In-water assessments of sea turtles at Glover's Reef Atoll, Belize

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ABSTRACT: The decline of sea turtle populations in the Caribbean has led to intensive recovery efforts. In Belizean waters, hawksbill turtles are seemingly making a comeback. At Glover's Reef Atoll particularly, juvenile hawksbill turtles are found in the fore-reef habitat. The population status and dynamics of this foraging aggregation were assessed to inform conservation management and to ascertain the national and regional importance of this site. During 12 sampling periods from 2007 to 2013, turtles of all species were counted, captured, and tagged. For hawksbill turtles, the capture-recapture histories were combined with the counts using a mark-resight analysis under a robust design. This provided estimates of abundance as well as survival and transition rates. From 2009 onward, distance sampling was also used to estimate density and abundance of hawksbill turtles and the less frequently encountered green and loggerhead turtles. Distance sampling provided a more cost-effective estimation method for multiple species and another more precise source of abundance estimates for hawksbills. This is the first study known to use either mark-resight or distance sampling methods during snorkel surveys of sea turtles. It produced reasonably congruent abundance estimates of >1000 juvenile hawksbills and an order of magnitude less of green and loggerhead turtles. The mark-resight analysis estimated an apparent juvenile hawksbill survival probability of 0.975 (95% CI: 0.936–0.99), indicating that mortality factors are low. The Atoll provides important developmental habitat for juvenile hawksbills, contributing to the recovery of the species on the national and regional scale.

KEY WORDS: Hawksbill turtle · Green turtle · Loggerhead turtle · Distance sampling · Mark-resight · Glover's Reef Atoll · Belize · Caribbean

INTRODUCTION

The Belizean Barrier Reef (BBR) forms part of the Meso-American Barrier Reef system, the second largest in the world. Glover's Reef Atoll (16° 44' N, 87° 48' W) is the southernmost of 3 offshore coral atolls in the BBR. This site was declared a marine reserve in 1993 (Glover's Reef Marine Reserve [GRMR]; see Fig. 1) and is managed by the Belize Fisheries De-partment (BFD). GRMR possesses the greatest range of reef types in the Caribbean Sea, supports high biological diversity, and is economically important. The Glover's Reef Living Seascape project spearheaded by the Wildlife Conservation Society (WCS) helped develop a strategic conservation plan for the site (Gibson et al. 2011). The approach used allowed for stakeholder participation and involved the selection of a suite of target species that represent the key

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habitats and threats at the site and that, if conserved, will help protect all the biodiversity sheltered under their collective conservation canopy (Sanderson et al. 2002, Coppolillo et al. 2004, Didier et al. 2009). The hawksbill turtle *Eretmochelys imbricata* was identified as one of the target species representing key marine and terrestrial habitats, as well as threats related to habitat loss and fisheries interactions. Selection of this species highlighted the need to maintain both nesting beaches on the cayes of the Atoll as well as foraging and developmental habitats within its waters. Although only sparse hawksbill turtle nesting still occurs on these cayes, measures that protect turtle nesting habitat will benefit this remnant nesting population as well as the other species in the GRMR that require this habitat, including green *Chelonia mydas* and loggerhead *Caretta caretta* turtles.

Hawksbills known to use nesting beaches and foraging habitats in Belize (e.g. Smith et al. 1992) fall within the Atlantic West/Caribbean Regional Management Unit (RMU) identified by Wallace et al. (2010). This RMU was classified as Low risk-High threat based on the consideration that hawksbill populations within this RMU were fairly robust in terms of their extinction risk, but if threats are not reduced, populations could decline; hence, intervention is necessary (Wallace et al. 2010). The current principal threats to sea turtle rookeries include loss of nesting beach habitat due to coastal development and erosion (possibly from climate change impacts) on the mainland and the cayes off-shore as well as predation of eggs and hatchlings by raccoons, dogs, cats, coatis, and pigs, particularly on mainland beaches (see review by Campbell 2014). Threats to in-water aggregations are less well known; however, fisheries interactions have been an important threat (Smith et al. 1992, Brautigam & Eckert 2006, Coleman & Majil 2014). Sites such as the GRMR and others (e.g. Scales et al. 2011), which include nesting, developmental, and feeding habitats for hawksbills, are highly valuable for recovery of the species in the Caribbean region.

Although hawksbills are widely distributed in the Caribbean Sea and Western Atlantic (Mortimer & Donnelly 2008, National Marine Fisheries Service & U.S. Fish and Wildlife Service 2013, Campbell 2014), they are currently listed as Critically Endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (IUCN 2015). Intensive harvest for their shells, meat, and eggs (Meylan & Donnelly 1999, Bjorndal & Jackson 2003) have resulted in substantial reductions in population numbers across their range throughout the tropical

and subtropical waters of the Atlantic, Pacific, and Indian Oceans (Rhodin & Pritchard 1999). Hawksbills spend their early years in oceanic habitats feeding on a variety of floating organisms (Bolten 2003, Witherington et al. 2012). In the Caribbean, when hawksbills shift from oceanic to neritic habitats as small juveniles, they become primarily spongivores (Meylan 1988) and are typically associated with reef habitats, such as the fore-reef habitat of the GRMR, but may also use seagrass habitat (see Bjorndal & Bolten 2010). Hawksbill turtles play a key functional role in the ecosystems they inhabit (Goatley et al. 2012), and reductions in hawksbill density have potentially important ramifications for those marine habitats. This is an additional reason why hawksbill turtles were included as a conservation target for the GRMR.

Conservation management of hawksbill turtles within the GRMR requires estimates of density and abundance as well as of vital rates associated with survival, fecundity, and movement. Across the range of hawksbill turtles, only a few studies have been conducted to estimate these parameters. This is due to reduced hawksbill numbers and their long life span, which encompasses multiple life stages in a variety of marine habitats that are geographically wide ranging. Indices that provide information on the relative abundance or relative density of the population of interest based on nesting beach and in-water surveys have been used to assess turtle population status (e.g. Diez & van Dam 2002). These relative indices are correlated to density, but the exact relationship is usually unknown and may change over time and space (Williams et al. 2002). Thus, actual or absolute estimates of density or abundance provide stronger inference and can more reliably be used to assess baselines and population trends or to make comparisons between sites, although studies providing such estimates are few (Bjorndal et al. 2010). To obtain these estimates for sea turtles using foraging habitat at GRMR, we used a unique sea turtle sampling protocol that included capture as well as direct observation of the turtles along transect lines. We analyzed the data using mark-resight (McClintock et al. 2009) and distance sampling methods (Buckland et al. 2001) that provided absolute estimates of density and abundance. The latter estimate was obtained from both analysis methods with additional insights into population dynamics provided by the mark-resight method.

Capture-recapture analyses based on data obtained from tagging turtles over time have been used to estimate abundance (Chaloupka & Limpus 2001, Bjorndal et al. 2005, overview in Bjorndal &

Bolten 2000) and/or other vital rates (Krueger et al. 2006, Sasso et al. 2006, Eguchi et al. 2010). Instead of using more traditional mark-recapture methods (Otis et al. 1978), we used mark-resight methods to obtain absolute estimates of abundance for hawksbill turtles as well as estimates of survival and transition rates between observable and unobservable states (McClintock & White 2009, McClintock et al. 2009). The method allowed us to combine individual turtle capture histories with in-water sightings of turtles with and without tags that were not captured. This combination was particularly useful in terms of robust estimation given the low recapture probabilities for these hawksbill turtles. Current mark-resight methods have moved beyond a single focus on abundance estimation (Bartmann et al. 1987, Arnason et al. 1991, Neal et al. 1993, Bowden & Kufeld 1995) and now more reliably allow for integrated estimation of survival and transition rates between observable and unobservable states (Kendall et al. 1995, 1997, Kendall & Nichols 2002). This is important for evaluating the status of this Belizean hawksbill turtle population over time because it provides information on long-term prospects for the population and movements in and out of the fore-reef study area. Mark-resight methods were initially applied to terrestrial mammals and birds (McClintock et al. 2006, 2009, McClintock & White 2009, Walsh et al. 2010, Wingard et al. 2011, Franzetti et al. 2012) with later applications to fish, cetaceans and seals in the marine realm (Hagen et al. 2010, Cordes 2011, Ryan et al. 2011, Mansur et al. 2012). This is the first known application of mark-resight methods to marine turtles.

Distance sampling has been successfully applied to a large variety of species in different habitats (Buckland et al. 2001, 2015). Previous distance sampling application to turtles include both aerial (Gómez de Segura et al. 2006, Houghton et al. 2006, Seminoff et al. 2014, Benson et al. 2007, Lauriano et al. 2011) and boat-based (Eguchi et al. 2007, Beavers & Ramsey 1998) surveys with turtle observations limited to the surface or just below. To our knowledge, this is the first use of distance sampling with snorkellers making observations to a greater depth below the surface. This approach reduces perception and availability bias that is problematic in aerial and boat-based surveys (Henwood & Epperly 1999, Pollock et al. 1996, Kenney & Shoop 2012, Fuentes et al. 2015). Distance sampling permitted the estimation of absolute density and abundance for hawksbill turtles as well as the less frequently encountered green and loggerhead turtles.

MATERIALS AND METHODS

Study area

GRMR is the fourth largest marine reserve in Belize with an area of almost 360 km^2. Management zones within the GRMR aim to maintain its incredible biodiversity and support sustainable fishing practices for economically important species for local and international markets, including Caribbean spiny lobster *Panulirus argus*, queen conch *Lobatus gigas*, black grouper *Mycteroperca bonaci*, hogfish *Lachnolaimus maximus*, and mutton snapper *Lutjanus analis* (Koslow et al. 1994). Zones include a general use zone (covering ~75% of the area), conservation zone (fishing is prohibited, aside from catch and release sport fishing), wilderness zone (all access is prohibited), and a spawning aggregation zone (the location of one of the Caribbean's largest and last remaining Nassau grouper spawning aggregations, where all fishing is prohibited) that overlaps with the seasonal closure zone (fishing is prohibited December through February; Fig. 1). The Atoll comprising GRMR has a well-developed spur and groove outer reef structure that surrounds a shallow lagoon interspersed with >800 patch reefs. The outer reef or fore-reef is covered by sparse and dense massive encrusting corals, and has a low relief spur and groove, an escarpment, wall, and deep reef (Mumby & Harborne 1999). Long-term turtle monitoring, particularly of hawksbills *Eretmochelys imbricata*, within the GRMR is one of the principal management goals for the reserve. Our pilot study determined that the fore-reef area was potentially important turtle foraging habitat for hawksbill turtles (in contrast to the lagoon habitat within the atoll, for example), with some occurrence of green *Chelonia mydas* and loggerhead *Caretta caretta* sea turtles as well. In addition, the GRMR does not include much of the off-shore area, such as the reef wall. Thus, the present study focuses on the fore-reef area (approximately 22 km^2) that slopes from the reef crest to the drop-off, which was accessible to the survey teams without scuba gear.

Turtle research guidelines and permits

Turtles were captured and tagged by the survey team according to internationally recognized guidelines and standardized methods for marine turtle tagging (Eckert & Beggs 2006) and general guidelines for research at the Glover's Reef Research Station (www.wcsgloversreef.org/wp-content/uploads/2013/
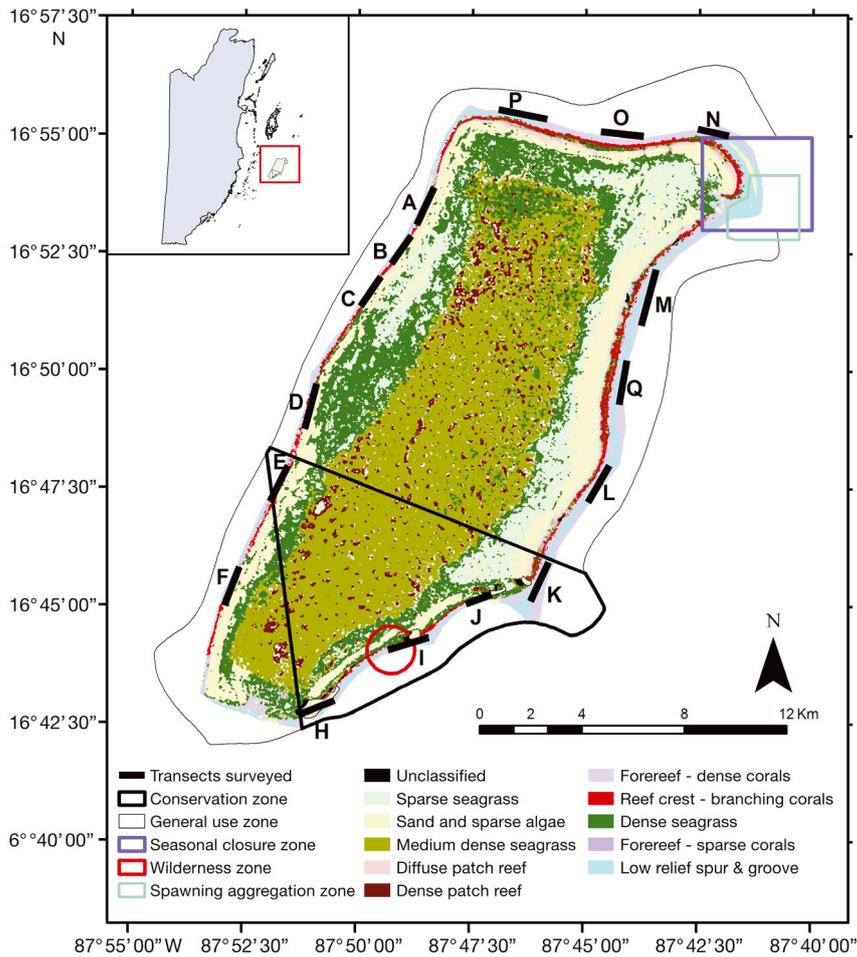
Fig. 1. Glover's Reef Atoll, Belize. Shown are the management zones and the 16 in-water sampling sites in the fore-reef habitat. Habitat classifications are based on Mumby & Harborne (1999)

04/GRRS-Research-Guidelines.pdf). The sea turtle survey work was initially conducted under permit number 000019-08 obtained from the BFD and subsequently within the framework of a Memorandum of Understanding between WCS and BFD.

Field survey methods

Snorkel surveys were conducted within the fore-reef habitat of Glover's Reef Atoll at 16 sampling sites (Fig. 1). Sites in the fore-reef habitat were selected by systematic design with a random start point to cover the circumference of the atoll, with some of the original sampling units moved or removed due to issues of accessibility or visibility. Hawksbills composing part of a foraging aggregation within the GRMR were the principal target of sampling surveys in the GRMR, with greens and loggerheads also occurring

in the fore-reef habitat included in the study. Turtle counts of all 3 species were collected during 1 h in-water transects by teams of 6 to 8 snorkellers spread from ~3 m depth to the reef edge (~20 m depth) with ~5 m between them. Snorkellers were accompanied by a boat-based crew that assisted with data recording (for example, taking GPS positions to mark the locations of turtle observations) and helped them maintain their correct survey position along the transect line between the start and end point that were located using the GPS. The same start and end points for each transect were used to orient the observers during every survey period. The survey protocol dictated that snorkellers raise their hand when a turtle was sighted to facilitate the recording of observations and to assess their independence. To avoid positively biased estimates of encounter rate, only independent duplicate observations were retained.

In addition, turtles were captured and brought to the boat by the snorkellers to collect biometric data, to tag newly caught individuals, or to read the tag information from turtles caught during previous sampling sessions. Because turtle capture and observation surveys were combined for reasons of efficiency, changes in survey effort in terms of the number of observers (due to capture activities or for other reasons) were recorded. Snorkel surveys were conducted at least twice a year from 2007 to 2010 to investigate potential seasonality in the target hawksbill turtle population, and then once a year from 2011 to 2013 (12 sampling periods in total). The initial aim was to use a capture-recapture method to estimate abundance over time (Otis et al. 1978), as well as other vital rates.

From 2009 onward, the perpendicular distance from each sighted turtle to the transect line swum by the observer was also recorded to permit assessments using distance sampling methods as well (Buckland et al. 2001). This permitted abundance estimation of not only hawksbill but also the less frequently encountered green and loggerhead turtles, and with minimal extra effort provided abundance estimates generated by a different method that could be compared to estimates obtained through turtle capture-recapture methods. This is useful because the latter may produce biased parameter estimates if

heterogeneity in capture probabilities is not accounted for during the analysis (e.g. Heupel & Bennett 2007). Distance sampling is robust to heterogeneity in detectability (Buckland et al. 2001), can efficiently provide estimates of density and abundance (Kulbicki & Sarramégna 1999) immediately for each survey period, and provides better precision more cost-effectively when populations are larger. Both capture-based and distance sampling account for catchability or detectability that may be influenced by factors such as weather conditions, visibility, observer ability, or attentiveness during the estimation process. This is critical for statistically defensible comparisons in space and time, avoiding the pitfalls of using a relative index such as encounter rate based on number of turtles observed over a given distance or period of time (Williams et al. 2002, Thompson 2002).

Tagging and biometrics

Turtles captured during the surveys were flipper tagged with Inconel #681 metal tags (National Band & Tag, Newport, KY, USA) on the trailing edge of each front flipper, proximal to the first scute. Straight carapace length measurements from nuchal notch to posterior tip (SCLnt) were taken following Bolten (1999) using a straight-line caliper. Turtles were weighed, except for turtles of very large size, as was the case for some loggerhead turtles; it was too difficult to obtain accurate measurements without the correct lifting device to weigh them, as well as being potentially unsafe to hoist these turtles onto a 8.5 m (28 ft) boat at sea.

Mark-resight methods

We applied a mark-resight analysis under Pollock's robust design (Pollock 1982) to the hawksbill turtle data for each of the 12 primary sampling periods from 2007 to 2013. The details of the timing and effort for each secondary period are shown in Table 1. Encounter histories of tagged individuals were compiled, and totals of marked unidentified and unmarked individuals overall and for each primary sampling period were obtained (Table 1; also shown are the captures and recaptures). The number of marked unidentified and unmarked turtles corresponds to the aggregate count of animals observed, but not captured, during the snorkel surveys that did and did not have tags, respectively. For the former group, the tag was seen, but because the turtle was not recaptured, individual identification was not possible. The analysis method assumes that tags are not lost over time, with assumption violations leading to positively biased abundance estimates. Generally, tag retention is high with the double tagging protocol and type of tags used in this study (e.g. Limpus 1992, Bjorndal et al. 2005). Tagged turtles can be uniquely identified when recaptured; however, the number of

Table 1. The year and month corresponding to the primary sampling periods, the number of days between primary sampling periods, the sampling effort (in days) associated with each of the secondary survey periods, and the total and primary period specific number of hawksbill turtles that were unmarked, marked unidentified, newly captured or recaptured

Year	Month	Primary sampling period	Inter-sampling period (d)	Secondary period effort (d)	Unmarked (no tag)	Marked (tagged) unidentified	Newly captured & tagged	Recaptures
2007	Apr	1		5	17	0	8	
	Sep	2	151	4	13	0	10	
2008	Apr	3	207	5	20	2	19	1
	Jul	4	93	6	30	0	16	2
	Nov	5	116	4	33	1	28	4
2009	Apr	6	149	5	38	3	16	3
	Nov	7	206	5	48	2	26	4
2010	Apr	8	150	6	48	5	46	4
	Nov	9	208	4	41	5	25	3
2011	Mar	10	120	5	37	2	27	2
2012	Apr	11	387	5	50	3	14	4
2013	Apr	12	360	5	59	3	20	4
Totals				59	434	26	255	31

tagged individuals within the study area at the time of each survey is unknown, and the same turtle can potentially be encountered more than once during a secondary sampling period. For this reason, we used an appropriate model that accounts for an unknown number of tagged individuals as well as sampling with replacement (McClintock et al. 2009, McClintock & White 2009). This model is also able to deal with heterogeneity in turtle sightability due to physical or behavioral differences and variation over time (McClintock et al. 2006) and functions for populations where there is potentially no demographic or geographic closure. In the latter case, animals move in and out of the study area during the time of a survey, and the abundance estimates are for a wider ranging 'superpopulation' associated with the study area.

The data were analyzed using the MARK software (White 2011), which provides estimates of the intercept for the mean resighting rate α, amount of individual heterogeneity σ^2, the number of unmarked individuals U, apparent survival ϕ, and transition rates γ'' (transition from an observable to an unobservable state) and γ' (remaining in an unobservable state). The abundance estimate for each survey, N, is derived from U, the overall mean resighting rate λ, and the total number of resightings of tagged individuals. Model selection was based on Akaike's information criterion values adjusted for sample size (AICc; Akaike 1973, Burnham & Anderson 2002) calculated within MARK. Models considered included those in which certain parameters (α, σ^2, U, ϕ, γ', and γ'') were either constant or different for each of the 12 encounter occasions. We also considered models where σ^2 or the transition rates were set equal to zero.

Distance sampling methods

A series of 7 distance sampling surveys were conducted in April 2009, November 2009, April 2010, November 2010, March 2011, April 2012, and April 2013. Survey teams generally comprised a majority of observers with prior experience with turtle observation and capture. Survey teams were provided training in the distance sampling method with an emphasis on meeting the assumptions underlying the method, namely perfect detection on or close to the transect line, exact distance measurements, and animal detection and distances recorded before movement in response to the observer occurs. Training was repeated to refresh memories and to account for new observers who joined the team.

Turtle density within the 22 km^2 fore-reef habitat of the GRMR was estimated as: $\hat{D} = \dfrac{n\hat{f}(0)}{2L}$, where n is the number of turtles of a particular species observed during the survey period, $f(0)$ represents the probability density function of the perpendicular distances evaluated at zero distance, and L denotes the total transect length (Buckland et al. 2001). Whenever there was a change in survey effort, in terms of total number of observers actively conducting the sighting survey (as opposed to capturing turtles or some other activity), the time and number of observers was recorded. The effective number of observers was calculated by aggregating the proportion of survey time that each observer grouping was in place multiplied by the total number of observers in that group. The effort for each transect was then calculated by multiplying the distance between the in-water start and end position by the effective number of observers over the 1 h survey period. The total effort was the aggregate length across all transects. $f(0)$ is inversely proportional to the effective strip half-width μ; there is an equal number of undetected and detected animals within and beyond half-width μ, respectively (Buckland et al. 2001). The effective area surveyed is given by $2\hat{\mu}L$. The abundance estimate was obtained by multiplying $\hat{D}$ by the 22 km^2 surface area of the same study area covered in each sampling period.

The Distance 6 software was used to analyze the data (Thomas et al. 2010). The variance of encounter rate (n/L) and $\hat{\mu}$ was estimated empirically from the 16 transects and using maximum likelihood methods, respectively. Data were plotted in detail to identify potential assumption violations, such as less than perfect detection on or close to the line, rounding of perpendicular distances to convenient values, turtle movement before perpendicular distance were obtained. A set of key functions and adjustment term combinations were considered to model the detection function, and to improve model fit, both right truncation of the data and grouping distances into intervals were considered. Buckland et al. (2001) note that good model fit at distances near zero is particularly important to avoid biased estimates of detectability. To ensure a sufficient number of observations to reliably fit the detection function, the data for all turtle species were combined. Distance sampling is robust to pooling data in this manner, and results are not biased even when there is variability in detectability between individuals because the result is an average detectability. Once a satisfactory truncation distance or distance intervals were identified, AICc was used in model selection. For hawks-

bills, the distance sampling density estimates were contrasted against each other sequentially in time using a *t*-test with a 5% significance level to determine whether a statistically significant difference could be detected between sampling periods.

RESULTS

Biometrics and life stages

The size distribution of green *Chelonia mydas* and hawksbill *Eretmochelys imbricata* turtles captured during in-water surveys was very similar, although green turtles tended to be smaller, and loggerheads *Caretta caretta* were consistently larger (Fig. 2). The mean straight carapace length notch to tip (SCLnt) for captured hawksbill turtles was 43.2 cm (SE = 0.62 cm, range = 20.0–75.1 cm, n = 214; only SCLnt for first capture was used). For green turtles, the mean SCLnt was 38.4 cm (SE = 2.34 cm, range = 22.9–61.8 cm, n = 18), and mean SCLnt for loggerhead turtles was 79.2 cm (SE = 3.7 cm, range = 68.9–91.2 cm, n = 6). The mean weight for hawksbill turtles was 12.13 kg (SE = 0.56 kg, range = 1.2–65 kg), for reen turtles was 9.53 kg (SE = 2.18 kg, range = 1.6–40 kg), and for loggerhead turtles was 81.98 kg (SE = 9.97 kg, range = 53–125 kg). The biometrics for loggerheads are negatively biased given that 2 of the larger turtles that were tagged in the water could not be measured. Based on carapace length, the life stages captured in the study were small and large juvenile hawksbills (and possibly adults infrequently), primarily small juvenile green turtles, and large juvenile and adult loggerheads.

Mark-resight analysis

Given the relative sparsity of the data and the low recapture rates (Table 1), higher-ranked models tended to be those with fewer parameters (Table 2). Numerical problems tended to arise for models in
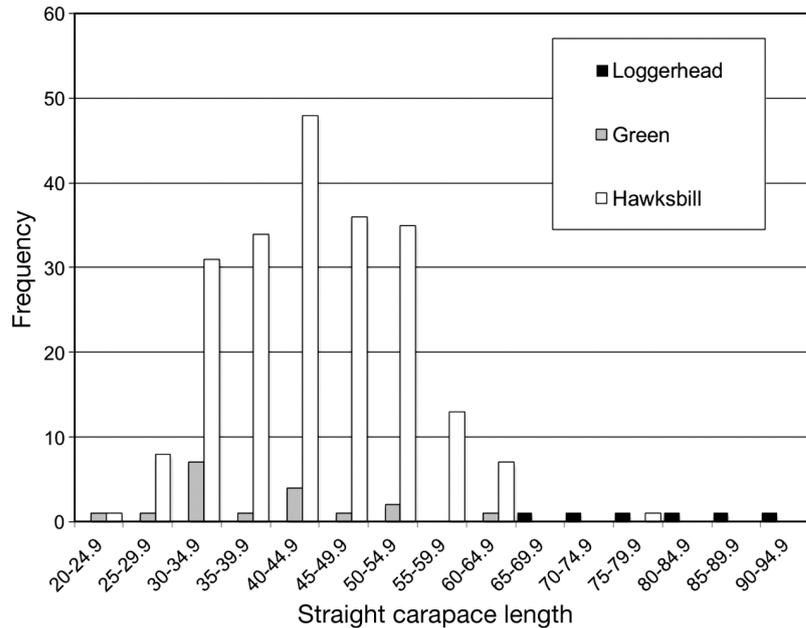

Fig. 2. Distribution of straight carapace length (notch to tip) of hawksbill, green, and loggerhead turtles captured at Glover's Reef Atoll, Belize, from 2007 to 2013

Table 2. The model results for the Glover's reef hawksbill turtle mark–resight analysis. The estimated parameters are the intercept for the mean resighting rate α, the number of unmarked individuals U, apparent survival φ, the probability of transitioning from an observable state to an unobservable state in the next survey γ″, and the probability of remaining in an unobservable state in the next survey when in an unobservable state in the previous survey γ′. These parameters were either set to constant (.), allowed to vary over time (*t*) or were set equal to zero (=0). Individual heterogeneity level σ^2 was fixed at zero for the models shown. The parameterization of each model is shown (Model), along with the difference in Akaike's Information Criterion (AICc) value between the top-ranked model and each model listed (ΔAICc), the relative support for the model given the data using weights (AICc weights), the strength of evidence of each model relative to the other models in the set (Model likel.) and number of parameters estimated (Num. par.). We only show models with an AICc weight > 5%

Model	ΔAICc	AICc weights	Model likel.	Num. par.
$\alpha_t \sigma^2_{=0} U.\phi.\gamma''_{=0}\gamma'.$	0	0.38936	1	14
$\alpha.\sigma^2_{=0} U_t \phi.\gamma''_{=0}\gamma'.$	0.1351	0.36393	0.9347	14
$\alpha_t \sigma^2_{=0} U.\phi.\gamma''.\gamma'.$	2.2324	0.12752	0.3275	15
$\alpha.\sigma^2_{=0} U_t \phi.\gamma''.\gamma'.$	2.3675	0.11919	0.3061	15

which >1 parameter was allowed to vary over time. Setting γ″ to zero always improved the AICc ranking of the model (for models in which γ″ was not set to zero, its estimated value was miniscule). This was not the case for γ′, and setting σ^2 to zero produced identically ranked models to those where σ^2 was set to constant for the 12 encounter occasions. Within the set of highest ranked mark-resight models, when α varied over time, U was set to constant and vice versa. For these models, γ″ was set to constant or zero,

σ^2 was set to zero, and the remainder of the parameters were set to constants (Table 2). For the model set in Table 2 that all have good support in the data, model averaged results were obtained from MARK. Hawksbill abundance estimates ranged from 1014 (95% CI: 105–1924) to 2159 (95% CI: 914–3405) turtles for the 12 survey periods (Table 3). Mean resighting rates ranged from 0.025 (95% CI: 0.008–0.075) to 0.053 (95% CI: 0.026–0.106), and the overall survival probability estimate was 0.975 (95% CI: 0.936–0.99; Table 3).

Distance sampling analysis

The majority of turtles observed were hawksbills (82.1%), with a much smaller number of greens (13.3%) and loggerheads (4.6%) observed (Table 4). The encounter rates (n/L) for hawksbill turtles are comparable across the first 5 surveys, with noticeably lower numbers in 2013 and particularly 2012 (Table 4), which also corresponds to the introduction of completely new and inexperienced observers in 2012. The encounter rates are more variable between surveys for green and loggerhead turtles, which is likely due, at least in part, to the generally low sample sizes for these 2 species. Loggerhead turtles were only encountered during the March or April surveys. The percent coefficient of variation (%CV) for n/L by species decreased or was comparable over time.

For the first 2 surveys, there were too many observations close to zero (heaping at zero), this was not evident in the later survey data. However, for all surveys, there was a tendency to round perpendicular distances to convenient values, e.g. 0, 5, 10, 15, 20 ft, and so on; thus, data were grouped into intervals for final analysis (with right-truncation to improve model fit). The final models selected for each of the 7 survey periods are shown in Fig. 3 (the associated key function and adjustment terms are detailed in the legend). The estimates for $\hat{f}(0)$ and $\hat{\mu}$ are shown in Table 5. Over the 7 sampling sessions, the effective area surveyed fluctuated between 4.2% and 7.6% of the 22 km² fore-reef habitat. The estimated detection probability ranged from 0.50 to 0.65, and this likely reflects the variability in visibility (water turbidity) and observers.

Table 3. The model averaged results over the model set in Table 2 for the Glover's reef hawksbill turtle mark–resight analysis. Shown are estimates of abundance $\hat{N}_m$ and mean resighting rate $\hat{\lambda}$ by primary season as well as the overall apparent survival $\hat{\phi}$ and the probability of remaining in an unobservable state $\hat{\gamma}'$. All estimates are shown with their 95% confidence intervals (95% CI) and percent coefficient of variation (%CV)

Survey	$\hat{N}_m$	95% CI	(%CV)	$\hat{\lambda}$	95% CI	(%CV)
Apr 2007	1014	(105–1924)	45.76	0.028	(0.011–0.068)	46.43
Sep 2007	1141	(113–2395)	56.09	0.025	(0.008–0.075)	56.00
Apr 2008	1438	(227–2649)	42.98	0.032	(0.013–0.072)	43.75
Jul 2008	1307	(569–2045)	28.77	0.035	(0.020–0.063)	31.43
Nov 2008	1636	(748–2523)	27.69	0.039	(0.022–0.067)	28.21
Apr 2009	1319	(599–2039)	27.90	0.043	(0.025–0.075)	27.91
Nov 2009	1652	(663–2641)	30.57	0.047	(0.025–0.086)	31.91
Apr 2010	2159	(914–3405)	29.41	0.047	(0.026–0.085)	29.79
Nov 2010	1671	(776–2566)	27.35	0.044	(0.025–0.076)	27.27
Mar 2011	1713	(792–2635)	27.44	0.039	(0.022–0.068)	28.21
Apr 2012	1453	(604–2302)	29.80	0.049	(0.027–0.089)	30.61
Apr 2013	1673	(531–2816)	34.85	0.053	(0.026–0.106)	35.85
Overall	$\hat{\phi}$	95% CI	(%CV)	$\hat{\gamma}'$	95% CI	(%CV)
	0.975	(0.936–0.99)	1.23	0.559	(0.211–0.857)	35.06

Table 4. The number of in-water observations by species (*n*) post right truncation, survey effort *L* (km) and the estimate of encounter rate (n/L) in observations km⁻¹ for each survey period by species (Ei = hawksbill, Cm = green, Cc = loggerhead) with the corresponding percent coefficient of variation (%CV) and 95% confidence interval (95% CI). Note that the survey effort takes into account the periods during which observers were off-effort during the sighting survey, for example, when capturing turtles

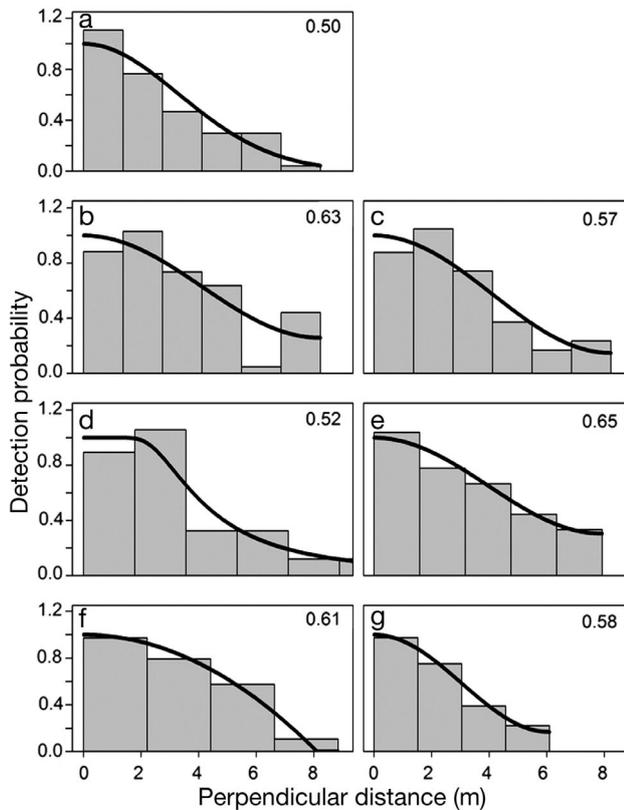| Survey	Species	*n*	*L* (km)	n/L (km⁻¹)	(%CV)	95% CI
April 2009	Ei	57	112.17	0.508	21.37	(0.322–0.802)
	Cm	10		0.089	48.87	(0.033–0.242)
	Cc	3		0.027	71.47	(0.007–0.107)
Nov 2009	Ei	68	160.55	0.424	13.88	(0.316–0.569)
	Cm	8		0.050	35.93	(0.024–0.105)
April 2010	Ei	88	168.83	0.521	18.04	(0.356–0.763)
	Cm	11		0.065	30.07	(0.035–0.122)
	Cc	3		0.018	73.31	(0.004–0.072)
Nov 2010	Ei	70	132.16	0.530	15.76	(0.379–0.740)
	Cm	13		0.098	31.06	(0.052–0.188)
March 2011	Ei	68	152.08	0.447	14.72	(0.327–0.611)
	Cm	13		0.086	33.65	(0.043–0.172)
	Cc	7		0.046	29.96	(0.025–0.086)
April 2012	Ei	41	150.37	0.273	13.33	(0.206–0.362)
	Cm	15		0.100	32.75	(0.051–0.197)
	Cc	8		0.053	51.10	(0.019–0.149)
April 2013	Ei	71	188.16	0.377	11.97	(0.293–0.487)
	Cm	5		0.027	48.52	(0.010–0.071)
	Cc	5		0.027	62.77	(0.008–0.091)

Fig. 3. Detection function fitted (key + adjustment terms) to the perpendicular distances of observations of all turtle species (bold black line) in (a) April 2009 — half-normal, (b) November 2009 — half-normal+cosine, (c) April 2010 — uniform+cosine, (d) November 2010 — hazard rate, (e) March 2011 — uniform+ cosine, (f) April 2012 — uniform+cosine, and (g) April 2013 — uniform+simple polynomial. The grey bars represent the frequency of observed perpendicular distances. The estimated detection probability corresponding to these detection functions is shown in the upper right corner of each panel

Hawksbill density estimates were consistently higher than for greens or loggerheads, making up >80% of turtle density in the majority of survey periods (Table 6). Abundance estimates for hawksbills ranged from 555 (95% CI: 410–750) to 1618 (95% CI: 1030–2540) turtles over the 22 km² study area (Table 6). The estimates of density and abundance were most precise for hawksbills because the n/L was the highest for this species. However, even for hawksbills, the difference in density between sequential surveys across all years of the surveys was not statistically significant at the 5% level, except for the April 2012 survey, when contrasted to each of its neighbors.

DISCUSSION

These are the first hawksbill assessments to use either distance sampling or mark-resight methods based on snorkel sighting and capture surveys. The results produced by the 2 methods are fairly congruent and indicate a healthy population of >1000 individuals. Comparing abundance estimation methods as applied to the juvenile hawksbills *Eretmochelys imbricata* in the fore-reef of the GRMR, the estimates from the mark-resight analysis are generally higher than those from the distance sampling analysis (Tables 3 & 6, respectively). This is likely explained by the capture of transient individuals or individuals that move in and out of the fore-reef habitat, and thus, the mark-resight abundance estimate is for a 'superpopulation' associated with the study region during a particular survey. Because we do not know the exact area corresponding to this 'superpopulation', we cannot easily derive density estimates from the mark-resight abundance estimates.

In contrast, distance sampling estimates density directly and then permits abundance estimation if the surface area of the study region is available. The fore-reef area in GRMR is clearly delimited by the reef crest and reef wall drop-off, and using the available fine-scale habitat map, it was possible to calculate the surface area of the fore-reef within the reserve. There was a statistically significant change in turtle density and abundance in April 2012 contrasted to earlier or later surveys. However, we do not believe this is a true change in the target population but rather an artifact of data collection problems in 2012 resulting from lack of experience and training in a new team of observers that season. Due to the observers' lack of understanding of distance sampling and their inexperience with turtle surveys in general, it is likely that key assumptions underlying the method were violated. A critical assumption underlying distance sam-

Table 5. Estimates of $\hat{f}(0)$, the probability density function of the perpendicular distances evaluated at zero distance, and its inverse the effective strip width ($\hat{\mu}$) obtained for each survey period with their 95% confidence intervals (95% CI) and corresponding percent coefficient of variation (%CV)

Survey	$\hat{f}(0)$ (m^{-1})	95% CI	$\hat{\mu}$ (m)	95% CI	(%CV)
April 2009	0.245	(0.202–0.296)	4.08	(3.38–4.94)	9.57
Nov 2009	0.193	(0.162–0.230)	5.18	(4.35–6.17)	8.81
April 2010	0.212	(0.187–0.239)	4.73	(4.18–5.34)	6.16
Nov 2010	0.182	(0.145–0.229)	5.49	(4.38–6.89)	11.46
March 2011	0.193	(0.162–0.231)	5.17	(4.34–6.17)	8.89
April 2012	0.185	(0.164–0.209)	5.41	(4.79–6.11)	6.08
April 2013	0.281	(0.243–0.325)	3.56	(3.08–4.12)	7.30

Table 6. Distance sampling estimates of turtle density ($\hat{D}$) in number km^{-2} and abundance ($\hat{N}$) for each survey period by species (Ei = hawksbill, Cm = green, Cc = loggerhead) and combined with their 95% confidence intervals (95% CI) and percent coefficient of variation (%CV). The abundance estimates for hawksbill turtles are in **bold** to facilitate comparison with abundance estimates obtained using the mark-resight method

Survey	Species	$\hat{D}$	95% CI	$\hat{N}$	95% CI	(%CV)
April 2009	Ei	62.22	(39.63–97.69)	**1618**	(1030–2540)	21.86
	Cm	10.92	(4.21–28.33)	284	(109–737)	46.81
	Cc	3.28	(0.80–13.41)	85	(21–349)	73.16
	Total	76.41	(50.99–114.50)	1987	(1326–2997)	20.00
Nov 2009	Ei	40.88	(29.27–57.10)	**1063**	(761–1485)	16.44
	Cm	4.81	(2.26–10.24)	125	(59–266)	36.99
	Total[a]	46.30	(33.81–63.39)	1204	(879–1648)	15.60
April 2010	Ei	55.12	(37.10–81.89)	**1433**	(965–2129)	19.06
	Cm	6.89	(3.65–13.00)	179	(95–338)	30.69
	Cc	1.88	(0.46–7.62)	49	(12–198)	73.56
	Total	63.89	(44.86–90.99)	1661	(1166–2366)	17.18
Nov 2010	Ei	48.22	(32.57–71.41)	**1254**	(847–1857)	19.48
	Cm	8.96	(4.56–17.58)	233	(119–457)	33.11
	Total[a]	57.86	(40.32–83.05)	1505	(1048–2159)	18.12
March 2011	Ei	43.22	(30.45–61.33)	**1124**	(792–1594)	17.19
	Cm	8.26	(4.05–16.33)	215	(105–438)	34.80
	Cc	4.45	(2.34–8.46)	116	(61–220)	31.26
	Total	55.93	(41.06–76.18)	1454	(1067–1981)	15.45
April 2012	Ei	25.21	(18.63–34.11)	**555**	(410–750)	14.65
	Cm	9.22	(4.64–18.34)	203	(102–403)	33.31
	Cc	4.92	(1.76–13.79)	108	(39–303)	51.46
	Total	41.81	(31.55–55.40)	920	(694–1219)	14.19
April 2013	Ei	52.98	(39.80–70.53)	**1166**	(876–1552)	14.02
	Cm	3.73	(1.39–10.00)	82	(31–220)	49.07
	Cc	3.73	(1.09–12.80)	82	(24–282)	63.19
	Total	62.68	(47.82–82.16)	1379	(1052–1808)	13.49

[a]These global estimates of density and abundance include the single sighting of indeterminate species

distance sampling, the achieved precision is not dependent on the proportion of the population that is sampled but is determined by the variability in encounter rate and detectability. On average for the 2009–2013 surveys, the percent coefficient of variation was 12% higher for the mark-resight estimates. Distance sampling along line transects was also less invasive and more cost-effective (less labour intensive during the survey itself, and only a single survey was required to obtain estimates for several species). However, distance sampling cannot provide information on vital rates and thus a capture-recapture based method was required to obtain such information.

Both methods worked well for a population of this size within this relatively small geographic area at depths that were accessible to snorkelers. In addition, the flight distance of the turtles made it possible to obtain distances before responsive movement occurred and to capture a substantial number of turtles. Mark-resight methods could potentially be applied less invasively using photo-based methods as has been demonstrated for juvenile hawksbills (Dunbar et al. 2014), which also eliminates problems caused by tag loss. Mancini et al. (2015) contrasted strip transect and photo-identification based capture-recapture methods for in-water surveys of green turtles *Chelonia mydas* in the Egyptian Red Sea. Their methods produced similar results, with strip transects being easier to implement in the field and with resulting data that were simpler to analyze. For any in-water turtle survey, its particular aims and constraints will dictate what sampling method is used (Bjorndal & Bolten 2000, Bjorndal et al. 2010, Mancini et al. 2015). A key advantage of the methods we used is that they account for detectability or catchability, which is important for the effective long-term management of turtle populations. The methods provided complementary results that allow us to make statistically defensible comparisons of population status and dynamics over time and between sites where similarly robust methods have been used.

pling is that animals on or close to the transect line are seen. It seems that in particular hawksbill turtles were missed on or close to the transect line because they are potentially better camouflaged, especially for the novice turtle observer. Another critical assumption underlying distance sampling is that animals are detected in their original location before responsive movement occurs. This assumption may also have been violated due to observer inexperience. In this case, where there is likely responsive movement away from observers, this would result in negatively biased density and abundance estimates.

The mark-resight estimates were consistently less precise, which is expected because a large proportion of the target population has to be sampled to achieve reasonable precision with this method. For

Juvenile hawksbill densities in the fore-reef of the GRMR (e.g. 52.98 juvenile hawksbills km^{-2} with a 95% CI of 39.80 to 70.53 for the 2013 survey) are likely tied to a combination of factors such as food availability and habitat structural complexity (Rincon-Diaz et al. 2011a). Estimates from this study are similar to those reported elsewhere; however, given methodological variation, comparisons should be viewed cautiously. Based on capture effort in 2 habitat types with different octocoral cover, Cuevas et al. (2007) estimated a density of 30 and 38 juvenile hawksbills km^{-2} in Caribbean Mexico. Leon & Diez (1999) reported juvenile hawksbill densities for 5 sites ranging from 5.6 to 96.8 turtles km^{-2} (combined area density was 8.1 km^{-2}) in the Dominican Republic, with their higher-density estimates found in the coral reef habitat. Diez & van Dam (2002) reported a density index of 24.1 juvenile hawksbills km^{-2} at Mona Reef, Puerto Rico. In the Pacific, Limpus (1992) reported a much lower density of 3.34 turtles km^{-2} for predominantly juvenile hawksbill at Heron Reef, Australia. None of the studies in the Caribbean account for detectability/catchability and in some cases are likely underestimates of actual density. In addition to differences in methodologies, there are differences in habitat types that confound efforts to make comparisons.

The high survival probability estimated for juvenile hawksbills (97.5% with a 95% CI of 93.6 to 99%) indicates a low level of natural and human-induced mortality. This is congruent with the possible loss of top predators in the ecosystem, e.g. the Near Threatened Caribbean reef shark *Carcharhinus perezi*, although there are indications that shark populations are less impacted in protected areas such as GRMR (Bond et al. 2012), but most likely due to no or little direct or incidental take of turtles in the waters of the Glover's Reef seascape, unlike in many other areas (e.g. Alio et al. 2010, and see review by Campbell 2014). Survival probabilities from 1st capture (51.2%) and from subsequent captures (81.8%) were lower for small juvenile hawksbills (<55 cm) and other age classes (88.5%) in the Bahamas (Krueger et al. 2006). Survivorship was also high for immature hawksbills (71.1% for males and 92.2% for females) found in a foraging aggregation in the northern Great Barrier Reef (Bell et al. 2012).

The size distribution of captured turtles clearly indicates that the population within our study area is composed predominantly of juvenile hawksbill turtles (Fig. 2). The biometrics of this juvenile population are comparable to aggregations found elsewhere in the region. Leon & Diez (1999) found predominantly juvenile and sub-adult hawksbills at their study site at

Jaragua National Park and Cabo Rojo, Dominican Republic. The size range of those turtles was very similar to ours, but the average size (43.2 cm) of the hawksbills in the GRMR fore-reef habitat was slightly larger with more representatives in the larger size classes. This was also the case for a study by Blumenthal et al. (2009b) in the Cayman Islands. In contrast, the predominantly immature hawksbills in the Union Creek Reserve, Bahamas, were larger on average (48.8 cm) with a larger lower limit (24.3 cm) in their size range (Bjorndal & Bolten 2010). These slight differences in size distributions among sites may be related to a variety of factors, such as capture methods and experience, and habitat type and structure.

In our study, habitat type was broadly defined, and thus, a more detailed assessment would improve our understanding of specific turtle dietary and habitat needs within the fore-reef and other habitats of the GRMR. This could be accomplished by means of telemetry and towed cameras, similar to the methods described by Walcott et al. (2014). Glover's Reef Atoll, despite its distance from the mainland and relatively high level of protection, has not entirely escaped the impacts of over-fishing that are evident throughout the Caribbean and that make systems less resilient to other impacts (Loh et al. 2015). A dramatic phase shift from coral-dominated to algal-dominated environments has already occurred at Glover's Reef Atoll (McClanahan & Muthiga 1998), and further habitat changes are likely to occur at this and other sites in the Caribbean due to warming waters (McClanahan et al. 2009, González-Rivero et al. 2011). Hawksbill turtles seem to exhibit substantial flexibility in their selection of food items (Rincon-Diaz et al. 2011b, Bell 2013), which bodes well for their survival in a changing marine environment. However, further studies of habitat diversity and distribution (e.g. Acosta et al. 2015) and monitoring in conjunction with studies quantifying the most important food sources and sheltering habitat are needed. Ensuring that the spatial configuration of the GRMR covers resistant and resilient areas in the key fore-reef and other habitats is important for the long-term survival of this juvenile hawksbill feeding aggregation and all the biodiversity that depends on this ecosystem for their survival.

Hawksbill turtles cover extensive geographic areas throughout their lives in the West Atlantic (Bolten 2003, Horrocks et al. 2011, Meylan et al. 2011, Hawkes et al. 2012), which requires a regional approach to their management and conservation (Horrocks et al. 2011, Moncada et al. 2012, Campbell 2014). Investigations of long-range movements (including ontogenetic habitat shifts) of turtles from Glover's Reef add to the

body of knowledge from previous studies in the region (e.g. Velez-Zuazo et al. 2008, Blumenthal et al. 2009a,b, Browne et al. 2010, Agusa et al. 2011, Horrocks et al. 2011, Rincon-Diaz et al. 2011a, Scales et al. 2011, Hart et al. 2012, Hawkes et al. 2012, Leroux et al. 2012, Dunbar et al. 2013) and advance our understanding of hawksbill ecology and management needs in Belize, as well as the relationship between this site and rookeries and feeding aggregations in the wider Caribbean region falling within the 'Atlantic, Western Caribbean/USA' RMU (Wallace et al. 2010). In addition, comprehensive genetic and contaminant analyses of the samples collected from 2010 to 2013 will provide further insights into the relationships between this population and others in the region. Preliminary genetic stock assessment results indicate a relatively high haplotype diversity (0.71) in this fore-reef habitat, with at least 10 haplotypes representing 8 rookeries (Otero et al. 2012). This diversity provides more evidence for GRMR's importance to hawksbill populations throughout the region.

Although much work remains to be done to increase our understanding of this population of juvenile hawksbills and to inform management for their recovery within the regional context, these estimates of their density and abundance can be used to assess the efficacy of conservation actions over time, as well as providing a baseline to look at potential changes due to climate change. With upward of 1000 juvenile hawksbills estimated within the 22 km^2 fore-reef habitat in the GRMR and an estimated high survival probability, this area provides extremely important developmental habitat for Caribbean hawksbills and undoubtedly contributes to their recovery in the region.

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