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Long-term monitoring of leatherback turtle diving behaviour during oceanic movements

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Abstract

The diving behaviour of four leatherback turtles (*Dermochelys coriacea*) was recorded for periods of 0.5–8.1 months during their postnesting movements in the Indian and Atlantic Oceans, when they covered 1569–18,994 km. Dive data were obtained using satellite-linked transmitters which also provided information on the dive depths and profiles of the turtles. Turtles mainly dove to depths <200 m, with maximum dive durations under 30–40 min and exhibited diel variations in their diving activity for most part of the routes, with dives being usually longer at night. Diurnal dives were in general quite short, but cases of very deep (>900 m) and prolonged (>70 min) dives were however recorded only during daytime. The three turtles that were tracked for the longest time showed a marked change in behaviour during the tracking, decreasing their dive durations and ceasing to dive deeply. Moreover, diel variations disappeared, with nocturnal dives becoming short and numerous. This change in turtle diving activity appeared to be related to water temperature, suggesting an influence of seasonal prey availability on their diving behaviour. The turtle diving activity was independent on the shape of their routes, with no changes between linear movements in the core of main currents or looping segments in presence of oceanic eddies.

Keywords: Deep scattering layer; Diel pattern; Diving activity; Postnesting movements; Dive profiles; Satellite telemetry

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1. Introduction

The biology of the leatherback turtle (*Dermochelys coriacea* Vandelli) is poorly known mostly because of its life habits. Leatherbacks are cosmopolitan and

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spend most of their life in the open sea travelling long distances while searching for pelagic prey (Bleakney, 1965; Pritchard, 1976; Boulon et al., 1988; Hughes et al., 1998). In contrast to other sea turtles, this critically endangered species is not limited to tropical or subtropical waters but is also found at high latitudes, probably thanks to its capacity to thermoregulate (Paladino et al., 1990). A central aspect of leatherback turtle behaviour is the diving activity that is intimately linked to foraging on pelagic prey. So far leatherback diving behaviour has been mostly studied during the so-called internesting period, i.e., between successive egg-layings of the reproductive cycle. These studies, in which turtles were equipped with data loggers, showed that leatherback turtles dive continually with surface intervals of short duration and are able to reach considerable depths (Eckert et al., 1986, 1989; Keinath and Musick, 1993; Southwood et al., 1999; Eckert, 2002; Reina et al., 2005).

Only recently, the use of satellite telemetry through the Argos system has made it possible to extend the study of leatherback diving behaviour to the postnesting journeys, when the diving activity most probably differs from that recorded during the internesting periods (Hays et al., 2004a). Since leatherback movements usually extend over a spatial scale of thousands of kilometres (Morreale et al., 1996; Hughes et al., 1998; Eckert, 1998; Ferraroli et al., 2004; Hays et al., 2004a,b) and may be strongly influenced by oceanographic factors (Luschi et al., 2003), the turtle diving behaviour can display spatial and temporal variations, being influenced by environmental factors such as water temperature or local availability and vertical distribution of food resources. As a consequence, leatherback diving behaviour can be expected to show a high degree of variation (Hays et al., 2004a). In the present study, the diving behaviour of four South African leatherbacks was monitored for up to 242 days as they moved in oceanic waters ranging over widely dispersed areas.

2. Materials and methods

2.1. Turtles T1 and T2

These turtles were encountered on the nesting beaches of the Maputaland Marine Reserve, Northern KwaZulu-Natal, South Africa, on 31 Jan. 1999, and were equipped with ST-6 platform transmitter terminals (PTTs; Telonics Inc., Mesa, AZ, USA) linked to the Argos system (see http://www.argosinc.com for details). The routes of these turtles, together with that of a further leatherback tracked in the same area in 1996, are described in another paper (turtles B and C in Luschi et al., 2003), where details about the PTT deployment and tracked routes can also be found. In short, turtles T1 and T2 generally followed the SW-directed course of the Agulhas Current, alternating straight segments and gyrations and reached the productive waters South and East of the continent, in one case even pushing as far as the southern Atlantic Ocean (Figs. 1, 2). Most parts of the turtle routes turned out to be determined by major oceanic features present in the areas crossed (Luschi et al., 2003).

Deployed PTTs had a salt water switch which suppressed their transmissions while the turtles were underwater and allowed the on-board software to calculate the number and the duration of dives in successive predefined 4-h time intervals. Submergences lasting less than 10 s were disregarded, so that transmitters recorded a dive as any time the salt water switch was wet for more than 10 s.

A pressure sensor measured turtle depth every 30 s and the single recordings were assigned to one of 8 depth intervals (bins): 0–10 m; 10–30 m; 30–70 m; 70–120 m; 120–200 m; 200–300 m; 300–500 m; 500–1400 m. At every surfacing of the turtle, the PTT transmitted 12 values: internal PTT temperature recorded immediately after previous transmission, mean dive duration, longest dive duration, number of dives, and total number of records for each of the 8 depth bins in a 4-h period. This method based on binned data rather than on individual dive profiles is frequently used to compress large amount of information to be transmitted by the PTT (see also Godley et al., 2002; Polovina et al., 2003).

Mean dive depth was calculated using the formula $[\sum n_{(\mathrm{Bin}\ X)} * (\mathrm{bin\ range}_x/2)]/N$, where $n_{(\mathrm{Bin}\ X)}$ is the number of records for the xth depth bin, bin range is the amplitude (in meters) of the xth bin and N is the total number of depth records during the 4-h period. Therefore, mean dive depth is a measure of the depth at which a turtle spent most of its time during each 4-h period. An estimation of total dive time per 4-h period

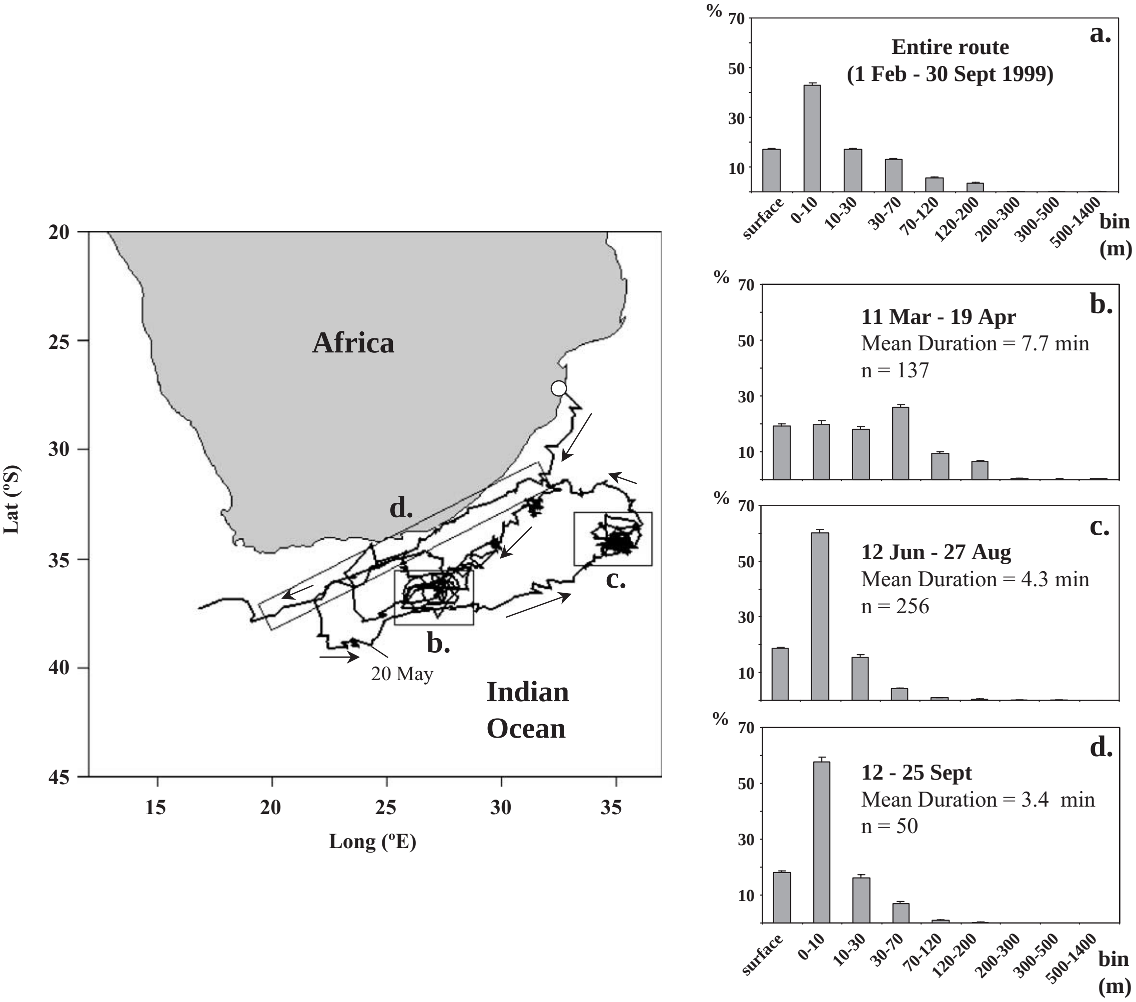

Fig. 1. Reconstructed track of turtle T1. Inserts show the turtle time-at-depth frequency distributions for the entire route (a) and for three differently shaped segments of the route (b–d, dates as indicated). Turtle position on 20th May is also indicated. The white circle indicates the location of the nesting beach.

was obtained by multiplying the number of submergences by mean dive duration in the same period, disregarding those cases in which data were erroneously processed or transmitted and led to a dive time percentage higher than 100%. Moreover, since depth was sampled every 30 s and data were summed per 4-h periods (i.e., 14,400 s), the maximum number of depth records in the 8 bins was expected to be 14,400/30 = 480, for every data set. Uplinks whose binned data had a value higher than 480 were therefore disregarded. These procedures led to discard 9.7% of total data sets.

2.2. Turtles T3 and T4

These turtles were approached while nesting on the Maputaland beach mentioned above on 13 Jan. 2002 (turtle T3) and on 29 Jan. 2003 (turtle T4). They were equipped with Satellite Relay Data Loggers, manufactured by the Sea Mammal Research Unit of the University of St. Andrews, UK. These Argos-linked transmitters employ a pressure sensor to measure depth every 4 s (to an accuracy of 0.33 m). A bespoke on-board software then processes the recorded depth data before transmission to satellites. A dive was con-

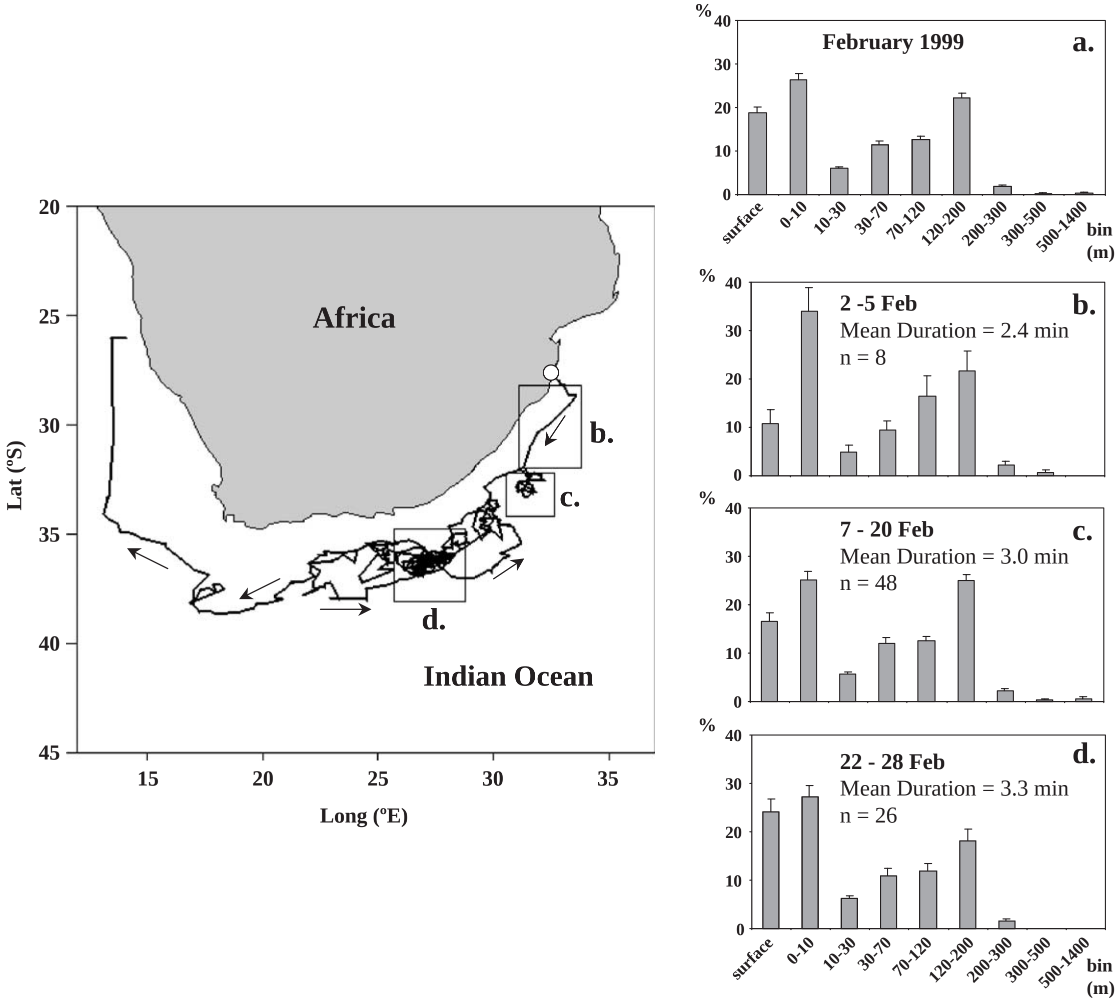

Fig. 2. Reconstructed track of turtle T2. Inserts show the turtle time-at-depth frequency distributions for February (a) and for three differently shaped segments of the route (b–d, dates as indicated). The white circle indicates the location of the nesting beach.

sidered to occur every time the turtle dove below 2.0 m for at least 30 s. Dives were distinguished between shallow and deep if the maximum depth reached was above or below 10 m, respectively. In the present analysis, only deep dives, which represent the vast majority of recorded dives, were considered. For each deep dive, the software examined the dive profile and determined the time and depth of the five most significant points of inflection during the dive. The time and depth of these five points along with the dive end-time and dive duration were then transmitted, allowing a reconstruction of individual dive profiles. For dives longer than 5 min, we also calculated the "bottom time percentage" as the percentage of time spent between the maximum depth for that dive and a threshold set equal to the 90% of this maximum depth.

In addition, each transmitter repeatedly relayed summary information averaged over 6 h on mean dive duration and mean and maximum depth (see also Hays et al., 2004a). The PTT used on turtle T4 also relayed temperature data recorded at various depths through a conductivity–temperature–depth sensor: for the present analysis, only data collected between 5 and 7 m were used, which best portray surface temperatures and are best comparable with the temperature data obtained in the other turtles.

2.3. Data analysis

For diurnal vs. nocturnal analysis, only data referring to periods which were completely nocturnal or diurnal were used. Day was considered to begin at the end of the morning nautical twilight and to end at the beginning of the evening nautical twilight. With a sample size of 4 turtles, statistical comparisons between subsets of data obtained from the same turtle (e.g., in different part of year or day) were limited by the lack of independence between multiple observations. Therefore, the relation between time series of temperature and various diving parameters (see below) was tested through Bravais–Pearson test, adjusting for autocorrelation effects by decreasing the degrees of freedom of tested datasets.

3. Results

3.1. Turtles T1 and T2

Turtles T1 and T2 were tracked for 242 and 223 days, and diving data after the discard procedures were obtained for 805 and 634 4-h periods, respectively. Since turtle T2's depth data were unavailable after 30 days of tracking (possibly due to a failure in depth sensor), only depth data for February ($n = 120$) were used; however, saltwater sensor-derived data on dive number and duration were successfully recorded all over the entire route.

3.1.1. General diving activity

The number of submergences and percentage of time spent submerged by turtles T1 and T2 during their journeys are reported in Table 1. In general, the turtles displayed a similar diving pattern (Fig. 3). Mean dive duration was mostly shorter than 8 min, with 10–20 dives being usually made per hour. Maximum dive duration in the single 4-h intervals was under 40 min in the 96.5–97.2% of cases. The percentage of time spent submerged was generally over 75% and showed few changes (Table 1). In turtle T1, the time-at-depth frequency distribution in the entire route had most recordings in 0–10 m depth range, with progressively fewer records in the deeper bins (Fig. 1a). Turtle T2 (in February) displayed a somewhat bimodal pattern with many records also in the 120–200 m depth range (Fig. 2a).

Table 1
Statistics of diving parameters recorded from the turtles during their entire journeys (mean ± S.E.)

Turtle	*n*	Mean dive duration (min)	Number of dives/h	Percentage of time spent diving
T1	805	5.54 ± 0.18	15.16 ± 0.32	84.89 ± 0.33
T2	634	4.24 ± 0.12	15.23 ± 0.32	77.70 ± 0.61
T3	41	16.86 ± 0.50	2.78 ± 0.12	74.21 ± 1.16
T4	301	14.90 ± 0.31	1.40 ± 0.05	34.36 ± 1.49

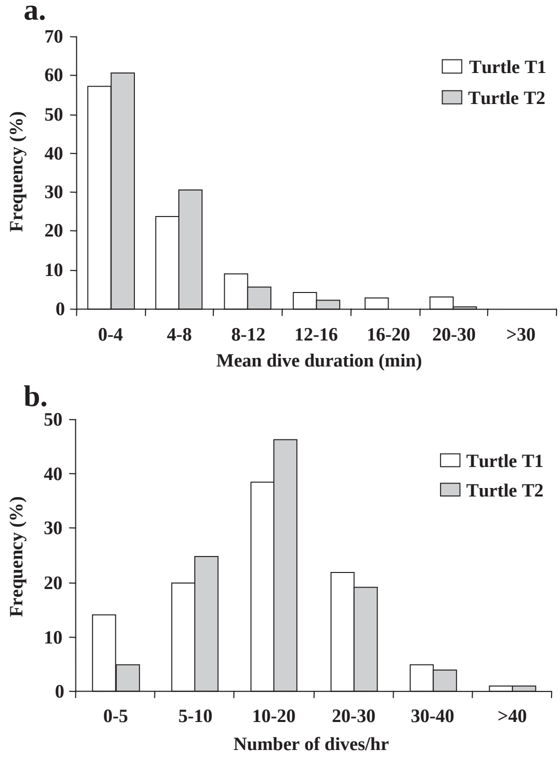

Fig. 3. Frequency distributions of mean dive durations (a) and number of dives per hour (b) recorded in 4-h intervals for turtles T1 and T2 during the entire routes.

Only occasional records were obtained for depths below 200 m, but the two turtles were also found to make very deep dives below over 500 m. These very deep dives were recorded in 21 different 4-h periods, nearly all in the central hours of the day. In these periods, longest dive duration exceeded 30 min, with a maximum duration of 59.7 min. In six instances, the turtles made dives longer than 70 min, with turtle T1 diving once for 82.3 min, to our knowledge the longest turtle dive ever recorded. During the three 4-h periods including dives longer than 70 min, the maximum depth reached by turtle T1 was always shallower than 200 m, and the same holds true for turtle T2 in the single period for which we have corresponding depth data.

3.1.2. Temporal changes in diving behaviour

During the 7–8 months of tracking, turtles T1 and T2 covered 18,994 and 14,063 km, respectively, moving over large areas in the South-western Indian Ocean and even shifting to the south Atlantic Ocean (Figs. 1, 2; Luschi et al., 2003). The diving behaviour of both turtles changed throughout the tracking period (Fig. 4). For turtle T1, major changes occurred after the first 3.5 months of tracking: it is therefore convenient to divide her route in two parts, before and after 20 May, a date after which she started to decidedly move NE-ward and then circled for months before re-entering the Agulhas Current mainstream (see Fig. 1). In the first part of the route, her dives were longer and deeper than in the second one (dive duration, means ± SEM: 7.2 ± 0.3 and 4.2 ± 0.2 min; dive depth: 51.5 ± 1.8 and 15.1 ± 1.0 m; $n = 358$ and 448, respectively).

In the first part, diurnal dives were shorter than nocturnal ones (means ± SEM: 3.7 ± 0.3 and 10.8 ± 0.6, $n = 156$ and 139, respectively, for day and night). The time-at-depth frequency distribution showed a more superficial pattern during daytime and a preference for the 30–70 m bin during the night (Fig. 4, insert [a]). However, since very deep dives below 300 m occurred exclusively during daytime, mean dive depth was shallower, albeit only slightly, during the night (means ± SEM: 53.0 ± 3.6 m for daytime and 47.2 ± 1.8 m for nighttime,

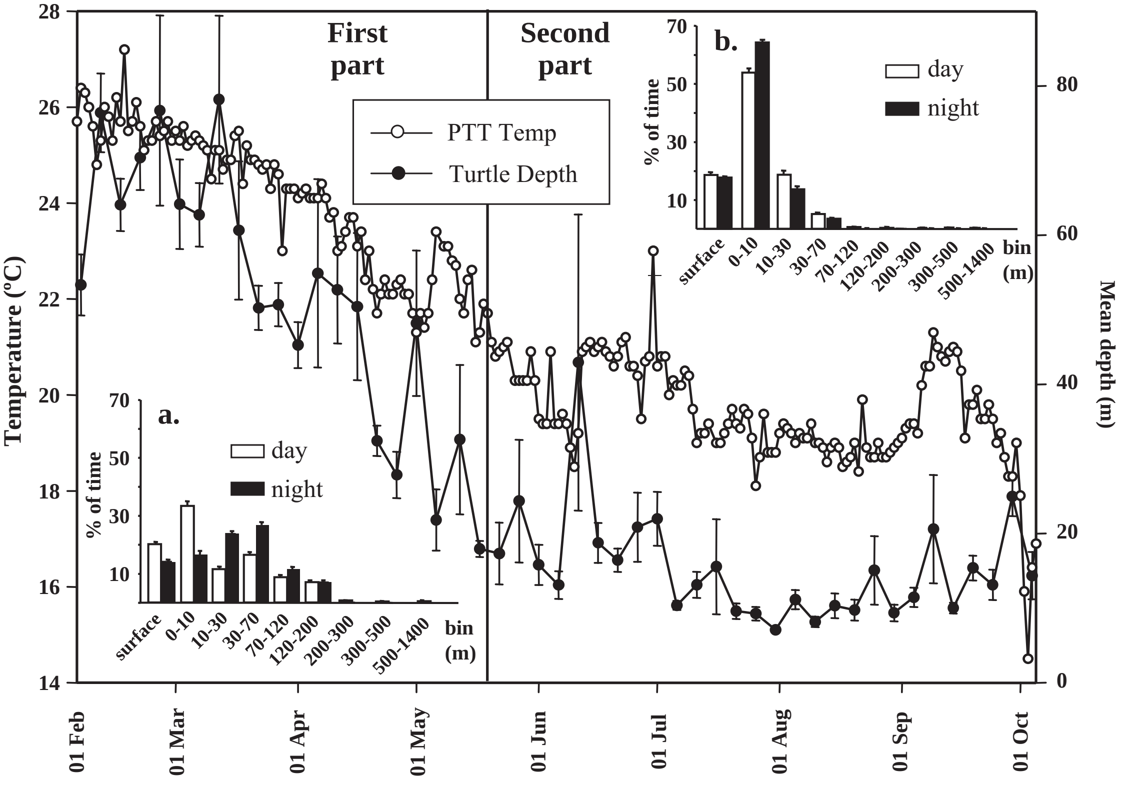

Fig. 4. Turtle T1: changes in dive depth (5-day means ± SEM) and in PTT temperatures (daily means) during the tracking period. Inserts show the time-at-depth frequency distributions (means ± SEM) during daytime (white) and nighttime (black), in the first ([a] Feb.–May) and second ([b] May–Oct.) part of the route. Diel differences in diving pattern disappeared in the second part of the turtle journey.

$n=156$ and 139, respectively). In the second period, these diel differences disappeared, as a result of a change in turtle diving behaviour at night, when dives became very short and shallow. Dive duration was indeed similar for day and night (means ± SEM: 4.8 ± 0.3 and 3.8 ± 0.1 min, $n=197$ and 212, respectively for day and night) and the nocturnal dive depth distribution shifted towards the surface (Fig. 4, insert [b]). Both diurnal and nocturnal dives were considerably shallower than in the previous period (means ± SEM of second vs. first period: diurnal dives, 20.5 ± 0.3 vs. 53.0 ± 3.6 m; nocturnal dives, 10.2 ± 0.3 vs. 47.2 ± 1.8 m). Again, submergences over 200 m were recorded only during daytime (Fig. 4, insert [b]).

One major change that occurred between these two periods was a decrease in water temperature as revealed by PTT-sensed temperature values. In the first period (Feb.–May), the turtle remained within the warm waters of the Agulhas Current system at a mean temperature of 24.1 °C, with lowest values never below 21.1 °C (Fig. 4). From May onward, a general decrease in temperature was evident, although with some variations. In this period, the temperature was nearly always below 22 °C (mean 19.6 °C in this period, with a minimum of 14.3 °C), even when the turtle moved northward and back into the warmer Agulhas Current in September (Figs. 1, 4; see also Luschi et al., 2003). Corresponding changes in temperature were qualitatively seen in AVHRR satellite images of sea surface temperature (see Luschi et al., 2003). Daily means of depth and PTT temperature only showed a trend towards a significant correlation (Bravais–Pearson test corrected for autocorrelation, $r=0.76$; $df=4$; $P=0.079$).

Turtle T2's diving behaviour mostly exhibited the same daily pattern shown by turtle T1 in the first part of her route, with nocturnal dives being more prolonged than diurnal dives (means ± SEM: 6.0 ± 0.2 and 2.8 ± 0.2 min, $n=198$ and 199, respectively for night and day). These differences were paralleled by a different diving activity at various depths, with a bimodal preference for near-surface submergences and the 120–200 m interval during daytime, and for the 30–200 m range at night (Fig. 5). Like for turtle T1, diel differences in dive duration disappeared in the very last part of turtle T2's route, with dives becoming short also during nighttime (means ± SEM: 2.7 ± 0.2 and 2.7 ± 0.5 min, respectively for night and day). In this period, the turtle was West of the African continent, presumably within the Benguela current (Luschi et al., 2003), when the PTT temperatures reached the lowest values (mean during the period: 15.5 °C). Also for turtle T2, deepest dives (over 300 m) occurred only during daytime.

3.1.3. Diving behaviour and shape of the route

The diving pattern of the tracked turtles appeared to be not related to the shape of the route. This is shown by comparing dive duration values in qualitatively similar or different parts of the routes (Figs. 1, 2). For instance, turtle T1's mean dive duration during

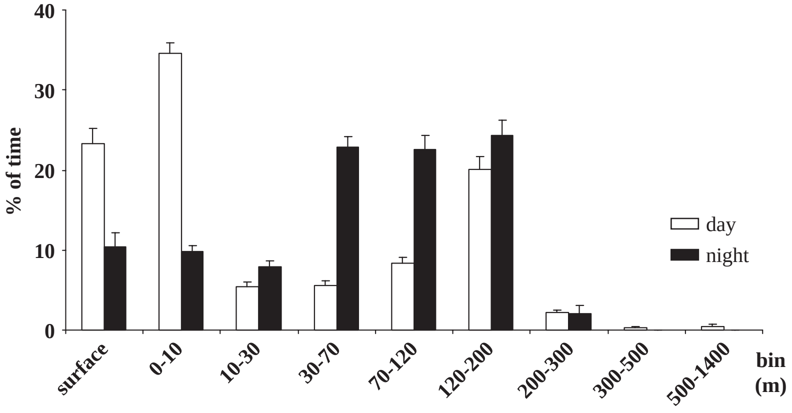

Fig. 5. Diel differences (day, white; night, black) in time-at-depth frequency distribution of turtle T2 during February (means ± SEM).

the prolonged circuitous movements performed between June and August in an oceanic eddy (Fig. 1c) was similar to that recorded during the successive linear movement in the core of the Agulhas Current (Fig. 1d), but it was different from that recorded during some similarly shaped loops previously made in March and April (Fig. 1b). Most noticeably, the same pattern emerges when analysing the time-at-depth distributions in distinct legs of the route. Dive depth distributions were different in two circling parts of the route (cf. Fig. 1b vs. c) but remained identical when the turtle ceased to circle in late August and successively covered a linear leg within the main course of the Agulhas Current (cf. Fig. 1c vs. d). Also in the February part of turtle T2's journey, dive depths were similar when she linearly drifted in the current mainstream (Fig. 2b) and when she performed extensive loops (Fig. 2c, d).

3.2. Turtles T3 and T4

Turtles T3 and T4 were tracked for 16 and 168 days, during which they covered 1569 and 8643 km. They initially followed a course generally similar to the previous turtles, moving SW with a straight path, mostly coincident with the mainstream of the Agulhas Current (Fig. 6). Like turtle T2, turtle T4 later on shifted from the Indian to the Atlantic Ocean, in the Benguela current area (Richardson et al., 2003), where she followed a more circuitous path.

3.2.1. General diving activity

Mean dive durations in 6-h periods were substantially longer than in the other turtles (Table 1). For turtle T4, the mean percentage of time submerged was much smaller than for the other three turtles (Table 1), as a result of major changes in this parameter which occurred throughout the tracking period (see below). Maximum depths reached were 240 m for turtle T3 and 940 m for turtle T4.

Dive profiles (Fig. 7) have been reconstructed for a total of 277 (turtle T3) and 1265 (turtle T4) dives. The vast majority of these dives were shorter than 30 min (100% for turtle T3; 98.7% for turtle T4), with a maximum duration of 44.5 min recorded in turtle T4 for a dive reaching a depth of 849.8 m.

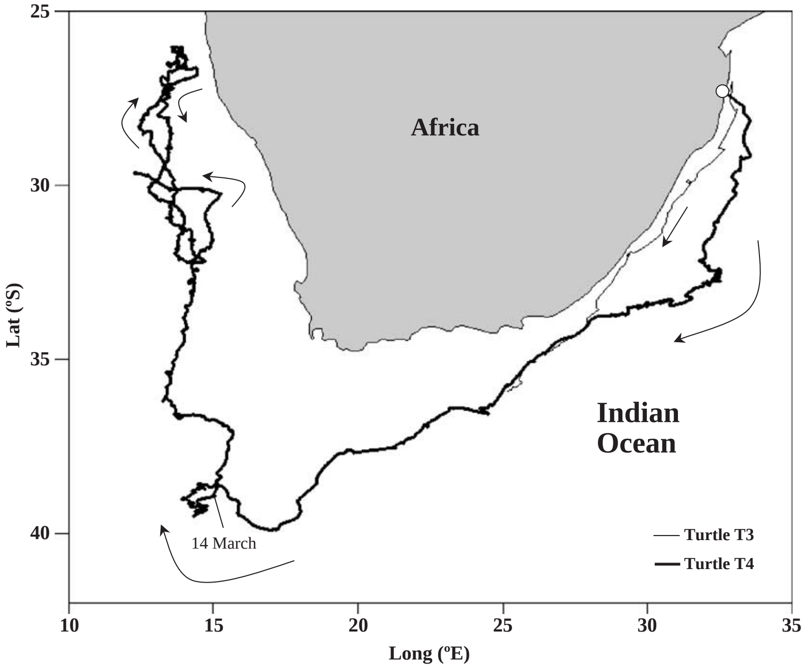

Fig. 6. Reconstructed tracks of turtle T3 (thin line) and T4 (thick line). The white circle indicates the location of the nesting beach.

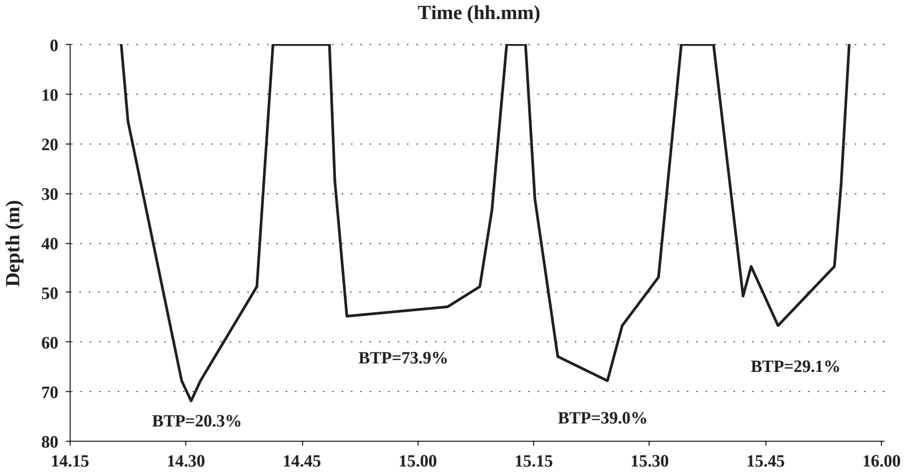

Fig. 7. Example of profiles of four consecutive dives made by turtle T4 on 1 April 2003. Bottom time percentage (BTP) calculated for each dive is also reported.

The turtle took 18.9 min to directly reach a depth of 786 m, then decreased her descent rate to reach the maximum depth in further 6.3 min. Her ascent was similar to the initial descent, as she swam for 19.3 min to reach the surface from 850 m depth. Bottom time percentage of dives longer than 5 min was mostly between 10 and 50% (256 dives out of 262, 97.7% in turtle T3; 1093 dives out of 1198, 91.2%, in turtle T4). This means that the vast majority of dives displayed a similar, basically V-shaped (Schreer et al., 2001), profile (Fig. 7). This prevalence remained constant throughout the tracking period.

3.2.2. Temporal changes in diving behaviour

Both mean dive duration and dive depth decreased markedly during turtle T4's route (Fig. 8a), especially from the beginning of March onward (i.e., when the turtle was moving in the Atlantic Ocean). A similar pattern was evident for the percentage of time spent submerged (Fig. 8b), which dropped from about 60% in early March to less than 10% in late June. As for turtle T1, these changes in turtle T4 diving behaviour appear to be related to water temperature: daily means of dive duration and depth were in this case significantly correlated to daily water temperature (Bravais–Pearson test corrected for autocorrelation, $r=0.759$; $df=7$; $P=0.018$ for duration; $r=0.612$; $df=12$; $P=0.020$ for depth). Similarly, the maximum depth reached in single dives displayed a significant correlation with water temperature (Bravais–Pearson test corrected for autocorrelation, $r=0.429$; $df=20$; $P=0.046$).

There were diel differences in the percentage of time spent diving, with turtle T3 diving on average for the 69.5% of the time during the day and 79.6% during the night and turtle T4 spending the 24.1% of time diving during the day and the 43.3% during the night. In turtle T3, no relevant diel differences were observed for dive depth and durations in data averaged over 6 h (mean durations ± SEM: 16.7 ± 0.7 and 17.2 ± 0.9 min for diurnal and nocturnal dives, $n=16$ and 12; mean depths ± SEM: 70.5 ± 2.5 vs. 66.5 ± 3.2 m; maximum depths ± SEM: 113.8 ± 5.5 vs. 110.1 ± 13.2 m).

In turtle T4, major differences in diel patterns of diving were noted in different part of the routes. These changes are most clearly shown by dividing her route in two parts, before and after 14 March, when she started her decided northward movement in the Atlantic Ocean (Fig. 6). In the first part, mean dive duration was slightly shorter during daytime than at night (means ± SEM: 19.2 ± 0.9 vs. 23.6 ± 0.8 min, $n=20$ and 14, respectively, for day and night) and dives were deeper during the day (mean depths ± SEM: 91.9 ± 12.2 vs. 75.0 ± 5.5 m; $n=20$ and 14, respectively for day and night). In

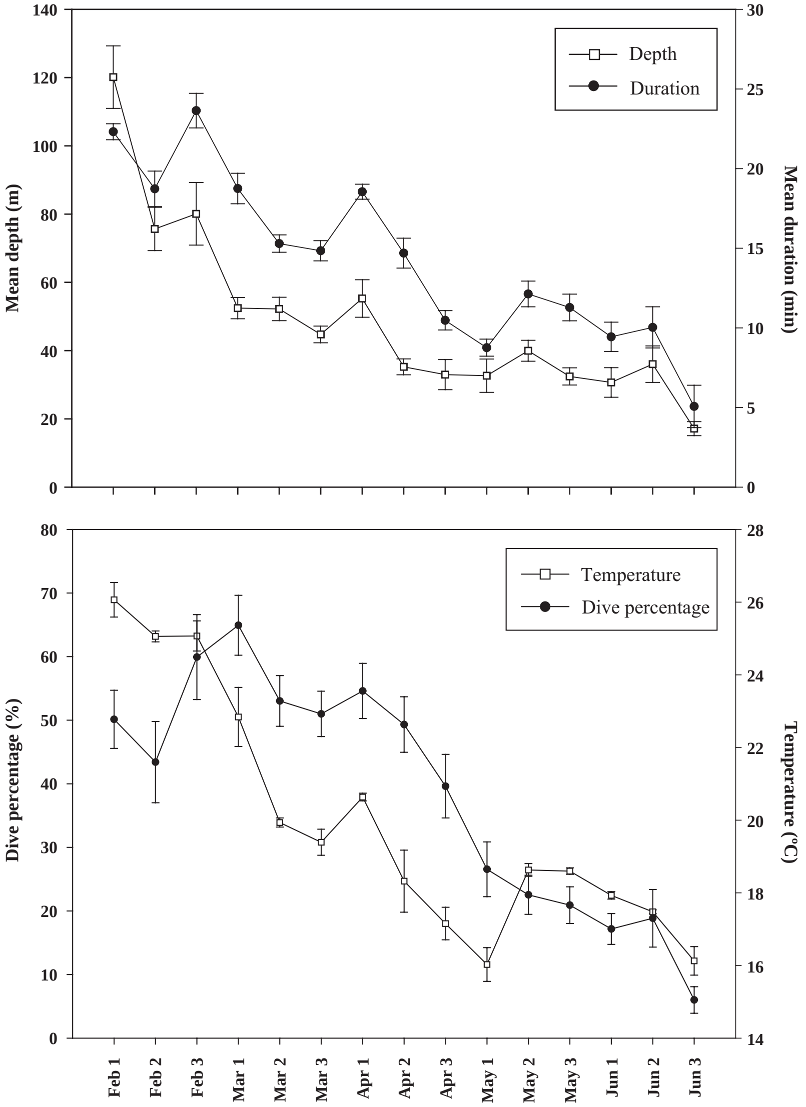

Fig. 8. Changes in dive percentage, mean depth and duration for turtle T4 and corresponding changes in surface water temperature throughout the tracking period. Data shown are 10-day means (± SEM) of the summary information on diving behaviour averaged over 6 h and of temperature values recorded at 5–7 m depth, as relayed by the transmitters.

the second part, no such diel differences in dive duration were observed (means ± SEM: 13.0 ± 0.5 and 12.6 ± 0.6 min for diurnal and nocturnal dives, $n = 47$ and 50), and both nocturnal and diurnal dives became shallower (mean depths ± SEM: 37.9 ± 2.7 m during daytime, and 30.4 ± 2.0 m at night, $n = 61$ and 56). Data derived from the recorded dive profiles showed the same pattern.

4. Discussion

4.1. General diving behaviour

Mean dive times recorded in turtles T1 and T2 (4.2–5.5 min; Table 1) are shorter than those recorded in other studies employing time–depth recorders during the internesting period (6.7–13.5 min; Eckert et al., 1989, 1996; Eckert, 2002; Southwood et al., 1999; Standora et al., 1984). This is most probably the result of the way Telonics transmitters were programmed. Since they regarded as dives all cases in which the salt water sensor was wet for more than 10 s, they could have considered as real dives also those instances in which turtles were just bobbing down near the surface (see also Keinath and Musick, 1993). These very short "dives" could therefore have artificially altered the overall values of dive number and duration. Dive duration values obtained through satellite telemetry are indeed lower (2.3–3.2 min; Keinath and Musick, 1993; Hughes et al., 1998). Similarly, mean dive times recorded in turtles T3 and T4 (16.9 and 14.9 min) are higher than the values of the other two turtles, and similar to those reported by Hays et al. (2004a) relying on the same PTT models, which only consider dives deeper than 10 m. In any case, we recorded instances of mean dive durations exceeding 20 min in turtles T1 and T2 as well (Fig. 3a), with single submergences being in 6 cases longer than 70 min.

The main pattern shown by the turtles was that of making continuous sequences of quite short dives, at least for the majority of their routes. This is in broad accordance with previous findings (e.g., Eckert et al., 1989; Southwood et al., 1999; Reina et al., 2005), and suggests that leatherbacks generally tended to remain within their aerobic diving limit, a strategy which is thought to allow to optimise the time spent underwater and to re-dive almost immediately once emerged (Eckert et al., 1986; Costa et al., 2001). While the at-sea aerobic dive limit of leatherback turtles has never been measured, Southwood et al. (1999) suggested that this limit is between 33 and 67 min in internesting leatherbacks, considering the postdive surface intervals of single recorded dives and the metabolic rates previously measured in nesting females. Hays et al. (2004a) estimated this limit to be around 40 min, having found that the dives of postnesting leatherbacks very rarely exceeded this duration. Our data, showing that dives of all turtles were mostly under 40 min (under 30 min for turtles T3 and T4), are in good agreement with these findings and confirm that 30–40 min constitutes an important threshold for diving leatherbacks. We however recorded several instances in which the leatherbacks undertook dives longer than this, even reaching the record duration of 70–80 min. Although for this finding the possibility of a failure in the opening of the salt water switch when the animals reached the surface to breathe cannot be excluded, dives of comparable durations have been recorded with data loggers in internesting leatherbacks (Southwood et al., 1999). Interestingly, when making these very prolonged dives, turtles did not reach large depths, but rather stayed in the upper part of the water column and so the prolonged submergence was not due to the attempt of reaching deep waters. The reason for these rare long dives remains enigmatic.

The tracked leatherback turtles sometimes dove to depths over 900 m, in accordance with data recorded in other leatherbacks making oceanic movements (Hays et al., 2004a,b). While depth data for turtles T1 and T2 were binned and referred to 4-h periods preventing to record parameters of each individual dive, dive profiles obtained for turtles T3 and T4 are in this respect much more informative and allow a better interpretation of the leatherback diving behaviour (see also Hays et al., 2004a). In most cases, dive profiles of turtles T3 and T4 had a similar shape, with turtles diving to a given depth and returning to surface rather directly (Fig. 7; Eckert, 2002). Only a few of them presented a prolonged flat-bottom part, as it is commonly found in other turtles during internesting (e.g., Hochscheid et al., 1999; Hays et al., 2000). This pattern resembles that recorded in internesting leatherbacks (Eckert et al., 1989; Southwood et al., 1999; Eckert, 2002; but see Eckert et al., 1996, Reina et al., 2005, who recorded also flat-bottomed dives to sea floor occurring during internesting) and indicates that turtles mostly travel through the water column without stopping at intermediate depths, probably exploring it in search for prey.

4.2. Diel variations

The four turtles exhibited a diel pattern in their diving behaviour, at least for most part of their routes. This is best shown by the time-at-depth distributions of turtles T1 and T2 (Figs. 4a; 5), in which a daytime preference for shallow depths (<10 m, with occasional dives to depths over 200 m) was clear, while the nocturnal activity was more evenly distributed roughly in the range 30–200 m. This pattern is thought to derive from turtles foraging within the deep scattering layer (Eckert et al., 1989), which consists in zooplankton that makes diel vertical movements in response to light levels, moving to the surface at night but descending below 600 m during the day (Eckert et al., 1989; Hays, 2003). Nocturnal dives were accordingly longer than during the day, as it is expected to occur when prey are more readily available and foraging success is high (Thompson and Fedak, 2001). Depths over 200 m were only reached during daytime, when occasional deep dives interrupted the common pattern of staying mostly near the surface, making short, shallow dives (most likely not related to feeding; Eckert et al., 1989; Reina et al., 2005). These occasional deep dives are thought to have an explorative function, whereby turtles search for their prey that are usually deeper during daytime.

4.3. Long-term variations in diving behaviour

There is little information available as to how leatherback diving behaviour changes during long-distance movements, when turtles are certainly bound to encounter variable environmental conditions. Hays et al. (2004a) have recently recorded marked changes in leatherback diving behaviour as their tracked turtles moved out of the Caribbean into the more productive Atlantic waters, with dives becoming longer. A similar tendency to increase dive durations in areas suitable for foraging has been found in a leatherback previously tracked in the southern Indian Ocean (Hughes et al., 1998).

Turtles T1, T2 and T4, which have been tracked for long periods, exhibited clear-cut changes during the last part of the tracking, their dives becoming shorter and shallower, as if they were in areas with a limited availability of prey. This however seems not to be the case for these turtles, which indeed visited productive waters such as those of the Subtropical Convergence or of the Benguela current system (Luschi et al., 2003). Furthermore, diel differences in diving behaviour disappeared, and turtles concentrated their activity in the most superficial water layers at any time, lacking the nocturnal shift towards longer dives. This constitutes an especially intriguing finding giving the wide occurrence of diel differences in diving behaviour of marine animals (e.g., Wilson et al., 1993; Putz et al., 1998; Bennett et al., 2001). The decrease in water temperature recorded for all turtles can provide a possible clue to explain these changes in diving behaviour, as indicated also by the positive correlations between PTT temperatures and turtle dive depth and duration. It is conceivable that the low temperatures encountered in the second part of their routes may per se have led the turtles to stay near the surface performing short dives (e.g., for thermoregulatory needs), but other factors that possibly co-changed with temperature may have affected turtle behaviour. A major role may have been played by temperature-dependent temporal (e.g., seasonal) changes in local distribution, composition and/or behaviour of prey. For instance, it is possible that a decrease in water temperature may have induced an higher availability of prey at shallower depths at any time of the day, leading turtles to shift to a pattern of numerous short dives in the second part of the routes, possibly improving diving efficiency (Houston and Carbone, 1992; see above). Instances of leatherback turtles feeding on jellyfish at the water surface during the day (i.e., on plankton that is not performing diel vertical movements) were reported by James and Herman (2001).

As previously found in another leatherback turtle tracked in the same area (Hughes et al., 1998), the diving activity of tracked turtles turned out to be independent on the shape of the route followed, with similar diving behaviour recorded in differently shaped segments (e.g., when turtles moved linearly in the Agulhas mainstream or circled within oceanic eddies), or different patterns recorded in similar looping segments (Figs. 1, 2). Moreover, even time profiles of the dives recorded in turtles T3 and T4 displayed little variation. This result provides support to previous findings on the strong influence exerted by current features on the horizontal movements of south African leatherback turtles (Luschi et al., 2003). Indeed, if the following linear or looping paths derived from the turtles' tendency to move to a new area or to stay in a particular patch of water, then one would predict that differences in diving behaviour would be detectable. For instance, green and loggerhead turtles have been shown to make short dives when migrating along straight paths and much longer dives when feeding in coastal waters at their foraging grounds (Hays et al., 1999; Godley et al., 2003). This was not the case in the present study, where leatherback turtles seemed to perform their dives independently from their actual geographical movements, that are therefore likely to be determined by major current features in the areas crossed, at least for most part of their journey (Luschi et al., 2003).

In conclusion, the present findings show how the prolonged monitoring of turtle movements and behaviour at sea can provide meaningful insights in many aspects of sea turtle biology. Such information is particularly important for endangered species, such as leatherbacks, that spend most of their life moving in remote oceanic areas far from land, and whose behaviour outside the nesting season is still very poorly known.

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