SEASONAL MOVEMENT AND HABITAT USE PATTERNS OF A DIAMONDBACK TERRAPIN (MALACLEMYS TERRAPIN) POPULATION

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ABSTRACT

The diamondback terrapin, *Malaclemys terrapin*, is unique among turtles as a long-lived, exclusively estuarine species that may demonstrate high site fidelity and high densities. These characteristics contribute to their usefulness as an indicator species for estuarine environmental health. Unfortunately, these traits also make this species vulnerable to habitat alterations. The status of terrapin populations in South Carolina is currently unknown.

Automated acoustic telemetry, manual radio telemetry, visual census, and mark-recapture methods were used to document temporal and spatial distributions and activity patterns of terrapins in Grice Cove, Charleston Harbor, South Carolina. From September 2002 through December 2003, automated acoustic receivers continuously monitored habitat types known to be important to terrapins: shallow water adjacent to a rocky seawall, mudflat, tidal creek, and a sandy beach where females have been observed nesting. In situ receivers recorded the presence of 12 tagged adult female diamondback terrapins in each habitat type.

The majority of detections of terrapins in the creek occurred during July and August, during the foraging period. Tagged females were detected in the water near the nesting beach from April-July. They were detected near the rocky shore in April-July and in October-November, when large aggregations of individuals and mounted pairs were observed in this area. In the mudflat, activity peaked in April and September.
However, habitat use was highly variable between individuals. Temporal movement patterns were tidally influenced. Terrapins were detected every hour of the day, especially late evening through early morning. Although they were not detected in the cove year round, most exhibited high site affinity by repeatedly returning to the study area over a long period. Sonic tagged females appeared to display two general residency patterns: females caught in the fall were more consistent residents than those caught in the spring, who may only visit the cove to mate and nest. Automated sonic telemetry proved to be an efficient tool to collect nearly constant movement data on multiple terrapins simultaneously, adding to our understanding of terrapin behavior.

Aggregations of individual and paired male and female terrapins observed in a small area of the cove during the spring seem to fit the criteria of a turtle lek. Like the marine iguana (*Amblyrhynchus cristatus*), the only known lekking reptile, male terrapins aggregated in the same area during three consecutive years. They were sighted at the aggregation site before females, and females left first. The aggregation area does not offer females useful resources such as food. The importance of female mate choice in the definition of a lek is highly debated, but it is possible that female terrapins distinguish between individual males by their unique shell and skin coloration. An aggregation of mating adult terrapins would be extremely vulnerable and should be well understood in order to effectively conserve this species.
INTRODUCTION

Ecology of Malaclemys terrapin

The diamondback terrapin, *Malaclemys terrapin*, is an important component of estuarine ecosystems along the Atlantic and Gulf of Mexico coasts of North America. Diamondback terrapins are small- to medium-sized turtles that exhibit strong sexual dimorphism. Females are significantly larger (10.0-22.1 cm carapace length) than males (7.5-12.2 cm carapace length) at reproductive maturity. Females also have larger, broader heads, thicker bodies, and shorter tails than males (Ernst *et al.*, 1994). Due to this dimorphism, adult male and female feeding niches overlap minimally (Tucker *et al.*, 1995). Males and small females of South Carolina populations forage on the small to medium salt marsh periwinkle, *Littorina irrorata*, while larger females feed on larger *L. irrorata*, fiddler crabs (*Uca pugnax*) and blue crabs (*Callinectes sapidus*) (Tucker *et al.*, 1995; Levesque, 2000). The foraging period lasts from shortly after emergence in early spring until early October (Hildebrand, 1929). Terrapins have distinct color patterns on their shells and skin. Carapace and plastron colors range from pale green and yellow to black and may have dark concentric rings or spots (Figure 1). Another distinguishing trait of terrapins is the large size of their hind feet in proportion to their bodies. This adaptation affords them greater mobility in strong tidal currents and undertows common in estuaries (Ernst *et al.*, 1994). Terrapins are long-lived, surviving up to forty years in captivity (Hildebrand, 1932).
Malaclemys terrapin is unique among chelonians in that it is the only exclusively brackish-water species in North America (Wood, 1977). This species inhabits coastal salt marshes, estuaries, and tidal creeks (Ernst et al., 1994). Diamondback terrapins occupy an extensive geographic range that encompasses the Atlantic and Gulf of Mexico coasts of the United States from Cape Cod, Massachusetts through Corpus Christi, Texas, including the Florida Keys (Seigel, 1984). This extensive latitudinal range may be attributed, in part, to the euryhaline nature of the species, another unique characteristic among chelonians. Diamondback terrapins can tolerate water salinities ranging from 0 to 34 ppt (Robinson and Dunson, 1976). However, in salinities above 21 ppt, terrapins are said to require a source of freshwater (Dunson and Mazzoti, 1989).

Malaclemys terrapin exhibits geographic variation throughout its range, which has prompted the description of seven subspecies. M. t. centrata, the Carolina diamondback terrapin, inhabits South Carolina and ranges from Cape Hatteras to northern Florida (Ernst et al., 1994). The geographic variation among these subspecies is not well defined. Analysis of mitochondrial DNA indicates very low divergence levels among subspecies; however populations along the Atlantic Coast are genetically different from those along the Gulf Coast (Lamb and Avise, 1992). In South Carolina, Hauswalt and Glenn (2005) analyzed microsatellite loci of terrapin populations and found no evidence for population genetic structuring within the Charleston Harbor or among other estuaries.

Due to the broad latitudinal distribution of M. terrapin, the annual activity cycle of this species varies among areas (Hildebrand, 1929; Yearicks et al., 1981; Ernst et al., 1994). Terrapins hibernate throughout much of the winter in the relatively open waters of marsh creeks. Hibernating terrapins have been found buried in creek banks or in
natural depressions along creek bottoms as solitary individuals or in groups. Terrapins will emerge temporarily on particularly warm days (Yearicks et al., 1981). In South Carolina, *M. t. centrata* are typically active from March thru November, and hibernate from December through February (Ernst et al., 1994; Lee, 2003).

*Mating Behavior of M. terrapin and Lekking Species*

Courtship and mating occur in early spring, shortly after emergence from hibernation, and are followed by nesting in late spring (Seigel, 1980; Zimmerman, 1992). There has been one documented observation of a terrapin mating aggregation in the field. Seigel (1980) observed groups of 6-75 male and female turtles in Florida during the spring. Residents near Seigel’s study area reported seeing up to 250 individuals within a 200 m² area, a density of 1.25 turtles per m² (Seigel, 1980). Mating in this aggregation occurred at the water surface during daylight, with the male mounted on the carapace of the female. Seigel (1980) reported that in Florida mating lasted from late March, more than one month after emergence, to April and only during late morning through late afternoon. Seigel stated that his observations were made as a brief side project and did not discuss the ratio of males to females in the aggregation or a possible relationship between tidal stage and this behavior. Greater knowledge of terrapin mating behavior is necessary to form sound management decisions to ensure the stability of this species.

Preliminary observations of terrapin aggregations in Grice Cove during the 2001 and 2002 spring seasons suggested that this population has a mating system similar to lek polygyny (David Owens, personal communication; personal observation). A lek mating system is characterized by an aggregation of males who defend small territories in which the males themselves are the only useful resources available to females. Females visit the
territories, which are tightly clustered in a traditional display area (the lek), for the sole purpose of mating. Females then leave to nest, without any additional parental investment from males (Willey, 1991). Although lek formation is most common in birds and insects and has not yet been described in aquatic turtles (Höglund and Alatalo, 1995; Jiguet et al., 2000), lekking has been well documented in another aquatic reptile, the marine iguana, *Amblyrynchus cristatus* (Trillmich, 1983; Wikelski et al., 1996; Partecke et al., 2002). Partecke et al. (2002) observed male *A. cristatus* defending small, clustered mating territories which were established two months prior to the mating season and offer no resources to females besides mating. Female iguanas mated once during the season before traveling a considerable distance from the lek to nest. Males typically returned to the same lek area in subsequent years (Partecke et al., 2002). Because the lek area offered no material resources, these authors suggested that the driving force behind the formation of such aggregations by male iguanas was to take advantage of the attractiveness of their neighbors. This is consistent with the hotshot model in which a female chooses a male based on his physical quality rather than the quality of another resource in his territory. By association, males near the popular ‘hotshot’ male have improved mating success (Partecke et al., 2002; Wikelski et al., 1996).

Like the marine iguana, terrapins in Grice Cove and in Florida (Seigel, 1980) form dense aggregations during spring months. For two consecutive spring mating seasons (2001 and 2002), a large group of male and female terrapins have been observed as mounted pairs in Grice Cove. This group was found in an area that does not appear to contain useful resources, such as *L. irrorata* (personal observation). One Grice female was captured on the nesting beach in spring 2001 with eggs. When she was recaptured
the following spring in the Grice Cove aggregation area, she possessed large follicles, but not eggs. This suggested that she was at an appropriate stage for mating and this Grice Cove site may be a mating aggregation area that appears to form yearly. These aggregations resembled a lek, so one goal of this study is to determine if this Grice Cove terrapin aggregation can be appropriately described as a reptile lek.

**Site Fidelity and Movements**

In addition to aggregating in certain areas, a limited number of studies have shown that terrapins also exhibit high annual fidelity to individual home ranges year after year (Hurd *et al.*, 1979; Spivey, 1998; Gibbons *et al.*, 2001). Gibbons *et al.* (2001) conducted a mark-recapture study over many years in a series of tidal creeks around Kiawah Island, South Carolina. In one small creek, approximately 1 km long, they recaptured 198 of 205 tagged terrapins during subsequent years. The majority of these terrapins were repeatedly recaptured up to nine consecutive years in the same creek. Many of these recaptures were within 100 m of the original capture site. This is a strong indication that terrapins have high fidelity to one particular creek. Similarly, Hurd *et al.* (1979) had a 26% recapture rate of terrapins in a short (<1 km) creek in Delaware. Radio-tagged terrapins in North Carolina had an average home range size of 257.7 ha (Spivey, 1998). Their home ranges included low marsh that frequently flood rather than open water or high marsh habitats. Females also exhibit fidelity to nesting beaches. Roosenburg (1990) found that terrapins in the Chesapeake Bay lay up to three clutches per year on the same beach and return to that beach in following years. Some degree of site fidelity has also been reported in the Florida red-bellied turtle, *Pseudemys nelsoni*,
(Kramer, 1995) and the alligator snapping turtle, *Macrolemys temminckii*, (Harrel et al., 1995) which remain in, or repeatedly return to, the same home ranges.

In contrast, some female terrapins have been reported to travel substantial distances to locate suitable nesting beaches. Hurd et al. (1979) recaptured a nesting female 8 km from her original home range. Another female terrapin near the Kiawah River, South Carolina reportedly made a 5.5 km roundtrip nesting migration (Gibbons et al., 2001). Therefore, an understanding of long distance migrations, as well as small scale movements made by terrapins, are equally important for devising an effective management plan for this species.

Preliminary observations, suggest a seasonal shift in habitat use by terrapins in Grice Cove, South Carolina. This small cove, approximately 30 ha, is adjacent to Charleston Harbor and contains apparent mating and foraging areas and a nesting beach.

To date, site fidelity of diamondback terrapins has only been addressed through mark-recapture or radio tracking studies. These studies give an incomplete picture of terrapin site fidelity and habitat use because it is impossible to know where the turtles are between locations of release and recapture or direct observation. Only by continuously tracking individuals can we more confidently state their degree of site fidelity and gain insight into their use of habitats on annual, daily, and hourly scales. Continuous or automated acoustic tracking has been used recently to study movement patterns and habitat use behavior of numerous fish species (Arnold and Dewar, 2000 for a review; Heupel and Hueter, 2000; Ohta et al., 2000; Arendt et al., 2001; Comeau et al., 2002; and Simpfendorfer et al., 2002). To assess the feasibility of using similar automated acoustic tracking techniques for continuous long-term monitoring of terrapins in Grice Cove, we
did a pilot radio tracking study of adult females caught in the cove. Although these observations were preliminary, they suggest this to be a resident population in Grice Cove, making it a suitable population for the study of movements, habitat use, and site fidelity of terrapins. Although various species of terrestrial, freshwater, and marine turtles have been tracked with radio, sonic, and satellite systems (Schubauer et al., 1990; Nieuwolt, 1996; McMaster and Herman, 2000; Schroeder et al., 2003) this will be the first time an automated, acoustic system is used to track turtles almost continuously.

The status of many terrapin populations is currently unknown and in many areas their numbers are declining due in large part to anthropogenic activities. Diamondback terrapins were once abundant in these habitats and supported a significant commercial fishery until the early 1900’s, when the species was nearly eliminated from most of its range due to over exploitation. Consequently, in 1902, the U.S. Bureau of Fisheries, then known as the U.S. Fish Commission, initiated studies in the Chesapeake Bay to determine the feasibility of propagating terrapins in captivity. Simultaneously, the U.S. Fisheries Biological Station in Beaufort, North Carolina conducted studies focused on behavior and life history of captive terrapins (Hildebrand, 1929).

Terrapin populations appear to have recovered somewhat since the early part of the last century, but the current status of *M. terrapin* populations is still in dispute. In 2003, the International Union for Conservation of Nature and Natural Resources (IUCN), listed terrapins as a lower risk/near threatened species in North America, which almost qualifies it for vulnerable status. Prior to 2000, there was a legal harvest season for terrapins in South Carolina that had not been active since the mid-1970s. A rewrite of South Carolina coastal fisheries laws in 2000 eliminated the commercial harvest season
for terrapins. Since then the Department of Natural Resources has had authority to grant permits for harvesting and selling diamondback terrapins in South Carolina. However, there have been no requests for permits. Currently, permits will not be issued due to the uncertain status of South Carolina terrapin populations (Dale Theiling, South Carolina Department of Natural Resources, personal communication).

This is in sharp contrast to other states where populations are considered stable, increasing, or retain “game status,” such as in Delaware and Texas (Seigel and Gibbons, 1995). According to Seigel and Gibbons (1995), there is an urgent need for more thorough research on terrapins in order to responsibly manage this species. Although commercial harvesting of *M. terrapin* has been markedly reduced, drowning in commercial and recreational crab pots, habitat alteration, nest and hatchling predation, as well as vehicle and boat induced mortalities continue to threaten the viability of natural populations (Bishop, 1983; Roosenburg, 1990; Zimmerman, 1992; Seigel and Gibbons, 1995; Roosenburg *et al.*, 1997; Hoyle and Gibbons, 2000).

The objectives of this study were to determine (i) the degree of site fidelity of diamondback terrapins, (ii) the movements of adult females associated with reproductive activities, and (iii) if terrapins have a lek mating system by evaluating the habitat use patterns of females and males in the spring and summer. To accomplish these goals, mark-recapture, radio tracking, and sonic tracking methods were used to document habitat use on various scales, from annual through hourly and to understand how movement patterns relate to environmental conditions. Since this study employed multiple tracking methods, it was possible to evaluate the efficiency of automated sonic versus active radio tracking technology in studying terrapin movement patterns.
MATERIALS AND METHODS

Study Area: Grice Cove and Surrounding Habitats

Grice Cove is a small brackish cove, adjacent to the southeast side of the Charleston Harbor and just east of the Fort Johnson peninsula of James Island in Charleston, South Carolina (Figure 2). The western portion of the cove is bordered by large granitic rocks, which serve as a man-made seawall for the College of Charleston’s Grice Marine Laboratory, located directly behind the rocks. The rocks comprise approximately half of the western shoreline closest to the harbor (about 350 m) with two short rock outcrops 73 m apart (the “rocks” study site). During three previous spring seasons (2001-2003), a large aggregation of individual and paired terrapins have been observed in the water between these outcrops and up to approximately 60 m from shore. This suggests that the rocks study site is an important mating and possibly inter-nesting habitat. The southern half of the cove is a mudflat surrounded by Spartina alterniflora marsh grass. A tidal creek cuts through the marsh in the back, southeast corner of the cove and is referred to as the “creek” study site. The eastern shoreline is a sand beach (“beach” site) that extends out of Grice Cove along the harbor shore approximately 1350 m to an area behind the Fort Sumter National Monument.

Sonic receivers were also deployed in other habitats, similar to those found within the cove, for short periods in 2003 to attempt to locate sonic-tagged terrapins that may have moved from the cove, as well as to compare terrapin activity outside of the cove (Figure 3). These areas included two nearby tidal creeks similar in size and vegetation to
the creek in Grice Cove, one directly to the south ("south creek-east" and "south creek-west" sites) and one to the east ("east creek" site). During spring high tides the marsh separating these two creeks from the cove is inundated with water, introducing the possibility that at least twice a month, during these tides, the turtles could access adjacent creeks from Grice Cove. A small mudflat in the harbor just outside the cove on the opposite side of the Fort Johnson peninsula was also monitored for a short period ("harbor mudflat" site). A rock wall and Spartina marsh border this area. Like the mudflat in the cove, it drains during spring low tides. The eastern, harbor side of the beach was also included in the study area ("Fort Sumter beach" site). This section of the beach is closer to the harbor mouth and was subjected to stronger wave activity. It is bordered by a small Spartina marsh to the east where it is separated from Fort Sumter by a short (~150m) channel and a shallow sandbar. This sandbar is only exposed at low tide. 

Spartina alterniflora is the dominant vegetation around the creek and mudflat. Vegetation behind the beach includes the searocket (Cakile harperi) and other species that are extremely dense in areas. Aquatic vegetation includes Ulva sp. and brown algae.

The semi-diurnal tides have amplitudes of approximately 2 m. During spring low tides the cove almost completely drains except the area closest to the harbor. Very importantly, the creek in Grice Cove maintains a 1-2 m deep channel between exposed mud banks, even at low tide. During most high tides, water spreads into the Spartina marsh grass surrounding the creek, rising to within a few inches of the top of the grass during spring high tides. Thus, the area of aquatic habitat available to terrapins varies considerably through a tidal cycle.
Capture Methods and Measurements

With the help of the Inshore Fisheries Group of the South Carolina Department of Natural Resources, terrapins were captured in Grice Cove with a trammel net. Sampling occurred from May through August 2001; in April, August, and October 2002; and in April, June, and October 2003. Captures were attempted in areas of the cove with the highest density of terrapins visible at the surface. Sampling techniques were the same as those described in Levesque (2000) and Lee (2003). The net was deployed parallel to the shore and anchored at each end to enclose the area of water between the net and the shoreline. The boat was driven between the net and shore to disturb the water while workers pounded the water with wooden poles to startle the turtles into the net. To catch turtles in the creek, the net was also deployed along the middle of the longest stretch of water without enclosing either side. All sets were made during ebb tides. Nesting females were also caught by hand on the nesting beach during May and June 2003. The location and time of each capture was recorded.

Terrapins were transported to Grice Marine Laboratory in buckets filled with water. There they were weighed and measured (straight mid-carapace length and width, straight mid-plastron length, head width, tail base to cloaca and cloaca to tail tip). Sex was recorded based on sexual dimorphic traits and later verified by ultrasound. Females with straight carapace lengths >14.0 cm and males with straight carapace lengths >9.0 cm were considered sexually mature (Hildebrand 1932; Hurd et al. 1979). Age was estimated from the number of scute rings on the carapace. For future identification, each animal was marked with a unique series of three or four notches on the marginal scutes using a method adapted from Cagle (1939). Each marginal scute was assigned a letter (A-X) and
V-shaped notches were made in the outer edge of the appropriate scutes using a triangular file (Figure 4). Bridge scutes (E-G and R-T) were not notched out of concern that it might weaken the integrity of the shell. All animals were returned to the water alive.

**Ultrasound Examinations**

All captured terrapins underwent an ultrasound examination. Individuals were held inverted in a tub of water with their pelvic region submerged. The transducing probe was placed on the skin just anterior to the rear leg. Both sides were examined. The resulting images enabled us to verify the sex, reproductive maturity, and reproductive stage of the terrapins. Follicles and eggs of females, and testes of males, were measured from a calibrated display screen. Adult female terrapins were grouped into four stages based on the size of the largest follicles or the presence of eggs: 0 = no visible structures; 1 = follicles < 2.0 cm; 2 = follicles > 2.0 cm; or 3 = eggs (Lee, 2003). Male reproductive condition was described by two categories based on the presence (category 1) or lack (category 0) of visually distinct testes. Printed images of gonadal structures of each terrapin documented the examinations. Following measurements and ultrasound, terrapins that did not receive a sonic or radio transmitter were released at the capture site.

**Pilot Study: Radio Telemetry**

In May 2002, 10 adult female terrapins were captured in Grice Cove, measured and tagged with radio transmitters (41 mm x 28 mm x 11 mm with a 25 mm antenna; Telonics, Mesa, Arizona), and released. Radio tags were attached with 2-part epoxy resin and fiberglass strips on posterior costal scutes. They were monitored from June through September 2001, when their transmitter signals were no longer detected. Radio signals travel far more efficiently through air than water, so signals could only be detected when
terrapins were at or near the surface. A stationary double-Yagi antenna was used to
detect signals and the receiver displayed the frequency of the signal. It was placed on a
raised platform behind the southern end of the rock wall. The antenna was attached to a
steel pole on a wooden mast with a total height of 5 meters above the platform, allowing
for a reception range of up to 815 m across the marsh. The direction of a tagged
individual was determined by slowly rotating the antenna until a signal was detected and
then continuing to rotate the antenna in the same direction until the signal faded. In this
“null zone” the antenna was pointing directly at the tagged turtle and signals from the two
antennas were canceling each other out. To ensure that the signal had not faded because
the terrapin had submerged the antenna was rotated slight further in the same direction.
If the signal immediately commenced then the antenna had been pointed at a tagged
terrapin and the antenna was returned to that direction. The bearing of the location was
determined with a compass. The frequency of the signal was recorded from the radio
scanner to identify the tag and the time was recorded. If an individual was detected for a
period of time, the antenna was turned slightly so that the signal could be heard. If the
audible signal was interrupted by intermittent periods of silence, these time periods were
recorded to determine the surface and submersion periods.

_Ultrasonic Telemetry_

_Transmitter Attachment_

Sonic telemetry was used to evaluate site fidelity and document movements of
adult female terrapins within Grice Cove. V8SC-2L-256 coded acoustic transmitters
were used (20 mm x 9 mm, 4.7 g in air; VEMCO Ltd., Shad Bay, Nova Scotia, Canada).
They emit sonic waves that travel most efficiently through liquid. The transmitters emit a
69 kHz pulse sequence at random intervals between 60 and 180 s, resulting in a potential battery life of 799 days. Although the frequencies of sound detectable by terrapins are still unknown, it is likely to be similar to that of other aquatic turtles. Previous studies on freshwater and marine turtle species indicated that their underwater hearing range is limited to low-frequency sounds. Three freshwater species in the same family as *M. terrapin*, family Emydidae, are most sensitive to low tones, below 500-700 Hz, and show a sharp decline in sensitivity to sound above these frequencies (Wever and Vernon, 1956). Similarly, loggerhead (*Carretta carretta*) and green (*Chelonia mydas*) sea turtles are most sensitive to low-frequency sounds (250 and approximately 400 Hz, respectively) and only detect frequencies below 750 Hz (Ridgeway et al., 1969; and Bartol et al., 1999). Therefore, it is likely that the 69 kHz signal emitted by the transmitters is also well above the terrapin hearing range and will not influence their behavior.

Other animals found in the study area produce sounds of similar frequencies that may also be detected by the receivers. The bottlenose dolphin, *Tursiops truncatus*, produces sounds ranging from 0.8-130 kHz (Thomson and Richardson, 1995) and can detect frequencies between ~1-100 kHz (Richardson, 1995). The snaps of the snapping shrimp, *Alpheus heterochaelis*, range from tens of hertz to greater than 200 kHz (Versluis et al., 2000). Snapping shrimp snaps and dolphin vocalizations can register with receivers as detections with random 4-5-digit transmitter ID numbers (Dale Webber, VEMCO Ltd., personal communication). Such detections were considered false since they were not produced by transmitters and therefore, were not included in the analysis.

In order to track individuals who are most representative of adult female terrapins in this cove, randomly selected females collected from areas of the current greatest
population density were tagged. Transmitters were attached to two randomly selected adult females who were caught and later released in the creek in August 2002. Six females caught near the mudflat site were tagged and released in October 2002. Two females from the rocks site and three from the creek site were tagged and released in April 2003. Following measurements and ultrasound exams, sonic transmitters were attached to the top of the posterior marginals of the carapace. This ensured that transmitters remained underwater, where they can be detected, even when the turtles surface for air. Barnacles and debris were removed from their carapaces, which were then cleaned with alcohol. For the first two females tagged in August 2002, two small holes were drilled in the posterior edges of the marginal scutes. Transmitters were wrapped in dark canvas and sealed with super glue. These transmitter packages were attached to terrapins with durable, wax-coated sail thread tied through the drilled holes (Figure 5a). It was later determined that the canvas slightly dampened the signal so a new method was devised for subsequent attachments. In October 2002 and April 2003, tags were attached to the edge of a posterior marginal scute with a small (1.6 mm wide) cable tie (Gardner Bender©) threaded through a small hole in the scute, around the transmitter, and fastened below the scute edge (Figure 5b). Excess tie length was removed and the end was sanded smooth. The transmitter, cable tie, and underlying scute surface were covered with epoxy (3 ml resin: 12 drops hardener mixture tinted with black dye; Evercoat© Premium Marine Resin) to further secure the tag. Terrapins were held only long enough to allow the epoxy to dry (not longer than 24 hours). They were then released at the site of their capture.
The location and method of attachment was selected to avoid inhibiting the terrapins' normal movements. The transmitters were small (9 mm x 28 mm) and weighed <2% of the average adult female body weight. Neither method of attachment was expected to be permanent.

**Receiver Array and Tracking**

One VR1 and three VR2 single channel receivers (VEMCO, Ltd.) were stationed in Grice Cove to monitor tagged terrapins, almost continuously, for approximately 16 months (Figure 3). These receivers recorded transmitter ID number, time, and date of signal reception. Tagged terrapins were monitored in the study area from September 2002 through early December 2003. Receivers were stationed in the water at each of the study sites: the rocks, beach, creek, mudflat, upper creek, harbor mudflat, south creek-east and -west, and east creek sites according to the monitoring schedule in Figure 6.

In order to collect the most continuous data possible, the receiver must be high in the water column throughout most of the tidal cycle while remaining submerged. Keeping the receiver near the surface provided the greatest possible vertical area through which transmitter signals could travel while minimizing signal attenuation from turbulence near the sediment level. Maximizing vertical area for signal propagation while minimizing interference results in the greatest possible horizontal signal reception. To increase the buoyancy of the receiver, enabling it to float near the water surface, each receiver was attached, with two stainless steel bolts (13 x 0.5cm), to a 52.5 x 19 x 0.8 cm section of Plexiglas which was tied with rope at the top to a yellow crab pot float (Figure 7). Bolts from the receiver passed through the Plexiglas and attached to a PVC pipe (42 x 6 cm) on the backside. To accommodate changes in water level, a vertical galvanized
steel pole (4.5 m x 3.2 cm) was placed through the PVC pipe so the receiver and Plexiglas backboard floated along the pole. Each pole was embedded in the mud and was as tall as the water level during a spring high tide. The hydrophone of each receiver thus remained approximately 0.5 m below the surface, except during spring low tides when the receiver was exposed. The poles anchored the receiver while allowing it to move vertically with changes in water level.

Detection data were retrieved from receivers weekly while terrapins were most active and less often during the winter. Data were downloaded in the field by inserting a PC interface probe into the receivers and saving the data to a laptop computer.

Prior to mooring the receivers in their final positions, it was verified that each receiver was omni-directional in the field. The optimum reception ranges of transmitters were tested at each site within the cove and creek during high tide on calm days. A transmitter was submerged 0.5 m below the surface for at least two signal-cycles (6-10 min.). The transmitter was tested at 10-meter intervals in a direct line from the receiver until the signal was no longer detected. To determine the effect of tide height and wind speed on signal reception in the creek and cove, a test transmitter was attached to a rope and crab pot float and moored near the creek and mudflat receivers for multiple days. The rope (4.3 m x 1 cm) was looped through the hole in a crab pot float and anchored by either a 5 lb weight in the creek or a PVC pole at the mudflat. At both sites the transmitter remained approximately 5 m from the receiver and 15 cm below the water surface throughout the test periods. However, during low tides at the mudflat the transmitter was on the mud bottom. These continuous tests occurred in the creek from 1/29/04-2/6/04 (186 hours) and at the mudflat from 8/29/03-9/1/03 (73 hours).
Other tracking methods

Two methods were used to attempt to find hibernating terrapins in the cove. During a low tide in January 2002, sticks were used to probe the mud of exposed and submerged creek banks, a method successfully used by Yearicks et al. (1981). On two days in January 2003 a directional hydrophone and one VR2 receiver were used in the upper reaches of the creek and along the mouth of the cove, in an attempt to locate terrapins outside the range of the receiver array. From May to August 2003, the entire nesting beach was searched 3-4 times a week for tagged or marked females.

Visual Census of Aggregation

The size of the terrapin aggregation in the water off the rock seawall was estimated by almost daily counts of terrapins in this area throughout 2002 and 2003. When terrapins surface to breathe their heads are visible above the surface. Sex of an individual is easily discerned by the relative size of the head, males being noticeable smaller. Based on the observation that the average submersion time of radio-tagged terrapins was three minutes, censuses were done for five minutes to ensure that counts were as representative of the total number of individuals as possible while minimizing resampling of individuals. The numbers of single males and females, and paired males and females that surfaced in the area between the rock outcrops were counted for five minutes. Counts were made from the rock seawall. Terrapins were considered paired if a male and female were less than the average adult female terrapin body length apart. Mounted pairs were easily distinguished due to the constant distance between the pair of heads, with the male behind the female. Qualitative observations of cloud cover, wind strength and direction, and wave height were recorded during each census. Surveys of
other sites in the cove and nearby areas were conducted approximately weekly in the spring and summer and at least every two weeks in the fall and winter in search of similar aggregations or pairs.

Data Analysis

To determine if there is a pattern in terrapin activity through time, combined total hourly detections of all tagged animals were analyzed with Fourier analysis. Fourier analysis, or harmonic analysis, describes a complex cycle or wave, which in this case occurs in a time series, by determining the frequencies and amplitudes of the constituent waves that sum to the complex wave (Bloomfield, 1976). Periodicity was found by dividing the total number of hours used in the analysis by the number of cycles in the time series. For example, 330 cycles during 4096 consecutive hours of observations occur with a periodicity of 12.4 hours. The dominant periodicities in the time series are the cycles with the greatest amplitudes, and were illustrated by plotting amplitude against the number of cycles per day.
RESULTS

Morphometrics

From May 2001-June 2004, 130 terrapins were captured for this study either by trammel nets in Grice Cove or by hand on the Grice Cove beach: 64 females (55 mature, 9 immature) and 66 males (mature based on carapace and tail length or the presence of testes visible by ultrasound). Terrapins were sampled in the cove at the mudflat, rocks, beach, and creek (Figure 2). Physical characteristics of these sites are described in the Methods section. The majority of captures occurred from April through August, with some sampling in October. During spring and summer, the number of terrapins caught per sampling day was highest in the creek. Males were more abundant in the creek and at the rocks than adult and juvenile females. However, no males were caught at the mudflat during these seasons. Males and juvenile females were never found on the beach. Juvenile females were only caught at the rocks and in the creek (Figure 8).

During October, the creek and mudflat were sampled (5 and 2 sampling days, respectively). Males were slightly more abundant than females at both sites (creek means ± SE: males= 3.0±0.89, females= 2.40±1.47; mudflat means ± SE: males= 2.50±2.50, females= 1.50±1.50). No immature females were caught.

Overall, the female: male ratio was approximately equal at the mudflat and creek (1:1.2 at both sites). However, almost twice as many males as females were caught at the rocks (1 female: 1.8 males). A larger portion of the population would need to be sampled for a more accurate estimate of the sex ratio of terrapins in Grice Cove.
Morphometric data for all sampled terrapins are summarized in Table 1. Females tagged with radio and sonic transmitters are not morphologically different from all other mature females sampled in Grice Cove, suggesting that they are morphologically typical of the female terrapins in Grice Cove (Table 2 and Table 3, respectively). During capture and tracking efforts (May 2001 through December 2003), water temperatures in or near the cove ranged from 8.5°C in January 2003 to 31.2°C in July 2002 (Figure 9).

Range Tests

Range tests showed that under optimal conditions of calm water, minimal winds, and high tide, the VR1 and VR2 receivers consistently detected the test sonic transmitter at a distance of 40-50 m at sites in the cove and up to 120 m in the upper creek (Table 4). At all sites, range decreased when the transmitter was moved closer to the surface. With the four receivers monitoring sites, the total area being monitored for tagged terrapins was about 2.5 ha of the approximately 30 ha cove. When a receiver was in the upper creek site the total monitored area increased to about 2.6 ha.

Tidal water level change and wind speed did not significantly affect signal detection capability during a continuous reception test in the creek during late January-early February 2004 (total hourly detections = -1.0143 [tide height] + 29.391, R² = 0.0326, n=186; total hourly detections = 0.0148 [wind speed] + 28.5, R² = 0.0003, n=186) (Figure 10 a and b). Because the signal interval of the transmitters varies randomly between 60-180 s, between 20 and 60 detections per hour or a mean of 30 detections per hour would be expected if 100% of detections were recorded. The observed mean of hourly detections (28.56 ± 0.20), was slightly below the expected
average, but well within the expected range. Mean detections varied hourly, but did not follow the tidal cycle. During periods of strongest winds (>10 knots), hourly detections were occasionally greater than expected values. The greatest reception (36 detections/hour) occurred during a period of relatively low wind speed on 2/03/04.

During a continuous reception test at the mudflat from 8/29/03 to 9/1/03, as tide height increased hourly detections increased (total hourly detections = $3.1377 + 0.5377$, $R^2 = 0.1153$, $n=73$) (Figure 11a). Hourly detections decreased as wind speed increased (total hourly detections = $-0.3611 + 5.5509$, $R^2 = 0.0176$, $n=73$) (Figure 11b). However, neither tide height nor wind speed significantly affected signal reception at the mudflat. The observed mean of hourly detections ($3.17 \pm 0.73$), was well below the expected average of 30 detections per hour.

*Visual Censuses*

Five-minute visual head counts of terrapins at the rocks site were conducted from February 2003 through November 2003. The census area was approximately 3,650 m². Preliminary censuses were performed in 2001 and 2002, but these data are less comprehensive and are not included here. Terrapins were observed in this area from March through November. The greatest mean terrapins per count occurred in April ($8.61 \pm 2.40$) and October ($6.52 \pm 1.39$) (Figure 12). The greatest number of terrapins counted during a single census was 79. Males appeared in the area before females and peaked in numbers before females. Females sustained greater numbers further into summer than males. No terrapins were observed in the area during August. Terrapins were seen forming male-female pairs in April-May and again to a lesser degree in September-October.
Individuals of both sexes, as well as pairs, were present during every hour of the day that the rock site was monitored, 0700-2000 h (Figure 13). More terrapins were observed in the evening (1900 h) than at any other time. Terrapins were also numerous during the early morning. During flood tides, the number of terrapins of both sexes, as well as pairs, counted at the rocks peaked during tide heights of 1.1-1.3 m. The number of females also peaked during low flood tides of 0.1 m. During ebb tides, the greatest numbers of terrapins were observed during low tide levels of 0.1-0.3 m (Figure 14).

**Radio Telemetry**

Ten adult female diamondback terrapins (16.0-18.3 cm SCL) were tagged with radio transmitters and released in Grice Cove in May-June 2001 (n=5) and August 2001 (n=5) (Table 2). Three were released on the beach in May. Two were released at the rocks, one each in May and June. Five were released in the creek in August. Radio tagged female terrapins were monitored from May 29, 2001 until December 18, 2001. During this time all 10 tagged terrapins were detected. The mean number of days that tagged terrapins were at large, or number of days from release date to the last date they were detected, was 78.90 (± 8.00) days. While at large, tagged terrapins were detected an average of 10.10 (± 2.83) days (Table 2). Based on detections, the greatest tag lifetime was 162 days.

The highest percent of radio tagged females were detected in June and August (100% and 90%, respectively). During all other months 50-60% of the tagged terrapins were detected, until November when terrapins were no longer detected in the cove (Figure 15). The three females caught on the beach in the spring were detected until June.
or August. However, all terrapins caught in the water were detected until late September or October (Table 2).

Terrapins were monitored and detected in the cove from 0900-2000 h. Terrapins were detected more in the evening than earlier in the day. However, this is also when the majority of the monitoring occurred (Figure 16). Terrapins were detected during tidal heights of −0.01-2.1 m. More detections occurred during ebb tides than flood tides, \((n=190, n=158, \text{respectively})\). Terrapins were detected more often when the water level was high (>1 m) (Figure 17).

*Ultrasonic Telemetry*

Thirteen adult female diamondback terrapins (16.0-18.7 cm SCL) were tagged with ultrasonic transmitters and released in Grice Cove in August and October 2002 \((n=8)\) and April 2003 \((n=5)\) (Table 3). Two each were released at the mudflat in August and October 2002. Five were released in the creek in October 2002. Three were released near the rocks and two were released in the creek in spring 2003. Twelve females were subsequently detected at the monitored sites. Transmitter #13 was never detected, even when the terrapin was released within 1 meter of a receiver, so it was excluded from data analysis. The transmitter was probably damaged by extended exposure to heat from the soldering iron during the activation process.

Ten sites in and around the cove were monitored with VR1 or VR2 receivers from September 14, 2002 through December 6, 2003 according to the schedule in Figure 6. Receivers recorded a total of 21,848 detections, 53% of which occurred at the creek site \((n=11,689)\). Tagged female terrapins spent an average of 55.89 ±8.38% of their detected days at more than one site (range= 27.27-100%). Mean detections of all 12 terrapins
were greatest at the creek, which was monitored for the longest period, and the mudflat, which was monitored for the next longest period (Figure 18). These were the only sites where all individuals with functioning transmitters were detected. Although eleven terrapins were detected at the rocks, the detection mean was low relative to the number of days the site was monitored. Eight females were detected at the beach, but the mean number of detections relative to the days monitored was also low. No terrapins were detected at the harbor mudflat or either south creek site. Over the course of the study tagged terrapins visited an average of 4.25 (+/- 0.33) sites, ranging from 2 to 6 sites per individual.

The number of tagged terrapins contributing to the total detections changed as more females were tagged. To account for this, a monthly detection index for each terrapin was calculated: the detection index = the total number of detections of an individual during a month/ the number of days the terrapin was tagged during that month. The monthly detection index mean for all tagged females varied significantly throughout the study ($\chi^2=54.2746$, 15 df, $P<0.0001$) (Figure 19). However, the monthly mean detection index mean for all tagged females did not vary significantly during the active period, from April through November ($\chi^2=13.4582$, 7 df, $P=0.0617$). This is also the period when all transmitters were deployed. The highest mean detection index occurred in October 2002 and was much greater than the following October. It was much cooler during October 2003, so terrapins may have begun hibernation earlier. Since receivers were occasionally moved, the number of days each site was monitored per month also varied and is indicated by dotted lines in this set of figures.
During the April through November active period, mean detection indices at the mudflat, rocks, and beach varied significantly, while there was no significant variation in detection indices at the creek. Terrapins were detected in the creeks every month except from December-February, with the majority of these detections during July and August ($\chi^2=5.3484$, 7 df, $P=0.6175$) (Figure 20). Terrapins were also detected in the mudflat area throughout the year except from December-February, with peaks in detections in April and September ($\chi^2=33.0245$, 7 df, $P<0.001$) (Figure 21). Tagged females were detected near the rocky shore in April thru July and October thru November ($\chi^2=30.8550$, 7 df, $P<0.001$) (Figure 22). This was also when aggregations of individuals and mounted pairs were observed in this area. Tagged females were also detected near the nesting beach from April thru July, coinciding with the nesting season ($\chi^2=13.7520$, 4 df, $P=0.0081$) (Figure 23). This area was not monitored until April, because this is known to be the beginning of the nesting season based on observations of the nesting beach from previous years.

Terrapins captured in the cove during the fall (late August and October 2002; $n=8$) showed a different detection pattern from those caught in the spring (late April 2003; $n=5$) (Table 3 and Figure 24). Females tagged in the fall were from the creek and mudflat, while females tagged in the spring were from the creek and rocks. In 2003, fall-tagged females were detected every week from late May through early November, with an increase in mean detections during mid-June through August. In contrast, the spring group was not detected in the cove for periods of weeks during the end of June and much of July and August. This group was not detected after mid-October.
Terrapins were detected during every hour of the day with the majority of detections occurring during the early morning hours, during 0500 and 0600 h (Figure 25). The fewest detections occurred in the afternoon, between 1500 and 1700 h. However, the mean number of detections did not vary significantly with time of day ($\chi^2 = 7.0196, 23$ df, $P=0.9994$).

Mean detections also varied significantly with wind speed ($\chi^2 = 212.89, 13$ df, $P<0.0001$), regardless of direction. Mean detections peaked during winds of 4-6 knots (Figure 26). The pattern of mean detections across wind speeds was almost identical to that of the frequency of wind speed observations during the study. Terrapins were detected during winds up to 25.8 kts. There was no significant difference in detections during winds from different directions ($\chi^2 = 3.3811, 3$ df, $P=0.3365$), however more detections occurred when winds were from the south or west. Marsh and trees protected the cove from wind from the south and west. The cove was less protected on the east side and open to the harbor from the north.

The mean number of detections varied significantly across tide heights (ebb tide heights: $\chi^2 = 67.1362, 13$ df, $P<0.0001$; flood tide heights: $\chi^2 = 83.1655, 13$ df, $P<0.0001$). Mean detections during flood tides were not significantly different than during ebb tides (Wilcoxon signed-rank test, $Z=0.144$, df=1, $P=0.885$). Terrapins were detected during tides as low as -0.4m. In the creek, detections of tagged females increased at the lower creek site with flood tides and peaked around mid-tide heights (Figure 27). Detections of females in the upper creek increased during higher flood levels, while detections at the lower creek decreased. During the highest water levels, females were not detected at either creek site. This pattern of detections reversed during ebbing tides. A similar tidal
synchrony of movement occurred at the mudflat (Figure 28). Detections at the rocks peaked during low tide heights, around 0.5 m (flood) or 0.1-0.3 m (ebb) (Figure 29). In contrast, detections at the beach peaked during mid-flood tide and near high and low ebbing tides (Figure 30).

Fourier analysis of 4096 hours of continuous detection data in the creek from the tagged terrapins in the spring and summer of 2003 revealed strong 12- and 24-hour periodicities and a weaker 8-hour cycle (Figure 31). Detection data from fall 2002 and 2003 (1,024 hours each) in the creek have revealed weaker periodicities of approximately 12 hours during fall 2002 and 12 and 24 hours during 2003. Analyses of detection data of individuals corresponded with these group results. Only individuals with transmitter numbers 1, 5, and 10 were detected enough in the creek during the spring through fall 2003 for analysis. Detections of Female 1 in the creek over 4,096 hours had dominant 12-and 24-hour cycles (each with an amplitude of approximately 2,000) and a weaker 8-hour cycle (approximately 1,000 in amplitude) (Figure 32). The dominant periodicity of Female 5 during 4,096 hours of monitoring was 24 hours (approximately 600 in amplitude) with weak 12-hour periodicity (amplitude of about 400). Female 10 was detected with 12-hour periodicity (amplitude of about 400).

Terrapins were not detected in the cove during the winter of 2002 and 2003. The water temperature during the 24 hours prior to the last or first detections was thought to be a prompt for commencing or ending hibernation, and the sites where detections stopped and later began should suggest where the terrapin hibernated. However, these ending and beginning temperatures varied between and among individuals. The mean temperature prior to when terrapins were last detected in the fall was lower in 2002.
(mean = 19.38 ± 1.73, n = 7) than in 2003 (mean = 22.44 ± 0.67, n = 5) (Table 5). Only one female tagged in 2002 was first detected in spring 2003 at the same site where she was last detected the previous fall, the creek.

**Ultrasound Examinations**

The largest ovarian structure of each adult female at the time of the ultrasound examination was used for analysis: eggs, large or small follicles, or nothing visible. Follicles were categorized as small (<1.0 cm diameter) or large (>1.0 cm diameter) according to Lee (2003). Eggs were observed as early as April 18 in a female caught at the rocks and as late as June 20. However, sampling occurred less frequently during late summer. Individuals with eggs had a mean of 4.5 eggs visible by ultrasound (+/-0.34; n = 20).

Ovarian structures of all females caught during the spring 2003 (April-June) were compared across capture sites: creek, beach, or rocks (Figure 33). At all three sites, about half of the females had eggs (creek: n = 7 of 14, beach: n = 8 of 16, rocks: n = 4 of 9), and the other half had only follicles. One female caught on the beach did not have visible follicles or eggs, indicating that she had laid her last or only clutch for the year.

**Individual Habitat Use**

Each individual had a unique pattern of habitat use. However, a distinction can be made between females caught in the fall and those caught in the spring. Of the females tagged with functioning transmitters, 100% of the spring-caught females and only 50% (or 4 of 8) fall-caught females were detected at both the beach and rocks habitats.

Only females with transmitters 1, 5, and 10 were detected over 2000 times (Female 1 = 6898 detections, Females 5 = 4746 detections, and Female 10 = 2683
detections). Individuals 1 and 5 were recaptured and their habitat use is detailed below. Female 10 was caught at the mudflat and tagged in late October 2002. She was subsequently detected in the creek during that fall. She was not detected for 156 days during the winter. During this time she was either outside of the study area, within the study area, but outside of the range of the receivers, or buried in the mud, which completely muffles transmitter signal. Her transmitter was functioning during this period because she was subsequently detected at all sites except the beach in spring 2003, and at the creek and mudflat during that summer. The following fall, she was only detected at the rocks and creek.

Terrapins 4, 6, 9, and 11 were detected over 1000 times (Female 4 = 1185 detections, Female 6 = 1298 detections, Female 9 = 1375 detections, and Female 11 = 1748 detections). Females 4 and 6 were initially caught in the creek in October 2002. Female 4 was detected at the mudflat and rocks that same month before an absence of 158 days. In the following spring and summer she spent time at the beach, creek, mudflat, and rocks. In October she was also detected once in the east creek. However, this was probably a false detection because it is likely that she would be detected more than once if she had been there. During the study, the receivers recorded 275 detections with identification numbers other than those of the transmitters. These were also considered false detections since they were not from the transmitters. Female 6 was at the creek, mudflat, and rocks into mid-November 2002. After being out of range for 155 days, she spent the spring at the beach, mudflat, and rocks. She was last detected at the beach in late May. Terrapin 9 was caught at the mudflat in late October 2002 and only detected for two more weeks. It could not be determined if her transmitter failed or if she left the study area since she
was never recaptured. During this period she spent time at the creek, mudflat, and rocks.

Female 11 was initially caught in late April 2003 in the creek. During the remainder of that month she was detected at the beach, mudflat, and rocks. She was then out of range during May. She returned to the same sites, as well as the creek, in June before leaving for two months. In October and November, she again returned to the same sites. This pattern of alternating intervals of detections and absences was common among the spring-caught females.

Females 8, 12, and 15 were all caught and tagged during the spring of 2003 and detected about 500-600 times (Female 8= 537 detections, Female 12= 598 detections, and Female 15= 609 detections). Female 8 was caught in the creek and only detected for two more weeks. Similarly, Female 15 was caught at the rocks and only detected through the end of June. During these periods, both females used all four main habitat types in the cove. Terrapin 12 was also caught at the rocks and spent the spring and summer at the same habitats as the other two females. In June she was detected at the Fort Sumter beach site, and was not detected again until September in the east Creek. She returned to Grice Cove in the spring and summer of 2004.

Terrapin 7 was only detected 150 times. She was recaptured and her habitat use is described below. Female 2 was caught in August 2002 at the mudflat, but was only detected 21 times in April and June 2003. She spent this short period in all four habitat types. Female 13 was caught at the rocks in April 2003, but was never detected, even during her release next to the rocks receiver. Although it appeared to be working when it was attached, it is likely that her tag was faulty and stopped functioning soon afterwards.
Recaptures

Some of the terrapins initially caught in Grice Cove were later recaptured within the cove ($n=19$ of 130 or 14.6% of the all terrapins marked in the cove). One adult female terrapin was recaptured twice. More than half of the recaptures occurred in the upper or lower areas of the creek (57%; $n=11$, Table 4). The majority of recaptured terrapins were found in a habitat other than where they were initially caught (68%; $n=13$). Systematic recapturing was not attempted.

Of the 83 terrapins originally caught in the creek, nine were recaptured and approximately half of these (55.6%) were found at sites other than the creek. Female terrapins, originally caught in the creek during October and April, were recaptured in either the creek or upper creek during the following October ($n=3$). Three male terrapins caught in the creek in April 2003 were recaptured there two months later, in June, while two originally caught in June 2003 were recaptured in the upper creek in October 2003. One male was recaptured at the rocks in April 2003.

Terrapins originally caught at the mudflat during August and October were recaptured in either the creek or upper creek ($n=2$ at both sites). None were recaptured at the mudflat. One female caught in August at the mudflat was recaptured during the following June in the creek. One female and one male were originally caught in October in the mudflat and recaptured the following October in the upper creek. Another male caught in October at the mudflat was recaptured in the creek in June.

A female originally caught at the rocks in June 2001 was recaptured almost two years later (April 2003) in the creek. Female terrapins originally found on the beach in
May (2001 and 2003) and June (2003), were caught again on the beach in May and June 2004, in the creek in June and August the same year, or at the rocks the following April.

Three females with sonic transmitters were recaptured. Females 5 and 7 were caught in the creek and tagged on 10/07/02 and recaptured exactly one year later in the upper creek. Ultrasound showed that both were undergoing ovarian maturation as they both had 2-3 large follicles (1.1-1.5 cm in diameter) during each capture. Female 7 also had many small follicles, less than 1 cm in diameter. In fall 2002, Female 5 was detected in the creek, mudflat, and at the rocks. She was not detected from 11/3/02-4/17/03. During spring-fall 2003 she was detected at both beach sites and all sites within the cove and creek. She was detected at both receivers near the nesting beach from April-July 2003. She was last detected on 10/7/03 in the creek. Female 7 was only detected from 10/10/02-10/29/02 at the creek and mudflat receivers. When she was recaptured her transmitter was still attached, but not functioning. It is not clear when the transmitter stopped transmitting. Both recaptured females had gained weight (19 and 45 g, respectively), indicative of good health.

Sonic-tagged Female 1 was originally caught on 8/26/02 in the mudflat. Ultrasound showed small, round structures that were possibly follicles, but she was probably not reproductively active. This female was detected the most during the study (6,898 detections or 31.5% of total detections of all tagged females). She was detected during fall 2002 in the creek and mudflat. From 11/19/02-3/16/03 she was not detected in the study area so she may have been hibernating. During spring-fall 2003 she was detected in the creek, mudflat, rocks, and upper creek. The two receivers at the nesting beach never detected her. Recaptured in the creek on 6/20/03, ultrasound revealed that
she had three eggs and two large follicles. Her transmitter was still functioning and she had gained 10 g. She was last detected on 11/4/03 in the creek.

Two females with radio transmitters were recaptured. The female with the radio tag #4019 was initially caught on the harbor side of the nesting beach on 5/25/01 and tagged with a radio transmitter. Ultrasound showed 4-5 eggs. She was captured again that summer (8/02/01) in the creek and had gained 20 g. Ultrasound was not performed. Three years later (6/02/04) she was caught on the same section of the beach. Probing of the inguinal region confirmed that she had eggs (Phil Allman, personal communication). The transmitter was no longer attached.

The female with the radio tag #4030 was first caught at the rocks on 6/26/01. No ultrasound was performed. She was only detected on 8/7/01 and 9/28/01, when she was southeast of the listening station, toward the creek. Recaptured in the creek almost two years later on 4/23/03, she had five eggs and possible follicles. She had gained 36g. The transmitter was attached, but no longer functioning.
DISCUSSION

Site Fidelity

With the exception of the individual who was never detected, all sonic-tagged females remained in the study area for at least part of the study period. Many repeatedly returned to Grice Cove following absences of up to 3-7 months. This supports the hypothesis that female terrapins exhibit site fidelity and that habitats found in Grice Cove are important to terrapins. The degree of site fidelity varied among individuals. Most, however, were detected repeatedly over several months between their release date and the last day they were detected. Eighty percent of the radio-tagged females \((n=8)\) were detected for 2.5 to 4 months. One individual (tag 4030) was recaptured in the cove more than 660 days after she was initially released. Of the terrapins tagged with sonic transmitters in fall 2002, 75% \((n=6)\) were detected over a period of at least seven months. Two were detected for longer than twenty months. These terrapins were never detected outside of Grice Cove and the area near the nesting beach. Three terrapins tagged with sonic transmitters in spring 2003 were detected for 7-13 months. One individual was detected for less than a month and one was never detected, probably due to a non-functioning tag. This group included the only female that was detected in a creek outside of the cove. No turtle tagged in Grice Cove has ever been recaptured somewhere else in the Charleston Harbor estuary despite repeated trammel netting of adjacent areas over several years (see also Lee, 2003).
On average sonic-tagged terrapins were detected a small portion (30%) of the days that sites were monitored. However, it must be considered that this included winter when none were detected for over 3 months. Collectively, the detection ranges of the receivers did not cover the entire cove (approximately 2.5 ha or 8.3% of the entire cove was covered). It is possible that individuals were within the cove during days that they were not detected.

Although they were not detected in the cove year round, most exhibited high site affinity by repeatedly returning to the study area over a long period. Sonic tagged females in Grice Cove appeared to display two general residency patterns. As a group, females caught in the fall at the foraging sites (creek and mudflat) spent relatively more days in the cove (33.7% of days that sites were monitored) than spring caught females (22.6% of monitored days). Fall-caught females were also more consistent residents.

In contrast, the five females caught during the spring mating season (late April) at the aggregation site or in the creek were more sporadic residents. They were absent from the cove for periods of weeks before reappearing. They were detected through the end of April or beginning of May. All five females were then absent for three weeks before revisiting the area in mid-June for only 2-3 weeks. They did not reappear next until eight weeks later, in early September, at the aggregation site. While in the cove they were primarily detected in the aggregation and nesting areas as well as the creek and mudflat. This residency pattern suggests that these females reside outside of the cove during the majority of the year and visit the cove to mate and nest.

The spring-caught group included the only female ever detected outside the cove. Female #12 was caught at the aggregation area during the mating season. In the nesting
season she was detected at the Fort Sumter end of the nesting beach. She was later detected in a creek to the east of the cove (east creek site) in September. She may have reached this creek by crossing a sand flat and marsh behind the nesting beach or by swimming around the east end of the island. She returned to the aggregation area the following spring.

Approximately 14% of the 130 terrapins captured in Grice Cove during this study were recaptured within the cove, often at the same site. This recapture rate is lower than previously reported rates of 97% (of 205 marked terrapins) (Gibbons et al., 2001) and 40% (of 547 mark terrapins) (Hurd et al., 1979) in small creeks, approximately 1 km long. However, the study by Gibbons et al. (2001) lasted 16 years and sampling was the primary focus of both studies. It is likely that the recapture rate of terrapins in Grice Cove would increase if this study was continued with more extensive sampling over several years. The return of terrapins to the same sites up to 22 months later is strong evidence of site fidelity. Management plans for this species need to consider that terrapins repeatedly return to relatively small areas, such as Grice Cove, and may remain there for extended periods.

Terrapins also exhibited fidelity to the nesting beach and the mating site in Grice Cove. Of tagged females detected at the beach, all visited this area on multiple days during the nesting season. Two females were caught on the beach during two different nesting seasons. One was recaptured on the beach within 400 m of where she was initially found and almost exactly one year later (5/29/03 and 5/15/04). This is consistent with Roosenburg’s (1990) finding that terrapins in the Chesapeake Bay return to the same nesting beach during consecutive years. Because the detection ranges of the two
receivers near the beach included only a fraction of the total shoreline (12%) and both receivers were not in the water the entire nesting season, it is likely that nesters were not always detected. Nests on this beach suffer very high predation by raccoons and possibly mink or otters, as well as dogs visiting with beachgoers. During beach surveys in 2003, predators had destroyed 100% of the 90 located nests (Ana Estrella, unpublished data). Disturbances by beachgoers may also deter terrapin nesting. During beach surveys, our presence often disturbed female terrapins on the beach and they immediately returned to the water. The only other suitable beach found in the southeastern portion of Charleston Harbor was Morris Island where far fewer tracks were seen (Dave Owens, personal communication). The lack of recruitment observed on this high-density nesting beach will likely devastate the local terrapin population over time. Only 9 of 130 terrapins caught in Grice Cove during this study were juveniles. Similarly, Gibbons et al. (2001) found that juveniles were notably absent from the terrapin population in Kiawah Island, South Carolina. None of the 1,274 terrapins they sampled had plastrons shorter than 9 cm or were less than 3 years old. This may be an indicator of low recruitment. However, it is also possible that the number of juveniles in these populations were underestimated because juveniles apparently remain in high marsh habitats for the first several years of life (Lovich et al., 1991).

All tagged females who were detected at the mating aggregation area repeatedly returned to this site. This behavior was also documented for females of the lekking marine iguana, *Amblyrynchus cristatus*, which return to the same rocky shore each breeding season to mate with displaying males (Wikelski et al., 1996). This area in Grice
Cove appears to be crucial for reproduction in the local terrapin population and should
remain undisturbed by boat traffic, at least during the mating season.

Habitat Use and Movements

In general, female terrapins showed site fidelity to Grice Cove; however on a finer
scale multiple habitats were used within and near the cove. Throughout this study 10
sites were monitored for terrapins, but terrapins were only detected at 7 sites. Of these 7
sites individuals were detected at an average of approximately 4 different sites.
Likewise, most recaptured individuals (68%) were caught at sites other than where they
were initially caught.

The amount of time sonic-tagged female terrapins spent in each habitat varied
throughout the year and is likely related to what they use each habitat for. Of the main
habitat types: creek, mudflat, rocks, and beach, sonic-tagged terrapins were detected most
in the creek habitat (detections at the three creek sites comprised 53% of total detections;
approximately 36% of the total monitoring effort was spent in the three creek sites). In
the creek, the majority of detections occurred during July and August, during the terrapin
foraging period (Hildebrand, 1929). Terrapins probably spent a large portion of these
months foraging in the Spartina alterniflora marsh surrounding the creeks, which has
abundant Littorina irrata snails. The fact that Littorina were scarce on the grass along
the creek shorelines, while abundant only a few meters into the marsh (personal
observation), suggested that terrapins had been feeding along the edges of the creeks.
However, it is also possible that blue crab (Callinectes sapidus), which also eats
Littorina, may forage in the grass near the creek margins during high tides as well.
Terrapin activity in the mudflat peaked in April and September. These were the months when individuals and pairs were seen aggregating at the nearby rocks. The mudflat may be a resting area for females when they are not mating. The creek and mudflat were the only sites used by all tagged females (excluding the individual that was never detected). Like the creek, the mudflat is surrounded by a Littorina-rich marsh. These two sites are likely important feeding and resting areas for terrapins.

At the rocks, tagged females were detected most during April through July and October. This is also when aggregations of individuals and mounted pairs were observed in this area. Although almost all tagged females \( n=11 \) used the aggregation area, the mean detection indices were lower here each month than those at the creek or mudflat. This may be because females visited the site only periodically and for relatively shorter periods, probably using the aggregation site only to mate and during internesting periods. This was illustrated by the weekly detections of sonic-tagged female #4 at both the beach and rocks sites (Figure 34). During visual census in June and July, significantly more females than males were observed at the aggregation area. However, none of these females were observed paired with males. Therefore, even though the mating season had ended and there is little food at the rocks, females continued to use the aggregation site during the nesting season. In August, females were no longer observed or detected at the rocks. This coincided with the end of the nesting season, when females were also no longer detected near the beach. In addition, no terrapin tracks were seen during beach surveys in August.

As expected, tagged females were also detected in the water near the nesting beach during late spring and early summer. This area was not monitored until April,
because this is known to be the beginning of the nesting season based on surveys from previous years. Terrapin tracks were found on the beach from mid-May to mid-June (Ana Estrella, unpublished data; personal observation). The presence of females in the foraging areas during the spring and summer suggests that they were also feeding during the nesting season.

Sonic-tagged terrapins were detected in the cove every hour of the day with a peak in detections during the early morning, between 0500-0700 h. This is in contrast to findings by Ernst et al. (1994) who concluded that terrapins must bury in the mud at night because they were not caught in seine nets. If the tagged females in this study spent the nights buried they would not have been detected by the receivers. However, it is possible that they become less active and perhaps rest on the bottom. If they were resting overnight within the range of a receiver, this would account for the relatively high detection of terrapins at night. During visual censuses, more females were also seen in the aggregation site during the morning, from 0700-0900 h (the earliest censuses), than any other time of day except 1900 h. This suggested an increase in activity around sunrise and during cooler evening hours. Females were detected least often between 1500 and 1700 h. This is typically the warmest time of day so they may become less active and bury in mud where receivers cannot detect them. Mean wind speed did increase in the afternoon hours, but the peak in wind speed did not correspond with the hours of fewest mean detections. Tests in the creek and mudflat confirmed that wind speed did not significantly affect signal detection capability of the receivers. Therefore, this pattern is most likely due to terrapin behavior rather than changes in signal reception capability.
Detectsions in the creek and upper creek sites, daily detection patterns of individuals, and direct observations all indicate that terrapin activity is strongly synchronized with tidal cycles. During flooding tides, tagged females were increasingly detected at the creek site. Detections peaked around mid-tide heights. As detections at this lower creek site decreased during higher water levels, females were detected more in the narrower and shallower upper creek. Females were not detected or visually observed in the creek during the highest water levels. This pattern of detections reversed during ebbing tides. When the tide ebbed, terrapins were detected in the upper creek before being detected at the lower creek site. This indicates that terrapins moved down creek during ebb tides. Studying detections of individual tagged females in the creek on an hourly scale supported this tidal movement pattern observed for the entire group. Female #5, among others, frequently followed this pattern (Figure 35). On numerous ebb tides, male and female terrapins were observed to appear in the upper creek soon after high tide, apparently entering the creek from the flooded marsh. The turtles then moved down creek with the current (personal observation). Tucker et al. (1995) observed similar behavior by females at Kiawah Island, South Carolina. Using radio telemetry to track terrapins in Spartina marshes, they found that females were moving from creeks into flooded marshes at high tide to feed on high densities of Littorina snails. As the tide ebbed, females either followed the water back into the creeks or buried in the marsh mud. Female terrapins in Grice Cove were probably also foraging in the marsh bordering the creek during high tide, which would explain why they were not detected.

The 12-hour periodicity of detections in the creek, determined by Fourier analysis, is further evidence that terrapin movement patterns were synchronized with tidal
cycles. Tidal periodicity of detections was stronger during spring and summer than in the fall. The less distinct detection pattern in the fall could be because fewer continuous hours of detection data were available for analysis. During the fall foraging period, before hibernation, female terrapins were no longer nesting so they may have remained in the creek and marsh for longer periods to feed rather than moving in and out of the creek, past the receivers. This could also account for the less pronounced tidal cycle of detections in the fall compared to the spring.

Zimmerman (1992) observed that female terrapins nest around high tide. Therefore, it was expected that detections of females near the nesting beach would increase immediately before and after high tides. The majority of detections during ebb tides did occur near high tide, perhaps as females returned to the water after nesting. During beach surveys, females were often seen before high tide in the water a few meters from the beach, occasionally moving parallel to the shore. It is thought that these females were looking for a suitable area of beach before leaving the relative safety of the water. This behavior may account for the peak in detections near the beach during mid-flood tide.

At the rocks, females were detected most often during low tide heights, around 0.5 m (flood) or 0.1-0.3 m (ebb). During spring tides, Grice Cove almost completely drains except for a narrow channel in the creek that retains less than 1 meter of water. During these times terrapins probably stay in the creek or leave the cove for the deeper harbor, passing the rocks on the way. Therefore, terrapins would pass the rocks near the mouth of the cove prior to and after low tides as they leave or reenter the cove.
Terrapins in South Carolina hibernate from November to March (Ernst et al., 1994). Radio-tagged females were never detected in Grice Cove during this period. Terrapins were also not observed at the aggregation site after November. Few sonic-tagged individuals \( n=6 \) were detected in November, as late as 11/27, and in late March \( n=1 \). Even though 12 of 13 sonic-tagged females had working transmitters during the winter of 2002, they were clearly not moving during this time. If they were within the range of the receivers, they must have been buried so the mud completely attenuated the transmitter signal. When the transmitter was 2 cm beneath the mud the signal could not be detected. The mean water temperatures during the 24 hour period prior to the last detections of individuals in the fall and first detections in the spring was thought to indicate the temperature that prompts the beginning or end of hibernation. However, since these temperatures varied between and among individuals in the two fall seasons, changes in other physical factors at the hibernacula, in combination with temperature, may signal the onset or end of hibernation. The amount of food consumed prior to hibernation may also account for individual variation in hibernation periods.

It is not known where terrapins hibernate in Grice Cove. Only one tagged female was first detected in the spring at the same site, the creek, where she was last detected in the previous fall. Yearicks et al. (1981) found terrapins hibernating in creek banks and along creek bottoms. No hibernating terrapins were found during a search along the edges of Grice Cove creek during the winter of 2002. However, it is likely that terrapins hibernate along the bottom of the deep channel in the middle of the creek, since this area remains submerged during low tides.
Do Terrapins Lek?

The spring aggregation of the Grice Cove diamondback terrapin population paritally fits the definition of a lek, as defined in Höglund and Atalato (1995). A lek is a mating system characterized by a dense aggregation of males defending small territories (the lek), that are established at the same site every mating season prior to the arrival of females. These sites offer no useful resources to females besides genetic material. Females visit the lek only to mate before nesting elsewhere, without additional male parental investment. Females may choose their mates, although this condition is not always considered necessary in defining a lekking species. This study was designed to determine if this terrapin population fits the basic requirements of a lek, not to describe territorial behavior of individual males or individual mating/reproductive success.

Aggregations of adult terrapin individuals and pairs were observed in the water adjacent to the rocky shore in Grice Cove during the spring seasons of 2001-2003, and again during October. The aggregation formed again in 2004, but these observations were not included in this study. Like the marine iguana, *Amblyrhynchus cristatus*, and other lekking species (Höglund and Atalato, 1995; Wikelski et al., 1996), terrapins returned to the same site during consecutive mating seasons. One hypothesis for why terrapins aggregate at the rocks each year is that this is an area of high female traffic in the spring, so males will have access to more females. This is true of the locations of marine iguana leks. The rocks are near a major nesting beach and males here may have access to more resident females as well as “visiting” females who may come to the cove mainly to mate and nest.
Male iguanas have been observed to arrive at lek sites up to two months before females. Likewise, male terrapins began to arrive at the aggregation area in March about one week before females arrived in early April and about three weeks before mounted pairs were observed. Although it was not verified that mounted pairs were mating, almost half of the females caught at the aggregation area during the spring had large follicles and no eggs (Figure 33). This indicated that females at this site were at an appropriate ovarian stage for mating.

Male terrapins do not appear to defend traditional “real estate” territories in Grice Cove. The aquatic environment inhabited by terrapins is not conducive to the parceling and defense of land as territories. Twice a day, during low tide, the majority of the cove, including the aggregation area, is nearly or completely dry. Terrapins leave the aggregation area during this time, presumably following the water as it recedes from the cove. If they had set territories, male terrapins would have to reestablish these twice a day upon their return during flood tides. It is possible that males use landmarks along the shoreline to delineate and return to areas of land. However, the mud bottom appears homogeneous in the aggregation area so it is unlikely to provide landmarks.

*Amblyrhynchus cristatus* males defend areas of rocky shorelines (Wikelski *et al.*, 1996). However, male terrapins were never seen on the rocks around the aggregation area.

Another hypothesis is that in a terrapin lek, females may function as the territories and mate-guarding by males may be a form of territory-defense. Males may mount females to prevent other males from mating with her, even if the pair was not actively mating. This is known to occur in sea turtles (David Owens, personal observation). Single males were often observed next to mounted pairs, perhaps to compete for the female.
When the aggregation occurred, terrapins were notably absent from the areas outside of the rock outcrops that appeared to define the borders of the aggregation area. To the human observer, there are no obvious differences in physical characteristics between these areas. The entire shoreline is bordered by rocks, is the same depth, and has pluff-mud sediment. This suggests that males are cuing into subtle characteristics of this area that make it unique and an ideal aggregation site, such as a unique current pattern.

Selection should favor males aggregating where they would have greatest access to receptive females during the spring mating season. This is true in bird and iguana leks (Wikelski et al., 1996; Westcott, 1997). During the spring all tagged females moved around a lot. They used multiple sites throughout the cove during 25-100% of the days they were detected. This would make it difficult for males to monopolize a mate (or mates) throughout her home range by constant guarding. Therefore, female movement patterns during the breeding season will determine where and when males will encounter potential mates. On average, females were detected less frequently near the beach during the peak breeding season relative to the mudflat and the creek. Approximately the same amount of time was spent near the rocks and beach (Figures 20-23). However, of the twelve sonic-tagged females whose transmitters were definitely functional, almost all were detected at the rocks (n=11). This suggests that males at the rocks may encounter a large portion of the female population in the Grice Cove area. The water near the beach is unprotected and often choppy, which would probably make it more difficult for males to mount females (personal observation). Males were never caught or observed on or near the beach.
Females were detected more in the mudflat than in the creek during the peak mating season (Figures 20 and 21). When females were not actively mating, the mudflat area may have been a resting or “spill-over” area. They may also have been foraging on the *Littorina* snails in the grasses surrounding the mudflat, because it is closer to the aggregation area than is the creek. This preferred food item was absent from the aggregation site (personal observation). Male marine iguanas fast during the mating season (Trillmich, 1983). It is not known if male terrapins leave the aggregation area to forage; however, males were not captured at the mudflat during the spring. Tracking male terrapins would give insight into their foraging patterns during the mating season. The mean detection index of tagged females at the aggregation area was highest during the mating season and again during October (Figure 22). Although the females tagged in this study were detected in the aggregation area less than in the creek or mudflat, males at this site would have access to potential mates from outside the cove as they enter from the harbor. The aggregation site is near the mouth of the cove (approximately 150 m), directly across from the nesting beach, and about 250 m from the mudflat.

There is evidence that some females who mate and nest in Grice Cove reside elsewhere during the majority of the year, traveling to the cove only for these activities. The sonic-tagged females who were caught in the spring at the aggregation area or creek were only periodically detected in the cove during the mating and nesting seasons. They reappeared during the fall aggregation. This presence-absence pattern of these females suggests that the lek and nesting beach attracted females from the surrounding areas, who would not be considered permanent residents of Grice Cove.
Female terrapins apparently only visited the aggregation area to mate before traveling elsewhere to nest. While at the aggregation site, females were observed paired with males, pursued by males, or swimming solo. They traveled to the beach on the opposite shore of the cove to nest (approximately 250 m away at the closest point). Females did return to the aggregation multiple times throughout the spring and summer. These return trips alternated with periods spent at the beach. This suggests that females also use this site as an inter-nesting area or they may mate on multiple occasions. The female with tag #4, among others, demonstrated this pattern of habitat use (Figure 34).

The presence of eggs in almost half (44%) of the females caught at this site in the spring is further evidence that this may be a resting site during internesting periods (Figure 33).

By not providing resources, such as food or nesting sites for females on their territories, or parental care to their offspring, male terrapins fulfill these criteria of a lekking species. As previously stated, the aggregation area does not offer females their preferred food (*L. irrorata*) and is not suitable for nesting. It is well known that, like the marine iguana, male turtles provide no parental investment beyond genetic material (Hildebrand, 1932). Males were never observed on the nesting beach or in the surrounding waters during this study.

Free mate choice by females was not observed or tested in the Grice Cove aggregation. However, the necessity of this condition for a lekking species is highly debated. The relatively strong sexual selection for certain male traits in leks, due to female choice, results in high variance in male mating success within an aggregation (Höglund and Alatalo, 1995). If female terrapins are choosing between potential mates, one possible cue for distinguishing between individuals may be coloration. Terrapins
have unique color patterns on their shells and skin. Carapace and plastron colors range from pale green, yellow or orange to black, or any color combination, and may have quite variable patterns including dark concentric rings ("diamond" patterns), spots, or solid color (Figure 1). Skin patterns vary from black to light gray or almost white with dark spots or stripes (Ernst et al., 1994). There is evidence of multiple paternity in New York, New Jersey, and North Carolina populations (Kristen Hart and Susanne Hauswaldt, personal communication). If females are choosing mates, there may be an advantage to more genetically varying mates. Color may be one factor on which females base their choice. However, the suggested guarding of females by males observed in the Grice Cove aggregation may prevent females from freely choosing mates. Future studies could investigate female mate choice.

Transmitter Reception and Evaluation of Methodology

Monitoring technologies of radio tracking, and sonic tracking were evaluated by comparing the efficiency of data collection and accuracy of animal location (Table 6). Sonic transmitters were more effective for long-term monitoring of terrapins because they have a longer battery lifespan and greater attachment time. The method of attaching sonic transmitters with cable ties through holes in the carapace in addition to epoxy may have been more secure, resulting in greater tag retention. However, it was not feasible to drill holes in a carapace that would accommodate the size of the radio transmitters. Transmitters attached to the surface of the carapace will be retained only until the scutes are shed. This was the case with radio transmitter 4060 which fell off during the study and was found in January 2002.
More data were collected per animal and per effort using automated sonic tracking than with radio tracking. Manually radio tracking was much more labor intensive than the automated sonic tracking system. Because terrapins spend no more than a few minutes at the surface, and because they could not be detected in the marsh due signal attenuation by the *Spartina* grass, there were only short periods when transmitters could be detected. It was often difficult to determine the direction of the signal during these short periods. The automated acoustic receivers provided nearly continuous reception of tagged terrapins, except in the cove during low tides, with less effort. Contrary to what had been expected, physical conditions such as high winds and sediment turbulence during low water levels did not significantly affect detections during continuous reception testing in the creek. However, the greatest number of detections per hour did occur during a period of low wind speed. The creek is more protected and deeper than the relatively open water of the cove. The cove may become choppier during windy periods and shallower during low tides, which did reduce signal reception in the mudflat and probably in the rocks and beach sites as well.

Since these sonic transmitters had previously not been used to track terrapins, it was necessary to recapture tagged individuals to assess the affect of the tag and attachment method on their health. Detections of sonic-tagged females at the mating aggregation area and near the beach, as well as the recapture of a tagged female on the beach, suggest that the sonic transmitters did not interfere with reproductive behavior. The three sonic tagged females that were originally tagged in fall 2002 and recaptured in spring 2003 had follicles and had gained weight when they were recaptured. This is further evidence that sonic tags did not negatively impact their health.
Summary

In general, female terrapins in Grice Cove in Charleston Harbor, South Carolina show site fidelity; this small, approximately 30 hectare, cove. This cove includes an important terrapin nesting beach, mating aggregation area, and foraging habitat. In this study, there appears to be some evidence of two degrees of site fidelity: some females are more resident while others seem to visit the cove more sporadically and were not detected for periods of weeks during the summer. These females may be visiting the cove mainly to mate at the spring aggregation and nest. This group also included the only female ever detected outside of the cove, in the creek to the east of the cove. Female terrapins also returned to the same mating site and nesting beach within a season and across multiple years.

On a finer scale terrapins did not stay in one habitat type within Grice Cove. This cove includes an important terrapin nesting beach, mating aggregation area, and foraging habitat. Terrapins were detected in the creek during almost all of their active period and the most intense part of the foraging period. Terrapin activity in the mudflat peaked in spring and late summer. During these times, *Littorina* were scarce along the shorelines, while abundant only a few meters into the marsh, suggesting that terrapins had been feeding along the edges of the marsh. Detections at the beach occurred in the spring and early summer, when hundreds of tracks of nesting females were seen on the beach. During the mating season, tagged females were detected at the rocks where aggregations of pairs and individuals were seen. The presence of large follicles in females caught at the rocks during the spring indicates that they were at the appropriate stage for mating.
Habitat use by female terrapins is apparently influenced by multiple factors including season, time of day, tide, and reproductive status. These factors should be considered when planning quantitative surveys. Depending on the time of the survey, sampling in different habitats could give markedly different results.

Although it cannot be stated that the terrapin aggregations observed in Grice Cove during the past few years fit all criteria of classically described leks, the strong similarities beg further study of terrapin mating behavior. In particular, marking and tagging males could give insight into possible spatial territoriality and genetics studies of clutches, and captive mating experiments may indicate female mate-choice.

Automated sonic telemetry was a more efficient method for tracking terrapins than manual radio telemetry, in terms of data collection and accuracy of animal location. For these reasons, automated sonic tracking is a valuable tool for studying terrapin behavior in the field.
LITERATURE CITED


Seigel, R.A. 1984. Parameters of two populations of diamondback terrapins \textit{(Malaclemys terrapin)} on the Atlantic coast of Florida. Pp. 77-86 In R. A. Seigel, L. E. Hunt,


Table 1. Mean (±1 SE) morphometrics for mature and immature female terrapins (n=55 and 9, respectively) and mature males (n=66) captured in Grice Cove from May 2001-April 2004. Tagged females are a subset of the mature females. Their mean is shown separately for comparison with mature females, as a group, and immature females. Recaptured terrapins are included as the mean of their measurements at each capture event. Mass is measured in grams. Straight carapace, straight plastron, tail and head measurements are in centimeters.
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<td>Head Width (cm)</td>
<td>3.7 (0.06)</td>
<td>2.2 (0.07)</td>
<td>2.6 (0.17)</td>
<td>2.5 (0.04)</td>
</tr>
<tr>
<td>Tail Length (cm)</td>
<td>2.3 (0.07)</td>
<td>1.8 (0.15)</td>
<td>2.6 (0.17)</td>
<td>2.5 (0.04)</td>
</tr>
<tr>
<td>Base-cloaca Width (cm)</td>
<td>3.7 (0.08)</td>
<td>2.7 (0.07)</td>
<td>2.7 (0.07)</td>
<td>2.2 (0.02)</td>
</tr>
<tr>
<td>Straight Plastron Length (cm)</td>
<td>15.2 (0.15)</td>
<td>15.1 (0.38)</td>
<td>11.0 (0.39)</td>
<td>10.2 (0.08)</td>
</tr>
<tr>
<td>Mass (g)</td>
<td>843.2 (20.25)</td>
<td>877.5 (44.07)</td>
<td>310.2 (26.92)</td>
<td>262.3 (6.33)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th></th>
<th>Straight Carapace Length (cm)</th>
<th>Mass (g)</th>
<th>Females (mature)</th>
<th>Tagged females (mature)</th>
<th>Females (immature)</th>
<th>Males (mature)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Straight Carapace Length (cm)</td>
<td>17.1 (0.14)</td>
<td>17.1 (0.28)</td>
<td>12.5 (0.47)</td>
<td>11.9 (0.18)</td>
<td>11.9 (0.18)</td>
<td>11.9 (0.18)</td>
</tr>
<tr>
<td>Mass (g)</td>
<td>843.2 (20.25)</td>
<td>877.5 (44.07)</td>
<td>310.2 (26.92)</td>
<td>262.3 (6.33)</td>
<td>262.3 (6.33)</td>
<td>262.3 (6.33)</td>
</tr>
</tbody>
</table>
Table 2. Summary of morphometric and turtle-days for 10 radio-tagged adult female terrapins in the Grice Cove study area in Charleston Harbor, South Carolina. Turtle-days at large are the total days between the release date and the last day the terrapin was detected. Since the cove was not monitored every day (52 total monitoring days), the days not detected are the number of monitored days after released that the terrapin was not detected. Recaptured individuals are indicated by an asterisk (*). Terrapins were captured and released at the same site. Detached tag of one individual (**) was found in the cove on 10-Jan-02 so it is possible that that terrapin was in the cove after it was last detected.
<table>
<thead>
<tr>
<th>ID</th>
<th>Release season</th>
<th>Mass (g)</th>
<th>SCL (cm)</th>
<th>Capture site</th>
<th>Release Date</th>
<th>Last detected</th>
<th>In study area</th>
<th>Not detected</th>
<th>At large</th>
</tr>
</thead>
<tbody>
<tr>
<td>*4019</td>
<td>Spring</td>
<td>850</td>
<td>17.1</td>
<td>Beach</td>
<td>25-May-2001</td>
<td>21-Aug-2001</td>
<td>22</td>
<td>30</td>
<td>88</td>
</tr>
<tr>
<td>4172</td>
<td>Spring</td>
<td>1100</td>
<td>18.3</td>
<td>Beach</td>
<td>25-May-2001</td>
<td>26-Jun-2001</td>
<td>3</td>
<td>49</td>
<td>32</td>
</tr>
<tr>
<td>4229</td>
<td>Spring</td>
<td>750</td>
<td>16.6</td>
<td>Beach</td>
<td>25-May-2001</td>
<td>21-Aug-2001</td>
<td>14</td>
<td>38</td>
<td>88</td>
</tr>
<tr>
<td>4332</td>
<td>Spring</td>
<td>900</td>
<td>17.6</td>
<td>Rocks</td>
<td>31-May-2001</td>
<td>5-Oct-2001</td>
<td>29</td>
<td>22</td>
<td>127</td>
</tr>
<tr>
<td>*4030</td>
<td>Spring</td>
<td>850</td>
<td>17.0</td>
<td>Rocks</td>
<td>26-Jun-2001</td>
<td>28-Sep-2001</td>
<td>2</td>
<td>30</td>
<td>94</td>
</tr>
<tr>
<td>**4060</td>
<td>Summer</td>
<td>840</td>
<td>17.0</td>
<td>Creek</td>
<td>1-Aug-2001</td>
<td>19-Oct-2001</td>
<td>8</td>
<td>6</td>
<td>79</td>
</tr>
<tr>
<td>4070</td>
<td>Summer</td>
<td>700</td>
<td>16.0</td>
<td>Creek</td>
<td>3-Aug-2001</td>
<td>19-Oct-2001</td>
<td>5</td>
<td>8</td>
<td>77</td>
</tr>
<tr>
<td>4080</td>
<td>Summer</td>
<td>890</td>
<td>17.8</td>
<td>Creek</td>
<td>3-Aug-2001</td>
<td>19-Oct-2001</td>
<td>6</td>
<td>7</td>
<td>77</td>
</tr>
<tr>
<td>4100</td>
<td>Summer</td>
<td>860</td>
<td>17.9</td>
<td>Creek</td>
<td>3-Aug-2001</td>
<td>19-Oct-2001</td>
<td>8</td>
<td>5</td>
<td>77</td>
</tr>
<tr>
<td>4040</td>
<td>Summer</td>
<td>720</td>
<td>16.0</td>
<td>Creek</td>
<td>30-Aug-2001</td>
<td>19-Oct-2001</td>
<td>4</td>
<td>1</td>
<td>50</td>
</tr>
</tbody>
</table>
Table 3. Summary of morphometric and turtle-days for 13 sonic-tagged adult female terrapins tagged in the Grice Cove study area in Charleston Harbor, South Carolina.

Turtle-days at large are the total days between the release date and the last day that any sites were monitored (12/06/03). Recaptured individuals are indicated by an asterisk (*).

Terrapins were captured and released at the same site. Recapture dates are included as one day in the study area. Terrapins detected in May 2004 (−) and terrapins detected in June 2004 (**) are indicated.
Table 4. Maximum distances at which sonic transmitters were detected by VR1 and VR2 receivers during range testing at Grice Cove study sites. The maximum distance verified at the rocks (*) was 25m although it is highly probable that the range was 40-50m, as the substrate was similar to that at the mudflat site.
<table>
<thead>
<tr>
<th>Receiver site and direction of transmitter</th>
<th>Distance at which receiver detected transmitter (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Creek</strong></td>
<td></td>
</tr>
<tr>
<td>upcreek</td>
<td>35-50</td>
</tr>
<tr>
<td>downcreek</td>
<td>50</td>
</tr>
<tr>
<td>crosscreek</td>
<td>15</td>
</tr>
<tr>
<td>channel bottom (on hard bottom)</td>
<td>50</td>
</tr>
<tr>
<td>outside channel (2cm below soft mud bottom) in <em>Spartina</em> grass</td>
<td>5-15</td>
</tr>
<tr>
<td></td>
<td>not detected</td>
</tr>
<tr>
<td><strong>Uppercreek</strong></td>
<td></td>
</tr>
<tr>
<td>downstream</td>
<td>120</td>
</tr>
<tr>
<td><strong>Mudflat</strong></td>
<td></td>
</tr>
<tr>
<td>toward harbor</td>
<td>40-50</td>
</tr>
<tr>
<td>toward marsh</td>
<td>40</td>
</tr>
<tr>
<td><strong>Rocks</strong></td>
<td></td>
</tr>
<tr>
<td>toward harbor</td>
<td>25*</td>
</tr>
<tr>
<td><strong>Beach</strong></td>
<td></td>
</tr>
<tr>
<td>toward harbor</td>
<td>40-50</td>
</tr>
<tr>
<td>toward middle of cove</td>
<td>40</td>
</tr>
</tbody>
</table>
Table 5. Dates and locations of the last detections of each sonic-tagged female Malaclemys terrapin in 2002 and the first and last detections in 2003. Water temperatures are the mean temperatures at the creek site during the previous 24 hours.

Water temperature was measured with a Tidbit® temperature logger. Female 2 was not detected in 2002. Females with transmitters 7 and 9 were not detected in 2003. Since females 8, 11, 12, 13, and 15 were released in Spring 2003, their first detections were not following hibernation and were included. Only detections that occurred in September–November were included as the last detections for each year.
Table 6. Comparison of V8SC-2L-256 ultrasonic (VEMCO, Ltd.) vs. radio (Telonics) transmitter performance during this study.
<table>
<thead>
<tr>
<th>No</th>
<th>% Coverage</th>
<th>Reproduction compromised (%)</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.2%</td>
<td>6.3%</td>
<td>35.1 (±1.1% - 1.3% 6.8)</td>
</tr>
<tr>
<td>3.4%</td>
<td>52.2%</td>
<td>168.0.6 (±4.5% - 4.2)</td>
</tr>
</tbody>
</table>
| 21.4% | 24% | 4.2

Compass bearing around receiver within range along a radius of 15-120m

- 8.1m
- 162
- 90%
- 100%
- 93.3%

- Epoxy and
- Epoxy and
- 13

<table>
<thead>
<tr>
<th>No</th>
<th>% Tag lifetime documented (days)</th>
<th>% of tags remaining attached</th>
</tr>
</thead>
<tbody>
<tr>
<td>4.2%</td>
<td>6.3%</td>
<td>35.1 (±1.1% - 1.3% 6.8)</td>
</tr>
<tr>
<td>3.4%</td>
<td>52.2%</td>
<td>168.0.6 (±4.5% - 4.2)</td>
</tr>
</tbody>
</table>
| 21.4% | 24% | 4.2

- Attachment method

<table>
<thead>
<tr>
<th>Sample size</th>
<th>Evaluation criteria</th>
</tr>
</thead>
<tbody>
<tr>
<td>Radio transmitters</td>
<td>Ultrasound transmitters</td>
</tr>
</tbody>
</table>
Figure 1. Two adult male *Malaclemys terrapin*, demonstrating the extreme color variation common among male terrapins. Both were captured on April 23, 2003 either at the rocks or in the creek.
Figure 2. Aerial photograph of the Grice Cove study area in the southeast side of the Charleston Harbor estuary in South Carolina. Terrapin aggregation, nesting, and probable foraging areas are indicated. Source: South Carolina Department of Natural Resources.
Figure 3. VR2 receiver locations in and around the Grice Cove study area. Receivers were at these locations from September 2002 through December 2003 according to the schedule in Figure 6. ♦ = original receiver location ○ = where receivers were later moved to locate sonically tagged females. Data from the receivers in each of the two circles are from similar habitat types and were combined for analysis. The name of the habitat type monitored by each receiver group is in bold and is used in data description and analysis. No terrapins were detected in the SW and SE creeks and the DNR sites.
Figure 4. Illustration of a diamondback terrapin carapace and the notching system used to mark terrapins with a unique alphabetical identification code (AJP is shown). Marginal scutes were notched with a triangular file. Bridge scutes E-G and R-T were excluded from filing, as they provide structural support for the shell. Figure from Levesque, 2000.
Figure 5. Two methods used to attach V8SC-2L ultrasonic transmitters to *Malaclemys terrapin* females: A. The transmitter, wrapped in dark canvas and sealed with super glue, was attached to the posterior marginal scutes with wax-coated sailing thread tied through two small holes. This method was used on two females tagged in August 2002. B. The transmitter was attached to posterior marginal scutes with a small cable tie threaded through a small hole and secured with black epoxy. The method was used on eleven females tagged in October 2002, and April 2003.
Figure 6. Schedule of sonic transmitter monitoring in Grice Cove from September 2002-December 2003. Black bars indicate dates that VR2 or VR1 receivers were stationed at each site to monitor tagged female terrapins. Sites are described in the Methods section.

The creek site was monitored during almost the entire study period.
Figure 7. VR2 receiver mounted to Plexiglas base and PVC tube with float. A temperature logger (Tidbit©) is attached near the bottom right corner of the Plexiglas.
Figure 8. Mean number of *Malaclemys terrapin* (+1 SE) captured per sampling day at sites in the Grice Cove study area from April-August. Data from 2001-2004 were combined. (■ = adult females, □ = adult males, □ = immature females) Number of sampling dates is below each site. Greatest densities occurred in the creek, a probable feeding area and staging area for mating and nesting, during spring and summer.
Figure 9. Mean monthly water temperature (C; +1 SE) in Grice Cove study area during the study: □ = 2001, ■ = 2002, ■ = 2003. Temperatures from May 2001 through August 2002 are from the NOAA National Ocean Service Center for Operational Oceanographic Products and Services station at the Cooper River entrance of the Charleston Harbor, SC (station #8665530). Temperatures during the sonic monitoring (September 2002 through November 2003) are an average from three temperature loggers (Tidbit©) at receiver stations in the cove.
Figure 10. a. Regression of total detections of a test transmitter per hour on tide height during a continuous reception test at the Grice Cove creek site during 1/29/04-2/6/04. b. Regression of total detections per hour on wind speed during a continuous reception test at the Grice Cove creek site during 1/29/04-2/6/04.
a. Total hourly detections = -1.0143 tide height + 29.391
R² = 0.0326

b. Total hourly detections = 0.0148 wind speed + 28.5
R² = 0.0003
Figure 11. a. Regression of total detections of a test transmitter per hour on tide height during a continuous reception test at the Grice Cove mudflat site during 8/29/03-9/1/03.

b. Regression of total detections per hour on wind speed during a continuous reception test at the Grice Cove mudflat site during 8/29/03-9/1/03.
a. Total hourly detections = 3.1377 tide height + 0.5377
   \( R^2 = 0.1153 \)

b. Total hourly detections = -0.3611 wind speed + 5.5509
   \( R^2 = 0.0176 \)
Figure 12. Monthly mean number of terrapins counted during visual censuses at the Rocks site from February through November 2003 (+1 SE): ■ = females, □ = males, □ - paired females and males. Each pair was counted as two terrapins.
Mean number of terrapins counted at the aggregation area (+1 SE)

- Feb
- Mar
- Apr
- May
- Jun
- Jul
- Aug
- Sep
- Oct
- Nov

x-axis: 0, 1, 2, 3, 4, 5, 6, 7, 8

Bars represent counts, error bars indicate standard error.
Figure 13. Mean numbers of terrapins counted during visual censuses at the Rocks site grouped by time of day (+1 SE): ■ = females, □ = males, □ = paired females and males.

Counts from February-November were combined. Terrapins were observed from 7:00 am through 8:00 pm.
Figure 14. Numbers of terrapins counted during visual censuses at the Rocks site, distributed according to the flood or ebb tide height during the count: ▲ = females, ■ = males, ● = paired females and males. Counts from February-November were combined. The distributions of all flood and ebb water levels observed during the study are indicated by gray dotted lines.
Figure 15. Percent of radio tagged female terrapins that were detected in the Grice Cove study area from May-December 2001.
Figure 16. Number of detections of radio tagged female terrapins in Grice Cove study area per hour spent listening for transmitters during each hour period from 0900-2000 hrs.
Figure 17. Mean detections (±1 SE) of radio tagged female terrapins per observation period during each tide height category. For example, mean detections during water levels ≥0.5m and <0.7m are plotted at tide height 0.5m. Mean number of detections occurring during flood tides (solid line) and those during ebb tides (dashed line) are plotted separately.
Figure 18. Mean detections of 12 female terrapins (+1 SE) at monitored sites in Grice Cove and surrounding areas. Data during the sixteen-month study period were combined for each site. The number of days each site was monitored is indicated by a black dot. Number of terrapins detected is below each month.
Figure 19. Monthly mean detection indices (+1 SE) of all sonic-tagged female terrapins at all receivers in Grice Cove (black bars). Monthly mean detection index = [Sum for all terrapin tagged during the month (total detections of a tagged terrapin during the month/n days that individual was tagged during that month)]/n terrapins tagged. The number of days during the month that sites were monitored is indicated by the dotted line. There was a significant temporal variation in mean detection index ($\chi^2=54.2746$, 15 df, $P<0.0001$) during the entire 16-month study period. However, during the active period (April-November 2003), variation in mean detection index was not significant ($\chi^2=13.4582$, 7 df, $P=0.0617$).
Figure 20. Monthly mean detection indices (+1 SE) of all sonic-tagged female terrapins at creek sites (lower creek, upper creek, and east creek) in Grice Cove (black bars). Refer to Figure 18 for the mean detection index equation. The number of days during the month that the site was monitored is indicated by the dotted line. Temporal variation during the active season (April–November 2003) was not significant ($\chi^2=5.3484$, 7 df, $P=0.6175$).
Figure 21. Monthly mean detection indices (+1 SE) of all sonic-tagged female terrapins at the mudflat in Grice Cove (black bars). Refer to Figure 18 for the mean detection index equation. The number of days during the month that the site was monitored is indicated by the dotted line. Significant temporal variation occurred during the active season and when all transmitters were deployed (April-November 2003) ($\chi^2=33.0245$, 7 df, $P<0.001$).
Figure 22. Monthly mean detection indices (+1 SE) of all sonic-tagged female terrapins at the rocks site in Grice Cove (black bars). Refer to Figure 18 for the mean detection index equation. Note scale of y-axis. The number of days during the month that the site was monitored is indicated by the dotted line. The temporal variation in mean detection indices was significant during the active season (April-November 2003) ($\chi^2=30.8550$, 7 df, P<0.001).
Figure 23. Monthly mean detection indices (+1 SE) of sonic-tagged female terrapins at the beach and Fort Sumter sites (black bars) from April through August varied significantly ($\chi^2=13.7520$, 4 df, $P=0.0081$). Note scale of y-axis. Refer to Figure 18 for the mean detection index equation. The number of days during the month that sites were monitored is indicated by the dotted line.
Figure 24. Weekly mean detections of sonic-tagged female terrapins tagged and released in fall 2002 (n=8; black line) and spring 2003 (n=4 with functional transmitters, dotted line) (+1 SE). Individuals in each group are listed in Table 3. Detections at all sites were combined.
Figure 25. Mean number of detections of sonic-tagged female terrapins during each hour of the day, indicated by black bars (n=12; +1 SE). Temporal variation in mean detections did not differ significantly ($\chi^2 = 7.0196$, 23 df, P=0.9994). Mean tide height (m; black line) and wind speed (kts; dotted line) are indicated. Water level data are from the NOAA National Ocean Service Center for Operational Oceanographic Products and Services station at the Cooper River entrance of the Charleston Harbor, SC (station #8665530). Wind speed data are from the NOAA National Marine Data Buoy Center station on Folly Island, SC (station FBIS1). Data from the sixteen-month study period are combined.
Figure 26. Mean number of detections of sonic-tagged female terrapins during various wind speeds, regardless of wind direction ($n=12$; +1 SE). Data from all sites during the sixteen-month study period are combined. Winds from all directions were combined according to speed. The number of times wind in each speed category occurred during the study period is indicated by the dotted line. Wind speed data are from the NOAA National Marine Data Buoy Center station on Folly Island, SC (station FBIS1). Wind speed was measured at ten-minute intervals. Mean number of detections varied significantly with wind speed ($\chi^2=212.89$, 13 df, $P<.0001$).
Figure 27. Number of detections of sonic-tagged females at the lower (black line) and upper (black dashed line) creek sites, distributed according to the flood or ebb tide height when they occurred. The distributions of all flood and ebb water levels observed during the study are indicated by lighter, dotted lines.
Figure 28. Number of detections of sonic-tagged females at the mudflat (black line),
distributed according to the flood or ebb tide height when they occurred. The
distributions of all flood and ebb water levels observed during the study are indicated by
lighter, dotted lines.
Figure 29. Number of detections of sonic-tagged females at the rocks site (black line), distributed according to the flood or ebb tide height when they occurred. The distributions of all flood and ebb water levels observed during the study are indicated by lighter, dotted lines.
Figure 30. Combined detections of sonic-tagged females at the beach and Fort Sumter sites, distributed according to the flood or ebb tide height when they occurred. The distributions of all flood and ebb water levels observed during the study are indicated by lighter, dotted lines.
Figure 31. Fourier analysis of detection periodicity for 4,096 consecutive hours of detections from 12 sonic-tagged terrapins in Grice Cove creek during the spring and summer of 2003 (3/29/03-9/14/03). Periodicities of 12 and 24 hours, as well as a weaker 8-hour periodicity, are evident.
Figure 32. Fourier analysis of detection periodicity for 4,096 consecutive hours of detections of sonic-tagged female 1 in Grice Cove creek during the spring and summer of 2003 (3/29/03-9/14/03). Periodicities of approximately 24 and 12 hours, as well as a weaker 8-hour periodicity, are evident.
Figure 33. Reproductive status of adult female terrapins captured at the crock (a), beach (b), or rocks (c) during the spring (April-June 2002 and 2003). Terrapins do move between these sites and this is representative of their location and reproductive status at the time of capture.
Figure 34. Weekly total detections of a female terrapin (sonic transmitter #4) during April through December 2003. This female was released in October 2002 and detected periodically in Grice Cove until June 2004, excluding the winter. Detections at the beach (solid line) and rocks (dashed line) sites are shown. She visited the aggregation area at the rocks multiple times during the spring, alternating with trips to the beach, and again during the fall. She was not detected at either site during the summer.
Figure 35. Hourly detections of a female terrapin (sonic transmitter #5) in the creek (solid grey line), upper creek (solid black line), and mudflat (dotted black line) during August 11-17, 2003. Water level (m) is indicated by the dashed grey line.