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Influence of oceanic factors on long-distance movements of loggerhead sea turtles displaced in the southwest Indian Ocean

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Abstract The routes of five satellite-tracked loggerhead turtles (*Caretta caretta*), subjected to an experimental translocation away from their usual migratory routes, have been analysed in relation to the concurrent oceanographic conditions. Remote sensing data on sea surface temperature and height anomalies, as well as trajectories of surface drifters were used, to get simultaneous information on the currents encountered by the turtles during their long-range oceanic movements. Turtles mostly turned out to move in the same direction as the main currents, and their routes were often influenced by circulation features they encountered. A comparison between turtle ground speeds with that of drifters shows that in several instances, the turtles did not drift passively with the currents but contributed actively to the overall movement. Two turtles embarked on an oceanic crossing, probably induced by seasonal changes in surface temperatures, a crossing that was largely determined by the main currents existing in the area.

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Introduction

Over the last two decades, the study of marine vertebrate movements has greatly benefited from the remarkable development of several tracking techniques allowing reconstruction of animal routes even in remote regions otherwise not readily accessible to humans (e.g. Andrews et al. 2008; Bestley et al. 2008; Shillinger et al. 2008). For air-breathing animals such as sea turtles, satellite-based radio telemetry has become the state-of-the-art technique, with a wealth of data now available on the routes followed by the various species in various geographical areas, in different stages of their life cycle and under both natural and experimental conditions (Godley et al. 2008; Luschi et al. 2003a).

Since movements in the ocean never occur in a stationary medium, the reconstructed, ground-related trajectories of turtles derive from two different components: that produced by the turtles' active swimming and that induced by the water movement itself, i.e. the current drift (for review see Luschi et al. 2003a). The relative importance of the two components varies depending on a number of factors such as the turtle feeding activity and motivations, the strength of oceanic currents or even the ontogenetic stage of the turtles, with the youngest stages being more strongly influenced by currents (e.g. Hays and Marsh 1997).

For ocean-dwelling species such as the leatherback turtle (*Dermochelys coriacea*), a fundamental role for marine currents in affecting their movements has recently been documented, thanks to the fruitful integration of the satellite tracking of animal movements and the remote sensing of ocean current features. This powerful combination has allowed researchers to document that leatherback movements in the Indian and Atlantic Oceans are actually strongly dependent on the prevailing marine currents, up to the point that turtles often appear to be passively

transported even over very long distances (Gaspar et al. 2006; Lambardi et al. 2008; Luschi et al. 2003b; Shillinger et al. 2008). Similar conclusions have been drawn for other cases of turtles spending long periods in the oceanic environment for foraging purposes, like juvenile loggerheads (Bentivegna et al. 2007; Revelles et al. 2007).

A relevant influence of main currents may not be surprising for pelagic turtles, which have an intimate link with the ocean circulation that is responsible for the distribution of the planktonic prey of these species. A different condition pertains to those turtle species which reside in coastal or neritic waters and cross the open sea only to migrate towards specific goals such as a breeding or a foraging area. In these cases, oceanic currents may have a detrimental effect since their drift can deflect the turtle courses, often decreasing their overall navigational performances (Girard et al. 2006; Luschi et al. 1998, 2007). In particular, this issue is of great interest for the adults of those species, such as loggerhead turtles and green turtles (*Chelonia mydas*), which periodically shuttle between their nesting beaches and individually specific feeding areas where they spend their inter-reproductive period. Knowledge of the extent to which turtle movements are affected by oceanic currents would also be important for the development of more suitable conservation plans needed to protect these endangered species. To date, however, the issue of evaluating the influence exerted by ocean currents and eddies on the long-distance movements of these turtles has been addressed in only a few cases (Girard et al. 2006; Luschi et al. 1998, 2007; Troëng et al. 2005).

In the present study, we used remote sensing data of current features to analyse the movements of five South African loggerhead turtles that had been artificially displaced in the open Indian Ocean at the beginning of their postnesting migration towards their foraging sites. Displacement experiments constitute a classical paradigm to study animal navigation in the field (Lohmann et al. 2008), as they offer the advantage of allowing researchers to study animals motivated to return to a specific site (the site of capture or, as in the present case, the foraging grounds), i.e. in a condition in which the turtles have to rely on their navigational abilities to overcome the experimental treatment. Assessment of current influence in these cases is expected to be particularly informative as it may hopefully provide insights into the turtles' actual navigational abilities (Girard et al. 2006; Luschi et al. 2007).

In a previous report (Luschi et al. 2003c), a detailed analysis of the spatial and diving behaviour of these displaced turtles was performed. In the specific experimental protocol we employed, the precise location of the foraging site of each displaced turtle was not known with certainty, but the general geographical distribution of the foraging sites for this population (along mainland Africa from

Mozambique up to southern Somalia, around Madagascar) could be inferred with reasonable accuracy from the many previous recoveries of flipper-tagged nesting females (see Luschi et al. 2003c for details). This is usually considered to be sufficient information to meaningfully interpret the navigational behaviour of displaced animals (e.g. Thorup et al. 2007). The three displaced turtles were able to relocate their presumed feeding grounds after displacement (although following circuitous routes not immediately directed towards the target) or at least to find a suitable foraging site in the neritic environment. The other two turtles, conversely, seemed to have completely failed to reach their coastal feeding areas and started long-distance oceanic wanderings leading them to cross the entire Indian Ocean. However, the analysis of the pure tracking data failed to provide a clear interpretation of some aspects of the turtles' behaviour, such as sudden changes in course directions or extended overlaps of the routes of different turtles (Luschi et al. 2003c). Here, we report additional information that shows that ocean currents, eddies and water temperature sometimes had a marked influence on the movements displayed by the tracked turtles, either by shaping their course to the target or by directly determining their movements in the open ocean.

Materials and methods

The turtles tracked belonged to the population nesting in the Maputaland Marine Reserve in KwaZulu-Natal, South Africa. Five females were captured at the end of their reproductive season and equipped with Argos-linked satellite transmitters in 1998 (turtles A1 and A2) and in 1999 (turtles B1, B2 and B3). A detailed description of the experimental procedures and of the analysis of Argos data can be found in Luschi et al. (2003c).

We have analysed the reconstructed turtle routes in relation to the main oceanographic features of the areas crossed. In particular, we used contemporaneous remote sensing data on sea surface temperature (SST), sea surface height anomalies (SSHA) and absolute geostrophic velocities (AGV).

Sea surface height anomalies images, derived from the measurements made by the TOPEX/Poseidon satellite, provide information about temporal variations in direction and speed of the main currents, thus allowing one to identify the occurrence of prominent mesoscale oceanographic features, such as current rings or eddies (Luschi et al. 2003b). The SSHA images are supplied daily from the Colorado Center for Astrodynamic Research (http://www-ccar.colorado.edu/ ~realtime/global-historical_vel/), 10-day averaged, with a resolution of 0.5° of latitude and longitude. SST images derive from multi-channel radiation sensed by the advanced

very high resolution radiometer (AVHRR), on board the NOAA 14 polar-orbiting satellite that measures infrared radiance of the ocean surface. SST data are processed into images of sea surface temperature with 1/8° spatial resolution and are available from the Naval Research Laboratory Stennis Space Center (http://www7320.nrlssc.navy.mil/altimetry/).

Absolute geostrophic velocities data were obtained from the database of dynamic topography measurements available from AVISO (Archiving, Validation and Interpretation of Satellite Oceanographic data, http://www.aviso.oceanobs.com/). Data were downloaded from Live Access Server (http://las.aviso.oceanobs.com/las/servlets/datasets) in the form of weekly maps of current fields (see e.g. Fig. 3), in order to get a portrayal of the general currents in the areas visited by the turtles. AVISO also provides numerical information on the zonal and meridional components of geostrophic currents, but we chose not to take these values into account to evaluate the currents' specific effects on tracked turtles, given that AVISO processing do not take the effect of winds into account (Dibarboure et al. 2009). The strength of the currents is therefore underestimated since the current's Ekman component is disregarded. Furthermore, these estimations are not reliable close to the coast, where turtles were tracked for long periods.

Finally, in order to obtain a more quantitative estimate of the drifting force associated with the presence of currents, we also compared turtle routes with the tracks of Lagrangian surface drifting buoys linked to the Argos system and tracked in the same region as the turtles. These drifters are designed to track near surface currents, i.e. those present in the upper (<100 m) layers of the water column, where ocean-moving, hard-shelled turtles spend most of their time (e.g. Polovina et al. 2004; Hays et al. 2001). For this analysis, we have only relied on drifters passing through a given region no more than 15 days before or after the turtles themselves. Drifter data were obtained from the Atlantic Oceanographic and Meteorological Laboratory (http://www.aoml.noaa.gov/phod/trinanes/xbt.html) that provides six-hourly interpolated positions.

Results

General turtle movements

As mentioned earlier, details of the turtle routes have been reported previously in a different context (Luschi et al. 2003c). Briefly, turtle A1 was released on 27 February 1998, south of Madagascar (Fig. 1a). After some days spent circulating in the release site region, the turtle headed towards the west, crossing the southern mouth of the Mozambique Channel and reaching the continental coast.

She then swam northwards along the African coast, until reaching a small coastal area off the town of Beira, Mozambique. Turtle A2 was released on 1 March 1998, east of Madagascar, near the island of La Reunion (Fig. 1a). After a short stay close to the release site, the turtle headed northwest, reaching the eastern Madagascar coast. She then circumnavigated the southern part of Madagascar before heading decidedly westwards towards the African mainland. This part of her route was surprisingly similar to that displayed by turtle A1 in the same area, several weeks before. When in the middle of the Mozambique Channel, however, the turtle abruptly changed her direction of movement to start a northwards leg leading her to the Mozambican coastline that she subsequently followed up to Zanzibar Island on the Tanzanian coast, with a detour to the Comoros Islands on the way.

The second group of turtles was released at the same time off Tanzania, on 18 February 1999 (Fig. 1b). Initially, all turtles moved in a northwards direction but, after a while, turtle B1 started moving southwards and found her presumed feeding grounds close to the coast, in the proximity of Mafia Island, where she remained for 7 months. Turtle B2 and B3 performed long-distance, often circuitous movements in the open sea, which led them to cross nearly the entire Indian Ocean from west to east. The two turtles thus covered more than 13,000 km in 10–11 months.

Influence of oceanic factors on turtle routes

Turtle A1

The initial westwards segment covered from the release site south of the Madagascar up to the continental coast coincided with the northern part of the retroflection loop of the East Madagascar Current's southern branch (Lutjeharms 1988; Siedler et al. 2006). During this leg, which was covered at a mean speed of 1.7 km/h, the path taken by turtle A1 was influenced by the anti-clockwise rotation of an eddy in the middle of the Mozambique Channel (Fig. 2a). The movement made by the turtle agrees very well with the currents along her path at the time, as shown in the corresponding AGV map (Fig. 2b). In addition, the southern mouth of the Mozambique Channel is usually characterised by a well-developed, zonal SST front (Lutjeharms 2006) that have been used by the turtle as a travel guide in this part of the trip.

When approaching the African mainland, the turtle started moving in a clockwise circuit without immediately reaching the coast. This apparently enigmatic behaviour may have derived from the influence of the well-documented clock-wise rotation known as the Delagoa Bight eddy, intermittently present in the region (Lutjeharms and Jorge da Silva 1988). It is evident in the SSHA and AVG
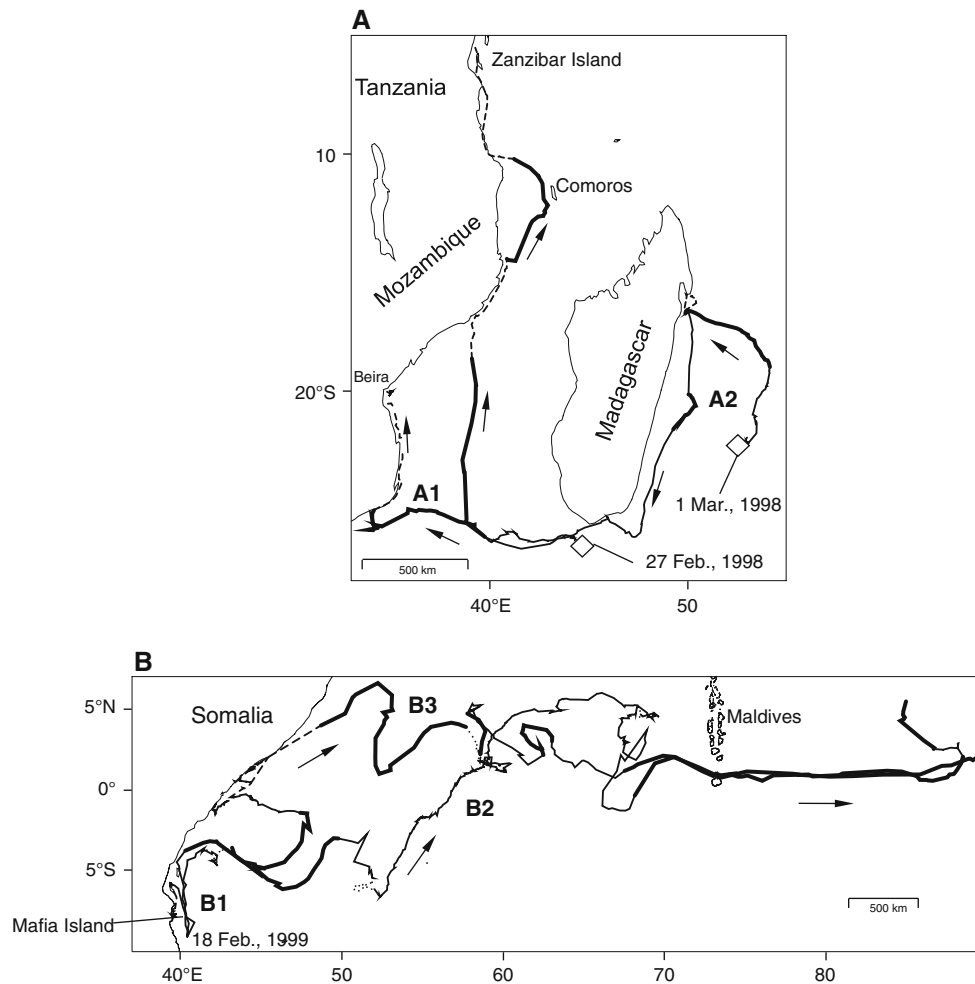
Fig. 1 Reconstructed tracks of turtles *A1* and *A2* (**a**) and *B1–B3* (**b**) after displacement. Different segments of the routes are plotted in different ways according to the relationship of a given segment with the oceanic currents. *Thick lines* indicate the segments covered in accordance with the current flow, as estimated from contemporaneous surface trajectories or SSHA images or AVISO charts; *thin lines* represent segments in which turtles moved independently from the currents, because currents were either weak or not in accordance with the turtle's course; *dotted lines* those segments in which turtles moved against the currents. For *dashed* segments, no reliable information on currents is available. *Diamonds* indicate the release sites. See text for further details

charts (Fig. 2). The speed of travel during this loop increased to 2.4 km/h. After reaching the coast to the north of this Bight, turtle A1 closely followed the coastline until the arrival at her presumed feeding grounds at about 20°S. No current assessments are available for this segment which was covered by the turtle at a mean ground speed of 1.4 km/h.

Turtle A2

The initial northern movement of this turtle occurred in a region where no strong currents are known to occur nor are any shown in AGV maps (Fig. 3a), and it is likely that the recorded movement, done at a mean speed of 1.9 km/h, was largely due to the turtle actively swimming. The northwest bend of her route from about 19°S (Fig. 4) was due to her encounter with the westwards-directed southern branch of

the South Equatorial Current. This is confirmed by the concomitant westwards movement of a surface drifter tracked during this period (no. 9729821; Fig. 4), which moved at a much lower speed than the turtle (0.9 vs. 2.2 km/h on average). Subsequently, the turtle mainly followed the direction of the southern branch of the East Madagascar Current which flows southwestwards parallel to the eastern coastline of Madagascar (Lutjeharms 2006). SSHA images show that at 21°S, the turtle passed though an eddy with a clockwise circulation. The influence of this circulation is seen as a slight eastwards and then westwards change in the path of the turtle (Fig. 1). Southeast of Madagascar the turtle seems to have been forced onto the continental shelf by the strong northeastwards currents existing here, which are not shown in the contemporary AVG charts. The turtle came close inshore here in a region known for its upwelling and increased biological productivity (DiMarco et al. 2000;
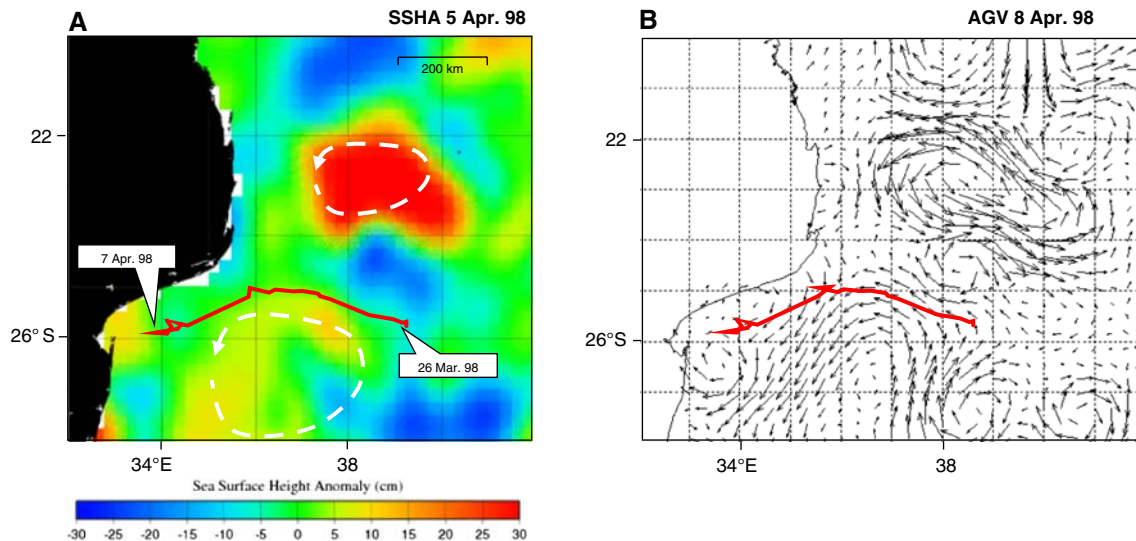
Fig. 2 Final part of the crossing of the Mozambique Channel by turtle A1 superimposed on **a** an SSHA image and **b** the corresponding AVG chart. The presence of eddies is indicated by the *dashed arrows* in correspondence of the large anomalies in **a** as well as by the looping current flow in **b**, e.g. in the central Mozambique channel. The SSHA image refers to the period 27 March–5 April 1998; the AVG chart to the period 2–8 April 1998

Lutjeharms and Machu 2000; Machu et al. 2002), without, however, spending extra time feeding here. During her westwards leg across part of the mouth of the Mozambique Channel, turtle A2's journey was at the border of two large eddies (Fig. 3b) and was slightly, but still noticeably, affected by the local eddy field. The general impression, from the combination of the turtle's movement and the contemporaneous current portrayal, therefore, is that this turtle was swimming strongly and with a defined direction, but was pushed off-track only slightly by eddies through which she had to pass.

The subsequent sudden change of direction displayed by the turtle in the middle of the Mozambique Channel stems from her encounter with a couple of anomalies residing in the middle of the Channel (Fig. 3c), whose strong northwards-setting currents could have also influenced the turtle's successive path leading her northwards (Fig. 3d). Also, her successive detour to the Comoros Islands and back to the African mainland was done strictly in accordance with the currents present in the area, as is evident in the corresponding AGV map (Fig. 3e). Finally, at the end of her travels, turtle A2 moved closely along the coast following the general flow of the current known to exist in the area (Lutjeharms 2006).

Turtle B1

Immediately after her release, turtle B1 headed north, covering a segment of 411 km following the branch of the equatorwards East African Coastal Current that exists only up to about 4°S during April, the end of the northeast monsoon season (Lutjeharms 2006). This current is shown in the AVG charts (Fig. 5) but is known to flow northwards at a lower speed than the turtle's one (mean 2.9 km/h). Having reached the northern Zanzibar coast, the turtle reversed her route to swim close inshore in the opposite direction as the main offshore current until she reached Mafia Island. The precise localizations of currents so close inshore is not possible with the altimetric dataset at our disposal.

Turtles B2 and B3

Like turtle B1, turtles B2 and B3 started their movements from the release site heading north with the East African Current (Fig. 5). Their average speed in this segment was 2.8–3.2 km/h, respectively, which is higher than the normal speed of the current. They then found themselves at a latitude of about 4°S where the strong Somali Current, flowing southwestwards along the coast, could have blocked their progress at this time of year, forcing them to move offshore. The two turtles turned eastwards with the southeastwards setting South Equatorial Counter Current, as clearly shown in the AVG charts (Fig. 6). Subsequently, both turtles executed a counter-clockwise motion very similar to that of a drifter (no. 9706574) tracked in the same region a few days later (Fig. 6). For both turtles, the speed of their movement was much higher than that of the drifter in this leg (mean 2.5 vs. 1.2 km/h for Turtle B2; 2.7 vs. 1.1 km/h for Turtle B3), indicating that the turtles were swimming actively at this time, although largely parallel to the ambient currents.

Later on, turtle B3 reached the Somali coast and then moved northeastwards crossing the Equator, somewhat contrary to the expected average direction of the coastal Somali Current at this time of year. Upon leaving the coast,
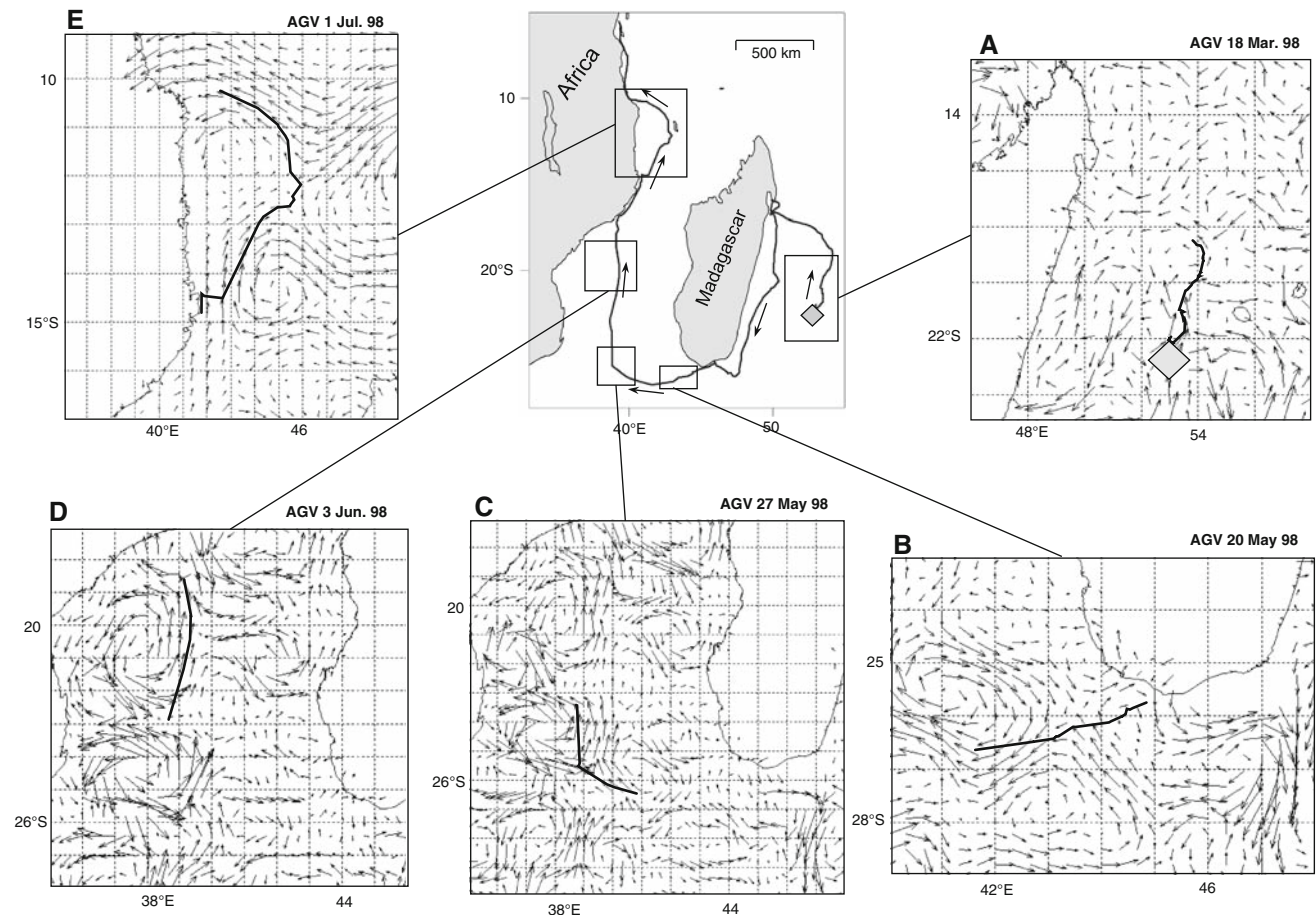
Fig. 3 Segments of turtle A2's route superimposed on the pertinent AVG charts showing the main surface currents. The dates for which AVG charts have been obtained are also shown

she then encountered a large and intense anti-cyclonic eddy, whose clockwise currents made her reverse her direction (Fig. 7). After that, turtle B3 headed northeastwards again along the main flow and then in a prevailing easterly direction like turtle B2 (Fig. 1b), thus starting the crossing of the entire Indian Ocean along the Equator. This movement was occurred broadly within the eastwards-flowing Equatorial Counter Current, which, however, lay somewhat further north than could normally be expected during a fully developed northeast monsoonal current system. In the last 2 months of their transmissions, the routes of turtles B2 and B3 were largely coincident with each other as they followed the flow of the Equatorial Jet Current that flows at high speed in an eastwards direction in October–December at equatorial latitudes (Wyrtki 1973). Large parts of the oceanic routes of both turtles show a close resemblance with those of buoy no. 9806375 that was tracked in the same region some days later (Fig. 8). For instance, before reaching the Maldive Islands turtle B2's path several times crossed that of the drifter also moving at a similar speed (1.6 vs. 1.3 km/h). Conversely, the drifter moved more rapidly than the turtle during the following straight approach to

the Maldives and the subsequent eastwards leg, where the turtle moved on average at 2.9 km/h (excluding a 7-day stop at Huvadu atoll, Maldives) and the drifter at 3.8 km/h. The same holds true for turtle B3's linear segment approaching the Maldives, which was similar to the one of the same drifter and was covered at a similar speed (1.9 km/h for the turtle vs. 1.8 km/h for the drifter). Finally, even the very last part of turtle B2's travel was covered according to the prevailing currents, as shown in the corresponding AVG charts (Fig. 9). We therefore conclude that the two turtles mostly moved with the prevailing currents during their oceanic crossing.

This eastwards movement of both turtles reflected the zonal variation of surface temperature occurring during the tracking period. The SST fields along the equator showed a zonal shift from May to September 1999, with warmer waters occupying more and more easterly zones as the season advanced. The turtles accordingly moved eastwards conceivably following the warmer waters (see Fig. 1 in supplementary material). This pattern was particularly evident in turtle B2, who managed to remain always in waters of at least 28°C.
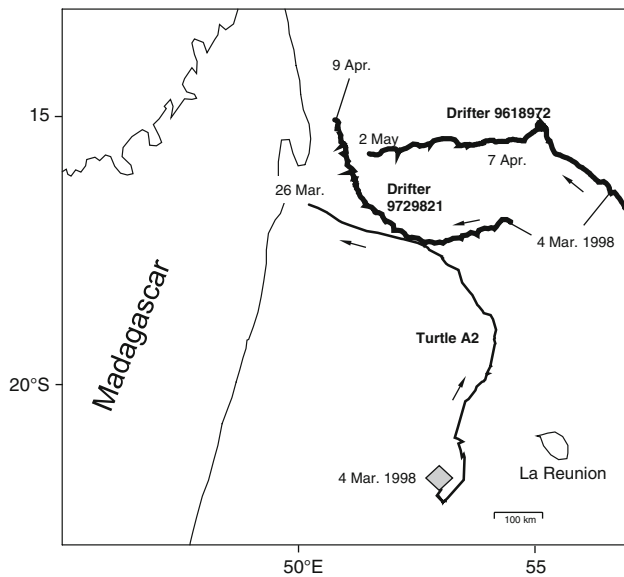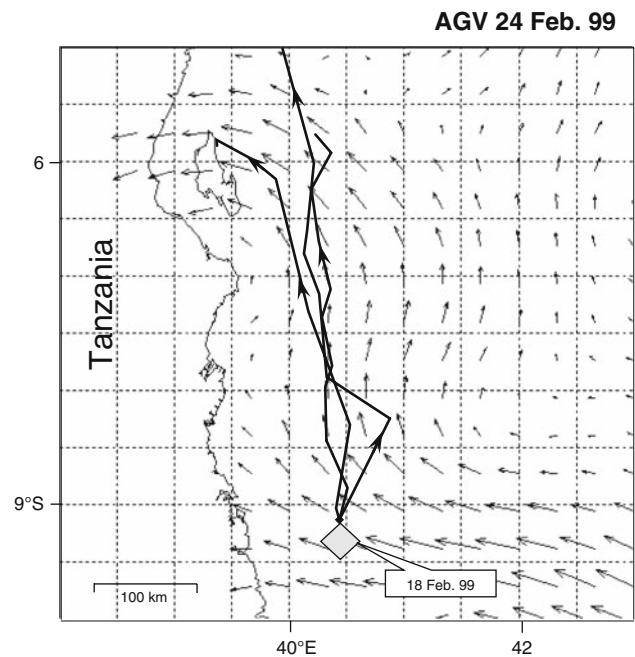
Fig. 4 Initial part of turtle A2's route (*thin line*) together with the contemporaneous trajectory of drifter no. 9729821 in the same area (*thick line*). The track of another drifter (no. 9618972) moving at a greater distance from the turtle is also shown to illustrate the general flow of the region


Fig. 5 Initial parts of the routes of turtles B1–B3 superimposed onto the contemporaneous AVG chart referring to 18–24 February 1999. The *diamond* indicates the release site

Discussion

The present analysis of the turtle routes after displacement in relation to concurrent ocean conditions has revealed a number of behavioural patterns of displaced turtles which were not readily evident after a simple analysis of their geographical movements tracked through the Argos system.

In general, turtles mostly moved in the same direction as the main currents of the areas they crossed, and we found only a few instances of movements clearly against the currents (Fig. 1). In some segments, in particular, the routes followed appear to have been heavily influenced by the oceanic features encountered. Clear examples of this pattern are found in the sudden northwards turn of turtle A2 in the middle of the Mozambique Channel (Fig. 2b), the strikingly similar curved path followed by turtles B2 and B3 after their initial straight movement (Fig. 5), the U-shaped turn of turtle B3 offshore of the Somali coast (Fig. 6), the final retroflection of turtle B2's route (Fig. 9). Also, in several other segments, the turtles moved in a direction coincident with that of the existing ocean currents. In all these cases, however, the turtles do not seem to have drifted passively with the currents and rather appear to have swum actively in the same direction of the main flow. This has been clearly shown for two route segments for which contemporaneous drifters were available: both for turtle A2's westwards leg towards Madagascar (Fig. 3) and for the earlier mentioned curved paths of turtles B2 and B3 (Fig. 5),

turtles turned out to move quicker than the drifter, most likely as a result of their active swimming. Turtle A1 was likely to move actively soon after release, albeit in a direction similar to the current flow. It is worth noting that the initial northwards move of turtle A2 as well as that of turtles B1-B3 was also partly due to the turtle actively swimming. If so, a pattern common to all displaced turtles seems to emerge, consisting in an active, directed response displayed after release.

A different situation is found in the oceanic crossing of turtles B3 and, especially, B2. Here, as already noticed by Luschi et al. (2003c), the main currents largely determined the observed paths. This is in quite a striking contrast with the initial response of these turtles upon release, which indeed was characterised by an active component. Most noticeably, the ground speed of turtle B2 in the oceanic legs is similar to that of a drifter which followed a similar trajectory (Fig. 7), which even seems to have moved more rapidly than the turtle itself. This prolonged transport with the flow, which in this region takes the form of jet currents (Wyrtki 1973), may have allowed the turtles to cross large areas with a limited energy expenditure, often reaching high ground speeds (up to nearly 3 km/h). It may be important to note here that these ocean-wide movements, which led turtles over 6,000 km away from the nesting beach, are hardly compatible with the life cycle of adult loggerhead turtles, which normally do not move so far away from their breeding area during the inter-reproductive period. The postnesting migrations of loggerheads are known

Fig. 6 Tracks of turtles B2 and B3 superimposed onto an AVG chart obtained for 31 March 1999 showing the main current flow in the area considered. The contemporaneous trajectory of drifter no. 9706574 (*thick line*) is also shown
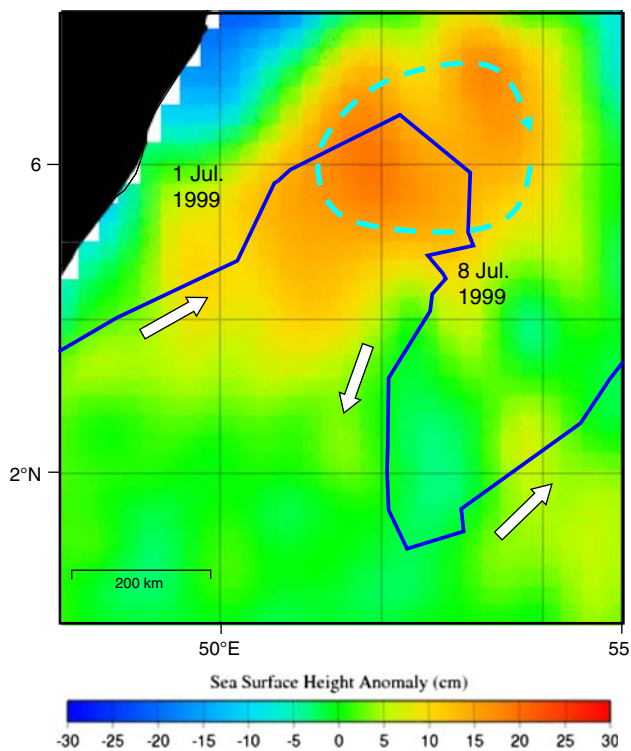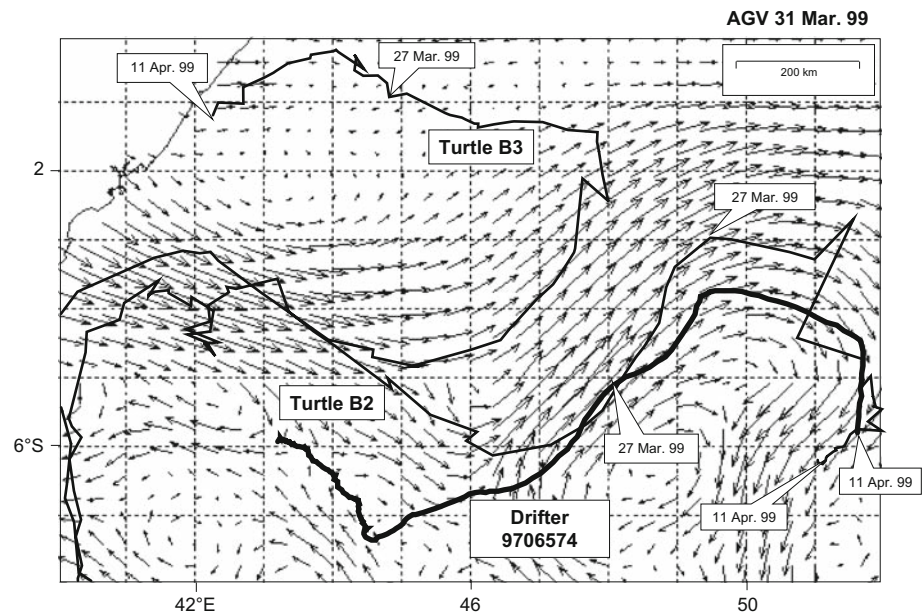
Fig. 7 Part of the track of turtle B2 superimposed onto an SSHA image showing an intense anomaly on 12 July 1999 (range 3–12 July). *White arrows* show the turtle's direction of movement

sometimes to extend for hundreds of kilometres, up to around 2,500 km (e.g. Hatase et al. 2002), but they remain confined to the same general geographical region as the breeding area. In the present case, the larger-scale movements shown were of a totally different nature (likely as a result of the displacement), deriving largely from a prolonged drift with the currents and being probably prompted

by the turtles' necessity to remain in warm waters to follow the seasonal zonal variation of sea surface temperatures.

It is quite difficult to compare the present findings with those obtained on other turtle species. Most studies on the oceanographic influences on turtle movements have been done on leatherback turtles (*Dermochelys coriacea*), whose routes have indeed been shown to be heavily affected by ocean currents (Gaspar et al. 2006; Lambardi et al. 2008; Luschi et al. 2003b), even when the tracked turtles maintained rather fixed headings (Shillinger et al. 2008). Leatherbacks, however, constitute a very different case from loggerheads: they are truly oceanic animals, spending most of their life wandering over immense oceanic areas and so any comparison with the loggerheads, which are more linked to neritic/coastal zones, is to be taken with caution (see also Luschi et al. 2006). Also, studied leatherbacks were tracked during their normal postnesting migrations and without any kind of experimental treatment.

The loggerheads of the present study were in a very special and demanding situation, having been subjected to long-range experimental displacements. Sounder comparisons can be made with other cases of turtles tracked while aiming at specific sites, like during the postnesting migrations directed towards a specific feeding area (Godley et al. 2008) or, again, after displacements. The effect of the currents on turtles in these situations has been investigated in some cases (Balazs 1994; Girard et al. 2006; Horrocks et al. 2001; Luschi et al. 1998, 2007; Sakamoto et al. 1997; Troëng et al. 2005), and turtles generally turned out to move actively, with their routes being largely independent, albeit affected to some extent, from the currents present in the area. Only three green turtles tracked by Troëng et al. (2005) during postnesting migration followed large circular
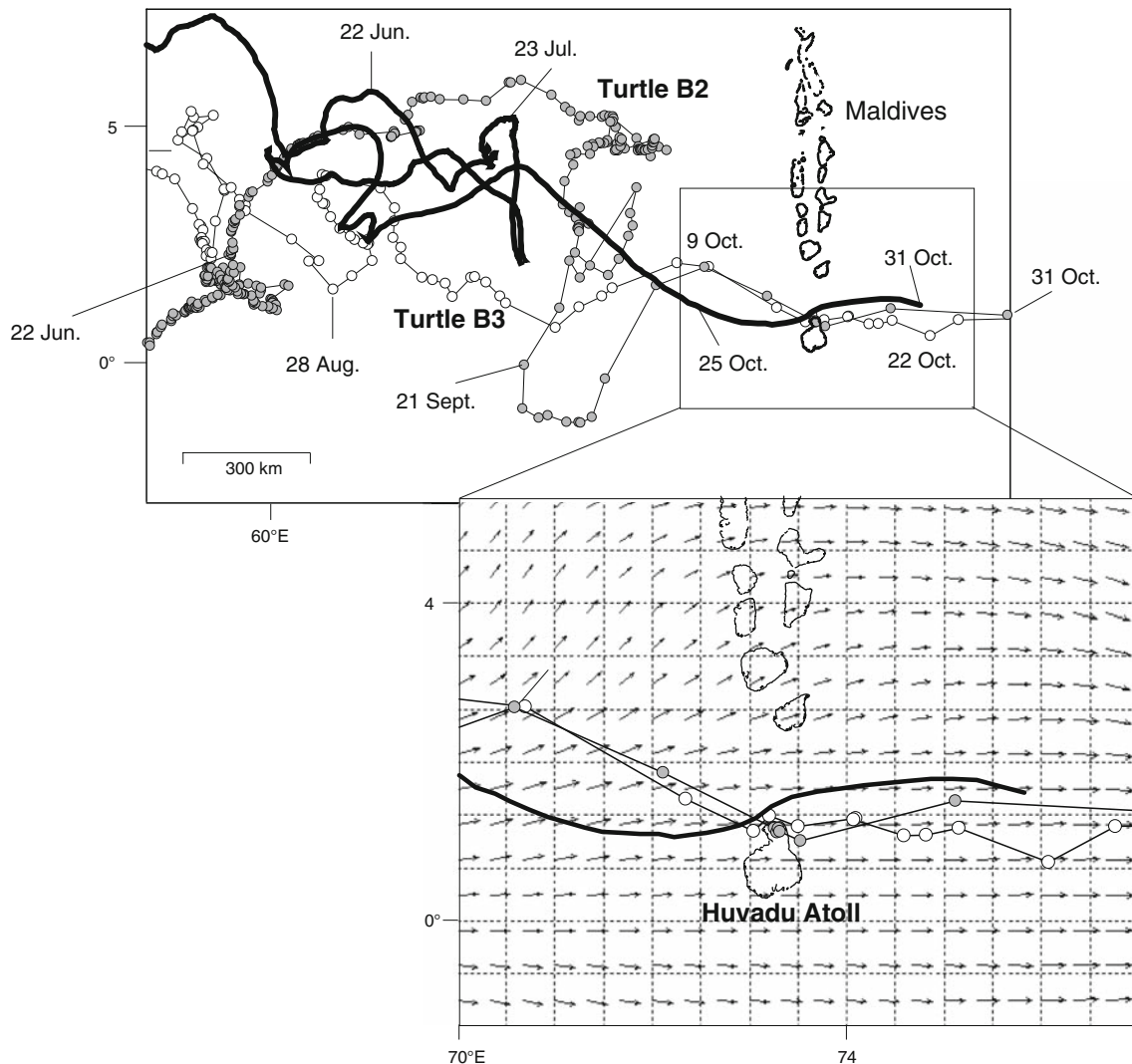
Fig. 8 Oceanic crossing and arrival at the Maldives of turtles B2 (*grey circles*) and B3 (*empty circles*) and the contemporaneous trajectory of surface drifter 980375 in the same region (*thick line*). The *inset* shows the turtles' final approach to Huvadu Atoll, Maldives superimposed on an AVG chart obtained for 20 October 1999

or semicircular paths corresponding to large SSHA. This resulted in apparently meaningless deflections from the expected migratory route towards their individually specific feeding grounds.

We started this oceanographic analysis with the main aim of drawing further inferences on the navigational abilities shown by the displaced turtles, besides those obtainable after a plain analysis of the spatial behaviour displayed (Luschi et al. 2003c). Indeed, considering the oceanographic factors involved in the turtle journeys has allowed us to reveal some aspects of turtle behaviour, such as the presence of prolonged periods of current-independent movements (Fig. 1), which likely derived from the turtles swimming actively. Since these movements were probably determined by the turtles' active orientation in a given direction, the turtles can therefore be assumed to have had some kind of information as to where to go at least during

some of these legs (e.g. in order to correct for the unwanted displacement from the usual migratory route). The presence of these active, oriented movements shows that these turtles were not just following the currents they encountered, but were rather aiming at reaching a specific area, possibly their foraging grounds, which they would have reached at the end of their postnesting migration had they not been experimentally displaced (see Luschi et al. 2003c for a further discussion).

Conversely, in the periods when the movements were largely dependent on current flows, the turtles were less reliant on their navigational abilities, and they may even have let themselves be drifted for long periods and over large distances, like in the ocean crossings of turtles B2 and B3. A clear effect of the current was noted also for the several changes in turtle course direction, like the abrupt turn in the middle of the Mozambique Channel of turtle A2
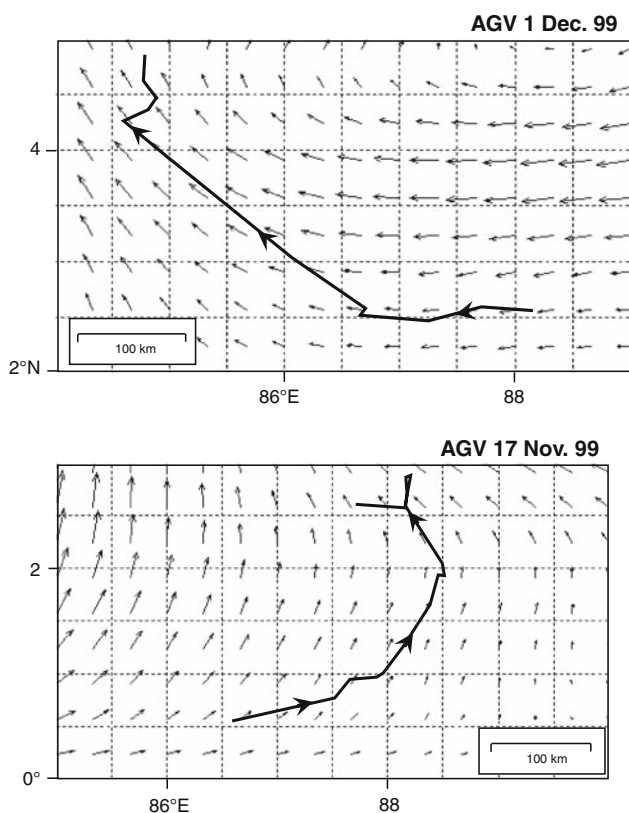
Fig. 9 Final part of turtle B2's route superimposed onto two AVG charts obtained for 17 November and 1 December 1999

(Fig. 2b) or the various turns displayed by turtles B2 and B3 in the second part of their journey (e.g. Figs. 6, 9). Such courses can be thought to derive from a corresponding change in the turtle orientation/navigation process(es), but the present analysis has indeed suggested that most of them were to some extent determined, or at least prompted, by the currents, with little, if any, contribution of the turtle's deliberate choice. These features of the tracked routes remain puzzling, and their interpretation is still elusive even after taking oceanic currents into account. Useful information on these aspects may be obtained by employing newly developed methods that allow quantitative estimations of the currents present in the areas visited by tracked turtles (e.g. Gaspar et al. 2006; Girard et al. 2006). However, as shown in a comprehensive validation study (Sudre and Morrow 2008), this system is unable to reliably estimate the currents close to the coast and in equatorial areas, so its suitability for the present case is doubtful. Also, future tracking experiments may take advantage of more accurate route reconstructions, for instance using the novel GPS tracking system (Schofield et al. 2007) that may allow one to get an improved idea of current effects, for instance by determining the exact position of turtles in relation to oceanographic features.

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