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Foraging ecology and habitat use of the northern diamondback terrapin (Malaclemys terrapin terrapin) in southern Chesapeake Bay

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Foraging ecology and habitat use of the northern diamondback terrapin (*Malaclemys terrapin terrapin*) in southern Chesapeake Bay

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In Partial Fulfillment
of the Requirements for the Degree of
Doctor of Philosophy

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by

Diane C. Tulipani
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APPROVAL SHEET

This dissertation is submitted in partial fulfillment of

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DEDICATION

To the loving memory of my grandmother, Mary Burns Hunt.

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ABSTRACT

The northern diamondback terrapin (*Malaclemys terrapin terrapin*) is the only estuarine turtle residing along western Atlantic and Gulf of Mexico coasts of North America. Through predation, terrapins may be a key species in coastal marine habitats by exerting top-down control on marsh invertebrates, and thereby help to maintain healthy marshes. Despite the terrapin's ecological importance, there has not been a thorough study of terrapin foraging ecology and movements in lower Chesapeake Bay. In this dissertation, the research focused on the foraging habits of diamondback terrapins and their effects within salt marsh and seagrass habitats of lower Chesapeake Bay. I provided detailed analysis of the diet of diamondback terrapins captured from both salt marsh and seagrass habitats that showed preferred foraging in seagrass beds when present, as well as prey differentiation by terrapin size, i.e., small vs. large terrapins. Three general patterns in dietary overlap based on terrapin size were common for *M. terrapin*. By habitat, there was substantial overlap in prey choice, though further analyses determined selectivity for barnacles *Balanus* spp. by small terrapins in seagrass beds. Small terrapins from marsh-mudflat habitats consumed more periwinkles than large terrapins from marsh-mudflat habitats or all terrapins from marsh-SAV habitats. The size of ingested periwinkles was related to terrapin size with snails ingested by mature females presenting a bimodal distribution. Two mesocosm prey choice experiments showed that terrapins had a preference for juvenile blue crabs (*Callinectes sapidus*) over periwinkles and mottled dog whelks (*Nassarius vibex*). A third revealed terrapins were less successful in finding and consuming blue crabs with increasing percent cover of vegetation. An acoustic telemetry study confirmed that small terrapins, which included all males and juvenile females, had better-defined home ranges than adult females and stayed mostly in shallow near-shore water in seagrass beds of lower York River, whereas large females entered these areas on flood and high tides. A logistic regression model predicted that small terrapins were less likely to move out of an area than large females. Males made infrequent, long distances trips within the study area not associated with mating. Both genders and size classes also frequently moved between non-connected *Zostera marina* beds in the study area. This research provided the first field evidence that terrapins ingested viable eelgrass seeds incidental to consuming *Z. marina* epifauna. A second logistic regression model revealed that small terrapins were more likely to consume seeds than large terrapins. The diamondback terrapin is considered a "species of concern" in Virginia, but it has minimal protection with little enforcement. This dissertation provides empirical evidence supporting the diamondback terrapin's ecological importance within Chesapeake Bay that can be incorporated into conservation strategies to promote recovery and protection of the species within Virginia.

AUTHOR'S NOTE

The chapters of this dissertation were written in manuscript format for scientific publication. Thus, each chapter is written in the third person to represent my co-authors, and is formatted to align with the guidelines of the journal to which the manuscript was or will be submitted. At the time of writing, citations for individual chapters are as follows:

CHAPTER 2
Tulipani, D.C. and Lipcius, R.N. *In prep.* Foraging by northern diamondback terrapins (*Malaclemys terrapin terrapin*) in seagrass beds and salt marshes of lower Chesapeake Bay: variation by size and habitat.

CHAPTER 3
Tulipani, D.C. and Lipcius, R.N. *In prep.* Selective foraging and search success of northern diamondback terrapins (*Malaclemys terrapin terrapin*) in lower Chesapeake Bay.

CHAPTER 4
Tulipani, D.C. and Lipcius, R.N. *In prep.* Tracking diamondback terrapins (*Malaclemys terrapin*) using ultrasonic telemetry: range and habitat use in submerged aquatic vegetation beds in southern Chesapeake Bay.

CHAPTER 5
Tulipani, D.C. and Lipcius, R.N. *In prep.* Eelgrass (*Zostera marina*) seed dispersal by northern diamondback terrapins (*Malaclemys terrapin terrapin*) in lower Chesapeake Bay.

Foraging ecology of diamondback terrapins in lower Chesapeake Bay

CHAPTER 1

Introduction

INTRODUCTION

The diamondback terrapin (*Malaclemys terrapin*) of the family Emydidae is a broadly distributed turtle found in coastal regions throughout temperate and subtropical regions of the eastern United States (Wood 1977). It is the only aquatic turtle in North America that is a permanent resident in the narrow strip of brackish water habitats from Massachusetts to Texas (Ernst and Lovich 2009). Other species, such as the common snapping turtle (*Chelydra serpentina*), sometimes venture into brackish portions of estuaries in search of food (Dunson 1986). Five of the seven marine turtles are seasonal migrants to various estuarine regions of the US coast with many venturing into Chesapeake Bay, Virginia's coastal bays, and locations farther north mainly in search of food (Ernst and Lovich 2009). Terrapins are an iconic turtle species within Chesapeake Bay (Roosenburg 1991). This species has had a long history of being overharvested as its culinary popularity increased through the early part of the 20th Century (Coker 1920; Hildebrand and Hatsel 1926). After most commercial harvest ended by the early 1930s, diamondback terrapin populations experienced some recovery until faced with negative impacts from habitat loss and as bycatch in the blue crab (*Callinectes sapidus*) pot fishery (Roosenburg 1991). The conservation status of populations in the United States varies greatly from state to state. Some populations are considered endangered or threatened while others are listed as stable. In Virginia, *M. terrapin* are considered a "species of conservation concern" (Roble 2013).

There are seven recognized subspecies of *Malaclemys terrapin* with distinctive physical characteristics and variations in life history traits adapted to their specific latitude (Wood 1977; Ernst and Lovich 2009). It is the northern diamondback terrapin subspecies, *M. t. terrapin* that is in Virginia (Ernst and Lovich 2009). Generally, terrapins in southerly locations emerge from hibernation earlier, mature, and reproduce at younger ages than those in the northern parts of the range (Roosenburg 1991; Baldwin et al. 2005; Ernst and Lovich 2009). Male and female terrapins become sexually mature at different ages with female terrapins maturing later and at a larger body size compared to males (Lovich and Gibbons 1990; Roosenburg 1991). *Malaclemys terrapin* exhibits gender-size dimorphism such that mature females can be more than twice as large as adult males, i.e., maximum straight carapace length (SCL_{max}) 28.8 cm and 14.0 cm, respectively (Ernst and Lovich 2009). Depending on location, males become sexually mature as early as 3 years old and females mature as early as 6 years old (Ernst and Lovich 2009). Mating season occurs shortly after emergence from hibernation commencing as early as March and ending in May depending on latitude (Ernst and Lovich 2009). Nesting follows through early July (Ernst and Lovich 2009). As with many turtle species, small clutch size and low survivorship result in low replacement within populations causing population declines (Roosenburg 1991). While predation on eggs by raccoons (*Procyon lotor*) is responsible for the majority of nest failures

(Munscher et al. 2012), population declines can be intensified by accelerated losses caused by bycatch mortality (Roosenburg et al. 1997).

Size dimorphism has evolved in many species and in most reptile groups (Cox et al. 2009). In several turtle groups, including Emydidae, Geoemydidae, and Trionychidae, females being bigger than males is common (Gibbons and Lovich 1990; Cox et al. 2009). Behavior and adaptions by species in the emydid genera *Graptemys*, *Chrysemys*, and *Trachemys* have been attributed to this adaption (Gibbons and Lovich 1990; Rowe 1997; Lindeman 2000). It is a common effect that being a large size increases reproductive output in females (Gibbons and Lovich 1990). *Malaclemys terrapin* has also been studied with respect to female size and reproductive output (Roosenburg and Dunham 1997). Proportionally, larger body size is accompanied by a larger head. In turtles, having a larger head implies ingesting larger prey (Cox et al. 2009). Lindeman (2000) addressed patterns in habitat use and food resources with respect to female head morphology in the *Graptemys* genus segregating species into three categories, i.e., microcephalic, mesocephalic, and megacephalic, based on head and alveolar widths. Preference was for molluscs in megacephalic turtle diet though it appeared to decrease in species with smaller head width (Lindeman 2000). Similar to *Graptemys*, mature female diamondback terrapins from South Carolina, Florida, and New York ate mainly gastropods and bivalves (Tucker et al. 1995; Butler et al. 2012; Erasmus 2012). In comparison, males of all *Graptemys* species fed on smaller prey groups similar to microcephalic females (Lindeman 2000). Diets of male and juvenile female *Graptemys* of similar body size typically overlap (Lindeman 2000).

Differences in body size may also support use of different habitats. In Maryland, males and juvenile female diamondback terrapins of similar size utilized different near-shore habitats than larger mature females (Roosenburg et al. 1999), though all sizes ventured farther into salt marshes on high tides to feed (Tucker et al. 1995). A variety of diet studies of diamondback terrapins described different prey preferences at different sites from Florida to New York (Tucker et al. 1995; Spivey 1998; Petrochic 2009; Butler et al. 2012; Erazmus 2012). Some of the variation between prey choices can be attributed to a latitudinal gradient of species (Brown 1984). Some variation may also be attributed to size differences and different prey assemblages based on habitat (Butler et al. 2012). Selectivity of prey by juvenile hawksbill sea turtles (*Eretmochelys imbricata*) on certain coral species resulted in low abundance of some species (Rincon-Diaz et al. 2011). Terrapins are top predators in salt marshes (Tucker et al. 1995). By selectively choosing certain prey, diamondback terrapins can exert top-down control in a given habitat (Silliman and Bertness 2002).

In Chesapeake Bay, coastal regions that are used by terrapins commonly include *Spartina*-dominated salt marshes (Reay and Moore 2009). Also located within Chesapeake Bay and Virginia's coastal bays and lagoons are seagrass beds dominated by *Zostera marina* (eelgrass) found subtidally adjacent to marshes, though the amount of seagrass has been in decline for many decades (Orth et al. 2011). Seagrass habitats provide many ecosystem services (Costanza et al. 1997). They support great abundance and diversity of species providing food and refuge for both permanent and transient organisms (Homziak et al. 1982). Salt marshes and subtidal habitats are linked through use of the two habitats and migration between them by various aquatic organisms including fishes (Irlandi and Crawford 1997; Orth et al. 2006). Aquatic species that provide this link are able to maximize the resources of each habitat (Irlandi and Crawford 1997). In North Carolina and Virginia, diamondback terrapins are found in seagrass beds (Spivey 1998; this study). However, there was no indication that terrapins were utilizing that habitat for foraging (Spivey 1998). In Virginia, diamondback terrapins become active in early April and complete mating by the end of May (Ernst and Lovich 2009). This coincides with the timing of maturation and release of *Z. marina* seeds (Silberhorn et al. 1983).

Since terrapins in lower Chesapeake Bay appear to utilize the near-shore marsh habitat where seagrass beds occur, they potentially are feeding in seagrass. Prior to this study, it had not yet been shown definitely that they were. While feeding on seagrass fauna, they can ingest mature *Z. marina* seeds. Seed dispersal by turtles does occur. Many previous studies have detailed dispersal of terrestrial and aquatic plant seeds by terrestrial and aquatic turtles, such as Galápagos tortoises (*Chelonoidis nigra*; Blake et al. 2012), Florida box turtle (*Terrapene carolina bauri*; Liu et al. 2004), black river turtle (*Rhinoclemmys funerea*; Moll and Jansen 1995), as well as red-eared sliders (*Trachemys scripta elegans*) and the common snapping turtle (*Chelydra serpentina*; Kimmons and Moll 2010). Determining whether a specific species is an effective seed disperser can be challenging (Schupp 1993). The combined criteria of number of seeds ingested and whether they produce adult plants determines if the turtle is positively or negatively impacting that plant

(Schupp 1993). Silliman and Bertness (2002) suggested that terrapin predation on marsh snails helped to maintain marsh plant abundance. In seagrass beds of Chesapeake Bay, diamondback terrapin predation on seagrass fauna may be beneficial to *Zostera marina*.

In this dissertation, I describe habitat use and the role of the terrapin in the food web of near-shore, brackish-water habitats by examining its movement patterns, foraging habits, and diet within seagrass beds and salt marshes of the lower York River subestuary. In Chapters 2 and 3, I describe the foraging habits of northern diamondback terrapin, *M. t. terrapin*, in *Z. marina* and salt marsh habitats of the York River, Virginia. In Chapter 2, I describe prey selection by size class (i.e., large vs. small) and by habitat (i.e., salt marsh with adjacent mudflats vs. salt marsh with adjacent subtidal seagrass beds) based on findings from a three-year diet analysis. In Chapter 3, I further examine terrapin prey selectivity as it relates to abundance of prey species in each habitat. In Chapter 4, I address habitat use and preference by diamondback terrapins as determined from an acoustic telemetry study centered on terrapin movements between *Zostera marina* beds in the lower York River. In Chapter 5, I consider the dispersal effectiveness of diamondback terrapins with respect to ingestion and dispersal of *Z. marina* seeds. The overarching goal of this dissertation is to provide the empirical and theoretical information needed to justify the terrapin's ecological importance in lower Chesapeake Bay, leading to improved conservation strategies that will foster population recovery and protection in Virginia.

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CHAPTER 2

Foraging by northern diamondback terrapins (*Malaclemys terrapin terrapin*) in seagrass beds and salt marshes of lower Chesapeake Bay: variation by size and habitat.

ABSTRACT

Diet analysis of the Northern Diamondback Terrapin (*Malaclemys terrapin terrapin*) based on fecal samples revealed foraging in submerged aquatic vegetation (SAV) beds over adjacent salt marsh habitat in southern Chesapeake Bay. Significant differences in prey selection varied by size class of terrapin in species consumed from both habitats regardless of gender. Multivariate analyses confirmed most variation in diet was because of terrapin size class. An ontogenetic shift occurred in females, which consumed barnacles and crabs when small to bivalves and crabs as head width increased to 30 mm and larger. The proportion of crab biomass in total fecal sample biomass also increased with terrapin size, e.g. small 6.5% vs. large 17.7%. Barnacles were consumed most frequently by small terrapins and by those captured in SAV habitats. The tunicate, *Molgula* manhattensis, was found more frequently in fecal samples from terrapins captured in marsh-mudflat habitats. When feeding subtidally on SAV epifauna, such as barnacles, terrapins significantly increased ingestion of plant matter compared to foraging in salt marshes. These findings indicate that Northern Diamondback Terrapin size and the type of habitat influence foraging behavior and prey species consumed in lower Chesapeake Bay. Of all terrapins captured in SAV beds, 81.5% had ingested pieces of eelgrass (*Zostera marina*) leaves. Of 118 terrapins captured in late spring, 34 had ingested eelgrass seeds. These findings represent the first field evidence of Northern Diamondback Terrapins foraging in eelgrass beds and ingesting eelgrass seeds, thereby expanding the modes of biological seed dispersal for *Zostera*.

INTRODUCTION

The complexities of community interactions, such as predation and competition, have challenged ecologists for decades (Hairston et al., 1960; Duffy, 2002). Abundant species greatly affect their community and habitat (Power et al., 1996) and that changes in species abundance can affect structure (e.g., *Pisaster* sp. in rocky intertidal habitat, Paine, 1974; and sea otters, *Enhydra lutris*, in kelp forest, Konar, 2000) and diversity within their community (e.g., large predatory fishes in eelgrass meadows, Bologna, 2007). Foraging within a habitat can result in changes in abundance of prey species, such that juvenile Hawksbill Sea Turtles (*Eretmochelys imbricata*) on coral reefs near Puerto Rico resulted in low abundance of some species of coral (Rincon-Diaz et al. 2011). There may be similar effects from foraging by a reptile within salt marshes of the eastern United States.

The Diamondback Terrapin, *Malaclemys terrapin*, is the only turtle of the family Emydidae in North America that resides exclusively in the coastal salt marshes and estuaries from Cape Cod to Corpus Christi (Ernst and Lovich, 2009). In Virginia, the Northern Diamondback Terrapin, *M. terrapin terrapin*, is an apex predator found in brackish water habitats throughout the state, including Chesapeake Bay, ocean-facing salt marshes of the Eastern Shore, and the state's southern shoreline. As a top predator in salt marshes, terrapins have filled a niche not occupied by other reptiles. As such, this species has the potential to strongly influence the community structure within this habitat through foraging and prey choice (Silliman and Bertness, 2002).

Similar to other emydid turtles such as *Graptemys* spp., Northern Diamondback Terrapins exhibit gender-size dimorphism with mature females being approximately twice as large as mature males (Ernst and Lovich, 2009). Head width of emydid turtles can determine size of prey ingested (Lindeman, 2000; Herrel et al., 2002). The bite strength was measured for diamondback terrapins from Oyster Bay, New York and showed that mature female terrapins have greater head width, which enables them to eat larger invertebrate prey with thicker shells that smaller turtles cannot crush (Petrochic, 2009). Juvenile females of species exhibiting similar size differences typically overlap in prey choice and prey size with males until the females attain sufficient size and shift to larger prey (Lindeman, 2000). Diamondback Terrapins feed mainly on hard-shelled marsh and benthic invertebrates including gastropods, bivalves, and decapod crustaceans near and in salt marshes in North Carolina, South Carolina, New York, and Florida (Coker, 1906; Tucker et al., 1995; Petrochic, 2009; Butler et al., 2012). Ingested plant material was considered incidental to feeding on epifaunal species (Ernst and Lovich, 2009; Butler et al., 2012).

Latitudinal differences in prey consumed by Diamondback Terrapins vary by species along the terrapin's range associated with the distribution of the species of prey (MacArthur, 1972; Tucker et al., 1995; Spivey, 1998; Butler et al., 2012). Some, like the marsh periwinkle *Littoraria* spp., are found along large portions of the terrapin's range. In a South Carolina marsh, periwinkles are the main prey consumed (Tucker et al., 1995). In North Carolina, small terrapins prefer the marsh snail *Melampus bidentatus* whereas medium and large terrapins prefer blue crabs *Callinectes sapidus*. Northern Diamondback Terrapins from Long Island Sound prefer the snail *Ilyanassa obsoleta* (Petrochic, 2009) whereas mature females from Jamaica Bay, New York, prefer bivalves (Erazmus, 2012). No explicit diet study had previously been conducted for Northern Diamondback Terrapins in Virginia or Chesapeake Bay (Roosenburg et al., 1999). It was reasonable to conclude that terrapin prey selection in Virginia would be similar to that in other regions since the state's coastal habitats and faunal composition are similar to other regions along its range.

Habitat preferences and food availability may shape dietary composition in a particular habitat (Moll, 1990), and prey preference may differ because of the specific habitat structure (Roosenburg et al., 1999; Gibbons et al., 2001). Availability of new prey, such as the invasive Zebra and Quagga mussels in Texas (Lindeman, 2006a), the Great Lakes (Lindeman, 2006b), and in Pennsylvania (Patterson and Lindeman, 2009), has altered foraging habits of two *Graptemys* spp. In Florida, preferred prey shifts when mature female terrapins feed in marsh creeks or at nesting beaches (Butler et al., 2012). In Chesapeake Bay, in addition to *Spartina alterniflora*-dominated salt marshes, there are extensive seagrass beds often found adjacent to salt marshes (Reay and Moore, 2009; Orth et al., 2011). Two seagrass species dominate the saline portions of Chesapeake Bay; eelgrass *Zostera marina* and widgeon grass *Ruppia maritima* (Orth et al., 2011). Seagrass beds are important coastal habitats that provide many ecological and economic ecosystem services, e.g., supply organic material to local food webs, provide refugia for many organisms including commercially important species, trap sediment and particles from the water column, stabilize sediments, and enhance primary production (Costanza et al., 1997; Short et al., 2007). They also support high biodiversity through increased vertical living space on leaves and amongst roots and rhizomes within sediments (Short et al., 2007). Spivey (1998) reported the presence of Diamondback Terrapins in seagrass beds in North Carolina. Northern Diamondback Terrapins have been observed in seagrass beds in Chesapeake Bay (D. Tulipani, pers. obs.). I am unaware of any publications prior to the commencement of this study in 2009 that described them as part of the temperate seagrass food web (Orth et al., 1984; Heck et al., 2008), though plentiful anecdotal evidence described the presence of this species in local seagrass beds.

The objective was to describe the diet of Northern Diamondback Terrapins in two habitat types, seagrass and salt marsh, as well as by size class, in the lower Chesapeake Bay. We hypothesized that Northern Diamondback Terrapin prey preference would differ between habitat types and would reflect differences in prey selection associated with head size regardless of habitat. Results by size class and habitat type were compared to the findings from previous reports.

MATERIALS AND METHODS

Northern Diamondback Terrapins were collected May through August of 2009, 2010, and 2011 along the York River and southeastern Mobjack Bay, Virginia (Fig. 1). Sites were categorized into habitat types by the presence or absence of submerged aquatic vegetation (SAV) beds adjacent to emergent salt marsh. Goodwin Islands, Green Point, Allens Island, Perrin Creek, Browns Bay, and Poquoson were "marsh-SAV" habitats; Catlett Islands and Felgates Creek were "marsh-mudflat" habitats. In salt marsh habitats, smooth cordgrass (*Spartina alterniflora*), the dominant salt marsh plant, was intermixed with saltmeadow cordgrass (*Spartina patens*) and black needlerush (*Juncus roemerianus*) at many sites. At seagrass sites, eelgrass (*Zostera marina*) and widgeon grass (*Ruppia maritima*) were the dominant species in the SAV beds.

Collection methods included a 4.9-m otter trawl, commercial crab pots modified with wire "chimneys" to allow access to surface to prevent drowning, dip nets, a bottom scrape, hoop nets, and hand capture. Each Diamondback Terrapin was notched with a unique turtle identification number (TID) on the marginal scutes (Cagle, 1939). An additional notch was made in the second left marginal scute (left of supracaudal scute) to differentiate terrapins captured for this study from previous studies conducted in the region. After laboratory processing, all live Diamondback Terrapins were released at the capture locations.

Biological and Morphological Information.—

Size of each terrapin was measured to the nearest 0.1 cm using tree calipers and recorded as straight carapace length (CL), carapace width (CW), and plastron length (PL; Fig. 2). Fine-scale calipers were used to measure head width (HW) to the nearest 0.1 mm across the skull at the tympana. Gender was determined by external morphological features of size, tail length, and position of cloacal vent relative to edge of supracaudal scutes. Only mature females had HW ≥ 30 mm (Ernst and Lovich, 2009). Male terrapins had longer, thicker tails with cloacal vent located posterior to the edge of supracaudal scutes (Gibbons and Lovich, 1990).

All measurements were summarized by year and three gender-size classes (Table 1): males (HW < 30 mm), small females (HW < 30 mm), and large females (HW ≥ 30 mm), similar to the classes in Tucker et al. (1995). Using R statistical programming language, morphological data were analyzed for significant differences using ANOVA ($\alpha = 0.05$) with Tukey Honest Significant Differences (Tukey HSD) test for multiple comparisons between gender-size classes within each year and for each gender-size class between years. Measurements for large females were analyzed separately as all size comparisons were significantly different from the small size class (Table 1). Size measurements of male and small female terrapins (HW < 30 mm) were compared by year and gender.

Diet analysis.—

Upon capture, individual terrapins were placed in buckets and transported to Virginia Institute of Marine Science. Specimens were maintained indoors in individual 19-L aquaria (mature females were kept in large plastic totes) for up to 5 d in either tap water or brackish water from nearby York River. Brackish water protected potentially viable egested eelgrass seeds in 2010 and 2011. Fecal samples were collected daily, rinsed through a 1-mm standard test sieve into small pre-weighed drying trays and air dried prior to sorting. Fecal material egested during transit to lab was also collected and sorted after being dried. In 2010 and 2011, after eelgrass seeds were removed, samples were rinsed with tap water to remove salt before being dried. Daily sample dry weight (DSDW) was recorded prior to sorting. All DSDWs for each turtle were summed to give total sample dry weight (TSDW). Dried samples were sorted according to taxon and plant material into separate, pre-weighed trays viewed through a dissecting microscope. Each subsample tray was weighed again and mass of each different organism was calculated. Items were sorted to the lowest identifiable taxon.

Each prey group was summarized by percent occurrence (i.e., percent of fecal samples containing a specific group), and percent mass of sample (i.e., total mass of prey group divided by TSDW). Percent occurrence and percent mass of sample were summarized for each year by size class based on HW ≥ 30 mm or HW < 30 mm (Tucker et al., 1995). Genepop v4.1.4 was used to compare percent occurrence between size classes and separately by habitat with a G-test of population differentiation using default settings (Butler et al., 2012). Each prey group was assigned one of two possible values indicated as "present" (barnacles = "0101", snails = "0202", bivalves = "0303", crustaceans = "0404", plant = "0505", fishes = "0606", insects = "0707", tunicates = "0808", and sand = "0909") or "absent"

("9999"). Comparisons were tested for population differentiation across all prey groups.

PRIMER 6 (version 6.1.6, PRIMER-E) was used to calculate Shannon Diversity (H'), Pielou's Evenness (J'), and Margalef's Richness (d) indices to describe the diversity of prey consumed by habitat and size class using mass of each prey (Magurran, 2004). Schoener's Overlap index (θ) was calculated to determine biological significance of resource partitioning of data summarized by the categories habitat and size-class, based on terrapin head width (Schoener, 1968; Tucker et al., 1995). Schoener's Overlap index (θ) was calculated as:

$$\theta = 1 - \tfrac{1}{2} \left(\ {}_{i=1}^{s} |P_{ij} - P_{ik}| \right) \qquad s = 1, \ldots, m$$

where P_{ij} and P_{ik} were proportions of the food resource i used by category j and k, and s is the total number of different resources used by each category (Tucker et al., 1995). Diversity overlap values range between 0 and 1, no overlap and complete overlap, respectively. Partitioning was considered minimal if $\theta < 0.4$ and biologically significant if $\theta > 0.6$ (Schoener, 1968; Zaret and Rand, 1971).

PRIMER 6 was also used to perform three multivariate analyses. Prior to analysis, fecal sample biomass data were first standardized as percent of total by individual turtle then square-root transformed. Bray-Curtis similarity measure was then used to construct similarity matrices. Non-metric multidimensional scaling (nMDS) ordination was used to compare diet composition across habitats and by terrapin size. ANOSIM, analysis of similarity routine, was used to determine significant differences, as indicated by the Global R value, between large and small size classes and between marsh-mudflat and marsh-SAV habitats. The R statistic was interpreted as *groups well-separated* when R > 0.74, *groups overlap but clearly different* when R > 0.5, or *groups barely separable* when R < 0.25 (Dreyer et al., 2005). SIMPER, similarity percentages routine, was used to examine contribution of various prey groups to Bray-Curtis dissimilarities between the same factors if ANOSIM indicated significant results.

RESULTS

Diet analysis was based on 141 males and 82 females (Table 1). Four males and two females marked in this study were recaptured once in a subsequent year, one male was recaptured in two different years, and two males were captured a second time within the same year they were marked. All recaptures occurred in the same location of original capture. Only two terrapins died during capture throughout the study.

Gender and size analysis.—

The overall sex ratio was 1.6:1 male to female (Table 1). Of all terrapins, 64% were captured from Goodwin Islands and Green Point sites at the mouth of the York River; 19% were from Allens Island and Perrin Creek cove; 10% were from the Catlett Islands; and 6% were from Browns Bay. One large female was captured each from Felgates Creek and Poquoson.

Size of large females with HW ≥ 30 mm (n = 45) did not differ significantly between years (all $P > 0.05$). The overall means (± SE) were CL = 20.5 ± 0.2 cm, PL = 18.5 ± 0.2 cm, HW = 38.8 ± 0.6 mm, and mass = 1,395.0 ± 44.2 g. For males and females with HW < 30 mm, of all recorded measurements only HW was significantly different ($P < 0.001$) between genders, and there was an interaction between year and gender ($P < 0.05$; Table 2). Differences in male HW and small female HW by year ranged from 1.5–4.2 mm with the largest difference occurring in 2011 (Table 2).

Many fewer females (HW < 30 mm) were captured in 2011 with four of the six having HWs approaching 30 mm. Though statistically significant, this was not considered biologically significant and all terrapins with HW < 30 mm were pooled into the small size class for diet analysis.

Diet analysis.—

Most terrapins in this study consumed several prey types or species (Table 3). For these terrapins, the number of prey consumed had a median = 4 and the range = 1-11. There was a significant difference (ANOVA $P < 0.01$) in number of prey ingested by terrapin size class. Large terrapins ingesting slightly more prey types than small terrapins; the mean number of prey types ingested by large was 5.3 (± 0.3) vs. mean ingested by small of 4.5 (± 0.1). However, there was no significant difference by habitat. Generally, animals in the samples included four types of crustaceans (barnacles, crabs, isopods, and amphipods), two types of molluscs (snails and bivalves), fish bones and scales, insect parts, and tunicates (Figs. 2, 3). Pieces of marsh, aquatic plants and algae occurred in most fecal samples (Figs. 2, 3). Sand grains were common in samples, though the mass was minor (i.e., mean < 0.007 g).

Small terrapins (HW < 30 mm) produced mean fecal sample mass of 1.895 ± 0.120 g and large terrapins produced 6.444 ± 1.522 g. Barnacles constituted 49% of diet mass for small terrapins, which egested a mean of 0.932 ± 0.103 g barnacles. Conversely, large terrapins only egested 0.269 ± 0.114 g barnacles, constituting only 4%. Bivalves dominated the diet of large terrapins and averaged nearly 60% of TSDW (Fig. 3A), but were less than 4% of TSDW for small terrapins (Fig. 3B). Other crustaceans, such as crabs, isopods and amphipods, and several snail species (e.g., *Bittium* sp., *Melampus bidentatus,* and *Littoraria irrorata*) also contributed to the diet of both size classes (Fig. 3).

Percent occurrence of barnacles, bivalves, and fishes differed between size classes (Table 4). Over 70% of large and 90% of small terrapins had consumed barnacles, over 85% of each size class had ingested other crustaceans, and greater than 68% of each had ingested snails (Fig. 4). Of large terrapins, 76% and 47% ingested bivalves and fish parts, respectively; small terrapins consumed these items infrequently (Fig. 4). Significantly more small terrapins had consumed barnacles ($P < 0.01$), whereas large terrapins more frequently ingested bivalves and fishes (both $P < 0.01$). Northern Diamondback Terrapins from marsh-SAV sites also consumed barnacles more often than those from marsh-mudflat sites, whereas tunicates were more frequently consumed at marsh-mudflat sites (Table 4).

Small horn snails *Bittium* sp. ($P < 0.05$) and the common marsh snail *Melampus bidentatus* ($P < 0.05$) were consumed more often by small terrapins than by large ones (Table 5). *Bittium* sp. was also consumed more frequently ($P < 0.01$) in SAV beds (Table 5). Consumption of marsh periwinkles *Littoraria irrorata* was higher ($P < 0.01$) for terrapins from marsh-mudflat sites (Table 5). Large terrapins ate blue crabs *Callinectes sapidus* more frequently ($P < 0.01$) than small ones (Table 5). The proportion of crab biomass in TSDW also increased with size from 6.5% TSDW for small terrapins to 17.7% TSDW for large terrapins. Within the small size class, the amount of egested crab was significant (ANOVA $P < 0.01$); small females egested more crab material than males. Blue and mud crabs were eaten more frequently in marsh-mudflat habitats (Table 5). Ribbed mussel *Geukensia demissa* and total clam prey categories were significantly more common in large terrapins than small ones ($P < 0.01$ for both), though there was no significant difference by habitat (Table 5).

When combined across years, plant material was ingested by 97.3% of all terrapins, though the percent TSDW for plant material varied per year and size class. When compared by habitat, terrapins from marsh-SAV sites more frequently ingested plant material than terrapins from marsh-mudflat sites (Table 4). In 2009, 2010, and 2011, egesta from large terrapins contained 10.8%, 1.7%, and 2.9% plant TSDW, respectively, whereas egesta from small terrapins contained 8.6%, 8.0%, and 16.6% plant TSDW, respectively. Of the identified plant material, eelgrass *Zostera marina* was ingested by 73% of all terrapins, and by 81.5% of ones from marsh-SAV sites regardless of size (Fig. 5).

Fecal samples from marsh-SAV terrapins contained *Z. marina* blades, spathes (seed pods), and seeds in all years. Over the three years, 34 terrapins egested a total of 82 *Z. marina* seeds. Widgeon grass *Ruppia maritima* blades were also identified in many marsh-SAV samples, though less frequently than *Z. marina* (Fig. 5). Sea lettuce *Ulva lactuca*, a marine alga, was identified in samples from both size classes and habitats, yet it contributed less than 1.4% plant TSDW. For all three years, smooth cordgrass *Spartina alterniflora* was ingested by 12.6% of terrapins, irrespective of size and habitat, though it accounted for less than 1% plant TSDW each year. Stem pieces of *S. alterniflora* were most common, and sometimes with mussels or barnacles still attached.

Shannon Diversity, Pielou's Evenness, Margalef's Richness, and Schoener Overlap (θ) indices of prey types frequently differed by habitat and size class, though not in a consistent manner (Table 6). Dietary evenness and diversity were nearly identical for both habitats. Species richness (d) based on mass of prey consumed was much greater for terrapins feeding in marsh-mudflat areas, possibly from feeding equally on more species; there was no difference by size class. Diversity and evenness of prey consumed by large terrapins was higher than those of the small size class (Table 6). Schoener Overlap (θ) indicated little overlap in prey type consumed by size class, yet moderate overlap by habitat neared biological significance (Table 6).

Multivariate analyses confirmed that most of the variation in diet was because of terrapin size (nMDS ordination and ANOSIM, $R = 0.416$, $P < 0.001$), though with some habitat effects ($R = 0.224$, $P < 0.003$) driven by prey choice of marsh-SAV terrapins (Figs. 6, 7). When analyzed by habitat, there was greater separation in prey groups consumed by size class for marsh-SAV individuals ($R= 0.47$, $P < 0.001$) and almost no separation by size class for those from marsh-mudflat habitat ($R= 0.031$, $P = 0.31$). Prey choice influenced by size class was particularly evident for barnacles, periwinkles of all gastropods, mussels, and blue crabs (Figs. 6, 7). Mussels and periwinkles were more frequently consumed by large terrapins, whereas barnacles were favored by small terrapins. Most of the dissimilarity in diet by size class was due to the abundance of barnacles (SIMPER analysis contribution: 20.1%), as well as mussels (contribution: 12.3%) and blue crabs (contribution: 10.7%). Although biomass of periwinkles was 3.4 times higher for large size class than the small size class, this difference only contributed 6.3% to dissimilarity in diet.

DISCUSSION

Northern Diamondback Terrapins exhibited significant differences by size in species consumed regardless of gender, similar to genus *Graptemys* (Lindeman, 2000). A shift occurred in prey ingested by females as head width increased to 30 mm and larger. When terrapins were captured in SAV beds adjacent to salt marshes, the composition of their fecal material was dominated by SAV-associated fauna and plants. A striking difference for southern Chesapeake Bay terrapins was the significant increase of plant matter ingested by those feeding in SAV beds. Earlier studies considered plant ingestion incidental (Tucker et al., 1995; Butler et al., 2012) whereas over 80% of terrapins captured in SAV beds had ingested pieces of eelgrass. An increase in ingested plant material may represent a transition to an omnivorous diet when terrapins feed in SAV beds. The findings presented here are the first field evidence of Northern Diamondback Terrapins foraging in eelgrass *Zostera marina* beds. The additional discovery of eelgrass seeds in 2009 fecal samples was a novel finding, thereby expanding the modes of biological seed dispersal for *Zostera marina*. Northern Diamondback Terrapin size and habitat influenced foraging behavior and type of prey consumed in Chesapeake Bay.

We identified 34 different genera or species in fecal samples collected over three years, which included mostly invertebrates and several species of aquatic and terrestrial plants (Table 3). Similar to earlier publications, hard-shelled invertebrates dominated the ingested prey. The range and number of prey types consumed were similar to values in Spivey (1998) and Petrochic (2009), though large terrapins consumed slightly more prey types on average. Side-by-side comparison with five recent studies, where results were ranked by highest percent occurrence reported per prey type for any size class, highlighted the variety in consumed prey by terrapins throughout their range (Table 7). Bivalve and gastropod molluscs were most frequently consumed (Table 7). Bivalves were ranked first in two studies, whereas gastropods were ranked first in three (Table 7). In North Carolina, as determined by percent mass, small terrapins preferred the gastropod *Melampus bidentatus* and large terrapins mainly consumed decapod crustaceans, as well as bivalves though to a much lesser extent (Spivey, 1998). Many of the species of preferred prey in other locations were also selected by terrapins in this study (Tables 3, 5). In Virginia, barnacles, crabs, and bivalves were ingested most often depending on terrapin size and habitat though plant material was the most frequently occurring item over all (Tables 4, 5; Fig. 4). In contrast to previous studies, barnacles contributed significantly to the diet of small terrapins, particularly those captured in SAV beds (Table 4). Of small terrapins captured in SAV beds, 92% had ingested barnacles. Bay barnacle *Balanus improvisus* and ivory barnacle *B. eburneus* were both identified and often found in samples still attached to pieces of *Z. marina* and *S. alterniflora*. On average, small terrapins egested nearly four times as much barnacle biomass per terrapin as did large terrapins.

Barnacles and other crustaceans were most frequently ingested by the majority of all terrapins in this study regardless of habitat (Table 4). Akin to mesocephalic *Graptemys* spp., diet composition for male terrapins was similar to females of comparable body size, e.g., juveniles, though females had slightly broader heads (Table 2; Lindeman, 2000). Male and juvenile female *M. t. centrata* captured from the same habitat also consumed the same prey with similar frequency (Butler et al., 2012). In Virginia, mature female terrapins (large size class) were primarily molluscivores preferring bivalves to gastropods (Fig. 3A) yet bivalves were ranked lower than gastropods by percent occurrence over all terrapins in this study (Table 7). *Geukensia demissa* plus all clam species accounted for the majority of fecal biomass from large females, unlike in North Carolina where crabs formed over 80% (Fig. 3A; Spivey, 1998). Within females, a shift in prey choice occurred as females grew larger, transitioning from primarily eating barnacles when small to eating bivalves as head width increased (Fig. 3). The proportion of "other crustaceans'" biomass, which was mainly crabs, also increased with female size (Fig. 3A). Decapod crustaceans were ranked second in five of seven studies (Table 7).

In addition to barnacles and other crustaceans, small terrapins frequently ate a variety of gastropod mollusks (Fig. 3), including *M. bidentatus* found in intertidal marshes (Kneib, 1984), *Bittium* sp., which live on eelgrass (van Montfrans et al., 1984), and the mottled dog whelk, *Nassarius vibex*, a mud snail found in muddy and sandy intertidal sediments of marshes and seagrass beds (Lippson and Lippson, 2006). Periwinkles were consumed more frequently by all sizes and genders from marsh-mudflat habitat than those from marsh-SAV habitat (Table 5). Male terrapins do not have sufficient bite strength to crush the shell of *Ilyanassa obsoleta* and only the snail's operculum is present in their fecal material (Petrochic, 2009). Mottled dog whelks were identified based on opercula found in fecal samples of 66 terrapins (62 males, 2 small and 2 large females). The maximum number egested was 186 opercula by a single mature male (HW = 23.0 mm). No shell fragments from this snail were identified and any soft tissue would have been digested. This suggests the entire snail was not ingested if it indeed was eaten. Mottled dog whelks were commonly found in SAV beds when trawling for terrapins (Tulipani, pers. obs.). Mottled dog whelk opercula are attached to the posterior dorsal area of their foot. It is possible that terrapins either snipped off this portion as the snail twisted its foot trying to right itself or the opercula were incidentally ingested (Petrochic, 2009).

This study is the first documented evidence of terrapins ingesting the tunicate *Molgula manhattensis* (Table 3). Terrapins from both habitats had consumed tunicates. Ingestion of tunicates was not incidental as tunicates formed 77-97% of fecal samples from six males captured from Green Point, a marsh-SAV habitat. In Gorgona National Park, Columbia, nearly 74% of juvenile Green Sea Turtle *Chelonia mydas* consumed pelagic species from the subphylum Tunicata (Amorocho and Reina 2007).

Diversity indices from this study indicated a generalist foraging strategy for diamondback terrapins based on habitat, though less so when based on terrapin size. Diversity measures based on size in this study (e.g., H' = 1.503 and 1.440, J' = 0.510 and 0.489, for large and small size classes, respectively) were within the range of values from other studies where highest averages were H' = 2.51, J' = 0.71 and lowest were H' = 0.983, J' = 0.499 from New York and North Carolina, respectively (Table 6; Tucker et al., 1995; Spivey, 1998; Petrochic, 2009; Erazmus, 2012). Evenness by size class reflected moderate variation in the large female diet (this study; Spivey, 1998; Petrochic, 2009). In other studies, preference typically varied between bivalves and crabs, except in South Carolina where periwinkles were preferred (Tucker et al., 1995; Spivey, 1998; Petrochic, 2009; Erazmus, 2012). In this study, dominance of consumed species by size class was higher than by habitat; bivalves were more frequently ingested by large terrapins and barnacles dominated the diet of small terrapins (Tables 4, 5, 6).

Moderate dietary overlap by habitat indicated that some of the prey types consumed were present in both habitats. The majority of terrapins from marsh-SAV habitat did not exclusively eat SAV-only species. Blue crabs, ribbed mussels, barnacles, *M. bidentatus*, mottled dog whelks, and periwinkles occurred in both habitat types where terrapins were captured. From this and other studies, we summarized three general patterns in dietary overlap based on size, *high overlap between males and small females that decreased as females grew*, *high overlap between medium and large sizes*, and *low overlap between small and large sizes* (Table 6; Tucker et al., 1995; Spivey, 1998; Petrochic, 2009). The first and third patterns applied to Diamondback Terrapins throughout their range and exemplified trophic morphology as described for broad-headed turtle species with gender-size dimorphism (Lindeman, 2000; Patterson and Lindeman, 2009).

The Northern Diamondback Terrapins used in previous diet studies were mostly captured in typical salt marsh habitats with extensive tidal creeks and bays, characteristically muddy sediments, varying tidal amplitudes, and dominated by *Spartina* spp. (Tucker et al., 1995; Spivey, 1998; Petrochic, 2009; Butler, 2012; Erazmus, 2012). Only Spivey (1998) and this study captured terrapins from regions with existing SAV beds dominated by eelgrass (*Z. marina*). Though both sites on Long Island, New York, were within the distributional range for eelgrass, both were situated in highly populated and urbanized regions where naturally occurring eelgrass beds were greatly reduced. Spivey (1998) was the first published account of terrapins in SAV beds though he determined they infrequently utilized the SAV habitat. He also did not report any aquatic or terrestrial plant material in his terrapin diet analysis (Spivey, 1998). One other publication about terrapin hibernacula described eelgrass as a deterrent to capturing brumating terrapins from subtidal areas in the vicinity of South Marsh Island, Maryland (Haramis et al., 2011).

From the start of this project in May 2009, pieces of eelgrass and associated epifauna were found in terrapin fecal material. I am unaware of any publications prior to 2009 that mentioned Northern Diamondback Terrapins foraging directly on eelgrass or even within an SAV habitat despite this species' well-documented use of shallow, near-shore regions of Chesapeake Bay, and elsewhere along its range, where SAV occurs (Spivey, 1998; Roosenburg et al., 1999; Short et al. 2007; Heck et al. 2008). Other turtle species forage on or within seagrass beds, e.g., the Green Sea Turtle *Chelonia mydas* is a marine herbivore that forages on tropical SAV (Thayer et al., 1984; Bjorndal 1985). Juvenile Loggerhead *Caretta caretta* and juvenile Kemp's Ridley *Lepidochelys kempii* sea turtles fed within temperate SAV beds in Chesapeake Bay (Seney, 2003). Though found in 30-60% of Loggerhead Sea Turtles and 30-44%

of Kemp's Ridley Sea Turtles, the amount of eelgrass was minimal and considered incidentally ingested (Seney, 2003; Seney and Musick, 2005). Widgeon grass *Ruppia maritima*, another seagrass in Chesapeake Bay, was found in less than 20% of samples.

The frequency and amount of plant material in fecal samples in this study was substantially greater than previously reported by others (Fig. 4; Coker, 1906; Tucker et al., 1995; Petrochic, 2009; Butler et al., 2012; Erazmus, 2012). The majority was eelgrass ingested when terrapins fed on epifauna, specifically barnacles (Fig. 4). The two New York studies likewise reported large percent occurrence of plant material in samples, 73% plants (Petrochic, 2009) and 52.7% plants and 48.8% algae (Erazmus, 2012). Barnacles attached to eelgrass blades were typically 2 mm or smaller in diameter (D. Tulipani, unpubl. data). To eat such small prey, terrapins would by necessity have to bite off pieces of leaf material with the barnacles. Visually, the eelgrass in fecal samples did not appear digested (D. Tulipani, pers. obs.). Even though the amount of eelgrass was much greater than other plant material reported, it was still likely incidental ingestion. Two questions arise from these findings: (1) do terrapins derive any nutrition from ingested eelgrass or other SAVs and algae? and (2) have terrapins adopted an omnivorous diet when feeding in SAV beds? Bjorndal (1991) described increased digestibility of duckweed *Spirodela polyrhiza* by Yellow-Bellied Sliders *Trachemys scripta scripta* when fed a mixed diet of duckweed and insect larvae. It is possible that Diamondback Terrapins may derive a similar positive associative effect by ingesting eelgrass with attached barnacles. Sea lettuce *Ulva lactuca* was found less frequently and typically with mussels in samples from large females. I concur that *U. lactuca*, frequently associated in samples with bivalves, was incidentally ingested (Erazmus, 2012). This study was also the first documented evidence of terrapins ingesting eelgrass seeds. Eelgrass seeds were first discovered in fecal samples collected in late May 2009. Erazmus (2012) listed plant seeds ingested by 8% of terrapins in her study yet did not identified them to species or whether they were from terrestrial or aquatic plants. In conjunction with rare occurrence of eelgrass in Jamaica Bay, New York, I surmise it would be highly unlikely they were eelgrass seeds. Although it is not unusual for aquatic chelonians to ingest seeds from aquatic and terrestrial plants, most documented occurrences are for freshwater species (Moll and Jansen, 1995; Bonin et al., 2006). Fewer still have been considered as potential seed dispersers like the tropical freshwater species *Rhinochlemmys funerea* (Moll and Jansen, 1995) or recently Red-Eared Sliders *Trachemys scripta elegans* and snapping turtles *Chelydra serpentina* (Kimmons and Moll, 2010). Some of the eelgrass seeds found in fecal samples in 2010 and 2011 were viable (Chapter 5) and suggested the potential of terrapins as additional biological vectors of seed dispersal for eelgrass within Chesapeake Bay.

As gleaned from all the diet studies, the most common prey species of Diamondback Terrapins were bivalves, gastropods, and decapod crustaceans. Species variability in the terrapin diet is to be expected particularly with its geographic range of approximately 6,000 km of shoreline spanning temperate and subtropical zones (Brown et al., 1996). An overarching theme of terrapin foraging ecology is the adaptations the species has made with respect to habitat-dependent prey availability. When various habitats are present, there is potential for increased variety in prey (Lindeman, 2006b). Although the types of organisms they consumed were not completely different from other regions, terrapins exploited the abundant resources in SAV meadows located in close proximity to salt marshes in the lower Chesapeake Bay. Not only do terrapins benefit from SAV resources for food and refuge, they may also help retention of eelgrass in shallow water areas of Chesapeake Bay by feeding on biofouling epifauna and dispersing viable seeds. An ongoing concern is the ability of Diamondback Terrapins to adapt to changes in prey availability brought about through negative anthropogenic effects, such as coastal development, environmental pollution and climate change resulting in habitat loss, as well as mortality from bycatch in the blue crab pot fishery (Radzio et al., 2013). Such presumably mutualistic benefits derived for local seagrass beds through foraging by this species can provide additional support for improved conservation of Northern Diamondback Terrapins within Virginia and the Chesapeake Bay region.

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Table 1.— Number of captured diamondback terrapins included in foraging analysis split by year for each size class and habitat.

	Size Class					Habitat		
	HW < 30 mm		HW ≥ 30 mm			Marsh-mudflat	Marsh-SAV	
Year	Males	Females	Females	Total	Year			Total
2009	43	11	15	69	2009	9	60	69
2010	47	20	8	75	2010	5	70	75
2011	52	5	22	79	2011	9	70	79
Total	142	36	45	223	Total	23	200	223

Table 2.— Size summary for diamondback terrapins captured along the York River, Virginia, 2009, 2010, and 2011. Values reported are mean (±SE) of straight carapace length (SCL), plastron length (PL), head width (HW), and mass for males (A) and two size classes of females (B and C). All males head widths < 30 mm.

A: Males HW< 30 mm

Year	n	SCL (cm)	PL (cm)	HW (mm)	Mass (g)
2009	43	12.7 (0.2)	10.8 (0.2)	21.1 (0.2)	323.9 (13.5)
2010	49	12.7 (0.2)	11.1 (0.2)	21.4 (0.2)	303.7 (10.3)
2011	52	12.7 (0.2)	11.0 (0.1)	21.4 (0.2)	304.5 (9.6)

B: Females HW< 30 mm

Year	n	SCL (cm)	PL (cm)	HW (mm)	Mass (g)
2009	13	12.9 (0.7)	11.6 (0.8)	22.6 (0.6)	310.7 (26.0)
2010	20	12.3 (0.4)	11.1 (0.4)	23.2 (0.6)	316.6 (29.2)
2011	6	13.6 (1.0)	12.2 (0.9)	25.6 (1.0)	420.7 (75.7)

C: Females HW ≥ 30 mm

Year	n	SCL (cm)	PL (cm)	HW (mm)	Mass (g)
2009	16	20.3 (0.5)	18.2 (0.3)	37.4 (1.1)	1,347.9 (74.1)
2010	11	20.5 (0.3)	18.7 (0.3)	38.9 (1.3)	1,340.6 (74.9)
2011	22	20.7 (0.4)	18.5 (0.4)	39.6 (1.0)	1,454.4 (73.6)

Table 3.—Species consumed by diamondback terrapins from the York River subestuary.

Phylum	Class	Genus/Species	Common Name
Arthropoda			
	Maxillopoda	*Balanus improvisus*	bay barnacle
		Balanus eburneus	ivory barnacle
	Malacostraca	*Callinectes sapidus*	blue crab
		Panopeus herbstii	black-fingered mud crab
		Sesarma reticulatum	marsh crab
		Uca sp.	fiddler crab
		Ampithoe valida	amphipod
		Ampithoe spp.	amphipod
		Dulichiella appendiculata	amphipod
		Elasmopus levis	amphipod
		Erichsonella attenuata	clinging isopod
		Idotea balthica	smooth seaweed isopod
		Edotea triloba	isopod
	Arachnida		spider
	Insecta		mosquito
			beetle
Mollusca			
	Bivalvia	*Geukensia demissa*	ribbed mussel
		Tagelus plebeius	stout razor clam
		Crassostrea virginica	eastern oyster
		Alegina elevata	clam
		Mya arenaria	soft-shelled clam
		Anadara transversa	transverse ark
		Gemma gemma	gem clam

Table 3.—continued.

Phylum	Class	Genus species	Common Name
	Gastropoda	*Littoraria irrorata*	salt marsh periwinkle snail
		Melampus bidentatus	coffee bean (salt marsh) snail
		Odostomia sp.	Odostome snail
		Nassarius vibex	mottled dog whelk
		Bittium varium	Grass cerith
		Crepidula convexa	slipper snail
		Mitrella lunata	lunar dove snail
Annelida			
	Polychaeta	Family Nereididae	jaw parts and parapodia
Chordata			
	Ascidiacea	*Molgula manhattensis*	sea grapes
	Actinopterygii	likely *Fundulus* sp.	Fishes (vertebrae, rib and skull bones, and teeth)
Bryozoa			
	Gymnolaemata	*Conopeum tenuissimum*	lacy crust bryozoan
Tracheophyta			
	Liliopsida	*Zostera marina*	Eelgrass (blades, spathes, and seeds)
		Ruppia maritima	widgeon grass
		Spartina alterniflora	salt marsh smooth cord grass
Chlorophyta			
	Ulvophyceae	*Ulva lactuca*	sea lettuce

Table 4.— Exact G test of population differentiation using Genepop comparing percent occurrence of prey groups found in fecal samples collected from 223 diamondback terrapins May-August 2009, 2010, and 2011 between size classes large (HW ≥ 30 mm) vs. small (HW < 30 mm) and habitats marsh-mudflat vs. marsh-SAV, with significant *P*-value at alpha = 0.5 in bold.

Prey Groups	Size class % occurrence Large	Small	*P* Large vs. Small	Habitat % occurrence Marsh-mudflat	Marsh-SAV	*P* Marsh-mudflat vs. Marsh-SAV
n	45	178		23	200	
Barnacles	71.1	91.0	**< 0.01**	69.6	89.0	**0.05**
Snails	64.4	77.5	0.08	65.2	46.0	0.31
Bivalves	77.8	41.6	**< 0.01**	60.9	47.5	0.27
Crustaceans	84.4	86.0	0.81	87.0	85.5	1.00
Fish	53.3	13.5	**< 0.01**	30.4	20.5	0.42
Insects	6.7	5.1	0.71	13.0	4.5	0.37
Tunicates	4.4	7.3	0.54	17.4	5.5	**0.05**
Plants	93.3	97.8	0.35	82.6	98.5	**< 0.01**

Table 5.— Exact G test of population differentiation using Genepop comparing percent occurrence of most common snail, crab, bivalve and barnacle species found in fecal samples collected from 223 diamondback terrapins May-August 2009, 2010, and 2011 between size classes large (HW ≥ 30 mm) vs. small (HW < 30 mm) and habitats marsh-mudflat vs. marsh-SAV, with significant *P*-value at alpha = 0.5 in bold.

	Size class			Habitat		
	% occurrence		*P*	% occurrence		*P*
Species	Large	Small	Large vs. Small	Marsh-mudflat	Marsh-SAV	Marsh-mudflat vs. Marsh-SAV
n	45	178		23	200	
Snails						
Bittium sp.	37.8	57.3	**<0.05**	13.0	58.0	**< 0.01**
Littoraria irrorata	26.7	17.4	0.20	52.2	15.5	**< 0.01**
Melampus bidentatus	4.4	16.3	**<0.05**	13.0	14.0	1.00
Nassarius vibex	2.2	15.2	**<0.05**	17.4	12.0	0.51
Crepidula convexa	13.3	15.2	0.82	21.7	14.0	0.35
Crabs						
Callinectes sapidus	51.1	24.2	**< 0.01**	52.2	27.0	**< 0.05**
Family Xanthidae	24.4	15.2	0.18	39.1	14.5	**< 0.05**
Bivalves						
Geukensia demissa	53.3	21.3	**< 0.01**	39.1	26.5	0.22
Clams (all species)	62.2	30.9	**< 0.01**	43.5	36.5	0.65

Table 6.— Shannon Diversity (H'), Pielou's Evenness (J'), Margalef's Richness (d) and Schoener's Overlap (θ) indices for diamondback terrapin diet by habitat and size class. Overlap indicates biological significance in terms of resource partitioning if $\theta > 0.6$ (Zaret and Rand 1971).

	$H'(\log_e)$	J'	d	θ
Habitat:				
Marsh-SAV	1.809	0.614	2.915	0.559
Marsh-mudflat	1.882	0.664	4.274	
Size Class:				
Small	1.440	0.489	3.249	0.224
Large	1.503	0.510	3.220	

Table 7.— Summary table for recent published diamondback terrapin diet studies. Common prey types ranked 1 (most common) to 7 (least common) by maximum reported percent occurrence in each study for the prey type. *nr* indicates prey type not reported, and *nv* indicates prey type mentioned but no value given. All studies included all size classes and both genders except Erasmus (2012), which only included large nesting females. Darker shading indicates higher percent occurrence. Plants included both terrestrial and aquatic species.

Prey Group	Tucker et al. 1995	Spivey 1998	Petrochic 2009	Butler et al. 2012	Erasmus 2012	Tulipani & Lipcius 2013
Barnacles	**3**	5	*nv*	5	*nr*	**3**
Bivalves	4	**3**	**3**	[illegible]	[illegible]	5
Decapod Crustaceans	**2**	2	4	**2**	**3**	**2**
Fishes	*nr*	4	5	4	*nr*	6
Gastropods	[illegible]	[illegible]	[illegible]	**3**	4	4
Insects	*nr*	*nr*	*nr*	*nr*	5	7
Plants	> 5	*nr*	**2**	*nr*	**2**	[illegible]

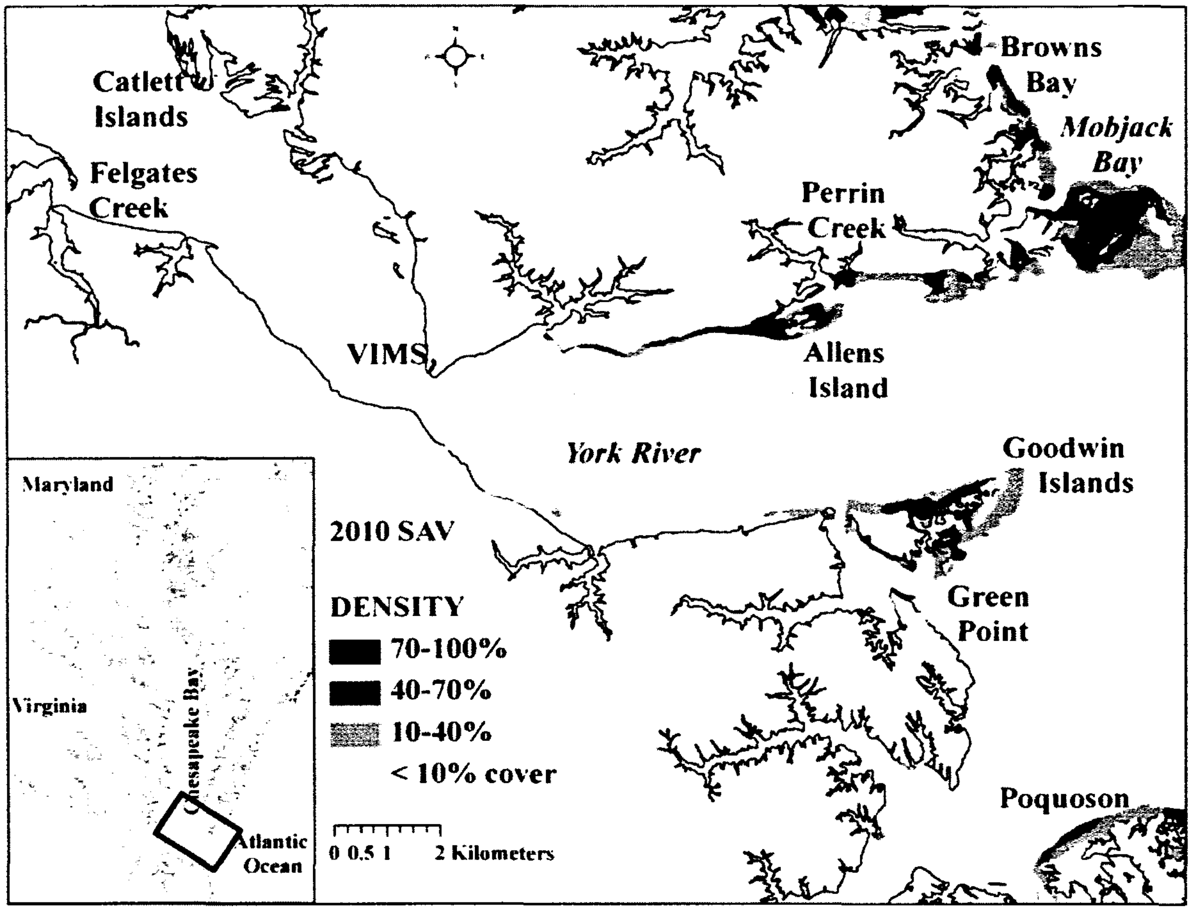


Fig. 1.— Collection locations for diamondback terrapins along the lower York River, Virginia, included Catlett Islands (upriver), Goodwin Islands and Green Point, cove near mouth of Perrin Creek, Allens Island, Browns Bay in southeastern Mobjack Bay, Felgates Creek and Poquoson in southwestern Chesapeake Bay (rectangle on inset). Gray shading indicates the spatial extent of submerged aquatic vegetation (SAV) in 2010 (modified from Orth et al. 2010).

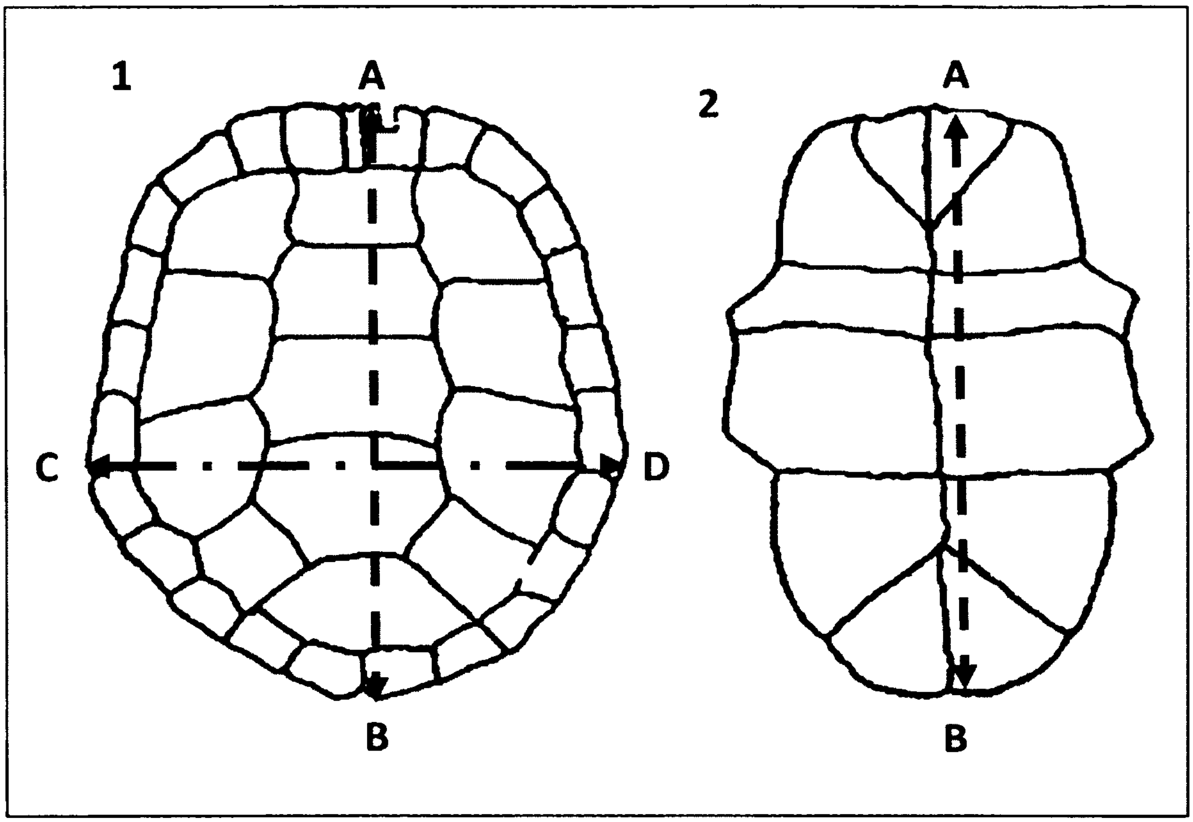


Fig. 2.— Standard measurements of shell dimensions for diamondback terrapin (*Malaclemys terrapin*) size where "A" is at the head and "B" is at the tail. (1) Carapace length A to B, carapace width C-D, (2) plastron length A to B.

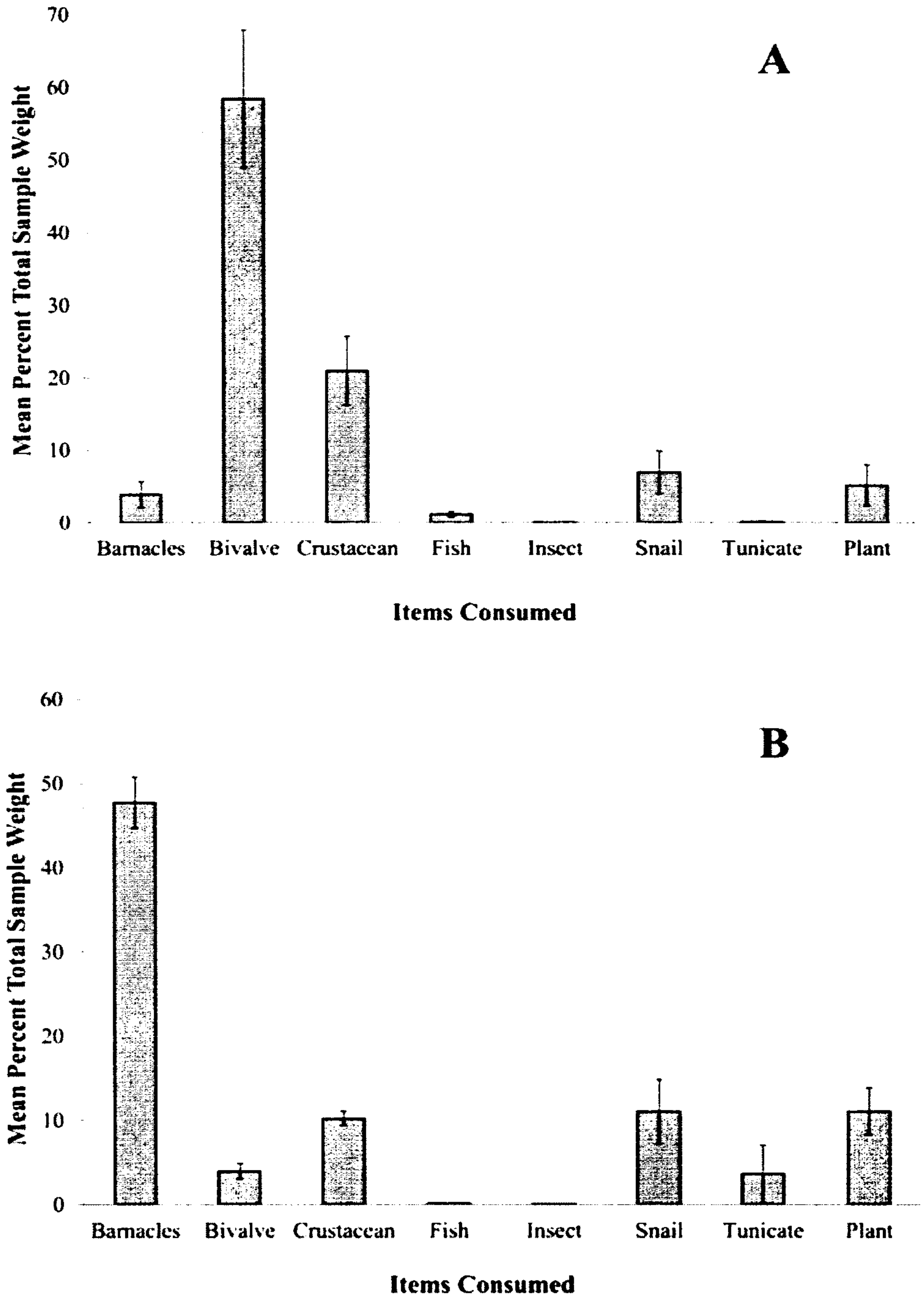


Fig. 3.— Mean percent total sample dry weight (TSDW) of items found in fecal samples over three years for two size classes of diamondback terrapins, (A) large (HW ≥ 30 mm) and (B) small (HW < 30 mm), captured along the York River and southeastern Mobjack Bay, Virginia. Error bars are standard error of mean.

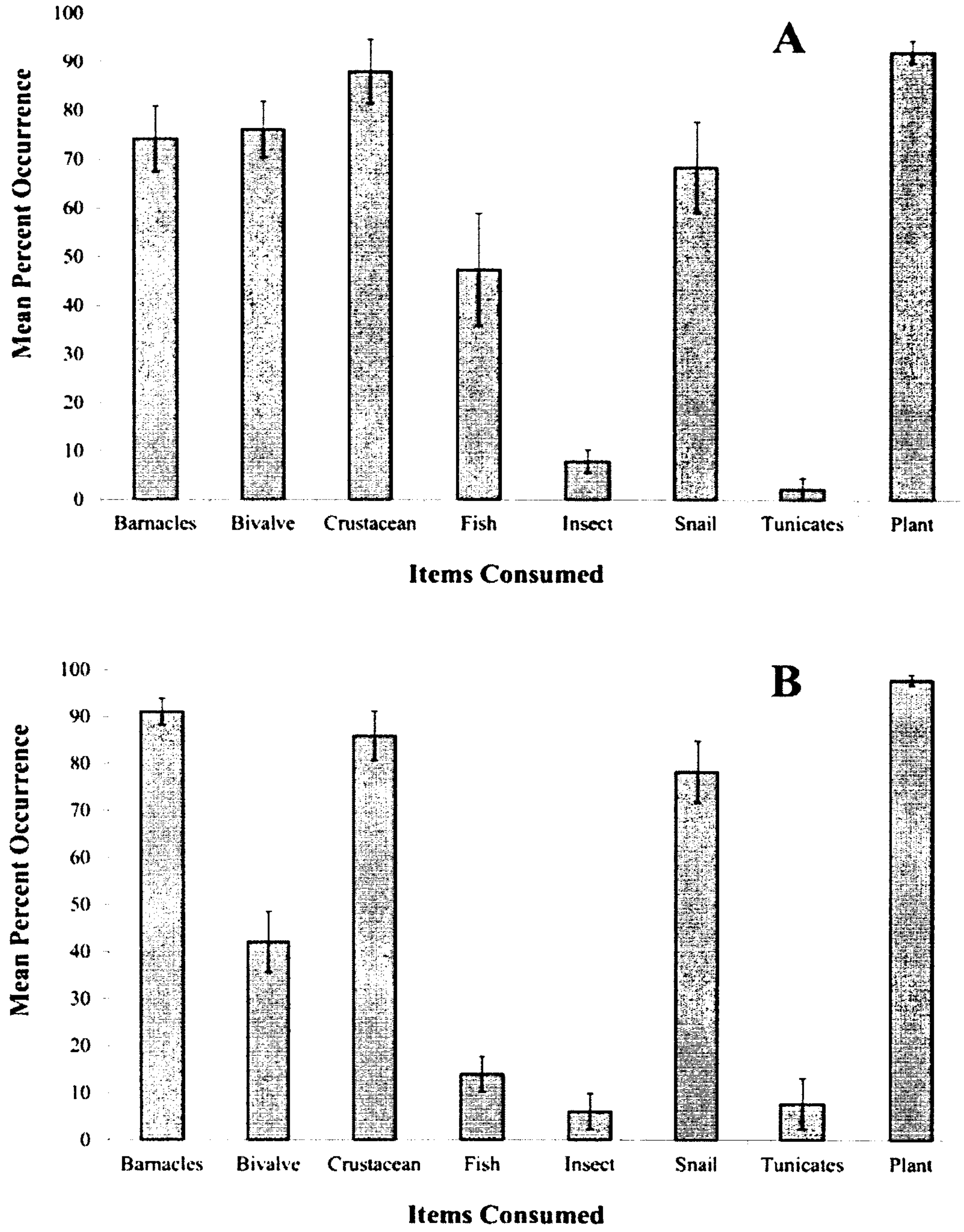
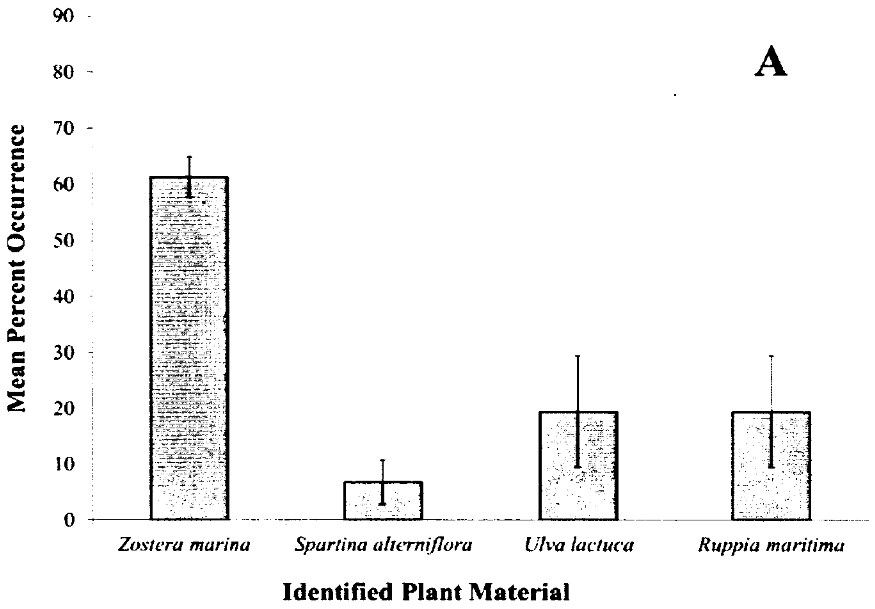


Fig. 4.— Mean percent occurrence of items ingested over threes year for two size classes of diamondback terrapins, (A) large (HW ≥ 30 mm) and (B) small (HW < 30 mm), captured along the York River, Virginia. Error bars are standard error of the mean.



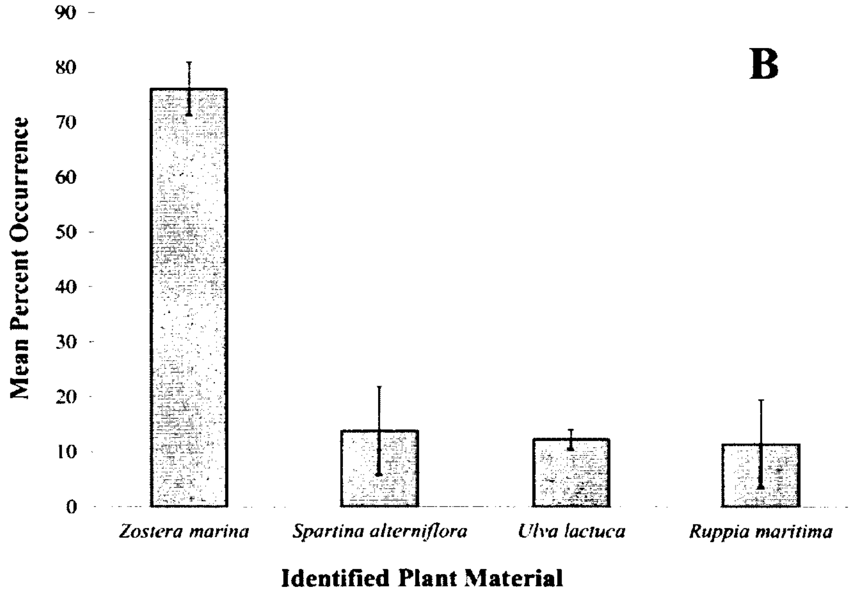


Fig. 5.— Mean percent occurrence of identified plant material found in fecal samples over three years for two size classes of diamondback terrapins, (A) large - HW ≥ 30 mm and (B) small - HW < 30 mm, captured along the York River and southeastern Mobjack Bay, Virginia. Error bars are standard error of mean.

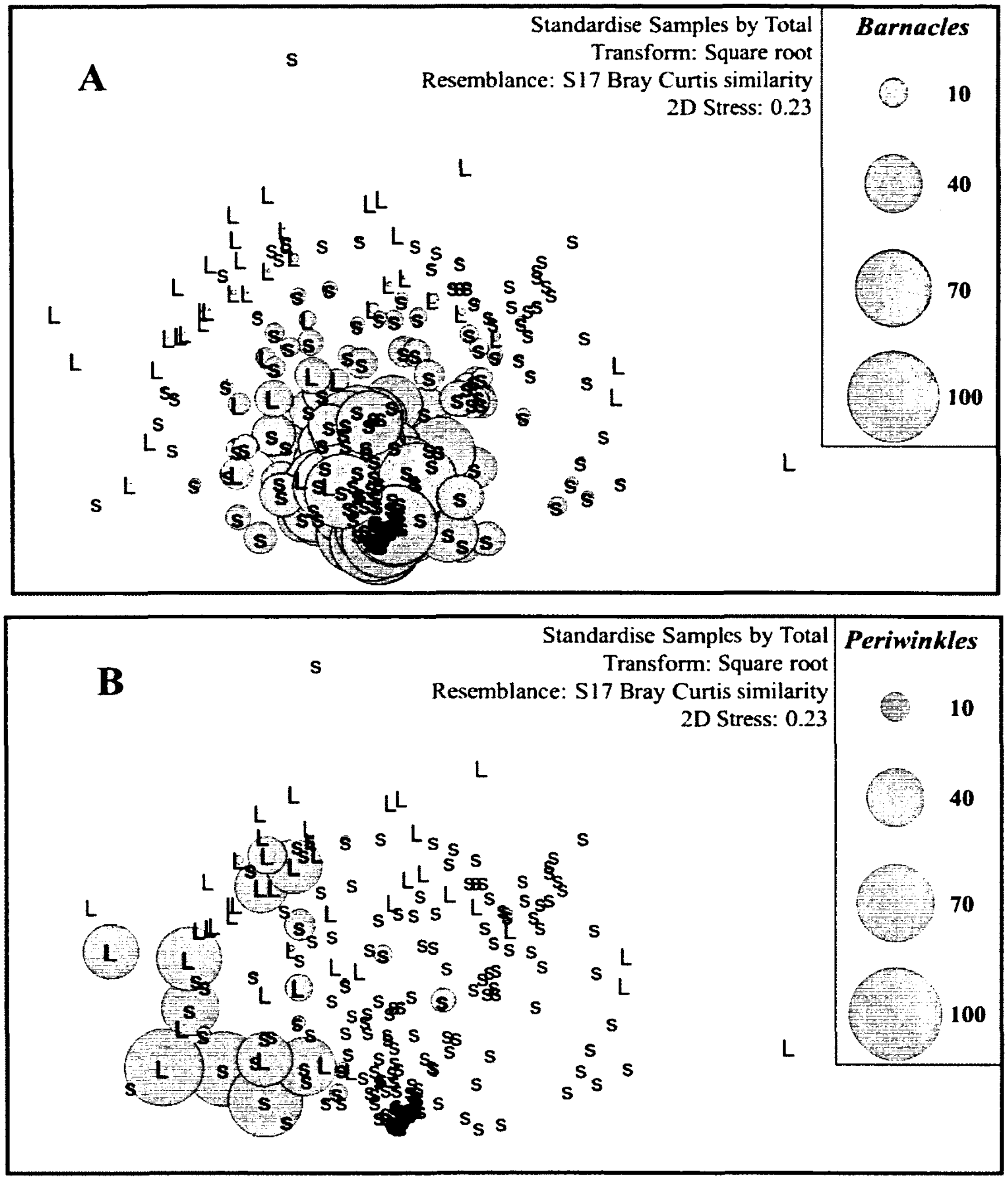


Fig. 6.— NMDS ordination bubble plots of diamondback terrapin fecal sample biomass by size class, L (large - HW ≥ 30 mm) and s (small - HW < 30 mm), overlaid with percent of total sample (gray bubbles) of barnacles (A), periwinkles (B) for each terrapin.

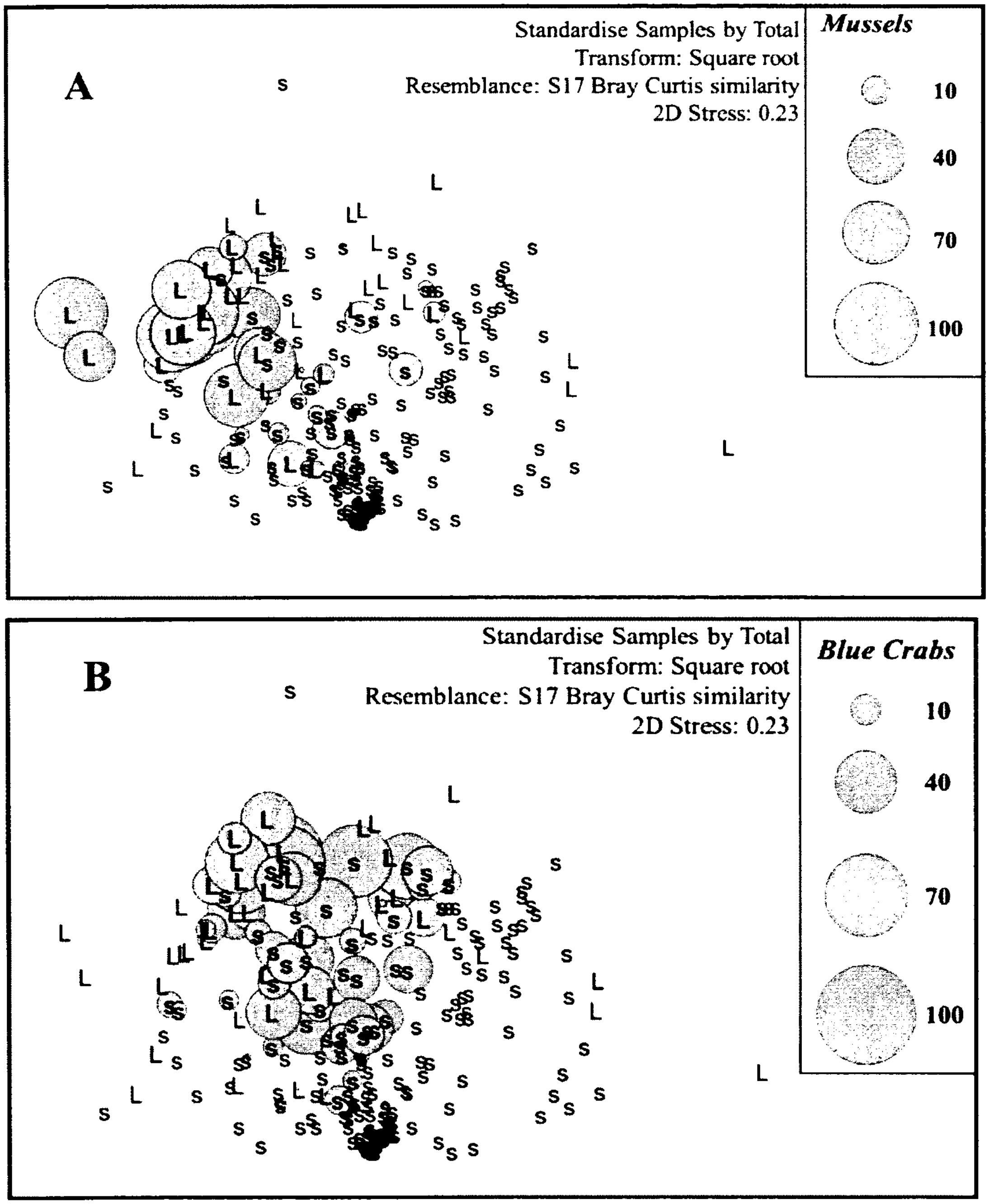


Fig. 7.— NMDS ordination bubble plots of diamondback terrapin fecal sample biomass by size class, L (large - HW ≥ 30 mm) and s (small - HW < 30 mm), overlaid with percent of total sample (gray bubbles) of mussels (A) and blue crabs (B) for each terrapin.

CHAPTER 3

Selective foraging and search success of northern diamondback terrapins (*Malaclemys terrapin terrapin*) in lower Chesapeake Bay

ABSTRACT

Prey selectivity of northern diamondback terrapin (*Malaclemys terrapin terrapin*) in seagrass beds and salt marshes of southern Chesapeake Bay was investigated in the field and in mesocosm experiments. Local seagrass beds where terrapins forage were characterized by plant density, faunal abundance, and prey diversity. Seagrass density was positively correlated with *in situ* prey diversity. The most abundant epifaunal prey were barnacles *Balanus* spp., an amphipod *Gammarus mucronatus*, and a gastropod *Bittium* sp. Manly-Chesson index (α) indicated distinct differences in prey selectivity by terrapin size class with small (head width < 30 mm) terrapins selecting barnacles and large (head width ≥ 30 mm) terrapins selecting bivalves. Comparison of size and number of periwinkle snails (*Littoraria irrorata*) ingested by terrapins to available *in situ* snail size distribution and abundance revealed small terrapins from marsh-mudflat habitat consumed more periwinkles than large terrapins from marsh-mudflat habitat, as well as all size classes from marsh-SAV habitats. In three mesocosm prey choice experiments, terrapins consumed more juvenile blue crabs (*Callinectes sapidus*) than periwinkles and mottled dog whelks (*Nassarius vibex*). Terrapins were also less successful in finding and consuming blue crabs with increasing percent cover of vegetation (*Gracilaria vermiculophylla*). While diamondback terrapins were mainly molluscivores, distinct prey selectivity was based on both morphological characteristics and the faunal assemblage, though not always the most abundant species, within the specific forage habitat being used.

INTRODUCTION

Many animals make specific prey choices that increase their survival. The green sea turtle *Chelonia mydas* exhibits an ontogenetic shift in diet from pelagic omnivory to benthic herbivory in the neritic zone foraging primarily on seagrasses (Arthur et al. 2008). The Texas river cooter *Pseudemys texana* feeds on aquatic plants with high digestible nutrients (Fields et al. 2003). Selectivity of prey may also be based on a preys' availability in the environment (Pyke 1984) like the leatherback sea turtle *Dermochelys coriacaea* survives by feeding on jellyfish that are abundant though metabolically energy-poor (Lutcavage and Lutz 1986).

The diamondback terrapin *Malaclemys terrapin* is a top predator in salt marshes throughout the species' range, which extends coastally from Massachusetts to Texas (Ernst and Lovich 2009). Terrapins regularly consume abundant hard-shelled invertebrates, such as crabs, snails, mussels, and clams (Coker 1906; Tucker et al. 1995; Butler et al. 2012; Erazmus 2012). Periwinkles *Littoraria* spp. are common prey throughout (Tucker et al. 1995; Butler et al. 2012). In Virginia, terrapins also feed on mobile fauna and epifauna in seagrass beds located near salt marshes (Chapter 2).

Through foraging, top predators exert top-down control thereby affecting community structure (Paine 1974; Valiela et al. 2004). Juvenile hawksbill sea turtles may contribute to low abundance of specific coral species on reefs near Puerto Rico

(Rincon-Diaz et al. 2011). Green sea turtles *Chelonia mydas* play a significant role foraging on tropical seagrasses (Thayer et al. 1984). In Chapter 2, I described the diet of diamondback terrapins feeding in seagrass beds in lower Chesapeake Bay finding that males and juvenile females fed mostly on barnacles attached to eelgrass (*Zostera marina*). By feeding on grazers and sessile organisms in salt marshes and in seagrass beds, terrapins may increase plant biomass and help sustain biodiversity (Silliman and Bertness 2002; Duffy et al. 2003; Chapter 2). As top predators, terrapins have potential to strongly influence the community structure within its habitat through foraging and prey choice (Silliman and Bertness 2002). Understanding plant-herbivore-predator interactions in seagrass ecosystems is crucial given the declines in distribution and abundance caused by increasing anthropogenic stresses such as global warming (Orth 1992).

Two earlier studies equated terrapin prey selection to prey abundance in salt marsh habitats (Tucker et al. 1995; Spivey 1998). In South Carolina, Tucker et al. (1995) focused on periwinkles and fiddler crabs *Uca pugnax*; Spivey (1998) surveyed blue crabs *Callinectes sapidus*, fiddler crabs, and periwinkles in a North Carolina marsh. In a Connecticut salt marsh where terrapins occur, the marsh snail *Melampus bidentatus*, the mud snail *Ilyanassa obsoleta*, fiddler crabs *Uca* spp., and marsh mussel *Geukensia demissa* were surveyed for abundance (Whitelaw and Zajac 2002). Periwinkles were very abundant and the preferred prey in South Carolina (Tucker et al. 1995) whereas blue crabs of specific sizes were identified as prey of choice for all except the smallest terrapins in North Carolina (Spivey 1998). Changes in prey selected by mature female terrapins were attributed to the different habitat from which they were captured, i.e., soft shell clam in salt marsh creeks or crabs and periwinkles at nesting beach (Butler et al. 2012). Terrapins preferentially fed on seagrass fauna when seagrass beds where adjacent to salt marshes (Chapter 2).

Eelgrass *Zostera marina* is one of the most commonly occurring species of seagrasses in Chesapeake Bay (Orth et al. 2011). It supports diverse assemblages of permanent and transient fauna (Orth et al. 1984). Faunal species commonly found in seagrass beds, as well as pieces of eelgrass, were found in fecal samples from nearly all terrapins captured in seagrass beds (Chapter 2). Conversely, periwinkles and other gastropods were ingested less often by this sample of terrapins (Chapter 2) when compared to the South Carolina population (Tucker et al. 1995). To what extent, then, does foraging by diamondback terrapins affect seagrass faunal community? What is the importance of seagrass fauna to the diamondback terrapin's diet?

This study further investigated the role of diamondback terrapins in food webs of seagrass beds and salt marshes of the lower York River subestuary. Specifically, prey selectivity of diamondback terrapins feeding in both habitats was examined with additional analysis of data from a previous terrapin diet study (Chapter 2). Local periwinkle *Littoraria irrorata* abundance and size distribution was determined through a survey where specimens were collected from four sites along the York River. Periwinkle size information was then used to estimate the size range of terrapin-ingested periwinkles. As blue crabs were a common prey in Virginia terrapin diet (Chapter 2), a mesocosm experiment tested the diamondback terrapin's ability to detect juvenile blue crabs (and blue crab survival) in various levels of algal cover (*Gracilaria vermiculophylla*). To examine specific prey choice, two additional mesocosm experiments tested terrapin choice between blue crabs and periwinkles (*L. irrorata*), and blue crabs (*C. sapidus*) and mottled dog whelk (*Nassarius vibex*).

MATERIALS AND METHODS

Study sites

Field sampling and collection of terrapins took place in the lower York River and southeastern Mobjack Bay (Figure 1). Sites located up river were Catlett Islands and Felgates Creek, which were categorized as "marsh-mudflat" habitat with smooth cordgrass (*Spartina alterniflora*) as the dominant salt marsh plant. Frequently intermixed with *S. alterniflora* was saltmeadow cordgrass (*Spartina patens*) and black needlerush (*Juncus roemerianus*) (Reay and Moore 2009). The remaining sites at Goodwin Islands, Green Point, Allens Island, Perrin Creek, Browns Bay, and Poquoson were emergent salt marshes with adjacent submerged aquatic vegetation (SAV) beds dominated by two species, eelgrass (*Zostera marina*) and widgeon grass (*Ruppia maritima*) (Reay and Moore 2009). These locations were categorized as "marsh-SAV" habitats. Catlett Islands and Goodwin Islands are part of the Chesapeake Bay National Estuarine Research Reserve in Virginia (Reay and Moore 2009).

Terrapin collection

Diamondback terrapins were collected during spring and summer of 2009, 2010 and 2011 for a terrapin foraging ecology project (Chapter 2). Most terrapins were captured by trawl, though some were captured with modified commercial crab pots or funnel traps. Terrapins were uniquely marked with a turtle identification number (TID; Cagle 1939). All were released at their original collection location. Gender and standard size measurements were recorded for each specimen, including head width (HW) at tympana in mm, straight carapace length (CL) and plastron length (PL) in cm, and mass (g). Gender was determined by tail length and position of the cloacal vent (Gibbons and Lovich 1990). Male terrapins have longer, thicker tails with the cloacal vent located posterior to the carapace edge, in contrast to females which have shorter tails with the cloacal vent anterior to the carapace edge (Gibbons and Lovich 1990). Terrapins were grouped in two size classes based on head width: small = HW < 30 mm and large = HW ≥ 30 mm (Chapter 2). Terrapins are gender-size dimorphic with adult females being substantially larger than adult males (Ernst and Lovich 2009), and no males in this study had HW > 25.0 mm; therefore, only females were included in the large size class.

Terrapin foraging in seagrass beds

The 2010 terrapin fecal sample data was collected and analyzed as part of an extensive three-year diet study (Chapter 2). On a daily basis, fecal samples were collected separately for each captured terrapin from time of capture up to 5 d post-capture (Chapter 2). Dried samples were sorted by prey type to the lowest taxonomic level, weighed by each prey type, and summed for each terrapin. Chapter 2 provides a detailed description of the diet study, including a list of prey ingested.

Zostera marina *density and faunal abundance estimates*

To estimate seagrass density and associated faunal abundance, random samples were collected over three consecutive weeks in May when seagrass biomass typically peaks (Orth and Moore 1983). Seventy-two (3 weeks x 4 regions x 6 replicate/region) 0.053-m^2 samples were collected in 2010 from three regions with SAV coverage > 40% around Goodwin Islands, i.e., north (GN), southeast (GSE), and southwest (GSW), and from Green Point (GP) (Figure 2; Orth et al. 2011). To collect each replicate, a 1-mm mesh bag was attached to the top of an 18.9-L bucket with the bottom half removed. The bucket's bottom edge was pressed into the sediment to isolate the sample, and was separated from the surrounding sediment with a shovel. Both bucket and shovel were inverted, dropping the sample into the attached bag. Samples were kept in river water during transport to VIMS and stored separately by region in outdoor holding tanks with flow-through river water. After reproductive shoots were removed for other analyses (Chapter 5), the remaining sample was placed in a large plastic bag and frozen until processed. Each replicate was sorted to remove all mobile fauna and epifauna, and sessile epifauna. Collected organisms were stored in 70% ethanol.

Seagrass in each sample was dominated by eelgrass, *Zostera marina*, but with scattered widgeon grass, *Ruppia maritima*. Seagrass was separated into blades and roots to estimate plant density above and within the sediment. Density of seagrass was based on amount of organic matter produced of the seagrass beds sampled by determining the ash-free dry weight (AFDW) was for each sample. Wet weight (g) was recorded before each portion was wrapped separately in aluminum foil and dried in a drying oven at 65°C. AFDW was the difference between the dried and ashed (550°C for 24 h cycle) weight (g) for each blade and root sample. Mean AFDW was calculated for each region and week sampled and analyzed by region and week with ANOVA. Blade and root AFDW data had log-normal distributions, so these data were natural log-transformed prior to analysis to meet assumptions of normality and homogeneity of variance. Linear regression was used to determine the association between roots and blades.

Diversity indices were calculated by region based on faunal counts (i.e., Margalef's species richness *d*, Pielou's Evenness *J'*, and Shannon Diversity *H'*), as well as number of individuals (N) and species (S), using PRIMER 6 version 6.1.6, PRIMER-E (Magurran 2004). The number of individuals was natural log-transformed to meet assumptions of normality and homogeneity of variance, and analyzed with ANOVA to test for differences by region and week. Linear regression was used to determine association between the independent variables blade AFDW, region, and week, and the response variables faunal abundance and diversity. Akaike Information Criterion with small sample correction (AIC_c) was used to select the best-fitting model (Anderson 2008).

Diet information from terrapins captured from Goodwin Islands and Green Point seagrass beds in 2010 (Chapter 2) and mean seagrass faunal counts were used to calculate the Manly-Chesson index (α) to determine the degree of prey selectivity by terrapins (Manly et al. 1972; Chesson 1983). Manley-Chesson index α_i is a ratio of the amount of food type *i* in the diet to the amount of food type *i* in the environment such that

$$\alpha_i = \frac{r_i\ n_i}{{}_{j=1}^{m}\ r_j\ n_j} \qquad i = 1,\dots, m$$

where r_i is the amount of food type *i* in the consumer's diet and n_i is the amount of food type *i* in the environment over the summation of *m* prey types of each proportion (r_j / n_j). Index values range from 0-1. When $\alpha_i = 0$ food type *i* is not in the diet, and when $\alpha_i = 1$ the consumer's diet consists entirely of food type *i* (Chesson 1983). The index was calculated for terrapin size classes using mean terrapin-egested biomass (Chapter 2) of five common prey types (i.e., barnacles, bivalves, crabs, gastropods, and isopods-amphipods) and mean biomass for the same sorted from the seagrass samples. Since terrapin-egested prey was measured in grams, faunal counts were converted to biomass (g) using methods in Edgar (1990).

Littoraria irrorata *population estimate & terrapin-ingestion by size class and habitat*

A survey for the marsh periwinkle snail (*Littoraria irrorata*) was conducted at Catlett Islands, Allens Island, Green Point, and Goodwin Islands along the lower York River in June and July 2012 to estimate periwinkle density where terrapins had previously been captured. Shorelines for each region were divided into 100-m wide cells from which 10 cells were randomly selected. At each cell, all periwinkles and coffee bean snails (*Melampus bidentatus*) were collected, and marsh grass *Spartina alterniflora* shoots were counted within three haphazard 0.25-m^2 quadrats. Snails were counted and shell lengths, shell widths, and operculum lengths measured (mm) using Vernier calipers. The width of the *S. alterniflora* zone was also recorded (m). Presence of mussels (*Geukensia demissa*) and oysters (*Crassostrea virginica*) was noted.

Periwinkle counts were log-transformed to meet assumptions of normality and homogeneity of variance, and then analyzed by region and *Spartina* zone using ANOVA. Linear regression was used to determine the relationship between periwinkle abundance, region, *Spartina* density (shoots per 0.25 m^2), and *Spartina* zone width. Shell length was chosen to represent snail size. To predict shell length from operculum length, parameter estimates were generated with linear regression using shell and operculum length measurements.

Periwinkles are an important food for terrapins in South Carolina (Tucker et al. 1995) and were identified in fecal samples from terrapins in lower Chesapeake Bay (Chapter 2). Although periwinkle shell pieces were unsuitable for estimating number and size ingested, the opercula were intact and used to estimate shell length from operculum length (Tucker et al. 1995). When present in fecal samples, opercula were retained from each terrapin, counted, and measured to the nearest 0.1 mm using Vernier calipers while viewed through a stereo microscope. Shell length was estimated using the linear equation derived from the periwinkle survey.

The predictive relationship between terrapin size (i.e., head width) and ingested snail size (i.e., operculum length) was examined with linear regression. Because terrapins exhibit gender-size dimorphism, data for small and large terrapins were analyzed separately. Operculum data for small terrapins were log-transformed, though it was not necessary for the data from large terrapins, to meet assumptions of normality and homogeneity of variance.

Terrapin prey choice mesocosm experiments

The three mesocosm experiments investigated prey choice of diamondback terrapins and their ability to locate prey in aquatic vegetation. Juvenile blue crabs (*Callinectes sapidus*) were used in all three experiments, whereas periwinkles and mottled dog whelks (*Nassarius vibex*) were used in the second and third experiments, respectively, along with the crabs. Within Chesapeake Bay, blue crabs occur in habitats with and without seagrass, periwinkles reside in salt marshes, and mottled dog whelks inhabit intertidal sand and mud flats. Blue crabs and periwinkles were selected for these experiments because both are well-known prey of terrapins (Tucker et al. 1995; Spivey 1998). Based on results from an earlier diet analysis, terrapins of the York River ingested both blue crabs and periwinkle snails (Chapter 2). In contrast, mottled dog whelks had not previously been recognized as terrapin prey, though another mud snail (*Ilyanassa obsoleta*) was frequently consumed by terrapins in Long Island Sound (Petrochic 2009). Mottled dog whelk opercula were found in fecal samples from many terrapins captured from the sites sampled along the York River.

Experiment 1: Blue crab survival as a function of percent algal cover

In 2009, four trials examined juvenile blue crab survival when exposed to terrapins in various levels of algal cover. Two trials were run simultaneously on two separate days in the Seawater Research Laboratory (SRL) at VIMS. The marine alga, *Gracilaria vermiculophylla*, and juvenile blue crabs were collected locally from the

York River. Treatments were 0, 25, 50, and 75 percent cover in four circular, 156-L tanks with flow-through river water, one treatment per tank. Percent cover was calculated based on maximum cylindrical volume of 9.7 L (34.9-cm tank radius and 2.54-cm height of *G. vermiculophylla*), where 25% = 2.4 L, 50% = 4.9 L, and 75% = 7.3 L of *G. vermiculophylla*. Twenty-five juvenile blue crabs were offered in each trial. Spine-tip to spine-tip carapace width (mm) and gender were recorded for all blue crabs. Terrapins were used only once, randomly assigned to a treatment (Appendix A), and then starved for 48 h before the trial. One terrapin was placed in each tank and allowed to acclimate for 24 h. A trial began when crabs were placed in the tank, and ended after 24 h when the terrapin was removed from the tank. Surviving crabs were counted, measured and gender identified. Terrapins were then isolated in individual aquarium tanks for three days after each trial and fecal material was collected to confirm ingestion of crabs.

Eight models were compared using AIC_c to select the factors (i.e., percent cover, terrapin gender or head width, plus interaction of gender and head width) that best predicted the size and number of crabs eaten. Carapace width of crabs eaten was natural log-transformed prior to analysis to meet assumptions of normality and homogeneity of variance. Whether a crab was eaten (1) or not (0) was analyzed using logistic regression to determine which factors best predicted crab survival. Model selection of the best-fitting generalized linear model (with binomial distribution and logit link function) was accomplished with AIC (Anderson 2008).

Experiment 2: Terrapin prey choice between blue crabs and periwinkles

In 2010, six mesocosm trials were conducted using blue crabs and periwinkle snails as prey to test if terrapin gender or size affects the number and size of consumed blue crabs and snails, and if terrapins showed preference for blue crabs or periwinkles. The three prey treatments were 20 blue crabs, 20 periwinkles, and 10 blue crabs plus 10 periwinkles. Mesocosms were three 156-L circular tanks with flow-through river water, one treatment per tank. The inside of each tank was ringed with 15-cm-wide copper flashing positioned 15 cm above the water's surface to prevent periwinkles from crawling out of the tanks. Outflow pipes were covered with plastic mesh caps to prevent escape of blue crabs and snails during the trials.

Of the terrapins available, three were randomly assigned to one treatment each trial. For each trial and treatment, we recorded carapace width (mm) and gender of blue crabs and shell length and width (mm) of periwinkles. Each terrapin was used only once (Appendix B) and starved for 48 h before each trial. One terrapin was placed in each tank and allowed to acclimate for 24 h. A trial began when crabs and snails were placed in the tank, and ended after 24 h when the terrapin was removed from the tank. Surviving crabs and snails were counted and re-measured. Terrapins were then isolated in individual aquarium tanks for three days after each trial and fecal material was collected to confirm ingestion of crabs and snails.

Linear regression was used to model the relationship between the number and size of blue crabs or snails consumed and terrapin size and gender. Five models using logistic regression were compared using AIC model selection to determine significant factors for survival. To address prey preference, treatment 3 results were analyzed using Fisher's exact test to test if the ratio of blue crabs eaten to periwinkles eaten differed from unity.

Experiment 3: Terrapin prey choice of crabs and whelks in simulated seagrass patches

Three prey preference trials were performed on June 30-July 1, July 14-16, and August 5-7 using blue crabs (*Callinectes sapidus*) and mottled dog whelks (*Nassarius vibex*) as prey in seagrass patches replicated in outdoor mesocosm tanks (1.2 m x 2.4 m) with flow-through York River water. Approximately 200 L of beach sand was distributed in each tank to form a central, flattened mound with slightly sloping sides. Eelgrass (*Zostera marina*) and widgeon grass (*Ruppia maritima*) were collected from local seagrass beds prior to each trial. Depending on the amount collected, 1-2 L eelgrass and 0.3-0.5 L widgeon grass were haphazardly planted in each tank to form the seagrass patches. The number, carapace width (mm), and gender of blue crabs, and number, shell length, and shell width (mm) of mottled dog whelks were recorded before and after each 48 h trial.

One terrapin was randomly selected for each treatment per trial (Appendix C), and used only once. Terrapins were starved for 24 h before each trial, and allowed to acclimate for an additional 24 h in the mesocosms prior to the start of a trial. After addition of the crabs and snails to experimental tanks, each trial ended after 48 h, at which time terrapins were removed from the tanks and placed in separate aquaria. Fecal material was collected from each terrapin over three days after each trial and the contents were examined to confirm prey ingested.

RESULTS

Terrapin foraging in seagrass beds

Fifty-five diamondback terrapins were captured from Goodwin Islands-Green Point seagrass beds in 2010 (Chapter 2). One large female (HW = 46.3 mm, mass = 1,839 g) was excluded from this analysis as it had produced an anomalously large fecal sample (60.2 g) that consisted mainly of ribbed mussel shells (51.2 g) and blue crab parts (8.1 g). This terrapin was approximately 20% larger than the other large females from this region. While the contents were consistent with other large female egesta, the amount was 16 times larger than the average fecal sample mass for the other five captured, which would have weighted the results heavily in favor of this single terrapin. For the five terrapins included in the large size class, their mean (± standard error) HW = 38.9 ± 0.7 mm and mass = 1,421.6 ± 45.0 g.

The small size class included 49 terrapins, 36 males and 13 juvenile females, having mean HW = 21.7 ± 0.3 mm and mass = 303.9 ± 13.6 g. Juvenile females had significantly larger HW than males, HW = 22.8 ± 0.8 mm vs. HW = 21.3 ± 0.3 mm, respectively, but did not differ by mass. Head width is important with respect to size and type of prey ingested yet diets of comparable-size juvenile females and males frequently overlap (Lindeman 2000). Based on findings in a comprehensive terrapin diet analysis (Chapter 2), males and juvenile females were combined into one group.

Zostera marina habitat at Goodwin Islands and Green Point

Eelgrass density

Goodwin Islands and Green Point SAV beds varied in area between 4.0 and 45.9 ha (Orth et al. 2011). Seagrass density varied among the regions with highest densities occurring along the York River and in coves along the southeast shoreline of Goodwin Island (Figure 2). The highest mean eelgrass blade AFDW occurred in GN and the lowest in GSW region (Table 1). Blade AFDW was significantly different by week sampled (p-value < 0.05), but not by region. Root AFDW was the opposite with differences between regions (p-value < 0.001), but not by week. GSW and GP regions had the lowest mean root AFDW while GSE was the highest (Table 1).

Faunal diversity

Six species were common to all areas. Two barnacles *Balanus improvisus* and *B. eburneus*, the amphipod *Gammarus mucronatus*, the isopod *Idotea baltica*, the snail *Nassarius vibex*, and the grass cerith snail *Bittium* spp. collectively comprised 67.2%, 77.0%, 87.7%, and 92.9% of total faunal abundance at GSE, GN, GSW, and GP, respectively (Table 2). In GN, the amphipod *Caprella penantis* contributed 13.9% to that region's total abundance, whereas it was rare in the other regions. The slipper snail *Crepidula convexa*, the blue crab *C. sapidus*, the clinging isopod *Erichsonella attenuata*, and the shrimp *Palaemonetes intermedius* were found in all regions except GN, whereas the amphipod *Amphithoe longimana* and the shrimp *P. vulgaris* were only found at GP and GSW. The gastropod *Mitrella lunata* and bivalve *Macoma* sp. were only found at GSW, and *Amphithoe valida* was only identified at GN. Other species summed to less than 2.0% of total abundance (Table 2, Appendix D).

Temporal and spatial differences were recorded and varied by diversity measure. Mean abundance differed significantly between regions ($P < 0.01$) with the highest mean number of individuals (N) occurring within region GP, which was dominated by barnacles (Table 3). Region GSW had highest mean number of species (S). Species richness (d') was similar in all regions with GP being slightly lower than the rest. S ($P < 0.05$) and d' ($P < 0.01$) were significantly different by week sampled but not by region. Evenness (J') was significantly different between regions ($P < 0.001$) indicating patchy distribution of species in different SAV beds (Table 3). Regions GN and GSE were most diverse and GP was least. Mean diversity (H') was significantly different ($P < 0.05$) between regions and week sampled. There was no significant interaction between region and week sampled for any of the measures.

Nine models were compared using AIC to determine which factor or combination of factors best predicted number of individuals, number of species, and each index (Appendix E). For number of individuals, model g(1), the full model, explained nearly all the variation in total number of individuals (Table 4A). For eelgrass density and region sampled, model g(3), best explained the variation in number of species, though model g(2) without the interaction term also ranked above 20%, which reflected species patchiness (Table 4B). Model g(9), week sampled, was the best predictor of species richness; however model g(4) which included eelgrass density also ranked high (Table 4C). Evenness was predicted best by model g(2) though model g(6) including region and week sampled was also a good fit (Table 4D). Model g(6) also best predicted diversity (Table 4E). Eelgrass density also partially influenced diversity in addition to region and week sampled as indicated by model g(2). Appendix F contains the full list of models ordered by AIC_c w_i. Parameter estimates for best fitted models only are listed in Appendix G.

Manly-Chesson index: diamondback terrapin feeding selectivity in seagrass beds

Terrapin feeding selectivity showed distinct preference by size class (Table 5). Small terrapins feeding in seagrass beds primarily consumed the highly abundant barnacles found attached to eelgrass blades. They also selected bivalves more than the remaining categories. Large terrapins overwhelmingly preferred bivalves that consisted mainly of ribbed mussels and a variety of clams (Chapter 2). Crabs were a distant second in food selectivity by large terrapins (Table 5). Gastropods were minimally selected ($\alpha < 0.02$) while the much smaller prey categories, barnacles and isopods-amphipods had $\alpha << 0.01$.

Littoraria irrorata: *population estimate & terrapin-ingested by size class and habitat*

Periwinkle abundance varied by region and by *Spartina* zone width ($P < 0.05$) with no significant interaction between region and zone width. AI had the highest mean snail density while GI was lowest (Figure 3). *Spartina* zone width and shoot density were also significantly different by region ($P < 0.001$) yet *S. alterniflora* shoot abundance had no effect on the snail abundance ($P = 0.78$; Figure 3, Table 6). In comparison, *S. alterniflora* shoot density in salt marshes along the lower York

River was substantially less than in a Connecticut salt marsh (Whitelaw and Zajac 2002). AI and CI mean *Spartina* zone widths were substantially wider than GI and GP though GI had the highest shoot density (Figure 3). AI had the highest mean snail abundance, snails per shoot, and widest *Spartina* zone while GP had second largest mean abundance of snails yet one of the narrowest *Spartina* zones and relatively low shoot density (Figure 3, Table 6). The periwinkle shell lengths had a median = 19.0 mm and a range = 3.2 to 27.0 mm. Mean periwinkle shell length differed among regions surveyed ($P < 0.01$) where CI snails were largest and AI were smallest on average (Table 6). Mussels were present at over 50% of locations surveyed while oysters were only observed at 4%.

Of the terrapins collected for the three-year diet analysis, periwinkle shell pieces and/or opercula were found in fecal samples from 43 terrapins (Chapter 2) of which 33 had egested opercula that could be measured. The number of opercula egested varied by collection region (Figure 4). Some terrapins from AI and GP egested many fewer periwinkles than the mean abundance (m^{-2}) estimated for those regions while others from CI and GI consumed more (Figure 4). Using the equation $y = 0.254 + 2.656x$ where x = operculum length and y = shell length, the size of periwinkles ingested by terrapins by size class and habitat type was estimated (Table 7). Male and female terrapins (HW < 30 mm) consumed similar proportions of periwinkles between 4.0 and13.0 mm shell lengths, though two males consumed larger snails (Figure 5). Large females (HW ≥ 30 mm) exhibited a bimodal size preference for periwinkles (Figure 5). Females of HW 30 - 40 mm ate snails of similar size range as smaller terrapins while ones with HW > 40 mm primarily ate snails larger than 16 mm shell length (Figure 5). The estimated size of periwinkles consumed was significantly different ($p < 0.001$) between both size classes and habitats (Table 7). One small terrapin from CI region egested over 250 opercula which was an extreme occurrence (Figure 6) that caused a significant difference in the number of opercula egested between size classes and habitats ($P < 0.001$; Table 7). When the analysis was rerun excluding the outlier, there was only significant difference by habitat in the number of opercula egested ($P < 0.05$). Only 4 out of 51 of the Goodwin Islands terrapins, a marsh-SAV habitat, consumed periwinkles; however, only two large females consumed 96 of 98 opercula reported for that region (Figure 4). One mature female terrapin was captured at each of three additional locations, i.e., Felgates Creek, Perrin Cove, and Poquoson, and all had ingested periwinkles (Figure 4). Felgates Creek (marsh-mudflat habitat) terrapin had egested 52 opercula while the other two from marsh-SAV habitats had consumed fewer periwinkles (Figure 4).

Experiment 1: Blue crab detection in varying algal percent cover

The terrapin specimens used represented three gender-size class combinations, 5 large female (HW ≥ 30 mm), 4 small females (HW < 30 mm), and 7 males (HW < 30 mm). Random assignment of terrapins to treatments resulted in each group being tested in each level of percent cover (Appendix A). A Student's t-test showed no difference by percent cover between mean size of crabs offered and mean size of crabs eaten ($P = 0.14$; Figure 7) but there was a significant difference by treatment between number offered and the mean number eaten ($P < 0.01$; Figure

8). Carapace width of crabs used in all the trials ranged from 10.0–35.6 mm. Nine models were tested (Table 8A) and number of crabs eaten was best predicted by model g(5) treatment only (AIC_c $w_i = 0.664$; Table 8A). The parameter estimates for model g(5) indicate the number of crabs eaten by terrapins decreased with increasing percent cover which was a significant factor ($P < 0.01$; Table 8B). HW possibly had some effect on number of crabs eaten i.e., model g(3) AIC_c $w_i = 0.141$, though HW alone was not a significant factor ($P = 0.94$). The full model, g(1), best predicted a crab being eaten or not (AIC_c $w_i = 0.633$; Table 9A). Model g(2) without the HW-gender interaction term also ranked AIC_c $w_i > 0.2$ (Table 9A). Most parameters negatively influenced whether a crab was eaten except gender, which was strongly positive (Table 9B). The size of crabs eaten was best predicted by model g(6) terrapin HW only (AIC_c $w_i = 0.242$; Table 10A). Size of a crab being eaten increased with increasing HW (Table 10B).

Experiment 2: prey choice blue crabs vs. periwinkle snails

The results from each treatment of this experiment supported the findings of the diet analysis, whereby terrapins from lower Chesapeake Bay more frequently consumed blue crabs than periwinkle snails (Chapter 2). The size of blue crabs consumed by terrapins was consistent between treatments 1 and 3. The low number of snails consumed in treatments 2 and 3 supported the earlier findings of the diet analysis that periwinkles were consumed less frequently terrapins from lower Chesapeake Bay (Chapter 2).

Treatment 1: Blue crabs only

Average number of crabs eaten was 7.7 ± 0.8 for the six trials. For the 120 blue crabs used, mean carapace width (CW) was 35.9 ± 1.2 mm and mean CW = 25.4 ± 1.5 mm for 46 crabs eaten. For each trial, mean CW of eaten was less than mean CW of offered. The difference between means was significant ($P < 0.01$) with mean difference = 9.8 ± 1.4 mm. Therefore, terrapins of all size classes preferred to eat crabs with CW < 35 mm (Table 11A). When crab size was regressed with terrapin HW, HW was not a significant predictor of size crab eaten ($P = 0.462$). However there were differences in prey consumed by size class, i.e., large vs. small, though all but one specimen were small. When trial 5 treatment 1 with the large female was excluded, terrapin HW was a significant predictor of crab size eaten ($P < 0.05$, $y = -15.613 + 1.881x_1$).

Of the six models compared, model g(4), terrapin HW and crab CW, explained the most variation and scored the highest AIC_c $w_i = 0.419$ (Table 11B). Model g(3), crab CW and terrapin gender-size, also had $w_i > 0.2$. However, when all three factors were combined in model g(5), a low AIC weight resulted (Table 11B). Therefore, terrapin HW and crab CW best predicted whether a terrapin ate a crab (Table 11C).

Treatment 2: Periwinkles only

There was a positive relationship between snail shell length (SL) and shell width (SW) where $SW = 1.8248 + 0.5726\ SL$ ($P < 0.001$, Pearson's correlation: 0.838), therefore snail SL was used to represent snail size. Mean SL was 13.6 ± 0.3 mm for the 120 snails offered (Table 12). Only five snails total were eaten for all six trials resulting in mean SL of eaten = 13.1 mm SE = 2.2. Testing the mean difference between snail size offered and eaten showed no significant difference in snail size ($P = 0.190$). Due to the few snails ingested by the terrapins, no further analyses were performed.

The terrapins in this treatment did not eat periwinkle snails. All terrapins used in this treatment were small (HW < 30 mm), as well as captured from marsh-SAV locations. The low number of periwinkles eaten by these terrapins agreed with the foraging study as both large and small groups ate periwinkles less frequently than other prey types, though some had consumed large numbers of the snail (Chapter 2).

Treatment 3: Choice between blue crabs vs. periwinkles

In the last treatment, both blue crabs and periwinkles were offered simultaneously to each terrapin (Figure 9; Table 13; Appendix B). Through random assignment of available terrapins to each treatment, only small terrapins (HW < 30 mm) were selected for this experiment (Appendix B). The comparison of the ratio of number of crabs eaten-not eaten (0.53) to number of snails eaten-not eaten (0.09) using Fisher's exact test ratio was not equal to 1 and this was highly significantly different ($P < 0.001$) which indicated small terrapins preferred blue crabs to periwinkles.

Experiment 3: Blue crabs and mottled dog whelks in simulated seagrass patches

Similar to 2009 results, more blue crabs were eaten by the terrapins than snails. In total for the three trials, ten crabs were eaten of fifty-three offered though the terrapin in trial 2 did not eat any crabs. Mean CW of crabs eaten = 38.7 mm (SE = 2.1) was less than overall mean CW of crabs offered = 42.1 mm (SE = 0.9), as well as less than CW of not eaten = 42.9 mm (SE = 1.0), though not significantly different (P = 0.09). Terrapin HW was a strong predictor of size of crab eaten ($P << 0.01$) and positively correlated (Pearson's correlation: 0.97).

In the three trials conducted, only three mottled dog whelks were eaten out of 57 offered, with one consumed per trial. The mean snail SW of eaten = 8.7 mm (SE = 1.3) was less than both mean SW of snails offered = 9.3 mm (SE = 0.2) and mean SW of snails not eaten = 9.3 mm (SE = 0.2), though not significantly different (P = 0.67). Mottled dog whelks have thick shells and would be harder to crush (Petrochic 2009). Additionally, terrapins in this treatment consumed small bivalves that entered the tank through the unfiltered flow-through water system.

DISCUSSION

Foraging in seagrass beds

Diversity of the faunal prey community was highest in seagrass beds with greatest blade density though temporal variability occurred over the 2010 sampling period (Tables 2 and 3). Seagrass beds in the study area were fortuitously sampled when plant density was high in May (Table 1) just prior to a near-complete die off of the eelgrass in June that was due to a rapid water temperature increase (Short et al. 2000; Moore et al. *accepted for publication*). Faunal abundance for each region sampled reflected a typical assemblage of eelgrass-associated organisms throughout the beds surveyed (Table 2; Appendix D; Marsh 1973; Orth et al. 1984). GSE had the most consistent assemblage of fauna compared to the other regions though evenness was relatively high for all areas (Table 4D). The number of individuals and species were both determined by eelgrass canopy density as well as temporal and spatial sampling factors (Tables 4A and 4B). Barnacles were the most abundant fauna by percent in three regions (Table 2) though the amphipod *Gammarus mucronatus* had higher estimated mean biomass (Table 5). More *G. mucronatus* were found in samples from GSE region, which consisted of many protected coves with dense eelgrass (Table 2). The other regions were exposed to stronger water currents, which benefit filter-feeding barnacles (Figure 2). Overall, faunal diversity within the seagrass beds was consistent across regions; however the low diversity region, GP, was overwhelmingly dominated by barnacles (Table 2).

Prey selectivity by diamondback terrapins foraging in seagrass beds was related to terrapin size. Large terrapins (HW ≥ 30 mm) had high selectivity for bivalves, low for crabs, very low for gastropods, and near zero for barnacles and small crustaceans such that they could be considered incidentally ingested (Table 5). Top preferences were similar to mature female terrapins in northeastern Florida though prey preference shifted with the different habitats used (Butler et al. 2012). Crabs and periwinkle snails were ingested most frequently by mature females at nesting beaches (Butler et al. 2012). Clams, and crabs to a lesser extent, were also preferred food for mature females in Jamaica Bay, New York, though no habitat differentiation was mentioned (Erazmus 2012). Mature females in the current study were consistent in their prey choice of bivalves and crabs in both marsh and marsh-SAV habitats, which included nesting beaches (Chapter 2).

The small size class (HW < 30 mm) primarily fed on barnacles *Balanus* spp. attached to eelgrass blades (Table 5; Chapter 2). The small and very abundant bay barnacle *B. improvisus* was the most frequently identified species found on eelgrass (Table 2). Barnacles, in general, are a ubiquitous species having a cosmopolitan distribution (Rainbow 1995). They can be found in salt marshes attached to *Spartina* sp. stems (Lippson and Lippson 2006) and adhered to many sessile marsh organisms, such as mussels (D. Tulipani, pers. obs.). Other diet studies found terrapins rarely egested barnacle shells or that barnacles contributed little to overall fecal sample mass, and thereby concluded barnacles were likely incidentally ingested (Tucker et al. 1995; Butler et al. 2012). In those studies, the terrapins were captured in salt marshes or along nesting beaches where seagrass was not present. Fecal samples from small terrapins feeding in seagrass beds frequently contained only barnacle shell, pieces of eelgrass (some with barnacles still attached), and the small epifaunal gastropod *Bittium* sp. that is associated with eelgrass (Chapter 2). *B. improvisus* were also found in fecal samples from terrapins captured in salt marsh areas without SAV though in much lower quantities similar to previous studies (Tucker et al. 1995; Spivey 1998; Chapter 2). Previous diet studies collected terrapins from typical *Spartina*-dominated salt marshes without abundant submerged aquatic vegetation present. The presence of eelgrass provided additional, easily accessible subtidal foraging areas with plentiful, low-risk prey, such as barnacles and *Bittium* sp., for smaller sized terrapins as was similarly described of the small bivalve *Mulinia literalis* in Florida (Irlandi and Crawford 1997; Heck et al. 2008; Butler et al. 2012). Feeding subtidally in near-shore areas could also reduce risk of predation when foraging in marsh areas during high tide. Since SAV habitat only occurs in areas where it is constantly submerged, they provide areas of constant refuge throughout the tide cycle (Whitelaw and Zajac 2002).

Gastropods are common prey for diamondback terrapins (Coker 1906; Ernst and Lovich 2009) and can be the primary item ingested (Tucker et al. 1995). However, in contrast to previous studies, selectivity for gastropods was low by both size classes of terrapins from marsh-SAV areas (Table 5). The most commonly found gastropods in seagrass beds (by percent total gastropod abundance and percent occurrence in seagrass samples) were *Bittium* sp. (69% and 71%, respectively), the slipper snail *Crepadula convexa* (13% and 44%, respectively), and the mottled dog whelk *Nassarius vibex* (11% and 49%, respectively). *Bittium* sp. was the most frequently found species in fecal samples (51%) yet it accounted for less than 1 g of fecal sample biomass. This species was the smallest type of gastropod ingested and was typically retained on 1.4-2.0 mm test sieves during biomass estimation. *C. convexa* was found in 16% and *N. vibex* in 15% of terrapin fecal samples and contributed less than 0.1 g each to total fecal sample biomass.

Periwinkles

Results of the periwinkle *Littoraria irrorata* survey in the lower York River concurred with previous abundance estimates for this species in Virginia, indicating a robust population with variation in density and size between regions sampled (Figure 3, Table 6; Silliman and Zieman 2001). The earlier diet analysis revealed that only 19% of captured terrapins ingested periwinkle snails (Chapter 2), which was substantially lower than South Carolina terrapins, i.e., 100%, (Tucker et al. 1995) and higher than reported for a Jamaica Bay, New York, population, i.e., less than 2%, (Erazmus 2012). Additionally, the number of periwinkles eaten was extremely low compared to the South Carolina population (Tucker et al. 1995). The number consumed in this study was not statistically different by terrapin size class after an outlier was excluded from the analysis (Figure 6A). The overall size-distribution pattern of consumed snails for small terrapins was similar to South Carolina terrapins (Figure 5; Tucker et al. 1995). This study's results were similar to previous studies where larger terrapins (HW ≥ 30 mm) consumed larger periwinkles than small terrapins (HW < 30 mm) (Table 7; Lindeman 2000). As females increased in size, they were able to eat larger snails (Figure 5; Petrochic 2009), though the snails eaten were slightly larger than reported from previous studies (Table 7; Tucker et al. 1995; Petrochic 2009). Large females (HW ≥ 30 mm) exhibited a distinct bimodal distribution of snail size preference depending on head width (Figure 5). Females HW 30-40 mm consumed a narrower range of smaller sizes than females HW > 40 mm that shifted to larger snails (Figure 5). The small size class, which included males and females, ate snails equivalent in size as those ingested by South Carolina terrapins (Tucker et al. 1995) and slightly smaller than those ingested by terrapins in Oyster Bay (Petrochic 2009). Despite the substantial geographic distance between the studied populations, diamondback terrapins of specific sizes consumed periwinkles within similar size ranges; however, the amount of periwinkles ingested varied greatly and decreased with increasing latitude.

Periwinkles are an abundant resource for diamondback terrapins in salt marshes of the York River; however, these terrapins showed low selectivity for periwinkles, and gastropods in general, in many of the regions surveyed (Figure 4; Rincon-Diaz et al. 2011). Habitat differences, i.e., absence of SAV, influenced greater inclusion of periwinkles in the terrapin diet (Figure 6B; Table 7). Terrapins from Catlett Islands and Felgates (marsh-mudflat habitats) had ingested the greatest number of periwinkles (Figure 6). It is likely that the abundant and diverse prey species found in seagrass beds reduced Chesapeake Bay terrapins' reliance on typical salt marsh species, such as periwinkles, thereby strengthening its generalist feeding strategy.

Prey selection experiments

All three mesocosm experiments supported the diamondback terrapins' preference to consume juvenile blue crabs. When prey choice was offered, i.e., crabs or snails, crabs were overwhelmingly preferred over snails (Tables 12 and 13). These results reflect small terrapins' preferred snail size as only one large terrapin (HW = 36.6 mm) was used in Experiment 2 (Appendix B). Small terrapins (HW < 30 mm) consumed small-sized snails, which was similar to the size selected by small terrapins for small littorinid snails of SL < 8 mm (Davenport et al. 1992). These results also were similar to the size preference egested by small terrapins (Table 7; Figure 5). Some snails avoided predation by finding refuge in various seams of the copper ring in the tank. Low snail ingestion during the experiment may also be due to only 3 terrapins being from marsh habitat and the rest from marsh-SAV habitat. Erazmus (2012) reported no periwinkles ingested in feeding trials; however, as she did not report sizes of terrapins and snails used, it is possible that the snails offered were not a preferred size.

Increased percent cover of aquatic vegetation increased crab survival in the mesocosm Experiment 1 (Figures 7 and 8). As the amount of *Gracilaria vermiculophylla* was increased, crabs obtained more refuge from being eaten by the terrapin in the dense branching of the alga. While plant density was low compared to *in situ* density, terrapins were successful in finding and eating blue crabs in constructed seagrass patches in Experiment 3. A terrapin's ability to eat juvenile blue crabs was also influence by its head width and gender as similarly described by Davenport et al. (1992). In their study, small male terrapins readily ate entire small crabs (carapace width < 25 mm) and "cropped" legs off larger crabs (Davenport et al. 1992). In feeding trials offering two crab species, Erazmus (2012) reported that all crab species were consumed by terrapins. With only mature female terrapins used, the results also indicated the terrapin's ability to eat crabs, though no specific size was mentioned (Erazmus 2012). In this study, terrapins preferred smaller sized crabs, i.e., in Experiment 1, crabs eaten were 17 mm smaller on average than uneaten crabs and 9.8 mm smaller on average in Experiment 2. In Experiment 3, while smaller crabs were consumed than were offered, the mean size eaten was much larger (38.7 mm carapace width on average) as was the size offered (42.1 mm carapace width on average). Two of the three crab-only trails used large terrapins (HW > 30 mm) both of which ate crabs; one small terrapin was used in a crab-only trial and it did not eat any crabs. In all three experiments, terrapin foraging behavior demonstrated selectivity for crabs over snails and suggested a preferred crab size.

Diamondback terrapins are generalist foragers (Ernst and Lovich 2009) that showed prey selectively based on gender-size dimorphism, prey availability within a habitat, and prey size based on terrapin head width. By foraging in seagrass beds where greater variety of prey at high density, terrapins potentially reduced search time and increased foraging success (Mueller and Fagan 2008). While the species consumed varied with geographical location, these patterns were common amongst all recent terrapin diet studies (Tucker et al. 1995; Spivey 1998; Petrochic 2009;

Butler et al. 2012; Erazmus 2012; Chapter 2). Terrapins provided top-down control within salt marsh ecosystems (Silliman and Bertness 2002); they also potentially helped regulate lower trophic levels within an eelgrass community. By feeding on fouling organisms and algal grazers within seagrass beds and on periwinkle snails in salt marshes, terrapins may aid the increase of plant biomass and help sustain biodiversity within their chosen habitats (Orth et al. 1983; Duffy et al. 2003). During times of intense die-back of eelgrass throughout Chesapeake Bay (Orth et al. 2010; Moore et al. *accepted for publication*), the terrapin population within the Bay persisted which is possibly attributable to terrapins also feeding in salt marshes. Terrapins provide a link between salt marsh and SAV habitats by moving materials and energy gained through foraging in both habitats (Irlandi and Crawford 1997; Heck et al. 2008). They also transfer some of the energy acquired from aquatic habitats to nearby terrestrial habitats through oviposition and as prey to raccoons *Procyon lotor* and other terrestrial and avian predators (Carlton and Hodder 2003; Munscher et al. 2012). The presence of seagrass beds adjacent to *Spartina*-dominated salt marshes in lower Chesapeake Bay provided terrapins additional exploitable resources for food and refuge from predation. By not solely relying on either salt marshes or seagrass habitats, terrapins have broadened their foraging strategy to include a variety of abundant food resources in Chesapeake Bay.

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Table 1. Mean (SE) AFDW (g per 0.053 m^2) for blade and root material from eelgrass samples collected from seagrass beds of Goodwin Islands and Green Point in May 2010.

Region	**AFDW Blades**	**AFDW Roots**
GN	8.3 (0.6)	4.9 (0.5)
GSE	7.3 (0.8)	7.4 (0.9)
GSW	5.2 (1.0)	2.9 (0.6)
GP	5.3 (1.4)	2.9 (0.5)

Table 2.— Percent abundance of identified species found in eelgrass from seagrass beds at Goodwin Islands and Green Point in May 2010. "Remainder" combined species each with < 2.0% total abundance in each region.

Region	Species	Percent	Region	Species	Percent
GN			GSW		
	Balanus spp.	36.2%		*Balanus* spp.	40.8%
	Gammarus mucronatus	26.9%		*Gammarus mucronatus*	23.3%
	Caprella penantis	13.9%		*Bittium* spp.	19.1%
	Idotea baltica	9.4%		*Idotea baltica*	3.7%
	Bittium spp.	3.0%		Remainder	13.1%
	Remainder	10.6%			
GP			GSE		
	Balanus spp.	73.8%		*Gammarus mucronatus*	23.1%
	Gammarus mucronatus	10.5%		*Balanus* spp.	16.9%
	Bittium spp.	6.0%		*Bittium spp.*	16.9%
	Remainder	9.7%		*Erichsonella attenuata*	13.1%
				Crepidula convexa	9.3%
				Idotea baltica	7.9%
				Callinectes sapidus	2.8%
				Nassarius vibex	2.4%
				Remainder	7.6%

Table 3. Mean (± SE) of number of individuals (N), number of species (S), Margalef's Species Richness (d), Pielou's Evenness (J') and Shannon Diversity (H'(log$_e$)) by region (A) and by sample (B) for seagrass beds from Goodwin Islands and Green Point based on samples collected three consecutive weeks in May 2010. N and S are means per 0.053 m^2 area sampled. Significance: [1] $p < 0.05$, [2] $p < 0.01$, [3] $p < 0.001$

A. By Region

Region	N[3]	S	d	J'[3]	H'(log$_e$)[1]
GN	64.4 (12.8)	7.8 (0.6)	1.9 (0.2)	0.737 (0.037)	1.5 (0.1)
GP	76.7 (14.9)	7.4 (0.7)	1.6 (0.2)	0.543 (0.053)	1.1 (0.1)
GSE	16.1 (2.1)	5.8 (0.5)	1.8 (0.2)	0.861 (0.017)	1.5 (0.1)
GSW	52.1 (6.5)	8.1 (0.8)	1.8 (0.2)	0.688 (0.035)	1.3 (0.1)

B. By Week Sampled (all regions)

Week Sampled	N	S	d[3]	J'	H'(log$_e$)[2]
1	50.7 (7.0)	6.9 (0.7)	1.6 (0.1)	0.675 (0.034)	1.2 (0.1)
2	65.2 (12.5)	6.4 (0.5)	1.5 (0.1)	0.677 (0.047)	1.2 (0.1)
3	41.1 (9.5)	8.5 (0.5)	2.3 (0.1)	0.770 (0.035)	1.6 (0.1)

C. Week Sampled By Region

Week Sampled by Region	N[3]	S[1]	d[2]	J'[3]	H'(log$_e$)[2]
GN-1	54.8 (10.2)	8.7 (1.4)	2.0 (0.4)	0.730 (0.044)	1.5 (0.1)
GN-2	122.0 (20.5)	8.2 (1.0)	1.5 (0.2)	0.613 (0.065)	1.3 (0.1)
GN-3	16.5 (4.0)	6.7 (0.7)	2.1 (0.2)	0.869 (0.031)	1.6 (0.1)
GP-1	69.5 (14.8)	7.7 (1.4)	1.6 (0.3)	0.548 (0.083)	1.1 (0.2)
GP-2	86.3 (30.8)	5.8 (1.1)	1.2 (0.3)	0.459 (0.112)	0.8 (0.3)
GP-3	74.3 (32.9)	8.8 (0.9)	2.0 (0.2)	0.623 (0.078)	1.3 (0.1)
GSE-1	14.2 (2.7)	4.5 (0.6)	1.3 (0.1)	0.835 (0.021)	1.2 (0.1)
GSE-2	16.2 (3.1)	5.5 (0.7)	1.6 (0.2)	0.835 (0.032)	1.4 (0.2)
GSE-3	18.0 (5.3)	7.5 (1.1)	2.4 (0.2)	0.913 (0.025)	1.8 (0.1)
GSW-1	64.3 (13.8)	6.8 (1.4)	1.4 (0.3)	0.588 (0.032)	1.1 (0.2)
GSW-2	36.2 (10.8)	6.2 (1.1)	1.6 (0.2)	0.799 (0.071)	1.4 (0.1)
GSW-3	55.7 (6.5)	11.2 (0.3)	2.6 (0.1)	0.676 (0.047)	1.6 (0.1)

Table 4. A-E. AIC-based model selection for factors of eelgrass abundance (N), species abundance (S), species richness (*d*), evenness (*J'*), and diversity (*H'*) for seagrass beds from Goodwin Islands and Green Point in May 2010. Number of parameters (k) for each model. Model definitions in Appendix E. Highest three models listed here and complete list in Appendix F. Model weights (w_i) in bold indicate model with best fit. Other model weights > 0.2 italicized.

A. Number of individuals (N)

Model	k	ΔAIC_c	w_i
g(1)	**14**	**0**	**0.984**
g(2)	8	8.888902	0.012
g(5)	13	11.322087	0.003

B. Number of species (S)

Model	K	ΔAIC_c	w_i
g(3)	**6**	**0**	**0.554**
g(2)	8	1.910078	*0.213*
g(1)	14	2.891188	0.131

C. Species richness (*d*)

Model	K	ΔAIC_c	w_i
g(9)	**4**	**0**	**0.503**
g(4)	5	0.26945	*0.440*
g(6)	7	5.36884	0.034

D. Evenness (*J'*)

Model	k	ΔAIC_c	w_i
g(2)	**8**	**0**	**0.460**
g(6)	7	1.62101	*0.205*
g(8)	5	3.00244	0.103

E. Shannon Diversity (*H'*)

Model	k	ΔAIC_c	w_i
g(6)	**7**	**0**	**0.693**
g(2)	8	2.50199	0.198
g(9)	4	5.00116	0.057

Table 5. Manly-Chesson index (α) of relative selectivity for five prey groups by two size classes of diamondback terrapins captured from seagrass beds of the Goodwin Island-Green Point region in 2010. Size class: s = small HW < 30 mm, L = large HW ≥ 30 mm (Chapter 2). * - high selectivity.

	Size Class	Barnacles	Bivalves	Crabs	Gastropods	Isopods-Amphipods
Mean Biomass (g)						
Eelgrass		19.8333	2.4035	24.7975	24.2826	24.3897
Terrapin	s	1.5932	0.0878	0.0591	0.0824	0.1700
	L	0.0026	1.1090	1.8024	0.2458	0.0074
Manly-Chesson α						
Terrapin	s	0.6199*	0.2817	0.0184	0.0262	0.0538
	L	0.0002	0.8472*	0.1335	0.0186	0.0006

Table 6. *Littoraria irrorata* total snails (n), mean (SE) shell length (SL, mm), shell length range (mm), *Spartina alterniflora*: mean (SE) zone width (m) from marsh edge, and number of snails/shoot in four regions where diamondback terrapins were captured. Significance: $^{1}p < 0.05$, $^{2}p < 0.01$, $^{3}p < 0.001$

	Littoraria irrorata			*Spartina alterniflora*	*L. irrorata/ S. alterniflora*
Region	n	SL$^{(3)}$	SL range	Zone$^{(3)}$	Shoot$^{(2)}$
AI	483	17.1 (0.2)	3.2 - 24.4	25.5 (2.7)	0.91 (0.17)
CI	289	19.4 (0.2)	4.6 - 24.5	23.0 (1.1)	0.75 (0.11)
GI	210	18.4 (0.3)	4.2 - 23.8	7.6 (1.3)	0.31 (0.07)
GP	265	19.0 (0.2)	5.5 - 27.0	8.0 (1.7)	0.70 (0.11)

Table 7. Mean (SE) number and length (mm) of periwinkle opercula egested by diamondback terrapins (n=33) with mean (SE), range, and median of estimated periwinkle shell length (SL, mm) by size class (s = small HW < 30 mm, L = large HW ≥ 30 mm) and habitat. *Significant difference (p < 0.001).

	Size Class*		Habitat*	
	s	L	Marsh-mudflat	Marsh-SAV
Number of terrapins	22	11	9	24
Opercula egested	24.6 (12.4)	17.8 (6.1)	54.8 (28.0)	10.2 (3.0)
Opercula Length	2.78 (0.04)	5.9 (0.1)	2.81 (0.04)	5.2 (0.1)
Estimated SL	7.6 (0.1)	15.8 (0.4)	7.4 (0.1)	13.9 (0.4)
Estimated SL size range	3.4 - 21.5	6.9 – 24.2	3.4 – 24.2	4.5 - 24.2
Estimated SL median	7.2	18.1	7.4	13.0

Table 8. 2009 prey detection models. A) Model set tested for number of crabs eaten regressed against percent cover, terrapin head width (HW), gender (G), and the interaction between HW and G. Best-fit and plausible models in bold. B) Parameter estimates of models with AIC_c $w_i > 0.20$.

A.

Model	**Intercept**	**Percent Cover**	**HW**	**G**	**HW*G**	**k**	**ΔAIC_c**	**w_i**
g(1)	β_0	β_1	β_2	β_3	β_4	6	9.415651	0.006
g(2)	β_0	β_1	β_2	β_3		5	5.105387	0.052
g(3)	**β_0**	**β_1**	**β_2**			**4**	**3.104027**	**0.141**
g(4)	**β_0**	**β_1**		**β_3**		**4**	**3.446147**	**0.119**
g(5)	**β_0**	**β_1**				**3**	**0**	**0.664**
g(6)	β_0		β_2			3	8.679823	0.009
g(7)	β_0			β_3		3	8.652283	0.009
g(8)	β_0		β_2	β_3		4	12.191273	0.001
g(9)	β_0		β_2	β_3	β_4	5	16.538059	0.001e-1

B.

Model	Parameter	Parameter Estimates	SE
g(5)	β_0	14.250	2.888
	β_1	-3.350	1.054

Table 9. 2009 prey detection models. A) Model set tested for crab eaten (1) or not eaten (0) regressed (logistic regression) against percent cover, terrapin head width (HW), gender (G), and the interaction between HW and G. Best-fit and plausible models in bold. B) Parameter estimates of models with AIC_c $w_i > 0.20$.

A.

Model	**Intercept**	**Percent Cover**	**HW**	**G**	**HW*G**	**k**	**ΔAIC_c**	**w_i**
g(1)	**β_0**	**β_1**	**β_2**	**β_3**	**β_4**	**5**	**0**	**0.633**
g(2)	**β_0**	**β_1**	**β_2**	**β_3**		**4**	**1.666306**	**0.275**
g(3)	β_0	β_1	β_2			3	4.8787141	0.055
g(4)	β_0	β_1		β_3		3	8.312313	0.010
g(5)	β_0	β_1				2	6.369956	0.026
g(6)	β_0		β_2			2	58.981895	0.099e-12
g(7)	β_0			β_3		2	57.516807	0.021e-11
g(8)	β_0		β_2	β_3		3	36.387688	0.081e-12
g(9)	β_0		β_2	β_3	β_4	4	61.106914	0.034e-12

B.

Model	**Parameter**	**Parameter Estimates**	**SE**
g(1)	α	3.628	1.070
	β_1	-1.025	0.143
	β_2	-0.085	0.032
	β_3	6.467	3.758
	β_4	-0.346	0.178
g(2)	α	3.637	1.066
	β_1	-0.944	0.135
	β_2	-0.091	0.032
	β_3	-0.844	0.372

Table 10. 2009 prey detection models. A) Model set tested for size of crab eaten regressed against percent cover, terrapin head width (HW), gender (G), and the interaction between HW and G. Best-fit and plausible models in bold. B) Parameter estimates of crab size eaten models with AIC$_c$ $w_i > 0.20$. Parameter estimates were back-transformed.

A.

Model	Intercept	Percent Cover	HW	G	HW*G	k	ΔAIC$_c$	w_i
g(1)	β_0	β_1	β_2	β_3	β_4	6	3.6776672	0.038
g(2)	β_0	β_1	β_2	β_3		5	4.3166143	0.028
g(3)	β_0	β_1	β_2			4	2.1738446	0.082
g(4)	β_0	β_1		β_3		4	2.7159200	0.062
g(5)	**β_0**	**β_1**				**3**	**0.5698332**	**0.182**
g(6)	**β_0**		**β_2**			**3**	**0**	**0.242**
g(7)	**β_0**			**β_3**		**3**	**0.5395403**	**0.184**
g(8)	β_0		β_2	β_3		4	2.0850150	0.085
g(9)	β_0		β_2	β_3	β_4	5	1.8626341	0.095

B.

Model	Parameter	Parameter Estimates	SE
g(6)	β_0	17.464	0.094
	β_2	0.997	0.068

Table 11. 2010 prey selection experiment treatment 1 - blue crabs only. A) summary of number and size of blue crabs offered, eaten, not eaten and difference between offered and eaten. B) AIC-based model selection for factors on treatment 1. Best-fit and plausible models in bold. C) Linear regression parameter estimates and standard errors for models with $w_i \geq 0.2$.

A.

Trial	n	Crabs Offered CW (mm) Mean (SE)	n	Crabs Eaten CW (mm) Mean (SE)	Difference (Offered – Eaten)	Crabs Not Eaten CW (mm) Mean (SE)
1	20	37.2 (1.8)	6	32.4 (2.8)	4.8	39.3 (2.1)
2	20	38.9 (2.0)	8	31.7 (1.9)	7.1	43.6 (2.3)
3	20	35.4 (3.2)	9	23.0 (3.0)	12.4	45.5 (2.5)
4	20	40.7 (2.6)	6	31.8 (5.4)	9.0	44.6 (2.3)
5	20	33.0 (3.7)	6	18.7 (4.2)	14.3	39.1 (4.0)
6	20	30.2 (3.9)	11	18.9 (2.6)	11.2	43.9 (5.2)

B.

Model	Intercept	Terrapin HW	Crab CW	Terrapin Gender-Size Class	k	ΔAIC_c	w_i
g(1)	**β_0**	**β_1**			**3**	**0**	**0.419**
g(2)	**β_0**		**β_2**		**4**	**0.5891282**	**0.312**
g(3)	β_0		β_2	β_3	2	2.0167308	0.153
g(4)	β_0	β_1	β_2		5	2.5715833	0.116
g(5)	β_0	β_1	β_2	β_3	2	53.1914540	0.118e-11
g(6)	β_0			β_3	3	55.0358692	0.469e-12

C.

Model		Parameter	Parameter Estimates	SE
g(4)	β_0	Intercept	6.67221	1.76258
	β_1	Terrapin HW	-0.10065	0.05176
	β_2	Crab CW	-0.13704	0.02417
g(3)	β_0	Intercept	2.97874	0.85704
	β_2	Crab CW	-0.14619	0.02605
	β_3	Terrapin gender-size class:		
		f-s	1.99603	0.89297
		m-s	1.55679	0.81785

Table 12. 2010 prey selection experiment treatment 2 - periwinkle snails only. Mean (SE) of snail length (SL, mm) for periwinkles offered to, eaten, difference (offered – eaten), and not eaten by diamondback terrapins.

Trial	n	Offered SL	n	Eaten SL	Difference	Not Eaten SL
1	20	14.7 (0.7)	1	18.0	-3.3	14.5 (0.7)
2	20	12.4 (0.6)	1	15.0	-2.6	12.2 (0.6)
3	20	12.5 (0.5)	1	7.9	4.6	12.7 (0.5)
4	20	14.5 (0.8)	2	12.2 (4.7)	2.3	14.8 (0.8)
5	20	12.0 (0.6)	0	0	12.0	12.0 (0.6)
6	20	15.4 (0.8)	0	0	15.4	15.4 (0.8)

Table 13. 2010 prey selection experiment treatment 3 – 10 blue crabs and 10 periwinkle snails. A) Mean (SE) and range of carapace width (CW, mm)of blue crabs offered, eaten and not eaten; B) Mean (SE) and range of shell length (SL, mm) for periwinkles offered, eaten, and not eaten by diamondback terrapins.

A.

	Blue Crabs							
	Offered		Eaten			Not Eaten		
Trial	Mean CW	CW Range	n	Mean CW	CW Range	n	Mean CW	CW Range
1	38.6 (1.6)	31.8-48.4	0	-	-	10	38.6 (1.6)	31.8-48.4
2	38.6 (2.2)	30.1-51.2	1	51.2	-	9	37.2 (1.9)	30.1-45.1
3	35.7 (5.2)	14.9-56.5	2	27.3 (12.4)	14.9-39.6	8	37.9 (5.9)	20.2-56.5
4	23.2 (2.9)	14.5-39.6	0	-	-	0	23.2 (2.9)	14.5-39.6
5	32.2 (4.6)	17.9-56.0	4	28.2 (9.3)	17.9 - 56.0	6	27.6 (5.1)	20.1-55.0
6	32.9 (5.1)	15.3-53.0	0	-	-	10	32.9 (5.1)	15.3-53.0

B.

	Periwinkles							
	Offered		Eaten			Not Eaten		
Trial	Mean SL	SL Range	n	Mean SL	SL Range	n	Mean SL	SL Range
1	14.8 (0.7)	10.9-17.6	2	14.5 (0.4)	14.1-14.8	8	14.9 (0.9)	10.9-17.6
2	14.9 (0.6)	11.1-16.6	0	-	-	10	14.9 (0.6)	11.1-16.6
3	11.6 (0.7)	7.9-15.6	0	-	-	10	11.6 (0.7)	7.9-15.6
4	14.8 (1.0)	9.9-19.4	0	-	-	10	14.8 (1.0)	9.9-19.4
5	12.3 (0.8)	9.1-16.6	0	-	-	10	12.3 (0.8)	9.1-16.6
6	13.8 (1.4)	7.4-22.6	3	12.8 (2.3)	9.7-17.2	7	14.2 (1.8)	7.4-22.6

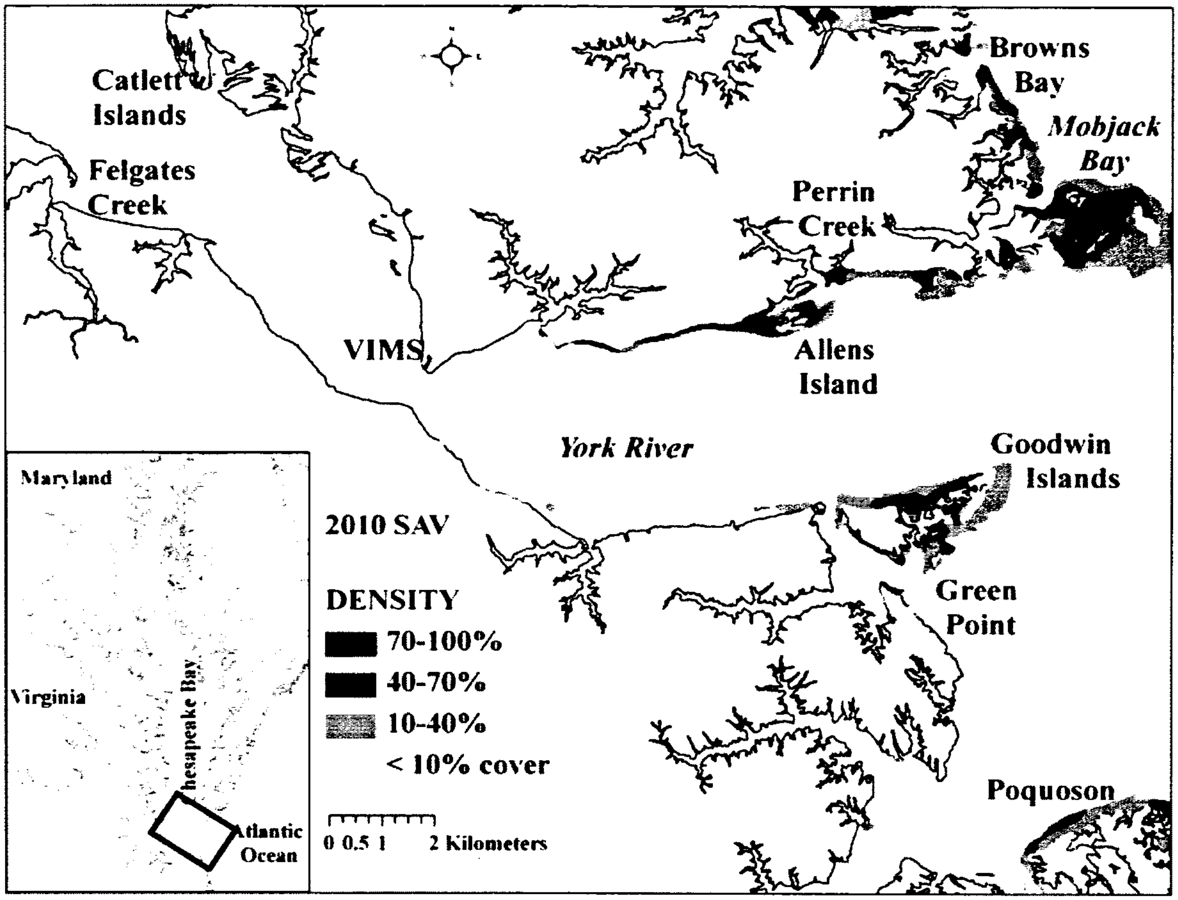

Figure 1. Collection locations for diamondback terrapins along the lower York River, Virginia, included Catlett Islands (upriver), Goodwin Islands and Green Point, cove near mouth of Perrin Creek, Allens Island, Browns Bay in southeastern Mobjack Bay, Felgates Creek and Poquoson in southwestern Chesapeake Bay (rectangle on inset). Gray shading indicates the spatial extent of submerged aquatic vegetation (SAV) in 2010 (modified from Orth et al. 2011).

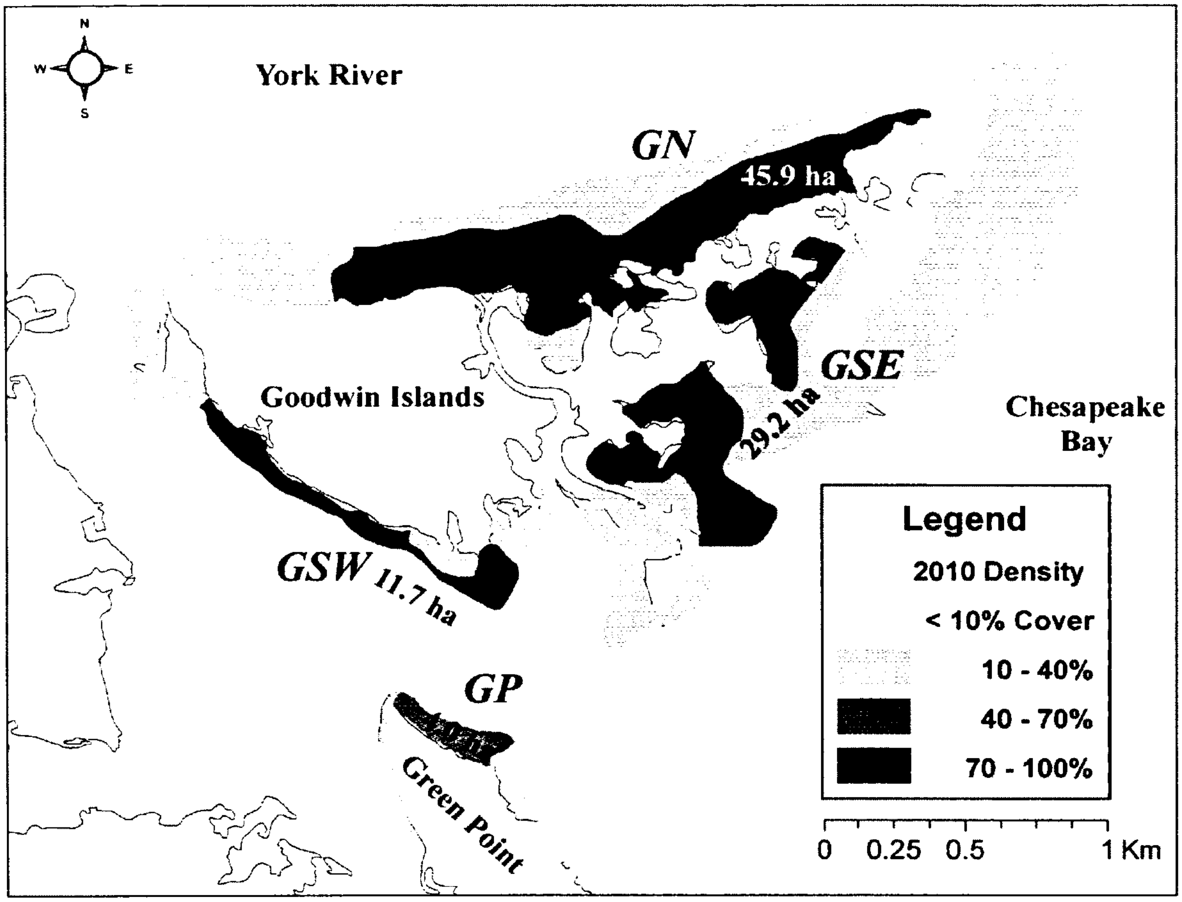

Figure 2. Regions with area (ha) where eelgrass samples were collected in May 2010 from seagrass beds adjacent to Goodwin Islands and Green Point where percent coverage ≥ 40% (modified from Orth et al. 2011).

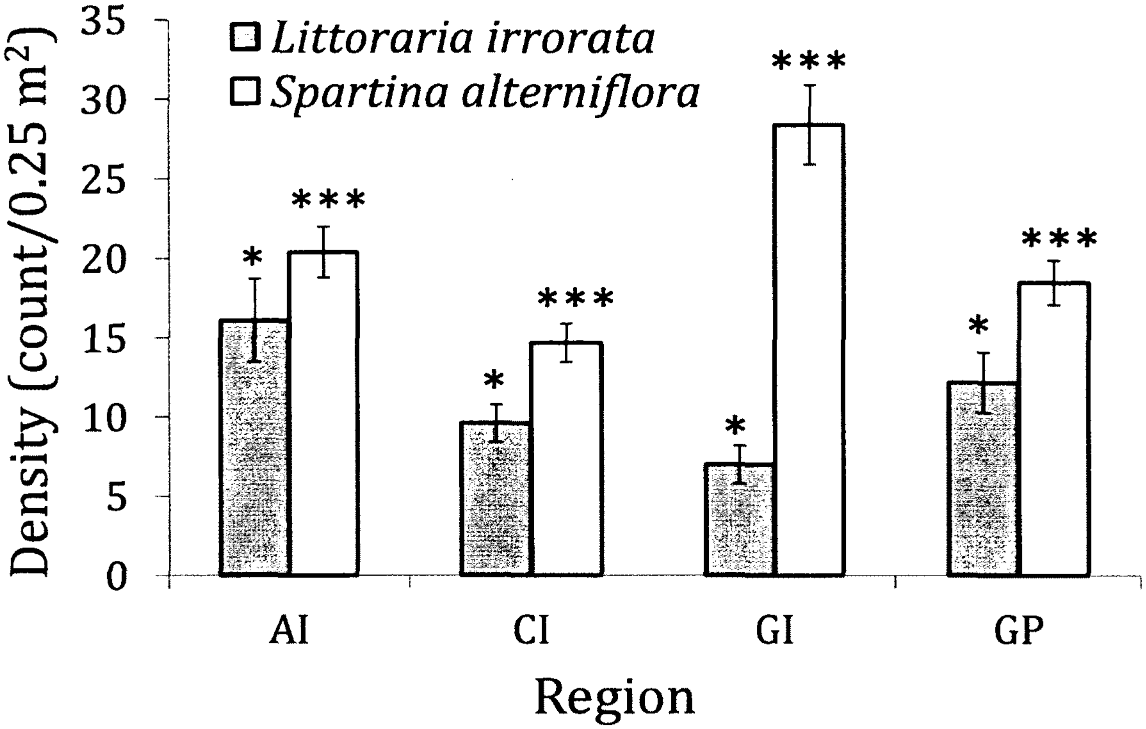

Figure 3. Mean (SE) *Littoraria irrorata* density (individuals 0.25 m^{-2}) and *Spartina alterniflora* shoot density (shoots 0.25 m^{-2}) in four regions where diamondback terrapins were captured. Error bars are standard error of the means. Significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$

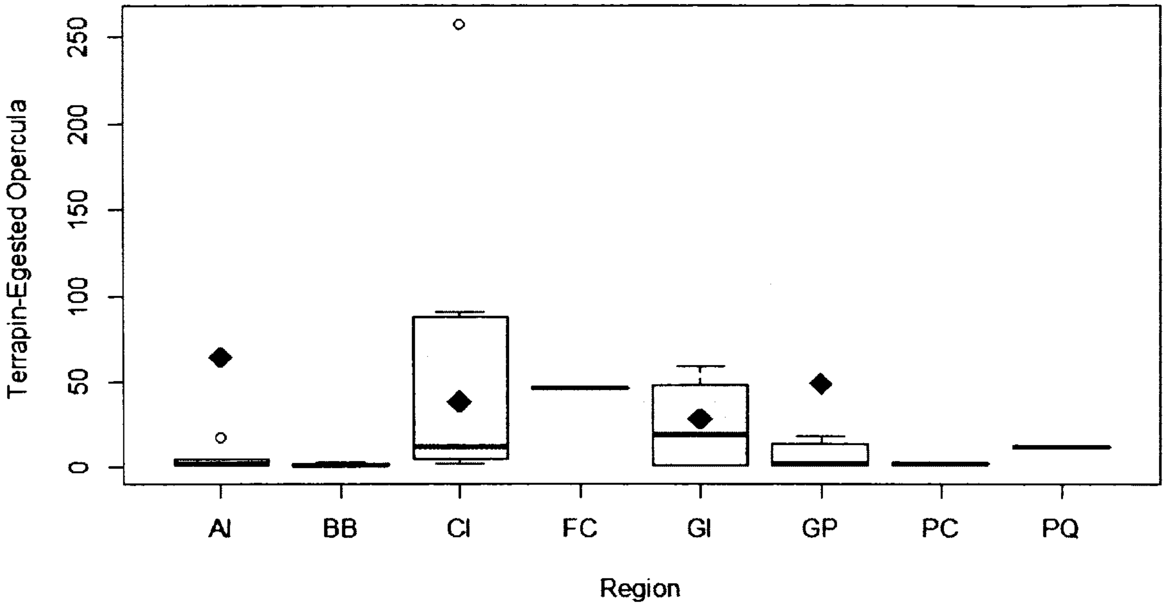

Figure 4. Number of periwinkle opercula egested by diamondback terrapins by region and mean periwinkle abundance m^{-2} (black diamonds) at four regions surveyed in 2012. Terrapins collected in 2009, 2010, and 2011, from Allens Island (AI), Catlett Islands (CI), Felgates Creek (FC), Goodwin Islands (GI), Green Point (GP), Perrin Cove (PC) along York River, Browns Bay (BB) in southeastern Mobjack Bay, and Poquoson (PQ) on Chesapeake Bay, Virginia

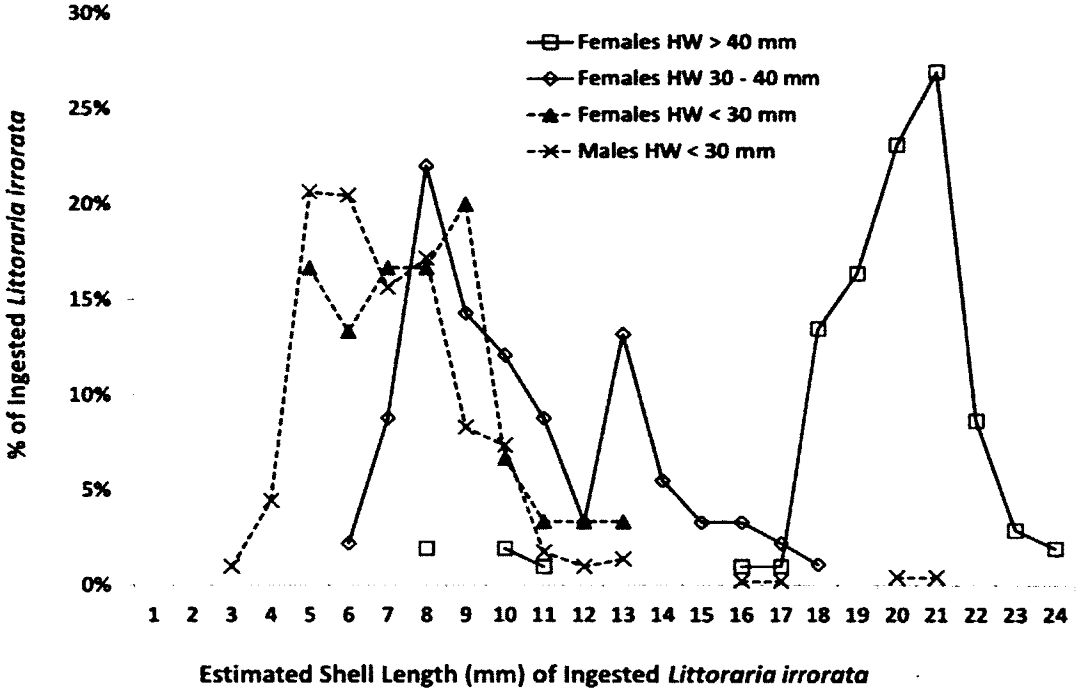

Figure 5. Size frequency distribution of estimated shell length of periwinkle (*Littoraria irrorata*) ingested by diamondback terrapins collected in 2009, 2010, and 2011 from York River, Virginia, by gender and size class, where large = HW ≥ 30 mm and small = HW < 30 mm. All males had HW < 30 mm.

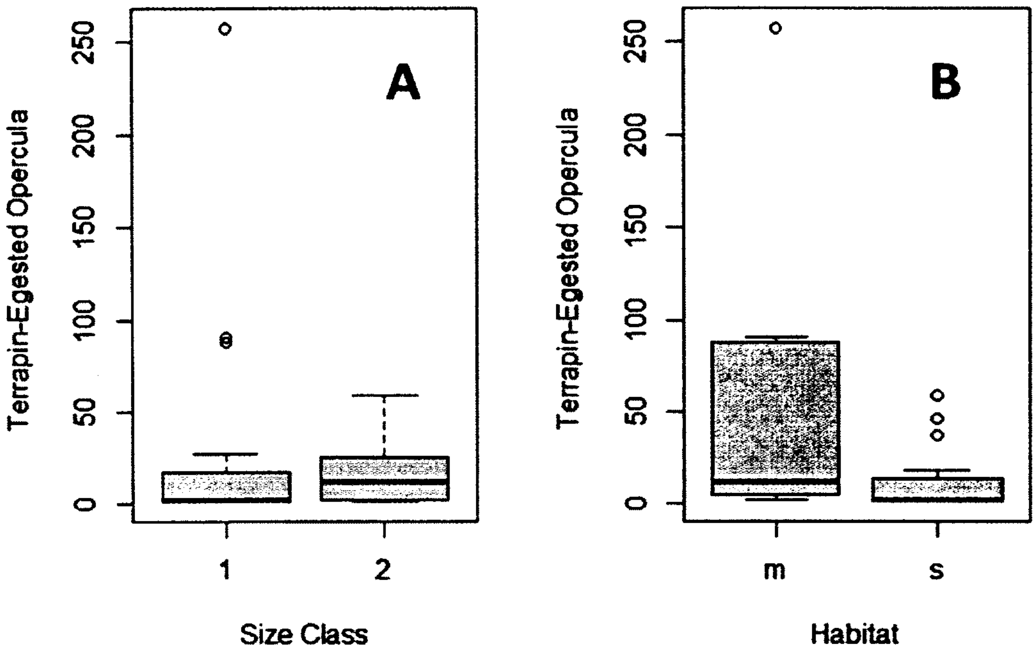

Figure 6. Number of periwinkle opercula egested by diamondback terrapins collected in 2009, 2010, and 2011 from York River, Virginia, by size class (1 = small, 2 = large) and habitat (m = marsh-mudflat, s = marsh-SAV).

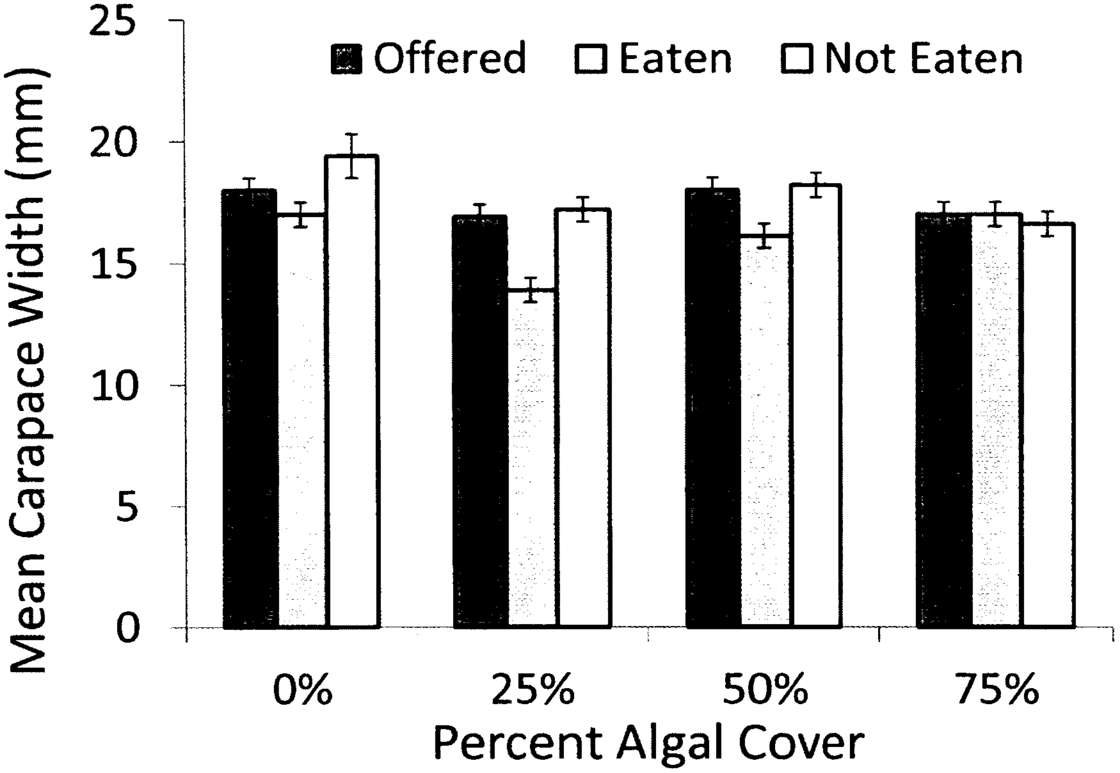

Figure 7. Mean (SE) carapace width (mm) of blue crabs (*Callinectes sapidus*) used in diamondback terrapin prey detection experiment (2009). Four trials tested increasing percent cover of *Gracilaria vermiculophylla* with 25 crabs offered per trial-treatment (4 trials). Overall mean (SE) for offered = 17.4 (0.2) mm, eaten = 16.7 (0.4) mm, and not eaten = 17.6 (0.3) mm. Error bars are standard error of the means.

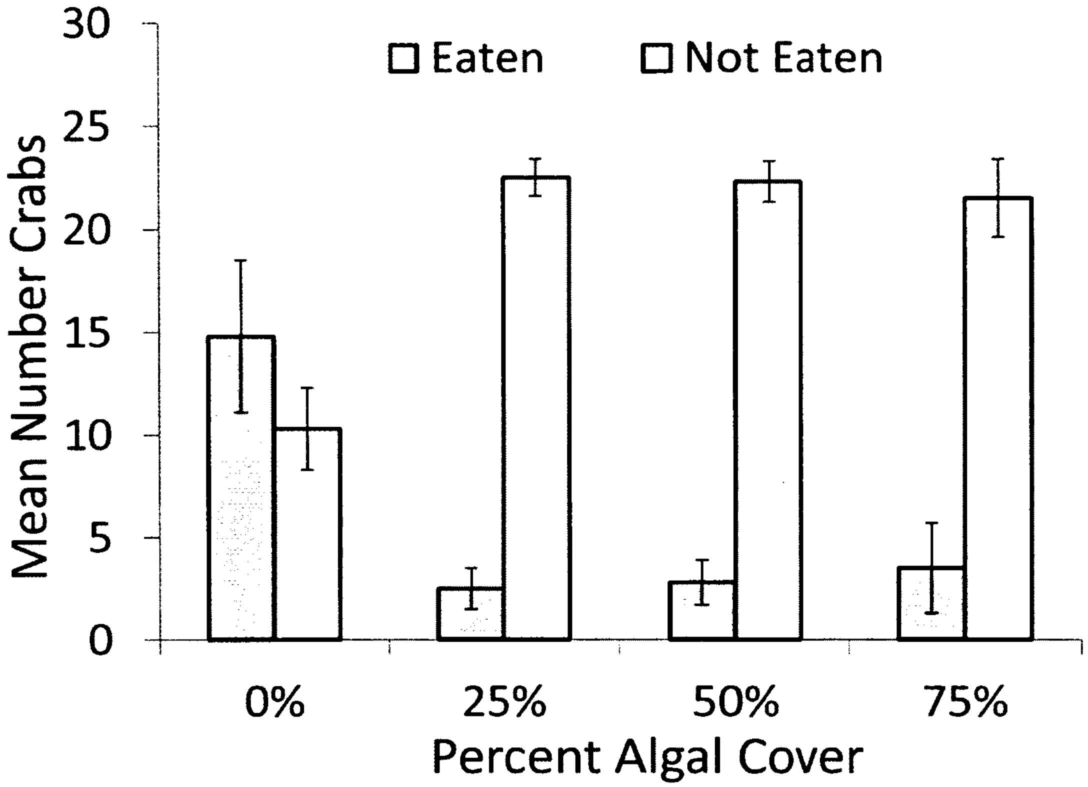

Figure 8. Mean (SE) number of blue crabs (*Callinectes sapidus*) used in diamondback terrapin prey detection experiment (2009). Four trials tested increasing percent cover of *Gracilaria vermiculophylla* with 25 crabs offered per trial-treatment (4 trials). For all trials, 400 crabs were used, 94 were eaten and 306 not eaten. Error bars are standard error of the means.

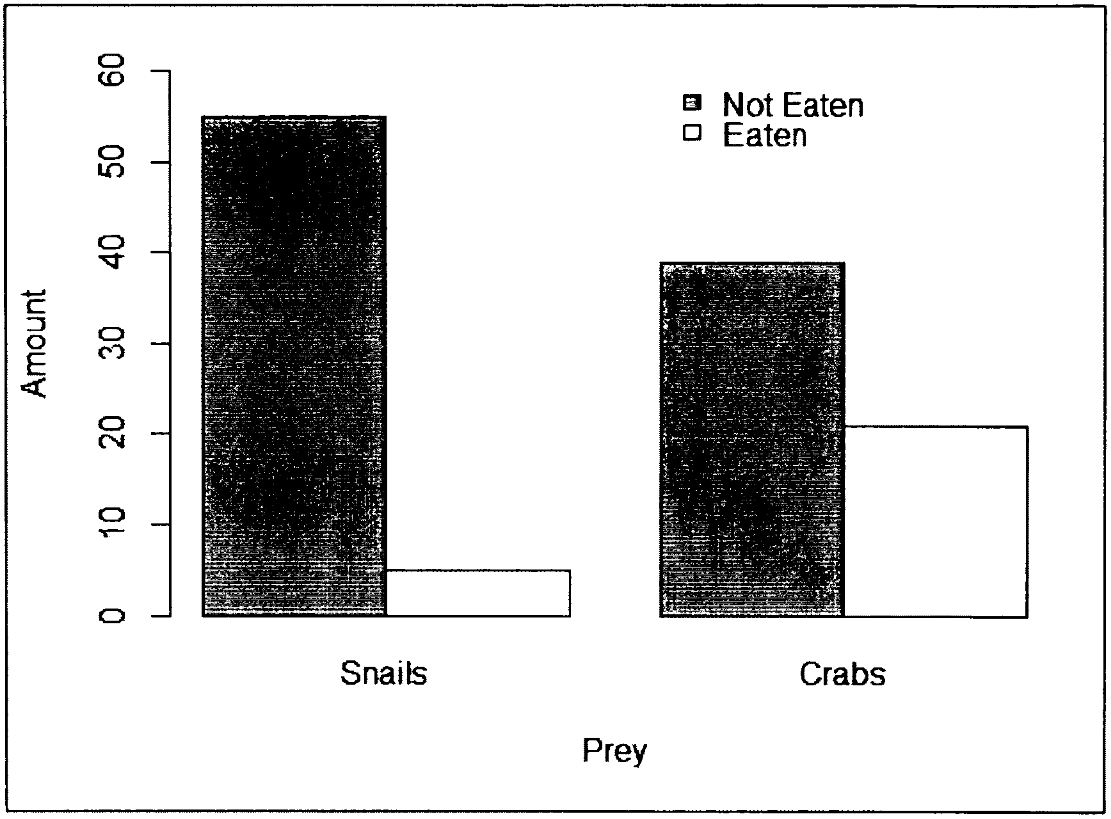

Figure 9. 2010 prey selection experiment treatment 3 – blue crabs vs. periwinkles showing total number of prey consumed by terrapins for all six trials. Each was offered 10 periwinkles and 10 blue crabs per trial.

Appendix A. Turtle identification number (TID), gender, mass (g), head width (HW, mm), carapace length (CL), and plastron length (PL) of diamondback terrapins (*Malaclemys terrapin*) used in 2009 prey detection experiment using four levels of algal cover per trial. Captured from CI - Catlett Islands, AI - Allens Island, GP - Green Point, GI - Goodwin Islands, and PC – Perrin Cove.

Trial	Percent Cover	TID	Gender	Mass	HW	CL	PL
1	0	PC-T007	f	1,085	33.0	19.4	17.4
	0.25	GI-T047	m	257	22.0	12.0	10.3
	0.5	CI-T006	m	331	22.0	13.0	11.1
	0.75	CI-T011	m	133	20.0	9.2	8.0
2	0	PC-T008	f	1,614	37.0	21.6	19.6
	0.25	GI-T040	f	1,226	35.0	19.8	17.9
	0.5	CI-T010	m	158	19.0	9.9	8.3
	0.75	AI-T005	f	431	26.0	13.8	12.8
3	0	CI-T013	m	153	21.0	9.6	8.7
	0.25	CI-T012	m	164	21.0	9.4	8.6
	0.5	GI-T043	f	1,026	31.0	18.7	16.9
	0.75	GI-T043	f	1,026	31.0	10.9	9.1
4	0	PC-T005	f	208	21.0	10.5	9.2
	0.25	PC-T006	m	362	22.0	13.5	12.0
	0.5	PC-T010	f	422	25.0	13.8	12.5
	0.75	AI-T006	f	316	24.0	12.7	11.6

Appendix B. Diamondback terrapins used in 2010 prey choice experiments. Treatments: 1 – crabs only, 2 – snails only, 3 – both. Captured from BB – Browns Bay, CI - Catlett Islands, AI - Allens Island, GP - Green Point, GI - Goodwin Islands, PC – Perrin Cove. Mass (g), HW – head width (mm), CL – straight carapace length (cm), PL – plastron length (cm).

Year	Trial	Treatment	TID	Gender	Mass	HW	CL	PL
2010	1	1	CI-T006	m	295	23.2	12.9	10.9
		2	GI-T091	m	380	22.4	13.9	11.8
		3	AI-T013	f	570	27.4	15.3	14.2
	2	1	AI-T006	f	367	24.9	13.5	12.3
		2	AI-T009	m	321	21.7	13.4	11.2
		3	AI-T012	m	461	23.8	15.2	12.7
	3	1	GP-T103	m	202	19.1	10.9	9.3
		2	BB-T003	m	342	21.5	13.3	11.5
		3	GP-T086	m	395	23.7	13.9	12.2
	4	1	BB-T002	f	259	23.3	11.7	10.9
		2	BB-T001	f	238	25.0	11.5	10.4
		3	CI-T016	f	237	22.5	11.0	9.9
	5	1	GP-T104	f	1,274	36.6	20.3	18.4
		2	GP-T094	m	301	23.0	12.6	11.0
		3	GI-T099	f	282	24.6	12.3	10.7
	6	1	PC-T012	m	337	22.0	13.2	11.4
		2	BB-T004	m	234	22.1	11.5	10.3
		3	CI-T018	f	216	21.5	11.1	9.9

Appendix C. Diamondback terrapins used in 2011 prey choice experiments. Treatments: 1 – crabs only, 2 – snails only. BB – Browns Bay, CI = Catlett Islands, AI = Allens Island, GP = Green Point, GI = Goodwin Islands. Mass (g), HW – head width (mm), CL – straight carapace length (cm), PL – plastron length (cm).

Year	Trial	Treatment	TID	Gender	Mass	HW	CL	PL
2011	1	1	BB-T007	f	916	31.9	17.9	16.7
		2	GP-T033	m	313	22.2.	13.0	11.2
	2	1	GI-T140	m	382	21.8	14.0	11.5
		2	BB-T006	f	211	22.1	10.6	9.5
	3	1	CI-T028	f	1,844	46.4	22.0	19.3
		2	CI-T027	f	1,578	44.8	21.3	19.1

Appendix D. Identified species found in eelgrass (*Zostera marina*) samples collected May 2010.

Type of fauna	Family/Genus/Species name
amphipod	*Ampelisca* sp.
	Ampithoe longimana
	Ampithoe valida
	Caprella penantis
	Corophium sp.
	Elasmopus levi
	Gammarus mucronatus
	Lembos smithi
bivalve	*Alegina elevata*
	Anadara ovalis
	Anadara transversa
	Anomia simplex
	Gemma gemma
	Geukensia demissa
	Macoma sp.
cirripedia	*Balanus* spp.
crab	*Callinectes sapidus*
	Family Xanthidae
fish	*Luciana parva*
	Syngnathus fuscus
isopod	*Edotea triloba*
	Erichsonella attenuata
	Idotea baltica
shrimp	*Palaemonetes intermedius*
	Palaemonetes pugio
	Palaemonetes sp.
	Palaemonetes vulgaris
	Upogebia affinis
snail	*Acanthodons pilosa*
	Anachis sp.
	Bittium sp.
	Crepadula convexa
	Littoraria irrorata
	Mitrella lunata
	Nassarius vibex

Appendix E: Models used in linear regression of eelgrass faunal abundance and diversity indices.

Model	Intercept	Eelgrass Blade AFDW	Region	Week Sampled	Region* Week Sampled
g(1)	β_0	β_1	β_2	β_3	β_4
g(2)	β_0	β_1	β_2	β_3	
g(3)	β_0	β_1	β_2		
g(4)	β_0	β_1		β_3	
g(5)	β_0		β_2	β_3	β_4
g(6)	β_0		β_2	β_3	
g(7)	β_0	β_1			
g(8)	β_0		β_2		
g(9)	β_0			β_3	

Appendix F. AIC-based model selection for eelgrass abundance (N), species abundance (S), species richness (*d*), evenness (*J'*), and diversity (*H'*) for seagrass beds from Goodwin Islands and Green Point in May 2010. Number of parameters (k). Model weights (w_i) in bold indicate model with best fit. Other model weights > 0.2 italicized. Model definitions listed in Appendix E.

A. Number of individuals (N)

Model	k	ΔAIC_c	w_i
g(1)	**14**	**0**	**0.984**
g(2)	8	8.888902	0.012
g(5)	13	11.322087	0.003
g(3)	6	14.184812	8.18E-04
g(8)	5	19.320368	6.28E-05
g(6)	7	21.043616	2.65E-05
g(4)	5	40.23912	1.80E-09
g(7)	3	40.33856	1.71E-09
g(9)	4	42.698755	5.26E-10

B. Number of species (S)

Model	k	ΔAIC_c	w_i
g(3)	**6**	**0**	**0.554**
g(2)	8	1.910078	*0.213*
g(1)	14	2.891188	0.131
g(7)	3	4.641916	0.054
g(4)	5	5.777501	0.031
g(6)	7	9.031701	0.006
g(5)	13	9.226785	0.005
g(9)	4	9.602754	0.005
g(8)	5	12.552373	0.001

Appendix F (continued).

C. Species richness (d)

Model	k	ΔAIC_c	w_i
g(9)	**4**	**0**	**0.503**
g(4)	5	0.26945	*0.440*
g(6)	7	5.36884	0.034
g(2)	8	6.34931	0.021
g(7)	3	13.1069	0.001
g(5)	13	13.7075	0.001
g(1)	14	14.9981	0.000
g(3)	6	19.0944	3.6E-05
g(8)	5	23.9288	3.2E-06

D. Evenness (J')

Model	k	ΔAIC_c	w_i
g(2)	**8**	**0**	**0.460**
g(6)	7	1.62101	*0.205*
g(8)	5	3.00244	0.103
g(1)	14	3.05029	0.100
g(5)	13	3.36041	0.086
g(3)	6	4.54948	0.047
g(9)	4	27.7454	4.3E-07
g(7)	3	29.3643	1.9E-07
g(4)	5	29.9279	1.5E-07

E. Shannon Diversity (*H'*)

Model	k	ΔAIC_c	w_i
g(6)	**7**	**0**	**0.693**
g(2)	8	2.50199	0.198
g(9)	4	5.00116	0.057
g(4)	5	6.26477	0.030
g(5)	13	9.45537	0.006
g(8)	5	9.66011	0.006
g(3)	6	9.85065	0.005
g(7)	3	10.8936	0.003
g(1)	14	12.4871	0.001

Appendix G. Parameter estimates and standard errors (SE) of models with AIC $w_i \geq 0.2$ for eelgrass diversity measures eelgrass abundance (N), species abundance (S), species richness (d), evenness (J'), and diversity (H') for seagrass beds from Goodwin Islands and Green Point in May 2010.

Abundance	Model		Parameter	Parameter Estimates	SE
N	g(1)	β_0	Intercept	27.634	0.309
		β_1	BLADES	1.078	0.021
		β_2	GP	1.523	0.021
			GSE	0.298	0.371
			GSW	1.212	0.371
		β_3	Sample 2	2.200	0.368
			Sample 3	0.266	0.369
		β_4	GP:Sample 2	0.548	0.521
			GSE:Sample 2	0.495	0.521
			GSW:Sample 2	0.282	0.524
			GP:Sample 3	2.344	0.527
			GSE:Sample 3	3.267	0.524
			GSW:Sample 3	3.576	0.521
S	g(3)	β_0	Intercept	5.386	0.867
		β_1	BLADES	0.296	0.075
		β_2	GP	0.500	0.883
			GSE	-1.704	0.857
			GSW	1.125	0.884
	g(2)	β_0	Intercept	5.584	0.957
		β_1	BLADES	0.246	0.080
		β_2	GP	0.350	0.882
			GSE	-1.754	0.852
			GSW	0.973	0.883
		β_3	Sample 2	-0.315	0.737
			Sample 3	0.963	0.766

Appendix G (continued).

Diversity Measures	Model		Parameter	Parameter Estimates	SE
d	g(9):	β_0	Intercept	1.579	0.119
		β3	Sample 2	-0.097	0.168
			Sample 3	0.688	0.168
	g(4):	β_0		1.437	0.156
		β_1	BLADES	0.024	0.017
		β_3	Sample 2	-0.078	0.168
			Sample 3	0.623	0.174
J'	g(2)	β_0	Intercept	0.777	0.057
		β1	BLADES	-0.009	0.005
		β_2	GP	-0.222	0.053
			GSE	0.114	0.051
			GSW	-0.078	0.053
		β_3	Sample 2	-0.005	0.044
			Sample 3	0.121	0.046
	g(6)	β_0	Intercept	0.705	0.045
		β_2	GP	-0.194	0.052
			GSE	0.124	0.052
			GSW	-0.050	0.052
		β_3	Sample 2	0.002	0.045
			Sample 3	0.096	0.045
H'	g(6)	β_0	Intercept	1.360	0.110
		β_2	GP	-0.389	0.127
			GSE	-0.015	0.127
			GSW	-0.127	0.127
		β_3	Sample 2	-0.013	0.110
			Sample 3	0.357	0.110

CHAPTER 4

Tracking diamondback terrapins (*Malaclemys terrapin*) using ultrasonic telemetry: range and habitat use in submerged aquatic vegetation beds in southern Chesapeake Bay

ABSTRACT

Descriptions of movement patterns and habitat use by diamondback terrapins (*Malaclemys terrapin*) were based on mark-recapture studies. Previous efforts primarily focused on movements of adult female terrapins. In a 2010 pilot study near the mouth of the York River, observed movements of seven terrapins, males and females, indicated distances traveled sufficient to move between non-connected eelgrass (*Zostera marina*) beds. In 2011 and 2012, ultrasonic telemetry confirmed movements of 16 male and female terrapins between non-connected eelgrass beds surrounding Goodwin Islands, York River. Tracking data indicated terrapin activity throughout both day and night, as well as during all tidal phases. Some traveled a single-direction distance of approximately 3.3 km, the minimal straight-line distance between the most distant telemetry receivers. A major implication of terrapin movement between non-connected eelgrass beds is the potential for dispersal of ingested eelgrass seeds beyond the bed of the parent plant. Dispersal of plants by turtles, particularly aquatic species, has not been extensively investigated. Given the ability of terrapins to traverse entire eelgrass beds, reasonable passage time of eelgrass seeds through the digestive track, and their home-range fidelity, terrapins may be an important dispersal vector for *Zostera* seeds within and between seagrass meadows.

INTRODUCTION

Investigations into animal migration has provided many insights that have uncovered use of different habitats for different purposes, i.e., reproduction, foraging, over-wintering area (Alerstam et al. 2003), as well as aiding understanding of the flow of genetic variation (Sheridan et al. 2010) and emigration due to habitat degradation (Wilcove and Wikelski 2008). Migrations occur within a defined region of specific dimensions and on different scales for different species, e.g., gray whale *Eschrichtius gibbosus* annual migration of 16,000 km between summer foraging grounds in Alaska and winter breeding grounds along the Baja, Mexico, peninsula (Pike 1962), caribou *Rangifer tarandus* migration from mainland to islands in northern Canada to avoid predation (Bergerud et al.1990), and Suwannee cooter *Pseudemys concinna suwanniensis* use of a 3.4 km stretch of the Santa Fe River, Florida (Kornilev et al. 2010).

For diamondback terrapins *Malaclemys terrapin*, movements are within a home range that includes foraging areas, reproductively important areas, and hibernacula, i.e., areas for brumation (Ernst and Lovich 2009). Terrapins exhibit strong fidelity within a home range, and often remain within a particular creek or marsh system (Roosenburg 1991; Tucker et al. 1995; Gibbons et al. 2001). In early spring shortly after emergence from brumation, adult male and adult female terrapins aggregate in large in-water mating groups (Seigel 1980; Ernst and Lovich

2009). When the mating period ends in May, males return to their home creeks and females move to nesting beaches up to several kilometers away (Roosenburg 1991; Estep 2005). Other than mating season, terrapins remain within a limited range (Gibbons et al. 2001; Estep 2005), though, like the Suwannee cooter, they could be considered a vagile species, actively swimming throughout their range (Kornilev et al. 2010).

Most of diamondback terrapin's active time is spent foraging (Montevecchi and Burger 1975; Davenport and Ward 1993). Its adaptation to a wide salinity range allows it to exploit highly productive coastal and estuarine ecosystems (Ernst and Lovich 2009). Because terrapins reside in estuaries and coastal bays, tides can influence their foraging habitat selection (Tucker et al. 1995; Ernst and Lovich 2009). Adult females are able to move higher into marsh creeks to feed during high tide (Ernst and Lovich 2009). Small terrapins can also be found in the flooded portion of a marsh amongst *Spartina* reeds during high tide (D. Tulipani, pers. obs.).

Research to determine movement patterns in animals employs various methods ranging from low-tech visual methods to more sophisticated technology including radio, satellite, and ultrasonic telemetry methods (Millspaugh et al. 2012). Several studies have successfully tracked diamondback terrapins using a variety of methods including fishing line and floats (Roosenburg et al. 1999), radio telemetry (Estep 2005), as well as ultrasonic telemetry (Estep 2005). Many tracking and mark-recapture studies of have followed adult female terrapins (Gibbons et al. 2001; Estep 2005; Butler 2002), though more recent research has included both genders (Harden et al. 2007; Sheridan et al. 2010). In Maryland, Roosenburg et al. (1999)

visually tracked terrapins of both genders and different sizes in creeks of the Patuxent River and determined movements were specific to both gender and size with little overlap between the groups. There was also a strong positive correlation between size and distance from shore with large adult females staying mainly in the deeper water (Roosenburg et al. 1999).

The study site for this project, the Goodwin Islands, is an archipelago of salt-marsh islands with adjacent subtidal *Zostera marina* (eelgrass) beds and is part of the Chesapeake Bay National Estuarine Research Reserve System in Virginia located at the mouth of the York River subestuary in Virginia (Reay and Moore 2009). It is more of an open-water environment than typical salt marsh creek and cove habitats of earlier studies. Given the nature of the area, we chose ultrasonic telemetry as the tracking method, which greatly increased "observation" time and spatially consistent coverage, as well as minimized human effects on terrapin behavior by reducing physical pursuit during tracking.

The purpose of this study was to determine the potential distance diamondback terrapins can travel and to determine what factors influence movement. We tracked 16 individual terrapins (10 males and 6 females) using ultrasonic telemetry in the vicinity of Goodwin Islands. This project was conducted in two phases, phase 1 in 2011 (5 terrapins) and phase 2 in 2012 (11 terrapins). We collected and analyzed detection data from a set of receivers located intermittently between the two regions to determine home range for individuals and estimates of longest distance traveled. A logistic regression model was developed to determine the probability of movement with respect to specific abiotic and biotic factors to further elucidate terrapin diamondback terrapin behavior within its home range.

MATERIALS AND METHODS

Pilot study 2010: Tracking diamondback terrapins in lower York River

A short-term pilot tracking study followed the movements of seven diamondback terrapins captured from the vicinity of the Goodwin Islands and Green Point. Three male and four female terrapins captured from these areas and weighing ≥ 300 g were chosen for the study (Table 1). Two terrapins were tracked on July 15, three on July 16, one on August 20, and one on September 1. Methods used were adapted from Roosenburg et al. (1999). Terrapin movements were followed by visual observation of a small, brightly painted, donut-shaped float. Floats were attached with 4 m of 9-kg test fishing line through a small pre-drilled hole in the third left rear marginal scute of each terrapin's carapace, which was chosen to reduce interference with swimming movements. Before and after drilling, the drill site was cleaned and disinfected twice alternating between 70% isopropyl alcohol antiseptic wipes then povidone-iodine wipes, similar to sea turtle iconel flipper tag attachment protocol (Balazs 1999). Immediately prior to a tracking session, one float was tied to the selected terrapin. One at a time, each terrapin was released at the site of its initial capture and tracked from a boat for up to 2 h while maintaining an approximate minimum distance of 50 m. Every 15 min, the terrapin's position was recorded using a Garmin GPS 76 handheld unit. At the end of its observation period, the terrapin was retrieved, the line and float removed, and the terrapin was released. Each recorded point for each terrapin was plotted in Google™ Earth and total distance (m) between the start and end point estimated with the built-in path measurement tool by connecting each point in chronological order.

Tracking with ultrasonic telemetry

Ultrasonic equipment

The model IBT-96-5 External transmitters and SUR models 2 and 3 receivers used in this study were purchased from Sonotronics, Inc., Phoenix, Arizona, USA. Each IBT-96-5E was uniquely coded with a combination of signal (ping) frequency (kHz), aural code for manual tracking, and ping interval time (Sonotronics, Inc.; Appendix A). This model had a 5-month battery life, in-water weight of 3.2 g, 36 mm length, and 13 mm diameter. This model was chosen for its reliability and small size, which was less than 2% of minimum terrapin body weight, to minimize effect on terrapin swimming. Transmitters were activated and tested for the programmed aural code with a hydrophone prior to attachment.

Each SUR operated with battery life of 7-12 months. SUR detection range of IBT tags when deployed in water less than 18 m deep was a 100-m radius (Sonotronics, Inc.). When activated, SURs scanned for up to 15 frequencies every 46 s based on the preset frequency map of deployed IBT tags. Receivers recorded SUR ID, date, time, IBT tag, tag frequency, and tag interval for each signal detected. SURs were initialized with the active IBT tag frequency map and the local date and time prior to deployment using the companion software SURsoft v6.8.12.

SUR detection range was tested in 2010 by deploying one SUR at four locations (two within seagrass beds and two in open water) within the study area.

An IBT was submerged 1 m below the water's surface for 1 min at 25 m intervals from the receiver from 0-200 m distance. Salinity, temperature, and turbidity were measured at each sample point with a multiparameter YSI sonde to verify possible effect on transmitter signal attenuation.

Phase 1: July - October 2011

Five diamondback terrapins, two captured from Goodwin Islands and three from Green Point were tracked during this phase (Table 1). Terrapins were selected based on the same weight criteria as the pilot study. One male captured at Green Point, GP-T033, was originally captured in 2009 from the same location. One uniquely coded transmitter (Appendix A) was attached to each terrapin's third left rear marginal scute to avoid interference with swimming and to insure transmitter remained submerged when the terrapin surfaced. Before and after drilling the attachment hole, the site was cleaned and disinfected (Balazs 1999). The transmitter was secured using a cable tie threaded through the hole and fastened tightly around the transmitter. To further prevent transmitter loss, marine epoxy was applied around the transmitter base and scute surface, and allowed to dry for 24 h (Estep 2005).

Five receivers were deployed on July 21 in approximately 1.5-2.0 m water depth and positioned greater than 200 m apart along Thorofare Channel-side of the Goodwin Islands. GI-1 deployed across from Green Point and GI-2 and GI-3 in different coves further east (Figure 1). GP-1 and GP-2 were positioned on either side of Green Point (Figure 1). Two additional receivers were deployed on September 22; GI- 4 was located near west end of Goodwin Islands along Thorofare Channel shoreline and GP-3 was located west of Green Point towards Back Creek, Seaford, Virginia (Table 1). The final receiver, GI-5, was deployed on September 30 along the York River shoreline at the east end of Goodwin Islands (Figure 1). All five tagged terrapins were released on July 21 after the first five receivers were deployed.

Tracking records were downloaded to a laptop on location approximately every 7 to 10 days through October 15 except for two weeks in August when the receivers were removed while two large storms moved through the area. Based on the list of activated IBT tags, records were identified and selected from the downloaded raw data files using Sonotronics, Inc. SonoDPC v6.8.11 SUR companion software with default interval tolerance = 2 ms. SonoDPC outputted text files with IBT-specific detections from each SUR. Records were aggregated by terrapin-IBT code and summarized using Microsoft™ Excel.

Phase II: May – September 2012

Phase II commenced in May 2012 with an additional 11 terrapins, seven from Goodwin Islands and four from Green Point, were tagged with new ultrasonic transmitters and released (Table 1). Eight receivers were redeployed on May 25 in the same locations as 2011. Tracking records were again downloaded on station approximately every 7 to10 days through September 6 when all receivers were retrieved.

Data management and statistical analysis

Additional descriptive fields merged with tracking records included terrapin gender and size class (e.g., 1 = small, 2 = large), tidal stage (e.g., flood, high, ebb, low), and day (d) or night (n). Terrapin size class was based on head width (HW) where small HW < 30 mm and large HW ≥ 30 mm (Chapter 2). Tidal stage durations were estimated from 2011 and 2012 tide charts such that each cycle was approximately 3 h in duration. A logic statement was developed using built-in functions in Microsoft™ Excel to evaluate the tidal stage and day-night for each tracking record of each terrapin and assign the correct value. The specific tidal stage was assigned to each tracking record using a logic statement evaluation of two fields, detection date and detection time, comparing both values to a tide cycle file. First, detection date was matched and then tide cycle was selected based on detection time range. Day-night codes were also assigned to tracking records based on detection date and time. If detection date matched and detection time was between sunrise and sunset, then "d" was assigned; if the detection time was between the times of that day's sunset and the following day's sunrise, then "n" was assigned. Additionally, for each tracking record of each terrapin, another logic statement was developed to populate movement field. SUR site and date of the current record was evaluated with the previous record. If both fields were the same, "0" (no move) was assigned. If either field, or both, were different "1" (move) was assigned.

Summary information included: number of detections each receiver, total possible detection days for each receiver, number of days each terrapin was detected, maximum distance traveled between two receivers and duration of travel, number of receivers each terrapin was detected by, maximum detections by a single terrapin at each receiver, and total terrapins detected by each receiver. The locations each terrapin frequented and its estimate home range were based on the frequency of IBT-specific detections at each receiver(s) and the frequency of detection overall. Differences in total detection counts by gender-tidal stage and gender-day-night were tested for goodness of fit with a X^2 test.

Terrapin Movement Predictive Model

A generalized linear mixed model was developed to predict terrapin movement patterns relative to biological (terrapin gender and size) and environmental factors (tidal stage, day-night). The generalized linear mixed effects model (GLMM) was fit to a binomial response variable indicating movement, move (1) vs. no move (0), between receiver detection areas to investigate how various factors affect the probability of terrapin movement between these locations. A generalized linear approach was chosen because the response variable contained a large number of zeros, thus these data were not normally distributed which violates one of the assumptions for general linear models (Kruger and Tian 2004). Tracking data for an individual organism are multiple measurements of location with respect to time for that individual. Such "repeated measures" required special consideration with respect to the inherent temporal autocorrelation in these data which was addressed by specifying the variance-covariance structure (Littell et al. 2006). Also, there were breaks in the tracking records (i.e., terrapins move out of receiver detection range and signal detection interval of receivers) such that the records were not continuous with respect to time, as well as the number of records for each sampling unit (i.e., terrapin) were vastly different resulting in an unbalanced structure to the data (Kruger and Tian 2004). Therefore, a repeated measures approach was incorporated with the GLMM to increase statistical power (Littell et al. 2006). The mixed effects model incorporated both fixed (i.e., terrapin gender, terrapin head width, receiver site, tidal stage, and day-night) and random effects due to random movements of individual terrapins and variance-covariance structure.

Following model development methods described in Henderson (2012), a generalized linear mixed effects model (GLMM) with a binomial response variable using the logit link function was constructed to interpret the tracking data (Bolker et al. 2009). The process comprised three parts (Henderson 2012). First, determine the preliminary variance-covariance structure using fixed effects without any interaction terms and the combined random effects of individual terrapins and variance-covariance structure. Next, develop a global model that included all possible main effects and any interactions between the main effects. The models tested were limited to the main effects to two-way interactions and three-way interactions (plus all two-way combinations of these factors); each interaction was included one at a time. The last step was testing various combinations of fixed effects, interactions terms, and random effects to find the model with best fit (Henderson 2012). Akaike Information Criterion with small sample correction (AIC_c) model comparison was used to select the variance-covariance structure, the global model, and the final mixed effects model to select the most parsimonious model. The best-fit model in each case had the lowest ΔAIC_c of the set considered (Anderson 2008).

SAS v9.3 for Windows® procedure GLIMMIX was used to run the analyses. Because a GLMM was employed, special options were required to use maximum likelihood to fit the parameters (Bolker et al. 2009). Specifically, Laplace's approximation to approximate likelihood enabled use of AICc (Bolker et al. 2009). Using Laplace's method also required using the containment method to estimate the denominator degrees of freedom as the default setting in SAS, the Kenward-Roger approximation, was not compatible (SAS 2013). The variance-covariance structures tested were: unstructured (un), compound symmetry (cs), variance components (vc), first-order autoregressive (ar-1), and first-order autoregressive-moving average (Littell et al. 2006; SAS 2013).

RESULTS

Tracking diamondback terrapins in the lower York River

Pilot study 2010

Seven diamondback terrapins, three males, two small females, and two large females, from Goodwin Islands and Green Point were visually tracked for up to 2 h each (Table 1). One male terrapin chosen for the study, GP-T086, was captured twice at Green Point in 2010. Total distance traveled varied among the terrapins with several moving nearly continuously the entire observation period, i.e., GP-T086, GP-T104, and GI-T100, while others swam to nearby marsh edge and hid, i.e., GI-T193 and GI-T194 (Table 2). Three terrapins moved away from near-shore shallow areas to deeper water of Thorofare Channel and each traveled greater than 1 km (Table 2). Upon release, GP-T086 started traveling towards the west around the tip of Green Point heading towards Back Creek (Figure 1 left of receiver GP-3). These results indicated that both male and female terrapins from Goodwin Island and Green Point had the potential to travel distances between each region, between non-connected SAV beds, as well as beyond the general area within a short period of time (Figure 1; Appendix B).

IBT-SUR Detection Range Test

IBT detection range varied slightly along each transect with the greatest detection distances recorded at two open water areas outside of seagrass beds. The signal was detected up to 200m away. The signal was only detected from 75-125 m away along the two transects that crossed through seagrass beds at Green Point (Figure 1). Salinity, temperature, and conductivity were consistent along all transects. Turbidity, however, was greater (ANOVA $\alpha = 0.5$, $p << 0.01$) along the Green Point transects than Goodwin Island. Turbidity is one factor that will attenuate transmitter signal (Sonotronics, Inc.). Based on these results, receivers were positioned greater than 200 m apart to avoid detection overlap and to cover the greatest area for the full study.

Tracking using ultrasonic telemetry

Diamondback terrapin movements were highly variable reflecting the active nature of this species. Number of detections was highly variable in 2011 (range = 17 to 14,188). The 2012 cohort was more consistently detected (range = 502 to 5,029) though still varied by individual. Most individuals in this study moved frequently within a preferred area yet made longer distance forays throughout the general region.

Phase 1: July – October 2011

SUR receivers were deployed for a total of 377 detection days (all days for all receivers) covering regions between Goodwin Islands and Green Point, as well as the eastern end, York River-side of Goodwin Island (Table 3; Figure 1). Receiver GI-3 went missing early August and GP-2 was lost during the last week of deployment in October. Deployment was interrupted for two weeks in late August due to Tropical Storm Lee and Hurricane Irene. Of all receivers deployed, GP-1 recorded the most signals followed by the other two receivers at GP (Figure 2). The two males from GP were detected most frequently by the all the GP receivers, which indicated that they resided in that area most often (Figure 3; Table 3).

Estimated single-direction distances between receivers ranged from approximately 400 m to 3,800 m, i.e., GP-1 to GP-3 and GP-3 to GI-5, respectively (Appendix B). The shortest distance between Goodwin Island and Green Point was approximately 500 m between the tip of Green Point and half-way between GI-1 and GI-4 (Figure 2; Appendix B). Terrapins traveled frequently between all the receivers, though males displayed a strong preference for specific areas (Table 3; Figure 3). All of the small terrapins, i.e., GP-T033, GP-T132, and GI-T136, traveled distances in excess of 1 km on a regular basis often being recorded by several different receivers within a single day.

All terrapins were detected by receivers at both Green Point and the Goodwin Islands, though none were detected by receiver GI-5 (Table 4). The males were detected more often by the same receivers than were females (Figure 2; Tables 3, 4). Female GP-T131 was detected only three days following its release by three different receivers, when it traveled from Green Point across Thorofare Channel to Goodwin Island then eastward toward receiver GI-3. Since this turtle was never detected at GP or any other receivers, it was likely that GP, possibly even Goodwin Island, was not its preferred area (Table 3). The other female, GI-T146, was only detected four days post-release by a GI-2 receiver (Table 2; Figure 3).

Males GP-T033 and GP-T132 were detected most often throughout phase 1 (Figure 3; Table 3). Both traveled around Green Point, as well as making trips across

Thorofare Channel to Goodwin Island (having been detected by GI-1 and GI-4) and back (Figure 3; Tables 3, 4). GP-T033 was initially captured in the vicinity of GP-2 in 2009 and again in June 2011. It was detected most often by receivers GP-1, GP-3, and GI-4 (Table 4B), though it spent most of its time near GP-1; it was never detected by GI-2, GI-3, or GI-5 receivers (Table 3). The longest recorded one-way distance that it traveled was between GP-3 and GI-4 (Table 4A; Appendix B). Male GI-T136 was initially captured in late June in the same cove where GI-2 was deployed (Figure 1; Table 3). It was detected by seven different receivers during the tracking period and by GI-2 receiver approximately 43% of the receiver's deployment days (Table 3). In October, GI-T136 traveled to the western end of Goodwin Island and Green Point remaining in the area for four days before returning to GI-2's detection area. Minimum distance traveled was approximately 3.4 km.

Phase 2: May – September 2012

Terrapins tracked in phase 2 showed similar patterns to movements as the ones in phase 1, such as preferred area as defined by detection pattern, though number of detections was much lower than 2011 (Table 2; Figure 2). All terrapins were recorded on receivers at both Green Point and Goodwin Islands with many moving regularly between both regions (Table 4). During this phase, terrapins were recorded near the GI-5 receiver (Table 3). Male GI-T018 was originally captured in 2009 near GI-5's location and was recaptured in the same area on June 20, 2012. This terrapin was also detected by receiver GP-1. An estimated single direction distance between GI-5 and GP-1 was 3,300 m. Over the course of 10 d, it had traveled from GI-5 to GI-1 to GP-1 then to GI-3, which totaled approximately 4.8 km. Female GI-T198, captured in the vicinity of GI-5, was recorded by receiver GP-3, traveling at minimum 3.8 km in one direction. It was regularly recorded at GI-1 and GI-2 receivers. Due to equipment loss or damage, coverage was intermittent at several locations, i.e., GI-3, GP-3, GP-4, and GP-2. This resulted in reduced tracking records, yet site fidelity by individual terrapins was still apparent.

Total detections for male and female terrapins were compared by tide cycle and day-night (Figure 4). Detections for females were significantly different by tide cycle (X^2 df = 1, $p << 0.01$) showing preference to near-shore areas on flood and high tides then decreasing with falling tides (Figure 4). Detections by tide cycle for male terrapins were not significantly different (X^2 df = 1, $p = 0.4595$); total detections for each tide cycle category were nearly evenly split (Figure 4). Total detections for both males and females were significantly different by day-night (X^2 df = 1, $p << 0.01$; Figure 4). Both genders were detected more often during the daytime (Figure 4).

Terrapin Movement Predictive Model

Variability in detection totals for the individuals tracked indicated randomness of movements by diamondback terrapins. When tested, the basic models (no interactions) tested with variance components (vc) structure resulted in the lowest AICc, though first-order autoregressive (lag = 1) structure was nearly equivalent (Appendix C). Determination of the global model revealed that the 3-way interaction of gender-head width-site was the best choice (AICc: 25525.77;

Appendix D). Five models that had the lowest AICc values all included site as a factor; gender and head width were factors in three each; day-night was in two and tide only appeared once. The model set tested included various combinations of main effects with the selected 3-way interaction and all combinations of the component 2-way interactions (Appendix E). Surprisingly, all the models with the 3-way interaction had no solution as the estimated G-sided matrices were not positive definite (Appendix E; SAS 2013). The best-fit model, model F13, included all variables plus all three 2-way combinations of gender, head with, and tide (Table 5; Appendix E). Model F18 with only one interaction between head width and day-night was also a plausible fit (AICc = 3.63). The representative equation for model F13 is:

$$logit\ \ y_{ig\hbar std} = \mu + \lambda_i + \gamma_i + \varsigma_s + \varphi_t + \pi_d + \lambda\gamma_{\ i} + \gamma\varsigma_{\ id} + \lambda\varsigma_{\ is} + \rho_i + \epsilon_{ig\hbar std}$$

where logit is the link function, y_{ighstd} is the binomial response for each terrapin (i) of gender (g), head width (h), receiver site (s), tide cycle (t), μ is the overall mean, λ is head width of terrapin (i), γ is gender of terrapin (i), φ is tide cycle (t = ebb, low, flood, high), ς is site (s = GI-1, GI-2, GI-3, GI-4, GI-5, GP-1, GP-2, GP-3), π is day-night (d or n), λγ is the interaction between terrapin head width and gender, γς is the interaction between gender and site, λς is the interaction between head width and site, ρ is the random effect for each terrapin (i), and ε is the random unexplained error. Model F13 indicated that site and gender decreased probability of a terrapin moving, i.e., move = 1 (Table 6). Variables representing tide and day-night conditions also had a negative effect on movement probability but not as strong.

Male terrapins stayed in the shallow regions nearest the receivers at all tide cycles (Figure 4). Of the interaction terms, gender x site had the strongest effect. These results support previous descriptions of terrapin habitat use (Roosenburg et al. 1999.)

DISCUSSION

Male diamondback terrapins have clearly defined home ranges (Table 3), yet will travel beyond their preferred area on occasion (Table 4; Figure 3). During mating season, terrapins travel to mating aggregation areas that often involve movement to areas outside their home range (Seigel 1980). Phase 1 of this study occurred from July through October 2011, which was well after terrapin mating season in Virginia (Ernst and Lovich 2009). Long distance travel occurred during this time, therefore the purpose of the long distance trips were not mating-related. Movements by an Amazon tortoise *Geochelone denticulata* included random long distance trips ranging 2.5–3.0 km, though the authors had no explanation for the purpose with respect to the tortoise itself (Guzmán and Stevenson 2008). Davenport and Ward (1993) described diamondback terrapins as voracious eaters. It is possible that the long distance travel by some smaller terrapins was related to searching for food. An increase in terrapin activity in late summer-early fall occurred in South Carolina and was attributed to an increase in foraging prior to brumation (Gibbons et al. 2001).

Signal detections for mature female terrapins were notoriously low during both phases of this study except for terrapin GP-T191 (Table 3). It had the second highest number of days detected of any tracked in 2012. Its preferred location was west of the point at GP and regularly moved to the eelgrass bed near GP-2 as well as the vicinity of GP-3, though it was detected by GI-3 on five separate days (Table 5). Based on the number of terrapins captured along Green Point, there was a fairly substantial, male-dominated group that frequented the area, whereas few mature females were captured there over three years (Chapter 2). Based on GP-T191's detection pattern, large females frequented GP as well. Low detections overall for mature females were likely due to their preference for deeper water except at flood or high tides (Figure 4). Though the receivers were typically deployed in water at 2-m depth at all times (unless an extreme low tide occurred), it may not have been suitable area for large females such that receiver locations may not have been in preferred foraging areas for them. Most receivers were located within or near the edge of eelgrass beds, which were preferred foraging areas for males and juvenile females (Chapter 2).

Estep (2005) described distinct habitat use and site fidelity for female terrapins tracked in South Carolina attributing movements and time spent in various locales to its use by the terrapin. In Virginia, nesting activity typically stops by the end of July (Ernst and Lovich 2009). Whereas Phase 1 commenced post-mating and near the end of nesting season, Phase 2 included the end of mating season and the entirety of nesting activity periods (Table 1). Four of the females tracked in this study were reproductively mature based on their size (Table 1). Low detections of mature females may also result from females migrating to their preferred nesting areas, which were outside the areas of detection (Figure 1). Only one receiver, GI-5, was located on the York River side of Goodwin Islands where sandy beaches are located that terrapins nest on (Rook 2009). Due to late delivery of equipment in Phase 1 and damage to the receiver in Phase 2, receiver coverage in this area started late each year whereby detections were underrepresented.

The combined estimated distances traveled and the detection locations for terrapins during each phase, indicated regular movement between Goodwin Islands and Green Point (Table 4). One-way direction travel distances were similar to ranges determined for male diamondback terrapins in other regions, i.e., 0.3–1.1 km (Harden et al. 2007) and 0.8–1.4 km (Sheridan et al. 2010). The most common one-way direction distance for mature females was 2.2 km (Table 4; Appendix B), which is much shorter than maximum distance of 8.5 km in New Jersey (Sheridan et al. 2010) and 12.5 km in North Carolina (Spivey 1998). Terrapins traveled much farther compared to the much smaller-sized musk turtle *Sternotherus odoratus* which averaged about 23 m per day, sometimes not moving at all (Wilhelm and Plummer 2012). Aquatic movements of the western pond turtle *Emys marmorata* varied greatly from 0.25 km to 5.0 km over many weeks with the greatest daily distance of 629 m by one female (Buskirk 2002). The type of aquatic habitat (e.g., stream, natural pond, man-made reservoirs) influenced frequency and distances traveled by *E. marmorata* (Buskirk 2002). Telemetry studies also revealed high frequency of terrestrial travel by *E. marmorata* not associated with oviposition and of distances up to 5.0 km (Buskirk 2002).

A few tortoises traveled distances similar to that of diamondback terrapins. The Galápagos tortoises *Chelonoidis nigra* moved an average of 394 m with a maximum distance traveled of 4.4 km (Blake et al. 2012) whereas the Amazonian tortoise *Geochelone denticulata* travel only 0.2–0.4 km over 3-17 d during the rainy season and about half that during the dry season (Jerozolimski et al. 2009). In a different study, typical distances for *G. denticulata* were less than 150 m (Guzmán and Stevenson 2008). Distances traveled in terrestrial and aquatic habitats may not be completely comparable as terrestrial landscapes often consist of dense vegetation, large rocks and other obstacles that would increase effort by the tortoise and restrict its movements.

All male and juvenile female terrapins frequented shallow, near-shore areas of the creeks (Roosenburg et al. 1999). There was some overlap of habitat use when adult females moved into the creeks to reach potential nesting locations (Roosenburg et al. 1999). The logistic regression of terrapin movement data supported the preference of male terrapins for shallow water areas (Figure 4), as well as indicating females visiting the same area at flood and high tides. The probability of not moving between sites was best predicted by terrapin gender and size with individuals showing preference for certain locations (Appendix E).

Zostera marina (eelgrass) beds lie adjacent to the Goodwin Islands and one side of Green Point. Terrapins frequent these areas to feed (Chapter 2). Terrapins ingested viable eelgrass seeds incidentally while feeding on epifauna during May and early June in this region (Chapter 2). Under normal dispersal conditions, the great majority of eelgrass seeds remain within the bed of the parent plant (Orth et al. 2003). Given the frequent trips (on the order of hours to days) between Goodwin Islands and Green Point, as well as the estimated one-way distances they can travel in that time (multiple kilometers at minimum), terrapins could disperse eelgrass seeds from one bed to a completely disconnected eelgrass bed (Figure 1; Appendix B). Moving seeds beyond the parent plant is beneficial to a plant's survival (Chambers and MacMahon 1994).

Habitat use by diamondback terrapins of the Goodwin Islands-Green Point region encompassed the entire area around Goodwin Islands and across Thorofare Channel to Green Point and likely west towards Back Creek (Figure 1). Patterns in signal detections indicated these individuals had preferred areas they visited regularly. The model results indicated that movement (no movement) was attributable to gender and size of the individual with males and small females more likely to stay at a specific site. Movements of large females within detection locations were related to tidal stage (flood and high), which had previously been described (Tucker et al. 1995; Spivey 1998). Further tracking of mature females from Goodwin Islands region would be beneficial in determining more accurately the extent of their travel within this region. Additionally, the distances these terrapins traveled have implications for eelgrass seed dispersal and eelgrass bed perpetuation as they regularly moved between unconnected beds. Their role as seed dispersers for eelgrass is an important ecosystem function that potentially benefits the health of Chesapeake Bay.

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Table 1: Diamondback terrapins used in the 2010 tracking pilot study (P) and the 2011 ultrasonic telemetry study (U) July 21 – October 13, 2011 and May 25 – September 6, 2012. Table lists capture site (GP – Green Point, GI – Goodwin Island), unique turtle identification number (TID) assigned at capture, gender-size class (male or female, large or small), straight carapace length (CL), mass, and date tracked for each terrapin.

Year	Study	Capture Site	TID	Gender-Size Class	CL (cm)	Mass (g)	HW (mm)	Date Tracked
2010	P	GP	T086	m-s	13.9	395	23.7	9/1
			T102	m-s	12.9	321	21.5	7/15
			T104	f-L	20.3	1274	36.6	8/20
			T192	m-s	13.7	345	21.3	7/16
	P	GI	T100	f-L	20.3	1518	39.0	7/15
			T193	f-s	15.0	517	24.5	7/16
			T194	f-s	15.7	552	26.1	7/16
2011	U	GP	T033	m-s	13.0	313	22.2	7/21 – 10/13
			T131	f-L	19.4	1141	34.9	7/21 – 10/13
			T132	m-s	13.3	349	23.0	7/21 – 10/13
	U	GI	T136	m-s	15.2	467	23.2	7/21 – 10/13
			T146	f-s	14.1	434	25.8	7/21 – 10/13
2012	U	GP	T086	m-s	13.8	424	24.3	5/25 – 9/6
			T187	m-s	13.2	339	22.1	5/25 – 9/6
			T191	f-L	21.2	1552	41.2	5/25 – 9/6
			T246	f-s	13.6	416	26.4	5/25 – 9/6
	U	GI	T018	m-s	14.8	400	23.1	6/18 – 9/6
			T151	m-s	14.9	426	23.0	5/25 – 9/6
			T152	m-s	14.3	426	23.0	5/25 – 9/6
			T154	m-s	14.4	439	20.0	5/25 – 9/6
			T172	m-s	13.8	408	22.0	5/25 – 9/6
			T197	f-L	20.3	1255	35.6	7/11 – 9/6
			T198	f-L	21.0	1501	39.9	7/11 – 9/6

Table 2. 2010 Pilot tracking study of seven diamondback terrapins with turtle identification number (TID), capture site (GP - Green Point, GI - Goodwin Island), gender-size class (male or female, large or small), capture/release site, date and duration observed.

Capture/Release Site	TID	Gender-Size Class	Date Tracked	Observation Period (h:mm)	Estimated Distance Traveled (m)
GP	T086	m-s	9/1/2010	2:00	1,415
	T102	m-s	7/15/2010	1:12	388
	T104	f-L	8/20/2010	2:10	2,126
	T192	m-s	7/16/2010	1:15	587
GI Southeast	T100	f-L	7/15/2010	1:48	1,403
	T193	f-s	7/16/2010	0:51	381
	T194	f-s	7/16/2010	1:15	121

Table 3. Number of days detected by receiver for 16 diamondback terrapins tracked in 2011 and 2012. Turtle Identification Number (TID), Gender-Size Class, and SUR ID; Total Receiver-Days Detected (A) is the number of days a terrapin was detected by each receiver; terrapins were frequently detected at multiple receivers on a given day. Total Possible Receiver Days (B) is the sum of total deployment days for each receiver a terrapin was detected by. Percent Detected (C) is the result of dividing the previous two columns (A/B).

TID (Gender-Size Class)	SUR										
	GP 1	GP 2	GP 3	GI 1	GI 4	GI 2	GI 3	GI 5	A	B	C
2011											
GPT033 (m-s)	70	28	22	25	19	0	0	0	164	267	61%
GPT131 (f-L)	0	1	0	1	0	0	5	0	7	168	4%
GPT132 (m-s)	21	40	3	19	5	0	0	0	88	267	33%
GIT136 (m-s)	3	2	3	2	3	33	1	0	47	366	13%
GIT146 (f-s)	0	0	0	0	0	4	0	0	4	77	5%
Total Terrapin Detection Days	94	71	28	47	27	37	6	0	310		
2011 Days SUR Deployed	77	69	22	77	22	77	22	11	377		
2012											
GIT018 (m-s)	0	1	0	4	0	2	0	9	16	251	6%
GIT151 (m-s)	1	1	0	1	0	1	0	16	20	357	6%
GIT152 (m-s)	7	0	6	0	3	3	0	3	22	334	7%
GIT154 (m-s)	6	6	0	3	1	4	0	0	20	446	4%
GIT172 (m-s)	10	1	4	3	3	3	5	0	29	548	5%
GIT197 (f-L)	1	0	0	0	35	1	0	0	37	276	13%
GIT198 (f-L)	0	0	1	25	34	0	0	0	60	253	24%
GPT086 (m-s)	65	28	23	8	1	0	7	0	132	484	27%
GPT187 (m-s)	45	31	14	4	1	0	3	0	98	484	20%
GPT191 (f-L)	74	22	20	6	0	1	5	0	128	442	29%
GPT246 (f-s)	29	1	18	6	4	2	8	2	70	565	12%
Total Terrapin Detection Days	238	91	86	60	82	17	28	30	632		
2012 Days SUR Deployed	106	64	41	106	106	64	61	17	354		

Table 4. A) Estimated distance (m) of farthest travel between two (or three) Goodwin Islands (GI) and Green Point (GP) and receivers detected for each diamondback terrapin tracked in 2011 and 2012. B) Total number of diamondback terrapins detected by each receiver and maximum detections by each receiver each year.

A.

Year	TID	Gender-Size Class	SURs Farthest apart	Est. Distance	Travel time	#SURS Detected
2011	GPT033	m-s	GP-3 to GI-4	880	1 day	5
	GPT131	f-L	GP-2 to GI-3	770	2 day	3
	GPT132	m-s	GP-3 to GI-1	1,330	1 day	5
	GIT136	m-s	GI-2 to GI-4	1,680	3 days	7
	GIT146	f-s	GI-2	-	-	1
2012	GPT086	m-s	GI-1 to GI-4 to GP-3	1,760	1 day	6
	GPT187	m-s	GI-2 to GP-2	1,360	1 day	6
	GPT191	f-L	GI-3 to GP-1	2,200	1 day	6
	GPT246	f-s	GI-3 to GP-1	2,200	2 days	8
	GIT018	m-s	GI-5 to GP-2	2,600	6 days	4
	GIT151	m-s	G1-1 to GI-5	2,500	1 day	5
	GIT152	m-s	GI-5 to GP-3	2,500	3 days	5
	GIT154	m-s	GI-2 to GP-1	1,700	18 h	5
	GIT172	m-s	GP-1 to GI-3	2,200	2 days	7
	GIT197	f-L	GI-3 to GP-1	2,200	3 days	3
	GIT198	f-L	GI-2 to GP-3	2,200	1 day	3

B.

		2011			2012	
		Maximum Detections			Maximum Detections	
SUR	Terrapins Detected	Total	Terrapin	Terrapins Detected	Total	Terrapin
GI-1	4	85	GPT033	9	1011	GIT198
GI-2	2	985	GIT136	8	1155	GIT197
GI-3	2	15	GPT131	8	9	GIT154
GI-4	3	476	GPT033	5	34	GIT172
GI-5	0	0	-	4	2558	GIT151
GP-1	3	8585	GPT033	10	3731	GPT191
GP-2	4	3762	GPT132	6	1624	GPT187
GP-3	3	1665	GPT033	8	406	GPT086

Table 5. Selection of models tested for the repeated measures generalized linear mixed effects model with combinations of main fixed effects, 2-way interactions, 3-way interactions (plus 2-way combinations), and random effects due to individual movements and variance components variance-covariance structure for which best predicted move (1) or no move (0) for diamondback terrapins tracked with ultrasonic telemetry. Tracking records included two years of detection data for 16 male and female terrapins (2011 – 5; 2012 – 11). Main Effects: gender (G), head width (HW), site (S), tide cycle (T), day-night (D-N)

	Main Effects					2-way Interactions			3-way Interaction		
Model	G	HW	S	T	D-N	G*HW	G*S	HW*S	G*HW*S	AICc	ΔAICc
F13	X	X	X	X	X	X	X	X		25179.00	0
F18	X	X	X	X	X		X			25182.63	3.63
F16	X	X	X	X	X		X	X		25185.00	6.00
F14	X	X	X	X	X	X	X			25186.58	7.58
F19	X	X	X	X	X			X		25188.14	9.14

Table 6. Parameter estimates for top ranked model (lowest AICc; Table 5) of the generalized linear mixed effects model to predict probability of movement by diamondback terrapins. Estimates: different tide cycles are relative to low, day-night are relative to night, gender are relative to male, site are relative to GP-3; estimates for interactions hw*gender are relative to male, gender*site relative to male sites, hw*site relative to GP-3. Table is continued on next page.

Effect	gender	Site	tide	day_nite	Estimate	SE	DF
Intercept					-1.5516	3.3256	12
tide			ebb		0.04518	0.03517	45953
tide			flood		0.1019	0.1073	45953
tide			high		0.2253	0.1174	45953
tide			low		0	.	.
day_nite				d	0.4757	0.1523	45953
day_nite				n	0	.	.
gender	f				0.7279	4.7982	45953
gender	m				0	.	.
hw					0.03032	0.3125	45953
Site		GI-1			4.9123	5.8926	45953
Site		GI-2			-6.2219	4.1748	45953
Site		GI-3			2.5887	3.5373	45953
Site		GI-4			-1.842	0.9964	45953
Site		GI-5			101.64	155.66	45953
Site		GP-1			-1.673	0.5711	45953
Site		GP-2			1.7225	1.7294	45953
Site		GP-3			0	.	.
hw*gender	f				-0.02289	0.246	45953
hw*gender	m				0	.	.

Table 6. continued

Effect	gender	Site	tide	day_nite	Estimate	SE	DF
gender*Site	f	GI-1			0.4925	1.6088	45953
gender*Site	f	GI-2			-1.3194	3.874	45953
gender*Site	f	GI-3			-0.7883	1.6844	45953
gender*Site	f	GI-4			-1.8767	0.4546	45953
gender*Site	f	GI-5			14.7466	22.456	45953
gender*Site	f	GP-1			-0.6482	0.345	45953
gender*Site	f	GP-2			2.4138	1.3344	45953
gender*Site	f	GP-3			0	.	.
gender*Site	m	GI-1			0	.	.
gender*Site	m	GI-2			0	.	.
gender*Site	m	GI-3			0	.	.
gender*Site	m	GI-4			0	.	.
gender*Site	m	GI-5			0	.	.
gender*Site	m	GP-1			0	.	.
gender*Site	m	GP-2			0	.	.
gender*Site	m	GP-3			0	.	.
hw*Site		GI-1			-0.2096	0.4298	45953
hw*Site		GI-2			0.1437	0.3627	45953
hw*Site		GI-3			-0.07416	0.3826	45953
hw*Site		GI-4			0.1117	0.3445	45953
hw*Site		GI-5			-4.6054	6.7261	45953
hw*Site		GP-1			-0.02197	0.4242	45953
hw*Site		GP-2			-0.2002	0.4117	45953
hw*Site		GP-3			0	.	.

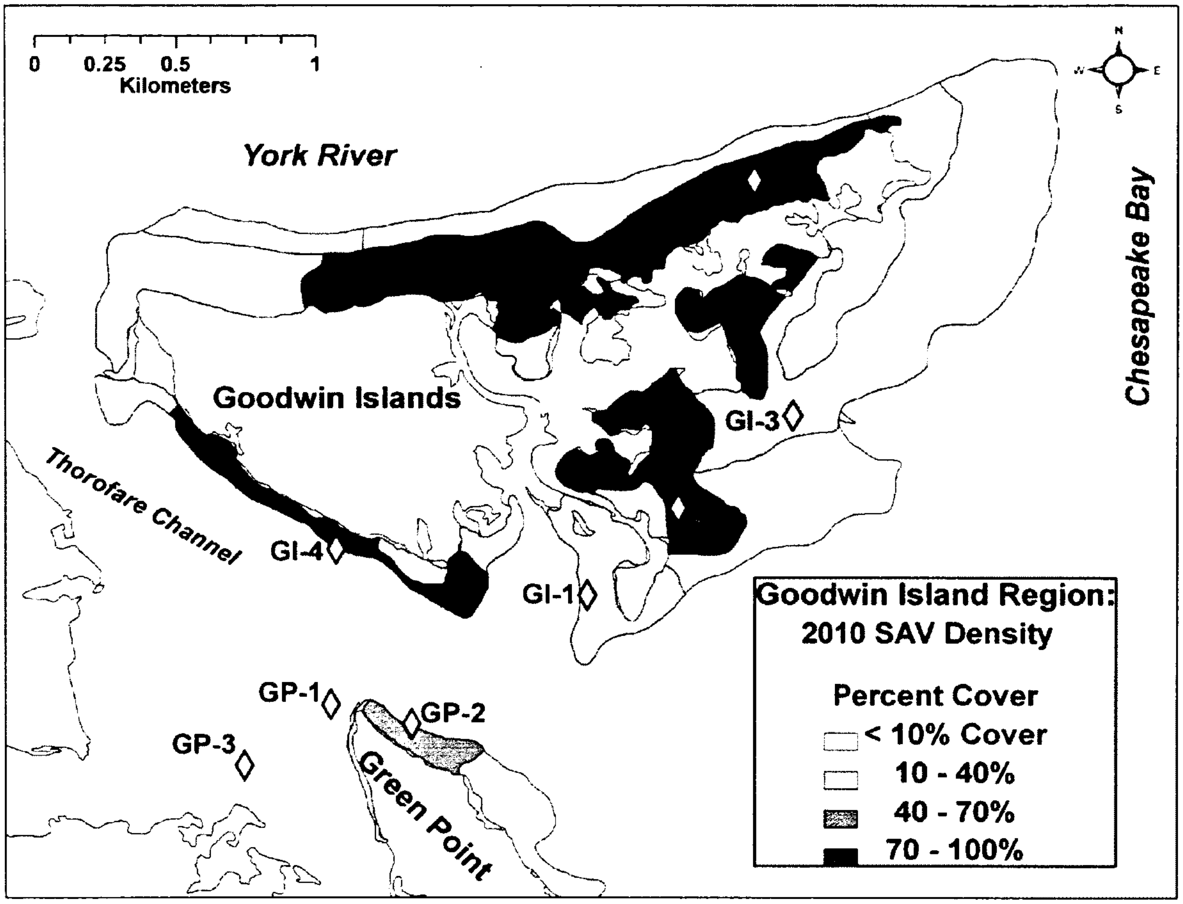

Figure 1. Site map of ultrasonic receiver placement at Goodwin Islands and Green Point for 2011 tracking study. Receivers placed in SAV beds with at least 40% estimated cover. Appendix A lists distances between receivers.

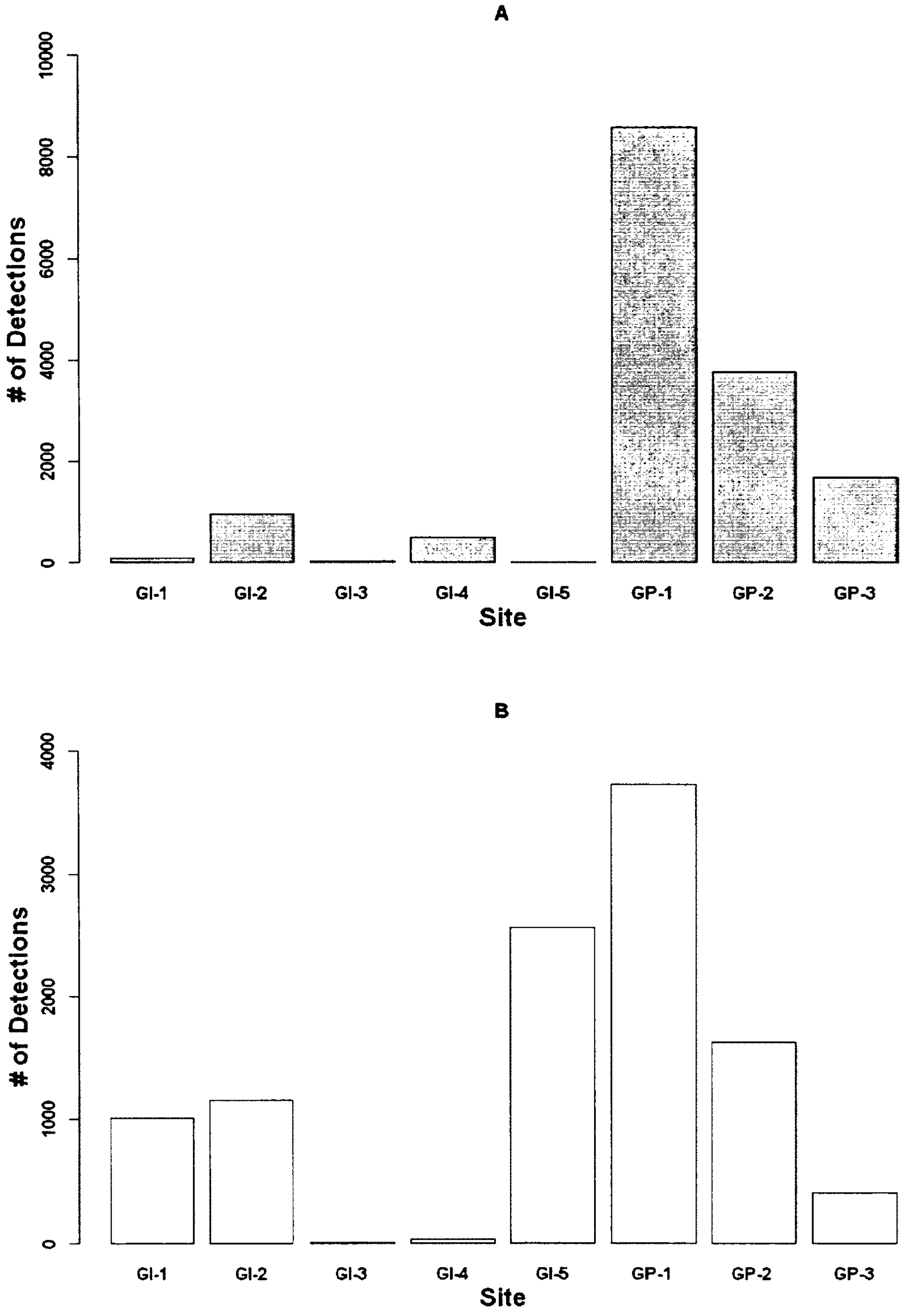

Figure 2. Total number of detections for each receiver during 2011 Phase 1 (A) and 2012 Phase 2. (B). Refer to Table 4 for number of diamondback terrapins detected by each receiver each year.

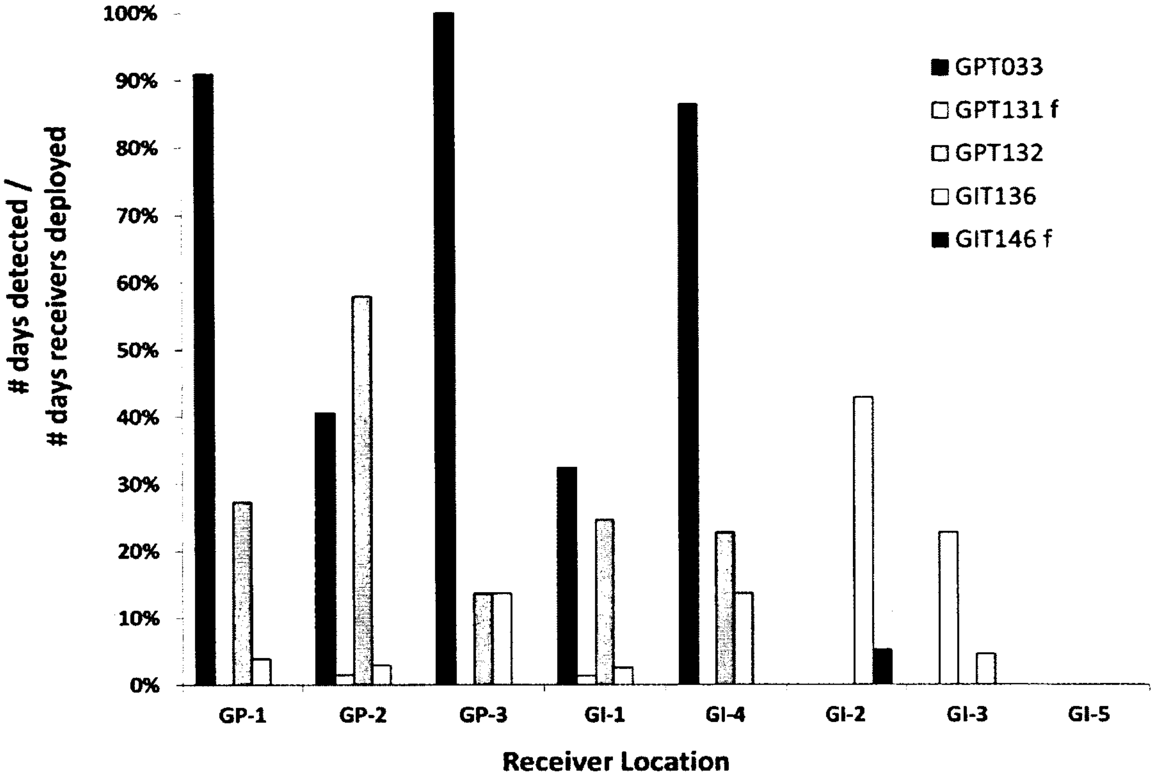

Figure 3. Percent days detected by total receiver days for each terrapin tracked in Phase 1 2011.

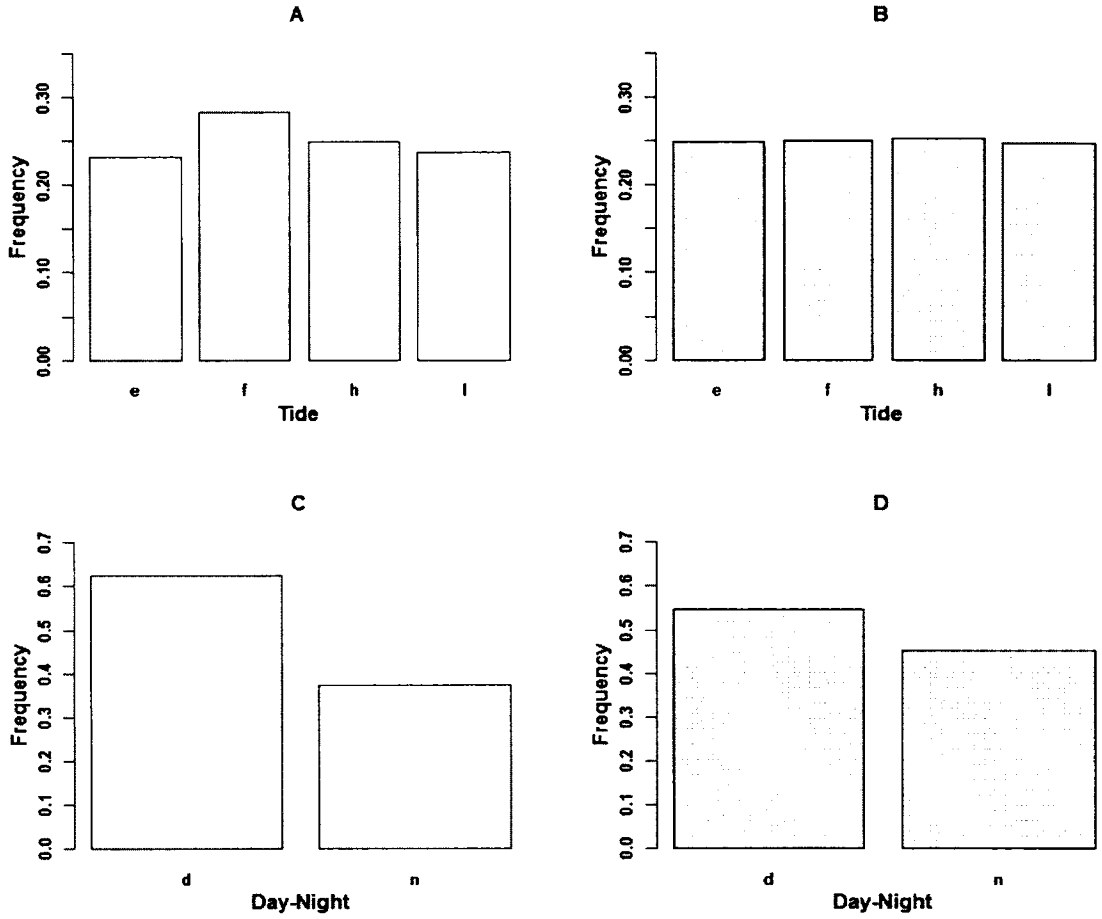

Figure 4. Percent frequency of detections of diamondback terrapins by time of day (i.e., d – day, n - night) and by tide cycle, (i.e., e - ebb, f - flood, h - high, l - low), for females only (A and C) and males only (B and D). Frequency is the number of detections by category divided by total detections for each gender separately.

Appendix A: Ultrasonic transmitter assignment to diamondback terrapins used in the ultrasonic telemetry study Phase 1: July 21 – October 13, 2011 and Phase 2: May 25 – September 6, 2012 with capture site Green Point (GP), Goodwin Island (GI), unique turtle identification number (TID) assigned at capture, and gender-size class (male or female, large or small), and Sonotronics-assigned transmitter frequency, interval and aural code for unique identification.

Year	Capture Site	TID	Gender: Size Class	Frequency (kHz)	Interval (ms)	Aural Code
2011	GP	T033	ms	73.0	910	4-4-7
		T131	fL	74.0	900	4-4-8
		T132	ms	71.0	890	3-6-5
	GI	T136	ms	70.0	860	3-3-4
		T146	fs	72.0	880	3-6-6
2012	GP	T086	ms	75.0	930	4-8-8
		T187	ms	79.0	970	3-3-5-4
		T191	fL	81.0	990	3-3-8-6
		T246	fs	77.0	950	6-7-7
	GI	T018	ms	83.0	1010	3-4-5-8
		T151	ms	80.0	960	3-3-5-5
		T152	ms	76.0	920	5-5-5
		T154	ms	78.0	940	6-7-8
		T172	ms	82.0	980	3-3-8-7
		T197	fL	71.0	1050	3-5-4-6
		T198	fL	72.0	1060	3-5-7-8

Appendix B. Estimated distances between locations of ultrasonic receivers deployed phase 1 2011 and phase 2 2012.

SUR	**GP-1**	**GP-2**	**GP-3**	**GI-1**	**GI-2**	**GI-3**	**GI-4**	**GI-5**
GP-1	-	440	400	930	1,700	2,200	700	3,300
GP-2	440	-	840	770	1,360	1,500	665	2,600
GP-3	400	840	-	1,330	2,200	2,700	880	3,800
GI-1	930	770	1,330	-	900	1,400	880	2,500
GI-2	1,700	1,360	2,200	900	-	500	1,680	1,600
GI-3	2,200	1,500	2,700	1,400	500	-	2,180	1,100
GI-4	700	665	880	880	1,680	2,180	-	3,300
GI-5	3,300	2,600	2,500	2,500	1,600	1,100	3,300	-

Appendix C. Random effects model selection for generalized linear mixed effect model fitting the binomial response variable, move (1) or no move (0), for diamondback terrapins tracked in 2011 and 2012 in the Goodwin Island-Green Point region. Variance-covariance structures tested included: unstructured (un), compound symmetry (cs), variance components (vc), first-order autoregressive (ar(1)), and first-order autoregressive-moving average (arma (1,1)). Model with lowest ΔAIC_c in bold.

Model	Random Terrapin effect	Variance-Covariance Structure	AICc	ΔAICc
1	**x**	**VC**	**25368.99**	**0**
3	x	AR(1)	25370.89	1.9
2	x	CS	25372.00	3.01
4	x	ARMA(1,1)	25372.89	3.9
5	x	UN	25613.91	244.92

Appendix D: Global model selection for generalized linear mixed effect model fitting the binomial response variable, move (1) or no move (0), for diamondback terrapins tracked in 2011 and 2012 in the Goodwin Island-Green Point region. Parameters included all main fixed effects, i.e., gender, head width (HW), site, day-night, tide, with 2-way interactions and 3-way interactions plus 2-way component combinations (only 3-way interaction listed). Model 1 includes main effects only; negative ΔAIC_c indicates better fit than model 1. Top five with lowest ΔAIC_c, (*) model with smallest ΔAIC_c.

Model	Interaction	AICc	ΔAICc
1	none	25924.71	0.00
2	gender*hw	25923.22	-1.49
3	tide*day_nite	25916.25	-8.46
4	gender*tide	25927.24	2.53
5	gender*day_nite	25843.36	-81.35
6	hw*tide	25925.68	0.97
7	hw*day_nite	25899.59	-25.12
8	gender*site	25685.83	-238.88
9	hw*site	25643.53	-281.18
10	tide*site	25854.25	-70.46
11	day_nite*site	25880.61	-44.10
12	gender*tide*day_nite	25836.60	-88.11
13	hw*tide*day_nite	25890.05	-34.66
14	gender*hw*tide	25905.09	-19.62
15	gender*hw*day_nite	25794.01	-130.70
16	**gender*hw*site**	**25525.77**	**-398.94***
17	tide*day_nite*site	25778.83	-145.88
18	**hw*tide*site**	**25564.05**	**-360.66**
19	**hw*day_nite*site**	**25576.41**	**-348.30**
20	**gender*site*tide**	**25605.02**	**-319.69**
21	**gender*day_nite*site**	**25571.81**	**-352.90**

Appendix E. Selection of models tested with combinations of main fixed effects, 2-way interactions, 3-way interactions (plus 2-way combinations), and random effects due to individual movements and variance components variance-covariance structure for which best predicted move (1) or no move (0) for diamondback terrapins tracked with ultrasonic telemetry. Tracking records included two years of detection data for 16 male and female terrapins (2011 – 5; 2012 – 11). Main Effects: gender (G), head width (HW), site (S), tide cycle (T), day-night (D-N)

	Main Effects					2-way Interactions			3-way Interaction		
Model	G	HW	S	T	D-N	G* HW	G*S	HW *S	G *HW*S	AICc	ΔAICc
F13	X	X	X	X	X	X	X	X		25179.00	0
F18	X	X	X	X	X		X			25182.63	3.63
F16	X	X	X	X	X		X	X		25185.00	6.00
F14	X	X	X	X	X	X	X			25186.58	7.58
F19	X	X	X	X	X			X		25188.14	9.14
F15	X	X	X	X	X	X		X		25190.00	11.00
F27	X	X	X		X	X	X	X		25198.61	19.61
F32	X	X	X		X		X			25204.33	25.33
F30	X	X	X		X		X	X		25205.05	26.05
F28	X	X	X		X	X	X			25207.86	28.86
F33	X	X	X		X			X		25209.16	30.16
F29	X	X	X		X	X		X		25211.03	32.03
F20	X	X	X	X		X	X	X		25353.93	174.93
F26	X	X	X	X				X		25361.91	182.91
F25	X	X	X	X			X			25363.13	184.13
F22	X	X	X	X		X		X		25363.79	184.79
F21	X	X	X	X		X	X			25366.83	187.83
F1	X	X	X	X	X					25368.99	189.99
F23	X	X	X	X			X	X		25369.01	190.01
F17	X	X	X	X	X	X				25371.96	192.96
F6	X	X	X			X	X	X		25379.90	200.9
F9	X	X	X				X	X		25381.68	202.68
F12	X	X	X					X		25389.54	210.54
F36	X	X	X		X					25391.35	212.35
F8	X	X	X			X		X		25391.41	212.41

Appendix E. continued

	Main Effects					2-way Interactions			3-way Interaction		
	G	HW	S	T	D-N	G*HW	G*S	HW*S	G *HW*S	AICc	ΔAICc
F11	X	X	X				X			25391.76	212.76
F31	X	X	X		X	X				25394.44	215.44
F7	X	X	X			X	X			25395.47	216.47
F35	X	X	X	X						25547.45	368.45
F24	X	X	X	X		X				25550.67	371.67
F34	X	X	X							25577.16	398.16
F10	X	X	X			X				25580.16	401.16
F2	X	X	X			X	X	X	X	NA	- *
F3	X	X	X	X	X	X	X	X	X	NA	- *
F4	X	X	X	X		X	X	X	X	NA	- *
F5	X	X	X		X	X	X	X	X	NA	- *

*These models runs resulted in G-matrices that were not positive definite indicating that the 3-way interactions should not be included.

CHAPTER 5

Eelgrass (*Zostera marina*) seed dispersal by northern diamondback terrapins (*Malaclemys terrapin terrapin*) in lower Chesapeake Bay

ABSTRACT

The initial discovery in May 2009 of eelgrass (*Zostera marina*) seeds in fecal samples of wild-caught northern diamondback terrapins (*Malaclemys terrapin terrapin*) was the first field evidence of eelgrass seed ingestion by this species. This finding suggested the potential of terrapins as seed dispersers in local eelgrass beds. Seeds were only found in feces of terrapins captured prior to June 8 in 2009, 2010, and 2011, which coincided with eelgrass seed maturation and release. Number of seeds found varied annually and decreased greatly in 2011 after an eelgrass die off in 2010. The condition of seeds found in terrapin feces were viable mature, germinated, damaged, or immature. Of terrapins captured May 1 through June 8 of which 97% were males and juvenile females (head width < 30 mm), 30% had ingested seeds. Logistic regression showed decreasing probability of ingestion with increasing head width. Diamondback terrapins are a philopatric species with defined home ranges. Estimated number of potential terrapin eelgrass seed dispersers ranged from 559 to 799 able to disperse between 1,341 and 1,677 seeds in the Goodwin Island region of the lower York River. Based on reported distances traveled, terrapins can traverse eelgrass meadow boundaries thereby dispersing seeds beyond the bed of origin.

INTRODUCTION

Plants rely on abiotic and biotic processes by which to transport their seeds to other suitable habitat (Chambers and MacMahon 1994). Some plants have adaptations for abiotic dispersal that slow the rate of descent, yet maximize horizontal distance (Chambers and MacMahon 1994). Biotic dispersal relies on other organisms to move seeds to new locations often further than abiotic processes can achieve (Nathan et al. 2008). Seed acquisition and transport can be achieved through active or passive involvement of the organism (Chambers and MacMahon 1994). Seed ingestion is the passive internal mode of dispersal and is an important mutualistic relationship between plants and animals (Chambers and MacMahon 1994). Dispersal by animals has been well studied, yet categorizing whether or not a species is an effective disperser can be challenging. Schupp (1993) defined disperser effectiveness as the part an animal plays in a plant's future reproduction, i.e., new adult plants produced from animal-dispersed seeds. Effectiveness depends on the number of seeds dispersed, i.e., quantity egested, and the probability a dispersed seed will produce future generations, i.e., quality indicated by germination rate (Schupp 1993).

Saurochory is dispersal of plants by reptiles (Moll and Jansen 1995). Specifically, dispersal of seeds by turtles is chelonochory (Elbers and Moll 2011). Many chelonian species of all foraging strategies are known to ingest seeds, though most of them are herbivorous (Bonin et al. 2006; Ernst and Lovich 2009). For instance, there are terrestrial species ingesting terrestrial plant seeds (e.g., Galápagos tortoises *Chelonoidis nigra*, Rick and Bowman 1961; Blake et al. 2012, Florida box turtle *Terrapene carolina bauri*, Liu et al. 2004, and the Amazonian tortoise *Geochelone denticulata*, Jerozolimski et al. 2009), aquatic or semi-aquatic species ingesting aquatic and terrestrial plant seeds (e.g., black river turtle *Rhinoclemmys funerea*, Moll and Jansen 1995) and aquatic species ingesting terrestrial plant seeds (red-eared sliders *Trachemys scripta elegans* and the common snapping turtle *Chelydra serpentina*, Kimmons and Moll 2010).

Most aquatic chelonid dispersers that have been studied occur in freshwater. Few reptiles are adapted to living in salt water and even fewer are turtles (Schmidt-Nielson and Fange 1958). Of the seven marine turtle species, green sea turtles *Chelonia mydas* are well-known consumers of the seagrass *Thalassia testudinum*, yet no information has been published about their potential as seed dispersers (Thayer et al. 1984). In North America, the diamondback terrapin *Malaclemys terrapin* is the only fully estuarine, aquatic species of turtle (Ernst and Lovich 2009). This species is well-known as an inhabitant of salt marshes from Massachusetts to Texas, and a recent diet study revealed they were foraging in seagrass beds in lower Chesapeake Bay (Chapter 2). The northern portion of the terrapin's range between the Outer Banks of North Carolina to Cape Cod, Massachusetts overlaps with the distribution of a primary species of seagrass, eelgrass *Zostera marina* (Moore and Short 2006; Ernst and Lovich 2009). Eelgrass is the dominant seagrass species found in Chesapeake Bay (Orth et al. 2011). Habitat preference of small terrapins is shallow, near-shore brackish water regions of estuaries and coastal bays (Roosenburg et al. 1999; Chapter 4), which overlaps with the location of eelgrass meadows in Chesapeake Bay and the coastal bays of Virginia's Eastern Shore peninsula (Moore and Short 2006).

In May 2009, eelgrass seeds were found in fecal samples from diamondback terrapins (Chapter 2). Prior to this finding, only waterfowl and several fish species had been considered as biotic dispersal agents for *Z. marina* in temperate seagrass habitats (Orth et al. 2006; Heck et al. 2008; Kendrick et al. 2012) though distances for fishes were small and timing of waterfowl ingestion was poor (Orth et al. 2006; Sumoski and Orth 2012). Because of physical characteristics of eelgrass seeds, nearly all seeds remain in the bed of origin despite abiotic processes that could transport the seeds greater distances (Orth et al. 1994). Long distance abiotic dispersal of floating *Z. marina* seed pods (spathes) can result in colonization of new seagrass beds (Harwell and Orth 2002). Finding that diamondback terrapins ingested *Z. marina* seeds raised the question of whether terrapins could be a vector for eelgrass seed dispersal at intermediate distances (i.e., less than long distance abiotic transport but farther than within the boundaries of an individual bed).

The aim of this study was to evaluate the role of diamondback terrapins in eelgrass seed dispersal in lower Chesapeake Bay. Through qualitative and quantitative analysis we addressed the following questions:

1. What is the frequency of occurrence of ingested *Zostera marina* seeds in fecal material of the northern diamondback terrapin *Malaclemys terrapin terrapin*?

2. Are egested seeds viable and will they germinate after egestion?
3. Is seed ingestion based on diamondback terrapin size and habitat use?
4. What is the potential of seed dispersal by diamondback terrapins and how far will they disperse eelgrass seeds?

MATERIALS AND METHODS

Diamondback terrapins were collected from submerged aquatic vegetation (SAV) beds adjacent to Goodwin Islands, Green Point, and Allens Island along the York River subestuary, and in Browns Bay from May to early June in 2009, 2010 and 2011 (Figure 1), as part of a diet study (Chapter 2). Most terrapins from SAV beds were captured using a 4.9 m trawl. Others were captured by hand, a bottom scrape, or commercial crab pots modified to prevent drowning. Captured terrapins were marked with a unique turtle identification number (TID) etched into marginal scutes along the right side of the carapace (Cagle 1939) plus one additional notch made in the second to the left, rear marginal scute to distinguish these captures from previous collections. Gender and standard morphological measurements for turtles were recorded, including head width (HW), straight carapace length (CL), plastron length (PL), and mass. Gender was determined by external characteristics of tail length and cloacal vent position with respect to the posterior edge of the carapace. Males have longer, thicker tails with the cloacal vent beyond the edge of the carapace (Gibbons and Lovich 1990). Terrapins were grouped into two size classes based on head width, as small (HW < 30 mm) and large (HW ≥ 30 mm). All were released at the original collection location.

Diamondback terrapin collection was authorized under Virginia Department of Game and Inland Fisheries (VA DGIF) scientific collection permits 034390 in 2009 and 038407 in 2010 and 2011, as well as Virginia Marine Resources Commission (VMRC) permits 09-012, 10-024, and 11-050 for 2009, 2010, and 2011, respectively. The Chesapeake Bay National Estuarine Research Reserve in Virginia (CBNERRVA) granted a scientific research permit from 2009 through 2011 to sample at the Goodwin Islands. This study was carried out in strict accordance with the recommendations in the Guide for the Care and Use of Laboratory Animals of the National Institutes of Health. Two three-year protocols, IACUC-2008-07-17-5364-rnlipc and IACUC-2011-08-05-7415-rnlipc, were approved by, and renewed annually with, the College of William & Mary's Institutional Animal Care and Use Committee.

Collection of eelgrass seeds ingested by terrapins

In 2009, each captured terrapin was placed in a separate bucket with freshwater and returned to a laboratory at the Virginia Institute of Marine Science (VIMS). Fecal material egested by each terrapin during transit to the lab was collected upon return. Terrapins were housed individually in aquaria for 3-5 d and were not fed during this period (Chapter 2). To stimulate defecation, terrapins were kept in fresh water and items were collected from fecal material (Tucker et al. 1995). Fecal samples were rinsed with freshwater through a 1-mm standard test sieve, condensed into small pre-weighed drying trays, and air-dried prior to sorting.

Discovery of dry eelgrass seeds in dried samples in June 2009 prompted the change to brackish water in the fecal material collection protocol for 2010 and 2011. From capture through fecal material collection, terrapins were kept in brackish water from the York River to maintain potentially viable egested eelgrass seeds. These samples were rinsed with brackish river water through the sieve, collected into drying trays, and then checked for presence of eelgrass seeds. For each sample in which seeds were found, the seeds were removed and stored in brackish water in individual glass vials.

Analysis of variance, ANOVA ($\alpha = 0.05$), was used to test for statistical significance of number of eelgrass seeds ingested by terrapins by gender or year collected. Presence of ingested seeds was analyzed using logistic regression to determine which factor (i.e., terrapin gender, head width, or year, plus interaction of gender and head width) best predicted ingestion of eelgrass seeds. Using a generalized linear model (GLM) with binomial distribution, nine candidate models were compared using Akaike Information Criterion with small sample correction (AIC_c) to select the most parsimonious model (Anderson 2008).

*Germination of "*in situ*-ingested" seeds*

In 2010 and 2011, potentially viable "*in situ*-ingested" seeds were planted and observed for germination. Collected seeds were stored for approximately 6 mos until ambient water temperature was less than 15 °C. [Eelgrass seeds germinate *in situ* in anoxic sediment when water temperature is near 0-10 °C (Moore et al. 1993).] Prior to planting, stored seeds were checked if still potentially viable. A seed was deemed viable if it was firm when gently squeezed with a pair of forceps. Five of the 11 viable seeds collected in 2010 and two of the five collected in 2011 were considered viable for planting. Following experimental design described in Sumoski and Orth (2012), each seed was planted in individual containers at approximately 0.5 cm depth in sieved sediment from the York River. Twenty non-ingested, viable eelgrass seeds (supplied by the Seagrass Ecology Lab) were also planted as experimental controls. All containers were placed in an outdoor tank with flow-through brackish river water. Containers were checked daily for visible leaf parts above the sediment, which indicated germination and plant growth. Seeds collected in 2010 were left in the flow-through tank until April 2011, at which time all cups were removed and checked for seed germination. The planted seeds collected in 2011 were removed in April 2012. Germination rate was calculated as number of seeds germinated divided by total number of seeds planted. Fisher exact test (two-sided) was used to test whether or not the ratio of germinated:planted for terrapin-egested seeds and control seeds was different from 1:1.

Viability of field-collected eelgrass seeds

To estimate eelgrass reproductive shoot and seed abundances in local SAV meadows, 72 samples (3 weeks x 4 regions x 6 replicates) were collected during peak reproductive shoot biomass and seed development (Orth and Moore 1983). Over three consecutive weeks in May 2010, SAV beds in three regions of Goodwin Islands, i.e., north (GN), southeast (GSE), and southwest (GSW), and from Green Point (GP) with at least 40% SAV cover were randomly sampled. Beds ranged in size from 4.0-45.9 ha (Figure 2; Orth et al. 2011). Each replicate was collected in a 1-mm mesh bag attached to the top of a bucket with the bottom half cut away. After inserting the cut end of the bucket into the sediment, the sample was separated from the surrounding SAV bed with a shovel, and then bucket and shovel were quickly inverted dropping the sample into the attached bag. Each replicate sampled 0.053 m^2 of the SAV bed. Samples were transported in totes containing brackish river water to our laboratory where they were stored by region in separate outdoor holding tanks with flow-through brackish river water until sorted to count and remove reproductive shoots.

Five reproductive shoots from each replicate were bagged separately and frozen to estimate number of spathes per shoot and number of seeds per spathe. If there were less than five shoots in a replicate, all shoots were frozen. If greater than five shoots, the extra shoots were returned to the region's holding tank for continued seed development and seed viability estimates. For each shoot, the number of spathes and seeds in each spathe were counted. Mean abundance per m^2 of reproductive shoots, spathes, and seeds were estimated for each region and week sampled and compared using ANOVA ($\alpha = 0.05$). Linear regression was used to determine which factor (i.e., region, week sampled, or region-week sampled) predicted eelgrass reproductive shoot abundance. Four candidate models were compared using AIC_c to select the most parsimonious model (Anderson 2008).

By mid-June 2010, each holding tank was drained through a 1-mm standard test sieve to collect eelgrass seeds. The sediment and detritus in the tanks were also checked for additional seeds because eelgrass seeds are negatively buoyant and sink when released (Orth et al. 2006). Recovered seeds were stored in jars containing York River water. A minimum of 10% of seeds collected from each region's holding tank (40% for GSW) was tested for viability, which was determined using the tetrazolium chloride staining method (Lakon 1949; Jarvis 2009). Prior to staining, the seed coat was removed from each seed to expose embryo and endosperm. Seeds were then placed by groups of five into separate cups and immersed in 1% tetrazolium chloride solution for 24 h. Trays were covered with aluminum foil and kept in a dark cabinet during staining period. A seed was deemed viable if the embryo was stained pink after 24 h. Percent viable was calculated as the number of pink-stained embryos divided by the total number of seeds immersed.

RESULTS

Eelgrass seeds ingested by terrapins

Over all three years, 118 terrapins were captured from early May through early June and examined for seeds; no seeds were found in fecal material from terrapins captured after June 8 each year. Of the 118 terrapins, 92% had ingested pieces of eelgrass leaves, which indicated foraging within the SAV beds (Chapter 2). The highest occurrence of ingested eelgrass seeds was in small terrapins ($HW < 30$ mm) of both sexes: 33% of small males and 35% of small females had ingested seeds, with little interannual variation (Table 1). In contrast, only 6% of large females had ingested eelgrass seeds (Table 1).

By early June 2009, 35 seeds had been found in dried fecal samples. An additional 28 and 19 seeds were found in 2010 and 2011, respectively (Table 2; Appendix A). The number of seeds ingested per terrapin averaged 2.4 ($SE = 0.1$) with a maximum of 13 for one small male. Of 18 large females ($HW \geq 30$mm), only one had ingested eelgrass seeds (Table 1), though pieces of eelgrass were in fecal material from all but four (Chapter 2). The most "*in situ*-ingested" seeds were collected from terrapins captured from the Green Point region (Figure 2).

Of the nine models tested, model g(1), with terrapin HW as the predictor variable, had the highest AIC_c weight ($w_i = 0.233$) (Table 3; Figure 3). Model g(1) parameter estimates were $\alpha = 0.864$ (intercept) and $\beta = -0.076$ (terrapin head width) predicted the probability of ingestion, y, decreased with increasing head width (Figure 3). Three other candidate models were a plausible fit though ranked lower by AIC_c weight (Table 3). All three included year as an explanatory parameter. Model g(5) tested head width and year, g(3) year only, and g(6) tested gender and year only (Table 3).

*Germination results for "*in situ-ingested*" seeds.*

None of the planted, viable *"in situ*-ingested" seeds from either year germinated though three of the five planted in 2010 were still considered marginally viable after they were removed from their containers in April 2011. The lack of germination for these seeds was likely due to issues relating to the ambient temperature at which the seeds were stored. Of the control seeds planted, 35.0% and 35.7% did germinate by April 2011 and April 2012, respectively. Control seeds were stored in a similar manner as the *"in situ*-ingested" though in a different location.

Goodwin Islands region Zostera marina *reproductive shoot and seed abundance estimates with seed viability estimates.*

Density of SAV varied throughout the beds sampled with the highest density beds occurring along the York River and in coves along the southeast shoreline of Goodwin Island (Figure 2). GSE had the greatest mean reproductive shoot density (Table 4). GSW, the least dense region, was nearly four times less dense than GSE (Table 4). Seed abundance increased with increased shoot abundance (y = 32.8 +

26.1x) and differed significantly by region ($P << 0.01$). GSE beds produced the highest mean seed abundance per m^2 (Table 4). GN had the second highest estimate of seed abundance though it was three times smaller than GSE (Table 4). Number of seeds produced per shoot also differed significantly by sample ($P << 0.01$) and there was a significant interaction between region and sample ($P < 0.01$). Of the four models compared, model g(4), which included all the parameters, had the highest AIC w_i and was the best-fit, though model g(3) with the next highest AIC_c w_i had a higher r^2 value than model g(4) (Table 5). This could indicate low importance of the interaction between region and week sampled in determining reproductive shoot abundance. Parameter estimates for g(4) and g(3) are in Appendix B.

Eelgrass seed viability estimate

GSW had lowest number of reproductive shoots in its samples, hence the fewest number of seeds were found in that region's holding tank (Table 6). Samples from region GSE contained the greatest number of reproductive shoots and therefore the largest number of seeds found in its tank (Table 6). The percent of viable seeds was lowest from region GN and highest from region GSW. This may have been due to fewer seeds stored in a single jar for GSW. For all regions combined, the percent of viable seeds was 59%.

DISCUSSION

In May 2009, the remains of *Zostera marina* (eelgrass) epifauna and benthic fauna as well as pieces of eelgrass leaves were found in fecal samples collected from diamondback terrapins of the York River, Virginia (Chapter 2). Eelgrass seeds were discovered in dried samples from eight terrapins during processing of their fecal samples shortly after initial collection (Chapter 2). While it is not uncommon for aquatic turtles to ingest aquatic or terrestrial plant seeds (Moll and Jansen 1995; Bonin et al. 2006; Kimmons and Moll 2010), finding seeds from a marine angiosperm in fecal material of diamondback terrapins was novel for this estuarine species. Prior to the start of this study, there was one published record of terrapins in eelgrass beds. Spivey (1998) radio tracked terrapins from Davis Marsh in North Carolina and determined minimal use by terrapins of SAV beds in the vicinity of the marsh. He also made no mention of any plant material, terrestrial or aquatic, in his analysis of the terrapin diet in that region (Spivey 1998). Since finding terrapin-egested eelgrass seeds in 2009, there has been only one published account of *in situ* seed ingestion by terrapins (Erazmus 2012). Unfortunately, neither the type (e.g., terrestrial or aquatic) nor the species of seeds were identified; the seeds were collected from fecal samples from large female terrapins (Erazmus 2012).

Habitat preference of small terrapins is shallow, near-shore brackish water regions of estuaries and coastal bays (Roosenburg et al. 1999), which overlaps with the location of eelgrass meadows in Chesapeake Bay and the coastal bays of Virginia's Eastern Shore peninsula (Moore and Short 2006). Fifty-five percent of all terrapins captured from May through early June were from an eelgrass bed along Green Point (Figure 2; Appendix A), which included over half of the terrapins that ingested eelgrass seeds. Ninety-two percent of terrapins from Green Point were in the small size class (Table 1). While feeding on barnacles, as well as other sessile and mobile eelgrass epifauna in this area, small terrapins incidentally ingested the seeds (Chapter 2). In fecal samples, barnacles were seen still attached to pieces of eelgrass blades, as well as on spathes (seed pods) of eelgrass reproductive shoots from collected eelgrass samples (Chapter 2; Tulipani pers. obs.). In a related analysis, barnacles were the most abundant species found within the Green Point eelgrass bed (Chapter 2). Large female terrapins characteristically preferred deeper water of coves further away from shore, yet they also utilized shallower intertidal areas particularly near nesting beaches (Roosenburg et al. 1999). They too had ingested pieces of eelgrass (Chapter 2).

The probability of seed ingestion decreased with increased head width (Table 3; Figure 3). Small terrapins had egested all but three of the eelgrass seeds found in fecal samples over the three years (Table 1). Additionally, the inclusion of year as a factor of seed ingestion reflected the effect of variable, annual seed ingestion by terrapins in this study as indicated by three additional models with AIC$_c$ $w_i > 0.100$ (Table 3). Fewer egested seeds were found in 2010 and 2011 despite increased effort to capture more terrapins during peak eelgrass seed development in May and completed seed release by mid-June (Table 2; Silberhorn et al. 1983; Orth et al. 1994). Many abiotic factors affected eelgrass seed production (Moore et al. 1993) and the temperature-induced die-off in June 2010 likely reduced the number of seeds produced in 2011 (Moore et al. *accepted for publication*), thereby decreasing opportunity for terrapins to ingest seeds.

One seed each from 2010 and 2011 found in fecal material had already germinated, while others were damaged (e.g., cracked or missing seed coat, or crushed seed) or immature (Table 2). Other viable seeds from both years were planted to test for germination. Though none of these terrapin "*in situ*-ingested" seeds germinated, eelgrass seeds fed to terrapins in a laboratory experiment and recovered from fecal material germinated when planted (Sumoski and Orth 2012). Germination rate for eelgrass seeds egested by terrapins was 14% (Sumoski and Orth 2012). Seed germination rates reported for other aquatic turtle species varied from 7% to 83% (Moll and Jansen 1995; Kimmons and Moll 2010), which were comparable to rates from herbivorous tortoises (Birkhead et al. 2005; Guzmán and Stevenson 2008; Jerozolimski et al. 2009).

During the related terrapin diet study (Chapter 2), fecal samples were collected daily. Terrapins typically stopped egesting "*in situ*-ingested" material within 5 days after capture and frequently stopped by day three post-capture (Tulipani, pers. obs.). Sumoski and Orth (2012) estimated gut retention time for terrapins ranging from 24-144 h. Wild animals exhibit captivity-induced stress with various behaviors, e.g., hyperactivity, hypoactivity, or interaction with transparent sides of aquaria (Morgan and Tromborg 2007). Captive terrapins kept in aquarium tanks sometimes responded with continuous swimming (hyperactivity), long periods of sleeping (hypoactivity), ignoring offered food, or halting defecation for several days (D. Tulipani, pers. obs.), which could result in longer-than normal retention rates in a laboratory experiment. *In situ* gut passage time likely varies with terrapin activity level and environmental stress (Holliday et al. 2009).

Several mark-recapture (Gibbons et al. 2001; Sheridan et al. 2010) and tracking studies (Spivey 1998; Butler 2002; Harden et al. 2007; Estep 2005) estimated home range size and distance traveled for diamondback terrapins. Greatest unidirectional distances reported (8.0-8.5 km) were always by mature females frequently traveling between marsh creeks and nesting beaches (Hurd et al. 1979; Butler 2002; Sheridan et al. 2010). After being captured in a commercial gill net and transported out of the study area, one mature female from North Carolina traveled 12.5 km to return to its home area (Spivey 1998). Distances for small terrapins were typically less than 1.5 km (Harden et al. 2008; Sheridan et al. 2010). In a related ultrasonic telemetry tracking project, estimated distance traveled for small terrapins was much greater than previously reported, i.e., 2.8-5.7 km based on detection records for the same male terrapin at numerous receivers for 2-d and 10-d periods (Chapter 4). Terrapins tracked in that study had preferred home areas similar in size, i.e., 50–455 ha, to terrapins in North Carolina (Spivey 1998), yet also engaged in occasional long-distance forays around the Goodwin Islands-Green Point region (Chapter 4). Hence, potential dispersal distances by small diamondback terrapins were much greater than previously estimated (Sumoski and Orth 2012).

Combining greater travel distances with their characteristically staunch home range fidelity (Gibbons et al. 2001), terrapins have the ability to routinely transfer ingested eelgrass seeds between completely separate eelgrass beds (Figure 2; Tulipani 2013).

Based on the times when seeds were found in terrapin fecal material, terrapins ingested eelgrass seeds directly from the reproductive shoots, with some still found in the spathe (D. Tulipani, pers. obs.). No seeds were found in fecal samples from terrapins captured after mid-June when annual seed release to sediments completed (Silberhorn et al.1983), though pieces of eelgrass blades continued to be egested throughout the collection period. In eelgrass beds, 80% of seeds were retained within the bed of origin (Orth et al. 1994) with in-sediment viability decreasing from 42% to less than 5% within 6 months (Jarvis 2009). By directly ingesting them from the plant, terrapins moved seeds at peak viability before they became part of the in-sediment seed bank.

To estimate number of terrapin dispersers and number of seeds potentially dispersed by terrapins for any day from mid-May through early June, we used a 2008 terrapin population estimate for Goodwin Islands (Rook 2009), the sex-ratio from a related terrapin diet study (Tulipani 2013), and the percent of terrapins with seeds by size class and average number of seeds per terrapin (this study; Appendix C). The estimated number of potential terrapin eelgrass seed dispersers ranged from 559 to 799 dispersing between 1,341 and 1,677 seeds each day (Appendix C). Because of temporal and spatial variability in reproductive shoot abundance and available seeds (Orth and Moore 1986), the potential number of dispersed seeds would vary as well (Table 4). While these estimates are an extremely small fraction of estimated total seeds produced in the Goodwin Islands-Green Point region, it may represent movement of a substantial number of viable seeds that might not otherwise survive (Table 4).

In seagrass literature as recently as 2012, neither diamondback terrapins *Malaclemys terrapin* nor any other temperate species of turtle were represented as an inhabitant (transient or permanent) of temperate seagrass habitats (Orth et al. 1994; Orth et al. 2006; Heck et al. 2008; Kendrick et al. 2012). Until the findings in May 2009, terrapins were not considered potential vectors of eelgrass seed dispersal unlike its well-known tropical relative, the herbivorous green sea turtle *Chelonia mydas* (Orth et al. 2006; Kendrick et al. 2012). Previously only waterfowl and several fish species had been considered biotic dispersal agents in temperate seagrass habitats (Orth et al. 2006). *Zostera marina* seed ingestion by this estuarine turtle is a novel finding. Supporting diamondback terrapins as seed dispersers is the convergence of terrapin distribution, its annual active period and habitat use, and its facultative omnivory on eelgrass overlapping with distribution of extensive meadows of *Z. marina* in Chesapeake Bay. The interplay between terrapins and eelgrass habitats in lower Chesapeake Bay exemplifies a different mutualistic relationship between diamondback terrapins and their habitat. Terrapins gain an abundant food resource and extended habitat beyond their typical salt marsh habitat. Meadows of *Z. marina* benefit from terrapin foraging through seed dispersal within and between beds, potentially increased genetic diversity (Howe and Smallwood 1982; Olivieri et al. 1995), reseeding failing eelgrass beds, and plant canopy maintenance by removal of biofouling epifauna and old leaf parts (van Montfrans et al. 1984). Further investigation of the digestive system of diamondback terrapins could reveal if terrapins were also gaining any nutritional benefit from eelgrass ingestion and digestion, as well as differences in intestinal microflora between those foraging in seagrass beds and those from salt marshes. Ongoing restoration of *Zostera marina* in Virginia's coastal bays lagoons of the state's Eastern Shore peninsula had been very successful (Orth et al. 2012). These are also areas where large populations of diamondback terrapin occur (Tulipani, unpubl. data). Through foraging, diamondback terrapins may play an additional, potentially substantive, role with respect to the health of *Zostera marina* in Virginia beyond that of a predator within seagrass beds. Conceivably, continuing anthropogenic threats to the diamondback terrapin population could lead to a negative cascading effect on *Zostera marina* in Chesapeake Bay.

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Table 1. Number of diamondback terrapins captured May-early June 2009, 2010, and 2011 by gender and size class, and number that egested eelgrass (*Zostera marina*) seeds. Mean (±SE) of CL = straight carapace length; HW = head width; Mass; s: HW < 30 mm; L: HW ≥ 30 mm.

Year Gender (Size Class)	Captured	With seeds	Percent terrapins with seeds	CL (cm)	HW (mm)	Mass (g)
2009						
males (s)	17	7	41%	13.0 (0.4)	20.7 (0.5)	340.8 (22.1)
females (s)	3	1	33%	11.3 (0.6)	21.3 (0.9)	265.3 (46.0)
females (L)	1	0	0%	22.0	47.0	1,710.0
Total	21	8	38%			
2010						
males (s)	26	11	42%	12.3 (0.3)	20.9 (0.3)	283.9 (15.0)
females (s)	11	4	36%	11.8 (0.5)	22.3 (0.9)	281.2 (33.2)
females (L)	2	0	0%	20.5 (1.0)	38.2 (0.7)	1,410.5 (102.5)
Total	39	15	38%			
2011						
males (s)	40	9	23%	12.5 (0.2)	21.2 (0.2)	290.2 (10.9)
females (s)	3	1	33%	14.2 (1.9)	26.2 (2.1)	479.7 (142.8)
females (L)	15	1	7%	20.7 (0.4)	38.8 (1.0)	1,419.9 (81.4)
Total	58	11	19%			
2009-2011						
males (s)	83	27	33%	12.5 (0.1)	21.0 (0.2)	298.6 (8.6)
females (s)	17	6	35%	12.1 (0.5)	22.8 (0.8)	313.4 (36.3)
females (L)	18	1	6%	20.7 (0.4)	39.2 (1.0)	1,434.9 (69.8)
Total	118	34	29%			

Table 2. Condition of eelgrass (*Zostera marina*) seeds in fecal samples from terrapins captured in SAV beds from May-early June 2010 and 2011.

Year*	Collected Seeds	Potentially Viable Seeds	Immature Seeds	Damaged Seeds	Germinated Seeds	Dead Seeds
2010	28	11	7	1	1	8
2011	19	5	7	1	1	5

* Thirty-five seeds found in 2009 were dried before discovered and could not be tested.

Table 3. AIC-based model selection with model weights (w_i) for nine candidate models to predict probability of terrapin eelgrass seed ingestion. Seed ingested (1) or not ingested (0) was regressed (logistic regression) against terrapin head width (HW), gender (G), year captured (Yr), and the interaction between HW and G. Best-fit and plausible models in bold.

Model	Intercept	HW	G	Yr	HW x G	k	ΔAICc	w_i
g(1)	**β_0**	**β_1**				**2**	**0**	**0.233**
g(2)	β_0		β_2			2	2.493153	0.067
g(3)	**β_0**			**β_3**		**3**	**1.081933**	**0.136**
g(4)	β_0	β_1	β_2			3	2.105079	0.081
g(5)	**β_0**	**β_1**		**β_3**		**4**	**0.866103**	**0.151**
g(6)	**β_0**		**β_2**	**β_3**		**4**	**1.321556**	**0.121**
g(7)	β_0	β_1	β_2		β_4	4	1.904298	0.090
g(8)	β_0	β_1	β_2	β_3		5	2.774923	0.058
g(9)	β_0	β_1	β_2	β_3	β_4	6	2.664346	0.062

Table 4. Estimates of mean (±SE) of eelgrass (*Zostera marina*) reproductive shoots, spathes, and seeds per m^2, spathes per shoot and seeds per spathe from samples collected May 2010 at Green Point (GP) and three areas adjacent to Goodwin Islands - north (GN), southeast (GSE), and southwest (GSW),York River. Estimated seed bank by region: SAV area (ha) x 10,000 (m^2/ha) x seeds/m^2 Figure 2 SAV area adapted from Orth et al. (2011).

Region	Shoots	Spathes	Seeds	Spathes per Shoot	Seeds per Spathe	Est. Total Seeds Produced
GN	90.0 (12.9)	399.4 (66.1)	2050.6 (333.8)	5.1 (0.7)	5.2 (0.2)	9.4×10^8
GSE	188.3 (26.8)	1305.9 (231.8)	6454.1 (1011.5)	7.5 (0.7)	5.1 (0.2)	1.8×10^9
GSW	48.1 (14.3)	294.5 (78.2)	1997.7 (477.3)	5.8 (1.7)	4.8 (1.3)	2.3×10^8
GP	58.6 (21.3)	326.4 (96.3)	2034.2 (570.6)	4.7 (1.1)	4.2 (0.8)	8.1×10^7

Table 5: AIC-based model selection for linear regression of eelgrass (*Zostera marina*) reproductive shoot abundance as a function of region (R), week sampled (Wk), and the interaction between R and Wk. Best-fit and plausible models in bold.

Model	Intercept	R	Wk	R x Wk	k	ΔAICc	w_i	r^2
g(1)	β_0	β_1			5	4.834352	0.064	0.288
g(2)	β_0		β_2		4	25.146394	0.000	0.039
g(3)	$\boldsymbol{\beta_0}$	$\boldsymbol{\beta_1}$	$\boldsymbol{\beta_2}$		**7**	**2.373648**	**0.219**	**0.439**
g(4)	$\boldsymbol{\beta_0}$	$\boldsymbol{\beta_1}$	$\boldsymbol{\beta_2}$	$\boldsymbol{\beta_3}$	**13**	**0**	**0.717**	**0.337**

Table 6. Estimate of percent viable eelgrass (*Zostera marina*) seeds from samples collected May 2010.

Region	Seed Collected	Seeds Stained	% Stained	Viable Seeds	% Viable
GN	222	25	11.3%	11	44.0%
GSE	822	82	10.0%	44	53.7%
GSW	35	14	40.0%	13	92.9%
GP	135	14	10.4%	11	78.6%

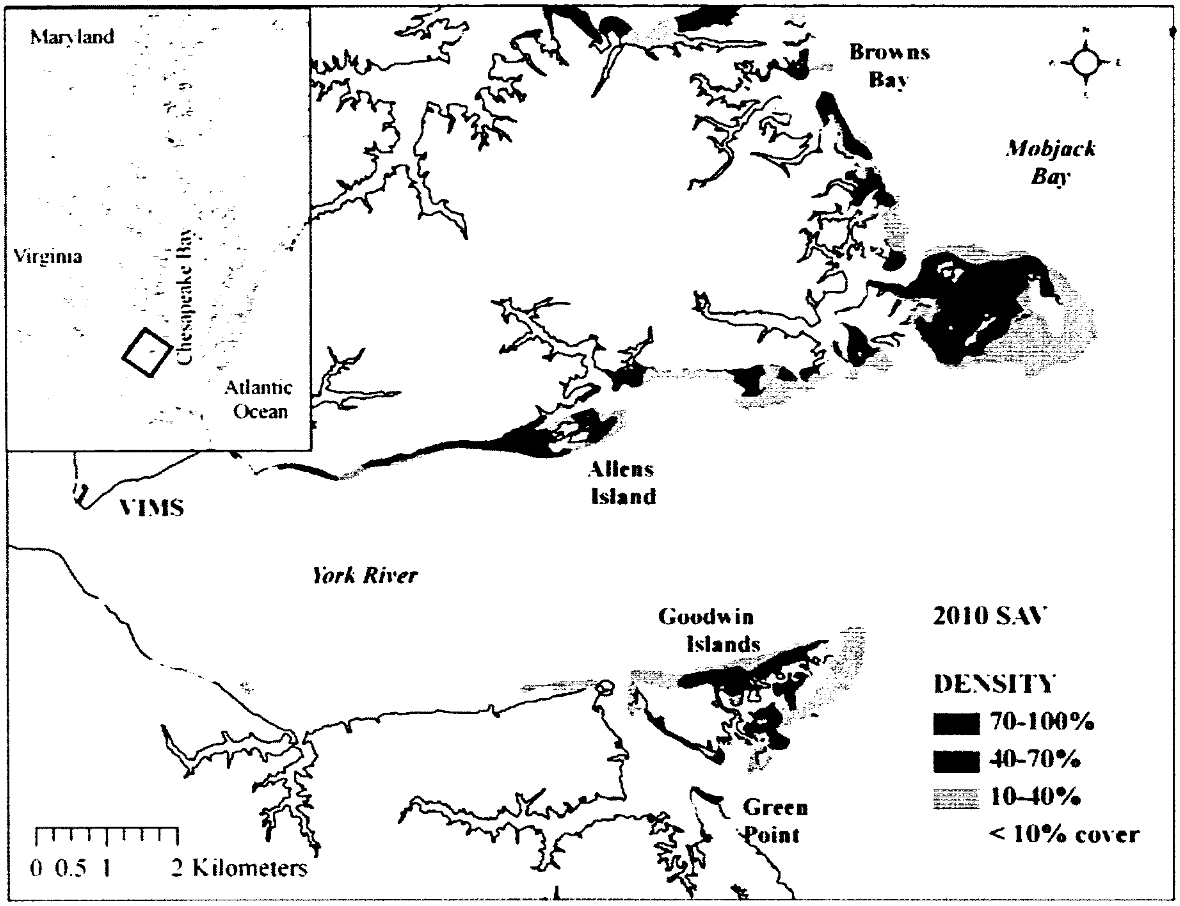

Figure 1. Collection locations for diamondback terrapins from SAV beds of (A) Allens Island, (B) Goodwin Islands, and (C) Green Point along the lower York River subestuary and from (D) Browns Bay in southeastern Mobjack Bay, southwestern Chesapeake Bay (rectangle on inset). Modified from Orth et al. 2010.

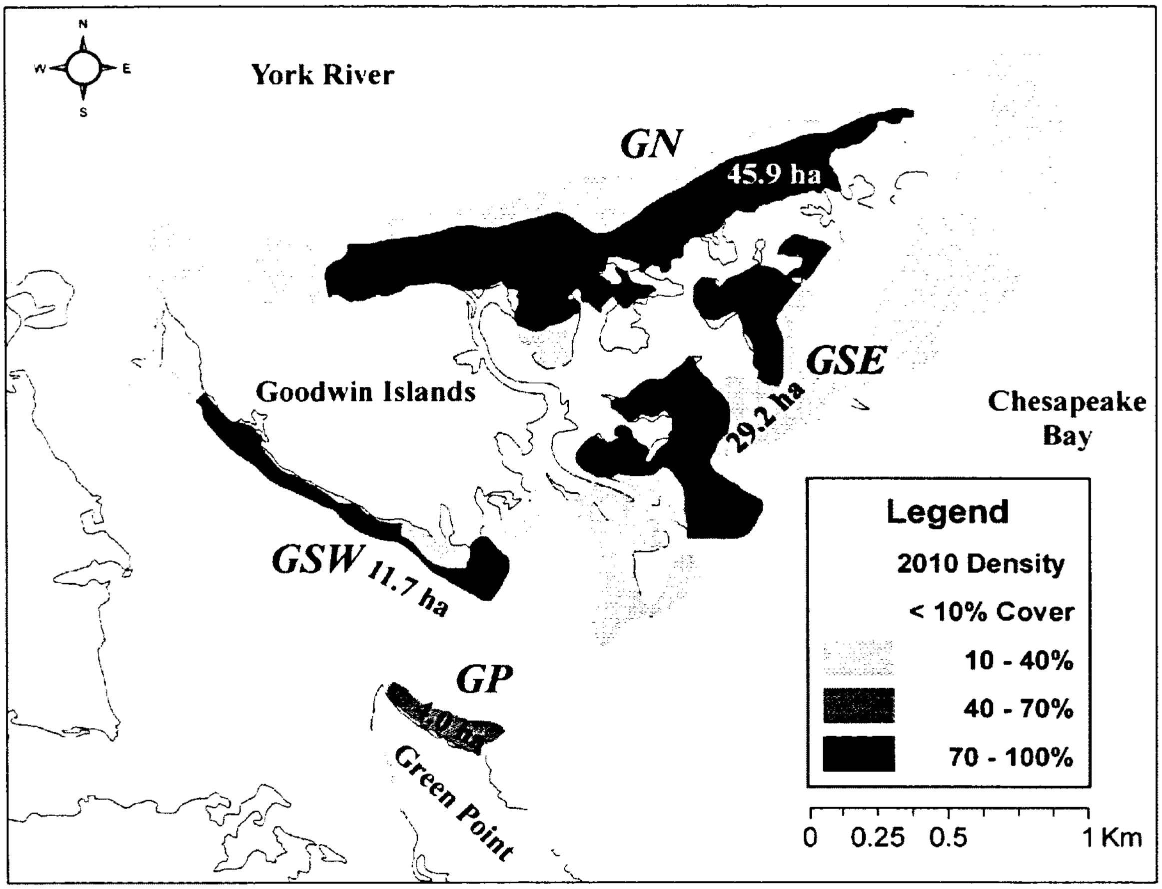

Figure 2. Regions with area (ha) where eelgrass samples were collected in May 2010 from SAV beds adjacent to Goodwin Islands (GN, GSW, GSE) and Green Point (GP) with percent coverage ≥ 40% (modified from Orth et al. 2010). GSE area included of two coves with > 70% cover.

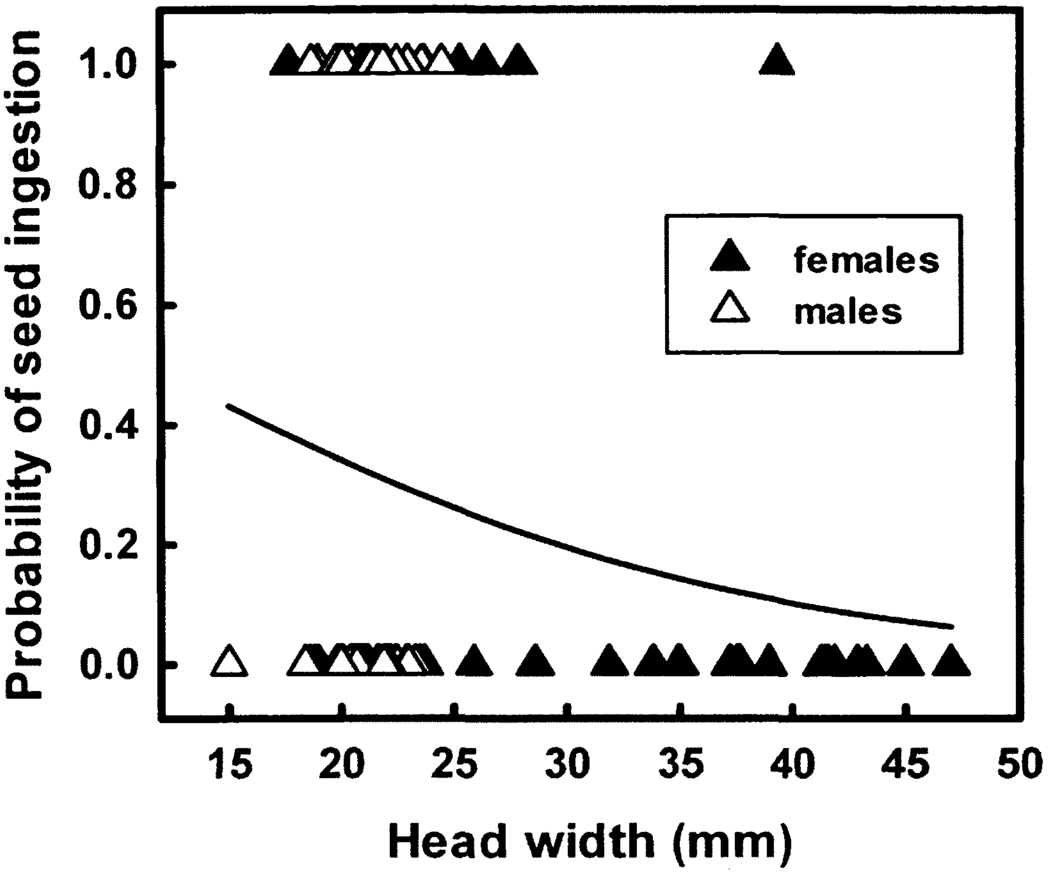

Figure 3. Presence (1) or Absence (0) of ingested seeds as a function of diamondback terrapin Head Width. The curve is the probability of eelgrass seed ingestion derived from logistic regression GLM-fitted model $g(1) = e^{(0.864 - 0.076x1)}/(1 + e^{(0.864 - 0.076x1)})$, with α 95% CI (-1.000, 2.728) and β 95% CI (-0.156, 0.004).

Appendix A. Eelgrass (*Zostera marina*) seeds found in fecal samples from terrapins captured in May 2009, May-early June 2010 and 2011 from SAV beds from regions Green Point (GP), Goodwin Islands (GI), Allens Island (AI), Perrin Cove (PC), and Browns Bay (BB).

Year	Region	Terrapins with seeds	Total terrapins caught	% Total Captured	Live seeds	Dried seeds	Total seeds
2009							
	GP	5	14	36%	0	19	19
	GI	2	4	50%	0	15	15
	AI	1	3	33%	0	1	1
	Total	**8**	**21**	**38%**	**0**	**35**	**35**
2010							
	GP	13	28	46%	20	6	26
	GI	1	8	13%	0	1	1
	AI	1	2	50%	0	1	1
	PC	0	1	0%	0	0	0
	Total	**15**	**39**	**38%**	**20**	**8**	**28**
2011							
	GP	1	23	4%	0	1	1
	GI	6	9	67%	10	2	12
	AI	2	16	13%	2	0	2
	BB	2	9	22%	4	0	4
	PC	0	1	0%	0	0	0
	Total	**11**	**58**	**19%**	**16**	**3**	**19**
2009-2011							
	GP	19	65	29.2%	20	26	46
	GI	9	21	42.9%	10	18	28
	AI	4	21	19.0%	2	2	4
	BB	2	9	22.2%	4	0	4
	PC	0	2	0.0%	0	0	0
	Total	**34**	**118**	**29%**	**36**	**46**	**82**

Appendix B. Best-fit models (AIC $w_i \geq 0.2$) parameter estimates and standard error of estimates from regressing reproduction shoot abundance with region, week sampled, and the interaction between region and week sampled.

Model	Parameter	Parameter Estimates	SE
g(4)	β0	3.8333	1.6055
	β1:		
	GP	-2.0000	2.2706
	GSE	2.3333	2.2706
	GSW	-2.6667	2.2706
	β2:		
	Sample 2	2.6667	2.2706
	Sample 3	0.6667	2.2706
	β3:		
	GP:Sample 2	-2.8333	3.2111
	GSE:Sample 2	6.5000	3.2111
	GSW:Sample 2	-2.0000	3.2111
	GP:Sample 3	3.8333	3.2111
	GSE:Sample 3	2.1667	3.2111
	GSW:Sample 3	3.3333	3.2111
g(3)	β0	2.917	1.234
	β1:		
	GP	-1.667	1.425
	GSE	5.222	1.425
	GSW	-2.222	1.425
	β2:		
	Sample 2	3.083	1.234
	Sample 3	2.500	1.234

Appendix C. Calculation estimating number of small and large terrapins potentially dispersing seeds in the Goodwin Island region. Amounts were rounded to nearest whole number. Small: males (m) and small females (sf); Large: large females (Lf).

	Low estimate: Number of Individuals			High estimate: Number of Individuals		
2008 population estimate (Rook 2009)	2,000			2,500		
	m	sf	Lf	m	sf	Lf
Sex ratio (m:f): 1.6:1 (Chapter 2)	1,250	375	375	1,563	469	468
	Small		Large	Small		Large
Total	1,625		375	2032		468
Percent of terrapins with seeds: Small: 33% Large: 6%	536		23	671		28
Estimated number of terrapin seed dispersers	**559**			**799**		
Seeds dispersed (2.4 seeds/terrapin)	**1,341**			**1,677**		

CHAPTER 6

Conclusions

CONCLUSIONS

This research examined foraging ecology of the northern diamondback terrapin in lower Chesapeake Bay. In the role of top predator, terrapins fed primarily on hard-shelled invertebrates found in both salt marshes and seagrass beds. This diet study provided the first field evidence that diamondback terrapins were foraging within local seagrass beds. Schoener's Overlap index, θ, supported the conclusion of prey differentiation by terrapin size with a low value indicating very little overlap in diet. There was discernible prey choice by size class, with large terrapins (HW ≥ 30 mm) primarily ingesting bivalves and blue crabs. Small terrapins captured from seagrass beds consumed small bay barnacles attached to the leaves of *Zostera marina*. Gastropods, which were the ingested most frequently by diamondback terrapins in South Carolina and New York (Tucker et al. 1995; Petrochic 2009), had a much reduced presence in the diets of terrapins in Virginia, especially if subtidal seagrass beds were present. When seagrass beds were not present, marsh snails were consumed more often by males than by females. Because many of the diamondback's intertidal prey can be found in both habitats, θ indicated substantial overlap in diet by habitat type. Three general patterns in dietary overlap based on terrapin size, *high overlap between males and small females that decreased as females grew, high overlap between medium and large sizes,* and *low overlap between small and large sizes* became apparent when this diet study was compared to previous research (Tucker et al., 1995; Spivey, 1998; Petrochic, 2009). As a species, the diamondback terrapin was consistent in dietary overlap due to limitations of its morphology. By feeding on sessile epifauna of *Zostera*, terrapins were removing organisms that covered the plant's leaves. Sessile epifauna can weigh down the plant and potentially reduce photosynthesis (van Montfrans et al., 1984). Similar to terrapin's control of periwinkle snail's harmful effects on *Spartina* marsh grass, terrapins may help maintain healthier *Zostera* beds through their predation on biofouling organisms.

Barnacles were the most abundant organisms found in *Zostera* beds around the Goodwin Islands and Green Point region of the York River. Periwinkle snails were also very abundant throughout the lower York River. The Manly-Chesson index of prey selectivity, α, which related prey choice in diet to prey abundance in the environment, also supported the conclusion that terrapins were selective in their choice of prey based on their size. When small terrapins did consume periwinkle snails, the sizes ingested were similar to ingested snail size ranges for terrapins in South Carolina and New York (Tucker et al. 1995; Petrochic 2009). Interestingly, large terrapins presented two distinct size range preferences based on terrapin head width where terrapins with HW 30–40 mm consumed snails with 6–17 mm shell length and terrapins with HW > 40 mm consumed snails with 17–24 mm shell length. This was different than reported for terrapins in South Carolina (Tucker et al. 1995). One trend that was suggested was that number of periwinkles ingested by terrapins decreased with increasing latitude. This may be a function of the availability of other "easier-to-consume" prey in the northern portion of its range.

The general trend suggested from the mesocosm prey choice experiments also confirmed that gastropods were not preferred prey when juvenile blue crabs were present. In each experiment, terrapins readily consumed the crabs. In the diet analysis, crabs were often ranked second or third of prey types consumed. In a third mesocosm experiment, blue crabs had better survival when vegetation percent cover was high, as expected. This may be one of the reasons that blue crabs, while important in terrapin diet, were not largely so. Juvenile blue crabs utilize eelgrass beds as refuge until they reach carapace width greater than 25 mm when they become more visible to predators amongst the vegetation (Lipcius et al. 2007). Terrapin's preference for juvenile blue crabs may be one reason why they enter blue crab pots, where they frequently drown before the pots are retrieved (Roosenburg et al. 1997).

The tracking study confirmed earlier findings on habitat use by small and large terrapins (Roosenburg et al. 1999). Small terrapins had better defined home ranges and stayed mostly in shallow near-shore water whereas large females entered these areas on flood and high tides. The logistic regression model predicted that small terrapins were less likely to move out of an area than large females. Even though males have preferred home ranges, they would frequently make long-distance forays to other parts of the Goodwin Islands region. Many of the long-distance movements were recorded after the mating season when terrapins are known to travel to mating aggregation areas (Seigel 1980). The long-distance trips made by terrapins in this study may be extended searches for food.

More importantly, the results of the tracking study revealed that both male and female terrapins regularly moved between Goodwin Islands and Green Point. A relatively deep channel separates Goodwin Islands from Green Point and along both shores are *Zostera marina*-dominated seagrass beds where the terrapin feed. Maximum unidirectional distance traveled by any terrapin was 2.6 km with one terrapin traveling 2.5 km within one day. This research also provided the first field evidence that terrapins ingested viable eelgrass seeds incidental to consuming epifauna, a first for this species or any temperate species of turtle (Orth et al. 2006; Kendrick et al. 2012). When compared to other modes of dispersal for eelgrass, biotic dispersal by terrapins may be a substantial contribution to local eelgrass propagation. By moving between non-connected eelgrass beds, terrapins can act as an intermediate distance dispersal agent for eelgrass. The frequency with which they migrate between different seagrass beds could help sustain beds in areas of less-than-ideal conditions. Alternately, terrapins could also destroy seeds through ingestion and digestion or they could deposit seeds in unsuitable habitats, such as muddy coves. Additionally, terrapins feeding on seagrass epifauna ingested more plant material than terrapins feeding within salt marshes, which suggests that terrapins were opportunistic omnivores when feeding in seagrass beds. The portions of the leaves bitten off were frequently the tips of the blades (Tulipani, pers. obs.), which likely were the oldest portion of the plant (van Montfrans et al.

1984). Terrapins feeding directly on eelgrass suggest an important ecological role of diamondback terrapins in Chesapeake Bay.

Diamondback terrapins are top consumers in salt marshes and seagrass beds providing important functions through foraging that are beneficial to each habitat. The reduction or extirpation of terrapin populations around Chesapeake Bay would be detrimental to the ecosystem as a whole. The goal of my research was to reveal the ecological role and importance of diamondback terrapins in Chesapeake Bay. Though the species is often ignored or overlooked with respect to management concerns, the collective findings of my research suggest that diamondback terrapins indeed play a key role in the functioning of coastal ecosystems. As such, this species should be afforded conservation strategies that will foster population recovery and protection in Virginia.

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