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ORIGINAL PAPER

The spatial ecology of juvenile loggerhead turtles (*Caretta caretta*) in the Indian Ocean sheds light on the "lost years" mystery

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Abstract While our understanding of the early oceanic developmental stage of sea turtles has improved markedly over recent decades, the spatial context for this life history stage remains unknown for Indian Ocean loggerhead turtle populations. To address this gap in our knowledge, 18 juvenile loggerheads were satellite tracked from Reunion Island (21.2°S, 55.3°E) between 2007 and 2011. Nine turtles swam north toward Oman (20.5°N, 58.8°E), where one of the world's largest rookeries of loggerheads is located. Three individuals traveled south toward South Africa and Madagascar, countries that also host loggerhead nesting grounds. Fourteen of the transmitters relayed diving profiles. A dichotomy between diurnal and nocturnal diving behavior was observed with a larger number of shorter dives occurring during the day. Diving behavior also differed according to movement behavior as individuals spent more time in subsurface waters (between 10 and 20 m) during transit phases. The study provides an understanding of the oceanic movement behavior of juvenile loggerheads in the Indian Ocean that suggests the existence of an atypical trans-equatorial developmental cycle for the species at the ocean basin scale in the Indian Ocean. These results address a significant gap in the understanding of loggerhead oceanic movements and may help with the conservation of the species.

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Introduction

Loggerhead sea turtles (*Caretta caretta*) have a global distribution throughout tropical and warm temperate waters, and the species is classified as endangered in the IUCN Red List (IUCN 2012). A striking feature of the life history of loggerheads is the large-scale, oceanic basin, development cycle. After entering the sea, hatchlings execute an intense, but brief, swimming phase known as the "swimming frenzy" (Wyneken and Salmon 1992). They then enter a neritic transitional phase lasting from a few days to a few months (Musick and Limpus 1997), after which they enter the oceanic zone. Juvenile and subadult loggerheads remain in the open ocean for many years, a phase referred to as the juvenile oceanic stage (Bolten 2003), during which their movements are driven essentially by the oceanic currents (Carr 1986). This stage of the development

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cycle was first referred to as the "lost year" (Carr 1952, 1986) and later as the "lost decade" (Musick and Limpus 1997) since it has long remained a stage of which little was known due to the difficulty of following the movements of hatchlings once they had departed the coastline. After this temporally variable oceanic stage (Bolten 2003), loggerhead juveniles return to neritic habitats before reaching sexual maturity (Bjorndal et al. 2000; Bolten 2003). It has been demonstrated, however, that some juveniles can frequent the oceanic environment until sexual maturity (McClellan and Read 2007; Mansfield et al. 2009; McClellan et al. 2010). Similarly, many adults also establish feeding ranges far removed from coastal zones (Hawkes et al. 2006; Hughes 2012). It has been suggested that these two strategies provide survival advantages. Whereas a neritic foraging strategy might be more energetically favorable for turtle development, an oceanic foraging strategy may reduce exposure to predation (Peckham et al. 2011).

In the North Atlantic Ocean, the loggerhead development cycle is spread across the entire basin (Bolten 2003), with turtles drifting from the western Atlantic nesting sites to the islands of Azores, Madeira and Canary Islands (Putman et al. 2012; Scott et al. 2012). Similarly, in the Pacific Ocean, genetic studies have demonstrated that the development cycle occurs on an even greater scale, originating from breeding sites in Japan, Australia and New Caledonia and reaching as far as the coasts of Baja California in Mexico (Bowen et al. 1995; Bowen and Karl 2007; Boyle et al. 2009).

While genetic and oceanographic studies have provided a better understanding of large-scale movement patterns of the loggerhead juvenile stage in the Atlantic and Pacific Oceans, information on their diving behavior remains scant. A diel diving behavior has been exhibited by loggerheads during the open sea juvenile stage (Godley et al. 2003; Polovina et al. 2004; Howell et al. 2010), with daytime dives being significantly shorter and more numerous than nighttime 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 (0–5 m) depths (90 % in 0–15 m). Moreover, this study revealed that the diving behavior was variable across mesoscale oceanic features, with turtles making deeper and longer dives when encountering more dynamic waters (Howell et al. 2010).

In the Indian Ocean, significant nesting sites for loggerheads are located at the edge of the western part of the basin in the northern and the southern hemispheres and on the northern coast of Western Australia (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 (ca. 30,000 nesters per year; Ross and Barwani 1995; Ross 1998; Rees et al. 2010). South Africa (27.1°S, 32.8°E), Mozambique (26.3°S, 32.9°E) and Western Australia are also known to host important nesting populations (ca. 500–1,000 nesters per year; Hughes 2010; Nel et al. 2013; Baldwin et al. 2003). In the southwestern 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 thought to be limited (Martel 2003; Rakotonirina 2011). Other minor nesting sites have also been identified in Yemen and Sri Lanka (Halpin et al. 2009).

Whereas recent studies have focused on the spatial dynamics of adult loggerheads in the western Indian Ocean (Oman: Rees et al. 2010; South Africa: Luschi et al. 2006), only one study focused on the juvenile stages (e.g., Hughes 1973), which produced few data on oceanic movements.

The main objective of our study was to document the foraging strategies of juveniles by determining the environmental conditions with which they were associated from their satellite-recorded large-scale oceanic movements. Our study thus aimed to provide a better understanding of these oceanic movements and the diving behavior of juvenile loggerheads, so as to provide key information for the survival of this species, which is of major concern both in the Indian Ocean (Petersen et al. 2009) and worldwide (Lewison et al. 2004).

Methods

Study area and sea turtle tracking

Late juvenile loggerheads are captured as bycatch by long-lining fishing boats from Reunion Island (21.15°S, 55.27°E). These vessels operate 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 declare to the official authorities (CROSS Réunion) any accidental captures of loggerheads for which onboard hook extraction is not possible. Individuals are then brought to "Kélonia Sea Turtle Observatory and Care Centre" (www.kelonia.org) where they receive veterinary surgery for hook extraction and are placed in tanks at the care center. General behavior and physiological parameters are regularly monitored.

A set of criteria has to be fulfilled before deciding that the animal has recovered sufficiently to be released: (1) the injuries have to be healed completely, (2) individuals must be able to ingest prey efficiently and regain body mass, (3) active swimming behavior must be resumed and (4) individuals must be free of anemia or infectious disease (confirmed through blood analysis). Between 2007 and 2011, a total of 56 individuals were brought to the care center. Fourteen individuals (25 %) died following the operation.

Table 1 Demographic (CCL, body mass), distribution and migration parameters 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	Captivity period (days)	CCL (cm)	Mass (kg)	Tag model	Release date	Tracking period (days)	Distance from released point (km)	Bearing from released point (°)	Mean travel speed (km day^{-1})
N1	171	69	44.7	A	19-Oct-10	244	4,521	4	48
N2	51	64	29.6	A	12-Nov-10	182	3,949	6	42
N3	199	66	40.3	B	23-Dec-10	134	3,620	8	42
N4	215	54	29.3	B	28-Mar-11	126	3,584	9	38
N5	338	61	26.5	D	15-Sep-11	219	4,591	9	37
N6	238	73	50.2	A	23-Dec-10	101	2,748	332	51
N7	876	72	54.4	A	23-Dec-10	144	3,115	349	37
N8	143	69	36.4	B	29-Mar-11	141	3,213	352	48
N9	44	61	28.5	D	16-Aug-11	260	3,417	351	30
S1	470	64	33.4	C	14-Oct-09	48	1,873	216	49
S2	212	68	44.0	B	23-Dec-10	157	2,037	213	35
S3	141	71	50.0	D	16-Nov-11	394	2,732	221	45
S4	332	65	32.4	D	11-Nov-11	401	3,221	121	24
X1	453	77	58.7	C	4-Mar-09	20	602	292	46
X2	28	67	37.2	C	11-Dec-09	59	348	249	31
X3	293	71	37.7	B	23-Dec-10	180	671	43	20
X4	224	71	54.2	A	17-Sep-10	171	1,157	331	29
X5	557	73	55.0	C	08-Oct-08	33	1,107	357	41

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 three locations per day

To date, 27 (48 %) have been released, of which 18 were fitted with Argos Platform Terminal Transmitters (PTTs). The mean ± SD curved carapace length of individuals released with a satellite tag was 67.7 ± 5.4 cm ($n = 18$).

We used four types of PTTs: A: TAM-4225, B: TAM-4325, 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, The Netherland). PTTs of types C and D were programmed to transmit data continuously, whereas PTTs of types A and B transmission followed a duty cycle involving 24 h "on" followed by 12 h "off" to extend life expectancy. Turtles were released approximately 3 km off the west coast of Reunion Island (21.15°S, 55.27°E) after periods of captivity ranging from 28 to 876 days (mean ± SD: 277 ± 209 days; Table 1).

Location and dive data acquisition

The mean ± SD lifetime of PTTs was 158 ± 112 days (maximum 401 days, type A: 168 ± 53, type B: 148 ± 21, type C: 40 ± 17 and type D: 268 ± 162, see Table 1). Location data were filtered in two successive stages: (1) ad hoc heuristic pre-filtering and (2) state–space model (SSM) filtering. Pre-filtering consisted in removing 0 and Z class locations (which, according to CLS/Argos hierarchy, are of low precision), as well as on-ground locations (i.e., which appeared more than 1 m 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 the hierarchical correlated random walk model described in Breed et al. (2009) under R and WinBUGS (5,000 iterations, a burn-in of 3,000, a thin of five and two MCMC chains, as in Hoenner et al. (2012) who previously used this procedure on sea turtles and demonstrated that location accuracy was improved significantly).

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 2.

Table 2 Depth parameters recorded by transmitter models A–C

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	12 h	24 h
Average dive duration (m)	12 h	24 h
Maximum dive duration (m)	12 h	24 h
Maximum dive depth (m)	12 h	–
Underwater percentage	12 h	24 h
Time-at-depth histograms	12 h	24 h
Dive qualification period	5 s	30 s

Model D (five tags) was not equipped with depth sensors

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 60 m and 20 m width from 60 to 120 m. 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 the surface down to 180 m.

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) and (3) sea surface currents and total kinetic energy (TKE) per water mass unit.

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, SST and photosynthetically active radiation. Datasets are available at 8-day interval with a spatial resolution of 9 km.
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 transport (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 based on latitude at last location: north (north of the equator), south (south of 30°S) or undetermined (all others), which were still in the vicinity of the released site when their PTTs stopped transmitting. Horizontal movements (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), which corresponds to a well-behaved extension of the first passage time, leading to a less noisy time series that therefore can be more easily segmented in different phases. Transit phases correspond to movements characterized by lowest residence times, which were assumed to occur in areas through which turtles were moving rapidly, whereas resident phases correspond to movements characterized by highest residence times, which were assumed to occur in concentrated-searching, food-rich areas. Because oceanic currents can have a major influence on sea turtles movements, 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, as the sum of the first passage time within the 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 reentry was not larger than a given threshold. This was set at 10 days in the present study. The 200 km radius was chosen because habitat selection of juvenile loggerheads is known to occur at a 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) being encompassed within the residence time computation. The residence time series was segmented using the Lavielle (2005) procedure, 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, with higher residence times corresponding to the resident period. The whole procedure was repeated with radii of 100 and 300 km, as well as with an unlimited time allowed outside the circle before reentry 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, when taking place less than 100 km from any coastal area (continent or island), were considered coastal, and beyond 100 km, oceanic.

Diving behavior

Based on distributions of dive depth and dive duration, we identified three categories of dives: shallow and short dives (Dss: depth < 30 m, duration < 13 min), shallow and long dives (Dsl: depth < 30 m, duration > 13 min) and deep and long dives (Ddl: depth > 30 m, duration > 13 min). Cutoffs of 13 min and 30 m were chosen as limits between classes based on dive depth and dive duration distributions, respectively (Fig. 1). When only dive duration was available (PTT type C), dives were assigned to either long dives (Dl; duration > 13 min) or short and shallow dives (Dss; duration < 13 min). The latter should have been considered simply as short dives, but it appeared that dives with duration inferior to 13 min were rarely deeper than 30 m (0.27 %, based on data from PTT types A and B). The dives that did not meet any of these criteria (0.17 %) were not assigned to any category.

Computations and statistical analyses

All results are presented as median ± IQR. For comparison of diving and environmental data, we either used a Kruskal–Wallis test for multiple group comparison, a Wilcoxon signed-rank test for paired comparison between two groups or a Mann–Whitney *U* test for unpaired comparison between two groups. When possible, exact *P* values were computed. Most analyses were performed using R software (R Core Team 2012). Current correction and residence time analyses were performed using Pascal programs developed by the authors. Lavielle (2005) segmentation was performed using his Matlab script (http://www.math.u-psud.fr/~lavielle/programs/dcpc.zip).

Results

Movement patterns

The tracks of these 18 individuals are shown in Fig. 2. Nine turtles were assigned to the northern group (N1–N9) and four to the southern group (S1–S4). Northern turtles

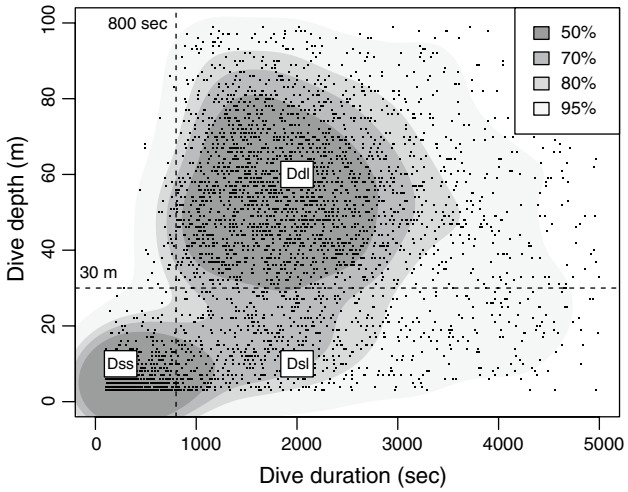


Fig. 1 Dive depth versus dive duration for pooled single dives of ten late juvenile loggerhead sea turtles. Density plot clearly outline two modes (*dark gray*) defined here as Dss and Ddl, respectively, representing short and shallow (<30 m, <800 s) and long and deep (≥30 m, ≥800 s) dives. Another number of dives, yet less numerous, was identified and defined as Dsl dives, long and shallow (<30 m, ≥800 s). Only dives superior to 30 s and 2 m were considered for the purpose of this analysis

reached the latitude of Arabian Peninsula in the northern hemisphere while southern individuals traveled beyond the latitude of South Africa. The remaining five either remained in the vicinity of the release site (X2–X4) or their transmitter stop transmitting shortly after deployment (X1 and X5; Table 1). There were no significant differences between the average sizes of individuals per group (Kruskal–Wallis test, $H_2 = 4.12$, $P = 0.13$). The total distance traveled was 2,932 ± 2,206 km ($n = 18$). The maximum straight distance traveled was 4,591 km (N5 reached the coast of the Sultanate of Oman). Turtles from the northern and southern groups traveled 3,584 ± 736 km (22.1 ± 8.6 km/day, $n = 9$) and 2,386 ± 857 km (10.6 ± 12.2 km/day, $n = 4$), respectively, away from the release point. The other turtles traveled 671 ± 505 km (6.8 ± 26.7 km/day, $n = 5$). There were no significant differences between the groups in the average daily straight-line distances traveled (Kruskal–Wallis test, $H_2 = 1.44$, $P = 0.49$). Neither was there any significant relationship between the size of the animals and the average daily straight-line distance traveled (Spearman rank correlation, $r_s = 0.04$, $n = 18$, $P = 0.97$).

The nine individuals of the northern group (N1–N9) displayed similar dispersal patterns. Their mean traveling direction corresponded roughly to the direction of Masirah Island (Oman) which hosts a major loggerhead rookery. N1–N5 traveled to the Omanese and Yemeni coasts more than 3,500 km away from the release point. N6–N9 headed to the south coast of Somalia and followed the coast northwards. N9 remained in a narrow strip some 30 km long off

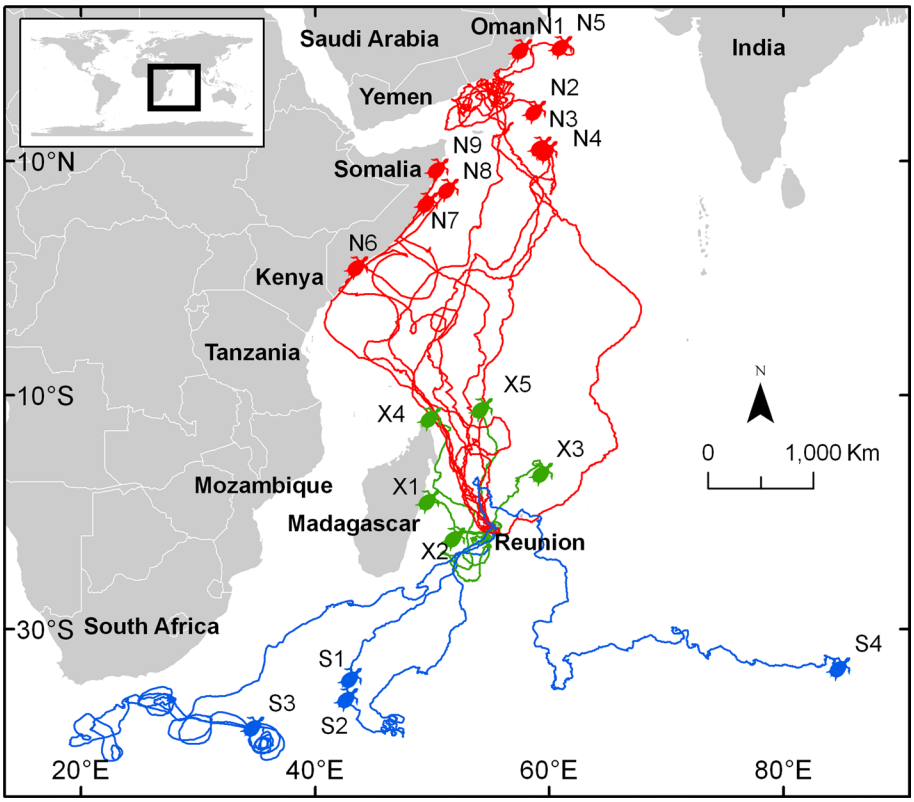


Fig. 2 Satellite tracks of 18 late juvenile loggerhead individuals released after accidental captured by longline fishing boats in the vicinity of Reunion Island. Individuals were classified into three groups: north (*red*), south (*blue*) and undetermined (*green*)

the Somali coast for more than 3 months. The PTTs of N6–N8 stopped transmitting while they were heading north.

The four southern turtles (S1–S4) traveled more than 1,500 km away from the release point. S1–S3 traveled southwest while S4 first went southward and later eastward in the middle of the southern Indian Ocean. It was the only tracked individual that crossed the 70°E meridian going eastward. All four turtles remained in the open ocean.

For the other turtles (X1–X5), last locations were within 1,500 km from the release point. X1 and X2 remained in the open ocean. They followed atypical westward pathways moving toward Madagascar either straight (X1) or with loops (X2). X3 followed a northerly route and remained in the vicinity of St. Brandon islands (670 km from Reunion Island) for more than 3 months. Similarly, X4 and X5 headed north, but they remained in the oceanic zone. Their movement patterns at the end of the transmission, around 1,100 km away from the release site, were similar to the patterns displayed by the turtles of the northern group.

Movement behavior types

Behavioral modes—OT, CT, OR or CR—along each current-corrected track are shown in Online Resource 2. Overall, turtles spent most of their time in transit and more specifically in ocean transit (OT: 51.5 ± 36.6 %, CT: 8.5 ± 19.0 %, OR: 1.8 ± 35.0 %, CR: 0.5 ± 12.3 %, $n = 18$). The PTTs of two 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 near the islands of Reunion and Mauritius shortly after release. None of them exhibited CR. 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 the open ocean or in the coastal areas of Somalia. N9 remained for 75 days in CR along a very narrow area of the Somalian coast. Once reaching the Omani and Yemeni waters, N1, N2 and N5 alternated long OR with short CR phases. Other individuals did not reach latitudes north of 10°N during their tracking periods.

Diving behavior

A total of 23,362 dive durations (from 14 turtles) and 18,688 dives depths (from 10 turtles) were recorded. The dive depth distributions show that 86.9 ± 8.2 % ($n = 10$) of dives were shallower than 30 m and that 98.5 ± 1.2 %

($n = 10$) of dives were shallower than 100 m. Another peak with larger dive frequencies appears around 55 m. Dive duration data demonstrated that 57.1 ± 12.9 % ($n = 14$) dives were shorter than 2 min and 88.9 ± 6.6 % ($n = 14$) shorter than 30 min where a second peak appears in the number of dives.

Mean frequencies of dives assigned to each dive type Dss, Dsl, Ddl and Dl were 80.0 ± 10.8 % ($n = 14$), 4.6 ± 3.8 % ($n = 10$), 13.1 ± 7.8 % ($n = 10$) and 9.9 ± 15.8 % ($n = 4$), respectively (Fig. 1).

There was a clear daily dichotomy in turtles' diving behavior (Figs. 3 and 4), with diurnal dives being significantly more numerous (Wilcoxon signed-rank test, $T = 55$, $P = 0.002$, $n = 10$, Fig. 3a) and shorter (Wilcoxon signed-rank test, $T = 1$, $P = 0.002$, $n = 10$, Fig. 3e; Table 3) than nocturnal dives. In addition, maximum dive depth was also significantly deeper at night (Wilcoxon signed-rank test, $T = 2$, $P = 0.006$, $n = 10$, Fig. 3c; Table 3). During daytime, turtles spent significantly more time just below the surface (53.5 ± 19.1 % in 0–10 m, $n = 10$, Table 3) than at night (20.7 ± 11.4 % in 0–10 m, $n = 10$, Table 3, Wilcoxon signed-rank test, $T = 55$, $P = 0.002$). At night, they spent half their time between 0 and 30 m (51.4 ± 22.2 % in 0–30 m, $n = 10$) with a 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 (4.3 ± 5.7 %, $n = 10$, Table 3) and night (5.2 ± 5.7 %, $n = 10$, Online Resource 1-Fig. 2, Table 3, Wilcoxon signed-rank test, $T = 36$, $P = 0.43$). These differences in diving behavior were confirmed by single dive parameters: short and shallow dives (Dss) were significantly more frequent during day hours (86.4 ± 12.8 %, $n = 14$, Table 3) than during night hours (73.0 ± 8.9 %, $n = 14$, Table 3; Fig. 4, Wilcoxon signed-rank test, $T = 104$, $P < 0.001$).

Relation between diving and movement behavior

Time spent just below the surface (0–10 m) was not clearly related to movement phases (OR, CR, CT and OT). A difference in the usage of the water column located between 10 and 20 m was observed, both during oceanic and coastal phases (Online Resource 1-Fig. 3). Turtles spent more time in this layer while they were in resident phases (24.9 ± 2.5 %, $n = 6$, Table 3) than during transit periods (8.8 ± 6.4 %, $n = 6$, Table 3, Mann–Whitney U test, $U = 13$, $P = 0.036$). The proportion of short and shallow dives (Dss) was slightly but not significantly more important during transit phases (85.5 ± 9.5 %, $n = 14$, Table 3) than during residency phases (74.5 ± 5.4 %, $n = 7$, Table 3, Mann–Whitney U test, $U = 13$, $P = 0.055$).

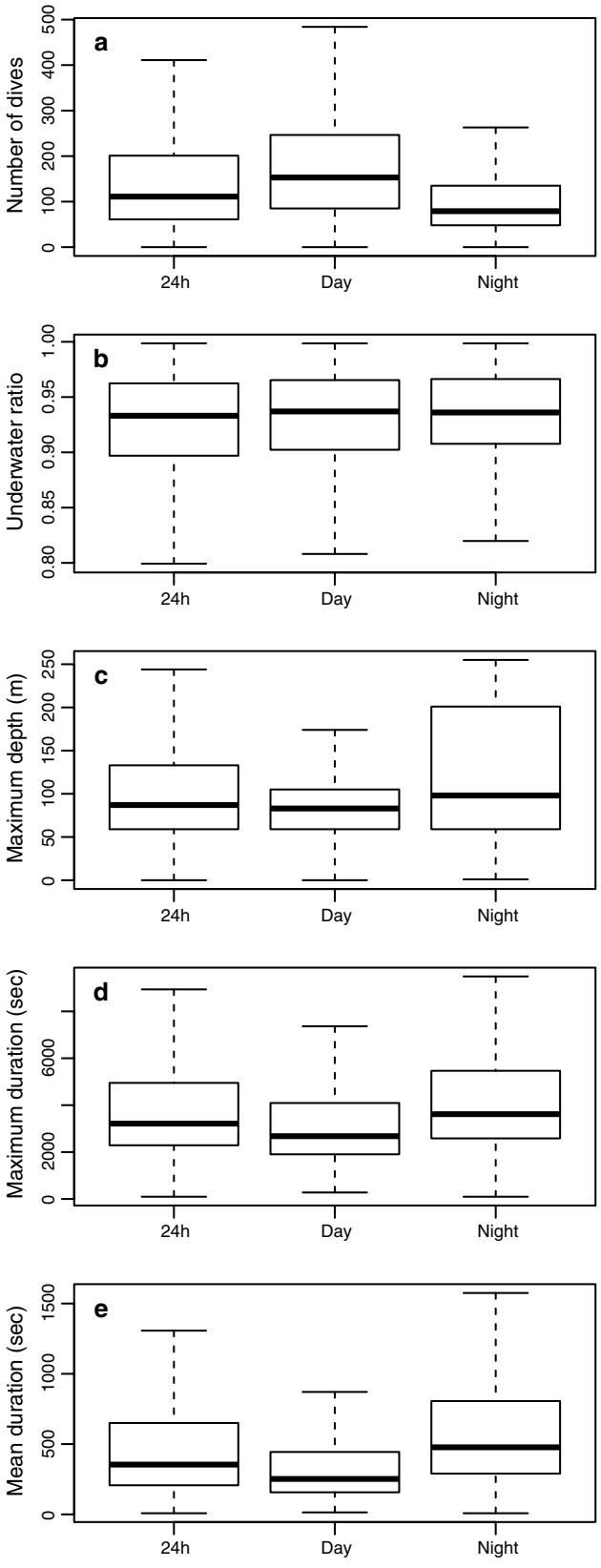
Slight differences were also observed in the usage of the deepest layers both during the open ocean and coastal phases (Online Resource 1-Fig. 3). The maximum dive depth of turtles during transit phases (121.2 ± 25.0 m, $n = 9$) was deeper than during resident phases (100.0 ± 50.0 m, $n = 9$, Table 3, Mann–Whitney U test, $U = 56$, $P = 0.039$). Nevertheless, the usage of the deepest layers (>40 m) was not significantly different whether animals were in resident (4.1 ± 5.7 %, $n = 7$, Table 3) or whether they were in transit (6.5 ± 5.1 %, $n = 14$, Table 3, Mann–Whitney U test, $U = 60$, $P = 0.44$).

Oceanic covariates

The distributions of SST, NPP and TKE are illustrated in Fig. 5, and oceanic environment values are summarized in Table 4 (an illustration of the oceanic covariates for each individual track is provided in Online Resource 3). Most (95 %) of the turtles locations were associated with SSTs ranging from 17.12 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). Turtles of the different groups were exposed to various levels of SST (Kruskal–Wallis test, $H_2 = 9.30$, $P = 0.009$). During residency phases (coastal and open ocean), individuals in the southern group were exposed to colder SST (19.4 ± 0.72 °C, $n = 3$) than individuals in the northern group (27.7 ± 0.61 °C, $n = 6$, Fig. 6a, Mann–Whitney U test, $U = 36$, $P = 0.028$). The other turtles were exposed to high SST of the same order of magnitude as northern turtles (27.8 ± 0.03 °C, $n = 2$, Fig. 6a, Mann–Whitney U test, $U = 16$, $P = 0.44$).

NPP levels were extremely variable along tracks, with 95 % of values ranging from 125.0 to 1,141.6 mg C m^{-2} day^{-1}. The highest levels of NPP were observed along the coast of the Arabian Peninsula, with the highest level of NPP being recorded for N5 at 7,801.1 mg C m^{-2} day^{-1} near the southeast coast of Oman. During residency phases, individuals were exposed to varying levels of productivity, depending on their groups (Fig. 6a; Kruskal–Wallis test, $H_2 = 8.07$, $P = 0.017$). Individuals of the undetermined group (231.1 ± 51.7 mg C m^{-2} day^{-1}, $n = 2$) were exposed to significantly lower NPP levels than individuals from the northern group (424.7 ± 345.3 mg C m^{-2} day^{-1}, $n = 5$, Mann–Whitney U test, $U = 5$, $P = 0.019$) or the southern group (396.9 ± 146.7 mg C m^{-2} day^{-1}, $n = 3$, Mann–Whitney U test, $U = 1$, $P = 0.016$).

OR phases occurred most frequently, but not exclusively, either below 30°S or above 10°N. Several individuals then described circular movements (N1, N2, N5, N6, S2 and S3; see respective figures in Online Resource 2). These OR phases were related to oceanic mesoscale structures (Online Resource 1-Fig. 4), as supported by higher TKE values observed along the tracks during OR phases (505.5 ± 451 cm^2 s^{-2}, $n = 10$) in comparison with OT phases (449.0 ± 202.5 cm^2 s^{-2}, $n = 18$, Fig. 6b,



Mann–Whitney U test, $U = 1$, $P = 0.61$). They were also exposed to higher levels of NPP during OR phases (405.2 ± 300 mg C m^{-2} day^{-1}, $n = 10$) than during OT phases (262.0 ± 80.6 mg C m^{-2} day^{-1}, $n = 18$, Mann–Whitney U test, $U = 39$, $P = 0.014$).

◂**Fig. 3** Pooled distributions of integrated parameters of late juvenile loggerhead sea turtles over 24, 12 h daytime and 12 h night time: **a** number of dives ($n = 14$), **b** underwater percentage ($n = 14$), **c** maximum dive depth ($n = 10$), **d** maximum dive duration ($n = 14$) and **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

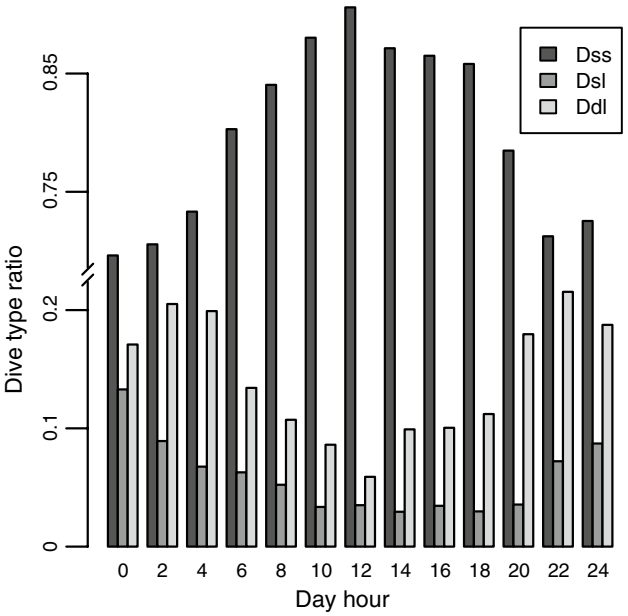


Fig. 4 Percentage of Dss, Dsl and Ddl dives of ten late juvenile loggerhead sea turtles according to day hour (GMT + 4). Dss are subsurface and short dives (<30 m, <800 s), Dsl are shallow and long dives (<30 m, ≥800 s), and Ddl are deep and long dives (≥30 m, >800 s). Short and shallow dives are more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

Discussion

All living organisms have to move at some point of their life history by either passive or active mechanisms (Holyoak et al. 2008). In a constantly changing and heterogeneous environment, animals interact with the physical environment, the resources and the habitats through their movement (Tilman and Kareiva 1997). Movement is therefore a key to the ecological dynamics of numerous species (Kendall and Fox 1998; Nathan et al. 2008). Sea turtles juvenile stage illustrates its importance. As our knowledge on juvenile loggerhead spatial ecology improves, there is growing evidence that the spatial fate of individuals during the early stages may have substantial effects on growth rates, life-stages duration and age at sexual maturity (Bjorndal et al. 2013). The results of the satellite tracking of 18 juvenile loggerheads in

Table 3 Distribution of diving parameters [median ± IQR (*n*)] for 14 late juvenile loggerheads over the all tracking period (overall), depending on day time (day and night) and depending on behavioral modes (OT, OT, CT and CR)

	Overall	Day	Night	OT	OR	CT	CR
(a) Dive summary							
Number of dives (24 h)	300.3 ± 117.3 (14)	356.3 ± 81.3 (10)	215.1 ± 100.4 (10)	326.4 ± 128.5 (14)	268 ± 184.7 (7)	405.5 ± 175.4 (13)	268.5 ± 38 (4)
Under water ratio (%)	90.8 ± 4.6 (14)	92.5 ± 2.8 (10)	92.3 ± 3.2 (10)	91.6 ± 4.5 (14)	80.7 ± 15.3 (7)	88.7 ± 6 (13)	91.5 ± 10.4 (4)
Maximum depth (m)	114.7 ± 18.6 (10)	88.6 ± 27.8 (10)	139.1 ± 40.9 (10)	126.7 ± 17.5 (10)	118.9 ± 35.6 (6)	109.3 ± 22.6 (9)	78.1 ± 32.5 (4)
Maximum duration (min)	66.9 ± 27.2 (14)	68.7 ± 31.5 (10)	72.6 ± 27.1 (10)	65 ± 28.1 (14)	80.5 ± 47.7 (7)	57.7 ± 18.6 (13)	56 ± 29.1 (4)
Mean duration (min)	8.5 ± 4.9 (14)	6 ± 3.8 (10)	10.7 ± 6 (10)	7.9 ± 4 (14)	6.3 ± 12 (7)	5.7 ± 2.7 (13)	6.3 ± 7 (4)
(b) Dive type							
Dss ratio (%)	75.9 ± 17.6 (10)	86.4 ± 12.8 (14)	73 ± 8.9 (14)	82.8 ± 12.1 (14)	72.1 ± 19 (7)	86.6 ± 8.4 (14)	76.4 ± 4.9 (4)
Ddl/(Ddl + Dsl) (%)	75.9 ± 17.6 (10)	64.6 ± 47.2 (10)	85.2 ± 28.2 (10)	86.6 ± 19.1 (10)	95.6 ± 33.5 (5)	79.3 ± 28.2 (10)	65.5 ± 15.2 (4)
(c) Time-at-depth							
1–10 m (%)	39.7 ± 11.2 (10)	53.5 ± 19.1 (10)	20.7 ± 11.4 (10)	37.6 ± 11.7 (10)	42.3 ± 13.8 (6)	43.2 ± 8.1 (9)	30.1 ± 6 (4)
11–20 m (%)	15.4 ± 11.7 (10)	6.2 ± 8.3 (10)	21.8 ± 14.3 (10)	8.9 ± 8.6 (10)	8.8 ± 15.1 (6)	5.5 ± 3.1 (9)	25.8 ± 13.1 (4)
21–30 m (%)	13.6 ± 6 (10)	8.2 ± 5.9 (10)	19.3 ± 9 (10)	15.1 ± 6.9 (10)	8.6 ± 9 (6)	8.8 ± 8.8 (9)	11.9 ± 4.4 (4)
31–40 m (%)	7.8 ± 3.9 (10)	5.2 ± 2.1 (10)	10.7 ± 7 (10)	9.3 ± 4.9 (10)	5.7 ± 3.6 (6)	8.1 ± 2.7 (9)	7.6 ± 3.8 (4)
40 m+ (%)	6.5 ± 6.2 (14)	4.3 ± 5.7 (10)	5.2 ± 5.7 (10)	6.4 ± 5.8 (14)	4.1 ± 5.4 (7)	6.5 ± 6 (13)	4.6 ± 5.5 (4)

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

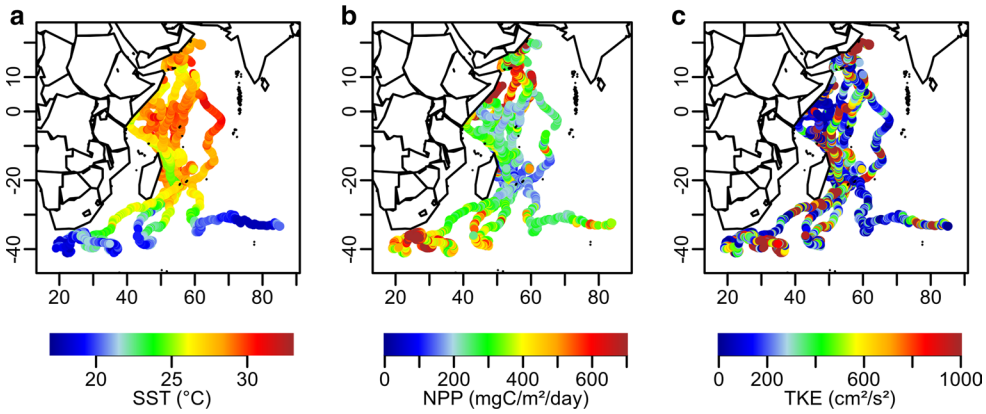


Fig. 5 Distributions of environmental variables along the 18 turtle's tracks: **a** SST (°C), **b** NPP (mg C m^{-2} day^{-1}) and **c** TKE (cm^2 s^{-2}). Coldest SST appears at the most southern locations. NPP levels are higher at more extreme latitudinal locations in the south and in the north and are lower in the equatorial locations. TKE values are more homogeneously dispersed

Table 4 Distribution of oceanic parameters [median ± IQR (*n*)] for the three spatial groups: north, south and undetermined and for the four behavioral modes: CR, CT, OR and OT

Group/mode	SST (°C)	NPP (mg C m^{-2} day^{-1})	TKE (m^2 s^{-2})
North	27.61 ± 1.27 (9)	296.07 ± 98.76 (9)	459.95 ± 177.17 (9)
South	21.65 ± 1.03 (4)	365.61 ± 62.9 (4)	433.7 ± 301.22 (4)
Undetermined	27.25 ± 1.44 (5)	204.67 ± 53.57 (5)	410.97 ± 126.07 (5)
OT	27.05 ± 2.39 (18)	261.92 ± 80.62 (18)	448.98 ± 202.46 (18)
OR	27.45 ± 5.96 (10)	405.18 ± 299.99 (10)	505.46 ± 451.61 (10)
CT	27.16 ± 1.64 (18)	208.11 ± 58.8 (18)	294.64 ± 288.41 (18)
CR	27.75 ± 0.45 (6)	427.23 ± 602.34 (5)	233.02 ± 244.11 (6)

the Indian Ocean provide new insight on the spatial ecology of the species in the region, but also first evidence of trans-equatorial movements with high latitudinal range.

Regional dispersal

One half (50 %) of the late juvenile loggerhead sea turtles tracked in this study went north toward one of the world's largest rookeries for the species (Fig. 2). Another important component (22 %) went southwest toward smaller rookeries (Fig. 2). The average size of first-time nesters is 84 cm in South Africa (Nel et al. 2013) and 91 cm in Oman (Ross and Barwani 1995) while the size of sexual maturity for this species is usually considered to be around 80–90 cm (Avens and Snover 2013). With an average curved carapace length of 68 cm, the individuals we tracked were likely to be close to sexual maturity, but not mature, and therefore to be heading toward their natal site, as sea turtles tend to exhibit philopatry. This suggests that late juvenile loggerheads frequenting the Reunion Island and East Madagascar waters (location of capture, Online Resource 1-Fig. 1) may originate mainly from northerly rookeries and also from southerly ones. This suggests a trans-equatorial development cycle for the individuals originating from the northern rookeries. Population genetics could be used to confirm this hypothesis as genetics have been used to characterize the origin of individuals at large distance from their natal site (Monzón-Argüello et al. 2010, 2012).

The distances traveled by the individuals were substantial as is generally the case for juvenile sea turtles (Hays and Scott 2013). Nevertheless, while in the other oceans the loggerhead development occurs typically over broad spatial scales (e.g., more than 10,000 km in the Pacific Ocean; Bowen et al. 1995; Boyle et al. 2009), it is normally confined to a single hemisphere (see exception in Bowen et al. 1995). The trans-equatorial development cycle in the Indian Ocean appears therefore atypical.

The spatiotemporal pathways followed by juvenile loggerheads to reach the southwest Indian Ocean are still to be determined. Ocean currents are known to play a crucial role in the spatial fate of juveniles sea turtles (Musick and Limpus 1997). Noticeably, in both the Atlantic and Pacific Oceans, large oceanic gyres are persistent and predominantly constrained in a single hemisphere. In the Indian Ocean, the unique characteristics of the monsoon phenomenon make hydrodynamics particularly complex: no annual, persistent and ocean scale gyre exists as cyclonic and anticyclonic complex gyres alternate during winter and summer monsoon periods (Schott and McCreary 2001; Schott et al. 2009). The pathway followed by hatchlings and early juvenile loggerheads from the Arabian Sea to the ocean waters around Reunion and Madagascar is likely to be more complex than in the other oceans.

Following the general scheme of Indian Ocean circulation described in Schott et al. (2009), we hypothesize that hatchlings from Oman may drift eastward with the

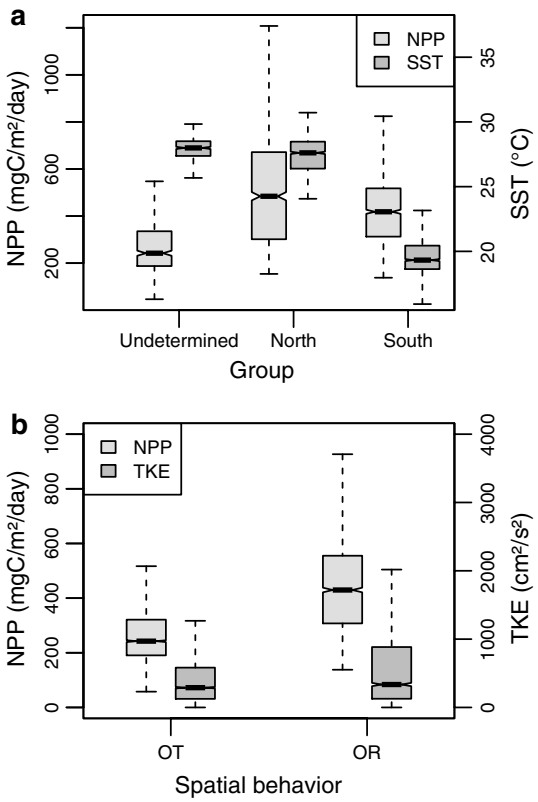


Fig. 6 **a** Comparison of NPP and SST between late juvenile loggerhead individuals from the northern group ($n = 11$) and individuals from the southern group ($n = 4$). NPP reaches higher levels for turtle of the northern and southern group. Individual from the southern group is exposed to lower SSTs. **b** Comparison of NPP and TKE during OT phases and OR phases. NPP levels are higher during resident phases. Higher TKE levels also occur during resident phases

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 westward toward the Mascarene archipelago. In the absence of strong supporting evidence, this hypothesis should, however, be treated with caution. Furthermore, considering the seasonal characteristics and the complexity of the oceanic circulation in the Indian Ocean, we can surmise that more variability in the development cycle and hatching dispersal of loggerheads may exist in Indian Ocean hatchling dispersal than for loggerhead populations in other oceans. Drift modeling should provide valuable information regarding these drift patterns as they are now extensively used (Hays et al. 2010; Putman et al. 2012; Scott et al. 2012; Shillinger et al. 2012; Gaspar et al. 2012).

Space utilization

In others oceans, various loggerhead foraging behaviors have been observed during the development stages. Juveniles generally settle in neritic habitats but may occasionally remain, or reenter, the open ocean environment (McClellan and Read 2007; Mansfield et al. 2009; McClellan et al. 2010). Both behaviors were observed in our study. Demographic implications of this alternative foraging strategy are discussed in Peckham et al. (2011). For example, while open ocean individuals may be exposed to slower growth rates due to lower prey availability, this disadvantage may be negated through having a lower predation risk than a purely coastal strategy.

It is noteworthy that three individuals remained in the vicinity of the coast of Yemen and Oman, and their movements were similar to the post-nesting movements of nesting adults from Oman that forage in the same area (Rees et al. 2010). It is also worth noting that no neritic settlement was observed in the southern group where all turtles remain in the open ocean. In contrast, to the northern group, movements of late juveniles of the southern group differed from the movements of adults nesting in South Africa that are known to forage in the neritic zone along the coast of South Africa (even along the Atlantic side, Hughes 1974), Mozambique (Luschi et al. 2006; Pereira, personal communication), Tanzania (Luschi et al. 2006) or Madagascar (Rakotonirina Berthin, IHSM, personal communication). Nevertheless, circular movements around the oceanic eddies of the Agulhas Rings have been observed in adult leatherback sea turtles (Luschi et al. 2006; Doyle et al. 2008; Galli et al. 2012), demonstrating the interest of the region for sea turtles during the oceanic phases.

Individual turtles did not generally spend much time around the island where they were captured and tended to leave the area shortly after release. The region must be regarded as transit zone or a migratory corridor for late juveniles heading toward more productive areas in the south or in the north and simply passing through Reunion Island waters where they are accidentally captured. More data are required to confirm this hypothesis.

Diving behavior

The diurnal versus 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). Howell et al. (2010) also found that late juvenile loggerheads 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 15 m during the day. With slightly different bins (0–10 m), we made similar observations. The dichotomy observed in the diving behavior may result from nocturnal resting dives and diurnal subsurface active dives (Godley et al. 2003).

During residency phases, turtles made more use of the 10–20 m layer than during transit periods, but made less

use of the deeper layers (>40 m). This was observed for both coastal and open ocean phases. For coastal phases, this may be explained by the shallower waters allowing turtles to reach ocean bottom. During open ocean phases, prey availability at shallower depth may occur under specific conditions and could explain the observed behavior of loggerheads. The association of OR 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 investigated more deeply in the future. Observations of occasional, and exceptionally deep dive events (>80 m) occurring mostly during transit phases, are difficult to interpret. Individuals may be inspecting the water column looking for prey as it has been suggested for the leatherback sea turtle (Houghton et al. 2008). They may also attempt to reduce silhouetting against the surface and exposure to predators or eventually to reach the sea bottom to check for the proximity of seamounts or coastal areas as these two behaviors have been suggested for green turtles (Hays et al. 2001; Rice and Balazs 2008).

Oceanic environment

Environmental conditions for northern and southern groups were drastically different. According to world Ocean partitioning of Longhurst (1998), the Indian Ocean consists mainly of two large biogeochemical provinces: the Indian Monsoon Gyre Province (MONS) in the north and the Indian South Subtropical Gyre Province (ISSG) in the south. MONS is bordered by the Northwest Arabian Sea Upwelling Longhurst province (ARAB). This province, included in the Arabian Large Marine Ecosystem, is considered a highly productive ecosystem (Heileman et al. 2009) with intense large-scale seasonal coastal upwelling and a productive phytoplankton bloom system (Lévy et al. 2007). The southern region also exhibits extensive 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). As a consequence, individuals of the northern and southern groups frequented more productive waters than the individuals that remained close to the release site.

There was a major difference in the SST to which turtles were exposed, with clearly higher temperatures for the northern group (27.6 °C) than for the southern group (20.4 °C; Fig. 6). Nevertheless, turtles from the southern group remained in relatively warm waters for loggerhead sea turtles. For example, in the Pacific Ocean, loggerheads frequent waters with temperatures between 14.5 and 20 °C (Kobayashi et al. 2008), and Coles et al. (2000) have suggested a lower thermal boundary of 13.3 °C. Such environmental difference should potentially lead to contrasted life histories. For example, growth rates have been shown to be strongly decreasing with lower SSTs and may therefore lead to lower growth rates for the turtles exploiting the southern habitats (Hughes 1974).

Conservation implications

Pelagic longlines, through incidental bycatch, have a high impact on loggerhead populations. (Lewison et al. 2004; Peckham et al. 2007). In the western Indian Ocean, longline bycatch was identified as one of the possible reasons explaining the slow recovery of the South African population (Petersen et al. 2009). The loggerheads tracked in this study were caught accidentally by the small French longline fishing fleet operating around Reunion Island and the East Madagascar EEZs (Evano and Bourjea Evano and Bourjea 2012). The number of individuals accidentally caught by this fishery is assumed to be low (Miossec and Bourjea 2003). The fact that most of the longline gears are set deeper than 40 m around Reunion Island could explain the relatively low incidence of turtle bycatch occurring within the area.

Considering the large size of loggerhead populations in the northern Indian Ocean from which a majority of individuals seems to originate, any negative impact of the Reunion Island longline fleet is likely to be moderate. Encouraging collaboration between fishermen and the local sea turtle care center (Ciccione and Bourjea 2010) should contribute to a reduction in this impact. Existing mitigation measures, such as the use of adapted circle hooks (Read 2007), the reduction in gear soak time, the avoidance of hotspots and the setting of gear below turtle-abundant depths (Polovina et al. 2003; Gilman et al. 2006; Howell et al. 2010), are also to be encouraged locally.

Summary

In the present study, the first evidence of ocean scale trans-equatorial movements was demonstrated for juvenile loggerhead turtles. This has value for conservation, as threats are identified and protection measures can be developed. It was also shown that southern and northern open ocean juvenile loggerhead turtles target waters with high levels of productivity, although the southern group was exposed to lower sea temperatures. The consequent influence on growth rates and on survival rates might have high impact on population dynamics, viability and recovery. While this is a modest advance in the knowledge of juvenile

loggerhead movement ecology, major questions remain. The routes followed by these individuals from their original rookeries to Reunion island waters are yet to be determined and whether the trans-equatorial development cycle suggested by the results for the northern rookeries is prevalent or whether it is only an artifact of the small number of loggerhead turtles tracked remains to be confirmed. Regional genetic and stable isotopes studies as well as drift simulations could help to answer key issues regarding the survival of loggerhead turtles from hatchling to adult.

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