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Shallow Water Diving by Leatherback Turtles in the South China Sea

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Abstract. – **Internesting dive behavior of 3 leatherback sea turtles near Rantau Abang, Malaysia, is presented. Diving patterns were similar to leatherbacks in the Caribbean in that there was almost no period when the turtles were not diving, and dives were influenced by time of day. Daytime dives were longer, deeper, and had longer post-dive surface intervals than night-time dives. Bottom durations were also longer during the day. Major differences between Caribbean and Malaysian leatherbacks were the depth and durations of the dives. Malaysian turtles were constrained by the shallow waters of the South China Sea to dives less than 60 m, and indeed many of their dives appeared to be to the bottom. Dive durations were much longer for Malaysian turtles. We suggest that this may be due to a lower metabolic demand of diving by Malaysian turtles, possibly because they were resting on or near the bottom on each dive. Bottom times were greater than 3 minutes in 47% of all dives, which is distinctly different than Caribbean leatherback diving. There was a strong correlation between dive depth and dive duration but only a weak relationship (if any) between dive duration and bottom time and none between dive duration and post-dive surface time.**

Key Words. – **Reptilia; Testudines; Dermochelyidae; *Dermochelys coriacea*; sea turtle; dive behavior; dive depth; dive duration; Malaysia**

The internesting dive behavior of the leatherback sea turtle, *Dermochelys coriacea*, has been well documented in the deep water environment of the northeast Caribbean Sea. By utilizing Time-Depth Recorders, Eckert et al. (1986, 1989) continuously monitored dives of 8 adult females during internesting intervals at St. Croix, U.S. Virgin Islands. A total of 6395 dives were documented during these two studies. The turtles tended to proceed directly to maximum depth and directly back to the surface. Very little time was spent at the bottom of the dive or on upward excursions during the dive. Dives were continuous throughout the day with an average depth of 35–122 m and a maximum in excess of 1000 m, averaging 6.9–14.5 min per dive (maximum = 42 min). There was no correlation between dive duration and post-dive surfacing time ($r^2 = 0.08–0.0003$), but there was a positive relationship between dive depth and dive time ($r^2 = 0.35–0.55$). Size of the turtle seemed to have no effect on average dive duration or dive time (however, the size range used in this study was limited because it included only adult females). The absence of a correlation between dive time and surface time led the authors to suggest that the leatherback relies primarily on aerobic metabolism for diving.

There was a strong diel influence on dive activity of the turtles at St. Croix. Day dives were deeper and longer than those at night (maximum dive depths usually occurred around 1200 h), but the hourly average depths were greatest in the early morning and shallowest at dusk. Total submergence time per hour and frequency of diving was highest at night with the least variation in dive depths. It was suggested that these patterns represented nocturnal foraging on vertically migrating prey associated with the Deep Scattering Layer. The hypothesis that the turtles were feeding was corroborated by weight-change data. Surface durations and periodicity were also influenced by time of day. Average surface times were longer during midday and might have represented basking by the turtles (Eckert et al., 1986, 1989).

The purpose of this study was to describe internesting dive behavior by gravid leatherbacks in the South China Sea where deep water is unavailable, and to compare the results with deep water studies conducted at St. Croix. The internesting habitat offshore at Terengganu State, Malaysia, barely reaches 60 m in depth, 50 km from shore. We were particularly interested in the effect of diving in shallow water on dive duration. Where applicable, we have reanalyzed St. Croix dive data to facilitate comparisons.

MATERIALS AND METHODS

The study was conducted near the village of Rantau Abang (5°52'N, 103°23'E) in Terengganu, Malaysia during June and July, 1989. Seasonal (May – September) nesting by leatherback turtles was concentrated on roughly 20 km of beach, with Rantau Abang centrally located. The beach was regularly patrolled during the nesting season by egg collectors licensed by the state government. We enlisted the support of these egg collectors in finding turtles as they came to shore to nest. Turtles were allowed to excavate the nest chamber and deposit a full clutch of eggs prior to our approaching them to attach instruments. Following egg-laying, a harness was fitted to the turtle and a VHF radio transmitter (Telonics Telemetry, model mk5) and a microprocessor controlled Time-Depth Recorder (TDR) (Wildlife Computers, model Mk 3+) were secured to the harness. The harness was constructed of 5 cm tubular nylon webbing with 2.5 cm flexible Polyvinyl ("Tygon") tubing inserted into the shoulder straps to act as padding. During fitting, the shoulder straps were brought up from under the turtle to meet the distal ends of the belly strap. All four ends (loops) were secured dorsally with multiple bands of 4.0 mm elastic cording. The single joining point simplifies installation and removal, permits easy harness adjustment, flexes with the animal to confer complete freedom of movement during swimming and diving, and avoids the necessity for multiple buckles or adjustment sites. The elastic cording disintegrates in 45–60 days to release the turtle from the harness should the opportunity for removal not arise (see Eckert and Eckert, 1986, for harness details).

The TDRs measure 2.5 x 15 cm, weigh 100 g, contain 64 k of memory, and are accurate to ± 2 m. Battery life is approximately two years, although the electronic memory may reach capacity in a matter of days. Interactive software developed by the manufacturer permits the user to program the TDR to record depth at predetermined intervals and to calculate surface time, ascent, and descent rates. During deployment of the first TDR (turtle 029A) the unit was programmed to sample dive depth every 10 sec. During all subsequent deployments, TDRs were programmed to sample dive depth every 20 sec. Each TDR was removed when the turtle returned to the beach to nest again (9–10 days later). A total of 5 turtles were fitted with TDRs as well as a radio transmitter, and an additional 7 turtles were fitted with radio transmitters alone. This paper will present only the data collected by the TDRs, the results of radio-tracking gravid females during the internesting period have been published separately (Chan et al., 1990).

Since behavioral dive data generally violates assumptions of normality, non-parametric statistical tests (e.g., Kruskal-Wallis) were used for statistical comparisons throughout the analysis. Comparisons were considered statistically significant at $P \leq .05$. Also, because of the non-normality of the data, we give both the mean and mode for each dive variable. The mean allows comparison with previous studies, but the mode probably represents 'typical' behavior of the turtles better.

Table 1. Turtle number, size (curved carapace length, CCL, in cm), and dates of deployment and recovery of Time-Depth Recorders on nesting female leatherbacks at Rantau Abang, Malaysia.

Number	CCL (cm)	Deployed	Recovered	Days
026	153	06 July	18 July	12
029A	149	15 June	23 June	8
029B	158	27 June	06 July	10

RESULTS

Of the 5 TDR deployments, 3 were successful. A total of 2422 dives was recorded. Dates of deployment and recovery as well as size data on each turtle can be found in Table 1. Mean dive times ranged from 7.9 min (sd = 3.59; mode = 10.0) to 12.14 min (sd = 4.94; mode = 12.33). Average dive depths ranged from 26.7 m (sd = 13.67; mode = 18.0) to 45.1 m (sd = 17.25; mode = 56.0). Summary dive data on individual turtles are in Table 2. Dives tended to be directly to maximum depth with the turtle remaining there a mean of 1.76 min (sd = 1.86; mode = 0.33) to 3.65 min (sd = 3.72; mode = 0.83) before ascending directly to the surface. Average individual descent rates were 0.15 m/s (sd = 0.065; mode = 0.14), 0.25 m/s (sd = 0.085; mode = 0.2) and 0.19 m/s (sd = 0.059; mode = 0.15). Average individual ascent rates were 0.25 m/s (sd = 0.15; mode = 0.20), 0.19 m/s (sd = 0.107; mode = 0.4), and 0.18 m/s (sd = 0.08; mode = 0.2). Frequency distributions for each of these variables are presented in Figs. 1–6.

A frequency distribution of the dive depths (Fig. 2) illustrates that turtles exhibited individual preferences in typical dive depths. Turtle 026 had a strong propensity for diving between 55 and 60 m, while turtle 029A's depth distribution was almost tri-modal with most dives between 0–5 m, 30–35 m, or 40–45 m. Turtle 029B's dive depth

Table 2. Summary statistics of dive behavior for 3 leatherback turtles during their internesting interval in the South China Sea.

	Mean	SD	Mode	Minimum	Maximum	*n*
Turtle 026						
Depth (m)	45.13	17.24	56.00	4.00	62.00	486
Dive Time (min)	12.14	4.49	12.33	1.00	27.67	486
Surface Time (min)	10.55	9.51	multiple	0.33	57.00	486
Descent Rate (m/s)	0.16	0.65	0.14	0.07	1.40	486
Ascent Rate (m/s)	0.25	0.15	0.20	0.02	2.80	486
Bottom Time (min)	3.65	3.72	0.33	0.33	21.33	486
Turtle 029A						
Depth (m)	27.48	11.79	18.00	4.00	48.00	626
Dive Time (min)	10.28	4.74	12.33	0.83	22.50	626
Surface Time (min)	6.65	8.24	2.83	0.17	85.83	626
Descent Rate (m/s)	0.25	0.08	0.20	0.09	0.80	626
Ascent Rate (m/s)	0.19	0.11	0.40	0.03	0.65	621
Bottom Time (min)	3.19	2.97	0.83	0.17	20.33	582
Turtle 029B						
Depth (m)	26.70	13.67	20.00	4.00	54.00	1158
Dive Time (min)	7.91	3.59	10.00	1.00	18.00	1158
Surface Time (min)	4.54	4.91	1.67	0.33	54.67	1158
Descent Rate (m/s)	0.19	0.06	0.15	0.50	0.50	1150
Ascent Rate (m/s)	0.18	0.08	0.20	0.00	0.70	1125
Bottom Time (min)	1.76	1.86	0.33	0.33	14.33	974

frequency distribution was bimodal with peaks at 20–25 m and 40-45 m. The frequency distributions of dive durations were somewhat bimodal for all turtles with peaks at 1 min and 9–15 min (Fig. 1).

Dives were analyzed for diel differences by comparing day (0500 h – 1859 h) and night (1900 h – 0459 h) dives. Daytime dives were statistically longer than night dives for turtle 026 ($P = 0.0002$) and 029B ($P = 0.014$), but not for 029A ($P = 0.886$). Dive depths were also deeper during the day for turtle 026 ($P = 0.00003$) and 029B ($P = 0.00003$), but not for 029A ($P = 0.551$). Surface intervals were distinctly longer during the day for all three turtles ($P = 0.00$, 0.0045, 0.00). Bottom time also was longer during the day ($P = 0.00$, 0.0193, 0.00) than at night.

There was a strong positive correlation between dive depth and dive duration for all turtles ($P = 0.00$) (Fig. 7). However, there was no correlation between dive depth and post-dive surface interval, suggesting that the turtles did not require immediate post-dive recuperation before diving again (Fig. 8).

Dive durations were distinctly longer for turtles in Malaysia than St. Croix (Mann-Whitney U test: $P = 0.000$) (Fig. 9A). Because dive depth and duration were positively correlated at both sites, we also compared dive durations for dives less than 62 m (the maximum dive depth for Malaysian turtles) (Fig. 9B). Dive durations in Malaysia were still longer ($P = 0.00$).

DISCUSSION

One of the most distinctive characteristics of diving by leatherbacks in Malaysia was that the dives were flat-bottomed rather than spike-like (Fig. 10). An average of 47% of all dives had bottom times longer than 3 minutes. The impression is that leatherbacks typically dove to the bottom, where they remained for a while before returning directly to the surface. This "bottom tracking" is clearly seen in the daily dive records of the 3 leatherbacks (Fig. 11). As turtle 029A left the nesting beach, dives followed the bottom contours by becoming progressively deeper until midday on the day after nesting. At that time she continued diving to depths that appeared to be near the bottom, but dive depths tended to become quite regular (as contrasted to the progressively deeper dives seen earlier). Based on radio tracking data we know that at approximately 1930 h on 15 June she was located about 10 km from shore in 30 m of water; at that time most dives were to 30 m. On 16 June at about 1900 h, she was located ca. 25 km from shore in 45 m

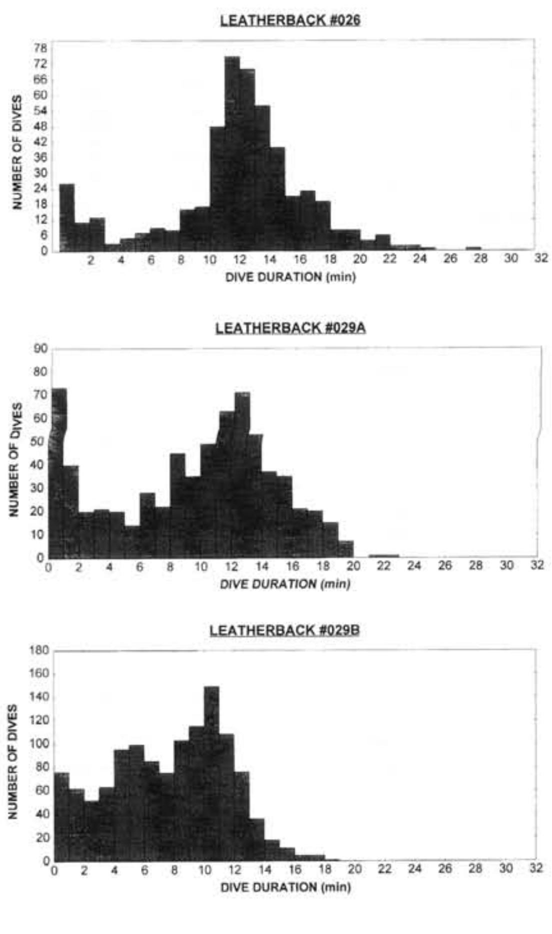

Figure 1. Frequency distributions of dive durations for 3 leatherbacks near Rantau Abang, Terengganu, Malaysia.

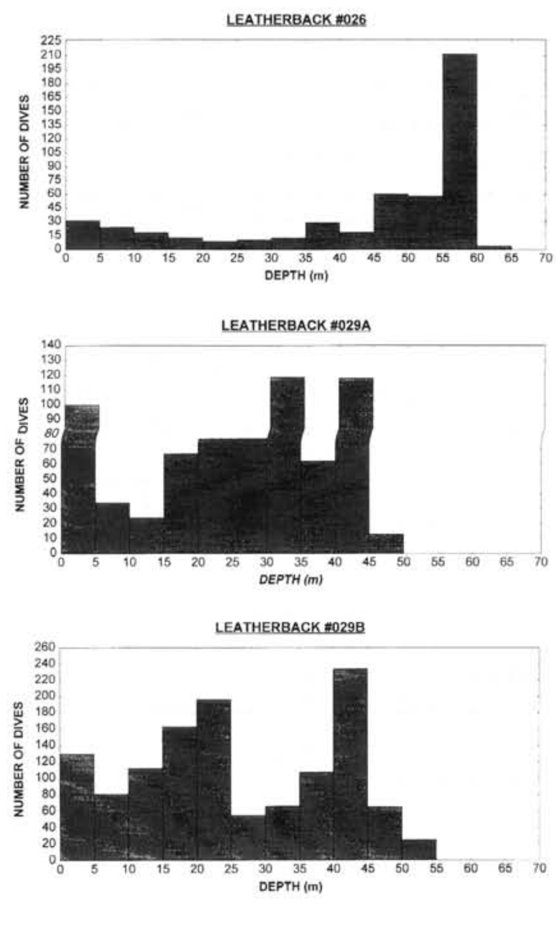

Figure 2. Frequency distributions of dive depths for 3 leatherbacks near Rantau Abang, Terengganu, Malaysia.

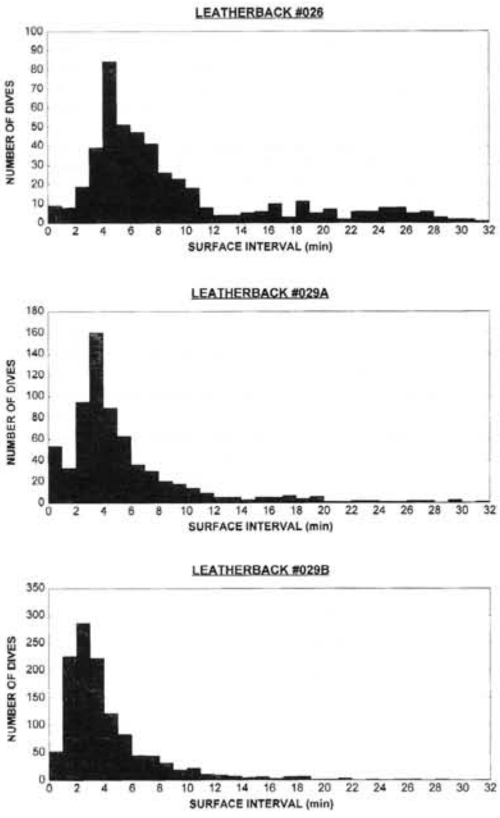

Figure 3. Frequency distributions of post-dive surface intervals for 3 leatherbacks near Rantau Abang, Terengganu, Malaysia.

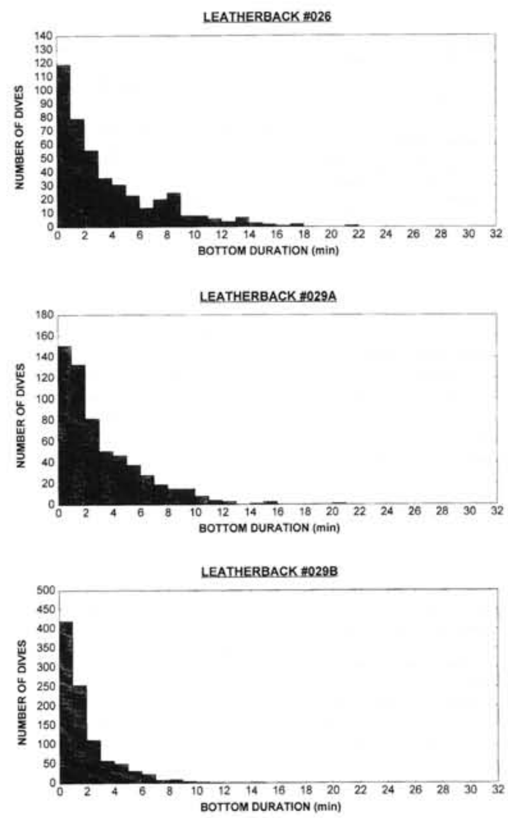

Figure 4. Frequency distributions of bottom durations (per dive) for 3 leatherbacks near Rantau Abang, Terengganu, Malaysia.

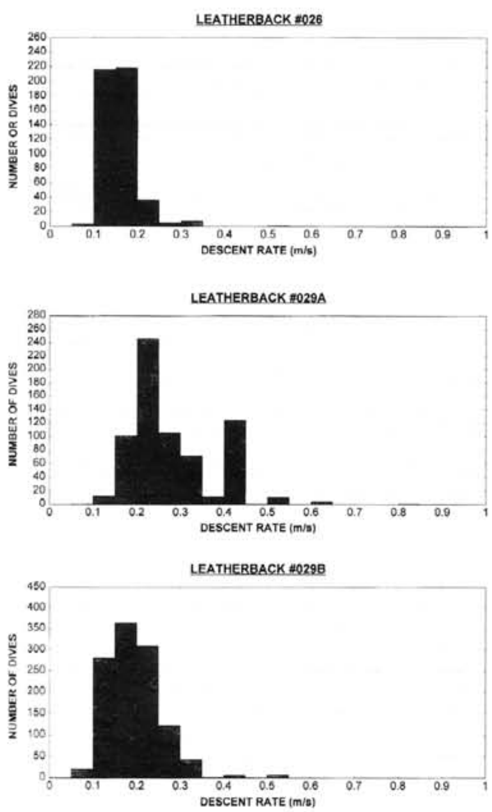

Figure 5. Frequency distributions of dive descent rates in meters per second for 3 leatherbacks near Rantau Abang, Terengganu, Malaysia.

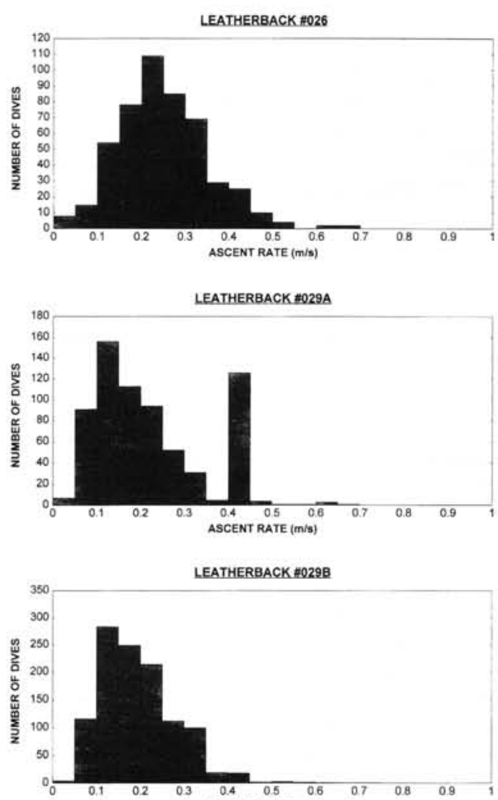

Figure 6. Frequency distributions of dive ascent rates in meters per second for 3 leatherbacks near Rantau Abang, Terengganu, Malaysia.

of water; typical dive depths were to about 45 m. Most subsequent dives were about 40 m deep until June 20, when the turtle was detected 8 km from shore in 26 m of water; dive depths were about 25 m.

Turtles 029B and 026 had similar dive depth behaviors, but their tracking records are not as complete. In all cases as the turtles returned to the nesting area, dive depths mirrored those at departure and became progressively shallower. Why the turtles dove to the bottom and whether they actually rested there is difficult to know. Once the turtles reached maximum depth, they tended to remain at that depth, moving upward only at the end of the dive. We do not know if the turtles were stationary at the bottom or swimming along near the bottom.

There was a strong relationship between dive duration and dive depth in the Malaysian leatherbacks (Fig. 7). The pattern is similar to that seen at St. Croix where these variables were also positively correlated. Interestingly, for two of the turtles there was almost no relationship between bottom duration and dive duration (Fig. 12), leaving us to conclude that the dive depth/duration relationship was established exclusively on the transit portion of the dive and that the rates of travel (swim speed) are probably fairly constant.

Dive durations were very different between St. Croix and Malaysia. Malaysian leatherbacks had consistently longer dive durations (Fig. 9A). This was even more pronounced if we eliminated St. Croix dives greater than 62 m (the maximum dive depth for Malaysian turtles) (Fig. 9B). In our work at St. Croix, we noted that there was no apparant relationship between size of the turtle and dive duration, and that the lack of post-dive recuperation time suggested that the species was primarily an aerobic diver that did not regularly exceed its Aerobic Dive Limit (Kooyman, 1989). Oxygen availability and its rate of consumption are extremely important in limiting dive durations of aerobic divers (Kooyman, 1989). In other works it has been suggested that leatherbacks rely heavily on oxygen stored in the tissues, in contrast to other turtles which utilize lung oxygen stores (Eckert, 1989; Lutcavage et al., 1990, 1992). Thus, reduction of oxygen stores by lung collapse due to increasing ambient pressure as has been suggested for green turtles (*Chelonia mydas*) (Berkson, 1966) should have little effect on leatherback dive durations. If this is true for the species, then we hypothesize that the longer dive durations in Malaysia may be due to decreased consumption rather than increased oxygen availability. Furthermore, the observation that dives at St. Croix less than 62 m were routinely shorter than Malaysian dive records lends credence to such an explanation. Either the Malaysian turtles are resting on the bottom, which might explain the flat-bottomed dive profiles, or possibly they are swimming slower (than St. Croix turtles) and thus reducing metabolic rates – and concurrently oxygen consumption. Further study on the purpose for such diving behavior as well as how leatherbacks manage oxygen consumption is needed to resolve this question.

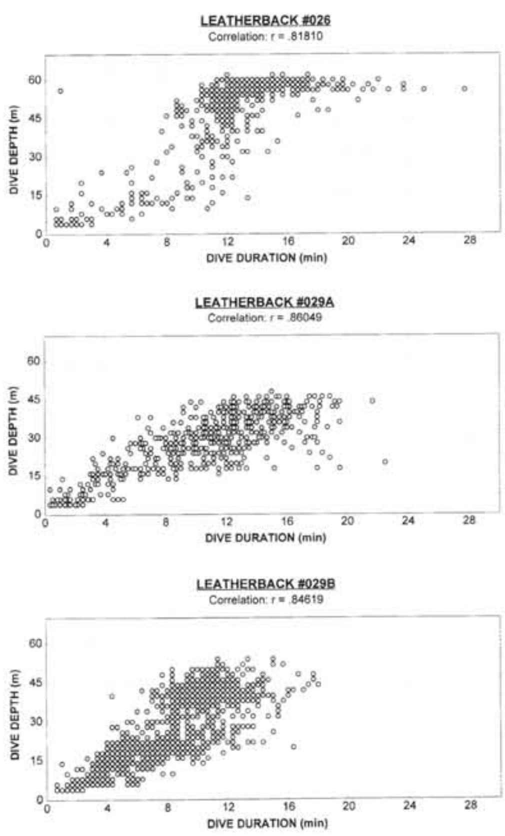

Figure 7. Scatterplot of dive duration vs. dive depth for 3 leatherbacks in the South China Sea.

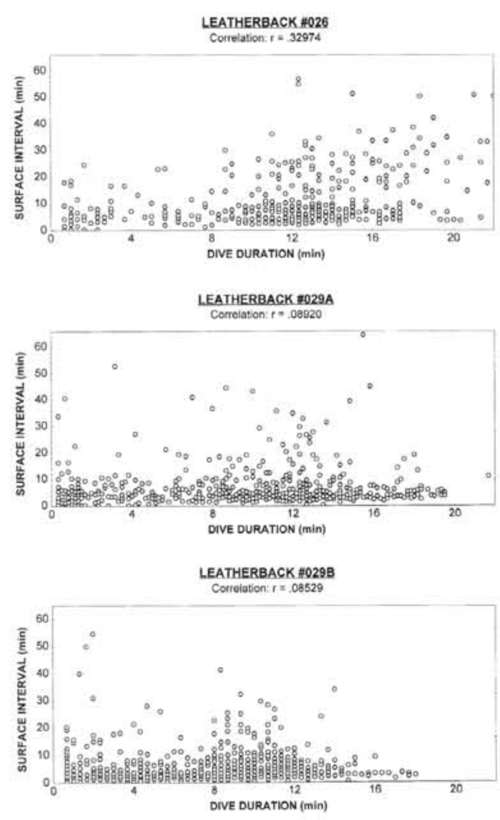

Figure 8. Scatterplot of dive duration vs. post-dive surface interval for 3 leatherbacks in the South China Sea.

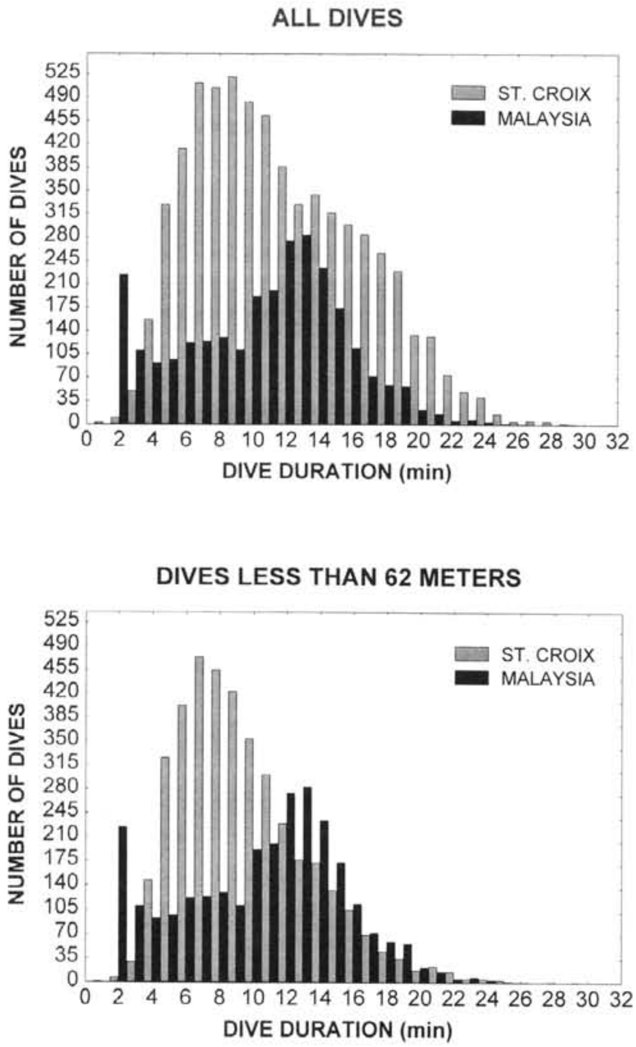

Figure 9. Frequency distributions comparing leatherback dive durations between St. Croix, U.S. Virgin Islands (Caribbean Sea) and Malaysia (South China Sea). **A.** All dives. **B.** Only dives less than 62 m.

In conclusion, diving by leatherback females during their internesting intervals in the shallow South China Sea are often characterized by diving near the bottom, remaining there for a short time, and returning directly to the surface. This pattern of diving directly to depth (with no excursions) and returning directly to the surface is similar to that seen at St. Croix, with the exception that the St. Croix dives exhibited virtually no bottom time. Had deep water been available, it is conceivable that Malaysian leatherback dives would have been spike-like as was observed at St. Croix. Dive depth and duration were related (deeper dives take longer) suggesting that swim speeds and ascent/descent rates are relatively constant. A major unexplained difference between leatherback dive profiles between the two sites concerns dive durations. Malaysian turtles made consistently and significantly longer dives. We hypothesize that this is due to a lower overall metabolic expenditure, which might be facilitated by slower swimming, or by resting on the bottom. Future studies comparing metabolic rates, oxygen management, and exercise behavior of turtles at the two sites should be undertaken if this difference in dive durations is to be understood.

Acknowledgments

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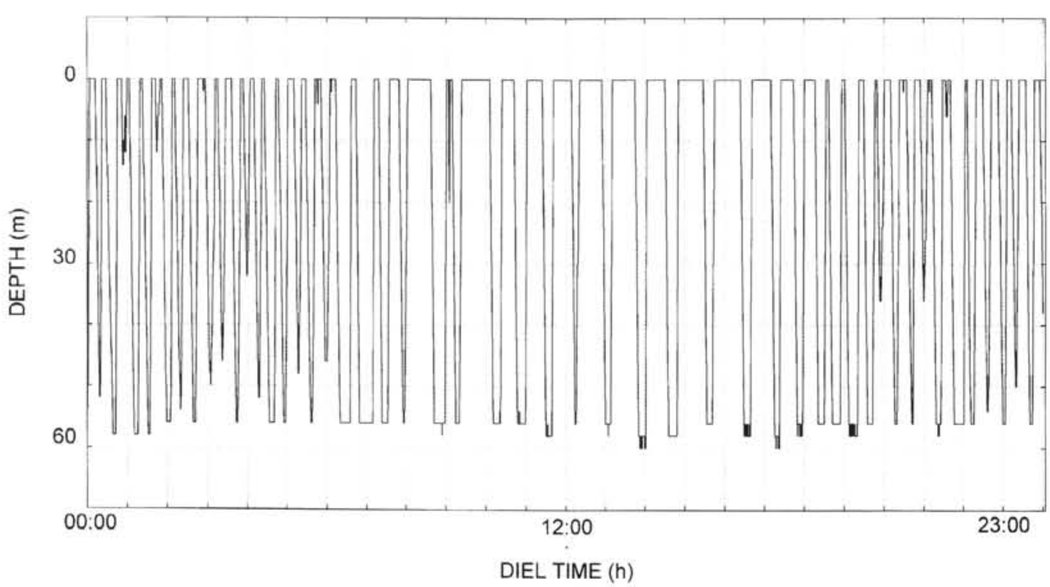

Figure 10. Example of a 24 hour dive pattern profile for leatherback 026 on 13 July 1989 in the South China Sea.

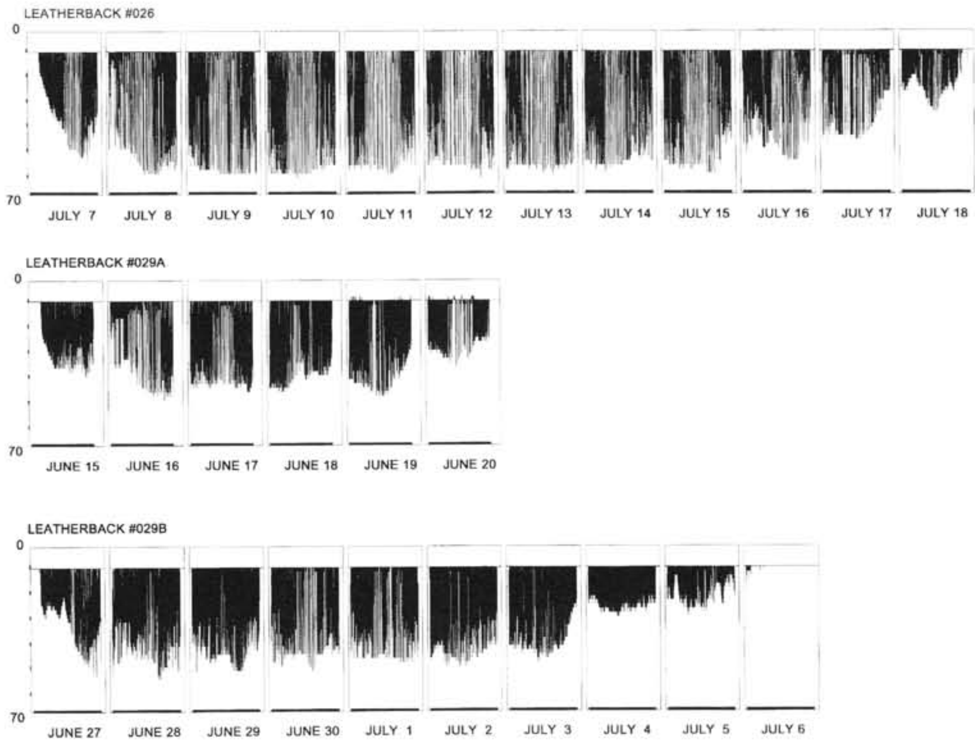

Figure 11. Dive pattern profiles for 3 leatherback females during their internesting intervals in the South China Sea, near the coast of Malaysia. Vertical axis is dive depth in meters. Note that the record of 029A is truncated, due to the instrument storage memory reaching capacity prior to the end of the internesting period.

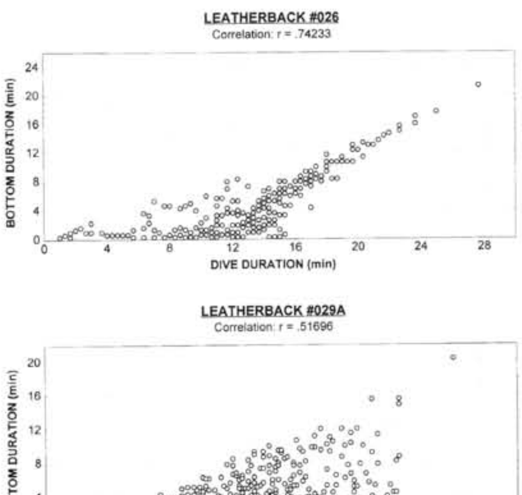

Figure 12. Scatterplot of dive duration vs. bottom duration for 3 leatherback females in the South China Sea.

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