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MAINTENANCE OF NEUTRAL BUOYANCY BY DEPTH SELECTION IN THE LOGGERHEAD TURTLE *CARETTA CARETTA*

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Summary

Time-series data of swimming speed and dive depth were recorded in six female loggerhead turtles *Caretta caretta* during the internesting period. The dive profiles of all animals indicated that they stayed at particular depths without swimming and that these depths were correlated with dive duration. These results support the hypothesis that lung air is used to achieve neutral buoyancy in the loggerhead turtle.

To test this hypothesis, female turtles were equipped with lead weights and time/depth recorders. The residence depth of the turtles increased when their specific gravity was artificially decreased. This indicates that they control depth rather than lung volume, suggesting that the residence depth of loggerhead turtles during the internesting period is not determined actively. They presumably remain at a particular depth exclusively to save energy for egg maturation during the internesting period.

Lung volume was estimated from the change in depth of weighted animals to be 50–150 ml kg^{-1}. The resulting residence depth of all turtles was within the range at which they maintained the neutral buoyancy.

Key words: loggerhead turtle, *Caretta caretta*, diving behaviour, buoyancy control, dive depth, swim speed, data logger.

Introduction

The ocean environment changes substantially with depth so that, if aquatic animals wish to stay at a preferred depth with minimal energy expenditure, they can achieve this by adjusting their specific gravity. At depth, where the animal's density differs from that of the water, particular depths can be maintained through behavioural responses necessitating additional energy expenditure. The appropriate control of buoyancy is therefore very important for aquatic animals. Some animals, such as elasmobranch fishes, increase the proportion of substances lighter than water in their tissues to achieve optimal buoyancy. Fat and oil, such as squalene, which have a specific gravity lower than that of sea water, will increase the animal's buoyancy (Schmidt-Nielsen, 1990). Marine mammals such as elephant seals *Mirounga angustirostris* also have large amount of fat under the skin partly to increase their buoyancy (Webb et al., 1998). Gas is particularly effective in increasing buoyancy because of its extremely low density. Many species of teleosts have swimbladders to give them neutral buoyancy (Schmidt-Nielsen, 1990) and, in the case of air-breathing diving animals, the lung may act as a buoyancy organ during the dive if the animal inhales enough air before diving. The volume of air in the lung will change with the depth according to Boyle's law. The air volume decreases with increasing water pressure, causing the total body density to increase with depth. Thus, neutral buoyancy is only possible at one particular depth. This problem makes the maintenance of neutral buoyancy by an air-mediated mechanism restrictive; animals will be subject to an overall upward force at shallower depths and a downward force due to gravity in deeper zones. This problem is particularly pertinent to air-breathing animals, which must undergo vertical movement to and from the surface for gas exchange by the lungs.

Sea turtles, which use pulmonary gas exchange, can selectively move lung gas to the front, back, right or left of the lungs to compensate for changes in body weight (Jacobs, 1939), and dive data from a loggerhead turtle *Caretta caretta* in the internesting period also suggest that these animals use their lungs to control their buoyancy (Minamikawa et al., 1997). This animal was able to maintain depth without swimming, indicating that buoyancy was close to neutrality at that depth. Furthermore, the preferred depth of the turtle varied and was correlated with dive duration, suggesting that the turtle stored more oxygen before performing a deeper dive. Since the

main oxygen-storage organ of turtles is the lung (Lutz and Bentley, 1985) and the total body volume of the turtle varies according to pulmonary air volume, it is possible that loggerhead turtles control their buoyancy by controlling pulmonary air volume.

There are two ways to achieve neutral buoyancy when using the lungs as buoyancy organs. (i) To adjust pulmonary air volume as a function of the preferred depth. This stationary depth is selected before diving by adjusting the pulmonary air volume. This is termed active depth selection (ADS). (ii) To adjust depth such that the stationary depth is a consequence of the air volume in the lungs. This is termed passive depth selection (PDS).

The first aim of this study was to examine the role of the lungs in buoyancy control in turtles. We recorded swimming velocity and dive depth simultaneously in free-ranging loggerhead turtles. The second aim was to determine whether ADS or PDS was used by loggerhead turtles. We examined changes in diving behaviour resulting from experimentally changing the turtles' specific gravity. If they use ADS, the turtles would maintain the same stationary depth after modification of their specific gravity, implying that there is probably a biological reason for the animals to stay at this particular depth. If the preferred depth changed after altering the specific gravity, the turtles would be using PDS.

Finally, the capacity of the lungs should restrict the range of depths at which the animals can achieve neutrality if their lungs control their buoyancy. We examined the extent to which the diving behaviour of loggerhead turtles supports this hypothesis.

Materials and methods

Equipment and field experiments

Experiment 1

Multi-channel data loggers (KS-PDT, developed by the National Institute of Polar Research and Little Leonardo, Tokyo, Japan) were attached to loggerhead turtles *Caretta caretta* (L.) to record their diving activities during the internesting period.

KS-PDT data loggers have a memory of 1 Mb and were programmed to record swimming velocity and depth at intervals of 5 s. Data were recorded over approximately 11 days. Swimming speed was measured by a stainless-steel impeller located at the front of the instrument, which turned at a rate determined by swimming speed and had a minimum threshold of 0.3 m s^{-1}. The measurement error of the velocity recorder was less than 0.1 m s^{-1}. Dive depth was measured by a pressure sensor located at the back of the device. KS-PDT loggers were classified by the thickness of the housing and the type of pressure sensor into three types: KS-200PDT, KS-200PDTt and KS-400PDTt. The range of measurement and resolution were, respectively, 0–380 m and 0.1 m (KS-400PDTt) and 0–190 m and 0.05 m (KS-200PDT, KS-200PDTt). The instruments had a diameter less than 32 mm, were less than 110 mm in length, and weighed less than 80.5 g in air.

All experiments were performed at Senri Beach, Minabe, Wakayama Prefecture, Japan, during June and July 1995 and 1996 (Fig. 1). We attached data loggers to nine female turtles after they had laid eggs and obtained the data from six individuals when they subsequently returned to the beach. We named these turtles 9501 (straight carapace length, SCL, 80.0 cm, body mass, M_b, 74.0 kg), 9502 (SCL 83.9 cm, M_b 73.0 kg), 9601 (SCL 85.8 cm, M_b 82.0 kg), 9602 (SCL 83.7 cm, M_b 80.0 kg), 9603 (SCL 79.2 cm, M_b 75.0 kg) and 9604 (SCL 76.0 cm, M_b 62.5 kg). All KS-PDT loggers were fixed to the frontal part of the carapace along the mid-line using epoxy resin.

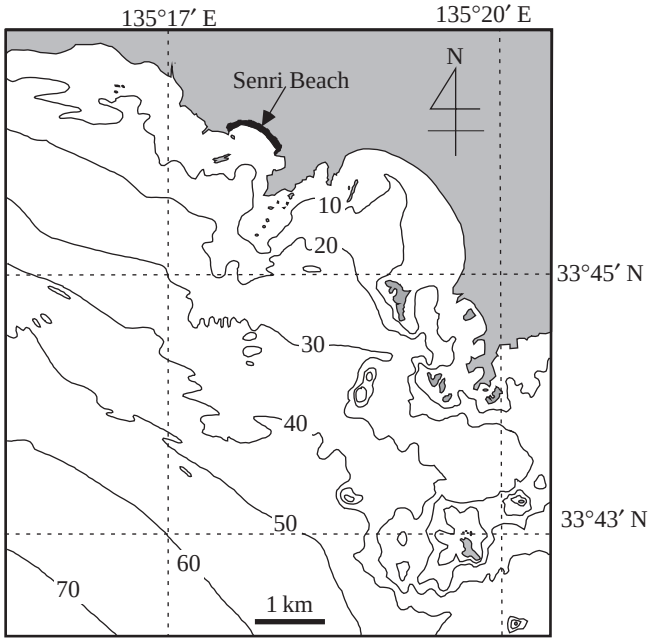

Fig. 1. Map of the site of field studies. Turtles were studied diving under natural conditions at Senri Beach. The numbers on contour lines indicate the depth of the water (m).

Experiment 2

We attached KS-PDT data loggers and lead weights with time-scheduled releasers to three female turtles as described above at Senri Beach during June and July 1996. The KS-PDT and time-scheduled weight releaser were attached to the centre front and centre rear part of the carapace, respectively. Holes in two lead weights were threaded with stainless-steel wire which was scheduled to be cut at a prescribed time to release the weights. The weights were stabilized by epoxy resin arches mounted on the right and left sides of the carapace. The time-scheduled weight releaser (developed by the National Institute of Polar Research, Tokyo and Nichiyu Giken Kogyo Co., Ltd, Saitama, Japan; 97 mm×27.5 mm diameter; mass 84 g) had an internal timer that was set to release the weights 100 h after attachment. Data were retrieved from two individuals (96A and 96B) after they had returned to their nesting beaches to lay eggs (see above). Straight carapace lengths were 86.3 cm and 91.3 cm, body masses were 88.0 kg and 113.0 kg and the total mass of the attached lead weights was 1128 g and 1494 g for 96A and 96B, respectively.

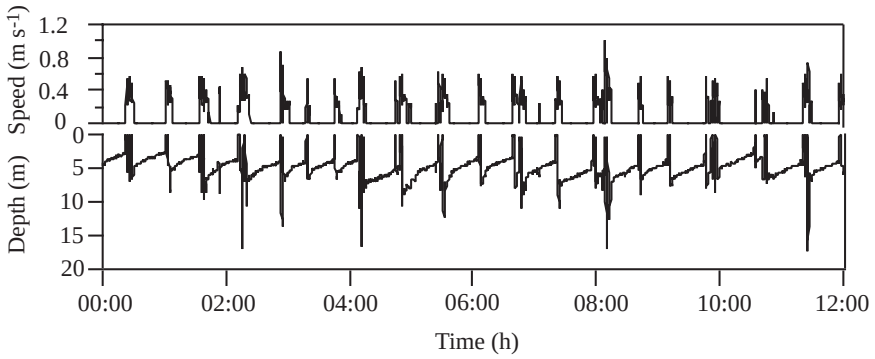

Fig. 2. An example of the recorded diving behaviour of a loggerhead turtle (9501) on 29 June 1995.

Data analysis

The impeller of the KS-PDT loggers attached to 9601 and 9602 did not rotate for some periods, perhaps for mechanical reasons, and data from these animals were discarded at such times.

The time-series data from each of the turtles showed similar patterns. They remained for periods at a certain depths without swimming. Fig. 2 presents a section of the time-series data showing dive depth and swimming speed retrieved from turtle 9501.

The dive of loggerhead turtles was characterized by a gradual ascent phase during which the turtle stayed at a relatively constant depth. Some dives could be divided into four phases (Fig. 3): first descent, first ascent, gradual ascent and final ascent, or three phases when the first ascent was absent. The summed total dive duration of these types of dives accounts for 66 % of the summed total dive duration of all dives, and the speed during the gradual ascent phase is approximately zero in approximately 50 % of these dives (Minamikawa et al., 1997). Therefore, we considered the typical dive of loggerhead turtles to have the following five points of inflection: start point of the dive (start point), the point of maximum depth during the dive (maximum point), the point of initiation of the gradual ascent (point A), the end point of the gradual ascent (point B) and the end point of the dive (end point). Some dives did not have first ascent or gradual ascent phases. The start point is defined as the first point for which the depth was greater than 0.4 m. The end point is the last point for which the depth was less than 0.4 m. We calculated the average ascent rate R of the dive as follows:

$$R = (D_{MAX} - D_{END})/(t_{MAX} - t_{END}), \quad (1)$$

where D_{MAX} and D_{END} are the depths at maximum point and end point, respectively, and t_{MAX} and t_{END} are the times of these points, respectively.

In addition we defined point A as the first point for which the ascent rate was less than the average ascent rate between the maximum point and end point over at least 5 s. Point B was identified as the last point for which the ascent rate was less than the average ascent rate between the maximum point and end point over 5 s.

However, point A determined in this way was not consistent with the first point of the gradual ascent phase determined visually because of small-scale variability in the depth recordings. We therefore performed the following correction to remove this effect.

We first smoothed the depth data by calculating a running mean over 13 points for each data point, centred on the point itself, and produced a dive profile based on these smoothed data. We then defined point A as the first point for which the ascent rate, over four consecutive points, was smaller than the average ascent rate. If such a point did not exist, it was defined in turn as the first point for which the ascent rate over three consecutive points, two consecutive points or one point was smaller than the ascent rate. Point B was defined as the last point for which the ascent rate was less than the average ascent rate of the smoothed data. Points A and B calculated in this way were consistent with the beginning and end of the gradual ascent as determined visually (see Fig. 3). Points A and B overlapped in V-shaped dives, which do not have a gradual ascent phase, and such dives were excluded from this analysis.

We defined the dive duration as the interval from the start to the end point; the initial speed was the swimming speed over the first 5 s from the start point, and the initial descent rate was the rate of change of depth during the first 5 s from the start point. Terminal speed and terminal ascent rate were the swimming speeds and the rate of change of depth calculated

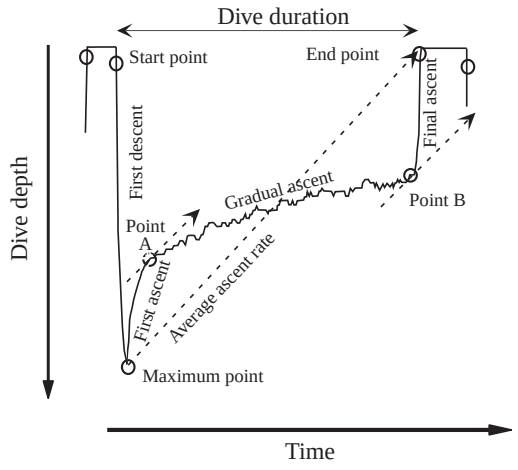

Fig. 3. The dive profile of a loggerhead turtle with definitions of the four phases.

over 5 s, 10 s before the end point (because the turtles did not always continue to ascend during the last 5 s).

Activity during the gradual ascent phase is likely to influence the rate of oxygen consumption and, consequently, dive duration. To analyse only dives in which oxygen consumption rates were as similar as possible and in which buoyancy during the gradual ascent phase was close to neutral, dives during which the average rate of impeller rotation during the gradual ascent phase was greater than 0.2 revs s^{-1} (=6×10^{-3} m s^{-1}) were also excluded.

Results

Experiment 1

Totals of 1285, 818, 493, 494, 817 and 1186 dives were obtained from animals 9501, 9502, 9601, 9602, 9603 and 9604, respectively. Using the above procedure, 1319 similar dives were selected from six turtles. These dives account for approximately 27–62 % (mean 43 %) of total dive duration of all dives for these individuals. Table 1 summarizes these selected dives.

There was a significant correlation for all turtles between dive duration and depth at point A (Spearman's rank correlation r_S: 9501, 0.341, N=205, P<0.0001; 9502, 0.216, N=98, P=0.0336; 9601, 0.538, N=99, P<0.0001; 9602, 0.673, N=92, P<0.0001; 9603, 0.725, N=432, P<0.0001; 9604, 0.563, N=392, P<0.0001). Fig. 4 shows the relationship between dive duration and depth at point A for each turtle.

Experiment 2

Totals of 1072 and 412 dives were recorded under the weighted and unweighted conditions for animal 96A; 403 and 455 dives were recorded, respectively, for 96B. Table 2 summarized the selected dives. There was a significant correlation between dive duration and depth at point A in both conditions for both turtles (Spearman's rank correlation r_S: 96A weighted, 0.498, N=455, P<0.0001; 96A unweighted, 0.657, N=170, P<0.0001; 96B weighted, 0.544, N=120, P<0.0001; 96B unweighted, 0.615, N=71, P<0.0001).

Fig. 5 shows the time-series data of 96A for 5 h before and after the weights were detached. The residence depth of 96A increased 17 min after the wire had been cut. The turtle descended from 2 m to 21 m and then ascended immediately to 3.6 m. The same pattern was also apparent in 96B. The depth at point A after the weights had been detached was significantly deeper than before detachment (Mann–Whitney U-test: 96A, U=16120.5, N_1=170, N_2=455, P<0.001; 96B, U=1643.5, N_1=71, N_2=120, P<0.001).

Fig. 6 shows the mean depth at point A for grouped dive durations for 96A and 96B. This depth was also shallower in the weighted condition for all dive duration groups in both turtles (Wilcoxon signed-ranks test: 96A, t=0, N=7, P=0.018; 96B, t=0, N=10, P=0.012).

Discussion

Loggerhead turtles remained at a constant depth without swimming during a large proportion of their dives. Although they actually ascend gradually during this time, the data suggest that their buoyancy is close to neutral.

Previously reported swimming speeds of loggerhead turtles are 28.1–40.2 km day^{-1} (i.e. 0.33–0.47 m s^{-1}) on the basis of the recapture of tagged turtles (Wyneken, 1996). Initial descent speeds in our results were similar to these values (Table 1). However, the average swimming speed during the internesting period determined by satellite telemetry is 0.45 km h^{-1} (i.e. 0.125 m s^{-1}) for loggerhead turtles (Wyneken, 1996), indicating that these animals do not move great distances

Table 1. *Summary of selected dives from individual turtles*

Individual	Dive duration (s)	Depth at point A (m)	Gradual ascent rate (cm s^{-1})	Initial speed (m s^{-1})	Terminal speed (m s^{-1})
9501	1556.1±629.7 [1665.0] (205)	4.70±1.48 [4.60] (205)	0.40±1.30 [0.10] (205)	0.37±0.10 [0.38] (205)	0.11±0.12 [0.00] (205)
9502	2392.5±13.5 [2510.0] (98)	10.58±5.00 [9.85] (98)	0.55±2.00 [0.10] (98)	0.23±0.14 [0.28] (98)	0.16±0.13 [0.19] (98)
9601	844.5±830.6 [435.0] (99)	4.29±2.40 [3.66] (99)	1.48±1.89 [0.29] (99)	0.39±0.11 [0.39] (99)	0.10±0.14 [0.00] (99)
9602	2125.1±818.2 [2090.0] (92)	8.16±3.63 [7.66] (92)	0.16±0.09 [0.13] (92)	0.50±0.15 [0.52] (92)	0.33±0.20 [0.33] (92)
9603	1208.2±460.7 [1315.0] (432)	4.17±1.67 [4.11] (432)	0.33±1.18 [0.12] (432)	0.21±0.11 [0.23] (432)	0.02±0.07 [0.00] (432)
9604	1278.7±3.87 [1358.0] (392)	4.56±1.85 [5.22] (392)	0.79±1.72 [0.09] (392)	0.36±0.11 [0.36] (392)	0.06±0.11 [0.00] (392)

Values are means ± S.D.; median values are given in square brackets and sample size in parentheses.
For details of selection criteria for dives, see Materials and Methods.
See Fig. 3 for definitions of points and rates during the dive profile.

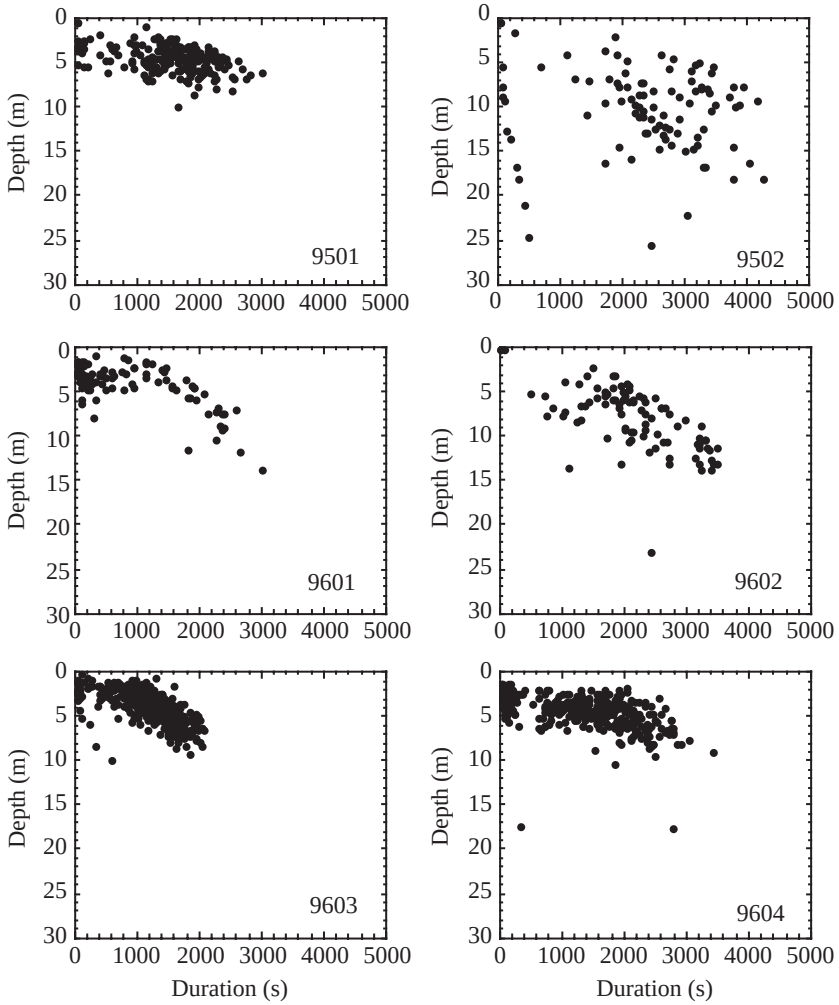

Fig. 4. Relationship between dive duration and depth at point A for each turtle studied. Statistics are given in the text. See Fig. 3 for definition of point A (the beginning of the gradual ascent phase of the dive).

horizontally during this period. Our observations that the turtles swam little during the gradual ascent phase, where they spend most of the time, are consistent with this (Fig. 2).

A positive correlation between residence depth and dive duration (Fig. 4) was found in all individuals. Correlations between dive duration and dive depth have been reported in many diving animals (Le Boeuf et al., 1987; Kooyman and Kooyman, 1995; Dolphin, 1987; Kooyman et al., 1992; Croxall et al., 1991; Croll et al., 1992). Houston and Carbone (1992) provide a model and data showing that dive duration will increase with depth. They consider dives of animals as foraging behaviour and conclude that an increase in dive

Table 2. *Summary of selected dives from individual turtles in experiment 2*

Individual	Dive duration (s)	Depth at point A (m)	Gradual ascent rate ($cm\,s^{-1}$)	Initial speed ($m\,s^{-1}$)	Terminal speed ($m\,s^{-1}$)
96A (weighted)	433.4±382.8 [305.0] (455)	1.90±0.73 [1.86] (455)	0.50±0.76 [0.18] (455)	0.292±0.177 [0.285] (455)	0.059±0.086 [0.000] (455)
96A (unweighted)	868.0±675.1 [747.5] (170)	3.48±1.73 [3.13] (170)	0.45±0.73 [0.16] (170)	0.356±0.150 [0.348] (170)	0.096±0.117 [0.000] (170)
96B (weighted)	1331.5±889.4 [1297.5] (120)	5.70±2.11 [5.39] (120)	0.31±0.53 [0.13] (120)	0.389±0.102 [0.387] (120)	0.146±0.118 [0.168] (120)
96B (unweighted)	1801.8±1279.1 [1945.0] (71)	8.85±3.07 [8.63] (71)	0.96±1.96 [0.13] (71)	0.511±0.083 [0.528] (71)	0.245±0.114 [0.272] (71)

Values are means ± S.D.; median values are given in square brackets and sample size in parentheses.
For details of selection criteria for dives, see Materials and Methods.
See Fig. 3 for definitions of points and rates during the dive profile.

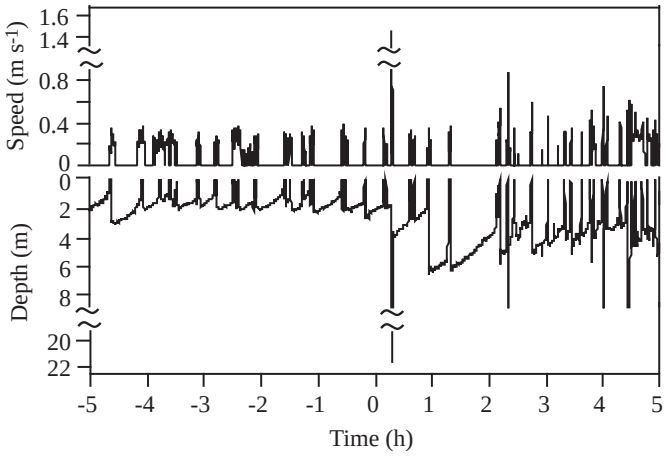

Fig. 5. Time-series data of turtle 96A for 5 h before and after the added weights were detached. The weights were detached at time zero.

duration with dive depth will maximize the proportion of time spent foraging. Loggerhead turtles are generally considered to be primarily carnivorous, feeding mainly on benthic invertebrates and coelenterates (Dodd, 1988). However, this species does not forage during the internesting period (Tanaka et al., 1995). Rather, they seem to dive to avoid unstable conditions at the sea surface (e.g. pitching and rolling due to wave action), and it is reasonable to suggest that a second function of such dives is to reduce energy expenditure to facilitate egg maturation. Whether the diving animals forage or not, dive duration should reflect the amount of oxygen stored. The primary oxygen-storage organs in loggerhead turtles are the lungs, which may store 71.6 % of the total oxygen available for dives (Lutz and Bentley, 1985). Thus, dive duration will reflect lung air volume, and the positive correlation between residence depth and dive duration in all individuals supports the hypothesis that buoyancy control is achieved by the lungs in loggerhead turtles.

There were dramatic changes in residence depth immediately following the release of the weights (Fig. 5). The 17 min time-lag from the release of the weights until the change in residence depth in 96A suggests that the weights may have remained on the carapace for this period. For a turtle to remain at a particular depth when the weights were attached, it must either swim to produce additional lift or inhale a larger amount of air to give additional buoyancy. However, our turtles simply changed their residence depth to maintain neutral buoyancy. These results suggest that the residence depth of loggerhead turtles during the internesting period is not determined actively, but is determined as a consequence of the breath volume before the dive and subsequent adjustment of buoyancy. Animals wishing exclusively to rest without relying on buoyancy must consume additional energy to enable them to commute down to and remain on the sea bed. Variability in residence depth would seem to be a consequence of fluctuations in tidal air volume. Indeed, if the observed depth changes are actually due to changes in buoyancy and the dive duration reflects pulmonary air volume, residence depth should be shallower in the weighted condition for dives of the same duration. The results shown in Fig. 6 are consistent with this prediction.

A diagram of the distribution of residence depth in weighted *versus* unweighted cases is shown in Fig. 7. This diagram can be applied provided that residence depth reflects pulmonary air volume, whether depth selection is passive or active. First, the time for a return trip to and from the target depth must increase with depth (line *A*), and this time determines the minimum dive duration. A turtle loads oxygen into the blood and muscles at the surface and it also needs a certain volume of pulmonary air to give it the buoyancy to remain passively at the residence depth (Minamikawa et al., 1997). The amount of oxygen in the blood and muscles determines the maximum dive duration and, because residence depth increases with increasing pulmonary air volume, maximum dive duration increases with increasing residence depth (line *B*). Lung capacity limits the controllable depth range of buoyancy (line *C*). Lines *B* and *C* shift upwards when the specific gravity of the animal is artificially increased

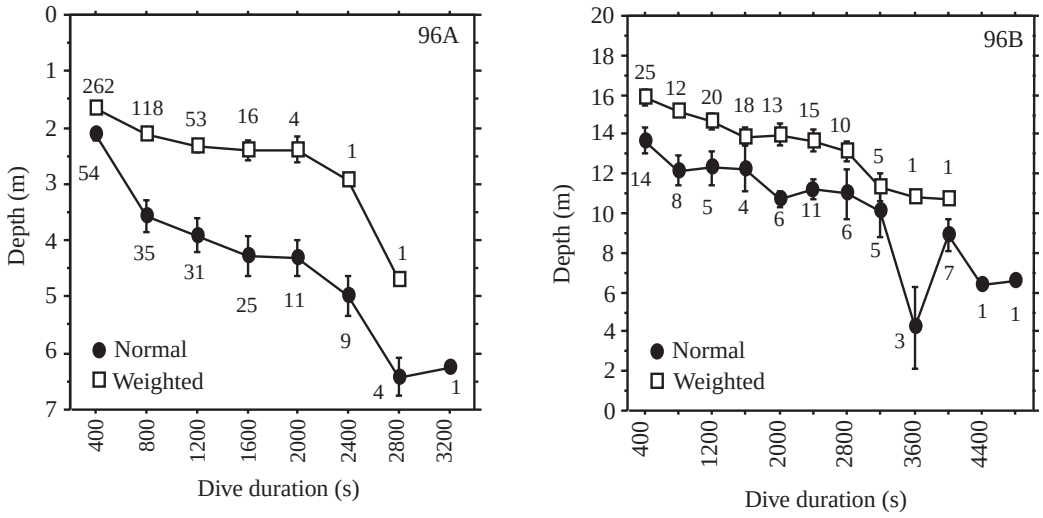

Fig. 6. Mean depth at point A for dive duration groups in animals 96A and 96B. The horizontal axis indicates the upper limit of the range of each dive duration. Circles and squares indicate mean values under unweighted and weighted conditions, respectively. Vertical bars indicate standard deviations. The numbers beside the symbols refer to sample size. See Fig. 3 for definition of point A (the beginning of the gradual ascent phase of the dive).

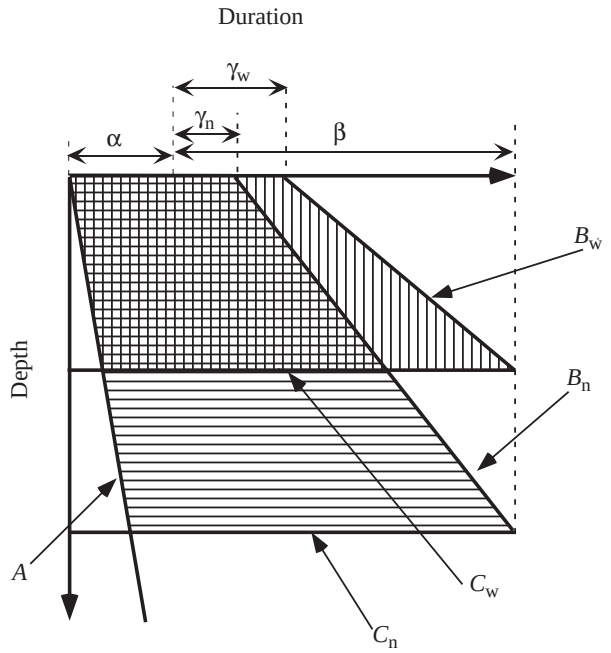

Fig. 7. The distribution of residence depth in a weighted animal (indicated by subscript w and the area delineated by vertical lines) and a normal (unweighted) animals (indicated by subscript n and the area delineated by horizontal lines). The residence depth lies within the area bounded by lines *A*, *B* and *C*. *A* is the limit determined by travelling time to each depth, i.e. indicating the time required to get to each depth. *B* is the limit determined by the amount of oxygen stored. *C* is the limit to the depth at which a turtle can achieve neutral buoyancy. α, range of dive duration determined by the oxygen in the blood and muscles; β, range of dive duration determined by the oxygen stored in the lungs; γ, dive duration determined by the oxygen present in the lungs at the time when the buoyancy of the turtle is neutral on the water surface.

(B_w, C_w). The resistance due to buoyancy during the initial phase of the dive is less in shallow dives and the cost of transport is also reduced, which means that overall energy expenditure commuting to the residence depth is minimal, increasing the likelihood that an animal may surface before its oxygen reserves are fully depleted. Conversely, commuting costs are high in deep dives, so the turtle should tend to remain under water until its oxygen reserves are exhausted. Consequently, dive duration should tend to be distributed around line *B* during deep dives. The duration distribution of animals 9601 and 9603 coincides particularly well with this predicted pattern. The difference in mean residence depth between the unweighted and weighted condition in 96A and 96B (Fig. 6) reflects the difference between line C_n and line C_w mainly in short dives and between lines B_n and B_w mainly in long dives, respectively.

If the depth of point A reflects the air volume in the lungs, we can estimate the pulmonary air volume of loggerhead turtles from our results. Loggerhead turtles have been reported to have a variable inspiration volume, which can be either greater or smaller than resting values (Milsom, 1975; Lutcavage et al., 1989). Even if the reasons for such variations are not clear, they result in changes in the depth of neutral buoyancy.

The results from the weighting experiments show that inspiration volume does not change according to the specific gravity of the turtle. Suppose that the pulmonary air volume per unit body mass (ml kg^{-1}) at the water surface is V_{LS}, the additional force due to the weights per unit body mass is W (g kg^{-1}) and the buoyancy is neutral at depth D_1 (m) in the weighted condition and at depth D_2 in the unweighted condition. Pulmonary air volume per unit body mass at D_1 and D_2 (m) is defined as V_{LD1} and V_{LD2}, respectively.

Because water pressure increases by 1 atmosphere (≈10^{-5} Pa) for every 10 m depth:

$$V_{LD1} = V_{LS}/(1 + 0.1D_1)\,. \quad (2)$$

Similarly,

$$V_{LD2} = V_{LS}/(1 + 0.1D_2)\,. \quad (3)$$

The depth difference (D_1–D_2) depends on the mass of the added weights. If the specific gravity of sea water is 1.03, then:

$$W = 1.03(V_{LD2} - V_{LD1})\,. \quad (4)$$

Substituting equations 2 and 3 into equation 4:

$$W = 0.103[(D_1 - D_2)/(1 + 0.1D_1)(1 + 0.1D_2)]V_{LS}\,. \quad (5)$$

From equation 5, V_{LS} can be derived as:

$$V_{LS} = W/\{[0.103(D_1 - D_2)]/[(1 + 0.1D_1)(1 + 0.1D_1)]\}\,. \quad (6)$$

Using equation 6, we can calculate the lung volume of loggerhead turtles from the dive depth data. Since lung capacity does not depend on the experimental condition, the maximum lung capacity is reflected by the maximum residence depth. We used the maximum value of the depth at point A under weighted conditions (96A, 4.94 m; 96B, 8.11 m) for D_1 and this depth under unweighted conditions (96A, 10.78 m; 96B, 19.92 m) for D_2. From these values, V_{LS} of 96A is 91.2 ml kg^{-1} and that of 96B is 145.1 ml kg^{-1}. Similarly, V_{LD2} is 50.3 ml kg^{-1} for 96A and 58.2 ml kg^{-1} for 96B. This means that the buoyancy of turtles is neutral when their lung volume reaches these values. The maximum lung capacity estimated for green turtles *Chelonia mydas* is 120 ml kg^{-1} (Tenney et al., 1974), and the measured lung capacity of loggerhead turtles is 65–170 ml kg^{-1} (Lutcavage et al., 1987, 1989). The estimated lung capacity in the present study is close to these values.

If the buoyancy of a loggerhead turtle is neutral when the lung volume is approximately 50 ml kg^{-1}, and the maximum lung capacity is approximately 120 ml kg^{-1}, the maximum lung capacity is 2.4 times the lung volume when the buoyancy is neutral. Because water pressure increases by 10^{-5} Pa for every 10 m depth, this means that the lungs of the turtle may control the buoyancy over a range of 14 m. The depth at point A is in agreement with this prediction (Tables 1, 2).

It is not known whether the consistent gradual ascent that occurs at the bottom of the dive is caused by a slight positive buoyancy of the turtle or by other factors. There are two alternative hypotheses. The resting rate of oxygen consumption

of a 20 kg loggerhead turtle is 40 ml O_2 kg^{-1} h^{-1} (Lutz and Bentley, 1985). Resting metabolic rate is proportional to $M_b^{-0.174}$ in green turtles (Prange and Jackson, 1976), and oxygen storage capacity is 22.2 ml kg^{-1} in loggerhead turtles (Lutz and Bentley, 1985). Applying these values to the individuals in our study, the rate of oxygen consumption at the residence depth is estimated to be approximately 9.0×10^{-3} ml kg^{-1} s^{-1}.

The main energy source during the internesting period is fat, because turtles do not forage at this time (Tanaka et al., 1995) and since the respiratory quotient of fat is 0.7, this results in a rate of production of carbon dioxide of 6.3×10^{-3} ml kg^{-1} s^{-1}. Therefore, if loggerhead turtles rely exclusively on the lungs to store and provide O_2, lung volume would decrease at a rate of 2.7×10^{-3} ml kg^{-1} s^{-1}. The median depth at point A was 4–5 m in most individuals. If we assume that 50 ml kg^{-1} is the lung volume that allows neutral buoyancy in loggerhead turtles, this air volume will be 75 ml kg^{-1} at the sea surface if the turtle is neutrally buoyant at a depth of 5 m. The initial concentration of oxygen in the lungs of the green turtle is 17.4 % (Berkson, 1966). Assuming that this value also applies to loggerhead turtles, after exhaustion of all oxygen stored in the lungs, the resulting volume converted to atmospheric pressure will be 71.1 ml kg^{-1}, a volume that produces neutral buoyancy at 4.2 m. The dive duration necessary to exhaust all the O_2 in the lungs is $(75\times0.174)/(9.0\times10^{-3})=1450$ s. If the turtle compensates actively for the sinking induced by the decrease in air volume caused by O_2 utilization during diving and maintains neutral buoyancy, the resulting ascent rate is calculated to be 5.5×10^{-4} m s^{-1}. This value is somewhat lower than the measured gradual ascent rate (Tables 1, 2). However, the actual metabolic rate during a dive is probably higher than the resting metabolic rate used in this calculation especially if the animal has to compensate actively for decreasing buoyancy, resulting in a more rapid exhaustion of the O_2 store in the lungs. In addition, all the carbon dioxide produced may not be released into the lungs during the dive; some will be contained in the blood. Thus, it is likely that the gradual ascent represents behavioural compensation to allow the animal to remain at neutral buoyancy despite a decreasing volume of air in the lungs. The dive profiles of the sea snake *Pelamis platurus* are similar to those of loggerhead turtles, and the same hypothesis has been proposed to explain the gradual ascent phases also observed in this species (Graham et al., 1987). Intracardiac blood shunting (right-to-left shunting) suppresses air loss from the lungs and minimizes the rate of buoyancy change in sea snakes (Graham et al., 1987). This shunt has also been observed for green sea turtles by Butler et al. (1984) and may serve the same function.

However, to accomplish such fine tuning would necessitate continuous, fine adjustment to the residence depth by active swimming. An alternative interpretation is that if the turtles are slightly buoyant at point A, because this point is just above their neutral buoyancy depth, they would be expected to accelerate towards the surface. However, the gradual decrease in lung volume discussed above may be sufficient to prevent this. This would obviate the problem of slow sinking during the dive caused by a loss of buoyancy. A recent study reported that the dive profiles of green sea turtles also have gradual ascent phases, and this was interpreted as a method of gradually gaining positive buoyancy (Hochscheid et al., 1999).

Our study shows that loggerhead turtles spent most of their time underwater at nearly neutral buoyancy by adjusting the depth to their lung volume. The reason why loggerhead turtles are not active during the gradual ascent phase is not clear. It is possible that this behaviour functions to save as much energy as possible because the turtles must allocate energy to preparing the next clutch of eggs during the internesting period. However, in this case, why do loggerhead turtles not stay at the bottom of the sea near to the beach? Further investigations are needed to clarify this.

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