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A Population Model for the Diamondback Terrapin: Implications for Conservation Management

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A Population Model for the Diamondback Terrapin: Implications for Conservation Management

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Introduction

　　The diamondback terrapin, *Malaclemys terrapin*, is America's only exclusively estuarine turtle. A resident of coastal marshes and shallow sub-tidal seagrass beds, terrapins are considered potential keystone species influencing community structure (Silliman and Bertness 2002). The turtle is declining throughout its range along the coast of Maine to southern Florida and Texas. Terrapins have very high site fidelity so they are especially vulnerable to local extinctions (Tucker et al. 2001; Hauswald et al. 2005).

　　Diamondback terrapins face two main threats as a result of human activity; the crabbing industry and urbanization. The crabbing industry primarily causes terrapin mortality as turtles enter crab pots and die as by-catch. Turtles caught in the traps drown when they are unable to exit the trap and surface for air (Grosse et al. 2009). As terrapins grow they are less able to fit inside the openings of the traps and the risk of mortality in crap pots decreases dramatically. However, only females grow large enough at sexual maturity to be excluded from the traps, while males remain small throughout their lives. As a result of this sexual size dimorphism, crab potting disproportionately affects adult males and juveniles of both genders (Wolak et al. 2010). This pattern of selective mortality has two overall effects on the terrapin population. First, it has been shown that this selection pressure has increased the average size and maturation rate of the species (Dorcas et al. 2007). Secondly, differential selection skews the gender ratio of a population to favor females (Dorcas et al. 2007). A shift in gender ratio could potentially decrease breeding efficiency and decrease reproduction rates, but this effect has never been studied. Furthermore, no studies to date have documented how small decreases in reproductive rates (e.g., via crab pot mortality) might affect the long-term viability of the species.

　　Fortunately, terrapin mortality in crap pots can be prevented through the use of by-catch reduction devices (BRDs). These devices are placed on the entrances of crab traps and make the openings more narrow. Crabs are still allowed to enter because they have a much smaller shell depth than turtles. When sized correctly, BRDs substantially reduce the number of terrapins which enter the trap but do not reduce crab harvests (Cole and Helser 2001; Rook et al. 2010; Morris et al. 2010). However, by-catch reduction devices are not a requirement in Virginia and many other states throughout the range of the Diamondback terrapin.

　　The second major threat faced by the diamondback terrapin is urbanization near nesting habitat. Since terrapins lay their eggs on land, development may lead to destruction of nesting sites and increased levels of natural nest predators. Mesopredators (also known as subsidized predators) including raccoons (*Procyon lotor*) and house rats (*Rattus norvegicus*) thrive in urbanized environments, increasing predation pressure on both nests and hatchings (Butler et al. 2004; Draud et al. 2004). Additionally, older females may be killed on roads as they travel to nesting sites (Avissar 2006). As with crab potting, it is not known whether these threats are the cause of decline in terrapin populations, or whether some populations are resilient against these specific pressures.

　　The purpose of my research was to develop a terrapin population model in order to determine the effects of specific selection pressures on the long-term population dynamics of the diamondback terrapin. The only published terrapin population model focused exclusively on

females and did not consider the interaction between the sexes (Mitro 2003). Male and female terrapin populations experiencing very low rates of mortality due to crab pots and nest predation should maintain population levels at or near the carrying capacity. However, as mortality rates are increased, there exists a threshold at which terrapin death rates surpass birth rates and the population gradually tends toward extinction. Identifying this threshold is very difficult to do via field observation because many sampling years are required to detect a slow, long-term decline in a population faced by many stochastic events. However, with the use of a mathematical model it is possible to determine the approximate level of mortality that causes a shift from population growth to decline. Another challenge with field studies is the difficulty of separating the effects of different sources of mortality, which almost always occur simultaneously. With the use of a model it is possible to examine the potential effects of road mortality, crab pot mortality, and nest predation individually. This has important implications for conservation planning since the model will show which human pressures have the greatest effect on the long-term viability of the species. Such knowledge could assist the development of management and policy decisions to prevent further decline of the Diamondback Terrapin.

Background

Very few reptile species can thrive in both salt and freshwater ecosystems. The diamondback terrapin is capable of surviving in both fresh and salt water and is one of few reptiles which actually prefer environments of intermediate salinity. The diamondback terrapin is able to withstand such a large range of conditions due to a variety of physiological and behavioral adaptations (Davenport and Magill 1996). Terrapins have a thick skin that is impermeable to water, allowing them to maintain a different solute level within their bodies as compared to the environment. They also have salt-glands that secrete a tear-like substance, enabling them to reduce salt levels in their body. The gland is analogous to tear glands found in sea turtles, though it is believed that they evolved independently. The salt gland only becomes active while the terrapins are in salt water (Cown 1974). Behaviorally, diamondback terrapins will drink fresh water whenever possible and minimize their intake of salt water. Terrapins may catch rain water directly in their mouth or drink from the small film of fresh water that forms on the water's surface. Feeding behavior decreases when terrapins are in salt water, which serves to minimize the incidental intake of salt water (Davenport and Ward 1993).

The diamondback terrapin also has a complex life history with sexual dimorphic traits (Table 1). As hatchlings and young juveniles, male and females are externally indistinguishable. At the age of 7, females begin to grow rapidly and may eventually grow to 20 cm in length. Females take several years to mature, and they go through an early breeding stage between age 8 and 11 before they reach full maturity. Males mature at a fast rate and are capable of breeding by age 5, but they only grow to approximately 10 cm in length at maturity (Hildebrand 1932). The larger size of the female may be an evolutionary advantage that allows them to have a larger clutch size, thereby increasing the number of potential offspring. Sexual size dimorphism may also minimize male and female competition for food (Tucker et al. 1995).

While terrapin males spend nearly their entire lives in the water, terrapin female come on to land to nest. Terrapins have evolved a reproductive strategy where females lay multiple clutches each nesting season over many successive years to compensate for heavy nest predation.

Early breeding females, "Immature breeders", will typically lay 1 clutch per year with 10 eggs per clutch. Mature breeders will lay 2-3 clutches per year, for a total of 20-30 eggs. Terrapin hatchlings also experience very high levels of predation. Young turtles spend several years growing until they are somewhat immune to predation before reproduction occurs (Graham 2009).

Table 1

Terrapin Life History		
Age Class	*Ages*	*Duration (Years)*
Female		
Hatchling	1-3	3
Juvenile	4-7	4
Immature Breeder	8-11	4
Mature Breeder	12-20	< 9
Male		
Hatchling	1-3	3
Juvenile	4	1
Mature Breeder	5-20	15

Nesting terrapin females are not immune to all risk, however. Eggs are laid on land, which exposes females to desiccation and natural predators including raccoons. Increasingly, females must also cross roads to reach nesting sites. Females may make several expeditions to land before laying eggs. Frequently, females abandon prepared nests without laying eggs due to human disturbances, including noise from traffic. Delayed nesting may be detrimental to the survival of the hatchlings if it occurs late in the year (Graham 2009). Once a nesting location is selected, females show a high level of site fidelity, returning to the same place every year (Hauswald et al. 2005).

Terrapins also vary their behavior seasonally. Terrapins breed during late spring and are active throughout the summer months. During the winter, terrapins burrow into the mud to brumate, a process similar to hibernation. During this time terrapin metabolism decreases dramatically, allowing the terrapins to survive months without replenishing their supply of oxygen (Baker et al. 2006). Turtles also stop eating as temperatures drop since brumation must occur with an empty gastrointestinal tract in order to prevent bacterial growth during the months of inactivity (Baker et al. 2006).

Interaction between humans and terrapins is certainly not new to the 21st century. The diamondback terrapin was often featured in Native American art and folklore and also served as an important food source. Terrapins were plentiful when European settlers arrived in the 1500s and as a result they were mostly fed to servants. Terrapin numbers declined and by the 1800s terrapin soup became a delicacy. A commercial terrapin industry developed and terrapin farming was attempted. It was around this time that terrapins from Texas were introduced to the Chesapeake Bay, blurring the boundaries between subspecies. Genetic evidence of this interbreeding still exists today (Hauswald et al. 2005). Changes in consumer demand and the

further decline of the terrapin effectively ended the terrapin fishing industry. However, terrapins continue to be harvested as by-catch in the crabbing industry.

Commercial crab potting occurs throughout the mid-Atlantic. The habitat of the blue crab (*Callinectus sapidus)* frequently overlaps with the diamondback terrapin, so crab pots are often placed in tidal waters utilized by the terrapin. Though recreational crab potting occurs on a much smaller scale than commercial crabbing, the effects of recreational crabbing are not entirely negligible. Recreational pots are much more likely to be lost or abandoned and these derelict traps drift into shallow water where males and juveniles most often reside. These traps are not removed from the water and they may continually catch turtles until they degrade (Hoyle and Gibbons 2000).

The Model

The model presented in this paper is a variation of the discrete time model often referred to as a Leslie Matrix model. A discrete time model does not consider continuous change in a population, rather it repeatedly predicts population levels after a set time interval. The population predicted for each time interval depends on the population from the previous time interval as well as parameters for survival and reproduction built into the matrix model. In the model presented below, the time between each time interval is one year (Equation 2). A discrete time model with step size of one year is especially well-suited for the Diamondback Terrapin since the turtles are active a relatively short portion of the year during the summer months. The model shows the resulting population after the end of each summer after the turtles have matured and reproduced. Since the terrapins brumate for the remaining part of the year, a continuous time model showing population change throughout the year would not be more useful or accurate compared to the discrete model.

Unlike the traditional Leslie Matrix, where there is a difference equation for each year of the organism's life, the model below is divided into age classes for both males and females. Females, indicated by 'X', are divided into four age classes: hatchlings, juveniles, immature breeders, and mature breeders. Males, indicated by 'Y', are divided into three age classes: hatchlings, juveniles, and mature breeders (Table 1). The likelihood of a turtle surviving in a given year is divided into two groups: turtles which will remain within in the same age class, 'p', and turtles which will progress to the following age class, 's'. Each age group has its own unique survival (*s*) and persistence (*p*) values, which regulates how the turtles progress throughout the model (Figure 1).

The age class specific survival and persistence values may be derived from the overall probability of survival, 'R', using the average duration of the given age class, 'n'.

Equation 1

$$s = R/n$$

$$p = \left(1 - \frac{1}{n}\right)R$$

This method of parameterization is reasonable since terrapins mature at different rates. The model represents the dynamics of the overall population rather than the course of an

individual. If one individual is followed throughout the model, it becomes apparent that it is possible for the individual to stay in one life stage indefinitely. However, this inaccuracy does not affect the accuracy of the overall results of the model since all individuals are assumed to be identical within an age group. So long as identical turtles progress to the next stage in the correct proportion, it does not matter that some turtles may remain in the same stage much longer than biologically possible.

The fecundity rates of the terrapins are designated by 'b$_i$', the fecundity of early breeders (immature breeders), and 'b$_m$', the fecundity of mature breeders. Immature breeding females by definition lay only one clutch per year, while older and more mature breeding females will lay as many as three clutches per year. As a result, 'b$_m$' values are always slightly larger than 'b$_i$' values. The total number of new hatchlings per year per female is divided in half to get the 'b' value, since the model includes male and female hatchlings separately. One assumption is that male and female hatchlings will be born at the same rate. While this assumption is reasonable in most cases, it has been shown that reptiles may vary the ratio of female and male hatchlings in response to temperature (Vogt 1982).

<u>Equation 2</u>
(A) The model written in matrix form
(B) The matrix model expanded into a series of difference equations

A.

$$
\begin{pmatrix} X_{H_{n+1}} \\ X_{J_{n+1}} \\ X_{I_{n+1}} \\ X_{M_{n+1}} \\ Y_{H_{n+1}} \\ Y_{J_{n+1}} \\ Y_{M_{n+1}} \end{pmatrix}
=
\begin{pmatrix}
p_h & 0 & b_i & b_m & 0 & 0 & 0 \\
s_h & p_j & 0 & 0 & 0 & 0 & 0 \\
0 & s_j & p_i & 0 & 0 & 0 & 0 \\
0 & 0 & s_i & p_m & 0 & 0 & 0 \\
0 & 0 & b_i & b_m & p_{h2} & 0 & 0 \\
0 & 0 & 0 & 0 & s_{h2} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & s_{j2} & p_{m2}
\end{pmatrix}
\begin{pmatrix} X_{H_n} \\ X_{J_n} \\ X_{I_n} \\ X_{M_n} \\ Y_{H_n} \\ Y_{J_n} \\ Y_{M_n} \end{pmatrix}
$$

B.

Females

$$X_{H_{n+1}} = p_h X_{H_n} + b_i X_{I_n} + b_m X_{M_n}$$

$$X_{J_{n+1}} = s_h X_{H_n} + p_j X_{J_n}$$

$$X_{I_{n+1}} = s_j X_{J_n} + p_i X_{I_n}$$

$$X_{M_{n+1}} = s_i X_{I_n} + p_m X_{M_n}$$

Males

$$Y_{H_{n+1}} = p_{h2} Y_{H_n} + b_i X_{I_n} + b_m X_{M_n}$$

$$Y_{J_{n+1}} = s_{h2} Y_{H_n}$$

$$Y_{M_{n+1}} = s_{j2} Y_{J_n} + p_{m2} Y_{M_n}$$

Table 2
Parameter Values

Parameter	Value	Description	Source
p_h	.2	Rate of Female Hatchling persistence as hatchlings per year	Estimation
s_h	.1	Rate of Female Hatchling survival to juvenile stage per year	Estimation
p_j	.525	Rate of female Juvenile persistence per year	Mitro 2003
s_j	.175	Rate of female Juvenile survival to Immature Breeding stage	Mitro 2003
p_i	.71	Rate of Female Immature Breeder persistence	Estimated based on Mitro 2003
s_i	.24	Rate of Female Immature Breeder survival to Mature Breeding stage	Estimated based on Mitro 2003
b_i	.5	Hatchlings per Immature Breeding Female per year	Roosenburg and Dunham 1997; Ruzicka master's thesis
p_m	.96	Rate of Female Mature Breeder persistence	Mitro 2003 ; Tucker et al. 2001
b_m	1.25	Hatchlings per Mature Breeding Female per year	Roosenburg and Dunham 1997; Ruzicka master's thesis
p_h2	.2	Rate of Male Hatchling persistence as hatchlings per year	Estimation
s_h2	.1	Rate of Male Hatchling survival to juvenile stage per year	Estimation
p_j2	0	Rate of Male Juvenile persistence per year	Mitro 2003
s_j2	.7	Rate of Male Juvenile survival to Mature Breeder stage per year	Mitro 2003
p_m2	.85	Rate of Male Mature Breeder persistence per year	Mitro 2003; Tucker et al. 2001

The only existing model for the diamondback terrapin, presented by Mitro in 2003, is also a discrete time model where terrapins are divided into age classes. However, the Mitro model only examines the female population. The number of males is assumed to equal the number of females which is not always the case in the presence of crab potting. The model also includes only three life stages for the female terrapin and does not distinguish between mature and immature breeding females.

Methodology

Field Work

A mark-recapture study was carried out in Felgate Creek during the months of June through July 2010 near Williamsburg, Virginia. The site is located on a restricted military base where no crab potting is permitted and urban development of the surrounding ecosystem is

sparse. Natural predators observed at the site included eagles (e.g. *Haliaeetus leucocephalus*), otters (*Lontra canadensis*), and raccoons (*Procyon lotor*).

In the summer of 2010, 10 chamberpots were placed in water approximately 1.5 meters deep at high tide and were checked daily. In the years 2007-2009, pots were placed in more shallow water approximately 1 meter deep at high tide. Traps were modified by the addition of a chimney that allowed turtles to access the surface for air. When turtles were captured, measurements were taken of the weight, carapace and plastron length and width, and shell depth. Age was estimated by counting age rings on the carapace or plastron. Gender was determined by physiological observation. Females have larger heads and thin tails, while males have smaller heads and thick tails, particularly at the base. Additionally, the cloaca in males is positioned past the posterior marginal scutes.

Turtles never previously captured were marked by filing notches into the marginal scutes of the terrapins. A binary system was used to mark the turtles, where the right posterior scute was designated as 1, and each scute in the anticlockwise direction doubled in value. The left posterior scute was designated as 256, and the value of scutes doubled in the clockwise direction. The number of the turtle was designated by adding the values of all marked scutes.

The Schumacher method was used to determine the population estimates for each sampling year (Krebs 1999). In this method 'N' is the estimated population, while C_t is the number captured terrapins and R_t is the number recaptured terrapins at sample 't'. M_t is the number marked in the population.

Equation 3
Schumacher and Eschmeyer method

$$N = \frac{\sum (C_t M_t^2)}{\sum (R_t M_t)}$$

Several assumptions about the population must hold true for these population estimates to be accurate. First, it must be assumed that samples are random and all individuals in the population have an equal likelihood of capture. Second, it must be assumed that the population stays relatively constant, with very little fatality or recruitment of new individuals (Krebs 1999). It is likely that the second condition was satisfied by the Felgate Creek population but the same cannot be said for the first condition. Recaptures were very common, particularly for a few individuals, so each individual may not have the same likelihood of being captured. Also sampling was not entirely random since the crab pots were placed in deeper water where females predominate. Very few pots were placed in the shallow water where males and young juveniles are mostly found. Also the majority of crab pots were placed in the same general area throughout the sampling period. If indeed terrapin movement is highly restricted, the population estimate would only estimate the number of the terrapins in the immediate vicinity of the traps and not the entire wetland. In general, the Schumacher method should give a reasonable estimate for the population in Felgate creek. However, it should be noted that violation of the first assumption would lead to an under-estimate of the population.

Modeling

Capture probabilities were determined by calculating the ratio of marked turtles that were recaptured within the same sampling year. Parameter values were either derived from data collected at Felgate Creek or from other studies (Mitro 2003; Tucker et al. 2001). Survival rates for adult female and juveniles were derived from Mitro (2003). Rates of survival for adult males and females in the presence of crab potting were derived from a study in Kiawah River, South Carolina. In this study the survival rates for several creeks with varying levels of crab potting were calculated. For adult females, all survival rates fell between .748 and .971. For adult males, survival was between .788 and .901 (Tucker et al. 2001). Little is known about the survival rate of hatchlings since they are too small to be caught in crab pots or by other methods.

The survival rate of terrapin nests was estimated by approximation to be 0.1 from Ruzicka's College of William and Mary master's thesis data from Goodwin Islands, Virginia. The number of eggs per clutch varies throughout the range of the terrapin, but the average is approximately 10 eggs. The number of clutches per female also varies, but mature female breeders lay an average of 2.5 clutches while immature female breeders lay 1 clutch (Roosenburg and Dunham 1997). The average number of hatchlings per breeding female was calculated from clutch size, survival, and clutches per female.

The population projections were created by evaluating the model numerically using MATLAB. Bifurcation diagrams were created by plotting the eigenvalues of the matrix model shown in Equation 1. The parameter values of interest were increased incrementally while all other parameters were held constant. All bifurcated 'p' values were held in the correct ratio with respective 's' values according to the duration of the age class.

Results

Field Work

For the population study in Felgate Creek in 2010, the total population of terrapins was estimated to be 98 (33 males and 65 females) using the Schumacher and Eschmeyer method (Figure 2). These estimates exclude hatchlings since no turtles from this age group were caught.

With 48 unique captures, approximately 51% of the total population was caught in the traps. For females, 38 unique captures indicates that 60% were captured. For males, approximately 65% were caught in the pots with 20 unique captures. This high rate of capture occurred within a single summer with only 10 crab pots. The possible mortality as a result of the potentially large number of commercial and recreational pots set each year in tidal creek habitats highlights the need to examine the scope of the problem throughout the Chesapeake Bay.

The data collected from Felgate Creek did not indicate any overall trend in the population of males or females (Figure 2), but instead documented the large interannual variability of the population estimates. The size data collected confirmed the sexual size dimorphism documented in the literature. Comparison of carapace length to age, as determined by counting growth rings, revealed that females undergo rapid growth starting around age 7 while males remain below 15 cm in length throughout their lives (Figure 3). Examination of shell depth revealed a similar

pattern (Figure 4). When compared to the width of a BRD of 4.5 cm, it was found that 96% of female terrapins caught in crab pots have a shell depth great enough to be excluded from the traps. For males, 78% percent were large enough to be excluded. Though some terrapins would still be able to enter the traps, even these individuals are less likely to enter (Morris 2010). This suggests that terrapins avoid the narrow opening of the BRDs regardless of their ability to fit.

Matrix Model

The matrix model has a single stable equilibrium where all age classes have a population equal to zero. An equilibrium point occurs when the values of each age class at time n remain the same at time n+1. The equilibrium is said to be stable when the population tends towards the equilibrium values. When the equilibrium is unstable the population will grow away from this point and tend towards infinity. However, it is assumed that any population predicted to grow without bound will eventually reach its carrying capacity. A carrying capacity was not built directly into this model because such capacities vary greatly from region to region and are not necessary for predicting the long-term growth or decline. Unbounded growth in the model implies the population will grow to reach its full carrying capacity while an overall decline shows the population is tending towards extinction.

With the parameters presented in Table 2, the model predicted long-term population growth. This is consistent with the findings in Mitro, where a female population with similar survival values was determined to be stable (Figure 5). In creeks heavily influenced by crab potting, the survival rates are predicted to be much lower. In Kiawah Creek, South Carolina, for example, survival rates are approximately .84 for adult females and .83 for adult males (Tucker 2001). In this case, the model predicted long-term decline and possible extinction within 85 years (Figure 6).

Discussion

Field Work

The particularly low population estimate in 2010 may be attributable to a number of factors (Figure 2). Below average rainfall in 2010 may have caused decreased water levels or increased salinity, shifting the general population away from the sampling site. An alternative explanation is that traps were placed in different locations in 2010 than in previous years. In previous years traps were placed in a larger variety of places while in 2010 the traps were placed in only two general vicinities. Little terrapin movement was detected between creek segments, so the entire terrapin population may not have been accounted for in the 2010 study.

Analysis of Matrix Model

The long term behavior of the model can be determined by examining the greatest positive eigenvalue of the matrix model, also known as the dominant eigenvalue (Equation 2B). When the dominant eigenvalue is greater than one, the population tends toward infinity (Figure 5). In this case, an increase in the value of the dominant eigenvalue corresponds with a faster rate of population growth. When the dominant eigenvalue is less than one, the population tends towards the zero equilibrium and therefore extinction, and a lower dominant eigenvalue implies a greater rate of decline (Figure 6). In this sense, the dominant eigenvalue, λ, is analogous to the growth rate, or the net replacement rate per individual.

Though it is known that human pressures, including crab potting and urbanization, put stress on the terrapin population, it is not clear how intense these pressures must be to cause a long term decline. To determine the effect of a given level of environmental stress, it is useful to examine how changes in survival affect the dominant eigenvalue, λ. For instance, the minimum level of pressure required to cause long term decline may be calculated by observing how greatly survival values must be decreased for λ to become less than 1. A plot of the changing eigenvalues in relation to changes in parameters is known as a bifurcation diagram. One value of this technique is that the effects of a specific pressure can be examined separately from other pressures by changing only the survival rates belonging to groups directly affected by that pressure.

Ecologically, a bifurcation diagram may be interpreted as a plot of the overall population replacement rate in response to the survival rate of a population subsection. In this model, subsections are based on age and gender. The plot may be used to determine thresholds where the fate of the population is drastically different above or below a particular subpopulation survival rate. Bifurcation plots may also be used to determine the sensitivity of the overall population to changes in the survival rates of population subsections. In other words, the plot shows how greatly the overall replacement rate is affected by changes in the survival of certain groups.

The bifurcation plots presented in this paper each have an irregular spike at a single point. The irregularity is due to numerical error and does not reflect on the true replacement rate for that point. Since the parameters were increased at distinct intervals for the bifurcation plots, only a single point was irregular for each plot, while surrounding values followed a continuous curve. Therefore, eigenvalues not at this irregular point are valid approximations of the population replacement rate.

Nest Predation

I examined the effects of nest predation through the use of a bifurcation diagram. Increased predation causes a decrease in the number of Hatchlings born per female (b_i and b_m). The values of the two parameters were set equal to zero and were increased incrementally (Figure 7). At the point where the dominant eigenvalue becomes greater than 1, the population will experience population growth. This point represents a threshold value for fecundity, or the minimum fecundity rate required for population survival. The diagram indicates that for populations which are not under pressure from crab potting, females must have an average of 1.75 eggs which successfully hatch each year. It is assumed that half of these will be female and the other half male.

Figure 7 also shows that the slope of the dominant eigenvalue is very small. Biologically, this indicates that the replacement rate of the population does not change rapidly in response to small changes in fecundity. However, it should be noted that near the bifurcation point, the population's fate may change drastically even in response to a small change in fecundity.

11

Road Mortality

The effects of road mortality on nesting females may also be examined (Figure 8). The bifurcation diagram indicates that adult female survival rates must drop below .86 before a population decline will occur. This does not seem likely to occur, though few studies have been done on the precise level of mortality caused by roads. Generally it is believed that roads do not play a major role in terrapin decline. Besides anecdotal evidence, one indication is that declining terrapin populations tend to have a greater ratio of females to males. If road mortalities were the cause of population decline, populations would tend to favor a higher proportion of males, since road mortality almost exclusively affects breeding females (Dorcas 2007).

However, Figure 8 also indicates that the survival of the population is very sensitive to changes in adult female survival rates since the slope of the dominant eigenvalue is very large. This means that even a small decrease in adult female mortality may significantly decrease the overall population replacement rate. Though adult female survival may still be above the bifurcation point, lowered replacement rates would make the population more vulnerable to other population pressures, including crabbing and nest predation. This result is consistent with the sensitivity analysis of Mitro's model presented in 2003, and it highlights the need to further examine other sources of adult female morality, including strikes from motorized boats.

Crab Potting

Crab potting has been shown to simultaneously decrease the survival of juvenile males (s_{j2}), juvenile females (p_j, s_j), and adult males (p_{m2}). Other age classes are not directly affected since larger females are unable to fit inside the opening of the trap, while young hatchlings are able to slip through the cull rings in the wire mesh of the trap. A bifurcation diagram was created by setting these parameters equal to zero and increasing each parameter in small intervals. At each interval the resulting eigenvalues were calculated and plotted (Figure 9). The point where the dominant eigenvalue transitions from less than 1 to greater than 1 is known as the bifurcation point. Below this point, the population will go extinct if conditions remain constant, while above this point the population will grow to the carrying capacity.

According to this method, terrapin populations begin to decline when adult male and juvenile survival rates are below 0.45. However, this method is not the most accurate way to determine the true effects of crab potting on the population. In the bifurcation diagram the survival rates for juveniles and male adults are set to the same value for each interval. In reality, the juvenile survival rate will always be lower than that for adult males since juveniles experience greater natural predation. Since male adult survival is naturally higher, this bifurcation point will correspond to a greater percent decrease for adult males than for juveniles. Using the parameters of a stable population (Table 2), male survival must be decreased by 47% while juvenile survival must only be decreased by 36% in order to achieve a survival rate of 0.45. However, the percent decrease in each group should be the same since each has an equal likelihood of crab pot mortality.

A more useful prediction would estimate the percent decrease in survival for male adults and juveniles required to create population decline. This can be achieved by altering the model in Equation 2 to include a crab potting term. For each group affected by crab potting, an additional

term was added that removes the average number of individuals that would die in pots each year (Equation 4). The intensity, 'ρ', is the proportion of an age group that dies each year as a result of crab potting.

Equation 4

Females

$$X_{H_{n+1}} = p_h X_{H_n} + b_i X_{I_n} + b_m X_{M_n}$$

$$X_{J_{n+1}} = s_h X_{H_n} + p_j X_{J_n} - \rho X_{J_n}$$

$$X_{I_{n+1}} = s_j X_{J_n} + p_i X_{I_n}$$

$$X_{M_{n+1}} = s_i X_{I_n} + p_m X_{M_n}$$

Males

$$Y_{H_{n+1}} = p_{h2} Y_{H_n} + b_i X_{I_n} + b_m X_{M_n}$$

$$Y_{J_{n+1}} = s_{h2} Y_{H_n} - \rho Y_{J_n}$$

$$Y_{M_{n+1}} = s_{j2} Y_{J_n} + p_{m2} Y_{M_n} - \rho Y_{M_n}$$

This method shows that only a 12% decrease in the population of adult males and juveniles each year will lead to population decline (Figure 10). A population projection of 10% crab pot mortality shows that extinction would occur within 160 years if conditions remained constant (Figure 11). The capture of 51% of the Felgate Creek population in 2010 demonstrates that a mortality of 12% may very easily occur in the presence of a small number of crab traps.

The use of by-catch reduction devices would potentially cause the rate of crab pot mortality to fall below the bifurcation point. In the Felgate Creek study, all but 2 females and 4 males would have been excluded from the traps based on their shell depth if BRDs had been installed. Given the population estimate of 65 females and 33 males, the percent of the population captured would have been reduced to 3% for females and 12% for males. Capture rates may be even lower with the use of BRDs since terrapins small enough to fit through a BRD appear to avoid the narrow opening (Morris 2010). In the case of Felgate Creek, the use of BRDs would allow the population to survive in the presence of crab potting purely based on size distribution.

Gender Ratio Change Due to Crab Potting

Another problem associated with crab potting is that it causes a demographic shift that favors a higher ratio of females to males (Dorcas 2007). This occurs because crab potting disproportionately affects males, while adult females experience very low rates of crab pot mortality. This trend may be seen by plotting the ratio of males to females in relation to the intensity of crab potting (Figure 12). As crab potting intensity is increased the ratio of females to males grows exponentially.

As a result of this trend, the model presented above is not entirely accurate for very high levels of crab potting. One assumption of the model is that females always have sufficient access to males for reproduction, but this cannot hold true when the ratio of females to males becomes too great. For instance, if all males were eliminated by crab potting, females would certainly not be able to continue reproducing at the same rate as they do in the model. However, this will not change the end result of the model since populations are typically close to extinction before the number of males becomes so low that the females' ability to reproduce becomes impaired.

Despite this, there is still value in examining the specific case where the ratio of males to females becomes very low. In the model above, it is possible that the predicted decline rate may be much more gradual than the decline of a real population affected by crab potting. At a certain point, these populations may begin decreasing more rapidly and may experience a population crash.

The potential decrease in fecundity as females lose access to males may be modeled by "removing" breeding females from the breeding population as the number of males becomes reduced. The specific number of females removed will depend on the number of females that may breed with a single male. Though this number is not known, a ratio of 5 males to 1 female maximized reproduction in captive breeding programs (Brennessel 2006). Based on this ratio, I assumed that one male may breed with up to 10 females. For each one male removed by crab potting, a total of 10 females would be "removed" from the reproductive population. These 10 females were divided among both the mature and immature breeding age classes. Assuming that males will mate with immature and mature breeding females at the same rate, I chose to remove 7 mature breeding females for every 3 immature breeding females since this was the typical ratio found in the Felgate Creek field studies. With these assumptions, the equations for hatchlings took the following form while all other equations remained the same as those in Equation 4.

Equation 5

$$X_{H_{n+1}} = p_h X_{H_n} + b_i X_{I_n} + b_m X_{M_n} - 0.3 \rho b_i X_{I_n} - 0.7 \rho b_m X_{M_n}$$

$$Y_{H_{n+1}} = p_{h2} Y_{H_n} + b_i X_{I_n} + b_m X_{M_n} - 0.3 \rho b_i X_{I_n} - 0.7 \rho b_m X_{M_n}$$

This model is only valid for populations where the ratio of females to males exceeds 10:1. Below this ratio, male abundance is in excess of that required for reproduction, so the removal of males should not affect the reproduction rate of females. For this reason, the values of 0.7 and 0.3 from Equation 5 were chosen with the assumption that the female to male ratio is

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10:1. This will ensure that approximately 10 breeding females are removed for every 1 male given a constant percent decrease in the population each year.

A bifurcation diagram of crab potting intensity for a population with more than 10 females per male revealed that the population would decline if 9% of the affected age groups were removed each year due to crab potting (Figure 13). For a population with sufficient males per female for reproduction, a 12% crab potting mortality was required to cause a population decline (Figure 10). This indicates that a population with reduced fecundity due to a high female to male ratio loses resilience against the effects of crab potting. Since crab potting itself contributes to a heavily female dominated population, there is the potential for a positive feedback mechanism which could make terrapin populations more difficult to recover once they are exposed to a certain level of crab potting. However, the model does not indicate that the rate of decline is significantly greater for those populations with reduced fecundity. As a result, the predicted time for extinction for a population would be similar regardless of the gender ratio.

Both Figure 10 and Figure 13 indicate that the overall sensitivity of the population is low in relation to the survival of juveniles and adult males. However, crab potting is still a major threat to the terrapin population due to the high fatality rates caused by crabbing relative to the bifurcation point. Data from Felgate Creek and other studies indicate that crab potting is capable of causing fatality much greater than 12% per year in juveniles and adult males (Grosse et al. 2009; Roosenburg 1997). Regardless of sensitivity, the matrix model predicts decline for all populations with crab pot mortality greater than 12%.

Conclusion

Management Implications
In the absence of a stochastic event, this model is a powerful tool for predicting the long-term population dynamics of the diamondback terrapin. As a result, it has many potential applications for both research and management for local terrapin populations and also throughout the Chesapeake Bay.

One important application of the model is that it can be used to evaluate the effectiveness of various management techniques. The model shows that population growth depends mostly on the survival of adults and juveniles rather than survival of hatchlings. For instance, the model showed that a 33% decrease in hatchling survival was required to destabilize the population, while only a 10% decrease in adult female mortality is required to cause population decline (Figure 14, Figure 8). For management of a declining population, the model can be used to determine which age groups should be targeted for conservation given limited resources. In general, the conservation of adult females would be the most effective strategy for most terrapin populations. This is consistent with the findings of the model presented by Mitro (2003). However, nest capping and head start programs for hatchlings could also be effective if the number of hatchlings per female and the hatchling survival rate were just below the bifurcation point. For this reason it is useful to rerun the model (Equation 3) with parameter estimates unique to each population examined.

Though the model indicates that population growth rates are not very sensitive to changes in juvenile survival, the bifurcation plots of crab pot mortality still highlight the need for by-catch reduction devices. The model indicates that crab potting is able to create levels of fatality beyond the maximum threshold which a terrapin population may withstand, while the use of BRDs lowers fatality rates below the threshold value.

The model can also be used as an important research tool to measure the impacts of the human footprint on terrapins within the Chesapeake Bay. With the use of the crab potting model in Equation 4, the impact of crabbing on the population may be quickly determined using an estimate of the number of crab pots within the terrapin habitat. With approximately .018 terrapin deaths per trap per day, the number of terrapin deaths for the population may be calculated (Roosenburg 1997). With a population estimate, it is possible to determine the percent of the population which dies in traps each year, ρ. This value alone would allow researchers to quickly predict the long-term viability of a population under pressure from crab potting. This eliminates the need to calculate the precise survival rates of each age class, a process which can take several years of field work.

Future Work

With more research it would also be possible to quickly estimate the effects of urbanization on nearby terrapin populations without calculating survival rates or the number of hatchlings per female. This may be achieved by quantifying the level of urbanization through such factors as road or housing density. These urbanization indicators would then need to be correlated with hatchling survival or the number of hatchlings per female. Additionally, road density and road distance from the stream could be used to find a correlation with adult female mortality. If a reliable correlation could be found, it would be possible to create a population projection using only a rough population estimate and information about the surrounding area.

The model can also be used to create population projections for populations simultaneously affected by crab potting and urbanization. In these cases, the two pressures act synergistically, creating an even more rapid decline than if they were acting separately. In these cases, a quick population projection could be made by using the number of hatchlings per females and hatchling survival rates as indicated by the level of urbanization. These parameters could then be used in the model for crab potting (Equation 4) with an estimate of ρ in order to account for both crab potting and urbanization.

In order for this model to be applied bay-wide, it must also be able to account for complex ecosystems where immigration and emigration may alter population dynamics. For these populations, a net migration term could be added to each age class. With more work, it would even be possible to determine the collective viability of two populations facing different pressures given a certain level of migration between them. This technique could be used to determine how sink-source dynamics affect the long-term growth or decline of multiple, interacting populations found within a wetland complex.

Overall, the model's versatility enables it to be employed in a variety of management and research situations. Since both genders and several age classes are included, the model can predict the viability of a population under any potential population pressure, including crab

potting. The model may also be adjusted to examine the population of the diamondback terrapin at any scale, whether the population of interest is contained in a single creek or within the entire Chesapeake Bay watershed.

Figure 1
The flowchart depicts the relationship between the age and gender classes of the Leslie matrix model for diamond terrapin population growth. 's' values represent the rate that turtles progress to the next group, while 'p' values represent the rate turtles stay within the same age class. 'b' values represent the number of hatchlings per female in the respective age class.
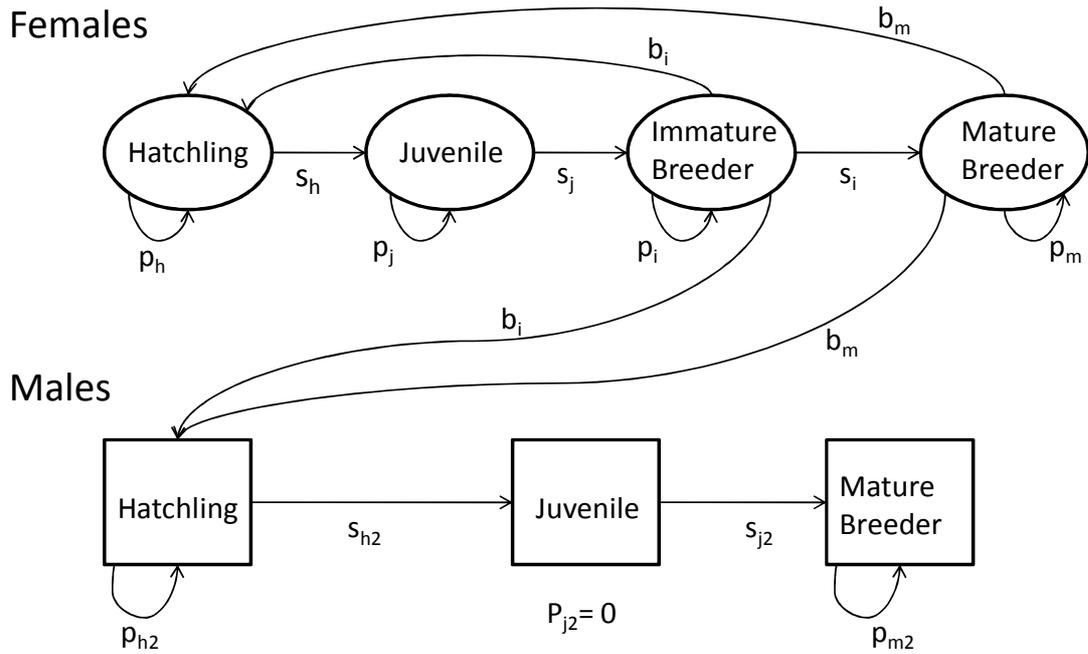
Figure 2

Population estimates for each gender for each sampling year. Estimates were taken using the Schumacher and Eschmeyer method.
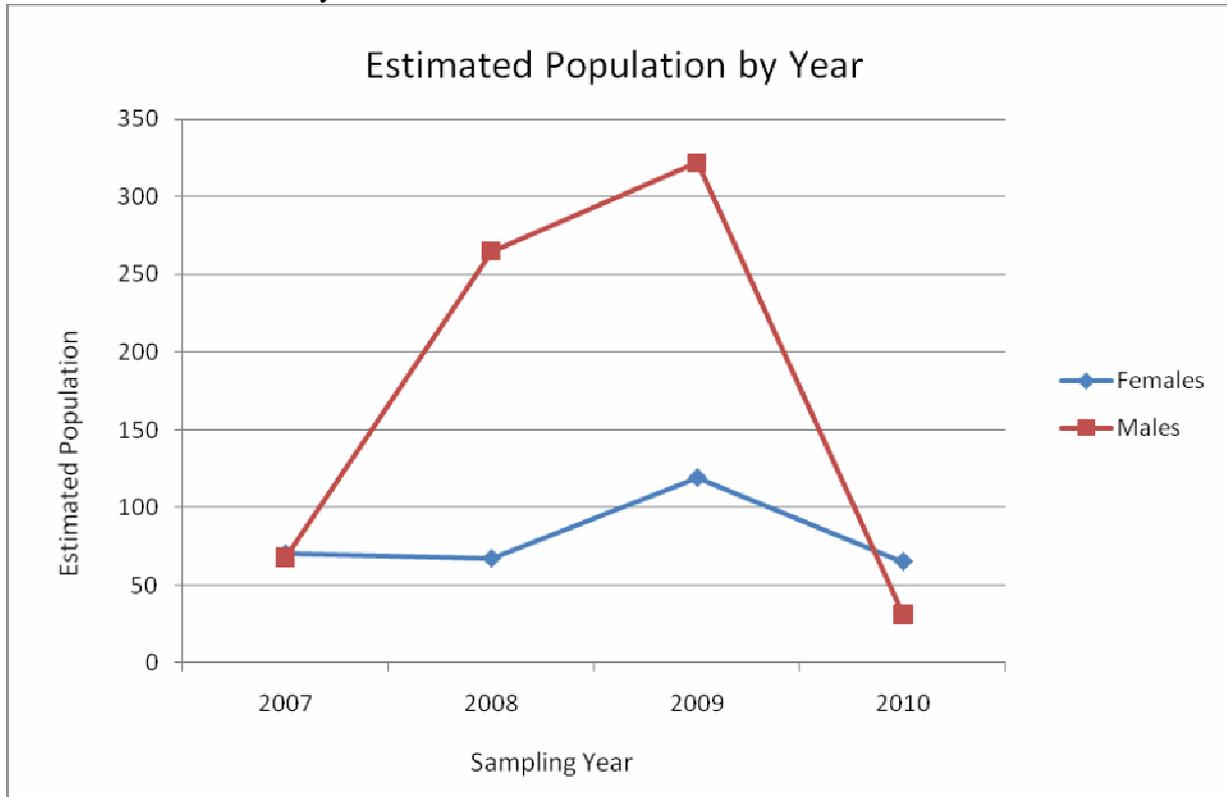
Figure 3
Relationship between age and carapace length according to gender, where age was estimated by counting growth rings on the terrapin's carapace. The maximum carapace length achieved by a male of any age was 15 cm. Females underwent a quick growth period around age 7.
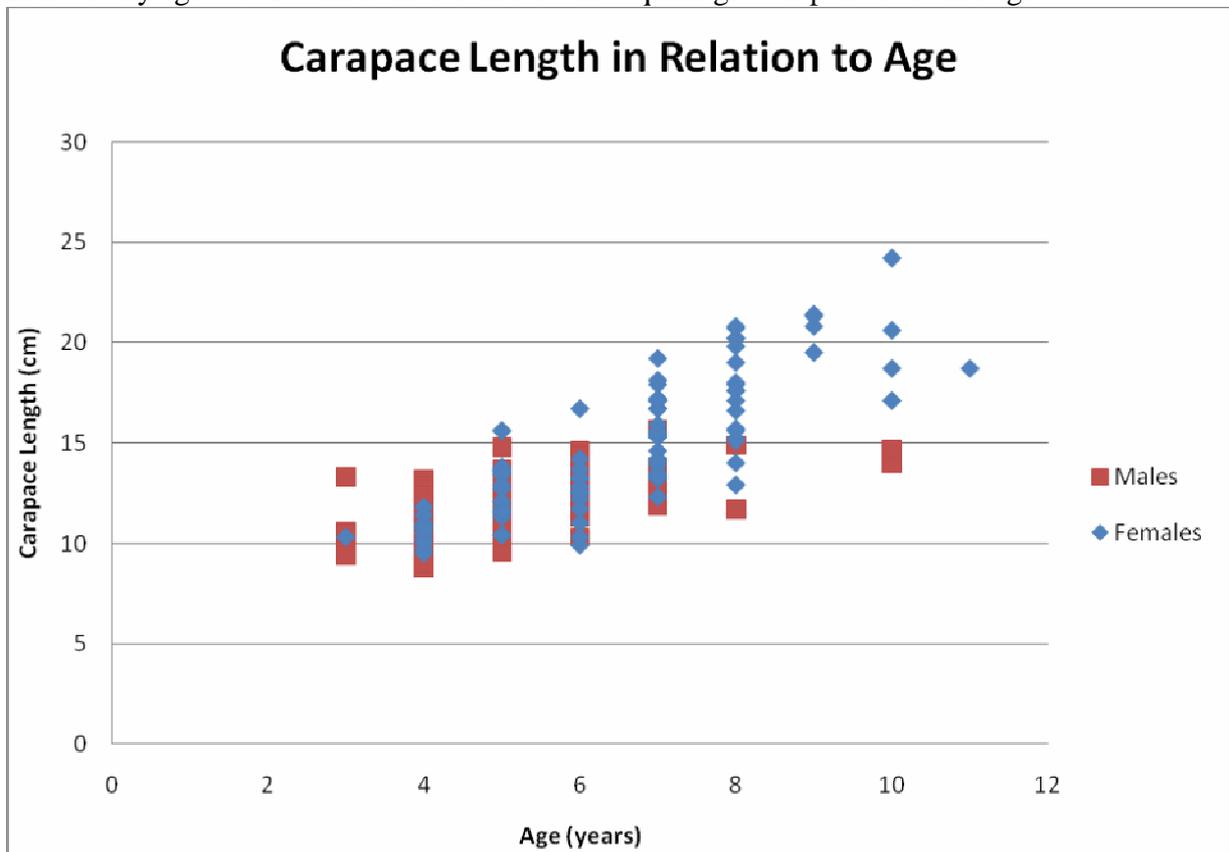
Figure 4
Relationship between age, gender, and shell depth. The solid black line indicates the typical size
of the opening of a BRD at 4.5 cm. All turtles with shell depth above this line would be excluded
by the device.
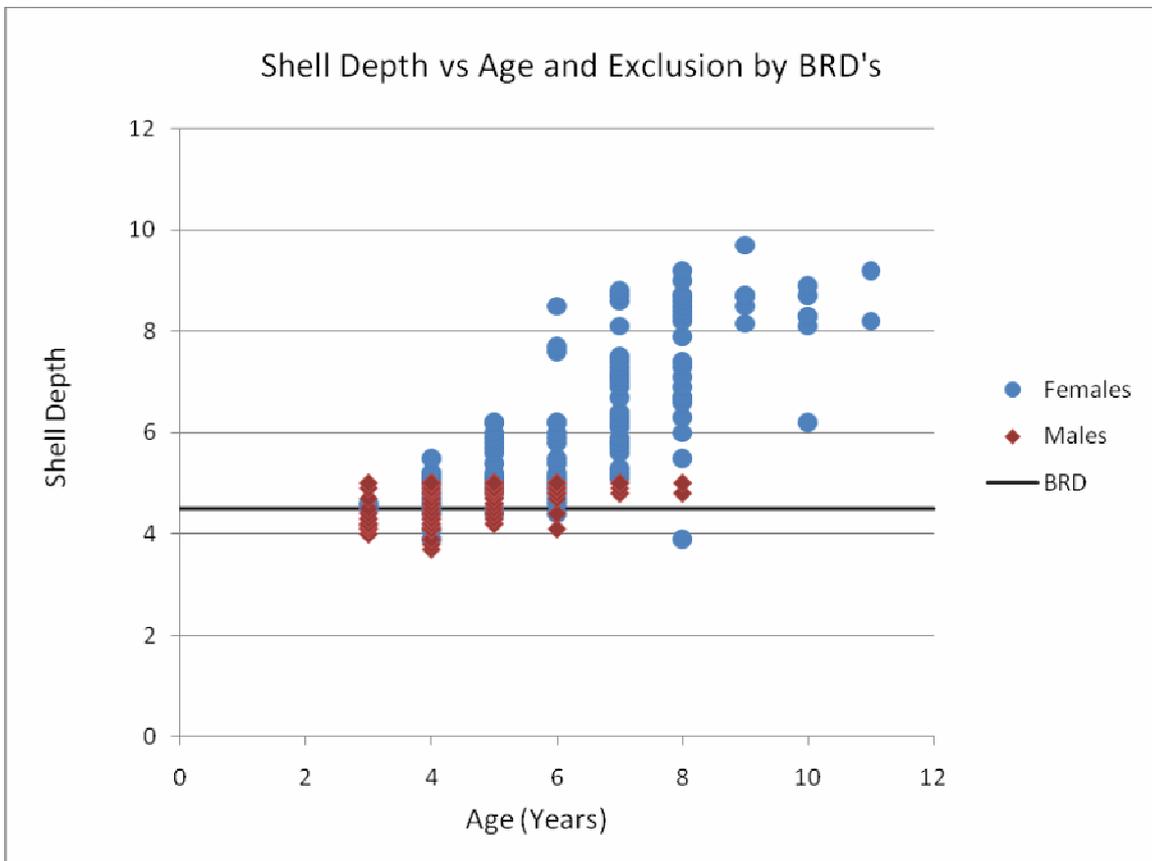
Figure 5
Population size predictions for females (A) and males (B) for each age class in a population with a positive growth rate. Adult female survival was set to 0.96 and adult male survival was 0.85.

A.
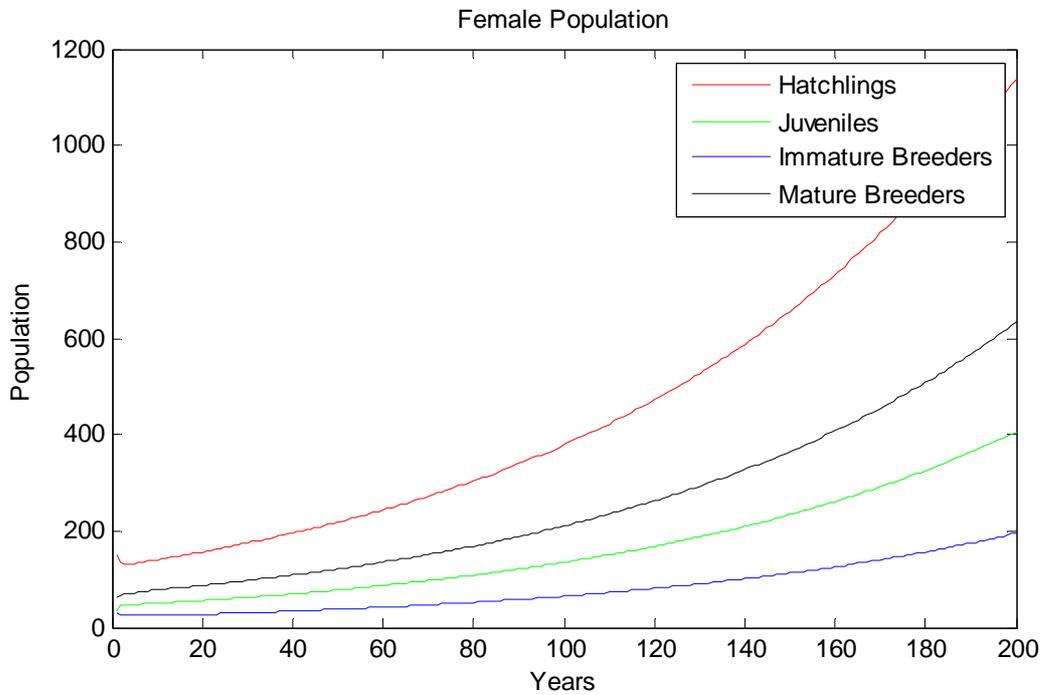
B.
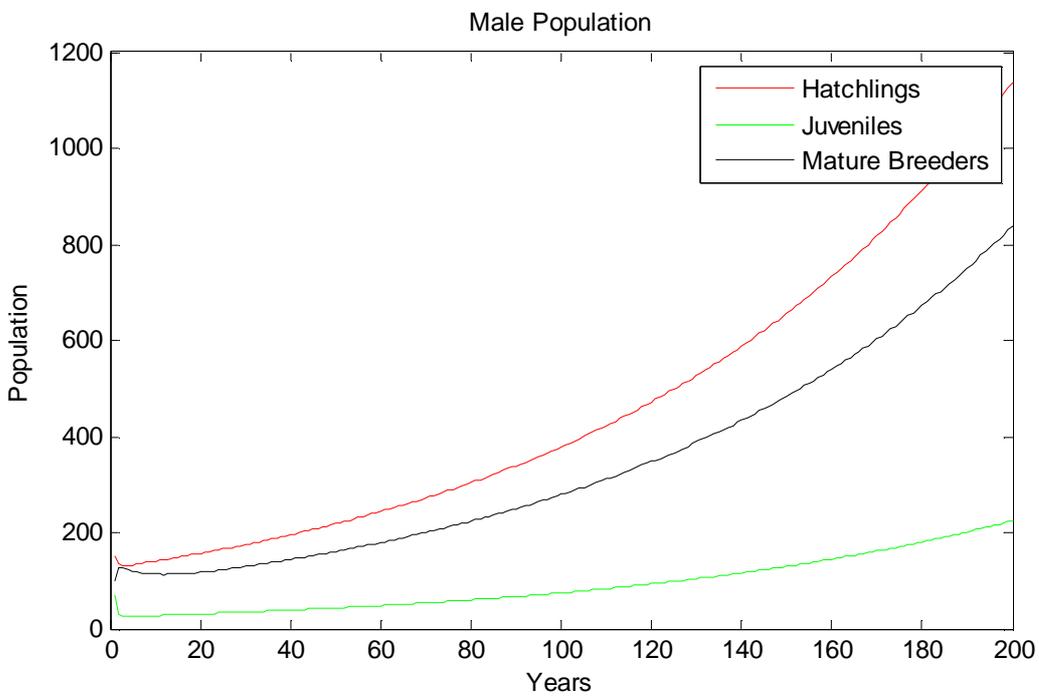
Figure 6

Population size projection for females (A) and Males (B) in a declining population. Parameters were specifically taken from Kiawah River, SC (Tucker). Extinction of the population is predicted to occur within 85 years.

A.
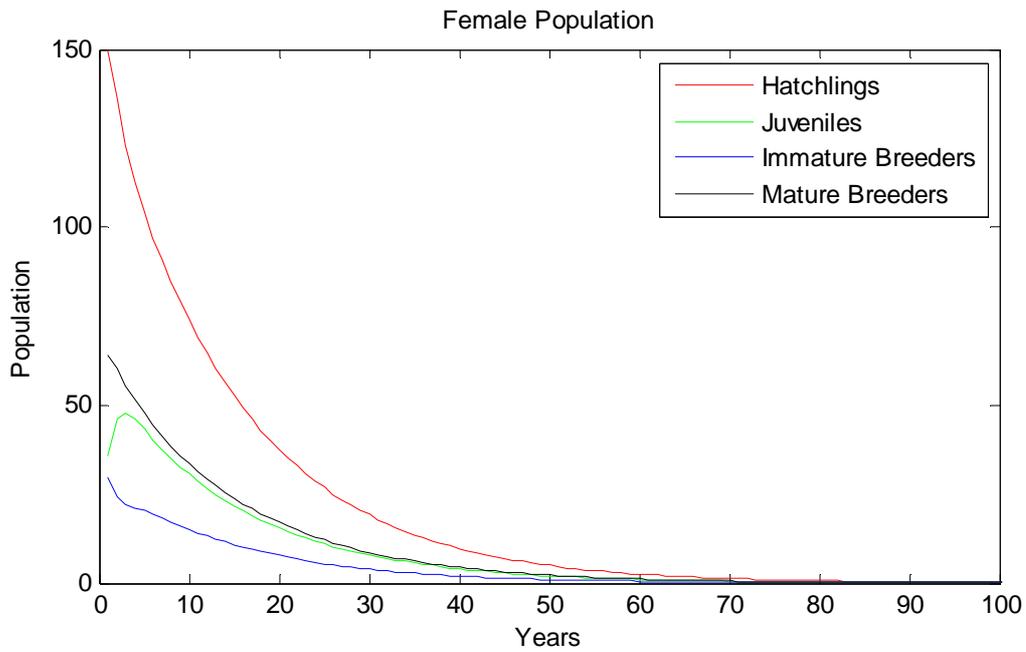
B.
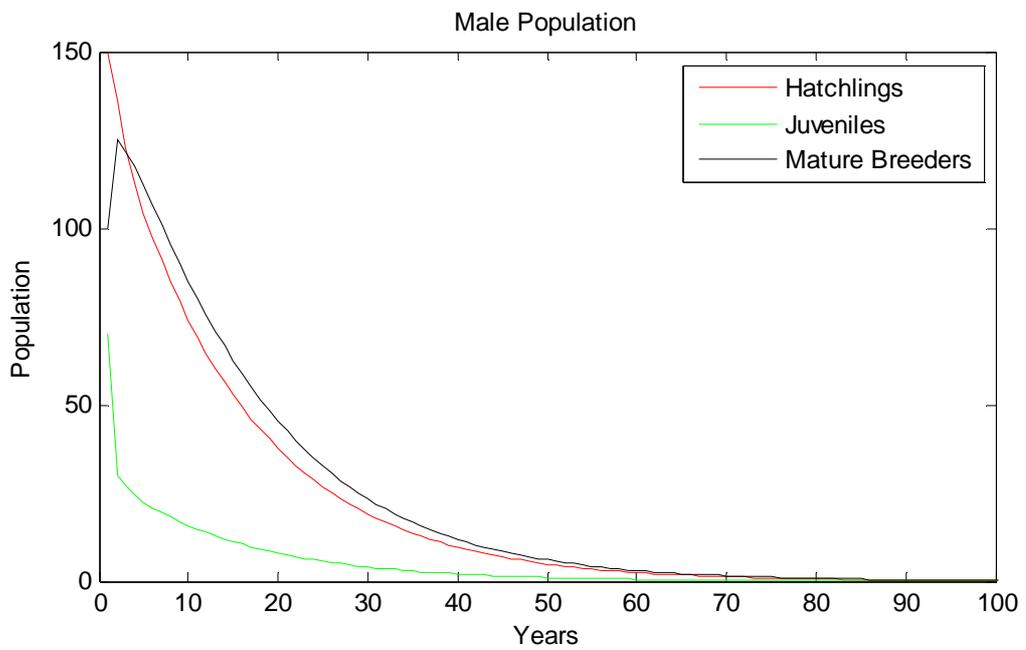
Figure 7
The bifurcation plot below investigates the effects of nest predation. The average number of hatchlings was set to zero and gradually increased, and the resulting eigenvalues were plotted. The population becomes stable when an average of 1.75 eggs per adult female survives to the hatchling stage.

Increased Nest Predation
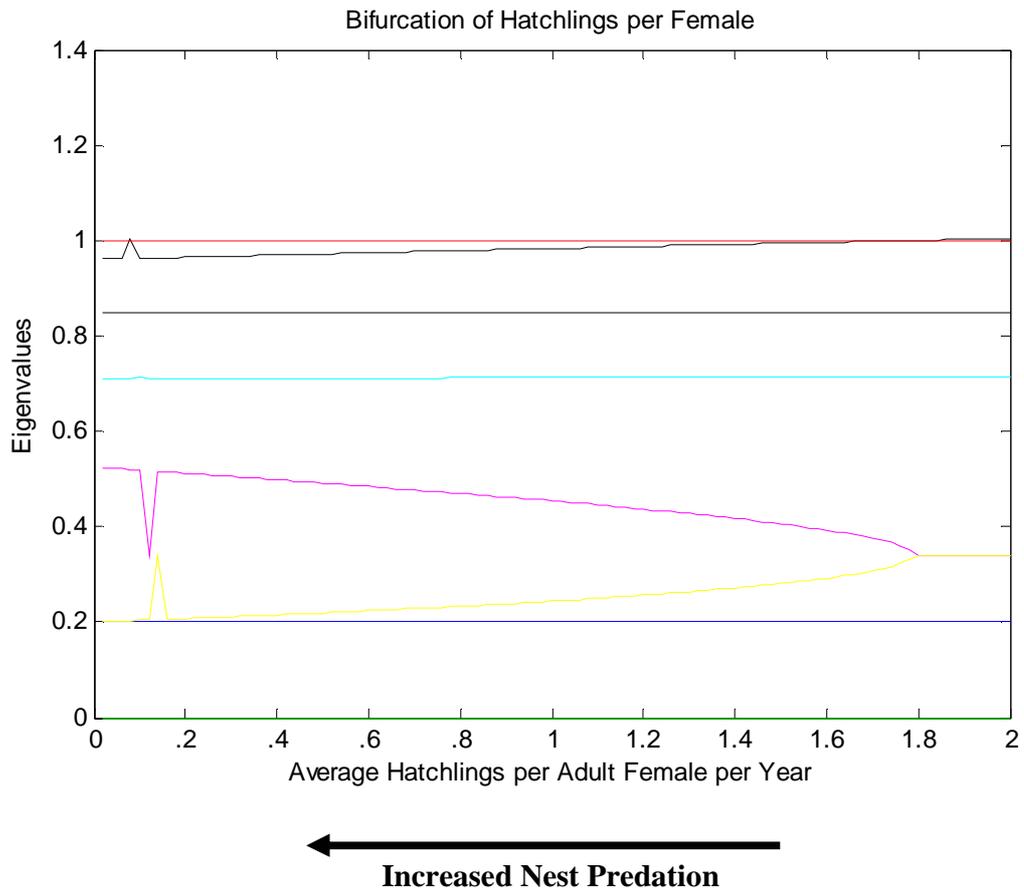
Figure 8
Bifurcation plot demonstrating the effects of adult female road mortality. The survival rate of adult females was set to zero and increased by increments of 0.01. The resulting eigenvalues were plotted for each increment and all other parameter values were held constant. The population will maintain positive growth at all values above the bifurcation point, where the dominant eigenvalue crosses the line $\lambda=1$. This point corresponds to approximately 86% adult female survival.
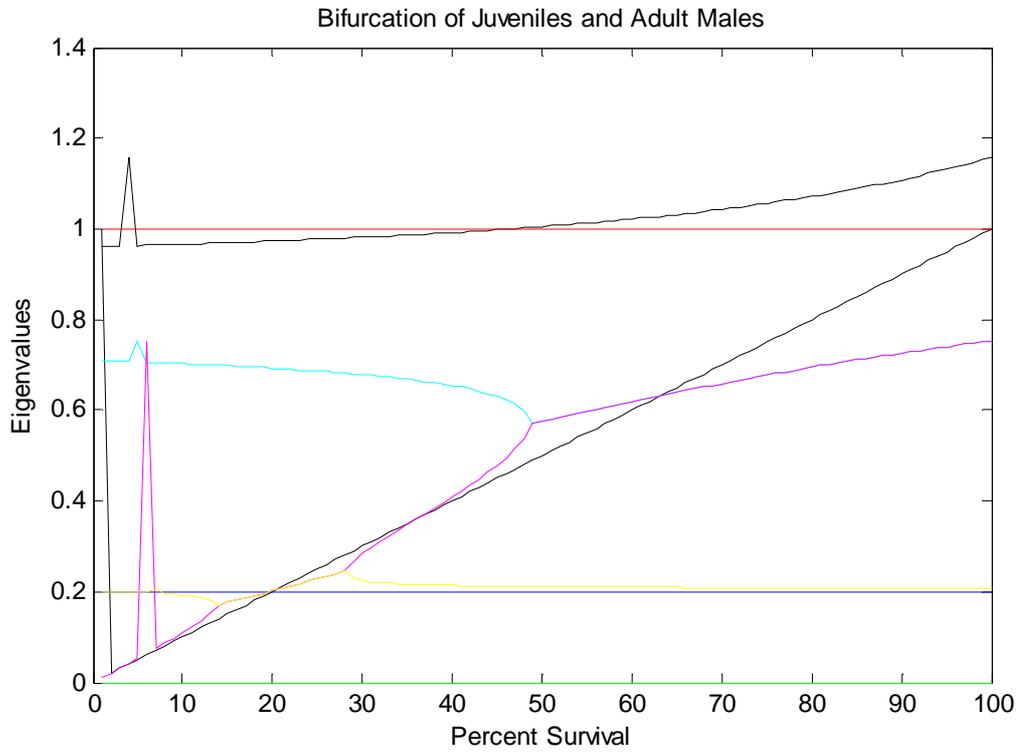

Increased Road Mortality
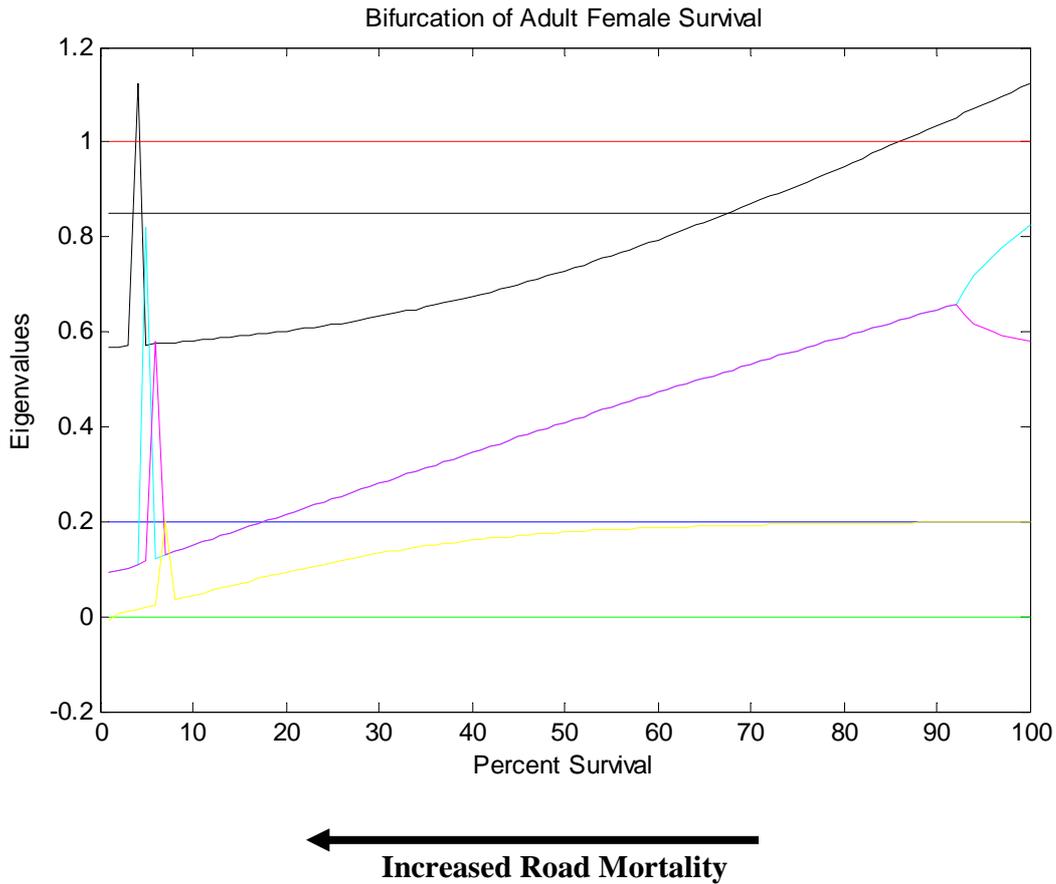
Figure 9

The bifurcation diagram shows how the growth rate of the population changes in response to crab potting. Survival rates for adult males and juveniles of each gender were plotted in relation to the resulting eigenvalues. The population is predicted to decline where adult male and juvenile survival falls below 45%.

Increased Crab Potting

Figure 10

The bifurcation diagram below shows how crab potting intensity affects the viability of the population. The bifurcation plot shows the eigenvalues in relation to crab potting intensity. It is predicted that the population will begin to decline when 12% of adult males and juveniles of both genders are removed each year.
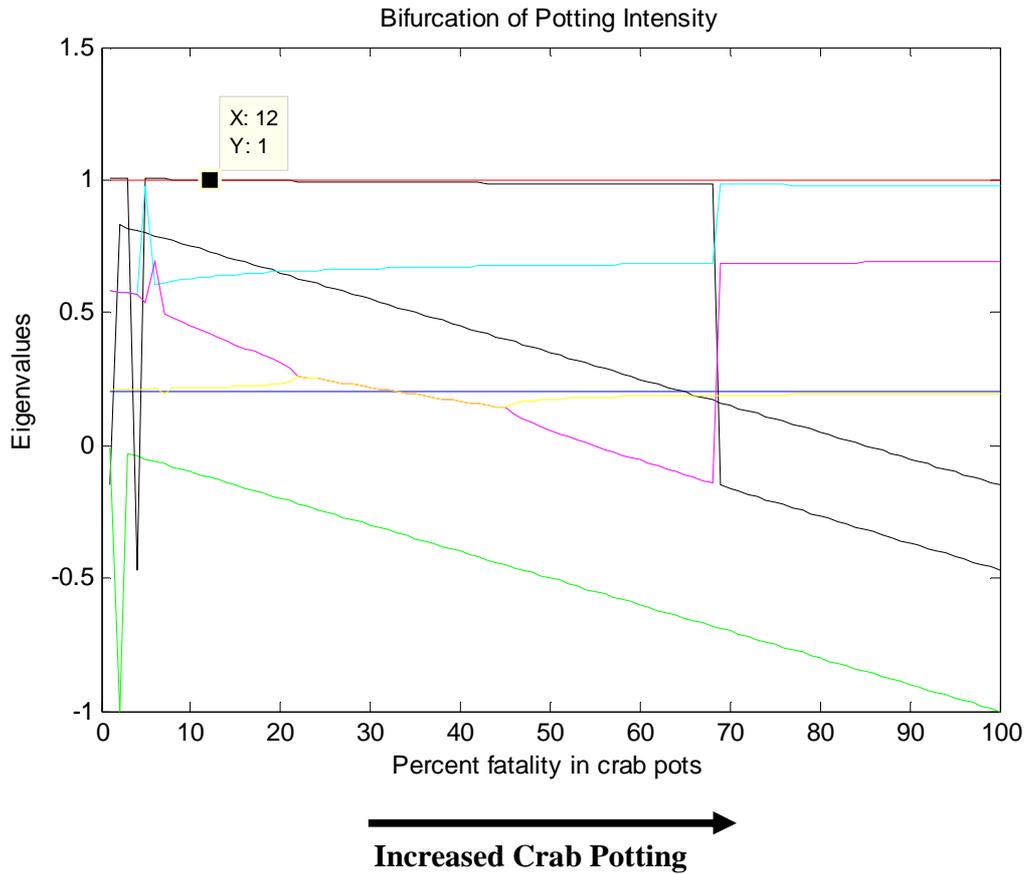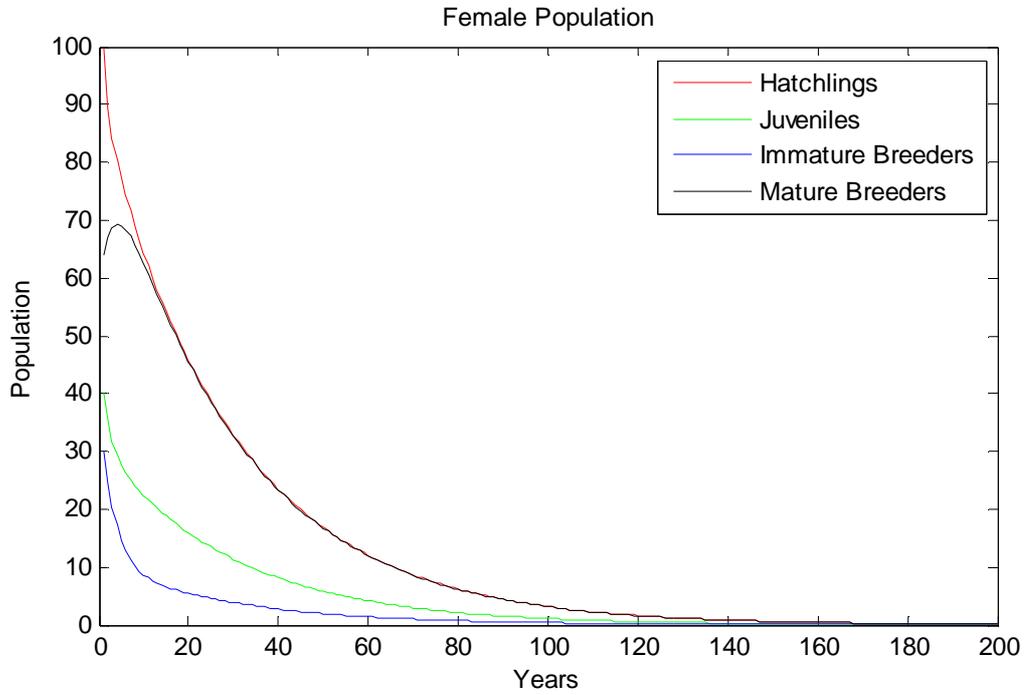

Bifurcation of Potting Intensity

Increased Crab Potting

Figure 11

Below is the population projection where ρ=0.1. This corresponds to where 10% of juveniles and adult males die due to crab pots each year. Extinction of the population is predicted to occur within 165 years.
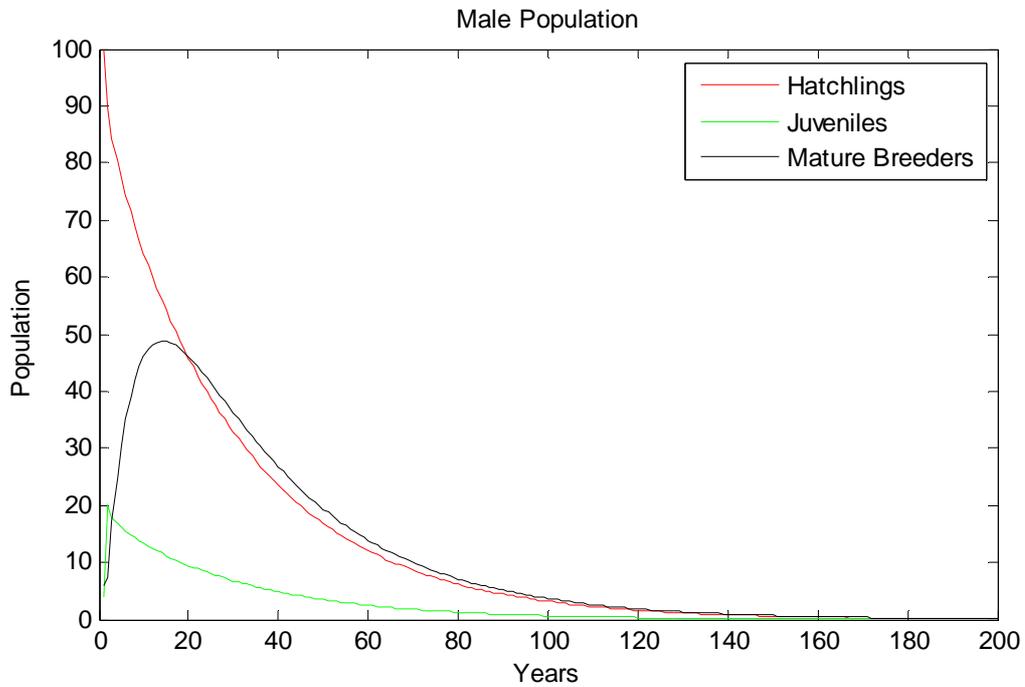
A.

B.

Figure 12
The plot below shows changes in gender ratio in response to crab potting. The female to male ratio surpasses 1 to 10 when 27% of juveniles and male adults die in crab pots each year. At this point, fecundity rates would start to decline as females lose access to males for reproduction.

Female to Male Ratio Bifurcation
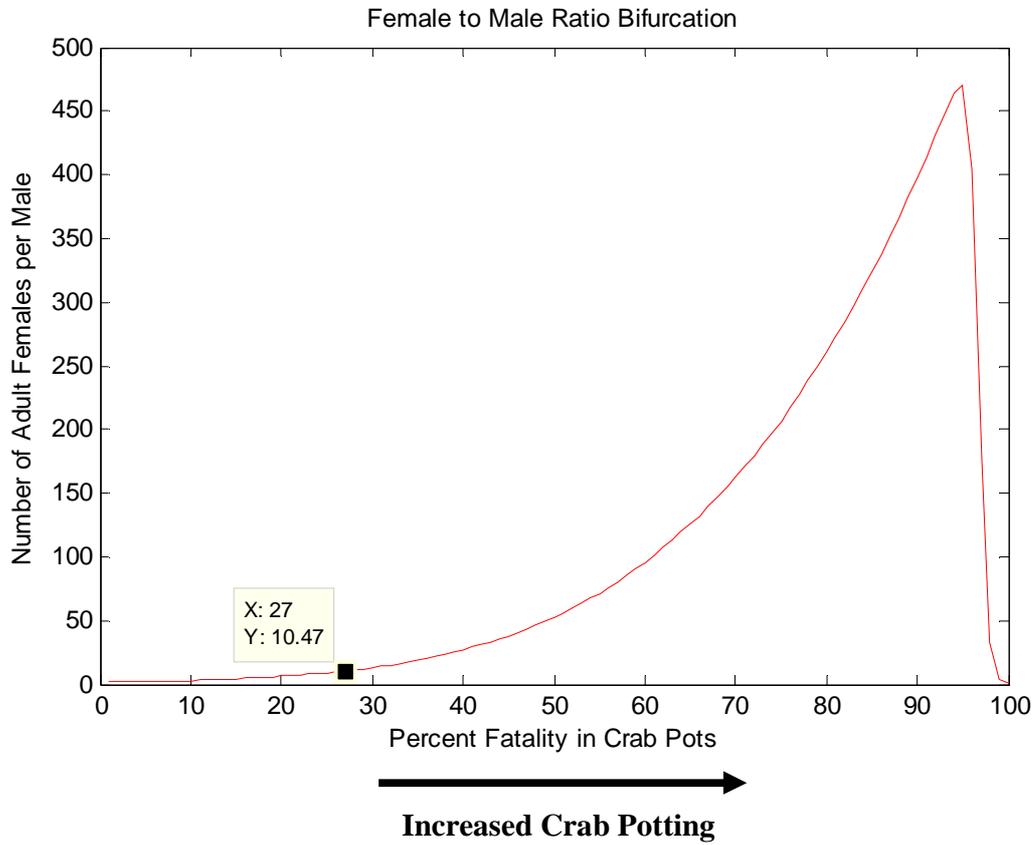
Increased Crab Potting

Figure 13
The bifurcation diagram shows how crab potting intensity affects the viability of a population with reduced fertility due to a female to male ratio greater than 10:1. In this case only 9% crab pot mortality for juveniles and adult males would cause a population decline.
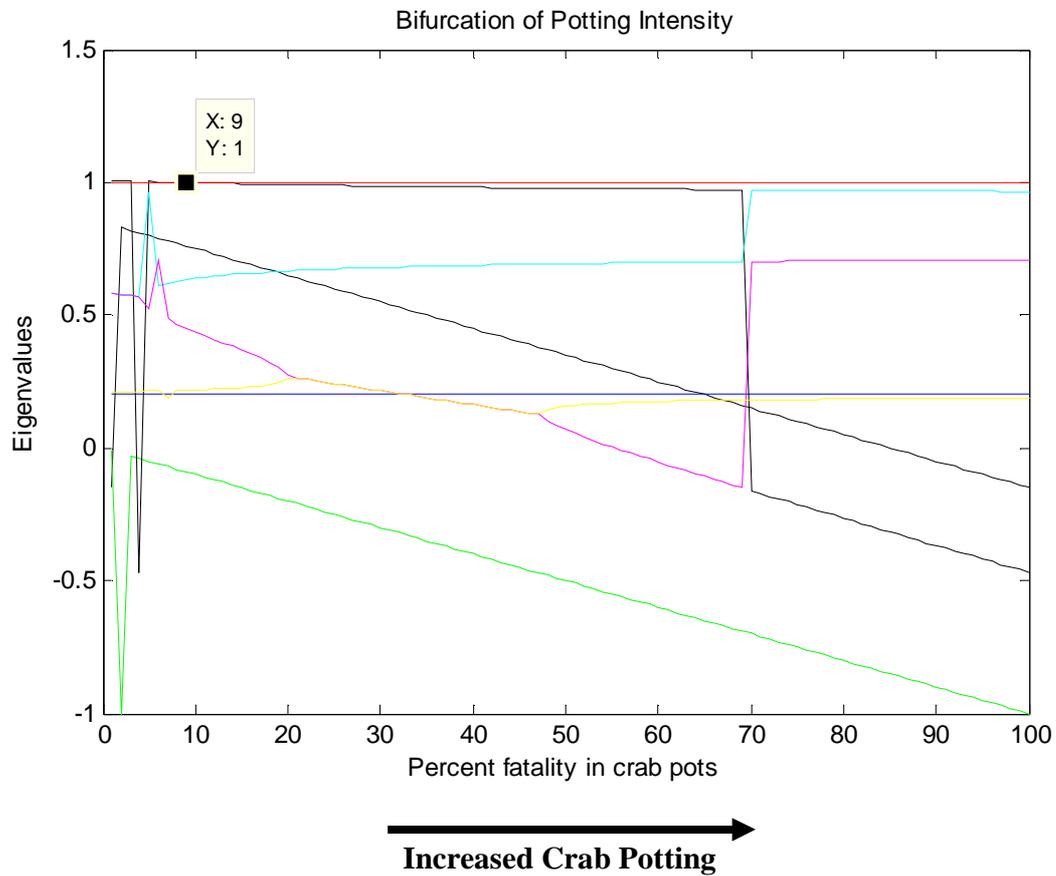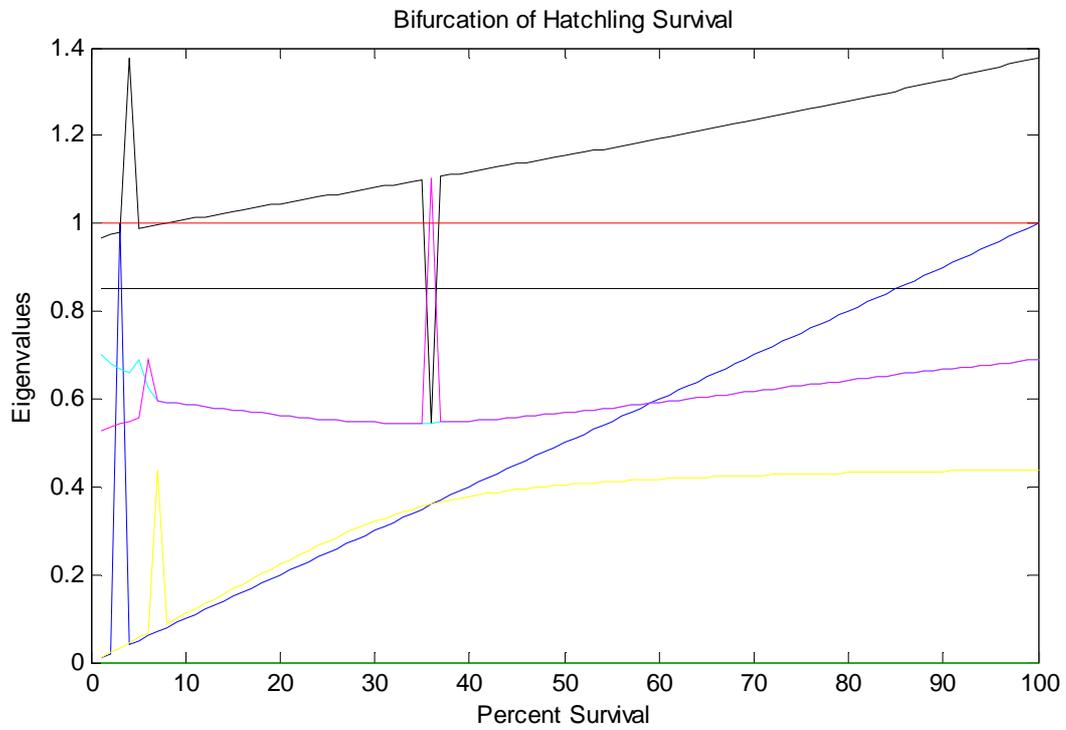

Bifurcation of Potting Intensity

Figure 14
In the bifurcation diagram, hatchling survival was increased incrementally while all other parameters were held constant. The diagram shows that in a stable population with high adult survival, 9% of hatchlings must survive for the population to maintain positive growth.

Bifurcation of Hatchling Survival

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