Prey Availability and Diet Analysis of Texas Diamond-Backed Terrapin (*Malaclemys terrapin littoralis*)

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Abstract. – The diamond-backed terrapin (*Malaclemys terrapin*) is the only North American turtle species specialized for living in brackish and saltmarsh environments. The Texas subspecies (*Malaclemys terrapin littoralis*) is found along most of the Texas Gulf Coast. Previous studies on the prey and diets of Atlantic and Florida subspecies found that the diet of terrapins primarily consisted of crustacean and molluscan species, although differences in dietary composition were observed between the sexes. Furthermore, prey availability had little effect on terrapin distribution within a marsh. We examined the prey availability and diet of Texas diamond-backed terrapins. Comparisons of random locations to terrapin capture locations indicated that prey availability is not a limiting factor affecting terrapin distribution in Texas marshes, but multiple significant seasonal and locational differences in prey were detected at capture sites. Fecal analysis, using multiple metrics, indicated Gastropoda and Decapoda as major components of the diets of Texas terrapins. Plicate horn snails (*Cerithidea pliculosa*) and fiddler crabs (*Uca* spp.) were important prey items for all terrapins. There were significant differences between the diets of male and female terrapins, among seasonal diets, and among diets of terrapins captured at different marsh sites. Our prey availability findings support previous studies, but results from fecal analysis indicate a slightly different diet for terrapins than previously reported in other studies. The combined results extend the basic knowledge and understanding of terrapin diets, which will be useful for ongoing conservation and management of *M. terrapin*, especially the Texas subspecies.

Key Words. – Reptilia; Testudines; Emydidae; *Malaclemys terrapin*; diamond-backed terrapin; ecology; prey availability; diet; fecal analysis; Texas

Diamond-backed terrapins (*Malaclemys terrapin*) occur along the Atlantic and Gulf coasts of North America from Massachusetts to Texas. There are 7 recognized subspecies across their range, with Texas diamond-backed terrapins (*Malaclemys terrapin littoralis*) inhabiting most of the Texas coast at the western range limit of the species (Dixon 2013). Throughout their range, terrapins occupy a narrow band of salt- and brackish-water habitats (Palmer and Cordes 1988). Terrapins are the only species of turtle specialized to live in saltmarsh and estuarine habitats in the temperate zone (Ernst and Lovich 2009). Terrapins exhibit sexual dimorphism, with females being larger and having larger, wider heads than do males (Tucker et al. 1995).

Previous prey availability studies indicate that available food resources are not likely to be a limiting factor in terrapin distribution (Tucker et al. 1995; Whitelaw and Zajac 2002). These studies documented high numbers of suitable terrapin prey items at various locations throughout the marsh, regardless of terrapin captures. They suggested, however, that food accessibility may be the most important factor limiting the distribution of terrapins (Tucker et al. 1995), but terrapins may be unable to acquire prey owing to some factor (e.g., tide level) that limits access to them.

Terrapin diet studies show that diets consist primarily of Crustacea and Mollusca, with gastropods such as *Littorina irrorata* and various crab species (*Sesarma* spp., *Uca* spp., *Callinectes sapidus*) being common (Davenport et al. 1992; Tucker et al. 1995; Butler et al. 2012; Denton et al. 2016). Studies have also recorded small clam species in terrapin dietary samples (Cagle 1952; Tucker et al. 1995; Roosenburg et al. 1999; Denton et al. 2016). Tucker et al. (1995) found that sexual size dimorphism allowed females to consume larger and different prey items than males, specifically larger marsh periwinkle snails (*L. irrorata*).

In contrast to the Atlantic Coast and Florida subspecies, there is a paucity of data on the dietary composition and prey selectivity of the Texas diamond-backed terrapin. Koza (2006) found that the scorched mussel (*Brachidontes exustus*) was the primary prey item observed in both male and female fecal samples in south Texas but also observed dietary differences between the sexes there at the extreme western range of the species and subspecies in south Texas. We examined prey available to,

Table 1. Breakdown of prey quadrats and fecal samples collected by marsh location. Bay system and global positioning system (GPS) coordinates given for marsh locations. Terrapin capture location quadrats per marsh given in parentheses, and dashes (—) indicate that no fecal samples were taken from that location.

Bay system	Site name	GPS coordinates	Prey quadrats, *n*	Fecal samples, *n*
Sabine Lake	Texas Point NWR	29.70568°N, 93.86867°W	11 (10)	—
East Galveston Bay	Bolivar Peninsula	29.51780°N, 94.54293°W	2	—
West Galveston Bay	South Deer Island	29.27209°N, 94.91174°W	144 (107)	35
	North Deer Island	29.28500°N, 94.92470°W	32 (22)	8
	Sportsman Road	29.25774°N, 94.90821°W	65 (49)	18
	Greens Lake	29.27432°N, 94.98524°W	29 (17)	2
	Sweetwater Lake	29.26768°N, 94.89235°W	6	—
San Bernard	San Bernard NWR	28.85145°N, 95.49290°W	2	—
Matagorda Bay	Coon Island Bay	28.66136°N, 96.20803°W	2	1
Total			293 (205)	64

and the diet of, *M. t. littoralis* along the upper Texas coast to determine sexual, spatial, and temporal differences.

METHODS

Study Area. — The main study area was West Bay, located within the Galveston Bay estuary, Texas, with secondary sites along the Texas coast (Table 1). The sites found in West Bay included North Deer Island, South Deer Island, Sportsman Road, Sweetwater Lake, and Greens Lake. Limited data were collected from secondary sites including Matagorda Bay, San Bernard National Wildlife Refuge (SBNWR), Bolivar Peninsula, and Texas Point National Wildlife Refuge (TPNWR). All locations were saltmarshes dominated by smooth cordgrass (*Spartina alterniflora*) consisting of tidal creeks, ponds, and larger, open-water areas. The other common plant species found in these marshes are saltwort (*Batis maritima*) and pickleweed (*Salicornia virginica*). However, Sweetwater Lake marsh had a slightly higher elevation than the others and was dominated by saltgrass (*Distichlis spicata*), with dense stands of black rush (*Juncus roemerianus*) interspersed. Additionally, we often found stands of salt-meadow cordgrass (*Spartina patens*) at TPNWR.

Data Collection. — We captured terrapins by hand during random searches at each site. During each sampling event at each site, starting points and compass direction for transect lines were randomly selected. Terrapins were measured and sexed using dimorphic characteristics (overall size, head width, tail length, and girth). Prey availability and density were assessed during each terrapin capture using a 1-m² quadrat around each capture location, and terrapins were collected from January 2013 through June 2014. Within each quadrat, we counted individual *L. irrorata* on vegetation and on the marsh surface and the number of fiddler crab (*Uca* spp.) burrows, and we noted the presence of plicate horn snails (*Cerithidea pliculosa*). Warren (1990) found that under appropriate conditions, the number of open burrows of fiddler crabs can be used to estimate crab abundance. Prey quadrat data were not collected when terrapins were found in aquatic settings (e.g., tidal creeks). Additionally, we conducted prey

surveys at random sites along the transect line. A timer was set for 5–15 min while walking transects to dictate when a random prey quadrat would be taken.

We collected fecal samples from April 2013 until May 2014, and only active terrapins were collected from capture sites in order to retrieve fecal samples. Therefore, terrapins were not collected during the months of December or January when terrapins are largely inactive (Williard and Harden 2011; B.J.A., *pers obs.*, December 2013). We chose fecal collection 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. Terrapins were maintained individually in plastic tubs containing 2–3 cm of fresh water for up to 48 hrs in our laboratory, sufficient time for defecation to occur (Tucker et al. 1995). We acquired most samples after 48 hrs, but some terrapins were held for only 24 hrs. Opportunistic fecal samples were also collected in the field when a terrapin provided one. Following sample collection, we released the terrapins at their original capture locations. Fecal samples were recovered from the containers by carefully pouring the water from the tub through a 0.5-mm sieve. We then recovered the samples and preserved them in vials containing 70% ethanol. The samples were thoroughly rinsed using a 0.5-mm sieve to wash away any preservative before drying. We used a desiccating oven (Model 10GC; Quincy Lab, Inc.) to dry samples at 100°C for 1 hr and then used a balance (Model E04130; Ohaus Explorer) to weigh the samples to the nearest 0.1 g. The drying process was repeated until sample weight became stable, at which time we recorded total sample weight. We separated each sample into component parts, identified the remains to the lowest possible taxon using a dissecting microscope, and then weighed each separate taxon.

Data Analysis. — We calculated frequency of occurrence (%F) as the percentage of fecal samples containing each prey taxon (Butler et al. 2012). Percent

Table 2. Number of prey quadrats surveyed and fecal samples collected by season with beginning date of season given. Terrapin capture location quadrats per season given in parentheses.

Season	Beginning date	Prey quadrats, n	Fecal samples, n
Spring	20 Mar	53 (38)	9
Summer	21 Jun	71 (52)	25
Fall	22 Sep	81 (70)	26
Winter	21 Dec	88 (55)	4
Total		293 (215)	64

weight (%W) of fecal components was calculated for each individual sample by dividing the weight of the prey item found in the sample by the total sample weight. We also calculated index of relative importance (IRI) for each prey taxon for male diet, female diet, and total diet using the following formula:

$$IRI = 100W_iF_i / \sum(W_iF_i)$$

where W_i is mean percent weight and F_i is percent frequency of occurrence (Bjorndal et al. 1997). Calculated IRI values add up to 100 and provide a more accurate measure of overall dietary importance of prey items than either %F or %W alone (Bjorndal et al. 1997).

We compared the median total weight of the fecal collection methods (48 hrs, 24 hrs, and field samples) using a Kruskal-Wallis 1-way analysis of variance (K-W) before proceeding to the other dietary analyses. We used K-W to test differences in median levels of prey availability between random and capture sites, between male and female capture locations, among seasons, and among marsh sites ($\alpha = 0.05$). When a significant difference was found between categories with more than 2 levels using K-W testing, Dunn's Multiple Comparison test was used post hoc to test for differences between categories (Zar 2009). Reported K-W values are those that were adjusted for ties when they occurred. Analyses were performed using Minitab 17 and Microsoft Excel software packages.

RESULTS

Prey Availability. — We collected data from a total of 293 prey quadrats, including 78 random locations and 215 terrapin capture locations. The data were collected from locations along the Texas coast from West Bay, Bolivar Peninsula, SBNWR, TPNWR, and Matagorda Bay, with West Bay sites making up the majority of quadrats (Table 1).

We commonly encountered *Uca* burrows or crabs (or both) and the snails *L. irrorata* and *C. pliculosa* in sampled quadrats. Occasionally, *C. sapidus* and *Melampus bidentatus* were encountered. Insects, spiders, and penaeid shrimp were also seen in quadrats. We did see the crab *Sesarma reticulatum* in the marsh, but never encountered

it in quadrats. Prey quadrat data were taken in all seasons (Table 2). Although aquatic prey quadrat data were not collected, small fish were often seen swimming in marsh ponds and tidal creeks.

Random locations had significantly more fiddler crab burrows than did capture locations ($H = 5.57$, $p = 0.018$). Significant differences were not detected in numbers of *L. irrorata* ($H = 0.32$, $p = 0.57$) or *C. pliculosa* ($H = 3.03$, $p = 0.082$) between random and capture locations. There were no significant differences in prey composition between quadrats where male terrapins were captured and quadrats where female terrapins were captured (all $p > 0.05$).

We detected multiple seasonal differences in prey availability. Number of fiddler crab burrows was significantly higher in summer and winter than in spring and fall ($H = 20.99$, $p < 0.001$). In contrast, *L. irrorata* numbers were significantly higher ($H = 18.58$, $p < 0.001$) in fall and winter than in summer and significantly higher in fall than spring.

Differences between marsh sites were analyzed using a reduced sample size of capture locations ($n = 205$; Table 1). We used data collected from most of the West Bay marshes and TPNWR to detect differences between marshes, but excluded Sweetwater Lake, Bolivar Peninsula, SBNWR, and Matagorda Bay from analyses because of low sample numbers (each $n = 2$). Significant differences were detected in the number of fiddler crab burrows among sites ($H = 15.48$, $p = 0.004$). South Deer, North Deer, and Sportsman Road all exhibited significantly higher numbers of burrows compared with Greens Lake. We found the numbers of marsh periwinkle snails to be significantly different among sites as well ($H = 24.12$, $p < 0.001$). Both North and South Deer had significantly higher counts of *L. irrorata* than did Sportsman Road and Greens Lake marshes. The occurrence of *C. pliculosa* was significantly different among sites ($H = 5.95$, $p = 0.003$). Horn snails were encountered in significantly more prey quadrats at South Deer, Sportsman Road, and Greens Lake compared with North Deer and were present in significantly more Sportsman Road quadrats compared with TPNWR.

Fecal Collection. — We collected 64 fecal samples from terrapins over the course of the study, with 35 from females and 29 from males. Straight plastron length ranged from 90 to 122 mm (mean, 111.5 ± 7 mm SD) for males and from 126 to 187 mm (mean, 169.2 ± 13.2 mm SD) for females. Samples from terrapins that were held for approximately 48 hrs constituted the majority of the collection ($n = 45$). Fewer samples came from terrapins that were only held for 24 hrs ($n = 8$), while the remainder ($n = 11$) were collected opportunistically in the field. There were no significant differences detected in total sample weights among fecal collection methods ($H = 4.91$, $p = 0.086$). Therefore, we were able to include all sampling methods in analyses.

Table 3. Percent frequency of occurrence of prey items found in Texas diamond-backed terrapin (*Malaclemys terrapin littoralis*) fecal samples for total, male, and female samples. Dashes (—) indicate that the item class was not found in samples.

Prey item	% Frequency of occurrence		
	Total ($n = 64$)	Male ($n = 29$)	Female ($n = 35$)
Class Gastropoda	70.3	62.1	77.1
Plicate horn snail (*Cerithidea pliculosa*)	59.4	58.6	60.0
Marsh periwinkle (*Littorina irrorata*)	25.0	3.4	42.9
Eastern melampus (*Melampus bidentatus*)	7.8	10.3	5.7
Class Bivalvia	9.4	6.9	11.4
Dwarf surf clam (*Mulina lateralis*)	6.3	3.4	8.6
Green jackknife clam (*Solen viridis*)	1.6	—	2.9
Ark clam A (Arcidae)	1.6	—	2.9
Ark clam B (Arcidae)	1.6	3.4	—
Subphylum Crustacea			
Order Decapoda	67.2	79.3	57.1
Fiddler crabs (*Uca* spp.)	40.6	41.4	40.0
Blue crab (*Callinectes sapidus*)	21.9	31.0	14.3
Purple marsh crab (*Sesarma reticulatum*)	3.1	6.9	—
Unidentifiable crab (unidentifiable pieces)	15.6	13.8	17.1
Unidentifiable shrimp (Penaeidae)	1.6	3.4	—
Order Sessilia			
Barnacle (*Balanus* sp.)	1.6	—	2.9
Class Insecta (insects)	18.8	13.8	22.9
Order Araneae (spiders)	7.8	10.3	5.7
Class Actinopterygii (ray-finned fishes)	14.1	17.2	11.4
Plantae	78.1	82.8	71.4
Algae (Monera, Protista, or both)	4.7	—	8.6

We found a total of 22 different items or categories, including biotic and abiotic items, in terrapin fecal samples, 7 of which were found in only 1 sample each. We found that most terrapins consumed more than one biotic item (mode, 3; range, 1–8). Prey items were found from the following animal groups: Gastropoda, Decapoda, Bivalvia, Insecta, Araneae, and Actinopterygii. Vascular plants and algae were also found in samples. Plant material consisted of the stems, leaves, and seeds of *S. alterniflora* and *Salicornia* spp. The majority of abiotic items encountered were pebbles, sand, and shell hash. Abiotic items or unidentifiable materials were not included in statistical analyses.

Frequency of Occurrence of Prey Items. — We found that the most frequently occurring prey items found in fecal samples of Texas diamond-backed terrapins were gastropods and decapods (Table 3). Overall, gastropods were more frequent in samples from females and decapods were more frequent in samples from males. Gastropods were found in 70% of all samples, including 62% of samples from males and 77% of samples from females. The most frequently encountered gastropod was the plicate horn snail (*C. pliculosa*) followed by marsh periwinkle snails (*L. irrorata*). We found little difference in the occurrence of *C. pliculosa* between males and females, but there was a large difference in occurrence of *L. irrorata* between the sexes, with females consuming *L. irrorata* much more frequently than did males. Decapod crustaceans occurred in 67% of all samples, including 79% of samples from males and 57% of samples from females. Fiddler crabs (*Uca* spp.) were the most commonly occurring decapod in samples, with occurrence being

similar for males and females. Blue crabs (*C. sapidus*) were found to be the second most frequently occurring decapod in terrapin fecal samples, with blue crabs occurring more frequently in samples from males than in samples from females. Other items occurring in fecal samples included *M. bidentatus*, *S. reticulatum*, bivalves (*Mulina lateralis*, *Solen viridis*, Arcidae), and spiders (Lycosidae, Salticidae, Linyphiidae).

Dietary Composition by Percent Weight. — The largest contributors to overall terrapin diets by weight were *C. pliculosa*, *L. irrorata*, and *Uca* spp., with *C. sapidus* also contributing in male diets (Table 4). We detected multiple significant differences in percent weight between the diets of male and female terrapins. Females consumed significantly more periwinkle snails ($H = 13.28$, $p < 0.001$) and total gastropods ($H = 5.95$, $p = 0.015$) than did males. 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 did females. Finally, male terrapins exhibited a significantly higher percentage of ingested plant matter ($H = 6.02$, $p = 0.014$) than did females.

We compared seasonal variation in percent weight of dietary items among spring, summer, and fall samples ($n = 60$); winter samples ($n = 4$) were excluded owing to low sample size. Multiple significant seasonal differences in percent weight of dietary items were detected. We detected a significant seasonal difference in percent weight of total gastropods ($H = 10.54$, $p = 0.005$). Consumption of snails was significantly higher during spring and fall compared with summer. Highly significant seasonal differences were detected in the percent of the diet

Table 4. Mean percent weight (%W), including standard deviation (SD) and range, for prey items found in Texas diamond-backed terrapin (*Malaclemys terrapin littoralis*) fecal samples for total, male, and female samples. Dashes (—) indicate that the item class was not found in samples.

Prey item	Total samples (n = 64) %W ± SD	Range	Males (n = 29) %W ± SD	Range	Females (n = 35) %W ± SD	Range
Cerithidea pliculosa	28.2 ± 40.3	0–100	24.6 ± 37.1	0–100	31.2 ± 43.2	0–99.9
Littorina irrorata	15.2 ± 34.1	0–98.9	0.02 ± 0.1	0–0.48	27.8 ± 42.3	0–98.9
Melampus bidentatus	1.7 ± 9.7	0–73	3.6 ± 14.3	0–73	0.1 ± 0.3	0–1.8
Mulina lateralis	0.02 ± 0.2	0–1.2	0.003 ± 0.02	0–0.09	0.04 ± 0.2	0–1.2
Solen viridis	0.001 ± 0.008	0–0.07	—	—	0.002 ± 0.01	0–0.07
Arcidae A	0.004 ± 0.03	0–0.2	—	—	0.01 ± 0.04	0–0.2
Arcidae B	0.1 ± 1	0–8.1	0.3 ± 1.5	0–8.1	—	—
Uca spp.	23.2 ± 37.5	0–100	23.5 ± 37.5	0–100	23.1 ± 38.1	0–99.9
Callinectes sapidus	7.7 ± 22	0–96.8	16.5 ± 30.7	0–96.8	0.4 ± 1.3	0–5
Sesarma reticulatum	3 ± 16.7	0–98.8	6.6 ± 24.6	0–98.8	—	—
Unidentifiable crab	2.3 ± 12.7	0–97.4	3.9 ± 18.2	0–97.4	1 ± 5	0–29.3
Unidentifiable shrimp	0.003 ± 0.02	0–0.2	0.01 ± 0.03	0–0.2	—	—
Balanus sp.	0.0002 ± 0.002	0–0.01	—	—	0.0004 ± 0.002	0–0.01
Insecta	0.2 ± 1	0–5.7	0.2 ± 1	0–5.4	0.2 ± 1	0–5.7
Araneae	0.02 ± 0.1	0–1.1	0.04 ± 0.2	0–1.1	0.001 ± 0.004	0–0.02
Actinopterygii	0.6 ± 3.3	0–26.1	1.2 ± 4.9–	0–26.1	0.1 ± 0.6	0–3.3
Plantae	2.9 ± 9.4	0–60	5 ± 13.2	0–60	1.1 ± 3.5	0–20
Algae	4.5 ± 20.5	0–100	—	—	8.2 ± 27.3	0–100

composed of fiddler crabs (*H* = 15.98, *p* < 0.001), with terrapins consuming a higher percentage of fiddler crabs in summer compared with other seasons. We also found that consumption of blue crabs varied seasonally (*H* = 8.15, *p* = 0.017), with terrapins consuming a significantly higher percentage of blue crabs in the fall than in summer. Seasonal differences in consumption of total Decapoda approached statistical significance (*H* = 5.79, *p* = 0.055), and terrapins consumed a significantly higher percentage of spiders (*H* = 7.00, *p* = 0.030) in fall than in summer. We detected seasonal differences in the amount of plant matter ingested (*H* = 11.74, *p* = 0.003) by terrapins, with significantly higher amounts of plant material being present in fall and summer than in spring.

We analyzed fecal samples from terrapins captured at three West Bay sites, South Deer, Sportsman Road, and North Deer to examine dietary differences among marsh sites (Table 1). Multiple significant differences were detected among the West Bay sites. We found a significant difference in percentage of horn snails among 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 did South Deer samples. We detected significant differences in *Uca* spp. consumption (*H* = 6.43, *p* = 0.040) between the sites. Terrapins from Sportsman Road were found to have significantly greater percentages of fiddler crabs in their diets than did those from both North and South Deer. Greens Lake and Matagorda samples were not included in the formal data analysis owing to low sample sizes (*n* ≤ 2). While not statistically analyzed, both Greens Lake fecal samples were dominated by *C. pliculosa* (> 99%) and the Matagorda sample contained *M. bidentatus* (73%) and *Uca* spp. (27%).

Index of Relative Importance. — Based on IRI, there are 4 primary prey items overall: *C. pliculosa*, *L. irrorata*, *Uca* spp., and *C. sapidus* (Table 5). For female terrapins, *C. pliculosa*, *L. irrorata*, and *Uca* spp. were the most important prey items. The most important prey species for males were *C. pliculosa, Uca* spp., and *C. sapidus*, with plant material ranking highly for males as well.

DISCUSSION

Effects of Prey Availability on Terrapin Distribution. — Prey quadrats at random and terrapin capture locations were not different in numbers of *L. irrorata* or presence of *C. pliculosa*, suggesting uniform distribution and availability of these snails within the studied marshes. Conversely, we observed higher numbers of *Uca* spp. burrows at randomly surveyed quadrats rather than at terrapin capture locations. Both random and terrapin capture quadrats were collected regardless of tide height, but the accuracy of these prey counts may have been affected by tidal stage. For example, *L. irrorata* were more easily observed during high tide, as they clump together and climb higher on plants (Warren 1985). However, fiddler crab burrows are better observed during periods of low tide. Our results suggest that prey availability is not a primary limiting factor in terrapin distribution within Texas saltmarshes. These findings are similar to those of previous terrapin prey studies conducted along the Atlantic Coast (Tucker et al. 1995; Whitelaw and Zajac 2002). Our study also indicates that male and female terrapins are not distributing themselves differently within the marsh based upon available prey.

Marsh periwinkle snail numbers were highest in fall and winter and lowest in summer. Fall numbers were also

Table 5. Mean percent weight (%W), percent frequency of occurrence (%F), and index of relative importance (IRI) for prey items found in Texas diamond-backed terrapin (*Malaclemys terrapin littoralis*) fecal samples for total, male, and female samples. Dashes (—) indicate that the item class was not found in samples.

Prey item	Total samples (*n* = 64)			Males (*n* = 29)			Females (*n* = 35)		
	%W	%F	IRI	%W	%F	IRI	%W	%F	IRI
Cerithidea pliculosa	28.2	59.4	48.1	24.6	58.6	41.2	31.2	60.0	44.9
Littorina irrorata	15.2	25.0	10.9	0.02	3.4	0.002	27.8	42.9	28.6
Melampus bidentatus	1.7	7.8	0.4	3.6	10.3	1.1	0.1	5.7	0.01
Mulina lateralis	0.02	6.3	0.004	0.003	3.4	0.0003	0.04	8.6	0.01
Solen viridis	0.001	1.6	0.00005	—	—	—	0.002	2.9	0.0001
Arcidae A	0.004	1.6	0.0002	—	—	—	0.01	2.9	0.0005
Arcidae B	0.1	1.6	0.01	0.3	3.4	0.03	—	—	—
Uca spp.	23.2	40.6	27.1	23.5	41.4	27.8	23.1	40.0	22.1
Callinectes sapidus	7.7	21.9	4.8	16.5	31.0	14.7	0.4	14.3	0.1
Sesarma reticulatum	3.0	3.1	0.3	6.6	6.9	1.3	—	—	—
Unidentifiable crab	2.3	15.6	1.0	3.9	13.8	1.6	1.0	17.1	0.4
Unidentifiable shrimp	0.003	1.6	0.0001	0.01	3.4	0.001	—	—	—
Balanus sp.	0.0002	1.6	0.00001	—	—	—	0.0004	2.9	0.00002
Insecta	0.2	18.8	0.1	0.2	13.8	0.1	0.2	22.9	0.1
Araneae	0.02	7.8	0.004	0.04	10.3	0.01	0.001	5.7	0.0001
Actinopterygii	0.6	14.1	0.2	1.2	17.2	0.6	0.1	11.4	0.03
Plantae	2.9	78.1	6.4	5.0	82.8	11.8	1.1	71.4	1.9
Algae	4.5	4.7	0.6	—	—	—	8.2	8.6	1.7

significantly higher than spring counts. Seasonal differences in tidal amplitude could explain the high fall numbers, as the tides are still high, which drives the snails farther up plant stems, facilitating easier detection and counting (B.J.A., *pers. obs.,* September 2013). However, we should have observed the same effect during the summer when tides were also generally higher, but instead we observed low numbers of *L. irrorata*. Furthermore, we would be likely to observe lower numbers on plant stems in winter when tides are generally lower instead of the high numbers observed. Winter is also a time when *L. irrorata* tend to move slightly offshore to deeper waters (Hamilton 1978). Therefore, we provide a more plausible mechanism that involves terrapins showing a preference for areas containing abundant fiddler crabs during summer months rather than areas containing periwinkle snails. This in turn would lead to higher survival and recovery of periwinkle snails during summer months, leading to the increased numbers in fall and winter. However, it should be noted that Warren (1985) found *L. irrorata* mortality, from causes other than predation, to be highest in summer. Fecal sample data support this claim that areas with *Uca* spp. are visited more often in summer than are areas containing high numbers of *L. irrorata*.

The only other observed seasonal prey differences were in numbers of fiddler crab burrows. Burrow counts were highest during the summer and winter seasons. We observed higher *Uca* spp. activity in the summer months, which is discussed in detail below. This is supported by, and explains, the higher burrow numbers counted during summer. Burrows are easier to detect in winter due to low tides exposing the marsh surface. Therefore, the higher counts in the summer were likely owing to higher numbers of active fiddler crabs while the high numbers in winter months were likely owing to the higher probability of

detection of older but still existent burrows from earlier seasons. Two species of fiddler crab were collected during the time of high summer activity at South Deer Island, *Uca rapax* and *Uca panacea*. Data from Louisiana showed that crab numbers range between 75% and 100% of burrow numbers, and an increase in *Uca spinicarpa* burrow densities occurred in the summer within lower reaches of the marsh (Mouton and Felder 1996). That study also noted high burrow densities in the early fall (September) for *Uca longisignalis* (Mouton and Felder 1996).

As with other analyses, individual marshes displayed differences in prey availability. Surprisingly, many of these differences were found among West Bay marsh sites. The only detected difference at TPNWR was the lack of horn snails. For every species exhibiting a significant difference in numbers, South Deer Island quadrats consistently displayed higher numbers in comparison to other locations. South Deer was observed as having more complex habitat than other areas (unpubl. data, 2015), which could explain the abundance of multiple prey items found there (Tews et al. 2004). The numbers and types of available prey at Sportsman Road marsh were similar to those at South Deer, with only one significant difference between the two, that being the number of *L. irrorata*. Both South and North Deer Islands exhibited higher numbers of *L. irrorata* than did the nearby barrier island and mainland sites at Sportsman and Greens Lake.

Greens Lake is unique compared with the other sites, specifically the other West Bay marshes, in having almost no fiddler burrows counted within capture quadrats. Greens Lake also had significantly lower numbers of periwinkle snails compared with the Deer Islands. Horn snails were found in a large percentage of Greens Lake capture locations. The difference in prey availability at Greens Lake likely explains why the 2 fecal samples from

Greens Lake 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 (~ 112 km; TPNWR to West Bay) but were observed between areas that are much closer together (≤ 8 km; multiple differences in West Bay). This may simply reflect an artifact of sample size, and increased effort at TPNWR may be able to identify differences in prey abundance in comparison to the West Bay Sites.

Terrapin Diet. — Terrapins on the upper Texas coast were found to consume multiple prey species, with the 2 most important groups of prey items in the diet of Texas terrapins being Decapoda and Gastropoda. Prey items from these groups were found frequently in fecal samples, made up large percentages of fecal samples by weight, and ranked highly in the IRI. We found the most important prey items to be *C. pliculosa*, *L. irrorata*, *Uca* spp., and *C. sapidus* but with consumption varying between the sexes.

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, we found remains of marsh periwinkle snails in only 1 male sample, implying geographic dietary differences. In contrast, by counting opercula we found that an individual female terrapin consumed over 200 *L. irrorata*, and periwinkle snails were shown to be the second most important dietary item for females. Furthermore, horn snail opercula of twice that number were found in the fecal sample of a separate female.

The plicate horn snail (*C. pliculosa*) is the most important dietary component for both male and female terrapins based on all 3 metrics used in our study. Horn snails are found along the western Gulf Coast (Rothschild 2004) and can be locally abundant (B.J.A., *pers obs.,* June 2013). However, this is the first study where consumption of this species by *M. terrapin* has been reported, although recent studies have recorded consumption of the congeneric ladder horn snail (*Cerithidea scalariformis*) in South Florida (Denton et al. 2015, 2016). Plicate horn snails are usually found on the sediment surface or just below the surface and are rarely found on vegetation (Rothschild 2004), unlike *L. irrorata*. The shells of *C. pliculosa* are much smaller in diameter than those of *L. irrorata* and would likely offer less resistance to both the large heads of females or to the much smaller male terrapins. It has been suggested that high processing costs associated with consumption of an abundant potential prey species may deter terrapins from consuming that species in favor of prey with lower processing costs (Tucker et al. 1997). Periwinkle snails are likely too large for male terrapins to consume efficiently and, with the abundance of other prey items (horn snails and decapods) and their ease of capture (*C. pliculosa* are found on the marsh surface rather than on plant stems), male terrapins may be ignoring the larger periwinkles in Texas marshes.

Overall, bivalves were found in few samples and therefore, no statistical analyses were performed on individual categories of bivalve. Terrapins in northern Florida consumed large numbers 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 our study sites (Koza 2006). However, the results of our study do not indicate bivalves are a major contributor to terrapin diets along the upper Texas coast.

We found that decapod crustaceans were more important to the diets of male Texas diamond-backed terrapins than to the diets of females. The sexes had nearly the same frequencies of occurrence in consumption of fiddler crabs (41% males, 40% females) but with differences in IRI. Males were shown to consume other species of decapods in higher frequencies than did females, including taxa that did not appear in the female diet, specifically *S. reticulatum*, which is a known herbivore of *S. alterniflora*. In a captive feeding experiment, male terrapins were shown to eat small green crabs (*Carcinus maenas*) whole, crop hind limbs from medium crabs, and avoid large crabs completely (Davenport et al. 1992). Tucker et al. (1995) found *C. sapidus* to be represented strongly 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 the present study, *C. sapidus* was the third most important prey item found in male samples but of little importance in female diets. Also, the *C. sapidus* remains found in fecal samples appeared to be whole small crabs (limbs, chelipeds, carapace, etc.). The hind limbs of larger blue crabs were found in some samples mixed with the remains of smaller crabs, indicating instances of limb cropping from larger crabs. This finding is similar to the blue crab remains found in female samples by Tucker et al. (1995), which were primarily cropped limbs.

A potential reason for blue crabs being more important to the diets of male terrapins in our study may be the presence of juvenile *C. sapidus* in areas where males more frequently visit. Alternatively, male terrapins on the upper Texas coast may be better at pursuing smaller blue crabs present in marshes than are females. Based on the present study, it appears that females primarily consume snail species; therefore, 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, likely reflecting 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. Our findings of fecal samples consisting of greater than 90% blue crab in fall support their data and indicate a dietary shift to this newly abundant resource.

Our study also noted another seasonal shift in terrapin diets. The amount of fiddler crab remains found in fecal samples during the summer was high compared with other seasons. In many instances, individual samples consisted almost entirely of *Uca* spp. remains and represented > 90% of the sample weight. Burrow numbers in prey quadrats were also significantly higher during the summer. The higher number of burrows reflects, and is consistent with, the increased fiddler crab activity observed in the field. Therefore, the increased consumption of fiddler crabs in the diet is likely because of increased seasonal availability of this prey species.

During daytime surveys in July and August 2013, large numbers of fiddler crabs were commonly seen moving throughout the marsh and hundreds were captured as bycatch in pitfall traps during a concurrent study (B.J.A., *pers. obs.,* August 2013). Many of the encountered crabs, found both walking through the marsh and in traps, appeared to be gravid females. Female fiddler crabs release their eggs at the water's edge, usually at night, with the falling tide (Salmon and Hyatt 1983). Herding behavior in *Uca pugilator* that feed in the intertidal zone at low tide, both diurnally and nocturnally, has also been noted (Salmon and Hyatt 1983), and hordes of *Uca* spp. go to the water's edge at low tide to wet their gills (Rothschild 2004).

There are 7 species of fiddler crab found along the Texas Gulf Coast, but only 5 species are likely to be found within the range of *M. t. littoralis*, including the 2 species identified from South Deer Island, *U. panacea* and *Uca rapax* (Barnwell and Thurman 1984; Rothschild 2004). The Gulf sand fiddler, *U. panacea,* is the Western Gulf's ecological equivalent to the Atlantic species *U. pugilator* (Rothschild 2004) and is likely to have similar behaviors to those mentioned above that would increase the probability of the crabs crossing paths with foraging terrapins. Teal (1958) also noted higher crab activity during flood tides, which would provide another opportunity for terrapins to capture marsh-dwelling crabs as the terrapins move higher into the marsh with the tide. Clarkson (2012) observed decreased nocturnal movement by terrapins on South Deer Island, but the increased tendency for nocturnal activity by fiddler crabs, combined with the abundance of their remains in terrapin diets, may indicate that terrapins were foraging at night.

While not an important dietary component, the bones and scales of ray-finned fishes (Actinopterygii) were found in fecal samples of both sexes and in numbers that may indicate consumption of more than one fish by an individual terrapin. Fishes commonly observed in Texas marsh habitats include killifishes (Fundulidae), sheepshead minnows (*Cyprinodon variegatus*), silversides (Atherinopsidae), gobies (Gobiidae), and juvenile members of the drum family (Sciaenidae; Rozas et al. 2007). We found both cycloid and ctenoid scales in samples, indicating that terrapins consumed fish from multiple families because all listed families have cycloid scales except for sciaenids.

Middaugh (1981) documented terrapin predation of spawning Atlantic silverside (*Menidia menidia*) but did not indicate the method of capture. It is unlikely that terrapins are very proficient at capturing free-swimming fish, but terrapins in aquaria have been observed cornering and consuming fish (B.J.A., *pers obs.,* June 2013). Most likely, the fish remains observed in fecal samples originated from fish stranded on the marsh surface as tides receded or remaining in isolated pools where they would be more easily captured.

It is doubtful that terrapins were intentionally consuming some items found in samples including the insects, spiders, and plant matter. Insects and spiders were commonly observed throughout the marsh and may have been unintentionally captured while terrapins consumed other prey, although our results did detect a seasonal difference in presence of Araneae in fecal samples. There is also a chance that spiders, and particularly insects, contaminated the enclosures used to house terrapins during transport, although their remains did appear to be thoroughly damaged, consistent with digestion. Both groups contributed minuscule amounts to the IRI and should perhaps be excluded if present in future diet studies.

While males ingested plant matter more frequently and in higher percentages than did females, these items were likely consumed incidentally while terrapins captured desired prey. Small bits of stems, leaves, and even reproductive structures (e.g., flower parts from *S. alterniflora* and seeds from *Salicornia* spp.) showed up in samples. 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 and noted that seeds were more likely to be found in samples from males and smaller females than in mature females (Tulipani and Lipcius 2014). It is possible that seed transport by terrapins may facilitate plant colonization of new areas. The results of our study support Tulipani and Lipcius (2014), who reported that male samples more frequently contained plant matter than did female samples.

The observed increase of fall and summer ingestion of 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 with female samples may suggest that males feed in terrestrial habits more often than do females. The intake of plant material may also be related to targeted prey items. For example, female terrapins' larger gape size and greater predation on *L. irrorata* may reduce incidental intake of plant material while the smaller males' greater intake of decapods may increase incidence of 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 sex-specific patterns in plant ingestion.

Conclusions. — The most important prey items for terrapins in our study were *C. pliculosa*, *L. irrorata*, *Uca* spp., and *C. sapidus*. However, availability of prey species does not appear to be a limiting factor in terrapin distribution within the marsh, although prey availability does change over space and time. Based on our diet analyses, distinct dietary differences were detected between male and female Texas diamond-backed terrapins. Our 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 *C. pliculosa*, at high frequencies and in high numbers, which has not been noted in previous studies. This snail species should be considered an important food source for terrapins in the northwestern Gulf of Mexico. Terrapins were shown to take advantage of seasonally abundant food resources, especially fiddler crabs. Continued research on the trophic interactions of terrapins along their entire range is needed to fully understand the dietary requirements of this unique, estuarine-dependent species. These data are critically needed for the successful management and conservation of diamond-backed terrapins.

LITERATURE CITED

BARNWELL, F.H. AND THURMAN, C.L., II. 1984. Taxonomy and biogeography of the fiddler crabs (Ocypodidae: Genus *Uca*) of the Atlantic and Gulf coasts of eastern North America. Zoological Journal of the Linnean Society 81:23–87.

BJORNDAL, K.A., BOLTEN, A.B., LAGUEUX, C.J., AND JACKSON, D.R. 1997. Dietary overlap in three sympatric congeneric freshwater turtles (*Pseudemys*) in Florida. Chelonian Conservation and Biology 2:430–433.

BUTLER, J.A., HEINRICH, G.L., AND MITCHELL, M.L. 2012. Diet of the Carolina diamondback terrapin (*Malaclemys terrapin centrata*) in northeastern Florida. Chelonian Conservation and Biology 11:124–128.

CAGLE, F.R. 1952. A Louisiana terrapin population (*Malaclemys*). Copeia 1952:74–76.

CLARKSON, E.L. 2012. Short term temporal trends in activity and habitat selection of the Texas diamondback terrapin. MS Thesis, University of Houston–Clear Lake, Houston, TX.

DAVENPORT, J., SPIKES, M., THORNTON, S.M., AND KELLY, B.O. 1992. Crab-eating in the diamondback terrapin *Malaclemys terrapin*: dealing with dangerous prey. Journal of the Marine Biological Association of the United Kingdom 72:835–848.

DENTON, M.J., HART, K.M., DEMOPOULOS, A.W.J., OLEINIK, A., AND BALDWIN, J.D. 2016. Diet of diamondback terrapins (*Malaclemys terrapin*) in subtropical mangrove habitats in South Florida. Chelonian Conservation and Biology 15:54–61.

DENTON, M.J., HART, K.M., DEMOPOULOS, A.W.J., WOOD, R., AND BALDWIN, J.D. 2015. *Malaclemys terrapin rhizophorarum* (mangrove diamondback terrapin). Diet. Herpetological Review 46:426–427.

DIXON, J.R. 2013. Amphibians and Reptiles of Texas: With Keys, Taxonomic Synopses, Bibliography, and Distribution Maps. Third edition. College Station: Texas A&M University Press, 447 pp.

ERNST, C.H. AND LOVICH, J.E. 2009. Turtles of the United States and Canada. Second edition. Baltimore, MD: John Hopkins University Press, 827 pp.

FIELDS, J.R., SIMPSON, T.R., MANNING, R.W., AND ROSE, F.L 2000. Modifications to the stomach flushing technique for turtles. Herpetological Review 31:32–33.

HAMILTON, P.V. 1978. Intertidal distribution and long-term movements of *Littorina irrorata* (Mollusca: Gastropoda). Marine Biology 46:49.

KOZA, B.R. 2006. Distribution, habitat selection, and resource partitioning of Texas diamondback terrapin (*Malaclemys terrapin littoralis*) in the Aransas National Wildlife Refuge area, Texas. MS Thesis, Texas A&M University–Corpus Christi.

MIDDAUGH, D.P. 1981. Reproductive ecology and spawning periodicity of the Atlantic silverside, *Menidia menidia* (Pisces: Atherinidae). Copeia 1981:766–776.

MOUTON, E.C., JR. AND FELDER, D.L. 1996. Burrow distributions and population estimates for the fiddler crabs *Uca spinicarpa* and *Uca longisignalis* in a Gulf of Mexico salt marsh. Estuaries 19:51–61.

PALMER, W.M. AND CORDES, C.L. 1988. Habitat Suitability Index Models: Diamondback Terrapin (Nesting)–Atlantic Coast. US Fish and Wildlife Service Biological Report 82 (10.151), Washington, DC, 18 pp.

ROOSENBURG, W.M., HALEY, K.L., AND MCGUIRE, S. 1999. Habitat selection and movements of diamondback terrapins, *Malaclemys terrapin*, in a Maryland estuary. Chelonian Conservation and Biology 3:425–429.

ROTHSCHILD, S.B. 2004. Beachcomber's Guide to Gulf Coast Marine Life: Texas, Louisiana, Mississippi, Alabama, and Florida. Third edition. Lanham, MD: Taylor Trade Publications, The Rowan & Littlefield Publishing Group, 200 pp.

ROZAS, L.P., MINELLO, T.J., ZIMMERMAN, R.J., AND CALDWELL, P. 2007. Nekton populations, long term wetland loss, and the effect of recent habitat restoration in Galveston Bay, Texas, USA. Marine Ecology Progress Series 344:119–130.

SALMON, M. AND HYATT, G.W. 1983. Spatial and temporal aspects of reproduction in North Carolina fiddler crabs (*Uca pugilator* Bosc). Journal of Experimental Marine Biology and Ecology 70:21–43.

TEAL, J.M. 1958. Distribution of fiddler crabs in Georgia salt marshes. Ecology 39:186–193.

TEWS, J., BROSE, U., GRIMM, V., TIELBORGER, K., WICHMANN, M.C., SCHWAGER, M., AND JELTSCH, F. 2004. Animal species diversity driven by habitat heterogeneity/diversity: the importance of keystone structures. Journal of Biogeography 31:79–92.

THOMAS, J.L., ZIMMERMAN, R.J., AND MINELLO, T.J. 1990. Abundance patterns of juvenile blue crabs (*Callinectes sapidus*) in nursery habitats of two Texas bays. Bulletin of Marine Science 46:115–125.

TUCKER, A.D., FITZSIMMONS, N.N., AND GIBBONS, J.W. 1995. Resource partitioning by the estuarine turtle *Malaclemys terrapin*: trophic, spatial, and temporal foraging constraints. Herpetologica 51:167–181.

TUCKER, A.D., YEOMANS, S.R., AND GIBBONS, J.W. 1997. Shell strength of mud snails (*Ilyanassa obsoleta*) may deter foraging by diamondback terrapins (*Malaclemys terrapin*). American Midland Naturalist 138:224–229.

TULIPANI, D.C. AND LIPCIUS, R.N. 2014. Evidence of eelgrass (*Zostera marina*) seed dispersal by northern diamondback terrapin (*Malaclemys terrapin terrapin*) in lower Chesapeake Bay. PLoS ONE 9:e103346.

WARREN, J.H. 1985. Climbing as an avoidance behaviour in the salt marsh periwinkle, *Littorina irrorata* (Say). Journal of Experimental Marine Biology and Ecology 89:11–28.

WARREN, J.H. 1990. The use of open burrows to estimate abundances of intertidal estuarine crabs. Australian Journal of Ecology 15:277–280.

WHITELAW, D.M. AND ZAJAC, R.N. 2002. Assessment of prey availability for diamondback terrapins in a Connecticut salt marsh. Northeastern Naturalist 9:407–418.

WILLIARD, A.S. AND HARDEN, L.A. 2011. Seasonal changes in thermal environment and metabolic enzyme activity in the diamondback terrapin (*Malaclemys terrapin*). Comparative Biochemistry and Physiology, Part A 158:477–484.

ZAR, J.H. 2009. Biostatistical Analysis. Fifth edition. Upper Saddle River, NJ: Pearson Prentice Hall, 960 pp.