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ORIGINAL PAPER

Hawksbill sea turtles in seagrass pastures: success in a peripheral habitat

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Abstract Hawksbill sea turtles, *Eretmochelys imbricata*, are closely associated with coral reef and other hard-bottom habitats. Seagrass pastures are peripheral habitats for Caribbean hawksbills. With the decline in quality and quantity of coral reefs, seagrass habitats may become more important for hawksbills. We use data from a 30-year mark-recapture study of hawksbills and green turtles, *Chelonia mydas*, in the southern Bahamas to assess the quality of a seagrass habitat for hawksbills. Size distribution, residence times, and body condition index for the seagrass hawksbill aggregation are similar to those of hawksbill aggregations over Caribbean reefs. Somatic growth rates of seagrass hawksbills are in the upper range of those reported for reef hawksbills. Based on these parameters, peripheral seagrass habitats can support healthy, productive hawksbill aggregations. During the 30-year study, a sixfold variation in green turtle density in the study area did not affect the productivity or body condition of hawksbills.

Introduction

Anthropogenic effects on habitats can affect the distribution of organisms and result in higher proportions of populations inhabiting formerly peripheral or sub-optimal habitats (Channell and Lomolino 2000; Naves et al. 2003; Namgail et al. 2007). Channell and Lomolino (2000) emphasized that conservation efforts should not necessarily be limited to core habitats; survival outlook of populations of endangered species may in fact be better in peripheral or sub-optimal habitats as a result of anthropogenic factors in core habitats. Understanding the ecology and demography of populations in these peripheral habitats is critical for appropriate conservation and management of both habitats and species.

The hawksbill sea turtle, *Eretmochelys imbricata*, is a circum-tropical species that is listed as Critically Endangered in the IUCN Red Book of Threatened Species (IUCN 2009) as assessed by Mortimer and Donnelly (2007). Similar to most sea turtle species, hawksbills appear to spend their first years in oceanic habitats (Reich et al. 2007) before recruiting to neritic habitats at a size of 20–35-cm carapace length. Once in neritic habitats, hawksbills are primarily associated with coral reefs, but also inhabit sponge reefs, reef walls, and other hard-bottom habitats (Meylan and Donnelly 1999). Their close association with coral reefs suggests that the survival outlook for hawksbills may be further jeopardized by the well-documented decline in quality and quantity of reef habitats (Pandolfi et al. 2003; Mora 2008) and reef-associated fauna (Jones et al. 2004; Wulff 2006).

Relatively little has been published on hawksbill ecology and demography, and many studies are characterized by small sample sizes because of low population levels. In the Atlantic, hawksbills feed primarily on sponges, coral-limorpharians, and zoanthids (Meylan 1988; León and Bjorndal 2002; Blumenthal et al. 2009). In the Pacific and Indian oceans, hawksbills have a broader diet that includes substantial quantities of algae in addition to sponges and other invertebrates (Bjorndal 1997; Whiting and Guinea 1998).

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Despite their close association with coral reefs and hard bottom habitats, hawksbills do inhabit seagrass pastures (Bjorndal and Bolten 1988; Diez et al. 2003), which can be considered peripheral habitats. If coral reef habitat continues to decline in abundance and quality, do seagrass pastures provide an alternative, good quality habitat, or are seagrass pastures sub-optimal habitat for hawksbills?

A 30-year mark-recapture study of sea turtles in the Union Creek Reserve (UCR), Bahamas, allows us to address this question. UCR, approximately 20 km^2 in area, is surrounded by and interspersed with mangroves, and has pastures of the seagrass *Thalassia testudinum*. Studies in UCR have focused on the larger aggregation of immature green turtles, *Chelonia mydas*, but we have also monitored the smaller aggregation of hawksbills that occur in the seagrass pastures in UCR.

To evaluate quality of seagrass habitat for hawksbills, we compare size distributions, growth rates, body condition index, and residence time with other hawksbill aggregations in Caribbean reef and hard-bottom habitats. We also assess potential effects of green turtles on hawksbills in a seagrass habitat using stable isotopes of carbon and nitrogen to compare dietary overlap and evaluating changes in hawksbill condition, growth, and relative population density with changes in abundance of green turtles in UCR.

Methods

Study site, data collection, and sample processing

Union Creek Reserve (UCR, 21.17°N, 73.57°W), approximately 20 km^2 in area, is located on the north coast of Great Inagua, the southernmost island in the Bahamas (Fig. 1). In the Bahamas, the term "creek" is applied to saltwater bays, not freshwater streams, as in some other countries. UCR is in the Bahamas National Park system, and sea turtles in UCR have legal protection from exploitation, which is well enforced by wardens of the Bahamas National Trust. The hawksbill aggregation in UCR is much smaller than the green turtle aggregation. Both hawksbill and green turtle aggregations in UCR are mixed stocks derived from several rookeries in the Atlantic, based on analyses of mtDNA sequences (Bowen et al. 2007; Bjorndal and Bolten 2008).

Annual capture effort occurred during a single 7–10-day interval. Hawksbills and green turtles were caught throughout the entire study area by diving on them from the bow of a motorboat following a brief chase. Turtles were tagged with flipper tags bearing an identification number, return address, and offer of a reward for return of the tag. To maintain individual identification of turtles, two to four tags were applied to each turtle and tags were replaced as needed upon recapture; no loss of any tag was reported for recaptured hawksbills. Straight carapace length (SCL) was measured for all hawksbills in all years to the nearest 0.1 cm from the anterior midpoint of the nuchal scute to the posterior tip of the longer of the pair of posterior marginal scutes with anthropometer calipers (GPM model 101, Switzerland). Body mass was measured for all hawksbills with a spring scale to the nearest 0.1 kg in a subset of years (1979, 1980, 1982–1985, 1986, 1989, 1998, 2005–2008). All measurements were made by ABB and recorded by KAB. The precision of SCL, determined as mean discrepancy between repeated measurements, is 0.046 cm (Bjorndal and Bolten 1988). Body condition index (CI) was calculated as Fulton's K ($CI = [mass/SCL^3] \times 10^4$; Ricker 1975).

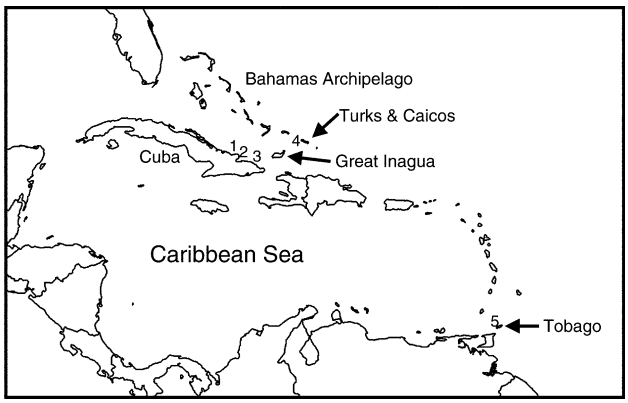

Fig. 1 Map showing the island of Great Inagua and locations of sightings of five hawksbills tagged in UCR. Hawksbills 1–4 were killed by fishers in Cuba and Turks and Caicos; hawksbill 5 was reported nesting on the island of Tobago

For stable isotope analyses, skin samples were collected from 42 resident green turtles and 22 hawksbills captured in UCR in 2002 and 2003. The hawksbills included seven residents (hawksbills captured in previous years) and 15 hawksbills captured for the first time. We used a sterile 6-mm biopsy punch (designed for collecting epidermis samples from humans) to collect samples of non-keratinized skin from the "shoulder" area of each turtle after cleaning the area with alcohol. Skin samples were stored in 70% ethanol at room temperature; storage in 70% ethanol does not affect stable isotope values in turtle skin (Barrow et al. 2008).

For stable isotope analysis, skin biopsy samples were rinsed in distilled water to remove any foreign material and cleaned with isopropyl alcohol swabs. The epidermis was removed, finely diced with a scalpel blade, and dried at 60°C for a minimum of 24 h. After drying, lipids were removed from all samples using an accelerated solvent extractor (ASE) with petroleum ether as the solvent. Approximately 550 μg of each dried, lipid-free sample was loaded into a pre-cleaned 4 × 6 mm tin capsule.

All samples were combusted in a COSTECH ECS 4010 elemental analyzer interfaced via a Finnigan-MAT ConFlow III device (Finnigan MAT, Breman, Germany) to a Finnigan-MAT DeltaPlus XL (Breman, Germany) isotope ratio mass spectrometer in the light stable isotope laboratory in the Department of Geological Sciences, University of Florida, Gainesville, Florida, USA. Stable isotope abundances were expressed in delta (δ) notation, defined as parts per thousand (‰) relative to the standard as follows:

$$\delta = \left(\left[R_{\text{sample}}/R_{\text{standard}}\right] - 1\right)(1000)$$

where R_{sample} and R_{standard} are the corresponding ratios of heavy to light isotopes ($^{13}C/^{12}C$ and $^{15}N/^{14}N$) in the sample and international standard, respectively. R_{standard} for ^{13}C was Vienna Pee Dee Belemnite (VPDB) and for ^{15}N was atmospheric N_2. Internal standards were inserted in all runs at regular intervals to calibrate the system and assess drift over time. The analytical precision of our measurements, measured as the SD of replicates of standards, was 0.09 for both $\delta^{13}C$ and $\delta^{15}N$ ($N = 88$ and 91, respectively).

Sampling design for growth and statistical analyses

The sampling design in this study was mixed longitudinal sampling (sampling with partial replacement). Age of the hawksbills was not known, as in most sea turtle studies, so year and cohort effects are confounded. Despite this confounding of environmental and cohort effects, the year covariate was included because it is a constraint of time series sampling design in all mark-recapture studies.

We modeled somatic growth statistically using generalized additive models (GAM). Our model had one response variable (absolute growth rate) and three potential growth covariates. The three covariates were all continuous (mean SCL, recapture interval, and year). Mean SCL is the arithmetic mean of SCL at initial capture and recapture. Mean SCL is the best approximation of SCL for the growth interval, particularly if the intervals are sufficiently short so that growth is linear. Recapture interval was included in the model to assess any bias from variable durations of these intervals. Year was assigned as the calendar year of the midpoint of the recapture interval.

The regression model comprised an identity link, a quasi-likelihood error function, and cubic smoothing splines. The significance of the contribution of each covariate to the overall model fit was evaluated with analysis of deviance. Significant covariates were evaluated for nonlinearity using a nonparametric F ratio test. The value of R^2 was calculated as (null deviance–residual deviance)/null deviance. The use of generalized additive models in the analysis of growth rates is discussed in more detail in Chaloupka and Limpus (1997).

Residence times were estimated by adding 0.5 years to the beginning and end of the capture record of each hawksbill. This addition accounted for the fact that we only surveyed once a year and that an individual turtle could have been in UCR before the first capture and after the last capture.

We used S-Plus software (S-Plus v. 7.0.3) for all statistical analyses. For all analyses, $\alpha = 0.05$.

Results

From 1979 through 2008, 91 hawksbills were captured a total of 129 times. The number of hawksbills captured each year varied from 0 to 14. SCL values ranged from 24.3 to 71.3 cm (mean = 48.8 cm, SD = 9.4 cm, $N = 129$; Fig. 2a). Multiple captures of individuals were 16 hawksbills captured twice, four hawksbills 3 times, three hawksbills 4 times and one hawksbill 5 times. Distances between successive capture locations of individual hawksbills were less than 500 m. Estimated residence times ranged from 1 to 7 years with 1 year as the overwhelming majority (Fig. 3).

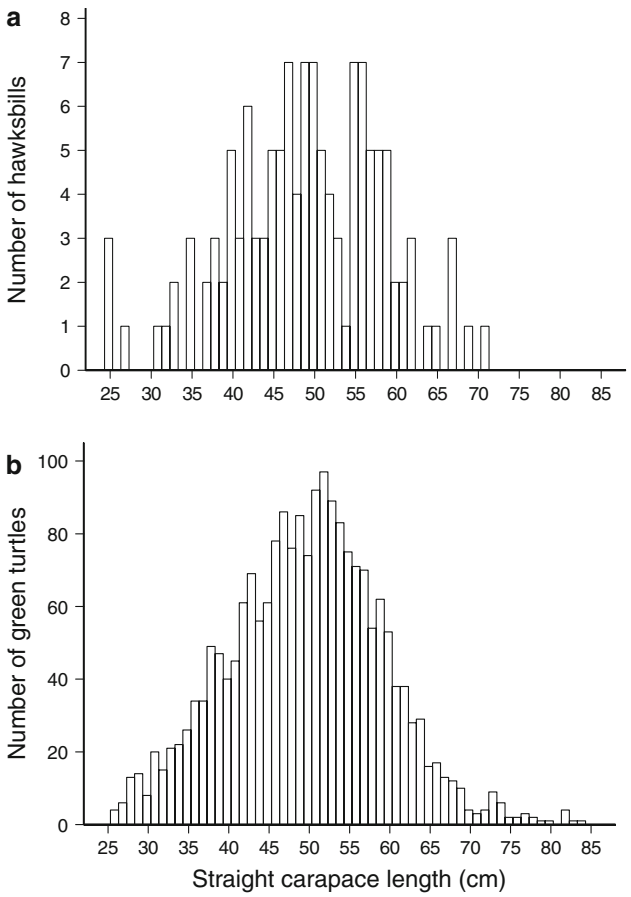

Fig. 2 Straight carapace length (cm) distributions for all turtle captures in UCR from 1979 through 2008 plotted on the same x-axis to facilitate comparison. **a** hawksbills, $N = 129$ and **b** green turtles, $N = 2{,}042$

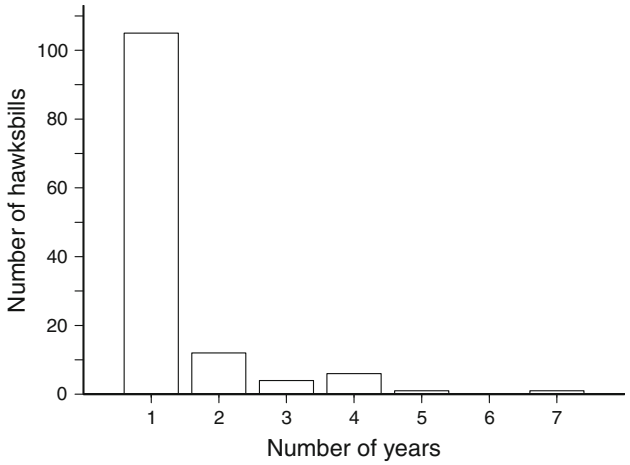

Fig. 3 Estimates of residence times for hawksbills in UCR

Most, if not all, of the hawksbills in UCR were immature. The largest turtles may have been adult females because the smallest hawksbill nesting at Mona Island, Puerto Rico, was 70.8 cm SCL (Diez and Van Dam 2002a), and 69.7 cm SCL was reported to be adult size in the Dominican Republic (León and Diez 1999). No hawksbills in UCR exhibited male secondary sex characteristics.

Body condition index (CI) of hawksbills in UCR ranged from 1.05 to 1.41 (median = 1.17, mean = 1.17, SD = 0.08, $N = 45$). Over the SCL range (24.8–68.4 cm) of CI values, the relationship between mass and SCL^3 is linear (least squares regression, $df = 43$, $R^2 = 0.9735$, $P < 0.0001$); CI was not significantly correlated with SCL (Spearman's rank, $\rho = 0.0319$, $P = 0.833$); and CI did not vary significantly among years (ANOVA, $df = 43$, $P = 0.425$). Thus, CI values could be compared and combined among size classes and years (Bolger and Connolly 1989).

Thirty-seven growth increments were measured in 24 hawksbills (Fig. 4a, open circles). Growth rates varied from 2.3 to 15.6 cm/year, with a mean of 6.0 cm/year and a median of 5.9 cm/year. Durations of all growth intervals were greater than 11 months. Intervals ranged from 330 to 1,179 days (median = 382 days, mean = 500 days, SD = 252); 78% of the intervals were between 11 months and 2 years.

The GAM regression analysis of growth rates indicated that only mean SCL had a significant effect ($P < 0.0001$), while the other two covariates (duration of growth interval and year) were not significant (Table 1; Fig. 5). The test for nonlinearity of SCL was not significant ($P = 0.0958$). Covariate function plots for the GAM model fit (Fig. 5) are centered on the response scale to ensure valid pointwise 95% confidence bands. However, these plots are more difficult to interpret visually, so the model fits with a smoothing spline ($df = 3$) are plotted in Fig. 4b on the original response scale. The curve is a monotonic declining

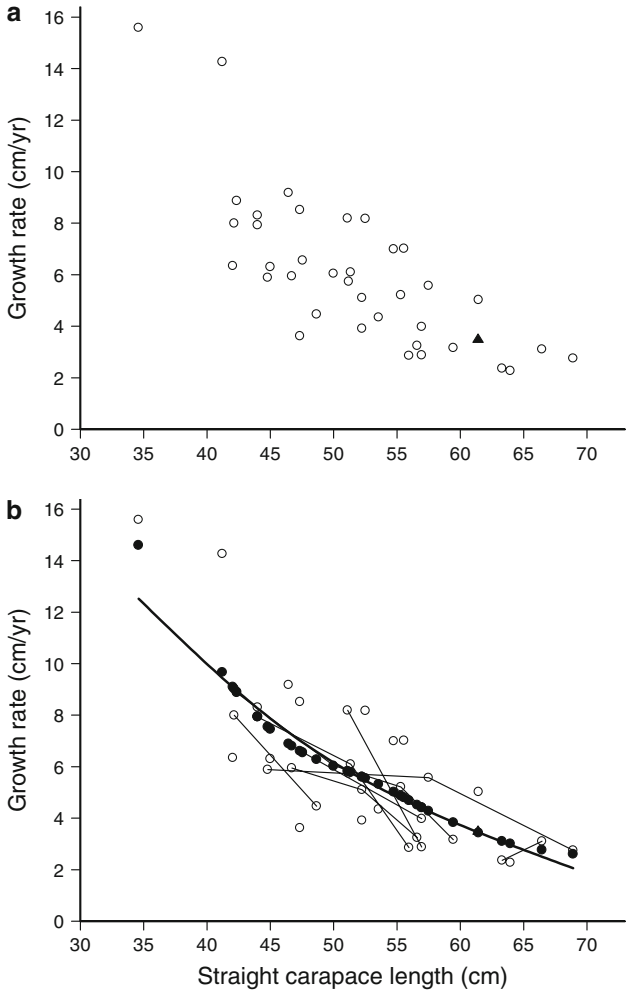

Fig. 4 Relationship of growth rate (cm/year) to mean straight carapace length (cm) for hawksbills tagged in Union Creek Reserve. **a** open circles are turtles tagged and recaptured in Union Creek Reserve; closed triangle is hawksbill first tagged in UCR and measured while nesting in Tobago–not used in growth analyses. **b** solid circles are GAM fits from model in Table 1, thick line is smoothing spline ($df = 3$); thin lines connect successive growth increments of 8 individual hawksbills; closed triangle of Tobago hawksbill is obscured under the spline

function with growth rates declining with increasing SCL. This model accounted for 74.9% of the variation in growth (Table 1).

Mean stable isotope signatures of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) for all hawksbill skin samples ($N = 22$) were −10.0‰ (SD = 1.4) and 5.3‰ (SD = 1.1), respectively (Fig. 6). For resident hawksbills (present in UCR at least one year) mean (SD) values were −10.32‰ (0.49) $\delta^{13}C$ and 5.72‰ (1.01) $\delta^{15}N$. For first-capture hawksbills in UCR, mean (SD) values were −9.83‰ (1.68) $\delta^{13}C$ and 5.13‰ (1.08) $\delta^{15}N$. Values for $\delta^{13}C$ and $\delta^{15}N$ were not significantly different between resident and first-capture hawksbills (*t*-tests, $P = 0.464$ for $\delta^{13}C$ and $P = 0.237$ for $\delta^{15}N$). Mean $\delta^{13}C$ and $\delta^{15}N$ for resident green turtle skin

Table 1 Summary of generalized additive regression analysis of growth in hawksbill sea turtles (identity link, quasi-likelihood error function, cubic smoothing splines)

Parameter	*df*	Deviance	Residual *df*	Residual deviance	*P*(Chisq)	Nonlinear effects (nonparametric)		
						df	*F*	*P*
3 parameter model[a]								
Null			36.000	47.217				
Mean SCL	1.00	27.996	35.000	19.221	<0.0001	3	2.373	0.096
Recapture interval	1.00	0.014	34.000	19.206	0.905			
Year	9.91	7.367	24.089	11.840	0.683			

P(Chisq) reported for analysis of deviance test. A significant nonparametric *F* means that the covariate is nonlinear; this test is only relevant for significant model covariates [*P*(Chisq)]

[a] Null deviance = 47.22, null *df* = 36, residual deviance = 11.84, residual *df* = 24.09, quasi-likelihood dispersion parameter = 0.500, $R^2 = 0.749$

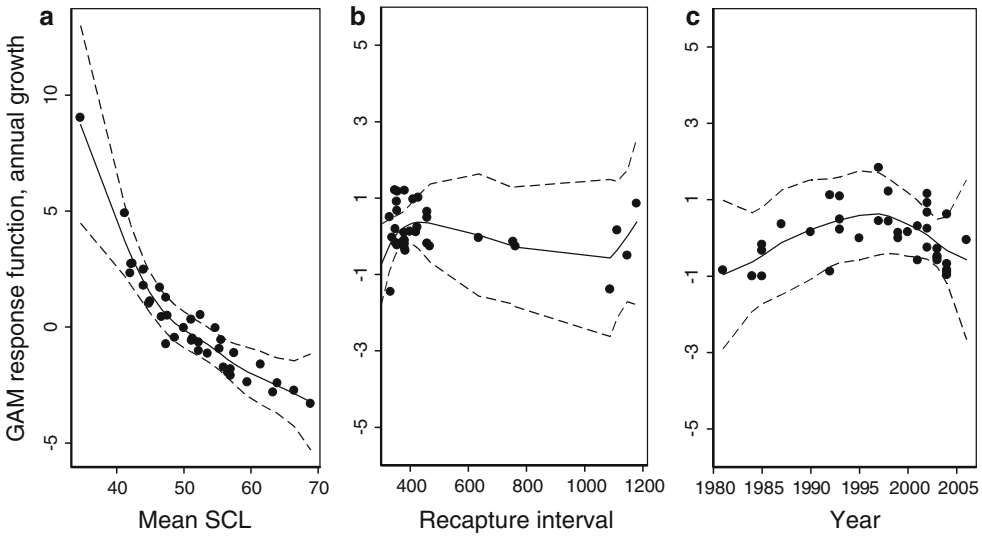

Fig. 5 Graphical summaries of generalized additive regression analysis of growth covariates of model in Table 1. **a** mean straight carapace length (SCL, cm), **b** recapture intervals (days), and **c** year. Only mean SCL is significant. The response variable (annual growth rate) is shown on the *y*-axis as a centered smoothed function scale to ensure valid pointwise 95% confidence bands around the fits (*dashed lines*). The *solid lines* are the cubic smoothing spline fits for each covariate conditioned on all other covariates in the analysis. *Solid circles* are residuals

samples ($N = 42$) were −5.8‰ (SD = 1.2) and 1.7‰ (SD = 1.2), respectively. Hawksbills and green turtles had significantly different δ^{13}C and δ^{15}N signatures (*t*-tests: δ^{13}C, $t = 12.523$, $df = 62$, $P < 0.0001$; δ^{15}N, $t = -11.701$, $df = 62$, $P < 0.0001$). Hawksbill SCL (30.3–63.9 cm) had a significant, positive correlation with δ^{15}N (Spearman rank, $\rho = 0.601$, $P = 0.006$), but no significant correlation with δ^{13}C (Spearman rank, $\rho = -0.085$, $P = 0.696$; Fig. 7).

Of the 91 hawksbills tagged in UCR, long-distance recaptures/sightings of five hawksbills have been reported to us (Fig. 1). All of these turtles had been captured only once in UCR, so we calculated the interval between tagging date and recapture/sighting date as the maximum time between leaving UCR and being recaptured, or maximum time at large. Fishers captured and killed four of the hawksbills. The three hawksbills recaptured in Cuba were all taken in Holguin Province and had maximum times at large of 1,795, 1,990, and 2,370 days. The hawksbill recaptured on Providenciales, Turks and Caicos, had a maximum time at large of 381 days. These recaptures are relatively short distances compared with some recaptures of juvenile hawksbills from elsewhere in the Atlantic (Meylan 1999; Bellini et al. 2000; Grossman et al. 2007; Blumenthal et al. 2009).

The hawksbill reported from Tobago was tagged in UCR on 2 February 1996 and was first seen nesting in Tobago on 13 June 2005 for a maximum time at large of 3,419 days or 9.37 years. In an earlier report of this recapture (Bjorndal et al. 2008), growth rate was calculated for curved carapace length measured from nuchal notch to posterior tip of the longer posterior marginal scute because that was the measure recorded in Tobago. Using the conversion equation presented in Bjorndal et al. (2008), we calculated growth in SCL to be consistent with the values presented in this paper. The mean size was 61.4 cm SCL, and growth rate in SCL was 3.5 cm/year (Fig. 4a). The growth increment of the Tobago recapture was not included in statistical analyses of growth presented here.

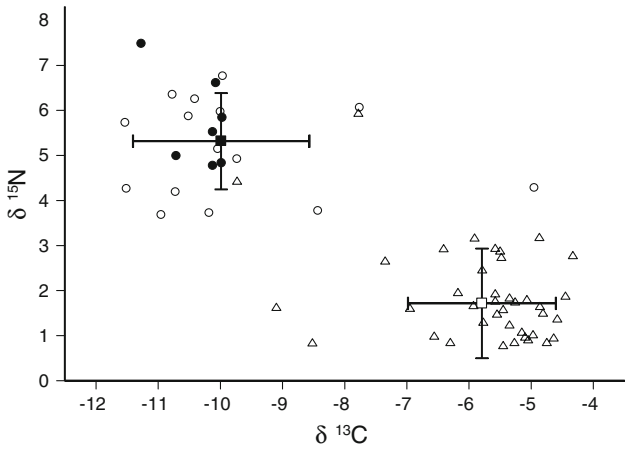

Fig. 6 Stable isotope signatures (‰) of carbon (δ^{13}C) and nitrogen (δ^{15}N) in skin samples. *Solid circles* are resident hawksbills ($N = 7$), *open circles* are first-capture hawksbills ($N = 15$), and *open triangles* are resident green turtles ($N = 42$). *Solid square* is mean value of all hawksbills ($N = 22$), and *open square* is green turtle mean value; *bars* represent 1 standard deviation. Hawksbill and green turtle signatures are significantly different (see text). The largest hawksbill δ^{13}C value is the smallest hawksbill

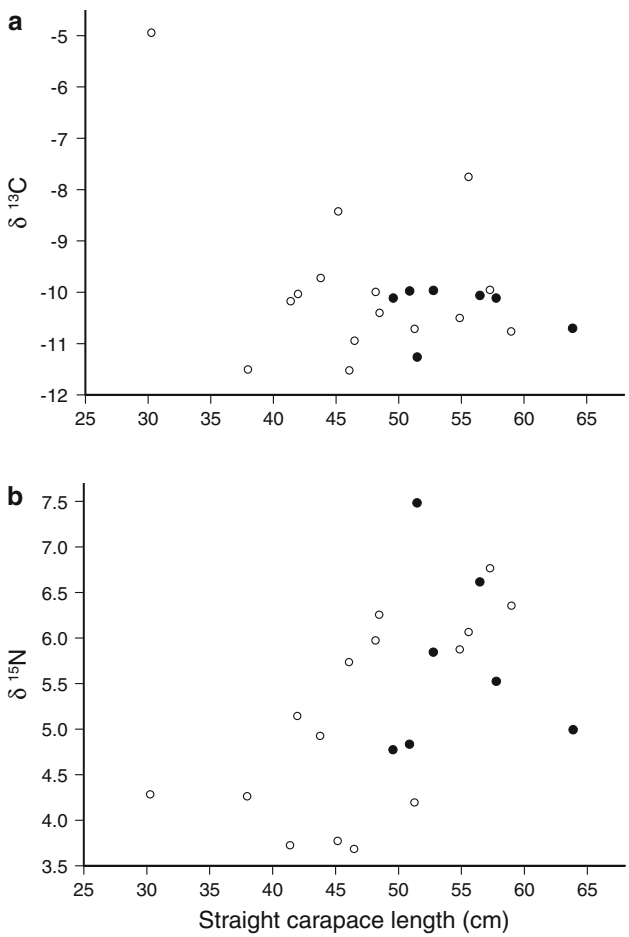

Fig. 7 Relationships between straight carapace length and stable isotope signatures (‰) of **a** carbon (δ^{13}C) and **b** nitrogen (δ^{15}N). *Open circles* are first-capture hawksbills in UCR; *closed circles* are resident hawksbills in UCR. Spearman rank correlation is not significant for δ^{13}C and is significant for δ^{15}N

Green turtles greatly outnumber hawksbills in UCR. The percentage of all turtles captured in UCR each year that were hawksbills ranged from 0 to 15.9% (mean = 6.6%, SD = 4.4). Numbers of hawksbills and green turtles captured each year were not correlated (Spearman rank test, $\rho = 0.147$, $P = 0.464$).

Discussion

Comparison of hawksbill foraging aggregations in seagrass and hard bottom habitats

Size distribution, residence time, and abundance

The size range of hawksbills in UCR (24.3–71.3 cm SCL, $N = 129$) is similar to that reported for other Caribbean hawksbill foraging aggregations in reef and hard bottom habitats: 22.5–67.5 cm SCL ($N = 63$) in St. Thomas, USVI (Boulon 1994); 19.5–69.7 cm SCL ($N = 275$) in Jaragua, Dominican Republic (León and Diez 1999); 20.0–84.5 cm SCL ($N = 197$) in three sites in Puerto Rico (Diez and van Dam 2002b); and 20.5–62.6 cm SCL ($N = 218$) in the Caymans (Blumenthal et al. 2009). The foraging aggregations in Puerto Rico included substantially larger turtles than the other aggregations, probably as a result of the much deeper waters and the presence of a nesting beach in the vicinity. All of the distributions share a characteristic shape–a uni-modal curve with a central tendency (Fig. 2a)–but the size range of the peak abundance varies. The smallest hawksbill captured in UCR was 1.8–4.8 cm larger than the smallest turtles captured in the other aggregations. It is not clear whether this size difference is biologically significant.

Residence times for hawksbills are difficult to compare among studies because of the variety of techniques used. Some studies report percentages of turtles caught various numbers of times. At Fernando de Noronha, Brazil (Sanches and Bellini 1999), of 125 hawksbills captured 63% were caught once, 12% twice, 7% 3 times, 3% 4 times and 15% ≥5 times. In Little Cayman, of 135 hawksbills captured, 72% were captured once, 19% twice, 7% 3 times, 2% 4 times, and 1% 5 times; in Grand Cayman, of 97 hawksbills captured, 88% were captured once and 12% captured twice (Blumenthal et al. 2009). The distribution for the 91 hawksbills captured in UCR was 73.6% captured once, 17.6% twice, 4.4% 3 times, 3.3% 4 times and 1.1% 5 times. The Fernando de Noronha aggregation has a higher proportion of multiple captures, whereas the Cayman aggregations have values similar to those of UCR.

However, these values must be interpreted with caution. In both Fernando de Noronha and the Caymans, capture effort was made throughout the year, so that minimum recapture duration in the Caymans was 11 days (Blumenthal et al. 2009), and one turtle in Brazil was captured 91 times during the 10-year study (Sanches and Bellini 1999). Because hawksbills were only captured during one interval each year in UCR, our minimum recapture interval is approximately 1 year. Thus, similar distributions of proportions for Caymans and UCR suggest that hawksbills are resident for longer in UCR than in the Caymans. However, the duration of the studies–8 years for the Caymans, 10 years for Fernando de Noronha, and 30 years for UCR–also affects the interpretation of these data; additional years of monitoring may yield longer residence times for Cayman and Fernando de Noronha hawksbills.

During an 8-year study at Mona and Monito Islands based on approximate annual surveys (Diez and van Dam 2002b), 197 turtles were captured 2 or more times. The elapsed time between first and last capture had a median value of 2.94 year, and the range was ~1–8 years. Because turtles only captured once were not included in the Diez and van Dam (2002b) study, the equivalent values for UCR are median = 1.58 year, mean = 2.06 year (SD = 1.33), and range = 0.9–6.2 years. Given the larger size distribution of hawksbills in the Mona and Monito foraging grounds, it is not surprising that they appear to remain resident for longer periods of time. Again, the deeper waters in the Puerto Rican foraging sites may be responsible. Sea turtles in the Atlantic tend to leave inshore, shallow water developmental foraging grounds as they increase in size and shift to deeper waters (Carr 1980; León and Diez 1999; Bjorndal et al. 2000).

Estimates of abundance of hawksbills in Caribbean study sites have been based on catch or sightings per unit effort (CPUE). We did not attempt to estimate abundance of hawksbills in UCR because the large proportion of green turtles dominate our capture effort and make any estimate of hawksbills based on CPUE questionable. However, in their survey of a hawksbill aggregation over a seagrass pasture at Saona Island, Dominican Republic, Diez et al. (2003) reported 7.7 hawksbill sightings/h. Parallel values recorded by the same investigators were 3.4 and 4.7 hawksbills per hour over reef and hard-bottom habitats off Mona-Monito islands and at Jaragua, Dominican Republic, respectively (Diez et al. 2003). These results indicate that hawksbill abundance over seagrass pastures can equal or exceed those over reef and hard-bottom habitats.

Condition index

Various indices are used to assess body condition in livestock and wildlife, such as the appearance and palpation of back and hind quarters in dairy cattle (Wildman et al. 1982) or observations of abdominal profiles in wild geese (Owen 1981). Although not without controversy (Green 2001; Hayes and Shonkwiler 2001; Schulte-Hostedde et al. 2005), condition indices are often used as measures of fitness and health. The most common indices are a function of body mass and body size. The CI we used ([mass/SCL^3] $\times$ 10^4) had significant predictive power in growth models for captive green turtles (Roark et al. 2009a) and was positively correlated with growth rates in green turtles in UCR (Bjorndal et al. 2000).

The same condition index has also been used for hawksbills at five study sites in reef and hard-bottom habitats. Diez and van Dam (2002b) reported CI values of 1.16, 1.18, and 1.24 for their three study sites in Puerto Rico. Hawksbills had mean CI values of 1.25 (SD = 0.17) at Little Cayman foraging grounds and 1.24 (SD = 0.18) at Grand Cayman (Blumenthal et al. 2009). The mean CI value for hawksbills in UCR (mean = 1.17, SD = 0.08, $N = 45$) were the same as values from two of the Puerto Rican foraging areas, and the range of values of individual hawksbills in UCR (1.05–1.41) encompassed all mean values reported for the five study sites. Thus, CI of hawksbills in UCR is within the range of CI values reported for hawksbills from hard-bottom habitats.

Growth rates

There is considerable overlap in growth rates among hawksbill aggregations in the Caribbean (Fig. 8a). The growth rates of hawksbills in UCR are in the upper range of the values reported to date.

Carapace length accounts for approximately 75% of the variation in growth rates of UCR hawksbills (Table 1). In all studies of hawksbill growth rates to date, except perhaps for Fog Bay, Australia (no apparent effect, but no analysis; Whiting and Guinea 1998), body size has had a significant effect on growth rates, although the shapes of the functions vary (Fig. 8a, b). In the Caribbean, growth rates reported for UCR, Dominican Republic (León and Diez 1999), USVI (Boulon 1994), and Caymans (Blumenthal et al. 2009) all demonstrated monotonic declining growth curves with increasing carapace length. However, Diez and van Dam (2002b) reported growth rates in the 20–30-cm size class were lower than those in the 30–40-cm size class at their three study sites in Puerto Rico, although at Monito the most rapid growth rates for the population were measured in the smallest (20–23 cm) turtles. Growth rates then declined with SCL following the peak in the 30–40-cm size class.

Comparing function shapes among these studies is difficult because the size ranges vary–note that both UCR and USVI do not include hawksbills in the 20–30 cm size class

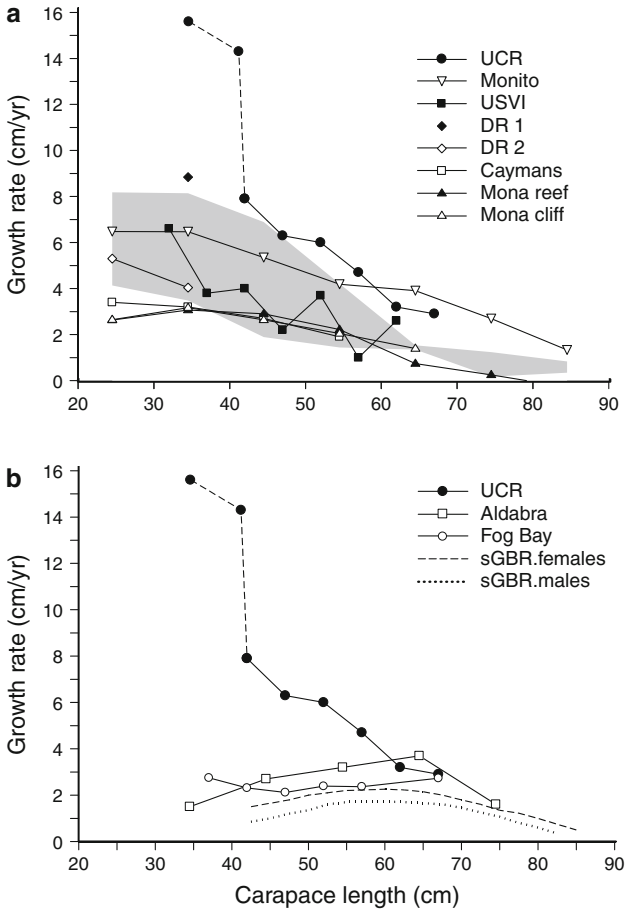

Fig. 8 Relationships of growth rate (cm/year) to mean carapace length (straight [SCL] and curved [CCL]). We did not convert CCL to SCL because, as shown for green turtles (Bjorndal and Bolten 1989), differences in growth rates between SCL and CCL are minimal in hawksbills (Bjorndal and Bolten, unpublished data). In both graphs, lines connect points that represent mean values of 5- or 10-cm CL increments except for the lines for sGBR females and males that are the cubic B-spline smooth fits from Chaloupka and Limpus (1997) and the first two UCR points. See text for sources of data. **a** Caribbean hawksbill foraging aggregations (all measured as SCL from the anterior midpoint of the nuchal scute to the tip of posterior marginal scute). UCR is Union Creek Reserve, USVI is US Virgin Islands, DR 1 is Lanza Zó, Dominican Republic, and DR 2 is combination of 3 other sites in the Dominican Republic. *Dashed line* highlights first 2 points from UCR that represent single individuals. Unpublished data from Barbados, Cuba, and Mexico (IUCN 2002) are presented as shaded area to protect publication rights of data owners. Upper and lower bounds of shaded area represent highest and lowest mean value of the 3 study sites for 10-cm SCL increments. **b** Pacific and Indian Ocean hawksbill foraging aggregations (all measured as CCL). sGBR is southern Great Barrier Reef; UCR data (growth in SCL) are repeated to facilitate comparison between (**a**) and (**b**)

that grow more slowly in other studies–and because the coarse grain of the 10-cm size classes can yield misleading results. The non-monotonic Caribbean growth functions are quite different from those in the Pacific and Indian oceans (Fig. 8b) because the peak growth rates are exhibited in a much smaller size class in the Caribbean. We suggest that the slower growth rates in the smallest hawksbill size class in the Caribbean may be a result of delayed growth during the transition from their oceanic diet to the digestively challenging sponge diet (see "Discussion" below). This period of limited nutrition could be followed by a period of compensatory, or "catch-up," growth during which turtles would exhibit more rapid growth. Compensatory growth and growth responses to periods of limit feeding followed by ad libitum feeding have been demonstrated in juvenile sea turtles (Bjorndal et al. 2003; Roark et al. 2009b). The very rapid growth rates recorded for two small hawksbills in UCR (14.3 and 15.6 cm/year, Fig. 8a) may well represent examples of compensatory growth. We are confident that both of these growth increments are accurate. Both of these hawksbills were tagged with four flipper tags, had reasonable recapture intervals (348 and 459 days, respectively), and had six linear measures recorded, which all showed equivalent growth rates. These rapid growth rates are of interest because they reflect the capacity for growth in wild hawksbills. Also suggestive of compensatory growth is the fact that successive growth rates for six of the eight turtles with more than one growth increment fall above and below the smoothing spline in Fig. 4b, similar to the pattern for loggerheads exhibiting compensatory growth (Bjorndal et al. 2003). That is, individual turtles do not grow at genetically determined rates. Rather, growth rates for individuals shift above and below the population mean over time and decrease the size variation within age cohorts.

Hawksbill aggregations in the Pacific and Indian oceans have very different growth functions, and growth rates tend to be slower, than those in the Caribbean (Fig. 8b). In Fog Bay, Australia (Whiting and Guinea 1998), there is no clear pattern. In the southern Great Barrier Reef (Chaloupka and Limpus 1997), males and females exhibit significantly different rates, but have a similar pattern of a unimodal curve with a peak at about 60 cm CCL. Aldabra had a pattern similar to the southern Great Barrier Reef, with peak growth rates in the 50–60 cm CCL size class (Mortimer et al. 2003). No explanation for this growth function has been offered. Higher growth rates in large juveniles suggest a higher plane of nutrition resulting from better quality or quantity of food available to the larger turtles. Improved nutrition in larger hawksbills could result from exploitation or interference competition between size classes, better quality foraging habitats, or a size-threshold to prey access, such as a nutritious sponge with a very tough cortex that only a large hawksbill can penetrate. Detailed studies on foraging habitats, intake, and diet quality are needed to address this question.

The departure of large subadult hawksbills from Caribbean study sites results in very limited data on growth rates in the years before sexual maturity and precludes accurate

estimates of age to sexual maturity. One hawksbill tagged in UCR (45.1 cm SCL) was recorded nesting on Tobago 9.4 years later (Bjorndal et al. 2008) at a size of 77.7 cm SCL (converted from 84.0 CCL). Because the growth rate for the 9.4-year interval falls on the growth curve (Fig. 4) and growth rates in hawksbills become negligible after sexual maturity (Bjorndal et al. 1985; Chaloupka and Limpus 1997), when resources are channeled to reproduction rather than growth, 9.4 years may be a good approximation of time to maturity in this 45-cm SCL hawksbill.

Seagrass pastures: shared habitats for hawksbills and green turtles

Seagrass pastures are the primary habitat for green turtles in the Caribbean, and grazing by green turtles on the seagrass *Thalassia testudinum* can change the structure from dense pastures with 20-cm leaf blades to stubble fields with 5-cm blades (Bjorndal 1980; Williams 1988). Grazing has substantial effects on the structure and nutrient content of *T. testudinum* pastures (Moran and Bjorndal 2005, 2007). Numbers of nesting green turtles are increasing at some Caribbean and Atlantic nesting beaches (Godley et al. 2001; Chaloupka et al. 2008), so the number of green turtles sharing seagrass pastures with hawksbills may be increasing.

To what extent do green turtles affect the quality of seagrass habitats for hawksbills? UCR is a good site to address this question because the green turtle population has fluctuated sixfold over the 30-year study as a result of changes in recruitment in response to changes in food availability (Bjorndal et al. 2005). The UCR green turtle aggregation has exhibited density dependent effects. At high green turtle densities, green turtle growth rates and condition indices were low because of depleted food resources, yielding a significant year effect on green turtle growth rates (Bjorndal et al. 2000). Green turtles have been at, or may have exceeded, carrying capacity in UCR during some intervals in the past 30 years (Bjorndal et al. 2000, 2005). Green turtles have a similar body size range as hawksbills in UCR (Fig. 2b).

If green turtle abundance affects habitat quality for hawksbills, we would expect at least one of three scenarios. First, numbers of green turtles and hawksbills captured each year would be correlated, either positively or negatively, depending on whether higher green turtle abundance improves or degrades the habitat for hawksbills. In UCR, there is no correlation between the numbers of green turtles and hawksbills captured each year.

Second, growth rates and condition indices in hawksbills would track changes in these parameters in green turtles. Although green turtle growth rates and CI have varied significantly among years and with green turtle density, hawksbill growth rates and CI have not.

Third, overlap in stable isotope signatures would reveal potential competition for food resources. We have not documented specific diet items consumed by hawksbills in UCR, but we have characterized their diet with stable isotope signatures of carbon (δ^{13}C) and nitrogen (δ^{15}N). Within the same community, differences in δ^{13}C and δ^{15}N values reflect differences in diet, and δ^{15}N values allow us to evaluate the relative trophic position of species or individuals (Newsome et al. 2007). Stable isotope signatures of hawksbills and green turtles (Fig. 6) demonstrate that the two species are feeding on different diets, and that hawksbills are feeding at a higher trophic level than green turtles. Green turtles in UCR feed primarily on the seagrass *T. testudinum* (Bjorndal 1980); the higher δ^{15}N values in hawksbills indicate that they are on a trophic level above primary consumers. There is almost certainly some diet overlap between green turtles and hawksbills in UCR because the chicken liver sponge, *Chondrilla nucula*, is consumed by green turtles in UCR (Bjorndal 1990) and is a very common diet species in hawksbills throughout the Caribbean (Meylan 1988; León and Bjorndal 2002). This diet overlap is clearly small, however, based on the stable isotope signatures. Unfortunately, we do not know of any other δ^{13}C or δ^{15}N values available for hawksbills with which to compare our data.

Bjorndal (1997) suggested that small Caribbean hawksbills, during the transition from their oceanic diet to a diet comprised primarily of sponges, may ingest a larger proportion of other invertebrates and algae than do larger hawksbills. This idea was based on three studies in which the smallest individuals had ingested substantial quantities of algae and invertebrates other than sponges. This transition diet could sustain the hawksbill as it adjusts to the physiological (toxins) and mechanical (silica spicules) challenges of feeding on a sponge diet. The positive correlation between δ^{15}N values and SCL (Fig. 7b) suggests there may be a shift from omnivory to more complete carnivory as hawksbills grow. In addition, the hawksbill with the highest δ^{13}C value (Figs. 6 and 7a) is the smallest hawksbill that we analyzed, also suggesting a different diet in this smallest individual. However, the increase in δ^{15}N values with size is also consistent with hawksbills feeding on the same diet, but with larger turtles growing more slowly and thus having a greater discrimination factor between diet and turtle tissues (Martínez del Rio and Wolf 2005; Reich et al. 2008).

Conclusions

Our results indicate that seagrass pastures, although apparently peripheral habitats for hawksbills, can support

healthy, productive hawksbill aggregations based on two measures of wellbeing and productivity. The condition index of hawksbills in UCR fell within the range of hawksbill aggregations at five other hawksbill aggregations on reef and hard bottom habitats in the Caribbean. Growth rates of hawksbills in UCR were in the upper range of rates measured at ten hawksbill aggregations in Caribbean reef and hard-bottom habitats. In addition, characteristics such as size distribution and residence times of hawksbills in UCR were consistent with those of hawksbill aggregations over hard-bottom habitats. Abundance estimates for a hawksbill aggregation over a seagrass pasture in the southern Dominican Republic exceeded parallel estimates of abundance for hawksbills over reef and hard-bottom habitats. Therefore, although seagrass habitats may not be as common a habitat for hawksbills as coral reefs and hard-bottom habitat, seagrass pastures may become more important, and can support equivalent productivity, for hawksbills if coral reefs continue to decline.

Although the quality of the habitat for hawksbills apparently did not change with the changes in green turtle population densities in UCR, even at the lowest densities, the green turtle densities in UCR were very high in comparison with most of the Caribbean. It is possible that grazed seagrass pastures, with their dramatic structural differences from ungrazed pastures, are better habitats for hawksbills than ungrazed pastures. If so, before the steep decline in green turtle populations that began hundreds of years ago (Jackson et al. 2001), hawksbills may have been more common in seagrass habitats. Additional studies of hawksbill aggregations in other seagrass pastures are needed to confirm the results reported here, and other factors that determine habitat quality, such as potential for increased vulnerability of hawksbills to predation or disease in seagrass habitats, should be evaluated. Structure and associated fauna of seagrass pastures vary greatly throughout the Caribbean, which may affect the quality of the habitat for hawksbills.

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