

Behaviour and buoyancy regulation in the deepest-diving reptile: the leatherback turtle

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SUMMARY

In the face of the physical and physiological challenges of performing breath-hold deep dives, marine vertebrates have evolved different strategies. Although behavioural strategies in marine mammals and seabirds have been investigated in detail, little is known about the deepest-diving reptile – the leatherback turtle (*Dermochelys coriacea*). Here, we deployed tri-axial accelerometers on female leatherbacks nesting on St Croix, US Virgin Islands, to explore their diving strategy. Our results show a consistent behavioural pattern within dives among individuals, with an initial period of active swimming at relatively steep descent angles (~–40 deg), with a stroke frequency of 0.32 Hz, followed by a gliding phase. The depth at which the gliding phase began increased with the maximum depth of the dives. In addition, descent body angles and vertical velocities were higher during deeper dives. Leatherbacks might thus regulate their inspired air-volume according to the intended dive depth, similar to hard-shelled turtles and penguins. During the ascent, turtles actively swam with a stroke frequency of 0.30 Hz but with a low vertical velocity (~–0.40 m s⁻¹) and a low pitch angle (~+26 deg). Turtles might avoid succumbing to decompression sickness ('the bends') by ascending slowly to the surface. In addition, we suggest that the low body temperature of this marine ectotherm compared with that of endotherms might help reduce the risk of bubble formation by increasing the solubility of nitrogen in the blood. This physiological advantage, coupled with several behavioural and physical adaptations, might explain the particular ecological niche the leatherback turtle occupies among marine reptiles.

Key words: gas solubility, endotherm, accelerometer, Boyle's law, cost of swimming, body density.

INTRODUCTION

Air-breathing marine vertebrates face a number of physical and physiological challenges as they perform prolonged breath-hold dives (Kooyman, 1989). They have to deal with physiological risks associated with the compression and decompression of the gases in the body upon changes in hydrostatic pressure, which increase with greater dive depth and frequency (Kooyman and Ponganis, 1998). Formation of nitrogen bubbles during decompression (i.e. decompression sickness), nitrogen narcosis and deep-water blackout are typical pathologies related to the effects of repetitive deep diving (Bennett and Rostain, 2003). They are particularly well documented for human divers (Brubakk and Neuman, 2003), but they have also been studied in marine mammals (Kooyman, 1989). In the latter case, mitigation of the problems occurs by restricting the amount of air in the lungs and absorption of nitrogen into the body tissues (Kooyman, 1989). Thus, to minimise deleterious effects, divers should exhale before deep diving (Boyd, 1997; Kooyman and Ponganis, 1998). For example, both Northern elephant seals *Mirounga angustirostris* and Weddell seals *Leptonychotes weddellii* exhale before submergence and repeatedly dive to many hundreds of meters (Le Boeuf et al., 1986; Ponganis et al., 1993; Sato et al., 2003; Mitani et al., 2009), without any obvious ill-effects (e.g. Castellini et al., 1988). However, dive duration is a function of oxygen stores, and so this strategy is at odds with maximising dive efficiency (i.e. the ratio dive duration/surface time) and, presumably,

for this reason, some divers also inhale before deep diving (Sato et al., 2002; Miller et al., 2004; Tyack et al., 2006). Divers that inhale adopt specific behaviours to reduce decompression risks. For instance, king penguins *Aptenodytes patagonicus* (Sato et al., 2002) and sperm whales *Physeter macrocephalus* (Miller et al., 2004), which both inhale before submergence, spend long periods either at the surface or performing shallow dives between successive deep dives, presumably to offload nitrogen and equilibrate to normal gas tensions in the tissues to prevent bubble formation.

Beyond its potential for physiological trauma, descending after inhalation also affects diving energetics because air-based oxygen in the respiratory spaces profoundly affects buoyancy and therefore the costs of swimming. Thus, for example, some seabirds adjust the amount of inspired air according to the intended dive depth, reducing the cost of counteracting buoyancy during the bottom phase to virtually zero, which increases dive efficiency (e.g. Wilson et al., 1992; Wilson, 2003), even in deep-diving species, such as king penguins (Sato et al., 2002) and Kerguelen shags *Phalacrocorax verrucosus* (Cook et al., 2010). However, divers that inhale are exposed to high energetic costs during the descent of the dives as they have to counteract air-mediated buoyancy by actively stroking (e.g. Sato et al., 2002; Hays et al., 2007), which might even constitute the majority of power requirements associated with diving (Lovvorn et al., 2004). Conversely, by exhaling, divers are able to glide during more of the descent, with the ratio of gliding/stroking depending

mainly on the body density of the animal [i.e. percentage of body lipids (e.g. Beck et al., 2000; Biuw et al., 2003; Sato et al., 2003)].

Deep diving and the associated strategies employed by marine birds and mammals are relatively well understood (Kooyman and Ponganis, 1998; Sato et al., 2002; Miller et al., 2004; Davis and Weihs, 2007), yet little is known about behavioural adaptations of marine reptiles performing deep dives. Morphological and physiological adjustments to repeated breath-hold diving have been studied in detail in hard-shelled turtles and sea snakes (e.g. Berkson, 1966; Seymour, 1974; Seymour and Webster, 1975; Lutz and Bentley, 1985; Lutcavage and Lutz, 1991; Wyneken, 2008), and it has been shown that individuals can adjust the amount of inspired air to be near neutral buoyancy at depth (Graham et al., 1987; Minamikawa et al., 2000; Hays et al., 2004b) in a manner similar to that of marine birds (Sato et al., 2002; Wilson, 2003; Cook et al., 2010). However, both groups are relatively shallow divers (Heatwole, 1999; Hochscheid et al., 1999; Hays et al., 2001; Houghton et al., 2002). The only true deep-diving marine reptile (defined here as exploiting typical mean dive depths ≥ 100 m) is the leatherback turtle, *Dermochelys coriacea* (Vandelli 1761), which is also the largest and most morphologically and physiologically distinct of the sea turtles. The thin flexible cartilaginous carapace and highly reduced plastron (Wood et al., 1996; Wyneken, 2001) in addition to compliant chest walls (Lutcavage and Lutz, 1997), compressible, cartilaginous tracheal tube (Davenport et al., 2009) and small collapsible lungs [i.e. relative to hard-shelled turtles (Lutcavage and Lutz, 1997)] are probably adaptations to the impressive diving abilities of this species. These physical attributes might allow complete lung collapse at depths of 80–160 m (Berkson, 1966) and the confinement of lung gas to nonrespiratory areas during deep dives, which help to prevent nitrogen supersaturation of tissues (Kooyman, 1989; Lutcavage and Lutz, 1997). In addition, having a larger oxygen store in the blood and tissues (15.2 ml kg^{-1}) than in the lungs (12.2 ml kg^{-1}) probably increases oxygen availability during deep dives (Lutcavage et al., 1992), and tachycardia at the surface might improve the removal of metabolic byproducts and uptake of oxygen after deep dives (Southwood et al., 1999). Several of these characteristics, very similar to those of deep-diving mammals (Kooyman, 1989), would suggest that leatherbacks are exhaling divers (Taylor, 1994). However, leatherbacks inhale before submergence (Reina et al., 2005), and the behavioural adaptations associated with this strategy, such as buoyancy regulation, have not been investigated yet. Contrary to some deep divers that exclusively forage in the mesopelagic zone and thus occupy relatively narrow vertical niches (Hooker and Baird, 1999; Tyack et al., 2006; Watwood et al., 2006), the leatherback turtle is characterised by a high behavioural plasticity associated with its trans-oceanic migrations (Hays et al., 2004a; Sale et al., 2006). In oceanic areas, leatherbacks feed on deep-scattering gelatinous zooplankton, whereas, in coastal areas, they forage on large shallow-water scyphozooan jellyfish (James and Herman, 2001; Witt et al., 2007; Fossette et al., 2010). This prey diversity requires flexibility in diving behaviour in order to optimise foraging efficiency (Hays et al., 2004a; Hays et al., 2006). The leatherback turtle thus performs the deepest dives (>1200 m) of any marine reptile, as well as routine dives generally shallower than 200 m and shorter than 25 min (Bradshaw et al., 2007; Houghton et al., 2008). Although the physical and physiological adjustments to this flexible diving behaviour are well understood, behavioural mechanisms associated with this strategy are still not clear. Most information on the fine-scale diving behaviour of this species comes from time-depth recorders and video cameras deployed on females during inter-nesting periods that have revealed typical underwater activities, such as

subsurface swimming, V- and U-shaped dives that varied in depth and duration and associated changes in swimming speed, vertical velocity and flipper stroke rates (Eckert, 2002; Reina et al., 2005; Fossette et al., 2007).

Here, we deployed tri-axial acceleration data loggers on female leatherbacks nesting on St Croix, US Virgin Islands in an attempt to understand how the diving strategy in these deep-diving reptiles compared with that of marine birds and mammals. We examined the relationships between dive depth and duration, body angle, stroke pattern and partial dynamic body acceleration (PDBA) as a proxy for the rate of energy expenditure (Wilson et al., 2006; Green et al., 2009; Gleiss et al., 2010) to test several hypotheses regarding the diving strategy of leatherbacks: (1) do leatherbacks control lung volume when diving?; (2) are they able to regulate lung volume to achieve neutral buoyancy at an intended dive depth as do other sea turtle species?; and (3) have they evolved behavioural adaptations in addition to physical and physiological adaptations to deal with decompression hazards when performing repeated deep dives?

MATERIALS AND METHODS

Field site and instrument deployment

The study was conducted in May 2007 in the northern Caribbean Sea at Sandy Point National Wildlife Refuge, St Croix, US Virgin Islands ($64^{\circ}54' \text{W}$, $17^{\circ}41' \text{N}$). Sandy Point National Refuge supports approximately 200 nesting leatherback turtles annually (Garner and Garner, 2009). The location of this colony provides a unique opportunity for the study of deep-water diving by leatherbacks. Indeed, the depth of the waters surrounding Sandy Point reaches 1000 m within 4 km of the nesting beach, potentially allowing leatherbacks to execute deep dives during the nesting season.

Five leatherbacks were equipped during the inter-nesting period with tri-axial acceleration data-loggers ['Daily diaries', dimensions $120 \times 20 \times 35$ mm, mass 90 g (Wilson et al., 2008)]. Three loggers either failed to record any data or recorded data for only the first few hours of the inter-nesting interval. However, this period is not considered stereotypical of leatherback diving behaviour, and hence these datasets were not analysed. Devices were set to record all acceleration channels at a frequency of 8 Hz and pressure at 2 Hz (0.05 m depth resolution). Devices measured acceleration in three orthogonal planes: heave (dorso-ventral acceleration), sway (lateral acceleration) and surge (anterior-posterior acceleration). Tri-axial acceleration data were recorded with 22-bit resolution in a 128 Mb flash RA memory with an absolute accuracy nominally better than $\pm 0.06 \text{ g}$. Device output was calibrated [to be converted to real g (9.8 m s^{-2})] by rotating the device through known angles in all orthogonal planes.

Devices were attached directly to the central dorsal ridge of the carapace (cf. Fossette et al., 2008a) by feeding 2 mm diameter, coated stainless steel wire through two holes in the ridge, ~ 6 cm apart, and crimping them together into two loops around the device and its base. The base of the device was constructed from platinum silicone putty (Equinox TM Series; www.smooth-on.com) to form a streamlined and snug fit to the top of the central ridge of the animal. The entire process took ~ 10 min and was undertaken during oviposition. Neither animal displayed any sign of discomfort during the attachment. Following recapture of the animals, the loggers were removed and the data downloaded.

Data analysis

Data were analysed using Origin Pro 8 (Origin Lab, Northampton, MA, USA) and custom-written software. For both turtles, the start- and end-time, the maximum depth, the duration of the

descent–bottom–ascent phases and the rates of descent and ascent were recorded for arbitrarily selected ‘shallow’ dives – that is, between 60 and 150 m ($N=45$ dives) and all deep dives – that is, >150 m ($N=36$ dives).

Acceleration data-loggers measure both dynamic acceleration (i.e. due to animal movement) and static acceleration (acceleration due to the Earth’s gravity). Dynamic acceleration of the heave signal was used to identify flipper beats of the turtles (cf. Shepard et al., 2008). We visually detected all individual flipper movements during each dive and defined the flipper beat duration as one complete sinusoidal cycle between acceleration maxima. Using the intervals between consecutive flipper beats, we calculated the instantaneous and the mean flipper beat frequency during descents and ascents.

We visually identified the start of the gliding phase during descents and ascents when cyclic variations in the dynamic heave, representing flipper strokes, were no longer detectable. This was done by one person (S.F.) to remove inter-observer variation. In order to validate this visual method, the periodic properties of dynamic acceleration of the heave signal of 15 randomly selected dives were analysed using Ethographer (Sakamoto et al., 2009) with Igor Pro 6.0 (Wavemetrics). This technique uses continuous wavelet transformation to identify the dominant cycle frequency of flipper beats, with gliding phases indicated where the wavelet transformation does not detect a dominant frequency (see, for example, Fig. 1). Each dive was therefore divided into four phases (Fig. 1): active descent (from the surface to the start of the gliding phase), gliding descent (from the start of the gliding phase to the maximum depth of the dive), active ascent (from the maximum depth of the dive to the start of the gliding phase) and gliding ascent (from the start of the gliding phase to the surface) (Fig. 1).

Body pitch was defined as the angle between the main body axis and the horizontal, with negative pitch angles being downwards directed and positive angles upwards directed. Pitch angles were derived from the arcsine of $\cdot g$, where $\cdot g$ is the static acceleration in the surging acceleration (anterior–posterior acceleration) (Yoda et al., 2001; Sato et al., 2003; Wilson et al., 2008). Static acceleration

was derived by calculating the weighted average following the method of Shepard and colleagues (Shepard et al., 2008).

Partial dynamic body acceleration (PDBA_{yz})

Acceleration data were first smoothed over 4 s (cf. Shepard et al., 2008) to yield static acceleration, which was then subtracted from total acceleration in each individual channel to yield dynamic acceleration (Wilson et al., 2006). Heaving and swaying dynamic acceleration were converted to absolute values and summed to yield the partial dynamic body acceleration of the y (heave) and z (sway) planes (PDBA_{yz}) (Halsey et al., 2008). PDBA_{yz} correlates with metabolic rate (Wilson et al., 2006; Halsey et al., 2008; Green et al., 2009) and therefore constitutes a proxy for the rate of energy expenditure (e.g. Gleiss et al., 2010). We examined the variation in PDBA_{yz} during the dives and defined the start of the gliding phases when PDBA_{yz} variations dropped off to values near zero.

Statistical analyses were carried out using SPSS 16.0 statistical software (SPSS, Chicago, IL, USA). Linear and nonlinear regressions were performed for each individual dataset to describe the relationships among diving parameters. Relationships were considered statistically significant when $P<0.05$.

RESULTS

General dive characteristics

A total of 61 and 20 dives from turtles T1 and T2, respectively, were analysed. Mean depths and durations (\pm s.d.; range) of the 81 dives were 151.8 ± 68.9 m (46.2–63.9 m) and 17.3 ± 3.2 min (3.6–11.1 min) for the two turtles, respectively (Table 1). Dive duration significantly increased with dive depth in T1 ($R^2=0.49$, $N=61$ dives, $P<0.01$), but the relationship was not significant in T2 ($R^2=0.06$, $N=20$ dives, $P>0.05$).

A consistent behavioural pattern within dives was found in both individuals. Turtles started diving at steep angles (mean \pm s.d. = -41.0 ± 6.8 deg; Table 1) and stroked continuously at the beginning of the dives, with a mean flipper beat frequency of 17.5 ± 1.8 strokes min^{-1} (Fig. 1). Pitch angle during the active descent

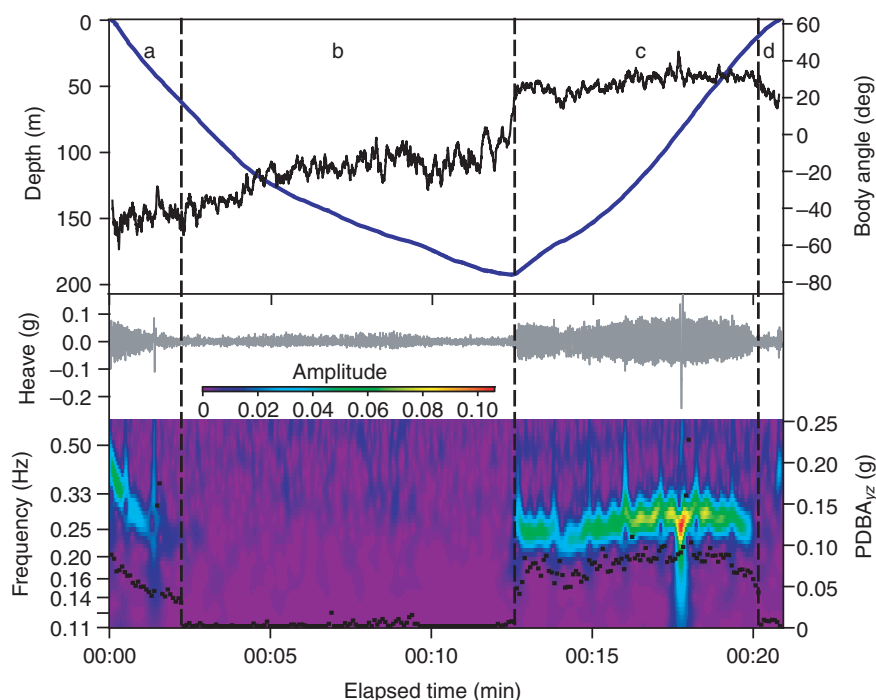


Fig. 1. Typical dive made by a female leatherback turtle (T1) during her inter-nesting period in the US Virgin Islands showing the variations in body angle (black line) and dive depth (blue line) (upper panel), heave acceleration (middle panel), flipper beating (amplitude and frequency, coloured scale inset) and partial dynamic body acceleration (PDBA_{yz}, black dots) (lower panel) throughout the dive (see Materials and methods for details). Vertical broken lines indicate the different phases of the dive: (a) active descent, (b) gliding descent, (c) active ascent and (d) gliding ascent.

Table 1. Summary of diving data for two female leatherback turtles during their inter-nesting period in the US Virgin Islands

| | T1 | T2 |
|---|-------------|-------------|
| Date of tag deployment | 18 May 2007 | 18 May 2007 |
| Standard curvilinear carapace length (cm) | 159.5 | 163.5 |
| Clutch rank | 5th | 5th |
| Number of dives analysed | 61 | 20 |
| Depth (m) | 151.3±76.1 | 153.3±41.7 |
| Duration (min) | 17.2±2.8 | 17.7±4.4 |
| Depth at initiation of gliding down (m) | 42.4±20.4 | 25.9±10.1 |
| Depth at initiation of gliding up (m) | 12.9±3.1 | 15.3±4.0 |
| Duration of gliding down (min) | 7.8±2.1 | 9.5±1.5 |
| Duration of gliding up (min) | 0.8±0.2 | 2.2±4.2 |
| Active descent rate (m s ⁻¹) | 0.43±0.11 | 0.52±0.09 |
| Gliding descent rate (m s ⁻¹) | 0.24±0.13 | 0.22±0.06 |
| Active ascent rate (m s ⁻¹) | 0.35±0.13 | 0.49±0.12 |
| Gliding ascent rate (m s ⁻¹) | 0.28±0.09 | 0.23±0.10 |
| Pitch angle during active descent (deg) | -38.8±6.8 | -46.5±4.6 |
| Pitch angle during gliding down (deg) | -20.6±9.1 | -23.8±9.1 |
| Pitch angle during active ascent (deg) | +20.9±4.4 | +27.8±5.4 |
| Pitch angle during gliding up (deg) | +21.1±4.1 | +13.1±5.6 |

T1, turtle 1; T2, turtle 2.
Values are means ± s.d.

increased significantly with the maximum depth of the dive (T1, $R^2=0.20$, $N=61$ dives, $P<0.01$; T2, $R^2=0.20$, $N=20$ dives, $P<0.01$; Fig. 2). The flipper beat frequency decreased as the descent progressed. Beat frequency typically dropped by ~30% during the active phase of each dive, from 0.37 ± 0.02 Hz to 0.26 ± 0.01 Hz (i.e. ~22 beats min⁻¹ down to ~16 beats min⁻¹; Fig. 1). T1 and T2 stopped stroking and began gliding at 42.4 ± 20.4 m (i.e. $28.6\pm 7.7\%$ of the maximum depth) and 25.9 ± 10.1 m ($17.3\pm 5.4\%$ of the maximum depth), respectively (Table 1). The gliding phase ended as turtles reached the maximum depth of the dive and started swimming up with a mean stroke frequency of 0.30 ± 0.02 Hz (i.e. ~18 beats min⁻¹) and a mean pitch angle of $+25.6\pm 4.7$ deg (Fig. 1). Pitch angle during the active ascent phase of the dives increased significantly with the maximum depth of the dive (T1, $R^2=0.56$, $N=61$ dives, $P<0.001$; T2, $R^2=0.35$, $N=20$ dives, $P<0.01$; Fig. 2). During the ascent, turtles started gliding at relatively shallow depths (12.9 ± 3.1 m and 15.3 ± 4.0 m for T1 and T2, respectively; Table 1) and at shallow angles ($+21.1\pm 4.1$ deg and $+13.1\pm 5.6$ deg for T1 and T2, respectively; Table 1 and Fig. 1).

Gliding descent

The depth at which turtles started gliding down increased significantly (T1, $R^2=0.63$, $N=61$ dives, $P<0.001$; T2, $R^2=0.23$, $N=20$ dives, $P<0.01$) and nonlinearly with the maximum depth of the dives,

reaching a plateau for T1 at ~80 m for dives deeper than 250 m (Fig. 3). Mean duration of the gliding phase was 8.3 ± 2.0 min and significantly increased with the duration of the descent phase in both turtles (T1, $R^2=0.92$, $N=61$ dives, $P<0.001$; T2, $R^2=0.97$, $N=20$ dives, $P<0.001$; Fig. 4). The percentage of time spent gliding during the descent was thus constant (mean±s.d.= $85.2\pm 6.7\%$ of the descent duration) regardless of the maximum depth of the dive. Pitch angle and vertical velocity during the gliding phase increased significantly with increasing dive depth (T1, $R^2=0.70$, $N=61$ dives, $P<0.001$; T2, $R^2=0.55$, $N=20$ dives, $P<0.001$ for pitch, and T1, $R^2=0.76$, $N=61$ dives, $P<0.001$; T2, $R^2=0.39$, $N=20$ dives, $P<0.001$ for vertical velocity; Fig. 3). In addition, for T1, pitch angle and vertical velocity during the gliding phase were significantly higher when the turtle started gliding at deeper depths ($N=61$ dives, $R^2=0.44$, $P<0.001$ for pitch, and $R^2=0.46$, $P<0.001$ for vertical velocity; Fig. 5). For T2, only the vertical velocity during the gliding phase increased when the turtle started gliding at deeper depths ($N=20$ dives, $R^2=0.26$, $P<0.01$; Fig. 5).

Gliding ascent

The depth at which T1 started gliding during the ascent increased significantly ($N=61$ dives, $R^2=0.32$, $P<0.001$) and nonlinearly with the maximum depth of the dives, reaching a plateau at ~18 m for dives deeper than 250 m (Fig. 3). This relationship was not significant for T2 ($N=20$ dives, $R^2=0.03$, $P=0.474$; Fig. 3). The mean duration of the gliding phase was 0.9 ± 0.4 min (i.e. $13.4\pm 6.5\%$ of the ascent duration) and increased significantly with the duration of the ascent phase, although the correlation coefficients were low (T1, $R^2=0.09$, $N=61$ dives, $P<0.05$; T2, $R^2=0.28$, $N=20$ dives, $P<0.05$; Fig. 4). Pitch angle and vertical velocity during the gliding phase increased significantly with increasing dive depth (T1, $R^2=0.35$, $N=61$ dives, $P<0.01$; T2, $R^2=0.29$, $N=20$ dives, $P<0.01$ for pitch, and T1, $R^2=0.50$, $N=61$ dives, $P<0.01$; T2, $R^2=0.50$, $N=20$ dives, $P<0.01$ for vertical velocity; Fig. 3). In addition, for T1, pitch angle and vertical velocity during the gliding phase were significantly higher when the turtle started gliding at deeper depths ($N=61$ dives, $R^2=0.12$, $P<0.01$ for pitch, and $R^2=0.18$, $P<0.01$ for vertical velocity; Fig. 5). There was no significant relationship between these parameters for T2 ($P>0.05$, Fig. 5).

PDBA_{yz} during dives

Variation of PDBA_{yz} throughout a dive showed a similar pattern to flipper beating (Fig. 1). PDBA_{yz} decreased as the descent progressed and then dropped off to values near zero (during gliding) until the maximum depth of the dive was reached. PDBA_{yz} increased during the ascent and remained high until the turtle was at 10–20 m from the surface, where it suddenly dropped off (again during gliding) to values near zero. We found a significant positive relationship

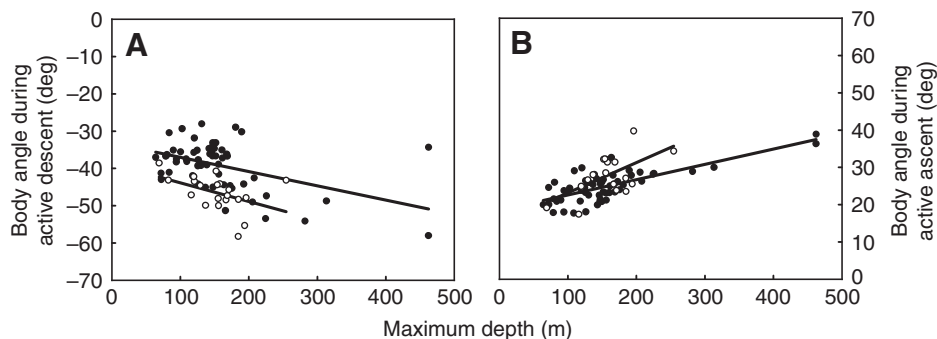


Fig. 2. Relationships between maximum depth of the dive and body angle during the (A) active descent and (B) active ascent of dives recorded for two female leatherback turtles (filled circles: turtle T1, $N=61$ dives; open circles: turtle T2, $N=20$ dives) during their inter-nesting period in the US Virgin Islands. Regression fits are shown in each graph for significant relationships. (A) T1: $y=-0.04x-33.2$; T2: $y=-0.05x-38.9$. (B) T1: $y=0.04x+18.5$; T2: $y=0.08x+15.1$.

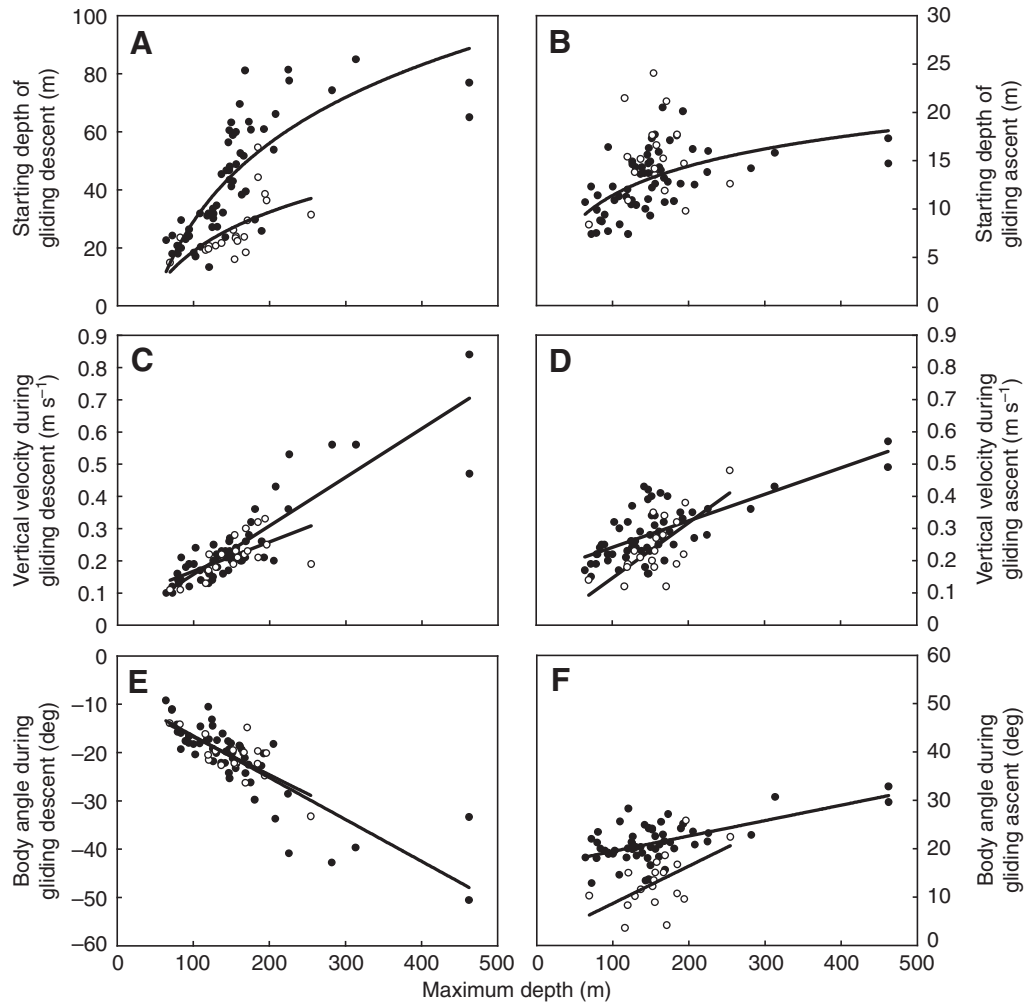


Fig. 3. Relationships between maximum depth of the dive and the depth at which the gliding phase began, vertical velocity and body angle during descent (A,C,E) and ascent (B,D,F) of dives recorded for two female leatherback turtles (filled circles: turtle T1, $N=61$ dives; open circles: turtle T2, $N=20$ dives) during their inter-nesting period in the US Virgin Islands. Regression fits are shown in each graph for significant relationships. (A) T1: $y=38.9\ln(x)-150.1$; T2: $y=16.3\ln(x)-55.3$. (B) T1: $y=4.4\ln(x)-8.7$. (C) T1: $y=0.002x+0.008$; T2: $y=0.001x+0.077$. (D) T1: $y=0.001x+0.16$; T2: $y=0.002x-0.03$. (E) T1: $y=-0.09x-7.9$; T2: $y=-0.08x-8.9$. (F) T1: $y=0.03x+16.3$; T2: $y=0.08x+0.95$.

between the starting depths of the gliding phases inferred from both methods (i.e. variation in $PDBA_{yz}$ vs visual analysis of flipper beats) during the descent (Spearman's correlation, $\rho=0.83$, $P<0.01$) and the ascent ($\rho=0.91$, $P<0.01$). There were significant differences in $PDBA_{yz}$ between the different phases of a dive (Kruskal-Wallis test, $H_3=35.4$, $P<0.001$). $PDBA_{yz}$ during the active ascent was significantly higher than during the three other phases (active and gliding descent and gliding ascent) (mean \pm s.d.= 0.08 ± 0.01 g, $P<0.001$). $PDBA_{yz}$ during the active descent was significantly higher than during both descending and ascending gliding phases (mean \pm s.d.= 0.05 ± 0.009 g, $P<0.001$). There was no significant difference in $PDBA_{yz}$ for the two gliding phases of the dive

(mean \pm s.d. during gliding descent= 0.01 ± 0.016 g, mean \pm s.d. during gliding ascent= 0.01 ± 0.013 g, $P=0.31$). There were significant positive relationships between maximum dive depth and $PDBA_{yz}$ during the active descent ($\rho=0.61$, $P<0.05$) and ascent ($\rho=0.71$, $P<0.01$) phases of the dives.

DISCUSSION

Our data are the first to relate buoyancy regulation and locomotory activity in the deepest-diving reptile, the leatherback turtle, which can be put into context in light of the different diving strategies employed by deep-diving vertebrates in general. While we only recorded data from two individuals, both animals had the same

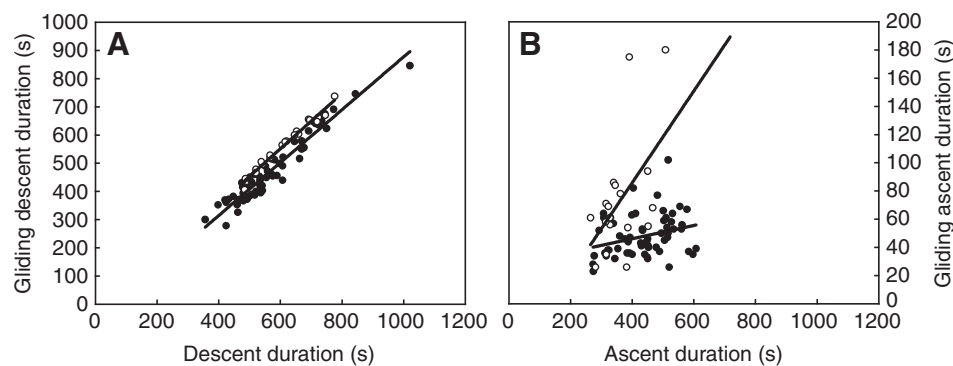


Fig. 4. Relationships between (A) the duration of the descent and of the gliding phase during the descent, and (B) the duration of the ascent and of the gliding phase during the ascent of dives recorded for two female leatherback turtles (filled circles: turtle T1, $N=61$ dives; open circles: turtle T2, $N=20$ dives) during their inter-nesting period in the US Virgin Islands. Regression fits are shown in each graph for significant relationships. (A) T1: $y=0.94x-60.5$; T2: $y=0.98x-36.1$. (B) T1: $y=0.05x+27.4$; T2: $y=0.33x-44.4$.

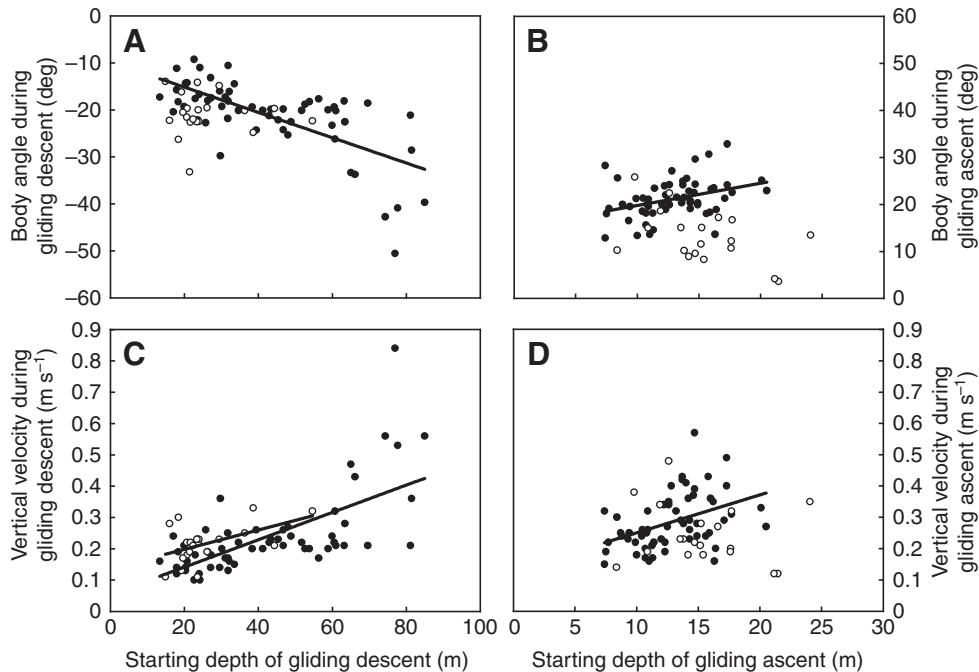


Fig. 5. Relationships between the starting depth of the gliding phase, the vertical velocity and the body angle during gliding descent (A,C) and gliding ascent (B,D) of dives recorded for two female leatherback turtles (filled circles: turtle T1, $N=61$ dives; open circles: turtle T2, $N=20$ dives) during their inter-nesting period in the US Virgin Islands. Regression fits are shown in each graph for significant relationships. (A) T1: $y=-0.27x-9.8$. (B) T1: $y=0.47x+15.1$. (C) T1: $y=0.004x+0.05$; T2: $y=0.003x+0.14$. (D) T1: $y=0.012x+0.13$.

diving patterns and showed all the characteristic dive profiles previously documented for leatherbacks at the US Virgin Islands and at other nesting sites (Eckert, 2002; Reina et al., 2005; Fossette et al., 2007). In addition, given that diving constraints are based primarily on universal physical laws, we expect individuals of the same species to have evolved similar strategies to deal with these constraints (Wilson et al., 1992; Hays et al., 2004b; Yasuda and Arai, 2009). Hence, despite our small sample size, we are confident that our results and conclusions will apply broadly to this species.

An inhaling deep diver

Most deep-diving vertebrates exhale before submergence and thus attain negative buoyancy at a constant depth during dives irrespective of the maximum depth attained. For example, Williams and colleagues (Williams et al., 2000) reported a very consistent pattern between dives for three marine mammal species, with animals starting to glide at depths of ~ 86 m, regardless of the maximum depth of the dive. Consequently, the time spent gliding during the descent increases with increasing dive depth. Contrary to many deep divers (Williams et al., 2000; Sato et al., 2003; Mitani et al., 2009), but similar to sperm whales and beaked whales (Miller et al., 2004; Tyack et al., 2006), leatherback turtles dive upon inhalation (Lutcavage et al., 1992; Reina et al., 2005). Accordingly, in this study, turtles started gliding down at deeper depth for deeper dives and thus spent a constant percentage of time gliding during the descent ($\sim 85\%$), regardless of maximum depth. Although they probably maximise their oxygen stores by inhaling, measures of $PDBA_{yz}$ during the active descent suggest that they are exposed to high energetic costs during this phase of the dives. Indeed, diving turtles initially actively swam down at relatively steep angles (~ 40 deg), with a mean stroke frequency of ~ 0.32 Hz (i.e. 19 strokes min^{-1}), presumably to overcome initial positive air-mediated buoyancy and minimise time in this energetically costly phase. Accordingly, high-speed swimming at the beginning of the dives had been recorded previously for female leatherbacks at the same nesting site (Eckert, 2002). In accordance with decreasing buoyancy with increasing depth (due to increasingly compressed

lung volumes), the flipper beat frequency and amplitude both decreased by $\sim 30\%$ by the time both individuals began gliding. Exactly this phenomenon has been shown in hard-shelled turtles (e.g. Hays et al., 2007). Conversely, both leatherbacks were active for most of the ascent, with beat frequencies of ~ 0.30 Hz (18 strokes min^{-1}). At shallow depths (~ 14 m), they started gliding up until they reached the surface. The mean flipper beat frequency of both leatherbacks deduced from the dorso-ventral acceleration was similar to the frequency measured by Reina and colleagues (Reina et al., 2005) using video images (i.e. 0.29 ± 0.03 Hz) from free-swimming female leatherbacks during their inter-nesting interval in Costa Rican waters. These results also match the general diving pattern reported for hard-shelled turtles (e.g. Hays et al., 2004c; Hays et al., 2007; Yasuda and Arai, 2009), marine mammals (e.g. Skrovan et al., 1999) and seabirds (e.g. Lovvorn et al., 2004).

The depth at which the gliding phase starts during descent is expected to be deeper than the true depth at which neutral buoyancy is attained, and *vice versa* during ascent (Davis and Weihs, 2007). In our study, the maximum depth at which the gliding phase began was 83 m for descent and 21 m for ascent for T1 and 52 m for descent and 25 m for ascent for T2. It is interesting to note that these values are close to those predicted for complete lung collapse in sea turtles (Berkson, 1966). In addition, this suggests that the maximum depth of neutral buoyancy of these leatherbacks diving with fully inflated lungs is probably situated half-way between 21 m and 83 m deep for T1 (i.e. ~ 52 m) and between 25 m and 52 m deep for T2 (i.e. ~ 38 m). This discrepancy between descent and ascent in the depth at which the gliding phase starts has already been described in hard-shelled turtles (Hays et al., 2007; Yasuda and Arai, 2009) and deep-diving mammals (Skrovan et al., 1999; Williams et al., 2000) and is due to the fact that glides can only be initiated once the buoyant force along the movement paths exceeds drag force, and this point can be substantially deeper if the animal is gliding at a low pitch-angle (Davis and Weihs, 2007), as is the case with the leatherbacks in our study. Another reason for the discrepancy might be that the consumption of lung oxygen during the dive results in pulmonary

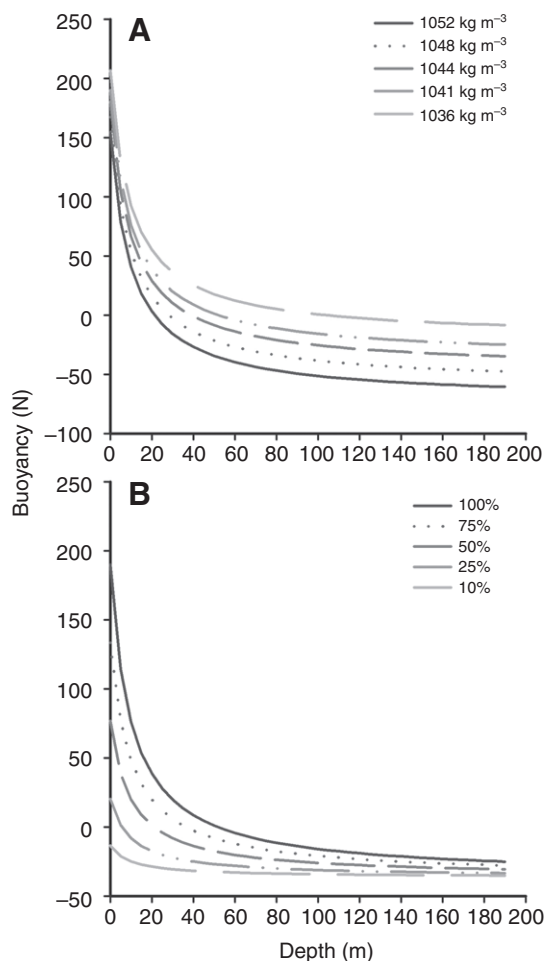


Fig. 6. Theoretical changes in buoyancy with depth in a leatherback turtle of mass 350 kg with a maximum initial lung volume of 64 ml kg^{-1} (Lutcavage et al., 1992) (A) diving with lungs fully inflated and a body density of 1056 kg m^{-3} (unbroken black line), 1051 kg m^{-3} (dotted black line), 1046 kg m^{-3} (black dashed line), 1041 kg m^{-3} (dashed-dotted grey line), 1036 kg m^{-3} (grey dashed line) and (B) with a fixed body density of 1041 kg m^{-3} and diving with lungs inflated at 100% (unbroken black line), 75% (dotted black line), 50% (black dashed line), 25% (dashed-dotted grey line) and 10% (grey dashed line). Buoyancy (N) was derived following Boyle's law and Archimedes' principal [for detailed equations, see Wilson et al. (Wilson et al., 1992)]. Note that, following lung collapse, air can move from the lungs to the upper airways (Bostrom et al., 2008).

gas loss and thus a decrease in buoyancy provided by the lungs during the ascent (Hochscheid et al., 2003). This might result in a shallower depth of neutral buoyancy, although this might be partly mitigated by corresponding increasing CO_2 volumes in the lung.

We found a difference between individuals in the mean starting depth of the gliding descent that is probably caused by differing body densities of the two individuals. If we consider that the point at which a typical 350 kg leatherback achieves neutral buoyancy is $\sim 50 \text{ m}$ (as observed in T1), with a maximum initial lung volume of 64 ml kg^{-1} – that is, 0.0224 m^3 (Lutcavage et al., 1992) – this would imply a body density of $\sim 1041 \text{ kg m}^{-3}$ (assuming seawater to have a density of 1030 kg m^{-3} ; Fig. 6A). If neutral buoyancy is achieved at $\sim 40 \text{ m}$ (as observed in T2), body density is expected to be more – that is, 1044 kg m^{-3} (Fig. 6A). Thus, the maximum depth of neutral buoyancy is probably indicative of body condition. Temporal

changes in such, particularly in amounts of lipid, are common in marine animals (e.g. Georges and Guinet, 2000; Biuw et al., 2003), and these have major impacts on buoyancy owing to the low density of fatty tissue (Schmidt-Nielsen, 1997). This subsequently affects diving patterns, including the modulation of stroking and gliding (Watanabe et al., 2006) and vertical velocity (Webb et al., 1998) in pinnipeds. Interestingly, in this study, there was no difference in the standard curvilinear carapace length (SCCL) or the number of egg clutches laid at the time of tag deployment between turtles, two parameters potentially linked with body condition (Table 1). However, it has previously been reported that body mass and body condition do vary between individuals (Georges and Fossette, 2006) and throughout the nesting season (J. Y. Georges and S.F., unpublished) in the leatherback turtle. This has also been reported in green turtles (Hays et al., 2002) and is expected to impact their diving patterns during inter-nesting intervals at sea as well. Indeed, diving characteristics could potentially be used to estimate body condition in leatherbacks, in a manner similar to that used in pinnipeds (Biuw et al., 2003; Watanabe et al., 2006).

Regulation of lung volume

As the turtles performed deeper dives, the depth at which gliding was initiated increased in tandem with body angles and vertical velocities during the active descent, suggesting that turtles might have been buoyed up by a larger air volume in their lungs during deeper dives. Accordingly, there were positive relationships between maximum dive depth and PDBA_{yz} during the active descent of the dives, suggesting that turtles are forced to increase their swimming effort during deeper dives to overcome increased buoyancy. This suggests that leatherbacks control their inspired air-volume according to the intended dive depth in a manner similar to that of hard-shelled sea turtles and seabirds (Minamikawa et al., 2000; Wilson, 2003; Cook et al., 2010). If we consider a typical 350 kg leatherback with a body density of $\sim 1041 \text{ kg m}^{-3}$, the point at which neutral buoyancy is achieved would vary between ~ 10 and 50 m for lungs inflated between 25% and 100% (Fig. 6B). In addition, leatherbacks appear to adjust their initial body angles and vertical velocities to descend quicker and at a steeper angle. This minimises the time spent travelling through the zone of highest buoyancy, thus reducing the overall energetic cost of diving with inflated lungs (Wilson, 2003; Yasuda and Arai, 2009; Cook et al., 2010; Wilson et al., 2010).

Despite many species of marine vertebrate modulating dive characteristics according to dive function (e.g. Wilson et al., 1996), only a few species are known to regulate their buoyancy according to the exploited depths (Minamikawa et al., 2000; Sato et al., 2002; Wilson, 2003; Hays et al., 2004b; Cook et al., 2010). Penguins regulate their inspired air volume in order to maximise foraging time during the bottom phase of the dives (Wilson, 2003), whereas green turtles maximise the time spent resting at the depth of neutral buoyancy (Hays et al., 2004b). By regulating their inhaled air-volume to the intended dive depth, leatherbacks might optimise the costs and benefits of buoyancy during dives and, notably, might modulate their depth of neutral buoyancy over a few tens of meters and therefore the time spent passively gliding during the descent of the dives. According to our results, during the nesting season in the US Virgin Islands, turtles seemed to regulate the amount of inspired air and thus glide passively an average of 85% of the time during the descent of any dive. During the inter-nesting intervals in the US Virgin Islands and at other nesting sites, deployment of mouth-opening sensors on gravid female leatherbacks has revealed rhythmic mouth opening during the descent of dives (Eckert, 2002;

Myers and Hays, 2006; Fossette et al., 2008b). This behaviour might allow turtles to use gustatory cues to sense their immediate environment and might be associated with foraging attempts (Myers and Hays, 2006). Animals commonly stop locomotory activity to sample their environment, as it increases the capacity of the sensory systems to detect relevant stimuli (Kramer and McLaughlin, 2001). Therefore, we suggest that turtles might use the advantage of negative buoyancy to increase the efficiency of their sensory systems for searching for prey while gliding, and a similar advantage could be exploited by other (non-reptilian) marine animals during glides.

Although V-shaped dive profiles are a relatively common feature of leatherbacks during their inter-nesting interval, most other species of turtle exhibit primarily U-shaped dives. It is likely that, during the inter-nesting interval, energy conservation is one of the primary drivers behind movement strategies, allowing turtles to divert surplus energy to developing their eggs. V-shaped dives in elephant seals (*Mirounga angustirostris*) have been shown to be the most energy-efficient dive strategy – that is, they result in the longest extension of the aerobic dive limit, owing to the large proportion of the dive spent gliding (Davis and Weihs, 2007). Thus, if leatherbacks are only opportunistically searching for a scarce resource (Myers and Hays, 2006), minimisation of dive costs are possibly central to a successful nesting season. Most other inhaling divers do so to select neutral buoyancy at a given foraging or resting depth. Although this might be energetically more expensive than a V-shaped dive in terms of locomotory cost (Davis and Weihs, 2007), it allows the maximisation of time spent at foraging or resting depth and thus foraging efficiency or energy conservation (Minamikawa et al., 2000; Sato et al., 2002; Wilson and Zimmer, 2004). Leatherbacks dive primarily shallowly in their high-latitude and coastal foraging grounds, and, according to our results, they would be able to attain neutral buoyancy (Fig. 6), which would benefit foraging efficiency [i.e. (surface+transit time)/time at foraging depth]. Deployment of accelerometers and high-resolution TDRs at foraging grounds will shed light on this issue and reveal whether leatherbacks inhale relatively more air to dive to the same depth as in the V-shaped dives we analysed here, which would provide them with neutral buoyancy. This behavioural plasticity might be crucial for this species to be able to balance the different physiological and energetic requirements of feeding either on deep-scattering gelatinous zooplankton or on shallow-water scyphozoan jellyfish (James and Herman, 2001; Hays et al., 2004a; Fossette et al., 2010). Flexibility in inspired air-volume might also give turtles more flexibility for dealing with potential changes in body condition, and thus buoyancy, throughout their migratory cycle.

Behavioural adaptations for dealing with decompression hazards

In this study, the body angles of both turtles during ascent were low ($\sim +26$ deg), as were the vertical velocities (~ 0.40 m s⁻¹), although they both increased with increasing maximum depth. Slow ascents near the surface might allow more time to scan for predators, given that the surface is generally a risky place for divers because of increased visibility due to surface silhouetting and reduced escape options (e.g. Glen et al., 2001). However, this behaviour might also help turtles to reduce the negative physiological and mechanical effects of gas expansion in the lungs or other tissues by slowly ascending to the surface. In the face of physical and physiological constraints due to hydrostatic pressure changes during breath-hold dives, deep divers have indeed evolved

behavioural and/or physiological adaptations to minimise the associated risks. Leatherbacks seem to fit the pattern shown by some marine mammals such as the northern bottlenose whale, *Hyperoodon ampullatus* (Hooker and Baird, 1999), and the beluga whale, *Delphinapterus leucas* (Martin and Smith, 1992), of diving upon inhalation and performing slow ascents to help reduce the risks of decompression sickness. This behavioural mechanism is coupled to several physical – for example, small collapsible lungs and compressible trachea (Lutcavage and Lutz, 1997; Davenport et al., 2009) – and physiological – for example, large blood and muscle oxygen stores (Lutcavage et al., 1992) and cardiovascular adjustments during diving (Southwood et al., 1999) – adaptations that might decrease the susceptibility of animals to the bends (Kooyman and Ponganis, 1998; Fahlman et al., 2006). However, body angles and vertical velocities during the ascent increased with increasing maximum depth, contradicting this hypothesis. This suggests that avoidance of the bends is probably not the only function of this behaviour. Beyond this, we note that, during the inter-nesting period, the body temperatures of female leatherbacks vary between 28.7°C and 31.1°C [i.e. 2–5°C above ambient water temperature (Southwood et al., 2005)] and are thus $\sim 10^\circ\text{C}$ lower than typical endotherm core body temperatures. The solubility of gases in liquids increases with decreasing temperatures (Weiss, 1970), which means, in the case of nitrogen, an increase in solubility of $\sim 20\%$ between 37°C and 27°C, so that leatherbacks will have a correspondingly decreased risk of bubble formation during decompression than endotherms operating at their higher body temperatures. Thus, ectotherms should be more tolerant to decompression sickness than endotherms, and this might explain the capacity of leatherbacks to perform serial dives to depths >150 m and, exceptionally, dives deeper than 1000 m (Houghton et al., 2008).

CONCLUSIONS

Contrary to many deep divers, but in a manner similar to that of other sea turtle species, the leatherback turtle dives upon inhalation and appears to regulate buoyancy through lung volume. This probably allows it higher plasticity in diving behaviour and energetics to deal with the diverse foraging conditions encountered during the migratory cycle (Hays et al., 2004a; James et al., 2005; Hays et al., 2006). Despite the dangers of decompression sickness that inhalation engenders, behavioural and physiological adaptations, some of them specific to marine ectotherms, seem to reduce the associated risks and might allow leatherbacks to perform repeated deep dives. Further experiments investigating the impacts of body composition changes or body temperature on diving strategy should help us better understand variations both between individuals and throughout the migratory cycle of this extraordinary marine reptile.

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