# Habitat Changes Associated with Mangrove Expansion in Coastal Marsh Systems

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## Final Report to the Coastal Bend Bays and Estuaries Program

## Project 1821

## 31 December 2019

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# PROJECT SUMMARY

The overall goal of this study was to assess the ecological changes associated with progressive black mangrove (*Avicennia germinans*) displacement of *Spartina alterniflora* marshes in the CBBEP study area. This preliminary study is focused on (1) the differences in sediment biogeochemical properties between the two habitats, (2) differences in the composition and abundance of infaunal and epibenthic species, and (3) the ability of fauna to assimilate organic carbon derived from either *Avicennia* or *Spartina* using stable isotopic methods. We occupied and sampled multiple plots at three sites characterized by pure but adjacent assemblages of *Avicennia* and *Spartina* at nearly identical elevations. We found that sediment TOC within *Avicennia* plots was well over 2% compared to *Spartina* plots, which were consistently less than 1.5%, revealing the high organic content of mangrove soils. Infaunal species were dominated by polychaetes in both vegetation types, with little detectable differences in overall species composition between *Avicennia* and *Spartina* habitats. Finally, the same species of fauna collected in both vegetative zones possessed clear isotopic distinctions that suggested fauna were equally capable of assimilating $^{13}C$ enriched *Spartina* carbon as they could $^{13}C$ depleted organic carbon derived from *Avicennia.* These results suggest that the changes in habitat utilization by benthic biota may be less profound than indicated by earlier studies, some of which had elevation as a confounding effect that compromised their ability to differentiate between elevation and plant assemblage effects.

# ACKNOWLEDGEMENTS

This study was funded by the Coastal Bend Bays and Estuaries Program (CBBEP) under Contract #1821. The PI (KHD) thanks our CBBEP Program Manager, Rosario Martinez who enabled an extension of this project to accommodate our recovery from Hurricane Harvey and her amazing patience with our reporting deadlines. I thank and acknowledge the highly experienced field team that worked on this project, initially led by Danny Fraser and including Kim Jackson, Nick Reyna, Caitlin Young, and Ashley Moreno. My deep appreciation to Susan Schonberg who spent countless hours building graphs, compiling data, and providing help with the editing and formatting the final report over the December holiday period. Finally, we extend our sincere appreciation to Frank Ernst who kept our field operation going through careful and constant maintenance of the Beachcomber, the airboat operated by Kim Jackson that provided us with access to the study sites.

# INTRODUCTION

The coastlines of the northern Gulf of Mexico exist along a relatively dramatic climatic gradient, ranging from low precipitation and semi-arid climate regimes to higher precipitation and humidity (Osland et al. 2014). Since the climate gradient of this ecotone changes so rapidly within only 3-4 degrees of latitude, any minor shifts in precipitation or temperature regimes from climate change will produce noticeable effects on the coastal environment within our lifetime (Osland et al. 2014; Gabler et al. 2017). Shifting precipitation regimes and fewer extreme cold weather events in the northern Gulf of Mexico are facilitating black mangroves (*Avicennia germinans*) expansion into wetlands previously dominated by smooth cordgrass (*Spartina alterniflora*) (Osland et al. 2013). Poleward expansion of *A. germinans* is limited by its sensitivity to hard freezes, but fewer severe winter freezes and ensuing mass die-offs have allowed *A. germinans* to move up the coasts of the Gulf of Mexico (Osland et al. 2013). Another reason for this transition is the contrast between *A. germinans* high salinity tolerance (Patterson and Mendelssohn, 1991) over *S. alterniflora* sensitivity to increased salinity (Stachelek and Dunton 2013).

*A. germinans* and *S. alterniflora* have similar ecosystem services, such as coastal protection, erosion control, carbon sequestration, and maintenance of fisheries (Barbier et al. 2011). The firmly packed plant structure of salt marsh ecosystems provides valuable ecosystem services by boosting the production of commercially and ecologically important fishery species such as shrimp, oysters, clams, and fishes (Barbier et al. 2011). The inundated pneumatophores of *A. germinans* and blades of *S. alterniflora* are known refuges for many types of juvenile nekton that are pivotal to fisheries recruitment, as well as various juvenile benthic organisms (Caudill 2005; Johnston et al. 2017). Shrimp mortality by predation is significantly higher on bare sand than among black mangrove pneumatophores (Nagelkerken et al. 2008). Coastal wetlands are also major carbon sinks because of their high primary productivity and biomass storage in belowground tissues (Chmura et al. 2003).

Even though these two foundation species have similar ecosystem services, they can differ in their sediment biogeochemistry. *A. germinans* habitat is correlated with decreased soil moisture, increased soil ammonium, increased redox potential, and increased elevation (Perry and Mendelssohn, 2013). *A. germinans* occupies higher elevations, while *S. alterniflora* is tolerant of frequent inundation characteristic of lower elevations (Caudill 2005). Many biogeochemical parameters of both *A. germinans* and *S. alterniflora* ecosystems are similar, but because these plants act as foundation species, even small changes can have major implications on ecosystem dynamics. Increased redox potential in mangrove ecosystems is a product of plant architecture, which includes the use of pneumatophores to provide air to belowground tissues. In contrast, *S. alterniflora* transports photosynthetically produced oxygen to belowground rhizomes using aerenchyma, effectively aerating soils and promoting establishment by infaunal invertebrates.

Mangroves are characterized by having higher above ground biomass, while salt marshes have a percentage of biomass in belowground tissues, which influences the organic content of the sediment. Because of the distribution in biomass, mangrove mineral trapping is at least four times higher and sediment organics are two times lower than salt marshes (Comeaux et al. 2012). Sediment formed by decaying mangroves also has decreased porosity and increased sediment strength, leading to more shoreline protection in storms than salt marshes (Comeaux et al. 2012).

Aside from these physicochemical differences, there are also differences in certain juvenile nektonic and infaunal species preferences between the two habitats. On the Atlantic Florida coast, blue crab juveniles showed preference for *S. alterniflora* dominated plots over *A. germinans* plots, as well as the juveniles having higher survivability rates in *S. alterniflora* plots in the presence of predators (Johnston et al. 2017). Similarly, in the northern Gulf of Mexico, both tanaids and polychaetes showed greater affinity for plots that were a mix of *A. germinans* and *S. alterniflora* or just *S. alterniflora* dominated plots, but not *A. germinans* dominated plots (Scheffel et al. 2018). Sheepshead Minnows and Gulf Killifish have also shown an affinity for *S. alterniflora* over *A. germinans* (Caudill 2005). These differences in habitat affinity by both lower and higher trophic level organisms could have far reaching implications with respect to ecosystem services (Caudill 2005; Johnston et al. 2017).

The Coastal Bend region (latitude 27°) is an ideal location to examine the ecological effects of mangrove expansion. Worldwide, the overlap in mangrove and marsh distribution occurs at latitude 27° in subtropical regions (Alongi 1997). South Texas estuaries clearly represent an ecotone between the two vegetative habitats

Over the past few decades climatic warming has produced some profound shifts in coastal vegetation along the Gulf coast. In south Texas in particular, competition between *Spartina alterniflora* (smooth cord grass) and *Avicennia germinans* (black mangrove) is apparent. The CBBEP study area straddles 27° N and the mixture of both mangrove and *Spartina* marsh habitats has been noted by wetland scientists here for many years. Regional changes in climate have also produced increased salinity, decreased precipitation, and increasing eustatic sea level changes (Krauss et al. 2011; Stachelek & Dunton 2013) that favor mangrove development. As winter freezing events have decreased in frequency along the Texas coast in recent decades, displacement of *Spartina* has accelerated, especially in the CBBEP study area as mangroves expand northward to areas previously inhabited by *S. alterniflora* (Cavanaugh et al. 2013; Lunt et al. 2013; Osland et al. 2013). In addition, *A. germinans* propagule establishment is facilitated in salt marshes because of favorable soil physicochemical conditions, effectively forcing salt marsh vegetation out of these areas (Osland et al. 2013; Peterson & Bell 2012).

The relative importance of carbon contributions to estuarine food webs that possess a diversity of primary consumers remains a complex problem. Some studies suggest that incorporation of mangrove/salt marsh carbon into estuarine food webs is limited, with greater dependence on more labile forms of carbon, like phytoplankton and benthic microalgae (Abrantes et al. 2015). Many larger metazoans (e.g. shrimp) cannot derive nutrition from plant detritus as they lack the microbial gut flora but may ultimately derive vascular plant carbon from lower trophic prey species that are assimilating plant carbon (Nagelkerken et al. 2008).

## Major Objectives

The overall goal of this work is to assess the ecological changes associated with progressive black mangrove (*Avicennia germinans*) displacement of smooth cordgrass (*Spartina alterniflora)* marshes in the CBBEP study area. This preliminary study is focused on (1) the differences in sediment biogeochemical properties between the two habitats, (2) differences in the composition and abundance of infaunal and epibenthic species, and (3) the ability of fauna to assimilate organic carbon derived from either *Avicennia* or *Spartina*.

In addition to basic water quality measurements of dissolved oxygen, pH, chlorophyll-*a*, conductivity, salinity, and water temperature, biogeochemical data included the collection of sediment total organic carbon (TOC), soil moisture, and porewater ammonium. Community composition was estimated by identification and enumeration of epifauna and infauna collected in sediment cores. The dependence of fauna on *Avicennia* vs. *Spartina* plant carbon was determined from the analysis of stable carbon and nitrogen isotope ratios of the flora and fauna collected at three sites over the course of a 12-m period.

# METHODS

We followed methodology established by the Mangrove Migration Network (MMN; Osland et al. 2014) to maintain continuity with a long-term Gulf-wide program. Texas currently has two MMN sites, one near Galveston and the second within the CBBEP area on the north side of Mustang Island. We established paired *Avicennia germinans* (black mangrove) and *Spartina alterniflora* (smooth cordgrass) vegetative assemblages at three locations in the CBBEP region (Fig. 1). Within each of the vegetative assemblages, we established four 100-$m^2$ plots (or polygons). A low-effort suite of plant community composition and structure measurements were taken within each 100-$m^2$ polygon to confirm our independent estimation of a 100% percent cover of mangrove (or marsh) vegetation. We used a YSI data sonde to collect water quality parameters at each site on each quarterly visit to the six study sites, including temperature, salinity, dissolved oxygen, pH, and chlorophyll *a*.

***(1) Quantify differences in sediment biogeochemistry*****:** Replicate sediment cores were taken within each of the four plots on each quarterly visit to the study sites for (1) total organic carbon, (2) soil moisture, (3) ammonium, and (4) porewater salinity.

***(2) Determine infaunal and epifaunal species composition*****:** We collected replicate 10-15 cm deep sediment cores within each plot to assess infaunal populations. Collections were made quarterly using a 9-cm diameter acrylic cylinder. To reduce variability related to the duration of tidal exposure, all cores were taken at one identical elevation as determined by water level. Cores were placed in plastic Ziploc bags and brought back to the lab for identification and enumeration.

***(3) Assess faunal dependence on ultimate carbon sources***: Stable isotopes of carbon and nitrogen were used to examine the ultimate sources and fates of plant organic matter. Origins of organic matter are based on the premise that potential sources are isotopically distinct from each other and do not change or change predictably as those materials are assimilated and transported through the food web. We sampled within large pure stands of *Avicennia* and *Spartina* vegetation assemblages to minimize potential mixing of the two carbon sources and the contributions by other primary producers (e.g. seagrasses or algae) that may interfere with the $C_4$ signal of *Spartina* carbon. Mangrove organic matter is characterized by depleted $\delta^{13}C$ (carbon) values (e.g. -25‰) compared to *Spartina* tissue, which has $\delta^{13}C$ values ranging from -12 to -15‰. We used these end member values to assess the relative importance of these two sources of carbon to marine consumers. In addition to core samples collected within each vegetative plot, we deployed an epibenthic sled in waters adjacent to the plots to collect nekton. All samples were seived, sorted, identified, and dried at 60º C for natural abundance isotope analysis at UTMSI.

### *Site Selection*

Our three sites (**Figure 1**) were located on the north side of Padre Island. From the north, the sites included Harbor Island (HI), Coyote Island (CI), and Packery Channel (PC). Coyote Island is unique from the other sites in that it appears to be the most elevated site, has the highest abundance of nekton, and may contain the youngest *Avicennia germinans* plot. We marked four paired 100 m$^{-2}$ polygons of homogeneous *Spartina alterniflora* and *A. germinans* at each site. We sampled at all three sites in late January and early February, mid-April, mid-July, and late October to capture the seasonal component of invertebrate recruitment of fauna.

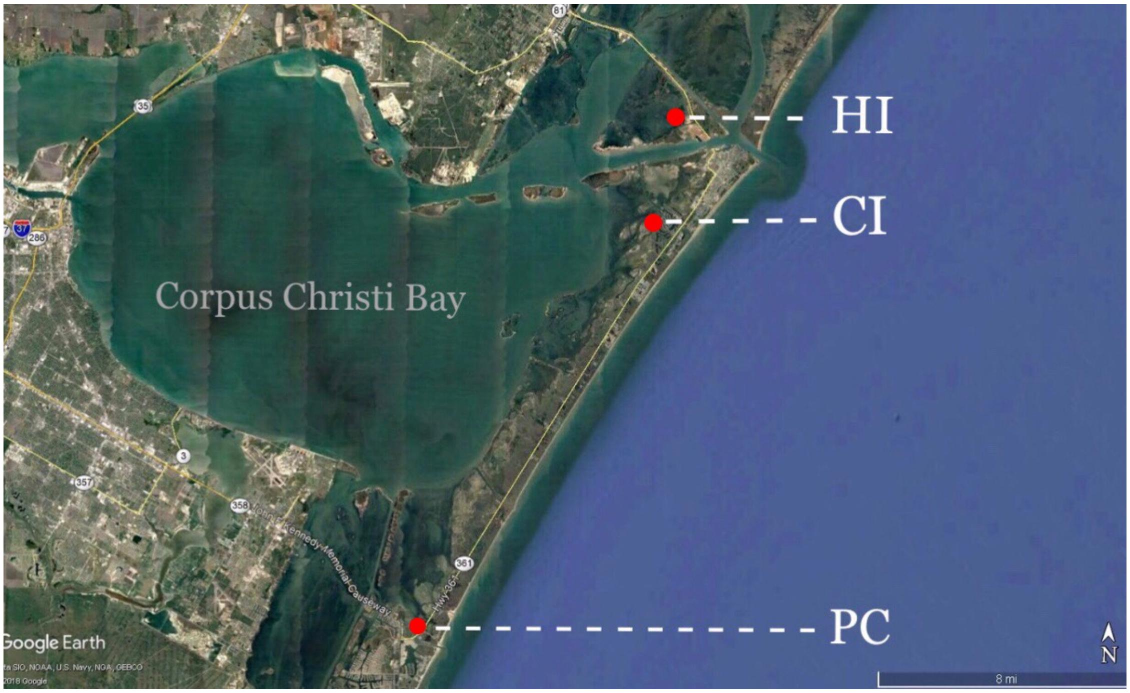

**Figure 1.** General location of three paired *Avicennia-Spartina* marsh study sites in the CBBEP project area. Locations were determined based on aerial surveys followed by ground truthing. Site coordinates (decimal degree format) include HI: Harbor Island (27.85 N; 97.08 W), CI: Coyote Island (27.80 N; 97.09 W), and PC: Packery Channel (27.62 N; 97.21 W).

### *Field Sampling*

At each of the three sites, a HOBO datalogger was installed in a main water inlet to record measurements of water temperature and salinity/conductivity. YSI 6920-V2 SONDE measurements were recorded for dissolved oxygen, pH, chlorophyll-*a*, conductivity, salinity, and water temperature at each site. An epibenthic sled, hand-pulled along an 18-m transect, was used three times per site to collect any epibenthic organisms for identification and isotopic analysis.

As described above, four paired 100 $m^{-2}$ polygons enclosed homogeneous *Avicennia* or *Spartina* plots. Within each plot, a 10 cm long (60 ml) syringe corer was used to extract four sediment cores for sediment total organic carbon (TOC), soil moisture, porewater ammonium, and porewater salinity. A 15 cm long, 9 cm diameter acrylic cylinder was also used within each plot to collect two infaunal cores for species identification and enumeration.

Plant tissue samples were taken for isotope analysis, with nine blades of nine different *S. alterniflora* and three terminal leaf nodes of three different *A. germinans* taken per plot. Percent coverage was estimated at each plot using 0.25 $m^{-2}$ quadrats subdivided into 100 gridded squares using monofilament line, with four replicates taken at random per plot. All sediment cores, infaunal cores, tissue samples, and epibenthic specimens were placed into pre-labeled Whirl-pak bags on ice until transported to UTMSI where they were stored frozen at -80°C, or live (at 4°C) until processed in the lab.

### *Lab Processing*

All infaunal cores were sieved at UTMSI after being transported from the field on ice and in Whirl-pak bags. A three-tiered sieve was used to separate sediment and vegetation from infauna before any organisms found were separated by taxa and enumerated to a minimum sieve mesh of 0.5 mm. For infauna that could not be immediately identified, at least one voucher specimen was stored in 100% ethanol for later identification by a taxonomist Susan Schonberg (UTMSI) or Mr. Rick Kalke (Harte Institute at TAMU-CC). After enumeration and identification was completed, all specimens were rinsed with deionized water, weighed, and stored at -80ºC for $\delta^{13}C$ and $\delta^{15}N$ isotopic analysis.

All sediment cores, except for cores used in soil moisture calculations, were frozen at UTMSI for later analysis. Soil moisture samples were homogenized and weighed to obtain their “wet weight”. Samples were then dried at 60 ºC for at least 24 hours, cooled to room temperature, and re-weighed to determine their “dry weight”. These weights were used to calculate the percent of soil moisture (the percent through difference between sample wet and dry weight):

$$\%\ soil\ moisture = ((wet\ weight\ - dry\ weight)\ \div\ wet\ weight\ ) * 100$$

TOC samples were thawed overnight, homogenized, and dried at 60 ºC for 24 hours. Samples were cooled to room temperature and then weighed to obtain their “60 ºC mass”. Samples were combusted at 550 ºC for 4 hours. Samples were cooled to room temperature and weighed again to obtain “550 ºC mass” (TOC is determined by loss on ignition by measuring the mass before and after combustion). These weights were used to calculate the total organic carbon percentage:

$$\%\ organic\ C = ((60℃\ weight\ - 550℃\ weight)\ \div\ 60℃\ weight) * 100$$

Biota collected for isotopic analysis were rinsed with milli-Q water and cleaned of epiphytes and other organic or inorganic matter. For animal tissues, any calcified structures were removed so that only muscular tissue remained. After samples were dried in a 60 ºC oven for at least 48 hours, each sample was homogenized into a fine powder using a mortar and pestle and placed in 10 ml polyethylene vials. All equipment used in preparation for isotope analysis was cleaned with ethyl alcohol before and after each use. Any samples frozen and stored were thawed for 24 hours before analysis. After homogenization, samples were placed into a Finnigan MAT Thermo Delta Plus XL isotopic ratio mass spectrometer (IRMS) interfaced through a Conflo-II to a Carlo Erba NC-2500 elemental analyzer.

Samples for porewater ammonium analysis were processed according to the guidelines in *Determination of Ammonia (The Alternative Method;* Parsons et al. 1984).

### *Data Analysis*

We used R-Studio to examine for statistically significant differences among our data using ANOVA, Tukey post-hoc analysis, and linear regression techniques in data analysis.

# RESULTS and DISCUSSION

## Water Quality

Basic water quality parameters showed expected seasonal variability in temperature but other indices (salinity, dissolved oxygen and pH) showed no clear seasonal pattern (**Table 1**) during 2019. With few exceptions the three sites were remarkably similar, especially with respect to salinity and temperature. Concentrations of chlorophyll *a* were consistently lower at Packery Channel during all four seasons and a high salinity (36) was recorded at Coyote Island in July (otherwise salinities generally ranged between 17 and 30 at all sites in all seasons).

**Table 1.** Summary of water column hydrographic parameters (recorded with a YSI 6920-V2 SONDE) by season and region.

| | **Temp (°C)** | **Salinity** | **DO (mg L$^{-1}$)** | **DO %** | **pH** | **Chl *a* (µg L$^{-1}$)** |
|---|---|---|---|---|---|---|
| **WINTER** | | | | | | |
| Harbor Island | 17.0 | 26.8 | 6.3 | 77.6 | 7.3 | 7.3 |
| Coyote Island | 19.3 | 27.6 | 4.5 | 57.4 | 7.4 | 2.3 |
| Packery Channel | 15.6 | 28.7 | 8.5 | 101.9 | 7.7 | 0.8 |
| **SPRING** | | | | | | |
| Harbor Island | 22.9 | 26.4 | 7.2 | 88.6 | 7.2 | 6.4 |
| Coyote Island | 25.2 | 25.6 | 10.0 | 138.6 | 8.3 | 6.0 |
| Packery Channel | 23.4 | 26.9 | 6.9 | 96.5 | 7.2 | 2.3 |
| **SUMMER** | | | | | | |
| Harbor Island | 28.9 | 33.5 | 3.0 | 47.2 | 7.4 | 9.1 |
| Coyote Island | 36.0 | 34.2 | 7.6 | 130.3 | 7.7 | 8.1 |
| Packery Channel | 29.8 | 34.2 | 5.9 | 78.3 | 7.2 | 4.7 |
| **FALL** | | | | | | |
| Harbor Island | 27.2 | 28.3 | 7.5 | 110.7 | 7.5 | 7.0 |
| Coyote Island | 24.7 | 29.3 | 5.0 | 72.9 | 7.5 | 2.8 |
| Packery Channel | 25.8 | 28.5 | 5.5 | 78.4 | 7.5 | 0.8 |

## Sediment Biogeochemistry

### *Soil Moisture and Total Organic Carbon*

Percent soil moisture ranged from 25 to 45% at the three sites, with no clear relationship between *Avicennia* and *Spartina* vegetation types (**Figure 2**). Coyote Island appeared to have a higher percent soil moisture (45%) than either the Harbor Island or Packery Channel sites. More interestingly, percent total organic carbon (TOC) was significantly ($p < 0.001$) different between *Avicennia* and *Spartina* vegetation types (**Figure 3**). Sediment TOC within *Avicennia* plots was well over 2% compared to *Spartina* plots, which were consistently less than 1.5%.

Our differences in soil moisture could be attributed to vegetation or the character of the sediments, and sediment grain size. We did not measure sediment grain size, but sediment comprised of clays versus porous sands would greatly affect water retention between sites. Vegetation may also affect soil moisture. The pneumatophores of *Avicennia* increase soil moisture by creating more channels through the sediment for water percolation. Preliminary analyses by co-author Fraser found a weak positive correlation ($r^2 = 0.33$) between increasing pneumatophore coverage and increasing soil moisture.

### *Water Depth, Porewater Ammonium and Salinity*

Mean water depths for *Avicennia* averaged 8-15 cm deeper than for corresponding water depths for *Spartina* at all three sites (**Figure 4**) but porewater salinity and sediment ammonium concentrations did not differ between vegetative types (**Figure 5**). Seasonal changes in porewater ammonium concentrations were not detected, but we expected lower concentrations in the spring as a result of increased ammonium uptake by marsh flora to fuel primary production (Perry and Mendelssohn 2013). A more in-depth look into ammonium differences between these two plot-types would be interesting, since our measurements may not be sufficiently sensitive to capture seasonal differences related to uptake and remineralization processes.

The lignin composition that make the *S. alterniflora* blades more structurally rigid than *A. germinans* leaves could possibly make them harder to be broken down by detritivores (Perry and Mendelssohn 2013). Regardless of the mechanism, *A. germinans* leaves and stems have been shown to have faster decomposition rates than *S. alterniflora* (Perry and Mendelssohn 2013). Greater amounts of particulate organic matter (POM) in the sediments of one plot-type or another could potentially support greater levels of bacterial growth with implications for significant differences in soil ammonium concentrations. Metagenomic comparisons between *A. germinans* and *S. alterniflora* sediments could provide future insight into any interactions between total organic carbon concentrations and the bacteria they could support.

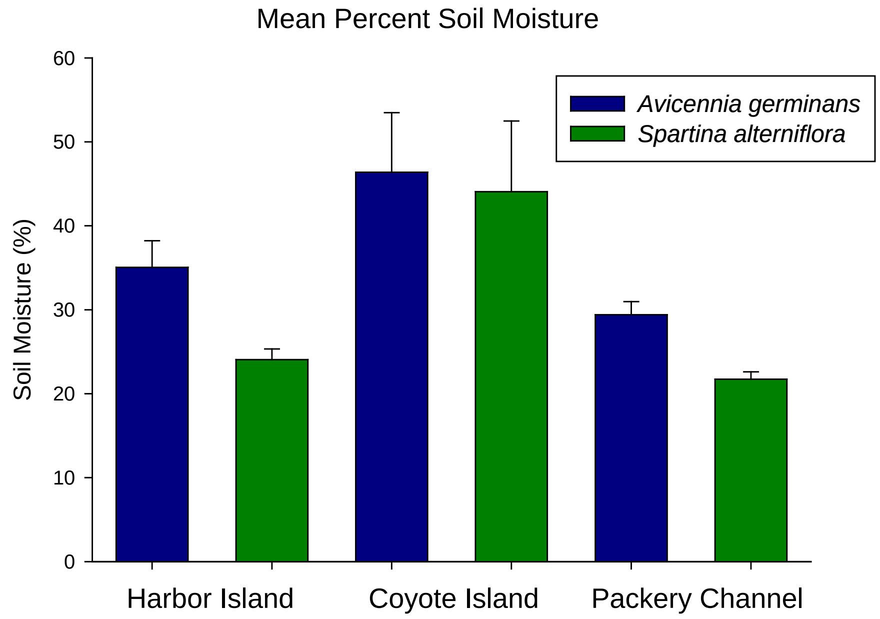

**Figure 2.** Comparison of percent soil moisture (means ±SE) between vegetative foundation species (*Avicennia* and *Spartina*) among sites. There were no significant differences ($p > 0.05$) among sites or vegetation assemblages.

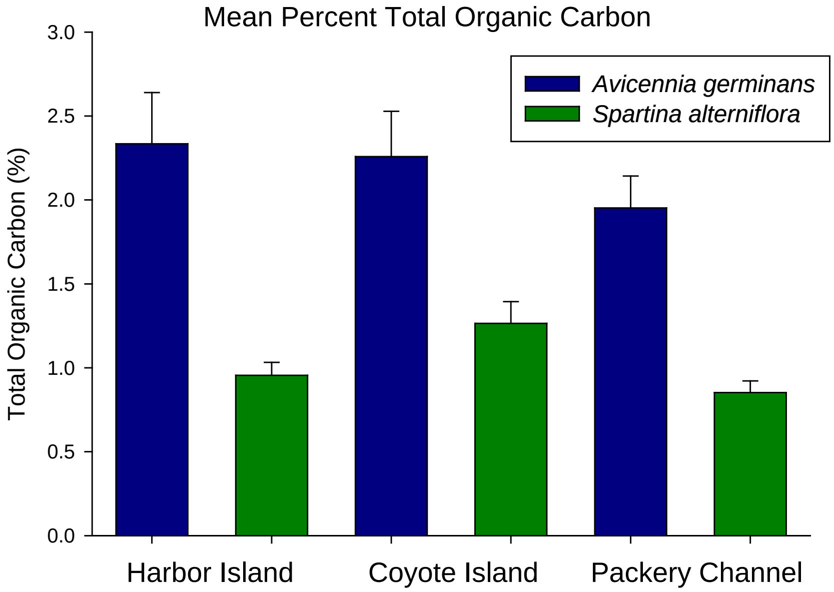

**Figure 3.** Comparison of total organic carbon (TOC) between vegetative foundation species (*Avicennia* and *Spartina*) among sites (means ±SE). TOC is significantly lower ($p < 0.001$) within *Spartina* habitats than within *Avicennia* habitats at all three sites.

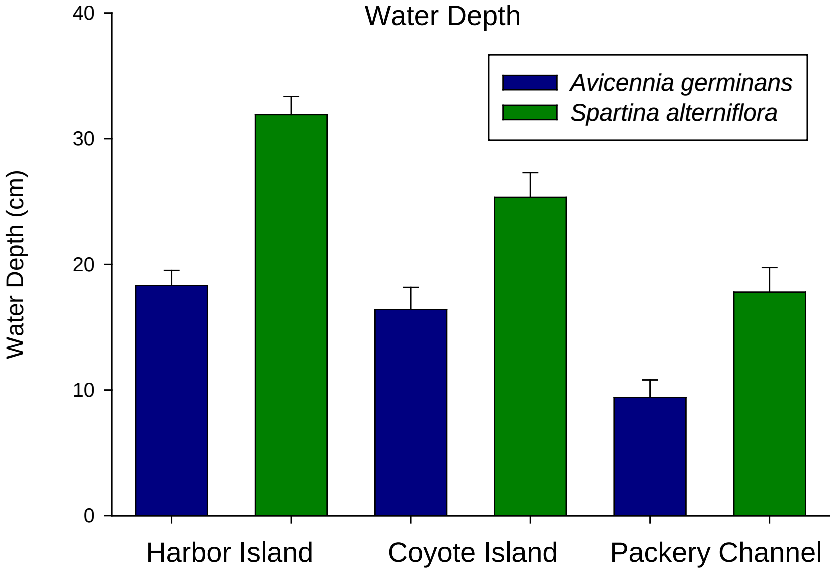

**Figure 4.** Comparison of water depths between vegetative foundation species (*Avicennia* and *Spartina*) among sites (means ±SE). Although water depths were significantly ($p < 0.011$) deeper at the *Spartina* plots than within the *Avicennia* plots, the difference only ranged about 10-12 cm.

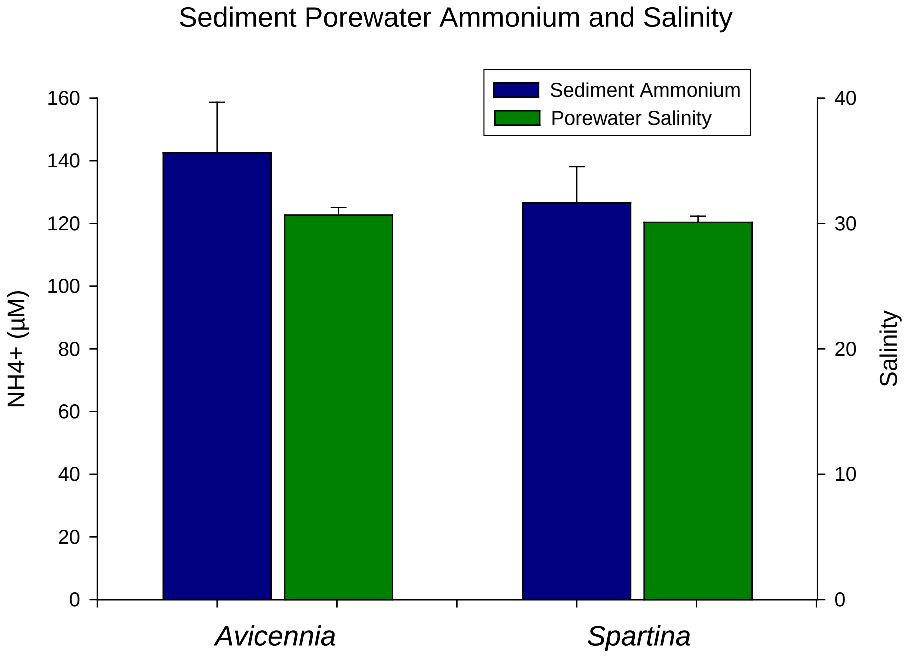

**Figure 5.** Pooled measurements of porewater ammonium and salinity within *Avicennia* and *Spartina* vegetation assemblages at all three sites. No significant differences ($p <. 0.05$) in either parameter was detected between plot types. Values are means ±SE.

## Infaunal Species Composition

A composite of all organisms collected and enumerated in benthic cores at all sites over the four collection periods reveal considerable overlap of species between both *Avicennia* and *Spartina* habitats (**Table 2**). Over 25 species and/or families of invertebrates were identified over the period of this study representing four major phyla, including Annelida (mostly polychaetes), Nemertea, Arthropoda (crustaceans), and Mollusca (bivalves and gastropods). Generally, the polychaetes and crustaceans were equally distributed between *Avicennia* and *Spartina* habitats, but more species of molluscs were collected in *Spartina* dominated habitats. Abundances generally ranged from a low of 7.4 individuals $m^{-2}$ in summer to a high of 739 individuals $m^{-2}$ in winter, which illustrates an extremely healthy wetland ecosystem, regardless of vegetative type (**Table 3**).

The distribution and abundance of infaunal biota also shows rather even distribution of fauna between vegetative assemblages and sites (**Figures 6-8**). Surprisingly, the abundance of biota is greatest in winter at all sites for both vegetative types. Moreover, the most dominant group are clearly the polychaetes on both temporal and spatial scales.

Polychaete abundance in the winter was shown to not differ significantly between plot-types but differed significantly between sites. Tukey ad-hoc analysis showed that the reason for this significant variance between sites was because Packery Channel nearly had twice as many polychaetes within each plot-type as the other two sites.

The major families of polychaetes between plot-types showing similar results include the Capitellidae, Arenicolidae, Nereididae, Spionidae, and Orbiniidae. These families were found throughout both *A. germinans* and *S. alterniflora* plots across all sites. Overall diversity was also dominated by polychaetes, but the presence of gastropods in *Spartina* habitats increased the number of species relative to *Avicennia* vegetated areas.

The lack of significant differences between plot-types for polychaete abundance fails to show any implications for infauna as wetlands shift from *Spartina* dominated to *Avicenna* dominated habitats. This result contrasts with other findings, which documented significant differences in faunal species composition between *Spartina* and *Avicenna* dominated habitats. However, such differences in faunal occurrence is likely a function of elevational differences between these two foundation species rather than the plant species themselves. The “typical” zonation of these wetland species places *Avicennia* at higher elevations than *Spartina*. In this study, we eliminated elevation as a variable by sampling both habitats at similar water depths (see **Figure 4**).

**Table 2.** Species composition (by family and/or genus) of fauna collected from benthic cores taken within *Avicennia germinans* and *Spartina alterniflora* vegetation types at each of the three sites in the CBBEP project area. Shaded cells indicate presence of the organism.

| | Organism | ***Avicennia*** | | | ***Spartina*** | | |
|---|---|---|---|---|---|---|---|
| | | HI | CI | PC | HI | CI | PC |
| POLYCHAETES | Arenicolidae | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | Capitellidae | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | Eunicidae | ▨ | | ▨ | ▨ | | ▨ |
| | Maldanidae | ▨ | | ▨ | ▨ | ▨ | ▨ |
| | Nereididae | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | Orbiniidae | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | Phyllodocidae | | | | ▨ | ▨ | ▨ |
| | Spionidae | | | ▨ | ▨ | ▨ | ▨ |
| | Unident. Polychaete | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| CRUSTACEANS | Tanaidacea | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | Amphipoda | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| | Copepoda | | | | | | ▨ |
| | Palaemonidae | | | ▨ | | | |
| MOLLUSCS | *Bulla striata* | | | | | ▨ | |
| | *Cyclinella tenuis* | ▨ | | | | ▨ | |
| | *Ceritheum atratum* | | | | ▨ | ▨ | |
| | *Neritina virginea* | | | | | ▨ | |
| | Tellinidae | | | | ▨ | | |
| | *Tagelus plebeius* | | | | ▨ | | |
| | *Amygdalum papyrium* | | | | ▨ | | |
| | *Crepidula* sp. | | | | | ▨ | |
| | *Phacoides pectinatus* | | ▨ | | | | |
| | Unknown Bivalve | ▨ | | | | ▨ | ▨ |
| MISC | Chironomidae | ▨ | | | | | |
| | Nemertea | | | | | ▨ | ▨ |
| | Oligochaeta | ▨ | | | | ▨ | |

**Table 3.** Total species abundance (m$^{-2}$) of infauna collected seasonally from 16 benthic cores taken within *Avicennia* and *Spartina* vegetation types at the three sites in the CBBEP project area.

| | 2019 | | | |
|---|---|---|---|---|
| SITE/ Foundation Assemblage | Winter | Spring | Summer | Fall |
| HARBOR ISLAND | | | | |
| *Avicennia* | 319.3 | 66.3 | 54.0 | 22.1 |
| *Spartina* | 329.1 | 137.6 | 29.5 | 41.8 |
| COYOTE ISLAND | | | | |
| *Avicennia* | 395.5 | 113.0 | 7.4 | 27.0 |
| *Spartina* | 469.1 | 361.1 | 7.4 | 110.5 |
| PACKERY CHANNEL | | | | |
| *Avicennia* | 739.3 | 149.8 | 39.3 | 31.9 |
| *Spartina* | 668.1 | 203.9 | 113.0 | 88.4 |

Inconsistencies in the results of Scheffel and Johnson (2018) also point to faunal differences not being a function of plant species. The research sites from this paper were off the coast of Mississippi and comprised of two islands, Horn Island and Chandeleur Island. The two islands had significant differences in the elevation of their *Avicennia* and *Spartina* plots, with similarly significant differences in their infaunal abundances. Horn Island's *Avicennia* plots were at relatively lower elevations and showed the highest amphipod density. Chandeleur Island's *Avicennia* plots were at relatively higher elevations and showed the lowest amphipod density. Horn Island's *Spartina* plots were at relatively higher elevations and exhibited no higher densities of infauna. Chandeleur Island's *Spartina* plots were at relatively lower elevations and exhibited higher polychaete abundance. The authors of this paper stated in their discussion that the results of this paper may be due to elevational differences (Scheffel and Johnson 2018).

The plots in this study were chosen to minimize these elevational differences, with a comparison of the interquartile ranges of water depths between *Avicennia* plots in the winter illustrating that this objective was largely accomplished. However, the mean water depths of these plots within each site were shown to be significantly different (Pr (>F) = 0.01165), but Tukey post-hoc analysis proved that the only significant factor for this variation was from Harbor Island. The few outliers of water depth at Harbor Island are probably responsible for this variation, but overall our sites are evenly comparable across water depths that we used as a proxy for elevation.

Our results show no significant difference in polychaete abundance between plot-types which were placed at similar elevations.  Consequently, we believe that unless elevation is removed as a confounding variable, reported differences in infaunal abundances between these two foundation species could be more of a function of elevation

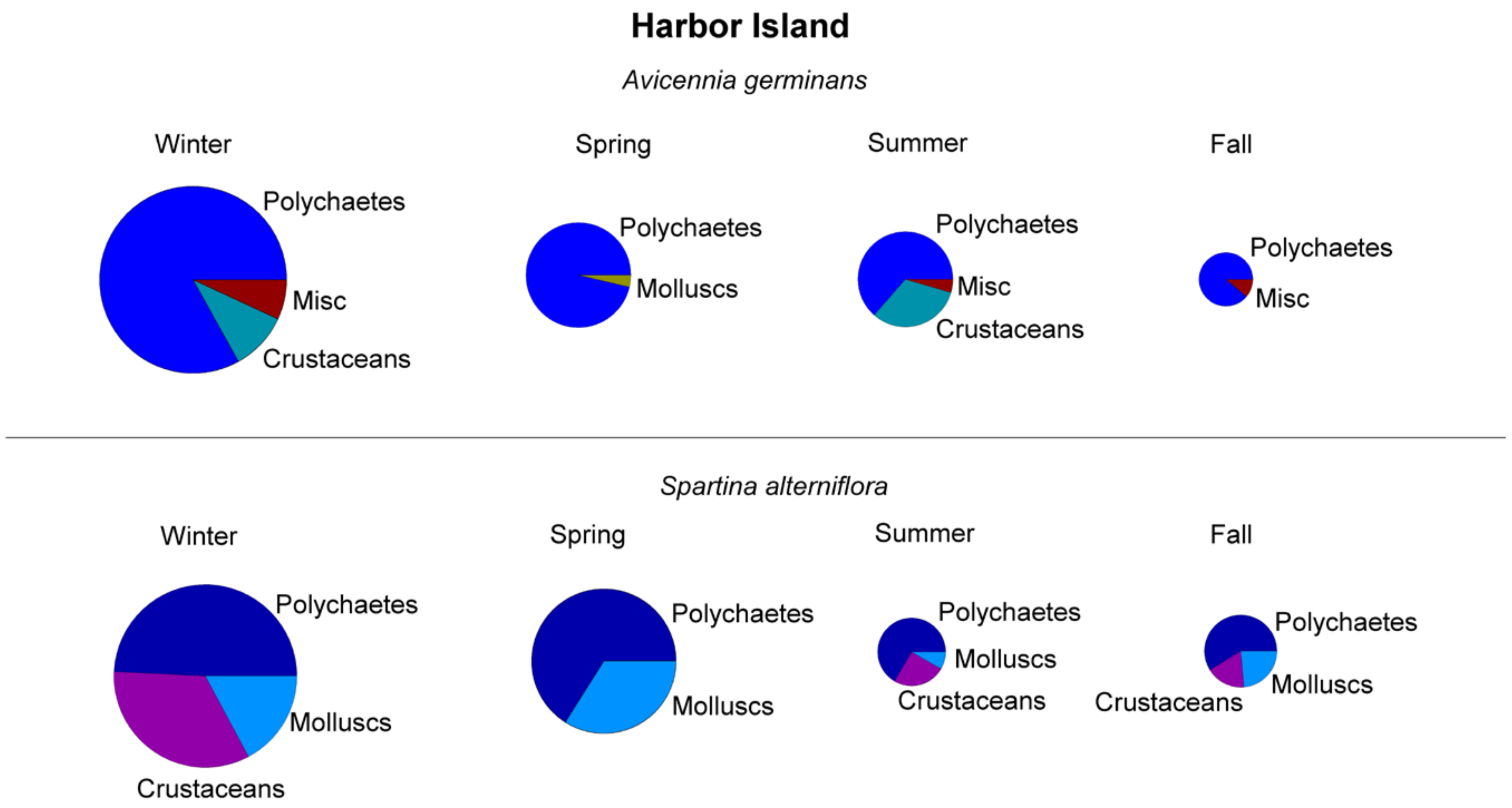

**Figure 6.** Harbor Island. Benthic infaunal species composition in *Avicennia* and *Spartina* plots by season in 2019. The size of the circle is proportional to the total species abundance as listed in Table 3.

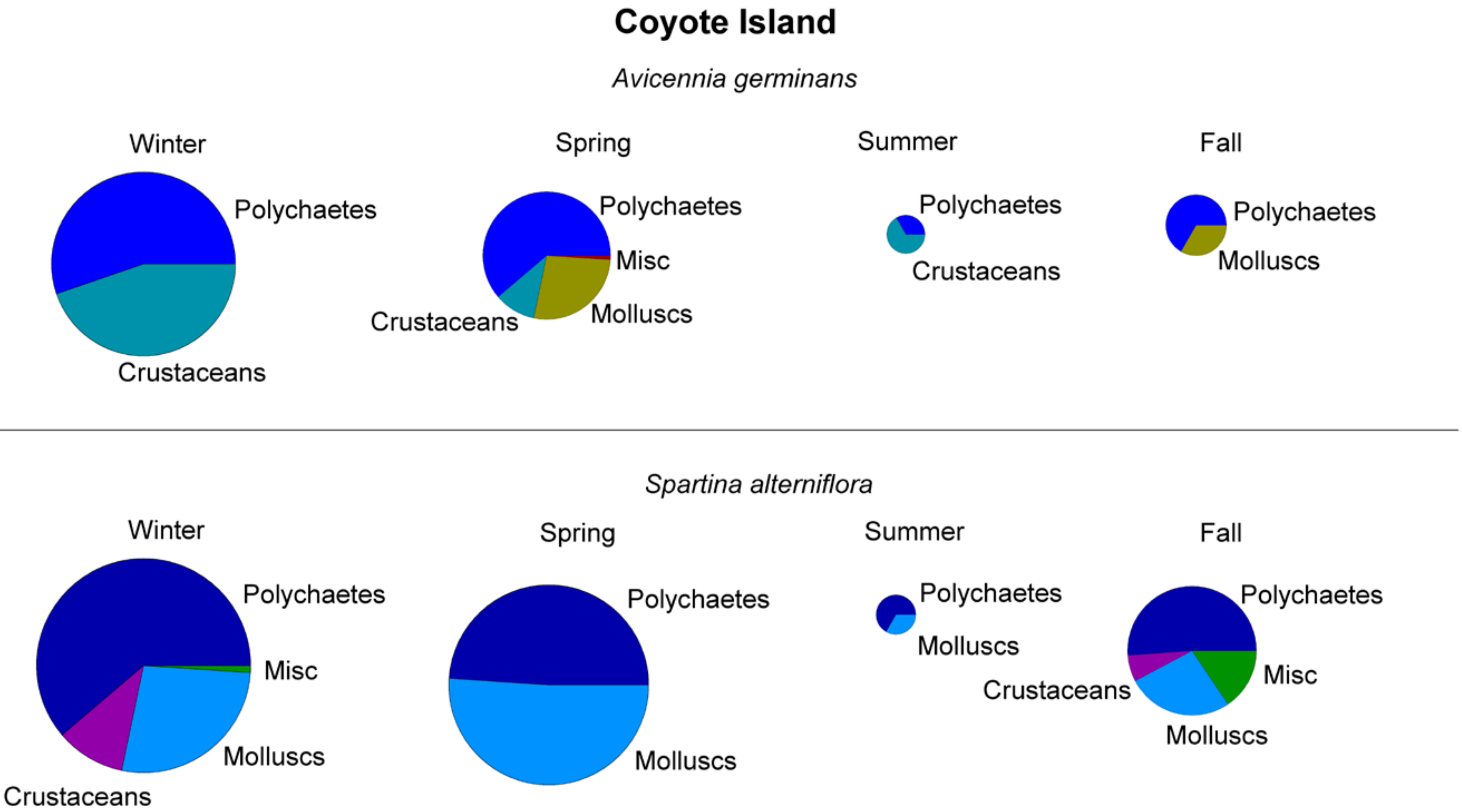

**Figure 7.** Coyote Island. Benthic infaunal species composition in *Avicennia* and *Spartina* plots by season in 2019. The size of the circle is proportional to the total species abundance as listed in Table 3.

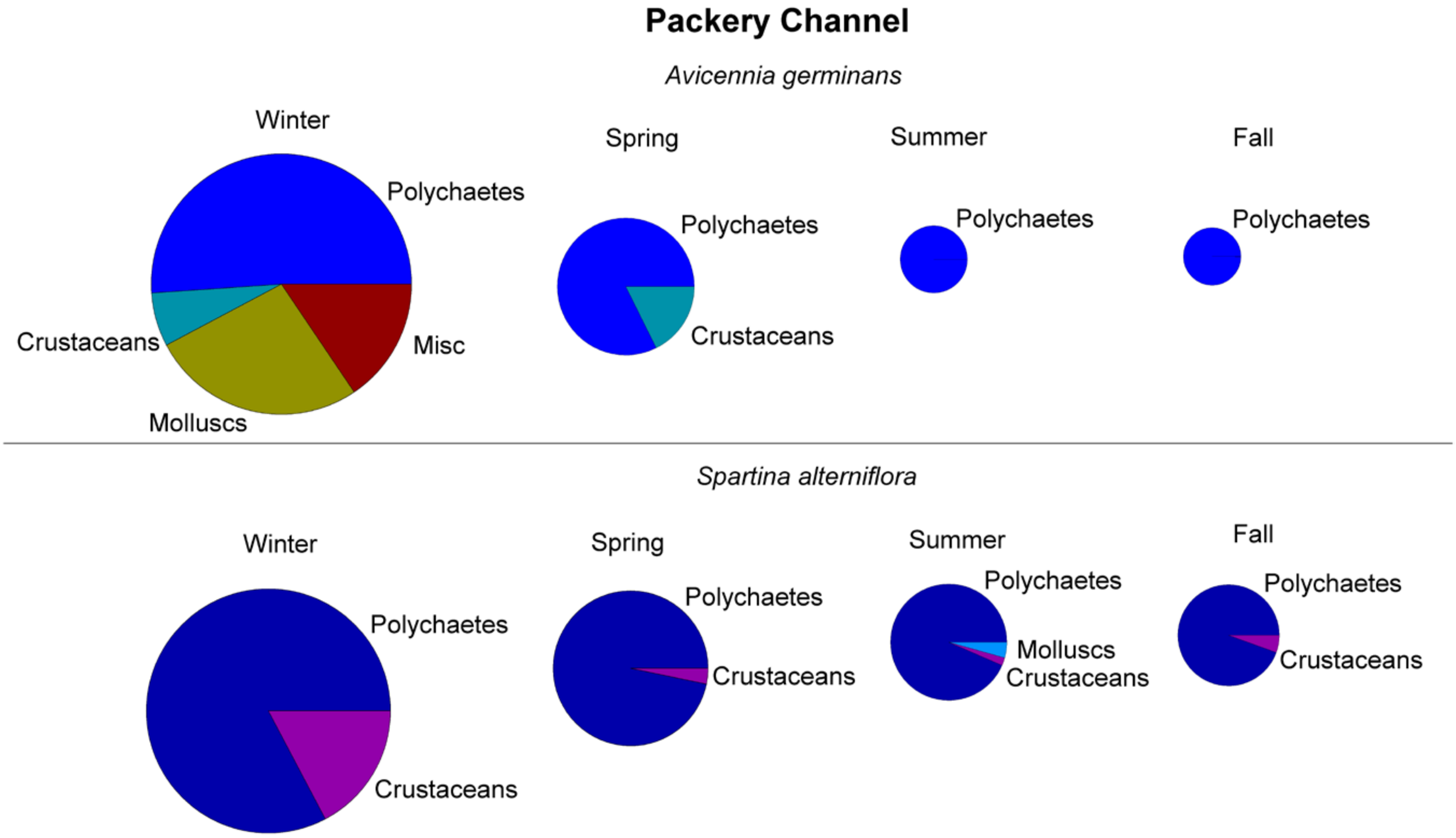

**Figure 8.** Packery Channel. Benthic infaunal species composition in *Avicennia* and *Spartina* plots by season in 2019. The size of the circle is proportional to the total species abundance as listed in Table 3.

abundances between these two foundation species could be more a function of elevation and not the plants themselves.

### *Avicennia* and *Spartina* as Sources of Organic Carbon: Isotopic Evidence

The stable isotopic values of the most common biota collected in benthic cores and in epibenthic nets (mullet), reveal that the δ$^{13}$C values (**Table 4**) fell within the range of the wetland end member δ$^{13}$C signatures for $^{13}$C depleted *Avicennia* (-24.6‰) and $^{13}$C enriched *Spartina* (-13.8.3‰). Tanaids were among the most $^{13}$C enriched of the benthic fauna (-15.4‰), while mullet were the most $^{13}$C depleted (-20.3‰).

In general, the same species of fauna collected in the *Spartina* habitat were isotopically heavier (more $^{13}$C enriched) than those collected in *Avicennia* habitats (**Figure 9**). The paired comparison provides good evidence for the assimilation of *Spartina* based carbon into benthic fauna which is potentially incorporated into higher trophic levels.

**Table 4**. Stable isotopic values (‰) of the most common organisms collected in vegetation assemblages dominated by either *Avicennia germinans* or *Spartina alterniflora*. Values are means ± SE (n). Mullet collected from tidal creeks adjacent to the study plots of both *Avicennia* and *Spartina* vegetative assemblages showed a δ$^{13}$C mean of -20.29‰ ± 1.22 (3) and δ$^{15}$N mean of 7.37‰ ± 0.19 (3).

| | ***Avicennia*** | | ***Spartina*** | |
|---|---|---|---|---|
| | δ$^{13}$C | δ$^{15}$N | δ$^{13}$C | δ$^{15}$N |
| *Avicennia germinans* | -24.60 ± 0.21 (6) | 3.10 ± 0.51 (5) | | |
| Amphipods | -16.63 ± 1.37 (3) | 4.52 ± 0.86 (3) | -15.80 ± 0.28 (3) | 3.79 ± 0.53 (3) |
| Arenicolidae | -19.82 ± 1.69 (2) | 4.73 ± 0.37 (2) | -15.90 ± 0.66 (6) | 5.29 ± 0.51 (5) |
| Capitellidae | -17.30 ± 1.01 (5) | 6.15 ± 0.39 (5) | -15.19 ± 0.58 (6) | 6.28 ± 0.69 (6) |
| Chironomid | -19.29 (1) | 4.36 (1) | | |
| Nereidae | -16.44 (1) | 7.63 (1) | -15.03 ± 0.81 (4) | 6.22 ± 1.11 (4) |
| Orbiniidae | -17.11 (1) | 2.68 (1) | -16.70 ± 0.83 (6) | 6.16 ± 0.81 (6) |
| Tanaids | -16.96 ± 1.17 (3) | 4.96± 1.61 (3) | -15.45 ± 0.68 (3) | 5.85 ± 0.51 (2) |
| *Spartina alterniflorna* | | | -13.75 ± 0.16 (6) | 1.82 ± 0.68 (6) |

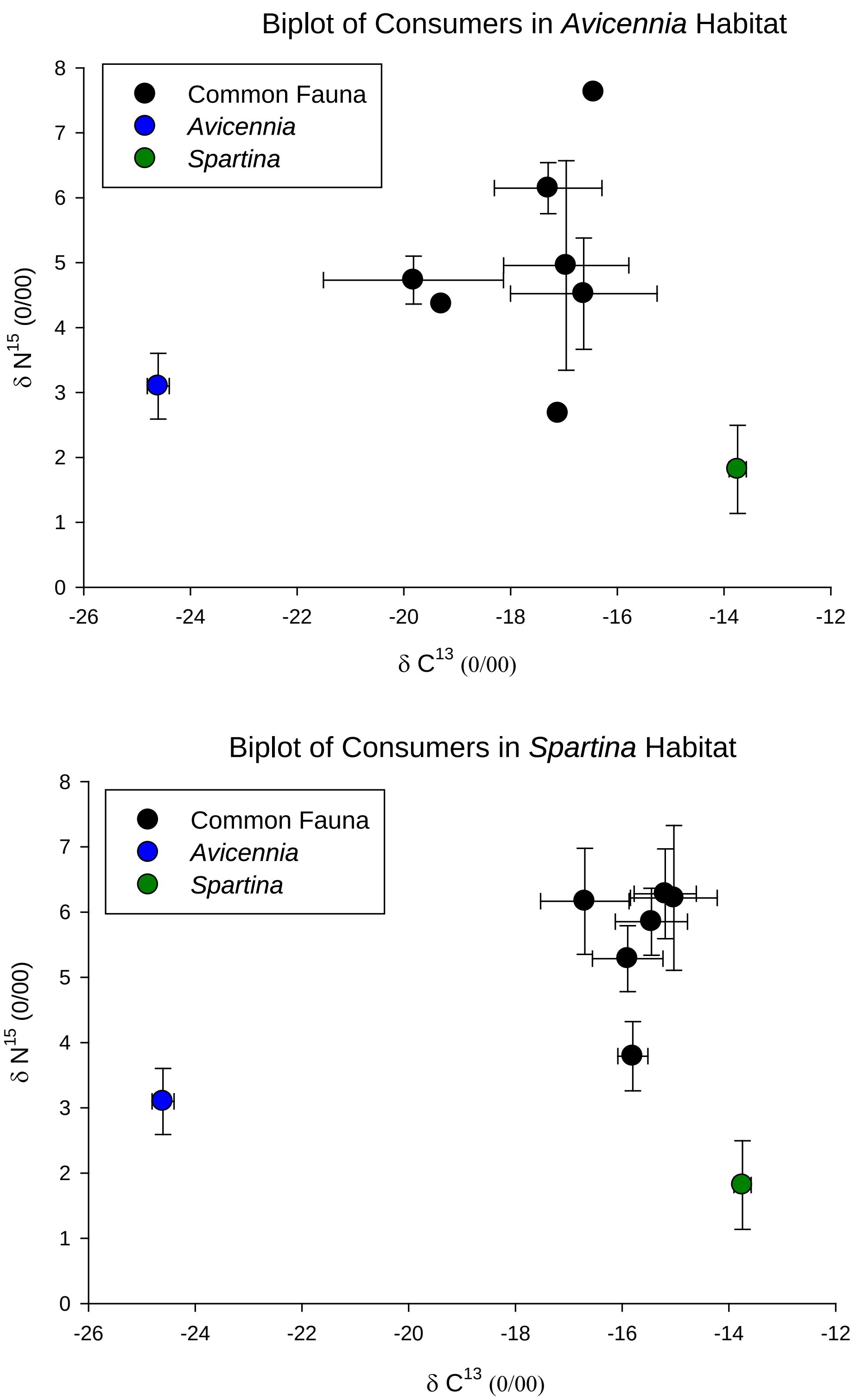

**Figure 9.** Biplot of $\delta^{13}$C and $\delta^{15}$N values (±SE) of the fauna listed in Table 4 collected within *Avicennia* plots (top panel) and *Spartina* plots (bottom panel). There is clear fidelity of fauna to $C_4$ derived carbon in *Spartina* habitats, but isotopic values of the same species diverge in *Avicennia* plots, reflecting the assimilation of mangrove ($C_3$) carbon.

## Conclusion and Recommendations for Further Work

The results of this study clearly demonstrated important differences between mangrove and marsh habitats with respect to sediment biogeochemical properties and the fidelity of fauna that inhabit these distinct but adjacent wetland habitats. Interestingly, we found that polychaetes, which dominated the infauna of both vegetation types, showed little detectable differences in overall species composition between *Avicennia* and *Spartina* habitats. We found that sediment TOC within *Avicennia* plots was well over 2% compared to *Spartina* plots, which were consistently less than 1.5%, revealing the high organic content of mangrove soils. The benthic invertebrate species collected in both vegetative zones possessed clear distinctions in their isotopic composition, indicating that these organisms move little between habitats types. This is not surprising for relatively sedentary polychaetes, but unexpected for mobile crustaceans such as amphipods and tanaid shrimp. Such observations suggest that there is considerable site fidelity by some biota, but our work did not adequately sample the epibenthic fauna which are considerably more mobile (e.g. snails, crustaceans and fish) that are known to move between these habitats (Smith et al. 2009; Rozas et al. 1990). Epibenthic habitats are challenging to sample, but future studies should focus on effective sampling strategies that can provide reasonably reliable estimates of the composition of the epibenthic fauna and their variable dependence on *Avicennia* and *Spartina* habitats.

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