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ORIGINAL PAPER

Foraging habitats and migration corridors utilized by a recovering subpopulation of adult female loggerhead sea turtles: implications for conservation

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Abstract From 1998 to 2008, 68 adult female loggerhead sea turtles (*Caretta caretta*) were instrumented with platform transmitter terminals at nesting beaches in Georgia, North Carolina (NC) and South Carolina (SC) on the East Coast of the United States of America (30°48′N, 81°28′W to 33°51′N, 77°59′W). The majority of post-nesting loggerheads ($N = 42$, 62 %) migrated to foraging habitats in the Mid-Atlantic Bight during May–October, with a subsequent migration occurring during November–March to foraging habitats south of Cape Hatteras, NC. Nine (13 %) loggerheads initially foraged in the near-shore, coastal areas of the South Atlantic Bight, but moved to offshore habitats—closer to the Gulf Stream—during November–March, while fourteen (21 %) loggerheads remained in foraging areas along the mid-continental shelf off of the eastern coast of Florida and/or continued southward to Florida Bay and the Bahamas. The present study delineates important, post-nesting foraging habitats and migration corridors where loggerheads may interact with commercial fisheries—providing managers opportunities to develop and implement optimally effective conservation actions for the recovery of this threatened species.

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DuBose B. Griffin has resigned from South Carolina Department of Natural Resources and Sally R. Murphy, John W. Coker, and Thomas M. Murphy have retired from South Carolina Department of Natural Resources.

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Introduction

Global loggerhead sea turtle (*Caretta caretta*) populations are considered to be declining (NMFS and USFWS 2007). As a result, loggerheads are listed as Endangered on the IUCN Red List (IUCN 2011) and they are protected as a threatened or endangered species under the United States of America (US) Endangered Species Act (ESA)—depending on the distinct population segment (DPS) in question (Federal Register 22 September 2011). Because loggerheads are a wide ranging species, consisting of

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multiple, geographically, and/or genetically distinct subpopulations, and they experience a variety of threats throughout different portions of their range, the US Loggerhead Recovery Team has established five recovery units (with the potential of six; Shamblin et al. 2011) across the western North Atlantic (including the Gulf of Mexico). By using this approach, recovery goals can be established for each unit and the contribution of each unit towards the recovery of the greater western North Atlantic loggerhead population can be adequately measured and monitored (NMFS and USFWS 2008; Jensen et al. 2013).

Loggerheads that nest in Georgia (GA), South Carolina (SC), North Carolina (NC), and Virginia (VA) comprise the smallest and most northerly situated recovery unit in US Atlantic waters (termed the "northern recovery unit" or NRU; Encalada et al. 1998; NMFS and USFWS 2008). Available data indicate that nest numbers in the NRU have declined 1.3 % annually from 1983 to 2008 (NMFS and USFWS 2008), although more recent analyses indicate that segments of this subpopulation may be stabilizing (Pfaller et al. 2013).

Satellite telemetry (Keinath 1993; Plotkin and Spotila 2002; Mansfield 2006; Hawkes et al. 2007, 2011), flipper tagging (Bell and Richardson 1978; Williams and Frick 2008), and isotopic research (Ceriani et al. 2012; Pajuelo et al. 2012a, b) indicate that the majority of NRU post-nesting loggerheads migrate to foraging grounds along the continental shelf from Cape Hatteras, NC to northern New Jersey. These feeding grounds or adult foraging areas (AFAs, Schroeder et al. 2003) are vital to post-nesting loggerheads for replenishing fat stores exhausted during the multiple nesting events and numerous, sometimes unsuccessful, nesting emergences associated with reproduction (Miller and Limpus 2003). Moreover, because loggerheads spend the majority of their adult life away from the nesting beach and in AFAs, it is important to identify the foraging areas and migration routes that these turtles utilize and to determine the spatial and temporal overlap with identified threats (e.g., commercial fisheries, military activities, and dredging; National Research Council 1990; NMFS and USFWS 2007, 2008) or potential threats (e.g., oil and gas exploration, organic pollutants and wind farms; Keller 2013).

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Despite extensive documentation of the incidental capture of sea turtles in some types of fishing gear (Wallace et al. 2010), many commercial fisheries in the western North Atlantic continue to operate unabated and without adequate or effective observer coverage (Murray and Orphanides 2013). As a result, there is little detailed information available on fishing effort, gear deployment location, and the incidental bycatch and mortality rates of sea turtles associated with the various fisheries operating in this region (Moore et al. 2009; Finkbeiner et al. 2011; McClellan et al. 2011). Regulations or enforcement to mitigate these captures are lacking. Examples of individual fisheries or types of gear that have been studied include scallop dredges (Murray 2007; Haas et al. 2008), pound nets (Lutcavage and Musick 1985; Mansfield 2006); gill nets (NCMFC 2006; Murray 2009), hook and line (Epperly et al. 1995b), pots and traps (Allen 2000), and trawls (Epperly et al. 1995a; Murray 2006, 2007; Warden 2011). A recent, comprehensive assessment of available bycatch data by Finkbeiner et al. (2011) demonstrates that loggerheads interact with more fishery types than any other sea turtle species in the USA—resulting in an estimated minimum of 1,400 mortalities annually. Such data underscore the necessity of identifying important migration corridors and foraging areas utilized by loggerhead turtles so that managers and legislators are afforded the opportunity to provide adequate protection to this vulnerable species (Hawkes et al. 2011).

The present study, which combines data from three independent research projects, supplements previous examinations (outlined above) of the post-nesting foraging habitats and migration corridors utilized by NRU loggerhead turtles. We compare and discuss our results with respect to the post-nesting behavior of NRU loggerheads reported elsewhere, and comparisons are made with respect to the post-nesting behavior exhibited by loggerhead turtles in other regions of the world. Our data highlight areas along the US Atlantic coast, where loggerheads might interact with commercial fishing operations and other anthropogenic activities, such as dredging, and they provide managers and legislators with useful, detailed information necessary for the development and implementation of protective measures to adequately facilitate the recovery of loggerhead sea turtles in the southeastern USA.

Materials and methods

Instrumentation

Sixty-eight adult female loggerhead turtles were instrumented with platform transmitter terminals (PTTs), from 1998 to 2008, at seven nesting beaches; these seven nesting

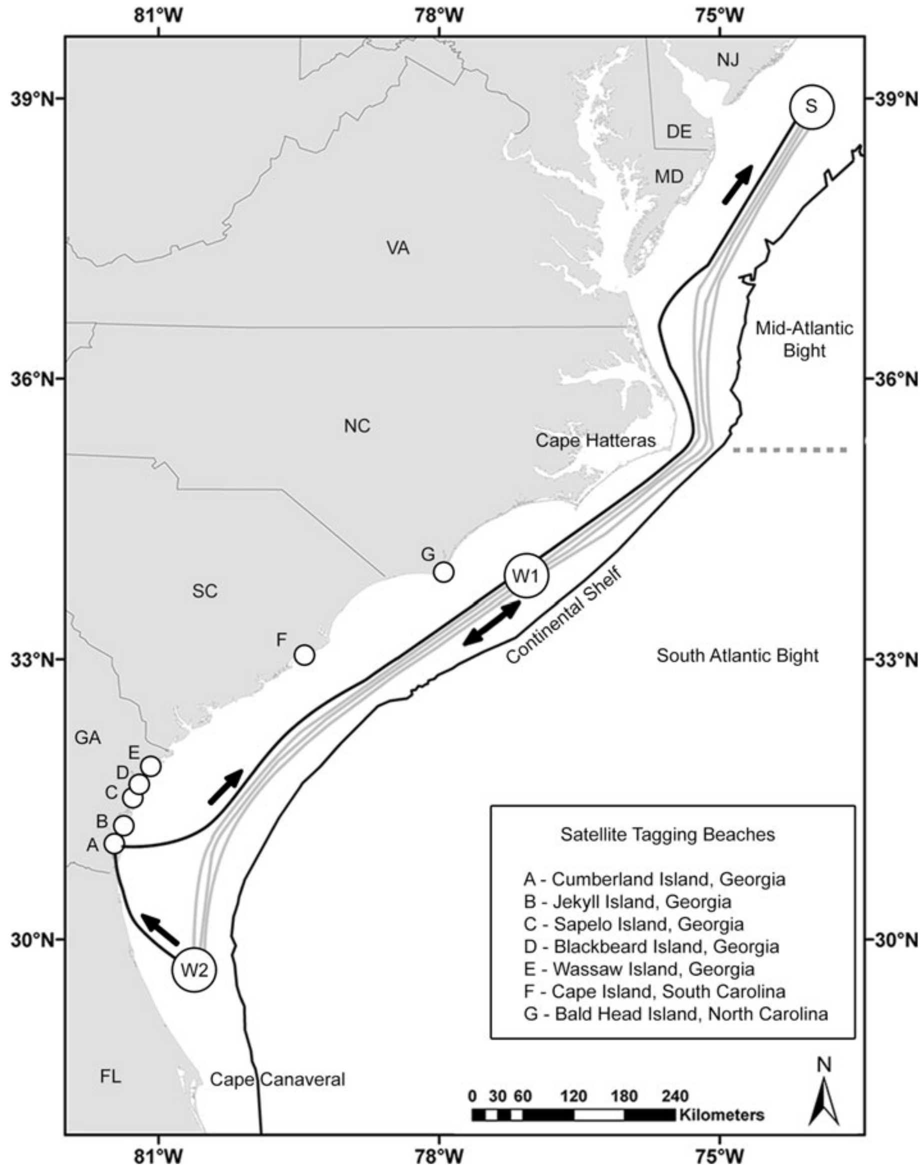


Fig. 1 Schematic of a two-year migration of a loggerhead turtle from a Georgia nesting beach. The migration includes the post-nesting northward migration segment (*black line*) from the beach to the summer adult foraging area (S), the inter-foraging migration segments (*grey lines*) between the summer and winter foraging areas (W1 and W2), and a breeding migration segment (*shorter black line*) back to the nesting beach. The *horizontal dotted line* separates the Mid-Atlantic and South Atlantic Bights. *DE* Delaware, *FL* Florida, *GA* Georgia, *MD* Maryland, *NC* North Carolina, *NJ* New Jersey, *SC* South Carolina, *VA* Virginia

beaches represent approximately one-third of the nesting effort in the NRU (Fig. 1): Cumberland Island (30°48′N, 81°28′W, $N = 6$), Jekyll Island (31°01′N, 81°26′W, $N = 4$), Sapelo Island (31°28′N, 81°21′W, $N = 10$), Blackbeard Island (31°10′N, 81°27′W, $N = 4$), Wassaw Island (31°03′N, 81°24′W, $N = 5$), GA, Cape Island, SC (33°02′N, 79°21′W, $N = 15$), and Bald Head Island, NC (33°51′N, 77°59′W, $N = 24$).

Data acquisition and filtering

Data transmitted by the PTTs were collected by the Argos system (CLS 2008) and downloaded into the Satellite Tracking and Analysis Tool program from seaturtle.org (STAT; Coyne and Godley 2005). See Appendix 1 for PTT parameters. Argos supplies location classes (LC), which represent error associated with each location (LC 3 < 150 m, LC 2 150–350 m, LC 1 350–1,000 m, LC 0 > 1,000 m, LC A and B: no estimate, LC Z: invalid, CLS 2008). Associated error can vary with space and time (Witt et al. 2010).

Data were filtered using STAT (Coyne and Godley 2005) and a custom script written for MATLAB (The Mathworks, Inc., Natick, MA). Data were used if they met the following criteria: LC 3, 2, 1, and A (Hays et al. 2001; van Vincent et al. 2002; Nicholls et al. 2007; Royer and Lutcavage 2008; Witt et al. 2010), speeds slower than 3.0 km h^{-1} (Limpus et al. 1992; Papi et al. 1997; Sakamoto et al. 1997), water deeper than 1.0 m, and one data point per 24 h to reduce the effects of autocorrelation (de Solla et al. 1999).

Terminology

A DPS is a vertebrate population or group of populations that is discrete from other populations of the species and significant in relation to the entire species (Federal Register 7 February 1996). A "recovery unit" is based on genetic differences, and a combination of geographic distribution of nesting densities, geographic separation and geopolitical boundaries. Recovery units are subunits of a listed species that are geographically or otherwise identifiable and essential to the recovery of the species (NMFS and USFWS 2008).

In this paper, summer months are May through October, and winter months are November through April. Turtle migrations occurred at the end and beginning of the summer or winter season, but they were of relatively short duration compared to their time on foraging areas. To maintain a larger sample size, only two seasons were used.

We classified loggerhead location data points as "migratory" or "foraging" based on the turtles' movement. Loggerheads that exhibited a constant unidirectional movement between consecutive locations were considered to be migrating. When location data received from a loggerhead were no longer unidirectional and the consecutive locations were in no particular direction, but concentrated in a distinct area, the loggerhead in question was assumed to be in its AFA (See map at: http://www.seaturtle.org/tracking/index/shtml?tag_id=49433&full=1&lang=). As a loggerhead migrated to its AFA, the last location outside of the concentration of points was designated as the end of migration. The next location located within the concentration of points was designated as the onset of foraging. The same method was used when loggerheads left their AFAs. The first location outside of the concentration of points was the onset of migration.

A migration is defined as a round trip. An adult female loggerhead migration consisted of two or three segments: post-nesting, inter-foraging (only those loggerheads moving between seasonal AFAs), and breeding (moving from the AFA back to the nesting beach). For analysis, some post-nesting and inter-foraging segments were combined over a 12-month period and labeled as "annual" so that they could be compared with year-round distances (Fig. 2; Table 1). Loggerheads exhibited three foraging strategies: (1) seasonal large-scale, (2) seasonal small-scale, and (3) year-round. "Seasonal" (large-scale and small-scale) loggerheads moved in response to changing temperatures. "Year-round" loggerheads remained in the same area regardless of the time of year (Fig. 2; Table 1) (see also Hawkes et al. 2007, 2011).

Migration and adult foraging strategies

Migration routes were mapped in ArcGIS 10.0 (ESRI, Redlands, CA) for individual loggerhead turtles using filtered location data. The geographic mean (centroid) of the location data was used to plot each AFA. The 20-m isobath contour was derived from NOAA's National Geophysical Data Center US Coastal Relief Model volumes 1, 2, and 3 (NOAA 2011). Distances were compared among post-nesting, inter-foraging, and "annual" migration segments (Fig. 2; Table 1). Annual segment distances were compared among foraging strategies. Welch's ANOVA and the Games–Howell post hoc test were used to compare migration segment distances among the foraging strategies (seasonal large-scale, seasonal small-scale, and year-round) as variances were not equal.

Foraging habitat areas

Adult foraging habitat areas (more than one loggerhead used the area at some point in time during the duration of the study, not necessarily at the same time) were identified by overlaying all filtered location data on a $0.01° \times 0.01°$ grid and counting the number of individual loggerheads in each cell. This area within each grid cell roughly approximates to 1 km^2 and incorporates the majority of error in Argos positions used in this study. The selected grid cell

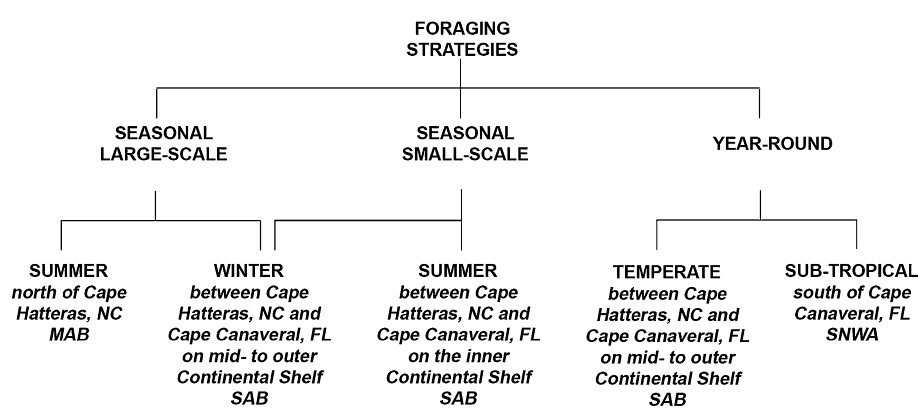


Fig. 2 Schematic of foraging strategies used by satellite tracked loggerhead turtles from Georgia, South, and North Carolina (NC) nesting beaches. Summer = May–October, winter = November–April. *MAB* Mid-Atlantic Bight, *SAB* South Atlantic Bight, *SNWA* Sub-tropical Northwest Atlantic, *FL* Florida

Table 1 Migration segments and foraging strategies used by satellite-tracked loggerhead turtles from Georgia, North and South Carolina nesting beaches

Category	Type	Description
Migration Segment	Post-nesting	Movement from nesting beach to summer foraging area after nesting
	Inter-foraging	North-to-south (west-to-east) and south-to-north (east-to-west) movement between summer and winter foraging areas
	Breeding	Movement from foraging area to nesting beach
	Annual (excludes breeding)	(1) seasonal foraging strategy: post-nesting plus inter-foraging segments;(2) year-round foraging strategy: post-nesting segment only
Foraging Strategy	Seasonal large-scale	Long, sustained movement in a north-to-south (or south-to-north) direction in response to temperature
	Seasonal small-scale	Gradual shift in a west-to-east (or east-to-west) direction in response to temperature
	Year-round	Loggerheads remain in their foraging area all months of the year

Summer May–October, *Winter* November–April

size expedited processing and, therefore, allowed for more efficient experimentation with modeling parameters to select optimal values. It is acknowledged that degree grid cells will have different areas (km^2) depending on latitude that could affect the results of any spatial analysis. However, this study does not conduct any spatial analyses, but provides an actual count of individual loggerheads from the location data. Foraging data were identified as seasonal (summer or winter) or year-round. If foraging data from seasonal and year-round loggerheads overlapped, the number of loggerheads in each grid cell represents this overlap. The number of individual loggerheads in each grid cell was determined using a custom script for MATLAB.

Results

Data summary

The mean curved carapace length for loggerheads in this study was 99.3 cm (SD ± 6.57 cm; range 82.8–112.0 cm; $N = 64$; four loggerheads were not measured). Mean PTT duration was 372 d (SD ± 210 days; range 19–997 days; $N = 68$). Thirty-seven PTTs functioned for longer than 365 days and two transmitted for <1 month. Locations with LC 3, 2, 1, and A comprised 40.3 % of the data received. Of the 68 instrumented loggerheads, 48 provided migration data, while 65 provided data to identify the foraging strategy (seasonal large-scale, seasonal small-scale, and year-round). Data from 63 loggerheads were used to (1) determine the location of the AFA and (2) warrant inclusion in the adult foraging habitat area grid.

Migration

Forty-two loggerheads utilized migration routes along the continental shelf. Six migration routes deviated away from the shelf [four loggerheads made oceanic excursions off of the shelf (mean = 105 days; SD ± 60.8 days; range 54–192 days), and two loggerheads crossed oceanic waters to reach the Bahamas]. All four loggerheads that exhibited oceanic excursions eventually returned to their respective foraging areas along the shelf. Three departed the shelf during the winter and returned to the shelf the following June, and one turtle left the shelf in November to return the following February. Loggerheads that traveled to a summer AFA north of Cape Hatteras (35°N latitude) to the Mid-Atlantic Bight (MAB; Cape Hatteras to Cape Cod, Massachusetts) exhibited a southward movement from mid-September through November to a winter AFA in the South Atlantic Bight [SAB; between Cape Hatteras and Cape Canaveral, Florida (FL)]. This was followed by a northward movement from April through June to return to their summer AFA (Figs. 1, 3). One loggerhead's PTT functioned long enough to document the breeding migration segment from a southerly winter AFA back to habitats adjacent to the nesting beach where the loggerhead was initially satellite-tagged 2 years prior (Fig. 1).

Typically, when a loggerhead left the nesting beach or their AFA, they each followed a distinct route rather than an overlapping route used by other turtles. During the post-nesting migration segment for these turtles, loggerheads headed directly toward Cape Hatteras and did not follow the "scalloped" contours of the NC coast. Loggerheads moving between seasonal AFAs were concentrated while passing through a migration corridor around Cape Hatteras where the shelf narrows (minimum width of shelf = ~38 km; Fig. 4). In general, loggerheads traveled through this corridor during 7 months of the year (July–August: post-nesting migration segment; mid-September–November: southward inter-foraging migration segment; April–June: northward inter-foraging migration segment; Fig. 3). Loggerheads that traveled south to Florida Bay or the Bahamas ($N = 4$) migrated close to the shore, along the

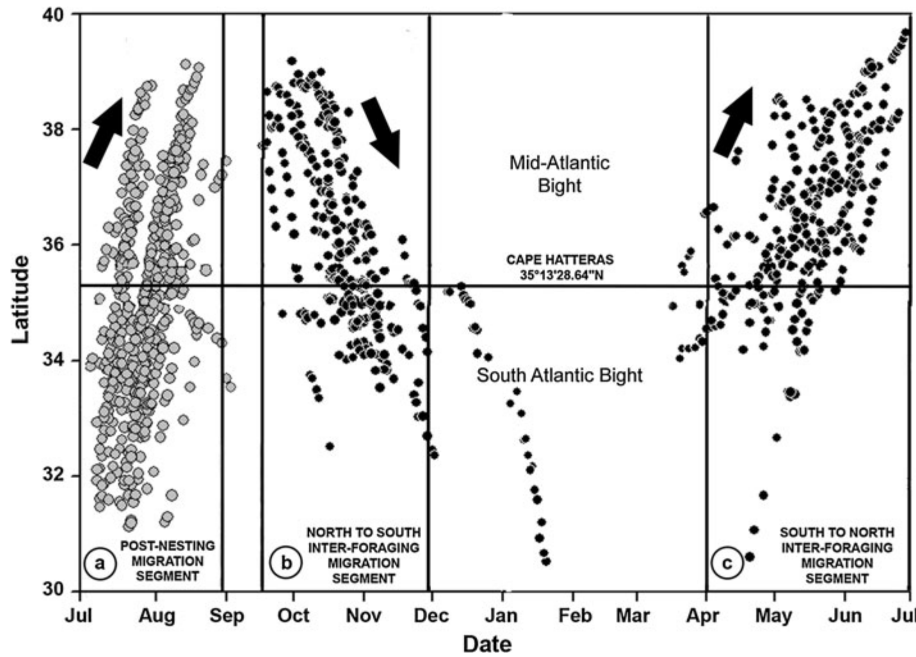


Fig. 3 Temporal and spatial seasonal migration distribution of satellite-tracked loggerheads during (*a*) post-nesting migration segment to summer adult foraging area (AFA), (*b*) inter-foraging migration segment from summer to winter AFA, and (*c*) inter-foraging migration segment from winter to summer AFA. The *horizontal line* represents Cape Hatteras, North Carolina and separates the Mid-Atlantic and South Atlantic Bights. Each *dot* represents one location point per day per loggerhead (there was not necessarily one point per loggerhead for every day). *Grey dots* represent post-nesting migration data. *Black dots* represent inter-foraging migration data

narrow shelf of south Florida (FL; minimum width of shelf = ~7 km).

Forty-eight loggerheads provided location data that allowed us to measure their migration segment distances (post-nesting, inter-foraging, and annual). Migration segment distances are reported in Table 2. There is a significant difference among the distances traveled by loggerheads that coincides with the particular foraging strategy exhibited by turtles (Welch's ANOVA, $F_{(2, 18.6)} = 50.1$, $P < 0.001$). Post hoc tests revealed that annual segment distances for loggerheads that utilized a seasonal large-scale foraging strategy were significantly greater than seasonal small-scale ($P < 0.001$) and year-round foraging strategies ($P < 0.001$). Seasonal small-scale and year-round foraging strategy distances were not significantly different ($P > 0.84$).

Adult foraging areas and foraging strategies

All AFAs were located along the continental shelf (Fig. 5a, b). Of the 68 loggerheads instrumented, 42 (62 %) traveled to a summer AFA that was generally north of Cape Hatteras in the MAB, indicating a seasonal large-scale foraging strategy. Loggerheads were typically present in these summer AFAs from May through October and present in winter AFAs (located in the SAB) from November to April. Nine (13 %) loggerheads traveled to summer AFAs that were located in the SAB and exhibited a small-scale foraging strategy (Table 3).

Fourteen (21 %) loggerheads exhibited a year-round foraging strategy within their AFAs. Year-round AFAs were situated in temperate zones along the mid-shelf (20–40 m isobaths) and along the outer shelf (40-m isobath to the shelf break; Aretxabaleta et al. 2006) of the SAB, or they were situated in the subtropical clines south of Cape Canaveral. Collectively, year-round AFAs ranged from the northern coast of SC to more southerly areas like Florida Bay and the Bahamas (Table 3). Three loggerheads (4 %) provided incomplete data that were insufficient for determining foraging strategy and location.

Adult female foraging habitat areas

Of the 65 loggerheads with a clearly discernible foraging strategy, 63 provided data useful in identifying foraging habitat areas along the continental shelf. The number of individual loggerheads per grid cell for summer, winter, and year-round foraging habitat areas ranged from 1 to 5, 1 to 12, and 1 to 3 loggerheads, respectively (Fig. 6a, b, c). Location data from 12 individual loggerheads with seasonal and year-round foraging strategies overlapped.

Summer: Grid cells that contained at least four individual loggerheads included (1) 92 km off the south coast of New Jersey, (2) within 20 km of the Delmarva Peninsula, (3) 35 km east of the mouth of the Chesapeake Bay, and (4) 15 to 45 km near-shore along the southern VA coast and the NC Outer Banks. These adult female foraging habitat areas are found in the MAB and are defined in Fig. 6a.

Winter: Higher turtle densities existed during the winter months with grid cells containing as many as 12 loggerheads (compared with a maximum of five individuals per grid cell for summer). The area with the highest concentration of adult female loggerheads was located 101 km

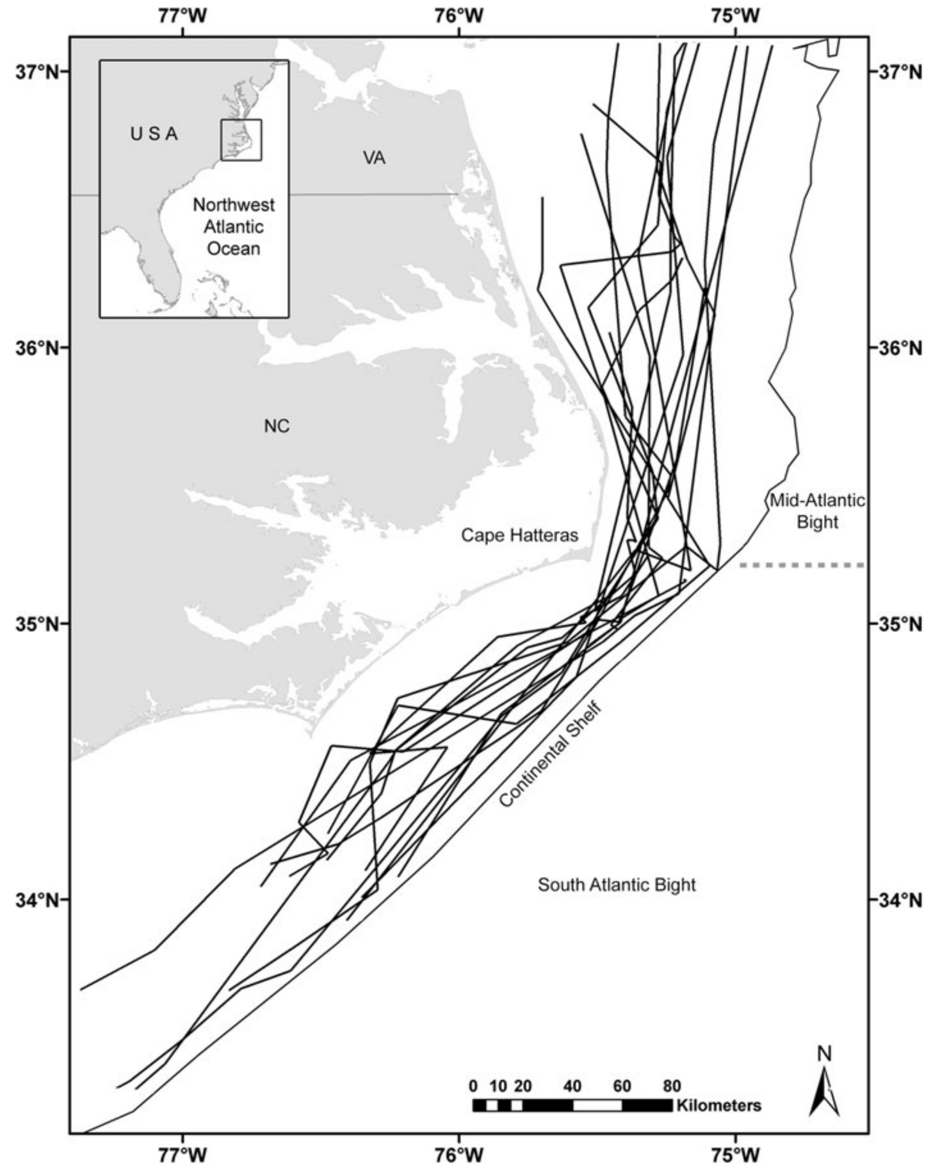


Fig. 4 Migration routes (post-nesting and inter-foraging segments) of satellite-tracked loggerhead turtles ($N = 15$) represented by individual *black lines* in the Cape Hatteras, North Carolina (NC) region. The *horizontal dotted line* separates the Mid-Atlantic and South Atlantic Bights. *USA* United States of America, *VA* Virginia

Table 2 Migration segment distances for each foraging strategy used by satellite-tracked loggerhead turtles from Georgia, North and South Carolina nesting beaches

Migration segment	Foraging strategy	Mean (km)	SD (±km)	Range (km)	No. of loggerheads
Post-nesting	All	696.0	307.1	115.0–1,253.0	48
	Seasonal large-scale	788.6	252.5	341.0–1,252.0	29
	Seasonal small-scale	376.4	213.8	181.0–727.0	5
	year-round	618.3	353.0	115.0–1,253.0	14
Inter-foraging	Seasonal large-scale	944.4	335.3	308.0–1,478.0	29
	Seasonal small-scale	172.8	41.8	116.0–232.0	5
Annual	All	1284.6	713.1	115.0–2,666.0	48
	Seasonal large-scale	1733.0	514.1	735.0–2,666.0	29
	Seasonal small-scale	549.2	181.2	363.0–843.0	5
	Year-round	618.3	353.0	115.0–1,253.0	14

Forty-eight loggerheads provided location data to measure their migration segment distances (post-nesting, inter-foraging, and annual)

SD one standard deviation

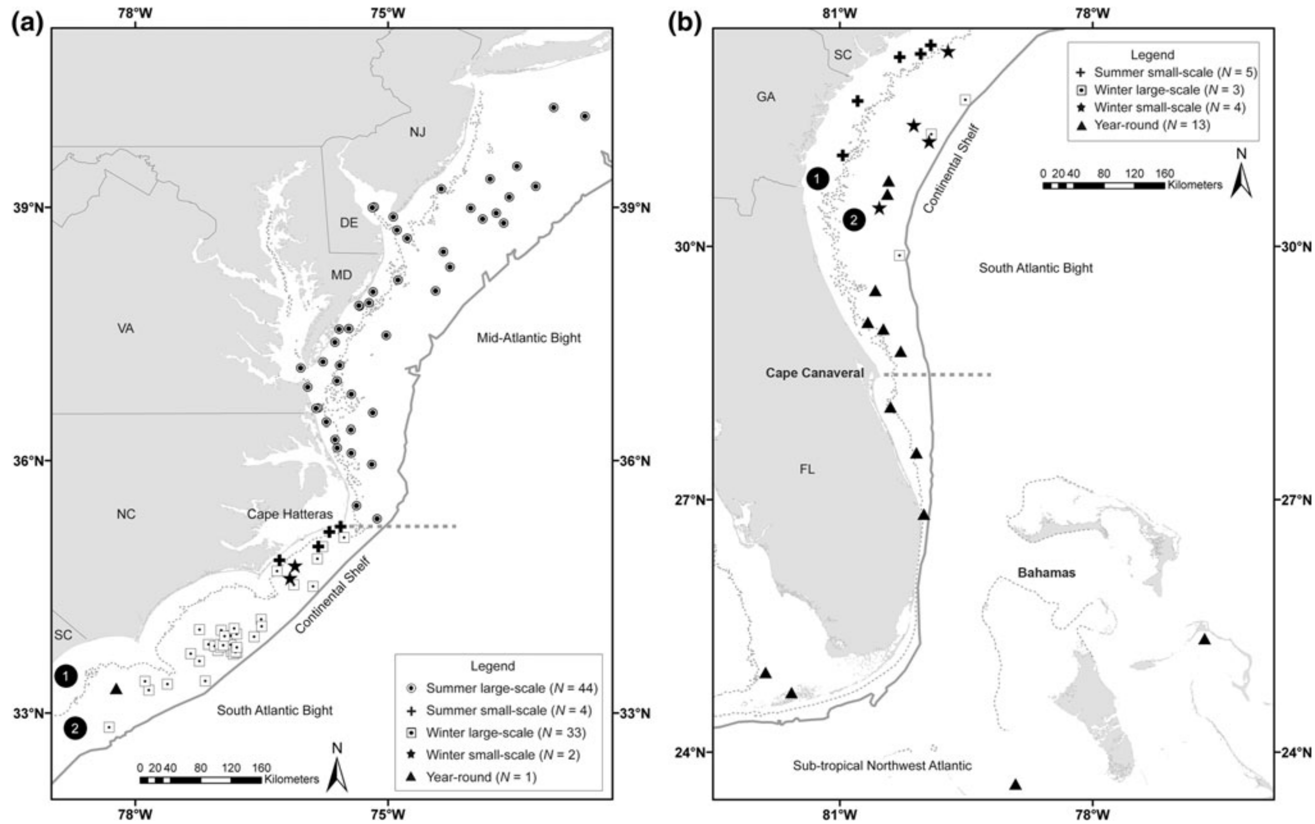


Fig. 5 **a** Geographic mean (centroid) of adult foraging areas (AFA) for satellite-tracked loggerheads on the Continental Shelf from northern South Carolina (SC) to New Jersey (NJ). There may be more than one AFA per turtle. The inner (1) and mid- to outer (2) continental shelf are separated by the 20-m isobath bar (*dotted line*). The horizontal dotted line separates the Mid-Atlantic and South Atlantic Bights. *DE* Delaware, *MD* Maryland, *NC* North Carolina, *VA* Virginia. **b** Geographic mean (centroid) of AFA for satellite-tracked loggerheads on the continental shelf from southern South Carolina (SC) to the Bahamas. There may be more than one AFA per turtle. The inner (1) and mid- to outer (2) continental shelf are separated by the 20-m isobath bar (*dotted line*). The *horizontal dotted line* separates the South Atlantic Bight from the sub-tropical Northwest Atlantic. *FL* Florida, *GA* Georgia

Table 3 Number (and percentage) of satellite-tracked loggerheads from Georgia (GA), North (NC) and South Carolina (SC) nesting beaches that exhibited each of the three foraging strategies (seasonal large-scale, seasonal small-scale and year-round)

Foraging strategy	GA	NC	SC	Total
Seasonal large-scale	20 (69 %)	13 (54 %)	9 (60 %)	42 (62 %)
Seasonal small-scale	4 (14 %)	5 (21 %)	0 (0 %)	9 (13 %)
Year-round	4 (14 %)	6 (25 %)	4 (27 %)	14 (21 %)
No data	1 (3 %)	0 (0 %)	2 (13 %)	3 (4 %)
Total	29	24	15	68

Sixty-five turtles provided location data to determine their foraging strategy

southeast of Onslow Bay, NC, between Frying Pan Shoals and Cape Lookout Shoals in the SAB (Fig. 6b). Loggerheads off of GA and SC moved farther offshore in the winter, departing AFAs along the inner shelf and travelling to foraging areas along the mid- or outer shelf (Fig. 6a, b).

Year-round: The lowest density of loggerheads was associated with a year-round strategy (most likely attributable to the small sample size of turtles performing this foraging strategy) with a maximum of three individuals in any one grid cell (Fig. 6c). The most pronounced area was ~55 km northeast of Cape Canaveral. Similarly, up to three individual loggerheads per grid cell were located 112 km off of the southern coast of GA and 110 km off of the northern coast of SC.

Discussion

The present study temporally and spatially identifies areas along the Atlantic Coast of the USA utilized by multiple, adult female loggerheads for migration and foraging. These areas are also recognized as important habitats for other loggerhead ontogenies and other sea turtle species, including adult male loggerheads (Arendt et al. 2012a, b), juvenile loggerheads, Kemp's ridleys (*Lepidochelys* *kempi*), and green sea turtles (*Chelonia mydas*); Byles 1988; Keinath 1993; Morreale and Standora 2005; Mansfield 2006; McClellan and Read 2007; Arendt et al. 2012c). Considering the significant number of sea turtles moving between habitats from New England to Florida during autumn and spring, effective conservation actions must occur in these areas in order to achieve the recovery goals initiated for each of these protected species.

Migration

Typically, when loggerheads leave the nesting beach or their seasonal AFA, they utilize the entire continental shelf as a migration corridor until it narrows at Cape Hatteras in the north of our study area and at Cape Canaveral in the south of our study area. A report by the Turtle Expert Working Group (2009) noted that loggerhead females in FL that depart the same nesting beach and share a similar post-nesting destination do not necessarily follow the same route. In areas where the shelf narrows, loggerheads are concentrated (Dodd and Byles 2003; see Fig. 12 in TEWG 2009) and, therefore, are likely more vulnerable to fisheries interactions and boat strikes in these "migratory bottleneck" corridors (sensu Mansfield et al. 2009). Cape Hatteras appears especially important in this regard as data from this study demonstrate that loggerheads pass through this corridor during 7 months of the year (during post-nesting and inter-foraging segments of their migration) and in considerable densities (see below). Conservation actions in these migratory bottleneck corridors would undoubtedly provide for recovery opportunities that are beneficial not only to the majority of the NRU adult female loggerhead population, but also to other sea turtle species and loggerhead life stages that also utilize these habitats (see Morreale and Standora 2005).

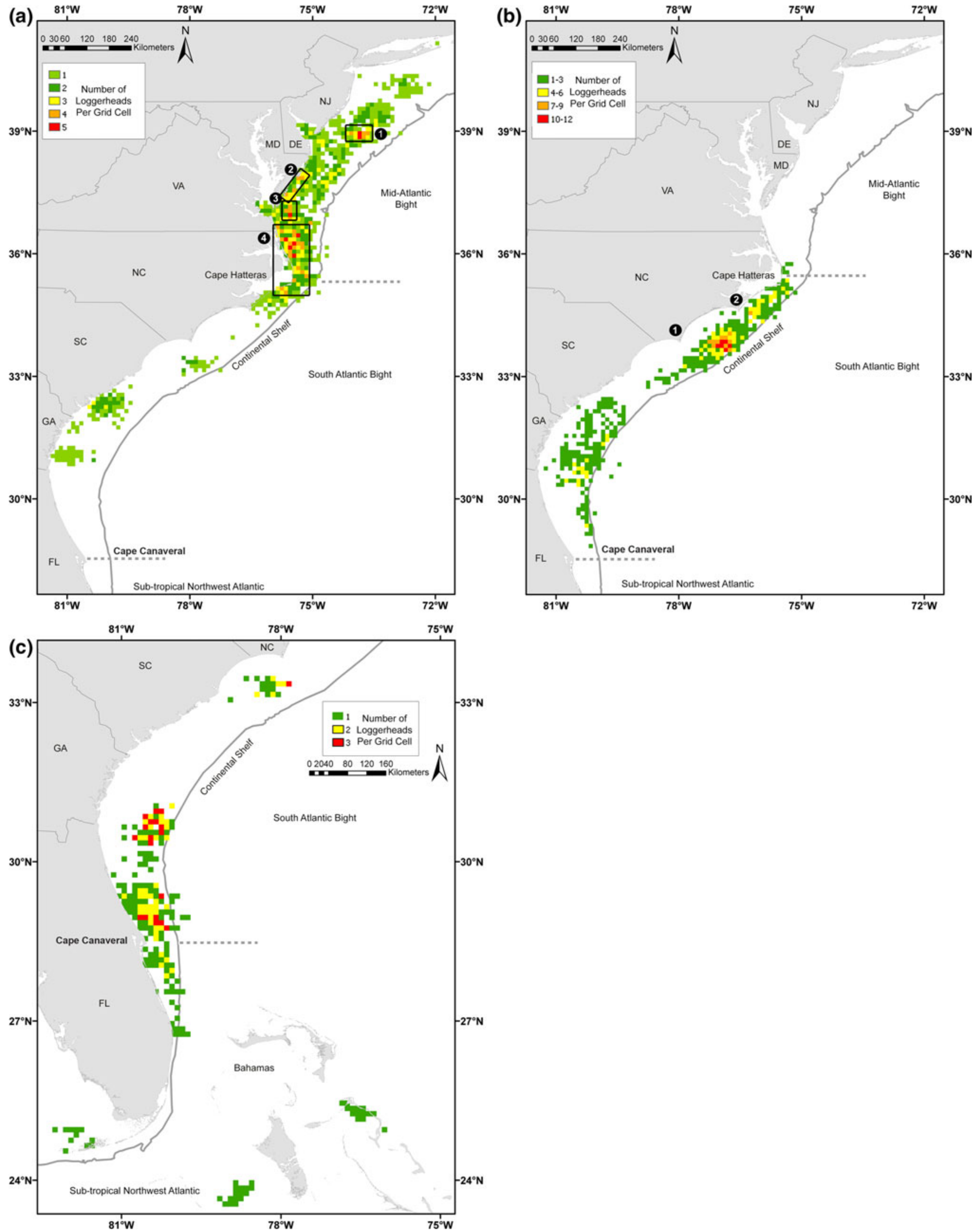
Foraging strategies

Loggerheads in this study exhibited three foraging strategies (seasonal large-scale, seasonal small-scale and year-round). The seasonal large-scale strategy appears to be based on a north/south temperature gradient and involves long distance travel between summer foraging areas (typically north of Cape Hatteras) and winter foraging areas (on the mid- and outer shelf south of Cape Hatteras). Loggerheads occupied summer AFAs from approximately May through October in coastal and shelf waters in the MAB (Fig. 6a). Presumably, as temperatures dropped in autumn (mid-September to November), loggerheads moved south of Cape Hatteras to a winter AFA primarily off of the coast of NC in the SAB and remained in this region from approximately November to April (south of 35°N; Fig. 6b). Other studies report similar data where satellite-tracked loggerheads and Kemp's ridleys migrated to the southern coast of NC during this time period (Keinath 1993; Renaud 1995; Morreale 1999). This portion of the NC coast is most likely favorable for winter time foraging by sea turtles because an elevated portion of the shelf located south of this region (the Charleston Bump) aids in bringing warmer water closer into shore. The Charleston Bump is a complex bottom feature of great bathymetric relief located 130–160 km southeast of Charleston, SC (31°42′N, 78°48′W; Sedberry et al. 2001). It deflects the trajectory of the offshore Gulf Stream into the shallower waters of the SAB, creating eddies, gyres and associated upwellings that provide influxes of warmer water to the region, and they condense pelagic and surface-oriented organisms (Bjorndal 1997; Sedberry et al. 2001). Post-nesting loggerheads in Florida, and in other regions of the world, utilize oceanic/pelagic habitats for foraging (Hatase et al. 2002; Hawkes et al. 2007; Reich et al. 2010), and our data provide the possibility that NRU post-nesting loggerheads also exploit pelagic resources in tandem with thermoregulation. It is unclear, however, whether NRU post-nesting loggerheads actively seek out pelagic foraging habitats along the outer continental shelf, or if their movements to these areas are purely in response to seasonal declines in water temperature. Moreover, we believe that movements of NRU post-nesting loggerheads from the outer continental shelf at Cape Hatteras into adjacent oceanic habitats represent entrainments into swift Gulf Stream-associated currents rather than foraging bouts.

Converse to the seasonal large-scale strategy, the small-scale strategy (not noted by Hawkes et al. 2007, 2011) appears to be based on a west/east (near-shore/offshore) temperature gradient where loggerheads move shorter distances along the western edge of the Gulf Stream (likely to remain in warmer water; see Coles and Musick 2000 and Hawkes et al. 2011). This occurs in the SAB temperate zone between Cape Hatteras and Cape Canaveral. Such west-to-east movements are documented for several juvenile loggerheads that migrated offshore during colder months to the warmer waters of the Gulf Stream and the North Atlantic Current (Keinath 1993; Renaud 1995; Morreale 1999).

The remaining foraging strategy we documented was exhibited by loggerheads that occupied their AFAs year-round (Figs. 5a, b and 6c). Individual turtles traveled to sub-tropical waters (south FL and the Bahamas) or to the mid- to outer shelf regions located in the temperate zone between Cape Hatteras and Cape Canaveral (where they remained within their AFAs until satellite transmission was lost). It is likely that these loggerheads did not move because their AFAs are located where water remains relatively warm throughout the year.

Seasonal foraging strategies similar to those presented herein have also been documented from post-nesting


(a)
81°W
78°W
75°W
72°W
39°N
36°N
33°N
30°N
0 30 60 120 180 240
Kilometers
N
1
2
3
4
5
Number of Loggerheads Per Grid Cell
NJ
MD
DE
VA
NC
SC
GA
FL
Mid-Atlantic Bight
Cape Hatteras
Continental Shelf
South Atlantic Bight
Cape Canaveral
Sub-tropical Northwest Atlantic
(b)
1-3
4-6
7-9
10-12
Number of Loggerheads Per Grid Cell
(c)
1
2
3
Number of Loggerheads Per Grid Cell
0 20 40 80 120 160
27°N
24°N
Bahamas

◀ **Fig. 6** **a** Number of individual loggerheads per 0.01° × 0.01° grid cell for summer (May–October). These data represent 51 individual loggerheads. Numbered boxes delineate areas that contained four or more individual loggerheads. Grid cells that contained at least four individual loggerheads included: (1) 92 km off the south coast of New Jersey, (2) within 20 km of the Delmarva Peninsula, (3) 35 km east of the mouth of the Chesapeake Bay, and (4) 15 to 45 km near-shore along the southern VA coast and the NC Outer Banks. *Horizontal dotted lines* separate the Mid-Atlantic Bight, the South Atlantic Bight, and the sub-tropical Northwest Atlantic. *DE* Delaware, *FL* Florida, *GA* Georgia, *MD* Maryland, *NC* North Carolina, *NJ* New Jersey, *SC* South Carolina, *VA* Virginia. **b** Number of individual loggerheads per 0.01° × 0.01° grid cell for winter (November–April). These data represent 42 individual loggerheads. Higher densities existed during the winter months with grid cells containing as many as 12 loggerheads (compared with a maximum of five individuals per grid cell for summer). The area with the highest concentration was found 101 km southeast of Onslow Bay, NC between Frying Pan Shoals (1) and Cape Lookout Shoals (2). Loggerheads off of GA and SC moved farther offshore in the winter leaving AFAs on the inner shelf and moving to foraging areas on the mid- or outer shelf. *Horizontal dotted lines* separate the Mid-Atlantic Bight, the South Atlantic Bight and the sub-tropical Northwest Atlantic. *DE* Delaware, *FL* Florida, *GA* Georgia, *MD* Maryland, *NC* North Carolina, *NJ* New Jersey, *SC* South Carolina, *VA* Virginia. **c** Number of individual loggerheads per 0.01° × 0.01° grid cell for all months of the year. These data represent 20 individual loggerheads. The lowest density of loggerheads existed for the year-round strategy (most likely due to the low sample size of loggerheads for this strategy) with a maximum of three individuals in any one grid cell. The most pronounced area was ~55 km northeast of Cape Canaveral, FL. Additionally, 112 km off the southern coast of GA and 110 km off the northern coast of SC indicate up to three individual loggerheads per grid cell. *Horizontal dotted lines* separate the South Atlantic Bight from the sub-tropical Northwest Atlantic. *FL* Florida, *GA* Georgia, *NC* North Carolina, *SC* South Carolina

loggerhead turtles in Florida (Girard et al. 2009), Japan (Hatase et al. 2002), Cape Verde (Hawkes et al. 2007), Oman (Rees et al. 2010) India (Papi et al. 1997), and Greece (Zbinden et al. 2011; Rees et al. 2013). Loggerhead populations in Australia do not exhibit seasonal foraging strategies as identified in this study. Limpus and Limpus (2003) documented recruitment of juvenile loggerheads from the oceanic habitat to resident coastal foraging areas off Queensland. These loggerheads were tracked until their first breeding season. After nesting, the neophyte nesters returned to the foraging area where they had grown to maturity (see Table 6.2 in Limpus and Limpus 2003). This brings up the question of *how* and *when* do loggerheads with a seasonal strategy select their summer and winter AFAs. Do juvenile loggerheads select these adult foraging areas when they transition to the neritic habitat, or do they exhibit some type of resource partitioning as they mature? For example, Epperly et al. (1995b) reported that loggerheads were generally smaller in Long Island Sound, New York, than in three other estuarine systems farther south. Similarly, the size distribution of juvenile loggerheads stranding primarily in Massachusetts and New York had a mean straight carapace length equal to 54.0 cm (see Fig. 2 in Rankin-Baransky et al. 2001). Unlike the Queensland model, it may be that US loggerheads transition between relatively widely spaced, geographically distinct foraging areas as they mature.

The effects of foraging strategy selection on nesting remigration intervals are unknown but may have significant consequences for reproductive output. The remigration interval is determined by how quickly a loggerhead can replenish fat stores exhausted during the nesting season. Annual segment distances for the large-scale foraging strategy were greater than distances for the small-scale and year-round foraging strategies; consequently, the large-scale foraging strategy is more energy demanding. In this study, a high percentage of loggerheads traveled to summer AFAs north of Cape Hatteras (seasonal large-scale), suggesting that the quality of this foraging habitat (e.g., abundant crustacean resources in the MAB) offsets any negative consequences associated with swimming greater distances. Alternatively, a year-round strategy may result in increased utilization of local food resources (12 months a year rather than seasonal occupation), which could lower the carrying capacity of these year-round foraging areas. However, wide ranging prey types that are commonly consumed by adult female loggerheads often reproduce more frequently than conspecifics in more temperate areas (see Williams 1984)—increasing the number of individual prey items available to foraging turtles within year-round habitats. Or, such an increased breeding periodicity in prey may also increase the possibility that foraging turtles will consume ovigerous (egg-bearing) individuals more frequently than turtles in temperate habitats, thus increasing the nutritional value of such prey items (see Frick et al. 2001). Nonetheless, further research is needed to determine how these strategies affect remigration intervals.

Adult foraging habitat areas

During the course of this study, it was evident that post-nesting loggerheads were selecting AFAs in certain locales and not just randomly spreading out onto the entire shelf. This is also evidenced by the high site fidelity to AFAs between seasons (Hawkes et al. 2011). This is not surprising because the shelf is a heterogeneous habitat that consists of a wide sandy plain interspersed with rocky outcroppings, shipwrecks, and artificial reefs. This is further supported by the fact that individual loggerhead AFAs ($N = 12$) overlap regardless of strategy, indicating they are selecting specific foraging areas (Fig. 6a, b, c).

During summer, adult loggerheads in the MAB appear to be utilizing particular foraging habitats that collectively span the entire continental shelf. Despite the small number of loggerheads (four to five) in these adult habitat foraging areas, it appears that some areas are utilized by loggerheads more than others. The rich and expansive estuaries of the mid-Atlantic coast (Chesapeake Bay in VA and Delaware Bay in Delaware)

are well known for resources such as crabs (particularly edible brachyurans), as well as chelicerates-like horseshoe crabs (*Limulus polyphemus*; Lutcavage and Musick 1985); both representing food types especially relished by loggerhead turtles (Seney and Musick 2007). Three of the four areas delineated in Fig. 6a are near-shore where such resources are particularly abundant (based on exports from these estuaries).

During winter, the concentration of loggerheads near the western edge of the Gulf Stream off of NC is striking in that grid cells contain as many as 12 loggerheads (Fig. 6b). Considering the vast area along the western edge of the Gulf Stream with temperatures suitable for loggerheads, the fact that 29 % (12 of 42) of the loggerheads were present at this locale at some point in time is noteworthy. Morreale and Standora (2005), using recapture records and satellite telemetry data on loggerhead and Kemp's ridley juveniles, reported that:

> "Another area where turtles become highly concentrated during winter months [same months as indicated in the 'terminology' section above] is Onslow Bay, NC up to 100 km offshore. This section of coastline between Frying Pan Shoals and Cape Lookout Shoals is protected and warmer because of the nearby Gulf Stream. In early winter, it appears that Kemp's ridleys and loggerheads migrating from the north often settle here. In some years, they may even spend the entire winter. Such winter gathering sites for turtles warrant special attention."

A comparison of Fig. 6a, b illustrates and supports the above observation that some loggerheads move offshore during the winter and into warmer waters along the western edge of the Gulf Stream along the mid- and outer shelf. This movement of loggerheads away from shore during the winter was also observed by Keinath (1993), Renaud (1995), Morreale (1999), Epperly et al. (1995a), and Dodd and Byles (2003).

The distribution of loggerheads reported in the present study reveals several areas where turtles occur year-round; the most pronounced being just northeast of Cape Canaveral. This well-known area is characterized by shallow, relatively warm water and extensive live bottom habitats, and is utilized by immature and adult loggerhead turtles alike, including post-breeding, resident male loggerheads (Hopkins-Murphy et al. 2003; Morreale and Standora 2005; Arendt et al. 2012a, b). Loggerheads also utilize habitats off of GA and SC year-round, including Grays Reef National Marine Sanctuary (Hopkins-Murphy et al. 2003).

Summarized data

If the post-nesting NRU loggerheads that used the MAB (present study; $N = 42$) are combined with additional studies [satellite telemetry: Mansfield et al. 2001 ($N = 2$), Plotkin and Spotila 2002 ($N = 4$); isotopic analysis: Pajeulo et al. 2012b ($N = 41$)], 89 of 144 (62 %) foraged in the MAB. Similarly, using stable isotope signatures, 14 of 37 (38 %) adult male loggerheads captured in the Port Canaveral Ship Channel in FL (Fig. 1b, 2 in Pajuelo et al. 2012a), and 21 of 71 (30 %) adult females nesting in the Archie Carr National Wildlife Refuge (Ceriani et al. 2012) also travelled to foraging grounds north of Cape Hatteras. Likewise, twelve adult female loggerheads (live captures and stranded carcasses bearing flipper tags) from NRU nesting beaches were also recovered in this region (Bell and Richardson 1978; Williams and Frick 2008; SCDNR unpubl data). These summarized data strengthen a picture of repeatable and predictable use of the MAB by adult female loggerhead turtles from the NRU and other rookery areas or recovery units from the southeastern USA.

The mean number of loggerhead nests laid each year within the NRU area is 5,215 (SD ± 1,523, range 1,804–7,681, 1989–2008; NMFS and USFWS 2008). Recent genetic analyses identify 5,358 individual nesting females within the NRU (B. Shamblin pers comm). If satellite-tagged and untagged nesting loggerheads within the NRU display similar post-nesting behavior as reported here, the estimated minimum number of adult female loggerheads utilizing the MAB as a post-nesting foraging habitat is over 3,300 (based on the 62 % above).

The recovery of sea turtle populations largely depends on greater life stage survivorship as dictated by deferred sexual maturity and longevity following adulthood (Crouse et al. 1987). Wallace et al. (2008) demonstrate how fisheries that operate in habitats that are also occupied by adult loggerheads (e.g., trawls in neritic areas) are actually negatively impacting the greater western North Atlantic loggerhead population than fisheries that operate in areas occupied by juvenile loggerheads (e.g., oceanic and pelagic longlines) by culling more reproductively "valuable" individuals from the population. Additionally, loggerheads that utilize foraging grounds at higher northern latitudes (areas adjacent to historically more human development) are at a greater risk of sublethal toxic effects resulting from high concentrations of organic pollutants when compared to loggerheads foraging in more southerly regions (Alava et al. 2011; Ragland et al. 2011). Although more data are needed, such is likely the case within the NRU loggerhead subpopulation of the western North Atlantic.

This study has delineated adult female foraging areas and two migration corridors where loggerheads are concentrated and may interact with commercial fisheries. Finkbeiner et al. (2011) reported that loggerheads interact with more fisheries (17 out of 18 fisheries analyzed) than any other sea turtle species in the USA resulting in a minimum of 1,400 annual deaths (see Table 5 in Finkbeiner et al. 2011). Loggerhead nesting in the NRU declined 1.3 % annually from 1983 to 2008 (NMFS and USFWS 2008), and nesting in FL declined 28 % between 1989 and 2006 and 43 % between 1998 and 2006 (Witherington et al. 2009), although recent trends indicate that nesting activity within the NRU may be stabilizing (Pfaller et al. 2013). According to Murray (2006, 2007, 2009), loggerhead bycatch in commercial fisheries has substantially contributed to these declines. The areas of concentrated loggerhead occurrence from the present study overlap with areas of predicted gill net/loggerhead bycatch instances identified by Murray (2009), and they overlap with predicted bottom trawl/loggerhead bycatch instances identified in Warden (2011). Thus, it becomes apparent and imperative to characterize fishery interactions with sea turtles through observer coverage, particularly within the MAB, and along the narrow shelf migration corridors adjacent to Cape Hatteras and southern FL. Such characterization is a necessary first step toward mitigating threats that would otherwise decrease the survival probabilities of loggerheads that utilize these areas.

Conclusion

Minimizing sea turtle mortality on and adjacent to rookery beaches is insufficient in recovering regional populations. Our data serve as a "case in point" for the greater western North Atlantic population by reporting the locations of adult female loggerhead foraging habitat areas and migrations corridors that overlap with the predictable gear deployment of commercial fisheries that are documented to kill numerous turtles annually. If loggerheads are not sufficiently protected in their foraging areas and while migrating between them, the greater western North Atlantic loggerhead population will continue to decline. Often, results from satellite telemetry studies are limited in scope due to a paucity of high-quality data, but by combining data across three states from the same recovery unit, this study provides a more robust analysis that supplements the detailed examinations of Hawkes et al. (2011) and Scott et al. (2012), which, when combined, provide managers and legislators with data that are critical for developing and implementing conservation measures that are critical for the conservation of this wide-ranging marine species.

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Appendix 1

See Table 4.

Table 4 Platform transmitter terminal (PTT) specifications for Georgia (GA), North (NC) and South Carolina (SC) satellite telemetry projects

Telemetry project	PTT model	Repetition period (seconds)	Duty cycle (hours)	Duration of duty cycle	Number of tagged loggerheads
GA 2001	Wildlife Computers SDRSSC3	45	16 on, 08 off	At all times	2
GA 2001	Telonics ST-6	45	Continuously on	At all times	1
GA 2002	Telonics ST-6	60	08 on, 52 off	At all times	1
GA 2002	Telonics ST-6	45	Continuously on	At all times	1
GA 2004	Telonics ST-20	45	Continuously 24 on, 24 off	Nesting migration/foraging	12
GA 2005	Telonics ST-20	45	Continuously on	At all times	12
SC 1998	Telonics ST-14	40	24 on, 12 off	At all times	5
SC 2002	Sirtrack Kiwi Sat 101	40	24 on, 12 off 24 on, 48 off	Nesting migration/foraging	5
SC 2003	Sirtrack Kiwi Sat 101	40	24 on, 24 off	At all times	5
NC 2003	Telonics ST-18/SMRU	45	Continuously on	At all times	3/1
NC 2004	Sirtrack Kiwi Sat 101/SMRU	45	Continuously on	At all times	3/1
NC 2005	Sirtrack Kiwi Sat 101	45	Continuously on	At all times	4
NC 2006	Sirtrack Kiwi Sat 101	45	Continuously on	At all times	2
NC 2006	Sirtrack Fastloc	45	Continuously on	At all times	2
NC 2007	Sirtrack Kiwi Sat 102	45	Continuously on	At all times	4
NC 2008	Sirtrack Kiwi Sat 102	45	Continuously on	At all times	4

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