Vol. 571: 221–232, 2017
https://doi.org/10.3354/meps12136

MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser

Published May 17

Movements and diving behaviour of inter-nesting leatherback turtles in an oceanographically dynamic habitat in South Africa

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ABSTRACT: Sea turtles congregate in specific in-water habitats during reproductive periods. These habitats are inherently tied to the location of their nesting beaches, but they are also influenced by the prevailing oceanographic conditions. Here, we characterized the movements and diving behaviour of leatherback turtles *Dermochelys coriacea* between nesting events at the iSimangaliso Wetland Park, South Africa. Furthermore, we characterized the general oceanographic features (sea surface temperature and ocean currents) in and around the identified inter-nesting habitats. To achieve this, we deployed satellite transmitters onto 10 inter-nesting leatherback turtles. Many of these turtles were tracked over multiple inter-nesting intervals; in total, we collected data over 25 inter-nesting intervals. Inter-nesting turtles generally stayed within 100 km of the coastline, but they moved large distances north and south, covering approximately 600 km of the coast. Even though sea surface temperatures increased notably over the nesting season, we did not observe any obvious change in the movement or diving patterns of leatherback turtles tracked over consecutive inter-nesting intervals, suggesting that turtles were not selecting inter-nesting habitats based on local sea surface temperature patterns. However, we propose that the fast-flowing Agulhas Current may provide a natural boundary for the movements of inter-nesting turtles. We hypothesize that inter-nesting turtles might be avoiding fast flowing waters to minimize energy expenditure or avoid being advected away from the nesting habitats.

KEY WORDS: Satellite telemetry · Thermal habitats · Spatial ecology · Temperature · *Dermochelys coriacea* · Conservation · iSimangaliso Wetland Park

INTRODUCTION

Sea turtles, like many migratory species, congregate in specific habitats during reproductive periods (Eckert et al. 2006, Fossette et al. 2007, Witt et al. 2008). The locations of high-use in-water habitats for gravid turtles are inherently tied to the turtles' nesting beaches, although the prevailing oceanographic conditions in nearby waters also play an important role in habitat selection (Wallace et al. 2005, Schofield et al. 2009, Fossette et al. 2012a). Indeed, the location of high-use inter-nesting habitats for leatherback turtles *Dermochelys coriacea* on the Pacific coast of Costa Rica appears to vary each year in association with dynamic fluctuations in sea surface temperature and net primary productivity

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(Shillinger et al. 2010). Thus, an understanding of the basic movement patterns of gravid sea turtles, as well as how oceanographic processes may affect habitat selection, can help guide the development of spatially explicit conservation measures.

Leatherback turtles are the largest of all sea turtle species and nest circumglobally on a variety of tropical and sub-tropical beaches. The nesting season commonly lasts about 4 to 6 mo, during which time each individual turtle will lay an average of 7 clutches (Reina et al. 2002). The inter-nesting period, defined as the time between consecutive clutches, lasts 8 to 14 d (Nel et al. 2013). During this time, leatherback turtles may migrate distances of over 400 km and turtles can conduct looping movements that take them hundreds of kilometres offshore (Georges et al. 2007, Hitipeuw et al. 2007, Stewart et al. 2014). Inter-nesting habitats for leatherback turtles can thus span large areas and encompass a range of different habitats and oceanographic features.

It is possible that leatherback turtles move such long distances during the inter-nesting period to search for prey (Fossette et al. 2008a, Fossette et al. 2009). Yet unlike other species of sea turtles, such as the green turtle *Chelonia mydas*, that will opportunistically feed during the inter-nesting period if there is ready access to food (Hays et al. 2002), most evidence suggests that leatherback turtles are capital breeders and thus do not feed extensively during the nesting season (Hays et al. 2004, Reina et al. 2005, Casey et al. 2010, Plot et al. 2013, Perrault et al. 2014). If leatherback turtles are not foraging or finding much prey during the inter-nesting interval, it would make sense that they would try to minimize energy expenditure. As ocean currents may advect gravid turtles in the direction of the prevailing flow (Gaspar et al. 2006, Galli et al. 2012), sea turtles might try to avoid strong currents in order to remain close to the preferred nesting area.

Leatherback turtles might also select inter-nesting habitats for thermoregulatory purposes. By selecting cooler habitats, leatherback turtles could shed excess heat accrued during nesting and possibly lower metabolic demand. Indeed, inter-nesting leatherback turtles in the eastern Pacific Ocean appear to preferentially select areas with lower sea surface temperatures, especially during hotter years (Shillinger et al. 2010). In another potential example of thermoregulatory behaviour, leatherback turtles make longer and deeper dives into cooler waters during the first half of the inter-nesting interval (Southwood et al. 2005, Wallace et al. 2005, Myers & Hays 2006).

The purpose of this study was to (1) characterize the movements and diving behaviour of inter-nesting leatherback turtles within the iSimangaliso Wetland Park, South Africa, an oceanographically dynamic coastal environment. We also aimed to (2) characterize the typical oceanographic conditions, specifically temperature patterns and currents, within these inter-nesting habitats and (3) identify whether changes occur in inter-nesting behaviour between nesting events and possibly in response to seasonal temperature changes. The iSimangaliso Wetland Park is a particularly interesting location to study due to the dynamic oceanographic features found just offshore from the nesting habitats. The Agulhas Current — one of the strongest boundary currents in the world (Johannessen et al. 2014) — flows along the east coast of South Africa and past the iSimangaliso Wetland Park. Additionally, waters adjacent to the park show a consistent increase in sea surface temperature (SST) over the leatherback turtle nesting season from October to March.

MATERIALS AND METHODS

Study site

The largest nesting population of leatherback turtles in the Western Indian Ocean is shared between the eastern coasts of South Africa and Mozambique. The majority of this population nests within the iSimangaliso Wetland Park, South Africa (28° S, 32° E) (Fig. 1A), a World Heritage Site that spans the 280 km of coastline that extends south from the South Africa–Mozambique border. The nesting area is characterized by a series of sandy beaches 5 to 15 km long and separated by short rocky headlands. Leatherback turtles nest along the northern 56 km of the park (Thorson et al. 2012), and this northern area was patrolled nightly over the 2011–2012 and 2012–2013 nesting seasons (Nov–Feb) to encounter nesting females.

Satellite tracking

MK10-PAT satellite transmitters (Wildlife Computers) were deployed onto 10 inter-nesting leatherback turtles using a tethering method (for full details, see Robinson et al. 2016). We chose the tethering method because it incurs less drag than conventional harness transmitter attachments (Jones et al. 2013, 2014). Moreover, studies have suggested that harnessed

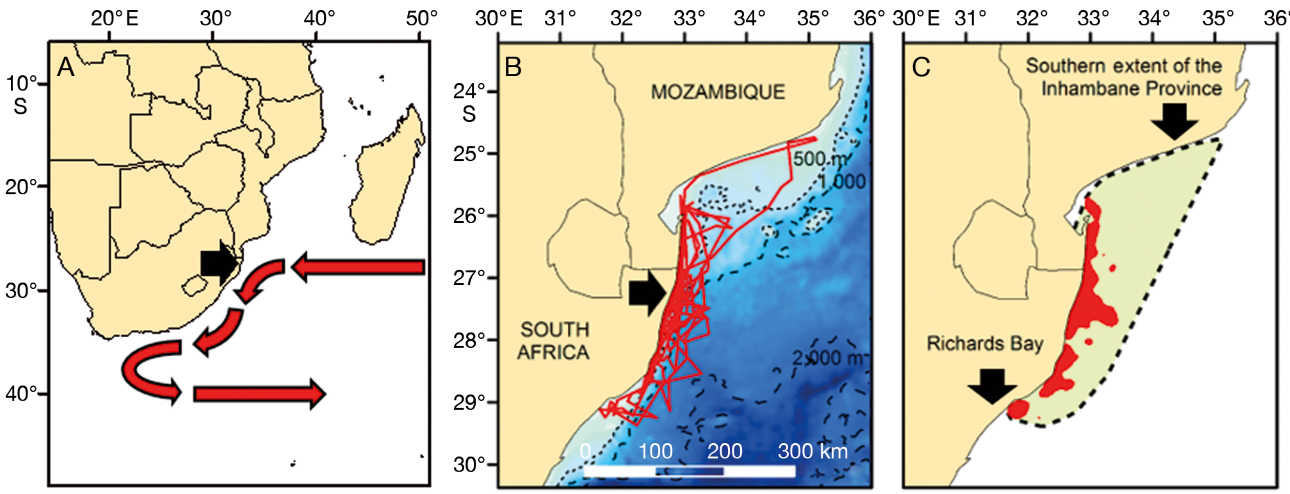

Fig. 1. (A) Black arrow indicates the location of the iSimangaliso Wetland Park, South Africa, within continental Africa. Red arrows represent the generalized flow patterns of the Agulhas Current, which flows along the east coast of southern Africa and past the iSimangaliso Wetland Park. (B) Pathways (red lines) between daily location estimates for 10 satellite tracked leatherback turtles over a combined total of 25 inter-nesting intervals. Black arrow indicates the tagging location. Dotted/dashed black lines represent the 500, 1000, and 2000 m bathymetry contours. (C) Minimum convex polygon (green-shaded area) encompassing all the daily locations from the 10 satellite tracked inter-nesting leatherback turtles, and the 95% utilization distribution (red-shaded area)

transmitters may not actually reflect natural behaviour, especially under conditions of high current flow (Fossette et al. 2008b, Robinson et al. 2016). Consequently, in this analysis, we did not combine our data with other satellite tracking data collected through the use of 'harnessed' turtles from within the iSimangaliso Wetland Park (e.g. Harris et al. 2015).

Prior to attaching each transmitter, we assessed the reproductive state of the female turtle using a Sonosite 180 Plus real-time portable ultrasound. This was achieved by scanning the ovaries of turtles just after they had finished laying to look for the presence or absence of vitellogenic follicles (Rostal et al. 1996). If an animal had over 10 vitellogenic follicles per ovary, it was assumed that the turtle would lay more clutches of eggs in the current this season (Blanco et al. 2012), and this enabled us to distinguish between inter-nesting and post-nesting animals (the tracks of which have been published in Robinson et al. 2016). If turtles with transmitters were encountered again on subsequent nesting attempts, the transmitter was recovered by clipping the tethered line and a new transmitter was deployed in its place. Recovery of the transmitters allowed us to access all the raw data that had been recorded by the devices, whereas the data from the transmitters that we were not manually retrieved were summarized and binned and transmitted to us remotely.

Transmitters were programmed to record depth and temperature every 10 s, and these data could be downloaded in their entirety if the transmitter was recovered. Otherwise, the diving data were summarized into 4-h binned frequency histograms before being relayed remotely. On-board software converted the raw depth and temperature data into dive summaries. A dive was defined as the movement in which the turtle descended below 3 m for more than 1 min. Dive metrics included the maximum depth of the dive as well as the total duration. The lower range of the dive depth bins were set to 0, 6, 10, 30, 50, 100, 150, 200, 300, 400, 500, 600, 800, 1000, and >1000 m. The lower range of the dive duration bins were set to 0, 2, 5, 10, 15, 20, 25, 30, 35, 40, 45, 50, 60, 90, and >90 min.

The transmitters relayed dive data via the Argos Satellite System, which concurrently derives the location of the transmitter. The transmitters did not have a specific duty cycle, but were programmed to relay a maximum of 52 messages per day, enough to relay all of the frequency histograms collected that day twice over. If any fewer than 52 messages were sent in a day, the unused messages were added to the message limit for the subsequent day. The transmitters were programmed to relay data that were collected within the past 10 d in priority over older data.

When a transmitter stopped reporting depths deeper than 10 m for a period of 10 d or more, it was assumed the transmitter had detached from the animal. Any data after the moment when diving ceased were not included for analysis.

Horizontal movement data

Location data were filtered by removing any locations that were on land using the GIS layer TM_WORLD_BORDERS-0.3 (available from http://thematicmapping.org/) and then applying a maximum-movement speed filter of 240 km d^{-1}. From the filtered data, we selected the most accurate daily locations using the location classes provided the Argos satellite system (3, 2, 1, 0, A, or B in descending order of assurance of accuracy). Because raw location data were not available for each day, we generated interceding daily location estimates using a Bayesian state-space model (see Jonsen et al. 2007). The state-space model was run with 2 chains for 30 000 Markov chain Monte Carlo samples with a 10 000 burn in (thin = 5).

To determine high-use inter-nesting habitats, we built a minimum convex polygon (MCP) that encompassed all the filtered transmitter data. We also used a fixed kernel density analysis, using a least-squares cross-validation method to calculate the smoothing factor (Worton 1989); from these, we created 95% utilization distribution (UD) maps.

Environmental data

A digital bathymetric map (ETOPO1: www.ngdc.noaa.gov/mgg/global/) with a spatial resolution of 0.017° was obtained from NOAA. Monthly composites of remotely sensed SST data for the South African continental shelf at a spatial resolution of 0.1° were obtained from POES AVHRR satellite imagery (http://coastwatch.pfeg.noaa.gov/) for each month when turtles were tracked (Nov 2011–Feb 2012 and Dec 2012–Feb 2013). Five-day composites of remotely sensed ocean current data at a spatial resolution of 0.33° were obtained from Ocean Surface Current Analysis Real-time (OSCAR) satellite imagery (http://podaac-www.jpl.nasa.gov/dataset/; search text: OSCAR_L4_OC_third-deg) for all months in which tracking data were available (Nov 2011–Feb 2012 and Dec 2012–Feb 2013). These spatial data were then compared to the MCP and 95% UD polygons to determine how oceanographic features influence the distribution of high-use inter-nesting habitats.

Changes in horizontal and vertical behaviour over inter-nesting intervals

To examine how the behaviour of individual turtles differs over consecutive inter-nesting intervals, we reverse-numbered each inter-nesting interval in relation to when the turtle began its post-nesting migration. For example, the final inter-nesting interval before a turtle migrated was considered *t*, the previous inter-nesting interval was $t - 1$, and then each prior inter-nesting interval was $t - 2$ and so on. We were able to determine the start and end date of each inter-nesting interval, as well as when turtles began post-nesting, by synchronously examining the ultrasound data and the animal's movement patterns.

Next, we calculated 5 behavioural metrics over each inter-nesting interval: (1) mean distance from land, (2) maximum distance from land, (3) total net horizontal distance travelled, (4) mean maximum dive depth (henceforth called mean dive depth), and (5) mean dive duration. These metrics were chosen because each of them alone or in combination could indicate how inter-nesting leatherback turtles might respond to changing environmental conditions within their inter-nesting habitats. For example, as activity can raise body temperatures in leatherback turtles (Bostrom & Jones 2007), changes in the horizontal movement patterns could indicate behavioural thermoregulation in response to increasing local temperatures. Alternatively, evidence that sea turtles dive deeper or longer during subsequent inter-nesting intervals could indicate that these animals spend more time in deep, cool waters as water temperatures increase. The metrics that focused on horizontal movement were calculated using Euclidean distances between the best daily locations. The mean dive depth and mean dive duration metrics were calculated using the binned data and thus represent the mean dive duration and mean dive depth per 4 h period.

Mapping

All mapping and spatial analyses were conducted in ArcGIS v10.3.

RESULTS

A total of 25 inter-nesting events were recorded from 10 leatherback turtles equipped with satellite transmitters (Table 1). This accounted for a total of 261 tracking days: 152 d in 2011–2012 and 109 d in 2012–2013. Inter-nesting intervals ranged in length from 8 to 12 d (mean = 9.8, SD = 1.0, n = 10). We recovered transmitters from 5 different turtles, which enabled complete data recovery for 13 inter-nesting intervals.

Table 1. Summary metrics for the behaviour of 10 inter-nesting leatherback turtles tracked from the iSimangaliso Wetland Park, South Africa. For 3 turtles, the transmitters did not record dive duration data (–). When calculating the mean values for all the individuals combined, we used the mean value for each individual over all their inter-nesting intervals. In this manner, we reduced the potential bias of having more inter-nesting data for some turtles than others. PTT: platform terminal transmitter

PTT no.	No. of inter-nesting intervals	Date tracked (d/mo/yr)	Mean distance travelled (km) (SD)	Mean distance to land (km) (SD)	Maximum distance to land (km) (SD)	Mean dive depth (m) (SD)	Mean dive duration (min) (SD)
107887	1	16/01/2013 to 26/01/2013	304.0	14.2	51.9	32.8	7.6
107892	1	13/01/2013 to 21/01/2013	144.8	26.8	67.2	46.4	10.25
107902	2	14/11/2011 to 06/12/2011	445.6 (74.0)	21.8 (6.5)	82.8 (13.4)	42.1 (8.2)	–
107903	2	11/12/2011 to 29/12/2011	352.5 (109.2)	25.7 (0.7)	54.9 (20.8)	44.6 (1.6)	–
107904	1	09/01/2012 to 19/01/2012	355.1	4.0	10.5	48.7	13.2
107908	4	13/02/2012 to 23/03/2012	237.6 (97.4)	24.2 (8.5)	54.8 (21.3)	54.5 (14.7)	17.8 (2.5)
377951	4	04/01/2013 to 05/02/2013 15/02/2013 to 25/02/2013	264.5 (88.1)	7.8 (2.3)	21.3 (6.6)	33.1 (11.4)	9.5 (1.9)
1079011	3	10/11/2011 to 14/12/2011	560.4 (127.2)	28.1 (14.5)	76.6 (42.7)	65.4 (3.4)	–
1079061	2	25/01/2012 to 13/02/2012	343.0 (8.4)	17.0 (1.3)	41.9 (8.7)	49.6 (16.0)	11.5 (1.6)
1079062	5	28/12/2012 to 12/02/2013	188.4 (46.0)	16.6 (13.4)	46.2 (32.5)	24.5 (3.3)	7.2 (0.9)
Grand mean			319.6 (122.3)	18.6 (8.2)	50.8 (22.5)	44.1 (11.8)	11.0 (3.6)

Horizontal and vertical movement patterns

The movements of the 10 inter-nesting turtles spanned from 24.7° to 29.4° S and 31.6° to 35.1° E. This covered a region as far south as the waters of the city of Richards Bay, South Africa, and as far north as the Inhambane province of Mozambique (Fig. 1B). The MCP containing all the turtle locations was contained in an area of 90 661 km^2, whereas the area defined by the 95 % UD was far smaller at 16 023 km^2 (Fig. 1C).

Inter-nesting turtles travelled net distances between 110 and 692 km per inter-nesting interval (mean = 319.6, SD = 122.3). Turtles spent most their time within 50 km of the coast, and the mean distance to land was 18.4 km (SD = 8.2). Thus, most turtles spent the majority of their time in waters less than 1000 m deep (Fig. 1B). However, 8 different turtles also conducted large looping movements that took them as far as 111 km offshore and into deeper water during at least one inter-nesting interval (mean maximum distance = 50.8 km, SD = 22.5).

There was no distinct change in either the movement patterns or total distance travelled by inter-nesting leatherback turtles between consecutive inter-nesting intervals (Figs. 2 & 3A,B). While the values for both the mean and maximum distance from land were smaller in the first inter-nesting interval ($t-4$), they remained relatively unchanged during the subsequent inter-nesting intervals (Fig. 3B); however, this could be attributable to the small sample sizes (n = 2) for early nests.

Similarly, we did not observe any distinct change in either the mean dive depth or mean dive duration of inter-nesting leatherback turtles over consecutive inter-nesting intervals (Fig. 3C,D). The dive depth frequency histogram showed that most (60 %) of the dives did not exceed 30 m (Fig. 4A), although dives up to 636 m were recorded. The mean dive depth was 44.1 m (SD = 11.8). The dive duration frequency histogram was skewed towards shorter dives, with 42 % of dives lasting less than 5 min (Fig. 4B). The mean dive duration was 11.0 min (SD = 3.6) and the longest dives lasted up to 35 min. In addition, there was an association between dive duration and dive depth (Fig. 4C). Dive duration increased with dive depth, although the rate of increase decreased with increased depth, especially after dive durations of ~20 min.

When it was possible to recover the satellite transmitters, repeated patterns were observed in the diving patterns of these animals over an inter-nesting interval. For the first half of the inter-nesting interval, turtles dove more frequently and to greater depths than during the latter half (Fig. 5). A diel diving pattern was also apparent, with turtles diving more frequently and to greater depths during the daylight hours, and the differences between daytime and night-time diving patterns became more distinct in the latter of half of the inter-nesting interval.

Thermal conditions

Regional SST in the waters of the iSimangaliso Wetland Park steadily increased from November until the following February in both the 2011–2012

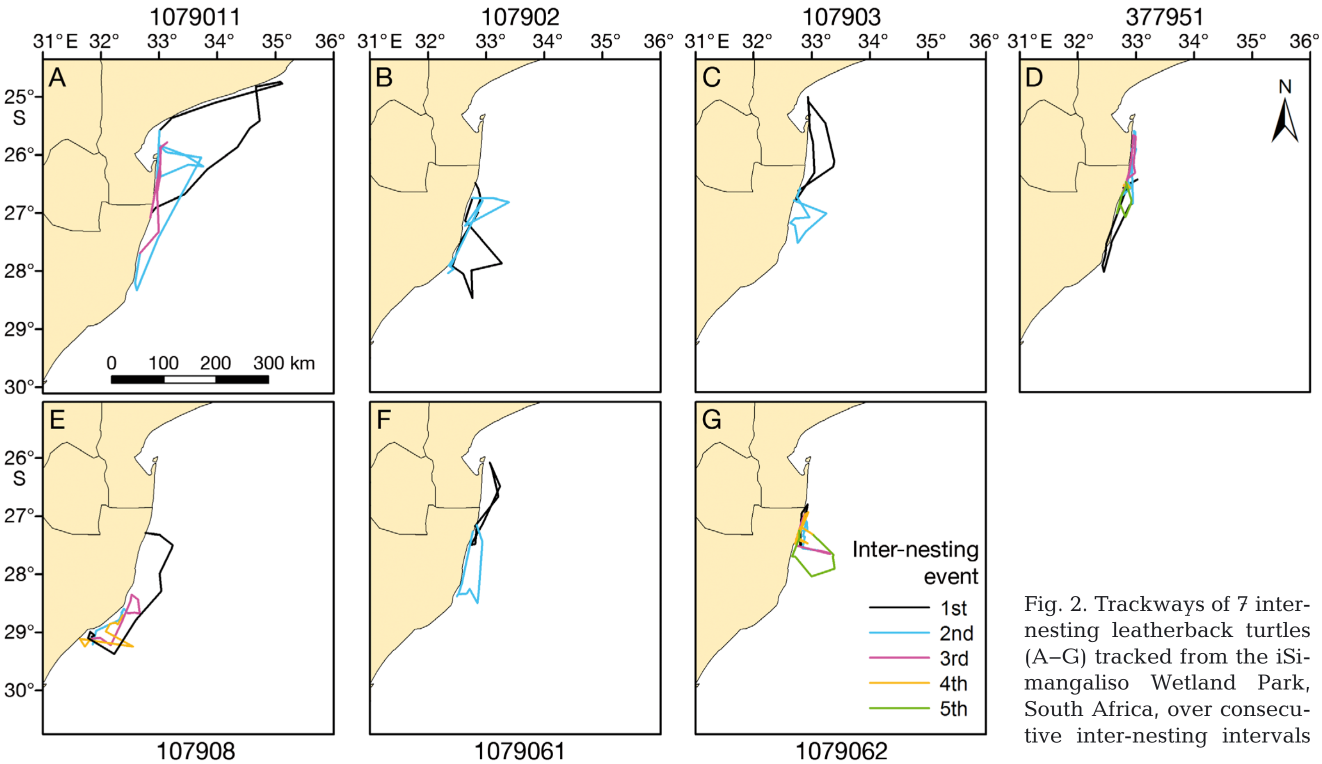

Fig. 2. Trackways of 7 inter-nesting leatherback turtles (A–G) tracked from the iSimangaliso Wetland Park, South Africa, over consecutive inter-nesting intervals

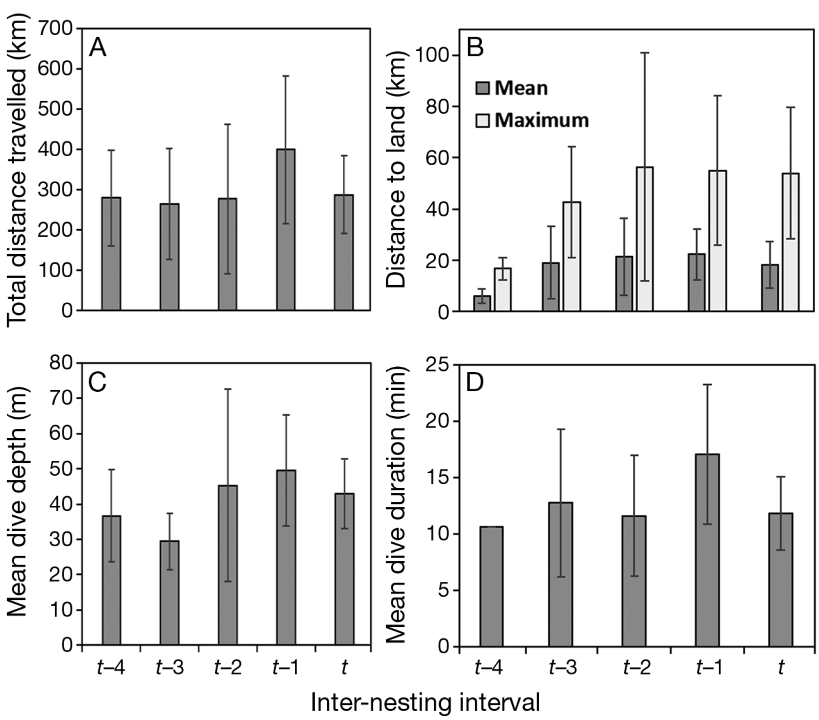

Fig. 3. Movement and diving metrics for leatherback turtles tracked from the iSimangaliso Wetland Park, South Africa, over consecutive inter-nesting intervals: (A) total distance travelled; (B) distance to land; (C) mean dive depth; and (D) mean dive duration. *t*: final inter-nesting interval before a turtle migrated; *t* − 1: the previous inter-nesting interval; *t* − 2,…: each prior inter-nesting interval. Error bars = 1 SD

and 2012–2013 seasons (Fig. 6). The Agulhas Current brings a flow of warm water than connects with the coast around 28° S and then continues to flow down the coast. In the earlier half of the nesting season, the waters south of the Inhambane Province remain up to 2°C cooler than the waters of the iSimangaliso Wetland Park where the Agulhas Current reaches the South African shoreline. The SST within the overall MCP that encompassed all of the turtles' inter-nesting movements ranged from 21.6 to 29.4°C. Although temperatures within the MCP were as low as 21.6°C, 96% of the temperatures recorded at the turtles' locations fell between 23 and 28°C.

The temperature data recorded by the transmitters indicated that inter-nesting turtles spent the majority of their time in the top 70 m of the water column, where water temperatures were very consistent, in the range of approximately 24–26°C (Fig. 5). Deeper than 70 m, there was an apparent

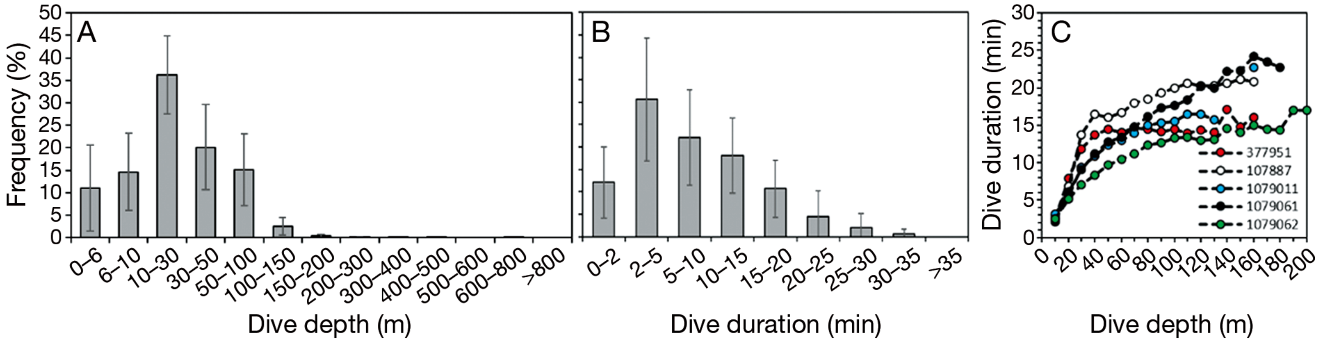

Fig. 4. (A) Dive depth and (B) dive duration frequency histograms for 10 inter-nesting leatherback turtles from the iSimangaliso Wetland Park, South Africa. Error bars = 1 SD. (C) The relationship between dive depth and dive duration for 5 leatherback turtles

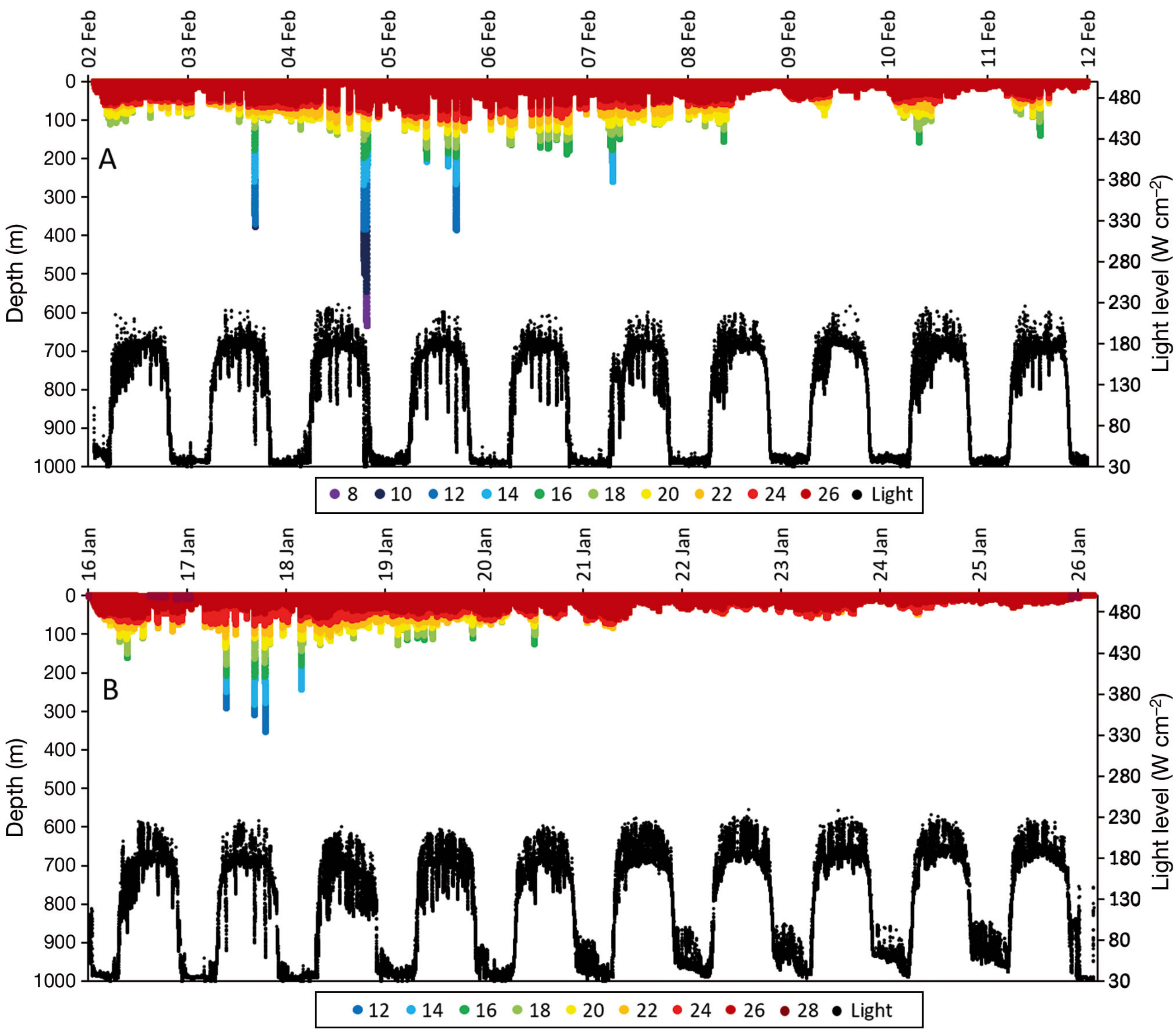

Fig. 5. Dive−temperature profiles of 2 different leatherback turtles (A and B) over an inter-nesting interval in 2013. Coloured dots represent the temperature (°C) at the different depths inhabited by the diving animal. Black dots represent light levels corresponding to day−night patterns

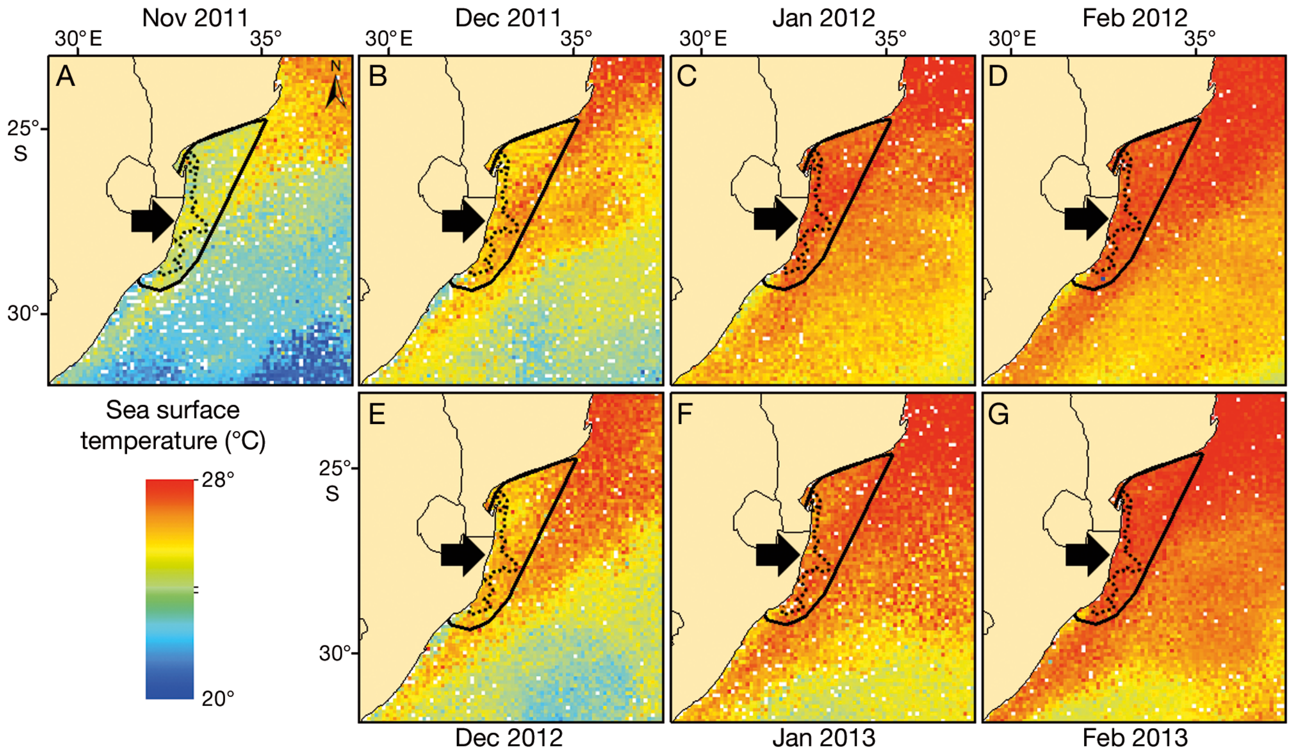

Fig. 6. Monthly composites of mean sea surface temperature (°C) in the Western Indian Ocean and surrounding the inter-nesting area as delineated by a minimum convex polygon (solid black line) and a 95% utilization distribution (dotted black line) encompassing the data shown in Fig. 1B. (A) November 2011, (B) December 2011, (C) January 2012, (D) February 2012, (E) December 2012, (F) January 2013, and (G) February 2013

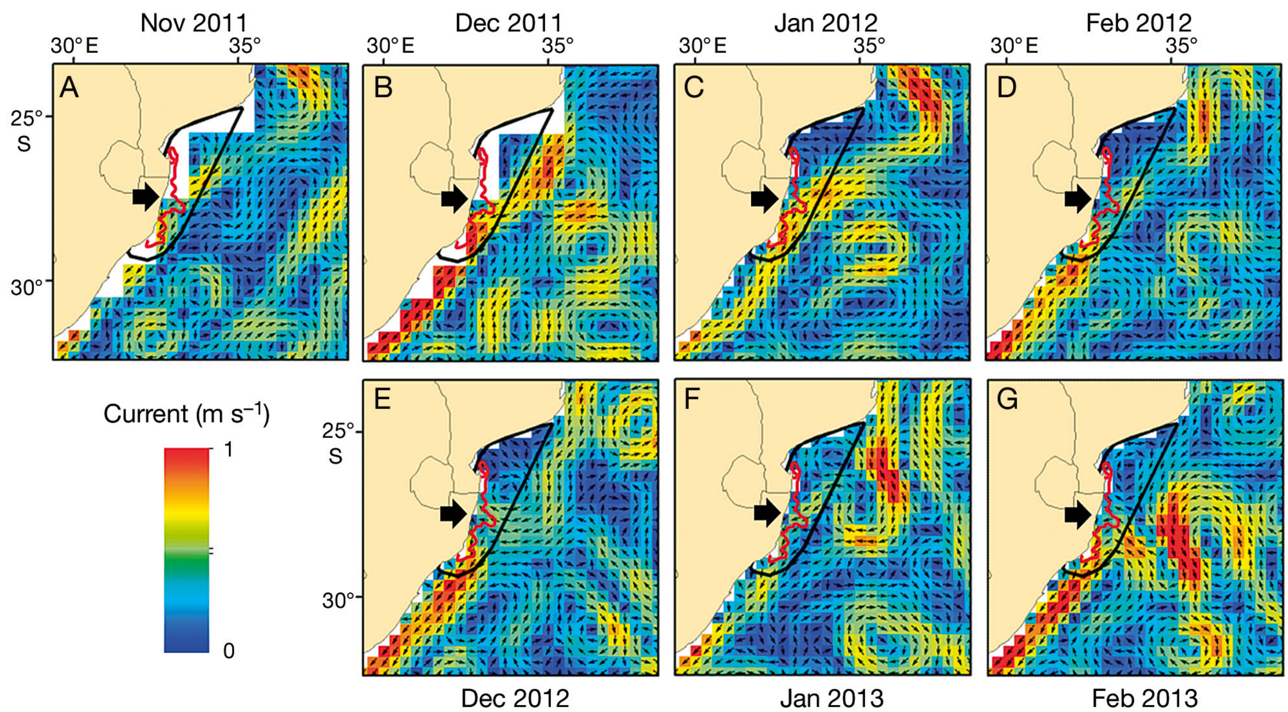

Fig. 7. Five-day composites of ocean currents in the Western Indian Ocean and surrounding the inter-nesting area as delineated by a minimum convex polygon (solid black line) and a 95% utilization distribution (red line) encompassing the data shown in Fig. 1B. Weekly composites of ocean current data were collected for the first week of the following months: (A) November 2011, (B) December 2011, (C) January 2012, (D) February 2012, (E) December 2012, (F) January 2013, and (G) February 2013

thermocline, and by depths of 200 m, the temperature decreased to around 14°C. During the deepest dive recorded in this study (636 m), the turtle encountered temperatures of 9°C.

Ocean currents

Ocean currents in the region ranged in velocity from 0 to 1.5 m s^{-1} (Fig. 7). In all months, there was a distinct and continual presence of the Agulhas Current flowing south at speeds generally in excess of 1.0 m s^{-1}. The Agulhas Current flows down the Mozambique coastline and heads out to sea after reaching the Inhambane Province at around 25°S, until it reaches the South African coast line at around 28°S, at which point it continues down the South African coastline. Notably, the primary flow of the Agulhas Current only intercepted the southern-most portions of the MCP and 95% UD of the inter-nesting leatherback turtles.

DISCUSSION

To understand an animal's movement patterns, we must have knowledge of the landscape or seascape through which it moves (Nathan et al. 2008). Here, we investigated the movement and diving patterns of gravid leatherback turtles on the southeast coast of Africa and characterized the general oceanographic features, specifically SST and ocean currents, relative to their inter-nesting habitats. Our data indicate that leatherback turtles from this nesting population can disperse distances in excess of 600 km in a single inter-nesting interval and dive to depths exceeding 600 m; however, for the majority of this time, these animals remain within 50 km of the coast and dive to depths shallower than 30 m. Our data also suggest that inter-nesting leatherback turtles do not adjust their movements or diving behaviour in response to seasonal temperature changes and that the Agulhas Current may play a role in defining the ultimate extent of the core habitat of inter-nesting turtles from the iSimangaliso Wetland Park.

Characterization of inter-nesting behaviour

Inter-nesting leatherback turtles spread out from the iSimangaliso Wetland Park over a length of coastline approximately 600 km long, ranging from 24.7 to 28.5° S. Interestingly, the northern extent of the inter-nesting habitat observed here matches the reported northern extent of leatherback turtle nesting in Mozambique (Costa et al. 2007). Thus, it may be that the inter-nesting habitat observed in this study provides a reasonable representation of the inter-nesting habitat for leatherback turtles over the entire range of this nesting population. In addition, while the MCP indicated that inter-nesting turtles can potentially inhabitant a very large area out to sea, the 95% UD indicates that the primary inter-nesting habitats are far smaller and confined to a region within 50 km of the coastline.

The mean net distance moved per inter-nesting period was 319 km (SD = 122, n = 10). This is comparable to the distances moved by inter-nesting leatherback turtles from Grenada (mean = 384 km, SD = 116, n = 14), but somewhat shorter than those of turtles from French Guyana (mean = 560 km, SD = 134, n = 14) or Gabon (mean = 656 km, SD = 144, n = 9) (Georges et al. 2007). Interestingly, the waters near the nesting beaches in South Africa and Grenada get deeper much closer to shore than those from Gabon and French Guyana. The differences in magnitude of movement could therefore reflect more ready access to deeper waters. Indeed, the inter-nesting leatherback turtles from South Africa and Grenada are diving to greater depths, while those turtles from Gabon and French Guyana are mainly moving horizontally and performing shallow dives. The mean dive depth for leatherback turtles in South Africa and Grenada was 44.1 m (SD = 11.8) and 54.7 m (SD = 37.9; Myers & Hays 2006), respectively, while it was only 9.4 m (SD = 9.2) for turtles in French Guyana (Fossette et al. 2007).

The relationship between dive depth and dive duration has often been considered an insightful indicator for assessing foraging behaviour in leatherback turtles (James et al. 2006, Myers & Hays 2006). Previous studies have shown that when diving to equivalent depths, migrating turtles conduct longer dives than inter-nesting turtles, presumably because of the lower foraging success of leatherback turtles in inter-nesting habitats (Hays et al. 2004). Although we do not compare data here on the relationship between dive depth and dive duration for both inter-nesting and migrating leatherback turtles from South Africa, the relationship observed in this study for inter-nesting turtles was very similar to that observed for inter-nesting, and presumably non-foraging, turtles in Grenada (Hays et al. 2004). Thus, we consider it likely that inter-nesting leatherback turtles in South Africa similarly do not feed during the inter-nesting period and are capital breeders, a conclusion that is supported by an increasing number of studies on inter-nesting leatherback turtles worldwide (Hays et al. 2004, Reina et al. 2005, Casey et al. 2010, Plot et al. 2013, Perrault et al. 2014).

Tracking turtles over consecutive inter-nesting intervals

Sea turtles can nest multiple times in a single nesting season, yet only a single study has previously examined changes in the behaviour of leatherback turtles over subsequent nesting events (Byrne et al. 2009). Knowledge of whether sea turtle behaviour changes between inter-nesting intervals could have important implications for characterizing the general behaviour of gravid turtles. Indeed, if sea turtles move increasingly large distances away from the nesting area over consecutive inter-nesting intervals, as observed by Byrne et al. (2009), then attempts to quantify core habitats for gravid sea turtles will be influenced by whether turtles are sampled at the beginning or end of their nesting season. Nevertheless, in this study, we did not observe any changes in horizontal or vertical movement patterns over multiple inter-nesting events. It is possible that the difference in our results may reflect our larger sample size (5 individuals versus 2 individuals) and records of individuals over as many as 5 inter-nesting intervals. Although we recommend that such studies are also undertaken at other nesting sites, our data suggest that leatherback turtles sampled at any time during their nesting season can provide an accurate representation of the movement patterns of these animals over the entire nesting season.

Environmental habitat selection

We observed that leatherback turtles from the iSimangaliso Wetland Park dive deeper and more frequently, taking them into cooler waters, during the first half of the inter-nesting period. This behaviour has also been observed for leatherback turtles at many other locations worldwide, and has been hypothesized to be a behavioural adaptation by which leatherback turtles can shed excess heat accrued during nesting (Southwood et al. 2005, Wallace et al. 2005, Myers & Hays 2006). Considering that SST increases by ~5°C over the nesting season in the iSimangaliso Wetland Park, if leatherback turtles are diving to thermoregulate, it may be expected that turtles in this area would dive deeper over consecutive inter-nesting intervals as SST increases. Yet, no changes were observed in any behavioural metric over consecutive inter-nesting intervals, suggesting that the deeper and longer dives during the first half of the inter-nesting interval are not driven by thermoregulatory needs.

While it could be argued that comparing consecutive inter-nesting intervals of leatherback turtles, which only last 8–14 d, might not encompass enough time to truly represent the response of these animals to seasonal temperature changes on a monthly scale, other evidence also suggests that leatherback turtles are not diving exclusively for thermoregulatory purposes. Indeed, if deep diving in leatherback turtles was solely for thermoregulatory purposes, then turtles may be expected to only dive to just below the thermocline (Houghton et al. 2008). However, this was not observed in this study, and diving turtles were almost constantly active and did not spend prolonged periods of time at any particular depth below the thermocline (Fig. 5).

To further investigate whether local SST variation is strongly affecting the location of high-use inter-nesting habitats of leatherback turtles from the iSimangaliso Wetland Park, we compared the general movements of these animals to remotely sensed SST data. In the early months of the nesting season, the waters north of the iSimangaliso Wetland Park, but south of the Inhambane province, are up to 2°C cooler than the Agulhas Current. Thus, if inter-nesting leatherback turtles were actively searching for cooler waters for thermoregulatory purposes, they might have been expected to spend more time in these northerly waters. Although this did not appear to be the case, the northern waters were only cooler in the earlier half of the nesting season. Different movement patterns could become apparent if a large enough number of turtles was tracked at the beginning and end of the season; this could be a possible avenue for further research.

Unlike regional SST, which demonstrated strong seasonal patterns over the nesting season, the primary flow of the Agulhas Current remained very constant throughout. The pattern was of strong current (>2.5 m s^{-1}) flowing down the east coast of Mozambique, heading out to sea, and then reaching the South African coastline again near 28° S. Thus, the primary flow of the Agulhas Current closely matched MCP in the northern extent, which was largely reflected in the movements of one animal that headed northeast until hitting the Agulhas Current, after which it immediately started swimming south and shoreward again. In addition, the Agulhas Current closely matches the eastward limits of the 95% UD in the southern range of this population's movements. Based on these observations, we hypothesize that leatherback turtles might be avoiding the strong flow of the Agulhas Current to conserve energy. Indeed, if a turtle did swim into the Agulhas Current, it must either expend energy by swimming to maintain a position near the nesting habitat or risk being advected south and away from the nesting area.

Similar observations that inter-nesting turtles might avoid strong currents have been previously noted by Georges et al. (2007), who observed that inter-nesting turtles in Grenada tended to avoid the strong currents on the other side of the island. Both this study and our study, however, have only compared the movements of a few individual turtles to broad-scale ocean current patterns. It is also unknown how sea turtles would be able to sense the directionality or strength on any current that they might be entrained in (Galli et al. 2012). Further studies are therefore needed to gain a deeper understanding of how inter-nesting sea turtle interact with ocean currents and to truly test the hypothesis of whether inter-nesting sea turtles avoid strong ocean currents. Such studies are likely to benefit considerably from utilizing satellite tracking devices with the capacity to generate location data with accuracy less than a few hundred meters, e.g. Fastloc-GPS (Dujon et al. 2014), along with ocean circulation models that generate data at similarly high resolutions (Fossette et al. 2012b, Putman & He 2013). When these more refined tools are combined, the data may reveal important information about the energetic strategies of sea turtles and help identify the factors driving habitat selection during the inter-nesting period.

Acknowledgements. Samir H. Patel, Wayne Brazier, Jenny Tucek, and Bernice Mellet all provided essential help in the field. This research was performed in accordance with permits granted by the Purdue University Animal Care and Use Committee and the Department of Environmental Affairs, South Africa (RES2013/10). Funding was provided by the Goldring Family Foundation, The Betz Chair Endowment of Drexel University, The Schrey Chair Endowment of Indiana University-Purdue University Fort Wayne, and The Leatherback Trust. N.J.R. was supported by the Bilsland Dissertation Fellowship granted by Purdue University.

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Editorial responsibility: Graeme Hays, Burwood, Victoria, Australia

Submitted: August 1, 2016; Accepted: April 2, 2017
Proofs received from author(s): May 6, 2017