ASSESSMENT OF PREY AVAILABILITY FOR DIAMONDBACK TERRAPINS IN A CONNECTICUT SALT MARSH

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ABSTRACT - Wheeler Marsh in Milford, Connecticut provides habitat for diamondback terrapins (*Malaclemys terrapin*), a unique estuarine turtle. To assess potential prey availability, the distribution and abundances of marsh snails (*Melampus bidentatus*), mud snails (*Ilyanassa obsoleta*), marsh mussels (*Geukensia demissa*), and fiddler crabs (*Uca* spp.) were studied in several sub-habitats (marsh surface, marsh edge, creek bank, and mudflats) of five tidal creeks. Almost all terrapins have been found in one section of the marsh, Turtle Creek, where all four prey species were present in large numbers. However, high numbers of some prey were found in other sections of the marsh as well, suggesting that resource availability may not be the primary determinant of terrapin distribution. The physical structure, plant density, and tidal amplitudes of salt marsh creeks may also be important determinants of terrapin distribution via their influence on resource accessibility.

INTRODUCTION

The northern diamondback terrapin (*Malaclemys terrapin*) ranges along the Atlantic Coast from Cape Cod to Cape Hatteras (Ernst et al. 1994). They are found in a variety of estuarine/brackish water environments, including coastal marshes, coves, tidal rivers, lagoons behind barrier beaches (Ernst et al. 1994), and also in inland tidal habitats (Roosenburg et al. 1999). In Connecticut and elsewhere along the eastern coast of the United States, *Malaclemys terrapin* is a species of management concern (Chambers 2000), yet relatively little information is available on its ecology. Wheeler Marsh in Milford, Connecticut provides habitat for diamondback terrapins with an estimated population of about 500 individuals (Chambers 2000). Adult terrapins have been found in several areas of the marsh complex, which is characterized by an extensive system of marsh creeks (Fig. 1), and turtles are known to nest on the sand spit on Milford Point. This indicates the importance of the marsh as a feeding and nesting habitat and/or refuge. Terrapins have been observed in several of the marsh creeks, but not in

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all of the creeks where searches were completed. In population studies, most of the terrapins were consistently captured in large numbers only in Turtle Creek (Chambers 1999, 2000). The local distribution of terrapins in the marsh is likely the function of several factors that determine habitat suitability, including migration patterns, accessibility, physical conditions within the tidal creeks, and food resources. The objective of this research was to assess prey availability for diamondback terrapins as one measure of habitat suitability.

Feeding Ecology

Little is known about terrapin food habits and how they change over the geographical distribution of the species. The natural diet of terrapins consists largely of crustaceans and mollusks (Carr 1952, Pope 1939, Spagnoli and Marganoff 1975). Captive terrapins feed readily on chopped fish, crabs, snails, oysters, clams, insects, marine annelids, and beef (Coker 1906). In Allen and Littleford's (1955) study in Maryland, terrapins were fed a mixed diet of fresh fish, clams, oysters, and snails to investigate their rate of growth. The terrapins

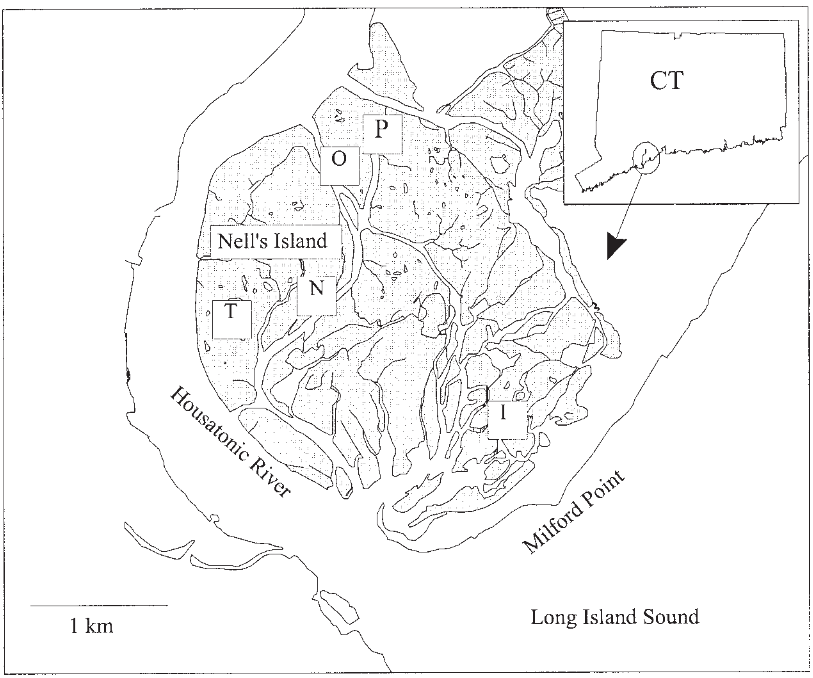

Figure 1. Location of the research area in Wheeler Marsh, at the mouth of the Housatonic River in Milford, Connecticut. Sites chosen for the prey availability study were located in three terrapin trapping creeks (Turtle [T], Princess [P] and New [N]) and two non-trapping creeks (Inner [I] and Outer [O]).

preferred shellfish and snails to all other foods offered. Young terrapins were indiscriminate in their initial feeding habits but rapidly developed food preferences that did not change after three weeks. Populations of potential terrapin prey were described by Montague et al. (1981) for Georgia salt marshes, where the population sizes of individual prey species were often large but species diversity was low. In the intertidal zone, 80 to 200 fiddler crabs (*Uca pugnax*), 400 to 700 marsh snails (*Littorina irrorata*), and 7 to 8 ribbed mussels (*Geukensia demissa*) m^{-2} of marsh were typical. In addition, the pulmonate snail (*Melampus bidentatus*), the marsh clam (*Polynesoda caroliniana*), and several polychaete worms were abundant. On adjacent mudflats, densities of *Ilyanassa obsoleta* ranged from 500 to 1600 m^{-2}.

Tucker et al. (1995) analyzed fecal samples of terrapins in South Carolina marshes and determined that their diets included snails (*Littorina irrorata, Melampus lineatus*), small crabs (*Gelasimus, Uca*), marine annelids (*Nereis irratabilis*), mussels (*Mytilus edulis*), clams (*Anomalocardia cuneimens*), captured or scavenged fish (*Menidia menidia*), and other material (*Sargassum*, unidentified grass fragments). Mark and recapture studies carried out by Hurd et al. (1979) in a salt marsh in Delaware indicated that terrapins ingested the blue mussel (*Mytilus edulis*) and other invertebrates, as determined by terrapin excretions. In a Maryland river system, which had limited *Spartina* marshes and a scarcity of *Littorina* and other salt marsh snails, terrapins fed primarily on soft-shell clams (*Mya arenaria*), razor clams (*Tagelus* spp.), and other smaller clams (*Macoma* spp. and *Gemma gemma*). These clams were most abundant on open sandy flats in deeper water (Roosenburg 1994, Roosenburg et al. 1999).

Tucker et al. (1995) investigated dietary preferences among different size classes of terrapins, which can range from 100–230 mm carapace length (Ernst et al. 1994, Pope 1939). Terrapins are sexually dimorphic, with males maturing at approximately 300 g between 4 to 7 years of age and females at 1100 g between 8 to 13 years of age (Roosenburg 1996). Small terrapins (head width ≤ 20mm) specialized on small snails (≤ 10 mm), with large snails (> 10 mm) and marsh clams being less important food items. Medium-sized terrapins (20–30 mm) still relied on small snails but apportioned more of their diet among large snails, blue crabs, and fiddler crabs. Large terrapins (≥ 30 mm) spread their dietary choices more evenly among large snails, small snails, blue crabs, mud crabs, and fiddler crabs. Roosenburg et al. (1999) noted that larger female terrapins were able to crush the shells of larger clams found on open sandy flats in deep water. However, small crustaceans and soft-bodied prey (amphipods, isopods, juvenile molting decapods) found in near-shore waters were a likely food resource for smaller terrapins.

Tucker et al. (1997) tested the shell strength of mud snails (*Ilyanassa obsoleta*) to determine if this deterred foraging by terrapins. The average shell strength of mud snails was twice that of *Littorina*, and three times that of *Uca*. They noted that if terrapins could process large *Littorina* they should be capable of crushing at least small *Ilyanassa*. However, an absence of *Ilyanassa* in diet samples (Tucker et al. 1995) suggested that for terrapins, it might be more efficient to harvest large *Littorina* than small *Ilyanassa* for the same processing effort (Tucker et al. 1997).

In the spring of 1998, we conducted a preliminary survey of prey availability in Wheeler Marsh and observed many of the species terrapins are known to consume elsewhere. These included *Melampus bidentatus*, *Ilyanassa obsoleta*, *Geukensia demissa*, *Uca pugnax,* and *Uca minax,* however *Littorina irrorata* and *Mytilus edulis* were not found. Several clam species were observed on the sandier flats, and small crabs, amphipods, and isopods were available on the marsh surface. We conducted the prey availability research presented here in the summer and fall of 1998, in coordination with the terrapin population research conducted by Chambers (1999). We sought to determine how prey species were distributed in the marsh and whether this helped to explain terrapin distribution.

METHODS AND MATERIALS

The Charles E. Wheeler salt marsh (Fig. 1) is located in a sheltered area behind Milford Point, at the mouth of the Housatonic River in Connecticut. This 850-acre wetland complex, owned by the Connecticut Department of Environmental Protection and included in the Stuart B. McKinney National Coastal Wildlife Refuge, provides habitat for *Malaclemys terrapin*. Based on mark and recapture analysis, it was estimated that 135-240 terrapins might inhabit the salt marsh (Chambers 1999). Follow-up research places this figure at around 500 individuals (Chambers, 2000).

Study Sites

We selected as study sites the same three creeks (Turtle Creek, New Creek, and Princess Creek) where the terrapin population research was conducted and two additional creeks (Inner Creek and Outer Creek), that were not sampled for terrapins, but where no terrapins had been previously reported (Fig. 1). In addition, no terrapins were observed in these two creeks during our sampling. Our approach to site selection was determined by the need to understand prey availability across various sections of the marsh in order to provide a basis for future terrapin studies. The following general habitat characteristics were observed for each site (Fig. 1):

- Turtle Creek, located in Nell's Island, was the deepest and widest creek studied. At the study location it was ~ 3 m deep in the center at high tide and ~ 20 m wide. Its steep banks were > 2 m high in some places. The broad marsh surface was covered in *Spartina alterniflora*. The creek bottom was mostly sandy in the center with firm mudflats closer to the banks. Even at low tide there was some water left in the central channel (~ 0.5 m deep). The entrance to this creek was closer to the Housatonic River and to a terrapin nesting area at Milford Point (Fig. 1) than the other creeks studied.
- New Creek, on the edge of Nell's Island, was narrower (~ 15 m) and shallower (~2 m). Its low banks were eroded in places and absent in others where the mudflats sloped up to the marsh surface. The marsh surface was covered in *S. alterniflora* and some *S. patens*.
- Princess Creek, located farther into the high marsh, was narrow (~10 m) and shallow (~1 m) at high tide and became intertidal at low tide. The low banks were highly eroded in places and absent in others. Some *S. alterniflora* and *S. patens* grew on the marsh but *Scirpus robustus* and *Phragmites australis* also grew there, unlike other creeks.
- Inner Creek was narrow (~2 m), shallow at high tide (~1 m) and closest to the land. It was located in the last area of the marsh to be reached by the high tide. The banks were low to absent. *S. alterniflora* and some *S. patens* covered the marsh. This creek was exposed for long periods of time at low tide.
- Outer Creek was narrow (~2 m), shallow at high tide (~1 m) and close to the Housatonic River. The banks were steep but eroded in places and the marsh was covered by *S. alterniflora*. This creek was flooded by the high tide quite early in the tidal cycle but exposed quickly at low tide.

Data Collection

We consistently chose locations that were near the middle of the three longer creeks (relative to the main drainage channels) and closer to the mouths of the two shorter creeks (Inner and Outer). At each of the five locations, we established three replicate 1 m^2 quadrats in each of four habitats: the marsh edge horizontal to the creek, the marsh surface perpendicular to the creek, the vertical creek bank, and the adjacent mudflats. There were no creek bank habitats at the Princess, New, and Inner Creek locations.

We assessed prey availability of three prey species, *Melampus bidentatus*, *Ilyanassa obsoleta*, and *Geukensia demissa,* by counting individuals in each quadrat. We counted the open burrows of *Uca pugnax* and *U. minax* in each quadrat to estimate the abundance of *Uca* spp. This method was proposed by Warren (1990) to overcome the difficulties of obtaining an actual count and to provide a quick and reliable index of the abundance of crabs. In each quadrat, we also counted plant stems to determine their density, because ease of movement could affect terrapin foraging on the marsh surface. We included *S. alterniflora* (found at all sites) and *S. patens, Scirpus robustus,* and *Phragmites australis* where they were found. Statistical analyses of prey abundance and distribution were conducted using NCSS (Hintze 1997) and NTSYS (Rohlf 1997) statistical software. Analytical details are provided in the results. Multiple tests in NCSS were used to check normality and homogeneity of variance assumptions of the statistical tests. In a few cases data were transformed to meet test assumptions. These cases are noted in the results.

RESULTS

Prey abundance varied considerably among and within creek sites and habitats (Fig. 2). *Uca* was present in all creeks but was most abundant on the bank and marsh edge of Turtle Creek and the marsh edge of Princess Creek. *Geukensia,* present in all creeks, was most abundant on the bank of Outer Creek, with similar density on the marsh and marsh edge at the other sites. *Melampus* was most abundant along the marsh edge of Turtle Creek, was present in Princess and New Creeks, but was absent from Inner and Outer Creeks. *Ilyanassa* was absent from most creeks and found predominantly on the mudflats of Turtle Creek.

No differences in abundance were found for *Uca*, *Geukensia,* and *Melampus* among sites (Table 1). However, there were within-site dif-

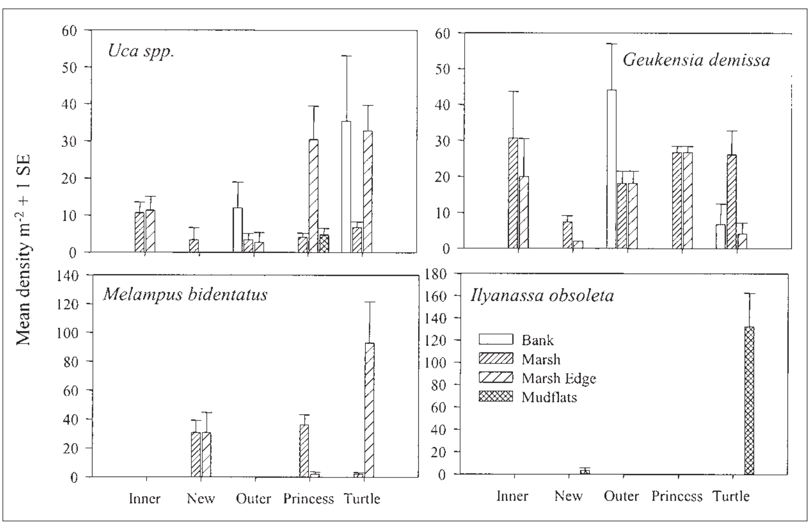

Figure 2. Mean ± 1 standard error (SE) prey density m^{-2} in different habitats at each study site.

ferences among marsh surface and edge habitats for *Melampus* and *Uca*. There were also differences in the density of *Ilyanassa* on the mudflats among the five sites (One way, random effects ANOVA, data log transformed, $p < 0.001$, $F_{4,10} = 47.37$, MSE = 2.4844).

Plant density varied considerably among and within creek sites and habitats. *S. alterniflora* was found in all five creeks (Fig. 3), and it was the only plant growing at the Turtle Creek location. It grew more densely along Inner, Outer, and New Creeks than in Princess and Turtle Creeks. There were differences in *S. alterniflora* stem density among sites, but not among the marsh edge and surface within sites (Table 2). *S. patens* grew more densely in New Creek than Outer or Princess Creeks and was absent from Inner and Turtle Creeks. There were no differences in *S. patens* among sites and habitats due to the high variation in stem density (Fig. 3, Table 2). *Scirpus robustus* and *Phragmites australis* were found only in Princess Creek, at stem densities of 508 ± 33.7 and 13.3 ± 13.3 respectively. Total stem counts of plants along the marsh edge ranged from a low of 111 m^{-2} in Turtle Creek to a high of 325 m^{-2} in Inner Creek. On the marsh surface, they ranged from a low of 136 m^{-2} in Turtle Creek to a high of 508 m^{-2} in Princess Creek. Total stem counts for the marsh and marsh edge combined were lowest at Turtle Creek (One way, random effects ANOVA, $p = 0.042$, $F_{4,31} = 2.82$, MSE = 60,220.5).

Table 1. Analysis of variance (ANOVA) of differences in mean density m^{-2} of prey among sites (five creeks) and among marsh surface and marsh edge habitats within creeks. The habitats were treated as a nested factor within the sites, and sites were tested using a random effects model ANOVA. *Uca* data were square root transformed. *Ilyanassa* were not found in these two types of habitat. Mudflats and creek banks were not included in the analysis because few or no individuals of the species investigated were found in these habitats. *Term significant at alpha = 0.05.

Species	df	Mean Square	F Ratio	P Value
Uca				
Site	4	11.70283	1.46	0.3384
Habitat (Sites)	5	8.00143	2.78	0.0407*
Error	24	2.88118		
Guekensia				
Site	4	295.57	0.79	0.5793
Habitat	5	374.93	1.76	0.1588
Error	24	212.67		
Melampus				
Site	4	1696.53	0.45	0.7689
Habitat	5	3750.58	13.95	0.0001*
Site/Habitat	24	268.92		

A clustering analysis was performed to assess the similarity among sites based on a combination of all prey and plant attributes considered in this study. Mean values based on replicate counts were used for each combination of site and habitat type. A similarity matrix was generated using the Bray Curtis coefficient followed by the unweighted pair-group method (UPGMA) of clustering (Rohlf 1997). This analysis revealed one large cluster of sampling sites (Group A), a smaller cluster (Group B), and several outliers (Fig. 4). Group A was comprised of all marsh edge and marsh surface sites, as expected due to the presence of the plants. Group B and the outliers were a combination of creek bank and mudflats habitats with no clear pattern, reflecting the highly variable

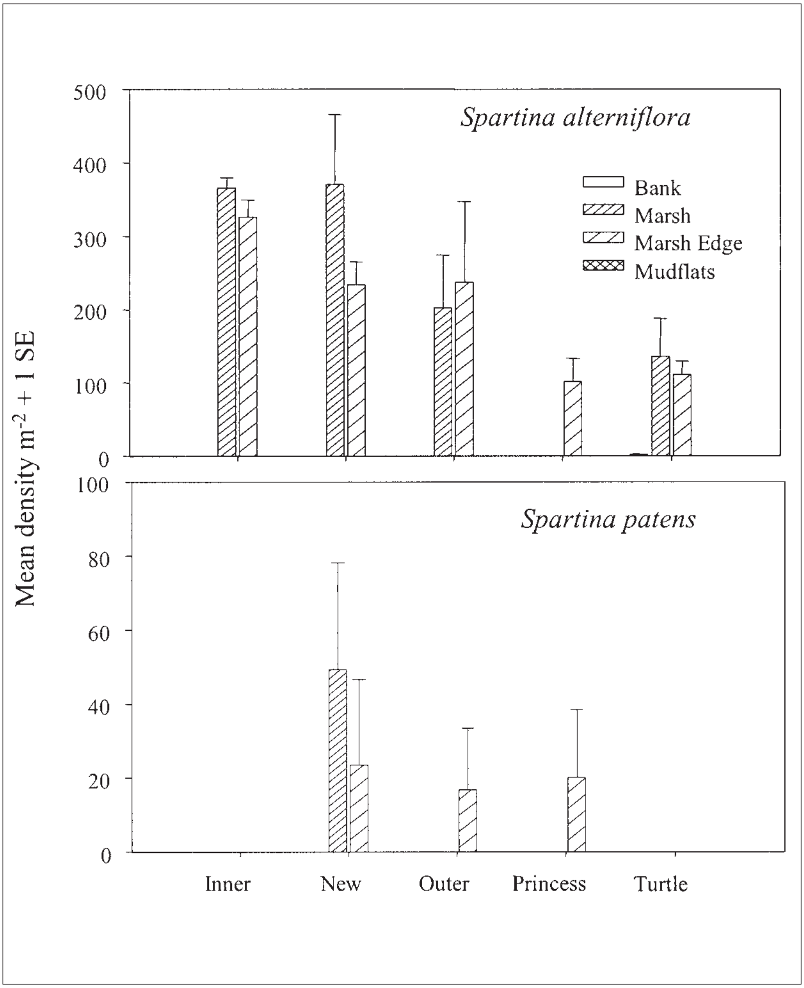

Figure 3. Mean ± 1 standard error (SE) plant stem density m^{-2} in different habitats at each study site.

composition of prey species at these sites (Fig. 2). These groups were clustered at low levels of similarity (< 10%) (Fig. 4).

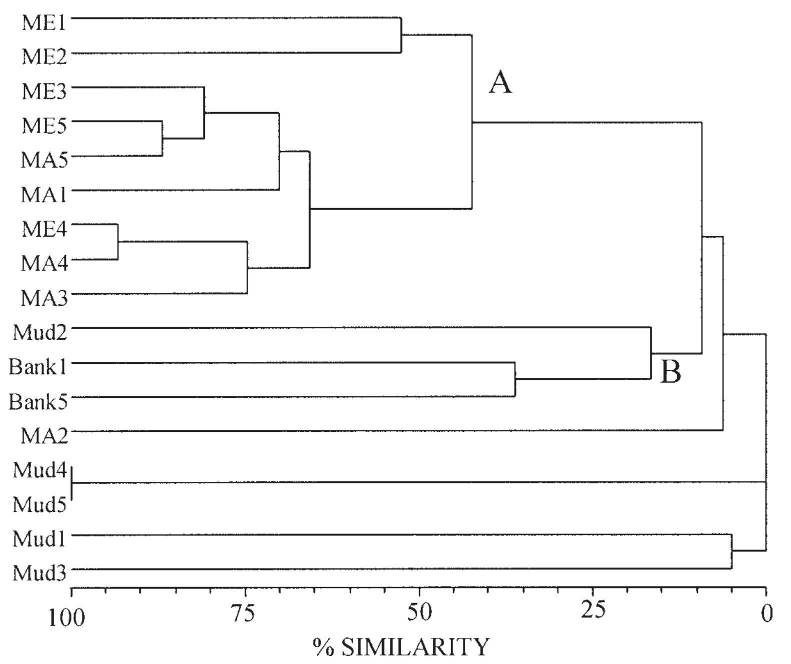

Figure 4. Dendrogram showing results of cluster analysis for plant community and prey species abundance data for habitats in Wheeler Marsh. ME = marsh edge; MA = marsh surface; Bank = creek bank; Mud = mudflats; 1 = Turtle Creek; 2 = Princess Creek; 3 = New Creek; 4 = Inner Creek; 5 = Outer Creek.

Table 2. Analysis of variance (ANOVA) of differences in *S. alterniflora* and *S. patens* stem density m^{-2} among sites (five creeks) and among marsh surface and marsh edge habitats within creeks. The habitats were treated as a nested factor within the sites, and sites were tested using a random effects model ANOVA. *Term significant at alpha = 0.05.

Species	df	Mean Square	F Ratio	P Value
S. alterniflora				
Site	4	98,891.15	9.22	0.0158*
Habitat (Site)	5	10,726.70	0.98	0.4470
Error	24	10,914.49		
S. patens				
Site	4	1,438.89	3.23	0.1155
Habitat	5	446.13	0.58	0.7180
Site/Habitat	24	774.77		

Within Group A, there were two smaller clusters, one containing marsh edge from Turtle and Princess Creeks and the other containing marsh edge and marsh surface from the remaining creeks. These smaller clusters represent a strong difference as they clustered at a similarity level < 40%. This difference is due to the higher densities of *Uca* and *Melampus* (Fig. 2) and the low density of *S. alterniflora* in Turtle and Princess Creeks (Fig. 3). The other creeks had higher densities of *S. alterniflora* and lower abundances of *Uca* and *Melampus* (Fig. 2).

DISCUSSION

All four prey studied were available in large numbers in Turtle Creek. Mean abundance was higher for *Uca* on the bank and marsh edge, *Melampus* on the marsh edge and *Ilyanassa* on the mudflats of Turtle Creek than all other creeks. However, there were no strong differences in overall prey availability among the creeks in Wheeler Marsh (Fig. 2), suggesting that all could provide food for diamondback terrapins. Yet, of the 182 terrapins captured over two field seasons, 126 were trapped in Turtle Creek. The remaining 56 were trapped in two additional creeks, not included in the 1998 study (Chambers 2000).

Habitat Characteristics

The preponderance of terrapins in Turtle Creek indicates that habitat characteristics at the site generate very suitable conditions for the terrapins. We suggest that two habitat factors, prey availability and prey accessibility, may be important in helping to generate this distribution. Cluster analysis of prey and plants revealed no "Turtle Creek" cluster, but did separate out the Turtle Creek marsh edge due to low densities of plants and higher abundances of some prey (Fig. 4). Dietary diversity in Turtle Creek was greater due to the presence of *Ilyanassa*, and all prey but *Geukensia* were more abundant there. This creek had the greatest availability of resources (Fig.2). In addition, plant density was lower on the marsh surface and edge habitats of Turtle Creek than all other creeks. In Princess Creek, where *Melampus* was found primarily on the marsh surface, the *Scirpus* density was the highest, possibly restricting access to prey by any but the smallest terrapins. In New Creek, total stem counts almost doubled in density from the marsh edge to the marsh surface, again possibly restricting access to prey away from the marsh edge. It would appear that the low plant density of Turtle Creek may assist the terrapins by making resources more accessible there than in other creeks.

Other factors such as creek morphology, locality, and tidal amplitude may also affect terrapin distribution. Turtle Creek differs physically from the other creeks. Located on Nell's Island, the oldest part of the marsh, it has the highest creek banks offering access to additional prey. The mudflats are firmer and the channels sandier than other creeks. It has the deepest channel, which fills early at high tide and drains late at low tide. This low-tide access to deep water presumably provides refuge for the terrapins at low tide (Chambers, personal communication).

Of the five creeks, we know for sure that two did not support terrapins via sampling done by Chambers, and no terrapins were ever observed in the two not directly sampled. Although we extended our analyses and interpretation to the latter two creeks, we believe that our findings help to set up hypotheses about where terrapins might or might not be found based on prey availability and salt marsh structure. Further research is needed to examine the actual consumption of prey by adult males and females and by juvenile terrapins, to refine the assessment of prey availability and accessibility and to consider these in relation to other habitat requirements of terrapins. In turn, these data can aid in the development of quantitative habitat suitability models. The cumulative effects of habitat degradation have the potential for negatively impacting the ability of diamondback terrapins to maintain viable populations in coastal ecosystems, especially those near the northern limit of the species range. Research on various aspects of terrapin ecology can help to develop management plans for systems like Wheeler Marsh that have resident populations of this unique species.

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