

HEART RATES AND DIVE BEHAVIOUR OF  
THE LEATHERBACK SEA TURTLE  
(*Dermochelys coriacea*)

by

AMANDA LEAH SOUTHWOOD

B.Sc., Auburn University, 1993

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF  
THE REQUIREMENTS FOR THE DEGREE OF

MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES

(Department of Zoology)

We accept this thesis as conforming  
to the required standard

The University of British Columbia

July, 1997

© Amanda Leah Southwood

In presenting this thesis in partial fulfilment of the requirements for an advanced degree at the University of British Columbia, I agree that the Library shall make it freely available for reference and study. I further agree that permission for extensive copying of this thesis for scholarly purposes may be granted by the head of my department or by his or her representatives. It is understood that copying or publication of this thesis for financial gain shall not be allowed without my written permission.

Department of Zoology

The University of British Columbia  
Vancouver, Canada

Date 5 August 1997

## ABSTRACT

Diving bradycardia, or a decrease in heart rate while diving, has been observed in a wide variety of species, from frogs to seals. The degree to which an animal lowers its heart rate during a submergence may vary depending on the behaviour of the animal. The leatherback sea turtle (*Dermochelys coriacea*) is an active diver, and has a metabolic rate that is higher than expected for a reptile of its size. The purpose of this research was to gain an understanding of the cardiovascular response to diving made by the leatherback turtle and to integrate this information with what is known of the turtle's diving behaviour and metabolism.

Instruments capable of recording heart rate, dive duration and dive depth were deployed on leatherback females as they lay eggs on a nesting beach. Heart rate and diving variables were recorded during the internesting interval when turtles were freely diving at sea. Instruments were recovered when the turtles returned to the nesting beach to lay more eggs. Relationships between the turtle's diving behaviour and heart rate were examined, and comparisons were made between diving heart rates, surface heart rates, and long-term heart rates.

Dive records show that leatherback turtles dive continually throughout the internesting interval. The brief amount of time spent at the surface between dives suggests that these turtles rely mainly on aerobic metabolism for routine dives, and all observed dives fell within the calculated aerobic dive limit. No significant diel differences existed for leatherback turtles from the Playa Grande nesting population, but dives became

shorter and shallower as the interesting interval drew to a close. Neither dive duration nor dive depth was strongly related to heart rate.

Diving heart rates were significantly lower than surface heart rates for leatherback turtles. The most likely cause of the observed diving bradycardia is increased pulmonary resistance accompanied by variable degrees of systemic perfusion. The fact that decreases in heart rate during diving were not extreme suggests that turtles do not drastically lower their metabolic rate while diving during the interesting interval. Long-term heart rates were more similar to diving heart rates than to surface heart rates.

## TABLE OF CONTENTS

ABSTRACT . . . . .	ii
TABLE OF CONTENTS . . . . .	iv
LIST OF TABLES . . . . .	v
LIST OF FIGURES . . . . .	vi
ACKNOWLEDGMENTS . . . . .	vii
INTRODUCTION . . . . .	1
METHODS . . . . .	8
Field Procedures . . . . .	8
Instrumentation . . . . .	12
Statistics and Analysis . . . . .	14
RESULTS . . . . .	17
Dive Behaviour . . . . .	17
Heart Rate . . . . .	22
DISCUSSION . . . . .	32
Dive Behaviour . . . . .	32
Heart Rate . . . . .	39
Conclusions . . . . .	48
BIBLIOGRAPHY . . . . .	50

## LIST OF TABLES

Table 1. Dive statistics for individual turtles . . . . .	20
Table 2. Mean dive variables for the first and second half of the internesting interval, as well as a diel comparison of dive variables . . . . .	24
Table 3. Heart rate statistics for individual turtles . . . . .	26
Table 4. Comparison of heart rate and metabolic rate for sea turtles . . .	46

## LIST OF FIGURES

Figure 1. Map of Costa Rica . . . . .	9
Figure 2. Diagram showing placement of recording instruments and ECG leads on turtle's shell. . . . .	10
Figure 3. Photograph of a turtle (PT2566) with data logger and and ECG leads attached to carapace . . . . .	11
Figure 4. Dive trace recorded from PT8866 on 11/11/96 . . . . .	18
Figure 5. Long duration dives recorded from PT8866 . . . . .	21
Figure 6. Comparison of mean dive depth and mean dive duration for each day of PT7610's 9-day interesting interval . . . . .	23
Figure 7. ECG recorded from PT7610 during a single dive cycle . . . . .	27
Figure 8. A single dive and the corresponding heart rate trace for PT7610 . . . . .	29
Figure 9. Dive record and corresponding heart rate trace for PT7610. . .	30
Figure 10. Dive record and corresponding heart rate trace for PT2566 . .	31

## ACKNOWLEDGMENTS

This study would not have been possible without the cooperation of numerous friends and colleagues. I am most grateful to my supervisor, David R. Jones, for his support of this project and to Russel Andrews for his generous donation of time and expertise. I also thank Molly Lutcavage for her encouragement throughout the course of this study. Robert George, Nigel West, Robin Liley, Charles Blaney, and Jennifer Goldstein all participated in the deployment of instruments on the beach. Frank Paladino, Pamela Plotkin, and Jim Spotila provided logistical support at the beach, and the Costa Rican government granted the permits to conduct research at Playa Grande. Earthwatch provided funds for travel and accomodation in Costa Rica, and Earthwatch staff and volunteers, as well as Las Baulas National Park personnel, assisted in the retrieval of instruments. I am indebted to them all. I would also like to express my gratitude towards the members of my research committee, Bill Milsom and Peter Hochachka. Finally, I would like to thank Timothy D. May for his unconditional support over the past two years. His kindness and strength are an inspiration to me.



## INTRODUCTION

The leatherback sea turtle (*Dermochelys coriacea*) is a migratory reptile that ranges from tropical to Arctic waters (Bleakney, 1965). With records existing for dives exceeding 1000 meters of seawater (MSW) (Eckert et al., 1989), the leatherback turtle is one of the deepest divers in the ocean, along with sperm whales and elephant seals (Kooyman, 1989). Adult leatherback turtles are the largest of the marine turtles, and commonly weigh 300 - 600 kg (Pritchard, 1971). Unlike all other species of sea turtles, the leatherback turtle is a pelagic forager, feeding primarily on jellyfish and the invertebrates and algae associated with the jellyfish (Brongersma, 1969; Eisenberg & Frazier, 1983; Grant et al., 1996). Perhaps because of their distinct foraging strategy, leatherback turtles display a different pattern of diving than is observed for other sea turtles (Hendrickson, 1980; Eckert et al., 1989). Chelonid sea turtles feed primarily on the algae, sea grasses, and invertebrates found on the ocean floor in coastal waters. As benthic foragers, these turtles spend large amounts of time either at the sea floor or suspended in the water column. In contrast, the leatherback turtle is an active diver that spends the majority of dive time traveling vertically through the water column, thereby optimizing its chance for encountering pelagic prey (Eckert et al., 1986; Eckert et al., 1989).

The leatherback turtle has a suite of morphological and physiological adaptations that support its foraging and diving behaviour and set it apart from chelonid sea turtles. Phylogenetically, the leatherback turtle is placed in a family of its own (Dermochelyidae)

while all other extant sea turtles belong to the family Cheloniidae. One of the leatherback turtle's more distinct morphological characteristics is its unique shell. Most turtles have a hard shell composed of bony scutes, but the leatherback turtle's shell is made of a cartilaginous matrix and covered by a smooth leathery dermis (Pritchard, 1971). The flexible shell provides a greater degree of compliance under increased hydrostatic pressure at depth (Kooyman, 1989). The shape of the shell is barrel-like anteriorly and tapers to a blunt tip posteriorly. This teardrop shape, combined with the carapace's prominent dorsal ridges, is beneficial in reducing drag and increasing swimming efficiency (Deraniyagala, 1936; Hendrickson, 1980). Some skeletal features of the leatherback turtle are also distinct from the patterns observed in chelonid sea turtles. The leatherback turtle has a distribution of bone and cartilage that is similar to the chondro-osseous morphology of cetaceans, manatees, pinnipeds, and penguins (Rhodin et al., 1981).

In addition to the similarities in bone and cartilage morphology, leatherback turtles and marine mammals also show similarities in certain physiological characteristics. In some ways, leatherback physiology more closely resembles marine mammal physiology than the typical reptilian physiology. For instance, leatherback turtles store the majority of oxygen for dives in the blood and tissues, whereas all chelonid sea turtles and sea snakes use the lungs as the major oxygen store (Butler & Jones, 1982; Lutcavage et al., 1992; Lutcavage, 1997). The leatherback turtle has a higher hematocrit (Hct) and hemoglobin concentration ([Hb]) relative to chelonid turtles, resulting in an increased blood oxygen carrying capacity. Also, a comparatively high concentration of myoglobin ([Mb]) allows an increased amount of O<sub>2</sub> to be stored in the muscle. By storing the majority of oxygen

in the blood and tissues, the leatherback turtle and deep-diving marine mammals may ensure that oxygen remains available during dives to depths where the lungs collapse.

For aerobic divers, the amount of oxygen available during a dive is a determinant of dive duration. The aerobic dive limit (ADL) is defined as "the maximum breath-hold that is possible without any increase in blood LA (lactate) concentration during or after the dive" (Kooyman et al., 1983), and is determined by the oxygen stores available during the dive and the rate at which oxygen is consumed (metabolic rate). Mass specific metabolic rate scales inversely with body size, so in a given class a larger animal has a lower mass-specific metabolic rate than a smaller animal (Schmidt-Nielsen, 1984). Large animals also have greater oxygen stores than do small animals, due in part to larger blood volumes (Schmidt-Nielsen, 1984). The relationship between body size and these two variables leads to the conclusion that large animals should have a longer ADL than smaller animals of a similar design (Schreer and Kovacs, 1997). The adult leatherback turtle's total oxygen store is  $27.4 \text{ ml O}_2 \text{ kg}^{-1}$  (Lutcavage et al., 1992; Lutcavage, 1997) and resting metabolic rate of turtles on a nesting beach ranges from  $0.25 \text{ ml min}^{-1} \text{ kg}^{-1}$  to  $1.15 \text{ ml min}^{-1} \text{ kg}^{-1}$  (Paladino et al., 1990; Lutcavage et al., 1992). Based on these figures, Lutcavage et al. (1992) calculated an ADL of 70 minutes for an average sized adult leatherback turtle. A subadult (15 kg) loggerhead turtle's total oxygen store is  $22.2 \text{ ml O}_2 \text{ kg}^{-1}$  (Lutz & Bentley, 1985) and the resting metabolic rate for a 13 kg loggerhead turtle is  $1.0 \text{ ml min}^{-1} \text{ kg}^{-1}$  (Lutz et al., 1989). Lutz calculated an ADL of 33 minutes for a 20 kg loggerhead turtle (Lutz and Bentley, 1985), which is considerably shorter than the adult leatherback turtle's calculated ADL. Although leatherback turtles have the ability to

remain submerged and metabolize aerobically for twice as long as the smaller loggerhead turtle, leatherback turtle dive durations seldom last over 30 minutes. In fact, the average leatherback turtle dive time (4 - 14.5 minutes)(Standora et al., 1984; Eckert et al., 1989; Keinath and Musick, 1993) is considerably shorter than the average loggerhead (14.8 - 30 minutes)(Sakamoto et al., 1990; Soma, 1985; Byles, 1988) or green turtle (9 - 23 minutes)(Brill et al., 1995) dive times, despite the leatherback turtle's size advantage. Decreased dive duration may be an indication that the turtle's metabolic rate during diving is higher than the resting metabolic rate observed on the beach. The ADL was calculated using resting metabolic rate, and does not take into account the effect of activity, such as swimming or foraging, on the rate of oxygen consumption.

Leatherback turtles may have a higher metabolic rate at sea than while resting on the beach due to the energetic cost of thermoregulation. Leatherback turtles are capable of maintaining an elevated core body temperature in relation to ambient temperature. Friar et al. (1972) found that a leatherback turtle captured off the coast of Nova Scotia could maintain a core body temperatures of 25°C in ambient water temperatures of 7.2°C. This observation led some to speculate that the leatherback turtle was a "warm-blooded" reptile (Greer et al., 1973; Goff and Stenson, 1988). A study by Paladino et al. (1990) revealed that the leatherback turtle's metabolic rate was greater than would be expected for a green turtle scaled to leatherback turtle size, but still only half that of a similarly sized mammal. They concluded that the leatherback turtle was not endothermic, rather, it had a unique thermal biology which they called "gigantothermy". The concept of gigantothermy is based on the relationship between volume and surface area. As an animal's size

increases, volume increases by a factor of three, whereas surface area only increases by a factor of two (Schmidt-Nielsen, 1984). Large animals have a smaller surface-to-volume ratio than smaller animals of a similar shape, and therefore have a relatively smaller surface area over which heat can escape. Paladino argued that even if the leatherback turtle had a reptilian metabolism, it would be able to maintain a high core body temperature in cold water by means of its large body size, countercurrent heat exchangers in the flippers (Greer et al., 1973), and the use of peripheral tissues as insulation.

Current knowledge of the leatherback turtle's physiology is based on studies conducted with nesting turtles. Those studies have provided valuable information about the partitioning of oxygen stores (Lutcavage et al., 1990), metabolism (Paladino et al., 1990; Lutcavage et al., 1992) and thermoregulation (Paladino et al., 1990). The physiological response to diving in the leatherback turtle has never been explored, due to the difficulties of studying an oceanic species in its natural habitat. Diving bradycardia is one of the main components of the "classical" dive response described by Irving (1941) and Scholander (1940). A decrease in heart rate results in slower delivery of oxygen to tissues, and may serve as a means for oxygen conservation during a dive. However, the rate of oxygen delivery to the tissues, as determined by cardiovascular adjustments, must be sufficient to meet metabolic demands if the animal is to maintain aerobic metabolism. Therefore, the degree to which an animal lowers its heart rate while diving depends on the nature and purpose of the dive. An animal foraging for underwater prey may display only a moderate diving bradycardia or no bradycardia at all, whereas an animal resting underwater may reduce heart rate to very low levels. The compromise between the dive

response and dive behaviour has been addressed often in the literature for marine mammals (Castellini et al., 1985; Fedak, 1986; Fedak et al., 1988; Butler, 1988; Castellini & Kooyman, 1989). Although several researchers have published accounts of the diving behaviour of leatherback turtles in the wild (Standora et al., 1984; Eckert et al., 1986; Eckert et al., 1989; Keinath et al., 1993; Morreale et al., 1996), none of these studies address the physiological mechanisms that underlie the observed behavior.

The diving physiology and behaviour of the leatherback turtle is of particular interest since this turtle is recognized as an endangered species by the U.S. Endangered Species Act and Canada's COSEWIC (Committee on the Status of Endangered Wildlife in Canada). The incidental capture of leatherback turtles in shrimp trawls, fishing nets, crab pots, and derelict fishing gear poses a major threat to the survival of this species (Goff & Lien, 1988; NMFS, 1992; Witzell & Cramer, 1995). A knowledge of diving patterns and the physiological limitations of the leatherback turtle are essential in devising and implementing conservation measures to prevent turtle mortality due to accidental capture in fishing gear.

One might suspect that the combination of large size and a reptilian metabolism would allow the leatherback turtle to make long duration voluntary dives, and perhaps even endure prolonged enforced submergence, by means of a large oxygen store, low metabolism, and low heart rate (Schmidt-Nielsen, 1984; Schreer & Kovacs, 1997). However, typical dive durations for a leatherback turtle are relatively short, and the turtle's metabolic rate is higher than would be expected for a reptile of this size. Thermoregulatory demands, as well as the energetic costs of reproduction and foraging,

may temper the effects of the "classical" dive response during the internesting interval.

The current research was undertaken to test the hypothesis that leatherback turtles experience a significant, but moderate, diving bradycardia while freely diving at sea during the internesting interval.

To test this hypothesis, data loggers capable of recording heart rate, dive depth, dive duration, and surface interval were deployed on female leatherbacks nesting on the northwest Pacific coast of Costa Rica. Like other species of sea turtles, female leatherbacks return to their natal beach every two to three years to lay eggs. The majority of information regarding leatherback physiology and behaviour is gained by studying turtles on a nesting beach, as intentional at-sea encounters with this species are rare. The nesting season for leatherbacks in the Eastern Pacific lasts from late October to early March. During this period of approximately four months, a female leatherback may lay as many as 10 clutches of eggs on the same beach, returning to the offshore waters for 7 to 14 days between nesting (Steyermarker et al., 1996). The period of time spent at sea in between nesting is referred to as the internesting interval. The leatherback turtle's instinctive behaviour of repeatedly returning to the same beach during a single nesting season provides the necessary paradigm for attachment and retrieval of physiological recorders.

## METHODS

### *Field Procedures*

Research for this thesis was conducted at Playa Grande, Guanacaste, a leatherback nesting beach located in Las Baulas National Park on the northwest Pacific coast of Costa Rica (Figure 1). Playa Grande supports one of the highest nesting populations of leatherback females in the Eastern Pacific Ocean (Steyermark et al., 1996). Over the course of the 1995-1996 and 1996-1997 nesting seasons, VHF radio transmitters and data loggers (see *Instrumentation*) were deployed on seven nesting leatherback females on the beach. Instruments were attached to the turtle's shell as she laid eggs and camouflaged her nest cavity. Figures 2 and 3 show where the instruments and electrocardiogram (ECG) leads were attached to the turtle's carapace. Three small holes (13/64" diameter) were drilled in the caudal peduncle region of the carapace using a battery-powered hand-held drill (Makita Corporation of America). Holes were immediately flushed with Betadine antiseptic and treated with Gentamycin Sulfate antibiotic cream. Flexible stainless steel wire surrounded by Tygon tubing was inserted in the holes in the carapace, then passed through loops in the recording instrument. The wire was pulled taut and the free ends of the wire were twisted together so that the recording instrument was secured to the shell. A layer of foam padding lay between the instrument and the turtle's carapace to prevent chaffing.

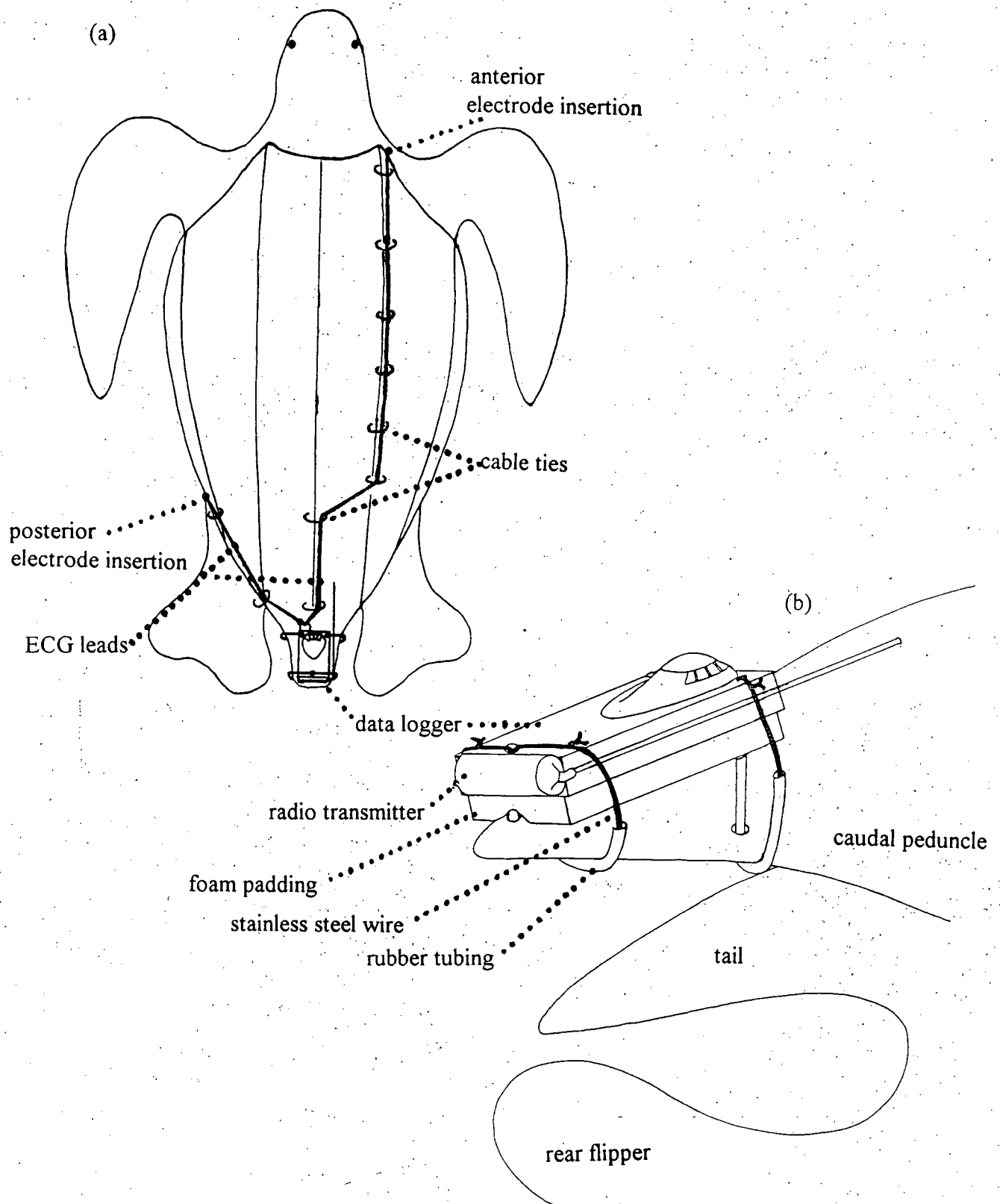
Heart rate was recorded using two stainless steel thin wire electrodes, which were inserted with an 18 gauge sterile needle at a point where skin and shell fused and



Figure 1.

Map of Costa Rica. The study was conducted in Las Baulas National Park on the northwest Pacific coast. The park is designated by the number "5" and is located south of the Gulf of Papagayo. Park boundaries are outlined in green on this map. (Map courtesy of M.L. Smith, ©1995)





**Figure 2.**  
 Diagram showing placement of recording instruments and ECG leads on turtle's shell.  
 (a) Dorsal view of a leatherback with a data logger and ECG leads attached to carapace.  
 (b) View of caudal peduncle with data logger attached.



Figure 3.

Photograph of a turtle (PT2566) with data logger and ECG leads attached to carapace. The data logger is secured to the rear portion of the shell (caudal peduncle) with flexible stainless steel wire. The anterior ECG lead (red wire) runs along the second from lateral ridge and is secured to this ridge with white plastic cable ties. The posterior ECG lead is not visible in this photograph. (Photograph courtesy of R.D. Andrews)

positioned along the inner surface of the shell. The anterior electrode was inserted 6" deep above the right forelimb, and the posterior electrode was inserted 10" deep immediately anterior to the left hindlimb. Electrodes were secured at the point of insertion by surgical silk sutures (Ethicon, Inc.). An additional ten holes (1/8" diameter) were drilled along the dorsal ridges (two holes on the median ridge, six holes on the second from 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 by cable ties passed through these holes.

ECG and diving variables were recorded during the interesting interval when the turtle was diving freely at sea. A radio transmitter was attached to the recording unit so that the turtle could be located when she returned to the beach to lay another clutch of eggs. The instruments and electrodes were removed at this time, and the data was downloaded onto a laptop computer.

### *Instrumentation*

Over the course of the two field seasons, various types of instruments were used to record ECG. Initially, ECG was recorded with a custom-designed Tattletale Lite data logger (Onset Computer Corp.) which will be referred to as TL1. The ECG amplifier in this data logger was based on a modified commercial sports monitor (Polar Electro Inc.). Data were recorded at a frequency of 50Hz and stored as analogue-to-digital (A/D) readings. This prototype data logger was also capable of recording dive depth and dive duration. The pressure circuit included a pre-calibrated Keller PSI pressure transducer



with a resolution of 4 MSW (meters of seawater) over a range of 0 - 1000 MSW. Depth was recorded every 5 seconds and stored as an A/D reading. This data logger had a memory of 512 kilobytes (kb) and was used to record ECG and diving variables from one turtle for 3 hours.

In order to record diving variables for a longer period of time, another instrument consisting of two Tattletale Lite data loggers was made. One of the data loggers (TL2) was used solely for recording ECG. The ECG circuit was identical to the circuit used in TL1. Memory of the data logger was 512kb, so the instrument was capable of recording ECG at a frequency of 50Hz for a period of 3 hours. The second data logger was modified to record dive depth and dive duration, and will be referred to as a TDR (time-depth recorder). The pressure circuit was identical to the circuit used in TL1 (resolution = 4 MSW over a range of 0 - 1000 MSW). With a memory of 512kb and a sampling frequency of 5 seconds, the TDR recorded diving variables for a period of 9.5 days. This combination of data loggers (TL2/TDR) was used with one turtle. A TDR without the accompanying TL2 was also deployed in order to record only dive variables from another turtle.

For the 1996 - 1997 field season, TDR resolution was increased to 1 MSW over a range of 0 - 500 MSW. The new TDR model was coupled with a Model 8 data logger (Onset Computer Corp.) to record ECG. The ECG circuit in the Model 8 also contained a modified Polar amplifier. The Model 8 had a 15 megabyte (Mb) memory and was capable of recording ECG at a frequency of 50Hz for 3.5 days. The M8/TDR combination was used to record ECG and diving variables from three turtles.

All of the instruments were encased in Sealtronics epoxy (Industrial Formulators of Canada, Ltd.). ECG electrode leads were soldered directly to the instruments, and the solder joints were coated with a layer of 5-minute epoxy (Industrial Formulators of Canada, Ltd. ) as well as an additional outer layer of Sealtronics epoxy for added protection. A VHF radio (Holohil Systems, Ltd.) was glued to each instrument with Fastweld™ 10 (Ciba-Geigy Corp.) epoxy.

### *Statistics and Analysis*

Dives were analyzed for maximum depth, dive duration and post-dive surface interval using the Dive Analysis (DA) program issued by Wildlife Computers. Dive depth was defined as the maximum depth attained during the dive. For the TL1 and TL2/TDR data loggers, only dives deeper than 8 MSW were analyzed. The M8/TDR data loggers had increased depth resolution, so dives deeper than 4 MSW could be analyzed. The turtle was considered to be at the surface if depth readings were less than 3 MSW. If turtles made a dive or series of dives to less than 3 MSW, the analysis program would not be able to distinguish these submergences from a surface interval. Due to the possibility that turtles make shallow dives to depths above the surface interval criterion, dives with surface intervals that were 3 times longer than the individual's mean surface interval were excluded from analysis.

Descriptive statistics and frequency distributions for depth and duration of dives, as well as surface intervals, were calculated for each individual turtle. The relationship between dive duration and dive depth was examined using a 2nd order polynomial

regression, and linear regression was used to examine the relationship between dive duration and the subsequent surface interval. Due to high variability in the diving data, comparisons between turtles were made using non-parametric tests. Linear regressions were used to determine if size influenced dive duration or dive depth.

Dive records were broken down into 24 hour periods beginning with the onset of the first dive of the record. The Kruskal-Wallis test was used to determine if there were day-to-day differences in the dive variables during the interesting interval. Additionally, dive records were divided into "day dives" (05:00 to 18:59) and "night dives" (19:00 to 04:59). Diel differences in turtle diving behaviour were analyzed using the Mann-Whitney test. Comparisons were considered significantly different at  $P < 0.05$ .

ECG was 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 were excluded from the analysis. Individual R-R intervals were measured in the Acknowledge program and subsequently converted to heart rate in  $\text{beats min}^{-1}$ . Heart rate was temporally coordinated with the dive record so that diving heart rate could be distinguished from surface heart rate. One turtle, PT5027, did not have a corresponding dive record, so diving rates and surface rates were distinguished based on the patterns observed in the ECG traces and dive traces of other turtles. The Mann-Whitney test (significance level  $P < 0.05$ ) was used to compare heart rates during diving and while at the surface. The relationship between mean dive heart rate and mean surface heart rate was examined using linear regression. Linear regression was also used to determine the relationship between dive duration and mean dive heart rate and between dive depth and

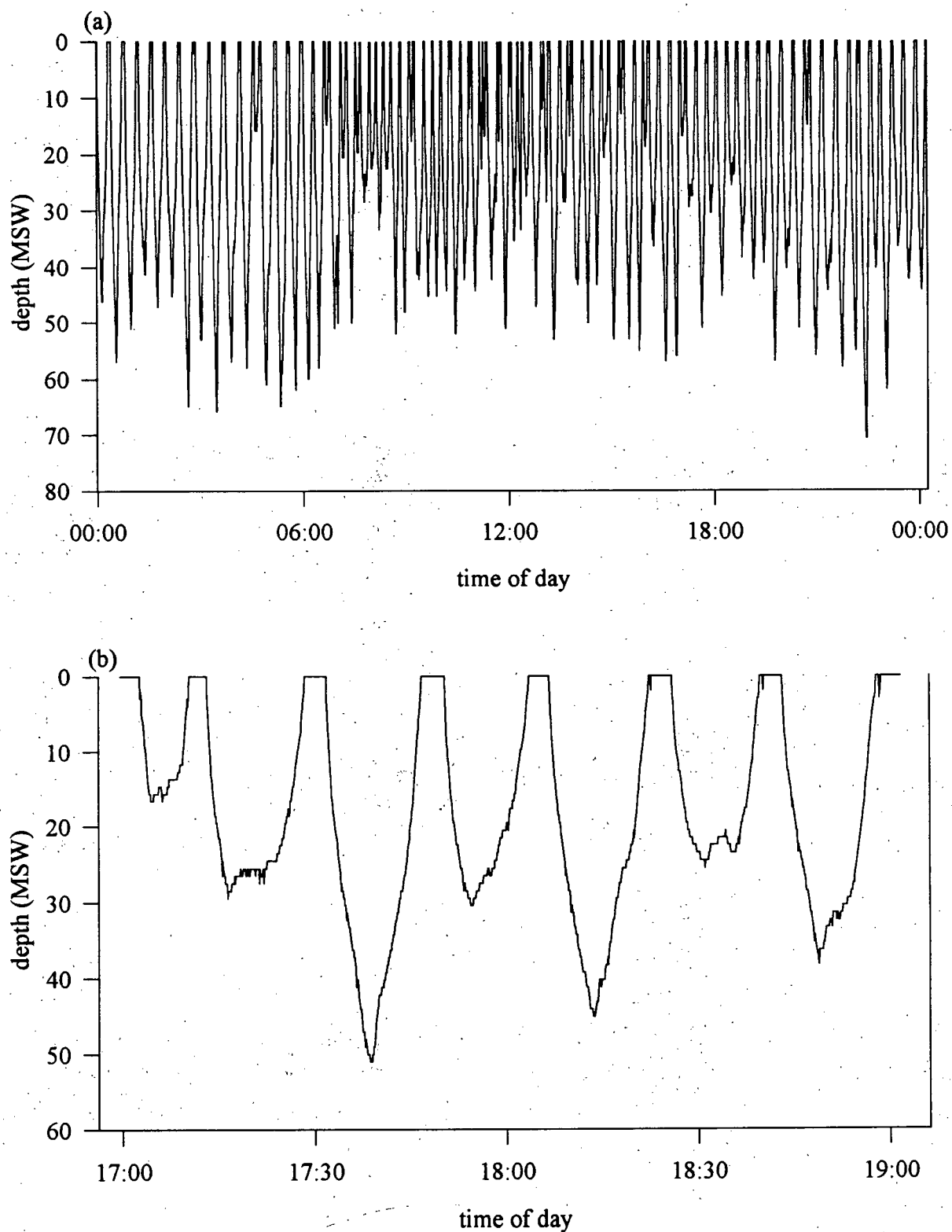
mean dive heart rate. Dives of varying duration and depth were chosen at random (random number generator - SigmaPlot for Windows) and plotted with corresponding heart rate to observe trends in the cardiac response to diving. Linear regression was used to determine if there was a relationship between heart rate and body size (curved carapace length, CCL).



## RESULTS

### *Dive Behaviour*

Dive records were obtained from a total of 5 turtles over the course of the 1995-1996 and 1996-1997 nesting seasons at Playa Grande. Curved carapace length (CCL) was used as a measure of size, and values ranged from 124 to 166 cm. Turtles were estimated to weigh between 250 and 400 kg. All turtles began diving immediately upon departure from 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 Figure 4, which depicts a typical 24-hour dive sequence from PT8866's TDR record (Fig. 4a), as well as a 2-hour sequence from that same day (Fig. 4b). Non-parametric analysis of variance (Kruskal-Wallis test,  $P < 0.05$ ) showed that there was a significant difference in the dive variables among the study animals. Therefore, data were not compiled and descriptive statistics were examined on an individual basis. Differences in dive variables were not due to size, as there was no relationship between CCL and dive duration or between CCL and dive depth. Average dive duration for individual turtles during the internesting interval ranged from 4.06 to 8.17 minutes, and the average surface interval between dives ranged from 1.61 to 5.26 minutes. The maximum observed submergence time was a 67 minute dive made by PT8866. While at sea, turtles spent 57.83% to 73.23% of the time submerged. The average dive depth for the entire recording period ranged from 14.58 to 21.31 MSW. Maximum dive depths ranged from 21 to 124 MSW, and were observed early on in the internesting interval. Dive statistics for individual



**Figure 4.**  
Dive trace recorded from PT8866 on 11/11/96. (a) 24-hour dive trace for 11/11/96.  
(b) 2-hour excerpt of dive trace from early evening on 11/11/96.

turtles are summarized in Table 1. Polynomial regression (2nd order) was used to examine the relationship between dive duration and dive depth. There was a significant positive relationship between these two variables for all turtles ( $P < 0.05$ ,  $R^2 = 0.61$ ). Linear regression demonstrated that there was no relationship between surface interval and the preceding dive duration.

Two exceptionally long dives were made by PT8866 during her interesting interval. The dive trace in Figure 5a shows that PT8866 was at the surface for only 10 seconds before initiating a 33.83 minute dive at approximately 05:20 on 13/11/96. She descended quickly to a depth of 17 MSW and remained at that depth for approximately 33 minutes. The extremely brief surface interval prior to this dive and the quick descent suggests that the turtle may have been avoiding a disturbance at the surface. The subsequent surface interval lasted only 3.67 minutes and the turtle continued to dive regularly afterwards, suggesting that the turtle maintained aerobic metabolism for the duration of this exceptionally long dive. The second noteworthy dive made by PT8866 was a 67.25 minute submergence made at 10:05 on 15/11/96 (Figure 5b). This is the longest recorded dive made by a leatherback turtle to date. Unfortunately, there is no simultaneous ECG recording for this dive. The 67 minute dive was preceded by a surface interval of average duration (2.75 minutes). The turtle dived to a depth of 39 MSW and remained at that depth for over 60 minutes before quickly ascending to the surface (ascent duration = 35 seconds). The turtle spent 3.67 minutes at the surface before initiating another dive, which lasted only 2 minutes and was followed by a post-dive surface interval of 31.25 minutes. The occurrence of an exceptionally long surface interval

**Table 1.**

Dive statistics for individual turtles

Turtle no.	Curved carapace length (cm)	Instrument	Date deployed	Date recovered	Recording time of TDR (hours)	No. of dives	Mean dive depth $\pm$ SD (MSW)	Mean dive duration $\pm$ SD (min)	Mean surface interval $\pm$ SD(min)
PT0367	124	TDR	10/01/96	21/01/96	230	920	17.92 $\pm$ 7.18	7.21 $\pm$ 3.66	5.26 $\pm$ 3.63
PT6573	146	TL1	11/01/96	21/01/96	1.5	12	14.58 $\pm$ 3.42	4.06 $\pm$ 2.04	1.61 $\pm$ 0.46
PT2566	140	TL2/TDR	21/01/96	31/01/96	230	1048	20.27 $\pm$ 9.96	8.17 $\pm$ 5.16	3.76 $\pm$ 2.24
PT8866	145	M8/TDR	09/11/96	18/11/96	230	1107	19.31 $\pm$ 18.95	7.66 $\pm$ 6.01	3.17 $\pm$ 2.16
PT7610	166	M8/TDR	14/11/96	22/11/96	230	1091	21.31 $\pm$ 20.44	6.66 $\pm$ 4.77	3.58 $\pm$ 2.80

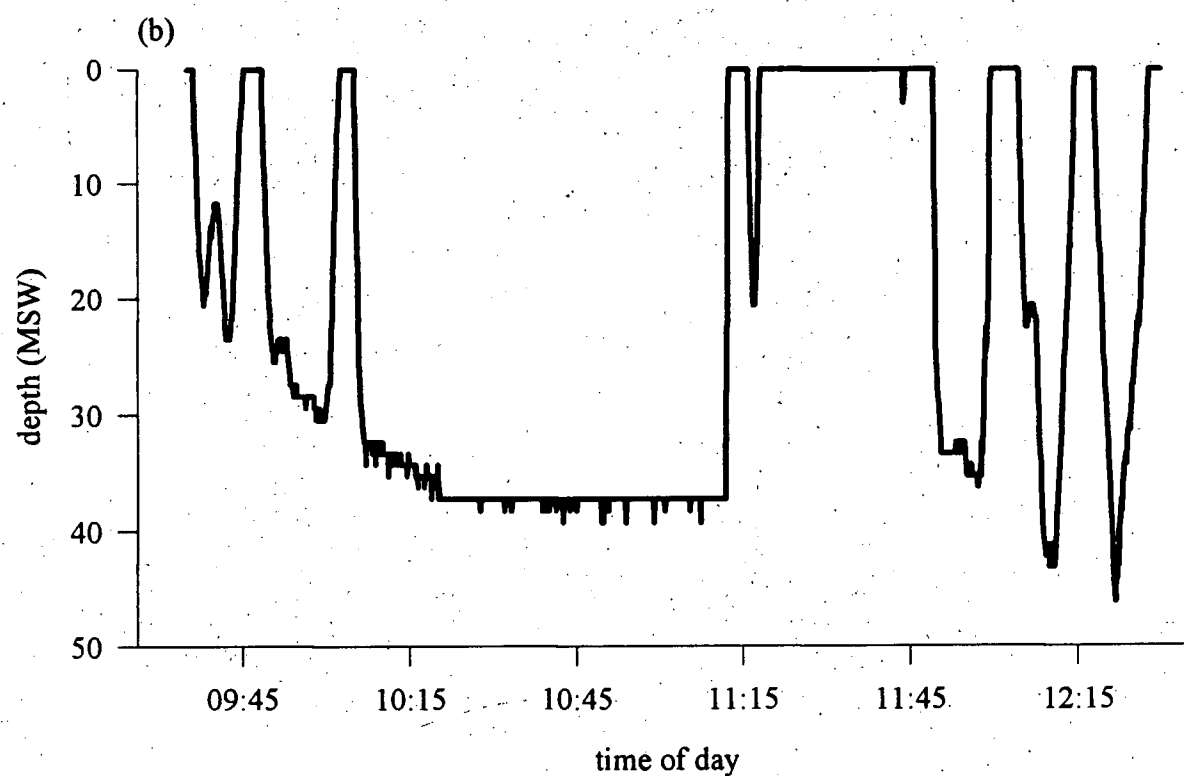
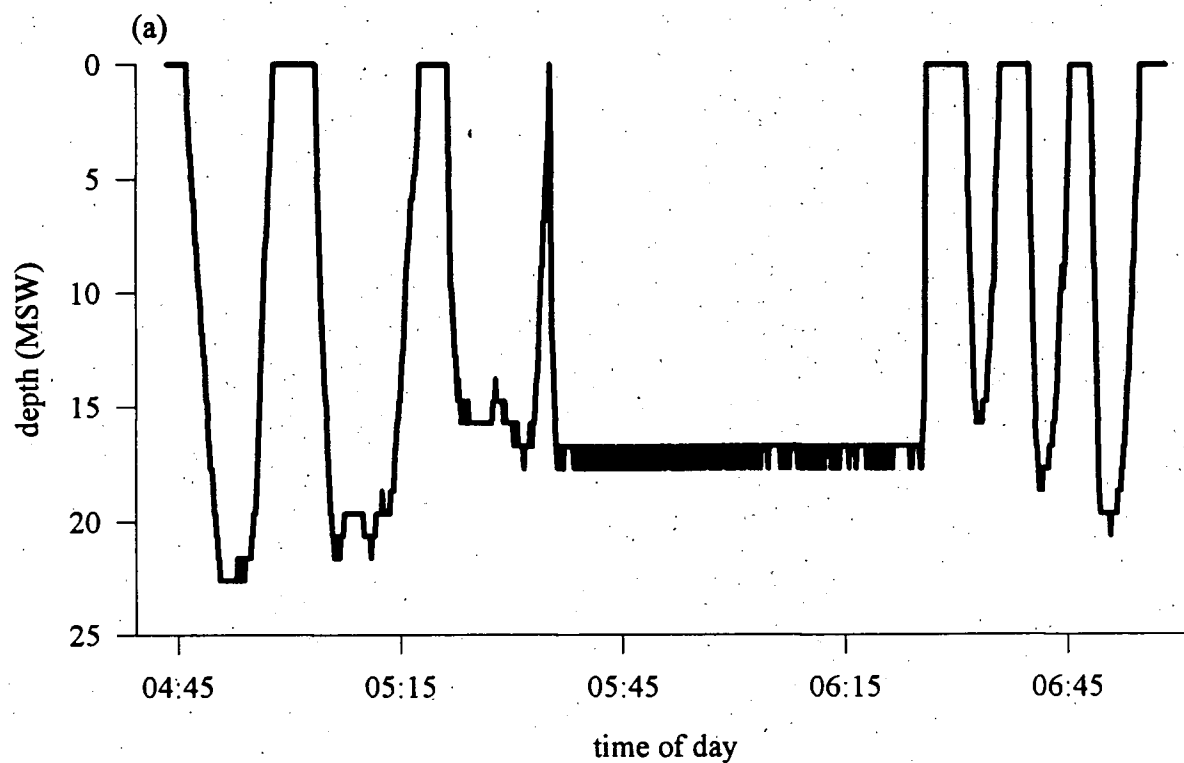


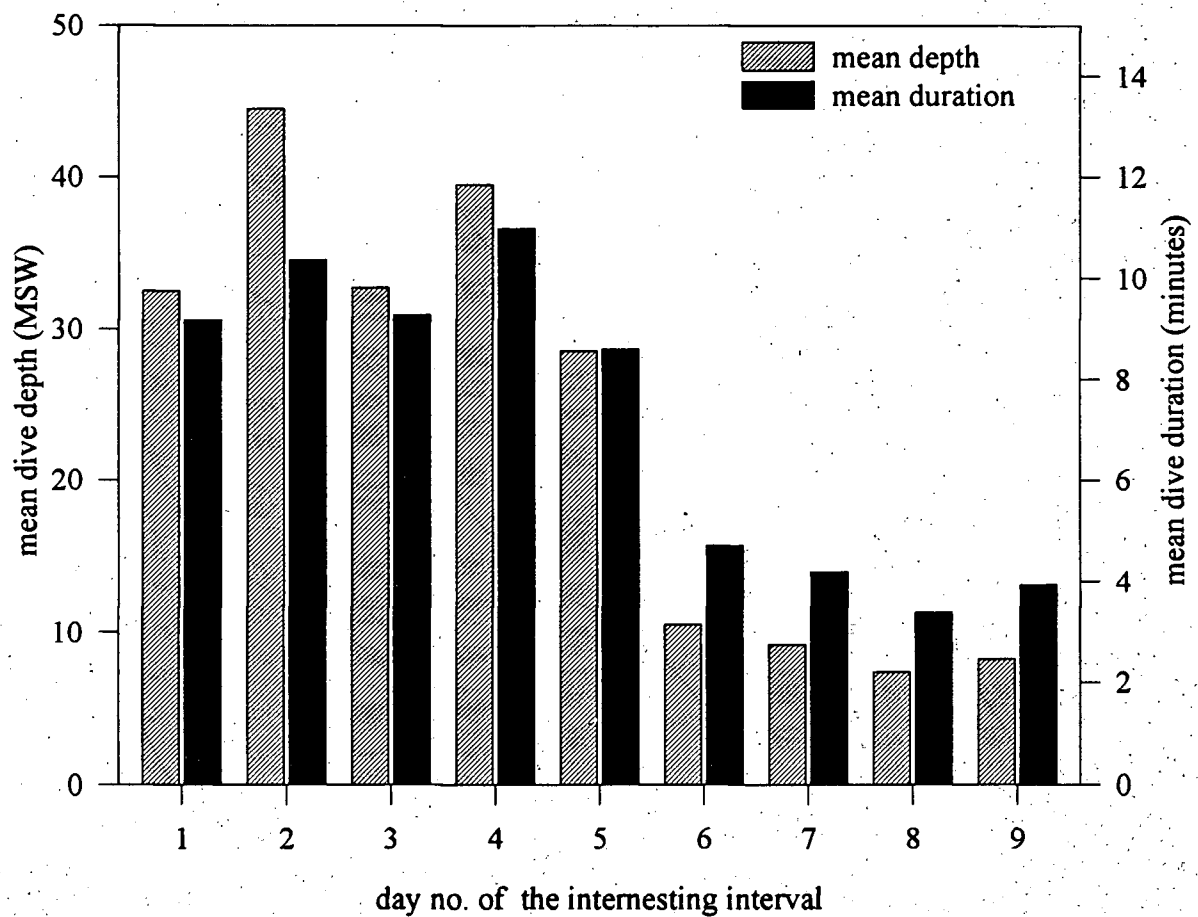
Figure 5.  
Long duration dives recorded from PT8866. (a) 2.5-hour dive trace including a 33 minute dive made at 05:20 on 13/11/96. (b) 3.5-hour dive trace including a 67 minute dive made at 10:05 on 15/11/96.

shortly after the 67 minute dive suggests that the turtle may have incurred an oxygen debt while submerged.

The Kruskal-Wallis test showed significant differences in daily mean dive depth and mean dive duration for 3 of the 4 turtles equipped with TDRs. PT6573's dive record is only one hour long, so daily comparisons were not possible for this turtle. Dive depths became shallower and dive durations became shorter for PT2566, PT8866, and PT7610 as their interesting intervals drew to a close. This trend is evident in Figure 6, which shows a comparison of daily mean depth and mean duration for PT7610. The mean dive depth for the first 5 days combined is 303% deeper than the mean depth for the remainder of the interval, and 65% deeper than the overall mean depth. Likewise, mean dive duration for the first 5 days combined is 137% longer than the mean dive duration for the rest of the interval, and 44% longer than the overall mean dive duration for this animal. Dives were significantly deeper and longer during the first half of the interesting interval compared to the second half of the interval for PT2566 and PT8866 also (Mann-Whitney test,  $P < 0.05$ ). Individual turtles showed slight differences in mean dive depth, duration, and surface interval between day (05:00 to 17:59) and night (18:00 to 04:59), but no consistent diel trend was obvious in the data. Table 2 summarizes dive variables during the day and night for individual turtles, and also lists the mean depth, dive duration, and surface interval for the first and second half of the interesting interval.

### *Heart Rate*

Heart rate was recorded from 5 leatherbacks. Descriptive statistics were done for



**Figure 6.**  
Comparison of mean dive depth and mean dive duration for each day of PT7610's 9-day interesting interval.

**Table 2.**

Mean dive variables for the first and second half of the interesting interval, as well as a diel comparison of dive variables.

Turtle No.	Day 1 - 5			Day 6 - 10			Day (05:00 - 18:59)			Night (19:00 - 04:59)		
	depth (MSW)	duration (min)	surface interval (min)	depth (MSW)	duration (min)	surface interval (min)	depth (MSW)	duration (min)	surface interval (min)	depth (MSW)	duration (min)	surface interval (min)
PT0367	19.0± 7.7	7.4± 3.5	5.3± 3.4	16.7± 6.3	6.9± 3.7	5.1± 3.7	18.9± 8.1	6.9± 3.5	5.9± 4.0	16.6± 5.6	7.5± 3.7	4.4± 2.9
PT2566	23.2± 10.8	9.9± 5.4	3.4± 1.7	15.9± 6.3	5.5± 3.1	4.1± 2.7	21.2± 10.3	8.3± 5.0	3.9± 2.4	18.8± 9.2	7.9± 5.3	3.4± 1.9
PT8866	33.4± 19.8	11.1± 5.4	3.8± 1.8	8.6± 8.2	5.0± 5.0	2.6± 2.2	19.7± 20.1	7.4± 5.9	3.1± 2.2	18.5± 16.9	8.0± 6.0	3.2± 1.9
PT7610	35.1± 21.9	9.5± 4.6	3.4± 2.3	8.7± 5.0	4.0± 2.9	3.6± 3.1	21.7± 21.2	6.8± 4.8	3.6± 2.9	20.7± 19.3	6.3± 4.6	3.5± 2.6

\* All values are given as Mean ± SD



each individual turtle, but data were not compiled due to the fact that there was a significant difference in heart rate among turtles (Kruskall-Wallis test,  $P < 0.05$ ). There was no relationship between heart rate and CCL, so differences in heart rate were not due to size. A summary of heart rate data for individual turtles is presented in Table 3. Dive data presented in Table 3 is for the ECG recording period only and not for the entire interesting interval. The overall mean heart rate for individual turtles during the interesting interval ranged from 18.0 to 22.2 beats  $\text{min}^{-1}$ . Mean dive heart rates ranged from 17.0 to 19.9 beats  $\text{min}^{-1}$  and mean surface heart rates ranged from 23.6 to 28.2 beats  $\text{min}^{-1}$ . Dive heart rates were significantly lower than surface heart rates (Mann-Whitney test,  $P < 0.05$ ) for all turtles tested. Figure 7 shows sections of ECG for PT7610 during a single dive cycle. Heart rate recorded while the animal was diving (Fig. 7a) is noticeably lower than heart rate recorded during the subsequent surface interval (Fig. 7b). 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 ( $R^2 = 0.239$ ,  $P < 0.05$ ). R-R intervals as long as 57.16 seconds (heart rate = 1.05 beats  $\text{min}^{-1}$ ) were recorded during a 33 minute dive made by PT8866. Heart rates at the surface were as high as 35.7 beats  $\text{min}^{-1}$ .

Trends in the nature of the diving bradycardia were determined by plotting randomly chosen dives alongside the corresponding heart rate trace. Heart rate began to fall upon initiation of a dive, and continued to decrease for the majority of the descent. During mid- dive, heart rates tended to stabilize between 15 and 19 beats  $\text{min}^{-1}$ . An anticipatory increase in heart rate was commonly observed during the ascent portion of

**Table 3.**  
Heart rate statistics for individual turtles

Turtle No.	Curved carapace length (cm)	Instrument used	Hours recorded	No. dives	Mean depth (MSW) $\pm$ SD	Mean dive duration (min) $\pm$ SD	Mean surface interval (min) $\pm$ SD	Mean dive heart rate (beats min <sup>-1</sup> ) $\pm$ SD	Mean surface heart rate (beats min <sup>-1</sup> ) $\pm$ SD	Mean long-term heart rate (beats min <sup>-1</sup> ) $\pm$ SD
PT6573	146	TL1	1.5	12	14.6 $\pm$ 3.4	4.1 $\pm$ 2.0	1.6 $\pm$ 0.4	19.9 $\pm$ 1.8	28.2 $\pm$ 2.9	22.2 $\pm$ 4.3
PT2566	140	TL2/TDR	3	13	31.5 $\pm$ 7.4	12.8 $\pm$ 3.4	2.7 $\pm$ 0.6	17.0 $\pm$ 2.8	23.6 $\pm$ 2.8	18.0 $\pm$ 3.7
PT8866	145	M8/TDR	84	344	32.6 $\pm$ 19.8	10.7 $\pm$ 5.5	3.6 $\pm$ 1.7	17.8 $\pm$ 4.5	26.9 $\pm$ 2.7	20.5 $\pm$ 6.2
PT7610	166	M8/TDR	84	367	36.7 $\pm$ 22.8	9.6 $\pm$ 4.7	2.8 $\pm$ 1.9	17.6 $\pm$ 5.3	25.4 $\pm$ 4.1	20.5 $\pm$ 6.7
PT5027	138.5	M8/TDR	84	*	*	*	*	18.6 $\pm$ 3.1	24.1 $\pm$ 1.9	20.0 $\pm$ 5.5

\* There was no dive record for PT5027

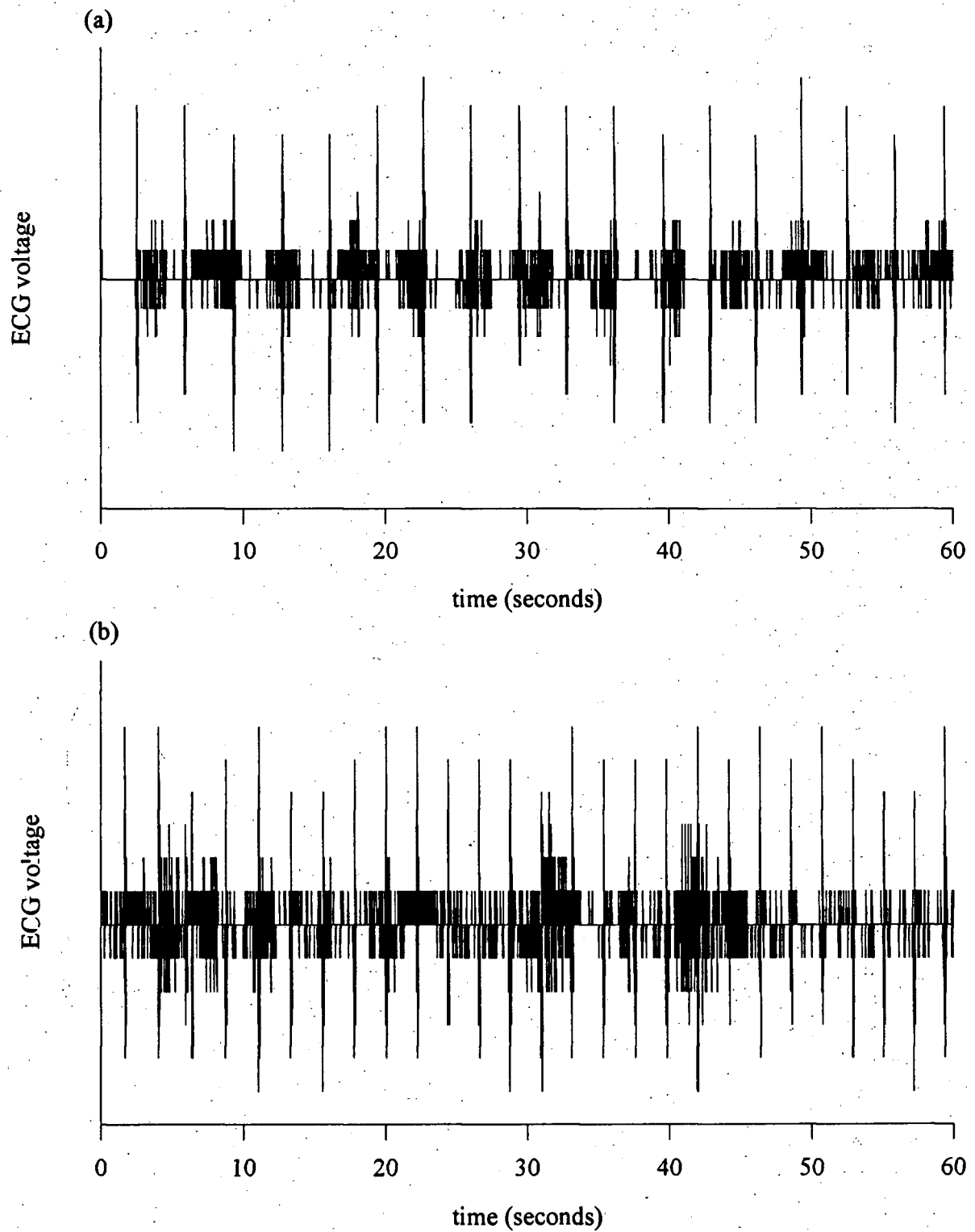


Figure 7.  
ECG recorded from PT7610 during a single dive cycle. (a) ECG recorded during a dive made at 03:15 on 16/11/96. (b) ECG recorded during the accompanying post-dive surface interval.

the dive. Figure 8 shows the cardiac response during a single dive made by PT7610.

For the majority of dives analyzed, diving heart rates stabilized around 17 beats  $\text{min}^{-1}$ . Figure 9 shows an excerpt of PT7610's TDR record which consists of dives of various duration and depth. The corresponding heart rate trace for this dive sequence shows that heart rate drops to a mean of 17 beats  $\text{min}^{-1}$  regardless of the depth of the dive or how long it lasted. A linear regression of dive duration and the mean dive heart rate showed that the negative relationship between these two variables was not strong ( $R^2 = 0.227$ ,  $P < 0.05$ ). Likewise, there is only a weak negative relationship between dive depth and mean dive heart rate ( $R^2 = 0.241$ ,  $P < 0.05$ ).

It is interesting to note that not all turtles in this study showed a uniform response to dives of varying duration and depth. For PT2566, the heart rate trace closely resembled the dive trace (Figure 10). While the animal was descending, heart rate steadily dropped. If the animal spent time at one certain depth in the water column, the heart rate remained at a constant level until the animal either increased or decreased depth. Decreasing depth resulted in an increase in heart rate.

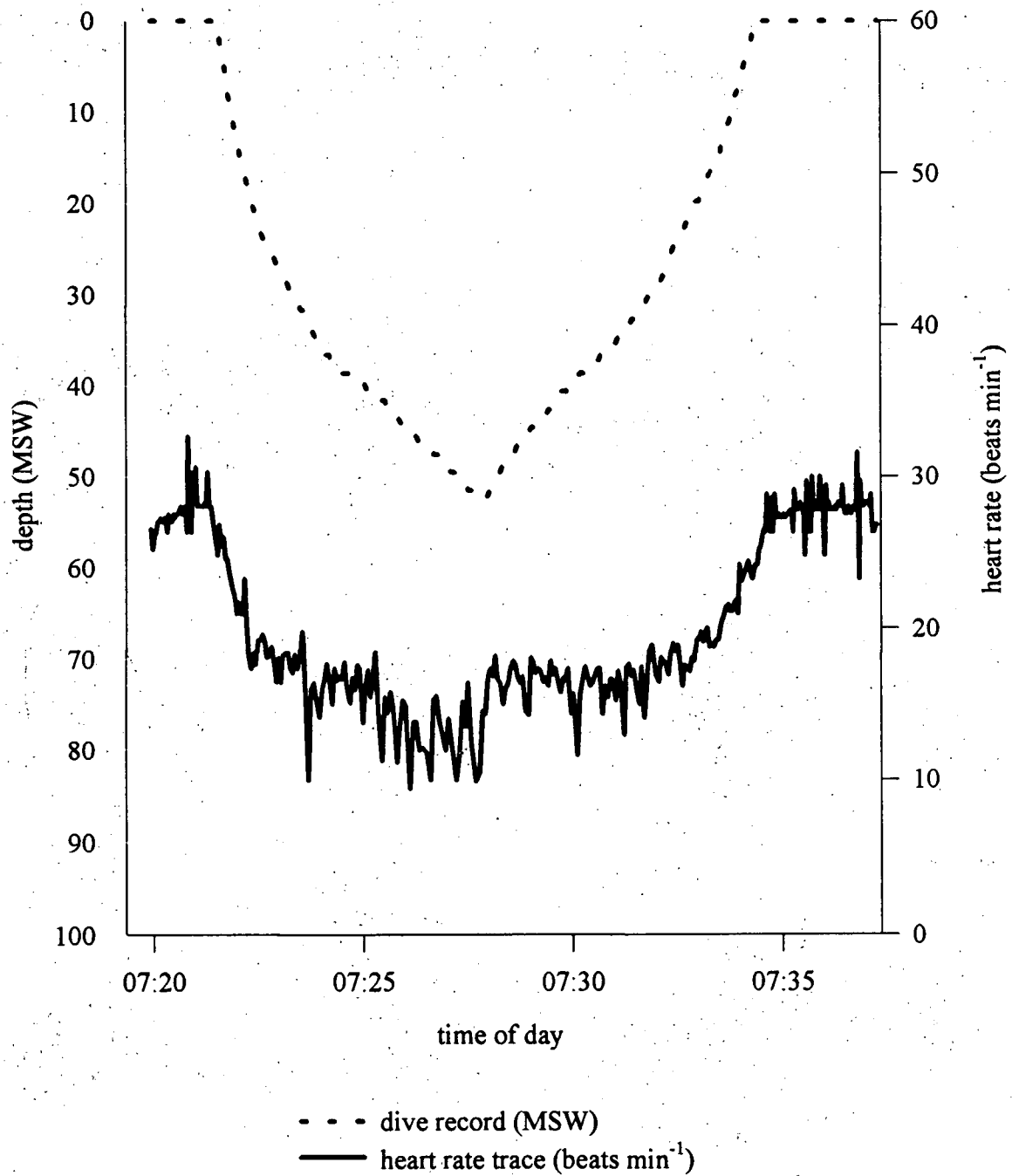


Figure 8.

A single dive and the corresponding heart rate trace for PT7610. Diving bradycardia develops slowly during the descent phase of the dive. An anticipatory increase in heart rate occurs before the turtle reaches the surface.

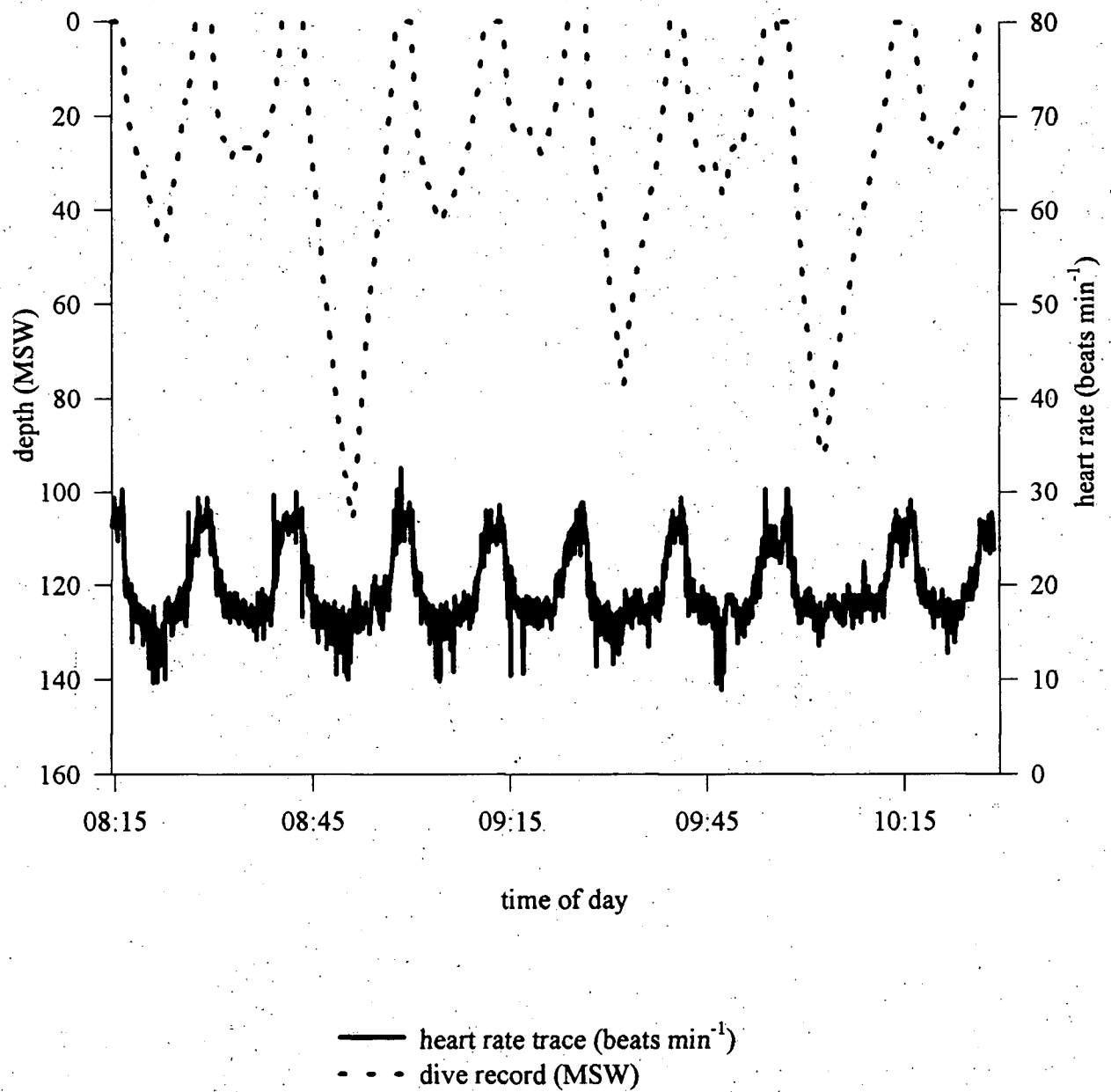


Figure 9.

Dive record and corresponding heart rate for PT7610. Dive durations range from 9 to 15 minutes and dive depths range from 26 to 106 MSW. This turtle shows a uniform cardiovascular response to dives of varying depth and duration.

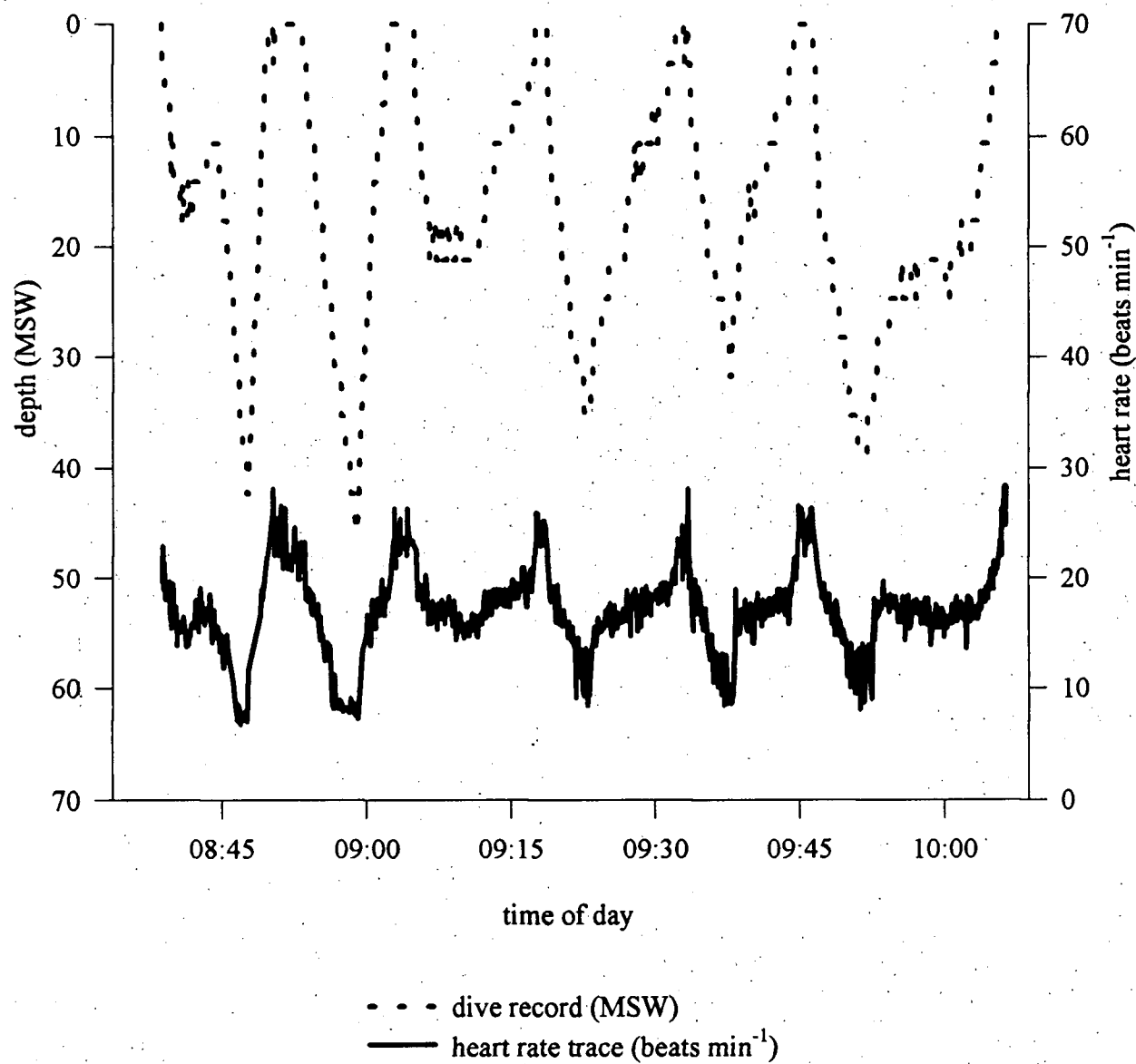


Figure 10.  
Dive record and corresponding heart rate for PT2566. Dive durations range from 8 to 18 minutes and dive depth ranges from 21 to 45 MSW. Heart rate varies with dive depth.

## DISCUSSION

### *Diving Behaviour*

Improvements in instrumentation were made throughout the course of this study. The TDRs used in the 1995-1996 nesting season had a depth resolution of 4 MSW. Only dives that were at least twice the depth resolution were subsequently analyzed, so dives under 8 MSW went undetected and were treated as a continuation of surface time. For the 1996-1997 season, TDR resolution was improved to 1 MSW. In theory, this would allow for dives as shallow as 2 MSW to be detected. However, a safety margin of 2 MSW was added to account for wave action. The parameters in the dive analysis program were set so that only dives deeper than 4 MSW were analyzed, and depths less than 3 MSW were treated as the surface. Consequently, any dives made to depths less than 3 MSW went undetected during dive analysis. The optimal depth for drag reduction, and hence increased swimming efficiency, is 3 body diameters below the surface (Blake, 1983). For an average leatherback turtle, this optimal depth would be 2 - 3 MSW, which would be too shallow to be considered a dive by the dive criterion used for analysis. Swimming velocity data from migrating leatherback turtles (Eckert, unpublished data) shows the occurrence of high swimming speeds during periods when turtles were supposedly at the surface (TDR resolution = 4 MSW). In the current study, there is a possibility that turtles are making shallow dives to depths above the dive criterion (4 - 8 MSW). This may result in extended surface intervals in the dive record during the period



of time when these shallow dives are occurring. For this reason, surface intervals longer than 3 times the average surface interval were excluded from analysis.

Turtles from the Playa Grande nesting population had lower mean dive depths (mean $\pm$ SD = 14.58 $\pm$ 3.42 to 21.31 $\pm$ 20.44 MSW) during the internesting interval than did turtles from the Sandy Point nesting population in the Caribbean (mean $\pm$ SD = 35.42 $\pm$ 23.22 to 110.37 $\pm$ 77.75 MSW)(Eckert et al., 1989). The difference in dive depth may be explained by bathymetric differences in the offshore habitats. In the northeast Caribbean there is a marked increase in depth close to shore. Turtles nesting at Sandy Point would have access to deep water almost immediately after departing the nesting beach. In contrast, water depth remains relatively shallow (60 - 125 MSW) off the Pacific coast of northwest Costa Rica for a distance of approximately 10 nautical miles offshore. Standora et al. (1984) showed that leatherback turtles are capable of swimming at speeds of 3 miles hour<sup>-1</sup>, so turtles nesting at Playa Grande are quite 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 diving depth of only 124 MSW suggest that turtles probably remain on the continental shelf during the internesting interval. This notion is supported by personal observations made while radio-tracking turtles from the beach. Intermittent radio signals were received from tagged turtles 3 to 4 days prior to the turtle's return to the beach. The range of the radio receiver was approximately 3 miles, so turtles must have been within 3 miles of the beach, and therefore on the continental shelf, for the radio signal to have been detected.

Leatherback turtles nesting in Malaysia also show a pattern of shallow diving during their interesting interval in the South China Sea (mean  $\pm$  SD = 26.7 $\pm$ 13.67 to 45.13 $\pm$ 17.24 MSW) (Eckert et al., 1996). However, some important differences exist between the Malaysian turtles and the Pacific turtles in this study. Most of the dives made by Pacific turtles were V-shaped, indicating that turtles spent the majority of dive time traveling to and from maximum depth. The noteworthy exceptions are the long dives (33 minutes and 67 minutes) to shallow depth. These dives were flat-bottomed, meaning a large portion of dive time was spent at maximum depth instead of traveling through the water column. Most of the dives made by Malaysian turtles were flat-bottomed instead of V-shaped (Eckert et al., 1996). Malaysian turtles dove to a maximum depth, presumed to be the ocean floor, and remained at that depth for several minutes before ascending to the surface. The authors were unable to determine if turtles were stationary or swimming at maximum depth. Frequency distributions show that dive durations tend to be longer for Malaysian turtles than for Caribbean turtles (Eckert et al., 1989; Eckert et al., 1996) and Pacific turtles (this study). Eckert hypothesized that Malaysian leatherback turtles may have a decreased oxygen consumption, due to slower swimming speed or inactivity during the portion of the dive spent at maximum depth, which may result in a longer mean dive duration.

A positive correlation between dive depth and dive duration ( $R^2=0.61$ ,  $P<0.05$ ) existed for the turtles studied at Playa Grande, as well as for Caribbean (Eckert et al., 1989), Malaysian (Eckert et al., 1996), and migrating leatherback turtles off the eastern coast of the U.S. (Standora et al., 1984). Therefore, it comes as no surprise that in

addition to having lower mean dive depths, Playa Grande turtles also had shorter mean dive durations (mean $\pm$ SD = 4.06 $\pm$ 2.04 to 8.17 $\pm$ 5.16 min) than turtles from the Caribbean (mean $\pm$ SD = 6.95 $\pm$ 2.37 to 13.51 $\pm$ 8.30 min) (Eckert et al., 1989) and Malaysia (mean $\pm$ SD = 7.91 $\pm$ 3.59 to 12.14 $\pm$ 4.49 min) (Eckert et al., 1996). There was no relationship between dive duration and the post-dive surface interval. Surface intervals were consistently lower in Playa Grande turtles than in turtles from the Caribbean and Malaysian populations. As a result, the percent of time spent submerged was similar for all three populations, even though mean dive duration was shorter for Playa Grande turtles.

Despite differences in mean dive depth, dive duration, and surface interval, a similar pattern of continual diving interrupted by brief surface intervals was observed in leatherback turtles from Malaysia, the Caribbean, and the Pacific. This pattern suggests that the leatherback turtle relies mainly on aerobic metabolism for routine dives (Ackerman & White, 1979; Seymour, 1979; Kooyman et al., 1980; Eckert et al., 1986). If an oxygen debt was incurred during diving, then long duration dives would require longer surface intervals to metabolize the oxygen debt. The leatherback turtle's surface intervals are longer than those observed for chelonid sea turtles, but this is probably due to its relatively small lungs (Standora et al., 1984; Byles, 1988). The smaller lung volume, combined with a lower blood oxygen affinity, necessitates a longer period of time at the surface to restore blood and tissue oxygen stores (Lutcavage et al., 1990).

Previous accounts of leatherback turtle diving behaviour have shown significant differences in mean dive depth, dive duration, and surface interval between day and night

(Eckert et al., 1989; Eckert et al., 1996). Dives were deepest and longest at daybreak. As the day progressed, dive depths decreased and dive durations declined, 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), as the DSL rises towards the surface at dusk to depths frequented by leatherback turtles (Boden & Kampa, 1967). There was no consistent diel difference in mean dive duration or depth in the current study, so it is unlikely that the foraging hypothesis is applicable to the Playa Grande nesting population. Although several studies have shown that leatherback turtles spend more time at the surface during the daylight hours (Standora et al., 1984; Eckert et al., 1989; Eckert et al., 1996), long duration surface intervals were observed during both day and night in the current study. No consistent diel trend in mean surface interval was obvious for Playa Grande turtles.

The phenomenon of decreasing dive depth and duration towards the end of the internesting interval has never been reported in the literature for leatherback turtles. However, this trend was quite obvious in dive records from 3 of the 4 turtles equipped with TDRs in the current study. The physiological significance of this shift in behaviour is difficult to ascertain, since there are no ECG recordings for the second half of the internesting interval and swim velocity was not recorded in this study. Most of the exceptionally long surface intervals (longer than 3 times the mean surface interval) occurred during the last few days at sea before nesting. If these long intervals are true representations of surface time, then turtles may be basking or resting at the surface. Eckert et al. (1989) reported that leatherback turtles are commonly seen in the Pacific

ocean offshore from Mexico, and "the animals almost appear to be in a stupor, or asleep". TDR records for Caribbean leatherback turtles showed instances of long surfacings between 10:00 and 14:00 which suggested basking behaviour (Eckert et al., 1989). Inactivity during the internesting interval has also been noted for other species of sea turtles. Olive ridley turtles (*Lepidochelys olivacea*) nesting on the northwest coast of Costa Rica actively swam for the first 2 - 3 days of the internesting interval, but were relatively inactive for the remainder of time at sea before returning to the beach (Plotkin, 1994). Unlike the leatherback turtles off the coast of Mexico, ridley turtles seem to spend extended periods of time (45 - 70 minutes) resting on the ocean floor instead of at the surface. Although the dive records from the current study indicate that Playa Grande turtles were spending long periods of time at the surface, this may not actually be the case. As explained previously, only dives deeper than 4 MSW were analyzed, and submergences to depths less than 3 MSW were treated as surface time by the analysis program. There is a strong possibility that turtles were actively diving to shallow depths during the extended "surface intervals". In either case, the question of why these turtles altered their diving behaviour in the middle of the internesting interval remains unanswered. Further research on foraging patterns, reproductive physiology and diving metabolism is necessary in order to fully understand the diving behaviour of leatherback turtles during the internesting interval.

The maximum calculated aerobic dive limit (ADL) for an average sized adult leatherback turtle is 70 minutes (Lutcavage et al., 1992). This calculation is based on metabolic rates of unrestrained turtles on a nesting beach, as the metabolic rate for freely

diving leatherback turtles is unknown. Dive durations during the interesting interval were much shorter than the calculated ADL, with the exception of the 67 minute dive made by PT8866. If the calculated ADL is correct, then oxygen stores towards the end of a 67 minute dive would be very low, if not depleted. PT8866's quick ascent to the surface at the end of the 67 minute dive, as well as the occurrence of a 31 minute surface interval shortly after this dive, implies that the turtle may have depleted her oxygen stores and resorted to anaerobic metabolism while submerged. It is interesting to note that this long duration dive had a maximum depth of only 39 MSW. A 33 minute dive made by the same turtle had a maximum depth of only 17 MSW. The purpose of making extended dives to shallow depths remains unclear, since dives of this nature were made by only one turtle (PT8866) during this study. In the case of the 33 minute dive, it seems likely that a disturbance at the surface, such as a passing boat, prompted the turtle to remain submerged for a long duration of time. However, the dive trace for the 67 minute dive gives no indication of a disturbance prior to the dive. The possibility that Pacific leatherback turtles may rest on the ocean floor cannot be ruled out, as this behaviour is well-documented in some species of chelonid sea turtles (Booth & Peters, 1972; Brill et al., 1994; Plotkin, 1994) and has been suggested for the Malaysian population of leatherback turtles (Eckert et al., 1996).

There was no significant relationship between size (CCL) and dive depth or size (CCL) and dive duration. Generally, larger animals have longer dive times and can dive deeper than smaller animals of a similar design (Schreer and Kovacs, 1997). The small number of turtles and narrow range of sizes in this study could account for the lack of a

relationship between these variables. It is interesting to note that Atlantic leatherback turtles are generally larger than Pacific leatherback turtles and also have longer mean dive durations and deeper mean dive depths (Eckert et al., 1986; Eckert et al. 1989).

### *Heart rate*

Leatherback turtles experience a significant decrease in heart rate while diving. There are several explanations as to how the cardiovascular response to diving is initiated and maintained in vertebrates. In general, diving bradycardia is caused by the inhibitory effects of increased parasympathetic activity at the heart via the vagus nerve, but the events that lead to the increased vagal activity may vary depending on the species. The rapid decline in heart rate experienced by many species of diving mammals (Dykes, 1974a; Dykes, 1974b; Drummond & Jones, 1979) and birds (Catlett & Johnston, 1974; Mangalam & Jones, 1984) at the onset of a dive is generally attributed to immersion-sensitive nasal receptors. These receptors serve the dual purpose of initiating apnea and bradycardia, and quite possibly have an effect on peripheral vascular resistance (Butler and Jones, 1982). Leatherback turtles and green turtles do not display an extreme bradycardia upon submergence, rather, heart rate decreases gradually throughout descent (Berkson, 1966; West et al., 1992). The lack of a quick cardiovascular response to submersion suggests that the nasal receptors do not play a direct role in the initiation of diving bradycardia in the sea turtles, as they do in some diving mammals and sea birds. However, nasal receptors are still an important factor in the initiation of apnea, and thus may indirectly affect heart rate (Bamford and Jones, 1976). When an animal stops

breathing, the lack of feedback from pulmonary stretch receptors tends to inhibit cardiovascular activity (Jones and Purves, 1970; Butler & Jones, 1982).

The slow decline in heart rate exhibited by the leatherback turtle may be mediated by peripheral chemoreceptors in the carotid bodies, as it is in amphibians (Jones, 1967; Lenfant & Johansen, 1967; Butler & Jones, 1982) and some species of ducks (Lacombe & Jones, 1991a). As the dive progresses,  $PO_2$  and pH levels decrease and  $PCO_2$  increases in the blood. In diving vertebrates, the changes in blood oxygen levels are detected by peripheral chemoreceptors which send a signal to the cardiovascular control center in the medulla. This results in a release of norepinephrine (NE) and epinephrine (EP) from the adrenal gland, as well as an increase in sympathetic nerve activity. Smooth muscle surrounding peripheral blood vessels is innervated by sympathetic nerves, and the increased firing of these nerve fibers results in peripheral vasoconstriction. As total peripheral resistance (TPR) increases, heart rate decreases in order to maintain a steady blood pressure. Past studies have shown that stimulation of peripheral chemoreceptors also has the direct effect of decreasing heart rate (Jones and Purves, 1970). In addition to the oxygen-sensitive peripheral chemoreceptors, most reptiles have central chemoreceptors which are sensitive to increasing  $PCO_2$  and decreasing pH. Stimulation of central chemoreceptors also results in increased peripheral resistance (Lioy et al., 1978; Hanna et al., 1979; Lioy et al., 1981; Jones et al., 1982).

If changes in systemic peripheral resistance have the effect of decreasing heart rate, then changes in pulmonary resistance could also have a profound influence on the initiation of diving bradycardia. Unlike mammals and birds, reptiles have an incompletely



divided ventricle which allows for differences in flow between the pulmonary and systemic circulations. Blood and tissue oxygen stores make up over 50% of the total oxygen store in the leatherback turtle (Lutcavage et al., 1992). If the leatherback turtle does not depend on the lung as its main source of oxygen during a dive, then the turtle may shunt blood away from the pulmonary circuit while submerged. A subsequent drop in heart rate or stroke volume would be necessary to maintain blood pressure with the increased resistance in the pulmonary circuit. Studies conducted with green sea turtles in a laboratory setting (West et al., 1992) showed that blood flow in the pulmonary artery dropped to extremely low levels at the onset of a submergence. This drastic decrease in pulmonary flow was accompanied by a fall in heart rate. The observed diving bradycardia in leatherback turtles may be indicative of increased pulmonary resistance resulting in a right-to-left (R - L) shunt. A R - L shunt would be beneficial for the turtle in a variety of ways. Reduction in lung-to-blood gas exchange would decrease the amount of N<sub>2</sub> loading in the blood, thereby reducing the risk of air-bubble formation during ascent (Seymour, 1974; Kooyman, 1989). If the leatherback turtle's lungs collapse at depths of 80 - 160 MSW, as do green turtle lungs (Berkson, 1967), then a R - L shunt would prevent perfusion of the non-functional lungs. Finally, by regulating pulmonary perfusion, the turtle may partition lung oxygen stores throughout the dive.

The degree to which leatherback turtles use their lung O<sub>2</sub> store while diving is difficult to assess without blood gas or blood flow data. In freshwater turtles, the degree and timing of pulmonary perfusion while diving varies greatly from species to species and with dive time. During long-duration dives in *Pseudemys scripta*, blood PO<sub>2</sub> dropped

steadily upon the initiation of a dive (Burggren and Shelton, 1979; Burggren, 1988). However, there was a temporary reversal of the diving bradycardia, concurrent with a large increase in blood  $PO_2$ , during mid-dive. The increase in heart rate and blood  $PO_2$  suggests that the turtles had restored blood flow to the lungs in order to load oxygen. Pulmonary perfusion was transient, and afterwards blood  $PO_2$  steadily declined to a low level. This pattern of intermittent blood flow to the lungs followed by large fluctuations in  $PO_2$  was repeated several times during a dive. A different strategy of pulmonary perfusion is evident during diving in *Chelodina longicollis*, the Australian side-necked turtle (Burggren et al., 1989). Although pulmonary perfusion was intermittent in this species, blood oxygen saturation remained at 80% to 95% throughout the dive. Frequent increases in pulmonary flow allowed the turtle to maintain consistent levels of  $PO_2$  in the blood. West et al. (1992) measured the pulmonary and systemic blood flow and heart rate in captive juvenile green sea turtles. They found that pulmonary blood flow changed rhythmically during periods of submergence, but these alterations in flow were not accompanied by changes in heart rate. Butler et al. (1984) maintain that total cardiac stroke volume in the green turtle varies as a result of changes in pulmonary flow, which could account for the lack of a response in heart rate during periods of pulmonary perfusion. Whether or not arterial  $PO_2$  is maintained at a constant level in *Chelonia mydas*, as it is in *Chelodina longicollis*, is unknown. In the leatherback turtle, the diving bradycardia is not drastically alleviated at any time during diving, except for the anticipatory increase in heart rate just before surfacing. However, as evidenced by the experiments with green turtles, changes in pulmonary perfusion may not be reflected in

heart rate if stroke volume varies. Based on the heart rate trace alone, it is difficult to say whether or not leatherback turtles intermittently perfuse their lungs to "top off" blood  $O_2$  stores while diving. Until values for blood and lung  $PO_2$  and pulmonary blood flow are known, caution should be taken when drawing conclusions about the role of lung oxygen stores during diving in the leatherback turtle.

Mean diving heart rate was not strongly related to dive duration or dive depth. Most of the dives observed in the current study were well within the aerobic dive limit, so the weak relationship between heart rate and dive duration is not surprising. However, the weak relationship between heart rate and dive depth is somewhat unexpected, considering that in green sea turtles the diving bradycardia is accentuated by increases in hydrostatic pressure (Berkson, 1967). Certainly, the dive trace recorded from PT2566 (Figure 10) shows that heart rate varied with dive depth. However, this turtle's ECG record is 3 hours long and only 12 dives occur during the recording period. Heart rates recorded from other turtles did not vary as greatly with depth. Overall, turtles displayed a fairly uniform cardiac response to dives of various duration and depth, suggesting that there may be an optimal heart rate for efficient delivery of oxygen to tissues during routine dives. Maintenance of the diving heart rate may be accomplished by the combined actions of chemoreceptors, baroreceptors, and circulating catecholamines. The accumulating metabolites in ischemic peripheral tissue act as vasodilators, and tend to reverse the initial vasoconstriction caused by increased sympathetic nerve activity. An increase in circulating catecholamines during diving helps maintain systemic peripheral resistance by countering the effects of increasing metabolites in ischemic peripheral tissues (Kooyman et

al., 1980; Lacombe & Jones, 1991b; Hurford et al., 1996). Catecholamines have the opposite effect in the pulmonary circuit, where they act as vasodilators. If intermittent perfusion of the lungs is governed by the  $PO_2$  and  $PCO_2$  levels in the blood, then stimulation of the chemoreceptors and the subsequent release of NE and EP may play a role in management of the lung oxygen stores. Arterial baroreceptors may sense blood pressure changes that occur with reperfusion of the lungs and adjust heart rate or peripheral resistance accordingly.

Many diving vertebrates that decrease heart rate while diving show an anticipatory increase in heart rate prior to surfacing. This phenomenon has been observed in green (Butler et al., 1984; West et al., 1992) and leatherback sea turtles (current study). One possible explanation is that the higher centers of the brain recognize that the turtle is about to surface. Peripheral resistance decreases and heart rate increases in anticipation of breathing. Restoring blood flow to peripheral tissues would flush out metabolites that may have built up in the ischemic tissue, allowing for a more efficient removal of metabolic by-products during recovery time at the surface. The anticipatory increase in heart rate prior to surfacing may also be explained by the effects of decreasing pressure during the ascent. As hydrostatic pressure decreases, the lungs expand and this may trigger pulmonary stretch receptors. Stimulation of these stretch receptors tends to override the effects of arterial chemoreceptor stimulation, and may result in an increase in heart rate and decrease in pulmonary vascular resistance (Kooyman, 1989).

In general, heart rate and mass specific metabolic rate scale inversely with body size (Schmidt-Nielsen, 1984). Therefore, one would predict that the enormous

leatherback turtle would have both a lower heart rate and lower metabolic rate than the smaller chelonid sea turtles. A summary of currently available metabolic and heart rate data for sea turtles is presented in Table 4. Typical diving and surface heart rates for a freely diving leatherback turtle weighing between 250 and 400 kg are similar to values obtained for juvenile green sea turtles (1 - 2 kg) resting in air and submerged. Although the leatherback turtle is certainly capable of dropping heart rate to extremely low levels during a dive ( $1.05 \text{ beats min}^{-1}$ ), this is seldom the case. Leatherback turtles have a moderate diving bradycardia (65% to 70% of surface rate) compared to the much larger decreases in heart rate observed in some species of marine mammals, such as the northern elephant seal (20% to 50% of surface rate)(Andrews et al., 1997). Green sea turtles in a laboratory setting reduced heart rate to 50% or less of resting surface heart rate during voluntary dives or periods of apnea (West et al., 1992). Obviously, diving heart rate is not simply a reflection of submergence, but also of the animal's behaviour. In contrast to olive ridley and green sea turtles, leatherback turtles rarely spend time resting on the sea floor. TDR records show that the majority of the leatherback turtle's dive time is spent traveling through the water column, where the turtle could be actively swimming or foraging. The leatherback's lack of an extreme bradycardia during routine diving may be an indication of the turtle's higher activity level. Metabolic rates of leatherback turtles are higher than expected from the allometric equations found in the literature (Prange and Jackson, 1976). Resting metabolic rate of leatherback turtles on the beach was three

**Table 4.**  
Comparison of heart rate and metabolic rate for sea turtles.

Species	Age & Weight	Conditions	Heart rate beats min <sup>-1</sup>	$\dot{V}O_2$ ml min <sup>-1</sup> kg <sup>-1</sup> STPD	Reference
Leatherback	hatchling (~ 50g)			4.76	Lutcavage & Lutz, 1986
	adult (250-400 kg)	beach - unrestrained		0.25 - 1.15	Lutcavage et al., 1990 Paladino et al., 1990
		beach - restrained	50	1.09	Lutcavage et al., 1992
		beach - active		3.7	Paladino et al., 1990
		at sea - surface	24 - 28		current study
		at sea - diving	17 - 20		current study
Green	hatchling (~ 50g)			5.61	Prange & Ackerman, 1974
	juvenile (1-2 kg)	swimming	46 - 68	3.7 - 5.6	Davenport et al., 1982; Butler et al., 1984
		rest	24 - 51	1.4 - 1.98	Davenport et al., 1982; West et al., 1992; Butler et al., 1984
	subadult (13-22 kg)	surface	22 - 24		Berkson, 1966
		force dive	2 - 10		Berkson, 1966
	adult (127-142 kg)	rest		1.1 - 2.4	Prange & Jackson, 1976
exercising (crawling)			2.7 - 4.5	Prange & Jackson, 1976 Jackson & Prange, 1979	
Loggerhead	hatchling (~ 50g)			3.5	Lutcavage & Lutz, 1986
	subadult (4-27 kg)	rest		1.0	Lutz et al., 1989
		swimming		3.0	Lutz et al., 1989

times higher than values predicted for a green turtle scaled to leatherback size (Paladino et al., 1990), and metabolic rates for leatherback turtles exercising on the beach were similar to resting values predicted for mammals of similar size (Paladino et al., 1990).

The effect of temperature on metabolism and heart rate should be taken into account when interpreting data collected from reptiles. The data in this study and all of the metabolic studies have been collected in the tropics. Metabolic and heart rate data is not available for migrating leatherback turtles in cold water, although Friar et al. (1972) showed that these turtles maintain high core body temperatures in the cold water off the coast of Nova Scotia. Leatherback turtles may have a higher heart rate in the tropics as opposed to temperate climates due to higher water temperature. To avoid overheating while nesting on the beach, leatherback turtles typically flush blood to the skin (Spotila et al., 1997). The increased blood flow to the periphery is especially noticeable around the throat and flippers, where the pale skin turns bright pink during the process of nesting. The moderate bradycardia observed during the internesting interval may be an indication that some degree of blood flow to peripheral tissues is maintained for thermoregulatory purposes.

Leatherback turtles spend approximately 60% to 75% of the internesting interval submerged. Long-term mean heart rates for individual leatherback turtles ranged from 18.0 to 22.2 beats  $\text{min}^{-1}$ , and were closer to diving heart rates than to surface heart rates. Based on experiments conducted with the freshwater turtle *Psuedemys concinna*, Belkin (1964) proposed that diving heart rates were the "normal" heart rates for turtles that spent

the majority of time underwater, and turtles actually experience a breathing tachycardia at the surface rather than a diving bradycardia while submerged. Leatherback turtles maintain an active diving pattern and have diving heart rates as high as 77% of surface heart rates. Turtles are producing eggs, maintaining a suitable body temperature, and possibly foraging during the interesting interval. Given that the majority of time at sea is spent submerged, it seems unlikely that the leatherback turtle suspends normal physiological functions, such as egg production and digestion, during routine dives. The leatherback turtle is probably capable of aerobically powering normal bodily functions within the range of heart rates observed while diving and at the surface. Therefore, the leatherback is in a "normal" condition both at the surface and during diving. Higher surface heart rates would allow the turtle to maximize gas exchange and O<sub>2</sub> loading during ventilation. By lowering heart rates during routine dives, turtles may supply tissues with a sufficient amount of oxygen at a reduced energetic expenditure.

### *Conclusions*

One of the major causes of sea turtle mortality is drowning due to entanglement in fishing gear. Experiments conducted with loggerhead, green, and Kemp's ridley sea turtles demonstrated that the stress of enforced submergence greatly reduced the turtles' ability to withstand anoxia (Lutz & Bentley, 1985; Henwood & Stuntz, 1987; Stabenau et al., 1991). Forced dives of less than 30 minutes resulted in large increases in lactic acid, and recovery time to restore acid-base balance took up to 20 hours (Henwood & Stuntz, 1987). Forced submergence experiments have never been conducted with leatherback



turtles, due to the difficulties of capturing these turtles and maintaining healthy animals in captivity. Conservation efforts for this species must be based on knowledge of the behaviour and physiology of freely diving animals.

The current study has demonstrated that the leatherback turtle has a lower heart rate while diving than while at the surface. However, this turtle does not experience an extreme diving bradycardia during routine dives. Diving heart rates are usually 65% to 77% of surface rates. Although the leatherback turtle is capable of remaining submerged for over an hour, typical dive durations are surprisingly short (4 - 8 minutes). The short dive durations, in addition to the moderate diving bradycardia, suggests that leatherback turtles do not drastically lower their metabolic rate while freely diving during the interesting interval. The energetic costs of thermoregulation, reproduction, or foraging may contribute to a higher oxygen consumption, and therefore a decreased aerobic dive limit. Data from the current study and previous studies of metabolic rate suggest that the leatherback turtle would have difficulty surviving a prolonged enforced submergence. The longest recorded voluntary dive for a leatherback turtle is 67 minutes, but this dive was followed by an extended period of time at the surface (>30 minutes), suggesting that an oxygen debt may have been incurred during the dive. As with chelonid sea turtles, the stress of entanglement and the energetic cost of struggling may decrease the amount of time the leatherback turtle can remain submerged without experiencing severe acidosis. Conservation efforts should take into account the variable nature of the diving bradycardia and the effects of stress on normal diving behaviour.

## BIBLIOGRAPHY

- Ackerman, R.A. and White, F.N. 1979. Cyclic carbon dioxide exchange in the turtle *Pseudemys scripta*. *Physiol. Zool.* 52:378-379.
- Andrews, R.D., Jones, D.R., Williams, J.D., Thorson, P.H., Oliver, G.W., Costa, D.P., and LeBoeuf, B.J. 1997. Heart rates of Northern elephant seals at sea and resting on the beach. *J. Exp. Biol.* in press.
- Bamford, O.S. and Jones, D.R. 1976. Respiratory and cardiovascular interaction in ducks; the effect of lung denervation on the initiation and recovery from some cardiovascular responses to submergence. *J. Physiol. (London)* 29:575-596.
- Berkson, H. 1966. Physiological adjustments to prolonged diving in the Pacific green turtle (*Chelonia mydas agassizii*). *Comp. Biochem. Physiol.* 18:101-119.
- Berkson, H. 1967. Physiological adjustments to deep diving in the Pacific green turtle (*Chelonia mydas agassizii*). *Comp. Biochem. Physiol.* 21:507-524.
- Blake, R.W. 1983. *Fish Locomotion*. Cambridge University Press. Cambridge, U.K.
- Bleakney, J.S. 1965. Reports of marine turtles from New England and Eastern Canada. *The Can. Fld. Nat.* 79:120-128.
- Boden, B.P. and Kampa, E.M. 1967. The influence of natural light on the vertical migrations of an animal community in the sea. *Symp. Zool. Soc. Lond.* 19:15-26.
- Booth, J. and Peters, J.A. 1972. Behavioural studies on the green turtle (*Chelonia mydas*) in the sea. *Anim. Behav.* 20:808-812.
- Boulon, R.H., Dutton, P.H., and McDonald, D.L. 1996. Leatherback turtles (*Dermochelys coriacea*) on St. Croix, U.S. Virgin Islands: fifteen years of conservation. *Chelonian Conserv. Biol.* 2(2):141-147.
- Brill, R.W., Balazs, G.H., Holland, K.N., Chang, R.K.C., Sullivan, S., and George, J.C. 1995. Daily movements, habitat use, and submergence intervals of normal and tumor-bearing juvenile green turtles (*Chelonia mydas L.*) within a foraging area in the Hawaiian islands. *J. Exp. Mar. Biol. Ecol.* 185:203-219.
- Brongersma, L.D. 1969. Miscellaneous notes on sea turtles, II A & B. *Proc. K. Ned. Akad. Wet.* 1:76-102.
- Burggren, W.W. and Shelton, G. 1979. Gas exchange and transport during intermittent breathing in chelonian reptiles. *J. Exp. Biol.* 82:75-92.

- Burggren, W.W. 1988. Cardiovascular responses to diving and their relation to lung and blood oxygen stores in vertebrates. *Can. J. Zool.* 66:20-28.
- Burggren, W.W., Smits, A., and Evans, B. 1989. Arterial homeostasis during diving in the turtle *Chelodina longicollis*. *Physiol. Zool.* 62(3):668-686.
- Butler, P.J. and Jones, D.R. 1982. The comparative physiology of diving in vertebrates. *Adv. Comp. Physiol. Biochem.* 8:179-364.
- Butler, P.J., Milsom, W.K., and Woakes, A.J. 1984. Respiratory, cardiovascular and metabolic adjustments during steady state swimming in the green turtle, *Chelonia mydas*. *J. Comp. Physiol.* 154B:167-174.
- Butler, P.J. 1988. The exercise response and the "classical" diving response during natural submersion in birds and mammals. *Can. J. Zool.* 66:29-39.
- Bytes, R.A. 1988. Behavior and Ecology of Sea Turtles from Chesapeake Bay, Virginia. PhD. dissertation, College of William and Mary, Williamsburg, Va.
- Castellini, M.A., Murphy, B.J., Fedak, M., Ronald, K., Goffon, N., and Hochachka, P.W. 1985. Potentially conflicting metabolic demands of diving and exercise in seals. *J. Appl. Physiol.* 58(2):392-399.
- Castellini, M.A. and Kooyman, G.L. 1989. Behavior of freely diving animals. *Undersea Biomed. Res.* 16(5):355-362.
- Catlett, R.H. and Johnson, B.L. 1974. Cardiac response to diving in wild ducks. *Comp. Biochem. Physiol.* 19:176-187.
- Davenport, J., Ingle, G., and Hughes, A.K. 1982. Oxygen uptake and heart rate in young green turtles (*Chelonia mydas*). *Proc. Soc. Zool., Lond.* 198:399-412.
- Deraniyagala, P.E.P. 1936. Some postnatal changes in the leathery turtle *Dermochelys coriacea*. *Ceylon J. Sci. B.* 19:225-239.
- Drummond, P.C. and Jones, D.R. 1979. The initiation and maintenance of bradycardia in a diving mammal, the muskrat, *Ondatra zibethica*. *J. Physiol. (London)* 290:253-271.
- Dykes, R.W. 1974a. Factors related to the dive reflex in harbour seals: Respiration, immersion bradycardia, and lability of the heart rate. *Can. J. Physiol. Pharmacol.* 55:248-258.
- Dykes, R.W. 1974b. Factors related to the dive reflex in harbour seals: Sensory contributions from the trigeminal region. *Can. J. Physiol. Pharmacol.* 52:259-265.

- Eckert, S.A., Nellis, D.W., Eckert, K.L., and Kooyman, G.L. 1986. Diving patterns of two leatherback sea turtles (*Dermochelys coriacea*) during interesting intervals at Sandy Point, St. Croix, U.S. Virgin Islands. *Herpetologica* 42(3):381-388.
- Eckert, S.A., Eckert, K.L., Ponganis, P., and Kooyman, G.L. 1989. Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). *Can. J. Zool.* 67:2834-2840.
- Eckert, S.A., Liew, H.C., Eckert, K.L., and Chan, E.H. 1996. Shallow water diving by leatherback turtles in the South China Sea. *Chelonian Conserv. Biol.* 2(2):237-243.
- Eisenberg, J.G. and Frazier, J. 1983. A leatherback turtle (*Dermochelys coriacea*) feeding in the wild. *J. Herpetol.* 17:81-82.
- Fedak, M.A. 1986. Diving and exercise in seals: a benthic perspective. *In* Diving in animals and man. Kongvold Symposium 1985, Royal Norwegian Society of Sciences and Letters. *Edited by* A.O. Brubakk, J.W. Kanwisher, and G. Sundnes. Tapir Publishers, Trondheim. pp. 11-32.
- Fedak, M.A., Pullen, M.R., and Kanwisher, J. 1988. Circulatory responses of seals to periodic breathing: heart rate and breathing during exercise and diving in the laboratory and open sea. *Can. J. Zool.* 66:53-60.
- Friar, W., Ackman, R.G., and Mrosovsky, N. 1972. Body temperature of *Dermochelys coriacea*: warm turtle from cold water. *Science* 177(4051):791-793.
- Girondot, M. and Fretey, J. 1996. Leatherback turtles, *Dermochelys coriacea*, nesting in French Guiana, 1978-1995. *Chelonian Conserv. Biol.* 2(2):204-208.
- Goff, G.P., and Lien, J. 1988. Atlantic leatherback turtle, *Dermochelys coriacea*, in cold water off Newfoundland and Labrador. *Can. Fld. Nat.* 102(1):1-5.
- Goff, G.P. and Stenson, G.B. 1988. Brown adipose tissue in leatherback sea turtles: a thermogenic organ in an endothermic reptile? *Copeia* 1988:1071-1074.
- Grant, G.S., Malpass, H., and Beasley, J. 1996. Correlation of leatherback turtle and jellyfish occurrence. *Herpetol. Review* 27(3):123-125.
- Greer, A.E., Lazell, J.D., Jr., and Wright, R.M. 1973. Anatomical evidence for a counter-current heat exchanger in the leatherback turtle (*Dermochelys coriacea*). *Nature* 244:181.
- Hanna, B.D., Lioy, F., and Polosa, C. 1979. The effect of cold blockade of the medullary chemoreceptors on the CO<sub>2</sub> modulation of vascular tone and heart rate. *Can. J. Physiol. Pharmacol.* 57(5):461-468.

- Hendrickson, J.R. 1980. The ecological strategies of sea turtles. *Am. Zool.* 20:597-608.
- Henwood, T. and Stuntz, W.E. 1987. Analysis of sea turtle captures and mortalities during commercial shrimp trawling. *Fish. Bull.* 85:37.
- Hughes, G. 1996. Nesting of the leatherback turtle (*Dermochelys coriacea*) in Tongaland, Kwa-Zulu-Natal, South Africa, 1963-1995. *Chelonian Conserv. Biol.* 2(2):153-158.
- Hurford, W.E., Hochachka, P.W., Schneider, R.C., Guyton, G.P., Stanek, K.S., Zapol, D.G., Liggins, G.C., and Zapol, W.M. 1996. Splenic contraction, catecholamine release, and blood volume redistribution during diving in the Weddell seal. *J. Appl. Physiol.* 80(1):298-306.
- Irving, L., Scholander, P.F., and Grinnell, S.W. 1941. Significance of the heart rate to diving ability of seals. *J. Cell. Comp. Physiol.* 18(3):283-297.
- Jackson, D.C. and Prange, H.D. 1979. Ventilation and gas exchange during rest and exercise in adult green sea turtles. *J. Comp. Physiol.* 134:315-319.
- Jones, D.R. 1967. Oxygen consumption and heart rate of anuran amphibia during submergence. *Comp. Biochem. Physiol.* 20:691-707.
- Jones, D.R. and Purves, M.J. 1970. The effect of carotid body denervation upon the respiratory response to hypoxia and hypercapnia in the duck. *J. Physiol. (London)* 211:295-309.
- Jones, D.R., Milsom, W.K., and Gabbott, G.R.J. 1982. Role of central and peripheral chemoreceptors in diving responses of ducks. *Am. J. Physiol.* 243 (Regulatory Integrative Comp. Physiol. 12):R537-R545.
- Keinath, J.A. and Musick, J.A. 1993. Movements and diving behavior of a leatherback turtle, *Dermochelys coriacea*. *Copeia* 1993(4):1010-1017.
- Kooyman, G.L., Wahrenbrock, E.A., Castellini, M.A., Davis, R.W., and Sinnett, E.E. 1980. Aerobic and anaerobic metabolism during voluntary diving in Weddell seals: evidence of preferred pathways from blood chemistry and behavior. *J. Comp. Physiol.* 138:335-346.
- Kooyman, G.L., Castellini, M.A., Davis, R.W., and Maue, R.A. 1983. Aerobic diving limits of immature Weddell seals. *J. Comp. Physiol.* 151:171-174.
- Kooyman, G.L. 1989. *Diverse Divers: Physiology and Behavior*. Springer-Verlag, Berlin, 200pp.

- Lacombe, A.M.A. and Jones, D.R. 1991a. Neural and hormonal effects on hindlimb vascular resistance of ducks during forced submergence. *Am. J. Physiol.* 261:R1579-R1586.
- Lacombe, A.M.A. and Jones, D.R. 1991b. Role of adrenal catecholamines during forced submergence in ducks. *Am. J. Physiol.* 30:R1364-R1372.
- Lenfant, C. and Johansen, K. 1967. Respiratory adaptations in selected amphibians. *Resp. Physiol.* 1967(2):247-260.
- Leslie, A.J., Penick, D.N., Spotila, J.R., and Paladino, F.V. 1996. Leatherback turtle, *Dermochelys coriacea*, nesting and nest success at Tortuguero, Costa Rica, in 1990-1991. *Chelonian Conserv. Biol.* 2(2):159-168.
- Lioy, F., Hanna, B.D., and Polosa, C. 1978. CO<sub>2</sub>-dependent component of the neurogenic vascular tone in the cat. *Pflugers Arch.* 374:187-191.
- Lioy, F., Hanna, B.D., and Polosa, C. 1981. Cardiovascular control by medullary surface chemoreceptors. *J. Auton. Nerv. Syst.* 3:1-7.
- Lutcavage, M.E. and Lutz, P.L. 1986. Metabolic rate and food energy requirements of the leatherback sea turtle, *Dermochelys coriacea*. *Copeia* 1986(3):796-798.
- Lutcavage, M.E., Bushnell, P.G., and Jones, D.R. 1990. Oxygen transport in the leatherback sea turtle *Dermochelys coriacea*. *Physiol. Zool.* 63(5):1012-1024.
- Lutcavage, M.E., Bushnell, P.G., and Jones, D.R. 1992. Oxygen stores and aerobic metabolism in the leatherback sea turtle. *Can. J. Zool.* 70:348-351.
- Lutcavage, M.E. 1997. Diving Physiology. *In The Biology of Sea Turtles, edited by Lutz, P.L. and Musick, J.A.* CRC Press, New York.
- Lutz, P.L. and Bentley, T.B. 1985. Respiratory physiology of diving in the sea turtle. *Copeia* 1985(3):671-679.
- Lutz, P.L., Bergey, A., and Bergey, M. 1989. Effects of temperature on gas exchange and acid-base balance in the sea turtle *Caretta caretta* at rest and during routine activity. *J. Exp. Biol.* 144:155-169.
- Mangalam, H.J. and Jones, D.R. 1984. The effects of breathing different levels of O<sub>2</sub> and CO<sub>2</sub> on the diving responses of ducks (*Anas platyrhynchos*) and cormorants (*Phalacrocorax auritus*). *J. Comp. Physiol. B* 154:243-247.
- Morreale, S.J., Standora, E.A., Spotila, J.R., and Paladino, F.V. 1996. Migration corridor for sea turtles. *Nature* 384:319-320.

National Marine Fisheries Service and U.S. Fish and Wildlife Service. 1992. Recovery Plan for Leatherback Turtles in the U.S. Caribbean, Atlantic, and Gulf of Mexico. National Marine Fisheries Service, Washington, D.C.

Paladino, F.V., O'Connor, M.P., and Spotila, J.R. 1990. Metabolism of leatherback turtles, gigantothermy, and thermoregulation of dinosaurs. *Nature* 344(6269):858-860.

Plotkin, P.T. The Migratory and Reproductive Behavior of the Olive Ridley, *Lepidochelys olivacea* (Eschscholtz, 1829) in the Eastern Pacific Ocean. PhD. dissertation, Texas A&M University, College Station, 1994.

Prange, H.D. and Ackerman, R.A. 1974. Oxygen consumption and mechanics of gas exchange of green turtle (*Chelonia mydas*) eggs and hatchlings. *Copeia* 1974:758.

Prange, H.D. and Jackson, D.C. Ventilation, gas exchange and metabolic scaling of a sea turtle. 1976. *Resp. Physiol.* 27:369-377.

Prescott, R.L. 1988. Leatherbacks in Cape Cod Bay, Massachusetts, 1977-1987, p.83-84. In B.A. Schroeder (comp.), Proceedings of the 8th Annual Workshop on Sea Turtle Conservation and Biology. NOAA Tech. Memo. NMFS-SEFC-214.

Pritchard, P.C.H. 1971. The leatherback or leathery turtle, *Dermochelys coriacea*. IUCN Monograph 1:1-39.

Rhodin, A.G.J., Ogden, J.A., and Conlogue, G.J. 1981. Chondro-osseous morphology of *Dermochelys coriacea*, a marine reptile with mammalian skeletal features. *Nature* 290:244-246.

Sakamoto, W., Uchida, I., and Kureba, K. 1990. Deep diving behavior of the loggerhead turtle near the frontal zone. *Nippon Suisan Gakkaishi* 56:1435.

Sakamoto, W., Naito, Y., Uchida, I., and Kureba, K. 1990. Circadian rhythm on diving motion of the loggerhead turtle *Caretta caretta* during interesting and its fluctuations induced by the oceanic environmental events. *Nippon Suisan Gakkaishi* 56:263.

Schmidt-Nielsen, K. 1984. Scaling: Why is Animal Size So Important. Cambridge University Press, New York.

Scholander, P.F. 1940. Experimental investigation on the respiratory function in diving mammals and birds. Hvalraadets Skrifter, No. 22. Det Norske Videnskaps Akademi I Oslo.

Schreer, J.F. and Kovacs, K.M. 1997. Allometry of diving capacity in air-breathing vertebrates. *Can. J. Zool.* 75:339-358.

- Seymour, R. 1974. How sea snakes may avoid the bends. *Nature* 250(5466):489-490.
- Seymour, R. 1979. Blood lactate in free diving sea snakes. *Copeia* 1979:494-497.
- Soma, M. 1985 Radio biotelemetry system applied to migratory study of the turtle. *J. Pac. Mar. Sci. Technol. Tokai Univ.* 21:47.
- Spotila, J.R., O'Connor, M.P., and Paladino, F.V. 1997. Thermal Biology. *In The Biology of Sea Turtles, edited by Lutz, P.L. and Musick, J.A.* CRC Press, New York.
- Stabenau, E.K., Heming, T.A., and Mitchell, J.F. 1991. Respiratory, acid-base and ionic status of Kemp's ridley sea turtles (*Lepidochelys kempii*) subjected to trawling. *Comp. Biochem. Physiol.* 99A:107.
- Standora, E.A., Spotila, J.R., Keinath, J.A., and Shoop, C.R. 1984. Body temperatures, diving cycles and movement of a sub-adult leatherback turtle, *Dermochelys coriacea*. *Herpetologica* 40:169-176.
- Steyermarker, A.C., Williams, K., Spotila, J.R., Paladino, F.V., Rostal, D.C., Morreale, S.J., Koberg, M.T., and Arauz, R. 1996. Nesting leatherback turtles at Las Baulas National Park, Costa Rica. *Chelonian Conser. Biol.* 2(2):173-183.
- West, N.H., Butler, P.J., and Bevan, R.M. 1992. Pulmonary blood flow at rest and during swimming in the green turtle, *Chelonia mydas*. *Physiol. Zool.* 65(2):287-310.
- Witzell, W.N. and Cramer, J. 1995. Estimates of sea turtle by-catch by the U.S. pelagic longline fleet in the western north Atlantic Ocean. NOAA Tech. Memo. NMFS-SEFCS-3559, 14p.