Current transport of leatherback sea turtles (*Dermochelys coriacea*) in the ocean

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While the long-distance movements of pelagic vertebrates are becoming known thanks to satellite telemetry, the factors determining their courses have hardly been investigated. We have analysed the effects of oceanographic factors on the post-nesting movements of three satellite-tracked leatherback turtles (*Dermochelys coriacea*) moving in the southwest Indian Ocean. By superimposing the turtle tracks on contemporaneous images of sea-surface temperatures and sea height anomalies, we show that current-related features dominate the shape of the reconstructed routes. After an initial offshore movement, turtles moved along straight routes when in the core of the current, or executed loops within eddies. Large parts of the routes were strikingly similar to those of surface drifters tracked in the same region. These findings document that long-lasting oceanic movements of marine turtles may be shaped by oceanic currents.

Keywords: oceanographic features; current drift; migration; remote sensing; sea currents

1. INTRODUCTION

Many marine vertebrates spend most of their life moving in oceanic waters and therefore have to face the sea currents they encounter. In sea turtles, newborn hatchlings are known to disperse following the general course of major currents (Hughes 1974; Carr 1987), but such a dependence on currents has never been documented for adults (Plotkin 2003). Rather, satellite telemetry has shown that adult turtles are generally able to contrast or overcome current action (Nichols *et al.* 2000; Polovina *et al.* 2000; Horrocks *et al.* 2001).

The leatherback turtle (*Dermochelys coriacea*) represents the most suitable species to investigate the effects of currents on adult movement patterns. Leatherbacks make the most extensive movements among turtles, wandering over large oceanic areas with fairly complex routes in which straight transfers, often along migratory corridors, are alternated with meandering segments, probably related to the turtles' feeding activity on macroplankton (Morreale *et al.* 1996; Eckert & Sarti 1997; Hughes *et al.* 1998).

In this investigation we aimed at testing whether physical factors influence leatherback movements by analysing the post-nesting routes of three leatherbacks wandering in the southern Indian Ocean in relation to the oceanographic features of the areas crossed. This region is particularly suited for this kind of study, as the physical environment exhibits extremes in temperature gradients, current speeds, and mesoscale variability. Surface circulation is dominated by the Agulhas Current, an intense, persistent current consisting of warm waters, with core speeds of up to 7.2 km h⁻¹, which flows southwest along the shelf edge of the eastern seaboard of southern Africa (Lutjeharms 2001). Bodies of water can be detached from the Agulhas Current, forming extensive eddies (Gründlingh 1988) that stand out thanks to their circular motion. Southwest of the continent, the Agulhas Current bends forming the Agulhas retroflection (Lutjeharms & Van Ballegooyen 1988), an unstable loop from which at irregular intervals large rings or filaments are pinched off. These rings subsequently drift off into the South Atlantic Ocean (Richardson *et al.* 2003). That part of the current that safely negotiates the retroflection flows eastwards as the Agulhas Return Current, which carries out a number of marked meanders along its course (Lutjeharms & Ansorge 2001), following closely the subtropical convergence.

2. MATERIAL AND METHODS

(a) Turtles and satellite tracking

Tracked turtles (turtles A, B, C; table 1) nested within the Maputland Marine Reserve, South Africa, in January 1996 and 1999. They were equipped with Argos-linked satellite transmitters (platform transmitter terminals (PTTs)) by a harness made of elastic cord (Hughes *et al.* 1998). Telonics (Mesa, AZ) PTTs were used, with sensors on board providing information about local water temperature.

The tracks were reconstructed by using all localizations provided by Argos (<http://www.argosinc.com/>), except those (19.1%) that inferred a speed exceeding 10 km h⁻¹ or were on land. Turtle speed over the ground was calculated by dividing the distance between successive fixes by the time between them.

(b) Remote sensing data

Data on sea-surface temperature were derived from the Advanced Very High Resolution Radiometer on board the NOAA 14 satellite (1 km spatial resolution). Measurements of sea-surface height anomalies (SSHA) were made by the TOPEX/Poseidon satellite. They provide information about temporal variations in course and speed of major currents determining mesoscale features, such as meandering and eddy shedding. These images are available from the Colorado Centre for Astrodynamic Research (http://www-ccar.colorado.edu/~realtime/global-real-time_vel/), in the form of 10 day averages. Tracks of Lagrangian surface drifting buoys were assembled from data at the Atlantic Oceanographic and Meteorological Laboratory (AOML). Buoys were located by the Argos system, and the data were quality controlled and optimally interpolated to 6 h intervals at the AOML.

3. RESULTS

All the turtles initially headed offshore, at right angles to the shoreline (see figure 3 in electronic Appendix A available on The Royal Society's Publications Web site). This movement, made in the absence of strong currents, led them to enter the Agulhas Current, as shown by the dramatic shift of their heading. Their successive south-westward movement was later interrupted by anticlockwise loops, which were in all cases superimposable on positive (anticyclonic) SSHA (figure 1a).

Thereafter, the turtles moved along straight routes at high speed (up to 6 km h⁻¹) when in the core of the Agulhas Current, or executed slower loops in eddies, indicated by SSHA. Turtle A quickly reached the waters south of the continent, with a 780 km long linear leg (figure 2a) following the course of the Agulhas Current, that in this area had

Table 1. Tracking summary of the three turtles.
(A leg of the journey was considered in the current mainstream when corresponding changes in turtle speed, direction of movement and PTT temperature were recorded. This was determined by eddies when superimposable to SSHA and circling in the same direction as the anomaly. Abbreviation: CCL, curved carapace length.)

turtle	CCL (cm)	deployment date	tracking duration (days)	total track length (km)	legs in mainstream (km)	legs in eddies (km)	legs not associated with current features (km)
A	163	16 January 1996	124	6195 ^a	3648 (58.9%)	1534 (24.8%)	1013 (16.3%)
B	153	31 January 1999	242	18 994	3893 (20.5%)	10 949 (57.6%)	4152 (21.9%)
C	168	31 January 1999	223	14 063	2770 (19.7%)	6961 (49.5%)	4332 (30.8%)

^a Excluding a 677 km long leg that could not be examined in relation to remote sensing data.

Figure 1. Examples of looping segments of the turtle tracks superimposed onto SSHA images recorded in the same period (10 day range as indicated). Turquoise line, turtle A; pink line, turtle B; white line, turtle C. Areas with positive anomalies (red in the images) are associated with warm, anticyclonic (i.e. anticlockwise) eddies, while negative anomalies (blue) are associated with cold, cyclonic eddies. The key to sea-surface height is provided within the figure. (a) Initial loops of turtle C (anomaly of 11–20 February 1999). (b) The crossing of an intense negative anomaly by turtle A (11–20 March 1996). Note that her successive counterclockwise loop was in accordance with her encounter of a positive anomaly. (c) The equatorward excursion of turtle A (19–29 April 1996). (d) The interruption of eastward movement and prolonged sojourn of turtle B (9 June to 27 August) inside an eddy. The image shown is for 9–19 August 1999, and the eddy persisted for months even after the turtle had left it.

a stable trajectory with no evident eddies as also shown by buoy tracks (figure 2b). Her successive series of loops corresponded to SSHA, but she also crossed an intense anomaly without having been influenced (figure 1b). Later on she moved eastwards at an increased speed, being located in the core of the Agulhas Return Current. After a large northward excursion shaped by a cyclonic eddy (figure 1c), she reached

the subtropical convergence in mid-May, as shown by the decline in PTT temperature (see figure 4 in electronic Appendix A) that reached values typical of the subtropical convergence (Lutjeharms & Valentine 1984). Turtles B and C displayed circuitous routes in correspondence with eddies that had formed off the seaward edge of the Agulhas Current, and moved along similar

Figure 2. (a) Reconstructed turtle routes superimposed to a low-resolution (50 km) image of sea-surface temperatures in the area on 3 July 1999, showing the general course of the Agulhas Current. Turquoise line, turtle A; white line, turtle B; dark blue line, turtle C. The dashed segment indicates the part of turtle A's route that could not be reconstructed. (b) Tracks of four surface drifting buoys followed by satellite in the same area in the same periods. Blue line, 21 April 1996 to 5 March 1997; white line, 8 January to 18 April 1999; red line, 26 April to 17 December 1996; black line, 2 January to 30 April 1999. The key to sea temperatures is provided within the figure.

paths for 119 days (figure 2a). From June onwards, turtle B made repeated clockwise circles for about 80 days in an area superimposable to a persistent cyclonic eddy (figure 1d), where PTT temperatures initially increased (see figure 4 in electronic Appendix A). She then approached the coast to re-enter the Agulhas Current (figure 2a), as shown by the change in direction and increase in PTT temperature and in speed. Turtle C re-entered the Agulhas Current further south in July and then reached the Atlantic Ocean (figure 2a), perhaps caught in a ring or filament. Surface buoys too sometimes display such interoceanic shifts (figure 2b). Turtle C's northward movement and drop in speed together with PTT temperature (see figure 4 in electronic Appendix A) indicated

that the turtle was within the northward drift of the Benguela Current.

4. DISCUSSION

The tracked turtles were involved in many oceanic features of different extent and nature, such as eddies or the core of the Agulhas Current, and their routes closely matched the mesoscale features encountered for the 69–84% of their length (table 1). In particular, most circuitous or curved segments were superimposable onto SSHA, and the sense of the turtle circling within the anomaly was always in accordance with the rotation of the water masses. Because these anomalies portray current eddies, the most likely explanation is that turtles were

caught by these features and started to circle accordingly. The linear parts of the routes, conversely, occurred within the current mainstream and showed a striking similarity in their course with those of surface buoys tracked in the same region. Surface circulation accurately portrays the conditions the turtles experienced during the tracking period, as turtles mostly remained in the upper part of the water column. Satellite-relayed depth data showed that turtles generally dived to depths shallower than 70 m, reaching depths below 500 m only a few times in the tracking period (A. Sale, P. Luschi, R. Mencacci, G. R. Hughes, G. C. Hays and F. Papi, unpublished data).

We conclude that the reconstructed routes were largely shaped by current-related features, and that the turtles were transported by current flow for large parts of their journey, following the detail of the mesoscale circulation. Even in the presence of a strong circulation like that linked to the Agulhas Current, this was not an entirely expected outcome, as it is not obvious that powerful swimmers such as leatherbacks are drifted in water currents. Satellite-relayed diving data indicate that the turtles were continuously diving throughout their journey, and so were not inactive. They concentrated their activity on swimming in the vertical plane to forage, rather than on swimming horizontally to move into different patches of water.

Many far-ranging nektonic animals are thought to be influenced by or take advantage of major currents during their oceanic movements (Dingle 1996). The available data only indicate that animals may follow the general current drifts during their oceanic journeys or select favourable tidal streams (Carr 1987; Hull *et al.* 1997; Healey *et al.* 2000; Arnold 2001). Our analysis further reveals that leatherbacks in the Indian Ocean intimately follow the detail of the mesoscale circulation for prolonged periods while ranging over wide extents. This has been shown previously in sharks and whales only for journeys tracked for short periods (Carey & Scharold 1990; Brill *et al.* 1993; Mate *et al.* 1997).

In the present case, it is likely that current transportation allowed leatherbacks to exploit macroplanktonic resources over large areas with minimal effort. Turtles B and C, for example, looped within eddies for months, and eddies in this region are known to support a well-structured food chain exploited by top predators (Pakhomov & Froneman 2000; Nel *et al.* 2001). Turtle A, conversely, made use of the flow of the Agulhas Current to quickly reach biologically rich areas such as the subtropical convergence. The leatherback post-nesting wanderings are therefore a consequence of their preference for oceanic current systems as foraging areas, and should not be considered migrations, a term usually referred to movements uninfluenced by the available resources (Dingle 1996). The turtles appeared to actively move in specific directions only when leaving the coastal waters and in some legs covered independently of the current flow, like during turtle A's northward movement, or turtle B's withdrawal from a persistent eddy.

It is currently unknown whether the strong influence of oceanographic features on leatherback routes that we have shown for movements in the Indian Ocean applies to journeys in other seas as well. The present analysis has, however, shown that the oceanographic features are key factors in determining the pattern of movements recorded, producing such different courses as large-scale straight movements or circuitous routes over small areas.

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