
VOL. 396, NO. 2
1 JANUARY 2011
ISSN 0022-0981
ELSEVIER
Journal of
EXPERIMENTAL
MARINE BIOLOGY
AND ECOLOGY

Journal of Experimental Marine Biology and Ecology 407 (2011) 122–129

Contents lists available at ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Insights into habitat utilisation of the hawksbill turtle, *Eretmochelys imbricata* (Linnaeus, 1766), using acoustic telemetry

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ARTICLE INFO

Article history:
Received 20 April 2011
Received in revised form 8 July 2011
Accepted 10 July 2011
Available online xxxx

Keywords:
Acoustic telemetry
Belize
Eretmochelys imbricata
Habitat use
Hawksbill turtle
Home range

ABSTRACT

Patterns of distribution, key biometric parameters and home range extent were determined for hawksbill turtles at Lighthouse Reef Atoll (LRA), Belize over two field seasons (16 days, 2009; 30 days, 2010). Relative abundance was determined using 49 sightings transects (≈1 km) distributed across the atoll and of all turtles encountered ($n = 68$), 91% were immature ($CCL_{min} \leq 65$ cm). Habitat type was significantly correlated with abundance, with more turtles encountered on the coral reef than in the lagoon (GzLMM, $\chi^2_2 = 6.85$, $p < 0.05$; CPUE reef = 1.41 turtles h^{-1}, CPUE lagoon = 0.62 turtles h^{-1}). Hawksbills were also significantly more abundant within protected areas (GzLMM, $\chi^2_1 = 8.69$, $p < 0.05$; CPUE Blue Hole Natural Monument (BHNM) = 2.96 turtles $person^{-1}$ h^{-1}; CPUE Half Moon Caye Natural Monument (HMCNM) = 2.34 turtles h^{-1}; outside boundaries = 0.88 turtles h^{-1}). Of 26 captures, 19 focal individuals were equipped with ultrasonic transmitters for active acoustic telemetry, and tracked for 6–25 days ($n = 10$, 2009; $n = 9$, 2010). Spatial habitat utilisation was found to be highly variable, with large areas of overlap between distinct home ranges. Home range averaged 31.2 ha ± 32.6 (range 5.1–111.3 ha) for the juveniles that were successfully tracked ($n = 15$), with maximum displacement in the order of 1.8 km ± 1.0 (range 0.5–4.0 km) and net displacement at 1.2 km ± 0.9. This offshore atoll constitutes an important developmental habitat for the regional population and although our tracking durations were limited, home range of juvenile hawksbills at this site is significantly more expansive than that documented elsewhere.

1. Introduction

Investigating marine vertebrate spatial ecology is problematic owing to the life history traits of focal taxa and the challenges of conducting research in the marine environment. Recent technological innovations in biotelemetry and biologging have considerably widened the scope of investigation (Cooke et al., 2004; Ropert-Coudert et al., 2009; Wilson et al., 2008). Satellite telemetry has become the prevalent method for tracking many marine megavertebrates (Coyne and Godley, 2005; Hart and Hyrenbach, 2009), but certain caveats are inherent in its application. Limitations in spatiotemporal accuracy preclude its usage for high-resolution habitat utilisation studies (Cooke, 2008; Hays et al., 2001; Yasuda and Arai, 2005), tags often fail (Hays et al., 2007) and surfacing is required for signal transmission (Cooke et al., 2004; Wilson et al., 2005). Emergent GPS-based tracking technologies generate data of improved spatial accuracy (Hazel, 2009; Schofield et al., 2007; Sims et al., 2009; Witt et al., 2010b) and require a surfacing duration of only milliseconds (Witt et al., 2010b). This rapid acquisition of GPS ephemeris has facilitated high-resolution habitat utilisation studies through the generation of up to 100 fixes per day for periods of up to a year or greater (Schofield et al., 2007; Schofield et al., 2010a; Senko et al., 2010).

Acoustic telemetry is a viable alternative method for use over limited spatiotemporal scales. As this method does not require surfacing for signal propagation or recapture for data retrieval (Arnold and Dewar, 2001; Sibert, 2001), it has primarily been used as a tool for fisheries management, particularly in informing MPA design (e.g. bluespine unicornfish *Nasa unicornis*, Meyer and Holland, 2005). Over recent decades, it has been subject to extensive cross-taxa utilisation in marine vertebrate spatial ecology (e.g. tiger sharks, *Galeocerdo cuvier*, Heithaus et al., 2002; green turtle, *Chelonia mydas*, Seminoff et al., 2002), and has generated insights of applied conservation value (e.g. active acoustic telemetry, Lowe et al., 2003; Meyer et al., 2000; Blumenthal et al., 2009a; passive acoustic telemetry, Parsons et al., 2003; Garla et al., 2006).

As the largest spongivore, the circum-tropically distributed (van Dam and Diez, 1997) hawksbill turtle could be regarded as a keystone species in coral reef habitats (Blumenthal et al., 2009a; Jackson, 1997; Léon and Bjorndal, 2002). At some sites, the hawksbill selects primarily for *Chondrilla nucula* (Bjorndal and Jackson, 2003; Léon and Bjorndal, 2002). This widely-distributed Caribbean sponge species takes place in

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0022-0981/$ – see front matter © 2011 Published by Elsevier B.V.
doi:10.1016/j.jembe.2011.07.008

40–50% of coral–sponge interactions and would overgrow the majority of corals in the absence of spongivory (Hill, 1998). At historical population density, spongivores such as the hawksbill turtle could therefore have played an instrumental role in the maintenance of biodiversity on Caribbean coral reefs (Bjorndal and Jackson, 2003) which are now considered to be in critical decline (Bellwood et al., 2004; Gardner et al., 2003; Pandolfi et al., 2003).

Anthropogenically-mediated threats have caused severe depletion of hawksbill populations in 22 of the 26 geopolitical units in the Caribbean for which data are available (Meylan, 1999; Troeng et al., 2005). However, nesting populations in some of the largest hawksbill rookeries in the Caribbean have shown significant growth in recent decades (Barbados, Beggs et al., 2007; Mona Island, Van Dam et al., 2008; Antigua, Richardson et al., 2006). This population recovery has been attributed to a reduction in juvenile and sub-adult mortality both nationally and regionally (Beggs et al., 2007) and linked to successful conservation initiatives (Van Dam et al., 2008).

There exists a relative paucity of knowledge of hawksbill spatial ecology when compared with the body of literature on other cheloniids. Habitat utilisation has been studied using direct observation (Houghton et al., 2003); point of capture habitat assessment and benthic habitat mapping (Cuevas et al., 2007); mark-recapture methodologies (Blumenthal et al., 2009b; Léon and Diez, 1999; van Dam and Diez, 1998), acoustic tracking (Blumenthal et al., 2009a; van Dam and Diez, 1998) and the use of Time-Depth Recorders (TDRs; Blumenthal et al., 2009a; van Dam and Diez, 1996; van Dam and Diez, 1997; Witt et al., 2010a). It has been postulated that individuals maintain a limited home range area (Blumenthal et al., 2009b; van Dam and Diez, 1997; van Dam and Diez, 1998) and exhibit specific site fidelity (Léon and Diez, 1999), particularly in selecting a nocturnal resting site (Blumenthal et al., 2009a; van Dam and Diez, 1997). These conclusions have, however, been generated from studies conducted at few locations. Anecdotal reports suggest that Lighthouse Reef Atoll (LRA), Belize, could be of potential importance for the regional hawksbill population. In order to augment the current understanding of hawksbill spatial ecology and assess the status of the population utilising LRA, we set out to i) determine patterns in relative spatial abundance and establish key biometric parameters of the population, and ii) ascertain extent of home range using active acoustic telemetry.

2. Materials and methods

2.1. Study site

Lighthouse Reef Atoll (LRA) is the most remote of three offshore coral atolls in the Belizean part of the Mesoamerican barrier reef system. It is located 75 km to the east of Belize City and is approximately 45 km long and 10 km wide. Within its coral-rimmed perimeter, LRA encompasses a shallow lagoon containing six small cayes and two no-take marine protected areas (MPAs), Blue Hole Natural Monument (BHNM) and Half Moon Caye Natural Monument (HMCNM) (Fig. 1). These MPAs are managed by the Belize Audubon Society (BAS, 2007) and form part of the Belize Barrier Reef Reserve System, designated a UNESCO World Heritage Site in 1996.

Active acoustic telemetry was predominantly carried out to the west of Long and Hat Cayes, within a ~5 km section of the western (leeward) forereef that spans approximately 40 km (Fig. 1). The western forereef is of variable width, approximately 300 m on average. It is comprised of a shallow reef crest, which occasionally breaks the surface, a forereef slope of variable depth, and a pronounced escarpment or wall at its westernmost extent. This escarpment, known here as the forereef edge, rapidly drops from ca. 15 m to over 500 m depth. The reef habitat surrounding HMCNM is composed of 30.7% coral cover, 24.7% macroalgal cover and 2.74% sponge cover, with *Montastraea annularis* and *Agaricia agaricites* the dominant coral species (Graham et al., 2005).

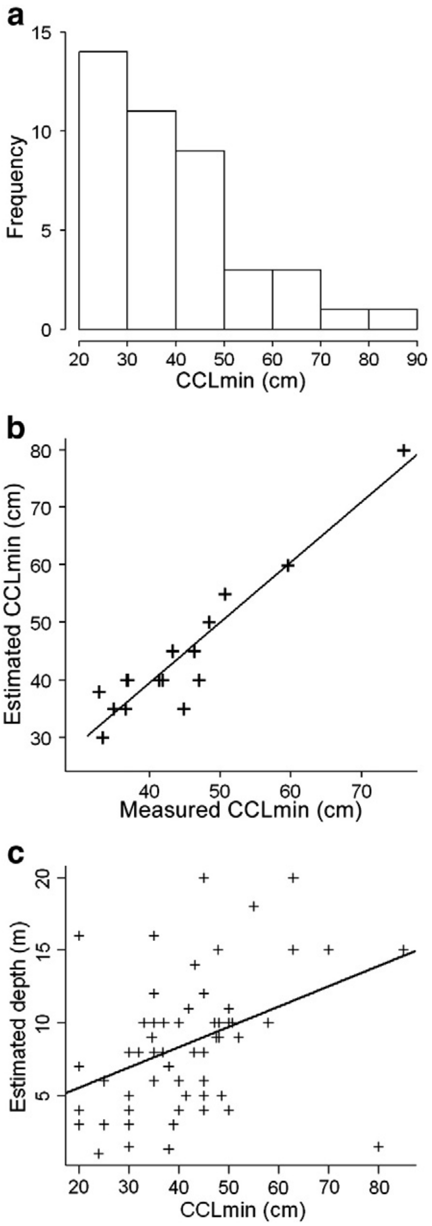

Fig. 1. Biometrics of hawksbills encountered on transects. Estimated CCL$_{min}$ (cm) of all turtles encountered on sightings transects (n = 42) in shown in (a), and (b) shows inter-observer calibration between estimated and measured sizes of captured turtles from the 2010 field season. Close correlation between estimated and measured sizes confirms accuracy of size estimations conducted by all observers. Correlation between depth at first sighting and estimated size are shown in (c). In general, larger individuals were encountered at greater depth.

2.2. Sightings transects

Sightings transects were conducted over the course of 30 days in April–May 2010 in an effort to determine patterns of abundance and identify key habitat zones. 180 random location points across all habitat zones were generated using the Hawths Analysis Tools v.3.27 plug-in extension (Hawthorne L. Beyer) for ArcGIS v.9.3.1 (ESRI Corporation, 2009). A random number generator (Randomness 1.5.2, Andrew Merenbach, 2010) was used to select 30 of these points within each habitat zone (western forereef, lagoon, eastern forereef). These 90 points were then pooled and approximately halved in number on the basis of adequate spatial coverage of the entire atoll, using a grid square system. Additional location points adjacent to HMCNM and BHNM were also included to assess relative abundance within protected areas. The resulting 49 location points were utilised as starting points for transects of 1 km length, conducted in a Southerly direction due to prevailing winds (Fig. 1). Our transect protocol involved a team of three snorkelers swimming southwards parallel to one another at a distance of approximately 10 m, and occasionally diving down to facilitate closer inspection of reef features. Upon sighting a turtle, the snorkeler would raise a hand as a signal to the boat crew. The boat captain would then navigate the boat to the snorkeler and a GPS location would be taken using a handheld GPS unit (Garmin GPSMap76). Estimated depth (m) and size (minimum curved carapace length (CCL_{min}, cm)) and behaviour at sighting were also recorded. Sightings transects were carried out between 0830 and 1230 or between 1330 and 1630. Where possible, repeats were carried out at the same time of day (am/pm), although time of day could not be completely controlled for due to logistical constraints. We aimed for an interval period of at least seven days before repeat transects were carried out.

2.3. Turtle captures

Searches were conducted using snorkelers and focused on areas that had been identified on the basis of accessibility and greater potential turtle population density. The major search effort took place over a ten-day period in 2009 (30 April–9 May) and a three-day period in 2010 (9–11 May). Once a turtle was sighted, it was captured by a team of 3–6 freedivers and brought on board a 7 m skiff. Capture location was recorded using a handheld GPS unit, alongside habitat, estimated size and behaviour at first sighting. For the 2010 dataset, estimated size at first sighting was compared to actual size for inter-observer calibration purposes (following Blumenthal et al., 2009b). All turtles were released at their capture location within 2 h.

2.4. Tagging and biometrics

Following capture, biometric measurements were taken prior to transmitter deployment. Firstly, each individual was suspended in a custom-made net and weighed. Mass of smaller individuals was determined to the nearest 500 g using a 20 kg spring balance and for larger individuals to the nearest kilogramme using a 50 kg spring balance. Minimum and maximum curved carapace lengths (CCL_{min}, CCL_{max}; Bolten, 1999) were recorded, with CCL_{min} used in all statistical analyses. Those individuals with $CCL_{min} < 65$ cm were classed as immature, following Witzell (1983).

Of 26 turtles captured, 15 individuals (n = 6, 2009; n = 9, 2010) were equipped with continuous ultrasonic transmitters in the range 51–84 kHz for active acoustic telemetry (Vemco V16-5H transmitters,16 mm diameter, 95 mm length; 16 g in water; pulse interval 1 s; power output 165 dB; 84-d battery life). In 2009, a further four were equipped only with R-coded passive transmitters (Vemco V16-6H transmitters, 16 mm diameter, 16 g in water, 69 kHz, random pulse interval 30–90 s; power output 160 dB; 1850-d battery life), which were utilised for active tracking. A total of 19 individuals (Table 1) were actively tracked over the two field seasons (n = 10, 2009; n = 9, 2010).

Prior to transmitter application the carapace surface was prepared using a metal paint scraper to remove epibionts, followed by coarse sandpaper and then wiped with acetone and dried. A two-part epoxy resin (Goop Marine Fix Fast 2 Epoxy Paste, n = 18; Power Fastners Pure2k, n = 1) was then used to attach the transmitter to the dorsal surface of the caudal marginal and costal scutes on the right-hand side of the carapace. Positioning was designed to minimise the risk of tag damage or loss owing to collisions with coral and to minimise hydrodynamic interference and to ensure that the transmitter was submerged at all times, including during surfacing. A frequency range of 51–81 kHz was utilised as the sonic impulses emitted are far outside the hearing range of marine turtles (30 Hz–1 kHz; Ridgway et al., 1969) and their predators (e.g. 10–640 Hz for Lemon sharks *Negaprion brevirostris*; Nelson, 1967). In addition, all captured individuals were marked with Inconel flipper tags (serial numbers BZ1035–BZ1073) on both front flippers.

Transmitters were deployed in bespoke casings of PVC tubing in the 2010 field season to facilitate tag recovery and potential redeployment (following Blumenthal et al., 2009a). The dry mass of the transmitters in air was 36 g and the bespoke housings 47 g. Mass of epoxy used was no greater than 100 g in any case. This represents a range of 0.8–3.1% of body mass, with a mean of 2.2%. The transmitter package was approximately neutrally buoyant and therefore virtually weightless in water. The lowest threshold of individual mass required for transmitter deployment was 5.0 kg. Of the fifteen turtles equipped with continuous transmitters, eleven were later relocated for transmitter removal.

2.5. Active tracking

Following a 24-hour post-deployment acclimation period, individuals were relocated using a VEMCO VR100 ultrasonic receiver. Firstly, an omni-directional hydrophone was deployed at the individual's last recorded location. If no regular signal was received, the vessel would widen its search redeploying the hydrophone every 200 m until a signal was received.

Upon detection using the omni-directional hydrophone, a directional hydrophone was deployed. Attached to a bespoke mechanical direction finder, the directional hydrophone was slowly turned through 360° to locate the direction from which the signal was strongest. The vessel then travelled in this direction at slow speed whilst the hydrophone was turned through a 180° arc. Visual corroboration determined that at a signal strength of 80 dB, the tag was located approximately 25 m in front of the hydrophone. This was deemed an acceptable level of spatial accuracy for a GPS location to be recorded. Whenever possible, visual corroboration of turtle presence and behavioural observation took place concurrently. We aimed to relocate each turtle every 24 h.

Tracking effort must be considered in studies utilising active acoustic telemetry, as biased effort may systematically over-record non-dispersers. Tracking effort is inevitably constrained by available resources and time pressures. Nevertheless, areas within the lagoon and western reef crest, forereef slope and forereef edge were included in the search effort in both years. No tracking was conducted on the eastern forereef due to inclement weather conditions and safety concerns. However, as 16 of the 19 focal individuals were regularly relocated on the forereef to the west of Long Caye, it is postulated that short-term movement from the western to eastern forereefs is rare.

Table 1
Key parameters of active tracking study. Key biometric and spatial habitat use measures for all turtles successfully tracked in both 2009 and 2010 field seasons.

Turtle ID	CCL_{min} (cm)	Mass (kg)	Home range area (ha)	Tracking duration (days)	Max. displacement (km)	Net displacement (km)
Ei01_2009	48.0	12.0	70.2	13	2.01	1.79
Ei02_2009	34.3	5.5	10.3	12	0.82	0.64
Ei04_2009	39.0	7.0	11.5	14	0.88	0.40
Ei05_2009	48.5	14.0	260.1	14	4.42	3.01
Ei06_2009	47.6	12.5	41.3	8	2.23	1.77
Ei07_2009	34.6	5.0	8.2	6	2.30	2.19
Ei08_2009	48.0	13.0	85.0	10	4.03	3.27
Ei10_2009	43.0	10.0	12.0	6	1.88	1.88
Ei01_2010	33.0	5.2	25.0	25	1.81	0.77
Ei02_2010	43.1	11.0	111.3	25	2.16	1.24
Ei03_2010	37.1	8.7	17.6	14	2.68	0.73
Ei04_2010	50.8	34.0	403.6	14	7.87	7.87
Ei05_2010	36.8	12.0	26.5	14	0.92	0.46
Ei06_2010	45.0	12.4	7.1	13	0.46	0.23
Ei07_2010	48.6	13.0	5.1	13	0.46	0.30
Ei08_2010	47.2	11.0	32.4	13	2.53	1.40
Ei09_2010	41.5	10.8	5.1	13	0.63	0.60

2.6. Statistical analyses

Pearson's product–moment correlation was used to assess the accuracy of size estimations from sightings transects, through determining the strength of correlation between measured and estimated CCL_{min} (cm) of all turtles captured in the 2010 field season ($n = 16$). Additionally, Pearson's product–moment correlation was used to determine correlation between turtle size (CCL_{min}) and estimated depth at first sighting for all turtle encounters that included an estimation of depth ($n = 61$). Generalised Linear Mixed Modelling (GzLMM) was utilised to determine the effects of habitat type and location (western forereef, eastern forereef, lagoon), latitude and time of day (am/pm) on turtle frequency per transect. A Poisson error structure was used and repeats were absorbed as a random effect. Similarly, the effects of protected area status were examined using GzLMM. Likelihood ratio tests using maximum likelihood simplification of minimal adequate REML models were incorporated to determine the degree of influence of explanatory variables.

Home range area was calculated using the Minimum Convex Polygon (MCP) method (Burt, 1943) and 100% of outer edges, using the Hawth's Analysis Tools v.3.27 plug-in extension for ArcGIS v.9.3.1. General Linear Modelling (GLM) was used to determine the levels of influence of body mass (kg), CCL_{min} (cm) and survey duration (days) on log-transformed MCP home range area, net displacement and maximum displacement. Net displacement describes the straight-line distance between capture location and last sighting, whereas maximum displacement describes the greatest straight-line distance between two locations for each individual. All statistical analyses were carried out using the statistical programming package R (R core development team, 2009). All means are followed by standard deviation (±s.d.).

3. Results

3.1. Sightings transects

Body size estimates of hawksbill sightings on transects ($n = 42$) ranged from 20.0 to 85.0 cm, with a mean of 40.9 cm ± 15.6 (Fig. 1a). A significant correlation between measured and estimated CCL_{min} confirms that the accuracy of size estimations was acceptable for all observers in 2010 (Pearson's product–moment correlation, $r = 0.94$, $t_{14} = 10.62$, $p < 0.05$, Fig. 1b). As the expedition team was largely the same over the two field seasons, we surmise that size estimations lay within an acceptable range of accuracy over the entire study. Estimated depth at first encounter was significantly correlated with body size, with larger turtles more likely to be encountered at greater depth (Pearson's product–moment correlation, $r = 0.40$, $t_{59} = 3.36$, $p < 0.05$, Fig. 1c). The surveys operated over a range of depths from 1 to 20 m, with a mean turtle encounter depth of 8.5 m ± 4.6 for those encounters over both field seasons that included a depth estimation ($n = 61$), with a mean body size of 41.1 cm ± 13.3 CCL_{min}. This may have influenced the body size distribution of the sample selected for acoustic tracking, owing to the difficulty of locating and catching larger turtles in deeper water.

Habitat type and location (western forereef, eastern forereef, lagoon) was found to have a significant influence on number of turtles encountered per transect (likelihood ratio test using maximum likelihood simplification of minimal adequate REML model, $\chi^2_2 = 6.85$, $p < 0.05$), with fewer turtles present in the lagoon. Latitude and time of day (am/pm) had no demonstrable influence on turtle abundance. For purposes of comparability, we report CPUE here both as number of turtles encountered per hour (turtles h^{-1}) and number of turtles encountered *per person* per hour (turtles $person^{-1}$ h^{-1}), in order to correct for effort. CPUE of transects ranged from 0.0 to 7.7 turtles h^{-1} (0.0 turtles $person^{-1}$ h^{-1} to 3.3 turtles $person^{-1}$ h^{-1}; Fig. 2), and was significantly higher in the coral reef habitat (1.41 turtles h^{1}; 0.48 turtles $person^{-1}$ h^{-1}) than in the lagoon (0.62 turtles h^{-1}; 0.20 turtles $person^{-1}$ h^{-1}).

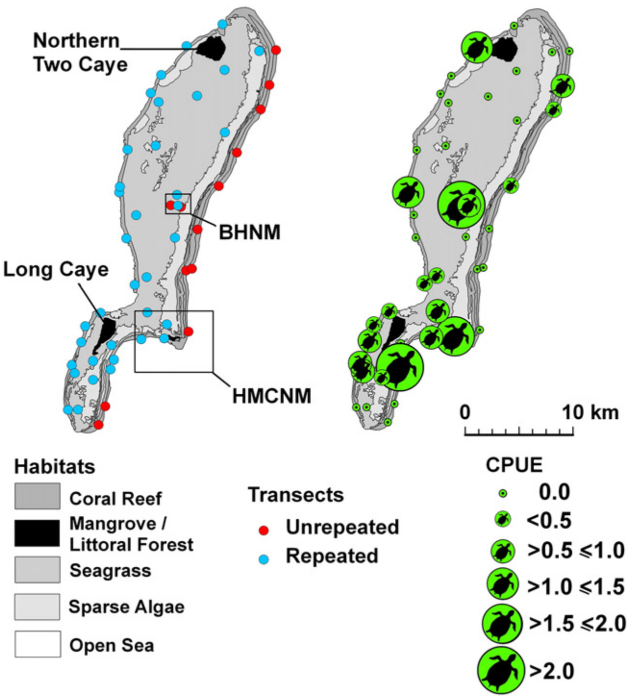

Fig. 2. Sightings transects to determine patterns in abundance at LRA. Transect start locations. 1 km transects conducted in Southerly direction. Blue circles show repeated transects; red circles show unrepeated. Location and extent of no-take marine protected areas (BHNM, HMCNM) shown. Catch Per Unit Effort (CPUE, turtles $person^{-1}$ h^{-1}) of *E. imbricata* encountered on each transect included. CPUE is appreciably higher within protected areas and in the coral reef habitat, although heterogeneity of abundance is evident. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

Of note, protected area status had a highly significant effect on turtle abundance (likelihood ratio test using maximum likelihood simplification of minimal adequate REML model, $\chi^2_1 = 8.69$, $p < 0.005$). CPUE was notably higher within protected areas (BHNM: 2.96 turtles h^{-1}, 0.99 turtles $person^{-1}$ h^{-1}; HMCNM: 2.34 turtles h^{1}, 0.77 turtles $person^{-1}$ h^{-1}) than outside their boundaries (0.88 turtles h^{-1}, 0.29 turtles $person^{-1}$ h^{-1}; Fig. 2). Furthermore, discarding transects within protected areas from the analysis shows an even stronger influence of habitat on turtle abundance (likelihood ratio test using maximum likelihood simplification of minimal adequate REML model, $\chi^2_2 = 11.47$, $p < 0.05$).

3.2. Population biometrics and home range extent

Of all turtles encountered over the two field seasons ($n = 68$), at least 91% were likely to be immature. CCL_{min} of all hawksbills captured ($n = 26$) over the two field seasons ranged from 32.0 to 76.1 cm (Fig. 3a), with a mean of 43.2 cm ± 9.5. Body mass ranged from 3.5 to 50.0 kg (Fig. 3b), with a mean of 12.4 kg ± 10.3. CCL_{min} of the 19 turtles captured for the active tracking study ranged from 32.0 to 50.8 cm, with a mean of 41.6 cm ± 6.3. Body mass ranged from 5.0 to 34.0 kg, with a mean of 10.8 kg ± 6.5. MCP home range area for the 17 turtles successfully tracked ranged from 5.1 to 403.6 ha, with a mean of 66.6 ha ± 107.4 (Fig. 4). Similarly, maximum displacement ranged from 0.45 to 8.4 km, with a mean of 2.3 ± 1.9 km, and net displacement ranged from 0.08 to 8.4 km, with a mean of 1.6 km ± 2.0. Of interest, the two largest turtles (Ei05_2009 = 14 kg; Ei04_2010 = 34 kg) tracked used a substantially more extensive home range area (Ei05_2009 = 260 ha; Ei04_2010 = 384 ha) than the other 15 tracked for this study. Analyses have been completed both with and without these data, as although a potential trend is identified, further sampling

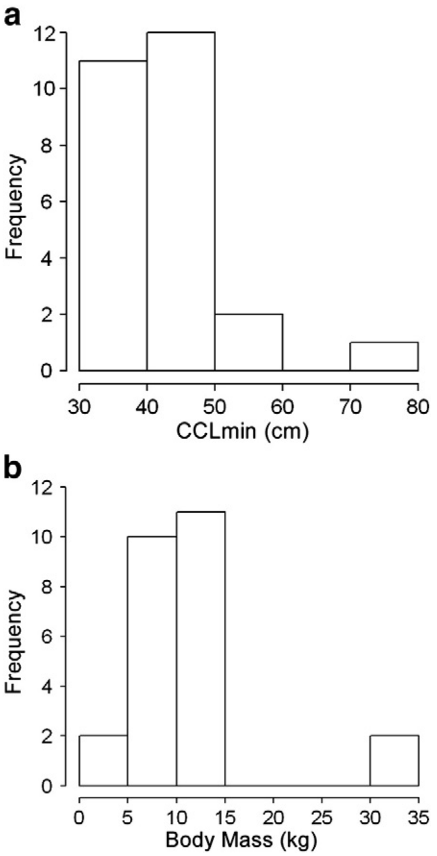

Fig. 3. Biometrics of all turtles captured for active tracking study. CCL$_{\text{min}}$ (cm) of all turtles captured in both field seasons ($n = 26$) is displayed in (a). Body mass (kg) of all turtles captured that could be accurately weighed ($n = 25$) is shown in (b). The largest turtle captured (CCL$_{\text{min}}$ = 76.1 cm) could not be weighed as our equipment was not sufficient. Biometrics indicates that the atoll is predominantly used by juvenile *E. imbricata* (CCL$_{\text{min}}$ < 65 cm).

of larger individuals would be essential to determine whether this trend is indicative of habitat use by mature hawksbills.

MCP home range area for the subsample of juveniles (<14 kg, $n = 15$) that were successfully tracked was highly variable and overlapping, ranging from 5.1 to 111.3 ha, with a mean of 31.2 ha ± 32.6. Individuals in this subsample ranged in size (CCL$_{\text{min}}$) from 33.0 to 48.6 cm with a mean of 41.8 cm ± 5.6. Body mass ranged from 5.0 to 13.0 kg with a mean of 9.9 kg ± 2.92. Maximum displacement was in the order of 1.7 kg ± 1.0, ranging from 0.5 to 4.0 km, whilst net displacement was 1.2 km ± 0.9, ranging from 0.2 to 3.3 km. Whilst there was no observed influence of body size on home range extent for this subsample population, a potential positive trend was identified upon analysis of the entire data set. Body mass (kg) was found to be highly significantly correlated to log-transformed MCP home range area (GLM, $F_{2,15} = 9.74$, $p < 0.05$, Fig. 5a), to net displacement (GLM, $F_{2,15} = 32.4$, $p < 0.05$, Fig. 5b) and to maximum displacement (GLM, $F_{2,15} = 23.6$, $p < 0.05$, Fig. 5c), whereas CCL$_{\text{min}}$ and, perhaps surprisingly, survey duration were not (please see Supplementary Fig. 2 for quantitative spatial documentation of survey effort).

Both field seasons were constrained by available tracking duration as a result of logistical constraints of operating at a very remote location. Although incremental plots (please see Supplementary Fig. 2) suggest that these figures represent an underestimation of true home range area, our findings are validated somewhat by the tracking of the same turtle in both field seasons (Ei7_2009; Ei03_2010; BZ1046). This individual exhibited a notably similar home range in terms of both location and extent, although not overlapping (8.2 ha, 6 day duration, 2009; 17.6 ha, 13 day duration, 2010).

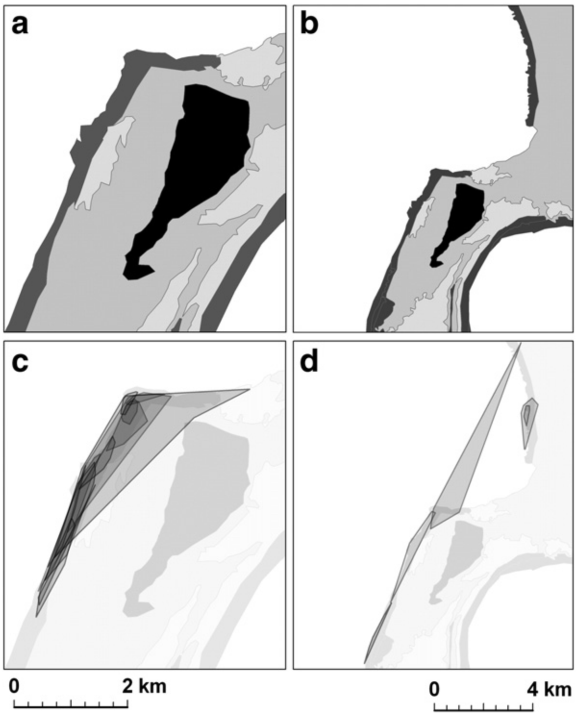

Fig. 4. MCP home range polygons generated from active tracking over two field seasons. Habitat maps are shown in small scale (a) and large scale (b). The majority of individuals maintained home ranges to the west of Long Caye, as shown in (c). A larger spatial scale is used in (d) to display the more expansive home ranges documented and those of the individuals tracked in more northern sections of the western forereef in 2009. A considerable degree of overlap between discrete home ranges is evident.

4. Discussion

The hawksbill turtle population utilising LRA is principally comprised of juveniles and sub-adults. Although juvenile hawksbills have been recorded sharing foraging grounds with adults (Diez and van Dam, 2002), populations in similar foraging habitats in the Caribbean also consist primarily of resident juveniles and sub-adults (Blumenthal et al., 2009b; Houghton et al., 2003; Léon and Diez, 1999; van Dam and Diez, 1998). An ontogenetic shift from developmental to adult foraging habitats has been hypothesised, characterised by increased depth with increasing body size (Blumenthal et al., 2009a; McGowan et al., 2008; Musick and Limpus, 1997). We therefore postulate that LRA is an important developmental habitat for juvenile hawksbill turtles, which may disperse when a certain level of maturity is reached.

Lighthouse Reef Atoll consists of approximately 73 km^2 of suitable hawksbill foraging habitat and could support a sizeable population. The range of CPUE for sightings transects at LRA is amongst the highest recorded in contemporary studies in this region (0.57–1.1 turtles h^{-1}, BVI; McGowan et al., 2008; 0.9–3.43 turtles h^{-1}, Dominican Republic; Léon and Diez, 1999; 0.4–2.38 turtles h^{-1}, Mona & Monito Islands, Puerto Rico; Léon and Diez, 1999), indicating the importance of LRA for the Caribbean hawksbill population. As might have been expected, based on the distribution of the sponges on which they feed, hawksbills are more abundant in the coral reef habitat than the lagoon with this latter habitat likely utilised primarily as a transit zone between foraging habitats. More remarkable, however, abundance in protected areas of LRA was appreciably higher than outside their boundaries. Superior habitat quality and/or protection from incidental catch in gill-net fisheries are likely contributing factors to this greater abundance. BHNM and HMCNM have been no-take zones since 1996 and are regularly patrolled.

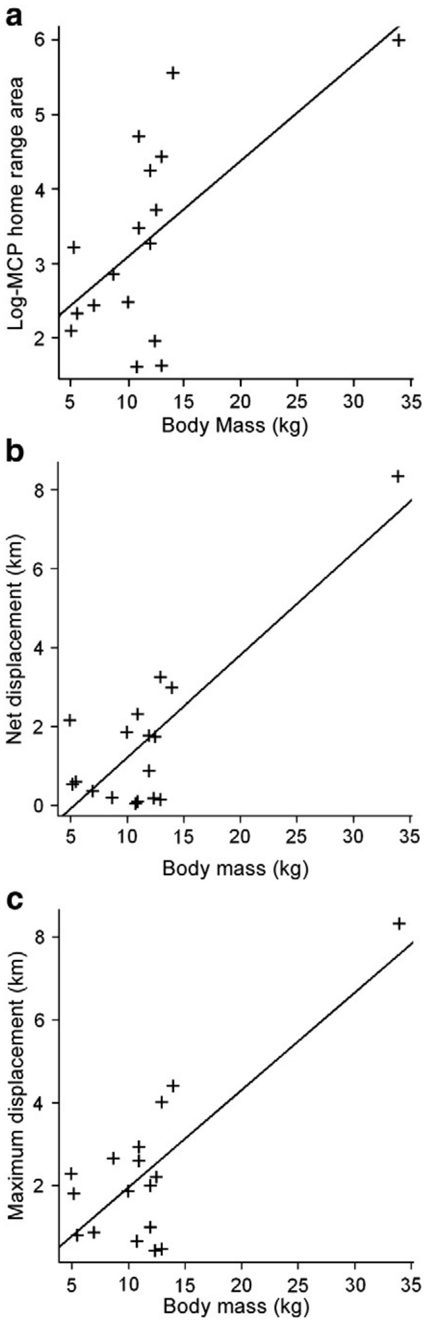

Fig. 5. Influence of body mass (kg) on (a) log-transformed MCP home range area, (b) net displacement (km) and (c) maximum displacement (km). All show a positive correlation, suggesting that larger individuals maintain a more expansive home range. However, the considerable degree of scatter within the data indicates significant variability within this subset of the population. Owing to lack of sample size for turtles of mass >14 kg, these trends should be treated as indicative only.

Our study strongly suggests that, despite high abundance, the home range of juvenile hawksbills at LRA is significantly more extensive than has been previously documented elsewhere. Indeed, mean home range area of hawksbills at LRA is more than double that exhibited in a similar habitat off Mona Island, Puerto Rico (7–14 ha, 11–16 day survey duration; van Dam and Diez, 1998). Considerable variability is evident within our sample population, but observed mean net displacement is an order of magnitude greater than the 545 ± 514 m documented in the Cayman Islands (11–360 day survey duration; Blumenthal et al., 2009b) and 450 m in Puerto Rico (465 days; van Dam and Diez, 1998). Of note, our measures are notably larger than comparable published values even after removal of the two outlying data points from the larger individuals. Our findings are concordant with those of Witt et al. (2010a), who inferred from dive profile data that juvenile hawksbills could be utilising home ranges of several square kilometres or more at Anegada, British Virgin Islands. Recent insights into the spatial ecology of other marine turtle species generated using GPS tracking suggest that home range areas may be as large as 662 ha ± 293.9 (Australia, Hazel, 2009) for adult green turtles, with daily activity ranges of up to 1575 ha also reported for this species (Baja California Sur, Mexico, Senko et al., 2010). Foraging home range areas of adult loggerhead turtles *Caretta caretta* have been demonstrated to be as large as 10 km^2 in neritic habitats and up to 1900 km^2 in oceanic habitats (Schofield et al., 2010b (Zakynthos, n = 10, duration 3–368 days); Hawkes et al., 2011 (N. Carolina, n = 13, duration 353 +/-89 days)). It is therefore likely that our findings represent a highly conservative estimate of the spatial habitat utilisation of juvenile hawksbills at LRA.

Values reported here are likely to be underestimations of true home range size as a result of several restrictive factors. Firstly, the short survey durations meant that incremental plots of home range area against tracking duration reached an asymptote in only one case, indicating that we likely did not establish true home range extent for the majority of the study population. It has been suggested that loggerhead turtles should be tracked for a minimum of 80 days to enable accurate estimation of home range extent (Hawkes et al., 2011). Secondly, our tracking study was restricted to daylight hours, which may have led to further underestimation. Hawksbills have been shown to exhibit a high degree of site fidelity to a specific nocturnal resting site (van Dam and Diez, 1997; Witt et al., 2010a) and inclusion of diel migration between resting and foraging sites may have enlarged calculated home range (cf. Hazel, 2009; Senko et al., 2010). Reported values should therefore be taken as highly conservative estimates of the utilisation of space by the population of juvenile hawksbills at LRA.

Accurate real-time tracking of marine vertebrates is constrained by the limitations of available technologies. Detectability of ultrasonic transmitters is influenced by ambient noise and sea state (Pincock, 2008; Xerri et al., 2002). In our experience, environmental conditions frequently limit the range of transmitters to within 100 m and detectability is highly variable between habitat types and water depth. False signals often exacerbate the complexities of real-time tracking, particularly in shallower areas such as the reef crest where interference of ambient noise is most frequent. Interference from false signals is most common for transmitters in the 81–84 kHz frequency band. In general, lower frequencies propagate better through the aquatic environment and are detectable at a greater distance than higher frequencies. Acoustic tracking error has been estimated at 7 m ± 4.5 compared with the 26 m ± 19.2 using 8 satellites determined for Fastloc-GPS (FGPS) (Hazel, 2009) and acoustic telemetry would therefore seem the preferential choice for real-time tracking of marine vertebrates in terms of accuracy. However, acoustic tracking is highly labour-intensive and weather dependent and is therefore often characterised by low spatiotemporal resolution. GPS data-loggers attached to sea turtles have generated up to 250 location fixes per day (Schofield et al., 2010a) compared with the 1–5 fixes obtained here, and so likely constitute a preferable method for high-resolution tracking of sea turtles.

Interpretation of our findings is limited by the existing body of knowledge of species ecology. Our *a priori* assumption is that home range extent is likely heavily influenced by habitat quality, so pronounced inter-population variability would be expected. The considerable degree of overlap between discrete home ranges at LRA suggests adequate resources to sustain a large population, suggesting that the extensive home range areas observed may not be a direct function of poor habitat quality. We also suggest that individual size, a proxy for maturity, could be an influential driver in habitat utilisation trends (cf. Blumenthal et al., 2009a; McGowan et al., 2008; Musick and Limpus, 1997). Determination of factors driving home range magnitude, including investigation of habitat quality and aspects of foraging and population ecology, would be of great utility in contextualising our findings. Habitat characterisation and exploration of selective feeding strategies (cf. Léon and Bjorndal, 2002), could contribute greatly to our current understanding of the foraging ecology of this species and elucidate factors driving home range magnitude. It has been suggested that hawksbill turtles are omnivorous following recruitment (Houghton et al., 2003), progressing to predominant spongivory as they mature (Léon and Bjorndal, 2002; Meylan, 1988; van Dam and Diez, 1998). Further inquiry into the degree of plasticity in hawksbill foraging strategies could also elucidate its potential level of resilience to environmental and climatic change (Blumenthal et al., 2009a; Hawkes et al., 2009). Alongside investigation of foraging ecology, determination of growth rates (cf. Blumenthal et al., 2009b; Boulon, 1994; Chaloupka and Limpus, 1997; Diez and van Dam, 2002) and sex ratios (cf. Léon and Diez, 1999) could generate valuable insights into population ecology, augmenting current explanation of observed habitat utilisation patterns.

Furthermore, genetic profiling of the population could determine its natal origins and degree of inter-relatedness with other Caribbean populations (cf. Bowen et al., 2007). Oceanic current modelling suggests that juvenile hawksbill turtles recruiting to the developmental habitat at LRA could have originated from nesting beaches all over the Caribbean and as far afield as Antigua, Barbados, Venezuela, and Puerto Rico (Blumenthal et al., 2009c). The developmental habitat at LRA may therefore be integral to the status of breeding aggregations across the Caribbean region. Further investigation into how the hawksbill turtle population is using this atoll could not only contribute to the conservation of this population of the species, but also generate valuable insights into more general aspects of species ecology.

Passive acoustic telemetry using a network of fixed-station ultrasonic receivers and coded transmitters is less labour intensive than active telemetry, generates longitudinal data to give insights into long-term site fidelity (Blumenthal et al., 2009a; Chapman et al., 2009; Dewar et al., 2008) and the true extent of home range (Morrissey and Gruber, 1993; Parsons et al., 2003) and is characterised by a larger sample size. The deployment of coded transmitters on turtles at LRA, in conjunction with the network of 18 fixed receivers already in-situ as part of the MarineMeganet acoustic array, would generate long-term insights into habitat utilisation trends over the entire atoll and perhaps a more accurate representation of home range extent for this population.

5. Conclusions

Lighthouse Reef Atoll constitutes a critical developmental habitat supporting the juvenile life stage of the regional population of hawksbill turtles. This primarily spongivorous, reef-dwelling marine turtle was once highly abundant in the Caribbean, playing a pivotal role in maintaining resilience of coral reef ecosystems. Caribbean coral reefs are now in critical decline, which could have deleterious effects on hawskbill populations in the region. Juvenile hawksbills maintain a much more expansive home range at LRA than elsewhere, despite abundant resources. Although likely driven by aspects of foraging ecology, we cannot yet explain the considerable variability in home range extent. Determination of the major factors driving patterns of abundance and habitat utilisation, particularly in the Caribbean, will be useful in the formulation of effective conservation measures for this species. There is a clear requirement for development of a globally-standardised transect protocol for estimating marine turtle population density, which would ensure reliability and repeatability. As technological innovation progresses, the utilisation of emergent GPS tracking technologies could be instrumental in generating fine-scale insights into marine turtle spatial ecology and facilitate applied conservation initiatives that enhance the survival chances of both hawksbills and marine vertebrates in general.

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.jembe.2011.07.008.

Acknowledgements

The financial support of the Wildlife Conservation Society (WCS), British Chelonia Group (BCG) and in kind support from the Belize Fisheries Department and Vemco is gratefully acknowledged. The research was conducted under WCS's research permit 22-10 extended by the Fisheries Department. Thanks also go to Sophie Thompson for her assistance with data collection and Levi and Clynton Pinfold for assistance with data processing. This study would not have been possible without the efforts of the expedition crew—Daniel Castellanos Sr., Darryn Castellanos, Demian Garbutt, Jason Castro, Mason Cuevas, Alex Garbutt, Kevin Castellanos, Orrington Burgess and Alistair Daly. **[SS]**

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Glossary

Archival loggers: devices that records data for later retrieval. In some cases, loggers must be retrieved, but increasingly data is acquired remotely through transmission to a satellite.

Biologging: recording of parameters pertaining to physiological, behavioural, environmental or energetic data.

Biotelemetry: remote measurement of physiological, behavioural or energetic data.

Home range: from Burt (1943), “that area traversed by the individual in its normal activities of food gathering, mating and caring for young. Occasional sallies outside the area, perhaps exploratory in nature, should not be considered as in part of home range”.

Telemetry: remote measurement of data.

Tracking: most basic form of telemetry that determines fine-scale movement and activity patterns through determining the spatial location of an animal through time.