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Foraging and overwintering behavior of loggerhead sea turtles *Caretta caretta* in the western North Atlantic

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ABSTRACT: Discerning the foraging habitat requirements of wildlife is key to providing for their conservation and management, especially with rare species. Sea turtles are slow-growing, late-maturing species that undertake wide-ranging migrations, making them especially susceptible to changes and disruptions in their environment. To protect and successfully manage these imperiled populations, an understanding of their spatial ecology is required; thus, characterizing critical habitats, identifying high-density areas, and identifying foraging regions is essential. We captured 30 loggerhead sea turtles *Caretta caretta* (male and female; juvenile and adult) in the estuarine waters of North Carolina (USA) and tracked them in western North Atlantic neritic (nearshore and offshore) waters. Using a combination of satellite telemetry and spatial modeling techniques, we characterized their movements and identified foraging and overwintering sites. Average core-use areas in the north had greater net primary production (NPP) and were smaller than those in the south, indicating more abundant marine resources in northern foraging regions. In summer, loggerheads migrated to both northern and southern foraging grounds, but most (53%) resided within North Carolina neritic waters. Likewise, the majority of loggerheads (67%) we tracked in winter remained in North Carolina neritic waters, underscoring the importance of this area as year-round foraging habitat, and lending to its consideration as potential critical habitat for both juvenile and adult loggerheads. The change to foraging behavior mode was significantly influenced by day of the year, geographic location, and NPP; however, individual-specific factors influenced switching probabilities relative to other covariates. Data highlighting 'hotspots' or densely used areas by foraging sea turtles can thus be used by conservation managers to make informed decisions concerning sea turtle conservation measures.

KEY WORDS: Foraging habitat · Overwintering · Core-use areas · State-space modeling · Loggerhead · *Caretta caretta*

1. INTRODUCTION

Discerning the foraging habitat requirements of wildlife is key to providing for their conservation and management, especially with rare species (Walsh & Harris 1996). Likewise, understanding which factors are influencing their spatial distribution, as it relates to foraging and/or reproductive habitat, can aid in predicting the consequences of human interactions and environmental changes on these species (Hei-

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thaus et al. 2002). However, knowledge of the spatial distribution of some wildlife, in particular, marine fauna, can be limited given the logistical difficulties in studying animals with wide-ranging habitats (Block et al. 2002). For example, sea turtles spend the majority of their lives in a vast oceanic habitat, making migratory journeys that cross ocean basins. Similar to other long-lived, late-maturing species, sea turtles are especially susceptible to high levels of mortality (Musick 1999), resulting in their threatened or endangered status. While many anthropogenic interactions with sea turtle populations exist, incidental capture in certain fishing gear has one of the greatest impacts on population declines (Lewison et al. 2004, Hamann et al. 2010, Wallace et al. 2013). Models that integrate sea turtle distributions with fishing effort have been developed to estimate the potential risk of sea turtle bycatch in certain fishing gear (Howell et al. 2008, Murray & Orphanides 2013). Additionally, some mitigation measures have been developed, including time-area restrictions for specific fisheries: bottom trawl fisheries in the western North Atlantic (NMFS 1996), California/Oregon drift gillnet fishery (NMFS 2003), and shallow longline sets in the Pacific Ocean (NMFS 2004). However, for these mitigation methods to be most effective, an understanding of sea turtle spatial ecology is required (National Research Council 2010, Ramirez et al. 2017). As such, studies characterizing critical habitats, identifying high-density areas, and identifying foraging regions are essential (Lewison et al. 2004, Hamann et al. 2010), and many have been conducted in the Gulf of Mexico (Hart et al. 2012, 2018, Shaver et al. 2013, Lamont et al. 2015a,b), the North Pacific (Polovina et al. 2004, Kobayashi et al. 2008, 2011), the North Atlantic (McCarthy et al. 2010), and the Mediterranean (Schofield et al. 2013). Because sea turtles are elusive and conduct wide-ranging migrations, collection of data on their habitat needs and movements can be challenging.

Satellite telemetry is a tool that has been used effectively to track the movements of wide-ranging animals such as sea turtles so that migratory and distributional data can be collected (Godley et al. 2008, Hart & Hyrenbach 2009, Costa et al. 2012). Over the years, limitations of satellite telemetry data have been addressed so that more accurate locations can be derived from animals that only surface briefly. For example, Fastloc-GPS transmitters can rapidly (within milliseconds) acquire high-resolution movement data for sea turtles (Dujon et al. 2014). Likewise, state-space modeling (SSM) techniques can provide more accurate positional information from lower-accuracy Argos locations, and also can infer the behavior of the animal (Jonsen et al. 2003, 2006). Once core foraging areas have been delineated, they then can be characterized by measuring a variety of environmental parameters (e.g. sea surface temperature [SST], net primary production [NPP], and bathymetry) so that informed management and conservation decisions concerning the temporal and spatial protection of these species can be made (Lewison et al. 2004).

The importance of western North Atlantic waters to loggerhead sea turtles has been well documented (Shoop & Kenney 1992, Epperly et al. 1995a,b,c, Plotkin & Spotila 2002, Morreale & Standora 2005, Arendt et al. 2012a,b, Winton et al. 2018), and several studies have integrated tracking data with environmental variables to characterize foraging habitat of neonate, juvenile, and adult loggerheads in these waters (Hawkes et al. 2007, 2011, Mansfield et al. 2009, 2014) or identified foraging grounds from the isotopic signatures of loggerheads (Ceriani et al. 2014). To develop effective management strategies for the conservation of loggerheads in western North Atlantic waters, however, additional studies are needed to identify and characterize foraging and overwintering habitats. Using a combination of satellite telemetry and spatial modeling techniques, we tracked male and female adult and juvenile loggerhead sea turtles in western North Atlantic neritic (nearshore and offshore) (Dujon et al. 2018) waters to: (1) identify high-use areas, including overwintering sites, and (2) examine the influence of SST, NPP, and bathymetry in the initiation of foraging and overwintering behavior.

2. MATERIALS AND METHODS

Loggerhead turtles were captured in pound nets set in Core and Pamlico Sounds or entanglement nets set in Cape Lookout Bight, North Carolina, USA (Fig. 1). Pound nets are a stationary fishing gear open to the surface of the water, so that as sea turtles enter, they are able to swim freely and come to the surface to breathe (see Epperly et al. 2007). Entanglement nets were 100 m, with a large mesh size of 30.5 cm to minimize bycatch of fish, and checked every 30 min to eliminate turtle drowning. After turtles were brought onboard the small research vessels used, we measured standard straight carapace length (SCL), affixed Inconel Style 681 tags (National Band and Tag) to each rear flipper, and injected a 125 kHz unencrypted passive integrated transpon-

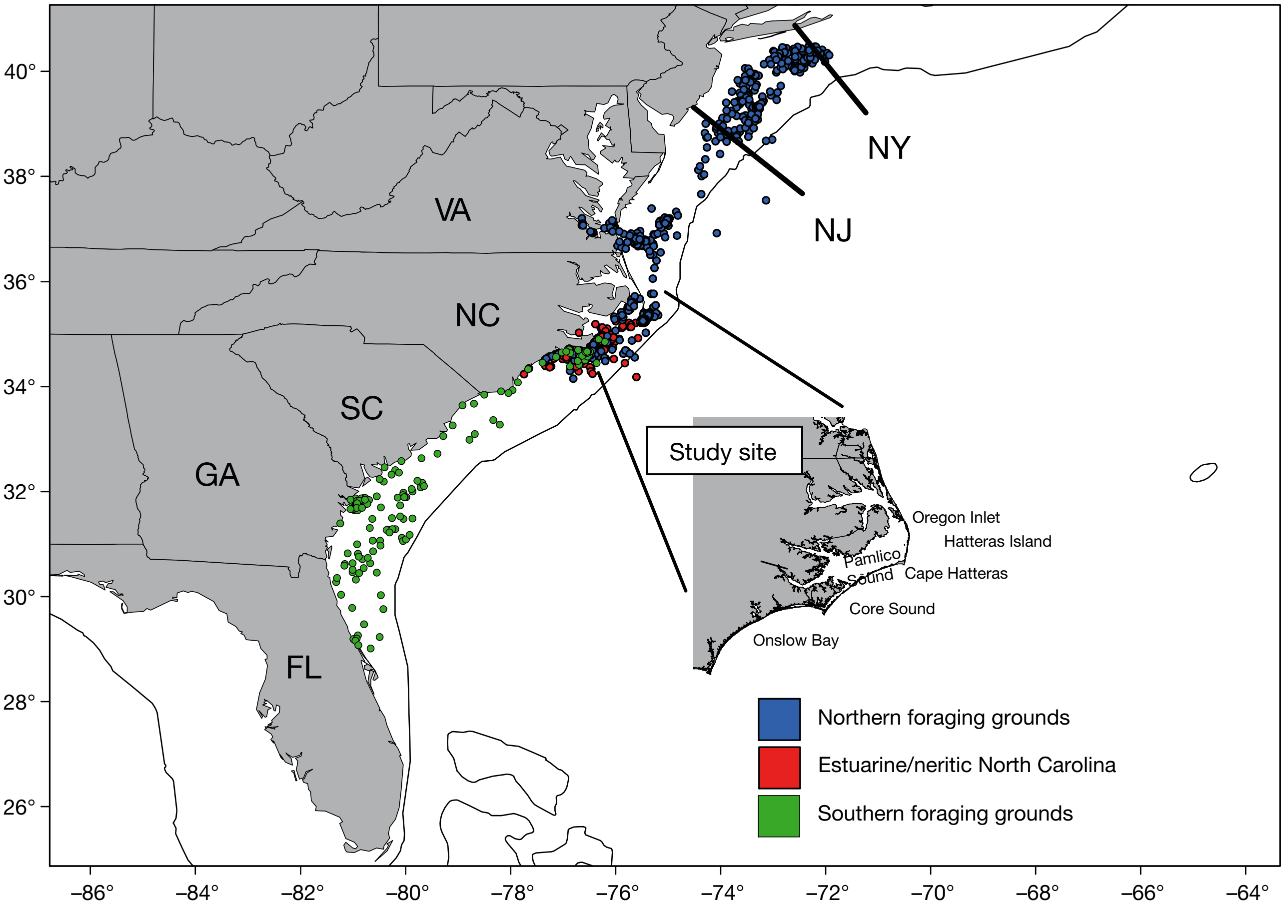

Fig. 1. Summer filtered Argos locations of loggerhead sea turtles *Caretta caretta* traveling to northern foraging grounds (blue; n = 11), remaining within estuarine or neritic waters of North Carolina (red; n = 16), or traveling south (green; n = 3). Black line depicts the 200 m isobath. Inset map depicts study site

der tag (Destron-Fearing) into their left front flipper triceps muscle. We categorized adults as having an SCL ≥82 cm (Turtle Expert Working Group 2009). We determined sex of juveniles using a testosterone radioimmunoassay technique (Owens 1997) that had been validated by a subset of loggerheads via laparoscopy, i.e. turtles were classified as male if testosterone levels were 433 pg ml^{-1} or greater, female if testosterone levels were 371 pg ml^{-1} or less, and unknown sex if testosterone values were between 372 and 432 pg ml^{-1} (Braun McNeill et al. 2016). We identified adult males by a relative tail length ≥0.3 cm (Ishihara & Kamezaki 2011).

2.1. Satellite data

Loggerhead sea turtles (n = 30) that were captured during summer and fall of 2007 (n = 8), spring and summer of 2008 (n = 18) and spring of 2014 (n = 5), were outfitted with satellite tags (Wildlife Computers) following established protocols (NMFS 2008). One turtle was recaptured and outfitted with another tag, resulting in 31 tags. After removing epibiota from the first 3 vertebral and costal scutes, the area was lightly scrubbed with fine-grit sandpaper, rinsed with fresh water, and dried with acetone (NMFS 2008). We attached the base of the transmitters using a high-strength, low-temperature epoxy adhesive (Power Fast; Mitchell 1998) and further secured the SPOT5 transmitters using fiberglass cloth and resin (Balazs et al. 1996). All tags and attachment materials weighed <1% of the turtle's body weight. We released turtles within 100 m of their capture site. We programmed tags to transmit daily over a 10 h period beginning just after dawn and ending near dusk. All tags were programmed to collect water temperature to determine the amount of time turtles were spending in each of 14 temperature bins (5, 8, 10, 12, 14, 16, 18, 20, 22, 24, 26, 28, 30, >30°C). We filtered satellite location data based on the accuracy of transmissions (Location Class of 0, 1, 2, 3, A, and B) (CLS America 2016), likely swimming speed between locations (≤ 6 km h^{-1}), and locations over water vs. land (topography < 0.5 m) using the Satellite Tracking and Analysis Tool (Coyne & Godley 2005). We also excluded those locations that occurred before or on the tagging date.

2.2. Switching SSM

We applied switching SSM to all of the raw satellite locations of each loggerhead track to characterize sea turtle movements off the US Atlantic coast (Breed et al. 2009); this included 6 years of data (2007–2010 and 2014–2015). Switching SSM allowed us to estimate locations from the observed satellite data at regular time intervals, using the satellite location quality class to account for error, and to infer behavioral mode so that 'movement' and 'foraging' behavior could be distinguished. We assumed that turtles remaining in a particular area for extended periods are in favorable habitat, and thus are foraging (Breed et al. 2009). We estimated locations at 8 h intervals (3 locations d^{-1}) and estimated model parameters by Markov chain Monte Carlo (MCMC) using WinBUGS via R from 2 independent chains. The convergence was visually assessed by observing a mixture of the 2 chains in the trace plot. We ran the 2 MCMC chains for 10 000 iterations, and after a burn-in of 7000 iterations, we sampled every fifth point of the remaining 3000 samples, resulting in 600 MCMC samples in each chain. We calculated a mean and variance for each location estimate and model parameter.

2.3. Core-use areas and home range estimations

We classified filtered locations (i.e. 'movement' or 'foraging') based on the SSM output and used them to produce mean daily locations (MDLs; point locations) in R version 1.1.383 (R Core Team 2017). We only calculated home range estimates for turtles which had at least 80 d of foraging data (Hawkes et al. 2011). We created kernel density estimates (KDEs) using MDLs (when $n \geq 20$) and minimum convex polygons (MCPs; when MDLs < 20) using filtered locations. KDE is a non-parametric means of differentiating core foraging areas (i.e. areas of disproportionately heavy use) within an animal's home range (Worton 1987, 1989, White & Garrott 1990). We used the package 'adehabitatHR' (Calenge 2006) in R to calculate KDEs with the fixed-kernel least squares cross-validation smoothing factor (hcv; Worton 1995, Seaman & Powell 1996). If the standard deviations of the x and y coordinates were unequal (<0.5 or >1.5), we rescaled data before conducting home range calculations (coordinates were divided by their standard deviation, following Seaman & Powell 1996). We considered 95% KDEs to represent the home range and 50% KDEs to represent the core-use area (Hooge et al. 2001).

We created MCPs at 95%, as this excluded a proportion of distant locations that might represent infrequent movements or explorations following Walcott et al. (2012). MCPs were generated when there were not enough MDLs for KDE analysis and at least 5 filtered locations. We used ArcGIS Desktop 10.4.1 (ESRI) to plot the data and to calculate the area (km^2) within each kernel density contour and each MCP. We also created centroid locations from 50% KDE contours and MCPs; if a 50% KDE had multiple activity centers, we used only the largest activity center.

2.4. Characteristics of foraging and overwintering regions

We defined 'foraging regions' when the filtered location was classified as 'foraging' from April to October; likewise, we defined 'overwintering regions' when the filtered location was classified as 'foraging' from November to March. To characterize each turtle's at-sea foraging region, we extracted SST, NPP, and bathymetry data for each turtle's daily location. We obtained bathymetry data from the National Oceanographic and Atmospheric Administration (NOAA) National Centers for Environmental Information (NCEI) site (https://ngdc.noaa.gov/mgg/global/global.html, accessed 28 April 2017). We obtained NPP data from Oregon State University ocean productivity data (www.science.oregonstate.edu/ocean.productivity/standard.product.php, accessed 14 April 2017), in which 8 d NPP was derived as a function of chlorophyll, light, and photosynthetic efficiency (Behrenfeld & Falkowski 1997). We obtained SST data from Duke University Marine Geospatial Ecology Tools (http://mgel.env.duke.edu/mget) to obtain 4 km resolution 8 d SST of Moderate Resolution Imaging Spectroradiometer (MODIS) Terra Global Level-3 Mapped Mid-IR SST (accessed 26 July 2018). We also used water temperature data from each turtle's satellite tag. We assessed differences between males and females and juveniles and adults with respect to foraging area destination using a chi-squared distribution. We calculated average SST, NPP, and bathymetry for each foraging region.

We used binomial generalized additive mixed models (GAMMs) (Wood 2006, Hazen et al. 2016, Breece et al. 2018) to evaluate the potential influence of different environmental factors on switching from one behavioral state to another. Specifically, we evaluated the change from movement to foraging and/or movement to overwintering (foraging during winter months) as delineated based on SSM results, with 'winter' classified as November through March. Base GAMMs incorporated day of the year (i.e. Day 1 to 365 within each calendar year), geographic location (latitude [Lat] and longitude [Lon]), SST, NPP, and bathymetry as continuous variables and either migrating/foraging or migrating/overwintering as the binary response. In addition, all models accommodated potential individual effects, and accounted for temporal autocorrelation by incorporating turtle ID as a random variable. Following base model runs, any non-significant factors were removed, and reduced models were run stepwise until significance was observed for all remaining factors. Best model fits were assessed using Akaike's information criterion (AIC; Burnham & Anderson 2002). All models were implemented using the 'gamm4' package in the statistical program R version 3.5.2 (R Core Team 2018).

3. RESULTS

3.1. Satellite data

Turtles varied in size from 54.0 to 104.4 cm SCL (mean ± SD: 73.8 ± 12.3 cm; Table 1), indicating a mixture of juveniles (n = 24) and adults (n = 6). We classified 14 turtles as male and 16 turtles as female, based on testosterone levels or tail length, resulting in a 1:1.1 M:F ratio for the sample. From a total of 4909 tracking days, average length of transmission was 158 d and ranged from 26 to 682 d. Turtles' average speed ranged from 0.32 to 1.79 km h^{-1} (mean ± SD: 0.94 ± 0.42), and their total distance traveled ranged from 93 to 4283 km (mean ± SD: 1218 ± 1181). On average, turtles were found in water depths ranging from 2 ± 4.75 m to 71 ± 131.96 m, with a maximum water depth of 762 m. According to extracted SST data overlaid with location data, overall turtles were found in SSTs ranging from 12.2 to 29.7°C; however, those turtles tracked during winter months (November through March) remained in water temperatures that averaged 19.6°C. Based on SST data collected from satellite tags, turtles spent <6 % of their time in water <15°C.

3.2. Foraging regions

During summer months, loggerheads foraged in 3 different regions (Fig. 1). Most (n = 16) turtles remained within estuarine or neritic waters of North Carolina, close (<150 km) to their capture/release location. Others traveled in a northern direction to either the neritic waters of Virginia or within the Chesapeake Bay (n = 5) or further north to New York or New Jersey (n = 6). Finally, 3 turtles traveled to southern foraging grounds (South Carolina, Georgia, and Florida). Turtles that made a northerly migration (Virginia, New Jersey, or New York) did so within days after being released. Likewise, 1 of the 3 turtles that traveled south began its southerly trek soon after being released in May; however, the other 2 turtles which were released in August did not begin traveling south until early September. All 3 turtles remained within neritic waters of South Carolina, Georgia, or Florida throughout the summer.

Although not statistically significant at $p < 0.05$ ($\chi^2 < 2$, df = 3), but of potential biological importance, more females (67 %; 2 adults, 9 juveniles) used the neritic waters of North Carolina for summer foraging while more males (64 %; 2 adults, 5 juveniles) used northern foraging areas (Virginia, New York, New Jersey). These percentages are more than would be expected given the nearly 1:1 sex ratio of turtles in the sample for this study. No significant difference at $p < 0.05$ ($\chi^2 < 0.5$, df = 3) was found in foraging site selection between juvenile (n = 24) and adult (n = 6) turtles.

3.3. Overwintering behavior

We documented the overwintering behavior of 12 turtles: most (67 %) used the neritic waters of North Carolina (Onslow Bay), while the rest (33 %) traveled as far as 1300 km to use waters to the south. Average SST at which these turtles remained during winter months (November–March) ranged from 18 to 25°C. Six individuals (4 juvenile females, 1 juvenile male, 1 adult female) that inhabited estuarine or neritic waters during the summer and early autumn, simply migrated to warmer North Carolina neritic waters with the onset of colder water temperatures (average winter temperatures in estuarine waters are generally below 8°C; Hettler & Chester 1982) and remained there during winter months (November to March, Fig. 2). For example, a juvenile male captured June 2008 in Core Sound (34.968° N, 76.222° W) remained within estuarine waters near its release location until late

Table 1. Satellite-tracking details and environmental parameters for 30 loggerhead sea turtles tagged in North Carolina (NC) estuarine waters during fall of 2007 (n = 8), spring and summer of 2008 (n = 18) and spring of 2014 (n = 5). *Turtle outfitted with 2 different tags. SCL: straight carapace length to tip; test.: testosterone; SST: sea surface temperature, NPP: net primary production; South: South Carolina, Georgia, and/or Florida waters; NA: overwintering data not available

ID	SCL (cm)	Sex	Test. level (pg ml^{-1})	At large (d)	Total distance traveled (km)	Avg distance from shore (km)	Avg speed (km h^{-1})	Max speed (km h^{-1})	SST (°C) mean ± SD (n)	Avg NPP (mg C m^{-2} d^{-1})	Avg water depth (m)	Max water depth (m)	Greatest distance from release location (km)	Over-wintering location	Foraging grounds
42599	54.9	F	195.8	98	282	1.85	1.11	2.71	22.3 ± 1.1 (12)	1840.66	6	16	159	NA	Neritic NC
43699	54.0	F	74.6	122	416	1.97	0.40	2.60	25.9 ± 2.5 (28)	1599.55	4	17	88	NA	Neritic NC
43697	59.8	M	498.6	69	175	1.28	0.51	4.19	25.3 ± 2.9 (13)	1223.03	4	20	23	NA	Neritic NC
75427	62.2	F	100.0	208	804	23.43	0.46	2.65	19.0 ± 4.5 (40)	1036.13	21	68	97	Neritic NC	Neritic NC
75426	64.1	F	138.4	31	221	2.62	0.57	2.66	27.4 ± 0.8 (10)	1830.50	10	20	71	NA	Neritic NC
76457*	66.4	F	214.3	187	845	16.32	0.98	4.98	21.6 ± 2.8 (54)	1377.49	30	762	72	Neritic NC	Neritic NC
42664*	67.1	F	205.2	47	148	3.56	0.34	1.22	25.6 ± 0.8 (6)	1113.29	10	29	27	NA	Neritic NC
76455	67.2	F	134.8	185	1090	18.40	0.62	3.32	18.1 ± 3.3 (50)	1131.83	20	38	110	Neritic NC	Neritic NC
42605	67.4	F	105.4	169	302	1.63	0.32	2.27	24.8 ± 2.8 (18)	2782.77	5	25	70	NA	Neritic NC
138101	69.2	M	882.8	49	336	5.79	1.21	4.15	22.4 ± 1.7 (22)	1769.92	10	19	78	NA	Neritic NC
42602	73.4	F	196.3	40	93	0.78	0.33	2.33	22.8 ± 0.9 (2)	3940.68	2	19	21	NA	Neritic NC
76456	76.0	F	178.6	192	1802	37.91	1.04	4.83	19.7 ± 2.7 (80)	1179.14	34	489	126	Neritic NC	Neritic NC
43639	78.8	M	1750.0	64	222	3.00	0.77	4.70	25.5 ± 0.8 (16)	1481.59	10	22	26	NA	Neritic NC
43638	78.9	M	1435.0	224	500	13.79	0.49	2.20	23.4 ± 2.5 (21)	1922.67	18	154	124	Neritic NC	Neritic NC
42603	82.8	F	138.3	26	99	1.83	0.45	1.75	26.2 ± 1.6 (9)	1789.99	4	19	12	NA	Neritic NC
42601	92.1	M	1893.0	45	268	3.92	1.16	4.29	25.4 ± 2.1 (10)	1593.17	11	20	74	NA	Neritic NC
138103	97.7	F	94.9	283	1329	22.25	0.99	4.88	24.2 ± 2.5 (208)	1009.50	21	36	139	Neritic NC	Neritic NC
43635	67.5	F	213.0	133	2160	53.87	1.31	4.92	23.0 ± 1.6 (95)	1573.25	48	273	709	NA	New York, Jersey
138102	71.6	F	164.6	69	1107	28.03	1.74	4.87	23.1 ± 1.7 (60)	4590.29	22	75	660	NA	New York, Jersey
43713	76.7	M	642.7	682	4210	46.07	0.98	5.93	21.2 ± 2.6 (103)	1679.22	36	349	642	Neritic NC	New York, Jersey
138104	76.9	M	1209.0	276	3063	61.12	1.79	4.99	21.2 ± 2.0 (127)	1666.52	49	76	755	South	New York, Jersey
43722	79.0	M	2002.0	269	4283	58.91	1.53	5.67	22.1 ± 1.9 (74)	1705.75	42	133	1825	South	New York, Jersey
43702	104.4	M	77450.0	198	2335	57.79	1.27	6.00	24.4 ± 1.7 (54)	1777.13	71	745	550	Neritic NC	New York, Jersey
75425	59.7	F	108.8	276	1342	32.14	0.70	4.11	20.6 ± 4.3 (62)	1067.03	19	34	332	South	South
42604	63.5	M	497.6	164	2281	31.13	1.04	3.47	26.4 ± 1.7 (74)	1437.03	19	42	852	NA	South
76454	85.1	M	1243.0	245	2358	50.41	0.99	4.93	22.6 ± 3.4 (115)	1604.60	33	544	552	South	South
42600	54.2	F	87.0	57	588	12.63	0.87	4.33	19.9 ± 2.8 (20)	3538.56	13	32	247	NA	Virginia
138100	67.4	F	126.3	123	1038	5.15	1.31	4.92	25.0 ± 2.1 (101)	2117.57	12	34	250	NA	Virginia
43716	73.3	M	1438.0	151	1243	53.49	1.54	5.91	24.3 ± 2.6 (38)	1297.53	41	368	337	NA	Virginia
66026	80.6	M	1019.0	146	2634	29.47	1.17	5.98	25.6 ± 1.5 (30)	1384.52	21	32	444	NA	Virginia
43715	94.6	M	5063.0	81	176	8.17	1.08	5.72	25.4 ± 1.6 (20)	5930.47	10	14	270	NA	Virginia

October when it moved into nearshore waters off Core Sound (Fig. 1). Average water temperature in Core and Pamlico Sounds that week was 14.7°C (NMFS Beaufort Lab unpubl. data). This turtle remained in the neritic waters of North Carolina, where average water temperature was 21.3°C, until his transmissions ceased on 1 January 2009, 224 d later. Two turtles (1 adult male, 1 juvenile male) that had migrated to neritic waters of New Jersey in the summer began a southerly journey in September and traveled over 500 km to remain within North Carolina neritic waters for the winter. Both turtles began their southerly migration when water temperatures were 19–20°C. Although the adult's transmitter lasted only until late November, the juvenile male spent the winters of 2009 and 2010 in these waters.

The other 4 turtles migrated to or remained in southern waters during the winter (Fig. 2). Two juvenile males that had traveled north for the summer traveled as far as 1300 km to spend winter months within the vicinity of Florida; they began their southerly migration in either late September from the coastal waters of New Jersey or early October from the coastal waters of New York when water temperatures had dropped to 19°C. One turtle was off the northern coast of Florida when transmissions ceased in February; however, the other turtle continued moving around the tip of Florida and was midway up the western coast of Florida by mid-January. Because both turtles were large juveniles (SCLs = 76.9 and 79.0 cm), they might have been approaching maturity and possibly seeking a breeding area. Finally, we have overwintering data on 2 of the turtles that traveled south upon release. An adult male was released the end of August and traveled over 500 km before reaching the South Carolina/Georgia border by late September. He remained within neritic waters of northern Georgia until transmissions ceased in March. A juvenile female was released in early September, traveled over 200 km before reaching northern South Carolina by early December, and remained there until transmissions ceased mid-April in the following year.

One juvenile male provided us with data for 2 winters. This turtle spent the winters of 2008–2009 and

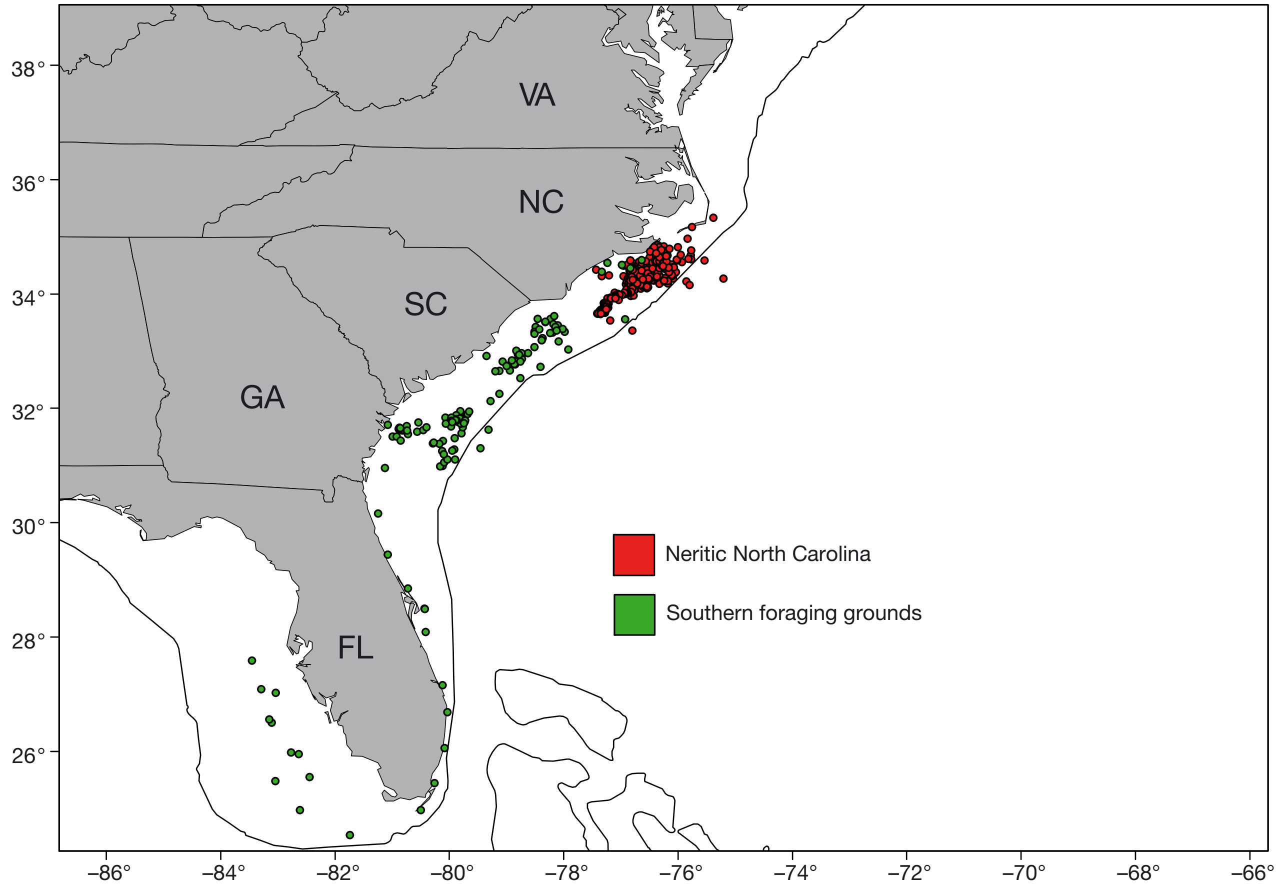

Fig. 2. Winter filtered Argos locations of loggerhead sea turtles *Caretta caretta* remaining within neritic waters of North Carolina (red; n = 8), or traveling south (green; n = 4). Black line depicts the 200 m isobath

2009–2010 in the neritic waters of North Carolina, enabling us to document his northward migration during the spring of 2009. However, we were not able to document a specific spring departure date due to a large gap in transmissions. The transmission received prior to its northward migration was on 19 April 2009, but it was not until 29 June 2009 that we received the next transmission when the turtle was off the southern end of New Jersey, over 500 km away. Also, transmissions ceased on 14 March 2010 before we could document an additional spring migration (2010).

3.4. Core-use areas and home range estimations

Of the 14 turtles that had >80 foraging days, we delineated 17 core-use areas (50% KDEs) that ranged in size from 11.5 to 13 902.4 km^2 (mean ± SD 1553.5 ± 3603.6 km^2; Fig. 3). Home ranges (95% KDEs) varied between 90.8 and 53 182.7 km^2 (mean 6591.5 ± 13701.2 km^2). Turtles that foraged in the south had an average core-use area (5370.5 km^2) that was much larger than that of turtles foraging in the North (New Jersey/New York; 950.4 km^2), while turtles foraging off Virginia or in the neritic waters of North Carolina had the smallest average core-use areas (190.4 and 274.3 km^2, respectively; Table 2). We detected no relationship between days-at-large and home range size (R^2 = 0.008, p < 0.5). Average SST ranged from 21.8°C (neritic North Carolina) to 25.5°C (Virginia). Average NPP was lowest in Virginia waters (933.1 mg C m^{-2} d^{-1}), comparable in neritic North Carolina (1197.8 mg C m^{-2} d^{-1}) and the south (1387.8 mg C m^{-2} d^{-1}), but highest for those foraging off New Jersey/New York (1622.1 mg C m^{-2} d^{-1}). Average water depth for core-use areas was comparable in neritic North Carolina (17.2 m) and the south (21.9 m), but was deeper off Virginia (34.3 m) and New Jersey/New York (46.4 m).

The change to foraging behavior mode was significantly influenced by day of the year, geographic

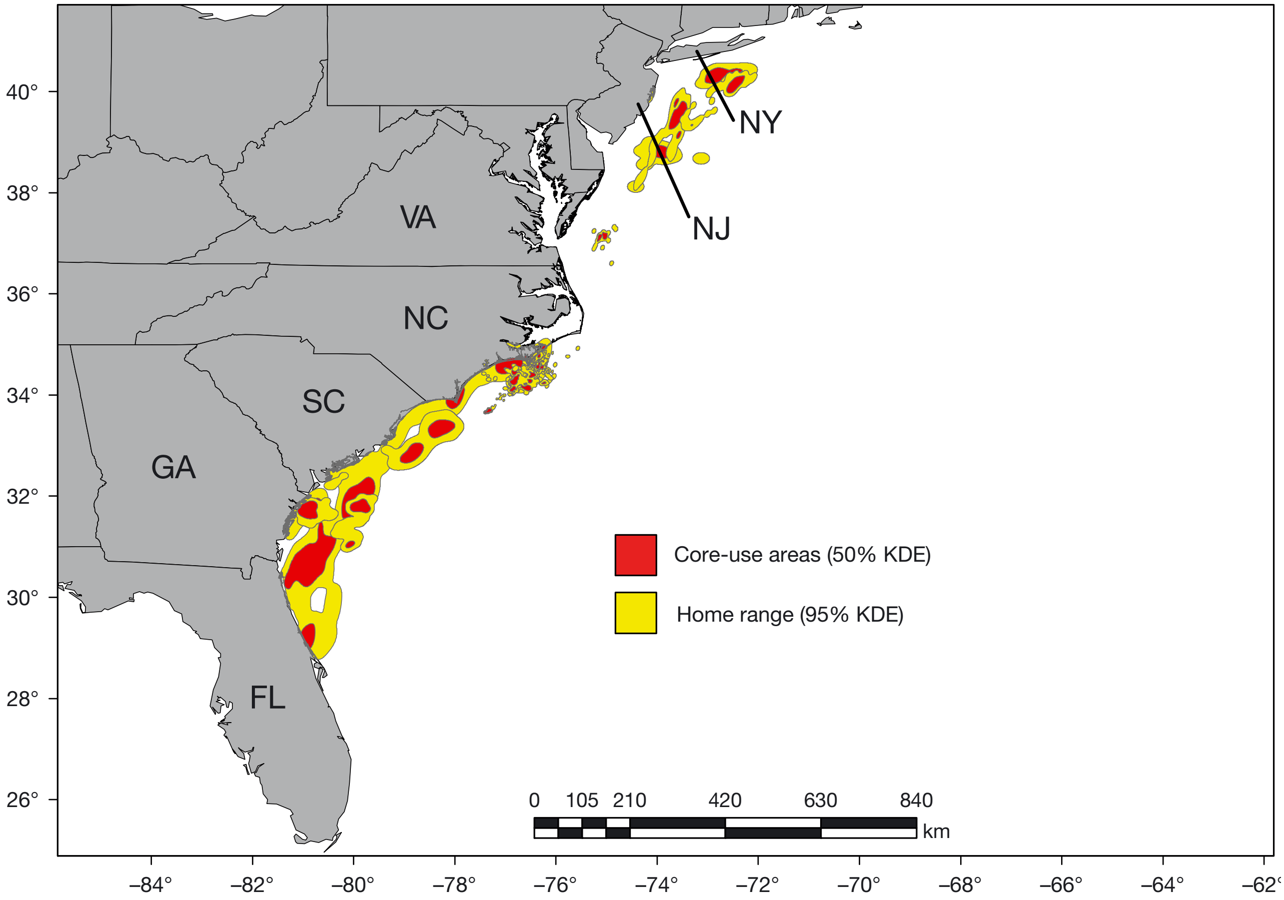

Fig. 3. Core-use areas (50% kernel density estimate, KDE; red) and home range (95% KDE; yellow) for 14 loggerhead sea turtles *Caretta caretta*

Table 2. Average size (range) of 50 and 95 % kernel density estimates (KDEs; core-use and home range areas, respectively) and average (range) sea surface temperature (SST), net primary production (NPP), and bathymetry for each foraging region. South: South Carolina, Georgia, and/or Florida waters. Only turtles that had >80 foraging days were used in the calculation of KDEs (Hawkes et al. 2011)

Foraging region	50 % KDE (km^2)	95 % KDE (km^2)	SST (°C)	NPP (mg C m^{-2} d^{-1})	Bathymetry (m)
New Jersey, New York (n = 4)	950.4 (640.2–1180.9)	4843.2 (4008.1–5833.3)	22.4 (21.2–24.0)	1622.1 (1326.0–1941.6)	46.4 (34.8–58.6)
Virginia (n = 1)	190.4	976.8	25.5	933.1	34.3
North Carolina (n = 6)	274.3 (11.5–692.6)	1365.2 (90.8–3048.9)	21.8 (17.9–26.7)	1197.8 (993.8–1490.8)	17.2 (1.3–31.3)
South (n = 3)	5370.5 (33.1–13902.4)	21246.6 (298.2–53182.7)	23.1 (21.4–26.3)	1387.8 (997.9–1720.3)	21.9 (19.8–25.5)

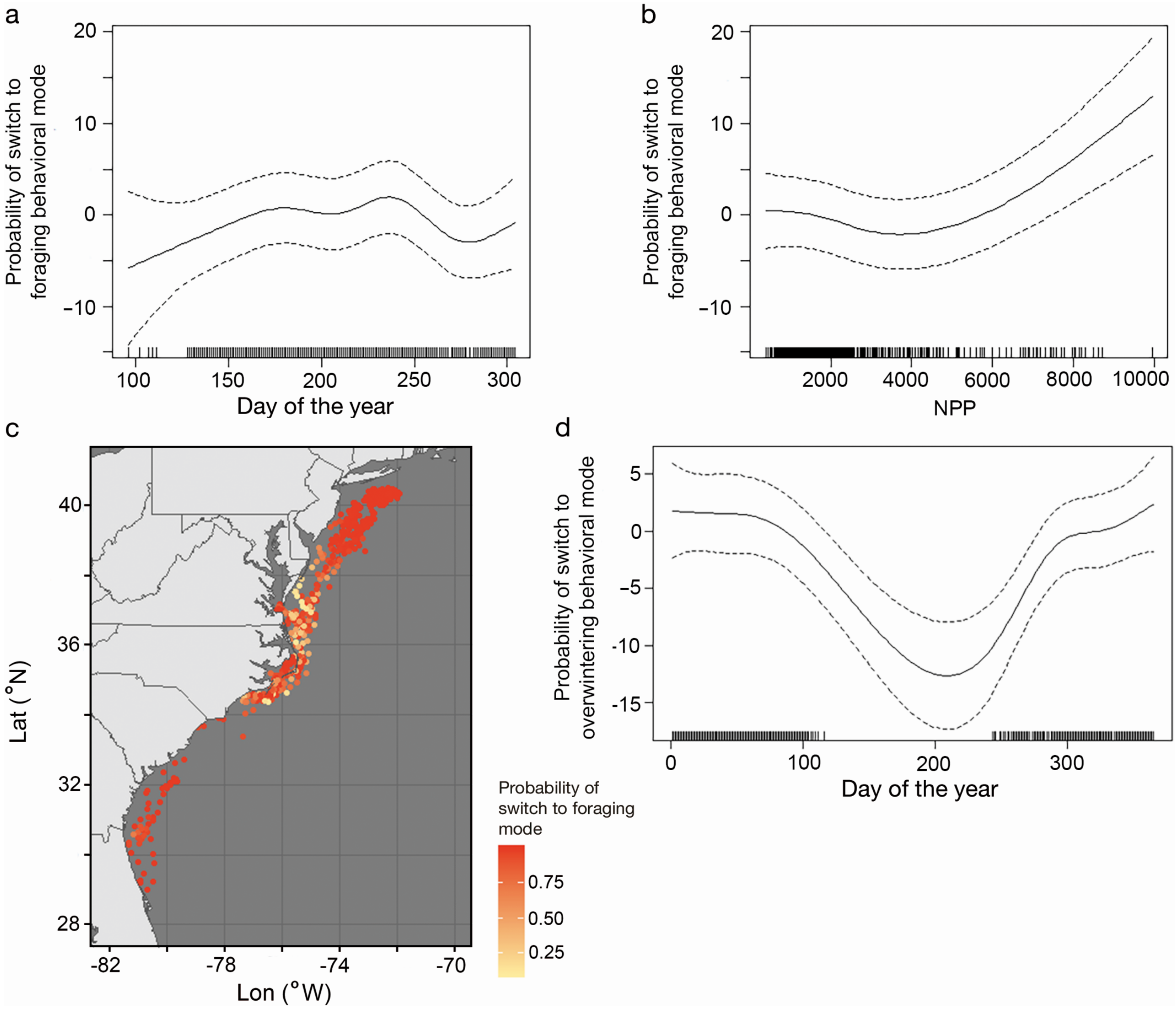

Fig. 4. Binomial generalized additive mixed models (GAMMs) applied to evaluate the potential influence of different environmental variables on the probability of loggerheads switching from migratory behavior to either (a–c) foraging or (d) overwintering behavior. Panel (c) represents the probability of switching to foraging mode relative to geographic location, as delineated by latitude and longitude associated with satellite track positions. For panels a, b, and d, solid lines represent mean GAMM response, dashed lines are 95 % credible intervals for the mean, and the rugplots represent the distribution of data for the sample

Table 3. Statistical output of binomial generalized additive mixed models applied to evaluate potential influence of environmental variables on the probability of loggerheads switching from migratory behavior to either foraging (April to October) or overwintering (November to March) behavioral states. Lat: latitude, Lon: longitude, SST: sea surface temperature, NPP: net primary production

Binomial GAMM	n	Adjusted r^2	Smooth terms				
			AIC	Variable	edf	χ^2	p
Foraging							
Day of year + Lat.Lon + SST + NPP + Bathymetry	885	0.002	428	Day of year	5.344	27.806	<0.001
				Lat.Lon	4.232	33.776	<0.001
				SST	1.175	0.549	0.531
				NPP	2.969	29.773	<0.001
				Bathymetry	1	1.006	0.316
Day of year + Lat.Lon + NPP	885	0.005	421	Day of year	5.451	41.73	<0.001
				Lat.Lon	4.342	34.91	<0.001
				NPP	3.176	33.37	<0.001
Overwintering							
Day of year + Lat.Lon + SST + NPP + Bathymetry	587	0.142	206	Day of year	5.366	21.862	<0.001
				Lat.Lon	3.164	1.411	0.738
				SST	1	1.516	0.218
				NPP	1	0.024	0.877
				Bathymetry	1	0.471	0.493
Day of year	587	0.236	186	Day of year	5.315	34.81	<0.001

location, and NPP (Fig. 4a–c). Adjusted r^2 values were low even for the best-fitting model (Table 3); however, random individual effects were significant ($p < 0.001$), indicating that turtle-specific behaviors likely had a great deal of influence on timing and location of foraging areas. Distribution of geographic location significance (Lat+Lon) was discontinuous, with an increased probability of foraging inshore, near the tagging location (dark red coloration), as opposed to the north and south, where foraging is more likely on the shelf (Fig. 4). With respect to overwintering behavior, the probability of switching from movement to overwintering mode was significantly influenced only by day of the year (Fig. 4d). Significant individual effects ($p < 0.001$) were again present, indicating that individual-specific factors influenced switching probabilities relative to other covariates. Overall, the probability of switching from movement to foraging behavioral mode increased following overwintering (beginning with March) through late June, after which it remained relatively stable until August when it began to decrease. Probability of switching to foraging mode remained relatively constant until NPP reached ~4000 mg C m^{-2} d^{-1}, after which it steadily increased. Finally, as would be expected, the probability of switching to overwintering behavior reached its nadir in mid-July, followed by a steady increase in probability through approximately October, after which the probability of switching remained relatively stable until it began to decrease again in mid-March.

4. DISCUSSION

Previous research has documented the extensive occurrence of loggerheads in North Carolina's estuarine waters, indicating the importance of this habitat to sea turtles (Epperly et al. 1995a,c). In the present study, we demonstrated that in addition to estuarine waters, North Carolina neritic waters, in particular those of Onslow Bay, are important habitat for loggerheads during both summer and winter months, and neritic waters from Virginia to New York/New Jersey serve as important summer foraging habitat. Most (67%) of the 12 turtles for which we documented overwintering behavior used North Carolina neritic waters (Onslow Bay), while the rest (33%) traveled to southern waters (South Carolina, Georgia, and Florida). The change to foraging behavior mode was significantly influenced by day of the year, geographic location, and NPP; however, individual-specific factors influenced switching probabilities relative to other covariates.

Loggerheads in this study inhabited 3 different summer foraging regions: (1) northern foraging grounds (either Virginia or New York/New Jersey, n = 11); (2) southern foraging grounds (South Carolina to Florida, n = 3); or (3) remained within neritic waters off North Carolina (n = 16). Despite energetic costs of migrating, those turtles traveling north are likely benefiting from more productive foraging areas (Hawkes et al. 2007, Schofield et al. 2013, Patel et al. 2015). NPP, which can be used as an indicator of pelagic marine resources, and has been linked with sea turtle foraging behavior (Polovina et al. 2000, 2001), was greater in the northern foraging areas (New York/New Jersey) than in neritic waters of Virginia, North Carolina, or areas farther south. This was demonstrated by the large percentage (37%) of loggerheads in our study that spent summer months foraging in a northern area. Another factor influencing summer dispersal patterns may be site fidelity to areas chosen for foraging by juveniles after transitioning from oceanic to neritic habitat, which might, in turn, influence where turtles forage as adults (Hawkes et al. 2007, Mansfield et al. 2009). For example, stable isotope analysis revealed that the majority (72–80%) of loggerheads nesting at northern beaches (North Carolina and Georgia) foraged in northern areas (New Jersey, Virginia, and Delaware) while those nesting at southern beaches (46–81%, Florida) foraged in southern areas (Bahamas; Pajuelo et al. 2012).

Similar to our study, other research on satellite-tracked loggerheads captured in more northern habitats (north of 34° N) in the western North Atlantic found that a majority of tracked turtles remaining in shelf waters used northern foraging areas. For example, Mansfield et al. (2009) found that from May to November, the majority (88%) of juvenile loggerheads captured in Virginia that remained in shelf waters foraged off Virginia and North Carolina. Likewise, in a study of juvenile loggerheads captured in North Carolina, McClellan & Read (2007) documented that most of the 13 tracked turtles remaining in shelf waters stayed off North Carolina. Finally, Hawkes et al. (2007) demonstrated that the majority (75%) of satellite tracked adult female loggerheads nesting in North Carolina (the northern part of the nesting range for this population), used foraging habitat between North Carolina and Delaware. Thus, these studies likewise highlight the importance of these northern foraging grounds to loggerheads inhabiting the western North Atlantic.

More than half (53%) of the loggerheads from this study remained within neritic waters of North Carolina. Loggerheads captured and satellite tagged in South Carolina displayed a similar, if not more pronounced, fidelity to their capture location where the majority (75%) of loggerheads were classified as 'seasonal residents' (Arendt et al. 2012c), remaining within 50 km of a Charleston, South Carolina, shipping channel. Only 5 of the 34 South Carolina turtles headed north: 4 to North Carolina and 1 to Delaware. Because juvenile loggerheads captured in South Carolina displayed such a restricted foraging range, Arendt et al. (2012c) proposed the idea of distinct foraging groups within a regional foraging ground. They also suggested that juvenile loggerheads could retain a lifelong affinity for a foraging habitat even during non-breeding periods. Evidence of such long-term association might also be evidenced by data indicating that after nesting in North Carolina, most (75%) female loggerheads used foraging habitat between North Carolina and Delaware (Hawkes et al. 2007). Likewise, a long-term foraging study of juvenile loggerheads in North Carolina estuarine waters revealed that residents were more specialized in resource use relative to the population over periods of years (Goodman Hall et al. 2015), again indicating preference for foraging areas containing those forage species. Further foraging ecology studies using stable isotope analysis might provide additional evidence of regional foraging area affinities.

Research on other loggerhead populations reveal a variety of foraging area sizes, with some studies estimating home range size (95% KDEs) and others estimating core-use areas (50% KDEs). Adult female loggerheads in the Mediterranean Sea had an average home range of 305 km^2 that varied from 3.5 to 1198 km^2 (Zbinden et al. 2008). In contrast, our average home range sizes (95% KDE) were much larger, and varied from 976.8 km^2 (Virginia neritic waters) to 21 246.6 km^2 (southern waters). However, when we compared average core-use areas (50% KDE) with other studies, those in Virginia (190 km^2) and North Carolina (274.3 km^2) were comparable to those of adult female loggerheads in the Gulf of Mexico (91.8 km^2) (Hart et al. 2012) while those in northern areas (950.4 km^2) were similar to those of adult female loggerheads in northeastern Brazil (889 km^2) (Marcovaldi et al. 2010), but larger than that of juvenile loggerheads in the northwest Gulf of Mexico (133.6 km^2) (Hickerson 2000). Our foraging area results included adults and juveniles of both sexes, which may be masking size differences between adults and juveniles. However, a quantitative comparison was not possible due to limited sample size for adults in each foraging region.

Interestingly, we also noted that a disproportionate number of males (both adults and juveniles) used northern foraging regions while a disproportionate number of females remained within North Carolina neritic waters. While inferences can be drawn as to the distribution patterns of the adult turtles, currently there is no literature on sex-related dispersal patterns of juvenile turtles. After breeding, male loggerhead sea turtles in the Mediterranean tend to use a broad spatial and temporal foraging habitat (Schofield et al. 2010), similar to females (Zbinden et al. 2008, Hays et al. 2010). As males expend high energy during the breeding season (Jessop et al. 2004) and foraging opportunities may be limited, a return to more productive foraging areas is likely (James et al. 2005). Although males generally depart breeding grounds at mid-season (Plotkin et al. 1996), some remain close to the breeding grounds (Van Dam et al. 2008, Arendt et al. 2012b). In fact, one-third of male loggerheads from the Mediterranean remained at the breeding grounds throughout the year, while females dispersed (Schofield et al. 2010, Hays et al. 2014). One of 4 adult male loggerheads in our study remained within North Carolina coastal waters; however, the other 3 used northern or southern foraging grounds.

Because of the impact of temperature on sea turtle physiology (Milton & Lutz 2003), population distributions are influenced geographically and temporally by water temperature. Although leatherbacks *Dermochelys coriacea* are exceptional among sea turtles in their ability to maintain an average core body temperature of 8°C above ambient temperatures (James & Mrosovsky 2004), hard-shelled turtles, such as the loggerhead, need to be in water above a certain minimum temperature for them to maintain physiological functions. If water temperatures fall rapidly or remain below that minimum for long periods, feeding behavior and locomotor movements will be negatively impacted (Milton & Lutz 2003). For example, loggerheads exposed to a drop in temperature from 30 to 10°C displayed behavioral changes at 15°C and experienced cold stunning and floated at 14°C (Lutz et al. 1989). However, several studies have documented active behavior of loggerheads despite low (<15°C) water temperatures. Loggerheads still remained active despite minimum water temperature of 11.8°C in the Mediterranean Sea (Hochscheid et al. 2007) and 10.3°C in the North Pacific (Narazaki et al. 2015). Although 5 of the loggerheads that we tracked were found in low water temperatures (12.2–13.7°C), none of these turtles experienced cold stunning (i.e. remaining at the surface for long periods of time), indicating that these turtles were active in water temperatures <15°C. Moreover, in a study of loggerhead behavior using a remotely operated vehicle-mounted video camera, Smolowitz et al. (2015) observed loggerheads in the Northwest Atlantic Ocean actively foraging in water temperatures below 10°C, a temperature range at which turtles have generally been thought to become cold stunned (Spotila et al. 1997). Thus, the capability of some loggerheads to remain active at temperatures previously anticipated to result in cold stunning or dormancy of others, reveals the wide range of temperatures at which this species is capable of remaining active.

In a study of winter sea turtle distribution in neritic waters of North Carolina, Epperly et al. (1995b) noted that the onshore movement of warm Gulf Stream frontal eddies in winter resulted in warmer water temperatures in Onslow Bay (between Cape Hatteras and Cape Lookout) than in other nearshore areas to the south. Frontal eddies consist of a filament of warm near-surface Gulf Stream water that wraps around a cold core of deeper Gulf Stream water (Lee & Atkinson 1983). These disturbances propagate along the shelf in a northward direction, transporting warm water across shelf waters. Loggerheads taking advantage of this favorable temperature regime may be the reason most (67 %) of the turtles we tracked in winter remained in these neritic waters.

In addition to water temperature, food resources also influence the distribution of sea turtles. Studies on home ranges of sea turtles have concluded that activities were concentrated in areas where food resources were optimal (Makowski et al. 2006). Gulf stream frontal eddies not only bring warm water to the shelf, they also facilitate the transport of nutrients to shelf waters (Lee & Atkinson 1983). Upwelled nutrients within the cold core result in increased primary production (Lee et al. 1991). When shelf waters are vertically well mixed (from November to April), phytoplankton production is primarily restricted to the outer shelf region; however, when shelf waters are vertically stratified (May to October), the nutrient-rich waters can reach the middle and inner shelf regions (Lee et al. 1991). Onslow Bay supports a diverse benthic community, largely due to a thin layer of sediment cover and numerous outcroppings of the underlying bedrock (Schneider 1976). In a survey of deep-water algae in the Carolinas, the majority of species found in Onslow Bay were tropical (Schneider 1976) while most of the benthic invertebrates were warm-temperate (inner shelf) or tropical (outer shelf) species (Cerame-Vivas & Gray 1966). Because the western North Atlantic loggerhead population as a whole feeds on a variety of prey including mollusks and crustaceans (Dodd 1988, Burke et al. 1993, Plotkin et al. 1993, Frick et al. 2001, Wallace et al. 2009), this habitat has the potential to provide food resources throughout the year, supporting their year-round distribution in the area.

Several studies have documented significant increases in dive duration (up to 10 h), coinciding with decreasing water temperature, indicating potential brumation (Hochscheid et al. 2005, 2007, Broderick et al. 2007, Hatase et al. 2007, Hawkes et al. 2007). Given that average water temperature experienced by turtles in this study during winter months was 19.6°C, and turtles spent very little (<6%) time in water temperatures <15°C, it is more probable that turtles are active and feeding in Onslow Bay during winter. In fact, Epperly et al. (1995b) observed that those turtles captured in a bottom trawl from November through February were generally active, not brumating or cold-stunned, and suggested that they had been on the bottom, likely feeding.

Bycatch in certain fisheries has been identified as detrimental to marine megafauna, including sea turtle populations (Lewison et al. 2004, Hamann et al. 2010, Wallace et al. 2013). Satellite telemetry has been used to indicate fishing-induced mortality (Hays et al. 2003, Byrne et al. 2017) with evidence for capture resulting from an increase in rate of good quality locations, transmitters moving toward coastal towns and villages, or submergence data, all indicating that transmitters had come out of the water. As none of the transmitters we deployed displayed this behaviour, we do not have evidence of capture. Nonetheless, because our data define several northern foraging grounds for loggerheads, they also reveal areas where sea turtle and fishery interactions might overlap. For example, the winter trawl fishery for summer flounder *Paralichthys dentatus* has regulations in place that require a turtle excluder device (TED) at all times of the year, but only when trawlers are operating south of 37° N (NMFS 1996). Thus when this fishery operates in waters to the north of 37° N, TEDs are not required. This trawl fishery, along with other bottom trawl fisheries, also operates north of the boundary (Orphanides & Magnuson 2007), and sea turtle bycatch occurs in the region where TEDs are not required (Murray 2007, 2008). Likewise, the monkfish (*Lophius* spp.) fishery, which uses large mesh (>20.3 cm) gill nets, has a seasonally adjusted closure that prohibits use of this gear based on water temperatures (NMFS 2002); however, this regulation is only implemented in waters south of Chincoteague, Virginia (37.9° N), while waters to the north of this area are not affected by this rule. In a study modeling loggerhead interactions with bottom trawl fisheries in the mid-Atlantic, Warden (2011) noted that because of the greater fishing effort, loggerhead interactions were estimated to be the greatest at latitude 37–39° N, an area in which 37% of the satellite-tagged loggerheads from this study spent summer and early autumn. Moreover, as warming ocean conditions manifest with current climate changes, sea turtles, like other marine species, may show a northward shift in distribution (Kleisner et al. 2016), resulting in an even greater percentage of sea turtles in these northern waters. Therefore, given that 12% of the North Carolina loggerhead foraging population originate from the Northwest Atlantic Ocean discrete population segment (Bass et al. 2004), which is at greatest risk for decline (Conant et al. 2009), it is imperative that additional protective measures are implemented and monitoring of loggerhead distributions is continued.

Through the use of satellite telemetry in conjunction with SSM, we demonstrated that neritic waters of North Carolina, in particular those of Onslow Bay, serve as important year-round foraging habitat for both juvenile and adult loggerhead sea turtles. In addition, this study highlights the importance of northern foraging grounds to loggerheads, an area with considerable fishing effort that lacks any mitigation of potential harmful interaction. Data such as ours, highlighting the spatial and temporal characteristics of densely-used foraging areas, can thus be used by conservation managers to make informed decisions concerning the establishment of marine protected areas or time/area fishery closures that successfully mitigate harmful human interactions.

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