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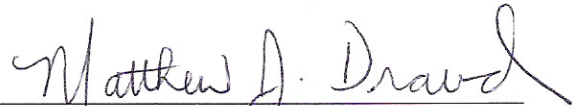
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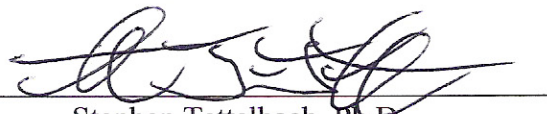
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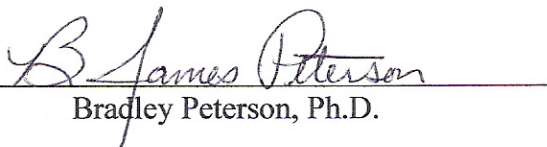
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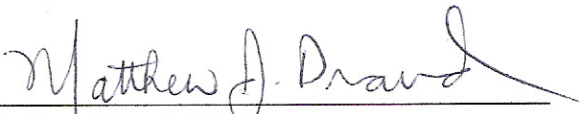
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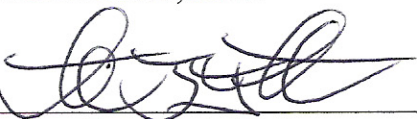
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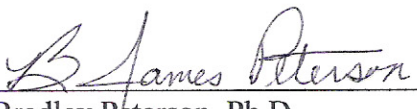
Feeding Ecology of the Northern Diamondback Terrapin, *Malaclemys terrapin terrapin*

A thesis submitted to the Faculty of the Graduate School in partial fulfillment of the
requirements for the degree of Master of Science (Biology)

APPROVED:


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22 April 2009
Date

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I. ABSTRACT

Malaclemys terrapin, the only estuarine turtle in North America, is believed to play an integral role in estuarine ecosystems. However, not much is known about its feeding ecology and its actual effect on community structure. This study measured bite force capability and utilized fecal analysis to examine various aspects of feeding ecology between sexes, among size classes, and over time in one subspecies, *M. terrapin terrapin*. It was determined that this subspecies, as a whole, is a dietary generalist that possesses relatively high bite forces. Diet and bite force were found to vary significantly among all groups. The relatively strong bite force of *M. t. terrapin*, and the large number of hard prey items found in samples indicated that terrapins may be able to take advantage of prey items that other organisms within the salt marsh ecosystem cannot consume, thereby making them a potential controller of community structure.

II. Chapter 1: A Brief Diamondback Terrapin History

The diamondback terrapin, *Malaclemys terrapin*, is the only estuarine turtle in North America. It is considered to be small to medium in size and is sexually dimorphic, with adult males having smaller carapaces (10-14 cm to adult females' 15-23 cm) (Ernst et al., 1994), longer tails, and smaller heads than adult females (Coker, 1906). Overall, diamondback terrapins are light skinned with dark markings ranging from specks to blotches. Their carapaces vary in color from light brown to black and have distinct concentric markings and grooves. The plastron is usually yellow to green or black and also can have dark markings. Each of *Malaclemys* seven subspecies has variations in shell shape, structure, and/or color unique to itself (Ernst et al., 1994).

Terrapins can be found in salt marshes and estuarine habitats in the temperate – sub-tropical zones (Hart & Lee, 2006) and each of its seven subspecies can be found at different latitude along the Atlantic and Gulf coasts from Cape Cod to the Florida Keys, into Texas, and possibly into Mexico (Fig. 1). The subspecies of interest, the northern diamondback terrapin (*M. t. terrapin*), can be found from Cape Cod to Cape Hatteras (Carr, 1952; Ernst et al., 1994).

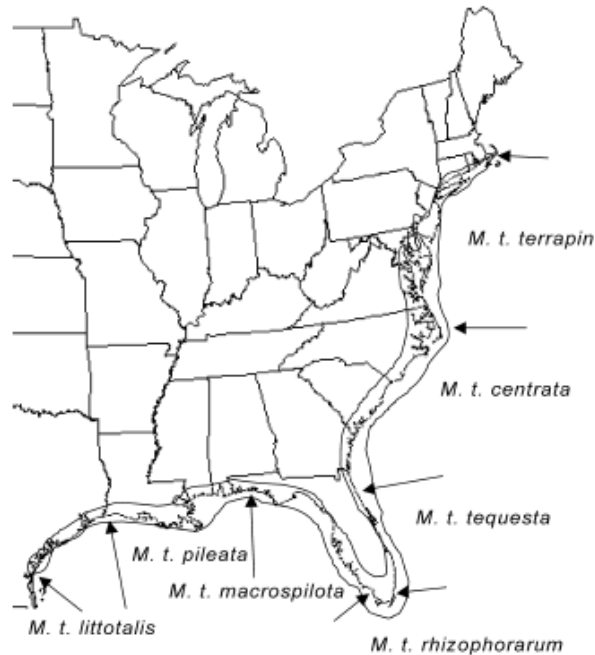


Figure 1: Ranges of the various diamondback terrapin sub-species (Hart & Lee, 2006).

While diamondback terrapin populations, as a whole, can be found over a large geographical range, individuals tend to exhibit high site fidelity and main stay within small areas as adults. Among populations in South Carolina, Gibbons et al, (2001), found little to no terrapin movement between adjacent creeks. Even females that underwent long journeys during nesting typically returned to the same marsh. A study of an Oyster Bay, Long Island, New York terrapin population found that adults have average home ranges of 278.26 ha and include both intertidal and shallow, sub-tidal habitats (Kumiga, 2004) adding support to this idea. Juveniles appear to utilize a different habitat from adults for the first 1-4 years of their life cycle (Gibbons et al., 2001; Lovich et al., 1991), with hatchlings staying in the intertidal areas of marshes using the dense wrack mats to hide from predators, stay cool, and gain access to a rich food source (Zimnavoda, 2004).

During winter months, terrapins undergo a period of hibernation, with adults primarily burying in soft mud that is covered by water (Yearicks et al., 1981). With few

exceptions, they do not surface or eat during this time period, but will become somewhat active on warm days. Juvenile terrapins hibernate terrestrially and are known to withstand short periods of freezing during hibernation (Baker et al., 2006; Coker, 1906).

After being harvested to the point of commercial extinction in the late 1800's and early 1900's (Carr, 1952; Coker, 1906), natural populations of diamondback terrapins are seemingly making a comeback (Gibbons et al., 2001). However, many within the field still consider most populations to be declining or believe that not enough information is known about terrapin populations to comment on their status (Butler et al., 2006), since even with the ending of large scale harvesting, many threats still remain for terrapin populations.

Crab traps are one of the biggest threats to terrapin populations today (Butler et al., 2006). Most terrapins that enter such traps are unable to escape and, as a result, drown. This threat is particularly high for males and small females, but less so for juveniles that are easily able to swim back out due to their smaller body size. Large females are also at a lower risk of this particular threat because they are too big to enter the trap to begin with (Hart, 1999). Traps that are abandoned or lost contribute significantly to mortality of terrapins in areas where crab fisheries dominate estuaries (Hart, 1999). One solution to this problem is the use of terrapin excluder devices (TED) on traps to prevent terrapins from entering them.

Other significant threats to terrapins populations today include changes in the estuarine habitats they occupy (Gibbons et al., 2001; Palmer & Cordes, 1988). Habitat loss and development can dramatically affect nesting site availability and thereby decrease population growth. For example, Chesapeake Bay terrapin populations are

losing nesting beaches due to homeowners' efforts to stabilize shorelines. Often bulkheads or other hardened structures are constructed and inadvertently prevent terrapins from accessing essential nesting areas above the intertidal zone. Since terrapins return to the same nesting areas year after year, hardening of these shorelines can dramatically decrease the number of terrapins that successfully breed by outright preventing nesting, causing the remaining suitable nesting sites to become overcrowded, or forcing terrapins to nest in areas where eggs are unlikely to hatch (e.g. sites that are flooded during high tide and therefore cause the eggs to drown) (Roosenburg, 1990). Development of marsh areas can also change freshwater input, which could have other drastic effects on terrapins (Hart, 1999).

Increased predation on terrapin eggs and hatchlings is another threat to the recovery of terrapin populations. Animals such as rats, crows, and raccoons are all known to be major predators of young terrapins in the wild (Draud et al., 2004). Other potential predators include crabs, fish, and several bird species (Coker, 1931). Plant roots can also be responsible for egg mortality if they grow through a nest (Coker, 1906; Hart, 1999).

Other, more recent, threats to consider are caused by increases in human recreational activities. As more people take part in boating activities, the numbers of terrapin injuries also increase. Females tend to be more at risk to such injuries than males, since they more often enter open water to reach nesting grounds (Gibbons et al., 2001; Hart, 1999). Adult females and hatchlings are also at risk of being crushed by motor vehicles when crossing roads to nest or after emergence from nests (Szerlag &

McRobert, 2006) and are susceptible to being run over by off-road vehicles on beaches adjacent to salt marshes (Palmer & Cordes, 1988).

In an effort to protect declining terrapin populations, certain steps can be taken. It has been suggested that limits should be placed on the number of crab traps that can be placed in high terrapin density areas. The use of TEDs on all traps, as well as removal of abandoned crab traps would also be a major step in limiting the number of terrapins killed by crab traps. Other ways to decrease terrapin mortality includes seasonally closing nesting beaches to human use, regulating dredging and placement of dredge material in marshes, regulating salt marsh drainage and impoundment, and prevention of bulkhead construction in salt marshes. Finally, educating the public about incidental terrapin mortality in crab traps could potentially help reduce the number of terrapins that are killed by recreational traps (Hart, 1999).

III. Chapter 2: Emydid Feeding Ecology

Emydidae is the largest family of living turtles with 33 genera and approximately 100 known species. They are the most abundant and ecologically diverse group of turtles in North America and occur in aquatic and terrestrial habitats, often utilizing both habitat types. They are capable of feeding on land, in water, or both, depending on species. Some species are active predators, while others are scavengers. Members of this family are known to feed on anything from aquatic and terrestrial vegetation, berries, and seeds to insects, mollusks, small crustaceans, and fish. Some have even been reported to consume small reptiles, amphibians, birds and mammals (Ernst et al, 1994).

Emydids are herbivores, omnivores, or carnivores, with most fitting into one of the following four general diet types - herbivory, insectivory, molluscivory, or omnivory. While most are omnivorous (Stephens & Wiens, 2003), some will undergo ontogenetic shifts as they age. Additionally, some turtle species may have dietary differences among size classes, sexes, or both, with the degree of dietary specialization often being determined by overall turtle community composition, prey availability (Moll, 1990), and/or differences in skull structure (Ward, 1980).

Two emydid species that have been found to undergo a shift in diet as they age are *Trachemys scripta* and *Chrysemys picta*. Both feed primarily on insects as juveniles and then shift to a mostly herbivorous diet as adults. Hart (1979) found that at ~120 mm, both species increased the amount of terrestrial vegetation consumed, while simultaneously decreasing the amount of insects consumed. After further study, it was

determined that *T. scripta* also has dietary differences between the sexes, with females being more herbivorous than males (Hart, 1983).

Map turtles (*Graptemys* spp.) are another good example of an emydid species with dietary differences between sexes and among size classes. They are aquatic turtles that primarily eat mollusks and aquatic insect larvae (Lindeman, 2006a). However, in a Pennsylvania population, it was found that adult females, including those equal in size to males, tended to focus on mussels, while males and juveniles fed primarily on insect larvae and small snails. This difference in diet was thought to be caused by females having larger jaws and alveolar surfaces (Lindeman, 2006b). Additionally, Lindeman (2000) discovered that females of different sizes classes also varied in degree of molluscivory. Females that possessed narrower heads consumed fewer mollusks than those with wider heads.

A study conducted by Moll (1990) found that turtles within a community consisting of multiple turtle species may modify their typical diets as a result of resource partitioning among species. In this particular community, *T. scripta*, *Kinosternon scorpioides*, and *K. leucostomum* had varying degrees of diet specialization among species. *T. scripta* females consumed mostly plants, males some insects and plants, and juveniles primarily insects, while the other two species were mostly carnivorous and had similar diets to each other. However *K. scorpioides* and *K. leucostomum* both became more specialized over the course of the study and their degree of dietary overlap decreased due to unknown reasons. While these diets were consistent with other studies, the degree of dietary specialization was thought to be affected by the presence of other turtle species within the community, most likely as a result of competition.

Another community composed of three species of map turtles (*Graptemys geographica*, *G. pseudogeographica*, and *G. ouachitensis*) was also found to exhibit resource partitioning (Vogt, 1981). Adult female *G. geographica* have much wider skulls than the other two species, while the skull of *G. ouachitensis* is only slightly wider than *G. pseudogeographica*; all three species are similar in shell length and body mass. In this community, *G. geographica* was found to have the least amount of dietary overlap with the other two species. Mollusks constituted a large part of its diet, while *G. pseudogeographica*, and *G. ouachitensis*, both consumed almost similar amounts of vegetation and animal material. While total vegetation was found to be consumed by the two species in roughly the same proportion, vegetation type was different.

It has been postulated that differences in skull shape alone can explain diet choices among turtles. The general trend is that insectivores have narrow alveolar surfaces, herbivores have broad ones, and molluscivores have jaw adaptations that allow them to crush hard prey items. These adaptations are often more prominent in adult females than males and therefore frequently account for the dietary differences between the sexes (Ward, 1980).

The general process by which emydids feed can be broken into a three step process of capture, chewing, and swallowing. Tearing and positioning of food items is often accomplished by using forefeet or jerking the head sideways. Molluscivores employ a grinding technique and herbivores take several bites before swallowing. The tongue is used to move food items within the mouth, to keep food items on the alveolar surface, or to hold them to the roof of the mouth. It also aids swallowing in all species (Ward 1980).

Other emydids, such as the eastern box turtle (*Terrapene carolina*), employ a suction feeding method accomplished by hyoid depression to capture aquatic prey. However, Summers et al. (1998) found that *T. carolina* (and perhaps most aquatic feeding turtles) do not actually produce enough suction force to bring prey items into the mouth, but rather only enough suction force to compensate for the pressure wave produced by the movement of the turtle's head toward the prey item. It was also determined that this species, as well as many others, are capable of regulating hyoid depression depending on feeding location (i.e. on land or in water).

When approaching prey items, turtles use multiple techniques. The diamondback terrapin, for example, will either make a swimming or slow walking approach depending on prey type. Once the prey item is in the terrapin's mouth, it is moved back and forth within the buccal cavity with the tongue to manipulate the item between the jaws in order to crush it (Bels et al., 1998).

According to Herrel et al. (2002), species that consume hard or large prey will bite harder for their body size than species that have a more generalized diet. They also found that species that evolutionarily shifted to diets that included large or hard prey, often had a corresponding evolutionary increase in bite performance since the ability to consume these items would free these turtles from the usual limitations of gape-limited predators, while also decreasing competition for food resources. This increase was found to result from an increase in head volume due to an increase in head height relative to carapace length.

In addition to prey size and hardness, prey availability and preference will also play a role in turtle diet. Given that *M. terrapin* has such a wide geographic range, it is

very likely that there will be dietary differences among subspecies. Also, since this is a sexually dimorphic species, it can be expected that males and females will have differences in diet (Shine, 1989). While few studies have looked at dietary differences between sexes and among size classes of diamondback terrapins, their general diet has been examined.

M. terrapin forage in shallow tidal creeks and sub-tidal mudflats (Palmer & Cordes, 1988), migrating into intertidal areas on incoming tides and then leaving with the out-going tide (Kumiga, 2004). They consume snails, fish, crustaceans, and beef in captivity (Coker, 1931), while wild terrapins feed mainly on crustaceans, and mollusks (Coker, 1931; Tucker et al., 1995). They also have been found to occasionally consume insects and marsh plants as well (Carr, 1952; Tucker et al, 1995).

Fecal analyses done by Tucker et al. (1995) found the marsh snail, *Littorina irrorata*, to be the major component of the diets of terrapins in South Carolina. The rest of the diet was comprised of various crabs (*Uca pugnax*, *Sesarma reticulatum*, and *Callinectes sapidus*), small marsh clams (*Polynesoda caroliniana*), and small barnacles (*Balanus sp.*). An insignificant amount of sediment and *Spartina sp.* was also found. Terrapins of Florida were found to consume mostly dwarf surf clams (*Mulina lateralis*) as well as smaller amounts of crab and *L. irrorata* (Butler, 2000).

While the importance of terrapins in their natural habitat is not fully known, they are believed to be an integral part of the salt marsh ecosystem (Hurd et al., 1979; Tucker et al., 1995). Terrapins are secondary consumers that potentially have major impacts on the benthic community in terms of diversity and biomass. They are often the main

predator on benthic invertebrates in the salt marsh ecosystem and, as such, may be acting as a top down controller of primary productivity.

Silliman and Bertness (2002) found that a typical marsh periwinkle (*Littorina irrorata*) population is capable of completely denuding areas of marsh cordgrass (*Spartina alterniflora*) in the absence of predators. Through the use of predator exclusion and tethering experiments, they concluded that marine predators are responsible for controlling the distribution and quantity of marsh periwinkle adults and recruits. This indirectly allows the high levels of primary production in marsh systems. They also believe that without predators, including terrapins, highly productive marsh areas could potentially be turned into mudflats by these grazers.

Many other ecological systems studied have been found to have top-down controls, as is possibly the case with terrapins in salt marsh systems. For example, in the presence of sea otters, urchin densities are low and macroalgae are able to flourish. If urchin densities are allowed to increase due to absence of otters, then macroalgae abundance is decreased (Estes et al., 1978). Additionally, Duggins (1980) found that removal of sea urchins is responsible for greater initial kelp diversity, but over the course of two years, diversity decreased with one species becoming dominant as plant competition became more important in determining community structure.

IV. Chapter 3: Examining Diamondback Terrapin Feeding Ecology

The overall goal of this study is to look at various aspects of the foraging ecology of *M. t. terrapin*, much of which is still unknown. I determined the diet of this subspecies in one Long Island population by examining fecal samples. I also determined bite force capabilities of the different sexes and female size classes. Seasonal differences in diet, as well as dietary differences among size classes and between sexes were also determined.

Since female terrapins have larger heads than males, it is to be expected that females will be capable of biting harder than males simply due to having larger jaw muscles. For the same reason, larger females should bite harder than smaller females. Differences in head size and bite force can potentially lead to differences in diet, both among size classes and between sexes. If such differences are found, large females should be found to consume larger and harder prey items than smaller females and males, due to few gape limitations and possessing a higher bite force.

Terrapin bite force was also compared to the closely related emydid species, *Trachemys scripta* (red eared slider). Since it is known that this species consumes primarily soft food items, and terrapins consume hard prey items, we believe terrapins should be capable of biting harder than red eared sliders of similar size.

Additionally, diet composition of the Oyster Bay *M. t. terrapin* population was compared to other *M. terrapin* subspecies found along the Atlantic coast. It is expected that while potential species available will differ due to differences in community composition, the types and ratios of prey items should be fairly consistent.

Methods:

Study Site

This study was conducted in Oyster Bay Harbor (Fig. 2b) on the north shore of Long Island, New York (40°57'N, 73°02'W) (Fig. 2a) where large terrapin populations are known to be found (Marganoff, 1970; Bossert & Draud, 2004). This bay ranges in depth from 2-9 m. The majority of the study took place in Mill Neck Creek (Fig. 2c) in the northwest portion of the bay. This small tidal creek is primarily surrounded by residentially developed land with lawns extending to the waterline at most points. It is backed by a two-lane paved road and has small borders of *Spartina* spp. or *Phragmites australis* where lawns have not been established. The creek itself is mostly muddy bottomed and becomes a mud flat during low tides. It supports benthic filter feeders such as clams, mussels, and oysters, as well as annelids, snails, and crustaceans such as crabs and shrimp.

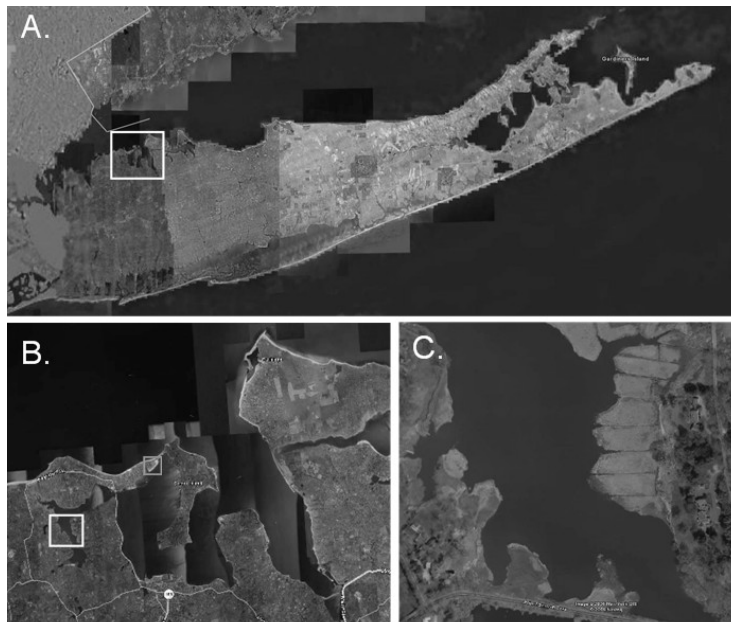


Figure 2: Map of study site. A. Long Island, NY- white square = Oyster Bay. B. Oyster Bay – white square = Mill Neck Creek; grey square = Center Island Beach. C. Mill Neck Creek

Study Animals

Terrapins captured in this study are part of a well known diamondback terrapin population. This particular population has been studied since 2000 and over 700 individuals have been tagged with passive integrated transponder (PIT) tags. They have also had one or more marginal scutes filed according to a coding system to indentify known individuals (Draud pers. Comm.).

Most animals examined in this study were captured between May 15th, 2007 and September 28th, 2007 in one of two locations in Oyster Bay; Mill Neck Creek or Center Island Beach (Fig. 2b). They were captured by seine net (n= 42) or baited crab trap (n= 87) in Mill Neck Creek or by hand while nesting (n= 4) on Center Island Beach. An additional 16 lab reared individuals were also used in the bite force and head shape analyses.

All captured terrapins were brought to the laboratory where measurements were taken. Weight of adult terrapins was measured to the nearest 25 g by placing an individual in a mesh bag and suspending it from a hanging fish scale (Chatillon). Juvenile (individuals that were too small to be accurately sexed) weight was measured using a digital scale (Ohaus Scout Pro SPE123) to the nearest 0.01 g. Shell measurements of all turtles included midline carapace and plastron lengths, maximum carapace width, and shell height at the deepest point between the highest ridge on the vertebral scutes and the plastron (Fig. 3). Head measurements were made to the nearest 0.1 mm using digital calipers (Mitutoyo) and shell measurements were taken to the nearest 1 mm using 50 cm Haglof tree calipers. The number of annuli present on the carapace was recorded when possible and any shell abnormalities were also noted.

Additionally, every terrapin that was not already tagged from previous studies had a PIT tag injected into its coelom with a hypodermic needle. Following procedures from previous studies (Draud, unpublished data), the injection site was located in the right hind leg region, slightly anterior to the pelvis, and beneath the bridge of the shell. Marginal scutes were also filed (Cagle, 1939) for future identification. Once all data had been collected, terrapins were released at their respective capture sites.

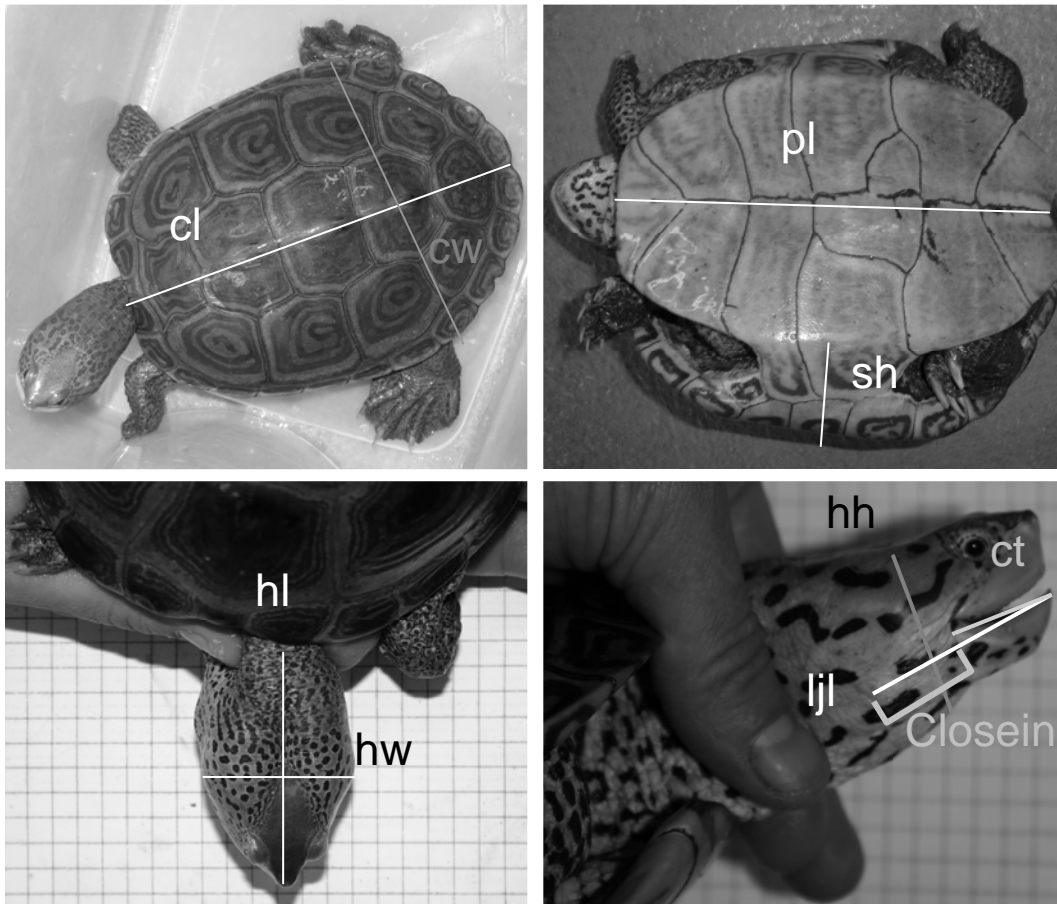


Figure 3: Terrapin morphometric measurements. cl- carapace length, cw- carapace width, pl-plastron length,sh- shell height, hl- head length, hw- head width, hh- head height, ct – coronoid to tip of lower jaw, ljl- lower jaw length.. Closein = size of the in-lever for jaw closing.

Bite Force

Bite forces of individual terrapins were measured using a gnathodynamometer (Kistler Inc.) (Fig. 4). This apparatus consisted of an isometric Kistler force transducer (type 9203) connected to a Kistler charge amplifier (type 5995). It recorded instantaneous force during the bite, as well as the peak pressure achieved. The plates of the apparatus were placed in the open mouths of the terrapins until they forcefully bit down. The peak force of the bite was recorded and the procedure was repeated five times per individual. The maximum bite force recorded was assumed to be the maximum force possible for that individual. The forces recorded were multiplied by 0.63 to correct for the lever arms of the apparatus and standardized for carapace length. These corrected and standardized forces were used to compare differences in male and female bite forces. Male and female diamond terrapin bite forces were also compared to male and female red eared sliders (Herrel et. al, 2002; Herrel & O' Reilly, 2006).

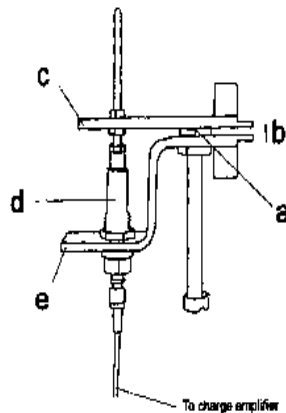


Figure 4: Gnathodynamometer used to measure bite force. a- fulcrum, b- bite plate, c- upper plate, d- force transducer, e- holder (Herrel et al., 2001)

Head Shape Analysis

Terrapins used in the bite force portion of this study were also used to determine differences in head shape between male and female terrapins. Head width, length, height, and volumes were standardized for carapace length and were compared for males and females. Head volume was calculated using the following equation:

$$\text{head volume} = \frac{(3.1415 * \text{head length} * \text{head width} * \text{head depth})}{6}$$

(Macías-Ordóñez & Draud, 2005).

Head shapes of male and female terrapins were also compared to those of similarly sized male and female red eared sliders (*T. scripta*), a closely related emydid species. Once again, head width, length, height, and volumes were standardized by carapace length.

Prey Resistance

The gnathodynamometer was also used to determine the compression resistance of several potential prey items including crabs, snails, mussels, and oysters. Each potential prey item was weighed to the nearest 0.001 g using a digital scale and measured to the nearest 0.1 mm using digital calipers. Carapace length, width, and height, along with claw length and width were measured for crabs. Shell height of snails (base to apex), shell length of bivalves (hinge to ventral margin), and width at the widest point of both snails and bivalves were measured. Snail operculum height and width were also taken when present.

All prey items were tested live to avoid potential structural changes to shell strength caused by death or temperature changes. The item was positioned on a flat surface in the way a terrapin would most likely bite it while a modified version (biting plates removed) of the gnathodynamometer was pressed down on the item until it was crushed and the force required for crushing was recorded. This method allowed for the determination of crushing force needed to break the prey items (Herrel et al., 2001).

Fecal Analysis

To quantify the diet of *M. t. terrapin*, fecal analyses were conducted. It was determined that examining only fecal content is adequate to ascertain major dietary components of terrapins because the few studies performed using other methods (primarily stomach content) have shown that the majority of terrapin prey items possess a calcareous or chitinous exoskeleton (Coker, 1951; Marganoff, 1970). Additionally, fecal analysis is the least invasive and harmful technique in determining diet and it was desirable not to harm individuals in this population.

Once terrapins were captured, they were transported to the laboratory where they were measured and placed individually in 90 L Rubbermaid totes with enough tap water to cover the carapace of the prone terrapin. Every terrapin was isolated for 72-96 hours at 28-32 °C and any fecal matter produced was removed daily from the totes. To collect the fecal samples, the individual was removed from the tote and placed in a dry bin. All water from the tote was passed through a number 18 sieve (1-mm) and the tote was washed with tap water until no feces remained in the tote. Fecal material was then removed from the sieve by either a reverse flow of water, inverting the sieve and forcing

contents onto a plexi-glass board, or a combination of the two methods. The retained material was then stored in individual jars in 90% ethanol until it was sorted. After fecal collection, the terrapin was placed back in the tote with fresh tap water until the collection period was over.

Fecal samples were processed after allowing the samples to air dry at least 8 hr on filter paper placed on a sieve. Each sample was sorted by hand, winnowing (Tucker and Fitzsimmons, 1992), or a combination of these methods. Winnowing was primarily used to separate the drastically lighter opercula and plant material from the heavier shell and other hard material.

Once separated, the fecal samples were examined and hard pieces were compared visually to known local species present at the study site. Opercula were separated into two species by comparing them to local species. Opercula lengths, widths, and area were measured using a microscope (Nikon SMZ1500) and NIS Elements Basic Research Imaging Software.

All fecal samples for an individual collected over the 3- 4 day period were combined since digestive turnover rates were not calculated. Percent occurrence and percent mass of each ingested species found were calculated and terrapins were placed in one of the following four size classes: males (all males and indeterminate sex), large females (carapace lengths >190 mm), medium females (carapace lengths 170-190 mm), and small females (carapace lengths <170 mm). Terrapins were also placed into one of four time periods: pre-nesting (May 15th - June 1st), nesting (June 2nd - July 27th), post-nesting (July 28th - August 31st), and pre-hibernation (September 1st - September 29th) roughly based on turtle movement patterns found by Kumiga (2004) (Fig. 5). Previous

studies of hibernating terrapins found no signs of foraging during hibernation (Coker, 1906; Yearicks et al., 1981) and therefore hibernating individuals were not sampled in this study.

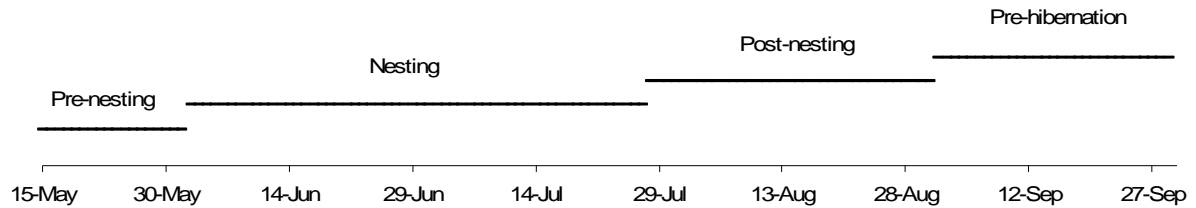


Figure 5: Time periods used in this study.

Similarity of terrapin diet (dietary niche breadth) among size classes and time periods was determined by the Shannon indices of diversity and evenness. The Schoener method was utilized to establish the dietary niche overlap of the above groups (Krebs, 1999).

Statistical Analysis

Multivariate regressions were used to compare maximum bite forces, head measurements and jaw measurements of male and female diamondback terrapins, male diamondback terrapins and male red eared sliders, and female diamondback terrapins and female red eared sliders. Weights of the various prey items found in samples, along with total sample weight and number of species found in samples were compared among the various size classes and time periods using Kruskal Wallis Non-parametric ANOVAs. Alpha levels for all ANOVAs were 0.05. Pairwise post-hoc nonparametric multiple comparison test (Zar, 1996), Tukey test or Dunn's method were used when necessary as follow-up tests to the ANOVAs.

To determine significance differences in diversity among size classes and time periods variation in H' and J' was created by a jackknifing technique. Ten calculations for each niche breadth and evenness were computed by systematically removing one individual from the sample set for each new calculation. No individual was removed more than once. Kruskal Wallis ANOVAs were then run using the created data set.

In all following box plots, the boxes represent the inter-quartile range, the middle line is the median, and the whiskers represent the data range. Groups connected with a horizontal line are not significantly different from each other.

V. Results

Bite Force

Bite force was measured on 52 terrapins (7 males and 46 females) captured between May 15th and May 25th, 2007 and 16 laboratory reared animals (13 juveniles, 1 male, 2 females). Overall corrected bite forces ranged from 1.6 N to 151.5 N with juveniles ranging from 1.6 N - 27.1 N, males 14.7 N - 29.0 N, and females 30.2 N – 151.5 N. Averages bite forces were 10.7 N, 23.4 N, and 98.4 N for juveniles, males, and females, respectively. Bite force of female terrapins was significantly harder than that of males when standardized for carapace length ($p=0.002$) (Table 2, Fig. 6). Differences in head width and cloacal size were found to be responsible for 99% of the variation in terrapin bite forces (Table 1) and therefore are the best predictor of bite force.

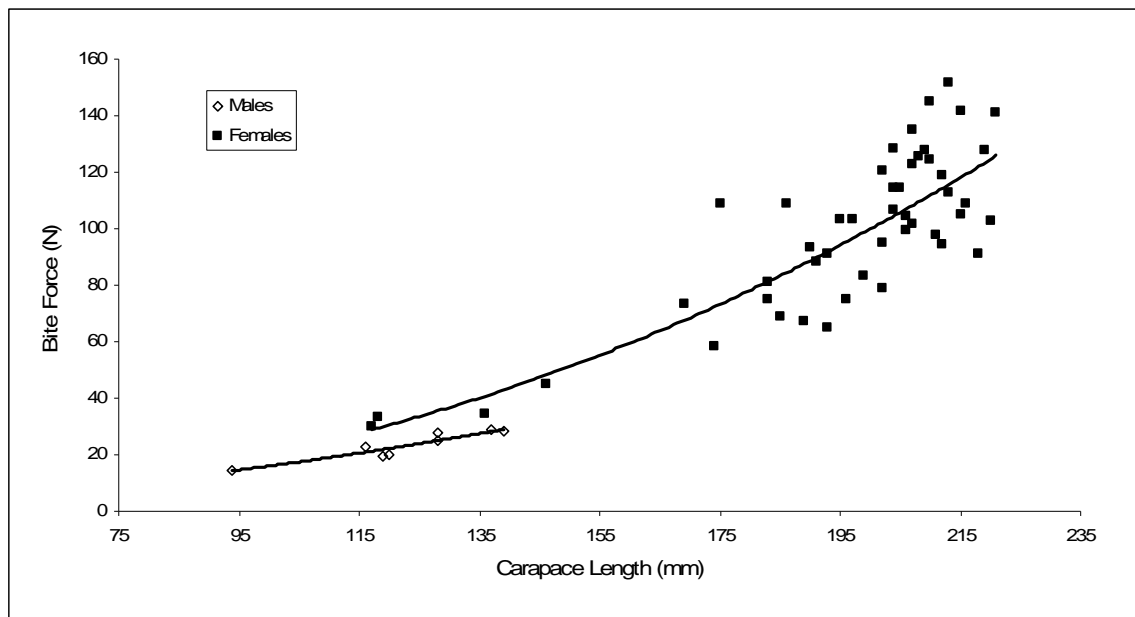


Figure 6: Bite forces of male and female Diamondback Terrapins of varying carapace sizes.

Table 1: Multiple regression analysis with bite force as the dependent variable.

Variable	Unstandardized Coefficients		Standardized Coefficients	t	Sig.
	B	Std. Error	Beta		
Constant	-1.795	0.058		-31.194	0.000
Head width	2.441	0.040	0.993	60.735	0.000
Constant	-1.793	0.062		-28.113	0.000
Head width	2.145	0.147	0.872	14.621	0.000
Closein	0.33	0.159	0.125	2.094	0.041

When compared to red eared sliders, both male and female diamondback terrapins had significantly higher bite forces ($p=0.032$, $p<0.001$ respectively) (Table 3, Fig. 7).

Head width, length, and height together explained 97% of the variation in bite force between terrapins and red eared sliders.

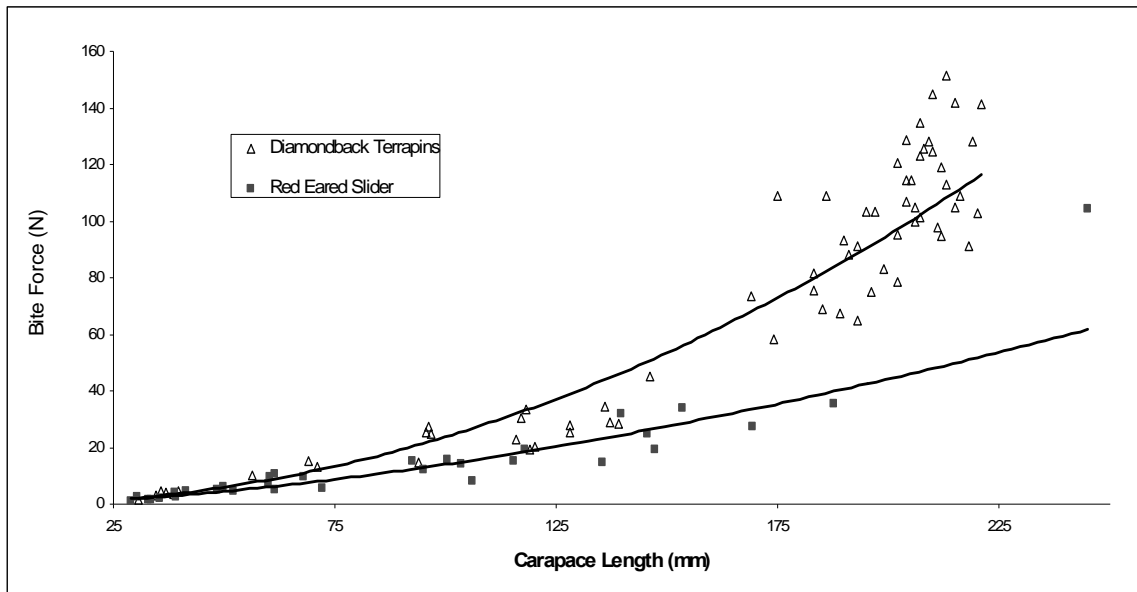


Figure 7: Bite forces of male and female Diamondback Terrapins and Red Eared Sliders of varying carapace sizes

Head Shape

Head measurements were taken on 52 individuals (7 males and 46 females) captured between May 15th and May 25th, 2007 and 16 laboratory reared animals (13 juveniles, 1 male, 2 females). Multivariate regression indicated that head width, height, and volume differed significantly in males and females ($p < 0.001$ for each) (Table 2) with females having more robust heads than males when standardized for carapace length. Heads of females ($\bar{x} = 24.1$ mm, 21.8-42.2 mm) were wider than heads of males ($\bar{x} = 14.0$ mm, 16.9- 22.3 mm) when standardized for carapace length. They did not differ in head length, lower jaw length, length from coronoid to tip of jaw, or the size of the in-lever for jaw closing (closein) (Table 2) when standardized for carapace length.

Table 2: Multivariate ANOVA comparing male and female Diamondback Terrapins standardized by carapace length. Numbers in bold indicate significant results.

Dependant Variable	Male Average	Female Average	df	F	Sig.
Plastron Length	102.4 mm	174.6 mm	1	10.082	0.003
Carapace Width	92.3 mm	150.5 mm	1	8.165	0.007
Carapace Height	45.0 mm	84.8 mm	1	4.446	0.041
Mass	304.9 g	1354.2 g	1	2.892	0.097
Head Length	39.7 mm	62.9 mm	1	0.671	0.417
Head Width	19.9 mm	35.8 mm	1	21.413	0.000
Head Height	14.0 mm	24.1 mm	1	21.094	0.000
Lower Jaw Length	24.0 mm	38.1 mm	1	2.264	0.140
Coronoid to Tip	12.8 mm	22.0 mm	1	3.147	0.084
Closein	11.2 mm	16.1 mm	1	0.345	0.560
Head Volume	5900.4 mm	29375.9 mm	1	19.994	0.000
Bite	23.4 N	98.4 N	1	11.270	0.002

Overall, diamondback terrapins have wider heads than red ear sliders when standardized for carapace length (Fig. 8). When compared by sex, male diamondback terrapins were significantly different from male red eared sliders in carapace width ($p = 0.002$), head length and height ($p < 0.001$ for both), and lower jaw length ($p = 0.005$, respectively) when standardized by carapace length (Table 3). Male terrapins typically

had a narrower carapace and longer, shallower heads with longer lower jaws and stronger bite forces than male red eared sliders of similar carapace length, but did not differ in mass or head width.

Female terrapins and red eared sliders standardized for carapace length differed significantly in mass and head length and width, ($p=0.034$, $p<0.001$, $p=0.002$, respectively) (Table 3). Female terrapins are heavier, have longer and wider heads, and bite harder than female red eared sliders of similar carapace length, but did not differ in carapace width, head height, or lower jaw length.

Table 3: Multivariate ANOVAs comparing male Diamondback Terrapins (n=6) and male Red Eared Sliders (n=10) and female Diamondback Terrapins (n=37) and female Red Eared Sliders (n=7) standardized by carapace length. Significant differences are in bold.

	Dependant Variable	df	Mean Square	F	Sig.
Males	Carapace Width	1	0.004	15.927	0.002
	Mass	1	0.010	3.384	0.089
	Head Length	1	0.037	85.111	0.000
	Head Width	1	0.000	1.035	0.327
	Head Height	1	0.009	22.443	0.000
	Lower Jaw Length	1	0.006	11.692	0.005
	Bite	1	0.064	5.791	0.032
Females	Carapace Width	1	1.40 E-005	0.066	0.798
	Mass	1	0.007	4.807	0.034
	Head Length	1	0.055	76.527	0.000
	Head Width	1	0.006	10.694	0.002
	Head Height	1	0.000	0.371	0.546
	Lower Jaw Length	1	0.002	2.692	0.108
	Bite	1	0.112	14.720	0.000

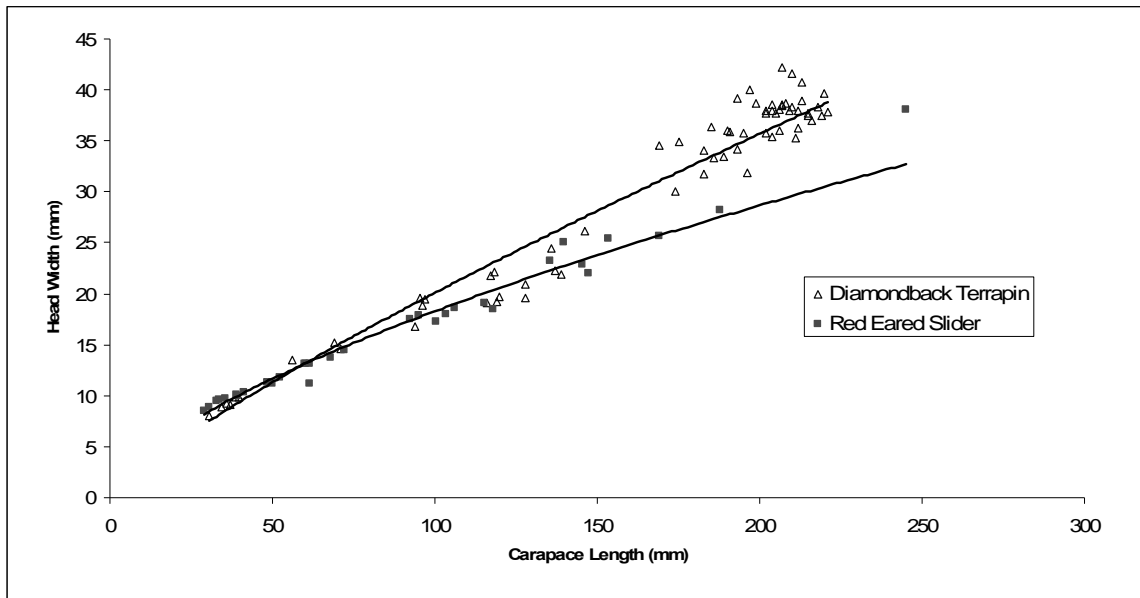


Figure 8: Carapace length and head width of male and female Diamondback terrapins and Red Eared Sliders.

Prey Resistance

A total of 30 mud snails (*Ilyanassa obsoleta*), 8 periwinkles (*Littorina* spp.), and 20 coffee bean snails (*Melampus bidentatus*) were crushed to determine the force needed to fracture the items. Mud snails ranged in size from 10.6-19.4 mm and required forces ranging from 24.1 N to over 240 N (max force capable with this method) to be crushed. Periwinkles ranged in size from 2.7-6.6 mm and required 4 N to 15.1 N to be crushed. Coffee bean snails ranged in size from 3.2-11.7 mm and required forces of 1 N to 39.1 N to be crushed (Fig. 9). Forces tended to increase with shell height for periwinkles and coffee bean snails, while force decreased slightly with shell height for mud snails.

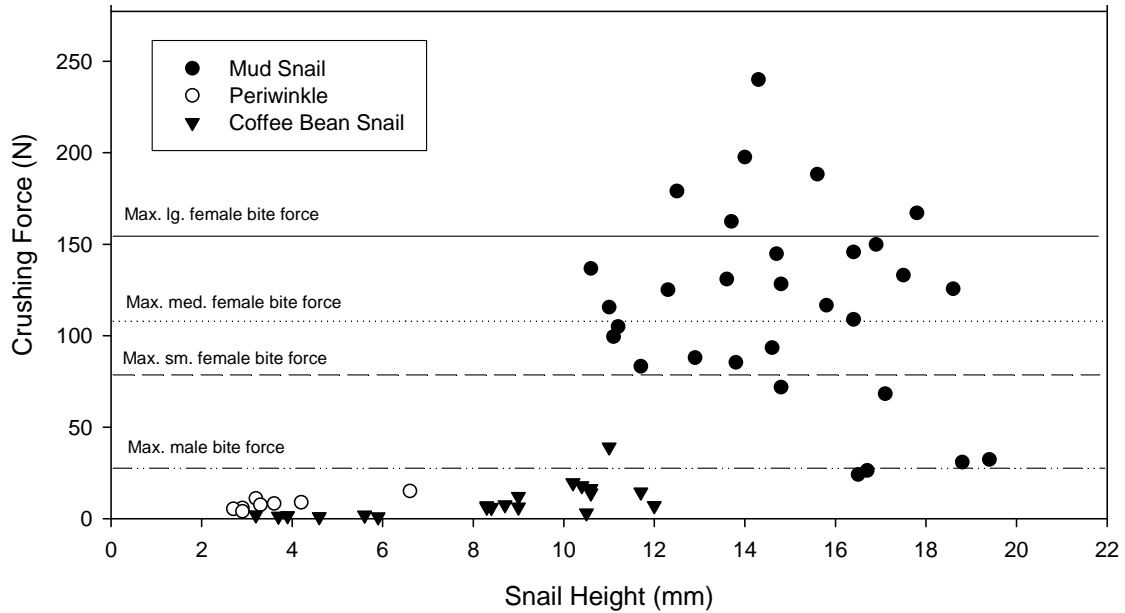


Figure 9: Forces required to crush various snail types with horizontal lines representing maximum force capable of the various size classes.

A total of four fiddler crabs (*Uca pugilator*), one green crab (*Carcinus maenas*), and six mud crabs (*Panopeus* sp., *Eurypanopeus* sp., or *Dyspanopeus* sp.) ranging in carapace sizes of 8.0-34.2 mm were crushed. The maximum force required to crush any crab was 32.9 N, but the majority were <10.5 N.

Maximum forces required to crush ribbed mussels (*Geukensia demissa*) and oysters (*Crassostrea virginica*) were 160 N and 29.9 N, respectively (Fig. 10). Mussels (n=14) ranged in length from 28.2- 92.6 mm in length while the 20 oysters ranged in length from 4.1-18.1 mm.

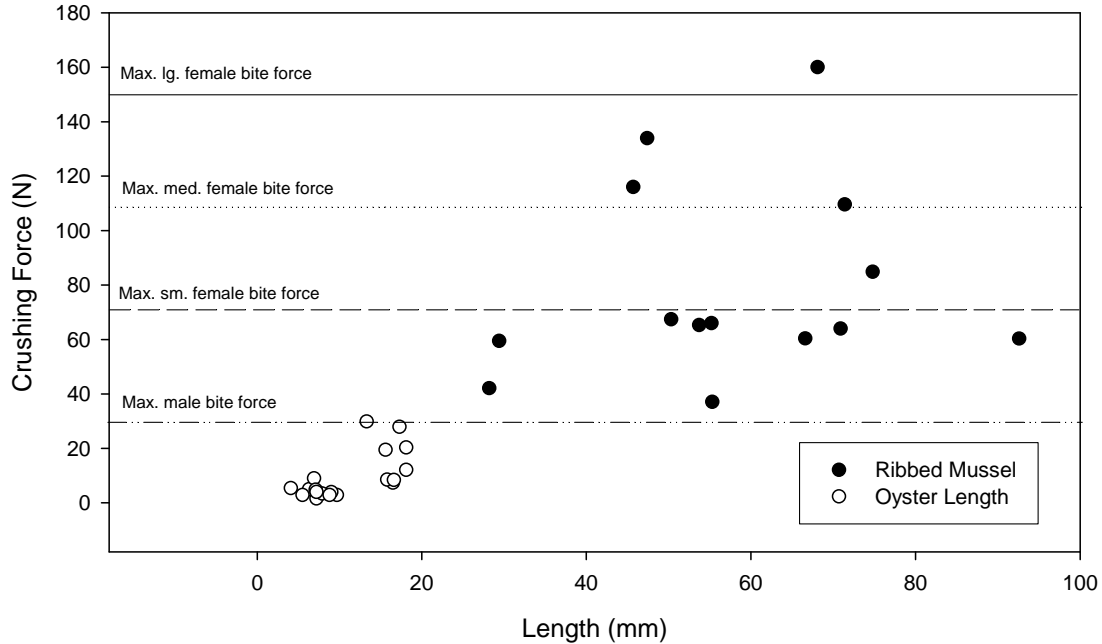


Figure 10: Force required to crush ribbed mussels (*Geukensia demissa*) and oysters (*Crassostrea virginica*) with horizontal lines representing maximum force capable of the various size classes.

Fecal Analysis

Fecal samples were collected from a total of 99 terrapins (35 males, 62 females, 2 indeterminate sex; 27 pre-nesting, 19 nesting, 28 post-nesting, 25 pre-hibernation) captured between May 15th and September 28th, 2007. A total of 12 species of prey items were found to make up the majority of the terrapins' diet (Fig. 11) based on presence in fecal samples. Additionally, small amounts of blue mussel (*Mytilus edulis*), razor clam (*Ensis directus*), unidentified barnacle fragments, mantis shrimp (*Squilla empusa*), and small rocks (<2mm) were also found. Most individuals consumed multiple species/prey groups (median = 4 spp., range 1-9 spp.) (Fig. 12) and overall species diversity by mass was 2.58 with an evenness of 0.72. Species diversity by occurrence was 3.29 with an evenness of 0.92.

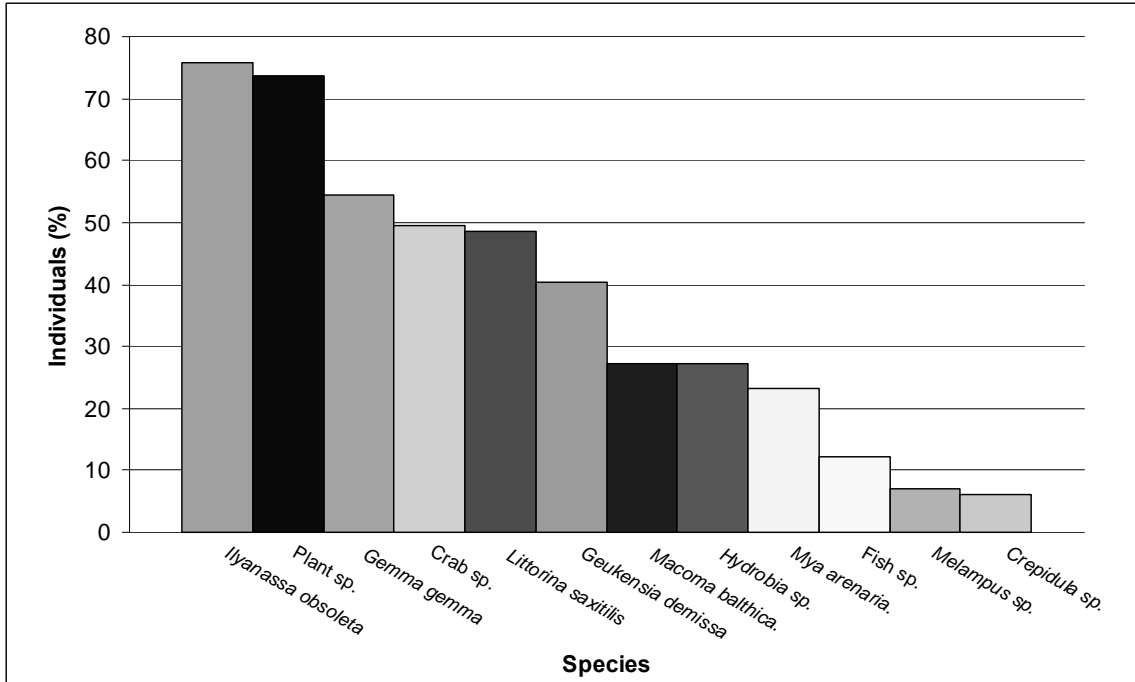


Figure 11: Percent of individual terrapins (n=99) that consumed the noted species/prey groups found in fecal samples over the course of the study.

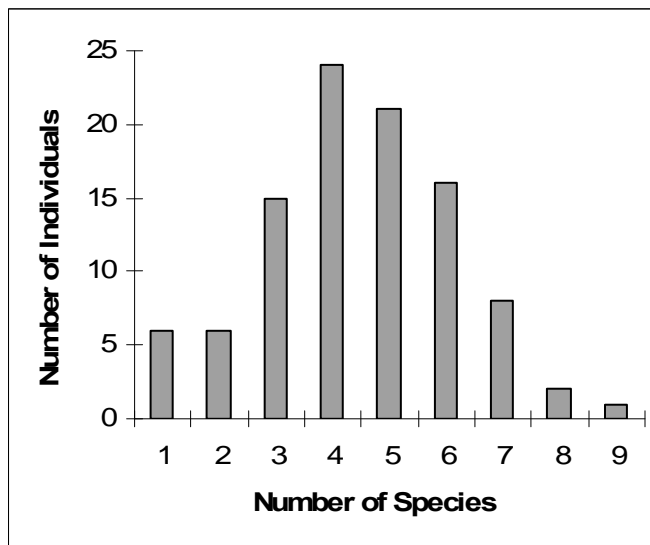


Figure 12: Distribution of fecal samples with varying numbers of prey species (range 1-9). Each fecal sample represents one terrapin

When comparing specific time periods, fecal samples of pre-nesting individuals had an average of 4.9 prey species, nesting had an average of 4.6 species per sample, post-nesting had an average of 4.3 species per sample, and pre-hibernation had an average of 3.7 species per sample. Pre-nesting terrapins consumed a significantly higher number of species than pre-hibernation terrapins (Kruskal-Wallis; $H=8.569$ $p=0.036$) (Fig.13), but no other significant differences were found.

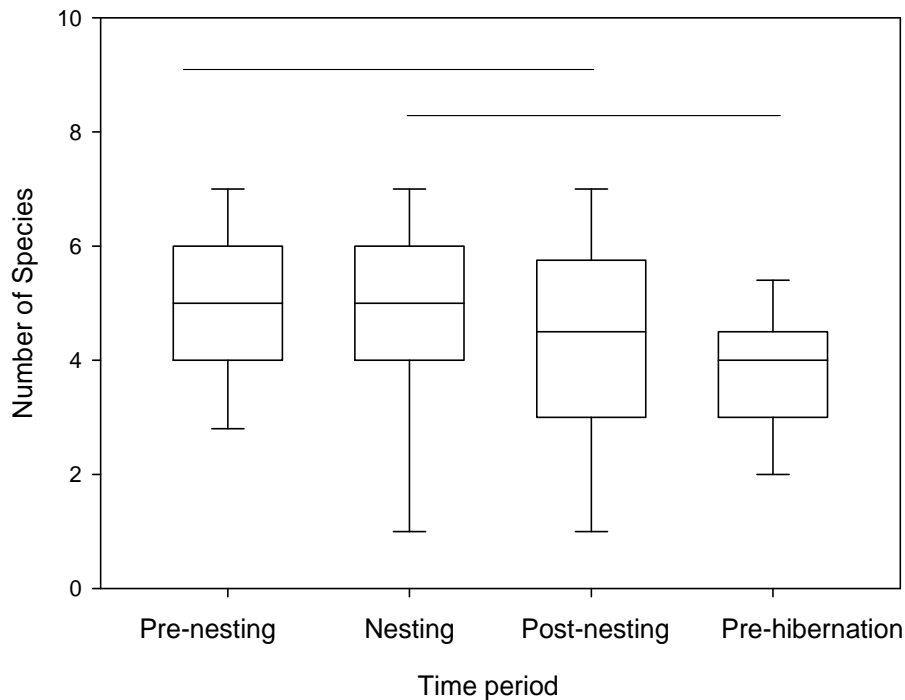


Figure 13: Number of species consumed during each time period (Kruskal- Wallis; $H=8.569$ $p=0.036$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

Niche breadth (H') by total weight of species ranged from 1.48 for post-nesting terrapins to 2.63 nesting terrapins (Table 4). Pre-nesting terrapins were found to have a significantly higher H' than post-nesting and pre-hibernation terrapins, while post-nesting terrapins were significantly lower than nesting terrapins (Kruskal-Wallis $H=36.603$,

$p < 0.001$). Evenness (J') was also found to be significantly different for the same time periods as H' (Kruskal-Wallis $H=36.60$, $p < 0.001$) and ranged from 0.42 for post-nesting terrapins to 0.79 for pre-nesting terrapins (Table 4).

Niche breadth by occurrence of prey species ranged from 2.96 for pre-nesting terrapins to 3.38 for pre-hibernation terrapins (Table 4). Pre-hibernation terrapins were found to have significantly higher H' than all other time periods and pre-nesting terrapins had significantly lower H' than nesting terrapins (Kruskal-Wallis $H=33.017$, $p < 0.001$). Evenness ranged from 0.09 for post-nesting terrapins to 0.94 for nesting and pre-hibernation (Table 4). Pre-hibernation terrapins were significantly different for all time periods except nesting and nesting terrapins were significantly different from post-nesting terrapins (Kruskal-Wallis $H=30.542$, $p < 0.001$).

Table 4: Comparison of Diversity (H') and Evenness (J') medians by mass and occurrence in the diet of diamondback terrapins captured at different time periods

Mass Proportion	Pre-nesting	Nesting	Post-nesting	Pre-hibernation
H'	2.51	2.63	1.48	2.21
J'	0.79	0.76	0.42	0.62
Occurrence				
H'	2.96	3.24	3.24	3.38
J'	0.93	0.94	0.90	0.94

The least dietary overlap, by mass, occurred between pre-nesting and post-nesting terrapins (25.39%) and by occurrence between pre-nesting and pre-hibernation (64.71%) (Table 5). Dietary overlap was greatest for pre-nesting and nesting terrapins for both mass (58.51%) and occurrence (85.81%).

Table 5: Dietary overlap of the different time periods.

	θ	
	Mass (%)	Occurrence (%)
Pre-nesting & Nesting	58.51	85.81
Pre-nesting & Post Nesting	25.39	80.89
Pre-nesting & Pre-hibernation	46.96	64.71
Nesting & Post-nesting	57.12	82.01
Nesting & Pre-hibernation	57.36	74.56
Post-nesting & Pre-hibernation	33.66	80.28

Differences in the amount of fecal matter collected over time, approached significance (Kruskal-Wallis; $H=7.671$ $p=0.053$) with the pre-nesting period being the most different from all other periods. This period had the largest samples and overall sample size gradually decreased as the summer progressed (Fig. 14). Median sample weight for pre-nesting terrapins was 2.444g, 1.930 g for nesting terrapins, 1.731 g for post-nesting terrapins, and 0.674 g for pre-hibernation terrapins.

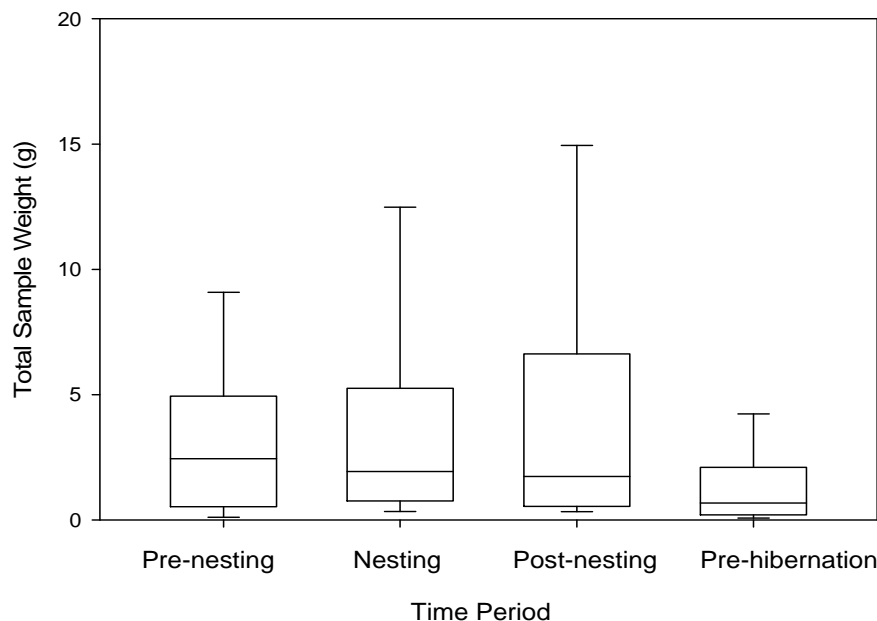


Figure 14: Amount of fecal sample collected during the different seasons. (Kruskal-Wallis; $H=7.671$ $p=0.053$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range.

Additionally, there was a significant difference in the length of periwinkle opercula consumed during all time periods (Kruskal- Wallis; $H=344.949$ $p<0.001$). The largest periwinkles were consumed during pre-nesting with a median of 3.6 mm. The smallest ones (median=2.4 mm) were eaten during the nesting season and then size of snails consumed increased over the course of the study (Fig. 15). The range of opercula length also appeared to narrow as time progressed. For the pre-nesting time period opercula lengths ranged from 1.6-5.8 mm, for nesting the range was 1.4–4.8 mm, 1.6-4.9 mm for post-nesting, and 1.7-4.6 mm for the pre-hibernation time period.

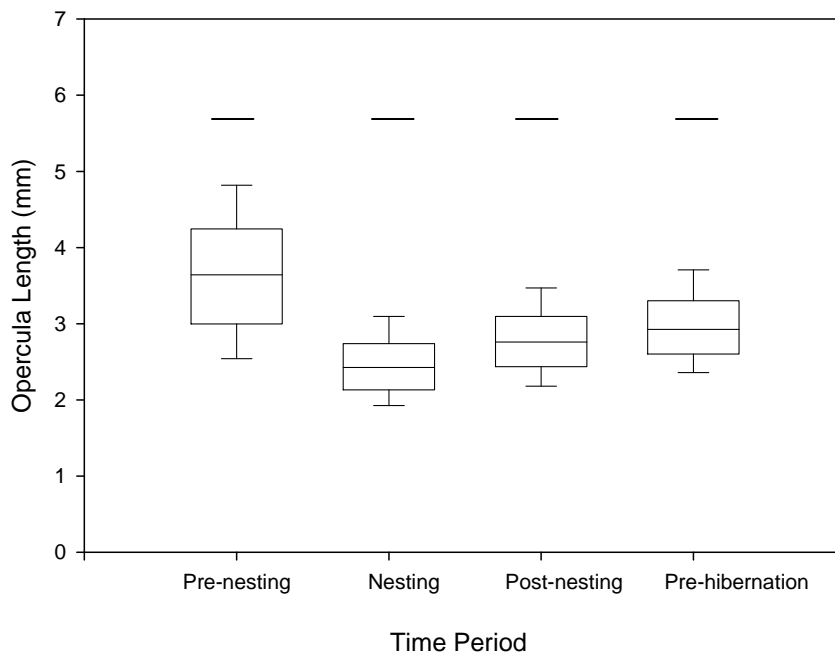


Figure 15: Opercula lengths of periwinkle (*Littorina saxatilis*) consumed during the different seasons (Kruskal- Wallis; $H=344.949$ $p<0.001$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

A gradual increase in opercula length of mud snails consumed during the time periods was also observed, however, it was found to be non-significant (Kruskal- Wallis; $H= 6.449$ $p=0.092$) (Fig. 16). Pre-nesting terrapins consumed the smallest mud snails (medium = 3.4mm) while pre-hibernation terrapins consumed the largest (medium = 3.6mm).

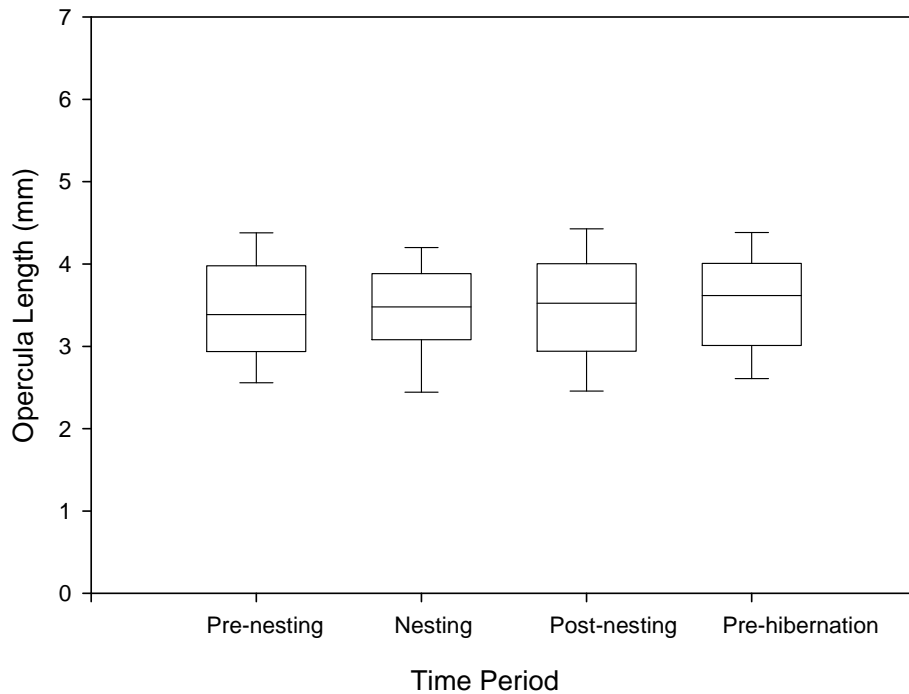


Figure 16: Opercula length of mud snails among the seasons (Kruskal- Wallis; $H= 6.449$ $p=0.092$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range.

A significant difference was found for the amount of *G. gemma* consumed during pre-nesting and post-nesting, as well as pre-nesting and pre-hibernation periods (Kruskal- Wallis; $H=33.232$ $p=<0.001$). Pre-nesting samples contained a median of 0.427 g of *G. gemma* shell, while post-nesting and pre-hibernation samples contained a median of 0.0 g of *G. gemma* shell (Fig. 17).

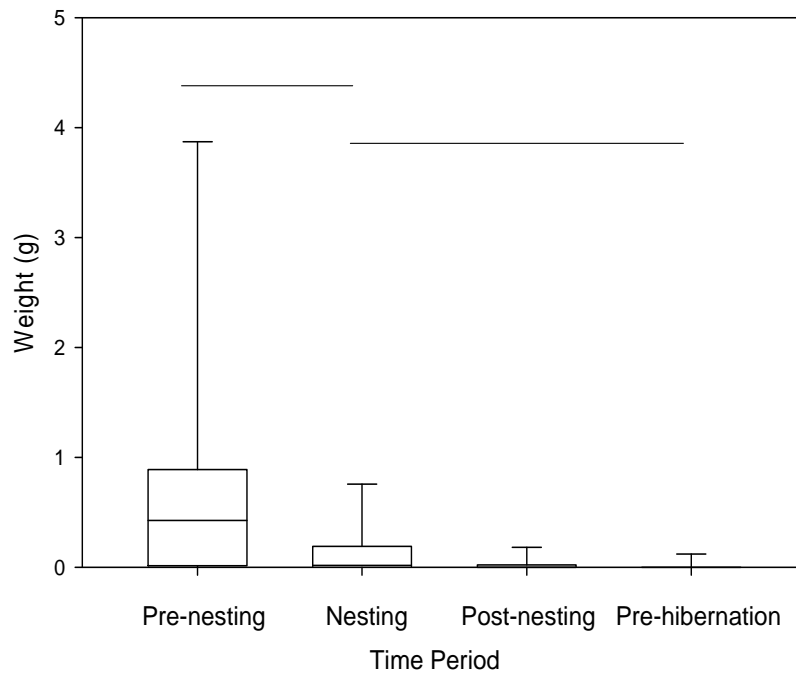


Figure 17: Weight of *G. gemma* shells consumed during each time period (Kruskal- Wallis; $H=33.232$ $p<0.001$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

Pre-nesting, nesting, and post-nesting terrapins all differed significantly from pre-hibernation terrapins in the amount of plant material present in fecal samples (Kruskal-Wallis; $H=22.537$ $p<0.001$) (Fig. 18). Pre-nesting individuals had the most plant material in their fecal samples (median= 0.03 g). From there, the amount of plant material found gradually decreased (nesting median= 0.02 g, post-nesting median=0.018 g, pre-hibernation median=0 g).

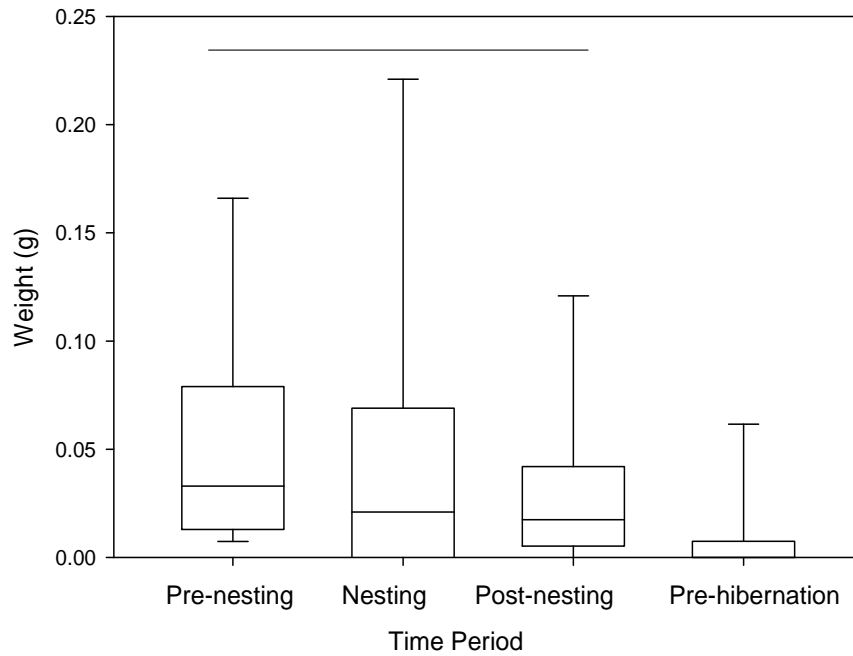


Figure 18: Weight of plant material consumed during each time period (Kruskal-Wallis; $H=22.537$ $p<0.001$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

There was a significant difference in the weight of bivalves found in fecal samples over time (Kruskal-Wallis; $H=19.731$ $p<0.001$). Pre-hibernation terrapins were found to have less bivalve material in fecal samples than pre-nesting, nesting, and post-hibernation terrapins (medians = 0.035g, 1.70g, 1.21g, and 0.690g respectively) (Fig.19).

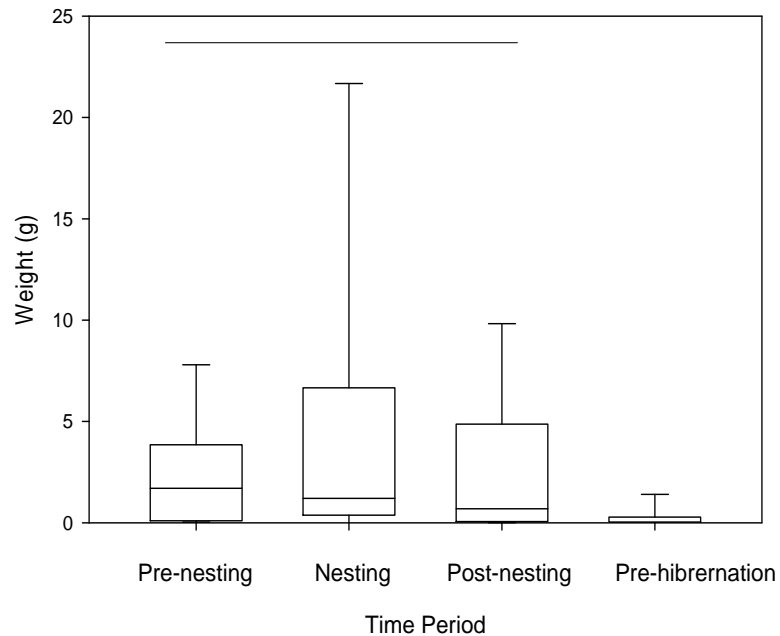


Figure 19: Weight of bivalves present in fecal samples during each season (Kruskal-Wallis; $H=19.731$ $p<0.001$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

There also appeared to be a change in the type of bivalves consumed over time. The amount of *G. gemma* and *Mya arenaria* decreased, while the amount of *Macoma balthica* increased. Ribbed mussels were the only bivalve for which the weight of shell material found in fecal samples remained roughly the same for the duration of this study (Fig. 20).

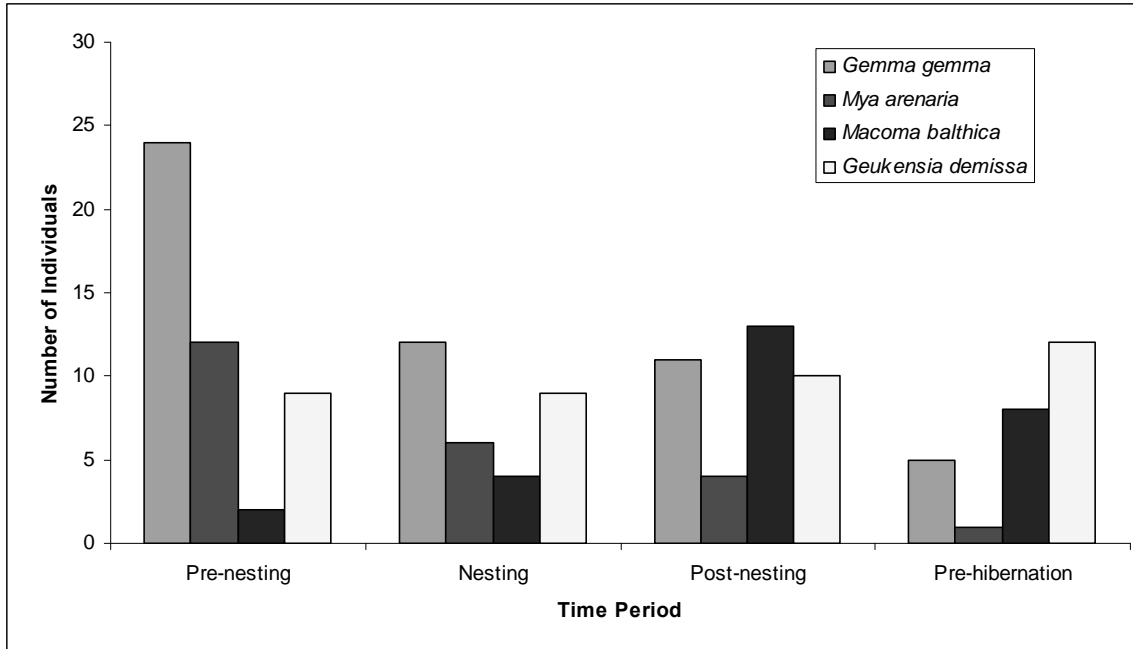


Figure 20: Number of individuals that consumed each bivalve type over time.

The weight of shell, the number of periwinkle and mud snail opercula, the number of fecal samples collected from each turtle in a single collection period, and the weight of crab and ribbed mussel consumed did not differ among time periods. Differences in the total weight of gastropods consumed were also not found to be significant.

When comparing terrapins by size class, a significant difference was found between the number of prey species consumed by males and medium females ($p=0.035$) with medium females consuming more species than males (Fig. 21). A significant difference was also found when comparing females of all size groups to males ($p=0.007$) (Fig. 22).

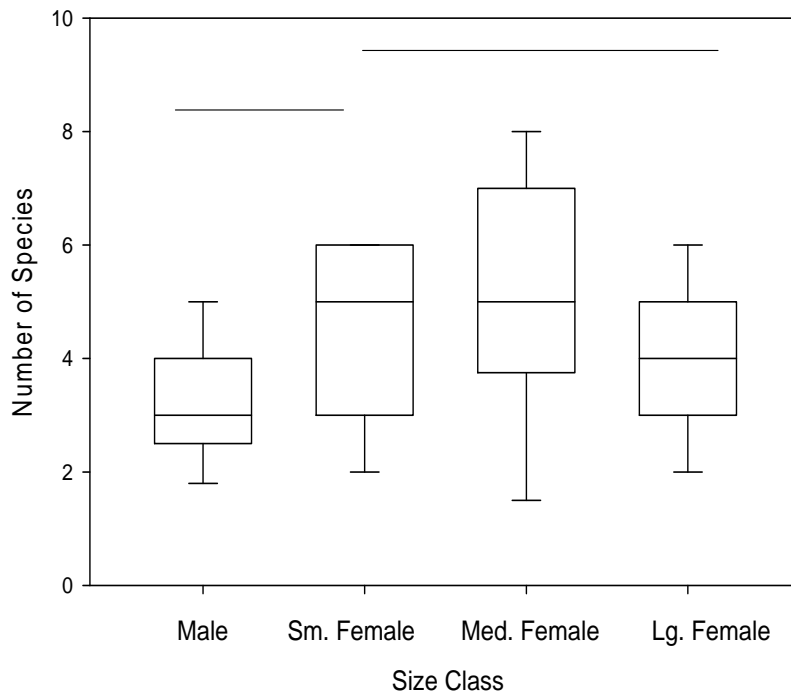


Figure 21: Number of species consumed by each size class. The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

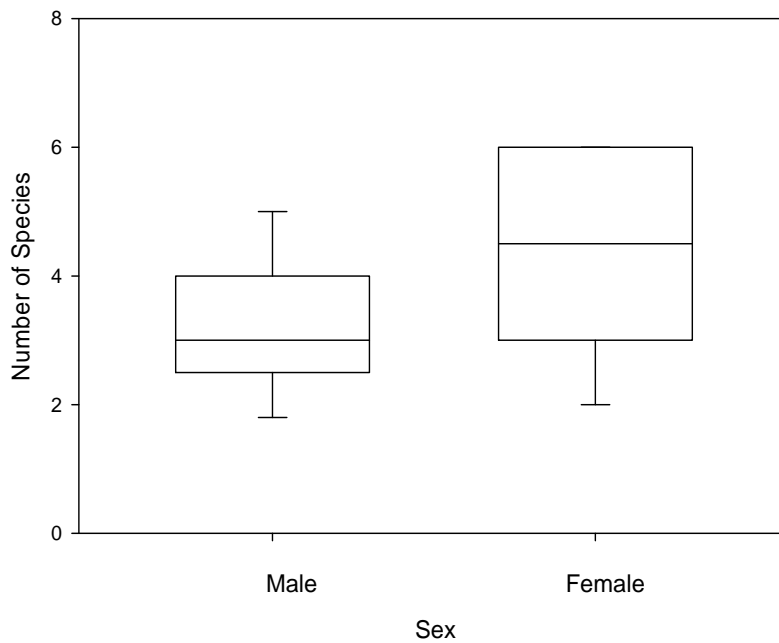


Figure 22: Comparison of the number of species consumed by each sex. The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

Niche breadths by mass ranged from 2.18 for large females to 2.65 for medium females (Table 6). Large females were found to be significantly different from all other size classes (Kruskal-Wallis $H=24.616$, $p<0.001$). Evenness values ranged from 0.61 for large females to 0.75 for small females (Table 6). Again, large females were significantly different from all other size classes (Kruskal-Wallis $H=26.157$, $p<0.001$).

Niche breadth by occurrence ranged from 3.21 for small females to 3.31 for medium females (Table 6). Small females were significantly different from medium females and males and large females were significantly different from medium females (Kruskal-Wallis $H=25.175$, $p<0.001$). Evenness values ranged from 0.90 for large females to 0.93 for small females (Table 6). Small females were significantly different from large females and males and large females were significantly different from medium females (Kruskal-Wallis $H=29.338$, $p<0.001$).

Table 6: Diversity (H') and Evenness (J') of diet when compared by size classes.

Mass Proportion	Male	Sm. Female	Med. female	Lg. Female
H'	2.64	2.58	2.65	2.18
J'	0.74	0.75	0.74	0.61
Occurrence				
H'	3.25	3.21	3.31	3.23
J'	0.91	0.93	0.92	0.90

Dietary overlap was greatest between medium and large females by both mass (74.54%) and occurrence (94.08%). Overlap was least between males and large females for both mass (22.18%) and occurrence (76.54%) (Table 7).

Table 7: Dietary overlap of the different time periods.

	θ	
	Mass (%)	Occurrence (%)
Male & Sm. Female	60.55	88.99
Male & Med. Female	30.67	76.84
Male & Lg. Female	22.18	76.54
Sm. Female & Med. Female	54.82	77.50
Sm. Female & Lg. Female	44.32	77.63
Med. Female & Lg. Female	74.54	94.08

The amount of fecal matter collected differed significantly by size class (Kruskal-Wallis; $H=48.469$ $p<0.001$). All females produced more fecal matter than males, but did not differ significantly from each other. Large females produced the most fecal matter (median=3.743 g) and males produced the least (median=0.046g) (Fig. 23).

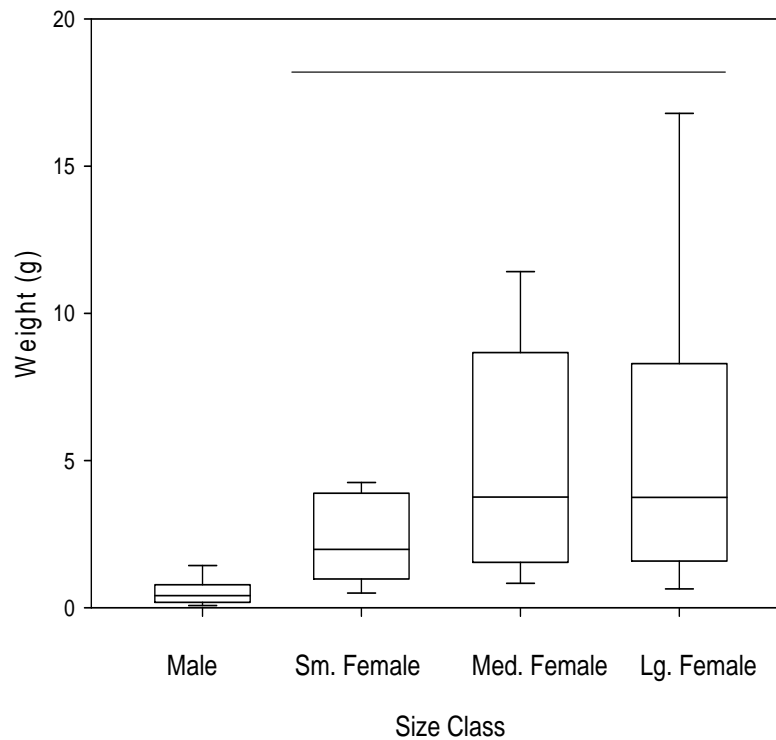


Figure 23: Amount of fecal mater collected for each size class (Kruskal-Wallis; $H=48.469$ $p<0.001$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

There was also a significant difference in the length of opercula for both mud snails and periwinkles found in samples among the different size classes (Kruskal-Wallis; mud snail $H = 173.669$ periwinkle $H=96.141$ $p<0.001$ for both). Mud snail opercula length was significantly different for all size classes, while periwinkle length was different for all size classes except for small and medium females. Large females tended to eat larger individuals of both types of snails (Figs. 24 & 25). The size of mud snail eaten gradually increased with larger terrapins consuming the largest mud snails. However, the lengths of periwinkles were greater for males than for small or medium females and greater for small females than medium females. Interestingly, mud snail shells were not found in male fecal samples, but opercula were, while female fecal samples contained both shells and opercula.

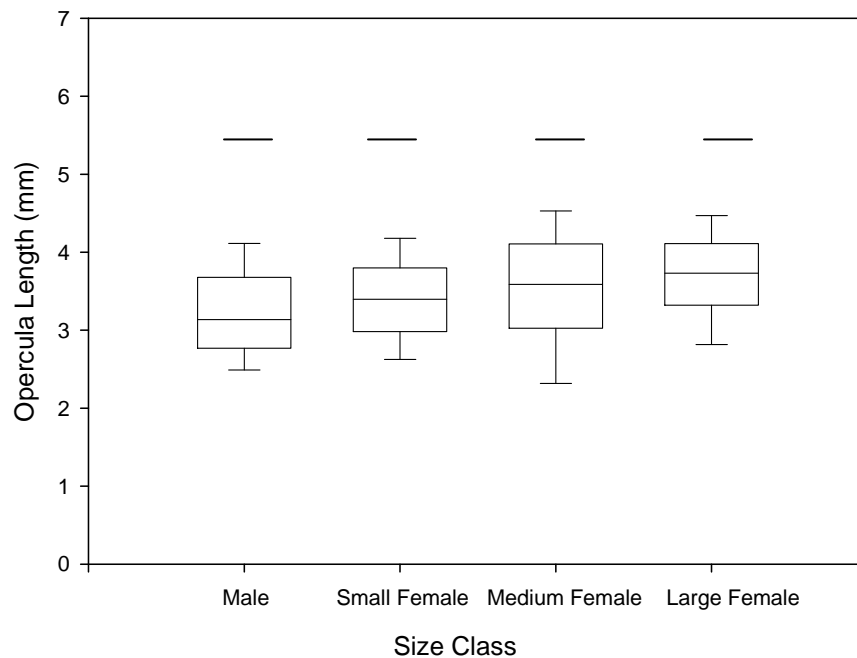


Figure 24: Opercula length of mud snail consumed by each size class (Kruskal-Wallis $H = 173.669$ $p<0.001$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

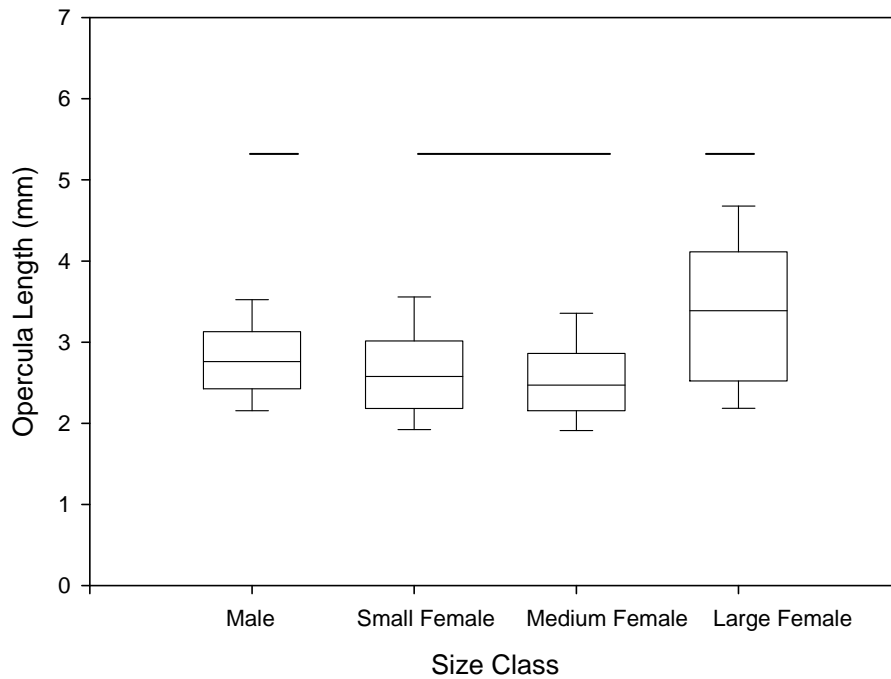


Figure 25: Opercula length of periwinkle consumed by each size class (Kruskal-Wallis $H=96.141$ $p<0.001$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

A significant difference was found among the different size classes and the number of periwinkle consumed (Kruskal-Wallis; $H=8.772$ $p=0.032$) (Fig 26). Small females consumed the most periwinkles (median = 3) and large and medium females consumed the least number of periwinkles (median=0 for both). A nonparametric comparison test found that males consumed significantly more periwinkles than medium and large females and small females consumed more periwinkles than medium females ($p< 0.05$).

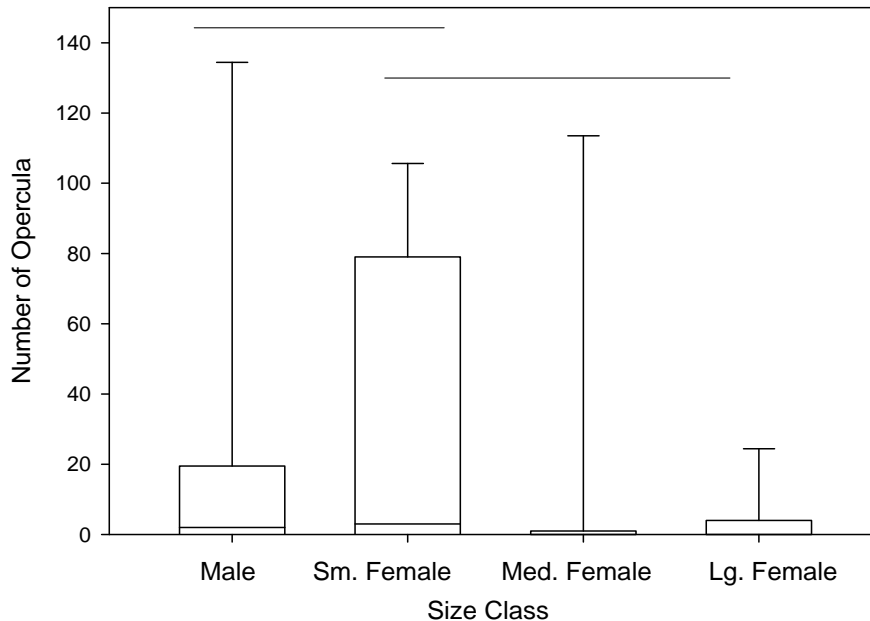


Figure 26: Number of periwinkle consumed in each size class (Kruskal-Wallis; $H=8.772$ $p=0.032$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

There was a significant difference in the amount of plant matter consumed by size class (Kruskal- Wallis; $H=7.987$ $p=0.046$) (Fig. 27). Medium females had the highest amount of plant matter in their fecal samples (medium=0.027 g). Large females had a similar amount of plant in their samples (medium=0.024 g). Males consumed the least amount of plant material (medium= 0.006 g). A nonparametric multiple comparison test found that males had significantly lower amounts of plant matter in fecal samples than all female size groups ($p < 0.05$).

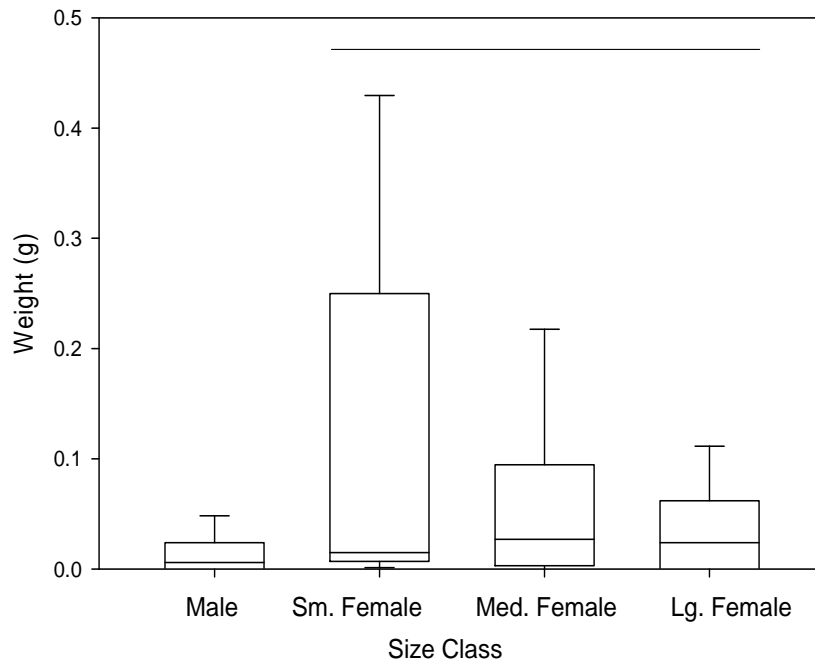


Figure 27: Amount of plant matter consumed by size class (Kruskal- Wallis; $H=7.987$ $p=0.046$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

The weight of crab matter found in fecal samples differed significantly by size class (Kruskal- Wallis; $H=11.467$ $p=0.009$) (Fig. 28). Large females consumed the most crab with a median of 0.031 g and males and small females consumed the least amount of crab with medians of 0.0 g each. Males were significantly different from large and medium females according to a nonparametric comparison test ($p < 0.05$).

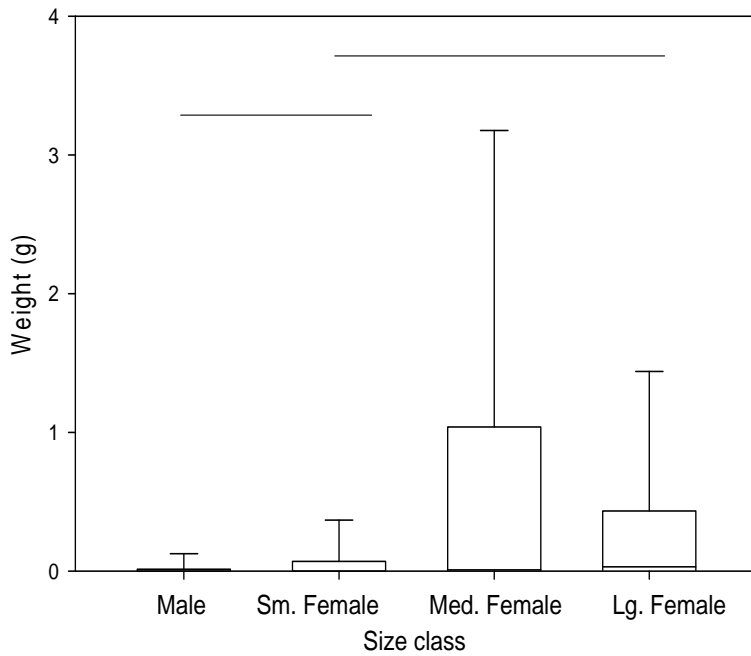


Figure 28: Amount of crab consumed by size class (Kruskal- Wallis; $H=11.467$ $p=0.009$). The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

There was also a significant difference in the amount of bivalves eaten by the different size classes (Kruskal-Wallis $H = 33.643$ $p = <0.001$) (Fig. 29). Males consumed less bivalve material than large and medium females, but not small females.

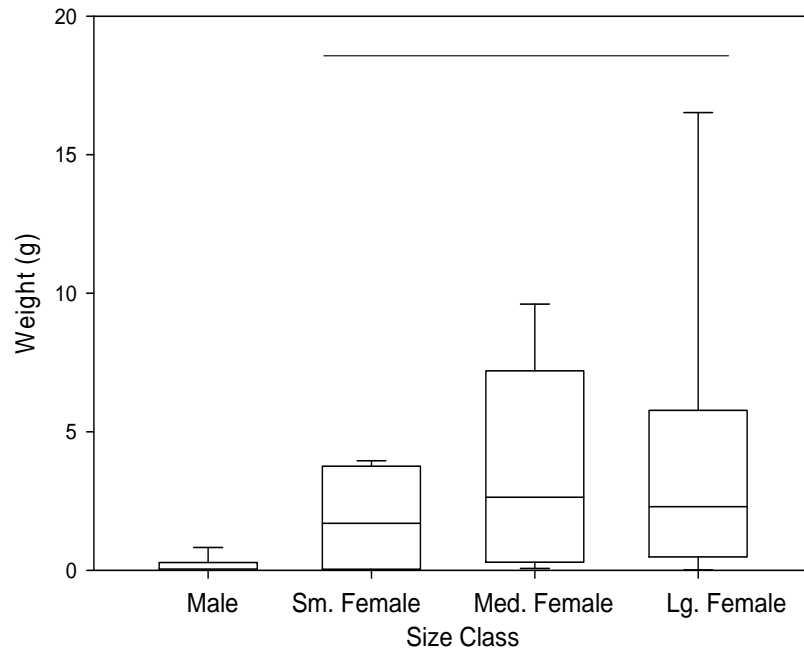


Figure 29: Amount of bivalves consumed by size class. The box represents the inter-quartile data range, the middle line is the median of the data, and the whiskers represent the data range. Unconnected periods are significantly different.

No significant difference was found among the four size classes for the number of mud snail opercula consumed, the number of fecal samples collected from a single turtle in a given collection period, or the amount of *G. gemma*, *Mya arenaria*, *Macoma bathica*, or *Geukensia demissa* consumed.

VI. Discussion

Overall Diet of M. t. terrapin

Terrapins appear to be dietary generalists since twelve prey items were consistently found and no one item was consumed in drastically larger amounts than the others. Values of evenness (both by mass and occurrence) were close to one, supporting the idea that terrapins are dietary generalists. Of the prey items found, seven can be considered heavily armored, with four of those species (mud snails, *G. demissa*, *Macoma balthica*, and *Mya arenaria*) being consumed by at least 40% of all individuals. This possibly suggests that they are taking advantage of prey items that other consumers may not be able to prey upon.

In addition to the twelve common prey species, several other species were found in the samples. One such group was unidentifiable plant matter. While present in a majority of samples, it is believed to have been unintentionally consumed while eating snails or other prey species (this study; Coker, 1906), as they are often found on plants. Additionally, plant material was not found in large amounts, suggesting it was not the targeted prey item. Other items thought to have been unintentionally eaten are *Crepidula* spp. and *Balanus* spp.. Due to low occurrence, I believe these species to have been accidentally consumed as a result of being attached to the focal prey item (this study; Marganoff, 1970).

Fish bones and scales were also found in several samples in this study and one done by Coker (1906), but it is unknown whether they were scavenged after death or

caught live. While terrapins are capable of catching live fish in confined areas (personal observation), it is likely that they were consumed dead, as there is some evidence that terrapins have scavenging tendencies (Ehret & Werner, 2004). Given that fish parts were not commonly found, fish are not believed to be a substantial part of the terrapin's diet. However, their presence supports the idea that terrapins are generalists and will take advantage of any food source that becomes available.

Seasonal Dietary Shifts

One of the main findings of this study is that terrapin diet changes over time. It appears that they become more specialized in August and September, as H' by mass for pre-nesting terrapins was significantly higher than that of post-nesting and pre-hibernation terrapins (Table 4). Fewer species are also consumed in later time periods (Fig. 13) further supporting this idea. Explanations for this decrease include a change in terrapin prey preference or changes in prey distribution, behavior, or abundance that make certain items more rare in later time periods.

One example that supports the possibility of a change in prey preference was the apparent shift from *Mya arenaria* to *Macoma balthica* over the course of this study (Fig. 20). It is possible that *Macoma balthica* is the preferred prey but that is not readily available until the end of the foraging season. Once *Macoma balthica* becomes available, terrapins shift their focus from *Mya arenaria*. However, this shift could also be explained by changes in distribution, behavior, or abundance of *Mya arenaria* and *Macoma balthica*.

A change in foraging location is another possible explanation for many of the dietary differences found among time periods. Kumiga (2004) found that home ranges of terrapins in Oyster Bay significantly increased by July and August. During these later months they expand their ranges from exclusively inter-tidal marsh areas to encompass both inter-tidal and sub-tidal areas. Such a change would expand the number of prey items available for terrapins. The author believed the expansion of home range was in direct response to a decrease in prey availability in their original location. The above example of a shift from *Mya arenaria* and *Macoma balthica* also supports a change in foraging location, since *Mya arenaria* is typically found in shallow or intertidal waters, while *Macoma balthica* is found offshore in bays (Weiss, 1995).

Changes in energy needs can also explain differences in diet over time. It is likely that energy demands are higher during certain time periods than others. After hibernation (pre-nesting), it is probable that energy stores need to be rebuilt and maintained in order to be able to successfully reproduce later on. In an effort to accomplish this, more species may need to be consumed, as is shown by more species being eaten during these two periods (Fig. 13). Then during pre-hibernation, the amount of prey consumed may need to be decreased in order to limit the number of undigested particles within the terrapin. Such particles could lead to harmful freezing of body fluids by acting as ice-nucleating particles during hibernation if exposed to sub-zero temperatures (Packard et al., 2001). This study found that the amount of fecal matter, as well as the number of species consumed decrease during the pre-hibernation time period.

In conjunction with terrapins themselves having variable energy need is that certain prey items may be better able to meet energy requirements than others.

Therefore, if such items become available, terrapins may shift their focus to these items depending on what its current energy needs are. Clark & Gibbons (1969) suggested that *P. scripta* juveniles may change from a mostly carnivorous diet to an herbivorous one because plant matter is more readily obtained and is better suited for meeting increased dietary requirements as they grow. At the beginning of the summer their energy requirements were not as great due to having a smaller body size so small insects (the main component of juvenile diet) are sufficient to meet their energy needs.

The size of periwinkles consumed was also found to vary over time. During the pre-nesting season, terrapins consumed larger periwinkles than during other periods. It is possible that these larger snails have survived from the previous season and that reproduction has yet to occur, thus making larger ones more abundant during this period. Then, during the nesting season, mature periwinkles begin to reproduce (Hughes, 1980 in Hull et al, 1999), thereby increasing the number of smaller periwinkles available. As smaller periwinkles become more abundant, it is likely that it is now more energetically worthwhile to consume smaller periwinkles than to search only for larger ones. Over the rest of the study period, the periwinkles continue to grow leading to larger snails once again being found in the terrapins' diet (Fig. 25).

Sex and Size Effects

Many of the differences found between the sexes and among size classes may simply be explained by differences in gape size. Naturally, larger individuals would be capable of consuming larger prey than smaller individuals. Since differences in head width and cloacal size were found to be responsible for the differences in bite forces among

size classes (Table 3), it is probable that gape limitation together with bite force are responsible for many of the differences among size classes.

One example of how gape limitations and differences in bite force affect terrapin diet was the differences in snail type consumed. This study found that all females are capable of producing bite forces necessary to crush mud snails, periwinkles, and coffee bean snails of varying sizes, while males could only readily crush coffee bean snails and periwinkles (Fig. 9). While it is interesting that larger mud snails appear to be easier to crush than smaller ones, males and medium and small females are unlikely to be able to take advantage of these larger, weaker snails because they are too large to manipulate. This stronger bite force may also allow females to take advantage of more/different prey items than males as is indicated by females consuming more species than males in this study.

Differences in the number of species consumed between the sexes could also be explained by differences in foraging techniques or locations. If males and females are foraging in completely different locations, it is likely that certain prey items would be encountered in one area and not another, since prey items are not uniformly distributed among all marsh zones. This can be seen in the findings of Tucker et al. (1995) that periwinkle size typically increased with distance from a creek drainage area. Competition among and within prey species also contributes to differences in prey distributions within different marsh zones, as has been shown by several experiments including Connell's (1961) barnacle zonation experiments and Navarrete & Menge's (1996) work on the effects of sea star and whelk predation on mussels.

Other support for different size classes utilizing different habitats is that large adult female terrapins tend to use deeper, more open water habitats in addition to occasionally using shallower inshore, while small males and juvenile females tend to stay in shallow inshore areas such as creeks. Large males tend to use habitat similar to large females, adding support to body size being a determining factor of habitat shifts (Roosenberg et al., 1999).

One example of a possible difference in foraging technique seen in this study is that only mud snail opercula were found in male fecal samples, while females had both opercula and shell pieces. It is possible that the males are only able to eat the foot of the snail because they cannot crush the snail's shell (Fig. 9). They may grab the foot of the snail while it is extended from the shell and then use its forelimbs to push the snail shell away and rip the foot from the snail. Since terrapins are known to use their forelimbs while feeding (Bels et. al., 1998, personal observation) this is a plausible explanation. While the force needed to crush mud snails appears to decrease with snail height (possibly due to eroding shells), males may still be unable to consume the whole snail due to gape limitations. Since females have larger heads and more powerful bite forces than males, it is possible that they are more easily able to fit the larger snails in their mouths and crush them, therefore having no need to only consume the foot. Another explanation for males only having mud snail opercula in their feces is that they are picking them up by consuming sediment. It is possible that there are differences in habitat of differently sized snails that correspond with the differences in male and female habitats.

A third, but less likely explanation for male samples only having mud snail opercula is that there are differences in gut residence time of shell material and opercula. Since terrapins were kept for three to four days, shell would be expected to be found in at least one of the multiple samples collected for each terrapin even with differences in gut residence times. It is highly unlikely that the majority of males captured were at the same time in the cycle of when shell would not be collected from them. Additionally, other types of shell were found in samples. Gut residence time of mud snail shell should not be so different from other shell material that it would not have been collected.

Other differences in diet between the sexes that are worth commenting on include the surprising evidence that males consumed larger periwinkles than small and medium females, while consuming smaller mud snails than all females. This is most likely explained by differences in foraging habitat between the sexes as mentioned above or by differences in prey preference. In the case of periwinkles, it is possible that females do not “waste” their time and energy in general because they are not worth the cost of searching for them. Supporting this is that fewer females consumed periwinkles than males (Fig. 26) and the ones that did either had few, indicating accidental ingestion, or large numbers of them, possibly indicating they had come across a large quantity of them which made them energetically worthwhile to consume.

As stated above for differences among time periods, differences in energy needs between the sexes may also explain differences in diet. According to Legler (in Shine, 1989), differences in turtle skull dimensions that give females the ability to crush large mollusks are likely linked to the females’ need for increased calcium for eggshell production. Females may also need increased calcium intake to maintain a larger shell

(Ward, 1980). Additionally, since males are characteristically smaller than most females, they should be able to maintain or gain body size with less food. Given both of these reasons and differences in energetic values of different prey items, it makes sense that males and females might have different prey preferences.

Among the different size classes of females, there were additional differences in diet. Large females consumed larger mud snails and periwinkles than smaller female terrapins. While all periwinkles and larger mud snails appear to fall within the range of forces capable by smaller females it is possible that they are physically unable to consume them due to the previously mentioned gape limitations. It is also possible that large females are either foraging in different locations than smaller females or are out-competing them for the larger snails.

In most cases, the size or amount of prey consumed decreased in ways that would be expected. One case where this is not true, however, is the size of periwinkles consumed. In this instance, small females ate larger periwinkles than medium females. As mentioned above in the case of males, larger females may not consume periwinkles until it is energetically worthwhile to do so. Since they have larger heads and stronger bite forces they can consume other larger and or harder prey items that are more energetically profitable to search for than periwinkles. Smaller females, as with the males, may be unable to consume these items, forcing them to rely on smaller items that fall within their range of bite force (i.e. periwinkles).

As noted in several places, males and small females had very similar diets in many ways. These similarities can be explained by the fact that males and small females are of similar body size. Since small females are immature, they may have similar

energy needs to that of males. They are not yet producing eggs and therefore do not have the same energy costs as larger, mature females. Also since smaller females would have smaller heads than larger females, they, like the males, may not be able to take advantage of all the prey items that the larger females can due to gape limitations. This is supported by the relatively high dietary overlap of 60.55% by mass (Table 7). The differences between males and small females can most likely be explained by the simple fact that while they are similar in body size, small females still have larger heads and therefore higher bite forces (Table 2; Lindeman, 2000).

Geographic Dietary Differences

Terrapins in New York had higher niche breadth and evenness than those in South Carolina (Tucker et al., 1995) as a result of consuming nearly twice as many prey items as terrapins in South Carolina. This provides evidence that northern populations have a more varied diet than southern populations. This may be caused by prey availability, competition, or differences in community composition.

Another major difference between the two studies is that periwinkles (*L. irrorata* in SC and *L. saxatilis* in NY) made up 76-79% of the material found in samples of South Carolina terrapins (Tucker et al., 1995), but were only found in 48% of terrapins in New York. The main prey item of New York terrapins' diets appears to be mud snail. It was found in 76% of New York terrapins sampled, but in none of the South Carolina terrapins despite being readily available (Tucker et. al. 1995). One possible explanation of why mud snails are eaten by New York terrapins and not by South Carolina terrapins could be that northern mud snails may not have as hard of shells as southern ones. This study

found that most mud snails required an average force of 117 N to break their shells. A similar study conducted in South Carolina found that mud snails, similar in size to those in New York, required an average force of 2108 N to break their shells (Tucker et al., 1997). Differences in shell strength can be caused by several environmental factors. One such factor is the chemical tributyltin a major component in organotin based antifouling paints, such as those used on boat bottoms, and is known to have drastic effects on mollusks such as shell thickening (Axiak et al., 1995).

Other items found to be present in higher numbers in New York terrapin diets include *G. gemma* (74%) and crabs (49%). The cases of *G. gemma*, crabs, and other prey items found in New York terrapin diets and not South Carolina terrapin diets can once again be explained by prey availability or differences in community structure. If more prey items are available, then more species should be found in the diets of individuals from that area.

Finally, terrapins from New York are a different sub-species than those from South Carolina. It is possible that there are enough differences in head shape or jaw muscles that New York terrapins are capable of greater bite force than South Carolina terrapins. South Carolina terrapins had wider heads on average (males =17.6 mm, females = 28.9 mm), but smaller ranges (males =14.6-20.5 mm; females = 16.4-39.5 mm) than New York terrapins (males \bar{x} =14.0 mm, range 16.9-22.3 mm; females \bar{x} = 24.1 mm, range 21.8-42.2 mm). These differences may explain the differences in diet, but more studies need to be conducted, as bite forces of South Carolina terrapins remain unknown (Tucker et. al., 1997).

Other geographic differences also exist. A study conducted in Florida (Butler, 2000) found that the dwarf surf clam (*Malina lateralis*) made up the majority of the diets of terrapins there. The rest of the diet consisted mostly of crabs and periwinkles (*L. irrorata* - the same species found by Tucker et al, 1995). Butler suggested that resources are not limited since he did not find significant differences in diet between the sexes, although he did discover that crabs and periwinkles were less important in the diets of males than females.

Maryland terrapins also appear to have a different dietary composition than South Carolina and Florida terrapins. These terrapins' diet consisted mostly of soft-shelled clams (*Mya arenaria*), stout razor clams (*Tagelus* spp.), *Macoma* spp., and *Gemma* spp. (Roosenburg et al., 1999). These results are more consistent with what was found for New York terrapins. The differences in diet among terrapin populations of different locations further support the idea that terrapins are foraging generalists that take advantage of what is available.

The diet of diamondback terrapins is also drastically different from that of the closely related freshwater turtle, the red eared slider. Red eared sliders have diets mostly composed of plants. Non-plant matter found included insects, carrion fish, and freshwater gastropods (Moll & Moll, 1990), none of which are considered heavily armored.

According to Herrel et al. (2002), species that consume hard or large prey bite harder than species (of similar body size) that eat softer, smaller prey. Consistent with this is our findings that red eared sliders do not have bite forces as high as those of diamondback terrapins. One explanation for this could be that the two species underwent

different selection pressures, leading to terrapins having a stronger bite force. A study conducted by Claude et al. (2004) comparing skull shapes of turtle species belonging to Testudinoidae and Emydidae found that habitat and diet contribute more to the variation in the evolution of skull design than that of phylogeny, making this a plausible explanation. Consistent with this is Ward's (1980) finding that characters of mollusivorous turtles can be found early in development even when individuals are fed a diet of soft food. However, this particular study found that differences in head measurements between the two species are sufficient to explain the differences in bite force.

Terrapins as Top-down Controllers

While this study was unable to directly examine terrapins as a major controller of community structure, some inferences can be made. Levesque (2000) found that terrapins are an important predator of *L. irrorata* in South Carolina salt marshes. Previous studies have estimated the terrapin population of Oyster Bay to be between 500 and 700 adults (Bossert, 2004). With a population of this size, it is possible that terrapins are a controlling factor of marsh diversity. By consuming large quantities of various species of snails, bivalves, and crabs, terrapins may be responsible for higher community species diversity by not allowing any one species to dominate.

Overall, this study found that terrapin appear to be foraging generalists that feed in the intertidal zone of marshes. Terrapin diets changes over time and while male and females do consume similar prey items, there are important differences. One of the major differences is that females tend to consume more heavily armored items than males. This

is to be expected due to their stronger bite force and larger heads. Terrapins, as a whole, are able to take advantage of harder prey than other species within their family. The relatively high crushing force of their jaws allows terrapins to broaden their niches with prey items that other inter-tidal predators may not be able to eat. While its potential as a top-down controller of benthic community structure is still unknown, this study shows that it may be having some sort of effect on snail abundance since it regularly consumes large amounts of this particular prey item.

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