

Review

Navigational challenges in the oceanic migrations of leatherback sea turtles

Alessandro Sale¹ and Paolo Luschi^{2,*}

¹*Institute of Neuroscience, National Research Council (CNR), via Moruzzi 1, 56100 Pisa, Italy*

²*Department of Biology, University of Pisa, via A. Volta 6, 56126 Pisa, Italy*

The open-sea movements of marine animals are affected by the drifting action of currents that, if not compensated for, can produce non-negligible deviations from the correct route towards a given target. Marine turtles are paradigmatic skilful oceanic navigators that are able to reach remote goals at the end of long-distance migrations, apparently overcoming current drift effects. Particularly relevant is the case of leatherback turtles (*Dermochelys coriacea*), which spend entire years in the ocean, wandering in search of planktonic prey. Recent analyses have revealed how the movements of satellite-tracked leatherbacks in the Indian, Atlantic and Pacific Oceans are strongly dependent on the oceanic currents, up to the point that turtles are often passively transported over long distances. However, leatherbacks are known to return to specific areas to breed every 2–3 years, thus finding their way back home after long periods in the oceanic environment. Here we examine the navigational consequences of the leatherbacks' close association with currents and discuss how the combined reliance on mechanisms of map-based navigation and local orientation cues close to the target may allow leatherbacks to accomplish the difficult task of returning to specific sites after years spent wandering in a moving medium.

Keywords: current drift; satellite telemetry; long-distance navigation; geomagnetic map

1. INTRODUCTION: DEALING WITH CURRENT DRIFT

In March 1741, the man-of-war 'Centurion' left the South Atlantic Ocean under the command of George Anson, directed towards the Pacific Ocean. At the eastern boundary of the South American continent, she steered towards southwest to pass Cape Horn, sailing offshore of this dangerous region. Being aware of the presence of a strong eastward current in the area, the captain continued along this route for nearly 40 days, until he esteemed to be some 10° westward of the continent. After veering northward, however, the ship unexpectedly found itself at the southern outlet of the Straits of Magellan, i.e. approximately 1000 km east of the expected position. The frustrating event delayed their reaching a location where it was possible to refit and halt the spread of scurvy, which eventually led to the loss of about half of the 400-man crew (Walter 1901). Such a great navigational mistake was by no means unusual in the past, when the lack of a reliable system of longitude determination forced seafarers to rely on dead reckoning to establish their position in the open sea. This navigational system is based on successive position updates obtained from the vessel's speed and course and so, by its very nature, cannot take into account the drifting effect of wind and currents.

The example of the Centurion clearly illustrates how detrimental it can be to navigate without taking the

currents' drift into consideration. Indeed, any object moving in the marine environment is inevitably subjected to the action of sea currents, which add their drifting forces to the object's active motion. If not adequately compensated for, the effect of drift can become deleterious, especially for movements taking place in the open sea, where the lack of stationary references prevents immediate realization of the deflection owing to current drift. Safe open-sea seafaring was only possible after the relatively recent developments of efficient systems of position fixing (Johnson & Nurminen 2007).

The same problems are faced by the multitude of marine animals that routinely travel in high seas during their life cycle, sometimes crossing entire ocean basins. In many cases, these movements are not randomly oriented but are directed towards specific sites, such as a spawning area or a foraging ground (e.g. Luschi *et al.* 1998; Bonfil *et al.* 2005; Mate *et al.* 2007). As in the case of ships, current drift alters the animals' water-related active movements, resulting in a ground-related course that may be substantially different from the intended one and thus may not be the most appropriate one to keep if a specific target is to be reached (Carr 1967; Girard *et al.* 2006). The effect is analogous to that detectable in birds flying in the presence of side winds (Åkesson & Hedenström 2007). However, the very fact that a variety of marine species are able to successfully reach their target after long oceanic legs shows that the animals have evolved appropriate navigational solutions to deal with current drift, well before human navigators.

Very little is known about how marine animals achieve this difficult navigational task and only recently has

* Author for correspondence (pluschi@biologia.unipi.it).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rspb.2009.0965> or via <http://rspb.royalsocietypublishing.org>.

relevant information on the topic emerged because of studies employing innovative approaches, such as testing specific hypotheses in field or laboratory conditions and integrating animal tracking data with oceanographic information (e.g. Lohmann *et al.* 2004; Polovina *et al.* 2004; Luschi *et al.* 2007; Weng *et al.* 2008). The most advanced studies have been conducted on one renowned group of oceanic navigators, marine turtles, for which some hypotheses have been put forward as to how they accomplish their navigational feats (e.g. Luschi *et al.* 2003a; Freake *et al.* 2006; Lohmann *et al.* 2008). The present review aims at extending these hypotheses to the remarkable case of leatherback turtles, the most widely ranging turtle species.

2. THE PARADIGMATIC CASE OF OCEAN-MOVING SEA TURTLES

All living species of sea turtles are well adapted to the marine environment, having a life cycle that, with the exception of very short periods by nesting females, takes place entirely in the sea. Since suitable foraging areas are usually located in different regions from the breeding grounds, most species have developed remarkable migratory habits, often involving journeys of hundreds of kilometres in the open sea (Luschi *et al.* 2003a). The impressive ability displayed by these powerful marine swimmers to reach remote goals without getting lost in the apparently featureless homogeneity of the ocean has long attracted the interest of ethologists and physiologists in search of the sensory and behavioural mechanisms underlying such performances (e.g. Carr 1967). Knowledge of the extent and course of the routes followed by sea turtles has increased considerably over the last few years, owing to the diffusion of satellite telemetry techniques, which allow tracking of air-breathing species in considerable detail.

The reconstructed tracks allow division of turtle migrations into two main spatial patterns (Luschi *et al.* 2003a; Godley *et al.* 2008). On the one hand, some species are characterized by a periodic shuttling between nesting beaches and individually specific feeding areas where they spend the inter-reproductive period (e.g. Luschi *et al.* 1998; Craig *et al.* 2004; Broderick *et al.* 2007; Van Dam *et al.* 2008). These turtles, best represented by the herbivorous green turtle (*Chelonia mydas*), usually aim at reaching specific targets during their migrations. Therefore, their journeys have to be controlled by navigational mechanisms allowing correct orientation and overcoming current drift, which may deflect the course to their destination (Luschi *et al.* 2003a; Girard *et al.* 2006). At present, most information regarding the orientation and navigational abilities of adult sea turtles has been obtained in these species, using various fruitful methods such as in-arena tests or field experiments with satellite-tracked turtles (Lohmann *et al.* 2008).

On the other hand, the olive ridley turtle (*Lepidochelys olivacea*) and, very typically, the leatherback turtle (*Dermochelys coriacea*), spend entire years in the oceanic environment, foraging in complex wandering movements apparently not directed towards any specific goal, often staying off any coasts. In adult females, spectacular examples of long-distance oceanic journeys have been

documented in the Pacific Ocean (Plotkin *et al.* 1995; Morreale *et al.* 1996; Eckert & Sarti 1997; Benson *et al.* 2007; McMahon *et al.* 2007), Atlantic Ocean (Ferraroli *et al.* 2004; Hays *et al.* 2004; James *et al.* 2005a,b,c; Eckert 2006) and Indian Ocean (Luschi *et al.* 2006), sometimes revealing the presence of persistent migratory corridors corresponding to high-use areas for migrating turtles (Morreale *et al.* 1996; Lambardi *et al.* 2008; Shillinger *et al.* 2008). Foraging may take place either in spatially limited hotspots (Ferraroli *et al.* 2004; James *et al.* 2005a,b) or during the long journeys in the open ocean (Hays *et al.* 2006; Lambardi *et al.* 2008). Little is known about the movements made by males and juveniles, but the available data suggest that they basically have the same spatial behaviour as female turtles (James *et al.* 2005a,b,c). Ocean-dwelling turtles have an intimate link with ocean currents, which constitute a very relevant environmental factor affecting their at-sea behaviour, besides being responsible for the distribution of the planktonic prey targeted by these species. Recent analyses performed on satellite-tracked leatherbacks moving in different oceanic areas, indeed, have shown that most of the recorded movements are actually strongly dependent on the main oceanic currents (Luschi *et al.* 2003b; Gaspar *et al.* 2006; Lambardi *et al.* 2008; Shillinger *et al.* 2008). These exert a dramatic influence on the turtle open-sea courses, up to the point that turtles often appear to be passively transported by the prevailing currents.

3. FLOWING WITH THE CURRENT: NEW DATA ON LEATHERBACK TURTLE MIGRATIONS

The integration of satellite-tracking data with oceanographic information has recently proved to be a most useful method to shed light on the influence exerted by ocean currents on leatherbacks' trajectories.

In South African leatherbacks, superimposition of reconstructed turtle tracks on remotely sensed images of sea surface temperatures and sea height anomalies (indicative of the presence of rotating water masses) has revealed that turtle movements are largely determined by the prevailing current features encountered by the animals (Luschi *et al.* 2003b; Lambardi *et al.* 2008). Turtles have been followed for long time periods (up to 223 days), during which they exhibited extremely long tracks (up to over 18 000 km). These cover a huge oceanic area that extends from the southwestern part of the Indian Ocean to the eastern Atlantic Ocean (figure 1a). The region is dominated by the Agulhas Current, an intense and persistent warm current that flows southwest along the eastern coast of southern Africa with core speeds of up to 7.2 km h^{-1} (Lutjeharms 2006). Most tracked turtles drifted southwest upon leaving the coastal waters of the nesting area in northern South Africa, covering straight tracts at high speed where the current has a stable course (figure 1a). Remarkably, oceanographic features had a dominant influence not only on these linear parts of the turtle routes, but also on those route legs, occurring mostly off the seaward edge of the Agulhas Current, which showed highly convoluted circular patterns. Superimposition of these segments on images of sea surface height anomalies showed clear correspondence with such anomalies, revealing the presence of eddies that are well known to occur in this region (Lutjeharms 2006).

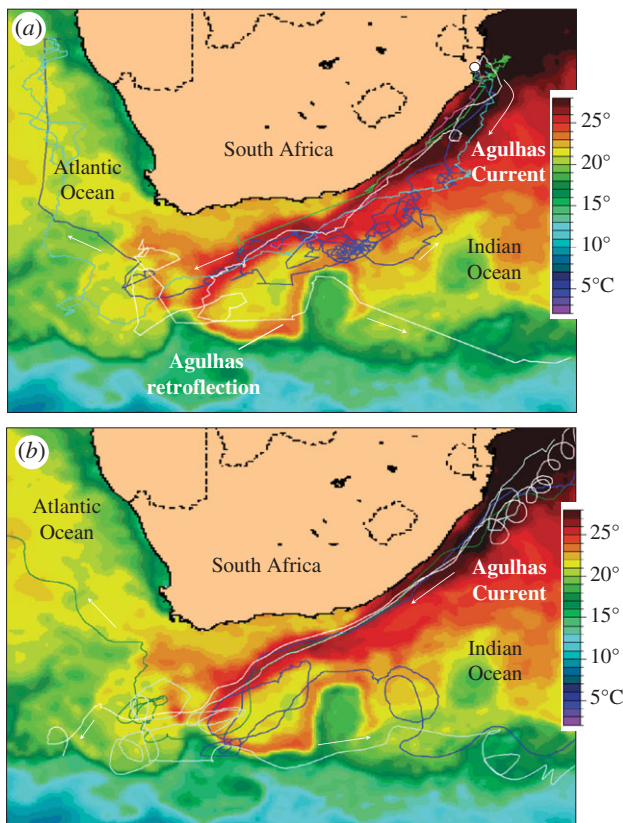


Figure 1. Trajectories of (a) five leatherback turtles and (b) four surface drifting buoys tracked by satellite in the southwestern Indian Ocean. The tracks are superimposed on a sea surface temperature image recorded on 1 February 2003, in which the position of the Agulhas Current mainstream is indicated as a ribbon of warm (red) water flowing along the east coast of South Africa and then retroflecting towards the East south of the continent (Lutjeharms 2006). The arrows indicate the general direction of movement, and the white dot indicates the turtle nesting beach.

Turtles remained engaged in prolonged rotations inside a given eddy for weeks, and their sense of circling was always in accordance with that of the water masses. Further evidence in favour of a major role for ocean currents in shaping the movements of South African leatherbacks derives from the observation that turtle courses closely resembled those of oceanographic drifters tracked in the same region (figure 1b). Overall, the authors calculated that the reconstructed turtle routes were determined by the current flows for 69–84% of their length, i.e. the turtles spent several months basically drifting with the current stream, while covering thousands of kilometres (Luschi *et al.* 2003b; Lambardi *et al.* 2008).

A profound impact of oceanic currents on leatherback routes has also been recently shown in a turtle nesting in French Guyana (South America) and then moving in the North Atlantic Ocean during her erratic post-nesting journey. Using a new quantitative approach allowing subtraction of the current vectors from the reconstructed animal movements, Gaspar *et al.* (2006) have been able to separate the otherwise combined effects of the animal's active swimming and the passive drift operated by the oceanic currents encountered. The analysis showed a dramatic impact of the Gulf Stream and the North Atlantic

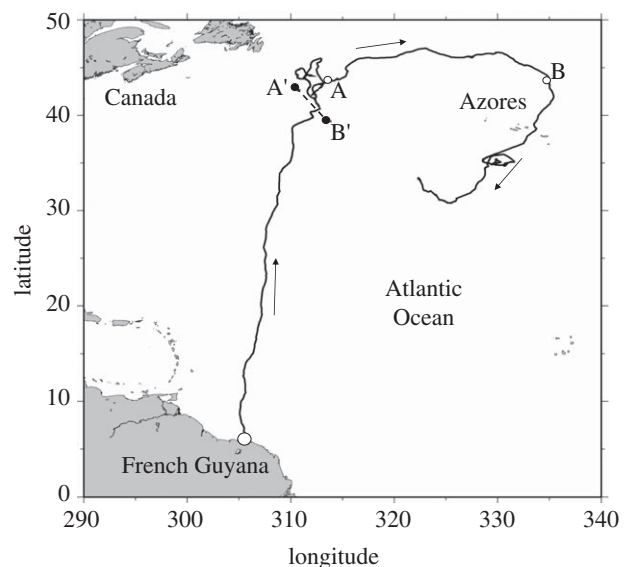


Figure 2. Route of a leatherback turtle tracked by satellite in the Atlantic Ocean between 29 June 2000 and 20 April 2001. The segment between A and B was covered within the Gulf Stream Extension and the North Atlantic Current and led to a substantial eastward displacement of 2144 km. Subtraction of the currents' action from the recorded (ground-related) segment, however, revealed that the active swimming of the turtle would have led her to move only between points A' and B' (dashed line). The larger white dot indicates the turtle nesting beach. Modified from Gaspar *et al.* (2006).

Current on the long-distance turtle movements, with large geographical displacements resulting to be completely determined by the action of currents. Most impressively, a two-month-long segment was identified during which the turtle was displaced eastward for 2144 km while her actual movements (current contribution excluded) would have led her to remain roughly in the same area with a displacement of only a few hundreds of kilometres (figure 2).

In the eastern Pacific Ocean, adult leatherbacks nesting at Playa Grande (Costa Rica), travel along a persistent migratory corridor that extends from the American coast southwesterly into the South Pacific Gyre (Morreale *et al.* 1996; Shillinger *et al.* 2008). During these journeys, leatherbacks cross areas of intensive stream transport owing to the presence of strong zonal currents such as the South Equatorial Current and the Equatorial Undercurrent. A recent estimate of the impact of current action on turtle routes revealed that Playa Grande leatherbacks, in their attempt to remain within a defined migratory corridor with a predominant southwesterly heading, increased their swimming speed when crossing those currents that tended to push them eastward or westward from the correct route. Despite this effort to overtake the action of the currents, the recorded turtle routes still presented multiple longitudinal deflections that proved to be entirely owing to the pushing effect of current drift (Shillinger *et al.* 2008).

4. CURRENT TRANSPORT AND SEA TURTLE NAVIGATION

The documented marked dependence on current action, completely unexpected for such a powerful swimmer as

the largest living turtle, is of great interest when analysed with respect to the entire leatherback life cycle. Indeed, leatherbacks, like other sea turtles, are known to display a remarkable site fidelity to their nesting beach. Genetic assays have revealed that upon reaching maturity, leatherbacks usually return to breed in the same general region where they had been born a few tens of years before (Dutton *et al.* 1999). Besides such a 'natal homing' behaviour (Carr 1967) that actually takes place once in a turtle's lifetime, each adult female also shows a reproductive faithfulness throughout her life, always choosing to nest on the same coastal areas where she bred in her previous nesting season, 2–3 years in advance (e.g. Hughes 1996). While this reproductive site fidelity is not absolute, with turtles sometimes found nesting away from the previous season's beach (e.g. Troëng *et al.* 2004), in most cases leatherbacks are thought to return to a specific, localized area to nest. In addition, fidelity to defined foraging sites has also been demonstrated in adults and juveniles (James *et al.* 2005b). Leatherbacks are able to show this multiple fidelity even after having spent long periods in the open sea, i.e. in a condition in which no animal can perceive the drifting action of currents, given the lack of stationary references.

The nature and physiological basis of the mechanisms allowing long-distance navigation towards specific targets after such a long-lasting period of life in a moving medium are largely unknown. The navigational challenges produced by current drift are not exclusive to leatherbacks, though, and other sea turtle species have to deal carefully with this deflecting factor when migrating in the ocean with the aim of reaching a specific target. A number of recent studies have provided empirical evidence on the abilities of oceanic navigation shown by other sea turtle species (e.g. Lohmann *et al.* 2004; Luschi *et al.* 2007). This has led to ground-based hypotheses as to how these turtles may find their way towards specific destinations (e.g. Freake *et al.* 2006; Lohmann *et al.* 2008). In leatherback turtles, these challenges are particularly relevant given their habit of spending years performing long-distance wanderings in close association with strong and variable ocean currents.

Sea turtles, like many other animals, can use various biological compasses to follow straight segments, even when coastal directional information (e.g. visual; Carr 1967) is not available. These compass mechanisms are fully available during their movements in the ocean: compass orientation based on the Earth's magnetic field has been demonstrated in newborn leatherback and loggerhead (*Caretta caretta*) turtles (Light *et al.* 1993; Lohmann & Lohmann 1993), while reliance on a sun compass seems to be well within the turtles' reach (Avens & Lohmann 2003).

This ability alone, however, is not sufficient to allow goal-directed navigation when turtles are subjected to passive drift (owing to intense and/or varying sea currents, Lohmann *et al.* 2008). Goal-directed navigation in these conditions would be impossible by using mechanisms sensitive to passive displacements during the trip, such as vectorial navigation (i.e. navigating along distinct segments whose length and direction are defined through either genetic or acquired information) or path integration (a sort of animal equivalent of seafarers' dead reckoning method: the animal continuously

updates its position with respect to the starting point by integrating the direction and length of each leg of the route covered) (Able 2001; Papi 2006). The case of the Guyana leatherback described earlier is particularly informative in this respect: how could that turtle be aware of being in the eastern Atlantic Ocean if her active movements would not have implied such a displacement? How can she take this displacement into account when moving towards a specific site like a nesting beach? Similar considerations probably apply to the other described cases of leatherback migrations for which a marked influence by oceanic currents has been documented (Lambardi *et al.* 2008; Shillinger *et al.* 2008).

It seems therefore necessary to hypothesize that ocean-moving turtles rely on more complex navigational systems when they have to reach specific targets. A first possibility is that turtles may account for the displacement operated by the currents by taking on-course readings of the drift they experience. For instance, the behaviour of leatherbacks moving offshore in the Pacific Ocean seems sometimes to reflect a direct appreciation of current drift, as tracked turtles adjusted their headings and speed in response to the different currents they encountered (Shillinger *et al.* 2008). Such an ability would permit navigation towards a given target, since the direction of the original nesting beach would be continuously updated, step by step, during the journey, by integrating all single segments covered both actively and passively, employing a sort of inertial navigation (Able 2001). In birds, compensation for cross winds is only possible in the presence of some fixed frame of reference, like when moving overland (Åkesson & Hedenström 2007). For birds flying over the sea, some help may still be derived from the wave pattern that can be used as a visual landscape feature (Alerstam & Petterson 1976)—a possibility precluded to swimming turtles. Detection of current flow has been hypothesized to occur in some fishes, e.g. through the ampullae of Lorenzini (Kalmijn 1974), but organs with such properties have never been described in sea turtles. Current flow detection would still be possible against some stationary reference point encountered by the turtles during their journey. This could occur, for instance, while being in visual or tactile contact with the sea floor or by sensing relative water movements at the border between the current and the surrounding waters, e.g. by lateral-line receptors (Montgomery *et al.* 1997) or the vestibular sense (Sand & Karlsen 2000). Unfortunately, similar processes are impossible when the animal moves in deep waters and within wide oceanic currents such as the Agulhas Current or the Gulf Stream. Most turtle tracks, indeed, lie inside the core of the current and so away from its borders or from the sea bottom, although leatherbacks tracked in the Indian Ocean have been sometimes observed to move at the oceanic border of the Agulhas Current (Luschi *et al.* 2003b; Lambardi *et al.* 2008), which may suggest the possibility of occasional current sensing in these turtles.

5. MAP-BASED NAVIGATION IN SEA TURTLES

Another possibility to explain leatherback ability to navigate towards specific sites after long-lasting passive displacement by the currents is that turtles take advantage of a position-fixing process. This would allow them to

establish their position with respect to a goal solely on the basis of local cues available at any given site, relying on some sort of navigational map. Such an efficient navigational system, which is usually referred to as true navigation or map-based navigation (Able 2001; Papi 2006, see Lohmann & Lohmann (2006) for a discussion of the map concept), would allow turtles to update their knowledge of the actual position with respect to the target area virtually anytime, or at least at some points along the journey. Reliance on a process of map navigation would minimize the course errors deriving from the displacing action of the current, making the problem of position fixing largely independent from where turtles may have been borne by the current flow.

But are leatherback turtles capable of true navigation? Some information can be drawn from the experimental findings obtained in other turtle species, although the results are not univocal and the picture emerging is still unclear (Alerstam 2006). The most informative experimental paradigm classically used to test true navigation ability is spatial displacement with respect to a goal that the animal is motivated to reach (Lohmann *et al.* 2008). Using virtual displacements of juvenile green turtles swimming in arenas, Lohmann *et al.* (2004) have provided the best evidence available today on the capacity of sea turtles to perform true navigation, focusing on the role of cues deriving from the Earth's magnetic field (Lohmann & Lohmann 2006; Lohmann *et al.* 2007). In particular, two magnetic parameters have been tested: magnetic field intensity and inclination (i.e. the strength of the geomagnetic field and the angle at which the geomagnetic field lines intersect the Earth's surface, respectively (figure 3)). These parameters vary quite uniformly over the Earth's surface, mostly showing a latitudinal gradient: magnetic intensity is minimal at the magnetic equator and increases moving towards the magnetic poles, and magnetic inclination ranges between 0° at the magnetic equator (where the field lines lie parallel to the horizon) and 90° at the magnetic poles (figure 3). Previous experiments had demonstrated that loggerhead hatchlings responded to experimentally induced changes in magnetic intensity and inclination (Lohmann & Lohmann 1996; Lohmann *et al.* 2001), thus showing the basic sensory abilities to use these cues for navigational purposes. By recreating in an arena the magnetic field parameters found at real locations in the sea, Lohmann *et al.* (2004) have shown that juvenile green turtles oriented in such a way as to compensate for the shift in magnetic parameters applied to the local magnetic field, a behaviour that would have allowed them to return to the capture area. Although the available data actually show displacement compensation only along the north–south axis, they strongly suggest that virtually displaced green turtles could rely on magnetic cues collected at the test site to fix their position and re-approach the goal, employing a sort of geomagnetic map (Lohmann & Lohmann 2006; Lohmann *et al.* 2007).

Challenged in the test-bed of the open sea using satellite telemetry, the attracting hypothesis of true navigation based on magnetic cues has initially failed to provide supporting evidence (Alerstam 2006). Initial displacement experiments on green turtles breeding on Ascension Island, in the middle of the Atlantic Ocean, revealed little ability of turtles to compensate for long-distance

translocations (Luschi *et al.* 2001; Hays *et al.* 2003). Transported by ship away from the island to distant (60–450 km) release sites in different directions, the turtles displayed circuitous movements not directed towards the target, which was eventually reached only from the northwest quadrant (Luschi *et al.* 2001; Hays *et al.* 2003). It therefore appears as if displaced Ascension turtles were generally unable to compensate for the displacement and to rely on a position-fixing mechanism (and so on any kind of map), as also suggested by similar experiments on turtles tested in the Indian Ocean (Luschi *et al.* 2003c; Girard *et al.* 2006).

Recent experiments performed on green turtles translocated from their nesting beach in Mayotte Island, in the Mozambique Channel (Luschi *et al.* 2007), depict a different scenario. Turtles were transferred by a boat to open-sea locations in different directions, 100–120 km away from the home beach, and were then tracked by satellite during their successive movements. Displaced turtles succeeded in homing back to the nesting beach, although generally with rather undirected routes, while the application of head-attached magnets to alter the local magnetic field resulted in a significant lengthening of the homing paths, leading to a decrease in turtle navigational performances (Luschi *et al.* 2007). This suggests that Mayotte turtles were relying on a navigation process based on a magnetic map that allowed them to compensate for the passive translocation they had been subjected to—a conclusion in general agreement with the arena experiments described earlier.

Can leatherbacks rely on magnetic navigation to guide their returns to specific nesting beaches after years spent wandering in the open ocean, largely at the mercy of ocean currents? Magnetic field conditions are theoretically favourable for reliance on a bi-coordinate broad-scale magnetic map at least over some of the oceanic areas crossed by leatherbacks during their roving life. For instance, in the tropical east Pacific Ocean, the isolines of magnetic intensity (isodynamics) and of magnetic inclination (isoclinics) form a nearly orthogonal grid theoretically suitable for long-distance magnetic navigation (Shillinger *et al.* 2008). In the southwest Indian Ocean, field intensity and inclination do not form an orthogonal grid, but vary longitudinally in a quite uniform manner (figure 4a), so that they may allow turtles to evaluate their longitudinal displacement. Information on latitude may be provided by an additional parameter, the magnetic declination (the angle between the magnetic vector and the geographical north; figure 3), for which, however, knowledge of the direction of geographical north is necessary (figure 4b). A somewhat reversed situation exists in the North Atlantic Ocean (electronic supplementary material, figure S1), where both isodynamics and isoclinics display a nearly latitudinal gradient, while isolines of magnetic declination are mostly aligned along the north–south axis, being thus able to provide information on longitude.

Regardless of the combination of magnetic parameters employed, such a bi-coordinate magnetic navigation would be likely to enable leatherbacks to deal with the navigational challenges they face when homing to the nesting beaches after years of absence. It is presently hard to assess to what degree they do actually rely on such a mechanism. For instance, very little is known on

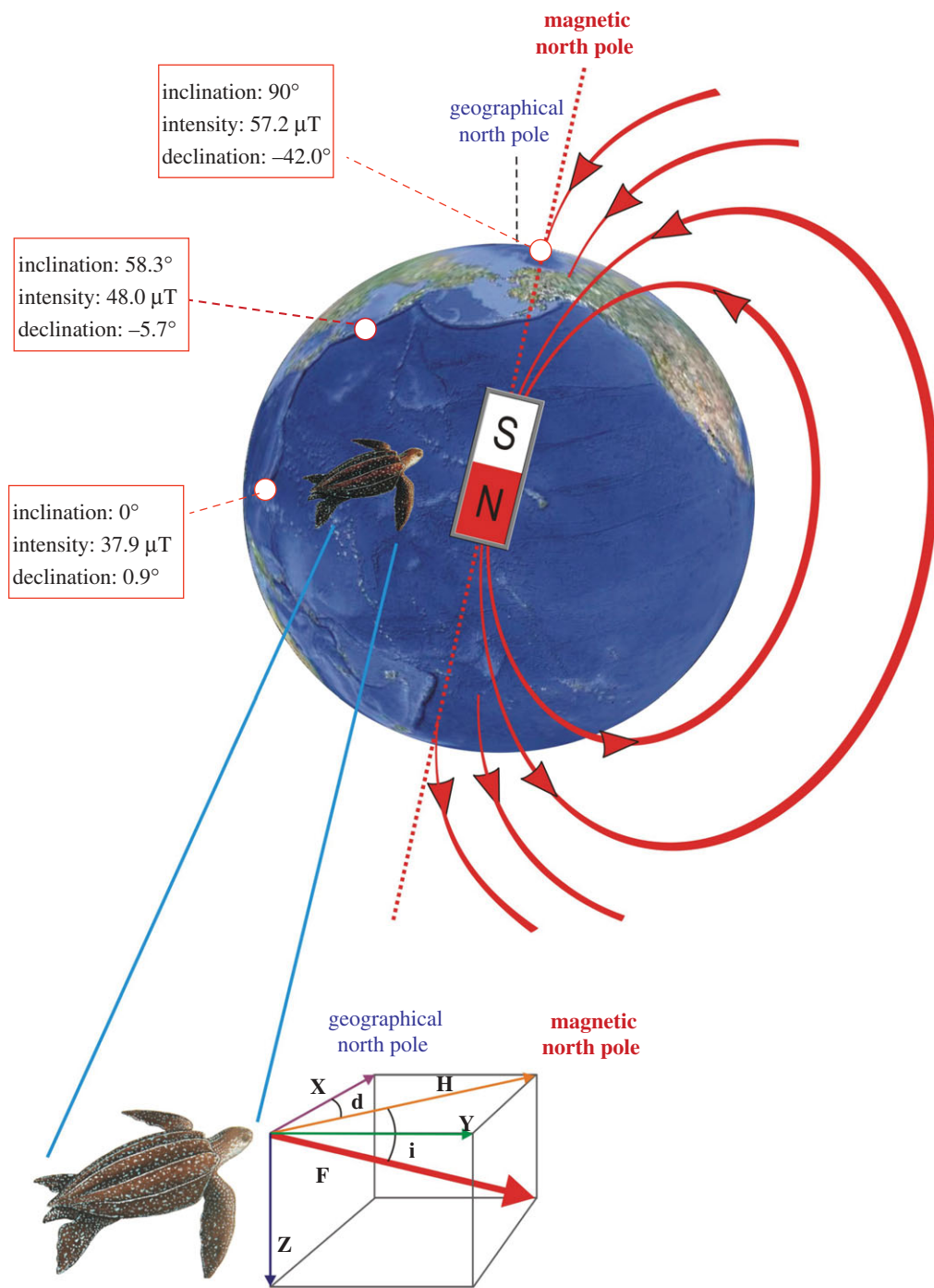


Figure 3. Graphical representation of the Earth's magnetic field and of the geomagnetic vector describing the field at any given location on the Earth's surface. To illustrate the geographical variation of the geomagnetic field, the values of magnetic intensity, inclination and declination are also shown for three different locations: the magnetic North pole, a mid-latitude point and the magnetic equator. Positive values of declination indicate a difference between true north and magnetic north towards the east and negative values towards the west. Magnetic parameters have been calculated for January 2009 according to the International Geomagnetic Reference Field model. d , declination; i , inclination; H , horizontal intensity; Z , vertical intensity; X , north–south intensity; Y , east–west intensity; F , total intensity.

the leatherbacks' magnetic sensitivity: they have been shown to use magnetic cues to steer in a given direction as hatchlings (i.e. to possess a magnetic compass; Lohmann & Lohmann 1993), but it is unknown whether they are also able to detect variations in magnetic inclination and intensity (i.e. if they have a magnetic map), an ability that has so far been demonstrated in loggerhead and green turtles only (discussed earlier). Moreover, it has to be considered that geomagnetic parameters are

known to change over time owing to the so-called secular variation of the geomagnetic field, and so the magnetic coordinates of a nesting site may shift during a turtle's absence from it, determining a non-negligible error for a turtle returning there only on the basis of magnetic navigation (see Freake *et al.* 2006; Lohmann *et al.* 2008 for thorough discussions of this point).

Notwithstanding these difficulties, it is important to note that any long-range navigational system used by

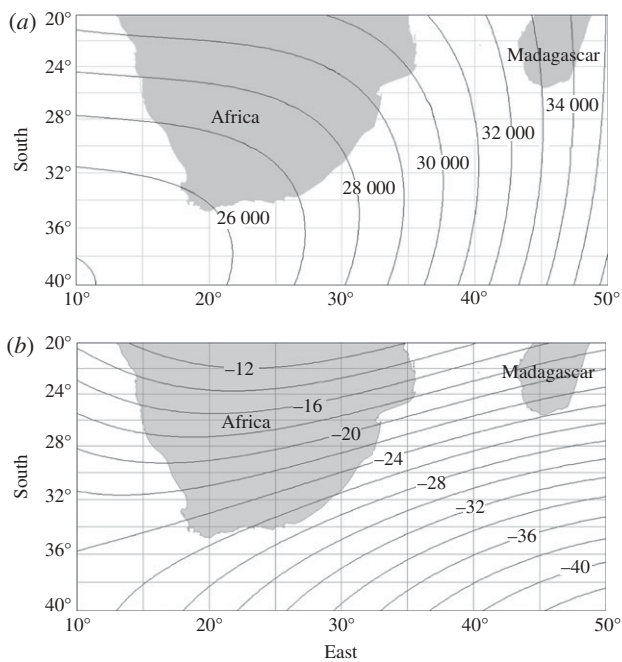


Figure 4. Chart of the southwestern Indian Ocean showing (a) lines of equal intensity (values in nT) and (b) lines of equal declination (values in degrees) of the Earth's magnetic field. Isoclinics in the area follow a pattern similar to isodynamics. Magnetic parameters have been calculated for January 2009 according to the International Geomagnetic Reference Field model.

leatherbacks to relocate their nesting beaches does not necessarily need to be very accurate, as it can be backed-up by other navigational mechanisms working at shorter scales. Reliance on a large-scale magnetic map may bring turtles back to the general breeding region, where regional cues may then intervene to allow precise homing to the nesting beach last visited by the turtles 2 or 3 years before. Sea turtle navigation has indeed been hypothesized to involve multiple mechanisms acting at different spatial scales, with distinct suites of cues mediating successive phases of the large-scale homing process (e.g. Bingman & Cheng 2005; Freake *et al.* 2006; Lohmann *et al.* 2008). Experimental evidence collected in displacement experiments with green turtles actually confirms this view. Turtles displaced from Ascension Island, for instance, more readily homed back to the nesting island when released downwind than upwind from the target (Hays *et al.* 2003), suggesting a role for wind-borne cues (or for any cue differentially available around the target) in assisting the final, fine-scale process by which turtles precisely pinpoint their target (Lohmann *et al.* 2008). On this connection, it might be worth noting that leatherbacks mostly nest on mainland beaches (e.g. French Guyana, South Africa) or on islands close to the mainland (e.g. Trinidad), whereas turtles nesting on isolated small islands tend to be those species (like green turtles) that have simpler post-breeding movements.

For leatherbacks, one additional factor that is worth considering is the action of the large current gyres that characterize all the world's oceans, determining a recirculation of water masses at different spatial scales within each basin (e.g. Stramma & Lutjeharms 1997). It may be hypothesized that leatherbacks, in the attempt to

return to their nesting area, may take advantage of these gyres that could bring them back into the region of the nesting area after years in the oceanic environment, just as some oceanographic drifters are known to return to areas crossed months or years before only owing to current action. Again, this relocation could be only spatially approximate but it may still have enough resolution to bring turtles within the 'catchment area' (Bingman & Cheng 2005) of local-scale navigation, triggering the fine-scale homing processes. Hitchhiking current gyres would then not only help leatherbacks in saving energy during their migrations, but would also transform a long-range navigational task into a more restricted one, for which locally available stimuli originating from the target may guide the final part of the journey. Probably such a system based on current gyres would not be sufficiently precise to allow return to a given place with high periodicity, owing to the variability and irregularity of current features. It is interesting to observe, however, that the proposed current-helped return is in agreement with the available tagging data of nesting leatherbacks, attesting a certain degree of irregularity in the duration of the interval between two successive reproductive seasons (e.g. in South African turtles; Hughes 1995).

6. CONCLUSIONS

We have highlighted how ocean-moving leatherback turtles constitute a particularly relevant case in the study of oceanic navigation. Because of their feeding habits, these turtles are closely linked to current systems and as such are bound to be highly affected by current drift, up to the point of being passively transported for long periods by current flows during their ocean-wide movements. Yet they do faithfully find the very same coastal stretch every few years to nest, thus proving to be able to navigate towards a specific target after long periods spent in oceanic areas dominated by strong currents. How do they accomplish this most difficult task is not known, although some considerations are possible on the basis of experimental results collected on other turtle species.

One fundamental piece missing in this puzzle is the reconstruction of the whole movements carried out by leatherbacks during their inter-reproductive movements, including the migrations towards the breeding areas, i.e. when they are expected to resort to their navigational abilities to return to their usual nesting beach. No one has been able, to date, to track leatherback movements across the ocean for a time sufficiently long as to permit monitoring of this mysterious part of their life cycle. At the same time, the experimental approaches that have proved to be so fruitful in studying turtle navigation (arena tests and displacements) have never been attempted in leatherbacks—which is not surprising given the enormous logistical problems associated with working with such huge and pelagic-dwelling animals. Essential progress is expected from the improvement of satellite telemetry techniques, for instance, through the employment of new attachment systems and of long-lasting transmitters, able to collect useful information such as the turtle's actual headings, independently from the current drift. In addition, more intensive efforts may be envisaged to apply some of the experimental approaches successfully

adopted to study the navigation of other turtle species, such as the application of magnets inducing specific disturbances during the leatherbacks' oceanic odysseys.

We are grateful to Floriano Papi and Graeme Hays who provided useful comments to the manuscript.

REFERENCES

- Able, K. P. 2001 The concepts and terminology of bird navigation. *J. Avian Biol.* **32**, 174–183. (doi:10.1034/j.1600-048X.2001.320211.x)
- Åkesson, S. & Hedenström, A. 2007 How migrants get there: migratory performance and orientation. *BioScience* **57**, 123–133. (doi:10.1641/B570207)
- Alerstam, T. 2006 Conflicting evidence about long-distance animal navigation. *Science* **313**, 791–794. (doi:10.1126/science.1129048)
- Alerstam, T. & Pettersson, S. G. 1976 Do birds use waves for orientation when migrating across the sea? *Nature* **259**, 205–207. (doi:10.1038/259205a0)
- Avens, L. & Lohmann, K. J. 2003 Use of multiple orientation cues by juvenile loggerhead sea turtles *Caretta caretta*. *J. Exp. Biol.* **206**, 4317–4325. (doi:10.1242/jeb.00657)
- Benson, S. R., Kisokau, K. M., Ambio, L., Rei, V., Dutton, P. H. & Parker, D. 2007 Beach use, interesting movement, and migration of leatherback turtles, *Dermochelys coriacea*, nesting on the north coast of Papua New Guinea. *Chelon. Conserv. Biol.* **6**, 7–14. (doi:10.2744/1071-8443(2007)6[7:BUIMAM]2.0.CO;2)
- Bingman, V. P. & Cheng, K. 2005 Mechanisms of animal global navigation: comparative perspectives and enduring challenges. *Ethol. Ecol. Evol.* **17**, 295–318.
- Bonfil, R., Meyer, M., Scholl, M. C., Johnson, R., O'Brien, S., Oosthuizen, H., Swanson, S., Kotze, D. & Paterson, M. 2005 Transoceanic migration, spatial dynamics, and population linkages of white sharks. *Science* **310**, 100–103. (doi:10.1126/science.1114898)
- Broderick, A. C., Coyne, M., Fuller, W. J., Glen, F. & Godley, B. J. 2007 Fidelity and over-wintering of sea turtles. *Proc. R. Soc. B* **274**, 1533–1538. (doi:10.1098/rspb.2007.0211)
- Carr, A. 1967 *So excellent a fish: a natural history of sea turtles*, 1st edn. Austin, TX: Texas University Press.
- Craig, P., Parker, D. M., Brainard, R., Rice, M. & Balazs, G. H. 2004 Migrations of green turtles in the central South Pacific. *Biol. Conserv.* **116**, 433–438. (doi:10.1016/S0006-3207(03)00217-9)
- Dutton, P. H., Bowen, B. W., Owens, D. W., Barragan, A. & Davis, S. K. 1999 Global phylogeography of the leatherback turtle (*Dermochelys coriacea*). *J. Zool. (Lond.)* **248**, 397–409. (doi:10.1111/j.1469-7998.1999.tb01038.x)
- Eckert, S. A. 2006 High-use oceanic areas for Atlantic leatherback sea turtles (*Dermochelys coriacea*) as identified using satellite telemetered location and dive information. *Mar. Biol.* **149**, 1257–1267. (doi:10.1007/s00227-006-0262-z)
- Eckert, S. A. & Sarti, L. 1997 Distant fisheries implicated in the loss of the world's largest leatherback nesting population. *Mar. Turtle Newslett.* **78**, 2–7.
- Ferraroli, S., Georges, J. Y., Gaspar, P. & Le Maho, Y. 2004 Where leatherback turtles meet fisheries. *Nature* **429**, 521–522. (doi:10.1038/429521a)
- Freake, M. J., Muheim, R. & Phillips, J. B. 2006 Magnetic maps in animals: a theory comes of age? *Q. Rev. Biol.* **81**, 327–347. (doi:10.1086/511528)
- Gaspar, P., George, J. C., Fossette, S., Lenoble, A., Ferraroli, S. & Le Maho, Y. 2006 Marine animal behaviour: neglecting ocean currents can lead us up the wrong track. *Proc. R. Soc. B* **273**, 2697–2702. (doi:10.1098/rspb.2006.3623)
- Girard, C., Sudre, J., Benhamou, S., Roos, D. & Luschi, P. 2006 Homing in green turtles *Chelonia mydas*: oceanic currents act as a constraint rather than as an information source. *Mar. Ecol. Prog. Ser.* **322**, 281–289. (doi:10.3354/meps322281)
- Godley, B. J., Blumenthal, J. M., Broderick, A. C., Coyne, M. S., Godfrey, M. H., Hawkes, L. A. & Witt, M. J. 2008 Satellite tracking of sea turtles: where have we been and where do we go next? *Endang. Species Res.* **4**, 3–22. (doi:10.3354/esr00060)
- Hays, G. C., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. & Luschi, P. 2003 Island-finding ability of marine turtles. *Proc. R. Soc. Lond. B* **270**(Suppl. 1), 5–7. (doi:10.1098/rsbl.2003.0022)
- Hays, G. C., Houghton, J. D. R. & Myers, A. E. 2004 Pan-Atlantic leatherback turtle movements. *Nature* **429**, 522. (doi:10.1038/429522a)
- Hays, G. C., Hobson, V. J., Metcalfe, J. D., Righton, D. & Sims, D. W. 2006 Flexible foraging movements of leatherback turtles across the North Atlantic Ocean. *Ecology* **87**, 2647–2656. (doi:10.1890/0012-9658(2006)87[2647:FFMOLT]2.0.CO;2)
- Hughes, G. R. 1995 Nesting cycles in sea turtles: typical or atypical? In *Biology and conservation of sea turtles* (ed. K. A. Bjørndal), pp. 81–89. Washington, DC: Smithsonian Institution Press.
- Hughes, G. R. 1996 Nesting of the leatherback turtle (*Dermochelys coriacea*) in Tongaland, KwaZulu-Natal, South Africa, 1963–1995. *Chelon. Conserv. Biol.* **2**, 153–158.
- James, M. C., Eckert, S. A. & Myers, R. A. 2005a Migratory and reproductive movements of male leatherback turtles (*Dermochelys coriacea*). *Mar. Biol.* **147**, 845–853. (doi:10.1007/s00227-005-1581-1)
- James, M. C., Myers, R. A. & Ottensmeyer, C. A. 2005b Behaviour of leatherback sea turtles, *Dermochelys coriacea*, during the migratory cycle. *Proc. R. Soc. B* **272**, 1547–1555. (doi:10.1098/rspb.2005.3110)
- James, M. C., Ottensmeyer, C. A. & Myers, R. A. 2005c Identification of high-use habitat and threats to leatherback sea turtles in northern waters: new directions for conservation. *Ecol. Lett.* **8**, 195–201. (doi:10.1111/j.1461-0248.2004.00710.x)
- Johnson, D. S. & Nurminen, J. 2007 *The history of seafaring*. London, UK: Conway Maritime Press.
- Kalmijn, A. J. 1974 The detection of electric fields from inanimate and animate sources other than electric organs. In *Handbook of sensory physiology*, vol. III/3 (ed. A. Fessard), pp. 147–200. Berlin, Germany: Springer Verlag.
- Lambardi, P., Lutjeharms, J. R. E., Mencacci, R., Hays, G. C. & Luschi, P. 2008 Influence of ocean currents on long-distance movement of leatherback sea turtles in the southwest Indian Ocean. *Mar. Ecol. Prog. Ser.* **353**, 289–301. (doi:10.3354/meps07118)
- Light, P., Salmon, M. & Lohmann, K. J. 1993 Geomagnetic orientation of loggerhead sea turtles: evidence for an inclination compass. *J. Exp. Biol.* **182**, 1–10.
- Lohmann, K. J. & Lohmann, C. M. F. 1993 A light-independent magnetic compass in the leatherback sea turtle. *Biol. Bull.* **185**, 149–151. (doi:10.2307/1542138)
- Lohmann, K. J. & Lohmann, C. M. F. 1996 Detection of magnetic field intensity by sea turtles. *Nature* **380**, 59–61. (doi:10.1038/380059a0)
- Lohmann, K. J. & Lohmann, C. M. F. 2006 Sea turtles, lobsters, and oceanic magnetic maps. *Mar. Freshwater Behav. Physiol.* **39**, 49–64. (doi:10.1080/10236240600563230)
- Lohmann, K. J., Cain, S. D., Dodge, S. A. & Lohmann, C. M. F. 2001 Regional magnetic fields as navigational

- markers for sea turtles. *Science* **294**, 364–366. (doi:10.1126/science.1064557)
- Lohmann, K. J., Lohmann, C. M. F., Ehrhart, L. M., Bagley, D. A. & Swing, T. 2004 Geomagnetic map used in sea-turtle navigation. *Nature* **428**, 909–910. (doi:10.1038/428909a)
- Lohmann, K. J., Lohmann, C. M. & Putman, N. F. 2007 Magnetic maps in animals: nature's GPS. *J. Exp. Biol.* **210**, 3697–3705. (doi:10.1242/jeb.001313)
- Lohmann, K. J., Luschi, P. & Hays, G. C. 2008 Goal navigation and island-finding in sea turtles. *J. Exp. Mar. Biol. Ecol.* **356**, 83–95. (doi:10.1016/j.jembe.2007.12.017)
- Luschi, P., Hays, G. C., Del Seppia, C., Marsh, R. & Papi, F. 1998 The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. *Proc. R. Soc. Lond. B* **265**, 2279–2284. (doi:10.1098/rspb.1998.0571)
- Luschi, P., Åkesson, S., Broderick, A. C., Glen, F., Godley, B. J., Papi, F. & Hays, G. C. 2001 Testing the navigational abilities of ocean migrants: displacement experiments on green sea turtles (*Chelonia mydas*). *Behav. Ecol. Sociobiol.* **50**, 528–534. (doi:10.1007/s002650100396)
- Luschi, P., Hays, G. C. & Papi, F. 2003a A review of long-distance movements by marine turtles, and the possible role of ocean currents. *Oikos* **103**, 293–302. (doi:10.1034/j.1600-0706.2003.12123.x)
- Luschi, P., Sale, A., Mencacci, R., Hughes, G. R., Lutjeharms, J. R. E. & Papi, F. 2003b Current transport in leatherback sea turtles (*Dermochelys coriacea*) in the ocean. *Proc. R. Soc. Lond. B* **270**, 129–132. (doi:10.1098/rsbl.2003.0036)
- Luschi, P., Hughes, G. R., Mencacci, R., De Bernardi, E., Sale, A., Broker, R., Bouwer, M. & Papi, F. 2003c Satellite tracking of migrating loggerhead sea turtles (*Caretta caretta*) displaced in the open sea. *Mar. Biol.* **143**, 793–801. (doi:10.1007/s00227-003-1117-5)
- Luschi, P., Lutjeharms, J. R. E., Lambardi, P., Mencacci, R., Hughes, G. R. & Hays, G. C. 2006 A review of migratory behaviour of sea turtles off southerneastern Africa. *S. Afr. J. Sci.* **102**, 51–58.
- Luschi, P., Benhamou, S., Girard, C., Ciccione, S., Roos, D., Sudre, J. & Benvenuti, S. 2007 Marine turtles use geomagnetic cues during open-sea homing. *Curr. Biol.* **23**, 126–133. (doi:10.1016/j.cub.2006.11.062)
- Lutjeharms, J. R. E. 2006 *The Agulhas Current*. Berlin, Germany: Springer.
- Mate, B. R., Mesecar, R. & Lagerquist, B. A. 2007 The evolution of satellite-monitored radio tags for large whales: one laboratory's experience. *Deep-Sea Res. II* **54**, 224–247. (doi:10.1016/j.dsr2.2006.11.021)
- McMahon, C. R., Bradshaw, C. J. & Hays, G. C. 2007 Satellite tracking reveals unusual diving characteristics for a marine reptile, the olive ridley turtle *Lepidochelys olivacea*. *Mar. Ecol. Prog. Ser.* **329**, 239–252. (doi:10.3354/meps329239)
- Montgomery, J. C., Baker, C. F. & Carton, A. G. 1997 The lateral line can mediate rheotaxis in fish. *Nature* **389**, 960–963. (doi:10.1038/40135)
- Morreale, S. J., Standora, E. A., Spotila, J. R. & Paladino, F. V. 1996 Migration corridor for sea turtles. *Nature* **384**, 319–320. (doi:10.1038/384319a0)
- Papi, F. 2006 Navigation of marine, freshwater and coastal animals: concepts and current problems. *Mar. Freshwater Behav. Physiol.* **39**, 3–12. (doi:10.1080/10236240600563057)
- Plotkin, P. T., Byles, R. A., Rostal, D. C. & Owens, D. W. 1995 Independent versus socially facilitated oceanic migrations of the olive ridley *Lepidochelys olivacea*. *Mar. Biol.* **122**, 137–143. (doi:10.1007/BF00349287)
- Polovina, J. J., Balazs, G. H., Howell, E. A., Parker, D. M., Seki, M. P. & Dutton, P. H. 2004 Forage and migration habitat of loggerhead (*Caretta caretta*) and olive ridley (*Lepidochelys olivacea*) sea turtles in the central North Pacific Ocean. *Fish. Oceanogr.* **13**, 36–51. (doi:10.1046/j.1365-2419.2003.00270.x)
- Sand, O. & Karlsen, H. E. 2000 Detection of infrasounds and linear acceleration in fishes. *Phil. Trans. R. Soc. Lond. B* **355**, 1295–1298. (doi:10.1098/rstb.2000.0687)
- Shillinger, G. L. *et al.* 2008 Persistent leatherback turtle migrations present opportunities for conservation. *PLoS Biol.* **15**, e171. (doi:10.1371/journal.pbio.0060171)
- Stramma, L. & Lutjeharms, J. R. E. 1997 The flow field of the subtropical gyre of the South Indian Ocean. *J. Geophys. Res.* **102**, 5513–5530. (doi:10.1029/96JC03455)
- Troëng, S., Chacón, D. & Dick, B. 2004 Possible decline in leatherback turtle *Dermochelys coriacea* nesting along Caribbean Central America. *Oryx* **38**, 41–49.
- Van Dam, R. P., Diez, C. E., Balazs, G. H., Colón Colón, L. A., McMillan, W. O. & Schroeder, B. 2008 Sex-specific migration patterns of hawksbill turtles breeding at Mona Island, Puerto Rico. *Endang. Species Res.* **4**, 85–94. (doi:10.3354/esr00044)
- Walter, R. 1901 *Anson's voyage round the world*. London, UK: Rivingtons.
- Weng, K. C., Foley, D. G., Ganong, J. E., Perle, C., Shillinger, G. L. & Block, B. A. 2008 Migration of an upper trophic level predator, the salmon shark *Lamna ditropis*, between distant ecoregions. *Mar. Ecol. Prog. Ser.* **372**, 253–264. (doi:10.3354/meps07706)