

Impacts of invasive *Phragmites australis* on diamondback terrapin nesting

Cassandra Elizabeth Cook

Farmington Hills, MI

Bachelor of Science, University of Michigan-Ann Arbor, 2010

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Cassandra Elizabeth Cook

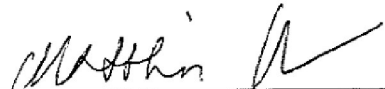
Approved by the Committee, June, 2016


Committee Chair

Professor Randy Chambers, Department of Biology
College of William and Mary



Professor Michael D. Lamar, Department of Biology
College of William and Mary



Professor Matthias Leu, Department of Biology
College of William and Mary

ABSTRACT PAGE

The diamondback terrapin (*Malaclemys terrapin*) is a species of turtle found exclusively in brackish water habitats. Terrapins are currently facing population threats including by-catch mortality in crab pots, predation, and habitat loss. The expansion of the exotic, invasive reed *Phragmites australis* is causing widespread structural and functional changes to coastal ecosystems throughout North America, which could negatively impact the nesting success of female terrapins by invading preferred nesting habitats. I examined the extent to which *Phragmites* affects nesting of a breeding population of diamondback terrapins at Fisherman Island National Wildlife Refuge on the eastern shore of Virginia, where *Phragmites* has recently expanded into known areas of terrapin nesting. With data collected from the 2015 nesting season I quantified the impacts of this expansion on terrapin nesting by: determining the extent to which nest incubation temperature is impacted by *Phragmites* shading, determining how *Phragmites* density impacts the risk of rhizome invasion into nests, and determining how the presence of *Phragmites* impacts predation of terrapin nests. I also examined landscape features to determine which factors may be associated with diamondback terrapin nest site use. I found that *Phragmites* cover greater than 50% would decrease incubation temperatures of terrapin nests sufficiently to produce predominantly male hatchlings. There was no effect of *Phragmites* cover on root growth into simulated nests, but cover by other dune plant species explained observed trends in root growth. I did not find a significant effect of *Phragmites* on nest predator activity, but did find that *Phragmites* had an impact on terrapin nest site use on Fisherman Island. Distance from nest to nearest marsh and tidal creek also influenced terrapin nest site use. With crab pots and roadways contributing to high adult mortality every year, high nesting success will be highly important to maintaining and propagating this charismatic species.

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Chapter 1: Impacts of *Phragmites australis* on incubating terrapin nests - Temperature and Root Invasion

Introduction

The diamondback terrapin is a specialized species of emydid turtle found only in brackish water habitats along the Atlantic Coast and Gulf of Mexico of the United States (Butler and Heinrich 2007; Feinberg and Burke 2003). Terrapins play an important role in the salt marsh ecosystems, acting as a top predator for invertebrate populations (Baldwin et al. 2005) as well as being prey for the Bald Eagle (*Haliaeetus leucocephalus*) (Butler et al. 2006). Diamondback terrapin populations were once large, but by the 20th century their numbers were greatly reduced by harvesting for the food industry (Baldwin et al. 2005). While terrapin meat is no longer in high demand, terrapin populations still face major threats including by-catch mortality in crab pots, nest predation, road mortality, and habitat loss (Butler and Heinrich 2007; Feinberg and Burke 2003). Due to these factors local terrapin populations declines are documented in states such as Florida and South Carolina, however terrapins are only protected by state laws in some parts of their range (Gibbons et al. 2001; Seigel 1993).

Terrapins face high risk of mortality in all life stages; crab pots and roadways result in high death rates in adults (Grosse et al. 2014), while predation is the greatest threat to the egg stage (Butler et al. 2006). Mortality in crab pots is documented as the main cause of decline for this species, and has been occurring for the last 60 years (Roosenburg 2004). Crab pots selectively kill adult males and juvenile females, as they are the size that can easily fit into the

openings designed for crab capture (Coleman et al. 2014). This is a major cause of concern because diamondback terrapins have relatively small home ranges, and a high rate of juvenile—particularly female—mortality could ultimately lead to population collapse, as has been found in other emydid turtles (Congdon et al. 1993). A study by Gibbons et al. (2001) documented that terrapins show high home range site fidelity from year to year, with a majority of terrapins recaptured in the same tidal creeks in consecutive years. To offset high rates of adult and juvenile mortality in a species with low dispersal rates, nesting success is imperative to support recruitment of local terrapin populations. Terrapins, like most turtle species, have life history traits (e.g., delayed maturity) that restrict their ability to adapt to a rapidly changing environment (Gibbons et al. 2001). Any changes, be it anthropogenic or natural, could cause dramatic changes in demography, and severely affect population recruitment.

Land-use change, climate change, alien or invasive species, and pollution are a few of the major factors impacting biodiversity (Didham et al. 2007; Wilcove et al. 1998). Among them, many scientists argue that habitat loss and invasive species are two of the largest threats to the proliferation of native species (Didham et al. 2007; Wilcove et al. 1998). These two phenomena are interlinked; human actions and land use change disturb ecosystems in such a way that makes them susceptible to colonization by invasive species (Galatowitsch et al. 1999; Zedler and Kercher 2004; Silliman and Bertness 2004). Invasive vegetation often further degrades ecosystems and impacts the survival of native species that may not be able to withstand severely modified conditions (Uddin et

al. 2014). In a study on reptile populations, Gibbons et al. (2000) found that exotic grasses degraded their native shrub habitat in Idaho, which resulted in a decrease of species richness by about 5% over 20 years. Invasive vegetation has a high probability of changing ecosystems to such an extent that native species cannot survive, therefore creating drastic habitat modification and impacting diversity.

Invasive vegetation can severely impact wetlands when made vulnerable by high amounts of disturbance. Anthropogenic activities such as runoff, sedimentation, nutrient inputs, and drainage degrade wetlands and cause them to be susceptible to colonization by invaders (Galatowitsch et al. 1999). Aggressive invaders, such as *Phragmites australis* (common reed, hereafter *Phragmites*), are able to thrive in areas of disturbance and displace native wetland plants (Silliman and Bertness 2004). *Phragmites* is rapidly colonizing Atlantic Coastal wetlands of the United States, particularly brackish wetlands (Gan et al. 2010; Chambers et al. 1999). In the last 100 years *Phragmites* has been increasing its range and has become a dominant species in some terrestrial and aquatic ecosystems (Chambers et al. 1999), including some around Chesapeake Bay. A study by Rice et al. (2000) of seven marshes in the Chesapeake Bay found greater rates of *Phragmites* expansion in saline marshes compared to tidal freshwater marshes. This prolific grass species forms dense monocultures mainly by rhizome spread and clonal growth. It establishes in well-drained areas bordering marshes and creeks, and then expands by rhizomes into the high marsh zone (Bart and Hartman 2003). *Phragmites* reproduction by clonal

integration has also enabled it to spread into increasingly saline habitats and rapidly colonize New England salt marshes (Silliman and Bertness 2004). Increasing habitat alteration and destruction along the Atlantic Coast enables *Phragmites* to successfully invade these ecosystems (Silliman and Bertness 2004) and will aid in the continued expansion of its range throughout New England and potentially further south. Currently *Phragmites* distribution has been documented to overlap with known terrapin habitat in Delaware (Meadows 2016) and Virginia (Denmon 2014), and may continue to overlap in other areas throughout the terrapin range.

Phragmites expansion is associated with many impacts on tidal marsh ecosystems, including; decreased plant diversity, altered vegetation structure, and modified hydrology and soil properties (Chambers et al. 1999; Bolton and Brooks 2010). The height and density of mature *Phragmites* stands enables it to become the dominant species by crowding out other species and reducing the amount of solar radiation at the soil surface, available soil nutrients, and soil moisture (Meyerson et al. 2000; Rice et al. 2000). These ecosystem changes may also directly impact the fauna that inhabit these marshes. *Phragmites* has been shown to fill in small creeks in brackish tidal marshes, impacting aquatic fauna by restricting movements into important feeding areas (Roman 1978). *Phragmites* also has a negative impact on wildlife diversity by reducing habitat that is important for nesting, stopover during migration, and foraging (Benoit and Askins 1999). *Phragmites* expansion and reduction of shallow aquatic breeding habitat was attributed as the most likely cause of Fowler's toad (*Anaxyrus*

fowleri) population decline in Ontario marshes (Greenberg and Green 2013). The results of *Phragmites* invasion can be quite severe and have the potential to greatly affect the survival of a wide variety of species in a wide variety of habitats.

Phragmites may impact diamondback terrapin nesting because of its ability to alter aspects of the environment imperative for nesting success, such as vegetation structure, soil temperature, and moisture (Bolton and Brooks 2010). Terrapins prefer sparsely vegetated, sandy areas above the intertidal zone to lay their nests (Feinberg and Burke 2003; W. M. Roosenburg 1994), and have been found to commonly nest in areas with less than 20% vegetation cover (Burger and Montevecchi 1975). Terrapins exhibit temperature dependent sex determination (TSD), where clutches incubated under warmer temperatures ($> 30^{\circ}\text{C}$) will produce females while cooler incubation temperatures ($< 27^{\circ}\text{C}$) produce males (Jeyasuria et al. 1994). Laboratory studies have found the pivotal temperature for sex determination – the temperature that produces a 1:1 sex ratio – to be roughly 28.5°C (Jeyasuria et al. 1994). These temperatures are key during the critical sex-determining period, which is thought to occur sometime around the middle to last third of incubation (Burke and Calichio 2014; Mrosovsky and Pieau 1991). *Phragmites* invasion into sites could drastically reduce the amount of preferred sparsely vegetated nesting areas, and could shade nests to such an extent that incubating temperatures are reduced enough to produce male-dominated clutches. Most studied terrapin populations are female biased (Baldwin et al. 2005), so a high rate of adult female mortality coupled with male-dominated clutches could greatly skew the ratio of a breeding population.

In addition to skewing the sex-ratio of a breeding population, *Phragmites* has the potential to severely reduce nesting success. Root invasion of terrapin nests has been documented to occur from various species, including American beachgrass (*Ammophila breviligulata*) as well as *Phragmites* (Bolton and Brooks 2010; Lazell and Auger 1981). Nest invasion by roots often results in nest failure, either due to egg destruction or prevention of hatchling emergence (Lazell and Auger 1981). *Phragmites* has an extensive underground root system and rhizomes may spread up to 2 meters either horizontally or vertically (Rice et al. 2000). Many studies have found that most root growth happens above a depth of 50 cm in the soil profile (Kudo and Ito 1988; Moore et al. 2012), with a majority of roots growing in the spring and rhizomes growing in the summer (Engloner 2009). This depth and timing of *Phragmites* root growth is of concern to terrapin nesting success. When female terrapins nest on sand dunes colonized by *Phragmites*, terrapin nests - which are typically dug to a depth of 15cm below the soil surface (Butler, Seigel, and Mealey 2006) - may experience a large risk of root and rhizome invasion over the nesting season. The nesting season varies among geographic regions (Butler, Seigel, and Mealey 2006), but encompasses a main portion of the spring and summer growing season during which *Phragmites* undergoes prolific root growth and could possibly destroy a large number of incubating nests.

The ability of *Phragmites* to alter ecosystem functioning could impact terrapin nesting efforts and nest survival. The sandy nesting beaches imperative to terrapin nesting are adjacent to salt marshes at high risk of degradation from

invasive species colonization. Effects of habitat degradation may be further exacerbated by the fact that diamondback terrapins exhibit nest site fidelity, where females return to the same beaches to nest each season (Sheridan et al. 2010; W. M. Roosenburg 1994). If females return to nest every year in sub-optimal habitat, this could lead to low nesting success or skewed sex-ratios and could severely reduce population recruitment and persistence. It is imperative to study the intersection of *Phragmites* and terrapin nesting activity and the resulting changes to tidal marsh ecosystems that may influence terrapin nest success. The rate of *Phragmites* expansion may be faster than the rate at which terrapins may be able to adjust to subsequent habitat changes. Expansion of *Phragmites* into the terrapin range may create additional hardship for nesting females (Chambers et al. 1999; Bolton and Brooks 2010) but has never been examined directly. Loss of optimal nesting habitat may make it extremely difficult for terrapin populations to rebound from high rates of adult mortality, greatly impacting the propagation of this species (Baldwin et al. 2005).

I examined the potential impacts on terrapin nesting ecology that could result from *Phragmites* colonization using a study site in Virginia where terrapin habitat and *Phragmites* distribution overlap. Fisherman Island National Wildlife Refuge on the eastern shore of Virginia is a popular nesting area for northern diamondback terrapins (Denmon 2014; Hackney et al. 2013). *Phragmites* is present on this refuge, and may be expanding in some sections every year (Leffel 2015). To achieve my project goal I addressed two research objectives:

Objective 1: Determine the shading regime of terrapin nests at varying *Phragmites* densities and the resulting impact on incubation temperature. I hypothesized that nests laid in areas with higher *Phragmites* canopy cover would experience a lower incubation temperature than nests laid in more open areas. I predicted that heavily shaded nests would have an incubation temperature below the pivotal sex-determination temperature, and would follow a regime that would produce mostly male hatchlings.

Objective 2: Determine how the density of aboveground *Phragmites* influences the potential for rhizome invasion of terrapin nests. I predicted that nests laid in areas with high density of aboveground *Phragmites* would experience greater prevalence of root and rhizome invasion, and thus greater potential for nest failure.

Methods

Study Site: This study was completed on Fisherman Island National Wildlife Refuge (37°5'44.49"N, 75°57'38.17"W). Fisherman is Virginia's southernmost barrier island found at the mouth of the Chesapeake Bay. This roughly 800-ha island is under the jurisdiction of the U.S. Fish & Wildlife Service and is part of the Eastern Shore of Virginia NWR ("About the Refuge" 2016). It is an area known to contain breeding habitat for diamondback terrapins with high rates of incidental observation of terrapin nesting activity (Denmon pers. com).

Phragmites has also become established on the Refuge, and USFWS employees have not managed for its spread since 2011 so its expansion has

been unhindered for up to 5 years (Leffel pers. com). This island was selected for this study because of the likelihood of overlap between nesting terrapins and sandy dunes containing various densities of *Phragmites* coverage. Only areas known to have high concentrations of terrapin nesting were utilized for this study (Fig. 1), as Fisherman Island is used by many nesting bird species and access to all parts of the island are restricted.

Determine the extent to which terrapin nest incubation temperature is impacted by *Phragmites* shading

Experimental Design

To evaluate potential changes in terrapin nest incubation regime due to *Phragmites* shading, I measured simulated incubation temperatures in sites with varying densities of *Phragmites* cover. I buried 15 Thermochron iButton temperature loggers (#DS1922L) to compare temperature regimes across different vegetation cover classes. *Phragmites* density was separated into three classes by percent stem density: low (0-20%), medium (21-50%), and high (51-75%). Study plots were determined by taking a stem density measurement within a 1-m² quadrat around an intended “nest” site and evaluating the percent of ground covered by *Phragmites* (Fig. 2). Two observers generated independent estimates that were averaged. Observers also estimated the average coverage of other, non-*Phragmites* vegetation within the study plots by the same method. I buried 5 temperature loggers per cover class in sites that met these vegetation density requirements. A sample size of 5 loggers per cover class was chosen by

considering the results of a power analysis¹. I coated the temperature loggers in Plasti Dip to prevent water damage, and glued them to wooden paint sticks to remain conspicuous aboveground for collection. I buried the loggers 15-cm deep – the depth of an average terrapin nest (Butler et al. 2006) – and set them to record hourly temperature measurements. I deployed the loggers in late May 2015 and collected them 65 days after deployment to simulate an average terrapin nest incubation period in Virginia (Ruzicka 2006). I downloaded the temperature data using OneWire Viewer (Walden 2015).

Data Analysis:

I performed all statistical analyses in SAS using MIXED procedures. I investigated the effects of week, *Phragmites* cover class, and the interaction of week and cover class on simulated terrapin nest incubation temperatures using a repeated measures mixed linear model. The factors of interest were week (repeated factor), *Phragmites* cover class (fixed factor), plot (random factor), and the dependent variable was temperature. Cover classes were denoted as 1 (0-20%), 2 (20-50%), and 3 (50-75%). *Phragmites* cover was analyzed as a categorical variable to increase statistical power. Data loggers recorded hourly measurements for each sampling site, so I calculated the mean temperature per week (9 one week samples total) for each logger over the nesting season and

¹Analysis performed in R. An estimate of the effect size for incubation temperature was determined from data obtained from Grosse et al. (2014) and considered a 3°C change in incubation temperature to be a relevant effect size to measure (the difference between all male and all female producing temperatures). The power calculated for 5 loggers in each of the 3 cover class categories with an alpha level of 0.05 was 98%.

used that in the analysis. I modeled the variance and covariance structures, and the unstructured model had the lowest AICc value so it was used in the analysis.

Determine how *Phragmites* density impacts degree of rhizome invasion into nests

Experimental Design

To evaluate prevalence of root invasion into nests due to aboveground density of *Phragmites*, I buried 21 in-growth bags in sites with varying densities of *Phragmites*, with 7 bags per each *Phragmites* cover class density: 0-20%, 21-50%, 51-75%. The in-growth bags were used as nest proxies, and should not have affected the growth or roots around or into the bags (Steingrobe et al. 2001). In-growth bags consisted of a nylon mesh tube fitted over a 2-in diameter PVC pipe. I dug 30cm deep soil cores to determine root growth for a deeper soil profile, to see where terrapin nests lie on the root growth gradient. I placed the tube with bag in the soil core hole and then filled it with substrate (mostly sand) to the soil surface. The PVC pipe was carefully removed, the nylon tied off, and then covered over with remaining sand. I deployed in-growth bags on May 22, 2015 and excavated them on July 26, 2015. The 65 days growth period was chosen to simulate an average nest incubation period. To excavate the bags, I used a shovel to dig a wide hole around the in-growth bag, and then used a trowel and scissors to carefully excavate bags and prevent roots from being pulled out. Bags were wrapped in plastic wrap in the field then refrigerated until analysis. In the lab, the root bags were sectioned into 10-cm increments to

examine root growth across the soil profile. I sorted roots from soil using tweezers and a soil sieve. I then washed the roots in tap water to remove excess soil particles, and dried them in a 60°C oven for 24 hours, or until dry. Dried roots were weighed using an analytical balance to the nearest 0.1 mg.

Data Analysis

I performed all statistical analyses in SAS using MIXED procedures. I investigated the effects of *Phragmites* cover class, other vegetation cover, and depth on root biomass in each in-growth bag. I ran an analysis of variance (ANOVA) on total in-growth bag root biomass (log transformed for normality) to determine the effects of *Phragmites* cover on root growth. Because roots were hard to distinguish as *Phragmites* or other vegetation, I also investigated the effects of other vegetation found around the in-growth bags. Other vegetation found at the study site included low herbaceous species, most commonly American beachgrass (*Ammophila beviligulata*) and other native species found on coastal marshes in Virginia. I used a linear regression analysis to determine if percent cover of other vegetation related with in-growth bag root biomass. I also ran an ANOVA analysis on root biomass (log transformed) in each 10-cm increment of each in-growth bag to parse out effects of *Phragmites* cover on root growth by depth. This experimental set-up involved nesting and blocking, and was analyzed with the in-growth bags serving as blocks that were nested in *Phragmites* cover class, with the depth intervals (0-10cm, 10-20cm, 20-30cm) serving as the treatments.

Results

Temperature

Diamondback terrapins nested regularly throughout the study period (May 28-July 24) on Fisherman Island (see Chapter Two for data collection methods) (Fig. 3). The results of the unstructured repeated measures model showed that there was no interaction between week and cover class, so the interaction term was removed from the model. *Phragmites* cover class had a significant effect on nest temperature ($F_{2,12} = 8.31$, $p < 0.01$). Average “nest” temperature for the whole 65 day incubation period was the highest for cover class 1 (0-20%), and the lowest for cover class 3 (50-75%) (Table 1). When temperatures were examined on a weekly basis throughout the incubation period, “nests” in cover class 1 consistently had the highest temperatures while nests in cover class 3 consistently had the lowest temperatures (Fig. 3). For even the earliest nesters, temperatures during the sex determining period in cover class 1 (0-20%) remained entirely above the pivotal temperature. Cover class 2 (20-50%) had temperatures that were mostly above the pivotal temperature, while cover class 3 (50-75%) was entirely below the pivotal temperature for the whole incubation period. There was also a significant effect of week on nest temperature ($F_{8,7} = 365.48$, $p < 0.01$). Average weekly temperatures were warmer at the end of the incubation period than the beginning for each cover class, with some variation throughout.

Roots and Rhizomes

Phragmites cover class had no significant effect on total root growth into in-growth bags ($F_{2,17}=0.35$, $p=0.71$). Mean root biomass was very similar across all three *Phragmites* cover classes (Fig. 4). Analysis on the impacts of other vegetation yielded a significant regression equation ($F_{1,19}=19.71$, $p<0.01$), with an R^2 of 0.51. Other vegetation was a significant predictor of total root weight (Fig. 5). I was not able to determine the identity of roots in the in-growth bags as they were all very fine and looked similar and no rhizome ingrowth was observed. The ANOVA for root growth by depth showed that neither *Phragmites* ($F_{2,18}=0.23$, $p=0.80$) nor depth ($F_{2,40}=3.17$, $p=.0527$) had a significant effect on root growth. There was no discernable pattern regarding root growth, depth, and *Phragmites* cover (Fig. 6).

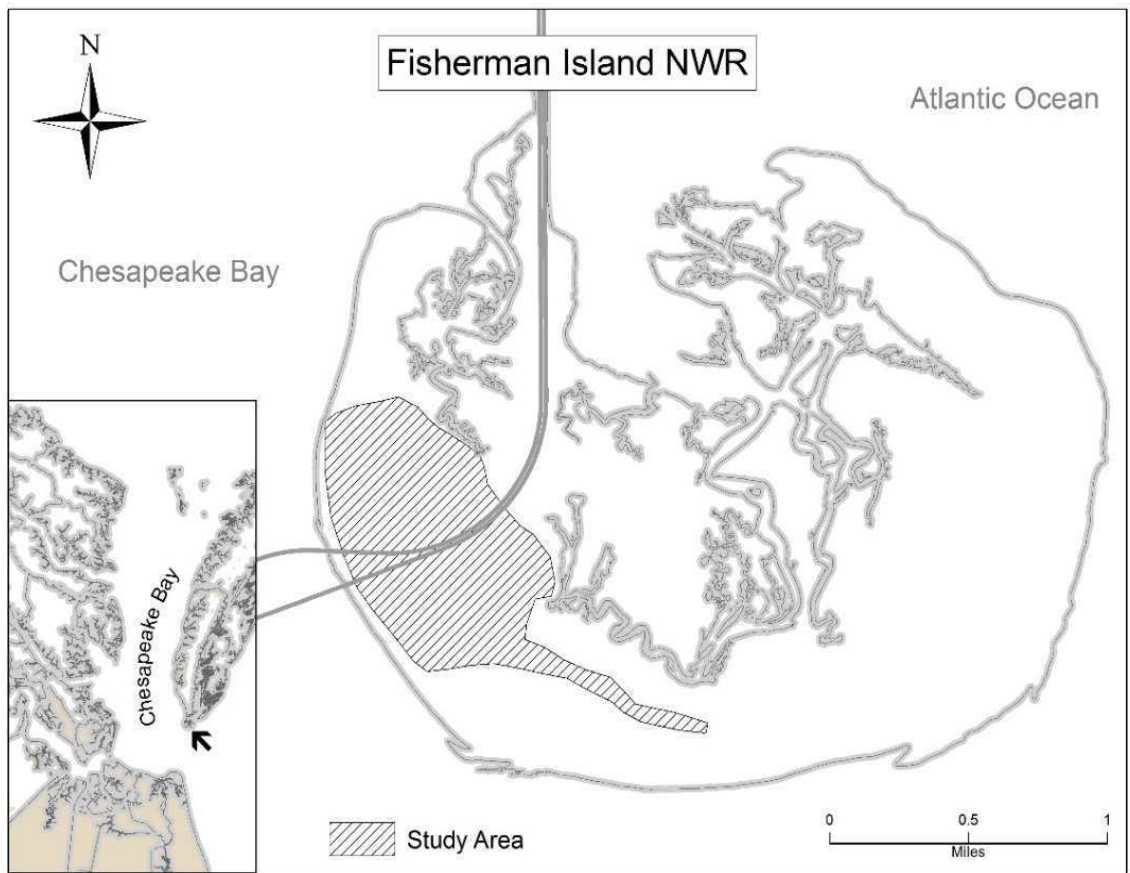


Figure 1. Map of Fisherman Island National Wildlife Refuge with a cross-hatched polygon of the study area. Fisherman Island is located on the eastern shore of Virginia, at the mouth of the Chesapeake Bay.

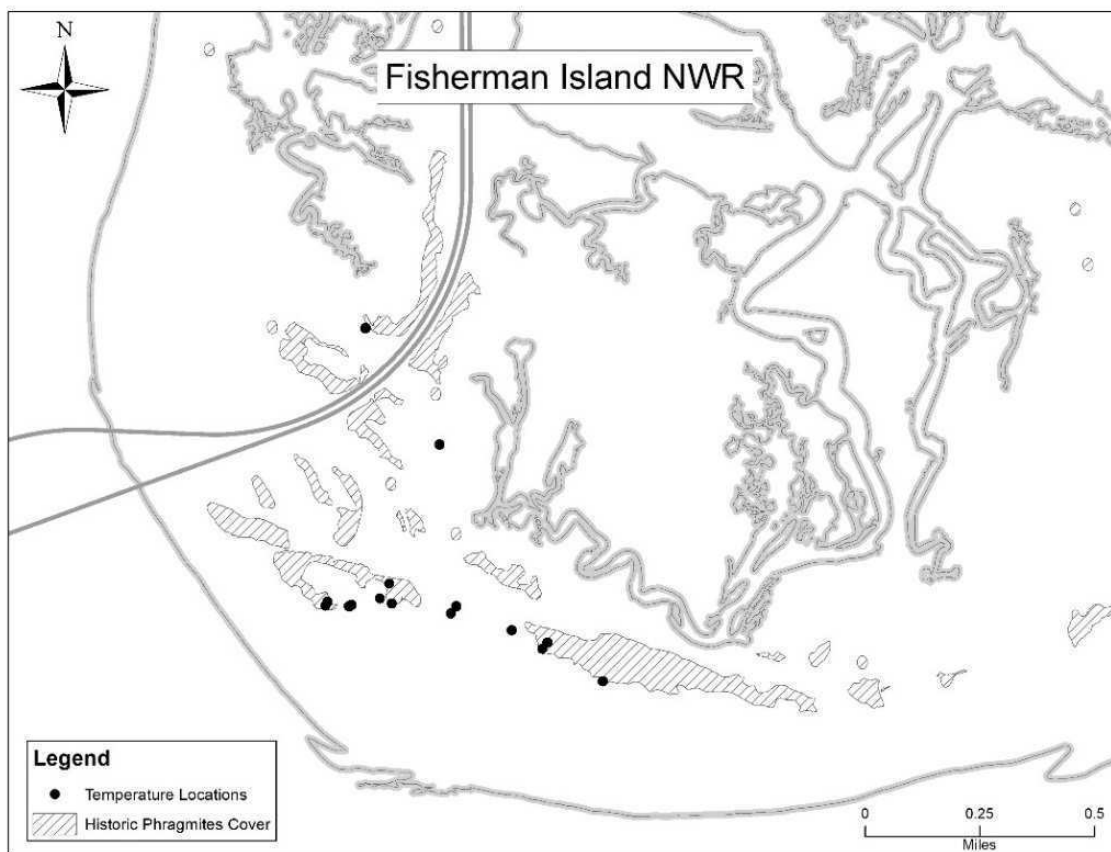


Figure 2. Locations where iButton data loggers were buried on Fisherman Island in relation to *Phragmites* occurrence

Table 1. Average "nest" temperatures for the total 65-day incubation period (May-July 2015) for each *Phragmites* cover class

Cover Class	Percent Cover	Mean Temperature
Low	0-20	28.2°C
Med	20-50	27.3°C
High	50-75	25.3°C

Table 2. Average "nest" temperature for each week during the 65-day incubation period (May-July 2015) for each *Phragmites* cover class

Cover Class	Mean Temperature by Week (°C)								
	1	2	3	4	5	6	7	8	9
Low	25.5	25.2	26.7	30.3	30.8	29.0	30.2	29.0	30.7
Med	24.7	24.5	25.7	28.9	29.4	28.1	29.1	28.1	29.6
High	22.6	23.0	23.6	26.6	27.1	25.9	26.9	26.2	27.3

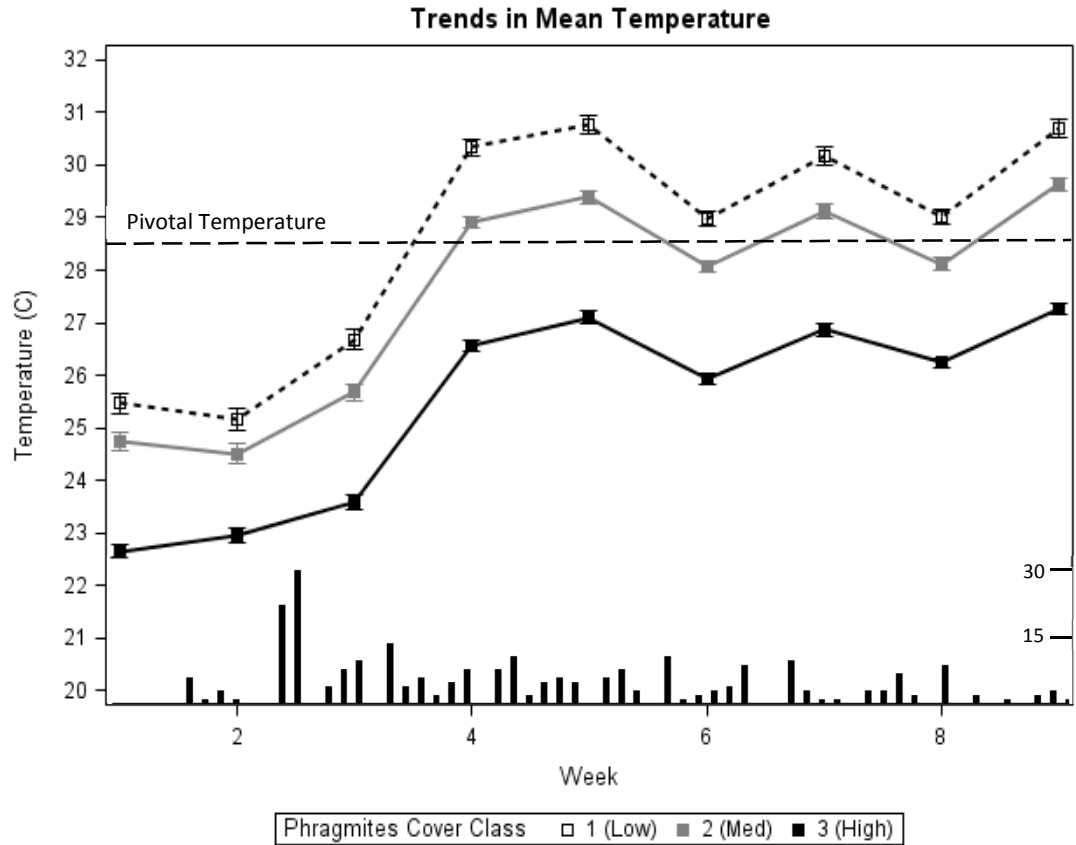


Figure 3. Means and 95% confidence intervals of “nest” temperature averaged by week for each *Phragmites* cover class (May-July 2015). Pivotal temperature shown (28.5°C). Bar plot of predated terrapin nests found per day.

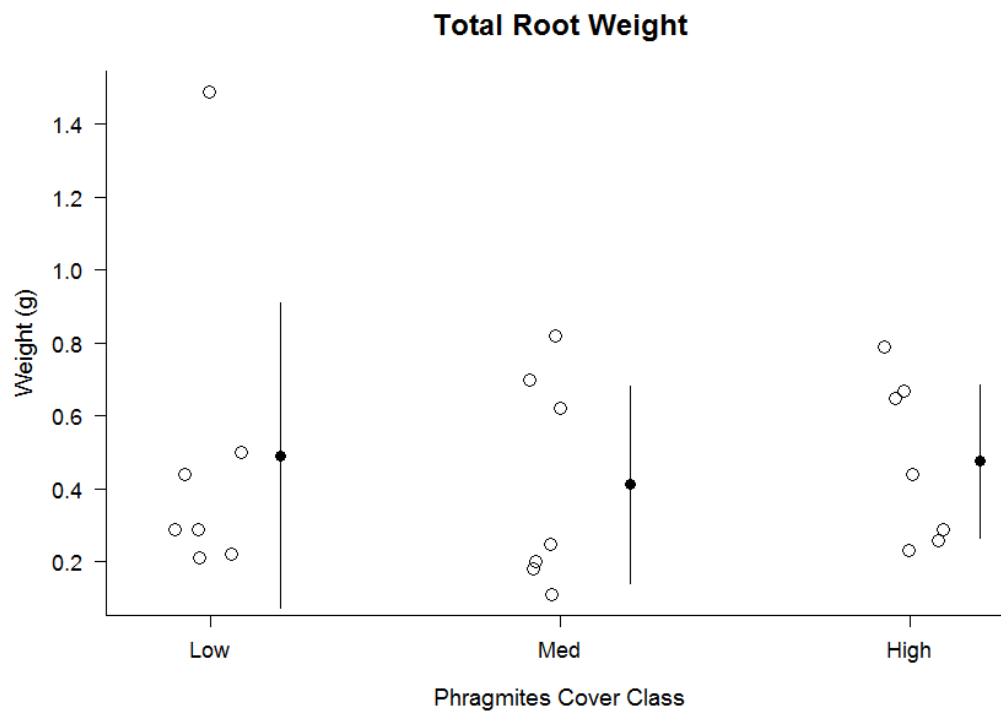


Figure 4. Means and 95% confidence intervals of total root weight of in-growth bags for each *Phragmites* cover class

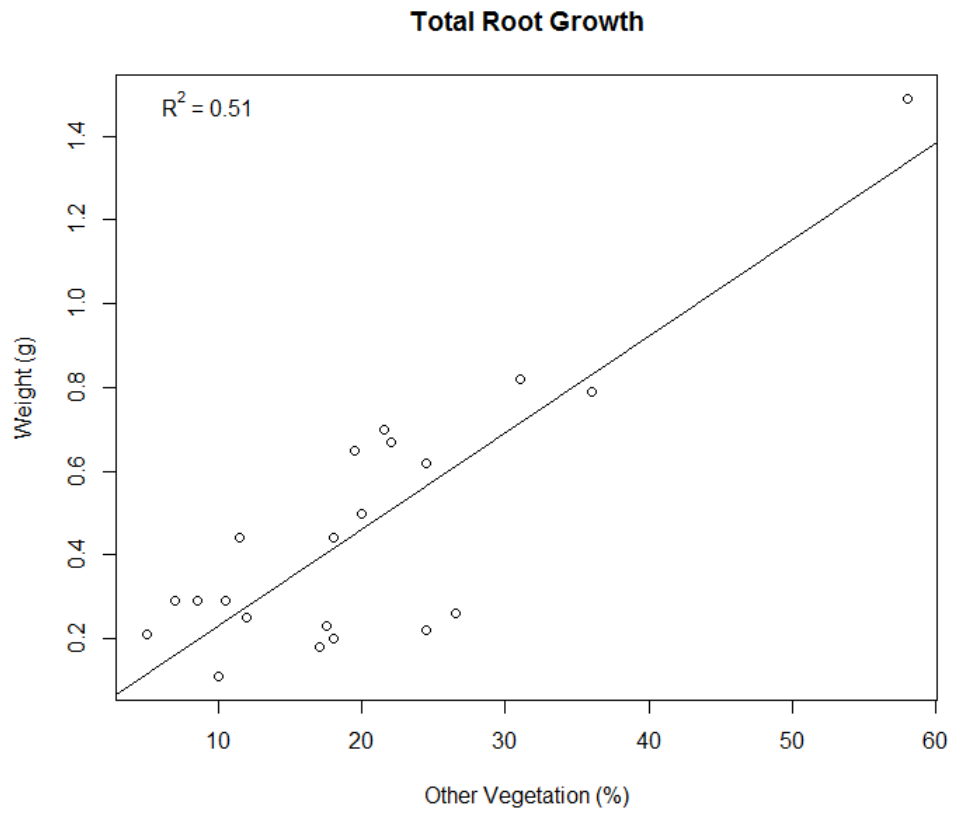


Figure 5. Plot of total root weight of in-growth bags by other above-ground vegetation cover.

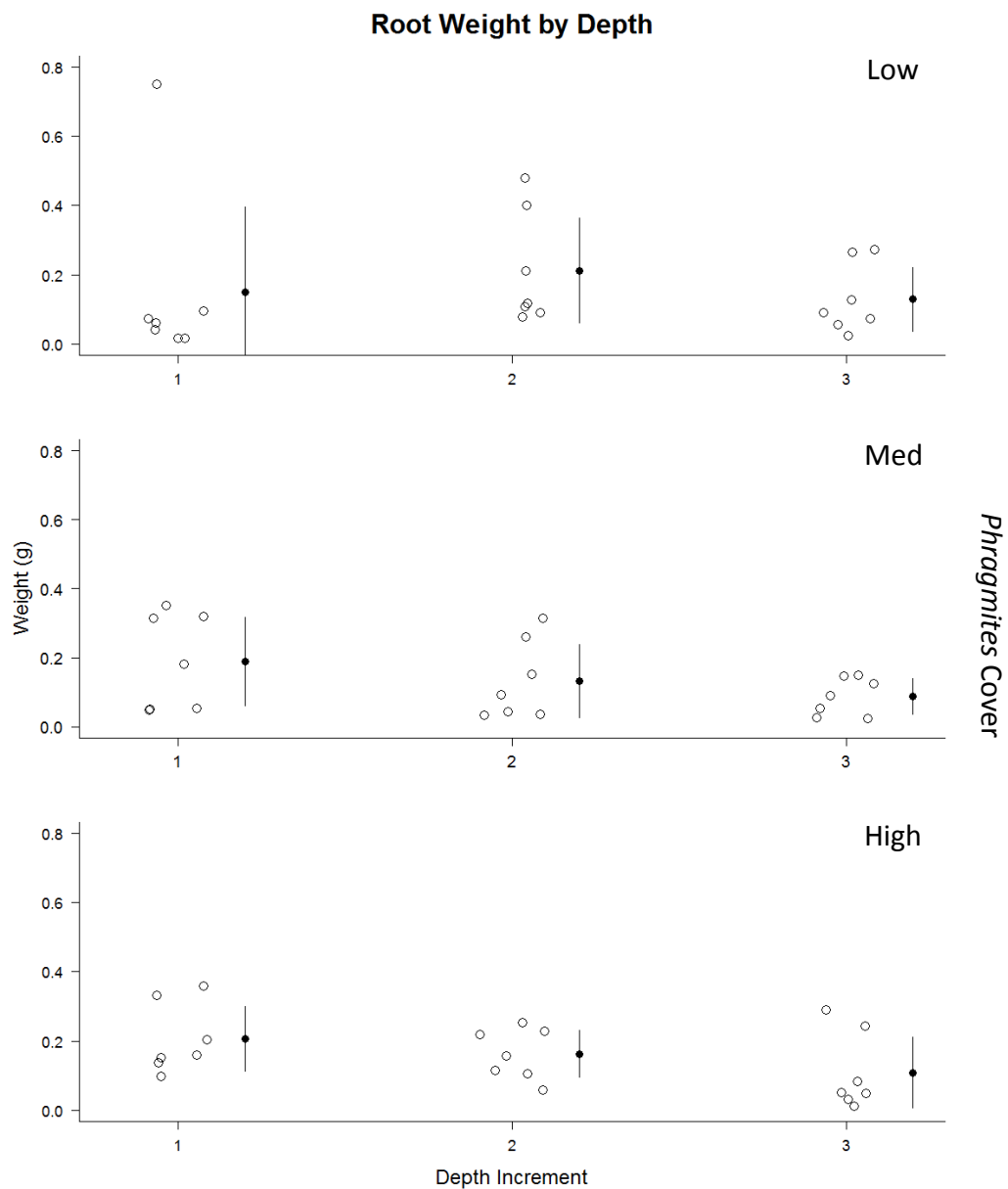


Figure 6. Means and 95% confidence intervals of root weight of in-growth bags by *Phragmites* cover class and by depth increment. 1=0-10cm, 2=10-20cm, 3=20-30cm

Discussion

I performed field studies to examine the potential of *Phragmites* to reduce incubating temperature of diamondback terrapin nests and increase the risk of rhizome and root invasion into nest chambers. I found that *Phragmites* cover from 0-50% still allowed nests to incubate at temperatures warm enough to produce both male and female hatchlings, whereas cover over 50% would most likely produce predominantly male hatchlings. This pattern was shown for the earliest nests laid in the spring, and would hold true for later nesters in cover classes 1 and 2 as ambient temperatures rise during the summer. It is undetermined if temperatures in cover class 3 would ever reach the pivotal temperature even for late nests that experience high mid-summer temperatures. I did not find significant differences in *Phragmites* root and rhizome growth among different aboveground cover classes, and there was not much evidence for *Phragmites* root growth into root bags at all. The changes in root weight in in-growth bags appear due mostly to other herbaceous species found on the sandy nesting dunes, as I found a significant positive correlation between root weight and other (non-*Phragmites*) vegetation cover. My work suggested the risk of *Phragmites* root invasion was low for terrapin nests, but other plant species may contribute to minor amounts of nest predation.

Though the effects of *Phragmites* on terrapin nests have never been studied directly, my findings are consistent with other studies concerning vegetation cover and reptile nest incubation. Grosse et al. (2014) found that diamondback terrapin nests incubated along hedgerows had average

temperatures below the pivotal incubation temperature (28.5°C), while nests in open grassy areas were much warmer. These differences were also consistent on a weekly basis across the incubation period. Bolton and Brooks (2010) documented that spiny softshell turtle (*Apalone spinifera*) nests shaded by *Phragmites* took over 10 days longer to incubate than unshaded nests, demonstrating that vegetation cover reduced nest temperatures sufficiently to affect development. These findings are important when considering sex-ratios and management of isolated populations of diamondback terrapins. Sex ratios in populations of diamondback terrapins seem to vary throughout the terrapin species range. Studies have estimated ratios to be female-dominant by 3:1 in Maryland (Roosenburg 1990), 5:1 in central Florida (Seigel 1984), and range from 9:1 to 21:1 in southern Florida (Baldwin et al. 2005), whereas Lovich and Gibbons (1990) found a slight male bias in South Carolina. This variability may be due to natural factors such as warmer ambient temperatures found in the south, or the fact that adult females tend to be easier to capture than males due to their large size. Crab pots also differentially kill male terrapins because of their smaller size (Baldwin et al. 2005). However, female bias seems to be common for populations of chelonians and crocodilians (Freedberg and Wade 2001). The potential consequences of *Phragmites* invasion on nest sites for terrapin populations are unknown, but could contribute to changing sex ratios and altering recruitment rates. If extensive *Phragmites* colonization of nesting sites causes a shift to mostly male hatchling production, it may cause some terrapin populations to go extinct. A model developed for a Rhode Island population of terrapins

showed that terrapin fecundity declines severely as mature females are increasingly lost to road mortality (Gilliand et al. 2014). This trend would be exacerbated if females were no longer being produced to replace the older population, and highlights the importance of female terrapin production and survival.

Significant *Phragmites* root growth was not found in this study; however, root growth into turtle nest chambers is a regular occurrence across species. *Phragmites* roots have been documented to grow into and destroy nests of spiny softshell turtles (*Apalone spinifera*) in Canada (Bolton and Brooks 2010), and root growth was documented to be responsible for destroying 23% of nests of loggerhead sea turtles (*Caretta caretta*) during one nesting season in Florida (Bouchard and Bjorndal 2000). *Phragmites* has the capability of being a severe belowground threat to turtle nests because of its growth habits. *Phragmites* underground biomass experiences peak growth in the early spring and late fall for roots, while rhizomes grow mostly in the summer (Engloner 2009) – so this is a threat that is present for most of the turtle nesting season. This growth pattern may also explain the lack of substantial *Phragmites* root growth into my in-growth bags – they were deployed when root growth was minimal. Nests laid on the periphery of *Phragmites* stands may also be under just as much threat of rhizome invasion as those laid within stands, as Sokup et al. (2002) found daily growth rate of rhizomes to be up to 23mm/day. Turtle species whose hatchlings overwinter in nests may experience even greater declines due to the longer time spent underground and increased accessibility by plant roots. Not much is known

about diamondback terrapin hatchling behavior once they leave a nest, but they have been found to overwinter in nests (Draud et al. 2004; Muldoon and Burke 2012) and may be more susceptible to *Phragmites* root invasion when in the nest chamber for an extended period of time. Root invasion is a threat to diamondback terrapin nest success, however further study will be needed to fully understand the specific threats due to *Phragmites*.

Additional work could enhance our understanding of the relationship between *Phragmites* invasion and diamondback terrapin nesting success. Terrapin nests and eggs were not used in this study due to logistical constraints, and this may be one major limitation of this study. Burger (1976), for example, found a significant difference in temperature between terrapin nests and the soil 5-cm from the nest at a study site in New Jersey. Daily mean temperatures in incubating nests were significantly higher than the surrounding soil. This finding was attributed to metabolic heat produced by the embryos. Placing temperature loggers in an experimental nest with terrapin eggs and taking into account metabolic heat could reduce the differences in incubation temperature I observed among *Phragmites* cover classes. The absence of terrapin eggs may have also impacted the root growth study results. Nesting turtles provide a source of nutrients to the nest sites they choose (through exudates or embryonic material), and may provide an important source of nitrogen in sand dunes where this nutrient is a limiting factor (Hannan et al. 2007; Stegmann et al. 1988). A study by Stegmann et al. (1988) found that American beachgrass (*Ammophila breviligulata*) grown in the presence of terrapin eggs grew much larger and had

many more branched, lateral roots than when grown without eggs. Terrapin eggs may be a source of nutrients for growing roots. Absence of terrapin eggs in the in-growth bags may not have accurately reflected the risk of root invasion for terrapin nests in nutrient poor sand dunes. Further study of the impacts of *Phragmites* (and vegetation) on incubating turtle nests should take this into account.

My study shows evidence of *Phragmites* impacting soil temperatures (potential nests) when present in great enough densities, but the question still remains whether terrapins will nest in areas with greater than 50% *Phragmites* cover. The answer is mostly likely no, because past studies have shown that terrapins tend to nest in relatively open, sandy areas (Roosenburg 1994). During the time of this study, terrapin nests were found in 25% *Phragmites* cover or less, indicating a preference to avoid stands of dense *Phragmites*. Increased *Phragmites* growth into terrapin nesting areas would make traveling and digging difficult, and would most likely exclude terrapins from those nesting areas. Experimental *Phragmites* removal from a known terrapin nesting beach in Delaware resulted in terrapins returning to nest at sites a few years after vegetation was removed (Meadows pers. com). Apparently, dense vegetation completely excluded the terrapins from nesting at these sites. When preferred open sand dunes disappear due to vegetation colonization, female terrapins must deviate from nest site fidelity and find new suites more suitable for nesting. Owing to the suspected limited plasticity in nest site selection by female

terrapins, management strategies to maintain suitable terrapin nesting habitat will be imperative to sustaining their populations.

Managing *Phragmites* comes at a high cost – in time and effort, as well as monetarily. Effective removal strategies include herbicide application and prescribed burning, but regular treatments 2-3 years after an initial treatment must be implemented in order minimize *Phragmites* regrowth (Ailstock et al. 2001; Meadows pers. com). My study results suggest that complete extirpation of *Phragmites* is not necessary to have successful terrapin nesting. On Fisherman Island, terrapins were found to nest in less dense stands of *Phragmites* and the results of the temperature and root study show that impacts of *Phragmites* on the fate of the nests would be minimal. As long as terrapins are still able to access nesting areas, they may still be able to reproduce unhindered if *Phragmites* coverage is minimal (or less than 50%).

My study was developed to determine the potential impacts of invasive vegetation on the reproductive success of an estuarine turtle species with temperature-dependent sex determination, and to aid land managers in making informed decisions about habitat and wildlife conservation. When studying the ecology of *Phragmites*, there is a great dichotomy of whether or not its role in ecosystems is a positive or a negative one. *Phragmites* has been shown to stabilize shorelines, remove excess nutrients from soil, and even provide nesting habitat for some bird species (Ailstock et al. 2001; Meyerson et al. 2009). However there are a suite of negative consequences to *Phragmites* invasion, including reduced and degraded habitat required for nesting turtles. Ensuring

higher rates of nesting success will increase the diamondback terrapin's ability to adapt to other environmental changes, and to rebound from high rates of adult mortality due to the blue crab fishery. While some Chelonian population models predict that juvenile or adult survivorship is the key driver behind population persistence (Crouse et al. 1987), increasing nesting success combined with strategies to reduce adult mortality will help ensure diamondback terrapin persistence. With anthropogenic disturbance contributing to the increase of *Phragmites* colonization (Silliman and Bertness 2004), overlap with diamondback terrapin habitat will increase and so must the effort in managing this invasive species. The effects of *Phragmites* are not only experienced by terrapins in brackish marshes; *Phragmites* is inhibiting reptile nesting in freshwater ecosystems and impacting other turtle species. We need a better understanding about natural sex-ratios in terrapin populations so that we can predict how shifts in hatchling sex determination may impact these populations. Expanding upon this study to make spatial models that highlight areas where existing terrapin populations are at high risk of negative effects from invasive *Phragmites* would be a great next step for effective management.

Chapter 2: Impacts of *Phragmites australis* on terrapin nest site use and nest predation

Introduction

In Chapter One the effects of *Phragmites australis* on diamondback terrapin nests was examined on a microhabitat scale. This Chapter will examine the impacts of *Phragmites* on a larger scale, considering how vegetation may impact terrapin nest site selection. Nest site selection by females is a large factor in determining predation risk of nesting species (Leighton et al. 2011). It can be a strong selector on maternal fitness due to its high influence on offspring survival (Spencer 2002). Vegetation structure of the habitat may determine where an animal is able to nest, and can also lead to uneven predation risk throughout the habitat (Leighton et al. 2011; Söderström et al. 1998). Plants create a three-dimensional structure throughout the landscape which often mediates predator-prey interactions (Pearson 2009). Exotic species invasions can change this landscape structure and thus alter the relationships between predator and prey. Pearson (2009) found that invasions of spotted knapweed (*Centaurea maculosa*) into western grasslands caused a shift in web spider community structure. Spotted knapweed allowed spiders to build larger webs than native vegetation, and thereby capture more prey. *Phragmites australis*, an invasive species to the United States, has the capacity to modify habitat features on a relatively rapid time scale because of its ability to colonize quickly and form dense monocultures (Silliman and Bertness 2004). This may cause changes that are beneficial to nest

predators, but detrimental to prey species that inhabit newly colonized *Phragmites*-dominant habitats.

The vegetation structure of diamondback terrapin nesting beaches is a factor that can have severe impacts on nesting success through its influence on foraging patterns as well as detectability of prey. Raccoons (*Procyon lotor*) and fish crows (*Corvus ossifragus*) are among the most prevalent predators of diamondback terrapin nests and have the potential to severely decrease nest success, but these species employ different foraging strategies (Schmidt 1999). Raccoons forage nocturnally by smell and are particularly adept at finding terrapin nests; one study at Jamaica Bay National Wildlife Refuge documented over 90% predation of monitored nests during one nesting season (Feinberg and Burke 2003). Raccoons are considered the most voracious predators of terrapin nests, and many studies have found that their foraging behavior is mediated by vegetation (Barding and Nelson 2008; Newbury and Nelson 2007). The influence of “Edge Effects” on raccoon (and other species) predation are both supported and negated throughout the literature (review by Lahti 2001), but if raccoon foraging is influenced by edges, then it is highly likely that *Phragmites* colonization of terrapin nesting beaches could further facilitate this pattern. Dense *Phragmites* stands create a well-defined vegetation edge for raccoons to forage along, providing both protective cover and a delineated travel corridor. These features may make *Phragmites*-dominant habitats more likely for raccoons to travel through and forage within terrapin nesting beaches, and increase terrapin nest failure due to predation.

Corvid species, such as crows, are also frequent predators of terrapin nests, but are diurnal visual predators (Huhta et al. 1996). They use cues such as egg visibility or activity of nesting females in order to locate nests (Sullivan and Dinsmore 1990), and search by air or on foot (Sugden and Beyersbergen 1986). Tall, dense vegetation cover can deter crows foraging on the ground, and conceal nests from their view. Sugden and Beyersbergen (1987) found that simulated duck nest survival from corvid predation was greater in sites with taller vegetation, and nests were found faster in sites with shorter vegetation.

Phragmites may impede the ability of crows to locate nesting terrapins and dig up freshly laid nests. In contrast with raccoons, *Phragmites* presence in a nesting area may actually reduce the amount of avian predation on terrapin nests.

Predictions of *Phragmites* effects on terrapin nest predation by different predator species might hold true if terrapins nested evenly across a habitat with *Phragmites* distributed heterogeneously across the landscape. However, if *Phragmites* limits the availability of total nesting area and restricts terrapins to nesting in certain areas (i.e. nesting is clumped), then predation rates may be higher by both raccoons and crows due to the impact of density dependence. Density dependent predation is the theory that predators will respond to and spend more time in areas where a food resource is more common than other areas of the landscape where food is scarce (Burke et al. 1998; Schmidt and Whelan 1999). Though some discrepancy exists in the literature on whether this pattern always holds true (Burke et al. 1998), medium-sized generalist predators (raccoons and crows) are more likely to exhibit this type of behavior. They have

relatively large home ranges that produce the opportunity to experience heterogeneous resource availability, and selectively spend time in areas that are more profitable (Schmidt and Whelan 1999). Mesocarnivores such as raccoons may develop search images that aid in allocating more time in these areas where resource availability is high (Byrne and Chamberlain 2012). Crows also have increased predation success with increased prey abundance because they generally return to sites of previous foraging success (Shields and Parnell 1986). *Phragmites* colonization of brackish marshes and nesting beaches may restrict the total available nesting habitat for terrapins, resulting in a high density of nests laid within a small area. Terrapins may experience greater nest predation by raccoons and crows at nesting areas spatially restricted by *Phragmites* due to the highly profitable area that has been created.

Maternal nest site selection not only influences predator detection of nests, but also controls incubation regime and success for oviparous species that lack parental care (Brooks et al. 1991; Horrocks and Scott 1991). Site characteristics of turtle nests such as vegetation, slope, and elevation have been shown to impact embryo survival and development (Bobyne and Brooks 1994; Wilson 1998). Examining predated turtle nests provides an opportunity to determine habitat features associated with nesting preference. Past studies have shown that diamondback terrapins typically nest on sparsely vegetated sand dunes above the high tide line (Feinberg and Burke 2003; Roosenburg 1994). Burger and Montevercchi (1975) found that terrapins nesting in New Jersey preferentially nested in high dune areas: likely to prevent flooding during

incubation. Nest site selection impacts reproductive success and should be a selective force for choosing sites that maximize offspring survival for species that lack paternal care (Crump 1991). It is imperative to understand the habitat characteristics required for successful terrapin nesting to offset high rates of predation.

Nest predation is considered one of the greatest threats to turtle offspring (Spencer and Thompson 2003), with average survivorship of terrapin eggs found to be roughly 1-3% (Baldwin et al. 2005). Presence of *Phragmites* and stand density in terrapin nesting sites has the potential to influence predation rates and to alter the species specific nature of predation. This has important conservation applications, as diamondback terrapin populations were in decline dating back to the early 20th century (Baldwin et al. 2005), and after a brief rebound are now thought to be declining again. Efforts to increase population recruitment are important for successful terrapin management. I examined predation of terrapin nests on a barrier island in Virginia to determine if any patterns exist in response to *Phragmites* presence which could be explained by vegetation structure changes. I also examined other nest site characteristics to determine if diamondback terrapin nesting on the eastern shore of Virginia matched and supported the existing literature on female nest site selection, as well as to provide more data on terrapin nesting activity in Virginia. To achieve my project goals I addressed two main research objectives:

Objective 1: Determine the extent to which predation of terrapin nests is influenced by *Phragmites* density. I hypothesized that *Phragmites* cover would impact the ability of predators to detect terrapin nests, and that predation patterns would vary with *Phragmites* density. If nests are laid evenly across the landscape in areas with and without *Phragmites*, I predicted that nests laid in areas with *Phragmites* present would experience less avian predation, relative to raccoon predation, due to reduced visibility of nesting activity for corvids. I predicted that there would be higher avian predation in areas without *Phragmites*, but not necessarily higher than raccoon predation. If *Phragmites* restricts terrapin movement and concentrates nesting into certain areas, then I would expect to see higher rates of predation by both corvids and raccoons in areas of higher nest density.

Objective 2: Determine whether nest site characteristics such as presence of *Phragmites*, elevation, and distance to marsh or tidal creek, could explain the observed variation in terrapin nesting density. I hypothesized that terrapins would nest at sites with low *Phragmites* coverage in order to reduce shading of incubating nests. I also hypothesized that female terrapins would nest closer to marsh and tidal creeks for ease of access to nest sites. Finally, I hypothesized that terrapins would nest at sites with higher elevation to reduce the risk of flooding of incubating nests.

Methods

Study Site: This study was also performed on Fisherman Island National Wildlife Refuge, chosen because of the high rate of diamondback terrapin nesting previously reported on the island, as well as relatively high rates of nest predation. The dominant terrapin nest predators found at this site are raccoons and fish crows (Denmon pers. com). Raccoon predation is also a threat to nesting shorebirds on the refuge, and the USFWS implements annual raccoon trapping to reduce predation on nests. Predator activity has been documented across the island, so it is likely that there will be areas of overlap of foraging predators, terrapin nests, and the presence and absence of *Phragmites*.

Examine predation of terrapin nests – predator behavior and landscape variation

Observational Study

I collected observational data on predated terrapin nests on Fisherman Island over the 2015 nesting season. While an observational study on all terrapin nests laid and the fate of each nest would provide the most comprehensive information, the scope of work is much too large for this Master's thesis. Due to the vast area to be covered by relatively few people and the large effort involved in determining if nests are successful, only predated nests were counted. I performed predated nest searches from late May to late July to encompass the majority of the terrapin nesting season. I surveyed the study area for a total of 50 days (non-consecutive) throughout the nesting season, with nest searches taking

place between 07:00 and 14:00 each day. Nests were considered to be predated if fragments of egg shell were present on the sand surface and there was evidence of digging. Predator type was determined by the state of the egg shells: shells ripped apart indicated raccoon predation whereas shells with hole punctures indicated crow predation. I took stem density measurements within a 1-m² quadrat centered on a predated nest and evaluated the percent of ground covered by *Phragmites* as well as other vegetation. Once a nest was documented as predated it was covered up and egg fragments were removed to prevent double counting during subsequent surveys. Coordinates of all nests were taken with a handheld Trimble GPS unit. GPS points were differentially corrected and 90% of points had sub-meter accuracy.

Nest Site Use

I examined other landscape features to determine which might be associated with diamondback terrapin nest site use. GPS points of predated nests were projected into ArcMap 10.2. To determine if landscape features had an effect on nesting occurrence, I imported shapefiles delineating areas of marsh and deep water of Fisherman Island, from the National Wetlands Inventory database (U.S. Fish and Wildlife Service 2013). Areas of deep water were delineated on a rather coarse scale, so I hand-digitized tidal creeks from a 2013 aerial image of Fisherman Island (Virginia Base Mapping Program). The “Near” spatial analyst tool was used to determine the shortest distance between a predated nest to marsh and to deep water tidal creeks. I also obtained elevation data from U.S. Geologic Survey National Elevation Dataset (Data available from

the U.S. Geological Survey). This provided raster data of elevations of most of the conterminous United States to a ~10m resolution. I used the “Extract Values to Points” tool to obtain an elevation for each predated nest.

Data Analysis

I performed all statistical analyses in SAS on predation data during the 2015 nesting season². I examined the impact of *Phragmites* on nest predator type using a chi-squared contingency test, with presence/absence of *Phragmites* as the independent variable and predator type as the dependent variable. Only nests for which the predator could be positively determined were used in this analysis. Data on terrapin nest site use were averaged across all nests to provide a general idea of preferred nest sites in relation to distance to marsh, distance to creek, elevation, presence of *Phragmites*, and percent of other vegetation cover. During this study, I found terrapin nesting (as identified by predated nests) to be clumped in two distinct areas on Fisherman Island: a high density area north of the highway and a low density area south of the highway. Possibilities for why this occurred were also explored in analysis of predated nest data and habitat characteristics. I performed a correlation analysis using the CORR procedure to determine if nest site variables were related. I then put the appropriate variables into a generalized linear model under a binomial distribution using the LOGISTIC procedure. A multivariate logistic regression was run. The binary dependent variable was high or low density nesting area, and the factors of interest were

² Past studies have been completed in Virginia examining terrapin nesting, however neither study recorded information on surrounding vegetation and thus were unable to be included in statistical analyses.

distance to marsh, distance to tidal creek, elevation, presence/absence of *Phragmites*, and percent other vegetation cover. All predated nests were used in this analysis.

Results

Nest Predation

A total of 259 predated nests were found during the 2015 nesting season (Fig. 7), with 232 (90%) nests having no *Phragmites* within 1-m² of the nest and 27 (10%) nests having *Phragmites* present. Raccoons depredated 170 (66%) nests, crows depredated 64 (25%) nests, and for 25 (9%) nests the predator was undetermined (no definitive shell fragments) (Fig. 8). For nests where predator type was determined, there was no evidence that nest predator type was dependent upon presence or absence of *Phragmites* in nest sites ($\chi^2=0.76$, $p=0.38$) (Fig. 9).

Nest Site Use

On average, terrapin nests found on Fisherman Island were 34-m (SD=25.6) from the closest marsh (range 0-90m) (Fig. 10), 80-m (SD=27.9) from tidal creek (range 11-147m) (Fig. 11), and 1.9-m (SD=0.6) above sea level (range 0.9-4.1m) (Fig. 12). A majority of nests were free of *Phragmites* (90%), and on average had 29% (SD=19) non-*Phragmites* vegetation cover (range 1-90%) (Table 3; Fig. 13). The high density area had roughly 0.024 nests/m² of nestable beach habitat, and the low density area had 0.003 nests/m². The

correlation analysis (Table 4) showed that no factors were highly correlated, so all were included in a logistic regression model.

Most factors fit the assumption of linearity between independent variables and the logit of the response, but distance to marsh and elevation required an $\ln(x+1)$ transformation. The data also satisfied the outlier influence assumption. When comparing factors between the high versus low density nesting sites, my generalized model was significant and fit under the binomial distribution (Hosmer-Lemeshow $\chi^2=5.57$, $p=0.7$, Likelihood Ratio $p<0.01$) (Table 5). Distance to marsh had a significant effect on location of terrapin nests (Wald $\chi^2=10.57$, $p<0.01$) with nests in the high density area being significantly farther from the marsh than the low density area. Distance to tidal creek had a significant effect on location of terrapin nests (Wald $\chi^2=6.09$, $p=0.01$) with nests in the high density area being significantly farther from creeks than the low density area. Elevation did not have a significant effect on location of terrapin nests (Wald $\chi^2=1.19$, $p=0.27$). However, a graph of the means and confidence intervals show that confidence intervals of the high and low nesting density areas do not overlap – indicating that elevation influences terrapin nest site use (Fig. 12). Presence of *Phragmites* had a significant effect on location of terrapin nests (Wald $\chi^2=22.78$, $p<0.01$) with nests in the high density area having significantly less instances of *Phragmites* surrounding them than nests in the low density area (Fig. 13). I saw no effect of other vegetation cover on the probability of terrapins nesting in the high or low density area (Wald $\chi^2=0.56$, $p=0.45$) (Fig. 14).

Table 3. Averages and std. dev for all factors associated with predated terrapin nests found May-July 2015

	Dist. Marsh	Dist. Creek	Elevation	Other Veg.	Prop. w/ <i>Phragmites</i>
Mean	33.9 m	79.9 m	1.9 m	29.2%	10%
Std. Dev.	± 25.6 m	± 27.9 m	± 0.6 m	± 19%	N/A

Table 4. Results of a correlation analysis, including Pearson Correlation Coefficients, *Prob > |r| under H0: Rho=0*

	Dist. Marsh	Dist. Creek	Elevation	Other Veg.
Dist. Marsh	1.00	0.57 <.0001	0.03 0.63	-0.12 0.05
Dist. Creek	0.57 <.0001	1.00	0.02 0.78	-0.05 0.43
Elevation	0.03 0.63	0.02 0.78	1.00	0.14 0.03
Other Veg.	-0.12 0.05	-0.05 0.43	0.14 0.03	1.00

Table 5. Results from the logistic regression on factors influencing terrapin nest site use

Factor	High Density (mean)	Low Density (mean)	β	SE	Wald χ²	P value	Effect Size
Dist. Marsh	39.1 m	10.8 m	0.51	0.16	10.57	0.0011	28.3 m
Dist. Creek	84.0 m	61.2 m	0.02	0.01	6.09	0.0136	22.8 m
Elevation	1.96 m	1.60 m	1.45	1.33	1.19	0.2745	0.36 m
Other Veg.	29.1%	29.6%	-0.01	0.01	0.56	0.4535	0.50%
<i>Phragmites</i>			1.41	0.3	22.78	<.0001	

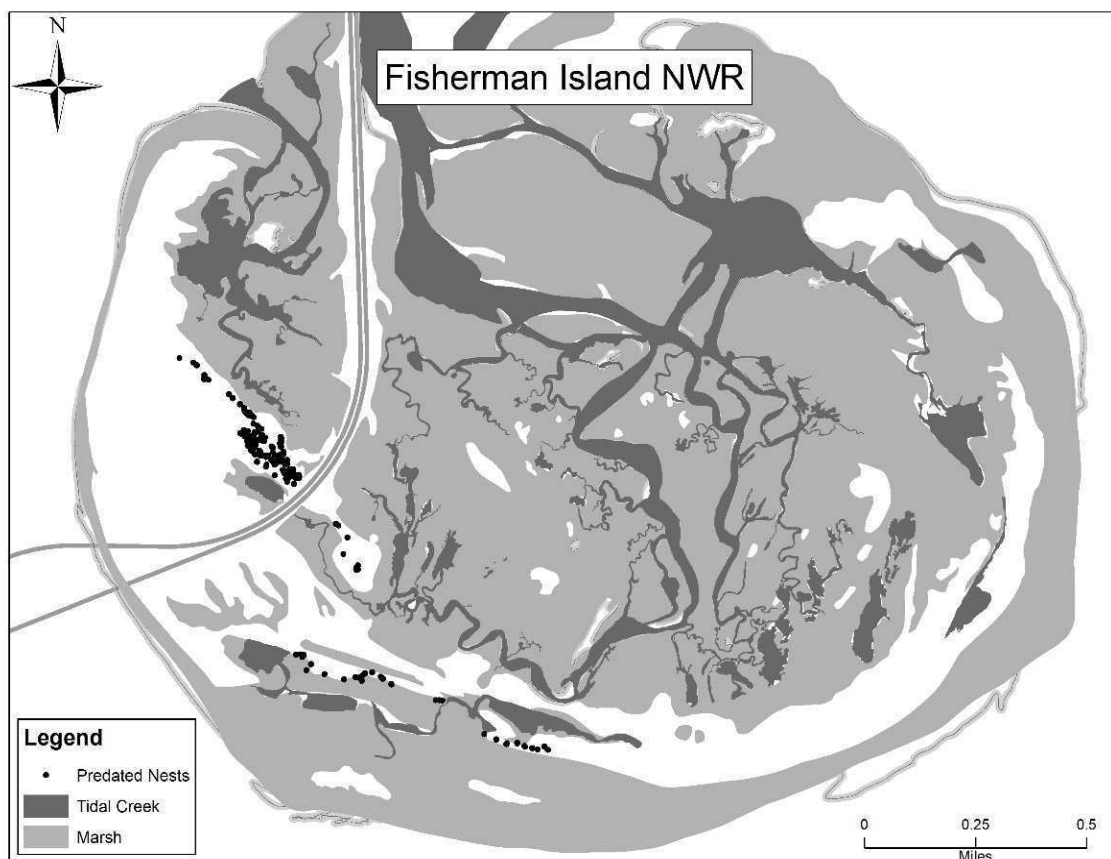


Figure 7. Map of locations of predated nests found during the 2015 nesting season.

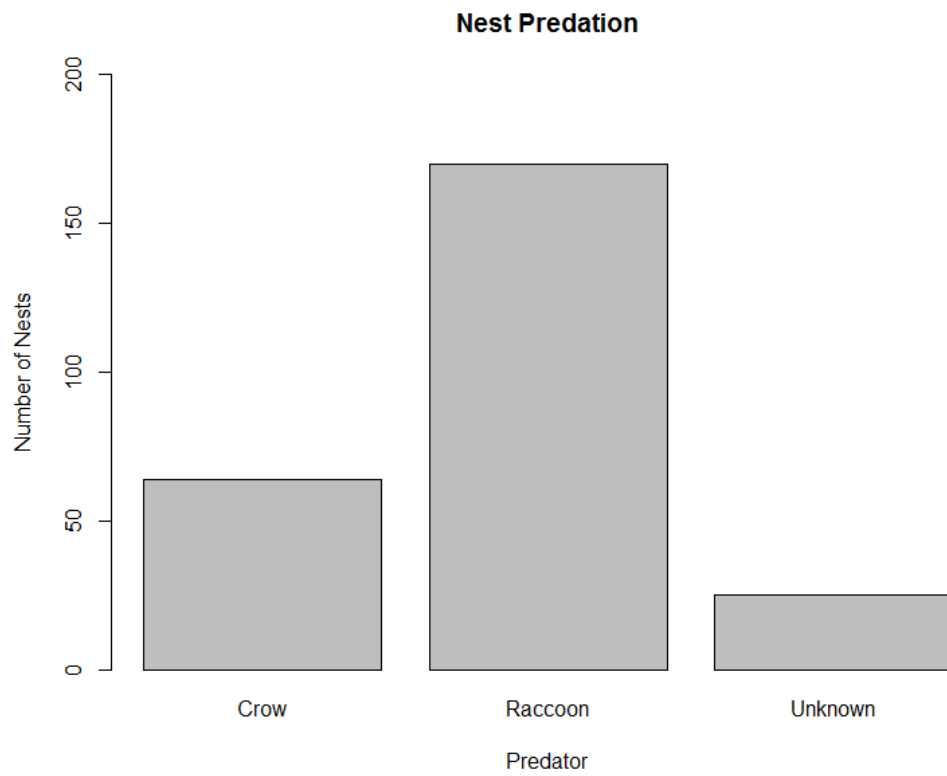


Figure 8. Number of nests predated by different predator species.

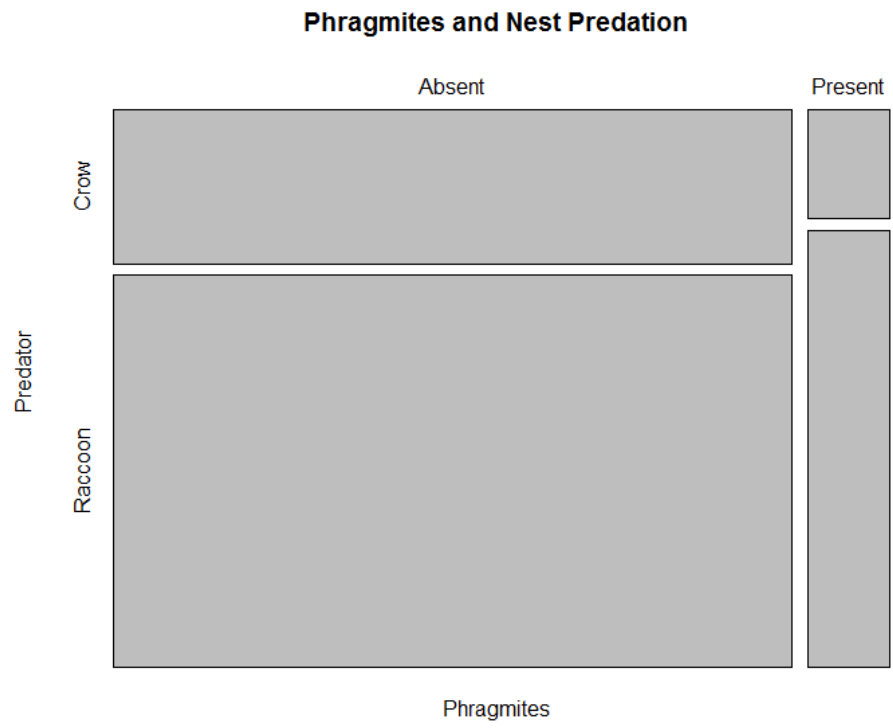


Figure 9. Mosaic plot of predator type by *Phragmites* presence.

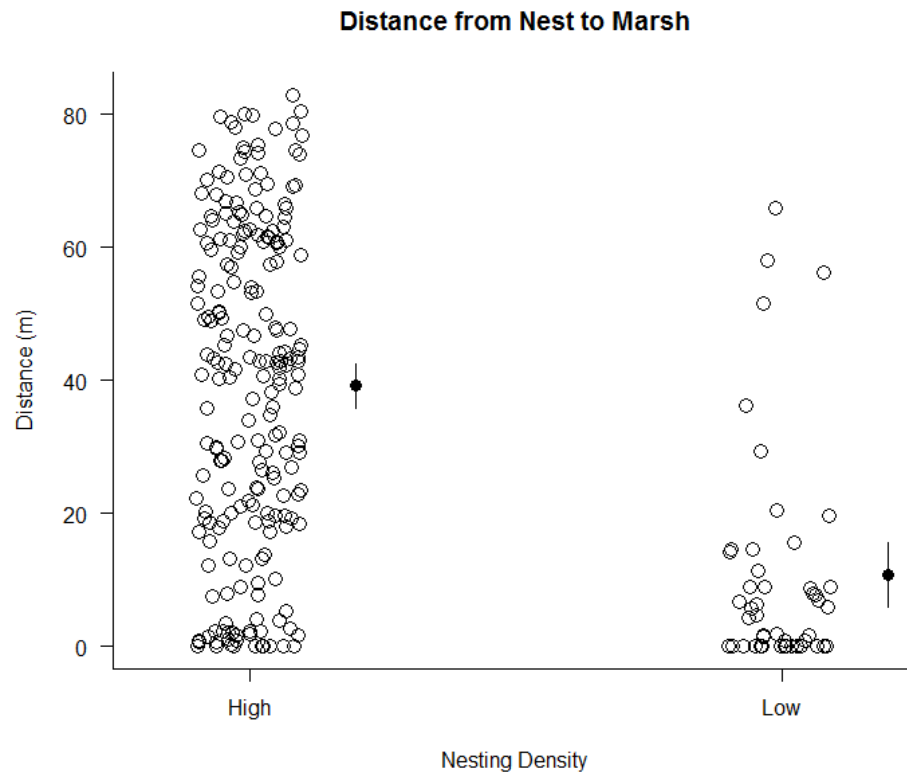


Figure 10. Distance of predated nests to nearest marsh (with means and 95% confidence intervals).

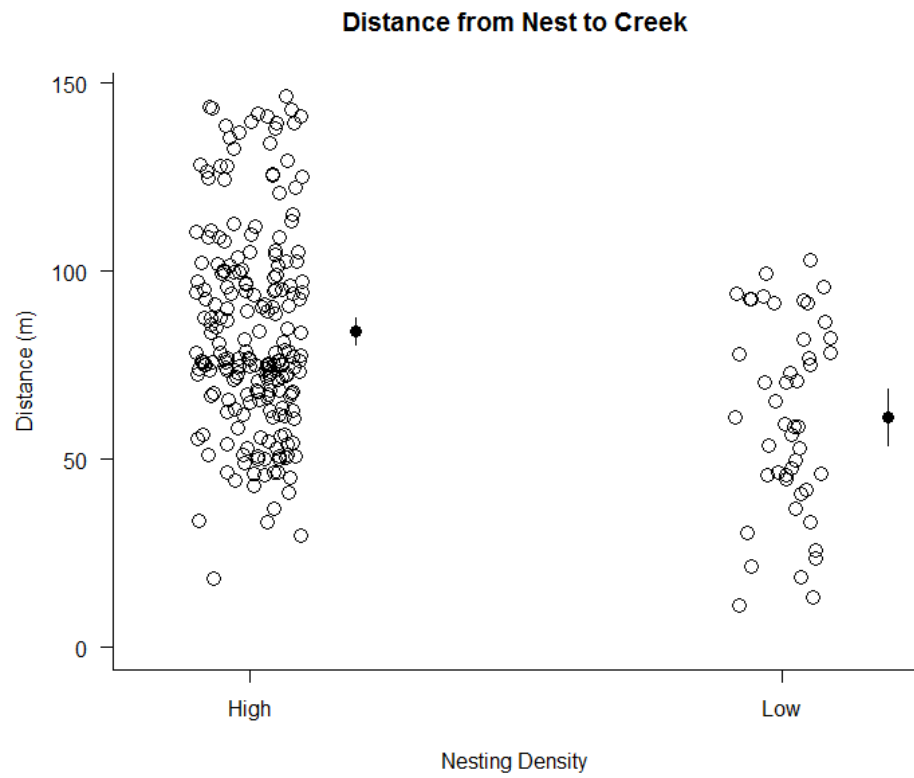


Figure 11. Distance of predicated nests to nearest creek (with means and 95% confidence intervals).

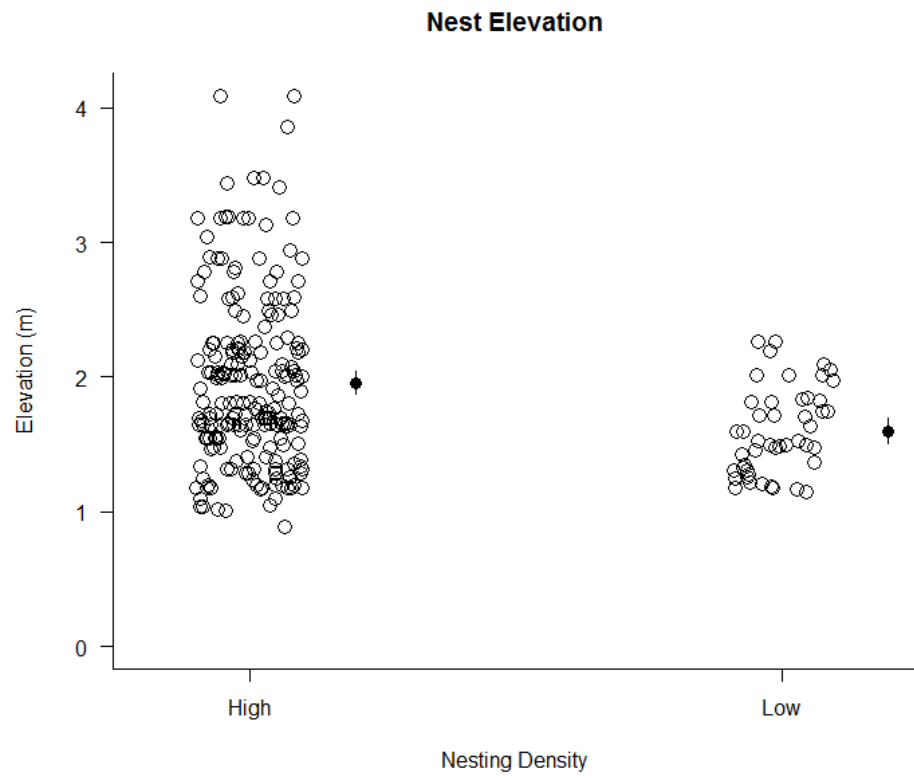


Figure 12. Elevation of predated nests (with means and 95% confidence intervals).

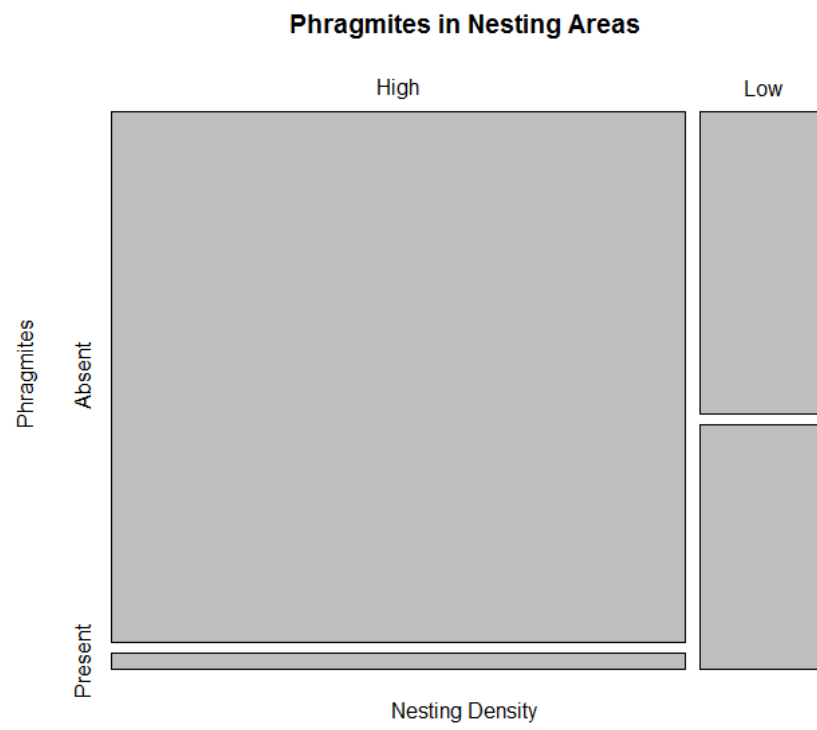


Figure 13. Mosaic plot of *Phragmites* presence vs. nesting density area.

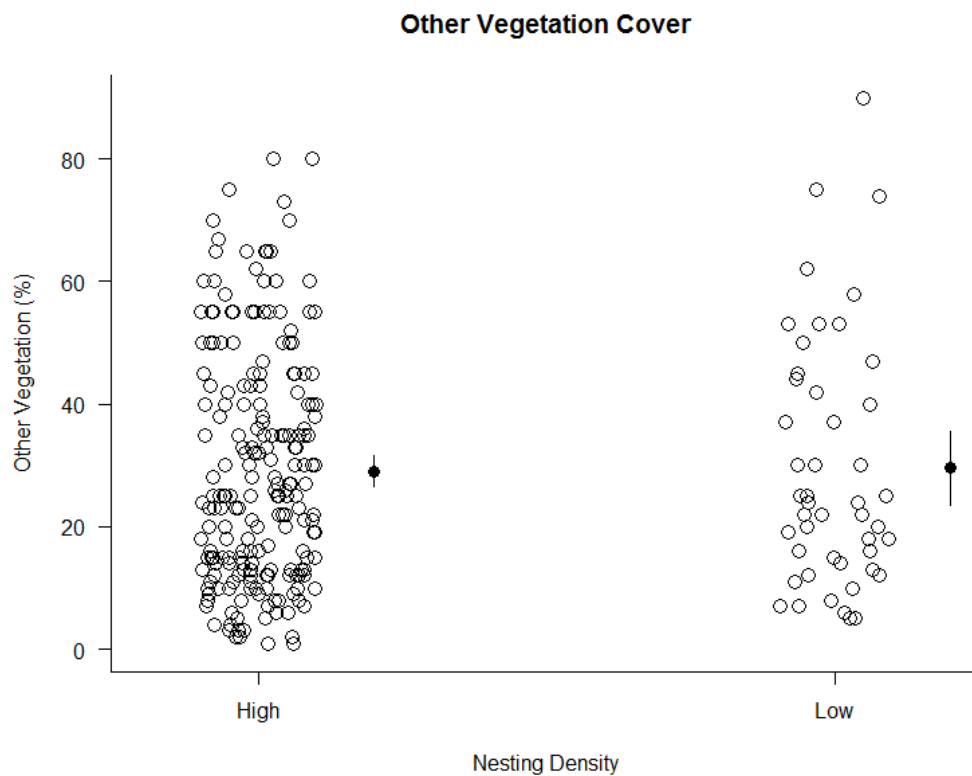


Figure 14. Other vegetation cover around predated nests (means and 95% confidence intervals).

Discussion

I performed a field study to examine the potential impact of *Phragmites* on predator foraging and detection of terrapin nests on Fisherman Island. I did not find a significant shift in dominant predator species when nests were found in sites with or without *Phragmites*. Proportions of raccoon to crow predation of nests did not change with the presence of *Phragmites* as I had hypothesized. This could be because the vegetation structure change caused by *Phragmites* did not influence the ability of crows and raccoons to detect nests. The *Phragmites* present around some nest sites may not have been dense enough to impact predation. Further, because so few nests were laid in areas with *Phragmites*, I had too small of a sample size to compare with non-*Phragmites* sites. I surveyed for predated nests and not total nests laid, but I feel confident that my surveys for predated nests encompassed most of the terrapin nesting activity of the 2015 season. Raccoon predation was very high that year, and the USFWS had to repeat trapping mid-summer to try to remove raccoons that were also heavily predating shorebird nests. Raccoons are such efficient predators of terrapin nests (Feinberg and Burke 2003), that with their prevalence during the nesting season I am confident they would have found other nests in the low nesting density site if they were present.

With few exceptions, most studies provide evidence for vegetation as a mediator of predator-prey interactions. Burger (1977) found that predated terrapin nests were significantly closer to vegetation than non-predated nests. Habitat fragmentation and the creation of edges also impacts predation rates of

edge breeders, as has been seen in many studies on birds (Huhta et al. 1996) as well as other species. A study on hawksbill sea turtles found that nest survival from mongoose predation increased as nests were laid farther away from vegetation edges (Leighton et al. 2011). No effects of *Phragmites* on nest predation were found in my study, but my experiments were limited by the distribution and extent of *Phragmites* cover. I believe there is still great potential for *Phragmites* to influence predation of terrapin nests. The distribution of *Phragmites* throughout my study site was not arranged in a way that produced a leading “edge” – it was mostly scattered throughout the dunes and found in localized clumps. Other terrapin nesting sites along their wide coastal range occur where there is a clear, horizontal gradient from aquatic habitat to nesting beach (Meadows pers. com) and thus would allow for a more direct test of *Phragmites* effects that my study was unable to detect. It is at these sites where *Phragmites*’ ability to create an edge and thereby influence foraging behavior of predators, such as raccoons, may be greater. If *Phragmites* is dense enough it may also create an impenetrable barrier to terrapin movement, causing them to nest on the border of the vegetation. High resource abundance along a foraging corridor would increase the likelihood of nest predation and reduce terrapin nesting success.

For further study on the relationship between *Phragmites* presence and predator behavior I would repeat this study at other sites and set up more structured experiments in areas with and without *Phragmites*. This would facilitate the determination of the exact proportion and rates of predation on

simulated nests. I was not able to access enough spatial area—separate from my observational study—to perform these studies because of USFWS restrictions due to nesting shorebirds on the island. I would also perform experiments at sites with a clear linear gradient from shore to vegetation. I believe more significant predation effects could be seen in this landscape type, and the results could be applied to other species that nest in this type of habitat, such as sea turtles and shorebirds.

I used habitat data collected for predated nests to examine the factors influencing diamondback terrapin nest site use on Fisherman Island. I found that distance to marsh, tidal creek, and presence of *Phragmites* all had significant effects on terrapin nesting in the high density versus the low density areas. The high density nesting area was farther away from marsh and tidal creek, and on average higher in elevation (though not significant) than the low density nesting area. These findings suggest that perhaps terrapins are nesting in areas that are relatively safe from flooding during the incubation period, and are consistent with other studies on turtle species (Burger and Montevecchi 1975; Cox and Marion 1978; Plummer 1976). Data on vegetation surrounding the nests were also consistent with the literature about terrapin preference for nesting in sites with little to no vegetation (Burger and Montevecchi 1975; Roosenburg 1996). On average, nests on Fisherman Island were surrounded by relatively low amounts of vegetation cover (29%) and terrapins used sites that were free from *Phragmites*. The use of non-*Phragmites* nesting areas could be because of the potential for negative impacts on nest development, such as shading and root

invasion, or due to difficulty digging in soil with high root mass. Turtle nest site selection in response to vegetation has been supported in many studies and there is evidence for maternal selection in regards to embryonic development and temperature dependent sex determination (Refsnider et al. 2013; Wilson 1998). From nest site data I conclude that females are preferentially choosing sites that would lead to a higher probability of nest success due to a reduction in risk of flooding and negative vegetation effects. As has been shown to occur in painted turtles (Hughes and Brooks 2006), natural selection would favor behaviors that increase offspring survival and female fitness. My analysis comparing the high versus low density nesting sites to illustrate female terrapin nest site use on Fisherman Island provides evidence to support previous studies on factors influencing turtle nest site selection.

The significant negative effect of *Phragmites* on terrapin nesting density could also be an outcome of *Phragmites* excluding diamondback terrapins from accessing potential nesting sites. The high density nesting area was relatively free from *Phragmites*, with only about 3% of predated terrapin nests having *Phragmites* present within 1-m² of the nest, as compared to 45% in the low density area. The low density area also had considerably more *Phragmites* surrounding the nesting dunes than the high density area. Terrapins may not be able to come ashore through *Phragmites*-bordered sand dunes, and so are concentrating their nesting in one small area where upland access is not limited. This may explain why predation rates were so high for terrapin nests – I saw a large number of predated nests in one concentrated area of nesting dunes, and

this intense predation seems to support the density dependent predation theory. The behavior of raccoons and crows to return to areas of successful foraging with high resource abundance (Byrne and Chamberlain 2012; Shields and Parnell 1986) may be the reason for extremely high predation rates. It also may explain the return of predators to the island every year, and the need for additional removal efforts. However, some terrapins are still nesting in the *Phragmites*-dominated area, suggesting at least some nests are successful, or females have not yet adapted to the habitat change associated with invasive plant growth. If more nests were successful but undetected from the low-quality nesting area, however, then *Phragmites* would be beneficial for terrapin nests, and yield a trade-off between habitat quality and predation risk. Further study is needed to determine the extent of this relationship as well as the response of females to degraded nesting dunes.

Phragmites not only has the potential to negatively impact terrapin nesting, but it can also have other negative consequences on terrapin life-history. By decreasing plant species diversity post-colonization, *Phragmites* has the capacity to reduce marsh habitat quality for terrapins, thus reducing time terrapins spend in invaded tidal marshes. *Phragmites* invasion has been linked to decreases in *Spartina* abundance in brackish tidal marshes (Medeiros et al. 2013) as well as decreases in invertebrate communities (Gratton and Denno 2006; Jivoff and Able 2003). The marsh periwinkle (*Littorina irrorata*) is a staple in the diamondback terrapin diet, as well as other crustaceans (Tucker et al. 1995). Marsh periwinkles selectively graze on *Spartina alterniflora* (smooth

cordgrass), and have not yet been shown to successfully graze on *Phragmites* (Hendricks et al. 2011). This is most likely due to a chemical defense that *Phragmites* produces that is unpalatable to marsh periwinkles (Hendricks et al. 2011). Decreased numbers of marsh periwinkles and other invertebrates could be a major factor in terrapins utilizing *Phragmites* marshes and thus nesting in the dune areas surrounding them. A study by Butler et al. (2012) found that female terrapins had significantly higher levels of marsh periwinkle in their diet than males, and females found at nesting beaches had significantly more than females found in creeks. The potential *Phragmites*-linked reduction in abundance of this important food resource could also be a driver behind decreased terrapin nesting activity near *Phragmites*-colonized salt marshes.

Invasive *Phragmites* was not shown to differentially impact nest predator behavior in this study, however there are certainly other terrapin nesting sites and other turtle species for which the nesting landscape includes a clear, linear gradient from water to beach to vegetation. In these areas it could be more likely to see an impact of *Phragmites* presence on predation rates. More conclusive evidence from this study shows *Phragmites* presence to be a major player in diamondback terrapin nest site use. Among many potentially important factors, unimpeded *Phragmites* colonization of tidal marshes would most likely reduce terrapin habitat use as well as nesting activity and/or success. With *Phragmites* presence in saltmarshes increasing around the Chesapeake Bay and other important terrapin nesting sites (Chambers et al. 1999; Rice et al. 2000), there will be an increased need for management strategies to remediate negative

effects to native species. As mentioned in Chapter One, it may not be necessary to completely eradicate *Phragmites* from sites to sustain successful terrapin nesting. Managing the landscape in a way to reduce *Phragmites* density and extreme habitat structure change to increase use and prevent setting up terrapin nests for failure should be sufficient for ensuring the survival of this turtle species.

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