Diet and Prey Choice of Female

Diamond-backed Terrapins (*Malaclemys terrapin*) in Jamaica Bay, New York

THESIS

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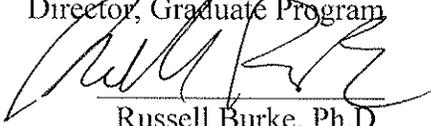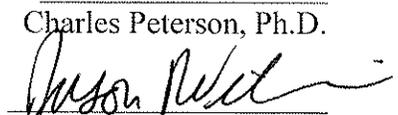
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Abstract

The diets of 129 adult female northern diamond-backed terrapins (*Malaclemys terrapin terrapin*) were examined by means of fecal analysis and controlled feeding trials during three consecutive nesting seasons at the Jamaica Bay Wildlife Refuge, Queens, New York. Only one thorough dietary study using fecal analysis has been published on *Malaclemys* diets, and none in the Northeast, where potential prey species differ from those that occur elsewhere in the range. Based on work from other locations in the *Malaclemys* range and to similarities in head morphology to the alabama map turtle (*Graptemys pulchra)*, I predicted that JB diamond-backed terrapins would consume primarily gastropods, bivalves and crustaceans. While I found that bivalves and crustaceans do make up 57% of their diet, there was very little evidence of gastropod consumption. I also found a higher abundance of vegetation, especially sea lettuce (*Ulva lactuca*), than previously documented, however, a correlation test between sea lettuce and soft shelled clams (*Mya arenaria)* supported the hypothesis that vegetation was accidently ingested when feeding on soft shell clams. Through the use of Monte Carlo simulations I also found that although the diets of *Graptemys*, *Trachemys* and *Malaclemys* were overall more similar than expected by chance, significant differences occurred in prey type consumption between all three species and between other *Malaclemys* diets studies using χ^2 tests. My results suggest that *Malaclemys* diets vary geographically, and cannot be determined from a single study. Multi-year studies throughout the entire range of *Malaclemys* will be necessary to fully characterize their dietary ecology.

Introduction

There are approximately 22 living species of emydid turtles (Fritz and Havas, 2007) within the Deirochelinae clade (Spinks et al., 2009; Weins et al., 2010). All are aquatic, and sexual dimorphism is widespread and sometimes extreme. The chicken turtle, *Deirochelys reticularia,* is the only strict carnivore; the others, such as the painted turtle, *Chrysemys picta,* are omnivorous (Ernst and Lovich, 2009). Species in the genera *Trachemys* and *Pseudemys* tend to undergo an ontogenetic shift from carnivory to herbivory as they mature (Hart, 1983; Parmenter and Avery, 1990; Bouchard and Bjorndal, 2006). This may be attributed to a habitat shift from shallow to deeper waters (Hart, 1983; Congdon et al., 1992) and changes in digestive physiology (Whelan et al., 2000; Bouchard and Bjornal, 2006). Among the 12 species in genus *Graptemys*, relative head width is correlated to differences in diet, with little molluscivory in microcephalic species, moderate to high molluscivory in mesocephalic species, and high molluscivory in megacephalic species (Lindeman, 2000). These comparisons are difficult to apply to *Malaclemys*, because *Malaclemys* are ambiguously sister to *Graptemys* and *Trachemys* (Spinks et al., 2009; Weins et al., 2010) and comparative studies based on morphology across these genera are rare (e.g., Stephens and Weins, 2008, 2009). However, all recent phylogenetic hypotheses indicate that the monotypic genus *Malaclemys*, which inhabits brackish water coastal environments, is derived from freshwater ancestors.

McDowell's (1964) taxonomic study grouped *Graptemys* into *Malaclemys* based largely on the similarity of their skulls and the triturating surfaces of their upper jaws. After examining many more specimens, Wood (1977) also noted the strong similarities between *Graptemys* and *Malaclemys* skulls, but reviewed numerous ecological

differences. Dobie (1981) noted that skull shape of adult female *Malaclemys* closely resembled that of adult female false map turtles (*G. pseudogeographica*), northern map turtles (*G. geographica*), barbour's map turtles (*G. barbouri*) and Alabama map turtles (*G. pulchra*), and predicted that these resemblances were probably due more to convergent evolution for feeding on similar food items than shared ancestry. However, given the close phylogenetic relationship between these taxa, these causes should not be considered mutually exclusive. These four *Graptemys* species were classified as either mega- or mesocephalic by Lindeman (2000), based on measurements of body size adjusted skull width and alveolar width; therefore I hypothesized that the prey species consumed by *Malaclemys* would be morphologically and ecologically similar to prey of those *Graptemys*.

Both false map turtles and northern map turtles consume gastropods, bivalves, annelids, crustaceans, insects, algae, and fish carrion. (Garman, 1890; Surface, 1908; Lagler, 1943; Penn, 1950; Vogt, 1981; White and Moll, 1992; Lindeman, 2006; Ernst, 2009). False map turtles also consume bryozoans, small vertebrates and vegetation (Garman, 1890; Cahn, 1937; Parker, 1939; Carr, 1952; Webb, 1961; Ernst and Barbour, 1972; Moll, 1980; Vogt, 1980; Shively and Vidrine, 1984; Johnson, 1987; Collins, 1993; Lindeman, 2000). There are only two published diet studies of Alabama map turtles, but the asian clam (*Corbicula manilensis*) may be a new important food source for adult females (Marion, 1986; Ernst, 2009). Female barbour's map turtles eat mostly gastropods and bivalves (Cagle, 1952) and males tend to consume small insects and insect larvae, small gastropods, and plant material (Lee et al., 1975).

Diet Study Methodology

Although stomach flushing can be used to obtain dietary samples of live turtles, it is invasive and can cause jaw, palate and esophageal injury (Fields et al., 2000). Because of this, stomach flushing was discouraged by the National Park Service, the permitting agency at my study site. Alternatives include fecal analysis and controlled feeding studies. Fecal analysis is noninvasive but effective, especially for prey with chitinous or calcareous exoskeletons. However, a disadvantage of fecal analysis is possible omission of soft-bodied prey species if they are well digested before excretion. Pairing fecal analysis with observational studies can produce more complete dietary data. This combination can also identify food preferences, such as whether predators eat particular soft-bodied prey species and to help identify and quantify hard-bodied prey consumption more accurately than through fecal analysis alone.

Terrapin Natural History

The diamond-backed terrapin (*Malaclemys terrapin*) is the only truly estuarine North American turtle. The seven subspecies inhabit the brackish waters of the Atlantic and Gulf coasts, ranging from Massachusetts to Texas. All exhibit extreme female-biased sexual dimorphism (Carr, 1952). The northern diamond-backed terrapin (*Malaclemys t. terrapin*) is the largest subspecies, in terms of body size and is found from Cape Cod Massachusetts to Cape Hatteras North Carolina (Carr, 1952; Ernst et al., 1994).

There are 14 previous studies pertaining to diamond-backed terrapin diets and all are no longer than a single year in duration. Studies based on observations of feeding in the wild and stomach dissections found that northern diamond-backed terrapins consume mostly marsh periwinkles (*Littoraria irrorata)* in North Carolina (Coker, 1906) and soft-

shelled clams (*Mya arenaria*) in Maryland (Roosenburg et al., 1999). Studies of captive

hybrids between carolina diamond-backed terrapins and northern diamond-backed

terrapins of all ages found that they willingly ate blue crabs, fish, oysters, clams, fiddler

crabs, canned fish, liver, beef and small mollusks (Hildebrand,1928; Allen and Littleford,

1955).

Five previous terrapin diet studies have used fecal analysis (Figure 1). Percent

frequency of occurrence (PFO) values showed carolina diamond-backed terrapins

consumed predominantly marsh periwinkles in South Carolina (Tucker et al., 1995) and

dwarf surf clams (*Mulina lateralis*) in northern Florida (Butler et al., 2000). Studies of

northern diamond-backed terrapins found the dominant prey item of adult females to be

Atlantic blue crabs (*Callinectes sapidus)* in North Carolina (Spivey, 1998) and eastern

mudsnails (*Ilyanassa obsoleta*) in New York (Petrochic, 2009). Diets of wild hatching

terrapins are not well known, however hatchling and yearling northern diamond-backed

terrapin in New York appear to be dietary generalists, feeding in the high intertidal marsh

and consuming mostly introduced (Grosholz and Ruiz, 1996) european green crab

(*Carcinus maenas*) (King, 2007). Results from 11 of the 14 diet studies show terrapins

exhibit moderate to high levels of molluscivory, much like *Graptemys*, however there is

considerable variation in both prey availability and prey consumption rates among study

sites. This variation has not been examined. At present, no substantial multi-year diet

studies have been performed on the northern diamond-backed terrapins. The most

significant previous dietary study (Tucker et al., 1995) is limited to Carolina diamond-

backed terrapins from a single nesting season and may not be representative of the

species as a whole. Multiyear studies of diamond-backed terrapins in Jamaica Bay are

necessary to determine how diets may fluctuate year to year and if changes in diet can be attributed to habitat alterations and climate change. Knowing more about diets in Jamaica Bay may provide knowledge into their exact role in the ecosystem. My study is the first statistically meaningful multi-year diet study of northern diamond-backed terrapins.

Methods

Study Site

JB is a polyhaline embayment at the extreme southwestern end of Long Island NY, part of the boroughs of Brooklyn and Queens NY, and connected to the Atlantic Ocean through Rockaway Inlet. The current average bay depth is about five meters, with an average flushing time of about 35 days (Swanson et al., 1992). The salinity varies from 28-32 parts per thousand near the Rockaway Inlet to 16-27 ppt near the Bergen Basin outfall (Frame, 2009a). Northern quahogs (*Mercenaria mercenaria*), soft shell clams and blue mussels (*Mytilus edulis*) are abundant in the mud flats and deep waters. Atlantic ribbed mussel (*Geukensia demissa*) and northern rock barnacles (*Semibalanus balanoides*) are prevalent in the upper half of the inter-tidal zone and both eastern mudsnails and common Atlantic slippersnails (*Crepidula fornicata*) dominate tidal creeks. Additionally, sea lettuce (*Ulva latuca*) and smooth cordgrass (*Spartina alterniflora)* are abundant throughout the nutrient-rich waters of the bay.

The history of diamond-backed terrapins and their prey in Jamaica Bay (JB), is unclear, but abundance and distribution of these species have probably experienced dramatic changes in the recent past. JB has undergone significant alterations in size and shape as a result of urbanization, similar to urbanization's effect on estuaries elsewhere in the diamond-backed terrapin range (Dean et al., 1987; Titus, 1988; Allen and Pye, 1992;

Wray et al., 1995). In the 1700s urbanization along much of the U.S. Atlantic coast increased sediment and sewage loads in salt marshes (Odum et al., 1984; Hanson and Lindh, 1993; Ehrenfeld, 2001) and in the 1800s wide-scale diking, dredging, and filling of urban salt marshes became common as shipping and industry expanded (Dahl, 2000). These factors, along with global climate change, have contributed to substantial salt marsh loss (Englebright, 1975; Hartig et al., 2002).

JB was relatively unaffected by urbanization until the mid-1800s (Black, 1981) however, the consequences of urbanization have altered its flushing time, tidal amplitude, nutrient composition, and salinity (Franz, 1985). During the past three centuries JB has lost 90% of its salt marshes and 95% of its freshwater wetlands (Frame, 2009). In 1900, JB encompassed 9712 hectares, with an estimated 6544 hectares of salt marsh land and 3169 hectares of open water (Franz, 1985). By 1970 the total acreage of JB was only 5261 hectares, of which 1619 were marshland (Englebright, 1975). Loss of terrapin habitat in JB is on-going; *Spartina* marshes continuously deteriorate due to combined effects of changes in sediment deposition patterns, nutrient pollution, and ocean level rise (NPS, 2001; Gornitz et al., 2002; Hartig et al., 2002). diamond-backed terrapins forage in shallow tidal creeks and subtidal mudflats (Palmer and Cordes, 1988), therefore the salt marshes changes described above may have probably influenced diamond-backed terrapin diet choice and prey availability.

Prior to the 1920s JB supported a substantial fishery with abundant fish, clams, and eastern oysters (*Crassostrea virginica*) (Black, 1981). The lower Hudson had 90,650 hectares of oyster beds along the shores on Brooklyn and Queens in Jamaica Bay, in the East River and on all shores of Manhattan (Kurlansky, 2006). Currently there are no

Eastern Oysters in JB due to overharvesting and pollution. Similar factors have dramatically lowered the oyster population in the Chesapeake Bay (Rothschild et al., 1994), resulting in greatly reduced water filtration rates and hypoxic conditions (Kemp and Boynton, 1984). Because of this, the Chesapeake Bay experienced a shift in dominant macroinfaunal species in deep muddy sediments from larger older bivalves to short-lived opportunistic species (Holland et al., 1987). A similar shift may have occurred in Jamaica Bay, thus altering the prey species available to Diamond-backed Terrapins, but historical records are insufficient to test this.

Since 2003 approximately 30 hectares of JB salt marsh have been restored and plans to restore an additional 8-14 hectares are underway (Patricia Rafferty NPS, pers. comm.). Additionally, researchers are investigating the potential for reintroduction of eastern oysters, Atlantic bay scallops (*Aequipecten irradians)* and eelgrass (*Zostera marina)* beds to restore JB native plant and animal communities and improve water quality (Frame, 2009b). These restoration projects could influence diamond-backed terrapin diet choice and prey availability,however, recent poor oyster survival rates in JB indicate that conditions have changed so dramatically that JB may no longer be able to support oysters.

Fecal Sample Collections

In June and July of 2008, 2009 and 2010 I collected female northern diamond-backed terrapins that had nested on the western half of Ruler's Bar, an island centrally located within JB. I induced defecation by soaking terrapins individually in fresh water (Tucker et al., 1995). I soaked diamond-backed terrapins indoors in 2008 and 2010 and

outdoors under a shade structure in 2009, in individual coolers, with approximately 23 liters of freshwater each, allowing for full coverage of their carapaces. I soaked terrapins individually, and for two days in 2008 and for five days in 2009 and 2010. Water was replaced in the coolers daily. Terrapins were released back into JB after fecal collection. Feces were collected daily by pouring the water into a sieve (1 mm standard size mesh) and preserving the solid material in formalin. All fecal samples from the same terrapin were pooled. Individual pieces of prey were separated from fecal samples using forceps and a dissecting microscope. Samples were air-dried in a hood and food items were identified to species where possible. Molluscan and crustacean pieces were compared to live specimens collected from JB and to Gosner's (1987) field guide to the Atlantic Seashore. Items that I could not identify to species were placed into more general categories.

Fecal Analysis

I classified fecal sample contents into the following groups: Plantae (leaves/stems, seeds, grass); Algae (sea lettuce and algae other than sea lettuce); Bivalvia (soft shell clams, Atlantic ribbed mussels, and amethyst gem clams (*Gemma gemma*)); Crustacea (crabs and ostracods); Gastopoda (eastern mudsnails, rough periwinkles, convex slippersnails (*Crepidula convexa*)); Bryozoa/Porifera; Insecta; Annelida (polychaete tubes); Invertebrate eggs (Atlantic horseshoe crab (*Limulus polyphemus*) eggs, and invertebrate egg masses); and unidentifiable animal tissue/detritus. I calculated the percent frequency of occurrence (PFO) by summing the number of times each prey species was identified in any of the fecal samples for a particular year and dividing that number by the total number of individuals whose feces were collected that year. PFOs

were calculated for each year (2008, n =36; 2009, n= 43, 2010, n=50) and for a

combination of all three years (n=129).

Comparisons with published diet data

  I searched the available literature for published *Malaclemys*, *Graptemys*, and

Trachemys diet data that met the following criteria: 1) Fecal analysis was the primary

method of sample collection, 2) During fecal collection, individuals were housed in

separate containers so percent frequency of occurrence could be calculated for each prey

item, and 3) Diet data were obtained primarily from adult females. I used major

taxonomic groups including Plantae, Bivalvia, Gastropoda, Crustacea, Algae, Insecta,

Gnathostomata, Annelida, Bryozoa/Porifera, and Invertebrate eggs to compare results

between different subspecies of *Malaclemys* and between *Malaclemys*, *Trachemys* and

Graptemys. Percent frequency of occurrence of prey items from literature meeting all

criteria was compared to my data using an adaptation of Pianka's symmetric equation

(see below).

Statistical analysis of diets

  First, I compared PFO for specific prey types between years using χ^2 tests in all

cases where PFO were greater than 30% for at least one season. Second, I used Pianka's

(1973) symmetric equation to calculate the overall similarity of the utilization frequencies

of prey items between years and between my combined (all years) data and data from

other studies. Pianka's equation is: where n is the number of prey categories, p_{ij} is

the proportion of prey item $_i$ in one year (or in one study when comparing one study to

another) and p_{ik} is the proportion of prey item $_i$ in another year (or in another study when

comparing one study to another). For example, using my data to compare diets from 2009

and 2010, p_{ij} would be 0.100 (the proportion of diamond-backed terrapins that ate crabs

eaten in 2010) and p_{ik} would be 0.069 (the proportion of diamond-backed terrapins that

ate crabs in 2009). When comparing my study to Butler (2000) p_{ij} would be 0.054 (the

proportion of diamond-backed terrapins that ate gastropods in my study) and p_{ik}would be

0.582 (the proportion of diamond-backed terrapins that ate gastropods in South

Carolina). This would be repeated for all prey categories. p_{ij} and p_{ik} are multiplied

together for all prey categories and the resulting values are summed. This value is then

divided by the square root of the sum of p_{ij}^2 (proportion of all prey items from 2010

squared) multiplied by the sum of p_{ik}^2 (proportion of all prey items from 2009 squared).

This produces an O value (letter O) between 0.0 (no overlap) and 1.0 (total overlap).

However, because the results of these calculations are non-parametric, meaningful

statistical comparisons cannot be made from O values alone. Instead, I used Monte Carlo

simulations created by using subsets my data to create pseudo-communities with

Lawlor's (1980) random RA3 algorithms. Pianka's equation was used to compare the

pseudo-communities to my collected data; however, p_{ik} was replaced with a_{jk} in which a_{jk}

represented a value randomly chosen from the Monte Carlo simulations. The RA3

procedure conserves niche breadth for each seasonal sample at each simulation, but

destroys the resource utilization matrix's zero structure, which means values taken from

observed data between zero and one were assigned to each prey category to create a

pseudo-community. Once an O value was calculated using Monte Carlo simulations for

each pair of years (2008-2009, 2009-2010, 2008-2010) the mean O value was calculated

for each year, then each pair of years was compared with the mean of the observed O

values. If the O value of the observed index was greater than or equal to the O value of

the simulated index, the p value was closer to 0.0000, indicating a significant difference. If the O value of the observed index was less than or equal to the O value of the simulated index the p value was closer to 1.0000, indicating no significant difference. Chi square tests were also performed on pseudo-communites to test for significant differences between individual prey categories.

<u>Feeding Trials</u>

During the summer of 2009, after fecal collection, 56 northern diamond-backed terrapins were housed individually in 37.8 liter tanks that each contained approximately 20 liters of water that had been treated with Instant Ocean (Spectrum Brands, Inc) to raise the salinity to approximately 18ppt. These diamond-backed terrapins and tanks were kept outdoors under shading and randomly assigned to experimental trials in which 10 potential prey species in different combinations were offered. In 32 treatments, a single prey species was offered; in 24 treatments two prey species were offered. Individual prey specimens were of similar size and numbers of each prey given were distributed equally based on weight. On the first day of each trial each terrapin was presented with potential prey and observed briefly. Terrapins were then left with prey items in the tanks for two additional days and the number of prey individuals remaining in the tank was recorded daily.

Potential prey species in single species trials were periwinkles (*Littorina* sp.) (2 trials, each offering 1 snail), Atlantic oyster drills (*Urosalphinx cinerea)* (1 trial offering one snail), bloodworms (*Glycera* sp.) (1 trial offering one worm), sea lettuce (7 trials, each offering 4 5cm x 5cm squares), eastern mudsnails (6 trials, each offering 5 snails), Atlantic ribbed mussels (13 trials each offering 30g of mussels), soft shelled clams (3

trials, each offering 30g of clams) and sea walnuts (*Mnemiopsis leidyi*) (3 trials each offering 5 sea walnuts); prey were collected live from Jamaica Bay. Periwinkles and eastern mudsnails were chosen because they were consumed heavily in other terrapin diet studies (Tucker, 1995; Petrochic, 2009). Bloodworms and sea walnuts were chosen as they are soft-bodied and cannot be detected through fecal analysis alone. Soft shelled clams, sea lettuces, Atlantic ribbed mussels and Atlantic marsh fiddler crabs were chosen to further investigate findings from fecal analysis from 2008.

Combinations of prey items offered included the following pairs: soft shell clams and ribbed mussels (30g each; 13 trials), asian shore crabs (*Hemigrapsus sanguineus*) and ribbed mussels (30g each; 5 trials), asian shore crabs and Atlantic marsh fiddler crabs (*Uca pugnax*) (20g each; 2 trials) and soft shell clams and soft shell clams wrapped in sea lettuce (20g each; 4 trials) which was done to test if terrapins may be consuming sea lettuce inadvertently while feeding upon soft shelled clams.

Statistical Analysis of Feeding Trials

I used a correlation test between soft shelled clams and sea lettuce occurrence to test for non-random patterns in a presence–absence matrix (Gotelli and Graves, 1996). I created a basic checkerboard unit, as described by Stone and Roberts (1990) using the observed presence/absence data of soft shelled clams and sea lettuce in diets of individual terrapins for all three years combined. I calculated a checkerboard score, or C-score, defined as the mean number of checkerboard units per species pair, from this unit (Stone and Roberts, 1990). The C-score measures the average pairwise species segregation for the entire matrix (Gotelli, 2000). Next, 5,000 pseudo matrices were generated by shuffling the observed data matrix, using a SYM4 randomization algorithm which

provides fixed species total but creates random proportional site totals (Luiselli et al., 2007). The observed C-score was then compared to the distribution of simulated C-scores. Co-occurrence patterns were considered statistically significant if the observed index was significantly larger than 95% of the simulated indices (Luiselli et al., 2007).

<u>Head Width Comparisons</u>

I measured plastron length, head width and alveolar width of adult female and male northern diamond-backed terrapin museum specimens from Connecticut, New York, New Jersey, Delaware, Virginia and Maryland. I used the methodology of Lindeman's (2000) study on *Graptemys* and the combined data to classify northern diamond-backed terrapins as microcelphalic, mesocephalic, or macrocephalic.

Results

<u>Fecal Analysis</u>

Of 145 Diamond-backed Terrapins soaked, 129 provided usable fecal samples (Table 1). Insects were lumped into a single category, as many could not be identified to species. Those that could be identified were from orders Coleoptera and Hemiptera and families of Dytisidae and Saldidae respectively. Crabs were also lumped together as some fragments could not be identified to species. Those that could be identified were flatback mud crabs (*Eurypanopeus depressus*), lady crabs (*Ovalipes ocellatus*), Atlantic sand fiddler crabs (*Uca pugilator*), and european green crabs (*Carcinus maenas*). In 2008 the prey items with the highest PFOs were Atlantic ribbed mussels and amethyst gem clams, but in 2009 and 2010, the prey items with the highest PFOs were sea lettuce and soft shelled clams (Table. 1). All white shell fragments were identified as soft shelled clams, however the baltic clam (*Macoma baltica*) is present in JB and is similar in appearance to

the soft shelled clam. Because all complete samples in which hinge structures were present were identifiable as soft shelled clams, similar samples lacking a hinge fragment were assumed to be soft shelled clams as well. Items found in fecal samples from this study, not yet reported in previous studies include Atlantic horseshoe crab (*Limulus polyphemus*) eggs and algae containing invertebrate egg masses.

The RA3 algorithm showed that overall diet composition was more similar than expected by chance in comparison between the three years (O=0.731, p< 0.001). Similarly, χ^2 tests from pseudo-communities revealed no significant differences between years in individual prey categories. However, χ^2 tests revealed significant differences in PFO values among all three years for soft shelled clams (p=0.02145), sea lettuce (p=0 .00039), grass (p= 0.01220), and Atlantic ribbed mussels (p= 0.00159).

When all fecal samples were combined over the three-year study the prey items with the highest PFO were sea lettuce (46.51%) and soft shelled clams (44.19%) (Table 1).

Comparisons with Published *Malaclemys* Diet Data

Although data from Petrochic (2009) did not fit my selection criteria because it included both male and female diamond-backed terrapins sampled across all seasons, I included her data in this analysis because it was especially valuable; her study was of the same subspecies and from Oyster Bay, NY (OB), a population only 48 km from JB. Instead of combining prey into general taxonomic groups as I did for all other comparisons, I used species-specific comparisons for analysis, as prey species are very similar in both Jamaica Bay and Oyster Bay. Comparison of JB diamond-backed terrapin PFO values (all years combined) to OB diamond-backed terrapins (Petrochic, 2009)

showed they neither more similar or different than expected by chance (O= 0.437, p= 0.31) . In contrast, I found significant differences using χ^2 tests and simulated data from Monte Carlo simulations between PFO's of OB and JB diamond-backed terrapins in rough periwinkle, Atlantic ribbed mussel, eastern mudsnail, amethyst gem clam, crab, baltic clam and *Hydrobia* sp. categories.

Comparison of JB diamond-backed terrapin PFO values (all years combined) to Carolina diamond-backed terrapins from South Carolina (Butler, 2000) showed they were neither more similar or different than expected by chance (O = 0.486, p = 0.322). In contrast, I found significant differences using χ^2 tests and simulated data from Monte Carlo simulations between PFO's of Carolina diamond-backed terrapins and JB diamond-backed terrapins in the plantae, gastropoda and crustacea categories.

Comparisons with Published *Trachemys* and *Graptemys* Diet Data

Comparison of JB diamond-backed terrapin PFO values (all years combined) to a megacephalic river population of Alabama map turtle (*Graptemys pulchra*) (Lindeman, unpublished data) showed they were more similar than expected by chance (O=0.774) p= 0.026. In contrast, I found significant differences using χ^2 tests and simulated data from Monte Carlo simulations between PFO's of Alabama map turtle data and JB diamond-backed terrapin PFO's pooled across three years in the bivalvia and plantae categories.

Comparison of JB diamond-backed terrapin PFO values (all years combined) to a mesocephalic lake population of northern map turtles (Lindeman, 2006a) showed they were more similar than expected by chance (O= 0.776, p = 0.021). In contrast, I found significant differences using χ^2 tests and simulated data from Monte Carlo simulations

between PFO's of northern map turtles data and JB diamond-backed terrapin PFO's pooled across three years in plantae, bivalvia, and gastropoda categories.

Comparison of JB diamond-backed terrapin PFO values (all years combined) to those of pond sliders (*Trachemys scripta)* (Thomas, 1993) showed they more similar than expected by chance (O = 0.735, p = 0.047). In contrast, I found significant differences using χ^2 tests and simulated data from Monte Carlo simulations between PFO's of Pond Sliders data and JB diamond-backed terrapin PFO's pooled across three years in algae and fish categories.

<u>Feeding Trials</u>

In the single prey type trials northern diamond-backed terrapins did not consume any periwinkles, Atlantic oyster drills, sea lettuce, or eastern mudsnails. It is unknown whether sea walnut was consumed, because in the feeding tanks we could not see them. In the single bloodworm trial, the northern diamond-backed terrapins consumed the entire worm within two minutes of introduction. Six of 13 diamond-backed terrapins consumed at least one Atlantic ribbed mussel during the trials. All soft shelled clams were consumed within 24 hours.

In the two-prey species trials, of the 13 diamond-backed terrapins given a choice between soft shelled clam and Atlantic ribbed mussel, all soft shelled clams were consumed first, then at least one Atlantic ribbed mussel was consumed in each trial. Of the five diamond-backed terrapins given a choice between the asian shore crab and Atlantic tibbed mussel, all consumed at least one Atlantic ribbed mussel, while three diamond-backed terrapins consumed at least one asian shore crab also. Of the two diamond-backed terrapins given a choice between asian shore crabs and the Atlantic

marsh fiddler crabs, both ate at least one of each crab species. Of the four diamond-backed terrapins given a choice between soft shelled clams and soft shelled clams wrapped in a sheet of sea lettuce, all consumed the unwrapped soft shelled clam first and then unwrapped the soft shelled clam from the sea lettuce and ate it. They apparently avoided consumption of sea lettuce. Correlation tests using Monte Carlo simulations show that soft shelled clams were associated non-randomly and more frequently with sea lettuce than expected by chance (C-score = 123.33, P < 0.0001).

Comparisons of *Malaclemys* and *Graptemys* head morphology

Maximum head width/plastron length values of female (n=22, from NY, MD, CT) and male (n=8, from NY, CT, RI, MD) northern diamond-backed terrapins were found to be 0.190 and 0.186 respectively. Alveolar width/head width values were 0.253 (females) and 0.259 (males). These values place northern diamond-backed terrapins within the megacephalic group of *Graptemys* as described by Lindeman (2000), more specifically, their head morphology is most similar to the alabama map turtle (Lindeman, 2000)

Discussion

Terrapins in Jamaica Bay

Diet analyses can be used to indicate predator feeding microhabitats. The highest prey species PFOs of JB Diamond-backed Terrapins were Atlantic ribbed mussels, amethyst gem clams, soft shelled clams and sea lettuce. Although detailed invertebrate distributions have not been studied in JB, soft shelled clams bury themselves in soft sediments (Zwarts and Wanink, 1989) and are found throughout JB (Franz, pers. comm.). Atlantic ribbed mussels embedded themselves in and amongst salt marshes sediments,

often attached to Smooth Cordgrass stalks (Bertness, 1980) in the upper half of the inter-tidal zone. Eastern mudsnails and common Atlantic slippersnails (*Crepidula fornicata*) are found primarily in tidal creeks. Sea lettuce is abundant throughout JB (Frame, 2009). Diamond-backed terrapins may feed on sea lettuce and soft shelled clams throughout much of JB, and may move into intertidal, *Spartina*-dominated habitats where Atlantic ribbed mussels, amethyst gem clams, and crabs are found. Kumiga (2004) and Palmer and Cordes (1988) also suggested that diamond-backed terrapins move into intertidal areas to feed.

Although statistical tests found that the diet of Jamaica Bay diamond-backed terrapins were more similar than expected over three years, my PFO values were different enough to show fluctuations in prey species consumption year to year. Unfortunately, have no data on prey availability so I cannot say what changes in prey availability occurred in JB during this time however, there is reason to suggest that in the recent past JB has undergone a state change that may influence Diamond-backed terrapin prey abundance and distribution (Hartig et al., 2002; Mackenzie Jr., 2005). One notable change in JB over the past century is the extirpation of eastern oysters. Because of their reef-forming and filtration capacity, oyster depletion leads to reduced water quality and less complex habitats (Lotze, 2005). It is likely that abundance and distribution of diamond-backed terrapin prey species that once inhabited oyster beds have also change. Studies from other regions of the eastern United States have shown that artificial or restored oyster reefs can be as successful as natural reefs for providing habitats for high densities of Atlantic ribbed mussels, common mud crabs, flatback mud crabs, soft-shelled

clams, amethyst gem clams, (Meyer and Towsend, 2000; Rodney, 2007) all of which are diamond-backed terrapin prey in JB.

The prey of JB diamond-backed terrapins may also be affected by urbanization and climate change. Although filling and dredging of wetlands have been a primary cause of marsh loss in the past, more recent losses may be attributed to three other causes. Local sea level rise within JB is higher than the global average (Hartig et al., 2002) and pollution, specifically nitrogen loading, has also been linked to current salt marsh loss and the growth of sea lettuce (Mackenzie Jr., 2005). Areas of JB that once had dense stands of smooth cordgrass are now covered with sea lettuce (Hartig et al. 2002) and unusually dense clusters of Atlantic ribbed mussel (which have been implicated in the deterioration of JB (Franz, pers. comm.)) are now common, attached to the bases of remaining smooth cordgrass stems (Hartig et al., 2002). Although under normal densities Atlantic ribbed mussels can help stabilize and provide nutrients to smooth cordgrass (Bertness, 1984), the anomalously high numbers of Atlantic ribbed mussels attached to smooth cordgrass stems in JB may be acting as a barrier preventing normal water drainage during ebb tide, subsequently causing marshes to become waterlogged (Hartig et al., 2002). Additionally it has also been suggested that the expansion of sea lettuce may be smothering smooth cordgrass (Hartig et al., 2002). The expansion of sea lettuce also reduces the number of macroinvertebrates on sediment surfaces in JB by nearly 100% (Franz and Freidman, 2002). Studies of nearby New Jersey estuaries have found similar impacts of sea lettuce mat expansion on populations of copepods, polychaetes, amethyst gem clams, eastern mudsnails, and soft shelled clams (MacKenzie, 2000; MacKenzie and McLaughlin, 2000), all of which are important prey items for diamond-backed terrapins

in JB.

Because JB is losing salt marshes at about 20 hectares per year (National Park Service, unpubl. data), it is likely that some diamond-backed terrapin prey species are decreasing in abundance. For example, rough periwinkles, which typically live in smooth cordgrass marshes, and are consumed by diamond-backed terrapins in Oyster Bay NY (Petrochic, 2009) and usually live on smooth cordgrass, are not abundant in JB (Frame, pers comm.;Franz, pers comm.). Additionally, Atlantic ribbed mussels typically inhabit the microhabitat at the base of smooth cordgrass stalks (Bertness 1980); ongoing loss of smooth cordgrass marshes is may be altering the availability of smooth periwinkles and Atlantic ribbed mussels and therefore diamond-backed terrapin prey.

Feeding Trials

Feeding trials demonstrated that wild-caught diamond-backed terrapins will feed readily in captivity when offered appropriate prey species. My choice experiments showed that JB northern diamond-backed terrapins preferred soft shelled clams over Atlantic ribbed mussels, they consumed all soft shelled clams offered and always consumed soft shell clams before other prey. In feeding trials JB northern diamond-backed terrapins also did not consume eastern mudsnails, Atlantic oyster rills or periwinkle but did eat Atlantic marsh fiddler crabs; these findings concur with the results of the fecal analysis. In feeding trials JB diamond-backed terrapins also readily consumed Asian shore crabs, an invasive species not found in fecal samples but commonly observed in JB in a variety of near-shore habitats that they share with non-native European green crabs (Jensen et al., 2002). I could not identify some crab fragments in fecal samples to species; some of these may have been Asian shore crabs. Similarly, Lindeman (2006)

noted northern map turtles had sufficient dietary flexibility to add two non-native clam species to their diets. Although they consume invasive species, it is unclear whether either of these turtles consumes enough prey to affect populations of any prey species. One study by Levesque (2000), suggests that diamond-backed terrapins may play a vital role in the top-down control of ecosystems; In South Carolina they may lower the density of the salt marsh periwinkles, which in turn consume large amounts of smooth cordgrass.

My correlation tests showed that diamond-backed terrapin consumption of soft-shelled clams was non-random and more frequently associated with sea lettuce than expected by chance. Also, JB diamond-backed terrapins avoided sea lettuce in my feeding trials. Together these results suggest that Diamond-backed Terrapins consume sea lettuce incidentally while predating soft-shelled clams. While accidental plant consumption by diamond-backed terrapins had been suggested previously (Coker,1906; Tucker et al., 1995; Ernst and Lovich, 2009), my study provides the first robust evidence that diamond-backed terrapins ingest plant material incidentally while grazing for invertebrates. Butler (2000) mentioned a small amount of "unknown plant" found in Florida diamond-backed terrapin diets and Petrochic (2009) found over 70% PFO of plant material in New York diamond-backed terrapin diets but did not identify this to species. I found a high PFO of sea lettuce in JB diamond-back terrapin feces, which has not been reported in diamond-backed terrapins elsewhere. Soft shelled clams are normally found buried in sand and mud, up to 25cm deep however, their burial depth decreases in the presence of macroalgal mats (Auffrey et al., 2004) In JB, soft shelled clams occur directly below sea lettuce mats, on top of sand, at low tide (pers. obs). I suspect that the unspecified plant material found in other diet studies was likely

consumed through accidental consumption and may be associated with the consumption of another invertebrate prey species, just as soft shelled clams are associated with sea lettuce in Jamaica Bay. This should be further examined in future dietary analysis.

JB Diamond-backed Terrapins and other *Malaclemys* Populations

Although previous diamond-backed terrapin diet studies (e.g., Tucker et al., 1995; Butler, 2006; Spivey, 1998 and Petrochic, 2009) provided valuable information regarding prey species, they reported diet data from fecal and/or stomach content analyses as percent volume and/or percent mass, which are highly variable according to prey type. This is especially problematic with prey items such as sea lettuce, carrion, and hard-shelled clams and small snails. Percent volume/mass of fecal content is a poor index of volume/mass of prey items before consumption, especially in crabs, gastropods and bivalves. Additionally, Tucker et al. (1995) and Spivey (1998) developed similarity indices with arbitrary significance values and which cannot be analyzed statistically.   I was also unable to directly compare my results to either Tucker et al. (1995) or Spivey (1998) because fecal collection in those studies was reported on multiple turtles (grouped by size), their data were not collected by turtle individually (Tucker, pers. comm., Spivey, pers. comm.).

Neither of my comparisons of complete diets (all prey categories) indicated differences between the two terrapins diets I examined (Butler, 2000 & Petrochic, 2009). I expected to detect dietary differences among different populations of diamond-backed terrapins, because the ranges of common prey species do not completely overlap with the entire diamond-backed terrapin range. For example, soft shelled clams, an important prey

species for JB diamond-backed terrapins, do not occur south of South Carolina, restricting its possible consumption to northern diamond-backed terrapins.

Using χ^2 tests from Monte Carlo simulations to compare two geographically close diamond-backed terrapin populations (JB northern diamond-backed terrapins and OB northern diamond-backed terrapins (Petrochic, 2009)), I found that OB diamond-backed terrapins ate significantly more periwinkles, Atlantic ribbed mussels, eastern mudsnails, amethyst gem clams, baltic clams, *Hydrobia*., and crabs. These differences are surprising because OB is muddy-bottomed and bordered by smooth cordgrass and common reed, similar to JB, and most of the same species of invertebrates are present. The high PFO of eastern mudsnails (75.76) in OBH diets is especially surprising because eastern mudsnails are very common at JB but northern diamond-backed terrapins but rarely consume them there (2.8 PFO). I have no explanation for their low occurrence in JB diamond-backed terrapins diets.

Using χ^2 tests from Monte Carlo simulations I found differences between JB Diamond-backed terrapins and Carolina diamond-backed terrapins (Butler, 2000) diets in plant, *Littorina* sp., and crab categories. JB northern diamond-backed Terrapins ingested four times more plant material than Carolina diamond-backed terrapins. This could be due to the close association of soft shelled clams with sea lettuce. Soft shelled clams are very abundant in Jamaica Bay but occur only as far south as Cape Hatteras (North Carolina), which explains why Carolina diamond-backed terrapins do not consume them (Gosner, 1978) and may not be ingesting sea lettuce. Carolina diamond-backed terrapins consumed four times more periwinkle (*Littoraria irrorata*) (Butler, 2000; Tucker,1995), than JB northern diamond-backed terrapins. Marsh periwinkle does not occur north of

New Jersey (Meinkoth, 1981) although smooth periwinkle and common periwinkle do. Flatback mud crabs, lady crabs, and marsh fiddler crabs are abundant in JB and are consumed by diamond-backed terrapins however not as much as Carolina diamond-backed terrapins consume the squareback marsh crab (*Sesarma cinereum*) and other various crabs.

Evolution of feeding strategies

 To better understand the evolution of diamond-backed terrapins from freshwater ancestors (Wood, 1977; McDowell, 1964), I compared diamond-backed terrapin diets to those of their sister taxa. Conflicting phylogenies place diamond-backed terrapins sister to either *Trachemys* or *Graptemys* (Weins et al., 2010; Spinks et al., 2009), however diamond-backed terrapin skull morphology is more similar to that of *Graptemys* (McDowell, 1964; Dobie 1981). When I compared head and jaw dimensions of northern diamond-backed terrapins with those of *Graptemys* as analyzed by Lindeman (2000) I found that the head and jaw dimensions of the northern diamond-backed terrapin were megacephalic, most similar to the derived megacephalic Alabama map turtle and three other *Graptemys* species. Mesocephaly appears to be primitive for *Graptemys*, with both microcephaly and macrocephaly being derived (Lindeman 2000). This means that megacephaly has evolved convergently in both a *Graptemys* clade and in diamond-backed terrapins.

My results suggest that diets of diamond-backed terrapin, megacephalic *Graptemys*, mesocephalic *Graptemys* and *Trachemys* are all broadly similar in ecological types, but not the same species. Therefore as these taxa evolved to exploit different habitats, they have maintained conservative food preferences.

JB Diamond-backed Terrapins and Sister Taxa Diets

Using χ^2 tests from Monte Carlo simulated data, I found significant differences between the diets of JB diamond-backed terrapins and northern map turtles, a mesocephalic species. One of those differences was that female northern map turtles consumed much higher amounts of gastropods and bivalves than JB northern diamond-backed terrapins. Northern map turtles diets are much more similar to those of other diamond-backed terrapin populations (e.g., Tucker et al., 1995; Petrochic, 2009) that consume more mussels and snails.

Using χ^2 tests from Monte Carlo simulated data, I found significant differences between the diets of JB diamond-backed terrapins and Alabama map turtles. Alabama map turtles ate nearly double the amount of bivalves than JB diamond-backed terrapins and JB diamond-backed terrapins ate more plant material than Alabama map turtles. Alabama map turtle diets are also more similar to other diet studies of diamond-backed terrapin populations (e.g., Tucker et al., 1995; Petrochic, 2009) that consume more mussels and snails.

Using χ^2 tests from Monte Carlo simulations, I found that JB northern diamond-backed terrapins had much lower PFOs of algae and fish than pond sliders did (Thomas, 1993). Petrochic (2009) and Spivey (1998) also found that diamond-backed terrapin diets have low PFO of fish. Both JB diamond-backed terrapins and pond sliders eat substantial amounts of algae (this study; Dreslik, 1999; Thomas, 1993; Hart, 1983), although pond sliders apparently consume plant materials intentionally (Ernst and Lovich, 2009; Carr, 2008) whereas JB diamond-backed terrapins apparently consume algae incidental to foraging for soft shelled clams.

<u>Conclusions</u>

My results that all diets compared were not significantly different were surprising because this statistical technique has detected diet differences between and within other turtle species (Del Vecchio et al. (2011); Luiselli, 2006a; Luiselli, 2008a) as well as lizards (Lorenzo and Luiselli, 2007; Luiselli, 2008b) and snakes (Luiselli, 2006b; Akani et al., 2008). It is unknown whether the inter-annual changes I observed in diamond-backed terrapin diets occurs at other locations. In general, comparison of diamond-backed terrapin diets throughout the range could have been more robust if a uniform methodology was used in each study and if prey consumption was reported using PFOs of each prey species instead of lumping prey into generalized categories. In addition to this, future studies should be multi-year in nature and should include statistical comparisons of diamond-backed terrapin diets at multiple sites along with simultaneous surveys on prey species in order to better understand prey choice. Head morphology should be compared as Lindeman (2000) did across to detect any regional patterns in prey choice associated with head width. Additionally, males should be included in dietary studies to explore the possibility that they may be more insectivorous, as are megacephalic male *Graptemys.* Lastly, nutritional studies in which diets are analyzed for nutrient content and digestibility (e.g., Bjorndal, 1980) have yet to be conducted in diamond-backed terrapins, but would further enhance diet studies.

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Figure 1.

Map of United States outlining diamond backed terrapin range (in red) and the locations

of five previous diet studies that used fecal analysis (a: New York (Petrochic, 2009) b.

New York (King, 2007) c. North Carolina (Spivey,1998) d. South Carolina (Tucker et al.,

1995) e. Florida (Butler et al., 2000)).

Table 1.

Percent frequency of occurrence prey species consumed by Jamaica Bay Diamond-backed Terrapins during each sampling year (2008 n=50, 2009 n= 43, 2010 n=36).

	2008	2009	2010	3 years combined
Plantae				52.7
Leaf/Stem	30.56	18.60	32.00	27.13
Seeds	8.33	18.60	7.02	8.00
Grass	11.11	34.88	36.00	28.68
Algae				48.8
Sea Lettuce (*Ulva lactuca*)	19.44	74.42	42.00	46.51
Algae (other than sea lettuce)	5.56	2.33	0.00	2.33
Bivalvia				58.9
Soft Shelled Clam (*Mya arenaria*)	27.78	62.79	40.00	44.19
Atlantic Ribbed Mussel (*Geukensia demissa*)	33.33	2.33	6.00	12.40
Amethyst Gem Clam (*Gemma gemma*)	33.33	0.00	0.00	9.30
Crustacea				17.1
Crab sp.	30.56	6.98	10.00	14.73
Ostracods	5.56	2.33	0.00	2.33
Gastropoda				5.4
Eastern Mudsnail (*Ilyanassa obsoleta)*	0.00	4.65	2.00	2.33

Periiwinkle (*Littorina* sp.)	0.00	4.65	0.00	1.4
Convex Slippersnail (*Crepidula convexa*)	0.00	0.00	2.00	.78
Annelids				.78
Polychaete tube	0.00	0.00	2.00	0.78
Invertebrate eggs				4.7
Horseshoe Crab Eggs (*Limulus polyphemus*)	2.78	4.65	0.00	2.33
Invertebrate egg masses	5.56	2.33	0.00	2.33
Bryozoan				0.78
Bryozoans	2.78	0.00	0.00	0.78
Insecta				10.08
Insects	0.00	11.63	16.00	10.08
Unidentifiable animal tissue	13.89	20.93	8.00	13.95