

Satellite tracking reveals unusual diving characteristics for a marine reptile, the olive ridley turtle *Lepidochelys olivacea*

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ABSTRACT: The movements, diving behaviour and thermal environment occupied by 4 adult female olive ridley turtles *Lepidochelys olivacea* in northern Australia were determined through satellite telemetry. Patterns of behaviour recorded were rather unusual compared to other sea turtles in that dives were mainly deep, largely benthic and exceptionally long (>2 h) in some cases, characteristics typical of over-wintering turtles in colder environments. One individual occupied shallow coastal foraging zones, while the others foraged far from land (probably on the seabed) in relatively deep water (>100 m). Individuals performed long dives (frequently >100 min), but from the short post-dive intervals we suggest that these dives were mainly aerobic. Maximum dive depth recorded was 200 ± 20 m (mean maximum depths ranged from 20.1 to 46.7 m across individuals; $n = 17\,328$ dives in total; depths ≥3 m were considered 'dives') and the maximum duration was 200 ± 20 min (mean durations ranged from 24.5 to 48.0 min across individuals). Temperature profiles indicate that turtles experienced temperatures ranging from 23 to 29°C at the surface, with the lowest temperature recorded (18.7°C) at a depth of 98 m. Only 6.9% of the dives were in water <20°C. From time-allocation at depth (TAD) scores, we demonstrated that many dives reaching the known or inferred sea bottom were U-shaped, but there was no apparent diel signal in dive depth. This suggests that many benthic dives were not associated exclusively with resting behaviour and likely had a foraging component as well. The ability to perform long benthic dives allows this species to exploit deeper benthic environments in addition to the shallow coastal areas more generally occupied by adult hard-shelled sea turtles (e.g. green and hawksbill turtles). Deep benthic dives also occur in certain marine mammals (e.g. narwhals) and sea birds (e.g. rockhopper penguins) and therefore seem to be a general foraging strategy exploited by animals that can perform long dives.

KEY WORDS: Aerobic metabolism · Benthic diving · Foraging strategy · Habitat selection · Movement · Northern Australia · Satellite-relayed data loggers · Temperature profiles

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INTRODUCTION

Phenotypic plasticity, a characteristic occurring in a wide variety of taxa (Tollrian & Harvell 1999), allows an organism to shift its response to different environmental conditions (Bradshaw 1965) via modifications in morphology, physiology and behaviour (Gabriel et al. 2005). As such, species with generalist diets, variable foraging behaviours and many reproductive stra-

tegies tend to be buffered from catastrophic environmental shifts that put specialist species at a higher risk of extinction when population sizes are low (Pimm 1991, McKinney 1997, Kotze & O'Hara 2003). In the marine environment, plasticity in foraging behaviour and diet has been demonstrated for many different higher vertebrate taxa including seabirds (Votier et al. 2004), marine mammals (Thompson et al. 1997, Harcourt et al. 2002) and some fish species

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(Ellis et al. 1996, Garrison & Link 2000, Bellwood et al. 2006).

Many species of marine turtles, on the other hand, are thought to have rather specialist dietary requirements and consequently, relatively predictable foraging strategies; although some species occasionally undergo pronounced ontogenetic niche shifts (Bjorndal 1997, Salmon et al. 2004, Seaborn et al. 2005). This may be a particularly important aspect of their life history and may help to explain their susceptibility to human activities (many species are Red-Listed with the International Union for Conservation of Nature and Natural Resources (IUCN), www.iucnredlist.org), because the over-exploitation of specific marine habitats on which foraging turtles depend may reduce carrying capacity. For example, adult hawksbill turtles *Eretmochelys imbricata* rely heavily on sponges within shallow coral reef systems (Meylan 1988, Leon & Bjorndal 2002), adult green turtles *Chelonia mydas* are largely herbivorous and feed mainly on marine algae and seagrasses (Lopez-Mendilaharsu et al. 2005), leatherback turtles *Dermochelys coriacea* feed almost exclusively on pelagic gelatinous invertebrates (e.g. scyphozoan jellyfish and pyrosomes) (Holland et al. 1990, Salmon et al. 2004) and Kemp's ridley turtles *Lepidochelys kempii* have been found to eat mainly crustaceans (Burke et al. 1994, Seney & Musick 2005).

Two other species of hard-shelled marine turtle seem to have more plastic foraging behaviour and diets. Loggerhead turtles *Caretta caretta* have a rather diversified diet including soft-bodied benthic invertebrates, molluscs, crustaceans and fish (Plotkin et al. 1993, Godley et al. 1997, Tomas et al. 2001), and olive ridley turtles *Lepidochelys olivacea* are thought to be much less of a foraging specialist given their deep-diving behaviour (to 300 m) (Landis 1965) and long-distance movement patterns relative to other marine turtle species (Plotkin et al. 1995, Plotkin 1998, Luschi et al. 2003, Plotkin 2003, Polovina et al. 2003, Polovina et al. 2004). Indeed, the available literature suggests that olive ridley turtle diet is highly variable among regions (reviewed in Bjorndal 1997). However, there are few contemporaneous collections of the movement and detailed diving behaviour data needed for a more complete interpretation of olive ridley turtle foraging strategies.

The advent in recent years of satellite-relayed data loggers (SRDLs) has provided a means to overcome the difficulties in obtaining detailed diving behaviour and relatively precise location data in the study of the foraging behaviour of wide-ranging marine vertebrates (Fedak et al. 2002, Hays et al. 2004b). These sophisticated instruments not only provide accurate locations in real time, they also give information describing the environmental conditions in which the animals forage

(McMahon et al. 2005) that is useful for quantifying habitat selection and range extents. This is especially important for species that range widely and spend the majority of their life cycles submerged (Myers et al. 2006). Thus, to address the gaps in our understanding of olive ridley turtle behaviour and to examine whether observations of this species' juvenile movement patterns elsewhere (Polovina et al. 2003, Polovina et al. 2004) imply a broad foraging niche for adults, we deployed SRDLs on 4 female turtles in northern Australia during the post-nesting migration. In addition to the important knowledge gap this research addresses, it also provides data essential for the effective management of olive ridley turtles in Australia. The predicted wide range of this species suggests a potentially high susceptibility to human fishing activities (e.g. Polovina et al. 2004) from several nations bordering the Arafura and Timor Seas, and it has fundamental social and practical management implications for different aboriginal groups attempting to manage this important seasonal food resource (Kennett et al. 2004).

MATERIALS AND METHODS

Satellite-relayed data loggers (SRDLs, manufactured by the Sea Mammal Research Unit [SMRU], University of St. Andrews, United Kingdom, www.smru.st-and.ac.uk) were attached to the carapaces of 4 female olive ridley turtles nesting in the Wessel Islands of Arnhem Land in the Northern Territory of Australia (Graham Island: 11° 45' S, 135° 57' E and Wunpirri Island: 11° 36' S, 136° 05' E) using quick-setting epoxy glue. Standard curved carapace length (SCCL) was measured for all individuals prior to SRDL-unit attachment, where SCCL is the distance from the anterior point at midline (nuchal scute) to the posterior tip of the supracaudal (Shanker et al. 2004). Weights were not measured, but we estimated mass from a SCCL-weight relationship derived from olive ridley turtles captured during a World Wildlife Fund for Nature (WWF) Australia program (5 turtles, morphometric measurements available from <http://wwf.org.au/ourwork/oceans/oliveridleytrackingbios/>).

The SRDL function and attachment procedures are summarized in detail elsewhere (Hochscheid et al. 2005, McMahon et al. 2005). However, we modified previous procedures by mounting the SRDLs prior to attachment onto an epoxy wedge (base = 125 mm, width = 70 mm, height = 32 mm, hypotenuse = 92 mm, slope = 20°) with glue so that the antenna would point perpendicular to the sea surface to improve communication with the satellites upon the turtle surfacing (SMRU SRDLs are constructed so that the antenna points forward at an angle of approximately 20°). We

observed that the long axis of olive ridley turtles swimming at the surface was $\sim 0^\circ$, so the SRDL-wedge configuration appeared to maximize the occurrence of a vertical antenna position when the animal first surfaces to breathe.

Argos location data were summarized such that average daily positions were interpolated from the scatter of points available for each day. For this analysis, only high-quality Argos locations of quality class A, 1, 2 and 3 were used (see Hays et al. 2001 for accuracy estimates for each class). We first interpolated these high-quality locations using custom R code (R Development Core Team 2004) developed by D. Pinaud (Pinaud & Weimerskirch 2005) with an interpolation distance set to 0.2 km. Using this interpolated set, the mean latitude and longitude were then calculated for each day of the trip.

In addition to Argos location data, SRDLs provided 4 measures of diving behaviour: (1) long-form dive profiles with information on dive shape (Myers et al. 2006); (2) short-form dives, recording information for single dives that only included surface duration, dive duration, time of end of dive and maximum dive depth (Hochscheid et al. 2005); (3) 24-h summary statistics of diving events based on all the data recorded by the SRDL (these statistics include mean \pm SD dive duration, maximum dive duration, mean \pm SD depth, maximum depth, number of dives and the proportion of time spent either diving or at the surface) (Hochscheid et al. 2005); and (4) temperature-depth profiles of the deepest dive over a minimum time interval of 2 h. Due to the limited bandwidth available with the Argos system, depth values, while measured accurately, were not relayed with detailed precision. Near the surface (to 10 m), depth was relayed to the nearest 1 m, but this precision decreased with depth such that at 140 m, depth was relayed to the nearest 20 m. Similarly, for short dives (0 to 10 min), dive duration was relayed to the nearest min, but precision decreased thereafter so that a dive of 180 min duration was relayed to the nearest 20 min. To examine diel patterns in diving behaviour, we calculated the local solar mid-time (LST) for each dive as $LST = GMT + (\text{longitude}/15)$ (Bradshaw et al. 2002) and examined patterns in mean dive duration, maximum depth and the proportion of time spent diving per LST hourly bin.

Depth and temperature were measured every 4 s, then key points of inflexion of the dive profile were determined at the end of a dive and relayed via the Argos system (Fedak et al. 2002). For long-form dives, up to 5 points of inflexion, dive duration and the end time of the dive were relayed. For temperature profiles, 12 points of inflexion were determined in a manner consistent with the processing of expendable bathythermograph (XBT) data. See Myers et al. (2006)

for a full description of depth profiles and McMahon et al. (2005) for a description of the how temperature profiles are measured by SRDLs. SMRU SRDLs have a 2000 m depth transducer with a 0.5 m resolution, and water temperature is accurate to 0.1°C (www.smru.st-and.ac.uk). The depth threshold for diving was ≥ 3 m (i.e. all dives < 3 m were considered at-surface noise). Sea surface temperatures (SST) were taken as those temperatures recorded in the uppermost depth bin.

To examine whether turtles were diving to the ocean floor, we determined the ocean depth for a particular dive location using the General Bathymetric Chart of the Oceans (GEBCO) (IOC/IHO/BODC 2003) and then established whether the maximum depth for a particular dive was within 10% of the depth described in the GEBCO atlas. However, bathymetric data were not always available for particular locations, so we consulted a hydrographic chart (Royal Admiralty 2003) to determine the depth of the sea floor. In some cases, the maximum-recorded dive depths exceeded the reported bathymetric maximum, so here we assumed the sea floor depth was equivalent to the maximum depth of the dive in question.

Long-form dive profiles have a variety of 'shapes' that can be quantified using the Time-Allocation at Depth (TAD) index developed for SRDL-collected data (Fedak et al. 2001). Our goal was to estimate the proportion of the bottom-attaining dives (as defined above) that followed the classic U-shape typically associated with benthic activities. The TAD index uses relevant data from dive profiles to highlight where in the dive an individual forager centres its activity with respect to depth (Takahashi et al. 2003):

$$\text{TAD} = \frac{\sum_i^n \frac{(d_{i+1} + d_i)(t_{i+1} - t_i)}{2} - \left(\frac{d_{\max}^2}{S}\right)}{(d_{\max} \times (t_n - t_1)) - \left(\frac{2d_{\max}^2}{S}\right)} \quad (1)$$

where d_i = an individual depth reading for depth reading i in a dive, t_i = the time of depth reading i , d_{\max} = the maximum dive depth and S = a predefined average rate of change of depth. For our analyses, S was set to 1.4 m s^{-1} . This ensured that the TAD index would vary between 0 and 1, with values near 0.5 corresponding to more V-shaped dives and values near 1.0 indicating more U-shaped (benthic) dives. We also tested the sensitivity of the TAD to variation in S ; reducing S to 1.0 m s^{-1} (-28%) changed the median TAD of Turtle A by only 0.4% (from 0.8679 to 0.8714), and increasing S to 2.0 m s^{-1} ($+43\%$) increased the TAD by only 0.3%.

The relationships between post-dive surface intervals and dive duration were examined using linear regression, with the strength of evidence for a relationship assessed using the information-theoretic evidence ratio (ER). This is equal to the Akaike's Information

Criterion (Akaike 1973) corrected for sample size (AIC_c ; Burnham & Anderson 2002) weight of the full model \div AIC_c weight of the intercept model, and the least-squares r^2 value to quantify structural goodness-of-fit.

Diel patterns in dive duration, maximum dive depth and the proportion of time spent diving were investigated using linear mixed-effects models (LME) using a reduced maximum-likelihood (REML) structure (Pinheiro & Bates 2000). Models considered only the hour-of-day covariate for each response model. Although this structure captures the main diel trends, it ignores any trends between days given the linear covariate of time set as hour of the day. Due to the autocorrelation inherent in time series of these behavioural indices, we assessed the first-order autocorrelation coefficients for each response variable and averaged these over all individuals. These mean coefficients were then set in the LME model structure (mean autocorrelation coefficients were 0.70, 0.54 and 0.41 for duration, maximum depth and proportion of time spent diving, respectively), with the random effect set to 'individual' (Pinheiro & Bates 2000). To correct for non-Gaussian distributions of the response variables, we log-transformed duration and maximum depth, and took the complementary log-log of the proportion of time spent diving. Model support was assessed using an information-theoretic index (AIC and ER) as outlined above, and structural goodness-of-fit was determined from the percent of the deviance explained (%DE) by the single-term models. All analyses were done using the R software package (R Development Core Team 2004), and all values are shown as means \pm 1 SD.

RESULTS

Morphometrics and data retrieval

The 4 female olive ridley turtles fitted with SRDLs had a SCCL of 68.5, 68.0, 69.6 and 68.8 cm (Turtles A–D, respectively). The SCCL-weight relationship from the WWF data was $\hat{W} = -75.0623 + 1.5715 \times \text{SCCL}$

(\hat{W} = estimated weight, $r^2 = 0.97$, $F_{1,3} = 125$, $p = 0.002$). This equation predicted weights of 32.6, 31.8, 34.3 and 33.1 kg for Turtles A–D, respectively. SRDLs provided large volumes of high-quality data (Table 1). We obtained a total of 534 turtle-days of tracking data (mean track duration = 134 d), giving 3043 locations ranging from Class B to 3 (Table 1). Of those locations, 630 (18.7%) were of highest quality (Location Classes 1 to 3). Conductivity data (not shown) suggested the units ceased transmission due to biofouling rather than battery failure or detachment.

Movement patterns

The individuals tracked went in 3 general directions after leaving the nesting beaches (Fig. 1): Turtles A and B spent approximately 26 and 18 d, respectively, in the vicinity of the island where they nested (possibly nesting again during this period) before departing the region (Fig. 1A,B). Turtles C and D left the nesting area immediately on northward and westward migrations, respectively (Fig. 1C,D). The duration of migrations to foraging areas ranged from 15 to 36 d (Fig. 1); 'foraging areas' were defined as the approximate regions where directed migrations ceased and were replaced by more convoluted and overlapping tracks (Fig. 1). Turtles A and B settled in single foraging areas, but Turtles C and D had 2 and 3 main foraging areas, respectively (Fig. 1A–D).

Dive patterns

SRDLs collected a total of 3501 long-form dive profiles, 13827 short-form and 496 24-h summaries (Table 1). We used information from the 24-h summaries to estimate the proportion of dives relayed for each turtle. Overall the number of dives relayed ranged from 69.6 to 96.8% of the total possible number of dives (Table 2), and of those relayed, the long-form represented between 15.3 and 22.7% of dives (Tables 1 & 2). Taking into consideration the decreas-

Table 1. *Lepidochelys olivacea*. Summary information from 4 satellite-relayed data logger (SRDL) deployments on post-nesting olive ridley turtles (A–D) from the Wessell Islands, Northern Territory, Australia. Dates given as dd/mm/yy

Turtle ID	Dates	Days tracked	Links in each Argos location class					Long-form dives	Short-form dives	24-h summaries	
			B	A	0	1	2				3
A	11/05/05–10/10/05	133	251	143	71	21	23	9	556	3055	126
B	10/05/05–27/07/05	78	72	57	128	66	21	11	414	1590	76
C	06/05/05–19/10/05	167	280	189	375	142	59	13	1192	4625	161
D	06/05/05–18/09/05	156	322	223	302	131	101	103	1339	4557	133
Total		534	925	612	876	360	204	66	3501	13827	496

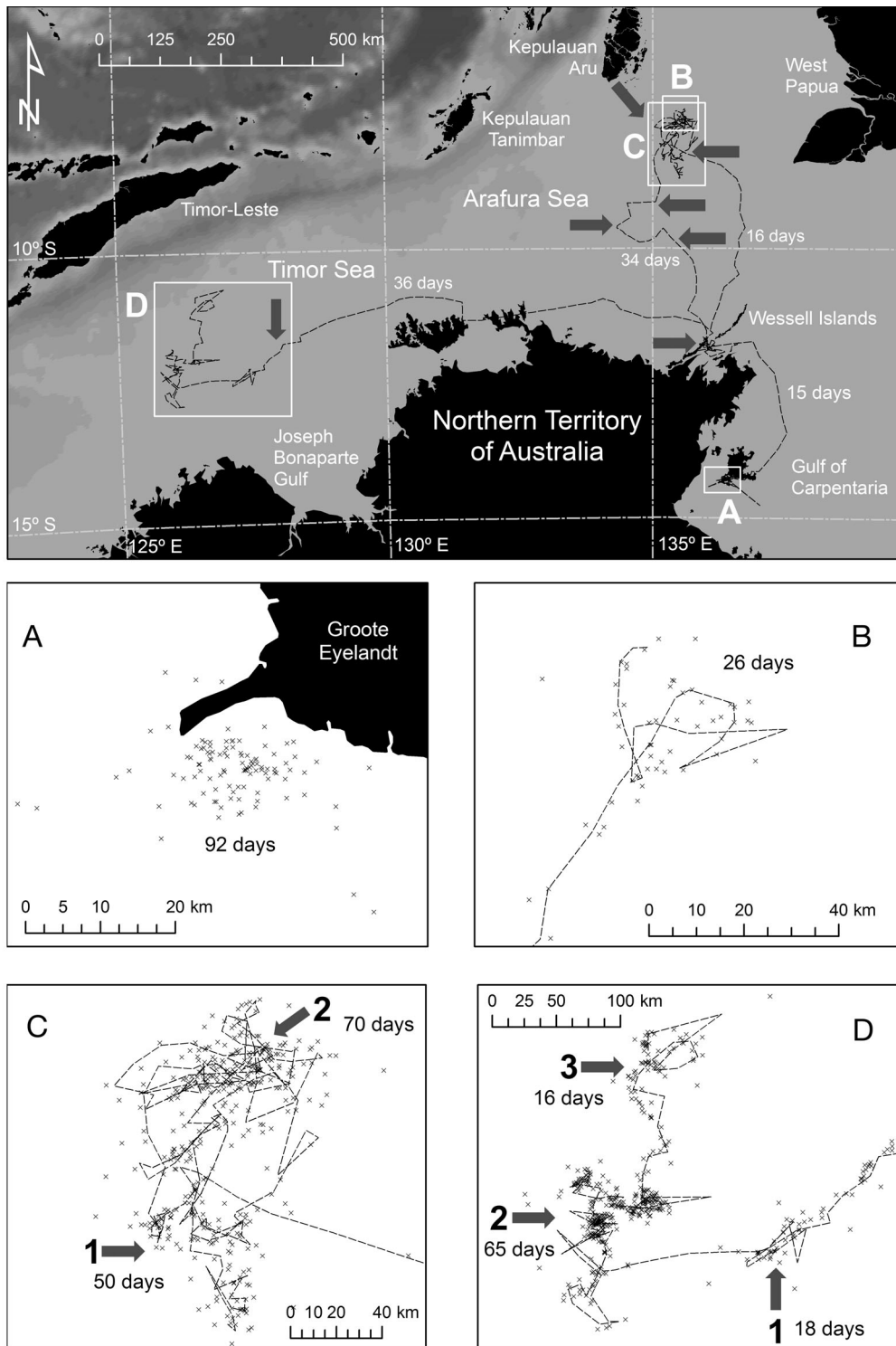


Fig. 1. *Lepidochelys olivacea*. Movement patterns during post-nesting migration and foraging of 4 olive ridley turtles tracked from the Wessel Islands in the Northern Territory of Australia. Top panel = general distribution of individuals relative to the nesting areas (mean daily interpolated positions and approximate duration of transit pathways and foraging phases in days). Top panel arrows = approximate positions of deepest dives. Grey-scale colour = bathymetry variation. Panels A–D = focal foraging regions for Turtles A–D, with mean daily interpolated track (Turtles B–D only) and distribution of high-quality (Argos Location Classes A, 1, 2, 3) locations. Arrows in panels C, D = major foraging areas. Days = approximate number of days in each foraging area

Table 2. *Lepidochelys olivacea*. Estimated proportion of total dives for Turtles A–D, as determined from the total number of dives and the 24-h summary for each turtle's satellite-relayed data logger (SRDL) record

Turtle ID	Mean dives d ⁻¹	Dives relayed	% of all dives relayed
A	39.0	3611	69.6
B	27.5	2004	93.4
C	36.0	5817	96.8
D	47.0	5896	80.4

ing precision of depth and times relayed with the increasing values of these parameters, the maximum dive depth relayed was 200 ± 20 m (precision indicates error associated with data compression at this depth range) and the maximum duration was 200 ± 20 min (3.33 ± 0.33 h). The deepest long-form dive profiles were from Turtle D at 140 m, followed by 120 m, 100 m and 50 m for Turtles B, C and A, respectively (Fig. 2). An examination of the median maximum dive depth and duration for the 3 phases identified for each track (i.e. pre-transit, transit and foraging area) revealed high variation among phases for each turtle (data not shown). However, there was a suggestion of an increasing maximum depth and duration from the pre-transit to the transit phase. There was little difference in these parameters between the transit and foraging-area phases.

Mean maximum dive depths were similar for Turtles B–D (46.7 ± 30.2 m, 46.0 ± 21.9 m and 46.2 ± 27.6 m, respectively) (Fig. 3), but Turtle A dived considerably shallower (20.1 ± 9.4 m), consistent with its travelling and foraging closer to land (Fig. 1). Most dives (66.3%) were shallower than 50 m, and only 0.4% were >100 m, with the 50, 75, 95 and 99 percentiles being 35, 50, 90 and 100 m, respectively. Mean dive durations were more variable, with Turtle B having the longest mean duration (48.0 ± 35.3 min), followed by Turtles A, C, and D (37.2 ± 27.5 min, 33.7 ± 17.0 min and 24.5 ± 17.2 min, respectively) (Fig. 3). Most dives (66.7%) were less than 40 min in duration, and 9.5% exceeded 60 min, with the 50, 75, 95 and 99 percentiles being 30, 45, 75 and 115 min, respectively. However, frequency histograms of dive duration do not demonstrate the allocation of time within each dive; therefore, we also plotted the proportion of total time spent within each duration bin (Fig. 4) to demonstrate that a large portion of the time was spent in dives of long duration. The relationships between dive duration and maximum depth were considerably different among turtles (Fig. 5). Plots of the mean and quartile ranges of mean duration vs. depth indicated that mean duration increased with depth up to approximately 28, 100, 30 and 50 m for Turtles A, B, C and D, respectively (Fig. 5). Fewer dives at depths >100 m than at <100 m complicates conclusions, but in general, those turtles diving the deepest did not necessarily dive for the longest durations.

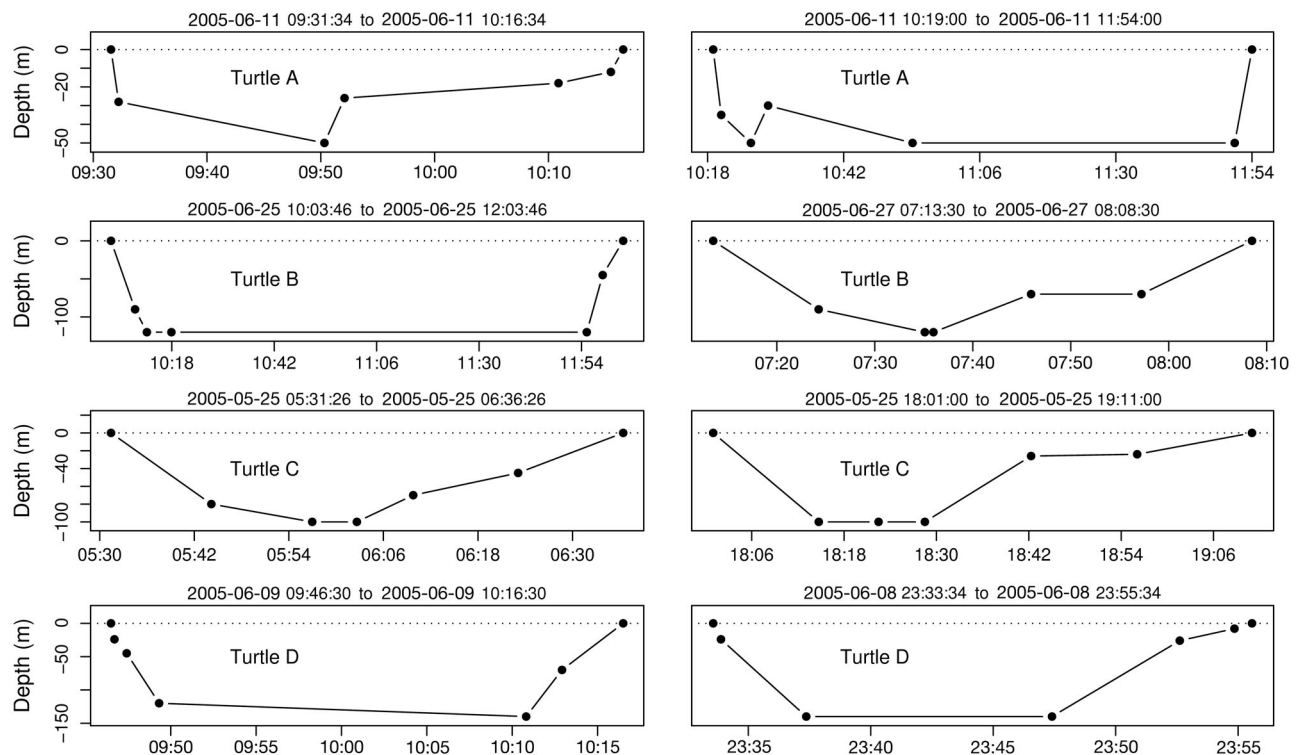


Fig. 2. *Lepidochelys olivacea*. Examples of 2 long-form dive profiles each from Turtles A–D with maximum depths vs. dates and times

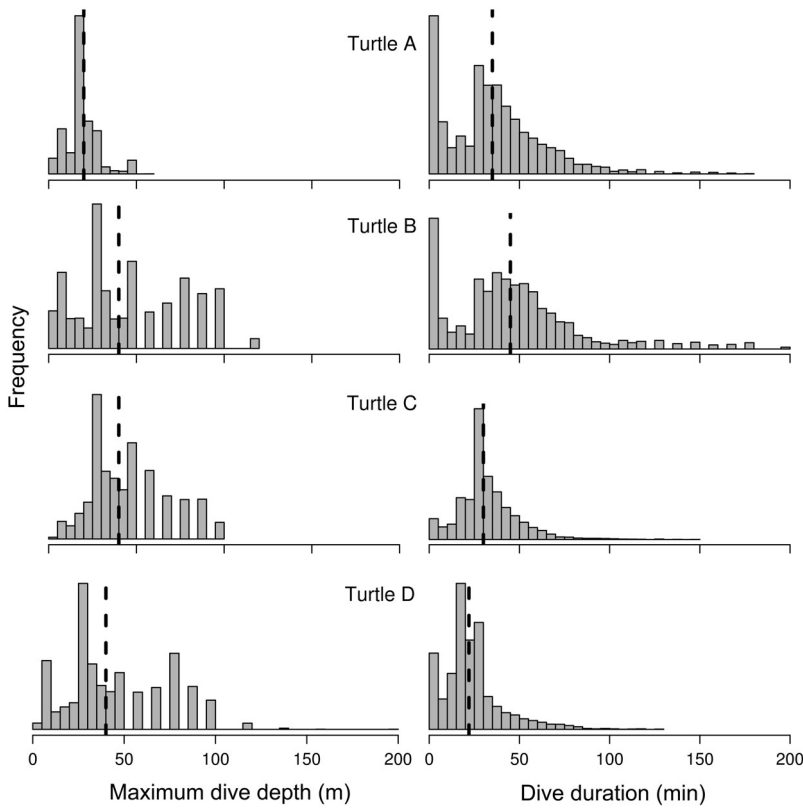


Fig. 3. *Lepidochelys olivacea*. Maximum dive depth and duration for Turtles A–D. Median values = dashed vertical line; y-axis values show relative frequency

After assuming that any dive with a maximum depth within 10% of the estimated bottom depth had reached the seabed, the majority of dives (66.0%) reached the bottom at least once during the dive. There was considerable variation among turtles; for example, Turtle A with the shallowest dives and the most in-shore foraging track (Fig. 1) had the majority of its dives at or

near the bottom (Fig. 6). Turtles C and D had a more oceanic distribution (Fig. 1) and considerably fewer dives reaching the bottom, although the majority of their dives were still considered bottom dives (Fig. 6). Turtle B had a similar foraging distribution to Turtle C, but the former had many more dives to the bottom. To examine if these bottom-reaching dives might relate, at least in part, to benthic foraging (i.e. most of the dive spent at the bottom; ‘U-shaped’ dive), we examined the distribution of TAD for each turtle. An examination of bottom dives with TAD >0.75 generally demonstrated a bottom phase suggestive of benthic behaviour, and the proportion of bottom dives with a TAD >0.75 were 0.62, 0.66, 0.47 and 0.43 for Turtles A, B, C and D, respectively. Of course, the decreasing precision with depth suggests that the true proportion of dives deemed ‘benthic’ might actually be smaller given that the flat bottom of deep, U-shaped dives may in fact be more variable than suggested by our data.

Diel patterns in diving behaviour demonstrated some interesting trends. Although there were no clear patterns in

mean maximum dive depth, there was some suggestion of a peak in mean depths during the later hours of the morning (09:00–10:00 h) and early evening (18:00–20:00 h), especially for Turtles B–D (Fig. 7, top-row left panel). However, the LME models demonstrated little support for an hour-of-day effect on the log of maximum dive depth ($ER < 1$, $DE \cong 0\%$). Mean dive

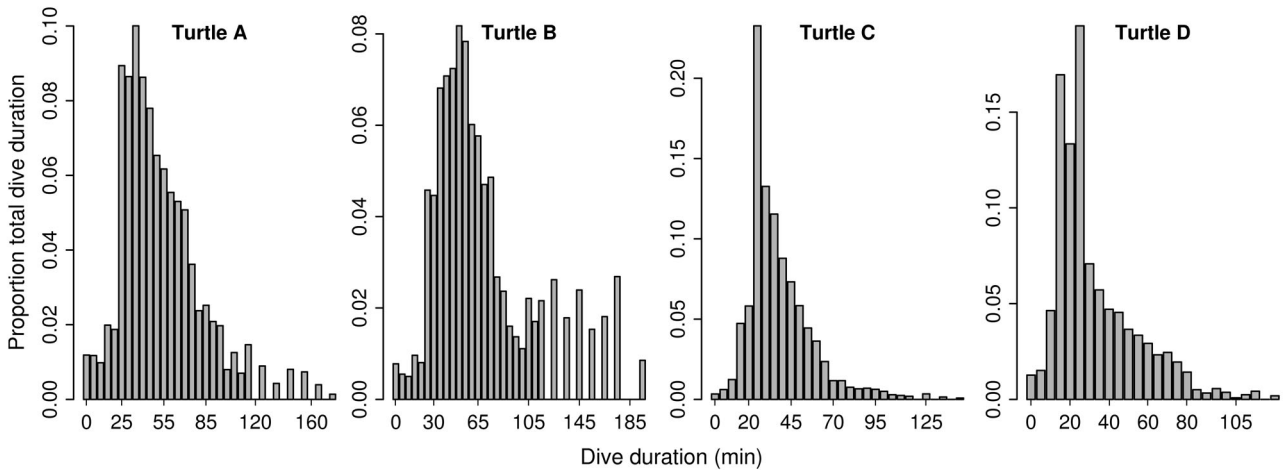


Fig. 4. *Lepidochelys olivacea*. Dive duration for Turtles A–D as proportion of the total time within each duration bin. Dive duration bins represent 5 min increments

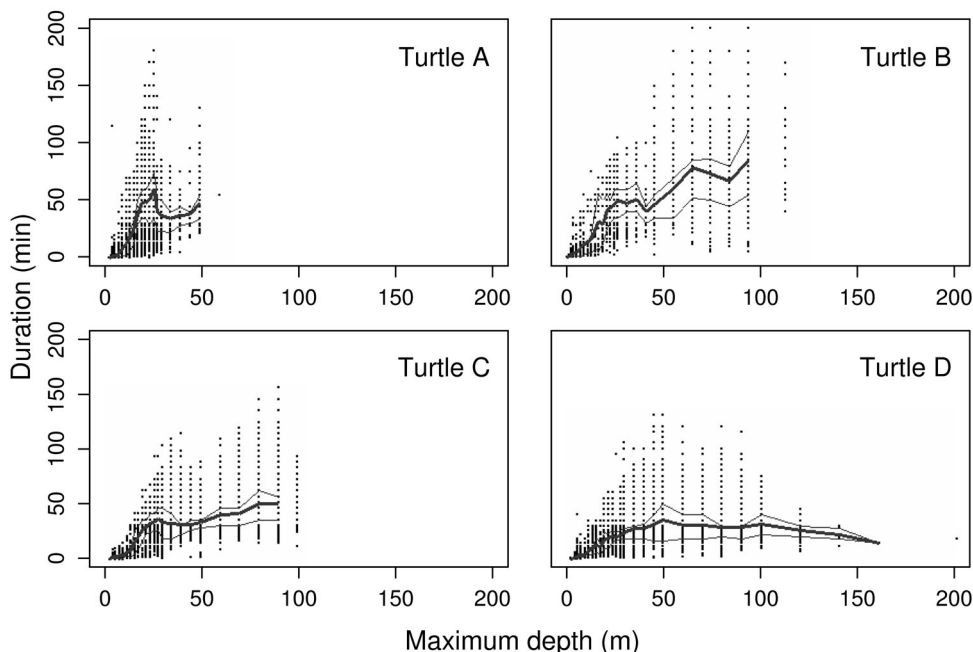


Fig. 5. *Lepidochelys olivacea*. Relationship between dive duration and maximum depth for Turtles A–D. Solid lines = mean duration per depth bin. Thin lines = 25 and 75% quartiles of duration at each incrementing depth bin

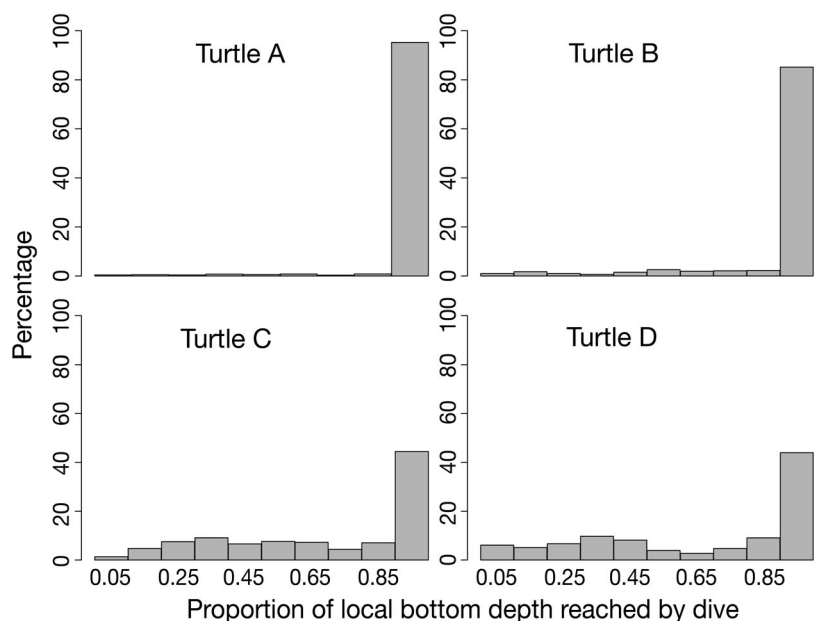


Fig. 6. *Lepidochelys olivacea*. Percentage of proportion of bottom depth reached by a dive for Turtles A–D

duration showed clear diel patterns with a maximum duration occurring at approximately 04:00 h local time and a minimum duration between 12:00 and 17:00 h local time (Fig. 7, top-row middle panel). The LME model supported an effect of hour-of-day on dive duration ($ER = 3.3 \times 10^{13}$); however, the deviance explained was low ($DE = 0.13\%$). This was mimicked by a maximum in the proportion of time spent diving (average range = 87.7–94.1%) between 03:00 and 05:00 h, and a minimum in this measure between 10:00 and 17:00 h

($ER = 7768$, $DE = 0.07\%$) (Fig. 7, top-row right panel). For bottom dives only, the diel patterns in maximum depth, duration and proportion of time spent diving were far more variable, and the patterns appeared to mimic those of all dive types (Fig. 7, bottom-row panels).

The post-dive surface interval and dive duration relationships varied substantially among individuals (Fig. 8). There was little suggestion of a positive relationship for Turtle A ($ER = 5.0$, $r^2 = 0.001$), but convincing positive relationships for Turtles B and C ($ER = 9.0 \times 10^{107}$ and 6.9×10^{157} , $r^2 = 0.22$ and 0.12 , respectively). There was perhaps a weak negative relationship for Turtle D ($ER = 2.1 \times 10^8$, $r^2 = 0.007$). These differences among individuals are due possibly to the variation in the number of dives of short duration, with the shorter-duration dives explaining the negative relationship for Turtle D (Fig. 8).

Turtles A–D experienced SST between 23 and 29°C during the course of their records, and median SSTs were similar for all individuals (overlapping 95% CI) (Fig. 9). However, there were some seasonal differences in daily SST experienced by each turtle. Overall there was a general pattern of cooling toward the end of July, and Turtles B and C experienced similar patterns throughout their records (Fig. 9). Turtle D experienced warmer average SSTs travelling west, and Turtle A encountered cooler temperatures upon heading

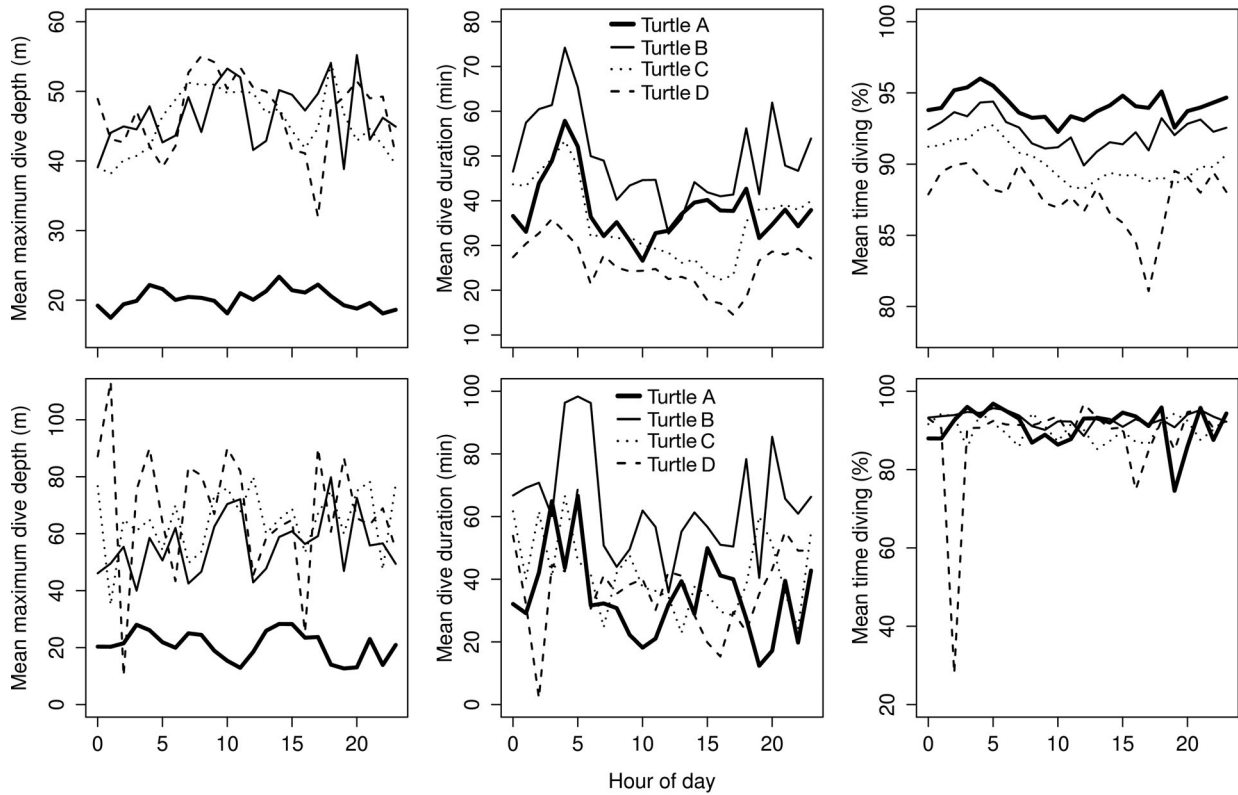


Fig. 7. *Lepidochelys olivacea*. Top-row panels = diel patterns for all dives with (center panel) mean duration, (left panel) mean maximum dive depth and (right panel) mean percent time diving. Bottom-row panels = diel patterns for bottom dives only. Times in local solar time (LST)

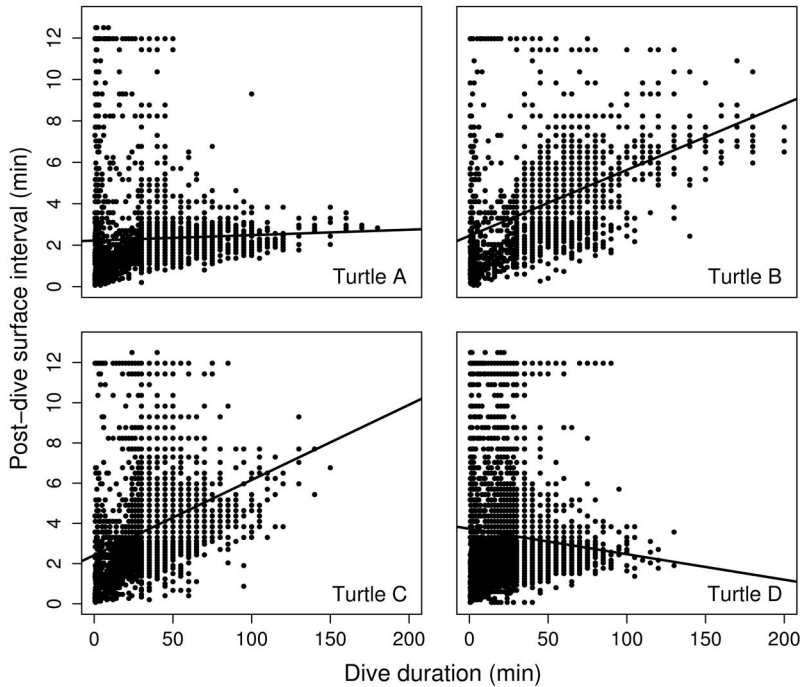


Fig. 8. *Lepidochelys olivacea*. Relationship between post-dive surface interval and dive duration for Turtles A–D with least-squares linear regression line of best fit for each

south into the Gulf of Carpentaria (Figs. 1 & 9). Examination of the depth-temperature profiles demonstrated that in some instances there was an approximate 9°C difference between surface and maximum depth temperatures (Turtle B). In other cases, even deep dives showed remarkably little temperature variation within the water column. The minimum temperature at depth was 18.7°C experienced by Turtle B on 8 June 2005 at a depth of 98 m; however, only 6.9% of the dives with temperature profiles were in water that was <20°C (Turtles B and C only).

DISCUSSION

Dives recorded during post-nesting migration and foraging from 4 olive ridley turtles supported the prediction that this species demonstrates high habitat plasticity by using a broad range of habitats (inshore coastal and oceanic)

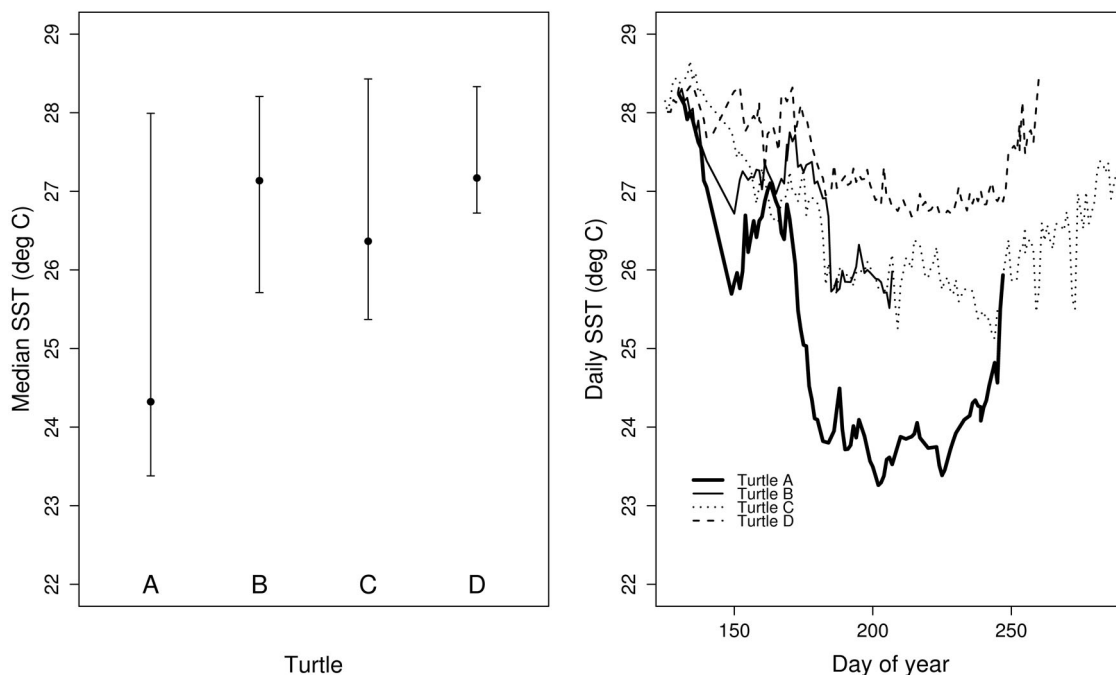


Fig. 9. *Lepidochelys olivacea*. Left panel = median ($\pm 95\%$ confidence limits) sea surface temperature (SST) for Turtles A–D for the duration of their satellite-relayed data logger (SRDL) record. Right panel = daily SST for Turtles A–D over their SRDL record (SRDLs typically record 1 temperature upcast each day)

within the water column and an emphasis on benthic diving. Although we had no direct data on the diet composition of the turtles from the population sampled, this generalist behaviour and benthic bias is consistent with previous descriptions of olive ridley turtles elsewhere having a generalist diet (Bjørndal 1997) and variable foraging behaviour (Polovina et al. 2003, Polovina et al. 2004). Of particular interest was the high proportion of dives that attained the bottom of the Arafura and Timor Seas and the evidence for a predominately benthic existence. The lack of a clear diel signal in the mean dive depths suggests that these benthic dives were not associated solely with resting or anti-predator behaviour (Fig. 7). As such, if these benthic dives comprise foraging activity, our results support previous inference about the behaviour and diet of olive ridley turtles which have shown frequent benthic activity (Polovina et al. 2003, Polovina et al. 2004) occurring often at great depths (Landis 1965). The hypothesised generalist mode of foraging is also congruent with the few studies and reports describing the diversified diet of this marine turtle species (e.g. salps, jellyfish, molluscs, crustaceans, bryozoans, fish eggs, sipunculids, ascidians, pelecypods, gastropods and algae) sampled elsewhere (reviewed in Bjørndal 1997).

However, distinguishing the true function of such benthic dives in marine turtles from profiles alone is not straightforward. Previously, resting dives made by marine turtles equipped with time-depth recorders

(TDRs) have been inferred by bouts of consistently U-shaped dives (mostly at night), with little or no variation in depth of the bottom phase consistent with a stationary animal (van Dam & Diez 1996, Hays et al. 2004c). In contrast, non-resting dives (e.g. foraging) have been inferred from profiles with far more variation in the bottom phase (van Dam & Diez 1996). In neritic hawksbill and green turtles, a strong nocturnal component to benthic resting has also been noted (van Dam & Diez 1996, Hays et al. 2000), whereas pelagically feeding leatherback turtles often demonstrate a nocturnal foraging pattern corresponding to the vertical migrations of plankton that are closer to the surface at night (Hays et al. 2004a). Hence, nocturnal vs. diurnal patterns of activity seem to vary across species. We can say with confidence that 3 of the 4 individuals we tracked made deep benthic dives, and the depth and prevalence of these dives is certainly unusual for hard-shelled turtles. However, distinguishing the function of these dives is complicated because there were few sequences of long-form dives with which to test for the existence of regular bouts of U-shaped dives. Certainly in shallow-diving species (e.g. hawksbill, green and loggerhead turtles), when individuals dive to the seabed, some dives typically serve a resting function while others are associated with foraging. It is therefore logical to expect that the benthic dives we recorded might have served these 2 functions.

Our data also revealed some interesting and unexpected traits of this species that have not been documented previously. Most turtles performed extraordinary long dives (nearly 10% lasted longer than 1 h), with the maximum dive lasting 3.33 ± 0.33 h, although others have noted relatively long dive durations for this species (Plotkin cited in Lutcavage & Lutz 1997). This is particularly remarkable considering the thermal environment in which these turtles live. Most turtles encountered SSTs within the range of 23 to 29°C, with few of the deep (≥ 100 m) dives measuring temperatures $< 20^\circ\text{C}$ at maximum depth. Previous studies of loggerhead turtle dive durations during winter conditions have measured dives of 7 h when SSTs were consistently $< 15^\circ\text{C}$, suggesting that extended diving times result from temperature-mediated reductions in diving metabolic rate associated with hibernation (Hochscheid et al. 2005). Although we did observe diel patterns in dive duration, i.e. longer durations during the early morning (Fig. 7), it is doubtful that any substantial variation in oceanic water temperatures occurred during this time. Further, the long dive durations observed for the shallower-diving Turtle A could not be explained by observations of low water temperatures at depth. Another possibility is that turtles were resting during the early hours of the morning and thus had lower metabolic rates, although the lack of a diel signal in dive depth suggests that any resting behaviour occurred at many different depths and times.

It is conceivable that the long dives we recorded were not a consequence of cold waters, but of anaerobic respiration during part of the dive. We can examine this possibility by considering the pattern of diving and surfacing. The relative length of dives and post-dive surface intervals is frequently used as an indication of whether animals are diving aerobically or anaerobically (Costa et al. 2001). Across a range of diving birds, mammals and reptiles, the prevailing view is that dives are mainly aerobic (e.g. Hays et al. 2000, Hindell et al. 2000, Croll et al. 2001), although there are exceptions (e.g. Kooyman et al. 1980, Costa et al. 2001). This is the best strategy for maximising the amount of the time that can be spent diving, because relatively little time is spent recovering at the surface between dives (Mori 1998, 1999, Thompson & Fedak 2001). The fact that dives by the instrumented olive ridleys were relatively long compared to their surface intervals suggests that in common with many other diving species, olive ridleys were diving aerobically. Even though we detected a positive relationship between the post-dive surface interval and dive duration for 2 turtles, longer surface intervals following long, aerobic dives are expected given the requirement of recharging oxygen stores. It is therefore plausible to hypothesise that this species of hard-shelled marine turtle is capable of achieving

either unexpectedly low diving metabolic rates or storing high concentrations of oxygen allowing it to exploit the benthic environment of shallow tropical seas. Indeed, the occasional manifestation of extremely long dives well beyond the median suggests that during these dives, olive ridleys approach or even go beyond their aerobic dive capacity. However, the competing hypotheses of low metabolic rates and high oxygen storage capacity still need to be tested using respirometry and direct measurements of oxygen stores in a laboratory setting (e.g. Lapennas & Lutz 1982, Southwood et al. 2003).

In general terms, olive ridley turtles seem to be able to occupy a different niche to other species of turtle (Polovina et al. 2003, Polovina et al. 2004). While the juveniles of several species live in an oceanic environment, possibly feeding on plankton and neuston (Bjorndal 1997), most hard-shelled species (e.g. green turtles, hawksbill turtles) spend their adult lives in shallow coastal environments (Lutz & Musick 1996, Seminoff et al. 2003, Lopez-Mendilaharsu et al. 2005). In contrast, adult leatherback turtles move extensively across ocean basins and dive deeply in the oceanic zone to feed on gelatinous plankton (Ferraro et al. 2004, Hays et al. 2004b). We showed clearly that olive ridley turtles diverge from these general paradigms in foraging turtles by spending long periods diving towards the seabed far from land in relatively deep water. This deep benthic activity seems unusual for sea turtles, but does occur in some diving mammals and birds. For example, grey seals *Halichoerus grypus* are largely benthic foragers (Thompson et al. 1991), and narwhals *Monodon monoceros* can forage on the seabed at depths of at least 800 m where they target deep-water fish and squid species (Laidre et al. 2003). Similarly, while penguins generally feed pelagically, it has been shown that in some situations certain species may dive deeply to feed near the seabed (Tremblay & Cherel 2000).

Our success to date in obtaining some of the highest quantity and quality of data for a hard-shelled turtle fitted with a satellite tag (cf. Plotkin et al. 1996, Plotkin 1998, M. Fedak pers. comm.) was perhaps due the application of a small wedge to improve communication between the unit and the Argos satellite network. This modification made the antenna point perpendicularly to the water surface when the animal breached. It is also possible that this species demonstrates a relative high surfacing rate that may facilitate communications with the Argos network, although previous work on the same species elsewhere has had lower success in data retrieval (Plotkin 1998, Plotkin et al. 1996).

Our results also have important implications for the management of this species in northern Australia and Southeast Asia. The extensive movements (> 1000 km)

measured from 4 tags and the variability in migration pathways suggest that this population is potentially susceptible to a wide range of human activities in the general region. The management of turtle egg harvest by Australian Aboriginal groups (Kennett et al. 2004) should therefore take into consideration the broader activities of clans across the entire range of the northern Australian coastline; and those responsible for turtle conservation in Australia must consider it likely that olive ridleys nesting in Australia are susceptible to threats in the oceanic region such as fishing by-catch (Poiner et al. 1990, Poiner & Harris 1996, Tucker et al. 1997, Salini et al. 2000) and direct predation by artisanal fisherman (Nuitja & Lazell Jr 1982, Limpus 1997, Meylan & Donnelly 1999) throughout Papua New Guinea, Indonesia and Timor-Leste.

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