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Diving behavior of immature hawksbills (*Eretmochelys imbricata*) in a Caribbean cliff-wall habitat

Abstract Time-depth recorders were attached to immature hawksbills (*Eretmochelys imbricata* Linnaeus, 1766) residing at the northwestern cliffs of Mona Island, Puerto Rico. Data on diving profiles obtained from four turtles of 32.0 to 53.4 cm straight carapace length revealed strong similarities in behavioral patterns. During daylight hours, turtles were active an average 8.4 h per day, surfacing 3.6% of the time. Length of foraging dives correlated with turtle size, with mean durations ranging from 8.6 to 14.0 min. Foraging dives, with a mean depth of 4.7 m, were associated with feeding on encrusting sponges. At night, turtles were mostly inactive, surfacing 1.8% of the time and with individual mean submergence intervals of between 30.4 and 37.1 min. From the surfacing behavior of turtles making deep and long dives, it is inferred that dives were aerobic, with the turtles making use of oxygen stores in addition to that of the lung.

Introduction

Juveniles of the circumtropically distributed hawksbill turtle *Eretmochelys imbricata* Linnaeus, 1766 are thought to take up residence in benthic habitats after the pelagic post-hatchling life phase (Carr et al. 1966). Information available on the behavioral ecology of

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juvenile and subadult hawksbills is limited, and consists mainly of anecdotal observations of wild and captive turtles, and inferences made from collected specimens. Behavioral studies of the species have largely focused on nesting females, when these animals are most accessible to researchers.

The hawksbill is well adapted for mechanically harsh benthic environments, with the carapace of the species featuring thick, abrasion-resistant, keratinized scutes. Characteristic beak-like jaws are used for snipping food out of crevices (Carr et al. 1966). The hawksbill diet consists of a wide variety of benthic invertebrates (den Hartog 1980) and, particularly in the Caribbean Sea, of sponges (Meylan 1988).

Due to the highly alert and mobile nature of sea turtles, it is difficult to make behavioral observations of them for extended time periods in the marine environment. Indirect methods are frequently used, and detailed behavioral information of turtles has been gathered with recording devices attached to them. Using time–depth recorders, Eckert et al. (1989) demonstrated the diel periodicity and deep diving capabilities of leatherback sea turtles, *Dermochelys coriacea*, during inter-nesting periods on St. Croix, US Virgin Islands. Similarly, Sato et al. (1994) used recorder technology to examine the thermal characteristics and diving behavior of loggerhead sea turtles (*Caretta caretta*) between nestings in Japan.

Published information on the behavioral patterns of free-ranging immature marine turtles is much less detailed. Standora et al. (1984) monitored the surfacing patterns and movement of one subadult leatherback for a period of 18 h off the coast of Rhode Island, USA. The behavior of juvenile green turtles (*Chelonia mydas*) on foraging grounds at St. Croix was studied for periods of up to 12 d by Ogden et al. (1983), and displayed marked diel foraging patterns. In this paper, we report on the detailed study of the diving behavior of immature hawksbill sea turtles inhabiting the vertical cliff walls of Mona Island. We establish the depth range of

feeding and resting habitats, and examine the activity patterns of these turtles. Furthermore, we explore the physiological basis for the observed types of dive.

Materials and methods

Data were obtained from August to November 1994 along the northwestern coast (18°07'N; 67°55'W) of Mona Island, Puerto Rico. The study site (Fig. 1) consists of a 2.3 km section of cliff coast, where a gently upward-sloping bedrock seafloor meets the vertical limestone cliff-face at 18 to 34 m depth. The cave-strewn wall of the cliff is heavily populated with an epifaunal assembly consisting of encrusting Porifera, calcareous and phaeophytic algae, and numerous other invertebrates. We found evidence for residency there of a population of *Eretmochelys imbricata* by repeated observations of physically distinctive and tagged individuals during field work from 1992 through 1994. Detailed diving data were collected by the attachment of custom-built time depth recorders (TDRs) to turtles caught at the study site. Turtles were hand-captured during daylight

Fig. 1 a Study area (*arrowed*) at cliff walls, Mona Island; **b** cross-sectional diagram of cliff wall habitat of hawksbill, *Eretmochelys imbricata*

hours by free-diving or with the aid of SCUBA, and were brought aboard a small boat for tagging, measurement and TDR attachment. All turtles participating in this experiment were immature (determined by size criteria. For individual identification, external stainless steel and plastic tags were applied to the trailing margin of both front flippers and a "passive integrated transponder" (PIT) tag was inserted subcutaneously to the right front flippers. Size measurements of turtles included straight-line carapace length (measured from the anterior nuchal notch to the posteriormost marginal scute) using 40 and 117 × 0.1 cm Haglof aluminum tree calipers, and body mass, weighed with a 20 × 0.1 kg Pesola spring-scale. Instrumented turtles were returned to the location of capture within 30 min. Capture locations were determined by landmarks and a Global Positioning System (GPS) receiver.

Two rectangular, epoxy-encapsulated electronic TDRs were used, both measuring 2.5 × 3 × 5 cm. TDR-1 weighted 102 g in air and 35 g in water, and was later modified with an additional battery, making the unit weight 135 g in air and 47 g in water. TDR-2 weighed 85 g in air and 28 g in water. The digital TDRs were designed to sample and record ambient water pressure at 8 s intervals for a maximum duration of 12.1 d. The units were calibrated using a standard-pressure station at Scripps Institution of Oceanography. TDR-1 had a water-depth resolution of 0.29 m and maximum registerable depth of ≥ 110 m. Resolution and maximum reading depth of TDR-2 was 0.36 and 85 m, respectively. TDRs were attached to the post-marginal scutes of turtles using two round-headed #10 stainless-steel screws of appropriate length. The screws were fitted with nylon washers to reduce abrasion against the carapace, and were inserted along the non-living tissue scute margins through holes made with a hand drill. The post-marginal scutes were chosen as the attachment site to minimize the instrument's hydrodynamic impact on the turtle and to ensure eventual disattachment by natural outgrowth should we fail to recapture the turtle for device-recovery.

To facilitate turtle recapture and instrument recovery, a sonic pinger tag was attached to three TDR-equipped individuals. The cylindrical 10 × 1.8 cm tags (Model CHP-87-L, 37 kHz, Sonotronics, Tucson, Arizona, USA) were attached with nylon-coated stainless-steel wire (crimped with a corrodible copper link) through two 1.5 mm holes in the edge of appropriate posterior marginal carapace scutes. An underwater acoustic locator receiver (Model N15A235B, Dukane Corp, St. Charles, Illinois, USA) was used to facilitate recapture of tagged turtles both from the boat and underwater.

Five records of diving behavior were obtained through the recapture of TDR-equipped immature hawksbills. During the deployment of TDR-1 on one turtle, the unit suffered battery depletion, causing the corruption of a large part of the dive information. We had failed to recapture on additional turtle (carrying TDR-2) by the end of the research period. Data for both these turtles are not presented here. Viable time-depth records were obtained from four turtles, yielding continuous behavioral records of between 10.9 and 11.8 d duration (Table 1).
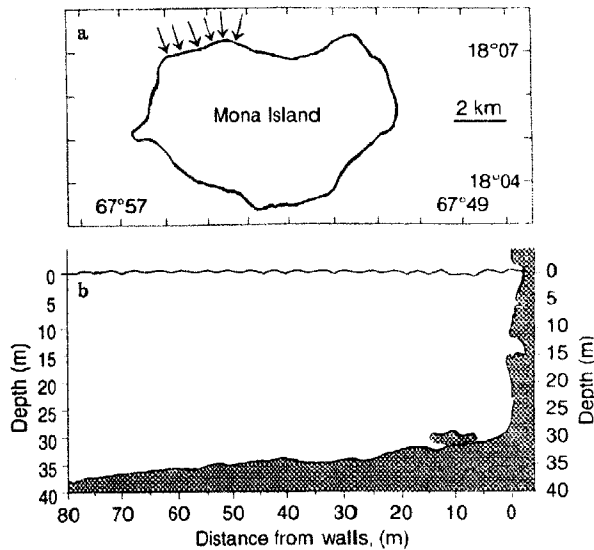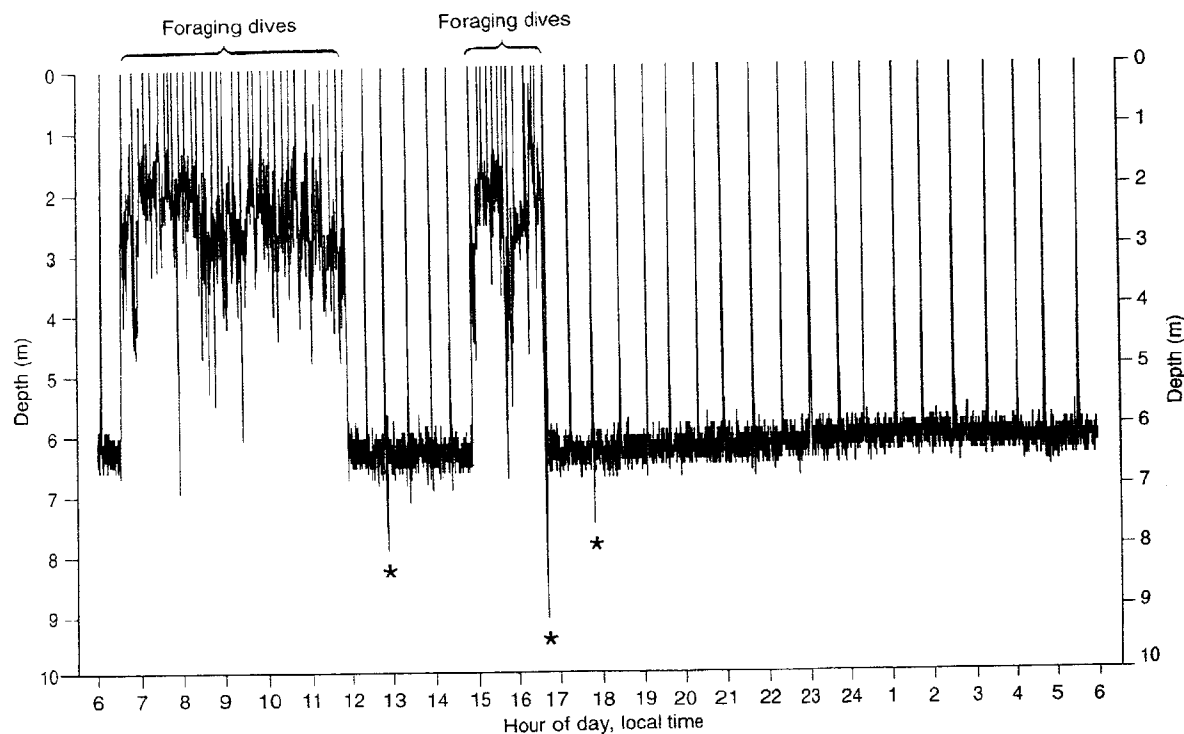
Table 1 *Eretmochelys imbricata*. Biological and experimental data for four immature hawksbill sea turtles equipped with time depth recorders (*TDR*). Turtle behavior was monitored continuously from time of instrument deployment. Experiment conducted during 1994 along northwest coast of Mona Island, Puerto Rico (*CL* straight-line carapace length; *Distance moved* distance between instrumented turtle-release site and location of recapture)

Turtle No.	CL (cm)	Body mass (kg)	TDR	Date (time) of TDR:		Length of behavioral record (d)	Distance moved (km)
				deployment	recovery		
94-038	32.0	3.7	TDR-1	19 August (16:42 hrs)	5 September (15:00 hrs)	11.8	1.98
93-053	32.1	3.8	TDR-1	16 October (16:06 hrs)	4 November (11:45 hrs)	11.8	0.86
94-041	50.5	16.2	TDR-1	4 October (12:35 hrs)	15 October (10:29 hrs)	11.0	1.02
94-085	53.4	17.2	TDR-2	25 August (17:20 hrs)	5 September (16:10 hrs)	10.9	0.11

Table 2 *Eretmochelys imbricata.* Summary of extent of dives of four immature hawksbills at northwestern cliffs of Mona Island. Data are means ± SE with minimum and maximum values in parentheses

Turtle No.	No. dives recorded	Dives/day	Surface interval (s)	Dive duration (min)	Dive depth (m)
94-038	971	82.1 ± 0.9 (49–159)	22.1 ± 0.4 (8–80)	17.1 ± 0.4 (0.1–57.7)	3.1 ± 0.1
93-053	901	77.7 ± 1.8 (25–208)	33.0 ± 0.6 (8–136)	18.3 ± 0.6 (0.1–81.1)	5.5 ± 0.2
94-041	714	63.3 ± 0.7 (26–84)	38.3 ± 0.7 (8–152)	21.4 ± 0.5 (0.1–78.0)	5.2 ± 0.2
94-085	767	71.3 ± 0.5 (46–94)	41.4 ± 0.9 (8–184)	19.9 ± 0.4 (0.1–52.0)	5.4 ± 0.2

Fig. 2 *Eretmochelys imbricata.* Diving by 32.1 cm (straight-line carapace length) Hawksbill 93-053 during 24 h time segment, starting on 23 October 1994 at 06:00 hrs (*Foraging dives* submergences exhibiting continuous variation in measured depth throughout dive; * excursions apparently related to finding habitual resting site)

Surveys to measure the extent and distribution of feeding scars on sponges were conducted along two ≈ 240 m-long segments of cliff wall at the study site. Feeding scars consist of exposed sponge choanosome or substrate material, and typically measure ~ 50 cm² (van Dam and Diez unpublished data). The number of feeding scars were counted independently by two SCUBA-equipped observers for bands 5 m in vertical extension and centered upon the 20, 15, 10, and 5 m isobaths. Counts along the wall from the surface to 2.5 m depth were made by swimming with snorkeling equipment.

the number of dives made per day, differences in the average number of daily dives were not significant between individuals (pairwise Mann–Whitney U-tests; $P > 0.001$).

Results

The four instrumented *Eretmochelys imbricata* exhibited remarkably similar patterns of diving and surfacing behavior. The dive and surfacing information collected for each turtle is summarized in Table 2. Any submergence exceeding 1 m in depth was considered a dive. While turtles exhibited considerable variation in

Foraging and resting dives

Fig. 2 chronicles the diving behavior of Hawksbill 93-053 for a 24 h period. The behavioral pattern appears typical of most conduct recorded for the four turtles, and comprises two markedly different dive

types. From 06:34 to 11:56 hr and again from 14:56 to 16:47 hrs on 23 October, Turtle 93-053 made movements resulting in continuous depth fluctuations throughout each submergene interval. We call these submergences "foraging dives" and these dives are labeled as such in Fig. 2. Dives with little change in measured depth other than variation attributable to wave action or breathing episodes are called "resting dives" (the unlabeled dives in Fig. 2).

Activity in the hawksbills examined displayed a strong diurnal component (Fig. 3). Periodic bouts of foraging dives were made for a mean of 8.4 h per day, mostly during daylight hours. The immature turtles spent an average of 3.6% of their time at the surface during the mean daytime period (from 06:30 to 18:30 hrs), whereas surfacing time was reduced to 1.8% at night, when turtles were largely inactive.

Dive duration and surface intervals

Immature hawksbill dives lasted an average of 19.0 min, and surface intervals were an average of 32.9 s duration. Partitioning of the data according to dive type exposed profound differences in the properties of foraging and resting dives (Table 3). For each turtle, foraging dives were of significantly shorter duration (Fig. 4) and had shorter post-dive surface intervals than resting dives (one-tailed Student's t-tests, assuming independence of samples; $P < 0.001$). Correlations between dive duration and post-dive surface interval were significant for foraging dives in all turtles ($0.307 \leq r \leq 0.528$, Pearson product-moment; $P < 0.001$), yet generally weaker and not consistently significant for resting dives ($0.098 \leq r \leq 0.308$). The duration of resulting dives increased steadily on average for 8 h after the onset of dusk (Fig. 5; data pooled for all turtles).

Fig. 3 *Eretmochelys imbricata.* Diel behavioral pattern recorded in four immature hawksbills. Percent time turtles spent during surfacings, foraging and resting dives are presented in 24 1-h segments; daylight period during study extended from 06:00–6:30 to 18:50–19:00 hrs local time
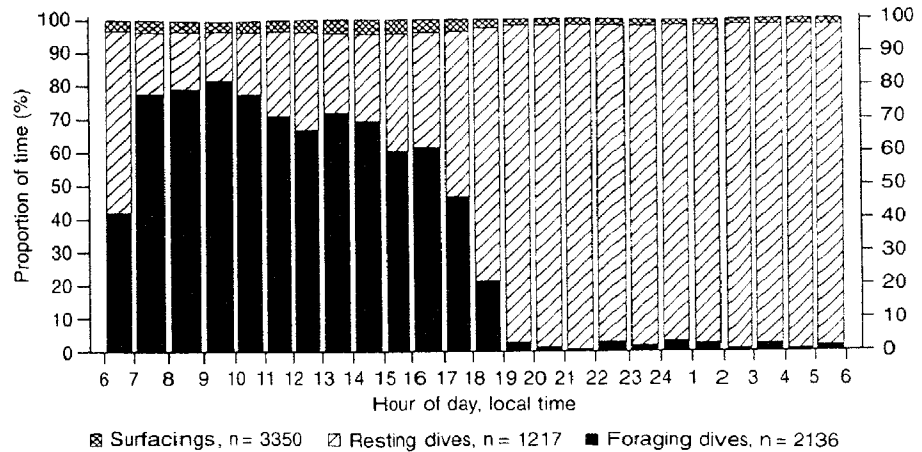
🕸 Surfacings, n = 3350   ▨ Resting dives, n = 1217   ■ Foraging dives, n = 2136

Table 3 *Eretmochelys imbricata.* Summary of immature hawksbill diving data after partitioning into "foraging" and "resting" dives (for dive-type criteria, see "Results – Foraging and resting dives"). Data presentation as in Table 2

Turtle No.	[N]	Post-dive surface interval (s)	Dive duration (min)	Dive depth (m)	Max. depth recorded (m)
Foraging					
94-038	[639]	18.4 ± 0.5 (8 56)	8.9 ± 0.3 (0.1–35.6)	2.7 ± 0.1	27.3
93-053	[596]	29.5 ± 0.8 (8 136)	8.6 ± 0.4 (0.1 54.9)	3.7 ± 0.2	34.3
94-041	[451]	34.2 ± 0.8 (8 122)	14.0 ± 0.4 (0.1 58.9)	4.7 ± 0.3	44.2
94-085	[450]	31.9 ± 1.1 (8 184)	12.5 ± 0.4 (0.1 52.0)	6.4 ± 0.3	72.1
Resting					
94-038	[332]	29.3 ± 0.7 (8 80)	33.1 ± 0.5 (2.7 57.7)	4.0 ± 0.1	32.6
93-053	[305]	39.7 ± 0.9 (8 88)	37.1 ± 0.9 (11.2 81.1)	9.1 ± 0.3	37.5
94-041	[263]	45.4 ± 1.1 (8 152)	33.9 ± 0.7 (10.9 77.5)	6.0 ± 0.2	31.1
94-085	[317]	54.9 ± 1.0 (8 104)	30.4 ± 0.5 (9.7 50.1)	6.2 ± 0.2	56.2

Fig. 4 *Eretmochelys imbricata.* Dive-duration distribution of 2136 foraging and 1217 resting dives as proportion of all dives made by four immature hawksbills
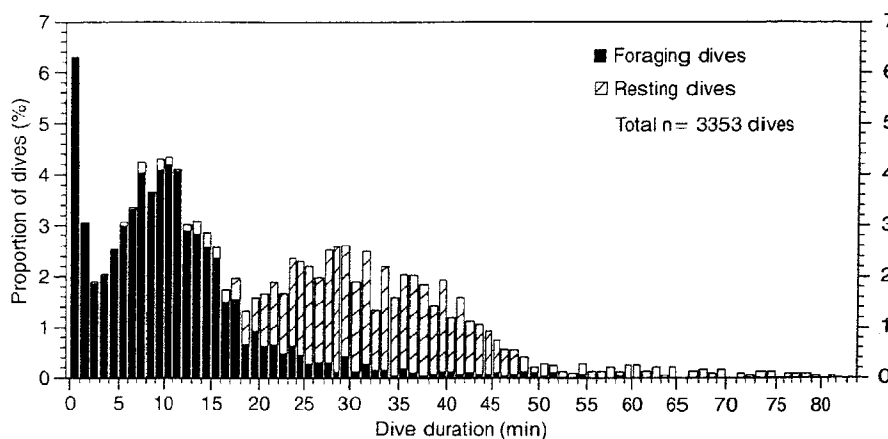
Correlations of turtle size (straight-line carapace length) with duration of foraging dives were strong and significant ($r = 0.951$; $P < 0.001$), while no such significant trend was evident in the length of the resting dives. However, surface intervals after resting dives did correlate significantly and postively ($r = 0.8843$; $P < 0.001$) with turtle size. The highly variable post-surface intervals of foraging dives exhibited no significant size-related trends.

Dive depth

The mean depth of foraging dives was significantly less than that of resting dives in three out of four turtles (Table 3; pairwise Mann–Whitney U-tests; $P < 0.001$; exception: Turtle No. 94-085). Fig. 6 illustrates the depth distribution of foraging and resting dives; the overall mean foraging dive depth was 4.7 m, while resting dives had a mean depth of 6.8 m. Foraging dive durations increased significantly with dive depth ($r = 0.1384$; Pearson product-moment; $P < 0.001$), but resting dive durations did not. Post-dive surface intervals were positively but weakly correlated with dive depth (foraging dives: $r = 0.1186$, resting dives: $r = 0.0699$; $P < 0.001$). Turtle size correlated significantly and positively with foraging dive depth ($r = 0.898$; $P < 0.001$), but differences in resting dive depth were not attributable to turtle size.

The dive records did not uniformly correspond to the pattern of alternating bouts of short, shallow, foraging dives and longer, deeper, resting dives. Fig. 7 depicts an example of deviations from the typical behavioral pattern by Turtle No. 94-085, the largest hawksbill examined. This turtle made three dives that were deeper and of longer duration than usual for foraging dives. While post-dive surface intervals were not notably longer than normal, the turtle did spend an unusual amount of time at the surface immediately prior to the dives (72, 128 and 144 s, respectively).
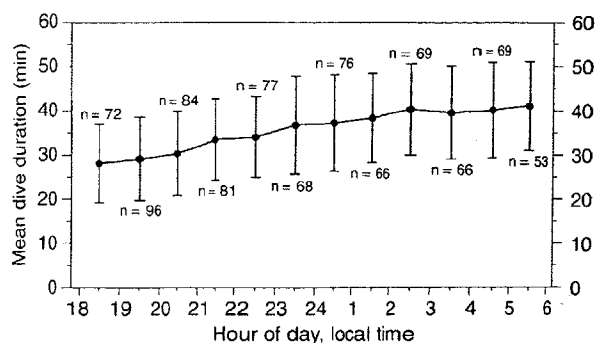

Fig. 5 *Eretmochelys imbricata.* Mean duration ($\pm$SD) of total of 887 nightly resting dives recorded at hourly intervals. Time at midpoint of dive was used as criterion for calculating hourly means

Horizontal turtle movement along the cliff wall as measured by the distance between TDR-development and recovery-capture locations varied strongly (from 0.1 to 2.0 km) between individuals. Dives of turtles beyond 34 m, the maximum depth of the cliff base, indicate movements away from the cliff wall. The dive depths of up to 72 m provide evidence of excursions by the turtles to waters several hundred meters away from the cliff wall.

Prey-sponge distribution

Densities of feeding scars on encrusting sponges surveyed along the cliff wall were high in the uppermost zone (from the surface to 2.5 m depth) and declined strongly at greater depth (Table 4). The observed scars were characteristic of those caused by hawksbill feeding on sponges. Hawksbill feeding-behavior in shallow water was observed by us on several occasions within the study area.

Fig. 6 *Eretmochelys imbricata.*
Mean depth distribution of 2136
foraging and 1217 resting dives
as proportion of all dives made
by four immature hawksbills.
Mean depth of dive calculated as
average depth during
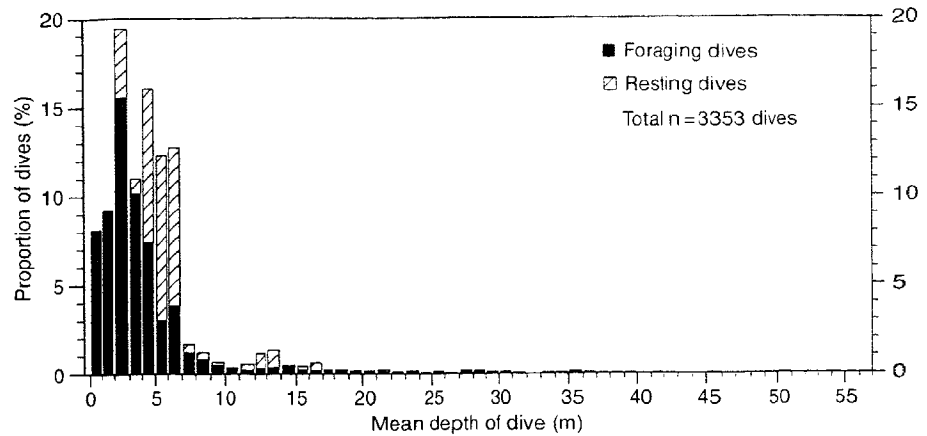submergence interval, including
descents and ascents

Fig. 7 *Eretmochelys imbricata.*
Foraging dives made by 53.4 cm
(straight-line carapace length)
Hawksbill 94-085 during 6 h
period starting 27 August 1994
at 07:30 hrs. Turtle made three
dives (starting at 8:30, 10:58
and 11:53 hrs, respectively)
exceeding 50 m in depth. Note
prolonged surfacing (*) prior to
each of these deep foraging
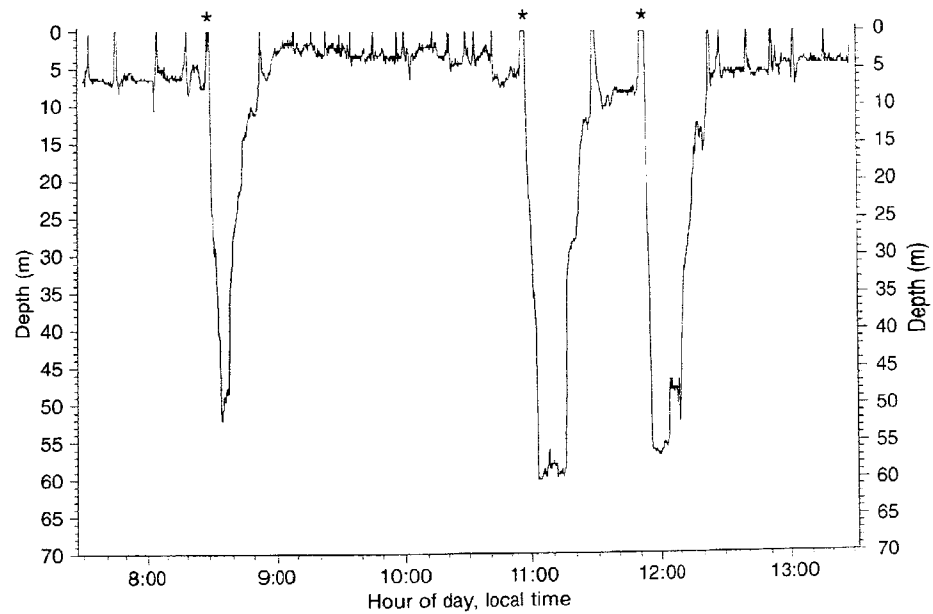dives, suggesting that turtle
anticipated extent of these dives

Table 4 Results of feeding-scar survey along cliff wall east of Esper-
anza cave and east of Espinal cave, Mona Island. Horizontal exten-
sion of both surveyed areas is ≃ 240 m. Base of cliff wall lies at
between 24 and 28 m depth for Esperanza area and between 16 and
25 m depth for Espinal area (*RVD/CED* observers)

Survey zone depth (m)	No. feeding scars, observed RVD/CED	Mean feeding scar density (m^{-2})
East of Esperanza		
0–2.5	208/130	0.282
2.5–7.5	44/61	0.044
7.5–12.5	9/12	0.009
12.5–17.5	4/1	0.002
17.5–22.5	7/4	0.005
East of Espinal		
0–2.5	154/130	0.237
2.5–7.5	85/45	0.054
7.5–12.5	15/26	0.017
12.5–17.5	3/2	0.002

Discussion and conclusions

Foraging patterns of immature *Eretmochelys imbricate*
are similar to those observed for juvenile green turtles
(*Chelonia mydas*) by Ogden et al. (1983) and Bjorndal
(1980), with feeding bouts during daylight hours and
resting behavior predominant at night. We found that
the daytime dive durations of hawksbills were mostly
longer than the 3 to 10 min reported for *C. mydas* (size
7 to 8 kg) on shallow seagrass beds (Ogden et al. 1983).

Feeding, predator avoidance and resting behavior

The recorded dive profiles represent the vertical com-
ponent of excursions by turtles surfacing for respir-
ation, foraging, resting, and/or predator avoidance.

Hawksbills along Mona Island's cliff wall are presented with a range of depth options and can make dives down to 34 m water depth without expending effort in horizontal movement. However, the vast majority of dives made by the turtles involved depths of ≤ 7 m (see Fig. 6). Given that the shallowness of foraging dives corresponds well with the distribution of feeding scars on encrusting sponges, most of which are found in the upper few meters along the wall, we feel confident that most dives labeled foraging dives did indeed involve feeding or prey-searching behavior. However, occasional foraging dives of turtles to deeper water probably reflect other behaviors such as predator avoidance or exploration. Large fish are potential predators of hawksbills [e.g. *Galeocerdo cuvier* (Randall 1967) and *Epinephelus itajara* (Cadenat 1957)], and these typically swim parallel to the cliff wall. Turtles may successfully evade these predators by descending to the cliff base and moving away from the wall to deeper water. This evasive behavior was frequently observed by us in our attempts to capture cliff-wall turtles, and many escaped using this maneuver. In contrast, a few deep dives appear preplanned, such as those to depths > 50 m illustrated in Fig. 7, and are not likely to be made in response to immediate external threats. These dives reflect purposeful behavior by the turtles, requiring substantial effort, for which the objectives remain unclear.

Turtles making resulting dives on perches near the surface risk being dislodged by water motion caused by waves colliding with the cliff wall. The majority of resting dives were made to depths of 2 to 7 m, and these depths probably represent compromises by the turtles aimed at minimizing disturbance by wave action and minimizing surfacing effort by remaining in shallower water. Turtles made an average of 16 to 31 trips to and from the surface per day between resting dives, and any decrease in dive depth would substantially reduce surfacing effort. Resting in shallow water may allow hawksbills to avoid lung collapse, thus enabling them to prolong bottom times by retaining access to lung oxygen-stores.

Oxygen stores and metabolic rates

The mean duration of hawksbill resting dives observed by us fall in the range of resting and night-dive durations noted by Parrish (1958) for an assembly of chelonid turtles (including *Eretmochelys imbricata*) held in tanks 5.5 m and shallower. Markedly longer durations of foraging dives in wild hawksbills compared to those observed in captive marine turtles may be attributed to greater environmental challenges and resulting physical conditioning faced by the former. Interestingly, those hawksbill dives along the cliff wall that were of longer than normal duration were mostly deep dives (for example see Fig. 7), during which the

lung oxygen-store may be less available due to lung collapse.

In a study by Lutz and Bentley (1985) of captive loggerhead turtles (*Caretta caretta*), the lung was determined to be the principal oxygen-store for diving. The hawksbills we studied, while extending surface intervals after long and deep dives, often also made longer than normal surfacing *prior* to these dives, suggesting that they anticipated the extent of the dives and hyperventilated, possibly to increase body oxygen-stores. Kontos and Eckert (1988), observing haksbills surfacing along the cliffs of Mona Island, found that juvenile and adult turtles took 3.51 and 5.85 breaths per surface interval, respectively. Such a respiratory pattern seems excessive for the mere repletion of oxygen in the lung when the tidal volumes of turtles are > 50% of their lung capacity (measured for *Chelonia mydas* by Tenney et al. 1974). Instead, free-ranging hawksbill turtles making extended dives probably utilize and recharge substantial oxygen-stores in their blood and muscle tissues during their routine diving cycles, as do wild diving birds and marine mammals (Kooyman 1989).

Although we found a correlation between foraging dive duration and the subsequent surface interval, surfacings after prolonged, deep-foraging dives were not of dramatically increased duration. This indicates that it is improbable that anaerobic metabolic pathways were used during the dives. Green turtles in forced diving experiments have been shown to require long (> 10 h) recovery periods to reduce lactic acid accumulations (Berkson 1966). Results supporting our observations were obtained for captive, 10 to 20 kg loggerheads by Lutcavage and Lutz (1991). These authors concluded that the loggerheads were capable of making aerobic dives of ≤ 1 h.

The significantly longer duration of resting submergence compared with foraging dives is attributable to lowered metabolic requirements when resting. Measurements of metabolic rates in juvenile green turtles by Prange (1976) demonstrate that, at rest, these turtles had rates up to four times lower than when swimming. The variation in nocturnal dive durations (Fig. 5) provides clues as to the dynamics of metabolic rates in hawksbills at rest. Assuming that we may use resting dive duration as an inverted gauge of metabolic rate, the increases in duration indicate that turtle metabolic rates fell continuously for 8 h after the onset (at dusk) of resting-dive sequences.

The cliff walls of Mona Island constitute an important developmental habitat for a wide size range of immature hawksbills. Because turtles appear able to find adequate food and shelter in the upper few meters of the sublittoral zone, little incentive exists for the hawksbills to make deep, prolonged dives that would approach their physiological limitations. Further investigations, both in the field and in the laboratory, should improve our understanding of the limitations and metabolic scope of breath-hold diving in these turtles.

References

Berkson H (1966) Physiological adjustments to prolonged diving in the Pacific green turtle (*Chelonia mydas agassizii*). Comp Biochem Physiol 18: 101–119

Bjorndal KA (1980) Nutrition and grazing behavior of the green turtle *Chelonia mydas*. Mar Biol 56: 147–154

Cadenat J (1957) Notes d'ichtyologie Ouest-Africaine. 17 Biologie. Régime alimentaire. Bull Inst fr Afr noire (Sér A: Sci nat) 19: 274–294

Carr A, Hirth H, Ogren L (1966) The ecology and migration of sea turtles, 6. The hawksbill turtle in the Caribbean Sea. Am Mus Novit 2248: 1–29

Eckert SA, Eckert KL, Ponganis P, Kooyman GL (1989) Diving and foraging behavior of leatherback sea turtles (*Dermochelys coriacea*). Can J Zool 67: 2834–2840

Hartog den JC (1980) Notes on the food of sea turtles: *Eretmochelys imbricata* (Linnaeus) and *Dermochelys coriacea* (Linnaeus). Neth J Zool 30: 595–610

Kontos A. Eckert S (1988) The relationship between the number of breaths, surface time and dive time of the hawksbill turtle (*Eretmochelys imbricate*) in the wild. Am Zool 28: 180A

Kooyman GL (1989) Diverse divers: physiology and behavior. Springer-Verlag Berlin Heidelberg

Lutcavage MF, Lutz PL (1991) Voluntary diving metabolism and ventilation in the loggerhead sea turtle. J exp mar Biol Ecol 147: 287–296

Lutz PL, Bentley TB (1985) Respiratory physiology of diving in the sea turtle. Copeia 1985: 671–679

Meylan A (1988) Spongivory in hawksbill turtles: a diet of glass Science, NY 239: 393–395

Ogden JC, Robinson L, Whitlock K, Daganhardt H, Cebula R (1983) Diel foraging patterns in juvenile green turtles (*Chelonia mydas* L.) in St. Croix United States Virgin Islands. J exp mar Biol Ecol 66: 199–205

Parrish FK (1958) Miscellaneous observations on the behavior of captive sea turtles. Bull mar Sci Gulf Caribb 8: 348–355

Prange HD (1976) Energetics of swimming of a sea turtle. J exp Biol 64: 1–12

Randall J (1967) Food habits of reef fishes of the West Indies. Stud trop Oceanogr, Miami 5: 665–847

Sato K, Sakamoto M, Matsuzawa Y, Tanaka H, Naito Y (1994) Correlation between stomach temperatures and ambient water temperatures in free-ranging loggerhead turtles. *Caretta caretta*. Mar Biol 118: 343–351

Standora EA, Spotila JR, Keinath JA, Shoop CR (1984) Body temperatures, diving cycles, and movement of a subadult leatherback turtle *Dermochelys coriacea*. Herpetologica 40: 169–176

Tenney SM, Bartlett Jr D, Farber JP, Remmers JE (1974) Mechanics of the respiratory cycle in the green turtle (*Chelonia madas*). Respir Physiol 22: 361–368