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Satellite tracking of migrating loggerhead sea turtles (*Caretta caretta*) displaced in the open sea

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Abstract Loggerhead turtles (*Caretta caretta*) are known to migrate towards fixed, individually-specific residential feeding grounds. To study their spatial behaviour and their navigational ability, five loggerheads nesting in South Africa were captured when about to start their postnesting migration and tracked by satellite after having been displaced from their usual migratory route. The first turtle, released south of Madagascar about 1,148 km from the capture site, moved west up to mainland Africa and then reached her feeding grounds by following the coast. A second turtle, released farther away (2,140 km) close to La Réunion Island, stopped for some time on the Madagascar east coast, then turned southwards to round the island and regain the African mainland in the northwest, without however allowing us to establish the location of her residential grounds. Three other turtles were released off the Tanzanian coast, 2,193 km north of their nesting area, at the northern edge of the distribution of the feeding grounds along the African coast. All of them headed north, and one turtle found her residential grounds located north of the release site. The other two females started long-distance oceanic wanderings in which they crossed nearly the entire Indian Ocean, apparently being transported by the sea currents of the region. We conclude that adult loggerhead turtles are apparently unable to compensate for the displacement and can return to a pelagic life style

characteristic of juvenile turtles. These findings suggest that South African loggerheads rely on simple orientation mechanisms, such as the use of the coastline, as a guide, and compass orientation, possibly integrated by spatiotemporal programmes and/or acquired maps of familiar sites.

Introduction

Most marine turtles migrate between their nesting beaches and their residential feeding grounds commonly located in the neritic zone. The two termini can be located at a relatively small distance or on the same stretch of a continental coast, but very exact migratory journeys can occur as well when the target is a tiny island in the middle of the ocean, thousands of kilometres away from the starting point (Mortimer and Carr 1987; Balazs 1994; Papi et al. 1995; Luschi et al. 1996, 1998; Cheng 2000). The navigational abilities underlying these journeys are poorly known, so that turtles are tentatively attributed with reliance on mechanisms that, according to findings for other animals, would permit the recorded navigational performances. In the case of alongshore migration, for instance, turtles might derive cues from the coast and, as long as they swim over shallow waters, from the sea floor (Timko and Kolz 1982; Luschi et al. 1996). Alternatively, when turtles maintain straight routes over deep waters, they could keep their course by making use of biological compass(es), which are widespread in the animal kingdom (Papi 2001). Finally, experimental findings on sea turtle hatchlings have suggested that more sophisticated mechanisms based on the perception of parameters of the earth's magnetic field could allow latitude determination or even a more or less precise determination of the geographic position over favourable areas (review in Lohmann et al. 1999). In this last case turtles would therefore rely on a true navigation system through a so-called bicoordinate grid map (Papi 1992) allowing them to fix their position with

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respect to the target, even from sites never previously visited. Experiments aimed at testing this eventuality have, however, failed to provide supporting evidence (Papi et al. 2000; Luschi et al. 2001).

A classic experiment to investigate the navigational mechanisms of an animal involves displacing it from the capture area to a new site, whose distance and degree of familiarity are varied in accordance with the nature of the underlying mechanism that the researcher aims to test. The capacity or failure to compensate for the displacement and the kind of course followed after release are then the basic facts from which to draw inferences. In the present paper we report the results of experiments in which five loggerhead turtles (*Caretta caretta*) nesting on the beaches of KwaZulu-Natal, South Africa, have been displaced at different distances and directions. Adult loggerheads are known to migrate between fixed nesting and feeding grounds. They generally leave their nesting area at the end of the reproductive season to reach specific foraging areas to which they display site fidelity, as shown by the repeated recoveries of tagged females within the same feeding area in successive seasons (Limpus et al. 1992). These feeding grounds are thought to be mostly in the neritic zone (Dodd 1988; Musick and Limpus 1997), where adult loggerheads can even establish small territories (Hughes 1974), although satellite telemetry has recently shown that a small contingent of a nesting community may also migrate towards pelagic areas (Hatase et al. 2002).

The loggerheads nesting in South Africa are being subjected to a long-lasting tagging programme, and a number of recoveries of tagged females is now available (Hughes 1974, 1989). Since recoveries of tagged turtles away from the nesting area mostly occur during their stay at the feeding grounds (Limpus et al. 1992), the general distribution of the feeding grounds of these loggerheads can be inferred from the recovery sites of the tagged animals. From these data (Fig. 1), it turns out that turtles belonging to this nesting community move to residential quarters in different areas, namely the East African coast north of the nesting area ($n=28$ turtles), the East African coast south of the nesting area ($n=9$), Madagascar's east coast ($n=2$), Madagascar's west coast ($n=9$) and the Seychelles ($n=1$). Satellite tracking of the post-nesting migration of four turtles showed that they indeed migrate northwards by closely following the coast (Papi et al. 1997).

Previous short-distance displacement experiments with turtles caught on the same beach showed some homing ability with quick return to the coast (Papi et al. 1997), and this encouraged us to perform further experiments at greater distance with low risk of endangering the life of the females used. We displaced the turtles at the end of their reproductive season, when they were about to start their postnesting migration towards their residential quarters. Since no South African turtle re-sighted away from the nesting beach has ever been found again while nesting, we could not use turtles for which the exact location of the feeding ground was

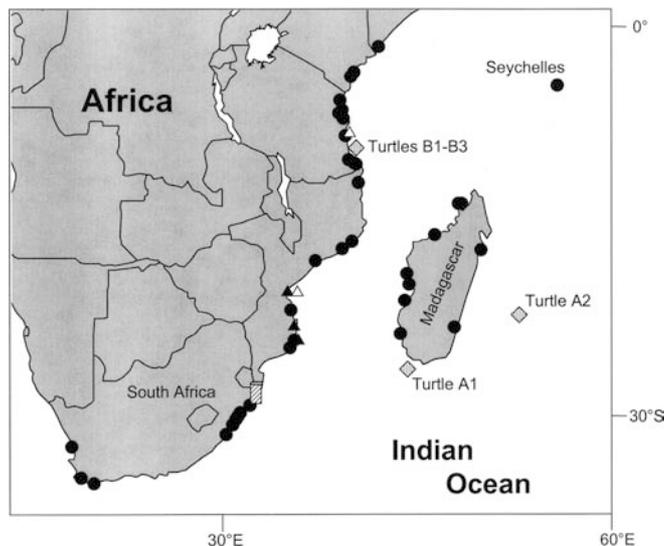


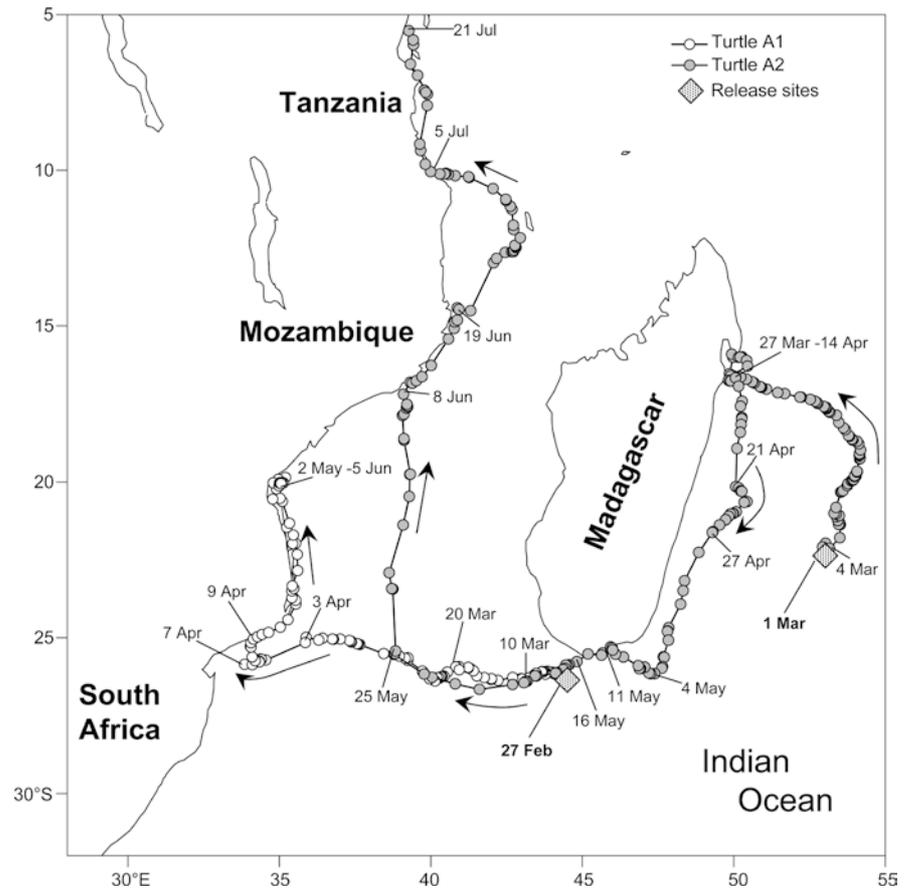
Fig. 1 *Caretta caretta*. Map of the feeding grounds of loggerheads nesting in Maputaland beaches (cross-hatched rectangle) as deduced by recovery sites of tagged loggerheads in years 1979–99 (black dots) and by the results of previous (Papi et al. 1997; black triangles) and present (white triangles) satellite tracking studies. Dotted diamonds indicate the release sites of the five turtles

known. Nevertheless, we assumed that each turtle should migrate towards a specific (possibly neritic) area within the geographical range identified by the recovery distribution, and expected that the turtle behaviour after displacement could give us some hints about the navigational systems they rely on. In particular, we aimed at determining whether South African turtles have a true global map of the area, or use simplified homing mechanisms, e.g. by detecting a latitudinally varying geomagnetic gradient in order to establish their position along the coast (Lohmann et al. 1999) or by using a piloting mechanism based on cues on the coast.

Materials and methods

Two experiments were performed with adult females captured after completing the final egg-laying of the season on their nesting beach in Maputaland, northern KwaZulu-Natal (Fig. 1). After capture, the turtles were placed in specially designed wooden crates and transferred by vehicle to Durban (about 370 km south of the capture site). There they were held in a tank at Sea World awaiting embarkation on an appropriate ship from Durban. In experiment A, two turtles (A1 and A2, curved carapace length 94 and 95 cm, respectively) were captured on 29 January 1998 in the region of Sodwana Bay (27°02'S, 32°51'E), equipped with an Argos satellite transmitter (ST-6 model, Telonics, Mesa, Ariz., USA) and embarked on 25 February on the freighter "Magdeburg", bound for Port Louis, Mauritius. The turtles were kept in the crates on the ship's deck, but prevented from seeing the sky by a curtain hanging above them. An officer of KwaZulu-Natal Wildlife looked after them, moistening them in sea water at regular intervals. Turtle A1 was lowered away on 27 February at a point (26°08'S, 44°09'E) south of Madagascar, from which the turtle could directly reach the African coast. Turtle A2 was released on 1 March at a point (21°58'S, 52°59'E) east of La Réunion (Fig. 2), from where the turtle had to bypass Madagascar to reach the continent. The release sites were, respectively, 1,148 km and 2,140 km (bee-line) from the capture site.

Fig. 2 *Caretta caretta*.
Reconstructed tracks of turtles
A1 and A2 after release
northeast of the nesting area



In the second experiment, three turtles (B1, B2 and B3) were involved. Their curved carapace length was 87, 96, and 93 cm, respectively; turtle B2 had the front right flipper truncated. The turtles were caught on 25 January 1999 at Sodwana Bay, equipped with Telonics transmitters (ST-14 model for turtle B1, ST-6 for the other two) and embarked on the freighter "Ariane", which left on 12 February for Dar es Salaam, Tanzania. The release occurred on February 18 at a point (09°09'S, 40°26'E) about 92 km offshore from Kilwa Masoko, Tanzania, 2,193 km north of the capture site (bee-line).

The transmitters were attached to the top of the carapace using standard methods (Balazs et al. 1996; Papi et al. 1997). Turtles were localised by the Argos satellite system which classifies the fixes into six classes of decreasing accuracy (within 1 km of the true location for the three most accurate classes). Turtle speed over the ground was calculated by dividing the distance between successive fixes by the time between them. The routes followed by the turtles were reconstructed disregarding those fixes that were considered erroneous (213 out of 1,438) either because they were on land or inferred a swimming speed exceeding 6 km/h (a threshold value estimated from speed values calculated from high-accuracy localisation only).

The transmitters also sent information about the turtles' diving parameters by means of an onboard software that took into account the pattern of closure of a salt-water switch suppressing underwater transmissions (see also Hays et al. 1999). Mean dive duration and number of dives in a specified time interval of 6 h were transmitted, disregarding submergences of less than 10 s. The percentage of time spent submerged in each interval was calculated by multiplying the number of submergences by their mean duration. Diving data were filtered by excluding those values leading to a percentage of time submerged higher than 100%.

In the analysis of the turtles' routes, we considered they had reached their feeding grounds when they were localised for more than 1 month in the same limited area and displayed a charac-

teristic diving pattern consisting in few and long submergences, typically recorded in turtles staying at their residential feeding quarters (Papi et al. 1997; Hays et al. 1999).

Results

Experiment A

The routes reconstructed for turtles A1 and A2 are shown in Fig. 2. Turtle A1 was first localised 28 h after her release on 27 February, when she was 26 km southeast of the release site. In the following days, she remained in the general area of release, circulating at low speed (Table 1), and making few, long submergences. On 10 March she then started to move decidedly westwards at a higher speed, and this led her to cross the Mozambique Channel in a gently winding route. Her speed generally remained >1.5 km/h during the whole crossing, except for a period between 20 and 23 March when she moved in a generally southwestern direction at a mean speed of 0.9 km/h. During the crossing, she made more submergences, shorter in duration (Table 1).

On 3 April the turtle was about 80 km east of mainland Africa, but did not orient immediately towards the coast, rather making a southwesterly divagation of about 260 km, more or less parallel to the coast (Fig. 2). In this divagation, the turtle moved at high speed (2.6 km/h) and made a large number of very

Table 1 Performances of turtles released in experiment A. The straightness index was calculated as the ratio between the direct-line distance between the first and the last fix of the leg and the total length of the leg (Batschelet 1981). SEM Standard error of the mean

Period (1998)	Mean speed (km/h)	Mean duration (min) of submergences in 6-h periods (mean \pm SEM)	Number of submergences in 6-h periods (mean \pm SEM)	Percent of time submerged in 6-h periods mean \pm SEM)	Straightness index
Turtle A1					
27 Feb–10 Mar	0.7	14.5 \pm 1.7	35.6 \pm 4.4	92.9 \pm 0.6	0.27
10 Mar–3 Apr	1.7	8.6 \pm 0.8	55.1 \pm 3.8	90.7 \pm 1.2	0.82
3 Apr–7 Apr	2.6	4.9 \pm 1.3	113.6 \pm 32.9	92.1 \pm 3.2	0.95
7 Apr–9 Apr	1.9	5.0 \pm 0.7	74.7 \pm 8.2	95.8 \pm 0.6	0.72
9 Apr–2 May	1.4	9.8 \pm 0.8	45.9 \pm 3.4	96.0 \pm 0.3	0.76
2 May–5 Jun	0.3	26.5 \pm 1.8	17.1 \pm 1.4	94.0 \pm 0.2	0.11
Turtle A2					
1 Mar–4 Mar	0.7	21.1 \pm 4.2	19.2 \pm 3.7	92.1 \pm 0.6	0.43
4 Mar–27 Mar	1.9	13.7 \pm 1.4	48.5 \pm 6.1	86.4 \pm 2.6	0.69
27 Mar–14 Apr	0.8	43.7 \pm 5.5	12.6 \pm 1.8	95.2 \pm 0.8	0.03
14 Apr–4 May	2.6	21.8 \pm 3.5	44.0 \pm 8.2	93.0 \pm 1.3	0.92
4 May–16 May	1.3	32.5 \pm 6.0	33.3 \pm 9.5	94.6 \pm 0.8	0.77
16 May–25 May	2.8	9.7 \pm 2.9	79.4 \pm 13.7	87.2 \pm 5.5	0.94
25 May–8 Jun	3.0	13.9 \pm 2.4	48.5 \pm 6.9	90.6 \pm 3.0	0.97
8 Jun–19 Jun	1.3	27.9 \pm 5.3	22.7 \pm 4.5	96.3 \pm 0.4	0.94
19 Jun–5 Jul	2.2	16.8 \pm 2.5	39.7 \pm 5.6	93.4 \pm 0.7	0.59
5 Jul–21 Jul	1.5	23.8 \pm 5.7	34.1 \pm 6.7	93.7 \pm 2.1	0.92

short submergences (Table 1). On 7 April she then stopped and changed her direction, swimming decidedly towards the coast, reaching it on 9 April. She then started to follow the Mozambique coastline, at a somewhat lower speed, increasing her mean submergence time and decreasing the number of dives (Table 1). After 2 May, she remained in a small area off the town of Beira where she was localised until the end of the tracking on 5 June, making very few and long submergences (Table 1). She was therefore assumed to have reached her residential feeding grounds.

Like her companion, turtle A2 remained in the general area of release for some days, displaying circuitous movements at low speed some 30 km south of the release site, and making few and long submergences (Table 1). On 7 March, she left this area, swimming northwards and then bearing westwards (Fig. 2), reaching the eastern coast of Madagascar slightly south of the Gulf of Helodrano Antongila on 27 March. During this open-sea track section, the turtle moved at higher speed, and made more and shorter dives (Table 1). During her stay in the coastal waters, she circuted at low speed and made few submergences of extremely long duration (Table 1). After 20 days, however, the turtle left this area, starting to move in a generally southward direction, following an offshore course more or less parallel to the east coast of Madagascar, with an occasional detour on 21 April. During this southward section, the turtle proceeded in a rather straight line at high speed, making many short submergences (Table 1), especially in the section between 27 April and 4 May (mean speed 3.5 km/h; number of submergences 62.7; mean dive duration 18.6 min). On reaching a latitude higher than the southernmost part of the island, she abruptly turned and swam northwestwards towards the coast, reaching it on 11 May, and left again a few days later, when a westward segment was observed. All these movements

were made at a rather low speed, and with fewer, longer submergences (Table 1).

From 16 May, the turtle increased her speed, starting to cross the Mozambique Channel in a route surprisingly similar to that taken by turtle A1 some months before (Fig. 2). Like her companion, turtle A2 made frequent and short dives (Table 1) but she swam at a higher speed (means 2.8 versus 1.7 km/h). However, she did not cross the whole channel, as she suddenly turned in the middle of it on 25 May, starting a 1,000-km-long straight movement in a northward direction at high speed, with many and short submergences (Table 1). In this way, she reached the continental coast of Mozambique on 8 June, which she followed for about 300 km, swimming at low speed, making fewer and longer submergences than before (Table 1). On 19 June, she left the coast for a short visit to the Comoros Islands, then back to the coast at a rather sustained speed and with short submergences (Table 1). Her last leg was a slow movement (Table 1) along the coast, up to north of Zanzibar Island, reaching it on 21 July. A few hours later, her transmitter began to emit from a point on land, with diving data indicating that it was out of water.

Experiment B

Upon release on 18 February 1999, turtles B1, B2 and B3 started to move decidedly northwards at some distance from the coast, covering 410–730 km in that direction (Fig. 3). They swam at a similar, high speed (means 2.9, 2.8 and 3.2 km/h, respectively), with submergences 15–18 min long (Table 2). On 24 February, turtle B1 stopped along the east coast of Zanzibar Island (Fig. 3), where she remained until 19 March wandering at low speed. She then slowly moved southwards, reaching the waters west of Mafia Island

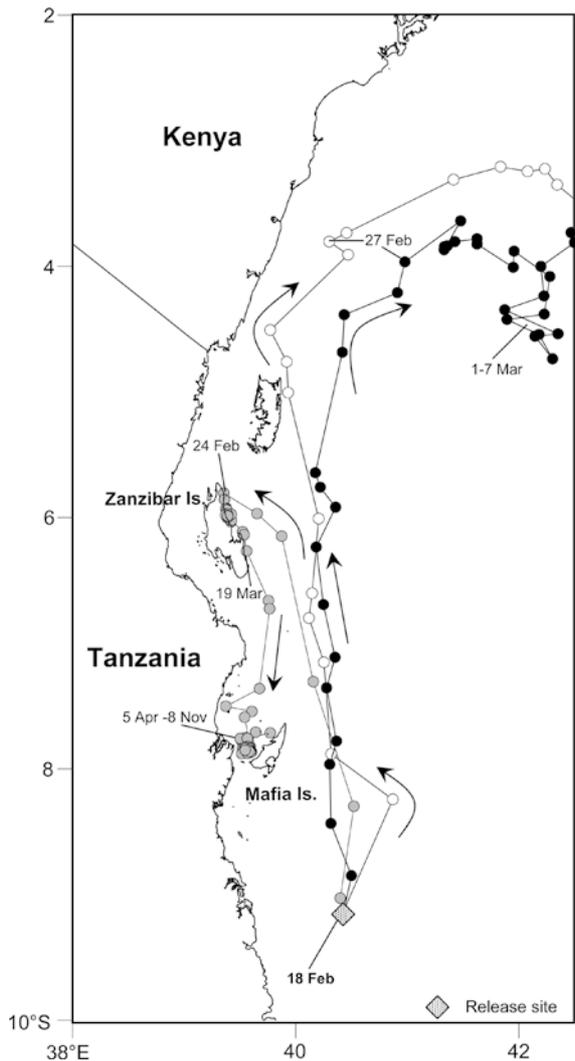


Fig. 3 *Caretta caretta*. Initial part of the routes of turtles B1 (shaded circles), B2 (black circles) and B3 (open circles) after their release off Kilwa Masoko, Tanzania

(Fig. 3) on 5 April, where she remained until 8 November. During this period she made very long and few dives (Table 2), and was assumed to have found her feeding grounds.

The other two turtles, in contrast, left the coast taking a very similar curved path until the end of March, first moving east, then southeast and finally northeast (Figs. 3, 4). During this period, they generally maintained a rather high speed and made short submergences (Table 2), especially during turtle B2's northeastward leg (mean speed reaching 4.4 km/h). An exception was a short circuitous section that turtle B2 made between 1 and 7 March (Fig. 3), when she proceeded at low speed (mean 1.3 km/h), making less frequent and prolonged dives (means of 14.1 dives, and 25.5 min duration).

Thereafter, the tracks of the two turtles diverged, with turtle B2 remaining in oceanic waters and turtle B3 returning to the coast. During the months of April to September, turtle B2 alternated straight and winding

sections, moving in a generally northeastward direction and crossing the equator (Fig. 4). She moved at variable speed (Table 2) and her diving behaviour did not correspond to that observed before (nor to that of the other turtles, either), as she started to spend much less time submerged than usual. From the beginning of April, for instance, 6-h periods in which the turtle spent less than 10% of the time submerged began to be recorded, and in 21 of these 6-h periods, the turtle made no submergences at all. In particular, between 3 and 22 May, the turtle stayed submerged on average for only 28.7% of the time, with 18 instances of no dive in a 6-h period.

After reaching the Somali coast on 4 April, turtle B3 made short movements at low speed along the coast until 18 June (Fig. 4; Table 2). Her submergences, which were short during her approach to the continent, became longer and fewer (Table 2), as if she had reached suitable feeding areas. Like turtle A2, however, she left the coast without having stopped for more than 21 days in any location visited, and first moved quickly northwards and then returned to the open sea from the end of June (Fig. 4). She then meandered in a general eastward direction, at a sustained speed and with rather short dives (Table 2). Between 28 and 31 July, in three instances, the turtle spent less than 5% of her time submerged, making no submergence in one 6-h period.

By the end of September, the two turtles were west of the Maldives Archipelago, about 450 km apart. Suddenly, they started to move quickly northeastwards, converging on an oceanic spot around 2.0°N, 70.5°E, where they passed, about 12 h apart, on 10 October. They then made a quick, coincident southeastward movement towards the atoll of Huvadū, Maldives, which they reached separately on 13 and 14 October (Fig. 4). During the section approaching the atoll, both turtles moved faster than before, with turtle B3 making fewer and much longer dives (Table 2). Turtle B2 remained in the water inside the atoll for 8 days making fewer and longer dives (Table 2), while turtle B3 was always located outside the atoll and passed by it in a few days (Fig. 4), only decreasing her speed and making longer dives (Table 2). She then continued to move eastwards at a sustained speed, taking a very straight, W–E oriented path, nearly reaching the coast of Sumatra (Fig. 4). Her last locations, around mid-November, indicated that she was decreasing her speed, being around 87°E at about 750 km west of Sumatra.

As she left Huvadū Atoll on 22 October, turtle B2 too made a straight eastward leg at high speed (Table 2), strikingly similar to that made by the other turtle some days before. During this leg, she made many dives of short duration (Table 2). On 13 November, while she was around 87°E, she started to turn northwards, decreasing her speed, and finally taking a northeastward direction from 23 November (Fig. 4), moving again at enhanced speed and making fewer and longer dives (Table 2). She was last located on 2 December, 380 km southeast of Sri Lanka.

Table 2 Performances of turtles released in experiment B

Period (1999)	Mean speed (km/h)	Mean duration (min) of submergences in 6-h periods (mean \pm SEM)	Number of submergences in 6-h periods (mean \pm SEM)	Percent of time submerged in 6-h periods (mean \pm SEM)	Straightness index
Turtle B1					
18 Feb–24 Feb	2.9	14.6 \pm 3.5	53.5 \pm 17.2	90.2 \pm 0.6	0.94
24 Feb–19 Mar	0.2	10.0 \pm 2.1	78.0 \pm 10.8	94.0 \pm 0.3	0.65
19 Mar–5 Apr	0.5	21.4 \pm 4.8	37.2 \pm 9.4	93.5 \pm 0.7	0.76
5 Apr–8 Nov	0.0	33.4 \pm 1.7	16.4 \pm 1.6	95.9 \pm 0.3	0.03
Turtle B2					
18 Feb–28 Feb	2.8	18.1 \pm 1.7	26.6 \pm 7.1	90.5 \pm 0.3	0.81
28 Feb–30 Mar	2.3	20.3 \pm 1.5	23.1 \pm 2.1	90.4 \pm 1.8	0.56
30 Mar–6 Apr	3.9	7.0 \pm 0.8	55.1 \pm 4.8	91.6 \pm 2.4	0.52
6 Apr–30 Sep	1.7	12.1 \pm 0.6	40.6 \pm 2.1	69.6 \pm 1.6	0.26
30 Sep–10 Oct	2.2	11.4 \pm 0.9	32.3 \pm 2.6	98.5 \pm 0.2	0.94
10 Oct–13 Oct	3.4	12.7 \pm 4.0	34.3 \pm 7.8	96.4 \pm 0.5	1.00
13 Oct–21 Oct	0.1	17.9 \pm 3.5	23.6 \pm 4.9	98.6 \pm 0.5	0.53
21 Oct–13 Nov	3.0	13.4 \pm 2.2	59.2 \pm 10.9	85.9 \pm 2.3	0.98
13 Nov–23 Nov	1.5	10.5 \pm 2.0	59.5 \pm 9.8	88.4 \pm 2.2	0.63
23 Nov–2 Dec	2.8	15.6 \pm 2.8	40.1 \pm 7.9	92.4 \pm 0.8	0.76
Turtle B3					
18 Feb–25 Feb	3.2	17.1 \pm 1.8	23.4 \pm 2.3	93.0 \pm 0.2	0.91
25 Feb–19 Mar	2.6	16.2 \pm 1.8	34.6 \pm 3.9	92.8 \pm 1.1	0.70
19 Mar–4 Apr	2.0	7.2 \pm 0.7	62.7 \pm 7.3	88.4 \pm 1.9	0.79
4 Apr–18 Jun	0.9	20.4 \pm 1.3	29.3 \pm 2.3	94.4 \pm 0.6	0.13
18 Jun–5 Oct	2.5	14.1 \pm 0.9	37.1 \pm 3.1	85.0 \pm 1.7	0.41
5 Oct–14 Oct	3.3	31.2 \pm 5.3	16.8 \pm 5.3	95.7 \pm 0.6	0.92
14 Oct–16 Oct	1.5	17.4 \pm 4.6	23.7 \pm 7.3	96.5 \pm 0.1	0.87
16 Oct–14 Nov	2.6	17.3 \pm 2.2	29.6 \pm 3.8	96.0 \pm 0.4	0.96

Discussion

Although necessarily based on a small sample size, the present findings allow some inferences on loggerhead spatial movements to be drawn. First, it is remarkable how turtles B2 and B3 wandered in the open ocean for as long as they were tracked, i.e. for 9 months or more, whereas adult loggerheads are considered to spend most of their life in fixed, commonly neritic habitats (Hughes 1974; Dodd 1988; Limpus et al. 1992; Musick and Limpus 1997). The turtle behaviour is not attributable to their incapacity to approach the coast, since they were released close to it and B3 even reached it again during her subsequent movements. Despite the fact that she had a front flipper truncated, turtle B2 did not appear to be handicapped with respect to her companion, their open-sea tracks being very similar. Adult loggerheads therefore seem able to deliberately switch to a pelagic lifestyle, a behaviour more typical of juvenile and sub-adult loggerheads, which spend most of the developmental phase in the oceanic environment (Musick and Limpus 1997), opportunistically feeding on pelagic invertebrates (Nichols et al. 2000; Polovina et al. 2000). It is noteworthy that this habit has recently been recorded in a few adults of the Japanese population (Hatase et al. 2002).

During her stay in the middle of the Indian Ocean, turtle B2 (and on a few occasions turtle B3, as well) exhibited long periods in which she spent a long time at

the surface, sometimes not diving for many hours. This is a rather unexpected behaviour, since loggerheads, and marine turtles in general, are known to stay for most of their time (usually above 90%) submerged (e.g. Renaud and Carpenter 1994; Papi et al. 1997; Hays et al. 1999). However, since juvenile loggerheads are known to concentrate their predatory activity on neuston (Polovina et al. 2000), it is very possible that our turtles were feeding on floating prey. Another possibility is that they were basking at the sea surface to regulate body temperature (Spotila et al. 1997), although it is unclear why they should have concentrated this behaviour only in a limited part of their long stay in open ocean.

Another interesting aspect of the turtle tracks is the long straight eastward movement of B2 and B3 turtles which first converged on the same spot as if they had been attracted to it (Fig. 4), and later followed the same course for 1½ months, covering over 1,600 km, independently of each other, 0.5–3 days apart. It is hard to hypothesise the existence of any attracting cue emanating from a very distant point in the open sea. Sea currents probably played a major role in this process. It is known that during the transition period between the southwest to northeast monsoons (i.e. September–October), an equatorial jet current flows eastwards in the Indian Ocean at a speed of around 3.6 km/h (Wyrski 1973). The speed recorded during the convergence of the two turtles and the subsequent eastward legs is close to this current speed (Table 2), supporting the explanation

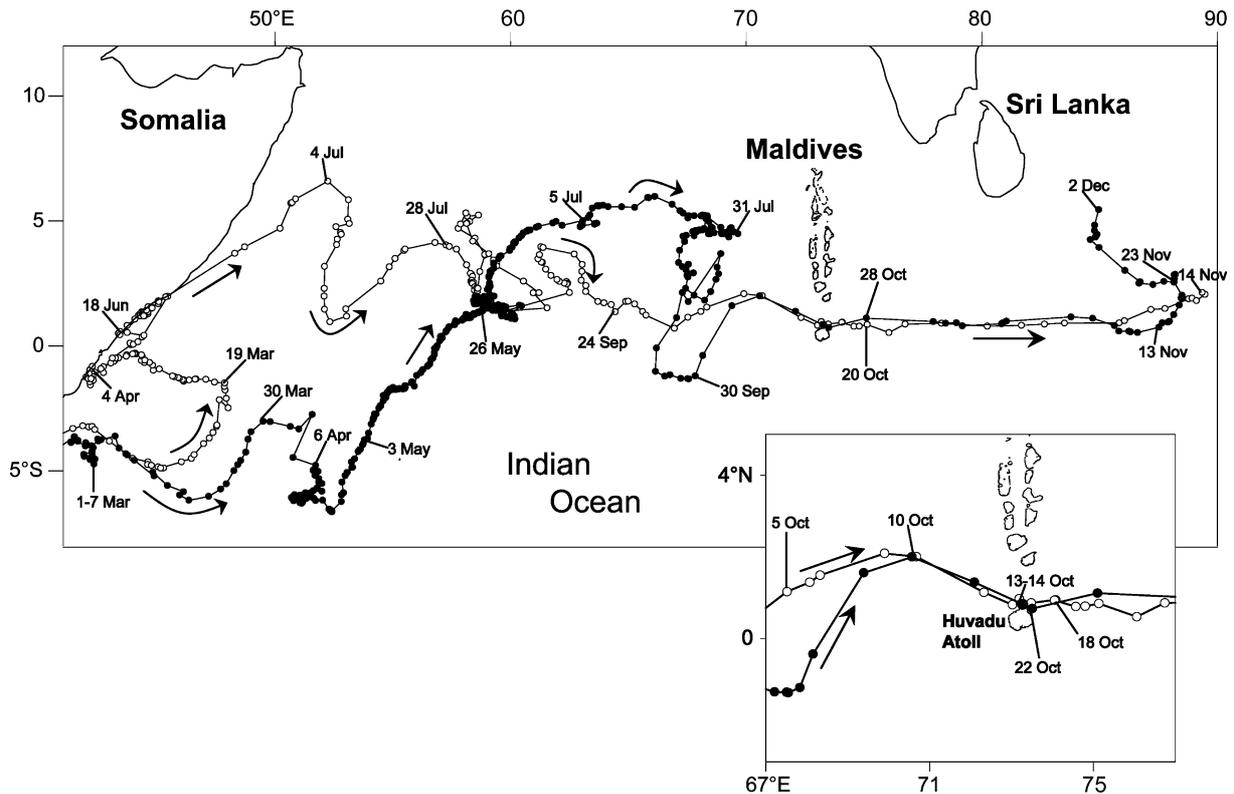


Fig. 4 *Caretta caretta*. Reconstructed oceanic movements of turtles B2 (black circles) and B3 (open circles). The inset box shows details of their contemporaneous approach to Huvadhu Atoll, Maldives

that the turtles were probably drifting with the current. The final change in course and the decrease in speed we observed may derive from the seasonal decline of the jet, as well as from other oceanographic processes at the eastern boundary of the jet (e.g. the presence of Kelvin and Rossby waves; Vinayachandran et al. 1999).

The present results also shed some light on the navigational mechanism(s) used by the displaced turtles. The turtles in the present experiments were captured at the end of their reproductive season, and their movements have therefore to be interpreted as aiming at reaching their residential feeding grounds which were shown to be individual-specific (Limpus et al. 1992). An alternative hypothesis is that loggerheads may not display fidelity to specific foraging sites, as has been recently argued, considering that their large prey spectrum may not impose any need on them to forage at a specific site (Godley et al. 2003). The behaviour of our displaced turtles was however not in accordance with this interpretation. Turtles A2, B1 and B3, for instance, stopped for up to 3 weeks in localised coastal areas displaying a movement and diving pattern typical of a stay in residential grounds, but then left these (presumably favourable) sites. This behaviour is what can be expected for a turtle having not found her residential area and thus having to search further for this specific target. Limpus et al. (1992) actually predicted that migrating loggerhead females, having made a previous

migration and having found a good foraging site, should not select a new feeding area even if closer to the one previously occupied.

A serious difficulty in evaluating the behaviour of the displaced turtles is that we did not know their intended destinations. The distribution of the recovery sites (Fig. 1), however, shows that their most probable destination was northwest of the release sites for turtles A1 and A2 and south of the release site for B1–B3 turtles, with the 75% of the recovery sites located on the East African coast. If turtles were endowed with a system of true navigation or with a simplified form limited to latitude determination, they would be expected to be able to use cues perceived at the release site (Wallraff 1991) and to compensate for their displacement either heading towards their target in direct routes or at least reducing their distance from home.

Under these premises, we can now examine the behaviour of each turtle. Turtles A1 and B1 most probably relocated their feeding grounds along the Mozambique coast. Turtle A1, however, did not orient directly towards her target (i.e. northwestwards from the release site). The most obvious interpretation of her behaviour is that she first moved westwards to reach the familiar stretch of the coast she knew to be oriented N–S with the open sea to the east and then swam northwards along the coast until she reached her feeding grounds. Similarly, turtle B1, in spite of the large distance of her displacement, turned out to have been released somewhat south of her feeding grounds. She actually moved north after release, but she went beyond the latitude of her feeding ground which she reached only after having

approached the coast of Zanzibar Island. Thus, she too was apparently unable to establish either her position or latitude for a long while after release.

The behaviour of turtle A2 is puzzling, mainly because her tracking was abruptly stopped thus preventing us from ascertaining whether she had found her target residential grounds. Since she moved northwards along a stretch of the African continental coast (roughly from 17° to 6°S; Fig. 2) without stopping, it is likely that her feeding grounds were north or south of this stretch. If they were at Zanzibar or north of it, her initial movements towards the north and west may be seen as the output of a true navigation mechanism allowing her to point directly towards this area. However, a more logical interpretation of this first leg is possible, by assuming that it represents a combination of a tendency to reach the African coast and to move according to the presumably migratory direction. Inconsistent with both interpretations is the fact that, when she found the formidable obstacle represented by Madagascar Island, she decided to swim around the south of it. This change of general orientation remains unexplained and we can only note that the turtle might have been influenced by the southern branch of the East Madagascar Current, flowing southwards (Tomczak and Godfrey 1994). The change of course in the middle of the Mozambique Channel also appears to be appropriate to move towards a northern target. The detour to the Comoros Islands appears energetically expensive and apparently useless. Such detours from the straight course have however been sometimes observed during the spontaneous movements of turtles (Cheng 2000). If, on the other hand, her feeding grounds were south of her point of approach to the continental coast, she was clearly unable to locate them, and all her movements have to be considered long-distance searches for her target.

The most interesting and revealing behaviour was that of turtles B2 and B3. Initially they moved northwards for about 650 km, then headed eastwards. If these turtles had their feeding grounds on the Madagascar coast, such a course would have been appropriate to lead them from their nesting beach to their target. Having been displaced, they found themselves in open sea. The successive oceanic movements of the two turtles were apparently not directed towards a target. In fact, it is very unlikely that they both were heading towards a feeding ground in the northern Indian Ocean, since this would entail a shuttling migration between sites more than 6000 km apart, a distance which largely exceeds the longest two-way migration known in any turtle species (Meylan 1982). We conclude that the feeding grounds of these two turtles were, as expected, south of the release site and that the turtles were unable to compensate for the northward displacement by detecting a latitudinally-varying factor such as geomagnetic inclination (Lohmann et al. 1999) or by using a true navigation mechanism.

A detailed interpretation of the factors affecting the single turtle journeys would only be possible by taking into consideration the various physical and biotic factors

that might have exerted an influence on turtles (e.g. sea currents and other oceanographic features, plankton distribution), which is beyond the scope of the present paper. We think however that even the plain analysis of the turtle behaviour after displacement has provided indications on the homing mechanisms used by loggerheads during their migrations. The present findings fail to provide clear evidence in accordance either with the hypothesis that South African loggerheads possess a true navigation system based on the earth's magnetic field or other physical parameters, nor that they are able to establish the local latitude. The behaviour of turtle A2 and, especially, of turtles B2 and B3 provided no indications that they were able to compensate for long-distance displacement, or even to appropriately react to latitudinal shift. These negative conclusions are in contrast with those drawn from previous displacements performed with this loggerhead colony (Papi et al. 1997) and with Malaysian green turtles (Luschi et al. 1996). These findings apparently revealed turtle ability to compensate for relocation, but the releases were made along coasts and/or at short distance from the capture site. On the other hand, the results of more systematic oceanic displacements recently carried out with green turtles nesting at Ascension Island are in good agreement with the present ones, showing a general lack of ability to compensate for the displacement by using true navigation (Luschi et al. 2001).

Additionally, the present findings and those of a previous study (Papi et al. 1997) allow the proposal of a general picture of the migratory behaviour and navigational ability of South African loggerheads. In many cases, these turtles have nesting and feeding grounds on the African continental coast, so they find it convenient to migrate along the coast until they recognise their target (be it the feeding or the nesting area). In this task they probably find support in simple spatiotemporal programmes (Berthold 1991), which inform them of the distance to be covered and make it easier to recognise the visual and/or chemical cues of the goal site, thus allowing them to avoid mistaking it for similar ones encountered in a probably monotonous replication of similar habitats encountered during the trip. In this recognition process, they neither estimate their latitude nor calculate their position on a true navigational map. Replicating their trips along the coast would even permit the turtles to acquire a map of familiar landmarks following one another along their linear trip. If displaced away from the coast during migration, a simple compass orientation towards the West, based on the knowledge of the relative position of the coast and the sea, would be sufficient for the turtles to regain the coast and to continue their coastwise migratory movement in a northward direction. Turtles nesting on the KwaZulu-Natal rookery but spending the non-reproductive years on the Madagascar or Seychelles coast have probably to rely on more complicated spatiotemporal programmes and/or to acquire a wider map of familiar sites inclusive of their relative geographic directions.

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