



# Predation refuge values of marsh and mangrove vegetation for the marsh periwinkle *Littoraria irrorata*

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**ABSTRACT:** Black mangroves *Avicennia germinans* are becoming increasingly common in coastal wetlands in the Gulf of Mexico (USA). As mangroves displace salt marsh vegetation, there may be consequences for associated wetland fauna. In a series of field studies, we compared prey refuge values between marsh and mangrove vegetation for a vertically migrating gastropod, the marsh periwinkle *Littoraria irrorata*. *Littoraria* were tethered to marsh grasses (*Spartina alterniflora*) or the aerial roots (pneumatophores) of *Avicennia* in arrays that fully crossed vegetation type (*Spartina* vs. *Avicennia*), tether height (base vs. canopy), and wetland location (edge vs. interior marsh platform). After 1 d, acute predation rates were twice as high on *Littoraria* tethered to the base of *Spartina* stems than on those tethered to pneumatophores, suggesting that mangroves provided superior refuge from benthic predators like blue crabs. In the canopy, *Spartina* reduced acute predation rates by 75 %, indicating that marsh grasses may provide superior refuge from aerial predators (possibly wetland birds). After 7 d, the effect of vegetation type diminished, but *Littoraria* mortality was 2 times higher on the benthos than in the canopy. Links between vegetation type and predation intensity on this important basal consumer may have broader consequences for trophic dynamics in coastal wetlands that are experiencing mangrove encroachment.

**KEY WORDS:** Ecotone · Woody encroachment · Predator–prey · Food web · Texas · Estuary

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## 1. INTRODUCTION

Vertical and horizontal habitat heterogeneity are key regulators of prey behavior and survival in coastal ecosystems. Prey refuge value is closely linked to variation in structural qualities such as differences in vegetation height or canopy structure, elevation, inundation, and connectivity to subtidal habitat (Warren 1985, Roberts et al. 1989, Hovel et al. 2001). In salt marshes, for example, keystone grazers such as the marsh periwinkle snail *Littoraria irrorata* (hereafter *Littoraria*) vertically migrate up smooth cordgrass *Spartina alterniflora* (hereafter *Spartina*) stems to reduce the risk of predation from benthic preda-

tors such as crabs (Warren 1985, West & Williams 1986, Vaughn & Fisher 1988, Hovel et al. 2001, Davidson et al. 2015, Carroll et al. 2018). Taller stems and more diverse plant assemblages can enhance the value of this vertical refuge (Hughes 2012). In tidal wetland habitats, there is also a refuge from aquatic predators further away from the wetland edge, especially for prey items such as *Littoraria* that are adapted to withstand periods of emersion (Minello & Zimmerman 1983, Dietl & Alexander 2009).

A shift in plant community composition could alter characteristics (e.g. canopy height and cover, stem density, plant rigidity) that influence prey refuge values (Dietl & Alexander 2009, Hughes 2012). A promi-

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nent example of this shift is apparent in many subtropical marsh–mangrove ecotones, where increases in minimum winter temperatures and sea level rise are contributing to increased black mangrove *Avicennia germinans* (hereafter *Avicennia*) cover and the subsequent displacement of salt marsh plant species (*Spartina*, *Batis maritima*, *Sarcocornia* spp.) (Comeaux et al. 2012, Osland et al. 2013, Cavanaugh et al. 2014, Armitage et al. 2015). Mangrove and marsh vegetation have distinctly different features that may be linked to prey refuge value. Mangroves are taller, with woody trunks, a leafy canopy, and dense aggregations of aerial root structures (pneumatophores) that emerge from the sediment. Marsh assemblages are comprised of a mixture of herbaceous species that are generally shorter than mangroves (see Fig. 1a). Therefore, as mangroves become more common, they may change features associated with prey refuge such as plant height, structural rigidity at the benthos, and canopy cover.

The transition from a herbaceous wetland to one dominated by woody vegetation may have many implications for food webs, including predator–prey interactions. Most previous predation studies on *Littoraria* have focused on the refuge value of *Spartina* and other marsh plant species (Warren 1985, Vaughn & Fisher 1988, Hovel et al. 2001, Hughes 2012, Davidson et al. 2015). In encroached ecotonal wetlands where *Avicennia* has become common, *Littoraria* are frequently associated with both mangrove and *Spartina* vegetation (see Fig. 1b,c; Armitage et al. 2020), but the potential differences in refuge value between vegetation types has not yet been quantified in the field. Additional layers of complexity in predator–prey relationships and prey refuge value are introduced by seasonal variations in *Littoraria* and predator activity (Rozas & Zimmerman 2000) and by contrasting temporal variations in canopy structure, with winter senescence in *Spartina* (O'Donnell & Schalles 2016) and evergreen productivity in *Avicennia* (Flores-de-Santiago et al. 2012). Therefore, our goal was to quantify if and how *Avicennia* vegetation affected spatial and seasonal variation in prey refuge value for *Littoraria*.

We used a series of *Littoraria* tethering experiments to explore vertical and horizontal variation in prey refuge value over 2 seasons. Based on our earlier mesocosm work (Glazner et al. 2020) demonstrating that mangrove pneumatophores restrict the movement of blue crabs *Callinectes sapidus* and the regional importance of blue crabs as a benthic predator of *Littoraria* (Moody & Aronson 2007), we hypo-

thesized that mangroves would provide superior refuge for *Littoraria* from predation in the field.

## 2. MATERIALS AND METHODS

### 2.1. Study area

All experiments were conducted in a tidal wetland at East End Lagoon in Galveston, Texas, USA (29.33° N, 94.75° W). This microtidal (typical tidal range <0.5 m) wetland is typical of the region, comprised of small stands of *Avicennia* shrubs interspersed among areas of marsh vegetation dominated by herbaceous grasses (primarily *Spartina*) and short-stature forbs (Fig. 1a). Within *Avicennia* stands, average ( $\pm$ SE) pneumatophore density was  $95.1 \pm 11.4 \text{ m}^{-2}$ . In *Spartina* stands, stem density was  $71.5 \pm 6.5 \text{ m}^{-2}$  (Glazner 2020). The amount of light

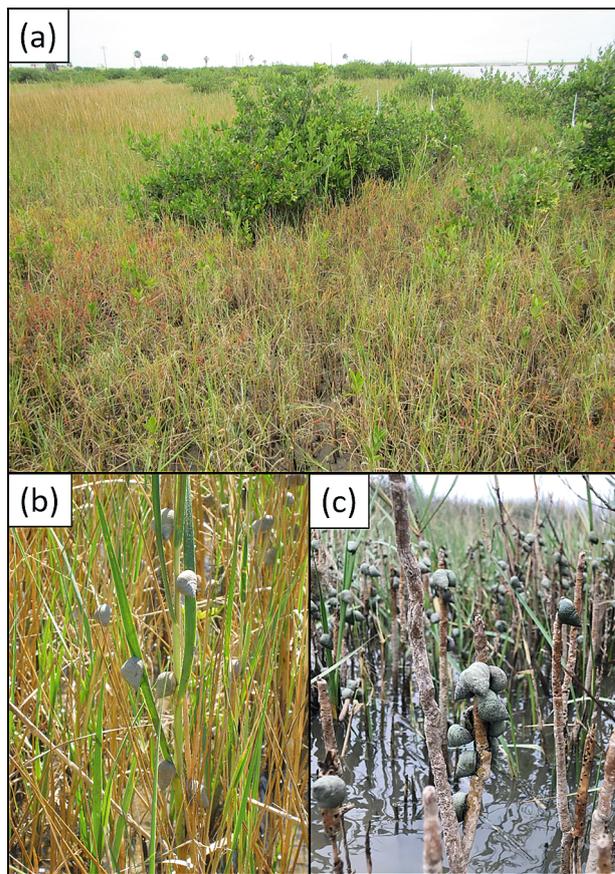


Fig. 1. (a) Black mangrove *Avicennia germinans* encroaching into a salt marsh dominated by smooth cordgrass *Spartina alterniflora*. (b) Marsh periwinkles *Littoraria irrorata* climbing *S. alterniflora* stems. (c) *L. irrorata* climbing *A. germinans* pneumatophores

reaching the benthos was  $44.7 \pm 4.8\%$  in *Spartina* stands and  $65.7 \pm 6.1\%$  in *Avicennia* stands (Glazner 2020). Maximum *Avicennia* pneumatophore height was generally  $<45$  cm, whereas mature *Spartina* stems were typically  $>100$  cm tall (Armitage et al. 2020).

## 2.2. Seasonal study

To assess whether the influence of vegetation (*Spartina* vs. *Avicennia*) on relative predation intensity varied between seasons, tethering trials were conducted in winter (February) and summer (June) 2019. For each of these trials a 50 m transect was established parallel to the shoreline, within 3 m of the vegetation–water interface. At randomly selected points along this transect (winter:  $n = 6$ ; summer:  $n = 5$  due to logistical constraints), one  $2 \text{ m}^2$  plot was established in the closest patch of *Spartina* vegetation, and one plot was placed in the closest *Avicennia* stand (winter: 12 total plots; summer: 10 plots).

Five snails per plot were tethered at the base of the primary vegetation type (winter: 30 per vegetation type, 60 total tethered snails; summer: 25 per vegetation type, 50 total). *Littoraria* with shell lengths of 17–22 mm were selected for tethering so that all snails were within the same adult size class (Vaughn & Fisher 1988). *Littoraria* were collected from the study site on the same day that they were deployed on tethers. Tethers were created using 10 cm of monofilament line; this length allowed snails to forage but minimized the risk of entanglement and limited the extent of vertical and horizontal migration (Silliman & Bertness 2002). On one end, the line was attached to galvanized steel wire, which was used to secure the tether to a plant. On the other end, the line was attached to the snail shell with cyanoacrylate glue (Fig. 2). These snails were able to move around the base of the plant but could not migrate more than 10 cm vertically upwards. Within each plot, snails were tethered to stems or pneumatophores dispersed throughout the  $2 \text{ m}^2$  plot to avoid overlapping tethers.

After 9 d (winter) or 7 d (summer; all snails were consumed by the 7<sup>th</sup> day so the trial was ended), the status (alive, consumed, missing) of all snails in each plot was recorded. *Littoraria* were marked as alive if the live snail was still attached to its tether. Snails were marked as consumed if the tether was attached to the plant but the line was severed and the snail was missing, or if only broken fragments of shell remained (Hovel et al. 2001). Snails were marked as

missing if the tether was completely absent (including the galvanized steel wire); this was deemed tether failure. From these data, daily predation rate (total no. of snails consumed / no. of days) and total percent snail mortality ( $100 - [100 \times \{\text{no. of surviving snails} / \{\text{total no. of tethered snails} - \text{no. of tether failures}\}]$ ) was calculated for each plot.

## 2.3. Spatial study

The second portion of this study explored vertical and horizontal heterogeneity in the influence of vegetation (*Spartina* vs. *Avicennia*) on relative predation intensity. In July 2019, a new set of 5 *Spartina* and 5 *Avicennia* plots was established within 3 m of the wetland edge, and an additional set of 5 *Spartina* and 5 *Avicennia* plots was established in the interior wetland platform, 20 m away from the water's edge. Both the edge and interior locations had similar tidal inundation regimes but differed in potential exposure to subtidal predators. The edge plots were immediately adjacent to subtidal habitat, whereas the interior plots



Fig. 2. *Littoraria irrorata* tethered to a *Spartina alterniflora* stem

had a 20 m buffer of vegetation that aquatic predators would need to traverse to reach the study plots. In each of the 10 plots, 5 snails were tethered to the base of the dominant vegetation as described above. An additional 5 snails were tethered 25–45 cm above the benthos (canopy) on 5 different *Spartina* stems and 5 different pneumatophores (10 snails plot<sup>-1</sup>, 200 total tethered snails). This tether height approximated the high water level in this microtidal wetland. These snails could not vertically migrate to the benthos and were able to remain at or above the waterline during typical flood tides.

Snail status (alive, consumed, missing) was recorded at the 1 and 7 d marks. From these data, acute predation rate was reported as the number of snails consumed within the first 24 h (sensu Moody & Aronson 2007). Daily predation rate and total percent snail mortality after 7 d were calculated for each plot as described above.

#### 2.4. Statistical analyses

All statistical analyses were conducted using R v.4.0.2 (R Core Team 2020). For the seasonal study (Section 2.2), generalized linear models (GLMs) were used to compare the fixed effects of season (winter vs. summer) and vegetation type (*Spartina* vs. *Avicennia*) on daily predation rate and total percent *Littoraria* mortality. For the spatial study (Section 2.3), separate GLMs were used to analyze acute (1 d) predation rates, daily predation rates over the 7 d period, and total percent mortality, where the fixed effects were vegetation type (*Spartina* vs. *Avicennia*), tether height (canopy vs. basal), and location (edge vs. interior). To ensure that data fit model assumptions, residuals of all models were visually inspected and Levene's tests ('car' package) confirmed homogeneity of variances; data were square root transformed to conform to model assumptions in the seasonal study. For all GLMs, significance of fixed effects was tested with Type III sums of squares using the ANOVA function in the 'car' package.

### 3. RESULTS

#### 3.1. Seasonal study

Daily predation rates were much higher (>0.7 snails d<sup>-1</sup>) in the summer than in the winter (<0.2 snails d<sup>-1</sup>,  $F_{1,18} = 26.10$ ,  $p < 0.0001$ ; Table 1, Fig. 3a). All tethered

Table 1. ANOVA output from generalized linear model showing the effects of vegetation type (*Spartina* vs. *Avicennia*) and season (winter vs. summer) on daily *Littoraria* predation rate and total percent mortality over the 9 d (winter) or 7 d (summer) study period. Significant p-values ( $p < 0.05$ ) are highlighted in **bold**

	SS	df	F	p
<b>Daily predation rate</b>				
Vegetation type	0.01	1	0.29	0.5989
Season	0.89	1	26.10	<b>&lt;0.0001</b>
Vegetation type × season	<0.01	1	0.13	0.7223
Residuals	0.61	18		
<b>Total mortality</b>				
Vegetation type	0.02	1	0.29	0.5989
Season	1.09	1	17.76	<b>0.0005</b>
Vegetation type × season	0.01	1	0.13	0.7223
Residuals	1.10	18		

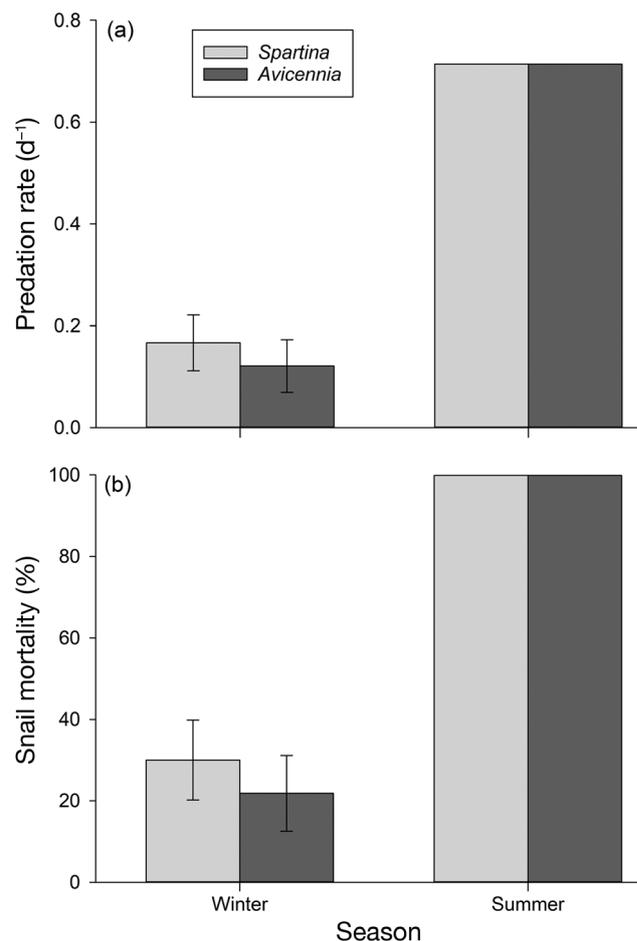


Fig. 3. (a) Daily predation rate and (b) average total percent mortality on *Littoraria irrorata* tethered to *Spartina alterniflora* stems or *Avicennia germinans* pneumatophores in the winter (9 d) and summer (7 d). Error bars: ± SE

snails (5 plot<sup>-1</sup>) were consumed in the summer, but less than 2 snails plot<sup>-1</sup> were consumed in the winter, regardless of vegetation type ( $F_{1,18} = 17.76$ ,  $p = 0.0005$ ; Table 1, Fig. 3b). There was no difference in predation rate or total percent mortality between snails tethered to *Spartina* or *Avicennia* vegetation in either season, and there was no interaction between vegetation type and season (Table 1). No tether failures were recorded during these trials.

### 3.2. Spatial study

Acute predation rates over the first 24 h of the study period varied across treatments, with a significant interaction between tether height and vegetation type ( $F_{1,32} = 7.23$ ,  $p = 0.0113$ ) (Table 2). At the benthos, acute predation rates were 2 times higher on snails tethered to *Spartina* than to *Avicennia* (edge: average 4.6 d<sup>-1</sup> on *Spartina*, 2.4 d<sup>-1</sup> on *Avicennia*; interior: 2.8 d<sup>-1</sup> on *Spartina*, 1.1 d<sup>-1</sup> on *Avicennia*)

(Fig. 4). Conversely, in the canopy, acute predation rates were lower on *Spartina* (0.2 d<sup>-1</sup>) than on *Avicennia* (0.8 d<sup>-1</sup>) in both the edge and interior locations (Fig. 4). Overall, acute predation rates were much lower in the canopy (<1 snail d<sup>-1</sup>) than on the benthos (1–5 snails d<sup>-1</sup>). Location (edge vs. interior) did not affect acute predation rates.

Daily predation rate was lower in the canopy (<0.3 snails consumed d<sup>-1</sup>) than on the marsh surface (>0.5 snails consumed d<sup>-1</sup>) ( $F_{1,32} = 6.64$ ,  $p = 0.0147$ ) (Table 2, Fig. 5a,b). Likewise, total mortality was nearly 100% for snails tethered to the benthos but less than 60% for snails in the canopy ( $F_{1,32} = 11.65$ ,  $p = 0.0017$ ) (Table 2, Fig. 5c,d). There were no differences in daily predation rates or total mortality over the 7 d study period among vegetation types or interior or edge locations, and there were no interactions among factors (Table 2). Some tether failures occurred across treatments, but these failures were relatively uncommon and were distributed across all treatments (Table 3).

Table 2. ANOVA output from generalized linear model showing the effects of vegetation type (*Spartina* vs. *Avicennia*), tether height (basal vs. canopy), and location (edge vs. interior) on acute (1 d) *Littoraria* predation rate, daily (over 7 d) predation rate, and total percent mortality. Significant p-values ( $p < 0.05$ ) are highlighted in **bold**

	SS	df	F	p
<b>One day predation rate</b>				
Vegetation type	1.48	1	5.46	<b>0.0259</b>
Tether height	1.17	1	4.30	<b>0.0463</b>
Location	0.20	1	0.73	0.3969
Vegetation type × tether height	1.96	1	7.23	<b>0.0113</b>
Vegetation type × location	0.06	1	0.23	0.6351
Tether height × location	0.10	1	0.37	0.5480
Vegetation type × tether height × location	0.03	1	0.11	0.7370
Residuals	8.68	32		
<b>Daily predation rate</b>				
Vegetation type	0.03	1	1.66	0.2065
Tether height	0.13	1	6.64	<b>0.0147</b>
Location	<0.01	1	0.13	0.7493
Vegetation type × tether height	0.05	1	2.54	0.1204
Vegetation type × location	0.02	1	0.83	0.3687
Tether height × location	<0.01	1	0.21	0.6516
Vegetation type × tether height × location	0.02	1	0.93	0.3408
Residuals	0.63	32		
<b>Total mortality</b>				
Vegetation type	0.02	1	0.62	0.4366
Tether height	0.38	1	11.65	<b>0.0017</b>
Location	0.01	1	0.19	0.6645
Vegetation type × tether height	0.05	1	1.69	0.2030
Vegetation type × location	0.02	1	0.75	0.3926
Tether height × location	0.03	1	0.86	0.3601
Vegetation type × tether height × location	0.03	1	0.77	0.3879
Residuals	1.04	32		

## 4. DISCUSSION

*Spartina* stems and *Avicennia* pneumatophores provided distinctly different short-term protection for *Littoraria* from acute predation risk, with densely packed pneumatophores providing superior refuge on the benthos and tall *Spartina* canopies reducing predation risk in the canopy over the first 24 h of the study (Fig. 4). Over short periods, tethering studies can be effective in documenting relative predation intensity (Mills et al. 2008, Perez et al. 2009), especially in areas with high predation pressure. Although tethering artifacts on acute predation rates can be pronounced for mobile prey that rely on escape behaviors to avoid predation (Baker & Waltham 2020), there is a lower risk of predation inflation due to tethering for less mobile prey that primarily utilize structural defenses (e.g. urchins or snails) (Boada et al. 2015). Therefore, the distinct difference between acute predation rates on *Littoraria* tethered to *Spartina* versus those tethered to *Avicennia* indicated that there was likely a functional difference in refuge value between the 2

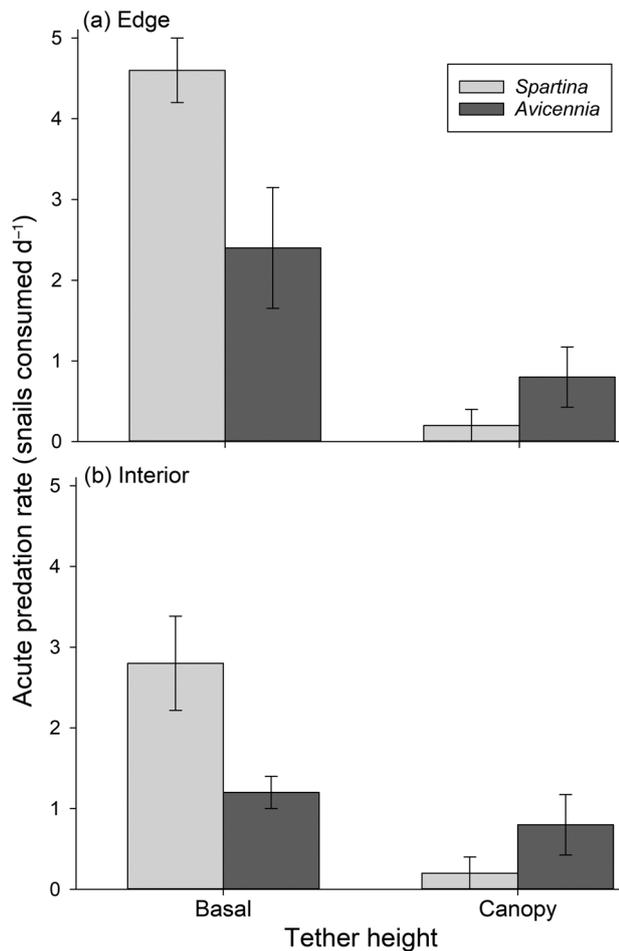


Fig. 4. Average rate of predation over a 24 h period on *Littoraria irrorata* tethered to *Spartina alterniflora* stems or *Avicennia germinans* pneumatophores at 2 different tether heights: basal (at the base of the stem or pneumatophore) or canopy (25–45 cm above the benthos). Tethers were deployed (a) at the lower tidal edge of the wetland and (b) in the wetland interior, 20 m from the vegetation–water interface. Error bars:  $\pm$ SE

vegetation types. After several days, that difference between vegetation types diminished (Fig. 5), though this may be partially due to the tethering approach. In habitats with high predation intensity, such as salt marshes, several days of tethering prolonged the snails' exposure to predation risk and increased the likelihood of being discovered by predators, and thus may have inflated the absolute mortality rate across vegetation types.

Acute predation rate showed distinct vertical variation within the wetland. Overall predation intensity was much higher at the benthos than in the canopy, possibly due to differences in basal and canopy predator identities. We deployed wildlife cameras to monitor predation activity on tethered snails (Glazner

2020) and detected light-footed clapper rails *Rallus crepitans* and white ibis *Eudocimus albus* foraging near the study plots. However, we were not able to capture footage of specific predation events on tethered snails, nor did the motion detectors on the cameras capture crab movement along the benthos. Regardless, snails tethered on the benthos were submerged for longer periods during high tide and therefore were more vulnerable to aquatic predators, most likely the blue crab *Callinectes sapidus*, which is abundant locally and exerts strong top-down pressure on *Littoraria* and other prey items near the benthos (Stanhope et al. 1982, Warren 1985, West & Williams 1986, Vaughn & Fisher 1988, Hovel et al. 2001, Silliman & Bertness 2002, Moody & Aronson 2007). The low predation intensity we documented in the winter aligns with the seasonal variations in blue crab foraging behavior (Jacobsen & Stabell 1999). In the canopy, *Littoraria* were likely less vulnerable to blue crab predation since crabs generally do not climb more than 20 cm above the water line (Vaughn & Fisher 1988), and therefore spend little time foraging in the canopy during low tide. Instead, snails tethered to the canopy may have been consumed by aerial predators such as light-footed clapper rails and other wading birds (Heard 1982, Zembal & Fancher 1988). *Littoraria* is a relatively minor dietary component of birds such as clapper rails (Rush et al. 2010), which was reflected in the much lower relative predation intensity in the canopy than near the benthos.

Acute predation rates were also linked to vegetation identity (Fig. 4). In this and other studies, benthic predators, presumably blue crabs, have more readily consumed snails and other prey items (e.g. small decapods) tethered to marsh than to mangrove vegetation (Johnston & Smith 2018, this study). The capacity of aquatic predators such as blue crabs to move through tidal wetlands may be restricted by vegetation features such as higher biomass, stem density, or stem rigidity (Dietl & Alexander 2009, Hughes 2012, Failon et al. 2020). Mangrove pneumatophore density was modestly higher than *Spartina* stem density at this site, potentially creating a barrier to crab movement. The relative rigidity of mangrove pneumatophores and stems has the potential to restrict the movement of aquatic predators and subsequently reduce predation intensity (Johnston & Smith 2018, Glazner et al. 2020). These complementary field and mesocosm studies (Johnston & Smith 2018, Glazner et al. 2020, this study) demonstrate that mangroves can potentially reduce predation intensity on certain prey items and may subsequently suppress some top-down controls in the system.

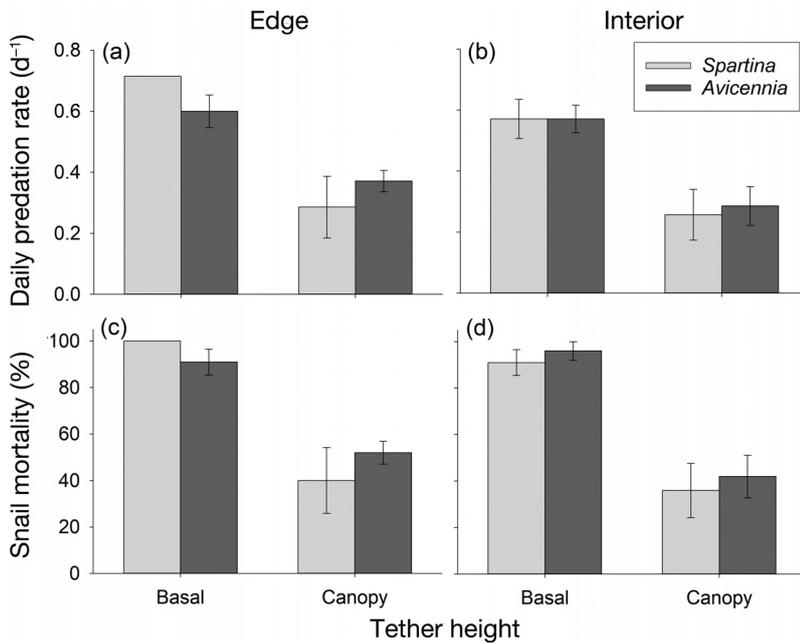


Fig. 5. (a,b) Daily predation rate and (c,d) average total percent mortality over a 7 d period for *Littoraria irrorata* tethered to *Spartina alterniflora* stems or *Avicennia germinans* pneumatophores at 2 different tether heights: basal (at the base of the stem or pneumatophore) or canopy (25–45 cm above the benthos). Tethers were deployed at the lower tidal edge of the wetland (a,c) and in the wetland interior (b,d), 20 m from the vegetation–water interface. All basal *Littoraria* tethered to *Spartina* were consumed within the first day; for all other treatments, error bars: ±SE

Table 3. Total number of tether failures in the spatial study at the acute (1 d) and 7 d time points in treatments that varied by vegetation type (*Spartina* vs. *Avicennia*), tether height (basal vs. canopy), and location (edge vs. interior). A total of 25 tethers were deployed in each treatment

		1 day		7 day	
		<i>Spartina</i>	<i>Avicennia</i>	<i>Spartina</i>	<i>Avicennia</i>
Edge	Basal	0	0	0	2
	Canopy	0	0	1	0
Interior	Basal	1	1	3	4
	Canopy	1	0	1	1

In the field, the realized vertical refuge from benthic predators may be influenced by stem height. *Avicennia* pneumatophores are substantially shorter than mature *Spartina* stems (Armitage et al. 2020), suggesting that pneumatophores may provide lower vertical refuge value. However, *Littoraria* are frequently associated with both vegetation types (Fig. 1), and in mixed assemblages, do not show strong affiliations for one vegetation type over another (Armitage et al. 2020). Despite the shorter height of pneumatophores, they are still tall enough to remain

above the waterline for much of the tidal cycle in this microtidal environment, where the typical tidal range is less than 50 cm. Therefore, at this site, both vegetation types may provide adequate height for snails to vertically migrate and mitigate predation risk from benthic consumers during high tide.

A different pattern of *Littoraria* predation emerged in the canopy, where acute predation rate was higher on *Avicennia* pneumatophores than on *Spartina* stems (Fig. 4). This difference may have been linked to canopy features. In particular, relative to *Avicennia* pneumatophores, the leaves of *Spartina* stems provided higher canopy cover (based on light attenuation; Section 2.1) and may have obscured line-of-sight foraging by visual predators such as wading birds (Farina et al. 2009, Johnston & Smith 2018). Wading bird foraging efficiency can be reduced in higher density emergent vegetation stands (Lantz et al. 2011), but this dynamic did not appear to be a factor in our system, where predation intensity in the canopy was higher among the somewhat denser mangrove pneumatophores. Given that *Littoraria* is a relatively minor component of bird diets (Rush et al. 2010), it is also possible that the canopy predation is attributable to aquatic predators such as blue crabs that can swim above the benthos during high tide or climb the rigid pneumatophores (Hamilton 1976), though this is a relatively uncommon occurrence (Vaughn & Fisher 1988). Regardless of the predator identities, it is clear that *Spartina* vegetation and *Avicennia* pneumatophores provided vertically

heterogeneous refuge from acute predation pressure. Although there was no significant effect of edge or interior location on acute predation intensity, absolute rates of predation were somewhat lower on basal *Littoraria* that were tethered further away from the wetland edge, regardless of vegetation type (Fig. 4). This pattern of horizontal refuge is common in coastal wetlands, where predation intensity decreases with increasing distance from the vegetation–water interface (Stiven & Hunter 1976, Silliman & Bertness 2002, Failon et al. 2020). Given the fairly

close proximity of the edge and interior plots (20 m) and the low elevation topography of the study site, we did not detect a strong horizontal gradient in acute predation intensity. The qualitatively higher predation rates at the wetland edge were most likely attributable to proximity to subtidal habitat and thus higher exposure to aquatic predators. There was no difference between edge and interior predation rates in the canopy, indicating that any horizontal refuge value was constrained to the benthos. This pattern suggests that the benthic and canopy predators were unlikely to have the same taxonomic identity or foraging strategy. Higher predation near the water's edge is characteristic of predators that are fully or partially constrained to subtidal habitats (e.g. blue crabs), whereas the activity of the canopy predators was not as closely linked to the proximity of aquatic habitat.

Tethering is an imprecise method to assess absolute predation rates but is a useful tool to compare relative predation intensity among stands of different vegetation types within a habitat, where predator identities are likely to be consistent across the study area (Moody & Aronson 2007). Furthermore, because untethered snails and other potential prey items occurred at the study site, tethering studies may actually underestimate absolute predation rates (Warren 1985). However, tethering has been repeatedly demonstrated to be an effective approach for assessing relative predation intensity on low-mobility organisms such as snails (e.g. Warren 1985, Silliman & Bertness 2002, Moody & Aronson 2007). Furthermore, blue crabs and wading birds will readily consume tethered prey items, with minimal behavioral artifacts (Englund & Krupa 2000, Hovel et al. 2001). Therefore, the tethering approach we used was an effective (though relative) method for the comparison of refuge value between vegetation types within the wetland.

Despite the potentially higher value of pneumatophores as refuge from blue crab predation, untethered *Littoraria* still often associate with *Spartina* in the field (Armitage et al. 2020) due to the trophic value of live and detrital leaves (Silliman & Zieman 2001, Silliman & Bertness 2002). Therefore, the preference of *Littoraria* for *Spartina* or *Avicennia* vegetation will likely reflect a balance between food and refuge values. *Littoraria* is a generalist herbivore that does not solely feed upon *Spartina* (Failon et al. 2020), so the leaves, detritus, or associated microalgae from *Avicennia* may also provide some trophic support, though this value is largely unquantified. Parsing out the relative importance of food selection and prey refuge is an important area for future explo-

ration in the quest to understand the consequences of mangrove expansion on coastal wetland food webs in the Gulf of Mexico.

Many coastal wetlands in the Gulf of Mexico are undergoing a rapid state change, where mangroves are displacing marsh vegetation (Osland et al. 2013, Armitage et al. 2015). Warmer winters, drought events, and near-term sea level rise may facilitate this shift over the coming decades (Ward et al. 2016, Osland et al. 2020). These modifications to foundation plant identity have the potential to profoundly alter faunal communities (e.g. Smee et al. 2017, Johnston & Gruner 2018, Armitage et al. 2021) and trophic interactions within wetland communities (Macy et al. 2019, Nelson et al. 2019, Goeke & Armitage 2021). These changes may be particularly pronounced for basal consumers that fill multiple roles in the ecosystem. In this case, *Littoraria* can dramatically reduce the amount of salt marsh vegetation when released from predation pressure (Silliman & Bertness 2002), potentially reducing ecosystem-level primary production and carbon storage potential. *Littoraria* is also a food source for aquatic animals including blue crabs, conch, and fishes (Warren 1985, West & Williams 1986, Vaughn & Fisher 1988, Hovel et al. 2001), as well as wetland birds such as the clapper rail (Heard 1982). Therefore, as mangroves enhance *Littoraria* refuge from certain benthic, aquatic predators, there are many potential consequences for other ecosystem functions. This study is a first step in elucidating how mangrove expansion may alter trophic dynamics within coastal wetlands.

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