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Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a caribbean reef habitat

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Abstract. Time-depth recorders were deployed on immature hawksbill turtles at the southwestern reefs of Mona Island, Puerto Rico, to examine patterns of diving behavior. Diving profiles of 10–12 day duration were obtained from five turtles ranging in carapace length from 27–52 cm. Turtles exhibited contrasting diurnal and nocturnal diving behaviors. During daylight hours, dives were made 92% of the time, featured continuous depth variation and were attributed to foraging activity. Foraging dive duration increased with turtle size; individual mean dive durations ranged from 19–26 min; mean post-dive surface intervals ranged from 37–64 s; mean depths ranged from 8–10 m. At night, dives were made 86% of the time to constant depths and were interpreted as resting behavior. Resting dive durations were not dependent on turtle size; individual mean dive durations ranged from 35–47 min; mean post-dive surface intervals ranged from 36–60 s; and mean depths from 7–10 m. Immature hawksbill turtles maintained short term home ranges several hundred meters in extension.

Introduction

The hawksbill turtle (*Eretmochelys imbricata*) is circumtropically distributed and frequently associated with coral reefs (Márquez 1990). Juvenile turtles with a carapace length of 20 cm and larger are thought to take up residency in hard-bottom neritic habitats after completing a pelagic post-hatching life phase (Carr et al. 1966). Adaptations to hard-bottom environments include thick, abrasion resistant keratinized scutes, and characteristic beak-like jaws used for snipping food out of crevices (Pritchard and Trebbau 1984). Hawksbill turtles feed on a variety of benthic invertebrates (den Hartog 1980); in the Caribbean they appear to be primarily spongivorous (Meylan 1988). Although the terrestrial nesting behavior of *Eretmochelys* has been described in detail (Deraniyagala 1939; Carr et al. 1966), few accounts of the at-sea behavior of the species are available. One report by Hirth et al. (1992) describes immature hawksbill turtles swimming and resting at a fringing reef in Papua New Guinea.

In this study, we document the diving behavior observed in immature hawksbill turtles at a reef site in the northern Caribbean. We compare the behavior of this species with that of the more extensively studied green turtle (*Chelonia mydas*), which has distribution and habitat preferences comparable to those of the hawksbill turtle.

Study area and methods

Data were collected during the 1992 to 1994 field seasons (July–November) in a study area along the southwestern coast (18°05′N, 67°57′W) of Mona Island, Puerto Rico (Fig. 1). The study area was divided into three sections named according to the adjacent beaches: Sardinera, Mujeres, Carabinero. All sections lie on the leeward side of the island and are thus relatively protected from prevailing winds and associated waves from the east and southeast. However, the reef profile and benthic composition of the areas are substantially different. The Sardinera area consists of a forereef with spurs and grooves at between 5 and 12 m depth, radiating outwards from a fringing reef. The reef spur structures seldom reach more than 1.5 m above the substrate. Cover at 10 m depth is dominated by macro-algae, scleractinians, plexaurids and other gorgonians. Beyond 12 m depth, about 500 m offshore, the spur-groove system breaks up into large coral patches surrounded by sand. At Mujeres, the reef patches at 4 to 18 m depth are better developed, with typical structure heights of 1 to 2 m (up to 4 m) and overhangs and ledges providing turtles with ample shelter. Patches are covered with macro-algae, hydrocorals, scleractinians, gorgonians, and the prominent encrusting sponge *Anthosigmella varians*. At Carabinero, a hard-bottom terrace

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is interrupted at 11 m depth, as close as 150 m from shore, by a vertical drop-off exceeding 75 m in depth. The narrow, almost flat terrace has extensive stands of *Pseudopterogorgia sp.* upon a substrate covered with *Dictyota sp.* and other macro-algae. Prominent sponges are *Aplysina sp.*, *Tethya sp.*, and *Xestospongia muta.*

The repeated observation, capture and recapture of numerous tagged immature hawksbill turtles in the nearshore area demonstrated the feasibility of deploying and recovering recording instruments on the turtles. Detailed diving data were collected by the attachment of custom built time-depth recorders (TDRs) on turtles caught in the study area. Turtles were hand captured in waters up to 18 m deep by free diving and occasionally with the aid of SCUBA, and brought aboard a small boat for tagging, measurement and TDR deployment. All turtles used in this experiment were immature. For individual identification, 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 in the right front flipper. Body size measurements included straight line carapace length (from the anterior nuchal notch to the posteriormost marginal scute) and body mass. Turtles were returned to the location of capture within 30 min. Capture locations were determined using a global positioning system (GPS) receiver. Throughout most visits to the study area, bathymetric information was collected by simultaneously recording depth and location on a portable computer linked to a ultrasonic depth sounder and a GPS receiver.

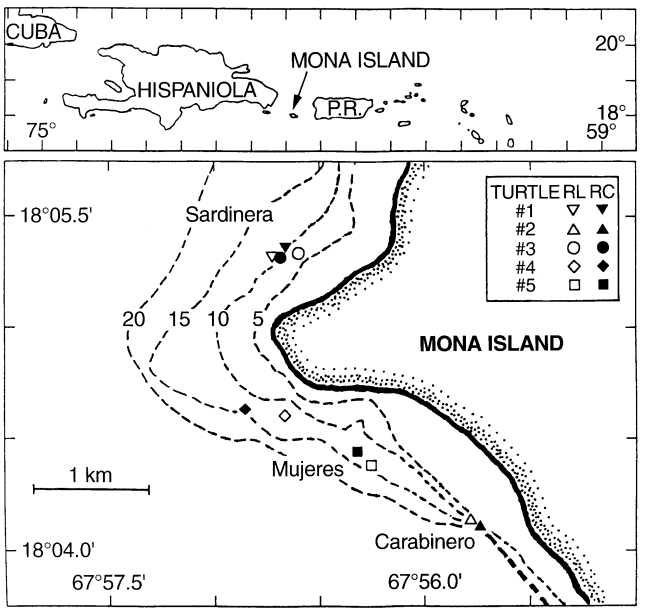

Fig. 1. Map of the study area along the southwestern coast of Mona Island, Puerto Rico. Isobaths beyond 20 m depth are not plotted. Symbols refer to the release (*RL*) and recapture (after 10–12 d) (*RC*) locations of immature hawksbill turtles fitted with time-depth recorders

Two rectangular, epoxy encapsulated electronic TDRs were used, both measuring approximately $2.5 \times 3 \times 5$ cm. TDR-1 weighed 102 g in air, 35 g in water and was later modified with an additional battery, making the weight 135 g in air, 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 12.1 day duration. The units were calibrated using a standard pressure station at the Scripps Institution of Oceanography. TDR-1 had a water-depth resolution of 0.3 m and maximum registerable depth of approximately 110 m. Resolution and maximum reading depth of TDR-2 was 0.4 m and 85 m, respectively. TDRs were attached to the post-marginal scutes of turtles. To locate turtles during TDR deployment and facilitate recapture for instrument recovery, a sonic pinger tag was attached to two TDR equipped animals.

Results

Five TDR equipped immature hawksbill turtles released and recaptured in the study area (Fig. 1) yielded continuous behavioral records for 10–12 days (Table 1). Distances between individual capture and recapture locations ranged from 100–340 m (Table 1). The turtles exhibited similar behavioral patterns, making an average 48.6 dives per day (SE = 5.1, range 37–64). Any submergence beyond a depth of one meter was considered a dive.

Two types of dives were recognized: "foraging" and "resting" dives. Dives with depth fluctuations greater than

Table 1. Biological and deployment data of five time-depth recorder equipped immature hawksbill turtles. Turtle behavior was monitored continuously from the time of instrument deployment. Net distance moved is distance between turtle capture locations of instrument deployment and recovery

Turtle	Straight-line carapace length (cm)	Body mass (kg)	Date and time of instrument deployment	Date and time of instrument recovery	Length of behavioral record (d)	Net distance moved (m)
1	27.1	2.4	9 Sep 1994 11:07	17 Sep 1994 15:55	10	140
2	29.3	3.1	5 Nov 1994 11:07	15 Nov 1994 10:36	10	100
3	38.5	7.4	9 Aug 1993 15:13	23 Aug 1993 17:45	12	250
4	41.8	8.8	27 Jul 1994 15:55	16 Aug 1994 6:36	12	340
5	51.6	18.4	2 Aug 1994 12:15	25 Aug 1994 10:41	12	170

0.5 m within 2 min during at least 50% of the submergence interval were indicative of turtle activity and were labeled foraging dives. All other dives were considered resting dives. Figure 2 illustrates this classification for dives made during a 24 h period by an individual turtle (4). The animal was active during the daytime (daylight period was 05:45–19:20 h on 1 August 1994), while making resting dives throughout the night.

The hawksbill turtles made foraging dives an average of 11.4 h per day. From dawn to dusk (05:45–06:30 to 18:05–19:20 h local time, times varied by TDR deployment date), turtles made foraging dives and surfaced on average 86% and 4% of the time, respectively. Nighttime behavior was dominated by inactivity; turtles made resting dives and surfaced on average 96% and 2% of the time, respectively. The proportion of time spent surfacing and making resting and foraging dives for each hour of the day is summarized in Fig. 3.

To compare the characteristics of foraging and resting dives, the dive data were separated according to dive type (Table 2). The dive duration frequency distribution (Fig. 4) illustrates the overall difference in dive length of foraging and resting dives. Foraging dives were roughly half the duration of resting dives for each individual turtle (eg. turtle 1: 18.9 ± 0.3 min versus 39.7 ± 0.6 min, Table 2; Mann-Whitney U-tests, $P < 0.001$).

The frequency distribution of dive depth for each turtle (Fig. 5) reveal differences between foraging and resting dives that are not apparent from the mean dive depths listed in Table 2. Foraging dive depths were normally distributed in four turtles (Shapiro-Wilks tests, $P > 0.001$), but had a non-normal, bimodal distribution in turtle 3. Maximum attained depths during foraging dives of Sardinera area turtles (1, 3) and of resting dives in all turtles did not fall far outside of the usual depth range (maximum depths were less than mean dive depth + 3 SD). The Mujeres and Carabinero turtles (2, 4, 5), however, made excursions classified as foraging dives to depths well outside of their habitual depth range (maximum depths were greater than mean dive depth + 6 SD).

Dive depths were positively and significantly correlated with the durations of foraging dives ($r = 0.49 \pm 0.16$, Pearson product moment; $P < 0.001$). Similarly dive depths were positively correlated with surface intervals after foraging dives in all turtles ($r = 0.46 \pm 0.14$; $P < 0.001$). However, resting dive durations and surface intervals after resting dives were not consistently correlated with dive depths. Foraging dive durations, post-dive

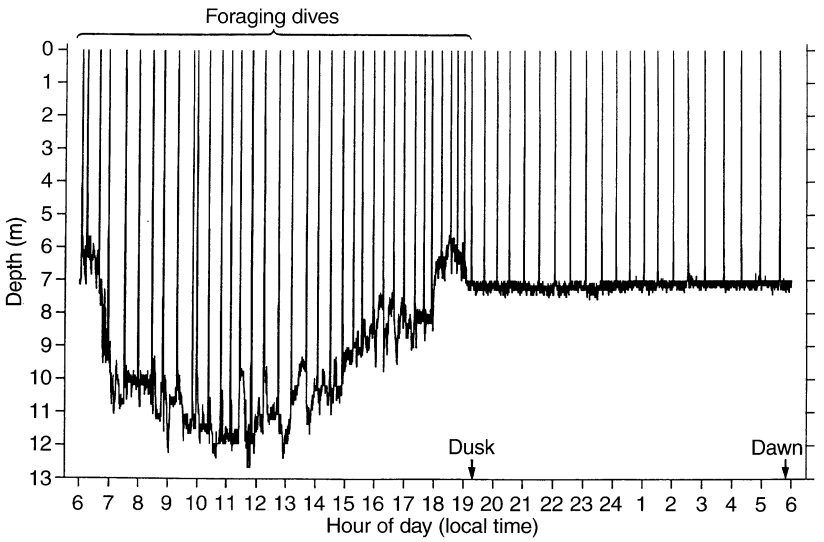

Fig. 2. Diving by an individual hawksbill turtle (4, Table 1) during a 24 h segment starting on 1 August 1994 at 06:00 h local time. Submergences exhibiting continuous variation in measured depth throughout the dive are labeled foraging dives; the remaining dives with little depth variation other than attributable to wave action and surface ascents and descents are named resting dives

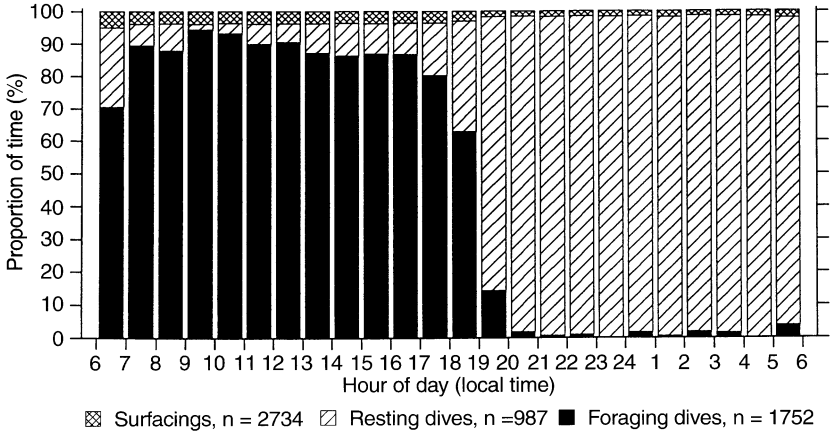

Fig. 3. Diel behavioral pattern recorded in 5 immature hawksbill turtles. The Percent time turtles spent during surfacings, resting and foraging dives are presented in twenty-four 1 h segments. The daylight period during TDR deployments extended from 05:45–6:40 to 18:00–19:20 h local time

Table 2. Summary of immature hawksbill turtle diving data after partitioning into foraging and resting dives (for separation criteria, see text)

	Turtle	*n*	Dive duration (min) mean ± SE min – max	Dive depth (m) mean ± SE	Maximum depth recorded (m)	Post-dive surface interval (s) mean ± SE min – max
Foraging dives	1	326	18.9 ± 0.3 1.2–43.5	7.9 ± 0.1	11.9	37 ± 1 8–64
	2	308	18.5 ± 0.3 0.4–38.1	8.1 ± 0.1	24.1	49 ± 1 8–200
	3	429	22.0 ± 0.3 0.1–39.6	10.2 ± 0.1	17.5	60 ± 1 8–120
	4	373	24.2 ± 0.3 3.5–36.5	9.9 ± 0.3	21.2	52 ± 1 8–112
	5	316	25.8 ± 0.5 1.1–49.7	8.4 ± 0.1	17.4	64 ± 1 8–152
Resting dives	1	206	39.7 ± 0.6 1.7–57.2	7.1 ± 0.1	12.1	36 ± 1 8–72
	2	178	46.6 ± 1.0 0.7–73.7	9.6 ± 0.0	12.2	50 ± 1 8–96
	3	179	41.0 ± 0.7 17.6–59.3	9.9 ± 0.2	17.5	52 ± 1 24–128
	4	224	35.2 ± 0.5 17.6–59.3	8.0 ± 0.1	14.0	37 ± 2 8–152
	5	200	43.7 ± 0.8 14.7–66.3	8.0 ± 0.0	11.6	60 ± 2 24–216

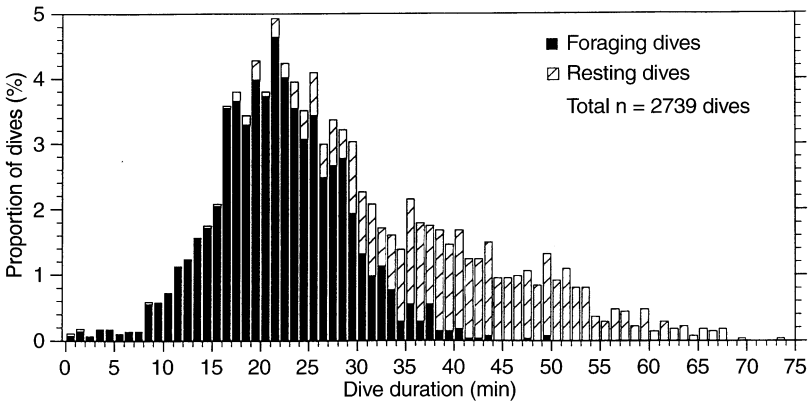

Fig. 4. Dive duration distribution in minutes of 1752 foraging and 987 resting dives as a proportion of all dives made by five immature hawksbill turtles

surface intervals and dive depths were dependent on turtle size, all increasing significantly with straight carapace length ($r = 0.40$, 0.44 and $r = 0.173$, respectively; $P < 0.001$). The duration and depth of resting dives were independent of turtle size ($P > 0.001$).

Discussion and conclusions

The immature hawksbill turtles studied at Mona Island exhibited diel behavioral patterns similar to those observed by Ogden et al. (1983) for juvenile green turtles on feeding grounds in the US Virgin Islands. Both turtle species were generally active during daylight hours and usually inactive at night. Hawksbill turtle activity in the present study was interpreted as related to foraging, but may have included other behaviors, such as travel and predator avoidance. Sightings of active immature hawksbills in the study area (when turtles were not apparently aware of observer presence) almost always confirmed foraging behavior, i.e., turtles busy sampling or ingesting benthic organisms, predominantly sponges (Van Dam and Diez, unpublished data).

A larger body size in hawksbill turtles was correlated with longer and deeper foraging dives (with longer post-dive surface intervals). It remains unclear whether extended dive capabilities in the reef environment confer any significant advantages to larger turtles of the size range examined. One possible measure of foraging success, the number of hours per day spent on foraging dives (mean 11.4 h/day, range 9.5–13.1), exhibits no significant relation turtle size (carapace length) (Pearson product moment; $P > 0.001$). If hawksbill turtles strive to maximize bottom times (as suggested by Eckert et al. 1989) so that dive durations are regulated primarily by physiological limitations, then the size dependence of foraging dive parameters and size independence of resting dive parameters is puzzling. This contrast between activity and resting

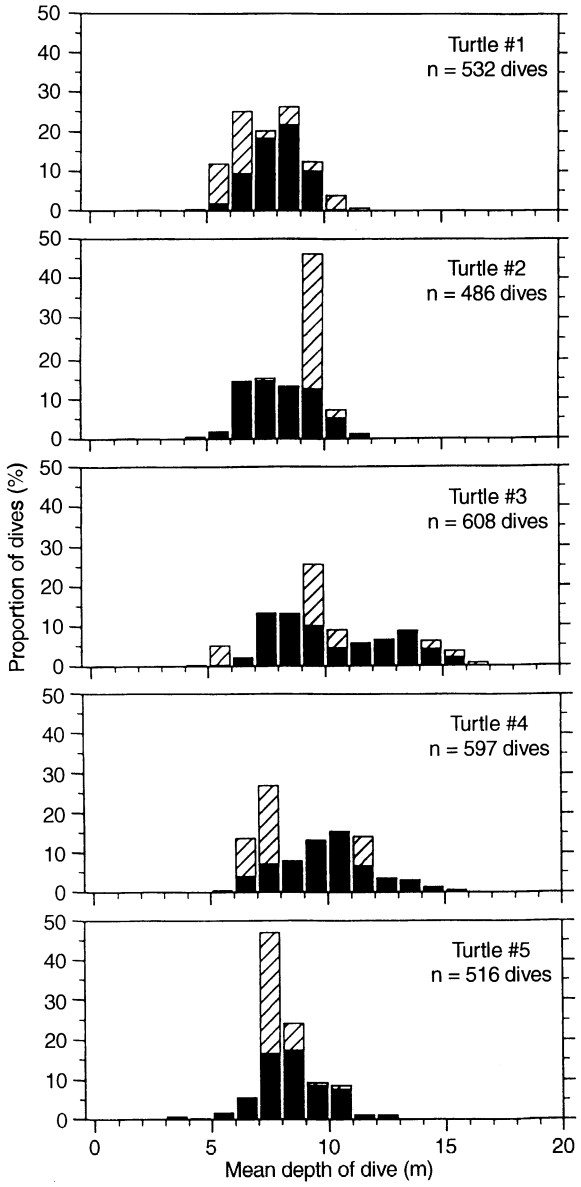

Fig. 5. Distribution by depth of foraging (black) and resting dives (diagonals) as a proportion of all dives made by each of 5 immature hawksbill turtles. Means per dive were calculated as average depth during the submergence interval, including descents and ascents

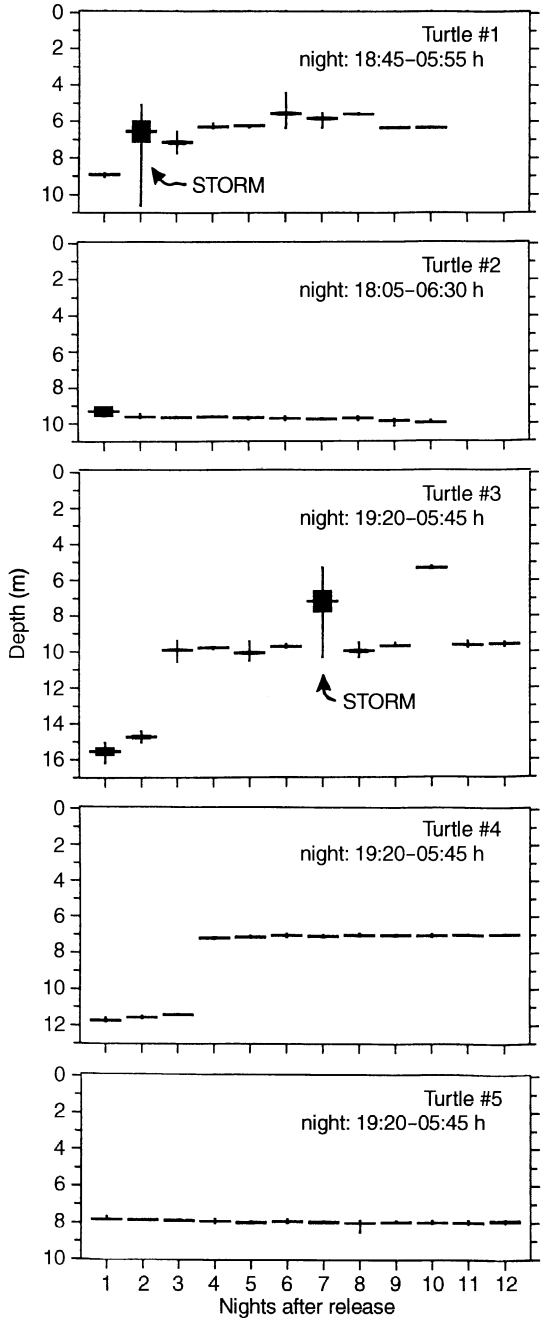

Fig. 6. Depth of nightly resting dives made by 5 immature hawksbill turtles. Mean depth (*horizontal line*), SE (*box*) and depth range (*vertical line*) of resting dives are given for each night after TDR deployment. Turtles made 11–21 resting dives per night

implies that different scaling relationships exist for the physiological mechanisms regulating dive duration (e.g. metabolic rate, oxygen storage capacity).

Occasional nightly, activity by green turtles was observed by both Bjorndal (1980) and Ogden et al. (1983) on shallow, nearshore seagrass grazing plots. The immature hawksbill turtles of the study area exhibited no such activity, even though light levels on moonlit nights appear sufficient for visual orientation on the reef (personal observation). The lack of nightly hawksbill turtle foraging activity may be attributed to difficulties in locating the patchily distributed and cryptic prey sponges, compared to the homogeneous stands of seagrasses on which green turtles graze.

Resting sites of immature green and hawksbill turtles on reefs at Wuvulu Island, Papua New Guinea, ranged in depth from 5.5 to 12.8 m (Hirth et al. 1992). Of the resting dives recorded for immature hawksbill turtles at Mona Island, 93% fall within this depth range. Depths of resting dives in the five turtles studied here were not correlated with turtle size. Furthermore, depths were remarkably constant on a per night basis under normal conditions (Fig. 6). The lack of variation in depth of resting dives suggests that turtles selected a resting place at dusk and

frequently managed to return to the same spot or one of very similar depth after surfacing. Fidelity to certain resting sites frequently continued on subsequent nights, especially notable in turtles 2, 4, and 5 (Fig. 6). Immature hawksbill turtles sighted during nighttime SCUBA dives in the study area were associated with crevices or ledges in the reef. The ability of turtles to return to their resting sites appears reduced during storms, as indicated by the increased range of resting dive depths recorded for turtle 1 on night 2 and turtle 3 on night 7 (Fig. 6). Both turtles resided in the northern section of the study area (Sardinera), where storms resulted in high (> 2 m) waves and caused a severe deterioration of underwater visibility (personal observation).

The immature green turtles observed by Ogden et al. (1983) moved between distinct feeding and resting areas differing in depth and biotic composition. We observed no such commuting of *Eretmochelys* on the reefs of Mona Island. The depth ranges of routine foraging and resting dives generally overlapped for individual hawksbill turtles (Fig. 5). Given the depth gradients present throughout the study area (Fig. 1), overlapping depth ranges are indicative of overlapping or at least proximate foraging and resting habitats. The two deepest dives recorded (to 24.1 and 21.2 m) were made immediately after the turtles were released (2 and 4, respectively) and should therefore be disregarded in the context of habitat preference.

Net movement of the five hawksbill turtles during the TDR deployment period of 10–12 days was limited to several hundred meters (Table 1), suggesting that turtles keep to a home range of limited area. Repeated sightings of tagged hawksbill turtles at fixed locations (Boulon 1983; Bjorndal et al. 1985), further support the observation that hawksbill turtles are relatively sedentary after reaching a good feeding area (Pritchard and Trebbau 1984). However, records of long-range dispersion by immature Caribbean hawksbill turtles (Boulon 1989) demonstrate that these turtles occasionally venture well beyond their home range.

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