02	1.45 \pm 0.02	1.52 \pm 0.03
	2	22.51 \pm 0.24	16.88 \pm 0.16	8.16 \pm 0.06	6.57 \pm 0.08	1.92 \pm 0.02	1.46 \pm 0.02	1.61 \pm 0.03
	3	23.32 \pm 0.13	17.58 \pm 0.09	8.50 \pm 0.06	6.93 \pm 0.10	1.95 \pm 0.05	1.50 \pm 0.02	1.65 \pm 0.03
	Mean	22.57 \pm 0.12	16.81 \pm 0.09	7.97 \pm 0.05	6.22 \pm 0.06	1.90 \pm 0.01	1.47 \pm 0.01	1.59 \pm 0.02
East Barataria	1	20.96 \pm 0.18	15.93 \pm 0.14	7.75 \pm 0.05	6.81 \pm 0.05	1.78 \pm 0.02	1.33 \pm 0.01	1.67 \pm 0.02
	2	21.81 \pm 0.16	16.72 \pm 0.11	8.16 \pm 0.04	7.24 \pm 0.04	1.90 \pm 0.02	1.43 \pm 0.01	2.02 \pm 0.02
	3	22.11 \pm 0.16	16.50 \pm 0.10	8.17 \pm 0.05	7.18 \pm 0.05	1.82 \pm 0.02	1.39 \pm 0.02	1.99 \pm 0.02
	Mean	21.51 \pm 0.11	16.34 \pm 0.08	7.99 \pm 0.03	7.05 \pm 0.03	1.83 \pm 0.01	1.38 \pm 0.01	1.87 \pm 0.01
Oyster Bayou	1	20.31 \pm 0.33	15.48 \pm 0.24	8.13 \pm 0.05	7.26 \pm 0.04	1.76 \pm 0.02	1.29 \pm 0.02	1.85 \pm 0.02
	2	20.33 \pm 0.26	15.53 \pm 0.19	8.12 \pm 0.06	7.10 \pm 0.05	1.69 \pm 0.02	1.31 \pm 0.02	1.68 \pm 0.03
	3	21.97 \pm 0.29	16.75 \pm 0.22	8.46 \pm 0.06	7.54 \pm 0.06	1.79 \pm 0.03	1.38 \pm 0.02	1.87 \pm 0.03
	Mean	20.63 \pm 0.19	15.74 \pm 0.14	8.19 \pm 0.03	7.26 \pm 0.03	1.74 \pm 0.01	1.32 \pm 0.01	1.79 \pm 0.01
Port Fourchon	1	22.98 \pm 0.28	16.94 \pm 0.18	8.26 \pm 0.08	7.16 \pm 0.06	2.25 \pm 0.12	1.62 \pm 0.02	2.12 \pm 0.02
	2	24.60 \pm 0.26	17.80 \pm 0.16	8.68 \pm 0.09	7.47 \pm 0.08	2.20 \pm 0.02	1.71 \pm 0.02	2.14 \pm 0.03
	3	22.01 \pm 0.45	16.31 \pm 0.30	8.03 \pm 0.12	6.99 \pm 0.10	2.07 \pm 0.03	1.63 \pm 0.03	2.16 \pm 0.02
	Mean	23.31 \pm 0.20	17.09 \pm 0.12	8.36 \pm 0.06	7.23 \pm 0.05	2.19 \pm 0.05	1.66 \pm 0.01	2.14 \pm 0.01
Terrebonne Bay	1	17.98 \pm 0.37	13.71 \pm 0.27	7.00 \pm 0.09	5.56 \pm 0.09	1.80 \pm 0.03	1.44 \pm 0.02	1.71 \pm 0.02
	2	17.80 \pm 0.27	13.64 \pm 0.20	6.29 \pm 0.10	4.40 \pm 0.08	1.69 \pm 0.02	1.27 \pm 0.02	1.29 \pm 0.03
	3	16.09 \pm 0.44	12.37 \pm 0.34	5.91 \pm 0.16	4.63 \pm 0.16	1.69 \pm 0.02	1.26 \pm 0.02	1.51 \pm 0.03
	Mean	17.32 \pm 0.21	13.27 \pm 0.16	6.37 \pm 0.07	4.97 \pm 0.07	1.72 \pm 0.01	1.32 \pm 0.01	1.48 \pm 0.02

Note: Values are means \pm SE of five distance points from the marsh edge with two replicates each ($n = 10$).

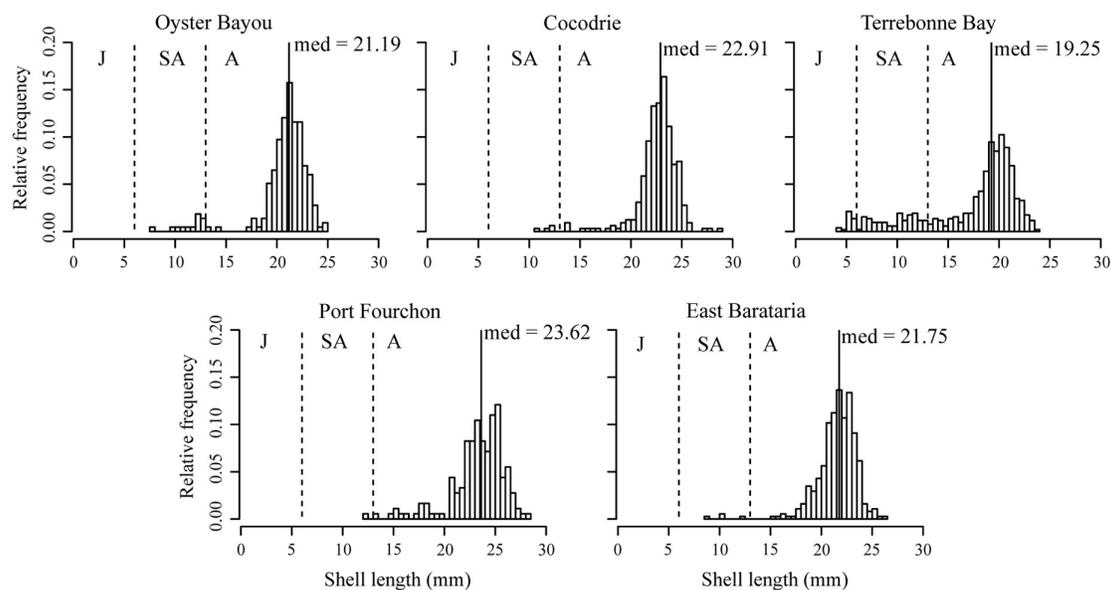


Fig. 4. *Littoraria irrorata* size class (mm) distribution for juvenile (J), sub-adult (SA), and adult (A) periwinkles across five regions in southeastern Louisiana (Oyster Bayou, Cocodrie, Terrebonne Bay, Port Fourchon, and East Barataria Bay). Vertical dashed lines represent cut offs for size classes, and vertical solid lines represent median values for each region.

for all regions ($r^2 = 0.96, 0.91, 0.72, 0.85,$ and 0.76 for OB, CO, TB, PF, and EB, respectively). *Littoraria irrorata* density had a significant negative relationship with *S. alterniflora* height ($P < 0.01$)

and a positive relationship with water depth ($P < 0.001$), but each only explained $\sim 14\%$ of the variation in density ($n = 74$). There was no relationship between *S. alterniflora* stem density and

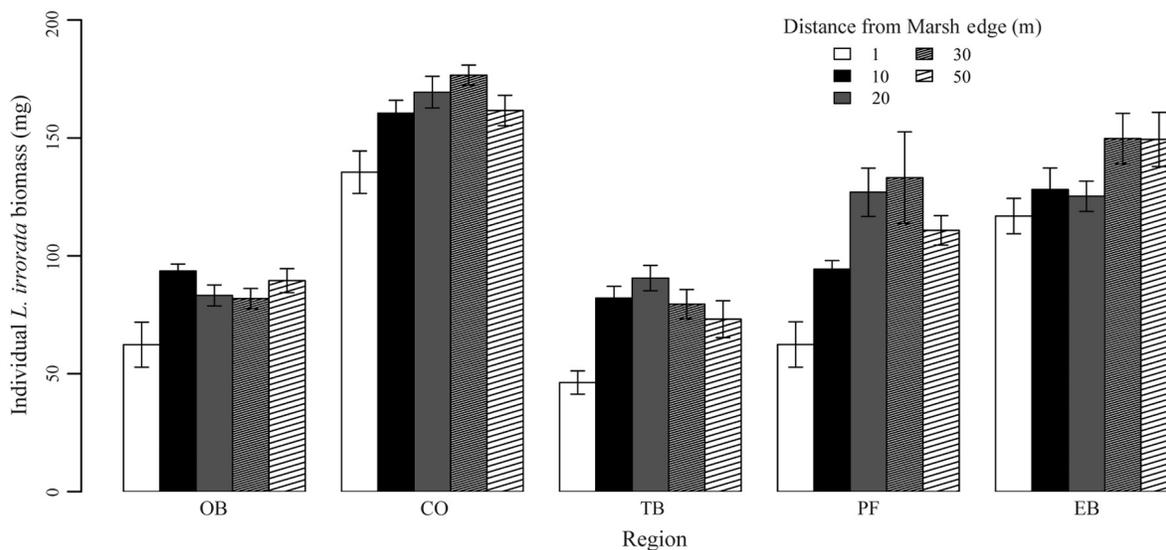


Fig. 5. Individual *Littoraria irrorata* biomass (mg) values across five regions in southeastern Louisiana, Oyster Bayou (OB), Cocodrie (CO), Terrebonne Bay (TB), Port Fourchon (PF), and East Barataria Bay (EB) with different bars representing different distances (m) from the marsh edge. Values are means \pm SE.

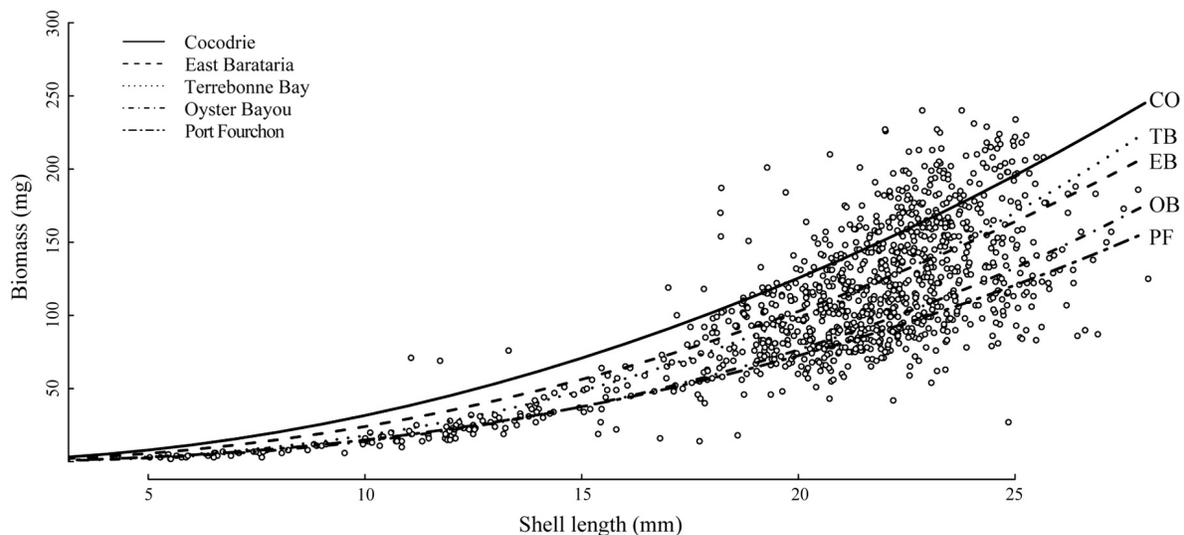


Fig. 6. Allometric relationships between shell length (mm) and biomass (mg) for *Littoraria irrorata* across five regions in southeastern Louisiana (Oyster Bayou, Cocodrie (CO), Terrebonne Bay (TB), Port Fourchon (PF), and East Barataria Bay). The allometric equations for each line are given in Table 2. The solid line represents CO; short dashed line, East Barataria; dotted line, TB; alternating dot-dashed line, Oyster Bayou; and alternating long-short dashed line, PF.

periwinkle density. Periwinkle density tended to increase with percentage N in *S. alterniflora* leaves across all samples, though this relationship was not significant ($P = 0.06$). However, when looking at regions separately, there was a significant negative relationship within the PF region ($r^2 = 0.32$, $P < 0.01$, $n = 15$), but no significant relationship in other regions ($P > 0.05$). When examining all regions together without PF ($n = 60$), we see a significant ($P = 0.04$), positive relationship where higher densities corresponded to higher N content; however, this only explains 5% of the variation.

Other snail species

The other snail species found in this study, *Melampus bidentatus* and *Neritina usnea*, were found at much lower densities than *L. irrorata*. Densities of *M. bidentatus* were significantly different between regions and distance from edge ($P = 0.02$, $n = 75$), with densities for OB, CO, TB, PF, and EB being 0 , 9.1 ± 3.6 , 4.3 ± 2.5 , 0 , and 11.2 ± 3.1 individuals/m², respectively. Densities of *M. bidentatus* were significantly lower at 20 m than at other distances from the marsh edge. Densities of *N. usnea* were only different by region ($P < 0.001$, $n = 75$), with densities for OB, CO, TB, PF, and EB

being 0.5 ± 0.5 , 0.5 ± 0.5 , 13.3 ± 5.8 , 1.1 ± 1.1 , and 3.7 ± 2.7 individuals/m², respectively.

DISCUSSION

Coastal Louisiana periwinkle densities based on our study (overall mean 172 ± 10 individuals/m²) may be higher than at other marshes along the Gulf and Atlantic coasts (most studies <100 individuals/m²; Table 3), with the possible exception of Sapelo Island, Georgia, USA, where densities up to 558 individuals/m² have been reported (Silliman and Bertness 2002, Silliman et al. 2005, McFarlin et al. 2015). Periwinkle densities did show differences based on marsh position and areal biomass closely tracked density, with densities being higher at 10 m and biomass peaking 10–30 m from the marsh edge across all regions. However, none of the variables we measured seemed to explain this within marsh distribution. While we initially expected a mid-marsh peak in density due to marsh edge predation pressures, shell repair frequency did not vary by marsh position. It is possible that our measure of predation was not accurate enough, being as we only measured unsuccessful predation that leaves behind shell scars. Some regions or marsh

Table 3. Studies reporting densities (ind./m²) of *Littoraria irrorata* within unimpacted marshes along U.S. Atlantic and Gulf of Mexico coasts.

Location	Snail density (m ⁻²)	Sources
Barataria Bay, LA	19 ± 4 to 190 ± 40	Alexander (1979), Spicer (2007), Silliman et al. (2012), Zengel et al. (2016a, b)
Port Fourchon, LA	27 ± 10 to 82 ± 12.6	Silliman et al. (2005), McFarlin et al. (2015)
Sabine NWR, LA to Bay St. Louis, MS	50 ± 25 to 75 ± 40	McCall and Pennings (2012)
Bayou Lafourche, LA	34 ± 29 to 133 ± 17	Stagg and Mendelssohn (2012), Tong et al. (2013)
Dauphin Island, AL	65.3 ± 12.3 to 144.8 ± 31.6	West and Williams (1986)
Wakulla Beach, FL	450	Warren (1985)
Sapelo Island, GA	145 ± 55 to 558 ± 121	Silliman and Bertness (2002), Silliman et al. (2005), McFarlin et al. (2015)
Ossabaw Island, GA	78 ± 17	Silliman et al. (2005)
Bryan County, GA	1.4 ± 0.8	Silliman et al. (2005)
Talahi Island, GA	68 ± 11	Silliman et al. (2005)
Lighthouse Marsh, GA	22–44	Schindler et al. (1994)
Dean Creek, GA	52–66	Schindler et al. (1994)
North End Marsh, GA	52	Schindler et al. (1994)
Bell Baruch, SC	49 ± 15 to 56 ± 17	Silliman et al. (2005)
Hog Inlet, SC	18–85	Hutchens and Walter (2006)
North Inlet, SC	36–74	Hutchens and Walter (2006)
Murrells Inlet, SC	31–115	Hutchens and Walter (2006)
Charleston, SC	96 ± 37	Silliman et al. (2005)
Kiawah Island, SC	42	Tucker et al. (1995)
Calico Creek, NC	19.8 ± 6.3 to 80	Stiven and Hunter (1976), Stiven and Kuenzler (1979)
Tar Landing Marsh, NC	11.3 ± 2.6 to 18.6 ± 4.5	Stiven and Kuenzler (1979)
Causeway Marsh, NC	0.4 ± 0.2 to 2.3 ± 0.9	Stiven and Kuenzler (1979)
Ft. Macon, NC	40	Stiven and Hunter (1976)
Russell's Creek, NC	60	Stiven and Hunter (1976)
Walden Creek, NC	33	Cammen et al. (1980)
Wallops Island, VA	12.1–14.2	Crist and Banta (1983)
Hog Island, VA	48	Silliman and Zieman (2001)

Note: Values are means ± SE or ranges when available.

positions may simply have a higher incidence of successful predation. Additionally, density relationships were not explained by *Spartina alterniflora* density or height, as has been observed in other studies (Kiehn and Morris 2009).

Periwinkle density increased with distance from the Atchafalaya River to a peak in the TB region and was again lower in two regions of Barataria Bay (PF and EB) that were closer to the Mississippi River. This general pattern is similar to that of *S. alterniflora* leaf N content where sites nearest to the two rivers had the lowest N content and the furthest from either river (TB) had the highest N content. Periwinkle density tended to increase with percentage N in *S. alterniflora* leaf tissue except in PF, where periwinkle density decreased as percentage N increased. This differing relationship and lower densities at PF appear to be related to predation, where we observed repair frequencies three to five times higher and

aperture ridges that were 14–24% thicker than in other regions. Similar to density, PF shell lengths decreased with increasing percentage N, but shell repair frequency increased. Taken together, these data are consistent with predation pressure being the main factor shaping the observed differences at PF compared to other regions. Generally, areas with higher percentage N tended to have more snails, which may indicate preference based on N content as has been found in other studies (Ialeggio and Nyman 2014), but in PF, interactions with predators may be changing this relationship.

The allometric relationship between shell length and biomass varied across southeastern Louisiana with sites nearer the coast (OB and PF) having similar, though still statistically different allometric relationships, and sites situated further inland (TB and East Barataria) having similar relationships. Cocodrie snail allometry was distinct, having more biomass for a given shell length than all

other regions in our study. Cocodrie sites were the most protected and furthest inland, which is consistent with the idea that periwinkle morphology responds to differing environmental pressures across the region. Interestingly, regional salinities alone do not explain observed differences in allometry. To test our models, we applied our regional equations (Table 4) to periwinkles that were measured and then dried and ashed in bulk, rather than individually. We found that in four out of five regions (OB, TB, PF, and EB), our models underestimated actual biomass values by between 7% and 35%, and in the last region (CO), our models overestimated biomass by 13%. The two regions in which our models performed the best were OB and TB where calculated biomass values underestimated actual values by 7% and 8%, respectively. At EB, our regional model performed the worst, where calculated values underestimated actual measured biomass values by 35%, likely due to EB having less diversity in periwinkle sizes than in other regions (Fig. 4), which can skew our derived models toward a certain size of periwinkle.

Predation pressures could be playing a role in these observed morphological differences. At PF, periwinkles of a given shell length weigh less than in other regions, which could be a response to long-standing predation pressures where investing in appearing larger may increase survival (Schindler et al. 1994). Indeed, PF had some of the largest shells we found in this study, but these snails had less biomass. Essentially, with increased predation pressure, periwinkles appear to devote more resources into building larger shells with thicker apertures and less into

biomass. The region most similar to PF in terms of allometry was OB; however, there we saw low shell repair frequencies. Shell repair frequencies at OB decreased in an inland direction away from Fourleague Bay, indicating higher predation rates closer to open waters. Due to our site selection, we may have failed to capture an accurate representation of predation at OB, which likely displays higher predation pressures along the edge of the bay than in channels as crab abundance in the bay would be expected to be higher than in a channel. Furthermore, shell repair frequencies were lowest at CO where snail shells tend to be larger and have more biomass and more intermediate at TB and East Barataria. These data imply that regional predation pressures are shaping periwinkle morphology and seem to be affecting these communities more so than variation in other environmental variables or *S. alterniflora* characteristics. These changes in periwinkle body size could produce spatially localized cascading effects in terms of *S. alterniflora* production and energy flow through marshes (Cammen et al. 1980, Silliman and Zieman 2001).

The fact that periwinkle allometry varies across the coast could pose a problem for studies that wish to apply such relationships to organisms from differing areas. For example, Stagg and Mendelsohn (2012) estimated biomass from shell length using a linear model derived from a log-linear regression of shell length and biomass. Their calculation of $273.3 \pm 209.5 \text{ g/m}^2$ with a density of only 133 ± 17 individuals/ m^2 is the highest reported areal biomass for this species. To put this in perspective, the largest areal biomass value found in our study was 57.61 g/m^2 that corresponded to a density of 248 individuals/ m^2 in East Barataria. It is possible that periwinkles gathered for equation calibration in Stagg and Mendelsohn (2012) exhibited different growth patterns and environmental pressures than the snails measured to estimate biomass; however, this is unknown. To further illustrate the degree to which allometric relationships differ regionally, we applied models derived from our two most different regions (CO and PF; Fig. 6) to one another. When the PF allometric model was applied to CO periwinkles, this underestimated actual biomass by 32%, and when CO models were applied to PF, values were overestimated by 42%.

Table 4. Allometric equations and range in shell lengths for five regions in southeastern Louisiana depicted in Fig. 6.

Region	Range in shell lengths (mm)	Equation	<i>n</i>
Oyster Bayou	7.62–24.61	$y = 4.77 \times 10^{-5} x^{2.46}$	173
Cocodrie	10.72–27.84	$y = 3.24 \times 10^{-4} x^{1.99}$	237
Terrebonne Bay	4.30–23.55	$y = 6.19 \times 10^{-5} x^{2.46}$	274
Port Fourchon	12.45–28.07	$y = 7.72 \times 10^{-5} x^{2.28}$	164
East Barataria	8.82–26.40	$y = 1.93 \times 10^{-4} x^{2.10}$	235

Note: Equations are of the form $y = kx^a$, where y = biomass (g) and x = shell length (mm).

Summary

In summary, we found that *Littoraria irrorata* density, allometry, and areal biomass exhibit strong regional and spatial patterns; however, general periwinkle morphology was much less variable between regions and along our marsh transects. We found a mid-marsh peak in density and areal biomass; however, these patterns did not relate to shell repair frequency. Our data indicate that predation pressure may influence periwinkle shell morphometry in multiple ways, as well as their distributions, in that periwinkles tend to put more resources into appearing larger where predation is likely higher and to aggregate away from areas expected to have higher predation rates near the marsh edge. Previous research would suggest that areas with more snails would correspond to higher densities of short *S. alterniflora* stems (e.g., Silliman and Zieman 2001, Kiehn and Morris 2009); however, we did not find this relationship. We observed a weak relationship between periwinkle density and percentage N in *S. alterniflora*, but found that this relationship can change for a given region (e.g., PF) based on predation pressure. Lastly, we observed an increase in periwinkle ridge thickness with higher predation pressure across regions; however, shell scarring and ridge thickness values did not exhibit spatial patterns along our marsh transects. Our findings show regional and spatial differences in snail densities, biomass, and allometry, and cautions against making generalizations about this species across geographic regions. Since the general ecology of this species is less understood than its impacts on marsh productivity, we encourage more researchers to examine patterns in *L. irrorata* morphology, density, and biomass along the Gulf and Atlantic coasts of the United States in order for us to better understand the ecological drivers of salt marsh periwinkle distribution and morphology.

ACKNOWLEDGMENTS

We thank Ariella Chelsky, Nicole Farley, David Klings, and Ronald Scheuermann for their help with sample collection and processing. This research was made possible by a grant from The Gulf of Mexico Research Initiative to the Coastal Waters Consortium. The funders had no role in the design, execution, or analyses of this project. Data are publicly available

through the Gulf of Mexico Research Initiative Information & Data Cooperative (GRIIDC) at <https://data.gulfresearchinitiative.org> (DOIs: <https://doi.org/10.7266/N7GQ6W4T> and <https://doi.org/10.7266/N779432B>).

LITERATURE CITED

- Alexander, S. K. 1979. Diet of the periwinkle *Littorina irrorata* in a Louisiana salt marsh. *Gulf Research Reports* 6:293–295.
- Cammen, L. M., E. D. Seneca, and L. M. Stroud. 1980. Energy flow through the fiddler crabs *Uca pugnax* and *U. minax* and the marsh periwinkle *Littorina irrorata* in a North Carolina salt marsh. *American Midland Naturalist* 103:238–250.
- Crist, R. W., and W. C. Banta. 1983. Distribution of the marsh periwinkle *Littorina irrorata* (Say) in a Virginia salt marsh. *Gulf Research Reports* 7:225–235.
- Dietl, G. P., and R. R. Alexander. 2009. Patterns of unsuccessful shell-crushing predation along a tidal gradient in two geographically separated salt marshes. *Marine Ecology* 30:116–124.
- Graça, M. A., S. Y. Newell, and R. T. Kneib. 2000. Grazing rates of organic matter and living fungal biomass of decaying *Spartina alterniflora* by three species of salt-marsh invertebrate. *Marine Biology* 136:281–289.
- Hamilton, P. V. 1978. Intertidal distribution and long-term movements of *Littorina irrorata* (Mollusca: Gastropoda). *Marine Biology* 46:49–58.
- Henry, R. P., C. J. McBride, and A. H. Williams. 1993. Responses of the marsh periwinkle, *Littoraria (Littorina) irrorata* to temperature, salinity and desiccation, and the potential physiological relationship to climbing behavior. *Marine and Freshwater Behavior and Physiology* 24:45–54.
- Herberich, E., J. Sikorski, and T. Hothorn. 2010. A robust procedure for comparing multiple means under heteroscedasticity in unbalanced designs. *PLoS ONE* 5:e9788.
- Hutchens, J. J., and K. Walter. 2006. Gastropod abundance and biomass relationships with salt marsh vegetation within ocean-dominated South Carolina, USA estuaries. *Journal of Shellfish Research* 25:947–953.
- Ialeggio, J. S., and J. A. Nyman. 2014. Nutria grazing preference as a function of fertilization. *Wetlands* 34:1039–1045.
- Kiehn, W. M., and J. T. Morris. 2009. Relationships between *Spartina alterniflora* and *Littoraria irrorata* in a South Carolina salt marsh. *Wetlands* 29:818–825.
- McCall, B. D., and S. C. Pennings. 2012. Disturbance and recovery of salt marsh arthropod communities following BP Deepwater Horizon oil spill. *PLoS ONE* 7:e32735.

- McFarlin, C. R., T. D. Bishop, M. W. Hester, and M. Alber. 2015. Context dependent effects of the loss of *Spartina alterniflora* on salt marsh invertebrate communities. *Estuarine, Coastal and Shelf Science* 163:218–230.
- Moody, R. M., and R. B. Aronson. 2007. Trophic heterogeneity in salt marshes of the northern Gulf of Mexico. *Marine Ecology Progress Series* 331:49–65.
- Moody, R. M., and R. B. Aronson. 2012. Predator-induced defenses in a salt-marsh gastropod. *Journal of Experimental Marine Biology and Ecology* 413:78–86.
- Newell, S. Y. 1993. Decomposition of shoots of a salt-marsh grass. *Advances in Microbial Ecology*. Springer, Boston, Massachusetts, USA.
- Newell, S. Y., and F. Barlocher. 1993. Removal of fungal and total organic matter from decaying cord-grasses by shredder snails. *Journal of Experimental Marine Biology and Ecology* 171:39–49.
- Newell, S. Y., R. D. Fallon, and J. D. Miller. 1989. Decomposition and microbial dynamics for standing, naturally positioned leaves of a salt marsh cordgrass: *Spartina alterniflora*. *Marine Biology* 101:471–481.
- Rietl, A. J., J. A. Nyman, C. W. Lindau, and C. R. Jackson. 2017. Gulf ribbed mussels (*Geukensia granosissima*) increase methane emissions from a coastal *Spartina alterniflora* marsh. *Estuaries and Coasts* 40:832–841.
- Schindler, D. E., B. M. Johnson, N. A. MacKay, N. Bouwes, and J. F. Kitchell. 1994. Crab: snail size-structured interactions and salt marsh predation gradients. *Oecologia* 97:49–61.
- Silliman, B. R., and M. D. Bertness. 2002. A Trophic cascade regulates salt marsh primary production. *Proceedings of the National Academy of Sciences of the United States of America* 99:10500–10505.
- Silliman, B. R., J. van de Koppel, M. D. Bertness, L. E. Stanton, and I. A. Mendelssohn. 2005. Drought, snails, and large-scale die-off of southern U.S. salt marshes. *Science* 310:1803–1806.
- Silliman, B. R., J. van de Koppel, M. W. McCoy, J. Diller, G. N. Kasozi, K. Earl, P. N. Adamn, and A. R. Zimmerman. 2012. Degradation and resilience in Louisiana salt marshes after the BP Deepwater Horizon oil Spill. *Proceedings of the National Academy of Sciences of the United States of America* 109:11234–11239.
- Silliman, B. R., and J. C. Zieman. 2001. Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia salt marsh. *Ecology* 82:2830–2845.
- Spicer, J. A. 2007. Comparison of channel morphology, marsh elevation, and biological processes in natural and dredged tidal salt marshes in Louisiana. Dissertation. Louisiana State University, Baton Rouge, Louisiana, USA.
- Stafford, E. S., C. L. Tyler, and L. R. Leighton. 2014. Gastropod shell repair tracks predator abundance. *Marine Ecology* 36:1176–1184.
- Stagg, C. L., and I. A. Mendelssohn. 2012. *Littoraria irrorata* growth and survival in a sediment-restored salt marsh. *Wetlands* 32:643–652.
- Stiven, A. E., and J. T. Hunter. 1976. Growth and mortality of *Littorina irrorata* Say in three North Carolina marshes. *Chesapeake Science* 17:168–176.
- Stiven, A. E., and E. J. Kuenzler. 1979. The response of two salt marsh molluscs, *Littorina irrorata* and *Geukensia demissa*, to field manipulations of density and *Spartina* litter. *Ecological Monographs* 49:151–171.
- Sullivan, M. J., and C. A. Moncreiff. 1990. Edaphic algae are an important component of salt marsh food-webs: evidence from multiple stable isotope analysis. *Marine Ecology Progress Series* 62:149–159.
- Tong, C., J. J. Baustian, S. A. Graham, and I. A. Mendelssohn. 2013. Salt marsh restoration with sediment-slurry application: effects on benthic macroinvertebrates and associated soil-plant variables. *Ecological Engineering* 51:151–160.
- Tucker, A. D., N. N. FitzSimmons, and J. W. Gibbons. 1995. Resource partitioning by the estuarine sea turtle *Malaclemys terrapin*: trophic, spatial, and temporal foraging constraints. *Herpetologica* 51:167–181.
- 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* (Rathburn) within *Spartina alterniflora* (Loisel) marshes. *Journal of Experimental Marine Biology and Ecology* 100:75–95.
- Williams, A. H., and A. G. Appel. 1989. Behavioral thermoregulation in *Littorina irrorata* by climbing. *Marine and Freshwater Behaviour and Phy* 16:31–41.
- Zengel, S., et al. 2016a. Impacts of the Deepwater Horizon oil spill on salt marsh periwinkles (*Littoraria irrorata*). *Environmental Science and Technology* 50:643–652.
- Zengel, S., et al. 2016b. Five years of Deepwater Horizon oil spill effects on marsh periwinkles *Littoraria irrorata*. *Marine Ecology Progress Series*. <https://doi.org/10.3354/meps11827>