Sea turtle nesting distributions and oceanographic constraints on hatchling migration

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Patterns of abundance across a species's reproductive range are influenced by ecological and environmental factors that affect the survival of offspring. For marine animals whose offspring must migrate long distances, natural selection may favour reproduction in areas near ocean currents that facilitate migratory movements. Similarly, selection may act against the use of potential reproductive areas from which offspring have difficulty emigrating. As a first step towards investigating this conceptual framework, we analysed loggerhead sea turtle (*Caretta caretta*) nest abundance along the southeastern US coast as a function of distance to the Gulf Stream System (GSS), the ocean current to which hatchlings in this region migrate. Results indicate that nest density increases as distance to the GSS decreases. Distance to the GSS can account for at least 90 per cent of spatial variation in regional nest density. Even at smaller spatial scales, where local beach conditions presumably exert strong effects, at least 38 per cent of the variance is explained by distance from the GSS. These findings suggest that proximity to favourable ocean currents strongly influences sea turtle nesting distributions. Similar factors may influence patterns of abundance across the reproductive ranges of diverse marine animals, such as penguins, eels, salmon and seals.

Keywords: *Caretta caretta*; loggerhead turtle; nest density; abundance; biogeography; Gulf Stream System

1. INTRODUCTION

Numerous animals range over vast expanses of land or sea but reproduce only in geographically restricted regions. Within these regions, there is often considerable spatial variation in the abundance of individuals (e.g. Page *et al.* 1991; Boyd 1993; Feldheim *et al.* 2002). The spatial variation is typically correlated with ecological resources and environmental conditions favouring the survival of offspring, including the presence of food, shelter and a relative lack of predation (Boyd 1993; Martin 1993; Olivier & Wotherspoon 2005).

For animals that migrate long distances, additional environmental factors might also influence survival. For example, the offspring of some fish, shorebirds, penguins and seals must successfully complete, at a very young age, a long-distance migration from the natal area to suitable developmental habitat (Butler *et al.* 1997; Azumaya & Ishida 2001; McConnell *et al.* 2002; Clarke *et al.* 2003). Because favourable winds and oceanic currents can greatly reduce the energetic costs of travel (Alerstam 1979; Butler *et al.* 1997; Guinet *et al.* 2001; Clarke *et al.* 2003), natural selection might select for the use of reproductive areas in which environmental conditions facilitate migration. We explore this possibility by examining the nesting distribution of an iconic long-distance migrant, the loggerhead sea turtle (*Caretta caretta*).

The loggerhead turtle has an itinerant lifestyle comprised of a series of migrations (Carr 1987). Along the southeastern US coast, young loggerheads emerge from nests deposited on sandy beaches and then migrate off-shore to the Gulf Stream System (GSS), becoming entrained in the North Atlantic Subtropical Gyre (Carr 1987; Witherington 2002). Juvenile loggerheads remain within the gyre for several years as they grow and mature, often taking up temporary residence in productive foraging areas (e.g. the Azores) before eventually returning to the North American coast (Bolten *et al.* 1998). As adults, turtles return to nest in the same geographic region where they themselves hatched, a behavioural pattern known as natal homing (Bowen & Karl 2007; Lohmann *et al.* 2008).

Sea turtle nesting has been studied extensively in the context of local environmental traits associated with individual nest sites (Carthy *et al.* 2003). Little is known, however, about factors that influence nest density across regional scales (Miller *et al.* 2003; Witherington *et al.* 2009). One possibility is that nesting distribution has been shaped by constraints on hatchling migration (Putman *et al.* in press). Reaching offshore currents is crucial to the survival of hatchlings because such currents provide shelter, food and a source of transport that facilitates long-distance migration to pelagic feeding areas (Carr 1987; Bolten *et al.* 1998; Witherington 2002; Boyle *et al.* 2009). Moreover, turtles that remain in near-shore areas are subjected to intense predation (Whelan & Wyneken 2007).

Given these considerations, hatchlings that emerge on beaches close to the GSS might have increased survival relative to hatchlings from beaches farther from the current. Because of natal homing, beaches that produce the most surviving hatchlings might also have the highest numbers of adults returning to nest. As a first step

towards investigating whether constraints on the hatchling migration shape patterns of nest abundance, we assessed how well the distance that hatchlings must travel to reach the GSS predicts nest distribution at regional and local scales.

2. METHODS

(a) *Regional-scale analysis of loggerhead nest density*

For purposes of analysis, the nesting range of loggerheads in the southeastern US was partitioned into 10 regions that correspond to geographical areas used in previous reports of nesting data (e.g. Meylan *et al.* 1995; Mast *et al.* 2007). Along the Gulf of Mexico, the regions were: (i) Texas; (ii) Louisiana and Mississippi; (iii) Alabama through to the western panhandle of Florida (from Alabama to Franklin County, Florida); (iv) northwestern Florida (Wakulla to Pasco County); and (v) southwestern Florida (Pinellas to Monroe County). Along the Atlantic Ocean, the regions were: (vi) southeastern Florida (from Miami to Cape Canaveral); (vii) northeastern Florida (from Cape Canaveral to the northern border of Florida); (viii) Georgia; (ix) South Carolina; and (x) North Carolina. The length of coastline for these 10 regions ranged from 154–700 km (figure 1; electronic supplementary material, table S1).

At this regional scale, loggerhead nesting data were obtained from two sources that used different methods for assessing nest abundance. Each dataset covered a different period of years and provided the basis for a separate, independent analysis.

The first dataset was obtained from the NOAA *Recovery plan US population of loggerhead turtles* (NMFS & USFWS 1991), hereafter referred to as 'NOAA (1985–1990)'. This provided the highest and lowest nesting totals for all US beaches that reported at least 100 loggerhead nests between 1985 and 1990. To obtain a single value of nest density (nests per kilometre of beach surveyed) for each of the 10 regions, the highest and lowest values of nest density at the beaches within each region were averaged (electronic supplementary material, table S1).

A second, independent analysis was done using the *State of the world's sea turtles report, vol. II* (Mast *et al.* 2007), hereafter referred to as 'SWOT (2005)' which compiled nesting data for 2005 from agencies responsible for monitoring sea turtle nesting (Dodd & Mackinnon 2007; FFWCC-FWRI 2007*a*; Godfrey 2007; Griffin 2007; Reynolds 2007; Shaver 2007). These data differ from the NOAA data in that they include all instances of loggerhead nesting across the Atlantic and Gulf coasts (not just nesting at the major beaches). Nesting data were compiled to determine the overall nest density (nests per kilometre surveyed) within each of the 10 geographical regions (electronic supplementary material, table S1).

(b) *Local-scale analysis of nest density*

For local-scale analysis, we calculated the average number of loggerhead nests per year from coastal Florida counties (n = 27) between 1990 and 2006 (FFWCC-FWRI 2007*b*), hereafter referred to as 'Florida counties (1990–2006)'. Local-scale nest density was determined by dividing the average number of nests per county by the estimated length of coastline in each county (derived from Google Earth software). The range of coastline lengths among counties was 18–140 km (electronic supplementary material, table S2).
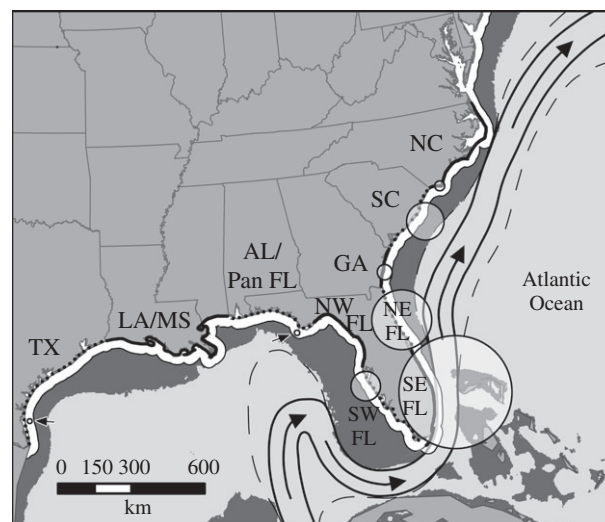

Figure 1. Map of loggerhead nesting range along the southeastern US coastline. Alternating solid and dotted black lines along the coast delineate the stretches of beach used for the regional analysis. The regions comprise Texas (TX), Louisiana and Mississippi (LA/MS), Alabama and the panhandle of Florida (AL/Pan FL), northwestern Florida (NW FL), southwestern Florida (SW FL), southeastern Florida (SE FL), northeastern Florida (NE FL), Georgia (GA), South Carolina (SC) and North Carolina (NC). Circles indicate relative nest density in each region (based on SWOT 2005 dataset; SE FL and TX nest density are not to scale). Circles are centred on the area within each region that has highest nest density. The white shading (line) immediately adjacent to the coast indicates the maximum distance (40 km) that a hatchling loggerhead can swim using the residual energy from its yolk sac (Kraemer & Bennett 1981). The dark grey shading shows the continental shelf (the area over which predation on young sea turtles is thought to be greatest). The solid black line demarcates the average position of the GSS (see text for details) and the surrounding dashed lines show the area over which the GSS meanders. Arrows indicate the direction of current flow.

(c) *Gulf stream system*

The GSS is a swift, warm current that flows through the Gulf of Mexico, the Florida Straits, and then northward and northeastward over the continental slope off the southeastern US (figure 1). The part of the GSS within the Gulf of Mexico is known as the Loop Current because the current's flow loops in a clockwise path within the eastern Gulf (Auer 1987). The current between southeast Florida and North Carolina is referred to as the Gulf Stream (Auer 1987). Near Cape Hatteras, North Carolina, the Gulf Stream separates from the continental slope, veering northeastward towards the Grand Banks and eventually eastward towards northwestern Europe, thus forming the northern portion of the North Atlantic Subtropical Gyre (Auer 1987). In this paper, we refer to the Loop Current and Gulf Stream as the GSS.

The GSS path undergoes meanders (time-varying lateral motions) that can shift the Stream about 5–40 km from its mean position along the east coast (Bane & Brooks 1979; Bane *et al.* 2001) and by as much as 125 km in the Gulf of Mexico (Molinari *et al.* 1977; Sturges 1992). These meanders are neither strictly seasonal, nor are they predictable from year to year (Molinari *et al.* 1977; Olson *et al.* 1983; Sturges 1992). As a result, the GSS is not consistently either shoreward or seaward of its average position during loggerhead nesting season.

Table 1. Results of regression analyses predicting nest density (n) as a function of each area's distance to the GSS (D) and latitude (L).

dataset	no. of areas	equation	predictor(s)	r^2	r^2 (adj.)	F	p
NOAA (1985–1990)	10	$n = 5410D^{-1} - 13.1$	GSS Dist	0.96	0.95	169.3	<0.001
NOAA (1985–1990)	10	$n = 7797L^{-1} - 233$	latitude	0.16	0.06	1.6	0.248
NOAA (1985–1990)	10	$n = 3390L^{-1} + 5173D^{-1} - 125$	latitude + GSS Dist	0.98	0.98	212.2	<0.001
SWOT (2005)	10	$n = 3962D^{-1} - 12.1$	GSS Dist	0.94	0.93	122.5	<0.001
SWOT (2005)	10	$n = 5893L^{-1} - 179$	latitude	0.17	0.06	1.6	0.236
SWOT (2005)	10	$n = 2676L^{-1} + 3775D^{-1} - 101$	latitude + GSS Dist	0.97	0.96	120.2	<0.001
Florida counties (1990–2006)	27	$n = 3622D^{-1} + 4.4$	GSS Dist	0.46	0.43	20.8	<0.001
Florida counties (1990–2006)	27	$n = 11\,709L^{-1} - 368$	latitude	0.07	0.04	2.0	0.171
Florida counties (1990–2006)	27	$n = 5172L^{-1} + 3695D^{-1} + 174$	latitude + GSS Dist	0.47	0.42	10.4	0.001

Because loggerhead sea turtles are long-lived and nest over many years, the turtles nesting at any one time presumably include individuals from numerous different cohorts, each of which experienced different states of the GSS as hatchlings. Moreover, the average state of the GSS is likely to reflect conditions representative of what loggerhead hatchlings have experienced over many years (Olson *et al.* 1983; Auer 1987), a time scale appropriate for assessing patterns of nest density.

For our analysis, we superimposed on maps from Google Earth the average position of the shoreward edge of the Loop Current, as described in Sturges (1992), and the average position of the shoreward edge of the Gulf Stream, as described in Olson *et al.* (1983). For the regional analysis, the distance from the coast to the edge of the GSS was measured at every half-degree of latitude within each region (or at every half-degree of longitude in the case of the Louisiana/Mississippi and Alabama/Florida panhandle regions, which are aligned approximately east–west). These measurements were used to calculate mean distance to the GSS for each region. For the local-scale analysis, a single measurement was taken from the centre of each Florida county to the GSS. In both cases, distance was measured to the nearest kilometre.

(d) Latitude

As an additional part of our analysis, we investigated whether nest density was correlated with latitude, which covaries with several climate-related variables that might be important in sea turtle nesting (Mrosovsky 1994). For the regional analysis, the mean latitude was determined by summing the latitude values at each half-degree of latitude (or at each half-degree of longitude in the case of the Louisiana/Mississippi and Alabama/Florida panhandle regions) and then dividing the sum by the number of half-degree intervals within the region. For the local-scale analysis, latitude was taken at the centre of each Florida county.

(e) Statistical analyses

Three linear regression models were used to investigate variation in loggerhead nest density (SPSS v. 16). Nest density was regressed against the inverse of the distance from the nesting area to the GSS because we expected nest density of an area to increase with decreasing distance to the GSS. Nest density was also regressed against the inverse of latitude because previous studies suggested that more turtles might nest in southern areas owing to effects mediated by temperature (Mrosovsky 1994). A multiple regression analysis was performed that included both distance to the GSS and latitude as predictors of nest density. To investigate a possible interaction between the effect of latitude and distance to the GSS, standard variance partitioning analyses were carried out using the adjusted r^2 values of the three regression models (Legendre & Legendre 1998). Regression and variance partitioning analyses were performed separately for regional nesting data obtained from NOAA (1985–1990) and SWOT (2005) owing to differences between survey methods. The analyses were also carried out for Florida counties (1990–2006).

3. RESULTS

Regression analyses (summarized in table 1) indicated that, as the distance to the GSS increased, loggerhead nest density decreased (figure 2). This pattern held for both of the regional datasets (NOAA: $r^2 = 0.96$, $p < 0.001$, $n = 10$; SWOT: $r^2 = 0.94$, $p < 0.001$, $n = 10$). Across Florida counties, the same general relationship was observed as in the regional analysis ($r^2 = 0.46$, $p < 0.001$, $n = 27$). Latitude was not a significant predictor of nest density at regional or local scales. Furthermore, including both latitude and distance to the GSS as predictors of nest density at regional or local scales did not appreciably increase the amount of nesting variance explained compared with the analyses using distance to the GSS alone (table 1).

Variance partitioning analyses also indicated that distance to the GSS robustly predicted nest density (figure 3). For the two regional datasets, distance to the GSS alone accounted for 92 per cent (for NOAA dataset) and 90 per cent (for SWOT dataset) of the variation in nest density. Latitude accounted for 3 per cent of the variation in nest density and the interaction between distance to the GSS and the latitude accounted for 3 per cent (for both datasets). Across Florida counties, distance to the GSS alone accounted for 38 per cent of the variation in nest density, whereas latitude accounted for less than 1 per cent, and the interaction between the GSS and the latitude accounted for 5 per cent.

4. DISCUSSION

The results indicate that, along the southeastern US coast, loggerhead nest density declines as the distance between the coast and the GSS increases. This pattern holds at
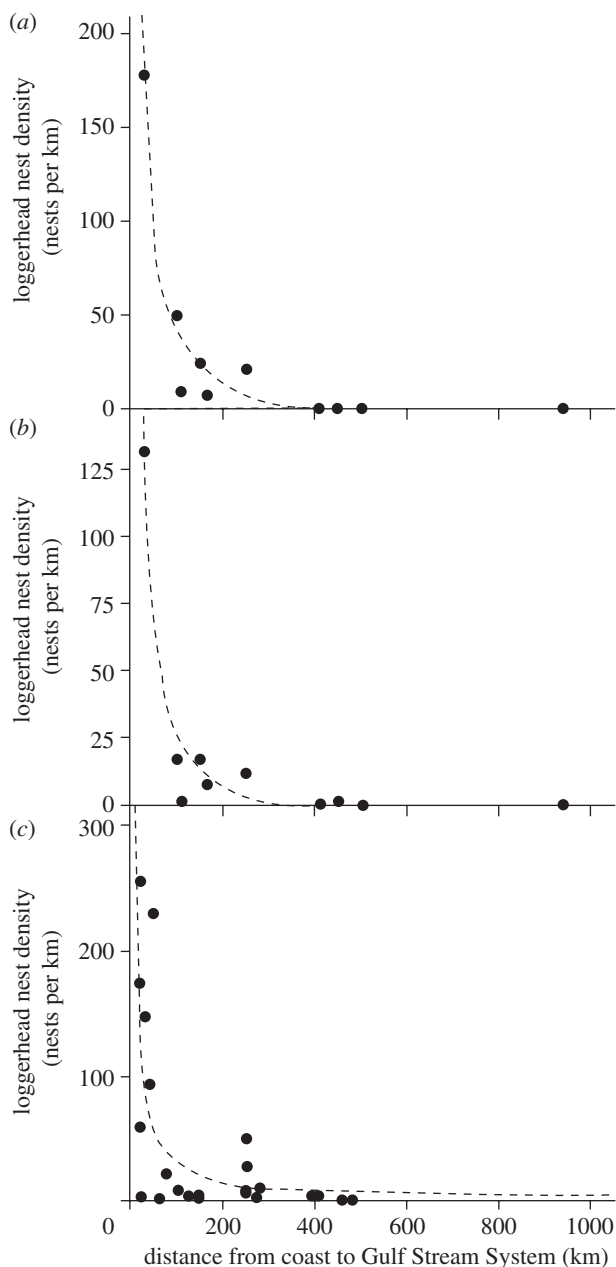
Figure 2. Graphs of loggerhead nest density plotted against distance from each nesting area to the GSS. Trend lines are estimated by regression. (*a*) Regional-scale results using the NOAA 1985–1990 dataset. (*b*) Regional-scale results using the SWOT 2005 dataset. (*c*) Local-scale results using nesting data from Florida counties for 1990–2006. See text for details.

both regional and local spatial scales. On a regional level, the distance to the GSS was able to account for more than 90 per cent of the variation in nest density (table 1; figures 2*a*,*b* and 3). On the smaller scale of Florida counties, distance to the GSS could account for at least 38 per cent of the variation (table 1; figures 2*c* and 3). These findings are consistent with the hypothesis that loggerhead nest distribution is influenced by the distance that hatchlings must migrate from the beach to the GSS.

(a) Offshore migration of hatchlings

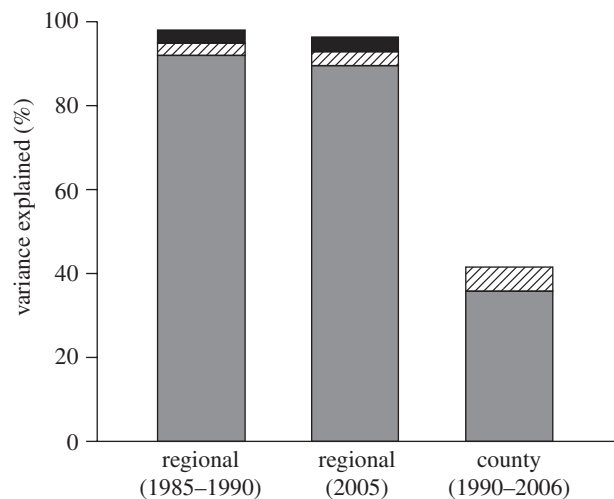Immediately after emerging from underground nests, hatchling loggerheads scramble to the ocean and migrate

Figure 3. The partitioning of variance of nest density of southeastern US loggerhead sea turtles by dataset into effects of (i) distance from nesting area to the GSS (grey), (ii) nesting area latitude (black) and (iii) variance explained by some combination of the two factors that cannot be uniquely ascribed to either (hatched).

seaward, using visual cues, ocean waves and the Earth's magnetic field to stay on course (Lohmann & Lohmann 1996). During the offshore migration, hatchlings rely on yolk reserves for sustenance and do not feed for several days (Wyneken & Salmon 1992). Analyses of loggerheads from Georgia suggest that the longest distance a hatchling can swim using the residual energy from its yolk is about 40 km (Kraemer & Bennett 1981).

Hatchlings that emerge on beaches within about 40 km of the GSS may thus have an increased likelihood of reaching their offshore destination. For these turtles, the energetic requirements of the migration can presumably be met without pausing to forage. Moreover, predation risk may be reduced because hatchlings reach the GSS sooner and can immediately take refuge in mats of floating sargassum (Carr 1987; Witherington 2002), whereas between the shore and the GSS, hatchlings typically lack places to hide and are likely to be exposed to intense predation (Whelan & Wyneken 2007). An additional benefit of migrating from beaches closer to the GSS is that hatchlings might embed themselves farther into the current, increasing the likelihood that they are transported along the gyre and not returned to coastal waters by filaments shed from the outer edges of the main current.

These considerations notwithstanding, hatchlings in some geographic areas still reach the GSS from beaches farther than 40 km away (figure 1). In such cases, however, whether hatchlings succeed may be influenced greatly by factors specific to each situation. Among these are near-shore currents that facilitate or impede offshore movements, the intensity of predation in particular coastal areas and the availability of food sources for hatchlings once the yolk reserve is depleted. Additionally, hatchlings may have evolved differences in migratory behaviour or physiology that are uniquely suited to particular geographical areas. For instance, loggerhead hatchlings from southwest Florida swam longer in the first week after emergence than did hatchlings from southeast Florida, a difference hypothesized to reflect

the greater distance hatchlings from southwest Florida must travel to reach the GSS (Wyneken *et al.* 2008).

(b) Spatial patterns of nesting

Patterns of nest abundance in loggerheads are likely to be maintained and reinforced by natal homing, the tendency of turtles to return to nest in the same geographical areas where they originated (Bowen & Karl 2007). Because they nest near their natal sites, females are likely to nest in greatest numbers at beaches that produced the most surviving hatchlings. Thus, if nesting beaches close to the GSS enhance the survival of hatchlings, then more turtles are likely to return to these areas to nest, and patterns of nesting density may persist through time.

Although a highly significant correlation exists between nest density and distance to the GSS at regional and local scales, the r^2 value of the local-scale analysis (0.46) was considerably lower than that for the regional analyses (0.96 and 0.94). At local scales, coastal geomorphology and human disturbances probably have some influence on specific nest site selection; for example, urban beaches with night-time lighting and human activity attract relatively few nesting turtles (Miller *et al.* 2003). These local influences might be masked at larger scales (Levin 1992).

At regional scales, the need of turtles to nest in close proximity to a major offshore current system might explain why no nesting occurs along some parts of the US coast that otherwise appear suitable. For example, almost no nesting occurs along the warm sand beaches from Mississippi to Texas, even though such beaches have temperatures and other characteristics that match those found on loggerhead nesting beaches elsewhere (Nelson 1988). It is possible that beaches in the north and west Gulf of Mexico are in effect cut off from the GSS, making them impossible for large numbers of loggerheads to colonize, even if all other necessary conditions exist.

(c) Nest density and latitude

In principle, temperature-mediated effects might have resulted in a correlation between nesting abundance and latitude. For example, the temperature of incubation determines the sex of sea turtle hatchlings, with warmer temperatures producing more females and cooler temperatures producing more males (Mrosovsky 1988, 1994). Because lower latitudes are associated with higher incubation temperatures, nest density might conceivably increase with decreasing latitude because more females are produced on southern beaches, resulting in more female adults returning to those areas to nest (Mrosovsky 1988). No correlation was found to exist between latitude and nesting density, however, either at regional or local scales (table 1; figure 3). With hindsight, this finding is perhaps not surprising in view of the fact that nest temperature can vary greatly over several metres (depending on proximity to the surf or vegetation), enough to substantially alter the sex ratio of clutches on the same beach (Kamel & Mrosovsky 2006). Such local effects might override any weak influence of latitude.

5. CONCLUSIONS

Our analyses suggest that the distance from a nesting area to the GSS might account for much of the variation in loggerhead nest density in the southeastern US. Other loggerhead nesting areas have not been analysed because comparable nest density data are not available. Thus, whether the same pattern exists elsewhere is not known. However, numerous major loggerhead nesting assemblages occur along continental coastlines in close proximity to ocean currents. Among these are Japan (Kuroshio Current), east Australia (East Australian Current), Marisah Island of Oman (Ras al Hadd Jet), Tongaland of South Africa (Agulhas Current), south equatorial Brazil (Brazil Current) and the eastern Yucatan Peninsula of Mexico (Yucatan Current; Bolten & Witherington 2003). Our findings might be directly applicable to these and other sea turtle populations. Moreover, the principles outlined in the study may prove helpful in understanding the geographical distribution of reproduction in diverse marine animals, such as seals (Guinet *et al.* 2001), penguins (Clarke *et al.* 2003), salmon (Azumaya & Ishida 2001) and eels (Kettle & Haines 2006).

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