Vol. 9: 113–121, 2010
doi: 10.3354/ab00222

AQUATIC BIOLOGY
Aquat Biol

Published online April 15

OPEN ACCESS

Life in (and out of) the lagoon: fine-scale movements of green turtles tracked using time-depth recorders

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ABSTRACT: Tracking fine-scale movements in relation to threats is fundamental to the management of exploited marine species, yet there is considerable difficulty associated with gathering such data at sea. By combining a capture-recapture study with deployment of time-depth recorders (TDRs) and ultrasonic tags, we elucidated distribution and daily movements of juvenile green turtles *Chelonia mydas* exposed to a legal marine turtle fishery in the Cayman Islands. For instrumented turtles, distinct diel activity patterns were observed: dives during the day were shorter and more active than those at night, implying diurnal foraging and nocturnal resting. Spatially, while capture and recapture locations suggested fidelity to a shallow lagoon, when turtles were fitted with TDRs and ultrasonic tags we demonstrated that they regularly moved out of the lagoon and onto the reef, where they could legally be captured in the marine turtle fishery. Our results are thus novel and valuable in a management context in that we demonstrated that seemingly protected aggregations of juvenile green turtles within a lagoon were, in fact, exposed to legal capture on a near-daily basis. This emphasizes the importance of assessing diel activity patterns of juvenile marine turtles, particularly with respect to directed take and other threats.

KEY WORDS: Green turtle · *Chelonia mydas* · Spatial ecology · Seagrass · Coral reef · Time-depth recorder · TDR

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INTRODUCTION

Due to spatial variability in intensity of threats, tracking movement is fundamental to the management of endangered animals (Cooke 2008, Bograd et al. 2010). As commercially valuable migratory species which often overlap in distribution with fisheries, marine turtles are susceptible to directed and incidental harvest throughout their range (Lewison et al. 2004). It is well established that impacts of fishery-related mortality cross geopolitical boundaries; for example, green turtles originating from both regionally important (Tortuguero, Costa Rica; Troëng et al. 2005) and critically reduced (Cayman Islands; Blumenthal et al. 2006) rookeries migrate to foraging grounds in Nicaragua, where a commercial turtle fishery persists (Campbell & Lagueux 2005). However, in addition to tracking transboundary migrations, characterization of fine-scale movements (e.g. with respect to the boundaries of local marine protected areas) has key implications for marine turtle management, as has been demonstrated in adult loggerheads (Schofield et al. 2007, Zbinden et al. 2007). For juvenile green turtles, while individuals on foraging grounds are known to make daily movements from foraging to resting sites (Mendonca 1983, Ogden et al. 1983), few studies have investigated how local movements determine vulnerability to anthropogenic threats.

Deployment of remote systems such as satellite transmitters (see Godley et al. 2008 for review) and light geolocation system tags (Storch 2003, Fuller et al. 2008) has been extremely effective in tracking long-range migrations of marine turtles, but location resolution of these instruments is generally insufficient to characterize fine-scale patterns of movement of resi-

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dent animals. On foraging grounds, long-established techniques such as in-water capture and flipper tagging have proven essential in establishing survivorship (Bjorndal et al. 2003a) and growth rates (Balazs & Chaloupka 2004, Chaloupka et al. 2004), but such methods are limited in their ability to elucidate diel movements between capture and recapture. Recently, radio and ultrasonic tracking (e.g. van Dam & Diez 1998, Seminoff et al. 2002, Taquet et al. 2006) and deployment of GPS loggers (Schofield et al. 2007) and Argos satellite-linked GPS tags (Schofield et al. 2009) has proven useful in unveiling local movements, and determination of movements via dead reckoning represents a promising emerging technology (Wilson et al. 2008). However, these methods are relatively resource- and/or time-intensive.

Time-depth recorders (TDRs) represent cost-effective and widely utilized instruments in marine turtle research (e.g. van Dam & Diez 1996, Hays et al. 2000, Ropert-Coudert et al. 2009), but lack a spatial context (i.e. depth but not location is recorded). In the Cayman Islands, drastic differences in bathymetry inside and outside a lagoon (sheltered area within a barrier reef) provide opportunities to infer locations of dives from depth profiles. In the present study, integration of TDR recordings with bathymetric data allowed us to determine location of instrumented turtles (inside or outside the lagoon), opening up the possibility of using TDRs to examine daily movements of juvenile green turtles and their resultant exposure to anthropogenic threats.

Turtle fishing in the Cayman Islands began shortly after European discovery (in 1503) and played an important role in shaping the economy and culture (Bell et al. 2006). However, due to heavy exploitation, nesting populations collapsed by the early 1800s (Lewis 1940). While rookeries are still critically reduced (Bell et al. 2007), a low-level legal fishery persists to this day (Bell et al. 2006). Since 1985, the fishery has been regulated through legislation licensing traditional fishers and setting quotas (Cayman Islands Government 1985), and harvest is well-monitored, with a requirement for fisheries officers to measure and document all captured turtles (Richardson et al. 2006). However, from 1985 to 2008, minimum size limits (protecting smaller green turtles and allowing only animals >54 kg to be taken) focused legal exploitation on larger individuals, including reproductive adults (Bell et al. 2006). In 2008, fishery size limits were revised in order to protect reproductively valuable subadult and adult turtles (Cayman Islands Government 2008); a ban was instituted on taking green turtles >60 cm (and also <40 cm) curved carapace length (CCL), where CCL of reproductive females on Cayman Islands nesting beaches is >100 cm (Cayman Islands Department of Environment unpubl. data). Thus, larger and smaller size classes are now protected, and juvenile green turtles from 40 to 60 cm CCL are vulnerable to legal exploitation in the Cayman Islands for the first time in more than 20 yr.

In addition to setting size limits and quotas, Cayman Islands turtle fishery licensing conditions establish geographic areas open to fishing. As turtles are protected within lagoons and exposed to legal take in some adjacent areas (Bell et al. 2006), habitat use and daily movements determine exposure to fishery-related threats. Thus, deployment of TDRs and ultrasonic tags on green turtles of legal size for capture in the marine turtle fishery allowed us to assess vulnerability and management requirements for an aggregation of juvenile green turtles in a Caribbean coastal ecosystem.

MATERIALS AND METHODS

In the Grand Cayman South Sound lagoon (Fig. 1), juvenile green turtles were captured using the turtle rodeo method (Limpus & Reed 1985), wherein animals were pursued in a small boat and caught at the surface of the water by a researcher diving from the bow. In an

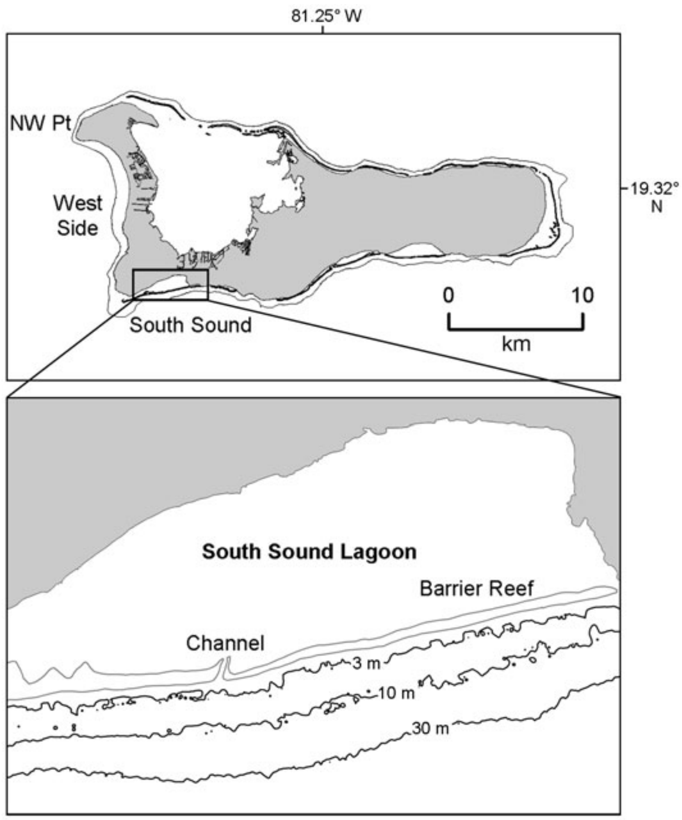

Fig. 1. South Sound, West Side and North West Point (NW Pt), Grand Cayman. Lower panel depicts 3, 10 and 30 m depth contours for the South Sound study area

effective modification to this technique, smaller turtles were pursued until they surfaced to breathe and then scooped out of the water with large long-handled nets (Aquatic Eco-Systems, part no. LN22). In order to reduce potential stress, no more than 3 attempts were made at capturing an individual using either methodology. In addition to rodeo capture in South Sound, green turtles were opportunistically hand-captured in western Grand Cayman (Fig. 1) when encountered during in-water surveys of hawksbill turtles (Blumenthal et al. 2009a).

Turtles were sighted from a small vessel and, although the search pattern was not truly random, the whole the lagoon was searched during the course of every survey bout. For each sighting, turtle habitat and GPS location were recorded. Measurements of mass, straight carapace length (SCL) and CCL (taken from the center of the nuchal notch to the posterior-most marginal scute) were recorded for all captured turtles and used to determine size distribution and calculate growth rate (Bjorndal & Bolten 1988). In order to allow individual identification, turtles were tagged with passive integrated transponder (PIT) tags and double inconel flipper tags (Blumenthal et al. 2009a). Additionally, a white grease pen was used to apply a temporary mark to the carapace of each turtle, preventing individuals from being caught more than once per capture occasion.

In November 2006, TDRs (LTD1110, Lotek) and ultrasonic tags (V13, VEMCO) were deployed on 6 green turtles captured in the South Sound lagoon. Instrument housings were constructed from Starboard polyethylene, with holes in the lids and sides of the housings to facilitate pressure equilibration for TDRs and transmission of signals from ultrasonic tags (Blumenthal et al. 2009b). To prepare for housing attachment, a rear lateral scute on each turtle was scrubbed, sanded and degreased with acetone, and housings were attached with 2-part epoxy. Turtles were released at the site of capture (confirmed by GPS). TDRs recorded depth and temperature at 10 s intervals for an 8 d period (depth accuracy: ±0.5 m; temperature accuracy: ±0.3°C).

A VEMCO VR100 receiver with directional and omni-directional hydrophones was used to locate instrumented turtles. Following recapture, housings were removed and TDRs were subsequently downloaded using manufacturer software (TagTalk 1100, Lotek). After conversion of TDR pressure data to depth (taking the density of saltwater as 1.03 g cm^{-3}), dive analysis software (MultiTrace MT-Dive, Jensen Software) was used to compute descriptive statistics (presented as means ± SD) for individual dives — i.e. duration and depth of the bottom phase of the dive (portion of the dive between points of inflection) — and the coefficient of variation (CV) of the depth of the bottom phase was calculated to evaluate activity level (Blumenthal et al. 2009b).

To determine movements, ArcView v.9.2 (ESRI) was used to overlay bathymetric contours (derived from single beam sonar, Cayman Islands Government unpubl. data) on a map of the study area, indicating that depths >3 m represented habitats outside the lagoon (Fig. 1). Thus, turtle location (inside or outside the protected lagoon) could be inferred based on dive depths and confirmed by ultrasonic tracking and direct observation.

Date- and location-specific sunrise and sunset times were obtained from the US Naval Observatory Astronomical Applications Department (http://aa.usno.navy.mil) in order to investigate diel patterns in diving behavior. To achieve normal distributions for the variables of dive depth, duration and CV, the following transformations were applied: $\log\{-\log[1-(\text{Depth}/100)]\}$, $\log(\text{Duration} + 1)$ and $\text{sqrt}(\text{CV})$. Then, using GenStat (11th edn), 3 linear mixed effects models (restricted maximum likelihood method) were constructed: (1) nocturnal versus diurnal dive depth; (2) nocturnal versus diurnal dive duration; and (3) nocturnal versus diurnal CV. Models included all dives, with individual turtle incorporated as a random effect in order to control for the effect of each individual and thus avoid pseudoreplication.

RESULTS

Capture data

Of 66 individual turtles tagged, 10 were recaptured on one occasion and one was recaptured on 2 occasions. The mean CCL for all captured turtles was 55.7 ± 11.5 cm, with a range of 32.8 to 80.7 cm. All 6 instrumented turtles were of legal size for capture under marine turtle fishery regulations: mean CCL was 52.9 ± 6.8 cm, with a range of 40.6 to 59.0 cm (Fig. 2).

In South Sound, all captures took place on shallow seagrass beds within the lagoon, with 85% of captures and sightings occurring within 500 m of a channel from the lagoon to the reef (Fig. 3a). For turtles tagged and recaptured in South Sound, mean time at large (n = 10 turtles) was 527 ± 212 d, with a range of 173 to 853 d. One green turtle initially captured in western Grand Cayman was recaptured >2 yr later in South Sound. Another individual had a titanium flipper tag from the Cayman Turtle Farm, indicating that the animal had been hatched and reared in captivity for approximately 8 mo. This captive-bred animal was released at North West Point, Grand Cayman, and was captured in South Sound after 7.2 yr in the wild.

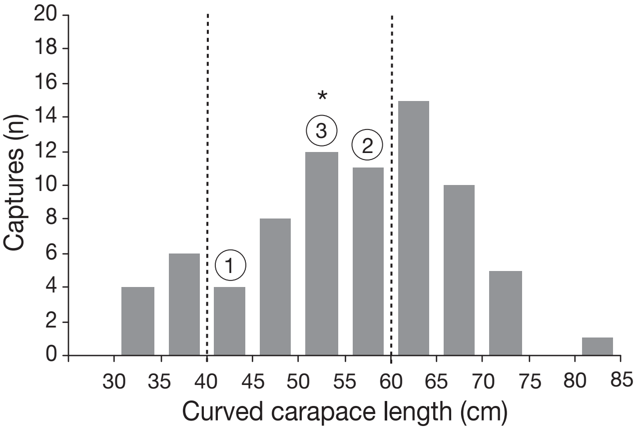

Fig. 2. *Chelonia mydas.* Size distribution (curved carapace length) for instrumented green turtles (O, no. of turtles in each size class is given within the circles, n = 6) in comparison with size distribution of all captured green turtles (bars). *: an instrumented individual which was not recovered. Dotted lines show minimum and maximum size limits for capture in the legal marine turtle fishery

Mean growth rate was 4.1 ± 2.2 cm yr^{-1}, with a range 0.5 to 7.5 cm yr^{-1} (n = 11, increments of >170 d). For the captive-bred turtle, size at recapture was 75.5 cm SCL and 62.5 kg. As size at release from the Cayman Turtle Farm averages 29 cm SCL and 3.6 kg (Wood & Wood 1993, Bjorndal et al. 2003b), this suggests a mean growth rate of 6.4 cm yr^{-1}.

Despite the shallow nature of much of the study area, use of ultrasonic tags greatly facilitated TDR recovery. The recapture rate for instrumented turtles was >80% (5 of 6 TDRs were retrieved) in comparison with a recapture rate of <17% for un-instrumented turtles in the South Sound capture-recapture study.

Movements

The majority of captures in the capture-recapture study occurred in close proximity to a narrow man-made boat channel through the barrier reef (Fig. 3a)

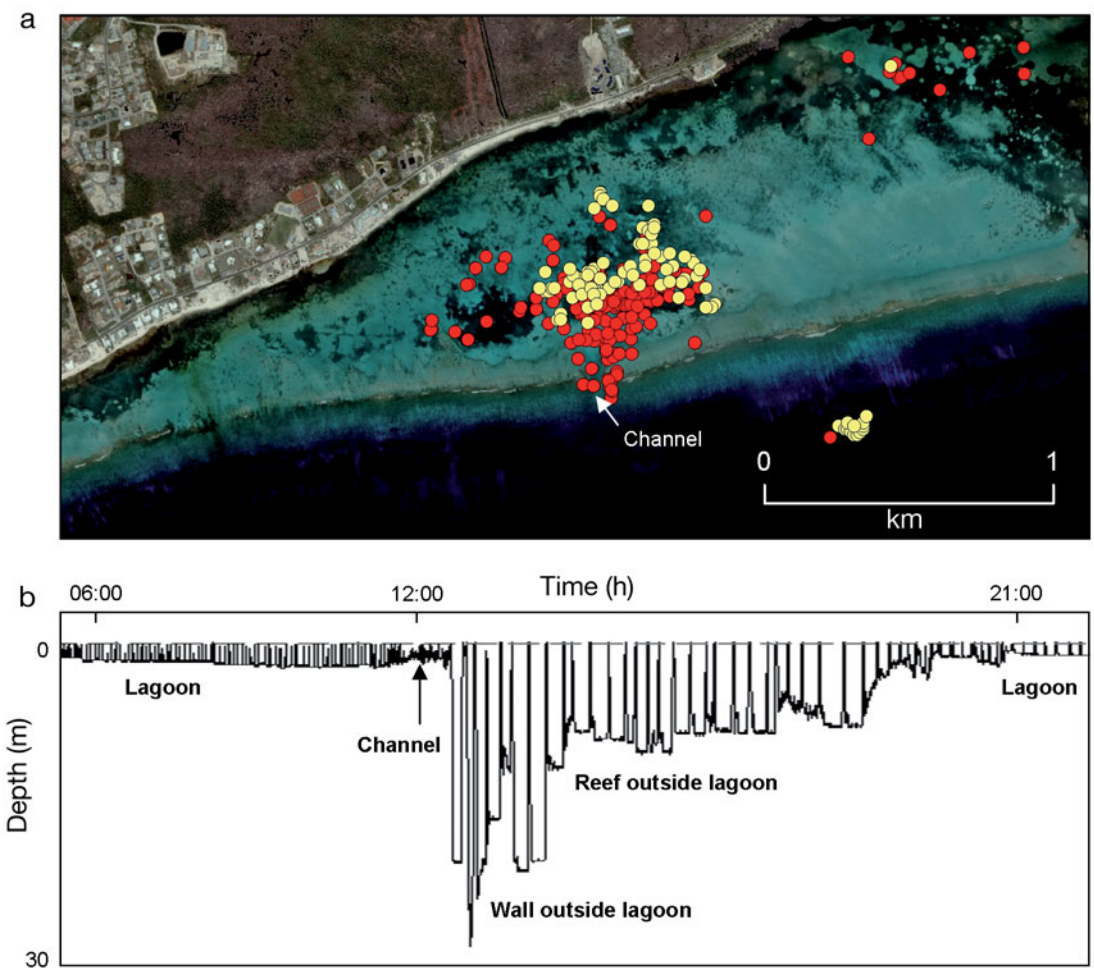

Fig. 3. *Chelonia mydas.* (a) Sighting and capture points (red circles) and ultrasonic detections (yellow circles) for green turtles in the South Sound lagoon. Captures clustered in a high-use area between a channel and a public boat launching ramp, but one instrumented turtle was sighted and detected outside the lagoon. (b) Time-depth recorder depth data suggest diverse habitat utilization within (<3 m) and outside the lagoon (>3 m)

and, when pursued during capture bouts, turtles often escaped through the channel into deeper waters. It was possible to infer turtle location from dive profiles (Fig. 3b) as, based on bathymetry for the study area, dives to depths >3 m must have occurred outside the lagoon. By examining dive depths, we determined that instrumented turtles regularly left their presumed habitat of the seagrass bed (where depths do not exceed 3 m) and traveled to the reef (maximum recorded dive depth 28 m).

Movement of instrumented turtles from the lagoon to the reef outside the lagoon was confirmed by ultrasonic tracking (n = 98 detections; Fig. 3a) and direct observation: one instrumented individual was detected and sighted outside the lagoon in 21 m of water, swimming along the bottom in coral reef habitat. This determination of movement from the lagoon to the reef was also supported when dive depths and sea temperatures were considered in concert; within the lagoon, temperatures increased steadily throughout the day (Fig. 4a), a drop in temperature was evident when turtles moved from lagoon to reef (Fig. 4b), and temperatures remained relatively constant outside the lagoon (Fig. 4c). Finally, photos obtained from underwater photographers confirm the presence of green turtles on the reef in habitats including hard-bottom, coral reef and reef wall (vertical drop-off/slope edge) (Fig. 5).

For instrumented turtles (n = 5 for which TDRs were recovered), mean dive duration was 3.8 ± 0.7 min for diurnal dives and 11.9 ± 8.3 min for nocturnal dives; dive depth was 2.1 ± 0.4 m for diurnal dives and 4.7 ± 5.1 m for nocturnal dives (Table 1). The CV of the depth of the bottom phase of the dive (examined to evaluate activity level) was 0.16 ± 0.01 for dives during the day and 0.13 ± 0.03 for dives at night (n = 5 ind.). Thus, dives during daylight hours were shorter than those at night (mixed effects model, Wald statistic = 3811.88, $p < 0.001$) and turtles were more active in daylight hours (Wald statistic = 194.85, $p < 0.001$). Dives during the day were not significantly shallower than dives at night (Wald statistic = 2.80, $p = 0.095$).

At night 3 turtles rested in the lagoon and 2 rested on the reef. During the day, several activity patterns were observed: all day in the lagoon, all day on the reef and portions of the day in and outside the lagoon. Though the study duration was limited, some turtles were consistent in dive patterns while others were more variable (Fig. 6). Overall, however, while 3 of the 5 turtles spent much more time in the lagoon, all turtles made forays outside the lagoon to the reef, where they were susceptible to legal capture.

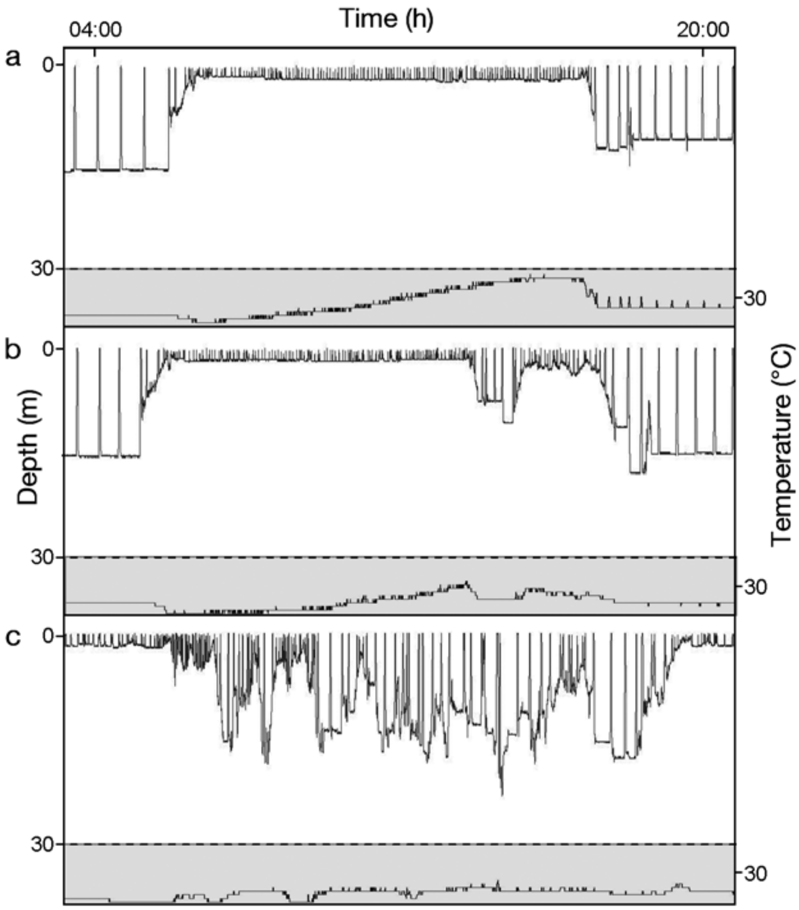

Fig. 4. *Chelonia mydas.* Selected daily profiles of depth (white background) and temperature (gray background) recorded by time-depth recorders (a) inside the lagoon during the day (outside the lagoon at night); (b) inside the lagoon during the day with an excursion to the reef in the afternoon (outside the lagoon at night); and (c) outside the lagoon during the day (inside the lagoon at night)

DISCUSSION

In the present study we combined a traditional capture-recapture method with deployment of TDRs, providing information on demography, distribution and diel movements of Caribbean green turtles. Size distribution suggests that the study area provides a developmental habitat for small juvenile to subadult turtles. While the number of recaptures in the present study was limited, mean growth rate was comparable to that found in other foraging grounds in the Caribbean and Bahamas (Boulon & Frazer 1990, Bjorndal et al. 2000), suggesting a similar time to maturity. In the South Sound capture-recapture study, capture locations suggested fidelity to

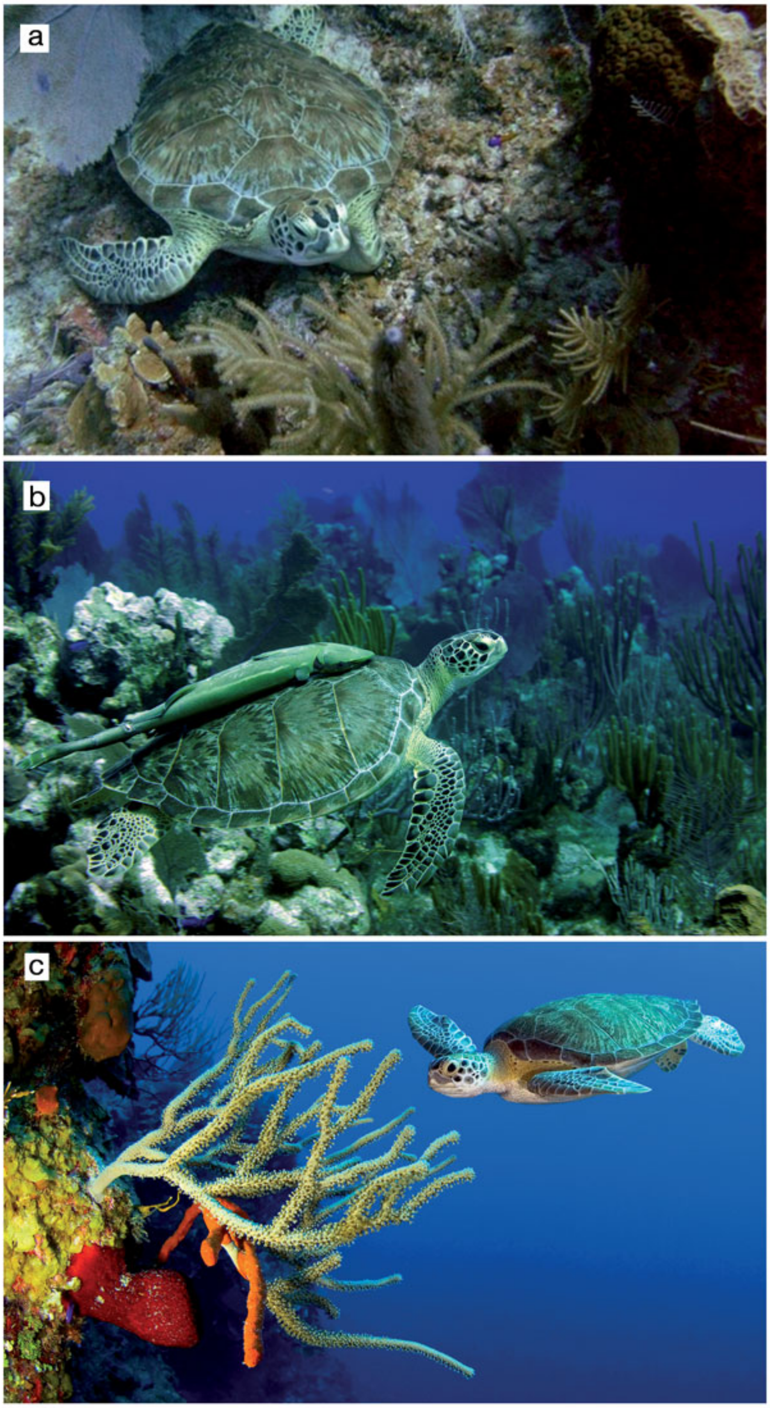

Fig. 5. *Chelonia mydas.* Cayman Islands green turtles outside the lagoon in (a) hard-bottom, (b) coral reef and (c) reef wall habitats

seagrass beds, the typical diurnal habitat of Caribbean green turtles based on previous studies (Mortimer 1981, Ogden et al. 1983). However, when turtles in the lagoon were instrumented with TDRs, we demonstrated that animals traveled through a narrow channel from the lagoon to the reef, often on a daily basis.

There are considerable difficulties associated with inferring activity from dive profiles (Seminoff et al. 2006, Blumenthal et al. 2009b), but for instrumented turtles in the Cayman Islands, dives at night were significantly longer and less active than diurnal dives, implying nocturnal resting. During the day, turtles were sighted on seagrass beds and sand patches in the lagoon, suggesting that both feeding and resting occurred. Diurnal excursions into deeper waters outside the lagoon could represent avoidance of predators or human disturbance (Seminoff et al. 2002), resting or thermoregulation (Mendonca 1983), visitation of cleaning stations (Losey et al. 1994), grazing algae (Musick & Limpus 1997) or self-cleaning by rubbing against rocks and sponges (Heithaus et al. 2002). In the present study, TDRs recorded a decrease in temperature as turtles moved from the lagoon to the reef and, anecdotally, green turtles on reefs in the Cayman Islands have been observed at cleaning stations and rubbing against coral heads and sea fans *Gorgonia* spp. Turtles may have fed on algae in the reef environment, but an alternative method such as deployment of video-linked TDRs would be needed to confirm the occurrence of foraging behavior (Seminoff et al. 2006). Generally, while foraging ecology and the ecological role of green turtles on seagrass beds has been relatively well documented (Moran & Bjorndal 2005), much remains to be determined regarding green turtles inhabiting or transiting through Caribbean coral reefs.

In addition to ecological implications, marine turtle distribution and local movement patterns may influence vulnerability to anthropogenic threats (McClellan & Read 2009). In the South Sound lagoon, green turtle distribution showed a substantial overlap with human activity: captures in the lagoon were concentrated in a high use area between the channel and a public boat launching ramp, and turtles used a single, narrow route from the lagoon to the reef, increasing susceptibility to vessel collision, illegal harvest and incidental capture in hook and line fisheries (Department of Environment unpubl. data). Harvest of breeding turtles at a nesting beach can be unsustainable and may result in reduction or loss of the nesting population (McClenachan et al. 2006). Sim-

Table 1. *Chelonia mydas.* Capture date, biometric data (straight carapace length [SCL], curved carapace length [CCL] and mass) and dive statistics (mean nocturnal and diurnal dive depth and duration) for instrumented turtles. One animal (Turtle 1) was not recaptured

ID	Capture date (2006)	SCL (cm)	CCL (cm)	Mass (kg)	Mean dive depth (m)		Mean dive duration (min)	
					Night	Day	Night	Day
1	6 Nov	49.9	52.7	15.7	–	–	–	–
2	6 Nov	55.3	59.0	22.6	1.2	1.9	6.1	3.5
3	7 Nov	50.1	51.0	30.2	12.4	2.8	23.4	4.9
4	7 Nov	53.9	59.0	23.3	7.6	1.8	18.1	3.8
5	7 Nov	37.8	40.6	18.1	0.9	1.8	5.5	2.9
6	7 Nov	52.2	54.9	15.5	1.4	2.0	6.5	3.8

ilarly, overharvesting in a high vulnerability area (e.g. capture in a lagoon or netting in a channel) could have a high impact on juvenile foraging aggregations.

While quotas on legal take may represent a partial solution to overharvesting (Heppell et al. 2005), these are difficult to enforce. Given limitations in enforcement capability, our results highlight the potential importance of maintaining restrictions against marine turtle harvest in high-use areas and routes where overexploitation can easily occur. In the Cayman Islands, setting of fixed nets (used to capture turtles on routes such as channels from the lagoon to the reef) was banned in 2008 and a restriction on taking turtles within lagoons has been maintained. When area restrictions are implemented, however, it becomes necessary to determine how individuals and populations move across these boundaries. Our results showed that individuals frequently moved between protected and unprotected habitats, a finding which may have implications for management of other marine turtle foraging aggregations, particularly as other Caribbean jurisdictions implement maximum size limits for legal take. At present, the Cayman Islands is the only Caribbean jurisdiction with a maximum size limit, though 13 Caribbean countries and territories maintain some form of legal marine turtle harvest (Dow et al. 2007) and it is widely recognized that populations of long-lived, late-maturing species have difficulty supporting harvesting of subadult and adult individuals (Heppell et al. 2005).

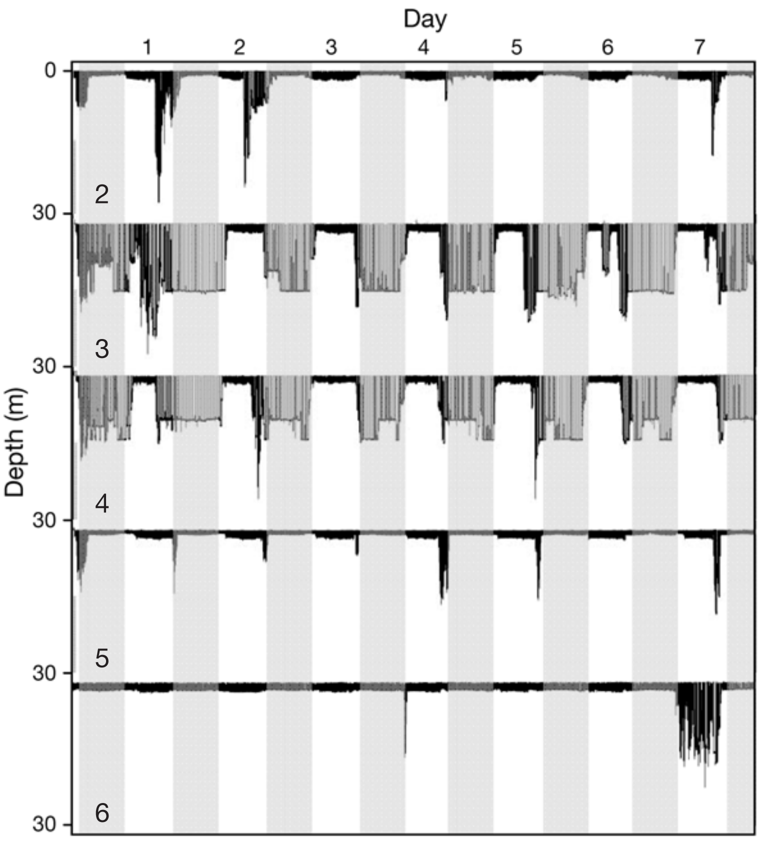

Fig. 6. *Chelonia mydas.* Dive profiles for Turtles 2 to 6 (Turtle 1 was not recaptured), showing movements from lagoon (less than 3 m depth) to reef (more than 3 m depth). Shading indicates night-time hours (sunset to sunrise)

It should be noted, however, that sample size, duration and geographic scope of the present study were limited. Also, in areas with unknown or more complex bathymetry, TDRs will be limited in their ability to resolve movements, and as dives are not always to the bottom, shallow dives cannot be assumed to have been made in shallow water. Nonetheless, as recorded dive depths in the present study frequently exceeded the depth of the water column inside the reef, we showed that turtles regularly left the protected lagoon and moved into unprotected habitats. This demonstrates that under certain circumstances, TDRs can provide a viable low-cost methodology for determining movements and exposure to threats.

In summary, capture-recapture methodology and integration of time-depth profiles and bathymetry proved a useful method for elucidating movements of marine turtles within a Caribbean foraging ground, indicating that turtles congregated in a high-use area in the lagoon, a channel from the lagoon to reef represented a high vulnerability habitat and movements beyond the boundaries of protected areas frequently occurred. Thus, we demonstrated that assessing daily movements may be an important component in revising fishery legislation, targeting law enforcement and managing protected areas and species.

Acknowledgements. For sharing the use of ultrasonic tracking 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 the following photographers for generously providing their images for Fig. 5: M. Braunstein, P. Weir (www.digitaldiver.biz) and K. and C. Alpers. For providing release data for the head-started green turtle, we thank J. Parsons and Cayman Turtle Farm. For assistance with fieldwork, we thank A. McGowan and L. Wright, and for logistical support, we thank Department of Environment administration, operations and enforcement staff. Work in the Cayman Islands and the UK was supported by the National Environment Research Council (NERC), the Darwin Initiative and the European Social Fund. We acknowledge support to J.M.B. (University of Exeter postgraduate studentship and the Darwin Initiative) and thank anonymous reviewers for input which improved the manuscript.

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Editorial responsibility: Brent Stewart,
San Diego, California, USA

Submitted: July 10, 2009; Accepted: January 11, 2010
Proofs received from author(s): March 31, 2010