HEART RATES AND DIVING BEHAVIOR OF LEATHERBACK SEA TURTLES IN THE EASTERN PACIFIC OCEAN

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Summary

Heart rates and diving behavior of leatherback sea turtles (*Dermochelys coriacea*) were monitored at sea during the internesting interval. Instruments that recorded the electrocardiogram and the depth and duration of dives were deployed on six female leatherback turtles as they laid eggs at Playa Grande, Costa Rica. Turtles dived continually for the majority of the internesting interval and spent 57–68 % of the time at sea submerged. Mean dive depth was 19 ± 1 m (mean ± S.D.) and the mean dive duration was 7.4 ± 0.6 min. Heart rate declined immediately upon submergence and continued to fall during descent. All turtles showed an increase in heart rate before surfacing. The mean heart rate during dives of 17.4 ± 0.9 beats min^{-1} (mean ± S.D.) was significantly lower than the mean heart rate at the surface of 24.9 ± 1.3 beats min^{-1} ($P<0.05$). Instantaneous heart rates as low as 1.05 beats min^{-1} were recorded during a 34 min dive. The mean heart rate over the entire dive cycle (dive + succeeding surface interval; 19.4 ± 1.3 beats min^{-1}) was more similar to the heart rate during diving than to the heart rate at the surface. Although dive and surface heart rates were significantly different from each other, heart rates during diving were 70 % of heart rates at the surface, showing that leatherback turtles do not experience a dramatic bradycardia during routine diving.

Key words: heart rate, diving, sea turtle, leatherback turtle, *Dermochelys coriacea*, reptile, data logger, behavior.

Introduction

The leatherback sea turtle (*Dermochelys coriacea*) is a pelagic reptile that makes long-distance oceanic migrations. Leatherback turtles may journey as far north as the Arctic circle, but every 2–3 years the female turtles return to a tropical nesting beach to lay eggs. Dive records for females offshore of a nesting beach in the Caribbean show that leatherback turtles dive continually and spend 55–80 % of the time at sea submerged (Eckert et al., 1989). Mean dive times for leatherback turtles during the internesting interval ranged from 6.9 to 13.5 min, and surface intervals between dives ranged from 2.3 to 10.5 min (Eckert et al., 1989, 1996). Migrating leatherback turtles also spend the majority of time at sea submerged and display a pattern of continual diving (Standora et al., 1984). This dive pattern suggests that the leatherback turtle primarily uses aerobic metabolism while diving, because a reliance on anaerobic metabolism would necessitate a lengthy recovery period at the surface to repay the oxygen debt incurred during the dive (Eckert et al., 1986).

For aerobic divers, the amount of oxygen available during a dive and the rate of oxygen consumption are determinants of dive duration. In the deep-diving leatherback turtle, the primary oxygen stores are in the blood and tissues, not in the lungs (Lutcavage et al., 1992), so oxygen remains available when the lungs collapse under increased hydrostatic pressure at depth (Berkson, 1967; Lutcavage et al., 1990; Lutcavage and Lutz, 1997). The utilization of blood oxygen stores can be regulated by cardiovascular adjustments, such as changes in blood flow, which may be reflected by changes in heart rate (Butler and Jones, 1997). Increases in heart rate and tissue perfusion upon surfacing would facilitate the exchange of gases and reduce the amount of time necessary to reload oxygen stores, thereby reducing surface intervals. Upon submergence, a decrease in heart rate would result in a slower delivery of oxygen to the tissues and might serve as a means for conserving oxygen during diving. However, the rate of oxygen delivery to the tissues during a dive, as determined by cardiovascular adjustments, must be sufficient to meet metabolic demands if metabolism is to remain aerobic.

Most diving animals experience a decrease in heart rate when submerged, but the degree of bradycardia varies depending on the species and the nature of the dive (Butler and Jones, 1997). For example, the northern elephant seal

(*Mirounga angustirotris*) experiences a significant bradycardia while making repetitive deep dives at sea (Andrews et al., 1997), but ducks (*Aythya* spp.) foraging underwater have dive heart rates that are the same as or higher than resting heart rates (Butler and Jones, 1997). The few studies that have examined heart rate in freely diving reptiles have shown that dive heart rates are only moderately lower than surface heart rates, but reptiles may drastically reduce their heart rate if they are disturbed during a dive (Smith et al., 1974; Heatwole et al., 1979).

Very little is known about the cardiovascular response to diving in sea turtles. Heart rates have been recorded from captive cheloniid turtles and from sea turtles on nesting beaches, but heart rates during diving have never before been recorded from any species of sea turtle in the wild. The dive response of the leatherback turtle is of particular interest to comparative biologists, because this pelagic turtle has many physiological features, such as a rapid growth rate (Zug and Parham, 1996), a large body mass (250–600 kg) and the ability to maintain high core body temperatures in cold water (Friar et al., 1972), which are comparable with features found in accomplished mammalian divers. However, leatherback turtles display a much less rigorous diving pattern than that observed for diving mammals in the same mass range (Butler and Jones, 1997), diving for shorter periods and spending a greater amount of time at the surface between dives. Typical dive times for the leatherback turtle are also substantially shorter than dive times for the much smaller cheloniid species of sea turtles (Lutcavage and Lutz, 1997), despite the fact that large animals usually have longer dive durations than smaller animals of a similar design because of a more favorable relationship between oxygen stores and mass-specific metabolic rate (Schreer and Kovacs, 1997). The goal of this study was to examine the heart rate response to diving in the leatherback turtle to gain a better understanding of the diving behavior in light of this turtle's physiology.

Materials and methods

Field procedures

Research was conducted at Playa Grande, Guanacaste, a leatherback turtle nesting beach located in Las Baulas National Park on the north Pacific coast of Costa Rica. Like other species of sea turtles, female leatherback turtles return to their natal beach every 2–3 years to lay eggs. The nesting season for leatherback turtles in the Eastern Pacific is from late October to early March. During this period, a female turtle may lay as many as 10 clutches of eggs on the same beach, returning to the offshore waters for 7–14 days between nesting (Steyermark et al., 1996). The instinctive behavior of the leatherback turtle in repeatedly returning to the same beach during a single nesting season provides the necessary conditions for attachment and retrieval of physiological recorders.

During the 1995–1996, 1996–1997 and 1997–1998 nesting seasons, VHF radio transmitters and data loggers (see *Instrumentation*) were deployed on six nesting leatherback
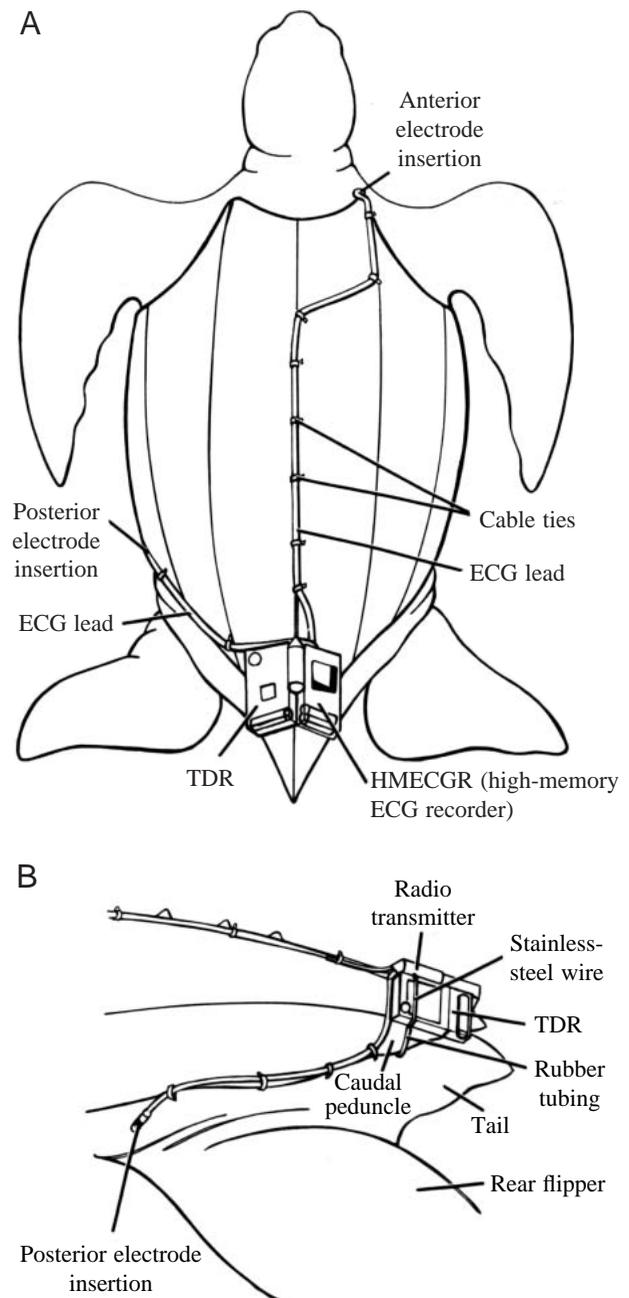

Fig. 1. Illustrations of data logger attachment to a leatherback sea turtle. (A) Dorsal view showing the placement of the data logger on the caudal peduncle and the electrode leads along the lateral ridges. (B) Left lateral view showing the data logger on the caudal peduncle and the posterior electrode insertion point. TDR, time/depth recorder.

females (Fig. 1). All procedures used for electrode insertion and instrument attachment were approved by the UBC Committee on Animal Care and the Costa Rican Ministry of Environment (MINAE). Instruments were attached to the turtle's shell as she laid eggs and camouflaged her nest cavity. Three pieces of flexible stainless-steel wire (1.6 mm in diameter) sheathed in polyvinyl tubing were anchored at one end to the instrument package. Three small holes (0.5 cm in diameter) were drilled in the caudal peduncle region of the

carapace using a battery-powered hand-held drill. Holes were immediately flushed with Betadine antiseptic (Purdue Frederick Inc., Pickering, Ontario, Canada) and treated with antibiotic cream (Polysporin; Warner-Lambert Inc., Scarborough, Ontario, Canada). The free ends of the stainless-steel wire were threaded through the holes in the caudal peduncle then wrapped around and secured to the instrument package. A layer of foam padding was placed between the instrument and the carapace of the turtle to prevent chafing.

The electrocardiogram (ECG) was recorded using two stainless-steel wire electrodes (20 gauge), which were inserted using a 14 gauge sterile needle at a point where the skin and shell fused and positioned along the inner surface of the shell. The anterior electrode was inserted above the right forelimb to a depth of 15 cm, and the posterior electrode was inserted immediately anterior to the left hindlimb to a depth of 25 cm. Electrodes were secured at the point of insertion using surgical silk sutures (Ethicon, Inc., Peterborough, Ontario, Canada). An additional 10 holes (3.2 mm in diameter) were drilled along the dorsal ridges (six holes on the median ridge, two holes on the second ridge from the lateral ridge on the right side, and two holes on the lateral ridge on the left side). Leads connecting the heart rate electrodes to the recording unit were secured to the dorsal ridges using cable ties passed through these holes. A passive induced transponder (PIT) tag (diameter 1.5 mm, length 15 mm) was injected into the left shoulder of each turtle before release so that she could be identified and monitored throughout the remainder of the nesting season and in future nesting seasons.

The ECG, dive depth and dive duration were recorded during the internesting interval when turtles were diving freely at sea. All the instrumented turtles returned to the beach to lay eggs after 9–12 days at sea and were located by radio telemetry. The instruments and electrodes were removed at this time, and the data were downloaded onto a laptop computer. Turtles showed no sign of infection and behaved normally on subsequent visits to the beach following instrument deployment (Table 1).

The ECG was also recorded from two leatherback females as they laid eggs on the beach. Two 18 gauge 3.8 cm needles inserted subcutaneously served as electrodes. One electrode was placed above the right front flipper, and the second electrode was placed above the left hind flipper. Each ECG was recorded with a hand-held ECG recorder and subsequently downloaded onto a laptop computer.

Instrumentation

Dive depth and duration were recorded using custom-built time/depth recorders (TDRs) previously described for use on elephant seals (Andrews, 1998). With a memory of 512 kilobytes (kb) and a sampling frequency of 5 s, a TDR recorded dive variables for a period of 9.5 days. TDRs with a depth resolution of 4 m over a range of 0–1000 m were used with two turtles during the 1995–1996 field season. During the 1996–1997 field season, TDRs with an improved depth resolution of 1 m over a range of 0–500 m were successfully used on two turtles.

Two types of instrument were used to record the ECG. In the 1995–1996 field season, the ECG was recorded using a custom-designed data logger previously described for recording the ECG of cormorants (Andrews, 1998). This low-memory ECG recorder (LMECGR) included an ECG amplification circuit and a single board computer (Tattletale Fast Lite, Onset Computer Corp., Pocasset, MA, USA) with a 512 kb memory that stored 3 h of ECG data when sampling at 50 Hz. To record the ECG for a longer period during the 1996–1997 and 1997–1998 seasons, we used a data logger in which the single board computer was replaced by a unit with a higher memory capacity. This high-memory ECG recorder (HMECGR) was based on a computer board (Model 8; Onset Computer Corp.) interfaced to a compact-flash memory expansion board (model CF8; Peripheral Issues, Mashpee, MA, USA). The HMECGR sampled the ECG at 50 Hz, so that its 15 Mb memory lasted 3.5 days. Each type of ECG recorder was bonded to a TDR and a VHF radio beacon (model SI-2sp; Holohil Systems, Carp, Ontario, Canada) to form the instrument package illustrated in Fig. 1.

Statistics and analysis

Submergences to depths of at least twice the depth resolution

Table 1. *Summary information for the instrumented leatherback turtles at Playa Grande, Costa Rica*

Turtle tag number	Curved carapace length (cm)	Estimated mass (kg)	Instrument	Date deployed	Date recovered	Internesting interval (days)	Documented returns*
0367	124.0	172	TDR	10 Jan 1996	21 Jan 1996	10.3	1
2566	140.0	250	TDR/LMECGR	21 Jan 1996	02 Feb 1996	10.0	2
8866	145.0	274	TDR/HMECGR	09 Nov 1996	18 Nov 1996	8.9	4
7610	166.0	377	TDR/HMECGR	14 Nov 1996	22 Nov 1996	8.9	3
5027	138.5	243	TDR/HMECGR	14 Nov 1996	26 Nov 1996	11.9	1
8364	148.5	291	TDR/HMECGR	04 Dec 1997	16 Dec 1997	11.5	6

CCL, curved carapace length; TDR, time/depth recorder; LMECGR, low-memory ECG recorder; HMECGR, high-memory ECG recorder; ECG, electrocardiogram.

*The number of times the turtle returned to the beach to lay eggs after instruments were deployed. Returns during subsequent nesting seasons are not documented in this table.

of the data logger were considered to be dives and were analyzed for maximum depth, dive duration and post-dive surface interval using the dive analysis (DA) program (Wildlife Computers, Redmond, WA, USA). Data loggers used during the 1995–1996 field season had a depth resolution of 4 m, so only dives deeper than 8 m were analyzed. For the 1996–1997 field season, data loggers had an improved depth resolution of 1 m, but we conservatively set the dive criterion at 4 m to account for the effects of wave action.

A dive cycle was defined as an individual dive and the accompanying post-dive surface interval. Dive depth was defined as the maximum depth attained during the dive. The turtle was considered to be at the surface if depth readings were less than the minimum dive criterion. If turtles made a dive or a series of dives to depths less than the minimum dive criterion, the analysis program would not be able to distinguish these submergences from a surface interval. Dive cycles with surface intervals that were three times longer than the mean surface interval of the individual were excluded from analysis to exclude the possibility that turtles might have made shallow dives to depths above the minimum dive criterion. Elimination of exceptionally long surface intervals also ensured that basking periods between dive bouts did not inflate the mean value for surface intervals occurring during a dive bout. Less than 5 % of all surface intervals were excluded from analysis by this criterion.

Descriptive statistics and frequency distributions for dive depth, dive duration and surface interval were calculated. Linear regression was used to examine relationships between the following variables: dive duration and dive depth, dive duration and the subsequent surface interval, body size (curved carapace length, CCL) and dive duration, and body size and dive depth.

Dive records were divided into 24 h periods beginning at 00:00 h on the night the instrument was attached. The Mann–Whitney rank test was used to determine whether there were differences in mean dive depth, dive duration and surface interval during the first and second halves of the internesting interval. Additionally, means for dive depth, dive duration and surface interval were calculated for each hour of the day to determine whether there were diel patterns in the diving behavior of the turtle (local sunrise, 05:30 h, local sunset, 17:30 h). Diurnal (05:00–17:59 h) and nocturnal (18:00–04:59 h) means for dive variables were compared using the Mann–Whitney rank-sum test. Comparisons were considered significantly different at $P<0.05$.

The ECG data were analyzed from the onset of the first dive to the end of the ECG recording. Sections of the ECG trace in which the QRS complex could not be distinguished (approximately 10–20 % in recordings from each turtle) were excluded from the analysis. Cardiac intervals (CI) were derived from the ECG trace by identifying QRS peaks by eye. The mean CI for each dive or surface interval was then converted to heart rate in beats min^{-1}.

Two turtles, 5027 and 8364, did not have dive records. Dive and surface heart rates for these turtles were distinguished on the basis of patterns observed in their ECG traces which were similar to patterns found in the ECG traces of the turtles for which diving records were available. Instantaneous heart rates of less than 20 beats min^{-1} were never observed during surface intervals in turtles for which both ECG traces and diving records were available. For turtles 5027 and 8364, if heart rate fell below 20 beats min^{-1} and remained below this level for longer than 1 min, this was considered to be the beginning of a dive. Data points occurring within 30 s of the initial fall in heart rate were eliminated from analysis to allow a reasonable margin for error. Similarly, if heart rate rose to $\geqslant$20 beats min^{-1} and remained at this level for longer than 1 min, this was considered to be the end of the dive. Data points within 30 s of the point when heart rate equaled or exceeded 20 beats min^{-1} were excluded from analysis.

Comparisons between mean dive heart rate, mean surface heart rate and mean dive cycle heart rate were made using a one-way analysis of variance (ANOVA) test (significance level $P<0.05$). Linear regression was used to determine whether there were significant relationships between the following variables: mean dive heart rate and mean surface heart rate, dive duration and mean dive heart rate, maximum dive depth and mean dive heart rate, and mean dive cycle heart rate and body size.

Curved carapace length was used as a measure of body size, since the turtles in this study were not weighed. Values for CCL ranged from 124 to 166 cm. Turtles were estimated to weigh between 170 and 380 kg on the basis of a regression (r^2=0.84) calculated with mass/length data from the literature (Eckert et al., 1989) and our own unpublished data.

Results

Diving behavior

Time/depth recorders were deployed on a total of six turtles (Table 1) over the course of this study, but usable TDR records were obtained from only four of the six turtles. All turtles began diving immediately after leaving the beach and dived continually for the majority of the recording period. This pattern of continual diving punctuated by short surface intervals is shown in Fig. 2, which shows the entire TDR data for turtle 8866 over the internesting interval (Fig. 2A), as well as a 2 h sequence from that record shown on an expanded time scale (Fig. 2B). Dives typically had a V-shaped profile, indicating that the turtle spent the majority of dive time traveling vertically through the water column. Mean dive duration for individual turtles during the monitoring period ranged from 6.7 to 8.2 min (grand mean 7.4±0.6 min), and the mean surface interval between dives ranged from 3.17 to 5.26 min (grand mean 3.94±0.91 min) (Table 2). While at sea, turtles spent 57.6–68.4 % of the time submerged. The mean dive depth for the entire recording period ranged from 17 to 21 m (grand mean 19±1 m) (Table 2). Maximum dive depths of individual turtles ranged from 56 to 124 m and were observed early on in the internesting interval. There was a
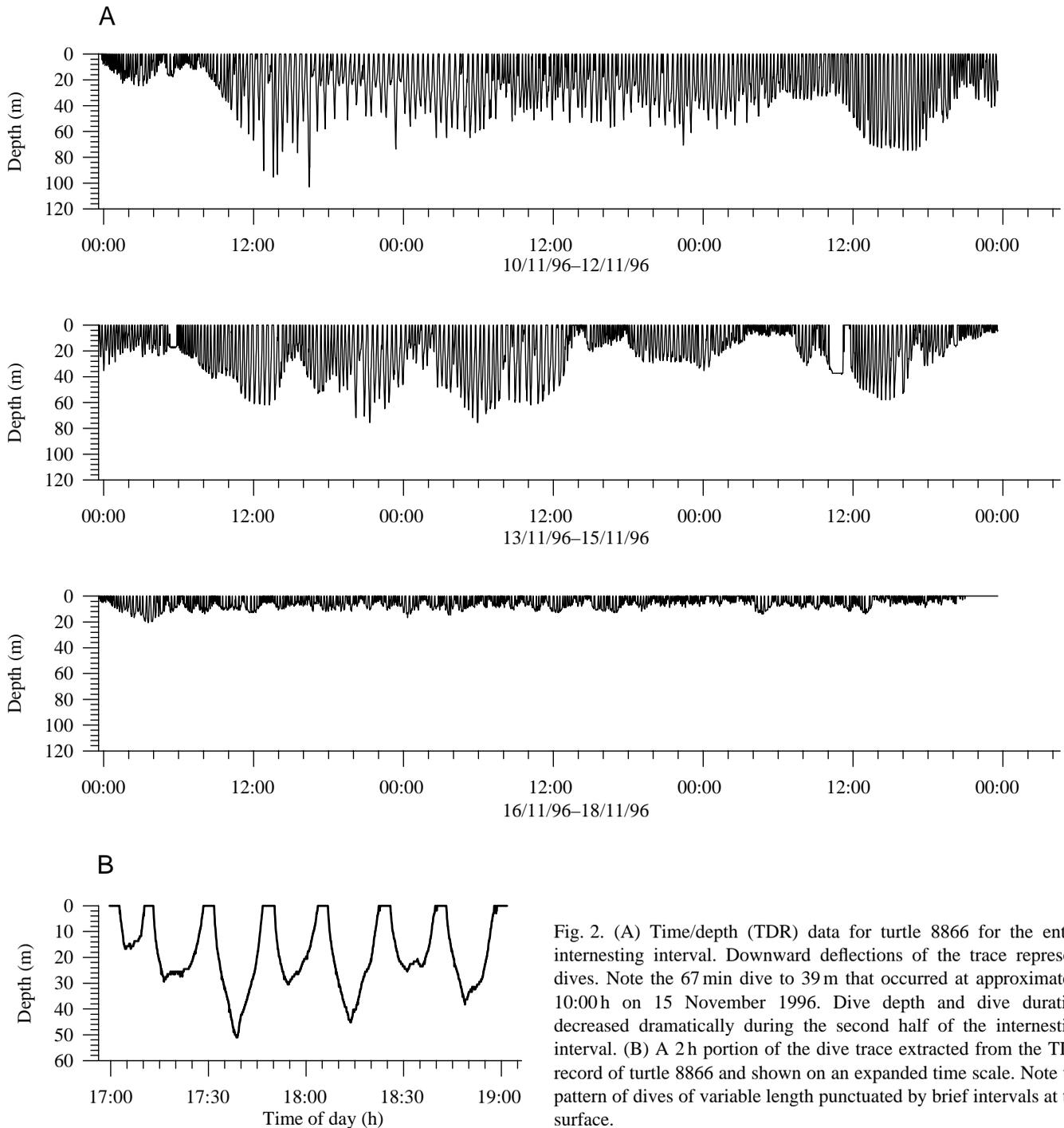
A

B

Fig. 2. (A) Time/depth (TDR) data for turtle 8866 for the entire internesting interval. Downward deflections of the trace represent dives. Note the 67 min dive to 39 m that occurred at approximately 10:00 h on 15 November 1996. Dive depth and dive duration decreased dramatically during the second half of the internesting interval. (B) A 2 h portion of the dive trace extracted from the TDR record of turtle 8866 and shown on an expanded time scale. Note the pattern of dives of variable length punctuated by brief intervals at the surface.

significant positive relationship between dive duration and dive depth ($P<0.05$, $r^2=0.53$). Linear regression demonstrated that there was no relationship between surface interval (time spent at the surface) and the preceding dive duration.

An exceptionally long dive was made by turtle 8866 during her internesting interval. This noteworthy dive lasted 67.3 min and is the longest recorded dive made by a leatherback turtle. The 67.3 min dive was preceded by a surface interval of average duration (2.8 min). The turtle dived directly to a depth of 39 m and remained at that depth for over 60 min before

rapidly ascending to the surface (ascent duration 35 s). Consequently, this dive had a flat-bottomed profile instead of the V-shaped dive profile typically exhibited by this population of leatherback turtles. The turtle spent 3.7 min at the surface before initiating another dive, which lasted only 2 min and was followed by a post-dive surface interval of 31.3 min.

There were significant differences in mean dive depth and mean dive duration during the first and second halves of the internesting interval for three of the four turtles equipped with TDRs. Dives became shallower and shorter for turtles 2566,

Table 2. *Summary statistics for dives during the first 9.5 days of the internesting interval*

Turtle tag number	Number of dives	Mean dive depth (m)	Mean dive duration (min)	Mean SI duration (min)	Mean % time submerged
First 5 days of recording period					
0367	470	19±8	7.4±3.5	5.3±3.4	58.2
2566	497	23±11	9.9±5.4	3.4±1.7	74.4
8866	477	33±20	11.1±5.4	3.8±1.8	74.5
7610	507	35±22	9.5±4.6	3.4±2.3	73.6
Grand mean	488	28±8	9.5±1.5	4.0±0.9	70.4
Last 4.5 days of recording period					
0367	450	17±6	6.9±3.7	5.1±3.7	57.5
2566	551	16±6	5.5±3.1	4.1±2.7	57.3
8866	630	9±8.0	5.0±5.0	2.6±2.2	65.8
7610	584	9±5.0	4.0±2.9	3.6±3.1	52.6
Grand mean	553	13±4	5.4±1.2	3.9±1.0	58.1
Entire recording period, 9.5 days					
0367	920	17±7	7.2±3.7	5.3±3.6	57.6
2566	1048	20±10	8.2±5.2	3.8±2.2	68.3
8866	1107	19±19	7.7±6.0	3.2±2.2	68.4
7610	1091	21±20	6.7±4.8	3.6±2.8	61.5
Grand mean	1041	19±1	7.4±0.6	3.9±0.9	62.1

Values are presented as mean ± S.D.; SI, surface interval (time spent at the surface).
Grand mean is the mean for all turtles.

8866 and 7610 as their internesting intervals progressed. This trend is evident in Fig. 3, which shows a comparison of daily mean depth and mean dive duration for turtle 7610. The mean dive depth for the first 5 days combined was three times deeper than the mean depth for the remainder of the interval and 65 % deeper than the mean depth for the entire internesting interval. Similarly, the mean dive duration for the first 5 days combined was 137 % longer than the mean dive duration for the rest of

the interval and 44 % longer than the mean dive duration for the entire internesting interval. Dives were also significantly deeper and longer during the first half of the internesting interval compared with the second half of the interval for turtles 2566 and 8866 ($P<0.05$).

Individual turtles showed slight differences in mean dive depth, dive duration and surface interval between day (05:00–17:59 h) and night (18:00–04:59 h), but none of the differences was statistically significant ($P<0.05$).

Body size (CCL) was weakly related to dive depth, dive duration and surface interval ($P<0.05$).

Heart rate

Heart rate was measured in five turtles while they were at sea. Fig. 4 shows the typical cardiac response to diving made by a leatherback turtle. Heart rate began to decrease from levels measured at the surface at the start of the dive and continued to fall throughout descent. At mid-dive, heart rates stabilized around the mean dive rate. An increase in heart rate was usually observed during the ascent portion of the dive.

Heart rate and dive variables for each turtle equipped with an ECG recorder are given in Table 3. Dive data presented in Table 3 are for the ECG recording period only and not for the entire internesting interval. The mean dive cycle heart rate for individual turtles during the internesting interval ranged from 18.0 to 20.5 beats min^{-1}. Mean heart rates during diving ranged from 16.1 to 18.6 beats min^{-1} and mean heart rates at the surface ranged from 23.6 to 26.9 beats min^{-1}. Instantaneous heart rates at the surface were as high as 35.7 beats min^{-1}. Cardiac intervals as long as 57.16 s (instantaneous heart rate
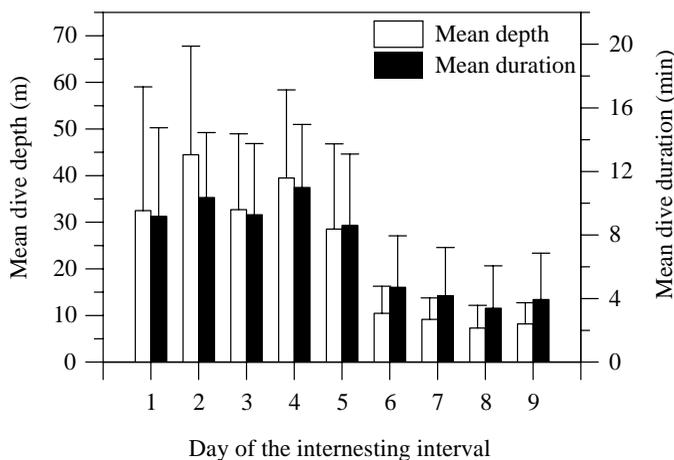

Fig. 3. Daily mean dive depth and mean dive duration over the internesting interval for turtle 7610. Dives are significantly deeper and longer during the first 5 days of the internesting interval compared with the last 4 days of the interval (Mann–Whitney rank test, $P<0.05$). Values are means + S.D.

Table 3. *Heart rates and dive variables for the period of ECG monitoring*

Turtle tag number	Hours analyzed	Number of dives	Mean depth (m)	Mean dive duration (min)	Mean surface interval (min)	Mean dive heart rate (beats min⁻¹)	Mean surface heart rate (beats min⁻¹)	Mean dive-cycle heart rate (beats min⁻¹)
2566	3	13	31±7	12.8±3.4	2.7±0.6	17.0±2.8	23.6±2.8	18.0±3.7
8866	84	344	32±19	10.7±5.5	3.6±1.7	17.8±4.5	26.9±2.7	20.5±6.2
7610	84	367	36±22	9.6±4.7	2.8±1.9	17.6±5.3	25.4±4.1	20.5±6.7
5027	64	230	*	*	*	18.6±3.1	24.1±1.9	20.0±5.5
8364	35	125	*	*	*	16.1±2.2	24.7±1.2	18.0±2.0
Grand mean			33±2	11.0±1.6	3.0±0.5	17.4±0.9‡	24.9±1.3‡	19.4±1.3

Values are presented as mean ± S.D.

*Dive variables are not available for turtles 5027 and 8364.

‡Significantly different from the dive cycle heart rate ($P<0.05$).

1.05 beats min⁻¹) were recorded during a 33 min dive made by turtle 8866.

Fig. 5 shows sections of the ECG trace for turtle 8866 during a surface interval (Fig. 5A), a typical dive (Fig. 5B) and the 34 min dive (Fig. 5C). Cardiac intervals (CIs) during diving were noticeably longer than CIs during the surface interval. Mean dive heart rate (17.4±0.9 beats min⁻¹) was significantly lower than mean surface heart rate (24.9±1.3 beats min⁻¹; $P<0.05$) and was also significantly lower than the mean dive cycle heart rate (19.4±1.3 beats min⁻¹; $P<0.05$; Table 3). Mean surface heart rate was significantly higher than the mean dive cycle heart

rate ($P<0.05$). A linear regression showed that there was a weak positive relationship between mean dive heart rate and the mean post-dive surface interval heart rate ($r^2=0.24$,
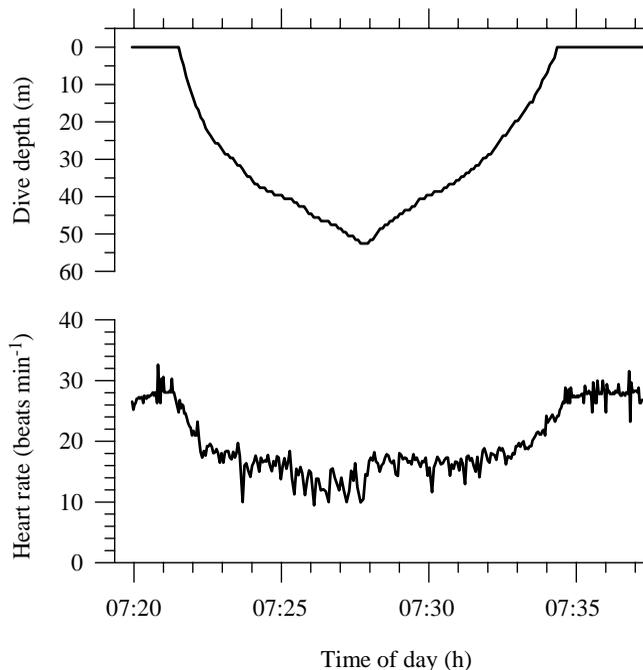

Fig. 4. Dive trace and corresponding heart rate trace for a single dive made by turtle 7610. Heart rate dropped as soon as the turtle submerged and continued to decline during descent. By mid-dive, the heart rate had stabilized between 15 and 17 beats min⁻¹. An increase in heart rate occurred during the ascent.
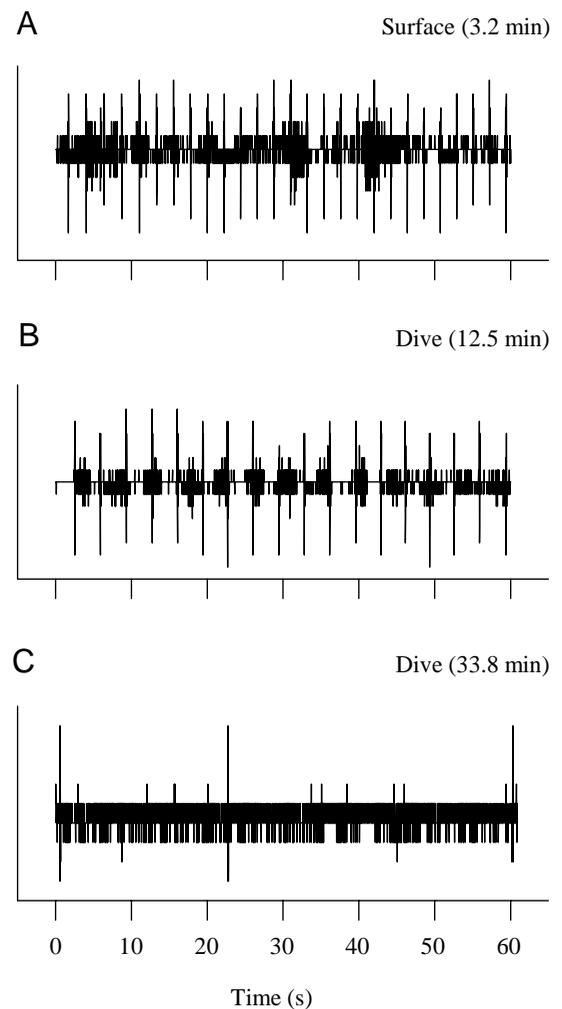

Fig. 5. Electrocardiogram (ECG) traces recorded from turtle 8866 during a surface interval of 3.2 min (A), a dive of 12.5 min (B) and a long-duration dive of 34 min (C). Mean heart rate during the 34 min dive was 3.6 beats min⁻¹, and heart beats occurred arrythmically.
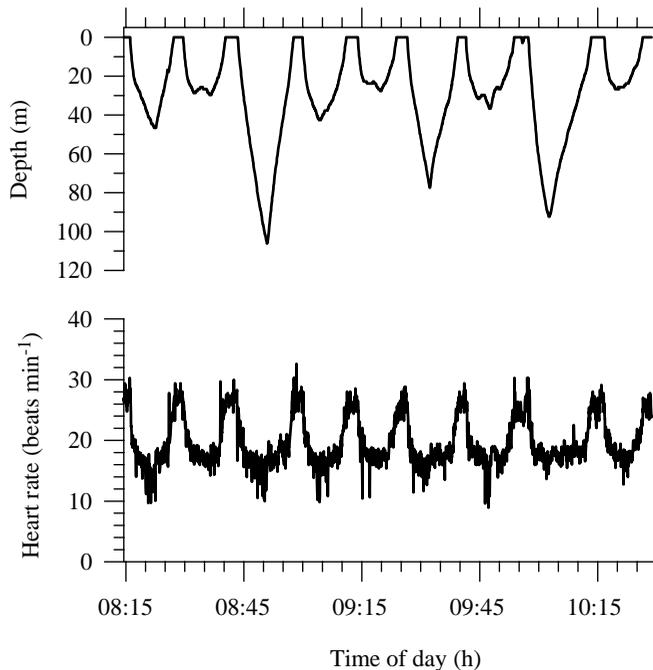
Fig. 6. A 2 h extract from a dive trace and the corresponding heart rate trace for turtle 7610. Although the depth and duration of the dives varied considerably, the heart rate response during diving was consistent. Heart rate dropped to a mean value of 16–17 beats min^{-1} during all dives illustrated.

$P<0.05$). There was no relationship between size as measured by CCL and the mean dive cycle heart rate.

The cardiac response of the leatherback turtle to submergence was fairly consistent from dive to dive. Fig. 6 shows an excerpt of the TDR record of turtle 7610, which consisted of dives of various durations (8–15 min) and depths (25–105 m). The corresponding heart rate trace for this dive sequence showed that the mean dive heart rate dropped to approximately 16 beats min^{-1} regardless of the depth of the dive or how long the dive lasted. A linear regression of dive duration on mean dive heart rate showed that the negative relationship between these two variables was not strong ($r^2=0.227$, $P<0.05$). Similarly, there was only a weak negative relationship between dive depth and mean dive heart rate ($r^2=0.241$, $P<0.05$).

The mean heart rate of turtles laying eggs on the beach was 18.3–22.3 beats min^{-1}. During egg deposition, the lowest instantaneous heart rate was 8.8 beats min^{-1} and the highest instantaneous heart rate was 29.4 beats min^{-1}.

Discussion

Diving behavior

Previous studies conducted in the Caribbean Sea and the South China Sea have described the dive patterns of leatherback females during the internesting interval. This study provides the first detailed records of dives performed by leatherback turtles from an Eastern Pacific nesting population.

Leatherback turtles from the Eastern Pacific, Caribbean and South China Sea all show a pattern of continual diving punctuated by brief surface intervals. However, turtles from the Playa Grande population displayed some trends in their diving behavior that have not been described for other populations of leatherback females. A trend of decreasing dive depth and duration as the internesting interval progressed was observed in three of the four turtles equipped with TDRs. The shallow diving towards the end of the internesting interval may indicate that turtles are close to shore, where dive depth may be limited by shallow water depth. In addition to the significantly shorter and shallower dives observed late in the internesting interval, most of the exceptionally long surface intervals (longer than three times the mean surface interval) occurred during this time. If these long intervals are true representations of surface time, then turtles may be basking or resting at the surface. However, since only dives deeper than 4 m were analyzed, and submergences to depths of less than 4 m were treated as surface time by the analysis program, there is a possibility that the turtles were making shallow dives to depths above the dive criterion. Whether or not turtles were basking or making shallow dives during the extended 'surface intervals', the question of why these turtles altered their pattern of diving behavior in the middle of the internesting interval remains unanswered.

Turtles from the Playa Grande nesting population dived to relatively shallow mean depths (mean 17–21 m) during the internesting interval. The continental shelf off the north Pacific coast of Costa Rica extends for a distance of approximately 18 km offshore and the water is only 60–125 m deep. Leatherback turtles are capable of swimming at speeds of 9 km h^{-1} (Standora et al., 1984; Keinath and Musick, 1993), so turtles nesting at Playa Grande are capable of reaching the deep water beyond the continental shelf during the 9–10 day internesting interval. However, the relatively shallow diving observed in these turtles and the maximum observed dive depth of only 124 m suggest that turtles may have remained on the continental shelf during this time.

Previous accounts of the diving behavior of the leatherback turtle have shown significant differences in mean dive depth, dive duration and surface interval between day and night (Eckert et al., 1989, 1996). Dives were deepest and longest at daybreak. As the day progressed, the depths and durations of the dives decreased, and by nightfall dives were consistently short and shallow. Eckert et al. (1989) hypothesized that the routine shallow dives made in the evenings represented foraging in the deep scattering layer (DSL), since the DSL rises towards the surface at dusk to depths frequented by leatherback turtles (Boden and Kampa, 1967). There were no consistent diel patterns for depth or dive duration in our study. Several studies have shown that leatherback turtles spend more time at the surface during the daylight hours than at night (Standora et al., 1984; Eckert et al., 1989, 1996), but there was no significant difference in surface intervals between day and night for turtles from the Playa Grande population. Long-duration surface intervals were observed during both day and

night in the current study, so basking behavior cannot fully account for extended periods at the surface.

Heart rate

In leatherback sea turtles, dive heart rates were significantly lower than surface heart rates. Overall, turtles displayed a fairly uniform cardiac response to diving, both in the pattern of heart rate changes and in the degree of change from the surface condition to the dive condition. In fact, the degree to which leatherback turtles lowered their heart rate during submergence was largely independent of dive depth and dive duration. The lack of a strong relationship between mean dive heart rate and dive depth (r^2=0.24, P<0.05) may be due to the fact that turtles from the Playa Grande population did not dive to a wide range of depths. The deepest dive we recorded in this study was only 124 m, and a frequency distribution shows that the majority of dives were less than 30 m. Similarly, the fact that the majority of dives made by Playa Grande turtles lasted for less than 10 min may account for the weak relationship between mean dive heart rate and dive duration (r^2=0.23, P<0.05). Heart rates during exceptionally long dives were well below the average dive heart rate, but these extended dives occurred rarely during the monitoring period. The longest dive that occurred during the ECG recording period lasted 33.8 min, and the mean heart rate during this dive was 3.6 beats min^{-1} (Fig. 5C), with instantaneous heart rates as low as 1 beat min^{-1} (CI=57.16 s).

Heart rate declined immediately upon submergence and continued to fall during the descent portion of the dive. During the ascent portion of the dive, leatherback turtles displayed an increase in heart rate. Many other diving animals increase their heart rate towards the end of a dive in anticipation of surfacing (Butler and Jones, 1997). Thompson and Fedak (1993) suggested that an anticipatory tachycardia might restore blood flow to peripheral tissues, flushing out metabolites that may have built up and allowing for a more efficient removal of metabolic by-products and uptake of oxygen during recovery time at the surface.

Leatherback turtles from the Playa Grande population spent 57–68 % of the internesting interval submerged. Belkin (1964) proposed that dive heart rates were actually the 'normal' heart rates for animals that spend most of their time submerged and that heart rates at the surface actually represented a tachycardia. Increases in heart rate at the surface allow a more rapid renewal of oxygen stores and removal of CO_2. The northern elephant seal has an extremely high surface tachycardia which allows it to spend a minimum of time at the surface between dives (Andrews et al., 1997). The mean surface heart rate (107.3 beats min^{-1}) for this species is 174 % higher than the mean dive heart rate (39.0 beats min^{-1}), and elephant seals typically spend 90 % of a dive cycle submerged. In contrast, heart rates of leatherback turtles at the surface (mean 24.9 beats min^{-1}) are only moderately higher (43 %) than heart rates (mean 17.4 beats min^{-1}) during diving. Differences in the degree of surface tachycardia may explain why leatherback turtles spend a greater proportion of time at the surface than do elephant seals. Relatively long surface intervals may also play a role in temperature regulation in the leatherback turtle.

Leatherback turtles also spend a lower percentage of time submerged and dive for shorter periods (4–14 min) than other species of sea turtles (Eckert et al., 1986, 1989; Lutcavage and Lutz, 1997; current study). Routine dive durations for adult loggerhead and Kemp's ridley turtles range from 13 to 30 min, and these turtles spend 80–96 % of their time at sea submerged (Sakamoto et al., 1990; Soma, 1985; Byles, 1988; Mendonca and Pritchard, 1986). Although measurements of at-sea heart rate are unavailable for any of the cheloniid sea turtles, laboratory studies with green turtles (*Chelonia mydas*) have shown that this species is capable of doubling its heart rate during ventilatory periods (Berkson, 1966; Butler et al., 1984; West et al., 1992). Cheloniid species of sea turtles use their lungs as the primary oxygen store while diving and have relatively large lung tidal volumes, which may also contribute to rapid CO_2 unloading and O_2 loading at the surface (Lutcavage and Lutz, 1991).

Apart from the current study, all heart rate data available for sea turtles have been collected in a laboratory or on a beach. Mean heart rates for green turtles resting in a laboratory swim channel ranged from 24 to 51 beats min^{-1}, and maximal rates of 46–68 beats min^{-1} were obtained from exercising turtles (Davenport et al., 1982; Butler et al., 1984; West et al., 1992). Green turtles that were forced to dived had heart rates as low as 2–10 beats min^{-1} (Berkson, 1966). Considering the large size difference between the adult leatherback turtles in this study (250–400 kg) and sub-adult green turtles (13–22 kg), the ranges of heart rates observed for both species are surprisingly similar.

There is little information available on heart rates in other voluntarily or freely diving reptiles. Laboratory studies with caimans, aquatic snakes and freshwater turtles show that these animals experience a moderate bradycardia during voluntary dives (Belkin, 1964; Gaunt and Gans, 1969; Jacob and McDonald, 1976; Ware, 1993). Smith et al. (1974) recorded heart rates from a freely diving alligator using radio telemetry, and found that there was no significant difference between the heart rate at the surface and the heart rate during short routine dives in the wild. Heatwole et al. (1979) recorded heart rate from sea snakes (*Aipysurus laevis* and *Acalyptophis peronii*) diving freely in a lagoon. Unlike the previous laboratory and field studies on the diving responses in reptiles, this study described heart rates for both resting and active dives. While heart rate during a resting dive (13 beats min^{-1}) was less than the heart rate at the surface (34 beats min^{-1}), heart rates for snakes that were swimming while submerged (21–42 beats min^{-1}) were similar to heart rates at the surface. The few data available on heart rates in reptilian divers show that, in general, surface heart rates and heart rates during routine voluntary dives are only moderately different from each other. The dive response of the leatherback turtle follows this general trend.

In the present study, heart rates during a single dive and the accompanying post-dive surface interval were combined to

calculate the mean dive cycle heart rate. Since leatherback turtles are probably aerobic divers, there should be no overall accumulation of metabolites or depletion of oxygen stores at the end of the dive cycle. If this is the case, then the mean dive cycle heart rate represents the heart rate necessary to meet the metabolic needs of the turtle. Dive cycle heart rates for leatherback sea turtles (18.0–20.5 beats min^{-1}) were more similar to dive heart rates (16.1–18.6 beats min^{-1}) than to surface heart rates (23.6–26.9 beats min^{-1}), reinforcing the idea that heart rates at the surface represent a tachycardia. Dive heart rates were slightly lower ($P<0.05$) than the dive cycle heart rates, suggesting that leatherback turtles may need to conserve oxygen to maintain aerobic metabolism while submerged.

The period that an animal may remain submerged without any build-up of lactate in the blood, during or after the dive, is referred to as the aerobic dive limit (ADL) (Kooyman et al., 1983). If blood lactate levels are not measured directly, then the ADL of an animal may be calculated by using estimates of metabolic rate and total available oxygen stores (ADL$_C$) (Kooyman et al., 1983; Butler and Jones, 1997). A 340 kg leatherback turtle has a total oxygen store of approximately 27 ml kg^{-1} (Lutcavage et al., 1990). At-sea measurements of metabolic rate are unavailable for the leatherback turtle, so the ADL$_C$ for this species has been calculated using metabolic rates of leatherback females on a nesting beach. Lutcavage et al. (1990) reported a mean $\dot{V}_{O_2}$ of 0.25 ml min^{-1} kg^{-1} for unrestrained leatherback females laying eggs and a mean $\dot{V}_{O_2}$ of 1.09 ml min^{-1} kg^{-1} for turtles restrained in a cargo net on the beach (Lutcavage et al., 1992). Paladino et al. (1996) reported similar values for $\dot{V}_{O_2}$ of restrained turtles (mean 1.2 ml min^{-1} kg^{-1}) and a mean $\dot{V}_{O_2}$ of 3.7 ml min^{-1} kg^{-1} for turtles covering nests or walking on a beach (Paladino et al., 1990). Using this range of values for $\dot{V}_{O_2}$, the ADL$_C$ for a 340 kg leatherback turtle is estimated to range from 5 to 70 min (Lutcavage et al., 1992).

Examination of heart rate data and diving records may allow us to narrow the wide range of ADL$_C$ estimates. Leatherback turtle heart rates during egg deposition ranged from 8 to 29 beats min^{-1}, with average rates of 18–22 beats min^{-1}. Heart rates of restrained turtles on the beach were much higher, 43–48 beats min^{-1} (Lutcavage et al., 1992). Given the similarity between dive heart rates (17–20 beats min^{-1}) and heart rates during egg deposition, the use of metabolic rates recorded from nesting turtles, as opposed to restrained or active turtles, may give a more valid estimate of the ADL$_C$ of the leatherback turtle. In this case, the leatherback turtle has an ADL$_C$ at the higher end of the range of estimates (up to 70 min).

The longest dive recorded in this study was a 67.3 min submergence (Fig. 2A). The rapid ascent of this turtle to the surface at the end of the 67.3 min dive, as well as the occurrence of a 31 min surface interval shortly after this dive, implies that the turtle may have exceeded her ADL. Another long-duration dive made by this same turtle lasted 33.8 min. The post-dive surface interval for this dive was only 3.7 min, and the turtle continued to dive regularly after this dive cycle.

The brief recovery time at the surface following this long-duration dive suggests that the animal had sufficient oxygen to last for the entire dive and did not exceed her ADL$_C$. It is reasonable to assume that the ADL$_C$ for this turtle (estimated mass 274 kg) is between 33 and 67 min.

Routine dive durations for leatherback turtles during the internesting interval are well below the estimates of ADL$_C$ for this species. Metabolic rates at sea may be higher than the metabolic rates observed during egg deposition because of the costs of reproduction, swimming and foraging. More detailed information about the behavior and metabolic rate of the leatherback turtle during the internesting interval may give insight into the dive patterns and the physiological response to diving exhibited by this turtle.

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