Ecological associations of *Littoraria irrorata* with *Spartina cynosuroides* and *Spartina alterniflora*

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Abstract

It is well-documented that marsh periwinkles (*Littoraria irrorata*) consume and inhabit smooth cordgrass (*Spartina alterniflora*), but their interactions with big cordgrass (*Spartina cynosuroides*) remain unknown. Plant communities in mesohaline marshes will change as sea-level rise shifts species from salt-intolerant (e.g., *S. cynosuroides*) plants to salt-tolerant (e.g., *S. alterniflora*) ones. Therefore, understanding how *L. irrorata* interacts with different habitats provides insight into this species' generalist nature and allows us to predict the potential impacts of changing plant communities on *L. irrorata*. We show, for the first time, that *L. irrorata* inhabits, climbs, and grazes *S. cynosuroides*. We compared both habitats and found snails were larger, plant tissue was tougher, and sediment surface temperatures were higher in *S. alterniflora* than *S. cynosuroides*. Snails had greater survivorship from predators in *S. cynosuroides* than in *S. alterniflora*. Further, snails grazed *S. cynosuroides* more than *S. alterniflora*, evidenced by a greater number of radulation scars. Despite these differences, snail densities were equal between habitats suggesting functional redundancy between *S. cynosuroides* and *S. alterniflora* for *L. irrorata.* Our results indicate *L. irrorata* is a habitat generalist that uses both *S. alterniflora* and *S. cynosuroides*, which may allow it to gain an ecological foothold as sea-level rises.

Keywords: brackish marsh, mesohaline marsh, salt marsh, ecological equivalence, sea level rise

Introduction

Tidal marshes cover approximately 45,000 km^2 globally (Greenberg et al. 2006) and contribute ecologically and economically to human well-being by providing erosion and flood control, recreation, improved water quality, carbon sequestration, and nursery habitat for commercially important fishes and invertebrates (Boesch et al. 2000; Beck et al. 2001; Shepard et al. 2011). There are 16,000 km^2 of tidal marshes in North America alone, with high concentrations on the South Atlantic coast and Gulf of Mexico (Greenberg et al. 2006). The Chesapeake Bay in the United States contains an estimated 1,240 km^2 of tidal marshes, with brackish marshes making up one-third of this area (Stevenson et al. 2000). A mesohaline marsh is a type of estuarine brackish marsh where saline and fresh waters mix, leading to salinities between 5 and 18 ppt on average (Odum 1988). Despite their abundance, mesohaline marshes are relatively understudied compared to their polyhaline counterparts (i.e., salt marshes, 18-30 ppt), especially regarding their flora and fauna.

Mesohaline marshes tend to have higher plant diversity than that of polyhaline marshes (Odum 1988) because a greater abundance of vascular plant species can tolerate lower salinities (Anderson et al. 1968; Wass and Wright 1969; Perry and Atkinson 1997). On the Atlantic coast of the United States, the lowest elevations of mesohaline marshes are dominated by two co-occuring species: the smooth cordgrass, *Spartina alterniflora*, and the big cordgrass, *Spartina cynosuroides*. Both species have similar growth forms, with leaves growing from a single tall stem (culm) and rhizamatous belowground biomass (Silberhorn 1992; McHugh and Dighton 2004). However, in the Chesapeake Bay region, *S. cynosuroides* ranges from 2 to 4 meters tall, whereas *S. alterniflora* ranges from 1 to 2 meters tall (Silberhorn 1992). Both species are flood tolerant, however *S. alterniflora* has a wider salt tolerance than *S. cynosuroides* (Penfound and

Hathaway 1938). *Spartina alterniflora* commonly dominates polyhaline marsh communities due to its ability to outcompete salt-sensitive species, however it can also thrive in lower salinity marshes (Stribling 1997; White and Alber 2009). In contrast, *S. cynosuroides* prefers oligohaline (0.5-5 ppt) environments but can tolerate freshwater to mesohaline conditions (Odum et al. 1984; Constantin et al. 2019). The co-occurrence of these plant species creates distinct habitat types with qualities that may attract similar fauna to each.

The marsh periwinkle (*Littoraria irrorata*) is an abundant and herbivorous gastropod found in tidal marshes along the Gulf of Mexico and Atlantic coast of the United States. It thrives in salinities ranging from 5 to 30 ppt; however, it can survive shorter periods of time (less than a week) in salinities from 0 to 5 ppt (Crist and Banta 1983; Henry et al. 1993). It is a critical component of saltmarsh food webs (McCann et al. 2017) as prey for fishes and crustaceans (Hamilton 1976) and as a consumer of live and dead *S. alterniflora*, marsh sediment, algae, diatoms, nematodes, foraminifera, ostracods, mites, copepods, and other microorganisms (Alexander 1979). *Littoraria irrorata* climbs plant stems to avoid rising tides and aquatic predators (Warren 1985; Carroll et al. 2018), as well as to cultivate fungus colonies on plant leaves for consumption (Silliman and Zieman 2001; Silliman and Newell 2003). At extraordinarily high densities, this fungal farming by *L. irrorata* can lower aboveground biomass of *S. alterniflora* (Silliman and Zieman 2001). During low tide, some snails move back to the sediment surface to feed and to avoid the threat of desiccation (Bingham 1972).

Littoraria irrorata is frequently studied in polyhaline marshes and therefore associated primarily with *S. alterniflora* (e.g., Hamilton 1976; Silliman and Zieman 2001; Silliman and Newell 2003; Deis et al. 2017; Zengel et al. 2017; Rietl et al. 2018). In the mesohaline marshes of the Chesapeake Bay, we have observed *L. irrorata* in both *S. alterniflora* and *S. cynosuroides* habitats. Here, we document, for the first time to our knowledge, the ecological use of *S. cynosuroides* by *L. irrorata* in a mesohaline marsh. Our goals were to compare the environmental characteristics, predation pressure, palatability of plant tissue, and algal-food availability between *S. alterniflora* and *S. cynosuroides* habitats in relation to *L. irrorata* use. We expected that *L. irrorata* climbed *S. cynosuroides* to avoid predation, similar to its behavior in *S. alterniflora*. However, we hypothesized that *S. alterniflora* was more palatable than *S. cynosuroides*, as the use of *S. alterniflora* as a preferred food source for *L. irrorata* is well-documented (e.g. Hendricks et al. 2011; Sieg et al. 2013). We also expected the difference in plant height between *S. alterniflora* and *S. cynosuroides* to influence the foraging behavior of *L. irrorata*. For example, taller *S. cynosuroides* may limit access to leaves or light penetration to the substrate, thus decreasing benthic diatom growth, an additional food for *L. irrorata* (Alexander 1979).

Methods

Study Site

Our study focused on the mesohaline marsh surrounding Taskinas Creek (37° 24' 54.79" N; 76° 42' 52.74" W; Fig. 1), within the Chesapeake Bay watershed in James City County, Virginia, USA. Access to this York River State Park site was possible through the Chesapeake Bay National Estuarine Research Reserve of Virginia (CBNERR-VA), which maintains marsh monitoring stations within the York River estuary. Taskinas Creek has an average salinity of 6 to 7 ppt (VECOS Database, accessed: July 16, 2019) with a semidiurnal tidal range of 0.85 m on average. The low marsh exists below the mean high-water level and is dominated by distinct, side-by-side, monotypic stands of *S. alterniflora* and *S. cynosuroides*, with *L. irrorata* found in both habitats. The high marsh above the mean high-water level is made up of mostly salt hay (*Spartina patens*) and saltgrass (*Distichlis spicata*).

Snail & Environmental Data

We established two, 20-meter transects one meter from the creek bank, one in a monotypic stand of *S. alterniflora*, and the other in a monotypic stand of *S. cynosuroides*. Along each transect, we haphazardly placed twenty 0.0625 m^2 quadrats (total of forty quadrats) to estimate stem heights and densities. Plant height was measured for all live plants within quadrats and the tallest plant from each quadrat was clipped from the base and stored in a -80°C freezer to await plant trait analysis. The second tallest plant from each quadrat was clipped from the base and processed with a penetrometer immediately for tissue toughness (see below). To evaluate *L. irrorata* densities in *S. alterniflora* and *S. cynosuroides*, thirty 0.0625 m^2 quadrats per habitat (total of sixty quadrats) were haphazardly sampled and all snails within each quadrat were counted. In a separate sampling effort, adult snails were haphazardly collected along each transect within each habitat (*S. alterniflora*, n=184; *S. cynosuroides*, n=128) and measured in the lab for height and width using digital calipers to determine average snail size. Height was measured from the tip of the shell spire to the bottom of the shell aperture. Width was measured diagonally from the widest part of the shell aperture to the body whorl. To assess leaf damage from snail grazing, fifteen 0.0625 m^2 quadrats were haphazardly placed within each habitat type. In each quadrat, five plants were chosen at random to measure heights and to count radulations. In addition, four Onset HOBO pendants were deployed from July 11th to August 6th, 2018 to measure light intensity and temperature in *S. alterniflora* and *S. cynosuroides* habitats, with two pendants per habitat. To estimate benthic algal biomass, a benthic chlorophyll *a* sample was taken to a depth of 3 mm from the sediment surface (volume = 0.29 mL) and placed in a cooler of ice. The samples were then stored in a -80°C freezer to await further processing. Chlorophyll *a* was extracted in 10 mL of 90% acetone for 24 hours and filtered through a 0.45μm Acrodisc with absorbance measured at 630, 647, 664, 665, and 750 nm against a 90% acetone blank (Brush MJ, *personal communication*). An additional acidification step allowed for phaeophytin correction. Chlorophyll *a* concentration was calculated using the following equation where V is the volume of extractant in mL (10 mL), SA is the core area in cm^2 (0.95 cm^2), and L is the light path length in cm (1 cm, UV-1601 Shimadzu UV Visible) (Lorenzen 1967; Jeffrey and Welschmeyer 1997).

$$\text{Chl}_a(\text{mg}\cdot\text{m}^{-2}) = \frac{26.7\ \times(\lambda665 - \lambda665_{\text{acid}})}{(\text{L})}\times\frac{\text{V}}{\text{SA}}\times\frac{1\text{ mg}}{1000\ \mu\text{g}}\times\frac{10000\text{ cm}^2}{1\text{m}^2}$$

Predation Assays

To examine predation pressure between the two habitats and the effect of distance from the creek bank, three predation trials were conducted on successive tides. Each trial consisted of tethers in both habitats positioned 1 m, 2 m, and 3 m from the creek. Each tether consisted of one adult snail attached with super glue to a 15 cm segment of 1.8 kg monofilament fishing line tied to a 30 cm clear plastic rod. For each distance from the creek bank, 8 snails were tethered and separated by at least 0.5 m from each other for a total of 24 snails per habitat. This design allowed us to assess predation pressure in relation to distance from the creek, as predators of *L. irrorata* arrive with the incoming tide. Within the vegetated habitats, each rod was placed near a single plant stem and pushed into the sediment until the tether and snail were flush with the sediment surface. The tether was long enough to allow snails to climb the adjacent plant stem to avoid predation, but short enough that they could not get tangled with any other nearby vegetation. The tethers were deployed at low tide and were retrieved after 24 hours.

Plant Traits

To determine tissue toughness of fresh leaves, we used a penetrometer consisting of an insect pin attached to a plastic tray which was suspended above leaf material (Pennings et al.1998; Siska et al. 2002). A plastic cup was placed on the tray and dry sand was added to the cup until the pin pierced the tissue. The mass of sand in kilograms required to pierce the tissue was indicative of leaf toughness. This was then converted into a measure of force in newtons (N). Toughness was assessed for each leaf and an average was determined for each plant. Frozen plants were freeze dried in a Labconco Freezone system for 72 hours. Dry mass was recorded, and plants were ground to a fine powder using a mini Wiley mill fitted with a 40-mesh sieve. Total soluble protein content was measured using a modified Bradford assay with absorbance read at 595 nm and compared to a Bovine Serum Albumin (BSA) standard curve. Total phenolic concentrations were determined using a modified Folin-Ciocalteu assay with absorbance measured at 760 nm and compared to a ferulic acid standard curve. Carbon [C] and Nitrogen [N] content were analyzed using a Fisher Scientific FlashEA system.

Statistical Analysis

All statistical analyses were conducted using R software (Version 3.5.1, R Core Team, 2018). The response variables snail height and width, C:N, %N, tissue toughness, benthic chlorophyll *a*, temperature, and light intensity were analyzed using one-way ANOVAs with habitat type as the factor, while protein content and phenolic concentration were analyzed with ANCOVA, with plant biomass serving as the covariate. For all responses the assumptions of normality and homogeneity of variance were tested; if data did not meet these assumptions, responses were transformed via Box-Cox transformations. For ANCOVA, the assumptions of linearity and equality of slopes were also tested. If there was no relationship between the response and the covariate, the covariate was removed from the model. Predation data was analyzed with a binomial logistic regression, while generalized linear models with a negative binomial distribution were used for radulations and snail count data. To account for differences in size between *S. alterniflora* and *S. cynosuroides*, the covariate, plant height, was included in the analysis of radulation data.

Results

Snail & Environmental Data

Habitat type had no significant effect on snail density (p=0.43), with an average of 42.15 ± 8.15 standard error (se) snails per m^2 across habitats. However, habitat type did influence snail height (p << 0.01; *S. alterniflora,* mean=19.27 ± 0.15 se; *S. cynosuroides*, mean=18.40 ± 0.10 se) and width (p << 0.01; *S. alterniflora*, mean=14.94 ± 0.11 se; *S. cynosuroides*, mean=14.35 ± 0.08 se), with larger snails found in *S. alterniflora*. One snail from *S. alterniflora* habitat was excluded from analysis as an outlier due to small size. There was a wider distribution of both heights and widths in *S. alterniflora* than *S. cynosuroides* (Online Resource 1). Habitat type also had a significant effect on the number of radulations (p=0.05, Fig. 2), with more found on *S. cynosuroides* than on *S. alterniflora*. There was no significant effect of the covariate, plant height, on the number of radulations (p=0.84). Additionally, habitat type had a significant effect on daily temperature (p=0.03, Online Resource 2a), with higher temperatures in *S. alterniflora* (Online Resource 2a), but no significant effect on daily light intensity (p=0.86, Online Resource

2b). Benthic chlorophyll *a* was similar between habitats ($p = 0.69$), for a combined mean of 36.19 ± 4.07 se mg/m^2.

Predation Assays

Trial number had no significant effect on survival ($p=0.67$), therefore data from each trial was pooled. We found that habitat type ($p=0.02$, Fig. 3a) had a significant effect on survival, with greater survival in *S. cynosuroides* than in *S. alterniflora*. In addition, distance from the creek also had a significant effect on survival ($p=0.01$, Fig. 3b), with the highest survival farthest from the creek (3 m away), and the lowest survival closest to the creek (1 m away).

Plant Traits

Plant type had a significant effect on both tissue toughness ($p \ll 0.01$, Fig. 4a) and total soluble protein content ($p < 0.01$, Fig. 4b), with the covariate, biomass, having no significant effect on protein content ($p=0.41$). *Spartina cynosuroides* had higher protein content while *S. alterniflora* tissues were tougher. In addition, plant type had no significant effect on either %N ($p=0.32$; *S. alterniflora*, mean=0.89 ± 0.03 se; *S. cynosuroides*, mean=0.94 ± 0.04 se) or C:N molar ratio ($p=0.59$; *S. alterniflora*, mean=54.25 ± 2.00 se; *S. cynosuroides*, mean=52.56 ± 2.33 se). Plant type and biomass had a significant interactive effect on total phenolic concentration ($p=0.03$, Fig. 5). Due to this significant interaction, main effects were not explored further.

Discussion

We demonstrate, for the first time to our knowledge, that *L. irrorata* will use *S. cynosuroides* in addition to *S. alterniflora* as habitat. Between the two habitats, we found significant differences in the size of *L. irrorata*, environmental characteristics, predation pressure, and palatability of plant tissue. In *S. alterniflora* habitat, we found significantly larger snail height and width, higher daily surface temperatures, and tougher plant tissues. In *S. cynosuroides* habitat, we found significantly higher plant protein content, safer habitat from predation, and a higher number of radulations. Despite these differences, snails were seen climbing the stems of both *S. alterniflora* and *S. cynosuroides* at high tide and densities were equal between habitats. This suggests that, from a population level, snails use both habitats similarly. Thus, from the perspective of *L. irrorata*, *S. cynosuroides* and *S. alterniflora* habitats may be functionally redundant. Research is needed in additional marshes to confirm these results, as this study was conducted in a single marsh.

Predation pressure on *L. irrorata* was higher in *S. alterniflora* than in *S. cynosuroides*, indicating that *S. cynosuroides* serves as better predation refuge for snails. One possible explanation for this trend is plant size. *Spartina cynosuroides* is much larger, in terms of biomass and height, than *S. alterniflora* and potentially provides more structure to impede incoming predators of *L. irrorata*, such as the blue crab (*Callinectes sapidus*), during tidal flooding. Although we found greater survivorship in *S. cynosuroides* than in *S. alterniflora*, snail densities did not differ between the habitats, suggesting that there is limited predator control of snail populations or that the effects of predation are ultimately offset by recruitment. While *L. irrorata* larvae settle over wide portions of the marsh, they do not move far from their settlement site over the course of their life (Hamilton 1978; Vaughn and Fisher 1992). Distance from the creek enhanced *L. irrorata* survival in both habitats, likely because plant shoots impede benthic predators such as crabs (Schindler et al. 1994; Lewis and Eby 2002). This indicates that snails are most susceptible to predators at the edge and that the interior provides a predation refuge, a trend seen for *L. irrorata* in mixed marshes of *J. roemarianus* and *S. alterniflora* (Hughes 2012) and for other mollusks in tidal marshes (ribbed mussels, *Geukensia demissa*, Lin 1989, coffee-bean snails, *Melampus bidentatus*, Johnson and Williams 2017).

We found that benthic chlorophyll *a* concentration was similar between the two habitats, which means that each habitat could provide comparable levels of algae for *L. irrorata* to consume. Although it is well-documented that *L. irrorata* will graze and fungal farm on *S. alterniflora* (Vaughn and Fisher 1992; Silliman and Zieman 2001), we found that they will also graze *S. cynosuroides*, as it had more radulations than *S. alterniflora*. In our study, *S. cynosuroides* had higher forage quality than *S. alterniflora*, as indicated by weaker tissues and higher protein content. Further, *S. alterniflora* produces Dimethylsulphoniopropionate (DMSP), a known deterrent to herbivores, whereas *S. cynosuroides* does not (Otte et al. 2004). The lack of DMSP production and higher forage quality of *S. cynosuroides* may be responsible for promoting more grazing on *S. cynosuroides*. Despite our finding that *L. irrorata* grazes more on *S. cynosuroides* than *S. alterniflora*, *L. irrorata* is a generalist feeder (Alexander 1979) and both plants may ultimately serve as a source of food for *L. irrorata*.

Our work contributes to the evidence that *L. irrorata* is a habitat generalist that will use marsh vegetation other than *S. alterniflora* as habitat (Lee and Silliman 2006; Hendricks et al. 2011; Hughes 2012; Sieg et al. 2013; Kicklighter et al. 2018). For instance, *L. irrorata* will use *Juncus roemarianus* as a refuge from predation over *S. alterniflora* in mixed-species marshes (Hughes 2012), however it remains unknown whether *J. roemarianus* can also serve as a food source. *Littoraria irrorata* prefers to inhabit and consume *S. alterniflora* over *Phragmites australis, Bolboschoenus robustus* (Kicklighter et al. 2018), *Batis maritima*, *Borrichia frutescens, Sarcocornia* sp., and *Iva frutescens* (Sieg et al. 2013), due to its low chemical defense and greater palatability (Hendricks et al. 2011; Sieg et al. 2013; Kicklighter et al. 2018). Further, both *P. australis* and *B. robustus* were better at inhibiting fungal growth than *S. alterniflora*, leading to a greater density of *L. irrorata* on *S. alterniflora* stems than these other species (Kicklighter et al. 2018).

Our results have implications for periwinkles adjusting to changing plant communities in mesohaline marshes due to sea-level rise. Mesohaline marsh vegetation is resilient to acute pulses of salinity from spatial and temporal changes in tidal salinity gradients (Jarrell et al. 2016; Li and Pennings 2018), however, chronic saline presses from sea-level rise could result in a shift in plant communities in mesohaline marshes from salt-intolerant (e.g., *S. cynosuroides*) to salt-tolerant plant species (e.g., *S. alterniflora*). In marshes where *S. cynosuroides* and *S. alterniflora* co-occur, this disparity in salt tolerance could lead to monotypic stands of *S. alterniflora*, as salt-water intrusion via sea-level rise drives salinity above the threshold for *S. cynosuroides*. Our results suggest that *L. irrorata* is a habitat generalist, one that will use both *S. alterniflora* and *S. cynosuroides* as functionally redundant habitats, which may allow it to gain an ecological foothold in brackish marshes as sea-level rises.

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Figure Captions

Fig. 1 a) Inset map of the state of Virginia. Boxed area indicates study region and arrow points to the Chesapeake Bay. b) Enlarged map of study region. Diamond is the location of Taskinas Creek with dotted rectangular region representing York River State Park

Fig. 2 Mean number of radulations per *S. alterniflora* and *S. cynosuroides* habitat. Error bars represent standard error

Fig. 3 Mean percent snail survival by a) *S. alterniflora* and *S. cynosuroides* habitat types and b) distance from the creek bank (habitats combined). The italicized letters above bars indicate the significant differences between levels

Fig. 4 Mean a) tissue toughness in Newtons and b) total soluble protein content in milligrams per gram dry weight for *S. alterniflora* and *S. cynosuroides* tissues. Error bars represent standard error

Fig. 5 Interaction of biomass and mean total phenolic concentration for a) *S. alterniflora* and b) *S. cynosuroides*. Trend lines represent smoothed, linear regression lines

Electronic Supplementary Material Captions

Online Resource 1 Size-frequency plots for shell height and width of *L. irrorata* found in a) *S. alterniflora* and b) *S. cynosuroides* habitats

Online Resource 2 Mean a) daily temperature and b) daily light intensity in *S. alterniflora* and *S. cynosuroides* habitats from July 12, 2018 through August 5, 2018. Error bars represent standard error