

A review of long-distance movements by marine turtles, and the possible role of ocean currents

Paolo Luschi, Graeme C. Hays and Floriano Papi

Luschi, P., Hays, G. C. and Papi, F. 2003. A review of long-distance movements by marine turtles, and the possible role of ocean currents. – *Oikos* 103: 293–302.

Sea turtle movements often occur in open-sea unsheltered areas, and are therefore likely to be influenced by major oceanographic processes. Only recently has work started to examine the possible relationships of these movements with dynamic oceanic features, and consequently a clear picture of such interaction is only available in a few cases.

Newborn sea turtles are thought to rely on oceanic currents to reach their pelagic nursery habitats. The actual extent and timing of these developmental migrations are known for only a few populations, but these movements probably last several years and range over thousands of km. Large juveniles that have been tracked during their pelagic stage were found to make long-distance movements, sometimes swimming against the prevailing currents. Older juveniles of most species leave the pelagic habitat to recruit to neritic developmental habitats. This is a very poorly documented phase of the sea turtle life-cycle, and the few available indications show that turtles may have to swim actively for enormous distances to counterbalance their previous drift with the current.

The course and extent of adult postnesting migrations vary greatly among different turtle species, but two main patterns are evident. Some species, like green, hawksbill and loggerhead turtles, shuttle between the nesting beach and a specific feeding area used for the entire inter-reproductive period. In these cases, individuals swim, rather than drift, to complete their journeys, with possible advection due to currents sometimes helping them to quickly reach their target, but sometimes providing navigational challenges.

Other species such as the olive ridley and the leatherback turtle, leave the coastal nesting areas to reach the pelagic environment where they forage, and perform wandering movements. Major oceanographic processes (such as main currents and eddies) have been recently shown to have a remarkable influence on leatherback movements, making it questionable whether these journeys are to be considered migrations or, rather, prolonged stays in vast feeding areas.

P. Luschi and F. Papi, Dipartimento di Etologia, Ecologia, Evoluzione, Univ. of Pisa, Via A. Volta 6, IT-56126 Pisa, Italy (luschi@discau.unipi.it). – G. C. Hays, School of Biological Sciences, Univ. of Wales Swansea, Singleton Park, Swansea, SA2 8PP UK.

Although greatly differentiated in their general life-style and feeding habits (Hendrickson 1980, Bjorndal 1997), the seven extant species of sea turtle still share a common lifecycle (Carr et al. 1978, Musick and Limpus 1997) that may encompass prolonged periods in the open sea at all developmental stages. During these periods, turtles are known to move widely between different habitats or specific locations, ranging over

large oceanic areas away from the continental shelf (Musick and Limpus 1997). In this environment, currents and related oceanographic features are likely to be important environmental factors affecting the behaviour and movements of sea turtles.

In recent years, many features of the open-ocean movements of sea turtles, such as their general extent, pattern and course, have become known, mostly thanks

Accepted 4 December 2002

Copyright © OIKOS 2003
ISSN 0030-1299

to the findings obtained through satellite telemetry. However, the effects of environmental factors on these movements are still poorly known, and only in a few cases has the integration of satellite tracking data with oceanographic techniques such as mathematical modelling of current fields and analysis of remote sensing data, provided useful clues on how turtle movements are affected by the current circulation pattern (Hays and Marsh 1997, Polovina et al. 2000, Horrocks et al. 2001).

In theory, there are a number of ways by which ocean currents can affect turtles. The main stream of major ocean currents will have an obvious effect on turtle movements, producing powerful forces which advect swimming turtles in a given direction not necessarily concordant with the intended swimming direction. Less predictable (and discernible) effects can be produced by weaker currents or at the border of main currents, where powerful processes such as eddies or rings often occur (Gründlingh 1988), producing small- to medium-scale rotatory drifts of the water. Sea turtle movements will be affected by these processes accordingly, just like bird flights are drifted by winds (Richardson 1990). Finally, currents might also indirectly influence turtles by determining the local availability of planktonic prey, that may be concentrated in preferential areas such as convergence zones or frontal systems (Olson et al. 1994). Most of these processes can now be recorded through satellite-derived remote sensing, by which it is possible to monitor various parameters such as sea surface temperature and height (showing the course of major currents and mesoscale oceanographic features, such as meanders and eddies), or chlorophyll content.

In the present paper, we briefly review the currently available data on sea turtle movements in the open sea and highlight the stages where currents can be supposed or have been shown to have a role. Since the study of oceanographic influences on sea turtle movements is still in its infancy, many considerations are based on limited findings, or are entirely hypothetical. The ecology of sea turtle movements differs greatly in the different life history stages and so the influence of oceanographic factors can be expected to vary accordingly. Following the terminology proposed by Musick and Limpus (1997), we will therefore examine separately the case of hatchling, juvenile and adult turtles.

Hatchling and early juvenile turtles

Until some years ago, so little was known about the fate of turtle hatchlings that the term 'lost year(s)' was used to refer to the first period of their life after they left the nesting beach (Witham 1980). A few hours after emerging on the beach surface from their underground

nest, hatchlings actively swim out into the open sea, and do not reappear in neritic areas until they are much older juveniles. Evidence suggests that hatchlings rely on major ocean currents to be transported away from the natal beach to their pelagic nursery habitats (Carr et al. 1978, Carr 1987, Musick and Limpus 1997), where they spend 1–10 years feeding on planktonic prey similarly drifted by currents and especially found in fronts and convergence zones (Musick and Limpus 1997, Witherington 2002). The only noticeable exception is the flatback turtle (*Natator depressus*), whose hatchlings apparently lack a pelagic phase in their development and always remain in neritic areas (Walker and Parmenter 1990).

These developmental migrations are generally thought to be on a macro-geographic scale but their actual extent and timing are well known for only a few populations. This is especially the case of loggerhead turtles (*Caretta caretta*) born in Eastern Florida beaches, which have been shown to entrain in the Florida Current and then the Gulf Stream to start a transoceanic journey towards the East Atlantic (Carr 1987). By remaining for a few years in the large circulating current system known as North Atlantic Gyre, loggerhead juveniles can then be transported back by the North Equatorial Current to the West Atlantic, to reach their natal areas where they will reproduce once attaining sexual maturity (Bowen and Karl 1997). These oceanic movements, which are probably performed by Florida green turtles (*Chelonia mydas*) as well (Witham 1980), have also been simulated by using a numerical model of North Atlantic general circulation (Hays and Marsh 1997).

Taking into account known current patterns in the areas involved, similar scenarios have been proposed for a few other turtle populations. A transpacific crossing is thought to occur for loggerheads born in Japan, that traverse the North Pacific carried by the Eastward-flowing California current to reach California waters (Bowen et al. 1995). Similar scenarios have been hypothesised for South African loggerheads (Hughes 1974), Costa Rican green turtles (Carr and Meylan 1980), and Kemp's Ridleys (*Lepidochelys kempii*) in the Gulf of Mexico (Collard and Ogren 1990). In other cases, virtually nothing is known about the location of nursery habitats of the various turtle species and populations, although this would represent a most important piece of information for conservation purposes. For the more pelagic turtle species (olive ridley *Lepidochelys olivacea*, and leatherback turtle *Dermochelys coriacea*), in particular, the period following their departure from the natal beach should still be considered 'lost years' (Musick and Limpus 1997).

Sea currents certainly play a major role in the movements of hatchlings and early juveniles of all species: it is far better for hatchlings to be 'sequestered' by currents (Collard 1990) than to remain in inshore wa-

ters, where predator concentration and the risk of being cast ashore is higher. Once in the current systems, hatchlings and juveniles are therefore in their optimal environment, and their (passive) dispersal movement with the current is not 'a developmental necessity but a consequence of drifting' (Collard 1990). It is even questionable whether these movements can be considered a real migration (see also below).

Since it is still impossible to track coin-sized hatchlings for long periods, the available evidence supporting the occurrence of a pelagic stage in turtles is still mostly indirect (e.g. size of turtles recovered in different pelagic areas, and knowledge in physical oceanography). Only a few pelagic loggerhead juveniles have been tracked, off Madeira Island in the Northern Atlantic (Dellinger and Freitas 2000), North of Hawaii Islands in the Pacific (Polovina et al. 2000) and in the Mediterranean (Bentivegna 2002). In all cases, turtles were found to make long-distance movements in different directions, often swimming against the prevailing currents (Polovina et al. 2000, Dellinger and Freitas 2000). This shows that larger juveniles are no longer totally dependent by current flow and can perform active movements probably linked to foraging needs (Polovina et al. 2000) and/or environmental factors (e.g. sea temperature, Bentivegna 2002).

Late juvenile sea turtles

After some years of pelagic life, older juveniles of most species are thought to recruit to neritic habitats, where they complete their development. These areas can be either shared with adults (and will constitute the adult residential foraging grounds where juvenile turtles will later spend their inter-reproductive periods), or be frequented only by juveniles, that will later shift to a different adult feeding area (Musick and Limpus 1997). In the best known cases, these late developmental habitats are likely to be closer to each turtle's natal (and future nesting) beach than their pelagic nursery habitats and consequently, arrival of juveniles at neritic feeding areas may be the result of a directed long-distance movement. In some cases, transport by current gyres is thought to facilitate this movement, but the actual extent of this help is hard to estimate. Rather, there might well be instances when turtles have to swim actively to counterbalance their previous drift with the current, and to do so for enormous distances and while heading towards a target.

This is by far the least known stage of sea turtle life-cycle, and the only indications we have come from tracking studies done on Japanese loggerheads, that have been tracked for part of their crossing of the Pacific Ocean from their pelagic feeding areas off California to their nesting area in Japan (Nichols et al.

2000, Polovina et al. 2000). For one female, the complete transoceanic journey was reconstructed: it was carried out along a constant westward trajectory and lasted nearly one year for a total length of about 11 500 km, slightly longer than the shortest possible distance between the start and end points (Nichols et al. 2000). A precise interpretation of this amazing finding is difficult (the tracked turtle had been in captivity for ten years and was probably sexually mature at the time of tracking), but it is most likely that her movements are truly representative of those of done by younger juveniles returning to Japan at the end of their pelagic period. The tracked turtles were not merely carried by current flow, and were rather found to swim against currents, or to be deflected from the optimal course (Nichols et al. 2000, Polovina et al. 2000).

Despite the great interest that this phase of sea turtle life has, no further data document the movements of late juveniles shifting from their pelagic to demersal phase. In a number of cases, juveniles have been tracked at a slightly later stage, during their stay at their developmental habitats (see Musick and Limpus 1997 for references). These studies have provided useful results on sea turtle habitat utilisation, site fidelity and seasonal migrations from higher to lower latitudes. No interaction with existing sea currents has been documented.

Adult sea turtles

The migratory behaviour of adult sea turtles is far better known than that of juveniles, thanks to an ever increasing number of satellite telemetry findings providing information on the course and extent of migratory movements of many turtle populations. Unfortunately, many of these results, even when impressive or thought provoking, are left unpublished or are improperly published (e.g. as non-refereed short reports, or even only on the Internet), thus preventing sea turtle students to fully benefit and correctly interpret these data. In most cases, females have been tracked during their postnesting migration away from the nesting beaches (Balazs 1994, Luschi et al. 1998, Cheng 2000, Ellis et al. 2000, Nichols et al. 2000, Polovina et al. 2000), although some journeys towards the nesting areas have also been reconstructed (Renaud et al. 1996) and a few males have been followed during their movements (Beavers and Cassano 1996, Hays et al. 2001b).

Although the findings obtained reveal quite a large degree of variation, even within the same species or population, two main patterns of movement are evident. Upon leaving the nesting area, some species swim towards a fixed feeding area, generally in the neritic environment, where they then stay for long time, possibly for the entire inter-reproductive period of 1–4 years

(Fig. 1, Balazs et al. 1994, Luschi et al. 1996, Cheng 2000, Ellis et al. 2000, Hays et al. 2002). At the following reproductive season, they will migrate back to their nesting area. Such shuttling migrations between defined feeding and nesting areas generally span a somewhat smaller scale than the pan-oceanic movements of juveniles, if only because each individual has to make the trip every few years and cannot waste too much energy

and time. In this case, therefore, migrating turtles aim to reach these specific targets with the minimum energy expenditure possible, and indeed they swim actively to reach their destination. These journeys are often carried out all along the coast (Luschi et al. 1996, Renaud et al. 1996, Papi et al. 1997, Ellis et al. 2000), but it is not uncommon that turtles cross open-sea stretches as well, especially (but not only) when their target area is on an

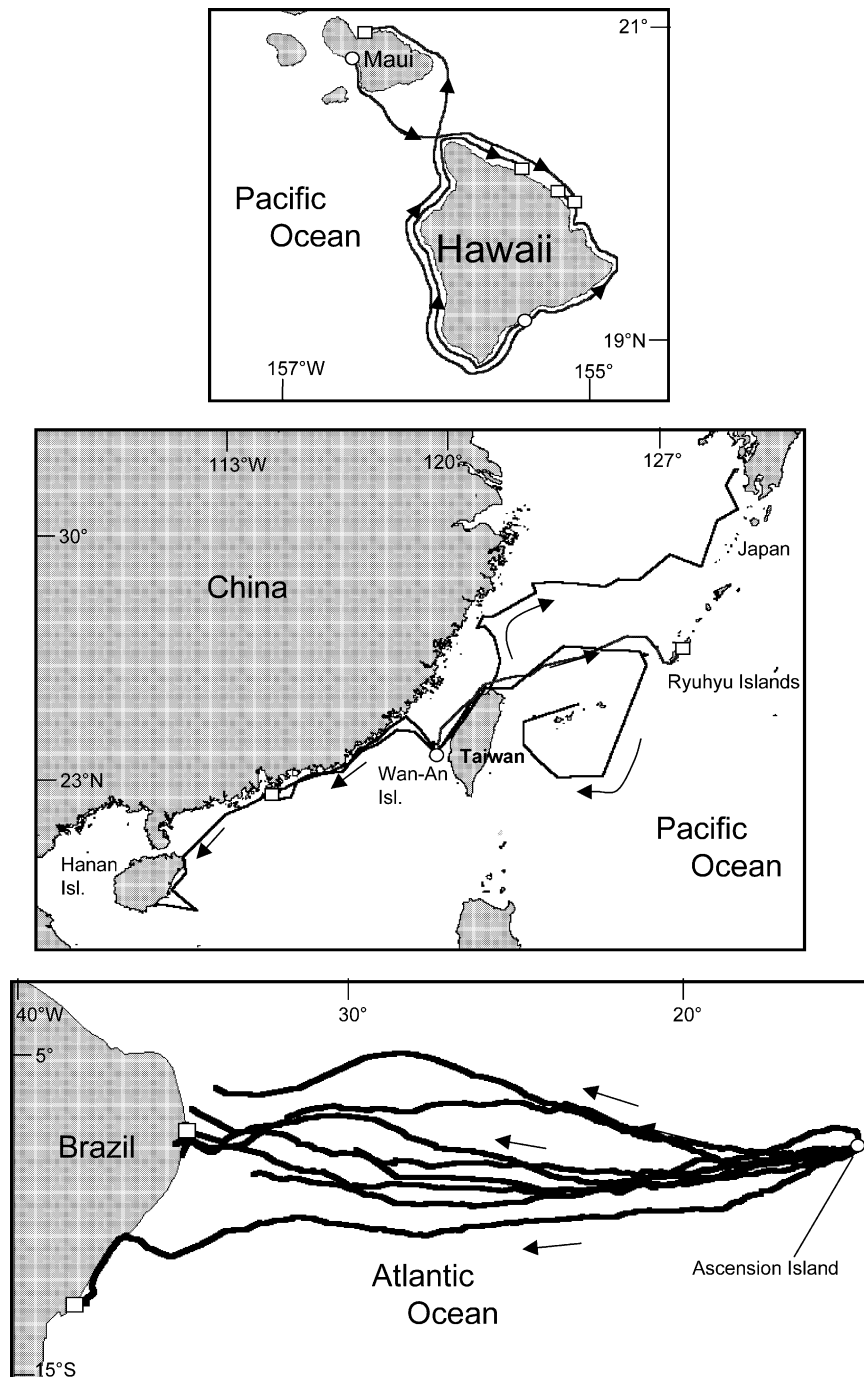


Fig. 1. Satellite-tracked postnesting migrations of turtles heading towards a specific feeding ground. Top: Short-range coastal migrations of hawksbill turtles in the Hawaiian islands (from Ellis et al. 2000). Middle: Routes of 5 turtles migrating from Wan-An Island, Taiwan towards different destinations, sometimes with very undirected routes (from Cheng 2000). Bottom: Routes of 8 Ascension turtles undertaking a transoceanic migration towards their feeding grounds along the Brazilian coast (from Luschi et al. 1998, Papi et al. 2000). White dots indicate the nesting beaches of the tracked turtles, white boxes their spatially-limited feeding grounds where they have been localised for long time.

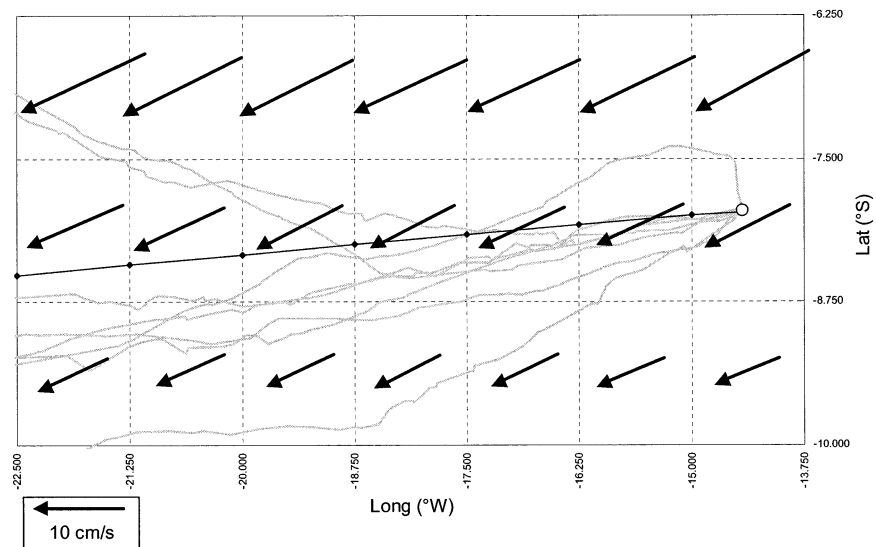
island (Balazs 1994, Luschi et al. 1996, 1998, Cheng 2000). Satellite tracking has often shown that the routes followed by these turtles are well directed towards their target, although individuals do not always take the most direct route to get to their destination, sometimes reaching it only after long detours (Cheng 2000, Hays et al. 2002). This choice often derives from the need to limit the time spent in the open sea, but there are also many cases in which such detours are apparently meaningless (Fig. 1). Sea turtles' diving behaviour reflects their active swimming to get to destination. Submergences are usually short (5–10 min) and frequent during the trip, compared to when turtles are resting at neritic sites where dive durations of 30–40 min are common (Papi et al. 1997, Hays et al. 1999).

Of course, sea currents interfere with these movements, especially when they occur in the open sea. Since migrating sea turtles most often dive shallow (< 20 m; Hays et al. 2001a), surface currents produce most of the effects. These effects are particularly harmful when they deflect individuals from the optimal route, as turtles then have to resort to their navigational abilities to compensate. The influence of currents on turtle journeys has been investigated in only a few cases (Balazs et al. 1994, Sakamoto et al. 1997, Luschi et al. 1998, Horrocks et al. 2001). For green turtles migrating from Ascension Island to Brazil, individuals usually leave the island heading slightly SW of their target, and this deflection has been ascribed to the SW-flowing South Atlantic equatorial current (Luschi et al. 1998, Fig. 2). However, preliminary results obtained from a computer simulation of Ascension turtle migration in relation to modelled surface currents actually indicate that turtles chose to swim in the same direction of the SW-flowing current while leaving the island (G. Santini, P. Luschi, G. C. Hays and R. Marsh, unpubl.), and that they

would have displayed a more westerly route if they were continuously swimming due West (Fig. 2). Indeed, a closer look at their migratory performances revealed that turtles actually took advantage of the current flow which increased their migratory speed, although not along the optimal direction, and allowed them to get to their destination quicker (Hays et al. 1999). Most interestingly, migrating birds and salmon, too, have been found to migrate more efficiently when they tolerate wind or current drift in some circumstances (Alerstam 1979, Healey et al. 2000). However, such comparisons between actual turtle routes and modelled data may be misleading, since models of current fields only show 'average' currents over large areas and periods and cannot account for the variability in currents, thus providing little information about the real currents migrating turtles have actually experienced during their journey. As such, comparison between the routes of turtles and those of drifters satellite-tracked during the same period may prove useful.

In other species, adults leaving the nesting area do not search for a specific residential site but rather move away from the coast to the pelagic environment where they begin to perform wandering movements, often over large distances, that are undirected towards a fixed site (Fig. 3). This pattern is typical for the olive ridley (Plotkin et al. 1995, Beavers and Cassano 1996) and, especially, for the leatherback turtle (Morreale et al. 1996, Eckert and Sarti 1997, Hughes et al. 1998), although open-sea wanderings have also been recorded for postnesting loggerheads as well (Stoneburner 1982, Hatase et al. 2002). In these cases, individuals are known to behave much like juveniles, feeding on current-transported plankton. Leatherbacks, for instance, have a very specialised diet exclusively composed of gelatinous planktonic invertebrates, that have to be

Fig. 2. Current field in the area West of Ascension Island in June, together with the first part of the routes of turtles leaving the island at the end of the reproductive season (grey lines; data from Luschi et al. 1998, Papi et al. 2000). The black line is the simulated trajectory of a turtle leaving the island heading due West with a constant speed (2.0 km h^{-1}) and encountering the depicted current field. See Luschi et al. (1998) for a full description of how these modelled currents were produced.



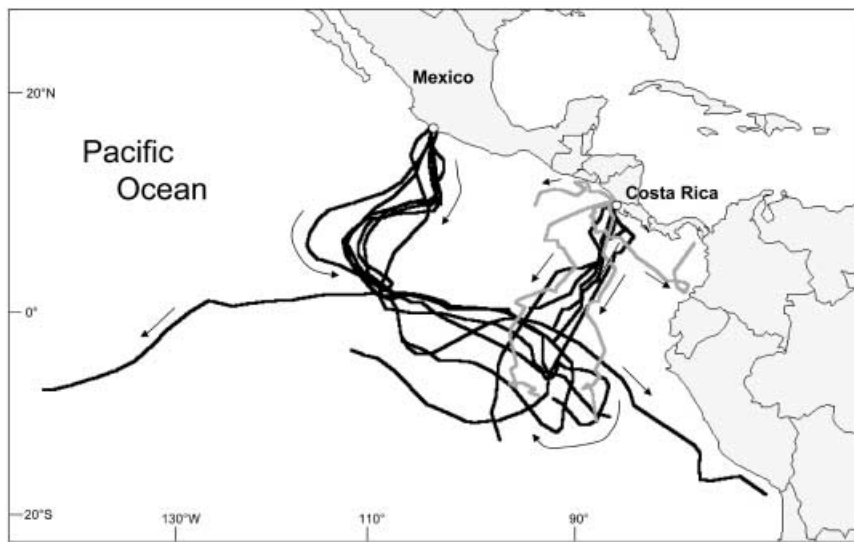


Fig. 3. Long-distance pelagic movements of leatherbacks (black tracks) and olive ridleys (grey tracks) migrating from Mexico (Eckert and Sarti 1997) and Costa Rica (Plotkin et al. 1995, Morreale et al. 1996) into the Pacific Ocean. The areas frequented by the turtles partly overlapped.

ingested in huge quantities to sustain the energetic demands of these giant turtles (Lutcavage 1996, Bjørndal 1997). The routes reconstructed by satellite for oceanically feeding species are often fairly complex, with meandering segments alternating with straight legs in corridors common to different individuals (Fig. 3, Plotkin et al. 1995, Beavers and Cassano 1996, Morreale et al. 1996, Eckert and Sarti 1997, Hughes et al. 1998, Luschi et al. submitted(a)). The diving patterns of leatherbacks seem to be linked to the activity of their pelagic prey, with dive depths of hundreds of meters being routinely attained (Eckert et al. 1989).

The role of oceanographic features in this kind of movement pattern has long been highlighted (Carr 1987, Lutcavage 1996) but rarely documented. Like in the case of juveniles, frontal systems have often been recognised as reliable and predictable foraging areas, and adult leatherbacks and olive ridleys are indeed habitually found associated with these features (Beavers and Cassano 1996, Lutcavage 1996, Morreale et al. 1996). In no case, however, have the areas visited by satellite-tracked leatherback turtles been analysed with respect to their productivity (e.g. derived from remote-sensing data on chlorophyll density, as has been done for juvenile loggerheads; Polovina et al. 2000). A detailed analysis of satellite-tracked movements of South African leatherbacks in relation to oceanographic features, has recently revealed that the reconstructed routes are largely shaped by processes such as current flows and eddies (Luschi et al. submitted(b)). These turtles actively left the coastal nesting area to enter the mainstream of the intense Agulhas Current, and then remained within it for months (Fig. 4). Large parts of the routes were superimposable to remotely-sensed oceanographic features occurring in those areas, which sometimes made turtle routes looping (when turtles were engaged in eddy circulating patterns) and some-

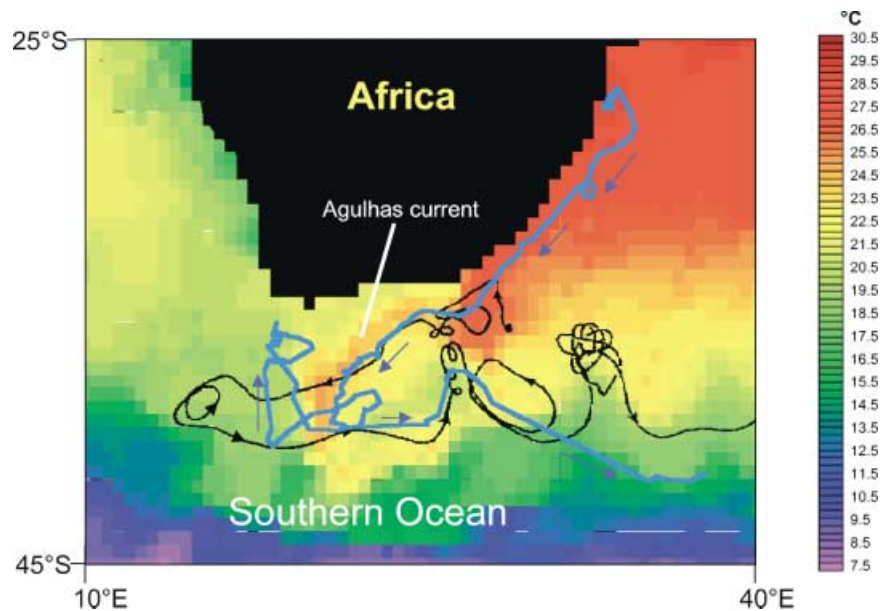
times straight (when they were in the current mainstream). Large adult leatherbacks are obviously able to swim actively out of current patterns when needed, but the tracked turtles nevertheless seemed to be carried by currents for most of the time, probably because they found abundant and predictable food within them. These journeys are therefore not to be considered migrations as defined by Dingle (Dingle 1996) but, rather, prolonged stays in a far-ranging feeding ground.

Such a strict, prolonged dependence on current systems has not been reported in other species. In olive ridleys, Beavers and Cassano (1996) found instances of transport with the prevailing currents, but mainly got indications of active swimming by turtles. On the other hand, two adult loggerheads wandering in the equatorial Indian Ocean, were found to be quickly transported by jet-like currents for 2 months, along a remarkable straight common leg, over 1600 km long (Luschi et al. submitted(b)). It is tempting to suggest that other examples of open-sea corridors common to different migrating leatherbacks (Fig. 3) might be derived from the turtles being transported by current systems.

Discussion: navigational consequences of current actions

For animals living and moving in the open sea, ocean currents and related features certainly represent an important environmental factor affecting their life and behaviour. Recent research has started to show that this is indeed the case for sea turtles, whose complex and truly marine lifecycle is fundamentally influenced by currents at all ontogenetic stages. Hatchlings and early juveniles live within major current systems, where they find suitable feeding areas, like fronts or conver-

Fig. 4. Postnesting wandering movement of a leatherback turtle (Hughes et al. 1998), superimposed to Sea Surface Temperatures (SST) in the area crossed. The SST image refers to 19 Mar. 1999 and shows the SW-directed course of the Agulhas current South of the African continent, where the current's warm waters are distinguishable from the surrounding cooler waters. The track of a drifting buoy (black line) followed in the same area (Gründlingh 1978) is also plotted. The turtle clearly followed the course of the current for long parts of her journey.



gence regions (Witherington 2002), and where they are safer than in coastal areas. Adults of pelagic species similarly exploit the biologically rich environments linked to current systems. As a counterbalance of such beneficial effects, currents typically carry pelagic sea turtles on macro-geographic journeys, often ranging over entire ocean basins. These (mostly passive) movements have no specific role in turtle development (Collard 1990) or inter-reproductive biology, and can rather be thought to have detrimental consequences, leading turtles away from their subsequent foraging or nesting areas where they move to sooner or later (see also below).

The effects of currents are also mostly harmful when turtles cross open-sea stretches heading towards a specific target, like during the adults' shuttling migrations. Even when the movement in one direction is done together with current flow, the return migration is often hindered to a similar extent, and so the net effect might be nil. Most importantly, lateral currents can deflect turtles from the optimal route towards their target, displacing them sideways. Although this drift might be helpful in some cases (Healey et al. 2000), it certainly poses most difficult navigational challenges. Sea turtles, like any other swimming animal, cannot perceive the drift of currents in the absence of external references (e.g. landmarks, or the border of two contrasting currents; Richardson 1990, Papi and Luschi 1996). As a consequence, they cannot immediately overcome the deflecting action of side currents in the apparent absence of non-drifting references of the open sea. During long open-sea stretches, this drift can eventually lead turtles largely away from the expected target.

Such errors have to be compensated for in some way (although not necessarily soon after they occur; Aler-

stam 1979), and indeed it is just to account for the ability to compensate for these deviations – also induced by inaccuracies in the turtle steering mechanism(s) – that sea turtles have often been postulated to rely on some system of true navigation allowing position-fixing on a global scale (Carr 1984, Lohmann and Lohmann 1996, Papi and Luschi 1996). However, such an ability has never been demonstrated in any turtle species, despite a series of recent efforts specifically aimed at testing this hypothesis (Papi et al. 2000, Luschi et al. 2001, Luschi et al. submitted(b), Åkesson et al. 2003). Conversely, a number of recent findings indicate that the navigational abilities of sea turtles may be less sophisticated than previously suspected: experiments have shown that Ascension green turtles find it difficult to compensate for experimental relocations (Luschi et al. 2001), and that they often fail to direct their open-sea postnesting migrations towards their residential feeding grounds, rather first reaching the Brazilian coast at any point, and then hugging the coastline until they find their intended goal (Hays et al. 2002, Fig. 1).

The hypothesised reliance of adult turtles on simpler orientation mechanisms, such as vectorial navigation (Luschi et al. 2001) is challenged by the fact that such vectorial mechanisms provide no way to compensate for induced deviations from the intended route. Their efficiency is therefore largely dependent on the action of deviating factors, such as turtle guidance inaccuracies and current drift. The accuracy of the compass mechanism(s) used by the turtles to keep a constant direction seems to be generally rather high, as shown by their frequently recorded ability to follow long straight courses in open seas (Balazs 1994, Balazs et al. 1994, Luschi et al. 1996, 1998). There might also be cases in

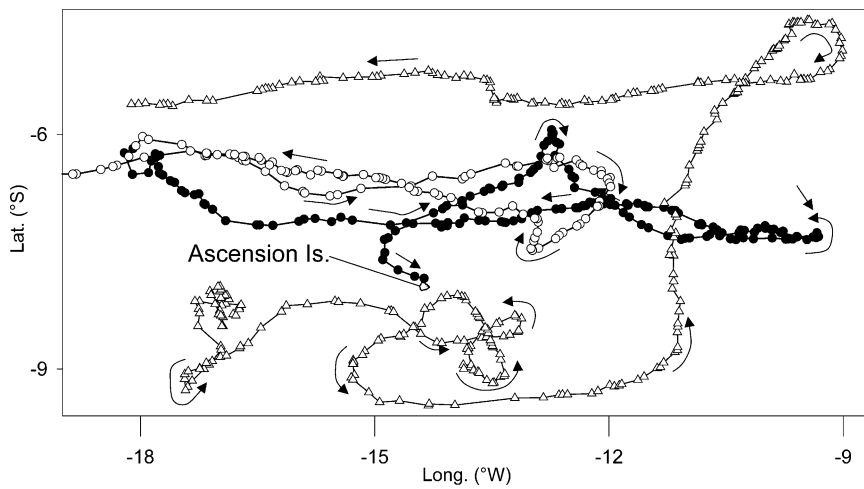


Fig. 5. Open-sea movements of green turtles searching for Ascension Island after having been displaced, showing retracing of previous paths and repeated returns to the same spot (from Luschi et al. 2001).

which current drift too is not particularly powerful. Ascension turtles displaced in the middle of the Atlantic Ocean, for instance, have been found to be able to pass again over previously visited sites (such as the release site) after long loops or to retrace previous movements with great precision (Fig. 5, Luschi et al. 2001). Such orientation feats are only possible in the absence of sustained current drift (by route-based orientation mechanisms; Papi 1992). Furthermore, vectorial programmes could be used in conjunction with shorter-range orienting cues that would help turtles to pinpoint their target (or to search for it) once in its general vicinity (Carr 1984, Wallraff 1991, Hays et al. 2002). For Ascension-bound turtles, a role of wind-borne cues has recently been highlighted, that would determine a direction-specific enlargement of the target island thanks to the constantly-blowing Southeast trade winds (Luschi et al. 2001, Åkesson et al. 2003). Such a role is however peculiar to the Ascension island area, and turtles migrating in different geographical areas (and meteorological conditions) may employ different mechanisms to pinpoint their target.

Reliance on systems unable to guarantee compensation for current drift seems to be rather unlikely for those turtles, like leatherbacks, that drift with the currents for a long time, ranging over vast distances (Fig. 4, Luschi et al. submitted(a)). At every reproductive season, these turtles face the same navigational problems of late juveniles, i.e. how to find their way back to their nesting (and natal) area, after 2 or 3 years of long-distance, mostly passive wanderings. The mechanisms they use are still totally unknown, unless we assume that in these species a position-fixing mechanism, not available to other turtles, is operating.

The first results obtained by studying the relationships between ocean currents and turtle spatial behaviour have started to produce a breakthrough in our understanding of sea turtle oceanic movements. Modern technology presently allows researchers to make

further important steps on this line. Detailed and meaningful post-hoc analysis can be done by integrating the findings obtained by satellite tracking sea turtles (and other marine migrants as well) with the available remote sensing data. This approach has recently allowed most useful insights into the determinants of long-distance turtle movements, and can be expected to provide further exciting results when applied to previously tracked journeys showing unexplained phenomena such as the occurrence of migratory corridors (Morreale et al. 1996, Luschi et al. 1998). In addition, attempts could be made to monitor current action while tracking the animals. A new generation of satellite-linked instruments has recently been developed, allowing the collection of useful environmental, physiological and behavioural data during animal tracking. Among these, the compass directions held by the moving animal is an important parameter to record in order to estimate the drift induced by currents (as well as to reconstruct fine-scale movements between successive satellite fixes). Whatever be the approach chosen, the findings reviewed in the present survey clearly show that any effort to study the relationships between sea turtle movements and oceanographic features is likely to be most fruitful and rewarding in the near future.

Acknowledgements – Part of the researches reported in the present paper were financed by grant awards from the Accademia Nazionale dei Lincei, the Italian Space Agency, the Natural Environmental Research Council of the UK (NERC) and from the Department of the Environment, Transport and Regions (DETR). Giacomo Santini (Florence) and Robert Marsh (Southampton) developed the model of Ascension turtle migrations.

References

- Åkesson, S., Broderick, A. C., Glen, F. et al. 2003. Navigation by green turtles, which strategy do displaced adults use to find Ascension Island? – *Oikos* 103: 363–372.

- Alerstam, T. 1979. Optimal use of wind by migrating birds: combined drift and overcompensation. – *J. Theor. Biol.* 79: 341–353.
- Balazs, G. H. 1994. Homeward bound: satellite tracking of hawaiian green turtles from nesting beaches to foraging pastures. – In: Schroeder, B. A. and Witherington, B. E. (eds), *Proc. 13th Ann. Symp. on Sea Turtle Biology and Conservation*. NOAA Tech Memo NMFS-SEFSC-341., pp. 205–208.
- Balazs, G. H., Craig, P., Winton, B. R. and Miya, R. K. 1994. Satellite telemetry of green turtles nesting at French Frigate Shoals, Hawaii, and Rose Atoll, American Samoa. – In: Bjorndal, K. A., Bolten, A. B., Johnson, D. A. and Eliazar, P. J. (eds), *Proc. 14th Ann. Symp. on Sea Turtle Biology and Conservation*. NOAA Tech Memo NMFS-SEFSC-351., pp. 184–187.
- Beavers, S. C. and Cassano, E. R. 1996. Movements and dive behavior of a male sea turtle (*Lepidochelys olivacea*) in the eastern tropical Pacific. – *J. Herpetol.* 30: 97–104.
- Bentivegna, F. 2002. Intra-Mediterranean migrations of loggerhead sea turtles monitored by satellite telemetry. – *Mar. Biol.* 141: 795–800.
- Bjorndal, K. A. 1997. Foraging ecology and nutrition of sea turtles. – In: Lutz, P. L. and Musick, J. A. (eds), *The biology of sea turtles*. CRC Press, pp. 199–232.
- Bowen, B. W. and Karl, S. A. 1997. Population genetics, phylogeography, and molecular evolution. – In: Lutz, P. L. and Musick, J. A. (eds), *The biology of sea turtles*. CRC Press, pp. 29–50.
- Bowen, B. W., Abreu-Grobois, F. A., Balazs, G. H. et al. 1995. Trans-Pacific migrations of the loggerhead turtle demonstrated with mitochondrial DNA markers. – *Proc. Natl. Acad. Sci. U. S. A.* 92: 3731–3734.
- Carr, A. 1984. The sea turtle. – Univ. of Texas Press.
- Carr, A. 1987. New perspectives on the pelagic stage of sea turtle development. – *Conserv. Biol.* 1: 103–121.
- Carr, A. and Meylan, A. B. 1980. Evidence of passive migration of green turtle hatchlings in sargassum. – *Copeia* 162: 366–368.
- Carr, A., Carr, M. H. and Meylan, A. B. 1978. The ecology and migrations of sea turtles. 7. The West Caribbean green turtle colonies. – *Bull. Am. Mus. Nat. Hist.* 162: 1–46.
- Cheng, I. J. 2000. Post-nesting migrations of green turtles (*Chelonia mydas*) at Wan-An Island, Penghu Archipelago, Taiwan. – *Mar. Biol.* 137: 747–754.
- Collard, S. B. 1990. The influence of oceanographic features on post-hatchling sea turtle distribution and dispersion in the pelagic environment. – In: Richardson, J. I., Richardson, T. H. and Donnelly, M. (eds), *Proc. 10th Ann. Symp. on Sea Turtle Biology and Conservation*. NOAA Tech. Memo. NMFS-SEFSC-278., pp. 111–114.
- Collard, S. B. and Ogren, L. H. 1990. Dispersal scenarios for pelagic post-hatchling sea turtles. – *Bull. Mar. Sci.* 47: 233–243.
- Dellinger, T. and Freitas, C. 2000. Movements and diving behaviour of pelagic stage loggerhead sea turtles in the North Atlantic: preliminary results obtained through satellite telemetry. – In: Kalb, H. J. and Wibbels, T. (eds), *Proc. 19th Ann. Symp. on Sea Turtle Biology and Conservation*. NOAA Tech. Memo. NMFS-SEFSC-443, pp., pp. 155–157.
- Dingle, H. 1996. *Migration*. – Oxford Univ. Press.
- Eckert, S. A. and Sarti, L. 1997. Distant fisheries implicated in the loss of the world's largest leatherback nesting population. – *Mar. Turt. Newsl.* 78: 2–7.
- Eckert, S. A., Eckert, K. L., Ponganis, P. and Kooyman, G. L. 1989. Diving and foraging behaviour of leatherback sea turtles (*Dermochelys coriacea*). – *Can. J. Zool.* 67: 2834–2840.
- Ellis, D. M., Balazs, G. H., Gillmartin, W. G. et al. 2000. Short-range reproductive migrations of hawksbill turtles in the Hawaiian Islands as determined by satellite telemetry. – In: Abreu-Grobois, F. A., Briseño-Dueñas, R., Márquez, R. and Sarti, L. (eds), *Proc. 18th Ann. Symp. on Sea Turtle Biology and Conservation*. NOAA Tech. Memo. NMFS-SEFSC 436., pp. 252–253.
- Gründlingh, M. L. 1978. Drift of a satellite-tracked buoy in the southern Agulhas Current and Agulhas Return Current. – *Deep-Sea Res.* 25: 1209–1224.
- Gründlingh, M. L. 1988. Review of cyclonic eddies in the Mozambique Ridge Current. – *S. Afr. J. Mar. Sci.* 6: 193–206.
- Hatase, H., Takai, N., Matsuzawa, Y. et al. 2002. Size-related differences in feeding habitat use of adult female loggerheads *Caretta caretta* around Japan determined by stable isotope analyses and satellite telemetry. – *Mar. Ecol. Prog. Ser.* 233: 273–281.
- Hays, G. C. and Marsh, R. 1997. Estimating the age of juvenile loggerhead sea turtles in the North Atlantic. – *Can. J. Zool.* 75: 40–46.
- Hays, G. C., Luschi, P., Papi, F. et al. 1999. Changes in behaviour during the internesting period and postnesting migration for Ascension Island green turtles. – *Mar. Ecol. Prog. Ser.* 180: 263–273.
- Hays, G. C., Åkesson, S., Broderick, A. C. et al. 2001a. The diving behaviour of green turtles undertaking oceanic migration to and from Ascension Island: dive durations, dive profiles and depth distribution. – *J. Exp. Biol.* 204: 4093–4098.
- Hays, G. C., Broderick, A. C., Glen, F. et al. 2001b. The movements and submergence behaviour of male green turtles at Ascension Island. – *Mar. Biol.* 139: 395–399.
- Hays, G. C., Broderick, A. C., Godley, B. J. et al. 2002. Bi-phasal long-distance migrations in green turtles. – *Anim. Behav.* 64: 895–898.
- Healey, M. C., Thomson, K. A., Leblond, P. H. et al. 2000. Computer simulations of the effects of the Sitka eddy on the migration of sockeye salmon returning to British Columbia. – *Fisheries Oceanogr.* 9: 271–281.
- Hendrickson, J. R. 1980. The ecological strategies of sea turtles. – *Am. Zool.* 20: 597–608.
- Horrocks, J. A., Vermeer, L. A., Krueger, B. et al. 2001. Migration routes and destination characteristics of post-nesting hawksbill turtles satellite-tracked from Barbados, West Indies. – *Chelonian Conserv. Biol.* 4: 107–114.
- Hughes, G. R. 1974. The sea turtles of South-East Africa. II. The biology of the Tongaland loggerhead turtle *Caretta caretta* with comments on the leatherback turtle *Dermochelys coriacea* and the green turtle *Chelonia mydas* in the study region. – *Rep. 36, Oceanogr. Res. Inst.*
- Hughes, G. R., Luschi, P., Mencacci, R. and Papi, F. 1998. The 7000-km oceanic journey of a leatherback turtle tracked by satellite. – *J. Exp. Marine Biol. Ecol.* 229: 209–217.
- Lohmann, K. J. and Lohmann, C. M. F. 1996. Detection of magnetic field intensity by sea turtles. – *Nature* 380: 59–61.
- Luschi, P., Papi, F., Liew, H. C. et al. 1996. Long-distance migration and homing after displacement in the green turtle (*Chelonia mydas*): a satellite tracking study. – *J. Comp. Physiol.* 178A: 447–452.
- Luschi, P., Hays, G. C., Del Seppia, C. et al. 1998. The navigational feats of green sea turtles migrating from Ascension Island investigated by satellite telemetry. – *Proc. R. Soc. Lond. B* 265: 2279–2284.
- Luschi, P., Åkesson, S., Broderick, A. C. et al. 2001. Testing the navigational abilities of oceanic migrants: displacement experiments on sea turtles. – *Behav. Ecol. Sociobiol.* 50: 528–534.
- Luschi, P., Sale, A., Mencacci, R. et al. submitted(a). Current transport in leatherback sea turtles (*Dermochelys coriacea*) wandering in the ocean. – *Proc. R. Soc. Lond. B*.
- Luschi, P., Hughes, G. R., Mencacci, R. et al. submitted(b). Satellite tracking of migrating loggerhead sea turtles (*Caretta caretta*) displaced in the open sea. – *Mar. Biol.*

- Lutcavage, M. E. 1996. Planning your next meal: leatherback travel routes and ocean fronts. – In: Keinath, J. A., Barnard, D. E., Musick, J. A. and Bell, B. A. (eds), Proc. 15th Ann. Symp. on Sea Turtle Biology and Conservation. NOAA Tech. Memo. NMFS-SEFSC-378., pp. 174–178.
- Morreale, S. J., Standora, E. A., Spotila, J. R. and Paladino, F. V. 1996. Migration corridor for sea turtles. – *Nature* 384: 319–320.
- Musick, J. A. and Limpus, C. J. 1997. Habitat utilization and migration in juvenile sea turtles. – In: Lutz, P. L. and Musick, J. A. (eds), *The biology of sea turtles*. CRC Press, pp. 137–164.
- Nichols, W. J., Resendiz, A., Seminoff, J. A. and Resendiz, B. 2000. Transpacific migration of a loggerhead turtle monitored by satellite telemetry. – *Bull. Mar. Sci.* 67: 937–947.
- Olson, D. B., Hitchcock, G. L., Mariano, A. J. et al. 1994. Life on the edge: marine life and fronts. – *Oceanogr. Soc. J.* 7: 52–60.
- Papi, F. 1992. General aspects. – In: Papi, F. (ed.), *Animal homing*. Chapman & Hall, pp. 1–18.
- Papi, F. and Luschi, P. 1996. Pinpointing ‘Isla Meta’: the case of sea turtles and albatrosses. – *J. Exp. Biol.* 199: 65–71.
- Papi, F., Luschi, P., Crosio, E. and Hughes, G. R. 1997. Satellite tracking experiments on the navigational ability and migratory behaviour of the loggerhead turtle *Caretta caretta*. – *Mar. Biol.* 129: 215–220.
- Papi, F., Luschi, P., Akesson, S. et al. 2000. Open-sea migration of magnetically disturbed sea turtles. – *J. Exp. Biol.* 203: 3435–3443.
- Plotkin, P. T., Byles, R. A., Rostal, D. C. and Owens, D. W. 1995. Independent versus socially facilitated oceanic migrations of the olive ridley, *Lepidochelys olivacea*. – *Mar. Biol.* 122: 137–143.
- Polovina, J. J., Kobayashi, D. R., Parker, D. M. et al. 2000. Turtles on the edge: movement of loggerhead turtles (*Caretta caretta*) along oceanic fronts, spanning longline fishing grounds in the central North Pacific, 1997–1998. – *Fish. Oceanogr.* 9: 71–82.
- Renaud, M. L., Carpenter, J. A., Williams, J. A. and Landry, A. M. J. 1996. Kemp’s ridley sea turtle (*Lepidochelys kempii*) tracked by satellite telemetry from Louisiana to nesting beach at Rancho Nuevo, Tamaulipas, Mexico. – *Chelonian Conserv. Biol.* 2: 108–109.
- Richardson, W. J. 1990. Wind and orientation of migrating birds: a review. – In: Berthold, P. (ed.), *Orientation in birds*. Birkahuser Verlag, pp. 226–249.
- Sakamoto, W., Bando, T., Arai, N. and Baba, N. 1997. Migration paths of the adult female and male loggerhead turtles *Caretta caretta* determined through satellite telemetry. – *Fish. Sci.* 63: 547–552.
- Stoneburner, D. L. 1982. Satellite telemetry of loggerhead sea turtle movement in the Georgia Bight. – *Copeia* 1982: 400–408.
- Walker, T. A. and Parmenter, C. J. 1990. Absence of a pelagic phase in the life cycle of the flatback turtle, *Natator depressa* Garman. – *J. Biogeogr.* 17: 275–278.
- Wallraff, H. G. 1991. Conceptual approaches to avian navigation systems. – In: Berthold, P. (ed.), *Orientation in birds*. Birkhauser, pp. 128–165.
- Witham, R. M. 1980. The ‘lost years’ question in young sea turtles. – *Am. Zool.* 20: 525–530.
- Witherington, B. E. 2002. Ecology of neonate loggerhead turtles inhabiting lines of downwelling near a Gulf Stream front. – *Mar. Biol.* 140: 843–853.