

Ecology of Hawksbill Turtles, *Eretmochelys imbricata*, on a Western Caribbean Foraging Ground

J.M. BLUMENTHAL^{1,2}, T.J. AUSTIN¹, C.D.L. BELL², J.B. BOTHWELL¹, A.C. BRODERICK²,
G. EBANKS-PETRIE¹, J.A. GIBB¹, K.E. LUKE¹, J.R. OLYNIK¹, M.F. ORR¹, J.L. SOLOMON¹, AND
B.J. GODLEY²

¹Cayman Islands Department of Environment, PO Box 486, Grand Cayman KY1-1106, Cayman Islands
[jblumenthal@seaturtle.org, DoE@gov.ky];

²Centre for Ecology and Conservation, School of Biosciences, University of Exeter Cornwall Campus,
Penryn TR10 9EZ UK [B.J.Godley@exeter.ac.uk; A.C.Broderick@exeter.ac.uk]

ABSTRACT. – We present results of an inwater research program focusing on basic ecology of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Cayman Islands. We made 206 captures of 135 hawksbills in Little Cayman and 103 captures of 97 hawksbills in Grand Cayman. The Cayman Islands aggregation demonstrated a broad size distribution (20.5–62.6 cm straight carapace length), slow growth rate (3.0 ± 0.9 cm/y), and multiple recaptures, suggesting long-term residence in some individuals. Demonstrated home range was small (mean distance from capture to recapture 545 ± 514 m, range 2–2080 m); although, an international tag return suggested a long-range developmental migration. Vertical features provided important habitat in Little Cayman, and larger turtles were generally captured in deeper waters. Behavior at sighting varied by habitat: resting, swimming, and feeding were observed in coral reef, reef wall, and hardbottom colonized by sponges and gorgonians, and resting was frequently observed in uncolonized hardbottom. Images obtained from underwater photographers show that hawksbills forage on sponges and occasionally on jellyfish. We observed an apparent commensal feeding relationship between hawksbills and 3 species of angelfish as well as aggressive interactions between hawksbills. We also documented causes of injury and mortality in the study area—including legal, illegal and incidental take, vessel collisions, hurricanes, and natural predation.

KEY WORDS. – Reptilia; Testudines; Cheloniidae; hawksbill; *Eretmochelys imbricata*; marine turtle; tagging; habitat use; behavior; Cayman Islands

Hawksbill turtles *Eretmochelys imbricata* are a migratory species of conservation concern. Adults travel hundreds or thousands of kilometers from foraging grounds to breeding areas (Horrocks et al. 2001; Tröeng et al. 2005; van Dam et al. 2008) and neonates are broadly dispersed by ocean currents (Carr 1987; Musick and Limpus 1997). Following the oceanic stage, juveniles recruit to neritic habitats including coral reef, hardbottom, seagrass bed, and cliff-wall (Musick and Limpus 1997). Recent genetic studies suggest that juveniles on foraging aggregations originate from multiple nesting beaches (Bowen et al. 1996; Bass 1999; Díaz-Fernández et al. 1999; Bowen et al. 2007a; Velez-Zuazo et al. 2008), and because hawksbills are commercially valuable, management of mixed stocks has been the subject of considerable controversy (Bowen et al. 2007b; Godfrey et al. 2007; Mortimer et al. 2007a, 2007b).

While movements across geopolitical boundaries attract considerable attention (e.g., Meylan 1999), juvenile hawksbills appear to remain resident on foraging grounds for extended periods (Limpus 1992; van Dam and Diez 1998a; León and Diez 1999; Sanches and Bellini 1999),

where local conditions determine survival. Inwater capture has provided information on size distribution and condition index (León and Diez 1999; Diez and van Dam 2002), and growth rate has proven to be habitat dependent and highly variable among study sites, suggesting variation in time to maturity (León and Diez 1999; Diez and van Dam 2002; IUCN 2002). Thus, monitoring demographic parameters from a variety of locations will aid in understanding population dynamics and evaluating resilience to harvesting.

Studies of hawksbill habitat use and behavior on foraging grounds may also elucidate ecological roles (León and Bjørndal 2002) and susceptibility to threats. For Caribbean hawksbills, ultrasonic tracking, point of capture habitat assessment, and benthic habitat mapping have begun to illuminate home range and habitat use (van Dam and Diez 1998a; León and Diez 1999; Cuevas et al. 2007). Deployment of time depth recorders has provided data on depth utilization (van Dam and Diez 1996, 1997; Blumenthal et al. 2009), yet inwater activities cannot be determined from dive profiles alone (Seminoff et al. 2006). In order to study behavior, increasingly sophisticated

technologies—such as video-linked time depth recorders (Heithaus et al. 2002; Seminoff et al. 2006), multi-sensor archival tags (Wilson et al. 2008), and inter-mandibular angle sensors (Hochscheid et al. 2005; Houghton et al. 2008)—are being developed and applied. However, direct inwater observation (Houghton et al. 2003; Schofield et al. 2006) may represent a complementary and substantially under-utilized method in marine turtle research, considering its potential to offer insights into inwater activities and aid in the interpretation of data gathered through instrumentation.

Despite an increasing number of inwater studies, national and international conservation efforts are hindered by a lack of basic demographic and ecological data on immature hawksbills (Mortimer and Donnelly 2007). While juvenile hawksbills are often sighted in the waters surrounding the Cayman Islands (Bell et al., in press), basic ecology and management needs of this aggregation have not previously been assessed. Here, we present results of a 7-year monitoring program, focused on providing relevant biological data from a Caribbean foraging ground. We conducted a capture–mark–recapture study, integrated point of capture habitat assessments with benthic habitat mapping, collected stranding data, and made direct observations of turtle behavior at sighting. Additionally, in order to supplement our observations, we requested photographs from recreational and professional underwater photographers documenting marine turtle habitat use, diet, and behavior. Thus, through diverse methods, we aimed to elucidate hawksbill management requirements within the foraging ground as well as implications for regional management.

METHODS

Study Site. — The Cayman Islands are located in the western Caribbean Sea, approximate 240 km south of Cuba (Fig. 1). For this study, 2 sampling sites were selected: Bloody Bay, Little Cayman (19°41'N, 80°05'W) and western Grand Cayman (19°18'N, 81°23'W). A narrow shelf surrounding each island consists of coral reef, hardbottom, and other habitats. In many locations, a former seacliff (“miniwall”) begins at depths of 8–10 m, marking the transition from shallow to deep terrace reefs. From the edge of the shelf (beginning at depths of 6–20 m), the near-vertical “reef wall” and deep slope extend to abyssal depths (Logan 1994; Roberts 1994). Both the miniwall and the reef wall are characterized by prolific coral reef colonization (Logan 1994; Roberts 1994).

Capture Methodology. — Hawksbill turtles were hand-captured by snorkelers (who swam in teams of 2 or were towed approximately 10 m behind a small boat). Catch per unit effort was recorded as hawksbills sighted per hour that observers were towed. For each sighting, GPS location, habitat type, water depth, turtle activity, and estimated turtle size were recorded (regardless of whether a turtle was captured). In order to qualitatively supplement

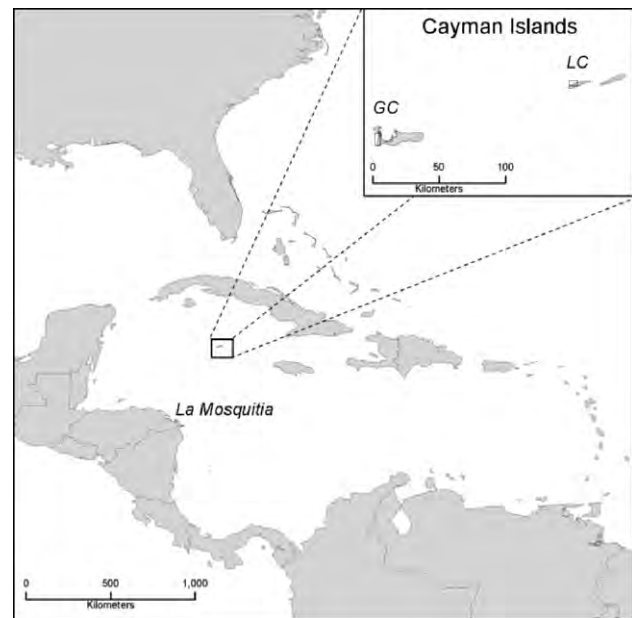


Figure 1. Location of the 3 Cayman Islands in the western Caribbean sea. Inset shows the study areas of western Grand Cayman (GC) and Bloody Bay Little Cayman (LC). One hawksbill turtle tagged in LC was later captured in La Mosquitia, Honduras, suggesting a developmental habitat shift.

observations, we requested photographs of marine turtle habitat use and behavior from underwater photographers.

Tagging. — To allow individual identification, all captured turtles were tagged according to standard protocols: a metal inonel tag was applied to the posterior edge of each front flipper and a Passive Integrated Transponder (PIT) tag was injected into the shoulder muscle (Balazs 1999). Additionally, to prevent individuals from being captured more than once per capture occasion, a white grease pen was used to apply a temporary mark to the carapace of each turtle.

Tag retention for inonel and PIT tags was calculated according to the equation $P_i = b_i / (a_i + b_i)$, where i is the elapsed time in whole years since tag application, P_i is the probability of tag loss i years after attachment, a_i is the number of tags present i years after attachment, and b_i is the number of tags lost i years after attachment (Limpus 1992; Bellini 2001). All tags were marked with a return address: the Archie Carr Center for Sea Turtle Research (from 2000 to 2002) and Wider Caribbean Sea Turtle Conservation Network (from 2002 to present). For each recaptured turtle, time at large was noted and straight-line distance from GPS capture site to GPS recapture site was calculated using Hawth's Analysis Tools for ESRI ArcGIS.

Size Frequencies, Condition Index, and Growth. — Measurements of mass and straight carapace length (SCL, measured from the center of the nuchal notch to the tip of the posterior-most marginal scute) were used to determine size distribution and calculate morphometric relationships (van Dam and Diez 1998b), growth rate (Bjorndal and Bolten 1988), and body condition index (mass/SCL^3)

(Bjorndal et al. 2000). In order to determine the accuracy with which turtle size could be estimated inwater, for captured turtles we compared estimated size (at first inwater sighting) and measured size, calculating mean difference from the absolute values.

Habitat Mapping. — Benthic habitat maps were produced from orthorectified and georectified true color aerial photography (0.12 m resolution), using the NOAA habitat digitizer extension for ESRI ArcGIS v. 9.2. Habitat categories included coral reef (spur and groove, aggregate reef, patch reef, and reef wall), colonized hardbottom (10%–70% colonization by sponges and gorgonians), uncolonized hardbottom (< 10% colonization), rubble, and sand.

Threats. — We collected data on hawksbill turtles captured in the legal marine turtle fishery (Bell et al. 2006) as well as on injured or dead hawksbills reported to Department of Environment (the agency responsible for responding to marine turtle strandings in the Cayman Islands). Where possible, necropsies were performed to determine cause of death.

RESULTS

From 2000 to 2007, we made 206 captures of 135 individual hawksbill turtles in Little Cayman and 103 captures of 97 hawksbills in Grand Cayman. Species composition of the aggregation was primarily hawksbills: limited sightings and captures were made of juvenile green turtles at both sites, and one juvenile loggerhead was sighted but not captured in Little Cayman. Catch per unit effort (mean $\pm$ SD) in Little Cayman (3.15 ± 0.98 hawksbill sightings per hour towing) was significantly greater than Grand Cayman (1.6 ± 0.45 hawksbill sightings per hour towing) (Mann Whitney $U = 9.000$, $p = 0.0001$).

Size Distribution and Body Condition Index. — Straight carapace length (mean $\pm$ SD) was 33.7 ± 8.6 cm for hawksbills captured in Little Cayman (Fig. 2a, $n = 125$ individuals for which a measure of notch-to-tip straight carapace length was obtained) and 31.4 ± 7.4 cm for hawksbills captured in Grand Cayman (Fig. 2b, $n = 93$ individuals), and size range for the aggregation was 20.5–62.6 cm. Condition index (10^{-4} kg/cm³) for Little Cayman (1.25 ± 0.17) and Grand Cayman (1.24 ± 0.18) was not significantly different (Mann Whitney $U = 7824$, $p > 0.05$, $n = 268$). Comparison of estimated with actual size for captured turtles indicated that size could typically be estimated to within 10 cm (mean accuracy $\pm$ SD: 4.66 ± 3.67 cm, $n = 85$).

Tag Retention and Recaptures. — Over the duration of the study, tag retention was nearly 100% for each tag (inconel, 98%; PIT, 100%), ensuring near certainty that triple-tagged turtles would remain individually identifiable for extended periods. In Little Cayman, ultrasonic tracking was used to facilitate recovery of hawksbills instrumented with time depth recorders, resulting in recapture of 19 of

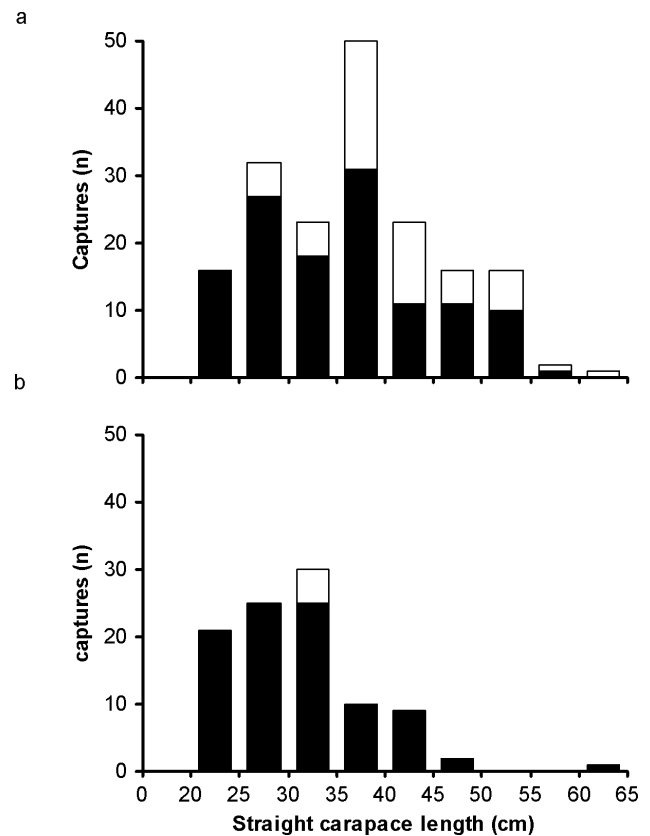


Figure 2. Straight carapace length for hawksbill turtles captured (filled bars) and recaptured (unfilled bars) in a) Little Cayman and b) Grand Cayman.

21 individuals (Blumenthal et al. 2009). Excluding recaptures facilitated by ultrasonic tracking, in Little Cayman 72% of hawksbills were captured once, 19% were captured twice, 7% were captured 3 times, 2% were captured 4 times, and 1% were captured 5 times. In Grand Cayman, 88% were captured once and 12% were captured twice.

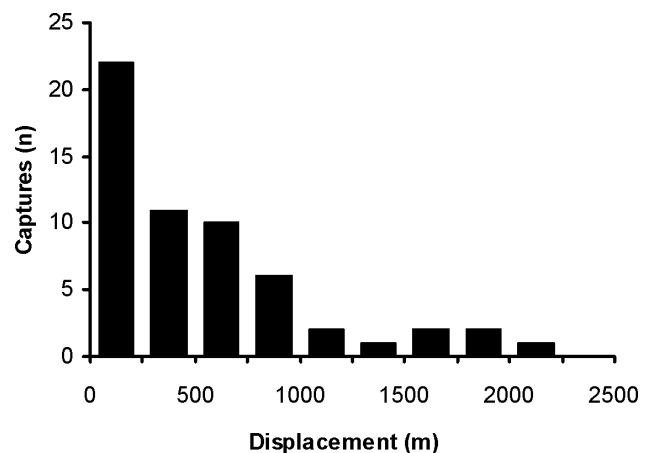


Figure 3. Straight-line displacement between capture and recapture points for hawksbill turtles. There was no significant correlation between displacement and turtle size (straight carapace length) or between displacement and time at large. Data for Little Cayman and Grand Cayman were combined.

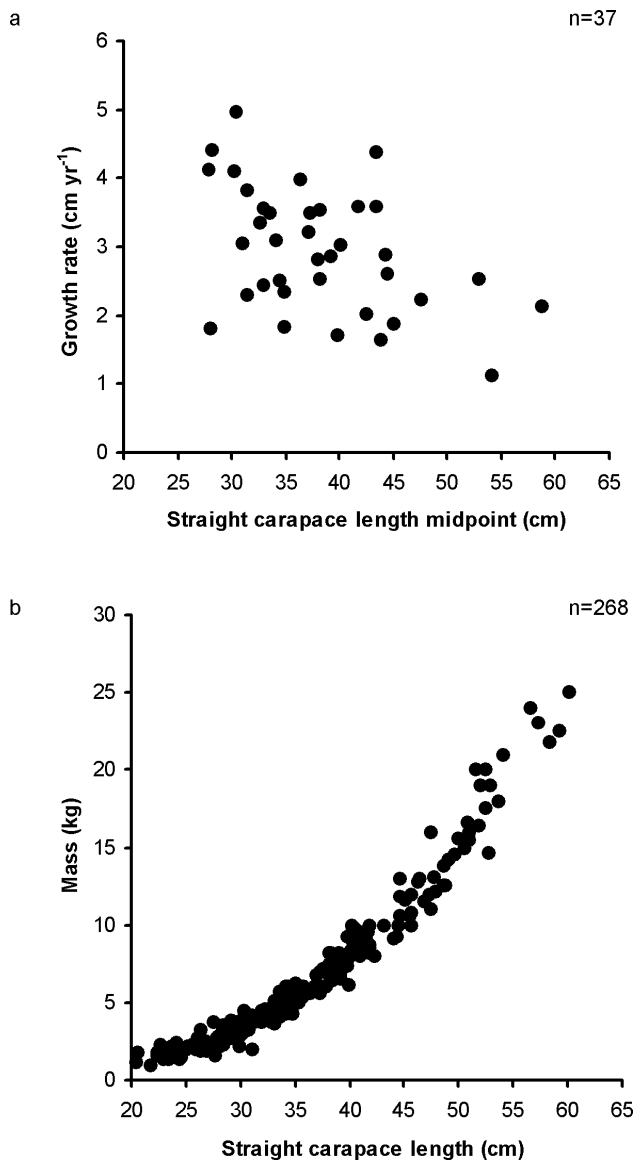


Figure 4. a) Turtle size (straight carapace length) and carapace length growth rate from first capture to last capture (cm/y) were significantly correlated. b) A highly significant correlation was observed between body mass and straight carapace length. Data for Little Cayman and Grand Cayman were combined.

Local recaptures occurred at intervals ranging from 11 days to 7.3 years. Distance traveled (mean $\pm$ SD) from first capture to last capture was 545 ± 514 m, range 2–2080 m, $n = 57$ (Fig. 3). There was no correlation between distance traveled and time at large (Spearman's $r = 0.06$, $p > 0.05$) or distance traveled and turtle size (midpoint between straight carapace length at capture and straight carapace length at recapture) (Spearman's $r = 0.09$, $p > 0.05$). One hawksbill turtle was tagged in Little Cayman and recaptured 6.7 years later in La Mosquitia, Honduras (likely as an opportunistic capture in an artisanal lobster fishery). Size of this animal at original capture in the Cayman Islands was 46.5 cm straight carapace length and size at recapture was not reported.

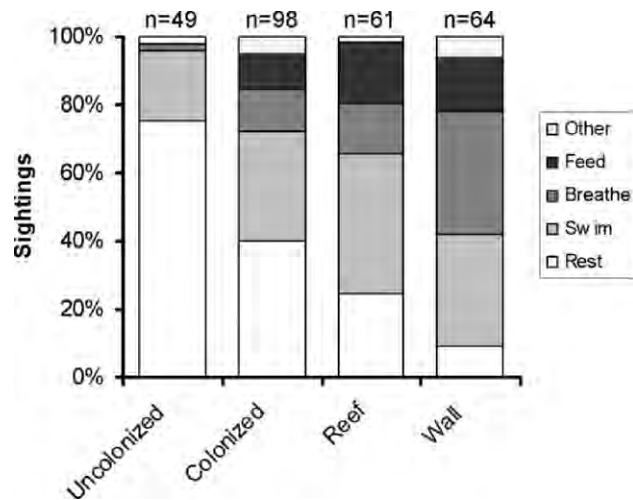


Figure 5. Activity with respect to habitat (uncolonized hardbottom, colonized hardbottom, reef, and reef wall). Turtles were observed feeding in colonized hardbottom, reef, and wall, while resting was more commonly observed in uncolonized habitats. Data for Little Cayman and Grand Cayman were combined.

Growth and Morphometrics. — Mean growth rate (of individuals, from first capture to last capture) was 3.0 ± 0.9 cm/y ($n = 37$ increments of > 1 year). Straight carapace length and growth rate were significantly correlated (Spearman's $r = -0.43$, $p < 0.01$) (Fig. 4a), and the correlation between straight carapace length and mass was highly significant (linear regression, $r = 0.96$, $p < 0.0001$) (Fig. 4b).

Behavior. — A wide range of behaviors were recorded at sighting. Turtles were observed resting (33%), swimming (31%), breathing (20%), feeding (10%), hovering (3%), fleeing (2%), and fighting (1%) ($n = 317$ observations). We were able to broadly assess how turtle activity varied according to habitat (Fig. 5, $n = 272$ observations for which both habitat and activity were obtained): turtles fed in colonized hardbottom, miniwall, reef, and reef wall, while resting was common in uncolonized habitats. In deeper areas (such as off edge of the wall in Little Cayman), turtles were more likely observed breathing at the surface.

In order to qualitatively supplement behavioral observations, more than 500 photographs documenting habitat use and behavior were obtained from underwater photographers. During the day, hawksbills were observed in colonized hardbottom (Fig. 6a), reef (Fig. 6b), and reef wall (Fig. 6c) and at night, hawksbills were seen resting on the bottom and wedged under ledges (Fig. 6d). Feeding behaviors included scraping the surface of the reef (Fig. 6e) and eating sponges [primarily the leathery barrel sponge (*Geodia neptuni*)]. Gray angelfish (*Pomacanthus arcuatus*), French angelfish (*Pomacanthus paru*), and queen angelfish (*Holocanthus ciliaris*) were documented feeding on sponges in association with hawksbills, nibbling sponges where the interior tissue was exposed (Fig. 6f) or eating crumbs dropped by turtles (Fig. 6g).



Figure 6. Habitat use, feeding behaviors and interspecies feeding associations of hawksbill turtles in the Cayman Islands: a) colonized hardbottom; b) coral reef at the edge of the miniwall; c) reef wall; d) nocturnal resting wedged under a ledge; e) hawksbill turtle scraping reef face; f) angelfish feeding on interior sponge tissue exposed a hawksbill; g) angelfish feeding on crumbs dropped by a hawksbill; h) hawksbill feeding on thimble jellyfish. Photographers: a) Michelle Foss, b) Gary Tayler, c) Patrick Weir, d) Eric Friberg, e) Gary Tayler, f) Katie and Chris Alpers, g) Joanna and Chris Humphries, h) Alexander Mustard.

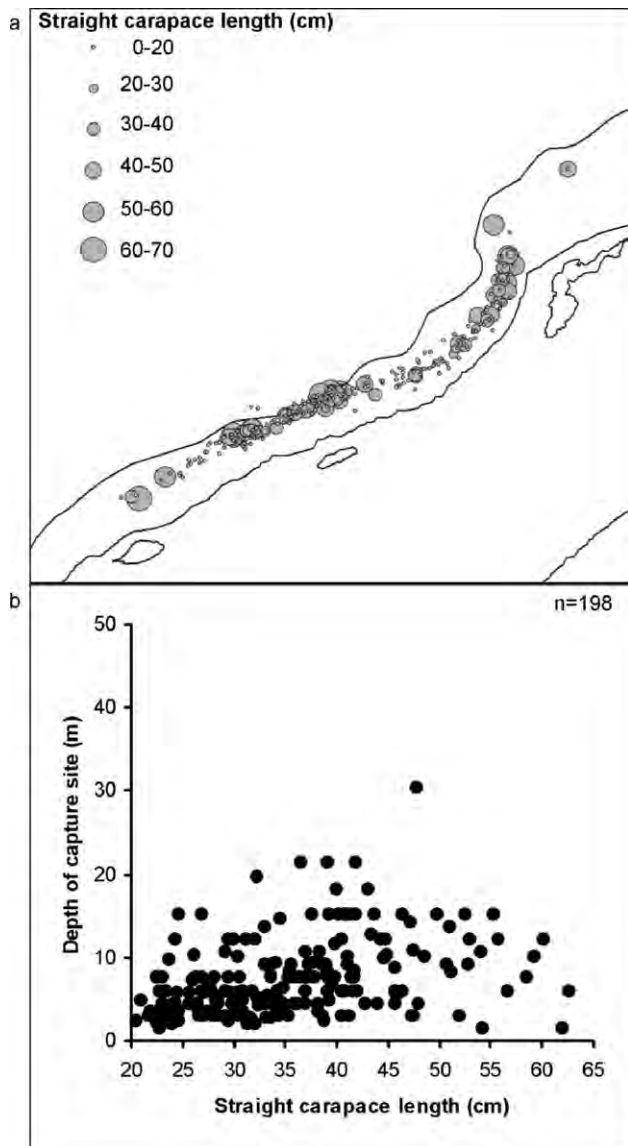


Figure 7. a) Sighting locations for hawksbill turtles in Little Cayman, scaled according to turtle size (estimated straight carapace length), show lack of horizontal habitat structuring. b) The significant relationship between turtle size (straight carapace length) and depth of water at the capture site indicates size-related vertical structuring.

Additionally, hawksbills were observed feeding on occasional summer swarms of thimble jellyfish (*Linuche unguiculata*) (Fig. 6h).

Habitat Use. — When GPS sighting locations were scaled according to turtle size, there was no apparent structuring of horizontal habitat use (Fig. 7a). However, a weak but highly significant correlation was observed between turtle size and depth of the water at capture (Little Cayman, Spearman's $r = 0.35$, $p < 0.001$; Grand Cayman, Spearman's $r = 0.44$, $p < 0.001$) (Fig. 7b).

In Little Cayman, turtles were sighted in coral reef (20%), reef wall (26%), colonized hardbottom (39%), and uncolonized hardbottom, rubble, or sand (14%). In Grand Cayman, turtles were sighted in coral reef (57%),

colonized hardbottom (17%), and uncolonized hardbottom, rubble, or sand (26%). When spatial data were integrated with benthic habitat mapping, sightings and captures of hawksbill turtles were dispersed in Grand Cayman (Fig. 8a) and clustered near the miniwall and reef wall in Little Cayman (Fig. 8b).

Threats. — Injury and mortality ($n = 41$ documented incidents during the course of the study) resulted from anthropogenic (61%), natural (30%), and unknown (10%) sources. Anthropogenic threats included legal (24%) and illegal take (17%), vessel collision (2%), and incidental capture, including entanglement in fishing line and ingestion of fishhooks (17%). Natural sources included hurricanes (15%) and possible shark-inflicted wounds (15%). Additionally, photographic evidence was obtained documenting the presence of hawksbill scutes in the stomach of a tiger shark (*Galeocerdo cuvier*) captured by fishermen in Grand Cayman in 2002. There is also potential for anthropogenic disturbance: Bloody Bay is heavily utilized for recreational diving and 98% of hawksbill sightings in Bloody Bay occurred within 200 m of a dive mooring.

DISCUSSION

Demographics. — Size distribution of captured hawksbills suggests that the Cayman Islands provide developmental habitat. Generally, hawksbills are first documented on foraging grounds at 20–35 cm curved carapace length (Musick and Limpus 1997; van Dam and Diez 1998b; León and Diez 1999; Sanches and Bellini 1999; Seminoff et al. 2003), indicating varying periods of oceanic drifting prior to recruitment to neritic habitats (Musick and Limpus 1997). For Cayman hawksbills, small size at initial capture suggests that the oceanic phase may be relatively brief, and the continued capture of small, unmarked juveniles throughout our study implies continual recruitment. Indeed, significant growth in some Caribbean hawksbill breeding populations has been observed (e.g., Beggs et al. 2007)—a trend that may ultimately be detected on foraging aggregations.

In some areas, adult and juvenile hawksbill turtles share foraging grounds (Limpus 1992; Broderick et al. 1994; Musick and Limpus 1997), while in others, the larger size classes are lacking (León and Diez 1999). The absence of the larger size classes may represent an artifact of past exploitation (León and Diez 1999), but emerging flipper tagging (Meylan 1999; Bellini et al. 2000; Grossman et al. 2007) and limited satellite tracking results (Whiting and Koch 2006) suggest migrations from juvenile to adult foraging grounds. In the Cayman Islands, the predominance of juveniles and a tag return from Honduras suggests developmental migration of sub-adults—as is also suspected for headstarted green turtles released from the Cayman Turtle Farm (Bell et al. 2005).

Within the Cayman Islands, local recapture of marked hawksbills occurred over periods of several years,

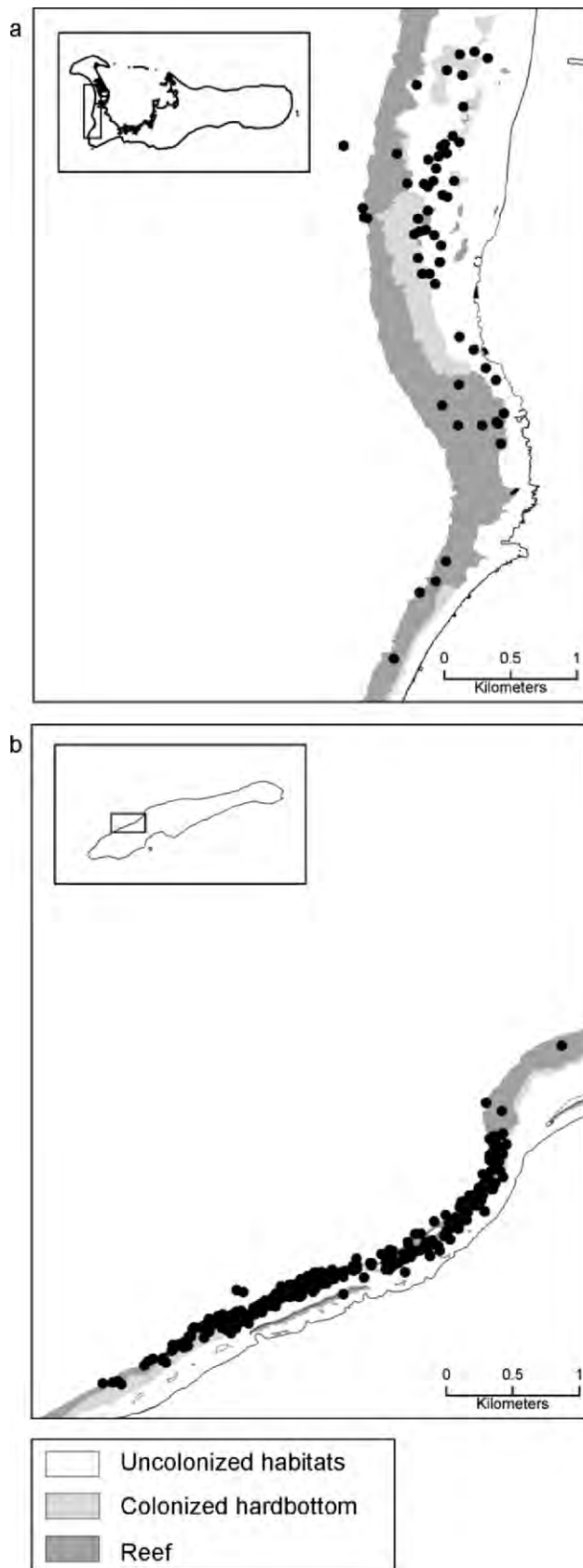


Figure 8. Sighting and capture locations for hawksbill turtles with respect to habitats within the study areas of a) western Grand Cayman (GC) and b) Bloody Bay, Little Cayman (LC). Captures in LC were clustered along vertical features (miniwall and reef wall) while captures in GC were more widely dispersed. Insets show the locations and geographic limits of the study areas.

indicating year round residence and long-term site fidelity in some individuals. Compared to sites in Puerto Rico (Diez and van Dam 2002), body condition index was relatively high, but growth rate was slow. Because of slow growth and extended residence in juvenile foraging habitat, anthropogenic and natural threats will have a cumulative impact during the years that hawksbills are present in the Cayman Islands—and stocks may have less resilience to exploitation.

Behavior. — Turtle activity varied according to habitat: resting was frequently observed in uncolonized areas and resting, swimming, and feeding were observed in coral reef, reef wall, and colonized hardbottom habitats. In deeper waters, turtles were more likely to be observed breathing, partly because when submerged they were likely out of view, but perhaps also because they spent more time at the surface preparing for or recovering from deep dives. Notably, little feeding was observed in the Cayman Islands in comparison to Puerto Rico, where turtles fed almost continuously (van Dam and Diez 1997). While turtles feeding by scraping the reef may be more easily disturbed than turtles feeding on sponges, for the most part, feeding turtles did not perceptibly react to the presence of observers or discontinue feeding.

Though hawksbills are generally considered solitary, aggressive interactions have been documented in captivity, when 2 captured hawksbills were placed in a boat together (Sanches and Bellini 1999) and in the wild, when 2 hawksbills attempted to feed on the same sponge (van Dam and Diez 2000). In Little Cayman, 2 aggressive—possibly territorial—interactions between hawksbills were observed along the reef wall: in both incidences, hawksbills were observed biting a conspecific.

Images from underwater photographers offered an opportunity to qualitatively enhance understanding of hawksbill habitat use and behavior. Turtles were photographically documented at a variety of depths (including those beyond the range of capture efforts). During the day, hawksbills were often observed in colonized hardbottom, reef, and reef wall, and at night, they were seen wedged under ledges. Thus, despite positive buoyancy, hawksbills may maximize dive duration and minimize surfacing effort by “assisted resting” (Houghton et al. 2003) in shallow water with fully inflated lungs.

Observations of foraging behavior included feeding on sponges and scraping the surface of the reef (a behavior which likely represents feeding on encrusting sponges, invertebrates or algae; Carr and Stanczyk 1975). Occasional consumption of thimble jellyfish was also photographically documented. As jellyfish are digested more rapidly than other food items, they may be under-represented in samples of stomach contents. Thus, like deployment of animal-borne video cameras (Heithaus et al. 2002), photo-documentation can provide dietary insights. Additionally, a commensal feeding relationship was noted between hawksbills and angelfish, in which angelfish nibbled

sponges where hawksbill feeding had exposed the interior tissues, or fed on crumbs dropped by turtles.

Many Caribbean reefs, including those in the Cayman Islands, are heavily used for dive tourism. While ecological impacts of recreational scuba diving (Tratalos and Austin 2001) and potential disturbance of marine turtles by inwater activities (Meadows 2004) are cause for concern, there is a corresponding but under-utilized potential to harness recreational divers for biology and conservation (Bell et al., in press). By requesting photographs from scuba divers, we were able to make use of the immense number of hours they spend observing the behaviors of marine turtles in the wild, without relying on anecdotal reports. Photographs collected from divers during this project offered insights into hawksbill diet, habitat use, and behavior—highlighting the utility of this technique in the study of charismatic marine animals.

Habitat Use. — For hawksbills in the Cayman Islands, distance traveled from capture to recapture was comparable to other studies (van Dam and Diez 1998a; León and Diez 1999), and individual turtles were recaptured in multiple habitats, suggesting that all of these must be encompassed in the design of marine protected areas. There was no apparent structuring of home range according to turtle size, but significant vertical structuring was observed, with larger individuals generally captured in deeper waters. In Little Cayman, hawksbill sightings and captures were clustered within narrow bands of highly colonized habitat along the miniwall (former seacliff marking the transition from shallow to deep terrace) and reef wall (near-vertical shelf edge). Given the narrow shelf, diving down the face of the reef wall substantially increases available habitat, and may buffer against anthropogenic and natural degradation of shallow habitats (Blumenthal et al. 2009). Thus, as in other areas (Limpus 1992), vertical features may provide critical habitat, yet these are necessarily under-represented on 2-dimensional habitat maps. Hawksbill density (catch per unit effort) was significantly greater in Little Cayman. However, caution must be taken in comparing catch per unit effort in this study with other studies, unless a similar method of towing observers is used.

Threats. — Though historically the Cayman Islands were noted for abundant nesting by green, loggerhead, leatherback, and hawksbill turtles (Lewis 1940), migratory green and loggerhead nesting populations are now critically reduced, and leatherback and hawksbill nesting appears to have been extirpated (Aiken et al. 2001; Blumenthal et al. 2006; Bell et al. 2007). Nevertheless, adult and subadult turtles, including hawksbills, were captured in a traditional turtle fishery (Bell et al. 2006). In 2008, the Cayman Islands government modified size limits for legal marine turtle take—protecting vulnerable breeding populations but allowing smaller turtles to be targeted for the first time in more than 20 years. However, a ban on legal take of hawksbill turtles has been implemented, based on results of this study—showing slow growth rate,

long-term residence, and resultant vulnerability to anthropogenic threats. Thus, by collecting diverse data on demographics, habitat use, behavior, and threats to hawksbills in the Cayman Islands, we have informed local management and set a baseline for an index inwater monitoring site in the western Caribbean.

Caveats and Considerations for Future Study

Our results illustrate how capture methods, survey design, and selection of study sites may profoundly influence findings. Study sites differed significantly in physical configuration: in Little Cayman, we were able to search the narrow shelf from near shore to the shallow drop-off, while in Grand Cayman, the drop-off began in deeper water. Likely due to lack of search effort in highly suitable deep habitats near the shelf edge, captures in Grand Cayman were more widely dispersed and fewer large turtles were captured. Generally, search effort in Little Cayman was more complete and capture occasions were more efficient (i.e., catch per unit effort was higher). Also, in Little Cayman, a much higher proportion of turtles were recaptured, allowing estimates of growth and home range to be made. However, while Little Cayman offered substantially greater insights into demographic parameters, it is possible that these results are not representative of all areas. Therefore, a balance must be found between monitoring a larger number of index sites—and diluting demographic data by providing fewer opportunities to capture and recapture individuals.

In this study, effort was not uniform across habitat types, as we aimed to maximize number of captures by searching more suitable areas. Additionally, a limited number of captures were made per capture occasion, representing an efficient survey design given resources and personnel, but precluding present estimation of population size and survival by capture–mark–recapture modeling. In the future—and in designing new monitoring programs—longer capture occasions could be undertaken, effort could be expanded to include deeper waters using scuba methodology, and habitat preference could be quantified using a random survey methodology. Based on our calculations of size estimation accuracy, uncaptured turtles can be assigned to 10 cm size classes—opening up the possibility of further studies of habitat use via sighting transects.

ACKNOWLEDGMENTS

We thank the following photographers for generously providing their images for Fig. 6: Michelle Foss, Gary Tayler, Patrick Weir (<http://www.digitaldiver.biz>), Eric Friberg, Gary Tayler, Katie and Chris Alpers (<http://www.indigodivers.com>), Joanna and Chris Humphries, and Alexander Mustard (<http://www.amustard.com>). For invaluable logistical support and assistance with fieldwork, we thank Department of Environment research, adminis-

tration, operations, and enforcement staff and numerous volunteers. Work in the Cayman Islands and the United Kingdom was generously supported by the National Fish and Wildlife Foundation (NFWF), the Turtles in the Caribbean Overseas Territories (TCOT) project at University of Exeter, the UK Department of Environment, Food and Rural Affairs (DEFRA), the National Environment Research Council (NERC), the European Social Fund, and the Foreign and Commonwealth Office for the Overseas Territories. We also acknowledge support to Janice Blumenthal (University of Exeter postgraduate studentship and the Darwin Initiative). The manuscript was improved by the comments from Robert van Dam and anonymous reviewers.

LITERATURE CITED

- AIKEN, J.J., GODLEY, B.J., BRODERICK, A.C., AUSTIN, T., EBANKS-PETRIE, G., AND HAYS, G.C. 2001. Two hundred years after a commercial marine turtle fishery: the current status of marine turtles nesting in the Cayman Islands. *Oryx* 35(2):145–151.
- BALAZS, G.H. 1999. Factors to consider in the tagging of sea turtles. In: Eckert, K.L., Bjorndal, K.A., Abreu-Grobois, F.A., and Donnelly, M. (Eds.). Washington, DC: Research and Management Techniques for Capturing and Handling Turtles, IUCN/SSC Marine Turtle Specialist Group Publication 4, pp. 101–109.
- BASS, A.L. 1999. Genetic analysis to elucidate the natural history and behavior of hawksbill turtles (*Eretmochelys imbricata*) in the wider Caribbean: a review and re-analysis. *Chelonian Conservation and Biology* 3:195–199.
- BEGGS, J.A., HORROCKS, J.A., AND KRUEGER, G.H. 2007. Increase in hawksbill sea turtle *Eretmochelys imbricata* nesting in Barbados, West Indies. *Endangered Species Research* 3: 159–168.
- BELL, C.D., BLUMENTHAL, J.M., AUSTIN, T.J., EBANKS-PETRIE, G., BRODERICK, A.C., AND GODLEY, B.J. Harnessing recreational divers for the collection of sea turtle data around the Cayman Islands. *Tourism in Marine Environments*. (in press).
- BELL, C.D., BLUMENTHAL, J.M., AUSTIN, T.J., SOLOMON, J.L., EBANKS-PETRIE, G., BRODERICK, A.C., AND GODLEY, B.J. 2006. Traditional Caymanian fishery may impede local marine turtle population recovery. *Endangered Species Research* 2:63–69.
- BELL, C.D., PARSONS, J., AUSTIN, T.J., BRODERICK, A.C., EBANKS-PETRIE, G., AND GODLEY, B.J. 2005. Some of them came home: the Cayman Turtle Farm headstarting project for the green turtle *Chelonia mydas*. *Oryx* 39:137–148.
- BELL, C.D., SOLOMON, J.L., BLUMENTHAL, J.M., AUSTIN, T.J., EBANKS-PETRIE, G., BRODERICK, A.C., AND GODLEY, B.J. 2007. Monitoring and conservation of critically reduced marine turtle nesting populations: lessons from the Cayman Islands. *Animal Conservation* 10:39–47.
- BELLINI, C. 2001. Metal tag loss in wild juvenile hawksbill sea turtles (*Eretmochelys imbricata*). *Herpetological Review* 32: 173.
- BELLINI, C., SANCHES, T.M., AND FORMIA, A. 2000. Hawksbill turtle tagged in Brazil captured in Gabon, Africa. *Marine Turtle Newsletter* 87:11–12.
- BJORNDAL, K.A. AND BOLTEN, A.B. 1988. Growth rates of immature green turtles, *Chelonia mydas*, on feeding grounds in the Southern Bahamas. *Copeia* 1988:555–564.
- BJORNDAL, K.A., BOLTEN, A.B., AND CHALLOUPKA, M.Y. 2000. Green turtle somatic growth model: evidence for density dependence. *Ecological Applications* 10:269–282.
- BLUMENTHAL, J.M., AUSTIN, T.J., BOTHWELL, J.B., BRODERICK, A.C., EBANKS-PETRIE, G., OLYNIK, J.R., ORR, M.F., SOLOMON, J.L., WITT, M.J., AND GODLEY, B.J. 2009. Diving behavior and movements of juvenile hawksbill turtles *Eretmochelys imbricata* on a Caribbean coral reef. *Coral Reefs* 28(1):55–65.
- BLUMENTHAL, J.M., SOLOMON, J.L., BELL, C.D., AUSTIN, T.J., EBANKS-PETRIE, G., COYNE, M.S., BRODERICK, A.C., AND GODLEY, B.J. 2006. Satellite tracking highlights the need for international cooperation in marine turtle management. *Endangered Species Research* 2:51–61.
- BOWEN, B.W., BASS, A.L., GARCIA RODRIGUEZ, A., DIEZ, C.E., VAN DAM, R., BOLTEN, A., BJORNDAL, K.A., MIYAMOTO, M.M., AND FERL, R.J. 1996. Origin of hawksbill turtles in a Caribbean feeding area as indicated by genetic markers. *Ecological Applications* 6:566–572.
- BOWEN, B.W., GRANT, W.S., HILLIS-STARR, Z., SHAVER, D.J., BJORNDAL, K.A., BOLTEN, A.B., AND BASS, A.L. 2007a. Mixed stock analysis reveals the migrations of juvenile hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Sea. *Molecular Ecology* 16:49–60.
- BOWEN, B.W., GRANT, S., HILLIS-STARR, Z., SHAVER, D.J., BJORNDAL, K.A., AND BOLTEN, A.B. 2007b. The advocate and the scientist: debating the commercial exploitation of endangered hawksbill turtles. *Molecular Ecology* 16:3514–3515.
- BRODERICK, D., MORITZ, C., MILLER, J.D., GUINEA, M., PRINCE, R.J., AND LIMPUS, C.J. 1994. Genetic studies of the hawksbill turtle *Eretmochelys imbricata*: evidence for multiple stocks in Australian waters. *Pacific Conservation Biology* 1:123–131.
- CARR, A. 1987. New perspectives on the pelagic stage of sea turtle development. *Conservation Biology* 1:103–121.
- CARR, A. AND STANCYK, S. 1975. Observations on the ecology and survival outlook of the hawksbill turtle. *Biological Conservation* 8:161–172.
- CUEVAS, E., DE LOS ÁNGELES LICEAGA-CORREA, M., AND GARDUÑO-ANDRADE, M. 2007. Spatial characterization of a foraging area for immature hawksbill turtles (*Eretmochelys imbricata*) in Yucatan, Mexico. *Amphibia-Reptilia* 28(3):337–346.
- DÍAZ-FERNÁNDEZ, R., OKAYAMA, T., UCHIYAMA, T., CARRILLO, E., ESPINOSA, G., MARQUEZ, R., DIEZ, C., AND KOIKE, H. 1999. Genetic sourcing for the hawksbill turtle, *Eretmochelys imbricata*, in the Northern Caribbean Region. *Chelonian Conservation and Biology* 3:296–300.
- DIEZ, C.E. AND VAN DAM, R.P. 2002. Habitat effect on hawksbill turtle growth rates on feeding grounds at Mona and Monito Islands, Puerto Rico. *Marine Ecology Progress Series* 234: 301–309.
- GODFREY, M.H., WEBB, G.J.W., MANOLIS, S.C., AND MROSOVSKY, N. 2007. Hawksbill sea turtles: can phylogenetics inform harvesting? *Molecular Ecology* 16:3511–3513.
- GROSSMAN, A., BELLINI, C., FALLABRINO, A., FORMIA, A., MBA, J.M., MBA, J.N., AND OBAMA, C. 2007. Second TAMAR-tagged hawksbill recaptured in Corisco Bay, West Africa. *Marine Turtle Newsletter* 116:26.
- HEITHAUS, M.R., McLASH, J.J., FRID, A., LAWRENCE, M.D., AND MARSHALL, G.J. 2002. Novel insights into green sea turtle behavior using animal-borne video cameras. *Journal of the Marine Biological Association of the UK* 82(6):1049–1050.
- HOCHSCHEID, S., MAFFUCCIA, F., BENTIVEGNA, F., AND WILSON, R.P. 2005. Gulp, wheezes, and sniffs: how measurement of beach movement in sea turtles can elucidate their behavior and ecology. *Experimental Marine Biology and Ecology* 316: 45–53.
- HORROCKS, J.A., VERMEER, L.A., KRUEGER, B., COYNE, M.,

- SCHROEDER, B.A., AND BALAZS, G.H. 2001. Migration routes and destination characteristics of post-nesting hawksbill turtles satellite-tracked from Barbados, West Indies. *Chelonian Conservation and Biology* 4:107–114.
- HOUGHTON, D.R., CALLOW, M.J., AND HAYS, G.C. 2003. Habitat utilization by juvenile hawksbill turtles (*Eretmochelys imbricata*, Linnaeus, 1766) around a shallow water coral reef. *Journal of Natural History* 37:1269–1280.
- HOUGHTON, D.R., CEDRAS, A., MYERS, A.E., LIEBSCH, N., METCALFE, J.D., MORTIMER, J.A., AND HAYS, G.C. 2008. Measuring the state of consciousness in a free-living diving sea turtle. *Journal of Experimental Marine Biology and Ecology* 356:115–120.
- IUCN. 2002. Hawksbill turtles in the Caribbean region: basic biological characteristics and population status. CITES wider Caribbean range state hawksbill turtle dialogue meetings. www.cites.org/common/prog/hbt/consolidated_paper.pdf (accessed 20 September 2008).
- LEÓN, Y.M. AND BJORNDAAL, K.A. 2002. Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. *Marine Ecology Progress Series* 245:249–258.
- LEÓN, Y.M. AND DIEZ, C.E. 1999. Population structure of hawksbill turtles on a foraging ground in the Dominican Republic. *Chelonian Conservation and Biology* 3:230–236.
- LEWIS, C.B. 1940. The Cayman Islands and marine turtle. In: Grant, C. (Ed.). *The herpetology of the Cayman Islands*. Kingston: Bulletin of the Institute of Jamaica Science Series, pp. 56–65.
- LIMPUS, C.J. 1992. The hawksbill turtle, *Eretmochelys imbricata*, in Queensland: population structure within a southern Great Barrier Reef feeding ground. *Wildlife Research* 19:489–506.
- LOGAN, A. 1994. Reefs and lagoons of Cayman Brac and Little Cayman. In: Brunt, M.A. and Davies, J.E. (Eds.). *The Cayman Islands Natural History and Biogeography*. Dordrecht: Kluwer Academic Publishers, pp. 105–124.
- MEADOWS, D. 2004. Behavior of green sea turtles in the presence and absence of recreational snorkelers. *Marine Turtle Newsletter* 103:1–4.
- MEYLAN, A.B. 1999. International movements of immature and adult hawksbill turtles (*Eretmochelys imbricata*) in the Caribbean Region. *Chelonian Conservation Biology* 3: 189–194.
- MORTIMER, J.A. AND DONNELLY, M. 2007. Marine Turtle Specialist Group. 2007 IUCN Red List status assessment hawksbill turtle (*Eretmochelys imbricata*). http://www.iucn-mtsg.org/red_list/ei/index.shtml (accessed 20 September 2008).
- MORTIMER, J.A., DONNELLY, M., MEYLAN, A.B., AND MEYLAN, P.A. 2007a. Critically endangered hawksbill turtles: molecular genetics and the broad view of recovery. *Molecular Ecology* 16:3516–3517.
- MORTIMER, J.A., MEYLAN, P.A., AND DONNELLY, M. 2007b. Whose turtles are they, anyway? *Molecular Ecology* 16:17–18.
- MUSICK, J.A. AND LIMPUS, C.J. 1997. Habitat utilization and migration in juvenile sea turtles. In: Lutz, P.L. and Musick, J.A. (Eds.). *The Biology of Sea Turtles*. Boca Raton, FL: CRC Press, pp. 137–164.
- ROBERTS, H.H. 1994. Reefs and lagoons of Cayman Brac and Little Cayman. In: Brunt, M.A. and Davies, J.E. (Eds.). *The Cayman Islands Natural History and Biogeography*. Dordrecht: Kluwer Academic Publishers, pp. 75–104.
- SANCHES, T.M. AND BELLINI, C. 1999. Juvenile *Eretmochelys imbricata* and *Chelonia mydas* in the Archipelago of Fernando de Noronha, Brazil. *Chelonian Conservation and Biology* 3: 308–311.
- SCHOFIELD, G., KATSELIDIS, K.A., DIMOPOULOS, P., PANTIS, J.D., AND HAYS, G.C. 2006. Behavior analysis of the loggerhead sea turtle *Caretta caretta* from direct in-water observation. *Endangered Species Research* 2:71–79.
- SEMINOFF, J.A., JONES, T.T., AND MARSHALL, G.J. 2006. Underwater behavior of green turtles monitored with video-time-depth recorders: what's missing from dive profiles? *Marine Ecology Progress Series* 322:269–280.
- SEMINOFF, J.A., NICHOLS, W.J., RESENDIZ, A., AND BROOKS, L. 2003. Occurrence of hawksbill turtles, *Eretmochelys imbricata* (Reptilia: Cheloniidae), near the Baja California Peninsula, Mexico. *Pacific Science* 57(1):9–16.
- TRATALOS, J.A. AND AUSTIN, T.J. 2001. Impacts of recreational SCUBA diving on coral communities of the Caribbean island of Grand Cayman. *Biological Conservation* 102:67–75.
- TROENG, S., DUTTON, P.H., AND EVANS, D. 2005. Migration of hawksbill turtles *Eretmochelys imbricata* from Tortuguero, Costa Rica. *Ecography* 28:394–402.
- VAN DAM, R.P. AND DIEZ, C.E. 1996. Diving behavior of immature hawksbills (*Eretmochelys imbricata*) in a Caribbean cliff wall habitat. *Marine Biology* 127:171–178.
- VAN DAM, R.P. AND DIEZ, C.E. 1997. Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. *Coral Reefs* 16:133–138.
- VAN DAM, R.P. AND DIEZ, C.E. 1998a. Home range of immature hawksbill turtles (*Eretmochelys imbricata* (Linnaeus)) at two Caribbean islands. *Journal of Experimental Marine Biology and Ecology* 220:15–24.
- VAN DAM, R.P. AND DIEZ, C.E. 1998b. Caribbean hawksbill turtle morphometrics. *Bulletin of Marine Science* 62:145–155.
- VAN DAM, R.P. AND DIEZ, C.E. 2000. Remote video cameras as tools for studying turtle behavior. In: Abreu-Grobois, F.A., Briseno-Duenas, R., Marquez, R., and Sarti, L. (Compilers). *Proceedings of the Eighteenth International Sea Turtle Symposium*. U.S. Dep. Commer. NOAA Tech. Memo. NMFS-SEFSC-436. pp. 168–169.
- VAN DAM, R.P., DIEZ, C.E., BALAZS, G.H., COLON, L.A.C., McMILLAN, W.O., AND SCHROEDER, B. 2008. Sex-specific migration patterns of hawksbill turtles breeding at Mona Island, Puerto Rico. *Endangered Species Research* 4:85–94.
- VELEZ-ZUAZO, X., RAMOS, W.D., VAN DAM, R.P., DIEZ, C., ABREU-GROBOIS, A., AND McMILLAN, O. 2008. Dispersal, recruitment and migratory behavior in a hawksbill sea turtle aggregation. *Molecular Ecology* 17:839–853.
- WHITING, S.D. AND KOCH, A.U. 2006. Oceanic movement of a benthic foraging juvenile hawksbill turtle from the Cocos (Keeling) Islands. *Marine Turtle Newsletter* 112:15–16.
- WILSON, R.P., SHEPARD, E.L.C., AND LIEBSCH, N. 2008. Prying into the intimate details of animal lives: use of a daily diary on animals. *Endangered Species Research* 4:123–137.

Received: 21 October 2008

Revised and Accepted: 9 February 2009