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ORIGINAL PAPER

Satellite tracking reveals a dichotomy in migration strategies among juvenile loggerhead turtles in the Northwest Atlantic

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Abstract Few data are available on the movements and behavior of immature Atlantic loggerhead sea turtles (*Caretta caretta*) from their seasonal neritic foraging grounds within the western north Atlantic. These waters provide developmental habitat for loggerheads originating from several western Atlantic nesting stocks. We examined the long-term movements of 23 immature loggerheads (16 wild-caught and seven headstart turtles) characterizing their seasonal distribution, habitat use, site fidelity, and the oceanographic conditions encountered during their migrations. We identified two movement strategies: (1) a seasonal shelf-constrained north–south migratory pattern; and (2) a year-round oceanic dispersal strategy where turtles travel in the Gulf Stream to the North Atlantic and their northern dispersal is limited by the 10–15°C isotherm. When sea surface temperatures dropped below 20°C, neritic turtles began a migration south of Cape Hatteras, North Carolina (USA) where they established fidelity to the waters between North Carolina's Outer Banks and the western edge of the Gulf Stream along outer continental shelf. Two turtles traveled as far south as Florida. Several turtles returned to their seasonal foraging grounds during subsequent summers. Northern movements were associated with both increased sea surface temperature (>21°C) and increased primary productivity. Our results indicate strong seasonal and interannual philopatry to the waters of Virginia (summer foraging habitat) and North Carolina (winter habitat). We suggest that the waters of Virginia and North Carolina provide important seasonal habitat and serve as a seasonal migratory pathway for immature loggerhead sea turtles. North Carolina's Cape Hatteras acts as a seasonal "migratory bottleneck" for this species; special management consideration should be given to this region. Six turtles spent time farther from the continental shelf. Three entered the Gulf Stream near Cape Hatteras, traveling in the current to the northwest Atlantic. Two of these turtles remained within an oceanic habitat from 1 to 3 years and were associated with mesoscale features and frontal systems. The ability of large benthic subadults to resume an oceanic lifestyle for extended periods indicates plasticity in habitat use and migratory strategies. Therefore, traditional life history models for loggerhead sea turtles should be reevaluated.

Introduction

The coastal and estuarine waters of Virginia and the Chesapeake Bay (USA) provide important seasonal developmental foraging habitat for juvenile loggerhead (*Caretta caretta*) sea turtles (Lutcavage and Musick 1985; Byles 1988; Musick and Limpus 1997; Keinath 1993). As ectothermic reptiles, the distribution, biology and behavior of cheloniid sea turtles are strongly linked to the thermal regimes of their environment (Bell and Richardson 1978; Spotila et al. 1997). The body temperature of loggerhead

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sea turtles can only exceed ambient water temperatures by a few degrees Celsius (Spotila and Standora 1985). Prolonged exposure to temperatures lower than 8–10°C may cause "cold-stunning" or a disruption in the turtle's metabolic pathways, resulting in loss of buoyancy and an inability to dive or swim (Schwartz 1978; Morreale et al. 1992; Spotila et al. 1997). Sea turtles must compensate for their inability to thermoregulate via other mechanisms including shifting habitat use or temporal changes in activity or geographic distribution (reviewed by Zug et al. 2001).

Virginia's estuarine and coastal waters are subject to large variation in temperatures annually. Winter sea surface temperatures (SST) can be as low as 1–5°C, while summer temperatures may exceed 30°C. Due to cold winter temperatures, sea turtles are not physiologically capable of utilizing near-shore waters along the northeastern USA coast as over-wintering habitat. Stranding and aerial survey data indicate that yearly migrations north into the Chesapeake Bay are strongly associated with vernal warming with the greatest concentrations of sea turtles found south of the 18°C isotherm (Lutcavage and Musick 1985; Byles 1988; Keinath 1993; Coles 1999). When SST cools in the early fall (September to October), turtles begin a migration southward (Lutcavage and Musick 1985; Byles 1988; Keinath 1993). Thus, sea turtles have a limited *residency* period (May through October) within northeastern USA waters, followed by a *non-residency* period (November through April).

Other oceanographic cues such as primary productivity, sea surface height, frontal systems, and oceanic current vectors also likely influence the movements of loggerheads (Polovina et al. 2000; Witherington 2002; Luschi et al. 2003; Kobayashi et al. 2008) and other species of sea turtle including green (*Chelonia mydas*) (Pelletier et al. 2003; Seminoff et al. 2007). Chlorophyll concentrations are important variables associated with habitat use and feeding behavior among juvenile loggerheads in the Pacific (Polovina et al. 2000; Kobayashi et al. 2008). Flotsam, fronts and downwelling lines provide important habitat for posthatchling, neonate Atlantic loggerheads and for Pacific oceanic juvenile loggerheads (Carr 1986; Polovina et al. 2000; Witherington 2002) and for postnesting green turtles in the Pacific (Seminoff et al. 2007). In order to develop time-sensitive management strategies within temperate regions where seasonal thermal regimes restrict turtle residency, it is necessary to understand the role of oceanographic conditions in the migration and distribution of sea turtles.

Juvenile loggerheads found in the Chesapeake Bay are genetically comprised of both the northern (54%) and southern (46%) USA loggerhead subpopulations (Norrgard 1996). The northern loggerhead subpopulation is geographically associated with nesting beaches ranging from northeastern Florida and Georgia, north through North Carolina and Virginia (Encalada et al. 1998). Some turtles hatching from Florida's nesting beaches occur in North Carolina's sounds as juveniles (Rankin-Baransky et al. 2001; Bass et al. 2004; Bowen et al. 2004). These studies indicate shared habitat use among juvenile turtles originating from different western Atlantic subpopulations.

Aerial surveys conducted between 2001 and 2004 indicate a 65–75% decline in the Chesapeake Bay sea turtle population since the 1980s (Mansfield 2006). During this period, Virginia sea turtle stranding deaths increased 200–300% (Mansfield 2006). The observed strandings increase may be due, in part, to changes in mortality rates, changes in sources of mortality, and/or changes in turtle distribution patterns as a result of recent declines in blue crab (*Callinectes sapidus*) and horseshoe crab (*Limulus polyphemus*) prey availability within the Chesapeake Bay (Lipcius and Stockhausen 2002; Mansfield 2006; Seney and Musick 2006). Localized sources of mortality affecting juvenile loggerheads will ultimately translate to population impacts among all USA loggerhead subpopulations. Identifying and understanding seasonal sea turtle distribution patterns, locating areas of high turtle density, and identifying regional wintering habitat will help managers mitigate these impacts.

Few data are available (Byles 1988; Keinath 1993; Morreale 1999) characterizing the movements and behavior of juvenile loggerheads from established seasonal foraging grounds in the northwestern Atlantic. The primary objectives of this study were to: (1) characterize the seasonal distribution and habitat use of juvenile loggerhead sea turtles; (2) identify the wintering habitat of juvenile loggerhead sea turtles seasonally found in northwestern USA waters; and (3) characterize the oceanographic conditions associated with the migration and distribution of immature loggerhead sea turtles in the northeastern USA, and northwest Atlantic.

Materials and methods

Satellite telemetry

We deployed 23 satellite tags on juvenile loggerhead sea turtles between 1986 and 2007. Sixteen turtles were captured on their foraging grounds within the Chesapeake Bay; seven turtles were headstarted animals (2–3 years of age) originating from North Carolina and Virginia. Headstarted turtles are collected on natal beaches as eggs or hatchlings and raised in captivity for later release as larger neonates or juveniles (Donnelley 1994; Meylan and Ehrenfeld 2000). A short-lived loggerhead headstart program was conducted using turtles collected from Virginia and North Carolina nesting beaches in the late 1980s and early 1990s. Telonics, Inc. (ST-3 ST-6, ST-14 and ST-18; $n = 15$), Wildlife Computers (SDR-T16; $n = 2$), and (Sirtrack Kiwisat 101; $n = 6$)

platform terminal transmitters (PTT's) were used. We attached tags to the turtles' carapaces with fiberglass filler (prior to 2000) or with a base layer of PowerFast™ two-part marine epoxy covered by SonicWeld™ putty epoxy. The SonicWeld™ was molded into a tear-drop shape to create a smooth, hydrodynamic surface. Transmitters deployed prior to 2000 had continuous duty cycles (24-h on). All other duty cycles were set to 12-h on, 48-h off. Transmitter data were collected and distributed by Service ARGOS (ARGOS 1988, 1996; CLS 2007) and managed using the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley 2005).

All turtles were measured, weighed and flipper-tagged prior to release. With the exception of two turtles released off of Cape Hatteras, North Carolina, turtles were released in the lower Chesapeake Bay and Bay mouth. Using one-way analysis of variance (ANOVA), we tested for differences in sizes (straight carapace length, or SCL) between headstart and wild turtles, and between turtles exhibiting different migratory strategies (McClellan and Read 2007).

Data filters

Location data were archived, filtered and summary statistics were generated using STAT (Coyne and Godley 2005). Transmitter location data were filtered to retain best quality Location Classes (LC) 3, 2, 1, 0, and A for tags deployed between 1994 and 2007 (Hays et al. 2001; Vincent et al. 2002, Tougaard et al. 2008) and Locator Indicator codes (LI) -3, -2, -1 and 0 for tags deployed before 1994. Location Indicator codes -3 to 0, correspond to locations where ≥ 3 satellite messages were received (similar to LC 0–3, A). We filtered all data for likely swim speed between locations (<5 km h^{-1}), minimum turning angle ($>3°$), likely distance between points (<50 km), and topography (<0.5 m). Filtered data were imported into ArcView 3.2 and reconstructed for spatial movement analyses. Tracks lasting at least 21 days ($n = 19$ of 23) were used for these analyses to ensure that tracks were not biased by small sample sizes or behavioral biases associated with the tagging event. To reduce spatial bias associated with autocorrelated data, we selected daily locations for each turtle from the STAT filtered dataset (De Solla et al. 1999; James et al. 2005a). Location data were quantified using STAT to determine the range in depth of the water column and mean distance from nearest shore (Coyne and Godley 2005).

Density utilization plots

Daily location data were tallied into hexagonal area bins. Each hexagonal area bin was larger in scale than the associated error of LC or LI (669–2,686 km^2 vs. approximately >4–10 km; Brothers et al. 1998; Britten et al. 1999; Millspaugh and Marzluff 2001; Hays et al. 2001; Vincent et al. 2002; Tougaard et al. 2008). We linearly interpolated locations for missing days (an artifact of tag duty cycle); distances between observed locations were divided among missing days (James et al. 2005a; TEWG 2007). Hexagon-binned maps were generated using all track data as well as a zoomed subset to identify neritic habitat use during periods of known Chesapeake Bay sea turtle *residency* (May–November) and *non-residency* (December–April). Each degree is represented by either two hexagons (all track data), where the area of each hexagon is approximately 2,686 km^2, or by four hexagons (zoomed neritic *residency* and *non-residency* maps), where the zoomed hexagon area equals approximately 669 km^2.

Movement analyses

The start of seasonal turtle migrations out of Virginia's waters was determined by an extended (>4 days) and significantly directional travel path (bearing). Using the Spatial Analyst and Animal Movement (AMAE) extension for ArcView 3.2, we tested individual track data for spatial randomness and orientation using circular point statistics and the Raleigh's z statistic; significant values were based on $P < 0.05$ (White and Garrott 1990; Zar 1999; Hooge et al. 2001). Turtles released mid- to late fall that exhibited extended (>4 days) directional movement immediately postrelease ($n = 2$) were not included in these analyses since we could not determine if their movements were influenced by the cold seasonal temperatures associated with a late release. We used Monte Carlo Random Walk (MCRW) simulations to test for site fidelity (1,000 replicates) using AMAE (Hooge et al. 2001). Site fidelity analyses excluded directed migratory movements. Tracks were tested for spatial randomness against randomly generated walks; significance was based on $P < 0.05$; low r^2 values represent higher relative site fidelity (Hooge et al. 2001). Tracks exhibiting site fidelity indicate that the turtles' movements were more spatially constrained compared to randomly distributed or dispersed movement data (Hooge et al. 2001).

Filters applied to location data help minimize erroneous locations in track reconstruction. The effects of location error bias were also minimized when examining large-scale migratory tracks or habitat use (Hays et al. 2001). Our results should be considered conservative for smaller-scale analyses of movement within discrete near shore or estuarine habitats. Spatial location error associated with directional movement or site fidelity analyses tend to provide less constrained or more randomly dispersed results. Therefore, if location accuracy were increased, tracks already exhibiting significant directional movement or site fidelity would likely result in even more significant P values.

Oceanographic composites

We sorted all track data (2003–2007) into seasonal bins (winter, spring, summer and fall) determined by solstice and equinox dates within the Northern Hemisphere. We used STAT to extract oceanographic data describing sea surface temperature, chlorophyll content and bathymetry for all filtered turtle locations occurring between 2003 and 2007 ($n = 10$ turtles) (Coyne and Godley 2005). These data were used to determine SST encountered by individual turtles the week prior to and the week following the start of directional fall migratory behavior. Oceanographic data prior to 2003 were not available in STAT.

We generated seasonal oceanic SST composites for the entire Atlantic basin using MODIS 9 km SST data, and seasonal coastal SST composites using MODIS 4 km SST data. Seasonal 9 km net primary productivity (NPP) composites were generated using the Vertically Generalized Production Model (VGPM). Seasonal sea surface height (SSH) anomaly composites were generated from Ssalto/Duacs and Archiving Validation and Interpretation of Satellite Data in Oceanography (AVISO). Track data were overlaid with each seasonal composite. All SSH anomaly data and STAT-derived SST and chlorophyll data were tested for normality using the Kolmogorov–Smirnov test ($P < 0.05$). We tested for differences in SST and chlorophyll encountered by turtles exhibiting different migratory strategies using the Mann–Whitney *U* test (Hawkes et al. 2006).

Results

General movements and turtle body size

Two strategies were observed: (1) neritic movements with shelf-constrained seasonal north–south migrations ($n = 17$); and (2) oceanic movement ($n = 6$) where turtles traveled in the Gulf Stream to the northwestern Atlantic. Neritic turtles remained on the continental shelf off Virginia and North Carolina ($n = 15$) or moved south along the shelf to Florida ($n = 2$). Six turtles (three headstart and three wild) traveled to oceanic waters, of which four continued to the northeast Atlantic. The remaining two turtles (both headstarted) remained adjacent to the coastal shelf; however, all oceanic turtles remained in deep waters (mean = 4,281 m ± 1,262 SD, range = 10–5,674 m). The turtles traveling to the northern Atlantic ranged as far east as 35°W, and between 24°N and 47°N (Fig. 1). Two of these turtles remained within oceanic waters for more than 1–3 years (458 days and 1,167 days) and ranged from 8 km (off of Bermuda) to 1,211 km from shore in the north Atlantic (mean = 461 km ± 241 SD).

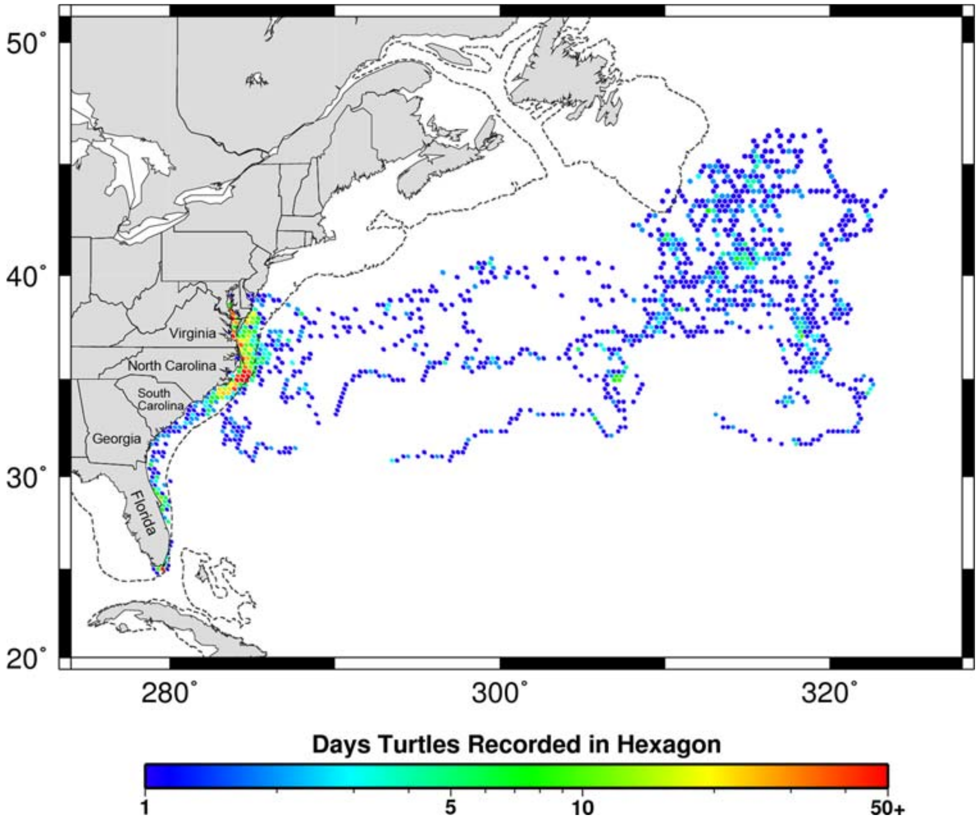


Fig. 1 Habitat use and movements of immature loggerhead sea turtles ($n = 23$; 3,535 track days; maximum 78 days per hexagon). The number of log-transformed track days spent per hexagon is represented by *color*. The 200 m isobath is represented by a *dashed line*. Each degree is represented by *two hexagons*; the area of each hexagon is 2,686 km^2

Turtles in this study (mean = 64.8 cm SCL ± 10.9 SD, range = 41.9–90.5 cm) were tracked for an average of 216 days (±320 days SD, range = 7–1,415 days) (Table 1). Wild turtles were significantly larger (mean = 68.0 cm SCL ± 9.3 SD, range = 53.3–90.5 cm) than headstarted turtles (mean = 56.0 cm SCL ± 9.3 SD, range = 41.9–64.8 cm; ANOVA $F_{1,21} = 7.26$; $P = 0.014$) (Table 1). Neritic turtles (mean = 63.5 cm SCL ± 10.23 SD, range = 41.9–80.9 cm) were not significantly larger than oceanic turtles (mean = 69.5 cm SCL ± 11.75 SD, range = 52.9–74.2 cm; ANOVA $F_{1,21} = 1.31$; $P = 0.226$). Excluding headstart animals, there were no significant size differences among wild neritic and oceanic turtles (ANOVA $F_{1,15} = 0.98$; $P = 0.360$).

Neritic turtles ($n = 17$)

The area of densest occupation occurred in the Chesapeake Bay particularly within the mouths of Bay tributaries, and in the region immediately south of Cape Hatteras, North Carolina (Fig. 1). High use areas during the *residency* period of spring through early fall (May through November) occurred in Virginia's coastal and Bay waters south to the North Carolina–South Carolina border (Fig. 2a). Two turtles showed significant site fidelity (MCRW $P \leq 0.001$; $r^2 \leq 0.035$) to discrete areas within the Chesapeake Bay or near-shore waters north of Cape Hatteras. Between September 20 and November 15 turtles (of 17) migrated south of Cape Hatteras (Table 1; Fig. 2b). With the exception of two headstart turtles that spent a short period (<2 weeks) north of Cape Hatteras along the outer continental shelf and the western edge of the Gulf Stream during early winter, no juvenile turtle occurred within near-shore or estuarine waters north of Cape Hatteras during the *non-residency* period (December through April) (Fig. 2b). Fall migrations began when SST dropped below 20°C. During the week prior to the start of the fall migration, mean SST was 19.9°C (±2.4 SD, range = 17.0–24.6°C). During the week following fall migration, mean SST was 18.8°C (±2.3 SD, range = 13.9–27.4°C). During the winter and early spring, eight turtles established significant fidelity (MCRW $P \leq 0.048$; $r^2 \leq 0.05$) to the waters south of Cape Hatteras,

Table 1 Summary data for tracked turtles including track ID; straight carapace length (SCL); release date; duration (days) of track; whether turtle was headstarted (Y) or wild (N); strategy adopted by each turtle (*S* shelf-based; *O* oceanic); start date of fall migration; and date of Gulf Stream dispersal if applicable

Track ID	SCL (cm)	Release date	Duration (days)	Headstart (Y/N)	Shelf (S) or oceanic (O) strategy	Start date of fall migration	Date of Gulf Stream dispersal
5873[a]	80.9	5-Oct-86	26	N	S	5-Oct-86	
5784	90.5	3-Dec-87	180	N	O		
4931	64.8	4-Oct-89	93	Y	O	2-Nov-89	
4932	59.9	9-Nov-89	200	N	S	13-Nov-89	
4933	69.6	9-Nov-89	225	N	S	16-Nov-89	
1228	–	18-Sep-91	26	Y	O		25-Sep-91
1230	57.3	18-Sep-91	24	Y	S		
1231[a]	60.3	18-Sep-91	16	Y	S	18-Sep-91	
1233	47.5	18-Sep-91	29	Y	S	26-Sep-91	
1234a[a]	41.9	18-Sep-91	7	Y	S	19-Sep-91	
4936	64.2	23-Oct-91	49	Y	O	8-Nov-91	
4935[a]	60.2	28-Oct-91	209	N	S	28-Oct-91	
1234b	71.8	13-Sep-01	40	N	S	30-Sep-01	
11583	64.5	15-Jul-03	1,415	N	S/O	13-Oct-03	15-Mar-04
11993a[a]	76.3	17-Jul-03	15	N	S		
41335	66.0	22-Oct-03	36	N	S	1-Nov-03	
41336[a]	68.4	22-Oct-03	15	N	S	15-Nov-03	
10378	53.3	10-Jun-04	371	N	S	16-Oct-04	
10692	63.5	16-Nov-04	458	N	O		22-Dec-04
10693	60.2	17-Jun-05	771	N	S	10-Oct-05; 20-Sept-06	
10401	76.0	17-Jun-05	225	N	S	14-Nov-05	
11993b	65.4	30-Aug-05	220	N	S	12-Oct-05	
11585	62.0	30-Aug-05	318	N	S	12-Oct-05	

[a] Directed migrational movement occurred within 1–4 days postrelease or track durations too short to include in movement analyses

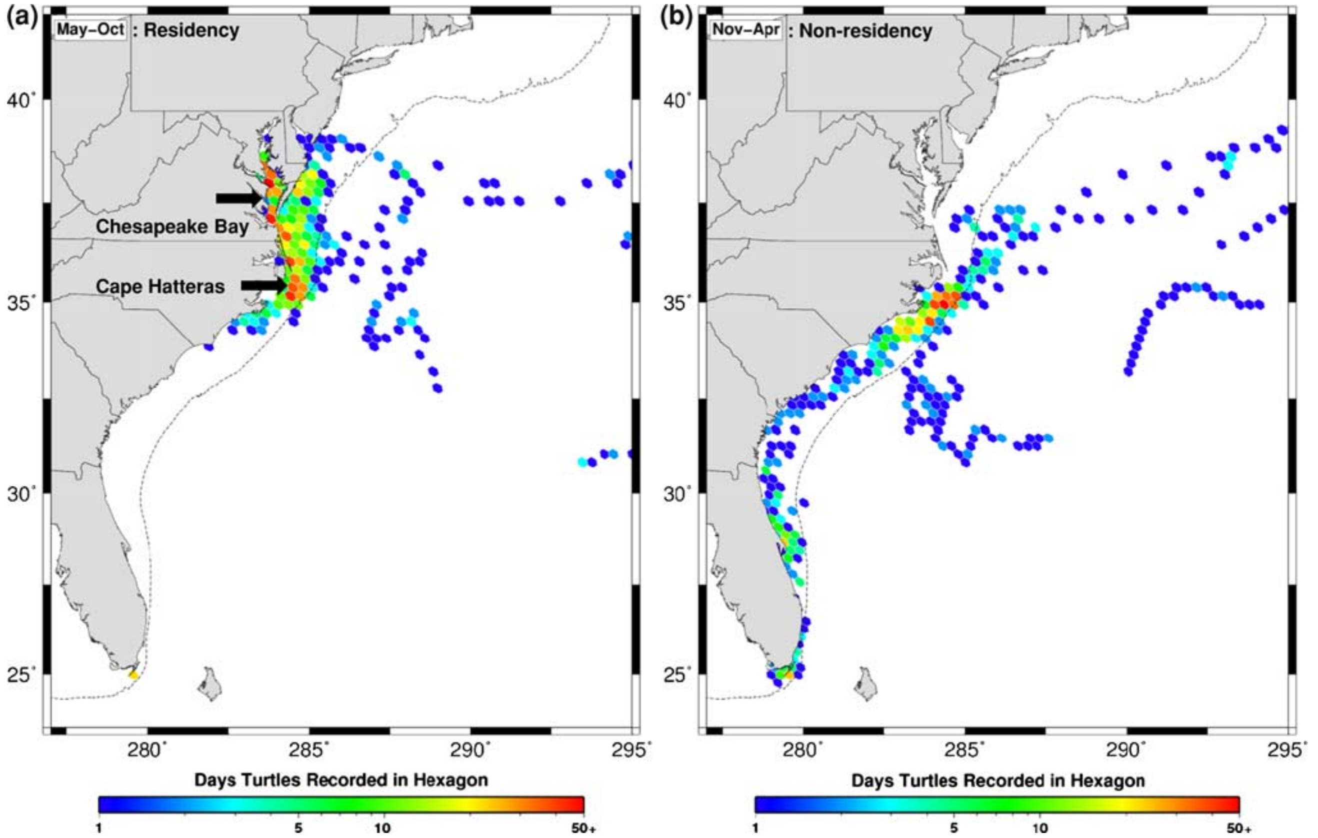


Fig. 2 Coastal habitat use and movements of immature loggerhead sea turtles during the months of seasonal northern *residency* (**a**), and *non-residency* (**b**) ($n = 23$ turtles; 3,535 track days). **a** *Residency* May through November ($n = 23$ turtles; 1,980 track days; maximum 58 days per hexagon). **b** *Non-Residency* December through April ($n = 13$ turtles; 1,515 track days; maximum 49 days per hexagon). The number of log-transformed track days spent per hexagon is represented by *color*. The 200 m isobath is represented by a *dashed line*. Each degree is represented by *four hexagons*; the area of each hexagon is approximately 669 km^2

between Cape Hatteras and Cape Fear; Fig. 3a, b) and the western edge of the Gulf Stream near the outer continental shelf. These turtles occurred farther offshore in association with the western frontal system of the Gulf Stream (Fig. 3a).

Two turtles continued migrating south along the continental shelf to Florida. One turtle traveled to the southern tip of Florida and the Florida Keys, establishing significant fidelity (MCRW $P = 0.001$; $r^2 = 0.037$) to this area prior to tag failure. The other turtle migrated south to Cape Canaveral, Florida where it established significant fidelity (MCRW $P = 0.001$; $r^2 = 0.018$) during the winter months. By March 16, this turtle migrated north again, reaching Cape Hatteras by May 10 (55 days later) and the mouth of the Potomac River in the western Chesapeake Bay by May 17th where it maintained significant fidelity (MCRW $P = 0.017$; $r^2 = 0.045$) close to where it had been captured the year before.

In addition to the Florida migrant, four turtles that wintered off Cape Hatteras returned to the Chesapeake Bay during subsequent summers. One of these turtles returned to waters south of Cape Hatteras for a second winter, followed by a third consecutive seasonal migration to the Chesapeake Bay, indicating interannual site fidelity (MCRW $P = 0.002$; $r^2 = 0.051$) to the vicinity of original capture near the mouth of the Potomac River and the upper Chesapeake Bay. Among the four Cape Hatteras turtles, northern springtime migrations commenced between May 21 and June 7 when SST warmed above 21°C (Fig. 3a–d). These turtles moved closer to shore prior to their northern spring migrations (Fig. 3b). Mean SST was 22.3°C (±1.9 SD, range = 17.0–23.8°C) the week prior to migration, and 21.6°C (±2.1 SD, range = 13.9–22.6°C) the week following the start of migration. Neritic turtles experienced higher SST and a broader range of chlorophyll values during the summer months compared to other seasons (Fig. 4a, b). All neritic turtles remained within normally distributed SST (Kolmogorov–Smirnov $P < 0.01$; KS = 0.189) ranging from 9.0°C in the winter to 29.3°C in the summer (Fig. 4a).

Oceanic turtles ($n = 6$)

Six turtles ranged farther from the continental shelf than the neritic turtles. Four turtles, including one headstart, entered

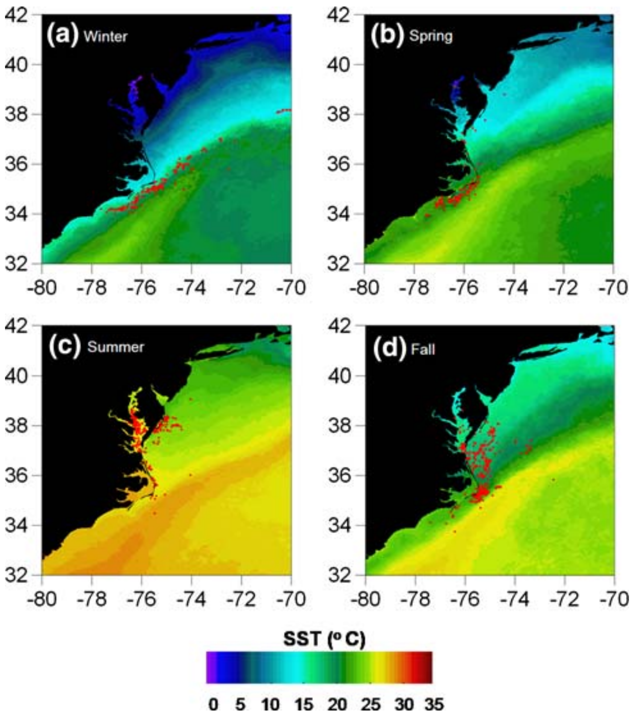


Fig. 3 Coastal sea surface temperature composites (2003–2007) by season overlaid with loggerhead track data (*red dots*) ($n = 8$). Winter (**a**); spring (**b**); summer (**c**); and fall (**d**) composites generated using MODIS 4 km SST data

the Gulf Stream near Cape Hatteras and moved with the current off the shelf to the east and north. Three of these turtles, including the headstart turtle, traveled in the current to the northwest Atlantic. After a summer of Chesapeake Bay foraging followed by a winter south of Cape Hatteras, one wild-caught turtle (11583) traveled to northwest Atlantic waters, remaining there for over 3 years (1,167 days). This track is among the longest recorded satellite tracks ($n = 1{,}415$ track days) for any loggerhead sea turtle to date. Turtle 10692 traveled in the Gulf Stream to northwest Atlantic waters where it moved east and south, making its way to Bermuda waters over a year after release. None of the oceanic turtles exhibited site fidelity to a discrete oceanic region.

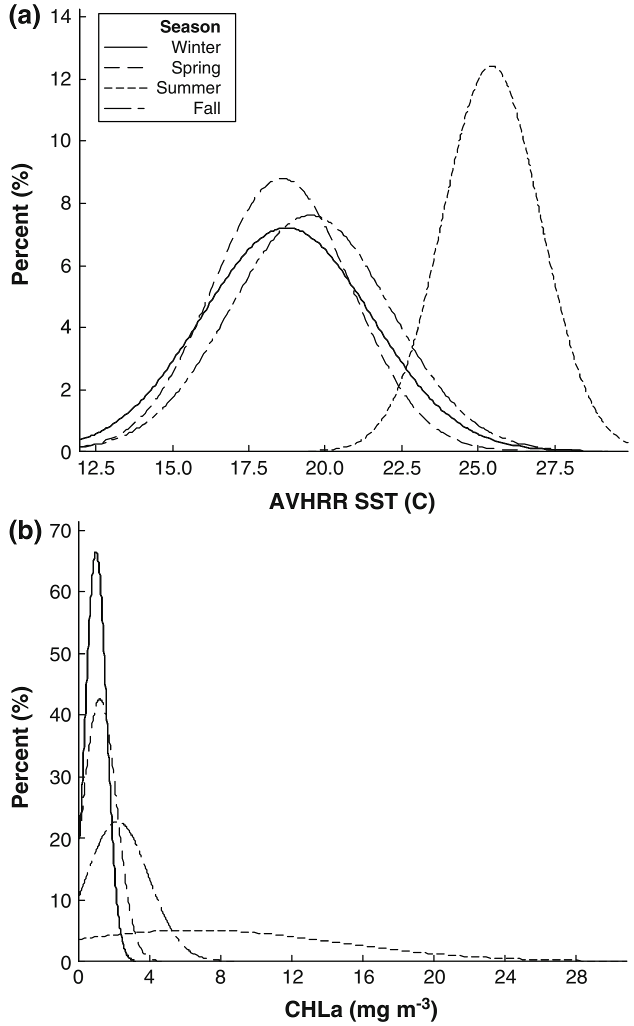


Fig. 4 Fitted seasonal density distributions for neritic turtle tracks (2003–2007; $n = 8$) including **a** sea surface temperature (°C) in the winter (18.7°C ± 2.8 SD, range = 9.0–21.5°C; $n = 100$), spring (18.6°C ± 2.3 SD, range = 13.6–24.4°C; $n = 86$), summer (25.5°C ± 1.6 SD, range = 22.9–29.3°C; $n = 275$) and fall (19.5°C ± 2.6 SD, range = 10.0–25.3°C; $n = 391$); and **b** chlorophyll *a* (mg m^{-3}) in the winter (0.97 mg m^{-3} ± 0.60 SD, range = 0.32–1.49 mg m^{-3}; $n = 133$), spring (1.19 mg m^{-3} ± 0.94 SD, range = 0.32–5.86 mg m^{-3}; $n = 92$), summer (6.60 mg m^{-3} ± 7.90 SD, range = 0.18–29.74 mg m^{-3}; $n = 162$) and fall (2.20 mg m^{-3} ± 7.76 SD, range = 0.17–10.67 mg m^{-3}; $n = 386$)

Oceanography

All oceanic turtles remained south of where the Gulf Stream meets the 10–15°C isotherm (Fig. 5a–d). All oceanic turtles remained within normally distributed (Kolmogorov–Smirnov $P < 0.01$; KS < 0.28) SST ranging from 10.9 to 29.0°C (Fig. 8a). These turtles were found in areas of high NPP and along the edges of mesoscale features distinguished by SSH anomalies (Figs. 6a–d, 7a–d). There were no differences (Mann–Whitney $U_{1,1093} = 475{,}368$; $P = 0.153$) in SST encountered by oceanic and neritic turtles; however, higher chlorophyll values (Mann–Whitney $U_{1,615} = 384{,}391$; $P < 0.001$) were encountered by the neritic turtles compared to the oceanic turtles. Oceanic turtles experienced warmer SST during the summer months than during other seasons (Figs. 5a–d, 8a); however, these turtles encountered higher chlorophyll concentrations during the spring months compared to the neritic turtles who experienced higher chlorophyll concentrations during the summer (Fig. 8b).

Turtle 11583 expanded its range south with the northwestern Atlantic spring bloom to approximately 30°N, and

Fig. 5 Seasonal oceanic sea surface temperature (SST) composites (2003–2007; *n* = 2) with loggerhead track data overlaid (purple dots). Winter (**a**); spring (**b**); summer (**c**); and fall (**d**) composites generated using MODIS 9 km SST data

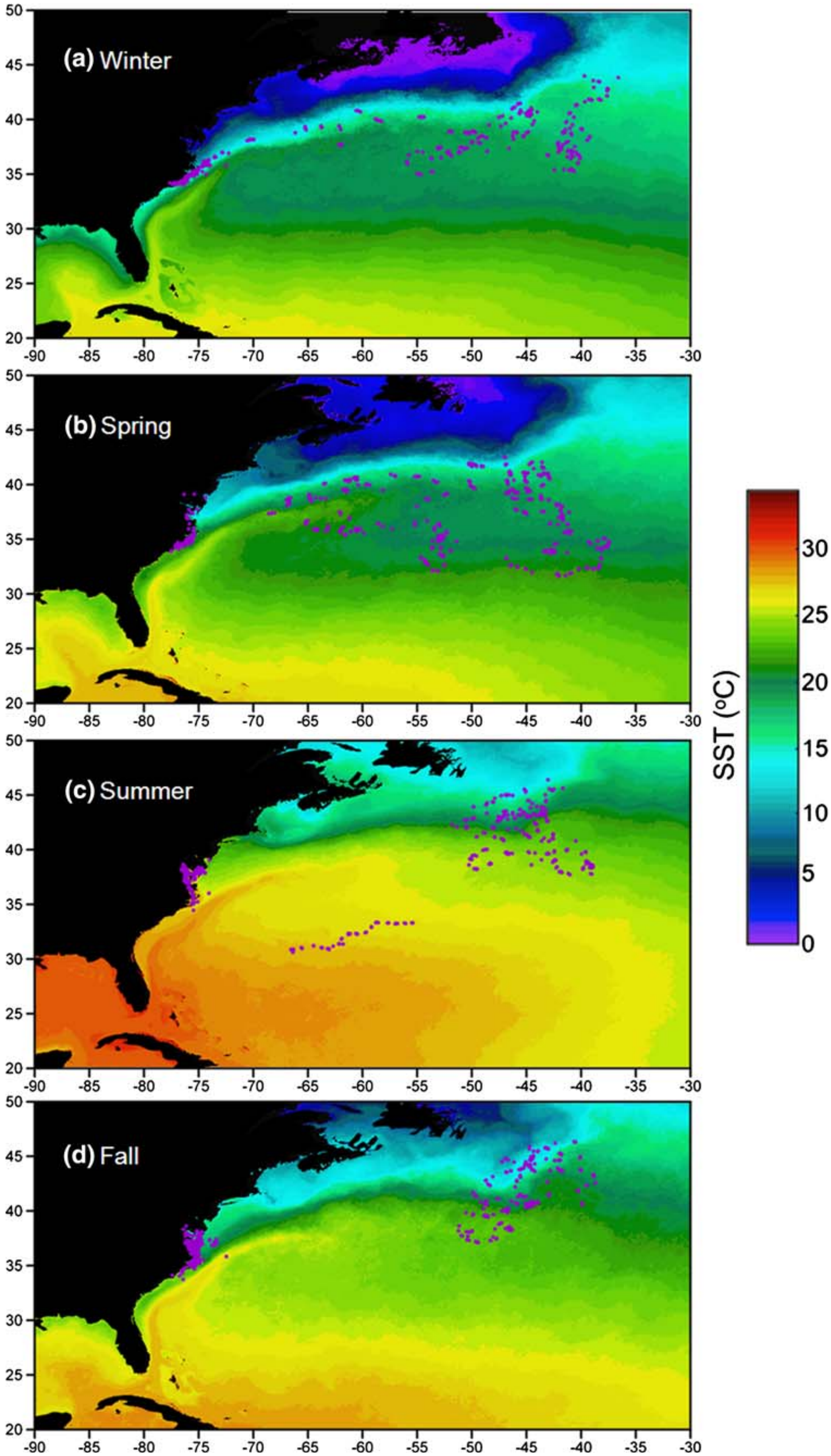
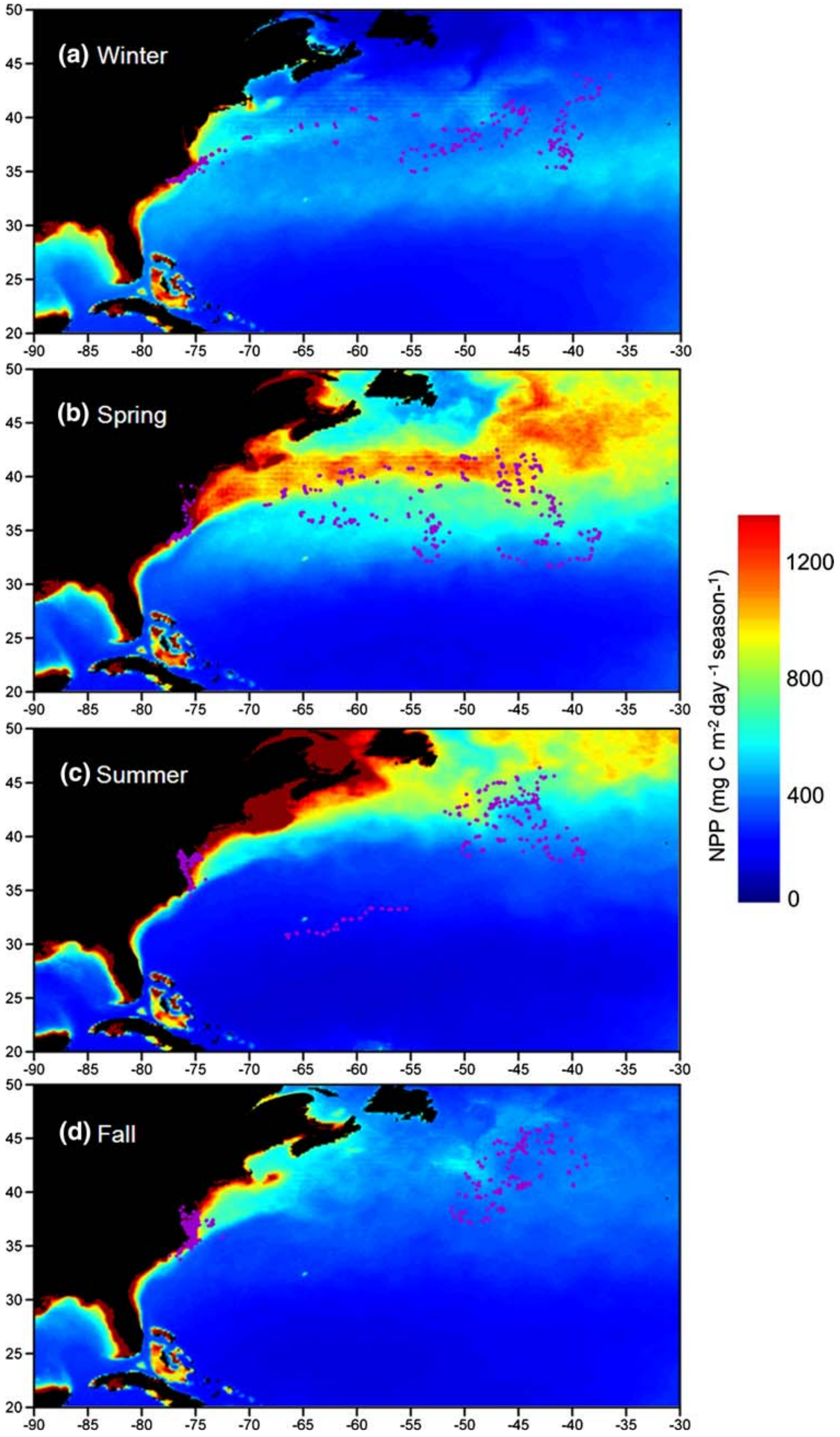


Fig. 6 Seasonal oceanic net primary productivity (NPP) composites (2003–2007; *n* = 2) with loggerhead track data overlaid. Winter (**a**); spring (**b**); summer (**c**); and fall (**d**) composites generated using the Oregon State University Ocean Productivity VGPM Model



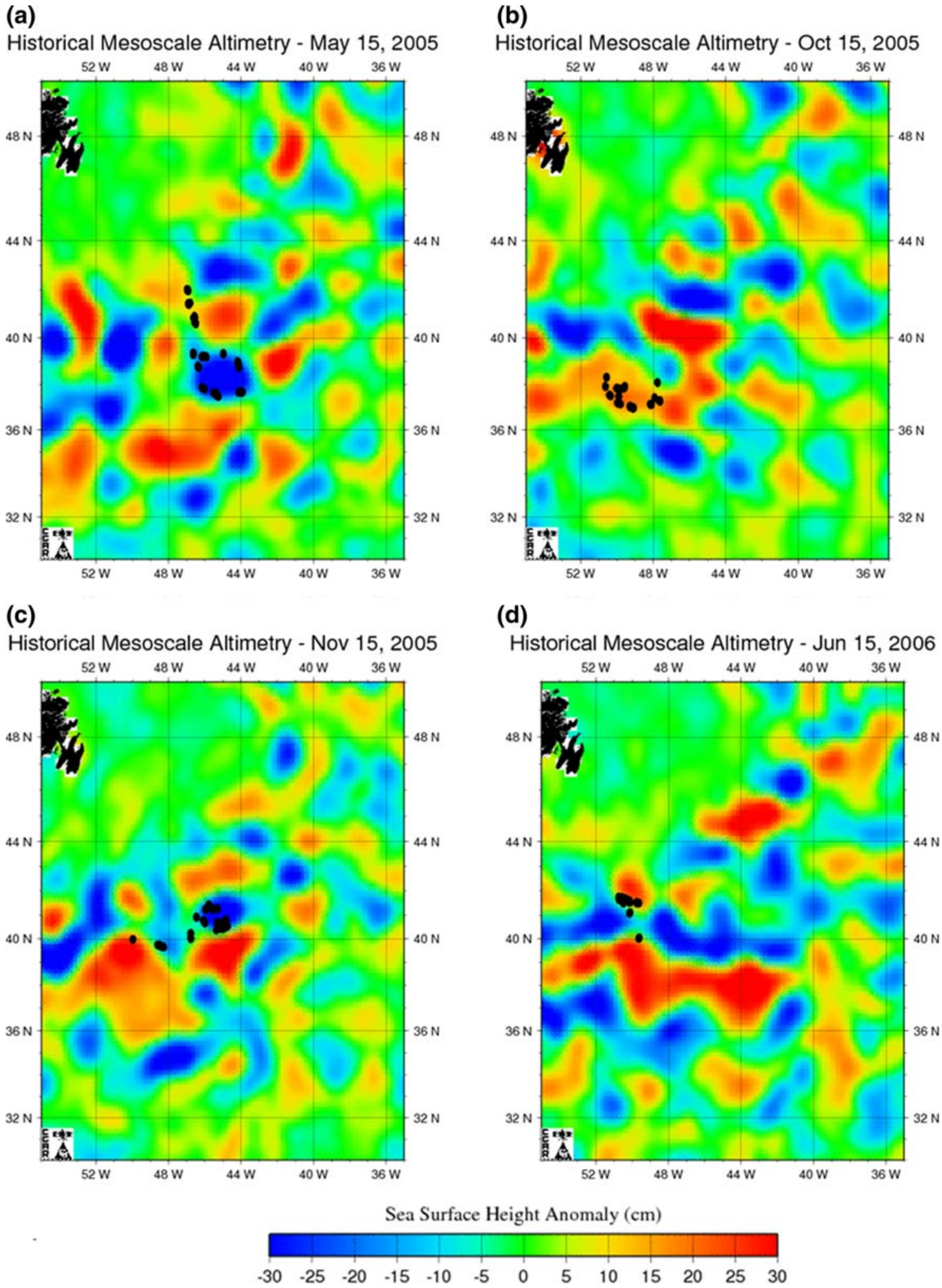


Fig. 7 Selected monthly oceanic sea surface height anomaly composites with turtle 11583 track data overlaid (*black dots*). Winter (**a**); spring (**b**); summer (**c**); and fall (**d**) composites generated from Ssalto/Duacs distributed by AVISO using data derived from TOPEX/Poseidon, Jason, and ERS-1/2

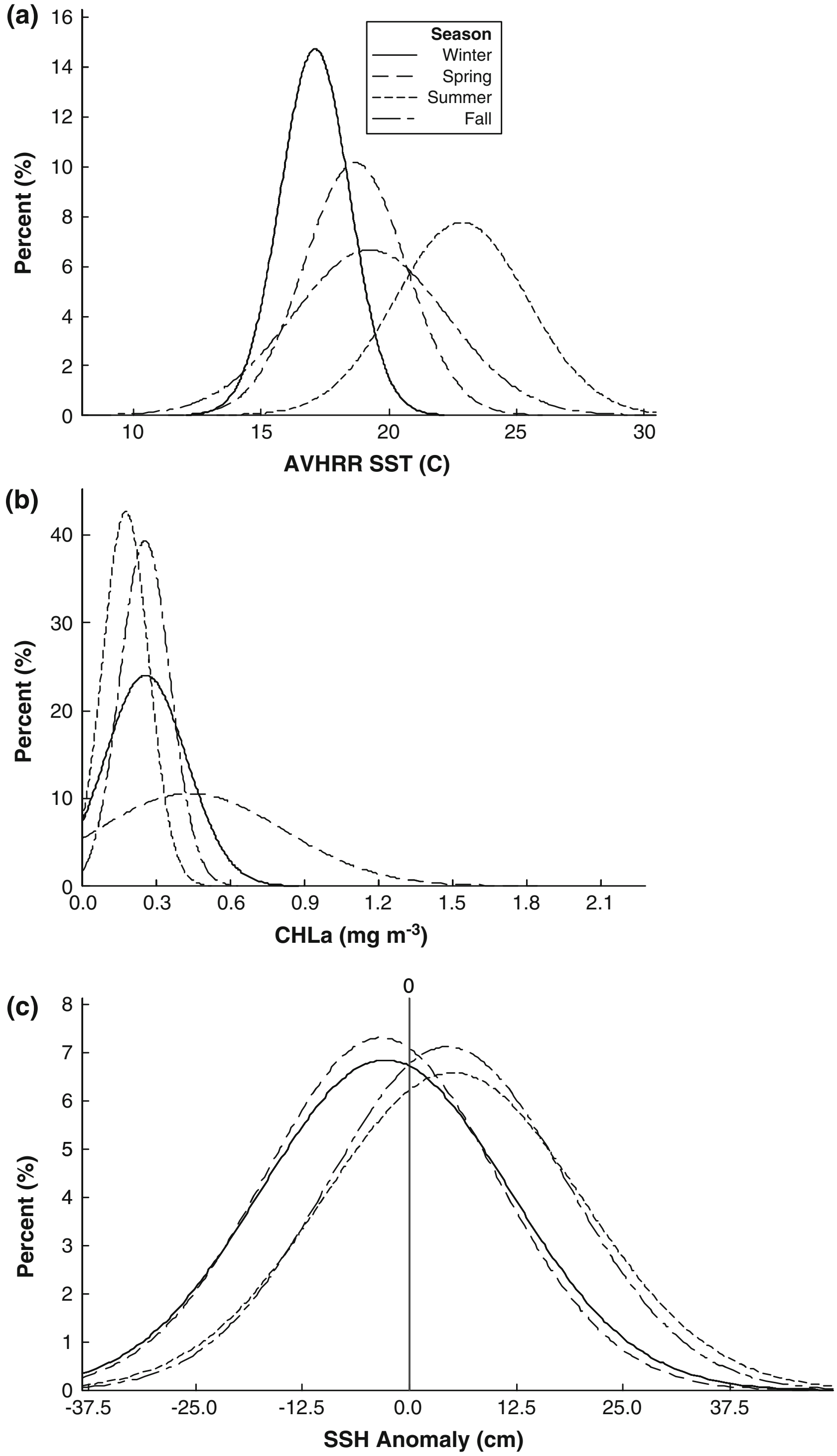


Fig. 8 Fitted density distributions for oceanic turtle tracks (2003–2007; *n* = 2) including **a** sea surface temperature (°C) in the winter (17.1°C ± 1.36 SD, range = 15.5–21.0°C; *n* = 176), spring (18.7°C ± 2.0 SD, range = 12.6–26.4°C; *n* = 443), summer (22.8°C ± 2.6 SD, range = 16.7–28.1°C; *n* = 251) and fall (19.3°C ± 3.0 SD, range = 13.2–24.4°C; *n* = 192); **b** chlorophyll *a* (mg m^{-3}) in the winter (0.26 mg m^{-3} ± 0.17 SD, range = 0.11–1.01 mg m^{-3}; *n* = 133), spring (0.44 mg m^{-3} ± 0.38 SD, range = 0.30–2.21 mg m^{-3}; *n* = 314), summer (0.18 mg m^{-3} ± 0.09 SD, range = 0.02–0.70 mg m^{-3}; *n* = 179) and fall (0.25 mg m^{-3} ± 0.10 SD, range = 0.10–0.83 mg m^{-3}; *n* = 136); and **c** sea surface height anomalies (cm) in the winter (−2.82 cm ± 14.53 SD, range = −28.6–40.6 cm; *n* = 177), spring (−3.34 cm ± 13.62 SD, range = −35.7 to 31.4 cm; *n* = 529), summer (5.07 cm ± 15.11 SD, range = −26.1 to 40.1 cm; *n* = 284) and fall (4.47 cm ± 13.97 SD, range = −24.9 to 42.6 cm; *n* = 301)

remaining north of 35°N during the other seasons (Fig. 5a–d). This track and that of 10692, when overlaid with SSH data, were associated with the outer frontal areas of either positive or negative SSH anomalies (Fig. 7a–d). Mean seasonal SSH data for these tracks were normally distributed (Kolmogorov–Smirnov $P = 0.01$; KS = 0.064) either slightly above zero (summer and fall) or slightly below zero (winter and spring) (Fig. 8c).

Discussion

Seasonal site fidelity

Several species of sea turtle exhibit fidelity to discrete foraging areas including loggerheads, greens and Kemp's ridleys (*Lepidochelys kempii*) (Byles 1988; Broderick et al. 2007; Shaver and Rubio 2008; Seney and Landry 2008).

Displaced loggerheads have been shown to return to original capture sites within a few days or weeks of relocation, exhibiting both homing behavior and site fidelity (Byles 1988; Keinath 1993; Ryder 1995; Musick and Limpus 1997; Avens 2003; Avens et al. 2003; Avens and Lohmann 2004; Mansfield 2006). Repeat captures of the same turtles from Chesapeake Bay pound nets indicate strong philopatry to specific foraging areas, both within and between years (Mansfield 2006). Mansfield (2006) reported that over 20% of individual loggerheads flipper-tagged ($n = 391$) were recaptured in study nets over 1–11 years. Similar interannual loggerhead recapture rates (21%) were reported among experimental pound nets fished in North Carolina's Core Sound (Sasso et al. 2006). These studies suggest that juvenile loggerheads have strong seasonal philopatry to foraging areas within North Carolina and Virginia waters.

In this study, seasonal philopatry to the waters of both Virginia (summer/early fall) and North Carolina (winter/early spring) was observed among most turtles tracked. These observations are consistent with radio and acoustic telemetry data observed by Byles (1988). While all neritic turtles remained in close proximity to Virginia and North Carolina waters immediately postrelease, few exhibited fidelity to discrete areas within this region. This may be due to the timing of release. Many turtles tracked in the 1980s and early 1990s were released during the fall, possibly coinciding with their fall migrations. Approximately half the neritic turtles exhibited fidelity to wintering habitat south of Cape Hatteras, North Carolina. The interannual habitat fidelity among turtles returning to northern foraging habitats ($n = 5$) is consistent with mark-recapture data from the western Chesapeake Bay where some juvenile loggerheads were recaptured for up to five consecutive years (Mansfield 2006).

It should be energetically beneficial for turtles to minimize migration distances between summer and winter habitats (Hawkes et al. 2007). For northern foragers, the region just south of Cape Hatteras provides the closest thermally habitable winter environment. In this area, the continental shelf narrows, and the Gulf Stream is located close to shore. The western edge of the Gulf Stream provides warm waters and possibly productive frontal zones. A recent algorithm designed to detect chlorophyll fronts (Belkin and O'Reilly 2009) shows strong frontal zones occurring near Cape Hatteras that may have large aggregations of prey. Aerial surveys conducted from North Carolina to Virginia suggest that turtles are rarely encountered in near shore waters north of Oregon Inlet or Cape Hatteras during the winter months (Keinath 1993; Epperly et al. 1995). Epperly et al. (1995) found that most turtles occurred south of Cape Hatteras in association with the fronts of Gulf Stream eddies. Similarly, our turtles occurred farther offshore in association with the western frontal system of the Gulf Stream, in areas with warmer waters and relatively high NPP (Figs. 3, 4, 7). There may also be strong chlorophyll frontal zones off Cape Hatteras that were not evident in this study. There are unpublished anecdotal observations of turtles brumating in near-shore waters during the winter months within this region. Hawkes et al. (2007) and Hoscheid et al. (2005) each reported one loggerhead turtle exhibiting extended 'hibernation' type dives, so it is possible that some turtles remain near-shore during the winter months; however, these observations are rare.

Ecologically, the Chesapeake Bay is highly productive and the interannual philopatry exhibited by neritic turtles in this study is likely an adaptive response to historically high productivity within the eutrophic Chesapeake Bay and northern coastal waters. Peak productivity in this region occurs primarily during the spring and summer months when turtles are established in their seasonal foraging grounds (Fig. 5b). The Bay may also provide refuge against predation from large coastal shark species which are mostly rare or absent in the brackish Bay salinities (Musick et al. 1993).

Migratory strategies and oceanography

Tracking studies of turtles captured from Florida to Virginia suggest that loggerhead sea turtles are not randomly distributed but are spatially limited or influenced by seasonal changes in SST (Keinath 1993; Nelson 1996). Most adult female loggerheads found nesting along the eastern coast of the United States exhibit a seasonal north–south migration pattern along the coastline (Hopkins-Murphy et al. 2003; Plotkin and Spotila 2002). Epperly et al. (1995) and Coles and Musick (2000) examined aerial sea turtle sightings in relation to AVHRR satellite imagery of SST. Loggerheads were mostly observed in temperatures $\geq 11°C$, ranging up to 29°C (Epperly et al. 1995; Coles and Musick 2000). Aerial turtle sightings off North Carolina during colder winter months suggest that favorable thermal sea turtle habitat occurs along the western edge of the Gulf Stream or outer continental shelf, particularly east and south of Cape Hatteras (Shoop and Kenney 1992; Epperly et al. 1995). Mansfield (2006) and Hawkes et al. (2007) observed satellite tracked adult female loggerheads from Virginia and North Carolina establish wintering habitat along the western edge of the Gulf Stream in waters off of both North Carolina and Florida.

Moon et al. (1997) reported that Kemp's ridleys exhibited hyperactive behavior (defined by continuous movement of the fore flippers) and remained at the surface for extended periods of time when temperatures dropped below 20°C. This suggests that one possible trigger for migration, at least among Kemp's ridleys, is a drop in SST (or maximum available temperature) below 20°C. Our data suggest that a similar 20°C temperature threshold may also apply to juvenile loggerheads followed by sustained directional movement at the time of migration. It is likely that these turtles were exhibiting behavior analogous to "migratory restlessness" or Zugenruhe. Migratory restlessness is common in migratory birds prior to seasonal migrations and is characterized, in part, by increased activity levels and directional orientation (Farner 1955; Helms 1963; Drickamer and Vessey 1986; Berthold 1996).

Large numbers of sea turtles migrate north of Cape Hatteras to forage during the warmer months (Shoop and Kenney 1992; Morreale and Standora 1988; Plotkin and Spotila 2002; Hawkes et al. 2007). They return south along this migration route in the fall (Shoop and Kenney 1992; Keinath 1993; Morreale and Standora 1988; Plotkin and Spotila 2002). For immature loggerhead sea turtles, Cape Hatteras acts as a seasonal "migratory bottleneck". It is at this juncture that four of our turtles entered the Gulf Stream, two of which (both wild) traveled to the north Atlantic gyre off the Grand Banks. A small number of other studies report similar oceanic dispersal strategies among loggerheads captured along the eastern USA coast (Byles 1988; Eckert and Martins 1989; Morreale and Standora 1988; McClellan and Read 2007). However, with the exception of McClellan and Read (2007), these studies have limited sample sizes or transmission days. One-third of ($n = 10$ of 30) wild juvenile loggerheads from North Carolina's waters traveled in the Gulf Stream to the north Atlantic (McClellan and Read 2007). Approximately a quarter ($n = 6$ of 23) of our study animals behaved similarly; and, excluding headstart turtles, one in five ($n = 3$ of 16) wild turtles adopted an oceanic lifestyle. Our data suggest plasticity in habitat use, and show that large benthic juveniles can resume an oceanic lifestyle for extended periods (up to 3 years), and can switch between neritic and oceanic habitats.

Data from this study and McClellan and Read (2007) suggest that there does not appear to be a phenotypic link between neritic versus oceanic habitat among juvenile loggerheads tracked from the western North Atlantic. These results differ from Hawkes et al. (2006) where smaller postnesting loggerheads from the Cape Verde Islands were found to forage oceanically, whereas larger postnesting females foraged coastally. Hatase et al. (2006) found that postnesting green turtles off the coast of Japan exhibited both neritic and oceanic foraging strategies; though, there was not a link between size of turtle and habitat use. However, Hatase et al. (2002) did find a size-based dichotomy in habitat use among postnesting loggerheads off of Japan. Regardless, behavioral and phenotypic dichotomies exist among different species and age classes of sea turtle and our data contribute to the arguments that classic life history models are not as simple as once assumed (Witzell 2002; McClellan and Read 2007).

In a study that compared diving behavior between headstart and wild turtles, Keinath (1993) reported that smaller headstarted turtles had higher dive frequencies per 12-h period, spent more time at the surface than larger wild turtles, and exhibited surface-based behavior indicative of the youngest age classes of loggerheads. Keinath (1993) suggested that these differences were due to their oceanic (vs. neritic habitat) selection and the relative ages of the headstart animals (2–3 years vs. an estimated 10–18 years for wild neritic juvenile turtles; NMFS SEFSC 2009). Prior to release, headstart turtles were fed a gel diet to accelerate growth in captivity. Thus, the sizes of headstart turtles were comparable to older wild juveniles found in the Chesapeake Bay (Coles 1999), yet the turtles were only between 2 and 3 years of age.

While none of the oceanic turtles in this study exhibited fidelity to a discrete oceanographic region their movements were constrained by SST to waters of >10°C. It is possible that this lack of fidelity to a specific area may reflect, in part, resource availability. The North Atlantic is one of the most productive regions among the world's oceans and is a common foraging habitat for leatherback sea turtles (*Dermochelys coriacea*) (Saba et al. 2008). However, the North Atlantic's harsh winters would restrict turtles to the warmer Gulf Stream waters during the colder months. This suggests that year-round oceanic foraging behavior may comprise two strategies: (1) in the later winter/early spring through the summer, turtles take advantage of the highly productive North Atlantic spring bloom when prey availability is high and SST begins to warm; and (2) during the fall and winter months, turtles must move closer to the warmer Gulf Stream, relying on frontal zones associated with the Gulf Stream and near-by mesoscale eddies for prey hotspots. Similarly, in the northeast Atlantic, Witt et al. (2007) noted decreased leatherback sightings in the late fall and winter, as well as a latitudinal size gradient where larger turtles were found further north. Leatherback turtles feed exclusively on gelatinous zooplankton and utilize the North Atlantic during the spring, summer, and fall (Saba et al. 2008) but have yet to be observed over-wintering there (James et al. 2005b) as one loggerhead did in this study. Leatherbacks are larger and can tolerate cooler temperatures (James et al. 2006) than loggerheads, yet they still return to tropical waters every winter. This suggests that prey associated with the northern Gulf Stream during the winter may not be suitable for leatherbacks, forcing the leatherbacks to migrate south for sufficient resources.

Migration associated with mesoscale eddies is not an uncommon behavior for loggerheads. Polovina et al. (2006) showed that juvenile Pacific loggerheads moved along eddies, likely taking advantage of the prey aggregations derived from both physical forcing and enhanced nutrients. Given the small number of turtles from this study that adopted an oceanic strategy with mesoscale eddy use, it appears that coastal foraging may be the more common strategy. Coastal areas are typically more productive than pelagic areas (Saba et al. 2008) and are closer to nesting beaches, thus the energetic costs/benefits of utilizing coastal areas may be more efficient.

Management considerations

While sea turtle migrations within the western Atlantic neritic zone correspond to seasonal changes in environmental conditions (e.g., SST), it is also probable that seasonal philopatry or site fidelity plays a strong role in determining habitat use among immature loggerheads. These changes may be 'predictable' and cyclical, driven by natural environmental and/or resource fluctuations (e.g., the thermal environment becomes seasonally inhospitable to the animal), or they may be due to changes in habitat quality over time (e.g., declines in prey availability). It is possible that observed declines in Virginia's sea turtle abundances since the 1980s may reflect recent declines in blue crab and horseshoe crab prey availability within the Chesapeake Bay, ultimately influencing sea turtle distributions (Lipcius and Stockhausen 2002; Mansfield 2006; Seney and Musick 2006). However, more telemetry data from immature loggerheads within the northwestern Atlantic are needed.

Our data support the argument that the Chesapeake Bay continues to provide important seasonal developmental habitat for immature loggerhead sea turtles for several years as they mature (Lutcavage and Musick 1985; Mansfield 2006). During their seasonal migrations north or south of Cape Hatteras, sea turtles are at risk of encountering coastal fisheries (Epperly et al. 1995) and hopper dredge operations. Recurring seasonal fidelity to a particular foraging or wintering habitat may increase the probability of incidental takes by fishing activities, particularly fixed fishing gears, cooccurring in these regions (Mansfield 2006). These data reinforce the importance of mitigating anthropogenic activities such as fishing and hopper dredging within immature loggerhead developmental foraging, migratory, and wintering habitat for turtles originating from both the northern and southern subpopulations. Localized sources of mortality (e.g., coastal fishing, hopper dredging) affecting juvenile loggerheads in North Carolina and Virginia will therefore ultimately affect the entire USA Atlantic loggerhead population. Special management consideration with an effort to reduce threats to sea turtle survival, particularly during periods of seasonal migrations, should be given to this region.

The classic loggerhead life history model assumes that once immature oceanic loggerheads reach a certain size, an ontogenetic shift occurs and turtles move from oceanic to neritic habitats (Carr 1987; Musick and Limpus 1997; Bjorndal et al. 2000; Snover 2002). However, our study, along with others (Morreale and Standora 1988; Witzell 2002; McClellan and Read 2007), suggests that a proportion of neritic juveniles resume an oceanic lifestyle for at least a year (and up to three). Our study suggests that historic sea turtle life history models should be reevaluated and that a large proportion (1:3, to 1:4 or 1:5) of immature loggerheads originating from northwestern Atlantic exhibit plasticity in habitat use (McClellan and Read 2007). Thus, when evaluating hazards and potential anthropogenic impacts for specific life stages of loggerhead sea turtles, managers must consider that larger juvenile loggerheads from western Atlantic populations may not remain strictly within the neritic zone.

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