DISTRIBUTION AND ECOLOGY OF THE DIAMONDBACK TERRAPIN
(MALACLEMYS TERRAPIN) IN SOUTH CAROLINA SALT MARSHES

By

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APPROVED BY

[Signatures of Major Advisor, Committee Members, and Dean of Graduate Studies with dates]
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ABSTRACT

The diamondback terrapin (*Malaclemys terrapin*) is a conspicuous resident of South Carolina estuaries. From 1995-1998, the Inshore Fisheries unit of the South Carolina Department of Natural Resources recorded incidental captures of terrapins during their trammel net sampling along the coast of South Carolina. I devised a statistical model to explain the distribution of terrapins in South Carolina using the occurrence of terrapins in trammel net sampling, and geographical and physical variables. The catch of *M. terrapin* remained stable over the four years that Inshore Fisheries recorded their abundance. Terrapins were caught in the highest density in the Ashley River, Charleston, SC (3.15 terrapins/trammel net set), and the lowest density in the ACE Basin (0.92 terrapins/trammel net set). *Malaclemys terrapin* was found in the highest densities during the spring mating season, when water temperatures were near 23.4°C. *Malaclemys terrapin* was a euryhaline organism, captured in almost all salinities, from completely fresh water to full strength seawater (0.3 ppt - 36.6 ppt).

Although local populations of South Carolina terrapins appear to be healthy, they have been ignored as an important predator in salt marsh food webs. I conducted exclusion and inclusion experiments in the Charleston Harbor estuary to determine the effect of *M. terrapin* on salt marsh periwinkles, *Littorina irrorata*. I found significantly higher densities of *L. irrorata* in cages that excluded terrapins compared to control plots, indicating that predation by *M. terrapin* may reduce the density of *L. irrorata*. The
results from the terrapin inclusion experiment were inconclusive, because Hurricane
Floyd hit Charleston, SC in the midst of the experiment.

I conducted a mark/recapture experiment in the Wando River, Charleston, SC, to
estimate terrapin population parameters. I captured a total of 87 terrapins and marked 76
over five sampling dates in April and May, 1999. No terrapins were recaptured during
the study. The sex ratio of 3.14 males: 1 female suggests that the Wando River terrapin
population is healthy, because stable populations generally have a male-biased sex ratio.
A biased sex ratio results from males being recruited into the adult population faster than
females because the former mature earlier. However, the stability of terrapin populations
may be challenged through incidental drowning in crab pots and habitat destruction.
Continued monitoring is vital to ensure healthy terrapin populations, an important
component of the estuarine ecosystem.
INTRODUCTION

The diamondback terrapin (*Malaclemys terrapin*) became a valuable natural resource in the late 1800's and early 1900's when terrapin soup became popular (Coker 1920; Ernst et al. 1994). By the 1920's, the market for this brackish water turtle had diminished as decreasing stock led to increased prices. As early as 1893, the U.S. Commission of Fish and Fisheries recognized the increasing scarcity of terrapins. They proposed that incentives be made for “fishermen and people of means to invest in terrapin culture...preserving the animal from extinction and putting it on the market at a price which while renumerative, will, nevertheless, be reasonable” (U.S. Commission of Fish and Fisheries 1895). However, commercial terrapin production did not come soon enough, and continued intense harvesting caused drastic reductions in wild populations. Recovery of *M. terrapin* populations was slow, because of long maturation times and heavy predation on eggs and hatchlings (Burger 1976; Arndt 1994). Yet in the years following large-scale commercial terrapin harvests, some populations recovered. Although commercial harvesting no longer threatens *M. terrapin*, habitat destruction and incidental drowning in crab traps (Bishop 1983; Seigel and Gibbons 1995; Hoyle 1997; Roosenburg et al. 1997) challenge the stability of terrapin populations.

Diamondback terrapins inhabit brackish water near *Spartina alterniflora* (salt marsh cordgrass) marshes along the Atlantic and Gulf coasts, from Cape Cod to Corpus
Christi (Ernst et al. 1994). They are the only permanent chelonian residents of estuarine habitats. Seven subspecies of *M. terrapin* are recognized: *M. t. terrapin* (Cape Cod to Cape Hatteras), *M. t. centrata* (Cape Hatteras to northern Florida), *M. t. tequesta* (Atlantic coast of Florida), *M. t. rhizophorarum* (Florida Keys), *M. t. macrospilota* (Florida Bay to the Florida panhandle), *M. t. pileata* (Florida panhandle to western Louisiana) and *M. t. littoralis* (western Louisiana to western Texas) (Ernst et al. 1994). There is tremendous phenotypic variation both among and within subspecies with carapace, plastron, and facial coloration (personal observation).

*Malaclemys terrapin* is a fairly long-lived species that displays sexual dimorphism, with female terrapins being larger than males. Mean plastron lengths, head widths, and masses of male *M. terrapin* were reported as 10.2 cm, 17.61 mm, and 242 g, while females were 14.8 cm, 28.88 mm and 705 g, with longevity of 20 years for both sexes (Seigel, 1984; Lovich and Gibbons 1990; Tucker et al. 1995). Resource partitioning among sexes and size classes of terrapins results from this distinct size difference (Tucker et al. 1995). Males and small female terrapins, which have narrow jaws, feed almost exclusively on the salt marsh periwinkle, *Littorina irrorata* (Tucker et al. 1995). Medium and large females, which have wide jaws and distinctive crushing plates, consume larger *L. irrorata* as well as crustaceans, particularly fiddler crabs (*Uca pugnax*) and blue crabs (*Callinectes sapidus*). Adults of both sexes also feed on marsh crabs (*Sesarma reticulatum*) and marsh clams (*Polynesoda caroliniana*) (Tucker et al. 1995). Perhaps because of their near elimination from the Atlantic and Gulf coast salt
marshes, this reptile has been ignored or dismissed as an important predator within salt marsh food webs (Teal 1962; Montague et al. 1981; Daiber 1982; Day et al. 1989).

Sex ratios of terrapins have been reported from various studies and range from strongly male biased to female biased. Lovich and Gibbons (1990) reported that the expected sex ratio of terrapins would favor males, due to an earlier age at maturity. Males are recruited into the adult population at approximately 4 years old while females reach maturity between 6 and 8 years of age. Therefore, assuming a 1:1 sex ratio upon hatching, a healthy terrapin population should favor males. Monitoring the sex ratio of terrapin populations may provide a way to assay the relative health of populations.

*Malaclemys terrapin* occurs in dense local populations and individuals display strong site fidelity from year to year (Lovich and Gibbons 1990; personal observation). Densities of 1.25-1.8 individuals per linear meter of creek were estimated in Florida and Delaware (Hurd et al. 1979; Seigel 1980, 1984, 1993; Tucker et al. 1995), and individual *M. terrapin* have been recaptured within meters of their original capture point in successive years (Lovich and Gibbons 1990). Terrapin abundance and site fidelity in salt marshes allow for fine-scale studies of interactions between *M. terrapin*, its prey and physical/biological conditions in its habitat.

Most studies on *M. terrapin* focus on feeding, growth and reproductive biology (Allen and Littleford 1955; Seigel 1980; Dunson 1985; Palmer and Cordes 1988; Davenport et al. 1992; Davenport and Ward 1993; Tucker et al. 1995; Roosenburg and Kelley 1996; Roosenburg 1996; Roosenburg and Dunham 1997; Spivey 1998). Furthermore, studies on the feeding habits of *M. terrapin* have focused on diet without
considering their ecological importance in salt marsh food webs. Few studies report the
distribution and density of *M. terrapin* (Hurd et al. 1979; Seigel 1984, 1993; Morreale
1992; Spivey 1998), despite the recent concern over declining populations. Demography,
habitat use, movement patterns and home range size, and long-term life history studies
were all identified as areas of research considered critical for managing *M. terrapin* at a
recent workshop (Seigel and Gibbons 1995).

I studied two aspects of diamondback terrapin ecology. I investigated the
abundance of *M. terrapin* in South Carolina and attempted to correlate it with physical
and geographical variables. By examining incidental catch records provided by Inshore
Fisheries (South Carolina Marine Resources Division, Department of Natural Resources),
I identified habitats and specific geographic locations preferred by *M. terrapin* throughout
South Carolina. I also determined the sex ratio of terrapins in the Wando River as a
means of assessing the relative health of the population. I also used manipulative
experiments to determine the importance of *M. terrapin* as a predator of salt marsh
periwinkles (*Littorina irrorata*), a conspicuous grazer in salt marsh food webs. I
designed a terrapin exclusion experiment to test several hypotheses. My first hypothesis
was that *M. terrapin* predation on *L. irrorata* significantly affects the density and size
structure of the *L. irrorata* population. The second hypothesis was that male and female
*M. terrapin* have different effects on the density and size structure of the *L. irrorata*
population due to the sexual dimorphism exhibited by terrapins. Since evidence of *M.
terrapin* as an important predator of *L. irrorata* would challenge traditional salt marsh
food webs, which generally omit terrapins, I designed a terrapin inclusion experiment to
verify the results of the exclusion experiment. Furthermore, the inclusion experiment allowed for a comparison of predation rates on *L. irrorata* between terrapins and another estuarine predator, the blue crab.
METHODS

Distribution of *Malaclemys terrapin* in South Carolina Salt Marshes

*Malaclemys terrapin* has been captured frequently by the Inshore Fisheries Program (South Carolina Department of Natural Resources, Marine Resources Division). Beginning in 1995, staff of Inshore Fisheries unit recorded the number of terrapins caught incidentally in each net haul. Sampling occurred along the entire South Carolina Coast in six geographically distinct locations: two areas in Cape Romain, Charleston Harbor, the Ashley and the Wando Rivers, and the ACE (Ashepoo-Combahee-Edisto) Basin (Fig. 1). Each area contained 25-30 sampling locations characterized by low water flow and mud flats with oyster bars adjacent to *Spartina alterniflora* marsh. This habitat is ideal for capturing red drum (*Scianops ocellatus*), spotted sea trout (*Cynoscion nebulosus*), southern flounder (*Paralichthys lethostigma*), black drum (*Pogonias cromis*), sheepshead (*Archosargus probatocephalus*) and striped mullet (*Mugil cephalus*), the target species of Inshore Fisheries projects.

Incidental catch of terrapins was recorded monthly at the six aforementioned estuarine locations from January 1995 - December 1998. Approximately 40% of the sampling locations at each site were randomly selected each month. At each location, a trammel net (184 m long, 2 m deep, with 36 cm and 6 cm mesh) deployed by a Florida net boat (Tremblay®), was set parallel to *Spartina alterniflora* marsh in ≤ 2 m of water.
The net was secured at each end by anchors to enclose an area between the net and marsh (Fig. 2). Crew members beat the water surface with long wooden poles to frighten fish into the pocketing of the net. The net was retrieved, and fish, terrapins and other organisms were removed. Species of interest were measured, weighed, tagged and released, and the number of terrapins was recorded. Air temperature, depth and time of the tow were recorded for each location. Water temperature, salinity and dissolved oxygen concentration were determined using a YSI Model 85 meter (Yellow Springs Instruments, Yellow Springs, OH).

**Role of *Malaclemys terrapin* in Salt Marsh Food Webs**

I used two experiments to investigate the role of *M. terrapin* in salt marsh food webs, particularly as a predator of *L. irrorata*. This two-fold design enabled me to examine the responses of *L. irrorata* in the presence and absence of *M. terrapin*. I simulated conditions in which *M. terrapin* was one of many possible natural predators at a very low density (exclusion experiment), or was the sole predator (inclusion experiment). This approach allowed me to estimate the predatory effects of *M. terrapin*, and the consequences of removing it from the salt marsh food web.

The inclusion experiment allowed me to test current salt marsh food webs, which show *C. sapidus* as the primary predator of *L. irrorata* (Hamilton 1976; Baxter 1983). By placing *M. terrapin* and *C. sapidus* in separate cages, I was able to compare their consumption rates.
Terrapin Exclusion Experiment

I erected terrapin exclusion cages in the Wando River Estuary, near Foster Creek, Charleston, South Carolina, May 16 - 30, 1998 (Fig. 3). The Wando River is one of three estuarine systems that empty into Charleston Harbor. It was approximately 1 km at its widest point and had an average depth of 1-3 m near the banks. The Wando River had little fresh water input, with salinity ranging from 12 - 30 ppt during my study. Foster Creek entered the Wando River from the eastern shore. The creek was approximately 100 m wide at the mouth and the average depth at the mouth was approximately 3 m. The experiment was set parallel to the shore on either side of Foster Creek. This site was characterized by oyster bars and mud flats exposed at mean low water; tidal amplitude in this region ranged from 1.5 - 2.2 m. A gentle slope graded into S. alterniflora, followed by a berm that clearly delineated low and high marsh. Blocks were located in the low marsh, in areas dominated by a population of tall S. alterniflora (Fig. 4).

The exclusion experiment had a randomized complete block design. Each of five blocks contained two experimental treatments and two controls. Treatment A consisted of a cage with holes cut in the mesh at the top, middle and sediment levels (Fig. 5). There were 27 holes on each side of the cage, and the holes were approximately 7.5 cm in diameter. This treatment allowed estuarine organisms smaller than M. terrapin to enter the cage. The difference in L. irrorata density and size between the controls and this treatment estimated the maximum predatory effect of all adult M. terrapin (and other large predators) on L. irrorata. Treatment B contained holes approximately 11.0 cm in diameter, allowing access only by male M. terrapin (and other small predators), which are significantly smaller than adult females (Tucker et al. 1995). The difference in L.
*irrorata* density and size between the controls and this treatment estimated the maximum predatory effect of male and small female *M. terrapin* (and possibly other predators of similar size) on *L. irrorata*.

The unmanipulated control was marked by PVC poles at the corners of a 4 x 4 m square plot of otherwise untouched marsh. This control estimated the natural population of *L. irrorata* in the marsh when all predators had unrestricted access. A manipulated control accounted for potential caging artifacts. The manipulated control consisted of PVC poles with mesh on only two sides of the plot. This control, like the unmanipulated control, allowed equal access by all predators in the salt marsh. Differences in *L. irrorata* density and size between the manipulated and unmanipulated control allowed estimation of caging artifacts (Connell 1997).

Each cage measured 4 x 4 m (Fig. 4). Cages were constructed of nylon mesh (0.31 cm square and 120 cm tall: Internet Inc., New Hope, MN) supported on a frame of 1.88 cm polyvinyl chloride pipe (PVC). Mesh was secured to the PVC with cable ties and hooks, which were fastened to a rope strung through PVC ‘tee’s at the top of the frame. The mesh was anchored in the sediment at three places on each side using hollow sections of PVC buried in the sediment (Fig. 5).

I collected data from each plot in September 1998. Each plot was divided into sixteen 1 m² sections, and two sections were randomly selected for sampling. All *L. irrorata* were collected from both subsamples and returned to the lab to be measured. *S. alterniflora* density was measured by randomly selecting \(\frac{1}{16}\) section of each quadrat to define the density of plant stems, which provide habitat for *L. irrorata*.
Terrapin Inclusion Experiment

I erected terrapin inclusion cages in the southern portion of the Charleston Harbor estuary, near the Marine Resources Research Institute, in Charleston, South Carolina August 3 - 22, 1999. The Charleston Harbor estuary is fed by the Ashley, Cooper and Wando Rivers, and empties into the Atlantic Ocean (Fig. 3). Salinity in Charleston Harbor during my study ranged from 2.2 - 35 ppt. The tidal amplitude in this region was the same as the Wando River (1.5 m - 2.2 m). The inclusion experiment was erected in an area of marsh with characteristics similar to the region in the Wando River where the exclusion experiment was conducted. However, experimental blocks were set up in a linear array instead of on both sides of a creek. The Charleston Harbor site also lacked an expansive area of high marsh. *Spartina alterniflora* growth in this area was recent, within the past twenty years (Charles A. Wenner, personal communication).

The inclusion experiment had a randomized block design. Three complete blocks each containing three experimental treatments and two controls were set parallel to the shore in the low marsh. Treatment A consisted of a cage that contained a single adult female terrapin. The difference in *L. irrorata* density and size between the controls and this treatment estimated the predatory effect of only adult female *M. terrapin* on *L. irrorata*. Treatment B consisted of a cage containing a single adult male terrapin. The difference in *L. irrorata* density and size between the controls and this treatment estimated the predatory effect of only adult male *M. terrapin* on *L. irrorata*. Significantly different densities and sizes of *L. irrorata* between Treatments A and B would indicate that female and male terrapins affected populations of *L. irrorata* in different ways, either by consuming different amounts of the snails or eating different sizes of snails.
Treatment C contained two adult blue crabs approximately equal to the mean mass of an adult male terrapin (\(\approx 279\) g). The difference in \emph{L. irrorata} density and size between the controls and this treatment estimated the predatory effect of adult \emph{C. sapidus} on \emph{L. irrorata}. Significantly different densities and sizes of \emph{L. irrorata} among Treatments A, B and C would indicate that female and male terrapins affected populations of \emph{L. irrorata} differently than blue crabs, either by consuming different amounts or eating different sizes of snails.

The unmanipulated control in this experiment was the same as in the exclusion experiment, and estimated the natural density of \emph{L. irrorata} in the salt marsh. The manipulated control consisted of a complete cage without any predators. Differences in \emph{L. irrorata} density and size between these controls allowed estimation of cage artifacts. Comparisons between the exclusion and inclusion experiments were important to verify the results of each experiment. Similar results would indicate that caging artifacts were minimal and differences in \emph{L. irrorata} size and density could be attributed only to predation by \emph{M. terrapin}. Differing experimental results could indicate the presence of caging artifacts as well as significant predation by predators other than \emph{M. terrapin}.

Each cage was \(4 \times 4\) m (Fig. 6), and was constructed of nylon mesh (0.625 cm square, 165 cm tall, Internet Inc.), with eight pieces of 1.88 cm PVC used for each frame. Mesh was secured to the PVC with cable ties, and anchored in the sediment at two locations on each side using hollow sections of PVC buried in the sediment. A plastic container (40 cm x 60 cm x 15 cm) submerged in the pluff mud until level with the marsh surface provided an aquatic refuge for experimental animals during low tide.
I collected data from each plot in September 1999, three weeks after terrapins and crabs were placed in the cages, and after Hurricane Floyd hit Charleston. Each plot was divided into sixteen 1 m² sections. Due to the cage design, only twelve of these sixteen sections were available for sampling (Fig. 7). The remaining four 1 m² sections were unsuitable because they were trampled during cage construction. The 1 m² sections were quartered and one 0.25 m² section was randomly selected for sampling. All L. irrorata were collected from the subsample, measured in the field and released immediately. Spartina alterniflora density was measured in the same 0.25 m² quadrat.

Population Dynamics of Malaclemys terrapin in South Carolina Salt Marshes

I conducted a mark/recapture study of M. terrapin in the Wando River estuary April 15 - June 16, 1999. Terrapins were captured using trammel nets deployed at locations routinely sampled during Inshore Fisheries surveys. Terrapins were captured and marked on four dates in April and May. On the final capture date in June, terrapins were not marked.

I used a marking method that allowed me to identify individual terrapins. I assigned a letter to each marginal scute from A - X (Fig. 8, Cagle 1939; Gibbons 1988). The bridge scutes (D - H and Q - U) were excluded, because notching these scutes might compromise the structural integrity of the shell. I marked each terrapin using either a triangular file or a Dremel tool to make V-shaped or rectangular marks in the marginal scutes. I also painted the three letter code on the plastron of each terrapin using a quick-dry paint marker, so individuals could be identified quickly once recaptured. This method allowed for 364 unique marks.
In addition to marking each terrapin, I also recorded sex, age, mass, head width, plastron length, and carapace width. Each terrapin was sexed by comparing the position of the cloaca relative to the edge of the carapace (Marganoff 1970; Lovich and Gibbons 1990). When the cloacal opening was posterior to the carapace edge, the terrapin was male; when the cloaca opened anterior to or at the edge of the carapace, the terrapin was female. I aged terrapins by counting the rings on a carapace scute (Brooks et al. 1997). Though previous studies used plastral scutes for aging terrapins (Morreale 1992; Tucker et al. 1995), I used carapace scutes because they were less worn. The scute I used to age the turtles was not standardized because wear varied; I chose the scute with the least wear. Each ring I counted was considered to be one year of growth. Terrapins with more than ten rings were given an age of 10+ years, because I could not accurately count beyond ten rings. Each terrapin was weighed in a bucket with a spring scale (Chatillon Model IN-50, NY) to determine mass. Head width, plastron length and carapace width were all measured with dial calipers.

Statistical Analysis

I developed a regression model explaining the distribution of *M. terrapin* as a function of six main effects: year, month, site, location nested within site, salinity and water temperature. I also included five interaction terms: year*month, year*site, month*site, year*month*site and water temperature\(^2\). The response variable was the number of *M. terrapin* caught per trammel net set. January, February and December were excluded from the analysis, because only 39 terrapins were caught in four years of sampling during these winter months. Terrapins were not available to the gear during
these months because they overwintered in creek banks or upland habitat (Coker 1920; Lawler and Musick 1972; Yearicks et al 1981).

I developed a regression model to further explore terrapin distributions within the Charleston Harbor estuarine system (Charleston Harbor, Ashley River and Wando River). This model contained six effects: site, channel depth at mean low water, river width and the distances from each sampling location to the nearest creek, suitable nesting habitat and developed area. These effects were chosen because they determine accessibility to feeding, mating, nesting and overwintering habitat of terrapins. I chose ten locations within each site: five locations with the greatest mean number of terrapins and five locations with the fewest mean number of terrapins. The response variable used was mean number of *M. terrapin* caught by Inshore Fisheries per trammel net set. I measured distances using infrared aerial photographs taken in 1994 (scale = 1:10,000), Charleston Harbor nautical charts (scale = 1:20,000) and digital calipers (Mitutoyo Model CD-6”BS, Mitutoyo Corporation, Japan).

I used two-way ANOVAs (α=0.05) to compare mean density of *L. irrorata* and *S. alterniflora* among blocks and treatments in the *M. terrapin* exclusion and inclusion experiments, and to compare the mean lengths of *L. irrorata* in the exclusion experiment. Due to heterogeneity of variances, the mean lengths of *L. irrorata* in the inclusion experiment were compared using a nonparametric alternative to a two-way ANOVA: Friedman’s method for randomized block designs. Block 1 was eliminated from the analysis because all except the female terrapin treatment, had missing values, a result of the destruction caused by Hurricane Floyd. Blocks were considered random effects, and
therefore were interchangeable. Orthogonal contrasts were employed to make *a priori* comparisons among significant block and treatment means. All statistical analyses were performed using JMP version 3.2.2 (SAS Institute, Inc., 1997).

I was unable to calculate population density of *M. terrapin* in the Lower Wando River because I did not recapture any marked terrapins. I determined sex ratio and mean ages, masses, plastron lengths, head widths, and carapace widths for male and female terrapins.
RESULTS

Distribution of *Malaclemys terrapin* in South Carolina Salt Marshes

From March 1995 through November 1998 (excluding January, February and December from each year), Inshore Fisheries recorded 4583 incidental captures of *Malaclemys terrapin* from 2528 trammel net sets along the South Carolina coast (\( \bar{x} = 1.81 \) *M. terrapin*/trammel net set). The statistical model I devised accounted for 32.6% of the variation in terrapin distribution (Fig. 9; Tab. 1). There were no significant differences in terrapin captures among years (Fig. 10), but terrapin abundance differed significantly among months. The highest captures occurred in the spring, with a peak in April (Fig. 11). Terrapin captures also differed significantly among sites. Terrapin captures in the Ashley River were significantly greater than in all other sites (mean +/− 1 S.E.; 3.15 +/− 0.34 terrapins/set; Fig. 10). Charleston Harbor had the next highest abundance of terrapins (2.09 +/− 0.32 terrapins/set), and had significantly higher captures than the ACE Basin (0.92 +/− 0.34 terrapins/set; Fig. 10). Terrapin captures in the Lower Wando River (1.50 +/− 0.36 terrapins/set) and Cape Romain (1.33 +/− 0.30 terrapins/set) did not differ significantly from each other (Fig. 10). Water temperature significantly affected terrapin captures. Captures peaked when the water temperature was approximately 23.4°C (Fig. 12). Captures of *M. terrapin* (a euryhaline organism; Dunson 1970; Robinson 1975), were not significantly affected by salinity (Fig. 13). The interaction terms year*month and month*site each explained a significant proportion of
the variation in terrapin distribution, suggesting that peaks in terrapin abundance occurred in different months depending on weather patterns during each year and peaks also occurred in different months at each of the five sites. The interaction terms year*site, year*month*site and water temperature² explained a minor amount of the variance in the model (F ≈ 1.00), so their Sums of Squares were pooled with the residual error.

The statistical model I devised to investigate habitat preferences of terrapins in the Charleston Harbor estuarine system did not account for a significant proportion of the variation in terrapin distribution (Tab. 2).

Role of Malaclemys terrapin in Salt Marsh Food Webs

Terrapin Exclusion Experiment

Densities of L. irrorata differed significantly among treatments and blocks (Fig. 14; Tab. 3). The density of L. irrorata did not differ between the unmanipulated (\( \bar{x} = 10.6 \text{ L. irrorata/m}^2 \)) and manipulated controls, (\( \bar{x} = 7.9 \text{ L. irrorata/m}^2 \)). Both treatments had significantly higher densities of L. irrorata than the controls. However, there was no significant difference in the density of L. irrorata between the treatment that excluded all terrapins (\( \bar{x} = 15.1 \text{ L. irrorata/m}^2 \)) and the treatment that only excluded large female terrapins (\( \bar{x} = 16.8 \text{ L. irrorata/m}^2 \)). The mean length of L. irrorata did not differ among treatments, but did differ among blocks (Fig. 15; Tab. 4). The density of S. alterniflora blades did not differ significantly among treatments or blocks (Fig. 16; Tab. 5).
Terrapin Inclusion Experiment

Two weeks after animals were placed in the experimental cages Hurricane Floyd approached the coast of South Carolina. Extreme high tides and winds caused over-wash of cages, which deposited S. alterniflora rack and other debris in the cages. The weight of the debris caused the mesh walls of my experimental structures to sag. No terrapins or blue crabs remained in the cages after the storm, suggesting experimental treatments were compromised.

Densities of L. irrorata did not differ significantly among treatments or blocks (Fig. 17; Tab. 6). The mean length of L. irrorata did not differ among treatments (Friedman’s method: $X^2 = 4.4$, $P>0.05$). There were no significant differences in the density of S. alterniflora among treatments or blocks (Fig. 19; Tab. 7).

Population Dynamics of Malaclemys terrapin in South Carolina Salt Marshes

I marked 76 terrapins on four sampling dates in April and May and caught 11 more on a final recapture day in June. Terrapins were captured in 17 different locations in the Wando River. I did not recapture any marked terrapins during the 1999 study. In March 2000, two marked terrapins were recaptured in their initial capture location. Both terrapins were male, and neither exhibited significant growth from the previous year.

The first recaptured terrapin, which had a mean pлаstron length of 10.9 cm and a mass of 325 g upon first capture, gained 0.1 cm and 25 g. The second turtle had a mean pлаstron length of 9.7 cm at first and second capture and a mass of 230 g upon first capture and 250 g at the time of second capture.
Mean head widths, plastron lengths, carapace widths, and masses of the 87 terrapins I sampled were 22.0 mm, 10.1 cm, 89.8 mm and 279 g for males from the Wando River, and 32.9 mm, 14.1 cm, 117.7 mm and 775 g for females. These measurements are compared to the Kiawah Island population in Table 8. The sex ratio of the Wando River terrapin population was 3.14:1 (male:female). The age of terrapins captured in this study was 3 - 7 years old for males and 5 - 10+ years old for females. A comparison of ages and sex ratios among the Wando River terrapins and other populations is shown in Table 9.
DISCUSSION

Distribution of *Malaclemys terrapin* in South Carolina Salt Marshes

At the 1994 “Workshop on the Ecology, Status, and Management of the Diamondback Terrapin” at the Savannah River Ecology Laboratory, the status of terrapins in Atlantic and Gulf coast states was discussed. Few states had undertaken recent or comprehensive surveys, and the status of *M. terrapin* in South Carolina was listed as “unknown” and “declining” based only on local surveys. My analysis of data on terrapin abundance collected by Inshore Fisheries is the most complete survey of *M. terrapin* populations in South Carolina to date. In the five sites sampled along the South Carolina coast, populations of *Malaclemys terrapin* remained stable for four years (1995-1998). These data suggest that most of the variation in terrapin abundance was determined by seasonal differences and inter-site variation within the five main sampling areas.

Each of the five sites sampled by Inshore Fisheries exhibited similar fluctuations in annual abundance. Terrapins were captured in trammel nets with the greatest frequency in the spring. Inshore Fisheries recorded as many as 46 terrapins in a single net set, specifically when the water temperature was approximately 23.4°C. This phenomenon can be explained by the heightened activity of terrapins during the spring mating season. In Florida, Seigel (1980) noted spring aggregations of terrapins involved in courtship. In North Carolina, Spivey (1998) also witnessed a higher density of
terrapins in the spring, which he attributed to mating aggregations and emergence from communal overwintering sites. In Delaware, Hurd et al. (1979) reported the seasonal distribution of terrapins as variable, with the greatest number captured during the June mating season.

The decrease in terrapin abundance after the mating season witnessed in this study was also documented by Hurd et al. (1979), who speculated that decreased densities in late summer were related to changes in food availability. However, there was a disproportionate decrease in females in their study, suggesting that nesting activity was partially responsible for the decrease in overall terrapin density. Zimmerman (1992) found female terrapins nesting from mid-May through June on Kiawah Island, SC, which is when terrapin captures declined in my study. A behavior first described by Spivey (1998) for a North Carolina population of terrapins may also explain the decrease in terrapin abundance during the hot summer months in South Carolina. Spivey (1998) found terrapins buried in marsh mud in the summers of 1996 and 1997. These aestivating terrapins sometimes remained buried for days, but upon excavation became active and returned to the water. Aestivation as a refuge from intense summer heat may be an alternative explanation for the decrease in terrapin abundance in my study, since South Carolina summers are similar to conditions experienced in North Carolina.

Terrapins were not caught during the winter in this study, because they overwinter and therefore were not available for capture with trammel nets. *Malaclemys terrapin* hibernates in the sides of creeks, in the high marsh or by resting on the bottom underwater (Coker 1920; Lawler and Musick 1972; Yearicks et al. 1981) either individually or in groups (Yearicks et al. 1981). This behavior contributed to the decline
of the species in some areas where industrious fishermen dug buried terrapins from their hibemacula and shipped them to market (Babcock 1926).

Terrapins may rest or bury themselves in the mud underwater as a defense mechanism. During stop net studies conducted by the South Carolina Department of Natural Resources in Charleston Harbor, many terrapin heads were seen bobbing at the surface at high tide. As the tide went out and the marsh mud became visible, terrapins were not captured by nets, nor were they found on the marsh surface. Instead, terrapins were found buried in the mud (William A. Roumillat, personal communication). 

_Malaclemys terrapin_ similarly may avoid the trammel nets used in my study. On numerous occasions I observed terrapins swimming alongside a trammel net, but when the net was hauled in, there were no terrapins. This indicates that my study provided a conservative estimate of true terrapin densities along the South Carolina coast.

Terrapins were captured in the greatest abundance in the greater Charleston area (Ashley River, Charleston Harbor and Wando River). Although the ACE Basin and Cape Romain are considered pristine areas (with very little development compared to the Charleston sites) terrapin densities there were not very high. The topography of the marshes in the ACE Basin and Cape Romain differs considerably from the other three sites. Marshes in the Charleston Harbor, the Ashley River and the Wando River have definitive banks that grade into high marsh and upland habitat. Sampling locations in the ACE Basin and Cape Romain are characterized by marshes with areas of new _S. alterniflora_ growth that do not have definitive banks and contain very little high marsh and upland habitat. Absence of marsh banks in a sampling location makes it difficult to completely enclose an area with the trammel net; therefore terrapins may escape more.
easily from these areas. The topography of the Charleston area also provides more accessible upland and beach habitat suitable as nesting sites by gravid females.

Topographical differences also may explain why there was more variation in terrapin distribution attributed to sampling locations within sites compared to differences among sites. As stated previously, some locations were easier to enclose with the net because of distinct banks, and therefore were more effective in capturing terrapins. Since prey distribution in salt marshes is not uniform (Kneib 1984), terrapin distribution within sites would not be expected to be uniform either; rather the highest concentration of terrapins would most likely inhabit areas richest in prey. In South Carolina, the large tidal amplitude (2 m) makes portions of higher marsh accessible to terrapins at high tide. Terrapins most likely select different foraging sites based on the time of the tide. Since Inshore Fisheries sampled each location at the same tidal stage every month, I could not determine whether water depth was a significant effect in determining the distribution of *M. terrapin*.

Terrapins were captured in salinities ranging from fresh water to full strength seawater (0.3 – 36.6 ppt) during this study. As expected for a euryhaline organism, salinity did not significantly affect the distribution of *M. terrapin*. Previous studies of adult *M. terrapin* also reported activity in a wide range of salinities (Hurd et al. 1979; Bishop 1983; Tucker et al. 1995; Spivey 1998). Hatchling and juvenile terrapins, which were not encountered during this study, have more restricted salinity requirements (Dunson 1985). Dunson (1985) found that terrapins raised in 25% seawater grew considerably faster than hatchlings raised in either freshwater or 50% seawater, and hatchlings raised in 100% seawater did not grow.
My analysis of terrapin abundance within Ashley River, Charleston Harbor and Wando River sampling locations did not indicate that channel depth, river width, distance to the nearest creek, nesting habitat or developed area significantly affected terrapin distribution. Palmer and Cordes (1988) identified tidal creeks as critical feeding habitat. The gentle slope of marshes in the Ashley River, Charleston Harbor and Wando River offer feeding habitat on the banks of these areas as well as in the creeks. As stated previously, terrapin distribution with respect to feeding is likely determined by the patchy distribution of prey within salt marshes. Although nest site selection varies geographically, female terrapins typically nest in areas above the high tide line in coastal upland habitat, characterized by sandy substrate with shrubs and grass (Palmer and Cordes 1988). Suitable nesting habitats were identified throughout the Charleston Harbor estuarine system. However, evidence presented by Hurd et al. (1979) suggests that female terrapins may travel great distances to nest rather than utilize the closest available nesting habitat. Hurd et al. (1979) found a female terrapin nesting 8 km away from her initial point of capture. Furthermore, my analysis did not reveal that terrapins were repelled by developed or disturbed areas. In fact, some of the closest developed areas to the sampling locations in the Charleston Harbor estuarine system also provided the closest available nesting habitat. Female terrapins are being killed by cars with increasing frequency as they cross roads to and from nesting sites (personal observation). Unfortunately, as development continues to encroach on salt marshes in the Charleston area, nesting females will face increased danger during the nesting season.

The status and distribution of *M. terrapin* populations in South Carolina are accurately portrayed through the analysis of Inshore Fisheries incidental catch data for
several reasons: 1) the sampling effort remained consistent over these four years, 2) the
gear remained constant, and 3) sampling locations within sites remained the same and
were randomly chosen each month. Consistent sampling effort and gear ensured that
trends in terrapin captures indicated the true status of *M. terrapin* populations. Random
selection of sampling locations allowed inferences about the distribution of terrapin
populations throughout these five major regions, and minimized the possibility of
confounding variables. These factors are vital in obtaining a realistic indication of the
status of *M. terrapin* populations. Inconsistencies in sampling strategies can lead to
incorrect assumptions about terrapin populations, which may translate into poor
management decisions.

**Role of Malaclemys terrapin in Salt Marsh Food Webs**

The exclusion study I conducted provided evidence that *M. terrapin* is an
important predator of *L. irrerata* in South Carolina salt marshes, but I did not find
evidence that male and female terrapins consumed different sizes of snails. This outcome
does not refute the findings of Tucker et al. (1995) who reported resource partitioning
among the sexes and size classes of *M. terrapin*; instead, it likely results from cage
avoidance by all *M. terrapin*.

I designed the exclusion cages to allow access to all known periwinkle predators
smaller than *M. terrapin* so any differences in *L. irrerata* density between controls and
treatments could be attributed only to predation by *M. terrapin*. Holes in the mesh
allowed access to crabs and fish, and birds could enter the cages because the tops were
open. Other predators of salt marsh periwinkles include blue crabs (*Callinectes sapidus*)
(Hamilton 1976; Baxter 1983; Stanhope et al., 1982), clapper rails (*Rallus longirostris*)
(Heard 1952), and oystercatchers (*Haemotopus ostralegus*) (Boates and Goss-Custard,
1992). These species are present throughout South Carolina. However, I never observed
oystercatchers in my study area and clapper rails were limited to the high marsh; my
experimental plots were in low marsh, an area with a longer period of tidal inundation,
and therefore more accessible to aquatic predators.

Blue crabs are conspicuous aquatic predators in the salt marsh, and were the
predators most likely to share the same feeding habitat as *M. terrapin* in my study area.
Hamilton (1976) reported that only 30% of the crabs he dissected on the Gulf Coast of
Florida had more than one *L. irrorata* operculum in their cardiac stomach. He further
noted that while a small percentage of crabs were heavily involved in periwinkle
predation, other crabs did not consume any periwinkles. Baxter (1983) claimed that *C.
sapidus* was the primary predator of *L. irrorata* in North Carolina salt marshes.
However, these results were based only on laboratory observations of blue crabs
consuming *L. irrorata*, the only prey offered to the crabs. Baxter’s study did not provide
evidence that blue crabs preferentially consumed *L. irrorata* in the field. While blue
crabs prey on a wide variety of organisms (Darnell 1958; Tagatz 1968) and individuals
usually consume the most accessible prey (Tagatz 1968), terrapins have a specific diet
that consists primarily of gastropods (Tucker et al. 1995; Spivey 1998). For example,
Tucker et al. (1995) found opercula of *L. irrorata* in the feces of all 294 terrapins
included in a dietary study. Opercula and shell fragments of *L. irrorata* comprised the
majority of fecal material I sampled from 32 terrapins from the Wando River (personal
observation, unpublished data).
Tucker et al. (1995) found that different sexes and size classes of *M. terrapin* consumed different sizes of *L. irrorata*. I designed the terrapin and blue crab inclusion experiment to estimate the differential effect of male and female terrapins on the *L. irrorata* population, and to compare terrapins’ per capita consumption to those of blue crabs. My results did not show *M. terrapin* or *C. sapidus* significantly reduced periwinkle densities. Although the densities of *L. irrorata* did not differ significantly among treatments, these results may be artifacts of Hurricane Floyd, which hit the coast of South Carolina in the midst of this experiment. Tidal amplitude during the storm was 1-2 m greater than normal; water washed over and carried a considerable amount of debris into the cages. Debris accumulated on cage walls collapsed them in some places, rendering them ineffective at retaining predators even after the storm waters subsided. I did not recover any blue crabs or terrapins from this experiment, and it is likely that they escaped during this storm event. This experiment should be repeated to confirm the results of the exclusion experiment, and to resolve current salt marsh food webs that ignore *M. terrapin* as an important consumer of *L. irrorata*.

**Population Dynamics of Malaclemys terrapin in South Carolina Salt Marshes**

I could not estimate the population size of *M. terrapin* in the Wando River estuary because no terrapins were recaptured during the mark/recapture study in the spring of 1999. It is unlikely that terrapins were negatively affected by the marking procedure. This method was used successfully in other studies to monitor populations and to identify individuals over long periods of time (Marganoff 1970; Morreale 1992; Tucker et al. 1995). It is more likely that the terrapin population is very large, or that marked animals
learned to avoid recapture in the trammel net. In spring 2000, one year after the mark/recapture study, two marked terrapins were recaptured in the Wando River in the same sites in which they were initially captured. Although the density of the Wando River terrapin population could not be determined from only two recaptures, the recaptures validated the permanence of the marks. Since both recaptured terrapins were found in the exact sites they were initially captured, the recaptures present additional evidence of site fidelity. Lovich and Gibbons (1990) have also reported site fidelity in a Kiawah Island, SC population of terrapins.

The plastron lengths, head widths and masses of male and female terrapins from the Wando River are similar to those of the Kiawah Island population of terrapins (Tucker et al. 1995). As in other population studies of *M. terrapin* (Coker 1906; Hurd et al. 1979; Lovich et al. 1991; Morreale 1992), only adults were captured in this study. While adult terrapins are conspicuous inhabitants of estuarine waters, juvenile terrapins are not found in the same habitat. Lovich et al. (1991) and Pitler (1985) suggested that juvenile *M. terrapin* reside in the high marsh, particularly under mats of vegetation. Groups of hatchling and juvenile terrapins have also been reported in high marsh habitat, sometimes near developed areas, in Charleston, SC (personal observation; Larry Goss, personal communication; Rebecca Yeomans, personal communication).

The male-biased sex ratio likely indicates that the terrapin population in the Wando River is healthy. Assuming a 1:1 sex ratio at hatching, male terrapins reach maturity earlier than females, and therefore are recruited into the adult population faster. Lovich and Gibbons (1990) attributed an uneven sex ratio in adult *M. terrapin* to this phenomenon. While a male-biased sex ratio may indicate a healthy population, a drastic
increase could indicate increased female mortality. Females are likely to face increased mortality while crossing roads to reach nesting habitat in areas that are being developed, and are vulnerable to predators such as raccoons. Alternatively, a female biased sex ratio would indicate increased male mortality, such as from drowning in crab pots, which they enter more readily than females. Reversals and/or sudden changes in sex ratios may provide advanced warning of declining populations.

Sex ratio estimates for other populations of *M. terrapin* have varied from strongly male biased to strongly female biased. Seigel (1984) reported female-biased sex ratios (0.10 and 0.11) for terrapin populations in the Indian and Banana Rivers in Florida; and population estimates were 404.7 and 212.5, respectively. When these populations were surveyed in 1992-1993, only 4-6 terrapins were found in the Indian River and just one in the Banana River. Bishop (1983) reported a 2.27:1 sex ratio for the Ashley and Wando Rivers, and I found a sex ratio of 3.14:1 for the Wando River. While I cannot estimate terrapin population sizes for these areas, the relative abundance data suggest that terrapin populations in South Carolina are stable. The stability of terrapin populations in the Charleston area (which exhibit a male-biased sex ratio), and the decline of the Florida populations (which exhibited a strongly female-biased sex ratio) suggest that monitoring sex ratios may give an early indication of population declines.
CONCLUSION

The diamondback terrapin (*Malaclemys terrapin*) is a conspicuous predator in South Carolina salt marshes, where they occur in dense local populations. Commercial and recreational crabbing and rapid coastal development threaten terrapin populations in South Carolina. Male terrapins are especially vulnerable to drowning in crab pots (Bishop 1983; Hoyle 1998; Roosenburg et al. 1997). Nesting females and dispersing hatchlings are placed at risk due to development, which is encroaching on high marsh habitat. Continued collection of data on the distribution, abundance and sex ratio of terrapins will provide the scientific evidence needed for wise management decisions.

To devise effective management plans, stage and sex-specific mortality rates within terrapin populations should be quantified. However, it is extremely difficult to directly determine the cause of terrapin mortality. Terrapins that drown in crab pots are usually not reported by commercial or recreational crabbers, and nesting female terrapins killed by cars often go unnoticed. Examining sex ratios of populations with differing vulnerabilities to various methods of “harvest” can be an effective method for monitoring changes within populations and determining the harvest methods most detrimental to the population (Paloheimo and Fraser 1981; Harris and Metzgar 1987). Once anthropogenic sources of terrapin mortality are quantified, management plans must be developed to protect local populations. Without such plans, South Carolina terrapin populations may
decline rapidly, as they have in other states. Populations in New Jersey, Maryland, North Carolina, Florida, Mississippi and Louisiana were identified as declining at the “Workshop on the Ecology, Status and Management of the Diamondback Terrapin” (Seigel and Gibbons 1994). However, only Massachusetts, which reported stable or increasing populations, ensured protection of *M. terrapin* through “Species of Special Concern” status.

Future investigations on the diet of *M. terrapin* in South Carolina will further understanding of terrapins’ role in salt marsh food webs. Such research will provide opportunities to monitor changes in the estuarine community, as coastal development continually challenges the community structure in these ecosystems.
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Figure 1. Nautical map showing the Inshore Fisheries (SCDNR) sampling areas. The Charleston Harbor estuarine system contains three sampling sites (Charleston Harbor, Ashley River, Wando River). The ACE Basin and Cape Romain are much larger in area than the other three sites.
Figure 2. Schematic of trammel net deployment. In each location, a trammel net (184 m long, 2 m deep, with 36 cm and 6 cm mesh) deployed by a Florida net boat (Tremblay®), was set parallel to *S. alterniflora* marsh in ≤2 m of water. The net was secured at each end by anchors, which enclosed an area between the net and marsh.
Figure 3. Nautical map showing locations of the terrapin exclusion and inclusion experiments. The exclusion experiment in the Wando River is depicted by three circles. The westernmost circle represents three blocks adjacent to Foster’s Creek, while the other two circles represent one block apiece. The three blocks of the inclusion experiment in Charleston Harbor are depicted by the square.
Figure 4. Schematic representation of experimental terrapin exclusion plot design, set in the Wando River Estuary, Charleston, SC. Solid lines indicate sides of the cages enclosed in mesh, while dotted lines indicate open sides. Each of five experimental blocks contained an unmanipulated and a manipulated control, and two treatments which either excluded all terrapins (treatment A) or only large, female terrapins (treatment B). Blocks were erected in the low marsh, in areas characterized by tall S. alterniflora.
Figure 5. Design of experimental exclusion cages. One side of the 16 m² cage is shown. The same cage design was used for the treatment, which excluded all terrapins (7.5 cm entrance holes) and the treatment, which excluded only large, female terrapins (11 cm entrance holes). Unmanipulated controls had two sides; one side had 7.5 cm diameter entrances and the other side had 11 cm diameter entrances. All cages used 0.31 cm (0.125 in) square mesh and 1.9 cm (0.75 in) PVC poles.
Figure 6. Schematic diagram of one block of the terrapin inclusion experiment in Charleston Harbor estuary, Charleston, SC. Solid lines indicate sides of the cages enclosed in mesh, while dotted lines indicate open sides. Each block contained an unmanipulated and manipulated (empty cage) control, and three treatments containing one female terrapin, one male terrapin, or two blue crabs. Treatments were randomly assigned to positions within spatial blocks, which were designed to minimize and account for spatial variation at the field site. Blocks were erected in the low marsh, in areas characterized by tall *S. alterniflora*. 
Figure 7. Top view of a terrapin inclusion cage. The disturbed area of the cage was not sampled because damage from foot traffic altered density of *Spartina alterniflora*. The sample area therefore was 12 m$^2$. Plastic containers were placed on the shoreward side of the cages to provide an aquatic refuge during low tide.
Figure 8. Alphabetical coding system used to assign a unique series of marks to the marginal scutes of terrapins. Each terrapin was marked on three separate scutes using a triangular file or a Dremel tool (the identification of the turtle pictured is AJP). The bridge scutes (D - H and Q - U) were eliminated from the marking system so to maintain the structural integrity of the shell. This system allowed for 364 unique marks (figure modified from Gibbons 1988).
Figure 9. Proportion of variation in terrapin captures attributable to month, site, month*site, year*month, location nested within site, and water temperature, as determined by multiple regression. Proportion of variation in terrapin captures attributable to year and salinity were not included on this chart because they did not explain a significant proportion of the variation. Data were collected by Inshore Fisheries section along the South Carolina coast, 1995 – 1998.
Partitioning the Variation
Model $R^2 = 0.326$

- Residual 67.4%
- Location (Site) 16.3%
- Water Temperature 0.2%
- Year*Month 1.6%
- Month*Site 2.9%
- Month 1.5%
- Site 1.1%
Figure 10. Mean number of *M. terrapin* (+/- 1 S.E.) caught per trammel net set by Inshore Fisheries (SCDNR) in different years and sites. The number of terrapins caught in different years did not change significantly. The five main study sites sampled were the Ashley River (AR\(\bigcirc\)), the Charleston Harbor (CH\(\blacksquare\)), the lower Wando River (LW\(\bullet\)), Cape Romain (CR\(\triangledown\)), and the Ace Basin (AB\(\blacktriangledown\)).
Figure 11. Mean number of *M. terrapin* (+/- 1 S.E.) caught per trammel net set during different months (circles depict the overall mean number of terrapins caught per trammel net set during each month, and bars show +/- 1 S.E.). Data collected by Inshore Fisheries (SCDNR) along the South Carolina coast, 1995 - 1998. Each square represents the mean number of *M. terrapin* caught in a particular year. The dashed line indicates the overall mean. The highest densities of terrapins occur in the spring during mating season.
Figure 12. Mean number of *M. terrapin* caught per trammel net set at different water temperatures. Data collected by Inshore Fisheries (SCDNR) along the South Carolina coast, 1995 – 1998. Mean number of *M. terrapin* = -2.8125 + 0.3554 water temperature (°C) - 0.0059 water temperature (°C)^2. The optimal water temperature for catching terrapins was approximately 23.4°C, which corresponds to water temperatures during the spring when terrapins were most abundant.
Figure 13. Mean number of *M. terrapin* caught per trammel net set at different salinities. Data collected by Inshore Fisheries (SCDNR) along the South Carolina coast, 1995 – 1998. Terrapin abundance could not be predicted by salinity, since they were captured from nearly fresh water to full strength seawater.
Figure 14. Mean density ( +/- 1 S.E.) of L. irrorata (number of snails/m²) by treatment in the terrapin exclusion experiment conducted in 1998 in the Wando River Estuary, Charleston, SC. Each square represents a mean from each treatment within a block. The dashed line is the overall mean. The density of snails in both of the exclusion treatments was greater than the density of snails in either of the controls, indicating that predator exclusion had a significant effect on snail density.
Figure 15. Mean length ( +/- 1 S.E.) of *L. irrorata* (mm) by treatment in the terrapin exclusion experiment conducted in 1998 in the Wando River Estuary, Charleston, SC.

Each square represents a mean from each treatment within a block. The dashed line is the overall mean. There was no significant difference in snail length between the controls and treatments.
Figure 16. Mean density (+/- 1 S.E.) of *S. alterniflora* (number of blades/m²) by treatment in the terrapin exclusion experiment conducted in 1998 in the Wando River Estuary, Charleston, SC. Each square represents a mean from each treatment within a block. The dashed line is the overall mean. There were no significant differences in *S. alterniflora* density among treatments.
Figure 17. Mean density (± 1 S. E.) of *L. irrorata* (number of snails/m²) by treatment in the terrapin inclusion experiment conducted in 1999 in the Charleston Harbor Estuary, Charleston, SC. Each square represents a mean from each treatment within a block. The dashed line is the overall mean. There were no significant differences in snail density among treatments. However, the experiment did not run as long as planned due to cage overwash caused by Hurricane Floyd.
Figure 18. Mean length of L. irrorata (mm) by treatment in the terrapin inclusion experiment conducted in 1999 in the Charleston Harbor Estuary, Charleston, SC. Each square represents a mean from each treatment within a block. Block 1 was eliminated from the analysis due to missing values. The dashed line is the overall mean. Snail length did not differ significantly among treatments (Friedman's method for randomized block designs).
Mean length of Littorina (mm)

Manipulated control

Blue crabs

Male terrapins

Female terrapins

Treatment
Figure 19. Mean density (+/- 1 S.E.) of *S. alterniflora* (number of blades/m$^2$) in the terrapin inclusion experiment conducted in 1999 in the Charleston Harbor Estuary, Charleston, SC. Each square represents a mean from each treatment within a block. The dashed line is the overall mean. There were no significant differences in *S. alterniflora* density among treatments.
Table 1. Results of the statistical model designed to explain the distribution of *M. terrapin* in South Carolina estuaries. Significant sources of variation were month, site, month*site, year*month, location nested within site and water temperature. Year was not a significant effect, which indicates that the terrapin population remained stable over the four years of the study. Salinity was not a significant effect either, since terrapins were captured in near freshwater to full strength seawater.
<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Year</td>
<td>3</td>
<td>47.325</td>
<td>1.139</td>
<td>0.3320</td>
</tr>
<tr>
<td>Month</td>
<td>8</td>
<td>657.888</td>
<td>5.936</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Site</td>
<td>4</td>
<td>486.921</td>
<td>8.787</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Month*Site</td>
<td>32</td>
<td>1287.527</td>
<td>2.904</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Year*Month</td>
<td>24</td>
<td>707.356</td>
<td>2.128</td>
<td>0.0011</td>
</tr>
<tr>
<td>Location (Site)</td>
<td>282</td>
<td>7256.755</td>
<td>1.858</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Water temperature</td>
<td>1</td>
<td>81.7266</td>
<td>5.900</td>
<td>0.0152</td>
</tr>
<tr>
<td>Salinity</td>
<td>1</td>
<td>0.1311</td>
<td>0.0095</td>
<td>0.9225</td>
</tr>
<tr>
<td>Error</td>
<td>2166</td>
<td>30,005.576</td>
<td>0.0095</td>
<td>0.9225</td>
</tr>
<tr>
<td>Total</td>
<td>2521</td>
<td>44,542.525</td>
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</tr>
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</table>
Table 2. Results of the statistical model designed to further explain terrapin distribution in the Charleston Harbor estuarine system (Charleston Harbor, Ashley River and Wando River). The mean number of terrapins/trammel net set did not differ significantly due to site, channel depth, river width or distances to the nearest creek, nesting habitat or developed area.
<table>
<thead>
<tr>
<th>Source</th>
<th>Site</th>
<th>Channel depth</th>
<th>River width</th>
<th>Distance to the nearest creek</th>
<th>Distance to the nearest suitable nesting habitat</th>
<th>Distance to the nearest developed area</th>
<th>Error</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>df</td>
<td>2</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>1</td>
<td>22</td>
<td>29</td>
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<tr>
<td>SS</td>
<td>12.261</td>
<td>0.583</td>
<td>0.216</td>
<td>0.001</td>
<td>0.4882</td>
<td>0.4012</td>
<td>0.8387</td>
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</tr>
<tr>
<td>P</td>
<td>0.5665</td>
<td>0.6467</td>
<td>0.9824</td>
<td>0.4882</td>
<td>0.4012</td>
<td>0.8387</td>
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<td></td>
</tr>
</tbody>
</table>
Table 3. Results of two-way analysis of variance on the density of *L. irrorata* (number of snails/m²) in the terrapin exclusion experiment. The blocks accounted for more variation in the density of *L. irrorata* than the treatments explained, probably because of natural patchiness in prey distribution.
<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>3</td>
<td>249.900</td>
<td>8.280</td>
<td>0.0030</td>
</tr>
<tr>
<td>Block</td>
<td>4</td>
<td>1682.675</td>
<td>41.814</td>
<td>&lt;0.0001</td>
</tr>
<tr>
<td>Error</td>
<td>12</td>
<td>120.725</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>19</td>
<td>2053.300</td>
<td></td>
<td></td>
</tr>
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</table>
Table 4. Results of two-way analysis of variance on the mean length of *L. irrorata* (mm) in the terrapin exclusion experiment. Lengths of *L. irrorata* did not differ significantly among treatments, but did differ significantly among blocks.
<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>3</td>
<td>4.299</td>
<td>1.285</td>
<td>0.3279</td>
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<tr>
<td>Block</td>
<td>4</td>
<td>15.892</td>
<td>3.562</td>
<td>0.0425</td>
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<tr>
<td>Error</td>
<td>11</td>
<td>12.269</td>
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<td></td>
</tr>
<tr>
<td>Total</td>
<td>18</td>
<td>33.518</td>
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</table>
Table 5. Results of two-way analysis of variance on the density of *S. alterniflora* (number of blades/m²) in the terrapin exclusion experiment. The density of *S. alterniflora* blades did not differ significantly among treatments or blocks.
<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>3</td>
<td>2662.400</td>
<td>0.349</td>
<td>0.7904</td>
</tr>
<tr>
<td>Block</td>
<td>4</td>
<td>8320.000</td>
<td>0.819</td>
<td>0.5375</td>
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<tr>
<td>Error</td>
<td>12</td>
<td>30,489.600</td>
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<tr>
<td>Total</td>
<td>19</td>
<td>41,472.000</td>
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</table>
Table 6. Results of two-way analysis of variance on the density of *L. irrorata* (number of snails/m²) in the terrapin inclusion experiment. The density of *L. irrorata* did not differ significantly among treatments or blocks.
<table>
<thead>
<tr>
<th>Source</th>
<th>df</th>
<th>SS</th>
<th>F</th>
<th>P</th>
</tr>
</thead>
<tbody>
<tr>
<td>Treatment</td>
<td>2</td>
<td>2214.400</td>
<td>1.2628</td>
<td>0.3597</td>
</tr>
<tr>
<td>Block</td>
<td>4</td>
<td>1538.133</td>
<td>1.7543</td>
<td>0.2335</td>
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<tr>
<td>Error</td>
<td>8</td>
<td>3507.200</td>
<td></td>
<td></td>
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<tr>
<td>Total</td>
<td>14</td>
<td>7259.733</td>
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</table>
Table 8. Mean head widths, plastron lengths, carapace widths, and masses of male and female terrapins in the Wando and Kiawah Rivers, S
<table>
<thead>
<tr>
<th></th>
<th>Head width (mm)</th>
<th>Plastron length (cm)</th>
<th>Carapace width (mm)</th>
<th>Mass (g)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Males</strong></td>
<td></td>
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<tr>
<td>This study</td>
<td>22.0</td>
<td>10.1</td>
<td>89.8</td>
<td>279</td>
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<td>Kiawah study</td>
<td>17.6</td>
<td>10.2</td>
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<td>242</td>
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<tr>
<td><strong>Females</strong></td>
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<td></td>
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<td></td>
</tr>
<tr>
<td>This study</td>
<td>32.9</td>
<td>14.1</td>
<td>117.7</td>
<td>775</td>
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<tr>
<td>Kiawah study</td>
<td>28.9</td>
<td>14.8</td>
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<td>705</td>
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Table 9. Comparison of ages and sex ratios among this and previous studies of *M. terrapin*.
<table>
<thead>
<tr>
<th>Reference</th>
<th>Location</th>
<th>M:F</th>
<th>Age</th>
<th>Gear Type</th>
<th>Status</th>
</tr>
</thead>
<tbody>
<tr>
<td>This study</td>
<td>Wando River, SC</td>
<td>3.14</td>
<td>3 - 7</td>
<td>Males 5 - 10+ Females 5 - 10+ Trammel nets</td>
<td>Stable</td>
</tr>
<tr>
<td>Spivey (1998)</td>
<td>North Carolina</td>
<td>0.69</td>
<td>5 - 9</td>
<td>Females 5 - 14 Trammel and gill nets, nesting and basking surveys</td>
<td>Not reported</td>
</tr>
<tr>
<td>Morreale (1992)</td>
<td>Long Island, NY</td>
<td>0.69</td>
<td>3 - 10</td>
<td>Females 3 - 10+ Trammel and seine nets, hoop traps, otter trawl, nesting surveys, snorkeling, SCUBA</td>
<td>Stable</td>
</tr>
<tr>
<td>Lovich and Gibbons (1990)</td>
<td>Kiawah River, SC</td>
<td>1.78</td>
<td>3 - 12</td>
<td>Females 3 - 15 Trammel and seine nets</td>
<td>Unknown</td>
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<tr>
<td>Seigel (1984)</td>
<td>Indian River, FL</td>
<td>0.10</td>
<td>&lt;1 - 4</td>
<td>Females &lt;1 - 7 Gill nets, nesting and basking surveys</td>
<td>Declining</td>
</tr>
<tr>
<td></td>
<td>Banana River, FL</td>
<td>0.11</td>
<td></td>
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</tr>
<tr>
<td>Bishop (1983)</td>
<td>Ashley &amp; Wando</td>
<td>2.27</td>
<td>Not given</td>
<td>Crab pots</td>
<td>Not reported</td>
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<tr>
<td></td>
<td>River, SC</td>
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<tr>
<td>Hurd et al. (1979)</td>
<td>Delaware</td>
<td>0.75</td>
<td>Not given</td>
<td>Females Otter trawl</td>
<td>Not reported</td>
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<tr>
<td></td>
<td></td>
<td>(1975)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>1.22</td>
<td>(1976)</td>
<td></td>
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</tr>
<tr>
<td>Marganoff (1970)</td>
<td>Long Island, NY</td>
<td>0.93</td>
<td>4 - 10+</td>
<td>Males 4 - 10+ Females 4 - 10+ Stop nets, dip nets, nesting surveys</td>
<td>Declining</td>
</tr>
<tr>
<td>Cagle (1952)</td>
<td>Louisiana</td>
<td>4.38</td>
<td>&lt;1 - 6</td>
<td>Females &lt;1 - 6 Not given</td>
<td>Not reported</td>
</tr>
</tbody>
</table>