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THEME SECTION

An alternative technique for the long-term satellite tracking of leatherback turtles

Sabrina Fossette[1], Hélène Corbel[1], Philippe Gaspar[2], Yvon Le Maho[1], Jean-Yves Georges[1,*]

[1]Département Ecologie, Physiologie et Ethologie (IPHC-DEPE), Université Louis Pasteur, CNRS, 23 rue Becquerel, 67087 Strasbourg, France
[2]Collecte Localisation Satellites, Direction Océanographie Spatiale, 8-10 rue Hermès, 31520 Ramonville, France

ABSTRACT: The satellite transmitter fixed on a harness was, until a short time ago, the commonly used attachment technique to follow oceanic movements of the soft-shelled leatherback turtle *Dermochelys coriacea*. However, harnesses have recently been reported to have a potential welfare impact during long-term deployments in this species. Here, we present the first long-term (3 mo) monitoring of 2 leatherback turtles tracked with satellite transmitters directly attached to the carapace and compare tracking data with 3 other turtles, that were concurrently satellite-tracked with traditional harnesses. There were significantly more good quality locations recorded for carapace-equipped turtles than for turtles with harnesses, which suggests that the satellite transmitter is better directly fixed to the carapace. The mean locomotor travel rate (i.e. turtle's own motion taking potential current drift into account) for turtles with harnesses was 16% slower (0.50 ± 0.01 and 0.59 ± 0.02 m s^{-1}, respectively) and dives were 12% shorter (23.2 ± 0.8 and 26.3 ± 0.8 min, respectively) than for carapace-equipped turtles, but all were to a similar depth (87.0 ± 3.1 and 80.7 ± 2.9 m, respectively). Despite our small sample sizes, these first results suggest a marked hydrodynamic impact of the harness on the leatherback's swimming and diving capabilities, and stress the need for further developments to improve long-term monitoring while reducing hydrodynamic constraints for this species.

KEY WORDS: Animal welfare · Endangered species · Long-term monitoring · Satellite-transmitter · Hydrodynamic impact · *Dermochelys coriacea*

INTRODUCTION

Telemetry and data-logging equipment have been increasingly deployed on free-ranging marine animals to study their movements and behaviour (review in Fedak 2004, Block 2005). Thanks to advances in microelectronics over recent years, transmitters have become small and light enough to minimize the physical and hydrodynamic impacts on the animals, so that their behaviour can be accurately related to environmental conditions (e.g. Craig et al. 2004, Gaspar et al. 2006) and/or human activities (Zbinden et al. 2007). For instance, satellite telemetry is being widely used in conservation management to identify potential hotspots of interaction with fisheries (e.g. Chan et al. 1991, Ferraroli et al. 2004, James et al. 2005b, Eckert 2006, Hays et al. 2006, Georges et al. 2007). However, attaching or implanting devices on animals can potentially have an effect on their physiology and/or their behaviour (Wilson et al. 1997, Watson & Granger 1998, Ropert-Coudert et al. 2000) that should be reduced as much as possible if reliable data are to be collected on their biology. Furthermore, methods used to fix external devices on animals such as collars, harnesses, tail

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*Corresponding author.
Email: jean-yves.georges@c-strasbourg.fr

mounts, glue, and suture may also have significant welfare implications and must be specially adapted to each species (see review in Hawkins 2004).

Satellite telemetry has been used to follow the oceanic movements of sea turtles since the late 1970s. For hard-shelled sea turtles (Cheloniidea), transmitters are attached to the scaly carapace using fibreglass or epoxy resin (e.g. Balazs et al. 1996, Godley et al. 2002, Seminoff et al. 2002). For soft-shelled leatherback turtles (Dermochelyidea), however, adhesive and resins are not effective methods for attaching transmitters, due to the leathery nature of the carapace. Accordingly, in addition to tethers (Morreale et al. 1996), different types of harnesses have been successfully used for tracking leatherbacks over the last 20 yr (Eckert & Eckert 1986, Duron-Dufrenne 1987, Hughes et al. 1998). Harnesses are generally made of 2 vinyl tube-covered straps that run over the shoulders and are connected to a strap made of nylon webbing that encircles the turtle's midsection, integrating corrodible links to ensure automatic release after several months of deployment (e.g. Eckert & Eckert 1986, James et al. 2005a). However, long-term retention may occur and may cause external injuries to the animal. For instance, Troëng et al. (2006) reported a unique recovery of a leatherback turtle coming ashore after a 2 yr migration that had retained its harness, as corrodible links had been replaced with non-corrodible ones to ensure the recapture of the turtle still equipped with harness and transmitter. The central hub of the retained harness was embedded into the central carapace ridge in 2 places, to depths of approximately 8 cm, and the waist strap and stainless steel rings used to attach the strap to the central hub were encrusted into the skin (Troëng et al. 2006). So it seems that even though harnesses have been a successful technique to study migration of leatherbacks for the last 20 yr — providing crucial information on their biology to facilitate their conservation — there are inevitable problems, as for any other tagging or tracking method (Wilson et al. 1997, Watson & Granger 1998, Gauthier-Clerc et al. 2004). Major advances have been made, such as the use of corrodible links (see Eckert & Eckert 1986, Eckert et al. 1996). More recently, other techniques have been used on leatherbacks to reduce drag. For example, carapace drilling (Southwood et al. 1999, Lutcavage et al. 2001, Fossette et al. 2007), suction cup (Reina et al. 2005) and cattle tags applied to the hind flippers (Eguchi et al. 2006) have been successfully used, but always for short-term deployments.

Here, we present the data for the first long-term monitoring of 2 leatherback turtles tracked with satellite transmitters directly attached to their carapace during their post-reproductive migration. During the same period, 3 other turtles were satellite-tracked using a traditional harness with corrodible links. We took this opportunity to compare the effects of the 2 attachment techniques on the dispersal and diving behaviours of the animals. We predicted that additional drag disturbance and potential injury would probably induce slower swim performances, resulting in some adjustments in the diving behaviour of harnessed turtles compared to turtles with sattelite transmitters attached directly to the carapace.

MATERIALS AND METHODS

Instrument deployment. Between 25 and 28 July 2005, we deployed 5 Series 9000 Satellite Relayed Data Loggers (SRDLs, manufactured by the Sea Mammal Research Unit, St. Andrews, UK, weight 370 g in air, 68 g in sea water, negative buoyancy, cross section: 28 cm) on female leatherback turtles nesting at Awala-Yalimapo beach (5.7° N, 53.9° W), French Guiana, South America.

For 3 turtles (H1, H2, H3), we fixed the SRDLs on the carapace using a customised harness (manufactured by S. Eckert, Wider Caribbean Sea Turtle Conservation Network, see Eckert & Eckert 1986 and Eckert et al. 1996), during oviposition. Harnesses were made of 2 vinyl tube-covered straps (5 cm diameter) that lace over the shoulders and are connected to a strap made of nylon webbing that encircles the turtle's midsection. The ends of the straps meet dorsally at a central elastic ring equipped with D-rings for ease of adjustment. The SRDL was fixed with epoxy resin on a platform attached to both tubes with metal ties. The straps and transmitter platform were painted with anti-fouling paint. The final weight of the harness was approx. 3 kg in air (900 g in sea water, negative buoyancy, cross section: 40 cm). This harness was built to automatically detach from the animals after several months, by way of the corrodible links (Eckert & Eckert 1986).

For the 2 other females (C1, C2), we fixed the SRDLs by drilling the central dorsal ridge of the turtle's carapace during oviposition (Fig. 1). Before drilling, the carapace was disinfected with Betadine® (Viatris Pharma), then locally anesthetised with a medical cold aerosol spray (Urgofroid Spray®, Laboratoires Urgo). Three holes were then made in the central ridge 3 to 4 cm from the top and perpendicular to the longitudinal body axis using a hand brace and a 6 mm diameter bit. Holes were then disinfected again with Betadine® before 4.5 mm wide nylon ties were introduced to tightly fix the base holding the SRDL on the carapace. The base consisted of a non-corrodible aluminium plate (20 cm long, 15 cm wide, 3 mm thick) with the lateral edges lined with plastic tubes, supporting it on each side of the central ridge of the carapace (Fig. 1).

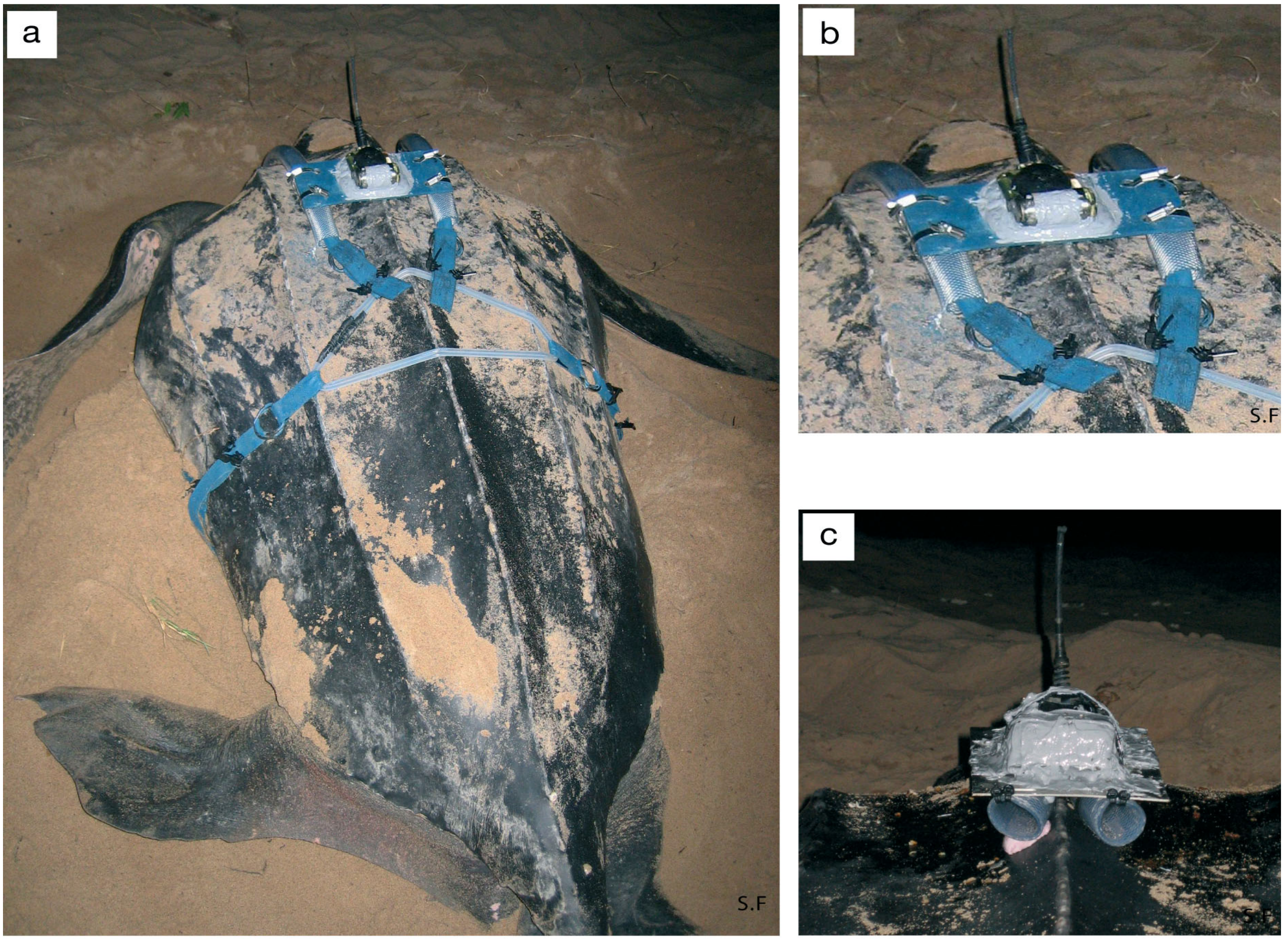

Fig. 1. *Dermochelys coriacea*. (a) Dorsal picture of a satellite-tracked leatherback turtle equipped with a harness while nesting inFrench Guiana in 2005. (b) Satellite Relayed Data Logger (SRDL) fixed with a harness. (c) SRDL directly fixed on the carapace of leatherback turtle

The base provided horizontal stability for the SRDL, improving the communication with the satellites when turtles surfaced. The final weight of the base was 250 g in air (132 g in sea water, positive buoyancy, cross section: 37 cm^2).

The technique of drilling the turtle's carapace to attach instruments has already been used for short-term deployments on leatherback turtles (Southwood et al. 1999, Fossette et al. 2007) and has been approved by the competent authorities (see 'Acknowledgements'). Our previous field experience shows that after 10 d at sea, holes were not infected and the turtles still had a normal nesting behaviour (S. Fossette unpubl. data). Each of the 5 turtles completed laying eggs and covered her nest normally before returning to the sea.

Reconstructing at-sea movements from the satellite data. The 5 turtles were tracked at sea using the Argos satellite location system (www.cls.fr). Their trajectories were edited following Gaspar et al. (2006): all Argos locations implying an apparent travel rate above 10 km h^{-1} were discarded and the track was smoothed and re-sampled at 3 h intervals using simple local linear regression with a time window of 2 d. We then computed the locomotor travel rate, i.e. the movement of the animals corrected for current drift, by subtracting the estimated surface current velocity from the apparent travel rate over the ground (Gaspar et al. 2006). The apparent travel rate was directly estimated by computing the distance between 2 successive positions of the re-sampled track divided by the time interval (3 h). As the surface current estimates used are unreliable in coastal areas (Gaspar et al. 2006), only those locations north of 8° N, well offshore of the Guiana shelf, were used. Turtles reached 8° N after 6.1 ± 0.9 d (range: 3.8 to 8.1 d). The shortest data transmission period was 98 d after the turtle reached 8° N. We thus decided to analyze equivalent track segments for all turtles, starting when they reached 8° N and ending 98 d later.

Reconstructing diving behaviour from the satellite data. SRDLs provided measurements of diving behaviour from a pressure sensor, which sampled depth every 4 s with an accuracy of 0.33 m. Individual shallow dives were recorded when depth exceeded 2 m for more than 30 s, and individual deep dives were recorded when the depth exceeded 10 m. Once a dive was completed, onboard software examined the dive profile and determined the time and depth of the 5 most relevant inflexion points during the dive (Fig. 2). The time and depth of these 5 points along with time of dive completion and dive duration were then transmitted via the Argos system, allowing a reconstruction of individual dive profiles (Fig. 2 and see Fedak et al. 2001). These dive parameters were buffered within the SRDL, with a capacity allowing up to 10 d delay to upload. Each dive was automatically numbered so that the number of dives for which data were not uploaded was known. In addition, the SRDL also provided summaries of dive information every 6 h (6 h summaries) (mean/max depth and duration) and diagnostic information showing transmitter performance (e.g. 'dry/wet' index).

Statistical methods. Due to the low replication level associated to the small sample size, the effect of group (harnessed turtles vs. carapace-equipped turtles) on repeated data (numbers of daily locations, locomotor travel rates and parameters of dives, namely depth, duration, descent and ascent rates) was examined using General Linear Mixed Models (GLMM). The GLMM approach allows pseudoreplication to be taken into account by including a repeated and a random factor (the temporal rank of data and the turtle identity, respectively). The structures of variance/covariance of the model were chosen following Akaike's Information Criterion (AIC). Analyses of variance (group effect on each dependent variable), and covariance (group effect on (1) the cumulative distance after correction for time, and (2) descent and ascent rates after correction for depth) were performed using SPSS 14.0. The percentage of dive duration spent at the bottom of the dive (i.e. the percentage of time spent between the maximum depth for the dive and 90% of this maximum depth, Fig. 2), and ascent and descent rates were calculated considering a random sample of 100 dive profiles per individual. Values are given as means ± SE, differences being considered as statistically significant when $p < 0.05$.

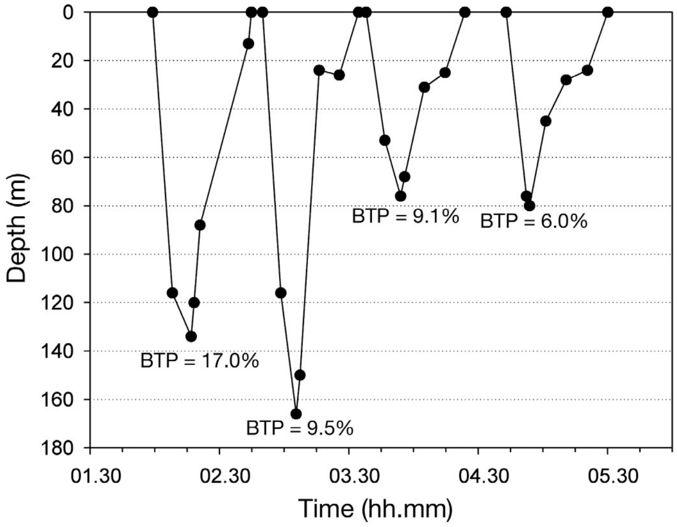

Fig. 2. *Dermochelys coriacea*. Example of profiles of 4 dives made by turtle H1. Black circles represent the dive profile inflexion points extracted and transmitted by the satellite transmitter. Bottom time percentage (BTP) calculated for each dive is also reported

RESULTS

For all 5 turtles, we analysed track segments of 98 d duration (see 'Materials and methods'). Of these 5 turtles, 4 headed northeast into the Atlantic Ocean, arriving near the Azores, while the fifth (C2) headed northwest, arriving near the eastern coast of the USA (Fig. 3). During these 98 d periods, individuals travelled between 3948 km (H3) and 5038 km (C1,

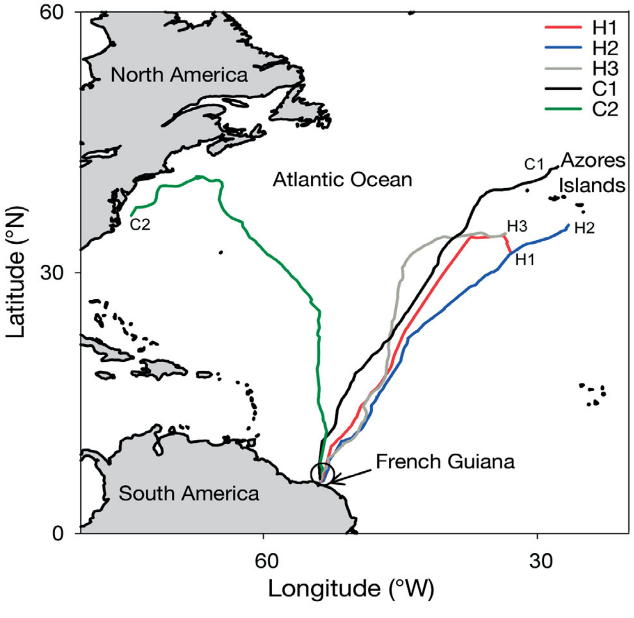

Fig. 3. *Dermochelys coriacea*. Post-nesting movements performed by 5 satellite-tracked leatherback turtles nesting in French Guiana in 2005, during the first 98 d of the post-nesting migration after turtles moved north of 8° N. Three turtles were equipped with satellite transmitter fixed on harness (H1–3) and 2 with satellite transmitter directly fixed on the carapace by drilling (C1,2). The circle corresponds to the low-latitude coastal area where the surface currents can not be correctly evaluated

Table 1. *Dermochelys coriacea*. Post-nesting movement characteristics of 5 satellite-tracked leatherback turtles nesting in French Guiana in 2005, during the first 98 d of the post-nesting migration after turtles moved north of 8° N. Three turtles were equipped with a satellite transmitter fixed on by harness (H1–3) and 2 with a satellite transmitter directly fixed on the carapace by drilling (C1, 2). SCCL: Standard Curved Carapace Length. Mean of the 2 groups: marginal means calculated from General Linear Mixed Models (GLMM). –: no data. *Significantly different from group H, GLMM, p < 0.001

Turtle ID #	Departure date	SCCL (cm)	Distance travelled (km)	Number of locations d^{-1}	Mean locomotor travel rate ($m\ s^{-1}$)
H1	26 July 2005	147	4353	0.69	0.51 ± 0.004
H2	26 July 2005	160	4374	2.24	0.52 ± 0.005
H3	28 July 2005	–	3948	1.58	0.47 ± 0.003
Marginal mean ± SE				1.52 ± 0.39	0.50 ± 0.013
C1	27 July 2005	–	5038	2.19	0.60 ± 0.007
C2	25 July 2005	149	4981	2.75	0.59 ± 0.006
Marginal mean ± SE				2.48 ± 0.47	0.59 ± 0.016*

Table 1). A total of 994 locations were recorded from the 5 SRDLs with 72% of the locations being of undefined accuracy (LCA and LCB). Mean number of daily locations varied between individuals from 0.69 locations d^{-1} to 2.75 locations d^{-1} (Table 1) but did not differ between harnessed turtles and carapace-equipped turtles (GLMM, $F = 2.46$, df = 1, 3, p = 0.214). Nevertheless, for 2 of the 3 harnessed turtles, satellite tags transmitted on average less than 2 locations d^{-1} (Table 1). In addition, there were significantly more locations of class 1, 2 and 3 for carapace-equipped turtles than for harnessed turtles (mean ± SE: 27.6 ± 0.1% and 14.2 ± 0.5% respectively; $\chi^2 = 7.356$, df = 1, p = 0.007). Transmission stopped 98 and 112 d after C1 and C2, respectively, reached 8° N (see 'Materials and methods'), whereas transmission stopped after 246, 409 and 257 d for the 3 harnessed turtles, H1, H2 and H3 respectively. For the carapace-equipped turtle C2, the 'dry' index (see 'Materials and methods') progressively decreased towards 50. For the 3 harnessed turtles, the number of daily locations after the first 98 d of tracking decreased until the last transmission and averaged 0.27 ± 0.40 locations d^{-1} (range: 0.14 to 0.42 locations d^{-1}).

Locomotor travel rate

During the 98 d periods, mean locomotor travel rate (i.e. turtle's own motion taking potential current drift into account) was 16% slower for harnessed turtles than for carapace-equipped turtles (GLMM: $F = 21.08$, df = 1,103, p < 0.001, Table 1). Indeed, the slope of the regression line of the cumulative distance on time since departure was significantly higher for carapace-equipped turtles (51.4 ± 5.3 km d^{-1}) than for harnessed turtles (44.0 ± 6.1 km d^{-1}, GLMM group × time: $F = 17.23$, df = 1, 3, p = 0.025, Fig. 4). At the end of the 98-d period, the fastest harnessed turtle (H2) had swum 607 km less than the slowest carapace-equipped turtle (C2) and the slowest harnessed turtle (H3) had swum 1090 km less than the fastest carapace-equipped turtle (C1).

Diving behaviour

The SRDLs recorded a total of 4917 dives summarized over 6 h periods (see 'Materials and methods') from the 5 turtles, with 46.7% of all recorded dives being performed by the 2 carapace-equipped turtles. Of the 4917 dives, 2341 dives were transmitted via Argos with enough dive parameters to be accurately analysed. The longest dive was also the deepest, reaching 1185.8 m in depth for 83.8 min in duration (C2). The overall mean of dive duration for the 5 turtles was 24.1 ± 1.5 min (range: 19.3 to 28.7 min, Table 2) and the overall mean of dive depth was 80.7 ± 8.0 m (range: 55.6 to 102.9 m, Table 2). Dives lasting longer than 35 min were mainly

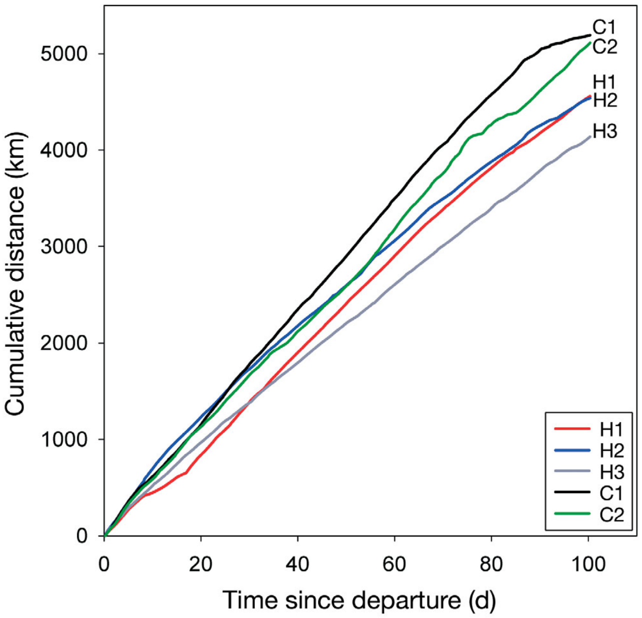

Fig. 4. *Dermochelys coriacea*. Cumulative distance calculated from locomotor travel rate throughout time for 5 Argos tracked leatherback turtles nesting in French Guiana in 2005, during the first 98 d of the post-nesting migration after turtles moved north of 8° N. H: harness attachment; C: direct carapace attachment

Table 2. *Dermochelys coriacea*. Diving behaviour characteristics of 5 satellite-tracked leatherback turtles nesting in French Guiana in 2005, during the first 98 d of the post-nesting migration after turtles moved north of 8° N. H: harness attachment; C: direct carapace atttachment. Mean of the 2 groups: marginal means calculated from GLMM. *Significantly different from group H, GLMM, $p < 0.006$

Turtle ID #	No. dives transmitted	Mean dive depth (m)	Mean dive duration (min)	Descent rate (m s^{-1})	Ascent rate (m s^{-1})
H1	180	55.6 ± 4.7	19.3 ± 1.1	0.20 ± 0.02	0.11 ± 0.01
H2	548	102.9 ± 3.5	24.8 ± 0.5	0.20 ± 0.01	0.16 ± 0.01
H3	365	78.6 ± 4.5	22.8 ± 0.9	0.26 ± 0.04	0.16 ± 0.02
Marginal mean ± SE		87.0 ± 3.1	23.2 ± 0.8	0.20 ± 0.01	0.14 ± 0.01
C1	451	92.1 ± 2.9	28.7 ± 0.7	0.23 ± 0.02	0.14 ± 0.01
C2	798	74.3 ± 2.6	24.9 ± 0.7	0.25 ± 0.03	0.15 ± 0.01
Marginal mean ± SE		80.7 ± 2.9	26.3 ± 0.8*	0.24 ± 0.02	0.15 ± 0.01

performed (69.8%) by the 2 carapace-equipped turtles. Dives performed by harnessed turtles were of a similar depth to those performed by carapace-equipped turtles (group effect on depth: $F = 2.26$, df = 1,520, $p = 0.133$, Table 2) but they were 12% shorter in duration (group effect on duration: $F = 7.52$, df = 1,360, $p = 0.006$, Table 2). Results were similar when considering the 4917 dives summarized over 6 h periods. For the 0–20 m, 40–60 m and 60–80 m depth classes, there was no significant difference between groups for the mean dive duration (Fig. 5, GLMM for each class, $p > 0.05$). For depth class 20–40 m, dives performed by harnessed turtles were significantly longer than those performed by carapace-equipped turtles (GLMM: $F = 7.17$, df = 1,24, $p = 0.013$, Fig. 5). Finally, dives deeper than 80 m were significantly shorter for harnessed turtles than for carapace-equipped turtles (Fig. 5, GLMM for each class, $p < 0.01$).

Considering all dives, both ascent and descent rates were similar between groups (GLMM: ascent: $F = 0.04$, df = 1,138, $p = 0.836$, descent: $F = 2.88$, df = 1,126, $p = 0.092$, Table 2). For dives deeper than 80 m only, no difference in descent rates was detected between groups (harnessed turtles: 0.22 ± 0.01 m s^{-1}; carapace-equipped turtles: 0.21 ± 0.01 m s^{-1}; GLMM: $F = 0.19$, df = 1,86, $p = 0.664$), whereas ascent rates were higher for harnessed turtles (0.16 ± 0.01 m s^{-1}) than for carapace-equipped turtles (0.13 ± 0.01 m s^{-1}; GLMM: $F = 4.61$, df = 1,76, $p = 0.035$). In the 2 groups, both descent and ascent rates significantly increased with depth for those dives deeper than 80 m (GLMM, $p < 0.001$ in all cases). The analysis of covariance failed to detect any group effect on slope ($F = 0.007$, df = 1,99, $p = 0.933$) and intercept ($F = 1.18$, df = 1,4, $p = 0.335$) for the descent rate, whereas the slope relating the ascent rate to depth was significantly higher for harnessed turtles than for carapace-equipped turtles (GLMM: $F = 17.49$, df = 1,87, $p < 0.001$). For harnessed turtles and for carapace-equipped turtles, the percentage of dive duration spent at the bottom of the dive was between 2 and 40% for 86.7 and 90.8% of the dives, respectively (Fig. 2).

DISCUSSION

The migratory tracks obtained in the present study were similar to those reported in previous years with other leatherback turtles satellite tracked with harnesses from French Guiana (Ferraroli et al. 2004, Gaspar et al. 2006) and from other Atlantic nesting sites (Hays et al. 2004, 2006, Eckert 2006). Remarkably, all 5 leatherbacks headed straight into the Northern Atlantic (e.g. Gaspar et al. 2006) until they arrived near potential feeding sites, namely the Azores (Eckert 2006) and the eastern coast of USA (James et al. 2005a). The diving performances recorded in the present study were within the range of those recorded for Atlantic leatherbacks during their migrations (mean

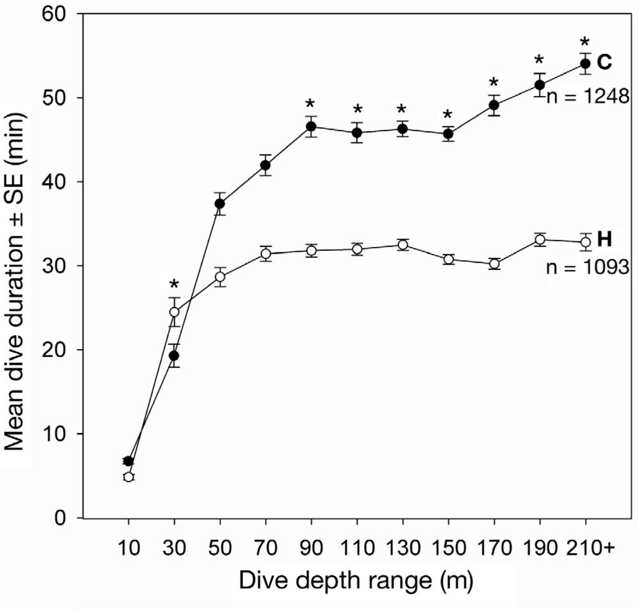

Fig. 5. *Dermochelys coriacea*. Relationships between mean ±SE dive duration (min) and dive depth class (m; given as class middle value) for turtles equipped with satellite transmitter fixed on harness (n = 3 ind., white circles, group H) and turtles equipped with satellite transmitter directly fixed on the carapace (n = 2 ind., black circles, group C) in 2005, during the first 98 d of the post-nesting migration after turtles moved north of 8° N. *Significantly different from group H, GLMM, $p < 0.05$

max. depth: 50 to 200 m and mean duration: 15 to 40 min, Hays et al. 2004, 2006, Eckert 2006), and the majority of the dives displayed a V-shaped profile as reported by Sale et al. (2006).

However, our results show significant differences in the data gathered by satellite tracking between harnessed and carapace-equipped turtles at 4 major levels.

First, data transmission ceased earlier for carapace-equipped turtles than for harnessed turtles. For one of the carapace-equipped turtles, the progressive reduction in the 'dry' index of the transmitter towards 50 suggests the build-up of biofouling that probably resulted in the transmission loss. For the second carapace-equipped turtle, the transmission may have stopped because of battery failure or transmitter loss. Data transmission lasted longer for harnessed turtles, but the mean number of daily locations dramatically decreased after the first 3 to 4 mo of tracking. This suggests that the direct attachment technique has to be improved to achieve records of similar duration to those obtained with harness. For instance, orthopaedic bioabsorbable mini-anchor screws might be used to more reliably fix the transmitter on the carapace (Lutcavage et al. 2001).

Second, there were significantly more recorded locations of low quality for harnessed turtles than for carapace-equipped turtles. In addition, for 2 of the 3 harnessed turtles, satellite tags transmitted on average less than 2 locations per day. Since the 5 satellite transmitters came from the same manufacturer and had the same technical specifications, the observed differences probably result from the stability of the transmitter on the turtle's back. Direct observations of harnessed leatherbacks crawling on the beach suggest that the harness may move laterally and/or longitudinally when the turtle swims (S. Fossette pers. obs.) meaning the transmitter may no longer be in an appropriate position for satellite transmission. Conversely, direct attachment permits the transmitter to be tightly fixed on the carapace and prevents it moving.

Third, the locomotor travel rate (i.e. the turtle's own motion when taking potential drift into account, see Gaspar et al. 2006) was 16% slower for harnessed turtles than for carapace-equipped turtles, the slowest carapace-equipped turtle still being faster than the fastest harnessed turtle. This difference suggests a marked hydrodynamic impact of the harness that may induce an additional drag effect for the animal. Further comparisons are required to confirm such differences. In addition, as sea turtles swim using front flippers as propellers (Wyneken 1997), the vinyl tubes of the harness that run over their shoulders may cause them discomfort (Troëng et al. 2006), limiting their fore-flipper movements and ultimately decreasing their travel rate and diving capabilities. If one considers that the Azores area is one of the major foraging grounds for Atlantic leatherback turtles (see Eckert 2006), leatherbacks should swim 4500 km straight from French Guiana to their feeding site. According to the mean travel rates we calculated in this study, a harnessed turtle is expected to arrive 16 d later than any carapace-equipped turtle. If leatherbacks feed in seasonal and ephemeral prey patches as suggested by Eckert (2006), food resources may have already declined when a turtle arrives 2 wk after the initiation of the patch.

Finally, the 5 leatherback turtles monitored during the study performed dives with a mean depth of 80 m. Carapace-equipped turtles performed slightly, yet significantly, longer dives than harnessed turtles, particularly in the case of dives deeper than 80 m. Such differences in the duration of dives of similar depth suggest that harnesses induce additional costs either due to unbalanced buoyancy (see below), drag effects (Ropert-Coudert et al. 2000) and/or physical constraints on flipper movements (Troëng et al. 2006). Harnessed turtles appear to compensate for these additional costs by reducing the time spent submerged, probably to avoid depletion of oxygen. Since the asymptote of maximum dive duration can be used to infer the diving metabolic rate in leatherback turtles (Bradshaw et al. 2007), the potential compensation related to the presence of a harness may be considered to revise these estimates. In this study, leatherbacks systematically descended to depths at a faster rate than when they ascended to the surface and spent almost no time at the bottom of the dives (Table 2). Both carapace-equipped and harnessed turtles showed similar descent rates regardless of depth, suggesting that buoyancy has a negligible impact on their diving behaviour. However, harnessed turtles increased their rate of ascent as dives exceeded 80 m depth. This indicates that, due to additional costs associated with wearing a harness, leatherbacks reduce the duration of their dives by resurfacing more quickly, probably by increasing their ascent angle. Behavioural differences observed between carapace-equipped and harnessed turtles are not biased by the random transmission of individual dive profiles via the Argos system, since we found similar results when considering dives provided by the 6 h summaries.

In conclusion, satellite telemetry is indispensable to the gathering of data in migrating species such as leatherbacks (e.g. Ferraroli et al. 2004, James et al. 2005b, Eckert 2006, Hays et al. 2006, McMahon & Hays 2006, Georges et al. 2007). Our study suggests that the harness technique commonly used on this species may induce significant impacts on the dispersion and diving capabilities, with potential impacts on their foraging efficiency. Despite the limited sample size used for this study, our results are consistent with previous studies (e.g. Wilson et al. 1997, Watson & Granger 1998, Ropert-Coudert et al. 2000). Yet, because of the low replication level, they should be appropriately considered as a warning to improve leatherback tracking methods. Satellite-transmitters fixed directly onto the carapace, as developed in this study, may be one solution which should benefit further investigations and improvements to reduce as far as possible the impact on turtles' hydrodynamic performance while improving the tracking duration.

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