BOTTOM-UP EFFECTS OF MANGROVE ENCROACHMENT ON BASAL CONSUMERS IN THE GULF OF MEXICO

A Dissertation

by

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ABSTRACT

Coastal wetlands are complex ecosystems that are shaped by the interaction of multiple environmental factors. As human activities alter the climate however, the structure of wetlands is changing. One such shift is occurring throughout the Gulf of Mexico where mangrove trees are encroaching into salt marshes as a result of climatic drivers including sea level rise and decreased frequency of winter freeze events. Along the Gulf Coast of Texas, black mangroves (*Avicennia germinans*), the primary encroaching species, are increasing in abundance and displacing salt marsh plants. The marsh plants being replaced are the primary food sources for many consumers at the base of salt marsh food webs, including fiddler crabs (*Uca* spp.) and marsh periwinkle snails (*Littoraria irrorata*). My research aimed to determine how these basal consumers respond to this shift in plant communities and the disappearance of their primary food sources. Through surveys and stable isotope analyses, I identified shifts in the distribution and diet of basal consumers in mangrove encroached marshes. Basal consumers in encroached wetlands were physically associated with mangrove structures but did not consume mangrove-derived plant matter. Lab mesocosm studies examined the trophic interactions of *Uca* and *Littoraria* with *Avicennia* in more detail through food preference and food quality experiments. I found that *Avicennia* was both an unpreferred and poor-quality food source that lowered the body condition of consumers to which it was fed. Field-collected consumers from mangrove encroached sites also had lower body conditions. Consumers at mangrove encroached sites replaced the marsh plants in their diet with fine organic matter, suggesting that either fine organic matter is less nutritive than marsh plants, or the presence of mangroves has negative non-consumptive effects on basal consumers. This research indicates that mangrove trees are not

equivalent to the marsh plants they are replacing and that their encroachment has negative trophic effects on basal consumers. These results have important implications for managing coastal wetland ecosystem functions such as nursery habitat and fisheries support and evaluating the restoration uses of mangroves.

DEDICATION

This dissertation is dedicated to Caroline Goeke and Eleanor Blumenschein, who never got the chance to read it but who worked and endured so I might someday have this chance to write it.

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1. TROPHIC IMPLICATIONS OF MANGROVE ENCROACHMENT: AN ONGOING SHIFT IN A THREATENED SYSTEM

Coastal wetlands are dynamic, complex, valuable, and, perhaps most importantly, threatened ecosystems. Naturally, they are shaped by tides, freshwater flow, erosion, accretion, and other environmental processes that interact to form highly productive ecosystems. However, humans have been altering these processes for years, disrupting the balance that forms these ecosystems. This can result in wetland loss due to rising sea levels and increased erosion, salinity-induced community shifts from changed freshwater flow, and changes in floral and faunal distributions and interactions as climate change affects environmental constraints on species ranges (Montagna et al. 2008, Osland et al. 2014, 2016, Armitage et al. 2015, Saintilan et al. 2018, Cavanaugh et al. 2019). Altogether, coastal wetlands around the world are shifting in response to changing factors, and researchers are racing to determine what the wetlands of the future may look like and how the millions of humans that interact with them will be affected.

Mangrove encroachment is one of the many disturbances shifting the balance in coastal wetlands around the world. Encroachment happens when mangrove trees are released from the environmental constraints that normally limit their range and are able to expand into adjacent habitats (Osland et al. 2016). In areas where mangroves are restricted by high soil salinity, they are encroaching landward due to rising sea levels, and at the latitudinal extremes of their range where they are freeze limited, they are expanding poleward as a result of increasing temperatures (Saintilan et al. 2014, 2018). In both cases, the most common adjacent habitat that is encroached upon are salt marshes. Salt marshes are normally dominated by short stature herbaceous vegetation such as graminoids and forbs, so the appearance of tall woody mangroves in the

ecosystem substantially shifts the vegetation community (Walker et al. 2019). While salt marshes and mangrove swamps are both economically and ecologically valuable systems, they differ somewhat in function and the extent to which they provide certain benefits, so this community shift is likely to have ecosystem-level effects (de Groot et al. 2012, Saintilan and Rogers 2015).

The myriad of interacting factors that shape coastal wetlands make it difficult to predict how ecosystems as a whole will respond to mangrove encroachment. Previous work has largely focused on studying the responses of single species and individual aspects of the system, and piece together the results of these separate studies. Researchers have so far identified geomorphic effects of mangrove encroachment including increased above and below ground biomass and carbon sequestration (Comeaux et al. 2012, Saintilan and Rogers 2015, Kelleway et al. 2017, Charles et al. 2020), increased erosion resistance (Comeaux et al. 2012, Armitage et al. 2020, Pennings et al. 2021), increased sediment accretion rates (Kelleway et al. 2017, Charles et al. 2020), and variable effects on decomposition rates (Perry and Mendelssohn 2009, Charles et al. 2020, Simpson et al. 2020). Effects of encroachment on faunal communities have also been recently identified, including decreased wading bird abundance and community composition shifts in nekton, epifauna, and infauna (Guo et al. 2017, Scheffel et al. 2018, Armitage et al. 2021). Unfortunately, such studies often focus on broad measures of biodiversity and richness while overlooking the details of the species interactions in these systems.

Species interactions in coastal wetlands support functions from fishery habitat provision (Silliman and Ziemann 2001, Cannicci et al. 2008, Holdredge et al. 2010) to nutrient cycling and soil aeration (Kristensen and Alongi 2006, Smith et al. 2009, Wang et al. 2010), so understanding how mangrove encroachment will alter interactions is vital to understanding overall ecosystem responses. Additionally, without knowledge of the suite of trophic and non-

trophic interactions that drives species abundance and distribution, it is difficult to monitor, protect, and restore food web health, energy flow, and other important aspects of these systems (Odum and Smalley 1959, Teal 1962, Harris et al. 2020). Such understanding of species interactions requires in-depth studies of the complex physiological and behavioral drivers of individual species responses to disturbances, and how these responses will affect other species in turn. It is not feasible to perform such in-depth analyses of all species in coastal wetland ecosystems, but by focusing on a small number of species that perform key roles, we can gain insight into consequential shifts in the system while minimizing research expenditure and maximizing potential applications to management and restoration.

In the coastal wetlands surrounding the Gulf of Mexico, it is simple to select the key species that likely have the largest roles in the system in relation to mangrove encroachment. *Avicennia germinans* (black mangrove) is the primary encroaching species throughout much of the Gulf, including along the Texas coast, and it is encroaching into wetlands typically dominated by *Spartina alterniflora* (Osland et al. 2013, Armitage et al. 2015, 2021). Many of the most influential fauna in these wetlands are invertebrate basal consumers that are interacting directly with the plant community. Such basal consumers consume and process plant carbon, making it available to higher trophic levels and serving as vectors for energy flow to higher trophic level predators (Cebrian 2004). Along the Gulf Coast of Texas. there are two particular basal consumers that perform additional roles and therefore have oversized effects on the ecosystem: *Littoraria irrorata* (marsh periwinkle snails) and *Uca* spp. (fiddler crabs, specifically *Uca rapax*, *Uca longisignalis*, and *Uca panacea*). *Littoraria* are abundant basal consumers in Gulf Coast salt marshes and are such voracious herbivores that they can influence the overall productivity and floral community composition in the marsh (Silliman and Ziemann 2001,

Silliman and Bertness 2002). *Uca* are considered ecosystem engineers because their constant burrowing activity affects soil aeration, nutrient cycling, and plant growth in marshes (Kristensen and Alongi 2006, Smith et al. 2009, Holdredge et al. 2010). Therefore, studying the interactions of *Littoraria* and *Uca* spp. with *Avicennia* and *Spartina* can yield insight into the bottom-up effects of mangrove encroachment on not only faunal community composition, but also food web structure, energy flow, productivity, and nutrient cycling in wetlands.

I investigated these interactions from physical, trophic, behavioral, and physiological perspectives. Chapter 2 focuses the physical and trophic aspects of the interactions by examining how the distributions and diets of basal consumers change between wetlands with and without mangroves. Chapters 3 and 4 then focus on *Uca* and *Littoraria*, respectively, by evaluating their interactions with *Avicennia* and *Spartina* through a series of in-depth lab feeding preference and food quality trials. These chapters aim to understand the causes and potential long-term effects of the dietary and distribution shifts documented in Chapter 2. Taken together, these chapters will fill an important knowledge gap regarding the bottom-up effects of mangrove encroachment on food webs, and the organism-level responses that lead to such community-level shifts. The results of this work will provide a broader understanding about mangrove encroachment effects on ecosystems and will inform decisions by coastal managers planning projects to restore and preserve the functions of wetlands within the mangrove-marsh ecotone.

2. A FOUNDATION SPECIES SHIFT CAUSES DIFFERENTIAL DISTRIBUTIONAL AND DIETARY RESPONSES IN COASTAL CONSUMERS

2.1 Introduction

Foundation plant species support and stabilize ecosystems both functionally and physically by facilitating the growth and survival of other species (Dayton 1972). A wide variety of species can be foundational plants in the right circumstances, from macroalgae in marine habitats, to grass in prairies, old growth trees in forests, or cushion plants in alpine environments (Ellison et al. 2005, Reid and Lortie 2012, Osland et al. 2013, Bittick et al. 2019). In recent years, some foundation species have disappeared as a result of changing environmental conditions (Osland et al. 2016), invasive species, pests and disease (Ellison et al. 2005), and human actions such as deforestation and overharvesting (Youngquist et al. 2017). The disappearance of foundation species can lead to decreases in biodiversity and species richness (Peters and Yao 2012, Baiser et al. 2013), a loss of services provided by an ecosystem (Boesch and Turner 1984, Ellison et al. 2005), and changes in the resource use patterns of fauna in the system (Sackett et al. 2011, Youngquist et al. 2017).

Foundational species disappearance also alters community assembly by influencing the fauna that rely on foundational species for food and habitat provision (Youngquist et al. 2017, Bittick et al. 2019). Such community level shifts can be distributional, trophic, or both. When a foundational species disappears, some organisms will shift to different locations due to changes in prey refuge value, sheltering structure presence, or preferred habitat (Bittick et al. 2019, Glazner et al. 2020), while other organisms will remain in the same physical location but change their feeding as a result of altered food preference rankings, differing food availability, or more

complex behavioral responses (Ó Brien et al. 2013). Knowledge of the type and extent of these resulting community level shifts will assist researchers in understanding the ecosystem level effects of foundational shifts. This will become increasingly vital in the coming years as climate change, species invasions, and other disruptions continue to cause foundational shifts, destabilizing ecosystems and threatening the services they provide.

Coastal ecosystems provide researchers with ideal conditions to examine the consequences of foundation species change on fauna, as coastal foundation species are controlled by temperature, precipitation, and sea level rise, and crossing abiotic control thresholds can cause abrupt transitions in foundation species abundance across a small geographical range (Osland et al. 2016, 2020). One ongoing and widespread coastal shift is the conversion of salt marshes to mangrove swamps. Here, I focused on the shift from *Spartina alterniflora* (marsh cordgrass, hereafter *Spartina*; other species in the genus are referred to by the entire scientific name) to *Avicennia germinans* (black mangrove, hereafter *Avicennia*) dominance in the Gulf of Mexico, USA as a result of changes in temperature and precipitation patterns (Osland et al. 2013, 2014, Cavanaugh et al. 2019). *Avicennia* has historically dominated southern Gulf of Mexico wetlands, but has been rare within the wetlands bordering the northern Gulf due to periodic mortality from low winter temperatures (Osland et al. 2013, Cavanaugh et al. 2014). Since 1990, temperatures in the northern Gulf of Mexico have rarely dropped below the threshold *Avicennia* can tolerate, allowing mangroves to encroach into wetlands previously dominated by *Spartina* (Saintilan et al. 2014, Armitage et al. 2015). One significant freeze event did occur in February 2021, resulting in at least temporary die-back of many *Avicennia* trees, but the long-term responses and survival rates have yet to be determined.

While *Spartina* and *Avicennia* are both foundation species, they differ in the roles they

perform and the services they support. For example, *Spartina* is a better choice for establishing structure and reducing erosion in recently restored sites (Yando et al. 2019), but large areas of *Avicennia* are more effective at protecting shorelines from hurricane induced erosion (Armitage et al. 2020, Pennings et al. 2021). While knowledge of such services has given us some insight into the ecosystem-level effects of mangrove encroachment, it is unknown if *Avicennia* and *Spartina* fill similar foundational roles for fauna, or if fauna will respond to the plant community shift as a foundational species disappearance. In particular, the displacement of *Spartina* may affect the high productivity and economically important fisheries associated with salt marshes (Boesch and Turner 1984), as there is no guarantee that *Avicennia* will fill the same trophic and structural roles.

Short-term effects of a foundational shift from *Spartina* to *Avicennia* are likely to be most apparent in low trophic level and mobility consumers, as they rely heavily on foundational plants for both food and shelter. In Gulf Coast salt marshes, the most common consumers that occupy this niche are *Littoraria irrorata* (marsh periwinkle snails) and *Uca* spp. (fiddler crabs). *Melampus bidentatus* (coffee bean snails) are less abundant overall but are common in some wetlands where other consumers are absent, and so were also included in this study. We investigated the physical and trophic responses of these three groups to mangrove encroachment in order to gain insight into how consumers may respond to recent shifts in foundation species. Specifically, we sought to address **1)** if the consumer abundance and distribution would shift with the encroachment of mangroves, and **2)** if the diet of these consumers would shift as a result of the changing plant community.

2.2 Methods

2.2.1 Experimental Sites

In order to investigate the co-occurrence and trophic relationships of basal consumers with mangroves in the field, two study regions with different degrees of mangrove encroachment were selected along the Texas Coast of the Gulf of Mexico. Port Aransas, the more southern site in the Coastal Bend region, is a barrier island with many entirely mangrove dominated sites along the back side (**Figure 2.1b**). Marsh sites dominated by *Spartina alterniflora* in the Port Aransas region are largely restricted to back bays further from tidal inlets. Galveston is 1.5° latitude farther north on the Upper Coast of Texas where mangroves are more sparsely distributed but have formed a patchy mix of mangroves and marsh vegetation in some areas (**Figure 2.1d**) since the last freeze-induced dieback in 1989 (Everitt et al. 1996). Many of the tidal wetlands on the back side of Galveston Island are still dominated by *Spartina.*

In each region, six study sites were selected: three encroached marshes with mangroves present, and three reference marshes without mangroves (**Figure 2.2**). Mangrove sites contained a mix of marsh vegetation and mangroves with 2-40% mangrove cover in Galveston sites and 50-75% mangrove cover in Port Aransas sites. In summer 2019, surveys were performed at each of these 12 sites to characterize the vegetation and basal consumer communities (**Section 2.2.2**). Additionally, samples of basal consumers and all likely end members were collected for stable isotope analysis (**Section 2.2.3**).

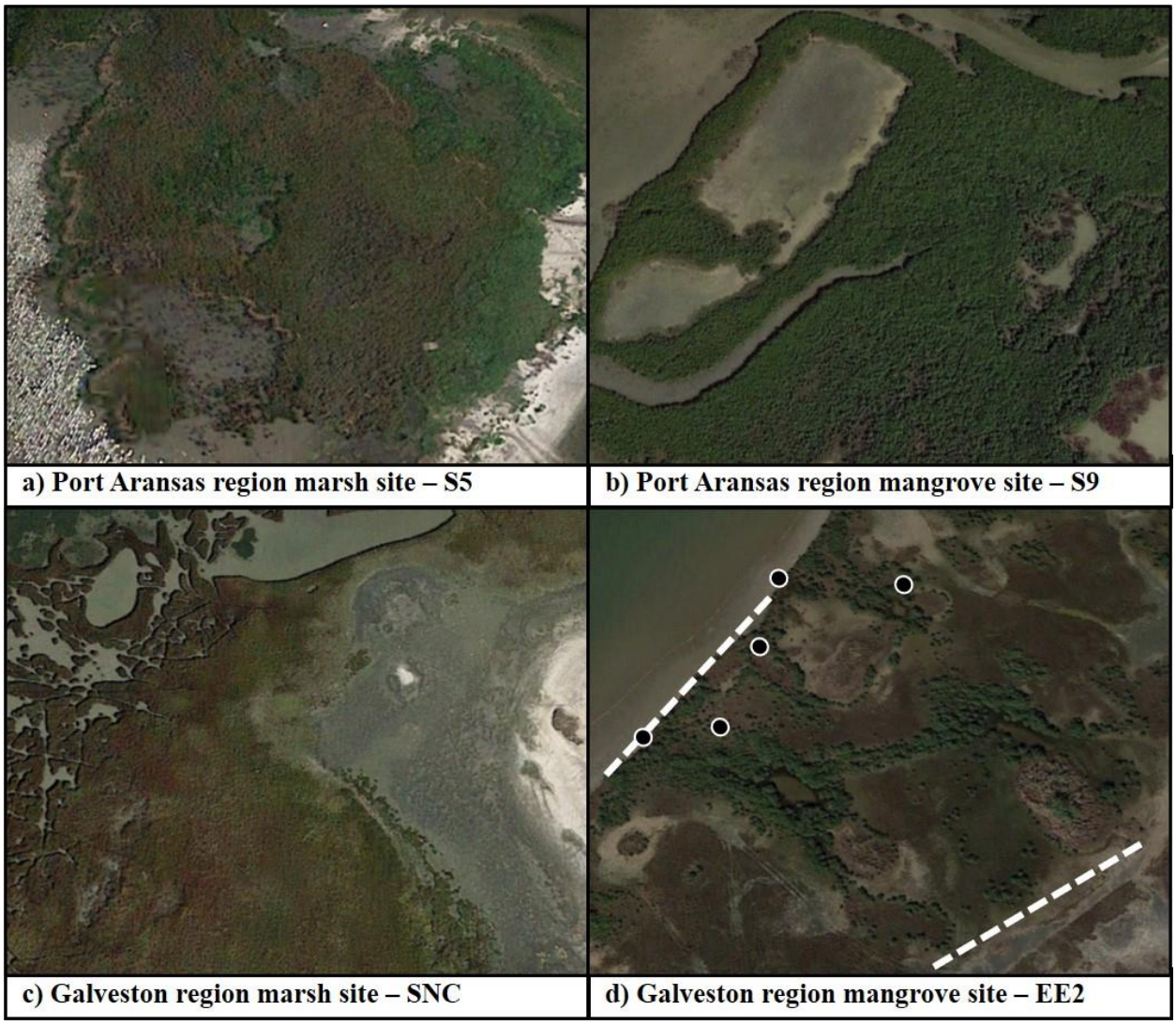

Figure 2.1: Examples of marsh and mangrove survey sites/ from the Port Aransas and Galveston regions. **a)** shows site S5 which contains only marsh vegetation, **b)** shows site S9 which is mangrove dominated, **c)** shows site SNC which is also only marsh vegetation, and **d)** displays a patchy mix of marsh vegetation (lighter colors) and mangroves (darker greens) with example transect (dashed lines) and sample collection locations (circles). Satellite imagery of sites obtained from Google Earth.

Figure 2.2: Map of study areas showing **a)** the two regions of the Texas coast where study sites were located, **b)** Galveston Island (Upper Coast) study sites locations and site types, and **c)** Port Aransas (Coastal Bend) area study site location and site types.

2.2.2 Surveys

At each of the 12 study sites, surveys were performed along two 100 m transects. One transect was in the low marsh, two meters from the water's edge, and the second transect was placed at the transition from low marsh to high marsh (**Figure 2.1d)**, for which the distance from the water's edge differed by site. The entire length of each transect was sampled with back-to-back 1 m^2 quadrats. Within each quadrat I recorded the percent canopy cover of each plant species present and basal consumer abundance. *Littoraria irrorata* and *Melampus bidentatus*

were counted directly, and the location of each snail (on the ground, on plant species A, on plant species B, etc.) was recorded. Due to the highly mobile nature of *Uca*, I was unable to count crabs directly. Instead, I recorded the number of burrows present within each quadrat and the percent cover of pseudofeces, which are a byproduct of crab feeding activity and therefore indicate that crabs are active in the plot. Burrow and pseudofeces counts were not possible in all quadrats, as some locations were flooded, obscuring the ground or softening the structure of burrows and pseudofeces beyond recognition. Flooded quadrats were marked as ND for these variables and were excluded from analyses of crab occurrence.

2.2.3 Sample Collections

Within each study site, samples for stable isotope analysis were collected from five stations (**Figure 2.1d**). Station locations were determined by randomly generating pairs of numbers in an (x,y) format, where x was distance along the shoreline, and y was distance into the marsh. Distances were measured from the starting point of the low marsh transect at each site. Stations were separated by a minimum of 20 m horizontally and were no more than 50 m from the shoreline.

At each station, samples of *Uca* spp., *Littoraria irrorata*, *Melampus bidentatus* and all likely end members were collected. Some consumers were absent from some study sites, but eleven of the twelve sites had at least two of the three consumers present **(Table 2.1)**. Five individuals of each basal consumer species present were collected from within 2 m of the station location. If five individuals of a species could not be located within 2 m, the search radius was expanded to 10 m and was canvassed for an additional 10 minutes. If I was not able to locate five individuals within that time, then collection was stopped with fewer than five individuals and I proceeded to the next station.

Table 2.1: Consumers found at each of the twelve study sites. The only site where fewer than two of the three consumers were found was S10, a marsh site in Port Aransas.

		Site	*Littoraria irrorata*	*Melampus bidentatus*	*Uca* spp.
Port Aransas	Mangrove	S3	**X**	**X**	**X**
		S4	**X**		**X**
		S9	**X**	**X**	**X**
	Marsh	S5	**X**	**X**	
		S6	**X**	**X**	
		S10		**X**	
Galveston	Mangrove	EE	**X**		**X**
		EE2	**X**		**X**
		SLP	**X**		**X**
	Marsh	SPM	**X**	**X**	**X**
		SNC	**X**		**X**
		IB	**X**		**X**

Sampled end members were particulate organic matter (POM), benthic organic material (BOM), and any vascular plant species present. Large quantities of macroalgae were not observed at any site so macroalgae was not included as an end member. POM was sampled by collecting 0.5 L of water from each station to be filtered in the lab, and BOM was sampled by collecting a scraping of the top 5 mm of sediment. For each plant species present, five to ten leaves were collected. When possible, five live and five dead leaves for each plant species were collected to evaluate isotopic variation between live and senescent plant material. Following collections, all samples were stored in a cooler with dry ice until they were transferred to a -20^{o}C freezer for storage prior to analysis.

2.2.4 Stable Isotope Processing and Analysis

Basal consumers were pooled by station to ensure there would be ample material for

analysis. Muscle tissue for analysis was obtained from the muscular foot of gastropods and from the legs of female and the large claw of male fiddler crabs. Tissue was rinsed in distilled water, then dried in an oven at 60^{o}C for 48 hours. Samples then were ground into a fine powder by hand with a mortar and pestle.

To collect particulate organic matter, water samples were thawed in the lab, then filtered through a 100 μm sieve onto pre-combusted glass fiber filters. Sieving removed any large detrital plant particles from the sample. Filters were dried in an oven at 60^{o}C for 48 hours, then stored in glass vials.

Benthic organic material was separated from the sediment using a density centrifugation protocol as outlined in Levin and Currin (2012). Fifteen mL of each sediment sample was rinsed twice with an equal amount of distilled water to remove salt. Twenty mL of Ludox (1.3 g/mL density**)** was added, and the sample was homogenized on a vortex mixer. Distilled water was carefully added without disturbing the surface of the Ludox to avoid mixing the Ludox and water layers and diluting the Ludox, and the sample was centrifuged again. Following centrifugation, the organic material from the sediment, including decaying plant matter, microalgae, and benthic meiofauna, were caught at the interface of the water and Ludox layers. This layer of organic material was pipetted onto a pre-combusted glass fiber filter through a 100 μm sieve to remove any larger masses of plant matter. Following filtration, the filter was dried in at 60^{o}C for 48 hours, then stored in a glass vial.

A complete list of the sampled vascular plants can be found in Appendix 1 (**Table A1)**. Plant leaves were rinsed thoroughly with distilled water, then dried at 60^{o}C for 48 hours. Most samples were then ground into a fine powder using a ball mill. Samples with very small leaves (e.g., *Batis maritima*) were ground by hand in a mortar and pestle to avoid the sample loss that

can occur with ball mills and ensure there would be enough material for analysis.

Analysis

Ground plant and animal tissues were weighed into tin capsules, and filters containing POM and BOM were placed in pre-combusted glass vials and cut into fine pieces using a pair of sterilized surgical scissors prior to shipment to analytical labs. The absence of carbonates was verified in a subset of POM and BOM samples following acid fumigation with 36% HCl. Stable isotope analysis of the majority of samples for $\delta^{13}C$ and $\delta^{15}N$ was performed at the Stable Isotopes for Biosphere Science Lab at Texas A&M University on a Costech elemental analyzer coupled with a DELTA V Advantage isotope ratio mass spectrometer. A subset of 50 samples was analyzed by the UC Davis Stable Isotope Facility on a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer due to an equipment malfunction at the SIBS lab. Analysis of duplicate samples showed no significant difference in the results produced by the labs. Vienna PeeDee Belemnite and atmospheric nitrogen were used as standards for carbon and nitrogen respectively. The accuracy of isotopic measurements was calculated as 0.07‰ for $\delta^{13}C$ and 0.03‰ for $\delta^{15}N$. All results are reported in standard delta notation.

2.2.5 Data Analysis

2.2.5.1 Site Surveys

Association of consumers with *Spartina* and *Avicennia* was analyzed using chi-squared tests. In order to perform chi-squared tests, the collected quadrat-level data was summarized by transect, then by group (transects from the same region, elevation, and site type). The quadrat-level data obtained from each transect consisted of percent cover by plant species, abundance of each consumer species (burrow count was used as a relative measure of *Uca* abundance), and the

locations of *Littoraria* and *Melampus* in each quadrat (on the ground, on plant species A, on plant species B, etc.). The data from each quadrat in the transect was combined. The quadrat-level values for percent cover of each plant and abundance of each consumer were averaged together to produce transect averages. The number of *Littoraria* and *Melampus* observed in each location was summed to determine the total number of each snail species occurring on each plant or on the ground. *Uca* burrows do not occur in association with a specific plant, so instead I identified the most common cover type in each quadrat where burrows were observed. The most common cover type was classified as the plant species that had the highest percent cover in that quadrat, or as "Bare" if the percent of bare ground was greater than the total plant cover. Following these calculations, I summed up the number of *Uca* burrows within all the quadrats dominated by each cover type. This allowed me to determine the total number of burrows found in association with each plant species and bare ground in each transect. Following these calculations, I had a set of summary values for each transect consisting of the average percent cover of each plant species, the average abundance of each consumer, and the total number of consumers located on or associated with each cover type.

Transects were then grouped based on region, site type, and elevation, resulting in 8 unique combinations such as Port Aransas-Mangrove-Low Elevation. Each transect group contained the three transects fitting that classification and the transect-level values calculated above. These transect-level values were averaged together within each group. This produced a single set of group average values for percent cover of each plant species, abundance of each consumer, and location/association of each consumer. The group values for the average number of consumers in each location and the average overall abundance of consumers were used to calculate the percent of each consumer that occurred in association with *Spartina* and *Avicennia*

in each group. Using these percent values, chi-squared tests were performed to investigate if *Littoraria* and *Uca* were randomly distributed across vegetation types, or if they co-occurred more often than expected with *Spartina* or *Avicennia*. The data analysis process is also summarized in **Figure A1**. *Melampus* was excluded from all distributional analyses because it was not widespread enough to address distribution. It was still used as a consumer in stable isotope analyses however because it was common at a small number of sites.

(2.1) $$\chi^2 = \frac{(O_p - E_p)^2}{E_p} + \frac{(O_e - E_e)^2}{E_e}$$

To test the null hypothesis that *Littoraria* and *Uca* were randomly distributed across vegetation types, the average percent of each consumer located on/associated with *Spartina* or *Avicennia* within a transect group was compared to the group average occurrence of *Spartina* and *Avicennia* themselves using chi-squared tests following equation **2.1**. O_p was the percent of the consumer observed in association with the plant of interest and O_e was the percent of consumers not associated with the plant of interest. E_p and E_e represented slightly different values for *Littoraria* and *Uca* chi-squared tests. For *Littoraria*, E_p represented the average percent cover of the plant of interest in the transect group and E_e represented the average percent of the group not covered by the plant of interest. For *Uca*, E_p was the average percent of non-flooded quadrats in the transect group dominated by the plant of interest and E_e was the percent of non-flooded quadrats dominated by other species. Non-flooded quadrats were used in the *Uca* tests to exclude flooded quadrats where burrows could not be counted from the analysis.

2.2.5.2 Stable Isotope Analysis

Dietary contributions of sources to consumers at each location were analyzed using Bayesian mixing models in MixSIAR in R (v 3.1.12, Stock et al. 2018). Models were run with

1,000,000 iterations and a burn-in of 500,000 and were thinned by 500. Trophic discrimination factors (TDFs) of 0.5 (±1.2) and 2.9 (±1.8) were used for C and N respectively (Vander Zanden and Rasmussen 2001). These values matched preliminary TDFs that we estimated from stable isotope analysis of *Littoraria* individuals restricted to *Spartina* or *Avicennia* diets for 60 days (S**ection 4.2.3**). The large standard deviations of these TDFs were used to account for uncertainty in estimated values and potential differences in TDFs between consumers.

There were minimal differences in the isotopic values of live versus senescent plant tissue, so plant condition was ignored in the diet analysis (**Table A1**). Physiologically similar plants had similar isotopic values, so plant species were separated into groups of graminoids, C3 photosynthesizers, and succulents. Particulate organic matter and benthic organic matter isotopic values also overlapped, and so the sources were combined into a single source referred to as fine organic matter (FOM) (**Table A1**). Grouping sources in this way is recommended by MixSIAR and ensures that the model will be able to differentiate between sources and fully resolve consumer diets (Stock et al. 2018). All groupings were supported with one-way ANOVA that confirmed the isotopic values of the sources within each group could not be distinguished from each other. All analyses were performed in R version 3.6.0 (R Development Core Team 2020).

2.3 Results

2.3.1 Surveys

Plant community differed between sites based on region, elevation, and encroachment level. *Avicennia* was the most common plant at the low elevation in Port Aransas mangrove sites (**Figure 2.3a**), but *Spartina* was most common at all other low elevations (**Figures 2.3b, 2.4a, 2.4b**). The low mangrove cover at Galveston mangrove sites (**Figure 2.4a**) is due to the patchy

nature of mangroves in Galveston (**Figure 2.1**). All high elevations had a diverse array of species present, but *Batis maritima* and bare ground were the most common cover types (**Figures 2.5a, 2.6a, 2.6b**), except for in the Port Aransas marsh sites, where *Distichlis spicata* was the most common (**Figure 2.5b**).

The distribution of consumers did not reflect the plant community of the sites where they occurred, indicating that consumers were actively selecting certain plants or areas of the wetland. *Littoraria* were most common in low elevation transects and were comparatively very rare at high elevations (**Table 2.2**). At the low elevations of all Galveston sites, where both *Spartina* and *Littoraria* were commonly found, snails occurred predominantly on *Spartina* (**Figures 2.4c, 2.4d, Table 2.2**). In both the marsh and mangrove sites in Galveston, the percent of *Littoraria* occurring on *Spartina* was higher than expected if snails were randomly distributed (**Table 2.2**). While some snails in the Galveston mangrove sites did occur on *Avicennia* (**Figure 2.4c**), the number was smaller than expected (**Table 2.2**). Despite *Spartina* being present at the high elevation of Galveston mangrove sites (**Figure 2.6a**), no *Littoraria* were found occurring on it, instead occurring predominantly on bare ground **(Figure 2.6c**).

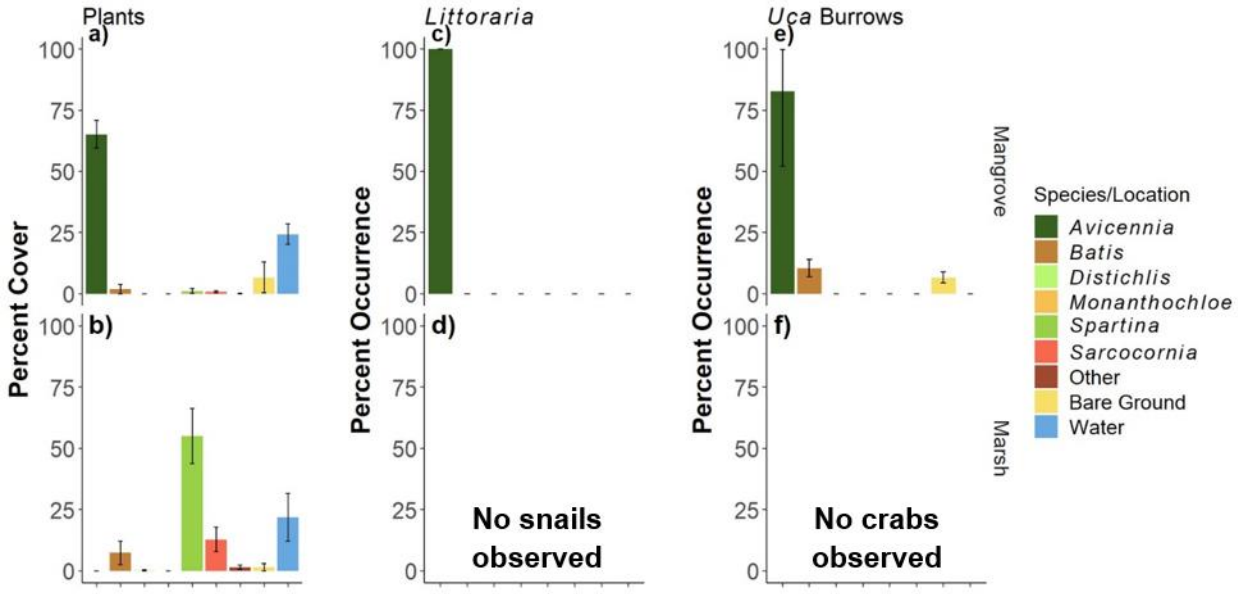

Figure 2.3: Plant and animal average relative abundances along low elevation transects at sites with mangroves (upper row) and without mangroves (lower row) in Port Aransas. **a-b)** plant percent cover, **c-d)** *Littoraria* percent occurrence on plants, and **e-f)** percent of *Uca* burrows associated with each cover type. All bars are mean ± standard error. No *Littoraria* or *Uca* burrows were observed in low elevation marshes.

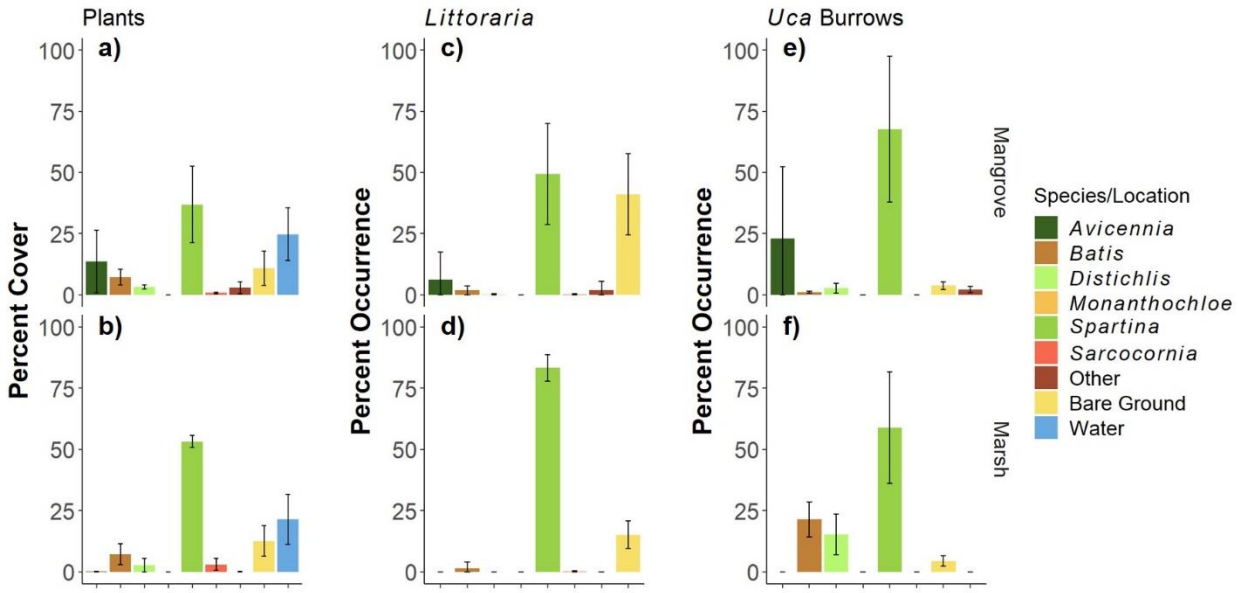

Figure 2.4: Plant and animal average relative abundances along low elevation transects at sites with mangroves (upper row) and without mangroves (lower row) in Galveston. **a-b)** plant percent cover, **c-d)** *Littoraria* percent occurrence on plants, and **e-f)** percent of *Uca* burrows associated with each cover type. All bars are mean ± standard error.

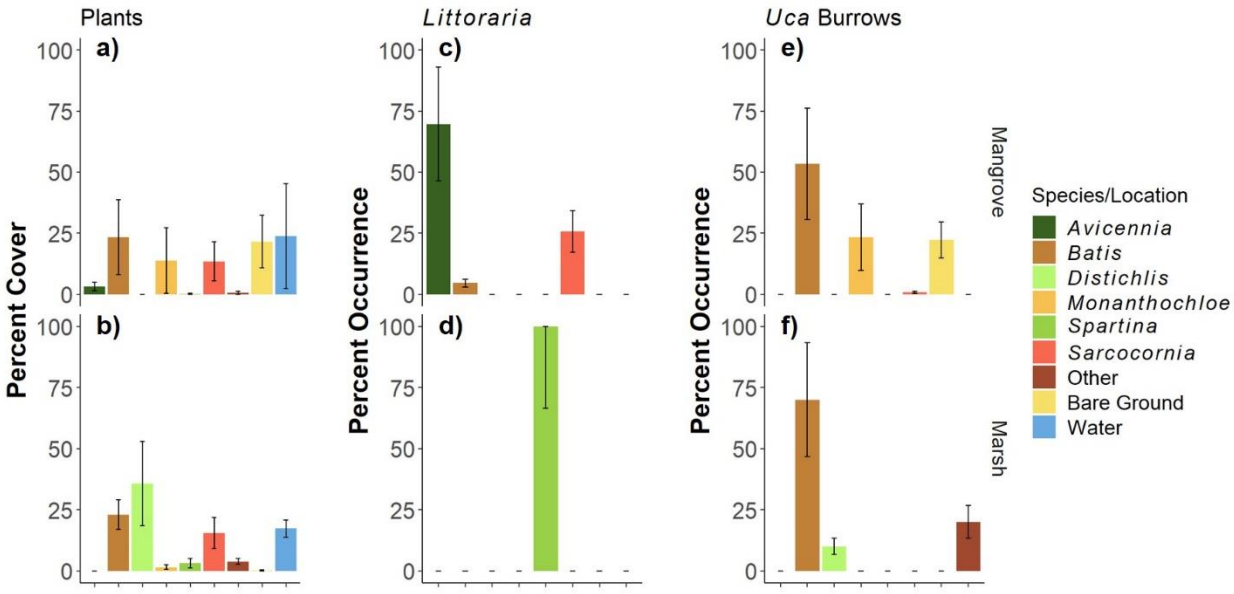

Figure 2.5: Plant and animal average relative abundances along high elevation transects at sites with mangroves (upper row) and without mangroves (lower row) in Port Aransas. **a-b)** plant percent cover, **c-d)** *Littoraria* percent occurrence on plants, and **e-f)** percent of *Uca* burrows associated with each cover type. All bars are mean ± standard error.

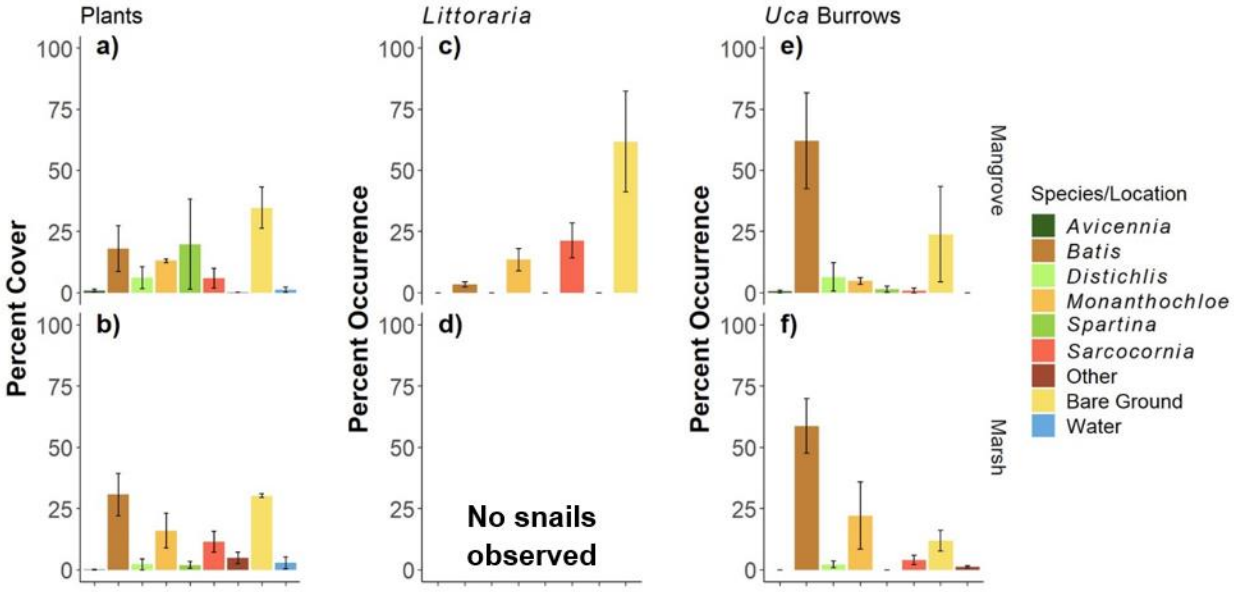

Figure 2.6: Plant and animal average relative abundances along high elevation transects at sites with mangroves (upper row) and without mangroves (lower row) in Galveston. **a-b)** plant percent cover, **c-d)** *Littoraria* percent occurrence on plants, and **e-f)** percent of *Uca* burrows associated with each cover type. All bars are mean ± standard error. No *Littoraria* were observed in the high elevation marshes.

The Port Aransas mangrove sites were almost entirely lacking in *Spartina* (**Figures 2.3a, 2.5a**), but despite the presence of other plant species, most *Littoraria* at both elevations were found on *Avicennia* (**Figures 2.3c, 2.5c**), which was a stronger association than was expected (**Table 2**). This association was especially notable in the high elevation at Port Aransas mangrove sites, where 70% of *Littoraria* occurred on *Avicennia* on average (**Figure 2.5c**) despite mangrove cover being lower than 5% (**Figure 2.5a**). Port Aransas marsh sites had abundant *Spartina* (**Figures 2.3b, 2.5b**), but *Littoraria* were almost entirely absent (**Figures 2.3d, 2.5d, Table 2.2**), so the co-occurrence of *Littoraria* and *Spartina* could not be analyzed for these sites. We were able to collect a small number of *Littoraria* from these sites for stable isotope analysis, but few of the located snails occurred within the predefined survey area.

Although *Melampus* distributions could not be statistically analyzed given their absence from many sites (**Table 2.1**), qualitative observations suggest that they occurred predominantly on *Spartina* in marsh sites and on *Avicennia* in mangrove sites. *Melampus* were most common in the *Spartina* dominated Port Aransas low elevation marshes, where *Littoraria* were almost entirely absent (**Table A2**). They were particularly common in site S10 (**Figure 2.2**), where 422 individuals were observed in the survey area. Fewer than 20 individuals were observed in all other surveys.

Table 2.2: The observed number of *Littoraria* and *Uca* found associated with *Spartina* and *Avicennia* at each site. Numbers in bold differ from the expected number of individuals, and the sign following the numbers indicates if the observed value was higher or lower than expected. * = p<0.05, ** = p<0.01, *** = p<0.001, p-values from chi-squared analysis

Location	**Port Aransas**				**Galveston**			
	Marsh Low	Marsh High	Mangrove Low	Mangrove High	Marsh Low	Marsh High	Mangrove Low	Mangrove High
Snails on Spartina (% ± SE)	0%	100 ± 33%	0%	0%	**83.3 ± 5.4% (+) *****	0%	**49.4 ± 21.2% (+) ****	0%
Snails on Avicennia (% ± SE)	NA	NA	**100 ± 0% (+) *****	**69.7 ± 23.2% (+) *****	NA	NA	**6.0 ± 11.4% (-) ****	0%
Total Snails in Survey area (Mean ± SE)	0	1 ± 1	186 ± 181	22 ± 22	269 ± 188	0	2272 ± 1150	30 ± 30
Burrows near Spartina (% ± SE)	ND	0%	0%	0%	**59.0 ± 22.8% (-) ****	0%	**67.6 ± 29.8% (+) ***	1.4 ± 1.3%
Burrows near Avicennia (% ± SE)	ND	NA	**82.9 ± 30.9% (+) *****	0%	NA	NA	22.9 ± 29.5%	0.6 ± 0.5%
Total Crab Burrows (Mean ± SE)	ND	17 ± 17	175 ± 173	832 ± 430	251 ± 135	953 ± 305	315 ± 210	598 ± 42

Fiddler crab burrows were most abundant (often exceeding 600 per transect) in high elevation transects, although many low elevation sites still contained 200-500 burrows within the belt transect survey area (**Table 2.2**). The Port Aransas low elevation marshes had high water levels at the time of data collection that made it impossible to locate burrows or pseudofeces, even at low tide, so the lack of recorded burrows in these marshes does not necessarily indicate an absence of fiddler crabs. The distribution of burrows at the other low elevation locations was similar to the observed distributions of *Littoraria*, with the majority of burrows occurring in association with the most common plant at each site (*Spartina* at the Galveston sites, *Avicennia* at the Port Aransas mangrove sites) (**Figures 2.3e, 2.4e, 2.4f**). The association with both *Spartina* and *Avicennia* was weaker in *Uca* burrows than it was in *Littoraria* (**Table 2.2**). Furthermore, in the low elevation Galveston marshes, despite the majority of *Uca* burrows occurring in *Spartina* dominated quadrats, there were still fewer burrows associated with *Spartina* than expected (**Table 2.2**). This is due to 21% of the burrows occurring in *Batis* dominated quadrats and 15% occurring in *Distichlis* dominated quadrats despite the low overall treatment average cover of both plant species (**Figure 2.4f**). The association of *Uca* with *Batis* was also found at high elevations where the majority of all burrows occurred in quadrats dominated *Batis* (**Figures 2.5e, 2.5f, 2.6e, 2.6f**). Fewer than one percent overall of recorded burrows at high elevations were associated with either *Spartina* or *Avicennia* (**Table 2.2**).

2.3.2 Stable Isotopes

C3 photosynthesizers, including *Avicennia* and succulents, contributed very little to the diets of *Littoraria* and *Uca* at all sites, even those heavily encroached by mangroves (**Figure 2.7**). All consumers had isotopic signatures that were highly distinct from those of C3 plants, and much more closely resembled the signatures of graminoid plants and FOM (**Figure 2.8**). Graminoid plants were consistently the dominant contributor to *Littoraria* and *Uca* diets but formed smaller proportions of consumer diets in mangrove sites compared to marsh sites, and in Port Aransas compared to Galveston (**Figure 2.7**). The contribution of graminoids to *Littoraria* diets was more than 15% lower in mangrove than in marsh sites in both Galveston and Port

Aransas. The graminoid proportion of *Littoraria* diets is likely formed mainly of *Spartina alterniflora*, which is by far the most abundant graminoid at the low elevations where *Littoraria* are predominantly found (**Figure 2.3b, 2.4a, 2.4b**).

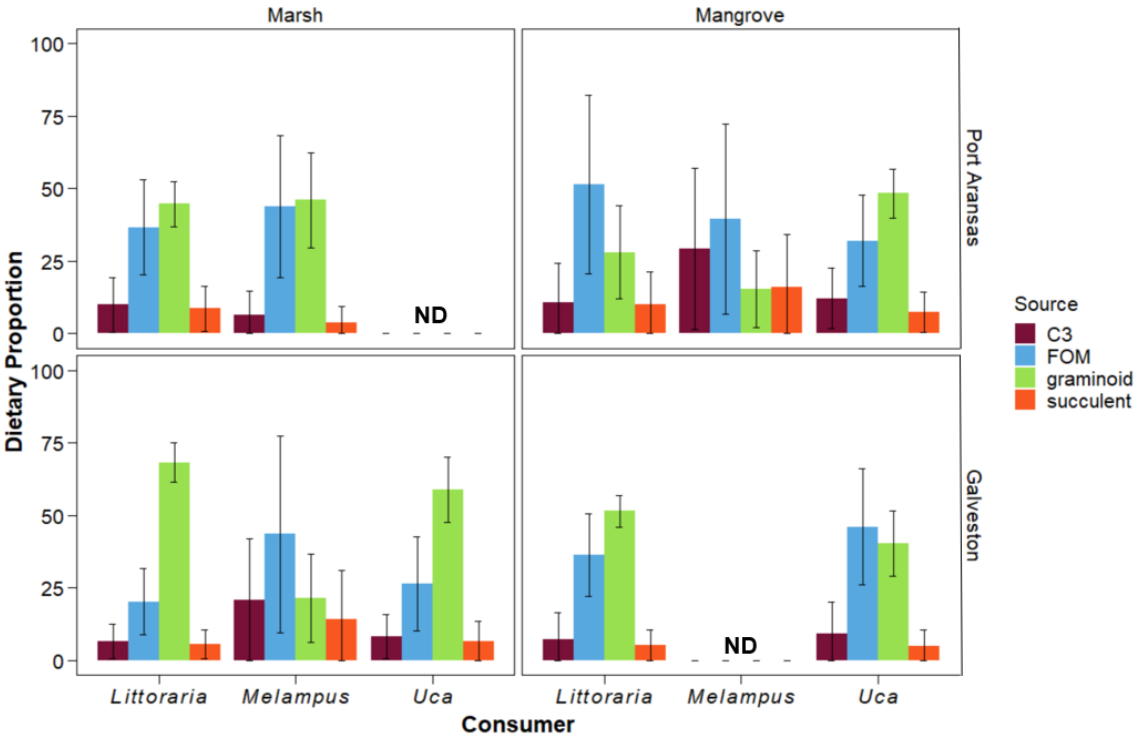

Figure 2.7: Mean (±SD) dietary proportions of *Littoraria*, *Melampus*, and *Uca* at each site as estimated by MixSIAR models.

The diets of *Uca* also contained more than 15% less graminoid material in mangrove sites than in marshes in Galveston (**Figure 2.7**), but the Port Aransas sites could not be compared as I was unable to collect crabs at the marsh sites. *Uca* burrows were abundant at both the high and low elevation of many sites, so contribution of graminoid plant material to *Uca* diets is likely from a combination of *Spartina* at low elevations and other grasses such as *Distichlis* and *Monanthochloe* at high elevations. The contributions of these high elevation graminoid species are likely especially important in the Port Aransas mangrove sites where graminoids still form

50% of *Uca* diets (**Figure 2.7**) and *Uca* isotopic signatures are similar to those of graminoid plants (**Figure 2.8**) despite *Avicennia* dominating the sites and *Spartina* being almost completely absent (**Figure 2.3a**).

For both *Littoraria* and *Uca*, a decrease in graminoid contribution to consumer diets between marsh and mangrove sites was mirrored by an increase in the contribution of FOM in all cases. This resulted in a noticeable shift in *Littoraria* and *Uca* isotopic signatures, although the signatures of both consumers remained far from those of *Avicennia* and other C3 plants (**Figure 2.8**). The estimated dietary proportion of FOM increased by 15-20% for both consumers between marsh and mangrove sites (**Figure 2.7**). This increase was substantial enough that FOM was the primary contributor to *Littoraria* diets in Port Aransas mangrove sites and to *Uca* diets in Galveston mangroves. In locations where it was not the primary food source FOM still composed a minimum of 20% of the diet, indicating that *Uca* and *Littoraria* were still consuming it in substantial amounts. There was a variation of ~4‰ in $\delta^{13}C$ between FOM sources at different sites (**Figure 2.8**), but the variation did not follow a consistent pattern with mangrove presence, and so is unlikely to reflect an influence of mangrove carbon on the FOM signature. This indicates that the increased consumption of FOM at encroached sites is not serving as a pathway for the incorporation of mangrove carbon into the food web.

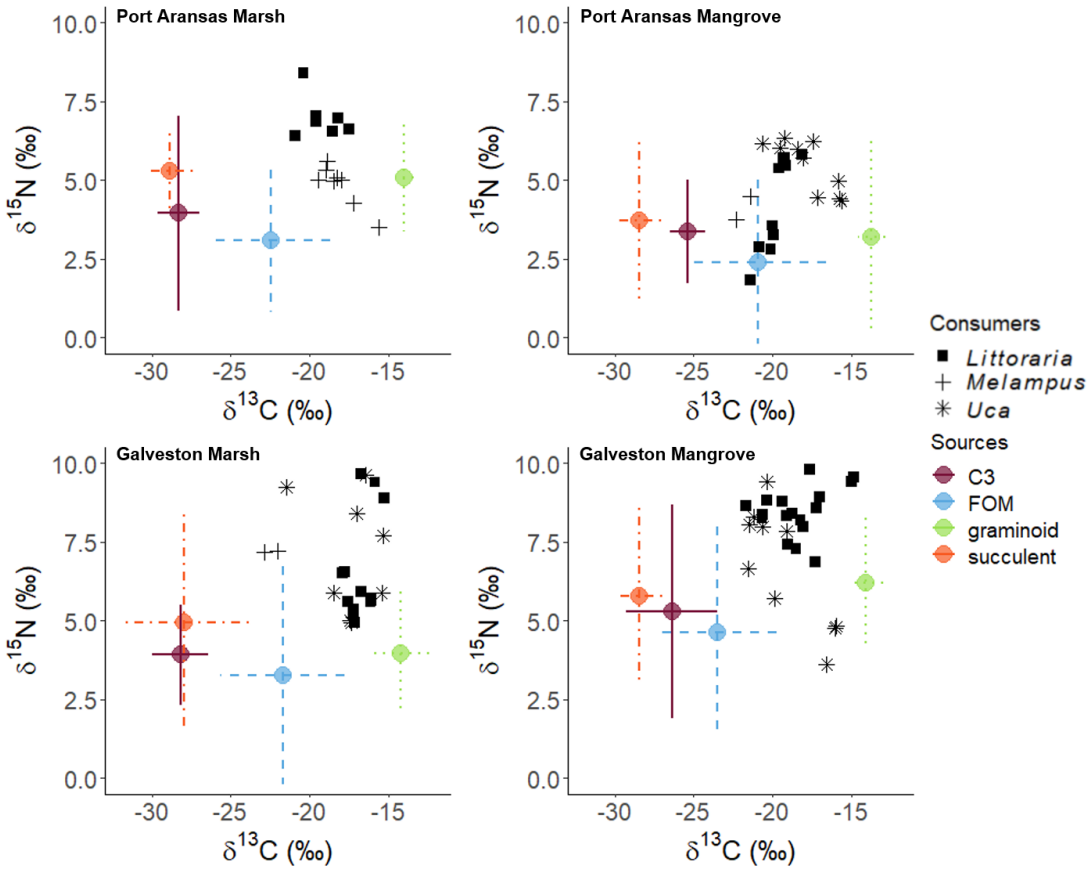

Figure 2.8: Stable isotope biplots showing the mean (±SD) carbon and nitrogen isotope ratios for each source group and consumer.

Melampus also consumed large quantities of both graminoids and FOM, especially at the Port Aransas marsh sites (**Figure 2.7**). Additionally, *Melampus* from the Port Aransas mangrove and Galveston marsh sites were the only consumers that incorporated moderate amounts of C3 plants and succulents into their diets, although the standard deviations on these dietary proportion estimates were very large (**Figure 2.7**). The low numbers of *Melampus* that were analyzed at these two sites (n =2 for each site) and the large standard deviations of all estimated source contributions may indicate that the models were unable to fully resolve the diets for *Melampus* at these two sites. Despite the uncertainty, models consistently found FOM or graminoid plants to be the primary contributor to *Melampus* diets at all sites, indicating that they

are relying on similar food sources and also incorporating little or no mangrove carbon into the food web.

2.4 Discussion

Consumer diets and physical associations with wetland plants shifted in mangrove encroached sites. The non-random distribution of consumers in wetlands indicated that they were selecting the habitats or plants with which they associate. All three consumers showed strong physical and trophic associations with *Spartina* at sites where it was abundant, although this association was most apparent in *Littoraria.* At the Port Aransas mangrove sites, both *Uca* and *Littoraria* switched to associating almost entirely with *Avicennia*, and no individuals were found associated with *Spartina* despite its occasional presence. Despite this strong physical association with mangroves, these species consumed little, if any, mangrove derived carbon even at the most highly encroached sites.

The stronger than expected associations of consumers with the most common plant at a site, regardless of its identity, suggests that this physical association is driven by the status of these plants as foundation species. Both *Spartina* and *Avicennia* possess rigid structures (the stems of *Spartina* and the pneumatophores of *Avicennia*) that allow *Littoraria* to vertically migrate away from predators and support the burrows of *Uca* (Vaughn and Fisher 1988, Lim and Rosiah 2007). The dense canopies formed by both of these plants also help prevent desiccation stress for *Littoraria* (Iacarella and Helmuth 2012) and protect *Uca* from predation by foraging wading birds (Lim and Heng 2007, Lantz et al. 2011). This functional similarity may explain why consumers strongly associate with *Avicennia* when *Spartina* is no longer present. At the Galveston mangrove site where both plant species were present, *Uca* and *Littoraria* were

strongly associated with *Spartina* and either avoided or associated randomly with *Avicennia* (**Table 2.2**), suggesting that *Spartina* was preferred as a foundation species. In the absence of *Spartina*, the characteristics of *Avicennia* appear to make it an acceptable substitute foundation species based on the strong reliance of basal consumers on *Avicennia* at the Port Aransas low elevation mangrove sites. In addition, it appears that *Batis maritima* may also be functioning as structural foundation species, at least for fiddler crabs, as there was a strong association between *Uca* and *Batis* at the high elevations of all sites. *Littoraria* showed no sign of association with *Batis* at high elevations and instead maintained their association with the most common plant species at the site.

It is important to note that plant community is not the only factor controlling basal consumer distribution. Environmental factors including salinity and hydrology can also affect faunal distributions (Thurman 1984, Montagna et al. 2008), as demonstrated by the lack of consumers at the Port Aransas marsh sites despite the abundance of *Spartina*. In order to locate sites lacking mangroves in Port Aransas, I had to travel to the back bay, away from the mouth of the estuary, where marsh sites are less saline and more hydrologically disconnected from the Gulf. As mangrove propagules and the aquatic larva of *Littoraria* and *Uca* are both reliant on tides and currents for dispersion (Bingham 1972, Press 2017), it is likely that these consumers have not established populations at these sites for the same reasons that *Avicennia* is absent. This discrepancy between *Spartina* and consumer occurrence demonstrates how foundation species and their associated fauna can become geographically decoupled in response to a foundational shift due to differences in environmental tolerances and dispersion techniques.

Basal consumer associations with particular plants do not serve as predictors of their trophic interactions. Despite associating strongly with *Avicennia* in some locations, *Littoraria*

incorporated very little mangrove carbon into their diets and instead begin to rely on FOM as a food source as their normal graminoid sources disappear. *Uca* also relied mainly on graminoids and FOM for food. Consumption of FOM as opposed to a combination of C3 and graminoid plants was difficult to determine based on $\delta^{13}C$ alone, as the $\delta^{13}C$ values of FOM sources were approximately the average of the values of C3 and graminoid plants at all sites. I was able to resolve the dietary contributions with the inclusion of $\delta^{15}N$ values in the models however, and the lack of C3 contribution is further supported by the food preference trials documented later in this dissertation (**Sections 3.3.1, 4.3.1**) that indicate basal consumers avoid consuming *Avicennia*.

The disconnect between physical and trophic association is further demonstrated by *Uca*, as despite the majority of burrows being located in the high marsh and associated with *Batis*, crabs incorporated almost no succulent carbon into their diet. The shifts in *Uca* diets with mangrove encroachment were less extreme than those in *Littoraria*, and graminoids continued to be the primary contributing source to *Uca* diets at the heavily encroached Port Aransas mangrove sites. This was unexpected, given the low abundance of graminoid plants at the heavily encroached sites, but is supported by other studies that have also found *Uca* to rely on graminoid carbon at mangrove dominated sites (Baker et al. 2021). As crabs were observed most commonly in the high marsh, they may be consuming *Monanthochloe*, which was the most common high marsh graminoid at the Port Aransas mangrove sites. *Monanthochloe* only covered 13% of the high marsh in these sites, but 23% of crab burrows were found in quadrats dominated by it. Additionally, these burrow counts may be underestimates, as *Monanthochloe* often occurred in very dense low-lying mats that made it difficult to observe burrows or pseudofeces on the ground.

The only basal consumer studied here that may be incorporating *Avicennia* into coastal wetland food webs was *Melampus*. While *Melampus* was too rare to assess patterns of physical association with vascular plants, stable isotope mixing models suggested that they consumed mainly FOM, supplemented by a moderate amount of C3 photosynthesizers at some sites. The uncertainty of these dietary estimates and overall low abundance of *Melampus* across sites means that it is unlikely *Melampus* are important consumers of mangrove carbon. However, at high abundances, they may have a role in incorporating carbon from mangroves or other recalcitrant plants into the food web.

Taken together, these observations indicate that while *Avicennia* is filling a foundational role structurally, it is not serving as a foundational species from a trophic perspective. This means that while basal consumers will continue to exist and find suitable habitat in encroached wetlands, they will have to turn to alternate energy pathways. Cases such as this involving a transition of foundational species and a loss of trophic, but not physical, functional support are very rare, so it is difficult to predict what the higher-level trophic consequences will be. Ecosystems that experience a foundational species disappearance often see a decrease in abundance of organisms that are trophically reliant on the foundation species and a loss in diversity (Ellison et al. 2005, Butterfield et al. 2012, Youngquist et al. 2017), but the continued abundance of crabs and snails in encroached marshes suggests this has not yet occurred in this region.

There is limited and somewhat contradictory evidence from other studies of shifts in faunal abundance and trophic interactions as a result of mangrove encroachment (Scheffel et al. 2018, Nelson et al. 2019, Walker et al. 2019, Armitage et al. 2021, Baker et al. 2021). Many of these studies have focused on highly mobile organisms such as nekton and fish, which can

change their distribution and locate alternative food sources more easily than benthic invertebrates like snails and fiddler crabs. The inability of benthic invertebrates to relocate means that they are more strongly affected by the characteristics of the site they inhabit and are likely to have the strongest and most immediate responses to foundational shifts. Other studies that focused on benthic invertebrates have also found distributional and trophic responses to mangrove encroachment. Walker et al. (2019) reported a slight pattern of higher crab burrow and snail abundance in marsh versus mangrove sites and Baker et al. (2021) also found that *Uca* do not incorporate mangrove carbon, even at mangrove dominated sites. While these studies did not look at distribution and trophic interactions together as I have here, they support my conclusions that basal consumers will associate physically with *Avicennia*, although they prefer *Spartina*, and that mangroves are not providing trophic support in the systems they encroach. Future efforts to determine the large-scale consequences of mangrove encroachment should seek to examine the responses of additional basal consumers in other regions and to clarify the uncertainty in the responses of more mobile fauna. Finding answers to these questions and detecting consistent responses across the different states and countries where mangrove encroachment is occurring will require long-term monitoring of sites undergoing encroachment and addressing natural geographic variation through standardized data collection and advanced statistical techniques (Ellison 2019, Ziegler et al. 2021).

In addition to understanding the large-scale effects mangrove encroachment will have on ecosystems and communities, we must also understand the small-scale behavioral and physiological changes that are driving these faunal shifts. Gaining insight into the reasons why basal consumers do not consumer mangrove plant matter and the effects of their shifting diets will help us understand how carbon sequestration and energy flow in marshes may change with

mangrove encroachment. Mangroves are valued for their high primary productivity in some systems (Nagelkerken et al. 2008), but without basal consumers processing the highly recalcitrant mangrove plant material in ways that make it more easily decomposable and biologically available to higher level consumers (Cebrian 2004), encroached wetlands may not gain these benefits. Knowing the details of the interactions between basal consumers and *Avicennia* will help us understand not only the ecosystem-level effects of mangrove encroachment, but the driving forces behind these effects.

Conclusion

This study exemplifies the importance of looking at multiple dimensions of plant-animal interactions, particularly those interactions with foundational species that have a strong potential to influence entire ecosystems. Co-occurrence cannot be assumed to indicate trophic reliance as shown by the discrepancy between *Uca* and *Littoraria* physical associations and dietary contributions. Similarly, plants that consumers are not interacting with trophically can still influence consumer diets. In this case, the presence of *Avicennia* led to increased reliance on FOM. Community-ecosystem linkages are highly complex and must be investigated from multiple angles, so researchers should avoid drawing general conclusions from the results found at a single site or in a single region. Collecting data from across multiple sites and regions, as I did here, is necessary to minimize the impact of site-specific factors. Even then, while the results presented here may reflect the responses of basal consumers to mangrove encroachment along the coast of Texas, consumers in Louisiana and Florida may not associate with *Avicennia* if other plants are present or environmental characteristics allow them to relocate, and may rely on food sources besides FOM if alternate producers such as different vascular plants, epiphytes, and macroalgae are present (Nelson et al. 2019, Baker et al. 2021). The results of this study

contribute to a growing body of literature that demonstrate the complex and multi-faceted ways that fauna are responding to mangrove encroachment and foundational shifts in general.

3. COASTAL WOODY ENCROACHMENT REDUCES FOOD QUALITY FOR A BASAL CONSUMER AND ECOSYSTEM ENGINEER*

3.1 Introduction

Woody encroachment is a phenomenon where native or invasive woody shrubs are released from their controls, often through anthropogenic ecosystem alterations, which leads to an increase in abundance or density of trees and shrubs at the expense of native grasses and forbs. Its occurrence has been well documented in terrestrial systems such as savannas, deserts, and grasslands (Eldridge et al. 2011, Naito and Cairns 2011). In these systems, woody encroachment often decreases plant species richness, increases soil carbon and nitrogen, increases carbon sequestration, and alters evapotranspiration dynamics (Eldridge et al. 2011, Ratajczak et al. 2012, Saintilan and Rogers 2015). Woody encroachment is also occurring in some subtropical coastal environments, where mangrove trees are overtaking salt marshes (Saintilan et al. 2014), and many similar trends have been identified in these environments (Saintilan and Rogers 2015, Kelleway et al. 2017, Armitage et al. 2021).

Such consequences of woody encroachment in both terrestrial and wetland ecosystems are well documented, but the bottom-up trophic effects of encroachment on basal consumers are largely unknown. Fauna may respond negatively when the plant community changes due to woody encroachment, but the majority of studies on this topic are focused on terrestrial systems, largely taxa specific, and focus more on faunal diversity than trophic effects (Blaum et al. 2009, Sirami et al. 2009, Stanton et al. 2018). Some recent findings in areas where mangrove

* Parts of the data reported in this chapter are reprinted with permission from "Coastal woody encroachment reduces food quality for basal consumers" by Janelle .A. Goeke and Anna .R. Armitage, 2021, *Ecosphere*, 00, e03511.

encroachment is occurring indicate that mangroves support different faunal assemblages than marshes (Smee et al. 2017, Scheffel et al. 2018, Armitage et al. 2021), but just as in terrestrial environments, the trophic consequences of these differences are unknown. Basal consumers control the entry of plant carbon into the food web, so understanding their trophic interactions with encroaching plant species is necessary for understanding how the flow of carbon through the food web could change in encroached ecosystems (Cebrian 2004).

Coastal wetlands are structured by a multitude of stressors including inundation, salinity stress, and wave action. These stressors create an ecosystem with relatively low plant and animal diversity (Hacker and Bertness 1999), and therefore provide a simplified landscape to examine the effects of woody encroachment on species interactions. The low diversity reveals strong and easily observable interactions between plants and their consumers, as opposed to the larger number of weak interactions expected in a higher diversity environment (Thébault and Loreau 2005). Overall, this makes coastal wetlands an ideal location to study the trophic responses of basal consumers to woody encroachment.

Along the Gulf Coast of Texas, the encroachment of black mangrove trees (*Avicennia germinans*, hereafter *Avicennia*) into salt marshes affects the density and abundance of the dominant grass species (*Spartina alterniflora*, hereafter *Spartina*) and common succulents (generally *Batis maritima* and *Sarcocornia* spp.) (Armitage et al. 2021). *Spartina* is an important dietary component of many salt marsh basal consumers, including gulf coast fiddler crabs (*Uca* spp.), which are abundant generalist consumers that typically consume detrital organic material derived from marsh plants (such as *Spartina*) and benthic microalgae (Currin et al. 1995). In addition to being important consumers, fiddler crabs are also ecosystem engineers. Their burrowing causes bioturbation, which increases soil aeration, boosts plant growth, reduces soil

organic content, and affects soil physical and biogeochemical processes (Reinsel 2004, Holdredge et al. 2010, Wang et al. 2010). As mangrove encroachment progresses, fiddler crabs may be forced to rely on new, mangrove-derived carbon sources. My objective was to enhance the understanding of how coastal woody encroachment affects basal consumers by evaluating trophic interactions between *Uca* spp. and *Avicennia* and *Spartina* plant matter. To this end, I investigated (1) if fiddler crabs exhibited a feeding preference for *Spartina* or *Avicennia* plant matter; and (2) if *Spartina* and *Avicennia* provided food sources of different quality for fiddler crabs. Based on the higher tannin and phenolic contents of *Avicennia* relative to *Spartina* (Erickson et al. 2004, Nordhaus and Wolff 2007), I hypothesized (1) that fiddler crabs would prefer to consume *Spartina* over *Avicennia* plant matter and (2) that *Spartina* would be a higher quality food source.

3.2 Materials and Methods

3.2.1 Background and Lab Preparations

Fiddler crabs were caught by hand in May 2018 and 2019 from four un-encroached marshes surrounding Galveston Bay (**Figure 2.2**). The majority of the crabs were sourced from the North Jetty on Bolivar Peninsula (29.37^{o} N, 94.75^{o} W), with a smaller number being obtained from Sportsman Road (29.25^{o} N, 94.92^{o} W), Sunset Cove (29.15^{o} N, 95.03^{o} W), and Clipper Marsh (29.31^{o} N, 94.82^{o} W) on Galveston Island. Crabs were placed in 10-gallon tanks (20-40 crabs per tank) with 20 ppt salinity filtered seawater and cleaned, store-bought sand to create a semi-terrestrial habitat with a non-submerged area of sand. During acclimation, crabs were fed store-bought hermit crab food.

There are three sympatric species of fiddler crabs that commonly occur along the Gulf

Coast of Texas: *Uca panacea*, *Uca rapax*, and *Uca longisignalis*. All three species occupy marsh habitats and fill similar ecological niches (Barnwell and Thurman 1984). Although I expected all species to respond similarly to mangrove encroachment, species was included as a factor to ensure detection of any unanticipated species-specific diet responses. All fiddler crab species feed by using their mouthparts to sift out organic matter from inorganic sediment. Organic matter is consumed, and sediment is deposited onto the surface as balls, called pseudofeces, which serve as an indicator of relative feeding activity (**Figure 3.1**).

Figure 3.1: Pseudofeces in a feeding dish following a feeding preference trial

Fallen dead *Avicennia* leaves and standing dead *Spartina*, including stems and leaves, were collected from an encroached marsh on Galveston Island. Plants were rinsed with distilled water, then dried in an oven at 60^{o}C for 24 hours. Dried plants were ground using a Thomas-Wiley Mill (model # 3383-L10) and filtered through 250 μm mesh to produce particles in the size range that fiddler crabs consume (Colpo and Negreiros-Fronsozo 2011). Experimental diets

were created by mixing ground plant powder with cleaned sand to emulate detrital food.

3.2.2 Food Preference Trials

To assess fiddler crab preference for *Spartina* and *Avicennia*, food preference trials were conducted where crabs were allowed to feed freely on the two plant diets and a control diet of cleaned sand. Five trials were performed with each of the three species. Trials were performed over the course of two summers due to time and equipment constraints, with eight trials in summer 2018 and seven trials in summer 2019. Trials for each species were evenly distributed among years, with 2-3 trials per species each year.

For each trial, five female and five male crabs of a single species were removed from the holding tanks and placed in a 10-gallon starvation tank, which contained 0.5 L of 20 ppt filtered seawater. Crabs were starved for 48 hours, then moved to a 2-m diameter feeding arena that contained three L of 20 ppt filtered seawater, nine dishes (three of each diet) evenly spaced around the circumference of the tank, and short sections of PVC pipe to simulate burrows (**Figure 3.2**). Each dish was filled with sand, and for the *Spartina* and *Avicennia* diets, 2 ml of the prepared diet was gently mixed with the sand surface. The surface was then smoothed to ensure that any pseudofeces produced would be easily detectable.

Dishes of each diet were placed around the tank in a random order, which was changed every trial. Crabs were allowed to feed freely for 24 hours, then the nine feeding dishes were removed from the arena, and the pseudofeces present on the surface of each dish were counted to determine relative feeding intensity.

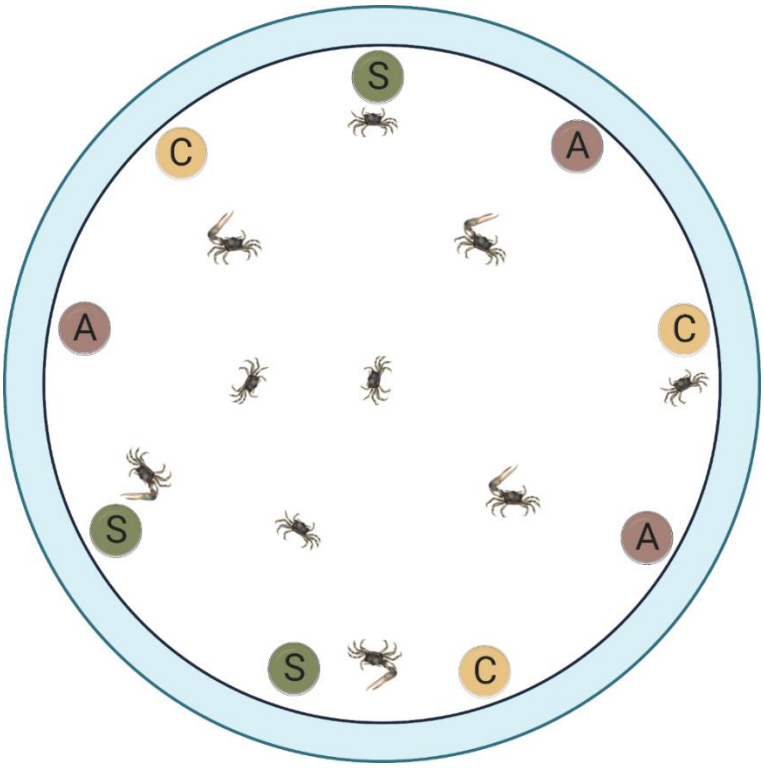

Figure 3.2: Feeding preference arena schematic. Letters in dishes represent diets (C = Control, S = *Spartina*, A = *Avicennia*) in example arrangement.

3.2.3 Food Quality

A food quality trial was used to compare *Uca* hepatopancreatic energy storage when crabs were restricted to a diet of either *Spartina* or *Avicennia* material for 60 days. Five males and five females of each species were assigned to each diet. Individual crabs were housed in 5.7 L plastic bins containing 0.35 L of 20 ppt filtered seawater, 0.5 L of cleaned sand, and 2 mL of their assigned diets spread over the surface of the sand. Bins were cleaned and provided with new food weekly for the duration of the experiment. Weight was recorded for each individual before and after the experiment, and all observed molts throughout the experiment were recorded. After 60 days, crabs were euthanized by freezing and the hepatopancreas was dissected out of each crab. The hepatopancreas was weighed then divided in two, half for use in CHN

analysis and half for lipid content analysis. The weight of the total hepatopancreas was used to calculate the hepatosomatic index (HSI) for each crab using equation 3.1.

(3.1) $$HSI = 100 \times \frac{Hepatopancreas\ wet\ weight}{Crab\ body\ wet\ weight}$$

Hepatopancreas lipid content was calculated to determine the relative diet quality of each food source. The hepatopancreas serves as the main energy storage organ in crustaceans and its lipid content is sensitive to the effects of starvation and energetically expensive processes, and is thus a proxy for physiological condition (Cockcroft 1997, Sánchez-Paz et al. 2007). Lipids are very carbon rich molecules, so a high lipid content also often corresponds with a higher C:N ratio. As the hepatopancreas is important for energy storage, calculating the HSI allows me to determine what proportion of an individual crab's weight is potentially being used for energy storage.

Lipid content of the hepatopancreas tissue was measured using methods adapted from Parrish (1999). Each hepatopancreas was weighed to determine the wet mass of the organ, then stored in chloroform at -20^{o}C until analysis. For analysis, methanol was added to make a 2:1 chloroform:methanol mixture and the sample was homogenized using a polystyrene pestle. The sample was centrifuged, the supernatant was removed by pipetting, and distilled water was added to the remaining sample. The mixture was then homogenized and centrifuged again. The lower organic layer, consisting of the isolated lipids, was transferred to a pre-weighed Eppendorf tube, and dried under a stream of nitrogen to evaporate the solvent. After drying, the tube was reweighed to determine the total mass of lipids.

Hepatopancreas tissue was prepared for CHN analysis by drying in an oven at 60^{o}C for a minimum of 24 hours. Dried tissue was ground to a powder and analyzed on a Costech ECS 4010 CHNSO Analyzer to determine the percent carbon and nitrogen content. These values were

corrected for molecular weight and used to calculate the hepatopancreatic C:N ratio.

3.2.4 Field Body Condition

To determine the effect of *Avicennia* on *Uca* physiological condition in the field, crabs were collected from a previously established experimental site in Port Aransas, Texas (27.86° N, 97.06° W). The experimental site consisted of 10 plots with mangrove cover ranging from 0 to 100%; this cover gradient has been experimentally maintained since 2012 (Guo et al. 2017). *U. rapax* is the most common fiddler crab species in these plots, so as many *U. rapax* as could be located (up to five per plot) were collected from each of the three lowest (0, 11, and 22%) and three highest (77, 88, and 100%) mangrove cover experimental plots. Crabs were collected from burrows within patches of the dominant vegetation of the site (marsh plants or *Avicennia*) in order to increase the likelihood of recent interactions with the targeted plant. Following collection, crabs were frozen until return to the lab. In the lab, the species was confirmed, and the sex of each collected crab was recorded. The HSI and hepatopancreas lipid content were determined for each *U. rapax* following the procedures outlined above, with the modification that the entire hepatopancreas was used in the lipid extraction since I did not analyze the C:N ratio of the field collected crabs.

3.2.5 Data Analysis

In the food preference trials, t-tests of pseudofeces counts showed no difference between years in the relative amount of feeding activity on either the *Spartina* diet ($t = -1.3029$, $df = 7.0087$, $p = 0.2338$) or the *Avicennia* diet ($t = -0.1050$, $df = 9.3311$, $p = 0.9186$), so year was excluded as a factor in the final analysis. Food preference of each fiddler crab species was analyzed using a permutation based randomization test as described by Bärlocher (2005) using R v. 3.6.0 (R Development Core Team 2020). The test statistic used was the sum of squared

deviations of the average pseudofeces counts, and the permutation was repeated 100,000 times for each species.

For the food quality trial, % weight change was calculated using the pre- and post-trial weights. Total lipid content was standardized by dividing by the hepatopancreas wet weight for each crab. The resulting % weight changes and hepatopancreas lipid concentrations were normally distributed and homoscedastic, as was HSI. Hepatopancreas C:N was homoscedastic but non-normally distributed, so was transformed with a reciprocal root transformation before further analysis. Weight change, hepatopancreas lipid concentration, HSI, and hepatopancreas C:N were then analyzed with separate three-way ANOVA, where the independent factors were crab sex, species, and diet.

The HSI and hepatopancreas lipid concentration of field-collected crabs were both normally distributed and homoscedastic. Both metrics were analyzed with two-way ANOVA using crab sex and dominant plot vegetation (marsh or mangrove) as independent factors. Identity of the six individual collection plots could not be used as a factor due to the low number of crabs found in some plots. Pooling data for the three low mangrove cover and three high mangrove cover plots yielded high enough sample sizes for analysis.

3.3 Results

3.3.1 Feeding Preference

Each of the three *Uca* species showed a strong preference for the *Spartina* diet (*U. rapax*: $S = 879.14$, $p = 0.0023$, *U. longisignalis*: $S = 1160.63$, $p = 0.0005$, *U. panacea*: $S = 3402.24$, $p = 0.0040$). All species produced at least three times more pseudofeces on the *Spartina* diet than on the *Avicennia* and control diets, and there was no preference for *Avicennia* plant matter over the

control diet (**Figure 3.3**). Pseudofeces counts were highly variable, particularly on the *Spartina* diet, where the average number of pseudofeces produced ranged from 5 to more than 180. Such extreme pseudofeces counts were uncommon however, and 11 of the 15 trials had *Spartina* pseudofeces counts between 20 and 70. Extreme values generally corresponded to a trial with abnormally high or low feeding across all diets. Counts on the other two diets were much less variable, with ranges from 3 to 27 for *Avicennia* and 0 to 11 for the control.

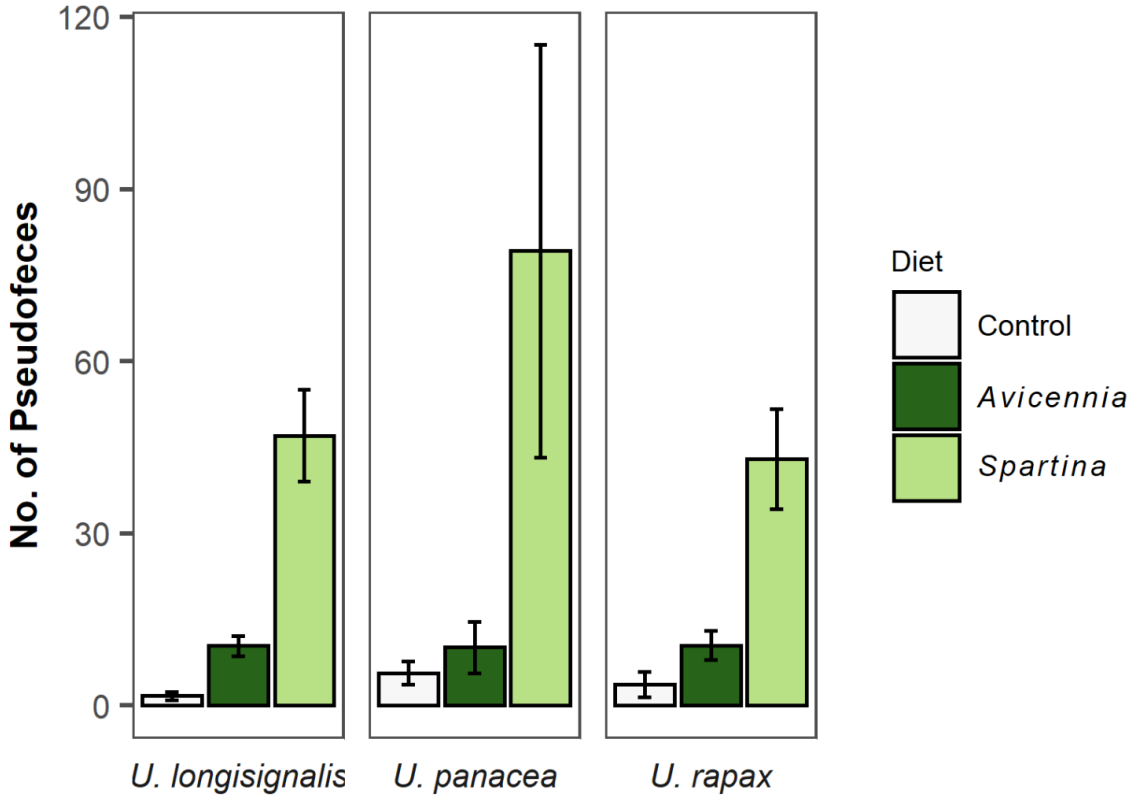

Figure 3.3: Average number of pseudofeces formed on each diet by *U. longisignalis*, *U. panacea*, and *U. rapax*. Colors represent different diet and bars are means ± standard error. (n = 5)

3.3.2 Food Quality

Survival was > 95% on both diets; one male *U. longisignalis* on the *Avicennia* diet and one female *U. longisignalis* on the *Spartina* diet died over the course of the trial and were excluded from the final analysis. *Uca* weight was not affected by diet, sex, or species over the course of the experiment (**Table 3.1**), and four crabs per diet molted. Lipid concentration of the hepatopancreas was 50-100% higher on the *Spartina* diet than on the *Avicennia* diet for all species (**Figure 3.4, Table 3.1**). There was an interaction between diet and species; the difference in lipid content between diets was most pronounced in *U. panacea* and least pronounced in *U. longisignalis* (**Figure 3.4, Table 3.1**). There was no effect of sex on lipid content, nor any other interactions between factors (**Table 3.1**).

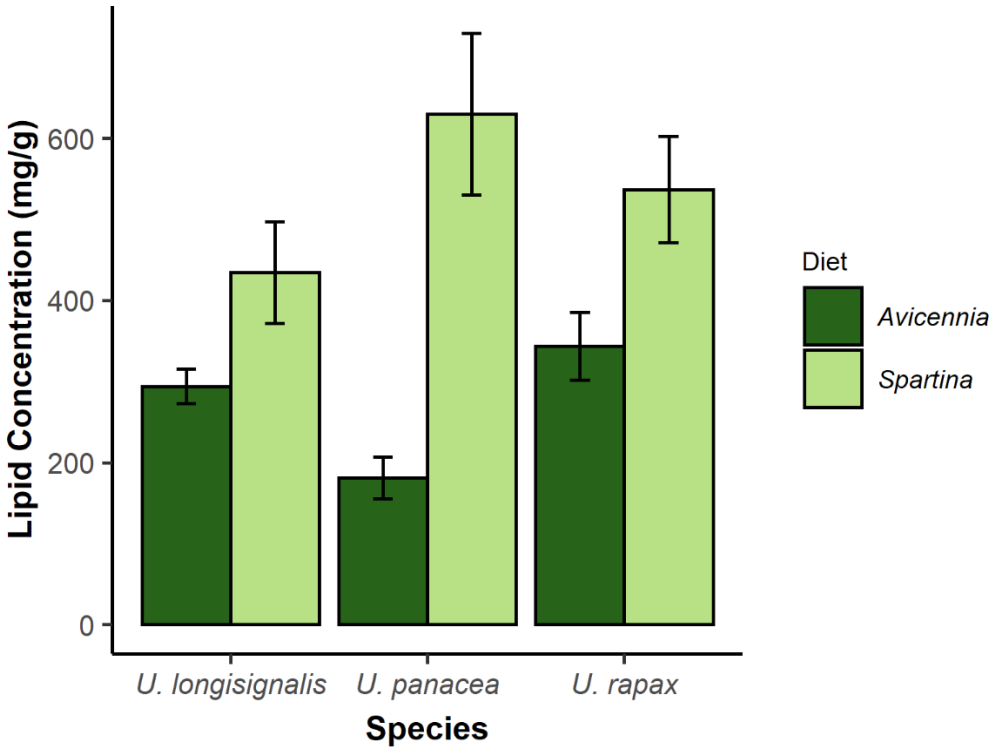

Figure 3.4: Average hepatopancreas lipid concentration of each species on each diet, standardized by wet weight of the hepatopancreas. There was no significant effect of sex on

hepatopancreas lipid concentration, so bars represent both sexes of a given species on a given diet. Colors represent diets and bars are means ± standard error (n=10).

Table 3.1: Results of three-way ANOVA of the effects of diet (*Avicennia* vs. *Spartina*), sex, and species (*U. rapax*, *U longisignalis*, and *U. panacea*) on hepatopancreas lipid content.

Lipid Content	**Degrees of Freedom**	**F-Statistic**	**p-value**
Diet	1	182.95	**<0.001 ***
Species	2	0.03	0.451
Sex	1	0.23	0.056
Diet:Species	2	13.53	**0.034 ***
Diet:Sex	1	1.39	0.388
Species:Sex	2	0.69	0.822
Diet:Species:Sex	2	0.80	0.922

Hepatopancreatic C:N was unaffected by sex, species, and diet over the course of the experiment (**Figure 3.5, Table 3.2**). HSI values were also unaffected by both sex and diet (**Figure 3.6, Table 3.3**). There was an effect of species, with the average HSI increasing from approximately 6 in *U. longisignalis* to 7.5 in *U. panacea* to 10 in *U. rapax*. This is most likely an artifact of species weight, as *U. longisignalis* crabs were naturally the heaviest, followed by *U. panacea* and *U. rapax* (**Figure 3.7**). A one-way ANOVA showed no difference in hepatopancreas weight by species ($F = 1.266$, $p = 0.29$), and a higher body weight at a given hepatopancreas weight results in a lower HSI. The relationship between HSI and species is therefore being driven by natural differences in size between species instead of species-specific changes in hepatopancreas weight.

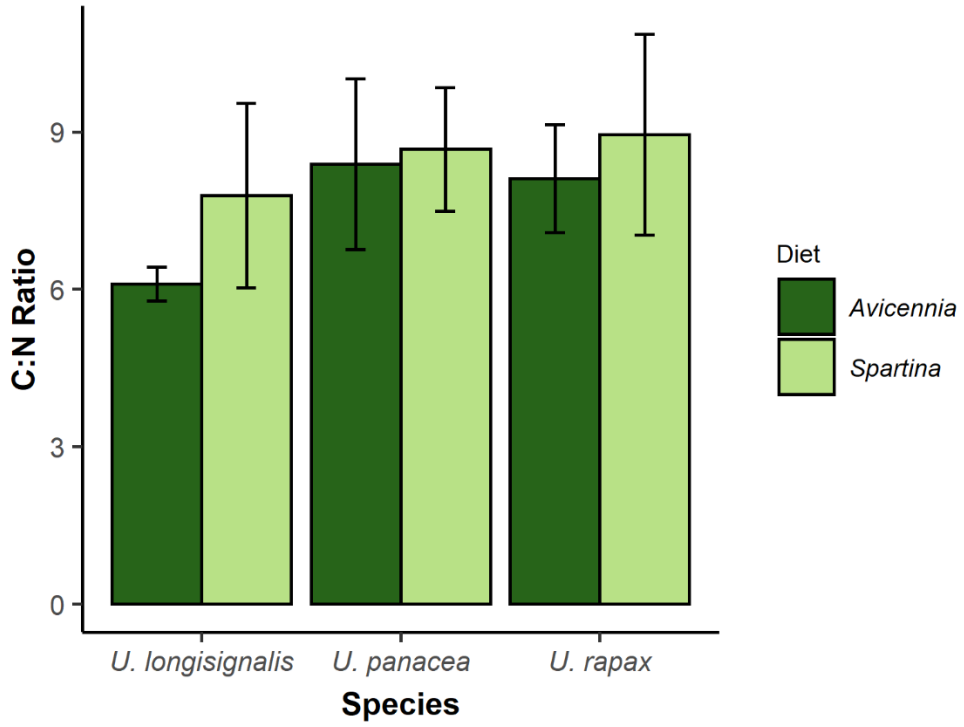

Figure 3.5: Average hepatopancreatic C:N ratio of each species on each diet. There was no significant effect of sex on C:N ratio, so bars represent both sexes of a given species on a given diet. Colors represent diets and bars are means ± standard error.

Table 3.2: Results of three-way ANOVAs of the effects of diet (*Avicennia* vs. *Spartina*), sex, and species (*U. rapax*, *U longisignalis*, and *U. panacea*) on hepatopancreatic C:N ratio of crabs over the 60-day experimental period.

C:N Ratio	**Degrees of Freedom**	**F-Statistic**	**p-value**
Diet	1	0.08	0.783
Species	2	0.21	0.810
Sex	1	1.66	0.205
Diet:Species	2	0.13	0.875
Diet:Sex	1	0.14	0.714
Species:Sex	2	0.36	0.702
Diet:Species:Sex	2	0.82	0.447

Table 3.3: Results of three-way ANOVA of the effects of diet (*Avicennia* vs. *Spartina*), sex, and species (*U. rapax*, *U longisignalis*, and *U. panacea*) on hepatosomatic index.

HSI	**Degrees of Freedom**	**F-Statistic**	**p-value**
Diet	1	0.07	0.789
Species	2	8.23	**<0.001 ***
Sex	1	2.21	0.144
Diet:Species	2	0.15	0.861
Diet:Sex	1	0.17	0.684
Species:Sex	2	2.02	0.144
Diet:Species:Sex	2	1.50	0.234

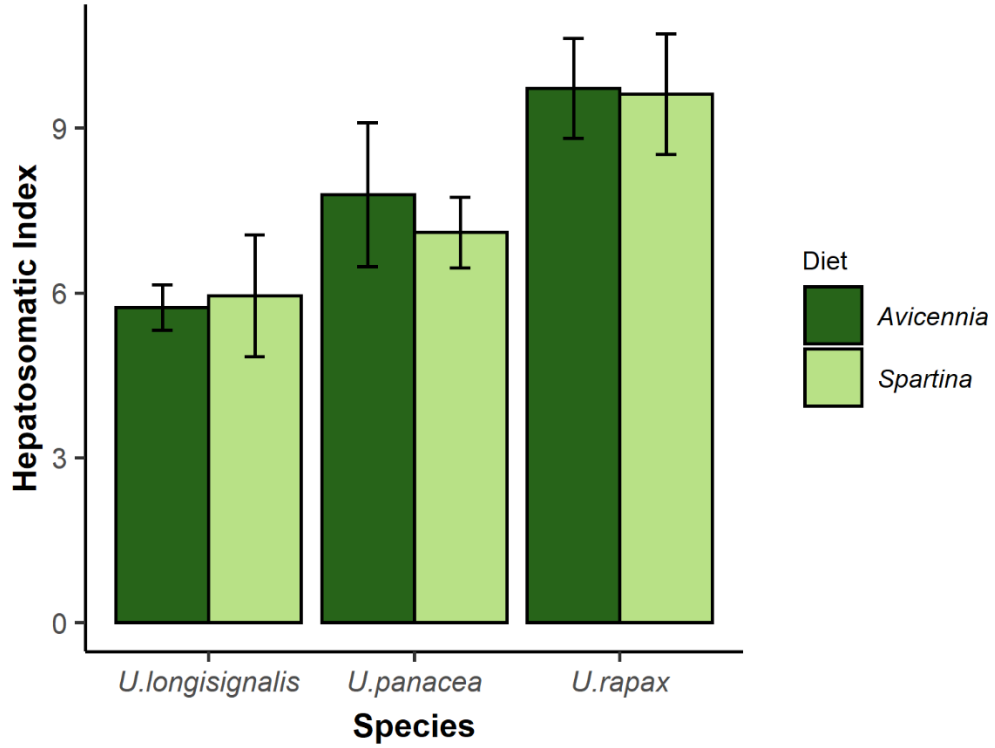

Figure 3.6: Average hepatosomatic index value of each species on each diet. There was no significant effect of sex on HSI, so bars represent both sexes of a given species on a given diet. Colors represent diets and bars are means ± standard error.

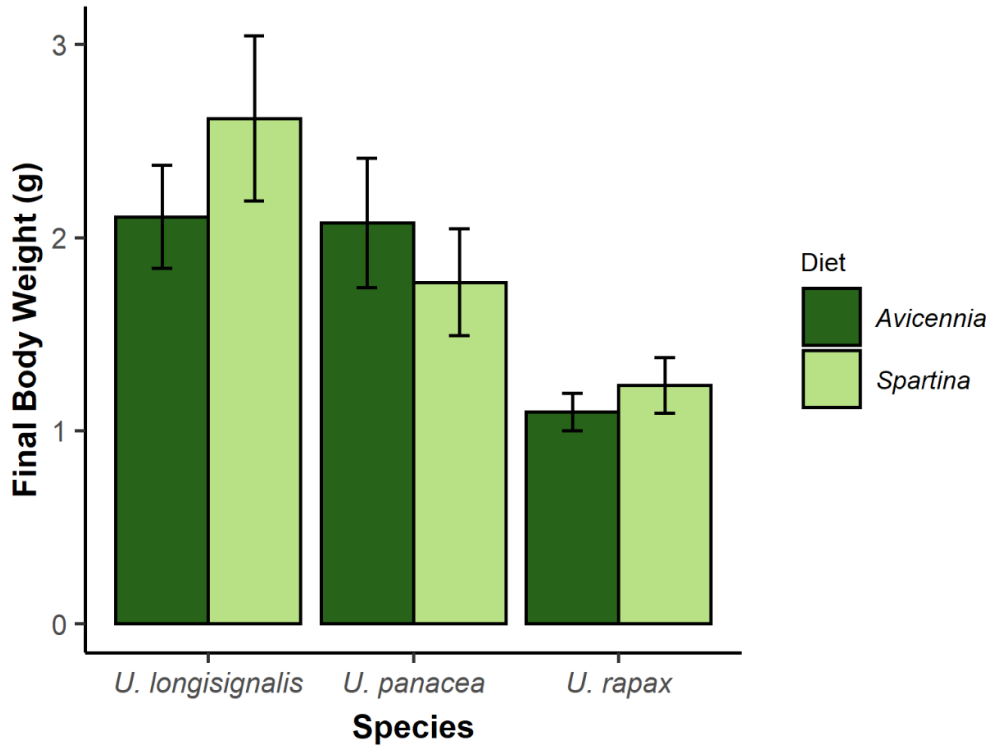

Figure 3.7: Average final body weights of each crab species. Bars are means ± standard error (n=20).

Table 3.4: Results of three-way ANOVA of the effects of diet (*Avicennia* vs. *Spartina*), sex, and species (*U. rapax*, *U longisignalis*, and *U. panacea*) on weight change of crabs over the 60-day experimental period.

Weight Change (%)	**Degrees of Freedom**	**F-Statistic**	**p-value**
Diet	1	0.08	0.783
Species	2	0.21	0.810
Sex	1	1.66	0.205
Diet:Species	2	0.13	0.875
Diet:Sex	1	0.14	0.714
Species:Sex	2	0.36	0.702
Diet:Species:Sex	2	0.82	0.447

Although there were weight differences between species, there was no effect of species, sex, or diet on weight change over the course of the experiment (**Figure 3.8, Table 3.4**). Only 5 of the surviving 58 crabs had gained weight by the end of the experiment, and 4 of those 5 were

crabs that had molted. The average percent weight loss across all crabs was -3.28 ± 3.94%. *Uca* are between 57 – 65% water by weight, and the percent water content fluctuates over time. The weight loss observed in this experiment is therefore most likely due to a slight decrease in water content between the initial and final weights, possibly as a result of a longer wait time between removal from tanks and weighing at the experiment end.

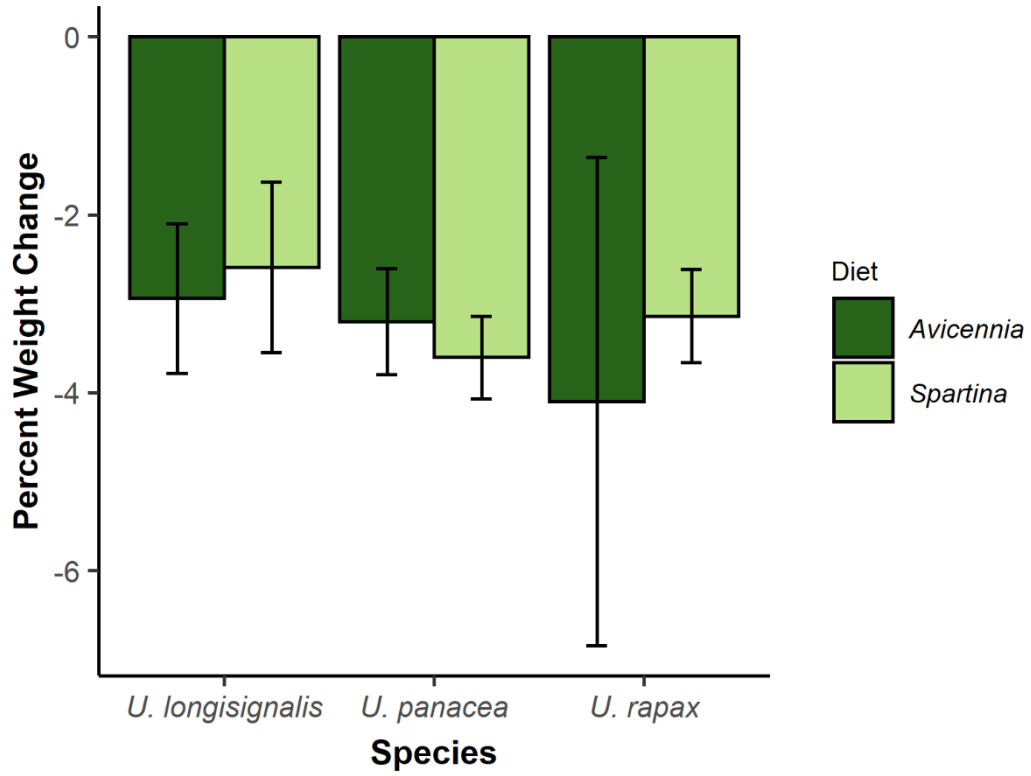

Figure 3.8: Average weight change of each species on each diet. There was no significant effect of sex on weight change, so bars represent both sexes of a given species on a given diet. Colors represent diets and bars are means ± standard error. (n=10)

3.3.3 Field Body Condition

Hepatosomatic index (HSI) of crabs collected from the field was highly variable

but was generally lower in sites with higher mangrove cover (**Table 3.5**, **Figure 3.9a**). Individual sex also had a strong effect on HSI with males having lower HSI values than females in all plots (**Table 3.5**). However, this was likely an artifact of male crabs having higher body weights owing to the presence of the major cheliped. Higher body weights in males was observed in the lab trials as well but was tempered by the larger sample sizes and the strong effect of species on HSI. Hepatopancreatic lipid concentration in field-collected crabs was also highly variable but was generally similar across all plots and sexes (**Table 3.6**, **Figure 3.9b**).

Table 3.5: Results of the two-way ANOVA of the effects of plot type and crab sex on hepatosomatic index (HSI) of *Uca rapax* crabs collected from Port Aransas experimental plots; p-values below 0.05 are indicated in bold.

HSI	**df**	**F-Statistic**	**p-value**
Plot Type	1	12.65	**0.002**
Sex	1	28.09	**<0.001**
Plot Type:Sex	1	2.15	0.158

Table 3.6: Results of the two-way ANOVA of the effects of plot type and crab sex on hepatopancreas lipid concentration of *Uca rapax* crabs collected from Port Aransas experimental plots; p-values below 0.05 are indicated in bold.

Lipid Concentration	**df**	**F-Statistic**	**p-value**
Plot Type	1	0.39	0.540
Sex	1	0.07	0.799
Plot Type:Sex	1	3.48	0.076

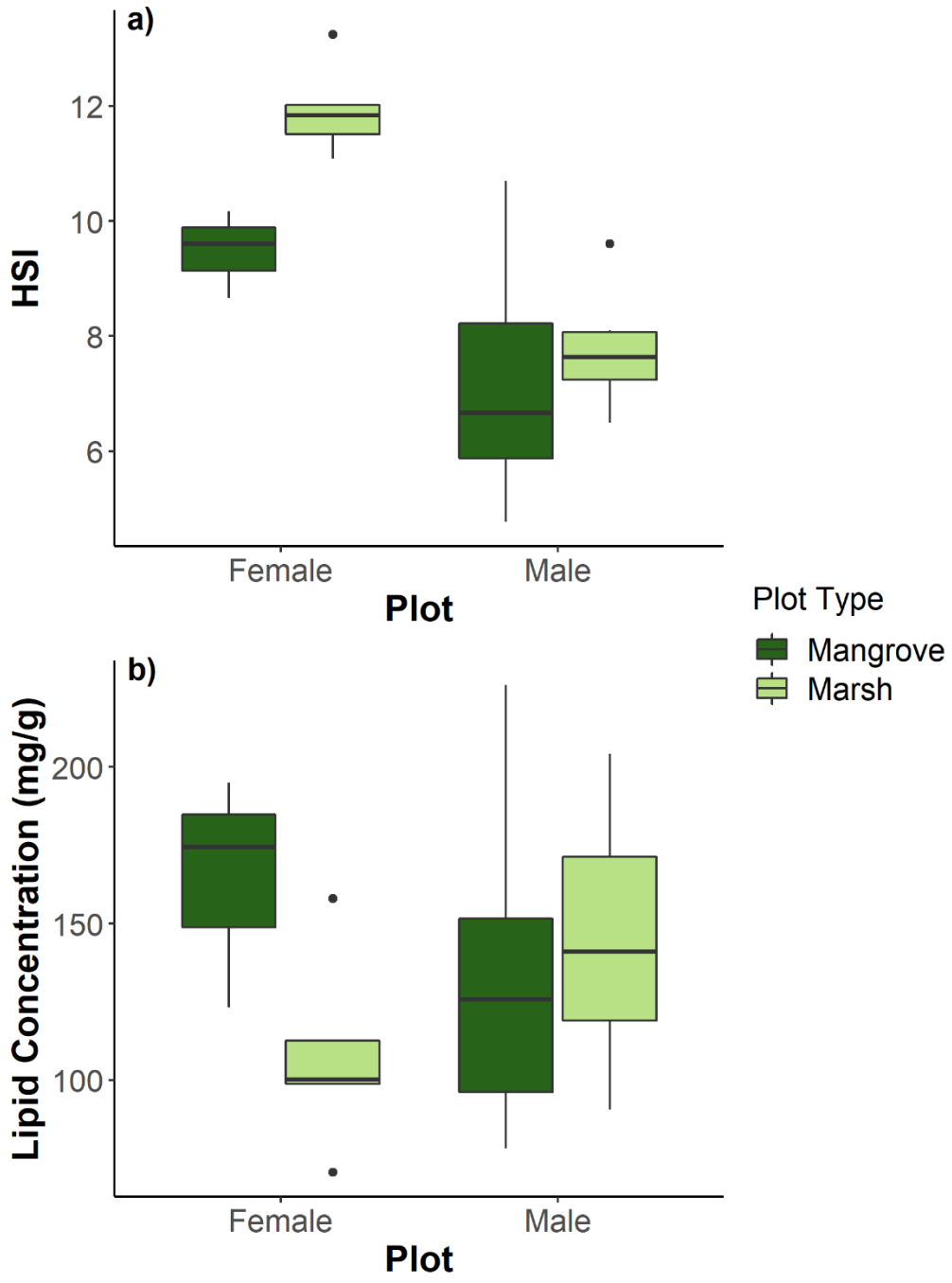

Figure 3.9: a) Hepatosomatic index and **b)** lipid concentration in the hepatopancreas of *Uca rapax* collected from mangrove and marsh experimental plots in Port Aransas. Number of crabs sampled per plot type was marsh (n = 11) and mangrove (n = 14)

3.4 Discussion

Plant matter from *Avicennia* was both less preferred and a lower quality diet for *Uca* spp. compared to *Spartina*. In food preference trials, consumption of the *Avicennia* diet was only marginally higher than consumption of the non-nutritive control diet. This indicates that Gulf Coast fiddler crabs either do not recognize *Avicennia* as a potential food source, or that characteristics of *Avicennia* plant matter discourage feeding by crabs. Generalist consumers are capable of exploring and assessing multiple food sources, and when presented with a high-quality novel food source, will often develop a preference for the novel food (Carroll and Wethey 1990). Therefore, it is likely that crabs were able to recognize *Avicennia* despite its novelty, and instead the apparent preference was driven by biochemical compounds in the plant matter. While food preference is a complex dynamic that can be influenced by factors including handling time, food accessibility, nutritional quality, and previous experience, the presence of secondary biochemical compounds is consistently one of the best predictors of preference in both lab and field studies (Pearse 2011, Tomas et al. 2011, Schwartz et al. 2016). The well-documented presence of secondary metabolites in both *Avicennia* and other woody encroaching species, as discussed below, supports both the observed preference in my study and the potential existence of a similar avoidance of woody shrubs in other encroached ecosystems.

Consumption of a low quality food source often negatively affects consumers, and in crustaceans, can be linked to decreased survival, growth, and fecundity (Cruz-Rivera and Hay 2000, Riley et al. 2014). In this case, although I did not see a difference in survival between diets, fiddler crabs raised on the *Avicennia* diet stored less energy in the form of lipids than those raised on the *Spartina* diet. Furthermore, crabs collected from mangrove dominated field sites had a lower HSI than those collected from nearby sites dominated by marsh vegetation. Higher

hepatopancreas lipid content and higher HSI in decapods are positively correlated with increased reproductive activity and molting frequency (Pillay and Nair 1973, Cockcroft 1997). The lower hepatopancreas lipid content of *Uca* raised on *Avicennia* diets therefore confirms *Avicennia* as a low-quality food source and, combined with the reduced HSI of *Uca* exposed to mangroves, indicates that long-term consumption of *Avicennia* may decrease fiddler crab growth and reproduction, leading to an overall reduction in fitness.

The interpretation of these results is complicated somewhat by the lack of change in weight, HSI, and hepatopancreas C:N in response to diet in the lab, and the lack of change in hepatopancreas lipid concentration with differing mangrove exposure in the field. However, all of these metrics are affected by factors beyond simply diet, including season, molt stage, and reproductive cycle (Pillay and Nair 1973, Wen et al. 2001, Hasek and Felder 2005, Tian et al. 2012). These confounding factors may have influenced the data, particularly the lipid concentrations in the field-collected crabs given the low sample size and the seasonal difference between the lab experiments and field collections. The non-responsive metrics in the lab-kept *Uca* could also be the result of these confounding factors, or may indicate that crabs feeding on *Avicennia* are using the nutrients they obtain to form biochemical compounds other than lipids. Possibilities include sugars (which are also very carbon rich), or glycogen (Pillay and Nair 1973, Tian et al. 2012). Storage of these compounds in the hepatopancreas could influence metrics, such as HSI and carbon content, causing them to respond in a way that does not correlate with hepatopancreas lipid levels. It is important to note that while confounding factors may have been present, it is highly unlikely that they drove the observed patterns in both sets of experiments given the strength of the observed responses.

Food preference and quality are often linked to biochemical characteristics, and generally

decrease with increased concentrations of secondary metabolites, such as phenolics and tannins (Erickson et al. 2004, Nordhaus and Wolff 2007). *Avicennia* was likely a less preferred and lower quality food source than *Spartina* due to the presence of such compounds. Concentrations of phenolic compounds, which are strongly linked to low palatability, are 3-6 times higher in *Avicennia* leaves than in *Spartina* (Valiela and Rietsma 1984, Erickson et al. 2004). Similarly, tannins, which are herbivory deterrents, are present in *Avicennia* leaves but generally absent from *Spartina* altogether (Bärlocher and Moulton 1999, Erickson et al. 2004). The high tannin and phenolic concentrations that lower the palatability and nutritive quality of *Avicennia* are characteristics that mangrove trees have in common with other woody encroaching species such as honey mesquite (*Prosopis glandulosa*), a woody species encroaching into terrestrial rangelands in the southeast US that also has higher levels of phenolics than the grass species it replaces. (Kurokawa et al. 2010, Ehsen et al. 2016).

The presence of secondary metabolites in plants also has physiological consequences for the herbivores that feed upon those plants. Secondary metabolites can decrease digestion, reduce growth rates, and even lead to toxicity in herbivorous insects (Barbehenn and Constabel 2011). Mammalian herbivores may also experience detrimental physiological effects, although some studies have reported tannins benefitting mammals by serving as antioxidants and protecting proteins from degradation (Dearing 1997, Iason 2005). In coastal systems, high concentrations of mangrove-derived tannins have been linked to smaller population sizes and slower population growth of sediment-dwelling meiofauna, and smaller body sizes of mangrove consuming crabs (Alongi 1987, Erickson et al. 2004).

In encroached coastal ecosystems, fiddler crabs are unlikely to incorporate a substantial amount of mangrove carbon into the coastal wetland food web. Basal consumers such as fiddler

crabs fill a vital role in the conversion of vascular plant derived organic matter into forms that are more accessible to the rest of the food web (Cebrian 2004). Therefore, the nutrients and carbon in mangrove leaves may be less accessible to other organisms in encroached wetlands. Furthermore, based on the strength of the observed individual-level effects in both the lab and the field, fiddler crabs may experience deleterious population-level effects in encroached areas where mangrove carbon is prevalent. This disruption at the basal consumer level may have negative consequences for organisms that feed on *Uca* spp., including economically important fishery species such as blue crabs and red snapper, and endangered birds like whooping cranes and sandhill cranes (Miles 1949, Hunt and Slack 1989, Dittel et al. 2000). As *Uca* spp. fill dual roles as basal consumers and ecosystem engineers, any population-level effects of woody encroachment could have a disproportionate impact on coastal wetland carbon flow and ecosystem services.

3.4.1 Conclusions

Studies examining basal consumer fitness responses to primary carbon source replacement as a consequence of woody encroachment are rare. Mangrove-encroached salt marshes provide a valuable opportunity to examine such trophic consequences. The dynamics of woody encroachment are well studied in terrestrial systems, but the effects on higher trophic levels are difficult to parse out due to higher interaction complexity and species diversity. Gulf Coast salt marshes do not share these challenges because they are dominated by a few plant species, and host fewer basal consumers that exert strong effects on the systems (e.g., *Uca* spp. and the marsh periwinkle *Littoraria irrorata*). This low diversity leads to a simplified food web that facilitates the identification of trophic consequences that could be obscured in more complex terrestrial systems.

Notably, my work demonstrated that the mangrove trees encroaching into Gulf Coast salt marshes are not trophically equivalent to the marsh plants they replace as a food source for basal consumers. Furthermore, the consistent responses of herbivores to secondary metabolites and the similarities among encroaching woody species across terrestrial and coastal systems suggest that similar patterns of food preference and quality may exist in woody shrub encroachment of terrestrial environments. Woody plants are likely to be poor food sources for basal consumers in such ecosystems, although consumer-specific responses will depend on consumer identity and diet diversity, and the extent to which a consumer can utilize other available food sources such as particulate organic matter. In both wetland and terrestrial systems, woody encroachment is likely to alter trophic interactions involving basal consumers and may subsequently impact carbon flow through the ecosystem.

4. MANGROVE ENCROACHMENT SHIFTS CONSUMPTION AND REDUCES ENERGY IN LITTORARIA

4.1 Introduction

Coastal wetlands in the Gulf of Mexico in the western Atlantic Ocean have historically played a large role in defining the culture and economy of surrounding human communities. Coastal wetlands support commercial and recreational fisheries and benefit ecosystems through flood mitigation, wastewater treatment, and habitat provision (Costanza et al. 2014). However, the structure of these wetlands is fundamentally changing, as the sub-tropical mangrove tree *Avicennia germinans* (black mangrove) is becoming more common in the region as a result of climatic drivers including decreased freeze events and increased hurricane activity (Osland et al. 2013, Feller et al. 2017). This results in mangroves encroaching into coastal marshes at the expense of marsh plants (Guo et al. 2017, Armitage et al. 2021). By displacing the currently dominant plant species, mangrove encroachment is changing the character and structure of these culturally and environmentally important systems.

Many studies have identified individual effects of mangrove encroachment, such as changes in soil organic content, decomposition rate, erosion and accretion rates, and faunal richness (Saintilan and Rogers 2015, Guo et al. 2017, Kelleway et al. 2017, Charles et al. 2020, Armitage et al. 2021). However, there is a need for a broader viewpoint that takes into account community-ecosystem linkages. In particular, mangrove effects on the abundance and interactions of certain key faunal species may have wide-reaching consequences, such as altering the value of fisheries (through fishery species presence), carbon cycling and sediment dynamics (through ecosystem engineers), and tourism and cultural value (through recreation attractiveness

and endangered species presence) (Stunz et al. 2002, Minello et al. 2003, Kristensen and Alongi 2006, Rush et al. 2009, Holdredge et al. 2010). In order to identify how wetlands will respond to mangrove encroachment, we must therefore understand how certain key species that influence the energy flow of these encroached marshes may be affected by mangrove encroachment.

Spartina alterniflora (smooth cordgrass) occurs throughout the Gulf of Mexico as both the dominant wetland macrophyte, and an important food source for many wetland basal consumers (Teal 1962, Currin et al. 1995). In addition, *Littoraria irrorata*, the marsh periwinkle snail, is an important faunal species that is ubiquitous in these wetlands. These snails have a range that extends along the coast from south Texas north through New England, and they occur at densities ranging from 20 snails/m^2 to >100 snails/m^2 in most coastal wetlands throughout this range (Silliman and Ziemann 2001).

Littoraria are voracious herbivores that feed by creating small wounds on leaves, particularly on *Spartina* blades, then feeding on the dead tissues and colonizing fungi that result from these injuries (Bärlocher and Newell 1994a, Silliman and Newell 2003). In New England marshes, they can decrease *Spartina* productivity by up to 75% and exert top-down control of *Spartina* density (Silliman and Ziemann 2001). At high enough densities, they are able to entirely denude areas of salt marsh (Silliman and Bertness 2002). *Littoraria* affect the New England coast so strongly through their interactions with *Spartina* that they have been designated as a keystone species in the area (Silliman and Ziemann 2001).

While *Littoraria* may not fill this same keystone role in the Gulf of Mexico (possibly due to environmental stressors or a more diverse plant community reducing the strength of the *Littoraria* - *Spartina* interaction), they remain a vital part of the ecosystem. In addition to consuming large amounts of *Spartina*, they are the main prey item for blue crabs (*Callinectes*

sapidus), which are an important fishery species in the Gulf of Mexico (Dittel et al. 2000), and are also consumed by other estuarine fishery species and coastal wading birds (Heard 1982, Tucker et al. 1995). A change in marsh periwinkle densities therefore has the potential to alter not only *Spartina* density and the vegetation community, but also trophic support for higher-level consumers.

Their strong interactions with *Spartina*, and their role as a basal consumer and important trophic link make marsh periwinkles an ideal indicator species to examine how faunal communities and food webs will respond to mangrove encroachment. To this end, I studied the interactions of *Littoraria* with both *Spartina* and *Avicennia* in Texas coastal wetlands. The Upper Coast of Texas is close to the current range limit of *Avicennia*, and the Texas coastline spans a gradient of mangrove encroachment.

The preference of *Littoraria* for diets of *Spartina* and *Avicennia* and their physiological response to those diets was quantitatively tested in the lab using mesocosms. Following that, the interactions were examined in a less controlled environment by analyzing the diet composition and physiological condition of snails exposed to different levels of mangrove encroachment in the field. Based on the strength of the well-known *Littoraria-Spartina* interaction, I hypothesized that snails would prefer to consume mostly *Spartina* in both the lab and the field. I also hypothesized that those snails that consumed *Spartina* would have better physiological conditions based on previous records of the growth of *Littoraria* on a variety of diets (Bärlocher and Newell 1994a). Based on the outcomes of this study, I will be able to determine how *Littoraria* will respond to the disappearance of their primary food source, both from a physiological and an energy flow perspective.

4.2 Methods

4.2.1 Background and Preparations

The snails used in lab trials were collected from marshes surrounding East End Lagoon in Galveston, TX (29.33 ^{o} N, -94.75 ^{o} W) in summer 2019 and 2020 (**Figure 1a**). Galveston is close to the current northern range limit of *Avicennia* and mangroves in the area have a patchy distribution, so snails in the region are likely to have had limited interactions and experience with mangroves. After collection and before being assigned to trials, snails were housed for no more than 72 hours in a 5.7 L plastic bin with ambient seawater from the collection site.

Plants used in all lab trials were collected from the same location as the snails. Four types of plant material were used across all lab experiments: live *Spartina*, dead *Spartina*, live *Avicennia*, and dead *Avicennia*. Live *Spartina* leaves were collected by selecting leaves showing no signs of herbivory damage from healthy plants, and dead *Spartina* leaves were taken from standing dead *Spartina* stems. Live *Avicennia* leaves were picked directly from adult mangroves and fallen dead *Avicennia* leaves were gathered from the ground. Leaves were brought back to the lab and rinsed with distilled water before being used in experiments, and all trials were started within 4 hours of leaf collection.

In order to confirm if the responses observed in the lab were also occurring in the field, snails were collected from marshes in Port Aransas, TX. Port Aransas is farther south than Galveston in an area where mangrove encroachment into marshes is more advanced, so snails were collected from previously established survey and experimental sites in the region in fall 2020 to assess the fitness of snails in close association with mangroves as opposed to marsh plants in situ. Snails were collected from survey sites **(Figure 1b)** that were either fully encroached “Mangrove” sites or un-encroached reference “Marsh” sites. In addition, snails were

collected from experimental plots that had either low (0-22%) or high (77-100%) mangrove cover (Guo et al. 2017). This site allowed me to examine the effects of increasing mangrove abundance while removing confounding geographic variation.

4.2.2 Lab Feeding Preference Trials

Three separate feeding preference trials were performed in April and July 2019 and October 2020. Trials were iterative, offering different combinations of food sources based on the observations from previous trials. Experimental set-up information including the food sources presented to snails in each trial are listed in **Table 1**. Food options were presented as full *Avicennia* leaves and 4-inch sections of *Spartina* leaves placed upright in containers with their cut basal end in 10 ml of 20 ppt salinity water. Trials included 20-25 experimental replicates and an additional five control replicates where water and leaves were kept in a container without snails for the length of the trial. Snails were allowed to feed freely on the presented leaves for the length of the trial and were monitored daily and provided with weekly water changes.

Feeding activity over the trial was measured as the change in leaf area. All leaves were photographed before being presented to snails and at the end of the trial. Area of the leaves in each photograph was measured using the program ImageJ. Any loss of leaf area between the beginning and end of the trial was assumed to be due to consumption.

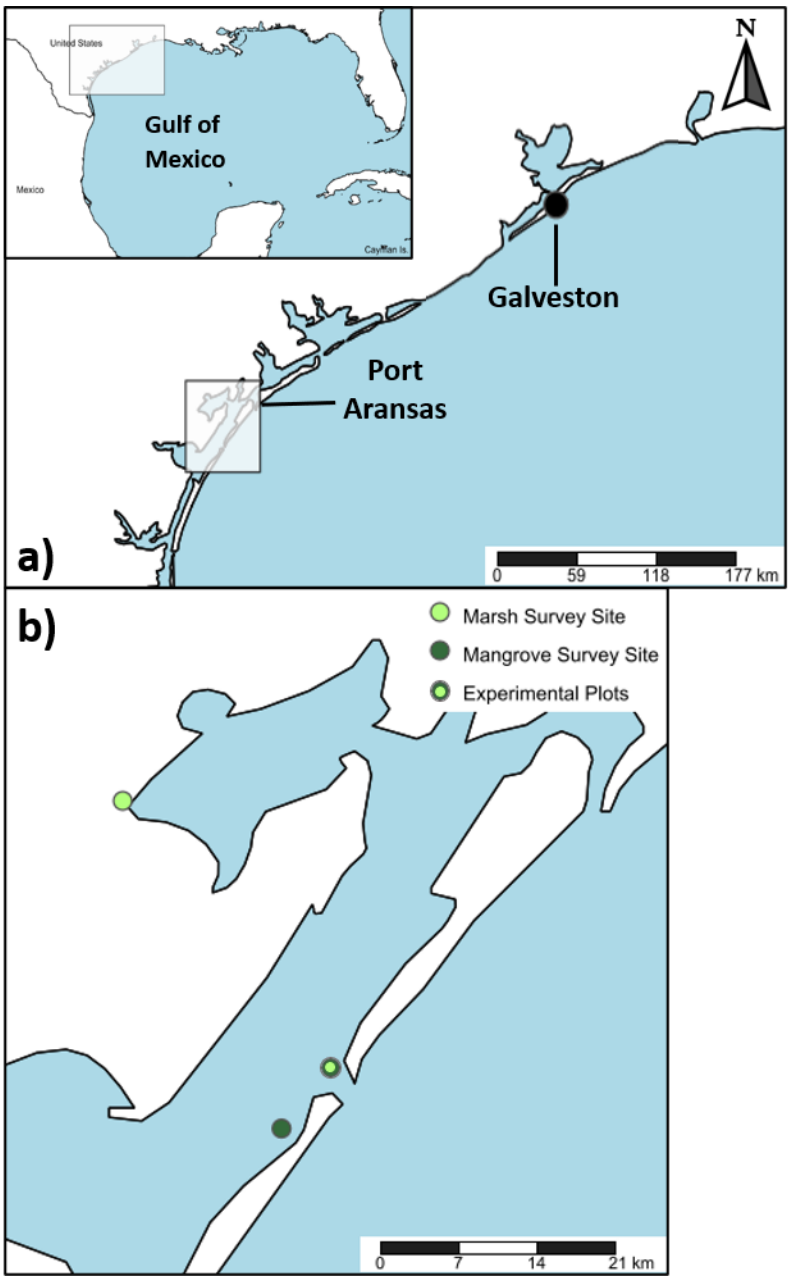

Figure 4.1: Maps of study sites used for snail collections. Map **a)** shows the locations of Port Aransas and Galveston along the Texas coast with an inset showing the Texas coastal bend region in relation to the Gulf of Mexico. The inset in map **b)** shows the locations of survey sites and the experimental plots in Port Aransas where snails were collected

Table 4.1: Summary of the three food preference trials, with presented food choices, trial length, environmental conditions, and number of snails used per replicate for each trial. The April 2019 trial was run for 45 days to determine if there would be changes in feeding patterns as time went on and leaves became more degraded. No change in feeding patterns was observed over time, so following trials were shortened to 14 days. Three snails per replicate were used in the October 2020 trial to ensure any feeding activity would be measurable despite the increased number of food options.

Trial Date	Offered Food Choices	Trial Length	Environmental Conditions	# Snails/ replicate
April 2019	Live *Avicennia*, Live *Spartina*	45 days	Lab maintained at 21°C	1
July 2019	Dead *Avicennia*, Live *Spartina*	14 days	Lab maintained at 21°C	1
October 2020	Dead *Avicennia*, Live *Avicennia*, Dead *Spartina*, Live *Spartina*	14 days	Partially shaded outdoor location exposed to ambient conditions*	3

*The October 2020 trial was performed outdoors due to the COVID-19 pandemic restricting lab access. The trial was performed in October as preliminary tests showed that the high outdoor air temperatures of Texas in spring and summer caused significant desiccation and thermal stress for snails and inhibited their feeding activity. The air temperatures during this trial were a daily average high of 23.7°C and low of 16.1°C (National Oceanic and Atmospheric Association 2021).

4.2.3 Lab Food Quality Trial

The quality of *Avicennia* and *Spartina* leaves as food sources for *Littoraria* was compared with a 60 day no-choice trial in summer 2020. Snails and plants for the lab food quality trials were collected from the Galveston site following the methods described above. The *Avicennia* diet consisted of living *Avicennia* branches containing 5-8 leaves, and dead *Avicennia* leaves from fallen branches and the marsh surface. The *Spartina* diet contained both living and standing dead stems with attached leaves, which were cut 6-12 inches from the marsh surface. Two hundred snails were collected in May 2020 and were randomly assigned to one of six 10-gallon aquarium tanks, with 25-35 snails per tank. All tanks contained 0.5 L of 20 ppt water and two stems/branches of both the living and dead material of one of the plant diets (n = 3 tanks per

diet). Tanks were covered with lids constructed out of window screening and were housed in a shaded outdoor location exposed to ambient temperature and humidity. Tanks were cleaned and provided with fresh food and water weekly. Salinity naturally fluctuated between 15 and 25 ppt due to the outdoor environment but was monitored and maintained as close as possible to 20 ppt through the addition of fresh or 20 ppt water as necessary.

After 60 days, snails were removed from tanks and frozen. After freezing, the shell length was measured, and snails were removed from their shells, the bodies were rinsed with distilled water, and then weighed to determine the wet body weight. Removing to shell prior to weighing minimizes the variability in water storage between organisms. Snail bodies were dried in an oven at 60^{o}C for 48 hours and reweighed to obtain the dry weight. The dry-weight density (DWD) of each snail was calculated as a ratio of dry body weight to shell-less wet body weight. DWD therefore represents the percent of an individual's total wet body weight that is attributed to tissue as opposed to water. In aquatic gastropods, such as *Littoraria*, energy stores are replaced with water as they are used, resulting in a negligible change in wet weight with a decrease in energy stores (Zonneveld and Kooijman 1989). Dry weight is sensitive to changes in energy storage, so calculating the dry-weight density of individuals allows me to determine the extent of a snail's available energy stores as a proxy for physiological condition (Zonneveld and Kooijman 1989).

4.2.4 Field Responses

The physiological condition of snails in the field was evaluated using snails collected from the experimental site and the survey sites in Port Aransas in November 2020 (**Figure 4.1b**). Five snails (the most that could be found at the time of the collection) were collected from one marsh survey site, and 10 snails were collected from one mangrove survey site and from each of

the three lowest (0, 11, and 22%) and three highest (77, 88, and 100%) mangrove cover experimental plots. Individuals from the experimental plots were collected in the vicinity of the dominant vegetation of the plot (i.e., within patches of marsh vegetation in marsh plots and underneath or on mangroves in mangrove plots). As *Littoraria* typically do not move more than a few meters over the course of months (Hamilton 1978), this method of collection was sufficient to ensure I was collecting individuals that were likely interacting with the vegetation of interest. Snails were frozen within five hours of collection and remained frozen until processing. In the lab, snails were processed to determine the dry-weight density (DWD) of snails at each site using the same procedure as described above for the lab food quality trials.

Stable isotope analysis was used to compare the $^{13}C/^{12}C$ ratios ($\delta^{13}C$ values) of a subset of these field-collected snails to those of snails raised on manipulated diets in the lab food quality trials. This was done to determine if fitness responses observed in the field were linked to diet shifts as they were in the lab. Plants with different photosynthetic pathways, such as C3 (*Avicennia*) or C4 (*Spartina*), have easily distinguishable isotopic carbon ratios, which are reflected in the organisms that consume them, so a diet shift between the two plants is easily detectable. Stable isotope analysis was performed on five snails raised on each the *Spartina* and *Avicennia* lab diets, and on twelve snails from the experimental site (**Figure 4.1b**); two individuals from each of the six sampled plots.

4.2.4.1 Sample Processing and Analysis

The muscular foot was dissected from each snail. Tissue was dried in an oven at 60^{o}C for 48 hours, then ground into a fine powder with a mortar and pestle. Ground tissue was weighed out into tin capsules for analysis.

Stable isotope analysis of all samples for $^{13}C/^{12}C$ isotopic ratios was performed at the UC

Davis Stable Isotope Facility on a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer. Vienna PeeDee Belemnite and air were used as standards for carbon and nitrogen respectively. Accuracy of the measured isotopic values was <0.2‰ for both $\delta^{13}C$ and $\delta^{15}N$ based on repeated analysis of a subset of samples. All results are reported in standard delta notation.

4.2.5 Data Analysis

All data sets were tested to ensure they conformed to assumptions of normality and homoscedasticity before analysis. Normality and homoscedasticity were tested with Shapiro-Wilk tests and Levene's tests (*car* package in R) respectively. All statistical analyses were performed in R version 3.6.0 (R Development Core Team 2020).

Food preference trials were analyzed with individual generalized linear models (GLMs, with the glm function). In all models the control treatment live *Spartina* leaves were used as a baseline, and treatment (control vs. experimental) and plant type (*Spartina* vs. *Avicennia*) were used as predictor variables to explain absolute leaf area change. Interactions between treatment and plant type were tested by creating an interaction term in the dataset and using it to perform Tukey tests with the glht function in the R package *multcomp*.

Leaf area change in both the April and July trials was transformed with a reciprocal root transformation prior to analysis in order to conform to assumptions of normality and homoscedasticity. Area change in the October trial was normally distributed but heteroscedastic in a way that could not be corrected by transformations. Heteroscedasticity for the October trials was addressed using weighted least squares to compensate for uneven variances.

Shell length, wet body weight, and dry-weight density of the snails in the food quality experiment all conformed to assumptions of normality and homoscedasticity. All variables were

analyzed using linear mixed effects models (lmer function in the *lme4* package in R) with diet as a fixed effect and tank number as a nested random effect. Reported results are from anova tables computed for fitted models

Body condition of snails collected from the field was analyzed with a GLM. DWD of the collected snails was the dependent variable and the mangrove cover at each site was the independent factor. The GLM was run using the DWD of snails from the 0% mangrove cover survey site as a baseline. DWD was both normally distributed and homoscedastic. The survey marsh site had 0% mangrove cover, and the survey mangrove site had 72% mangrove cover as calculated from transect surveys (**Table A4**).

$\delta^{13}C$ values of snails from the field and the lab food quality trials were normally distributed and homoscedastic. Separate t-tests were performed on the lab snails and field snails to determine the effect of vegetation type exposure (mangrove vs. marsh) on $\delta^{13}C$ values in each group.

4.3 Results

4.3.1 Lab Food Preference Trials

The only apparent feeding during the April trial occurred on *Spartina*, where snails consumed an average of 1.77 cm^2 of each leaf (**Figure 4.2**). This amounted to approximately 25% of the available *Spartina* leaf area. Absolute area change of experimental *Spartina* leaves was greater than that of both control *Spartina* leaves and experimental *Avicennia* leaves (**Table 4.2**), indicating that snails consumed *Spartina* preferentially over *Avicennia*. There was no apparent consumption of *Avicennia* leaves, as indicated by the lack of difference in area change

between experimental and control *Avicennia* (**Table 4.2**).

Littoraria consumed substantial amounts of both *Spartina* and dead *Avicennia* leaves in the July trial (**Table 4.2, Figure 4.2**). More *Spartina* than dead *Avicennia* was consumed on average (0.90 cm^2 per leaf vs. 0.68 cm^2 per leaf), but there was a large amount of variability and no clear preference between leaf types (**Table 4.2**). However, the measured consumption of the dead *Avicennia* leaves may have been overestimated, as snails were observed mechanically degrading the fragile dead *Avicennia* leaves by moving over the leaf surface, contributing to the total area change. I was unable to differentiate between changes in leaf area due to mechanical and consumptive effects.

Live and dead *Spartina* leaves were both heavily consumed during the October trial (**Figure 4.2, Table 4.2**). After 14 days, live *Spartina* leaves had lost on average 1.01 cm^2 of leaf tissue, amounting to 25% of their total area, and dead *Spartina* leaves lost 1.62 cm^2 (37%) of their area. This difference in consumption between live and dead *Spartina* was relatively minor, and both *Spartina* leaf types were consumed more than either type of *Avicennia* leaf (**Figure 4.2, Table 4.2**). Neither type of *Avicennia* leaf was consumed, as area change was not different between the experimental and control leaves, or between live and dead experimental leaves (**Table 4.2**).

Table 4.2: Results of Tukey post-hoc tests on GLMs comparing diet choices in each trial. Reported comparisons involve only experimental treatments, as there were no significant differences between any of the control treatments. Significant results are in bold.

	Diet Comparison	***Estimate***	***SE***	***z- value***	***p - value***
April 2019	*Spartina* – Control *Spartina*	-0.3272	0.0743	-4.405	**<0.001**
	Avicennia – Control *Avicennia*	0.0055	0.0743	0.074	0.999
	Avicennia – *Spartina*	0.3360	0.0470	7.154	**<0.001**
July 2019	*Spartina* – Control *Spartina*	0.2269	0.0806	2.815	**0.0229**
	Dead *Avicennia* – Control Dead *Avicennia*	0.1511	0.0806	1.875	0.227
	Dead *Avicennia* – *Spartina*	-0.0888	0.0465	-1.907	0.213
October 2020	*Spartina* – Control *Spartina*	0.8108	0.1744	4.649	**<0.001**
	Dead *Spartina* – Control Dead *Spartina*	1.5036	0.2188	6.871	**<0.001**
	Avicennia – Control *Avicennia*	0.0293	0.1128	0.260	1.000
	Dead *Avicennia* – Control Dead *Avicennia*	0.0387	0.1193	0.324	1.000
	Spartina – Dead *Spartina*	-0.6114	0.2387	-2.561	0.156
	Spartina – *Avicennia*	0.9415	0.1639	5.743	**<0.001**
	Spartina – Dead *Avicennia*	0.9563	0.1664	5.746	**<0.001**
	Dead *Spartina* – *Avicennia*	1.5529	0.1925	8.069	**<0.001**
	Dead *Spartina* – Dead *Avicennia*	1.5677	0.1946	8.056	**<0.001**
	Avicennia – Dead *Avicennia*	0.0148	0.0881	0.168	1.000

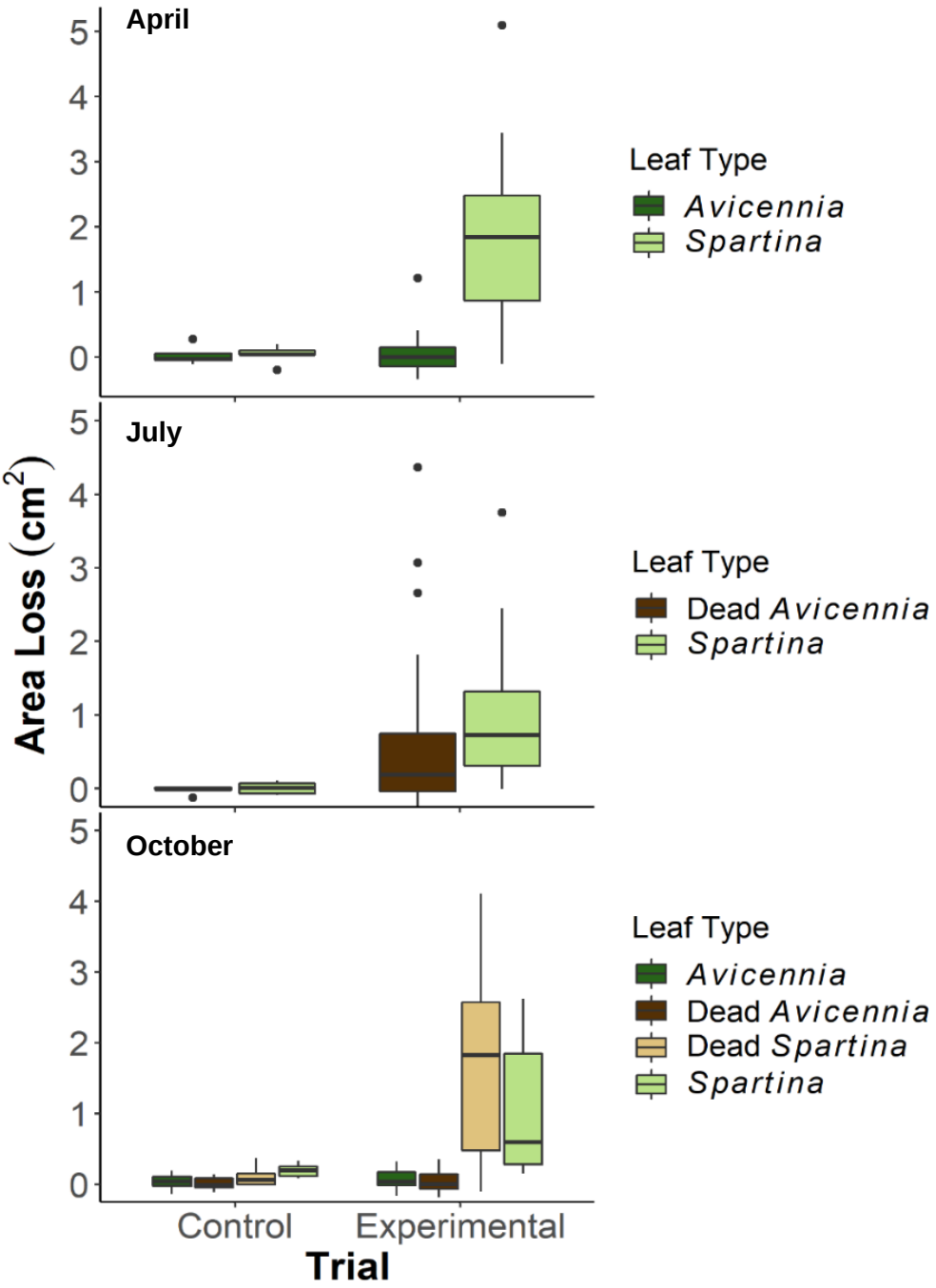

Figure 4.2: Area lost by leaf type in control and experimental replicates. Panels show area change in the April trial (n = 20) comparing live *Avicennia* to live *Spartina*, the July trial (n = 25) comparing dead *Avicennia* to live *Spartina*, and the October trial (n = 20) comparing live and dead *Spartina* to live and dead *Avicennia*.

4.3.2 Lab Food Quality Trials

Survival rate of snails was 100% on both diets. At the experiment end, there was no difference in *Littoraria* size on the two diets as measured by either shell length (**Table 4.3**, **Figure 4.3a**) or wet body weight (**Table 4.3**, **Figure 4.3b**). However, diet did affect dry-weight density (DWD), with *Littoraria* raised on the *Spartina* diet having DWDs that were on average 1.6 higher (**Table 4.3**, **Figure 4.3c**). This represents a difference of 1.6% in the contribution of organic tissue to total body weight. *Littoraria* are only 15–20% tissue by weight, so this difference of 1.6% indicates a gain or loss of approximately 10% of the body tissue.

4.3.3 Field Responses

The level of mangrove percent cover at a site strongly affected the DWD of the *Littoraria* collected from that site. Snail DWD values were ~21 in both the marsh survey site and 0% mangrove cover experimental plot (**Figure 4.4**), and DWDs at both sites were higher than at any other locations (**Table 4.4**). Even small numbers of mangroves in the 11% and 22% mangrove cover plots substantially decreased DWD (**Table 4.4**). At the highest percent mangrove cover sites DWD decreased to ~16, which was similar to the DWD of *Littoraria* raised on a mangrove diet in the lab food quality trials (**Figure 4.4**). The DWD of *Littoraria* from the mangrove survey site, with 72% mangrove cover, was higher than that of snails from any of the highly encroached experimental sites, but still approximately 1.6 lower than the DWD of snails from the marsh survey site (**Table 4.4**).

Table 4.3: ANOVA table results of the effect of diet (*Avicennia* vs *Spartina*) on each dependent variable in the lab food quality trials.

Dependent Variable	Sum of Squares	DF	F	p-value
Shell length	0.362	1	0.262	0.6325
Wet body weight	0.005	1	0.634	0.4662
Dry weight density	31.087	1	8.202	**0.0464**

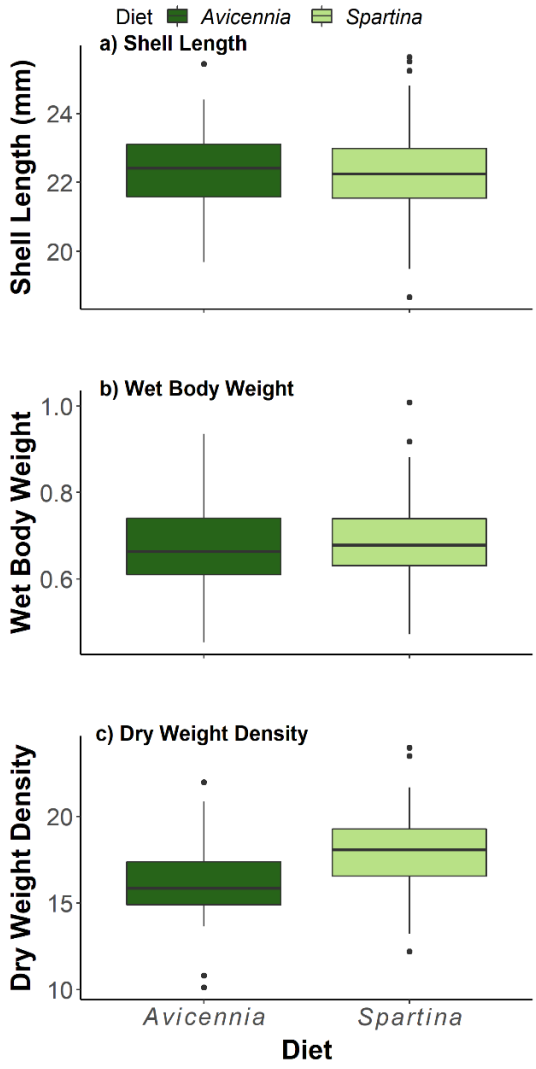

Figure 4.3: Comparison of **a)** shell length, **b)** wet body weight, and **c)** dry-weight density on *Spartina* and *Avicennia* diets after 60 days.

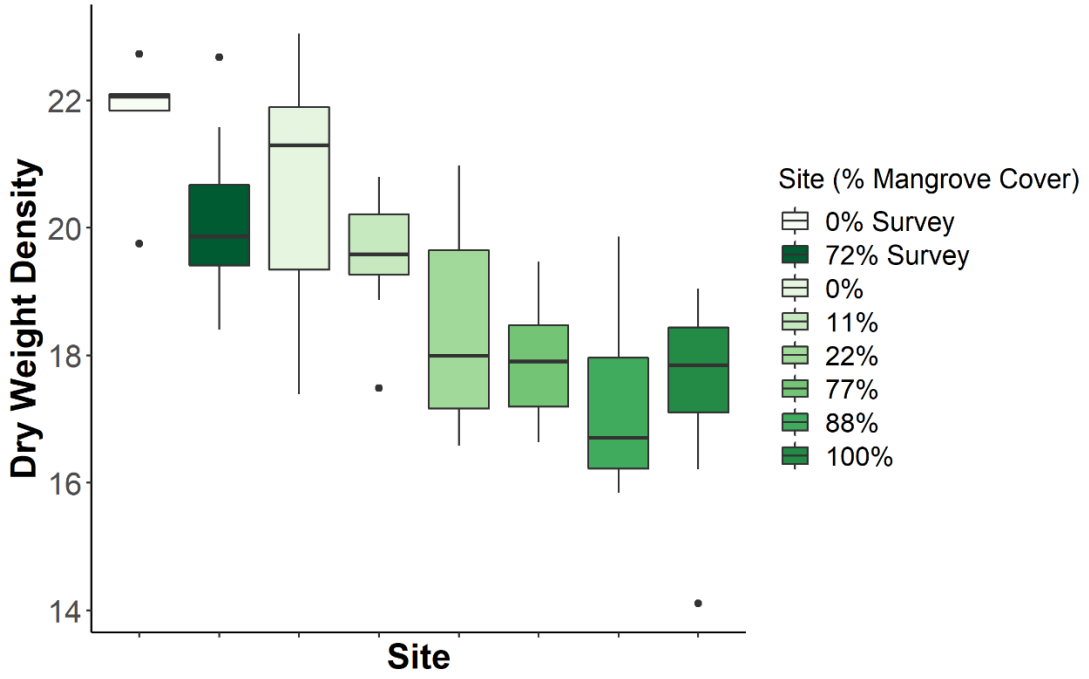

Figure 4.4: Body condition, as measured by dry-weight density, of *Littoraria* collected from sites with varying levels of mangrove cover in November 2020.

Table 4.4: GLM on dry-weight density of *Littoraria* snails collected from Port Aransas survey and experimental plots, using the 0% mangrove cover survey site as a baseline.

Site (% Mangrove Cover)	Estimate	Standard Error	t value	p-value
Intercept	21.6961	0.6015	36.068	**<0.001**
72% (Survey Site)	-1.5441	0.7367	-2.096	**0.0399**
0%	-0.9977	0.7367	-1.354	0.1803
11%	-2.0965	0.7367	-2.846	**0.0059**
22%	-3.3075	0.7367	-4.489	**<0.001**
77%	-3.8052	0.7367	-5.165	**<0.001**
88%	-4.3949	0.7503	-5.858	**<0.001**
100%	-4.2176	0.7367	-5725	**<0.001**

Dominant vegetation type influenced the $\delta^{13}C$ values of snails in both the field and the lab. The $\delta^{13}C$ values of snails collected from mangrove plots in the field were consistently 3-4‰ more negative than the values of snails collected from marsh plots ($t = -7.0385$, $df = 9.6155$, $p < 0.001$, **Figure 4.5a**). This difference is nearly identical to that observed between the snails raised on an *Avicennia* diet versus a *Spartina* diet in the lab ($t = -7.2601$, $df = 5.4539$, $p < 0.001$, **Figure 4.5b**). This indicates that the decreased DWD in snails from mangrove plots in the field is associated with a shift in diet that is similar to the shift simulated in the lab food quality trials.

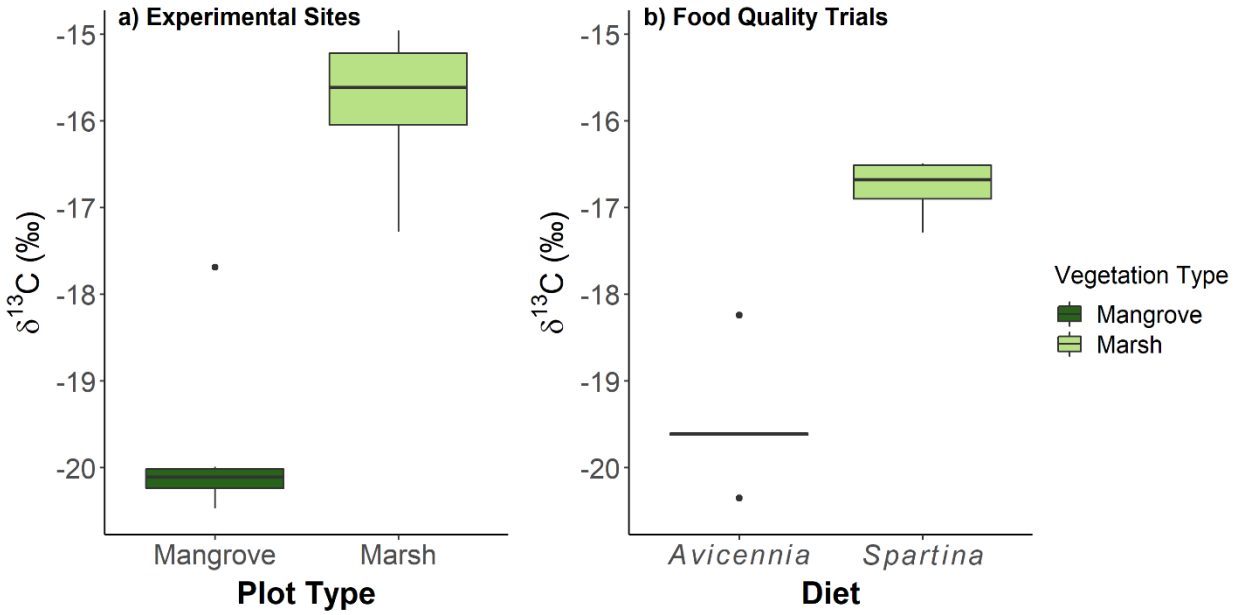

Figure 4.5: $\delta^{13}C$ values of *Littoraria* exposed to different vegetation types in **a)** the Port Aransas sites with experimentally manipulated mangrove cover and **b)** the lab food quality trials.

4.4 Discussion

The presence of mangroves decreased the body condition of *Littoraria* despite snails strongly avoiding feeding on *Avicennia* leaves. Preference trials in the lab indicated that

Littoraria clearly prefer to consume *Spartina* over *Avicennia*, as *Spartina*, whether live or dead, was the most consumed food source in each of the three lab feeding trials. Live *Avicennia* was never consumed by snails, and dead *Avicennia* was not consistently consumed across trials. Food preference is a complex dynamic that is affected not only by exposure to new food sources, but by environmental conditions, presence of chemical compounds in the food sources, and the fluctuating nutritional requirements of organisms (Cox and Murray 2006, Barbehenn and Constabel 2011, Hughes 2012, Iacarella and Helmuth 2012, Morton 2018). It is difficult to determine if any of these factors contributed to the patterns observed here, but the knowledge that *Littoraria* avoid consuming *Avicennia* has important implications for energy flow in encroached wetlands where *Spartina*, their preferred food source, is disappearing.

Interestingly, snails with decreased access to *Spartina* as a food source in both the experimental plots and the food quality experiment had lower energy stores, as measured by dry weight density. A variety of environmental factors have been shown to impact *Littoraria* species feeding and growth, including the presence of pollutants such as heavy metals (De Wolf and Rashid 2008), production of fatty acids and phenolic compounds by plants (Bärlocher and Newell 1994b, Sieg et al. 2013), and the sediment dynamics and *Spartina* cover of marshes (Stagg and Mendelssohn 2012). Based on the controlled nature of the lab food quality experiment and the proximity of the experimental plots to each other in order to minimize environmental variation, the most likely factor contributing to changes in *Littoraria* dry weight in my study is differing access to *Spartina*. *Littoraria* growth rates are positively correlated with *Spartina* abundance in the field (Stagg and Mendelssohn 2012), and *Littoraria* in the lab grow faster on a *Spartina* diet than on 14 other compared diets, including a benthic diet made of a marsh surface scraping (Bärlocher and Newell 1994a).

Alternatively, *Littoraria* may have been exposed to phenolic compounds and secondary metabolites from *Avicennia* leaves (McKee 1995, Erickson et al. 2004). As discussed above, the presence of these compounds can decrease the attractiveness of food sources and may contribute to the avoidance of *Avicennia* as a food source (Barbehenn and Constabel 2011). In addition, when dead leaves begin to decompose on the marsh surface or in the tanks of the food quality trials, these compounds leach out into the environment (Steinke et al. 1993, Kristensen et al. 2008), and the leached compounds may have negative effects on sediment dwelling fauna (Alongi 1987, Goeke and Armitage 2021).

The shift in $\delta^{13}C$ isotopic values between marsh and mangrove-associated snails provides some insight into the decreased body condition of *Littoraria* when exposed to *Avicennia* and restricted from *Spartina* by indicating that a dietary shift is occurring simultaneously with the reductions in energy storage. The $\delta^{13}C$ isotopic value of an organism reflects its diet, and can serve as an indicator of a shift in diet when the potential food sources have easily distinguishable carbon signatures (DeNiro and Epstein 1978). The $\delta^{13}C$ values of snails associated with marsh vegetation were between -16 and -17‰, while snails associated with mangroves had values of -19 to -20‰. *Spartina* and *Avicennia* respectively have $\delta^{13}C$ values of approximately -15‰ and -25‰ (**Section 2.3.2**). Therefore, the change in $\delta^{13}C$ values between marsh and mangrove-associated snails likely reflects a shift from the consumption of *Spartina* to either the consumption of a combination of *Spartina* and *Avicennia* material or the reliance on an entirely separate food source, even in the controlled lab trials.

Stable isotope analysis and dietary proportion mixing models of *Littoraria* collected from a variety of marsh and mangrove encroached sites along the Texas coast also found that *Littoraria* consumed minimal amounts of *Avicennia* at mangrove dominated sites, and instead

relied primarily on sources such as particulate organic matter and benthic macroalgae (**Section 2.3.2**). The observed $\delta^{13}C$ values of these alternate sources match the observed values of *Littoraria* in my study, suggesting that even *Littoraria* raised in the lab may be consuming algae and microorganisms that colonize dead mangrove leaves, as opposed to the leaf tissue itself. The decreased DWD of mangrove-exposed snails is therefore either an indication that these microorganisms serving as a replacement food source are nutritionally inferior to *Spartina*, or that the exposure to *Avicennia* and its associated secondary compounds decreases *Littoraria* body condition, even when alternate food sources are abundant.

Based on these results, food webs of encroached marshes are likely to experience trophic shifts, at least at the basal consumer level, as *Spartina* becomes less common. The decreased consumption of *Spartina* by *Littoraria* and corresponding decreased energy storage and body conditions could threaten the stability of the higher trophic levels in the food web. Gastropod body condition is correlated with respiration and metabolism (Henry et al. 1993, Baums et al. 2003, Ter Maat et al. 2007), can be used to help model the contribution of snails to the energy flow of a system (Odum and Smalley 1959), and is linked to the number of eggs produced during reproduction (Hughes and Roberts 1980, Zonneveld and Kooijman 1989). This decrease in condition may therefore affect *Littoraria* populations over time and decrease the availability of *Littoraria* as a prey species for higher trophic levels.

The diverse basal consumers present in marshes undergoing encroachment will likely have equally diverse responses to encroachment. The strong trophic relationship between *Littoraria* and *Spartina* (Silliman and Ziemann 2001, Stagg and Mendelssohn 2012) and the abundance of *Littoraria* in these ecosystems may amplify their responses. However, many other basal consumers also rely on *Spartina* for at least a portion of their diet (Teal 1962, Currin et al.

1995, Nelson et al. 2019), so I expect their responses to mangrove encroachment to reflect that of *Littoraria* to a degree. While studies of the physiological fitness implications of *Avicennia* presence are rare, many previous studies provide evidence that benthic and nektonic fauna, such as herbivorous fish fry and filter feeding shrimp, actively avoid mangroves in encroached systems (Smee et al. 2017, Scheffel et al. 2018, Armitage et al. 2021). Additionally, recent studies have found that a variety of basal consumers avoid consuming *Avicennia* in both the lab and the field, and often consume benthic material instead (Nelson et al. 2019, Harris et al. 2020, Goeke and Armitage 2021). Taken together, the shifting diet and body condition of *Littoraria* and the changing abundance and avoidance of *Avicennia* in other consumers supports the idea that there will be a shift in the energy flow of encroached wetlands at the basal consumer level, and possibly beyond.

4.4.1 Conclusions

The food webs of coastal wetlands are complex but are based on the interactions of basal consumers and foundational plant species. This work demonstrates the importance of examining all aspects of such interactions. By rigorously testing multiple aspects of the relationship between encroaching mangroves and a vital basal consumer, I was able to gain insight into how trophic interactions and food web structure are likely to change in coming years. While there are still many unknowns regarding how higher trophic levels will change in response to mangrove encroachment, based on my results I can surmise that there will indeed be changes. *Littoraria* is an abundant and vital part of coastal wetlands, so its shifting diet and decreased physiological conditions are likely to have effects on the variety of predators that consume it. Additionally, *Littoraria* is not the only basal consumer being affected by encroachment (Smee et al. 2017, Scheffel et al. 2018, Armitage et al. 2021, Goeke and Armitage 2021). The number of apparent

effects at the base level indicate that in the coming years we will likely start seeing shifts in the populations and diets of higher order consumers at sites that have been encroached for longer periods of time. As the economic and ecological benefits of coastal wetlands are being increasingly recognized (Costanza et al. 2014), more questions are being asked regarding the relative values of *Spartina* and mangroves for restoration and the support of ecosystem services (Yando et al. 2019). We must therefore continue to monitor the progress of mangrove encroachment, the disappearance of *Spartina* in coastal wetlands, and a range of consumer responses in order to ensure we are able to maintain the function of these dynamic systems and the important economic and cultural services they provide.

5. CONCLUSIONS

Mangrove encroachment is a disturbance that can be viewed through multiple lenses. It is a change in the foundational species of coastal wetlands, it alters ecosystem structure and soil and nutrient dynamics as a type of woody encroachment, and it impacts the roles of important species such as *Spartina* and *Littoraria* (Saintilan and Rogers 2015, Yando et al. 2019). Regardless of the lens through which it is viewed, the structural and functional shifts resulting from mangrove encroachment are readily apparent. Along the Gulf Coast of Texas, mangrove encroachment shifts the plant structure of wetlands from one dominated by flexible graminoid stems to rigid, woody mangrove pneumatophores and branches. Previous studies have documented the effects this structural vegetation shift can have on a variety of geomorphic and hydrological features (Walker et al. 2019, Yando et al. 2019, Armitage et al. 2020). However, the work in Chapter 2 shows that this shift has minimal effects on basal consumer distributions, as consumers were still abundant in the sites lacking *Spartina* and frequently associated with *Avicennia* structures.

While *Avicennia* may serve as a structural replacement for *Spartina*, it does not replace it trophically. The stable isotope analysis results presented in Chapter 2 show that basal consumers at marsh sites have diets composed primarily of *Spartina*, but consumers at sites where mangroves have replaced *Spartina* consume almost no *Avicennia*. Instead, consumers turn to alternate food sources such as particulate organic matter and benthic algae. The results of the food preference trials in Chapter 3 and Chapter 4 suggest that this lack of consumption is because consumers avoid *Avicennia* as a food source, even when it is abundant. Combined, the results of these experiments indicate that very little *Avicennia* carbon is likely to be incorporated

into coastal wetland food webs, and that basal consumers are not processing *Avicennia* plant matter to make it accessible to higher trophic level consumers.

The lack of incorporation of *Avicennia* into food webs may be beneficial, as the food quality experiments in Chapter 3 and Chapter 4 show that the consumption of *Avicennia* material reduces the body condition and energy storage of basal consumers. However, field-collected basal consumers exposed to various levels of mangrove encroachment showed similar reductions in energy storage to what was observed in the lab, despite the absence of *Avicennia* from their diet. This implies that either **1)** basal consumers in encroached locations are relying on food sources that are more preferred than *Avicennia*, but still nutritionally inferior to *Spartina*, or **2)** the presence of *Avicennia* in an environment reduces basal consumer body condition whether or not it is being consumed. Further research is necessary to identify which of these circumstances is occurring, and whether the lowered body conditions of basal consumers at encroached sites will have long term effects on reproduction, growth, and population size. Furthermore, the body conditions of consumers at higher trophic levels should be studied in order to determine if predators that consume *Littoraria* and *Uca*, such as blue crabs, are also being physiologically affected by mangrove encroachment.

The research presented in this dissertation shows the importance of studying species interactions in detail as opposed to simply relying on estimates of abundance or diversity. Based on the results of Chapter 2 alone, it might seem as though mangrove encroachment is having negligible effects on basal consumers, as it structurally replaces *Spartina* as a foundation species and consumers are able to find alternate food sources to rely on. However, the more comprehensive view of basal consumer-*Avicennia* interactions provided by the following chapters demonstrates that mangrove encroachment is negatively impacting basal consumers

through the removal of a high quality and strongly preferred food source. While this work occurred specifically on the Gulf Coast of Texas, these results are likely applicable throughout the eastern United States where *Spartina alterniflora* dominates most salt marshes. In other locations, such as Australia, where other graminoids dominate marshes and other species of mangroves are encroaching, the interaction dynamics may be different depending on the specific characteristics of the involved plant species. The research in this dissertation provides a framework that can be used to understand the responses of basal consumers in any system undergoing mangrove encroachment.

The ability of mangrove trees to reduce erosion and protect shorelines has led to increasing consideration of their utility as a restoration tool in recent years. This research shows that the goals and desired outcomes of a project must be carefully considered before involving mangroves however, as their inclusion may have negative consequences for the food web health and fishery support capacity of a system. These risks are present for basal consumers even at levels of mangrove cover as low as 30% (in the Galveston survey sites) or 22% (in the Port Aransas experimental plots), which are the levels at which this dissertation reports diet shifts (**Figure 2.7**) and reduced body conditions (**Figures 3.9, 4.4**) respectively.

Mangrove encroachment is a large-scale shift in a very complex ecosystem, and many of its impacts are still not fully understood. This work fills an important knowledge gap regarding the responses of basal consumers and gains additional insight by including a novel evaluation of the physiological impacts of encroachment. As shifts such as mangrove encroachment continue to destabilize coastal systems, research that investigates multi-level responses, from the organism to the ecosystem, will help scientists understand the forms these systems will take and the functions they will support in the face of changes. This understanding is an important step in

ensuring that the diversity, complexity, and value of coastal ecosystems will be preserved for years to come.

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APPENDIX A

Table A1: Site names and descriptions for each of the Galveston region sites referenced in Chapter 2. Wetland sizes are defined as small < 25000 m^2, medium 25000-100000 m^2, and large >100000 m^2.

Site Type	Site Name	Site Abbreviation	Description
Mangrove	East End	EE	Large wetland area on the eastern side of East End lagoon on Galveston Island. Popular fishing and recreation site with frequent human activity. Moderately encroached with 10-20% mangrove cover.
	East End 2	EE2	Large wetland area on the western side of East End lagoon on Galveston Island. Popular fishing and recreation site with moderate human activity. Moderately encroached with 30-40% mangrove cover.
	San Luis Pass	SLP	Medium wetland area fringing Galveston Bay on the western end of Galveston Island. Surrounded by condos and developments, but with infrequent foot traffic. Lightly encroached with ~5% mangrove cover.
Marsh	Sportsman Road	SPM	Large wetland area on the bay side of Galveston Island. Popular fishing and recreation site with frequent human activity.
	Indian Beach	IB	Medium wetland area on an inlet of Galveston Bay on Galveston Island. Near a small residential neighborhood, but with infrequent foot traffic.
	Sunset Cove	SNC	Medium area donated to Texas A&M University on the bay side of Galveston Island. Within a gated housing development, with well-preserved wetlands. Infrequently human activity outside of a variety of scientific research projects happening within the site.

Table A2: Site names and descriptions for each of the Port Aransas region sites referenced in Chapter 2. Wetland sizes are defined as small < 25000 m^2, medium 25000-100000 m^2, and large >100000 m^2.

Site Type	Site Name	Description
Mangrove	S3	Large wetland area on the bay side of Mustang Island in Port Aransas. on Galveston Island. Moderate human activity in the form of recreational fisherfolk. Mangrove cover near 100%.
	S4	Medium wetland area on the bay side of Mustang Island in Port Aransas. Popular fishing and recreation site with frequent human activity. Mangrove cover near 100%.
	S9	Medium wetland area on the bay side of Mustang Island in Port Aransas. Infrequent foot traffic but located adjacent to a small regional airport. Mangrove cover near 100%.
Marsh	S5	Small wetland area on an inlet of Aransas Bay on mainland Texas. Near a busy road and popular fishing location, but with infrequent foot traffic.
	S6	Small wetland area on an inlet of Aransas Bay on mainland Texas. Popular recreation site with signs of frequent human activity
	S10	Large wetland area on an inlet of Aransas Bay on mainland Texas. Wetlands are within the Aransas National Wildlife Refuge and have infrequent human activity outside of approved government and research personnel.

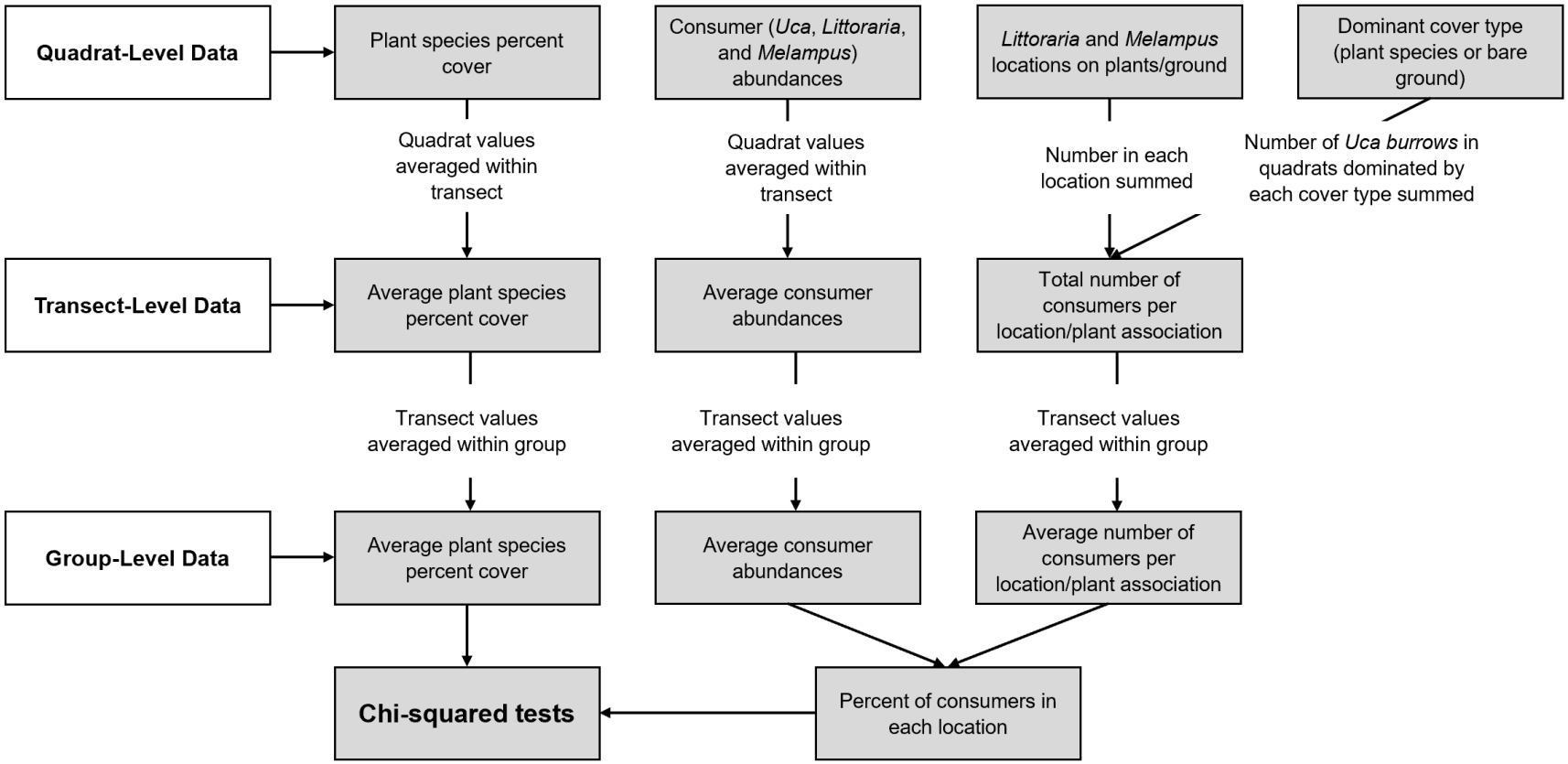

Figure A1: Flow chart demonstrating the approach used to summarize and analyze the data obtained from the transect surveys in **Section 2.2.2**.

Table A3: Source grouping and mean ± standard deviation of each source sampled for stable isotopes. Live and dead plant source values are displayed separately but were combined for analysis. Means reported are overall averages across all sites where sources were collected.

Source	Grouping	Plant Condition	n	δC^{13}(‰)	δN^{15}(‰)
Spartina alterniflora	graminoid	Live	13	-13.82 ± 0.21	4.47 ± 1.67
		Dead	12	-13.86 ± 0.29	4.36 ± 1.65
Distichlis spicata	graminoid	Live	6	-14.34 ± 0.81	6.10 ± 1.60
		Dead	5	-14.51 ± 0.63	5.30 ± 1.69
Monanthochloe littoralis	graminoid	Live	2	-14.41 ± 0.30	5.01 ± 1.00
		Dead	2	-15.26 ± 0.30	4.76 ± 0.78
Spartina spartinae	graminoid	Live	1	-13.67	5.00
		Dead	2	-13.01 ± 0.01	3.38 ± 0.54
Avicennia germinans	C3	Live	7	-25.34 ± 0.43	4.76 ± 1.62
		Dead	7	-25.66 ± 0.62	4.74 ± 1.69
Borrichia frutescens	C3	Live	5	-28.81 ± 0.37	2.55 ± 1.14
		Dead	2	-28.85 ± 0.11	3.45 ± 1.32
Juncus roemerianus	C3	Live	1	-27.39	4.82
		Dead	1	-27.40	3.08
Schoenoplectus robustus	C3	Live	2	-27.85 ± 1.19	5.48 ± 0.89
		Dead	2	-27.94 ± 0.17	4.55 ± 0.94
Symphyotrichum subulatum	C3	Live	1	-27.97	4.97
		Dead	1	-28.96	3.47
Batis maritima	succulent	Live	12	-28.66 ± 0.52	5.01 ± 1.28
		Dead	6	-26.59 ± 2.12	3.86 ± 1.77
***Sarcocornia* spp.**	succulent	Live	11	-29.27 ± 0.45	5.49 ± 1.31
		Dead	8	-28.24 ± 0.35	5.51 ± 1.43
Benthic organic matter	FOM	*NA*	54	-21.96 ± 2.52	3.47 ± 1.54
Particulate organic matter	FOM	*NA*	60	-22.26 ± 1.93	3.23 ± 1.84

Table A4: Summary of the site surveys for the low elevation Galveston sites. Burrow, *Littoraria*, and *Melampus* counts are averaged across all quadrats in the survey (or all non-flooded quadrats for burrows) and reported as the average number per m^2. All other values are percent covers averaged across all quadrats in the survey. ND indicates the ground was flooded and burrow and pseudofeces data could not be collected.

Elevation	**Low**					
Site Type	**Marsh**			**Mangrove**		
Site	Indian Beach	Sunset Cove	Sportsman Road	East End	East End 2	San Luis Pass
Burrows (per m^2)	*ND*	3.7	7.0	8.3	5.0	*ND*
Littoraria (per m^2)	0.2	1.4	6.3	45.3	10.9	11.3
Melampus (per m^2)	0	0	<0.1	0	0	0
Pseudofeces	*ND*	0.1	13.6	36.9	9.9	*ND*
AGP	0	0	0	0.7	30.5	0.3
AG	0	0.1	0	1.6	39.1	0.2
SA	57.2	48.8	53.6	60.1	7.1	43.5
BM	0	14.7	6.7	1.5	12.7	7.6
SS	1.1	7.7	0.2	0.1	1.4	0.7
Lyc	0	0	0	0	<0.1	0
BF	0	0	<0.1	0	2.7	0
Lim	0	0	0	0	<0.1	0
DS	0	0	8.2	2.0	5.0	2.4
SP	0	0	0	0	2.0	0
JR	0	0	0	0	2.7	0
Sym	0	0	0	0.1	0.3	0
SvP	0	0	0	0.7	0	0
Bare	41.7	28.8	31.4	34.0	26.9	45.6
Littoraria Locations	SA	88% SA, 8% BM, 3% Ground, 1% SS	82% SA, 18% Ground	56% Ground, 43% SA, 1% AG, <1% SvP	35% AG, 27% SA, 19% Ground, 7% BM, JR, 3% BF, 1% DS, SS, <1% SP, Sym	96% SA, 4% BM, <1% SS, AG
Melampus Locations			Ground			

Abbreviation Key for Tables A2-A5: AGP – *Avicennia germinans* pneumatophore, AG – *Avicennia germinans*, SA – *Spartina alterniflora*, BM – *Batis maritima*, SS – *Sarcocornia* spp., Lyc – *Lycium carolinianum*, ML – *Monanthochloe littoralis*, SL – *Suaeda linearis*, BF – *Borrichia frutescens*, Lim – *Limonium carolinianum*, RP – *Rayjacksonia phyllocephala*, SP –

Spartina patens, JR – *Juncus roemerianus*, Sym – *Symphyotrichum subulatum*, SvP – *Sesuvium portulacastrum*, EC – *Eleocharis* spp., ScR – *Schoenoplectus robustus*, CP – *Croton punctatus*, SpS – *Spartina spartinae*

Table A5: Summary of the site surveys for the high elevation Galveston sites. Burrow, *Littoraria*, and *Melampus* counts are averaged across all quadrats in the survey (or all non-flooded quadrats for burrows) and reported as the average number per m^2. All other values are percent covers averaged across all quadrats in the survey.

Elevation	**High**					
Site Type	**Marsh**			**Mangrove**		
Site	Indian Beach	Sunset Cove	Sportsman Road	East End	East End 2	San Luis Pass
Burrows (per m^2)	5.6	9.4	16.0	6.8	6.1	5.7
Littoraria (per m^2)	0	0	0	0	0	0.9
Melampus (per m^2)	0	0	<0.1	0	0	0
Pseudofeces	48.6	45.2	36.3	18.1	14.3	41.3
AGP	0	0	0	0.7	0.2	<0.1
AG	0	0.1	<0.1	1.9	0.6	0.1
SA	0.1	1.0	4.6	2.4	56.6	0.5
BM	39.0	13.6	39.6	35.1	2.7	16.3
SS	13.8	17.3	3.1	4.2	0	13.5
Lyc	0.1	0.1	0.8	0.2	0	<0.1
ML	10.6	30.1	7.1	12.1	12.7	14.6
SL	0.1	2.9	0			
BF	0.1	0.2	1.2	0	0	<0.1
Lim	<0.1	<0.1	0	0.2	0	<0.1
RP	0	0.05	0	0	0	0
DS	0	0	6.6	14.7	3.7	0.1
SP	0	0	0.9	0	0	0
JR	0	0	3.5	0	0	0
EC	0	0	0	0	0	0.10
Bare	36.3	30.9	32.0	29.4	23.8	54.8
Wrack and Debris	0	3.9	0.7	6.8	0	0
Littoraria Locations						62% Ground, 21% SS, 14% ML, 3% BM
Melampus Locations			Ground			

Table A6: Summary of the site surveys for the low elevation Port Aransas sites. Burrow, *Littoraria*, and *Melampus* counts are averaged across all quadrats in the survey (or all non-flooded quadrats for burrows) and reported as the average number per m^2. All other values are percent covers averaged across all quadrats in the survey. ND indicates the ground was flooded and burrow and pseudofeces data could not be collected.

Elevation	**Low**					
Site Type	**Marsh**			**Mangrove**		
Site	S5	S6	S10	S3	S4	S9
Burrows (per m^2)	*ND*	0	NA	0	9.7	*ND* *
Littoraria (per m^2)	0	0	0	<0.01	0.1	5.4
Melampus (per m^2)	<0.1	0	4.8	0	0	0.2
Pseudofeces	*ND*	0	*ND*	*ND*	25.9	*ND*
AGP	0	0	0	37.3	27.7	37.7
AG	0	0	0	69.6	54.0	72.1
SA	42.8	77.6	44.7	0.3	2.9	0
BM	3.6	1.5	16.9	0	5.8	0.1
SS	10.5	5.4	22.3	0	1.7	0.7
Lyc	0	0	<0.1	0	0.1	0
BF	0.3	0	1.4	0	<0.1	0
DS	0.6	0	0	0	0	0
Sym	<0.1	0	1.7	0	0	0
SvP	0	0	0	0	0.1	0
ScR	0.9	0	<0.1	0	0	0
CP	0	0	0	0	0	0
Bare	41.3	15.5	13.0	30.2	35.5	27.1
Littoraria Locations				AG	AG	AG
Melampus Locations	SA		93% SA, 5% SS, 2% BM, <1% BF, Sym, ScR			AG

*4 *Uca* were observed climbing on AGP

Table A7: Summary of the site surveys for the high elevation Port Aransas sites. Burrow, *Littoraria*, and *Melampus* counts are averaged across all quadrats in the survey (or all non-flooded quadrats for burrows) and reported as the average number per m^2. All other values are percent covers averaged across all quadrats in the survey. ND indicates the ground was flooded and burrow and pseudofeces data could not be collected.

Elevation	**High**					
Site Type	**Marsh**			**Mangrove**		
Site	S5	S6	S10	S3	S4	S9
Burrows (per m^2)	*ND*	7.1	*ND*	12.3	17.1	*ND*
Littoraria (per m^2)	<0.1	0	0	0	0	0.7
Melampus (per m^2)	0	0	0	0	0	0
Pseudofeces	*ND*	0	*ND*	62.1	71.6	*ND*
AGP	0	0	0	3.0	<0.1	1.4
AG	<0.1	0	0	6.5	1.3	1.5
SA	6.9	1.2	1.3	0.6	0	0
BM	34.7	19.5	14.7	53.5	13.6	3.2
SS	27.9	11.5	6.9	1.8	10.0	28.7
Lyc	0.1	0.9	0.3	0	0.3	0
ML	0	3.4	1.1	0.7	40.6	0
SL	0.3	0	0	0	1.6	0
BF	2.0	4.5	1.3	0	0	0
Lim	0	0	0.1	<0.1	0.1	0
RP	0.3	0	0	0	0	0
DS	2.3	44.9	60.0	0	0	0
Sym	0.1	0	<0.1	0	0	0
SvP	0.5	0	0	0	<0.1	0
ScR	0.6	0.1	<0.1	0	0	0
CP	0.2	0	0	0	0	0
SpS	0	0.2	0	0	0	0
Bare	24.2	14.0	14.3	36.8	32.6	66.6
Wrack and Debris	0.1	0	0	0	0	0
Littoraria Locations	SA					70% AG, 26% SS, 4% BM
Melampus Locations						