DIET ANALYSIS AND ASSESSMENT OF HABITAT AND PREY AVAILABILITY ASSOCIATED WITH TEXAS DIAMOND-BACKED TERRAPIN (*MALACLEMYS TERRAPIN LITTORALIS*)

by

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DEDICATION

For my grandmother, Yvonne Alleman (1934-1994).

Thanks for fostering and encouraging my curiosity of the natural world at a young age, and starting me on my path.

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ABSTRACT

DIET ANALYSIS AND ASSESSMENT OF HABITAT AND PREY AVAILABILITY ASSOCIATED WITH TEXAS DIAMOND-BACKED TERRAPIN (*MALACLEMYS TERRAPIN LITTORALIS*)

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The Diamond-backed Terrapin (*Malaclemys terrapin*) is a species of turtle specialized for living in brackish and saltmarsh environments, and due to diet is likely a keystone predator. The Texas Diamond-backed Terrapin (*M. t. littoralis*) is the subspecies found along most of the Texas Gulf Coast. Past studies have been conducted on the diet and prey of the Atlantic subspecies of Diamond-backed Terrapin. Previous studies indicate a diet primarily consisting of various crustacean and mollusk species with variations along their range. Due to body size sexual dimorphism, studies also show differences in diet between males and females. There is currently a paucity of data on the diet of this species along the coast of the Gulf of Mexico, and specifically on the Texas Gulf Coast. This study examined the prey availability and diet of the Texas Diamond-backed Terrapin. Dietary analysis via fecal analysis indicated Gastropoda and Decapoda as major components to Texas terrapin diet. The remains of plicate horn snails (*Cerithidea pliculosa*) and fiddler crabs (*Uca* spp.) were the most common prey items found in all samples. There were significant differences between the diet of male and female terrapin, specifically in amounts and proportion of periwinkle snails (*Littorina irrorata*), blue crabs (*Callinectes sapidus*), total Gastropods, and total Decapods consumed. Female terrapin consumed more *L. irrorata* and total Gastropods than males, while males were found to consume more *C. sapidus* and total Decapods than females. Males also demonstrated higher dietary diversity. Significant seasonal differences in diet were detected between seasons for total Gastropods, *C. sapidus*, and *Uca* spp. Additional dietary differences were detected for less common dietary components.

Randomly selected sites lacking terrapin exhibited a significantly higher number of plant species and vegetation coverage when compared to terrapin capture locations. No significant difference in the coverage of dominant plant species *Spartina alterniflora* was detected at terrapin capture versus non-capture sites. Randomly selected sites lacking terrapin had significantly higher numbers of *Uca* spp. burrows than capture locations. Multiple significant seasonal and location differences in vegetation and prey were detected at capture sites. However, no differences for any prey or habitat factor were detected between sexes at capture locations. Results from fecal analysis indicate a slightly different diet for terrapin than previously reported in other studies. However, habitat and prey availability findings support previous studies. The combined results extend the basic knowledge and understanding of diet and habitat utilization by this species which will be useful for ongoing conservation and management of *M. terrapin*, especially the Texas subspecies.

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INTRODUCTION

Life History

The Diamond-backed Terrapin (*Malaclemys terrapin*) is a medium-sized semi-aquatic turtle attaining a carapace length of up to 238mm (Dundee and Rossman 1989). Diamond-backed Terrapin exhibit sexual dimorphism with larger females having larger, wider heads, than males (Tucker et al. 1995). The carapace of the Diamond-backed Terrapin is oblong and ranges in color from light gray to black, and can have concentric growth rings, which gives the species its name (Butler et al. 2006). Their skin can be light gray to blue to black, with dark spots or patterns present.

Terrapin occur along the Atlantic and Gulf coasts of North America from Massachusetts to Texas. There are seven recognized subspecies across their range with the Texas Diamond-backed Terrapin (*M. t. littoralis*) present along most of the Texas coast (Dixon 2013). However, recent genetic studies are indicating that perhaps subspecies should be viewed instead as evolutionary management (Glenos 2013, Drabeck 2014, Hart et al. 2014).

Throughout their range, terrapin occupy a narrow band of salt and brackish water habitats (Palmer and Cordes 1988). Within this zone, terrapin live in the marshes, tidal creeks, coves, and lagoons behind barrier beaches (Palmer and Cordes 1988). According to Dixon (2013), Diamond-backed Terrapin can be found in thirteen Texas counties. Adult female terrapin can be found farther offshore in deeper estuarine waters while males and juveniles are usually found closer to shore in shallower waters (Roosenburg et al. 1999).

Terrapin are the only species of turtle specialized to live in saltmarsh and estuarine habitats in the temperate zone (Hart and Lee 2006). Terrapin are unique in this aspect as a North American turtle species, and perhaps when considering all species (Lamb and Osentoski 1997). Most North American Emydid turtles are adapted to freshwater ecosystems (Davenport and Ward 1993). The freshwater species group, map turtles (*Graptemys*), are the Diamond-backed Terrapin's closest relatives (Wood 1977, Lamb and Osentoski 1997). Diamond-backed Terrapin are adapted in both behavior and physiology to their estuarine ecosystems and are able to survive in full strength seawater for extended periods of time. Terrapins are able to live in saline environments by controlling water and salt levels in their body fluids (Dunson 1985, Davenport and Macedo 1990). In contrast, some turtle species that are normally found in freshwater systems, such as *Batagur baska* and *B. borneoensis* from Southeast Asia, are able to survive brief ventures into saltwater by avoiding drinking or eating while exposed to high salinities (Davenport and Wong 1986, Davenport et al. 1992b).

Terrapin face a number of human induced threats. Much of their habitat has been degraded or destroyed by human activities (Sierra and Burke 2007). Terrapin are also threatened by drowning in crab pots fished near their preferred habitat (Roosenburg et al. 1997). Due to these threats, many local populations or subspecies are listed by various states as either endangered, threatened, or species of concern (Glenos 2013).

Terrapin Diet

Compared to other turtles in the family Emydidae, the appetite of Diamond-backed Terrapin is enormous. Davenport and Ward (1993) noted terrapin in captivity consumed 8-10 times more food items by weight before satiation than other closely related species. Past studies have shown that terrapin diets consist primarily of Crustacea and Mollusca, with Gastropods such as marsh periwinkle snails (*Littorina irrorata*) and various crab species (*Sesarma* spp., *Uca* spp., *Callinectes sapidus*) being common (Davenport et al. 1992a, Tucker et al. 1995, Butler et al. 2012). Hatchling turtles in New York were shown to consume green crabs (*Carcinus maenas*) and amphipods (King 2007). Cagle (1952) and Tucker et al. (1995) also noted the presence of small clams in intestinal contents and in fecal samples. Koza (2006) found that the scorched mussel (*Brachidontes exustus*) was the primary prey item observed in both male and female fecal samples. Decapoda and Gastropoda were found in fecal samples of south Texas terrapins, but not as frequently as *B. exustus* (Koza 2006). Roosenburg et al. (1999) found that marsh periwinkle and other common marsh snails were not the primary food source for a Maryland terrapin population due to absence or scarcity of these species in the estuary. Instead, they found that the primary prey items in a Maryland estuary were small clams including soft-shelled clams (*Mya arenaria*) and razor clams (*Tagelus* spp.) (Roosenburg et al. 1999). Razor clams and soft shell clams were also noted in the stomachs of terrapins captured in New York (Spagnoli and Marganoff 1975). Fecal samples from New York terrapin also show *M. arenaria* (Erazmus 2012). Spivey (1998) noted that terrapins in Core Sound, North Carolina ate little *L. irrorata*. These Diamond-backed Terrapin consumed *C. sapidus, Uca* spp., and *Melampus bidentatus* in high percentages by mass (Spivey 1998). Presence of beetle larvae in terrapin gut contents point to possible scavenging by Diamond-backed Terrapin (Ehret and Werner 2004).

Tucker et al. (1995) studied the Carolina subspecies (*M. t. centrata*) to examine the influence of body size and sex on diet and resource partitioning. They found that the sexual size dimorphism seen in Diamond-backed Terrapin allowed larger sized females to consume larger and different prey items than males, specifically larger *L. irrorata* (Tucker et al. 1995). Evidence collected during a mercury pollution monitoring study support the previous study's findings of females consuming larger snails (Blanvillain et al. 2007). Blanvillain et al. (2007) documented higher levels of mercury in large periwinkles, and in turn higher levels of mercury in female terrapin. Koza (2006) found that *Brachidontes exustus* and Foraminifera were observed at greater frequencies in female fecal samples. In contrast, Decapoda and Gastropoda were observed at greater frequencies in male fecal matter. Based on his data he suggested that prey preference may be a function of individual size as much as sexual dimorphism (Koza 2006). This type of resource partitioning has been seen in other, closely related species (*Graptemys versa*) as well as in unrelated turtle species (*Hydromedusa maximiliani*) (Souza and Abe 1998, Lindeman 2003). In the past, dietary diversity has been shown to be higher in female terrapins (Tucker et al. 1995).

Due to their diet, Diamond-backed Terrapin may serve the role of a keystone predator in saltmarshes (Sierra and Burke 2007). It has been suggested that predation of major saltmarsh grazers by terrapins reduces herbivory on wetland plants. For example, *L. irrorata* and *Sesarma* spp. are major herbivores which graze on *Spartina alterniflora* (Silliman and Zieman 2001, Silliman and Bertness 2008). Removal or lack of species which prey upon these grazers would likely cause a trophic cascade leading to the reduction or collapse of the saltmarsh ecosystem (Altieri et al. 2012). It has been suggested that excess terrapin mortality caused by humans may contribute to these trophic cascade processes (Bertness and Silliman 2008, Altieri et al. 2012).

Prey Availability

Past studies have attempted to quantify terrapin prey species in order to determine how prey availability affects terrapin distribution. These studies indicate that available food resources are not likely to be determinant factors in terrapin distribution (Tucker et al. 1995, Whitelaw and Zajac 2002). Both studies noted high numbers of terrapin prey items in locations throughout the marsh, regardless of terrapin captures. It is suggested, however, that food accessibility may be the limiting factor in terrapin distribution (Tucker et al. 1995). Meaning food resources are present, but terrapin are unable to acquire them due to some factor (i.e. tide level).

Objectives and Hypotheses

The primary objective of this study was to examine and describe the diet of Texas Diamond-backed Terrapin over space and time through fecal analysis. A secondary objective within the diet study was to compare fecal analysis methodologies. Also, this study recorded available prey items and habitat parameters to document their potential effects on terrapin distributions in Texas saltmarshes.

Based on past literature, I hypothesize that there will be significant differences between the diets of male and female terrapins. I also hypothesize that diet composition of terrapin will change seasonally as well as by the marsh where terrapin are captured. Fecal analysis techniques are expected to have little or no influence on the results of diet composition. Locations of terrapin capture were expected to exhibit differences in prey availability as well as in various habitat parameters when compared to randomly selected locations within the marsh that did not contain terrapin.

METHODS

Study Site

This study was conducted in areas where terrapin surveys have historically occurred and were concurrently occurring, as well as areas added over the course of the study. The Environmental Institute of Houston has been monitoring terrapin in an ongoing study since 2008. The main study area was West Bay located within the Galveston Bay estuary, Texas with secondary sites along the Texas Coast (Figure 1). The sites found in and around West Bay include: North Deer Island, South Deer Island, Sportsman Road marsh, and Greens Lake (Figure 2). All previously mentioned locations are saltmarshes dominated by smooth cordgrass (*S. alterniflora*). The other common plant species found in the low marsh are *Batis maritima* and *Salicornia virginica*.

Figure 1. Imagery indicating surveyed sites along Texas Gulf Coast.

Figure 2. An aerial image that shows West Galveston Bay, Texas sites.

North Deer and South Deer are small islands in West Galveston Bay. North Deer is an approximately 56 hectares island, while South Deer is smaller at nearly 30 hectares (Figure 2). Both islands have areas of low and high marsh interspersed by tidal creeks and ponds. The perimeters of each island are primarily composed of shell hash and high marsh vegetation like *Iva frutescens*. There is a narrow strip of shrubby upland vegetation on South Deer Island. Whereas, North Deer has more upland habitat due to spoil from dredging in the Intracoastal Waterway, which is directly north of the island. Each island also has a larger open water area (lagoon) with connections to tidal creeks and narrow outlets to West Bay. The waters surrounding each island have numerous subtidal and intertidal oyster reefs near shore. North Deer Island is located 1.1 km to the northwest of South Deer with open bay water between the two. Both islands have been surveyed for numerous years, and seem to support large terrapin populations. Terrapin originally captured on one island have later been recaptured on the other island, denoting movement between the islands.

Other frequently surveyed sites in the West Bay study area were the saltmarshes located off Sportsman Road and Greens Lake. The Sportsman Road marsh is located 1.2 km to the south of South Deer Island with open water between the two (Figure 2). This large marsh (72 hectares) is located on the barrier island of Galveston. This area shares similar features and vegetation with the Deer Islands. However, it lacks shell hash beaches and large upland areas, but does have extensive sand flats. The actual road separates the studied marsh from West Bay, and is lined by residences on the bay side. However, there are passages to the bay through a large bayou connected to the marsh system by a series of tidal creeks. These creeks drain a much larger lagoon than those lagoons found on the Deer Islands. Terrapin movement between South Deer Island and Sportsman has been previously documented (unpublished data). The Greens Lake study area is a moderately sized (48 hectares) marsh area consisting of similar vegetation and features as the other previously described areas (Figure 2). However, the marsh encloses a much larger secondary bay, Greens Lake itself, rather than the small lagoons found at the Deer Islands. It is located approximately 5 km due west of North Deer Island. The Intracoastal Waterway forms the southern boundary of this marsh, but there is little to no spoil from dredging efforts. There have been no documented cases of individuals moving between Greens Lake and the other West Bay sites.

Limited data was also collected from other Texas coastal sites. These sites included Matagorda Bay (Figure 1 and Figure 3), San Bernard Nation Wildlife Refuge, Bolivar Peninsula, and Texas Point (Figure 1 and Figure 4). These sites exhibit comparable habitat that is similar to the West Bay locations. There is one additional West Bay location where terrapins have been captured that has a different dominant plant species. This site, located near Sweetwater Lake on Galveston Island, is a marsh with slightly higher elevation than the other, nearby areas (Figure 5). As a result, the dominant plant species are *Distichlis spicata* with *Juncus roemerianus* being present in dense stands as well.

Figure 3. An aerial image that shows the Matagorda Bay, Texas site.

Figure 4. An aerial image that shows Texas Point National Wildlife Refuge.

Figure 5. Image indicating location of Sweetwater Lake study site in relation to South Deer Island and Sportsman Road.

Terrapin Capture

Diamond-backed Terrapin were captured by hand during random searches at each site. Terrestrial terrapin surveys were conducted by walking random strip transects for at least a two hour period by each surveyor. Strips had a width of approximately 2.4 m. Once a surveyor reached an impassable obstacle (usually deep water), the transect was extended by making a 45° angle turn and following a new straight line transect. If and when a terrapin was encountered during the search the stopwatch was paused while data was recorded. When a terrapin is captured for the first time, they are uniquely marked by notching marginal scutes with a small triangular file (Cagle 1939), and by insertion of Passive Integrated Transponder (PIT) tags into their left, hind leg. Location (GPS), time, vegetation, and morphometric data were collected at each terrapin capture location. The morphometric data included carapace lengths and widths, plastron lengths and widths, head width, and weight. All biological sample collection was conducted under an approved IACUC protocol (IACUC 10.005).

Prey Availability

Prey availability was assessed during each terrapin capture. A 1 m^2 quadrat around the point at which a terrapin was captured was surveyed for prey abundance, plant community composition, and physical habitat (Figure 6). Within each quadrat sampled, the following data was collected: time, date, vegetation height class, percent vegetation cover, percent cover by species, presence of standing water; distance to the nearest standing water, air temperature at marsh surface, water temperature if standing water present, soil surface temperature, and soil temperature at burrow depth. In addition to the above data, the numbers of *L. irrorata* were counted. Individual *Littorina* were counted on the stems of *Spartina* and on the marsh surface. Shell length and width measurements of *L. irrorata* were taken using small calipers. Length measurements were taken at the longest point (Figure 7), from the apex to the lower edge of the shell, while width measurements were taken at the widest point of the shell (Figure 8). Along with counting available snails, the burrows of fiddler crabs (*Uca* spp.) were counted. Warren (1990) found that under appropriate conditions the number of open burrows of fiddler crabs can be used to estimate crab abundance. A study by Skov and Hartnoll (2001) shows support for this technique as well. In the summer, Louisiana fiddler crab numbers range between 75% and 100% of burrow numbers (Mouton, Jr. and Felder 1996). An attempt to collect the above data before thoroughly disturbing an area was made so as to obtain more accurate details. Prey quadrat data was collected during January 2013 through June 2014.

Figure 6. The 1-m^2 quadrat used in the field.

Figure 7. Photograph showing measure of *Littorina* length.

Figure 8. Photograph showing measure of *Littorina* width.

Additionally, surveys were conducted at random sites along the transect line. In all cases, these were areas where terrapin were not captured. A timer was set for times of 5-15 minutes while walking transect lines to dictate where/when a random prey quadrat would be taken. Once the timer went off, the above environmental, available prey, and location data were collected.

Tidal stage may have played a part in the accuracy of these prey counts. For example, the snails were more easily observed during high tide as they clump together and climb higher on the plants (Warren 1985). However, fiddler crab burrows are better observed during periods of low tide. In addition, other potential prey species and indicators including bivalve mollusks, snails, and crustaceans were counted in the field. Voucher specimens of potential prey items were collected.

Fecal Collection

Subsamples of captured, individual terrapins were taken from the sites in order to retrieve fecal samples. Fecal collection was chosen over stomach flushing because it is a less invasive technique. Stomach flushing has the potential to damage a turtle's jaw, palate, or esophagus (Fields et al. 2000). A disadvantage of using fecal analysis, however, is the possible overestimation of hard-bodied prey items while underestimating soft-bodied items.

The terrapins were brought to the UHCL animal care facility. They were maintained individually in plastic tubs containing a small amount (2-3cm) of fresh water (Figure 9) for up to 48 hours. This is sufficient time for defecation to occur (Tucker et al. 1995). Following this period, the terrapin were released at their capture sites. The majority of samples were acquired after 48 hour holding times, but due to logistical constraints some terrapins were only held for 24 hour periods. Also, opportunistic samples were also taken while in the field. Fecal samples were collected from the containers by carefully draining the water from the tubs. Water from the tubs was poured over a 0.5mm sieve to collect the fecal matter (Figure 10). The samples were then recovered and preserved in vials containing 70% ethanol (Figure 11). Some samples were initially preserved in 10% formalin before changing the solution to ethanol. Using a 0.5mm sieve, the samples were thoroughly rinsed to wash away any preservative before drying. Samples were dried in a desiccating oven at 100°c for one hour and then weighed to the nearest tenth of a gram (g) (Figure 12). This process was repeated until sample weight became stable.

Figure 9. Female Diamond-backed Terrapin in storage bin during fecal collection.

Figure 10. Fecal remains on 0.5mm sieve after being poured from collection bin.

Figure 11. Two vials containing fecal samples and preservative.

Figure 12. Aluminum container and fecal sample used during drying and weighing.

Once reaching a stable weight, the total sample weight was recorded. Each sample was next separated and sorted into its component parts. Sorting and identification of fecal remains took place in the lab using forceps and a dissecting microscope. Parts of organisms found in fecal samples were used to identify to lowest possible taxon. Once a sample was sorted, each separate taxon was weighed. The proportions of each taxon in an individual's sample were then calculated by dividing each taxon weight by the sample weight. In addition to the previous calculation, a percentage over all samples was calculated. Weights of each taxon category were summed and divided by the summed value of all individual sample weights.

Volumetric analysis was also examined and compared with the gravimetric technique above. Following weighing, the component parts from each sample were placed into graduated cylinders containing tap water (Figure 13). Displacement for each taxon was recorded in milliliters (mL) to the nearest 0.1 mL. If a sample displaced less than 0.1 mL, volume was visually estimated to be either 0.05 or 0.01 mL. The total sample volume was calculated by adding up the volumes of each taxon group. Size of the graduated cylinder and water amount in each cylinder used varied depending on size of the fecal sample being examined. Therefore, large samples were measured in larger cylinders with more water. Percent volume was calculated in a manner consistent with the calculations for percent weight described above.

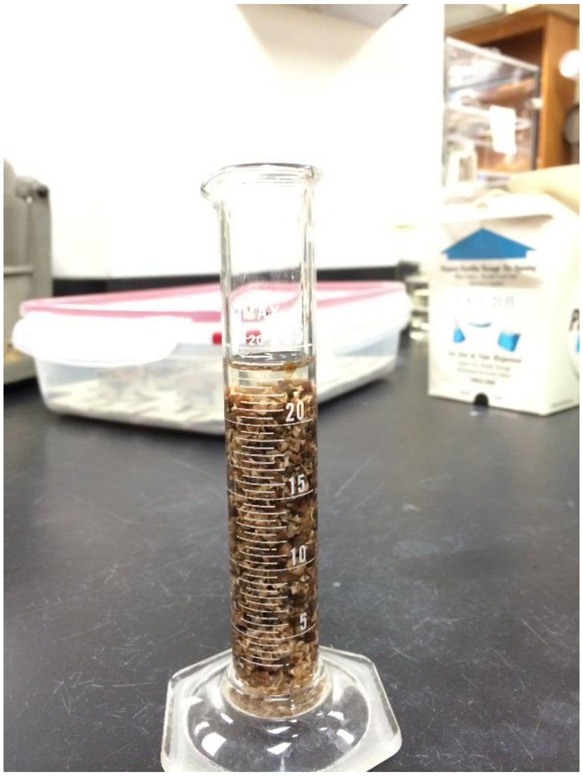

Figure 13. Graduated cylinder (25mL) containing partial fecal sample and water.

Fecal sample collection began in April 2013 and concluded May 2014. Terrapins were only taken from the field for fecal samples when they were found to be active. Therefore, no terrapins or samples were collected during the months of December or January when they usually burrow and brumate.

Data Analysis

A technique commonly used for diet analysis studies for terrapin, as well as other species, is percent frequency of occurrence (Ottonello et al. 2005, Butler 2012 Erazmus 2012). Frequency of occurrence was calculated as the percentage of fecal samples containing each, individual food item. This is a presence or absence technique. Percentages of food items by weight and volume were also calculated. These percentages were reached by computing total volume and weight for individual prey items and then dividing by the total sample (all samples) volume and weight. A modification of this technique is used for calculating percentages for individual samples. In this case, it is individual component weight divided by individual sample weight (or volume).

Prior to performing statistical analyses, data were tested for normality (Lengendre and Lengendre 2012). Datasets did not fit a normal distribution. Therefore, non-parametric statistical methods were employed for analyses. A Kruskal-Wallis one-way analysis of variance (KW-ANOVA) was used to analyze differences by sex, season, and location for both fecal and prey availability data. When an overall significant difference was found between groups with more than two levels using the overall KW-ANOVA test Dunn’s multiple comparison test was used post hoc to test for differences between individual groups (Zar 2009). The Mann-Whitney U-test was used to compare fecal analysis methods (gravimetric versus volumetric), and it was used to compare air temperature at ground level to that at breast height. Mann-Whitney testing was used in those cases because the data was paired. Reported Kruskal-Wallis and Mann-Whitney values are those that were adjusted for ties when they occurred. For all the below boxplots, the outer white box represents the interquartile range, inner shaded box is 95% confidence interval, horizontal line and dot are the median, and whiskers are the data range, unless otherwise noted. Diversity estimates for diet were calculated using Shannon Diversity (H’), Evenness (E), and Berger-Parker Index (BPI). Statistical analyses were performed using Minitab 17 and Microsoft Excel software packages.

RESULTS

Prey Availability and Habitat

Over the course of this study, data were collected from a total of 293 prey quadrats in the field. Data were gathered at both random locations (n = 78) and terrapin capture locations (n = 215). Terrapins that provided fecal samples made up a subset of this larger terrapin capture number (n = 55). These data were collected from locations along the coast of Texas from the following areas: West Bay, East Bay, San Bernard, Sabine Lake, and Matagorda Bay. West Bay sites made up the vast majority of locations (n = 276), and consisted of North Deer Island (n = 32), South Deer Island (n = 144), Sportsman (n = 65), Greens Lake (n = 29), and Sweetwater Lake (n = 6). Multiple prey quadrats were collected from Texas Point NWR (n = 11) in the Sabine Lake area. East Bay data were collected from marshes located on Bolivar Peninsula (n = 2). Other locations with low sample numbers included San Bernard NWR (n = 2) and Matagorda Bay (n = 2).

Similar habitats were found at all sites, and *Spartina alterniflora* was the dominant plant species encountered at both capture and random locations followed by *Batis maritima* and *Salicornia* spp. (Figure 14). Most vegetation encountered was 0-60 cm tall and appear to be consistent between the location types (Figure 15). Commonly encountered prey items, or prey indicators, encountered at sites were *Uca* burrows or the crabs themselves, along with the snails *L. irrorata* and *C. pliculosa*. Occasionally, *C. sapidus* and *Melampus bidentatus* were encountered. Insects, spiders, and Penaeid shrimp were also seen in quadrats. Various fish species were seen swimming in the marsh ponds and tidal creeks and the crab species, *Sesarma reticulatum*, were seen in the marsh, but neither was encountered in quadrats. Prey quadrat data were taken in all seasons (Table 1). In instances where a terrapin was encountered in a completely aquatic setting, prey quadrats were not conducted.

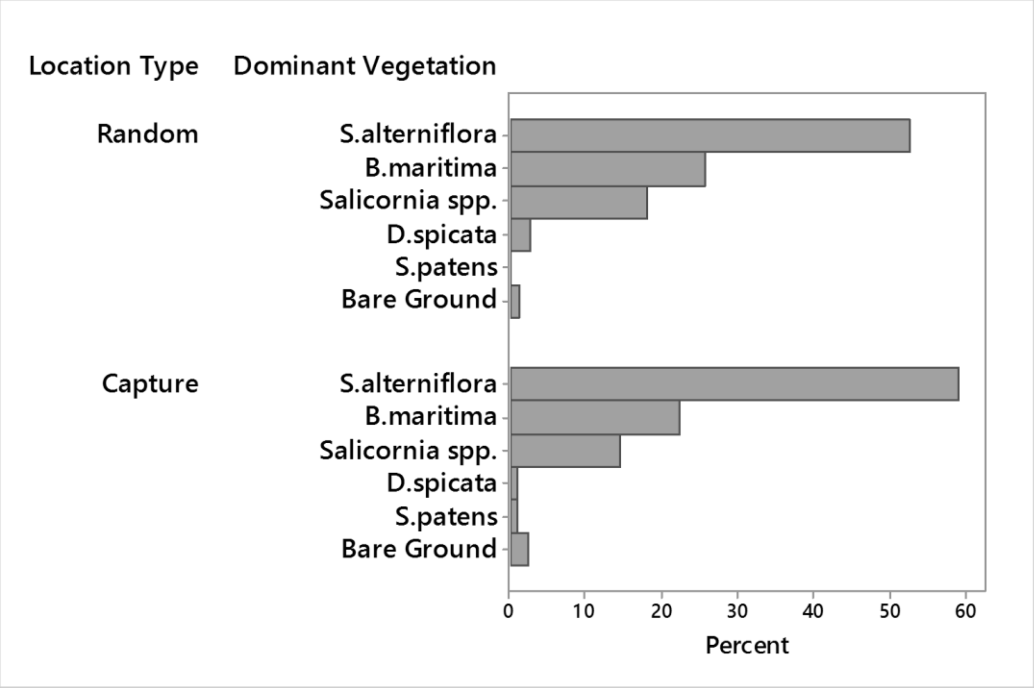

Figure 14. Percentage of 1 m^2 quadrats with listed species as the dominant plant species at random (n = 78) and capture (n = 215) locations.

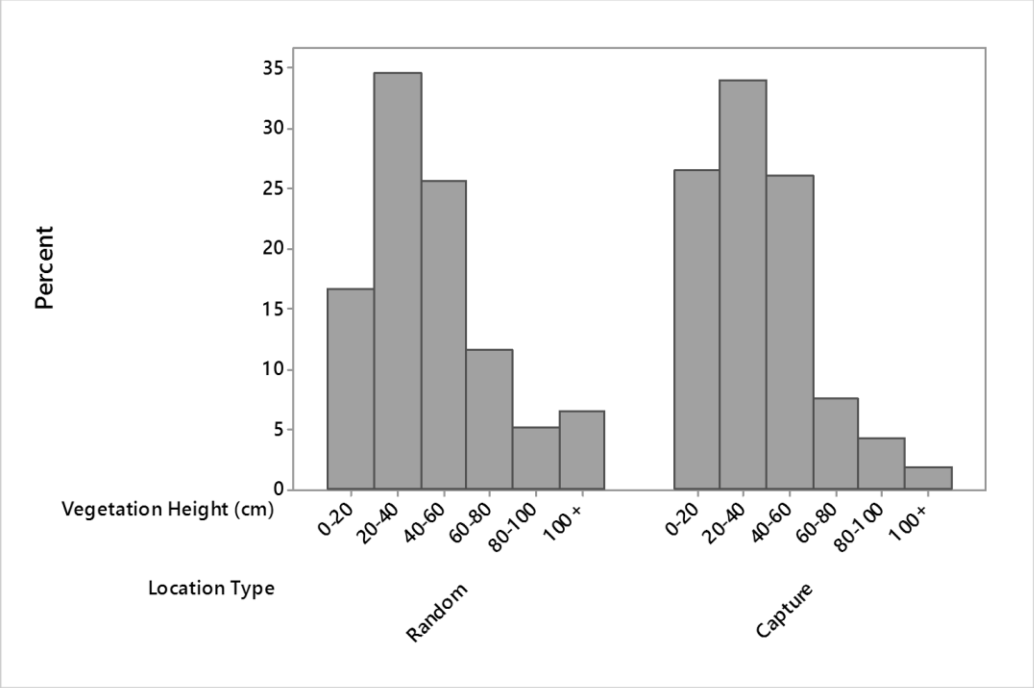

Figure 15. Percentage of 1 m^2 quadrats with listed vegetation heights at random (n = 78) and capture (n = 215) locations.

Table 1. Number of prey quadrats collected by season.

Season	Beginning Date	Sample Number
Spring	March 20	53
Summer	June 21	71
Fall	September 22	81
Winter	December 21	88

Habitat Quadrats at Random Versus Capture Locations

Multiple significant differences in habitat metrics were detected using Kruskal-Wallis analysis. The number of plant species present was significantly higher (H = 12.69, $p < 0.001$) at random locations than at capture locations (Figure 16). Most terrapin captures (92%) occurred at locations with only one plant species present (53%) or with two species present (39%) (Figure 17). The bulk of random locations (98%), on the other hand, consisted of three groups, and were as follows: one species (37%), two species (35%), and three species (26%) (Figure 17). Vegetation height was significantly different between random and capture locations (H = 4.48, p = 0.034). Plants at random locations were significantly taller than at capture locations (Figure 18). Random locations had significantly higher vegetation cover (H = 8.97, p = 0.003) than did terrapin capture locations (Figure 19). Significant differences in species coverage were found between location types as well. Coverage of *Batis maritima* at random locations was significantly greater (H = 5.24, p = 0.022) than at terrapin capture locations (Figure 20). Also, *Salicornia* spp. coverage was significantly greater (H = 6.47, p = 0.011) at random locations than at capture locations (Figure 21). No difference (H = 0.80, p = 0.372) was detected when examining *Spartina alterniflora* percent cover (Figure 22).

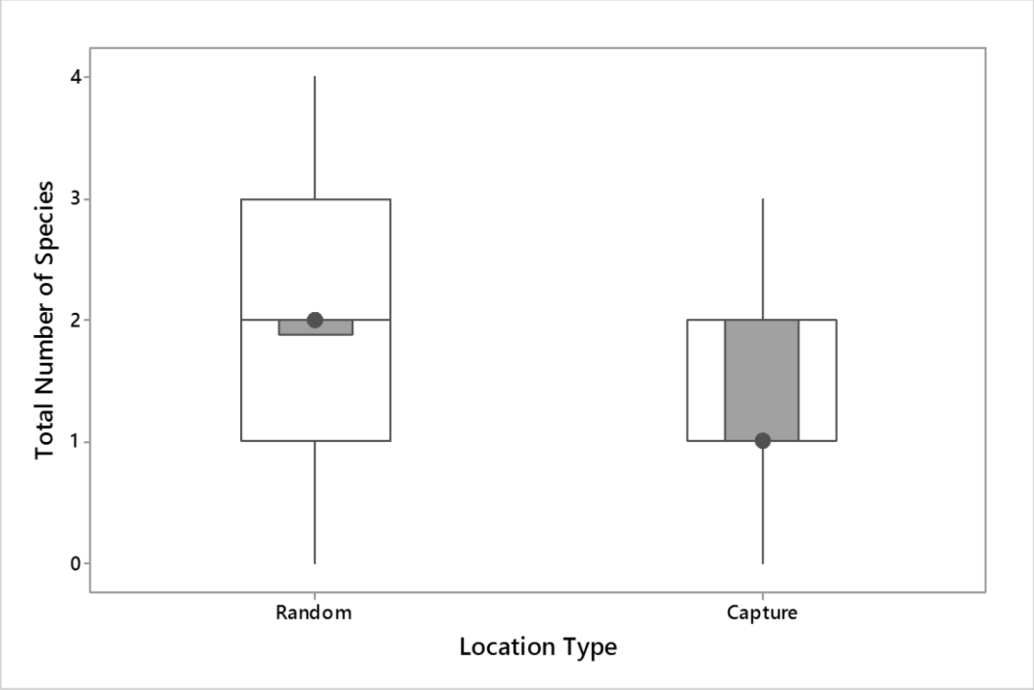

Figure 16. Boxplot depicting location differences of number of plant species in 1 m^2 prey quadrats (Kruskal-Wallis; H = 12.69, $p < 0.001$). The inner shaded box represents the 95% confidence interval for the median.

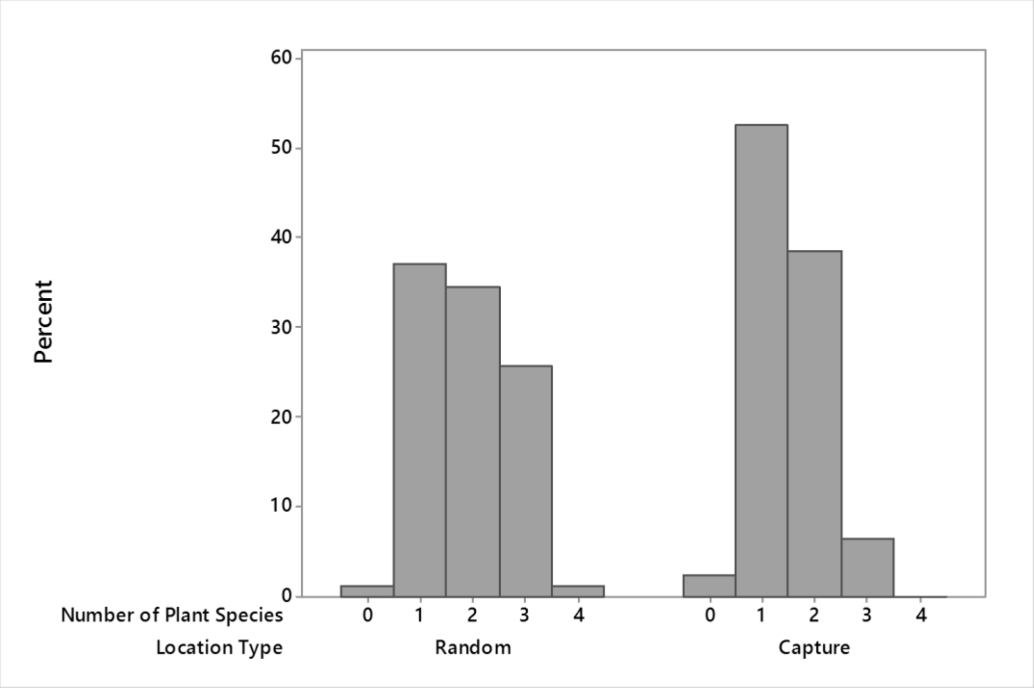

Figure 17. Histogram depicting percentage of prey quadrats from random (n = 78) and capture (n = 215) locations containing a given number of plant species.

Figure 18. Boxplot depicting location differences of vegetation height in 1 m^2 prey quadrats (Kruskal-Wallis; $H = 4.48$, $p = 0.034$). The inner shaded box represents the 95% confidence interval for the median.

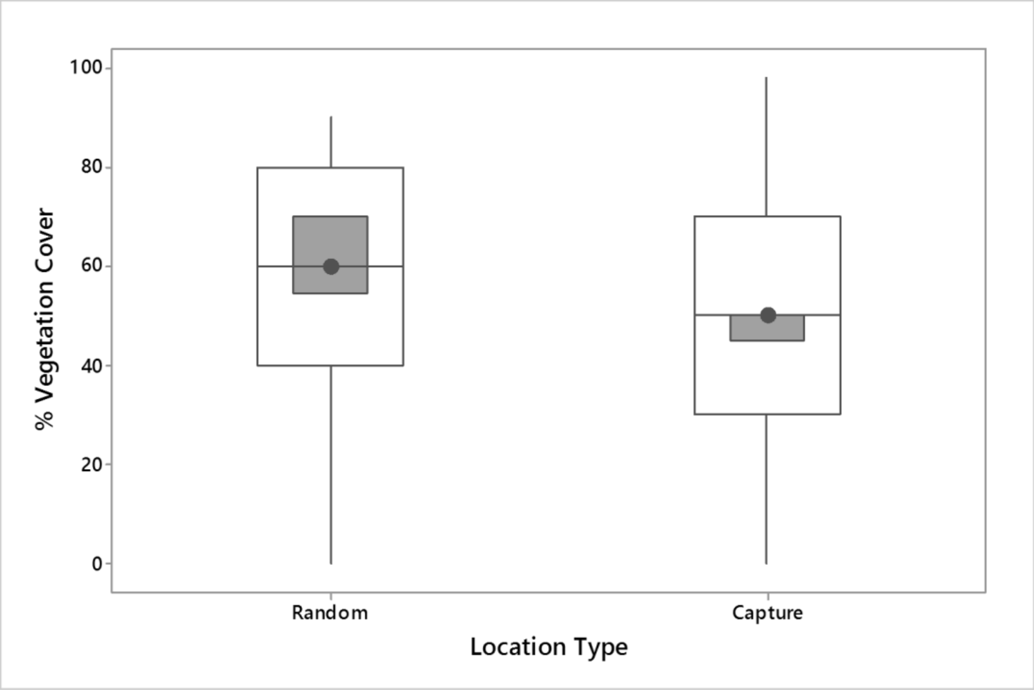

Figure 19. Boxplot depicting location differences of vegetation cover percentage in 1 m^2 prey quadrats (Kruskal-Wallis; H = 8.97, p = 0.003). The inner shaded box represents the 95% confidence interval for the median.

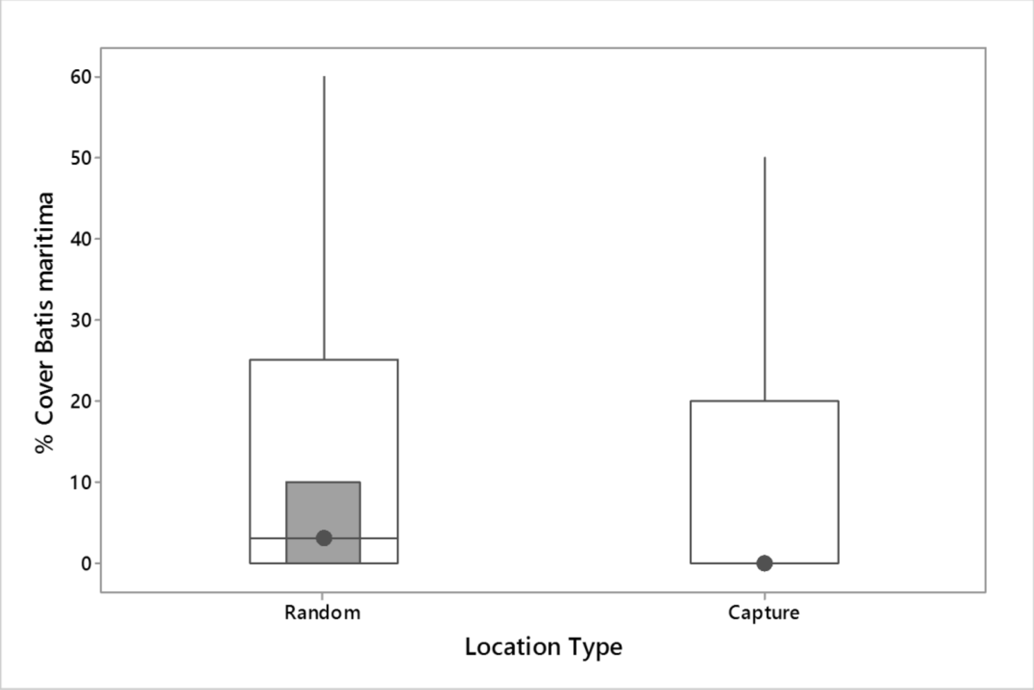

Figure 20. Boxplot depicting location differences of *Batis maritima* coverage percentage in 1 m^2 prey quadrats (Kruskal-Wallis; H = 5.24, p = 0.022). The inner shaded box represents the 95% confidence interval for the median.

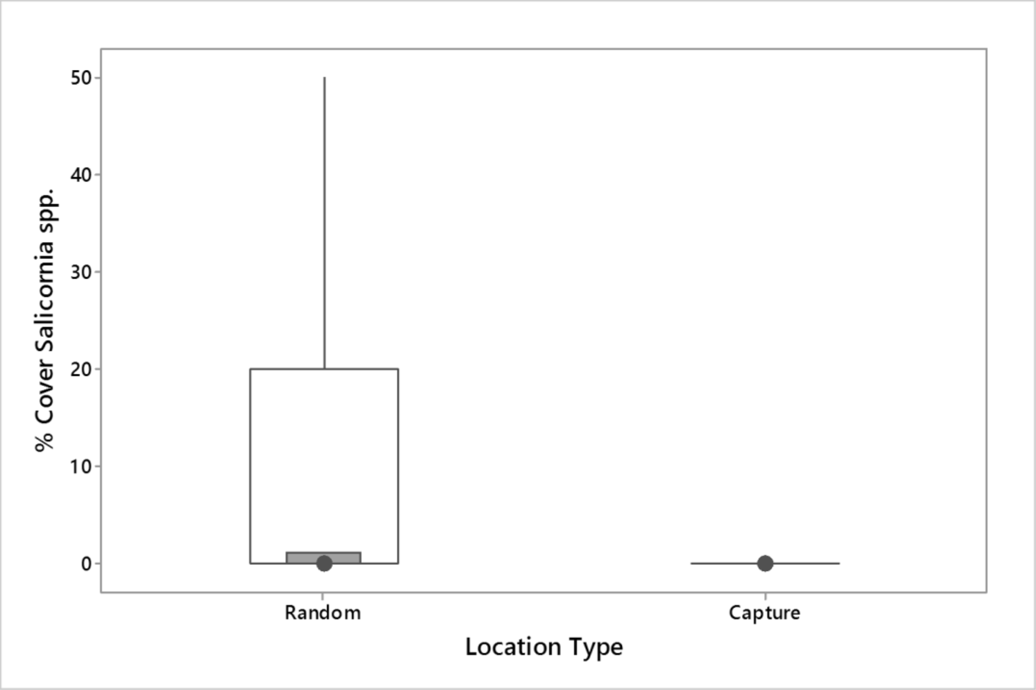

Figure 21. Boxplot depicting location differences of *Salicornia* spp. coverage percentage in 1 m^2 prey quadrats (Kruskal-Wallis; H = 6.47, p = 0.011). The inner shaded box represents the 95% confidence interval for the median.

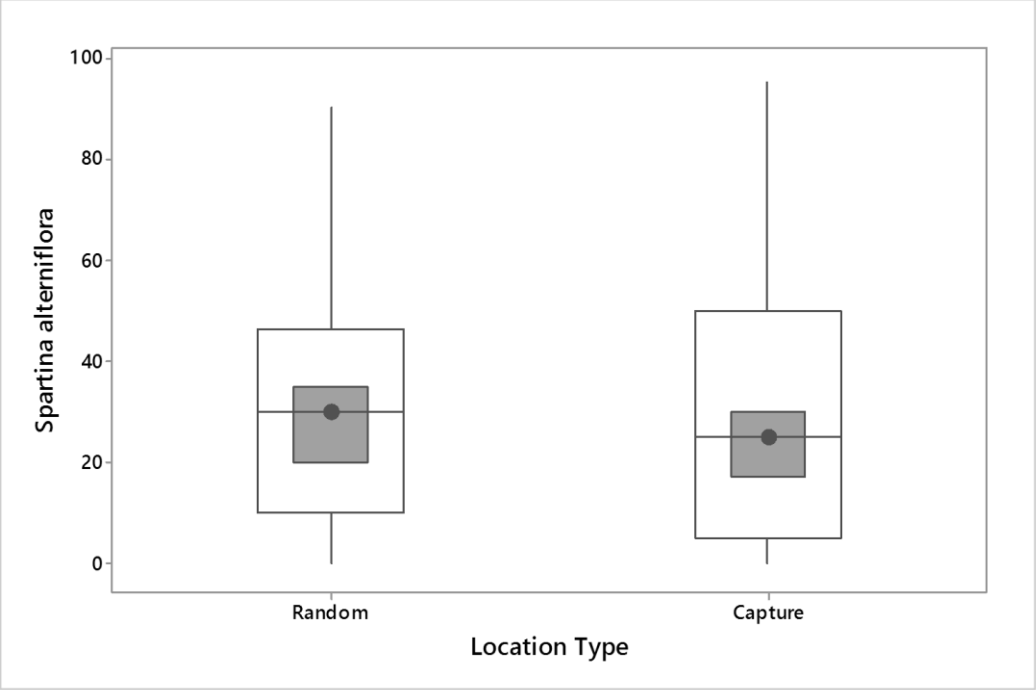

Figure 22. Boxplot depicting location differences of *Spartina alterniflora* coverage percentage in 1 m^2 prey quadrats (Kruskal-Wallis; H = 0.80, p = 0.372). The inner shaded box represents the 95% confidence interval for the median.

Habitat Quadrats by Season at Capture Locations

When specifically examining locations where terrapins were captured, no differences between sexes were found for any of the different habitat categories. However, significant seasonal differences were detected at capture locations. Seasonal differences in percent *S. alterniflora* were found to be strongly significant ($H = 31.24$, $p < 0.001$) at capture locations. Diamond-backed Terrapins were encountered in areas with significantly higher *S. alterniflora* ground cover in winter and spring than in summer and fall (Figure 23). No difference between winter and spring was detected. Interestingly, no significant seasonal differences for total vegetation cover at capture locations were detected ($H = 5.80$, $p = 0.122$). The opposite effect was detected in regards to coverage by *Batis maritima* (Figure 24). Capture locations had significantly greater percent cover of *B. maritima* in summer and fall than did spring and winter captures ($H = 14.61$, $p = 0.002$). Ground cover of *Salicornia* spp. was significantly higher in fall than in winter and spring ($H = 20.58$, $p < 0.001$). There was no significant difference between fall and summer (Figure 25).

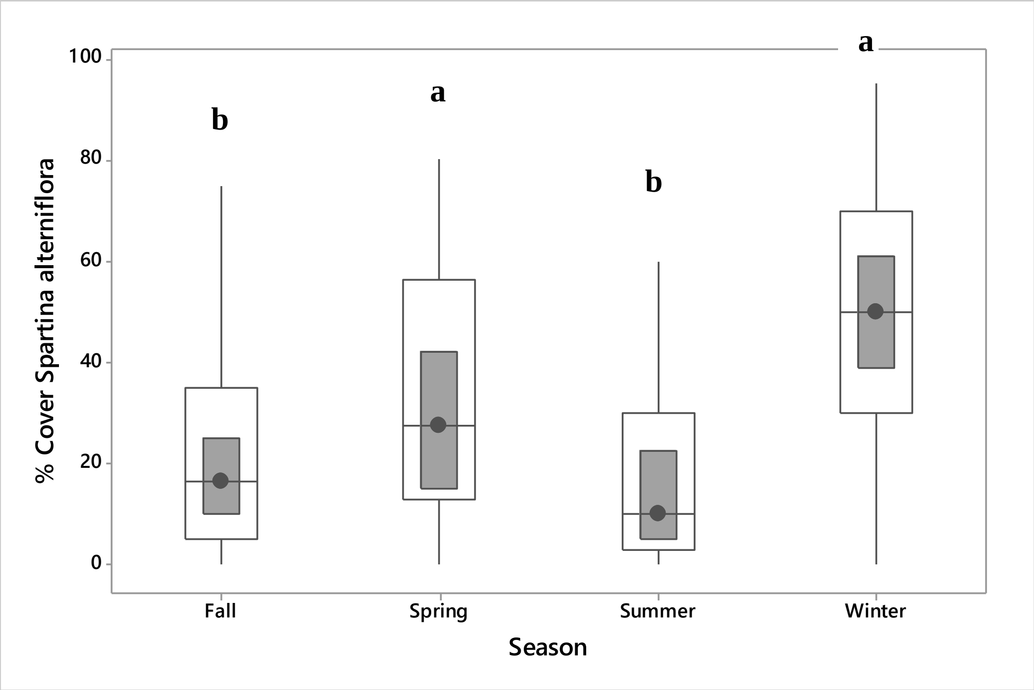

Figure 23. Boxplot depicting seasonal differences of *Spartina alterniflora* coverage at terrapin capture locations in 1 m^2 prey quadrats (Kruskal-Wallis; H = 31.24, p < 0.001). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

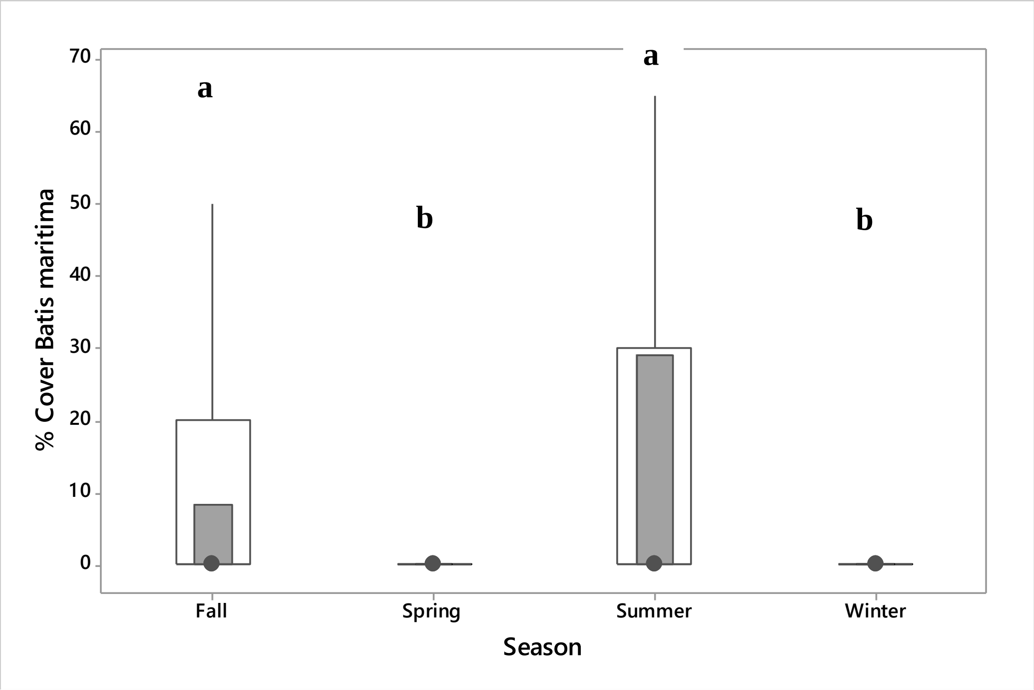

Figure 24. Boxplot depicting seasonal differences of *Batis maritima* coverage at terrapin capture locations in 1 m^2 prey quadrats (Kruskal-Wallis; H = 14.61, p = 0.002). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

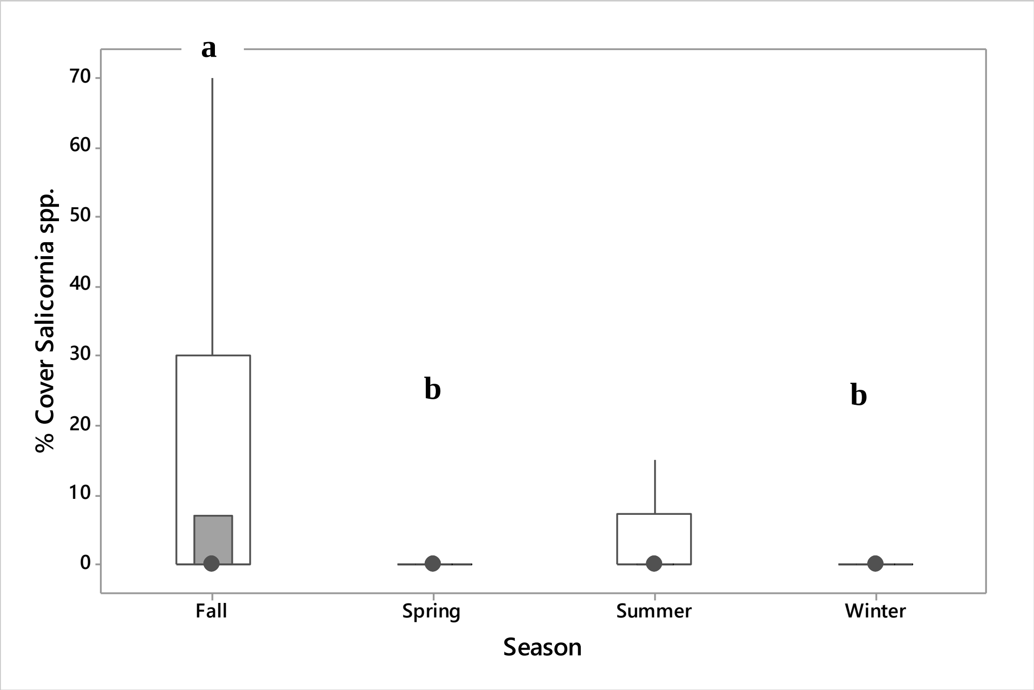

Figure 25. Boxplot depicting seasonal differences of *Salicornia* spp. coverage at terrapin capture locations in 1 m^2 prey quadrats (Kruskal-Wallis; $H = 20.58$, $p < 0.001$). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

Habitat Quadrats by Marsh Site at Capture Locations

Kruskal-Wallis analysis was employed to check for site differences ($n = 205$). Most West Bay marshes and Texas Point ($n = 10$) were included in these analyses. The West Bay sites examined included South Deer Island ($n = 107$), North Deer Island ($n = 22$), Sportsman Road ($n = 49$), and Greens Lake ($n = 17$). Due to low sample sizes, San Bernard ($n = 2$), Matagorda ($n = 2$), and Sweetwater ($n = 4$) sites were excluded from statistical analysis. Quadrats were not sampled at Bolivar capture locations. Vegetation height demonstrated significant location differences ($H = 10.71$, $p = 0.030$). North Deer had significantly taller vegetation than Sportsman Road with no other differences detected between sites (Figure 26). Sites also showed significant differences in number of plant species found within the quadrats ($H = 20.99$, $p < 0.001$). South Deer possessed a significantly higher number of species than both Sportsman and Texas Point, and a significantly higher number of plant species was detected at North Deer compared with Sportsman (Figure 27).

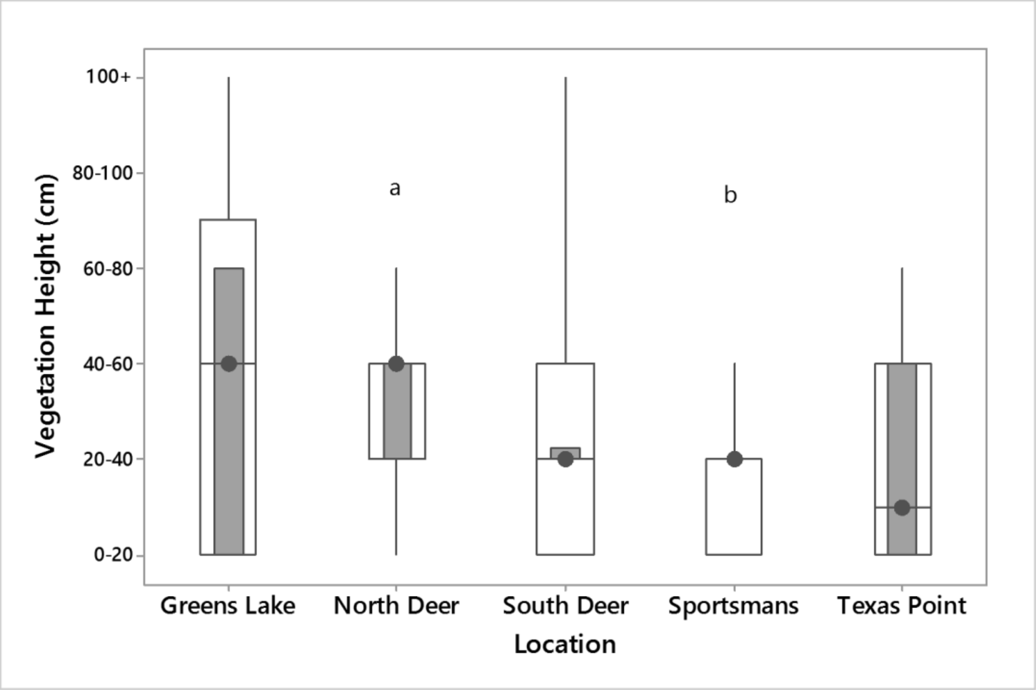

Figure 26. Boxplot depicting marsh differences at capture locations of vegetation height in 1 m^2 prey quadrats (Kruskal-Wallis; H = 10.71, p = 0.030). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

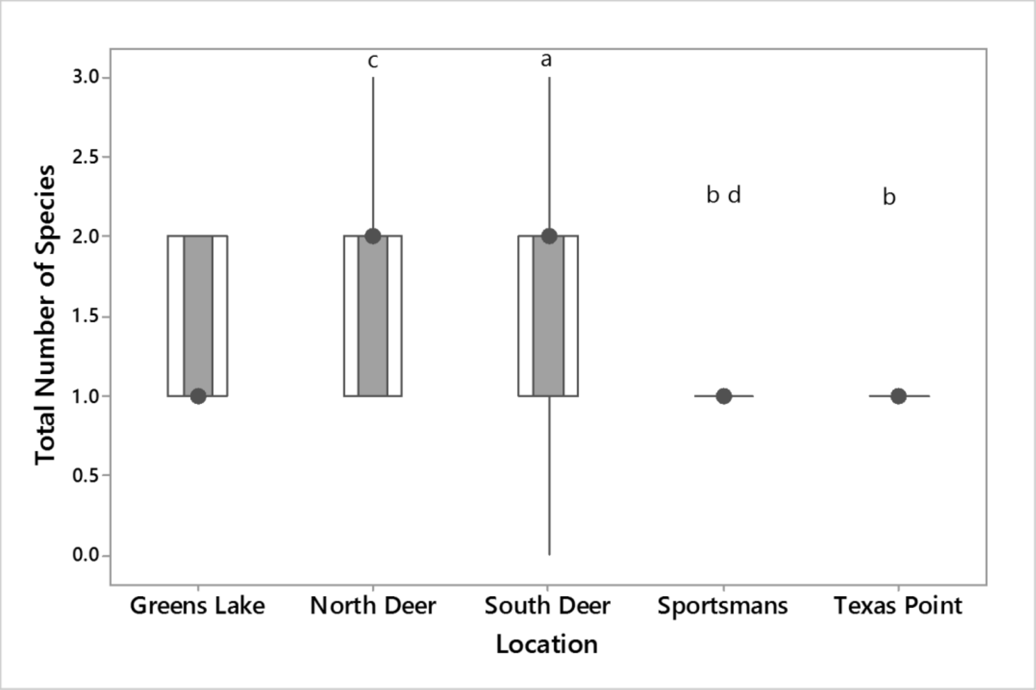

Figure 27. Boxplot depicting marsh differences at capture locations of number of plant species in 1 m^2 prey quadrats (Kruskal-Wallis; H = 20.99, $p < 0.001$). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b* and *c* > *d*)

There were no significant differences amongst the West Bay sites when comparing percent vegetation cover (Figure 28). However, North Deer, South Deer, and Sportsman had significantly higher vegetative coverage than did Texas Point (H = 14.49, p = 0.006). When examining percent cover of individuals plant species, there were no significant site differences in cover of *S. alterniflora* (H = 6.05, p = 0.196), *D. spicata* (H = 9.34, p = 0.053), or *Salicornia* spp. (H = 8.90, p = 0.064) between locations. *Batis maritima*, however, showed significant differences (H = 35.51, $p < 0.001$) between sites. South Deer had higher coverage of *B. maritima* than did North Deer, Sportsman, and Texas Point (Figure 29). Finally, *Spartina patens* showed significant location differences (H = 39.19, $p < 0.001$). Texas Point quadrats contained higher percentage of *S. patens* than did any of the four West Bay sites (Figure 30).

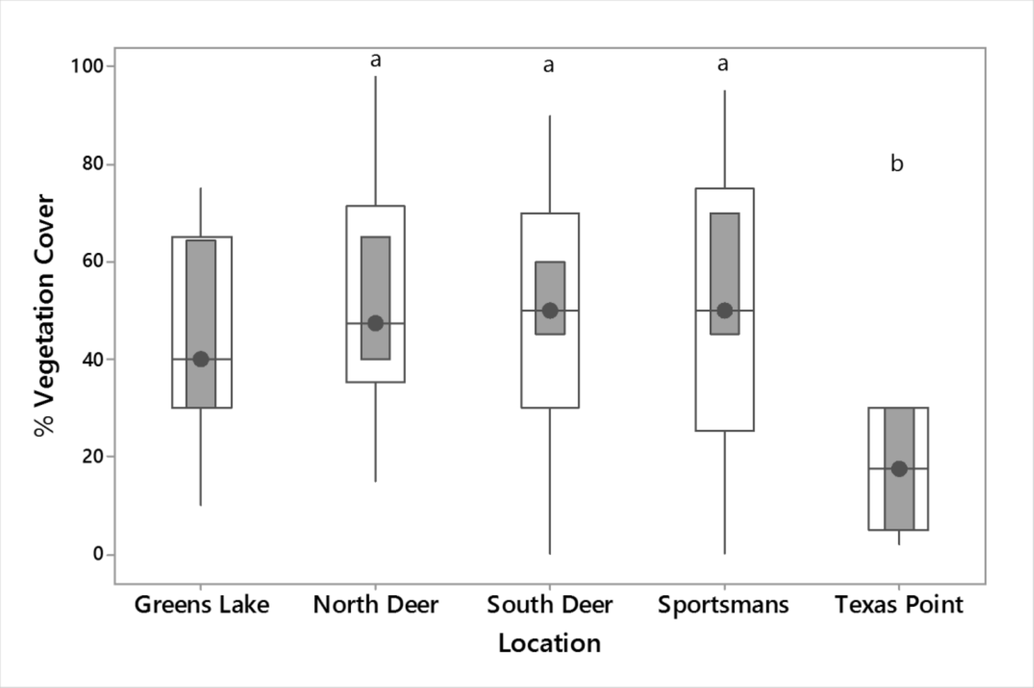

Figure 28. Boxplot depicting marsh differences at capture locations of vegetation coverage in 1 m^2 prey quadrats (Kruskal-Wallis; H = 14.49, p = 0.006). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

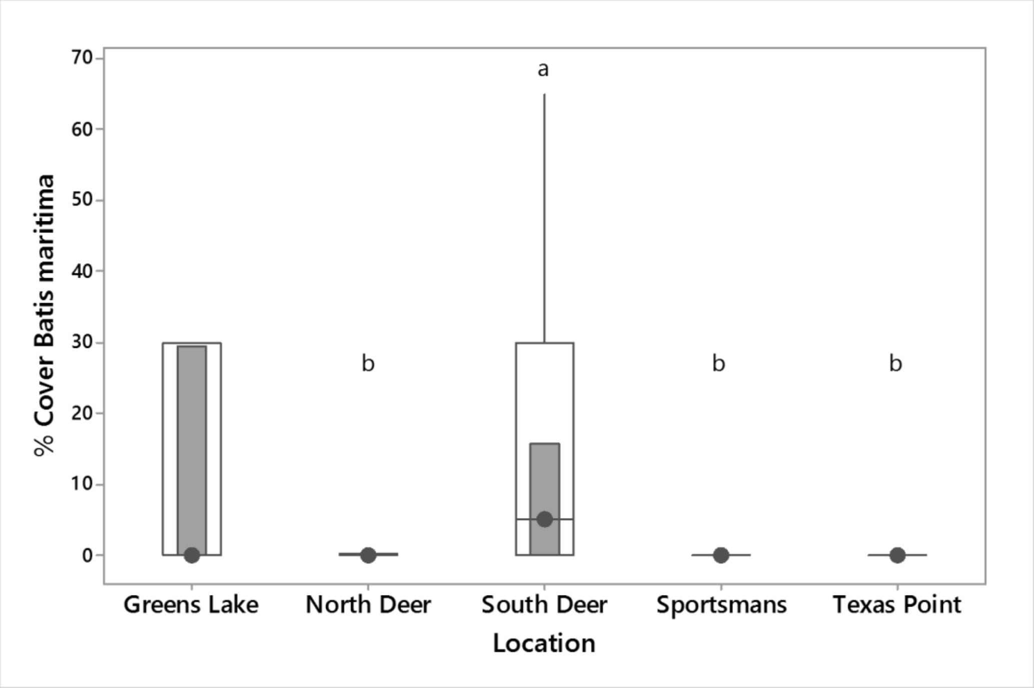

Figure 29. Boxplot depicting marsh differences at capture locations of *Batis maritima* coverage in 1 m^2 prey quadrats (Kruskal-Wallis; H = 35.51, p < 0.001). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

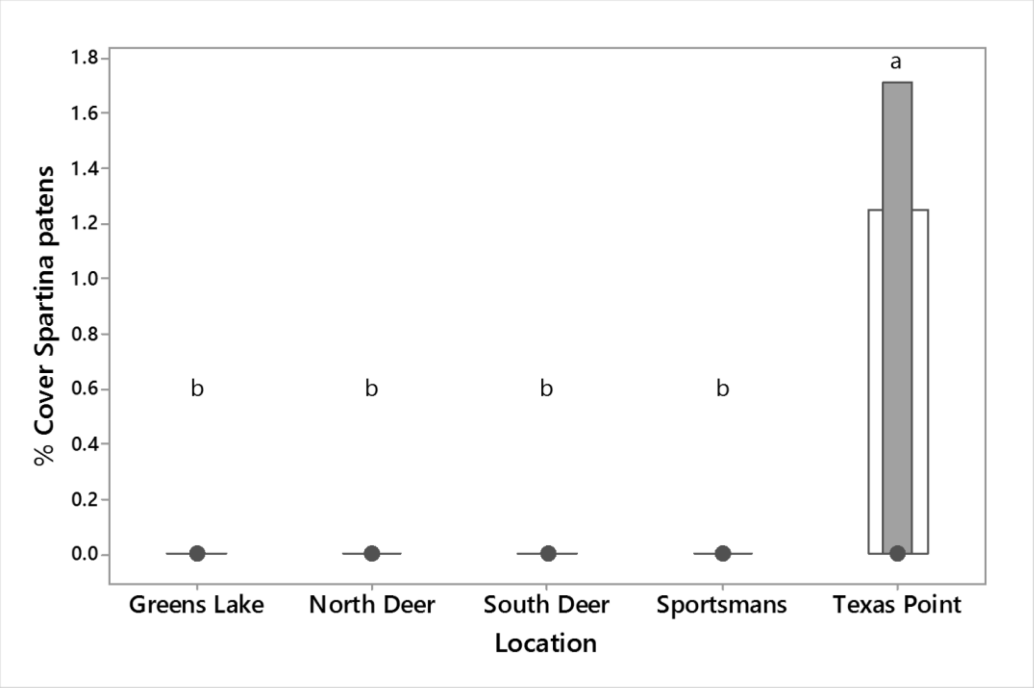

Figure 30. Boxplot depicting marsh differences at capture locations of *Spartina patens* coverage in 1 m^2 prey quadrats (Kruskal-Wallis; H = 39.19, p < 0.001). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

Habitat and Temperature

Water and soil temperature data were not statistically analyzed due to low sample size. However, air temperatures at breast height and ground level were taken more often, and therefore used in analysis. When analyzing all quadrats with air temperature data, Mann-Whitney testing detected no significant difference between air temperatures (p = 0.1962) at different heights (Figure 31). Median temperatures (26 °C) at breast height (n = 276) were no different than temperatures (27 °C) at ground level (n = 195). Therefore, when further examining temperature relationships below, temperature at ground level was used since it more accurately reflects to what terrapins are exposed.

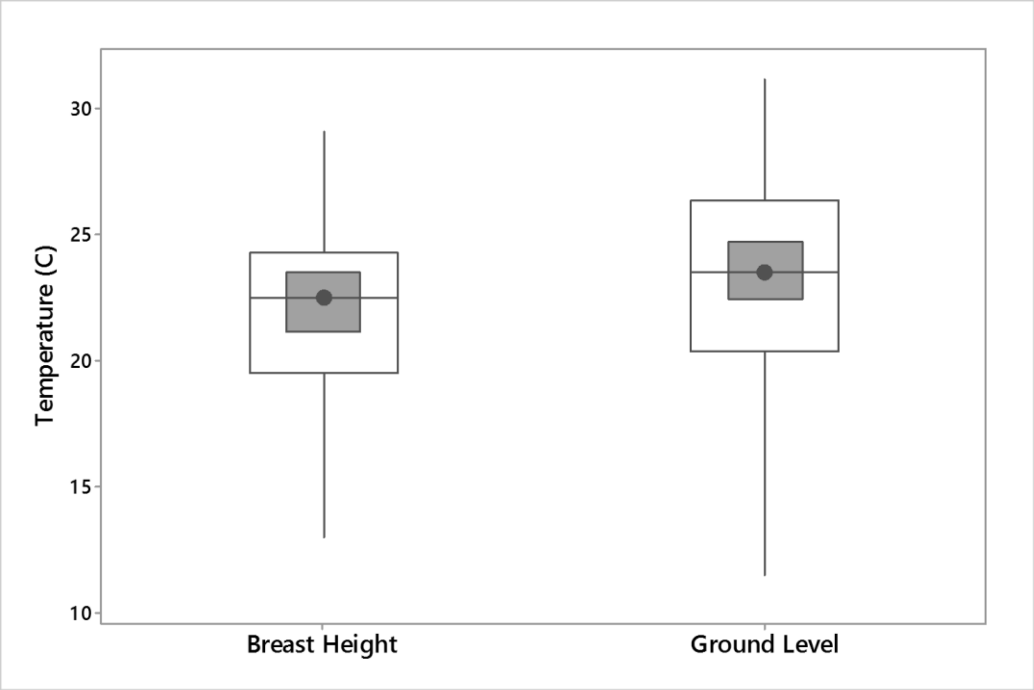

Figure 31. Boxplot depicting median temperatures at breast height (26.25 °C) and ground level (27. 00 °C) at both random and capture locations. Significant difference between median values (Mann-Whitney U-test; p = 0.1962). The inner shaded box represents the 95% confidence interval for the median.

Ground level air temperatures were recorded at a total of 195 locations. A significant (H = 4.19, p = 0.041) difference in ground level air temperature was detected between random (n = 61) and capture (n = 134) locations. Median temperatures at capture locations (27.6 °C) were significantly higher than at random locations (25.3 °C) (Figure 32). At terrapin capture sites, air temperatures exhibited significant differences (H = 23.93, p < 0.001) between vegetation height group classes. The shortest vegetation class (0-20 cm) exhibited significantly warmer temperatures than three of the taller classes (40-60 cm, 60-80 cm, 80-100 cm) (Figure 33). The tallest class was not included in analysis due to few quadrats (n = 4) with that vegetation height. Temperatures were also significantly different when comparing dominant vegetation (H = 18.57, p < 0.001). Sites dominated by *B. maritima* and *Salicornia* spp. were significantly warmer than *S. alterniflora* dominated quadrats (Figure 34). The remaining capture sites (n = 4) dominated by bare ground, *D. spicata*, and *S. patens* were again excluded from statistical analyses due to low sample numbers.

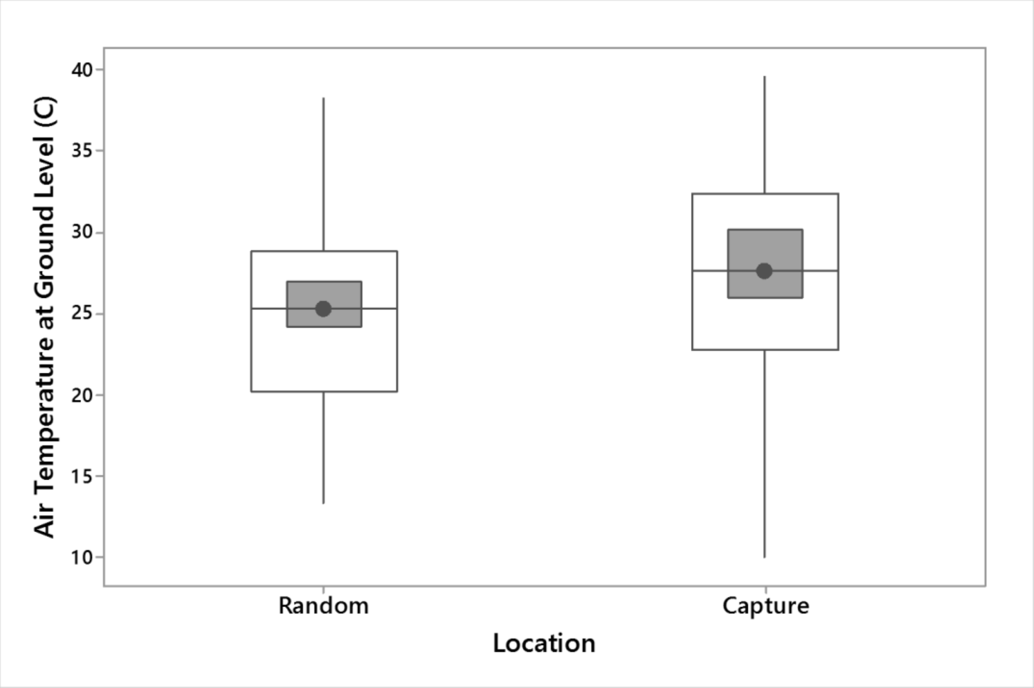

Figure 32. Boxplot depicting location differences of air temperature at ground level recorded at 1 m^2 prey quadrats (Kruskal-Wallis; H = 4.19, p = 0.041). The inner shaded box represents the 95% confidence interval for the median.

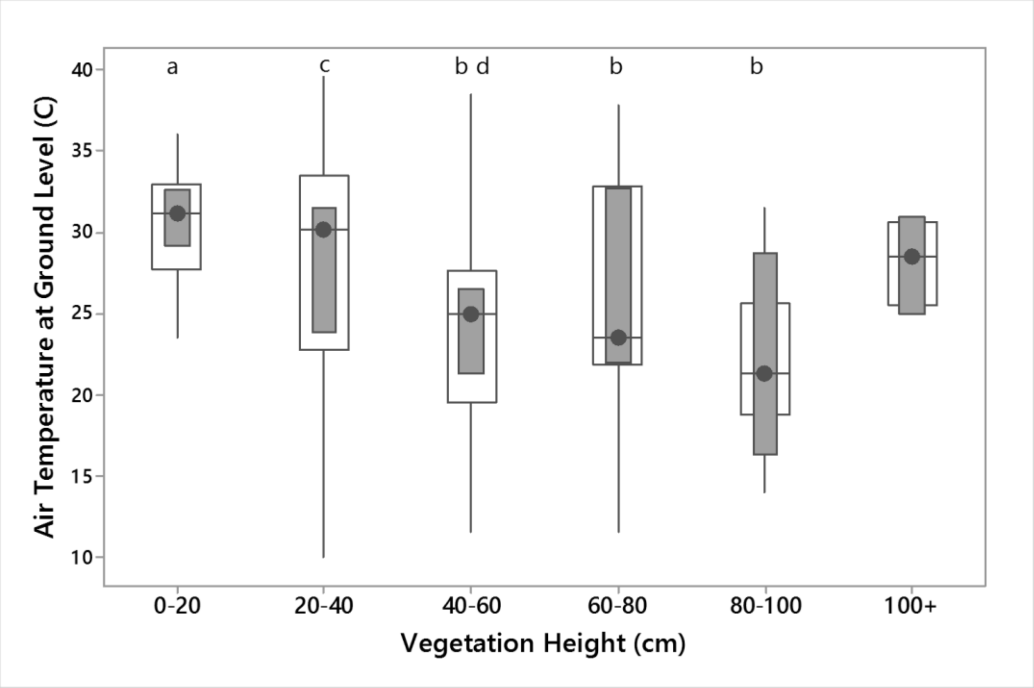

Figure 33. Boxplot depicting vegetation height differences in air temperature at ground level recorded at 1 m^2 prey quadrats at terrapin capture locations (Kruskal-Wallis; H = 23.93, $p < 0.001$). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b* and *c* > *d*; 100+ cm height excluded)

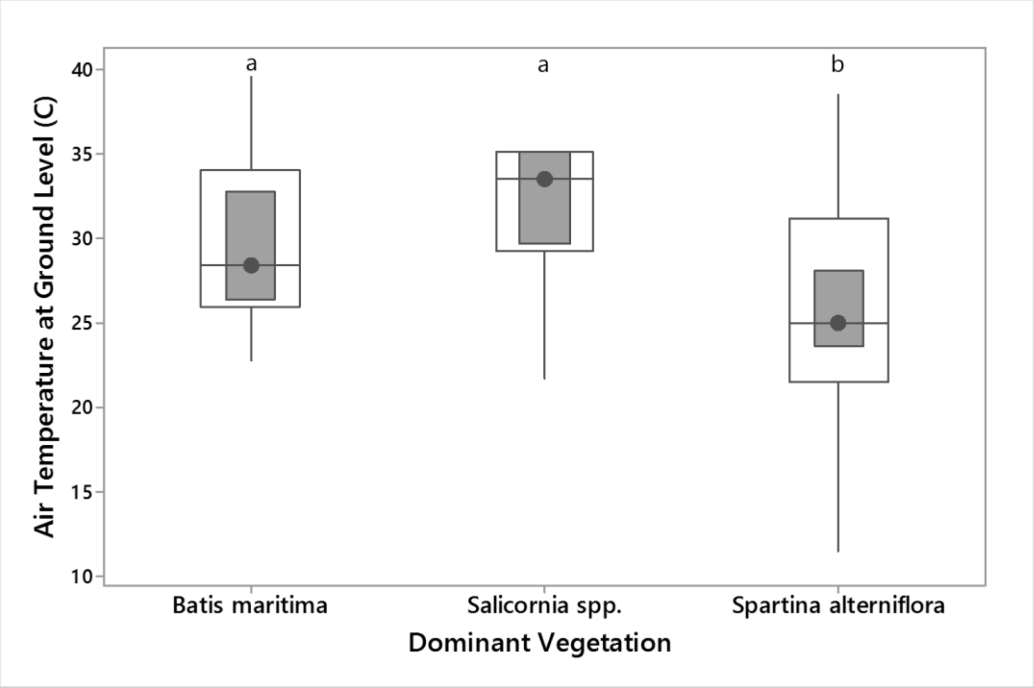

Figure 34. Boxplot depicting dominant vegetation differences in air temperature at ground level recorded at 1 m^2 prey quadrats at terrapin capture locations (Kruskal-Wallis; H = 18.57, $p < 0.001$). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

Prey Quadrats at Random versus Capture Locations

When comparing random locations to terrapin capture locations, there was only one significant difference in variables detected. Random locations had significantly more fiddler crab burrows (Kruskal-Wallis; H = 5.57, p = 0.018) than did capture locations (Figure 35). A significant (H = 0.32, p = 0.571) difference in number of *Littorina* snails was also lacking between location types (Figure 36). No differences between locations were detected when examining average length (H = 1.06, p = 0.302) of *L. irrorata* or average width (H = 0.70, p = 0.402). A significant difference in presence *C. pliculosa* (H = 3.03, p = 0.082) was also lacking between the location types.

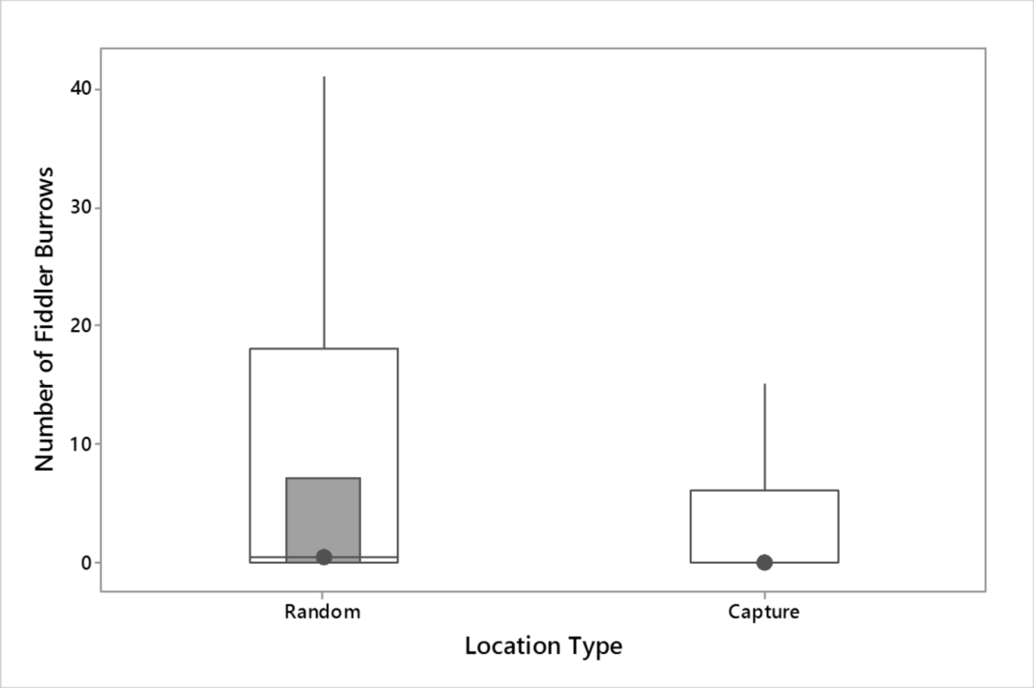

Figure 35. Boxplot depicting fiddler crab (*Uca* spp.) burrow number differences between random and terrapin capture locations in 1 m^2 prey quadrats (Kruskal-Wallis; H = 5.57, p = 0.018). The inner shaded box represents the 95% confidence interval for the median.

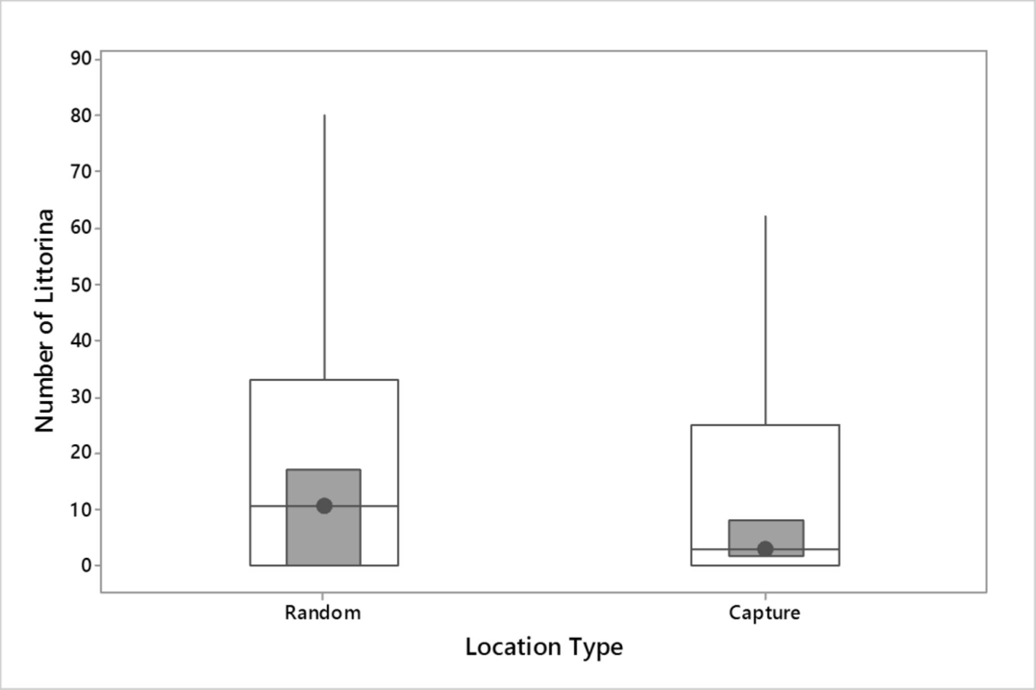

Figure 36. Boxplot depicting *Littorina irrorata* number differences between random and terrapin capture locations in 1 m^2 prey quadrats (Kruskal-Wallis; $H = 0.32$, $p = 0.571$). The inner shaded box represents the 95% confidence interval for the median.

Prey Quadrats by Season at Capture Locations

No significant differences in prey composition were detected between sites where males were captured versus females in regards to field category of prey item. However, significant differences were detected in multiple prey conditions by season at terrapin capture locations. Number of fiddler crab burrows was significantly higher in summer and winter than in spring and fall ($H = 20.99$, $p < 0.001$) (Figure 37). The number of marsh periwinkle snails counted within prey quadrats also showed significant seasonal differences ($H = 18.58$, $p < 0.001$). *Littorina* numbers were significantly lower in summer than in both winter and fall, and spring was also significantly lower than fall (Figure 38). No seasonal differences in average width ($H = 6.60$, $p = 0.086$) or length ($H = 6.84$, $p = 0.077$) of *L. irrorata* were detected.

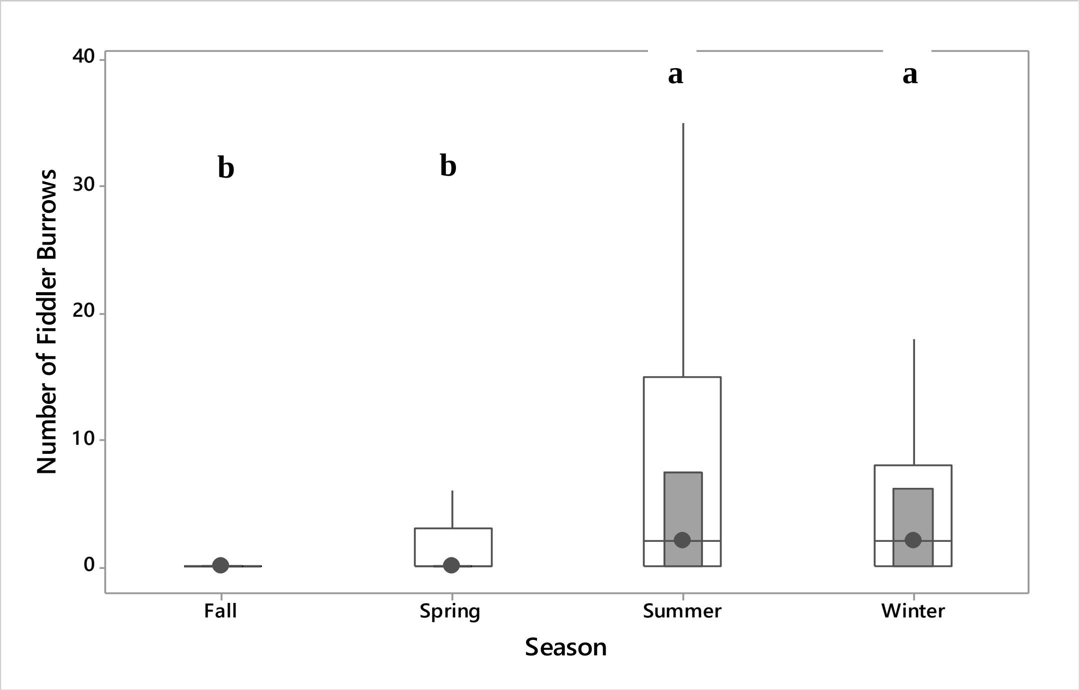

Figure 37. Boxplot depicting seasonal differences of *Uca* spp. burrows at terrapin capture locations in 1 m^2 prey quadrats (Kruskal-Wallis; H = 20.99, $p < 0.001$). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

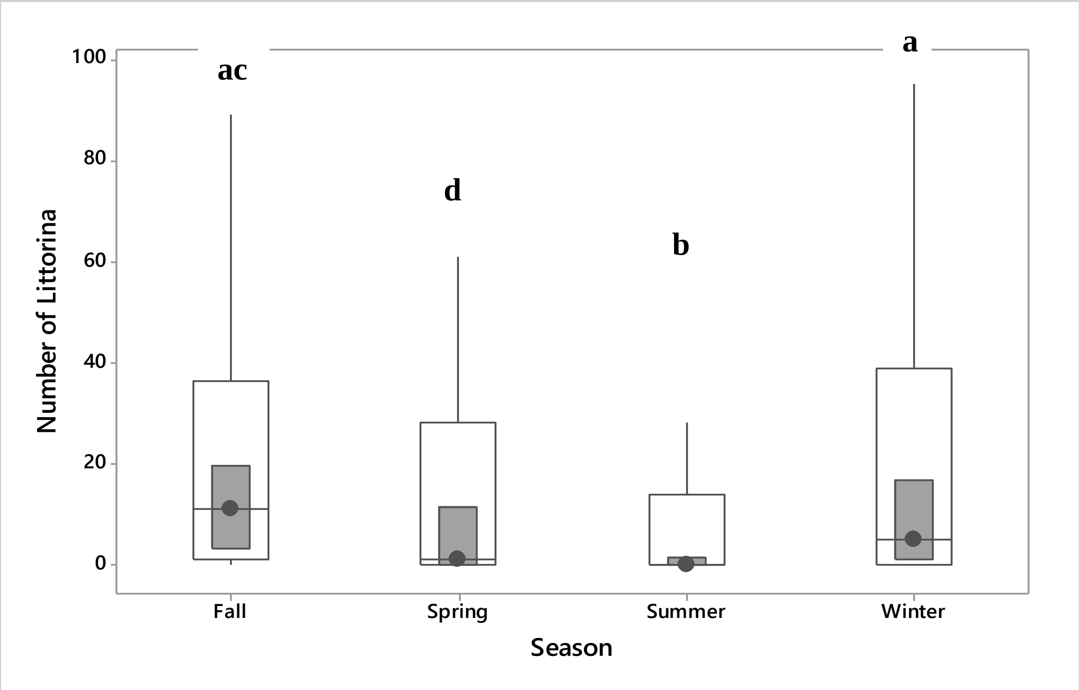

Figure 38. Boxplot depicting seasonal differences of *Littorina irrorata* at terrapin capture locations in 1 m^2 prey quadrats (Kruskal-Wallis; H = 18.58, $p < 0.001$). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b* and *c* > *d*)

Prey Quadrats by Marsh Site

Analyses to detect prey differences between marshes at terrapin capture locations in West Bay and Texas Point were conducted using the same number of samples as previously described for habitat characterization. Significant differences in the number of fiddler crab burrows were detected between sites (H = 15.48, p = 0.004). South Deer, North Deer, and Sportsman Road all exhibited significantly higher numbers of burrows compared to Greens Lake (Figure 39). The numbers of marsh periwinkle snails were found to be significantly different amongst sites as well (H = 24.12, p < 0.001). Both North and South Deer had significantly higher counts of *Littorina* than Sportsman and Greens Lake marshes (Figure 40). No differences were detected in either average periwinkle length (H = 0.68, p = 0.953) or width (H = 3.74, p = 0.443). The occurrence of *C. pliculosa* was significantly different between sites (H = 15.95, p = 0.003). Horn snails were encountered in significantly more prey quadrats at South Deer, Sportsman, and Greens Lake when compared to North Deer, and presence at Sportsman was also significantly different than Texas Point (Figure 41). Presence of other potential prey items also showed location differences (H = 17.90, p = 0.001). Other prey items were encountered at South Deer and Sportsman in significantly more quadrats than at North Deer (Figure 42).

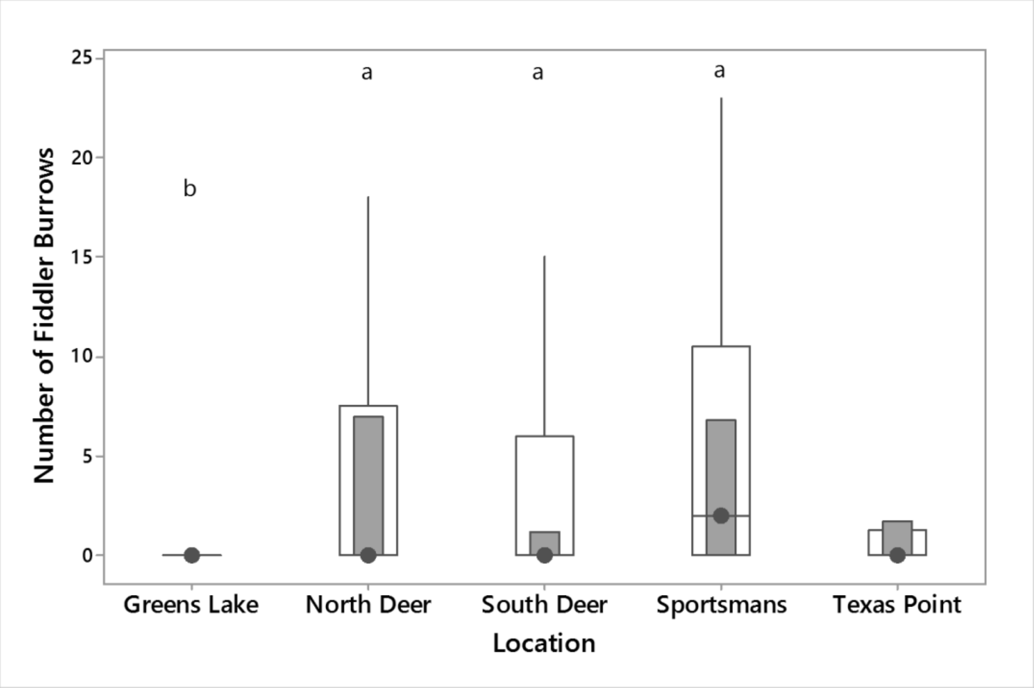

Figure 39. Boxplot depicting marsh differences at capture locations of *Uca* burrow numbers in 1 m^2 prey quadrats (Kruskal-Wallis; H = 15.48, p = 0.004). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b* and *c* > *d*)

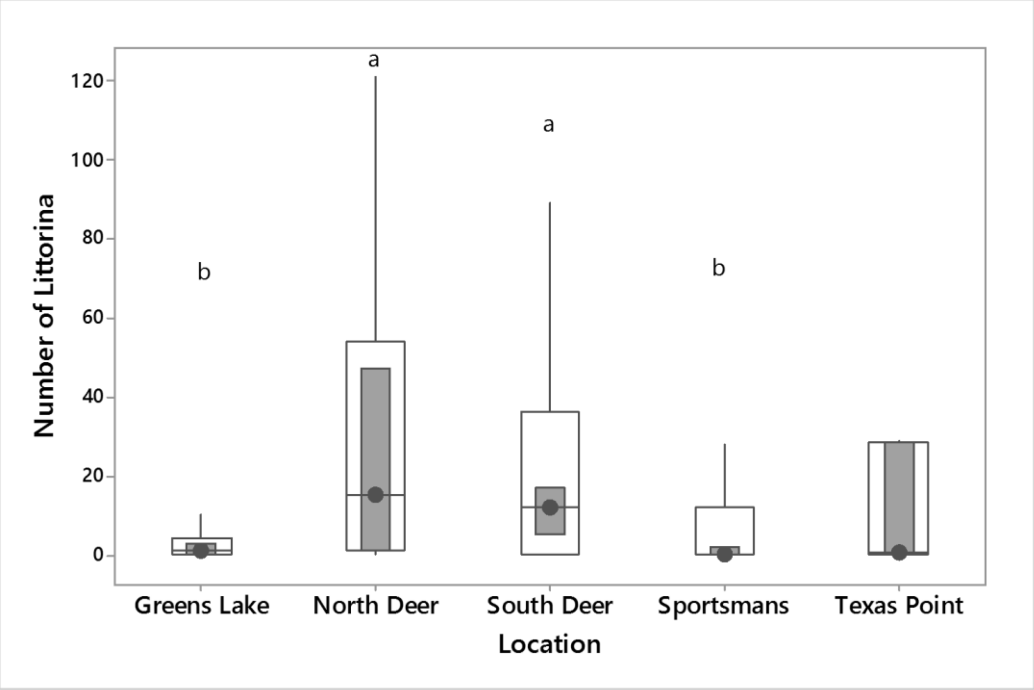

Figure 40. Boxplot depicting marsh differences at capture locations of *Littorina irrorata* numbers in 1 m^2 prey quadrats (Kruskal-Wallis; H = 24.12, p < 0.001). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

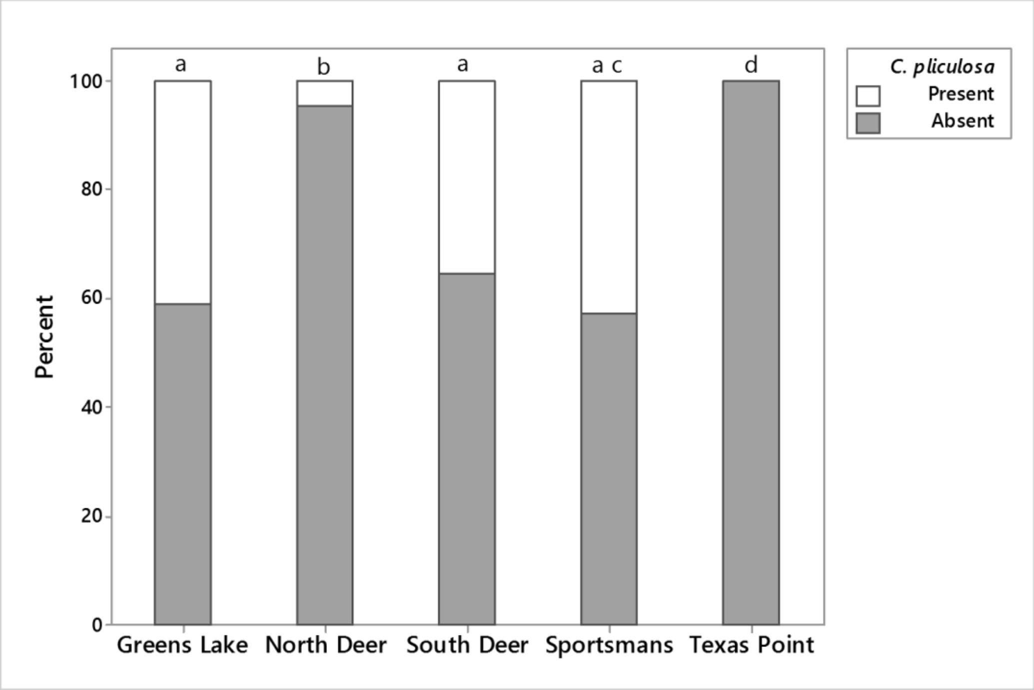

Figure 41. Marsh differences at capture locations of *Cerithidea pliculosa* presence in 1 m^2 prey quadrats (Kruskal-Wallis; H = 15.95, p = 0.003). Bars represent each site and show percentage of quadrats where *C. pliculosa* was present or absent. (Significant group differences: *a* > *b* and *c* > *d*)

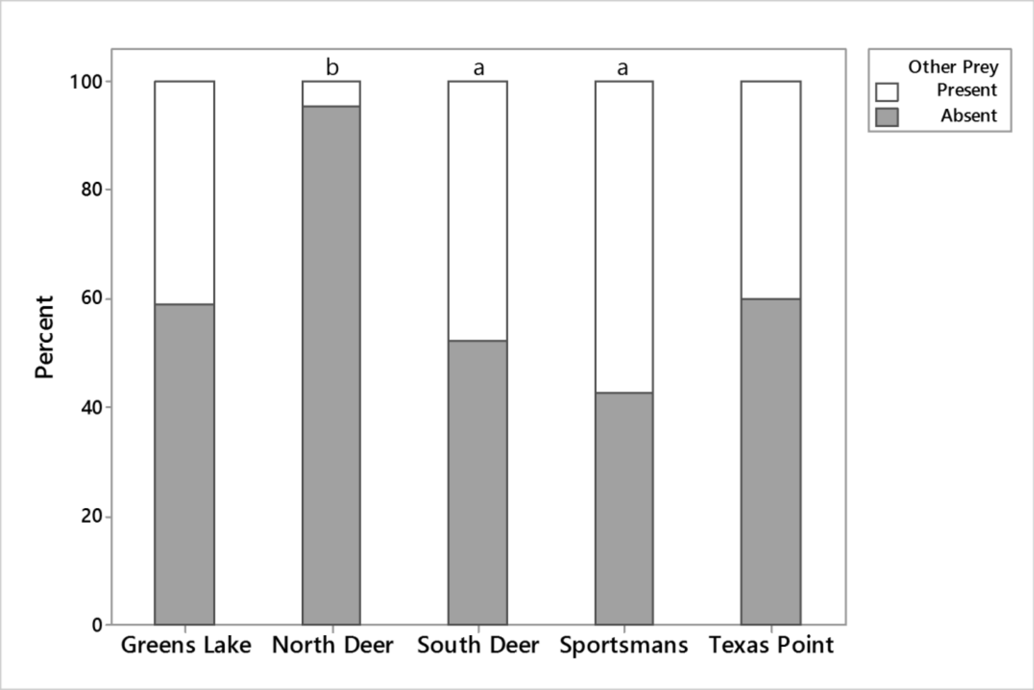

Figure 42. Marsh differences at capture locations of presence of other potential prey items in 1 m^2 prey quadrats (Kruskal-Wallis; H = 17.90, p = 0.001). Bars represent each site and show percentage of quadrats where C. pliculosa was present or absent. (Significant group differences: *a* > *b* and *c* > *d*)

Fecal Analysis

A total of 64 fecal samples were collected from terrapin over the course of the study with 35 female samples and 29 male samples. Samples from terrapins that were held for approximately 48 hours made up the majority of the collection (n = 45). Fewer samples came from terrapin that were only held for ~24 hours (n = 8), while the remainder (n = 11) were collected opportunistically from the field. There were no significant differences detected between collection methods for either gravimetric (Kruskal-Wallis; H = 4.91, p = 0.086) or volumetric (Kruskal-Wallis; H = 2.97, p = 0.226) techniques (Figure 43). Therefore, samples collected by all three methods were analyzed together. Sixty of the samples were collected from different individual terrapins. However, the four remaining samples represented subsequent samples collected from individuals that had been sampled previously. These samples were included in the analyses since they were collected in different seasons or using different techniques (field sample vs. 48 hour sample). Samples were collected from four West Bay locations: South Deer Island (n = 35), North Deer Island (n = 8), Sportsman Road (n = 18), and Greens Lake (n = 2). Also, a single sample of opportunity was taken from a site in the Matagorda Bay system (n = 1). Samples were collected across all four seasons: spring (n = 9), summer (n = 25), fall (n = 26), and winter (n = 4) (Table 2).

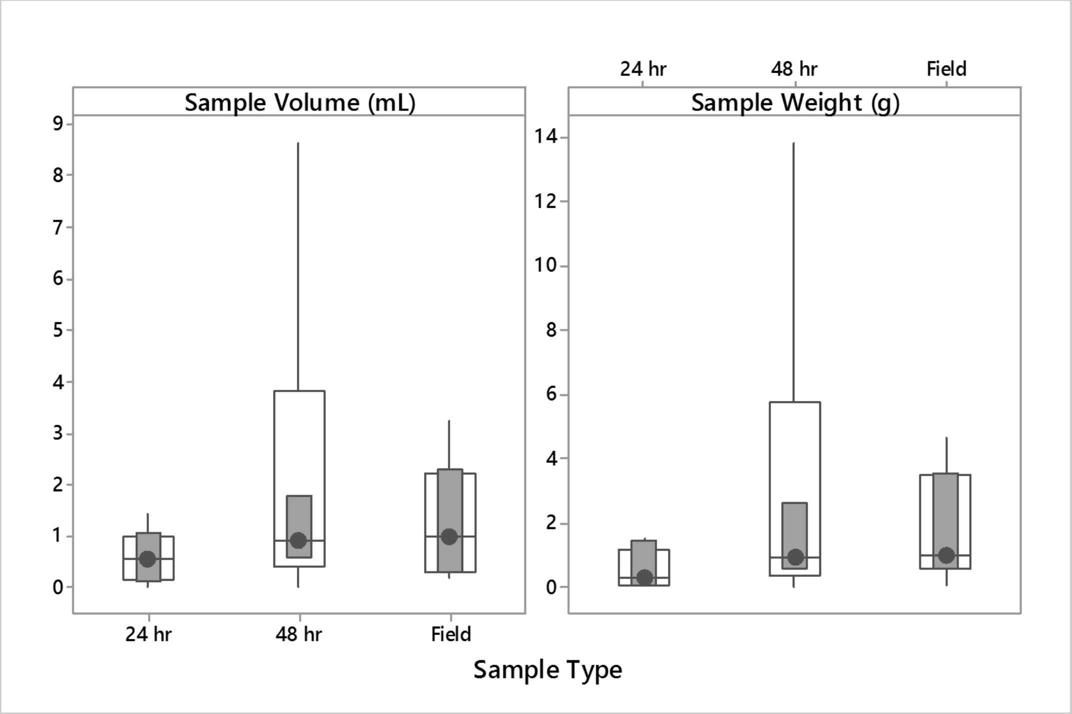

Figure 43. Boxplots depicting total sample volume (mL) (Kruskal-Wallis; H = 2.97, p = 0.226) and weight (g) (Kruskal-Wallis; H = 4.91, p = 0.086) showing no significant differences in median values between the three collection techniques. The gray inner box represents the 95% confidence interval for the median.

Table 2. Number of fecal samples collected by season.

Season	Beginning Date	Sample Number
Spring	March 20	9
Summer	June 21	25
Fall	September 22	26
Winter	December 21	4

A total of 22 different items were found in terrapin fecal samples, seven of which only showed up in one sample. One of these categories, Unknown Crab, was used as a “catch all” for particles of crab carapace that did not have any identifiable characteristics. Additionally, some categories were not included in most analyses due to rarity, being abiotic in nature, or if unidentifiable biological matter. The majority of abiotic items encountered were sediments, which included small rocks, sand, or shell hash. An item that appeared to be a small amount of plastic was found in a single sample. Most terrapins were found to have consumed more than one, biotic item (mode = 3), and the number of different items found in an individual sample ranged from 1-8 items (Figure 44). Prey items were found from the following animal groups: Gastropoda, Decapoda, Bivalvia, Insecta, Araneae, and Actinopterygii. There was one instance where an unknown egg cluster was found in a sample. Vascular plants and algae were also commonly found in samples. Plant material consisted of the marsh species *S. alterniflora* and *Salicornia* spp, and all materials (stems, leaves, seeds, etc.) were grouped together.

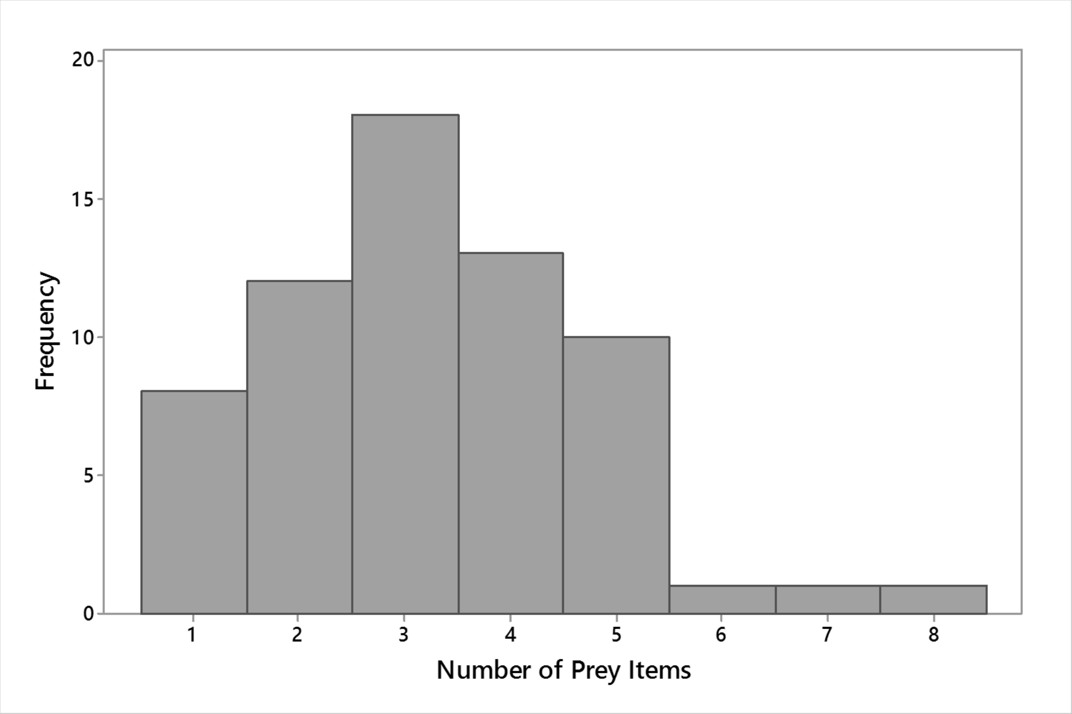

Figure 44. Frequency of varying numbers of prey items found in individual fecal samples (n = 64).

Diversity Indices

Estimates of dietary diversity varied by fecal analysis technique (Table 3). Overall Shannon-Weiner (H') diversity indices for terrapin diet were slightly higher for volumetric analysis (H'_{mL} = 1.34) than for gravimetric analysis (H'_{g} = 1.13). Overall Shannon Evenness (E) were again higher for volumetric (E_{mL} = 0.46) than for gravimetric (E_{g} = 0.39). Berger-Parker Index (BPI) values were similar between both techniques

(BPI_g = 0.48, BPI_{mL} = 0.49). The diets of male terrapins (H'_g = 1.41, H'_{mL} = 1.56) were shown to be more diverse than that of females (H'_g = 0.99, H'_{mL} = 1.18) using either fecal analysis technique. Male diets also exhibited a higher evenness (E) than females. Based on the results of gravimetric analysis, male diets had an E_g of 0.52 compared to the diet of females at 0.37. Volumetric analysis yielded similar evenness results for males (E_{mL} = 0.58) and females (E_{mL} = 0.43). Berger-Parker Index scores were similar across all categories and techniques. Volumetric BPI for male terrapins (0.46) was slightly lower than BPI for females (0.50). Whereas, male gravimetric BPI scores (0.52) were higher than females (0.47).

Table 3. Shannon-Weiner (H'), Shannon Evenness (E), and Berger-Parker (BPI) indices of diversity for *M. t. littoralis* diet. Estimates are given for total samples, males, and females for both gravimetric and volumetric techniques.

	Gravimetric (g)			Volumetric (mL)		
	Total	**Male**	**Female**	**Total**	**Male**	**Female**
Shannon-Weiner (H')	1.13	1.41	0.99	1.34	1.56	1.18
Shannon Evenness (E)	0.39	0.52	0.37	0.46	0.58	0.43
Berger-Parker (BPI)	0.48	0.52	0.47	0.49	0.46	0.50

Frequency of Occurrence

During the study, Diamond-backed Terrapins most frequently ingested Gastropods (Table 4). Gastropods, composed of three identified species, were found in 70% of fecal samples. The percent occurrence of Gastropods was lower in males (62%) in contrast to females (77%). The most frequently encountered Gastropod was the plicate horn snail (*Cerithidea pliculosa*) (59%) followed by marsh periwinkle snails (*Littorina irrorata*) (25%). There was little difference in the occurrence of *C. pliculosa* between males (58%) and females (60%). *L. irrorata* occurred in 43% of female samples, but only 3% of male samples. The third Gastropod species found in terrapin diet was eastern melampus (*Melampus bidentatus*). Melampus snails were found in 8% of all samples, 10% of male samples and 6% of female samples.

Table 4. Frequency of occurrence of prey items found in terrapin fecal samples. Percentages given for total, male, and female samples.

		% Frequency of Occurrence		
Prey Item		**Total (n = 64)**	**Male (n = 29)**	**Female (n = 35)**
Class Gastropoda		70.3	62.1	77.1
Cerithidea pliculosa	Plicate Horn Snail	59.4	58.6	60.0
Littorina irrorata	Marsh Periwinkle	25.0	3.4	42.9
Melampus bidentatus	Eastern Melampus	7.8	10.3	5.7
Class Bivalvia		9.4	6.9	11.4
Mulina lateralis	Dwarf Surf Clam	6.3	3.4	8.6
Solen viridis	Green Jackknife Clam	1.6	0.0	2.9
Arcidae A	Ark Clam A	1.6	0.0	2.9
Arcidae B	Ark Clam B	1.6	3.4	0.0
Subphylum Crustacea Order Decapoda		67.2	79.3	57.1
Uca spp.	Fiddler Crabs	40.6	41.4	40.0
Callinectes sapidus	Blue Crab	21.9	31.0	14.3
Sesarma reticulatum	Purple Marsh Crab	3.1	6.9	0.0
Unknown Crab		15.6	13.8	17.1
Unknown Shrimp		1.6	3.4	0.0
Order Sessilia				
Balanus sp.	Barnacle	1.6	0.0	2.9
Class Insecta		18.8	13.8	22.9
Order Araneae		7.8	10.3	5.7
Class Actinopterygii		14.1	17.2	11.4
Kingdom Plantae		78.1	82.8	71.4
Algae (Monran and/or Protista)		4.7	0.0	8.6
Unknown Egg Cluster		1.6	3.4	0.0

The second most common animal group was Decapod crustaceans (Table 4). Decapods were categorized into five groups, and were found in 67% of all samples. A higher percentage of male samples (79%) contained Decapoda compared to female samples (57%). Fiddler crabs (*Uca* spp.) were found in 41% of all samples and did not differ much between males (41%) and females (40%). Blue crab (*Callinectes sapidus*) remains were found in 22% of terrapin samples. There were differences in blue crab occurrence between males (31%) and females (14%). Purple marsh crabs (*Sesarma reticulatum*) were not encountered in any female samples; however, 7% of male samples contained this species. This accounts for only 3% of total samples. Unidentifiable particles of crab carapace found in samples were put into the category Unknown Crab. Items in this category were found in 16% of all samples, and within 14% of male samples and 17% of female samples. An unidentified shrimp was found in a single male sample (3%), which is less than 2% of the total. However, the shrimp was largely intact and hardly digested which may indicate contamination of the sample in some way rather than ingestion by the turtle.

The most frequently encountered group, overall, was vascular plants (Table 4). Plant material of some sort showed up in 78% of all samples, and was more frequently observed in male (83%) versus female (71%) samples. Infrequently consumed items included algae, Bivalvia, Araneae (spiders), Insecta, and Actinopterygii (ray-finned fishes). Bivalves consisted of four different types; two were identified to species while the other two could only be identified to family. The species identified were dwarf surf clam (*Mulina lateralis*) and green jackknife clam (*Solen viridis*), while the two others appear to be from the family Arcidae (ark clams). Three families of spiders were identifiable from remains: Lycosidae (wolf spiders), Salticidae (jumping spiders), and Linyphiidae (sheet web spiders). The insect items were not able to be identified and therefore put into a single group. A fragment of barnacle (*Balanus* sp.) and an egg mass were encountered in one sample each (2% of samples).

Gravimetric Analysis

Gravimetric analysis indicated that the bulk of terrapin diet consists of snails with crabs ranking second (Table 5). For all samples combined, Gastropods represented 88% of total weight while Decapods composed 10%. The major taxonomic contributors to these percentages were: *C. pliculosa* (47%), *L. irrorata* (40%), *Uca* spp. (7%), and *C. sapidus* (3%). All other dietary items represented less than 1% of the total. Male diet was composed of 54% Gastropod, most of which was horn snails (50%). Another 41% of the diet by weight was Decapod mainly made up in equal parts fiddler crab (17%) and blue crab (17%). Purple marsh crab represented 6% of the male diet. Female diet was primarily composed of snails (91%) with crabs representing 7% of the total weight. Females consumed *C. pliculosa* and *L. irrorata* in similar amounts, 47% and 44% respectively. Fiddler crabs (6%) were the main Decapod component of their diet.

Table 5. Percentages of prey items by weight (g) found in terrapin fecal samples. Percentages given for total, male, and female samples.

		% by Weight (g)		
Prey Item		**Total (n = 64)**	**Male (n = 29)**	**Female (n = 35)**
Class Gastropoda		87.6	54.5	91.3
Cerithidea pliculosa	Plicate Horn Snail	47.2	50.8	46.8
Littorina irrorata	Marsh Periwinkle	39.9	0.01	44.4
Melampus bidentatus	Eastern Melampus	0.4	3.6	0.1
Class Bivalvia		0.08	0.02	0.08
Mulina lateralis	Dwarf Surf Clam	0.06	0.004	0.06
Solen viridis	Green Jackknife Clam	0.008	0.0	0.009
Arcidae A	Ark Clam A	0.01	0.0	0.01
Arcidae B	Ark Clam B	0.001	0.01	0.0
Subphylum Crustacea Order Decapoda		10.4	40.6	6.9
Uca spp.	Fiddler Crabs	6.8	16.7	5.7
Callinectes sapidus	Blue Crab	2.6	17.0	1.0
Sesarma reticulatum	Purple Marsh Crab	0.6	6.1	0.0
Unknown Crab		0.3	0.9	0.2
Unknown Shrimp		0.0009	0.009	0.0
Order Sessilia *Balanus* sp.	Barnacle	0.0009	0.0	0.001
Class Insecta		0.007	0.03	0.005
Order Araneae		0.004	0.02	0.002
Class Actinopterygii		0.2	1.6	0.05
Kingdom Plantae		0.4	1.0	0.3
Algae (Moneran and/or Protista)		0.2	0.0	0.4
Unknown Egg Cluster		0.0009	0.009	0.0

Based on the results of Kruskal-Wallis ANOVA multiple significant differences in percent weight between the diets of male and female terrapins were detected. Females consumed significantly more periwinkle snails (H = 13.28, p < 0.001) and total Gastropods (H = 5.95, p = 0.015) than did males (Figure 45 and Figure 46). In contrast, males showed a significantly higher percentage of blue crab consumption (H = 3.87, p = 0.049) and Decapods overall (H = 5.30, p = 0.021) than females (Figure 47 and Figure 48). Finally, male terrapin exhibited significantly higher percentage intake of plant matter (H = 6.02, p = 0.014) in comparison to females (Figure 49). No other significant (p ≤ 0.05) differences in quantities or percentages of dietary items were detected between the sexes.

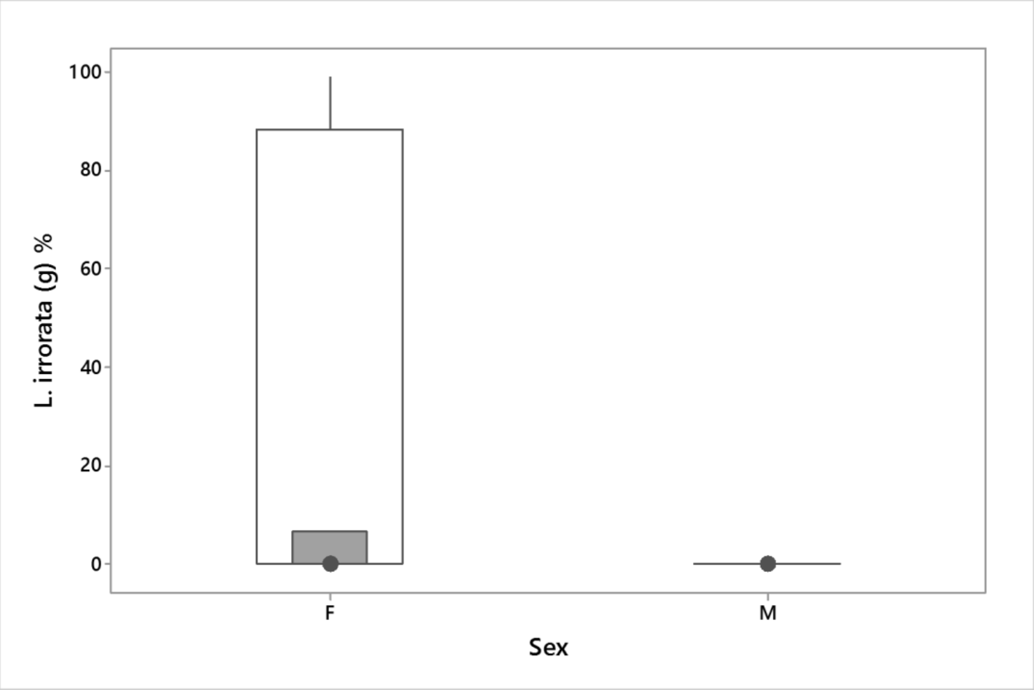

Figure 45. Boxplot depicting percent weight differences between male (M) and female (F) diet of *Littorina irrorata* (Kruskal-Wallis; H = 13.28, p < 0.001). The inner shaded box represents the 95% confidence interval for the median.

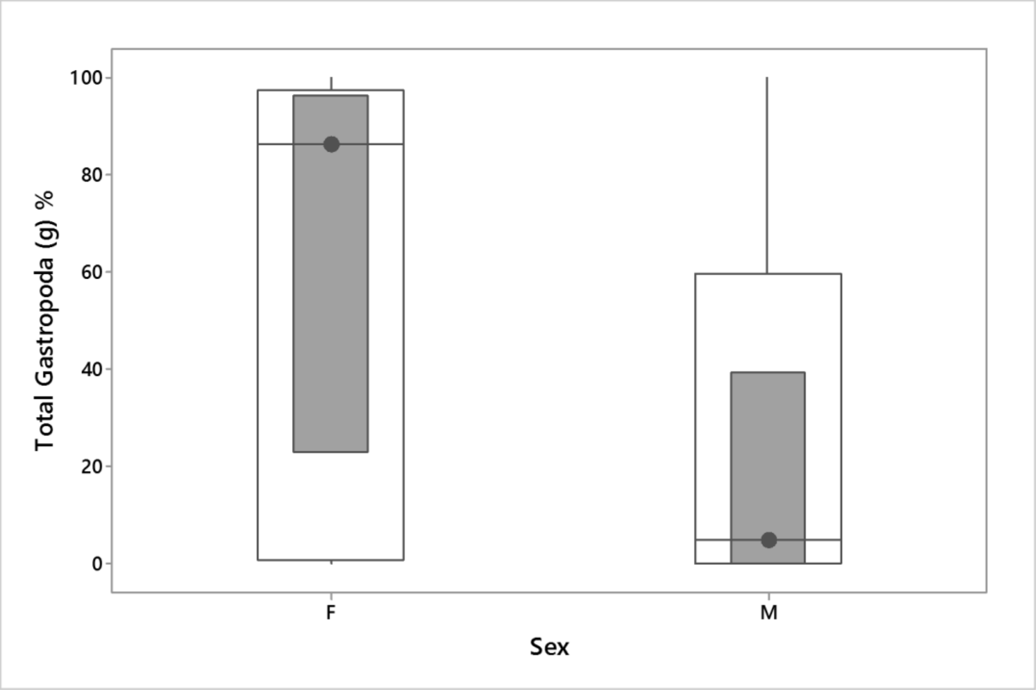

Figure 46. Boxplot depicting percent weight differences between male (M) and female (F) diet of Total Gastropoda (Kruskal-Wallis; H = 5.95, p = 0.015). The inner shaded box represents the 95% confidence interval for the median.

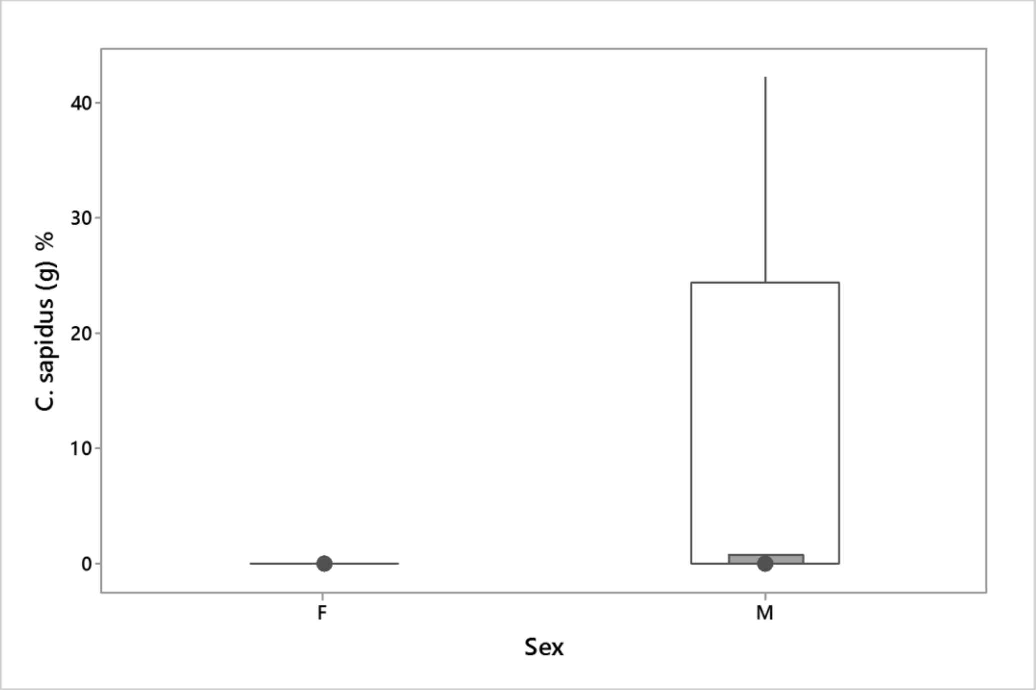

Figure 47. Boxplot depicting percent weight differences between male (M) and female (F) diet of *Callinectes sapidus* (Kruskal-Wallis; H = 3.87, p = 0.049). The inner shaded box represents the 95% confidence interval for the median.

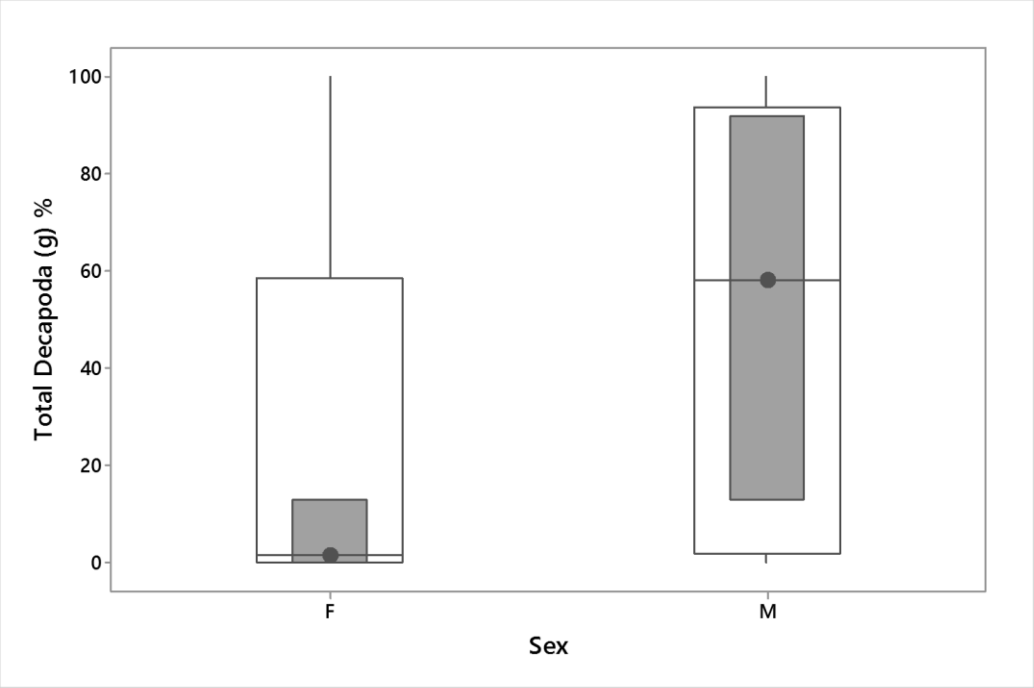

Figure 48. Boxplot depicting percent weight differences between male (M) and female (F) diet of Total Decapoda (Kruskal-Wallis; H = 5.30, p = 0.021). The inner shaded box represents the 95% confidence interval for the median.

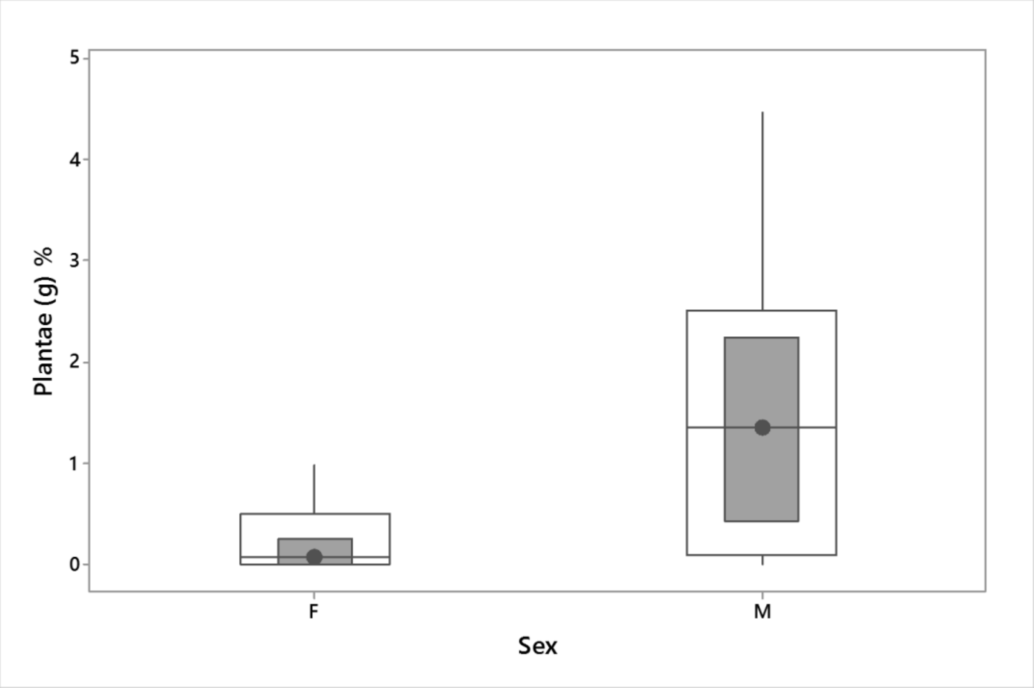

Figure 49. Boxplot depicting percent weight differences between male (M) and female (F) diet of Plantae (Kruskal-Wallis; H = 6.02, p = 0.014). The inner shaded box represents the 95% confidence interval for the median.

Due to winter having a small sample size (n = 4), seasonal statistical analyses were limited to spring, summer, and fall. However, winter data were included in graphical representations. Significant seasonal variations in diet were evaluated using Kruskal-Wallis analysis and the *post hoc* Dunn's multiple range test. A significant seasonal difference was found in the percent weight of total Gastropods (H = 10.54, p = 0.005). Consumption of snails was significantly higher during spring and fall compared with summer (Figure 50). Highly significant (H = 15.98, $p < 0.001$) seasonal differences were detected in the percent of diet composed of fiddler crabs. Terrapins consumed a higher percentage of fiddler crabs in summer in comparison to other seasons (Figure 51). Consumption of blue crabs also varied seasonally (H = 8.15, p = 0.017). Diamond-backed Terrapin consumed a significantly higher percentage of blue crab in the fall than in summer (Figure 52). Seasonal differences in consumption of total Decapoda approached statistical significance (H = 5.79, p = 0.055) (Figure 53). Diamond-backed Terrapin consumed a significantly higher percentage of spiders (H = 7.00, p = 0.03) in fall than in summer (Figure 54). Based on results of the Kruskal-Wallis test (H = 11.74, p = 0.003) seasonal differences in the amount of plant matter ingested by terrapin were detected. The amount of plant material in their diet was significantly higher in fall and summer than in spring (Figure 55).

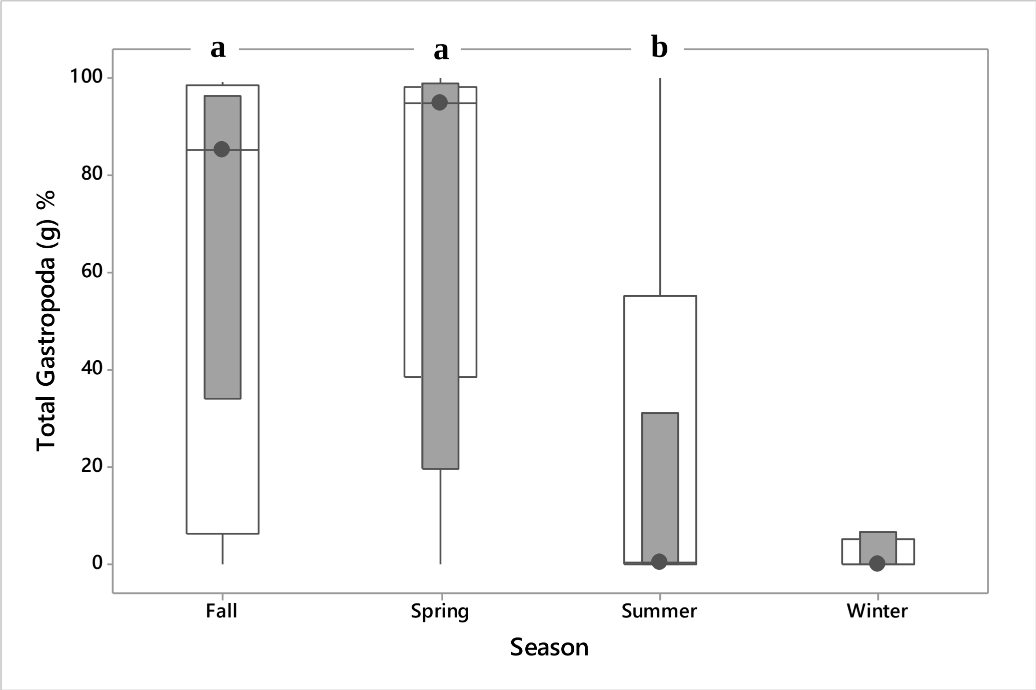

Figure 50. Boxplot depicting seasonal dietary differences in percent weight of total Gastropoda (Kruskal-Wallis; H = 10.54, p = 0.005). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*; winter excluded from analysis)

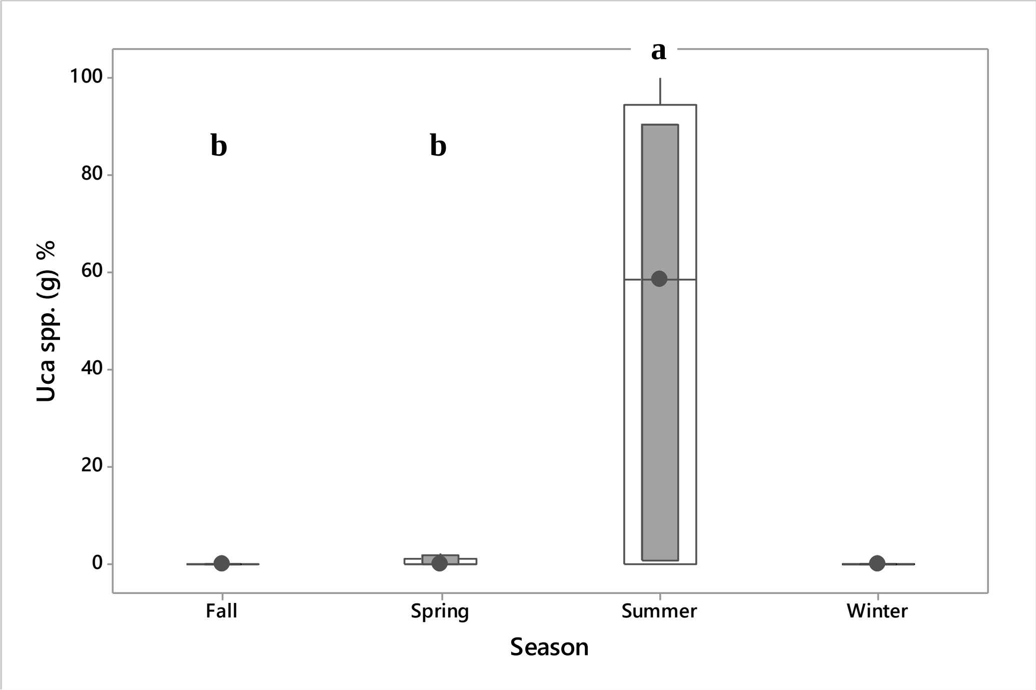

Figure 51. Boxplot depicting seasonal dietary differences in percent weight of *Uca* spp. (Kruskal-Wallis; H = 15.98, p < 0.001). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*; winter excluded from analysis)

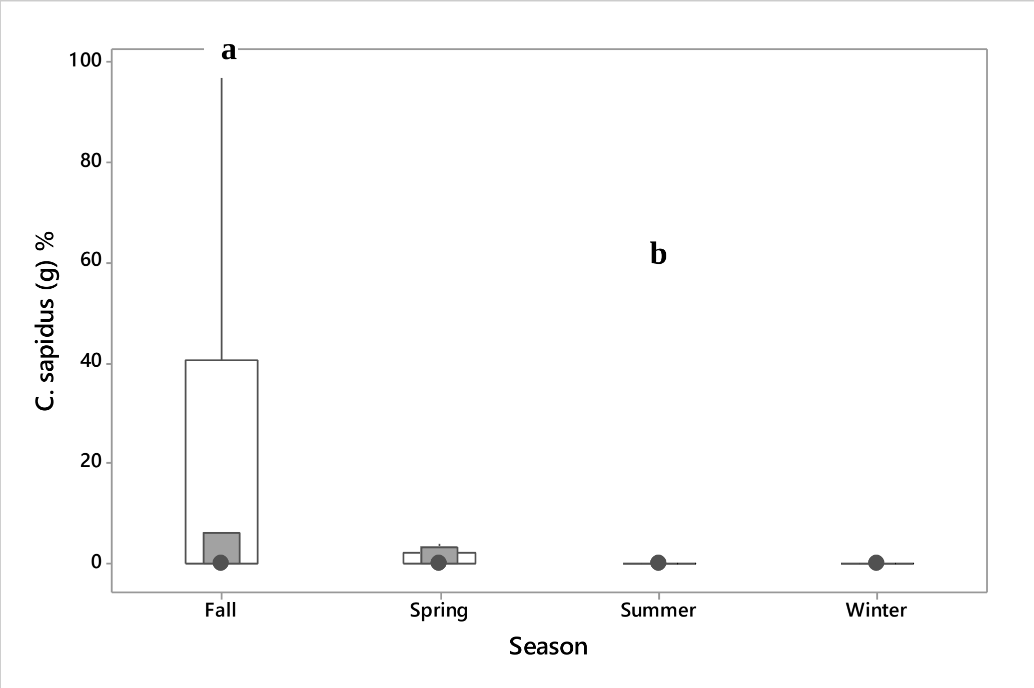

Figure 52. Boxplot depicting seasonal dietary differences in percent weight of *Callinectes sapidus* (Kruskal-Wallis; H = 8.15, p = 0.017). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*; winter excluded from analysis)

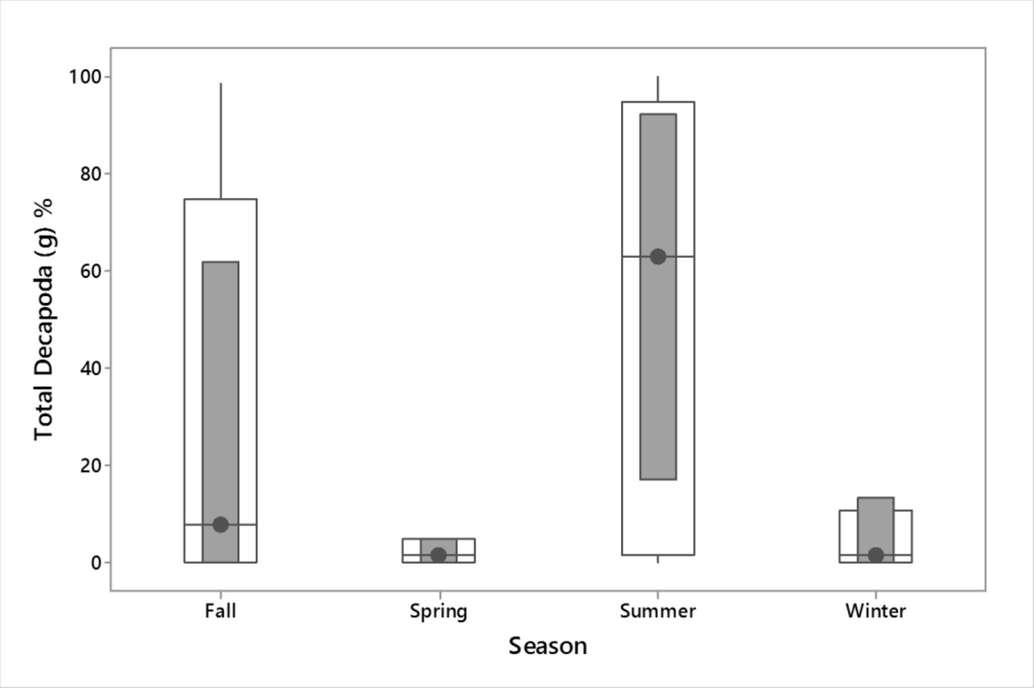

Figure 53. Boxplot depicting seasonal dietary differences in percent weight of total Decapoda (Kruskal-Wallis; H = 5.79, p = 0.055). The inner shaded box represents the 95% confidence interval for the median. (winter excluded from analysis)

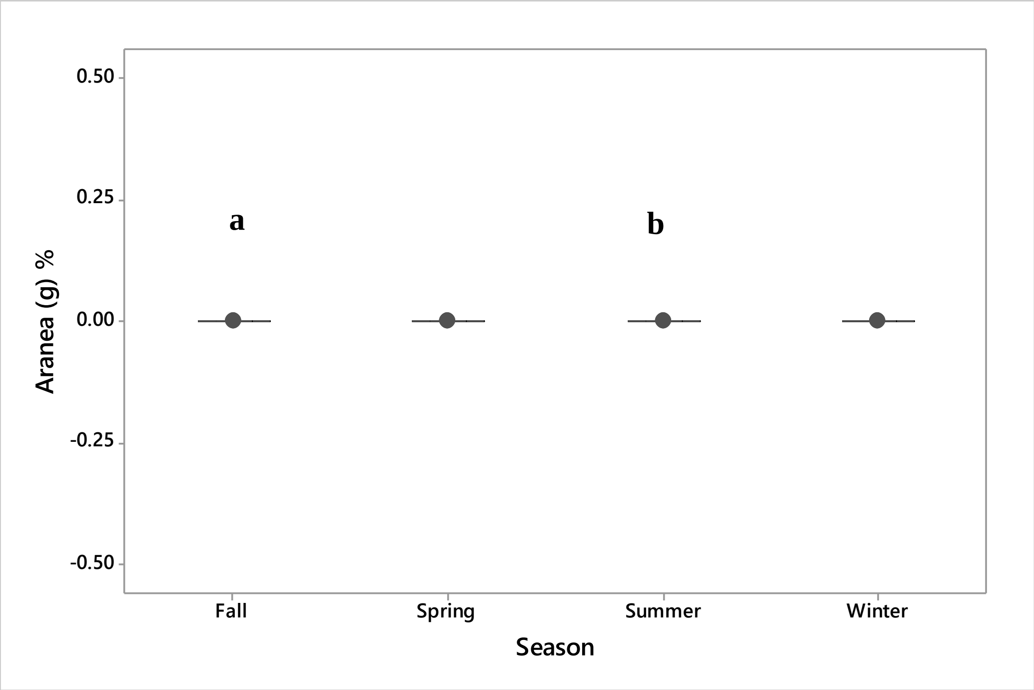

Figure 54. Boxplot depicting seasonal dietary differences in percent weight of Araneae (Kruskal-Wallis; H = 7.00, p = 0.03). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*; winter excluded from analysis)

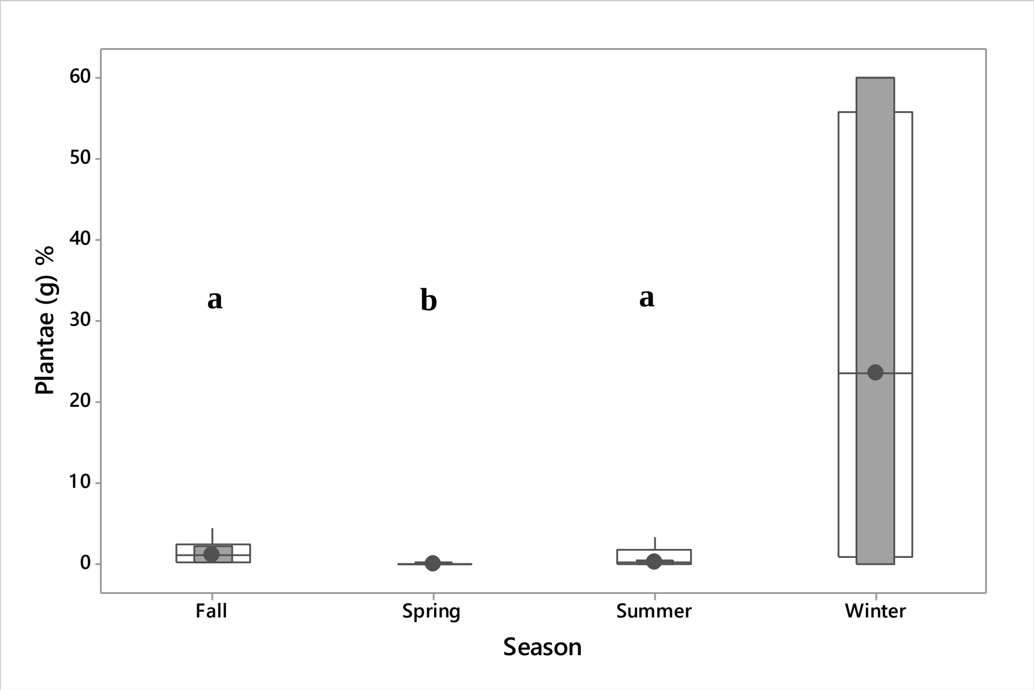

Figure 55. Boxplot depicting seasonal dietary differences in percent weight of vascular plants (Kruskal-Wallis; H = 13.74, p = 0.003). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*; winter excluded from analysis)

In order to examine dietary differences between sites, results of gravimetric analyses from terrapin captured at three West Bay sites including South Deer (n = 35), Sportsman Road (n = 18), and North Deer (n = 8) were included in the formal statistical analyses. Greens Lake (n = 2) and Matagorda (n = 1) were not included in the formal data analysis due to low sample size. While not statistically analyzed, Greens Lake terrapin diets were dominated by > 99% *C. pliculosa*. The Matagorda diet sample contained *M. bidentatus* (73%) and *Uca* spp. (27%).

A significant difference in percent horn snails found in terrapin diet was detected between the three sites (H = 6.60, p = 0.037). Both North Deer and Sportsman Road terrapins had significantly higher percentages of *C. pliculosa* in their fecal samples than South Deer samples (Figure 56). Significant location differences in *Uca* spp. consumption (H = 6.43, p = 0.04) were also detected. Terrapin from Sportsman Road were found to have significantly greater percentages of fiddler crabs in their diets than both those from North and South Deer (Figure 57).

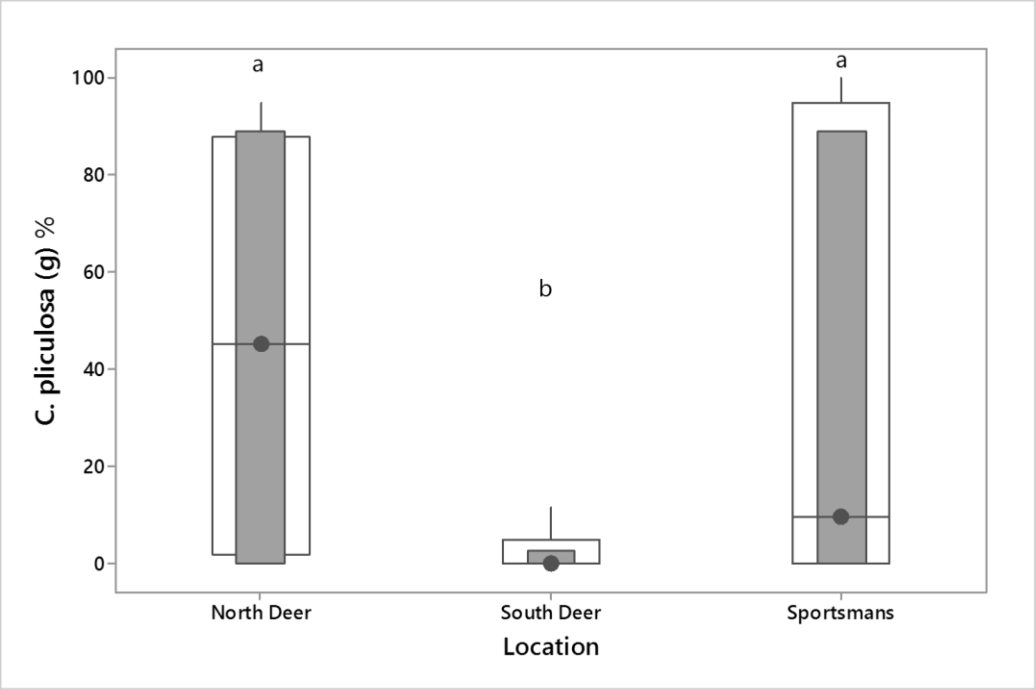

Figure 56. Boxplot depicting dietary differences by location in percent weight of *Cerithidea pliculosa* (Kruskal-Wallis; H = 6.60, p = 0.037). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

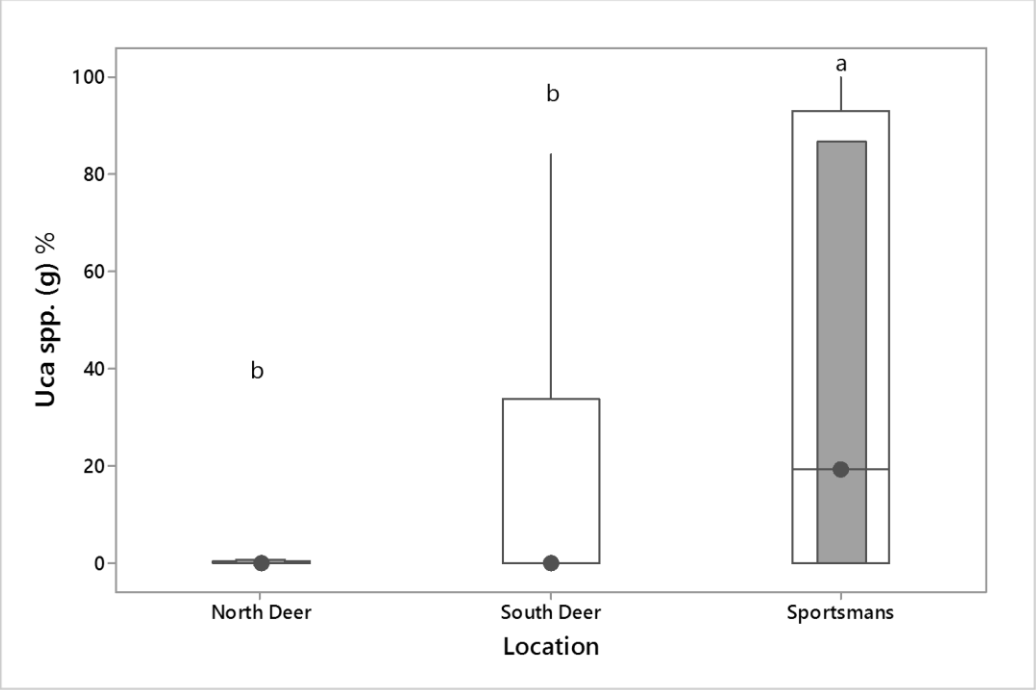

Figure 57. Boxplot depicting dietary differences by location in percent weight of *Uca* spp. (Kruskal-Wallis; H = 6.43, p = 0.04). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

Volumetric Analysis

Gastropods made up the highest percentage (79%) of total terrapin diet by percent volume (Table 6). Decapods made up the second highest percentage (15%) of total diet. Plant material represented 3% of the total terrapin diet. All other items contributed less than 1% of the total volume. Plicate horn snails were the largest contributor (48%) to the Gastropod category followed by marsh periwinkles (30%). Overall the main Decapod species consumed by volume were *Uca* spp. (10%) and *C. sapidus* (3%). Male terrapin consumed 47% snails by volume, which were composed of 45% *C. pliculosa*. Crab species represented 39% of the diet of male terrapins. Fiddler crabs (19%) and blue crabs (14%) were the dominant Decapod taxa consumed. Another Decapod species, *Sesarma reticulatum*, represented the reaming 5% consumed. Plants made up a fairly large portion (8%) of the male terrapin diet. The female terrapin diet consisted of Gastropoda at 84% by volume, 49% horn snails and 35% marsh periwinkle. In contrast to males, Decapods made up less of female diet (10%). Fiddler crabs represented 9% of the Decapod volume, while blue crab contributed only 1%. Plant material composed 2% of the female terrapin diet.

Table 6. Percentages of prey items by volume (mL) found in terrapin fecal samples. Percentages given for total, male, and female samples.

		% by Volume (mL)		
Prey Item		**Total (n = 64)**	**Male (n = 29)**	**Female (n = 35)**
Class Gastropoda		78.5	46.5	84.4
Cerithidea pliculosa	Plicate Horn Snail	48.1	44.5	48.7
Littorina irrorata	Marsh Periwinkle	29.9	0.05	35.4
Melampus bidentatus	Eastern Melampus	0.5	1.9	0.3
Class Bivalvia		0.2	0.1	0.2
Mulina lateralis	Dwarf Surf Clam	0.1	0.05	0.1
Solen viridis	Green Jackknife Clam	0.007	0.0	0.009
Arcidae A	Ark Clam A	0.04	0.0	0.04
Arcidae B	Ark Clam B	0.007	0.05	0.0
Subphylum Crustacea Order Decapoda		14.8	39.1	10.3
Uca spp.	Fiddler Crabs	10.2	18.9	8.7
Callinectes sapidus	Blue Crab	3.1	14.3	1.0
Sesarma reticulatum	Purple Marsh Crab	0.7	4.7	0.0
Unknown Crab		0.7	1.1	0.6
Unknown Shrimp		0.007	0.05	0.0
Order Sessilia				
Balanus sp.	Barnacle	0.007	0.0	0.009
Class Insecta		0.1	0.2	0.1
Order Araneae		0.1	0.3	0.03
Class Actinopterygii		0.4	1.6	0.2
Kingdom Plantae		2.6	8.1	1.6
Algae (Moneran and/or Protista)		0.8	0.0	0.9
Unknown Egg Cluster		0.007	0.05	0.0

Kruskal-Wallis test of volumetric data yielded multiple significant differences between the sexes. There was a strong significant difference in consumption of marsh periwinkle snails between the sexes (H = 13.28, p < 0.001), with females consuming more than males (Figure 58). Females also consumed significantly more Gastropods (H = 6.25, p = 0.012) than did males (Figure 59). Male terrapins were found to have significantly higher percentages of *C. sapidus* (H = 4.02, p = 0.045) in their diet than females (Figure 60). Total Decapoda intake was significantly greater in males (H = 4.15, p = 0.042) than females (Figure 61). Finally, male fecal samples contained higher percentages of plant material (H = 9.97, p = 0.002) than what was found in female fecal samples (Figure 62).

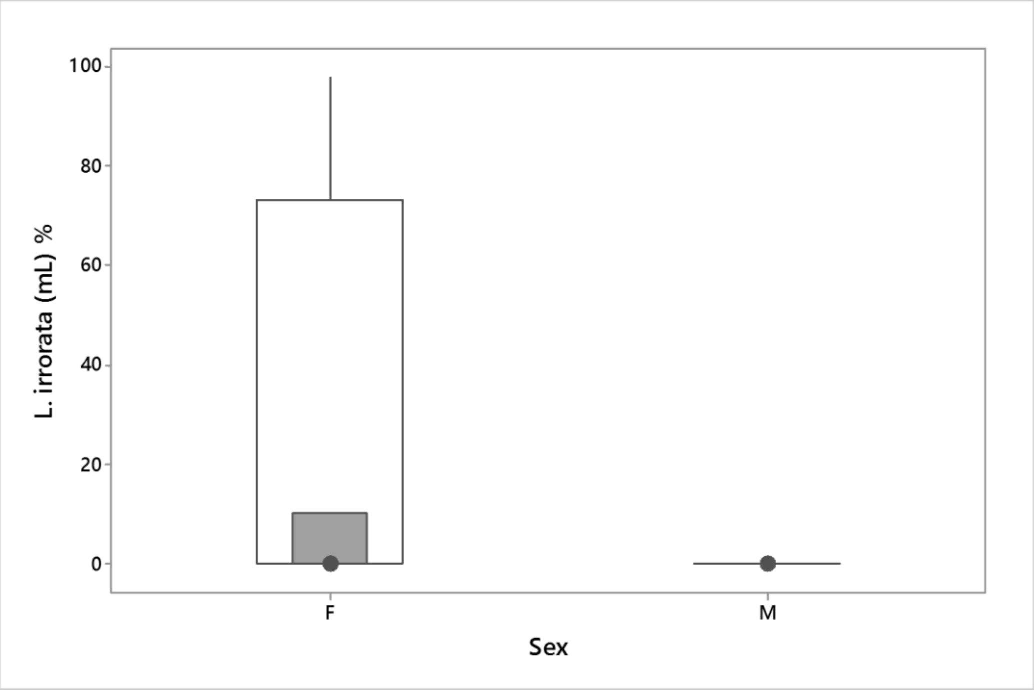

Figure 58. Boxplot depicting percent volume differences between male (M) and female (F) diet of *Littorina irrorata* (Kruskal-Wallis; H = 13.28, p < 0.001). The inner shaded box represents the 95% confidence interval for the median.

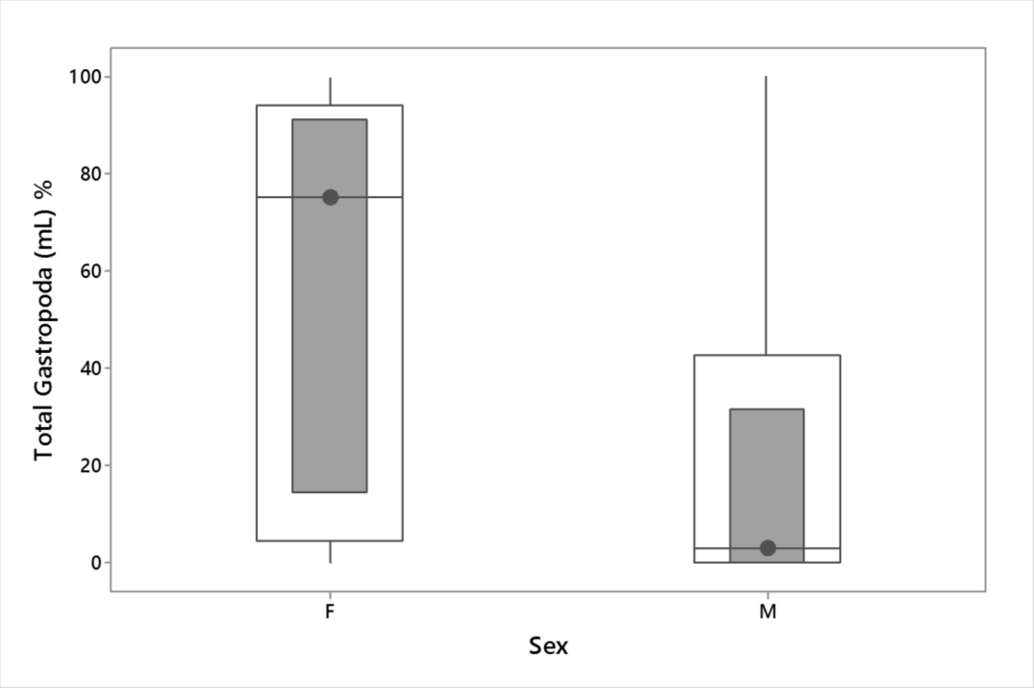

Figure 59. Boxplot depicting percent volume differences between male (M) and female (F) diet of Total Gastropoda (Kruskal-Wallis; H = 6.25, p = 0.012). The inner shaded box represents the 95% confidence interval for the median.

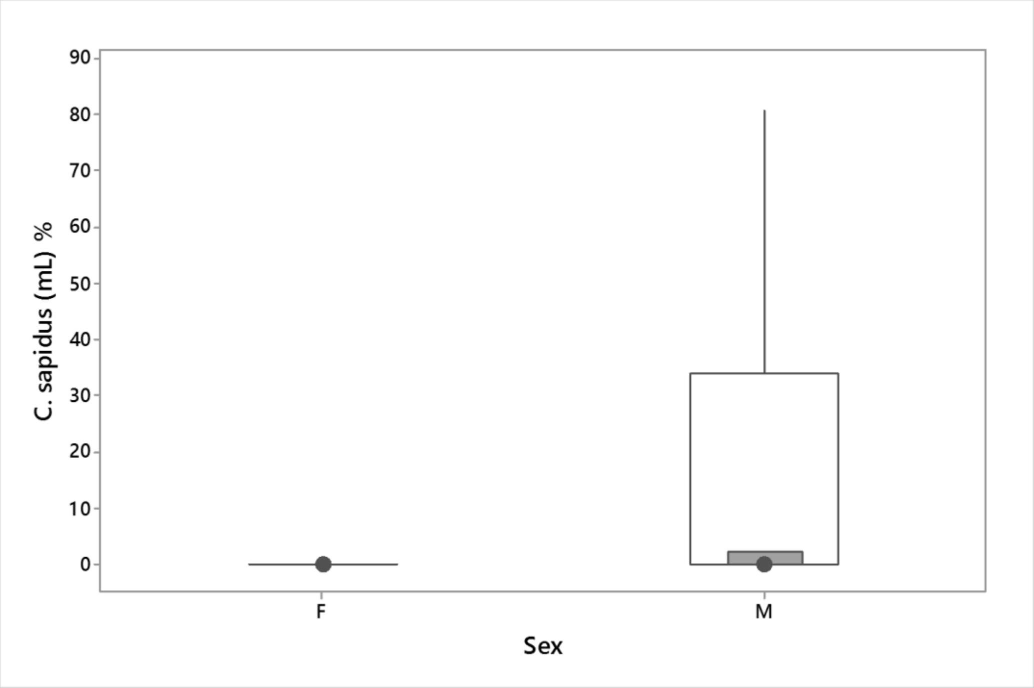

Figure 60. Boxplot depicting percent volume differences between male (M) and female (F) diet of *Callinectes sapidus* (Kruskal-Wallis; H = 4.02, p = 0.045). The inner shaded box represents the 95% confidence interval for the median.

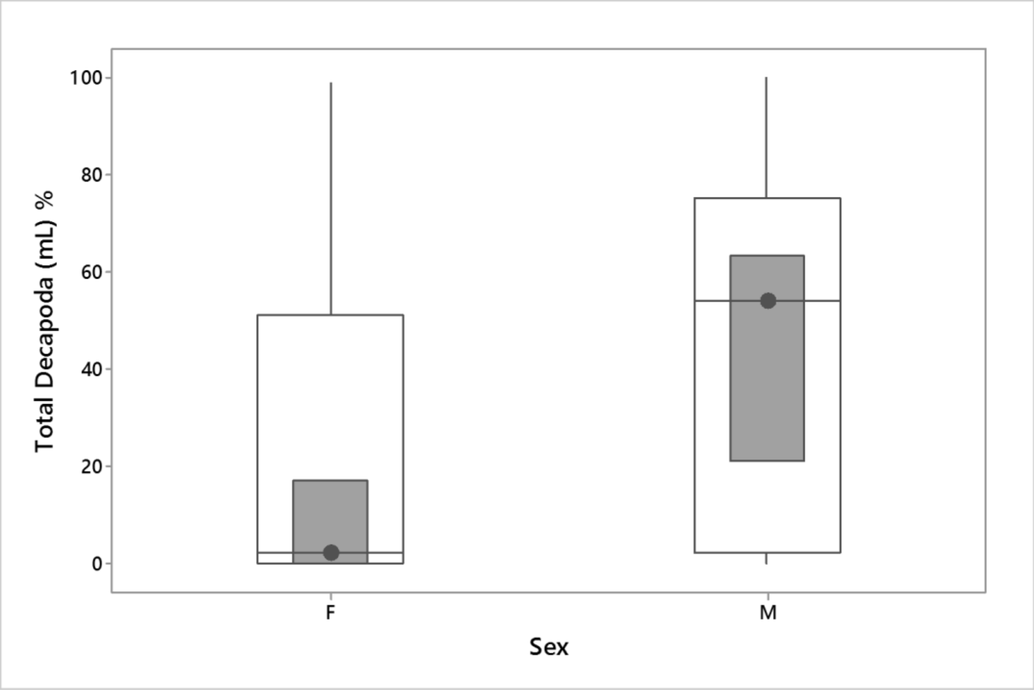

Figure 61. Boxplot depicting percent volume differences between male (M) and female (F) diet of Total Decapoda (Kruskal-Wallis; H = 4.15, p = 0.042). The inner shaded box represents the 95% confidence interval for the median.

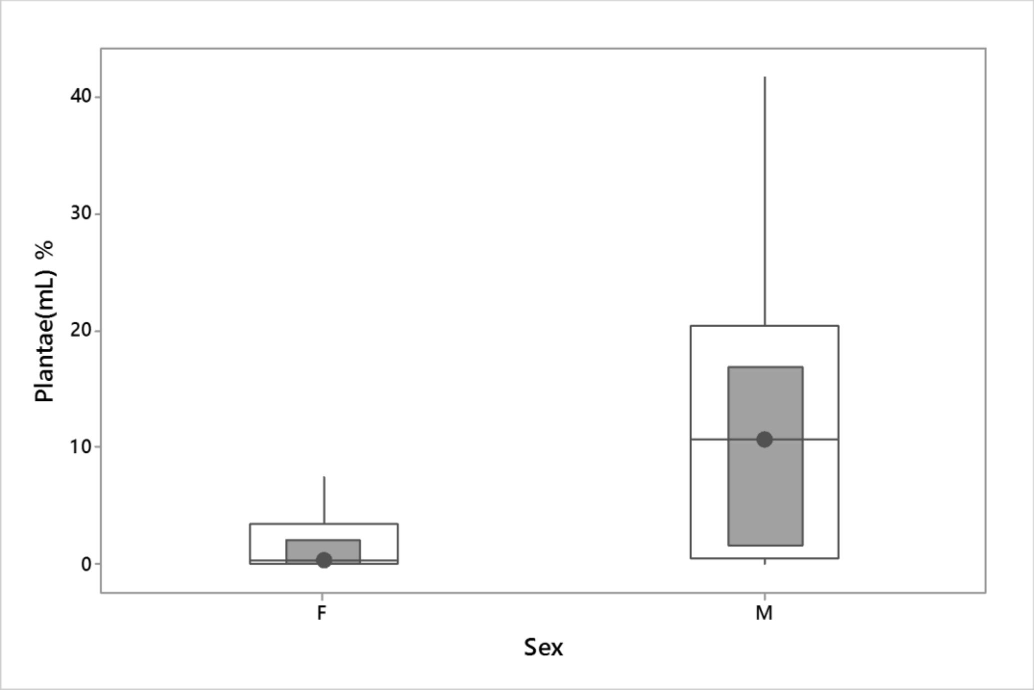

Figure 62. Boxplot depicting percent volume differences between male (M) and female (F) diet of Plantae (Kruskal-Wallis; H = 9.97, p = 0.002). The inner shaded box represents the 95% confidence interval for the median.

Seasonal variations in volumetric diet data were detected using Kruskal-Wallis ANOVA. There was a significant seasonal difference (H = 10.69, p = 0.005) in total Gastropoda consumed. Based on results of Dunn's multiple comparison test terrapin captured during the spring and fall had significantly higher amounts of total Gastropods in comparison to summer (Figure 63). A significant seasonal difference for *Uca* spp. was detected as well (H = 16.33, p < 0.001). Terrapin consumed higher percentages of fiddler crab species in summer compared to both fall and spring (Figure 64). There was a significant seasonal difference for *C. sapidus* (H = 8.26, p = 0.016). Fall was significantly higher than summer in percentage of blue crabs consumed (Figure 65). There was also a significant seasonal difference in total Decapoda (H = 7.23, p = 0.027) consumption. The consumption of Decapods was significantly higher in the summer in comparison to spring (Figure 66). Significant seasonal differences in consumption of spiders were detected (H = 7.00, p = 0.030). A higher percentage of spiders were consumed in fall than in summer (Figure 67). Terrapin captured during the summer and fall ingested a significantly higher (H = 14.44, p = 0.001) percentage of plant material in comparison to spring specimens. Fall was also significantly different than summer (Figure 68).

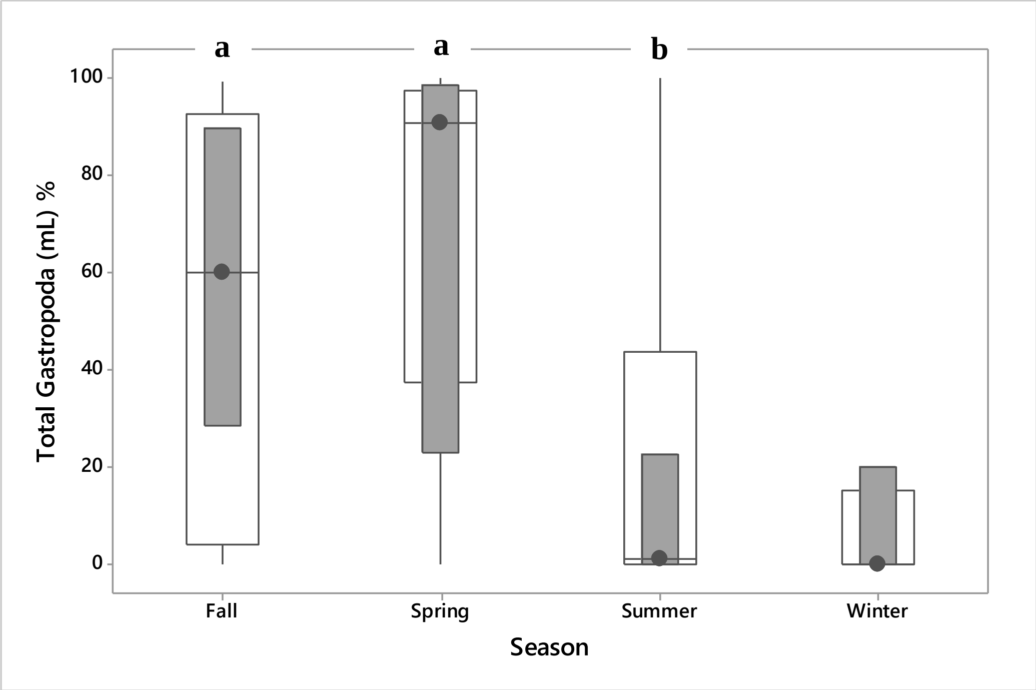

Figure 63. Boxplot depicting seasonal dietary differences in percent volume of total Gastropoda (Kruskal-Wallis; H = 10.69, p = 0.005). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*; winter excluded from analysis)

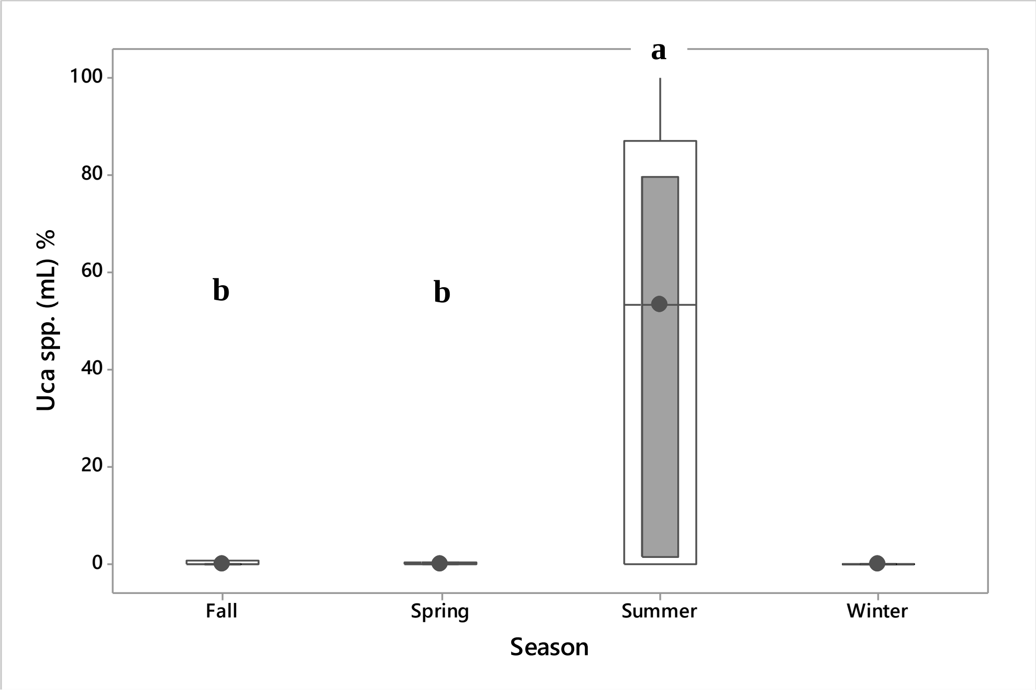

Figure 64. Boxplot depicting seasonal dietary differences in percent volume of *Uca* spp. (Kruskal-Wallis; H = 16.33, p < 0.001). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*; winter excluded from analysis)

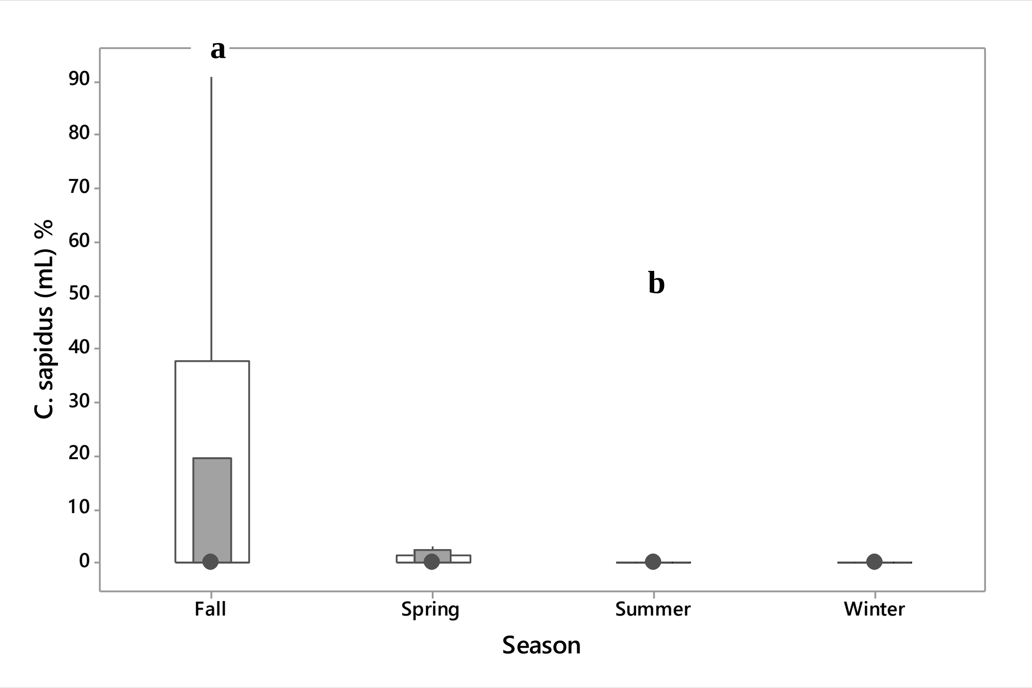

Figure 65. Boxplot depicting seasonal dietary differences in percent volume of *Callinectes sapidus* (Kruskal-Wallis; H = 8.26, p = 0.016). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*; winter excluded from analysis)

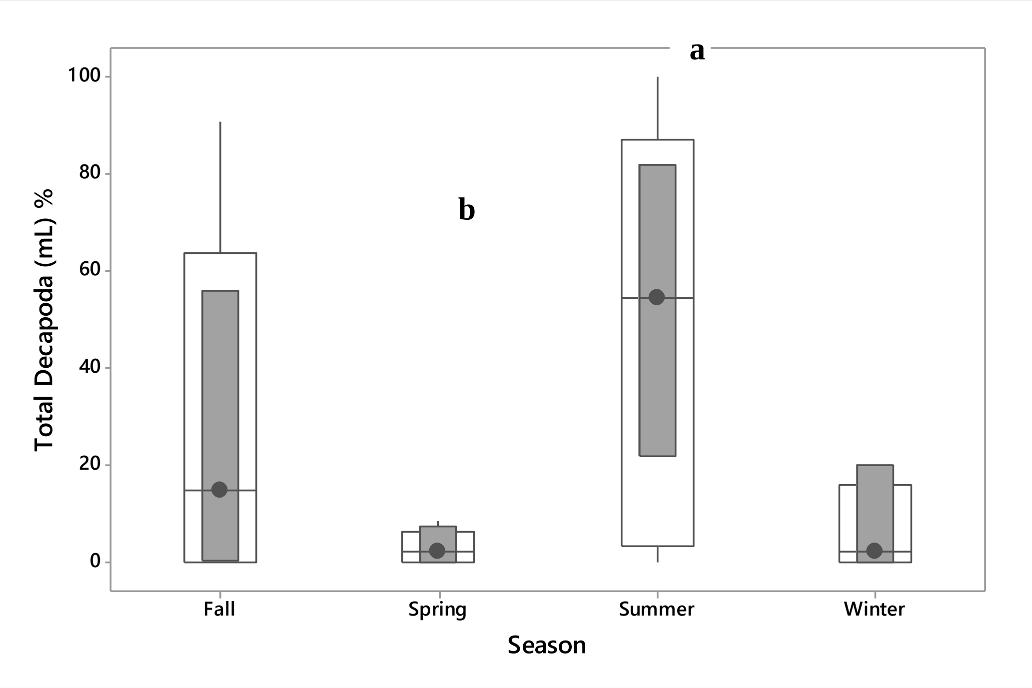

Figure 66. Boxplot depicting seasonal dietary differences in percent volume of total Decapoda (H = 7.23, p = 0.027). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*; winter excluded from analysis)

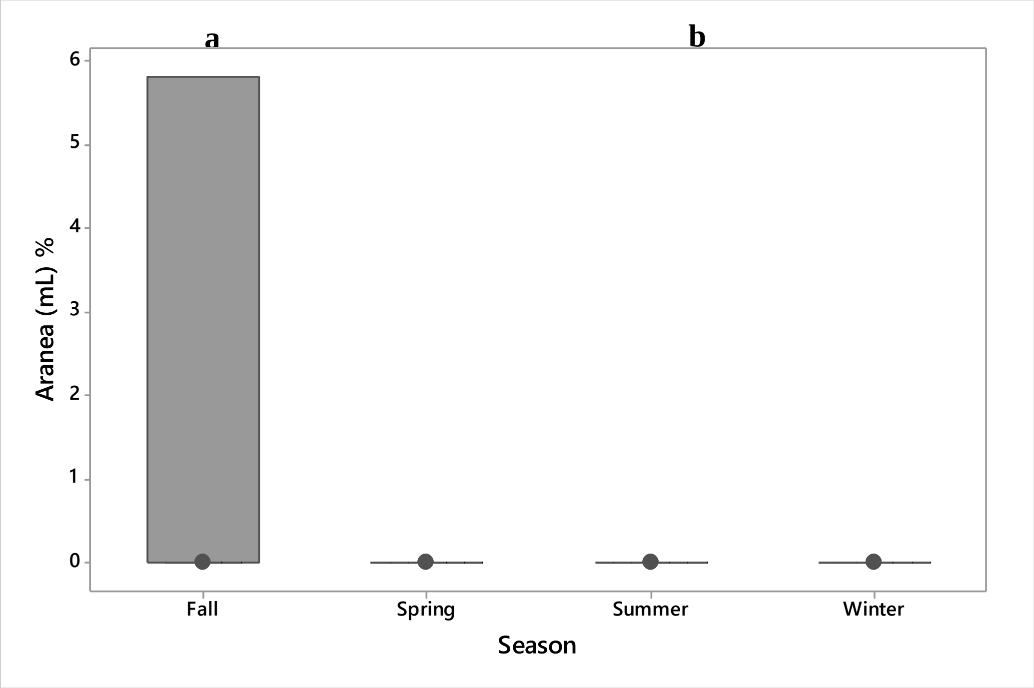

Figure 67. Boxplot depicting seasonal dietary differences in percent volume of Araneae (H = 7.23, p = 0.027). The shaded box represents the data range. (Significant group differences: *a* > *b*; winter excluded from analysis)

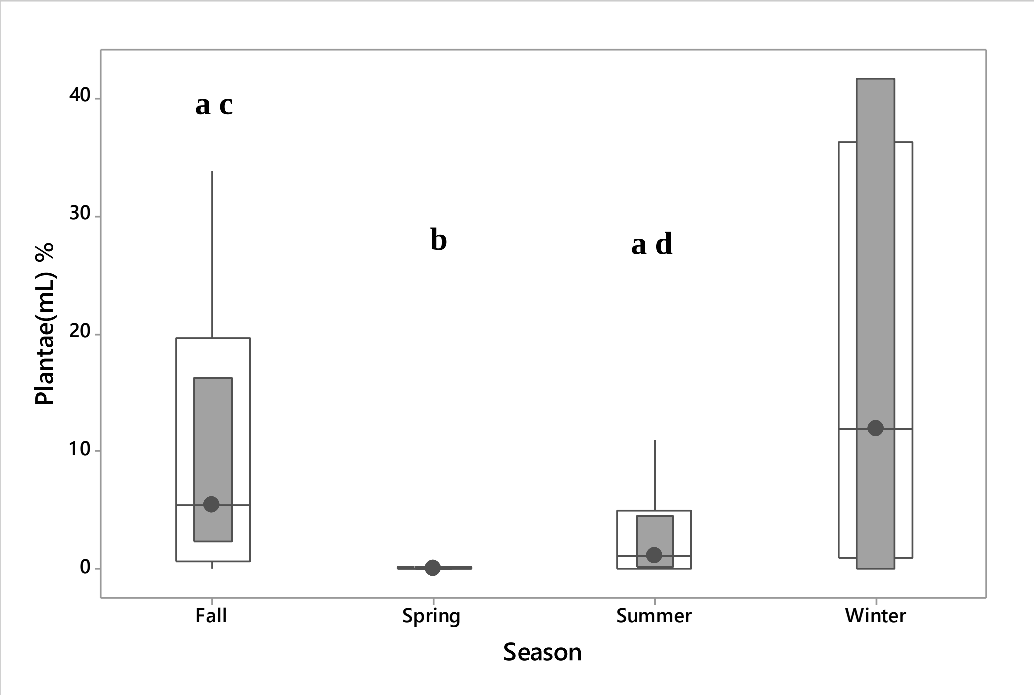

Figure 68. Boxplot depicting seasonal dietary differences in percent volume of vascular plants (Kruskal-Wallis; H = 14.44, p = 0.001). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b* and c > d; winter excluded from analysis)

During examination of dietary differences between sites, results of volumetric analyses from terrapin captured at three West Bay sites including South Deer (n = 35), Sportsman (n = 18), and North Deer (n = 8) were included in the formal statistical analyses. Greens Lake (n = 2) and Matagorda (n = 1) were not included in the formal data analysis due to low sample size. The Matagorda sample consisted of *M. bidentatus* (65%) and *Uca* spp. (32%). Greens Lake samples were almost entirely composed of *C. pliculosa* (> 99%). Based on volumetric data a significant difference in percent horn snails found in terrapin diet was detected between the sites (H = 6.91, p = 0.032). Terrapin collected at Sportsman Road were found to have significantly higher percentages of *C. pliculosa* in their fecal samples than South Deer samples (Figure 69). Significant location differences in the percent of diet composed of *Uca* spp. (H = 6.11, p = 0.047) were also detected. Terrapin from the Sportsman Road area had significantly greater percentages of fiddler crabs in their diets than both those from North and South Deer (Figure 70).

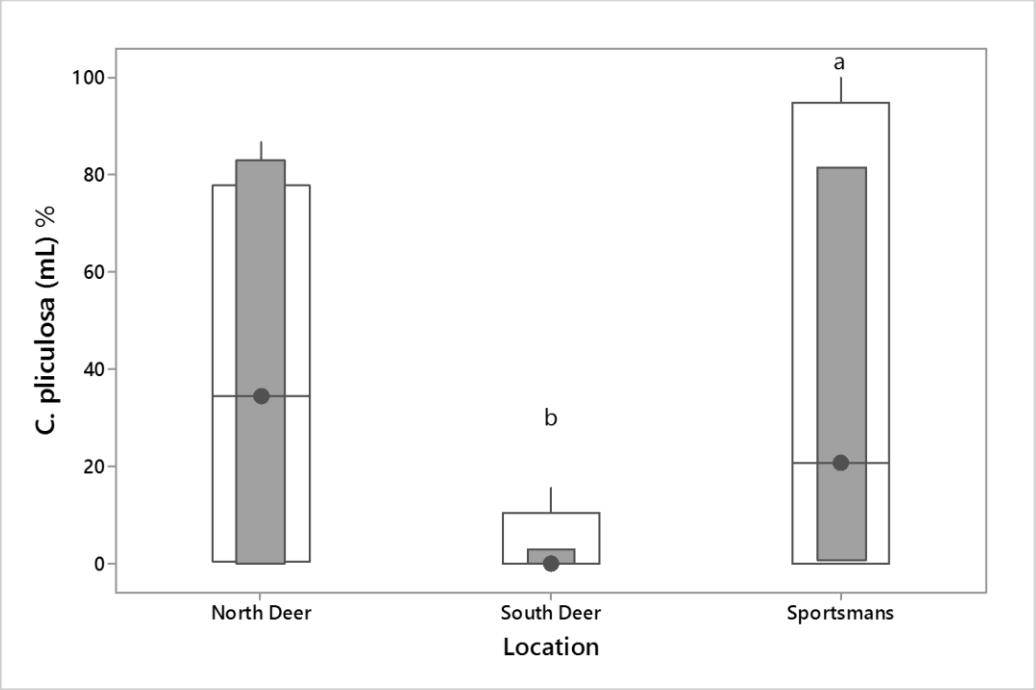

Figure 69. Boxplot depicting dietary differences by location in percent volume of *Cerithidea pliculosa* (Kruskal-Wallis; H = 6.91, p = 0.032). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

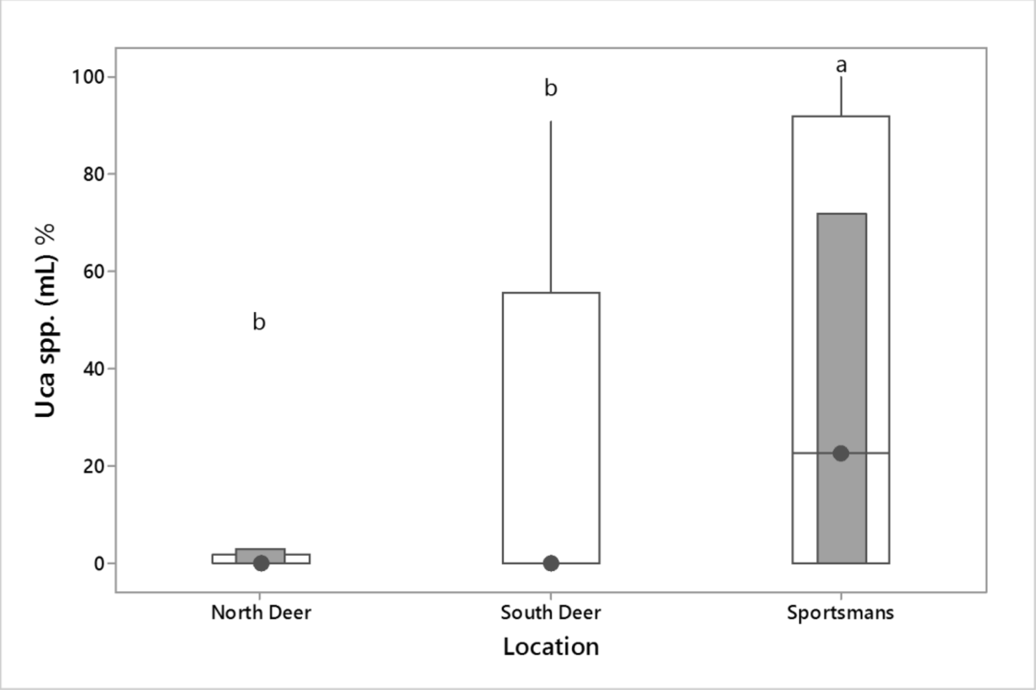

Figure 70. Boxplot depicting dietary differences by location in percent volume of *Uca* spp. (Kruskal-Wallis; H = 6.11, p = 0.047). The inner shaded box represents the 95% confidence interval for the median. (Significant group differences: *a* > *b*)

Volumetric vs. Gravimetric

No significant differences were found between most prey groups when comparing percent volume (n = 64) versus percent weight (n = 64) using Mann-Whitney U-test. There was, however, one group with a significant difference. Percentage of plant matter was found to yield significant differences between the two analysis techniques (p = 0.0204). The median value for percentages of plant material based on volumetric analysis (1.613) was significantly higher than gravimetric analysis (0.243) (Figure 71). While there are no other significant differences, volumetric analyses did result in slightly higher dietary percentages for a number of other groups especially crabs when compared to gravimetric (Table 5 and Table 6).

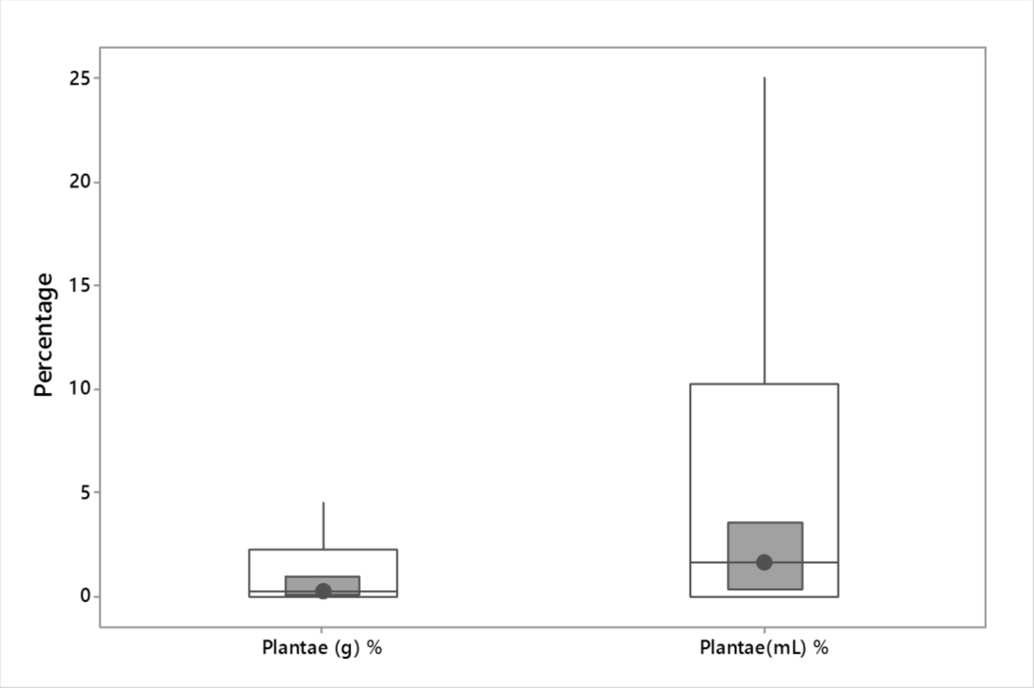

Figure 71. Boxplot depicting median values for gravimetric (0.243) and volumetric (1.613) for Plantae percentage in terrapin diet. Significant difference between median values (Mann-Whitney U-test; p = 0.0204). The white box represents the interquartile range, colored box is 95% confidence interval, horizontal line and dot are the median, and whiskers are the data range.

DISCUSSION

Effects of Habitat on Terrapin Distribution

Saltmarsh habitats throughout this study were found to have similar vegetation structures. Marsh vegetation tended to be less than a meter tall (≤60 cm), and composed of three common species. The dominant plant species encountered over the course of this study was smooth cordgrass (*Spartina alterniflora*). It was present in over half of the prey quadrats including both random survey and capture locations. Two less dominant but frequently encountered plants included *Batis maritima* and *Salicornia* spp. Terrapins were found significantly more often in areas of the marsh with low plant species richness (one or two species) compared to random locations. Overall percent vegetation cover within a quadrat was significantly higher at random locations than at points of capture. Vegetation was also significantly taller at random locations. These results suggest terrapins prefer areas without an extremely complex plant structure. Dense vegetation likely impedes efficient locomotion by terrapins. However, it is also possible that terrapins utilize areas with vegetation coverage similar to those detected within random quadrats, but may have gone undetected in such areas. Observers could have difficulty locating terrapins in areas of dense or tall vegetation.

No significant difference in *S. alterniflora* density was detected between capture and random locations. However, the other common species showed differences. Not finding differences in coverage of *S. alterniflora* gives credence to its commonality across Texas saltmarshes. Coverage of both *B. maritima* and *Salicornia* were significantly higher at random locations. These species are usually found at slightly higher marsh elevations than smooth cordgrass. These results may indicate infrequent usage of areas with high coverage of these species by terrapins. The random sampling method likely resulted in collection of data in some quadrats located at higher elevations where terrapin are infrequently observed.

Significant differences in seasonal vegetation density preference or any other habitat metrics were not detected between male and female terrapins. However, Clarkson (2012) found that male terrapins on South Deer Island occurred more frequently in less dense vegetation during March but in denser vegetation during August. In contrast, South Deer Island females occurred in denser vegetation during February, May, and August in contrast to the months of March and April (Clarkson 2012). Those findings differ from the results of this study where no sexual differences in use of vegetation density were detected. This study did, however, document overall seasonal changes in habitat use by terrapin.

During winter and spring, terrapins were more often captured in areas containing higher coverage of *S. alterniflora*. While in the summer and fall, terrapins were captured in areas consisting of higher density *B. maritima*. These seasonal habitat differences may be attributable in part to differing tidal amplitudes observed during each season. Terrapins in fall were also caught in areas of higher *Salicornia* cover. Tidal waters more often inundate areas containing *Batis* and *Salicornia* at high tides in summer and fall due to prevailing south winds. Diamond-backed Terrapin are known to follow tides as they rise into the marsh (Tucker 1995). It is also possible thermoregulation is a factor in habitat preference. Temperature results from this study indicate that ground level air temperatures of *S. alterniflora* dominated quadrats were significantly cooler than those of *B. maritima* and *Salicornia*. Therefore, it is unlikely that terrapin are using smooth cordgrass for warmth in winter. Past studies indicate that differences in plant canopy structure can affect microclimate resulting in lower maximum soil temperature and lower daily temperature amplitudes (Teasdale and Mohler 1993). The general structure of *S. alterniflora*, which is usually taller and denser than *Batis* and *Salicornia*, could result in more stable temperatures and less variation in temperature over short and long time periods. Whereas, the shorter, more open canopy structure of both *Batis* and *Salicornia* allows for more sunlight to reach the marsh surface and likely provides less insulation allowing for greater temperature swings. According to Akins et al. (2014), terrapins can experience drastic temperature changes depending on season and time of day. In North Carolina saltmarshes, terrapins experiences daily temperature variations of 7 °C in summer and 9 °C in winter (Williard and Harden 2011). Cordgrass structure also may make it more suitable for predator avoidance for the same reasons. Thus, *S. alterniflora* likely makes for good burrowing habitat during cold weather brumation.

Significant differences in habitat structure between marshes were detected based on data from capture location solely. These comparisons were made between capture locations at the three West Bay sites (North Deer, South Deer, Sportsman, and Greens Lake) and Texas Point. The only significant difference in vegetation height detected was between North Deer and Sportsman Road. The difference in vegetation height between North Deer and Sportsman Road may be due to different species composition between the two marshes. North Deer's taller vegetation when compared to Sportsman Road could be due to the presence of larger expanses of the taller *S. alterniflora* or less *B. maritima* or *Salicornia*. The amount of *Batis* cover was however low at both North Deer and Sportsman Road. The Sportsman Road and Texas Point marshes had a lower number of plant species present in quadrats than those of South Deer Island. The number of species was also significantly lower at Sportsman Road when compared to North Deer. Based on these results, South Deer Island's wetlands have more complex habitat than both Sportsman Road and Texas Point, and North Deer exhibited higher complexity than Sportsman. These differences in habitat complexity could potentially affect types and numbers of prey species (Tews et al. 2004).

West Bay marshes all had similar vegetation coverage, and all but Greens Lake were significantly greater than Texas Point. However, this may simply be a product of bias due to the locations where most of the Texas Point data were collected. The Texas Point captures were few in number and made in areas of little vegetation. In contrast all the West Bay sites showed similar vegetation coverage due to proximity of all the sites. However, there were differences in species coverage in West Bay. Coverage of *Batis* at South Deer was higher than Texas Point, North Deer Island, and Sportsman Road.

While South Deer had no significant height differences compared to other marsh sites, the island's higher coverage of *B. maritima* contributes to a somewhat lower vegetation height. Marshes at Texas Point had higher composition of *S. patens* than did all other sites. In fact, terrapin were never captured in association with saltmeadow cordgrass in West Bay. This species occurs infrequently at the West Bay sites (personal observation). The presence of saltmeadow cordgrass at Texas Point suggests that the area has slightly higher elevations and/or lower salinities based on the environmental preferences of this species (Bertness 1991).

Effects of Prey Availability on Terrapin Distribution

Terrapin capture locations and random locations showed similar numbers of *L. irrorata* and *C. pliculosa* suggesting uniform distribution and availability of these snails found within quadrats throughout the studied marshes. On the other hand, higher numbers of *Uca* burrows were observed at randomly surveyed quadrats. Fecal results demonstrate that terrapin take fiddler crabs in large numbers, specifically in summer. The fact that random sites had higher burrow counts than capture locations, with no other detected differences, suggests prey availability is not a driving factor in terrapin distribution within Texas saltmarshes. These findings are similar to previous terrapin prey studies (Tucker et al. 1995, Whitelaw and Zajac 2002).

As previously stated there were no significant differences in prey availability metrics between male and female capture locations. Marsh periwinkle snail numbers were highest in fall and winter, and lowest in summer. Fall numbers were also significantly higher than spring counts. Tidal amplitude could explain the high fall numbers, as the tides are still high which drives the snails further up plant stems making for more obvious targets to count. The same effect should also be seen in summer which makes the low *Littorina* numbers during that time period difficult to explain. However, terrapins may be showing a preference for areas containing abundant fiddler crabs in summer rather than areas with high counts of periwinkle snails. Fecal samples support this claim that areas with *Uca* spp. being visited more often in summer months than areas containing high amounts of *L. irrorata*.

The only other observed seasonal prey differences were in numbers of fiddler crab burrows. Fiddler burrow counts were highest during the summer and winter seasons. I observed higher *Uca* spp. activity in the summer months, which is discussed in detail later. Two species of fiddler crab were collected during this time of high activity at South Deer Island, *Uca rapax* and *U. panacea*. This is supported by and explains the higher burrow numbers counted during this season. Summer months generally had higher tidal amplitudes than winter, and high tides make it difficult to detect burrows. The opposite tidal effect is likely responsible for the winter burrow numbers. Low winter tides expose the marsh surface making counts easier to perform. Therefore, the higher counts in the summer were likely due to higher numbers of living fiddler crabs while the high numbers in winter months were likely due to the higher probability of detection of older but still existent burrows from the earlier summer and fall periods. Data from a Louisiana study showed increased *Uca spinicarpa* burrow densities in the summer within lower reaches of the marsh (Mouton, Jr. and Felder 1996). That study also noted high burrow densities in the early fall (September) for *U. longisignalis* (Mouton, Jr. and Felder 1996).

As with other analyses, individual marshes displayed differences in prey availability. Surprisingly, many of these differences were found between West Bay marsh sites. The only detected difference for Texas Point was in presence of horn snails, as none were encountered in Texas Point quadrats. For every species exhibiting a significant difference in numbers, South Deer Island quadrats consistently displayed higher numbers in comparison to other locations. As previously suggested, the more complex habitat found at South Deer likely explains the abundance of different prey items found there (Tews et al. 2004). The numbers and types of available prey at Sportsman Road marsh were similar to South Deer with only one significant difference between the two. Both South and North Deer Islands exhibited higher numbers of *Littorina* snails than the nearby, barrier island and mainland sites at Sportsman and Greens Lake.

Greens Lake stands out from the other sites, specifically the other West Bay marshes, as having basically no fiddler burrows counted within capture quadrats. Greens Lake also had significantly lower numbers of periwinkle snails compared to the Deer Islands. Large percentages of capture locations at Greens Lake contained *C. pliculosa*. The difference in prey availability at Greens Lake likely explains why the two fecal samples from Greens were almost exclusively composed of horn snails.

These results lead to somewhat contradictory conclusions. Differences in multiple prey metrics were not detected over large geographic distances (Texas Point to West Bay), but were observed between areas that are much closer together (multiple differences in West Bay). This may simply reflect an artifact of sample size. Increased effort at Texas Point may be able to identify differences in prey abundance at this site in comparison to the West Bay Sites.

Terrapin Diet Analyses

Terrapins on the Upper Texas Coast consumed multiple prey species. Contrary to previous studies (Tucker et al. 1995), male Texas Diamond-backed Terrapin displayed higher diversity in their diets than females. However, the diversity of prey items was found to be lower in Texas than in the South Carolina study. The two most important groups of prey items in the diet of Texas Diamond-backed Terrapin on the Upper Coast found in this study are Decapoda and Gastropoda. Prey items from these groups were found frequently in fecal samples, and also made up large percentages of fecal samples by weight and volume. Within these groups, three species and a genus occurred frequently in samples, but with rates of occurrence varying between sexes. The most frequently encountered snail species found in fecal samples were *Littorina irrorata* and *Cerithidea pliculosa*.

Both sexes consumed *C. pliculosa* in nearly equal frequencies, but female samples contained *L. irrorata* much more frequently than did male samples. Tucker et al. (1995) found large amounts of *Littorina* (76-79% of dietary volume) in both male and female fecal samples. However, remains of marsh periwinkle snails were recovered from only one male sample in this study which consisted of a single operculum with no shell pieces included. In contrast, an individual female terrapin was found to have consumed over 200 *L. irrorata* in this study. Furthermore, the remains of twice that number of horn snails were found in a single female fecal sample. However, female diets generally consisted of equal parts horn snails and marsh periwinkles. An infrequently encountered snail (*Melampus bidentatus*) in this study was an important prey item taken by small (male) terrapin in a Georgia study (Spivey 1998). This is another indicator of dietary change over geographic range.

The plicate horn snail (*C. pliculosa*) appears to be an important dietary component for terrapins in West Bay. Plicate horn snails made up similar percentages of the diets of both male and female terrapins. Horn snails are found along the Western Gulf Coast (Rothschild 2004), and can be locally abundant (personal observation). However, this is the first study where consumption of this species by *M. terrapin* was recorded. Horn snails are usually found on the sediment surface or just below the surface, and are rarely found on vegetation (Rothschild 2004). The shells of *C. pliculosa* are much smaller in diameter than those of *L. irrorata*, and would offer lesser resistance to both the large heads of females or to the much smaller male terrapins. Periwinkle snails may be too large for male terrapin to efficiently consume, and with the abundance of other prey items (horn snails and Decapods) male terrapin may be ignoring the larger periwinkles in Texas marshes.

Overall, Bivalves were found in few samples, and only contributed a miniscule percentage by weight and volume to the overall diet of terrapin. Therefore, no statistical analyses were performed on individual categories of Bivalves. However, Bivalves occurred more frequently in female versus male samples. This may indicate that female Texas Diamond-backed Terrapin forage more often in deeper, open water than males do as documented in previous studies (Roosenburg et al. 1999). Despite finding small amounts of clam remains, all four fecal samples containing *M. lateralis* were collected from terrapins captured at Sportsman Road. This may imply greater abundance of dwarf surf clams at Sportsman Road. Dwarf surf clams have not been collected when salinity was below 20 ppt along the Texas coast (Mannino and Montagna 1997). Therefore, the species is likely present throughout Galveston Bay (≥ 30 ppt., personal observation). Previous terrapin diet studies have shown high bivalve consumption. Terrapin in northern Florida consumed large amounts of *M. lateralis* (Butler et al. 2012). Mussels have been found to be abundant in the diets of terrapins, especially females, from the Coastal Bend area of the Texas Coast, which is located south of the current study sites (Koza 2006). However, the results of this study do not indicate Bivalves are a major contributor to terrapin diet along the upper Texas Coast.

Male Texas Diamond-backed Terrapin consumed significantly more Decapod crustaceans both by percent weight and volume than did females. The sexes had nearly the same frequencies of occurrence in consumption of fiddler crabs (41% males, 40% females), but males were shown to consume other species in higher frequencies than females including taxa that did not appear in the female diet. These taxa included purple marsh crabs, a known herbivore of *S. alterniflora*.

In a captive feeding experiment, male terrapins were shown to eat whole small green crabs (*Carcinus maenas*), crop hind limbs from medium crabs, and to completely avoid large crabs (Davenport et al. 1992a). Tucker et al. (1995) found the presence of *C. sapidus* to be strongly represented only in diets of medium and large terrapins (head width >20 mm), indicating that crab remains were found more frequently in female versus male terrapins. In this study *C. sapidus* remains occurred more frequently in male samples than in female samples (31% vs. 14%), and male terrapins were found to have significantly higher percentages of blue crab remains in fecal samples than what was found in female samples. Also, the *C. sapidus* remains found in fecal samples appeared to be whole small crabs (limbs, chelipeds, carapace, etc). The hind limbs of larger crabs were found in some samples mixed with the remains of smaller crabs indicating instances of limb cropping from larger crabs. This is similar to the blue crab remains found in female samples by Tucker et al. (1995), which were primarily cropped limbs. Spivey (1998) also recorded the presence of cropped limbs in diets of medium and large sized terrapins.

A potential reason that male terrapin in West Bay consume much higher percentages of blue crabs than females is likely the presence of juvenile *C. sapidus* in areas where males more frequently visit. This may indicate that male terrapins on the upper Texas coast are better at pursing smaller blue crab in Texas marshes than females. Based on this study it appears that females primarily consume species of snail on the upper coast of Texas, blue crabs may be a resource that females fail to utilize as much as males do. The percentage of blue crab remains found in fecal samples was higher in fall than in other seasons. This likely reflects seasonal patterns of the availability of prey. Thomas et al. (1990) found that the highest abundances and smallest specimens of blue crabs occurred during late summer and fall in West Bay and adjacent saltmarshes. Their data supports observations collected during the current study including individual fecal samples consisting of greater than 90% blue crab in fall, indicating a diet shift to this newly abundant resource. During the current study, another seasonal shift in diet was observed in fiddler crab consumption.

The amount of fiddler crab remains found in fecal samples during the summer was extremely high. In many instances, individual samples consisted almost entirely of *Uca* spp. remains and represented >90% of the sample by weight. The elevated percent *Uca* spp. remains in summer fecal samples was highly significant when compared to fall and spring. Significantly higher numbers of fiddler burrows in prey quadrats were observed during the summer months. The higher number of burrows reflects and is consistent with increased fiddler crab activity observed in the field. Therefore, the increased consumption of fiddler crab in the diet is likely due to increased seasonal availability of this prey species.

During daytime surveys in July and August, large numbers of fiddler crabs were commonly seen moving throughout the marsh, and hundreds were captured as bycatch in pit fall traps during a concurrent study (personal observation). Many of the encountered crabs, both found walking through the marsh and found in traps, appeared to be sponge crabs (pregnant females). Fiddler crab females release their eggs at the water's edge, usually at night, with the falling tide (Salmon and Hyatt 1983). In addition to the previous behavior, Salmon and Hyatt (1983) noted herding behavior, in an Atlantic species (*Uca pugilator*), to feed in the intertidal zone at low tide both diurnally and nocturnally. These hordes of *Uca* also go to the water's edge at low tide to wet their gills (Rothschild 2004).

There are seven species of fiddler crabs found along the Texas Gulf Coast (Barnwell and Thurman II 1984, Rothschild 2004). However, only five species are likely to be found within the range of *M. t. littoralis*, as two of the species are found farther south than terrapin's range (Rothschild 2004). As mentioned previously, individuals collected at South Deer Island were identified as two of the five species, *U. panaceae* and *U. rapax*, found along the Upper Texas Coast. The Gulf sand fiddler, *Uca panaceae*, is the Western Gulf's ecological equivalent to the Atlantic species *U. pugilator* (Rothschild 2004), and is likely to have similar behaviors. The above mentioned fiddler crab behaviors, herding near water's edge and releasing eggs in water, would increase the probability of crabs crossing in the path of foraging terrapins. Teal (1958) also noted higher activity in crabs during flood tides. Flood tides would provide another opportunity for terrapins to capture marsh dwelling crabs as they begin to move higher into the marsh. The increased tendency for nocturnal activity by these crabs combined with the abundance of their remains in terrapin diet may indicate that terrapin also forage at night. However, Clarkson (2012) observed decreased nocturnal movement by terrapin on South Deer Island.

The bones and scales of ray-finned fishes (Actinopterygii) were found in 14% of the fecal samples. These remains were found more frequently in male samples (17%) than in female samples (11%). Both cycloid and ctenoid scales were found. Fishes commonly observed in marsh habitats include: killifishes (Fundulidae), sheepshead minnows (*Cyprinodon variegatus*), silversides (Atherinopsidae), gobies (Gobiidae) and drums (Sciaenidae) (Rozas et al. 2007). Only members of the drum family have ctenoid scales while the other groups have cycloid scales. The bones collected included: vertebrae, ribs, pharyngeal teeth, and other bones that make up the skull. It is unlikely that terrapins are very proficient at capturing free swimming fish, but the number of bones collected from terrapin caught in the same area, on the same day, seems to indicate consumption of multiple fish by each terrapin. However, Middaugh (1981) documented predation of spawning Atlantic silverside (*Menidia menida*) by terrapin but didn't not observe the method of capture. Petrochic (2009) also found remains of fish in fecal samples from Long Island, NY. Most likely the fish remains observed in fecal samples originated from fish stranded on the marsh surface or remaining in isolated pools during the receding tide. If alive these fish would be more easily cornered and captured by terrapin. Terrapin in aquaria have been observed feeding using this mode of capture (personal observation). It has been suggested that terrapin will occasionally eat carrion (Ehret and Werner 2004). Terrapins have also been documented to be attracted to fish entrails and dead fish (e.g. menhaden used as bait in crab pots), and congregate near fish cleaning stations (Cochran 1978, personal observation).

It is doubtful that terrapins were intentionally consuming plant matter even though plant material was frequently observed in fecal samples. Males ingested plant matter more frequently and in higher percentages than did females. Small bits of stems, leaves, roots, and sometimes reproductive structures showed up in samples, and were likely consumed incidentally while terrapins captured desired prey items. Reproductive structures that were ingested included flower parts from *S. alterniflora* and seeds from *Salicornia* spp. Most of the *Salicornia* seeds appeared to pass through the terrapins entirely intact without evidence of digestion. A recent study suggested that terrapins could be seed dispersers for eelgrass (*Zostera marina*) in the Lower Chesapeake Bay (Tulipani and Lipcius 2014). So it is possible that terrapins can transport seeds to new areas therefore facilitating the spread of various plant species. Tulipani and Lipcius (2014) noted that seeds were more likely to be found in samples from males and smaller females than in mature females. These results are consistent with the results of this study where males more frequently possessed plant matter in their feces.

Most of the plant parts and seeds showed up in fecal samples in the fall season corresponding to when the parts and structures were likely being deposited on the marsh surface. Fall and summer fecal samples contained significantly higher percentages of plant material compared to spring. This increase in ingestion of more plant material corresponds with peak production and deposition of plant material on the marsh surface. The higher frequency and percentages of plant matter in male samples compared to female samples also suggests that males feed in terrestrial habits more often than females. This intake of plant material may also be related to other prey items consumed. For example, female terrapins' larger gape size and greater predation on Gastropods may reduce incidental intake of plant material, while the smaller males' greater intake of Decapods increases plant material. The exact mechanism of these interactions between different prey items and plant ingestion is, however, currently unknown. More research is needed to determine the cause of these size and/or sex specific patterns in plant ingestion.

While algae only showed up in three samples, each of those samples consisted almost entirely of algae. Unlike ingestion of vascular plants, the three samples containing algae suggest that the intake was not accidental. All three samples were from female terrapin caught at South Deer Island. Due to the low sample numbers containing algae, no statistical analysis was conducted. However, there appears to be seasonal consumption for algae. Two samples were from spring and the third from summer. South Deer had abundant algae present during these seasons in the shallow bay waters surrounding the island and within the tidal creeks (personal observation). This may be another example of utilizing a seasonally abundant food item. This may also be an indicator of females feeding in open waters more often than males.

Dietary Analysis Techniques

Statistical comparisons between volumetric and gravimetric dietary techniques yielded only one significant result. Percentage of vascular plant material was statistically different between the techniques where plant matter contributed a greater percentage to terrapin diet when using volumetric analysis. Also, while not significantly different, other prey taxa were higher using the volumetric technique, specifically crabs. The discrepancy is likely due to low density of these materials compared to their volume.

Future Work

Based on the findings of this study further research is needed to further evaluate the relation and interactions of tidal regime, habitat, prey availability, and trophic interactions between terrapin and prey items. Expanding on this study by expanding the effort to collect more fecal samples would be valuable. Larger samples sizes at the sites visited in this study, as well as expanding to other Texas marshes, would greatly benefit understanding on this unique species and how their food habits change throughout their range. With the increased sample size, additional information could be gleaned such as trophic level interactions. Supplementary analysis using stable isotopes and DNA analysis of food items would also increase our ability to accurately describe the trophic interactions of this species. Stable isotope analysis normally uses carbon and nitrogen ratios to determine food web interactions (Layman et al.2007). New genetic methods could be used to potentially identify prey items that go undetected using more traditional diet analyses (Waits and Paetkau 2005). Also, fecal samples may be useful as a noninvasive technique for collecting individual terrapin DNA (Bellemain et al. 2005) for demographic analysis and population size estimation, potentially expanding on previous Texas genetics work (Glenos 2013).

In concurrence with the increased fecal study, analysis of terrapin parasites should be conducted. Horn snails in Galveston Bay are noted for having trematode parasites (Rothschild 2004). This study demonstrated horn snails as important terrapin dietary items. The trematode worm (*Pleurogonius malaclemys*) parasite infects terrapins by using another snail species (mud snails, *Illyanassa obsoleta*) as a host, and can potentially be used to estimate terrapin abundance (Byers et al. 2011). Therefore, examining the effects, if any, of these parasites on terrapin and the role of terrapin as further hosts in the parasites lifecycle would be useful in further understanding the interactions of terrapins and their surrounding ecosystem.

Conducting a study to compare foraging costs and caloric return associated with terrapins feeding on horn snails, marsh periwinkles, fiddler crabs, and blue crabs would also provide information on the effects of limitations of these species on terrapin health and possibly help explain any selection observed for a particular species. A study with crushing experiments for Texas prey items, similar to the Tucker et al. (1997) study on *Ilyanassa obsoleta*, could serve as basis of this research. Such a study could explain why male terrapins here seem to not utilize abundant *Littorina*. Also, large numbers of *C. pliculosa* (~400 individuals) have been taken by single female terrapins in this study, while half that number of *L. irrorata* was recovered from samples. The larger, thicker periwinkles likely provide more calories but will have higher energy costs associated with consuming them due to their shells.

In addition to examining aquatic prey items, a better effort at quantifying horn snail numbers is necessary. This study did not thoroughly record numbers of *C. pliculosa* in the marsh, but only noted its presence. When this study began, it was not known how important this snail species was to the diets of Texas Diamond-backed Terrapin on the Upper Coast. As previously mentioned the horn snail is not often on vegetation and spends much of its time on the sediment surface, making it difficult to notice (Rothschild 2004). Future examination of prey species should include a more thorough count of this less visible snail.

Terrapins spend a lot of time using their aquatic habitats. Therefore, an effort to quantify aquatic and associated benthic prey availability is needed. This component was missing during this study. Shallow benthic grabs could be used to assess the density and composition of macrobenthic organisms such as the clams, mussels, and worms which are common members of this community. In order to sample nekton in creeks and ponds, seine tows could be used. However, Rozas and Minello (1997) suggest using enclosure traps (throw traps or drop samplers) due to low, variable catch efficiency of seines. Larger sample numbers are required with these traps as they are often small, but they provide reliable data for nekton in shallow estuarine habits (Rosa and Minello 1997). Due to the seasonal nature of terrapin diet and of the nekton community, I would suggest a monthly or seasonal sampling schedule for both nekton and benthic organisms. Sampling should be performed in all aquatic habitats (tidal creeks, ponds, larger lagoons, and bay edges) used by terrapin.

Further investigation into the effects physical habitat plays on behavior of terrapin is also needed, specifically examining how plant structure affects the behavior of terrapin. This could be accomplished by placing temperature recording devices beneath the different plant communities within the marsh to monitor microclimate over the short and long term. Differences in plant structure have been shown to affect air and soil temperature (Fliervoet and Werger 1984, Teasdale and Mohler 1993). This data could then be compared with terrapin capture data.

CONCLUSIONS

Volumetric and gravimetric dietary analysis techniques used during this study were found to yield similar and equivalent results, and therefore either technique can be employed to test terrapin diets. Based on my analyses distinct dietary differences were detected between male and female Texas Diamond-backed Terrapins. Male *M. t. littoralis* displayed higher dietary diversity than females. This study also confirmed dietary differences in terrapins over space and time. Broader spatial differences in *M. terrapin* diet were exhibited when comparing this study with other studies, spanning from southern Texas to the Atlantic coast. Terrapins on the Upper Texas Coast consumed plicate horn snails, at high frequencies and in high numbers, which has not been noted in previous studies. These snails should be considered a major food source for terrapins found along the Northwestern Gulf of Mexico. Terrapin were shown to take advantage of seasonally abundant food resources, especially fiddler crabs. Supporting evidence for increased consumption of fiddler crab was obtained from prey quadrat surveys.

Prey quadrat data from this study provided additional evidence indicating that prey numbers alone are not the primary factor predicting *M. terrapin* distribution in saltmarshes. A multitude of factors, including both of physical habitat and available prey, influences the distribution of Diamond-backed Terrapin. Continued research on the trophic and habitat interactions of terrapin along the entire range of terrapin is needed to fully understand the dietary and habitat requirements of this unique, estuarine dependent species. These data are critically needed for the successful management and conservation of this species.

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