Dispersal and dive patterns during the post-nesting migration of olive ridley turtles from French Guiana

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ABSTRACT: Behavioral plasticity allows migrating animals to adjust their migration patterns in relation to the environmental conditions they encounter during their movements. Sea turtles display long post-nesting migrations which vary considerably between species and populations. To date, there has been no description of migratory patterns of the large population of olive ridley turtles *Lepidochelys olivacea* in the west Atlantic. Here, we investigated dispersal and dive patterns in relation to environmental conditions of 7 satellite-tracked olive ridley females from French Guiana during their post-nesting migration. After they left the nesting beach, turtles followed a consistent northwestward direction and then remained in the restricted yet productive neritic domain of the continental shelf of French Guiana and Suriname. Despite this restricted dispersal range, turtles demonstrated variability in the habitats they exploited, i.e. the coastline, the continental shelf, and the continental slope, illustrating some plasticity. Moreover, turtles showed 2 different foraging strategies, either directly reaching a specific foraging area off river mouths, or meandering over the neritic area exploiting several foraging areas. In addition, turtles showed different dive patterns related to their habitat, although mostly exploiting the seabed by routinely performing U-shaped benthic dives. Overall, turtles vertically exploited non-stratified water masses characterized by warm surface temperatures consistent with their preferential thermal habitat. The migration strategy used by olive ridleys from French Guiana raises conservation concerns, since turtles may be exposed to coastal human-induced activities that must be considered in the implementation of accurate management measures for this still poorly studied population.

KEY WORDS: Migration strategy · Diving behavior · Satellite tracking · Atlantic Ocean · Olive ridley turtle

INTRODUCTION

Organisms may adapt to spatiotemporal heterogeneity in resource availability through migration. Migration can be defined as the to-and-fro movements between areas where conditions are alternatively favorable and unfavorable; for instance, animals return to their general breeding area but may stage their movements through a succession of non-breeding areas, and may use different paths on the outward and return journeys (Dingle & Drake 2007).

Migration may occur at different stages of life (i.e. from the ontogenic phase to adulthood) and forms an essential component of the life history (Dingle & Drake 2007). A variety of taxa, both terrestrial (e.g. Lack 1959, Urquhart & Urquhart 1978, Madsen & Shine 1996, Berger 2004) and marine (e.g. Brown 1957, Moriarty 1962, Block et al. 1998), perform migrations, sometimes over great distances. When resources are predictable in time and space, migratory patterns are relatively static, whereas when resource distribution and abundance are variable

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and unpredictable, organisms tend to adopt movement patterns that parallel the dynamic of their environment (Roshier & Reid 2003).

Oceans are highly dynamic and unpredictable environments driven by physical and biological processes operating at different scales of time and space (Mann & Lazier 1991). Oceanographic fronts occur at the interface between 2 water masses contrasting in their physico-chemical properties, and result in high biological productivity (Olson et al. 1994). These frontal areas provide suitable foraging areas for fish, sea birds, marine mammals, and sea turtles (e.g. Guinet et al. 1997, Georges et al. 2000, Polovina et al. 2001, Etnoyer et al. 2006, Bost et al. 2009, Kitagawa et al. 2009). Therefore, marine biogeography follows the basic geometry of these oceanographic features (Olson et al. 1994), often leading to common migration corridors for numerous species (Block et al. 2011) and to hotspots of biodiversity (Worm et al. 2005). However, migrating organisms may also show some behavioral plasticity, i.e. they may shift their behavior in response to environmental conditions (Gabriel et al. 2005) and/or to their individual physiology, gender, age, or size (Wearmouth & Sims 2008, Southwood & Avens 2010), resulting in some variability in the observed migration patterns.

In addition to horizontal movements, vertical movements of aquatic species (i.e. diving behavior) may also be affected by environmental conditions associated with the water column structure (e.g. thermocline depth), but also with resource distribution and interactions with other species (e.g. competition, predation). For instance, dive depths of the little penguin *Eudyptula minor* are related to the presence/absence and the depth of the thermocline (Pelletier et al. 2012). The diving behavior of the leatherback turtle *Dermochelys coriacea* displays diel patterns related to the vertical distribution of prey (Hays et al. 2006). Individual diving strategies due to inter-specific competition have also been reported in pinnipeds (Villegas-Amtmann et al. 2013).

In sea turtles, migration occurs from the hatchling stage to adulthood, with age-related migration patterns (Hendrickson 1980, Luschi et al. 2003, Bolten 2003, Godley et al. 2008). At the adult stage, females perform migration between nesting seasons, hereafter referred to as post-nesting migration (Miller 1997, Plotkin 2003): they travel hundreds to thousands of kilometers between the nesting beach and discrete foraging sites where they remain for long periods or travel continuously from one foraging site to another (Plotkin 2003, Hays & Scott 2013). Post-nesting migration is resource-driven and allows adult females to compensate for the high energetic needs of reproduction (Miller 1997, Plotkin 2003, Plot et al. 2013). Migration distances vary substantially among species (Hays & Scott 2013), with the most impressive distances being reported for leatherbacks (Benson et al. 2011). Over the last 20 yr, numerous satellite tracking studies have been conducted on sea turtles, and concurrently with an increased availability of oceanographic data, have produced breakthroughs in our understanding of sea turtle migrations (reviewed by Luschi et al. 2003, Godley et al. 2008). Several studies have suggested that mesoscale oceanographic features such as currents and eddies may influence the offshore movements of sea turtles (e.g. Polovina et al. 2001, Gaspar et al. 2006, Lambardi et al. 2008, Shillinger et al. 2008, Galli et al. 2012, Mansfield et al. 2014), sometimes drawing migration corridors (e.g. Morreale et al. 1996, Shillinger et al. 2008). Yet it is still unclear how sea turtles assess and/or compensate for such environmental forcing processes (Gaspar et al. 2006, Galli et al. 2012). Furthermore, post-nesting migration patterns may vary intra-specifically, in relation with phenotypic factors such as gender (Shaver et al. 2005, Van Dam et al. 2008) or body size (Hawkes et al. 2006, Hatase & Tsukamoto 2008, Zbinden et al. 2011, Rees et al. 2012, Richardson et al. 2013).

Among sea turtles, olive ridley turtles *Lepidochelys olivacea* show different post-nesting migration patterns depending on location. In the north and east tropical Pacific Ocean and in the Indian Ocean, olive ridley turtles exhibit an oceanic migration pattern (Polovina et al. 2004, Ram et al. 2009, Plotkin 2010), whereas they exhibit a neritic migration pattern in the Sea of Oman (Rees et al. 2012). Such differences also occur at smaller geographic scales: in the west Pacific, olive ridley turtles from 2 distinct nesting sites in north Australia have been reported to display a mixed oceanic–neritic migration pattern (McMahon et al. 2007) or a neritic migration pattern (Whiting et al. 2007). This diversity of migration patterns has not been investigated yet.

In the Atlantic Ocean, the post-nesting movements of olive ridley turtles have only been investigated in the eastern population (Pikesley et al. 2013), but data are lacking for the largest population nesting in French Guiana, whose conservation status is highly concerning (Kelle et al. 2009, Wallace et al. 2011, Plot et al. 2012). Considering the high oceanographic dynamism along the coast of French Guiana (Frouin et al. 1997, Fromard et al. 2004) and the contrasting migration patterns of olive ridleys reported else-

where (see above), one may predict a pronounced behavioral plasticity in the migration of olive ridley turtles after they have left their nesting site in French Guiana. Here, we tested this prediction by investigating (1) the dispersal pattern and (2) the diving behavior, in relation to environmental conditions during the post-nesting migration of olive ridleys nesting in French Guiana. By doing so, we further provide scientifically based data of interest for management issues related to the species in the region.

MATERIALS AND METHODS

Study site and equipment

The study was conducted during the nesting season 2006 on Cayenne/Rémire-Montjoly beaches (4° 53′ N, 52° 16′ W, French Guiana, South America). Seven olive ridley turtles were equipped with Satellite-Relayed Data Loggers (SRDL 9000X; Sea Marine Research Unit, SMRU, St Andrews, UK, www.smru.st-and.ac.uk/, unit mass = 660 g) while nesting. SRDL units were glued on the highest scale of the carapace using 2-component fast set epoxy (Powerfast), with the antenna pointing perpendicular to the sea surface to improve communication with the satellites upon the turtle surfacing. Standard curved carapace length (SCCL) was measured with a flexible measuring tape (±0.5 cm) for all individuals prior to SRDL attachment. Individuals were weighed after SRDL attachment and once they had completed oviposition using a handmade harness and a handheld spring scale (±0.1 kg). Individual body mass was then calculated by subtracting the SRDL mass.

Horizontal movements

At-sea movements were reconstructed using the Argos system (www.argos-system.org/). Location data were recovered from Collecte Localisation Satellites, CLS (www.cls.fr), and each track was processed following Gaspar et al. (2006). Argos locations of any accuracy were used except those implying an apparent speed above 1.5 m s^{-1} (i.e. 5 km h^{-1}), as travel rates above this threshold are considered to be biologically unlikely (Whiting et al. 2007, Rees et al. 2012). The track was smoothed and re-sampled with a fixed sampling period of 3 h. It has been demonstrated that surface currents may contribute to sea turtles' offshore movements (Gaspar et al. 2006), and such evidence has been considered in previous studies (e.g. Fossette et al. 2010a,b, Galli et al. 2012). However, estimates of surface currents are not reliable at low latitudes and close to the shore (Gaspar et al. 2006, Pascual et al. 2006), preventing us from integrating potential current drift in our analyses. Haulout events, identified by means of the SRDLs' wet–dry sensors, were used for determining whether a potential nesting event had occurred and thus for distinguishing the inter-nesting and the post-nesting periods in our study animals. Six of the 7 tracked turtles laid 1 clutch after being equipped with the SRDLs: their inter-nesting behaviors have been previously described by Plot et al. (2012) and were not included in the analysis in the present study.

We describe turtles' horizontal movements by characterizing their direction (i.e. the main course turtles followed after leaving the nesting beach) and the dispersal pattern (i.e. the way they scattered during the tracking period). For each individual track, we calculated the total distance traveled, the maximum distance from the departure beach (hereafter called dispersal range), the daily distance traveled (i.e. the cumulative distance traveled every day), and the daily travel rate (i.e. the mean travel rate calculated between successive Argos locations obtained every day).

Vertical movements

SRDLs provided measurements of diving behavior from pressure sensors. A dive was considered when depth was below 2 m. SRDLs provided 24 h summary statistics for each day of the tracking duration, including the mean and maximum dive duration (±10 s), the mean and maximum dive depth (±1 m), the total time spent diving, and the total number of dives performed. These 24 h summaries were used to assess the general characteristics of the vertical movements for each individual and to investigate potential differences in diving parameters between traveling and foraging phases (see next sub-section).

In addition, SRDLs relayed a sample of individual dives, and provided information consisting of a time-at-depth profile with 5 points of inflection, i.e. the time–depth points where the dive trajectory changes most rapidly (Fedak et al. 2001). These dive profiles were used to calculate the time of allocation at depth (TAD) index (Eq. 1). The TAD index is designed to use relevant information from dive profiles and highlights, independently of the depth and duration of the dive, where the diver centers its activity with respect to depth during a dive (Fedak

et al. 2001, Takahashi et al. 2003). It is expressed as follows:

$$\text{TAD} = \sum_{i}^{n} \frac{\frac{(d_{i+1} + d_i)(t_{i+1} - t_i)}{2} - \left(\frac{d_{max}^2}{C}\right)}{[d_{max} \times (t_n - t_1)] - \left(\frac{2d_{max}^2}{C}\right)} \qquad (1)$$

where d_i = individual depth reading for depth reading i in a dive, t_i = time of depth reading i, n is the total number of individual dives recorded, d_{max} = maximum dive depth, and C = predefined average rate of change of depth. C was set to 1.4 m s^{-1} as recommended by McMahon et al. (2007). We used the TAD index to characterize the shape of each recorded dive. TAD values vary from 0 to 1, with $0.5 \le \text{TAD} < 0.75$ being associated with V-shaped dives (assumed to be exploratory) and $0.75 \le \text{TAD} < 1$ being associated with U-shaped dives (where the diver's activity is centered at the bottom of the dive; Fedak et al. 2001, Takahashi et al. 2003). Individual dive records were also used to assess potential diel dive patterns, with day hours set from 06:00 to 18:00 h local time.

Identification of traveling and foraging behaviors

Identifying specific behaviors of marine animals by relying on indirect information, such as that provided by satellite telemetry devices, is challenging. It is generally assumed that traveling is associated with straight movements whereas foraging is most likely associated with convoluted movements (Batschelet 1981, Benhamou 2004). Such changes in behavioral modes are assumed to be accompanied by an alteration of travel speed, foraging being associated with lowered travel rate (Robinson et al. 2007), and may also be concurrent with changes in vertical (diving) behaviors (James et al. 2005, Fossette et al. 2010a). In order to investigate turtle behaviors along their tracks, we first used a straightness index (S) as a proxy to distinguish traveling and foraging phases. The straightness index is defined as the ratio of the straight line to the actual distance traveled by the animal (Batschelet 1981): S values vary from 0 to 1, with values near 0 indicating a sinuous path associated with foraging behavior, whereas values near 1 indicate a straight path associated with traveling behavior. Along each individual track, we calculated a daily straightness index with respect to the time-step of the dive data provided by SRDLs. Similarly to Gaspar et al. (2006) and Fossette et al. (2010a), visual examination of the frequency distribution of the straightness index values showed a bimodal distribution, with $S = 0.8$ as the threshold value (see Fig. S1 in Supplement 1

at www.int-res.com/articles/suppl/n026p221_supp/), suggesting that foraging and traveling could be identified for $S < 0.8$ and $S > 0.8$, respectively. In addition, we considered the travel rate during the traveling and foraging phases delineated by the straightness index. Finally, we investigated whether diving parameters changed between foraging and traveling phases.

Environmental parameters

Water temperature

The thermal habitat of migrating olive ridley turtles was assessed using sea surface temperatures (SSTs) provided by CLS for each Argos location and *in situ* temperature records provided by the SRDL units. SRDLs monitored the depth during the central phase of the 2 deepest dives in each 2 h period and collected temperature data (±0.1°C) every 4 s on the ascent. Data were then processed on board, and temperature-at-depth profiles (with 12 temperature–depth pairs) were produced and relayed via the Argos system. These profiles allowed us to characterize the water column in terms of a thermal gradient and to calculate the mean water temperature experienced by the turtles throughout the water column.

Bathymetry

For each Argos location, an ocean depth estimation was calculated from a satellite bathymetry grid (ETO PO2v2, National Geophysical Data, US National Oceanic and Atmospheric Administration), provided by CLS. In order to characterize dives in relation to ocean depth of the areas exploited by the turtles over the tracking duration, we compared the mean daily dive depth (provided by the 24 h summary) for each turtle with the associated estimated ocean depth. For each day of tracking, we assumed that dives reached the seabed (i.e. benthic dives) when the difference between dive depth and ocean depth was <5 m.

Statistical analyses

Results are given as means ± SE. All data were analyzed using R 2.10.1 (R Development Core Team) with α = 0.05. Normality was checked before each test using the Shapiro-Wilk test. Statistical tests were used according to the data considered. When all individuals were considered, mixed models including

individual identity as a random factor were used in order to control for pseudoreplication; when residuals fitted a normal distribution, a linear mixed effect model (LME) was used; otherwise, a generalized estimating equation model (GEE) was used.

RESULTS

The 7 female olive ridley turtles fitted with SRDLs measured 68.1 ± 1.3 cm in length (range = 62.5–72.0 cm) and weighed 36.1 ± 1.2 kg (range = 31.6–39.4 kg). For all data reported below, n = 7 unless otherwise noted.

Horizontal movements: dispersal patterns

Tracking duration lasted on average 112.4 ± 21.2 d (overall mean; individual tracking duration range: 59.4–218.3 d; Table 1), during which turtles traveled on average 3426.4 ± 512.4 km (overall mean; individual total distance traveled range: 1657.2–5589.0 km), with the farthest point being ca. 600 km from the departure beach (individual dispersal range: 144.0–596.6 km, Table 1). Total distance traveled and dispersal range were neither related to turtle body mass nor SCCL (linear regressions, p > 0.1 in both cases for total distance traveled; p > 0.6 in both cases for dispersal range). On average, turtles traveled 31.4 ± 1.8 km d^{-1} (overall mean; daily distance traveled range: 25.5–38.8 km d^{-1}), i.e. with a daily travel rate of 0.35 ± 0.02 m s^{-1} (overall mean; daily travel rate range: 0.28–0.42 m s^{-1}; Table 1).

All 7 individuals headed north/northwest from the nesting beach (except turtle 353, which moved slightly east during the first 6 d, i.e. up to 90 km from the beach before heading west) and scattered throughout the continental shelf without crossing the continental slope (except turtle 404, see below). Turtles 353 and 391 exclusively exploited waters off French Guiana, whereas the others also exploited waters off Suriname to the border with Guyana (turtles 387, 390, 404; Fig. 1). Three major dispersal patterns were observed: (1) in most cases, turtles (353, 387, 403, and 404) traveled directly toward the continental slope where they
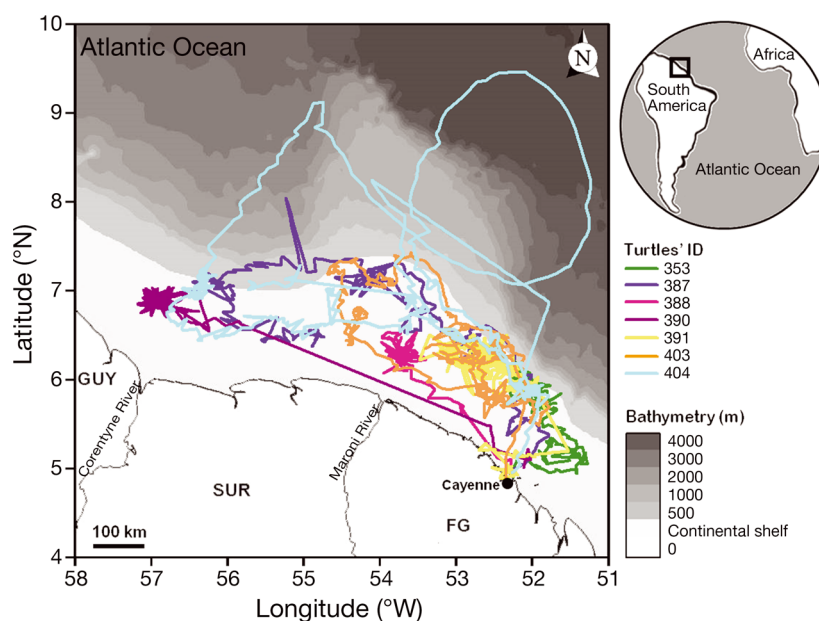

Fig. 1. Reconstructed horizontal movements of 7 olive ridley turtles *Lepidochelys olivacea* satellite-tracked during their migration after they nested in French Guiana (FG) in 2006. (See Supplement 2 at www.int-res.com/articles/suppl/n026p221_suppl/ for animated movements of turtle 404.) Each individual's track is represented by a different color. Bathymetry (from ETOPO2v2) is illustrated in greyscale, with the continental shelf in light grey. SUR: Suriname; GUY: Guyana

Table 1. General characteristics of the horizontal movements of 7 olive ridley turtles *Lepidochelys olivacea* satellite-tracked during their migration after nesting in French Guiana in 2006. Daily values are given as means ± SE with ranges in parentheses

Turtle ID	Date of departure (dd/mm)	Tracking duration (d)	Total distance traveled (km)	Daily distance traveled (km)	Dispersal range (km)	Daily travel rate (m s^{-1})
353	27/07	61.6	1657.2	26.7 ± 1.7 (9.4–82.5)	144.0	0.30 ± 0.02 (0.11–0.77)
387	01/07	77.3	3027.9	38.8 ± 2.1 (10.9–94.0)	519.7	0.42 ± 0.02 (0.12–1.06)
388	26/07	59.4	2014.1	33.6 ± 2.4 (4.7–80.8)	255.7	0.37 ± 0.03 (0.05–0.85)
390	07/08	133.7	4402.7	32.9 ± 1.6 (0.9–96.0)	596.6	0.37 ± 0.02 (0.01–1.08)
391	08/08	103.7	3551.9	34.2 ± 2.0 (1.9–93.8)	202.7	0.37 ± 0.02 (0.02–1.02)
403	07/07	133.1	3742.3	27.9 ± 1.4 (2.4–81.1)	405.0	0.31 ± 0.01 (0.03–0.91)
404	08/07	218.3	5589.0	25.5 ± 1.5 (1.4–103.7)	544.2	0.28 ± 0.02 (0.02–1.17)

remained for most of their time (Fig. 1); (2) turtles 388 and 390 first traveled in a straight line for 4 and 10 d, respectively, before they stopped off the mouths of the Maroni and the Corentyne Rivers, respectively, where they remained until transmission stopped (Fig. 1); (3) finally, turtle 391 remained close to the shore for ca. 20 d before heading to the continental shelf (Fig. 1). Dispersal patterns were related neither to turtle body mass nor to body size.

Anecdotally, turtle 404 initially followed pattern (1) but crossed over the continental slope and entered deep waters on 2 occasions: first, at the beginning of the tracking period, this turtle performed a 20 d clockwise loop in deep waters before arriving about 800 km offshore, straight off the mouth of the Corentyne River; second, on Day 125 while heading back to French Guiana, it again reached deep waters and initiated a similar, but aborted, clockwise loop and went back to the waters off Cayenne (Fig. 1, and see the animation in Supplement 2 at www.int-res.com/articles/suppl/n026p221_supp/).

Vertical movements: diving behavior

General characteristics

According to the 24 h summaries provided by the SRDLs, all 7 turtles dived continuously throughout the tracking duration, spending on average 88.4 ± 1.3% of their time at depths deeper than 2 m (overall average; individual range of mean daily time spent diving: 81.2–90.8%, Table 2). On average, dives were 43.7 ± 4.0 m deep (individual mean dive depth range: 29.4–58.2 m) and 47.6 ± 3.4 min long (overall mean; individual mean dive duration range: 31.9–60.8 min; Table 2). Turtle 404 performed the deepest dive (220 m) and turtle 403 performed the longest

dive (3.0 h; Table 2). Diving performances (i.e. mean and maximum dive depths, mean and maximum dive duration) were neither significantly related to turtle body mass nor to body size (linear regressions, p > 0.2 for each case). Turtles performed on average 31.2 ± 3.6 dives d^{-1} (overall mean; individual mean daily dive frequency range: 24.1–52.4 dives d^{-1}; Table 2).

Comparison of daily mean dive depth and associated estimated ocean depth showed that on average, 28.9 ± 6.9% of the recorded dives reached the seabed (overall mean; individual proportion ranging from 4.8–62.4%; Table 2). Of note, 15.5 ± 4.4% of the recorded dives were deeper than the estimated bathymetry (overall mean; individual proportions ranging from 4.8–62.4% for benthic dives and 4.0–35.0% for dives deeper than the estimated bathymetry; Table 2).

Diving patterns

In total, we recorded 3452 individual dives (deeper than 2 m) by the 7 turtles. Individual dive duration was significantly positively related to maximum dive depth (LME, p < 0.001). Post-diving surface duration was significantly positively related to the duration of the preceding dive (GEE, p < 0.001, χ^2_{Wald} = 12.4; with maximum dive depth as covariate).

Olive ridleys performed 6.1 ± 1.1% (overall mean; range = 3.6–12.3%) of shallow dives (≤10 m) and 5.7 ± 1.3% (overall mean; range = 1.2–10.9%) of short dives (≤5 min). Only 3.3 ± 1.2% of the dives (overall mean; range = 0.6–8.2%) were longer than 100 min. There was a pronounced inter-individual variability in terms of diving patterns. Individual median maximum dive depth ranged from 30 to 60 m, and median dive duration ranged from 30 to 50 min (Fig. 2). Interestingly, some individual turtles showed highly

Table 2. General characteristics of the diving behavior of 7 olive ridley turtles *Lepidochelys olivacea* satellite-tracked during their migration after nesting in French Guiana in 2006, determined from the 24 h summary provided by satellite-relayed data loggers. Values are given as means ± SE (ranges in parentheses)

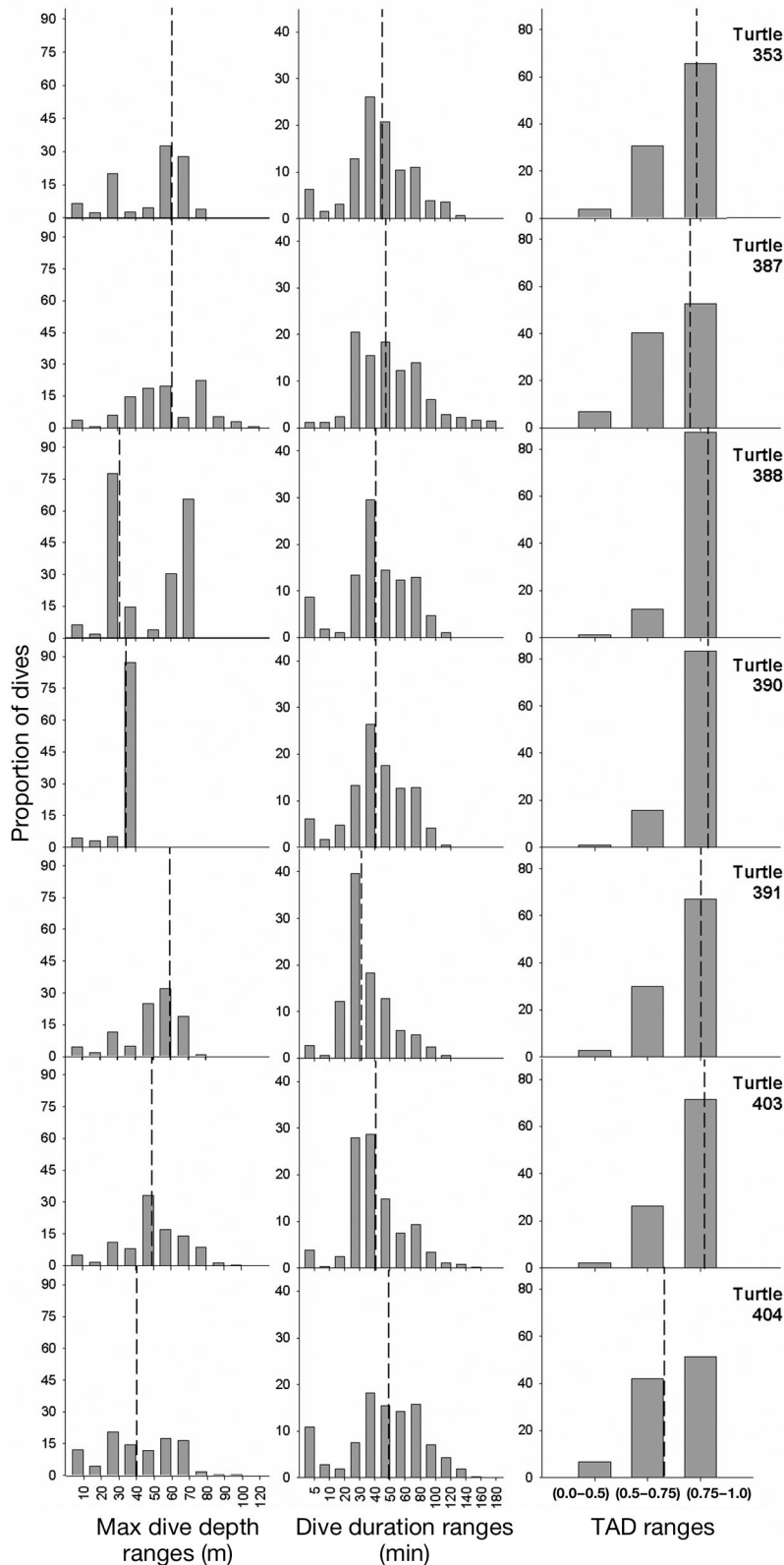| Turtle ID	Time spent diving (%)	No. of dives	Dive depth (m)	Max. dive depth (m)	Dive duration (min)	Max. dive duration (h)	Benthic dives (%)	Dives deeper than estimated bathymetry (%)
353	89.6 ± 0.5 (81.8–96.0)	27.8 ± 0.9 (14.0–45.0)	51.4 ± 1.4	80.0	48.2 ± 2.0	2.3	19.0	4.0
387	88.9 ± 0.8 (56.6–97.6)	24.1 ± 1.1 (7.0–62.0)	58.2 ± 1.7	160.0	60.8 ± 3.1	3.7	38.4	4.3
388	90.8 ± 0.5 (76.3–95.2)	27.8 ± 0.6 (21.0–41.0)	29.4 ± 0.3	40.0	46.8 ± 1.2	2.0	62.4	12.7
390	90.5 ± 0.4 (63.7– 96.0)	30.0 ± 0.8 (14.0–102.0)	32.7 ± 0.4	40.0	44.9 ± 1.1	2.0	4.8	26.3
391	81.2 ± 2.0 (3.1–96.0)	52.4 ± 4.1 (15.0–236.0)	41.6 ± 2.1	80.0	31.9 ± 2.0	2.8	34.0	7.7
403	90.2 ± 0.5 (43.3–95.2)	30.0 ± 0.8 (17.0–86.0)	50.9 ± 1.3	100.0	46.3 ± 1.3	3.0	24.6	35.0
404	87.8 ± 0.6 (50.3–95.2)	26.3 ± 0.9 (11.0– 82.0)	41.2 ± 0.9	220.0	54.5 ± 1.5	2.8	19.3	18.3

Fig. 2. Maximum dive depth, dive duration, and time of allocation at depth (TAD) index ranges (from left to right) recorded for 7 olive ridley turtles *Lepidochelys olivacea* satellite-tracked during their migration after nesting in French Guiana in 2006. Turtle IDs are indicated on the right of each set of graphs. Dashed vertical lines are median values

stereotyped behaviors: for example, more than 75% of the dives performed by turtles 388 and 390 ranged between 21 and 30 m and between 31 and 40 m, respectively, and lasted 31 to 40 min (Fig. 2). The other individuals exhibited more heterogeneous dive depths and durations, especially turtles 387 and 404 (Fig. 2).

The TAD index calculated from the individual dive time–depth profiles ranged from 0.75 to 0.92 (individual median values), indicating that turtles mainly performed U-shaped dives. Overall, 68.5 ± 5.1% of the dives (range = 51.7–87.0%) were U-shaped dives and 28.0 ± 4.2% were V-shaped dives (overall mean; proportion of V-shaped dives ranging from 11.9% to 41.5%). Interestingly, almost half the dives performed by turtles 387 and 404 were U-shaped and half were V-shaped (Fig. 2).

There was a slight but significant diel dive pattern: turtles performed on average shorter (day: 43.3 ± 0.6 min vs. night: 46.7 ± 0.6 min, GEE, p = 0.03, χ^2_{Wald} = 4.7) but deeper dives during daytime compared to nighttime (day: 47.5 ± 0.5 m vs. night: 43.3 ± 0.5 m, GEE, p = 0.007, χ^2_{Wald} = 11.4). Although TAD indices were significantly higher during daytime dives (day: 0.82 ± 0.02 vs. night: 0.79 ± 0.02, GEE, p = 0.007, χ^2_{Wald} = 7.19), turtles performed mostly U-shaped dives during both day and night.

Traveling and foraging behaviors

Based on the straightness index calculated along each turtle's track, we distinguished foraging and traveling phases. Importantly, the travel rates calculated during each phase differed significantly, and were slower during foraging phases than during traveling phases (0.12 ± 0.01 m s^{-1} vs. 0.25 ± 0.02 m s^{-1} respectively, GEE, p = 0.007, χ^2_{Wald} = 21.9). Yet, diving parameters (mean daily dive depth, mean daily dive duration, and mean daily TAD index) did not significantly differ between foraging and traveling phases (GEE, p > 0.1 in all cases).

Based on the *S* index, turtles traveled for 0 to 2 d after leaving the beach before entering into their first foraging phase. Traveling time before the first foraging phase was neither related to turtle body mass nor body size (linear regressions, p ≥ 0.73 in both cases). Afterwards, all turtles alternated traveling and foraging phases: on average, individual tracking duration comprised 15.6 ± 3.0 traveling phases (overall mean; range of individual number of traveling phases = 9–32) and 15.7 ± 2.9 foraging phases (overall mean; range of individual number of foraging phases = 9–31). Interestingly, traveling phases were significantly shorter (2.1 ± 0.3 d) than foraging phases (5.1 ± 0.4 d, GEE, p = 0.008, χ^2_{Wald} = 19.2), with the longest traveling phase lasting 10% of the tracking duration (turtle 404) and the longest foraging phase lasting 28% of the tracking duration (turtle 388). Consequently, 76.6 ± 5.5% of the tracking duration consisted of foraging (range of individual foraging phases = 46.6–89.7% of the tracking duration). The percentage of time spent foraging during the tracking duration was related neither to body mass nor to body size (linear regressions, p ≥ 0.29 for both cases).

Water temperature

During the tracking period, olive ridleys experienced daily SSTs ranging from 25.6 to 30.0°C, with slight inter-individual differences in the mean daily SST (ranging from 27.0 ± 0.1 to 28.2 ± 0.1°C, Kruskal-Wallis, K-W, test, p = 0.042, K-W χ^2 = 28.94; Table 3). No seasonal pattern in SSTs was detected, despite a slight cooling in SSTs experienced by turtle 404 in early December (~Day 150; Fig. 3), associated with a cooling of the overall environment (data not shown).

Overall examination of the turtles' depth–temperature profiles showed that temperature at the surface was 2.0 ± 0.4°C warmer than at depths (overall mean; paired *t*-tests or Wilcoxon paired test, p < 0.01 for each case, see Table 3). Interestingly, depth–temperature profiles of turtles 388 and 390 demonstrated very small differences in temperature between surface and maximum depth (0.6 and 0.8°C, respectively) compared to other turtles. The maximum difference between surface and maximum depth temperatures (9.8°C) was experienced by turtle 387 on 25 August 2006 at a depth of 104 m. Minimum temperatures at depth were above 20°C for all turtles except turtle 387 (see Table 3) and were recorded during their deepest dives (except for turtle 404 because no depth–temperature profiles were recorded during its deepest dive, which reached 220 m). It is noteworthy that for turtle 387 the minimum temperatures at depth below 20°C were only recorded 3 times throughout the tracking period and were associated with relatively deep dives (>100 m). Other minimum temperatures at depth recorded for turtle 387 were all above 20°C.
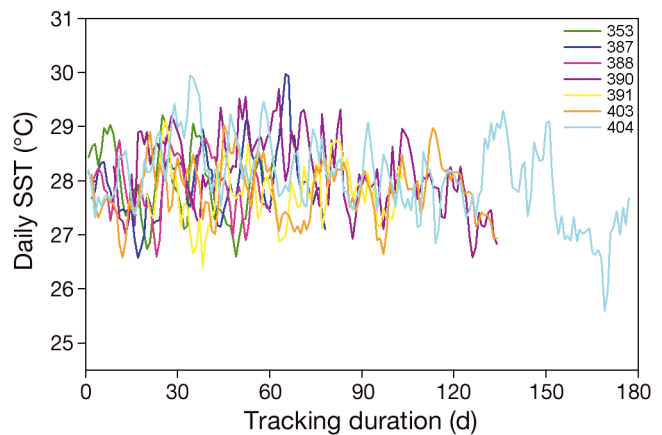

Fig. 3. Daily sea surface temperatures (SST) experienced by 7 olive ridley turtles *Lepidochelys olivacea* satellite-tracked during their migration after nesting in French Guiana in 2006. Each color represents an individual turtle

Table 3. Sea surface temperatures (SST) and *in situ* water temperatures experienced by 7 olive ridley turtles *Lepidochelys olivacea* during their migration after nesting in French Guiana in 2006. Δtemp.: difference in *in situ* temperature between the surface and the maximum depth reached during the dive. Values are means ± SE (with range in parentheses for SST)

Turtle ID	Daily SST (°C)	Water column temp. (°C)	Δtemp. (°C)	Δtemp. within water column Max. Δ temp. (°C)	Max. depth (m)	Min. temp. at depth Min. temp. (°C)	Depth (m)
353	28.0 ± 0.1 (26.4–29.4)	28.9 ± 0.1	1.7 ± 0.1	4.8	66	26.3	78
387	28.0 ± 0.1 (26.6–30.7)	26.1 ± 0.1	3.5 ± 0.2	9.8	104	18.2	100
388	27.0 ± 0.1 (26.6–29.0)	27.5 ± 0.1	0.6 ± 0.1	1.4	34	26.9	30
390	28.2 ± 0.1 (26.5–30.2)	28.6 ± 0.1	0.8 ± 0.0	2.3	40	26.2	30
391	27.8 ± 0.1 (26.4–29.3)	28.6 ± 0.2	2.7 ± 0.1	5.2	82	22.9	78
403	27.8 ± 0.1 (26.4–29.5)	26.7 ± 0.1	2.0 ± 0.1	5.7	84	22.5	102
404	28.0 ± 0.0 (25.5–30.2)	26.9 ± 0.1	2.5 ± 0.1	8.0	102	20.3	102

DISCUSSION

As far as the western Atlantic Ocean is concerned, only 1 occurrence of post-nesting migration movements has been documented for olive ridley turtles through flipper tag returns of a single female nesting in Brazil (Reis et al. 2010). In the present study, we investigated the post-nesting migration of 7 satellite-tracked olive ridley females from French Guiana and described their dispersal and diving behavior in relation to the environment they exploited.

Migration dispersal

Our study shows that during their post-nesting migration, olive ridleys from French Guiana remained in the restricted neritic domain of the continental shelves of French Guiana and Suriname. This contrasts with the long-distance movements suggested from tag recovery for the above-mentioned single female observed from northern Brazil (Reis et al. 2010). Our results also contrast with most studies conducted on other olive ridley populations where females display exclusively long-distance movements, traveling up to several thousands of kilometers away from the nesting beach, either in the oceanic (Plotkin 2003, 2010, Polovina et al. 2004, Pikesley et al. 2013) or in the mixed neritic–oceanic domain (McMahon et al. 2007). However, limited dispersal range has also been described in a population in the western Pacific Ocean (Whiting et al. 2007) and in the Sea of Oman (Rees et al. 2012), where individuals traveled on average ca. 400 km from the nesting beach, as was also the case in our study.

Olive ridley females from French Guiana followed a common northwestward direction when initiating their post-nesting migration. This contrasts with reports for conspecifics from other populations where no particular migration route was noted (Indian Ocean: Sasamal & Panigraphy 2006, Ram et al. 2009; Sea of Oman: Rees et al. 2012; Pacific Ocean: Polovina et al. 2004, McMahon et al. 2007, Whiting et al. 2007, Plotkin 2010; east Atlantic Ocean: Pikesley et al. 2013). The common route observed for olive ridleys at their departure from French Guiana may be related to the main northwestward currents along the French Guianese coast which result from the strong North Brazilian and Guianas Currents (Frouin et al. 1997). However, after their initial northwestward movements, most turtles traveled eastward and remained over the continental shelves of Suriname and French Guiana throughout the tracking period, suggesting that either these currents do not occur on the shelf or that turtles can compensate for them. Remarkably, while located near the continental slope, 1 turtle (404) performed a large loop off the continental shelf (Fig. 1). The influence of oceanic currents and mesoscale oceanographic features on offshore movements of sea turtles has been previously reported (e.g. Gaspar et al. 2006, Lambardi et al. 2008, Mansfield et al. 2014), notably the influence on olive ridleys (Beavers & Cassano 1996, Polovina et al. 2004, Sasamal & Panigraphy 2006, Ram et al. 2009). We thus suggest that the remarkable offshore movement of turtle 404 was associated with the local oceanographic features, such as the eddy occurring off the continental shelf, illustrated in the animation in Supplement 2. Unfortunately, we could not further investigate potential current drifts because estimates of current velocities are not reliable at low latitudes (see 'Materials and methods'). Turtle 404 achieved its oceanic loop by swimming straight to neritic waters off the mouth of the Corentyne River (Supplement 2). Studies on orientation have suggested that sea turtles can use chemical information (Luschi et al. 2001, Lohmann et al. 2008). In the Guianese region, large rivers discharge large amounts of low-salinity water that subsist up to 200 km offshore (Frouin et al. 1997). Such a low salinity signature may act as an orientation cue and may have driven turtle 404 back to the continental shelf.

Habitat use

Over the course of tracking, olive ridleys frequented sea surface waters with SSTs ranging from 25.6 to 30.0°C. These temperatures are slightly warmer than SSTs occupied by their conspecifics in other oceanic basins (Polovina et al. 2004, McMahon et al. 2007, Swimmer et al. 2009, Rees et al. 2012, Pikesley et al. 2013), most likely because of the neritic low latitude area they exploit. Moreover, in the study area, the local upwelling created by the counter-current localized close to the continental slope is not accompanied by a pronounced lowering of the SSTs (Artigas et al. 2003). These particularities may explain the narrow 5°C SST range recorded in our study, which is consistent with the narrow preferential thermal habitat reported in the species (Polovina et al. 2004, McMahon et al. 2007, Swimmer et al. 2009). Moreover, turtles vertically exploited warm, non-stratified water masses. Therefore, the Guianese continental shelf offers a favorable thermal habitat for olive ridley turtles nesting in French Guiana during their post-nesting migration.

Despite the restricted area exploited during the tracking period, olive ridleys exploited 3 contrasting habitats, i.e. the coastline, the continental shelf, and the continental slope, illustrating some plasticity in dispersal pattern. Moreover, although turtles mainly performed U-shaped dives, they demonstrated inter-individual variability in dive depth patterns. U-shaped dives are typically associated with benthic activities (i.e. close to the seabed; McMahon et al. 2007). We may thus expect that dive depths were limited by the bathymetry of the different habitats the turtles exploited. According to the bathymetry data, ca. 30% of dives reached the seabed. Additionally, 15% of dive depths were greater than the estimated ocean depth, which may suggest that, on average, ca. 45% (up to 75%, Table 2) of dives were associated with the seabed. This latter result, similar to the findings of Padman et al. (2010), implies that ocean depth estimates based on satellite bathymetry grids should be interpreted cautiously in such fine-scale analyses. Oceanographic surveys conducted in French Guianese waters have reported that the continental shelf presents a smooth slope, with depth increasing gradually from the coastline to the continental slope, reaching 80 to 100 m (CREOCEAN internal report 2011, www.creocean.fr). Therefore, turtles had potential access to contrasting depths depending on whether they exploited the coastline, the continental shelf, or the continental slope. This supports the hypothesis that the dive patterns reported for olive ridleys reflect the bathymetry and further suggests that turtles exploited the benthic area.

Finally, the continental shelves of French Guiana and Suriname are under the influence of the Amazon River which contributes to a local increase of nutrient inputs, enhancing biological productivity (Frouin et al. 1997, Froidefond et al. 2002, Fromard et al. 2004). Notably, benthic prey of olive ridleys, i.e. mollusks and crustaceans (Bjorndal 1997), are abundant (CREOCEAN internal report 2011). Therefore turtles most likely had access to multiple favorable benthic foraging areas despite their restricted dispersal range.

Foraging behavior

Similar to other studies investigating sea turtle behavior during the post-nesting migration (James et al. 2005, Fossette et al. 2010a,b), we found that turtles reduced their travel rate during foraging phases. Our results thus support the change in behavior modes (traveling vs. foraging) delineated by the straight-

ness index. However, these changes in horizontal patterns were not associated with significant changes in dive parameters. Concurrent modifications in the horizontal and vertical behaviors have previously been reported in leatherback turtles during their trans-Atlantic post-nesting migration where they follow distant patches of pelagic prey (see James et al. 2005, Fossette et al. 2010a,b). Although such changes in vertical patterns are biologically relevant for pelagic leatherbacks, in the present study they were not expected to occur in olive ridley turtles due to their benthic, i.e. bathymetry-related, behavior.

According to our results, olive ridley turtles reached their first foraging area within a maximum of only 2 d after they left the nesting beach, and then continued foraging for most of the tracking period. Interestingly, turtles exhibited 2 different foraging strategies. On the one hand, 2 individuals performed straight movements to a single location at the mouths of 2 different rivers, where they remained to exploit these resource-rich habitats (CREOCEAN internal report 2011) until the end of the tracking period. On the other hand, all other individuals alternated between short traveling phases and longer foraging phases and were distributed more erratically without showing fidelity to any particular foraging spot, i.e. meandering on the Guianese shelf and occasionally stopping to forage.

In contrast to dive data recorded by time−depth recorders (recording-only devices), SRDL dive profiles do not capture subtle depth variations, which are used to characterize dive shapes indicative of multiple behaviors, such as foraging (e.g. Hassrick et al. 2007, Fossette et al. 2008). However, the TAD index inferred from SRDL dive profiles allows us to characterize specific dive shapes by highlighting the center of activity with respect to depth during a dive. Together with information on the turtles′ environment, the TAD index is an important clue to assess turtle behavior. Olive ridleys mainly performed U-shaped dives (i.e. activity is centered at the bottom of the dive, Fedak et al. 2001), most likely associated with the seabed (see previous subsection), in an environment where their benthic prey are abundant (CREOCEAN internal report 2011). We thus suggest that the U-shaped dives were indicative of foraging behavior, consistent with olive ridleys being primarily benthic foragers (Bjorndal 1997). Moreover, 2 turtles (387 and 404) exploited deeper depths (>100 m) on the continental slope and displayed a substantial proportion of V-shaped dives. V-shaped dives are assumed to be exploratory dives (Fedak et al. 2001), during which divers

search for potential prey. The oceanographic survey conducted in the region shows that the thermocline is located at ca. 100 m depth, at the edge of the continental shelf (CREOCEAN internal report 2011). Accordingly, these 2 turtles may have reached the thermocline during the V-shaped dives; this is supported by the fact that the coolest water temperatures recorded *in situ* by the SRDLs were measured at the bottom of these dives. Polovina et al. (2004) previously suggested that olive ridleys in the oceanic waters of the North Pacific exploit the thermocline to feed. Therefore, while beyond the continental shelf waters, where benthic prey are most likely out of reach, olive ridleys may search for potential alternative prey near the thermocline.

Migration strategies of olive ridley turtles and conservation implications

This study suggests that the particularly favorable environmental conditions of the Guianese continental shelf, in terms of oceanic conditions, food resource abundance, and temperatures, may contribute to the fact that olive ridley turtles nesting in French Guiana did not migrate beyond the neritic area. Similarly to the present study, olive ridley turtles nesting in Oman (Rees et al. 2012) and Australia (Whiting et al. 2007), where environmental conditions are also favorable, remain in coastal areas relatively close to the nesting site during their post-nesting migration. In contrast, in the northern and eastern tropical Pacific regions, individuals exploit deep oceanic waters where food resources are scattered and unpredictable, traveling far from the nesting beach and over long distances (Polovina et al. 2004, Plotkin 2010). We thus propose that the different migration patterns observed in olive ridley populations worldwide, i.e. oceanic vs. neritic, may be specific to the ecological conditions of the areas near the nesting sites.

In other Chelonidea species, intra-population phenotypic differences have been related to variation in migration patterns: larger turtles perform neritic migrations, whereas smaller turtles perform oceanic migrations (Hatase et al. 2002, Hawkes et al. 2006, Hatase & Tsukamoto 2008, Zbinden et al. 2011, Richardson et al. 2013). In our study, the lack of relation between individual biometrics and migration patterns may have resulted from the fact that all turtles shared the same neritic pattern. If phenotypic-related migration patterns hold at the inter-population level, it is worth noting that olive ridley turtles

displaying a mixed oceanic–neritic migration pattern (McMahon et al. 2007) are smaller and lighter than the neritic turtles in our study. Although biometric details in tracking studies of olive ridleys from other populations are too scarce to draw any conclusions, we hypothesize that neritic migration may be a more advantageous migration strategy than oceanic migration. Further studies should assess body mass gain of turtles during post-nesting migration in order to investigate this hypothesis.

From a conservation perspective, such differences in migration patterns imply that management plans must be implemented case by case, in accordance with every single olive ridley population. For instance, the close-range migration pattern used by olive ridleys from French Guiana raises conservation concerns, since turtles may be exposed to coastal human-induced activities, such as local and international trawling fisheries and the recent oil exploitation, which may jeopardize their survival. Furthermore, the fact that turtles cross and/or exploit international borders must be considered in order to implement accurate trans-boundary management measures for the Guianese olive ridley population.

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