

available at www.sciencedirect.comjournal homepage: www.elsevier.com/locate/biocon

Crab trapping causes population decline and demographic changes in diamondback terrapins over two decades

Michael E. Dorcas^{a,*}, John D. Willson^b, J. Whitfield Gibbons^b

^aDepartment of Biology, Davidson College, Davidson, NC 28035-7118, USA

^bUniversity of Georgia Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29802, USA

ARTICLE INFO

Article history:

Received 3 November 2006

Received in revised form

14 February 2007

Accepted 20 February 2007

Available online 12 April 2007

Keywords:

By-catch reduction device

Crab trap

Malaclemys terrapin

Mortality

Salt marsh

Turtle

ABSTRACT

Diamondback terrapins (*Malaclemys terrapin*) are thought to be declining throughout their range. Although many factors have been proposed to contribute to terrapin declines, including increased predation of nests and adults, habitat loss and degradation, road mortality, commercial harvest for food, and mortality as bycatch in crab traps, few studies have provided evidence linking these agents to population declines. Because male and small female terrapins are most susceptible to mortality in crab traps, population declines should coincide with shifts in the age and size distributions of the population and a shift to a more female-biased sex ratio. We used twenty-one years of mark-recapture data (>2800 captures of 1399 individuals) from a declining diamondback terrapin population in South Carolina to test the prediction that the decline is the result of mortality in crab traps. Since the 1980s, the modal size of both male and female terrapins has increased substantially and the proportion that are females is higher than in earlier samples. Additionally, the population now contains more old and fewer young individuals than before. The changes in demography and sex ratio we observed suggest that this terrapin population has declined as a result of selective mortality of smaller individuals in crab traps. The use of bycatch-reduction devices on crab traps may help prevent terrapins from entering the traps, but current models are too large to prevent mortality of males and many females in this population. Future research should focus on design and testing of effective bycatch-reduction devices for specific regions and other methods to prevent terrapin mortality in crab traps.

© 2007 Elsevier Ltd. All rights reserved.

1. Introduction

Reptile populations worldwide are suffering from anthropogenic impacts (Gibbons et al., 2000). Like many reptile species, declines in diamondback terrapin (*Malaclemys terrapin*) populations have been noted throughout their range (Seigel and Gibbons, 1995). These declines have been attributed to a variety of factors including human-subsidized predators of nests and adults (Butler et al., 2004; Draud et al., 2004),

collisions with boats, habitat loss, road mortality and commercial harvest for food (Seigel and Gibbons, 1995; Wood and Herlands, 1997; Feinberg and Burke, 2003). Diamondback terrapins have long life-spans, delayed sexual maturity, low reproductive rates, and strong site fidelity; therefore, elimination of just a few individuals over several years can result in substantial population declines or even local extirpations (Seigel and Gibbons, 1995; Tucker et al., 2001).

* Corresponding author: Tel.: +1 704 894 2727; fax: +1 704 894 2512.

E-mail addresses: midorcas@davidson.edu (M.E. Dorcas), willson@srel.edu (J.D. Willson), gibbons@srel.edu (J.W. Gibbons).

0006-3207/\$ - see front matter © 2007 Elsevier Ltd. All rights reserved.

doi:10.1016/j.biocon.2007.02.014

Bycatch in crab traps poses potential problems for many marine animals small enough to enter a trap. Abandoned, or “ghost” traps, can continue to trap and kill animals for extended periods of time (Guillory, 1993). Mortality of terrapins as a result of bycatch in crab traps has been proposed as a contributing factor to the decline of diamondback terrapins (Bishop, 1983; Wood, 1997; Hoyle and Gibbons, 2000; Tucker et al., 2001; Roosenburg, 2004). Several studies have documented mortality in crab traps, but few studies have documented declines in terrapin populations where crab trapping is suspected as the primary cause (but see Gibbons et al., 2001). Most published studies have shown high mortality rates based on bycatch analysis of crab traps, interpreted these high mortality rates as detrimental to terrapin populations, and considered them likely agents of terrapin population declines (Roosenburg et al., 1997; Roosenburg, 2004). However, no studies have provided evidence implicating mortality in crab traps as the causative agent in a terrapin population decline.

Identifying population declines in long-lived species with low recruitment rates, such as diamondback terrapins, is challenging and requires intensive, long-term sampling (Tucker et al., 2001). Moreover, separating true declines from natural fluctuations in many animal populations can be difficult (Pechmann et al., 1991), and attributing terrapin declines to mortality due to crab trap bycatch requires more than documenting terrapin mortality in crab traps. Smaller terrapins, primarily males and immature females, are apparently more susceptible to mortality in crab traps than adult females because they can more easily enter trap openings (Roosenburg et al., 1997; Gibbons et al., 2001). Thus, terrapin populations suffering declines as a consequence of crab trap mortality should exhibit changes in population demography as smaller (i.e., males and young females) turtles are removed. Specifically, the average body size and age of individuals in the population should increase and the sex ratio of the population should become female biased as immature animals are recruited at reduced levels and adult males are removed.

We used data from a long-term, intensive study of a diamondback terrapin population at Kiawah Island, South Carolina, in which declines have been documented, to examine the effects of crab trapping on the size and age distributions and the sex ratio of the population. We hypothesized that if the decline of this population was due to the detrimental impacts of crab trapping, the population would show an increase in overall turtle size, age, and female:male sex ratio over time.

2. Material and methods

2.1. Study site

This study was conducted in the tidal creek tributaries of the Kiawah River adjacent to the southwestern tip of Kiawah Island, Charleston County, SC (80°08'W, 32°36'N). Terrapins were studied in 4 tidal creeks bordered by extensive salt marsh dominated by *Spartina alterniflora* (Fig. 1; for specific site descriptions see Gibbons and Harrison, 1981; Lovich and

Gibbons, 1990; Lovich et al., 1991; Tucker et al., 1995, 2001; Hoyle and Gibbons, 2000; Gibbons et al., 2001).

Since the mid 1980s, the human population of Kiawah Island, both resident and tourist, has greatly increased concomitant with considerable development (e.g., golf courses, housing) of upland habitats adjacent to the salt marsh. In 1983, a dock was built on the Kiawah River directly across from the mouth of one of the creeks, facilitating an increase in recreational crab trapping (Hoyle and Gibbons, 2000) and boat traffic.

2.2. Sampling

Sampling was initiated in Terrapin Creek (Fig. 1) at Kiawah Island in 1983 and has continued as part of an on-going, long-term study of diamondback terrapins (Gibbons et al., 2001). Sampling was expanded to include Fiddler Creek in 1988, Oyster Creek in 1990, and Sandy Creek in 1992. Sampling most years was irregular, but in general, each creek was sampled at least once annually, with the exceptions of 2000–2002 when minimal sampling occurred. This paper includes data from 1983 to 2004, representing more than 2800 captures of 1399 individual terrapins.

We captured terrapins primarily at low tide using trammel nets and seines (Lovich and Gibbons, 1990). A few supplemental captures were made by hand, dipnet, or cast net. For each turtle captured, we measured plastron length to the nearest 1 mm and individually marked each animal by notching the marginal scutes (Sexton, 1959). Sex was determined by tail length and age was estimated at initial capture based on growth rings on the carapace and plastron when possible (generally for turtles less than 11 years old).

Previous research has documented that terrapin populations at Kiawah Island are declining (Gibbons et al., 2001; Tucker et al., 2001). The goal of this study was to examine changes in population demography concomitant with this decline, rather than to quantitatively evaluate population trends, survivorship, or recruitment. However, to provide a graphical representation of terrapin captures and general trends in population size within the 4 tidal creeks, we calculated population sizes between consecutive years with >5 captures per year using the Peterson estimator and used Chapman's modification for low recaptures when there were <10 recaptures between years (Heyer et al., 1994). We recognize that closed population models make several simplifying assumptions, some of which may not hold for our populations. However, our estimates provide conservative “snap shots” of population size that are indicative of population trends within the creeks.

To evaluate temporal changes in size and age structure within the population, we grouped turtles into four time periods based on their capture dates. Year groupings were chosen to include similar numbers of captures within each group. To evaluate temporal changes in age structure, we only used turtles of known ages and only used individual turtles once in each year. Because our ability to age turtles by counting annuli is generally limited to turtles less than 11 years old, we only used turtles less than 11 years old in this analysis. To evaluate changes in terrapin sizes over time, we used the



Fig. 1 – Map of study site. Note the close proximity of the dock to the entrance to Terrapin Creek and the distance of Sandy Creek from access points.

plastron length measurement for each turtle's first capture of each year.

To examine changes in population sex ratio, we used linear regression to examine the relationship between year and the percentage of all turtles captured annually that were female (only first capture per year for each turtle was used). Because of the bias associated with trapping techniques (females are more likely to be captured in trammel nets than in seines and proportionately more males than females are captured in seines than in trammel nets; M. Dorcas, unpublished data), we analyzed turtles captured by seines separately from those captured by trammel nets. Linear regressions were conducted using Microsoft Excel, and an alpha of 0.05 was used for all analyses.

In 2004, the maximal shell width and height to the nearest mm was measured for 29 adult turtles. These data were then used to generate linear relationships between plastron length and shell width and height for each sex (R^2 's 0.46–0.96), allowing us to estimate these parameters for all individual terrapins captured in the study at their first capture. To evaluate effectiveness of bycatch-reduction devices (BRDs) placed on crab traps, we generated size distributions for all turtles at their first capture and then calculated the percentage of each sex that would be excluded by the BRD's recommended in previous studies (Roosenburg and Green, 2000; 45×120 mm).

3. Results

Our data showed substantial reductions in diamondback terrapin population sizes in 3 of the 4 creeks sampled (Fig. 2). The most intensively sampled creek, Fiddler Creek, showed a steady decline in its terrapin population from 1989 (approximately 400 terrapins) until 2004 (fewer than 100 terrapins). Except for a few years in the late 1980s and 2000–2002, Terrapin Creek was sampled regularly since 1983 and showed a marked decline with virtually no captures since 1990. The same adult female terrapin was captured in 1996 and 2004, and was the only turtle captured in Terrapin Creek since 1990. Oyster creek showed an apparent reduction in estimated population size since 1992, but insufficient sampling from 1996 to 2003 makes calculation of population sizes difficult. Sandy Creek was the only tidal creek to show no apparent reduction in its terrapin population since sampling began.

In conjunction with the decline in terrapin populations, the age of the overall terrapin population in the tidal creeks sampled increased. The modal age of terrapins changed from 5 years old in 1983–1992, to 6 years old in 1993–1997, to 8 years old from 1998–2004 (Fig. 3). Concomitantly, the number of young terrapins captured declined substantially. The change in the age of the population is also reflected in an increase in the size of individual terrapins from the early 1980s until 2004. The number of large female terrapins increased sub-

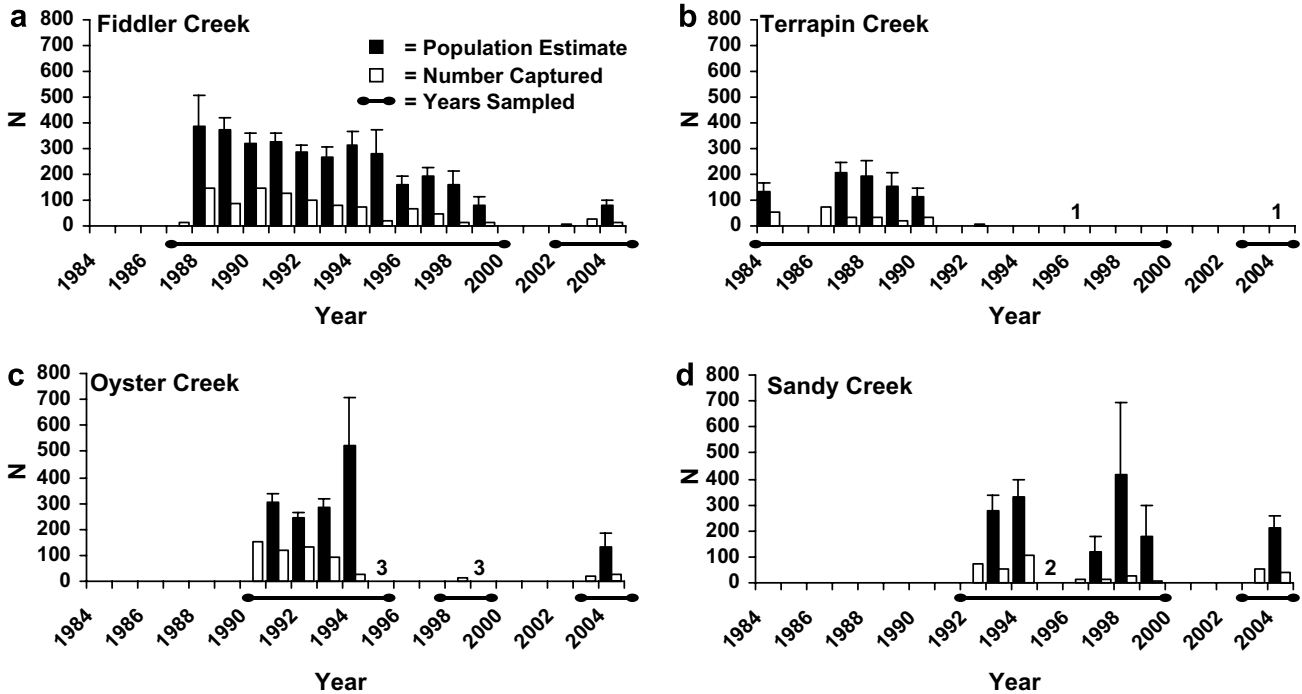


Fig. 2 – Changes in number of captures (open bars) and estimated population size (shaded bars, with associated standard errors) of diamondback terrapins in four tidal creeks associated with Kiawah Island between 1983 and 2004. Years in which creeks were sampled are indicated by lines beneath the X-axis of each graph. Population estimates were generated between years with >5 captures using the Peterson estimator with Chapman’s modification for low recaptures for years with <10 recaptures.

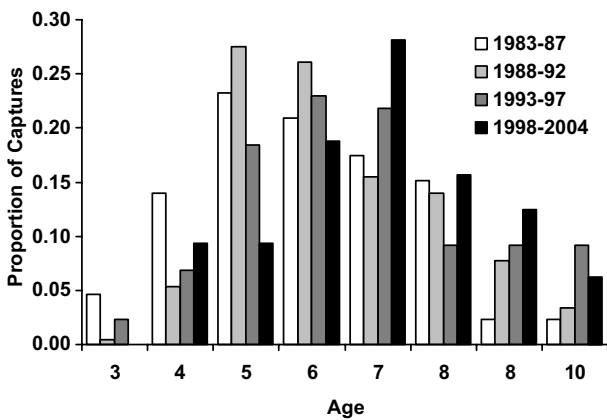


Fig. 3 – Age frequency distributions over time for all diamondback terrapins captured between 1983 and 2004. Year groupings were chosen to include similar numbers of captures in each group.

stantially from 1999 to 2004 and the modal size of male terrapins increased from 100 to 105 (plastron length; mm) from 1983 to 1998 to 105–110 (plastron length; mm) from 1999 to 2004 (Fig. 4).

Our data also show a significant shift in the sex ratio of the terrapin population from the mid 1980s to 2004. In the mid 1990s, the percent of female turtles captured in trammel nets was approximately 45%, apparently indicative of an equal sex ratio. However, by 1997 the proportion of captures of female

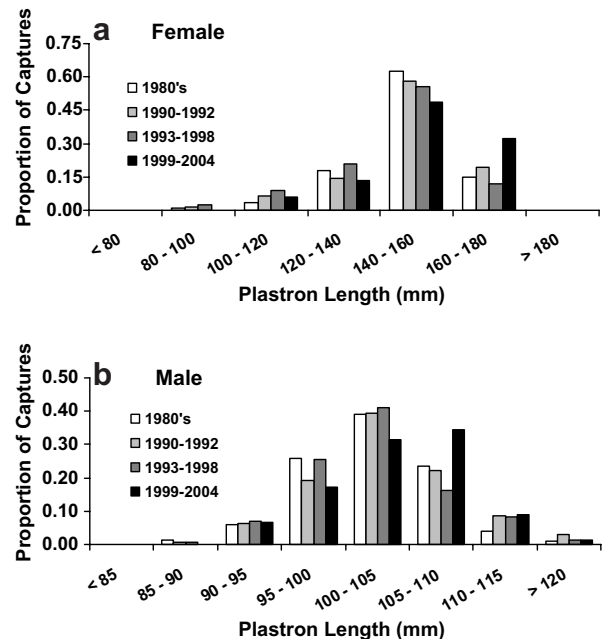


Fig. 4 – Size frequency (plastron length) distributions over time for female (a) and male (b) terrapins with all capture methods combined. Year groupings were chosen to include similar numbers of captures in each group.

terrapins in trammel nets had increased to greater than 80% (linear regression; $R^2 = 0.71$; $p = 0.001$; Fig. 5). Likewise, the proportion of female terrapins captured with seines in the

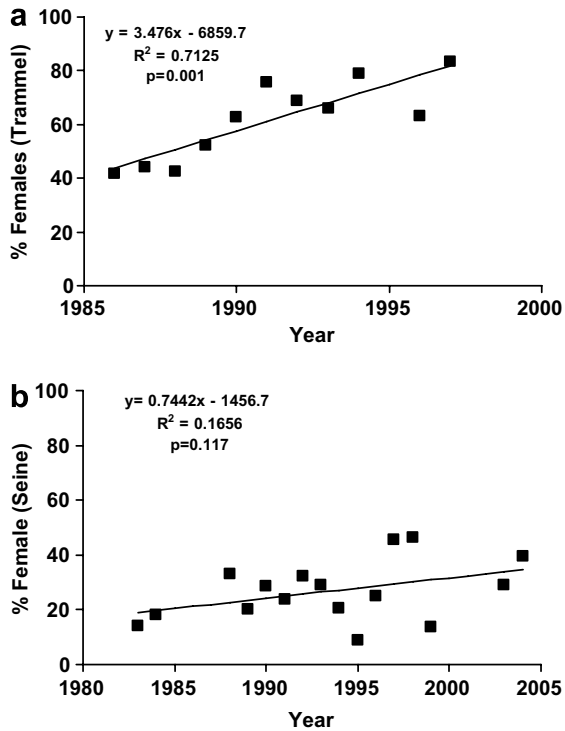


Fig. 5 – Percent of female of terrapins captured with trammel nets (a) and with seines (b). Individual turtles were only counted once per year. Years were eliminated if the total capture for that year for that technique was fewer than 12 individuals.

mid 1980s was approximately 20% and increased to approximately 40% by 2004 (linear regression; $R^2 = 0.166$; $p = 0.177$; Fig. 5).

Our results show that because of the depth of their shell, 81% of adult female turtles from the Kiawah Island terrapin population would be excluded from crab traps outfitted with bycatch-reduction devices of the dimensions recommended by Roosenburg and Green (2000); Fig. 6. Twenty-one percent of females would be excluded by shell width alone. No male turtles from the Kiawah Island terrapin population would be excluded from crab traps outfitted with bycatch-reduction devices of the dimensions recommended by Roosenburg and Green (2000; Fig. 6).

4. Discussion

This study represents the first to document temporal changes in age and size distributions and sex ratio of a declining terrapin population consistent with mortality due to bycatch in crab traps. We found that from 1983 until 2004, concomitant with a decline in overall population size, the population shifted toward larger sizes, older ages, and a female-biased sex ratio.

The population declines at Kiawah Island were most dramatic in tidal creeks close to access points for human recreation (Fig. 1; Gibbons et al., 2001). The dock that was built in 1983 on the Kiawah River across from the mouth of Terrapin Creek increased human access to this creek and is likely what

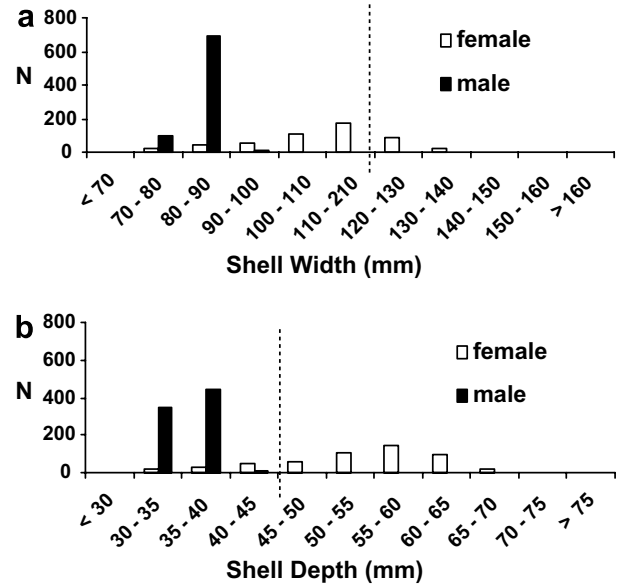


Fig. 6 – Maximal shell width (a) and depth (b) of terrapins from Kiawah Island, South Carolina, in relation to maximum dimensions of terrapin excluder devices (dashed vertical lines) designed to prevent terrapins from entering crab traps (Roosenburg et al., 1997). Maximal shell width and depth were estimated for all individual terrapins captured at Kiawah from plastron length based on linear regressions of shell width and depth on plastron length from 29 terrapins measured in 2004.

contributed to the drastic population decline. Sandy Creek, which is the most distant from any access point, has experienced no detectable decline. Because commercial crab fishermen generally deploy crab traps in all the creeks sampled, this pattern of declines is consistent with mortality due specifically to recreational crab trapping, (M. Dorcas, personal observation). Additionally, recreational crab trappers are more likely to abandon traps than commercial trappers, thus posing a continual threat to terrapins (Hoyle and Gibbons, 2000).

Other potential causes for terrapin population declines at Kiawah Island include disruption of nesting habitats and road mortality, both agents blamed for declines elsewhere (Seigel and Gibbons, 1995), and increased sedimentation resulting in habitat alteration. Disruption of nesting habitats could result in reduced levels of recruitment and a shift in the population size and age similar to what we have documented. However, nesting habitats on Kiawah Island, which include hammocks and a large dune area near the mouth of the Kiawah River, have, for the most part, remained intact, although human traffic (fishing, kayaking) in the dune area has increased substantially since 1983 (W. Gibbons, personal observation). Moreover, reduced overall recruitment would not result in the shift in sex ratio we observed. Unlike some other sites where road mortality of nesting females can be high, road mortality appears to be less of a factor on Kiawah Island. At Kiawah Island, no roads pass directly through known nesting areas and few road-killed terrapins have been found despite frequent travel over local roads by us during

the nesting season. However, no systematic survey of road mortality has been conducted on Kiawah Island, and the potential future contribution of road mortality to the terrapin decline remains enigmatic. If road mortality of nesting females was a significant contributing factor in terrapin declines, then a change to a more male-biased sex ratio would be expected. An increase in natural nest temperatures over time would tend to produce more female terrapins (Ewert and Nelson, 1991), however, nest temperature changes would not explain our documented changes in age and sizes of both sexes. Increased sedimentation since 1983 is evident in most creeks (W. Gibbons, pers. observ.), presumably as a consequence of local development and agricultural activities, and may result in a degraded salt marsh habitat. Such environmental alterations would presumably affect both sexes of terrapins in a similar manner and not result in detectable shifts in sex ratio.

Although concern about declines in terrapin populations is high, few studies have provided quantitative evidence of terrapin declines over time (but see Seigel, 1993; Gibbons et al., 2001; Tucker et al., 2001). The decline in the terrapin population at Kiawah Island has been documented previously by a reduction in overall capture rates since 1983 and by a decline in estimated adult survivorship (Tucker et al., 2001). Gibbons et al. (2001) and Tucker et al. (2001) both concluded that changes in survivorship were most likely due to terrapin mortality in crab traps. Seigel and Gibbons (1995) report that across the terrapin's geographic range, mortality due to drowning in crab traps appears to be a major cause of both documented and apparent declines.

Because smaller individuals can more easily gain entrance to crab traps, adult males and younger turtles of either sex have higher probability of being captured than adult females (Roosenburg et al., 1997). The demographic changes seen in the Kiawah terrapin population are consistent with this phenomenon. Apparently, a high proportion of young turtles and males become trapped in crab traps and drown, resulting in shifts towards larger and older individuals and a higher proportion of females within the population. Unlike road mortality, which typically results in male-biased populations (Gibbs and Steen, 2005), mortality due to crab trapping apparently eliminates males from the population at a higher rate and would seemingly have a lower impact on reproduction than other sources of mortality that selectively eliminate females. However, because young turtles of both sexes are reduced in number, fewer female turtles will survive to replace older females that die. Thus, although adult female turtles are relatively safe from mortality in crab traps, long-term viability of the population is likely still threatened by crab trapping through reduced recruitment of young females.

Alternative crab trap designs, including BRD's, have been proposed as methods by which mortality of terrapins in crab traps can be reduced (Roosenburg et al., 1997; Wood, 1997). Roosenburg et al. (1997) proposed a modified crab trap design that allows terrapins to surface and breathe. However, this design substantially increases the size of the trap and would likely be unacceptable to most crabbers. Small, rectangular BRDs that are easily attached to existing crab traps have been shown to increase crab captures while effectively reducing the number of turtles entering and drowning in crab traps

(Wood, 1997; Butler and Heinrich, 2007). However, it is important that the dimensions of any BRD exclude a significant number of terrapins in the area they are deployed. Using the dimensions provided by Wood (1997; 45 × 100 mm), BRDs deployed at Kiawah Island would prevent large females from entering traps due to shell depth (= height) but would not exclude males. Consequently, we recommend designing BRDs that effectively exclude a broader spectrum of individual sizes. Thus, the BRD opening may need to be reduced in regions where turtles are smaller.

An additional approach is to alter the orientation of the BRD. Preliminary research shows that vertical alignment of BRDs in the trap openings may more effectively exclude terrapins while having little or no effect on crab captures (Hoyle and Gibbons, 2000; Cole and Helser, 2001; C. Belcher and T. Sheirling, unpublished data). More research is required to examine BRD configurations and test their effectiveness for eliminating terrapins and their impacts on crab catch. Collaborations between cooperative crabbers and researchers will greatly facilitate such testing. Additionally, cooperative efforts with the public, regulatory organizations and researchers are needed to educate appropriate audiences about the impacts of crab trapping and to develop effective strategies that ensure the conservation of terrapin populations while ensuring the livelihood of people who rely on crab fisheries.

Acknowledgments

We thank Marilyn Blizard, Sophia McCallister, Bill Daniel, and Resort Quest Kiawah Island Vacation Rentals for providing lodging or arranging for housing while we were conducting our research at Kiawah Island. Marilyn Blizard and Meg Hoyle were especially helpful in facilitating interactions with regulatory agencies and the Town of Kiawah Island. Judy Greene managed the database and greatly assisted with numerous other tasks. Kristen Cecala, Leigh Anne Harden, Steven Price, Charlotte Steelman and Caitlin Westfall provided comments that improved the manuscript. We thank the numerous UGA-SREL and Davidson personnel for assistance with sampling and processing terrapins. This research was approved by the Davidson College Institutional Animal Care and Use Committee (Protocol# 3-04-11). Funding was provided by Duke Power, the Department of Biology at Davidson College, National Science Foundation Grants (REU DBI-0139153 and DEB-0347326) to MED, and the Environmental Remediation Sciences Division of the Office of Biological and Environmental Research, U.S. Department of Energy through Financial Assistance Award number DE-FC09-96SR18546 to the University of Georgia Research Foundation.

REFERENCES

- Bishop, J.M., 1983. Incidental capture of diamondback terrapins by crab pots. *Estuaries* 6, 426–430.
- Butler, J.A., Heinrich, G.L., 2007. The effectiveness of bycatch reduction devices on crab pots at reducing capture and mortality of diamondback terrapins in Florida. *Estuaries and Coasts* 30, 179–185.

- Butler, J.A., Broadhurst, C., Green, M., Mullin, Z., 2004. Nesting, nest predation and hatchling emergence of the Carolina diamondback terrapin, *Malaclemys terrapin centrata*, in Northeastern Florida. *American Midland Naturalist* 152, 145–155.
- Cole, R.V., Helsler, T.E., 2001. Effect of four by-catch reduction devices on diamondback terrapin (*Malaclemys terrapin*) capture and blue crab (*Callinectes sapidus*) harvest in the Delaware estuary. *North American Journal of Fisheries Management* 21, 825–833.
- Draud, M., Bossert, M., Zimnavoda, S., 2004. Predation on hatchling and juvenile diamondback terrapins (*Malaclemys terrapin*) by the Norway rat (*Rattus norvegicus*). *Journal of Herpetology* 38, 467–470.
- Ewert, M.A., Nelson, C.E., 1991. Sex determination in turtles: diverse patterns and some possible adaptive values. *Copeia* 1991, 50–69.
- Feinberg, J.A., Burke, R.L., 2003. Nesting ecology and predation of diamondback terrapins, *Malaclemys terrapin*, at Gateway National Recreation Area, New York. *Journal of Herpetology* 37, 517–526.
- Gibbons, J.W., Harrison III, J.R., 1981. Reptiles and amphibians of Kiawah and Capers islands, South Carolina. *Brimleyana* 5, 145–162.
- Gibbons, J.W., Lovich, J.E., Tucker, A.D., Fitzsimmons, N.N., Greene, J.L., 2001. Demographic and ecological factors affecting conservation and management of the Diamondback Terrapin (*Malaclemys terrapin*) in South Carolina. *Chelonian Conservation and Biology* 4, 66–74.
- Gibbons, J.W., Scott, D.E., Ryan, T.J., Buhlmann, K.A., Tuberville, T.D., Metts, B.S., Greene, J.L., Mills, T., Leiden, Y., Poppy, S., Winne, C.T., 2000. The global decline of reptiles, Déjà vu' amphibians. *Bioscience* 50, 653–666.
- Gibbs, J.P., Steen, D.A., 2005. Trends in sex ratios of turtles in the United States: implications of road mortality. *Conservation Biology* 19, 552–556.
- Guillory, V., 1993. Ghost fishing in blue crab traps. *North American Journal of Fisheries Management* 13, 459–466.
- Heyer, W.R., McDiarmid, R.W., Donnelly, M., Hayek, L. (Eds.), 1994. *Measuring and Monitoring Biological Diversity: Standard Methods for Amphibians*. Smithsonian Institution Press, Washington, DC.
- Hoyle, M.E., Gibbons, J.W., 2000. Use of a marked population of diamondback terrapins (*Malaclemys terrapin*) to determine impacts of recreational crab pots. *Chelonian Conservation and Biology* 3, 735–737.
- Lovich, J.E., Gibbons, J.W., 1990. Age at maturity influences adult sex ratio in the turtle *Malaclemys terrapin*. *Oikos* 59, 126–134.
- Lovich, J.E., Tucker, A.D., Kling, D.E., Gibbons, J.W., Zimmerman, T.D., 1991. Behavior of hatchling diamondback terrapins (*Malaclemys terrapin*) released in a South Carolina salt marsh. *Herpetological Review* 22, 81–83.
- Pechmann, J.H.K., Scott, D.E., Semlitsch, R.D., Caldwell, J.P., Vitt, L.J., Gibbons, J.W., 1991. Declining amphibian populations: the problem of separating human impacts from natural fluctuations. *Science* 253, 892–895.
- Roosenburg, W.M., 2004. The impact of crab pot fisheries on terrapin (*Malaclemys terrapin*) populations: where are we and where do we need to go? In: Swarth, C., Roosenburg, W.M., Kiviat, E. (Eds.), *Conservation and Ecology of Turtles of the Mid-Atlantic Region: A Symposium*, Salt Lake City, UT, pp. 23–30.
- Roosenburg, W.M., Cresko, W., Modesitte, M., Robbins, M.B., 1997. Diamondback terrapin (*Malaclemys terrapin*) mortality in crab pots. *Conservation Biology* 11, 1166–1172.
- Roosenburg, W.M., Green, J.P., 2000. Impact of a bycatch reduction device on diamondback terrapin and blue crab capture in crab pots. *Ecological Applications* 10, 882–889.
- Seigel, R.A., 1993. Apparent long-term decline in diamondback terrapin populations at the Kennedy Space Center, Florida. *Herpetological Review* 24, 102–103.
- Seigel, R.A., Gibbons, J.W., 1995. Workshop on the ecology, status, and management of the diamondback terrapin (*Malaclemys terrapin*), Savannah River Ecology Laboratory, 2 August 1994: final results and recommendations. *Chelonian Conservation and Biology* 1, 240–243.
- Sexton, O.J., 1959. Spatial and temporal movements of a population of the painted turtle, *Chrysemys picta marginata* (Agassiz). *Ecological Monographs* 29, 113–140.
- Tucker, A.D., FitzSimmons, N., Gibbons, J.W., 1995. Resource partitioning by the estuarine turtle, *Malaclemys terrapin*: trophic, spatial, and temporal foraging constraints. *Herpetologica* 51, 167–181.
- Tucker, A.D., Gibbons, J.W., Greene, J.L., 2001. Estimates of adult survival and migration for diamondback terrapins: conservation insight from local extirpation within a metapopulation. *Canadian Journal of Zoology* 79, 2199–2209.
- Wood, R.C., 1997. The impacts of commercial crab traps on Northern Diamondback Terrapins, *Malaclemys terrapin terrapin*, in: Van Abbema, J. (Ed.), *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference*, Purchase, NY, pp. 46–53.
- Wood, R.C., Herlands, R., 1997. Turtles and tires: the impact of roadkills on northern diamondback terrapin, *Malaclemys terrapin terrapin*, populations on the Cape May Peninsula, southern New Jersey, USA. In: Van Abbema, J. (Ed.), *Proceedings: Conservation, Restoration, and Management of Tortoises and Turtles – An International Conference*, Purchase, NY, pp. 46–53.