
Movement and diving behavior of late juvenile loggerhead sea turtles (*Caretta caretta*) in the Western Indian Ocean

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ABSTRACT

We conducted a satellite tracking study on juvenile loggerhead sea turtles in the Indian Ocean, where they have been poorly studied up to date. Eighteen individuals were released from Reunion Island (21.2°S, 55.3°E) to investigate movement and diving patterns of late juvenile stage in the region. Eleven turtles roughly swam towards Oman (20.5°N, 58.8°E), where one of the world largest rookery of loggerheads is located. Three individuals contrastingly went southwards off the coast South-Africa and Madagascar, countries that also host loggerhead nesting grounds. Fourteen transmitters allowed the processing of animal diving profile and we observed a dichotomy between diurnal and nocturnal diving behavior with a greater number of shorter dives occurring during the day. Diving behavior also differed according to movement behavior as individuals spent more time at subsurface (<10m) during transit phases. Our study provides a better understanding of the oceanic movements and diving behavior of juvenile loggerheads, and key information for conservation of this species, which is of major concern in the Indian Ocean and worldwide.

INTRODUCTION

Loggerhead sea turtles (*Caretta caretta*) are widely distributed worldwide throughout tropical and warm temperate waters. Despite this broad distribution, this species is classified as endangered in the IUCN red list (IUCN 2012). A striking life history trait of loggerheads is certainly their large-scale (ocean basin) developmental cycle. Basically, following an intense short swimming phase known as the “swim frenzy” (Wyneken and Salmon 1992) and a neritic transitional phase lasting from a few days to a few months (Musick and Limpus 1997), hatchlings enter the oceanic zone. Individuals then remain in the open ocean for numerous years, a phase referred here as juvenile oceanic stage (Bolten 2003). This stage of the developmental cycle was earlier referred as the “lost years” (Carr 1952; Carr 1986) or “lost

decade” (Musick and Limpus 1997) since it has long remained a stage with a lack of knowledge due to the hardly accessibility of this life stage. After this oceanic stage whose duration remains highly variable (Bolten 2003), loggerhead juveniles may recruit in neritic habitats before reaching sexual maturity (Bjorndal et al. 2000; Bolten 2003). However, neritic recruitment is not systematic and potentially reversible as it was shown that individuals can frequent the oceanic environment until sexual maturity (McClellan and Read 2007; Mansfield et al. 2009; McClellan et al. 2010). These two identified strategies both provide advantages in their life cycle; whereas neritic foraging strategy might be more energetically favorable for turtle development, oceanic foraging strategy may minimize exposure to predation (Peckham et al. 2011).

In the North-Atlantic Ocean, loggerhead development cycle occurs across the whole basin (Bolten 2003), from the western Atlantic nesting sites to the eastward islands of Azores, Madeira and Canary. Similarly, in the Pacific Ocean, genetic studies demonstrated that development cycle occurs at ocean scale from breeding sites in Japan, Australia and New Caledonia to the coast of Baja California and peninsula of Mexico (Bowen et al. 1995; Bowen and Karl 2007; Boyle et al. 2009). Nevertheless, if these studies provided a major step in the understanding of large scale movement patterns of the loggerhead juvenile stage in the Atlantic and Pacific Oceans, few focused on their diving behavior worldwide. A diel diving behavior has been observed on loggerheads during the open sea juvenile stage (Godley et al. 2003; Polovina et al. 2004; Howell et al. 2010), with daily dives being significantly shorter and more numerous than nightly dives. Recently, Howell et al. (2010) showed that, in the North Pacific Ocean, oceanic juveniles spend 80% of the time, day and night, at very shallow (0-5m) waters (90% in 0-15m). Moreover, this study revealed that the diving behavior was variable across meso-scale oceanic features, with turtles making deeper and longer dives when associated with more dynamic waters (Howell et al. 2010).

In the Indian Ocean, main nesting sites for loggerheads are located at the edge of the western part of the basin in the northern and the southern hemispheres (Baldwin et al. 2003; Halpin et al. 2009). Masirah Island (Sultanate of Oman; 20.5°N, 58.8°E) in the North is considered one of the world's largest nesting sites for this species (Ross and Barwani 1995). South-Africa (27.1°S, 32.8°E) and Mozambique (26.3°S, 32.9°E) are also known to host important nesting populations (Hughes 2010; Nel et al. 2013). In the south-western coast of Madagascar (23.8°S, 43.7°E), nesting events have also been reported, but nesting activity in this area is poorly documented and is known to be limited (Martel 2003; Rakotonirina 2011). Other secondary nesting sites have also been identified in Yemen, Sri Lanka or Australia (Halpin et al. 2009).

Whereas recent studies have addressed spatial dynamics of adult loggerheads in the western Indian Ocean (Oman: Rees et al. (2010); South Africa: Luschi et al. (2006)), only a minority concerns juvenile stages (*e.g.* Hughes (1973)), especially oceanic stage. The present study aims at investigating large movements and diving behavior of late juvenile loggerheads at oceanic stage in the western Indian Ocean. The main objective is to use satellite telemetry to characterize their large scale movement patterns in association with the environmental conditions in order to identify their foraging strategies. Our study thus aims at providing a better understanding of the oceanic movements and diving behavior of juvenile loggerheads, so as to provide key information for conservation of this species, which is of major concern in the Indian Ocean (Petersen et al. 2009) and worldwide (Lewison et al. 2004).

METHOD

Study area and sea turtle tracking

Late juvenile loggerhead individuals were accidentally captured by longliner fishing boats from Reunion Island (21.15°S, 55.27°E) operating in French and Madagascar exclusive economic zones (between 25°S and 16°S, and 49°E and 57°E; Online Resource 1 - Fig.1).

Following a collaboration protocol, fishermen declared to the official authorities (CROSS Réunion) any accidental capture of loggerheads for which on board hook extraction was not possible. Individuals were then brought to 'Kélonia Sea Turtle Observatory and Care Centre' (www.kelonia.org) where they received veterinary surgery for hook extraction and were placed in tanks at the care center after the surgery. General behavior and physiological parameters were regularly controlled by a vet.

A set of criteria had to be fulfilled in order to consider that the animal had recovered its natural body condition and could consequently be released: the wound had to be totally healed, the turtle had to feed correctly, put on weight, be able to swim actively and free of anemia or infectious disease (checked by blood analysis). Between 2007 and 2011, a total of 56 individuals were retrieved. Fourteen individuals (25%) died in the days following the operation. To date, 27 (48%) have been released, among which 18 were satellite tracked with Argos Platform Terminal Transmitters (PTTs).

We used four types of PTTs: A: TAM-4225, B: TAM-4325 and C: A-225 (Telonics, Inc., Mesa, Arizona), and D: SPOT-5 (Wildlife Computers, Inc., Bellevue, Washington). PTTs were attached on the second vertebral carapace scute with epoxy resin (Power-Fast and Pure2k; Powers Fasteners Inc., Wieringerwerf, Nederland). PTTs of types C and D were programmed to transmit data continuously whereas for PTTs of types A and B, transmission followed a duty cycle involving 24 hours "on" followed by 12 hours "off" to expand PTTs life expectancy. Turtles were released approximately 2 nautical miles off the west coast of

Reunion Island (21.15°S, 55.27°E) after a captivity period ranging from 33 to 260 days (Table 1).

Location and dive data acquisition

The mean \pm SD duration of PTTs was 158 ± 112 days (maximum 401 days, type A: 168 ± 53 , type B: 148 ± 21 , type C: 40 ± 17 , type D: 268 ± 162 , see Table 2). Location data were filtered in two successive stages: *ad-hoc* heuristic pre-filtering and state-space model (SSM) filtering. Pre-filtering consisted in removing 0 and Z class locations (which are of low precision according to CLS/Argos hierarchy), as well as on-ground locations (i.e. which appeared more than 1m above sea level on Gebco Gridded Global Bathymetry Data (Arendt et al. 2012; Mansfield et al. 2009) and locations involving a speed exceeding 15 km h^{-1} . SSM filtering was run using Breed et al. (2009)'s hierarchical correlated random walk model under R and WinBUGS (5000 iterations, a burn-in of 3000, a thin of 5 and two MCMC chains, as in Hoenner et al. (2012) who previously used this procedure on sea turtles and demonstrated that sea turtles locations accuracy was significantly improved).

PTTs of types A, B and C were equipped with depth sensors. Two kinds of parameters were recorded: single dive parameters and integrated dive parameters. Single dive parameters corresponded to last dive duration and maximum depth. Integrated parameters corresponded to number of dives, average duration, maximum duration, maximum depth, underwater percentage and time-at-depth histograms. They were computed over a given timeframe of either 12 h (types A and B) or 24 h (type C). Details of measured parameters and sampling frequency for each type of device are provided in

Table 3.

Types A and B were programmed to tabulate integrated dive data into 12-h periods 06:00-18:00 and 18:00-06:00 GMT+4 (roughly corresponding to daytime and night periods in the study area). The depth bins for the time-at-depth distributions were 10 m-width from surface up to 60m, and 20 m-width from 60 m to 120m. Two additional bins were used for deepest dives: 120-160-m and larger than 160 m. Type C was programmed to tabulate dive data into 24-h periods with 20 m-width depth bins from surface up to 180m.

Oceanic environment

The following environmental parameters were extracted along the filtered tracks using linear temporal and bilinear spatial interpolation: (1) sea surface temperature (SST), (2) net primary production (NPP), (3) sea surface currents and total kinetic energy per water mass unit (TKE). (1) Satellite-derived SST data were taken from the Moderate Resolution Imaging Spectroradiometer (MODIS), a major NASA EOS instrument aboard EOS-Aqua satellite (<http://oceancolor.gsfc.nasa.gov>; Savtchenko et al. (2004)). Datasets are available daily with a spatial resolution of 4.63 km. (2) Ocean NPP data were downloaded from Oregon State University (<http://www.science.oregonstate.edu/ocean.productivity/>). NPP calculation is based on the Vertically Generalized Production Model (Behrenfeld and Falkowski 1997). Datasets used for NPP calculation include MODIS surface chlorophyll concentrations, sea surface temperature and photosynthetically active radiation. Datasets are available at 8-days interval with a spatial resolution of 9km. (3) The surface currents were extracted from the GEKCO database which provides a satellite surface current product on daily basis at quarter degree resolution with a global coverage from 82°N to 82°S (Sudre et al. 2013). These current estimates are the sum of geostrophic current (resulting from the balance between the horizontal pressure gradient and the Coriolis force) and Ekman current (resulting from the

balance between the frictional stress due to the wind and the Coriolis force). These data were used both to compute motor (water masses-related) movements from recorded (ground-related) tracks and TKE ($TKE = 1/2 s^2$ where s is the current speed; Howell et al. (2010)).

Movement behavior

Turtles were divided into three groups depending on bee-line distance d traveled from release point and on overall bearing b . We distinguished turtles heading North ($d > 1,000$ km and $b > 295^\circ$ or $b < 65^\circ$), heading South ($d > 1,000$ km and $115^\circ < b < 245^\circ$) and non-dispersal (all others: $d < 1,000$ km). Horizontal movement bouts (hereafter simply refer to as movements) were classified as “oceanic transit” (OT), “coastal transit” (CT), “oceanic residency” (OR), or “coastal residency” (CR). Transit and resident phases were distinguished in terms of residence time (Barraquand and Benhamou 2008). Transit phases correspond to movement bouts characterized by lowest residence times, which are therefore assumed to occur in areas where turtles were just quickly passing through, whereas resident phases correspond to movement bouts characterized by highest residence times, which are therefore assumed to occur in concentrated-seaching, food-rich areas. Because oceanic currents can have a major influence on sea turtles tracks, we first computed the current-corrected tracks, corresponding to "motor" movements (*i.e.* performed with respect to water-masses) by subtracting the current effects to the ground-related (*i.e.* Argos recorded) tracks (see Girard et al. (2006) for details). Residence time was then computed within a 200 km-radius circle sliding along the motor track of each turtle. It corresponds to a well-behaved extension of the first passage time, which makes it possible to get a less noisy time series that can therefore more easily be segmented in different phases (see Barraquand and Benhamou (2008) for details). It was computed as the sum of the first passage time within the 200 km-radius circle and possibly of additional backward and forward time(s) spent in the circle with due care that the time(s) spent outside the circle before

re-entering it is not larger than a given threshold, set to 10 days in the present study. The 200 km radius was chosen because habitat selection of juvenile loggerheads is known to occur at scale of hundreds rather than tens of kilometers (Revelles et al. 2007). The limit of 10 days was set up to avoid irrelevant movement portions (further or prior to location) to be encompassed within residence time computation. The residence time series was segmented using Lavielle (2005) procedure applied to the mean resident time with a maximum number of 10 segments and a minimum of 20 locations in a segment. Segments were assigned to either transit or resident phases based on mean resident time over the segment, higher residence times corresponding to resident period. The whole procedure was repeated with radii of 100 and 300 km instead of 200 km, as well as with an unlimited time allowed outside the circle before re-entering it instead of 10 days so as to check that our results were not too sensitive to the choice of these parameters. No major differences were observed in the identification of the resident and transit phases. These phases were furthermore considered coastal, when taking place less than 100 km from any coastal area (continent or island) and oceanic otherwise.

Diving behavior

Regarding joint distributions of dive depth and dive duration, we identified three categories of dives: shallow and short dives (Dss: depth<30m, duration<13 min), shallow and long dives (Dsl: depth<30m, duration >13 min) and deep and long dives (Ddl: depth>30m, duration >13 min). Cut-offs of 13 min and 30m were chosen as limits between classes based on dive depth and dive duration distributions. When only dive duration was available (PTT type C), dives were either assigned to long dives (Dl; duration >13 min) or to short and shallow dives (Dss; duration < 13 min). Strictly speaking, the latter should have been considered only as short dives but, as dives with duration lesser than 13min were rarely deeper than 30m (0.27%,

based on data from PTT types A and B), they were very likely to be both short and shallow. The dives that did not meet any of these criteria (0.17%) were not assigned to any category.

Computations and Statistical analyses

Most analyses were performed using R software (R Core Team, 2012). Current-correction and residence time analyses were performed using home-made Pascal programs. Lavielle (2005) segmentation was performed using his Matlab script (<http://www.math.u-psud.fr/~lavielle/programs/dcpc.zip>).

RESULTS

Dispersal patterns

The mean \pm SD curved carapace length of individuals released with a satellite tag was 67.7 ± 5.4 cm (N = 18). The tracks of these 18 individuals are shown on Fig. 1. Eleven turtles were assigned to the northern group and four to the southern group. Northern turtles reached the latitude of Arabian Peninsula in the northern hemisphere while southern individuals traveled beyond South-African southern latitude. The remaining three were considered non-dispersal (Table 2). The mean \pm SD total distanced travelled was $2584 \text{ km} \pm 1354 \text{ km}$ (N = 18). The maximum beeline distance was 4,591 km (CC17 that reached the coast of the Sultanate of Oman). Turtles from the northern group and southern group respectively travel 22.0 ± 7.9 km/day and 17.1 ± 15.7 km/day away from the release point. There was no significant relationship between the size of the animals and the average daily straight-line distance travelled (Spearman rank correlation, $r_s = 0.04$, N = 18, P = 0.97). Neither was there any difference between the average size of individuals per group (Kruskal-Wallis test, $H_{25} = 1.35$, P = 0.51).

The 11 individuals of the northern group (N1-N11) displayed similar dispersal patterns. Their mean traveling direction roughly corresponded to the direction of Masirah Island (Oman), which host the main loggerhead rookery. N1-N5 traveled off the coast large of the Omanese and Yemeni coasts more than 3500 km away from the release point. N6-N9 headed to the south coast of Somalia and followed the coast to the north. N9 remained in the vicinity of the Somalian coast for more than 3 months in a narrow area of around 30 km long but the PTTs of N6-N8 however stopped transmitting while individuals were heading north. N10-N11 also moved north and their PTTs stopped transmitting when turtles reached the 12°S parallel.

The four southern turtles (S1-S4) traveled more than 1500 km away from the release point. S1-S3 travelled south-west from the released point. In contrast, S4 first went southward and later eastwards in the middle of the southern Indian Ocean. It was also the only tracked individual that crossed the 70°E meridian going eastward. All four turtles remained in oceanic areas.

For non-dispersal turtles (X1-X3), PTT transmissions stopped when turtles were still within 700 km from the release point. X3 followed a northerly route and remained in the vicinity of St-Brandon islands (670 km from Reunion Island) for more than 3 months. X1 and X2 remained oceanic. They followed atypical westward pathways moving toward Madagascar either straight (X1) or with loops (X2).

Movement behavior types

Behavioral modes – oceanic transit” (OT), coastal transit (CT), oceanic residency (OR), or coastal residency (CR) – along each track are shown in Online Resource 2. Overall, turtles spent most of their time in transit, and more specifically in oceanic transit (mean \pm SD, OT: 56.9 \pm 26.2%, CT: 18.4 \pm 25.3%, OR: 13.4 \pm 11.0%, CR: 11.3 \pm 22.5%, N = 18). The PTTs

of two non-dispersal turtles, X1 and X2, stopped transmitting while they were considered in OT. X3 spent 100 days in CR off St-Brandon islands and remained there until transmission was interrupted. Turtles of the southern group (S1-S4) exhibited almost exclusively OT or OR. These individuals did not travel along coastal areas except islands of Reunion and Mauritius shortly after release. None of them exhibited coastal residency. S2 and S3 noticeably exhibited long OR periods (113 days (72.7%) and 288 days (73.3%) respectively). Both turtles traveled along large circles (150-300 km of radius) either clockwise or anti-clockwise. S4 exhibited a slightly different movement behavior than other southern turtles as it spent most its time (53.2%) in OT. Individuals of the northern group traveled longer distances either in oceanic waters or in coastal areas of Somalia. N9 remained for 75 days in CR along a very narrow area of the Somalian coast. When reaching the Oman and Yemen waters, N1, N2 and N5 alternated long OR with short CR phases. Other individuals did not go northern than latitude 10°N.

Diving behavior

A total of 23362 dive durations (from 14 turtles) and 18688 dives depths (from 10 turtles) were recorded. The dive depth distributions show that $84.4 \pm 6.8\%$ (mean \pm SD; N = 10) of dives were shallower than 30 m and that $98.5 \pm 1.2\%$ (N = 10) of dives were shallower than 100 m. Another peak with larger dive frequencies appears around 55 m. About dive duration, $55.9 \pm 13.5\%$ (N = 14) of dives were shorter than 2 minutes and $86.2 \pm 9.0\%$ (N = 14) shorter than 30 minutes where second peak appears in the number of dives.

Mean frequencies of dives assigned to each dives types Dss, Dsl, Ddl and Dl were $78.8 \pm 13.8\%$ (N = 14), $5.8 \pm 4.8\%$ (N = 10), $14.8 \pm 6.8\%$ (N = 10) and $22.9 \pm 22.7\%$ (N = 4), respectively (Fig. 2).

There was a clear daily dichotomy in turtles diving behavior (Fig. 3 and Fig. 4), with diurnal dives being significantly more numerous (Exact two-tailed permutation test, $P = 0.002$, $N = 10$ Fig. 3a) and shorter (Exact permutation test, $P = 0.002$, $N = 10$, Fig. 3e, Table 4a) than nocturnal dives. In addition, maximum dive depth was also significantly deeper at night (Exact two-tailed permutation test, $P = 0.002$, $N = 10$, Fig. 3c, Table 4a). For daytime, turtles spent almost half time at subsurface (mean \pm SE = $53.7 \pm 4.1\%$ in 0-10 m, $N = 10$, Table 4c) while at night they spent almost half time between 0-30 m ($52.9 \pm 4.9\%$ in 0-30 m, $N = 10$) with relatively homogenous distribution in the water column (Online Resource 1-Fig. 2). Time-at-depth for deepest layers (> 40 m) did not differ between day ($6.4 \pm 1.6\%$, $N = 10$, Table 4c) and night ($5.6 \pm 1.2\%$, $N = 10$, Online Resource 1-Fig. 2, Table 4c). These differences in diving behavior were confirmed by single dives parameters: Dss dives were more frequent during day hours while frequency of long dives (Dsl and Ddl) was greater during night hours, especially for Ddl dives (Fig. 4).

Relation between diving and movement behaviors

Time spend at subsurface (0-10 m) was not clearly related to movement phases (OR, CR, CT, OT). Noticeably there was a significant difference in the usage of the water column located between 10m and 20m both during oceanic and coastal phases (Online Resource 1-Fig. 3). Turtles spent more time in this layer while they are in resident phases (mean \pm SE; OR: $15.3 \pm 6.0\%$, $N = 6$; CR: $27.3 \pm 8.0\%$, $N = 4$, Table 4c) than during transit periods (OT: $9.4 \pm 1.6\%$, $N = 10$; CT: $8.1 \pm 1.9\%$, $N = 9$, Table 4c). Proportion of short and shallow dives (Dss) was more important during transit phases ($80.0 \pm 3.8\%$, $N = 14$, Table 4b) than during residency phases ($74.0 \pm 6.4\%$, $N = 7$, Table 4b).

A difference was also observed in the usage of deepest layers (> 40 m) both during oceanic and coastal phases (Online Resource 1-Fig. 3). These layers were more rarely

frequented when animals were resident (mean \pm SE; OR: $6.7 \pm 3.1\%$, N = 7; CR: $4.8 \pm 1.7\%$, N = 4, Table 4c) than when they were in transit (OT: $9.1 \pm 1.9\%$, N = 14; CT: $8.6 \pm 1.9\%$, N = 13, Table 4c). Maximum dive depth of turtles during transit phases was deeper than during resident phases (mean \pm SE; CT: 109.93 ± 9 m, N = 9; CR: 78.1 ± 15.3 m, N = 4; OT: 125.8 ± 4.5 m, N = 10; OR: 103.9 ± 14.5 m, N = 6; Table 4a). Proportion of long and deep dives (Ddl) compared to long and shallow dives (Dsl) was generally larger during transit phases (OT: $83.7 \pm 3.7\%$, N = 10, Table 4b) than during residency phases (OR: $74.4 \pm 17.3\%$, N = 5, Table 4b).

Oceanic covariates

Distribution of SST, NPP and TKE are illustrated in Fig. 5 and oceanic environment values are summarized in Table 5 (An animation of the oceanic covariates for each individual tracks is provided in Online Resource 3). Most (95%) turtles' locations were associated with SSTs ranging from 17.12°C to 30.05°C . S4 experienced the coldest SST (11.5°C by 32.2°S) and N6 was exposed to the highest SST (31.9°C by 11.8°S). During residency phases (coastal and oceanic), individuals of the southern group were exposed to colder SST (mean \pm SE = $19.59 \pm 0.42^{\circ}\text{C}$, N = 3) than individuals of the northern group ($27.9 \pm 0.36^{\circ}\text{C}$, N = 6, Fig. 6a). Non-dispersal turtles were globally exposed to high SST of the same order of magnitude than northern turtles ($27.8 \pm 0.03^{\circ}\text{C}$, N = 2, Fig. 6a).

NPP levels were extremely variable along tracks, with 95% of values ranging from $125.0 \text{ mg C m}^{-2} \text{ day}^{-1}$ to $1141.6 \text{ mg C m}^{-2} \text{ day}^{-1}$. Highest levels of NPP were observed along the coast of the Arabian Peninsula with the highest level of NPP recorded for CC17 at $7801.1 \text{ mg C m}^{-2} \text{ day}^{-1}$ near the south-eastern coast of Oman. During residency phases, individuals were exposed to varying levels of productivity, depending on their groups (Fig. 6a; mean \pm SE: $543.3 \pm 117 \text{ mg C m}^{-2} \text{ day}^{-1}$, N = 5, for northern group; $419 \pm 85.4 \text{ mg C m}^{-2} \text{ day}^{-1}$, N = 3, for southern group; $224.9 \pm 60 \text{ mg C m}^{-2} \text{ day}^{-1}$, N = 2, for non-dispersal group).

In the open ocean, turtles were exposed to slightly higher TKE values when resident (mean \pm SE = $590.03 \pm 112.02 \text{ cm}^2 \text{ s}^{-2}$, N = 10) than in transit ($502.1 \pm 45.13 \text{ cm}^2 \text{ s}^{-2}$, N = 18, Fig. 6b). They were also exposed to higher levels of TKE during residency phases ($400.11 \pm 68.82 \text{ cm}^2 \text{ s}^{-2}$, N = 10) than during transit phases ($224.25 \pm 16.34 \text{ m}^2 \text{ s}^{-2}$, N = 18). OR phases were related to oceanic mesoscale structures (Fig. 6b), particularly for southern individuals for which most residency phases were associated with mesoscale eddies (Online Resource 1-Fig. 4). Interestingly, OR phases also occurred in majority, but not exclusively, either below 30°S or above 10°N .

DISCUSSION

Dispersal patterns

Most late juvenile loggerhead sea turtles (61%) went north towards one of the world largest rookeries of loggerheads (Masirah Island, Sultanate of Oman, with ca. 30,000 nesters per year; Ross and Barwani (1995); Ross (1998); Rees et al. (2010); ca. 4,600 km from the release point; Fig. 1). Another part (22%) went south-west towards the small South-Africa and southern Mozambique rookeries (ca. 500 nesters per year, Nel et al. (2013); Fig. 1). With an average curved carapace length of 68 cm, released loggerheads were considered to be at late juvenile stage. Average size of nesters is 84cm in South-Africa (Nel et al. 2013) and 91cm in Oman (Ross and Barwani 1995) and common size of sexual maturity for this species is usually considered to be around 80cm to 90cm (Avens and Snover 2013). Tracked individuals are therefore likely to be close to sexually maturity, but not mature. This suggests that late juvenile loggerheads frequenting the French Reunion Island and East Madagascar waters (location of capture, Online Resource 1-Fig. 1) may originate from both rookeries, and most frequently from the northern one. It will be necessary to perform genetic studies to confirm

this hypothesis and to more accurately determine the proportion of individuals from each rookery accidentally captured by French Reunion longliners.

While it is not very surprising that loggerheads from southern rookeries frequent Reunion Island waters, it is more astonishing to find individuals from rookeries of the northern hemisphere. In other oceans, although loggerhead developmental cycle has been demonstrated to take place at large scale (*e.g.* more than 10,000 km in the Pacific Ocean; Bowen et al. (1995); Boyle et al. (2009)), it is usually confined to a single hemisphere. Up to date, the juveniles from Baja California (Mexico) are an exception since they have been demonstrated to originate from both Japanese (northern hemisphere) and Australian rookeries (southern hemisphere; Bowen et al. (1995)).

This study thus provides the first evidence of a trans-equatorial developmental cycle at Indian Ocean basin scale for the world largest nesting population of loggerhead sea turtle. However, the spatio-temporal pathway followed by these turtles to reach the south-west Indian Ocean is still to be determined. Oceanic currents probably play a key role as their importance in loggerhead sea turtle developmental cycle has long been documented in other oceans (see review Musick and Limpus (1997)). In the northern Atlantic Ocean, it has been demonstrated that juveniles tend to remain in the North Atlantic gyre (Lohmann et al. 2001). In the North Pacific Ocean, juvenile loggerheads make use of oceanic habitats, particularly the Kuroshio Extension Bifurcation Region, a region with high eddy kinetic energy and high planktonic productivity (Polovina et al. 2006). However, in both Atlantic and the Pacific Ocean, loggerhead developmental cycles take place in oceanic gyres that are constrained in a single hemisphere. In the Indian Ocean, the unique characteristics of the monsoon phenomenon make hydrodynamics particularly complex: no annual persistent ocean scale gyre exists as cyclonic and anti-cyclonic complex gyres alternate during winter and summer monsoon periods (Schott and McCreary Jr 2001; Schott et al. 2009). The pathway followed

by hatchlings and early juvenile loggerheads from the Arabian Sea to the oceanic waters of Reunion and Madagascar is yet to be clarified. Following the general scheme of Indian Ocean circulation described in Schott et al. (2009), we hypothesize here that, depending on the monsoon season, individuals may be carried out South with the water flow either by the Somalian or the South-west Monsoon Currents. Young turtles may then drift eastward with the South-Equatorial Counter Current (SECC), possibly up to the eastern part of the Indian Ocean Basin. They may then join the permanent South-Equatorial Current (SEC) and drift back westward towards the Mascarene archipelago. In the absence of real evidence, this hypothesis should however be taken with care. Such a cycle is likely to take multiple years to be completed, a reason that could explain the absence of small individuals (<50cm) accidentally caught by the Reunion Island longline fleet. Furthermore, considering the seasonal particularities and the complexity of the oceanic circulation in the Indian Ocean we can suppose that more variability in the developmental cycle does exist in the Indian Ocean for loggerheads hatchling dispersal than in populations from other oceans.

Movement behavior

After an oceanic phase and before sexual maturation, juveniles in most species of sea turtles settle in coastal habitats during a phase referred as juvenile neritic or sub-adult stage (Type 2 in Bolten (2003)). Nevertheless, for loggerheads at late oceanic stage, various foraging behaviors were observed in other oceans. Juveniles do not systematically settle in neritic habitats but may remain or reenter the oceanic environment (McClellan and Read 2007; Mansfield et al. 2009; McClellan et al. 2010). We observed both behaviors in the present study. Demographic implications of this alternative foraging strategy are discussed in (Peckham et al. 2011). While oceanic individuals might be exposed to slower growth rate due

to the lower prey availability, this disadvantage might be counterbalanced by lower predation risk than coastal strategy.

Interestingly, three individuals remained in the vicinity of the coast of Yemen and Oman and their movement behaviors were similar to the post-nesting movements of nesting adults from Oman that forage in the same area (Rees et al. 2010). This reinforces the hypothesis that the individuals accidentally caught off Reunion Island coast originated from the Omanese rookery or other rookeries of the northern hemisphere. It is worth noting that no neritic settlement was observed in the southern group where all turtles remain oceanic. Contrastingly to the northern group, movements of late juveniles of the southern group differed from the movements of adults nesting in the South West Indian Ocean that are known to mostly forage along the coast of Mozambique (Luschi et al. 2006)(Pereira, Pers. Com.), Tanzania (Luschi et al. 2006) or Madagascar (Rakotonirina, Pers. Com.). Risk and benefits of oceanic and neritic strategies for late juveniles might be contrasted between the northern and the southern individuals. Our results suggest that oceanic strategies might be more common for late juvenile loggerheads coming from the southern rookeries. Although, considering that only a few tracked individuals headed southwestward and that these individuals were captured in the oceanic zone, it might not represent all existing foraging strategies used by southern individuals.

Surprisingly, turtles did not generally spent much time around the oceanic zone where they were captured and thus tended to leave this zone shortly after release. Only a few individuals (X2 and X3) among those we tracked remained resident between 30°S and 10°N. This behavior might be induced by the capture event and subsequent captivity. In other words, turtles being captured and kept in tank might be lead to migrate towards their natal rookery just after release. Another, more likely hypothesis is that the region is a transit zone or migratory corridor for late juveniles heading more productive areas in the South or in the

North and therefore crossing on the way the Reunion Island waters where they are accidentally captured. Nevertheless the oceanic zones visited prior to this transit are at this time hard to determine.

Diving behavior

The diurnal vs. nocturnal dichotomy in diving behavior, with more dives occurring during the day and longer dives at night, has already been observed (Renaud and Carpenter 1994; Houghton et al. 2002; Godley et al. 2003; Howell et al. 2010). It may result from nocturnal resting dives and diurnal subsurface active dives (Godley et al. 2003). Howell et al. (2010) found that loggerhead turtles spend more time in the 0-15 m depth layer during the night than during the day and that they make more dives deeper than 15m during the day. With slightly different bins, we found that turtles spend a majority of their time during the day in the 0-10 m in particular during transit period.

During transit phases, late juveniles spent most of their time at subsurface (0-10 m), but also used deep layers (>40m) relatively frequently. While swimming actively, turtles make a majority of short and shallow dives. During residency phases, turtles spent a similar proportion of time in the 0-10 m and 10-20 m depth layers. They consequently made more usage of the 10-20 m layer than during transit, but made less usage of the deeper layers (>40 m). This was observed for both coastal and oceanic phases. This seems relatively straightforward for coastal phases since depth near the coast is shallower and may allow turtles to reach ocean bottom. During oceanic phases, prey availability at shallower depth may occur at specific conditions, and could explain the specific observed behavior of loggerheads. The association of oceanic residency phases with oceanic frontal zones, as commonly observed in a variety of taxonomic groups such as birds and large pelagic fishes (Fonteneau et al. (2008); Tew Kai et al. (2009); Tew Kai and Marsac (2010); Online Resource 1-Fig. 4)

supports this hypothesis but needs to be deeper investigated in the future. Justification of occasional and exceptionally deep dive events (>80 m) occurring mostly during transit phases is difficult to interpret. Individuals may be inspecting the water column looking for prey or for attempting to reach the sea bottom, and so check for the proximity of seamounts or coastal areas.

Oceanic environment

Environmental conditions for northern and southern groups were drastically different. According to world Ocean partitioning of Longhurst (1998), based on global hydrodynamics and water color data, the Indian Ocean is mainly constituted by two large biogeochemical provinces: the Indian Monsoon Gyre Province (MONS) in the north and the Indian South Subtropical Gyre Province (ISSG) in the south. Both are separated at around 12°S of latitude by the hydrodynamic and biogeochemical front known as South Tropical Front. MONS is bordered in the Northwest by the Northwest Arabian Sea Upwelling Longhurst province (ARAB). This province is also included in the Arabian Large Marine Ecosystem considered a highly productive ecosystem (Heileman et al. 2009) with intense large scale seasonal coastal upwelling and productive phytoplanktonic bloom system (Lévy et al. 2007). The southern region also exhibits a productive coastal upwelling leading to the productive Agulhas Current large marine ecosystem (Heileman et al. 2009). In addition, interactions between mesoscale structures that take place in the Mozambique Channel generate strong frontal mixing zones favorable to the production and aggregation of organic matter (Tew-Kai and Marsac 2009). Therefore, individuals of the northern and southern groups frequented more productive waters than the non-dispersal individuals. During residency period, productivity levels for individuals of the northern group were slightly higher than productivity level of southern group individuals. In addition and more strikingly, there is a major difference in the sea

surface temperature to which turtles were exposed with clearly higher temperature for the northern group (27.6°C) than the southern group (20.4°C; Fig. 6). Nevertheless turtles from the southern group remained in waters above the 16°C isotherm that has been stated to be a lower thermal boundary for loggerhead sea turtle (McMahon and Hays 2006).

Such a strong environmental difference should potentially lead to slower growth rates for individuals exploiting southern hemisphere foraging habitats in comparison to individuals from the northern hemisphere. Assuming that northern and southern groups originate respectively from the Omanese and the South Africa/Mozambique rookeries, such a difference in food availability could contribute explaining the major difference in total number of nesters between both rookeries (ca. 30,000 annual nesters for Oman (Ross and Barwani 1995) vs. ca. 500 annual nesters for South-Africa (Nel et al. 2013)). There is a clear lack of data to validate this hypothesis at the moment, especially in terms of food availability and its energetic value in both northern and southern foraging habitats.

Ecological and conservation implications

Pelagic longlines, through incidental catch, has a high impact on loggerhead populations. Lewison et al. (2004) estimated that, in 2000, more than 200 000 loggerheads were likely taken worldwide as pelagic longline bycatch. In the Western Indian Ocean, longline bycatch was identified as one of the possible reason explaining the slow recovery of the South-African population with a bycatch rate of 0.02 turtle per 1000 hooks for the South African longline fisheries (Petersen et al. 2009). The loggerheads we tracked were initially caught accidentally by the small French longline fishing fleet composed of 41 boats (3.2 million hooks per year) operating in Reunion Island and Est-Madagascar EEZs (Evano and Bourjea 2012). The estimated amount of individuals accidentally caught by this fishery is assumed to be low (0.004 turtle per 1000 hooks, Miossec and Bourjea (2003)). Considering the large size of

loggerhead populations in the northern hemisphere from which a majority of individuals seems to originate from, the impact of the Reunion Island longline fleet activity on this species is likely to be moderate. We observed that loggerheads around Reunion Island displayed relatively short residence times. This supports the idea that the region is rather a transit zone than an identified foraging area for oceanic juvenile loggerhead sea turtles. We do believe that, contrastingly to other small scale fisheries worldwide (Peckham et al. 2007), it does not constitute a major threat for the species in the Western Indian Ocean. Encouraging collaboration between fishermen and local sea turtle care center (Ciccione and Bourjea 2010) should also contribute to minimize this impact.

Other mitigating measures have also been advanced to decrease bycatch of sea turtles such as the use of adapted circle hooks (Read 2007), the reduction of gear soak time, the avoidance of hotspots and the setting of gear below turtle-abundant depth (Polovina et al. 2003; Gilman et al. 2006; Howell et al. 2010). We demonstrated that in the Indian Ocean, late juvenile loggerheads spend a vast majority of their time between 0 and 30m depth. The deployment of fishing gears such as drifting longlines at depth deeper than 40m should prevent a majority of the bycatch. Nevertheless, this solution is mainly constrained by its impact on the target species catch rates (Beverly et al. 2009). Most of the longline gears are set deeper than 40m around Reunion Island, which could explain the relative small number of bycatch occurring within the area. Moreover, as most loggerheads are captured alive, this indicates that interaction with the longline gear occurs at the end of the set at the hauling time, suggesting that mitigation measures targeting the bait quality and hook form should be also further investigated in the future.

In the present study, we showed first evidence of ocean scale trans-equatorial movements. Oceanic strategy and neritic settlement is the most observed behavior for late juveniles in the region. This is of major interest for conservation, as threats and hence protection measures in

both cases are highly contrasted. We also showed that southern and northern oceanic loggerhead turtles target waters with high level of productivity, although southern group was exposed to lower levels of sea temperatures. The consequences on growth rates and on juvenile survival rates might have high impact on population dynamics, viability and recovery. While this is an advance in juvenile loggerhead movement ecology, major interrogations remain. The incoming paths followed by these individuals from their original rookeries to Reunion island waters are yet to be determined and we still ignore whether the trans-equatorial developmental cycle suggested by our results for the northern rookeries is prevalent or if it's only an artifact of the small number of individual tracked. Regional genetic and stable isotopes studies as well as drift simulations could help answering these key issues regarding the survival of loggerhead turtles from hatching to the adult stage.

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FIGURES

Fig. 1 Satellite tracks of 18 late juvenile loggerhead individuals released after accidental captured by long-line fishing boats in the vicinity of Reunion Island.

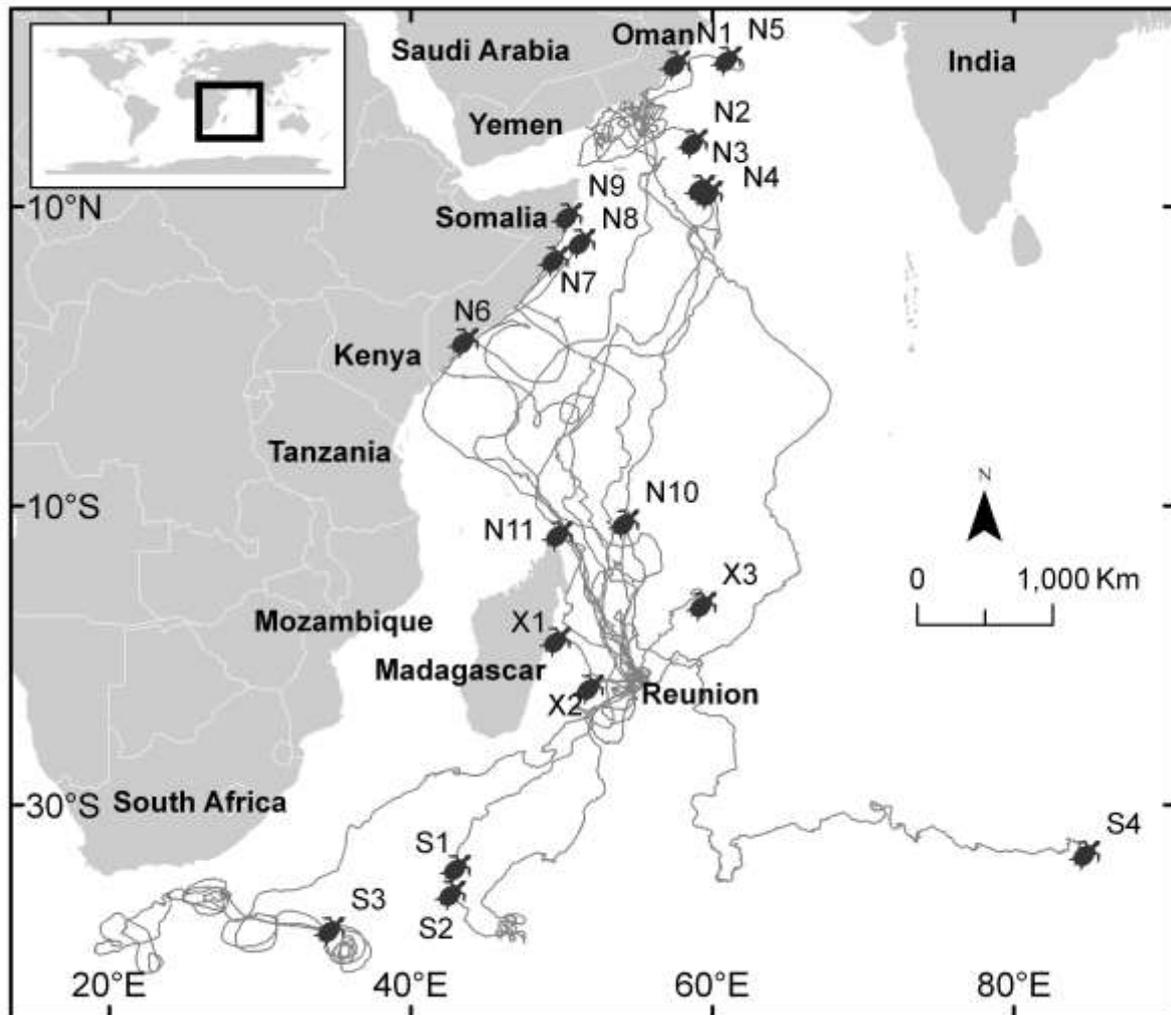


Fig. 2 Dive depth vs. dive duration for pooled single dives of 10 late juvenile loggerhead sea turtles. Density plot clearly outline 2 modes (darkgrey) defined here as Dss and Ddl, respectively representing short and shallow (<30m, <800sec) and long and deep (>=30m, >=800sec) dives. Another number of dives, yet less numerous, was identified and defined as Dsl dives, long and shallow (<30m, >=800sec).

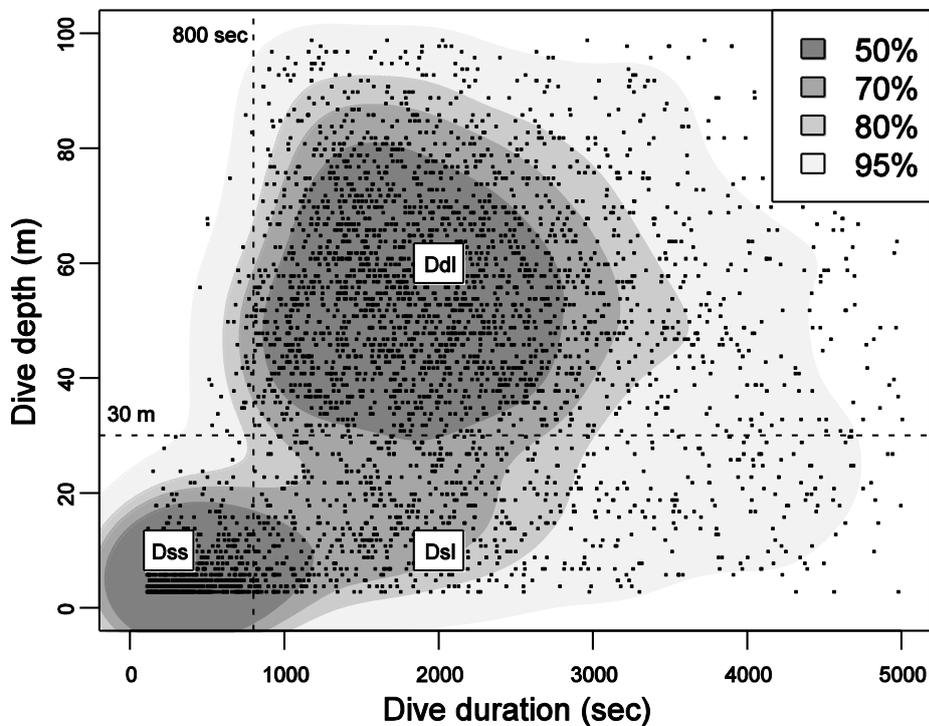


Fig. 3 Pooled distributions of integrated parameters of late juvenile loggerhead sea turtles over 24h, 12h daytime and 12h night time: (a) Number of dives (N = 14), (b) underwater percentage (N = 14), (c) maximum dive depth (N = 10), (d) maximum dive duration (N = 14), (e) mean dive duration (N = 14). Diurnal dives are more numerous and shorter than nocturnal dives. Maximum dive depth is also significantly deeper at night.

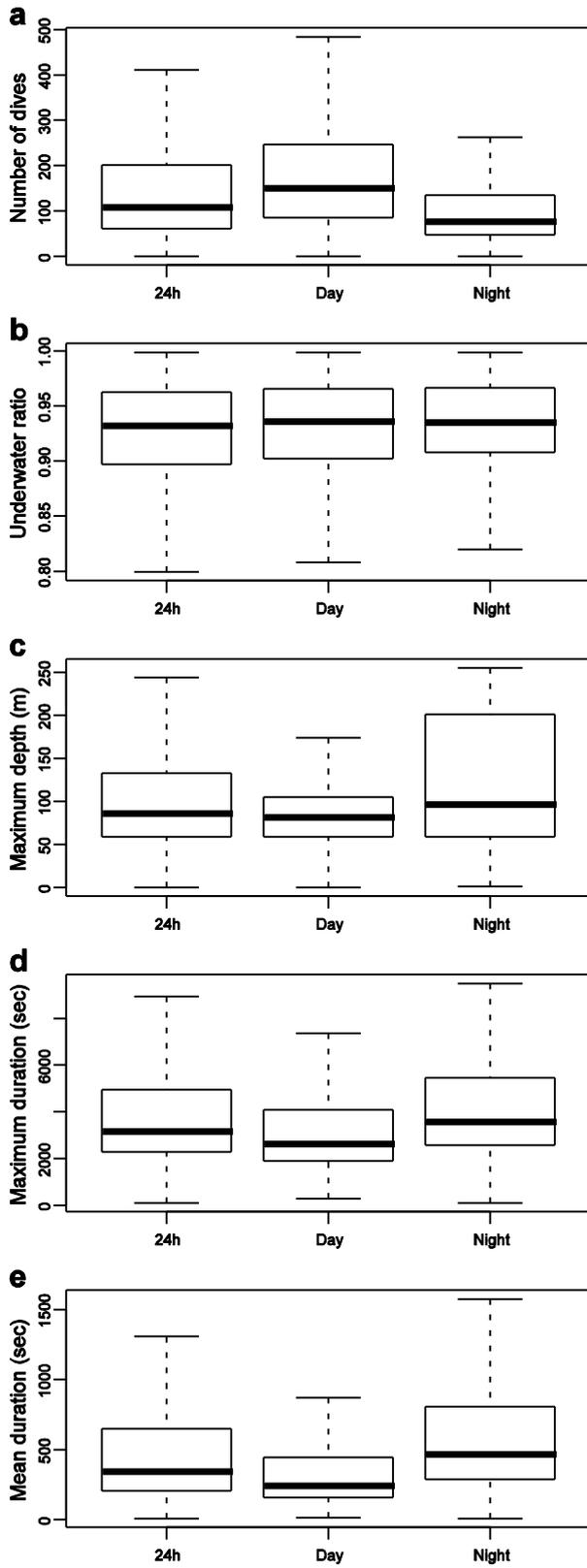


Fig. 4 Percentage of Dss, Dsl and Ddl dives of 10 late juvenile loggerhead sea turtles according to day hour (GMT+4). Dss are subsurface and short dives (< 30 m, < 800 s), Dsl are shallow and long dives (<30 m, >= 800 s) and Ddl are deep and long dives (>= 30 m, > 800 s). Short and shallow dives are more frequent at day time while longer dives are more frequent during night time.

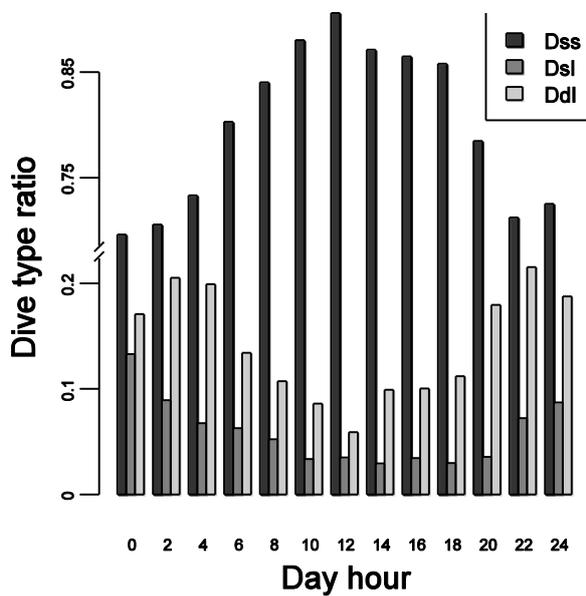


Fig. 5 Distributions of environmental variables along the 18 turtle's tracks: (a) Sea Surface Temperature ($^{\circ}\text{C}$), (b) netprimary production ($\text{mgC m}^{-2} \text{ day}^{-1}$), (c) total kinetic energy ($\text{cm}^2 \text{ s}^{-2}$). Coldest SST appears at the most southern locations. NPP levels are higher at more extreme latitudinal locations in the South and in the North and are lower in the equatorial locations. TKE values are more homogeneously dispersed.

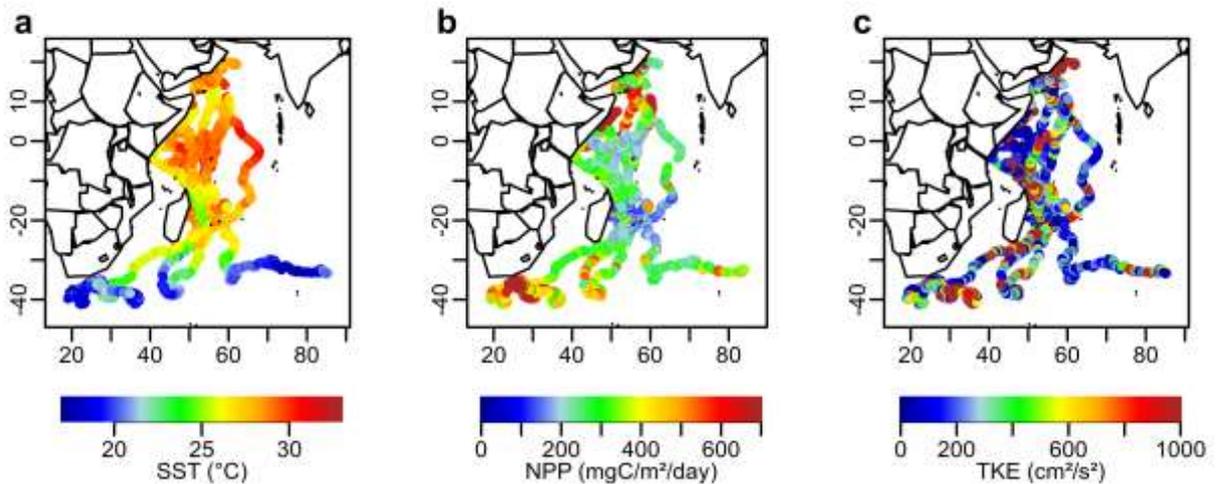
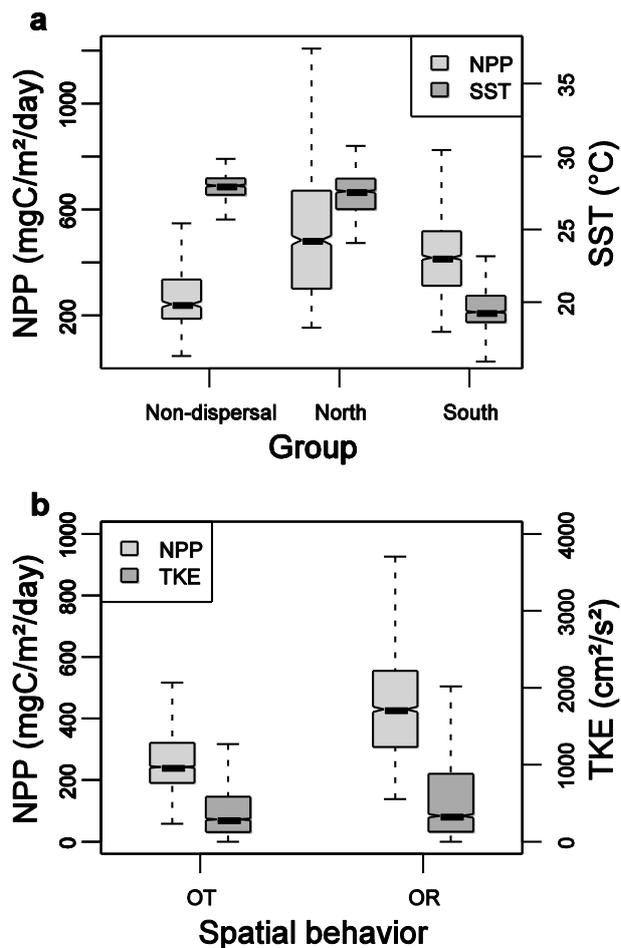


Fig. 6 (a) Comparison of Net Primary Production (NPP) and Sea Surface Temperature (SST) between late juvenile loggerhead individuals from the northern group (N = 11) and individuals from the southern group (N = 4). NPP reaches higher levels for turtle of the northern and southern group. Individual from the southern group are exposed to lower SSTs. (b) Comparison of NPP and Total Kinetic Energy (TKE) during oceanic transit phases (OT) and oceanic resident phases (OR). NPP levels are higher during resident phases. Higher TKE levels also occur during resident phases.



TABLES

Table 1 Demographic (CCL, body mass) and distribution data for 18 late juveniles loggerhead sea turtles satellite-tagged after accidental capture from long-liners from Reunion Island, Indian Ocean (Online Resource 1-Fig. 1).

| Turtle ID | Left flipper tag ID | Argos ID | Captivity period (days) | CCL (cm) | Mass (kg) | Tag model | Release date | Last location date |
|------------------|----------------------------|-----------------|--------------------------------|-----------------|------------------|------------------|---------------------|---------------------------|
| N1 | RUN0244 | 66839 | 171 | 69 | 44.7 | A | 19-Oct-10 | 19-Jun-11 |
| N2 | RUN0309 | 66840 | 51 | 64 | 29.6 | A | 12-Nov-10 | 12-May-11 |
| N3 | RUN0594 | 66818 | 199 | 66 | 40.3 | B | 23-Dec-10 | 5-May-11 |
| N4 | RUN0301 | 66823 | 215 | 54 | 29.3 | B | 28-Mar-11 | 31-Jul-11 |
| N5 | RUN0317 | 53434 | 338 | 61 | 26.5 | D | 15-Sep-11 | 21-Jun-12 |
| N6 | RUN0315 | 66846 | 238 | 73 | 50.2 | A | 23-Dec-10 | 2-Apr-11 |
| N7 | RUN0314 | 68845 | 876 | 72 | 54.4 | A | 23-Dec-10 | 15-May-11 |
| N8 | RUN0278 | 66837 | 143 | 69 | 36.4 | B | 29-Mar-11 | 16-Aug-11 |
| N9 | RUN0322 | 57684 | 44 | 61 | 28.5 | D | 16-Aug-11 | 01-May-12 |
| N10 | RUN0586 | 84473 | 557 | 73 | 55.0 | C | 8-Oct-08 | 9-Nov-08 |
| N11 | RUN0592 | 66838 | 224 | 71 | 54.2 | A | 17-Sep-10 | 6-Mar-11 |
| S1 | RUN0241 | 84477 | 470 | 64 | 33.4 | C | 14-Oct-09 | 30-Nov-09 |
| S2 | RUN0593 | 68819 | 212 | 68 | 44.0 | B | 23-Dec-10 | 28-May-11 |
| S3 | RUN0323 | 53509 | 141 | 71 | 50.0 | D | 16-Nov-11 | 14-Dec-12 |
| S4 | RUN0316 | 53435 | 332 | 65 | 32.4 | D | 11-Nov-11 | 16-Dec-12 |
| X1 | RUN0587 | 84475 | 453 | 77 | 58.7 | C | 4-Mar-09 | 23-Mar-09 |
| X2 | RUN0090 | 84476 | 28 | 67 | 37.2 | C | 11-Dec-09 | 7-Feb-10 |
| X3 | RUN0313 | 68821 | 293 | 71 | 37.7 | B | 23-Dec-10 | 20-Jun-11 |

Table 2 Migration parameters of 18 juvenile loggerhead sea turtles.

Spatial group, distance from released point and bearing from released point are evaluated from last tracking location. Mean travel speed is calculated using tracks interpolated with 3 locations per day.

| Turtle ID | Tracking period (days) | Distance from released point (km) | Bearing from released point (°) | Mean travel speed (km.day⁻¹) |
|------------------|-------------------------------|--|--|--|
| N1 | 244 | 4521 | 4 | 48 |
| N2 | 182 | 3949 | 6 | 42 |
| N3 | 134 | 3620 | 8 | 42 |
| N4 | 126 | 3584 | 9 | 38 |
| N5 | 219 | 4591 | 9 | 37 |
| N6 | 101 | 2748 | 332 | 51 |
| N7 | 144 | 3115 | 349 | 37 |
| N8 | 141 | 3213 | 352 | 48 |
| N9 | 260 | 3417 | 351 | 30 |
| N10 | 33 | 1107 | 357 | 41 |
| N11 | 171 | 1157 | 331 | 29 |
| S1 | 48 | 1873 | 216 | 49 |
| S2 | 157 | 2037 | 213 | 35 |
| S3 | 394 | 2732 | 221 | 45 |
| S4 | 401 | 3221 | 121 | 24 |
| X1 | 20 | 602 | 292 | 46 |
| X2 | 59 | 348 | 249 | 31 |
| X3 | 180 | 671 | 43 | 20 |

Table 3 Depth parameters recorded by transmitter models A-C. Model D (5 tags) was not equipped with depth sensors.

| Recorded parameter | Model A and B | Model C |
|---------------------------|----------------------|----------------|
| # of tags deployed | 10 | 4 |
| Dive duration (s) | Single dive | Single dive |
| Dive depth (m) | Single dive | - |
| Dive counter | 12h | 24h |
| Average dive duration (m) | 12 h | 24h |
| Maximum dive duration (m) | 12 h | 24h |
| Maximum dive depth (m) | 12 h | - |
| Underwater percentage | 12 h | 24h |
| Time-at-depth histograms | 12 h | 24h |
| Dive qualification period | 5s | 30s |

Table 4 Distribution of diving parameters (Mean \pm SE (N)) for 14 late juvenile loggerheads over the all tracking period (overall), depending on day time (Day and Night) and depending on behavioural modes (OT, OT, CT and CR). (CR: Coastal Residency, CT: Coastal Transit, OR: Oceanic Residency and OT: Oceanic Transit, Dss: Short and shallow dives, Ddl: Deep and long dives, Dsl: Deep and shallow dives)

| | Overall | Day | Night | OT | OR | CT | CR |
|-------------------------|-----------------------|-----------------------|-----------------------|----------------------|----------------------|-----------------------|----------------------|
| a. Dive summary | | | | | | | |
| Number of dives (24h) | 296.1 \pm 24.8 (14) | 366.1 \pm 33.2 (10) | 213.2 \pm 18.6 (10) | 297.8 \pm 27 (14) | 240.2 \pm 50 (7) | 392.5 \pm 34.8 (13) | 261.8 \pm 30.2 (4) |
| Underwater ratio (%) | 90.3 \pm 1 (14) | 91.6 \pm 1.1 (10) | 91.5 \pm 1.4 (10) | 91.5 \pm 0.8 (14) | 83.1 \pm 3.7 (7) | 88.6 \pm 1.6 (13) | 90.1 \pm 3.9 (4) |
| Maximum depth (m) | 108.1 \pm 9.1 (10) | 85.4 \pm 7.7 (10) | 130.2 \pm 13.3 (10) | 125.8 \pm 4.5 (10) | 103.9 \pm 14.5 (6) | 109.9 \pm 9.1 (9) | 78.1 \pm 15.3 (4) |
| Maximum duration (min) | 70.9 \pm 5.3 (14) | 65.9 \pm 6.9 (10) | 77.9 \pm 7.4 (10) | 69.4 \pm 6.2 (14) | 97.7 \pm 29.9 (7) | 69.2 \pm 10.5 (13) | 58.5 \pm 11.2 (4) |
| Mean duration (min) | 10.8 \pm 1.8 (14) | 7.4 \pm 1.2 (10) | 14.1 \pm 2.8 (10) | 9.7 \pm 1.8 (14) | 11.5 \pm 3.1 (7) | 6.5 \pm 1.3 (13) | 11 \pm 5.2 (4) |
| b. Dive type | | | | | | | |
| Dss ratio (%) | 78.8 \pm 3.7 (14) | 83.5 \pm 3.7 (14) | 71 \pm 3.5 (14) | 77.5 \pm 4.9 (14) | 71.9 \pm 7.2 (7) | 79.2 \pm 6.7 (14) | 75.4 \pm 2.2 (4) |
| Ddl/(Ddl + Dsl)(%) | 71.3 \pm 6.9 (10) | 63.5 \pm 9.3 (10) | 75.4 \pm 7 (10) | 83.7 \pm 3.7 (10) | 74.4 \pm 17.3 (5) | 75.6 \pm 7.5 (10) | 65 \pm 11.1 (4) |
| c. Time-at-depth | | | | | | | |
| 1-10m (%) | 38.4 \pm 2.3 (10) | 53.7 \pm 4.1 (10) | 23.6 \pm 2.5 (10) | 36.5 \pm 2.7 (10) | 39.6 \pm 4.2 (6) | 46 \pm 4.6 (9) | 32.3 \pm 4.3 (4) |
| 11-20m (%) | 14.5 \pm 2.9 (10) | 8.9 \pm 2 (10) | 20 \pm 3.9 (10) | 9.4 \pm 1.6 (10) | 15.3 \pm 6 (6) | 8.1 \pm 1.9 (9) | 27.3 \pm 8 (4) |
| 21-30m (%) | 14.3 \pm 1.6 (10) | 7.8 \pm 1.1 (10) | 20.6 \pm 2.8 (10) | 16.9 \pm 1.7 (10) | 10.9 \pm 2.8 (6) | 11.2 \pm 2.3 (9) | 12.3 \pm 1.5 (4) |
| 31-40m (%) | 8.4 \pm 1.3 (10) | 6.3 \pm 1.2 (10) | 10.4 \pm 1.5 (10) | 10.3 \pm 1.5 (10) | 7.8 \pm 3.3 (6) | 7.6 \pm 1.5 (9) | 7.3 \pm 1.3 (4) |
| 40m+ (%) | 8.5 \pm 1.9 (14) | 6.4 \pm 1.6 (10) | 5.6 \pm 1.2 (10) | 9.1 \pm 1.9 (14) | 6.7 \pm 3.1 (7) | 8.6 \pm 1.9 (13) | 4.8 \pm 1.7 (4) |

Table 5 Distribution of oceanic parameters (Mean \pm SE (N)) for the three spatial groups: North, South and Non-dispersal; and for the 4 behavioral modes: Coastal Residency (CR), Coastal Transit (CT), Oceanic Residency (OR) and Oceanic Transit (OT).

| Group / Mode | SST ($^{\circ}$C) | NPP (mgC m⁻² day⁻¹) | TKE (m² s⁻²) |
|----------------------|-------------------------------------|--|---|
| North | 27.47 \pm 0.33 (11) | 324.93 \pm 41.91 (11) | 508.15 \pm 48.86 (11) |
| South | 21.69 \pm 0.33 (4) | 377.04 \pm 46.08 (4) | 514.66 \pm 189.77 (4) |
| Non-dispersal | 27.89 \pm 0.35 (3) | 210.02 \pm 34.66 (3) | 373.6 \pm 104.42 (3) |
| OT | 26.76 \pm 0.49 (18) | 261.11 \pm 15.71 (18) | 502.1 \pm 45.13 (18) |
| OR | 25.4 \pm 1.29 (10) | 400.11 \pm 68.82 (10) | 590.03 \pm 112.02 (10) |
| CT | 27.21 \pm 0.31 (18) | 224.25 \pm 16.34 (18) | 317.44 \pm 53.18 (18) |
| CR | 27.94 \pm 0.35 (6) | 556.38 \pm 147.64 (5) | 296.1 \pm 76.18 (6) |

ONLINE RESOURCE

Online Resource 1

OR1. Fig. 1 Capture positions of loggerhead sea turtles by long-liners fisheries from Reunion Island between 2007 and 2011 (N = 46). Black symbol show capture positions for individuals released with a satellite tag.

OR1. Fig. 2 Time at depth histograms (Day (D) vs Night (N)) of 10 late juvenile loggerhead sea turtles. The subsurface layer (<10m) is the most frequented during the day while turtles make more usage of layers between 11 and 40m.

OR1. Fig.3 Time at depth histograms according to behavioral mode of 10 late juvenile loggerhead sea turtles (OT: Oceanic Transit; OR: Oceanic Residency; CT: Coastal Transit; CR: Coastal Residency). Turtles exhibit similar usage of the subsurface layer (<10 m) for all behavioral modes. They made more usage of the 11-20 m layer during resident phases (OR and CR) but more usage of the deepest layer (>40 m) during the transit phases (OT and CT).

OR1. Fig. 4 Examples of tracks associated with oceanic eddies in the northern hemisphere for N5 (a) and in the southern hemisphere for S2 (c) and S3 (c and d). (c) and (d) During a oceanic and resident phase lasting 288 days, S3 clearly associated repeatedly with eddies in the Agulhas retroflexion region at large of the South-African coast. This constitutes the most striking example of association with eddies observed in the Western Indian Ocean.

Online Resource 2

Representation of individual's track and behavioral mode, time-at-depth distribution, and dive depth distribution according to behavioral mode.

Online Resource 3

Animations representing the distributions of oceanic environmental variables along track.