Coral Reefs (2009) 28:55–65
DOI 10.1007/s00338-008-0416-1

REPORT

Diving behavior and movements of juvenile hawksbill turtles *Eretmochelys imbricata* on a Caribbean coral reef

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Received: 1 June 2008 / Accepted: 7 August 2008 / Published online: 12 September 2008

Abstract As historically abundant spongivores, hawksbill turtles *Eretmochelys imbricata* likely played a key ecological role on coral reefs. However, coral reefs are now experiencing global declines and many hawksbill populations are critically reduced. For endangered species, tracking movement has been recognized as fundamental to management. Since movements in marine vertebrates encompass three dimensions, evaluation of diving behavior and range is required to characterize marine turtle habitat. In this study, habitat use of hawksbill turtles on a Caribbean coral reef was elucidated by quantifying diel depth utilization and movements in relation to the boundaries of marine protected areas. Time depth recorders (TDRs) and ultrasonic tags were deployed on 21 Cayman Islands hawksbills, ranging in size from 26.4 to 58.4 cm straight carapace length. Study animals displayed pronounced diel patterns of diurnal activity and nocturnal resting, where diurnal dives were significantly shorter, deeper, and more active. Mean diurnal dive depth (±SD) was 8 ± 5 m, range 2–20 m, mean nocturnal dive depth was 5 ± 5 m, range 1–14 m, and maximum diurnal dive depth was 43 ± 27 m, range 7–91 m. Larger individuals performed significantly longer dives. Body mass was significantly correlated with mean dive depth for nocturnal but not diurnal dives. However, maximum diurnal dive depth was significantly correlated with body mass, suggesting partitioning of vertical habitat by size. Thus, variable dive capacity may reduce intraspecific competition and provide resistance to degradation in shallow habitats. Larger hawksbills may also represent important predators on deep reefs, creating a broad ecological footprint over a range of depths.

Keywords Hawksbill turtle · Time depth recorder · TDR · Marine protected area · Ultrasonic tracking · Deep reef

Introduction

Hawksbill turtles *Eretmochelys imbricata* are the largest spongivores on coral reefs and are thought to be associated with maintaining biodiversity (Hill 1998; Leon and Bjorndal 2002). However, the species is now of conservation concern (IUCN 2007) and coral reefs are increasingly threatened (Gardner et al. 2003). As marine turtles range widely (Musick and Limpus 1997; Plotkin 2003), spend the majority of their time submerged (Lutcavage and Lutz 1997), and are capable of diving to considerable depths (Eckert et al. 1989; Sakamoto et al. 1990), three-dimensional movements must be accounted for in evaluating habitat use, ecological role, and susceptibility to environmental degradation and other anthropogenic threats (Hindell et al. 2002; Seminoff et al. 2002; Cooke 2008).

In many marine vertebrates, dive capacity and habitat use is influenced by body size (Schreer and Kovacs 1997). For hardshell turtles, increases in oxygen stores in proportion to body size are greater than the corresponding increases in metabolic rate (Hochscheid et al. 2007). Thus,

Communicated by Biology Editor Dr Mark McCormick

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larger animals are capable of longer dives, but for turtles in the wild, the role of body size in determining spatiotemporal structuring of habitat utilization has been inconclusive (van Dam and Diez 1996, 1997a; Storch 2003). As marine turtles are slow growing and late maturing, individuals of the same species in the same habitat can vary in body length by a factor of four (Diez and van Dam 2002; McGowan et al. 2008) and in body weight by a factor of 20 (Storch 2003). However, to date, there has been no project where a large number of time depth recorders (TDRs) have been deployed on turtles across a wide range of body sizes, enabling investigation of scaling in dive capacity and habitat use.

Despite the importance of resolving movements in endangered marine vertebrates, there is considerable difficulty associated with gathering such data at sea (Hays et al. 2000a). In recent years, application of technologies, such as satellite transmitters and archival tags, has provided insight into migration and diving behavior in a variety of species, ranging from seabirds (e.g., Tremblay and Cherel 2000; Wilson and Quintana 2004) to seals (e.g., Kooyman 1975; Krafft et al. 2002) and whales (e.g., Croll et al. 2001; Baird et al. 2002). Satellite transmitters and satellite transmitters with dive recording capability have been used in a multitude of marine turtle studies, including tracking of juvenile green (Godley et al. 2003) and loggerhead turtles (Polovina et al. 2000). However, due to limitations such as large instrument size, high cost, and low positional accuracy and dive resolution, at present these technologies are most suitable for tracking migrations of larger individuals.

While long-distance migratory movements of reproductive adult turtles, including hawksbills (van Dam et al. 2008), have recently been the subject of much attention (Godley et al. 2008), juvenile hardshell turtles spend extended periods confining their movements to foraging grounds (Mendonca and Ehrhart 1982; van Dam and Diez 1998). Radio and ultrasonic tracking have been successfully used to determine home range on juvenile foraging grounds (van Dam and Diez 1998; Seminoff et al. 2002), but these technologies are limited to two-dimensional movements. In contrast, TDRs provide depth data devoid of a spatial context. While use of TDRs and ultrasonic tracking in concert (Makowski et al. 2006) has elucidated movements and diving behavior of juvenile green turtles, manual tracking is labor-intensive (Seminoff et al. 2002; Seminoff and Jones 2006) and underwater activities cannot be inferred from instrument recordings alone (Seminoff et al. 2006). Ultra-high resolution multi-sensor archival tags (Wilson et al. 2008) offer future utility in monitoring movements and behavior, and video-linked TDRs have been deployed on adult leatherbacks (Reina et al. 2005) and large juvenile green and loggerhead turtles (Heithaus et al. 2002b; Seminoff et al. 2006) in order to link underwater activities with dive profiles. However, video technologies are currently large, costly, and memory constrained, limiting their use on smaller animals (Moll et al. 2007).

In this study, TDRs and ultrasonic tags were deployed on 21 juvenile hawksbill turtles in Little Cayman, Cayman Islands. The study area provided animals of a wide range of body sizes, all of which had close access to essentially unlimited oceanic depths. Focal observations were conducted in order to link underwater activities with dive profiles, and an array of moored fixed station receivers around the island allowed movements to be evaluated in relation to the boundaries of marine protected areas. Thus, this study enabled an evaluation of movements, behavior, and scaling of dive capacity, informing management of hawksbill turtles on Caribbean coral reefs.

Materials and methods

Study site

The Cayman Islands are located in the western Caribbean Sea, approximate 240 km south of Cuba (Fig. 1). Due to a historical commercial turtle fishery and continuing traditional take (Bell et al. 2006), once abundant migratory green and loggerhead rookeries in the Cayman Islands have become critically reduced (Blumenthal et al. 2006; Bell et al. 2007). Hawksbill nesting appears to have been extirpated in recent years (Bell et al. 2007), but juveniles are frequently sighted around all three islands, with Bloody Bay, Little Cayman providing key habitat (Bell et al. 2008). In the study area of Bloody Bay (19°40′41″ N, 80°05′38″ W), a narrow shelf (coral reef and colonized hardbottom) provides access to a wide range of depths: the near-vertical slope ("wall") begins approximately 400 m from the shoreline and extends from 6 to 12 m to near abyssal depths.

Study animals and deployment of TDRs

Twenty-one juvenile hawksbill turtles, ranging in size from 26.4 to 58.4 cm straight carapace length, were hand-captured in two survey bouts (Table 1). Ten individuals (turtles 1–10) were captured in September 2005 and 11 individuals (turtles 11–21) were captured in November 2005. Lotek LTD-1110 time-depth recorders (TDRs) were used to record dive profiles. VEMCO V16 and V13 coded transmitters ("pingers") and VEMCO VR100 and VR2 receivers facilitated observation and recapture and offered insights into movements with respect to the boundaries of marine protected areas. Housings for TDRs and pingers were constructed from plastic (StarBoard polyethylene; Fig. 2). Combined mass of housings and instrumentation

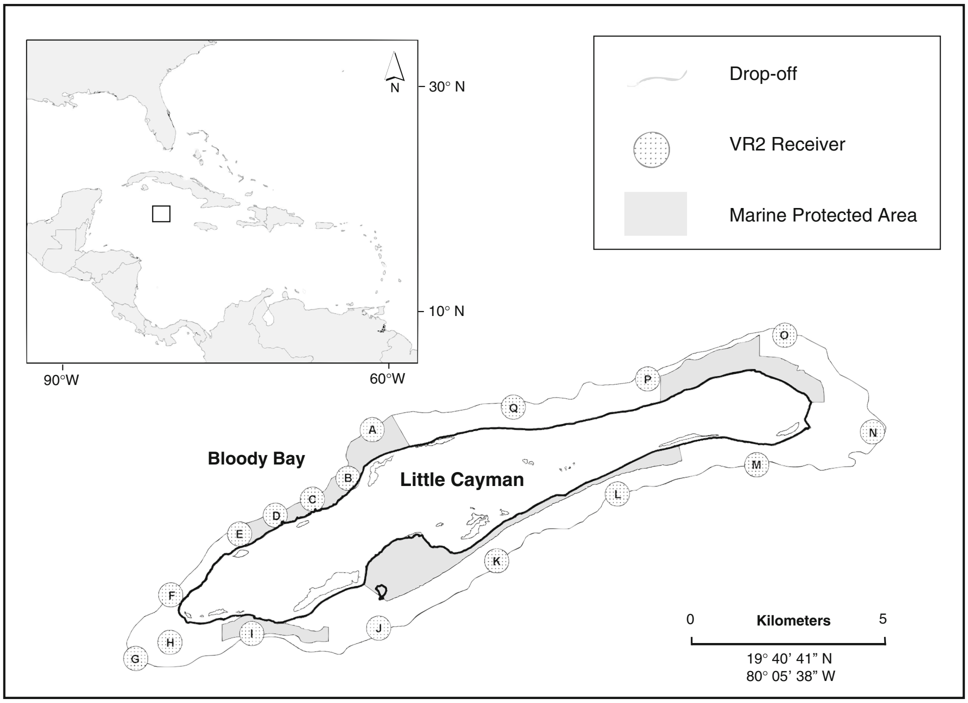

Fig. 1 An array of VEMCO VR2 ultrasonic receivers was installed around the island of Little Cayman (mean receiver separation ca. 1,000 m). Receivers were tethered at depths of 3–8 m on mooring lines with subsurface floats. Receiving range for the stations was approximately 400 m. Inset: Location of the Cayman Islands in the Caribbean Sea (19°40′41′′ N, 80°5′38′′ W)

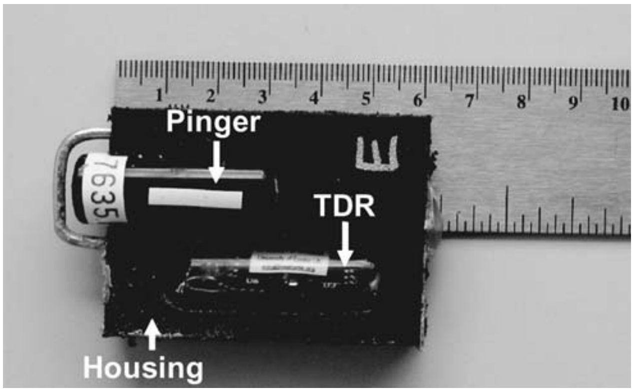

Fig. 2 Lotek LTD-1110 time-depth recorders (TDRs) and VEMCO V16 and V13 coded ultrasonic transmitters (pingers) were deployed in Starboard polyethylene housings. Holes in the lids of housings (not shown) over the TDRs facilitated water flow and pressure equilibration. Housings were attached to a rear scute of each turtle with two-part epoxy

ranged from 48 to 85 g in air (1–3% of body mass of study animals), representing a negligible weight in water. For instrument attachment, the carapace of each turtle was prepared by scrubbing to remove epibionts, sanding lightly, and cleaning with acetone. Units were attached to a rear lateral scute with two-part epoxy. In order to enable individual identification for observations, housings were labeled with a large numeral which was legible from a distance. Measurements of mass and straight and curved carapace length at time of first capture were collected and animals were tagged according to standard protocols (passive integrated transponder (PIT) tag and double inconel flipper tags; Balazs 1999). All turtles were released at GPS site of capture. Following an 8-day TDR recording period, animals were re-captured and housings were removed (pingers remained active until turtles were recaptured, or until batteries depleted at >365 days). For a summary of deployment and recapture information for all individuals, see Table 1.

Observations and ultrasonic tracking

Observations of behavior at sighting were made when turtles were captured and recaptured. Additionally, a VEMCO VR100 receiver with omni-directional and directional hydrophones was used to locate instrumented animals for observation (and recapture). For turtles observed during the TDR recording period, activity and time of sighting were recorded, allowing correlation of behaviors with TDR dive profiles. All observations were conducted during daylight hours.

Pingers were also detected via an array of VEMCO VR2 fixed station ultrasonic receivers. Seventeen VEMCO VR2s were located around Little Cayman at depths ranging from 3 to 8 m below the surface (Fig. 1). Receivers were placed with a mean separation of 1,000 m and had a mean range of 400 m. Thus, although there was coverage in a large proportion of the shallow waters around the island, there were some “dead zones” among stations. VR2 data indicated the frequency with which individual instrumented turtles came within range of each receiver (presence, not distance or bearing), regardless of whether turtles were ultimately recaptured. Stations were continuously active

Table 1 *Eretmochelys imbricata.* Summary of capture and biometric data for study animals: turtle ID, capture date, straight carapace length (SCL), curved carapace length (CCL), mass, displacement (straight-line distance from capture to recapture), time at large, and detections of instrumented turtles on ultrasonic receivers (A–I)

ID Turtle	Capture date	SCL (cm)	CCL (cm)	Mass (kg)	Displacement (m)	Time at large (d)	Turtle detections at VR2 stations								
							Receiver ID and days detected (*n*)								
							A	B	C	D	E	F	G	H	I
1	8 Sep 2005	26.4	27.5	1.9	579	63			*8*	*45*					
2	8 Sep 2005	35.8	38.3	5.5	381	11		*2*	*9*	*7*					
3	8 Sep 2005	37.0	39.0	5.9	661	11		*10*	*5*						
4	8 Sep 2005	37.0	40.1	5.8	758	13			*4*	*13*					
5	8 Sep 2005	37.3	39.6	5.6	539	11			*11*						
6	9 Sep 2005	41.3	44.2	8.5	1,190	12		*13*							
7	9 Sep 2005	36.2	38.2	5.7	150	11			*9*	*6*					
8	9 Sep 2005	28.1	29.6	2.2	331	11			*9*	*2*					
9	9 Sep 2005	38.6	41.5	7.6	285	62		4	*15*	*19*	*10*	1			
10	9 Sep 2005	39.9	41.5	6.2	529	11			*11*	*2*					
11	7 Nov 2005	29.8	31.0	3.0	760	316				*13*	*1*				
12	7 Nov 2005	33.2	34.5	3.7	2,080	22				*13*					
13	7 Nov 2005	58.4	61.0	21.8	N/A	>365		2	*6*	*21*					
14	8 Nov 2005	26.9	27.6	1.9	117	20		*4*							
15	8 Nov 2005	47.9	51.5	12.1	380	21		*22*							
16	8 Nov 2005	51.9	56.2	16.4	566	21		*22*							
17	8 Nov 2005	45.7	47.9	10.8	285	20		*12*							
18	8 Nov 2005	47.3	49.5	11.9	N/A	>365		*86*	*2*		3	3		3	1
19	9 Nov 2005	44.0	46.5	9.1	242	20		*12*							
20	9 Nov 2005	41.2	44.2	8.6	170	20		*17*							
21	9 Nov 2005	41.8	45.1	8.2	63	20		*16*							

Italicized values denote detections by VR2 receivers during the TDR recording period; numbers in cells denote total number of days detected by each station. As turtles could be detected at more than one receiver per 24-h period, days detected at each receiver may total more than the number of days at large. NB: There were no transmissions received at stations J–Q. For position of VR2 receivers, refer to Fig. 1

for the duration of the study and data were downloaded every 1–3 months.

Data analysis

TDRs recorded for 8 days at 10 s intervals, with an accuracy of ±1% of the maximum depth scale (0.1–1 m). Time and depth data were analyzed with bespoke dive analysis software (MultiTrace MT-Dive, Jensen software) to generate descriptive parameters of individual dives. Date and location specific sunrise and sunset times were obtained from the US Naval Observatory Astronomical Applications Department, http://aa.usno.navy.mil. For nocturnal and diurnal dives, Coefficient of Variation (CV) of the depth of the bottom phase (portion of the dive between points of inflection) was calculated in order to evaluate activity level. Relationships between turtle body mass and dive performance (dive depth and duration) were investigated with linear correlation (Pearson's *r*) and paired *t*-tests were used to compare nocturnal and diurnal coefficients of variation and dive depths and durations (log10 transformed).

Results

Size range and recaptures

All 21 turtles were detected on VEMCO VR2 fixed station ultrasonic receivers. Out of 21 TDRs deployed, 19 were recovered. Download of TDRs resulted in 18 usable dive datasets. Recaptured turtles spanned a broad range of sizes (mean straight carapace length (±SD) 37.9 ± 7.0 cm, range 26.4–51.9 cm; mass 7.7 ± 4.9 kg, range 1.9–21.8 kg) in a distribution resembling the more extensive dataset of marked animals in the population (Fig. 3a, b). Recovery effort for recaptured turtles ranged from 1 to 5 days actively searching in the study area with a VR100 ultrasonic receiver. Two animals remained at large at the conclusion of the study.

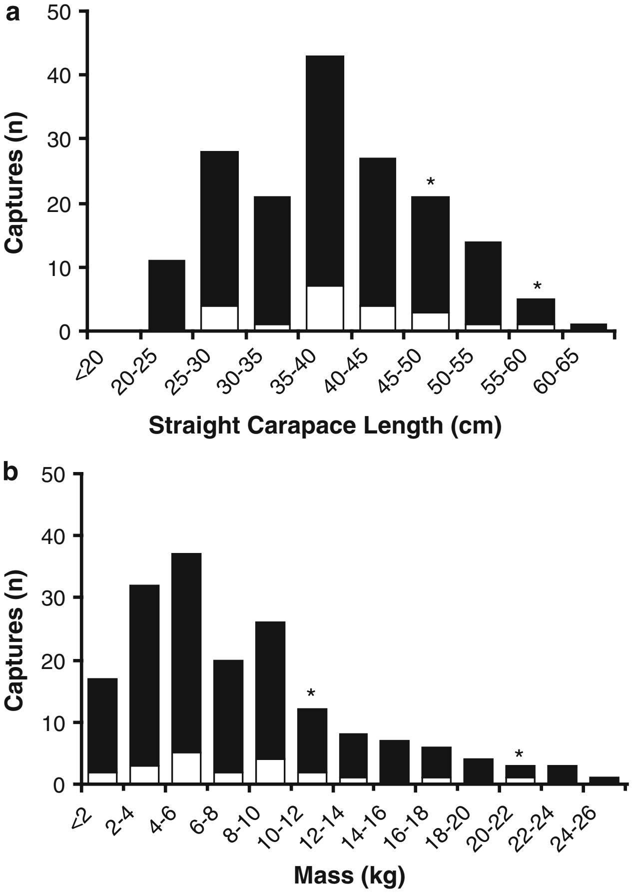

Fig. 3 *Eretmochelys imbricata.* Size distribution (**a**) straight carapace length and (**b**) mass for instrumented turtles (unfilled bars, $n = 21$) in comparison with population size distribution (filled bars). * indicates an un-recovered instrumented turtle

Diving

Study animals displayed pronounced diel patterns of diurnal activity and nocturnal resting. Diurnal dives were characterized by greater variability in the depth of the bottom phase: Coefficient of Variation (CV) of the depth of the bottom phase (mean ± SD) was 0.14 ± 0.04, range 0.06–0.20 for dives during the day and 0.07 ± 0.04, range 0.02–0.15 for dives at night. Thus, turtles during diurnal dives were more active (paired *t*-test, $t_{17} = 6.77$, $P < 0.0001$, Fig. 4a, b). Dives during the day were shorter than dives at night (paired *t*-test, $t_{17} = 3.03$, $P < 0.01$): mean dive duration (±SD) was 16 ± 7 min, range 8–36 for diurnal dives and 25 ± 14 min, range 8–53 min for nocturnal dives. Diurnal dives were also significantly deeper than nocturnal dives (paired *t*-test, $t_{17} = 3.05$, $P < 0.01$): mean depth of diurnal dives (±SD) was 8 ± 5 m, range 2–20 m and mean depth of nocturnal dives was 5 ± 5 m, range 1–14 m.

Mean dive duration was significantly correlated with body mass (Night: Pearson's $r_{16} = 0.73$, $P < 0.001$, Fig. 5a. Day: Pearson's $r_{16} = 0.55$, $P < 0.05$, Fig. 5b) and a significant correlation was observed between body mass and mean dive depth for nocturnal dives (Pearson's $r_{16} = 0.58$, $P < 0.05$, Fig. 5c). For nocturnal dives, smaller turtles (<5 kg) appeared to rest at shallower depths, larger turtles (>10 kg) at deeper depths, and intermediately sized turtles utilized depths across the range, with some individuals apparently switching resting sites during the course of the study period. For diurnal dives, mean dive depth was not significantly correlated with body size (Fig. 5d), but there was a significant correlation between body size and

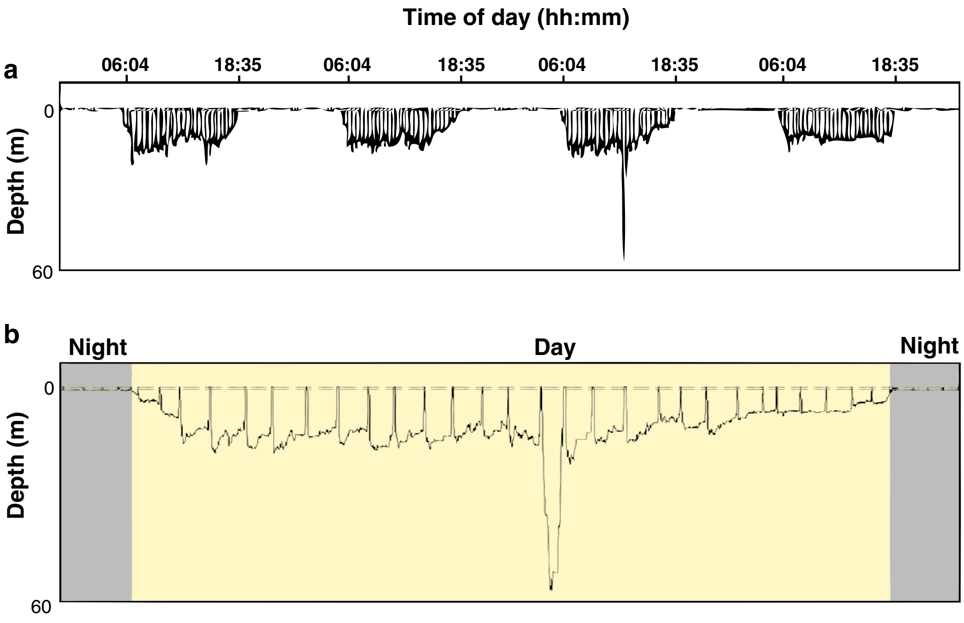

Fig. 4 *Eretmochelys imbricata.* (**a**) Dive pattern over a 4-day period; (**b**) dive pattern over a 1-day period

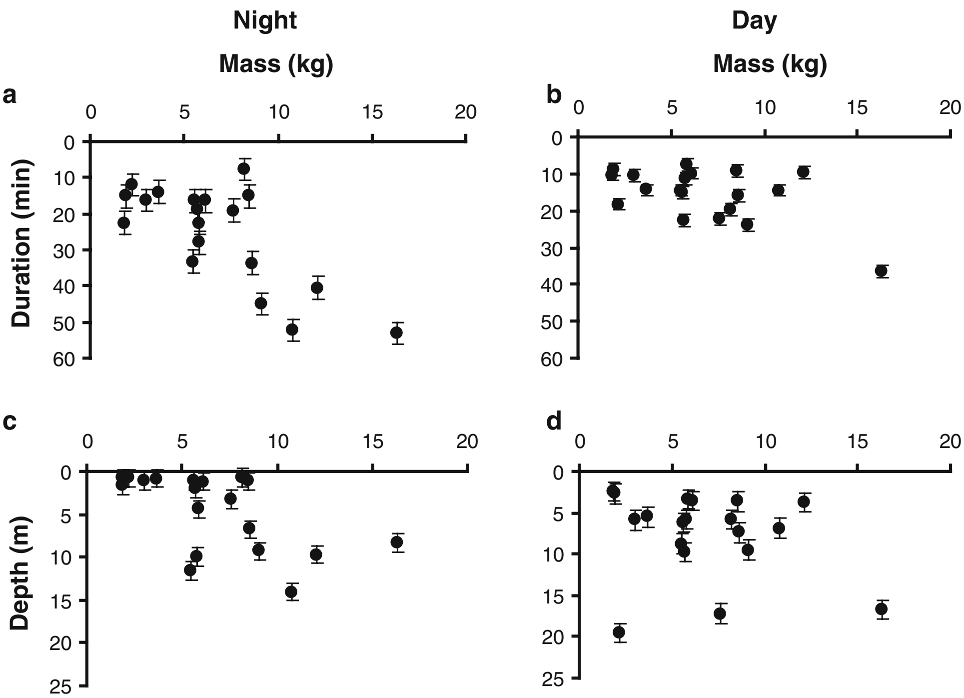

Fig. 5 *Eretmochelys imbricata.* Relationship between turtle mass and dive duration (**a**, **b**) and depth (**c**, **d**) for nocturnal and diurnal dives (mean ± SE). Each point represents data from one turtle

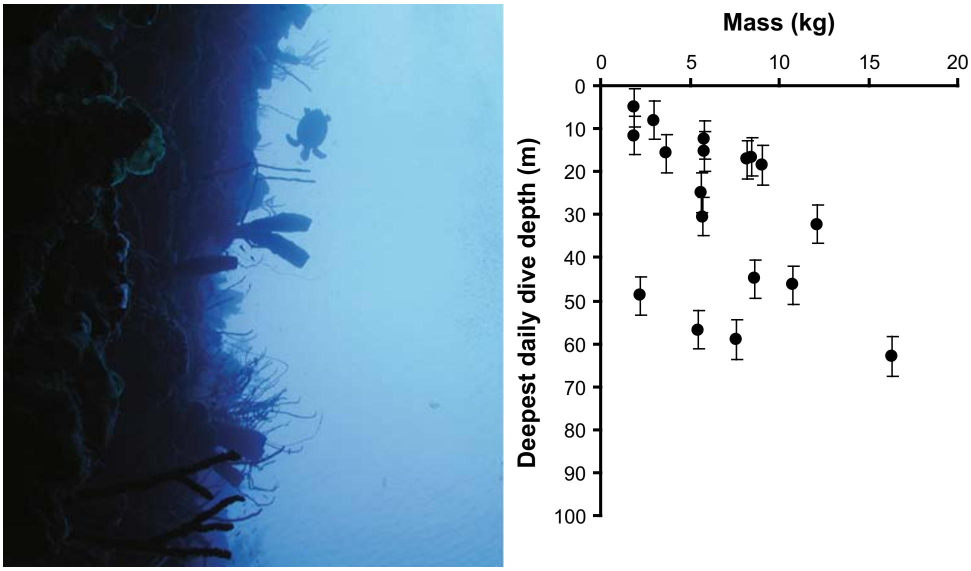

Fig. 6 *Eretmochelys imbricata.* Relationship between turtle mass and deepest daily dive depth (mean ± SE). Each point represents data from one turtle. Image: Hawksbill turtle, Little Cayman wall

maximum diurnal dive depth (Pearson's $r_{16} = 0.56$, $P < 0.05$), and deepest daily dive depth (mean of means for all daily maxima) (Pearson's $r_{16} = 0.51$, $P < 0.05$, Fig. 6). Among individuals, a high level of variation in depth utilization was observed, ranging from shallow (Fig. 7a) to deep (Fig. 7b) diving. Maximum diurnal dive depth was 43 ± 27 m, range 7–91 m and deepest daily dive depth was 29 ± 19 m, range 5–63 m.

Visual observations

Instantaneous behavioral observations were made at time of turtle capture and recapture ($n = 39$ observations). For all turtles, 13% of observations at sighting were of feeding. Other behaviors included breathing (5%), swimming (35%), hovering above the bottom (3%), fleeing the observer at time of observation (5%), or resting/motionless on the bottom (40%). As multiple behaviors were observed during diurnal dives, it is evident that "active" dives represented a range of searching, traveling and other behaviors in addition to feeding.

In addition, to correlate TDR profiles with behavior, visual observations were conducted during TDR recording. Eleven instantaneous daytime observations were made of activity at sighting, as well as continuous observation of one complete dive (Fig. 8). When descent from the surface

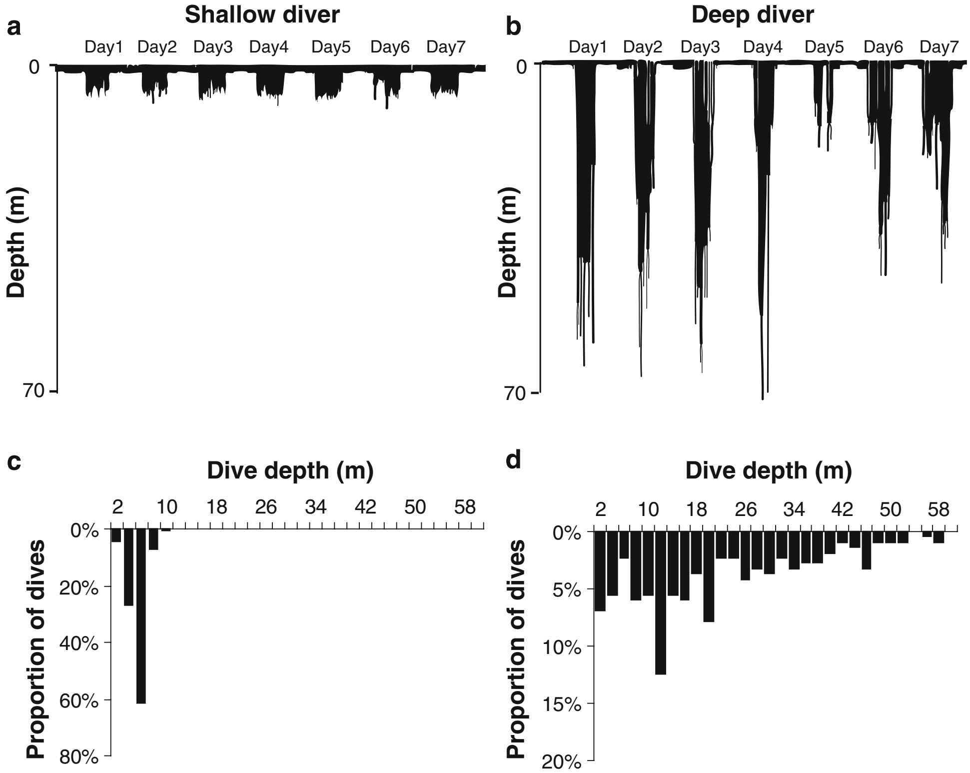

Fig. 7 *Eretmochelys imbricata.* Time depth recorder profiles (**a**, **b**) show diel patterns, contrasting the behavior of a shallow diving turtle and a deep diving turtle. Histograms (**c**, **d**) depict proportion of diurnal dives to each depth

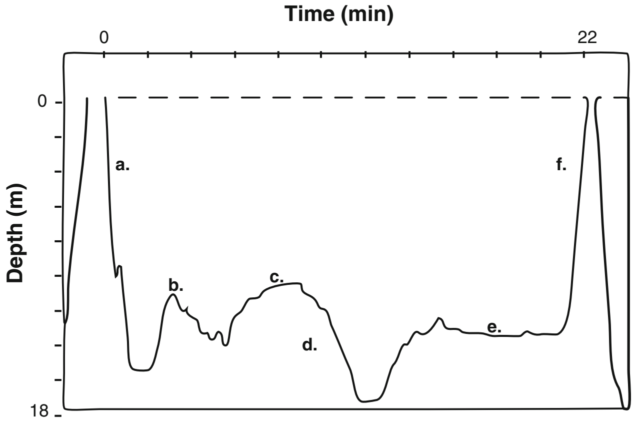

Fig. 8 *Eretmochelys imbricata.* Time depth recorder (TDR) profile for turtle 15, visually observed during TDR recording. (**a**) Descent: swim down then glide (**b**) Searching (**c**) Feeding (**d**) Swimming across sand (**e**) Feeding (crawling along the bottom). (**f**) Ascent: swimming upward, then gliding to surface. Dive duration: 22 min

to a depth of *ca.* 15 m was observed (Fig. 8a), behavior coincided with previous observations of hawksbill (van Dam and Diez 1997b) and green turtles (Hays et al. 2007): the turtle actively finned downward, then glided to the bottom from the apparent point of negative buoyancy. Pulling along the bottom with flippers (Fig. 8e) suggested that negative buoyancy was attained during the bottom phase of the dive. Ascent (Fig. 8f) was accomplished by actively swimming upward, followed by gliding to the surface from the apparent point of positive buoyancy.

Horizontal movements

For recaptured turtles, time at large (mean ± SD) was 37 ± 69 days, range 11–316 days and distance from capture site to recapture site was 530 ± 466 m, range 63–2,080 m (Table 1). There was no significant correlation between displacement and body mass or displacement and time at large. Horizontal movements were also detected via a network of VEMCO VR2 ultrasonic receivers (Table 1). During the course of the TDR recording period, all 21 study animals remained within the boundaries of the Bloody Bay Marine Protected Area (Table 1; Fig 1). Ten turtles were detected on only one station, nine turtles were detected on two stations, and two turtles were detected on three stations. Two turtles remained at large approximately 60 days. Of these, one turtle was detected on two stations, and the other turtle was briefly detected on five stations, one of which was located outside the Bloody Bay MPA. Three turtles remained at large for >300 days. Of these, two turtles were detected only in Bloody Bay MPA, while the third individual was detected on six stations. There was a significant correlation among number of stations upon which turtles were detected (a proxy for range) and time at large (Pearson's $r_{19} = 0.60$, $P < 0.01$).

Discussion

Over recent centuries, reductions in marine megavertebrate populations may have led to long-term shifts in Caribbean ecosystem dynamics (Jackson et al. 2001; Pandolfi et al. 2003). Hawksbill turtles might still represent important spongivores on coral reefs (Hill 1998; Leon and Bjorndal 2002). However, concerns have recently been raised regarding the ability of marine turtles to adapt to anthropogenic degradation of foraging grounds and changes in global climate (Bjorndal and Jackson 2003; Chaloupka et al. 2008). In order to evaluate ecological role and management needs of hawksbill turtles, an understanding of habitat use on coral reef foraging grounds is required. By combining TDRs, ultrasonic tags, and an array of ultrasonic receivers, diving behavior and movements of juvenile hawksbill turtles were elucidated on a Caribbean coral reef.

In hawksbills and other hardshell turtles, lung volume scales with body mass (by a factor of 0.92; Hochscheid et al. 2007). As the lungs contain the majority of the oxygen store needed for diving (Lutz and Bentley 1985), larger turtles are capable of longer aerobic dives. However, behavioral observations showed variations in diurnal activity, which may result in corresponding variations in metabolic rate and diurnal dive duration (cf. Hays et al. 2000a, b). In contrast, oxygen usage is likely to be consistent for resting nocturnal dives, explaining the stronger correlation between nocturnal dive duration and body mass.

Turtles are capable of adjusting buoyancy by controlling lung volume, and often dive with partially inflated lungs (Hays et al. 2004; Hochscheid et al. 2007). As turtles often do not dive to their maximum capacity, there is a need to characterize depth utilization in the wild. Differences in dive depths among Caribbean foraging areas (Table 2) suggest that depth utilization may be influenced by a variety of factors such as distribution of resources (Hays et al. 2006), physical conditions, such as wave action (van Dam and Diez 1996), and avoidance of predators (Heithaus et al. 2007).

In this study, mean nocturnal dive depth was significantly correlated with turtle size, while mean diurnal dive depth was not. For diurnal dives, turtles across a broad size range overlapped in mean dive depth distribution, most likely in order to utilize a relatively narrow band of reef habitat. For resting nocturnal dives, turtles might be expected to select a physiologically optimal depth, minimizing energy expenditure and maximizing dive duration by selecting depths which provide neutral buoyancy with fully inflated lungs (Hays et al. 2000a, 2004). However, in addition to the significant influence of body size, selection of nocturnal resting sites may have been influenced by the distribution of rugose reef and rubble in the study area. These habitats may provide protection from tiger and bull sharks which are present in the Cayman Islands (Simpfendorfer 2000; Simpfendorfer and Burgess 2000) and are known to be predators of juvenile turtles (Compagno 1984; Heithaus et al. 2002a). Additionally, hawksbills in the Cayman Islands are occasionally observed wedged under ledges at night (J. Blumenthal pers. obs.), suggesting that despite positive buoyancy, turtles may maximize dive duration and minimize surfacing effort by “assisted resting” (Houghton et al. 2003) in shallow waters. Thus, diel dive patterns may be influenced by a complex interaction of physiological and environmental factors.

In contrast to the non-significant relationship between body mass and mean diurnal depth utilization, there was a significant correlation between body mass and maximum diurnal dive depth and deepest daily dive depth. Within the study area, colonized shelf area is relatively narrow. However, turtles were able to increase available habitat by diving down the face of the reef wall, where they may feed on abundant sponges. Thus, vertical partitioning of habitat may decrease intraspecific competition and increase the carrying capacity of the foraging ground. The deepest dives may allow turtles to forage in the “sponge belt,” a proliferation of sponges at depths of 80–120 m (Ghiold et al. 1994). Perhaps due to lower temperatures, deep sponges on the wall grow to extraordinary size (Ghiold et al. 1994). Ecosystem dynamics of this assemblage are virtually unknown, but as deep divers, larger hawksbill turtles may represent important predators and may also benefit from access to relatively pristine deep ecosystems. In the Caribbean, serious declines in species diversity and biomass of shallow reef sponges have been observed (Wulff 2006). Sponges are

Table 2 *Eretmochelys imbricata*. Summary of dive data from published studies of hawksbill turtles

Study site	Mass	Carapace length	Dive depth (m)		Max dive depth (m)	Size/depth correlations		*n*
	Range (kg)	Range (cm)	Mean night	Mean day		Significance night	Significance day	
Puerto Rico cliffwall	3.7–17.2	32–53.4	6.8	4.7	72.1	NS (mean)	SIG (mean)	4
Puerto Rico reef	2.4–18.4	27.1–51.6	7–10	8–10	24.1	NS (mean)	SIG (mean)	5
Cayman Islands reef	1.9–16.4	26.4–51.9	5	8	91	SIG (mean)	NS (mean) SIG (max)	18

Information includes mass, straight carapace length, mean dive depth, maximum dive depth, correlation between body size and dive depth, and sample size (*n*). NS, not significant; SIG, significant. Source data: Puerto Rico cliffwall (van Dam and Diez 1996); Puerto Rico reef (van Dam and Diez 1997a, b). Cayman Islands reef (this study) increasingly threatened by disease (Webster 2007) and hurricanes and tropical storms strip such fauna from shallow environments (Woodley et al. 1981; Blair et al. 1994; Wulff 1995). Thus, deep dive capacity in hawksbills may provide a buffer against the impacts of hurricanes and anthropogenic degradation of shallow habitats.

Use of ultrasonic transmitters facilitated location of turtles (increasing recapture rate to >90%) and allowed instrument recordings to be correlated with observations of behavior. A previous study involving deployment of video-linked TDRs on green turtles resulted in the observation of multiple behaviors for each dive type (Seminoff et al. 2006). The methodology used in this study is feasible for smaller individuals and resulted in a similar observation for juvenile hawksbills (albeit with a limited number of observations). In Puerto Rico, hawksbills were observed to spend the majority of "active" dives feeding (van Dam and Diez 1997a). However, in the Cayman Islands, there were few observations of feeding and many observations of apparent traveling or searching. Resting behavior may be over-represented in the dataset if turtles detected the presence of observers prior to recording of behavior, but feeding turtles did not react perceptibly to the presence of observers or discontinue feeding. As there were very few mid-water sightings of turtles it can be inferred that the majority of dives were to the bottom.

In addition to characterization of diving behavior, horizontal movements were evaluated. Distances from capture to recapture were comparable to displacements observed in Puerto Rico (van Dam and Diez 1998) and there was no significant correlation between displacement and time at large. Deployment of ultrasonic tags and an array of receivers enabled description of horizontal movements of hawksbills with respect to the boundaries of marine protected areas (MPAs). In the short term, hawksbills remained resident within the Bloody Bay MPA. Of the three turtles which remained at large for more than 300 days, two appeared to remain within Bloody Bay, while 6 months after deployment the third individual undertook a movement of 10 km, entering a second MPA on the south coast of Little Cayman. Thus, daily home range was small, but longer term movements brought turtles through unprotected areas. In contrast to the non-significant relationship between time at large and displacement from capture to recapture, there was a significant correlation between time at large and mean number of receivers upon which turtles were detected (a proxy for range). Long-term movements and emigration patterns have implications in designing MPAs and in evaluating open versus closed populations for capture-mark-recapture modeling (Cooke 2008). In addition to tracking hawksbills, ultrasonic receivers were used to monitor the movements of endangered Nassau grouper (*Epinephelus striatus*), providing an opportunity for synergistic research and highlighting the potential of this method to aid in the management of mixed species assemblages.

Despite concerns regarding the decreasing state of Caribbean coral reefs (Gardner et al. 2003), significant growth in some regional hawksbill populations has been observed (e.g., Beggs et al. 2007). Thus, it is possible that hawksbills might survive or thrive on the successional communities formed after the demise of coral reefs. Alternatively, it could be that patches of high quality habitat serve as refugia, or that deep dive capacity has thus far buffered hawksbills from degradation in shallower habitats. Given the threats of changing climate to coral reefs (Knowlton 2001; Hughes et al. 2003), it is important to gauge the susceptibility of hawksbills to ecosystem change across a variety of depths, and to evaluate the footprint of hawksbill turtles as possible keystone predators in coral reef ecosystems.

Acknowledgments For generously sharing the use of ultrasonic equipment, we thank B. Semmens, S. and S. Heppell, L. Whalen, B. Johnson, P. Bush, C. McCoy, and K. Luke of the Grouper Moon Project—a collaborative effort between REEF and the Cayman Islands Department of Environment with funding provided by the NOAA International Coral Reef Conservation Program and PADI Project AWARE. We thank M. Slattery and the NOAA Twilight Zone Expedition Team for their insights and for providing the image used in Fig. 6. For invaluable logistical support and assistance with fieldwork, we thank J. Mills, P. Lopez, K. Donnawell, and Department of Environment administration, operations, and enforcement staff. Work in the Cayman Islands was supported by the National Environment Research Council (NERC) and the Darwin Initiative, and work in the UK was supported by the European Social Fund. We acknowledge support to J. Blumenthal (University of Exeter postgraduate studentship and the Darwin Initiative) and M. Witt (NERC Postgraduate studentship) and thank anonymous reviewers for input which improved the manuscript.

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