# A review of migratory behaviour of sea turtles off southeastern Africa

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**The survival of sea turtles is threatened by modern fishing methods, exploitation of eggs and habitat destruction. Forming keystone species in the ocean, their extinction would disrupt the marine food chain in ways as yet unknown. The Indian Ocean has many breeding areas for sea turtles, the southernmost ones being on the Maputaland coast of KwaZulu-Natal, where loggerhead and leatherback turtles nest in large numbers thanks to long-lasting protection programmes. For the leatherback this is the only known nesting site in the entire western Indian Ocean. At the end of the reproductive season, both loggerheads and leatherbacks undertake migrations towards disparate feeding areas. To contribute to their conservation, the migratory behaviour of these animals needs to be understood. Here we review 10 years studying this behaviour using transmitters that telemeter data via satellite. It emerges that these species frequent widely dispersed areas ranging from the Atlantic Ocean to the Mozambique Channel. The migratory behaviour of leatherback and loggerhead turtles is, however, very different, probably due to their differing food requirements. While loggerhead postnesting movements have a truly migratory nature, the large-scale wanderings of leatherbacks are better described as prolonged sojourns in extended feeding areas.**

## Introduction

The seas around South Africa are home to a variety of marine animals which spend the greatest part of their life in the open sea, often travelling over extended regions during the various stages of their life-cycles.[1] Examples of such oceanic travellers can be found in groups as diverse as squids, lobsters, fishes, sea turtles and whales.[2–4] Because of their elusive life habits, scientific knowledge of these species is limited, and the available information on many important aspects of their behaviour at sea is fragmentary and far from providing a well-defined picture.

Marine turtles represent a partial exception to this pattern, since the females need to spend some time out of water when crawling onto a beach to lay eggs, making them relatively more accessible to scientific studies. Although this period spent out of the sea (a few hours every 2–3 weeks, for 3–4 months every two or more years)[5] represents only a tiny fraction of adult turtles' lifetime, it offers the opportunity for scientists to easily approach a truly marine animal. For instance, systems to investigate turtle behaviour when they subsequently return to the sea are routinely deployed on nesting turtles to monitor various aspects of their behaviour, such as diving and feeding activity,[6–8] and/or to keep track of their movements.

Indeed, sea turtles have been favourite subjects for the development of marine tracking systems, and in particular of satellite telemetry techniques. Their ability to migrate long distances,[9] together with their large size and need to emerge from water to breathe (albeit for a few seconds only), make them well suited to such telemetric systems, which are able to provide worldwide localizations. Information about the general extent and courses of migrations of adults and, to a lesser extent, of juveniles, is now available for all the species,[9,10] and even specific aspects of their at-sea behaviour (for instance, diving and their interactions with environmental factors) are becoming accessible with accuracies and details once unimaginable.[11,12]

Two species of sea turtle reproduce on the sandy beaches of Maputaland, the loggerhead (*Caretta caretta*) and the leatherback (*Dermochelys coriacea*; Fig. 1). Turtle nesting activity in this area (Fig. 2) has been monitored and protected for more than 40 years.[13,14] Recoveries of tagged individuals indicate that they migrate for long distance after completing their reproductive cycles, reaching widely distributed areas from the Seychelles to the Cape region.[13,15,16] In recent years, satellite tracking experiments have been performed on females followed during their postnesting migrations.[16–19] Adults of these two species represent two extremes among life styles of sea turtles: loggerheads are primarily adapted to live in the neritic environment (e.g. shallow shelf waters), whereas leatherbacks represent a paradigmatic

**Fig. 1**. A loggerhead (**a**) and a leatherback (**b**) turtle nesting on a Maputaland beach. The loggerhead is equipped with a satellite transmitter and is about to leave the nesting beach, to begin her postnesting migration.

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example of pelagic-dwelling turtles that frequent vast and remote oceanic regions. These ecological differences are reflected by differences in the morphology and physiology of the two species, and may affect a number of behavioural aspects such as foraging activity, diving ability or general movement patterns and their relation to oceanographic conditions. In this paper, we review the results from a decade of turtle satellite tracking in South Africa, which have revealed many aspects of at-sea behaviour of adult loggerheads and leatherbacks. Such a comparison between turtles nesting in the same region, yet frequenting widely diverse environments during the non-breeding period, appears a most suitable way to illustrate the range of adaptations to the marine environment evolved by sea turtles.

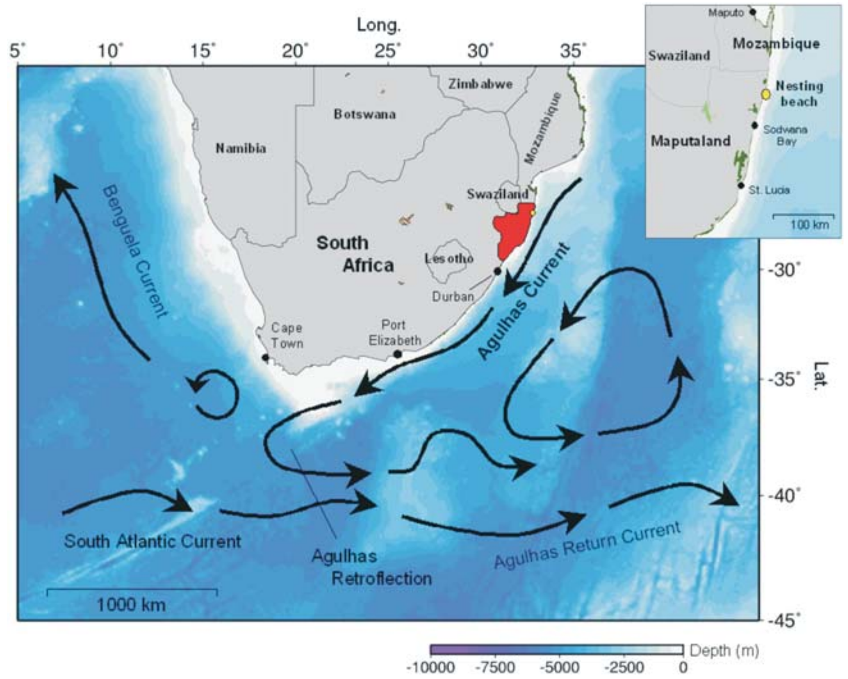


**Fig. 2.** Schematic diagram of major surface currents around southern Africa (after ref. 54, modified). The red area represents the Zululand–Maputaland region. Insert shows the area around the Maputaland Marine Reserve, with the position of the nesting site of tracked turtles.

### Oceanographic setting

Sea currents and related oceanographic features heavily characterize the marine environment of the South-West Indian Ocean, where the postnesting movements of both species take place. A brief overview of the oceanography of the region is therefore useful. The area is dominated by the greater Agulhas system (Fig. 2). Much has been learnt about this system over the past decade, but large regions remain relatively unstudied.[20,21]

The northern Agulhas Current is perhaps the best-studied part of the system. This major western boundary current is fully formed somewhere between the city of Maputo in Mozambique and St Lucia along the KwaZulu-Natal coast, although the exact location where it starts having a decisive influence on shelf waters is not known. Downstream of here, the current follows the shelf edge quite closely.[22] The general influence of the Agulhas Current on the waters overlying the narrow shelf is to force these waters to move parallel to the Agulhas Current.[23] The only intermittent exception occurs when a large, singular meander — the Natal Pulse[24] — disrupts the trajectory of the current and reverses the flow direction on and near to the shelf for a few days as it passes downstream. The surface waters of the Agulhas Current move at a rate of about 2 m/s;[25] the inner edge of the current is much more distinct than its offshore edge.[26] In fact, bodies of warm water have been observed to become detached from this seaward edge.[27] Offshore, intense eddies coming from the Mozambique Channel[28] and from east of Madagascar have a dramatic influence on the circulation in this region.[29]

South of Port Elizabeth, the Agulhas Current starts to meander sideways more consistently and, on passing the tip of the African continent, it turns back on itself (forming the Agulhas retroflection) with the majority of its water subsequently moving eastwards as the Agulhas Return Current[30] (Fig. 2). This retroflection loop is unstable and pinches off Agulhas rings at intervals of about 2–4 months. These rings drift into the South Atlantic Ocean where they dissipate.[31] Water from the Agulhas Current can also leak into the South Atlantic as filaments of warm surface water.[32]

The source regions of the Agulhas Current are far more complex. The flow in the Mozambique Channel is dominated by warm, anti-cyclonic eddies drifting poleward from the narrows of the channel.[33] Some of them may eventually be absorbed by the Agulhas Current.[34] The circulation in the rest of the channel is poorly known and may consist of weak and variable currents.[35] Along the mainland coast the currents are in general weak. The influence of passing Mozambique eddies seems to be small, but few observations are available to support this.

The surface waters of the Agulhas Current as well as of deep-sea eddies in the region are generally considered to be oligotrophic. Enhanced primary productivity is found at some upwelling cells inshore of the current[36,37] but their influence remains restricted to the continental shelf.

## Methods

### Sea turtles and transmitters

Over the years 1996–2003, a total of 19 female turtles (eight loggerheads and 11 leatherbacks) have been equipped with Argos-linked satellite transmitters in the Maputaland Marine Reserve, South Africa. Turtles were captured on the beach immediately after an egg-laying event, and transmitters were attached to their carapace by standard means.[38,39]

Several types of satellite transmitters were employed. During the years 1996–2001, transmitters manufactured by Telonics (Mesa, Arizona, U.S.A.) were used (models ST-14 and ST-6). To make batteries last longer, three of them had the on-board processor programmed with a specific duty cycle, by which they transmitted continuously for the first month after deployment and then every 5 days for the remaining time. In years 2002–03, four turtles were equipped with special transmitters (SRDL, Satellite Relay Data Loggers), manufactured by the University of St Andrews, U.K. Further details on procedures and equipment are provided elsewhere.[17,18,40]

### Satellite tracking and data analysis

Turtles were tracked by the Argos system, which provides worldwide geographical locations through measurements of the Doppler effect of signals received from transmitters (www.argosinc.com). Argos locations are assigned to different accuracy classes. Routes were reconstructed by using filtered data which excluded erroneous locations leading to unlikely travel rates (5 km/h for loggerheads, and 10 km/h for leatherbacks) or were over land.[17,18] This commonly used procedure led to us discard a small percentage of data, which did not affect the main features and overall courses of tracked routes .

Besides geographical locations, a number of satellite-relayed sensor data, recorded and processed on board the transmitters, were also obtained. For Telonics transmitters, these included information on the mean and maximum duration and number of dives made by the turtles in predefined 4-h or 6-h intervals, as derived from the pattern of salt-water-switch openings and closures. A pressure sensor was included in two units deployed on leatherbacks, which measured depth every 30 seconds and relayed binned data on the depth preference of the turtles over successive 4-h periods. SRDLs also employed a pressure sensor to measure depth every 4 seconds, and were able to provide more detailed diving data such as individual dive profiles or summary information (averaged over 6 h) on dive duration and maximum depth.[11,40]

### Oceanographic data

Luschi and co-workers[19] analysed the long-distance routes of the three leatherbacks tracked during 1996 and 1999 with respect to the oceanographic conditions of the oceanic areas crossed. Major oceanographic processes, such as eddies, filaments and meanders, were studied by considering contemporaneous remote-sensing information on sea-surface temperature and height anomalies obtained by NOAA 14 and Topex/Poseidon satellites, and made available by the Naval Research Laboratory, Stennis Space Center (Mississippi, U.S.A.) and by the Colorado Center for Astrodynamic Research, University of Colorado, Boulder, respectively. False-colour images deriving from such remote-sensing information were superimposed on reconstructed turtle tracks to show correspondences between different route segments and major oceanographic events. Qualitative comparisons with the routes of Argos-tracked surface drifters in the same region have been done by relying on the drifter database at the Atlantic Oceanographic Meteorological Laboratory (Miami, Florida, U.S.A.).

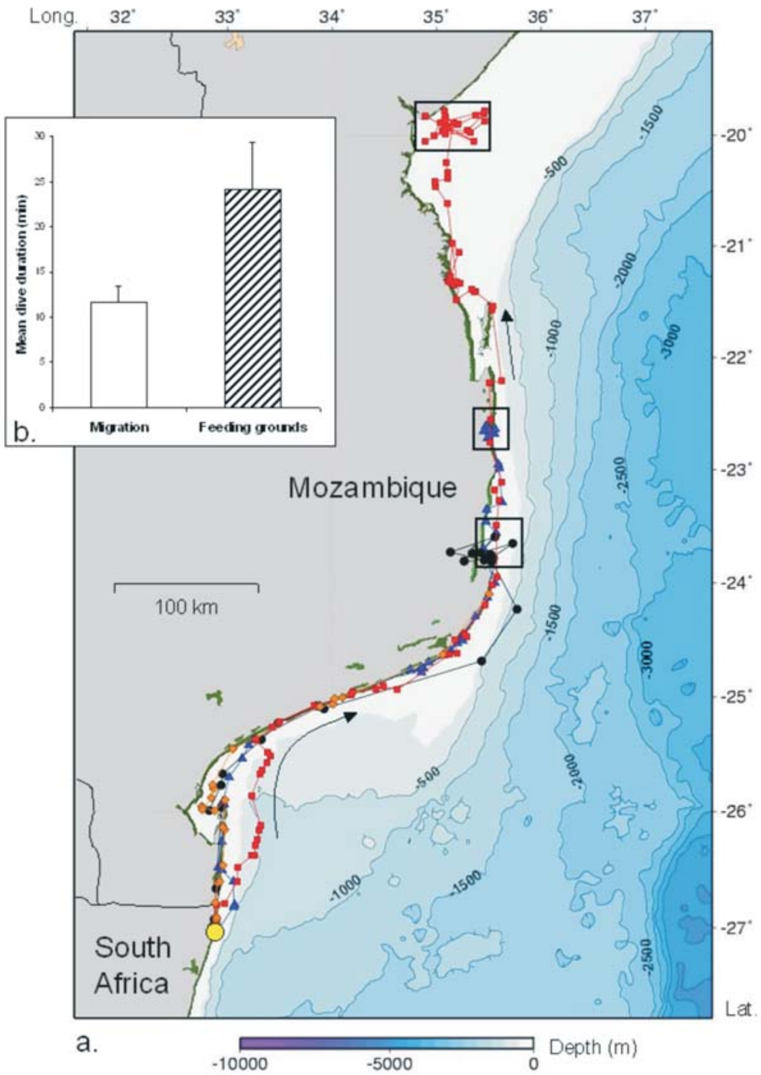


**Fig. 3**. Migratory routes of four Maputaland loggerhead turtles tracked by satellite. The rectangles indicate the residential foraging areas where turtles have been localized for prolonged periods.[17] Inset: mean (± s.e.m.) duration of dives of three loggerheads during the migration and while at the feeding grounds. Yellow dot shows the nesting beach.

## Results

### General migratory behaviour: loggerheads

Only four of the eight equipped loggerheads were successfully followed during their postnesting movements. They all displayed a remarkably similar behaviour, as they all moved northward, hugging the Mozambique coast (Fig. 3a). After 16–46 days of migration, three of them began to localize within spatially limited areas in shallow shelf waters along the Mozambique coast, where they then remained for more than 2 months. It is assumed that these were the individual-specific feeding grounds of tracked turtles, representing the endpoint of their migratory journeys.[41] The tracking of the fourth turtle stopped before she reached the foraging grounds, that is, her destination. The four turtles migrated for 510–930 km (mean ± s.e.m. 663.8 ± 95.2 km), at average speeds of 1.1–1.8 km/h (mean ± s.e.m. 1.3 ± 0.2 km/h); values comparable to those recorded in other postnesting migrating loggerheads.[42–44] The currents on the shelf regions crossed by these turtles were most probably weak and turtle movements were not likely to be influenced by a strong off-shelf current.

Satellite-relayed information on the diving behaviour of three loggerheads showed marked changes in dive duration during and after migration (Fig. 3b). While migrating, turtles made a large number of relatively short submergences (mean ± s.e.m. 11.7 ± 1.8 min, range of means 8.6–16.0 min). This pattern is known to occur also in other migrating turtles[44–46] and is thought to derive from the turtles' need to breathe frequently because of their active swimming during the migratory phase. Once in their neritic feeding grounds, they shifted to more prolonged dives (mean ± s.e.m. 24.1 ± 5.2 min, range of means 14.9–33.0 min).

### General migratory behaviour: leatherbacks

In total, 11 leatherback turtles were tracked between 1996 and 2003 as they left the Maputaland coast after having completed their egg-laying cycle. Nine turtles were tracked for long periods (up to 8 months: mean ± s.e.m. 131.1 ± 24.1 days; range 17–242 days), enabling us to outline their migratory pathways and to identify the pelagic areas frequented. The three turtles equipped with duty-cycled transmitters (that is, which were not transmitting continuously and were thus expected to last longer) were not tracked for longer than the other ones. Probably, the duration of the tracking was more affected by contingent factors (such as harness resistance or position, or turtle actual survival) than by the batteries' lifetime. For one turtle, anomalous diving data were collected, indicating that she may have been captured by fishermen about 140 km offshore southwest of Port Elizabeth, outside South African territorial waters.[47]

Upon leaving the nesting areas, four turtles remained for at least some weeks in low-latitude waters, two of them making large off-shore loops east and north of the nesting beach, and two moving around in the shelf between the Delagoa and Natal bights (Fig. 4). The five other turtles consistently moved immediately southwestward, keeping similar courses parallel to the coastline, which quickly led them to high-latitude waters, east and south of the African continent (Fig. 5). Such a movement has also been shown by two of the four turtles which initially spent some time at lower latitudes (black and yellow turtles in Fig. 5). Three turtles were tracked until they reached the oceanographically very dynamic area south of the Agulhas Bank and further on. One of them (white in Fig. 5) veered east after some circuitous movements, probably following the Agulhas Current retroflection (see also below), while the other two (blue and red in Fig. 5) entered the southeast Atlantic Ocean, thus displaying the first inter-oceanic shift documented for marine turtles.

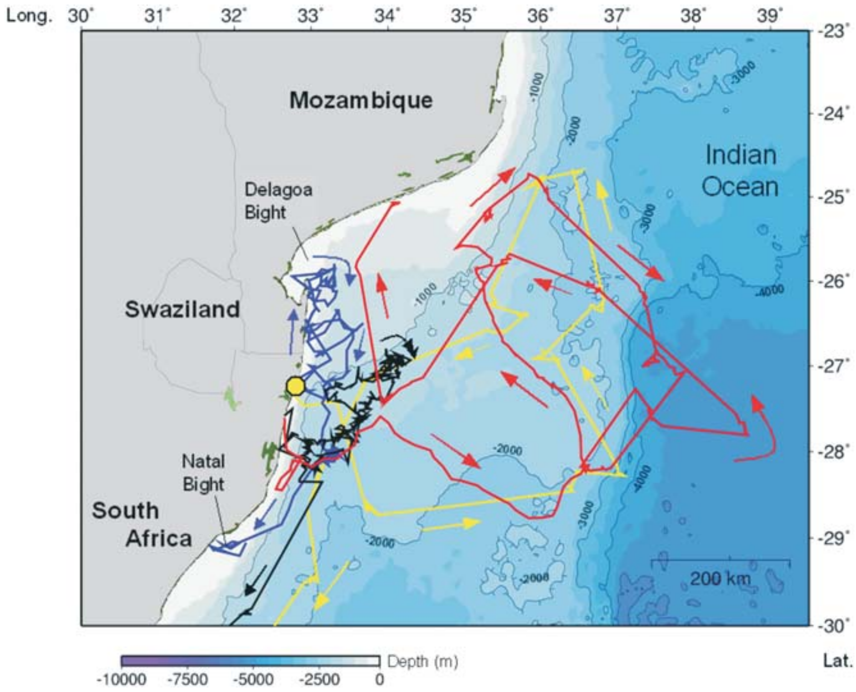


**Fig. 4.** Routes of four leatherbacks which remained in low-latitude areas upon leaving their nesting area (yellow dot).

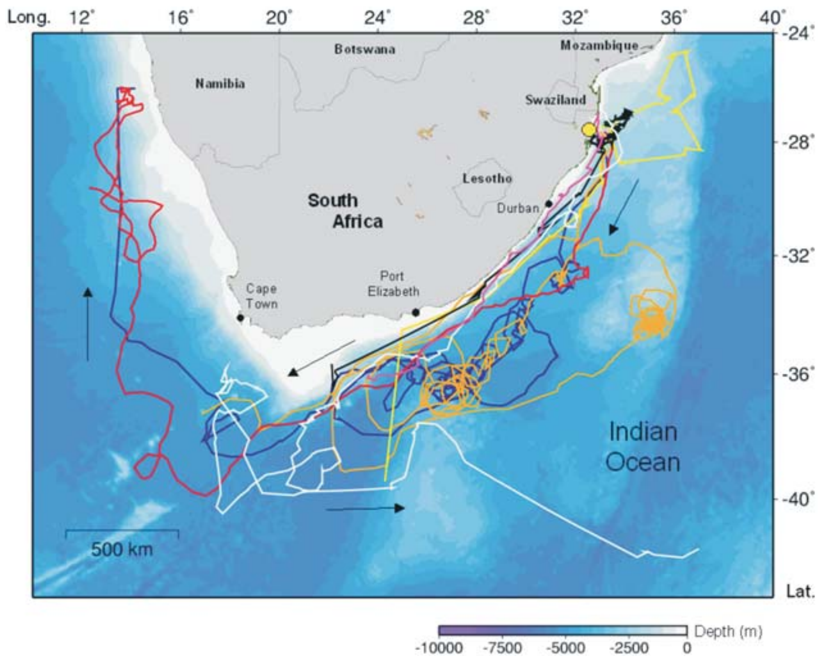


**Fig. 5.** Postnesting journeys of six leatherbacks tracked by satellite in years 1996–2003, showing movements towards the oceanic areas south and west of the continent. Yellow dot shows the nesting beach.

The diving behaviour of leatherback turtles is very complex, as it reflects their seemingly continuous predatory activity, targeting pelagic macroplankton such as jellyfish or salps.[48] Unlike loggerheads, leatherbacks feed on prey that are usually (but not only) found in pelagic waters and which may reside at great depths. The four tracked leatherbacks whose dive behaviour has been recorded made a large number of quite short dives (mean ± s.e.m. 10.4 ± 3.2 min), spending 34–85% (mean ± s.e.m. 67.8 ± 11.4%) of their time submerged. The most common pattern was that of diving to 30–70 m during the night and to remain in the superficial part of the water column (<10 m) during daytime. Such a pattern is a common feature of leatherback diving activity (e.g. refs 7, 49), and is thought to derive from the turtles' predation on zooplankton carrying out diel vertical migrations in the water column.[49,50] The deepest dives were, however, performed in the central hours of the day, when the record depths of 850 and 940 m were observed. These are most probably exploratory dives by which the turtles search for prey at great depths, interrupting their typical daytime pattern of shallow dives.[40] Long-lasting (but not particularly deep) dives (up to 82 min) have also been recorded at night, with turtles remaining, however, at shallower depths (<200 m)[40] than during middle-day dives. For the three turtles that were tracked longer, consistent changes in diving behaviour were qualitatively observed throughout the tracking period.[40] As the season proceeded, turtles' dives became briefer and shallower, and a much shorter period of time was spent submerged (dive time percentage dropped to around 10% at the end of the tracking). Moreover, the clear diel pattern in diving behaviour observed early in the tracking period disappeared, with the turtles always exhibiting a diurnal-style, superficial diving pattern. Such dramatic changes in diving behaviour were paralleled by corresponding decreases in water temperature, leading to the hypothesis that colder waters lead turtles to dive shorter and shallower, possibly as a result of a different prey distribution.[51] It is worth noting that a broadly similar phenomenon has recently been observed in leatherbacks moving in the northern Atlantic Ocean.[52]

## Leatherback interactions with oceanographic features

Being pelagic dwellers feeding on plankton, leatherbacks are the best candidates to evaluate the profound influence of sea currents and related aspects on open-sea movements of turtles, as their oceanic movements are likely to be affected by sea current circulation. Such influences can take place not only through the forces exerted on turtles' movements, but also more indirectly by determining the local availability of their patchily-distributed drifting prey, that concentrate in areas such as fronts, eddies or upwelling zones.[53]

The drifting role of currents is best shown for the case of the seven turtles that travelled down the east coast of Africa. They clearly moved along the Agulhas Current mainstream, and their courses closely resembled those of oceanographic surface drifters tracked in the same region (Fig. 6). For the three turtles that went through an eastward course change or entered the Atlantic Ocean, the correspondence with the drifters extends further. Their routes virtually replicated the movement of some drifters, being advected through the Agulhas Current retroflection and then continuing eastward in the Agulhas Return Current, or being involved in the inter-ocean exchange of waters occurring south of the continent.[54] The turtle moving eastward found herself within the highly productive Subtropical Convergence, where planktonic prey are known to abound.[55] Similarly, the turtles that moved to the Atlantic most likely took advantage of the upwelling areas along the west coast of southern Africa.[56]

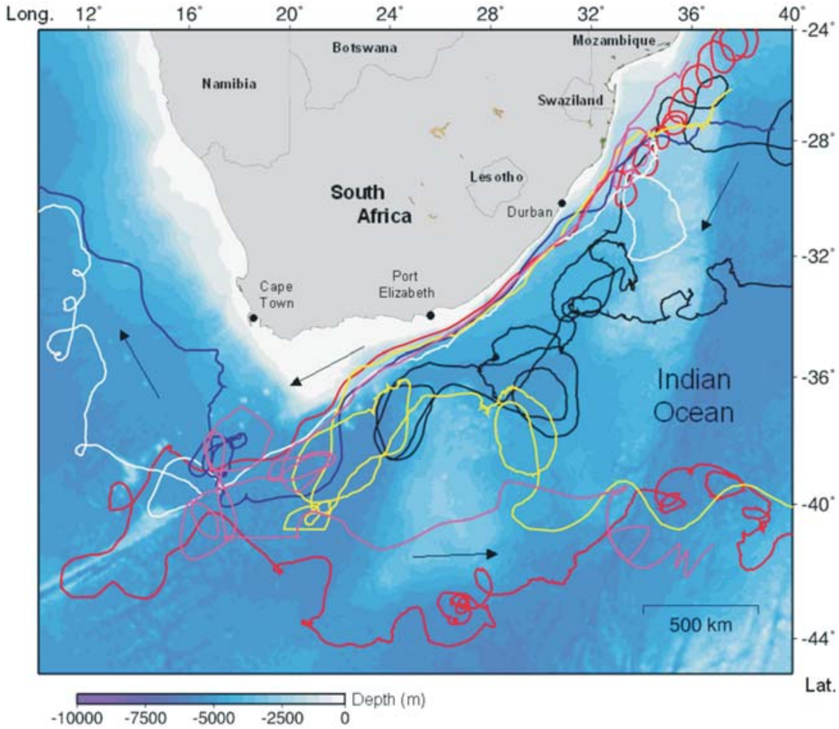


**Fig. 6.** Routes of surface drifters tracked in the South-West Indian Ocean in years 1996–2003, showing transport within the Agulhas Current mainstream, advection in the Agulhas retroflection, and inter-oceanic shift to the Atlantic Ocean.

Oceanographic features also greatly influenced the legs of turtle routes, which showed convoluted circular patterns (Fig. 7). The superimposition of these segments on images of sea-surface height anomalies showed clear correspondences with positive anomalies (red in Fig. 7). These are indicative of the presence of anticlockwise rotating eddies, which are actually known to occur in this region.[29] On these occasions, turtles sometimes remained in the same eddy for weeks (most probably having found abundant prey provisions), and their sense of circling was always in accordance with that of the water masses, showing that their movements in these periods were entirely determined by water movements.

## Discussion

The results of satellite-tracking experiments have clearly shown that the two species of turtles breeding in Maputaland undertake extensive migrations, leaving the nesting area upon completing breeding to reach distant foraging grounds, which were delimited and coastal in loggerheads, dispersed and pelagic in leatherbacks. The occurrence of long-distance migrations in the Maputaland populations has already been postulated on the basis of the distant recoveries of individuals tagged while nesting in this area.[13,15,16] Since most recoveries occurred in coastal areas, however, these data underestimated pelagic migrations and are indeed mostly limited to loggerheads. The satellite findings have allowed accurate identification of the feeding areas exploited, the migratory pathways followed, and the at-sea diving behaviour of tracked turtles. The present results have been obtained only for females, which are always available on beaches and easy to fit with instruments. The migratory behaviour and routes of adult loggerhead and leatherback males is very poorly known, although it may be postulated that their movement patterns should not be different from those displayed by females.[52,57,58]

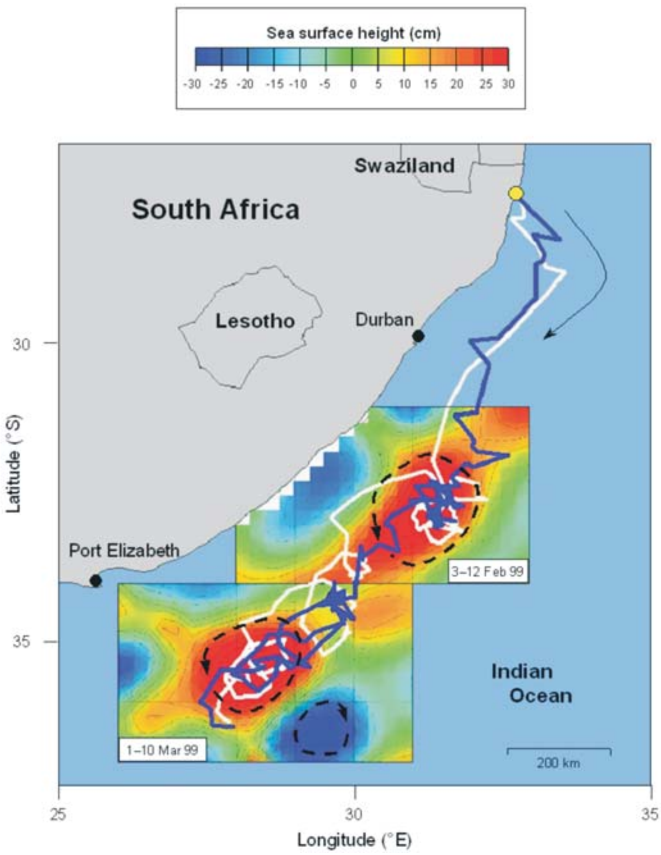


**Fig. 7**. Initial parts of the routes (31 January – 12 March 1999) of two leatherback turtles moving off the east coast of southern Africa[19] superimposed on maps of sea surface height anomalies referring to period shown. The presence of eddies (sense of rotation indicated by arrows) is shown by the large blue and red anomalies in correspondence with turtles' looping movements. Yellow dot shows the nesting beach.

The migratory patterns exhibited by the two species nesting in the same beaches could not be more different. Tracked loggerheads migrated actively hugging the coast, and ended up in individually-specific neritic feeding grounds. The reaching of suitable feeding areas at the end of the migratory trip was clearly indicated by the prolonged permanence of three tracked turtles in the same restricted areas for weeks and the dramatic changes in their diving parameters. This is in accordance with the most common pattern known in loggerheads, which are thought to perform shuttling migrations between nesting and residential areas.[41] Loggerheads are known to display fidelity to foraging grounds,[43,44] where they can establish feeding home ranges.[59] The increases in dive duration once at the feeding grounds recorded for South African loggerheads, have been observed in satellite-tracked green turtles[45,46] as well. They are attributable to a general decrease in activity of these herbivorous turtles, which spend a long time in seabed resting when at their feeding grounds.[45] It is uncertain whether this applies to carnivorous loggerheads as well, whose feeding is known to be targeted mostly on benthic prey[48,60] and may not involve such an activity decrease. Indeed, dive durations of loggerheads tracked during the residence at the feeding grounds may be quite short (<5 min on average)[44] and are usually quite variable (e.g. seasonal or daily).[44,61]

Conversely, leatherbacks have been found to be wanderers, ranging over vast oceanic areas while searching for their planktonic prey. In most cases, tracked leatherbacks frequented high-sea regions, although one of them stayed along the continental shelf during her whole tracking (blue track in Fig. 4). This double strategy of feeding over shelf and pelagic areas has been shown also for other tracked leatherbacks[52] and is probably linked to differential prey availability in the various regions.[48] The close association of leatherbacks with specific open-sea features (oceanic eddies in particular) is also common to pelagic-feeding turtles[12,53] and to pelagic birds,[62] who take advantage of the enhanced productivity around these discontinuity zones. The leatherbacks' search for prey within the water column does not appear to be affected by their advection by currents, as their diving behaviour does not change when in the presence of diverse oceanographic features.[40] Details of leatherback predation patterns at depth are, however, unknown, and so are the possible influences of currents.

The postnesting movements reconstructed for Maputaland leatherbacks are broadly similar to those recorded in the Atlantic and Pacific oceans, showing an alternation of straight paths, sometimes along migratory corridors, and shorter-distance meandering segments, usually covered at lower speed.[52,63–65] These two types of movements have usually been ascribed to different needs of migrating leatherbacks, with straight sections deriving from rapid transfers towards more suitable areas (e.g. thermally), and circuitous paths displayed in periods/areas where foraging activity is high.[18,52] This view is, however, challenged by the strong influence of current-related features on leatherback turtle paths.[19] The recorded differences in travel speed may not necessarily be a consequence of different turtle activities, but rather derive from differences in the speeds of currents encountered. This is further supported by the discovery that leatherback diving patterns did not differ in distinct route segments,[40] as it may be expected if turtles were indeed attending to such different activities as transferring and feeding (as discussed above[44–46]).

One of the most novel conclusions drawn from the tracking studies on South African leatherback turtles is the strong influence exerted by oceanic currents on the movements recorded. The shape of most segments of the turtles' movements turned out to be conditioned by the oceanographic features of the area crossed, which determined such variable paths in turtle journeys as circuitous loops or linear segments. The resemblance between many parts of turtle journeys with the courses of inanimate drifters is quite striking in this respect, and is in full agreement with evidence collected by analysing other oceanographic parameters.[19] This leads us to hypothesize that, for large part of the routes, turtles may not have been swimming actively (at least in the horizontal plane), and that the geographical movements observed mainly derived from the action of oceanic currents, with little, if any, contribution provided by the turtles' active motion.

To summarize, the tracking data indicate that while South African loggerheads migrate by actively swimming until they reach discrete feeding areas, the behaviour of leatherback turtles consists mainly of continuous diving activity (that is, movements within the water column), with currents providing most of the horizontal displacement. If so, the postnesting phase of Maputaland leatherbacks would be better described as a prolonged sojourn in vast feeding areas than as a true migration, a term more appropriate for the active movements of loggerheads.[66] The far-ranging postnesting displacements recorded in leatherbacks would be, therefore, mainly a consequence of their preference for feeding areas linked to major current systems, which exposes them to large drifts with the currents (sometimes even to unsuitable regions), in much the same way hatchlings are carried away from their natal areas during their developmental oceanic stage.[67] The turtles' diving activity would continue for as long as prey are available, largely regardless of the actual geographical location at which they find themselves. If needed, leatherbacks can always leave unprofitable or unsuitable areas through active horizontal movements, made independently from (or even against), currents — an ability which undoubtedly is well within the reach of such powerful animals.

During the postnesting phase, tracked loggerhead and leatherback turtles visited pelagic and neritic areas extending over large regions of two oceans, and spanning from temperate waters south of Africa to the tropical areas of the Mozambique shelf. This clearly highlights how Maputaland turtles are an internationally-shared resource, whose life cycle mostly takes place in shelf and offshore waters outside South Africa. Protecting breeding grounds, although most helpful,[13,68] cannot be fully effective if supplementary measures are not taken also to protect turtles during their prolonged and wide-ranging stays at sea. Many anthropogenic threats are known to affect turtles' marine life,[69] amongst which the impact of fishery activities is particularly harmful, especially (but not only) in the offshore waters frequented by leatherbacks. The fate of one of our tracked leatherbacks, that was possibly captured outside South African territorial waters,[47] clearly illustrate such dangers. On the other hand, fishery pressure is not expected to be lower in inshore areas,[69] and so turtles frequenting coastal waters (like loggerheads) are presumably vulnerable to a similar extent. Regulating the interaction of turtle populations with fisheries, and enforcing rules over such large oceanic areas, is not going to be a straightforward task. Identifying the marine areas most commonly frequented by turtles constitutes a first, albeit fundamental, step in developing ground-based, effective conservation and management programmes.

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