

Only some like it hot — quantifying the environmental niche of the loggerhead sea turtle

Lucy A. Hawkes¹, Annette C. Broderick¹, Michael S. Coyne²,
Matthew H. Godfrey³ and Brendan J. Godley^{1*}

¹Marine Turtle Research Group, Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Penryn, TR10 9EZ UK, ²SEATURTLE.ORG, 1 Southampton Place, Durham, NC 27705, USA, ³North Carolina Wildlife Resources Commission, 1507 Ann Street, Beaufort, NC 28516, USA

*Correspondence: Brendan J. Godley, Marine Turtle Research Group, Centre for Ecology and Conservation, School of Biosciences, University of Exeter, Cornwall Campus, Penryn, TR10 9EZ UK. E-mail: b.j.godley@exeter.ac.uk

ABSTRACT

Although the Atlantic waters of North America support hundreds of thousands of loggerhead sea turtles (*Caretta caretta*), remarkably little is known regarding their migratory ecology and habitat use. We integrate satellite tracking with remotely sensed oceanographic data to uncover two different migratory strategies used by loggerhead turtles at the northern part of their range. Most turtles travelled from the nesting beach to forage at higher latitudes in summer, before migrating south to wintering grounds in the autumn. Others moved south after nesting to forage for up to 514 days and did not make an autumn migration. Both groups utilized warm waters at the very edge of the Gulf Stream during winter: for southerly turtles obviating seasonal migration, and for northerly turtles minimizing the distance, time and energy required to reach northern areas for subsequent foraging seasons, avoiding lethally cold winter temperatures in inshore waters at the same latitude, and reducing energy costs that would be incurred within the fast-flowing Gulf Stream. Females made long resting dives of up to 7 h 24 min, effectively hibernating during the colder months. Offshore federal waters of the USA constitute a more important habitat for both foraging and wintering turtles than previously appreciated. These areas are potential hotspots for interaction with fisheries and proposed US military training activities and should receive special monitoring efforts to fully assess the extent of overlap.

Keywords

Loggerhead turtle, *Caretta caretta*, environment, North America, satellite tracking, niche model.

INTRODUCTION

Variability in environmental conditions can profoundly affect diversity, distribution, and abundance of animals and plants. In temperate and polar regions species must adapt to highly variable seasons (see review by Cockell *et al.*, 2000) in order to survive inclement conditions. Animals cope with adverse conditions by either tolerating them (through physiological mechanisms, e.g. blubber, antifreeze proteins, or behavioural mechanisms, e.g. hibernation, huddling) or by avoiding them (by migrating to alternative, more favourable habitat). As a strategy, migration allows animals to seasonally exploit profitable summer foraging areas that are unavailable on a permanent basis (Alerstam *et al.*, 2003) and some of the most spectacular long distance migrations are exhibited in the marine realm (Block *et al.*, 2001; Bonfil *et al.*, 2005; James *et al.*, 2005; Ream *et al.*, 2005; Phillips *et al.*, 2006).

Distribution of the loggerhead sea turtle (*Caretta caretta*) is the most temperate of the hard-shelled marine turtles. The species

is ectothermic with only small (1–2 °C) temperature differences being maintained between the core body temperature and the water temperature (Spotila & Standora, 1985). The south-eastern USA hosts one of the largest populations in the world with an estimated quarter of a million post-oceanic stage loggerhead turtles (including > 40,000 adult nesting females; TEWG, 1998) that have been recorded ranging as far north as Canada in summer (to 43° latitude, Squires, 1954) with range of regular distribution north to New Jersey (Shoop & Kenney, 1992). Although the neritic waters of North America support these large numbers of loggerheads, little is known about the spatial and physiological ecology of this species. Aerial and shipboard surveys, flipper tag returns, and limited published satellite tracking studies have revealed that adult turtles seasonally shuttle north and south along the North American coast (Plotkin & Spotila, 2002; Dodd & Byles, 2003; Hopkins-Murphy *et al.*, 2003; Schroeder *et al.*, 2003), winter in significant aggregations off the coast of the south-eastern USA (Epperly *et al.*, 1995a,b,c; Morreale & Standora, 2005), and that

their distribution is often associated with the Gulf Stream (Hoffman & Fritts, 1982; Morreale & Standora, 2005).

Although there have been reports of sea turtles potentially hibernating to survive the winter (Felger *et al.*, 1976; Carr *et al.*, 1980; Ogren & McVea, 1995; Godley *et al.*, 2002), no adult hibernacula have been confirmed for the species in North America. In this paper we use the term 'hibernation' in its literal translation from the Latin of 'winter residence' (as per Ultsch, 2006) without any inferences to shifts in metabolic or physiological state. However, in marine turtles, low temperature can cause lethargy, inhibit foraging, and eventually lead to starvation and death (Schwartz, 1978; Spotila *et al.*, 1997b; Milton & Lutz, 2003). We set out to quantitatively describe how and why this species seasonally exploits its foraging and wintering grounds by integrating long-term satellite tracking (2003–2006; mean duration 428 days), dive recorders, and remotely sensed oceanographic data on post-nesting adult female turtles.

METHODS

Twelve adult female turtles were tracked following nesting in North Carolina in the 2003, 2004, and 2005 nesting seasons. Satellite transmitters, attached following Godley *et al.* (2002), were Sirtrack Kiwisat 101's ($n = 7$), Telonics ST-18's ($n = 3$), and Sea Mammal Research Unit 9000× Satellite Relayed Data Loggers ($n = 2$; Table 1). Data were automatically downloaded, interpreted and analysed using the Satellite Tracking and Analysis Tool (STAT; Coyne & Godley, 2005) program from SEATURTLE.ORG, and integrated with a range of oceanographic data within the package [sea surface temperature (SST), sea surface current, and bathymetry data]. Data describing morphometrics, clutch metrics, and inter-nesting and remigration frequencies were collected as part of a long-term sea turtle monitoring project (see Hawkes *et al.*, 2005). All location data were filtered using STAT before analysis (transit speeds of more than 5 km h^{-1} and turning angles of less than 5 degrees), and one data point per 24 h used to reduce the effects of autocorrelation within the data (first location received). Sea surface current (geostrophic velocity vector) data were obtained from AVISO (http://www.aviso.oceanobs.com/html/donnees/tools/citations_uk.html) and U and V components sampled for all filtered locations. Bathymetric data were sampled from the General Bathymetric Chart of the Oceans (GEBCO, http://www.bodc.ac.uk/projects/international/gebco/gebco_digital_atlas) for filtered locations. Sea surface temperature data were sampled daily from NOAA GOES and monthly from the Advanced Very High Resolution Radiometer (AVHRR) data. Migratory and foraging stages of post-nesting behaviour were determined by plotting displacement from the site of deployment and identifying stages of behaviour (inter-nesting, migrating, foraging, wintering) from inflections in the curve (e.g. Blumenthal *et al.*, 2006).

Models of habitat suitability were developed based on the environmental characteristics of the North America shelf, where the attributes of interest were bathymetry (GEBCO) and SST data. Each cell in 1-min ($\sim 4 \times 4 \text{ km}$) bathymetry and monthly SST grids was scored 0 or 1 according to suitability. Suitability

was based on previously published thermal preference data (values greater than $13.3 \text{ }^\circ\text{C}$; Coles & Musick, 2000) and maximum dive depth data from our study (values shallower than 104.4 m) since there is a paucity of available data for depth utilization for adult foraging loggerheads. The overlap of both suitable bathymetry and SST was determined by multiplying the suitable bathymetry grid against each suitable SST grid to generate monthly grids of suitable habitat for months from January 1998 to December 2006 ($n = 108$ months). Temporal availability of habitat was calculated by dividing the number of months that each cell was suitable against the total number of months analysed. Similarly, suitability of the northern foraging habitat was calculated for summer months only (May to October from 1998 to 2006) and scaled accordingly ($n = 54$ months). The resulting habitat deemed suitable for turtles through time and space will hereafter be referred to as the 'niche' (see Guisan & Zimmerman, 2000).

RESULTS

Data highlighted two distinct movement patterns: type 1 — northward migration in summer to higher latitude areas above 35° N , 330–752 km distant from the nesting beach (turtles a–i, Fig. 1a), followed by autumnal southward migration to areas below 35° N (Fig. 1b; see Fig. S1 (movie) in Supplementary Material) and type 2 — southerly migration to lower latitude subtropical waters 576–895 km from the nesting beach (turtles j–l, Fig. 1a) with residency throughout winter at the same sites (Fig. 1b). Based on previously published information (Hopkins-Murphy *et al.*, 2003 and references therein), from this point on we will refer to northerly summer areas and southerly low latitude subtropical areas as 'foraging areas'.

Turtle d undertook a modification of type 1 pattern from her wintering area, making an extended excursion into the Gulf Stream in March 2005 and travelling over deep oceanic waters for 87 days before returning to the coastal zone near her departure point in June 2005 (Fig. 1c; Fig. S1). All turtles exhibited an intraannual ($n = 12$ turtles, types 1 and 2) and interannual (type 1, $n = 5$ and type 2, $n = 3$; tracked for > 381 days) fidelity to relatively discrete foraging and wintering areas (Fig. 2). For all type 1 turtles, wintering areas were significantly smaller than summer foraging areas (mean \pm SD north–south diameter foraging areas: $97.7 \pm 57.2 \text{ km}$, range 33.6–207.2 km; wintering areas: $51.9 \pm 29.5 \text{ km}$, range 17.5–95.4 km; Wilcoxon $z = -2.80$, $P < 0.01$).

Turtles predominantly stayed in shallow coastal waters (99.7% of highest quality locations were centred in water $< 100 \text{ m}$ deep) where they are likely able to exploit benthic prey. However, turtles wintered at significantly greater depths than they foraged in summer (bathymetry data derived from tracking locations of type 1 individuals; winter median = 38.3 m, range of medians 27.9–70.5 m, $n = 9$ turtles; summer median = 25.0, range of medians 9.8–46.8 m, $n = 9$ turtles; Wilcoxon $z = -2.31$, $P < 0.05$). At these locations, on the edge of the Gulf Stream, SSTs experienced by turtles typically ranged from 14 to $26 \text{ }^\circ\text{C}$ during winter, at minimum some $4 \text{ }^\circ\text{C}$ warmer than closer inshore where winter temperatures regularly fell below $8\text{--}10 \text{ }^\circ\text{C}$, sufficiently cold to

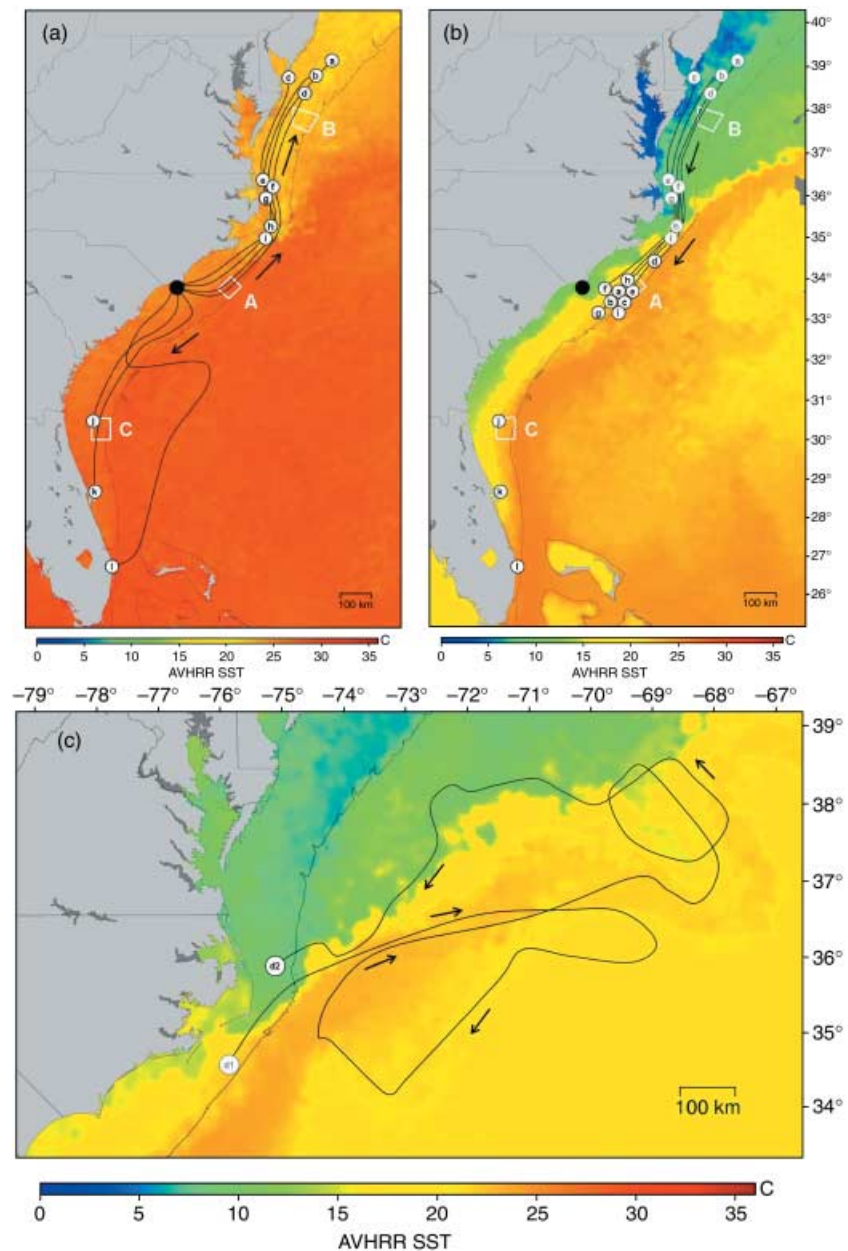


Figure 1 Migratory routes, foraging areas, and wintering areas.

(a) Reconstructed route (black line) to foraging areas (labelled circles) for individuals a to l from release location (filled circle). Coloured background shading shows mean sea surface temperature (SST) for September 2004, and the 250-m isobath is delineated. (b) Reconstructed route (black line) from foraging areas (grey labelled circles) to wintering areas (black labelled circles) for individuals a to g (type 1). Individuals j, k, and l (type 2) are shown but did not make an autumnal migration. Coloured background shading shows mean SST from January 2004, and the 250-m isobath is delineated. (c) Pelagic excursion of turtle d between 15 March and 8 June 2005; coloured background shading shows mean SST for April 2005. For (a) and (b) polygons indicate three proposed sites for US Navy undersea warfare training ranges off (a) south-eastern North Carolina, (b) north-eastern Virginia, and (c) north-eastern Florida (Navy, 2005).

cause 'cold stunning' (Schwartz, 1978; Witherington & Ehrhart, 1989; Spotila *et al.*, 1997). Within the Gulf Stream, surface current speeds are significant and data received from turtle d suggest that they may be strong enough to divert turtles off course. However, areas utilized in winter by turtles are on the edge of the Gulf Stream, thus minimizing the effort required to maintain their position while maximizing the exposure to warm temperatures (Figs 2d & 3b).

Although turtles undertaking the type 2 pattern of movement (Fig. 1a,b) did not make migrations to wintering areas, there were some similarities with conditions experienced by both groups. Specifically, type 2 turtles occupied the edge of the southerly portion of the Gulf Stream, on the coastal shelf (Fig. 1b). In winter, type 2 turtles experienced mean monthly SST to a minimum of 17 °C, while closer inshore, temperatures

fell as low as 10.8 °C, suggesting that these sites may therefore be selected under similar criteria as those for type 1 turtles (Fig. 3). Additionally, although type 2 turtles do not expend energy on seasonal shuttling migration, based on our limited sample size, they do not demonstrate differences in recorded fecundity measures relative to type 1 turtles (clutch frequency, clutch size, body size, remigration, and inter-nesting intervals; Mann–Whitney U, $P > 0.05$; see Table S1 in Supplementary Material).

Two turtles (a and f) exhibiting type 1 pattern were deployed with dive recording telemetry devices. Behaviour at summer foraging and wintering areas contrasted markedly (Fig. 4). At summer foraging areas, mean \pm SD dive duration for turtle a was 19 ± 10 min (maximum duration: 47 min, Fig. 4a) and 35 ± 20 min for turtle f (maximum duration: 51 min, Fig. 4b) in a series of short dives. At wintering areas, dive duration was

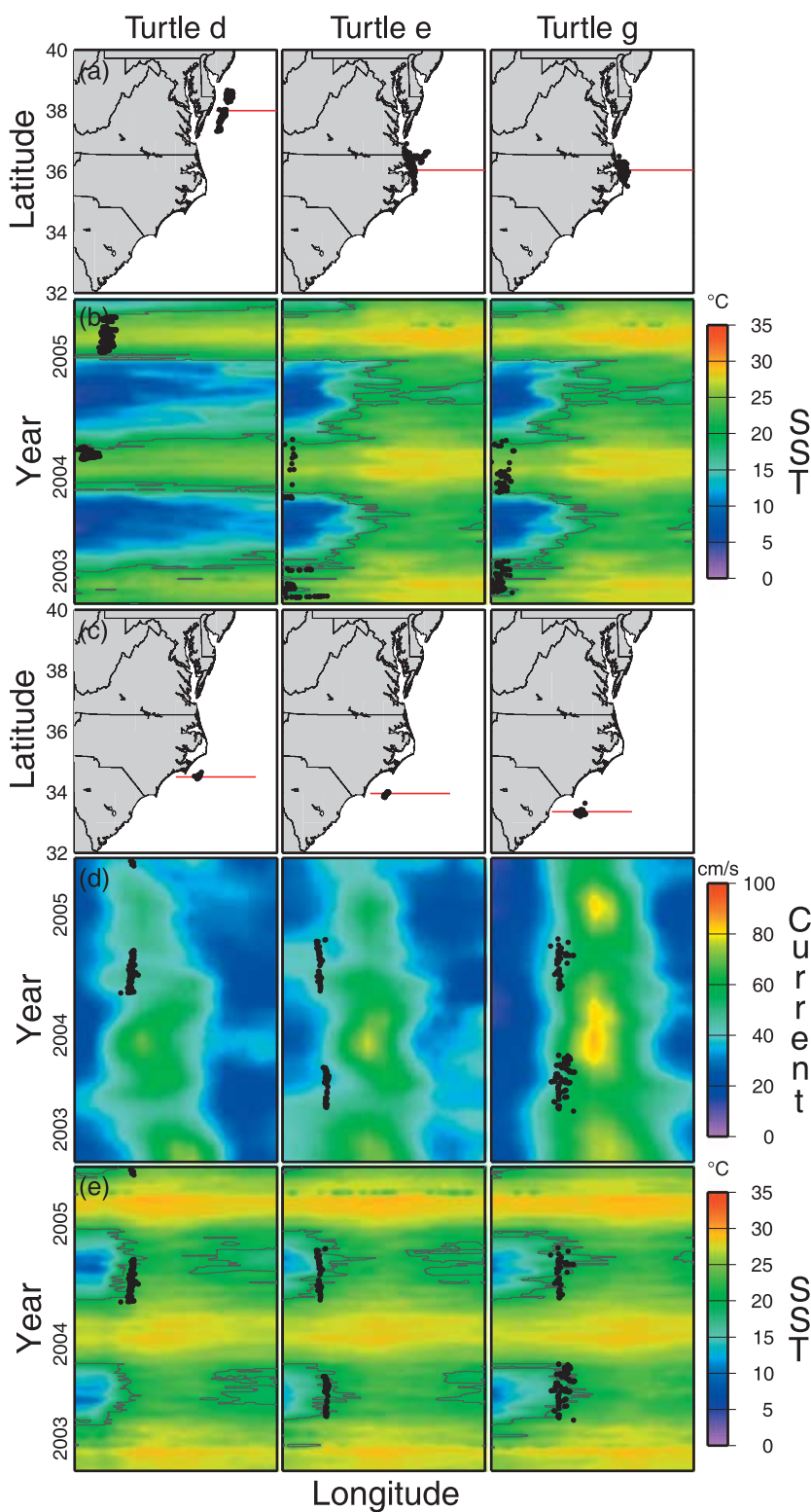


Figure 2 Linking oceanography to spatial patterns in type 1 turtles (d, e, and g). (a) Map detail of foraging areas. Black dots represent turtle locations received highlighting intraseasonal and interannual fidelity, red line shows mean latitude of locations used as sampling latitude for SST data; (b) sea surface temperature (SST) at sample latitude plotted on axes of longitude against time (from July 2003 to November 2005). Black dots show filtered locations received from turtles at foraging areas in consecutive years. The 20 °C isotherm is shown (black line); (c) map detail of wintering areas. Black dots represent turtle locations received, highlighting intraseasonal and interannual fidelity; red line shows mean latitude of locations used as sampling latitude for SST and current data; (d) sea surface current; and (e) SST at sample latitude plotted on axes of longitude against time (from July 2003 to November 2005). Black dots show filtered locations received from turtles at wintering areas in consecutive years. The 20 °C isotherm is shown (black line) in part e.

significantly longer than dive duration at summer areas (turtle a Mann–Whitney $U_{1,1570} = 6154$, $P < 0.001$; turtle f Mann–Whitney $U_{1,1570} = 72,623$, $P < 0.001$), diving for mean durations of 2 h 8 min and 4 h 9 min (turtles a and f, respectively). During the study, we recorded maximum dive durations of 7 h 24 min

(Fig. 4d), one of the longest published dive durations recorded for an air-breathing marine vertebrate. In both individuals a and f, bouts of long dives were interspersed with shorter dives. One of the dive logging transmitters also sent thermal data that allowed us to validate remotely sensed data sets.

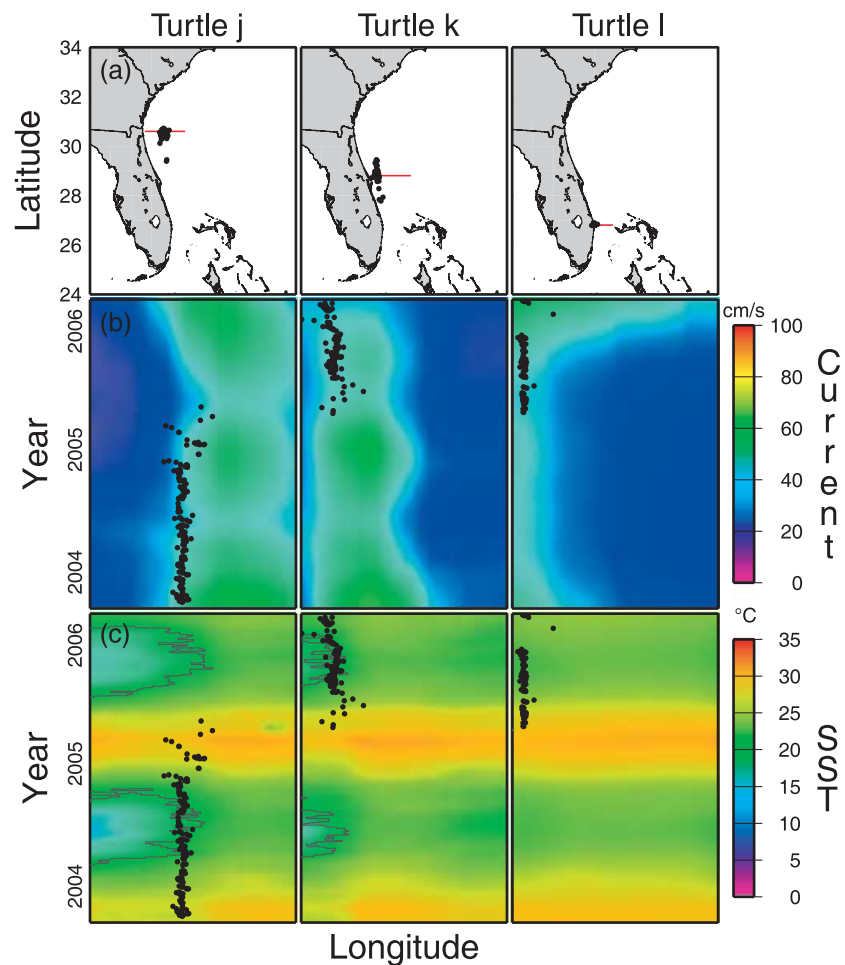


Figure 3 Linking oceanography to spatial patterns in type 2 turtles (j, k, and l). (a) Map detail of foraging areas. Black dots represent turtle locations received, red line shows mean latitude of locations used as sampling latitude for SST and current data; (b) sea surface current; and (c) SST at sample latitude plotted on axes of longitude against time (from August 2004 to May 2006). Black dots show filtered locations received from turtles. The 20 °C isotherm is shown (black line) in part c.

Despite the difficulties of monitoring migratory animals in the marine environment, we have detailed tracking information over long periods for a number of individuals. This allows us to explore the utility of ecological niche modelling (Nix, 1986; Peterson, 2001) to predict consistently suitable or marginal areas for species over a long period of time (Fig. 5). It is clear that turtles are using benthic neritic habitats and, as ectothermic reptiles, are under profound influence of temperature. Due to the influence of the Gulf Stream, there is a core offshore area that is suitable for loggerheads year-round with more northerly areas only available on a seasonal basis, with progressive temporal restriction as latitude increases (Fig. 5). Wintering areas for type 1 and locations of type 2 turtles are clearly within the year-round availability. When proportional availability is viewed from a summer-only context (May to October Fig. 5 inset), it is even more apparent that while type 1 turtles were found as far north as Delaware, the time of year when these northern neritic areas are available, including the waters of several north-eastern states of the USA, Canada, and the Georges Bank, is extremely limited. Unsurprisingly, given the concordance between the composite thermal profile for our study animals (Fig. 5b) and the lower thermal threshold used in this model, the fit of our location data to consistently suitable areas is very close.

DISCUSSION

Long-term deployment of reliable tracking units integrated with remotely sensed data in this study have highlighted the extreme importance of the Gulf Stream to turtles in the south-east USA. In particular, some adult loggerheads have developed a highly optimized strategy for taking advantage of this environmental resource throughout much of their winter range. Previous studies on sea turtle diving suggest that summer dives observed in this study are consistent with foraging behaviour while winter dives are suggestive of inactivity (Hays *et al.*, 2000; Hochscheid *et al.*, 2005; Myers *et al.*, 2006). By wintering at the edge of the Gulf Stream, type 1 turtles likely minimize migratory distance, time, and energy required to reach northern foraging areas; avoid lethally cold winter temperatures in inshore waters at the same latitude; and reduce energy costs required to maintain a position within the strong currents of the Gulf Stream. That the two turtles with dive recording transmitters were recorded making long resting dives suggests that for at least some of the winter, turtles remain quiescent, if not actually hibernating. The ramifications of this are profound. We suggest that large numbers of adult North American loggerheads are making long resting dives at the edge of the Gulf Stream in winter, enabling them to sit-out cold periods

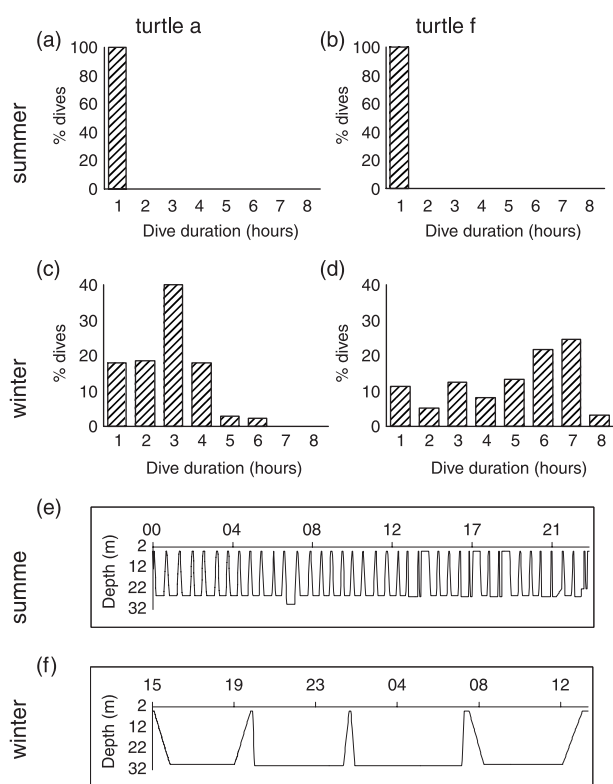


Figure 4 Diving in foraging and wintering areas. (a–d) Frequency histograms (in hourly bins) of summer and winter dive durations for turtles a and f deployed with dive recording transmitters. (e, f) Dive profiles for 24 h for individual f on (e) the 4 October 2003 demonstrating foraging behaviour and on (f) the 16 of January 2004 demonstrating resting dives.

in the winter while exploiting highly productive waters in higher latitudes on a seasonal basis. Hibernation as a strategy in sea turtles is not a new concept (Ogren & McVea, 1995; Godley *et al.*, 2002; Hochscheid *et al.*, 2005; Ultsch, 2006), but has never been demonstrated before for North American loggerheads.

Environmental constraints to turtle distribution can be quantitatively defined. North American loggerhead turtles generally feed on the benthos in shallow waters but our study illustrates how some turtles capitalize on more seasonally productive northern foraging areas, which are inaccessible in mid-winter when temperatures drop well below the thermal tolerance of loggerheads. Turtles not only head south in winter to avoid these inclement conditions, but also head offshore since nearshore water temperatures regularly fall below 10 °C in midwinter, temperatures at which turtles become lethargic and buoyant, and may die (Schwartz, 1978; Milton & Lutz, 2003). The Gulf Stream exerts a profound warming influence on these coastal waters, especially around North Carolina (Mallin *et al.*, 2000), with the north–western boundary of the Gulf Stream skirting sea turtle wintering areas identified in this study (Fig. 2). Here we have begun to describe the parameters that will allow detailed predictive modelling of the seasonally relevant geographical range of this species. However, estimation of the range, effectively the niche, can be confounded by two major factors: (1) errors of omission

Table 1 Metrics for tracked turtles showing turtle ID (turtles a to l), date of deployment, strategy adopted by each individual (where 1 = northerly foraging with shuttling winter migrations, 2 = southerly foraging), curved carapace length in centimetres (CCLn-t, following Bolten, 1999; + denotes not measured), duration of transmitter life in days where * indicates transmitters still active at time of press, and type of transmitter used for each turtle).

| Turtle ID | Deployed | Type | CCL | Duration | Transmitter |
|-----------|--------------|------|-------|----------|-------------|
| a | 09 July 04 | 1 | 93.0 | 297 | SMRU |
| b | 12 June 04 | 1 | 109.3 | 127 | Kiwisat |
| c | 09 July 03 | 1 | 104.7 | 304 | Telonics |
| d | 11 June 04 | 1 | 102.8 | 565 | Kiwisat |
| e | 03 July 03 | 1 | 102.5 | 643 | Telonics |
| f | 03 July 03 | 1 | 106.5 | 197 | SMRU |
| g | 02 July 03 | 1 | + | 652 | Telonics |
| h | 01 August 05 | 1 | 102.0 | 468 | Kiwisat |
| i | 22 July 05 | 1 | 103.0 | 381 | Kiwisat |
| j | 11 June 04 | 2 | 104.3 | 476 | Kiwisat |
| k | 23 July 05 | 2 | 99.3 | 534 | Kiwisat |
| l | 24 July 05 | 2 | 89.2 | 542* | Kiwisat |

SMRU, Sea Mammal Research Unit.

— underestimation when areas inhabited by turtles are not recorded (e.g. due to small sample sizes or short tracking durations from limitations of battery life or durability for satellite transmitters, especially in marine applications) or (2) errors of commission — when areas potentially habitable by turtles are not actually inhabited, i.e. are not part of the realized niche (e.g. because of lack of food, or due to competition or predation), and caution should therefore be appropriately applied. For example, we have identified suitable wintering habitat off the coast of Georgia, in which we have not tracked wintering individuals. These two factors can only be resolved with future increased tracking efforts and parameterization of more sensitive models (Fielding & Bell, 1997; Peterson *et al.*, 1999). Our model suggests potential habitat at a large scale whereas individual turtles appear to use more discrete areas and are probably driven by local-scale factors in the areas where they are foraging or wintering, perhaps associated with underwater features or structures.

Possible future climate change could lead to a change in the location and magnitude of the Gulf Stream (Rahmstorf, 1997; IPCC, 2001). Having now demonstrated that turtles in USA coastal waters use the Gulf Stream to maintain thermally accessible habitat through winter, changes to the Gulf Stream could mean that existing turtle foraging and wintering areas would not be suitable in the future. Although turtles have survived through millennia of changing natural conditions, their ability to adapt to the rapid, anthropogenically forced change in climate that is predicted to occur in the next century (IPCC, 2001) is uncertain.

Regulation of the threats posed by fisheries and other anthropogenic activities throughout the range of these turtles from New Jersey to Florida should be less complicated than in many other parts of the world due to the involvement of only one,

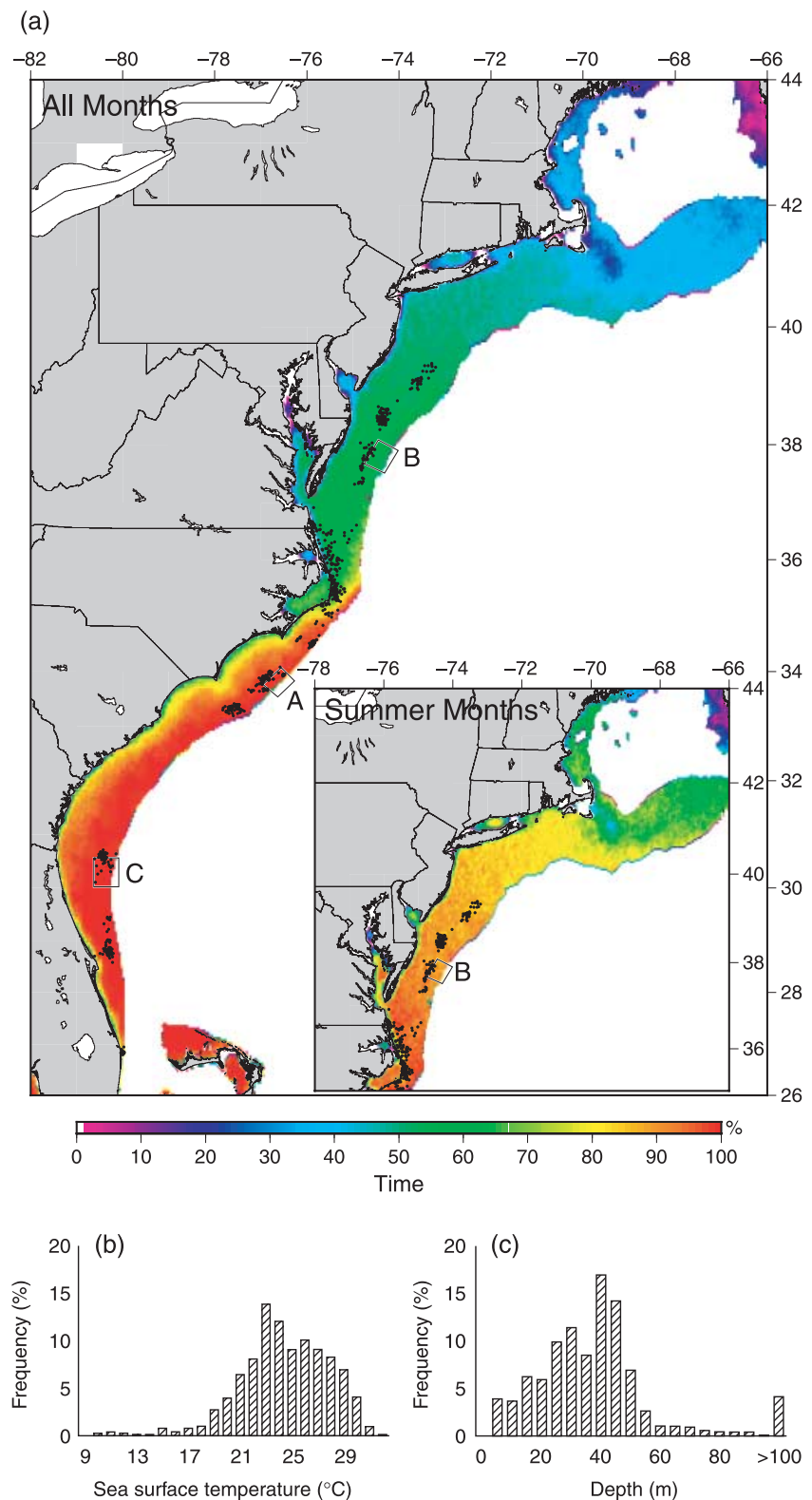


Figure 5 Modelling habitat suitability. (a) Habitat suitability model for loggerhead turtles on the eastern seaboard of the USA. Colour bar depicts proportional monthly suitability (where SST ≥ 13.3 °C and GEBCO bathymetry ≤ 104.4 m; source data from January 1998 to December 2006) for turtle survival for winter months on a 1-min grid. Polygons indicate proposed sites for US Navy Undersea Warfare Training Ranges, as in Fig. 1. (b) Frequency histogram of SSTs collected for all turtle locations for entire tracking period (mean 21.8 ± 3.0 °C, range 12.8–30.4 °C). (c) Frequency histogram of GEBCO bathymetry collected for all turtle locations for entire tracking period (mean 37.1 ± 16.0 m, range 0.25–104.4 m).

highly developed nation in much of the adult range. However, conservation efforts will likely be complicated by the presence of multiple migratory strategies in this population (see also Hatase *et al.*, 2002; Hawkes *et al.*, 2006), as well as the fragmented nature

of US ocean resource management (Crowder *et al.*, 2006). In addition, turtles from this population may exhibit more plastic foraging strategies than previously thought — we cannot exclude the possibility that turtle d may have foraged pelagically

during her 87-day excursion into the Gulf Stream and that this may make up a part of the foraging repertoire of this population. Despite the magnitude of nesting in Florida (Ehrhart *et al.*, 2003) few tracks of loggerheads have been published. Information currently available suggests that northerly, neritic foraging may be a common strategy in nesting turtles from the USA (Plotkin & Spotila, 2002; Dodd & Byles, 2003), with some diversity in movements including the use of the Bahamas Bank, which from our habitat suitability model offers a significant neritic area, potentially suitable to loggerhead turtles on a year-round basis.

The occurrence of two different migratory strategies poses some interesting points with regard to acquisition and allocation of resources for marine turtles. Although type 1 turtles expend energy on seasonal migrations and likely undergo fasting at least during part of the wintering period, they evidently net sufficient energy not only for maintenance but also for reproduction. Additionally, although type 2 turtles do not expend energy on seasonal shuttling migration, based on our limited sample size, a lack of differences in recorded fecundity measures relative to type 1 turtles suggests that neither strategy confers a significant advantage. This dichotomy may result from a constraint related to the settlement location of juvenile turtles to the North American shelf after an oceanic developmental period (Bolten, 2003). Post-settlement juvenile loggerheads are found seasonally over a wide range between 24° and 42° N, with some individuals moving southward in winter months (Hopkins-Murphy *et al.*, 2003). It may be that strong site fidelity (Avens *et al.*, 2003) to initial foraging areas after settlement leads to the development of the two migratory foraging strategies. These strategies are maintained in the long term because foraging habitats provide sufficiently rich feeding conditions, potentially evidenced by the relatively large body size of turtles from this population vs. Pacific, Mediterranean, and Indian Ocean loggerheads (Van Buskirk & Crowder, 1994; Tiwari & Bjørndal, 2000). Additional tracking of turtles and synthesis with other similar studies will help to elucidate the frequency of the two strategies within the population and perhaps identify selective pressures associated with the different behaviours.

The clear ecological niche constraints to loggerhead turtles elucidated in this study highlight how, in the future, predictive models may be used to inform management of commercial fisheries and other anthropogenic activities for the reduction of potential interactions (NRC, 1990). Currently, in waters off North Carolina and Virginia, the commercial use of large-mesh gillnets targeting monkfish has been restricted to months with < 11 °C water temperature (NMFS, 2002), and much effort has been expended on mitigation of specific fisheries in the USA such as shrimp trawls (Epperly, 2003) and pelagic longlines (Watson *et al.*, 2005). Although turtles must swim in the nearshore zone as part of the nesting process, our data show that turtles spend much of their time offshore in deeper federal waters, especially during winter. By-catch in these areas may not be easily detected, particularly as there are few on-board observer programmes for specific fisheries. Moreover, as a result of the strong current influence, any carcasses in this region are less likely to wash ashore

and be recorded as strandings. Additionally, the US Navy has proposed the establishment of an undersea warfare training range off south-eastern North Carolina (Navy, 2005). This could pose a significant opportunity for interaction during construction, maintenance, and operations, with potentially large aggregations of loggerhead sea turtles in and around the proposed sites off North Carolina, Virginia, and Florida (Fig. 1b; Fig. S1). Based on our results, some of the mitigation measures proposed by the US Navy to minimize impacts on sea turtles may be insufficient. For example, our results suggest that turtles may only surface four to six times a day in winter months, which would greatly hinder the efficacy of surface observers during construction to detect the presence of sea turtles (Navy, 2005; Okamura *et al.*, 2006).

We have highlighted the waters of North Carolina as a likely hotspot of loggerhead occurrence in the USA, particularly during winter months, building on the findings in early satellite tracking studies of small numbers of females from Georgia and Florida (Plotkin & Spotila, 2002; Dodd & Byles, 2003). Satellite tracking and remote sensing are revolutionizing our knowledge and understanding of the ecology of migratory marine vertebrates. It is clear that subsequent synthetic overviews, including tracking data from other projects underway elsewhere in the USA and overseas, may lead to reliable predictive continental-scale niche models leading to tremendous insights into both the fundamental and the applied ecology of these species.

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SUPPLEMENTARY MATERIAL

The following supplementary material is available for this article.

Figure S1 Animation of the mean weekly positions of turtles (a–l, represented by lower case letters). Coloured background shows average weekly sea surface temperatures (SST) for the study period (2003–2005); 250-m isobath and 20 °C isotherm are delineated. Grey polygons indicate proposed sites for US Navy undersea warfare training ranges off (a) North Carolina, (b) north-eastern Virginia, and (c) north-eastern Florida (21). The Gulf Stream is clearly visible off the coastal shelf. Grey patches indicate missing SST data due to cloud cover.

Table S1 Reproductive metrics for tracked turtles (where 1 = northerly foraging with shuttling winter migrations and 2 = southerly foraging) showing turtle ID (turtles a to l), body size (CCLn-t, following Bolten, 1999), remigration interval, inter-nesting interval, and clutch frequency.

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