Diversity and Distributions, (Diversity Distrib.) (2011) **17**, 624–640

BIODIVERSITY RESEARCH

A Journal of Conservation Biogeography

Diversity and Distributions

Home on the range: spatial ecology of loggerhead turtles in Atlantic waters of the USA

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ABSTRACT

Aim Although satellite tracking has yielded much information regarding the migrations and habitat use of threatened marine species, relatively little has been published about the environmental niche for loggerhead sea turtles *Caretta caretta* in north-west Atlantic waters.

Location North Carolina, South Carolina and Georgia, USA.

Methods We tracked 68 adult female turtles between 1998 and 2008, one of the largest sample sizes to date, for 372.2 ± 210.4 days (mean ± SD).

Results We identified two strategies: (1) 'seasonal' migrations between summer and winter coastal areas ($n = 47$), although some turtles made oceanic excursions ($n = 4$) and (2) occupation of more southerly 'year-round' ranges ($n = 18$). Seasonal turtles occupied summer home ranges of 645.1 km^2 (median, $n = 42$; using α-hulls) predominantly north of 35 ° latitude and winter home ranges of 339.0 km^2 ($n = 24$) in a relatively small area on the narrow shelf off North Carolina. We tracked some of these turtles through successive summer ($n = 8$) and winter ($n = 3$) seasons, showing inter-annual home range repeatability to within 14.5 km of summer areas and 10.3 km of winter areas. For year-round turtles, home ranges were 1889.9 km^2. Turtles should be tracked for at least 80 days to reliably estimate the home range size in seasonal habitats. The equivalent minimum duration for 'year-round' turtles is more complex to derive. We define an environmental envelope of the distribution of North American loggerhead turtles: warm waters (between 18.2 and 29.2 °C) on the coastal shelf (in depths of 3.0–89.0 m).

Main conclusions Our findings show that adult female loggerhead turtles show predictable, repeatable home range behaviour and do not generally leave waters of the USA, nor the continental shelf (< 200m depth). These data offer insights for future marine management, particularly if they were combined with those from the other management units in the USA.

Keywords

Environmental niche, habitat model, ocean management, satellite tracking, spatial ecology.

INTRODUCTION

Studies investigating the movements of migratory marine species have increased dramatically since the advent of remote tracking and biologging technologies (Bonfil *et al.*, 2005; James *et al.*, 2005a,b, Ream *et al.*, 2005). As the size, type and variety of tracking devices available (Ropert-Coudert & Wilson, 2005; Schofield *et al.*, 2007; Wilson *et al.*, 2008) and tools with which to analyse and interpret such data (Coyne & Godley, 2005) improve, studies can now contextualize tracking data with a

DOI:10.1111/j.1472-4642.2011.00768.x
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range of environmental variables to determine their possible influence on migratory behaviour. Accordingly, we can now describe habitat use of many species in multiple dimensions – through time and horizontal and vertical planes (Brischoux *et al.*, 2007), thermal and dynamic environments (Ream *et al.*, 2005; Lambardi *et al.*, 2008) and prey fields (Friedlaender *et al.*, 2006, Witt *et al.*, 2007a).

Understanding the spatio-temporal distribution and abundance of migratory species and their persistent use or re-use of areas after seasonal migrations (e.g. James *et al.*, 2005a,b; McMahon & Hays, 2006, Kobayashi *et al.*, 2008; McPherson & Myers, 2009) is important for the effective management of large marine vertebrate species of conservation concern. Effective conservation planning should include spatially and temporally explicit information about target species and habitats (Hyrenbach *et al.*, 2000; Parnell *et al.*, 2006), and projects exist to compile these data (e.g. OBIS-SEAMAP: Halpin *et al.*, 2009). Further, incorporating animal tracking data with data describing threats (for example, from fisheries: Lewison *et al.*, 2004 & Witt *et al.*, 2011; coastal development: McFadden *et al.*, 2007; pollution: Shahidul Islam & Tanaka, 2004; and climate change (Halpern *et al.*, 2008; Robinson *et al.*, 2009, Witt *et al.*, 2010a) may yield information that could significantly aid such management.

With the increase in satellite tracking has come a wealth of spatio-temporal data for a variety of taxa, with almost every large marine vertebrate taxon having now been satellite tracked (e.g. satellite tracking data for 2285 animals across four taxa hosted online at http://www.wildlifetracking.org; teleost fish (e.g. Block *et al.*, 2005; Holdsworth *et al.*, 2009; Sims *et al.*, 2009), cetaceans (e.g. Heide-Jørgensen *et al.*, 2006, Mate *et al.*, 2007; Andrews *et al.*, 2008), elasmobranchs (e.g. Eckert *et al.*, 2002; Bonfil *et al.*, 2005) seals & sea lions (e.g. Breed *et al.*, 2009; Kuhn *et al.*, 2010), seabirds (e.g. Weimerskirch *et al.*, 2000; Lynnes *et al.*, 2002; Croxall *et al.*, 2005) and marine turtles (Godley *et al.*, 2008). Much of these data have been published in location-specific studies but few have been used in meta-data studies, or to derive population-wide parameters. Marine turtles are wide-ranging, long-lived, late maturing and are susceptible to anthropogenic threats such as direct and indirect capture in fisheries (Zug *et al.*, 1995; Lewison *et al.*, 2004; Epperly *et al.*, 2007). All species of marine turtles have been satellite tracked in various ocean basins (reviewed in Godley *et al.*, 2008), and data now exist to describe spatio-temporal patterns of marine turtle occurrence in a number of populations.

Adult female marine turtles generally migrate between three types of home ranges on a seasonal to multi-annual basis: (1) inter-nesting ranges, occupied by turtles for the duration of the nesting season (Schofield *et al.*, 2007; Witt *et al.*, 2008) (2) foraging areas (usually coastal benthic areas for cheloniid turtles: Plotkin & Spotila, 2002; Dodd & Byles, 2003) and oceanic areas, previously thought only for leatherback turtles *Dermochelys coriacea* (Hatase *et al.*, 2002; Polovina *et al.*, 2004; James *et al.*, 2005a,b; Hawkes *et al.*, 2006; Houghton *et al.*, 2006, Hatase *et al.*, 2007; Kobayashi *et al.*, 2008; Seminoff *et al.*, 2008; Rees *et al.*, 2010) and olive ridley turtles (*Lepidochelys olivacea*, Polovina *et al.*, 2004; Plotkin, 2010) and in some temperate areas, (3) wintering areas where some turtles remain quiescent for extended periods in waters just warm enough for survival (Broderick *et al.*, 2007; Hawkes *et al.*, 2007).

The loggerhead sea turtle (*Caretta caretta*) is found in temperate and tropical waters of the Atlantic (Ehrhart *et al.*, 2003), Mediterranean (Margaritoulis *et al.*, 2003), Pacific (Kamezaki *et al.*, 2003; Limpus & Limpus, 2003) and Indian (Baldwin *et al.*, 2003) oceans, with the world's second largest nesting assemblage utilizing the Atlantic coast of the south-eastern USA (Ehrhart *et al.*, 2003). Comprising this nesting assemblage are three genetically distinct subpopulations, now recognized as three of five Atlantic 'recovery units': (Encalada *et al.*, 1998; National Marine Fisheries Service & Fish and Wildlife Service, 2008). Despite the nesting population being well studied, in many respects, there have been comparatively few data published about specific aspects of their spatial and temporal distribution and habitat utilization of adults; information that is important for the designation of appropriate protected areas and commercial fisheries impact mitigation (Palumbi, 2004; Braun-McNeill *et al.*, 2008). In the context of heterogeneous ocean governance in the USA (Crowder *et al.*, 2006; McClellan *et al.*, 2011) and given conservation concern for marine turtles, we quantify home ranges for adult females from the northern recovery unit (nesting from Virginia south to the Florida/Georgia state border) and parameterize a model for their occurrence based on oceanographic conditions. Including post-pelagic juveniles, turtles from this unit number in the thousands, inhabit commercially fished areas (Lewison *et al.*, 2004; McClellan & Read, 2007) and occupy waters of one of the most highly developed countries bordering the Western North Atlantic. This study brings together one of the largest tracking datasets for adult female loggerhead sea turtles to date, allowing us to define the scale, location and drivers of home ranges for turtles from this subpopulation and also to begin to reveal the level of fidelity shown to these home ranges.

METHODS

Satellite telemetry

Sixty-eight adult female loggerhead turtles from the northern recovery unit were instrumented at the nesting site following clutch deposition in North Carolina (NC, $n = 24$), South Carolina (SC, $n = 15$) and Georgia (GA, $n = 29$), with platform transmitter terminals (PTTs) between 1998 and 2008 (supplemental Table S1). Tags were affixed to the second vertebral scute of the carapace using marine grade epoxy (PowerFast+, Powers Fasteners, NY, USA) and turtles released *c.* 1 h later at the capture site. Tags were programmed to transmit when at the surface, as indicated by a saltwater switch. For tag performance metrics, see supplemental Table S1. Data were downloaded and managed using the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley, 2005). Argos satellite tracking data consist of varying quality of estimates of location, and a variety of filtering techniques exist with which to identify the most plausible locations to use in analyses (Swihart & Slade, 1985; Luschi *et al.*, 1996; Hays *et al.*, 2001; White & Sjöberg, 2002, Tremblay *et al.*, 2006; Kuhn *et al.*, 2009; Witt *et al.*, 2010b). To filter the data, we benefited from the deployment of two GPS 'Fastloc' PTT's (M.S. Coyne unpublished data) with which we were able to construct an optimal filtering schedule for our study. Based on this schedule, we retained for analysis only location classes 3, 2, 1 and A, and turning angles > 25 ° (as acute turning angles are usually indicative of erroneous, 'off-track' locations) and the best location received on that day (defined as highest quality location class received that day; where two or more high-quality locations were received, we only used the first received that day). We used filtered data to construct home ranges for each turtle, where applicable. Migration, summer and winter phases in the data were extracted by plotting displacement from deployment site (Fig. 1). Migration was considered to have ceased when displacement began to plateau, likewise summer and winter phases were considered to have ended when displacement values started to change again.

Home ranges

In this study, we define a home range as the area that accommodates all regular activities of an individual and consider that when animals migrate, they move between separate seasonal home ranges, which may include breeding, summer and winter home ranges. Home ranges were constructed using data-sets describing the area used by each turtle until subsequent migration. Therefore, in this study, a home range was considered valid only if the turtle was tracked until leaving the home range, or if it had occupied the home range for 6 months or more (57 of 68 turtles, see Supplementary Table S1 for numbers carried forward for analyses). Where turtles were tracked through multiple years, unless data from one individual were being compared between seasons, only the first recorded home ranges were analysed (eight seasonal turtles completed a second summer foraging season and three completed a second wintering season, see Fig. S1). We also considered that summer foraging home ranges immediately post-nesting would normally be expected to be shorter than, and therefore potentially smaller than, foraging ranges in non-breeding years, and we therefore discuss these separately.

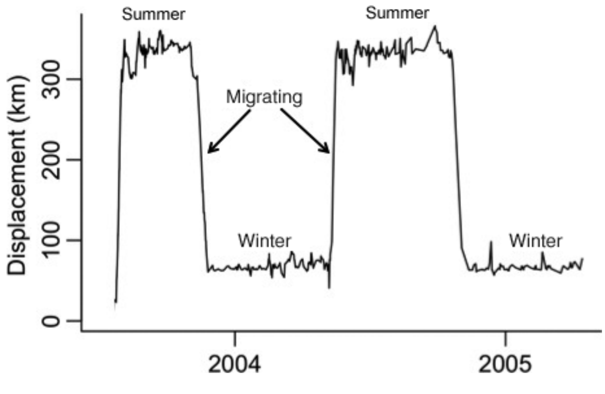

Figure 1 Displacement from release site plot of a seasonal turtle migrating between summer and winter home ranges off the coast of southern NC. Phases of migration are represented by rapid changes in displacement distance; summer, winter and year-round home ranges can be seen where displacement values plateau.

We estimated home ranges using two techniques: the minimum convex polygon (MCP) and the α-Hull technique. The MCP estimates home range by drawing the smallest convex polygon that incorporates all locations. MCPs are simple to generate and understand, require little computing power and are therefore widely used. However, MCPs can include areas of habitat that are likely not visited by tracked animals (Burgman & Fox, 2003), e.g. concave distributions, such as in marine applications, terrestrial features (islands or peninsulas) around which animals may be distributed, but do not occupy. The MCP technique can be improved upon by using the α-Hull technique, which estimates species ranges in a four-step process (see full details in Burgman & Fox, 2003) and has been used to estimate marine turtle home ranges previously (Witt *et al.*, 2008). First, all filtered locations are joined together by non-intersecting lines to form a Delauney triangulation network. The lengths of all the joining lines are then measured to obtain the mean line length. All lines greater than the mean line length multiplied by (α) are discarded. In building an α-hull complex, adjustments in 'α' change the cohesiveness of the overall estimated home range, moving from a discontinuous, fragmented network to an MCP. In this study, through iteration, we determined the optimal (α) to be three standard deviations of the mean triangle length within each network for each turtle and applied the same α value to all turtles, such that the home range was smaller than the MCP. The area encompassed by the remaining triangles in the network is then summed to calculate the resultant home range area. The effect of 'α' thus scales proportionately to the spatial architecture of the turtle's movements and is dominated by the mean triangle side length, rather than the multiplier value. In addition, α-hull estimates do not inflate the estimate of 100% occupation outside the MCP, as would other techniques such as Kernel Density Estimates (Laver & Kelly, 2008), yet improve upon the MCP by cropping out low-use areas objectively. We generated MCPs using Hawths tools for ArcGIS, and α-Hulls were processed and mapped using custom script written for MATLAB (MJW). Data were mapped in ArcGIS 9.3.1 (ESRI, Redlands, CA, USA). For each home range, we also calculated the centroid position, defined as the median latitude and longitude for all filtered location data.

Fidelity

We quantified the extent of site fidelity between consecutive seasons using the distance between median centroid locations.

Environmental data

We extracted remotely sensed environmental data (using custom scripts in MATLAB, MJW) for the best daily ARGOS locations of the turtles. We used 8-day oceanography products for sea surface temperatures (SST, from NOAA Geostationary Operational Environmental Satellite and monthly from the Advanced Very High Resolution Radiometer). Surface current geostrophic velocity vector data (AVISO, Ssalto-Duacs 0.3×0.3 ° gridded absolute dynamic topography, http://www.aviso.oceanobs.com, all available satellites merged) were extracted at best temporal resolution, which varied over the duration of all deployments (weekly, improving to daily). Bathymetric data used were GEBCO (General Bathymetric Chart of the Oceans, http://www.bodc.ac.uk/projects/international/gebco/gebco_digital_atlas).

Habitat suitability model

We quantified the environmental characteristics of habitats occupied by turtles to develop a method for predicting the occurrence of loggerhead turtles along the USA coast, a product of key utility for mitigating threats. First, we used the habitat suitability model for the eastern United States coast published in Hawkes *et al.* (2007), describing suitable habitat as where SST were warmer than 13.3 °C (Coles & Musick, 2000) and seafloor was shallower than 104 m (using 12 turtles that are also reported in this study). We tested the performance of this model by plotting all filtered satellite location data from 53 of the remaining 56 turtles for which there was sufficient data onto the model surface and enumerated the proportion of locations that fell in the modelled suitable habitat. Finally, we constructed a new improved model for summer and winter by reporting the range of SSTs and bathymetry used by all turtles with sufficient data.

We analysed data using nonparametric statistics in R 2.10.1, using Wilcoxon signed-rank test with continuity correction for matched pairs (function Wilcox.test) and Spearman's rank tests.

RESULTS

Turtles were tracked for 372.2 ± 210.4 days (mean ± SD, range 19–997, $n = 68$ turtles) and the majority followed one of two different post-nesting strategies; some turtles ($n = 18$) migrated to foraging areas south of 34 °N where they remained year-round, (Type A1; Godley *et al.*, 2008; Figs 1b, 2a & S1). All except two of these animals headed south relative to their nesting beach release sites. The majority of turtles ($n = 47$) migrated north to seasonal foraging areas above 35 °N with subsequent migration south for winter (Type A2; Godley *et al.*, 2008; Figs 1a & 2a,b). From this point onwards, we refer to these as 'year-round' and 'seasonal' turtles, respectively, and we deal with them separately. Three turtles did not transmit for sufficiently long enough to be assigned to either strategy and were omitted from further home range analyses (see Fig. S1). There was no apparent relationship between post-breeding strategy and the State in the USA in which the turtle originally nested (NC: 15 seasonal, three with oceanic excursions, 9 year-round; SC: 8 seasonal, one with oceanic excursion, 4 year-round, three could not be assigned to a strategy; and GA 19 seasonal, 5 year-round, five could not be assigned to a strategy). With the exception of two turtles that foraged in the Bahamas, and oceanic excursions noted below, which took place on the high seas, all remaining turtle locations were received from USA Exclusive Economic Zone waters. We were able to delineate single home ranges for each turtle's seasonal foraging and wintering period, respectively, as well as one range for year-round turtles, but smaller-scale space use was not evident from our data (Fig. 1).

Year-round turtles

On average, year-round turtles ($n = 13$) occupied foraging areas 482.6 km away from their nesting site (mean value, ± 282.1 SD, range 71.6–956.4) and were recorded in the waters of South Carolina, Georgia, Florida and the Bahamas for 353.1 days (± 88.7 days, range 197.8–491.4, $n = 13$ turtles). Year-round turtles did not make marked migrations to distinct winter home ranges and remained in the same general vicinity for the duration of tracking (Fig. 1b). However, some turtles ($n = 8$) made short excursions from their home ranges (moving up to 100 km away from their home range centroid in varying directions) over several weeks (median excursion start March to end July). These movements were not sufficiently distinct from overall movements around the home range to be analysed separately, and the function of the movements, and whether they were environmentally driven, is not clear. Year-round turtles occupied home ranges of median 4371.9 km^2 (using MCP, 789.3–6492.7 IQR, $n = 13$) and 1889.9 km^2 (using α-hull, 615.2–3356.9 IQR, $n = 13$).

Seasonal turtles

Post-nesting foraging areas for seasonal turtles ($n = 42$) were located 683.7 km away from their nesting site (± 265.2 SD, range 173.5–1165.7) and occupied waters of New Jersey, Delaware, Maryland, Virginia and North Carolina. Seasonal turtles remained in their first summer foraging areas for an average of 71.3 days (mean value, ± 26.6 SD, range 31.4–124.2) before turning south for winter (median date 13 October, earliest 27 August to latest 23 December). Seasonal turtles occupied winter areas 293.7 km away from their original deployment site (mean value, ± 202.8 SD, range 69.7–640.2, $n = 24$ turtles) for 103.1 days (mean value, ± 35.9 SD, range 22.3–172.9). In the spring (median date 09 March, range 4 February to 14 May), turtles departed again to the north for summer foraging areas. Four seasonal turtles (individuals 7, 8, 13 and 16; Table S1) made extended eastward oceanic excursions from their wintering ranges (22 Nov to 26 Feb; 02 Feb to 20 Aug; 04 Mar to 05 Jun; 05 Apr to 14-Jun,

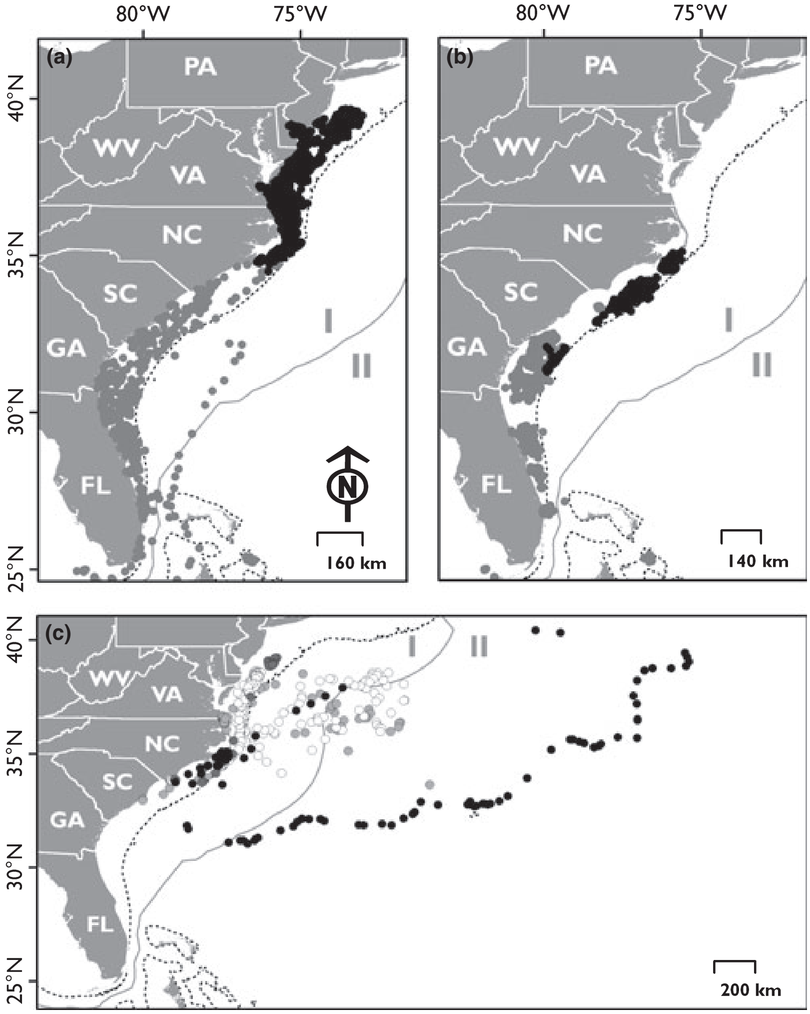

Figure 2 Filtered Argos locations received from (a) 42 seasonal (black dots) and 13 year-round (grey dots) loggerhead turtles during summer; (b) 24 seasonal (black dots) and 13 year-round (grey dots) during winter; and (c) from four seasonal turtles during oceanic excursions (shown as black, grey and white dots and light grey triangles). Legally designated waters are labelled as I: USA Exclusive Economic Zone (EEZ) and II: International Waters; 200 m bathymetry is shown as black dashed line, note different scales.

Fig. 2c) ranging from 1020 to 2673 km off the continental shelf (maximal displacement from deployment site). These excursions over deep waters lasted for 96–218 days (Fig. 2c) before turtles returned to the coastal shelf to previously occupied summer home ranges (all four turtles). These turtles were not tracked long enough to ascertain whether excursions were repeated in subsequent seasons. Seasonal turtles occupied median summer home ranges of 1045.7 km^2 (using MCP, 366.2–1919.6 IQR, $n = 42$) and 645.1 km^2 (using α-hull, 278.5–1262.2 IQR, $n = 42$; Fig. 3). In winter, seasonal turtles occupied home ranges of median 405.1 km^2 (using MCP, 78.3–1397.2 IQR, $n = 24$) and 339.0 km^2 (using α-hull, 51.0–1028.9 IQR, $n = 24$). Winter home ranges were on average smaller than summer home ranges, but were not significantly different (Wilcoxon matched pairs test: winter vs. summer MCP $V = 217$, $P > 0.05$, winter vs. summer α-hulls $V = 216$, $P > 0.05$). Seasonal turtle home ranges (both summer and winter) were significantly smaller than year-round turtle home ranges (Wilcoxon test, using MCP: $V = 206$, $P < 0.05$ and using α-hull: $V = 85$, $P < 0.05$).

Eight seasonal turtles were tracked through a complete second summer season (Fig. 4a–f). Turtles consistently returned to the same vicinity during summer, 623 km away from the original breeding site (mean value, range 266–1162 km, as compared to 683.7 km in the first year post-nesting), only 14.5 km away from the centroid of the previous years foraging area (median value, range 1.6–111.5 km). They remained there for 133 days (mean value, range 70–178 days, as compared to 71.3 days post-nesting). Three turtles were tracked for a complete second winter (Fig 4g–i) and occupied areas only 3.8, 10.3 and 19.5 km away from their original wintering site centroid (three turtles respectively), remaining there for 97, 171 and 123 days. More data were transmitted by PTTs in the first home ranges (median 55.9 and 6.3 locations per week for summer and winter, respectively) than in the subsequent ones (27.6 and 3.7,

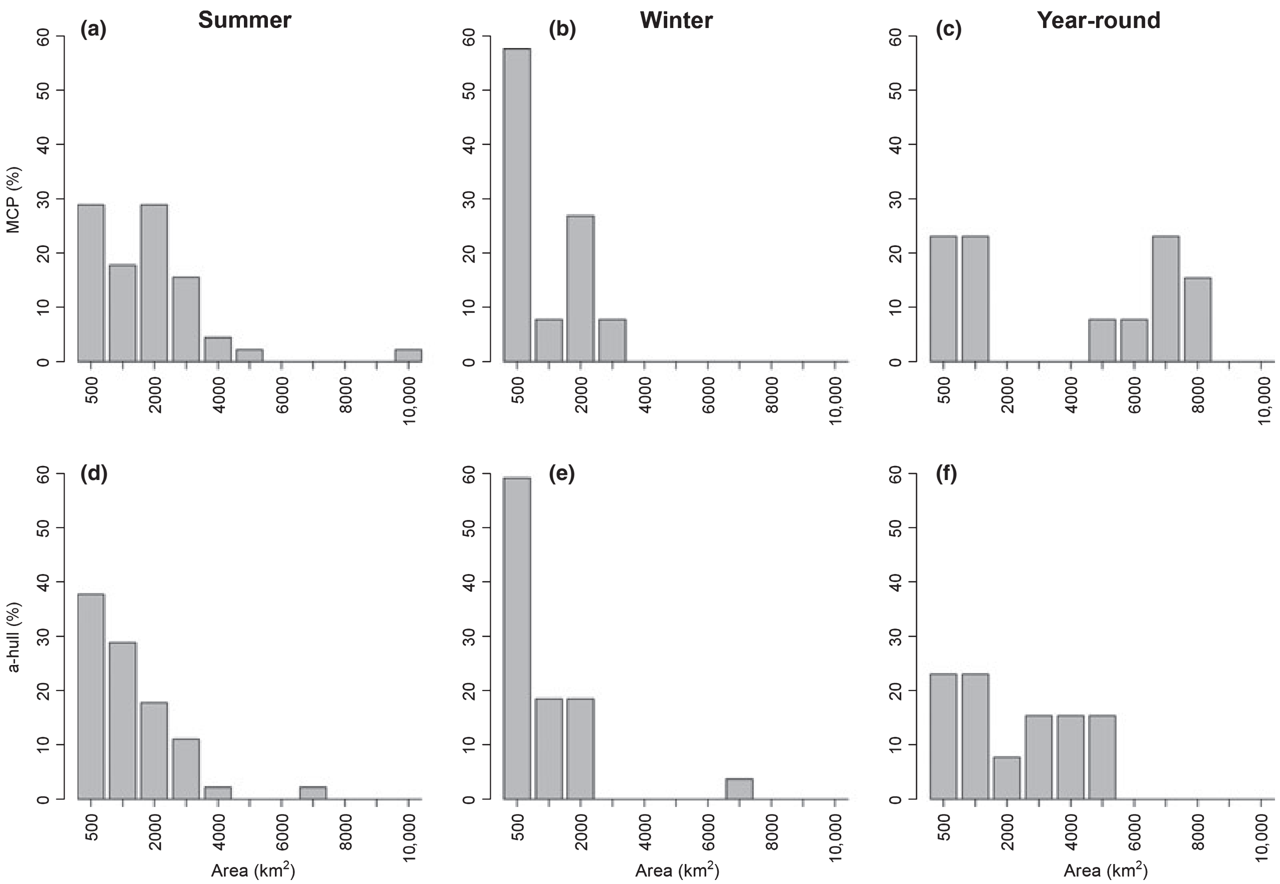

Figure 3 Frequency distribution of home range sizes for loggerhead turtles in summer (a,d), winter (b,e) and year-round (c,f) using minimum convex polygons (a–c) and α- hulls (d–f).

respectively), leading to home ranges that were almost always larger in the first year of tracking (using α-hulls, summer 1567.6 km^2 first year vs. 1149.2 km^2 second year; winter 1461.1 km^2 first year vs. 198.7 km^2 second year). Because of this sampling artefact, we did not compare home range size or overlap between years.

Estimates derived using MCPs were on average 1.5 times larger than α-Hull estimates (Fig. 3), but the results from the two methods were highly correlated (Spearman's Rank Correlation, summer $r_s = 0.96$, $P < 0.001$, winter: $r_s = 0.98$, year-round: $r_s = 0.83$, $P < 0.001$).

Environmental parameters

Median values for environmental variables per turtle were generated and are used in summary statistics from here on. Year-round turtles foraged in waters 28.1 m deep (median value, range 1.0–113.1) and in water 25.7 °C (median value, range 20.8–28.8) and experienced surface currents of 34.6 cm.sec^1 (median value, range 34.0–100.5, Fig. 5). In general, year-round turtles also spent the winter months generally, but not significantly, further offshore than the summer (further offshore in September to March: median 44.6 km range 7.1–99.8 than in April to August: median 39.4 km, range 14.3–89.9, Wilcoxon matched pairs test $P > 0.05$).

In summer, seasonal turtles foraged in warm, shallow waters (median 21.7 m deep, range 10.3–59.9 and median 23.4 °C, range 20.5–27.2) with surface currents between 7.1 and 37.6 cm s^{-1} (median 14.3, Fig. 5). In their wintering areas, seasonal turtles occupied cooler, deeper waters (median 39.3 m deep, range 30.3–83.3 m and median 21.1 °C, range 17.8–23.5) with surface currents between 18.1 and 44.9 cm s^{-1} (median 30.6 cm s^{-1}). Seasonal turtles used home ranges significantly further offshore in winter than in summer (median distance to shore in winter 75.5 km, range 25.6–107.4; summer 17.2 km, range 3.0–93.2; Wilcoxon matched pairs test $V = 3$, $P < 0.001$) and experienced stronger surface currents likely due to their relative proximity to the Gulf Stream (Wilcoxon matched pairs test winter vs. summer currents $V = 5$, $P < 0.001$).

Habitat suitability model

The habitat suitability model in Hawkes *et al.* (2007) was tested using turtles in this study not previously included in Hawkes *et al.* (2007). Between 60% and 100% of locations for all turtles were within the modelled suitable distribution (median 99%, the lowest two model fits from turtles that made oceanic excursions). We then refined the suitability model for adult female USA loggerhead distribution using all data from summer and winter home ranges (including all data from all turtles).

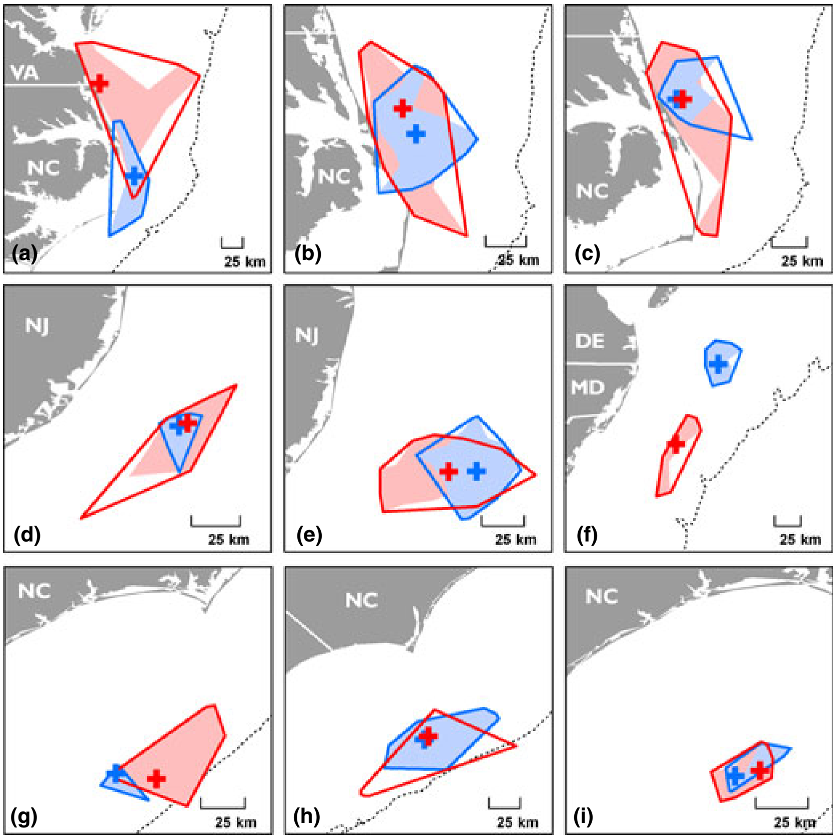

Figure 4 Repeat summer (a–f) and winter (g–i) home ranges for seasonal turtles that were tracked through two complete successive years (year one shown in red, year two shown in blue), $n = 6$ summer home ranges and $n = 3$ repeat winter home ranges. Home ranges are shown as minimum convex polygons (red line for year one, blue line for year two) and α- hulls (pink polygon for year one, pale blue polygon for year two), crosses show median centroid for each home range, respectively; 200-m bathymetric contour is shown as black dashed line.

Based on all environmental data collected from suitable turtles in our study, we suggest a more conservative distribution (Fig. 6): loggerheads from this subpopulation are unlikely to be found at temperatures lower than 18.2 °C (median of the 2.5 percentile of SSTs experienced per turtle) or higher than 29.2 °C (median of the 97.5th percentiles). Compared with previous ranges, they are normally found in depths between 3.0 m and 89.0 m (median of 2.5th and 97.5th percentiles of depths recorded for each turtle). Habitats where surface current speeds are > 50 cm s^{-1} are unlikely to contain turtles. Turtles are unlikely to be found north of latitude 35 °N later than the end of December and during colder months (November to April) are likely to be concentrated in large numbers off the coast of NC.

Estimating the whole home range

Complete first-year home range data received for seasonal turtles in summer and winter were used to estimate the minimum time required to estimate the maximum home range (Fig. 7). Home ranges should reach an asymptote after a threshold number of tracking days as the turtle traverses the maximum extent of its home range, indicating the minimum temporal period over which a turtle must be tracked to reliably estimate its home range (reviewed in Laver & Kelly, 2008). Our data suggest that to estimate 90% of the summer home range, an average seasonal turtle should be tracked for at least 80 days in its summer foraging area. Estimates for winter are harder to derive because of the lower number of locations received per week (approximately half as many). This coupled with the spatial error in some Argos location classes confounded our ability to reach an asymptote at all in some cases. In addition, the proportion of high-quality fixes decreases over time, meaning that repeat home ranges generally have higher inherent spatial error. Consequently, we were unable to determine time to generate maximum home range for repeated summer and winter home ranges. For year-round turtles, occupying single ranges over long periods, this is further complicated, as subtle, small offshore movements take place in winter that are difficult to separate from the total home range, giving no clear ability to reliably estimate the size of their home ranges in the same way.

DISCUSSION

Home range size and repeatability

Building on results in Hawkes *et al.* (2007), we have been able to refine the details of the spatial occupation of coastal seas by turtles from the northern recovery unit. Home ranges

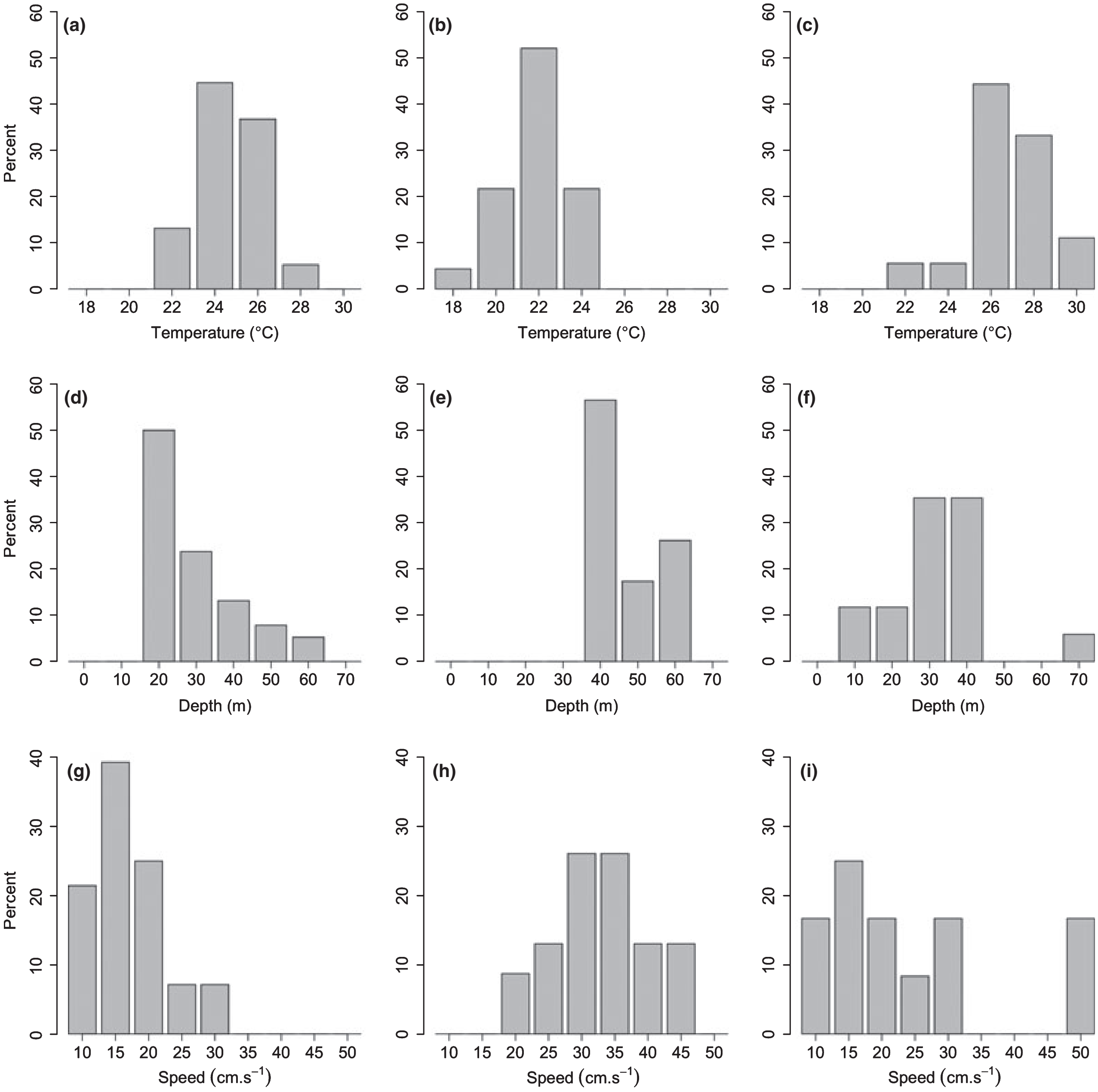

Figure 5 Environmental metrics for filtered locations received from seasonal and year-round loggerhead turtles in summer and winter home ranges. Remotely sensed sea surface temperature (a–c), bathymetry (d–f) and sea surface current velocity (g–i). Environmental metrics are reported for turtles that were tracked for the first tracking year only (n = 42 summer and 24 winter seasonal turtles and 13 year-round turtles). Surface current data are only available for a subset of these turtles.

are not well understood for marine turtles, despite the fact that hundreds of loggerhead turtles have been satellite tracked to date (n = 854; 518 of those in the USA; figures from the STAT at http://www.seaturtle.org; see also Plotkin & Spotila, 2002; Dodd & Byles, 2003; Godley *et al.*, 2008; Tucker, 2010). We show that home ranges for the northern recovery unit are large (typically of the order of thousands of square kilometres, see also Renaud & Carpenter, 1994) but are relatively consistent across individuals and are repeatable between years. The home range size estimate is clearly affected by the estimator used, and we recommend using multiple estimators for comparison, including the widely comparable MCP. However, some common patterns emerge: summer foraging home ranges are almost always much larger than winter ranges and all turtles, regardless of strategy, send many fewer location data from wintering ranges (see also for green turtles Broderick *et al.*, 2007). Data from dive recording PTTs (n = 2) previously published in Hawkes *et al.* (2007) demonstrated that instrumented turtles remained on the bottom at these sites for long periods with individual dives lasting up

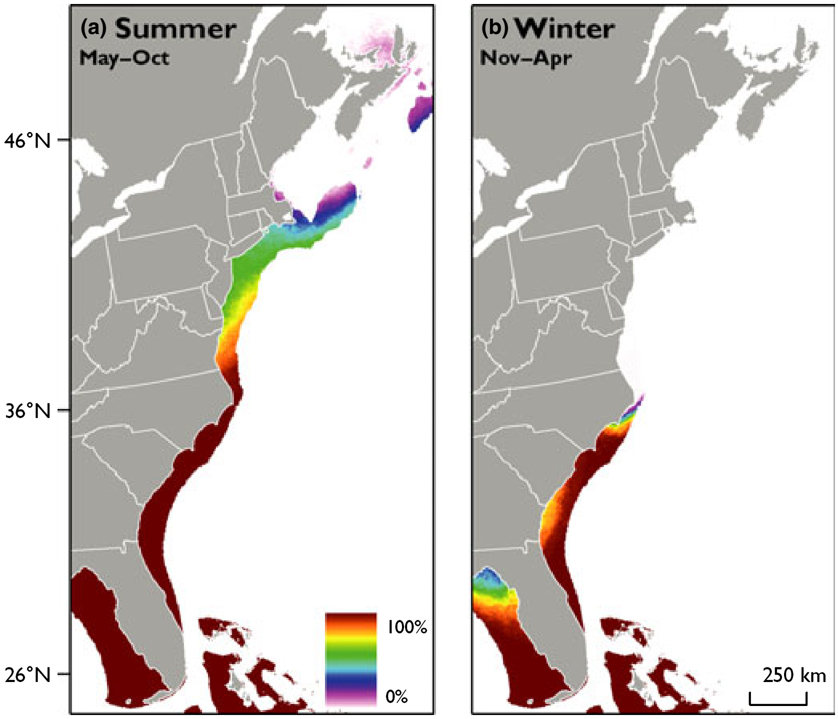

Figure 6 Ninety-five percent habitat suitability model for north Atlantic adult female loggerhead turtles based on sea surface temperature (warmer than 18.2 °C) and bathymetry (shallower than 89.0 m) from all turtles in this study, showing summer months (May to October) and winter months (November to April). Monthly ranges were selected based on median arrival and departure dates from summer and winter home ranges for seasonal turtles. Coloured scale bar shows habitat suitability from 1 (habitat is suitable for 100% of the locations received) to 0 (habitat is never suitable).

to 7.5 hours (Hawkes *et al.*, 2007). The frequency at which location data can be collected, may therefore be reflective of much behavioural and physiological changes. Finally, individual turtles are likely to be found in the same home range(s) year after year, confirming patterns of site fidelity established for loggerhead and other sea turtle species (Limpus *et al.*, 1992; Tröeng *et al.*, 2005; Broderick *et al.*, 2007; Zbinden *et al.*, 2008; Schofield *et al.*, 2010a), as well as for juvenile loggerheads (Avens *et al.*, 2003; Hopkins-Murphy *et al.*, 2003; Avens & Lohmann, 2004).

Comparison with other populations

Estimates of home range size for other marine turtle populations vary. Hawkes *et al.* (2006) showed that home range size for neritic foraging adult female loggerhead turtles from the Cape Verde islands in the eastern Atlantic were an order of magnitude smaller than those in this study, although a larger portion of the Cape Verdean population forage in the oceanic zone and consequently travel over enormous areas (almost 500,000 km^2). Marcovaldi *et al.* (2010) reported foraging home ranges for post-nesting adult female loggerheads between 500 and 1500 km^2. Two studies detailing the movement of juvenile loggerhead turtles from the northern recovery unit (McClellan & Read, 2007; Mansfield *et al.*, 2009) showed a dichotomy in behaviour with many juvenile turtles exhibiting a similar shuttling migration pattern to the adults in this study. These studies did not, however, publish the home range sizes for these juvenile turtles. Adult male and female loggerheads in the Mediterranean use home range areas on average smaller than those in this study (Broderick *et al.*, 2007; Zbinden *et al.*, 2008; Schofield *et al.*, 2010a) but Schofield *et al.* (2010b) and Hart *et al.* (2010) showed that inter-nesting home ranges for loggerhead turtles are an order of magnitude smaller. Tracking of juvenile loggerhead turtles in the Pacific ocean has demonstrated enormous ranges that extend over much of the Pacific ocean (Polovina *et al.*, 2004, 2006; Kobayashi *et al.*, 2008), although estimates for home range sizes for adult Pacific loggerheads appear not to have been published. Home ranges for adult olive and Kemp's ridley turtles may be similar to those of loggerheads (Shaver *et al.*, 2005; Whiting *et al.*, 2007; Seney & Landry, 2008; Shaver & Rubio, 2008). However, green turtles (*Chelonia mydas*) appear to occupy smaller home ranges than loggerhead turtles (Seminoff *et al.*, 2002: 39 km^2, Makowski *et al.*, 2006: 2.4 km^2, Broderick *et al.*, 2007: 77 km^2), and limited description of hawksbill turtle *Eretmochelys imbricata* home ranges suggests they are smaller still (0.2 km^2; Van Dam & Diez, 1998; max distance moved from release location 3.7–9.2 km; Witt *et al.*, 2010c). By comparison, James *et al.* (2005a,b) described a small proportion of high-use areas for Atlantic leatherback turtles (*Dermochelys coriacea*, adult males, females and juvenile turtles), compared with the total area travelled through, demonstrating a low fidelity to any particular area.

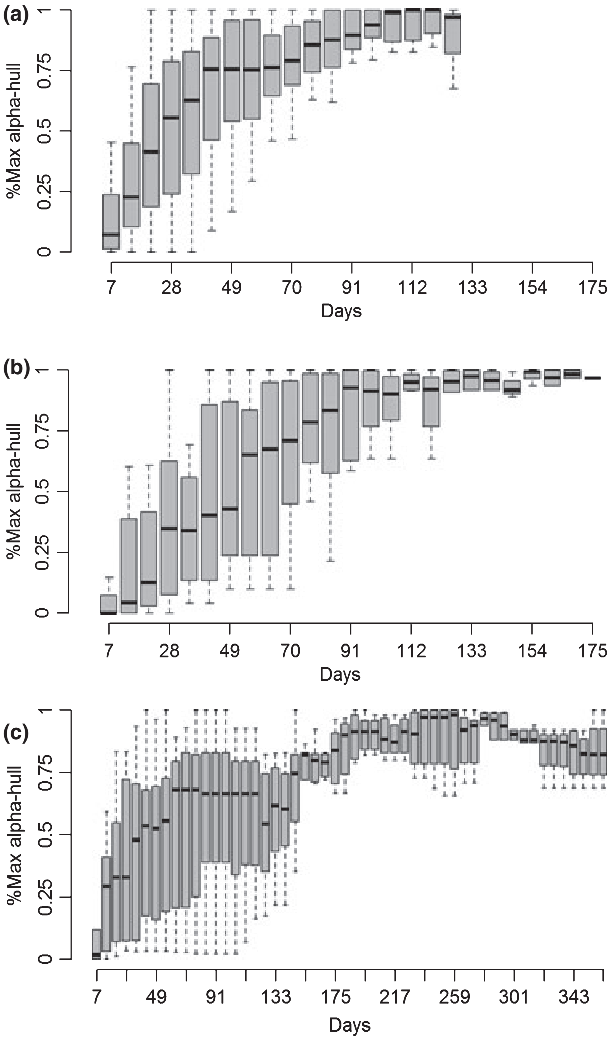

Figure 7 Weekly proportion (shown as box and whiskers, where box denotes inter-quartile range, whiskers denote 2.5–97.5th percentiles and median shown as black horizontal bar) of the maximum home range occupied by (a) seasonal summer, (b) seasonal winter and (c) year-round home ranges of loggerhead turtles, estimated using α-hulls. Note different *x*-axis on part (c).

Methodological approaches

The factors that lead to the selection of individual home ranges could not be addressed in detail in this study because of the spatial limitations of Argos error, which do not facilitate interpretations of fine-scale behaviour. Such factors, including biological (e.g. prey availability and predator avoidance), physical (e.g. habitat structure and shelter; Indermaur *et al.*, 2009) and intra-individual interactions (e.g. territoriality) have yet to be described for any species of marine turtle. Recent development in biologging tools, including the use of telemetry tags incorporating GPS [e.g. Fastloc, Costa *et al.*, 2010; Witt *et al.*, 2010b), as well as archival GPS devices (Schofield *et al.*, 2010a,b)], will facilitate this process and would help to identify core areas of occupation and hence key factors that make a habitat suitable 'home range'. Although satellite telemetry has until recently been the only available method with which to remotely obtain spatial information about a large number of tracked animals, there are inherent, variable and for some classes, unknown errors in the Argos location data (Hazel, 2009; Kuhn *et al.*, 2009), which have important repercussions for spatial analyses. While a number of different approaches exist to deal with location error (e.g. track modelling using likelihood based methods: Royer & Lutcavage, 2008 and Bayesian state-space models: Bailey *et al.*, 2008), most often, simple rejection filtering is used (Freitas *et al.*, 2008), discarding many potentially useful points. The recent advent of Kalman Filtering by Argos (http://www.cls.fr) should improve the filtering regimes and data retention of many projects. Thus, we recommend that satellite transmitters should not be duty cycled at <100%-on so that best estimates of home ranges may be attained. Indeed, our data highlight that short-term (< 6 months) tracking may not be sufficient to set conservation regulations based on assumed spatial distribution. Finally, while longer-term tracking permits for the investigation of fidelity behaviours, it should be noted that frequency of reporting declines with deployment duration, so that estimates become less robust.

Environmental niche

We have also shown that the environmental niche occupied by northern recovery unit turtles is actually rather conservative. While an increasing body of work is now demonstrating plasticity in migratory strategies in cheloniid marine turtles (Hatase *et al.*, 2002; Witzell, 2002, Hawkes *et al.*, 2006; McClellan & Read, 2007; Seminoff *et al.*, 2008; Mansfield *et al.*, 2009; Rees *et al.*, 2010; Zbinden *et al.*, 2011; Schofield *et al.*, 2010a), we show that North American loggerhead turtles may in fact be rather predictable. This may not be entirely surprising. While depths occupied by these turtles could be expected to be constrained by diving ability (maximum dive recorded for a loggerhead 233 m; Sakamoto *et al.*, 1990), temperature is likely the most influential factor governing distribution, as winter temperatures below 10 °C have been shown to lead to physiological stress in this species (Schwartz, 1978, Spotila *et al.*, 1997; Milton & Lutz, 2003; Ultsch, 2006). Turtles should therefore rarely be expected to be found in waters colder than this (Epperly *et al.*, 1995). Reports of overwintering turtles have been returned for loggerhead and green turtles for the Atlantic, Mediterranean and Pacific oceans (Felger *et al.*, 1976; Carr *et al.*, 1980; Ogren & McVea, 1995; Godley *et al.*, 2002; Hochscheid *et al.*, 2005, 2007; Hawkes *et al.*, 2007). Seasonal turtles in our study most likely move to winter areas to avoid temperatures that drop to as low as 5 °C in their summer home ranges, whereas for year-round turtles residing further south, surface temperatures do not fall below 18 °C in winter and thus winter migration to avoid cool temperatures would not be necessary. In their winter grounds, seasonal turtles could use deeper offshore waters, which would be more thermally stable, and waters on the periphery of the Gulf Stream, which may be warmer (see also Epperly *et al.*, 1995; Hawkes *et al.*, 2007; Mansfield *et al.*, 2009). However, fast currents in the Gulf Stream (up to 60 cm s^{-1}, Minobe *et al.*, 2008) could theoretically constrain the distance from shore for home ranges if extra energetic costs were incurred for turtles maintaining static home ranges in fast-moving offshore currents (Hays *et al.*, 2010). Note, however, that upper temperature limits for turtles in this study may not reflect preference or tolerance as much as availability, as the waters occupied by the southern recovery unit are more tropical and therefore reach warmer maximum temperatures. While the mechanisms by which the environment may drive distribution of loggerhead turtles are worthy of future investigation, the fact that we can confidently predict the environmental niche of these turtles lends itself well to climate change planning. Predictive modelling of species range changes in response to climate change (e.g. Beaugrand *et al.*, 2002; Pearson & Dawson, 2003; Richardson & Schoeman, 2004; Cotton *et al.*, 2005; McMahon & Hays, 2006; Chaloupka *et al.*, 2008; Witt *et al.*, 2010a) depends on such data, preferably incorporating many individuals and multiple years and should ultimately aid managers in directing future conservation efforts and funding appropriately in space and time. However, note that it is not yet understood how loggerhead turtle dietary breadth and prey distribution may change with future climate (Hawkes *et al.*, 2009; Witt *et al.*, 2010a), and efforts should be integrated with the modelling of prey distribution (McFarlane *et al.*, 2000; Edwards & Richardson, 2004; Sims *et al.*, 2006; Witt *et al.*, 2007a).

The oceanic excursions by four turtles observed in our study may reflect a shift back to the oceanic zone in adult loggerhead turtles, as has been observed for large juvenile turtles from the USA population (McClellan & Read, 2007; Mansfield *et al.*, 2009) from both the northern and southern recovery units (Rankin-Baransky *et al.*, 2001; Bass *et al.*, 2004; Bowen *et al.*, 2004) and suggested as one of several explanations for the gradient noted from stable isotope analysis of nesting turtles from Florida (Reich *et al.*, 2010). The extent of active choice by turtles, and role of surface currents, in making these excursions was not possible to ascertain using data in this study.

Summary statement

Loggerhead turtles, including both sexes and juveniles, likely number hundreds of thousands in United States eastern seaboard waters (Shoop & Kenney, 1992; Ehrhart *et al.*, 2003; Mansfield *et al.*, 2009). In this study, we show that they exhibit a broad dichotomy in foraging strategies, but broadly conform to the model behaviour for adult loggerhead turtles (Hopkins-Murphy *et al.*, 2003). The wide continental shelf off South Carolina and Georgia is likely occupied by roughly one-third of the northern recovery unit (*c.* 1250 adult female turtles, Ehrhart *et al.*, 2003), and these turtles occupy year-round home ranges of *c.* 2000–4000 km^2. Conversely, the other two-thirds of the northern recovery unit (*c.* 2500 turtles; Ehrhart *et al.*, 2003) occupy a seasonal range extending northwards as far as the waters of New Jersey during summer, retracting to a narrow coastal shelf area (< 30,000 km^2) during winter months (November to April, see also Lutcavage & Musick, 1985; Shoop & Kenney, 1992; Hawkes *et al.*, 2007). Although some turtles make oceanic excursions into deep water for several months, these are infrequent when compared with other populations of loggerheads where oceanic living is routine for a significant proportion of the population (Hatase *et al.*, 2002; Hawkes *et al.*, 2006; Rees *et al.*, 2010). These turtles are unlikely to be found outside the USA EEZ, potentially simplifying strategies for their conservation relative to populations of marine turtles that inhabit multiple range states (Blumenthal *et al.*, 2006; Hawkes *et al.*, 2006; Schofield *et al.*, 2010a). Work from the considerably more numerous peninsular Florida recovery unit (Girard *et al.*, 2009) has revealed that many turtles travel away from the USA as far south as Mexico and Cuba (11 of 28 turtles), thus introducing complications for effective conservation strategies for the USA population as a whole. Given reported declines in nesting numbers for the peninsular Florida recovery unit (Witherington *et al.*, 2009), this is of increasing importance.

Our collaborative approach, compiling almost all the satellite tracking datasets that exist for adult female loggerheads from the northern recovery unit from four different long-term projects, highlights how such an approach provides robust data, which can be used to build spatio-temporal occurrence models and to construct species-specific bioclimatic envelopes (see also Georges *et al.*, 2007). Such an approach is in line with the identified 'global research priorities for sea turtles' (Hamann *et al.*, 2010) to elucidate what parameters influence the biogeography of sea turtles and to locate their key foraging habitats. Integration of our models with anthropogenic threat data (e.g. from commercial fisheries; Lewison *et al.*, 2004; Witt & Godley, 2007, Halpin *et al.*, 2009; Witt *et al.*, 2011; climate change: Robinson *et al.*, 2009; Halpern *et al.*, 2008; Hawkes *et al.*, 2009; Witt *et al.*, 2010a) can then be successfully achieved, identifying key areas of overlap, which can then be prioritized for conservation management. A meta-population suitability model for the entire USA loggerhead population, incorporating available tracking data from all loggerhead recovery units (Encalada *et al.*, 1998; National Marine Fisheries Service and US Fish and Wildlife Service, 2008) should be synthesized as a conservation priority.

ACKNOWLEDGEMENTS

We thank the staff, volunteers and supporters of the Bald Head Island Conservancy and the Georgia Department of Natural Resources. The NC transmitters were funded collaboratively by the Bald Head Island Conservancy, the British Chelonia Group, Juanita Roushdy, Natural Environmental Research Council, WAVE Foundation/Newport Aquarium Cincinnati, PADI project AWARE, SEATURTLE.ORG, and the Whitener Foundation. We thank the USFWS Savannah Coastal Refuges, G.G. and S.D. at Cape Romain National Wildlife Refuge, J.F. at Cumberland Island National Seashore and F.H. at Sapelo Island, W.C., C.H., and M.S. for providing complete project support. Georgia and South Carolina satellite telemetry research is funded in part by an Endangered Species Act Section 6 Cooperative Agreement with NOAA Fisheries and the Grays Reef National Marine Sanctuary. The authors acknowledge using Beyer, H.L. (2004) Hawth's analysis tools for ArcGIS. http://www.spatialecology.com/htools. Sea surface current (geostrophic velocity vector) altimeter products were produced by Ssalto/Duacs as part of the Environment and Climate EU Enact project (EVK2-CT2001-00117) and distributed by Aviso, with support from CNES. Sea surface temperature data are from NASA MODIS Aqua/Terra satellites, NOAA GOES satellites, distributed by National Oceanographic Data Center, and Advanced Very High Resolution (AVHRR) satellite-based sensors. L.A.H. is supported by a University of Exeter Postgraduate Scholarship and the Anning-Morgan Bursary. M.J.W. is supported by the Peninsula Research Institute for Marine Renewable Energy (PRIMaRE) through the South West of England Regional Development Agency. B.J.G. and A.C.B. acknowledge the additional support of the Darwin Initiative, European Social Fund and the Natural Environment Research Council. This work is the result of a major collaborative effort: B.J.G., D.G., M.C., M.D., M.G.F., M.H.G., K.L.W. and S.M. deployed the satellite tags, L.A.H. and M.J.W. analysed the data, L.A.H. and B.J.G. led the writing with contribution from all authors.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Summary of data used in analyses.

Table S1 Deployment details for the 68 turtles released in this study (note turtles 1 to 12 were previously published in Hawkes *et al.*, 2007) from NC (North Carolina), SC (South Carolina) and GA (Georgia).

BIOSKETCH

Lucy Hawkes is a physiological ecologist, whose work focuses on the costs and drivers of migration in vertebrates using techniques such as satellite telemetry, heart rate recording and metabolic rate measurements. Her work has also investigated the impact of external forcing factors, such as climate change, on migration and breeding ecology. This work constituted part of her doctoral thesis with ACB and BJG at the University of Exeter, working in the Marine Turtle Research Group alongside MJW. Further information about LH and publications can be found at: http://publicationslist.org/l.a.hawkes.

Editor: David Richardson