# Recent Occurrence, Spatial Distribution, and Temporal Variability of Leatherback Turtles (*Dermochelys coriacea*) in Nearshore Waters of South Carolina, USA

THOMAS M. MURPHY<sup>1</sup>, SALLY R. MURPHY<sup>2,3</sup>, DuBose B. Griffin<sup>2</sup>, and Charlotte P. Hope<sup>1</sup>

<sup>1</sup>South Carolina Department of Natural Resources, 585 Donnelley Drive #2, Green Pond, South Carolina 29446 USA [murphyt@dnr.sc.gov, hopec@dnr.sc.gov];

ABSTRACT. – Based on museum and stranding records, leatherback turtles (*Dermochelys coriacea*) were previously considered a rare migrant in South Carolina nearshore waters with only 9 recorded prior to 1980. In 1989, leatherback sightings increased, both alive and dead, in large numbers. From 1980 to 2003, 141 leatherback carcasses stranded. These leatherback strandings were highly seasonal, with a major peak in spring and a minor peak in fall. Based on 23 necropsies, there were 7 males and 16 females (1:2.3). From 1994 to 2003, during April–June, 1131 live leatherbacks (0.04 per km) were observed during 50 nearshore aerial surveys flown parallel to the South Carolina coast. The highest concentration during a single flight was in May 2002, with 175 leatherbacks seen over 605 km of transect line or 0.29 per km. Leatherbacks were not randomly or uniformly distributed, but had a contagious (clumped) distribution. Numbers observed varied significantly between inner and outer transect lines, among years, and among flights within a year. These lines of evidence demonstrate the recent occurrence, spatial distribution, and temporal variability of leatherbacks in South Carolina nearshore waters.

KEY WORDS. – Reptilia; Testudines; Dermochelyidae; *Dermochelys coriacea*; sea turtle; strandings; aerial surveys; Cnidaria; Scyphozoa; *Stomolophus meleagris*; cannonball jellyfish; South Carolina; USA

Leatherback turtles (*Dermochelys coriacea*), traversing entire ocean basins, are the most itinerant of the sea turtle species (Pritchard 1976; Carr and Meylan 1984; Girondot and Fretey 1996; James et al. 2005). Leatherbacks are protected as Endangered in US waters by the Endangered Species Act (16 USC 1531–1543) and are classified as Critically Endangered worldwide (International Union for the Conservation of Nature and Natural Resources 2004). The biology of nesting females is better known, while foraging habitats and migratory movements are poorly understood. Information on the leatherback's biology while at sea can be obtained from stranded animals, tag recoveries, fishery bycatch data, aerial surveys, and satellite telemetry.

Previous pelagic aerial surveys in the Atlantic documented low numbers of leatherbacks on the continental shelf. They were seen off northeast Florida during February, off the mid-Atlantic states and in northern waters off New England and Nova Scotia in summer and fall (June–November; Thompson and Shoop 1983; Shoop and Kenney 1991; Epperly et al. 1995).

In South Carolina, the Charleston Museum's historical records (established in 1773) indicate that leatherback strandings and sightings prior to 1980 were rare events (n = 9). The earliest was a specimen from 1853 that is mounted and still on display. There were 2 records from the 1930s (including DeSola and Abrams 1933), 2 from

the 1950s (including Schwartz 1954), 1 from the 1960s, and 3 from the 1970s (including Pritchard 1976). The most recent record in the museum's file was in 1975, which predated establishment of the South Carolina Sea Turtle Stranding and Salvage Network (STSSN) in 1980.

Baldwin and Lofton (1940) began the sea turtle program at the Cape Romain National Wildlife Refuge in the late 1930s, and refuge personnel have been active on those beaches up to the present. Any sightings of leatherback strandings or occurrences in nearshore waters within the refuge would have been recorded in their annual reports. Ulrich (1978) monitored strandings in South Carolina during 1976 and 1977, but coverage was not statewide. Ulrich recorded 124 and 123 sea turtle carcasses, respectively, but no leatherbacks were noted. Between 1912 and 1915, shrimp fishermen used otter trawls-which became the standard gear-and by the 1930s, these devices accounted for approximately 90% of the catch (McKenzie 1974). This fishery would have resulted in strandings had leatherbacks been present. These historical records suggest leatherbacks rarely visited the South Carolina coast before the 1980s.

Recently, however, leatherbacks have been observed in Georgia and South Carolina nearshore waters (out to 5.6 km) from March to May and April to June, respectively (M. Harris, *pers. comm.*, 1993, this study). Using several lines of evidence, we describe the historical and recent

<sup>&</sup>lt;sup>2</sup>South Carolina Department of Natural Resources, PO Box 12559, Charleston, South Carolina 29422-2559 USA [griffind@dnr.sc.gov];

<sup>&</sup>lt;sup>3</sup>Present Address: PO Box 136, Sheldon, South Carolina 29941 USA [dacha1@earthlink.net]

occurrence, spatial distribution, and temporal variability of leatherbacks in South Carolina nearshore waters.

#### **METHODS**

Strandings. — In 1980, the South Carolina STSSN was established. Beaches (developed and undeveloped) were monitored daily for strandings during patrols (May-October) for loggerhead nesting and hatchling emergence. On developed beaches without loggerhead nesting surveys, stranded turtles were reported by the public to the stranding network. These 2 methods covered approximately 79% of the coastline. Beginning in 1991, remote beaches were monitored for strandings by monthly aerial stranding surveys (see below) flown north to south at an altitude of 61 m (200 feet) at 185 km/h (100 kt). These monthly aerial surveys increased coverage to approximately 99% of the coastline. One flight per month provided reasonable temporal coverage because previously documented skeletal remains of carcasses above the high tide line were seen during the next aerial survey. Beach patrols, reports from the public, and monthly aerial surveys would have detected any stranded leatherbacks on the coast.

Morphometric data were obtained when possible from carcasses. Fresh specimens were salvaged for postmortem examination to document food habits, sex, reproductive condition, and possible cause of death.

Aerial surveys. — During March, April, and May 1981 and April 1982, surveys were flown off the South Carolina coast. Ten transect lines of 105 km (65 miles offshore, the approximate western edge of the Gulf Stream) were flown perpendicular to the coastline, totaling 1275 km/survey, with distances between lines ranging from 31.1 to 40.7 km. A twin-engine, high-wing Aero Commander was flown at an altitude of 152 m (500 ft) at 222 km/h (120 kt). Two observers, seated left and right rear, reported sea turtles to a recorder seated front right.

On monthly surveys to document carcasses on the beach (mentioned above), the opposite route was flown 1.6 km from shore and parallel to the coast from Port Royal Sound to Murrells Inlet, totaling 191 km/survey. These surveys were conducted once a month from May 1991 to September 2003. A single-engine, high-wing Cessna was flown at an altitude of 274 m (900 feet) at 222 km/h (120 kt). Observers, seated left and right, counted live sea turtles. The pilot and recorder counted commercial shrimp trawlers.

Surveys flown specifically for leatherbacks from 1993 to 2003 were conducted weekly, from mid-April to early June, in a twin-engine, high-wing Aero Commander at an altitude of 274 m (900 feet), and at a speed of 222 km/h (120 kt). Observers were seated left and right rear. Surveys began at approximately 0900 hours and were rescheduled if there were rain or high winds. The early morning start took advantage of calmer sea conditions. Leatherback locations were recorded using Loran-C and Global Positioning Satellite technology. Other sea turtle species

and commercial shrimp trawlers were also counted. Thirty-six waypoints were programmed into the aircraft's computer, with the aircraft flown on autopilot to ensure the same route was covered.

In 1993, surveys consisted of transect lines perpendicular to the coastline. Greater numbers of leatherbacks were observed nearer to shore on the first 3 flights. Therefore, on remaining flights, a transect line parallel to shore was tried. More leatherbacks were observed on the parallel survey routes, thus, this design was used in subsequent years. A standardized route was used rather than a random flight design because of limited flight days and variable conditions affecting observations.

From 1994 to 2003, parallel transect lines were flown 2.8 and 5.6 km from shore along the entire South Carolina coast (Fig. 1). Since some leatherback mortality is fishery-related, distances were selected based on information that commercial shrimpers usually trawled within 6.5 km of shore (W. Shaffer, *pers. comm.*, 1993). Total lengths were 303.8 and 301.2 km (605 km/survey) for the inner and outer transect lines, respectively.

Spatial Distribution and Temporal Variability. — Data from 48 of 50 parallel flights (1994–2003) were analyzed in ArcView 3.2 in the UTM83, Zone 17 projection/datum. Inner and outer transect lines were divided into 5 equal segments of 60.8 and 60.2 km, respectively. Using a contingency table, we tested whether leatherback observations among years and segments were independent. We repeated this analysis with 10 equal segments of 30.4 km (inner) and 30.1 km (outer) to test for possible effects of spatial scale on the analysis (Fig. 1).

We tested whether distances between consecutive leatherback observations during each flight were randomly distributed. Distances between observations were calculated using the Path with Distances and Bearings, v.3.2 extension (Jenness 2005a). We tested goodness of fit to both a normal and uniform distribution using Shapiro-Wilk W and Kolmogorov-Smirnov tests, respectively. The index of dispersion (variance to mean ratio of the distances) to determine the degree of spatial clumping also was calculated (Pielou 1977; Perry and Mead 1979).

Leatherback density could not be determined because the rate of observation was too low to calculate meaningful estimates for turtles visible at the surface. Also, a population estimate for leatherbacks (visible at the surface and submerged) in shallow nearshore waters could not be calculated because residency time and surfacing behavior were unknown.

We tested whether the number of leatherback observations differed between inner and outer transect lines, among years, and among flights within a single year, using the nested analysis of variance. Data were used only when both inner and outer transect lines were flown. Whenever leatherback data did not follow a normal distribution, samples were transformed as  $\log_{10}(x+1)$ . The log-transformed data were normally distributed based on the Shapiro-Wilk W goodness-of-fit test.

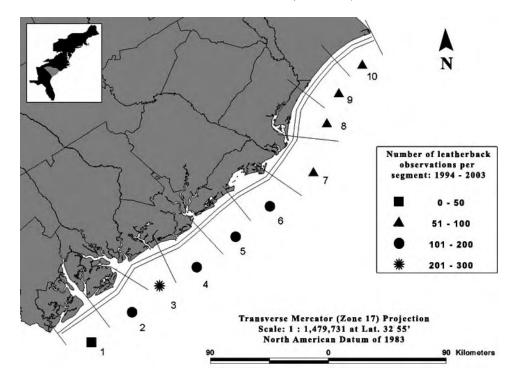


Figure 1. Locations of coastal segments (n = 10) and inner and outer transect lines flown during nearshore aerial surveys.

We also tested whether mean water depth was different between the inner and outer transect lines. One hundred points were placed at equal distances along each transect line (inner and outer) using the Add Points Evenly Along a Line, v.1.3 extension (Lead 2005). Forty points along each line were randomly chosen for analysis using the Random Point Generator, v.1.3 extension (Jenness 2005b). Data were not normally distributed, therefore, differences were tested with the Mann-Whitney statistic. All statistical analyses were conducted using JMP v.5.0.1a (SAS Institute, Inc, Cary, NC).

# **RESULTS**

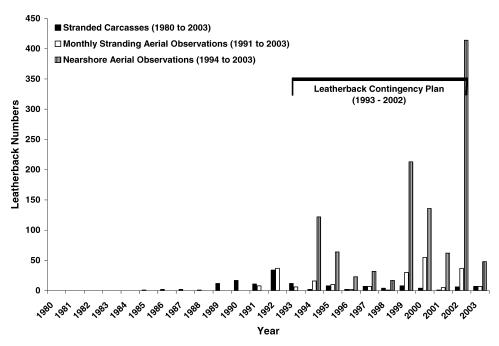
Strandings. — No leatherback strandings were recorded by the South Carolina STSSN coverage during the first 5 years (1980 to 1984), and only 6 were recorded from 1985 through 1988. Strandings increased dramatically from 1 in 1988 to 34 in 1992. Overall, 141 leatherback carcasses have stranded since 1980 (Fig. 2). Leatherback strandings were highly seasonal, with a major peak in spring and a minor peak in fall (Fig. 3). Mean curved carapace length of measurable leatherbacks was 151.7 cm (range 116–185 cm; n = 105). Twenty-seven were juveniles and 78 were adults (1:2.9), based on the size of nesting females at St. Croix, US Virgin Islands, most of which were > 144 cm (Boulon et al. 1996). Thirty-four of the animals had indications of propeller cuts and ship collisions, but it was not always possible to determine if this occurred pre- or postmortem. Six stranded adult females bore flipper tags from nesting beaches in the western Atlantic basin, including Colombia, Costa Rica, French Guiana (2), Puerto Rico, and Trinidad.

Twenty-six carcasses were recovered for postmortem examination. Sex could be determined for 23; there were 7 males and 16 females (1:2.3). Of these, 18 contained cannonball jellyfish (*Stomolophus meleagris*) and spider crab parts (*Libinia dubia* and *L. emerginata*) in the stomach or esophagus, 3 contained only spider crabs, and 5 had no food items.

Aerial Surveys. — During spring of 1981 and 1982, no leatherbacks were observed during 4 surveys covering a total of 5100 km. However, other species of sea turtles were seen (n = 145). From 1991 to 2003, 221 live leatherbacks were recorded during 141 monthly stranding surveys covering 26,931 km. The highest counts by month were 76 in April, 114 in May, and 20 in June (Fig. 3). Only 10 leatherbacks were seen in the other 9 months.

From 1994 to 2003, 1131 leatherbacks were seen during 50 nearshore aerial surveys that covered 30,250 km or 0.04 per km. The highest concentration during a single flight was in May 2002 with 175 leatherbacks seen over 605 km or 0.29 per km. Total annual leatherback observations ranged from 17 to 414 with the mean per flight ranging from 5.3 to 69.0 (Table 1). Almost twice as many turtles were observed on segment 3 off Edisto Island (Table 2; Fig. 1).

Spatial Distribution and Temporal Variability. — Numbers of leatherback observations in each segment for each year were not randomly distributed among 5 segments ( $\chi^2 = 108.64$ , df = 36, p < 0.0001) or 10 segments ( $\chi^2 = 221.88$ , df = 81, p < 0.0001; Table 2).



**Figure 2.** Annual numbers of stranded carcasses and live leatherback observations during monthly stranding (n = 121) and nearshore (n = 50) aerial surveys in South Carolina, respectively.

The frequency distribution was significantly different from normal (Shapiro-Wilk W, W = 0.60, n = 1047, p = 0.0000) and uniform (Kolmogorov-Smirnov, D = 0.27, n = 1047, p < 0.0100). The index of dispersion (I = 41.18) was substantially greater than 1, indicating a contagious or highly clumped distribution.

Numbers of leatherbacks observed differed significantly between inner and outer transect lines ( $F_{1,44} = 24.17$ , p < 0.0001). Of 892 observations used in the analysis, 581 (65.1%) and 311 (34.9%) were observed on the inner and outer transect lines, respectively.

Observations also differed significantly among flights within a year ( $F_{35,44} = 2.68$ , p < 0.0011) and among years ( $F_{9,44} = 4.11$ , p < 0.0011; Table 1). Mean water depths (in meters) for the inner and outer transect lines were  $6.7 \pm 2.1$ SD and  $9.0 \pm 2.1$ SD, respectively, and were significantly different (U = 300.5, p = 0.0000).

#### **DISCUSSION**

This study presents data from strandings and several types of aerial surveys that have demonstrated the sudden

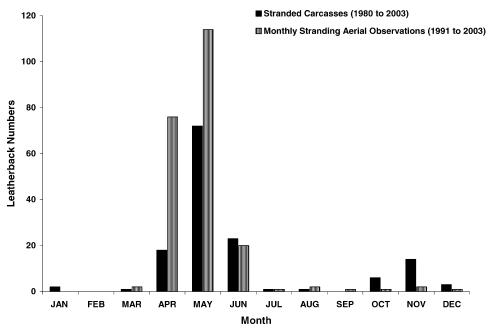


Figure 3. Numbers of stranded carcasses and live leatherback observations during monthly stranding aerial surveys (n = 121) in South Carolina.

**Table 1.** Number of leatherback turtle (*Dermochelys coriacea*) observations during nearshore aerial surveys (n = 50) from 1994 to 2003.

	Flight dates and numbers								
	22–27 Apr	28 Apr–4 May	5–11 May	12–18 May	19–26 May	27 May–3 Jun	Annual	Annual mean	Shrimp fishery opening date in
Year	1	2	3	4	5	6	total	per flight	state waters
1994	44	15	18	16	25	4	122	20.3	26 May
1995	35	14	13	2	no flight	no flight	64	16.0	16 May
1996	no flight	0	2	15	6	no flight	23	5.8	6 Jun
1997	5	5	5	7	8	2	32	5.3	14 May
1998	no flight	16	no flight	1	0	no flight	17	5.7	26 May
1999	69	27	38	41	26	12	213	35.5	26 May
2000	45	19	35	21	7	9	136	22.7	24 May
2001	14	22	14	5	7	no flight	62	12.4	25 Jun
2002	58	60	175	48	53	20	414	69.0	15 May
2003	no flight	10	10	26	no flight	2	48	12.0	10 Jun
Total	270	188	310	182	132	49	1131		
Mean	38.0	18.8	34.4	18.2	16.5	8.2			

and persistent occurrence of leatherbacks in South Carolina nearshore waters from the late 1980s to the early 2000s.

Strandings. — From 1853 to 1988, few leatherbacks were sighted in nearshore waters and/or stranded on the beach. During the first 5 years of the STSSN, when there were no leatherback strandings, 1475 other sea turtles were documented in South Carolina. In 1989, fishermen and South Carolina Department of Natural Resources marine law enforcement personnel reported numerous leatherbacks in nearshore waters. Carcasses also began to strand in unprecedented numbers (Fig. 2). Likewise, leatherback strandings on the east coast of Florida and Georgia, primarily around the Georgia/Florida border, increased from 7 in 1986 to 47 in 1987 (Schroeder 1988).

Annual landings by the commercial shrimp fishery in South Carolina have remained relatively constant from 1980 to 2003 (South Carolina Department of Natural Resources, unpubl. data). If leatherbacks had been in nearshore waters in high numbers prior to 1989, stranding records would have documented their presence, because turtle excluder device (TED) openings were inadequate to exclude leatherbacks. Therefore, increased leatherback

strandings beginning in the late 1980s cannot be attributed to increased shrimping effort.

Strandings and monthly aerial observations of live turtles document the seasonal occurrence of leatherbacks (Fig. 3). While the opening date of the shrimp trawl fishery in state waters (0 to 5.6 km) may vary from year to year (Table 1), trawlers can be active in federal waters from May until December 31 or early January. Thus, if leatherbacks were present in numbers outside of the spring months, shrimp fishery interactions would have reflected this in the form of strandings on the beach.

Most stranded leatherbacks were adults, and females were reproductively quiescent based on examination of reproductive tracts and tagging data. Juveniles were in the larger size classes. Therefore, these animals were either immature or reproductively inactive adults. As shown by loggerhead population models (Crouse et al. 1987), these size classes are most valuable to recovery of a population.

Unbiased sex ratios of free-ranging leatherbacks are hard to obtain because of the difficulty in collecting fresh carcasses and capturing and handling live leatherbacks in the water. Twenty males and 28 females (1:1.4) were identified from the national STSSN (US Gulf of Mexico and Atlantic coast) from 1980 to 1999, based on stranded

**Table 2.** Annual leatherback turtle observations in each of 10 equal segments of the South Carolina coast during nearshore aerial surveys.

Year	Total	Segment									
		1	2	3	4	5	6	7	8	9	10
1994	122	4	7	13	21	17	22	8	12	12	6
1995	64	1	7	6	7	11	14	10	4	1	3
1996	23	2	4	4	1	1	4	2	2	3	0
1997	32	3	1	9	3	6	7	0	2	0	1
1998	17	0	8	3	3	1	0	0	0	1	1
1999	213	6	28	57	16	16	16	18	17	31	8
2000	136	3	16	35	11	19	19	6	9	13	5
2001	62	0	3	7	14	9	8	2	3	8	8
2002	414	6	37	113	28	38	37	28	42	30	55
2003	48	3	1	21	3	6	10	0	0	1	3
Total	1131	28	112	268	107	124	137	74	91	100	90

juvenile leatherbacks (< 145 cm) where sex was determined by necropsy (National Marine Fisheries Service [NMFS] Southeast Fisheries Science Center 2001). Our study used all size classes to determine sex ratio (1M:2.3F) from necropsied leatherbacks because they stranded in South Carolina away from nesting beaches. Female biased sex ratios are frequently reported for other sea turtle species (Wibbels 2003).

As a result of the higher numbers of strandings in Georgia (n = 36; M. Dodd, pers. comm., 2003) and South Carolina (n = 34) in 1991 and 1992, respectively, multiple state and federal agencies developed a Leatherback Contingency Plan (LCP) to reduce leatherback mortality in shrimp trawls. Leatherback Conservation Zone regulations were established to implement the LCP in waters north of Cape Canaveral, Florida, to the North Carolina-Virginia border (60 FR 25260, May 12, 1995; 60 FR 25663, May 12, 1995). If aerial sightings exceeded 10 leatherbacks per 50 nm (92.60 km) of track line, NMFS closed waters within one degree of latitude to shrimp trawlers for 2 weeks, unless they used a TED modified with the leatherback exit opening (60 FR 47713, Sept. 14, 1995). The success of the LCP can be seen in Fig. 2, as leatherback strandings were low relative to aerial observations. The LCP was discontinued when NMFS required leatherback-sized TEDs in all waters at all times on 15 April 2003.

Aerial Surveys. — Leatherbacks are now present in South Carolina nearshore waters during the spring in unprecedented concentrations. This nearshore occurrence has persisted every year since 1989. Leatherbacks arrive across nearshore waters rapidly along the entire coast each spring. The staggered arrival and departure dates of leatherbacks in the southeastern states (Florida, Georgia, and South Carolina) in spring would indicate a northward migration. This idea is supported by James et al. (2005) in which satellite telemetry documented seasonal leatherback migrations (round-trip) between temperate feeding areas and tropical waters. Our seasonal occurrence of leatherbacks in South Carolina nearshore waters may represent a small segment of this migration.

March stranding surveys document the absence of leatherbacks. April leatherback surveys had some of the highest counts, which show a rapid arrival. It is also clear that most leatherbacks were leaving in early June (Table 1) despite the continued availability of cannonball jellyfish. This is further supported by the seasonality of strandings and monthly stranding aerial survey observations before and after this spring occurrence (Fig. 3).

Sporadic leatherback concentrations in the western Atlantic and Gulf of Mexico have been reported, but none have been sustained within season or among years. Leary (1957), on a single flight, observed an estimated 100 leatherbacks in association with cannonball jellyfish approximately 70 m off the Texas coast. This flight covered 30 miles (48.3 km), which converts to 2.07 leatherbacks per km. Extensive aerial surveys in the Gulf

of Mexico in 1980 and 1981 reported 47 leatherbacks in relatively shallow continental shelf waters (Fritts et al. 1983). During the Southeast Turtle Surveys flown in 1982 and 1983, leatherbacks were seen in relatively low numbers throughout the survey area. Even though 98 leatherbacks were observed, 31 of these were in survey block 8 off northern Florida during a single summer. In survey blocks 3, 4, and 5, which were off the coast of South Carolina, 28 leatherbacks were observed during the 11-month survey, with only 14 (none nearshore) seen in April and May 1982 (Thompson and Shoop 1983). In Florida, 128 leatherbacks were observed, but 116 were seen during summer surveys (1982 to 1984), and 58 of these were seen in the summer of 1983 (Schroeder and Thompson 1987). Right whale surveys flown off the coast of northern Florida from 1984 to 1988 did not observe any leatherbacks until February 1988 when 168 were counted in nearshore waters over a two-week period. The highest concentration (68 leatherbacks) was seen between St. Augustine and Sebastian Inlet. Two transect lines were flown equaling approximately 504 km or 0.14 leatherbacks per km (Knowlton and Weigle 1989).

An increase of leatherback observations since 1989 could be attributed to increased nesting populations in the western Atlantic (Boulon et al. 1996; Pritchard 1996; Spotila et al. 1996). However, gradual increases in nesting populations in the western Atlantic do not explain the sudden arrival of leatherbacks in South Carolina nearshore waters. It also does not explain their absence when historic nesting populations in French Guiana were approximately 15,000 (Pritchard 1971).

Spatial Distribution and Temporal Variability. — Leatherback distributions in South Carolina nearshore waters were clumped, with higher numbers along the inner transect line and segment 3 off Edisto Island (Table 2; Fig. 1). Leatherback movements are influenced by the distribution and abundance of their preferred food items (Pritchard 1971, 1976; Lazell 1980; Shoop et al. 1981). Distributions of cannonball jellyfish can be highly clumped and concentrated due to the "continental barrier effect" (Kraeuter and Setzler 1975; Arai 1997; Graham et al. 2001). This may explain the observed clumped distribution and higher numbers on the inner transect line and segment 3 off Edisto Island, especially because cannonball jellyfish and their associated crabs (Gutsell 1928; Hildebrand 1954; Phillips et al. 1969) were the primary food items found during necropsies. Cannonball jellyfish observations during aerial surveys were not included because they were not visible from our altitude.

Higher numbers on the inner transect line may be attributed to shallower water depth. Mean water depth on the inner transect line was 6.7 m compared with 9.0 m on the outer transect line. However, even on the shallower inner line, leatherbacks were able to dive below our visibility threshold, therefore we do not attribute differences to water depth.

Water clarity may also be a factor. Although South Carolina nearshore waters tend to be relatively turbid, this is not uniformly true. Waters tend to be clearer during an incoming tide; off the center of barrier islands away from inlets and sounds; in segments 8, 9, and 10 (no major river discharges); and along the outer transect line. Sightings may have been more difficult on the outer transect line due to slightly higher sea state, but better visibility in these clearer waters could offset this. Leatherbacks were visible below the surface to 2 m (estimated), depending on the relative turbidity both spatially and/or temporally. Therefore, significant differences among flights within a year could result from varying flight conditions—such as sea state, glare, and/or turbidity-rather than the actual number of leatherbacks present in the water during the surveys.

Various factors that resulted in the significant difference in leatherback observations among years remain unknown. However, we speculate the difference is related to the relative abundance of cannonball jellyfish and the residency time and/or surfacing behavior of leatherbacks relative to feeding. All of these factors would be influenced by the temperature-dependent arrival of cannonball jellyfish overlapping with the seasonal migration of leatherbacks.

There is a conundrum as to why leatherbacks were not abundant in South Carolina waters prior to 1989. Calder and Hester (1978) noted cannonball jellyfish were sometimes so abundant they curtailed commercial shrimping; the "Georgia Jumper" TED was originally invented to exclude cannonball jellyfish (S. Boone, pers. comm., 1987). Additionally, South Carolina Department of Natural Resources, Marine Resources Division's (SCDNR MRD) Southeast Area Monitoring and Assessment Program - South Atlantic Shallow Water Trawl Survey (SEAMAP-SA), have documented the presence of cannonball jellyfish in the South Atlantic Bight since 1986. Spring, summer, and fall survey tows (n = 102 per season) were conducted each year in shallow coastal waters from Cape Hatteras, North Carolina, to Cape Canaveral, Florida. Surveys were conducted in 4- to 10-m depth contours (J. Boylan, pers. comm., 2003). Therefore, absence of leatherbacks until the late 1980s is not explained by a lack of cannonball jellyfish prey.

There are few studies that examine the relationship between sea turtle migration and behavior and basinwide climate shifts (Limpus 1989), such as the North Atlantic Oscillation (NAO; Hurrell et al. 2003; Visbeck et al. 2003). One recent study shows that individual reproductive investment and length of the nesting season of leatherbacks in French Guiana were significantly negatively correlated to NAO winter index lagged by 3 years (Rivalan 2004). Although a longer time series is needed to establish any relationship between these climate shifts and our aerial survey data, it is worth mentioning because the sudden appearance of leatherbacks in 1989 coincided with highest positive NAO winter index in recent decades.

## **Management Implications**

Leatherbacks are susceptible to capture by commercial fisheries, including longline gear (Hildebrand 1987; Goff and Lien 1988; National Marine Fisheries Service and US Fish and Wildlife Service 1992; Witzell 1999; Lewison et al. 2004), fish trap warps, buoy anchor lines, and other ropes and cables (National Marine Fisheries Service and US Fish and Wildlife Service 1992), drift and set gill nets (Balazs 1982), lobster and crab pots (Prescott 1988; D. Griffin, *pers. obs.*, 2005). Although leatherback TEDs reduced mortality from the commercial shrimp fishery, they are not required in other trawl fisheries (cannonball jellyfish, whelk, summer flounder, and crab trawl fisheries).

Japan imports up to 10,000 tons of jellyfish products valued at US\$25.5 million annually (Omori and Nakano 2001). Currently, Asian countries are developing fisheries management plans to conserve jellyfish because they are unstable or declining due to pollution, overfishing, or climate change. Consequently, dealers are looking for new sources of jellyfish. Interest in cannonball jellyfish from the United States increased recently because of high consumer demand in Asia (Hsieh et al. 2001). A fishery in Florida has processed cannonball jellyfish since 1992 (Rudloe 1992), and a commercial trawl fishery for cannonball jellyfish in Georgia exists (M. Dodd, *pers. comm.*, 2003). Rising demand in Japan and southeast Asia may create an international market for cannonball jellyfish in state and federal waters off South Carolina.

This new, sudden occurrence of leatherbacks in South Carolina nearshore waters represents a significant management unit away from nesting beaches. It has a high relative abundance of leatherbacks in the western Atlantic and has persisted annually for 14 years. Turtles in this area are temporally predictable, include a wide range of size classes and both sexes, and represent a wide geographic area. Early aerial surveys by Fritts et al. (1983), Thompson and Shoop (1983), and Shoop and Kenny (1992) reported low densities over extensive areas. Although a direct comparison cannot be made, it is clear that the abundance of leatherbacks in South Carolina nearshore waters is much higher. We need to document residency times and surfacing behavior to further evaluate this assemblage of leatherbacks.

Negative impacts to this major assemblage of Atlantic leatherbacks could have significant consequences to the population. Management decisions in state and federal waters must consider the effects of incidental mortality on leatherbacks from existing commercial fisheries and other anthropogenic activities. Additionally, the impacts on turtles of a new commercial fishery harvest of cannonball jellyfish, an important food resource, must be considered.

#### ACKNOWLEDGMENTS

We are grateful to our pilots for their expertise: S. Bogan, B. Harris, M. Lucas, J. Madden, C. McIntosh, A.

Poston, and D. Scott. J. Coker was an excellent observer during flights, and J. Seithel provided invaluable technical and administrative assistance. We also acknowledge the assistance of A. Sanders of the Charleston Museum; J. Fauth, P. Good, and E. Wenner for advice on statistical analyses; and J. Boylan for providing cannonball jellyfish data from SCDNR MRD SEAMAP-SA Shallow Water Trawl Survey. J. Boylan, J. Fauth, F. Holland, and D. Owens provided insightful comments on an earlier draft. We acknowledge and thank 3 anonymous reviewers for extensive comments. These studies were funded in part through National Oceanic and Atmospheric Administration, National Marine Fisheries Service, under an Endangered Species Act Section 6 Cooperative Agreement.

## LITERATURE CITED

- Arai, M. N. 1997. A Functional Biology of Scyphozoa. London: Chapman and Hall, 316 pp.
- Balazs, G.H. 1982. Driftnets catch leatherback turtles. Oryx 16: 428–429.
- Baldwin, W.P., Jr. and Lofton, J.M., Jr. 1940. The loggerheads of Cape Romain. In: Baldwin, W.P., III and Fulcher, Patty (Eds.). Cape Romain Migratory Bird Refuge, US Biological Survey. McClellanville, SC: The Village Museum, pp. 1–36.
- Boulon, R.H., Jr., Dutton, P.H., and McDonald, D.L. 1996. Leatherback turtles (*Dermochelys coriacea*) on St. Croix, US Virgin Islands: fifteen years of conservation. Chelonian Conservation and Biology 2:141–147.
- CALDER, D.R. AND HESTER, B.S. 1978. Phylum Cnidaria. In: Zingmark, R.G. (Ed.). An Annotated Checklist of the Biota of the Coastal Zone of South Carolina. Columbia, SC: University of South Carolina Press, pp. 87–93.
- CARR, A. AND MEYLAN, A. 1984. Testudines. Herpetology Review 15:13.
- CROUSE, D.T., CROWDER, L.B., AND CASWELL, H. 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68:1412–1423.
- DeSola, C.R. and Abrams, F. 1933. Testudinata from southeastern Georgia, including the Okefinokee Swamp. Copeia 1933(1):10–12.
- Epperly, S.P., Braun, J., and Veishlow, A. 1995. Sea turtles in North Carolina waters. Conservation Biology 9:384–394.
- Federal Register 60 FR 25260, May 12, 1995.
- FEDERAL REGISTER 60 FR 25663, May 12, 1995.
- FEDERAL REGISTER 60 FR 47713, September 14, 1995.
- FRITTS, T.H., IRVINE, A.B., JENNINGS, R.D., COLLUM, L.A., HOFFMAN, W., AND McGEHEE, M.A. 1983. Turtles, birds, and mammals in the northern Gulf of Mexico and nearby Atlantic waters. Washington, DC: US Fish and Wildlife Service, Division of Biological Services. FWS/OBS-82/65, 455 pp.
- GIRONDOT, M. AND FRETEY, J. 1996. Leatherback turtles, Dermochelys coriacea, nesting in French Guinea, 1978– 1995. Chelonian Conservation Biology 2(2):204–208.
- GOFF, G.P. AND LIEN, J. 1988. Atlantic leatherback turtle, Dermochelys coriacea, in cold water off Newfoundland and Labrador. Canadian Field Naturalist 102:1–5.
- Graham, W.M., Pages, F., and Hamner, W.M. 2001. A physical context for gelatinous zooplankton aggregations: a review. Hydrobiologia 451:199–212.
- Gutsell, J.S. 1928. The spider crab, *Libinia dubia*, and the jellyfish, *Stomolophus meleagris*, found associated at Beaufort, North Carolina. Ecology 9(3):358–359.

- HILDEBRAND, H.H. 1954. A study of the fauna of the brown shrimp (*Penaus azteus Ives*) grounds in the western Gulf of Mexico. University of Texas Publications, Institute of Marine Science 3(2):233–366.
- HILDEBRAND, H. 1987. A reconnaissance of beaches and coastal waters from the border of Belize to the Mississippi River as habitats for marine turtles. Final Report to the National Oceanic and Atmospheric Administration, National Marine Fisheries Service, Southeast Fisheries Center, Panama City Lab, pp. 63.
- HSIEH, Y-H. P., LEONG, F.M., AND RUDLOE, J. 2001. Jellyfish as food. Hydrobiologia 451:11–17.
- HURRELL, J.W., KUSHNIR, Y., OTTERSEN, G., AND VISBECK, M. 2003. An overview of the North Atlantic Oscillation. In: Hurrell, J.W., Kushnir, Y., Ottersen, G., and Visbeck, M. (Eds.). The North Atlantic Oscillation: Climate Significance and Environmental Impact. Geophysical Monograph Series 134:1–35.
- International Union for the Conservation of Nature and Natural Resources. 2004. Red List of Threatened Species. http://www.redlist.org.
- JAMES, M.C., OTTENSMEYER, C.A., AND MYERS, R.A. 2005. Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. Ecology Letters 8:195–201.
- JENNESS, J. 2005a. Path, with distances and bearings (pathfind.avx) extension for ArcView 3.x, v. 3.2. Jenness Enterprises. http://www.jennessent.com/arcview/path.htm.
- Jenness, J. 2005b. Random point generator (randpts.avx) extension for ArcView 3.x, v. 1.3. Jenness Enterprises. http://www.jennessent.com/arcview/random\_points.htm.
- Knowlton, A.R. and Weigle, B. 1989. A note on the distribution of leatherback turtles *Dermochelys coriacea* along the Florida coast in February 1988. In: Eckert, S.A, Eckert, K.L., and Richardson, T.H. (Compilers). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. National Oceanic and Atmospheric Administration Technical Memorandum, National Marine Fisheries Service Southeast Fisheries Center 232:83–85.
- KRAEUTER, J.N. AND SETZLER, E.M. 1975. The seasonal cycle of Scyphozoa and Cubozoa in Georgia estuaries. Bulletin of Marine Science 25:66–74.
- LAZELL, J.D. 1980. New England waters: critical habitat for marine turtles. Copeia 1980(2):290–295.
- LEAD, S. 2005. Add Points Evenly Along a Line extension for ArcView 3.x, v. 1.3. http://arcscripts.esri.com/details. asp?dbid=11406.
- LEARY, T.R. 1957. A schooling of leatherback turtles, *Dermochelys coriacea*, on the Texas coast. Copeia 1957(3):232.
- Lewison, R.L., Freeman, S.A., and Crowder, L.B. 2004. Quantifying the effects of fisheries on threatened species: the impact of pelagic longlines on loggerhead and leatherback sea turtles. Ecological Letters 7:221–231.
- LIMPUS, C.J. 1989. Environmental regulation of green turtle breeding in Eastern Australia. In: Eckert, S.A., Eckert K.L., and Richardson, T.H. (Comps.). Proceedings of the Ninth Annual Workshop on Sea Turtle Conservation and Biology. National Oceanic and Atmospheric Administration Technical Memorandum, National Marine Fisheries Service - Southeast Fisheries Center 232:93–95.
- McKenzie, M.D. 1974. Description of industry: harvesting sector. South Carolina Marine Resources Center Technical Report Number 5:36–69.
- NATIONAL MARINE FISHERIES SERVICE, SOUTHEAST FISHERIES SCIENCE CENTER. 2001. Stock assessments of loggerhead and leatherback sea turtles and an assessment of the impact of the pelagic longline fishery on the loggerhead and leatherback sea turtles

- on the western North Atlantic. US Dep. Commer., NOAA Tech. Memor. NMFS-SEFSC-455, 343 pp.
- NATIONAL MARINE FISHERIES SERVICE AND US FISH AND WILDLIFE SERVICE. 1992. Recovery plan for leatherback turtles in the US Caribbean, Atlantic and Gulf of Mexico. Washington, DC: National Marine Fisheries Service, pp. 65.
- OMORI, M. AND NAKANO, E. 2001. Jellyfish fisheries in southeast Asia. Hydrobiologia 451:19–26.
- Perry, J.N. and Mead, R. 1979. On the power of the index of dispersion test to detect spatial pattern. Biometrics 3:613–622.
- PHILLIPS, P.J., BURKE, W.D., AND KOENER, E.J. 1969. Observations on the trophic significance of jellyfishes in Mississippi Sound with quantitative data on the associative behavior of small fishes with medusae. Transactions of the American Fisheries Society 98(4):703–712.
- Pielou, E.C. 1977. Mathematical Ecology. New York: John Wiley and Sons, 385 pp.
- PRESCOTT, R.L. 1988. Leatherbacks in Cape Cod Bay, Massachusetts, 1977–1987. In: Schroeder, B.A. (Comp.). Proceedings of the Eight Annual Workshop on Sea Turtle Conservation and Biology. National Oceanic and Atmospheric Administration Technical Memorandum, National Marine Fisheries Service Southeast Fisheries Center 214:83–84.
- PRITCHARD, P.C.H. 1971. The leatherback or leathery turtle Dermochelys coriacea. IUCN Monographs 1:1–39.
- PRITCHARD, P.C.H. 1976. Post-nesting movements of marine turtles (Cheloniidae and Dermochelyidae) tagged in the Guianas. Copeia 1976(4):749–754.
- PRITCHARD, P.C.H. 1996. Are leatherbacks really threatened with extinction? Chelonian Conservation and Biology 2:303–305.
- RIVALAN, P. 2004. La dynamique des populations des tortues luths de Guyane Française: recherché des facteurs impliqués et application à la mise en place de strategies de conservation. Ph. D. Dissertation. Universite de Paris XI Orsay Laboratoire Systématique et Evolution; 2004, 249 pp.
- ROUNTREE, R.A. 1983. The ecology of *Stomolophus meleagris*, the cannonball jellyfish, and its symbionts, with special emphasis on behavior. Unpublished manuscript. Wilmington, NC, University of North Carolina, 69 pp.
- RUDLOE, J. 1992. Jellyfish: a new fishery for the Florida panhandle. A report to the US Department of Commerce Economic Development Administration. EDA Project No. 04-06-03801, pp. 35.
- Schroeder, B.A. 1988. Sea turtle strandings and salvage network (STSSN): 1987 results. In: Schroeder, B.A. (Comp.). Proceedings of the Eight Annual Workshop on Sea Turtle Conservation and Biology. National Oceanic and Atmospheric Administra-

- tion Technical Memorandum, National Marine Fisheries Service - Southeast Fisheries Center 214:99–101.
- Schroeder, B.A. and Thompson, N.B. 1987. Distribution of the loggerhead turtle, *Caretta caretta*, and the leatherback turtle, *Dermochelys coriacea*, in the Cape Canaveral, Florida area: results of aerial surveys. In: Witzell, W.N. (Ed.). Ecology of East Florida Sea Turtles. NOAA Tech. Rep. National Marine Fisheries Service 53:45–53.
- Schwartz, A. 1954. A record of the Atlantic leatherback turtle (*Dermochelys c. coriacea*) in South Carolina. Herpetologica 10:7.
- Shoop, C.R., Doty, T.L., AND Bray, N.E. 1981. Sea turtles in the region between Cape Hatteras and Nova Scotia in 1979. In: A Characterization of Marine Mammals and Turtles in the Midand North-Atlantic Areas of the US Outer Continental Shelf (CeTAP), Executive Summary, pp. 68–75.
- SHOOP, C.R. AND KENNEY, R.D. 1991. Seasonal distributions and abundances of loggerhead and leatherback sea turtles in waters of the northeastern United States. Herpetological Monographs 6:43–67.
- SPOTILA, J.R., DUNHAM, A.E., LESLIE, A.J., STEYERMARK, A.C., PLOTKIN, P.T., AND PALADINO, F.V. 1996. Worldwide population decline of *Dermochelys coriacea*: are leatherback turtles going extinct? Chelonian Conservation and Biology 2:209–222.
- THOMPSON, T.J. AND SHOOP, C.R. 1983. Southeast Turtle Survey (SETS), pelagic surveys. Final report to the National Marine Fisheries Service. Groton, CT: Aero-Marine Surveys, Inc., 76 pp.
- ULRICH, G.F. 1978. Incidental catch of loggerhead turtles by South Carolina commercial fisheries. Report to the National Marine Fisheries Service, Contract No. 03-7-042-35151 and 03-7-042-35121, 36 pp.
- VISBECK, M., CHASSIGNET, E.P., CURRY, R.G., DELWORTH, T.L., DICKSON, R.R., AND KRAHMANN, G. 2003. The ocean's response to North Atlantic Oscillation Variability. In: Hurrell, J.W., Kushnir, Y., Ottersen, G., and Visbeck, M. (Eds.). The North Atlantic Oscillation: Climate Significance and Environmental Impact. Geophysical Monograph Series 134:113–145.
- WIBBELS, T. 2003. Critical approaches to sex determination in sea turtles. In: Lutz, P., Musick, J.A., and Wyneken, J. (Eds.). The Biology of Sea Turtles Volume II. pp. 103–134.
- WITZELL, W.N. 1999. Distribution and relative abundance of sea turtles caught incidentally by the US pelagic longline fleet in the western North Atlantic Ocean, 1992–1995. Fishery Bulletin 97:200–211.

Received: 5 December 2003

Revised and Accepted: 10 March 2006