OCEANOGRAPHIC AND GEOMAGNETIC INFLUENCES ON SEA TURTLE MIGRATIONS

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Abstract

NATHAN F. PUTMAN: Oceanographic and Geomagnetic Influences on Sea Turtle Migration
(Under the direction of Dr. Kenneth J. Lohmann)

The research presented here explores the migratory behavior of sea turtles from behavioral, ecological, and evolutionary perspectives. Turtles display long-distance migratory movements at all stages of their lives; as hatchlings they migrate offshore from nesting beaches, as juveniles they navigate oceanic gyres, and as adults they move between foraging and reproductive grounds. For each of these migrations I examine how behavioral processes mediate large-scale biogeographic patterns.

Analyses revealed a relationship between sea turtle nest abundance and offshore oceanic conditions. A disproportionate number of nests were deposited on beaches near ocean currents that facilitate the successful migration of hatchling turtles. This nesting pattern may persist through time because turtles return to nest near their natal beaches; thus, areas that produce the most surviving hatchlings and juveniles might also have the highest number of adults returning to nest.

Laboratory experiments demonstrated that young turtles are capable of extracting latitudinal and longitudinal information from the earth's magnetic field to assess their position along their open ocean migration. Computer simulations indicated that even limited swimming in response to these magnetic cues exerts considerable influence on the open-ocean distribution of turtles. Specifically, magnetic navigation behavior appears to increase the number of turtles that encounter high-productivity foraging grounds and decrease the number that enter or remain in suboptimal oceanic regions. Additionally, the synthesis of results from a decade of behavioral assays on magnetic navigation in turtles, combined with geomagnetic and ocean circulation models, provided the first quantitative insight into how environmental conditions select for the evolution of this behavior.

Finally, geomagnetic models were used to explore the long-standing mystery of how female turtles return to their natal beach after dispersing thousands of kilometers over a decade or more. Analyses indicate that a simple strategy of imprinting on the magnetic field of the natal site and using this information to return at maturity can account for the known homing precision of several different species of sea turtles. Moreover, the predictions from this hypothesis are consistent with the population structure for numerous sea turtle nesting assemblages across the world, as well as other spatiotemporal patterns in nest abundance.

La trahison des images
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CHAPTER 1

INTRODUCTION

The movement of organisms is a fundamental component of nearly all ecological and evolutionary processes, providing insights into phenomena at all levels of biological organization from physiology and behavior of individuals to broad-scale biogeographic patterns (Nathan 2008; Nathan et al. 2008). For example, the amount of gene flow among populations appears to be largely controlled by the movement capacity of a species (i.e. vagility). Species with a greater capacity for movement typically have increased gene flow among populations whereas less vagile species tend to have more structured populations (McCracken et al. 1994; Hamrick & Godt 1996). As a result, over evolutionary timescales, organisms with low capacity for movement may be more likely to evolve adaptations to localized selective agents (e.g. the environment, specific competitors, certain predators, or a specialized food source) which could eventually lead to speciation. In contrast, panmixia (random mating throughout a species' range) is likely to occur for species with high movement capacity and local adaptations may be less likely to evolve (Avise 2009).

However, exceptions to this generalization on the relationship between gene flow and species vagility are common. Although some exceptions can be attributed to historical barriers to gene flow that are no longer present, many exceptions result from the directionality of organism locomotion (Avise 2009) or the directionality of environmental factors such as ocean currents and wind (Treml et al. 2008). Biases in the direction of organism movement frequently confound the simple model of gene flow among populations being a function of geographic distance and dispersal ability (Avise 2009). These discrepancies suggest that, along with movement capacity of species, a key aspect of organism movement is that it is inherently directional. Thus, detailed examination of the environmental and biological factors that promote, impede, and directionally bias the movement of organisms is likely to provide the optimal framework for studying ecological and evolutionary phenomena (Alerstam et al. 2003; Holyoak et al. 2008; Bowlin et al. 2010).

In studying the complexities of organism movement, long-distance migratory animals have proven to be excellent model systems (Alerstam 2006; Åkesson & Hedenström 2007; Nathan 2008). The clear directionality of migration can often be highly amenable to hypothesis generation and experimentation with regard to the factors that animals use to assess their position and orient their movements. Additionally, the extensive distances traveled by migrants help to highlight how movement is a crucial component of energy acquisition, reproduction, and the evolution of traits associated with these tasks (Alerstam et al. 2003; Åkesson & Hedenström 2007). Likewise, the specialized adaptations in behavior and physiology that permit migrants to successfully navigate across heterogeneous landscapes provide opportunities to explore how the movement of individual organisms varies depending on environmental conditions.

From a phylogenetic perspective, migrants are not very different from non-migratory animals. Indeed, sister taxa or even populations within a species may differ greatly in the degree of migratory behavior (Mettke-Hoffman 2003; Alerstam 2006). This fact suggests that the adaptations for long-distance movement are likely to be simple extensions of the characteristics that control more localized movements and are thus useful for conceptually understanding the movements of non-migrant species as well (Grinnell 1931; Alerstam 2006). Studies of long-distance animal migration can even provide insight into the movement process of phylogenetically distant taxa such as plants and fungi that lack neuromuscular systems. Although such organisms might be dismissed as incapable of directed movement, they have nonetheless evolved diverse and numerous adaptations that allow them to bias how and when they travel (typically as seeds or spores) (Holyoak et al. 2008). This in turn results in highly non-random distributions, which can be similar to those observed in animals that take a more active role in the movement process (Levin et al. 2003; Wright et al. 2008).

In my dissertation I address unresolved issues fundamental to animal movement, particularly in long-distance migrants. Among these are the following: (1) the navigational mechanisms that guide long-distance movements; (2) how the mechanisms used influence the path of animals and errors in navigation; (3) how environmental constraints on migration influence the evolution of navigation strategies; and (4) the ecological and evolutionary implications of migrations for populations. I explore these questions by studying diverse aspects of the migratory behavior in sea turtles. The broad and multidisciplinary approach I present here is unified by the goal of describing how the directed movement of individuals shapes the biogeographic patterns exhibited in sea turtle species.

My dissertation is organized around three types of migrations that sea turtles undertake: (1) the offshore migration of hatchlings from the natal site; (2) the pelagic foraging phase of juveniles; and (3) the return to the natal site by adults for reproduction. Each migration is the focus of a single chapter that is further subdivided into sections that represent studies providing insight into the navigational mechanisms utilized by sea turtles during migration, aspects of the physical environment that shape turtle movement, and the population-level consequences arising from the interaction between sea turtles' migratory behavior and environmental factors.

Chapter two, "The offshore migration of hatchling sea turtles" comprises two sections that examine patterns of nest abundance along the reproductive range of different sea turtle species in the context of oceanic conditions that promote or impede the hatchling migration. Chapter three, "The pelagic migration of juvenile sea turtles", comprises five sections that examine how loggerhead sea turtles (*Caretta caretta*) utilize the earth's magnetic field to assess their position in the open ocean to direct their swimming. Additionally, I examine the ecological implications of magnetic navigation and the oceanic and geomagnetic factors that shape the evolution of such a system. Chapter four, "The magnetic imprinting hypothesis of natal homing" comprises three sections that examine the magnetic imprinting hypothesis of natal homing from navigational and ecological perspectives. This chapter addresses whether such a homing mechanism is compatible with known environmental constraints and, if so, how this navigational mechanism would be expected to shape phylogeographic and spatiotemporal patterns in sea turtle nesting. The final chapter provides a broader context for these studies by highlighting the implications of my research to the field of movement ecology, as well as potential applications to conservation and management initiatives in sea turtles.

CHAPTER 2

THE OFFSHORE MIGRATION OF HATCHLING SEA TURTLES

Historically, the nesting beach has been the most studied habitat of sea turtles, and yet no research has been carried out to address what factors influence spatial variation in nest density across the reproductive grounds of any sea turtle species. Instead, research to determine the factors that influence the spatial distribution of sea turtle nesting has largely focused on environmental parameters that ensure successful incubation (e.g. appropriate temperature, substrate, moisture, etc.) at individual nesting beaches (Carthy et al. 2003; Miller et al. 2003). However, the data from these studies are often conflicting and an unambiguous picture of what drives the spatial distribution of nesting has yet to emerge at the scale of the nest site (Miller et al. 2003). It is therefore difficult to extrapolate from these fine-scale studies what influences variation in nesting abundance across the nesting range of any sea turtle species.

Extensive monitoring of sea turtle nesting shows that some areas consistently have higher numbers of nests than others (Ehrhart et al. 2003). In this chapter I provide the first conceptual model that accounts for the variation in nest density across the nesting range of two sea turtle species. While there are certainly many factors that contribute to the observed spatial pattern in marine turtle nesting, I show that characteristics of the ocean rather than the beach are likely to exert the greatest influence the nesting distribution.

Immediately after emerging from underground nests, hatchling loggerheads scramble to the ocean and migrate 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 their yolk sacs for sustenance and do not feed for several days. It is thought that sea turtles evolved this behavior to escape intense predation that occurs over the continental shelf and to access distant high-productivity foraging grounds (Wyneken & Salmon 1992).

Because sea turtles return to nest in the vicinity of their natal beach, nesting locations that allow for the survival of more hatchlings should result in a greater number of adults returning to nest (Bowen & Karl 2007; Lohmann et al. 2008a). Thus, in principle, locations where the hatchling migration is facilitated might accumulate higher nesting abundance compared to locations where the migration is impeded. In this chapter I present evidence that suggests that beaches in close proximity to oceanic currents that aid hatchling migration have higher nest abundance than beaches where turtles must swim farther to reach favorable currents.

Is the geographic distribution of nesting in the Kemp's ridley sea turtle shaped by the migratory needs of offspring?

Summary

Across the geographic area that a species uses for reproduction, the density of breeding individuals is typically highest in locations where ecological factors promote reproductive success. For migratory animals, fitness depends, in part, on producing offspring that migrate successfully to habitats suitable for the next life-history stage. Thus, natural selection might favor reproduction in locations with conditions that facilitate the migration of offspring. To investigate this concept, the Kemp's ridley sea turtle (*Lepidochelys kempii*) was studied to determine whether coastal areas with the highest levels of nesting have particularly favorable conditions for hatchling migration. The passive drift of young Kemp's ridley turtles was modeled from seven nesting regions within the Gulf of Mexico to foraging grounds using the particle-tracking program ICHTHYOP and surface-current output from HYCOM (HYbrid Coordinate Ocean Model). Results revealed that geographic regions with conditions that facilitate successful migration to foraging grounds typically have higher abundance of nests than regions where oceanographic conditions are less favorable and successful migration is difficult for hatchlings. Thus, these findings are consistent with the hypothesis that, for the Kemp's ridley turtle and perhaps for other migrants, patterns of abundance across the breeding range are shaped in part by conditions that promote or impede the successful migration of offspring.

Introduction

Across a species' breeding grounds, abundance is patchy and typically highest in locations where ecological factors promote reproductive success (Horrocks and Scott 1991; Martin 1993; Boulinier 1997). For migratory animals, part of what determines reproductive success is whether offspring successfully complete their first migration to a geographic region that provides suitable habitat for the next life-history stage. Thus, natural selection might favor adults that reproduce in geographic areas with conditions that facilitate the migration of their young. For species in which adults return to reproduce in their natal area (Bowen and Karl 2007; Lohmann et al., 2008), the locations that produce the greatest number of surviving individuals may, over time, come to have higher abundance due to the higher reproductive success of individuals that breed in such places. Patterns of distribution within breeding areas of migratory species might thus remain relatively stable over considerable periods of time.

This conceptual framework is explored in a migratory sea turtle, the Kemp's ridley (*Lepidochelys kempii*). This species nests mostly within a limited area of coastline on the east coast of Mexico near Rancho Nuevo (23.2° N, 97.5° W), but scattered nesting also occurs from Texas, U.S.A. to southern Campeche, Mexico (Márquez 1994; Plotkin 2007) (Fig. 2.1). Hatchlings enter the sea and immediately migrate offshore to pelagic waters, thereby escaping intense nearshore predation that occurs over the continental shelf (Wyneken and Salmon 1992). After a period ranging from several months to two years, turtles enter coastal foraging grounds (Zug et al. 1997, Zimmerman 1998; TEWG 2000), typically either in the Gulf of Mexico between Texas and southwestern Florida or in locations along the eastern U.S. coast from Florida to Nova Scotia (Carr 1957; Hildebrand 1982; Ogren 1989; Metz 2004; Geis et al. 2005). In these coastal areas, turtles forage for benthic invertebrates such as the blue crab *Callinectes sapidus* (Shaver 1991; Werner 1994; Metz 2004). At 10-15 years of age, Kemp's ridleys return to their natal region to mate and nest (Caillouete 1995; Zug et al. 1997), after which they migrate back to distant foraging grounds and repeat this cycle every 1-3 years throughout their lives (TEWG 2000).

Although sea turtle nesting has been studied extensively in the context of local environmental variables associated with individual nest sites (e.g. Mortimer 1990; Horrocks and Scott 1991; Carthy et al. 2003), little is known about factors that influence density of nests across regional scales (Miller et al. 2003). Oceanic currents are likely to be of primary importance for facilitating young sea turtles' migration to areas where juveniles forage (Carr 1980; Carr and Meylan 1980; Carr 1987; Collard and Ogren 1990). Surprisingly, however, currents and their effects on hatchling migration have seldom been incorporated into attempts to explain spatial patterns of nesting. This study investigates whether the regions within the Gulf of Mexico where most Kemp's ridleys nest have oceanographic conditions that are particularly favorable for facilitating the migration of young turtles from their natal beach to suitable coastal foraging grounds.

Methods

A simple model was developed to investigate whether differences in relative abundance of nests across the Kemp's ridley nesting range can potentially be explained by how well different regions facilitate young turtles' migration to their foraging grounds. The Kemp's ridley nesting range was partitioned into seven regions: Texas (29°N, 94.3°W - 26°N, 96.55°W); North of Rancho Nuevo (25.75°N, 96.55°W - 24.25°N, 97.1°W); Rancho Nuevo (23.75°N, 97.3°W - 22.9°N, 97.3°W); South of Rancho Nuevo (22.8°N, 97.2°W - 21.75°N, 96.95°W); Veracruz (21.3°N, 96.8°W - 18.95°N, 94.5°W); South Campeche (18.9°N, 94.5°W - 19.45°N, 91.5°W); and North Campeche (19.4°N, 91.4°W - 21°N, 90.95°W) (Fig. 2.1).

To simulate the movement of young turtles through the ocean Global HYCOM (HYbrid Coordinate Ocean Model) surface currents (0 m depth) were used (Bleck 2002). This model has a spatial resolution of 0.08° (~5-7 km) and a temporal resolution of one day. Young turtles were simulated using the particle tracking program ICHTHYOP v. 2 (Lett et al. 2008). Simulated turtles were released in a zone 45-55 km offshore from each of the seven regions, a distance from shore that hatchling sea turtles are known to reach (Witherington 2002). One thousand simulated hatchlings were released at one-week intervals starting June 1 and continuing through July 20 (eight total release events per year, per region). Turtles were allowed to drift passively for up to two years. HYCOM output is available from 2004-2009; therefore two years of dispersal for four yearly cohorts of hatchlings (2004 –2007) were simulated. The simulation for each year-class was replicated ten times. Thus, the dispersal of 320,000 turtles was simulated from each of the seven nesting regions.

Juvenile Kemp's ridley turtles predominantly recruit to coastal waters within the Gulf of Mexico between Texas and southwestern Florida, or to areas along the east coast of the U.S. and

Canada between Florida and Nova Scotia (Carr 1957; Hildebrand 1982; Ogren 1989; Metz 2004; Geis et al. 2005). Some reports also suggest that young Kemp's ridley might recruit to coastal areas in Campeche Bay, Mexico (Márquez 1994). For purposes of analysis, the foraging grounds of juveniles were partitioned into five coastal areas: (1) Campeche Bay; (2) Texas; (3) Louisiana – West Florida; (4) East Florida – North Carolina; and (5) Virginia – Nova Scotia. These areas extended from the coast across the continental shelf, to a depth of 200 m (Fig. 2.1). Because very young turtles are unlikely to survive in nearshore waters due to intense predation (Collard and Ogren 1990), turtles could only recruit to a coastal region after reaching a minimum age of six months (Zimmerman 1998, TEWG 2000). Additionally, a turtle had to remain in a region for three days before it was considered to have recruited there. Each turtle could only recruit to one region.

How well a region facilitates migration of young sea turtles is likely determined by (1) how quickly hatchlings get offshore (thereby minimizing time spent over the continental shelf, where the risk of predation is probably highest) and (2) the percentage of hatchlings that reach suitable foraging grounds. Thus, for each region, measurements were taken of the percentage of simulated hatchlings that reached pelagic waters (i.e., water with a depth > 200 m) within four days, as well as the percentage of turtles that reached known coastal foraging grounds (Fig. 2.1) within two years.

A two-way ANOVA with replication determined whether there were differences among nesting regions in the percentage of simulated turtles that reached pelagic waters (within four days) and coastal foraging grounds (within two years). To assess which regions best facilitated this migration, mean recruitment to pelagic habitat over the four years simulated as well as the mean recruitment to foraging grounds were determined. In accordance with statistical procedures recommended by Hurlbert and Lombardi (2003) and Lombardi and Hurlbert (2009), two-tailed, paired t-tests were used to compare each region with all others. A separate analysis was conducted for each of the two metrics. For each, regions were ranked relative to one another (the better a region was at facilitating migration, the lower its rank). Regions that were not significantly different shared the same rank. In the event that regions 1 and 2 were not significantly different and regions 2 and 3 were not significantly different, but region 1 was significantly different from region 3, then regions 1 and 2 shared the same rank and region 3 was given that rank plus 0.5. The mean of both ranks was taken as the relative “migratory quality” of each region.

An additional analysis was carried out to assess patterns of movement and the geographic locations where juvenile Kemp’s ridley turtles recruited to coastal feeding grounds. For simulated turtles starting from each of the seven nesting regions, the mean percentage of turtles that reached each of the five foraging areas (defined in Fig. 2.1 and in the text) was determined.

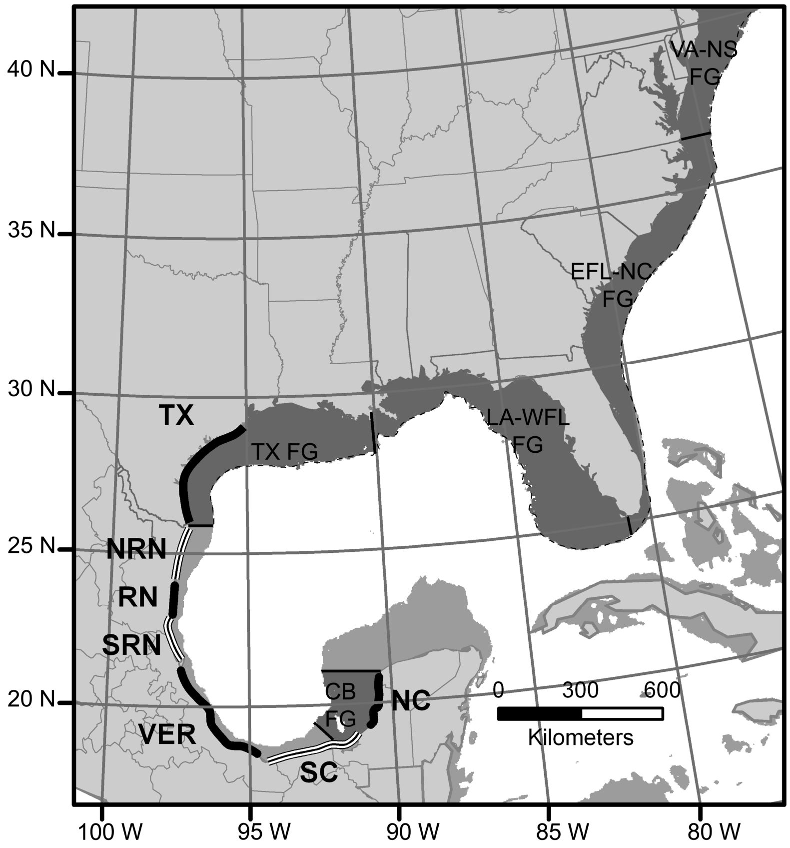

Figure 2.1 Map of the study region. Alternating black and striped lines along the western edge of the Gulf of Mexico show the nesting range of the Kemp’s ridley and delineate the seven nesting regions defined in the model. The regions, as labeled on the map, are TX = Texas, NRN = North of Rancho Nuevo, RN = Rancho Nuevo, SRN = South of Rancho Nuevo, VER = Veracurz, SC = South Campeche, and NC = North Campeche. Shaded areas along the coastline indicate the continental shelf (depth < 200 m). Dark gray areas indicate known or suspected foraging grounds of juvenile Kemp’s ridleys. Black lines extending from the coast across the continental shelf demarcate the partitioning of the foraging grounds in the model (abbreviations are: CB FG = Campeche Bay foraging grounds; TX FG = Texas foraging grounds; LA-WFL FG = Louisiana - West Florida foraging grounds; EFL-NC FG = East Florida - North Carolina foraging grounds; and VA-NS FG = Virginia - Nova Scotia foraging grounds). Pelagic waters are shown in white (depth > 200 m).

Results

The mean number of simulated turtles that reached pelagic habitat within four days was significantly different among nesting regions (ANOVA two-factor with replication, $F_{6,\,252} = 130927$, $p < 0.0001$). Over the four years simulated, pelagic recruitment success was highest for Veracruz, Rancho Nuevo and South Campeche. Paired t-tests revealed no significant difference between Veracruz and Rancho Nuevo ($p = 0.072$) or Rancho Nuevo and South Campeche ($p = 0.489$), although pelagic recruitment success was significantly higher for turtles from Veracruz than for turtles from South Campeche ($p < 0.0001$). From other regions, approximately an order of magnitude fewer simulated Kemp's ridley reached pelagic waters within four days (Table 2.1, Fig. 2.2).

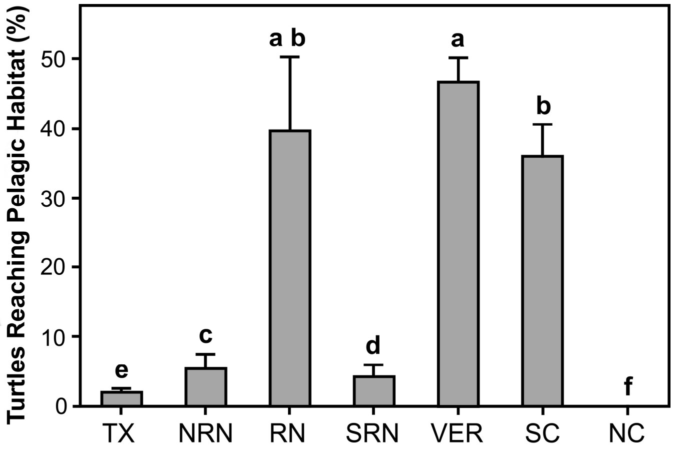

Figure 2.2 Graph of the mean percentage of simulated Kemp's ridley hatchlings from each nesting region that reach pelagic habitat (water deeper than 200 m) within four days. Nesting regions indicated on the horizontal axis correspond to the abbreviations in Figure 1. Error bars represent the 95% C.I. of the mean. Bars marked by different letters are significantly different (paired t-test, two-tailed, $p < 0.05$) whereas bars marked by the same letter do not differ significantly.

The mean number of turtles reaching foraging grounds within two years was significantly different among nesting regions (ANOVA two-factor with replication, $F_{6,\,252} = 16890$, $p < 0.0001$). The regions with the highest percentage of turtles entering foraging grounds were South Campeche, Rancho Nuevo, and Veracruz. Paired t-tests revealed no significant difference between South Campeche and Rancho Nuevo ($p = 0.105$). However, turtles from South Campeche and Rancho Nuevo had significantly higher recruitment success than did turtles from Veracruz ($p < 0.001$, $p = 0.023$ respectively). All other regions had significantly lower recruitment success than these three ($p < 0.001$ for each comparison) (Table 2.1, Fig. 2.3).

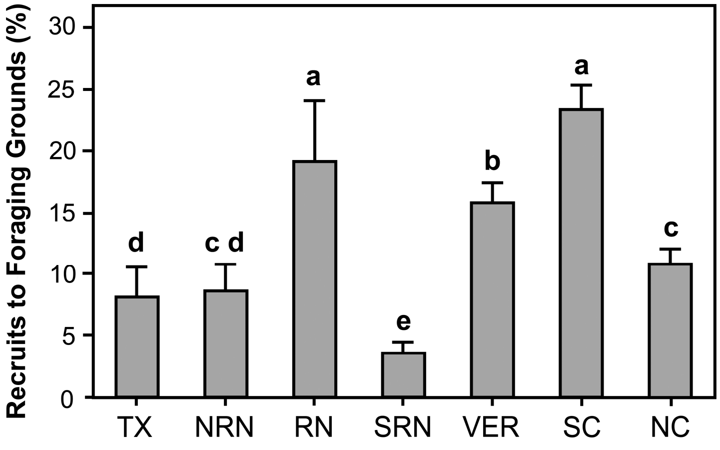

Figure 2.3 Graph of the mean percentage of simulated Kemp's ridley hatchlings that recruit to coastal foraging grounds within 2 years. Conventions as in Figure 2.

Table 2.1 Mean percentage of simulated turtles that reach pelagic habitat within four days and recruit to foraging grounds within two years. Results are given for each year and for each nesting region and are based on ten replicates for each year (see Methods for details). Numbers in italics indicate the 95% C.I. for the mean.

Year	**Texas**	**North RN**	**Rancho Nuevo**	**South RN**	**Veracruz**	**South Campeche**	**North Campeche**
2004 Pelagic Habitat	1.58% *(0.08%)*	12.94% *(0.23%)*	35.06% *(0.28%)*	8.09% *(0.19%)*	57.84% *(0.45%)*	52.15% *(0.33%)*	0.0% *(0.0%)*
2004 Foraging Grounds	3.55% *(0.22%)*	7.87% *(0.18%)*	22.53% *(0.22%)*	2.93% *(0.17%)*	14.65% *(0.22%)*	18.79% *(0.43%)*	8.35% *(0.18%)*
2005 Pelagic Habitat	2.93% *(0.10%)*	4.98% *(0.17%)*	58.60% *(0.33%)*	1.43% *(0.12%)*	50.20% *(0.51%)*	23.66% *(0.32%)*	0.0% *(0.0%)*
2005 Foraging Grounds	3.74% *(0.19%)*	11.27% *(0.28%)*	18.19% *(0.30)*	3.55% *(0.17%)*	17.50% *(0.22%)*	20.62% *(0.30%)*	14.27% *(0.30%)*
2006 Pelagic Habitat	1.86% *(0.11%)*	0.0% *(0.0%)*	0.0% *(0.0%)*	0.0% *(0.0%)*	36.55% *(0.34%)*	41.62% *(0.35%)*	0.0% *(0.0%)*
2006 Foraging Grounds	8.72% *(0.20%)*	0.09% *(0.03%)*	1.73% *(0.09%)*	0.55% *(0.07%)*	11.11% *(0.27%)*	31.27% *(0.41%)*	12.74% *(0.22%)*
2007 Pelagic Habitat	2.37% *(0.07%)*	4.07% *(0.19%)*	65.67% *(0.39%)*	7.78% *(0.24%)*	42.83% *(0.47%)*	26.51% *(0.33%)*	0.0% *(0.0%)*
2007 Foraging Grounds	17.02% *(0.32%)*	15.17% *(0.25%)*	34.56% *(0.20%)*	7.29% *(0.17%)*	20.51% *(0.25%)*	22.82% *(0.25%)*	7.98% *(0.22%)*
Mean Pelagic Habitat	**2.18%** ***(0.17%)***	**5.50%** ***(1.52%)***	**39.83%** ***(8.30%)***	**4.33%** ***(1.18%)***	**46.86%** ***(2.59%)***	**35.99%** ***(3.75%)***	**0.0%** ***(0.0%)***
Mean Foraging Grounds	**8.26%** ***(1.77%)***	**8.60%** ***(1.80%)***	**19.25%** ***(3.81%)***	**3.58%** ***(0.78%)***	**15.94%** ***(1.13%)***	**23.37%** ***(1.55%)***	**10.83%** ***(0.89%)***

Paired t-tests for the two migratory metrics (mean recruitment to pelagic habitat and coastal foraging grounds) and subsequent ranking of the seven nesting regions revealed that, for the four years modeled, Rancho Nuevo best facilitated the migration of the turtles. Rancho Nuevo was followed closely by South Campeche and Veracruz whereas North of Rancho Nuevo, Texas, North Campeche, and South of Rancho Nuevo were considerably worse in facilitating the migration (Table 2.2, Fig. 2.4).

Table 2.2 Relative migratory success by nesting region. Nesting regions are ranked relative to one another from high (1) to low (7) for each metric used to measure migratory success (percentage of turtles that reach pelagic habitat within four days and percentage of turtles that reach foraging grounds within two years). See text for details. The overall migratory rank of a region (determined by the mean of ranks) is in the fourth column. The final column provides the range of recent estimates of nest abundance (Read et al. 2010).

Nesting Region	Reach Pelagic Habitat	Reach Foraging Grounds	Overall Relative Migratory Success (Mean)	Estimate of Nest Abundance
Rancho Nuevo	1	1	1	3200 – 16000
South Campeche	1.5	1	1.25	1 – 25
Veracruz	1	3	2	728 – 3675
North RN	4	4	4	0 – 0
Texas	6	4.5	5.25	55 – 325
North Campeche	7	4	5.5	0 – 0
South RN	5	7	6	201 – 1025

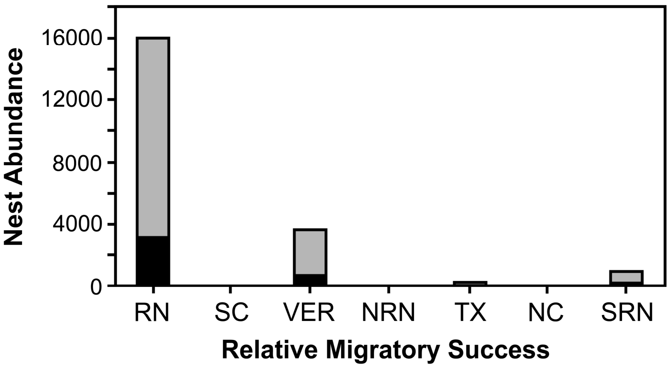

Figure 2.4 Bar graph showing estimated nest abundance for each nesting region. Nesting regions are ordered from left to right based on the degree to which oceanic conditions facilitate the migration of young Kemp's ridleys (Table 2.2) (see text for details). The region with the most favorable conditions is on the far left and the region with the least favorable conditions is on the far right. Abbreviations of nesting regions correspond to Figure 1. Nest abundance is taken from Read et al. (2010) with the minimum estimated nest abundance of a region in black and maximum estimated nest abundance in grey.

Nesting regions had significant differences in the percentage of simulated Kemp's ridley that recruited to the five defined foraging grounds (ANOVA two-factor with replication $F_{4, 180} > 20000$, $p < 0.0001$, for each nesting region). Out of all the simulated turtles that reached coastal foraging grounds (regardless of the location from which they started), the largest percentage recruited to coastal Texas (52.8 %), followed by Louisiana to W Florida (33.9 %), East Florida to North Carolina (12.9 %), Virginia to Nova Scotia (0.3 %), and Campeche Bay (<0.1 %). Table 2.3 provides the distribution of Kemp's ridley recruits by nesting region.

Table 2.3 Mean percentages of simulated turtles that recruit to foraging grounds (columns) when starting from different nesting regions (rows). Means are based on simulations of four two-year periods (2004-2006; 2005-2007; 2006-2008; 2007-2009). Italicized numbers below indicate the 95% C.I. of the mean.

Nesting Region	**Texas**	**Campeche Bay**	**LA – WFL**	**EFL – NC**	**VA – Nova Scotia**
Texas	5.140%	0.005%	2.462%	0.636%	0.016%
	(1.500%)	*(0.002%)*	*(0.373%)*	*(0.109)*	*(0.005%)*
North RN	4.207%	0.007%	2.781%	1.568%	0.038%
	(1.387%)	*(0.003%)*	*(0.526%)*	*(0.482%)*	*(0.014%)*
Rancho Nuevo	9.163%	0.016%	6.955%	3.037%	0.082%
	(2.790%)	*(0.007%)*	*(1.240%)*	*(0.822%)*	*(0.025%)*
South RN	1.877%	0.001%	1.153%	0.528%	0.014%
	(0.655%)	*(0.001%)*	*(0.187%)*	*(0.149%)*	*(0.006%)*
Veracruz	8.096%	0.024%	5.465%	2.311%	0.046%
	(1.330%)	*(0.009%)*	*(0.254%)*	*(0.612%)*	*(0.015%)*
South Campeche	12.669%	0.025%	8.161%	2.461%	0.058%
	(1.510%)	*(0.009%)*	*(0.866%)*	*(0.527%)*	*(0.021%)*
North Campeche	6.253	0.008%	3.508%	1.042%	0.023%
	(0.595%)	*(0.005%)*	*(0.382%)*	*(0.274%)*	*(0.008%)*

Discussion

Models of oceanic circulation indicate that the migratory success of young turtles (the percentage of simulated turtles that quickly reach pelagic waters and also successfully reach foraging grounds) is highly variable across the Kemp's ridley nesting range. Thus, from the standpoint of the ease with which young turtles are likely to complete their initial migration, the different regions of coastline are not equal.

This analysis has provided an initial exploration of the hypothesis that coastal areas where Kemp's ridley turtles nest in high numbers represent locations where offshore oceanographic conditions are favorable to the migration of hatchlings. The lack of standardized nest counts across the Kemp's ridley nesting range precludes a detailed quantitative analysis, but recent estimates of the numbers of nests in different geographic areas (Read et al. 2010) suggest that, in general, nesting is highest at locations with conditions that most effectively facilitate successful migration, whereas less nesting occurs in regions where successful migration is more difficult (Fig. 2.4, Table 2.2). The findings are consistent with the hypothesis that patterns of nest abundance are influenced, at least in part, by oceanographic conditions that facilitate or impede the migration of young turtles. Moreover, patterns of nest distribution are likely to be sustained over time by the natal homing of adults, inasmuch as nesting locations that facilitate the migration of young turtles to foraging grounds lead to increased survival of juveniles, which in turn leads to increased numbers of adults returning to the same nesting locations where they themselves began life.

Departures from the Predicted Pattern

Although oceanographic factors that facilitate migration may influence which nesting beaches are used, such factors by themselves are clearly insufficient to account fully for the present distribution of nesting in the Kemp's ridley. In at least two cases (South Campeche and South of Rancho Nuevo), the number of nests reported deviated from the predicted pattern. Interestingly, however, it is possible that special circumstances explain each departure.

According to the metrics used in the model, South Campeche possesses oceanographic conditions that facilitate both the offshore migration of young turtles and their subsequent movement to coastal foraging grounds. Nevertheless, this area has very little nesting. Evidence suggests, however, that the lack of nesting is a relatively recent development, and that a large population once existed in this area before it was nearly extirpated due to intense harvesting of adults and eggs by humans (Márquez 1994; Guzmán et al. 2007).

A second region that deviates from the predicted pattern is South of Rancho Nuevo. This area ranked among the worst in terms of metrics of migratory success and thus, according to predictions, few turtles should nest there. However, this area attracts the third highest number of nesting turtles. Clearly, additional or alternative factors must be important in shaping the pattern of nesting.

South of Rancho Nuevo is immediately adjacent to the largest nesting assemblage at Rancho Nuevo. An interesting speculation is that some nesting in this region might result from navigational errors by adult Kemp's ridley turtles attempting to return to Rancho Nuevo. If so, then it is unclear why the errors are asymmetrical, inasmuch as considerably more nesting occurs in the South of Rancho Nuevo area than in the North of Rancho Nuevo area. Conceivably, asymmetrical navigational errors might occur if turtles imprint on the magnetic field of the natal beach and then return to a slightly different location because the earth's field has shifted in their absence (Lohmann et al. 2008a). Indeed, geomagnetic modeling suggests that, over the past 400 years, adult Kemp's ridley turtles attempting to relocate Rancho Nuevo after a 10-15 year absence would arrive at Rancho Nuevo or slightly to the south if they imprinted on magnetic inclination angle (Putman and Lohmann 2008). Whether this occurs is not known.

Yearly variation in migratory success

In some of the geographic regions, migratory success was relatively constant across the time period of the analysis, but in other areas, it varied considerably from year to year (Table 2.1). In general, the nesting regions of Texas, Veracruz, South Campeche, and North Campeche had relatively constant percentages of recruitment for each of the four cohorts of hatchlings, both in terms of percentages reaching pelagic habitat and percentages reaching coastal feeding grounds. In contrast, year-to-year recruitment success was more variable at the central nesting regions (North of Rancho Nuevo, Rancho Nuevo, and South of Rancho Nuevo) (Fig. 2.5). Whether the observed temporal patterns are consistent features of the various regions is not known. Regardless, these findings suggest some promising avenues for future research.

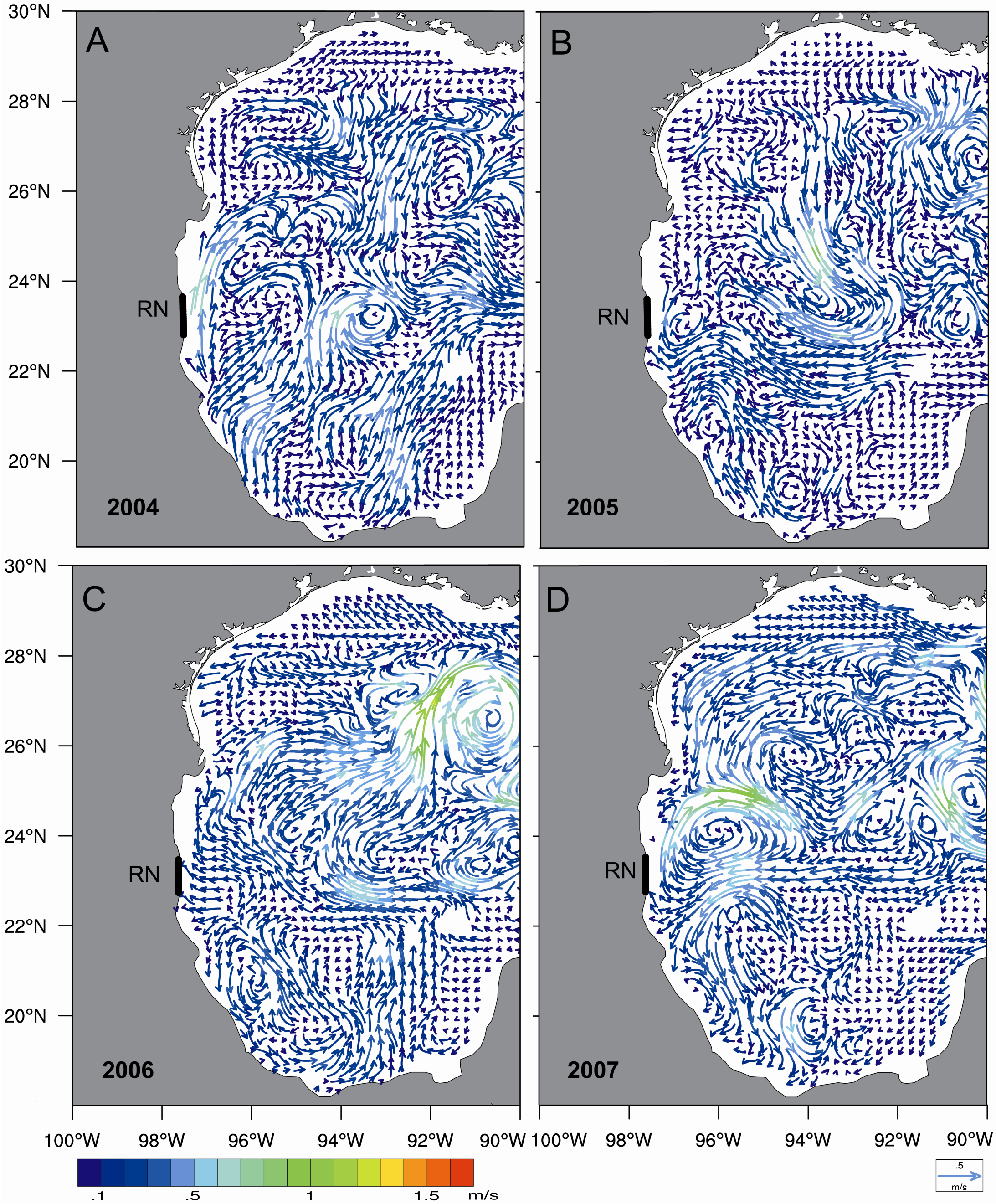

Figure 2.5 Surface current velocity in the Gulf of Mexico based on HYCOM output. The location of Rancho Nuevo is marked by the thick black line labeled "RN." Images show surface currents on June 1, the beginning of the Kemp's ridley hatching season, for the following years (A) 2004; (B) 2005; (C) 2006; and (D) 2007. Typical flow off the coast of Rancho Nuevo appears to be north-northeastward, which results in offshore transport of hatchlings (A, B, D). The year in which the largest percentage of turtles reached pelagic habitat and foraging grounds was 2007. During this period, there was a well developed anti-cyclonic eddy immediately offshore of Rancho Nuevo that resulted in strong seaward movement of simulated hatchlings (D). In contrast, the fewest turtles reached pelagic habitat and foraging grounds in 2006. Westward flow opposed the offshore movement of simulated hatchlings from Rancho Nuevo, which led to very few of the passively drifting particles reaching pelagic habitat (C).

For instance, averaged over the four periods simulated, the regions of Rancho Nuevo, South Campeche, and Veracruz all had similar high recruitment success to pelagic habitat and to foraging grounds. However, recruitment success in different periods was not constant. During certain periods of limited duration, oceanic currents at Rancho Nuevo transported exceedingly large numbers of young turtles offshore and subsequently to foraging grounds (Table 2.1). The most favorable conditions occurred during the 2007-2009 simulation. During the 2007 hatching period, there was a well developed anti-cyclonic eddy directly offshore of Rancho Nuevo, resulting in strong offshore movement of simulated hatchlings (Fig. 2.5). In contrast, there was an unusually poor period for recruitment to pelagic habitat and foraging grounds during the 2006-2008 simulation. The oceanographic cause seems to have been a northward shift of a semi-permanent westward flowing current (Fig. 2.5). Typically, this current bifurcates to the south of Rancho Nuevo, resulting in north-northeastward flowing water transporting hatchlings offshore, but in 2006, this westward flow was centered at Rancho Nuevo, directly opposing offshore progress of turtles. In the model, this led to very few turtles reaching pelagic habitat because they were washed shoreward; the limited number of turtles reaching the open sea in turn led to fewer turtles recruiting to foraging grounds. It is possible that the frequency of oceanic conditions which facilitate or impede the offshore migration of hatchlings might be an important but previously overlooked factor in the population dynamics of the Kemp's ridley.

Modeled Distribution of Juvenile Kemp's Ridley

In addition to exploring a possible relationship between nesting distributions and surface currents, these results also provide insight into how currents might influence the distribution of young Kemp's ridley turtles across coastal areas. The model recorded which of the known foraging areas (Fig. 2.1) each simulated turtle encountered first (see Materials and Methods). The results provide a preliminary indication of the geographic locations to which juvenile turtles may be most likely to recruit (Table 2.3).

The vast majority of Kemp's ridley hatchlings originate at Rancho Nuevo (Márquez 1994; Plotkin 2007; Read et al. 2010). Discussion will therefore be limited to the simulation involving this nesting region. Because the defined coastal foraging grounds (Fig. 2.1) vary in length from 490-1650 km, measures of recruitment are standardized by calculating, for each of the five regions, the percentage of turtles that recruited per 100 km of continental shelf length (Fig. 2.6).

Simulated turtles from Rancho Nuevo most commonly reached the coastal waters of Texas (9.2% of the total simulated turtles; 0.99% per 100 km of continental shelf). Fewer simulated turtles reached other known foraging areas, including: Louisiana-West Florida (7.0% of the total; 0.58% per 100 km); East Florida-North Carolina (3.0% of the total; 0.20% per 100 km); Virginia-Nova Scotia (0.08% of total; 0.005% per 100 km); and Campeche Bay (0.02% of total; 0.003% per 100 km).

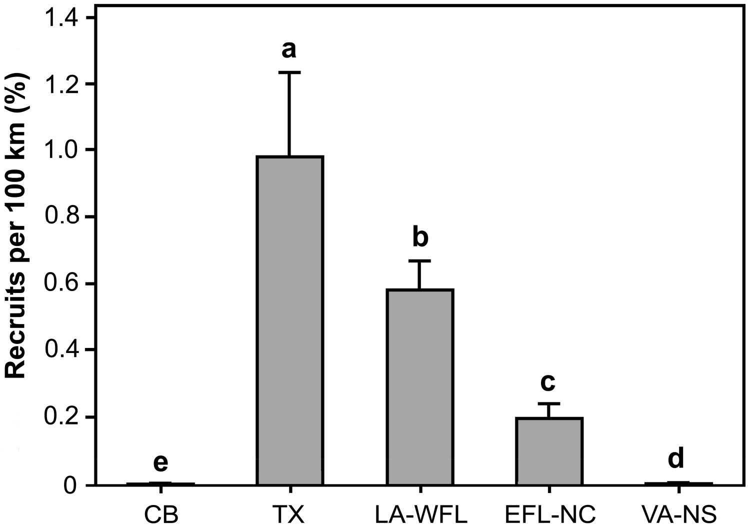

Figure 2.6 Graph of the mean percentage of simulated Kemp's ridley hatchlings from Rancho Nuevo that recruit to the five regions of Fig. 2.1. Recruitment were standardized by calculating the percentage of turtles that recruited per 100 km of continental shelf length along each of the five regions. Abbreviations correspond to Fig. 1. Error bars represent the 95% C.I. of the mean. Bars marked by different letters are significantly different (paired t-test, two-tailed, $p < 0.05$).

These results are consistent with a descriptive study by Collard and Ogren (1990), which indicated that turtles embarking on their migration from Rancho Nuevo would typically be transported offshore and to coastal locations along the Gulf and Atlantic coasts of the U.S. These findings also appear consistent with the numerous accounts of juvenile Kemp's ridley turtles inhabiting coastal waters of the southeastern U.S. (Carr 1957; Hildebrand 1982; Ogren 1989; Metz 2004; Geis et al. 2005). That ocean currents do not carry many Kemp's ridley from Rancho Nuevo to

Campeche Bay may also help explain why no juvenile turtles have been found there, despite seemingly suitable habitat (Carr 1980; Márquez 1994).

Implications for Conservation

These findings are consistent with the hypothesis that patterns of nest abundance for sea turtles are strongly influenced by oceanic conditions that promote or impede the successful migration of young turtles. Such considerations have important implications for conservation efforts. For example, in a program begun about 30 years ago, approximately 24,000 Kemp's ridley eggs and hatchlings were relocated from Rancho Nuevo to Texas (Márquez et al. 2003, Shaver and Wibbels 2007). The goal was to establish a second area where the turtles nest and thus avert the possibility of a population collapse. Although there has been much debate on the merits of this project, it is now apparent that at least some of these "head-started" turtles are returning to Texas to nest (Shaver and Wibbels 2007). The findings here, however, suggest that conditions off the Texas coast are relatively poor in terms of facilitating the migration of young turtles (Figs. 2.2, 2.3), which might make it difficult for a large population to become established. Although protecting Kemp's ridley nesting across Texas is certainly important to aid in the conservation of this critically endangered species, without concurrent protection of the Rancho Nuevo and Veracruz regions (which allow for high migratory success and presently have high abundance of nests), the efforts in Texas may be of limited value.

Additionally, attempts to predict the impact of climate change on sea-turtles' nesting distribution may benefit from a consideration of the migratory requirements of young sea turtles, integrated with previously studied factors such as beach temperatures and coastal substrate. Furthermore, the oceanographic modeling approach used in this study might be useful for predicting the distribution of hatchling and juvenile stages of other species of sea turtles.

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Sea turtle nesting distributions and oceanographic constraints on hatchling migration

Summary

Patterns of abundance across a species' 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 favor 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 toward investigating this conceptual framework loggerhead sea turtle (*Caretta caretta*) nest abundance along the southeastern U.S. coast was analyzed 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% of spatial variation in regional nest density. Even at smaller spatial scales, where local beach conditions presumably exert strong effects, at least 38% of the variance is explained by distance from the GSS. These findings suggest that proximity to favorable 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.

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 favoring 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 favorable 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 promote the use of reproductive areas in which environmental conditions facilitate migration. This hypothesis is examined for the nesting distribution of an iconic long-distance migrant, the loggerhead sea turtle (*Caretta caretta*).

The loggerhead turtle has an itinerant lifestyle comprising a series of migrations (Carr 1987). Along the southeastern United States coast, young loggerheads emerge from nests deposited on sandy beaches and then migrate offshore to the Gulf Stream System, 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 behavioral pattern known as natal homing (Bowen & Karl 2007; Lohmann et al. 2008a).

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. 2010a). 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 nearshore areas are subjected to intense predation (Whelan & Wyneken 2007).

Given these considerations, hatchlings that emerge on beaches close to the Gulf Stream System 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 toward investigating whether constraints on the hatchling migration shape patterns of nest abundance, regression analyses were performed to determine whether the distance that hatchlings must travel to reach the Gulf Stream System predicts nest distribution at regional and local scales.

Methods

Regional-scale Analysis of Loggerhead Nest Density

For purposes of analysis, the nesting range of loggerheads in the southeastern U.S. was partitioned into 10 regions that correspond to geographic 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: (1) Texas; (2) Louisiana and Mississippi, (3) Alabama through the western panhandle of Florida (from Alabama to Franklin County, Florida); (4) northwestern Florida (Wakulla to Pasco County) and (5) southwestern Florida (Pinellas to Monroe County). Along the Atlantic Ocean, the regions were: (6) southeastern Florida (from Miami to Cape Canaveral); (7) northeastern Florida (from Cape Canaveral to the northern border of Florida); (8) Georgia; (9) South Carolina; and (10) North Carolina. The length of coastline for these 10 regions ranged from 154-700 km (Fig. 2.7, Table 2.4).

At this regional scale, loggerhead nesting data were obtained from two sources which 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 Species Recovery Plan for the Atlantic Loggerhead (NMFS & USFWS 1991). This provided the highest and lowest nesting totals for all U.S. beaches that reported at least 100 loggerhead nests between 1985 and 1990. To obtain a single value of nest density (nests per km 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 (Table 2.4).

A second, independent analysis was done using the State of the World's Sea Turtles (SWOT Report, Vol. II) (Mast et al. 2007), which compiled nesting data for 2005 from agencies responsible for monitoring sea turtle nesting (Dodd & Mackinnon 2005; FFWCC-FWRI 2007a; 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 km surveyed) within each of the 10 geographic regions (Table 2.4).

Table 2.4 Regional scale data from loggerhead nesting range along the southeast U.SA.

Geographic Area	**Average Nests km^{-1} (1985-1990)**	**Total Nests km^{-1} (2005)**	**Coastline Length (km)**	**Average Latitude (°)**	**Average Dist. to GSS (km)**
Texas	0.0	0.005	590	27.7	940
La/Ms	0.0	0.0	700	30.2	504
Al/Panhandle Fl	0.0	1.4	452	30.0	450
Northwest Florida	0.0	0.0	380	29.2	410
Southwest Florida	22.7	11.9	332	26.5	250
Southeast Florida	177.2	131.5	331	27.0	29
Northeast Florida	49.7	16.9	252	29.5	100
Georgia	7.8	7.8	154	31.5	164
South Carolina	25.2	17	240	33.0	150
North Carolina	9.7	1.3	500	34.5	109

Local-scale Analysis of Nest Density

For local-scale analysis, the average number of loggerhead nests per year from coastal Florida counties (n = 27) between 1990 and 2006 (FFWCC-FWRI 2007b) was calculated. 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^{TM} software). The range of coastline lengths among counties was 18-140 km (Table 2.5).

Table 2.5 Local (county) scale data from loggerhead nesting range along Florida, U.S.A.

Florida County	Average Nests km^{-1} (1990-2006)	Beach Length (km)	Latitude (°)	Dist. to GSS (km)
Escambia	2.3	18.0	30.30	480
Santa Rosa	0.2	48.0	30.39	482
Okaloosa	0.6	40.0	30.39	485
Walton	0.91	40.5	30.26	475
Bay	1.1	80.0	30.1	460
Gulf	2.7	105.0	29.68	410
Franklin	2.9	100.0	29.58	397
Pinellas	2.9	64.6	27.86	272
Hillsborough	1.2	30.0	27.57	275
Manatee	6.5	40.0	27.38	250
Sarasota	49.7	54.5	27.18	250
Charlotte	27.5	27.0	26.81	252
Lee	9.3	68.0	26.45	250
Collier	9.8	90.0	26.00	280
Monroe	2.0	111.0	25.50	60
Miami-Dade	3.0	140.0	25.62	22
Broward	59.0	38.6	26.23	18
Palm Beach	173.7	73.0	26.72	18
Martin	254.8	34.0	27.10	22
St. Lucie	146.6	34.7	27.40	29
Indian River	92.9	37.0	27.74	40
Brevard	229.5	113.6	28.45	47
Volusia	22.2	78.6	29.20	76
Flagler	8.9	28.6	29.55	102
St. Johns	3.8	66.7	29.93	124
Duval	2.4	27.5	30.40	145
Nassau	4.5	20.6	30.63	145

Gulf Stream System

The Gulf Stream System 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 U.S. (Fig. 2.7). The part of the Gulf Stream System 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 portion of 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, Canada and eventually eastward towards northwestern Europe, thus forming the northern portion of the North Atlantic Subtropical

Gyre (Auer 1987). Together, the Loop Current and Gulf Stream are referred to as the Gulf Stream System (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 not 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 shoreward or seaward of its average position during loggerhead nesting season.

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 analysis, the average position of the shoreward edge of the Loop Current, as described in Sturges (1992), and the average position of shoreward edge of the Gulf Stream, as described in Olson et al. (1983) were superimposed on maps from Google Earth. 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 center of each Florida county to the GSS. In both cases, distance was measured to the nearest kilometer.

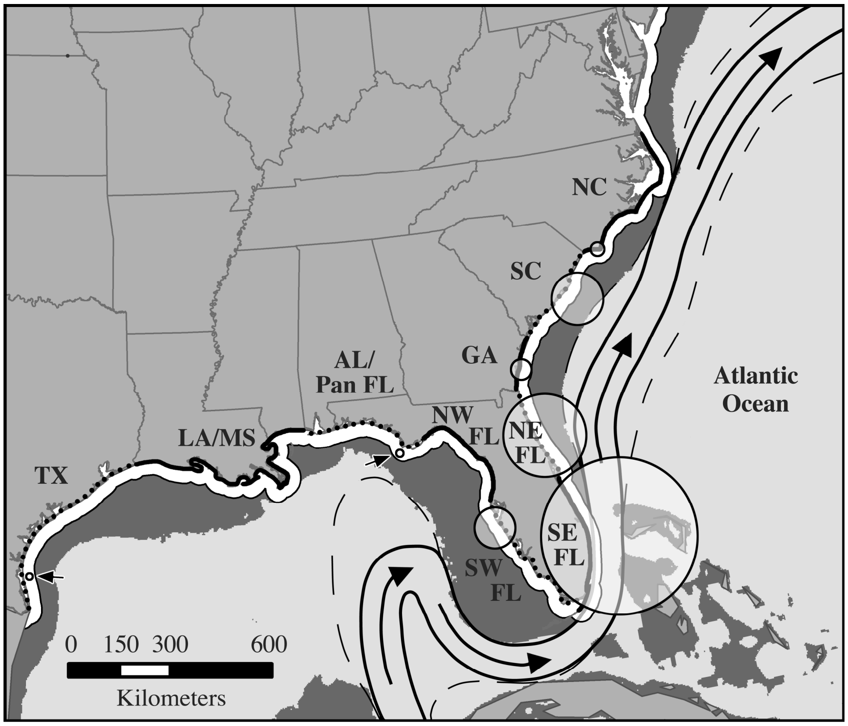

Figure 2.7 Map of loggerhead nesting range along the southeastern U.S. coastline. Alternating solid and hashed black lines along the coast delineate the stretches of beach used for the regional analysis. The regions include Texas (TX), Louisiana and Mississippi (LA / MS), Alabama and the panhandle of 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 Texas nest density are not to scale). Circles are centered 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 gray 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.

Latitude

An additional analysis investigated whether nest density was correlated with latitude, which co-varies 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 center of each Florida county.

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 nest density of an area was expected 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 due to effects mediated by temperature (Mrosovsky 1994). A multiple regression analysis was performed which 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) due to differences between survey methods. The analyses were also carried out for Florida counties (1990-2006).

Results

Regression analyses (summarized in Table 2.6) indicated that, as the distance to the GSS increased, loggerhead nest density decreased (Fig. 2.8). This pattern held for both of the regional datasets (for NOAA dataset (1985-1990), $r^2 = 0.96$, $p < 0.001$, $n = 10$; for SWOT dataset (2005), $r^2 = 0.94$, $p < 0.001$, $n = 10$). 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 to the analyses using distance to the GSS alone (Table 2.6).

Table 2.6 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. 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	<0.001
NOAA (1985-1990)	10	$n = 7797L^{-1}- 233$	Latitude	0.16	0.06	2	0.248
NOAA (1985-1990)	10	$n = 3390^{-1}+ 5173D^{-1} -125$	Latitude + GSS Dist	0.98	0.98	212	<0.001
SWOT (2005)	10	$n = 3962D^{-1}- 12.1$	GSS Dist	0.94	0.93	123	<0.001
SWOT (2005)	10	$n = 5893L^{-1}- 179$	Latitude	0.17	0.06	2	0.236
SWOT (2005)	10	$n = 2676L^{-1}+ 3775D^{-1} -101$	Latitude + GSS Dist	0.97	0.96	120	<0.001
Florida Counties (1990-2006)	27	$n = 3622 D^{-1}+ 4.4$	GSS Dist	0.46	0.43	21	<0.001
Florida Counties (1990-2006)	27	$n = 11709L^{-1}- 368$	Latitude	0.07	0.04	2	0.171
Florida Counties (1990-2006)	27	$n = 5172L^{-1}+ 3695D^{-1} + 174$	Latitude + GSS Dist	0.47	0.42	10	0.001

Variance partitioning analyses also indicated that distance to the GSS robustly predicted nest density (Fig. 2.9). For the two regional datasets, distance to the GSS alone accounted for 92% (for NOAA dataset (1985-1990)) and 90% (for SWOT dataset (2005)) of the variation in nest density. Latitude accounted for 3% of the variation in nest density and the interaction between distance to the GSS and latitude accounted for 3% (for both datasets). Across Florida counties (1990-2006), distance to the GSS alone accounted for 38% of the variation in nest density whereas latitude accounted for < 1% and the interaction between the GSS and latitude accounted for 5%.

Discussion

The results indicate that, along the southeastern U.S. coast, loggerhead nest density declines as the distance between the coast and the GSS increases. This pattern holds at both regional and local spatial scales. On a regional level, the distance to the GSS was able to account for more than 90% of the variation in nest density (Table 2.6, Figs. 2.8a, b, 2.9). On the smaller scale of Florida counties, distance to the GSS could account for at least 38% of the variation (Table 2.6, Figs. 2.8c, 2.9). 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.

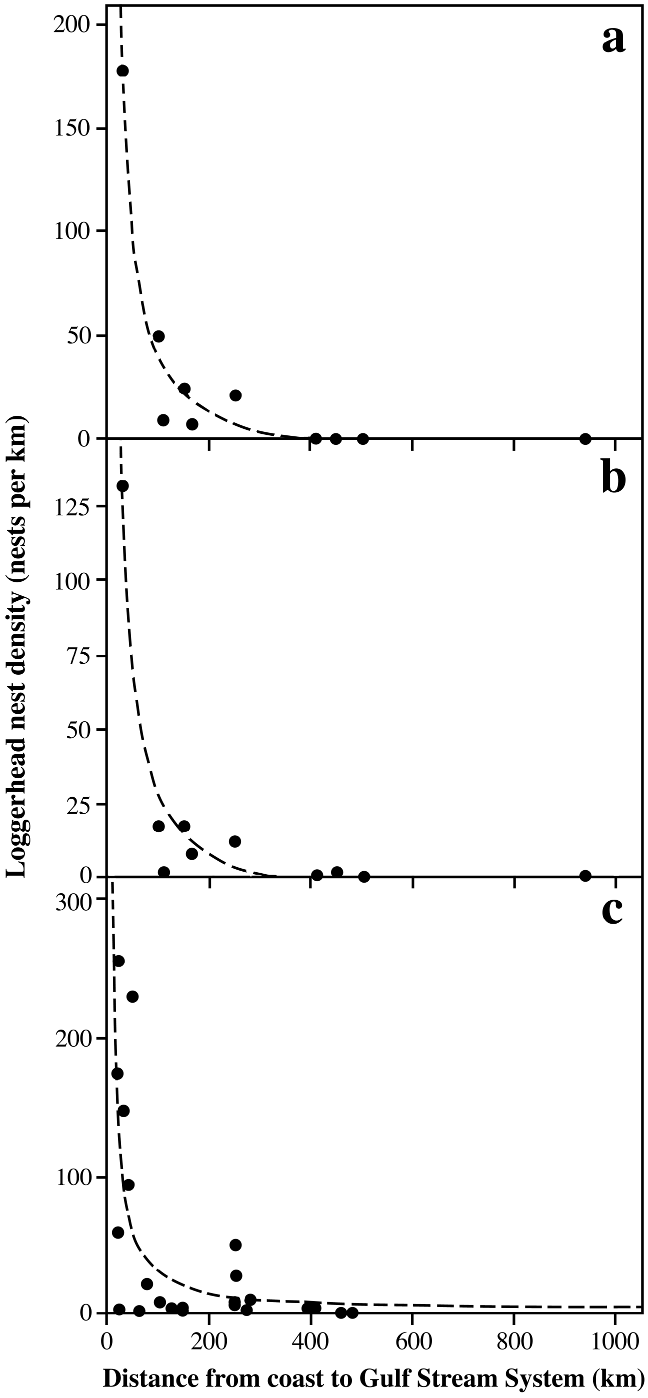

Figure 2.8 Graphs of loggerhead nest density plotted against distance from each nesting area to the GSS. Trend lines are estimated by regression. (a) Regional scale results using the NOAA 1985-1990 dataset. (b) Regional scale results using the SWOT 2005 dataset. (c) Local scale results using nesting data from Florida counties for 1990-2006. See text for details.

Offshore Migration of Hatchlings

Immediately after emerging from underground nests, hatchling loggerheads scramble to the ocean and migrate 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 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 (Fig. 2.7). In such cases, however, whether hatchlings succeed may be influenced greatly by factors specific to each situation. Among these are nearshore 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 behavior or physiology that are uniquely suited to particular geographic 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).

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 geographic 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 nighttime 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 U.S. 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.

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 2.6, Fig. 2.9). With hindsight, this finding is perhaps not surprising in view of the fact that nest temperature can vary greatly over several meters (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.

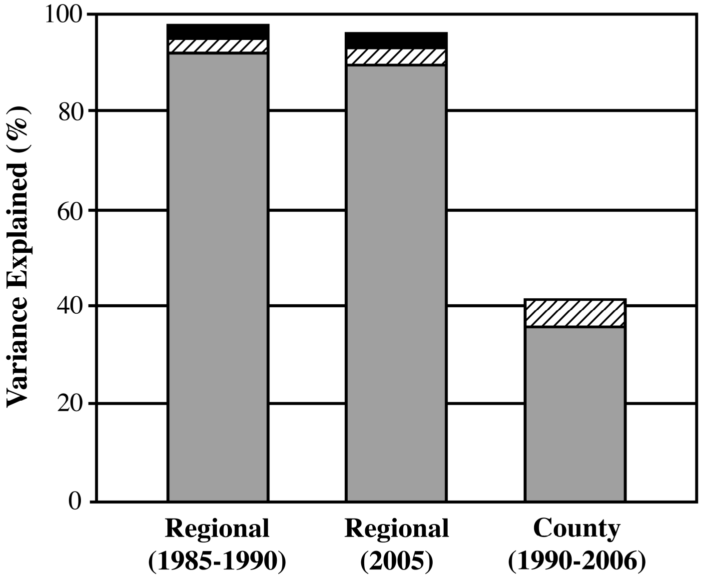

Figure 2.9 The partitioning of variance of nest density of southeastern U.S. loggerhead sea turtles by dataset into effects of: (1) distance from nesting area to the GSS (gray); (2) nesting area latitude (black); and (3) variance explained by some combination of the two factors that cannot be uniquely ascribed to either (hashed).

Conclusions

These 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 U.S. Other loggerhead nesting areas have not been analyzed 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). The findings presented here might be directly applicable to these and other sea turtle populations. Moreover, the principles outlined in the study may prove helpful in understanding the geographic 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).

Special Thanks

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Citation

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CHAPTER 3

THE PELAGIC MIGRATION OF JUVENILE SEA TURTLES

The pelagic migration of juvenile loggerhead turtles is one of the longest documented migrations of any marine animal. The loggerheads that emerge on beaches along the southeastern United States coast migrate eastward to the North Atlantic Subtropical Gyre. Turtles remain within the gyre for a period of years, during which they gradually migrate around the Atlantic before returning to the North American coast (Lohmann et al.1999). It was once assumed that turtles drifted passively and that the distribution of young loggerheads was entirely dependent on ocean currents (Carr 1987). More recently, experiments have demonstrated that hatchling loggerheads, when exposed to magnetic fields replicating those found in three widely separated oceanic locations, respond by swimming in directions that would help keep them within the currents of the North Atlantic Subtropical Gyre and facilitate movement along the migratory pathway (Lohmann et al. 2001). These results imply that young loggerheads possess the ability to assess their geographic position (i.e. use the magnetic field as a kind of "map").

Animals capable of detecting certain magnetic parameters (e.g. intensity and the angle of field lines relative to the earth's surface) can assess their geographic position due to the positional information inherent in the main-dipole field (Fig. 3.1). How turtles (and other animals) organize magnetic information into a "map," however, is poorly understood.

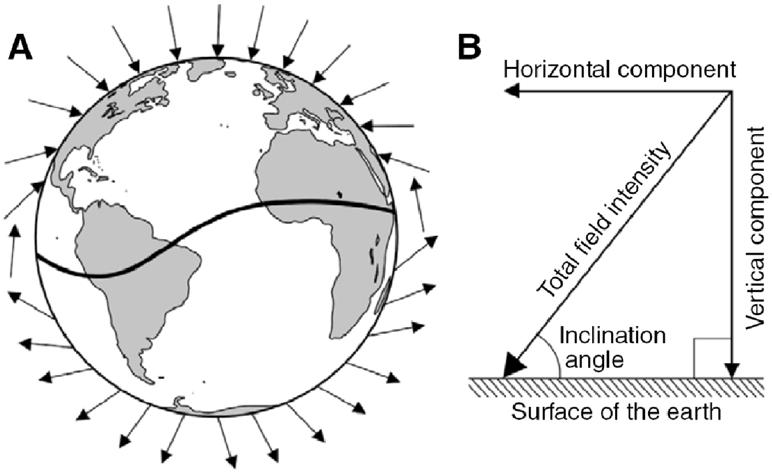

Figure 3.1 Representations of the earth's magnetic field (Lohmann et al. 2007) The movement of the liquid outer core generates a self-exciting dynamo which produces the earth's main-dipole magnetic. The two poles of this magnetic field correspond, approximately, to the location of the geographic north and south poles. Field lines exit the southern hemisphere and reenter the northern hemisphere and the related magnetic parameters vary systematically from the poles to the equator. This results in inherent positional information in the main-dipole field. (A) Diagrammatic representation of the Earth's magnetic field illustrating how field lines (represented by arrows) intersect the Earth's surface, and how inclination angle (the angle formed between the field lines and the Earth) varies with latitude. At the magnetic South Pole, field lines are directed away from the earth, perpendicular to its surface. The field lines become progressively less steep as one travels towards the magnetic equator (the thick curving line across the Earth), where the inclination angle is 0°. Then, moving from the equator towards the magnetic North Pole, field lines are directed down into the Earth and become progressively steeper until the field lines are directed straight down into the Earth and the inclination angle is 90°. (B) Diagram illustrating four elements of geomagnetic field vectors that might, in principle, provide animals with positional information. The field present at each location on Earth can be described in terms of a total field intensity and an inclination angle. The total intensity of the field can be resolved into two vector components: the horizontal field intensity and the vertical field intensity. Sea turtles have been shown to detect total field intensity and inclination angle. Whether they (or other animals) are able of resolve the total field into vector components, however, is not known.

In this chapter I present data from several experiments in which the orientation behavior of hatchling sea turtles was monitored as they were presented with magnetic fields that exist along their migratory route. Additionally, I use a high-resolution ocean circulation model and particle tracking software to simulate magnetic navigation by young turtles to assess how this behavior shapes the distribution of turtles in the open-ocean. Additionally, I synthesize the findings from the behavioral assays into a framework that explains the nature of the turtle magnetic map as well as the selective pressures that maintain it.

Exploring the geospatial organization of the magnetic map of hatchling loggerhead sea turtles

Summary

Hatchling loggerhead sea turtles (*Caretta caretta*) from eastern Florida undertake a transoceanic migration in which they gradually circle the North Atlantic Ocean before returning to the North American coast. During this migration, magnetic fields that exist at widely separated geographic areas appear to function as navigational markers, eliciting changes in the turtles' swimming directions at crucial geographic boundaries. In principle, nearly all locations along the migratory route can be assigned to one of three geomagnetic regions: (1) the northwest Atlantic where both inclination angle and intensity of the field are greater relative to values at the home beach in Florida; (2) the northeast Atlantic where the inclination is greater but the intensity is less; (3) the southern Atlantic where both inclination and intensity are less than values at the home beach. To test the hypothesis that the geospatial organization of the loggerhead "magnetic map" consists of these three large magnetic regions, hatchlings were exposed to magnetic fields that do not exist in nature but which match the magnetic criteria of the three regions that are described above. In two of the three treatments the orientation of hatchlings was difficult to reconcile with the migratory route over the oceanic region where such fields exist. These findings imply that the magnetic map of hatchling loggerheads is not solely organized around an algorithm of enhanced or diminished intensity and inclination; at a minimum, the magnitude of field change is likely incorporated into the geospatial organization of their magnetic map.

Introduction

Diverse migratory animals such as sea turtles, lobsters and newts use "magnetic maps" to navigate (Lohmann et al. 2004; Boles & Lohmann 2003; Fischer et al. 2001). Specifically, they rely on the Earth's magnetic field to assess their geographic position (Lohmann et al. 2007). Elements of the geomagnetic field vary predictably across the surface of the earth. In most parts of the world the inclination angle (the angle at which field lines intersect the earth's surface) steepens and the total field intensity (the strength of the field) strengthens poleward. In its simplest form, a magnetic map might provide geospatial information based entirely on whether detected magnetic field elements were increased or decreased relative to a goal field. For example, a migrating animal that encounters a steeper inclination angle and stronger intensity than the field at its geographic goal could know that it was poleward of its goal and must therefore orient equatorward. Likewise, if it encountered a less steep inclination angle and a weaker intensity than the field marking its goal, the animal could know it was equatorward of its goal and should orient poleward. In such a case, the geospatial organization of the animal's magnetic map is to place all locations into one of two regions relative to its goal magnetic field: a poleward region and an equatorward region. Alternatively, an animal could learn or inherit a magnetic map that allows for a more precise assessment of its geographic location along its migratory route by taking into account the magnitude as well as direction of field change.

Few experiments have been designed to characterize the geospatial organization of magnetic maps (Lohmann et al. 2007). Thus it is unknown whether most animals use magnetic information in a simple, "directional" way of determining position or whether magnetic maps are more spatially complex (e.g., incorporate the magnitude of field parameters). Here, this first possibility is examined for the hatchling loggerhead sea turtles (*Caretta caretta*), a species with a well-established magnetic map sense.

Loggerhead hatchlings from the east coast of Florida, U.S.A. migrate offshore and are transported by the Gulf Stream northward and then eastward across the North Atlantic Ocean (Carr 1987; Bolten 2003). Loggerheads remain in the circular current system of the North Atlantic Subtropical Gyre for 5 to 10 years before returning to their natal coast (Bjorndal et al. 2000a; Bowen & Karl 2007).

In principle, the loggerhead's pelagic migratory route can be organized into three geomagnetic regions: (1) the northwest Atlantic where both inclination angle and intensity of the field are increased relative to values at the home beach in Florida, (2) the northeast Atlantic where the inclination is increased but the intensity decreased, and (3) the southern Atlantic where both inclination and intensity are decreased (Fig. 3.2). Lohmann et al. (2001) presented hatchling loggerheads with specific pairings of inclination and intensity that occur within these three magnetic regions. When exposed to these fields, turtles swam in directions that would facilitate their pelagic migration had they actually been in the location that was simulated (Lohmann et al. 2001). However, from this experiment it is unclear whether the magnetic map is geospatially organized in a simple way that only considers the change in field parameters relative to the home beach or whether they inherit more detailed magnetic information to assess their position along their migratory route.

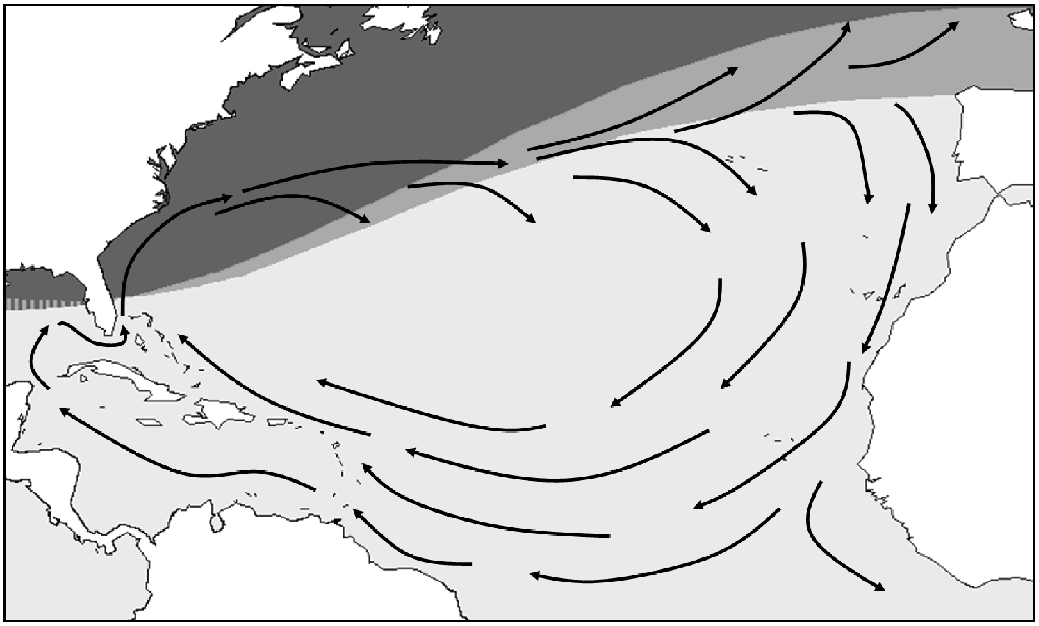

Figure 3.2 Hypothetical geospatial organization of the magnetic map of loggerhead sea turtles. The map assumes loggerheads from Florida U.S.A. calibrate their responses to magnetic fields based on the intensity and inclination angle at their home beach. The isoline of intensity at their home beach bends more northwards across their migratory route than the isoline of inclination angle; thus the loggerhead pelagic migratory route can be divided into three magnetic regions relative to the home-beach in Florida: (1) the northwest region where inclination angle is steeper and intensity is stronger (dark gray), (2) the northeast region where inclination angle is steeper and intensity is weaker (medium gray), and (3) the southern region where inclination angle is less steep and intensity is weaker (light gray). Arrows indicate the direction of surface currents of the North Atlantic Subtropical Gyre (after Tomczac & Godfrey 1994). Experiments by Lohmann et al. (2001) suggest that magnetic fields resembling those that occur in the dark gray area elicit east-southeastward orientation by turtles, fields associated with the area in medium gray elicit southward orientation, and fields that resemble those found in the light gray area result in west-northwestward orientation.

To test the hypothesis that hatchling loggerheads inherit a simple, “directional” magnetic map, turtles were exposed to one of three magnetic fields that correspond to the magnetic regions of their pelagic migratory route. The specific pairings of inclination angle and intensity used in this study do not presently occur in the North Atlantic to avoid the possibility that turtles had evolved a response to a specific field. However, the values of each element are within the range that loggerheads have responded to in previous experiments (Lohmann & Lohmann 1994, 1996; Lohmann et al. 2001). Thus, if the magnetic map is organized to only take into account whether inclination angle and intensity are higher or lower than the field of their home beach, turtles should swim the same direction as the corresponding treatment of the experiment by Lohmann et al. (2001). However, if the magnetic map also relies on the magnitude of field, turtles might be disoriented or misoriented when exposed to these fields.

Methods

Animals

Hatchling loggerheads were obtained from Melbourne Beach, Florida, U.S.A. Nests were checked daily from early July through mid-August based on the predicted date of emergence. In the late afternoon, a few hours before the turtles would otherwise have emerged, 15 to 30 hatchlings were gently removed from their nest. Turtles were immediately placed in lightproof Styrofoam coolers and transported to a nearby facility for experimentation. Hatchlings were maintained outside in the local ambient magnetic field and in darkness. Each hatchling was tested once that night and then released.

Orientation Tank and Data Acquisition

Hatchlings were tested outdoors in a circular, fiberglass tank 1.22 m in diameter. The tank was filled with fresh water to a depth of about 30 cm. In each trial, a hatchling was placed into a nylon–Lycra harness that encircled its carapace without impeding swimming. The harness was connected by a 16.5 cm monofilament line to a 25.5 cm Plexiglas lever-arm, thus each hatchling swam within a 42 cm radius from the center of the tank. The lever-arm rested on a digital encoder inside a plastic post mounted in the center of the arena. The lever arm was free to rotate in any direction and tracked the orientation of the turtle as it swam. The digital encoder in the central post was wired to a computer inside the facility (Fig. 3.3). The computer recorded the position of the turtle (to the nearest degree) every 10 seconds.

Control of the Ambient Magnetic Field

A computer-controlled magnetic coil system consisting of two independent four-coil systems (Merritt et al. 1983) arranged orthogonally was used to produce a uniform magnetic field. The first coil was aligned with the north-south magnetic axis and was used to control the magnitude of the horizontal field vector. The second coil was aligned perpendicular to the first coil and controlled the vertical field vector. Computer-controlled power supplies provided current to each coil and software developed for this system controlled the exact values for the inclination angle and intensity experienced by turtles. The computer and power supplies were located away from the coil inside the facility (approximately 20 m away) (Fig. 3.3).

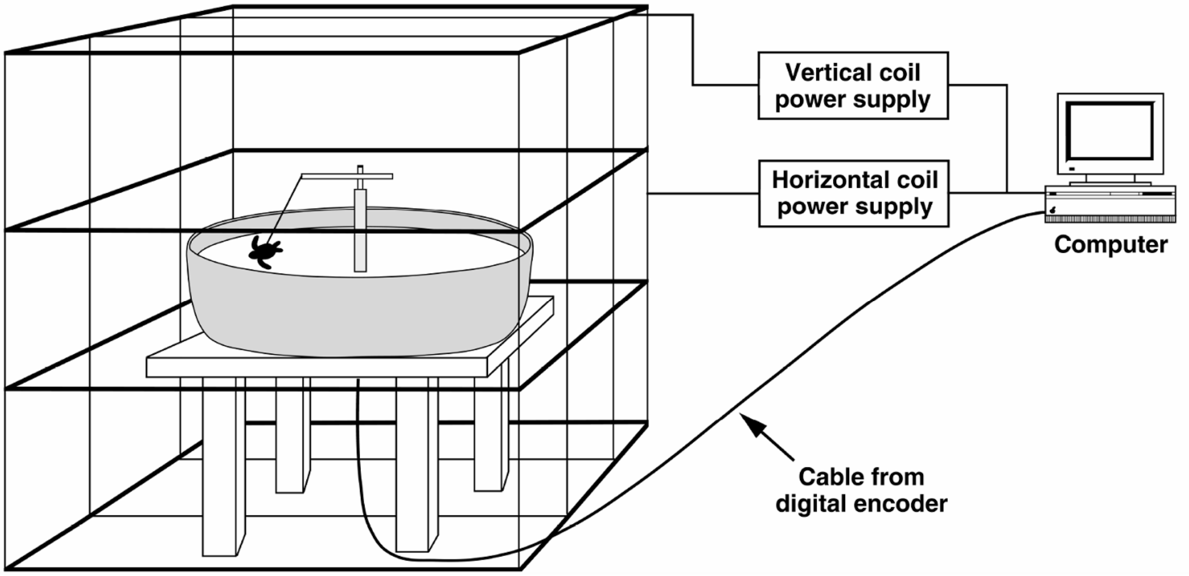

Figure 3.3 Schematic of experimental apparatus, including the orientation arena, magnetic coil structure, and data acquisition system (not to scale) (Füxjager et al. 2011). Turtles were tethered to a lever arm mounted to a digital encoder and capable of rotating 360° within the horizontal plane. The tracker arm monitored the direction in which the turtle swam via signals sent from the encoder to the computer system located in an adjacent facility. The arena was housed outdoors and enclosed by a magnetic coil structure capable of replicating specific values of inclination angle and total field intensity that exist in the North Atlantic.

To confirm field parameters, measurements of the magnetic field were taken inside the orientation arena at the northern, southern, eastern, and western edges as well as the center of the orientation arena. Measurements with a tri-axial fluxgate digital magnetometer (Applied Physics Systems, Model 520) showed that the magnetic fields produced by the coil varied by no more than 0.1 μT across the area where turtles swam.

Testing procedure

All experiments were conducted in July and August 2007. Trials were carried out at night between 19:30 h and 0:2:00 h, the time when most loggerhead hatchlings emerge from their nests and enter the sea (Witherington et al. 1990).

The orientation arena was covered with a plywood top and foam weather stripping was laid on the edges to seal out light. Prior to each trial, three layers of black 6 mm thick plastic were fastened around the entirety of the tank to further inhibit light from entering the arena. This was in addition to a tarp that was fastened around the outside of the coil that blocked natural and anthropogenic sources of light. Inside the arena, a single light emitting diode (LED) with a peak wavelength of 550 nm was suspended 2-3 cm above the water in the east. Each hatchling was harnessed and released in the orientation arena in the local magnetic field. As in previous experiments (Lohmann 1991; Lohmann and Lohmann 1994; 1996; Lohmann et al. 2001), most hatchlings (over 90%) quickly established a course towards the light (± 45°).

The light was presented because hatchlings that enter the ocean on dark, natural beaches encounter a dim glow of reflected skylight along the seaward horizon, and such light cues may play a role in establishing the magnetic directional preference of hatchlings leaving their natal beaches (Lohmann 1991). In addition, the response of each hatchling to the light source verified whether the turtle was healthy and capable of maintaining an oriented course. The few turtles that failed to establish a course towards the light within about 3 minutes were replaced with other hatchlings.

After a turtle swam towards the light for 10 minutes in the Earth's local magnetic field (intensity = 46.5 μT; inclination angle = 57.2°), the light was turned off and the hatchling swam in darkness for the ensuing test period.

In all trials, the magnetic field was changed immediately after the light was turned off. Turtles were given 3 minutes to adjust to the altered conditions. Data acquisition then began, and the position of the turtle was recorded each 10 seconds for the next 5 minutes. Individual turtles were assigned to one of three magnetic treatments, which corresponded to the northwest, northeast, and southern geographic regions of their pelagic migratory route (Table 3.1). The first treatment group experienced a field with intensity 3.0 μT stronger and an inclination angle 3.0° steeper than the home beach (intensity = 49.5 μT; inclination angle = 60.2°), the second treatment group experienced a field with intensity 3.0 μT weaker and an inclination angle 3.0° steeper than the home beach (intensity = 43.5μT; inclination angle = 60.2°), and the third treatment group experienced a field with intensity 3.0 μT stronger and an inclination angle 3.0° less than the home beach (intensity = 43.5 μT; inclination angle = 54.2°).

Statistics

At the conclusion of each trial, the computer calculated a mean angle for each hatchling using all of the 10 second measurements obtained during the 5-minute test period in darkness. The mean angles for each treatment were then analyzed with a Rayleigh test (Batschelet 1981) to determine the average direction of each treatment and whether the turtles were significantly oriented as a group. The multi-sample Watson-Williams F-test was used to test for differences among treatments (Batschelet 1981). Statistical tests were performed using Oriana (v. 2.02).

Results

Turtles presented with a magnetic field with a stronger intensity and steeper inclination angle relative to their home-beach (simulating the northwest region) were significantly oriented as a group with a mean heading to the southeast (Rayleigh test, mean angle = 153.1°, $n = 32$, $p = 0.045$). The orientation of turtles presented with a stronger intensity and less steep inclination angle relative to their home-beach (simulating the northeast region) was indistinguishable from random (Rayleigh test, mean angle = 206.7°, $n = 31$, $p = 0.529$). Turtles subjected to a magnetic field with a weaker intensity and less steep inclination angle (simulating the southern region) were significantly oriented as a group with a mean heading to the east (Rayleigh test, mean angle = 82.6°, $n = 32$, $p = 0.038$). Significant differences exist among the means of the three treatment groups (Watson-Williams F-test, $F = 8.34$, $p < 0.001$). Field parameters and results are summarized in Table 3.1.

Table 3.1 Information on the magnetic treatments presented to hatchling loggerheads.

Simulated Region	Field relative to home beach	Intensity (µT)	Inclination Angle (°)	Mean Direction (°)	Rayleigh r	Rayleigh p	n
NW Atlantic	+ 3.0 µT; + 3.0°	49.5	60.2	153	0.310	0.045	32
NE Atlantic	-3.0 µT; + 3.0°	43.5	60.2	207	0.144	0.529	31
South Atlantic	-3.0 µT; - 3.0°	43.5	54.2	83	0.318	0.038	32

Discussion

The results from this study are inconsistent with the hypothesis that hatchling loggerheads inherit a simple, “directional” magnetic map calibrated relative to the loggerheads’ home beach. In only the treatment simulating magnetic fields in the northwest Atlantic did turtle orientation (east-southeast) match the expectations of Lohmann et al. (2001). The treatment with steeper inclination angle and weaker intensity (simulating magnetic fields in the northeast Atlantic), should have elicited southward orientation, but the turtles’ orientation could not be distinguished from random. In the treatment with less steep inclination angle and weaker intensity (simulating magnetic fields in the southern Atlantic), west-northwestward orientation was expected, but loggerheads were significantly oriented eastward. While the orientation responses of turtles to the magnetic treatments are difficult to interpret because the specific fields presented do not exist along their migratory route, the experiment appears sufficient to conclude that the direction of field change relative to the turtles' home beach does not completely explain the orientation responses observed in loggerhead hatchlings (Fig. 3.4). Furthermore, the hypothetical geospatial organization of the loggerhead magnetic map (Fig. 3.2) is likely an oversimplification; the magnitude of magnetic elements is also taken into account.

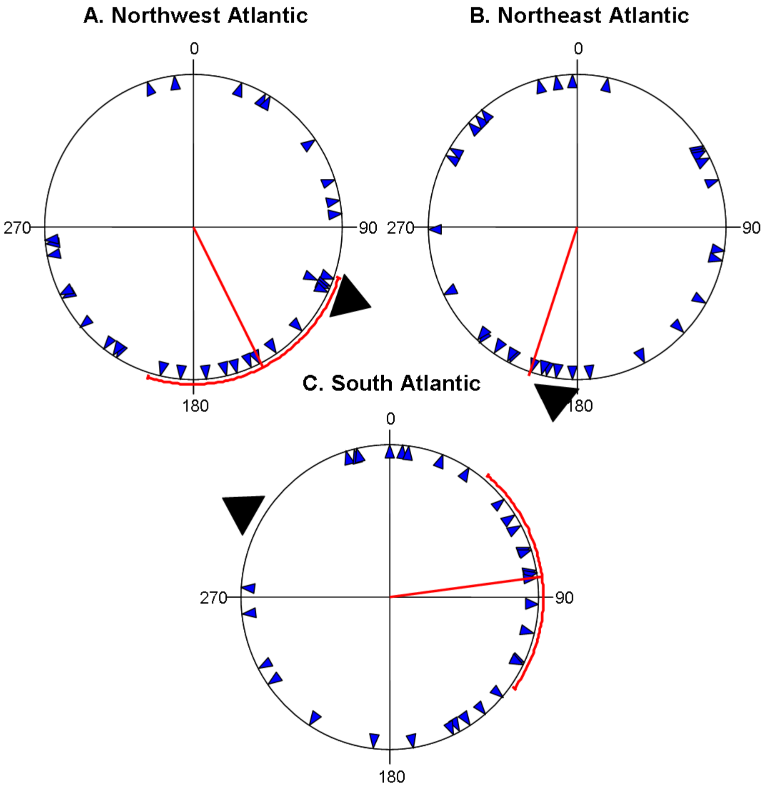

Figure 3.4 Circle diagrams representing the magnetic treatments turtles were exposed to. The red line indicates the mean direction of the entire group of turtles. The red shading outside the circle indicates the 95% confidence interval for the mean (not calculated for non-significant distributions). Blue triangles represent the mean heading of individual turtles and are plotted relative to magnetic north = 0°. Black triangles outside the circle show the expected orientation direction based on results from Lohmann et al. 2001. (A) Hatchlings exhibited southeasterly orientation when exposed to a magnetic field representative of the northwest North Atlantic Ocean. (B) Hatchlings' orientation in a field that simulates the northeast Atlantic could not be distinguished from random. (C) Easterly orientation was elicited in a field that simulates magnetic conditions of the southern North Atlantic. For statistics and field parameters see Table 3.1.

While a three-part magnetic map of the North Atlantic based only on magnetic parameters set relative to the turtles' home beach seems conceptually simple and might require relatively little neurological processing, the spatial resolution might be too coarse to provide appropriate geographic information needed by young loggerheads during their pelagic migration. The demands of the migration likely require the ability to discriminate among geographic areas on the scale of hundreds of kilometers, whereas the geographic resolution of the hypothetical magnetic map proposed here (Fig. 3.2) is on the scale of several thousand kilometers. Although there are non-magnetic cues turtles could possibly use to further assess their geographic position (Lohmann et al. 2008), inheriting a strategy that also takes into account the magnitude of magnetic elements would be helpful in resolving geographic position over the scale of hundreds of kilometers.

However, for an inherited magnetic map to have evolved, it must be able to withstand the gradual shifting of the Earth’s field due to secular variation (Courtillot et al. 1997; Alerstam 2006; Lohmann et al. 2007). Therefore, while the geospatial organization of an inherited magnetic map is likely a function of the ecological requirements imposed on the navigational task, it must also be a function of secular variation. Specifically, spatial resolution of the magnetic map is expected to increase as complexity of the navigational task increases, yet as spatial resolution increases, its stability over evolutionary time likely decreases. In principle, a spatially complex magnetic map could evolve if specific magnetic fields consistently correspond to highly important geographic locations. In such cases natural selection might favor turtles that detected the magnitude of these fields and biased their swimming direction “appropriately” (e.g. towards areas where productivity is consistently high or away from where currents diverge that could sweep them out of the North Atlantic Subtropical Gyre) and remove from the population turtles that did not orient appropriately. Whether this actually occurs is not known.

This present study suggests that the magnetic map of hatchling loggerheads is not solely organized around an algorithm of enhanced or diminished intensity and inclination relative to a home field. At a minimum, the algorithm must also consider the magnitude of field change. Recent studies suggest that this is indeed the case (Putman et al. 2011; Füxjager et al. 2011). Further research is needed to reveal the resolution with which these turtles use the magnitude of geomagnetic elements and how the geospatial organization of the magnetic map functions in an ecological context - including how secular variation shapes the resolution of hatchling loggerheads' magnetic map.

Special Thanks

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Longitude perception and bicoordinate magnetic maps in sea turtles

Summary

Long-distance animal migrants often navigate in ways that imply an awareness of both latitude and longitude. Although several species are known to use magnetic cues as a surrogate for latitude, it is not known how any animal perceives longitude. Magnetic parameters appear to be unpromising as longitudinal markers because they typically vary more in a north-south direction than east to west. However, to test whether longitude detection is possible using the magnetic field, hatchling loggerhead sea turtles (*Caretta caretta*) from Florida, were exposed to magnetic fields that exist at two locations with the same latitude but on opposite sides of the Atlantic Ocean. Turtles responded by swimming in different directions that would, in each case, help them advance along their circular migratory route. The results demonstrate for the first time that longitude can be encoded into the magnetic positioning system of a migratory animal. Because turtles also assess north-south position magnetically, the findings imply that loggerheads have a navigational system that exploits the Earth's magnetic field as a kind of bicoordinate magnetic map from which both longitudinal and latitudinal information can be extracted.

Introduction

How animals that migrate long distances determine their geographic position has been debated for more than a century (Viguier 1882; Alerstam 2006; Gould 2008). Several animals are now known to determine geographic position along a north-south axis using information in the Earth's magnetic field (Lohmann & Lohmann 1994; Fischer et al. 2001; Phillips et al. 2002; Boles & Lohmann 2003; Lohmann et al. 2004). Some migrants, however, can also determine their geographic position east to west (Avens & Lohmann 2004; Thorup et al. 2007; Chernetsov 2008). Because the Earth's magnetic field in most geographic areas varies primarily with latitude, extracting longitudinal information from the field appears difficult or impossible (Åkesson et al. 2005; Alerstam 2006; Gould 2006; Thorup &

Holland 2009). The mechanism or mechanisms that underlie longitude perception, however, have remained enigmatic.

Hatchling loggerhead turtles (*Caretta caretta*) from eastern Florida, U.S.A., embark on a trans-oceanic migration immediately after entering the sea. Hatchlings initially swim eastward to the North Atlantic Subtropical Gyre (the circular current system that flows around the Sargasso Sea), and remain within the gyre for several years, during which they gradually migrate around the Atlantic before returning to the North American coast (Lohmann et al. 2001; Lohmann & Lohmann 2003).

Sea turtles use magnetic cues to approximate position along a north-south axis (Lohmann & Lohmann 1994; Lohmann et al. 2004). To determine whether loggerheads can also use magnetic information to distinguish among positions along an east-west axis, hatchlings were subjected to fields replicating those found at two locations, both of which lie along the migratory route but on opposite sides of the Atlantic Ocean. Each location had the same latitude but differed by approximately 3700 km in longitude (Fig. 3.5a).

Methods

Methods have been described in detail previously (Lohmann & Lohmann 1994; Lohmann et al. 2001) and in section 1 of Chapter 3 of this dissertation. Briefly, each turtle was tethered to an electronic tracking unit in the center of a water-filled orientation arena. The arena was surrounded by a computerized coil system which was used to control the magnetic field in which the turtles swam (Fig. 3.3). Each turtle began its trial in a magnetic field matching that found at the natal beach (inclination = 57.7°; intensity = 46.5 μT) and was allowed to establish a course towards a dim light (an LED with peak wavelength = 550 nm) in magnetic east. After 10 minutes, the light was turned off and the magnetic field simultaneously changed to either: (1) a field replicating one near Puerto Rico; or (2) a field replicating one near the Cape Verde Islands. Turtles were allowed to acclimate to the new field for 3 minutes. A computer then monitored the direction that each turtle swam during the next 5 minutes and calculated a mean heading.

Each turtle was tested a single time under one of the two field conditions. No more than two turtles from the same nest were tested in the same field. The field used to approximate magnetic conditions near Puerto Rico had an inclination of 46.4°; and a total intensity of 39.0 μT (as assessed by 4 independent measurements with an Applied Physics Systems tri-axial fluxgate magnetometer, model 520A). The field used to approximate conditions near the Cape Verde Islands had an inclination of 26.1° and an intensity of 35.0 μT. The experimental fields were selected on the basis of estimates provided by the International Geomagnetic Reference Field Model (IGRF-10) (Macmillan & Maus 2005) for July 2007 (the date when the experiment began) using latitude 20.0° N, longitude 65.5° W for Puerto Rico and latitude 20.0° N, longitude 30.5° W for Cape Verde Islands. The IGRF-10 declination estimates for the target locations were -13.1° for Puerto Rico and -12.9° for the Cape Verde Islands. Experiments were conducted in Melbourne Beach, Florida (declination = -6.0°) (Table 3.2).

The coil system consisted of two different coils arranged orthogonally. The coil controlling the horizontal component of the magnetic field measured 2.41 m on a side and the coil controlling the vertical component measured 2.54 m (Fig. 3.3). Both were constructed in accordance with the 4-coil design by Merritt et al. (1983). Turtles were restricted to the center of the coil in an area defined by a horizontal circle of radius 42 cm and a vertical area of about 5 cm; in this region, calculated (Merritt et al. 1983) and measured deviations from perfect field uniformity were less than 1%.

Table 3.2 Information on the magnetic treatments presented to hatchling loggerheads.

Simulated Region	Latitude Longitude	Intensity (μT)	Inclination Angle (°)	Mean Direction (°)	Rayleigh r	Rayleigh p	n
Puerto Rico	20.0° N 65.5° W	39.0	46.4	50	0.393	0.032	22
Cape Verde Islands	20.0° N 30.5° W	35.0	26.1	217	0.336	0.018	35

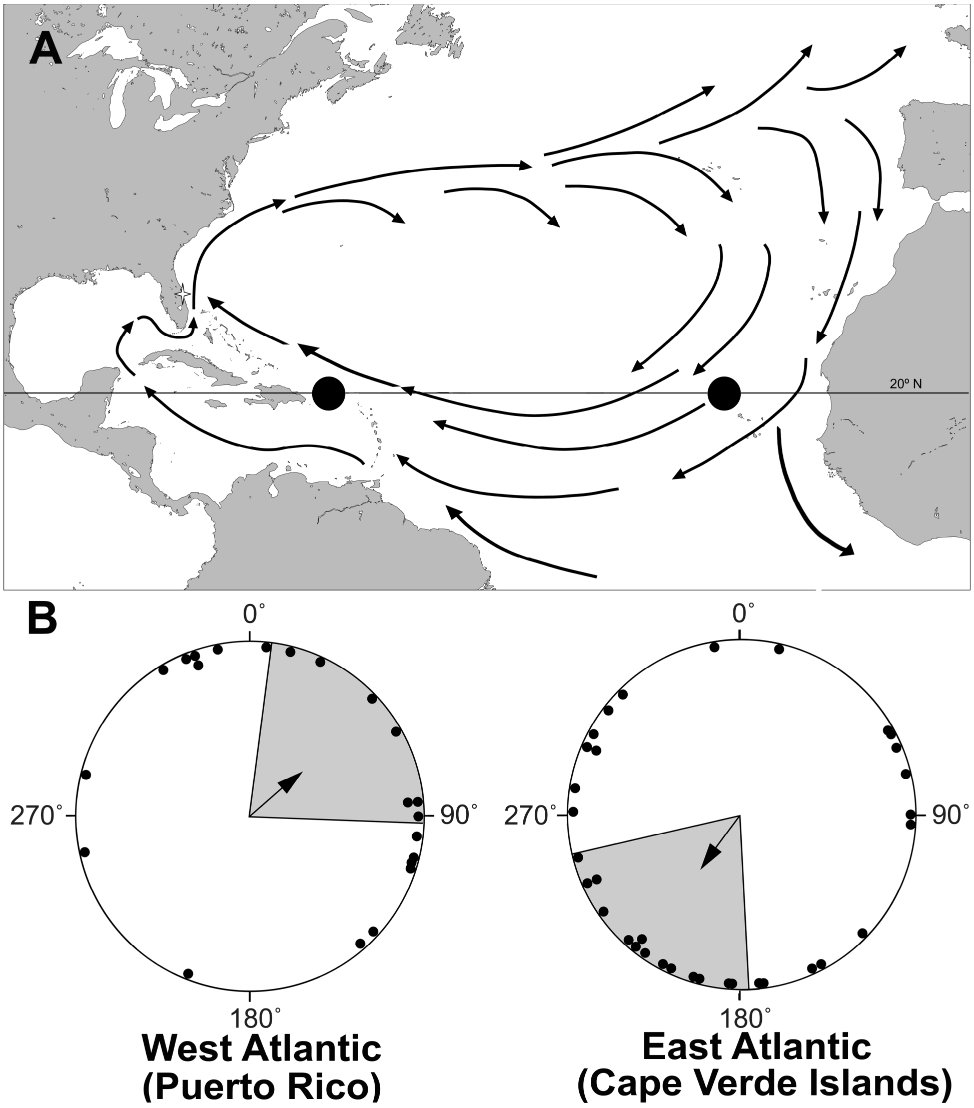

Figure 3.5 (A) Schematic of North Atlantic Subtropical Gyre (after Tomczak & Godfrey (1994)). Arrows indicate the generalized main currents. Hatchling loggerheads were exposed to the magnetic fields that exist at two locations (marked by black dots) with the same latitude but on opposite sides of the Atlantic. The test site and natal beach of the turtles is marked by the open star on the east coast of Florida, USA.
(B) Orientation of hatchling loggerheads tested in a magnetic field from the west side of the Atlantic near Puerto Rico (left) and in a field from the east side of the Atlantic near the Cape Verde Islands (right). Each dot represents the mean angle of a single hatchling. The arrow in the center of each circle indicates the mean angle of the group; the arrow length is proportional to the magnitude of the mean vector r, with the radius of the circle corresponding to r = 1. Turtles tested in the Puerto Rico field were significantly oriented with a mean angle of 50°. Turtles tested in the Cape Verde field were also significantly oriented but in approximately the opposite direction (mean angle = 217°). Shaded sectors indicate the 95% confidence interval for the mean angle. Data are plotted relative to geographic north (N = 0°). For statistics and field parameters see Table 3.2.

Results

Turtles exposed to a field like one that exists on the west side of the Atlantic near Puerto Rico swam approximately northeast (Fig. 3.5b). Those exposed to a field like one that exists on the east side of the Atlantic near the Cape Verde Islands swam approximately southwest (Fig. 3.5b). Both groups were significantly oriented at $p < 0.03$ or less (Fig. 3.5b) and the two distributions were significantly different (Watson test, $p < 0.002$). Thus, the results show that loggerhead turtles can distinguish between magnetic fields that exist at different longitudes along the same latitudinal parallel.

Discussion

Functional Significance of Orientation Responses

The orientation behavior elicited by the two fields is consistent with the interpretation that these responses have functional significance in the migration (Mouritsen 2001; Wiltschko & Wiltschko 2005; Lohmann et al. 2007). Near the Cape Verde Islands, southwesterly orientation coincides with both the migratory pathway and the direction of the wide, slow-moving Canary Current (Tomczak & Godfrey 1994) (Fig. 3.5). Swimming southwest in this area presumably helps turtles move back toward North America. It might also help them avoid the Guinea Current, the southeast-flowing branch of the Canary Current that can potentially displace turtles from the gyre and carry them along the coast of the African continent.

Near Puerto Rico, the gyre currents are slowed and diverted as they meander through the numerous islands and reefs of the Antilles and Bahama Archipelagos, but in deeper water to the northeast, the Antilles Current flows unobstructed toward Florida (Gunn & Watt 1982; Tomczak & Godfrey 1994). Northeasterly orientation near Puerto Rico is thus likely to help turtles stay within the gyre and embed in currents that facilitate movement back toward the North American coast, where most Florida loggerheads spend their late juvenile years (Lohmann & Lohmann 2003).

These results add to the growing evidence that specific regional magnetic fields elicit orientation responses that help young loggerheads remain in the gyre and advance along the migratory route (Lohmann and Lohmann 1994; 1996; Lohmann et al. 2001). The hatchlings that were tested had never been in the ocean, demonstrating that turtles do not need migratory experience in order to recognize and respond to fields that exist along their oceanic pathway. Because the earth's field gradually changes, this orientation behavior is consistent with the hypothesis that strong selective pressure acts to maintain an approximate match between the responses of turtles and the fields that mark critical positions along the migratory pathway at any point in time (Lohmann et al. 2001, Lohmann & Lohmann 2003).

Organization of the Turtles' Magnetic Map

The results indicate that, for sea turtles, the problem of perceiving longitude and the problem of perceiving latitude share a common solution. In each case, magnetic information can be used to distinguish among different geographic regions.

The ability of turtles to derive both latitudinal and longitudinal information from the earth's field necessarily implies that turtles exploit at least two different geomagnetic features that vary in different directions across the Atlantic. Thus, the results demonstrate that turtles use a kind of bicoordinate magnetic map in position-finding, an ability that has long been hypothesized to exist in animals (Viguier 1882; Gould 1982; Lohmann & Lohmann 1996; Phillips 1996; Lohmann et al. 2007) but has never before been demonstrated.

The precise way in which the turtles' magnetic map is organized is not yet known. Along the migratory route, the four magnetic parameters that might hypothetically provide a turtle with positional information all have isolines that trend east-west and intersect meridians on both sides of the Atlantic (Fig. 3.6). Thus, although any one of these parameters might be used as a surrogate for latitude, none of them, by itself, appear suitable for assessing longitude over the entire migratory route.

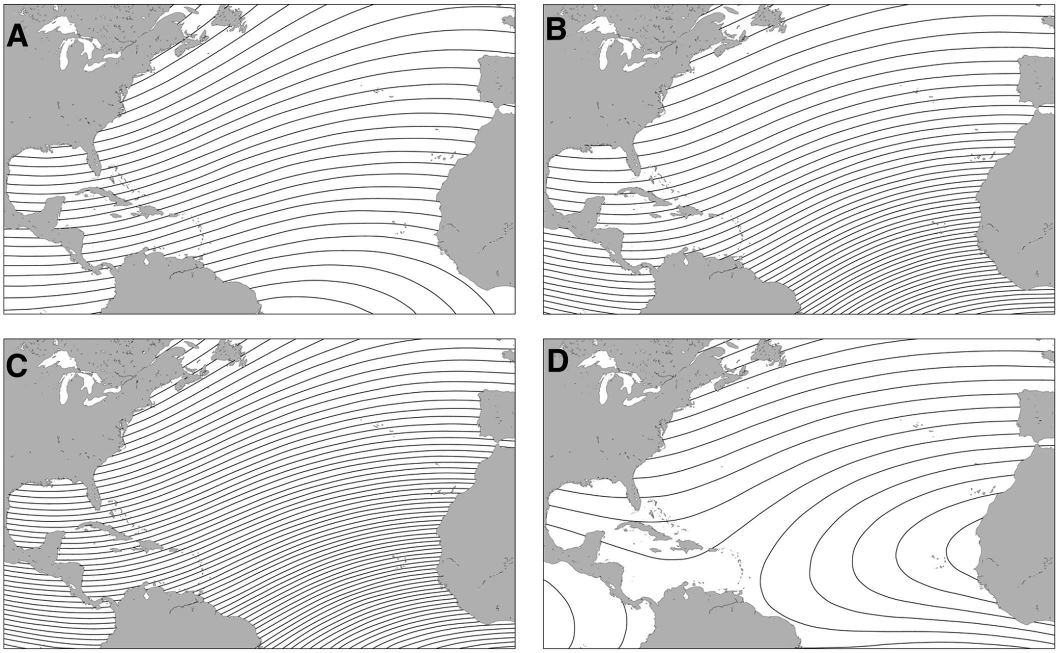

Figure 3.6 Maps of magnetic elements in the North Atlantic Ocean. (a) Total field intensity; contour interval = 1 μT. (b) Inclination angle; contour interval = 2°. (c) Vertical intensity; contour interval = 1 μT. (d) Horizontal intensity; contour interval = 1 μT. Isolines of each element trend east-west across the North Atlantic and intersect numerous meridians; thus, none of these parameters, used alone, can function as a surrogate for longitude. Although loggerheads detect both inclination angle and total field intensity (Lohmann & Lohmann 1994, 1996), it is not known whether they can resolve the vector components of the magnetic field (i.e. vertical and horizontal intensity). Declination was not changed in the experiment, nor is any animal known to perceive it (Gould 2008). Maps of magnetic information were generated using the International Geomagnetic Reference Field (IGRF-11) (Macmillan & Maus 2005) for 2010.

It is not necessary, however, to assume that turtles exploit one magnetic parameter as a surrogate for latitude and another as a proxy for longitude. Nearly all geographic regions along the migratory route, including the two used in this experiment, have fields defined by unique combinations of inclination and intensity; two magnetic parameters loggerheads detect (Lohmann & Lohmann 1994, 1996) (Fig. 3.7). A reasonable hypothesis is thus that turtles can distinguish among different longitudes using these unique “magnetic signatures.” Such a strategy appears feasible, in that the fields that exist in locations with the same latitude but on opposite sides of the Atlantic always differ in both inclination and intensity (Fig. 3.7), with the differences exceeding what turtles are known to perceive Lohmann & Lohmann 1994; 1996; Lohmann et al. 2004). Likewise, use of “magnetic signatures” might also explain how turtles distinguish among geographic regions that differ in latitude

(Lohmann & Lohmann 1994; Lohmann et al. 2001). Viewed in this way, turtles might have a bicoordinate magnetic map based on inclination and intensity, one that does not encode latitude and longitude *per se*, but that nonetheless provides turtles with both east-west and north-south positional information along the migratory pathway.

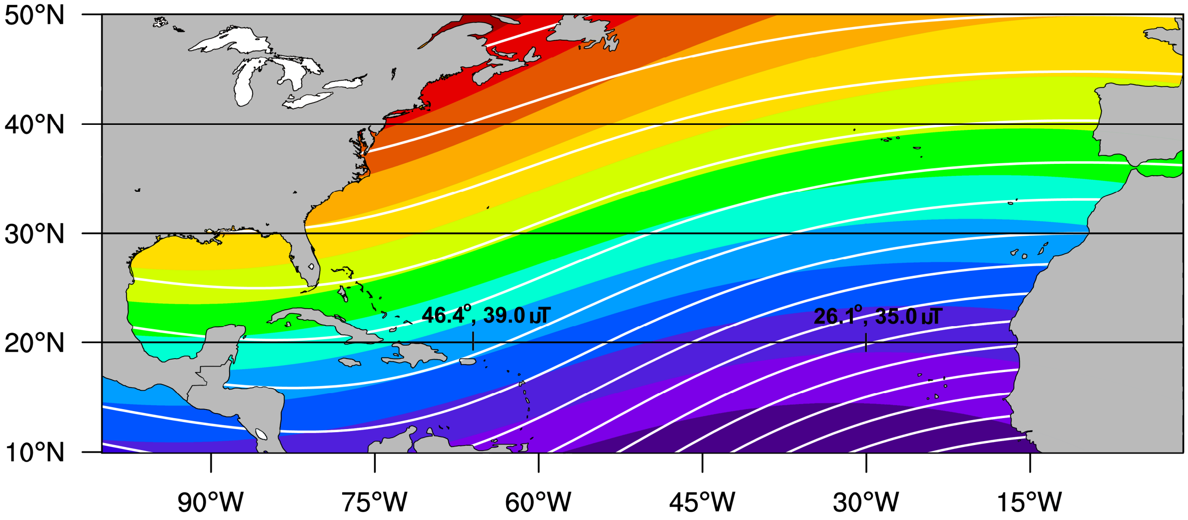

Figure 3.7 Map illustrating the feasibility of turtles using unique combinations of magnetic inclination and intensity to distinguish among longitudes at the same latitude but on opposite sides of the Atlantic. Background colors reflect total field intensity. Each color band encompasses 2 μT. White isolines indicate inclination angle in 5° increments. Horizontal black lines show 3 different latitudinal parallels that intersect the migratory route of loggerheads on both sides of the Atlantic. Numbers along the 20°N parallel are values of inclination and intensity for the fields used in the experiment. Vertical marks on the 20°N parallel indicate the location where each field exists. Along any latitudinal parallel, the differences in inclination and intensity that exist between locations on opposite sides of the Atlantic exceed what sea turtles are known to detect (Lohmann & Lohmann 1994, 1996, Lohmann et al. 2004). Magnetic information was generated using IGRF-11 (Macmillan & Maus 2005) for 2010.

In stating that turtles have a bicoordinate magnetic map, the term “map” is used in accordance with recent usage (Walcott 1996; Gould 1998; Mouritsen 2001; Alerstam 2006; Lohmann et al. 2007) that makes no assumptions about the nature of the internal spatial representation (if any) that an animal has. It is possible, and perhaps even likely, that hatchling turtles lack any real conception of their geographic location, and that they advance blindly along their migratory route by swimming in particular directions in response to specific magnetic fields. It is also possible that other cues besides magnetic fields play a role in guiding the transoceanic migration, and that the navigational system of young turtles provides a foundation on which additional strategies or mechanisms needed for the navigational tasks of older turtles (Lohmann et al. 2004; Luschi et al. 2007) can be added during maturation. Indeed, the experience of migrating across the Atlantic and back may provide turtles with an extended opportunity to acquire information (magnetic and otherwise) that can be incorporated into later navigational processes.

Other Animals

Whether animals other than sea turtles extract both latitudinal and longitudinal information from the Earth's field is not known. In principle, some animals might have bicoordinate maps in which each of the two axes depends on a different kind of sensory information; moreover, different ways of assessing longitude might have evolved in different animal groups. It is interesting to note that human navigators first solved the longitude problem in a very different way than turtles: by developing a precise and reliable clock which allowed time of day at a given location to be compared with that at a distant site (Gould 2008). For an animal to determine longitude in a similar way, it would presumably need a biological clock that did not reset to local time (or at least not immediately). A recent experiment designed to investigate whether migratory birds might assess longitude using two clocks, one of which synchronizes to local time more rapidly than the other, failed to find evidence in support of this mechanism (Kishkinev et al. 2010). These results are consistent with the interpretation that birds, like turtles, have evolved a way to assess longitude that is independent of time-keeping. Other possible mechanisms that animals might hypothetically use involve olfactory cues (Papi 1990; Wallraff 2004), infrasound (Kreithen 1979; Hagstrum 2000), or the use of declination in geographic areas where this parameter varies longitudinally (Åkesson et al. 2005).

Regardless of these considerations, these results provide the first demonstration that longitude can be encoded into the magnetic positioning system of an animal. In addition, the findings demonstrate the existence of bicoordinate magnetic maps, which are capable of simultaneously providing animals with both latitudinal and longitudinal information. Similar mechanisms may help explain some of the most impressive feats of navigation in the animal kingdom, including those of diverse long-distance migrants such as insects (Reppert et al. 2010; Miller et al. 2011), fish (Bonfil et al. 2005), birds (Wiltschko & Wiltschko 2003), and marine mammals (Stevick et al. 2011).

Special Thanks

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Citation

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Orientation responses of loggerhead sea turtles to magnetic fields in the North Atlantic

Summary

Loggerhead sea turtle (*Caretta caretta*) hatchlings' use of the earth's magnetic field as a "map" has been extensively studied. For more than a decade it has been known that hatchlings from Florida, U.S.A. are capable of detecting both field intensity (strength) and inclination angle (the angle at which field lines intersect the surface of the earth), two magnetic parameters that vary predictably across the surface of the globe. More recently, young loggerheads were shown to use magnetic parameters to extract latitudinal and longitudinal information from within the North Atlantic Subtropical Gyre. However, it is unclear whether young turtles inherit orientation responses to magnetic fields that exist across the entire gyre system, or only respond to fields at locations where displacement from the gyre is possible. In this experiment, hatching loggerheads were presented with five magnetic fields that exist along the North Atlantic Subtropical Gyre and correspond to potentially important locations (coastal Portugal, the Straits of Gibraltar, the Canary Islands, coastal Suriname, and Barbados). Two fields (coastal Portugal and Barbados), elicited oriented swimming in directions that appear to facilitate the loggerheads' transatlantic journey. The other fields, however, failed to elicit swimming behavior that could be distinguished from random orientation. These findings suggest that not all magnetic fields along the loggerhead migratory route elicit robust orientation responses and that the magnetic map of loggerheads may be more complicated than previously recognized.

Introduction

The magnetic navigational system of loggerhead sea turtles (*Caretta caretta*) is one of the best described of any marine animal (Wiltschko & Wiltschko 2005; Gould 2011). Hatchlings from Florida, U.S.A. are capable of detecting both field intensity (strength) and inclination angle (the angle at which field lines intersect the surface of the earth) - two parameters that might provide turtles with geospatial information (Lohmann & Lohmann 1994; 1996). Further experimentation has demonstrated that young loggerheads extract latitudinal and longitudinal information from the earth's magnetic field within the North Atlantic Subtropical Gyre (Lohmann et al. 2001; Putman et al. 2011). The emerging picture is that hatchling loggerheads are endowed with an elaborate set of orientation responses to regional magnetic fields that facilitate their movement along their transatlantic migratory route.

However, numerous questions remain as to the extent and resolution of the turtles' magnetic map. For instance, do turtles inherit a magnetic map that permits them to assess their position anywhere along the North Atlantic Subtropical Gyre, or do magnetic orientation responses exist only at a few locations? To better understand the navigational and ecological significance of these orientation responses, hatchling loggerheads were presented with five magnetic fields that exist along the North Atlantic Subtropical Gyre and correspond to potentially important locations. Three of these fields occur within the Canary Current System, a broad, productive, and slow south-flowing eastern boundary current. Specifically, fields were chosen that exist in locations where young loggerheads from the southeastern U.S. are frequently observed: (1) between the Azores and Portugal, (2) at the Straits of Gibraltar, and (3) near the Canary Islands. The two other fields exist on the western side of the basin corresponding to coastal Suriname and Barbados, near the confluence of the North Equatorial Current and the Guiana Current, two rapid, west-flowing currents that funnel water into the Caribbean Sea.

Methods

Methods have been described in detail previously (Lohmann & Lohmann 1994; Lohmann et al. 2001; Füxjager et al.2011) and in section 1 of Chapter 3 of this dissertation. Briefly, each turtle was tethered to an electronic tracking unit in the center of a water-filled orientation arena. The arena was surrounded by a computerized coil system which was used to control the magnetic field in which the turtles swam (Fig. 3.3). Each turtle began its trial in a magnetic field matching that found at the natal beach (inclination = 57.7°; intensity = 46.5 μT) and was allowed to establish a course towards a dim light (an LED with peak wavelength = 550 nm) in magnetic east. After 10 minutes, the light was turned off and the magnetic field simultaneously changed to either: (1) a field replicating one near coastal Portugal, (2) a field replicating one near the Straits of Gibraltar, (3) a field replicating one near the Canary Islands, (4) a field replicating one near the northern coast of Suriname, and (5) a field replicating one near Barbados. Table 3.3 provides further details on field locations and parameters. The experimental fields were selected on the basis of estimates provided by the International Geomagnetic Reference Field Model (IGRF-10) (Macmillan & Maus 2005) for July 2007 (the date when the experiment began). After turtles were initially exposed to new field conditions they were allowed to acclimate for 3 minutes. A computer then monitored the direction that each turtle swam during the next 5 minutes and calculated a mean heading. Each turtle was tested a single time under one of the five field conditions. No more than three turtles from the same nest were tested in the same field.

The coil system consisted of two different coils arranged orthogonally. The coil controlling the horizontal component of the magnetic field measured 2.41 m on a side and the coil controlling the vertical component measured 2.54 m (Fig. 3.3). Both were constructed in accordance with the 4-coil design by Merritt et al. (1983). Turtles were restricted to the center of the coil in an area defined by a horizontal circle of radius 42 cm and a vertical area of about 5 cm; in this region, calculated (Merritt et al. 1983) and measured deviations from perfect field uniformity were less than 1% (as assessed by 4 independent measurements with an Applied Physics Systems tri-axial fluxgate magnetometer, model 520A).

Circular statistics (Batschelet 1981) were used to determine whether the orientation of turtles differed among magnetic treatments and how well orientated each treatment was.

Results

First, the Mardia-Watson-Wheeler Test revealed significant differences in orientation of the turtles among the five magnetic treatments (W = 17.634, p = 0.024), indicating an influence of the magnetic treatment on hatchling orientation behavior. Second, two fields (coastal Portugal and Barbados) elicited oriented swimming. In the coastal Portugal field, turtles were oriented southwards (mean angle = 178.3°, r = 0.322, p = 0.043, n = 30). In the Barbados field, turtles were oriented northwards (mean angle = 5.2°, r = 0.401, p = 0.027, n = 22). The other three fields, however, failed to elicit swimming behavior that could be distinguished from random orientation (Table 3.3).

Table 3.3 Information on the magnetic treatments presented to hatchling loggerheads.

Simulated Region	Latitude Longitude	Intensity (μT)	Inclination Angle (°)	Mean Direction (°)	Rayleigh r	Rayleigh p	N
Portugal	43.0° N 15.5° W	45.7	58.8	178	0.322	0.043	30
Straits of Gibraltar	36.0° N 6.0° W	42.6	49.5	138	0.124	0.730	21
Canary Islands	30.0° N 20.0° W	39.4	41.1	293	0.208	0.242	33
Suriname	11.0° N 50.5° W	31.8	26.1	164	0.151	0.484	32
Barbados	13.0° N 59.6° W	34.1	35.5	5	0.401	0.027	22

Discussion

These findings suggest that some, but not all, magnetic fields along the loggerhead migratory route elicit oriented swimming in hatchlings. In the two treatments where magnetic fields elicited oriented swimming, the average direction chosen appears to facilitate the loggerheads' transatlantic journey (Fig. 3.8). In the field that occurs near Portugal, the southward orientation that was elicited is likely to facilitate the turtles' movement along the broad, south-flowing Canary Current System. Additionally, southward orientation in the vicinity of Portugal may decrease turtles' chances of being carried north into fatally cold waters (Lohmann et al. 2001). This southward swimming is consistent with previous findings by Lohmann et al. (2001) and Füxjager et al. (2011) that presented turtles with magnetic fields that exist in close proximity to this location. Likewise, northward orientation elicited by the field near Barbados likely increases the chances of turtles following currents that will transport them back to the North American coast, where older juveniles take up residence and where mating and nesting eventually occurs (Lohmann et al. 2001; Lohmann & Lohmann 2003)

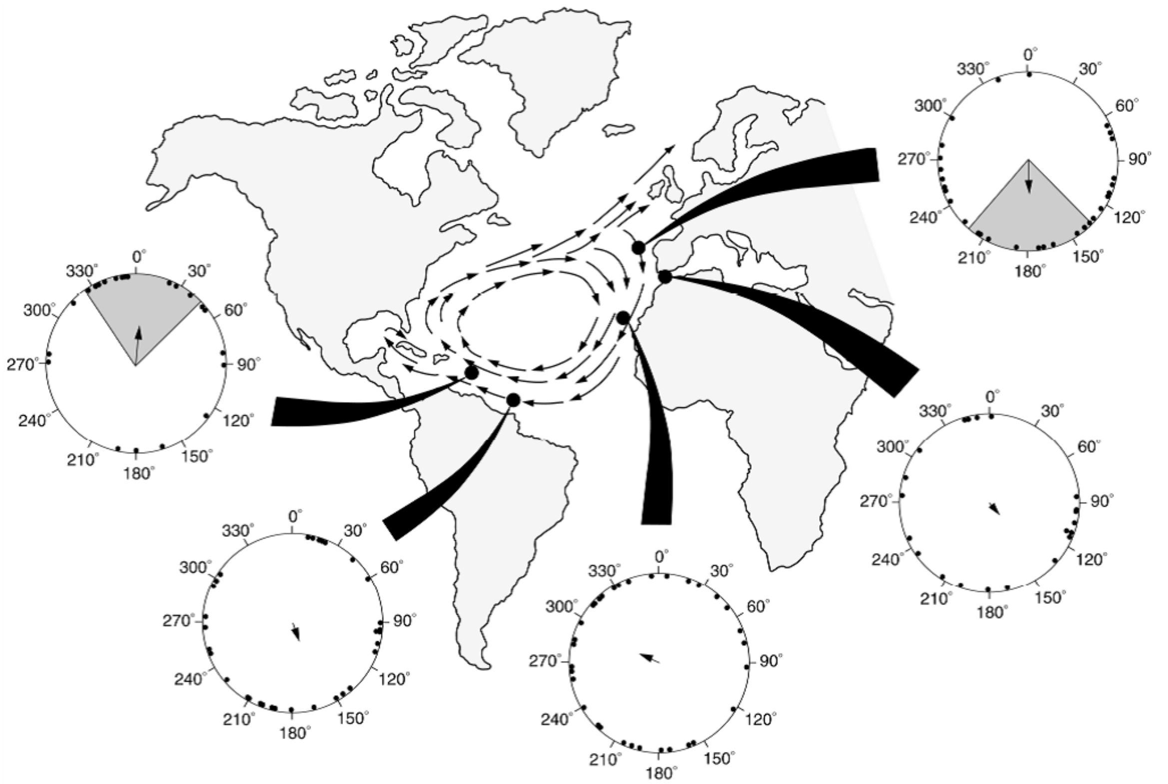

Figure 3.8 Map of the North Atlantic Subtropical Gyre. The orientation circles represent the headings of turtles tested in magnetic fields that exist at the location specified on the map. Each dot within a circle diagram represents the mean angle of a single hatchling. The arrow in the center of each circle indicates the mean angle of the group; the arrow length is proportional to the magnitude of the mean vector r, with the radius of the circle corresponding to r = 1. The 95% C.I. for the mean is indicated by grey shading within the circle diagrams for distributions that are significantly oriented ($p < 0.05$). See Table 3.3 for field parameters and statistics.

In contrast, the other three fields failed to elicit swimming behavior from turtles that could be distinguished from random orientation (Fig. 3.8). Although it is not clear why the magnetic fields that occur at the Straits of Gibraltar, the Canary Islands, and north of Suriname did not elicit oriented swimming from turtles, the lack of responses to these fields may provide key information about the nature of the hatchling loggerheads' magnetic map. It is conceivable that magnetic orientation to regional fields evolved as a mechanism to rapidly move turtles from a location that is dangerous (in terms of being displaced from the gyre) or unfavorable (such as low prey availability) to a safer or more favorable one (Lohmann & Lohmann 1994). Thus, fields that occur at locations that are neither dangerous nor unfavorable would not elicit strongly oriented swimming by turtles.

That magnetic fields within the central portion of the Canary Current System failed to elicit oriented swimming by loggerhead hatchlings is consistent with the above hypothesis. Numerous juvenile loggerheads from the southeastern U.S. are found within this part of the Canary Current, including waters on both the Atlantic and Mediterranean sides of the Straits of Gibraltar (Carreras et al. 2006) and near the Canary Islands (Monzón-Argüello et al. 2009). The eastern Atlantic is highly productive (Brochier et al. 2008) and it is unclear whether there would be an adaptive benefit for turtles to rapidly move through this particular region. It is possible that the lack of strong orientation to the magnetic fields that exist at these two locations is due to natural selection favoring turtles that remain in these areas for an extended period. Additionally, there is evidence from satellite-tracked juvenile loggerheads caught near the Azores and Madeira Islands that turtles spend extended periods in the Canary Current System and even make seasonal migrations north and south within it (McCarthy 2006).

In attempting to understand the lack of orientation by turtles to the field north of Suriname, two different factors may be at work. First, unlike the Canary Current System, it is not known whether loggerheads from the U.S. enter this oceanic region. It is possible therefore, that turtles never encounter the field and thus have never evolved a response to it. Alternatively, if turtles do enter this oceanic region, it may be that the swift and consistently westward currents (Tomczak & Godfrey 1994) safely carry turtles along the gyre and the risk of exiting the gyre is low. In this case also, presumably there would be little selective pressure on the loggerhead population to orient in a particular direction.

Regardless of the possible interpretations, the present findings suggest that the magnetic map of loggerheads may be more complicated than previously recognized. Some fields along the North Atlantic Subtropical Gyre elicit robust orientation responses whereas other fields, even nearby, do not. Further exploration of the magnetic map of loggerhead sea turtles is warranted, both adding to the number of magnetic fields presented to turtles and a comprehensive analysis of the existing data.

Special Thanks

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Transoceanic migratory dispersal of young sea turtles: a little navigation goes a long way

Summary

Young loggerhead sea turtles (*Caretta caretta*) from eastern Florida, U.S.A., undertake a transoceanic migration in which they gradually circle the Sargasso Sea before returning to the North American coast. Young turtles are weak swimmers but have a navigational system in which regional magnetic fields elicit changes in swimming direction at crucial points along the migratory pathway. Here I examine how these navigational responses interact with ocean currents to shape the distribution of turtles in the open sea. Using a high-resolution ocean circulation model, I simulate the movements of young turtles under several different scenarios, including one in which turtles drifted passively, and others in which turtles swam briefly in accordance with experimentally derived data on magnetic navigation. Results indicate that even small amounts of oriented swimming in response to regional magnetic fields can profoundly affect migratory routes and endpoints. Turtles that engaged in directed swimming for as little as 1-3 hours per day were 43-187% more likely than passive drifters to reach the Azores, a productive foraging area frequented by Florida loggerheads. They were also more likely to remain within warm-water currents favorable for growth and survival, avoid areas on the perimeter of the migratory route where predation risk and thermal conditions pose threats, and successfully return to the open-sea migratory route if carried into coastal areas. These findings imply that marine animals traditionally viewed as ineffective swimmers may be able to exert unexpectedly strong effects on their migratory trajectories and open-sea distributions through simple navigation responses and minimal swimming.

Introduction

Oriented locomotion in response to specific environmental cues is the essence of animal navigation. In many mobile species, such behavior plays a crucial role in guiding movement across various spatial scales (Dingle 1996; Nathan 2008; Bowlin et al. 2010). For animals that migrate long distances, navigation behavior has the potential to shape the geographic distribution of a species, as well as influence fundamental biological processes such as dispersal, gene flow and colonization (Alerstam 2006; Åkesson & Hedenström 2007). For marine animals, however, the mechanisms that guide most species are poorly understood, and dispersal models have typically assumed that individuals move randomly or drift passively with ocean currents (e.g. Dawson et al. 2005; Sims et al. 2008; Humphries et al. 2010; Pous et al. 2010). Few attempts have been made to incorporate realistic navigational processes into models of animal movement or to determine how such behavior influences animal distributions (Holyoak et al. 2008; Boyer & Walsh 2010).

The navigational system that guides the migration of young loggerhead turtles (*Caretta caretta*) is the most thoroughly studied of any marine animal (Wiltschko & Wiltschko 2005; Gould 2011). Young loggerheads from Florida, U.S.A., embark on a transoceanic migration around the Sargasso Sea, a pathway that approximately coincides with the warm-water current system known as the North Atlantic Subtropical Gyre (Carr 1986, 1987; Bolten et al. 1998). Young turtles use positional information in the Earth's magnetic field as a kind of "map" to guide their swimming within the gyre (Lohmann et al. 2007). Specifically, regional magnetic fields function as navigational markers and elicit changes in swimming direction at different locations along the migratory route (Lohmann & Lohmann 1994, 1996; Lohmann et al. 2001; Merrill & Salmon 2010; Putman et al. 2011; Füxjager et al. 2011). These empirical results, together with the existence of high-resolution ocean circulation models, provide a rare opportunity to investigate how navigation behavior interacts with ocean currents to affect the distribution of a migratory species in the open sea.

Using particle-tracking software (ICHTHYOP v. 2.21) (Lett et al. 2007) in combination with the ocean circulation model Global HYCOM (Hybrid Coordinate Ocean Model) (Bleck 2002), the first 5 years of the loggerhead migration were simulated assuming several different behavioral scenarios. The results demonstrate that a few simple navigational responses, expressed as small amounts of oriented swimming in response to regional magnetic fields, can have a disproportionately large effect on the migratory movements of turtles. The findings have important implications for numerous marine species traditionally assumed to depend on ocean currents for transport.

Methods

The duration of the pelagic migration of Florida loggerhead turtles is typically about 6-12 years (Bjorndal et al. 2000a). The simulation was restricted to 5 years, with an emphasis on migratory movements near the northern boundary of the North Atlantic Subtropical Gyre (Fig. 3.9).

The movement of young turtles was simulated using the particle-tracking program ICHTHYOP v. 2 (Lett et al. 2007), which interpolates surface currents from Global HYCOM (Bleck 2002). Global HYCOM output has a spatial resolution of 0.08° (~5-7 km) and a daily timestep. HYCOM uses data assimilation to produce "hindcast" model output that better reflects *in situ* and satellite measurements of oceanic conditions. Global HYCOM thus resolves mesoscale processes such as meandering currents, fronts, filaments, and oceanic eddies (Bleck 2002, Chassignet et al. 2006), which are important in realistically characterizing dispersal scenarios of turtles (Witherington 2002; Bolten 2003). For advection of particles through HYCOM velocity fields, ICHTHYOP implements a Runge-Kutta 4th order time-stepping method (Lett et al. 2007). The study domain extended from the Equator to 47°N and from 100°W to the Prime Meridian (Fig. 3.9).

Release Conditions

Simulated turtles (i.e. virtual particles) were released in an offshore zone that paralleled the east coast of Florida. The release zone was located between latitudes 26.0° N and 28.5° N and spanned an area that was 30-50 km from the coast. Releasing turtles offshore served to minimize the influence of coastal processes not characterized by the Global HYCOM model. Moreover, 40 km (the center of the release zone) is the approximate distance that hatchling loggerheads swim using the residual energy from their yolk sacks (Kramer & Bennett 1981); 30-50 km is also a distance from shore where post-hatchlings are routinely observed (Witherington 2002).

Previous modeling studies on hatchling dispersal suggest that the interannual variation in ocean current conditions can greatly influence the outcome (Hays et al. 2010; Putman et al. 2010). To make this analysis as broadly applicable as possible and to avoid outcomes that result from conditions unique to any particular year, each simulation extended over a 5-year period. In addition, 6 different years were used as a starting point (2004-2009). Simulations starting in 2004 and 2005 ran through 2009 and 2010, respectively. Simulations starting in 2006, 2007, 2008, and 2009 ran through 2010 and then looped back over to resume in 2004. For example, the simulation that began in 2006 ran until 2010 and then continued from 2004 to 2005. This "looping technique" is common in oceanographic simulations (e.g., Brochier et al. 2009) and diminishes the potential impact of a single, anomalous year. Similarly, to reduce possible effects of storms or other unusual events that might yield atypical oceanic conditions, releases each year were at 5-day intervals starting on July 1 and continuing through September 18, a period that encompasses the main loggerhead hatching season in Florida (Weishampel et al. 2003).

Behavioral Scenarios

For each behavioral scenario modeled, a total of 900,000 simulated turtles were tracked. This total consisted of 15 total release events of 1,000 turtles each (see above), replicated 10 times each year, for each of 6 different years. Replications within each year differed in two parameters: (1) the exact release sites of individuals within the release zone, which were assigned randomly; (2) the exact direction that individual turtles swam within each navigation zone, which was assigned randomly from a range of directions derived from empirical results (see below). The approach of tracking 900,000 simulated turtles in each of the behavioral scenarios allowed nearly all possibilities of transport to be observed and the use of statistics to determine the likelihood of each possibility.

Modifications were made to ICHTHYOP to simulate the swimming behavior of young turtles. For the active swimming scenarios, three geographic regions along the northern portion of the turtles' migratory route were designated as "navigation zones" (Fig. 3.9). Each zone encompasses the location of a specific magnetic field that is known to elicit directional swimming in loggerhead hatchlings (Lohmann et al. 2001; Füxjager et al. 2011). The magnetic fields were defined by intensity (field strength) and inclination (the angle at which field lines intersect the earth's surface). Because the precise boundaries of each navigation zone have not been determined empirically, each zone was arbitrarily extended outward +/- 3.0 μT of intensity and +/- 3.0° inclination (or until this extrapolation brought the zone into contact with an adjacent navigation zone). This process yielded navigation zones that were wider in the east-west axis than in the north-south axis (Fig. 3.9), a pattern attributable to the fact that the magnetic field in the North Atlantic varies more with latitude than with longitude (Putman et al. 2011).

In the simulations turtles were transported passively by currents unless they entered one of these three navigation zones, at which point additional velocity was imparted to them in a direction that depended on the zone (see below). When active, turtles swam 0.20 m/s, a speed that both hatchlings and juveniles are capable of sustaining (O'Hara 1980; Salmon & Wyneken 1987; Revelles et al. 2007). The duration of swimming bouts varied among scenarios and included 1 hour per day (maximum distance = 0.72 km/day), 2 hours per day (maximum distance = 1.44 km/day) and 3 hours per day (maximum distance = 2.16 km/day). These swimming durations and corresponding distances are well within the physiological capabilities of young loggerheads (O'Hara 1980; Kramer & Bennett 1981; Salmon & Wyneken 1987; Revelles et al. 2007).

Seven behavioral scenarios were modeled (Table 3.4). One assumed that turtles drifted passively. Three scenarios assumed that turtles swam 1, 2, or 3 hours per day by orienting to regional magnetic fields. The directions that turtles swam matched those of actual turtles that were tested in the same magnetic fields that defined each of the navigation zones [data from Lohmann et al. (2001) and Füxjager et al. (2011)]. At the start of every hour that a simulated turtle swam, a directional heading was assigned. The heading was selected randomly from a range of orientation bearings suitable for each navigation zone. All headings in a given zone were within +/- 40° of the mean heading elicited by the corresponding field. The 80-degree range of orientation angles used approximately matches the 95% confidence interval observed in behavioral experiments (Lohmann et al. 2001; Füxjager et al. 2011)). Additionally, three other scenarios assumed turtles swam within navigation zones for equivalent periods but in random directions. Parameters for each behavioral scenario are summarized in Table 3.4.

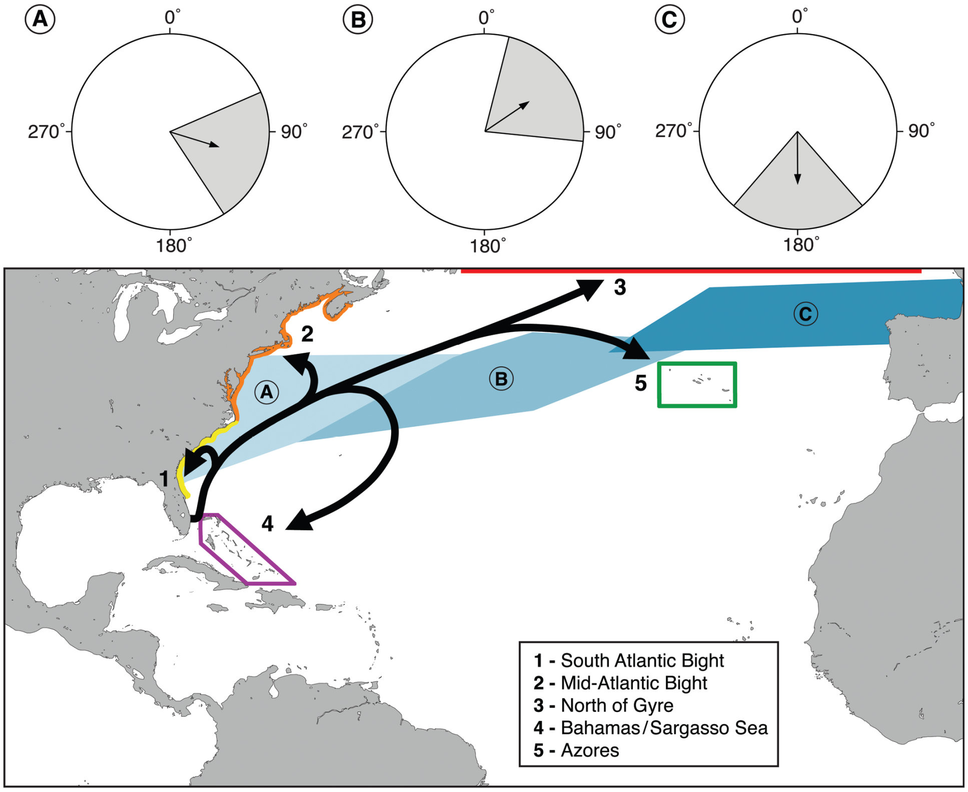

Figure 3.9. Map of possible dispersal routes of juvenile loggerheads migrating from southeast Florida, U.S.A. Given surface currents in the North Atlantic, turtles can be transported along five main trajectories: (1) into the South Atlantic Bight (yellow coastline); (2) into the Mid-Atlantic Bight and Gulf of Maine (orange coastline); (3) north of the subtropical gyre system (north of red line); (4) within the western portion of the Sargasso Sea around the Bahamas (purple polygon), or (5) to the eastern Atlantic passing through the Azores (green rectangle). Blue shaded regions (A, B, and C) demarcate three "navigation zones" defined by regional magnetic fields known to elicit navigational responses in young loggerheads (Lohmann et al. 2001; Füxjager et al. 2011). Zones are irregularly shaped because of how the Earth's field varies across the Atlantic (see Methods). The direction turtles swam in each navigation zone is shown by the gray-shaded area in the corresponding circular diagram. Each hour per day that a turtle swam, it adopted a new heading, randomly chosen from within this gray area. The trajectories of simulated turtles that swam for brief periods when inside the navigation zones were compared to trajectories of turtles that drifted continuously (see Results).

Analyses

To determine how the swimming behavior of turtles influences the dispersal trajectory of loggerheads in the North Atlantic, the percentage of turtles entering five different regions was calculated: (1) the South Atlantic Bight, (2) the Mid-Atlantic Bight and Gulf of Maine, (3) any area north of 46° latitude, (4) the Bahamas, and (5) the Azores (Fig. 3.9). The percent change from passive drift was calculated for turtles entering each region for scenarios involving simulated swimming behavior. Additionally, a two-way ANOVA with replication was used to determine whether the modeled behavior influenced the probability of turtles entering the productive oceanic region near the Azores, a location where young loggerheads are frequently observed (Carr 1986, 1987; Bolten et al. 1998). This region was arbitrarily defined by a rectangle around the archipelago with sides corresponding to latitude 40°N, longitude 32°W, latitude 36°N, and longitude 24°W.

Table 3.4 Parameters of the four behavioral scenarios. Turtles either drifted passively or swam in response to regional magnetic fields for periods of 1, 2, or 3 h per day (see Methods). The distance that simulated turtles swam was calculated from empirical data (O'Hara 1980; Salmon & Wyneken 1987; Revelles et al. 2007) and assumes movement in still water (no contribution of ocean currents). For simulations of swimming turtles, the three swimming directions indicate the mean angle of orientation elicited by the magnetic field that defines each navigation zone (Fig. 1). Swimming direction is based on data obtained by Lohmann et al. (2001) and Füxjager et al. (2011), corrected for average declination over each navigation zone. For each hour that a turtle swam, a new directional heading was randomly assigned from a pool of headings within 40° of the mean angle (see Methods and Fig. 3.9)

Behavior	Swim Duration (hrs/day)	Distance Swum (km/day)	Swimming Direction in North-West Navigation Zone	Swimming Direction in North-Central Navigation Zone	Swimming Direction in North-East Navigation Zone
Passive Drifting	0	0.00	n/a	n/a	n/a
Random Orientation	1	0.72	107° (± 180°)	55° (± 180°)	180° (± 180°)
Random Orientation	2	1.44	107° (± 180°)	55° (± 180°)	180° (± 180°)
Random Orientation	3	2.16	107° (± 180°)	55° (± 180°)	180° (± 180°)
Magnetic Navigation	1	0.72	107° (± 40°)	55° (± 40°)	180° (± 40°)
Magnetic Navigation	2	1.44	107° (± 40°)	55° (± 40°)	180° (± 40°)
Magnetic Navigation	3	2.16	107° (± 40°)	55° (± 40°)	180° (± 40°)

Results

For each scenario of passive drifting and oriented swimming we determined the number of turtles that moved along each of 5 dispersal trajectories (Fig. 3.9). Results indicated that the relative proportions of turtles that followed the various trajectories differed significantly depending on turtle behavior (Fig. 3.10; ANOVA two-factor, $F_{4,6} > 101$, $P < 2.86 \times 10^{-34}$).

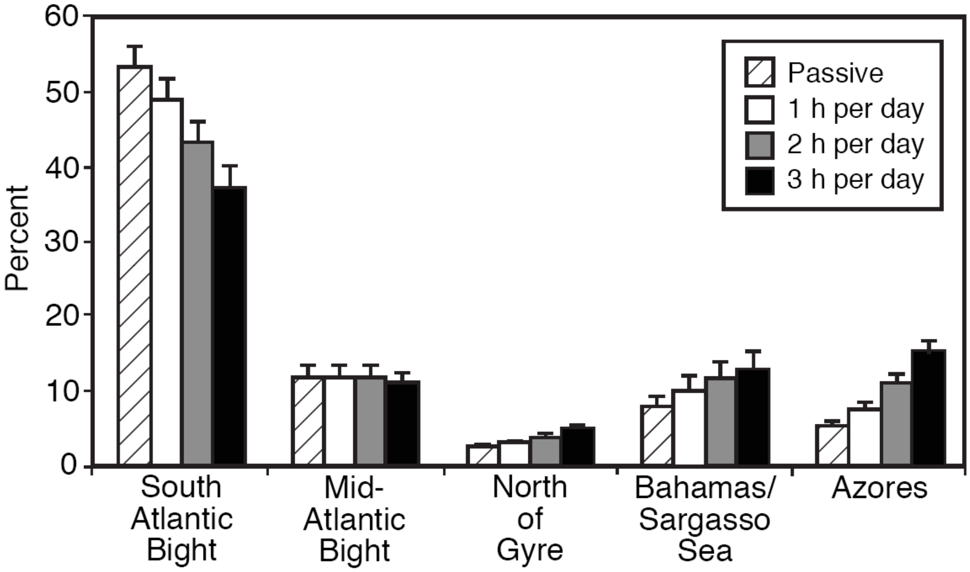

Figure 3.10 Mean percentages of turtles entering specific geographic regions within 5 years. Regions coincide with the trajectories shown in Fig. 3.9 (South Atlantic Bight indicates trajectory 1 in Fig. 1, Mid-Atlantic Bight indicates trajectory 2, North of gyre (latitudes higher than 46° N) indicates trajectory 3, Bahamas/Sargasso Sea indicates trajectory 4, and Azores indicates trajectory 5.) Hashed bars indicate results from simulated turtles that drifted passively. White bars indicate results obtained from simulated turtles that engaged in 1 h of oriented swimming per day, gray bars indicate 2 h of oriented swimming per day, and black bars indicate 3 h of oriented swimming per day. Results of random orientation are not shown because they did not differ from passive drift. Error bars indicate 95% C.I. of the mean.

To better visualize the effects of navigation on the large-scale distribution of turtles, we generated colorized maps of the North Atlantic that highlighted locations where turtle behavior affected the predicted abundance (Fig. 3.11). These maps indicate that, relative to passive drifting, simulated navigation behavior generally led to higher concentrations of turtles within the North Atlantic Subtropical Gyre (Fig. 3.11), an area favorable for the growth and survival of young loggerheads (Carr 1986, 1987; Bolten et al. 1998). In contrast, passive drifting led to more turtles along the margins of the gyre (Fig. 3.11).

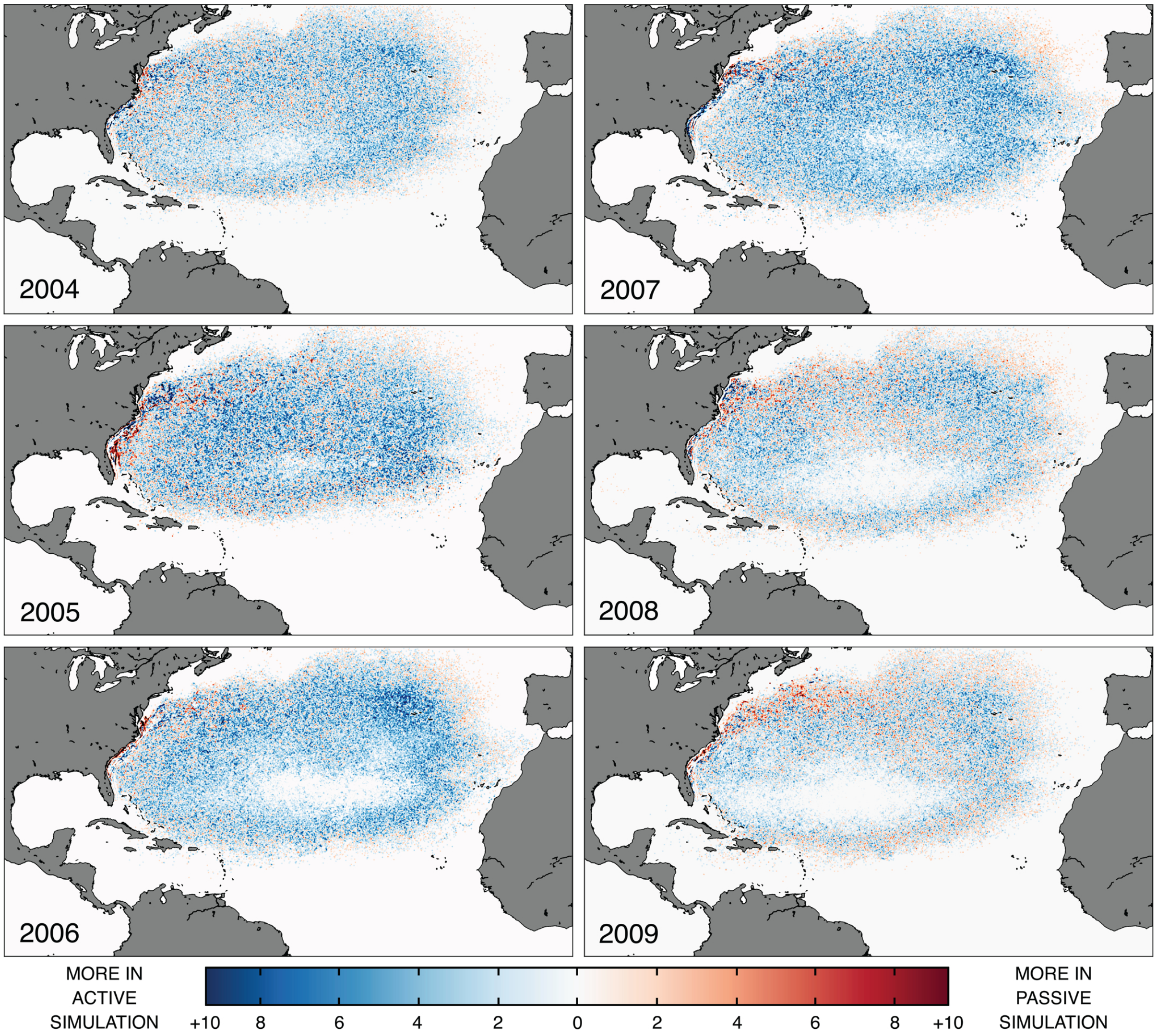

Figure 3.11 The relative difference between the predicted distributions of turtles that drifted passively vs. turtles that engaged in 2 h of oriented swimming per day (distance swum was approximately 1.44 km per day). Red colors indicate areas where the passive drifting scenario predicts more turtles than the swimming scenario; blue colors indicate areas where the magnetic navigation scenario predicts more turtles than the passive scenario. Areas shaded white had the same number of turtles in both scenarios. For each 5-year period modeled, one of the ten replicates of passive drifting and one of the ten replicates of magnetic navigation (2 h per day of swimming) were selected at random. Starting September 15 of each hatching season, the locations of all turtles were plotted at 25-day intervals for the duration of the simulation. A custom Python^{TM} script then highlighted differences in abundance between the two behavioral scenarios at each location in the North Atlantic. Although there is variation in predicted distributions among years, several general patterns are apparent in the output of all simulations. For example, a faint red ring is visible around the periphery of the gyre, indicating that a higher abundance of passively drifting turtles is associated with the gyre's margins. A cluster of blue always exists in the vicinity of the turtles' foraging grounds near the Azores, indicating that magnetic navigation is likely to increase the number of turtles that arrive there. Indeed, for turtles leaving the coast of Florida in 2004 there is a 110% increase in the number of turtles reaching the Azores relative to passive drifters. In 2005, this increase is 117%; in 2006 it is 122%, in 2007 it is 141%, in 2008 it is 75%, and in 2009 it is 57%.

Within the gyre, simulated navigation behavior resulted in a noticeable increase in turtle abundance near the Azores Islands (Fig. 3.11), a high-productivity area known to function as developmental habitat for many Florida loggerheads (Carr 1986, 1987; Bolten et al. 1998). Analyses revealed that even small amounts of oriented swimming had an outsized effect on the likelihood of reaching the Azores (Fig. 3.12). For example, one hour of oriented swimming per day (which resulted in a movement of only 0.72 km) led to a 43.6% increase in the number of turtles reaching the Azores. For 2 and 3 hours of swimming per day, the increases were 106.1% and 187.6% respectively.

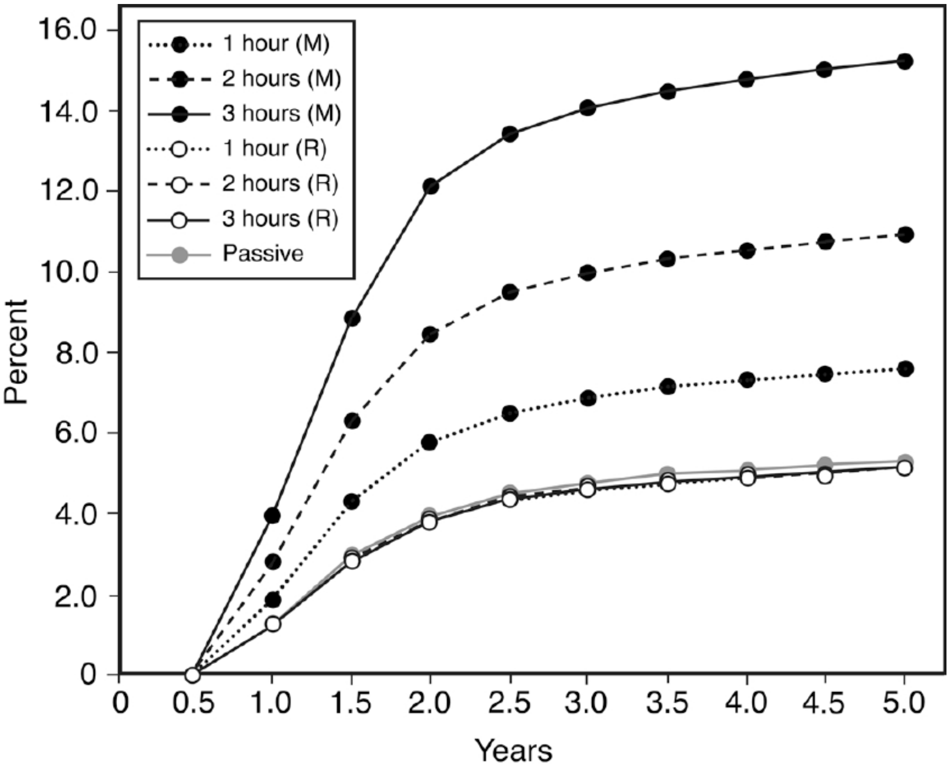

Figure 3.12. The mean percentage of turtles reaching the Azores for the 4 different behavioral scenarios. Grey circles indicate passively drifting turtles. Black circles indicate turtles swimming in response to regional magnetic fields (M). Open circles indicate turtles swimming in random directions (R). The dotted line indicates simulated turtles that swam 1 h per day (approximately 0.72 km per day), the dashed indicates 2 h of swimming per day (approximately 1.44 km per day), and the solid line indicates 3 h of swimming per day (approximately 2.16 km per day). Data points are cumulative (i.e., each percentage reflects the total number of simulated turtles that reached the Azores on or before each point in time).

Results also indicate that, although navigation behavior did not prevent turtles from entering suboptimal oceanic regions (Fig. 3.10), such behavior is likely to help turtles escape from such areas to resume their open-sea migration (Fig. 3.13). For example, among turtles that entered the South Atlantic Bight, those that swam just 1 h per day were 214% more likely to reach the Azores than were those that drifted passively. Greater amounts of swimming further increased the likelihood of escaping these coastal waters and arriving at the Azores (by 542% for turtles that swam 2 h per day and 1418% for those that swam 3 h per day) (Fig. 3.13a). Similarly, turtles that entered the Mid-Atlantic Bight but swam 1-3 h per day were 25-101% more likely to reach the Azores than were passive drifters (Fig. 3.13b), and turtles that crossed latitudes north of 46˚ N were 5-25% more likely to arrive at the Azores if they swam (Fig. 3.13c).

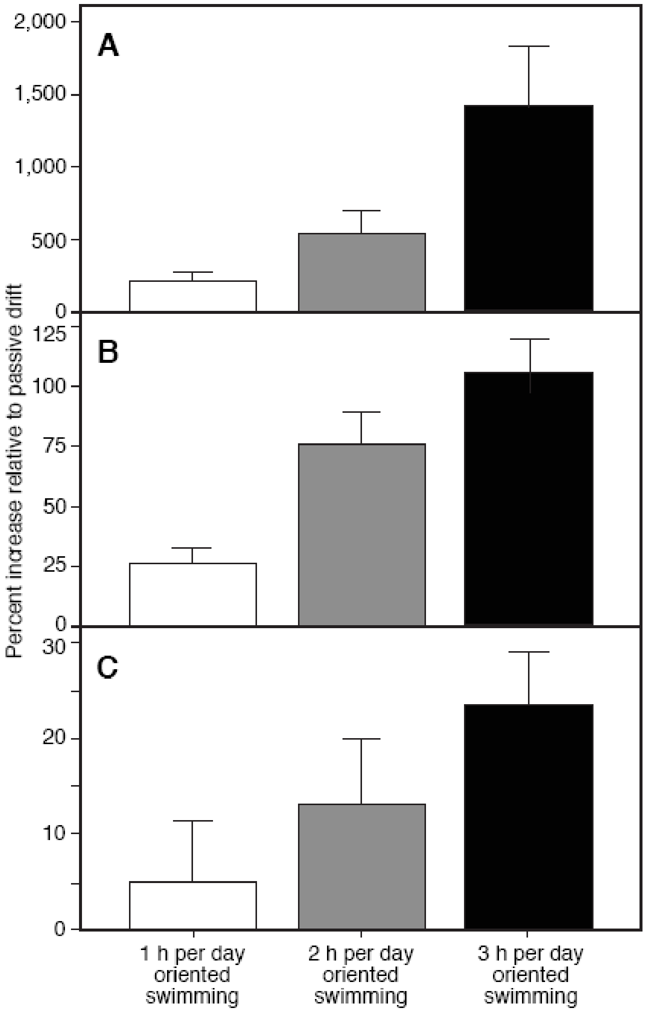

Figure 3.13. Graph showing the effects of directional swimming behavior on outcomes for turtles that enter suboptimal oceanic regions (trajectories 1-3 (Fig. 3.9)). The white bars indicate the mean percent increase of turtles reaching the productive waters of the Azores given 1 h of swimming per day as compared to passive drifting. Grey bars correspond to 2 h of swimming per day, and black bars correspond to 3 h of swimming per day. Error bars represent 95% C.I. of the mean. (A) Results for turtles that entered the South Atlantic Bight. (B) Results for turtles that entered the Mid-Atlantic Bight. (C) Results for turtles that crossed the area north of the gyre.

Discussion

These results imply that young turtles can exert considerable influence on their migratory trajectories despite swimming at velocities much slower than those of many ocean currents (Fig. 3.10-3.13). A simple navigational strategy, in which a few regional magnetic fields elicit directional swimming, greatly increased the probability of turtles reaching habitats favorable for growth and development (Fig. 3.11), while simultaneously reducing the likelihood of turtles entering or remaining in suboptimal geographic areas (Figs. 3.10, 3.13). Moreover, these effects were observed despite a set of conservative assumptions, such as that turtles engage in only brief periods of swimming (1-3 h per day), that they travel distances of just 0.72 - 2.16 km per day (Table 3.4), that they only swim in response to three regional magnetic fields along the northern edge of the gyre, and that they are only weakly oriented (±40° of mean direction, as in laboratory experiments (Lohmann et al. 2001; Füxjager et al. 2011)). The findings presented here suggest a reassessment of the paradigm that small turtles are powerless to influence their migratory movements, and that their distribution on an ocean-wide scale is completely dependent on ocean currents (Carr 1987; Collard & Ogren 1990; Luschi et al. 2003; Hays et al. 2010; Okuyama et al. 2011). Similarly, the results imply that other marine animals viewed as ineffective swimmers may exert greater control over long-distance movements than has long been assumed.

The simulations imply that, rather than relying on an energetically costly strategy of continuous swimming, turtles can advance along the migratory route with relative ease by using limited directional swimming to help them become entrained in currents that will carry them to appropriate oceanic regions. Behavioral experiments also suggest that the headings adopted by turtles in response to each regional field have been selected to take advantage of surface circulation patterns of the North Atlantic Subtropical Gyre (Lohmann et al. 2001; Putman et al. 2011; Füxjager et al. 2011).

In some cases, the advantages that result from a small amount of directional swimming are likely to be considerable. For example, among turtles that entered the predator-rich South Atlantic

Bight, those that engaged in oriented swimming were up to 14 times more likely to reach the Azores than turtles that drifted passively (Fig. 3.13a). These and related findings (Figs. 3.10-3.13) imply that such navigation behavior may have considerable adaptive value. If so, then such behavior is likely to be strongly favored by natural selection and will presumably spread rapidly through a population once it arises. Similarly, as the earth's magnetic field gradually changes over time (Skiles 1985), strong selective pressure is likely to ensure that the navigation responses of turtles evolve in parallel with the changing field, so that fields that exist along the migratory route at any point in time consistently elicit orientation that facilitates movement toward favorable oceanic regions (Lohmann et al. 2001; Lohmann & Lohmann 2003).

To date, all attempts to model the pelagic dispersal of sea turtles have assumed that turtles drift passively (e.g. Hays & Marsh 1997; Blumenthal et al. 2009; Godley et al. 2010; Putman et al. 2010; Okuyama et al. 2011). Although such models can provide a useful first step toward understanding large-scale patterns of distribution, the present results demonstrate that including empirically derived navigational behavior of sea turtles in particle-tracking models can greatly alter predicted patterns of abundance (Fig. 3.11). Thus, models that assume passive drift should be interpreted with caution. In particular, such models may not yield accurate estimates of the contributions that specific nesting populations make to distant mixed-stock foraging grounds or other geographic areas. Incorporating navigation behavior into models of dispersal is likely to provide better predictions of animal distributions, as well as an improved understanding of the ecological and evolutionary processes shaped by animal movement (Werner et al. 1993; Paris et al. 2007; Holyoak et al. 2008; Koehl & Hadfield 2010; Hamann et al. 2011).

Finally, the finding that young turtles can exert an unexpectedly strong influence on their migratory movements has important implications for diverse, weakly swimming marine animals such as larval eels (McCleave et al. 1998; Bonhommeau et al. 2009), juvenile salmon (Azumaya & Ishida 2001), juvenile reef fish (Fisher & Hogan 2007; Paris et al. 2007), and invertebrate larvae (Jeffs et al.

2005). These and other ocean migrants, whose movement appears strongly dictated by currents, might employ similar strategies to increase their probability of reaching appropriate habitat.

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The evolution of magnetic waypoint navigation in sea turtles

Summary

The environmental factors that promote the evolution of long-distance navigational behavior are poorly understood. Here I use a quantitative approach to gain insights into the evolution of magnetic waypoint navigation by hatchling loggerhead sea turtles (*Caretta caretta*) from eastern Florida. These turtles respond to numerous regional magnetic fields that exist along the North Atlantic Subtropical Gyre by swimming in directions that would, in each case, help them advance along their migratory route. However, not all fields that exist in the North Atlantic elicit robust orientation responses by hatchling turtles. To investigate, a geomagnetic model (IGRF-10) was used to map the location of each magnetic field over the past century and oceanic variables were extracted from an ocean circulation model (Global HYCOM) within the area occupied by each field. Multiple-regression analyses show that the strength of orientation of turtles (measured by Rayleigh r-value) to a given magnetic field increases as (1) the area over which the field has drifted between 1900-1975 decreases, (2) the average sea surface temperature over that area increases, (3) the average surface current velocity over that area decreases, and (4) the standard deviation of surface current direction over that area increases. These variables can account for as much as 84% of the variance in orientation strength among magnetic treatments. The findings suggest that the evolution of oriented swimming in response to regional magnetic fields is strongly linked to the geographic stability of specific fields and oceanic factors within those regions that select for directed swimming by turtles.

Introduction

Animals that engage in long-distance migrations possess numerous traits and adaptations that allow them to successfully travel hundreds or thousands of kilometers. Among these adaptations are navigation behaviors that help them follow migratory pathways and locate goal areas. Navigation behavior, in particular, appears to be highly flexible and can evolve rapidly, in only a few decades in some cases (Helbig 1991, 1996; Berthold et al. 1992; Bearhop et al. 2005). However, little is known about the factors that promote the evolution of long-distance navigation behavior or maintain it within a population of migrants. Here the environmental factors associated with navigational behavior are examined in young loggerhead sea turtles (*Caretta caretta*) along their migratory pathway. By determining the environmental correlates of directed swimming by turtles, inferences can be made about the factors that promote and maintain the evolution of navigation behavior.

Juvenile loggerhead turtles from Florida, U.S.A. undergo one of the most spectacular migrations known. Upon emerging from their nests, hatchling loggerheads swim offshore to the Gulf Stream, the western limb of the North Atlantic Subtropical Gyre (Carr 1987). These turtles gradually migrate around the entire North Atlantic basin, taking 6-12 years before eventually returning to the North American coast (Bjorndal et al 2000a; Bowen & Karl 2007). A fascinating aspect of this migration is that young loggerheads appear to guide their movements, at least in part, by using the earth’s magnetic field (Lohmann et al. 2007). Loggerheads orient their swimming in directions that facilitate migration in response to magnetic fields that occur along their migratory route (Lohmann & Lohmann 1994; 1996; Lohmann et al. 2001; Putman et al. 2011; Füxjager et al. 2011). Findings indicate that young loggerheads possess a “magnetic map” based on pairings of the field parameters intensity (field strength) and inclination (angle that field lines intersect the earth’s surface), which provide turtles with information about their location along the gyre (Putman et al. 2011). Perhaps most impressive is that hatchlings are capable of appropriate orientation to fields along their migratory route immediately after emerging from their nests, suggesting that the large-scale magnetic map is inherited, or at least not based on prior navigational experience.

However, recent laboratory experiments show that not all magnetic fields that occur in the North Atlantic elicit strong orientation responses from hatchling turtles (Füxjager et al. 2011; Putman et al. in prep). It is not known why loggerhead turtles have evolved orientation responses to some magnetic fields that occur in the North Atlantic, but not to others. To address this question quantitatively, orientation responses were pooled from studies in which hatchling loggerheads from southeast Florida were exposed to magnetic fields that occur in the North Atlantic. Analyses were carried out to determine whether orientation strength is likely to be influenced by: (1) the stability of a given magnetic field (i.e. rate of secular variation); and/or (2) oceanic variables that occur across the area where the magnetic field exists.

Methods

To determine whether certain environmental factors associated with the fields presented to hatchling loggerheads can predict the variation in orientation strength, a multiple regression approach was used. First, orientation data were taken from previous studies (Lohmann et al. 2001; Putman et al. 2011; Füxjager et al. 2011; Putman et al. in prep) that tested loggerhead hatchlings from southeast Florida in a total of 12 magnetic fields that exist in the North Atlantic. Strength of orientation was measured with the Rayleigh r-value (Batschelet 1981) for each of the 12 treatments (Table 3.5). For further analysis, the magnetic parameters of inclination angle and total field intensity were recorded for each field (Table 3.5).

Table 3.5 Experimental parameters and orientation responses of turtles to magnetic fields that occur in the North Atlantic. 1. Lohmann etl al. (2001); 2. Putman et al. (2011); 3. Füxjager et al. (2011); 4. Putman et al. (in prep).

Present Location	Inclination (°)	Intensity (μT)	Mean Heading (°)	Rayleigh R	Rayleigh P	N
Barbados[4]	35.5	34.1	5.2	0.401	0.027	22
Canary Islands[4]	41.1	39.4	293.1	0.208	0.242	33
Cape Verde Islands[2]	26.1	35.0	230.3	0.336	0.018	35
Straights of Gibraltar[4]	49.5	42.6	138.1	0.124	0.739	21
Greenland[3]	69.0	51.1	121.0	0.16	0.506	27
Mid Atlantic[3]	59.4	46.7	70.8	0.332	0.036	30
NE Florida[1]	59.3	49.1	117.0	0.42	0.01	29
Portugal[1]	59.1	45.2	188.0	0.36	0.05	24
Puerto Rico[2]	46.4	39.3	62.7	0.393	0.032	22
Southern Gyre[1]	16.7	31.0	297	0.35	0.05	26
Suriname[4]	26.1	31.8	163.7	0.151	0.484	32
SW Portugal[3]	54.3	44.0	242.0	0.362	0.028	27

Geomagnetic Secular Variation

To provide a measure of the geographic stability of a given inclination and intensity pairing (hereafter referred as a “magnetic point”) the area over which the field drifted from 1900-1975 was measured (i.e. amount of secular variation). To some extent, how well a turtle resolves inclination and intensity determines the area over which a magnetic point occurs (e.g., the higher the resolution, the smaller the area). Although the resolution of loggerhead sea turtles’ magnetic sense is not known, the following possibilities were considered: that turtles resolved inclination at ± 0.5, 1.0, or 2.0° and intensity with ± 0.5, 1.0, or 2.0 µT. For each field, the inclination angle and intensity were plotted using Kimmo Korhonen’s online mapping tool (http://www.ava.fmi.fi/MAGN/igrf/) which utilizes the International Geomagnetic Reference Field – 11th Generation (IGRF-10) (Macmillan & Maus 2005). The plots of inclination and intensity were overlaid in Adobe Photoshop to determine the location of the magnetic point for the years 1900, 1925, 1950, and 1975.

Initial results revealed that several magnetic points from the southern portion of the gyre only existed prior to 1975 at the coarsest magnetic resolution assumed (2.0° and 2.0 µT). For consistency, the rest of the analysis was therefore restricted to the coarsest resolution plots. Magnetic points from 1900-1975 were overlaid on the same map and the area over which the field drifted was estimated by multiplying the straight-line longitudinal and latitudinal distance that each point spanned (Table 3.6).

Oceanic Factors

For consideration of oceanic factors that might influence orientation strength, model output of the surface conditions of the North Atlantic was extracted from the Hybrid Coordinate Ocean Model (HYCOM) (Beck 2002) using a custom Python script. Daily HYCOM hindcast output (data assimilated) was extracted over 6 years (2004-2010) to generate the following variables for each area marked by one of the twelve magnetic fields: (1) mean temperature; (2) standard deviation of the mean temperature; (3) mean current speed; (4) standard deviation of the mean currents speed; and (5) standard deviation of the mean current direction (Table 3.6). For completeness, the mean current direction over the area is also reported, though it was not included in the analyses.

Estimates of oceanic conditions are meant to reflect the long-term features of ocean circulation associated with particular areas. Although the model output only captures the past 6 years (in contrast to the past century for the magnetic data), ocean circulation in the Atlantic has been similar to present for the past several million years, approximately since the closure of the isthmus of Panama which separated the Atlantic from the Pacific basin (Iturralde-Vinent & MacPhee 1999). Moreover, the annual North Atlantic Oscillation (NAO) indices for the time period examined (2004-2010) appear to be representative of conditions since 1865 (http://ncar.ucar.edu/). Paired T-tests reveal no significant differences between the NAO indices reported for 2004-2010 and other continuous 6-year periods since 1865 (T-test, range of p values = 0.052 - 0.994). Because the NAO is correlated with variability in surface circulation in the North Atlantic (Bellucci & Richards 2006), this suggests that the metrics used in this study are appropriate as proxies of "typical" oceanic conditions that occur across each region.

Table 3.6 Secular variation and oceanic factors associated with each magnetic point. 1. Lohmann et al. (2001); 2. Putman et al. (2011); 3. Füxjager et al. (2011); 4. Putman et al. (in prep).

Present Location	Field Drift 1900-1975 (km^2)	Temp. Mean (°C)	Temp. Std. Dev. (°C)	Current Speed Mean (m/s)	Current Speed Std. Dev. (m/s)	Current Direction Std. Dev. (°)	Current Direction Mean (°)
Barbados[4]	3.42×10^6	28.20	0.95	0.299	0.150	70.0	294.4
Canary Islands[4]	1.84×10^7	20.83	1.97	0.139	0.074	66.3	186.8
Cape Verde Islands[2]	2.88×10^6	23.02	2.25	0.156	0.070	49.0	255.7
Straights of Gibraltar[4]	2.19×10^7	19.41	2.68	0.121	0.071	98.5	236.5
Greenland[3]	7.56×10^6	15.42	2.58	0.301	0.176	87.2	59.5
Mid Atlantic[3]	1.65×10^7	21.55	3.03	0.190	0.104	92.0	110.1
NE Florida[1]	9.11×10^6	25.67	2.39	0.181	0.095	109.9	182.7
Portugal[1]	1.15×10^7	18.66	2.59	0.123	0.073	95.3	228.3
Puerto Rico[2]	1.36×10^7	26.50	1.19	0.129	0.073	65.3	288.1
Southern Gyre[1]	6.74×10^6	27.53	0.92	0.349	0.217	85.6	45.7
Suriname[4]	4.11×10^6	28.09	0.59	0.535	0.187	18.3	314.2
SW Portugal[3]	1.80×10^7	23.35	2.28	0.111	0.064	109.3	210.7

Multiple Regression Analyses

An information theoretic approach was used to assess the possible influence of the environmental variables associated with a magnetic point and the strength of orientation for hatchling turtles. Multiple regression analyses were performed using all possible combinations of the 6 explanatory variables (63 separate analyses). Linear regression analyses were performed in the software package R (v. 2.701). To select the best model, Akaike Information Criteria (AIC) values were calculated and an AIC weight was assigned to each regression model using standard methods (Burnham and Anderson 2002). The AIC weight is the likelihood that, of a candidate set of models, a given model best explains the variance of the dependent variable (in this case, strength of orientation measured by the Rayleigh r-value). All models that had an AIC weight greater than 5.0% were explored in further detail. Finally, for the best model (based on AIC weight and adjusted R^2 value), the coefficients of the explanatory variables and p-values were examined to assess the possible functional relationship between the environmental variables and strength of orientation.

Results

Of the 63 candidate models generated to explain the strength of orientation by turtles to regional magnetic fields, 6 had an AIC weight greater than 5.0% (Table 3.7). The model with the greatest AIC weight (36.9%) was more than twice as likely to be the best fitting model as the next closest. Moreover, the model with greatest AIC weight also had the highest adjusted R^2 value (adj. $R^2 = 0.754$, $F_{4,7} = 9.41$, $p = 0.006$) (Table 3.7).

The variables included in the best model were: (1) area over which the field drifted from 1900-1975; (2) mean temperature; (3) mean current speed; and (4) standard deviation of current direction. All variables significantly contributed to the explanatory power of the model at $p < 0.05$ (Table 3.8). Regression coefficients indicated that the orientation strength (Rayleigh r-value) increased as: (1) the area over which the field drifted decreased; (2) mean temperature increased; (3)

mean current speed decreased; and (4) the standard deviation of current direction increased (Table 3.8).

Table 3.7 AIC metrics used in model selection and results of multiple regression analyses.

Variables in Model	AIC	Δ_i	AIC Weight	R^2	adj. R^2	F	P	df
field drift, mean temp, mean speed, & s.d. direction	-30.78	0	36.9%	0.843	0.754	9.41	0.006	(4,7)
field drift, mean temp, s.d. temp, mean speed, & s.d. direction	-28.87	1.91	14.2%	0.844	0.715	6.51	0.021	(5,6)
field drift, mean temp, mean speed,s.d.speed, & s.d. direction	-28.81	1.97	13.8%	0.844	0.713	6.47	0.021	(5,6)
mean temp & s.d. temp	-27.12	3.66	5.9%	0.438	0.31	3.51	0.075	(2,9)
field drift, mean temp, s.d. speed & s.d. direction	-27.09	3.69	5.8%	0.787	0.665	6.45	0.020	(4,7)
field drift, mean temp, s.d. temp, mean speed, s.d. speed, & s.d. direction	-27.03	3.75	5.7%	0.846	0.662	4.59	0.058	(6,5)
mean of all other (58) models	-18.18	12.60	0.3%	--	--	--	--	--

Table 3.8 Regression coefficients and significance levels of variables contributing to the best model.

Variables in "Best" Model	Coefficients	Standard Error	t statistic	P-value
Intercept	-0.00091	0.148248	-0.00615	0.995265
Area of Field Drift (1900-1975)	-1.1×10^{-8}	3.37E-09	-3.21272	0.0148
Mean Temperature	0.017787	0.004455	3.992868	0.0052
Mean Current Speed	-0.63187	0.180856	-3.49376	0.0101
Std. Dev. of Current Direction	0.001871	0.00078	2.400002	0.0475

Discussion

Examination of AIC weights of the candidate models to explain orientation strength of hatchling loggerheads to regional magnetic fields clearly reveals a single superior model (Table 3.7). The next two best fitting models each included an additional parameter (standard deviation of temperature or standard deviation of current speed) that contributed only 0.3% of explanatory power to the model when they were both added to the best model (R^2 of the best model = 0.843, R^2 of the full model = 0.846). Further analysis shows that the four variables that comprise the best model (the area over which the field drifted, mean temperature, mean current speed, and the standard deviation of current direction) are highly relevant to understanding what environmental factors are associated with strong orientation to regional magnetic fields (Table 3.7, 3.8). Additionally, they provide insight into general environmental conditions that promote the evolution of navigation behavior.

Field Drift

The earth's magnetic field is generated and maintained by a self-exciting dynamo produced by the movement of the earth's liquid outer core. The field produced can be thought of as that of a bar magnet (Skiles 1985). However, unlike a simple bar magnet, the dynamo process does not create a static field, but one that undergoes long-term, non-periodic changes known as secular variation. Secular variation causes parameters of the magnetic field (e.g. inclination and intensity) to gradually shift across the globe with the rate of change varying by location and throughout time (de Santis et al. 2002; Macmillan & Maus 2005) (Fig. 3.14).

Some researchers have questioned how animals could inherit a map based on continuously shifting magnetic information (Courtillot et al. 1997; Walker et al. 2002; Alerstam 2006). The findings of this study suggest that secular variation does impose constraints on the evolution of an inherited magnetic map. Magnetic points such as those presently associated with the Straits of Gibraltar and the Canary Islands have shifted from the Caribbean Sea to the eastern Atlantic during the past century. Because of the extensive secular variation, it is not surprising that these fields do not elicit strong orientation responses from hatchling turtles. Presumably, evolving an orientation response to a magnetic field that does not consistently mark an oceanic region would be impossible. Over the past century, most fields in the Atlantic, however, have not drifted as far and turtles can, apparently, use them as reliable navigational markers.

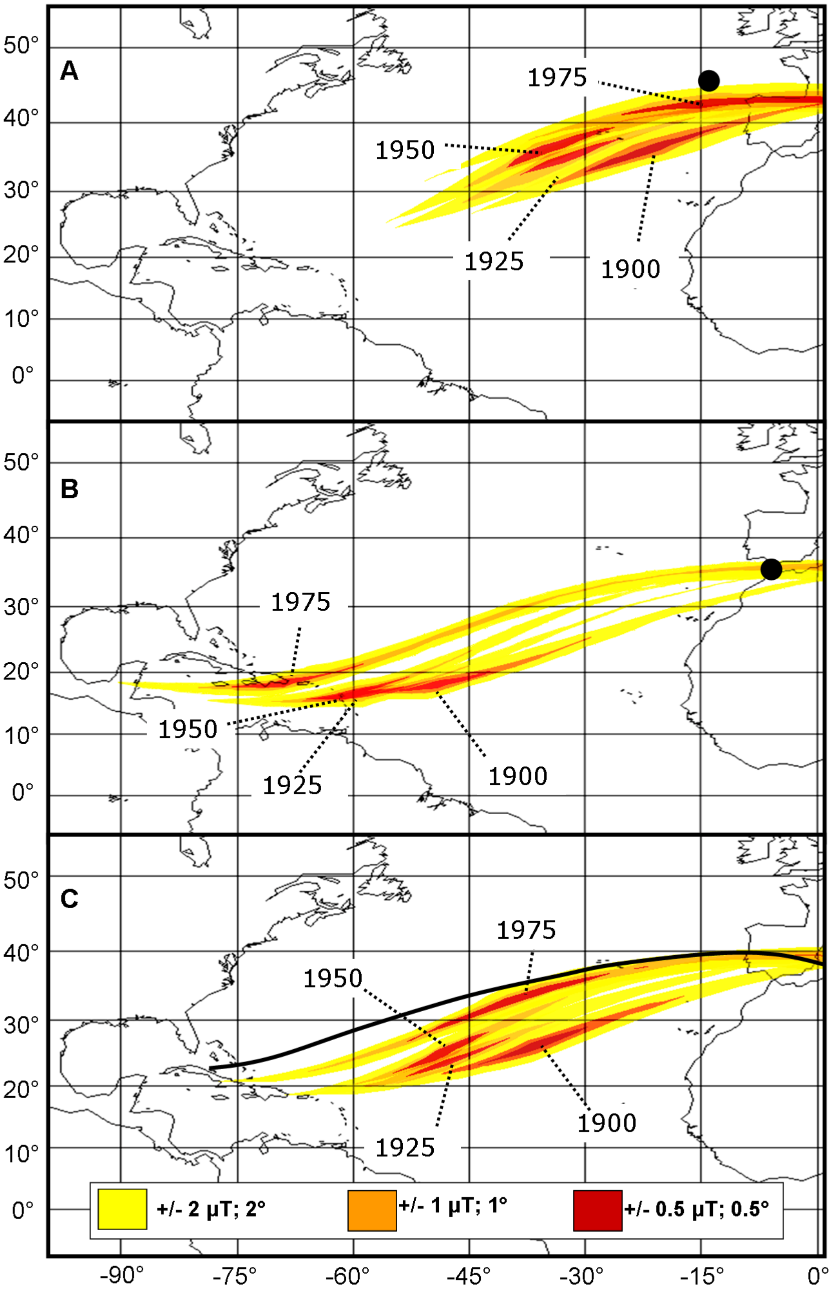

Figure 3.14 Maps of secular variation for three magnetic points in the North Atlantic from 1900-1975 from IGRF-10 output. Colors correspond to the area covered by each point assuming different resolution of magnetic intensity and inclination angle by turtles. (A) During the past century the magnetic field that exists near Portugal (black circle) unambiguously marked the northeastern portion of the gyre. This field elicited southward orientation from turtles (Lohmann et al. 2001) which would facilitate movement away from unsuitably cold waters (Fig. 3.15). (B) The field that exists near the Straights of Gibraltar (black circle) moved from the Caribbean Sea to Mediterranean Sea in the past 100 years and would be unlikely to serve as a navigational marker in an inherited map. This field elicited orientation from turtles that could not be distinguished from random (Putman et al. in prep). (C) The field denoted as SW Portugal by Füxjager et al. (2011) presently spans the width of the North Atlantic (black line); however, during the past century the field primarily corresponded to the central portion of the gyre. This field elicited west-southwest orientation from hatchlings, which in the past century would have promoted transport along the southern edge of the gyre where currents are faster and moving towards North America (Fig. 3.16). Similarly directed swimming along the present location of this field would also promote transport back to North America, where older juveniles take up residence.

For young loggerheads, moderate rates of secular variation do not seem to pose an insurmountable navigational problem for the evolution of an inherited magnetic map. Migratory behavior appears to be highly flexible over relatively short timescales (Alerstam 2006; Bearhop et al. 2005; Berthold et al. 1992), and change in orientation behavior appears to be controlled by only a few genes (Helbig 1996). Whether the orientation of loggerhead turtles to magnetic points evolves at a pace similar to other migrants is not known. However, a recent study modeling loggerhead navigation suggests that even minimal orientation precision and swim duration in response to magnetic points can increase the probability of young turtles reaching their foraging grounds by 40% to 180% compared to passive drifting (Ch. 3, Section 4). It is therefore reasonable to assume that orientation to magnetic fields confers a strong selective advantage, and thus, the continued selection for appropriate orientation responses is likely to match rates of secular variation for most magnetic points.

Oceanic Conditions

Regression analyses indicate that, as mean sea surface temperature over an oceanic area increases, the strength of orientation to the magnetic point that marks that area increases. Strong orientation responses are unlikely to evolve to magnetic points that mark regions consistently associated with cold temperatures. This might be because lethargic swimming by turtles, regardless of the direction, might be insufficient to confer a fitness advantage and thus not selected for. Perhaps the most extreme scenario is for the “Greenland” magnetic point, which throughout the century remained in oceanic areas much colder than is suitable for loggerheads (Witt et al. 2010). Presumably turtles encountering this area would not survive and any orientation bias to this field could not be selected for. Indeed, turtles exposed to this field exhibited orientation behavior that could not be distinguished from random (Füxjager et al. 2011).

Even within the gyre, magnetic fields that mark warmer areas are likely to elicit stronger orientation responses than colder areas because activity level and swim speed increase with temperature (O’Hara 1980; Spotila & Standora 1985). Turtles with increased swimming behavior may be better able control their position and natural selection might favor specific directional swimming.

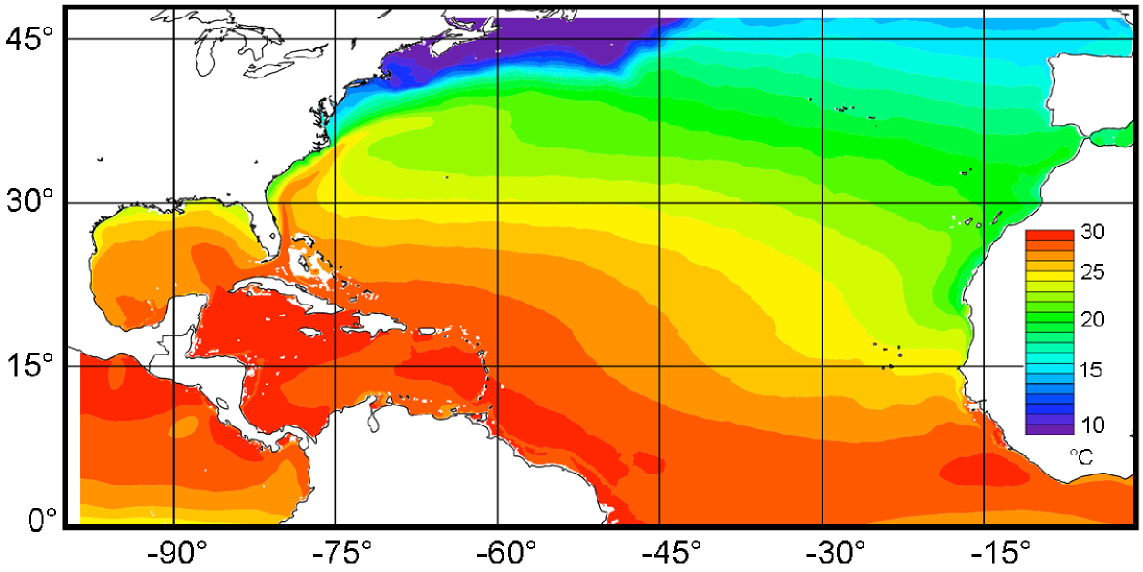

Figure 3.15 Mean surface temperature across the North Atlantic from Global HYCOM output (2004-2010). Magnetic fields that exist at locations with warmer temperatures elicited stronger orientation responses than did fields marking locations with cooler temperatures.

As the mean current speed over an oceanic area increases, the orientation strength to the magnetic point marking that area decreases. Across regions where surface currents are typically fast, the direction that turtles swim might be of little consequence because turtles may be unable to control their direction of travel. In contrast, evolution of strong orientation responses to magnetic points is likely to be promoted for fields that exist across oceanic regions where currents are relatively slow, because turtles can potentially “choose” a direction to travel and natural selection will have selective consequences. Moreover, turtles encountering oceanic regions with slower currents may be served well by actively moving into faster flowing portions of the gyre where their migratory transport will be enhanced by stronger currents.

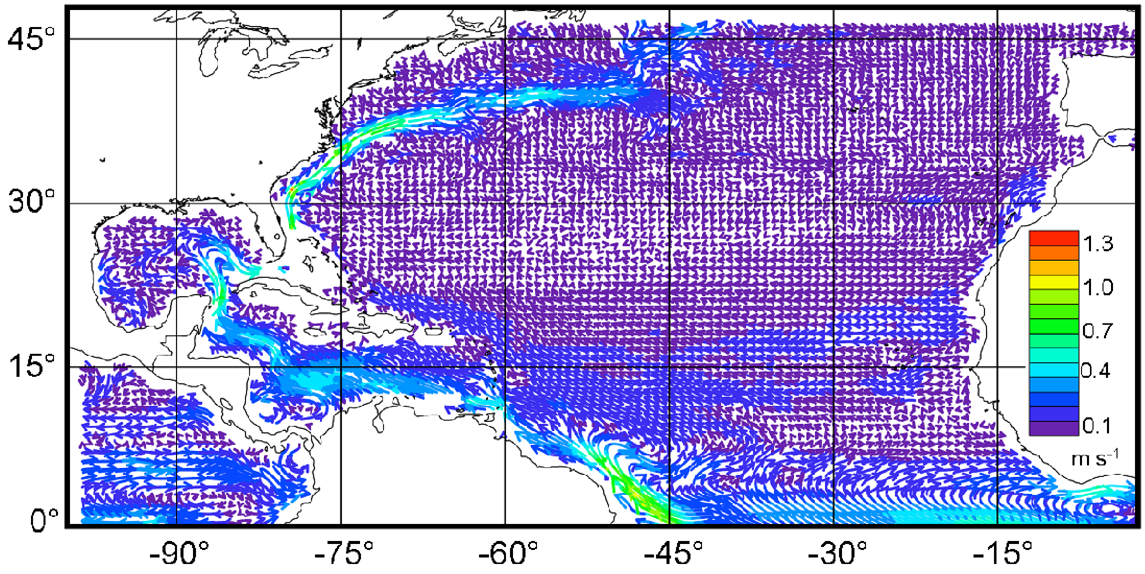

Figure 3.16 Mean surface velocity across the North Atlantic from Global HYCOM output (2004-2010). Magnetic fields that exist at locations with lower current velocities elicited stronger orientation responses than did fields marking locations with higher velocities. Presumably locations with consistently low current velocity require turtles to make progress along the migratory path under their own power, possibly by swimming in directions that would lead them into faster flowing waters to mitigate the energetic cost of swimming.

The standard deviation of current direction is positively correlated with orientation strength. Areas where current direction has a high standard deviation necessarily correspond to locations where the direction of currents is highly variable (Fig. 3.17). Across stretches of ocean where current direction is temporally variable, a selective advantage might be gained by turtles that orient their movements in a particular direction to ensure that they advance along the main migratory pathway. Oriented swimming in such circumstances might make the migration more predictable, over the timescale of multiple generations, by allowing turtles from a given population to consistently encounter certain oceanic areas. Ensuring predictability might be an important aspect of a navigational system that is largely inherited. Turtles following trajectories that are atypical of the population as whole might have difficulty returning to the migratory path if they are transported to areas marked by magnetic fields to which the population has not evolved an orientation response. Indeed, it might be difficult for the population to evolve responses to magnetic fields that mark locations that turtles rarely encounter because the natural selection process would be restricted to only a few individuals.

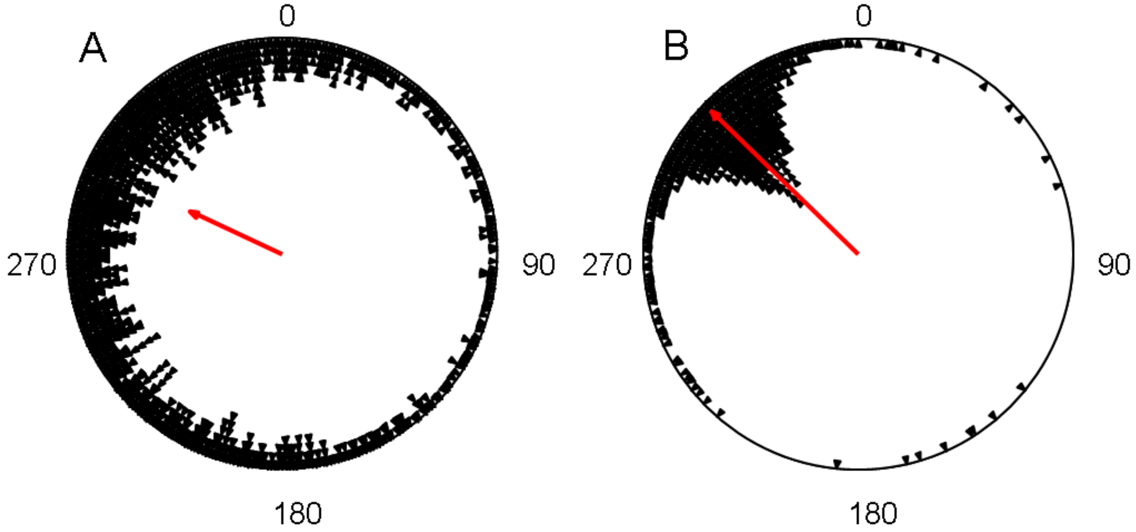

Figure 3.17 Example of variability in current directions at two locations in the North Atlantic from Global HYCOM output (2004-2010). In circle diagrams 0 corresponds to geographic north. Black triangles represent the current direction for a single day (some data overlap). The red arrow indicates the mean direction of the current, with the length proportional to the Rayleigh r-value. The areas possess similar mean temperature and mean current velocity but differ significantly in the degree of scatter. (A) The region marked by the "Barbados" magnetic point corresponds to the southern end of the Guinea Current where water predominately flows either into the Caribbean Sea or north along the Antilles Archipelago (standard deviation of mean = 70.0°). Turtles exposed to this field were well oriented to the north. (B) The area marked by the "Suriname" magnetic point corresponds to a region south of "Barbados" well within the North Brazil Current, a fast flowing northwesterly current. The orientation of turtles exposed to this field could not be distinguished from random.

Conclusions

The findings of this study suggest several important generalizations that can be made about the evolution of orientation behavior by migratory animals. First, orientation responses are likely to evolve only to stable navigational markers, those that consistently demarcate a particular geographical area. For animals that rely on magnetic information, this means that the rate of secular variation needs to be low. However, the same consideration of "cue stability" holds for navigational markers based on other sensory modalities of navigation, such as those that utilize chemical, auditory, or visual information. Of equal importance, orientation responses, observed at the population level, are most likely to evolve under environmental conditions that allow selection for (or against) the directed movements of animals. This likely means that the orientation cue must be perceived at locations where conditions are safely within an animal’s physiological limits (e.g. an appropriate temperature); otherwise the animal will be incapable of engaging in directed locomotion and the orientation phenotype will not experience natural selection. Similarly, for marine animals, if oceanic currents consistently overwhelm the swimming direction chosen, that orientation phenotype will be exposed to reduced selection compared to areas where currents are slower. Additionally, stronger orientation responses are likely to evolve under conditions in which failing to choose a direction leads to unpredictable and potentially negative results. In the case of marine animals, areas of high temporal current variability are likely to be such locations. Finally, this study highlights the importance of considering environmental conditions along the migratory routes of animals when determining how navigation behavior evolves and is maintained. The findings presented here are likely to be broadly applicable to other animals that rely on inherited positional information to navigate.

Special Thanks

K.J. Lohmann will be a co-author on the published m.s.

CHAPTER 4

NATAL HOMING AND THE MAGNETIC IMPRINTING HYPOTHESIS

Diverse ocean migrants, including some sea turtle, fish, mammal, and bird species, begin life in particular reproductive areas, disperse across vast expanses of sea, and then return as adults to their natal areas to reproduce (Lohmann et al. 2007). Little is known about how these and other marine animals guide themselves to their natal region from hundreds or thousands of kilometers away after absences ranging in duration from a few months to a decade or more. One hypothesis is that animals imprint on the magnetic field of their home area and use this information to return (Lohmann et al. 1999). Because the Earth's field varies predictably across the globe, different geographic areas are marked by distinctive magnetic fields that might, in principle, provide unique magnetic signatures for natal areas (Lohmann et al. 2007). A potentially serious complication, however, is that the Earth's field changes gradually over time (Lohmann et al. 1999; 2007). Thus, the fields marking natal areas slowly drift, and might make natal homing via magnetic imprinting challenging (Courtillot et al. 1997; Lohmann et al. 1999; Alerstam 2006). Although it has been established that navigational errors associated with natal homing can have important consequences, such as the colonization of new areas, promoting gene flow, or reducing fitness of the straying animal or its offspring (Quinn 2005; Lohmann et al. 2008a; Lin et al. 2008), it is unclear how secular variation might act on the natal homing process. In this chapter I use models of secular variation to quantitatively assess whether magnetic imprinting is compatible with the known precision of animals engaging in natal homing and the ecological implications of secular variation for the process of natal homing by magnetic imprinting.

Compatibility of magnetic imprinting and secular variation

Summary

Diverse ocean migrants begin life in particular reproductive areas along coastlines, disperse across vast expanses of sea, and then return as adults to their natal areas to reproduce. Although it is unknown how marine animals guide themselves to the correct coastal region from hundreds or thousands of kilometers away, one hypothesis is that animals imprint on the magnetic field of their home area and use this information to return. A potentially serious complication for this hypothesis is that the Earth's field changes gradually over time, causing the magnetic signatures that define natal areas to slowly drift. This secular variation could make natal homing via magnetic imprinting impossible if the magnetic signatures moved too far from the natal area. To investigate whether magnetic imprinting is compatible with secular variation, navigational errors associated with magnetic imprinting were modeled for the Kemp's ridley sea turtle (*Lepidochelys kempii*), an endangered species that ranges widely over the Gulf of Mexico, northern Caribbean, and the eastern U.S. coast, but returns to nest along a single, limited region of coastline in northern Mexico. Results spanning 1600-2010 indicate that by relying on the magnetic inclination angle, a field parameter turtles are known to detect, first-time nesters could consistently home to the narrow stretch of beach where 98% of the species presently nests. This demonstrates that the magnetic imprinting hypothesis is compatible with recent rates of secular variation and can potentially account for how the Kemp's ridley turtle, and perhaps other species, return to natal regions along continental coastlines even after absences of a decade or more.

Introduction

Diverse ocean migrants, including some sea turtles, elephant seals, and salmon, begin life in particular reproductive areas along coastlines, disperse across vast expanses of sea, and then return as adults to their natal areas to reproduce (Lohmann et al. 1999; McConnell 2002; Quinn 2005). Little is known about how such marine animals guide themselves to the correct coastal region from hundreds or thousands of kilometers away and after absences ranging in duration from a few months to a decade or more. One hypothesis is that animals imprint on the magnetic field of their home area and use this information to return (Lohmann 1999). The Earth's field varies predictably across the globe, so different geographic areas are marked by distinctive magnetic fields that might, in principle, provide unique magnetic signatures for natal areas (Lohmann et al. 2007).

A potentially serious complication for this hypothesis is that the Earth's field changes gradually over time (Lohmann et al. 1999; 2007), causing the magnetic signatures that define natal areas to slowly drift. This secular variation could make natal homing via magnetic imprinting impossible if the magnetic signatures moved too far from the natal area (Courtillot et al. 1997; Lohmann et al. 1999; Alerstam et al. 2003). To investigate whether magnetic imprinting is compatible with secular variation, a species with a life history that poses challenges for the hypothesis was chosen, because if magnetic imprinting is consistent with natal homing under unfavorable circumstances, then it would also be plausible in most other cases. The Kemp's ridley sea turtle (*Lepidochelys kempii*) was chosen because it ranges widely over the Gulf of Mexico, northern Caribbean, and the eastern U.S. coast, but returns to nest along a single, limited region of coastline in northern Mexico (Plotkin 2007). This species requires approximately 10–15 years to reach sexual maturity (Plotkin 2007) and is thus absent from its natal area for much longer than animals such as salmon and elephant seals (McConnell 2002; Quinn 2005). Given this long absence, the Kemp's ridley appears to be particularly susceptible to effects of secular variation if it relies on magnetic imprinting.

In principle, an animal might exploit geomagnetic cues in several different ways to identify its natal area, with the optimal strategy differing depending on whether the target area is along a continental coastline or on an island (Lohmann 1999; 2007). For species such as the Kemp's ridley that nest along continental coastlines, each coastal area typically has a different magnetic field associated with it (Lohmann et al. 1999; 2007) (Figure 4.1). Sea turtles detect two elements of the magnetic field: the inclination angle (angle at which the field lines intersect the Earth's surface) and the total field intensity (Lohmann et al. 1999). This model, based on a hypothetical strategy of magnetic navigation proposed previously for turtles that nest on continents (Lohmann et al. 1999), assumes that Kemp's ridley turtles imprint on one of these geomagnetic elements and return at sexual maturity to the coastal location marked by the same magnetic value. One analysis assumed turtles mature at 10 years, whereas a second assumed 15 years; these values bracket most estimates of time to maturation (Plotkin 2007). The model further assumed that turtles could not compensate for field change. Two geomagnetic models (Barraclough 1974; MacMillan & Maus 2005) were used in combination with GIS software to quantify the movement of the magnetic field between the years 1600 and 2010 at Rancho Nuevo, the beach with the highest nesting density (Figure 4.1).

Methods

Magnetic Models

The International Geomagnetic Reference Field 10th generation model (IGRF-10) was used to determine changes in the magnetic field from 1900-2010 (MacMillan & Maus 2005). This software predicts the main-field values of magnetic elements at any latitude and longitude for the years1900-2010. The main field coefficients are functions of time and for the IGRF-10 the change is assumed to be linear over five-year intervals. For the most recent five-year epoch (2005-2010), the rate of change is given by predictive secular variation coefficients. Values produced for the magnetic elements of this model have a high degree of accuracy (rms errors for the main field are listed for each range of coefficients: 100 nT from 1900-1940, 300-100 nT decreasing linearly from 1945-1960, 50 nT from 1965-1990 and 10-20 nT from 2000-2010). The calculator used in this study is available on the NOAA National Geophysical Data Center website (http://www.ngdc.noaa.gov/seg/geomag/jsp/IGRFWMM.jsp).

Changes in the magnetic field from 1600-1900 were calculated using a second geomagnetic model based on data from the British Geological Survey (Barraclough 1974) and provided online by the U.S. Geological Survey (http://geomag.usgs.gov/models/models/). The main field coefficients are again functions of time and the change is assumed to be linear; however, due to larger time scales the model provides coefficients for 50-year intervals. Rms errors for the main field are not available for this model.

Calculating Navigational Errors

To quantify how elements of the magnetic field moved along the coastline over time and thus calculate expected navigational errors of returning turtles, the geomagnetic models were used to determine magnetic fields that existed at various points in time at Rancho Nuevo and at locations every 0.05° of latitude north and south of that point along the Mexican coastline. For example, the values of inclination and total field intensity were determined for Rancho Nuevo in 1900. To determine the navigational error expected for a turtle leaving the coast in 1900 and returning in 1910, another analysis was done for Rancho Nuevo and the rest of the Mexican coastline for 1910. In this way, the location (in 1910) of the inclination angle and intensity that existed at Rancho Nuevo in 1900 could be determined, and the distance that each field parameter drifted during the hypothetical absence of the turtle from its natal beach could be measured. Measurements of distance were made using Google Earth^{TM} software, and reflected distance along the coastline (not straight-line distance).

Results

Results indicate that Kemp’s ridley turtles imprinting on the inclination angle of Rancho Nuevo between 1600 - 1900 would return to the coast an average of about 34 km away from their natal site if absent for 10 years or an average of about 51 km if absent for 15 years (Figs 4.1a 4.2, Table 4.1). For the more recent and detailed model (1900 - 2010), imprinting on inclination angle and returning to the natal site after 10 years would lead to average navigational errors of 23 km or an average of 34 km if absent for 15 years. Between 1600 and 1900, imprinting on field intensity would lead to returns that average 54 km from the natal site for a 10-year absence and 83 km for a 15-year absence (Figs 4.1b, 4.2, Table 4.1). For the 1900-2010 model, imprinting on intensity would result in an average navigational error of 89 km if turtles returned after 10 years or 133 km if returning after 15 years (Figs. 4.1b, 4.2, Table 4.2)

Table 4.1. Modeled navigational errors for Kemp's ridleys assuming time to maturity at 10 and 15 years, imprinting on either inclination angle (Inc) or total field intensity (Int) based on BGS from 1600-1900. Whether the navigational error is south (S) or north (N) of Rancho Nuevo, Mexico is noted.

Year	10 yr Inc (km)	15 yr Inc (km)	10 yr Int (km)	15 yr Int (km)
1600	5.6 S	5.6 S	144.7 N	217.1 N
1650	89.1 S	133.6 S	27.8 S	50.1 S
1700	55.7 S	83.5 S	72.4 S	111.3 S
1750	16.7 N	22.3 N	16.7 N	22.3 N
1800	27.7 S	44.5 S	11.1 N	16.7 N
1850	11.2 S	16.7 S	50.2 N	77.9 N
Mean:	**34.3**	**51.0**	**53.8**	**82.6**
95% CI:	**25.7**	**39.2**	**40.0**	**59.8**

Table 4.2. Modeled navigational errors for Kemp's ridleys assuming time to maturity at 10 and 15 years, imprinting on either inclination angle (Inc) or total field intensity (Int) based on IGRF-10 from 1900-2010. Whether the navigational error is south (S), north (N) or at Rancho Nuevo, Mexico (RN*) is noted.

Year	10 yr Inc (km)	15 yr Inc (km)	10 yr Int (km)	15 yr Int (km)
1900	56.3 S	90.3 S	33.0 N	66.3 N
1905	67.8 S	90.3 S	55.2 N	99.5 N
1910	56.3 S	78.9 S	77.3 N	127.2 N
1915	44.4 S	62.2 S	93.9 N	144.1 N
1920	38.8 S	56.3 S	93.9 N	132.8 N
1925	38.8 S	44.4 S	77.3 N	110.5 N
1930	27.7 S	16.6 S	66.3 N	93.9 N
1935	RN*	5.5 N	55.2 N	93.9 N
1940	11.0 N	27.7 N	66.3 N	105.0 N
1945	16.6 N	22.1 N	77.3 N	110.5 N
1950	22.1 N	16.6 N	71.7 N	110.5 N
1955	RN*	5.5 N	66.3 N	105.0 N
1960	RN*	5.5 N	77.3 N	127.2 N
1965	11.0N	RN*	88.4 N	155.4 N
1970	5.5 S	11.1 S	116.1 N	166.8 N
1975	11.1 S	27.7 S	116.1 N	166.8 N
1980	16.6 S	27.7 S	99.5 N	144.1 N
1985	22.1 S	22.1 S	93.9 N	172.5 N
1990	11.1 S	RN*	116.1 N	200.8 N
1995	11.0 N	22.1 N	155.4 N	219.1 N
2000	22.1 N	-	166.8 N	-
Mean:	**23.4**	**31.6**	**88.7**	**132.6**
95% CI:	**8.5**	**12.7**	**13.7**	**16.9**

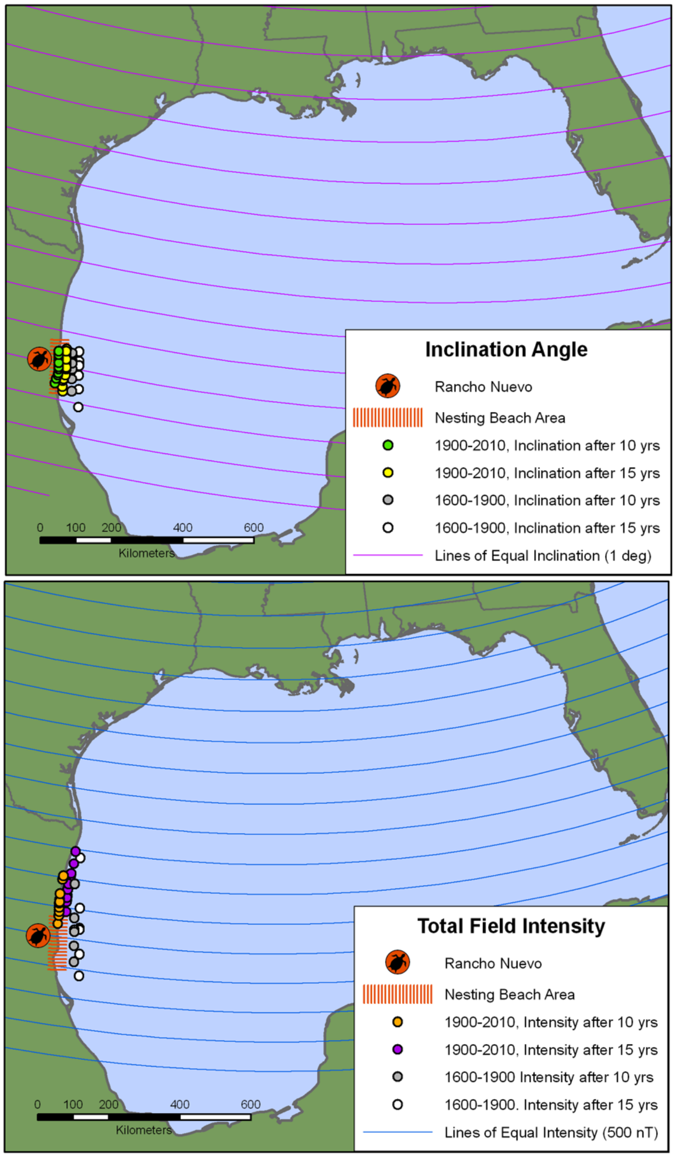

Figure 4.1: Map of the Gulf of Mexico indicating the nesting area of the Kemp's ridley turtle and the locations to which turtles would hypothetically return under two simple magnetic imprinting strategies. The red hatched lines indicate the region of coastline (approximately 160 km) in which 98% of nests of the species are deposited (Marquez et al. 2001; Plotkin 2007). The turtle symbol indicates the location of Rancho Nuevo, Mexico (23.20°N, 97.77°W), the site of peak nesting density (Marquez 2001; Plotkin 2007). Isolines in (A) indicate 1º increments of magnetic inclination; in (B) they indicate 500 nT increments of total intensity.
(A) Predicted locations of returns if turtles imprint on the magnetic inclination angle at Rancho Nuevo and then return 10 or 15 years later to the coastal location with the same inclination angle. Each colored dot indicates the return location for a turtle leaving the coast in a specific year (1900, 1905, and so on). Because some return locations are nearly identical, not all dots are visible results.
(B) Predicted locations of returns if turtles imprint on the magnetic intensity at Rancho Nuevo. Conventions are as before.

Discussion

The results demonstrate that the precision of natal homing predicted by the magnetic imprinting hypothesis is consistent with the precision known to occur in the Kemp's ridley turtle. The modeled returns of turtles imprinting on the inclination angle at Rancho Nuevo indicate that, for the last 400 years, first-time nesters could consistently home to the narrow stretch of beach where 98% of nests are presently deposited by this species (Fig. 4.1a). Though modeled returns of Kemp's ridley show that imprinting on field intensity does not always lead turtles directly back to the species' main nesting area, turtles would arrive near their natal region (Fig. 4.1b). In principle, simple strategies of magnetic imprinting can return turtles to their natal region, at which point they might use other, local cues to pinpoint particular nesting areas. Short-range cues available in the vicinity of nesting beaches might include pheromones secreted by females aggregating offshore in preparation for mass nesting events (Plotkin 2007), visual cues associated with the nesting areas, or distinctive chemical cues from the nesting beach leaching into the sea. Thus, magnetic imprinting might serve to return turtles to a general coastal location, around which they search for their final target. The precision of magnetic navigation might improve after the initial return migration because female Kemp’s ridley turtles nest every 1–2 years once they have matured (Plotkin 2007). Thus, experienced nesters return at much shorter intervals which provide less time for the field to change; moreover, turtles might update their knowledge of the magnetic field at the nesting beach each time they visit and use this information to target the natal area more accurately (Lohmann et al. 1999).

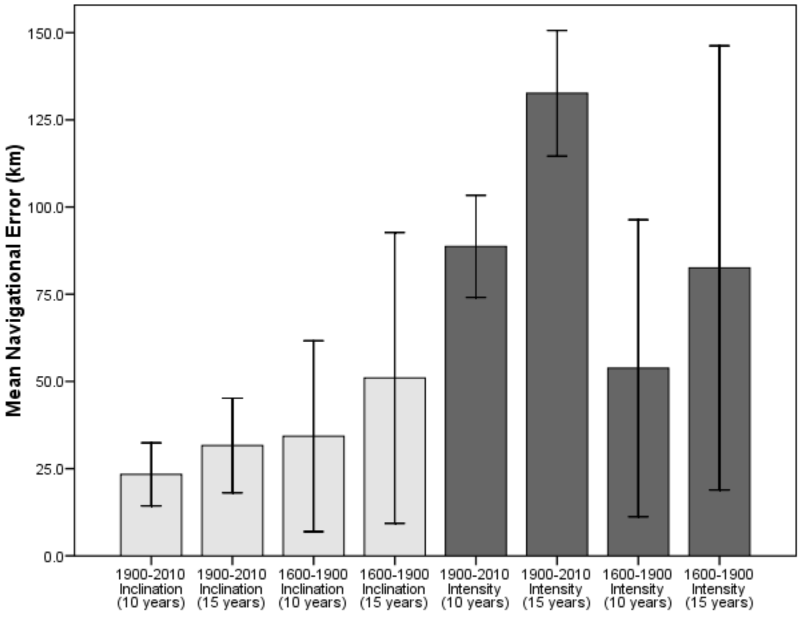

Figure 4.2. Bar graph showing hypothetical navigational errors for turtles that imprinted on inclination angle or intensity at specific points in time and returned to the coastal location marked by the same magnetic value 10 or 15 years later. For simplicity all turtles were assumed to enter the ocean as hatchlings at Rancho Nuevo (indicated by 0 km on the vertical axis), the beach with the highest concentration of nesting. Light-colored bars on the left half of the graph indicate outcomes if turtles imprint on inclination angle; the different means indicate results for different periods (1900–2010 or 1600–1900) and different assumptions about time to maturation (10 years or 15 years) as indicated below each bar. Dark bars on the right half of the graph indicate outcomes if turtles imprint on total intensity. Error bars indicate the 95% confidence interval for the mean.

Secular Variation at Rancho Nuevo Relative to Other Geographic Areas

Field elements change at different rates in different geographic areas and at different points in time (Macmillan & Maus 2005); thus, there is no single rate of field change that can be applied to all locations worldwide. The rate of change in field elements at Rancho Nuevo, however, falls well within the range of rates occurring at other geographic areas used by species that undergo natal homing (Table 4.3).

Table 4.3. Average rate of field change (1900 - 2010) at various coastal locations where sea turtles, salmon, and elephant seals return to reproduce. Data were calculated by the IGRF – 10 model available on the NOAA National Geophysical Data Center website (http://www.ngdc.noaa.gov/seg/geomag/jsp/IGRFWMM.jsp). The data for the Kemp's ridley nesting location are italicized. Data are listed in alphabetical order by geographic location.

Geographic Location	**Latitude and Longitude**	**Marine Migrant**	**Δ Inclination (per year)**	**Δ Intensity (per year)**
Alaska, USA	58.50, -158.00	Salmon	0.00°	31 nT
California, USA	37.12, -122.33	Elephant Seals	0.01°	73 nT
Costa Rica	10.45, -83.45	Sea Turtles	0.07°	99 nT
East Australia	-24.80, 152.44	Sea Turtles	0.01°	29 nT
Florida, USA	27.95, -80.50	Sea Turtles	0.09°	127 nT
French Guiana	5.74, -53.93	Sea Turtles	0.29°	64 nT
Greece	37.72, 20.94	Sea Turtles	0.02°	38 nT
India	20.60, 86.88	Sea Turtles	0.13°	68 nT
Norway	61.00, 5.00	Salmon	0.00°	40 nT
Oman	20.35, 58.80	Sea Turtles	0.10°	56 nT
Oregon, USA	46.25, -124.10	Salmon	0.02°	72 nT
Pacific Mexico	15.68, -96.63	Sea Turtles	0.03°	86 nT
Rancho Nuevo, Mexico	*23.20, -97.77*	*Kemp's Ridley Sea Turtle*	*0.03°*	*95 nT*
South Africa	-27.36, 32.74	Sea Turtles	0.04°	21 nT
South Japan	30.30, 130.42	Sea Turtles	0.02°	19 nT

The exact navigational error that would occur in each case depends upon the rate of field change, the pattern of isolines in the specific geographic area, the alignment of the coastline, whether the animal can compensate for secular variation (it was assumed not in this study), and the length of time that the animal is absent from the natal area. In some cases, animals return to a natal area well before they are ready to reproduce; this occurs, for example, in some populations of loggerhead turtles (Sears et al. 1995; Bowen et al. 2004) but is not known to occur in the Kemp's ridley, the subject of the present study. In addition, not all species of sea turtles show the same precision in natal homing as the Kemp's ridley.

Alternative Methods of Magnetic Navigation

In this study, turtles were assumed to relocate their nesting areas in accordance with a simple strategy of magnetic navigation that has been proposed previously (Lohmann et al. 1999) for turtles that nest along continental coastlines. The strategy involves detecting a single magnetic element (such as inclination or intensity), imprinting on the value that exists at the natal beach, and returning later to the coastal area marked by the same magnetic value that once existed at the natal site. Although this navigational strategy appears to be the simplest one possible for animals returning to locations along coastlines, more complex, alternative navigational strategies are also possible. For example, turtles or other animals might simultaneously exploit two magnetic elements in a bicoordinate magnetic map (Lohmann et al. 1999; 2007). Viewed in this way, every coastal location is defined by a unique combination of magnetic parameters (e.g., one value of inclination and one value of intensity). The task of returning to the natal area might then involve attempting to relocate the area marked by the unique combination of these two magnetic parameters. In the case of the Kemp's ridley turtle, modeling navigational errors that arise if animals use a bicoordinate magnetic map based on inclination and intensity is difficult because the values marking the natal site often drift inland to locations that are inaccessible to the turtles; thus, it is not possible to predict the location where a turtle using such a strategy would first encounter the coast because it depends on the approach direction of a turtle and how the turtle behaves when it is prevented (by the coastline) from reaching the desired location. For this reason, no attempt has been made in this initial study to model bicoordinate magnetic navigation. The results demonstrate that at least one simple strategy of magnetic imprinting is compatible with secular variation, but they should not be interpreted as evidence for any particular model of magnetic navigation; in particular, they do not rule out the possibility of bicoordinate navigation.

Yet another strategy of magnetic navigation could also hypothetically be used: turtles might imprint on both inclination and intensity, but treat these as independent markers (rather than using them together in a classical bicoordinate magnetic map). During most of the period studied, isolines of inclination at Rancho Nuevo have drifted southward (Fig. 4.1) whereas isolines of intensity have tended to drift north (Fig. 1B). Thus, if turtles were to swim first to the coastal area marked by the inclination angle that once existed at the natal beach and then to the area marked by the natal intensity (or vice versa), the animals would nearly always find the nesting beach between the two. In this way, inclination and intensity might be used to bracket the area of coastline to be searched.

Can Turtles Compensate for Secular Variation?

If turtles or other animals can detect field drift during the time when they are absent from the natal area and compensate for it, then they might be able to diminish or eliminate navigational errors that would otherwise occur. At present, there is no evidence that animals can compensate for field drift, although the issue has not been studied. This model assumed that turtles cannot compensate for drift (thus providing a “worst-case scenario” for navigational errors), although it is worth considering whether this assumption is correct. The basic challenge in attempting to compensate for field drift is that secular variation is not consistent over time; moreover, the rates and direction of secular variation vary among different geographic areas. Thus, for turtles such as Kemp’s ridleys that mature in widely dispersed locations far from their natal region, some individuals in distant locations might encounter field changes that roughly parallel those that occur at the natal region, whereas individuals in other locations will invariably encounter field drift that is significantly faster or slower. It seems conceivable that turtles can gain some indication of the direction, if not the rate, of field change, although whether this occurs is not known (Lohmann et al. 2007). However, any ability to compensate would serve only to improve the precision of natal homing beyond what has been estimated, further bolstering the conclusion that magnetic imprinting is compatible with secular variation.

Magnetic Imprinting on Islands

The present study focuses on the Kemp's ridley turtle, one of several sea turtle species that nest exclusively on continental coastlines. Interestingly, marine turtles in some populations of other species nest on islands, and at least a few such populations are thought to display natal homing. Whether turtles that nest on continental coastlines find their natal regions in the same way as turtles that nest on islands is not known; it is possible that different species and populations have evolved different strategies appropriate for the specific navigational task that each group confronts (Lohmann et al. 1999; 2007). In principle, navigational strategies exist that permit island-finding with a single magnetic element such as inclination or intensity (see "Swimming the Isoline" in Lohmann et al. 2007). Alternatively, turtles that nest on islands might need to rely on bicoordinate magnetic maps (as described above) or even, for a first return, on a strategy such as following an experienced conspecific. For detailed discussions of island-finding, see references (Lohmann et al. 1999; 2007; 2008b)

Stability of Nesting Areas

The nesting sites of sea turtles possess certain, specific attributes. For example, the beach must consist of sand rather than rock or mud, and the sand must possess qualities favorable for nest construction and egg incubation. The area must be free of steep inclines or other obstacles that block access from the sea. Appropriate temperatures for incubation and sex determination are required, as are low densities of egg predators and close proximity to ocean currents that can help transport hatchlings to suitable environmental habitats (Putman et al. 2010a, b). Given this suite of environmental factors, it is clear that nesting areas are created and destroyed rapidly over evolutionary time. Changes in sea level and climate, as well as storms and erosion, quickly render favorable areas unusable and produce suitable sites where none existed previously. Given that nesting areas have undoubtedly changed rapidly over evolutionary time, the process of magnetic imprinting might provide a way for turtles to rapidly change nesting areas when the need arises. Turtles returning to a natal area that is no longer suitable for nesting (e.g., one destroyed by a storm) would presumably seek out another site some distance away; offspring would then imprint on this new location and return there to reproduce.

Conclusions

This study demonstrates that the magnetic imprinting hypothesis can plausibly account for how the Kemp's ridley turtle, and perhaps other species, return to natal regions along continental coastlines even after absences of a decade or more. Additional studies will be needed to determine whether magnetic imprinting does in fact occur in sea turtles, as well as in other diverse migrants.

Special Thanks

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Citation

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Island finding: magnetic imprinting, bicoordinate navigation, and secular variation at eight major green turtle nesting sites

Summary

Several populations of island nesting green sea turtles (*Chelonia mydas*) disperse as hatchlings and, upon reaching maturity, migrate extraordinary distances to return to their natal site for reproduction. The mechanism by which turtles accomplish this navigational feat has generated much speculation but has yet to be adequately explained. One hypothesis is that, as hatchlings, turtles imprint on two magnetic parameters (inclination angle and total field intensity) that mark an oceanic island and then use that information to return to the island at maturity. Here geomagnetic models of 1900-2010 are used to calculate the navigational errors expected due to secular variation (field drift) for 8 geographically disparate nesting islands. The findings suggest that, if turtles are absent from their islands and unable to compensate for secular variation, the navigational errors accrued during a 25 year absence might preclude this bicoordinate magnetic imprinting strategy for natal homing in many instances; or at least make it unlikely without the use of supplemental mechanisms or strategies. Although use of inclination and intensity pairings might be better suited for island finding after the initial migration had first been completed, a simpler navigational strategy relying on a single magnetic coordinate in combination with local cues emanating from the island appears to be highly stable over time periods ranging from 5-25 years and may be compatible with known homing precision.

Introduction

Numerous animals disperse from their natal site and, upon reaching maturity, migrate extraordinary distances to return to their natal region for reproduction. The exact mechanism by which animals accomplish this navigational feat has, thus far, eluded researchers (Lohmann et al. 2008a, b). Particularly vexing is how some marine animals such as albatross, seals, and sea turtles can relocate isolated islands in a vast and seemingly featureless ocean (Koch et al. 1969; Moll 1983; Papi

& Luschi 1996; Lohmann et al. 2008b). The localization of such specific goal area is thought to require the use of at least two coordinates (e.g. humans utilize an orthogonal latitude and longitude system, though the coordinates need not be perpendicular) (Benhamou 2003; Gould 2008). For other animals, it has been proposed that certain parameters of the Earth's magnetic field could serve as a crude surrogate for latitude and longitude (Lohmann & Lohmann 1996; Papi & Luschi 1996; Freake et al. 2006; Lohmann et al. 2007; Gould 2008; Putman et al. 2011).

The Earth's main-dipole magnetic field is a pervasive environmental feature that varies predictably across the surface of the Earth (Skiles 1985). For example, at each location on the globe, the magnetic field lines intersect the Earth's surface at a specific angle (known as the inclination angle). At the magnetic equator, the field lines are parallel to the Earth's surface and the inclination angle is 0°. The field lines become progressively steeper toward the magnetic poles; at the poles themselves, the field lines are perpendicular to the Earth's surface (90°). Total field intensity (and its vector components, horizontal and vertical intensity) also vary predictably across the Earth's surface. In most areas of the world, the intensity gradient is not parallel with the inclination angle gradient. Thus, an animal capable of detecting both inclination angle and intensity possesses the needed sensory abilities to use the magnetic field as a bicoordinate map (Lohmann & Lohmann 1996; Freake et al. 2006; Lohmann et al. 2007; Gould 2008).

Sea turtles have been shown to use inclination angle and total field intensity to orient their movements (Lohmann & Lohmann 1994; 1996), extracting both latitudinal and longitudinal information from the field (Putman et al. 2011). Additionally, sea turtles can use the field to accurately determine their geographic position relative to a goal (Lohmann et al. 2004). Thus, these marine reptiles appear to be excellent candidates for possessing a bicoordinate geomagnetic map (Åkesson 1996; Lohmann & Lohmann 1996; Lohmann et al. 1999; 2007). Presumably, then, an island nesting sea turtle could imprint on the inclination angle and intensity at its natal island as a hatchling, disperse from the island, and, upon reaching maturity, relocate the island by searching for the oceanic location marked by those same magnetic coordinates (Lohmann et al. 1999). However, one complication of this hypothesis is that the magnetic field gradually shifts over time. Thus, geomagnetic secular variation could result in the magnetic target no longer coinciding with the geographic target.

Recent geomagnetic modeling studies indicate that the precision by which sea turtles return to their natal regions is, in at least some cases, compatible with rates of secular variation (Putman & Lohmann 2008; Lohmann et al. 2008a). However, these studies modeled the homing returns of sea turtles that nest along continental coastlines. In these cases, the coastline functions as a fixed coordinate and the magnetic isoline functions as a second coordinate. The navigational task of the animals is thus reduced to finding the coastline and swimming along it until reaching the appropriate magnetic marker (Lohmann et al. 1999; 2008b; Putman & Lohmann 2008). How secular variation influences a strategy of bicoordinate magnetic imprinting in regards to island finding has not been investigated in a quantitatively rigorous manner, but initial results suggest that whether secular variation is a problem depends on the geographic region studied and the length of time the returning migrant is absent (Lohmann et al. 1999; Freake et al. 2006; Lohmann et al. 2008b).

Here, secular variation at eight geographically disparate islands used for nesting by green turtles (*Chelonia mydas*) was examined using a geomagnetic model to quantitatively assess whether magnetic imprinting on values of intensity and inclination angle would allow for the successful natal homing of island nesting sea turtles. Because a turtle might update its magnetic information of an island after each nesting migration, so as to compensate for secular variation in its subsequent migrations (Lohmann et al. 2007; 2008b; Putman and Lohmann 2008), this possibility is also considered.

Methods

A simple magnetic homing strategy at eight geographically disparate islands used by green turtles for nesting was modeled. Choosing islands in different parts of the world was important, because rates of secular variation differ across the globe (Skiles 1985; Macmillan & Maus 2005). The selected islands include Ascension Island (equatorial Atlantic), Aves Island (Caribbean Sea), French Frigate Shoals (north-subtropical Pacific), French Polynesia (south-subtropical Pacific), Galapagos Islands (east-equatorial Pacific), Ogassawra (west Pacific), Raine Island (Coral Sea), and Mayotte Island (Indian Ocean) (Fig. 4.3). It should be noted that the green turtle populations nesting at these islands are not all known to precisely home back to their natal island. However, to make the results as broadly applicable as possible, these islands were chosen as a representative sample of how this navigational strategy might function for green turtle rookeries in different parts of the world.

Sea turtles detect inclination angle and intensity (Lohmann & Lohmann 1994, 1996) and it was assumed turtles imprint on the values of both of these magnetic elements that exist at the island. Because diurnal variation in the magnetic field and crustal anomalies likely preclude perfect resolution of the Earth's main-dipole magnetic field (Skiles 1985; Lohmann et al. 2007) it was further assumed that the green turtles resolved inclination angle within ± 0.1° and intensity within ± 0.1 μT.

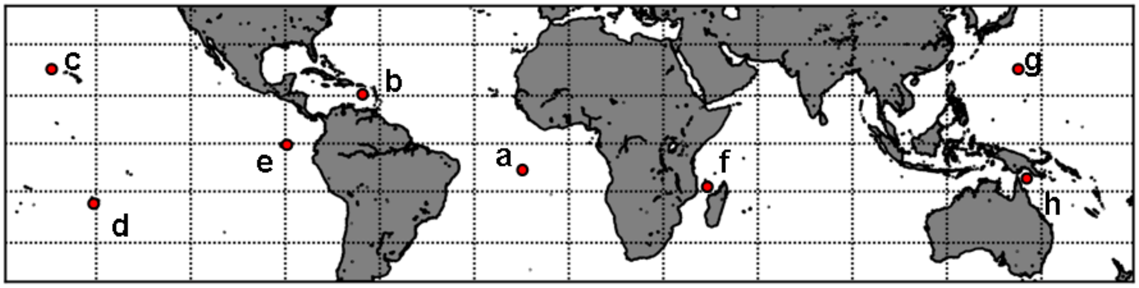

Figure 4.3 Location of islands used in this study. (a) Ascension Island, U.K., (b) Aves Island, Venezuela, (c) French Frigate Shoals, U.S.A., (d) French Polynesia, (e) Galapagos Islands, Equador, (f) Mayotte, France (g) Ogasawara, Japan and (h) Raine Island, Australia.

The values for inclination angle and intensity were taken at the center of each island using the IGRF-10 model (Macmillan & Maus 2005) at 5 year intervals from 1900-2010. Although there is variation among populations, green turtles were assumed to reach maturity in 25 years (Frazer & Ehrhart 1985; Frazer & Ladner 1986; Buskirk & Crowder 1994). Additionally, after reaching maturity, many green turtle populations migrate between nesting sites and distant foraging grounds every 3-5 years (Bjorndal 1980; Mortimer & Carr 1987). It has been proposed that turtles might update their knowledge of the magnetic field after each nesting event (Lohmann et al. 2007; 2008b; Putman & Lohmann 2008). Thus the movement of the field from each island was measured assuming absences of both 25 and 5 years (using Kimmo Korhonen's IGRF applet, available at http://www.ava.fmi.fi/MAGN/igrf/).

Maps of inclination angle and intensity were overlaid in Adobe Photoshop; the area where the values of inclination and intensity intersected was designated as the "magnetic target." The following measurements were made (i) closest distance from the magnetic target to the island, (ii) angle from the magnetic target to the island, (iii) distance spanned by the magnetic target, (iv) closest distance from the isoline of inclination to the island, (v) angle from that point along the inclination isoline to the island, (vi) closest distance from the isoline of intensity to the island, and (vii) angle from that point along the intensity isoline to the island. These seven measurements were made for each of the eight islands under both scenarios of turtles returning to nest after a 25 and 5 year absence.

Results

Natal Homing: 25 Years of Secular Variation

The distance the magnetic target drifted from a green turtle's natal island between 1900 and 2010 varied greatly among the islands (Table 4.3, Fig. 4.4). At the Galapagos Archipelago and Aves Island the mean distance the magnetic target moved from each island was greater than 1000 km. For French Frigate Shoals and Mayotte Island the mean movement of the magnetic target exceeded 750 km. Field movement at Ascension Island and French Polynesia exceeded 475 km. At Raine Island, the mean distance that the field drifted was more than 240 km. Mean field drift at Ogasawara Island was 55 km.

The mean size of the magnetic target varied among the islands, with relatively small distances spanned for Mayotte, Ogasawara, and Ascension Islands (134-152 km), whereas at Aves Island, French Polynesia, and French Frigate Shoals the magnetic target spanned 300-462 km. The mean distance spanned by the magnetic targets associated with Raine Island and the Galapagos Archipelago was 988 km and 1915 km respectively.

The direction of field drift for each island was highly consistent for the Galapagos Archipelago, French Frigate Shoals, French Polynesia, and Ascension Island (Rayleigh R-value > 0.97, p < 0.0001, n = 18; for each). Similarly, the direction of field movement for Aves Island and Mayotte Island was also consistent (Rayleigh R-values > 0.88, p < 0.0001, n = 18; for both). The direction of field drift was less consistent at Raine Island (Rayleigh R-value = 0.78, p < 0.0001, n = 18) and unpredictable at Ogasawara (Rayleigh R-vaule 0.39, p = 0.095, n = 18). For a summary of statistics see Table 4.4.

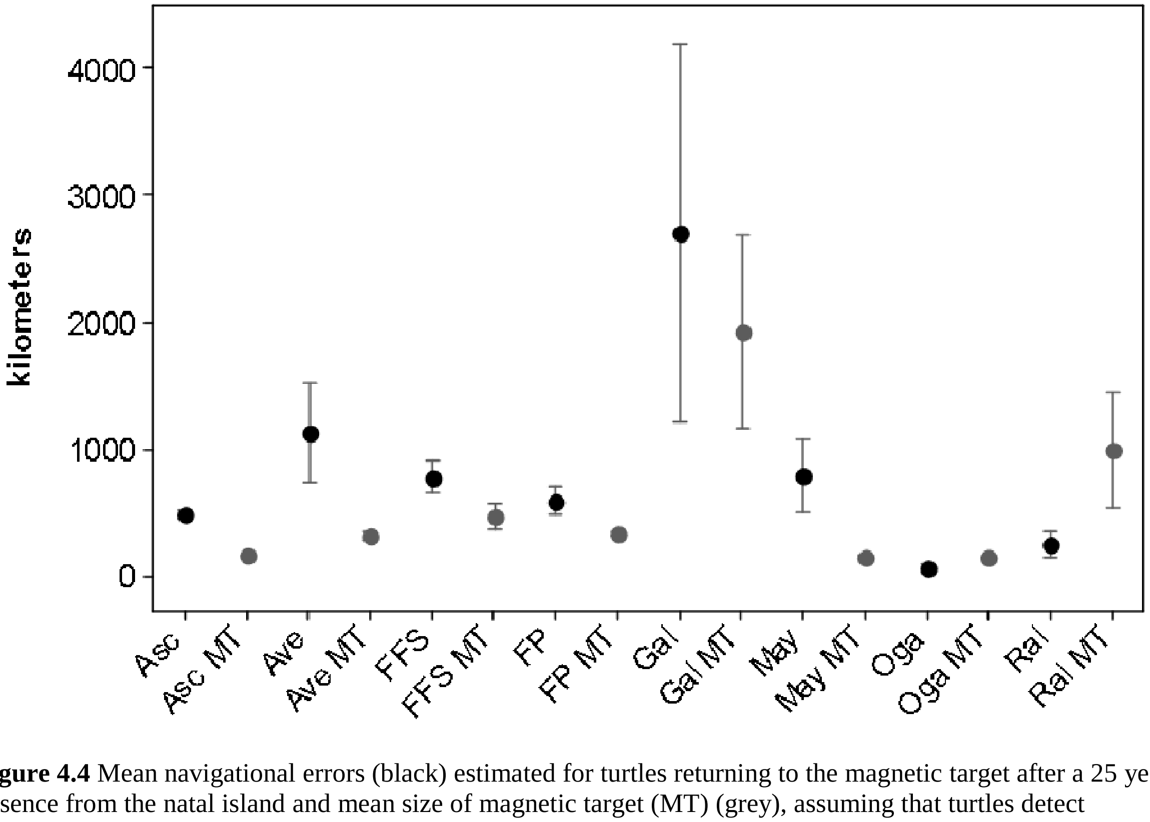

Figure 4.4 Mean navigational errors (black) estimated for turtles returning to the magnetic target after a 25 year absence from the natal island and mean size of magnetic target (MT) (grey), assuming that turtles detect inclination within 0.1° and intensity within 0.1 μT. Error bars represent 95% C.I. of mean. Distance measured in km. Abbreviations along x-axis denote islands from which measurements were made. Ascension Island (Asc) corresponds to (a) in Fig 4.3, Aves Island (Ave) corresponds to (b), French Frigate Shoals (FFS) corresponds to (c), French Polynesia (FP) corresponds to (d), Galapagos Islands (Gal) correspond to (e), Mayotte (May) corresponds to (f), Ogasawara (Oga) corresponds to (g), and Raine Island (Rai) corresponds to (h). Abbreviations of islands followed by MT show denote the mean size (length) of the magnetic target associated with the island.

Remigration: 5 Years of Secular Variation

After 5 years, the mean distance the magnetic target moved from each island decreased significantly compared to 25 years of secular variation (Fig. 4.5). Only at the Galapagos Archipelago and Mayotte Island was mean field drift greater than 100 km (134 km and 244 km respectively). The direction that the magnetic target moved from the island was slightly less consistent over 5 years; only at Ascension Island did field drift result in a Rayleigh R-value greater than 0.90 (Rayleigh R-value 0.95, $p < 0.0001$, $n = 22$). The distances spanned by the magnetic target were similar for all islands except the Galapagos Archipelago, where the mean distance decreased from 1915 km to 304 km. For a summary of statistics see Table 4.5.

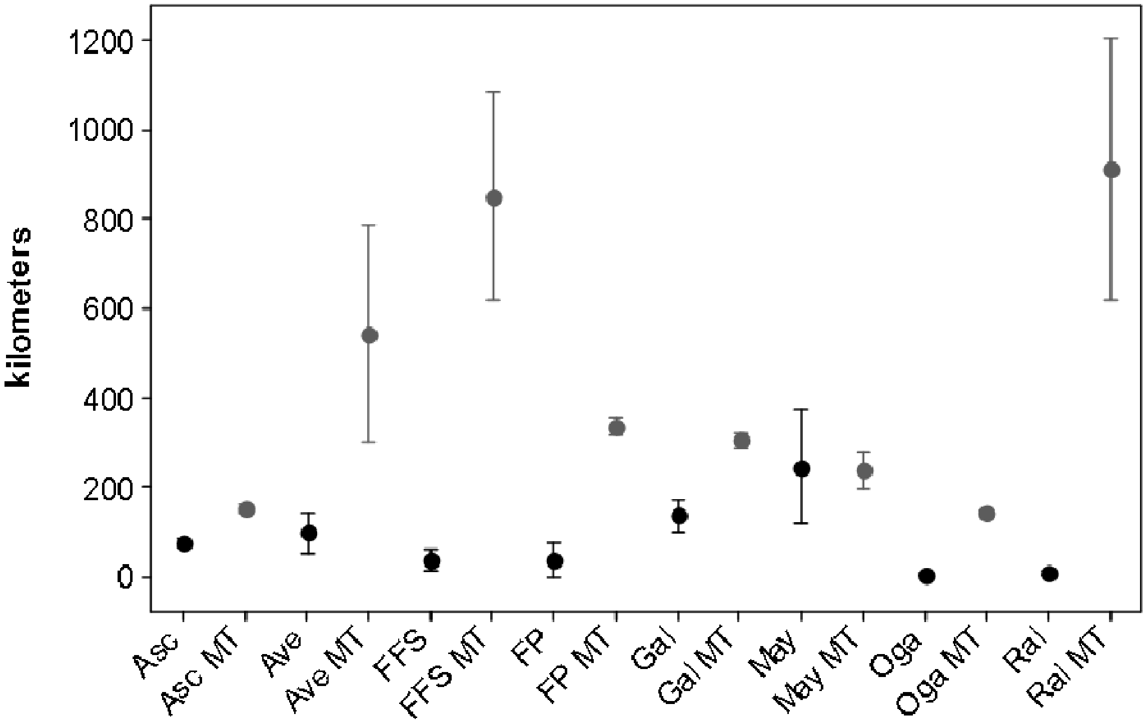

Figure 4.5 Mean navigational errors (black) estimated for turtles returning to the magnetic target after a 5 year absence from the natal island and mean size of magnetic target (grey). Error bars represent 95% C.I. of mean. Conventions as in Figure 4.4.

Discussion

Using an inclination angle and intensity coordinate system appears to be an attractive solution for the localization of a target; however, there are clearly problems in the case of island finding via magnetic imprinting by sea turtles. The results from mapping geomagnetic secular variation for the past century at 8 geographically disparate green turtle nesting sites strongly suggest, at a minimum, that the strategy of bicoordinate magnetic imprinting modeled here, by itself, is unlikely to be a global solution for natal homing to small oceanic islands.

The crucial issue is that, due to secular variation, the coordinates are inherently unstable. With two moving coordinates (inclination angle and intensity), slight amounts of field drift in both elements can be compounded so that the magnetic target moves great distances over a relatively short time. Secular variation also leads to the “bending” of inclination and intensity isolines, i.e. changes in the angle that isolines of inclination and intensity intersect. Thus, after 25 years, the values of inclination and intensity might drift no more than several 10s of kilometers away from an island, but the point of intersection can move substantially (Table 4.4). With the magnetic target drifting on average more than 400 km from 6 of the 8 islands studied, it is unclear how bicoordinate magnetic imprinting would be more precise than simpler navigational mechanisms.

In principle, the problem of “bending isolines” leading to substantial distances of field drift could be overcome if turtles decreased the resolution with which they measure inclination and intensity. This can be conceptualized as the pertinent isolines increasing in thickness; thicker isolines result in the magnetic target not drifting as far from the island. However, this is not a perfect solution because as the resolution of inclination and intensity becomes coarser the larger the area of the ocean covered by the magnetic target. Thus, if turtles have a broad tolerance of magnetic field values the area over which they must search increases. In contrast, if a turtle measures the field with exceptional precision then the distance that the magnetic target moves increases. In both cases finding a specific island with only this information would be exceptionally difficult.

Assumptions about Green Turtle Life-History

Although bicoordinate magnetic imprinting seems incompatible with rates of secular variation, this does not imply that magnetic information is not used by sea turtles to locate nesting islands. Luschi et al. (2007) found that placing magnets on green turtles’ impaired their ability to return to Mayotte Island (though the turtles did eventually locate the island). It is worth considering, therefore, how the assumptions of this model influence the results of navigational precision presented. In this study, several assumptions may not always hold true for all island nesting turtles. First, the age that green turtles reach maturity may be less than or greater than 25 years of age (Frazer & Ladner 1986; Zug et al. 2002; Chaloupka et al. 2004). For green turtles that mature later than 25 years, the effects of secular variation would, in almost every case, cause the magnetic target to drift further from the natal site. Presumably, if turtles matured more quickly, the field drift would be lessened (as shown by modeling 5 years of secular variation), though problems with the large size of the magnetic target still remain. If green turtles returned to nesting islands prior to reaching maturity they might be able to lessen navigational errors due to secular variation. Early natal homing behavior has been observed in some populations of loggerheads (Bowen & Karl 2007), and green turtles from French Frigate Shoals as young as 4 years old have been found near their reproductive grounds (Zug et al. 2002). Whether this behavior applies across other populations of island nesting green turtles is not known.

Additionally, this model assumes that turtles only remember two pieces of magnetic information (value of inclination angle and intensity at the island). It is possible that turtles learn considerably more about the magnetic topography around their island (e.g. the angle of field gradients, the axis of the field, etc.). If this were the case turtles might be able to employ a much more sophisticated (and accurate) bicoordinate (or multicoordinate) magnetic search for their island than modeled here. For a more complex strategy to work, it seems likely that a turtle would have to spend some amount of time in the vicinity of its island acquire additional information on the magnetic topography of its natal area. Although hatchling sea turtles from most continental nesting populations quickly migrate away from their natal site (making this solution unlikely), this may not be the case for all island nesting turtles. For instance, hatchlings from Ascension Island do not appear to engage in sustained offshore movements (Dalton 1979). It is suspected that the intense predation pressure exerted on hatchlings along continental coastlines may be relaxed for hatchlings entering the water from oceanic islands because turtles do not have to swim as far to reach pelagic waters where predation risk decreases (Wyneken & Salmon 1992). If this were the case, it might provide island nesting turtles the opportunity to learn magnetic (or other) information associated with their natal island for use in subsequent migrations. Whether young turtles are capable of performing such complex measurements remains to be determined.

Compensation for Secular Variation

The model of island finding proposed here assumed no compensation for secular variation between leaving the island and attempting to return. Whether any animal is capable of compensating for secular variation is unknown and would be difficult to demonstrate empirically; however, if a turtle could assess or predict how the field was changing it might be able to lessen navigational errors due to secular variation. Measurements of field drift revealed that at 7 islands, the magnetic target consistently moved in the same direction, assuming a 25 year absence for turtles (Fig. 4.6). Freake et al. (2006) proposed that some sea turtle populations might locate their islands by first swimming to the magnetic target and then adopting an appropriate compass direction towards its island. For this to be an evolutionarily feasible strategy, the direction of field drift may have to be consistent beyond the period modeled in this study.

An Easier Solution?

However, island finding with magnetic cues need not rely on complicated measurements of field gradients or compensation for secular variation. Some populations might utilize a strategy referred to as "sailing the isoline" (Lohmann et al. 1999; 2007). This strategy is analogous to the natal homing mechanism proposed for turtles nesting along continental coastlines (Putman & Lohmann 2008; Lohmann et al. 2008a). Essentially, a turtle begins its migration in a foraging area, locates the value of inclination or intensity by swimming up or down the gradient, and then swims along that isoline until intersecting the island or some localized cue emanating from it. Measurements of the movement of individual isolines of inclination and intensity show that for many oceanic regions, one or both of these parameters remain quite stable over 25 year periods. At 6 of the 8 islands the mean movement of the inclination angle is less than 100 km and at 4 of the 8 islands the mean movement of the intensity is less than 150 km. Only at Aves Island did neither parameter fall within these two ranges.

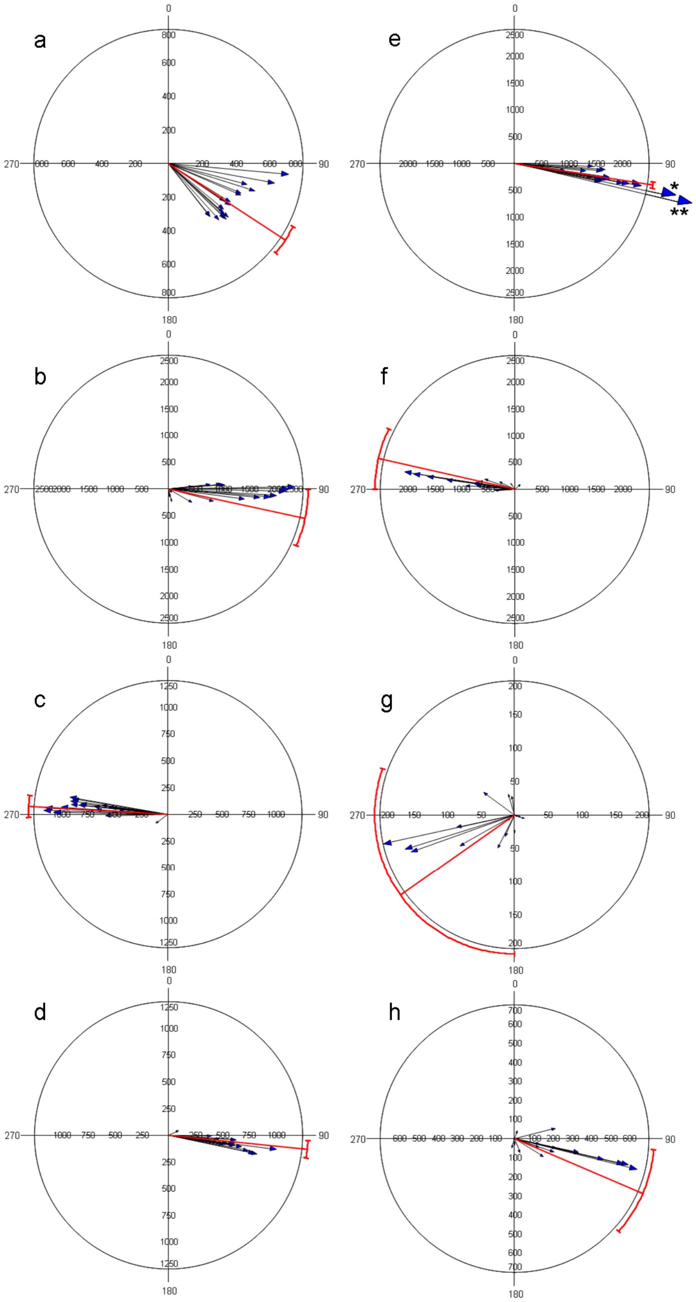

Figure 4.6 Direction of island from the magnetic target. The center of the circle represents the closest location of the magnetic target to the island. Each arrow head represents the location of the island from magnetic target for a different year, the lengths of arrows correspond to geographic distance (distance in km, based marked by values within the circle). The red line indicates the mean angle of the group, and red semi-circle represents the 95% C.I. of the mean. (a) Ascension, (b) Aves, (c) French Frigate Shoals, (d) French Polynesia, (e) Galapagos, n.b. two vectors have arrow heads outside the circle, these represent two years in which the field drifted 11,222 and 10,460 km from the island, (f) Mayotte, (g) Ogasawara, and (h) Raine.

The most striking example can be seen for the Galapagos green turtles. Many green turtles that nest in the Galapagos have coastal foraging grounds along mainland central and South America

(Green 1984; Seminoff et al. 2008). If these turtles imprinted on the value of inclination angle at the Galapagos as hatchlings, to relocate the island they would simply need to swim along the coastline of their foraging grounds until reaching the same value of inclination angle and then swim westward from that point following the isoline of inclination towards the island (Fig. 4.7). If Galapagos green turtles utilized this method for natal homing the mean navigational error would be 88 km (s.d. 69) to the south. This navigational error is quite small compared to the error expected if turtles search for a bicoordinate magnetic target (2702 km; s.d. 2991). Presumably, if a turtle could get relatively close to the target then it might encounter local cues emanating from the island that could be used to further localize it (Lohmann et al. 2008c). Such “multi-modal” homing has been proposed for a number of migratory animals in which one set of cues is used for navigation over large spatial scales and another is used over smaller scales (Lohmann et al. 2008a, b, c; Putman & Lohmann 2008).

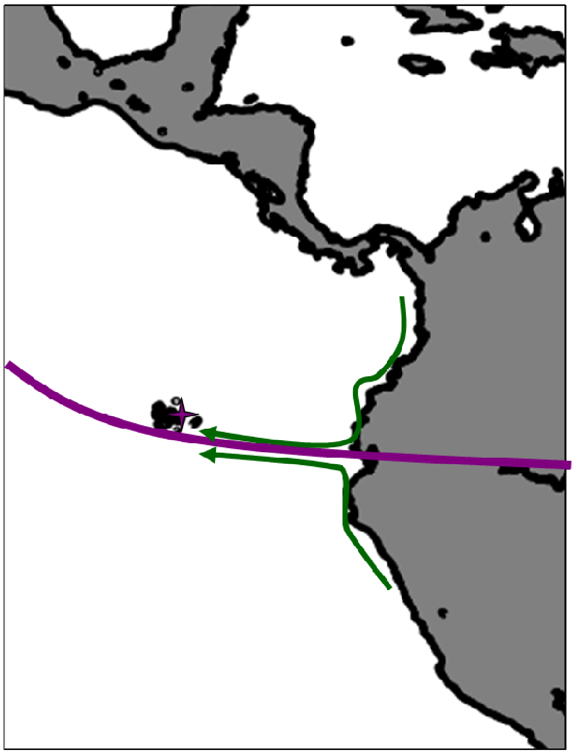

Figure 4.7 Hypothetical strategy for locating an island with a single magnetic coordinate. In this case, the coastline of South America functions as one coordinate (where adult green turtles forage) and magnetic inclination angle (purple line) functions as the second. Dark green arrows show the hypothetical path taken by turtles employing the strategy of imprinting on the value of inclination angle at the Galapagos Islands (marked by purple star) and attempting to return in 25 years later. The turtles could simply swim along the coastline from their foraging grounds in the direction of the imprinted inclination value and then, upon reaching the value of inclination angle, swim west until reaching the Galapagos Archipelago (or some secondary cue associated with the island).

Interestingly, a mechanism of “sailing the isoline” does not necessarily permit a high degree of navigational precision. This hypothesis predicts some degree of genetic exchange among nesting locations marked by the same isoline, as is observed for loggerhead (*Caretta caretta*) nesting beaches along the Florida peninsula (Shamblin et al. 2010). Numerous genetic studies for green turtles indicate that natal homing occurs over "regional" spatial scales and that there is little genetic differentiation between nearby islands (Bourjea et al. 2007). Geographically distant nesting sites in the same ocean basin often share the same haplotypes (Bourjea et al. 2007; Bowen & Karl 2007), which may be indicative of imprecise homing over evolutionary timescales. Perhaps then, it should not be surprising if the mechanism for natal homing is somewhat imprecise as well.

Finally, because sea turtles detect inclination and intensity, turtle populations associated with different oceanic regions might be capable of evolving a strategy that utilizes the most stable coordinate for island finding in each situation. There is no *a priori* reason that all populations of island nesting turtles locate targets the same way. For instance, turtles might follow the inclination angle isoline to home to French Frigate Shoals, French Polynesia, the Galapagos Archipelago whereas at Ascension Island and Raine Island the intensity isoline might be utilized. At Ogasawara Island, perhaps a bicoordinate magnetic imprinting strategy could be selected for. In each case, turtles that chose the "correct" strategy and isoline(s) would presumably increase their probability of encountering mates and accessing nesting locations and thus that particular strategy would be selected for. Regardless of these possibilities, however, any homing mechanism based on the earth's magnetic field by itself appears insufficient to allow for the localization of small oceanic islands. Instead, it is likely that turtles must also rely on an additional suite of mechanisms, such as a search strategy (Åkesson et al. 2003) or the use of cues emanating from the island (Hays et al. 2003).

Special Thanks

K. Stapput and. K.J. Lohmann will be co-authors of the forthcoming m.s.

Table 4.4. Mean field movement from 1900-2010 over 25 year periods at 8 green turtle rookeries (based on 18 measurements).

	Ascension Island	**Aves Island**	**French Frigate Shoals**	**French Polynesia**	**Galapagos Archipelago**	**Mayotte Island**	**Ogasawara Island**	**Raine Island**
Oceanic Region	Equatorial Atlantic	Caribbean Sea	N Subtropical Pacific	S Subtropical Pacific	Eastern Pacific	Indian Ocean	Western Pacific	Coral Sea
Latitude	-7.956	15.7	23.7	-16.8	-0.75	-12.8	27.1	-11.6
Longitude	-14.414	-63.63	-166.1	-153.95	-90.25	45.15	142.2	144.017
Mean Closest Dist. of MT (km) (Std. Dev.)	478 (83)	1117 (788)	772 (265)	586 (210)	2702 (2991)	787 (577)	55 (62)	243 (214)
Mean Dir. from MT from GT (deg) (Rayleigh R-value)	123 (0.970)	102 (0.904)	273 (0.986)	96 (0.991)	99 (0.999)	283 (0.887)	235 (0.395)	113 (0.777)
Mean Dist. Spanned by MT (km) (Std. Dev.)	152 (19)	312 (70)	462 (206)	326 (30)	1915 (1538)	134 (34)	142 (7)	988 (923)
Mean Closest Dist. of Inc. Isoline (km) (Std. Dev.)	387 (30)	220 (110)	31 (33)	18 (20)	88 (69)	30 (32)	19 (16)	48 (28)
Mean Dir. from Inc. Isoline to GT (deg) (Rayleigh R-value)	157 (0.991)	155 (0.420)	188 (0.988)	200 (0.079)	9 (0.997)	17 (0.145)	175 (0.500)	182 (0.762)
Mean Closest Dist. of Int. Isoline (km) (Std. Dev.)	113 (99)	285 (207)	177 (97)	129 (38)	200 (113)	750 (562)	12 (17)	12 (19)
Mean Dir. from Int. Isoline to GT (deg) (Rayleigh R-value)	53 (0.999)	162 (0.988)	196 (0.993)	20 (0.999)	179 (0.999)	270 (0.864)	330 (0.556)	179 (0.502)

Table 4.5. Mean field movement from 1900-2010 over 5 year periods at 8 green turtle rookeries (based on 22 measurements).

	Ascension Island	**Aves Island**	**French Frigate Shoals**	**French Polynesia**	**Galapagos Archipelago**	**Mayotte Island**	**Ogasawara Island**	**Raine Island**
Oceanic Region	Equatorial Atlantic	Caribbean Sea	N Subtropical Pacific	S Subtropical Pacific	Eastern Pacific	Indian Ocean	Western Pacific	Coral Sea
Latitude	-7.956	15.7	23.7	-16.8	-0.75	-12.8	27.1	-11.6
Longitude	-14.414	-63.63	-166.1	-153.95	-90.25	45.15	142.2	144.017
Mean Closest Dist. of MT (km) (Std. Dev.)	75 (21)	96 (104)	33 (56)	34 (86)	134 (81)	244 (290)	2 (7)	6 (6)
Mean Dir. from MT from GT (deg) (Rayleigh R-value)	139 (0.947)	132 (0.559)	209 (0.809)	249 (0.804)	87 (0.890)	269 (0.620)	20 (0.872)	180 (0.529)
Mean Dist. Spanned by MT (km) (Std. Dev.)	150 (19)	543 (551)	851 (530)	333 (40)	304 (39)	236 (92)	143 (9)	913 (661)
Mean Closest Dist. of Inc. Isoline (km) (Std. Dev.)	67 (14)	35 (20)	5 (7)	2 (4)	19 (17)	0 (2)	1 (3)	5 (6)
Mean Dir. from Inc. Isoline to GT (deg) (Rayleigh R-value)	153 (0.995)	157 (0.355)	181 (0.998)	195 (0.336)	12 (0.881)	185 (1.000)	175 (1.000)	180 (0.625)
Mean Closest Dist. of Int. Isoline (km) (Std. Dev.)	8 (24)	41 (38)	15 (22)	7 (15)	22 (22)	180 (207)	0 (0)	2 (4)
Mean Dir. from Int. Isoline to GT (deg) (Rayleigh R-value)	44 (0.984)	162 (0.987)	195 (0.983)	13 (0.948)	180 (1.000)	278 (0.516)	- (-)	0 (0.500)

Ecological implications of natal homing by magnetic imprinting in loggerhead sea turtles

Summary

Diverse animals perform impressive feats of natal homing after an extensive dispersal stage. While the navigational mechanism remains unknown, one hypothesis is that these migrants imprint on specific geomagnetic field values at their natal site and use positional information inherent in the field to return. However, the field values that exist at any particular geographic location gradually shift over time. This field movement, known as secular variation, might have several important ecological implications for populations that rely on magnetic imprinting to return to their natal region. Geomagnetic models describing the earth's field from 1900-2010 were used to explore this possibility with a quantitative model simulating natal homing via magnetic imprinting over the past century at eight geographically disparate loggerhead sea turtle (*Caretta caretta*) nesting assemblages. Modeled navigational errors for loggerheads were consistent with previous findings that the rate of secular variation at major nesting beaches is compatible with known homing precision of sea turtles. Moreover, nesting assemblages that have been shown to have relatively fine-scale population structure (Florida, U.S.A., Greece, and Japan) have had less extensive navigational errors this past century than those with coarse or no population structure (Brazil and the Cape Verde Islands). Additionally, at two of the three specific beaches analyzed (Cape Lookout, North Carolina, U.S.A. and Brevard County, Florida, U.S.A), the rate of field change over the average length of time to maturity for loggerheads, explained as much as 20 to 30% of the temporal variation in nest abundance. These findings provide strong support for the magnetic imprinting hypothesis of natal homing and highlight a potentially overlooked driver of ecological processes: the navigational mechanisms of animals.

Introduction

Numerous animal species disperse widely from their natal regions before returning to reproduce. How these migrants navigate back to their natal region after dispersing hundreds or thousands of kilometers is unknown. One hypothesis is that some species might imprint on the magnetic field of their natal region and use that information to return (Lohmann et al. 1999, 2008; Putman & Lohmann 2008). The elements of the Earth's magnetic field vary predictably across the globe; thus, with knowledge of even a single magnetic parameter (e.g. values of inclination angle or intensity) geographic position relative to a known magnetic goal can be deduced (Lohmann et al. 2007). Typically, geographic regions are marked by distinctive magnetic values. Young animals might therefore imprint on the fields at natal locations prior to dispersal and then use this information to facilitate the subsequent return migration (Lohmann et al. 1999, 2008a).

One notable aspect of the magnetic imprinting hypothesis is that secular variation of the Earth's field results in the homing cue(s) shifting over time. The secular variation of the magnetic field occurs across the globe in a somewhat unpredictable manner and rates of secular variation differ greatly by regions (de Santis et al. 2002). Unless an animal repeatedly updates its knowledge of the magnetic terrain of a particular region, compensation for secular variation is unlikely. Thus, secular variation is likely to impose a degree of imprecision on geomagnetic homing (Lohmann et al. 1999; 2007; 2008a; Southwood & Avens 2010). In principle, errors due to secular variation can be assessed if the following are known: (1) which magnetic element is being used; (2) its rate of secular variation; (3) the pattern of magnetic isolines in the specific geographic area; (4) the size and alignment of the target area; (5) how well the animal can resolve magnetic values; and (6) the length of time that the animal is absent from the natal area. Recent studies using geomagnetic models suggest that secular variation does not preclude several species of marine migrants from successfully employing a magnetic imprinting strategy to return to the vicinity of their natal site (Putman & Lohmann 2008; Lohmann et al. 2008a). However, little consideration has been given to how navigational errors associated with secular variation might affect evolutionary and ecological processes.

Here, a quantitative model of natal homing by magnetic imprinting (Putman & Lohmann 2008) was applied to make predictions about the spatiotemporal pattern of straying over the past century at eight geographically disparate loggerhead sea turtle (*Caretta caretta*) nesting assemblages.

At locations where data were available, whether secular variation provided explanatory power for phylogeographic patterns along nesting assemblages and temporal variation in nest abundance was examined.

Methods

Life-History of the Study Species

After hatching, loggerhead sea turtles disperse thousands of kilometers from their natal shores, remaining in the open ocean for 6-12 years (Bjorndal et al. 2000a; Musick & Limpus 1997). After this pelagic stage, they return to their natal coast while still immature. Upon reaching maturity they nest in the same geographic region where they hatched (Bowen & Karl 2007). Atlantic and Indian Ocean loggerheads begin nesting at about 20 years of age (Parham & Zug 1998; Baldwin et al. 2003) whereas Pacific Ocean loggerheads begin nesting around age 30 (NMFS & USFWS 1998). Once loggerheads reach maturity they typically make reproductive migrations every 2-4 years from foraging grounds to their natal region to mate and nest (Bolten & Witherington 2003). Thus, the longest period that loggerheads are out of contact with their natal region (and presumably unable to directly compensate for secular variation) occurs during their initial dispersal stage.

The Model

Using the methods of Putman and Lohmann (2008), a simple magnetic homing strategy was simulated for eight major loggerhead nesting assemblages (southeast USA, Cape Verde, Greece, Brazil, South Africa, Oman, Japan, and east Australia) (Table 4.6, Figure 4.8). Loggerheads detect inclination and intensity (Lohmann & Lohmann 1994, 1996) and it was assumed that turtles imprinted on the value of one of these magnetic elements. The location with the highest nest density at each loggerhead nesting assemblage was taken as the starting location for all analyses. Two separate analyses assumed that turtles return to the coastal region marked by the same magnetic value after exiting the pelagic stage and upon reaching maturity. In natural populations, the duration of the pelagic phase and time to reach maturity vary due to differences in environmental parameters (e.g., food availability and temperature) experienced by individuals (Musick & Limpus 1997). To simplify for this model, it was assumed that loggerheads exited the pelagic stage at five years old. For loggerheads in the Atlantic and Indian Ocean Basins maturity was assumed to be reached in 20 years (Parham & Zug 1998; Baldwin et al. 2003), whereas in the Pacific maturity was assumed at 30 years (NMFS & USFWS 1998). Thus, these analyses bracket the range of time that a typical loggerhead is away from its natal region.

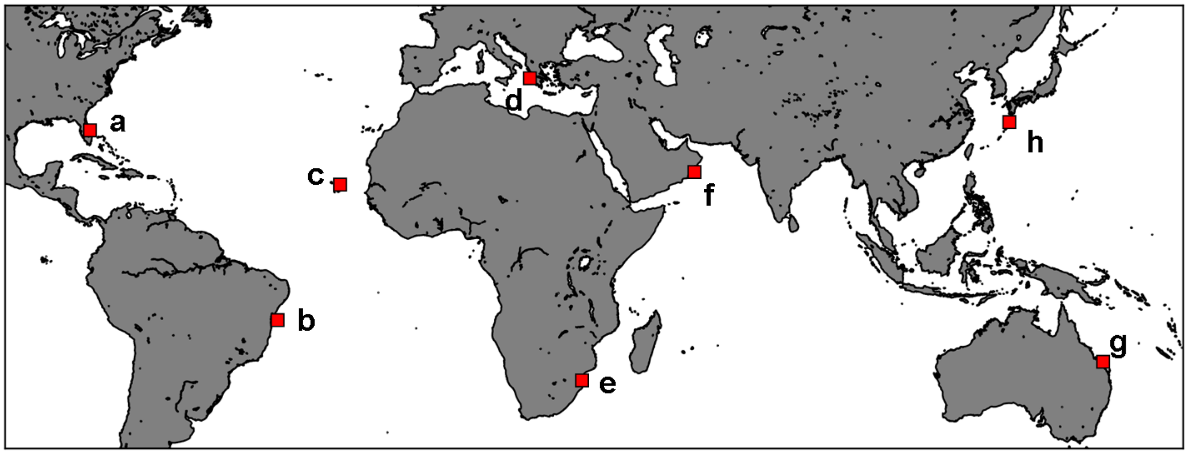

Figure 4.8 Maps of the eight major loggerhead nesting beaches where simulations of natal homing via magnetic imprinting were modeled: (a) Florida, U.S.A., (b) Brazil, (c) Cape Verde Islands (d), Zakynthos, Greece, (e) Tongaland, South Africa, (f) Marisah Island, Oman, (g) Mon Repos, Australia, and (h) Yakushima, Japan.

International Geomagnetic Reference Field 10th generation software (IGRF-10) was used to calculate return locations of loggerheads, based on changes in the magnetic field from 1900-2010 (Macmillan & Maus 2005). IGRF-10 predicts the main field values of magnetic elements from 1900-2010 at the Earth’s surface. Magnetic fields produced by minerals in the Earth’s crust are not taken into account by IGRF-10, but they did not need to be considered because crustal fields remain static over the time scales of interest. Loggerhead return locations were measured with a spatial precision of 0.05° latitude and longitude from 1900-2010 at five year intervals in accordance with changes in the main field coefficients given by IGRF-10. The distance from the natal beach to the modeled return location was measured using Google Earth^{TM} software. Homing was modeled under the following scenarios: (1) turtles imprinted on inclination angle and returned in five years; (2) turtles imprinted on intensity and returned in five years; (3) turtles imprinted on inclination angle and returned at maturity; and (4) turtles imprinted on intensity and returned at maturity. These analyses were performed for all nesting assemblages except South Africa because from 1900-1945 field lines of intensity ran parallel to the coastline; thus, the same value of intensity at the natal site was found at multiple locations along the eastern coast of Africa making a meaningful assessment of turtles imprinting on intensity impossible. For this region only analyses of turtles imprinting on inclination angle were performed. Secular variation rates are nearly identical across the length of a nesting assemblage, so modeling homing precision based on magnetic imprinting at one location gives a reasonable indication of the precision possible across the entire range

Comparing Model Output to Observed Homing Precision

Several techniques exist to test this model's predictions against a population's known precision of natal homing, though not all are available for each loggerhead nesting assemblage. The most definitive analysis would be to mark turtles as hatchlings and determine where they returned to nest as adults. Due to the considerable obstacles of this undertaking, relatively few turtles have been studied in this way (Baldwin et al. 2003; Hughes 2010). However, at Mon Repos, Australia, a major tagging study was undertaken on hatchling sea turtles in the mid-1970s to determine age at maturity and homing precision. At present, only anecdotal reports of adult turtles returning to the region of hatching have been reported by the Queensland government (http://www.derm.qld.gov.au/wildlife-ecosystems/wildlife/watching_wildlife/turtles/turtle_tracking/premiere.html).

The use of mtDNA markers has proved valuable in verifying and understanding natal homing in sea turtles (Bowen & Karl 2007). By comparing haplotype frequencies at nesting beaches across a nesting assemblage the precision of natal homing can be determined; a significant difference in haplotype frequency between two areas is assumed to demonstrate independent populations and the geographic distance between those areas indicates the natal homing precision (Bowen & Karl 2007). Phylogeographic analyses suitable for comparisons to the model output have been conducted for Florida, U.S.A. (Bowen & Karl 2007; Shamblin et al. 2010), Greece (Schroth et al. 1996), Japan (Hatase et al. 2002), Brazil (Reis et al. 2009), and Cape Verde (Monzón-Argüello et al. 2010)

For nesting assemblages where no tagging or genetic data are available, the next best option was to compare modeled homing precision to the range limits of the nesting assemblage. At a minimum, such comparisons can rule out the modeled navigational strategy for natal homing if errors consistently exceeded the nesting range of a population by a wide margin.

Temporal Variation in Nest Abundance

Additionally, whether the rate of secular variation at a given nesting beach provides any predictive value for temporal trends in sea turtle nest abundance was examined. Numerous variables likely influence the temporal variation in nesting on a given beach. However, if sea turtles imprint on the magnetic field as a homing mechanism, then the probability of turtles returning to their natal site should increase as the rate of secular variation decreases. To assess this possibility, a thorough search of the literature was conducted to find datasets in which more than 10 continuous years of standardized nest counts had been obtained. A number of long-term nest monitoring studies have been carried out across the world (Australia, Japan, South Africa, Brazil, U.S., and Greece), but only three have published their data in an accessible format. These datasets include Zakynthos, Greece (1984-2002) (Margaritoulis 2005), Florida, U.S.A (1990-2009) (Florida Fish & Wildlife), and Cape Lookout North Carolina, U.S.A (1990-2005) (Cordes & Rikard 2005). For the Florida dataset, records were available for all Florida counties; however, Brevard County was selected for analysis because it consistently has the highest nest abundance across the state (Witherington et al. 2009). The latitude and longitude of the area with highest nest abundance for each nesting beach was input into IGRF-11 to determine the amount of field drift for inclination angle and intensity that occurred during the years of available data. In the Atlantic basin loggerheads are thought to mature by age 20 (Parham

& Zug 1998); therefore the amount of field change for the 20 years before was calculated for each year in which nesting data was available. Linear regressions were performed to determine whether the change in inclination angle, intensity, or time (i.e. an increasing or decreasing trend in nesting during the observation period) correlated with the corresponding nest abundance for each beach.

Results

Model Results

Simulations of turtles returning at maturity show that using inclination angle, loggerheads could return, on average, within ± 100 km of their natal beach in the southeast U.S.A., Greece, South Africa, Oman, Japan, and east Australia. Along the Cape Verde Islands turtles would return on average within 275 km from their natal beach. Across the Brazilian coast turtles would return within 780 km of their natal site. Simulations of homing via intensity led to turtles returning within 100 km along Japan and East Australia. Turtles from the southeast U.S.A., Cape Verde, Brazil, and Oman would return within 265 km of their natal site. Along the coast of Greece turtles would return on average 657 km from their natal site.

For simulations in which loggerheads returned after exiting the pelagic stage (five years), most scenarios of imprinting on either the inclination angle or intensity would have consistently led loggerheads, on average, within 65 km of their natal beach. Only two scenarios differ from this pattern. Imprinting on the inclination angle in Brazil led to navigational errors that averaged 240 km from the natal site and imprinting on intensity in Greece led to returns that averaged 100 km from the natal site. For full results of the simulations in their geographical context see Fig. 4.9 and Table 4.6.

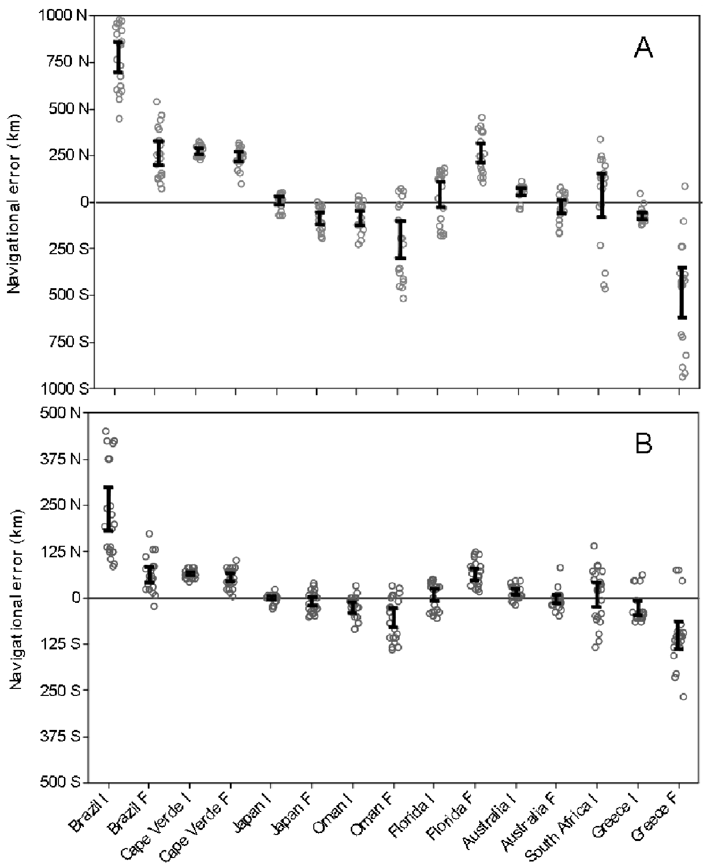

Figure 4.9 (a) The graph shows results from simulations between 1900 and 2010 for turtles leaving the natal site and returning at maturity to the location marked with either the same inclination (I) or same intensity (F) as the natal site. See text for details. Data is plotted so that the natal site for all beaches is at 0 km (marked by the solid line) and modeled returns above this location were north of the nesting beach, whereas returns below 0 km were to the south of the nesting beach. Open circles represent individual data points, error bars represent the 95% confidence interval of the mean. (b) The graph shows results from simulations between 1900 and 2010 for turtles leaving the natal site and returning after five years to the location marked with either the same inclination or intensity as the natal site.

Table 4.6 Loggerhead nesting assemblages where navigational errors based on secular variation from 1900-2010 were modeled. The last four columns give mean navigational error (and 95% CI in italics) relative to natal site for each simulation.

Nesting Assemblage	Latitude and Longitude	Age at Maturity (years)	Inclination Juvenile (km)	Inclination Mature (km)	Intensity Juvenile (km)	Intensity Mature (km)
Southeast, USA (Melbourne Beach)	27.950 N 80.497 W	20	8 N *9 S - 25 N*	37 N *30 S - 105 N*	63 N *48 - 79 N*	262 N *208- 316 N*
Cape Verde (Boa Vista)	16.123 N 22.908 W	20	65 N *60 N - 70 N*	273 N *258 - 288 N*	54 N *43- 66 N*	240 N *214-265 N*
Greece (Zakynthos)	37.723N 20.934 E	20	24 S *40 S - 8 S*	67 S *88 - 46 S*	97 S *127 - 67 S*	657 S *931 - 384 S*
Brazil (Salvador)	12.900 S 38.300 W	20	240 N *182 - 297 N*	779 N *697- 860 N*	61 N *40 - 82 N*	262 N *196 - 327 N*
South Africa (Tongaland)	27.362 S 32.739 E	20	7 N *25 S - 40 N*	35 N *80 S - 150 N*	N/A	N/A
Oman (Marisah Island)	20.350 N 58.801 E	20	27 S *40 - 13 S*	88 S *128 - 47 S*	53 S *78 - 28 S*	201 S *99 - 303 S*
Japan (Yakushima Island)	30.296 N 130.415 W	30	1 N *4 S - 6 N*	6 N *17 S - 29 N*	10 S *23 - 2 N*	89 S *122 - 55 S*
East Australia (Mon Repos)	24.795 S 152.443 E	30	17 N *9 - 25 N*	57 N *36 - 77 N*	5 S *16 S - 7 N*	26 S *60 S - 8 N*

Comparison to Known Precision of Natal Homing

Phylogeographic studies from the southeast U.S.A. (Encalada et al. 1998; Shamblin et al. 2010) and eastern Mediterranean (Schroth et al. 1996) suggest that the precision of loggerhead natal homing is on the order of 50-100 km (Bowen & Karl 2007). Analyses indicate that Florida and Mediterranean loggerheads that imprinted on inclination angle could return to their natal region at maturity with this level of precision. Loggerheads from Florida imprinting on inclination angle would return on average 37 km north (± 68 km) of their natal site if returning at maturity, whereas imprinting on intensity would lead to returns on average 262 km north (± 54 km) of their natal site. Modeled navigational errors from Greece suggest that loggerheads imprinting on inclination angle could return loggerheads on average 67 km south (± 21 km) of their natal site, whereas imprinting on intensity would lead to returns that average 657 km south (± 274 km) of the natal site.

Less fine-scaled phylogeographic analysis from Japan suggests that natal homing is at least as precise as 100-200 km (Hatase et al. 2002). Modeled homing precision of Japanese loggerheads indicates that imprinting on inclination angle would return turtles on average 6 km north (± 23 km) of their natal site, whereas imprinting on intensity would lead to returns that average 26 km south (± 34 km) of their natal site. In this case, both inclination angle and intensity are reliable homing cues and could equally account for the known precision of natal homing by Japanese loggerheads.

For the Brazil nesting assemblage, phylogeographic patterns were described based on political boundaries of four coastal states (Reis et al. 2010). Unfortunately, this does not provide sufficient resolution to infer homing precision beyond the assessment that a significant difference in the haplotype frequency of nesting turtles can be detected after travelling 900 km south from the northernmost state included in the analysis. The modeled navigational errors for turtles in Brazil are quite high and consistently to the north. Imprinting on inclination angle resulted in turtles returning, on average, 778 km to the north and using intensity the return location is 260 km north. Interestingly, southerly nesting beaches comprise turtles with a single haplotype (~99% of sampled loggerheads) and the northern beaches have this same haplotype (~83% of sampled loggerheads). Therefore, the genetic markers used in this study would not be able to differentiate turtles from southern beaches "straying" due to northerly field drift. Even though relying on magnetic imprinting for regional homing would result in large errors, these errors appear compatible with the known phylogeography of this nesting assemblage.

At the Cape Verde Islands, unlike at other nesting assemblages, no difference in haplotype frequency was observed within the archipelago (though haplotype frequencies across the archipelago are distinct from other nesting assemblages in the Atlantic) (Monzón-Argüello et al. 2010). Likewise, modeled navigational errors suggest that turtles would consistently be able to return to the vicinity of the nesting assemblage if they relied on magnetic imprinting, but distinguishing nesting locations among islands would not be possible. Navigational errors from the natal site for inclination angle would be, on average, 273 km (± 15 km) and 240 km (± 25 km) intensity. Although these distances seem large, the furthest the inclination drifts from the archipelago is only 75 km to the northwest. With the next closest beaches more than 600 km to the east, imprinting on either inclination angle or intensity would be sufficient to return turtles to this nesting assemblage.

Only in East Australia have individual loggerheads been marked upon hatching and then their precise nesting location verified. Anecdotal reports indicate that at least one loggerhead hatchling marked in 1975 returned 29 years later within 8 km of her natal site (http://www.derm.qld.gov.au/wildlife-ecosystems/wildlife/watching_wildlife/turtles/turtle_tracking/premiere.html). The remarkable homing accuracy reported for this turtle is consistent with model predictions that loggerheads leaving Mon Repos in 1975 and returning in 30 years to the imprinted inclination angle would return 7.2 km from their natal site (loggerheads imprinting on intensity would return 181.6 km from their natal site). Although this precision is not typical for the past century, the mean rate of field change for both inclination angle and intensity are quite low (57 km north and 26 km south respectively). Thus, it appears that throughout most of the century relatively precise natal homing is possible using magnetic imprinting in East Australia.

For the other two nesting assemblages (Oman and South Africa), modeled navigational errors can only be compared to the nesting range. At Marisah Island, Oman, imprinting on inclination angle led turtles, on average, 88 km south ($\underline{+}$ 41 km) of their natal site, well within the range of loggerhead nesting beaches between Oman and Yemen (Baldwin et al. 2003). In contrast, imprinting on intensity led turtles an average of 201 km south ($\underline{+}$ 102 km) of their natal site. For South Africa, the average navigational error for turtles that imprinted on inclination angle was 35 km north ($\underline{+}$ 115 km). The inclination angle drifted sometimes substantially over the past century (as much as 464 km to the south); however, the net location was consistently near the home beach and within the known nesting range (Baldwin et al. 2003). Along east South Africa, intensity isolines run parallel to the coastline making it unlikely to be useful to turtles as a navigational marker.

Regression Analysis of Temporal Variation in Nest Abundance

Regression analyses of temporal variation in nest counts for Cape Lookout, North Carolina, U.S.A. between 1990 and 2005 indicated that as the rate of field change for inclination angle increased, nesting decreased ($r^2 = 0.311$, $p < 0.025$, $n = 16$). No relationship was observed with the change in intensity ($r^2 = 0.045$, $p > 0.430$, $n = 16$) or time ($r^2 = 0.126$, $p > 0.178$, $n = 16$).

Regression analyses of temporal variation in nest counts for Brevard County, Florida, U.S.A. indicated a decreasing trend of nest counts between 1990 and 2009 ($r^2 = 0.369$, $p < 0.001$, $n = 20$). Additionally, as the rate of field change for inclination angle increased, nesting decreased ($r^2 = 0.562$, $p < 0.001$, $n = 20$). Likewise, the rate of field change of intensity also corresponded with decreased nesting ($r^2 = 0.599$, $p < 0.001$, $n = 20$). However, the rate of secular variation of inclination angle and intensity are highly correlated (Pearson's $r = 0.949$, $p < 0.001$, $n = 20$). The correlation between nest abundance and the rate of intensity field change is likely spurious because the observed phylogeographic patterns are incompatible with model output of turtles relying on intensity for magnetic imprinting (Fig. 4.9a). Variance partitioning of a multiple regression analysis (Legendre & Legendre 1998) of time and change in inclination angle ($r^2 = 0.570$, $p < 0.001$, $n = 20$) revealed that

0.8% of the temporal variation in nest abundance could be attributed to time, 20.1% is accounted for by the change in inclination angle, and 36.1% of the variation explained cannot be uniquely ascribed to time or change in inclination angle.

Regression analyses exploring temporal variation in nest counts between 1984 and 2002 for Zakynthos, Greece revealed that neither time, change in inclination angle, nor change in intensity provided any explanatory power ($r^2 < 0.046$, $p > 0.377$, $n = 20$; for each).

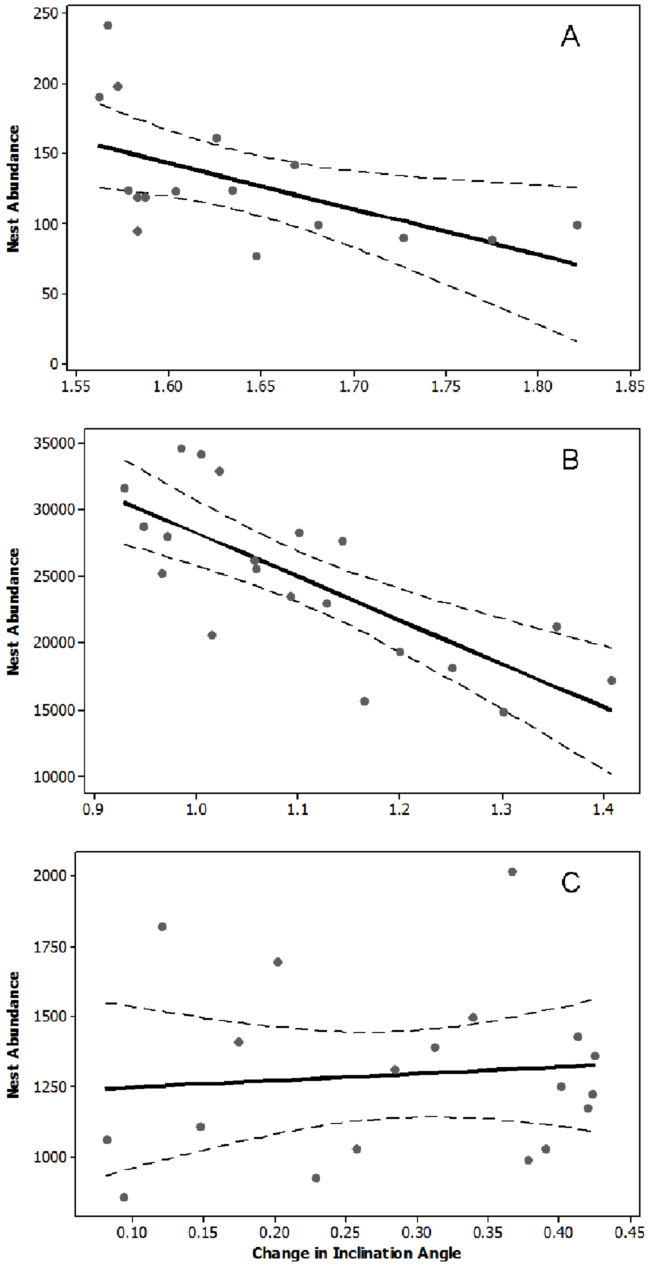

Figure 4.10 Linear regressions of loggerhead nest abundance vs. the change in inclination angle over a twenty year period. Dashed lines indicate 95% C.I. of the estimated best fit line. (A) Nest abundance at Cape Lookout, North Carolina U.S.A. from 1990 to 2005, showed a significant relationship with the change in inclination angle ($r^2 = 0.31$, $p < 0.02$, $n = 16$). (B) Nest abundance at Brevard County, Florida, U.S.A. from 1990 to 2009 showed a significant relationship with the change in inclination angle ($r^2 = 0.56$, $p < 0.001$, $n = 20$). However, because at this beach there is a general decrease in the number of nests laid through time a variance partitioning analysis was performed examining the effect of change in inclination angle and time. This analysis revealed that 20.1% of the variation in nest abundance was accounted for by the change in inclination angle, approximately 1% was accounted for by time, and the remaining 36% could not be uniquely ascribed to either time or the change in inclination angle. (C) Nest abundance at Zakynthos, Greece from 1984 to 2002 did not show a significant relationship with the change in inclination angle. See text for further discussion.

Discussion

The nesting sites of sea turtles possess a suite of necessary criteria that allow for the successful incubation and dispersal of offspring. For example, appropriate substrate and incubation temperature are required (Carthy et al. 2003; Miller et al. 2003), as is close proximity to ocean currents that can help transport hatchlings to suitable nursery habitats (Putman et al. 2010a, b). Some coastal locations provide better nesting habitat than others, yet the critical components for successful nesting are probably difficult or impossible for turtles to assess directly. By nesting in their natal region, females are assured the location has the attributes needed for successful reproduction as it allowed for their own successful growth and development (Lohmann et al. 2008a). However, similarities in environmental conditions among nearby coastal locations might not require (or permit) turtles to evolve a mechanism of pinpoint homing accuracy. Thus, a homing strategy that returns turtles to the vicinity of their natal site is likely sufficient to ensure that offspring encounter appropriate environmental variables. This quantitative assessment of the magnetic imprinting hypothesis suggests that such a strategy is well-suited for this navigational task.

The model's results indicate that the precision of natal homing would not be the same across all loggerhead populations, or even year to year in the same region. Interestingly, nesting assemblages where there is evidence for relatively structured populations (i.e. precise natal homing) such as the southeast U.S.A., Greece, and Japan have much lower rates of secular variation this past century compared to nesting assemblages such as Brazil and the Cape Verde Islands where the field has been changing more rapidly and population structure is less well defined, or not observed. Regardless, at all eight nesting assemblages, assuming turtles return to the coast at maturity, imprinting on inclination angle returned modeled turtles with approximately the same precision that is known for each population. In contrast, in the southeast U.S.A., Greece, Oman, and South Africa navigational errors modeled for turtles imprinting on intensity appear incompatible with the estimates of natal homing precision. In Brazil and the Cape Verde Islands, imprinting on intensity leads to smaller navigational errors than inclination angle (though navigational errors of inclination angle are still compatible with known homing precision at those two nesting assemblages).

It is not necessary to assume, however, that all loggerhead populations use the same magnetic parameters to locate their natal region. Because widely separated nesting assemblages of loggerheads are reproductively isolated (Bowen & Karl 2007) and novel navigational strategies can evolve relatively rapidly (Berthold et al. 1992; Helbig 1996) it is plausible that loggerheads could evolve strategies that most effectively guide homing based on the selective pressures of a given region. Furthermore, juvenile natal homing (Bowen et al. 2004; Bowen & Karl 2007) could serve as a compensatory mechanism for secular variation. Though the precision of juvenile natal homing has not been determined, these results indicate that it could considerably increase homing accuracy (using either inclination angle or intensity) (Fig. 4.9b). These early returns to the natal coast could serve to ensure that natal homing for future nesting efforts is successful, by allowing turtles to update their knowledge of the field in their natal region and compensate for secular variation long before their first reproductive migration. Whether this occurs, of course, is speculative, though the recalibration of navigational systems appears quite common in birds (Able & Able 1990; Cochran et al. 2003).

Although recalibration of the magnetic information remembered by sea turtles and the use of more localized cues could be used to further refine a turtle’s search for a natal region, in many cases it appears that natal homing is not particularly precise. It has been suggested that this lack of precision could be attributed to the use of magnetic cues for homing (Shamblin et al. 2010). For instance, phylogeographic analyses using mtDNA indicate that Florida loggerheads differentiate their natal region in terms of north-south, but not east-west. When published, this enigmatic phylogeographic pattern was not explained (Encalada et al. 1998); however, in a more recent and detailed analysis it was suggested that this pattern could be the result of loggerheads relying on a single magnetic cue to locate the beach on which to nest (Shamblin et al. 2010). The Florida peninsula is oriented north-south, whereas isolines of inclination and intensity run approximately east-west. Consequently, at a given latitude, the east and west coasts of Florida are marked by the same inclination angles and intensities, but northern and southern Florida are marked by different values of inclination and intensity (Fig. 4.11).

Presumably then, Florida loggerheads could readily determine whether they were north or south of a location using magnetic cues, but determining differences between east and west coasts of Florida would be impossible using a single magnetic cue, because the east and west coast are marked by the same magnetic values. Thus, if regional homing were accomplished by magnetic imprinting, over time straying from east to west across Florida might cause those populations to develop a homogenized haplotype frequency, whereas significant differences in haplotype frequency would be maintained north to south. Indeed, several individuals have been documented nesting on both sides of the Florida peninsula, a behavior consistent with this interpretation (LeBuff 1974; Bowen et al. 1993).

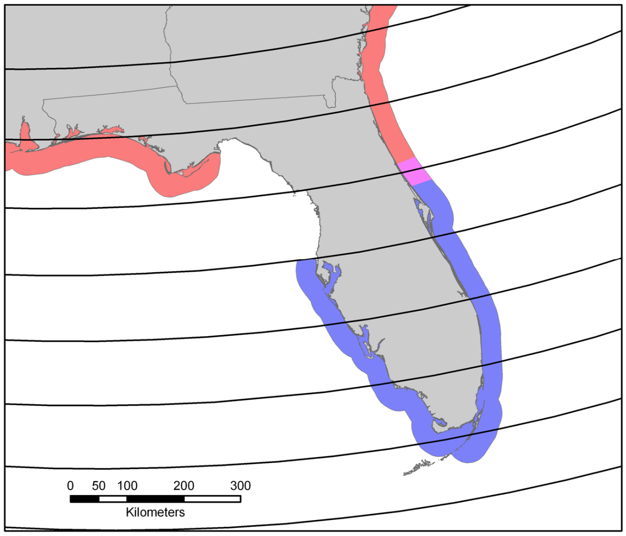

Figure 4.11 Map of Florida, U.S.A. and inclination angle (plotted at 1° intervals). Nesting beaches with significantly different haplotype frequencies are in different colors (red and blue). The area of haplotype frequency overlap is colored purple. Beaches that have the same inclination angle on the east and west coasts of Florida do not have significantly different haplotype frequencies. Inclination angle would not provide turtles with the information needed to distinguish the east from the west coast of Florida. Turtles could use inclination angle to differentiate nesting beaches north to south and differences in haplotype frequency are observed north to south.

In addition to natal homing by magnetic imprinting influencing spatial patterns over evolutionary timescales, it also appears that, in at least some cases, it might help explain temporal variation in sea turtle nesting at individual beaches. For turtles attempting to relocate their natal site using magnetic cues, it should be expected that a greater number of turtles could successfully locate their nesting beach if the field changed little between the year that they left and the year they attempt to return. During periods with high rates of secular variation drift of the homing cue might lead turtles to nest at locations distant from their natal site and not be counted in nesting surveys.

At the three nesting beaches where the relationship between nest abundance and secular variation was explored (Cape Lookout, North Carolina, U.S.A., Brevard County, Florida, U.S.A., and Zakynthos, Greece), one would expect that if turtles relied on magnetic imprinting they would use inclination angle because the rate of change in inclination angle for the past century is compatible with observed phylogeographic patterns whereas the change in intensity is too great. (Although NC was not specifically examined in the spatial modeling analysis, the rate of field change and navigational errors for inclination angle and intensity are similar to those at Florida.) The discussion will therefore be restricted to secular variation of inclination angle.

Regression analyses indicated that the amount that the inclination angle changed after a 20-year time-lag (the average age to maturity for loggerheads in the Atlantic) was a significant predictor of nest abundance at Cape Lookout, North Carolina and Brevard County, Florida. In these cases, the greater the change in inclination angle the fewer nests were laid. (Fig. 4.10) The change in inclination angle predicted approximately 30% of the variation in nesting between 1990 and 2005 at Cape Lookout. For Brevard County, Florida, the findings were somewhat more complicated. Initial analyses showed that 55% of the variation in nesting between 1990 and 2009 could be accounted for by the change in inclination angle. However, there also was a significant decrease in nesting over the monitored period (see also Witherington et al. 2009). After performing variance partitioning for a multiple regression analysis considering the change in inclination angle and the decreasing temporal trend, it was apparent that the change in inclination angle accounted for 20% of the variation in nesting with 36% of the variation unable to be uniquely ascribed to either time or the change in inclination angle. These findings provide the strongest evidence to date that sea turtles rely on a magnetic imprinting mechanism to return to their natal site. Additionally, they suggest that the mechanism by which animals navigate has profound, though previously unrecognized, ecological implications.

In Zakynthos, Greece, however, nest abundance was not correlated with the change in inclination angle over 20 years (Fig. 4.10). The differences between the Zakynthos nesting beach and the beaches on the western Atlantic basin may provide some insights into the nature of the navigational task for loggerheads engaging in natal homing and the possible role of magnetic imprinting. First, the rate of field change over the periods of nesting are much greater for North Carolina and Florida (range: 1.56 - 1.82 degree change in inclination angle over 20 years) than in Greece (range: 0.08 - 0.42 degree change in inclination over 20 years). Therefore, it is possible that the rate of secular variation in Greece was sufficiently low during this period that it did not pose a problem to returning loggerheads. Consistent with this explanation is the existence of a positive correlation between the magnitude of field drift and the amount of variation in nesting explained by field drift (Fig. 4.12).

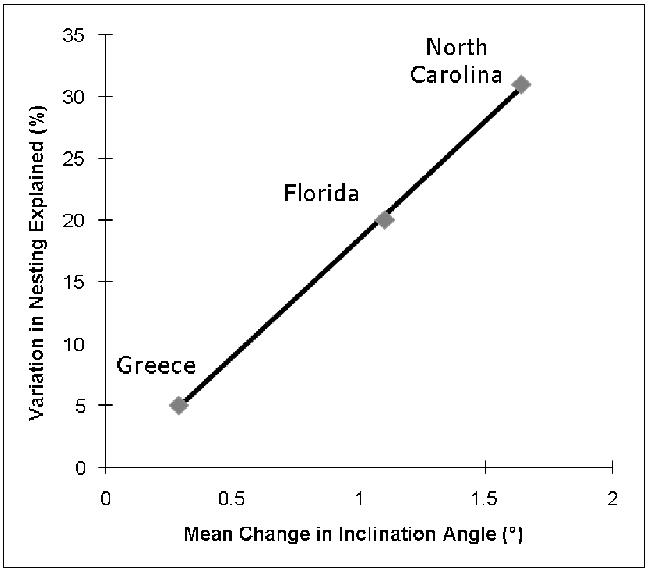

Figure 4.12 Percent variation in nest abundance explained by the change in inclination angle regressed against the mean change in inclination angle over the study period. For the three regions studied, there was a positive correlation between the mean magnitude of change in inclination angle and the percentage of variation in nest abundance that was explained by this field drift ($R^2 = 0.99$, $p < 0.001$, $n = 3$). Although this is a small sample size, the trend suggests that the greater the amount of field drift at a particular beach, the more pronounced the effect it has on temporal patterns of nesting in sea turtles.

Another possible reason for the difference among nesting sites in how well secular variation of inclination angle accounted for variation in nest abundance is major coastal geomorphology differences between nesting beaches in Greece and the eastern U.S. Sandy beaches in Greece are typically characterized as “pocket beaches” relatively short in length and marked by intervening regions of rocky coast. In contrast, North Carolina and Florida have hundreds of kilometers of uninterrupted sandy beach along their coastlines. Turtles searching for the appropriate inclination angle along Florida and North Carolina might be led north or south of the natal site due to secular variation, but would still find a sandy beach and might not rely on localized cues as heavily as turtles nesting in Greece that must search for non-rocky coast for nesting. Additionally, loggerheads from North Carolina and Florida travel the width of the North Atlantic basin over a period of 6 to 12 years making it unlikely that they could keep track of the secular variation occurring at their home beach. Turtles from Greece, on the other hand, may spend their lives largely within the Mediterranean Sea (Bolten 2003). Thus, keeping compensation for secular variation might be possible for this population (Lohmann et al. 2007).

Irrespective of these considerations, the findings presented here provide the strongest evidence to date that is consistent with the magnetic imprinting hypothesis of natal homing. Further research on how secular variation might influence temporal trends in nesting is warranted, particularly including more beaches for analysis. Ongoing phylogeographic studies along nesting assemblages will be a critical aspect of testing this hypothesis to determine if changes in haplotype frequency over time can be explained by the direction and magnitude of secular variation. Likewise, as genetic markers become more precise and less expensive to analyze it may soon be possible to test additional predictions of the magnetic imprinting hypothesis. Although such indirect methods are informative, only a carefully controlled experiment will answer this longstanding mystery of animal navigation. This present study may stimulate additional research on the topic of magnetic imprinting as a mechanism for natal homing and, more generally, how the mechanisms of animal navigation shape ecological and evolutionary patterns.

Special Thanks

S.A. Moore and. K.J. Lohmann will be co-authors of the forthcoming m.s.

CHAPTER 5

CONCLUSIONS

Migratory behavior in sea turtles is fundamental to understanding all aspects of their life-history, ecology, and evolutionary trajectories. The conclusions reached in this dissertation provide key insights to sea turtle biology that can inform conservation and management efforts, studies on other animals, and movement ecology theory. In particular, it has been shown that animal navigation and migration studies can help address long-standing questions in the larger biological disciplines of ecology and biogeography.

In Chapter 2 of this dissertation I showed that, within the reproductive range of sea turtles, nesting beaches in close proximity to ocean currents that aid the offshore movements of young turtles typically have higher nest abundance than beaches further from such currents. This biogeographic pattern along nesting beaches is likely mediated by adult sea turtles returning to the vicinity of their natal site for reproduction; a greater number of adults nest at locations that favor survival to maturity (Bowen & Karl 2007; Lohmann et al. 2008a). After I published these findings in 2010 (Putman et al. 2010a, b), the hypothesis has found additional support from modeling studies on hatchling sea turtle dispersal in Japan (Okuyama et al. 2011) and Australia (Hamann et al. 2011). The concordance among these and my own studies strongly suggests that the relationship between nesting distributions and oceanic conditions that influence dispersal is a global biogeographic phenomenon in sea turtles.

Additionally, my empirical and theoretical work on the sensory aspects of sea turtle migrations has greatly advanced the understanding of the function of magnetic information in animal navigation. The hypothesis that the earth’s magnetic field functions as a bicoordinate magnetic map in animal navigation has been debated for more than a century (Viguier 1882; Alerstam 2006; Gould 2008). In my dissertation I add to this discussion by providing new insights for how magnetic information might be used as a bicoordinate map in different contexts. In 1994 and 1996 it was discovered that sea turtles are capable of detecting two magnetic parameters, inclination angle and intensity (Lohmann & Lohmann 1994; 1996). From these discoveries it was hypothesized that these two parameters might serve as the basis of bicoordinate magnetic maps in sea turtles and other animals. It was suggested that such maps might function in a myriad of ways, ranging from providing spatial information to juvenile loggerhead turtles following a circular migratory route around the North Atlantic to providing adult turtles with a mechanism to locate isolated oceanic islands for nesting (Lohmann & Lohmann 1996).

Although potentially rich in explanatory power for how long-distance migrants navigate, bicoordinate magnetic maps have been viewed with much skepticism (e.g. Courtillot et al. 1996; Freake et al. 2006; Åkesson & Hedenström 2007; Thorup & Holland 2009). Across many parts of the world magnetic parameters are best suited for determining latitude and it was thought that the magnetic field was unlikely to provide longitudinal information (Gould 2008). However, I showed that hatchling turtles can extract longitudinal position from the earth's field (Putman et al. 2011), a finding that was heralded as the first compelling empirical evidence for the existence of a bicoordinate magnetic map in any animal (Gould 2011). This finding was obtained by exposing newly hatched loggerheads to magnetic fields that exist on the eastern and western sides of the North Atlantic at 20°N (near the southern edge of their migratory route). The young loggerheads likely utilize specific pairings of inclination and intensity; these pairings differ north to south and east to west over most of the Atlantic.

These results, combined with findings of hatchling turtles' swimming responses to various other pairings of inclination and intensity, provide growing evidence that turtles possess a large-scale magnetic map of the North Atlantic. Because all turtles tested had no migratory experience, the findings imply that their navigation system is based on inherited information. Further evidence from ocean circulation and geomagnetic models suggests that the evolution of the turtle map is strongly linked to the geographic stability of specific pairings of inclination and intensity (based on secular variation) as well as the oceanic factors within those regions that select for directed swimming by turtles. Such environmental factors may be the same selective agents that influence navigational behavior in diverse taxa, and their identification provides a starting place for further research.

Interestingly, although a bicoordinate magnetic map based on pairings of intensity and inclination angle appears to function well in providing spatial information to young loggerheads along their North Atlantic migratory route, such a map may be ill-suited for other navigational tasks. Geomagnetic models extending over the past century suggest numerous complications for adult sea turtles attempting to use of pairings of inclination and intensity to locate isolated oceanic islands. If one assumes that turtles resolve the magnetic parameters in such a way that filters out “noise” due to diurnal variation and crustal anomalies, in most parts of the world the area covered by pairings of inclination and intensity would span a relatively large geographic area. Such a system would be sufficient for marking broad oceanic regions (e.g. for the juvenile loggerheads’ magnetic map) but would, necessarily, not allow localization of an individual island without some additional information (e.g. for island nesting green turtles). Moreover, the rate of secular variation would typically result in magnetic parameters drifting large distances during the period prior to maturity when turtles of many populations are absent from their nesting island. Such field drift would make pairings of inclination and intensity inadequate markers for small islands.

My detailed analyses on the navigational systems of sea turtles have also provided a new avenue of research with important implications for movement ecology theory. Oriented locomotion in response to specific environmental variables is the essence of animal navigation and, intuitively, a crucial component of animal movement (Dingle 1996; Nathan 2008; Bowlin et al. 2010). Surprisingly, navigation behavior is rarely represented in models of animal movement. Instead, models typically assume individuals move randomly (e.g. Sims 2008; Humphries et al. 2010) or, in the case of weakly-swimming marine animals, drift passively with ocean currents (e.g. Dawson et al. 2005; Bonhommeu 2009; Hays et al. 2010).

Whether such simplifying assumptions lead to inaccurate representations of animal distributions is difficult to determine because the navigational mechanisms are not known for most animals (Holyoak et al. 2008). By modeling the magnetic navigation responses of young loggerheads, however, I show that, over time, even weakly directed locomotion is likely to have a profound effect on a population’s spatial distribution; thus, it is sufficiently important to be included in models of animal movement. Moreover, models of homing using magnetic cues appear to be highly informative in understanding the population structure of reproductive grounds in loggerhead sea turtles. These and other results from my dissertation imply that models assuming random locomotion of animals (e.g. Lèvy flights and random walks) may skew our understanding of animal movement and how it shapes fundamental ecological and evolutionary processes including individual fitness, species interactions, dispersal, gene flow, and colonization. Including explicit navigation behavior into these models is likely to provide new insights into how spatiotemporal patterns in migratory animals arise and are maintained.

Indeed, the methodologies of the research presented in this dissertation can be readily applied to address similar questions for a number of other migratory animals including certain species of invertebrates, fish, birds, and marine mammals. Conducting such studies on diverse taxa will be useful as a comparative approach and help elucidate how animal movement (and navigation behavior in particular) shapes biogeographic patterns, which in turn can be used to address conservation and management questions in migratory animals.

Understanding the factors that shape the biogeography of a species (e.g. spatial patterns of abundance) is a fundamental aspect of conservation biology and a critical aspect of prioritizing habitat preservation (Lomolino et al. 2005). Resources for habitat conservation are limited, and priority must be given to the areas of which preservation will be most likely to promote the population growth of at risk species (TEWG 2000). Particularly important are the environmental factors that predict abundance at the reproductive grounds, where the parental selection of appropriate conditions has unquestionably vital importance for offspring fitness. For sea turtles, a key feature of nesting grounds which I have identified is the nearby oceanic conditions that promote the hatchling offshore migration. To prioritize protection of nesting habitat in a way that will have the greatest chance of promoting population growth, beaches that possess offshore conditions favorable for hatchling migration should be identified. Such identification could be carried out in a manner similar to the work from my dissertation, using long-term measurements of ocean currents and ocean circulation models. With this information it should be possible to determine which beaches are most likely to produce the largest contributions of turtles to the population, and thus which should be allocated the greatest resources for conservation.

There has been a resurgence in discussion within the scientific community about “assisted colonization” of plant and animal species threatened by anthropogenic disturbance, especially climate change (Hoegh-Guldberg et al. 2008). This has generated considerable debate as to whether such measures would lead to ecological instability, whether they would be financially expedient, and whether it is even ethical to consider them (Ricciardi & Simberloff 2009). One of the greatest concerns with “assisted colonization” is that too little is known about most species to successfully assist their movement into suitable habitat (Hoegh-Guldberg et al. 2008). In the case of sea turtles, there is a history of attempting to introduce turtles to nesting beaches where their protection can be assured (Mrosovsky 1983; Carr 1986; TEWG 2000). This conservation measure has been viewed as largely unsuccessful (NOAA Tech Meth. 1996; TEWG 2000; but see Shaver & Wibbels 2007). Regardless, as “assisted colonization” continues to gain support, these questions will be revisited by sea turtle conservationists and researchers. If this conservation measure is to be successfully applied to sea turtles, it is critical that the suitability of offshore conditions for hatchling migration be examined. Choosing beaches where the migration of young turtles is facilitated will maximize a project’s possibility of success.

A recent case in which consideration of the factors that influence sea turtle nest abundance would have been useful is with the conservation measures taken by U.S. Fish & Wildlife to protect hatchling loggerhead sea turtles during the Deepwater Horizon Oil Spill of 2010. After a drilling accident released millions of liters of oil into the Gulf of Mexico, U.S. Fish & Wildlife officials deemed that any hatchlings migrating offshore from Mississippi, Alabama, and Florida panhandle beaches would be doomed. A decision was made to translocate all loggerhead sea turtle nests deposited along these stretches of coastline to the east coast of Florida, where eggs were incubated until they hatched. Afterwards, turtles were released on a nearby beach to crawl into the Atlantic.

Immediately after this plan was put forth, questions were raised as to whether this was the most effective conservation measure (http://www.newscientist.com/article/dn19177-gulf-turtle-evacuees-could-get-lost-at-sea.html). Because the distance that hatchlings must swim to reach the Gulf Stream System appears to be a limiting factor in the number of adults that return to nest (Putman et al. 2010b), it was suggested that hatchling turtles should be transported directly to the Gulf Stream. This would substantially increase the number of turtles reaching the Gulf Stream System compared to typical years, because Gulf of Mexico beaches are relatively far from the path of this current (Auer 1987; Sturges 1992). This increase might have had very positive effects on the number of turtles reaching maturity from these beaches allowing this hatchling cohort to substantially contribute to this relatively small population. Additionally, translocating hatchlings to the Gulf Stream (instead of translocating eggs to the east coast of Florida) would eliminate mortality induced by jostling eggs, which can cause the embryo to detach from the egg wall. Likewise, placing turtles directly into the Gulf Stream would minimize losses due to intense predation in coastal waters (Whelan & Wyneken 2007) and alleviate concerns that hatchlings from south-facing beaches in the Gulf of Mexico might not swim eastward to the Gulf Stream when released on east-facing beaches along the Atlantic coast.

The project ran from July through August 2010 and was deemed a success after 14,216 hatchlings were released from 265 translocated nests (http://www.nmfs.noaa.gov/pr/health/oilspill/turtles.htm). However, assuming that 100 eggs are laid per nest (Crouse et al. 1987) this means that only 53.6% of turtles survived the translocation process. Considering that the estimate of survivorship for eggs and hatchlings within the entire first year is 67.5% (Crouse et al. 1987), it seems clear that this conservation method increased mortality compared to turtles left undisturbed. Perhaps most unfortunate, however, is that the long-term merits of this conservation practice will be impossible to assess. Officials decided that hatchlings would not be marked for subsequent identification, even though such methods have been successfully employed on other loggerhead hatchlings (e.g. Baldwin et al. 2003; Hughes 2010). When the next oil spill occurs, conservationists will still be guessing as to the most effective method to protect young turtles.

Regardless, the successful conservation of sea turtles requires not only protection of habitat at reproductive grounds but also across the seascape that they traverse. Away from the nesting beach, however, there is little information on the abundance of sea turtles and studies correlating environmental factors with abundance in the open ocean, analogous to those examining nest density (Putman et al. 2010b), are not possible. A promising approach to assess patterns of turtle abundance in the open ocean is to apply particle-tracking software to numerical ocean circulation models. By releasing virtual particles at the reproductive grounds of sea turtles and tracking the particles' advection by modeled ocean currents, predictions can be made regarding turtles subsequent distribution (Fig. 5.1). These estimates of abundance can be used to identify potentially important dispersal pathways or residence areas and could give an indication of the likelihood of turtles encountering anthropogenic disturbances such as fisheries. Similar techniques have been successfully applied to numerous fish populations in order to predict commercial landings (e.g. Lehodey et al. 2003).

A word of caution, however, is warranted in interpreting the predictions made by such simulations. Findings from numerical experiments (Chapter 3, section 4 from this dissertation) indicate that even moderate amounts of weakly oriented swimming can have a profound influence on the distribution of young turtles. Specifically, simulations assuming passive drift always underestimated the number of turtles reaching locations thought to be high-quality habitat compared to simulations in which turtles engaged in “navigation behavior.” Such discrepancies suggest that omitting oriented swimming behavior by sea turtles from particle-tracking experiments introduces systematic biases in predictions of their abundance. The extent of this bias should be further studied and, if possible, parameterized using a combination of behavioral, physiological, and numerical experiments on young sea turtles. If the navigation behavior of some populations of young sea turtles can be accounted for sufficiently, it should be possible to estimate the error for predicted distributions generated under the assumption of passive drift.

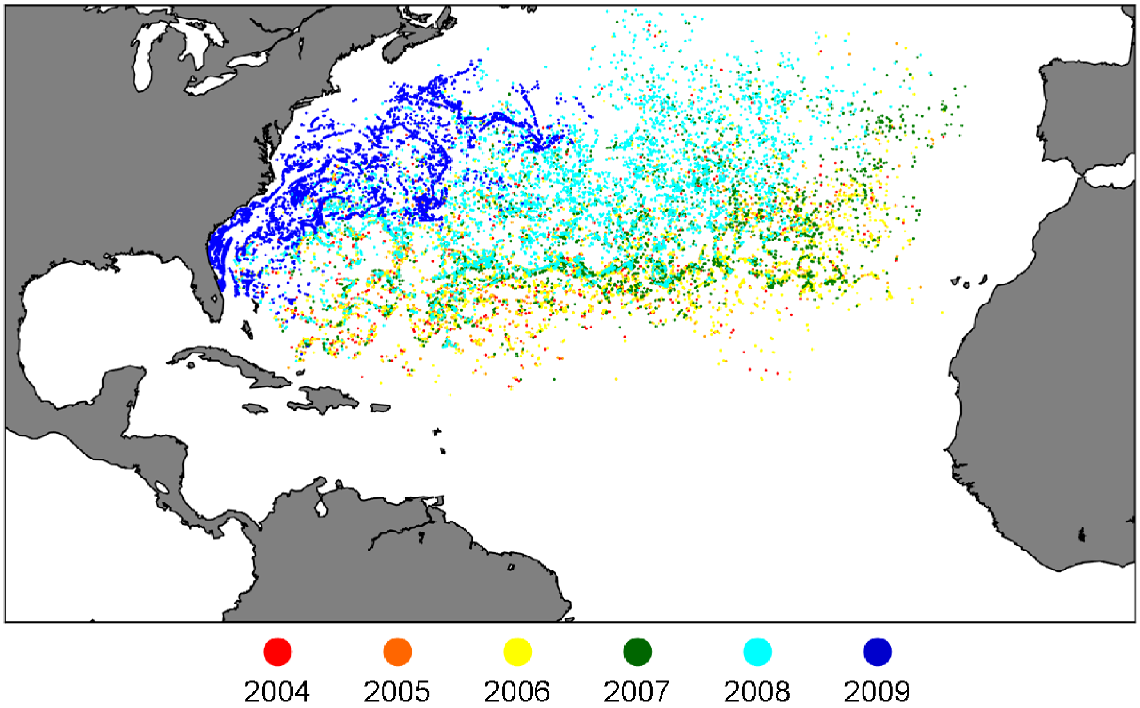

Figure 5.1 Map of the North Atlantic showing a “snapshot” of the predicted open ocean distribution of loggerhead sea turtles emerging from the southeast coast of Florida, U.S.A. Each dot represents the location of a simulated turtle in September 2009 based on Global HYCOM surface currents and the assumption of passive drift in ICHTHYOP particle-tracking software. Different colors correspond to the summer that simulated turtles departed Florida (release events occurred from July 1 through September 15 at 5 day intervals).

Along with understanding spatial patternss of abundance, identifying the factors that influence temporal variation in abundance is a crucial aspect of developing appropriate conservation and management plans (e.g. Morstad & Baker 2009). For sea turtles, temporal variation in population abundance is frequently attributed to anthropogenic causes (e.g. Broderick et al. 2006; Witherington et al. 2009). However, taking into account natural variability in hatchling survival is crucial when attempting to assess the efficacy of conservation measures. Without this, good programs may be terminated or ineffective ones might be retained as a result of temporal fluctuations in the population not attributable to anthropogenic activities. For instance, results from particle tracking experiments modeling the dispersal of hatchling sea turtles indicate that year-to-year variation in ocean circulation can have a substantial impact on the probability of young turtles reaching appropriate nursery habitat (Putman et al. 2010a). This variability likely results in differential survival among hatchling cohorts, which, in turn, presumably influences the numbers of turtles returning to nest upon reaching maturity. Further examination of variability in oceanic currents may prove useful in understanding the population dynamics of sea turtles.

Additionally, there may be factors that do not affect turtle mortality that can result in apparent temporal fluctuations in sea turtle populations. Most population assessments occur along a limited stretch of nesting beach. Therefore, variability in factors that influence the probability of turtles nesting within the monitored area contributes to the perceived fluctuations in population abundance. For example, adult sea turtles use some external cue(s) to locate their natal beach for reproduction. Errors in homing likely arise due to the navigational cue(s) not precisely corresponding to the nesting beach. If the navigational cue(s) were identified, presumably the magnitude and direction of the corresponding errors could be estimated and help account for temporal variation in nest abundance. For example, the hypothetical homing strategy of magnetic imprinting predicts that navigational errors would result from the gradual shifting (secular variation) of the earth’s magnetic field (Putman & Lohmann 2008; Lohmann et al. 2008a). Regression analyses from Chapter 4, section 3 of this dissertation indicate that, at some beaches, the rate of secular variation accounts for 20-30% of the temporal variation in nest abundance; fewer nests were deposited in years when secular variation was greater.

Mechanisms for regional homing, local site-selection, and the relative weight and interaction between them have the potential to influence recruitment of nesting adult females to specific beaches.

These mechanisms are largely unknown and, unfortunately, the value in assessing them appears to be an overlooked aspect of most recovery plans (NMFS & USFWS 1991; 1998; 2009; TEWG 2000). Knowing how sea turtles select nesting areas could be informative in predicting gene flow among beaches and even estimating the likelihood of beaches being re-colonized if turtles are locally extirpated. Moreover, it could also provide an indication as to the extent that different nesting areas contribute to the overall population. For example, a nesting beach might have unfavorable conditions for hatchling turtles, but maintain higher than expected levels of nesting because adult turtles produced at other beaches subsidize its losses. Clearly, effort allocated to protecting such an area would be better spent elsewhere.

Along with providing much needed insights into the conservation of migratory species and new understanding to the function of animal movement in ecological and evolutionary processes, the work from my dissertation highlights the value of integrative research. By combining techniques from diverse scientific fields (e.g. ethology, physical oceanography, and geology) I developed novel ways to address long-standing questions in biology. It is my hope that this research will inspire others to look for ways to approach their research from perspectives outside of their own discipline and seek out collaborations with scholars in disparate areas of study.

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