Marsh and mangrove vegetation provide different prey refuge values for the marsh periwinkle *Littoraria irrorata*

Running head: Mangrove and marsh prey refuge value

Rachael Glazner[1], Jake Ballard[2], Anna R. Armitage[2*]

[1] Texas A&M University, College Station, TX, 77843

[2] Department of Marine Biology, Texas A&M University at Galveston, Galveston, TX 77553

* Corresponding author: armitaga@tamug.edu

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 fauna. In a series of field studies, we compared prey refuge values between marsh and mangrove vegetation for a vertically migrating gastropod, *Littoraria irrorata* (marsh periwinkle). *Littoraria* were tethered to marsh grasses (*Spartina alterniflora*) or the aerial roots (pneumatophores) of *Avicennia*. *Littoraria* were tethered to the base of these plants at the wetland edge during periods of low (winter) and high (summer) predation intensity. Overall, more *Littoraria* survived in the winter than the summer, but after seven days, there was no detectable difference in *Littoraria* survival between vegetation types. In the summer, *Littoraria* were also tethered in the wetland interior (20 m from the shoreline), and at heights >25 cm above the benthos, and survival was monitored daily. At the end of the 7-day period, *Littoraria* survival was 55% higher in the canopy than on the benthos, and 8% higher in the interior zone than at the edge. Survival analysis revealed that on the benthos, *Littoraria* were consumed more rapidly when tethered to marsh grasses than to mangrove pneumatophores, suggesting that mangroves provide superior refuge from benthic predators (e.g., blue crabs). In the canopy, *Littoraria* survival was higher on marsh plants, indicating that marsh grasses provide superior refuge from predation by aerial predators (e.g., wetland birds). These results suggest that marsh and mangrove provide protection against different types of predators.

Key words: Avicennia; Spartina; trophic; predator-prey; food webs; community ecology

1. Introduction

Coastal habitats are heterogeneous across vertical and horizontal scales. Vertical heterogeneity exists as variation in vegetation height or canopy structure, and horizontal variability is linked to elevation and inundation (Warren 1985, Roberts et al. 1989, Hovel et al. 2001). In coastal wetlands, these forms of heterogeneity are often linked to prey refuge value. For example, prey can adjust their vertical location up a plant (Warren 1985) to escape from benthic predators. The marsh periwinkle snail (*Littoraria irrorata*) vertically migrates up smooth cordgrass (*Spartina alterniflora*) stems during flood tides to avoid benthic aquatic predators such as blue crabs (*Callinectes sapidus*) (Warren 1985, West & Williams 1986, Vaughn & Fisher 1988, Hovel et al. 2001, 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, organisms such as *Littoraria* that are adapted to withstand periods of emersion may also experience enhanced prey refuge at higher elevations further from the wetland edge, where the time of exposure to aquatic predators is lower and denser vegetation can restrict predator movement during flood tides (Minello & Zimmerman 1983, Dietl & Alexander 2009).

The magnitude of vertical and horizontal prey refuge values are influenced by plant characters such as canopy height and cover, stem density, and plant rigidity (Dietl & Alexander 2009, Hughes 2012). Therefore, a shift in plant community characteristics within coastal wetlands could influence prey refuge values. A prominent example of this shift is apparent in many subtropical marsh-mangrove ecotones, where a variety of abiotic and biotic drivers, including sea level rise and increases in minimum winter temperatures, are contributing to increased black mangrove (*Avicennia germinans*) cover and the subsequent displacement of salt marshes dominated by smooth cordgrass (*Spartina alterniflora*) and succulent species (*Batis maritima*, *Sarcocornia* spp.) (Comeaux et al. 2012, Osland et al. 2013, 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 (Fig. A1). As mangroves become more common, they may change the features associated with prey refuge such as height, structural rigidity at the benthos, and canopy cover.

The transition from an herbaceous wetland to one dominated by woody vegetation has many implications for food webs, including predator-prey interactions. Most previous predation studies on *Littoraria irrorata* (hereafter *Littoraria*) have focused on the refuge value of *Spartina alterniflora* and other marsh plant species (Warren 1985, Vaughn & Fisher 1988, Hovel et al. 2001, Hughes 2012). In encroached wetlands where *Avicennia* is common, *Littoraria* are frequently associated with both mangrove and marsh vegetation (Fig. A1), but the potential differences in refuge value between vegetation types has not yet been quantified. Mesocosm studies suggest that rigid structures such as pneumatophores could restrict the movement of important predators such as blue crabs (*Callinectes sapidus*), thus suppressing prey capture rates (Glazner et al. 2020), but this dynamic remains to be tested in the field. Therefore, our goal was to quantify if and how predation pressure differed across vertical and horizontal gradients between marsh and mangrove vegetation. Our general approach was to compare relative predation pressure in marsh and mangrove environments with a series of *Littoraria* tethering experiments.

Based on our earlier mesocosm work (Glazner et al. 2020) demonstrating that mangrove pneumatophores restrict the movement of blue crabs, a key predator of *Littoraria*, we hypothesized that mangroves would provide superior prey refuge value in the field.

2. Methods

2.1. Study array

All experiments were conducted at East End Lagoon in Galveston, Texas (29.33°N, 94.75°W). This site is a mangrove-marsh mix, comprised of small stands of *Avicennia germinans* (hereafter mangroves) interspersed among areas dominated by marsh vegetation (primarily *Spartina alterniflora*, hereafter marsh).

We conducted a series of trials using arrays of 4-m^2 plots spaced at least one meter apart. In the winter, a single array was established along an elevation contour at the vegetation-water interface. Six plots were placed in randomly selected areas of marsh vegetation, and six plots were place among mangroves. In the summer, two arrays were established – one along the water's edge and another 20-m away from the water's edge; each array contained five marsh and five mangrove plots. Pneumatophore density was slightly higher than *Spartina* stem density, but canopy cover was higher in marsh plots compared to mangrove plots (Glazner 2020; Table A1).

2.2. Snail tethering

In each plot, five *Littoraria* were tethered at the base of either *Spartina alterniflora* stems or *Avicennia germinans* pneumatophores (basal). In the summer, five additional *Littoraria* were tethered 25-45 cm above the benthos (canopy). Tethering at least 25 cm above the base of the plant allowed the snails to remain above the waterline during flood tide (Failon et al. 2020). Within each plot, individual snails were tethered a minimum of 20 cm apart to avoid overlapping tethers.

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 East End Lagoon the same day that they were deployed on tethers. Tethers were created using 10 cm of monofilament line; this length allowed snails to move and exhibit natural foraging behaviors with the exception 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. 1).

Prior to the experiment, a pilot study was conducted to confirm that the tethers were functional (Glazner 2020). In brief, *Littoraria* were tethered within cages enclosing either *Spartina alterniflora* or mangrove pneumatophores; cage mesh was small enough (~0.28 mm mesh) to exclude predators and prevent snail escape. *Littoraria* were tethered at the base and at least 25 cm above the base of the plant. After 19 days, all snails remained attached to their tethers.

2.3. Phase 1: Seasonal Comparison

The objective of this phase was to compare predation intensity between winter and summer, and between vegetation types (marsh vs. mangrove). Two trials focused on basal predation at the wetland edge: the first in winter 2019 and the second trial in summer 2019. Cumulative snail survival was recorded after nine days in the winter and seven days in the summer trial.

Littoraria survival was reported as the percent of snails in each plot that remained on their tethers at the conclusion of the monitoring period. If a tether was attached to the plant but the snail was missing or only broken fragments of shell remained, this was marked as a predation event (Hovel et al. 2001). In one case, the tether was completely missing from the plant (including the galvanized steel wire); this snail was excluded from analysis as it was deemed a tether/user failure.

2.4. Phase 2: Vertical and Horizontal Comparisons

The second phase of this study explored vertical and horizontal heterogeneity in refuge value in marsh and mangrove vegetation in summer 2019. Five marsh and five mangrove plots were established at the wetland edge, and an additional five marsh and five mangrove plots were established at the wetland interior (Fig. 2). In the first trial, predation intensity was assessed by documenting percent *Littoraria* survival in each plot after seven days. In the second trial, *Littoraria* survival was recorded daily over a seven-day period.

2.5. Statistical Analyses

All statistical analyses were conducted using R Studio 3.6.0. In Phase 1, a two-factor ANOVA was used to determine the effects of season (winter vs. summer) and vegetation type (marsh vs. mangrove) on cumulative *Littoraria* survival. In the first trial of Phase 2, a three-factor ANOVA was used to determine the effects of vegetation type (marsh vs. mangrove), height (basal vs. canopy), and location (edge vs. interior) on cumulative *Littoraria* survival. In the second trial of Phase 2, survival analyses with multivariate Cox Proportional-Hazards regressions were used to determine if there were differences in daily *Littoraria* survival between vegetation types (marsh vs. mangrove) and locations (edge vs. interior). Separate survival analyses were conducted for basal and canopy snails. For the survival analysis, a status of “0” indicated that snail was consumed and “1” indicated that a snail was alive and still tethered. Therefore, positive coefficients were interpreted as higher survival in the survival analyses.

3. Results

3.1. Phase 1: Seasonal Comparison

Vegetation type did not affect the cumulative survival of basal edge snails during either season, but average snail survival exceeded 70% in the winter and was 0% in the summer (Table 1, Fig. 3).

3.2. Phase 2: Vertical and Horizontal Comparisons

In the summer, cumulative *Littoraria* survival was over 60% in the canopy but only 4% on the benthos. Additionally, cumulative snail survival was 15% higher in the interior than in the edge zone (Table 2, Fig. 4). There was no effect of vegetation type on cumulative snail survival.

Survival analysis indicated that in the canopy, *Littoraria* survival was higher on marsh vegetation (Table 3); this pattern persisted but diminished in magnitude over the 7-day survey period (Fig. 5a, b). *Littoraria* survival in the canopy was similar between interior and edge zones (Table 3). Conversely, *Littoraria* tethered near the benthos were more vulnerable when tethered to marsh vegetation than to mangrove pneumatophores (Table 3, Fig. 5c, d). In addition, basal snail survival was higher in the interior zone relative to the edge (Table 3). For both canopy and basal snails, there were no interactions between vegetation type and zone, and so interactions were not included in the Cox PH models.

4. Discussion

Marsh vegetation and mangrove pneumatophores provided *Littoraria* refuge values that were distinctly different from each other, and varied across vertical and horizontal scales within the wetland. Overall predation intensity was much higher at the benthos than higher in the canopy, likely due to differences in basal and canopy predator identities. Basal *Littoraria* were vulnerable to aquatic predators, most likely the blue crab *Callinectes sapidus,* which 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). The low predation intensity we documented in the winter aligns with the foraging behavior of blue crabs and other intertidal predators, which are less active during the winter (Jacobsen & Stabell 1999). In the canopy, *Littoraria* were vulnerable to aerial predators such as Light-footed Clapper Rails (*Rallus crepitans*) and other wading birds (Heard 1982, Zembal & Fancher 1988). However, *Littoraria* is a relatively minor component of Clapper Rail diets (Rush et al. 2010), which was reflected in the much lower relative predation intensity in the canopy than near the benthos.

Predation intensity was also linked to vegetation identity. 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 (this study; Johnston & Smith 2018). 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 (Table A1), potentially creating a barrier to crab movement. In addition, 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 (this study, Johnston & Smith 2018, Glazner et al. 2020) demonstrate that mangroves can potentially reduce predation intensity for certain prey items and may subsequently suppress some top-down controls in the system.

The inverse *Littoraria* survival pattern emerged in the canopy, where predation intensity was higher on mangrove pneumatophores than on marsh grasses. This difference may be linked to canopy features. In particular, relative to mangrove pneumatophores, the leaves of marsh grasses generated higher levels of canopy cover (Table A1) 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 was higher among the somewhat denser mangrove pneumatophores. Given that

Littoraria is a relatively minor component of Clapper Rail 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). We deployed wildlife cameras to monitor predator activity (Glazner 2020), and although we detected potential predators such as Clapper Rails and White Ibis (*Eudocimus albus*) foraging near the study plots, we did not observe specific predation events on tethered snails. Regardless of the predator identities, it is clear that marsh vegetation and mangrove pneumatophores provided distinct prey refuge values in different microhabitats within the wetland.

Benthic predation intensity was lower on *Littoraria* that were tethered further away from the wetland edge, regardless of vegetation type. 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). However, there was no difference between edge and interior survival in the canopy, indicating that horizontal refuge value was constrained to the benthos. This pattern provides further evidence 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 within each study site, tethering studies tend to 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 (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 was an effective, though relative method for the comparison of refuge value between vegetation types within the wetland.

The goal of this study was to compare the relative refuge value of marsh and mangrove vegetation for a common basal consumer, but the absolute value of a habitat for prey refuge is much more complex, influenced by many factors. For example, wrack accumulations comprised of macroalgae and other organic material are common in coastal wetlands (Smith et al. 2018). Benthic invertebrates often aggregate in wrack as a refuge from predators as well as from environmental stress (Rodil et al. 2008, Colombini et al. 2009). The distribution of wrack accumulations at our site was very patchy (Table A1), so it did not have a clear or consistent effect on prey refuge dynamics in this case. Another potentially important influence on the value of a given site for prey refuge is the pattern of tidal inundation. Benthic consumers such as blue crabs are more likely to forage within the wetland during high tide (Hovel et al. 2001), but wading birds tend to forage during low tide (Lantz et al. 2011). However, the microtidal wetlands typical of the Gulf of Mexico coastline have a relatively consistent level of inundation. This relatively unchanging tidal environment provided an ideal system to parse out the effects of vertical location, horizontal location, and vegetation type on prey refuge value.

Despite the higher value of pneumatophores as refuge from blue crab predation, untethered *Littoraria* may still elect to associate with *Spartina alterniflora* due to the trophic value of live and detrital leaves (Silliman & Zieman 2001, Silliman & Bertness 2002). Therefore, the preference of *Littoraria* for marsh or mangrove vegetation will likely reflect a balance between food and refuge values. While *Littoraria* is a generalist herbivore that does not solely feed upon *Spartina alterniflora* (Failon et al. 2020), 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 exploration in the quest to understand the concequences of mangrove expansion on coastal wetland food webs in the Gulf of Meixco.

Shifts in foundation plant identity have the potential to profoundly alter trophic interactions within wetland communities (e.g., Macy et al. 2019, Nelson et al. 2019). 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, thus reducing primary production and carbon storage potential (Silliman & Bertness 2002). *Littoraria* is also a food source for aquatic animals including blue crabs, conchs, 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 an important first step in elucidating how mangrove expansion may alter trophic dynamics within coastal wetlands.

Acknowledgements

This work was supported in part by an Institutional Grant (NA18OAR4170088) to the Texas Sea Grant College Program from the National Sea Grant Office, National Oceanic and Atmospheric Administration, U.S. Department of Commerce. Additional support was provided by the Texas A&M University at Galveston Boost Fellowship. We thank Nicolas Dunn, Marco Chacon, and Keilana Borja for their extensive help in the field and lab.

Literature Cited

Armitage AR, Highfield WE, Brody SD, Louchouarn P (2015) The contribution of mangrove expansion to salt marsh loss on the Texas Gulf Coast. PLoS One 10:e0125404

Carroll JM, Church MB, Finelli CM (2018) Periwinkle climbing response to water-and airbone predator chemical cues may depend on home-marsh geography. PeerJ 6:e5744

Colombini I, Mateo MÁ, Serrano O, Fallaci M, Gagnarli E, Serrano L, Chelazzi L (2009) On the role of *Posidonia oceanica* beach wrack for macroinvertebrates of a Tyrrhenian sandy shore. Acta Oecol 35:32-44

Comeaux RS, Allison MA, Bianchi TS (2012) Mangrove expansion in the Gulf of Mexico with climate change: Implications for wetland health and resistance to rising sea levels. Estuar Coast Shelf Sci 96:81-95

Dietl GP, Alexander RR (2009) Patterns of unsuccessful shell‐crushing predation along a tidal gradient in two geographically separated salt marshes. Mar Ecol 30:116-124

Englund G, Krupa JJ (2000) Habitat use by crayfish in stream pools: influence of predators, depth and body size. Freshw Biol 43:75-83

Failon CM, Wittyngham SS, Johnson DS (2020) Ecological associations of *Littoraria irrorata* with *Spartina cynosuroides* and *Spartina alterniflora*. Wetlands

Farina S, Tomas F, Prado P, Romero J, Alcoverro T (2009) Seagrass meadow structure alters interactions between the sea urchin *Paracentrotus lividus* and its predators. Mar Ecol Prog Ser 377:131-137

Glazner R (2020) Effects of vegetation type on predation success: implications of mangrove expansion. PhD dissertation, Texas A&M University, College Station, TX

Glazner R, Blennau J, Armitage AR (2020) Mangroves alter predator-prey interactions by enhancing prey refuge value in a mangrove-marsh ecotone. J Exp Mar Biol Ecol 526: 151336

Hamilton PV (1976) Predation on *Littorina irrorata* (Mollusca: Gastropoda) by *Callinectes sapidus* (Crustacea: Portunidae). Bull Mar Sci 26:403-409

Heard RW (1982) Observations on the food and food habits of Clapper Rails (*Rallus longirostris* Boddaert) from tidal marshes along the East and Gulf coasts of the United States. Gulf Res Rep 7:125-135

Hovel KA, Bartholomew A, Lipcius RN (2001) Rapidly entrainable tidal vertical migrations in the salt marsh snail *Littoraria irrorata*. Estuaries 24:808-816

Hughes AR (2012) A neighboring plant species creates associational refuge for consumer and host. Ecology 93:1411-1420

Jacobsen HP, Stabell OB (1999) Predator-induced alarm responses in the common periwinkle, *Littorina littorea*: dependence on season, light conditions, and chemical labelling of predators. Mar Biol 134:551-557

Johnston CA, Smith RS (2018) Vegetation structure mediates a shift in predator avoidance behavior in a range-edge population. Behav Ecol 29:2214-1131

Lantz SM, Gawlik DE, Cook MI (2011) The effects of water depth and emergent vegetation on foraging success and habitat selection of wading birds in the Everglades. Waterbirds 34:439-447

Macy A, Sharma S, Sparks E, Goff J, Heck KL, Johnson MW, Harper P, Cebrian J (2019) Tropicalization of the barrier islands of the northern Gulf of Mexico: A comparison of herbivory and decomposition rates between smooth cordgrass (*Spartina alterniflora*) and black mangrove (*Avicennia germinans*). PLoS One 14:e0210144

Minello TJ, Zimmerman RJ (1983) Fish predation on juvenile brown shrimp, *Penaeus aztecus* Ives: the effect of simulated *Spartina* structure on predation rates. J Exp Mar Biol Ecol 72:211-231

Moody RM, Aronson RB (2007) Trophic heterogeneity in salt marshes of the northern Gulf of Mexico. Mar Ecol Prog Ser 331:49-65

Nelson JA, Lesser J, James WR, Behringer DP, Furka V, Doerr JC (2019) Food web response to foundation species change in a coastal ecosystem. Food Webs 21:e00125

Osland MJ, Enwright N, Day RH, Doyle TW (2013) Winter climate change and coastal wetland foundation species: salt marshes vs. mangrove forests in the southeastern United States. Glob Change Biol 19:1482-1494

Roberts D, Rittschof D, Gerhart DJ, Schmidt AR, Hill LG (1989) Vertical migration of the clam *Mercenaria mercenaria* (L.) (Mollusca: Bivalvia). Environmental correlates and ecological significance. J Exp Mar Biol Ecol 126:271-280

Rodil IF, Olabarria C, Lastra M, Lopez J (2008) Differential effects of native and invasive algal wrack on macrofaunal assemblages inhabiting exposed sandy beaches. J Exp Mar Biol Ecol 358:1-13

Rush SA, Olin JA, Fisk AT, Woodrey MS, Cooper RJ (2010) Trophic relationships of a marsh bird differ between Gulf Coast estuaries. Estuar Coasts 33:963-970

Silliman BR, Bertness MD (2002) A trophic cascade regulates salt marsh primary production. Proc Natl Acad Sci USA 99:10500-10505

Silliman BR, Zieman JC (2001) Top-down control of *Spartina alterniflora* production by periwinkle grazing in a Virginia saly marsh. Ecology 82:2830-2845

Smith RS, Blaze JA, Osborne TZ, Byers JE (2018) Facilitating your replacement? Ecosystem engineer legacy affects establishment success of an expanding competitor. Oecologia 188:251-262

Stanhope HS, Banta WC, Temkin MH (1982) Size-specific emergence of the marsh snail, *Littorina irrorata*: effect of predation by blue crabs in a Virginia salt marsh. Gulf Res Rep 7:179-182

Stiven AE, Hunter JT (1976) Growth and mortality of *Littorina irrorata* in three North Carolina marshes. Chesap Sci 17:168-176

Vaughn CC, Fisher FM (1988) Vertigal migration as a refuge from predation in intertidal marsh snails: a field test. J Exp Mar Biol Ecol 123:163-176

Warren JH (1985) Climbing as an avoidance behavior in the salt marsh perwinkle, *Lirrorina irrorata* (Say). J Exp Mar Biol Ecol 89:11-28

West DL, Williams AH (1986) Predation by *Callinectes sapidus* (Rathbun) within *Spartina alterniflora* (Loisel) marshes. J Exp Mar Biol Ecol 100:75-95

Zembal R, Fancher JM (1988) Foraging behavior and foods of the Light-footed Clapper Rail. Condor 90:959-962

Table 1. Results of a two-factor ANOVA comparing *Littoraria* survival on marsh vegetation and mangrove pneumatophores in summer (n = 5 per vegetation type) and winter (n = 6 plots).

Factor	**Df**	**Mean Sq**	**F value**	**P-value**
Vegetation	1	110	0.358	0.557
Season	1	29943	97.777	<0.001
Vegetation x Season	1	91	0.298	0.592
Residuals	18	306		

Table 2. Results of a three-factor ANOVA comparing *Littoraria* survival on marsh vegetation and mangrove pneumatophores in two locations and two canopy heights (n = 5 per treatment).

Source	**Df**	**Mean Sq**	**F value**	**P-value**
Vegetation	1	551	2.509	0.1176
Height	1	60566	275.667	<0.001
Location	1	1328	6.046	0.0163
Vegetation x Height	1	63	0.285	0.595
Vegetation x Location	1	68	0.312	0.5785
Height x Location	1	17	0.079	0.7798
Vegetation x Height x Location	1	341	1.553	0.2168
Residuals	72	220		

Table 3. Cox Proportional-Hazards snail survival analysis (n = 50 snails initially deployed in each location and vegetation type). Positive coefficients indicate higher survival.

Canopy	Coefficient (SE)	Z	df	p
Vegetation (Marsh)	0.205 (0.083)	2.476	1	0.013
Location (Interior)	-0.007 (0.082)	-0.086	1	0.931

	Likelihood ratio test	df	p
	6.16	2	0.046

Basal	Coefficient (SE)	Z	df	p
Vegetation (Marsh)	-0.687 (0.139)	-4.954	1	<0.001
Location (Interior)	0.464 (0.135)	3.447	1	<0.001

	Likelihood ratio test	df	p
	38.15	2	<0.001

Figure 1. *Littoraria irrorata* tethered to *Spartina alterniflora* stem.

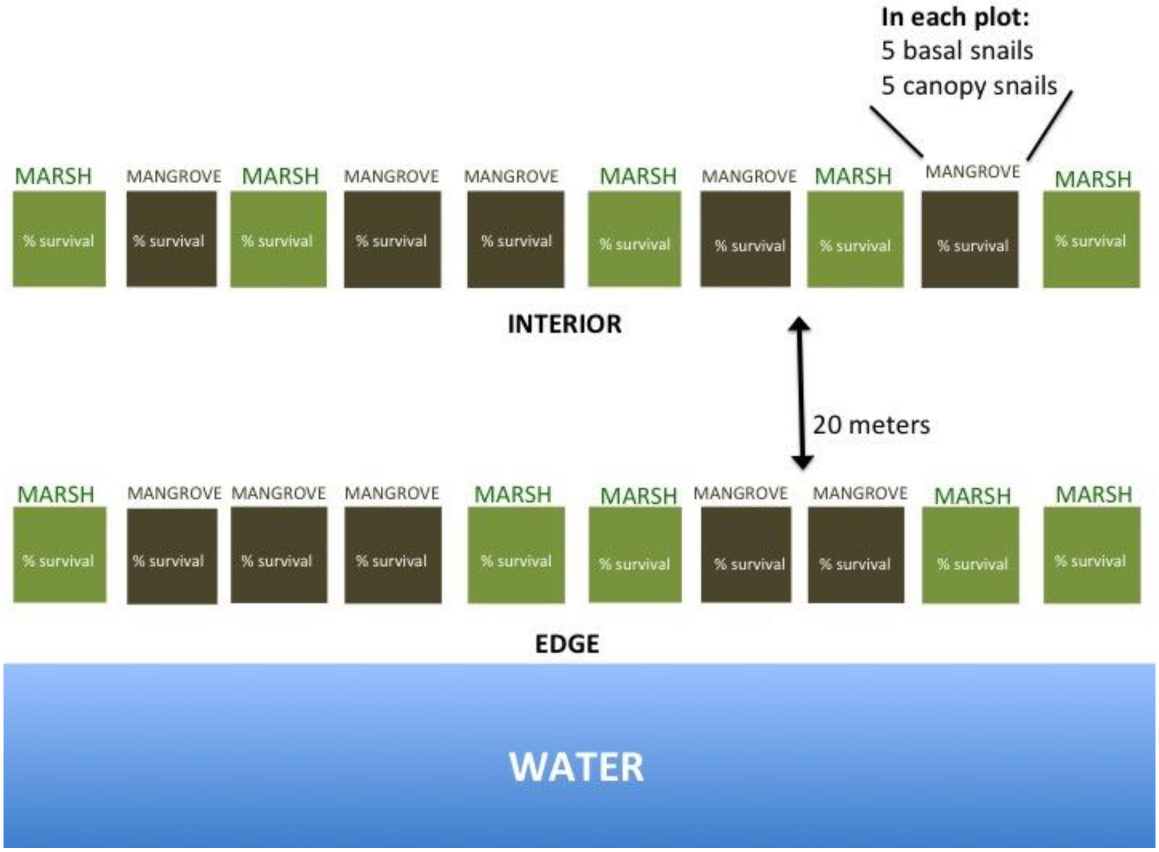

Figure 2. Experimental setup for Phase 2 summer trials. Each plot was approximately 2-m^2, and there was a minimum of one meter between plots (illustration not to scale).

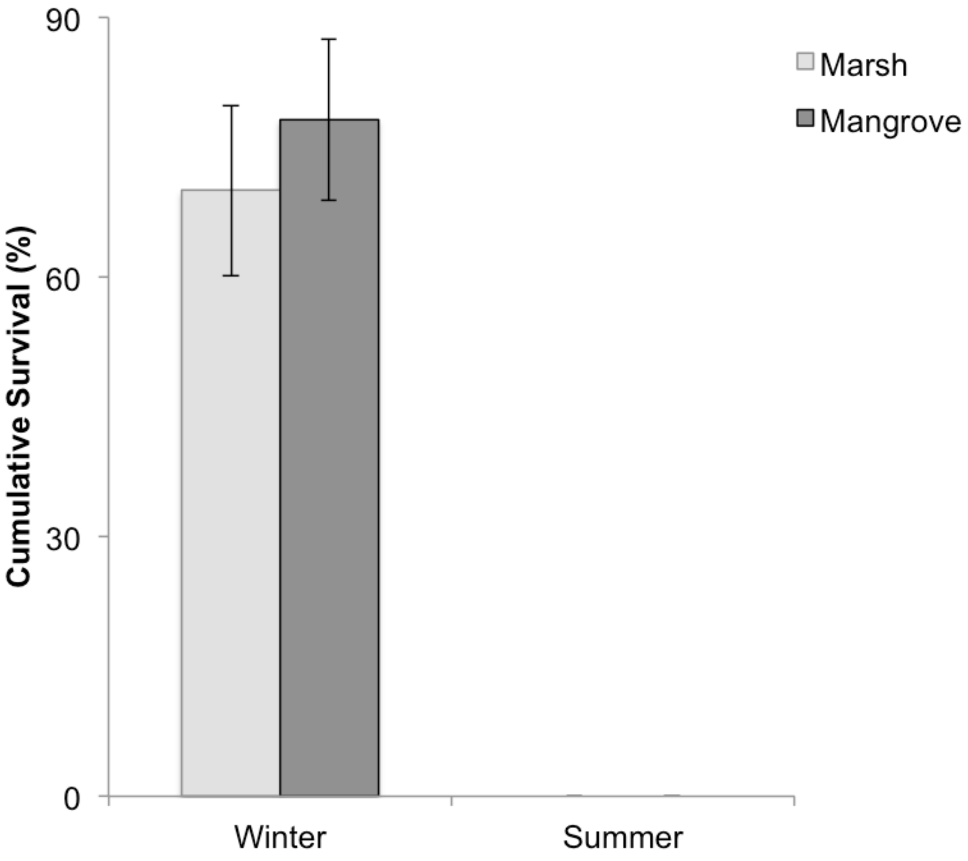

Figure 3. Cumulative *Littoraria* survival on marsh vegetation and mangrove pneumatophores in the winter (nine days) and summer (seven days). Error bars represent standard error.

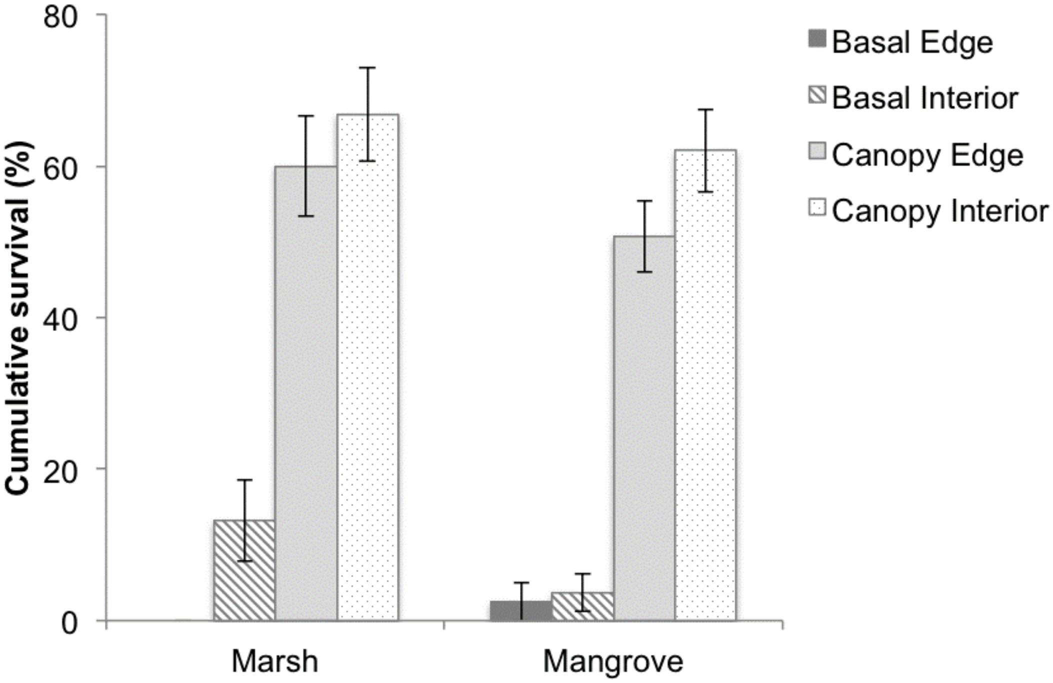

Figure 4. Cumulative *Littoraria* survival on marsh vegetation and mangrove pneumatophores at different locations within the wetland and at varying canopy heights. Error bars represent standard error.

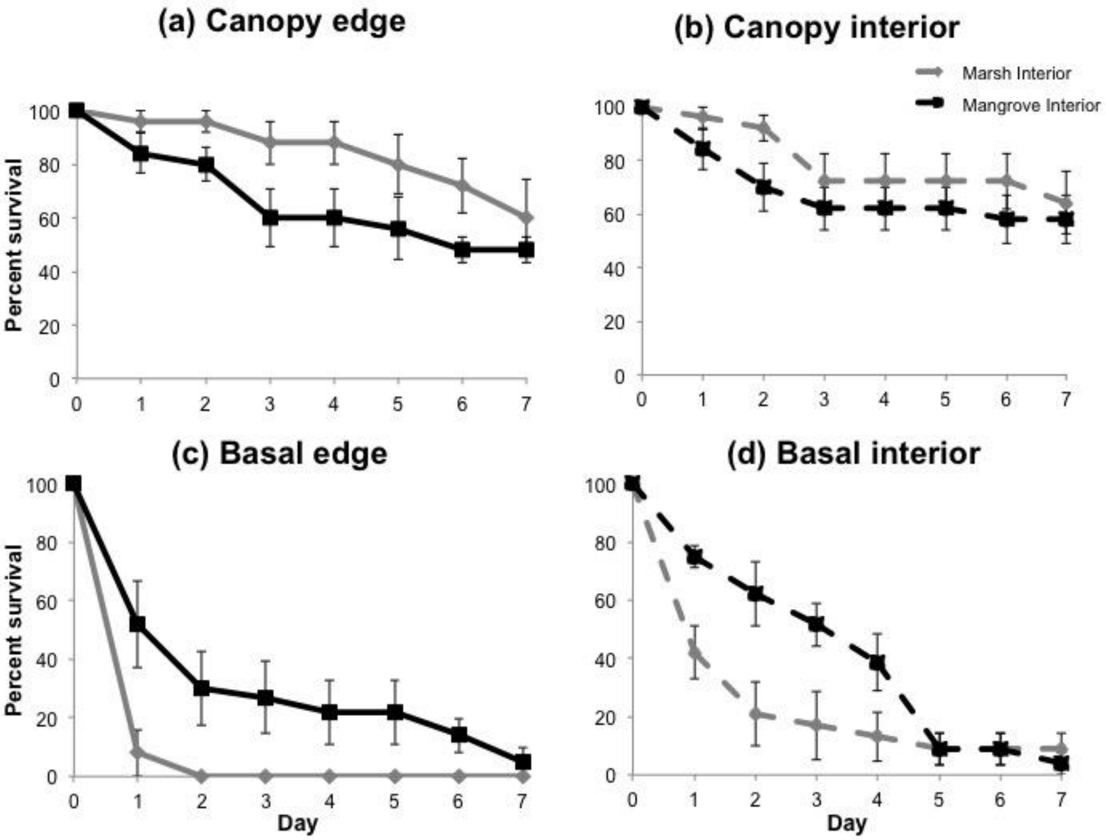

Figure 5. Summer *Littoraria* survival for a) canopy edge, b) canopy interior, c) basal edge, and d) basal interior. Error bars represent standard error

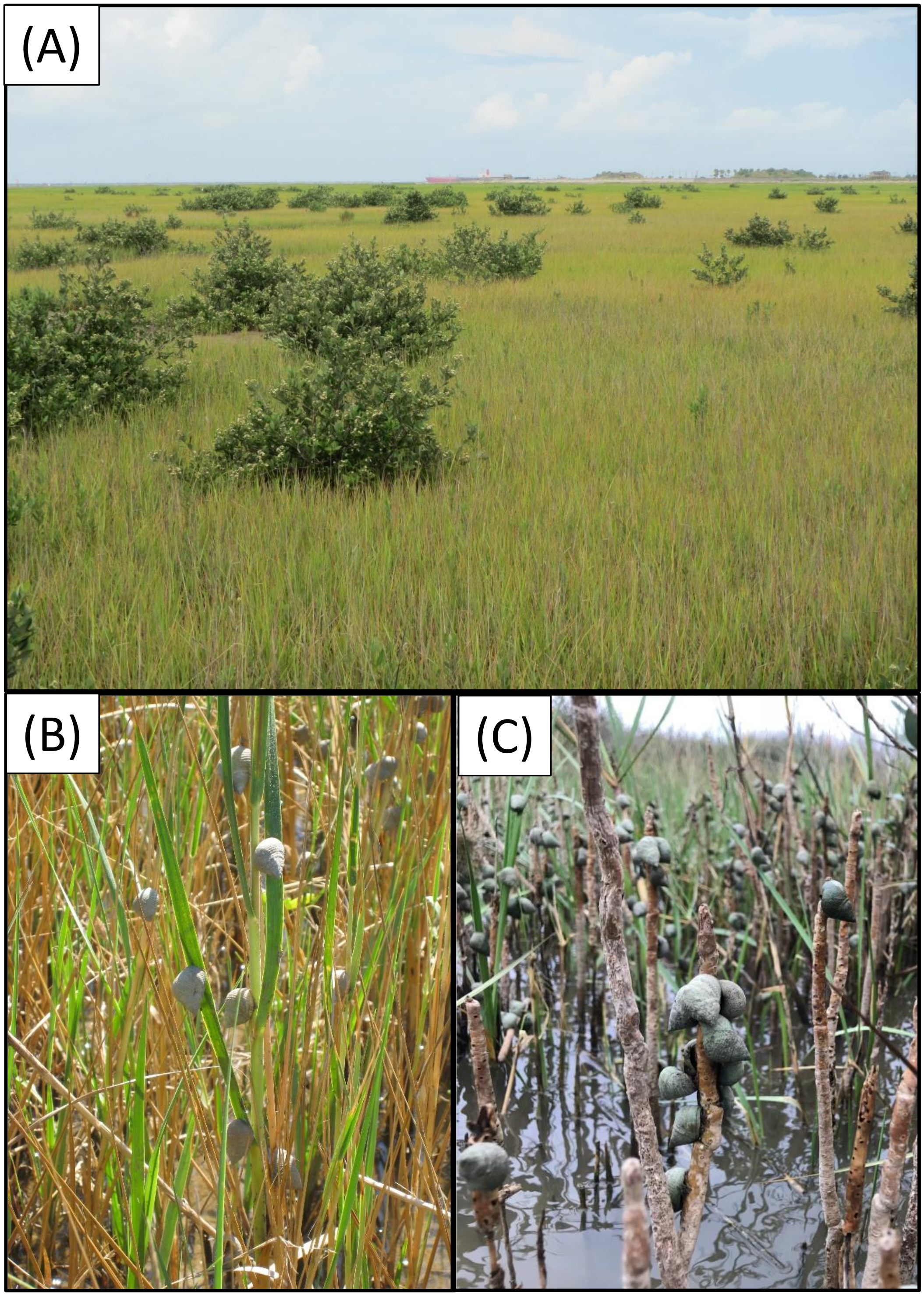

Figure A1. (A) *Avicennia germinans* encroaching into a salt marsh dominated by *Spartina alterniflora*. (B) *Littoraria irrorata* climbing *Spartina alterniflora* stems. (C) *Littoraria irrorata* climbing *Avicennia* pneumatophores.

Table A1. Means +/- standard errors of environmental characteristics in marsh and mangrove plots, modified from Glazner (2020).

	Marsh Mean (+/- SE)	**Mangrove Mean (+/- SE)**
Stem density (stems/m^2)	71.5 +/- 6.5	95.1 +/- 11.4
Number of species	1.5 +/- 0.3	2.7 +/- 0.4
Percent light	44.7 +/- 4.8	65.7 +/- 6.1
Wrack presence[a]	0.1 +/- 0.1	0.8 +/- 0.1

[a] Wrack was recorded as present (1) or absent (0)