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Goal navigation and island-finding in sea turtles

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Abstract

Juvenile and adult sea turtles often navigate to specific feeding areas during long-distance migrations, and adults periodically return to particular geographic areas for mating and nesting. In addition, turtles displaced from feeding or nesting areas often home to the site of capture. Relatively little is known, however, about how turtles navigate to particular goal areas.

Both juvenile and adult turtles use the Earth's magnetic field as a source of navigational information. Laboratory experiments have provided evidence that juvenile green turtles learn the magnetic topography of their feeding grounds and acquire a “magnetic map” that facilitates navigation toward particular locations. Adult green turtles displaced from nesting beaches on an island in the Indian Ocean showed diminished homing ability when magnets were attached to their heads, implying that mature turtles also exploit magnetic cues when navigating to islands or other specific destinations.

Although geomagnetic information appears to be an important component of sea turtle navigation, it is unlikely to be the only cue used. Additional experiments in which nesting green turtles were displaced from islands have highlighted the possible involvement of local, non-magnetic cues in the final phase of island-finding. Thus, a reasonable hypothesis is that turtles use multiple cues to navigate in the marine environment, perhaps relying on a magnetic map to navigate into the vicinity of a distant target and then using non-magnetic cues to guide themselves to the final goal.

Keywords: Magnetic; Migration; Navigation; Olfactory; Orientation; Review; Sea turtle; Secular variation

1. Introduction

Sea turtles of most species migrate intermittently throughout their lives. As hatchlings, turtles establish courses toward the open sea, then follow complex migratory pathways that sometimes lead across entire ocean basins and back (Carr, 1986; Bowen et al., 1995; Bolten et al., 1998, 2003). Older juveniles of some species, such as loggerheads (*Caretta caretta*) and green turtles (*Chelonia mydas*), eventually leave the open-ocean environment and take up residence in neritic feeding grounds, sometimes migrating seasonally between summer and winter habitats (Musick and Limpus, 1997). In contrast, other species, such as the leatherback *Dermochelys coriacea*, typically remain in the open-sea environment, often wandering over vast areas in search of food. As adults, turtles of nearly all species migrate from their feeding grounds to specific mating and nesting areas and back again. The highly mobile lifestyle of sea turtles is thus dependent on an ability to navigate reliably through the ocean environment.

For logistical reasons, most studies on orientation and navigation in sea turtles have focused on hatchlings. Hatchlings are small, seasonally abundant, easy to manipulate in laboratory and field studies, and strongly motivated to migrate offshore. Considerable progress has been made in characterising the orientation cues that guide hatchlings out to sea, as well as cues that help guide young turtles along their migratory path during their first transoceanic migration (Lohmann and Lohmann, 1996a, 2003; Lohmann et al., 2001).

In comparison to hatchlings, relatively little is known about the mechanisms of orientation and navigation used by juvenile and adult sea turtles. Because ontogenetic changes in orientation and navigation occur in some animals (Wiltschko, 1983; Able and Bingman, 1987; Rodda and Phillips, 1992; Able and

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Able, 1996), the strategies and mechanisms used by juvenile turtles, as well as by adults, may differ significantly from those used by hatchlings beginning their first migration. Moreover, older turtles migrate to specific locations whereas hatchlings do not; thus, the navigational tasks confronted by each age group differ in important ways.

The size of juvenile and adult turtles, and the open-sea environment that they often inhabit, present significant logistical obstacles to experimentation. Nevertheless, reconstructions of the migratory routes of turtles, as well as both laboratory and field experiments, have begun to provide insights into the navigational processes underlying long-distance movements (e.g. Papi and Luschi 1996; Lohmann et al. 1999, 2004; Hays et al., 2003; Lohmann, 2007; Luschi et al., 2007). In this paper we summarise what is known about how juvenile and adult sea turtles navigate, particularly when moving to specific goal areas such as feeding grounds and nesting beaches.

2. Goal navigation in juvenile and adult turtles

After a period of years spent in developmental migrations in the open ocean, juvenile turtles of several species leave the oceanic environment and take up residence in feeding grounds in shallow areas, often along coastlines (Musick and Limpus, 1997). Juvenile loggerhead and green turtles in these neritic habitats often show fidelity to specific foraging areas, returning to them reliably after long, seasonal migrations or experimental displacements (Ireland, 1980; Byles, 1988; Musick and Limpus, 1997; Avens et al., 2003a).

Adult sea turtles, like juveniles, can locate small, isolated feeding areas. For example, tag returns have shown that loggerheads and green turtles that nest along the Great Barrier Reef return afterwards to specific, widely dispersed feeding grounds that are sometimes located hundreds or thousands of kilometres away from their nesting sites (Limpus et al., 1992). The feeding grounds of different individuals may lie in nearly any direction from the nesting region, but adult turtles often show fidelity to both their feeding and nesting areas and migrate between them at appropriate times. A similar pattern exists in green and loggerhead turtles that nest in Cyprus. When the same turtles were tracked by satellite telemetry during post-nesting migrations in multiple years, each turtle was found to migrate to its own specific foraging area in Libyan waters, and to follow remarkably similar paths on different occasions (Broderick et al. 2007).

For many years researchers hypothesised that adult turtles nest on or near the same beaches where they themselves emerged as hatchlings (Mrosovsky, 1983). Genetic analyses have now confirmed that the adults of at least some species do indeed return to their natal region for nesting after spending years in distant oceanic regions, in neritic foraging grounds, or both (e.g., Meylan et al., 1990; Bowen et al., 1993, 1994, 1995).

In many cases, natal homing appears to be on a regional scale rather than at the level of highly specific nest sites. In loggerheads, for example, both the pattern of population genetics and the nesting locations of individual turtles suggest that although females return to nest within the general geographic region of their natal beach, they may select nest sites anywhere within a considerable area, possibly spanning a few hundred kilometres along coastlines (Richardson, 1982; Bjorndal et al., 1983; Bowen and Avise, 1995; Miller, 1997). Under some circumstances, however, turtles may return to much more specific nesting areas (e.g. Schroth et al. 1996; Hatase et al. 2002; Lee et al. 2007). In the future, improved methods of analysing molecular data may be helpful in resolving how finely tuned natal homing is to individual beaches, and whether differences in natal homing precision exist among different populations and geographic areas (Lee, 2008-this issue).

An interesting but unresolved question is whether nesting turtles use the same navigational strategy during all of their reproductive migrations, or whether instead the cues and strategies used change as a turtle gains migratory experience. It is possible, for example, that first-time migrants (some of which may have been absent from the natal region for a decade or longer) use one set of cues to locate the natal beach region during their initial reproductive migration, whereas older, more experienced turtles use different cues during subsequent reproductive migrations (Lohmann et al., 1999). For long-lived animals that undertake a similar long-distance migration every few years, the possibility of acquiring information that enhances navigational performance over time is both plausible and likely.

Although natal homing has long been discussed in the context of nesting adult turtles, a relatively recent finding is that similar homing (at least on a regional scale) also occurs earlier in the life cycle of loggerheads when juveniles transition from the oceanic developmental stage to the neritic phase. When juvenile loggerheads leave the open ocean, they choose foraging grounds within their general natal region more often than would be expected by chance (Sears et al., 1995; Engstrom et al., 2002; Bowen et al. 2004, 2005). Thus, juvenile loggerheads appear to take an active role in returning to the natal region years before they are ready to reproduce, despite having traveled great distances away during their developmental migrations. The navigational mechanisms involved are entirely unknown.

In sum, there are three distinct points in the life cycles of loggerheads, and perhaps also in some other turtle species, when the animals return to their natal region. The first occurs during the transition from the oceanic to neritic phase. The second occurs when a turtle reaches reproductive maturity and migrates for the first time to nesting areas in the general vicinity of its natal beach. The third occurs when an experienced migrant returns on multiple occasions (typically separated by intervals of 2–4 years) to the nesting area that it has chosen to use as its own. In each case, the precision of the natal homing (i.e., how close to the actual natal site turtles return to) is not known. In addition, whether turtles use the same navigational mechanisms in each situation, or instead use different cues and strategies in each case, remains to be determined.

Natal homing in all of its forms probably requires some type of goal navigation, inasmuch as a target area exists in each case. The specificity of the target, however, may vary at different life stages. For example, juvenile turtles may return only to a broad geographic region, whereas experienced nesting turtles may target a much more restricted area along a coastline.

3. Studying sea turtle navigation

The American zoologist Archie Carr was among the first to take a scientific interest in sea turtle navigation (e.g., Carr 1956, 1963, 1967, 1972). Long before the migratory nature of sea turtles was fully understood, incidents described to Carr by Caribbean turtle fishermen helped convince him that turtles have remarkable navigational abilities. In one such anecdotal account, a turtle captain in the Cayman Islands described how two green turtles captured in Nicaraguan waters were branded and loaded onto a ship bound for market in Key West, Florida. As the vessel approached Florida, however, a violent storm capsised the boat and the turtles escaped into the sea. Fishermen later recaptured the marked turtles in Nicaragua in the same location where they had been caught initially (Carr, 1956; Fig. 1). This incident, and others like it, led Carr to conclude that “green turtles … have some sort of extra sense, or some clever way of using the ordinary senses, that lets them make long, controlled journeys in trackless seas” (Carr, 1956).

At the time of Carr’s early investigations, techniques for studying turtle navigation were limited; moreover, little was known about where turtles migrated, or even whether they did. As a result, efforts were initially focused on establishing general migratory patterns of different turtle populations using simple methods such as recoveries of tagged turtles. Nevertheless, Carr provided thoughtful considerations on the subject of turtle navigation, as well as useful suggestions about future experiments that could not be conducted at the time (e.g. Carr, 1967, 1972). Moreover, he foresaw that advances in tracking technologies would one day make it possible to reconstruct the migratory routes of turtles and that such information might allow inferences about navigational mechanisms. Years later, with the arrival of satellite telemetry, analyses of the reconstructed routes of turtle migrations did indeed provide some useful, albeit general, insights into navigational strategies and mechanisms. For example, early tracks revealed that turtles often move almost directly toward goal areas from considerable distances away, and that they can maintain straight routes over long distances even when moving across water currents (e.g. Papi and Luschi 1996; Lohmann et al., 1999).

Carr was also involved with several early attempts to study turtle navigation through displacement experiments. This is a traditional method of studying navigational abilities of an animal by capturing it, moving it away to a distant site, and then observing its subsequent behaviour. If the animal is motivated to return to the place where it was captured, it may home to the capture site and, while doing so, use the same navigational mechanisms that it used during its initial trip.

Early turtle displacement experiments relied on clever but labor-intensive techniques for monitoring movements, such as attaching balloons to turtles and following them by boat (Fig. 2). Such methodologies proved cumbersome and, perhaps not surprisingly, yielded relatively little information because turtles could be followed only briefly (Carr 1963, 1972; Baldwin, 1972). Nevertheless, these early attempts marked the start of a continuously evolving stream of techniques for tracking turtles, which now include radio, satellite, and GPS

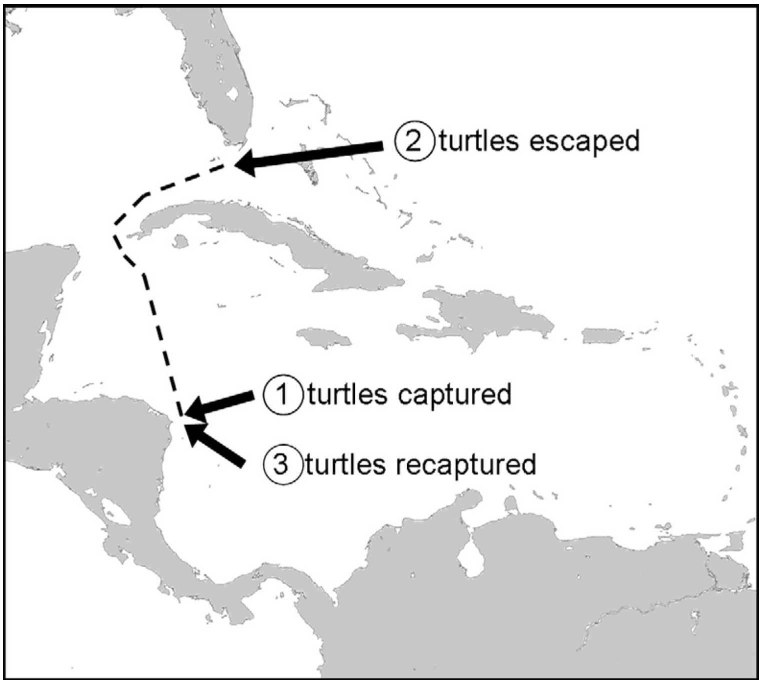

Fig. 1. An early anecdote about sea turtle navigation from a Cayman Islands turtle fisherman, as reported by Carr (1956). In this incident, green turtles captured in feeding grounds along the Nicaraguan coast were branded (so that the fishermen who caught them could be paid) and loaded onto a boat bound for market in Key West, Florida. The boat was capsised by a violent storm as it neared Florida and the turtles escaped into the sea. Some months later, two of the marked turtles were recaptured in Nicaragua almost exactly where they had been caught originally.

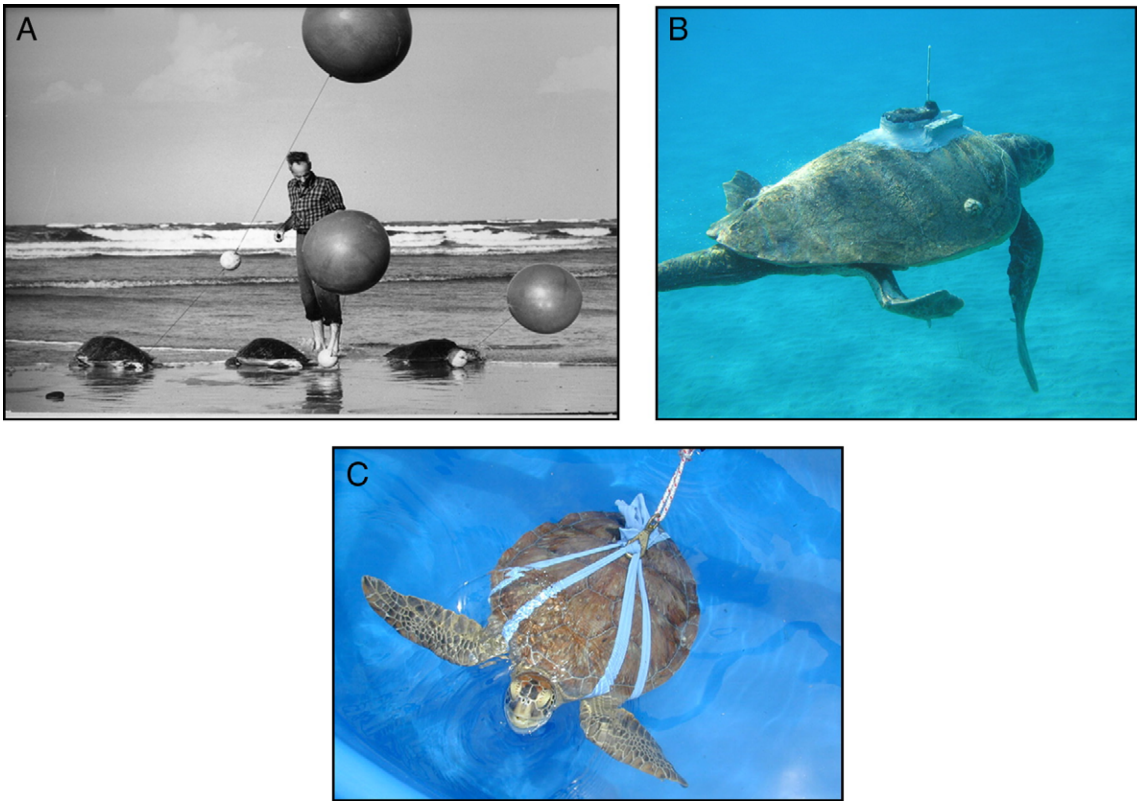

Fig. 2. Developments in techniques for studying navigational mechanisms of sea turtles. A) An early method of visually tracking turtles through the ocean. This method, used in the 1960s by Archie Carr and his colleagues, involved attaching helium balloons to turtles and following each animal in a boat. Researchers had to remain in visual contact with the balloons, which limited the time and range over which a turtle could be followed, particularly in the open ocean. B) Satellite transmitters and satellite-linked GPS receivers are now widely used to monitor movements of turtles. Both are capable of tracking animals anywhere in the ocean and can be used to reconstruct the migratory routes of turtles. C) A method for monitoring the directional movements of juvenile turtles in the lab during navigational experiments. Turtles are placed into a soft cloth harness and tethered to an electronic tracking device which records their swimming movements, permitting tests of navigational mechanisms under controlled laboratory conditions (e.g., Lohmann et al., 2004; see text for details). Photo credits: Mimi Carr (A), Mike Sheldon (B), Ken Lohmann (C).

telemetry (Fig. 2). These modern technologies allow continuous tracking of migrating and homing turtles, so that valuable information about the routes that turtles follow can be obtained with relative ease.

During the past several decades a number of studies involving displacements have been carried out with sea turtles of various species, ages, and size classes. In several studies, juvenile turtles were displaced and released at various distances (approximately 2–70 km) away from capture sites (e.g., Carr, 1967; Ireland, 1980; Standora et al., 1995; Avens et al., 2003a). In each case, many returned to the capture area, implying that the turtles have navigational mechanisms that enable them to compensate for displacements and to home to specific locations.

Similar results have been obtained with adult turtles. Because female turtles can be captured easily when they emerge on beaches to nest, displacing females during the nesting period (when they are likely to be motivated to home back to the nesting beach to complete their breeding cycle), has been the most commonly used approach. Experiments with female turtles displaced from their nesting beaches and then tracked using radio or satellite telemetry have confirmed that turtles frequently return to their nesting areas after displacements (e.g., Murphy and Hopkins-Murphy, 1990; Papi et al., 1995, 1997; Luschi et al., 1996, 2001, 2007). Paths of turtles were highly variable, with some individuals rapidly establishing paths toward the capture area and others following more circuitous routes, especially when released in the open sea. The reason for this variation is not known. Contributing factors might include differences in the physiological and motivational state of the turtles, differences in methodology (e.g., some turtles had transmitters placed on their heads where the magnetic fields of the transmitters might impair magnetoreception), and differences in the environment (e.g., some turtles were taken from continental nesting beaches and others from islands). What is evident, however, is that adult turtles displaced from nesting beaches often home back to the capture area.

In addition to traditional displacement experiments, an alternative method for studying homing behaviour of displaced turtles under laboratory conditions has recently been developed (Avens and Lohmann, 2004; Fig. 2). Juvenile loggerhead and green turtles captured in coastal waters of North Carolina, U.S.A., were displaced along circuitous routes while deprived of visual cues. Instead of being released, the turtles were tethered in a circular, water-filled arena (on land) and permitted to swim while their orientation was monitored. Turtles oriented in directions that corresponded closely with the most direct route back to their capture locations, providing a laboratory equivalent of homing behaviour, and one that can be studied under carefully controlled conditions.

4. Compasses, “maps”, and open-sea navigation

Animals capable of homing are often said to possess both a positional or “map” sense and a directional or “compass” sense; the map sense is used to determine position relative to a destination (or at least the direction toward the goal), while the compass sense is used to maintain a heading toward the appropriate direction once the animal begins to home (Kramer, 1961; Able, 2001). Although this widely used model is helpful in highlighting the importance of both positional and directional information, it is important to recognise that it often oversimplifies the navigational processes used by an animal. In reality, all animals studied to date rely on multiple sources of information when navigating. A given animal often has several different ways of maintaining headings, and it may also have multiple sources of positional information available to it. Moreover, the cues and/or strategies used may change depending upon whether the animal is close to its target area or far away.

Sea turtles are known to have several mechanisms that can be used to maintain headings. For example, they have a magnetic compass sense (Lohmann, 1991; Light et al., 1993; Lohmann and Lohmann, 1993). In addition, juvenile turtles possess a second mechanism for maintaining headings, possibly based on a sun compass or on patterns of skylight polarization (Avens and Lohmann, 2003). Finally, hatchling loggerheads, green turtles, and leatherbacks are able to derive directional information from the movement of ocean waves (Lohmann et al., 1990; Wyneken et al., 1990; Lohmann and Lohmann, 1992; Lohmann et al., 1995), an ability which might confer upon older turtles a third way of maintaining headings in oceanic regions where wave direction is relatively stable.

A compass by itself is not sufficient to explain some of the navigational tasks turtles are known to perform. For example, pinpointing an isolated target during migrations spanning hundreds of kilometres through the open sea appears to be impossible by relying exclusively on a directional sense. A compass cannot detect deviations from an intended course or correct for them, and even small deflections can lead to large errors in prolonged journeys. For instance, a systematic error in directional steering as small as a few degrees will cause a turtle migrating from the Brazilian coast to Ascension Island to miss its 11-km wide target after the 2200 km-long oceanic trip (Fig. 3). Given that animal compasses are generally thought to have limited accuracy (e.g., some estimates of compass accuracy are about ±40° (Wiltschko and Wiltschko, 1995)), reaching the island with a compass alone appears impossible.

In addition to errors caused by compass inaccuracy, naturally-occurring deflections are the rule in oceanic trips because of ocean currents. In the absence of stationary reference points, current drift is difficult or impossible for a swimming animal to detect. Currents, especially when they are temporally or geographically variable, thus have the potential to carry animals away from their intended routes. A few recent studies have investigated how current drift affects the routes of turtles homing toward oceanic islands after displacements (Girard et al. 2006; Luschi et al. 2007). The results indicated that, when turtles encountered currents, they did not immediately alter their movements in such a way that the original direction of travel was preserved. As a result, currents sometimes deflected turtles away from the courses they had initially been following.

Given the errors that will inevitably accumulate during long-distance migrations to islands and other goals in the open sea, the involvement of navigational mechanisms other than compasses has to be hypothesised. In principle, several different types of information might be used by turtles to supplement their sources of directional information in the open ocean. Most research, however, has focused on two different possibilities: chemosensory information emanating from target areas and the Earth’s magnetic field. Because long-distance migrants frequently use multiple cues in navigation, the two ideas are not mutually exclusive.

5. Current-borne cues and navigation

Sea turtles, like nearly all other aquatic organisms (Carr, 1988), can detect chemicals dissolved in water (Manton et al.,

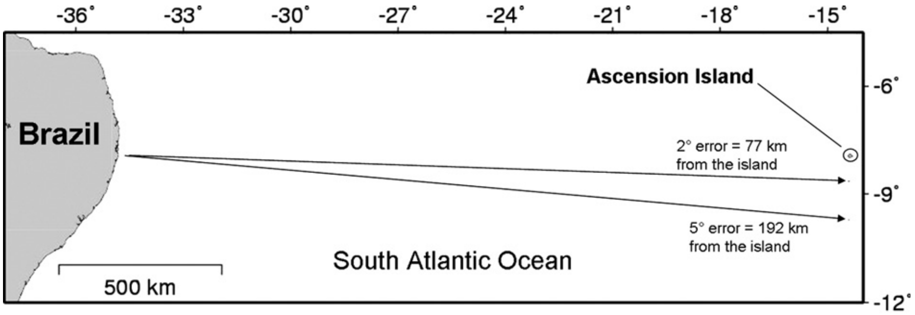

Fig. 3. Diagram illustrating the effects of hypothetical steering inaccuracies in a turtle migrating from Brazil to Ascension Island. Arrows connect a site in Brazil at the same latitude of Ascension to the points where turtles making systematic southward errors would cross the longitude of Ascension. Even if turtles can somehow locate the part of the Brazilian coast closest to the island and also somehow know the exact compass heading needed, a compass alone is insufficient to guide the turtles to the island because slight errors in compass direction will cause the animals to miss the small target. An error of just 2°, for example, leads to a path that misses Ascension by 77 km. In reality, additional errors seem certain to accumulate because ocean currents will drift the turtle off its course. The need for positional information of some kind during this migration appears inescapable.

1972a,b; Grassman and Owens, 1982). Such cues have been proposed to play a role in the long-distance migrations of adult turtles. For example, in an attempt to explain the migration of green turtles from the coast of Brazil to Ascension Island, Koch et al. (1969) hypothesised that green turtles detect a chemical plume that originates at the island and then follow it across more than 2000 km of ocean to its source. The putative chemical markers would need to persist in the sea without degrading for at least several weeks, and a sufficient gradient would need to exist so that turtles in distant locations could detect not only the chemical but the direction of the increasing gradient (Carr, 1967, 1972).

As the migratory paths of turtles have become better characterised, however, evidence against the use of such cues in long-distance navigation has begun to accumulate (Lohmann et al., 1999). Analyses of homing routes of displaced turtles in relation to the main currents they encounter have failed to provide evidence that turtles use current-borne cues emanating from targets (Luschi et al. 2001; Girard et al. 2006). Moreover, satellite tracking experiments have revealed that turtles often follow essentially straight paths to target areas hundreds of kilometres away (Balazs et al., 1994; Papi and Luschi, 1996; Luschi et al., 1996, 1998), even when swimming directly across water currents (Papi et al., 1995; Luschi et al. 1998). Because animals orienting in a chemical plume are seldom able to move directly to the source without employing a search strategy that involves frequent course changes (Baker, 1985; Dusenbery, 1992; Carr, 1972), the consistency of the headings casts doubt on the hypothesis that turtles follow such plumes over great distances (Papi et al. 1995; Papi and Luschi, 1996; Lohmann et al., 1999).

Even if waterborne chemical cues are not involved in long-distance navigation, they might still enable turtles to recognise a specific nesting area (for example, one adjacent to a river mouth) after other navigational mechanisms have brought the turtles into close proximity of the goal (Lohmann et al., 1997, 1999). Whether this occurs is not known.

6. Magnetic maps

In addition to providing turtles with directional information, the Earth's magnetic field provides a potential source of positional or "map" information over large geographic areas. Several geomagnetic elements vary in a predictable way across the surface of the Earth (Skiles, 1985; Lohmann et al., 1999, 2007). For example, at each location on the globe, the magnetic field lines intersect the earth's surface at a specific angle of inclination (Fig. 4). At the magnetic equator, the field lines are parallel to the Earth's surface and the inclination angle is said to be 0°. The field lines become progressively steeper, however, as one moves toward the magnetic poles; at the poles themselves, the field lines are perpendicular to the Earth's surface. Thus, inclination angle varies predictably with latitude.

In addition to inclination angle, at least three other magnetic field elements vary predictably across the Earth's surface and might hypothetically be used in assessing position. These include: (1) the intensity (strength) of the total field; (2) the intensity of the horizontal field; (3) the intensity of the vertical field.

Hatchling sea turtles can detect inclination angle and field intensity (Lohmann and Lohmann, 1994, 1996b) and can also distinguish among the magnetic fields that exist in different oceanic regions (Lohmann et al., 2001). Evidence that older turtles also use positional information from the Earth's field was obtained in experiments in which juvenile green turtles several years of age were captured in coastal feeding grounds at a site along the east coast of Florida, USA (Lohmann et al., 2004). At a nearby outdoor test site, each turtle was placed into a cloth

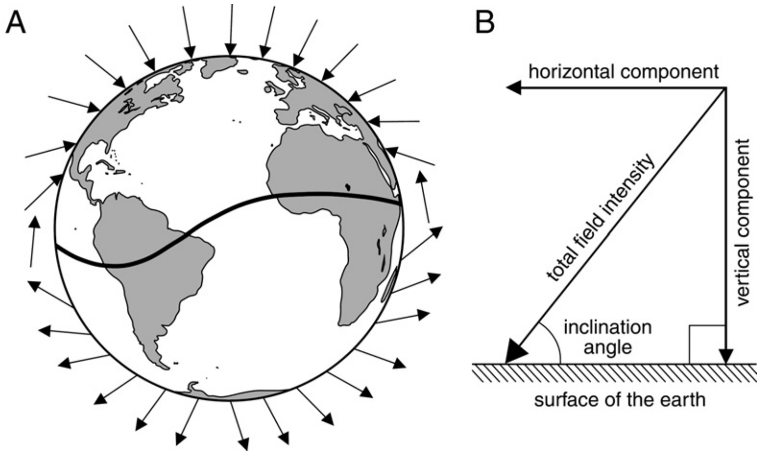

Fig. 4. A) Diagrammatic representation of the Earth's magnetic field illustrating how field lines (represented by arrows) intersect the Earth's surface, and how inclination angle (the angle formed between the field lines and the Earth) varies with latitude. At the magnetic equator (the curving line across the Earth), field lines are parallel to the Earth's surface. The field lines become progressively steeper as one travels north toward the magnetic pole, where 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 turtles 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. (Whether turtles or other animals are able to resolve the total field into vector components is not known.)

harness and tethered to a computerised tracking system inside a circular arena filled with water. The arena was surrounded by a coil system that was used to control the ambient magnetic field. The orientation of each turtle was monitored as it swam in a field equivalent to that which exists at one of two distant locations.

Turtles exposed to a magnetic field that exists in a location 337 km to the north swam southward (Fig. 5). By contrast, those exposed to a field matching that of an area an equivalent distance to the south swam northward (Fig. 5). Thus, turtles responded to each field by orienting in a direction that would have led them toward the capture site had they actually been at the location where each field occurs naturally.

These findings indicate that juvenile turtles use magnetic information as a component of a classical navigational map which facilitates navigation to specific geographic locations (Lohmann et al. 2004). Because different turtles leave the open ocean and settle in widely dispersed feeding areas, a juvenile turtle's ability to navigate to specific locations appears to be based at least partly on the animal's experience and learned understanding of how the Earth's field varies over a considerable geographic area.

The "magnetic map" of sea turtles may be organised in several fundamentally different ways (Lohmann and Lohmann, 2006; Lohmann et al., 2007). In addition, little is known about the capabilities and limitations of such maps. Although it is clear that such maps enable turtles to distinguish among geographic areas located several hundred kilometres apart (Lohmann et al., 2004), whether such maps can also be used over considerably shorter distances remains to be determined. Preliminary experiments with hatchling loggerheads have suggested that turtles have magnetic sensitivity considerably better than what would be needed for detecting only locations separated by hundreds of kilometres (K. J. Lohmann, unpublished data). Evidence from a few other animals, such as spiny lobsters (Boles and Lohmann, 2003) and newts (Phillips et al., 2002), suggest that magnetic map navigation may be possible over distances as short as a few kilometres under at least some conditions. Nevertheless, the spatial scale over which a sea turtle's magnetic map operates remains unknown.

Interestingly, the capabilities and limitations of magnetic maps may vary greatly among different geographic areas (Lohmann et al., 1999; Lohmann and Lohmann, 2006). In some parts of the world, the magnetic elements shown in Fig. 4 vary in similar directions over the surface of the Earth. In others, the gradients of inclination and intensity are aligned almost perpendicularly, so that each location is marked by a unique magnetic field (Lohmann and Lohmann, 1996b; Lohmann et al., 1999, 2007). In some areas, a turtle might thus be able to use a single magnetic element (such as inclination) to determine

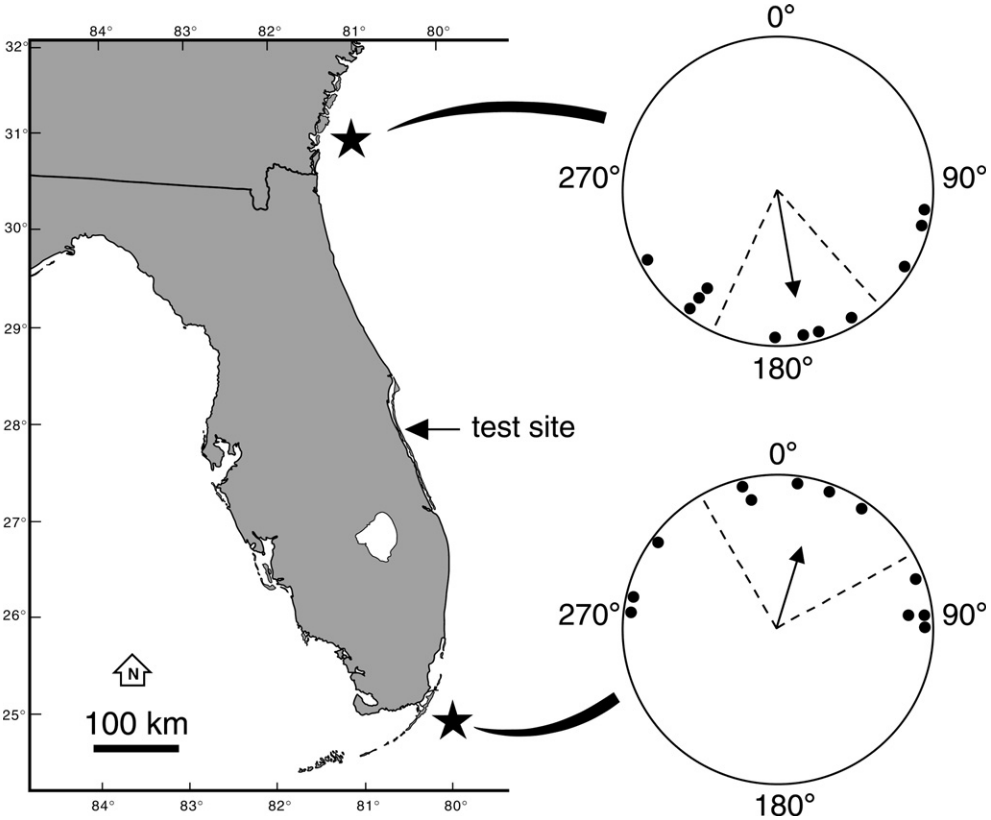

Fig. 5. Evidence for a magnetic map in juvenile green turtles. Juvenile turtles were captured in feeding grounds near the test site in Melbourne Beach, Florida, U.S.A. Each turtle was exposed to a magnetic field that exists at one of two distant locations (represented by stars along the coastline). Turtles exposed to the field from the northern site swam approximately southward, whereas those exposed to the field from the southern site swam approximately north. In the orientation diagrams, each dot represents the mean angle of a single turtle. The arrow in the center of each circle represents the mean angle of the group. Dashed lines represent the 95% confidence interval for the mean angle. Figure is modified from Lohmann et al. (2004). See text for details.

position only in one direction (for example, whether it is north or south of the goal), whereas in others, it might be able to use a bicoordinate magnetic map to assess its position relative to the goal when on any side of the target. Perhaps no universal magnetic map exists for sea turtles; each population might exploit the field in a different way, depending on the magnetic topography of the area and the navigational tasks that must be accomplished (Lohmann et al., 2007).

Conducting experiments in orientation arenas, as has been done with juvenile turtles (Lohmann et al., 2004; Avens and Lohmann, 2003, 2004), is not possible with adult turtles because of their size. In a recent field experiment, however, the possible involvement of magnetic cues during homing was investigated by placing magnets onto the heads of adult green turtles which had been displaced from their breeding island in the Indian Ocean (Luschi et al. 2007). The magnets were attached in such a way that they could move, and the turtles were thus exposed to strong, varying magnetic fields that presumably masked the much weaker field of the Earth.

Turtles treated in this way displayed diminished homing performance relative to control turtles carrying non-magnetic brass bars; the magnet-carrying turtles took longer to home and followed more convoluted routes. In this study, the currents encountered by homing turtles were quantitatively estimated and their contribution to the observed (ground-related) turtle movements removed, so that the movements resulting from the turtles' swimming could be assessed. Differences in performances between experimental groups were thus evaluated by considering the actual directional choices of the turtles during the oceanic journey, a behavioural measure similar to the turtles' directional choices recorded in still water during arena experiments (Lohmann et al., 2004).

An unexpected finding was that magnets adversely affected navigation regardless of whether turtles were exposed to them while homing, or only exposed during transport to the release site (but released without magnets) (Fig. 6). Two interpretations of the latter finding are possible. One is that turtles can use their magnetic sense to derive some general information on the direction of displacement during transport. Alternatively or additionally, the application of strong magnets might produce an effect on magnetoreceptors that persists well beyond the time that the magnets are removed.

These findings clearly showed that magnetic cues play a role in turtle homing under natural conditions. Although the magnets affected homing, the exact part of the turtles' navigational system that was affected cannot be determined. One possibility is that the magnets disrupted a magnetic map sense like that known to exist in juvenile green turtles (Lohmann et al., 2004), which would presumably be used in a navigational task such as returning to an island after displacement. Alternatively or additionally, the effect might have been on a magnetic compass.

An additional finding of interest was that most of the magnetically-treated turtles did eventually return to the island, despite following paths more convoluted than those of controls. This suggests that the turtles may have unknown alternative mechanisms that can, if necessary, allow them to relocate the nesting area even with an impaired magnetic sense.

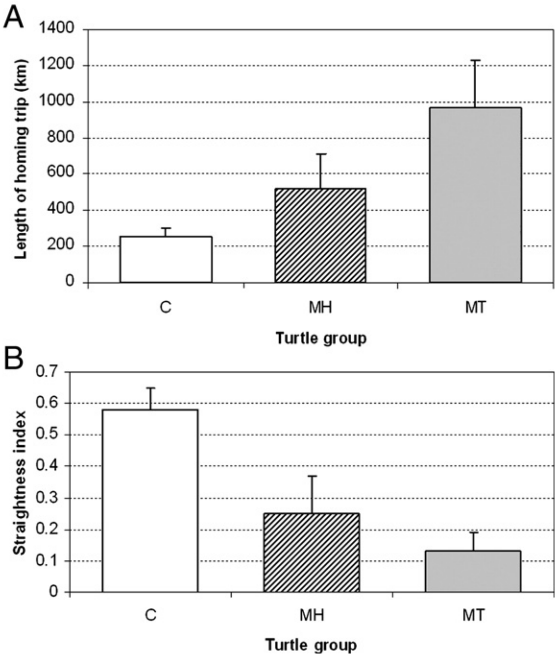

Fig. 6. Homing performances of different groups of green turtles displaced from an oceanic island in the Mozambique Channel. C indicates control turtles, MH indicates turtles which had magnets attached to their head during the homing trip, and MT indicates turtles which had magnets attached to their head during transportation to the release site. A) Mean (±SEM) length of the homing trip; B) Mean (±SEM) straightness index of the homing path calculated on the swimming directions chosen by the turtles, excluding the contribution of ocean currents. Data are from Luschi et al. (2007).

The procedure of attaching magnets to turtles was used in one previous study with Ascension Island turtles beginning their post-nesting migration back towards Brazil (Papi et al., 2000). At the time, it seemed possible that the magnets would disrupt navigation entirely, but instead the manipulation did not reveal major effects on the turtles' post-nesting migrations. The circumstances of the earlier study, however, differed greatly from those of Luschi et al. (2007). In the more recent study, turtles had been displaced from an island and thus had to home to a small goal, whereas in the earlier study, turtles were tested during a part of their migration when oceanic position-fixing was not strictly necessary (because turtles could potentially reach the Brazilian coast simply by swimming west). Thus, the navigational tasks that the turtles had to solve in each case, and the information required to do so, were probably not the same.

7. Secular variation of the geomagnetic field

A potential complication for all strategies of magnetic map navigation is that the Earth's field is not static but instead changes gradually over time. This change in field elements, known as secular variation (Skiles, 1985), means that the magnetic field that exists at a given location will not necessarily remain the same over the life span of a long-lived animal. Similarly, the pattern of magnetic isolines throughout a given oceanic region gradually changes.

For juvenile and adult turtles that spend much of their time in a particular coastal feeding ground, this gradual change seems likely to be incorporated into the learned magnetic map of an area, in much the same way that humans relying on visual landmarks adjust their knowledge of an area when old buildings in a city block are replaced by new ones. For adult turtles migrating to a nesting area only once every several years, however, the change that occurs in the geomagnetic field during a turtle's absence has the potential to cause navigational errors during return migrations if the turtle were to rely solely on a magnetic map (Lohmann and Lohmann, 1998; Lohmann et al., 1999).

Accurately estimating the magnitude of magnetic navigational errors that might occur due to secular variation is difficult for several reasons (Lohmann et al., 1999). Among these is that the rate of field change varies among different geographic regions and at different points in time, so that no "typical" worldwide value exists. In addition, the rate of change in different magnetic field elements differs, so that in any area, some elements are more stable than others. Finally, several fundamentally different strategies of magnetic map navigation are possible (Lohmann and Lohmann, 2006), and the same field change may affect each differently.

Two examples illustrate the complexity of the issue and the range of possibilities. At beaches along the east coast of Mexico where the Kemp's ridley turtle (*Lepidochelys kempii*) nests, the isolines of inclination and intensity have remained remarkably stable during the past century. In this area, a hypothetical strategy of returning to a coastal nesting area marked by a specific inclination angle would presumably be effective, inasmuch as the isoclinic (inclination isoline) that exists at a given nesting area seldom drifts more than a few kilometres away during a typical year (Putman and Lohmann, in preparation). Moreover, these turtles are thought to nest every 1–2 years (Miller, 1997).

The situation is different elsewhere. For example, the field at Ascension Island is presently changing more rapidly than the field in eastern Mexico. If turtles at Ascension Island use a magnetic navigational strategy that involves a bicoordinate map based on inclination and total intensity (one of several possibilities), then the magnetic coordinates marking the island are presently moving by approximately 15–20 km per year (Lohmann et al., 1999). Thus, a nesting turtle absent for 3 years, as is probably typical of Ascension female turtles (Carr, 1975; Bjorndal et al. 1983; Miller, 1997), might miss the island by some 45–60 km on her next trip if she were to rely exclusively on a magnetic map (Lohmann et al., 1999). The same strategy, if used at Tromelin Island in the Indian Ocean, would result in a smaller navigational error of about 18 km for the same 3-year interval (Lohmann et al., 1999).

As these examples illustrate, quantifying errors that secular variation might cause for magnetic map navigation is fraught with uncertainty, inasmuch as the outcome is dependent both on geographic location and assumptions about unknown navigational processes (Lohmann and Lohmann, 1998, 2003; Lohmann et al., 1999). Secular variation may matter little or not at all for turtles returning to nesting beaches along continental coastlines, especially given that some loggerheads deposit nests over stretches of coastline spanning several hundred kilometres (Richardson, 1982; Bjorndal et al., 1983; Miller, 1997). In contrast, secular variation may cause greater navigational problems for turtles seeking islands; if such turtles rely on magnetic maps, then they may need additional cues or strategies to help them localise islands once they have drawn near.

8. Long-range and short-range cues in island-finding

In many long-distance migrants, one set of cues is used when the animal is moving over long distances, whereas another is used for localisation of particular target areas once the animal approaches the final destination (Bingman and Cheng 2005). Thus, the possibility exists that sea turtles may use one strategy and set of cues to move into the general vicinity of feeding grounds or a nesting beach, and another set of cues to actually pinpoint the goal (Lohmann et al., 1999). Turtles nesting on remote islands provide a particularly interesting example of a situation in which use of different cues at different distances from the target area might be advantageous.

Once they have arrived in the general vicinity of an island, turtles might potentially exploit a number of different short-range cues to help them pinpoint the island's location and to find suitable nesting beaches (Lohmann et al., 1999; Luschi et al., 2001). One interesting possibility is that airborne cues (e.g., odorants or sounds) might be detected by turtles as they draw near (Luschi et al., 2001; Hays et al., 2003). In some cases, such cues might be dispersed over considerable areas by winds, a process that might, in effect, enlarge the target for a turtle in the open sea.

As a first step toward investigating this possibility, 6 turtles were captured after nesting at Ascension Island and displaced to locations 60 km upwind or downwind from the island (Hays et al., 2003). Ascension Island lies in a region where trade winds

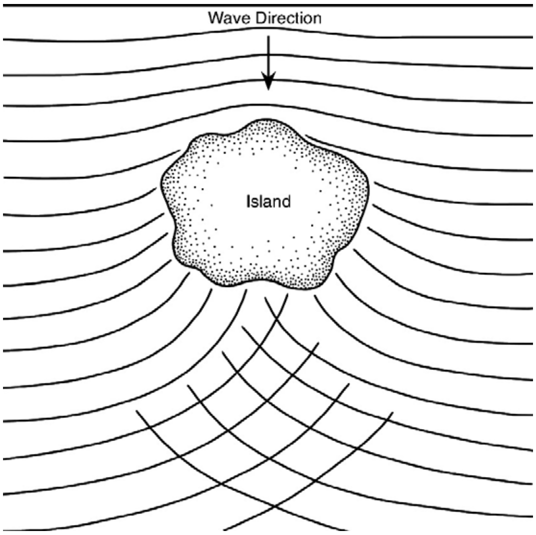

Fig. 7. Diagrammatic representation of wave refraction patterns around an island in the open ocean. As a wave passes around an island, the parts closest to land encounter shallow water and are slowed relative to the parts remaining over deeper water. As a result, refraction occurs and a pattern of wave interference is often formed on the leeward side of the island. In principle, turtles might exploit such wave patterns to help them localise islands once they have drawn near.

blow almost continuously from the southeast to the northwest, and the expectation was thus that turtles released downwind from the island might be able to detect the presence of the island more easily than those placed upwind from it. The results were consistent with this prediction; the 3 turtles released downwind returned to the island more rapidly, and by more direct routes, than did the 3 turtles released upwind.

Although these initial findings are consistent with the hypothesis that turtles detect windborne cues, alternative explanations are also plausible. For example, waves generally move in the downwind direction and are often bent or refracted as they pass around islands, creating characteristic interference patterns on the leeward side (Bascom, 1980; Fig. 7). Traditional Polynesian navigators used such wave patterns to detect the presence of islands too far away to be seen (Lewis, 1978), and turtles, with their acute sensitivity to accelerations and water movements associated with waves (Lohmann, 1992; Lohmann et al., 1995; Manning et al., 1997; Wang et al., 1998; Avens et al., 2003b), might do the same. In addition, the downwind (northwest) release site was relatively close to the protected side of the island where turtles nest and where they typically remain between nesting bouts (Mortimer and Portier 1989; Hays et al. 1999); as a result, this area might have been more familiar to the turtles than the southeastern side, where the turtles might never before have been. Nevertheless, the hypothesis that turtles detect and use windborne cues remains viable and warrants further study.

Several other potential cues might be useful in locating an island at the end of a migration. Among these are long-range visual landmarks such as mountains (Carr, 1967), the sounds of waves breaking (Mrosovsky, 1972; Luschi et al., 1996), sounds produced by snapping shrimp (Knowlton and Moulton, 1963; Carr, 1967) or fish (Gray and Winn, 1961) inhabiting shallow areas, pheromones from nesting or mating conspecifics (Ehrenfeld and Ehrenfeld, 1973), and waterborne chemical cues unique to a natal beach area (Grassman et al., 1984). The range over which such potential cues might extend is not known.

During the final stages of island-finding, mechanisms involving interactions with other turtles are also possible, inasmuch as turtles that have navigated into the appropriate region for the first time might encounter other members of the population that are migrating to the same goal. Thus, following an experienced conspecific at the end of a migration might lead an inexperienced turtle to an appropriate nesting site (Hendrickson, 1958; Owens et al., 1982).

Finally, search patterns initiated at the end of a migration might also help a turtle to locate an island, just as searching behaviour enables desert ants to overcome accumulated errors

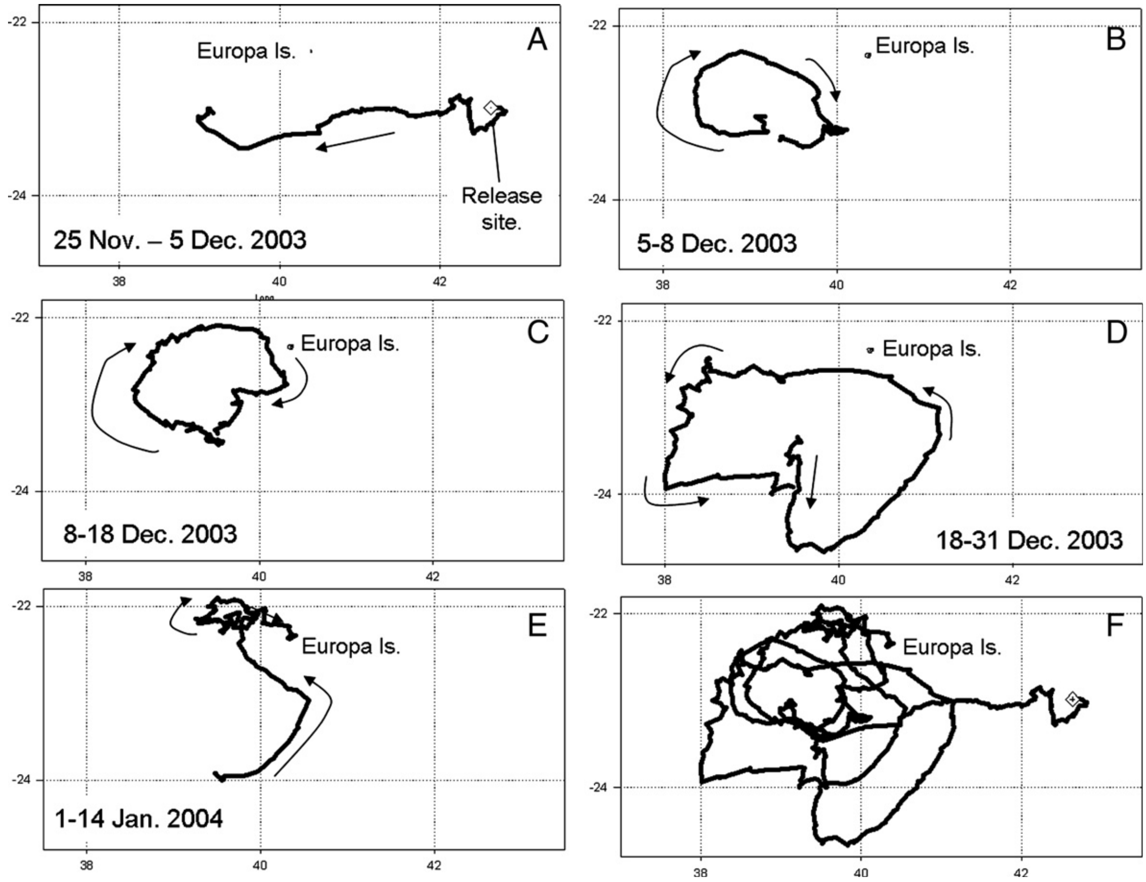

Fig. 8. Successive legs of the homing route of a turtle displaced 245 km SE of Europa Island in the Mozambique channel. A: initial westward movement; B–E: successive loops made by the turtle (dates shown); F: whole route (3515 km in 59 days). Circulating currents associated with eddies may have contributed to some of the loops, but others appear to be attributable to movements of the turtle. Axes show latitude and longitude degrees; 2° of longitude = approximately 220 km. Data are from Girard et al. (2006).

and locate a tiny nest entrance at the end of long foraging trips (Wehner and Srinivasan, 1981). Many convoluted paths shown by green turtles released after displacements (Luschi et al. 2001; Hays et al. 2003; Girard et al. 2006) indeed resemble the ants' searching spirals, although taking place over a far larger spatial scale, often ranging over at least 100 km (Fig. 8).

9. Summary and conclusions

The logistical obstacles to studying large, mobile marine animals are considerable, and it is therefore not surprising that the investigation of navigational mechanisms used by juvenile and adult sea turtles is still at an early stage. A few experiments have been carried out with juvenile turtles under controlled laboratory conditions, but the relatively large size of these animals, and the even greater size of adults, precludes many of the simple experiments that have proven so useful in unraveling the guidance mechanisms of hatchlings. Field experiments are feasible, but here too the challenges of working in the ocean impose significant constraints. Moreover, the natural marine environment is filled with numerous potential sources of navigational information; experimental designs must thus take into consideration the fact that animals frequently exploit multiple cues and strategies and can often switch between them if the need arises.

Despite these impediments, considerable progress has been made. Results obtained so far indicate that juvenile and adult turtles are able to exploit the Earth's magnetic field as a source of directional and positional information. Such a role for magnetic cues has been highlighted in independent experiments carried out both in orientation arenas on land and under more natural conditions in the ocean (Avens and Lohmann, 2003; Lohmann et al., 2004; Luschi et al., 2007). Juvenile turtles can also maintain headings using a compass that is independent of geomagnetism and apparently based on celestial cues (Avens and Lohmann, 2003).

This short list of known navigational cues is likely to expand as studies progress. For example, adult turtles have also been hypothesised to exploit chemical cues in water or in air, particularly when nearing a final target area (Koch et al. 1969; Grassman et al., 1984; Lohmann et al., 1999; Luschi et al., 2001; Hays et al., 2003). Juvenile and adult turtles seem likely to retain the ability of hatchlings to orient movements relative to the direction of ocean wave propagation (Lohmann et al., 1990; Wyneken et al., 1990; Lohmann and Lohmann, 1992). Over short distances, other cues that might plausibly be used include visual landmarks, pheromones from mating conspecifics, and the sounds of waves breaking on a coast or island. Over long distances, cues worth considering include water temperature (Hays et al., 2001), day length (which varies with latitude but also with season), infrasound signals (Sand and Karlsen, 1986), and various astronomical cues such as star patterns, sunrise azimuth, and sun transit arcs. Perhaps still more ideas will come from improved techniques of relating movements of turtles to remotely sensed oceanographic and topographic data (Kobayashi et al., 2008-this issue).

How sea turtles navigate to specific goals is not yet fully understood. Moreover, because only two species (loggerheads and green turtles) have been studied in this regard, the degree to which present findings represent other species is not known. Current results, however, are consistent with the hypothesis that turtles rely on multiple cues to guide their journeys in the marine environment, possibly organised in a two-step process. In the first, a magnetic map may guide turtles into the vicinity of the target area; in the second, local cues (probably non-magnetic), perhaps combined with search strategies, enable turtles to pinpoint their final destinations. Additional studies will be needed to confirm or refute this tentative view of goal navigation in turtles.

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