

The Population Ecology of a Headstart Supplemented Population of Diamondback
Terrapins (*Malaclemys terrapin*) at the Poplar Island Environmental Restoration Project
in the Middle Chesapeake Bay

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This thesis titled
The Population Ecology of a Headstart Supplemented Population of Diamondback
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in the Middle Chesapeake Bay

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ABSTRACT

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The Population Ecology of a Headstart Supplemented Population of Diamondback Terrapins (*Malaclemys terrapin*) at the Poplar Island Environmental Restoration Project in the Middle Chesapeake Bay (71 pp.)

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The efficacy of headstarting programs to supplement populations of long-lived, late-maturing organisms is unknown. Despite this fact, headstarting programs have been criticized for not addressing or mitigating the actual causes for population declines. Over the last five years, 642 diamondback terrapin (*Malaclemys terrapin*) hatchlings were headstarted and released at the Poplar Island Environmental Restoration Project (PIERP) in the Chesapeake Bay. I conducted a mark-recapture study to determine the effectiveness of headstarting in this population. I trapped terrapins using fyke nets and tall crab pots. Captured terrapins were tagged and I recorded morphometrics, mass, sex, and age. I compared the PIERP population to a 23 year mark-recapture study in the Patuxent River (PR) of a non-headstart supplemented population where data were collected in the same manner and commercial crab fishing does not occur. The sex ratio of the PIERP population was highly female biased (9:1). There was no difference in size or age distributions among the two populations, with both skewed toward larger and older individuals. I estimated the population size at PIERP to be 204-406 individuals and a stage-structured Leftkovich matrix population model indicated that the PIERP is declining ($\lambda=0.940$). The low population growth rate and similarities between the PIERP and PR populations suggest that headstarting is not increasing hatchling and juvenile

survival. I suggest that the lack of juvenile and male turtles in the PIERP population and ineffectiveness of headstarting are caused by differential mortality of these groups due to bycatch in crab pots and support the conclusion that headstarting is a “halfway technology” that does not address the initial causes for population declines. I recommend that headstarting not be considered a viable management strategy until mortality caused by crab pot bycatch is resolved through the use of bycatch reduction devices and spatial restrictions on commercial crab pots.

Approved: _____

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INTRODUCTION

Cultural History and Conservation Threats of Diamondback Terrapins

Conant (1975) describes diamondback terrapins (*Malaclemys terrapin*) as the “most celebrated of [North] American turtles” due to the long history of terrapin exploitation in the Eastern United States for food and incorporation of diamondback terrapins into the cultural heritage of many regions. As early as the 1700’s, diamondback terrapins were harvested to feed the Continental Army and later, slaves on tidewater plantations (Hart and Lee 2007). Likewise, records from Maryland from 1880 to 1936 indicate that the commercial harvest of terrapins peaked in 1891 at nearly 40,438 kg (this figure does not include illegal harvest), but rapidly declined in the years to follow (McCauley 1945). The total estimated legal harvest of diamondback terrapins from 1880 to 1936 in Maryland was 139,706 kg (McCauley 1945), representing nearly 200,000 individual turtles, of which most were likely large, adult females (Burke et al. 2000). By 1878, Maryland enacted regulations prohibiting the harvest of terrapins during certain seasons (Burke et al. 2000), but populations continued to decline drastically throughout the state during the early 20th century (McCauley 1945, Tucker 1993). Due to a combination of prohibition — one of the main ingredients in terrapin stew is sherry — and rising terrapin prices, demand dwindled and populations began to recover (Burke et al. 2000, Hart and Lee 2007).

Sustainable harvest of diamondback terrapins may be impossible due to the following reasons: 1) large, reproductive individuals are more frequently harvested rather

than smaller individuals (Burke et al. 2000) 2) low reproductive rates (Roosenburg 1991) and 3) delayed maturity (females between 8-13 years and males between 4-7 years; Roosenburg 1991). Because of this suite of life history traits, terrapin populations remain vulnerable to severe declines when exploited. Although demand for terrapin never rebounded to historic levels, diamondback terrapins continued to be harvested in Maryland to support both a small domestic and strong Asian demand for terrapin meat (Roosenburg 1991, Burke et al. 2000). In 1990, an estimated 8,000 – 12,000 terrapins were harvested annually in Maryland (Roosenburg 1991), some of which ended up in New York markets where approximately 10,000 terrapins are sold per year (Burke et al. 2000). Recently, Maryland legislators recognized that the state reptile of Maryland and mascot (*Testudo*) of the University of Maryland was harvested to support an international trade in terrapin meat. Thus, on 24 April 2007, the commercial fishery for terrapins was closed in Maryland (Roosenburg et al. 2008). Although it is too soon to tell whether or not populations will recover from the effects of harvest, other threats to diamondback terrapins in the Chesapeake Bay—crab pots (Roosenburg 1991, Roosenburg et al. 1997, Roosenburg and Green 2000, Hart and Lee 2007), habitat destruction (Roosenburg 1991, Hart and Lee 2007), and motor boats—remain.

In Maryland, and in particular the Chesapeake Bay, the commercial fishing industry is a way of life and engrained in the cultural heritage of the region, which made the closure of the terrapin fishery difficult (Roosenburg et al. 2008). Ironically, the commercial and recreational fishing industries, albeit blue crab instead of terrapin, still remain the most prominent threats to the persistence of terrapin populations in the Chesapeake Bay and elsewhere (Seigel and Gibbons 1995, Roosenburg and Green 2000,

Roosenburg 2004, Butler and Heinrich 2007, Dorcas et al. 2007). Due to their size and use of shallow, open water habitats, adult male and juvenile female terrapins most frequently drown in crab pots, effectively removing these age classes from the population (Roosenburg et al. 1997). This problem is further exacerbated by recreational crab pot fishing in shallow tributaries to the Chesapeake Bay, where capture rates may approach $0.17 \text{ terrapins} \cdot \text{pot}^{-1} \cdot \text{day}^{-1}$ resulting in 15-78% declines in the population annually (Roosenburg et al. 1997). The subsequent use of razor clams as crab pot bait, a preferred food of terrapins in the Chesapeake Bay, further increase the likelihood of terrapin capture in areas where recreational fishing occurs (Roosenburg 2004). Fortunately, Roosenburg and Green (2000) tested the efficacy of bycatch reduction devices (BRD's) on crab pots in the Chesapeake Bay and demonstrated an 80% reduction in terrapin mortality in crab pots. Concomitantly, Butler and Heinrich (2007) found a 73.2% decrease in terrapin mortality when BRD's were installed on traps in Florida. Unlike the previous two studies, however, Dorcas et al. (2007) argue that current BRD's do not significantly reduce mortality of males and most females within in a population from South Carolina. Although regulations in Maryland require the use of BRD's in recreational crab pots, the state lacks the ability to enforce this requirement and does not require their use on commercial crab pots (Roosenburg et al. 2008).

Headstarting as a Conservation Tool

The relocation and repatriation of headstarted wildlife to re-establish or bolster depleted populations has become a popular conservation strategy during the last 20 years. As of 1989, nearly 700 translocations occur per year in North America alone, most

involving endangered or game species (Griffith et al. 1989). Most of these relocation and repatriation programs were ineffective with a 56% failure rate (Griffith et al. 1989).

Likewise, Dodd and Seigel (1991) reviewed 25 repatriation programs for reptiles and amphibians, finding only 19% to be successful. Headstarting and repatriation programs, however, have been successful for many species of reptiles not reviewed by Siegel and Dodd (1991) including Galapagos tortoises (*Geochelone* spp. [Milinkovitch et al. 2004]), gopher tortoises (*Gopherus polyphemus* [Tuberville et al. 2005]), Mona Island iguanas (*Cyclura cornuta* [Perez-Buitrago et al. 2008]), and plains gartersnakes (*Thamnophis radix* [King and Stanford 2006]). These successes give hope to headstarting as a management tool for reptiles including long-lived organisms like turtles.

Turtle headstart programs were initiated experimentally in Florida as early as 1959 where managers wanted to increase endangered populations of green sea turtles (*Chelonia mydas* [Huff 1989]) and subsequently have been used for other sea turtle species (Byles 2001), western pond turtles (*Emys marmorata* [Spinks et al. 2003]), and tortoises and freshwater turtles (Seigel and Dodd 2000). Simply stated, a headstart program involves collecting eggs or hatchlings from the wild and rearing them in captivity for several months (Heppell et al. 1996, Spinks et al. 2003, Mitrus 2005). The two main goals of headstart programs are – 1) raise hatchlings in a controlled environment until they reach a size that reduces high mortality often associated with their first year of life (Heppell et al. 1996) and 2) increase the survivorship of the juvenile age classes to adulthood. Furthermore, if conditions are ideal, Hildebrand (1932) reports that reproduction may occur at a younger age due to the increased growth achieved within the first year. Roosenburg (1991) predicted that a female terrapins must reproduce at

maximal reproductive output (3 clutches/year, 13 eggs/clutch) for three years during her lifetime in order to replace herself as a hatchling in the population. Replacement becomes more probable with headstarting because it increases hatchling survival and these individuals may breed at a younger age than their wild conspecifics.

The ultimate goal of headstarting programs is to increase the number of reproductive individuals in the population. Heppel et al. (1996) argue that the true measure of success for a headstarting program is a significant increase in population growth, implying that simply bolstering juvenile cohorts is not an effective conservation method. Not only must headstarted individuals survive, but they must also reproduce and nest successfully. Because headstarting programs focus on juvenile cohorts, other conservation issues including high adult mortality and habitat loss are sometimes overlooked.

The most significant threat to turtle conservation in many species is bycatch from other fisheries (Frazer 1992, Roosenburg et al. 1997, Roosenburg and Green 2000). Methods to decrease or regulate turtle bycatch include BRD's on crab pots for terrapins (Roosenburg and Green 2000) and turtle excluder devices (TED's) in shrimp trawler nets for sea turtles (Frazer 1992). However, when populations drop below their effective population size, protecting habitat and reducing adult mortality may not restore populations, particularly when adults are harvested (Burke et al. 2000) or killed inadvertently as bycatch (Roosenburg 1991, Roosenburg et al. 1997, Roosenburg and Green 2000). In these situations, an input of younger age classes may be required to supplement current populations so that a more balanced age structure and sex ratio

(typically 3:1 female biased; Roosenburg 1991) may be attained. Headstart programs could be used to supplement younger age classes and bolster declining populations.

The true efficacy of turtle headstart programs remains unknown, largely because extensive information and long-term data sets for these programs are unavailable and survivorship for many populations has not been assessed (Heppell et al. 1996, Seigel and Dodd 2000). However, Frazer (1992) refers to headstarting as a halfway technology, because it only addresses one aspect of conservation and fails to “address the causes or provide amelioration for the actual threats turtles face.” This view of headstarting is reinforced by models from yellow mud turtles (*Kinosternon flavescens*), Kemp’s Ridley sea turtles (*Lepidochelys kempii*), and European pond turtles, where if subadult and adult survival is reduced, headstarting will fail to compensate for those losses (Heppell et al. 1996, Mitrus 2005). Failure to address the initial cause for population declines was also noted in western pond turtles in California, where invasive species are contributing to the population declines in some areas (Spinks et al. 2003). For these reasons, Dodd and Seigel (1991) and Frazer (1992) challenged the use of headstarting as a management tool for long-lived organisms including turtles. In Maryland, the prohibition on harvesting diamondback terrapins should increase adult survival, but the presence of crab pots, both active and ‘ghost pots’ (Roosenburg et al. 1997, Roosenburg and Green 2000, Roosenburg 2004), still represent real threats to terrapin survival and may negate terrapin headstarting activities.

Other potential issues with headstarting programs also exist. Headstarted turtles may not behave the same as their wild hatchling conspecifics (Nagelkerken et al. 2003, Spinks et al. 2003, Mitrus 2005). Similar suggestions have also been made for

headstarting programs in Caribbean rock iguanas (*Cyclura* sp.) where some headstarted individuals have not shown predator avoidance behaviors (Alberts 2007). Observations from Kemp's Ridley sea turtles revealed that many five month old headstarted turtles did not develop predator or human avoidance responses typically shown by wild turtles (Meylan and Ehrenfeld 2000). The same results, however, were not observed in western pond turtles, where recapture rates for wild and headstarted turtles were not significantly different (Spinks et al. 2003). Some opponents have also raised the threat of disease transmission as a risk involved with headstarting programs (Dodd 1988, Jacobson and Gaskin 1990, Flanagan 2000). It is suspected that upper respiratory disease, caused by *Mycoplasma agassizii*, was introduced to desert tortoise (*Gopherus agassizii*) populations from captive reared individuals released into the natural habitat (Seigel and Dodd 2000). Definitive examples of this risk, however, have not been observed or studied in headstarted turtle populations. Screening headstarted turtles should be a prerequisite before release to avoid contamination of wild populations (Dodd and Seigel 1991, Seigel and Dodd 2000).

Previous studies have determined that survivorship of headstarted turtles is directly related to size at release. In European pond turtles, Mitrus (2005) found 41.5% survivorship in headstarted turtles, likely influenced by larger size (carapace length) and body mass. This was more than five times the natural survival rate measured from the same population of wild hatchlings (Mitrus 2005). Spinks et al. (2003) used headstarting as a management option for a declining western pond turtle population in the University of California-Davis arboretum from 1996-1999. During this time, 31 headstarted turtles were released into the waterway, of which 24 survived to adulthood (77.4% survival

rate), six of which are now probably reproductively active (Spinks et al. 2003). Lastly, a less extensive study from Massachusetts of red-bellied slider (*Pseudemys rubriventris*) survival determined that larger headstarted turtles have a higher rate of survival for the first two years after released, after which turtles reached a size where threats to survival are limited (Haskell et al. 1996).

Although headstarting has been used as a management tool for terrapin populations (Herland et al. 2004), no study has yet determined the efficacy of such efforts. Therefore, the primary goal of this study was to compare the population ecology of a headstart supplemented population of diamondback terrapins at the Poplar Island Environmental Restoration Project (PIERP) to a population with natural recruitment in the Patuxent River (PR) in order to determine whether or not headstarting programs are a viable management strategy for the species. Because headstarting increases hatchling and juvenile survivorship, I predicted that the PIERP population would have a higher proportion of juvenile and subadult terrapins and higher survivorship of those size classes than the PR population. Furthermore, I provide specific management recommendations for the PIERP population through the use of stage-based population growth models that identify sensitive life cycle stages that can benefit from effective management.

METHODS

Study Species

The diamondback terrapin is a small to medium-sized, estuarine, emydid turtle (Roosenburg 1991, Tucker et al. 2001), characterized by concentric markings on their carapace (not always overtly apparent) and light colored skin with dark flecks or spots (Ernst et al. 1994). Currently, seven subspecies of diamondback terrapins are recognized based on carapace morphology and skin color, although they are most easily identified by geographic location (Ernst et al. 1994, Hart and Lee 2007). They are strongly sexually dimorphic; females are larger than males with a carapace length averaging between 1 and 13 cm longer than males (Ernst et al. 1994). Furthermore, females have wider heads, deeper shells, and shorter tails (Ernst et al. 1994). Diamondback terrapins range from Cape Cod to the Gulf Coast of southern Texas. Throughout their range, they live in the brackish waters of tidal wetlands and flats, salt marshes, and estuarine areas (Carr 1952). Their diet mainly consists of hard-shelled prey including bivalves, gastropods, and crabs but they occasionally consume carrion, fish, marine annelids, and plant materials (Ernst et al. 1994). In Maryland, the northern diamondback terrapin (*M. t. terrapin*) can be found in coastal marshes and other suitable habitats throughout the Chesapeake Bay and its tributaries. Carapace color in the northern diamondback terrapin ranges from light brown with concentric rings to black with an orangish to green-gray plastron (Ernst et al. 1994).

Terrapins rely on the external environment and behavioral adaptations to maintain body temperature and thus physiological processes, implying that local climates will limit the period when they are active. Activity patterns of terrapins vary due to extensive latitudinal variation in the range of the species (Ernst et al. 1994). In South Carolina, terrapins remain active from March until November or even December when they enter a state of brumation, which lasts until the following spring (Ernst et al. 1994, Hart and Lee 2007). In comparison, the active season for northern diamondback terrapins begins in late-May or early June, but ends in November (Ernst et al. 1994). Roosenburg et al. (2009) report similar dates for terrapin activity around the PIERP in the middle Chesapeake Bay.

Similar to behavior patterns, the phenology of reproduction varies by geographic location. Both sexual maturity and reproductive activities also are controlled by environmental temperatures (Ernst et al. 1994). Males mature at a much smaller size than females (ca. 90 mm; Ernst et al. 1994). Lovich and Gibbons (1990) report similar minimum size and age for males in South Carolina, but also found that females mature between 132-176 mm in plastron length (PL). However, maturity can occur at significantly younger ages when conditions for rapid growth are present (Hildebrand 1932). Due to colder environmental temperatures and shorter activity seasons, maturation in Maryland occurs much later, with females not becoming reproductively active until they reach approximately 163 mm in PL and males at 100 mm PL (Roosenburg 1991). Mating and copulation in terrapins occurs offshore in mating aggregations when water temperatures approach 24.8 to 27.0°C (Ernst et al. 1994), which

is not typically reached in the Chesapeake Bay until mid to late May. This is why nesting in Maryland does not commence until late May to June (Roosenburg 1994).

Across their range, female terrapins nest on sandy to vegetated beaches above mean high tide (Burger and Montevocchi 1975) by digging a flask-shaped nest where they lay between 4-18 eggs with an apparent trade-off between clutch and egg size (Ernst et al. 1994). Nesting behavior in Maryland differs from that in other regions. First, in most cases nesting is diurnal in Maryland, with peak nesting occurring between 10 a.m. and 2 p.m. (Roosenburg 1994). Second, terrapins in Maryland usually nest in open areas between vegetation (Roosenburg 1994). On PIERP, females may lay 1-3 nests with an average clutch size of 13-14 eggs (Roosenburg et al. 2009). Nest success varied between 61.9-72% and egg survivorship between 65.7-93%, considerably higher than the rates observed from the PR (Roosenburg et al. 2009). Despite relatively high reproductive output in most populations, low recruitment combined with a delayed age at first reproduction makes species such as the diamondback terrapin particularly susceptible to perturbations in population size and structure (Roosenburg 1991, Seigel and Dodd 2000).

Study Site

The Poplar Island archipelago is located near the eastern shore in Talbot County, Maryland and is formed by three islands: Poplar Island, Coaches Island, and Jefferson Island. However, by the mid-20th century, all that remained of Poplar Island were three small remnants of land composing ca. 4 hectares. PIERP is an ongoing restoration of Poplar Island (Fig. 1). The substrate on PIERP is mainly composed of shipping lane dredge material from the Baltimore Harbor approach channels; although, once the perimeter dyke was completed in 2002 natural sand beaches began to accrete around the

perimeter of the island providing nesting habitat for terrapins along the windward side. Adjacent to Coach's Island, beaches were formed with sand pumped out of the inland cells. The shallow waters around PIERP and restored wetlands provide suitable habitat for all diamondback terrapin life stages. The surrounding bay waters provide ample foraging and breeding areas for adults. The wetland cells in the interior of the island, when completed, and area between PIERP and Coach's Island provide hatchling and juvenile terrapin habitat that is sheltered from the Chesapeake Bay. The wetland cells also are where some headstarted and all non-headstarted wild hatchlings were released.



Figure 1. The Poplar Island Archipelago including PIERP, Jefferson Island, and Coaches Island. Fyke net trapping site = ▲ ; Tall crab pot trapping site = ⊕

These data collected from PIERP were compared with a 23 year mark-recapture data set from the Patuxent River in St. Mary's County, ca. 20 km southwest of PIERP on the western shore of the Chesapeake Bay in Maryland. However, in the PR population, no headstarting has occurred and there are no commercial crab pots were present.

Diamondback Terrapins on PIERP

Terrapin monitoring began on the PIERP in 2002 after terrapins were first found nesting on the island following the completion of the perimeter dike. Because of the absence of predators, terrapin nests have high success and hatchlings incur lower predation rates than they otherwise would in mainland populations. However, predation rates on PIERP have increased recently due to fish crows (Roosenburg et al. 2009). In response, researchers covered known nests with hardware cloth held in place by flags to deter predators (Roosenburg et al. 2009). The monitoring program involves the capture and subsequent measurement and tagging of hatchlings after they emerged from nests. Before release, terrapins were marked by notching the marginal scutes with a scalpel. All hatchlings in one year are considered a cohort and every cohort was assigned a unique shell ID. For example, all hatchlings in 2007 were marked by notching the 12th right marginal scute and the 11th left marginal scute, making the cohort ID 12R11L (Cagle 1932, Roosenburg et al. 2009). Furthermore, wild hatchlings were tagged with individually coded wire tags (CWTs, Northwest Marine Technologies®) subcutaneously in the right rear leg using a 25-gauge needle and injector. Along with nest protection, researchers used headstarting to try to increase diamondback terrapin populations on PIERP.

In conjunction with the Arlington Echo Outdoor Education Center and National Aquarium in Baltimore, researchers initiated a terrapin headstarting program in which 150-200 hatchling terrapins per year were raised in classrooms and released at PIERP. The hatchlings in this program were captured on PIERP as they emerged from nests and each nest was assigned a unique cohort shell ID. Like the wild hatchlings, each headstarted hatchling was wire tagged, although prior to release all headstarted animals were also tagged with a Passive Integrative Transponder (PIT) tag that allows for the future identification of individual terrapins. This program, Terrapin Connection, provides an important opportunity to teach young students about the environment in both a classroom and a field setting. Special care is taken to ensure that terrapins do not habituate to humans through limiting the handling to only times when measurements or veterinary care was needed. During headstarting, terrapins were raised according to protocols recommended by Dr. Eileen Manyin, D.V.M., who is also the veterinarian who oversees the health and prescribes treatment for the terrapins in the program. Each week, all participating classrooms recorded growth data, behavioral data, and weekly husbandry practices. These practices ensure that only healthy individuals were released into the PIERP population.

The PEIRP headstart program has successfully released 664 marked turtles on the island, most at sizes characteristic of 2-5 year old wild terrapins (Roosenburg et al. 2009). Another 240 hatchlings are currently being raised for release in the spring of 2010. Additionally, more than 7,000 non-headstarted hatchlings have been processed and released on PIERP. These large numbers of headstarted non-headstarted hatchlings

provide a unique opportunity to study the efficacy of headstarting programs for diamondback terrapins in the Chesapeake Bay.

Mark-Recapture

I captured diamondback terrapins using fyke nets, crab pots, and by hand. Two to four fyke nets were set in the shallow waters surrounding PIERP perpendicular to the shore line with a lead line staked near shore and two wings on either side of the lead line, which acted as funnels into the trap. Trapping locations changed weekly in most cases. Trapping effort shifted between two areas, the first between Coaches Island and PIERP and the other between Jefferson Island and PIERP. Fyke nets were set every Monday from June 15 until August 7 and removed every Friday. I checked all nets daily to avoid prolonged trap stress and mortality. In order to determine whether terrapins near PIERP enter crab pots, I also set three baited, tall crab pots (30"x30"x6') beginning on July 27 and ending on August 7. These crab pots were taller than normal pots, maintaining a permanent airspace that allowed terrapins to breathe. Like fyke nets, crab pots were set every Monday and pulled every Friday and checked and re-baited with crab and fish daily. Terrapins were also opportunistically captured by hand whenever located. I took all captured terrapins to a lab on PIERP where the animals were measured, marked, sexed and subsequently released at the point of capture.

I weighed captured terrapins to the nearest gram with an Ohaus Scout[®] digital scale and recorded the following morphological measurements to the nearest millimeter using Mitutoyo electronic digital calipers: plastron length (PL), straight line carapace length, shell width, shell height, and head width. I noted any shell anomalies or injuries. All new terrapins were marked with a small, metal monel tag in 9th marginal scute on the

right side, and injected with a PIT tag (Biomark, Inc., Boise, ID) subcutaneously in front of the right rear leg using a sterile 12-gauge needle. Similarly, I PIT tagged any recaptured terrapins that had not previously been implanted with a tag. I identified recaptured terrapins by the notched marginal scutes and by scanning using the Northwest Marine Technologies' V-detector and a PIT tag scanner. I recorded the shell ID, as well as the presence of a wire tag or individual identification number from a PIT tag for all recaptured terrapins.

I determined the sex of the terrapins by extending the tail and looking at the location of the cloaca in relation to the posterior edge of the carapace. The male's cloaca extends beyond the carapace and the tail is robust; the female's cloaca does not extend beyond the carapace and the tail is noticeably shorter. In some cases, terrapins were too small to determine sex and were thus considered juveniles. For female terrapins that were of reproductive size ($PL \geq 163$ mm; Roosenburg 1991) I palpated in front of the rear legs within the inguinal pouch for the presence of shelled eggs.

Age was determined by counting annuli on plastral scutes and double checked by at least one field assistant and/or myself to ensure accuracy. If age could not be determined from scute annuli, terrapins were considered to be adults if females had a $PL \geq 163$ mm (the smallest reproductive female based on palpation) and males had a $PL \geq 100$ mm (Roosenburg 1991).

The same methods were used to capture, measure, weigh, and sex terrapins in the PR population except terrapins were individually marked by notching the marginal scutes (Cagle 1939).

Analyses

Catch per unit effort (CPUE) was calculated as the number of terrapins captured divided by the total number of trap-nights (calculated as the number of traps set night⁻¹). I calculated CPUE for pooled trap types, as well as individually for crab pots. CPUE for crab pots was used as a measure for terrapin mortality in commercial crab pots within the Poplar Island harbor. I compared PL as a measure of size among trapping locations and trap types. To do so, I pooled male and female size measurements excluding within year recaptures. Because I compared size for all terrapins captured and not among ages or sexes, these data were non-parametric. Therefore, I compared PL using a Mann-Whitney *U*-test.

Sex-ratios for the PIERP, PR, and several other terrapin populations were compared based on the proportion of males and females in each population. I calculated age and size distributions for both the PIERP and PR populations by multiplying the proportion of terrapins captured in each age or size class within a population by one thousand. I then compared age and size distributions of females and males independently using a Kolmogorov-Smirnov two-sample test. To compare size structure data between the PIERP and PR populations, I separated male and female size measurements by age-class. Because these data were not normally distributed, differences in PL were compared using Friedman's Analysis of Variance (ANOVA) on Ranks, with the smallest measure of PL given a rank of one. This test is the equivalent of a two-way ANOVA; however, it uses ranks rather than scalar measurements when making comparisons. *Post-hoc* Mann-Whitney *U*-tests were applied to determine significant differences in PL at each age-class.

For the PIERP population, I used the program JOLLY (Pollock et al. 1990) to estimate the capture probability and population size for both the entire population and females using the Jolly-Seber (JS) model. Along with assuming that the population is open, the basic JS model also assumes that: 1) the sample taken is representative of the entire population, 2) there is an equal probability of capture for all individuals, and 3) marks are permanent and do not affect recapture or survival (Donnelly and Guyer 1994, Lancia et al. 2005). Aside from the basic JS model, JOLLY also calculates population size estimates using four other models with varying assumptions for the openness, survival rates, and capture rates. The JS model of best fit was determined using a Chi-squared goodness-of-fit test. For this program, I divided the eight-week trapping period into four trapping “sessions” consisting of two-weeks each due to the low rate of among week recaptures. If an individual terrapin was captured more than once during a trapping “session”, only the first capture was included in the analysis.

I developed a stage-structured Leftkovich matrix population growth model for the PIERP population (see matrix below; Leftkovich 1965, Heppell et al. 1996, Donovan and Welden 2001). I divided the female population into four classes based on size as follows: hatchlings (h), juveniles (j), subadults (sa), and adults (a). I considered young of the year hatchlings, all hatchlings that survived into the next year and individuals with a PL < 123 mm juveniles, individuals with a PL \geq 123 mm (the size at which individuals can no longer be captured in crab pots; Roosenburg et al. 1997) but < 163 mm subadults, and all individuals with a PL \geq 163 mm (the minimum size of first reproduction at PIERP; this study) adults.

The initial population size for each size-class was calculated by multiplying the proportion of individuals from the PR population within each of the three largest size classes, by the mean female population estimation from PIERP, as calculated in the program JOLLY. I calculated the number of hatchlings by multiplying the initial number of reproductive adults by their fecundity.

$$\begin{vmatrix} P_{h,h} & F_j & F_{sa} & F_a \\ P_{h,j} & P_{j,j} & 0 & 0 \\ 0 & P_{j,sa} & P_{sa,sa} & 0 \\ 0 & 0 & P_{sa,a} & P_{a,a} \end{vmatrix}$$

Fecundity (F) is a measure of the reproductive output for an individual female terrapin. I calculated fecundity (F_a) by multiplying the number of nests female⁻¹ year⁻¹ (1.207; Mitro 2003) by the number of female hatchlings nest⁻¹ on PIERP (0.94 female hatchlings nest⁻¹ * 13.47 eggs nest⁻¹ * 0.737 nest success; Roosenburg et al. 2009). The fecundity of subadults (F_{sa}) was based on the proportion of subadults moving into the adult stage-class within each year.

The survival probabilities ($P_{i,i}$) given on the principal diagonal represent the probability that an individual will survive but remain in the same size class. The survival probabilities ($P_{i,j}$) were calculated as the survival from one class to the next (i.e. $P_{h,sj}$ is the probability that a hatchling will survive to become a juvenile) and are given on the subdiagonal. Survival from one class to the next is a function of the proportion of

individuals within one year's growth of the next size class (based on average PL) and the total survival for the size class (i.e. $P_{j,sa}$ is the proportion of individuals within the juvenile size class with a PL ≥ 110 mm but ≤ 122 mm * 0.5625). The sum of the two survival probabilities for each stage equals total survival rate for that size class. I calculated hatchling survivorship by dividing the number of juveniles at $t=0$ by the number of hatchlings at $t=0$. Likewise, I calculated total juvenile survivorship by dividing the number of subadults at $t=0$ by the number of juveniles at $t=0$. Due to constraints of the model, however, it is likely that hatchling survivorship is underestimated due to the fact that $P_{h,j}$ includes multiple age classes of juvenile terrapins, not just those that survive the first year. Survival rates for subadults and adults (0.8582) were considered equal and determined from the PR female population using the program JOLLY, and were comparable to female survival rates from a population in South Carolina (0.840; Tucker et al. 2001).

The total population size (N_t) was calculated for time ($t+1$) through the summation of multiplying the Leftkovich matrix by the population vector at time (t) as follows (Donovan and Welden 2001):

$$\begin{pmatrix} n_h(t+1) \\ n_j(t+1) \\ n_{sa}(t+1) \\ n_a(t+1) \end{pmatrix} = \begin{pmatrix} P_{h,h} & F_j & F_{sa} & F_a \\ P_{h,j} & P_{j,j} & 0 & 0 \\ 0 & P_{j,sa} & P_{sa,sa} & 0 \\ 0 & 0 & P_{sa,a} & P_{a,a} \end{pmatrix} \times \begin{pmatrix} n_h(t) \\ n_j(t) \\ n_{sa}(t) \\ n_a(t) \end{pmatrix}$$

I was then able to calculate a time-specific population growth rate (λ), where $\lambda_t = N_{t+1} / N_t$. The population was projected for 100 years.

Using the calculated population survivorship probabilities, fecundity, and growth rate, I calculated sensitivity and elasticity values for the PIERP population. These values reveal how an incremental change in survival or fecundity within one age class with all other values being held constant will affect population growth. So, the sensitivity of a matrix element ($a_{i,j}$) is a function of the vector of the reproductive value (v) and the vector of the stable-stage distribution (w), where:

$$a_{i,j} = \frac{\partial \lambda}{\partial a_{ij}} = \frac{v_i w_j}{\sum_{k=1}^{Last\ stage\ class} v_k w_k}$$

Because sensitivities do not measure survival and fecundity on the same scale, I also calculated elasticities, which are essentially proportional sensitivities on growth rate (λ), where:

$$b_{i,j} = (\text{sensitivity of } a_{i,j}) \times \frac{a_{i,j}}{\lambda}$$

Sensitivity and elasticity values can then be compared among themselves to determine which vital rate will have the greatest impact on the population growth rate (λ) (Donovan and Welden 2001, Mills 2007).

Using the population growth model, I projected the impacts of feasible management options by manipulating the survival probability parameters within the

original Leftkovich matrix. Because there are no known direct impacts on adult and subadult survival probabilities at PIERP which can be mitigated through feasible management, manipulations of survival probabilities focus on hatchling and juvenile size classes. Three potential management options exist: 1) increase nest survivorship through protection from predators, 2) headstart hatchlings and reintroduce them to the population, and 3) eliminate mortality in crab pots around PIERP. The first two management options both focus on increasing hatchling survivorship and are already being performed in this population, and thus their impacts are already projected by the original growth model. Therefore, I projected expected population growth based on the current headstarting efforts by increasing the survival probability of hatchlings by 0.13. I also projected the expected population growth based on the removal of crab pots by increasing both hatchling and juvenile survival probabilities. For this projection, I increased the juvenile survival probability to 0.672, the average juvenile survival for freshwater emydid turtles (Iverson 1991) and increased hatchling survivorship until $\lambda \geq 1$.

All statistics were performed using SPSS version 17.0 with an α -level of 0.05, with exception to modeling the growth of the population and sensitivity and elasticity estimations, which were performed in Microsoft Excel.

RESULTS

A total of 288 terrapins were captured during this study, of which 85 (29.5%) were recaptured. Nine headstarted terrapins and eight previously marked PIERP hatchlings were captured. Due to low capture rates, the headstart and PIERP hatchling cohorts could not be compared statistically, however, there appears to be no correlation between size at release and survivorship of headstarted terrapins (Fig. 2

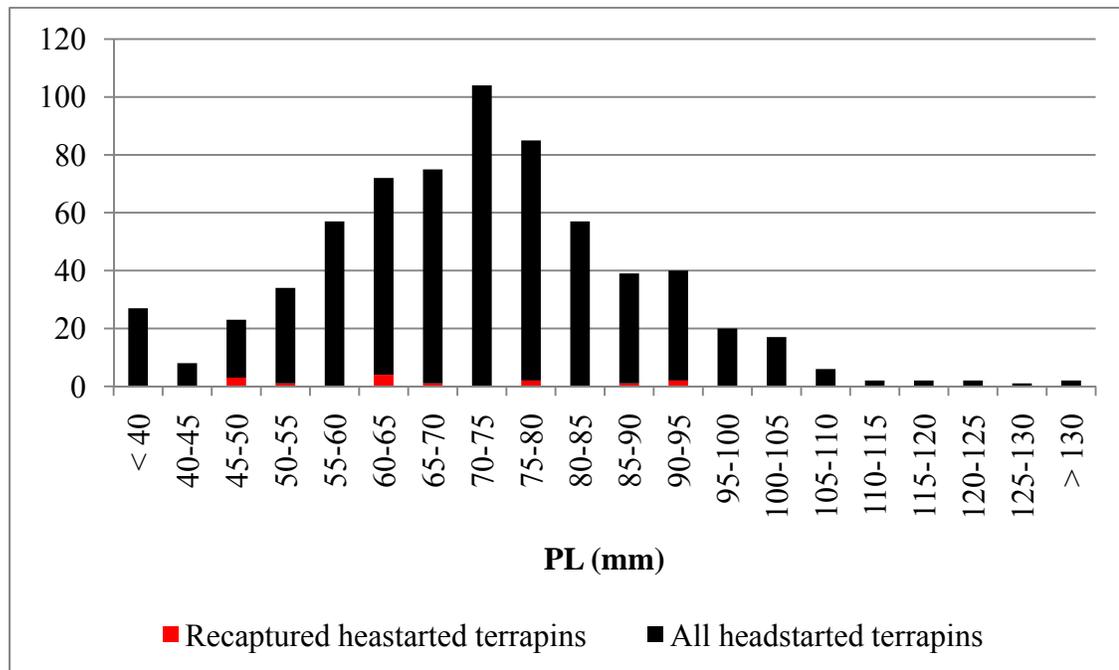


Figure 2. The size distribution for all headstarted terrapins at release and all recaptured headstarted terrapins at release. Initial size at release appears to have no impact on the survival probability of headstarted terrapins.

A total of two terrapins died during trapping. The CPUE for all trapping effort was 3.8 terrapins trap⁻¹ night⁻¹ over the course of the study, although 32% of our first captures occurred during the first week of trapping. For crab pots, the CPUE was 0.38 terrapins crab pot⁻¹ night⁻¹. Injuries to the shell or limbs were present on 31 (10.7%) of individual terrapins captured. There was a difference in PL among terrapins captured near Coaches and Jefferson Islands, with those caught near Jefferson's Island being larger (Mann-Whitney U = 3341.50, $p < 0.001$; Table 1). Likewise, terrapins in fyke nets had a larger PL than those captured in crab pots (Mann-Whitney U = 248.00, $p < 0.001$; Table 1).

Table 1.

Mean plastron length (PL) for all terrapins captured at both trapping locations and in two trap types

		Sample size	Mean PL (mm)	SE
Trap Location	Coaches Island	n=75	138.07	4.485
	Jefferson Island	n=200	177.07	2.133
Trap Type	Fyke Net	n=269	167.32	2.224
	Crabpot	n=9	108.89	7.29

The PIERP population had a strongly female biased sex ratio (9:1), which was different from expected ratios reported in other populations (Fig. 3). This population also showed marked sexual dimorphism, with adult females having a significantly larger PL

($\bar{X} = 191.9 \text{ mm} \pm 0.72$) than adult males ($\bar{X} = 119 \text{ mm} \pm 1.81$; Mann-Whitney $U < 0.01$, $p < 0.001$; Fig. 4). There was no difference in size distribution between the PIERP and PR populations for females (Fig. 5) or males (Fig. 6) (Kolmogorov-Smirnov $Z = 0.857$ and 0.707 , $p = 0.454$ and 0.699 respectively). Likewise, there was no difference in age distribution between the PIERP and PR populations for females (Fig. 7) or males (Fig. 8) (Kolmogorov-Smirnov $Z = 0.707$ and 1.179 , $p = 0.699$ and 0.124 respectively). There was no difference in PL for males when comparing age classes among populations (Friedman's ANOVA on ranks; $F_{1,3} = 1.367$, $p = 0.251$). The populations did, however, differ in PL at some age classes for females (Friedman's ANOVA on ranks; $F_{1,7} = 3.037$, $p = 0.003$), although differences can probably be attributed to low sample size (Fig. 9). However, the PIERP four year old females included four headstarted individuals with a PL ($\bar{X} = 148.33 \text{ mm}$) greater than that for the PR population at the same age class ($\bar{X} = 100.33$), which may have unproportionately increased the mean PL for the PIERP population (Mann-Whitney $U = 2836.00$, $p < 0.001$).

The estimated total population size for the PIERP population from JOLLY was 306 ± 102 ($N \pm \text{SE}$; 95% CI of 107 – 505) with a capture probability of 0.1799 ± 0.0343 ($p \pm \text{SE}$; 95% CI of 0.1127 - 0.2471). This estimate was based on the assumptions of Model D (χ^2 Goodness-of-Fit test; $\chi^2 = 0.6362$, $df = 5$, $p = 0.9863$), where survival rate is constant over a time period and there is a constant capture probability. Likewise, the population estimate for females using Model D ($\chi^2 = 0.9734$, $df = 5$, $p = 0.9647$) was 257 ± 88 (95% CI 84 – 431) with a capture probability of 0.1840 ± 0.0362 (95% CI 0.1130 - 0.2550).

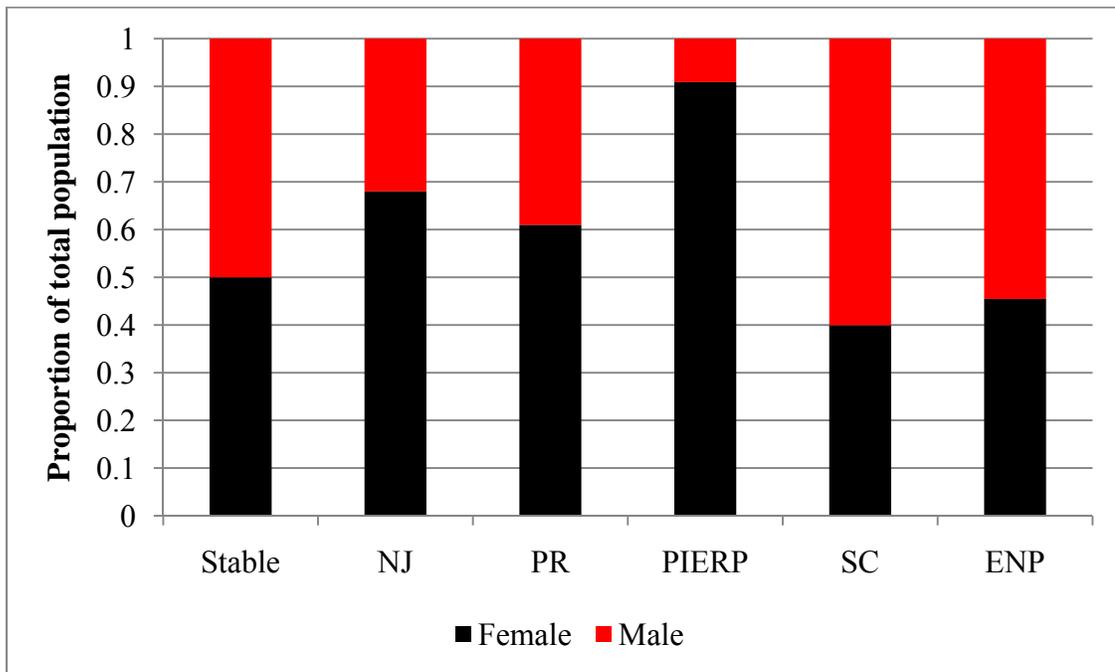


Figure 3. Sex ratios for the PIERP, evolutionarily stable (Gibbons et al. 2001), Patuxent River (PR; Roosenburg 1990), New Jersey (NJ; Avissar 2006), South Carolina (SC; Gibbons et al. 2001), and Everglades National Park (ENP; Hart and McIvor 2008) represented as the proportion of individuals of each sex within each population.

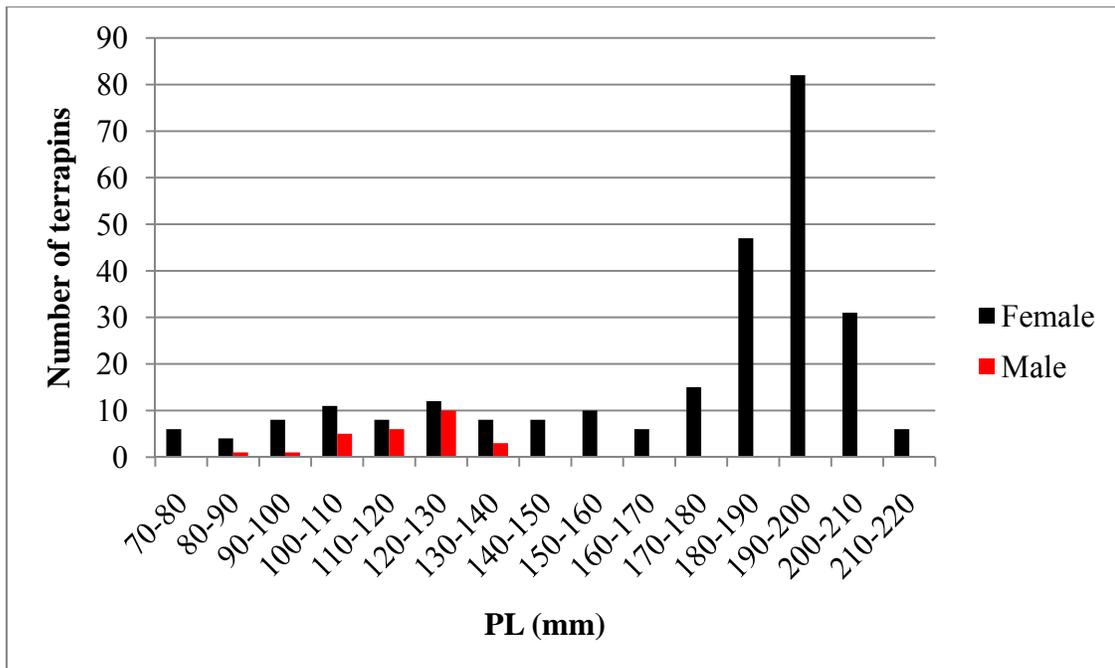


Figure 4. The size distribution of PL for female and male terrapins in the PIERP population. There is a marked size difference due to sexual dimorphism between males ($\bar{X} = 119 \pm 1.81$) and females ($\bar{X} = 192 \pm 0.72$).

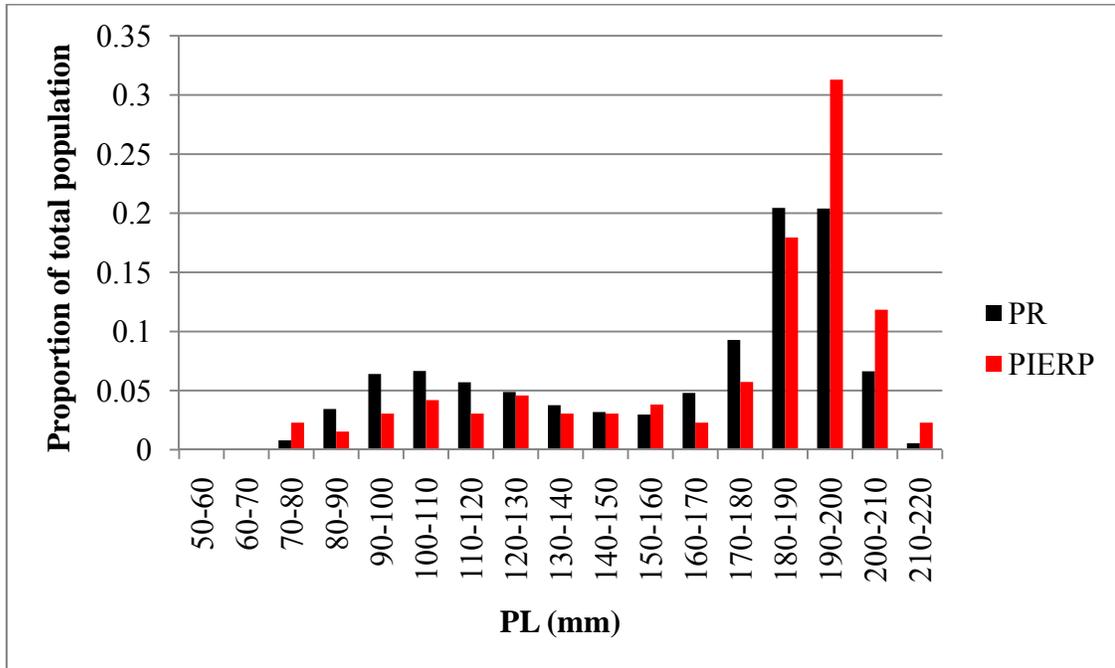


Figure 5. A comparison of size distributions for female terrapins between the Poplar Island Environmental Restoration Project (PIERP) and Patuxent River (PR) populations. There was no difference among the female size distributions ($p = 0.454$); however, proportions of 80 – 120 mm PL individuals in the PR population are nearly double those from the PIERP population.

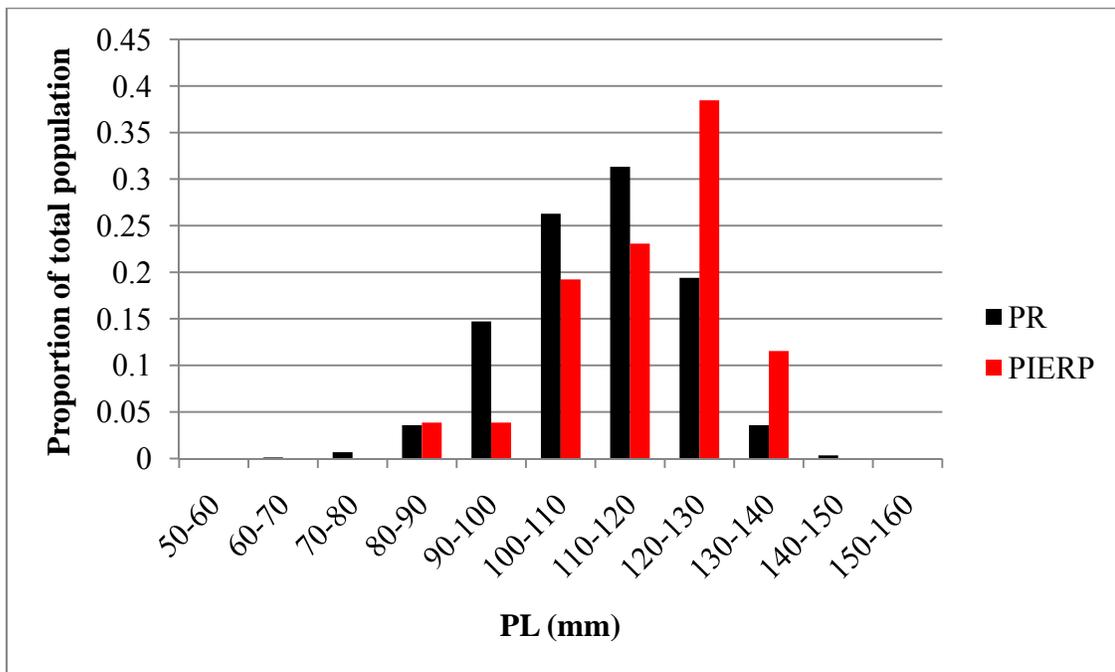


Figure 6. A comparison of size distributions for male terrapins between the Poplar Island Environmental Restoration Project (PIERP) and Patuxent River (PR) populations. There was no difference among the PR and PIERP male size distributions ($p = 0.699$).

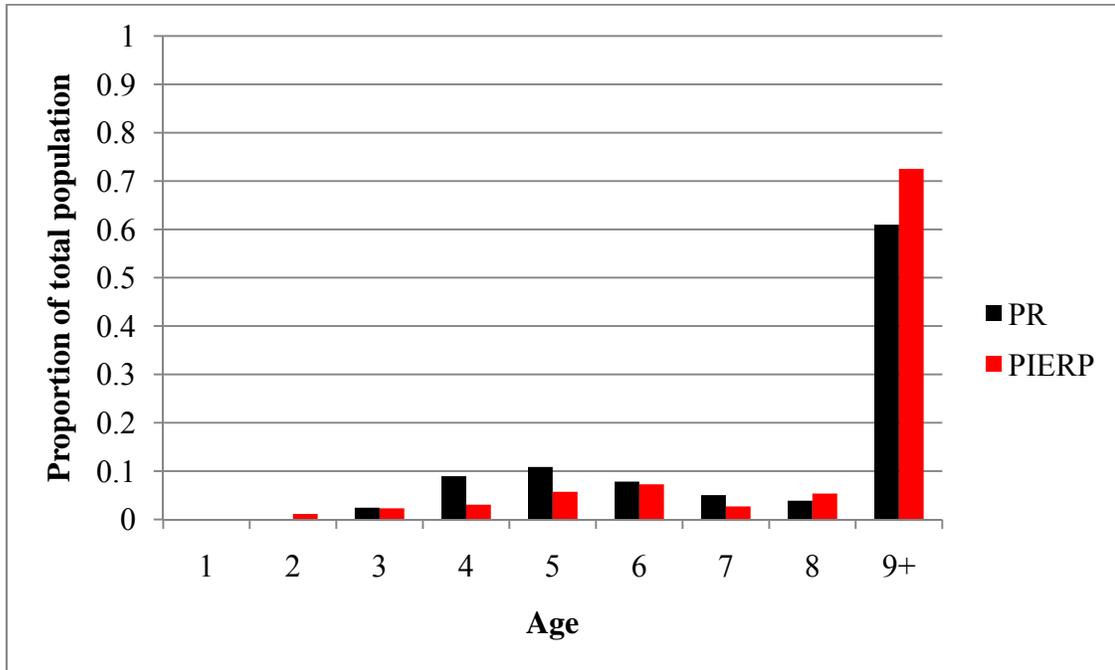


Figure 7. A comparison of age distributions for female terrapins between the Poplar Island Environmental Restoration Project (PIERP) and Patuxent River (PR) populations. There was no difference among the PR and PIERP female age distributions ($p = 0.699$).

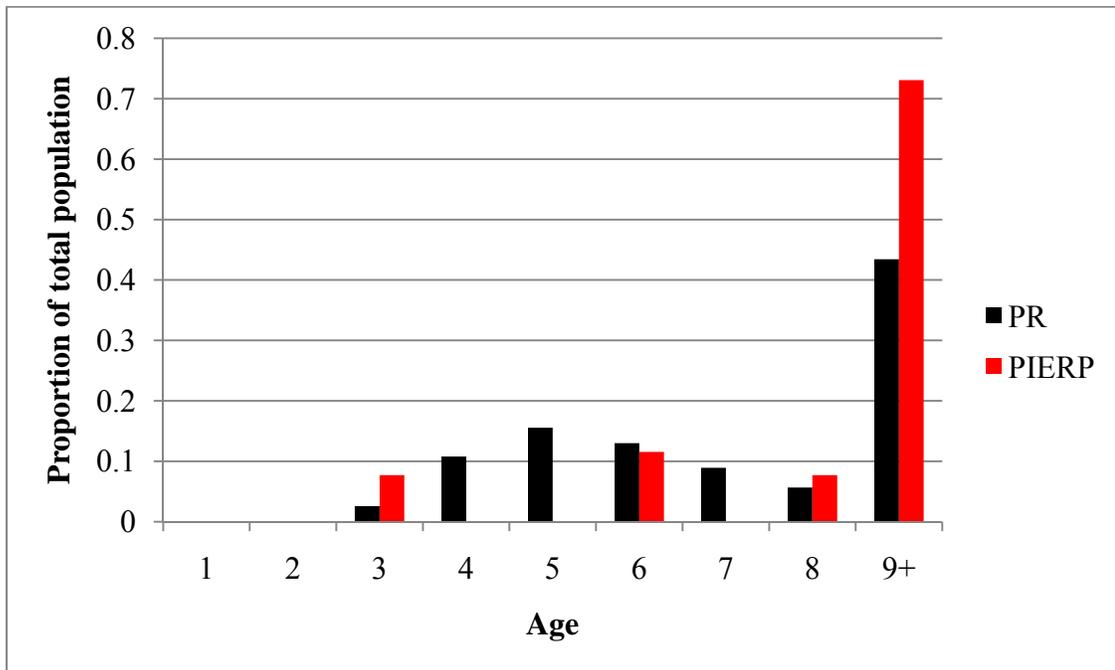


Figure 8. A comparison of age distributions for male terrapins between the Poplar Island Environmental Restoration Project (PIERP) and Patuxent River (PR) populations. There was no difference among the PR and PIERP male age distributions ($p = 0.124$).

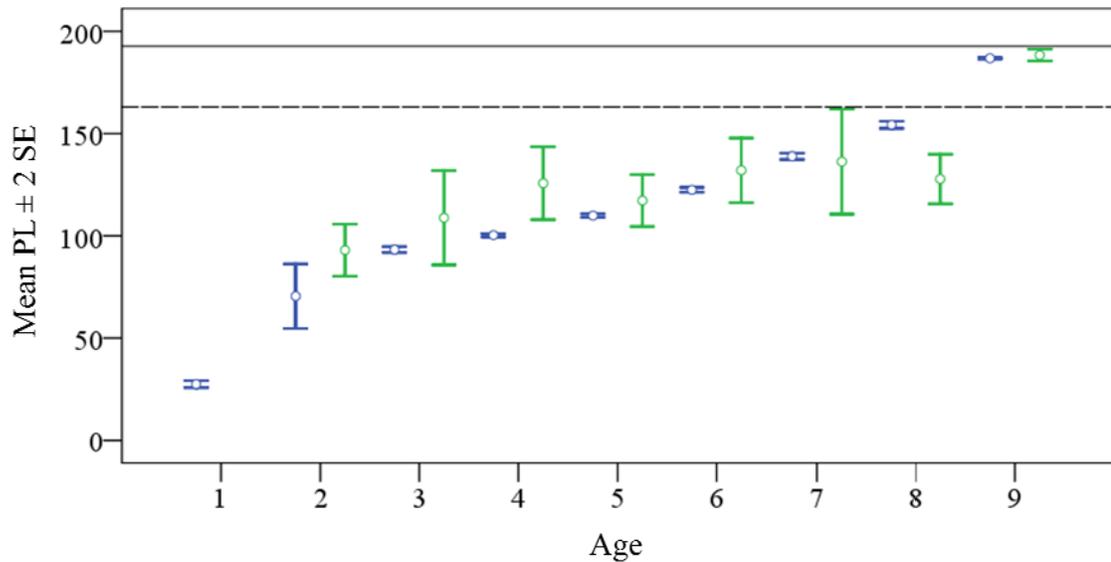


Figure 9. Mean PL for females in each age class for the PR (Blue) and PIERP (Green) populations. Four year old individuals from PIERP were larger than the same age class from PR ($p < 0.001$), although this may have been due to the larger mean PL for 4 year old headstarted females ($\bar{X} = 148.33$). The dashed horizontal line indicates the smallest reproductive females encountered in the PIERP population and the solid horizontal line indicates the mean reproductive size for diamondback terrapins.

The Leftkovich matrix population growth model indicates that under current conditions, the population will decrease ($\lambda = 0.940$) to a total population size of 18 individual female terrapins after 100 years (Fig. 10). Discounting hatchlings, the total juvenile, subadult, and adult female terrapin population would consist of three individuals. The vector of reproductive value (v) and stable-stage distribution (w) vector were used to calculate sensitivity and elasticity for each size class (Table 2).

Table 2.

The stable-stage distribution (w) and reproductive value (v) vectors for each size class

Stage Class	Stable-Stage Distribution (w)	Reproductive value (v)
Hatchling	0.83	0.01
Juvenile	0.07	0.11
Subadult	0.04	0.37
Adult	0.07	0.51

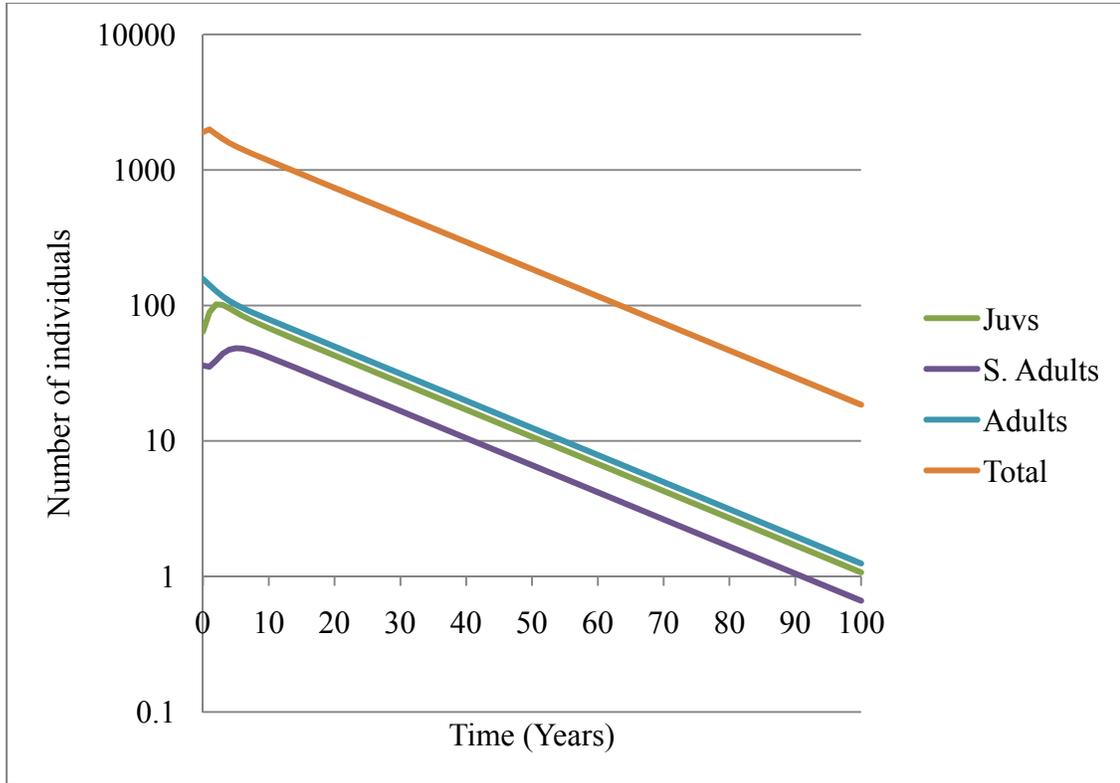
Sensitivity analysis indicates that an increase in survival probabilities for the younger size classes ($a_{h,j} = 1.55$ and $a_{j,sa} = 0.407$) will have the greatest impact on population growth (Table 3). However, elasticity analysis indicates that an increase in survival probabilities for older age classes ($b_{s,a} = 0.170$ and $b_{a,a} = 0.500$) will have the greatest impact on population growth, although these values are biased due to the importance of these size classes for reproduction and the higher proportion of adults and subadults in the PIERP population (Table 3; Mills 2007).

Table 3.

Sensitivity and elasticity values for fecundity (F) and survivorship probabilities (P) by size class

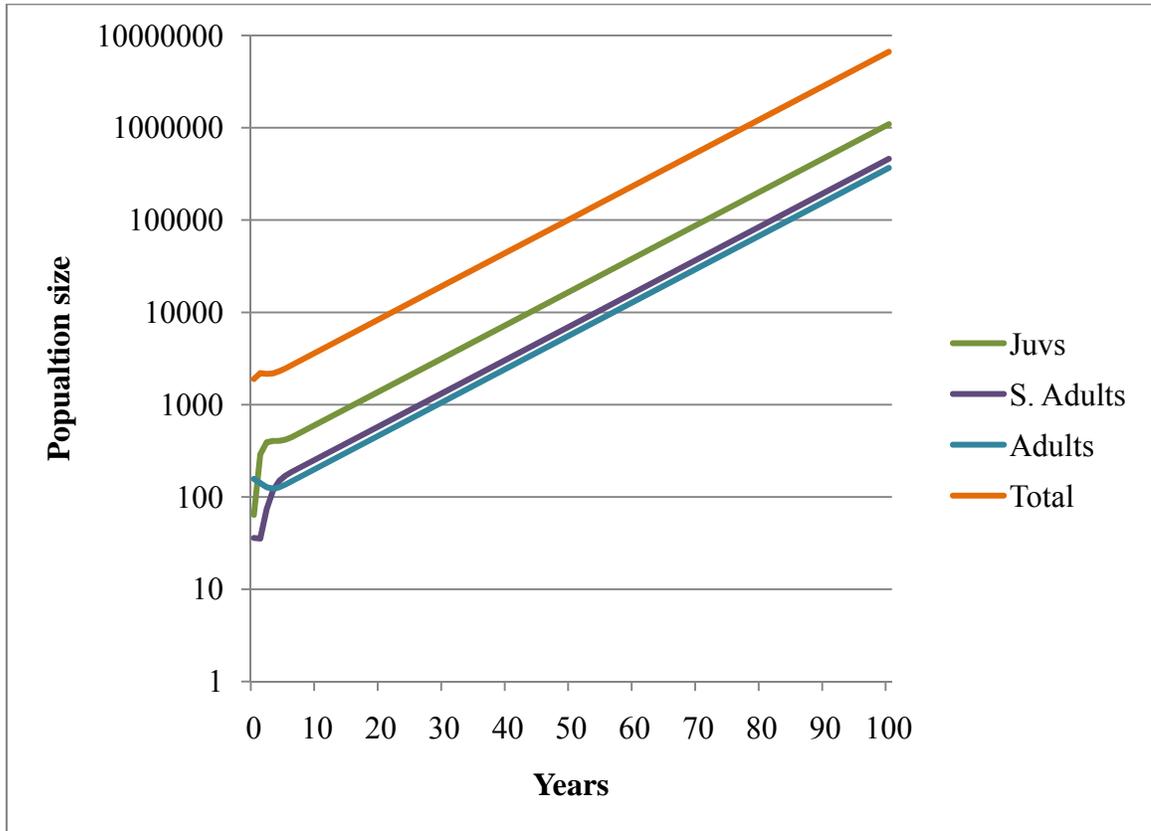
	F_{sa}	F_a	$P_{h,j}$	$P_{j,j}$	$P_{j,sa}$	$P_{sa,sa}$	$P_{sa,a}$	$P_{a,a}$
Sensitivity	< 0.01	< 0.01	1.55	0.12	0.41	0.24	0.33	0.56
Elasticity	0.01	0.06	0.07	0.05	0.07	0.17	0.06	0.50

The predicted stage-structured Leftkovich population matrix based on the current rate of headstarting indicated that the PIERP population should be increasing ($\lambda=1.07$; Fig. 11) at a drastically higher rate than projected with the measured fecundity and survival probabilities ($\lambda = 0.940$). I projected this by increasing the hatchling survival probability to 0.16, which is the estimated survival based on the proportion of PIERP hatchlings headstarted per year. The model also predicted that a small increase in juvenile survival to 0.672 combined with a 0.022 increase in hatchling survival, representing a removal of crab pots from the area, will maintain the population at its current level ($\lambda=1.00$; Fig. 12). A subsequent increase in either juvenile or hatchling survival probabilities beyond those rates led to population increase ($\lambda>1.00$; Fig. 13).



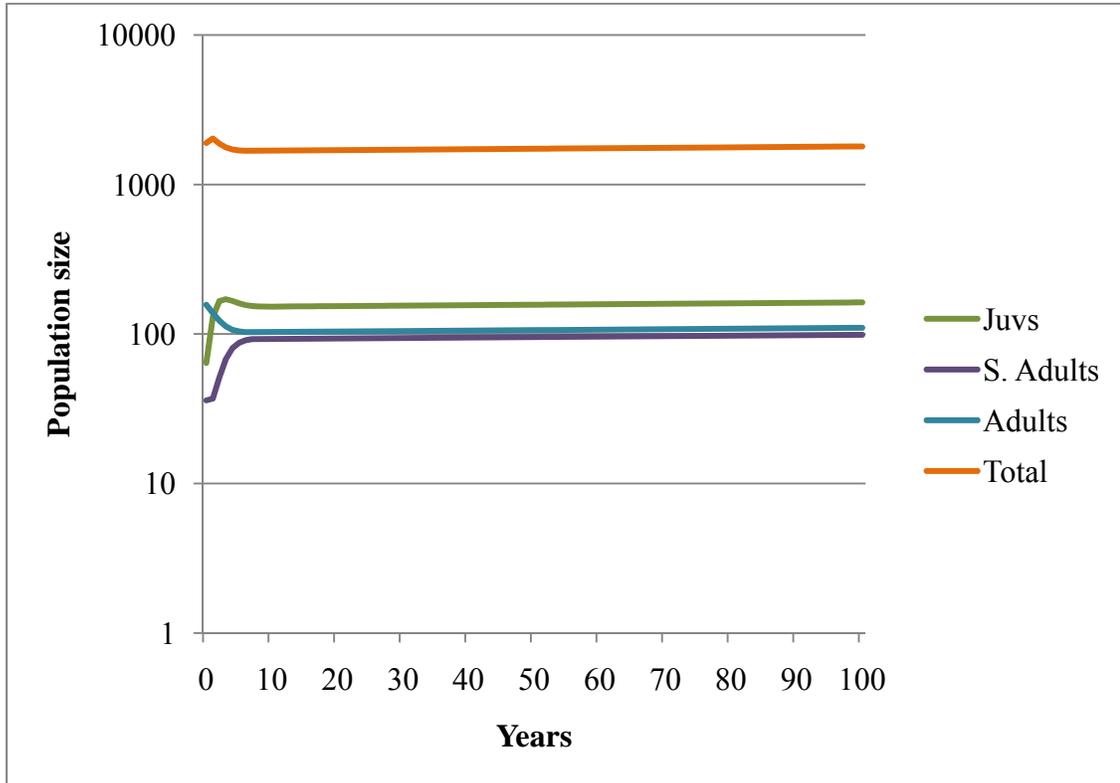
$$\begin{array}{cccc|c|cccc}
 P_{h,h} & F_j & F_{sa} & F_a & = & 0 & 0 & 2.951111 & 10.32889 \\
 P_{h,j} & P_{j,j} & 0 & 0 & & 0.038999 & 0.38981 & 0 & 0 \\
 0 & P_{j,sa} & P_{sa,sa} & 0 & & 0 & 0.172688 & 0.675246 & 0 \\
 0 & 0 & P_{sa,a} & P_{a,a} & & 0 & 0 & 0.182754 & 0.858
 \end{array}$$

Figure 10. Projected population growth for the PIERP population using a stage-based Leftkovich matrix model based on measured survival probabilities ($\lambda = 0.940$). For all model projections, total population size includes hatchling (not shown), juvenile, subadult, and adult population sizes.



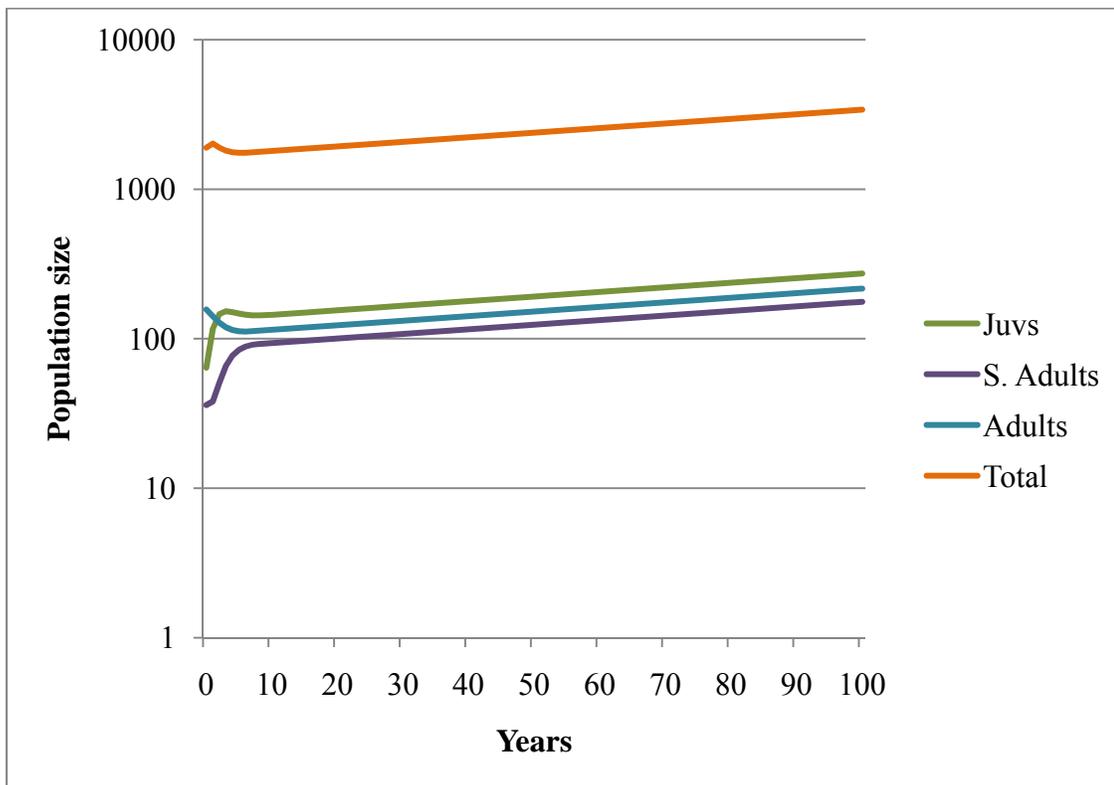
$P_{h,h}$	F_j	F_{sa}	F_a	=	0	0	2.951111	10.32889
$P_{h,i}$	$P_{i,i}$	0	0		0.160999	0.38981	0	0
0	$P_{i,sa}$	$P_{sa,sa}$	0		0	0.172688	0.675246	0
0	0	$P_{sa,a}$	$P_{a,a}$		0	0	0.182754	0.858

Figure 11. Predicted population growth for the PIERP population using a stage-based Leftkovich matrix model with increased hatchling survivorship based on the current rate of headstarting (~ 200 hatchlings year⁻¹) in the population ($\lambda=1.07$). Increases in survival probabilities (P_i) compared to the initial Leftkovich matrix are highlighted in gray.



$P_{h,h}$	F_j	F_{sa}	F_a	=	0	0	2.951111	10.32889
$P_{h,j}$	$P_{j,j}$	0	0		0.052	0.465696	0	0
0	$P_{j,sa}$	$P_{sa,sa}$	0		0	0.206304	0.675246	0
0	0	$P_{sa,a}$	$P_{a,a}$		0	0	0.182754	0.858

Figure 12. Predicted population growth for the PIERP population using a stage-based Leftkovich matrix model with increased hatchling and juvenile survivorship due to the removal of the commercial crab pots from around the island ($\lambda=1.00$). Increases in survival probabilities (P_i) compared to the initial Leftkovich matrix are highlighted in gray.



$P_{h,h}$	F_j	F_{sa}	F_a	=	0	0	2.951111	10.32889
$P_{h,j}$	$P_{i,j}$	0	0		0.052	0.4851	0	0
0	$P_{j,sa}$	$P_{sa,sa}$	0		0	0.2149	0.675246	0
0	0	$P_{sa,a}$	$P_{a,a}$		0	0	0.182754	0.858

Figure 13. Predicted population growth for the PIERP population using a stage-based Leftkovich matrix model with increased hatchling and juvenile survivorship due to the removal of the commercial crab pots from around the island ($\lambda > 1.00$). Increases in survival probabilities (P_i) compared to the initial Leftkovich matrix are highlighted in gray.

DISCUSSION

I was unable to detect a difference in population growth or structure between the PIERP and PR populations, the former which has been supplemented by headstarted terrapins. The size and age distribution for the PIERP population is heavily skewed towards larger and older individuals and low number of captures of smaller size classes suggests that their survivorship is low. Furthermore, I was unable to detect any difference in the size or age distributions between the PIERP and PR populations despite the nest protection and headstart efforts occurring at PIERP. These findings combined with a highly female biased sex ratio appear to indicate that the PIERP population is facing threats affecting survival of both juvenile size classes and all males. One factor causing these population characteristics may be low recruitment of hatchlings into the population, which appears to be the case in the PR population (Roosenburg pers. comm.). A second factor may be the migration of young age classes and males out of the population, but this is not likely as terrapins show high site fidelity throughout their lives (Gibbons et al. 2001, Tucker et al. 2001). However, it appears more likely that differential mortality in crab pots for males and juvenile females caused the PIERP population to become heavily biased towards females and large individuals (Roosenburg 1991, Roosenburg et al. 1997) and, without mitigation, may result in the local extirpation of the species (Tucker et al. 2001, Dorcas et al. 2007).

Population Ecology

Biased sex ratios may result from many factors including sampling gear bias, geographic variation in population biology, gender bias in mortality rates, or sex ratios at hatching due to factors related to nest temperature (Lovich and Gibbons 1990, Butler et al. 2006). Siegel (1984), Roosenburg et al. (1997), and Avissar (2006) have reported female-biased terrapin sex ratios, yet the 9:1 female biased ratio from this study represents the highest female bias reported for any population. Due to the non-discriminating nature of fyke nets, it is unlikely that the capture method I used differentially captured males or females; therefore, the strong female bias is likely the result of both gender bias in mortality rates due to crab pots and the female biased sex ratio of hatchlings (9.5:1; Roosenburg pers. comm.) produced on PIERP. Terrapins have temperature dependent sex determination rather than genetic sex determination (Lovich and Gibbons 1990). High nest temperatures on PIERP result in a highly female biased hatchling sex ratio; however, the sex ratio of hatchlings from CI and JI are likely not severely female biased due to lower nest temperatures caused by the presence of shade on nesting beaches (Smeenk pers. obs.). Although I did not capture any males in crab pots during this study, the average PL (119 mm) for adult males at PIERP is smaller than the size at which terrapins are no longer susceptible to mortality in crab pots (123 mm PL; Roosenburg et al. 1997), suggesting that adult males are vulnerable to drowning in crab pots. The PIERP population shows a highly female-biased sex ratio, supporting the conclusion that differential mortality in crab pots is the predominant factor leading to such a skewed sex ratio.

Injuries from boat propeller strikes and associated mortality have been recorded for many populations of terrapins. The injury rate for PIERP terrapins (10.7%) is lower than observed rate for the PR population (20%; Roosenburg 1991) and a sampled population from Florida (16%; Hart and McIvor 2008). However, the rate of injuries for males (19%) is higher than that for females (11%) in the PIERP population, which differs from those studies. Roosenburg (1991) suggested propeller strikes were the primary source of mortality for females in the PR population due to a higher propensity for females to be struck by boats when they bask on the surface of the water. This does not appear to be the case for the PIERP population, which may be the result of reduced boat traffic due to less recreational boating in the waters around the island and the remoteness of PIERP. This does not, however, explain the higher rate of injuries for male terrapins in this population. The higher rate of injuries on male terrapins may further elucidate the causes for the female biased sex ratio at PIERP.

During this study, more terrapins were captured near Jefferson Island (JI; n=200) than Coaches Island (CI; n=75), although this was biased by the first day of trapping when 32% of first captures occurred near JI. Terrapins captured near CI had a significantly smaller PL (138.1 mm) than those captured near JI (177.1 mm). This suggests that habitat use of terrapins around PIERP varies between size classes, as the waters near JI are on the windward side of the island and thus subjected to significant wave action when compared to the waters near CI, which are sheltered by the presence of both PIERP and CI. This parallels findings from the PR population, where larger terrapins use deep water habitats further from shore and smaller, juvenile terrapins used shallow, inshore waters (Roosenburg et al. 1999). These habitat use differences can

likely be attributed to prey availability (Tucker et al. 1995, Roosenburg et al. 1999). The presence of smaller, softer prey items like *Littorina* and other salt march snails near CI, a primary food source for juvenile terrapins (Ernst et al. 1994), as well as nesting beaches adjacent to this area support the observed differences in size based habitat use. Another contributing factor may be the lack of crab pots between PIERP and CI due to shallow waters limiting boat access to the area compared to high crab pot density around JI (Smeenk pers. obs.).

I anticipated that size and age structures of the PIERP population would have more individuals in the younger age and smaller size classes than the PR population because of the headstarted terrapins. Despite the of headstarted terrapins in the PIERP population, there was no difference in the size or age structures between the populations. There could be two causes for distribution skewed towards larger and older individuals. First, it is assumed that due to the erosion of Poplar Island, terrapins lost much of the nesting habitat that was once available to them. With little nesting habitat available, there would have been minimal recruitment of terrapins into younger age classes. The fact that the size and age distributions were the same may suggest that the population structure at PIERP was improving, although this cannot be tested because no population data is available prior to the construction of PIERP. It further suggests that headstarting may have helped some, but this appears unlikely due to the low rate of recaptures of headstarted individuals. Second, the populations could be facing similar survival threats to smaller and younger age classes due to differential mortality of young and adults. If this is the case, it is likely that the presence of crab pots in Poplar Harbor is causing the

skewed distributions at PIERP, while low recruitment of hatchlings is the cause in the PR population (Roosenburg 1991, Roosenburg et al. 1997, Roosenburg and Green 2000).

Estimates of terrapin population size vary widely between locations and states, and many suggest that terrapins may be locally common in undisturbed habitats (Butler et al. 2006a). Using mark-recapture and a Jolly-Seber model, I estimated the PIERP population to be 204-408 individuals with 169-345 of those individuals female. Population estimates from Florida range from 213 to 3147 individuals (Seigel 1984, Butler 2002, Hart 2005) and an estimate from Delaware is similarly large (1655; Hurd et al. 1979). Roosenburg et al. (1997) estimated the total PR terrapin population at 2778-3730. It appears likely that many terrapin populations may be in decline. Most researchers cite crab pot mortality as the major contributing factor to declining terrapin populations (Butler et al. 2006b). In fact, a single abandoned crab pot in the PR held 49 terrapin shells and the remains of others, representing estimated mortality of up to 3% of the population (Roosenburg 1991). Due to the high density of crab pots in the PIERP harbor (Smeenk pers. obs.), it is likely that crab fishing is also causing declines in the PIERP population.

The stage-based Leftokovich matrix population growth model estimated hatchling survival of 0.039 based on the relative proportion of juveniles to hatchlings. I considered all individuals hatchlings for the first year and after which I considered them juveniles until they reached 123 mm PL. This is nearly 0.02 lower than the average hatchling survivorship for other emydid turtle species (Heppell 1998). Likewise, juvenile survivorship was calculated to be only 0.56, nearly 0.14 less than the average for other emydid turtles (Heppell 1998). Adult and subadult survivorship probabilities were

assumed to be equal and were similar to those reported for other emydid turtles at 0.86 (Iverson 1991, Heppell 1998). Using the average estimated female population size for the four size classes in the model, I calculated a population growth rate (λ) of 0.940, which would lead to local extirpation in less than 100 years (Fig. 9). These differences indicate that mortality is high in the PIERP population and it again appears probable that crab pots may be limiting survivorship of young age classes due to increased mortality caused by drowning.

Headstarting at PIERP

Although headstarting has been used in conservation efforts for many reptile and amphibian species, the utility of such efforts is largely unknown (Dodd and Seigel 1991). Recalling that the two main goals of headstarting are to increase hatchling and juvenile survival probabilities and decrease the age at first reproduction, I examined whether either of these goals have occurred with the headstarting of diamondback terrapins on PIERP. Based on minimum survivorship of headstarted terrapins and similar size and age structures between PIERP and a non-headstart supplemented population in the PR, I suggest that headstart efforts have failed to increase juvenile survival probabilities (i.e. $P_{j,j}$ and $P_{j,sa}$). However, the recapture of one female that was of reproductive size indicates that headstarting does produce larger turtles at younger ages and may influence age of first reproduction although this individual was not gravid.

The calculated hatchling survival for the PIERP population was only 0.039, thus exacerbating the population decline ($\lambda=0.940$; Fig. 8). Based on the rate of headstarting and nest protection that has occurred at PIERP (200 hatchlings/year or 13% of all hatchlings and 0.737 nest success), I predicted that hatchling survivorship should be

closer to 0.16, a rate drastically higher than what was calculated, due to the guarantee that 13% of all hatchlings survive to become juveniles. Likewise, juvenile survivorship was lower than predicted based on average survivorship of juveniles in other emydid turtles (Iverson 1991). Because I know that the hatchling survivorship probability is high on PIERP, the increase in mortality is occurring in the juvenile size class. When I modeled the population using the expected hatchling survivorship (0.16), the population growth rate (λ) increased to 1.07 despite low juvenile survivorship (Fig. 9). The disparity between the calculated and expected hatchling survivorship probability is likely caused by external factors affecting juvenile survivorship, such as drowning in crab pots (Roosenburg et al. 1997).

I recaptured one four year old, female, headstarted terrapin that had a PL of 169 mm and mass of 1177 g. This female was larger than the smallest gravid female (163 mm and 1163 g) that was captured on PIERP. Even though the headstarted female was not gravid, this suggests that headstarting could decrease the age of first reproduction for headstarted females. Although the potential for this phenomenon was noted by Hildebrand (1932) in non-headstarted, captive individuals, it has still yet to be determined from headstarted turtles in the wild.

Over the last five years, 642 headstarted terrapins have been released at PIERP; however, I was only able to recapture nine of those terrapins. This gives a minimum estimate of 0.014 (9/642) survivorship for headstarted terrapins over that time period. In comparison, the survival rate for headstarted red-bellied sliders (n=63) averaged 0.823 over three years (Haskell et al. 1996), a rate higher than what one would expect to occur in wild cohorts (0.699; Heppell 1998). Although lower than estimates for red-bellied

sliders, survivorship for headstarted western pond turtles approached 0.65 (Spinks et al. 2003) and European pond turtles ranged from 0.32-0.35 (Mitrus 2005). Similarly, it is a prediction of headstarting that larger individuals are more likely to survive than their smaller, wild counterparts. Haskell et al. (1996) found that larger red-bellied sliders had a higher survival rate than smaller individuals. This does not appear to be the case with the diamondback terrapins at PIERP, where there is no indication that larger headstart individuals survive better than smaller individuals (Figure 2). This may, however, be caused by the differential use of wetlands by some individuals, an area where I did not sample. Although many of these species occur in areas much more sheltered than the Chesapeake Bay, my survivorship rate of 0.014 is exceedingly low.

The estimated minimum survivorship of headstarted turtles, size and age structure comparisons between PIERP and PR, and population growth models all suggest that headstarting has had no effect on the population growth or structure of the PIERP population. All of these factors point to low hatchling and juvenile survivorship probabilities as the reason for the failure of this headstart program. Due to the density of crabpots in the Poplar Harbor and propensity for juvenile terrapins to enter crab pots (Roosenburg et al. 1997, Butler and Henrich 2007, Dorcas et al. 2007), I suggest that crab pots are the cause for the low survival probabilities. It is due to these external factors like mortality in crab pots that opponents of headstarting programs criticize these efforts, arguing that headstarting only works if other threats to survival have already been mitigated in wild populations (Dodd and Seigel 1991, Reinert 1991, Frazer 1992). The results of this study support the criticisms of headstart programs, and I recommend that

causal factors for terrapin declines and decreased survivorship must be addressed prior to beginning a new or continuing the current headstart program.

Interactions with Crab Pots

The population ecology of terrapins at PIERP shows no effects from the headstarting of hatchlings or protection of nests. I expected to find a population structure with a higher proportion of juvenile and subadult terrapins and a stable or increasing population growth rate. In comparison, I found that both the size and age distributions and sex ratio are similar to those found in the PR population, a non-headstarted population of terrapins. The skewed size and age distributions and female biased sex ratios in the PIERP population are consistent with what one would expect from a population where increased mortality of males and juvenile female occurs due to bycatch in crab pots (Dorcas et al. 2007). Furthermore, population modeling suggests that the PIERP population is declining ($\lambda=.940$) and, without implementation of viable management strategies, the population will be functionally extirpated in less than 75 years. Models of management strategies indicate that with incremental increases in hatchling and juvenile survival, the PIERP population can be maintained or even increased over time (Figs. 12 and 13).

To determine if crab pots were a causal factor for low juvenile and male terrapin survival probabilities in the PIERP population, I set three tall crab pots for a total of 24 trap-nights. The CPUE over that period was 0.38 terrapins crab pot⁻¹ night⁻¹. This CPUE represents one of the highest reported rates of capture for terrapins in crab pots (Table 4). Over the course of the 90 day crab fishing season, I estimate that there are between 100 and 200 crab pots in Poplar Harbor per night, potentially drowning 3420-6840 male and

juvenile female terrapins, representing > 100% of the juvenile and male population. In order to mitigate this mortality, three logical management options exist that can be used in the Poplar Harbor: 1) require the use of bycatch reduction devices on commercial crab pots 2) prohibit shallow water crab potting during certain times of the year or 3) ban the use of crab pots in Poplar Harbor.

Table 4.

The catch per unit effort (CPUE) for diamondback terrapins in crab pots from across their range

State	CPUE (Terrapins crabpot⁻¹ day⁻¹)	Study
South Carolina	0.16-0.24	Bishop 1983
	0.027	Hoyle and Gibbons 2000
Maryland	0.17	Roosenburg et al. 1997
	0.044-0.23	Roosenburg and Green 2000
	0.38	This study
New Jersey	0.0054-0.06	Mazzarella 1994
	0.071-0.49	Wood 1997
North Carolina	0.15	Grant 1997

Bycatch reduction devices (BRD's) are small, rectangular wire or plastic devices that are affixed to the entrance of crab pots, reducing the width and height of the entrance (Hart and Lee 2007). BRD's prevent the entry of most turtles into crab pots, yet do not reduce the rate or size of crabs captured (Roosenburg and Green 2000, Butler and Heinrich 2007) and thus the use of these devices is now required several states (Butler et al. 2006, Hart and Lee 2007). However, even with the addition of BRD's, the maximum

reduction in capture is ca. 80% (Roosenburg et al. 1997). Extrapolated out to the CPUE for this study, the capture rate would still be 0.076 terrapins crab pot⁻¹ night⁻¹ or 7.6-15.2 terrapins per night. Over the course of the season, this would mean a loss of 684-1368 terrapins, > 100% of the total population. This implies that efforts to only increase hatchling survival through headstarting and nest protection will fail without a substantial reduction of terrapin mortality in crab pots. Furthermore, it suggests that the required use of BRD's around PIERP would not be sufficient in reducing juvenile female and male mortality.

Temporal or spatial restrictions on the use of crab pots can be used to limit the exposure of male and juvenile female terrapins to the threat of bycatch (Tucker et al. 2001). Both recreational and commercial crab pots are deployed in areas that are frequently used by male and juvenile female terrapins (Roosenburg et al. 1999), and where these overlaps of use occur bycatch mortality may cause the local extirpation of terrapin populations in a relatively short period of time (Tucker et al. 2001, Dorcas et al. 2007). Previous studies indicate that most crab pot mortality occurs during post-hibernation feeding (Bishop 1983, Hart 2005, Butler 2002); however, when I deployed crab pots in late-July and early-August I recorded a high capture rate. If previous estimates are correct, this suggests that mortality in crab pots may actually be higher during early seasonal activity periods than what I measured. Therefore, it is likely that a temporal restriction of crab pot deployment around PIERP would not be effective in reducing bycatch and increasing survival probabilities, particularly when considering the crab pot density around PIERP. Rather, a more effective management strategy would be

to ban crab pots in the shallow water in Poplar Harbor because this eliminates the overlap in temporal and spatial use between crab fishermen and small terrapins.

Management Recommendations

The population of diamondback terrapins at PIERP has a skewed size and age distribution, a female biased sex ratio, and appears to be in decline despite headstarting and nest protection efforts. The high capture rate of terrapins in crab pots during this study indicates that differential mortality of male and juvenile female terrapins in crab pots may be the cause for the skewed population structure and estimated population decline. Although many studies have recommended the implementation of BRD's on crab pots due to their ability to reduce terrapin bycatch (Gibbons et al. 2001, Tucker et al. 2001, Dorcas et al. 2007), this does not appear to be an option for the PIERP population due to high rates of capture and an already diminished male and juvenile population. The use of BRD's is also very difficult to enforce, particularly when hundreds of thousands of crab pots are being used annually in the Chesapeake Bay. Due to these factors along with the estimated high density of crab pots in Poplar Harbor and overlap of spatial and temporal use of the shallow waters surrounding PIERP by crab fishermen and diamondback terrapins, I recommend that the crab fishery be closed within Poplar Harbor. Not only will this minimize exposure of small terrapins to crab pots, but it will likely increase survivorship and recruitment of these size classes in the population. In fact, population modeling suggests that incremental increases of survivorship in these age classes through a reduction of bycatch mortality will maintain or even increase this population. The removal of crab pots would also allow for the study and comparison of the terrapin population structure at PIERP before and after the removal of crab pots.

When combined with more extensive trapping efforts with crab pots and within wetland cells, the information gathered will providing scientific support for informed management decisions.

Despite the limitations of headstarting, I recommend that headstarting on PIERP continue due to the nature of the Terrapin Connection headstarting program and the Arlington Echo Environmental Education Center. Terrapin Connection provides needed environmental education to the youth growing up along the Chesapeake Bay and its tributaries using the headstarting of terrapins as a hook to promote such education in classrooms. However, no further headstarting efforts should be initiated with the intent of terrapin conservation through increasing hatchling and juvenile survival prior to addressing this issue of crab pot bycatch. Without the reduction of bycatch mortality in crab pots, terrapin headstarting will continue to fail as a conservation mechanism to supplement population growth. Although it may have slowed the decline of the PIERP population, this study lends support to the conclusion that headstarting is a “halfway technology” until the initial causes for decline are addressed (Frazer 1992).

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