

The role of infrequent and extraordinary deep dives in leatherback turtles (*Dermochelys coriacea*)

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SUMMARY

Infrequent and exceptional behaviours can provide insight into the ecology and physiology of a particular species. Here we examined extraordinarily deep (300–1250 m) and protracted (>1 h) dives made by critically endangered leatherback turtles (*Dermochelys coriacea*) in the context of three previously suggested hypotheses: predator evasion, thermoregulation and exploration for gelatinous prey. Data were obtained via satellite relay data loggers attached to adult turtles at nesting beaches ($N=11$) and temperate foraging grounds ($N=2$), constituting a combined tracking period of 9.6 years ($N=26,146$ dives) and spanning the entire North Atlantic Ocean. Of the dives, 99.6% ($N=26,051$) were to depths <300 m with only 0.4% ($N=95$) extending to greater depths (subsequently termed 'deep dives'). Analysis suggested that deep dives: (1) were normally distributed around midday; (2) may exceed the inferred aerobic dive limit for the species; (3) displayed slow vertical descent rates and protracted durations; (4) were much deeper than the thermocline; and (5) occurred predominantly during transit, yet ceased once seasonal residence on foraging grounds began. These findings support the hypothesis that deep dives are periodically employed to survey the water column for diurnally descending gelatinous prey. If a suitable patch is encountered then the turtle may cease transit and remain within that area, waiting for prey to approach the surface at night. If unsuccessful, then migration may continue until a more suitable site is encountered. Additional studies using a meta-analytical approach are nonetheless recommended to further resolve this matter.

Key words: diving behaviour, gelatinous zooplankton, jellyfish, diel vertical migration, foraging, migration.

INTRODUCTION

Deep diving behaviour is well documented for a wide range of air-breathing marine vertebrates including pinnipeds (e.g. Le Boeuf et al., 1988; Sato et al., 2002), penguins (e.g. Kooyman et al., 1992; Ryan et al., 2004) and cetaceans (e.g. Hooker and Baird, 1999; Amano and Yoshioka, 2003). Such behaviours are typically associated with foraging deep in the water column or at the seabed, yet dives well beyond the usual depth range (i.e. extraordinary deep dives) are rarely considered explicitly as an important behavioural component. Nevertheless, it is known that exceptional behaviours may provide insights into performance maxima for species and reveal previously hidden aspects of their behavioural ecology. Indeed, infrequent and extraordinarily deep dives may provide tantalising insights into the ecology of air breathing marine vertebrates, although establishing the exact role of such behaviours is not easy as they may occur infrequently and in remote locations (Boyd, 1999).

An intriguing example of infrequent and extraordinary deep dives is found in leatherback turtles (*Dermochelys coriacea* Blainville 1816), which possess a highly adapted respiratory and cardiovascular physiology for prolonged and deep diving (>1 h, >1200 m) (Lutcavage et al., 1992; Hays et al., 2004a; Wallace et al., 2005), yet range infrequently below the epipelagic zone. Given this apparent inconsistency between physiological capabilities and behaviour, the exact nature of exceptionally deep dives in leatherbacks remains unclear. For other deep divers such as elephant

seals (*Mirounga leonina*) and sperm whales (*Physeter macrocephalus*), excursions into deep waters appear to play a more central role within their foraging ecology and occur far more frequently (Watkins et al., 1993; Watkins et al., 2002; Slip et al., 1994; McConnell and Fedak, 1996). Indeed, data-logger deployments have recently identified prey search and prey capture at great depths by deep-diving sperm whales (Watwood et al., 2006). Thus, if deep dives to similarly extreme depths have a critical function for other air-breathers but not leatherbacks, why do leatherbacks perform them? This question has generated considerable interest amongst sea turtle biologists and has led to the formulation of numerous hypotheses that, until recently, have been difficult to test empirically (Eckert et al., 1986; Eckert et al., 1989; Davenport, 1998).

Unravelling the function of deep dives in leatherbacks therefore constitutes a long-standing goal for sea turtle biologists as this exceptional behaviour has been recorded at tropical breeding grounds for many years (e.g. Eckert et al., 1986; Eckert et al., 1989; Mrosovsky, 1987; Eckert, 2002; Myers and Hays, 2006; Fossette et al., 2008). Nevertheless, it is difficult to extrapolate behaviours observed throughout the breeding season to the rest of the year given a distinct behavioural plasticity whereby diving behaviour changes markedly once turtles move into open oceanic waters (Hays et al., 2004a). The opportunity to consider deep dives in this broader context, however, has been made possible through

the development of satellite relay data loggers (SRDLs; Sea Mammal Research Unit, University of St Andrews, Fyfe, Scotland) (e.g. Bennett et al., 2001; Sparling and Fedak, 2004; Hays et al., 2004a; Biuw et al., 2007) that convey not just location, but information regarding the diving behaviour and corresponding environmental conditions *via* the Argos network. Utilising this technological advance, we set out to revisit three specific hypotheses put forward to explain the role of exceptionally deep dives in this species. (1) Rates of descent between exceptionally deep and more typical dive events were compared to explore the idea of deep evasive dives, with further consideration of how the ensuing post-dive recovery periods at the surface might increase detection by predators. (2) Water temperatures experienced by leatherbacks during their transit to great depths were examined to revisit the idea that they may serve some thermoregulatory function at warmer latitudes. (3) The temporal and spatial patterns of deep diving during different migratory phases were mapped to examine the potential benefits of such behaviour for prey detection and acquisition on transit to principal foraging grounds.

MATERIALS AND METHODS

Instrument deployment

Movements and behaviour of migrating leatherback turtles were determined using SRDLs. These devices provide information not simply on location but also on a host of variables including dive depth and water temperature. Twelve SRDLs were deployed upon leatherback turtles at two sites over 4 years (Table 1). Three transmitters were attached to nesting females on Levera Beach, Grenada, West Indies (12.1°N, 61.7°W) in 2002 with a further eight devices deployed from the same site in 2003. One transmitter was attached to a female turtle at sea off the Dingle Peninsula in County Kerry, Ireland (52.24°N, 10.30°W) in July 2005, with a second transmitter deployed on a male in June 2006 (Table 1).

For all but the 2006 deployment, transmitters were attached to turtles using a soft harness system (Hays et al., 2004a; Myers and Hays, 2006). For the 2006 deployment, direct attachment was used involving drilling three small holes through the median dorsal ridge. A transmitter glued to a highly streamlined catamaran-style base plate (designed to sit either side of the ridge) was attached using biodegradable, plastic cable ties that were passed through the holes. For a full description of this method see Doyle et al. (Doyle et al., 2008).

Deriving movements from satellite data

SRDLs were located with the Argos system (<http://www.clsamerica.com>; <http://www.argos-system.org>). Each Argos location is provided with a measure of its accuracy, called the location class. Location classes A, B and 0 are the least accurate, and classes 1, 2 and 3 are the most accurate (e.g. Hays et al., 2001) and were the only ones used in this study. These movement data have been the focus of numerous previous studies (e.g. Hays et al., 2004a; Hays et al., 2004b; McMahon et al., 2005; Hays et al., 2006) and are only included here as a reference for the location of specific diving behaviours (Fig. 1).

Dive data

Owing to the limited bandwidth of the Argos system, depth was relayed to an accuracy within 2 m for dives to 65 m, and within 4 m for dives between 65 m and 128 m, decreasing to ~30 m for dives >500 m [see Myers et al. for a validation of dive profiles relayed *via* the Argos satellite system (Myers et al., 2006)]. Using bespoke software, these depth data were analysed onboard the SRDL prior to transmission. Data for individual dives were generated when the depth exceeded 10 m. Start times for dives were determined by salt-water switches on the SRDL that perceived the transmitter was fully submerged, with the end of the dive defined when the transmitter again broke the surface or a depth <2 m was recorded. To account for drift in the recording of depth values, SRDLs perform a zero-point calibration on-board by re-setting their internal zero-offset whenever the saltwater switch detected that the device was at the surface, i.e. ensuring that a depth of zero metres is recorded for this time (Myers and Hays, 2006).

Once a dive was completed, onboard software examined the dive profile and determined the time and depth of the five most prominent points of inflection during the dive. The time and depth of these five points, together with the time of the end of the dive and dive duration were then transmitted. To ensure effective transmission of data, information for each dive was stored within a buffer on the SRDL so that it would be transmitted randomly for the next 10 days. In this way, the specific dive profiles obtained *via* the Argos system were not simply a function of the surfacing behaviour of the turtle immediately subsequent to each dive (Hays et al., 2004a). A dive number accompanied the depth and time data for each dive, so that it was possible to determine the number of dive profiles that were not received *via* Argos.

Table 1. Overview of dive data obtained from 13 SRDL deployments for leatherback turtles

PTT no.	Turtle no.	Deployment date	Deployment location	No. of days tracked	No. of dives recorded	No. of deep dives recorded	Maximum depth (m)	% of dives >300 m	Mean \pm s.d. depth of all dives (m)
15119	1	10 July 2002	Grenada, WI	376	2329	9	474.0	0.4	58.2 \pm 53.8
15120	2	09 July 2002	Grenada, WI	13	245	0	166.0	0.0	49.7 \pm 40.7
15121	3	05 July 2002	Grenada, WI	323	2616	4	626.0	0.2	48.7 \pm 52.4
4394	4	15 June 2003	Grenada, WI	180	1862	4	1010.0	0.2	61.6 \pm 57.7
4395	5	18 June 2003	Grenada, WI	247	2467	24	946.0	1.0	66.1 \pm 75.1
21914	6	28 June 2003	Grenada, WI	406	918	6	658.0	0.7	68.0 \pm 66.4
21915	7	19 May 2003	Grenada, WI	358	1787	12	882.0	0.7	69.0 \pm 60.6
21920	8	06 April 2003	Grenada, WI	322	4527	16	722.0	0.4	69.0 \pm 53.1
21923	9	31 March 2003	Grenada, WI	517	1911	6	506.0	0.3	46.1 \pm 47.5
29358	10	09 July 2003	Grenada, WI	241	3655	4	562.0	0.1	50.9 \pm 49.8
29359	11	06 July 2003	Grenada, WI	2	17	0	80.0	0	40.1 \pm 17.9
49818	12	31 August 2005	Co. Kerry, Ireland	313	1558	0	182.0	0	32.5 \pm 28.1
66360	13	29 June 2006	Co. Kerry, Ireland	220	2293	9	1250.0	0.4	40.6 \pm 57.8

PTT, platform terminal transmitter (each given an identifying code); SRDL, satellite relay data logger.

Turtles were located at Levera Beach, Grenada, West Indies (12.1°N, 61.7°W) or at sea off the Dingle Peninsula in County Kerry, Ireland (52.24°N, 10.30°W).

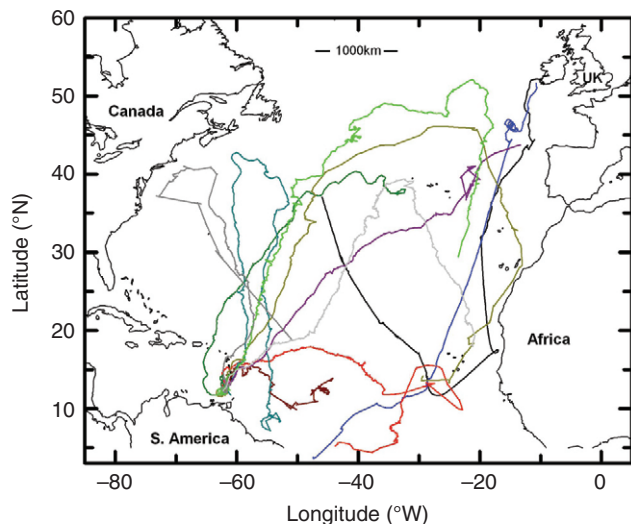


Fig. 1. Movements of 12 leatherback turtles tracked between 2002 and 2006. Composite figure based on previously published work (Hays et al., 2004a; Hays et al., 2006; McMahon and Hays, 2006; Doyle et al., 2008). All tracks originate in Grenada with the exception of the two turtles tracked from the west coast of Ireland, shown in black (2005) and dark blue (2006).

In conjunction with data for individual dives, a summary of all dive information for 6 h periods was also generated by each SRDL. Each summary period contained data for a range of parameters including (1) percentage of time spent at the surface (i.e. saltwater switch was dry for longer than 10 min); (2) percentage of time spent shallower than 10 m; (3) percentage of time spent deeper than 10 m; (4) mean depth of dives to over 10 m; (5) mean dive duration for dives to over 10 m; and (6) maximum depth attained. Although SRDLs include a speed sensor, this always rapidly clogged and ceased to function, so these limited data are not considered here.

Classification of deep dives

A frequency histogram of maximum dive depth was constructed for all dives recorded by each turtle combined ($N=26,146$ dives; Fig. 2). Data were broken down into 100 m depth bins, revealing that 99.6% of all dives ($N=26,051$) were to depths <300 m with only 0.4% ($N=95$) extending to greater depths. In this paper the term 'deep dives' therefore refers to all dive events >300 m (Fig. 2).

Determining local time of sunrise and sunset

The time of each deep dive was converted from GMT to local time by using the interpolated longitude for where each dive occurred. Day length and the time of sunrise and sunset (i.e. when the sun was at zero degrees elevation) were calculated for the interpolated position of each dive using bespoke online software (<http://www.csgnetwork.com/sunriset.html>).

Determining vertical rate of descent during deep dives

Vertical descent rate was calculated from the five points of inflection assigned to each dive profile. This was achieved in two ways. First, the depth of the first point of inflection (D_1) was divided by the time it took the turtle to reach this depth (T_1). However, the first point of inflection can occur at varying stages along the descent phase and may therefore not be consistently representative of the overall vertical rate of descent down to the maximum depth. A second approach was therefore also adopted whereby the deepest

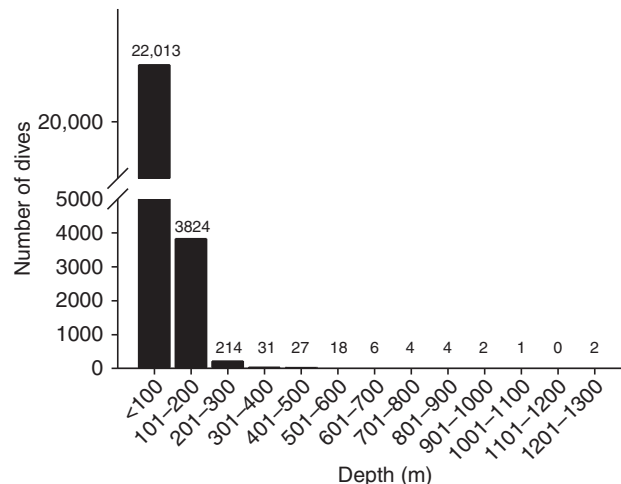


Fig. 2. Frequency histogram of all dives completed by the 13 turtles combined, where maximum depth data were available ($N=26,146$ dives).

point of inflection (D_{\max}) was divided by the corresponding time it took to reach this depth.

Temperature data

A detailed description of how SRDLs measure water temperature is given in McMahon et al. (McMahon et al., 2005). Temperature and depth (pressure) were sampled at 1 Hz, and the results averaged into 1 dbar bins (1 dbar increase in pressure being equivalent to 1 m of seawater; 1 dbar is 10 kPa). Twelve depth–temperature points were obtained for each profile.

RESULTS

Overall movements of turtles

The combined movements for the 13 leatherback turtles are given in Fig. 1. This constitutes a total of 3518 days of tracking data (Table 1) spanning substantial areas of the northern Atlantic Ocean. Full consideration of these tracking data has been published previously (Hays et al., 2004a; Hays et al., 2004b; Hays et al., 2006; Doyle et al., 2008) and is included here purely for reference.

Overview of dive data

The following generic data for the 13 tracked turtles are given in Table 1: (1) total number of dives recorded; (2) maximum depth; (3) number of deep dives recorded; (4) percentage of all recorded dives >300 m; and (5) mean depth of all dives. From a total of 26,145 individual dives recorded, 4949 were <10 m, which is below the threshold at which points of inflection are recorded during dives. For these dives only maximum depth data are available. For the 21,196 dives >10 m the mean maximum dive depth for all animals combined was 52.9 m (s.e.m., 0.35 m). The deepest dive, to 1250 m, was conducted by turtle 13, the large male tracked from County Kerry in Ireland on 30 December 2006 (18.58°N, 25.79°N). To further ascertain whether our proxies of descent rate (i.e. rate to D_1 and D_{\max}) were appropriate for all dives >10 m, we plotted each profile in turn ($N=21,196$ dives) prior to analysis. This revealed a marked uniformity in the shape of the dive profiles (i.e. they were of a similar V-shaped profile with brief bottom times and direct descent and ascent phases) rendering the classification of dives into different profile types (e.g. Houghton et al., 2002; Reina et al., 2005) unnecessary. Interestingly, the distinct U-shaped dive profiles detailed by Reina and colleagues (attributed to brief periods of sea

bed resting) were not identified during this preliminary analysis (Reina et al., 2005). This is perhaps understandable as this previous study suggested this unusual leatherback behaviour reflected the constrained bathymetry surrounding their study site.

Vertical rate of descent and duration of deep dives

To test for irregularities in deep-diving behaviour that may be indicative of periodic threats or predator evasion, the rate of descent was determined for all dives where five points of inflection were recorded ($N=20,497$ dives). Significant, yet weak, linear relationships were found between maximum dive depth and the rate of descent to D_1 ($F_{1,20496}=0.001$, $r^2=0.26$, $P<0.0001$) and D_{\max} ($F_{1,20496}=2391$, $r^2=0.09$, $P<0.0001$). To further elucidate these two relationships, data were classified into 100 m bins of dive depth (e.g. 0–100 m, 101–200 m) and mean rates of descent were calculated (Fig. 3). The midpoint of each depth bin (e.g. 50 m, 150 m) was then plotted against the mean rate of descent for that bin, revealing highly significant log-normal relationships for descent to D_1 ($F_{3,5}=23.11$, $r^2=0.93$, $P<0.0001$; Fig. 3A) and D_{\max} ($F_{3,5}=121.78$, $r^2=0.98$, $P<0.0001$; Fig. 3B).

Next, to test whether a slower vertical rate of descent during deep dives manifested itself in an increased duration, mean durations (± 1 s.d.) were determined for each of the 100 m depth bins used to derive vertical descent rates (Fig. 3C). Bradshaw and colleagues (Bradshaw et al., 2007), working from the same SRDL data set, used the maximum duration of dives at different depths to infer the aerobic dive limits (ADL), defined by Kooyman and colleagues as the dive duration beyond which blood lactate levels begin to rise above resting levels (Kooyman et al., 1980). The mean maximum ADL for the nine leatherback turtles considered was 37.6 ± 6.1 min (c.v., 16%) and ranged from 19.2 to 48.1 min (Bradshaw et al., 2007). This maximum ADL is shown on Fig. 3C, revealing that dives >800 m appear to be anaerobic, yet dives between 300 and 800 m largely fall within the aerobic diving capabilities for the species. The accumulation of lactate resulting from anaerobic respiration requires an air-breathing diver to spend time recovering at the surface between long dives (Thompson and Fedak, 1993), and this is expressed as a positive relationship between dive duration and post-dive surface intervals (Costa et al., 2001). SRDLs provide numerous measures of diving behaviour (for details, see Hays et al., 2004a; McMahon et al., 2007), but not all consecutive dive profiles are measured. Where data were available, therefore, we reconstructed dive profiles leading up to and following deep dives greater than 800 m and the inferred maximum ADL of 48.1 min (where data were available $N=5$ dives; Fig. 4). As suspected, each deep dive was followed soon after by a prolonged post-dive surface interval (mean, 2.1 ± 0.85 h; maximum, 2.61 h; minimum, 1.04 h) supporting the inference that such events are anaerobic (Fig. 4C). These times at the surface could represent resting or might possibly encompass periods of extremely shallow swimming (Eckert, 2002). Nonetheless, the salient point remains that repeated bouts of diving beyond 2 m were not evident for protracted periods of time following anaerobic dives, with the overall inference that oxygen debts needed to be repaid.

Temperatures experienced during deep dives

It has previously been suggested that diving behaviour may serve some thermoregulatory function in leatherback turtles (Paladino et al., 1990; Wallace et al., 2005; Southwood et al., 2005). To assess the range of temperatures experienced by leatherback turtles during rare and exceptional deep dives (>300 m), we examined the temperature–depth data from the SRDLs. To avoid issues of inter-

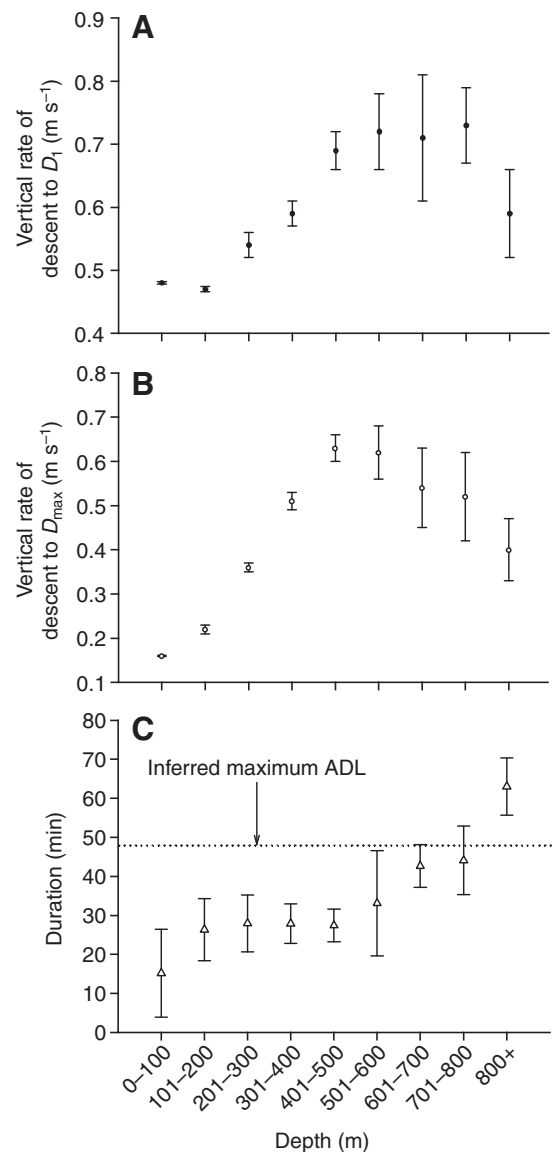


Fig. 3. (A) Mean (± 1 s.d.) vertical rate of descent to the first point of inflection (D_1) for all turtles combined, classified into 100 m depth bins ($N=22,085$ dives); (B) mean (± 1 s.d.) vertical rate of descent to the deepest point of inflection (D_{\max}) for all turtles classified into 100 m depth bins ($N=21,196$ dives). For both parts of the figure all data are from dives displaying five points of inflection. (C) Dive depth versus dive duration for dives where data were available ($N=21,196$ dives). Dotted line shows maximum inferred aerobic dive limit (ADL) for leatherbacks (Bradshaw et al., 2007).

annual variation we considered data for the 2003 Grenada deployments in isolation. In total, temperature–depth records were available for 1544 dives between 4 and 52°N . Unfortunately a software malfunction within the on-board software coded all data from depths >500 m as a single value of 500 m, rendering all data in excess of this depth invalid (i.e. analysis could only be conducted for data <500 m). Once this error had been taken into account, valid temperature–depth data were available for 147 dives >300 m but <500 m. Examples of nine temperature profiles from increasing latitudes are given in Fig. 5A, revealing that, independent of latitude, water temperature typically decreases very slowly below 350 m. Using the power relationships derived from each profile, predictions

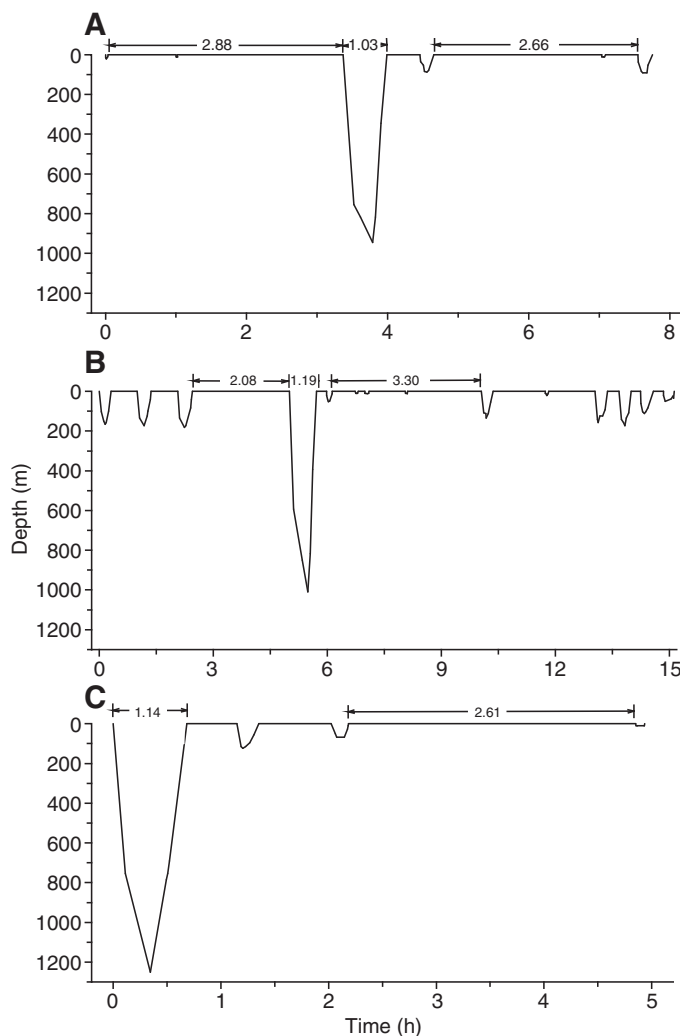


Fig. 4. Satellite relay data logger (SRDL) dive profiles showing deep-diving behaviour. (A) Turtle 5 (platform terminal transmitter, PTT no. 4935) 23 July 2003, 25.54°N, 58.85°W, 946 m; (B) turtle 4 (PTT no. 4934) 13 August 2003, 24.41°N, 60.81°W, 1010 m; (C) turtle 13 (PTT no. 66360) 30 November 2006, 18.58°N, 25.79°W, 1250 m (the deepest dive ever recorded for the species). Arrowed numbers represent duration in hours for pre-dive, dive and post-dive surfacing events.

of water temperature at 50 m intervals were made. The rate of thermal change through the water column (ΔT) was determined as the decrease of temperature within a 50 m depth band, confirming that, in each case, the rate of temperature decrease slowed significantly below 350 m (Fig. 5B).

Temporal patterns in deep-diving behaviour

The timing of deep-diving events was converted from GMT to local time, revealing a normal distribution (Kolmogorov–Smirnov test, $P=0.07$) in daily time of occurrence. A Gaussian 3-parameter curve was then fitted, revealing a peak in occurrence just after midday ($F_{2,20}=63.93$, $r^2=0.86$, $P<0.0001$; Fig. 6).

Spatial patterns in deep-diving behaviour

Deep dives were recorded throughout the entire North Atlantic Ocean (Fig. 7A). The greatest number of deep dives recorded for an individual turtle was 24 (turtle 8), with a minimum of 0 recorded for three individuals (turtles 2, 11 and 12), although turtle 11 was

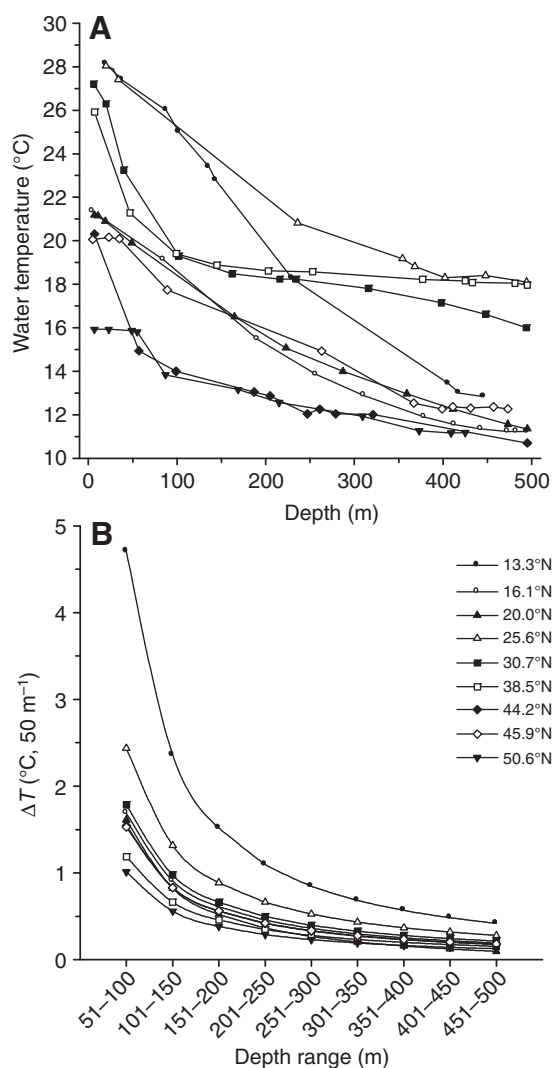


Fig. 5. (A) Each profile represents temperature data gathered from an individual turtle during a single dive. Data are given in raw format to demonstrate how profiles varied with latitude (marked in the key to the side of the figure). (B) Rate of temperature change (ΔT , °C) at 50 m depth intervals based upon power relationships derived from the temperature profiles given in A.

only tracked for a period of 2 days (Table 1). The apparent weighting of deep dives towards lower latitudes reflects the bias of data towards the Caribbean and proximate tropical Atlantic given that 11 of the 13 turtles were tracked from Grenada. This is compounded by the fact that post-nesting females may only reach the more productive waters of the northern Atlantic during the autumn months when decreasing water temperatures or shifting prey fields may truncate their residency and drive the animals further south (Ferrari et al., 2004; Houghton et al., 2006a; McMahon and Hays, 2006). To account for this bias, deep dive data were normalised by taking into account the number of dive profiles recorded within different 4° latitudinal bands (e.g. 4.00–7.99°N; Fig. 7B). This revealed a highly significant log-normal relationship showing that deep dives were not uniformly distributed throughout the northern Atlantic with a peak occurring between 15 and 30°N ($F_{2,11}=31.64$, $r^2=0.88$, $P<0.0001$).

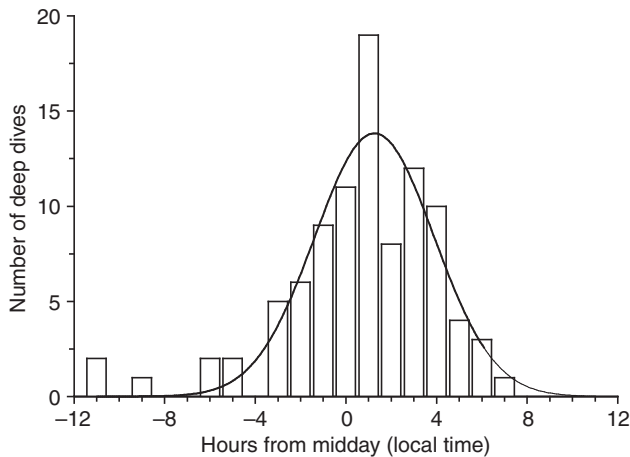


Fig. 6: Frequency distribution of all dives >300 m ($N=95$) revealing a peak in occurrence just after midday.

Deep diving during different phases of migration

'Distance from home' data (i.e. distance from the deployment site) were plotted against time for all post-nesting turtles leaving their breeding grounds in the Caribbean (Fig. 8). Unfortunately, for two turtles (turtles 4 and 5; Table 1) these data were incomplete and were therefore excluded from the analysis. Additionally, the male and female turtles tracked from Dingle (turtles 12 and 13) were not included as their stage within the 2–3 year reproductive cycle was not known, rendering comparison with post-nesting individuals impossible. For the six remaining turtles, post-nesting migrations were divided into four separate phases: (1) the internesting interval (i.e. movements within the Caribbean between subsequent nesting events); (2) the transit phase (i.e. movements from breeding to foraging sites in the northern or eastern tropical Atlantic); (3) the resident phase (signified by the end of the transit phase at which point individuals remain for protracted periods within specific oceanic or coastal areas); and (4) the post-residence phase (i.e. movements away from residence areas). These phases were defined using a simple criterion for distance from home. For example, interesting intervals were defined as the time from transmitter deployment to the time the female left the Caribbean after her last nest. The transit phase began once the female had left the Caribbean until a time when the distance from home slowed to a rate of <50 km per week for two consecutive weeks. Once this minimum threshold was passed the turtle was said to be 'resident' in temperate waters. The post-residence phase was taken to begin once movements south were again >50 km per week for two consecutive weeks. Although this method captures the distinct phases of migration well, more robust analyses using switching state–space models are required for future studies (Jonsen et al., 2007). To assess how deep-diving behaviour varied between different phases of the migration, the maximum depths recorded during 6 h summary periods were plotted against time and distance from home (Fig. 8). Next, the proportion of 6 h periods with a maximum depth >300 m was determined for each turtle during each phase of the migration and arc-sin transformed. Data for both the internesting interval and transit phase were only available for three turtles (turtles 7, 8 and 9) as transmitters were deployed on the remaining turtles during their last nesting event of the season so that they commenced transit directly after re-entering the water. Student's t -tests revealed a slight increase in the number of deep dives during transit when compared with the internesting interval ($t=-2.25$, $P>0.05$). However, it should be noted that this

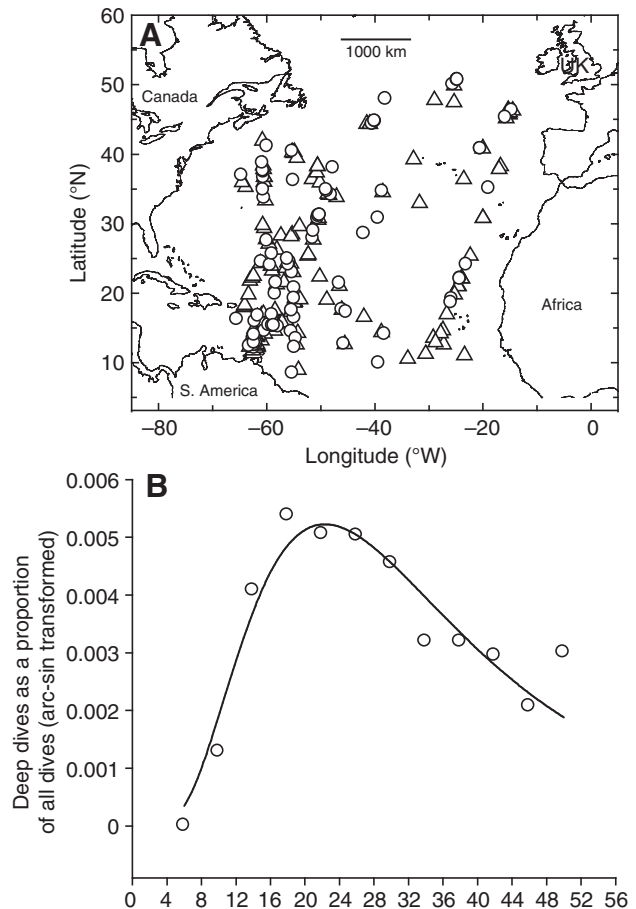


Fig. 7. (A) Spatial pattern of deep dives (>300 m) throughout the North Atlantic. Data from individual depth profiles are shown as open circles ($N=97$ dives). On occasion a maximum depth >300 m would be recorded in the summary data without an actual profile being recorded. To account for these events, all summary periods with maximum depths >300 m are shown as open triangles ($N=147$ periods). (B) The occurrence of deep dives as a proportion of the total number of dives recorded at different latitudes (combined into 4° bins). Data are given as mid-points for 4° latitude bins. The decreased occurrence of deep dives between 4.00 and 7.99°N should be interpreted with caution as data were only available for these latitudes from three of the 13 turtles.

behaviour was quite common during the internesting period. A more distinct behavioural shift was evident between transit and residence, with a significant decrease in the proportion of deep dives at the end of the transit period ($t_5=4.67$, $P=0.002$; Fig. 8). No such difference was detected between the residence and post-residence phases, although deep dives were recorded during the latter for two of the six turtles. Lastly, the proportion of deep dives was greater during transit than in the post-residence phase ($t_5=2.69$, $P<0.05$), although this was possibly a function of insufficient data for the latter as a result of decreasing transmitter efficiency with time.

DISCUSSION

The principal challenge for many migratory species is often how to cross large areas, such as deserts and oceans, without a suitable habitat for refuelling (Klasson, 1996). Such problems of prey availability may be further compounded by an increased risk of predation or exposure to sub-optimal environmental conditions, each in turn applying its own evolutionary pressure to the migrant. This

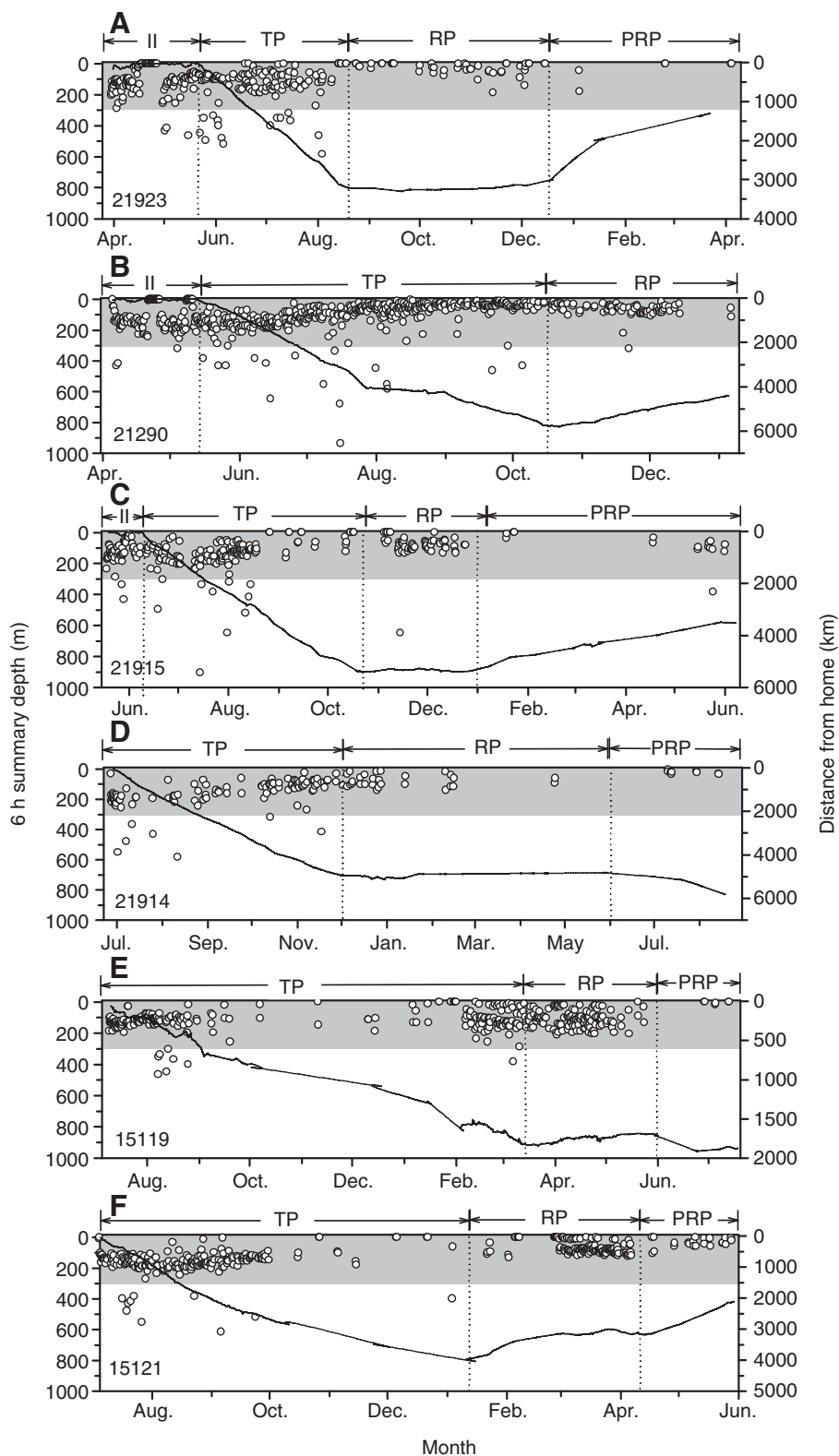


Fig. 8. The maximum depth recorded in 6 h summary periods for the entire tracking period are given for six turtles tracked from Grenada in 2002 and 2003 (PTT number given on individual figures). Depths <300 m are shaded on each figure to help identify deep dives according to our classification. Distance from home (i.e. Grenada) is also given on the secondary y-axis and denoted by a solid line. Time is classified into different stages of migration, which can be observed from changes in the distance from home data: II, interesting interval; TP, transit period; RP, residence period; PRP, post-residence period.

Predator avoidance

One of the earliest explanations put forward was that leatherbacks dive deeply to evade predators encountered *en route*. Certainly, they may be attacked by sharks (Keinath and Musick, 1993) or killer whales (*Orcinus orca*) around breeding sites in the Caribbean and whilst foraging in the northeast Pacific (Caldwell and Caldwell, 1969; Pittman and Dutton, 2004). However, Cropp documented essentially surface evasive behaviour in a leatherback turtle in the presence of a white shark, *Carcharodon carcharius* (Cropp, 1979). This included erratic diving, rolling at the surface and violent flailing of the turtle's flippers as it floated on its back. Even though this anecdotal evidence suggests that leatherbacks may not immediately dive to avoid predators, there is certainly a vertical and thermal overlap in range between white sharks and leatherbacks [adults recorded to depths of 980 m in waters as cold as 3–4°C (Bonfil et al., 2005)], although such studies of this predator in the Atlantic are currently lacking. Nevertheless, questions regarding evasive deep-diving behaviour in marine reptiles extend back much further than extant species, with Motani and colleagues speculating that ichthyosaur genera, with poor visual acuity at depth, may have contracted the bends during exceptionally deep predator avoidance dives (Motani et al., 1999). Extrapolating this idea to the present, there is some scope for suggesting that exceptionally deep dives in leatherback turtles may also reflect a periodic and exceptional predator avoidance response, especially as high partial pressures of carbon dioxide in the blood (through departure from normal diving patterns) have been recorded

scenario is clearly demonstrated by leatherback turtles, which often spend the greater part of any reproductive year transiting between jellyfish-rich temperate foraging grounds (Houghton et al., 2006a; Eckert, 2006; James and Herman, 2001) and jellyfish-poor nesting sites in tropical regions (James et al., 2005a, James et al., 2005b). Within this behavioural framework, the exact role of deep dives remains intriguing.

for sea turtles (Rothschild, 1991). However, our data suggest that this is not the case here. For example, during an evasive dive the vertical descent rate should logically be in excess of more typical behaviours within shallower waters (i.e. travelling or foraging dives), yet turtles appear to descend at a reduced rate for dives greater than 600 m (Fig. 3B). Additionally, the physiological demands of pushing beyond the ADL appear to require substantial pre-dive preparatory

and post-dive recovery periods at the surface (Costa et al., 2001) (Fig. 4) that would do little to alleviate the risk of predation. Although the exact nature of these post-dive surface (or near-surface) events is difficult to define, owing to the issues of resolving dive events <2 m (Eckert et al., 2002; Myers and Hays, 2006), an overall reduction in diving activity is clearly evident after deep dives. This may reflect one of the two strategies used by reptiles to reduce overall metabolic demands during periods of moderate to severe hypoxia (Hicks and Wang, 2004). Firstly, they can use behavioural reductions in preferred body temperature that, through the direct effect of temperature on biochemical processes (the 'Q₁₀ effect'), decreases the aerobic demands of the tissues. Secondly, at a constant body temperature, animals can actively down-regulate ATP demands (Hicks and Wang, 2004). So whether breathing at the surface or remaining fairly inactive in the top 2 m, the proposition that extremely deep dives elicit a metabolic and behavioural response in leatherbacks remains valid.

Some consideration must also be given to the possibility that leatherbacks dive to shed the transmitters themselves, which under natural scenarios might represent behaviour to dislodge commensal or parasitic species such as remoras (*Echeneis* spp.). This seems unlikely, however, as leatherbacks with only small time–depth recorders wired onto flipper tags have also been shown to exhibit deep-diving behaviour (Myers et al., 2006). Moreover, the inability of other turtle species to dive deeply, which may be prone to commensal organisms during oceanic transit phases (e.g. green turtles moving between Brazil and Ascension Island), suggests that this factor alone would be insufficient to explain the deep-diving behaviour described here. This reservation also extends to the documented behaviour of female sea turtles diving to dislodge male turtles during mating attempts (Reina et al., 2005). Although turtles clearly employ this strategy to avoid unwanted attention close to nesting sites (where mating takes place), the predominance of deep dives during post-reproductive migrations suggests this factor cannot explain the majority of such events.

Thermoregulation

The physiological adaptations of leatherback turtles (including low metabolic rate, large thermal inertia, blood flow adjustments and peripheral insulation) allow them to maintain elevated body temperatures in cold water and avoid overheating in the tropics (Paladino et al., 1990; Southwood et al., 2005; Wallace et al., 2005). The combined inference from previous studies is that leatherback turtles with increased activity levels (through nesting behaviour) might avoid overheating by increasing the proportion of time spent in cool waters, thus behaviourally moderating their body temperature by using cooler water as a heat sink (Paladino et al., 1990; Southwood et al., 2005; Wallace et al., 2005). In support of this concept, it has been shown that leatherback turtles spend the highest percentage of time in cooler waters in the early third of the internesting period, implying that increased heat loads incurred during nesting require shuttling to colder, deeper waters (Wallace et al., 2005). Therefore, could exceptionally deep dives be simply extreme examples of this cooling behaviour? Fig. 5B indicates that this is probably not the case as temperature decreases at a negligible rate below 350 m, implying that the opportunities to shed heat to the external environment would be only fractionally better deep in the water column (e.g. ≥800 m) than at more moderate depths (300–400 m), and would incur far greater transport costs. However, given the importance of swim speeds to metabolic rate, and thus heat generation (e.g. Southwood et al., 2005; Bostrom and Jones, 2007), this finding alone is not conclusive. Unfortunately, as the SRDL speed sensors all failed soon

after deployment (presumably through impeller clogging), it was not possible to conduct any analysis of directly measured swim speeds. This behavioural component should therefore be incorporated into future investigations of deep diving to thoroughly resolve the issue of their thermoregulatory potential. Moreover, such investigations should include direct measurements of leatherback body temperatures, dive behaviours, water temperatures, metabolic rates and blood flow simultaneously to provide the basis of an integrated bio-energetic model (Wallace and Jones, 2008).

Prey detection and acquisition

Attempts to locate prey might explain the decreased descent rate of dives >600 m, with turtles possibly surveying the water column as they descend. Certainly, for leatherbacks the occurrence of deep dives during the daytime supports the notion of speculative excursions in search of gelatinous zooplankton within the deep scattering layer (Eckert et al., 1989; Hays et al., 2006). This biological stratum comprises a wide range of potential prey items including siphonophores, salps and pelagic medusae (Barham, 1963; Barham, 1966; Michel and Foyo, 1976; Roe et al., 1984) that are often concentrated below 600 m during the day and move near the surface at night in response to diminishing light levels (Backus and Clarke, 1964; Eckert et al., 1989). Consequently, the idea that feeding, or attempted feeding (Myers and Hays, 2006; Fossette et al., 2008), takes place predominantly at night when prey are far more accessible is gaining acceptance (e.g. Eckert et al., 1989; Hays et al., 2004a; Hays et al., 2006; Jonsen et al., 2007). Put differently, the transit costs associated with deep daytime feeding may simply be too expensive as the gelatinous prey of leatherbacks would offer a minimal payback (Doyle et al., 2007). This notion of night-time feeding is supported by the visual adaptations of leatherbacks such as the concentration of ganglion cells in the superior temporal portion of the retina called the area temporalis. It is thought that leatherbacks probably use this concentrated area of visual cells to spot gelatinous zooplankton in the water column below them (Oliver et al., 2000). Additionally, it has been suggested that leatherbacks may use the bioluminescence of certain deep-sea gelatinous zooplankton, such as pyrosomes, to assist with locating suitable prey items (Davenport and Balazs, 1991). However, this suggestion prompts the question that if leatherbacks are perfectly capable of finding prey in low light levels, why do they simply not look for suitable patches at night, negating the requirement to dive to extreme depths during the day? The possible answer may relate to the dichotomy within leatherback diving behaviour whereby repeated dives to potential foraging sites occur during the night and extended periods of travelling occur during the day (Hays et al., 2004a; Hays et al., 2004b). Thus, the decisions of whether or not to keep moving or stay in a particular area need to be made during periods of transit (i.e. daylight hours) if leatherbacks are to maximise their rate of travel to more productive temperate waters. Although not ideal, the predominance of deep dives around midday certainly suggests that leatherbacks may make the best of a bad job by searching for prey when ambient light levels throughout the water column are at their greatest.

The notion of deep speculating dives during the internesting season comes, however, with a major caveat as it has been suggested that feeding may be suppressed in gravid sea turtles (Owens, 1980). This theory was indirectly supported by Reina and colleagues who integrated time–depth recorder data and video footage to investigate leatherback internesting behaviour in Pacific Costa Rica (Reina et al., 2005). During this study potential prey items such as scyphozoan jellyfish, ctenophores and salps in aggregations or singly were observed in the turtle's field of view at least once per hour in all

deployments but there were no visible indications of feeding activity. Alternatively, recent studies using beak-opening sensors have provided good, yet indirect, evidence to suggest that attempts to feed are indeed made, although further work to resolve feeding from drinking events are required (Myers and Hays, 2006; Fossette et al., 2008). Nevertheless, even if we accept that the issue of interesting foraging is unresolved, the key point remains that deep dives occur predominantly during transit to foraging grounds (where dietary suppression should not come into effect), yet cease to occur once the individual enters the residence stage (Fig. 8). This pattern is consistent with previous studies of migrating leatherbacks, which revealed a more generic shift between deeper, longer dives during transit (Jonsen et al., 2007; Reina et al., 2005) and extended periods of very shallow dives at high latitudes (Hays et al., 2006). Most probably, this behavioural plasticity represents a change in available prey from mid-water gelatinous zooplankton such as salps, siphonophores and pyrosomes during transit [found at 500–700 m during the day, rising to the top 100 m at night (Angel and Pugh, 2000)], to surface aggregations of medusae (e.g. Cnidaria: Scyphozoa) within temperate and coastal waters (James and Herman, 2001; Houghton et al., 2006a; Houghton et al., 2006b; Witt et al., 2007). Bringing all this evidence together, we therefore suggest that infrequent, exceptionally deep, daytime dives allow leatherbacks to assess whether adequate (nocturnally ascending) prey are present at depth and are not foraging dives in their own right.

Viewed in a migratory context, our findings suggest that if suitable resources are encountered during a deep dive then the turtle may cease transit and remain within that area, waiting for prey to approach the surface at night. If unsuccessful, then migration may continue with deep dives being employed periodically to assess the water column. This idea is compliant with the findings of Doyle and colleagues who recorded the long-term residence (76 days) of a leatherback within a meso-scale feature in the temperate north east Atlantic (Doyle et al., 2008). Upon leaving this inferred 'prey patch' there was a distinct change in the turtle's behaviour characterised by numerous deep dives (>500 m) over a 2 week period. Whether foraging conditions had deteriorated or the turtle had simply wandered out of a suitable patch is unknown, yet once the period of deep-diving behaviour ended the turtle began to move south at a significant rate (67.2 km day^{-1}) implying a decision to abandon searching for prey at high latitudes.

To conclude, leatherback turtles appear not to fit the general model of migration when responses to prey are suppressed during transit (Hays et al., 2006), but operate as 'income breeders' (Jonsson, 1997) supplementing their existing reserves *en route* until some threshold prey abundance is surpassed. Within this context, deep exploratory dives appear to play an important role in prey location, particularly during periods of extensive transit. However, further studies are required to address this theory, perhaps through a meta-analytical approach combining information on deep dives from leatherbacks at different geographic locales. Further empirical data are also required on the mid- and deep-water prey fields available to leatherback turtles so that the potential rewards of exploratory deep dives can be more clearly defined. For example, if leatherback turtles were merely adapted to feed upon epipelagic jellyfish aggregations found at temperate latitudes, then the evolutionary pressure would lie in getting back to such areas as quickly and efficiently as possible and not in the ability to dive to great depths. Furthermore, as leatherbacks spend significant time away from temperate shelf waters, where the abundance of jellyfish medusae is greatest, it seems evident that mid-water prey may form a more integral part of their diet than once thought.

LIST OF ABBREVIATIONS

ADL	aerobic dive limit
D_1	depth to first point of inflection during dive descent
D_{\max}	depth to deepest point of inflection during dive descent
T_1	time to first point of inflection during dive descent
T_{\max}	time to deepest point of inflection during dive descent
GMT	Greenwich mean time
PTT	platform terminal transmitter
SRDL	satellite relay data logger
ΔT	rate of temperature change ($^{\circ}\text{C}$)

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