



Habitat use and diving behaviour of gravid olive ridley sea turtles under riverine conditions in French Guiana



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ABSTRACT

The identification of the inter-nesting habitat used by gravid sea turtles has become a crucial factor in their protection. Their aggregation in large groups of individuals during the inter-nesting period exposes them to increased threats to their survival - particularly along the French Guiana shield, where intense legal and illegal fisheries occur. Among the three sea turtle species nesting in French Guiana, the olive ridley appears to have the most generalist diet, showing strong behavioural plasticity according to the environment encountered. The large amounts of sediments that are continuously discharged by the Amazon River create a very unusual habitat for olive ridleys, i.e. turbid waters with low salinity. This study assesses the behavioural adjustments of 20 adult female olive ridleys under such riverine conditions. Individuals were tracked by satellite from Remire-Montjoly rookery in French Guiana using tags that recorded the location and diving parameters of individuals, as well as the immediate environment of the turtles including the in situ temperature and salinity. Data concerning potential preys was provided via collection of epifauna by a trawler. Multiple behavioural shifts were observed in both horizontal and vertical dimensions. During the first half of the inter-nesting season, the turtles moved away from the nesting beach (21.9 ± 24.7 km), performing deeper (12.6 ± 7.4 m) and longer (29.7 ± 21.0 min) dives than during the second half of the period (7.4 ± 7.8 km, 10.4 ± 4.9 m and 25.9 ± 19.3 min). Olive ridleys remained in waters that were warm (range: 26–33 °C) and which fluctuated in terms of salinity (range: 19.5–36.4 psu), in a relatively small estuarine habitat covering 423 km². If olive ridleys were foraging during this period, the potential preys that might be available were mostly crustaceans (43%) and fish (39%), as expected for the diet of this generalist species during this period. This study highlights the numerous behavioural adaptations of this species in response to the unusual riverine conditions of the French Guiana continental shelf.

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1. Introduction

The tracking of highly mobile organisms through satellite telemetry helps to identify key breeding and foraging areas that play a crucial role in species conservation (Stokes et al., 2015). Given the high inter-individual plasticity of these migrant organisms, long-term monitoring is usually required to delineate adequate protected areas based on species distribution (Schofield et al., 2010). A better understanding of how animals interact with their environment is therefore needed to implement efficient conservation measures, especially when dealing with threatened species such as sea turtles.

The use of satellite tracking to study sea turtles movements and their habitat use during the breeding-nesting season highlighted strong site fidelity for both males and females (Schofield et al., 2010; Hays et al., 2014; Chambault et al., 2016b). The identification of such habitat is of major importance due to the large aggregation of individuals close to the nesting beaches during this period. Additionally, such periods make sea turtles particularly vulnerable due to the high energy costs of the reproduction and the nesting activities. An evaluation of the home range is an essential tool to establish a picture of the core activity areas for the protection of such endangered species (Scott et al., 2012; Schofield et al., 2013; Pendoley et al., 2014). This tool has been widely used to support conservation initiatives for leatherback (Witt et al., 2008), kemp ridley (Seney and Landry, 2008), loggerhead (Schofield et al., 2010; Hart et al., 2010), green (Richardson et al., 2013; Hart et al., 2013; Blanco et al., 2013), hawksbill turtles (Marcovaldi et al., 2012; Hart et al., 2012; Revuelta et al., 2015) and olive ridleys (Maxwell et al., 2011).

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During the inter-nesting season, olive ridley sea turtles show a strong behavioural plasticity in their dispersal and diving behaviour (Hamel et al., 2008; Maxwell et al., 2011; Pikesley et al., 2013). According to the geographic area and therefore the resources available, olive ridleys can adopt either a capital breeding strategy, in which they store fat reserves at their foraging grounds and then cease to feed during the breeding-nesting season (Drent and Daan, 1980), or use an income breeding strategy, whereby they continue to feed throughout the reproduction period (Miller, 1997; Colman et al., 2014).

The olive ridley is distributed across all tropical and subtropical waters, and appears to be the most abundant sea turtle species (Godfrey and Godley, 2008). This species has been studied in the Pacific (Polovina et al., 2004; Swimmer et al., 2006, 2009; Plotkin, 2010), the Arafura Sea off Northern Australia (Whiting et al., 2007; McMahan et al., 2007; Hamel et al., 2008; Pikesley et al., 2013), and in the Indian (Rees et al., 2012) and Atlantic Oceans (Reis et al., 2010; Maxwell et al., 2011). In the western part of the Equatorial Atlantic, French Guiana hosts one of the largest population of olive ridleys (Kelle et al., 2009; *The State of the World's Sea Turtles*, 2016). This olive ridley population has already been tracked during post-nesting migration (Plot et al., 2015; Chambault et al., 2016a), but only one study to date has focused on the movements and diving behaviour of this species during the inter-nesting season, highlighting the surprising reproductive synchrony of olive ridleys nesting in French Guiana (Plot et al., 2012).

The Guianese continental shelf is strongly enriched by the large amounts of sediments and suspended materials that are continuously discharged by the Amazon River (Milliman and Meade, 1983; DeMaster et al., 1996), creating turbid and warm waters that fluctuate drastically in terms of salinity between the dry and the rainy season. Given the active behaviour adopted by this population during the post-nesting migration (Chambault et al., 2016a) and the inter-nesting season (Plot et al., 2012), and in view of the abundance of potential prey for olive ridleys over the French Guiana shield (Guéguen, 2000), we hypothesize that gravid females nesting in French Guiana will dive consistently, adjusting their behaviour to the fluctuating conditions encountered on the Guianese continental shelf.

To assess olive ridley behavioural shifts in response to estuarine conditions, twenty adult females were equipped with satellite tags on Remire-Montjoly beaches (French Guiana) in 2013 and 2014. The tags recorded the behaviour (location and diving parameters) of animals and sampled the in situ temperature and salinity of their immediate environment. Combined with the details of available prey collected in trawl nets, the information supplied by these tags will help to characterize (1) the displacements and (2) the diving behaviour of this vulnerable species in this unusual habitat during the energetically costly inter-nesting season.

2. Methods

2.1. Ethics statements

This study meets the legal requirements of the countries where this work was carried out, and follows all institutional guidelines. The protocol was approved by the “Conseil National de la Protection de la Nature” (CNPN, <http://www.conservation-nature.fr/acteurs2.php?id=11>), the French Ministry for Ecology, Sustainable Development and Energy (permit Number: 09/618) acting as an ethics committee in French Guiana. After the evaluation of the project by the CNPN, fieldwork was carried out in strict accordance with the recommendations of the Police Prefecture of French Guiana, Cayenne, France, in order to minimize the disturbance of animals.

2.2. Study site and animal tagging

During the inter-nesting seasons in 2013 and 2014, 20 adult female olive ridleys were fitted with satellite tags on Remire-Montjoly beaches

(4.53°N, –52.16°W, Cayenne, French Guiana). From 26/06/13 to 29/06/13, 8 Argos-linked Fastloc GPS tags (MK10, Wildlife Computers Redmond, WA, USA) and 2 Conductivity Temperature Depth Fluorometer-Satellite Relayed Data Loggers (CTD-SRDL, Sea Mammal Research Unit, University of St. Andrews, Scotland) were deployed. From 25/06/14 and 30/07/2014, 10 additional CTD-SRDL tags were fitted on olive ridleys. The attachment procedure followed the standard methods described in Baudouin et al. (2015).

2.3. Data collection

2.3.1. Nocturnal patrols

Nesting events were identified using direct observation during nocturnal surveys rather than evidence of haul-outs from tracking data. This choice is explained by the lack of precise resolution from the Argos (>1500 m) and GPS locations (<100 m) and the potential inaccuracy of the GEBCO database in such coastal habitat, making the identification of nesting events unreliable if based on tracking data alone. Daily nocturnal patrols were therefore performed from April to September in 2013 and 2014 on Remire-Montjoly and Cayenne beaches to observe the entire nesting season of olive ridley turtles. Using the same procedure as that described in Chambault et al. (2016a), each observed female was scanned with a TROVAN Reader to identify a Passive Integrated Transponder (PIT) and if the individual was not tagged, a PIT was inserted in the top right triceps muscle. To complete these nocturnal patrols, daily counts of female's traces on the beach were conducted each day to ensure that no nesting event was missed.

2.3.2. Argos-linked Fastloc GPS tags

The procedure to extract the inter-nesting route data was identical to that used in Baudouin et al. (2015). The Argos-linked Fastloc GPS tags recorded Argos locations and GPS positions at 4-hour intervals (<1% of the locations transmitted). These tags also provided diving data, i.e. maximum dive depths, dive durations and in situ temperature data, binned as 4-hour period histograms. Maximum depths were collected in different bins, every 10 m from 10 to 100 m, then every 50 m from 100 to 250 m. Maximum dive durations were stored from 30 s to 1 min, then every minute from 1 to 5 min, and finally every 10 min from 10 to 60 min. In situ temperatures were recorded during dives from 20 to 32 °C, every one degree Celsius.

2.3.3. CTD-SRDL tags

The CTD-SRDL tags provided the locations of animals via Argos data and recorded simplified profiles of the diving parameters (dive depth, time at depth, dive duration and post-dive surface interval) and oceanographic data in the form of vertical temperature and salinity profiles taken during the ascent phase of turtle dives (Boehme et al., 2009). The CTD-SRDL tags were programmed to send summarized dive profiles using the compression algorithm described by Fedak et al. (2001), providing four depth records for each dive (instead of the single maximum depth per dive provided by Argos-linked Fastloc GPS tags). Temperature and salinity data were quality controlled using the procedure described in Roquet et al. (2011), with an estimated accuracy of 0.02 °C in temperature and 0.05 psu in salinity.

2.3.4. Prey abundance from trawler

Over the French Guiana continental shelf, 31 samples of potential olive ridley prey (epifauna) were collected during a survey carried out by IFREMER using a bottom trawler between 15/11 and 20/11/2014. The fauna was sampled with a shrimp trawl (1 m vertical opening, 6.7 m horizontal opening, 45 mm cod-end mesh size). The trawl hauls were performed on the seafloor at depths of 10 to 60 m. All the individuals collected at each location were identified and counted. As it was not possible to identify the specific species of some individuals, we classified the preys into five groups: cephalopods, crustaceans, cnidarians, molluscs and osteichthyes (fishes).

2.4. Data pre-filtering

As the tags were deployed at the beginning of the inter-nesting season, they also recorded locations from the post-nesting migration. Following the procedure described in Chambault et al. (2015), the average daily speed during the inter-nesting season was calculated, a speed filter of 30 km.d^{-1} was set, and only the positions associated with a daily speed $>30 \text{ km.d}^{-1}$ were set to migration phase and then excluded for the analysis. Following the same procedure as Chambault et al. (2015), only the positions corresponding to the inter-nesting season were retained for the analysis.

Using the same approach as Heerah et al. (2013), a Kalman-filtering algorithm was then applied (CLS, *Collecte Localisation Satellites*, Toulouse, France) to enhance tag position estimates by accounting for Argos location errors (Patterson et al., 2010; Lopez et al., 2014). The General Bathymetric Chart of the Oceans database (GEBCO, <http://www.gebco.net/>, 30-arc-second 1 km grid) was used to discard any locations on land (13% and 10% of the locations recorded in 2013 and 2014, respectively). Positions associated with a speed of over 5 km.h^{-1} (2% in 2013 and 2% in 2014) (Hays et al., 2004; Schofield et al., 2013) and those with location class Z (class associated with the raw location before Kalman filtering, 1 location recorded in 2013) were considered insufficiently accurate and were removed.

The *trackDistance* function from the *trip* package on R (Luque, 2007) was used to calculate the distance travelled and the elapsed time between locations. The observed speed was then derived from these values. The distance to the nesting site, i.e. the location where each turtle was initially tagged, was also calculated for each position.

2.5. Habitat use

In order to display the residency patterns, both the Argos and GPS positions were used to estimate the home ranges by mapping the kernel density distributions (Worton, 1989). Although GPS locations are much more accurate than Argos locations for the quantification of home ranges (Schofield et al., 2010), we could not base the kernel calculation only on GPS data due to the very low amount of GPS locations transmitted (1%). To minimize autocorrelation in spatial analyses, median daily locations were generated for each turtle (Schofield et al., 2010, 2013; Revuelta et al., 2015). Based on the coordinates expressed in decimal degree (limiting possible errors given the proximity to the equator), a kernel density analysis was then designed combining both years of tag deployment using the *kernelUD* function from *adehabitatHR* package on R (Calenge, 2006). As the kernel density cannot always be calculated using the least square cross-validation method (Seaman and Powell, 1998), the smoothing parameter h was fixed using the default approach, i.e. the ad hoc method with $h = 0.08$ (Calenge, 2006). Ninety percent contours were used to represent the broad home range, and 50% density contours were used to define the core area. The corresponding area (expressed in km^2) was then calculated within each kernel contour.

2.6. Diving behaviour

For the diving variables, we discriminated between benthic and pelagic dives by calculating the difference between the bathymetry at the dive location and the maximum dive depth recorded by the CTD-SRDL for the same location for each dive. Therefore, dives with a maximum depth within 0 m of the seabed were classified as benthic dives, and those with a maximum depth above 0 m of the seabed were pelagic dives. Data from the Argos-linked Fastloc GPS tags ($n = 8$) were not used due to their coarser resolution (one dive depth every 10 m). At some locations, depth difference was greater than the bathymetry depth, possibly due to the error generated by the shift between the incorrect Argos positions and the considerable movements of the turtle during the dive or due to GEBCO errors in such coastal habitats.

To obtain an idea of the dive patterns, we calculated the Time of Allocation at Depth (TAD) index by using the four inflection points of the summarized profiles provided by the CTD-SRDL tags. Based on Fedak et al. (2001)'s method, TAD calculation makes it possible to obtain relevant information about where turtles concentrate their activity within the dives, i.e. V-shaped dives for $0.5 \leq \text{TAD} < 0.75$ (exploratory dives) and U-shaped dives for $0.75 \leq \text{TAD} < 1$ (activity centered at the bottom of the dive, linked to either foraging or resting activity). Following the method of Plot et al. (2015), the average rate of change of depth was fixed at 1.4 m.s^{-1} .

2.7. Statistical analyses

All statistical analyses were performed using R software version 3.2.2 (R Core Team, 2015). Before being submitted to statistical tests, all samples were checked for normality and homogeneity of variance by means of the Shapiro-Wilk test. Depending on these results, parametric or nonparametric tests were used, with a significance level of $\alpha = 0.05$. Values are means \pm SD.

3. Results

3.1. Horizontal movements

3.1.1. Capture-mark-recapture data

During the period from April to September, a total of 1644 gravid female olive ridleys were observed nesting in Remire-Montjoly and Cayenne beaches in 2013 and 1125 gravid females in 2014. The activity peak occurred in July of both years, with 859 nesting events recorded in 2013 and 654 in 2014. Nocturnal patrols recorded an average 1.1 ± 0.3 and 1.2 ± 0.4 nesting events per turtle in 2013 and 2014, respectively (range: 1–4).

3.1.2. General tracking data

Among the ten females equipped in 2013, two individuals (#131354 and #131355) started their post-nesting migration directly after the tag deployment, and were therefore discarded from the analyses. In 2014, four turtles (#130765, #136775, #136776 and #136778) were also removed from the analyses due to very short tracking duration (3, 1, 8 and 4 days, respectively). The data for the horizontal movements of the 14 remaining turtles are summarized in Table 1. On average, 212 ± 93 locations were recorded per tag, for an average tracking duration ranging from 23 (#130767 and #130769) to 54 days (#130765a and #136773, Table 1).

The total distance travelled varied from 342 km (#136772) to 1101 km (#130771), for an average distance of 592 ± 237 km (Table 1). The average travel speed was $1.1 \pm 0.1 \text{ km.h}^{-1}$ (range: $0.8 \pm 0.8 \text{ km.h}^{-1}$ #136772 vs. $1.4 \pm 1.1 \text{ km.h}^{-1}$ #130771). The distance travelled differed significantly among individuals in 2013 (Kruskal-Wallis rank sum test: $\chi^2 = 34$, $df = 7$, $p < 0.001$), and in 2014 (Kruskal-Wallis rank sum test: $\chi^2 = 14$, $df = 5$, $p < 0.05$). In 2013, the daily speed ranged from $16.9 \pm 9.6 \text{ km.d}^{-1}$ (#136770) to $24.4 \pm 11.3 \text{ km.d}^{-1}$ (#130771), for an average daily speed of $20.1 \pm 10.8 \text{ km.d}^{-1}$. In 2014, the daily speed ranged from $16.6 \pm 9.9 \text{ km.d}^{-1}$ (#136779) to $23.8 \pm 21.8 \text{ km.d}^{-1}$ (#130776), for an average daily speed of $17.2 \pm 10.5 \text{ km.d}^{-1}$. Similarly, the daily speeds also differed significantly among individuals in 2013 but not in 2014 (2013: Kruskal Wallis rank sum test, $\chi^2 = 15$, $df = 7$, $p < 0.05$; 2014: $\chi^2 = 2.3$, $df = 5$, $p = 0.79925$, respectively).

3.1.3. Distance to the nesting beach

The distance to the nesting beach varied over the inter-nesting period. Although the turtles moved farther away in 2013 compared to 2014 (up to 38 km vs. 20 km, Figs. 1 and 2A), the same pattern was observed for both years: a sharp increase was observed in the distance to the nesting site during the first half of the tracking (2013: 24.3 ± 25.9 km

Table 1

Summary of the horizontal movements of the olive ridleys equipped in 2013 and 2014. PTT refers to the turtle ID, and Nloc to the number of locations recorded.

PTT	Instrument	Start date	Migration start	Nloc	Tracking duration (d)	Distance travelled (km)	Speed (km.h ⁻¹)
130764a	MK10	27/06/13	22/07/13	178	25	371	1.1 ± 0.9
130765a	MK10	26/06/13	19/08/13	445	54	939	1.1 ± 1.0
130766	MK10	27/06/13	06/08/13	277	40	778	1.2 ± 1.1
130767	MK10	28/06/13	21/07/13	159	23	346	0.9 ± 1.1
130768	MK10	27/06/13	03/08/13	239	37	726	1.3 ± 0.9
130769	MK10	27/06/13	20/07/13	102	23	390	1.3 ± 1.1
130770	MK10	28/06/13	04/08/13	259	37	528	1.1 ± 1.0
130771	MK10	27/06/13	08/08/13	334	42	1101	1.4 ± 1.1
130764	CTD-SRDL	29/07/14	27/08/14	190	29	529	1.1 ± 1.0
136772	CTD-SRDL	25/07/14	20/08/14	115	26	342	0.8 ± 0.8
136773	CTD-SRDL	29/07/14	21/09/14	205	54	803	1.1 ± 1.0
136774	CTD-SRDL	30/07/14	28/08/14	139	29	449	1.3 ± 1.3
136777	CTD-SRDL	30/07/14	28/08/14	178	29	514	1.0 ± 0.9
136779	CTD-SRDL	25/07/14	29/08/14	150	35	484	0.9 ± 0.9
				212 ± 93	35 ± 10.3	592 ± 237	1.1 ± 0.1

vs. 2014: 24.2 ± 25.5 km), followed by a decrease with turtles remaining within 10 km of the nesting beach (Fig. 1). During the second phase of the nesting season, the turtles remained an average 7.4 ± 8.0 km from the beach in 2013, and up to 7.4 ± 7.9 km in 2014. However, the distance to the nesting beach varied among individuals for each year (2013: Kruskal-Wallis rank sum test, $\chi^2 = 115$, $df = 7$, $p < 0.001$; 2014: Kruskal-Wallis rank sum test, $\chi^2 = 46$, $df = 5$, $p < 0.001$).

3.1.4. Home range

There was a slight inter-annual variability regarding the core home range (50% kernel estimator) used by the turtles as it covered 434 km² in 2013, compared to 398 km² in 2014. The broad home range (90% kernel estimator) was twice higher in 2013 (3257 km²) compare to 2014 (1587 km²). The total home range for both years of tag deployment extended over 2916 km², and the turtles centered their activity (50% kernel contours) within a 423 km² area (Fig. 2B).

3.2. Vertical movements

3.2.1. Maximum depth, dive duration and surface interval

Among the 20 tags deployed in 2013 ($n = 10$) and 2014 ($n = 10$), 14 were retained for the diving behaviour analyses, with the Argos-linked Fastloc GPS tags providing 4904 depth records and 4788 dive durations, and the CTD-SRDL tags recording 696 dives.

3.2.1.1. Argos-linked Fastloc GPS tags. In 2013, the maximum dive depth differed significantly between individuals (Kruskal-Wallis rank sum test: $\chi^2 = 316$, $df = 7$, $p < 0.001$), and ranged from 0 to 50 m (mean: 12.6 ± 6.7 m), with 82% of the dives performed in the upper 10 m (Fig. 3A). Dive durations differed significantly between individuals

(Kruskal-Wallis rank sum test: $\chi^2 = 206$, $df = 7$, $p < 0.001$) and ranged from 0 to 70 min (mean: 30.6 ± 19.8 min), with 44% of the dives lasting up to 20 min (Fig. 3B).

3.2.1.2. CTD-SRDL tags. In 2014, the maximum dive depth differed significantly between individuals (Kruskal-Wallis rank sum test: $\chi^2 = 28$, $df = 5$, $p < 0.001$), and ranged from 0 to 35 m (mean: 5.6 ± 4.4 m), with 90% of the dives performed in the upper 10 m (Fig. 3C).

Dive durations differed significantly between individuals (Kruskal-Wallis rank sum test: $\chi^2 = 16$, $df = 5$, $p < 0.005$) and ranged from 0 to 95 min (mean: 8.6 ± 12.4 min), with 77% of the dives lasting up to 10 min (Fig. 3D).

Post-dive surface interval ranged from 0.06 s to 9 min, for an average duration of 1.0 ± 0.9 min. Eighty-eight percent of the post-dive surface intervals lasted <2 min, and differed significantly between individuals (Kruskal-Wallis rank sum test: $\chi^2 = 35$, $df = 5$, $p < 0.001$, Fig. 3E).

3.2.2. Dive shape

Eighty-three percent of the dives performed by the turtles tracked in 2014 were benthic dives, and 16% were pelagic dives. The average TAD was 0.76 ± 0.14, indicating mainly U-shaped dives. Fifty-nine percent of the dives were associated with a TAD ranging between 0.75 ≤ TAD < 0.1 (resting U-shaped dives), and 37% were associated with a TAD between 0.5 ≤ TAD < 0.75 (exploratory V-shaped dives).

V-shaped dives were predominant at the beginning of the tracking period, then decreased until the week 5 and then increased again (Fig. 4). Inversely, the U-shaped benthic dives increased over the period, i.e. from week 1 to week 5, and then decreased again. The U-shaped pelagic dives were the less abundant type of dives.

3.2.3. Diving behavioural shifts over the inter-nesting season

The diving behaviour varied over the inter-nesting season. Although the turtles dived deeper and for longer durations in 2013 compared to 2014 (up to 17.8 m vs. 7.8 m; up to 44.1 min vs. 13.1 min), the same pattern was observed for both years but less pronounced in 2014, with deeper and longer dives during the first three weeks of tracking for both years, followed by shallower and shorter dives for the rest of the inter-nesting season (Fig. 5A and B). The post-dive surface interval recorded in 2014 followed the same pattern (Fig. 5C).

3.2.4. Habitat characterization

3.2.4.1. Potential preys collected from the trawler. The data for prey sampled by the trawler (IFREMER French Guiana) between 15/11 and 20/11/2014 provided 31 records from depths of 12–51.8 m along the French Guiana coast. During the sampling period, a total of 8730 organisms belonging to five different groups were collected: crustaceans ($n = 4489$), osteichthyes (fish, $n = 3063$), molluscs ($n = 976$),

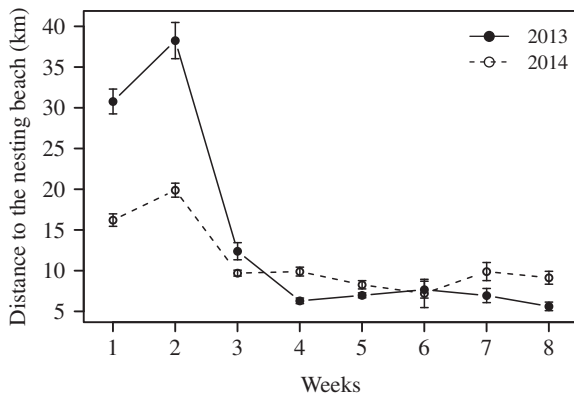


Fig. 1. Distance to the nesting beach in 2013 (filled dots) and 2014 (open dots) over the weeks during the inter-nesting season.

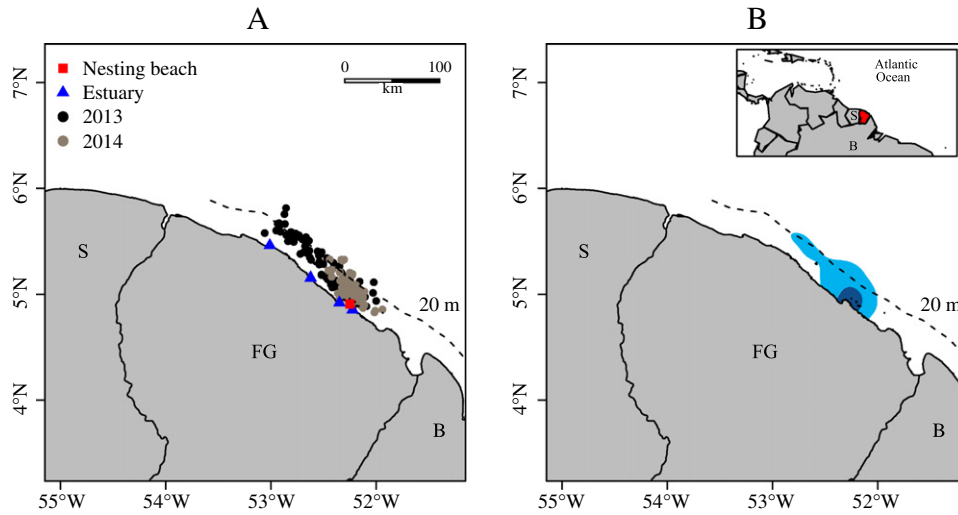


Fig. 2. (A) Median daily locations of the 14 olive ridleys tracked in 2013 (black dots) and 2014 (grey dots) and (B) kernel contours (90% shown in turquoise and 50% shown in dark blue) of the 14 olive ridleys tracked in 2013 and 2014. French Guiana is highlighted in red in B. FG stands for French Guiana, S for Suriname and B for Brazil.

cephalopods ($n = 162$) and cnidarians ($n = 17$). Over the 31 samplings, the crustacean group was the most abundant, representing 51% of the samples, followed by the osteichthye group (35%). Seven samples were collected within the 90% kernel contour of 2014 (Fig. 3A), and mainly contained two highly abundant groups: crustaceans (43%) and osteichthyes (39%) – see Fig. 6B.

3.2.4.2. Oceanographic data recorded by the tags. In 2013, the Argos-linked Fastloc GPS tags recorded 1224 temperature values, ranging from 26 to 33 °C, for an average temperature of 28.3 ± 1 °C (Fig. 7A). Seventy-six percent of the dives were performed in warm waters with temperatures between 27 and 29 °C.

In 2014, the CTD-SRDl tags recorded 91 temperature values, ranging from 26.1 and 28.1 °C (mean: 26.7 ± 0.4 °C), and 84 salinity values, ranging from 19.5 to 36.4 psu (mean: 32.8 ± 5 psu) – see Fig. 7B. All turtles had used a broad range of oceanographic structures, crossing three different density patches.

4. Discussion

The tracking of these 20 gravid olive ridleys over the French Guiana continental shelf provides crucial information about (i) their habitat use and (ii) behavioural shifts that occur during the energetically costly inter-nesting season.

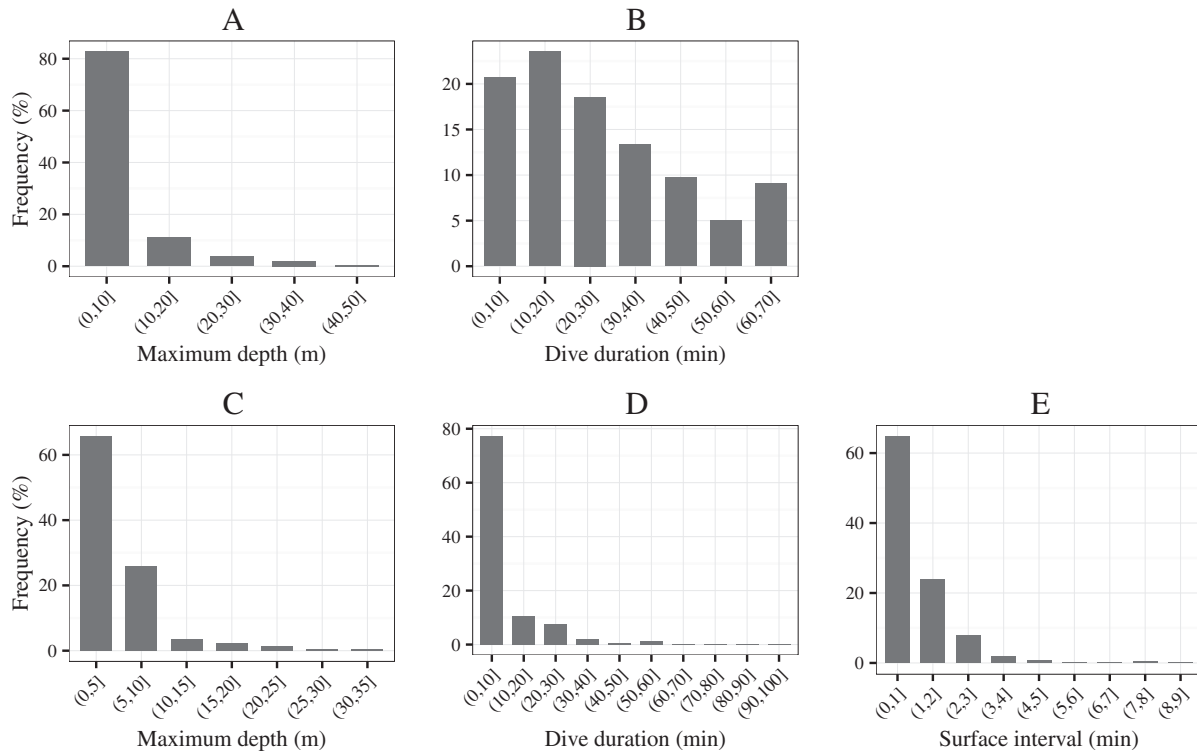


Fig. 3. Histograms of the diving variables recorded by the Argos-linked Fastloc GPS tags (A and B) and the CTD-SRDl tags (C, D and E): maximum dive depth (A and C), dive duration (B and D), and post-dive surface interval (E) for all individuals.

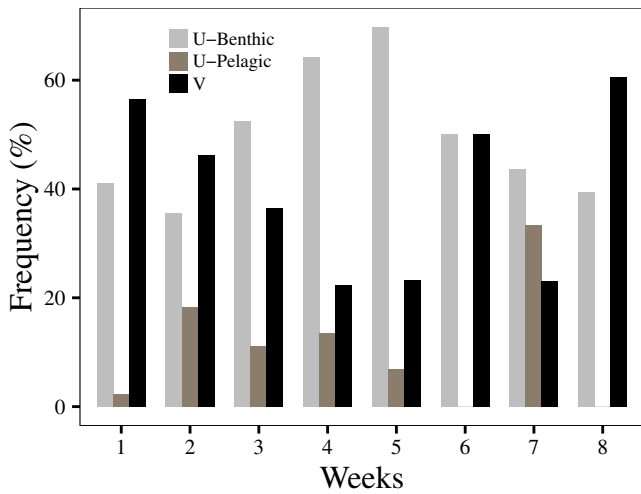


Fig. 4. Bar plots of the dive shape over weeks recorded by the six CTD-SRDL tags in 2014.

4.1. Habitat use

The kernel analysis indicated that the turtles spent most of their time in a relatively small area, covering 423 km² (50%). To date, the literature on the home range of this species is very limited, and only one study conducted in Central Africa has described a core range used by olive ridleys, covering 1267 km² (Maxwell et al., 2011), being bigger than in the present study (423 km²). Such difference might be due to the different methods used to calculate the home range (Minimum Convex Polygon vs. kernel densities) and also to the core range definition, as in Central Africa it was defined as 80% vs. 50% in our study. Turtle movements were close to the shore, generally not crossing the 20 m isobaths and remaining in shallower waters than those previously observed in other olive ridley populations, which usually occupy waters with depths of up to 50 m (Whiting et al., 2007; Maxwell et al., 2011; Rees et al., 2012). As habitat use is dictated by metabolic rate, such behaviour could therefore reduce the costs of locomotion by limiting their movements (Slavenko et al., 2016). This assumption is reinforced by the low travel speeds found in our study ($1.1 \pm 0.1 \text{ km.h}^{-1}$), compared to those recorded by Chambault et al. (2016a,b) ($2.5 \pm 0.6 \text{ km.h}^{-1}$) during the post-nesting migration of the same individuals. The limited displacements were also highlighted by the short distances travelled, with females remaining within $19.6 \pm 23.6 \text{ km}$ from the nesting beach, which is in accordance with the findings of Maxwell et al. (2011) in Central Africa ($27.7 \pm 22.3 \text{ km}$). This behaviour is also

identical to that shown by the same olive ridley population during tracking in the inter-nesting season in French Guiana in 2006–2007 ($18.4 \pm 2.9 \text{ km}$, Plot et al., 2012). This site fidelity probably enables turtles to remain in favourable conditions during oviposition, enhancing their fitness. A species which does not provide any parental care will attach great importance to its choice of nesting beach in order to favour the survival of its offspring (Kamel and Mrosovsky, 2005; Péron et al., 2013).

The prey data collected by the trawler (IFREMER, French Guiana) within the 90% kernel contour has shown the presence of crustaceans (43%), osteichthyes (39%), molluscs (8%), cnidarians (8%) and cephalopods (2%). Despite the temporal mismatch between olive ridleys tracking (From June to September) and the trawler sampling (November), the most abundant species found in olive ridleys home range were crustaceans and fish. This species is known to feed mainly on crustaceans and fish during the inter-nesting season, as demonstrated via stomach content analysis in northeast Brazil (Colman et al., 2014). Although no direct evidence of a feeding activity on such animals has been observed in French Guiana to date, the overlapping of potential resources with the distribution of olive ridleys suggests that if olive ridley were foraging during this period, their potential preys that might be available would include mostly crustaceans (43%) and fish (39%). Such behaviour would suggest that the turtles may adopt an income breeding strategy to cope with the energy loss that is inherent to reproduction and oviposition. To confirm this assumption, 3D accelerometers and cameras need to be deployed on this species, as previously carried out in green and loggerhead turtles (Fossette et al., 2012; Cheng et al., 2013), and complementary approaches such as isotopic analyses and oesophageal lavages/gut content analysis are also necessary (Hatase et al., 2006; Amorocho and Reina, 2007).

The oceanographic conditions of this habitat were warm (range: 26–33 °C) with highly fluctuating waters in terms of salinity (range: 19.5–36.4 psu). The thermal range was close to that experienced by other populations of olive ridleys nesting in Australia (23–29 °C, McMahon et al., 2007, Hamel et al., 2008) and Costa Rica (22–28 °C, Swimmer et al., 2006). However, the turtles crossed environments with varying levels of salinity that ranged from polyhaline (>18 psu) to ultrahaline (>33 psu) depending on their proximity to the shore. The turbid and low salinity waters can be explained by the large discharges coming from the Amazon River plume and other rivers that continuously flow into the French Guiana continental shelf (Jounneau and Pujos, 1988; Froidefond et al., 2002). The neritic domain off the shores of French Guiana is classified into three water classes based on their reflectance, and the olive ridleys concentrated their activity in the green waters (water column depth < 20 m isobaths) and beige waters (at the river mouths). In the latter, the levels of suspended matter are high ($\sim 115 \text{ mg.l}^{-1}$) and

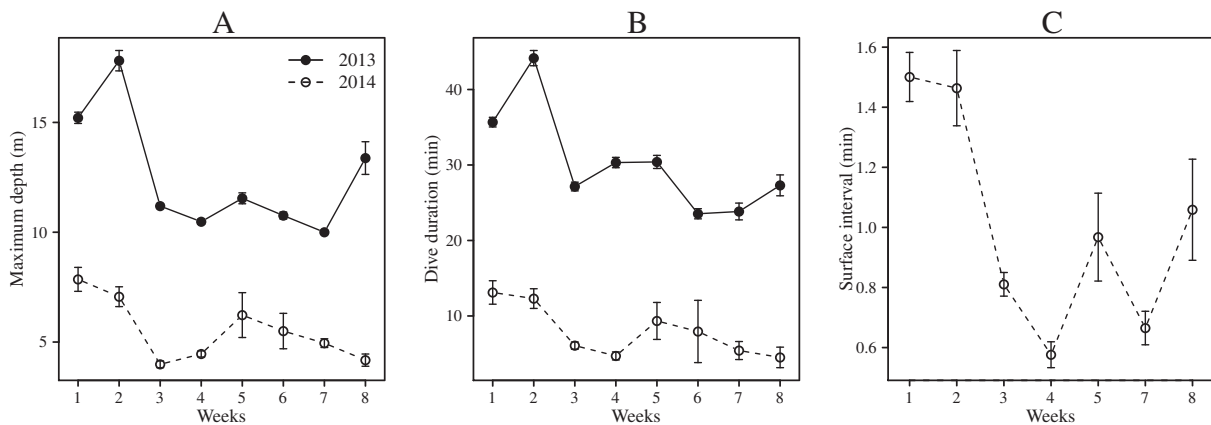


Fig. 5. Average diving variables (+SD) recorded in 2013 (filled dots) and 2014 (open dots) over the weeks of the inter-nesting season. (A) Maximum depth, (B) dive duration and (C) post-dive surface interval.

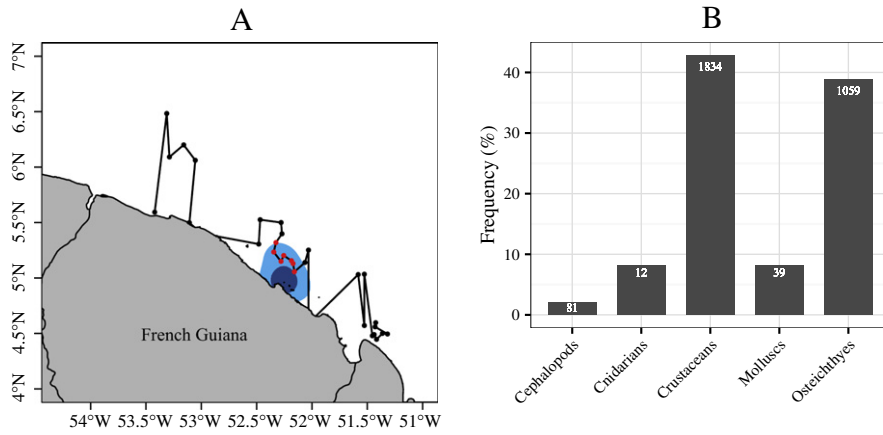


Fig. 6. (A) Trawler transect in relation to the kernel densities for 2014 (90% shown in turquoise and 50% shown in dark blue). (B) Percentage of individuals sampled for each prey group within the 90% home range in 2014 (shown by red dots in A). The white numbers in B refer to the individual abundance sampled within each group.

the chlorophyll *a* concentration is low: 2–3 mg.m⁻³ (Froidefond et al., 2002). Similar to the Kemp's ridley tracked in the Gulf of Mexico (4.5–36 psu, Metz, 2004) and the loggerhead turtles in southwest Florida (0–40 psu, Foley et al., 2006), the olive ridleys nesting in French Guiana show a high tolerance to a wide range of environments.

4.2. Behavioural shifts over the nesting season

Multiple behavioural shifts were observed in olive ridleys for both years of tag deployment, and the inter-nesting season could be divided into two phases. The distance to the nesting site increased during the first half of the period (0–21 days: 21.9 ± 24.7 km), then the turtles remained close to the beach (7.4 ± 7.8 km). The satellite tracking of the same olive ridley population followed in 2006 and 2007 indicated similar results (Plot et al., 2012), highlighting a unique reproductive synchrony in this species with individuals moving closer to the nesting beach after 21 days (Plot et al., 2012). These results reinforce the argument for a mass-nesting phenomenon, also called *arribadas*, which has been evidenced in several olive ridley populations in Mexico, Costa Rica and French Guiana (Eguchi et al., 2007; Plot et al., 2012). In French Guiana and Costa Rica, it has been reported that the inter-nesting interval of this species is approximately 28 days (Plotkin, 2007; Plot et al., 2012) and 18 days in Central Africa (Maxwell et al., 2011), which coincides with the moment when the individuals remain close to the

nesting beach, i.e. 21 days after the last nesting event, and is probably related to landing synchrony (Plot et al., 2012). However, inter-annual variability has been observed, as the turtles tracked in 2014 moved closer to the nesting beach after only 14 days, indicating possible shorter inter-nesting intervals, as previously observed in other populations (Whiting et al., 2007; Hamel et al., 2008). Such variability in the inter-nesting interval could be explained by the behavioural plasticity of the females during the pre-breeding migration (i.e., a remigration interval that can last from one to two years) and by the different foraging grounds used before or during the nesting season (McMahon et al., 2007; Chambault et al., 2016a,b). Indeed, one turtle tracked in 2014 had already been observed in 2013, confirming the uncommon and short remigration interval of this species.

Some behavioural shifts were also observed in diving behaviour, and comprised the same two distinct phases that were identified in the horizontal dimension. Similar to Plot et al. (2012), the turtles performed longer (29.7 ± 21.0 min) and deeper dives (12.6 ± 7.4 m) during the first three weeks of the inter-nesting season compared to the second half of the tracking (25.9 ± 19.3 min, 10.4 ± 4.9 m). These results are consistent with other studies showing that breeding females decrease their dive duration in the few days preceding a nesting event (Hays et al., 1999; Fossette et al., 2007; Houghton et al., 2008; Hamel et al., 2008; Plot et al., 2012), and may be related to the selection of the nesting beach (Plot et al., 2012). At the beginning of the inter-nesting

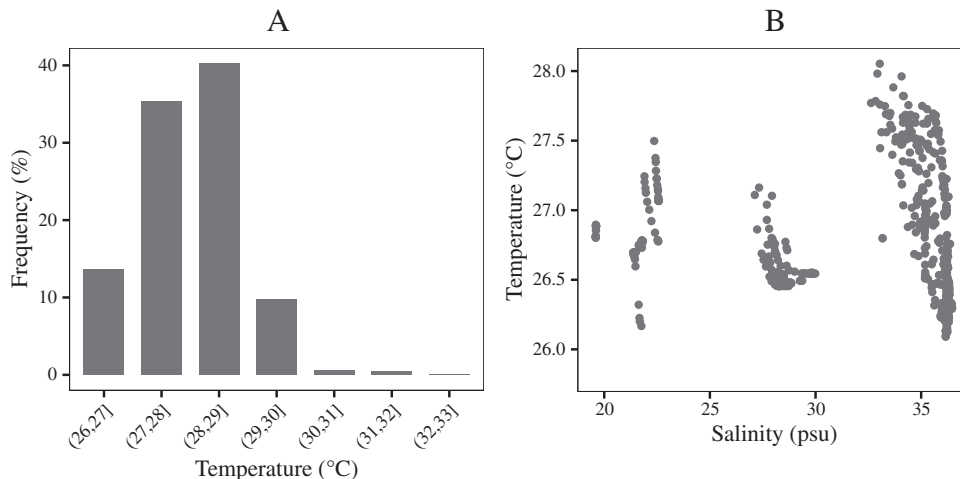


Fig. 7. (A) Histogram of the temperatures recorded by the Argos-linked Fastloc GPS tags in 2013, and (B) Temperature-Salinity diagram from the CTD-SRDL tags deployed in 2014.

season, such behaviour may indicate either a foraging or a resting activity (Hays et al., 1999; McMahan et al., 2007), especially when turtles perform mostly benthic dives (92%). This diving behaviour indicates that they follow the seabed, as previously described in leatherback turtles (Fossette et al., 2007). As olive ridleys performed mainly V-shaped dives (56%) during the first three weeks, such a pattern is more likely to be associated with exploratory behaviour and could be associated with an opportunistic feeding behaviour. In contrast, the dives were mainly benthic and U-shaped during the second half of the period (70%), which can be interpreted as either a resting or a foraging activity. Unlike the tracking during the post-nesting migration period, where the dives were mainly pelagic (Chambault et al., 2016a,b), the predominance of benthic dives in the present study excluded the use of hunting time index as a proxy for the foraging behaviour of this species within dives. Further studies therefore need to be conducted at a finer scale using 3D accelerometers on gravid olive ridleys to distinguish between these two activities during the inter-nesting season.

5. Conservation implications

The satellite tracking of these French Guianese population of olive ridleys provided crucial information on (i) habitat use and (ii) the behavioural shifts that could be used by these females during the inter-nesting season. The estuarine habitat was confined close to the shore, characterized by turbid waters that were strongly influenced by the river discharges along the Guiana coast (Froidefond et al., 2002). Such conditions make this species critically vulnerable due to reduced visibility (Metz, 2004; Chambault et al., 2016a,b) and the high energetic costs of reproduction and nesting activities during this period. The strong occurrence of illegal drifting net fisheries in the coastal area of the Guiana shield (Levrel, 2012; Cissé et al., 2014) exposes this vulnerable species to lethal interactions via bycatch (DEAL Guyane and Agence des Aires Marines Protégées, 2013). This situation requires the implementation of highly coercive but geographically localized measures in this small area (423 km²) used by breeding turtles. A further investigation on the interactions between olive ridleys and fisheries is therefore needed to support the application of adequate measures to ensure the conservation of this threatened species.

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