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NOTE

Oceanic overwintering in juvenile green turtles *Chelonia mydas* from a temperate latitude foraging ground

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ABSTRACT: Green turtles *Chelonia mydas* spend the first several years of life in oceanic nursery habitats before recruiting to coastal developmental habitats as juveniles. Traditional green turtle life history models assume that the ontogenetic habitat shift is permanent and associated with a transition from omnivory to herbivory, and that seasonal movements between temperate foraging sites to thermally appropriate overwintering sites occur within the neritic zone. We deployed satellite transmitters on juvenile green turtles captured at a temperate latitude foraging site to document seasonal movement patterns and identify overwintering strategies. We found that the majority (73%) of juvenile green turtles left the neritic zone and exploited oceanic habitats during the late fall or winter. While previous studies have indicated that juvenile green turtles may spend time in deep (>200 m) waters near the continental shelf break during the winter, ours is the first to report long-distance migratory movements, and presumably foraging, in the open ocean. Our findings contradict the widely held notion that juvenile green turtles adopt a strictly herbivorous, benthic foraging pattern after recruitment to the neritic zone and illustrate that there is plasticity in the ontogenetic habitat shift. These results have important implications for understanding somatic growth and population dynamics for this endangered species.

KEY WORDS: Sea turtle · Movements · Foraging · Growth · Ontogenetic shift · Seasonal

INTRODUCTION

Traditional views of green turtle *Chelonia mydas* life history hold that hatchlings are passively dispersed to oceanic nursery habitats, and subsequently recruit to neritic foraging grounds as juveniles (Carr et al. 1978, Meylan et al. 2011). A rapid shift from an omnivorous to primarily herbivorous diet is assumed to occur with the ontogenetic habitat shift (Bjorndal 1997, Reich et al. 2007). In the northwestern Atlantic Ocean, juvenile green turtles recruit to the coastal waters of the United States at a straight carapace length (SCL) of 20 to 35 cm (Meylan et al. 2011), and assume a pattern of benthic foraging on seagrass and/or algae in sounds, lagoons, and estuaries from Florida to New York (Bjorndal 1997). Green turtles that forage in shallow water habitats at temperate latitudes must migrate to warmer waters in the fall in order to avoid cold-stunning, a condition triggered by temperatures <10°C that is characterized by loss of buoyancy, lethargy, and reduced capacity for physiologic function (Innis et al. 2007).

The overwintering strategy adopted by juvenile sea turtles has important implications for energetics,

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growth rates, time to maturity, and hence, population dynamics of this endangered species. Dormancy, characterized by inactivity, prolonged periods of submergence, and reduced metabolism, has been documented for green and loggerhead turtles *Caretta caretta* at temperatures below 15°C (Felger et al. 1976, Hawkes et al. 2007). A temperature-induced reduction in metabolism would result in energetic savings and may allow turtles to match energy expenditure with seasonal fluctuations in food availability or quality; however, it would also reduce growth rate. If resources are available year-round and if thermal conditions permit, then it would benefit juvenile turtles to continue feeding during the winter months, as this would result in continued growth and accelerated time to maturity (Williard 2013). In fact, continued foraging and activity by green turtles, albeit at reduced levels, is observed at temperatures above the 15°C threshold (Mendonça 1983, Read et al. 1996).

We used satellite telemetry to document seasonal movements and provide insight into the overwintering strategy of juvenile green turtles captured at a temperate latitude foraging site. Juvenile green turtles arrive in North Carolina's nearshore waters in the spring to forage on seagrass and algae in shallow water sounds (McClellan & Read 2009); as water temperatures decrease in the fall, the turtles move out of the sounds and into offshore waters (Epperly et al. 1995). Once turtles have entered offshore waters, they have multiple options for overwintering: (1) utilize nearby thermal refugia in neritic waters south of Cape Hatteras (Hawkes et al. 2007, Mansfield et al. 2009); (2) migrate to warm water neritic habitats at lower latitude (González Carman et al. 2012, Fukuoka et al. 2015); or (3) enter the Gulf Stream and utilize warm waters in oceanic habitats (McClellan & Read 2007, Mansfield et al. 2009). Use of nearby thermal refugia off the coast of North Carolina would reduce energetic costs of seasonal migration, but foraging options may be limited and temperature-induced reduction in metabolism would be likely (Hawkes et al. 2007). Alternatively, migration to warm water, either at lower latitude or in the oceanic zone, would incur an energetic cost but permit continued foraging and growth throughout the winter. The primary goal of our study was to identify the predominate overwintering strategy of juvenile green turtles, and to assess the implications of seasonal movements and behavior for green turtle life history models and population dynamics.

MATERIALS AND METHODS

We deployed satellite transmitters (SPOT5, Wildlife Computers) on 20 juvenile green turtles (see Table 1) captured by commercial pound net fishermen in Back Sound and Core Sound, North Carolina, USA, during fall of 2009 (n = 2), 2010 (n = 14), and 2011 (n = 4). Upon capture, turtles were measured for SCL (notch to tip) and examined for identification tags. If no identification tags were present, a passive integrated transponder (PIT) tag was injected in the muscle of the left front flipper. Transmitters were attached to the turtle's carapace using marine epoxy according to previously published methods (Seney et al. 2010) and turtles were released on the day of capture within 6 km of the capture site.

Transmitters were programmed for a 24 h duty cycle. CLS America provided location estimates and accuracies (CLS America 2007), and data were downloaded and analyzed using the Satellite Tracking and Analysis Tool (STAT) program available at www.seaturtle.org (Coyne & Godley 2005). We used a multistep filtering procedure similar to that employed by Mansfield et al. (2009) to exclude implausible locations from analyses. Locations that met the following criteria were included in the dataset: (1) speed <5 km h^{-1} in neritic waters; (2) topography <0.5 m; and (3) turning angle $>5°$. For each day of a turtle's tracking period, the location estimate with the best accuracy was selected from the filtered data and plotted in ArcMap 10.1 (ESRI). We documented the date of last location in inshore waters from the filtered data, and determined overwintering habitat for turtles tracked for at least 4 wk offshore (McClellan & Read 2007). Daily location data for turtles offshore were collated into hexagonal area bins, and hexagon-binned maps were generated to illustrate overwintering habitat (Mansfield et al. 2009). We categorized overwintering habitat as oceanic if the turtle utilized waters off the continental shelf (>200 m depth), and neritic if the turtle remained on the shelf (≤ 200 m depth). A Mann-Whitney test was used to compare SCL of oceanic and neritic turtles to determine if differences in migration pattern were associated with differences in size (McClellan & Read 2007, Mansfield et al. 2009).

Our tracking data and previous work (Epperly et al. 1995) indicated that sea turtles generally leave inshore waters of North Carolina by early December and return as early as the end of March. Monthly sea surface temperature (SST) values were extracted from MODIS 9 km SST (Ocean Color Web; http://oceancolor.gsfc.nasa.gov, accessed 14 July 2016) for each daily turtle location during the typical overwintering period (1 December to 31 March). The Mann-Whitney test was used to compare mean winter SST experienced by oceanic and neritic turtles.

RESULTS

We could not determine winter habitat for 9 of 20 turtles, as some transmitters failed prior to emigration from sounds (n = 6) or within 4 to 27 d of emigration (n = 3). Of the 11 turtles tracked >4 wk offshore (Table 1), 8 utilized oceanic waters (oceanic tracking duration, $\bar{x}$ ± SD: 154 ± 44 d, range: 95 to 218 d; Fig. 1a) while 3 restricted movements to the shelf (neritic tracking duration: 84 ± 35 d, range: 46 to 113 d; Fig. 1b). All but one of the oceanic turtles remained on the continental shelf offshore of North and South Carolina for some time (36 to 68 d) prior to entering the Gulf Stream and initiating oceanic movements. Oceanic turtle 72941 was the exception; this turtle travelled to Florida before entering the oceanic zone after 80 d on the shelf, and returned to neritic waters off North Carolina on 5 May 2011. Transmissions for all other oceanic turtles ceased between late January and late June while turtles were still in oceanic waters (Table 1).

Of the 3 neritic turtles, one (72947) moved south along the shelf, with final transmission offshore of Florida on 30 November 2010. The other 2 remained offshore of North and South Carolina for the duration

Table 1. Descriptive information for 11 juvenile green turtles *Chelonia mydas* tracked by satellite telemetry while overwintering in the North Atlantic Ocean. SCL: straight carapace length

Turtle ID	SCL (cm)	Capture date	Last date in sounds	Date of last transmission	Offshore tracking duration (days)
Oceanic					
72940	28.6	30 Aug 2009	3 Dec 2009	2 May 2010	150
72941	27.6	10 Oct 2010	17 Oct 2010	7 May 2011	201[a]
72944	26.7	20 Sep 2010	3 Oct 2010	27 Jan 2011	116
72946	28.7	26 Sep 2010	7 Nov 2010	23 Mar 2011	136
72948	29.0	29 Sep 2010	26 Oct 2010	29 Jan 2011	95
72953	29.3	10 Oct 2010	19 Nov 2010	25 Jun 2011	218
72954	31.2	1 Oct 2010	13 Nov 2010	22 May 2011	190
110346	35.0	30 Sep 2011	26 Dec 2011	5 May 2012	130
Neritic					
72947	33.0	26 Sep 2010	15 Oct 2010	30 Nov 2010	46
72952	32.8	4 Oct 2010	6 Nov 2010	8 Feb 2011	94
110349	32.2	8 Oct 2011	3 Dec 2011	11 Jun 2012	113[b]

[a] Turtle re-entered Core Sound on 05 May 11 and remained in inshore waters for the rest of track duration

[b] Turtle re-entered Core Sound on 26 Mar 12 and remained in inshore waters for the rest of track duration

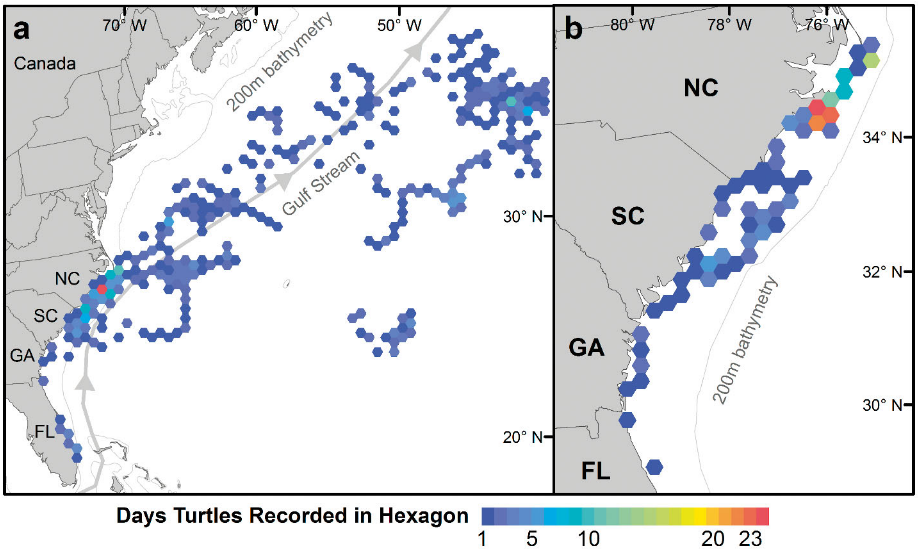

Fig. 1. Movements of juvenile green turtles *Chelonia mydas* after exiting sounds in North Carolina, USA, in the fall. Hexagons are color-coded to represent days of presence for (a) oceanic turtles (n = 8881 track days; hexagon area 2686 km^2), and (b) neritic turtles (n = 3281 track days; hexagon area 669 km^2)

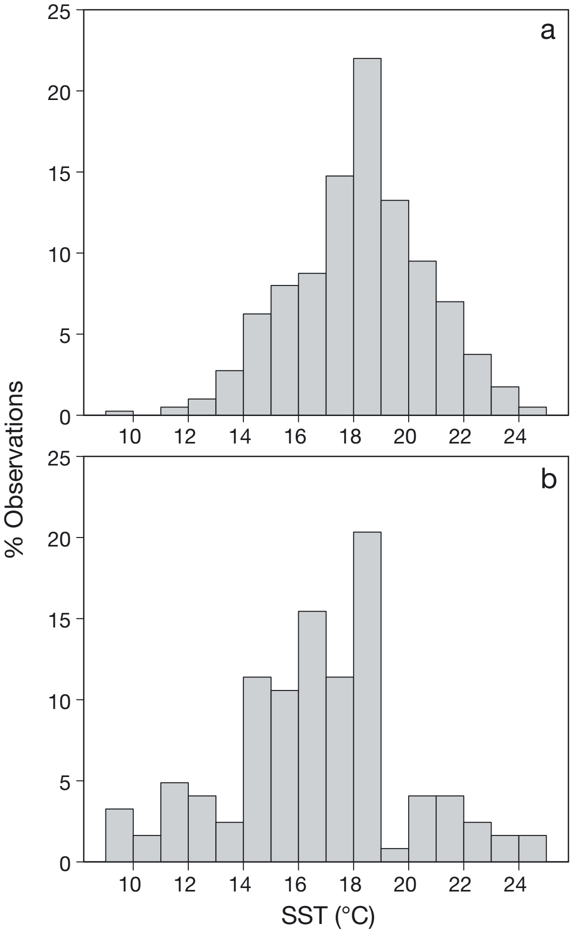

Fig. 2. Sea surface temperatures (SST) experienced by juvenile green turtles *Chelonia mydas* from December through March in (a) oceanic (n = 8) and (b) neritic (n = 2) habitats. Monthly SST values were extracted from MODIS 9 km SST for each daily turtle location. Oceanic turtles experienced significantly warmer mean SST than neritic turtles (Mann-Whitney $U_{1,8} = 0.0$, $p = 0.044$) during winter

of the overwintering tracks (Fig. 1b). One of these 2 turtles (110349) re-entered Core Sound on 26 March 2012 after a period of 113 d offshore.

There was no significant difference in SCL between oceanic (29.5 ± 2.6 cm) and neritic turtles (32.7 ± 0.4 cm; Mann-Whitney $U_{1,9} = 3.0$, $p = 0.085$). Oceanic turtles experienced significantly warmer mean SST (18.3 ± 2.4°C, range: 9.8 to 24.6°C) than neritic turtles (15.8 ± 2.2°C, range: 10.5 to 21.5°C; Mann-Whitney $U_{1,8} = 0.0$, $p = 0.044$) during winter (Fig. 2).

DISCUSSION

Seasonal migrations are an important component of reproductive, foraging, and thermal ecology in a wide variety of vertebrate and invertebrate taxa. For ectothermic reptiles, movements between summer and winter habitats permit exploitation of ephemeral food sources and avoidance of unsuitable thermal conditions. As is typical of reptiles, there is a positive relationship between environmental temperature and metabolism in green turtles (Kraus & Jackson 1980). Consequently, both the thermal environment and available foraging opportunities in the overwintering habitat will impact energetics, growth, and population dynamics of this endangered species. Juvenile green turtles captured at a temperate latitude coastal foraging site exhibited a variety of winter movement patterns, but the majority (73%) left the continental shelf for open ocean habitats. The oceanic pattern was adopted by turtles in all years of the study (Table 1).

Our findings contradict expectations, based on traditional views of green turtle life history, that post-recruitment juvenile turtles remain in the neritic zone year-round. Previous studies have found evidence for a rapid and discrete ontogenetic shift from oceanic foraging on invertebrate prey to neritic foraging on seagrasses and algae for juvenile green turtles in the western Atlantic Ocean (Bjorndal 1997, Reich et al. 2007); however, our telemetry data indicate the ontogenetic shift is facultative, with some juvenile green turtles returning to oceanic habitats on a seasonal basis. Reversal of the oceanic-to-neritic habitat shift has also been documented for juvenile loggerhead turtles *Caretta caretta* that forage seasonally in the nearshore waters of North Carolina (McClellan & Read 2007) and Virginia (Mansfield et al. 2009). Up to 43% of satellite-tagged loggerhead turtles from this region utilized oceanic habitats during the winter months, with the remainder overwintering on the continental shelf between Cape Hatteras and southern Florida. Similarities in winter habitat utilization for these 2 species highlights the possibility that facultative ontogenetic shifts are more common for juvenile sea turtles that must accommodate broad seasonal fluctuations in environmental conditions. Factors that affect growth rates, such as temperature and food availability, are key drivers of ontogenetic habitat shifts (Werner & Gilliam 1984), and are highly variable at temperate latitude foraging grounds. Results from our study and studies with juvenile loggerhead turtles from the northwest Atlantic (McClellan & Read 2007, Mansfield et al. 2009) show no clear link between turtle size and seasonal migration pattern.

Oceanic turtles experienced significantly warmer water temperatures compared with neritic turtles, and thus would be capable of sustaining higher metabolic rates (Kraus & Jackson 1980) and greater food intake rates (Avery et al. 1993), given sufficient foraging opportunities. The open ocean areas used by juvenile green turtles overlapped with areas used by juvenile loggerhead turtles (McClellan & Read 2007), and stable isotope studies have demonstrated that oceanic-stage green and loggerhead turtles are foraging at a similar trophic level (Reich et al. 2007, Cardona et al. 2010). Green turtles that return to oceanic habitats seasonally are likely to resume their pre-recruitment diet of epi-pelagic invertebrates, as has been demonstrated for loggerhead turtles (McClellan et al. 2010). Growth rates and digestive efficiency of green turtles are higher when fed a high-protein diet compared with a plant-based diet (Bjorndal 1985, Amorocho & Reina 2008), and inclusion of animal matter in the diet may be particularly important for young turtles that have not yet cultivated the appropriate intestinal microflora to break down the complex structural carbohydrates found in the cell walls of seagrass and algae (Bjorndal 1985). Results from our study and others suggests that juvenile green turtles at temperate latitudes continue to rely on animal prey to meet nutritional needs following initial recruitment to neritic habitats (Cardona et al. 2010, González Carman et al. 2014).

Juvenile green turtles that overwintered in neritic waters offshore from North and South Carolina spent approximately one-third of their time in areas where SST was less than 15°C (Fig. 2), the temperature threshold for sea turtle activity (Felger et al. 1976, Williard 2013). Loggerhead turtles that overwinter in this region exhibit prolonged dive durations (>7 h) indicative of metabolic downregulation (Hawkes et al. 2007), but there is also evidence that juveniles continue to forage opportunistically on epi-pelagic prey throughout the winter, as thermal conditions permit (McClellan et al. 2010). The diet of green turtles overwintering offshore of the Carolinas has yet to be determined, but would certainly differ from their inshore grazing patterns. Benthic algae on the continental shelf in this region occurs at depths (50 to 60 m) beyond the routine and maximum dive depths reported for juvenile green turtles (Williard 2013), so turtles may opt to forage on more accessible prey items within the water column. Although turtles overwintering in neritic habitats at temperate latitudes may continue to feed, low temperatures would result in a reduction in food intake (Avery et al. 1993), digestive efficiency (Bjorndal 1985), and growth.

Previous studies have documented seasonal movements of juvenile green turtles between high and low latitude foraging grounds (González Carman et al. 2012, Fukuoka et al. 2015), but this movement pattern was rare for green turtles tagged in North Carolina. Of the 2 turtles that travelled south to Florida after leaving inshore foraging grounds, oceanic turtle 72941 ultimately entered the Gulf Stream and neritic turtle 72947 was tracked to the coast of central Florida before the tag ceased transmitting on 30 November 2010. It is possible that neritic turtle 72947 eventually entered the Gulf Stream as well, given that the track ended early in the season. Juvenile green turtles that travel south to neritic habitats on a seasonal basis would need to invest significant energy into migration, and would face competition from resident juvenile and adult turtles for limited resources (Meylan et al. 2011). Feeding at a higher trophic level in oceanic habitats may allow green turtles to strike a more favorable balance between energy invested in migration and energy gained through foraging.

Size-specific growth rates for juvenile green turtles from the North Carolina foraging aggregation are exceptionally low compared with growth rates documented at tropical or sub-tropical latitudes (Goshe et al. 2010). The discrepancy in growth rates may be due to a number of factors, including the genetic composition of the foraging aggregations, diet, thermal habitat, and differences in energy allocation. Juvenile green turtles at low latitude foraging grounds may remain in the same area year-round (Mendonça 1983). In contrast, juvenile green turtles that forage in coastal areas at temperate latitude must migrate in the fall to avoid lethally cold temperatures. Turtles that make use of offshore thermal refugia close to coastal foraging sites reduce energetic costs of seasonal migration, but foraging options may be limited and temperature-induced reduction in metabolism and growth would be likely (Hawkes et al. 2007). Turtles utilizing oceanic habitats or migrating to lower latitudes during winter experience warmer temperatures, but energetic costs of migration may offset energy gains from foraging and reduce the amount of energy allocated to growth (Hawkes et al. 2007). In either scenario, the low growth rates typical of juvenile green turtles at temperate latitude foraging sites extend the time to reproductive maturity, with consequences for recovery of populations. Variability in overwintering strategies should be considered when assessing population dynamics and developing recovery plans for this endangered species.

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