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Insights on leatherback turtle movements and high use areas in the Southwest Atlantic Ocean

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ABSTRACT

Leatherback sea turtles, *Dermochelys coriacea*, undertake broad oceanic movements while traveling between breeding and foraging areas. While satellite telemetry has been used to investigate long-term movements and diving patterns of leatherback turtles around the world, behavioral information for this species in the South Atlantic Ocean is limited. Here we present the first data on movements, habitat use and diving behavior of leatherback turtles in the Southwest Atlantic Ocean (SWA). Four leatherback turtles (two females, one male and one subadult) were fitted with satellite relayed data loggers (SRDL) in 2005 and 2006 after being incidentally captured by industrial (high seas pelagic longlines) and artisanal (coastal bottom-set gillnets) Uruguayan fisheries. Turtles tended to remain in the western side of the South Atlantic Ocean where specific areas were frequented, in one instance showing a round-trip migration between temperate and tropical waters. Previously unidentified high use areas were recognized along continental shelf and break waters in the SWA, both in temperate and tropical regions. Leatherback turtles exhibited seasonal migration patterns and displayed marked changes in diving behavior between high use areas. Furthermore, our results highlight the importance of the Rio de la Plata estuary as a key foraging area for *D. coriacea* in the SWA which should be considered a central focus of attention for future research and conservation efforts.

1. Introduction

The Leatherback turtle, *Dermochelys coriacea*, is a cosmopolitan species that spends most of its life in the open ocean, occurring throughout tropical, temperate and polar oceans of the world (Pritchard, 1973; James et al., 2006a). They are specialized predators of gelatinous zooplankton such as coelenterates (class Scyphozoa, and Siphonophora) and pelagic tunicates such as pyrosomas and salps (Davenport, 1998; James and Herman, 2001; Estrades et al., 2007; Witt et al., 2007). Hence, their diving behavior can display spatial and temporal variations, which is affected not only by environmental factors but also by the local availability and vertical distribution of prey species (Hays et al., 2004a; Sale et al., 2006; Luschi et al., 2006). This preference for patchily distributed pelagic prey causes this species to travel over large regions in search of macrozooplankton (Hays et al., 2004b; Sale et al., 2006).

Leatherback turtle's movements may be strongly influenced by oceanographic features such as frontal zones which are commonly found where currents converge or along their margins, producing different behaviors such as large scale straight displacements or tortuous routes over small areas (Ferraroli et al., 2004; Hays et al., 2006; Luschi et al., 2006). Leatherback turtles globally undertake long-distance migrations over thousands of kilometers (Benson et al., 2007). Satellite transmitter data from post-nesting leatherback turtles revealed divergent migratory behaviors between ocean basins. For instance, it has been suggested that post-nesting Atlantic leatherbacks disperse widely throughout North Atlantic waters and demonstrate inter-individual behavioral variation (Ferraroli et al., 2004; Hays et al 2004b; Eckert, 2006), whereas post-nesting females departing from the Eastern Pacific share the same directional heading within a persistent migration corridor towards general high seas habitats in the eastern tropical and South Pacific (Morreale et al., 1996; Shillinger et al., 2008).

Reproductively active adults converge on natal tropical and subtropical coastal habitats to breed and nest (Miller 1997).The main nesting areas for *D. coriacea* in the Atlantic, are located in north-eastern South America (i.e., French Guiana and Suriname) and

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Trinidad (Eckert, 2006; Fossette et al., 2008) and in western Central Africa (i.e., Gabon and Congo) (Fretey, 2001; Fossette et al., 2008). In the Southwest Atlantic (SWA), leatherback nesting is restricted to the northern coast of the state of Espírito Santo (Brazil) (referred to as ES from this point foward) where a small number (<20) of leatherback females nest every season (Thomé et al., 2007). Also, leatherbacks tagged while nesting in Gabon (Africa) have been recovered along the SWA (as a result of incidental capture in fisheries and stranding events) documenting the first link between these two areas located on either sides of the Atlantic Ocean (Billes et al., 2006).

The incidental killing of leatherbacks by commercial fisheries and the unsustainable egg harvest have been implicated in the dramatic decline at major leatherback nesting beaches, mainly in the Pacific Ocean (Chan and Liew 1996; Spotila et al., 2000; Sarti Martínez et al., 2007). Following the global population decline over the past 2 decades, the leatherback turtle is currently listed as Critically Endangered on the World Conservation Union Red List 2007 (IUCN, 2007). Although nesting trends in the Atlantic are stable or even increasing (NOAA, 2007) there is a high level of bycatch occurring in interesting habitats in the Guianas, Trinidad and Gabon (Turtle Expert Working Group, 2007) as well as in the oceanic environment (Domingo et al., 2006; Carranza et al., 2006, Giffoni et al., 2008). Spatially limited estimates of population size and distribution and the lack of long term monitoring on some index beaches (Fossette et al., 2008), makes it very difficult to assess the global status of leatherback populations.

Understanding the movement of endangered species throughout their range is important for species conservation. Over the past 2 decades the use of satellite telemetry has delineated foraging areas and also provided valuable information regarding wide-range migrations of leatherbacks into oceanic and coastal waters (James et al., 2005b; Hays et al., 2006; Eckert, 2006; Doyle et al., 2008) however, information on leatherback movements in the SWA remains limited.

The aims of this study are to document the movements, identify high use areas and analyze the diving behavior of individuals of *D. coriacea* in the SWA using satellite relayed location and dive information.

2. Materials and methods

Four leatherback turtles, two adult females, one adult male and one sub-adult of undetermined sex were fitted with satellite tags (Satellite Relay Data Loggers, SRDLs, manufactured by the Sea Mammal Research Unit, St Andrews, UK) along the SWA (see Table 1 for details). Three of the tags were deployed by on-board scientific observers (Programa Nacional de Observadores Abordo de la Flota Atunera-PNOFA, Dirección Nacional de Recursos Acuáticos, DINARA, Uruguay) on leatherbacks incidentally captured during pelagic longline fishing operations targeting swordfish, tunas and sharks in the SWA. The turtles were entangled on the mainline and branch lines of the fishing gear. The fourth tag was deployed on an adult female that was brought to the beach after incidental capture in an artisanal bottom-set gillnet in the Rio de la Plata (RP) estuary, Uruguay (Table 1).

Captured individuals were measured, sexed and equipped with a satellite tag, and conventional flipper tags. Those with a curved carapace length (CCL) greater than 145 cm were assumed to be sexually mature adults (following Eckert, 2002).

Two types of harnesses were used to attach the SRDLs to the leatherback turtles' carapace. An elastic harness system made of tubular nylon webbing filled with rubber cords and covered with polyvinyl tubing was used to attach the tag to turtle T1 whereas harnesses made of non-elastic nylon webbing straps covered with polyvinyl tubing and a silicone/elastic flexible tubing ring, which incorporated corrodible steel links to ensure release were used for turtles T2, T3 and T4. The SRDLs of turtles T2, T3 and T4 were coated with antifouling paint to reduce bio-fouling.

Satellite transmitters were located with the Argos system (http://www.argosinc.com). Argos locations are assigned to different accuracy classes, called the location class (LC). Location classes 3, 2, 1, 0 are categorized to lie within 150 m, 150–350 m or 350–1000 m, >1000 m respectively of the tag's true position, while locations classes A and B have no location error estimate (ARGOS UsMO, 2007). Routes were reconstructed using LC 1–3 positions and filtered Argos positions (LC 0, A and B) based on a maximum rate of travel of 5 km/h, which is consistent with 99% of rates of travel calculated for this species (James et al., 2005a).

Dive data were analysed and compressed onboard the SRDL and maximum depth and duration of each dive relayed via Argos (Myers et al., 2006). Dive events were considered when leatherbacks dived deeper than 2 m and ≥30 s. Dives were distinguished as deep or shallow when greater than or less than 10 m, respectively. In addition to providing location data and dive information, the SRDL also relayed temperature data recorded at various depths through a conductivity–temperature–depth sensor (see McMahon and Hays, 2006). When temperature data were not available from the SRDLs, data were downloaded and analysed in the Satellite Tracking and Analysis Tool (STAT; Coyne and Godley, 2005) which provided information about sea surface temperatures associated with turtles' locations.

GIS software (ArcGis 9.3, Environmental Systems Research Institute, Inc.) was used to plot leatherback turtle movements and analyze the overall spatial use. To identify leatherbacks' high use areas a grid composed of 0.5 × 0.5 cells was overlaid with the study region. A single best daily position for each turtle was used to calculate the total time (days) spent by the turtles in each cell. High use areas (HUAs) for leatherback turtles were indicated by >5 geographic positions (days) within a single cell. The 200 m isobath was used to distinguish continental shelf waters from oceanic waters. The seasons were defined as follows: summer (January–March), fall (April–June), winter (July–September) and spring (October–December). Data on individual dives were used to examine spatial patterns in depth utilisation and dive duration. Student's t test was used to analyze differences in diving behavior (i.e., mean dive depth and duration) of leatherbacks along the identified HUAs.

3. Results

3.1. General migratory paths

The movements and behavior of four leatherback sea turtles (*D. coriacea*) were monitored for 383 ± 172 days (range: 237–631 days), during which time they travelled from 6178 to 21,203 km (Table 1). Turtles remained exclusively in the western side of the

Table 1
Summary information for leatherback turtles *D. coriacea* (n = 4) equipped with satellite tags along the SW Atlantic, from June 2005 to July 2008.

Turtle ID	Length CCL (cm)	Sex	Tag type	Release location (coordinates)	Date deployed	Last location	Days tracked	Minimum distance traveled (km)
T1	148.0	Female	SRDL	HS (29.5°S, 41.7°W)	15/06/2005	24/04/2006	313	8968
T2	159.0	Male	SRDL	HS (28.3°S, 44.0°W)	31/07/2006	25/03/2007	237	6761
T3	126.0	Unknown	SRDL	HS (28.2°S, 44.3°W)	14/08/2006	29/07/2007	349	6178
T4	155.5	Female	SRDL	RP (34.7°S, 56.7°W)	29/10/2006	21/07/2008	631	21,203

CCL, Curve carapace length (cm); SRDL, Satellite Relayed Data Loggers; HS, High Seas; RP, Rio de la Plata Estuary (Uruguay).

South Atlantic and most of them (with the exception of turtle T1) spent the majority of their time (71%, 56%, and 75% for T2, T3, T4, respectively) over the continental shelf (Fig. 1). None of leatherbacks tracked in this study ventured into the North Atlantic Ocean.

The turtles showed diverse movement patterns. Turtle T1 (a mature female) performed a long distance migration throughout oceanic waters heading NE for 165 days, and then turned around with a SW heading, not remaining at any specific area during the tracking period. Regular transmissions diminished from February to March but resumed during the last month of the tracking period when she arrived near the Rio de la Plata (RP) estuary off Uruguay (Fig. 1). Turtle T3 (a sub-adult) remained within Brazilian oceanic and continental shelf waters off the states of Santa Catarina, Paraná, São Paulo and Rio de Janeiro (~23–29°S) throughout their tracking duration, performing tortuous paths (Fig. 1). Turtle T2 (a mature male) quickly left the area where he was tagged and moved northward to tropical waters off the state of Espírito Santo (ES) in Brazil (Fig. 2). After spending 40 days (from the end of August to October 2006) in the proximity of the nesting beaches (range: 50–250 km from the coast) the male started to move southwards, arriving to the RP estuary in December 2006 where he remained until transmission ceased 3 months later (Fig. 2).

After tagged (October 2006) turtle T4 (a mature female) left the RP estuary and moved southwards into oceanic waters (~41–44°S), then performed circuitous loops before she headed back to the RP estuary (Fig. 2). After 13 weeks of residency (February–May, 2007), it left the estuary again and migrated north towards Brazilian shelf waters off the state of Rio de Janeiro (RJ) were she spent 3 weeks at the end of July. Then the turtle moved close to Espírito Santo nesting beaches but after a few days headed back towards high latitudes, arriving into waters of the RP estuary during the summer (January 2008). After spending 18 weeks in the estuary, she headed north towards tropical waters before transmissions ceased (Fig. 2).

3.2. High use areas

Most of the HUAs identified for the leatherback turtles in the present study were located over the continental shelf and slope within jurisdictional waters of Brazil, Uruguay and Argentina. The Rio de la Plata area was the most intensively used area when all turtles' satellite tracks were considered (Fig. 3). Long term residency of leatherback turtles in the RP estuary was observed for T2 and T4 which spent 121 days (51%) and 250 days (40%) of their respective total tracking durations in the RP estuary.

Other HUAs were recognized at lower latitudes within Brazilian waters, on areas adjacent to nesting beaches off the state of Espírito

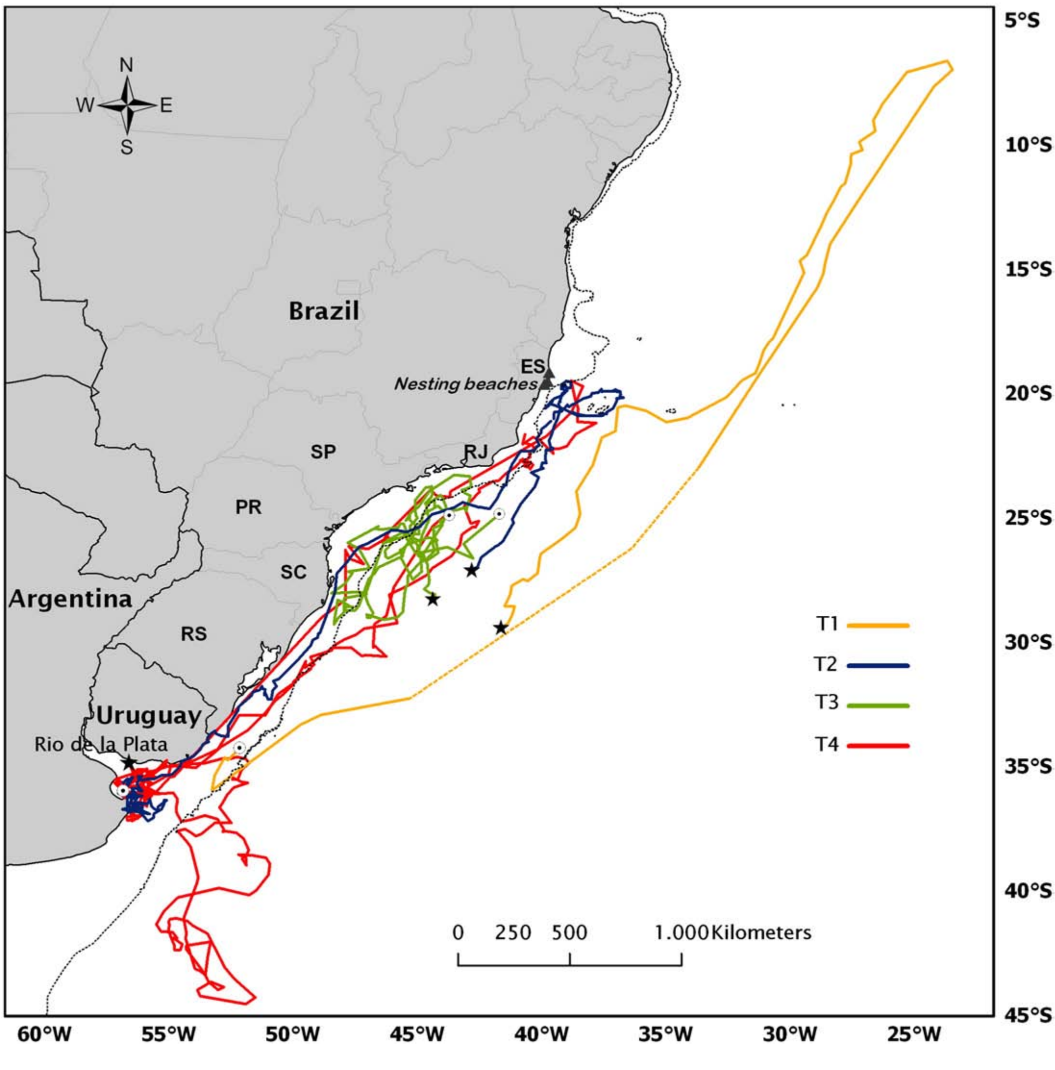

Fig. 1. The complete track of four leatherback turtles, satellite-tagged in the Southwest Atlantic Ocean. Tag deployment location is indicated by a filled symbol and last transmission location by a white circle. Bathymetric contour (dashed line = 200 m) shows turtles T2 (mature male), T3 (subadult) and T4 (mature female) spent the majority of their time over the continental shelf and break. On the contrary, Turtle T1 (mature female) remained in oceanic waters, venturing into shallower waters on the continental shelf at the end of the journey.

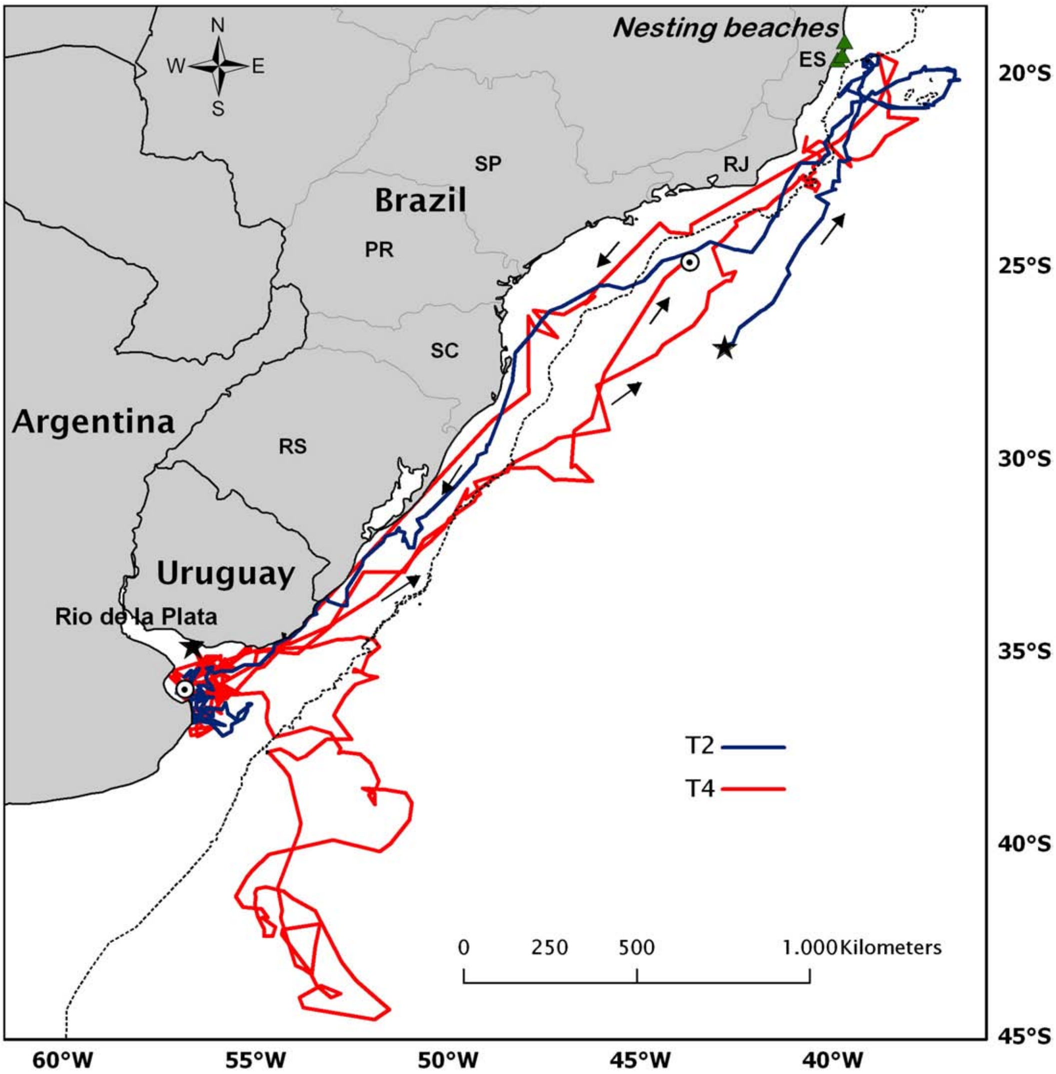

Fig. 2. Migratory paths performed by two individuals of *D. coriacea*, T2 (mature male) and T4 (mature female), monitored along the SW Atlantic Ocean. Northward and southward movements are indicated by arrows.

Santo and along the continental shelf and break of the northern portion of the state of Rio de Janeiro. For turtle T3 (subadult) the HUAs were located close to the continental break and adjacent oceanic waters off the states of São Paulo and Santa Catarina.

3.3. Seasonality of movements

In the present study leatherbacks exhibited seasonal north–south movements. HUAs were located at lower latitudes during winter (T1, T2, T4) and at higher latitudes (RP estuary) during the summer and part of the fall (T2, T4). Except for the immature individual (T3) which remained at mid-latitudes (~23–29°S), in general leatherbacks spent the summer at latitudes higher than 35°S, and during winter they mainly were at latitudes lower than 25°S (Fig. 4).

Turtles T2 and T4 presented a similar seasonal pattern in their long-distance movements (T4, also in two consecutive years), traveling from the HUAs in the RP estuary to those off the states of Rio de Janeiro and Espírito Santo (RJ-ES) mainly in late fall and backwards during spring, although both remained at the HUAs during part of these seasons (Fig. 4). Turtles T2 and T4 arrived at the RP estuary between December and February and remained within the region for up to 18 weeks.

Sea surface temperatures experienced by leatherbacks during the tracking period varied between 12 °C and 28 °C. Water temperature ranged from 18 to 28 °C for T1, 16–24 °C for T2, 20–26 °C for T3 and 12–26 °C for T4. Except for T2 which remained at mid-latitudes, turtles experienced minimum water temperatures at high latitudes in the RP estuary and adjacent waters both in late fall (e.g. T1 and T4) and spring (e.g. T2). Noteworthy, after marked decreases in water temperature (12–15 °C) recorded at the end of May of 2007 and 2008, turtle T4 left the RP estuary and migrated towards lower latitudes.

3.4. Overview of diving activity

Mean and maximum dive depths and durations for each turtle are reported in Table 2. Mean dive depth and mean dive duration recorded for all turtles ranged from 18.4 ± 19.5 m to 66.7 ± 73.6 m and 12.7 ± 11.8 min to 22.3 ± 12.5 min respectively. Turtle T1's mean dive depth was considerably deeper than the others. Turtle T1 also exhibited the longest and deepest dive record among the turtles tracked (Table 2). The dive took place in oceanic waters off the southern coast of Brazil during migration towards high latitudes (see López-Mendilaharsu et al., 2008). For all turtles combined the mean dive depth and mean dive duration were 25 ± 33.5 m and 15.6 ± 13.1 min ($n = 5687$ dives), respectively.

Ninety-three percent of all dives were to depths less than 70 m and only 16 dives (0.3%) were deeper than 200 m (Table 3).

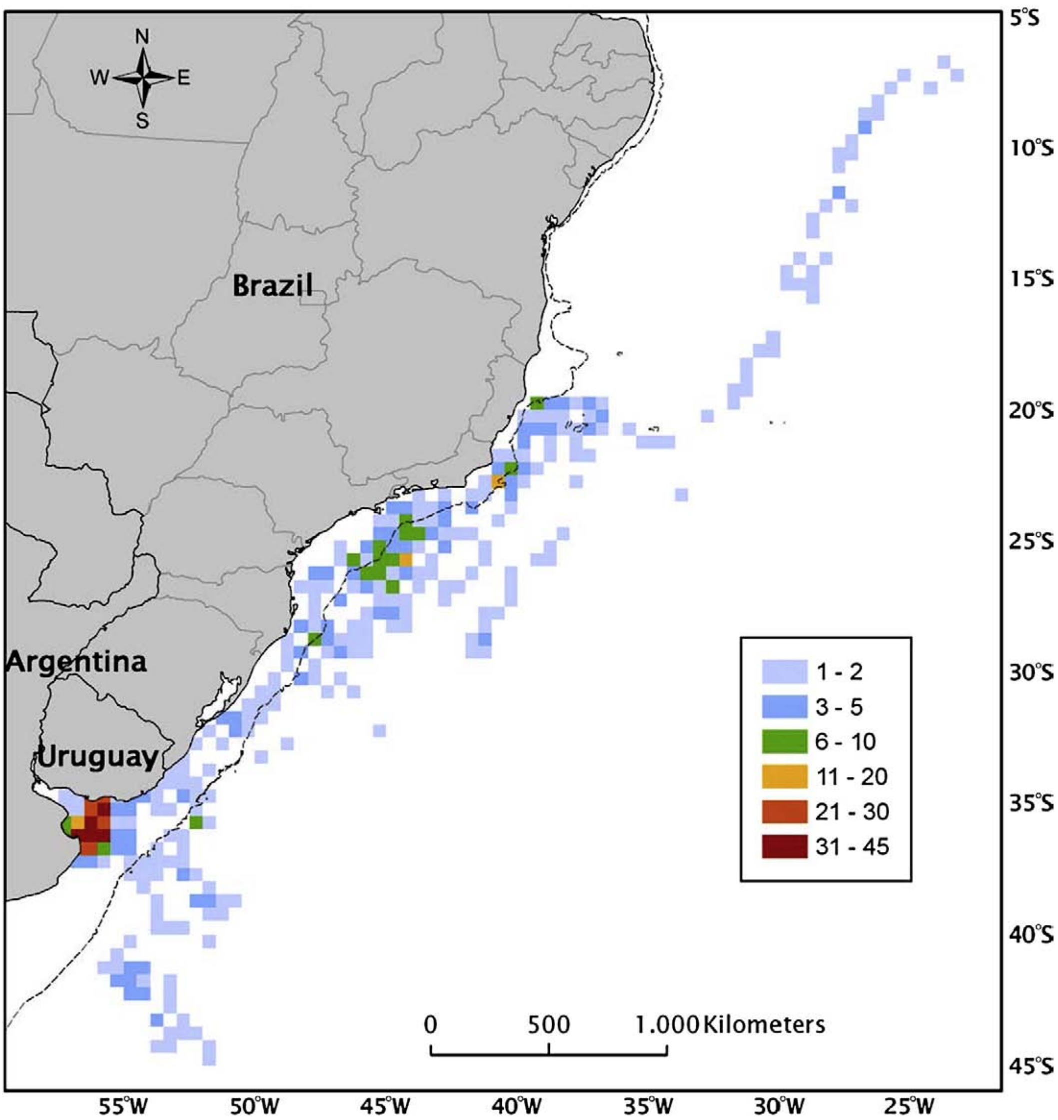

Fig. 3. Habitat utilization by tracked leatherback turtles ($n=4$), using a single daily position, from their respective reconstructed routes. The legend indicates total time (days) turtles spent in each cell (0.5 × 0.5°). Dashed black line indicates 200 m bathymetric contour.

3.5. Spatial changes in diving behavior

Two months after release turtle T1 started a long distance migration where its dive duration increased from 18.9 ± 6.6 ($n=159$) to 27.5 ± 14.8 min ($n=141$), then close to the end of the tracking period its dive durations became shorter 11 ± 15 min ($n=17$) while it was in continental shelf waters off Uruguay (Fig. 5A). Turtle T2 displayed marked changes across HUAs, with short (mean 5.9 ± 3.5 min; $n=885$) and shallow dives (mean 10.9 ± 4.5 m, $n=885$) along the RP estuary and longer and deeper dives (mean 24.4 ± 14.8 min, $t_{1246}=34.8$, $p<0.001$; mean 39.6 ± 56.5 m, $t_{1246}=14.9$, $p<0.001$; $n=363$) while in tropical HUAs (e.g., Espírito Santo and Rio de Janeiro) (Fig. 5B). For turtle T3, mean dive depth and duration became deeper (from 28.7 ± 24.7 m to 43.5 ± 42.1 m, $t_{987}=-6.9$, $p<0.001$; $n=658$ and $n=331$, respectively) and longer (from 15.2 ± 9.2 m to 27.9 ± 16.5 m, $t_{987}=-15.5$, $p<0.001$; $n=658$ and $n=331$, respectively) towards the end of the tracking period (between May and July 2007) while moving through oceanic waters off the coast of São Paulo, Brazil (Fig. 5C). Turtle T4 changed her diving behavior during the course of the journey as well. Mean dive depth and durations were deeper (mean 24.7 ± 19.3 m; $n=130$) and longer (mean 32.9 ±

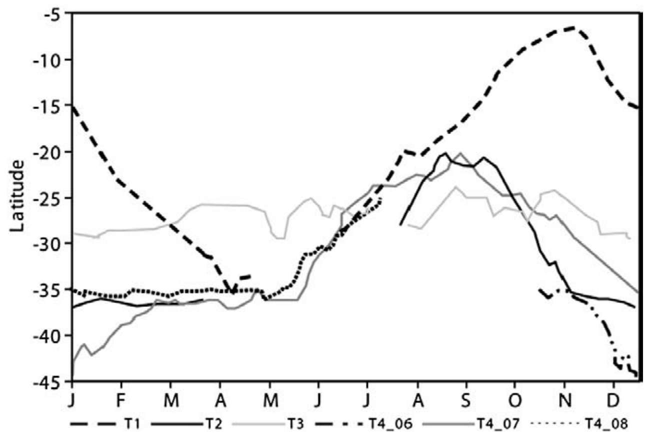

Fig. 4. Latitude versus the months of the year to indicate the leatherbacks' seasonal pattern of movement, In general, leatherbacks spent the summer at higher latitudes (>35°S) and winter months at lower latitudes lower (<25°S), with the exception of the immature individual (T3) which remained at mid-latitudes (~23–29°S), Northern movements begun at the end of May (fall) while southern movements started during spring (November–December). Turtles T1, T2, T3, T4_06 (turtle T4-2006 track), T4_07 (turtle T4-2007 track) and T4_08 (turtle T4-2008 track).

Table 2
Diving parameters recorded from the leatherback turtles ($n = 4$) tracked by satellite telemetry from June 2005 to May 2008 in the SW Atlantic Ocean (mean ± SD).

Turtle ID	No. of dives recorded	Max. dive depth (m)	Max. dive duration (min)	Mean dive depth (m)	Mean dive duration (min)
T1	317	1186	86.5	66.7 ± 73.6	22.3 ± 12.5
T2	1711	626	49.8	22.5 ± 33.0	12.7 ± 11.8
T3	989	506	61.8	33.6 ± 32.4	19.5 ± 13.5
T4	2624	506	72.5	18.4 ± 19.5	15.2 ± 13.2

Table 3
Frequency (%) of dives performed by each leatherback turtle, *D. coriacea*, at different depth ranges and for all turtles combined, along the Southwest Atlantic Ocean from June 2005 to May 2008.

Turtle ID	0–10 m	>10–30 m	>30–70 m	>70–120 m	>120–200 m	>200 m
T1	11.4	7.6	35.3	43.5	0.9	1.3
T2	40.7	38.7	14.5	5.2	0.5	0.3
T3	19.8	38.8	30.2	9.2	1.6	0.3
T4	38.6	41.7	18.6	0.9	0.1	0.2
All	34.1	38.6	20.2	6.3	0.6	0.3

22.8 min; $n = 130$) at low-latitudes near Rio de Janeiro shelf waters compared with those observed during her permanence at the RP estuary in 2007 (mean depth 11.8 ± 4.8 m, $t_{850} = -15.6$, $p < 0.001$; mean duration 14 ± 10.6 min, $t_{850} = -14.9$, $p < 0.001$; $n = 722$) and in 2008 (mean depth 9.9 ± 3.6 m; $t_{617} = 16.1$, $p < 0.001$; mean duration 7.6 ± 5.7 min; $t_{617} = 22.1$, $p < 0.001$; $n = 489$) (Fig. 5D).

4. Discussion

These satellite tracking data suggest that some leatherback turtles foraging in the SWA remain for periods of up to at least 631 days in this area utilizing similar movement paths up and down along a coastal corridor. Conversely, it has been shown that individuals tracked in the North Atlantic, from temperate foraging areas and tropical nesting beaches, traveled broadly across the ocean and did not migrate to and from northern areas along regular routes (Hays et al., 2004b; Ferraroli et al., 2004; James et al., 2005a,b).

In general, turtles tracked in the present study did not move across different oceanic environments but tended to remain mostly over the continental shelf and break during the entire tracking period (e.g., T2, T3, T4) even while migrating between temperate and tropical areas (e.g., T2 and T4). The transit over the continental shelf may provide cost effective movements (e.g., shorter distance displacement) between the HUAs located over the continental shelf and break of South America. In a study of post-nesting leatherback females from mid-latitude nesting beaches (i.e., Florida, USA), Eckert et al. (2006) noted that the turtles tended to spend a large portion of their time over the continental shelf of North America when moving to high-latitude foraging areas. However, other satellite telemetry studies of leatherbacks in the Atlantic showed that the individuals disperse far from coastal waters after leaving tropical nesting beaches or high-latitude foraging areas, traveling throughout oceanic environments for prolonged periods (Ferraroli et al., 2004; Hays et al., 2006; James et al., 2005a,b; Eckert, 2006; Doyle et al., 2008). Post-nesting females departing from western Pacific beaches also display a variety of migration routes in almost all directions including transoceanic

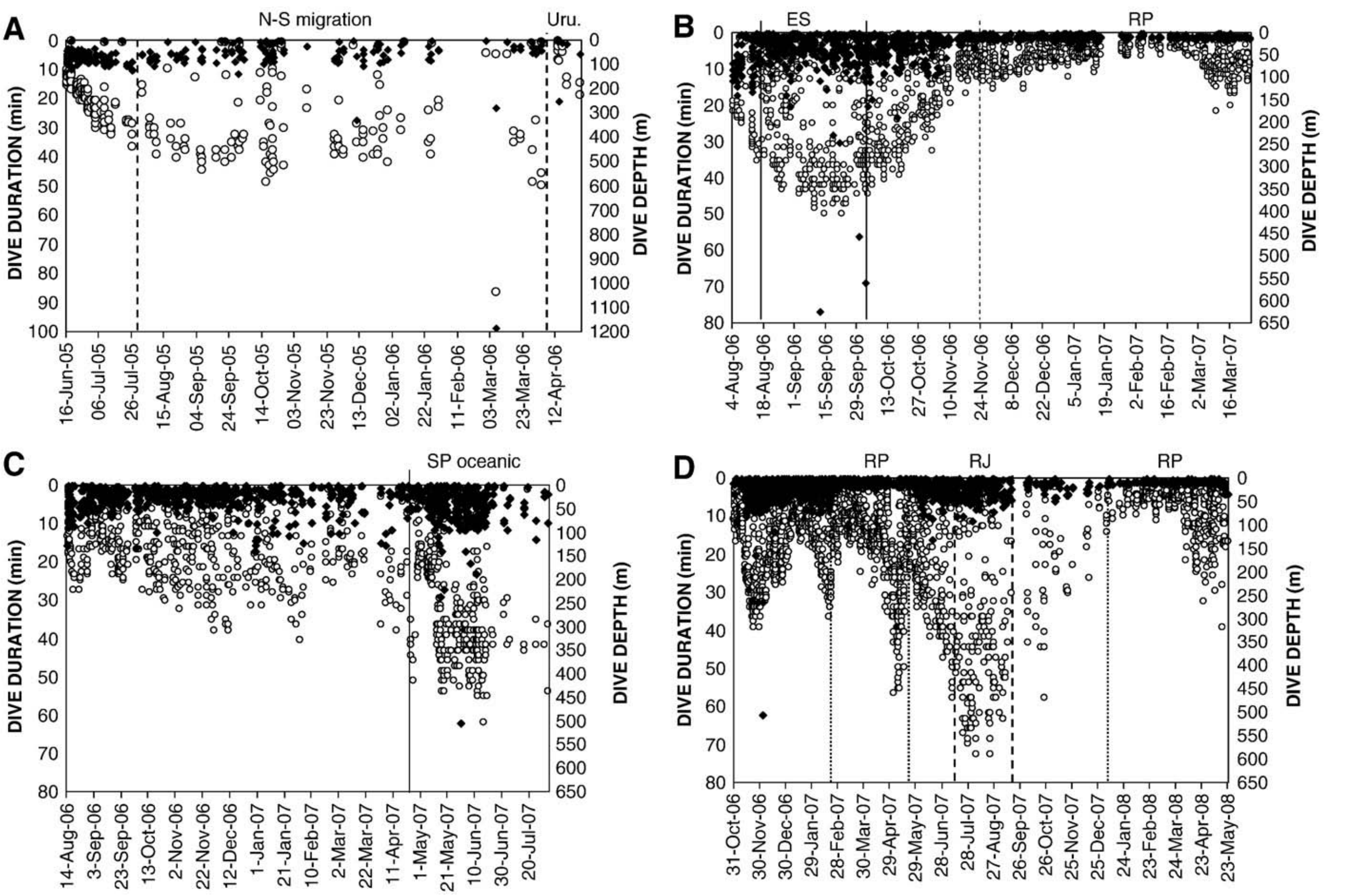

Fig. 5. Seasonal shifts in dive depth (filled symbol) and dive duration (open symbol) of A (turtle T1, a mature female); B (turtle T2, a mature male); C (turtle T3, a subadult); D (turtle T4, a mature female). Data come from individual dive profiles relayed during the tracking period. N–S migration (north–south migration), Uru. (waters off Uruguay), RP (Rio de la Plata estuary), ES (waters off the estate of Espírito Santo), RJ (waters off the estate of Rio de Janeiro), SP Oceanic (Oceanic waters off the estate of São Paulo).

movements (Benson et al., 2007). Thus, as suggested in previous studies, migratory destinations of leatherbacks might be related to the timing of prey availability in different regions (Eckert, 2006; Benson et al., 2007) which can result in extensive wandering movements over broad geographic regions or direct movements destined to fixed foraging areas.

It has been noted that leatherbacks may undertake annual north–south migrations between temperate foraging grounds and tropical waters, even during non-breeding years (James et al., 2005b,c). A similar behavior was observed for turtle T1, which moved from the subtropical Atlantic to the equatorial Atlantic, and then into the temperate Atlantic. This also occurred for T4 during the first year, where she approached tropical nesting beaches, and after a few days she headed back south towards the temperate foraging grounds.

The adults encompassed larger spatial migrations and utilized a broader region of the ocean compared to the subadult, which remained in tropical and subtropical waters between latitudes 23 and 29°S. James et al. (2005b) also noted that subadults as well as females during their internesting years encompassed similar spatial migrations between northern foraging grounds and southern tropical waters; however more data on subadult movements in the South Atlantic is needed to draw further conclusions.

Specific regions were frequented by the leatherbacks in the SWA, suggesting high site fidelity, for instance turtle T4 came back to the same area (RP estuary) occupied the previous year. A remarkable fact is that this turtle arrival to the RP was not synchronized every year. The turtle was captured in the area during spring (October, 2006), and then after an excursion to the south she arrived back to the RP estuary during February 2007. The following summer, she entered into waters of the RP estuary on January 2008 directly from the HUA off RJ-ES. This finding documents the first round-trip migration between temperate feeding areas and tropical waters in the SWA. The same behavior has been observed on individuals tracked from foraging grounds off Nova Scotia, Canada where turtles return to broadly the same area (e.g shelf and slope waters off Canada and the north-eastern United States) after performing annual round-trip migrations (James et al., 2005a,b). To the date leatherback tracking results have shown that they seem to maintain fidelity to broad geographic areas (e.g. northeast Atlantic, western Atlantic) (Hays et al., 2006) without evidence for fidelity to specific bays or localized areas (Houghton et al., 2006). However, here we show that leatherbacks can be faithful to a specific area (i.e. the RP estuary) at least during consecutive years.

Our data indicate a trend of residence in high latitudes during summer and fall (e.g., turtles T2 and T4) and migration towards lower latitudes during winter (e.g., turtles T1, T2, T4). For instance, north migrations by T4 in 2007 and 2008 begun right after marked decreases of surface temperatures at the RP estuary in late fall, suggesting that low temperature values (<15 °C) may have triggered the northern migration. This behavior is consistent with the pattern observed for leatherback turtles foraging in the North Atlantic (James et al., 2005a; Hays et al., 2006). In this way, McMahon and Hays (2006) noted that the seasonal occupation of high latitudes is primarily driven by water temperature and suggested that surface waters below 15 °C may represent a thermal constraint on the movements of leatherback turtles.

Leatherback turtles are known to present behavioral plasticity as a result of changes in prey distribution and availability (Hays et al., 2006). In general turtles changed their diving activity depending on the areas frequented, but showed similar trends while staying at regionally specific areas. Individuals in the RP estuary performed shallow and relatively short dives whereas at lower latitudes their dives were comparatively longer and deeper. The RP estuary is characterized by shallow waters (depths<20 m), thus, the turtles were diving close to the bottom. This behavior is consistent with the distribution of one of their main prey species, *Lychnorhiza lucerna* (Scyphozoa) (Estrades et al., 2007). Acoustic data and net samples surveys in the RP estuary (Alvarez-Colombo et al., 2003; Cabreira et al., 2006) showed that some species of scyphozoan medusae (e.g *L. lucerna* and *Chrysaora lactea*) tend to aggregate at the bottom, mostly beneath the halocline (vertical salinity gradient). The convergence of water masses and the resulting strong halocline at the tip of the salt wedge in the RP estuary cause an accumulation and retention of organic matter and plankton where marine species aggregate (Cabreira et al., 2006). Thus, leatherback turtles probably take advantage of the high biological productivity of this system that concentrates large amounts of their preferred prey species, resulting in the observed trend of longer residence at RP estuary by the tracked turtles. The use of temperate coastal waters by leatherbacks including estuarine systems has been noted before (James et al., 2005b; Houghton et al., 2006) however this is the first time that long term residency of leatherbacks within a relatively confined area–the RP estuary–is documented.

It is not clear if the male's deeper and longer dive durations in waters off the nesting beaches may be explained by foraging excursions into deeper waters (allowed by the narrow continental shelf) or by mating attempts (Eckert et al., 1989; Reina et al., 2005). The tracking of leatherback males from foraging grounds in the Northwest Atlantic have revealed that they usually arrive in waters adjacent to nesting colonies before the beginning of nesting season and depart from them during the peak of the nesting activity (James et al., 2005c). The male tracked in the present study showed a similar behavior and timing accordingly to nesting activity of the Espírito Santo nesting colony, as he arrived just before the beginning of the nesting season (August) and departed in October before the nesting peak (November; Thomé et al., 2007). James et al. (2005c) suggested that this behavior would increase the reproductive fitness of males arriving in breeding areas early as they could potentially maximize their expectancy for mating with multiple females before the females' first clutches of eggs are laid.

Although leatherback turtles are known to dive very deeply on a few occasions (Hays et al., 2004b; Doyle et al., 2008), the turtles in this study usually restricted their diving to less than 120 m depth. This behavior corroborates previous long-term telemetry results that also indicate that leatherbacks spend most of their time diving in the epipelagic zone (<200 m) (Hays et al., 2004b). This general shallow water diving, even in oceanic waters, at least partly reflects their requirement to surface and breath meaning that deep aggregations of gelatinous plankton are probably beyond the turtles' routine diving range. This conclusion has been reached by comparing the depth utilisation of leatherbacks with another predator of gelatinous zooplankton the ocean sunfish (*Mola mola*), with the finding that while in the same area the sunfish often spend a lot of time much deeper than leatherbacks (Hays et al., 2009).

Interestingly, turtle T1 performed a remarkably deep dive of 1186 m which lasted 86.5 min, representing the longest dive record for a leatherback turtle so far (López-Mendilaharsu et al., 2008). Estimated aerobic dive limit for leatherback turtles is around 40 min and most of the dives performed by leatherbacks fall within this limit (Bradshaw et al., 2007), so this exceptional dive was most probably anaerobic. It has been suggested that exceptionally deep and long dives appear to play an important role in prey location and assessment of the profitability of staying at a particular area, particularly during migration or extensive periods of transit (James et al., 2006b; Houghton et al., 2008).

Even though the sample size in this study is small, the data provides the first information available on long-term movements of leatherback turtles from the South Atlantic. We believe we were cautious so as not to make broad generalizations, but the fact that all the individuals were tracked for long periods (>7 months) produced interesting and novel observations that further demonstrate that they have great plasticity depending on where they forage and breed.

Here we identify previously unrecognized HUAs along the continental shelf and slope waters of the SWA. The RP estuary and adjacent waters were clearly detected as a HUA due to the large amount of time that two of the turtles spent within this relatively small geographic area. The fact that T4 returned to the RP estuary in two consecutive years (2007 and 2008) supports the importance of this area for leatherback turtles. Future studies should pay special attention to the location of other HUAs along the Brazilian continental shelf and slope waters as the area between Cape Frio (23°S) and Cape Santa Marta Grande (28°45′S) is characterized by local upwelling events (Acha et al., 2004) which can favor the aggregation and abundance of gelatinous prey for leatherbacks (Graham et al., 2001). Although the individuals tracked in this study used heavily the continental shelf area, longline bycatch studies have determined that leatherback turtles also occur on a larger area over the shelf break and oceanic waters of the Southwest Atlantic Ocean throughout the year (Domingo et al., 2006; López-Mendilaharsu et al., 2007; Giffoni et al., 2008). These bycatch studies revealed a high occurrence of leatherback in the area, but their movements and habitat use along oceanic environments off Southern Brazil and Uruguay yet remain unknown.

In summary, based on clear changes in spatial movements (e.g., from almost constant travel to tortuous movements), residency for long periods including remigration in consecutive years, a clear seasonality and changes in diving behavior of leatherback turtles, we recognize that the RP estuary could be described as a costal hotspot for leatherback turtles in the SWA. We highlight the RP estuary and adjacent continental shelf waters as a prey rich spot along the SWA, and therefore potentially supporting high densities of foraging leatherbacks as documented by frequent records of turtles incidentally captured in artisanal and industrial fisheries (Fallabrino et al., 2006; Domingo et al., 2006; Laporta et al., 2006; Miller et al., 2006) and massive stranding events of this species in the area (Anonymous, 2008).

Finally we recommend that key areas targeted by leatherback turtles repeatedly during their migratory cycles, such as those documented in this study, should be considered as important sites to focus future research and conservation efforts.

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