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ORIGINAL PAPER

Ecology of juvenile hawksbills (*Eretmochelys imbricata*) at Buck Island Reef National Monument, US Virgin Islands

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Abstract Surveys of juvenile hawksbills around Buck Island Reef National Monument, US Virgin Islands from 1994 to 1999 revealed distributional patterns and resulted in a total of 75 individual hawksbill captures from all years; turtles ranged from 23.2 to 77.7 cm curved carapace length (CCL; mean 42.1 ± 12.3 cm SD). Juveniles concentrated where Zoanthid cover was highest. Length of time between recaptures, or presumed minimum site residency, ranged from 59 to 1,396 days (mean 620.8 ± 402.4 days SD). Growth rates for 23 juveniles ranged from 0.0 to 9.5 cm year^{-1} (mean 4.1 ± 2.4 cm year^{-1}SD). Annual mean growth rates were non-monotonic, with the largest mean growth rate occurring in the 30–39 cm CCL size class. Gastric lavages indicated that Zoanthids were the primary food source for hawksbills. These results contribute to our understanding of juvenile hawksbill ecology and serve as a baseline for future studies or inventories of hawksbills in the Caribbean.

Introduction

Understanding the ecology of juvenile marine turtles in developmental habitats is vital for designing strategies to ensure persistence of the species, especially when the habitat and species may be at risk (Meylan et al. 2011). As juveniles, Chelonidae species spend the greatest period of their lives within developmental habitats, and their association with particular sites may last for decades. When they reach sexual maturity (20–30 years), adults leave foraging grounds to make temporary reproductive migrations (Limpus 1994). Juvenile hawksbill sea turtles (*Eretmochelys imbricata*) in particular have been observed spending many years in developmental habitat (Witzell 1983; Van Dam and Diez 1997, 1998), and previous studies have shown they have small home ranges in these areas (~1 km^2 or less; Van Dam and Diez 1997, 1998; Berube

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2012; Scales et al. 2011; also see Cuevas et al. 2007). Additionally, these developmental habitats can be home to juveniles from many different nesting aggregations, each often consisting of genetically distinct subpopulations (Bass et al. 1996; Velez-Zuazo et al. 2008).

Hawksbills primarily occupy coral reef habitats throughout most of their Caribbean range (Carr et al. 1966; Mortimer and Donnelly 2008). In parts of the eastern Pacific, they also inhabit mangrove estuaries (Gaos et al. 2012). Although hawksbills are circumtropically distributed, they are considered endangered in all parts of their range (National Marine Fisheries Service [NMFS] and United States Fish and Wildlife Service [USFWS] 1993; NMFS and USFWS 1998). The hawksbill was listed as critically endangered on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species in 1996, based on overall decline in the species of over 80 %, and extensive subpopulation declines in all ocean basins (Mortimer and Donnelly 2008). There are few places in the Caribbean where aggregations of hawksbill turtles, adults or juveniles, remain today (NMFS and USFWS 1993). Previous studies on juvenile hawksbill populations in the Caribbean have been conducted in Puerto Rico (Van Dam and Diez 1997, 1998), the Cayman Islands (Blumenthal et al. 2009a, b), Honduras (Dunbar et al. 2008; Berube 2012), and the Dominican Republic (Leon and Diez 1999). Limited hawksbill population surveys have also been conducted in near-shore waters of the Virgin Islands (Boulon 1994, see Pemberton 2001). Still, the ecology of this species during the juvenile life stage is not well understood.

Buck Island Reef National Monument (BIRNM), US Virgin Islands (USVI) is the only fully protected site in the Caribbean where hawksbills both forage and nest (USFWS and NMFS 1993). The Hawksbill Recovery Plan identifies the need to determine (for all life stages) distribution, abundance, seasonal movements, foraging areas (Section 121 and 2,211), growth rates, and survivorship (Sect. 2,213; USFWS and NMFS 1993); these data are key for making inferences about hawksbill population demographics. In particular, juvenile growth rates can eventually affect the rate and potential of nesting stock growth and recovery (see Kubis et al. 2009).

This study was designed to conduct baseline surveys for abundance and distribution of juvenile hawksbills, identify benthic composition in foraging areas, determine diet through lavages, and gather data on growth rates and minimum residency from recaptured turtles. Our specific objectives involved using three approaches from 1994 to 1999, including (1) in-water distribution surveys to determine occurrence of hawksbills and relative abundance in relation to specific habitat features; (2) in-water capture efforts to tag and recapture individuals, collect biometric data, and assess habitat use; and (3) gastric lavages to determine the diet of juvenile hawksbills captured in shallow areas of BIRNM.

Materials and methods

Study site

BIRNM includes a 0.71-km^2 uninhabited island (Buck Island) located on the shallow St. Croix shelf (approx. 15–20 m depth range), 2.4 km northeast of the island of St. Croix in the USVI at N17° 47.4′, W64° 37.2′ (Fig. 1). The coral sand beaches on the island dominate the southwest side and serve as nesting habitat for hawksbill, loggerhead (*Caretta caretta*), green (*Chelonia mydas*), and leatherback (*Dermochelys coriacea*) sea turtles. An emergent bank-barrier reef girdles the island from the southeast to the northwest, enclosing a lagoon 50–150 m wide (Fig. 1). This reef is primarily made up of dead elkhorn coral (*Acropora palmatta*), the dominant reef-building coral in the Caribbean; this reef experienced extensive damage from white-band disease in the 1970s and 1980s and from Hurricane Hugo in 1989 (Gladfelter 1982; Bythell et al. 1993). In the forereef (seaward of the barrier reef), these *A. palmata* corals create "haystacks" that rise to the surface from a depth of 9 m, with the east forereef representing one of the densest stands around St. Croix. Other dominant coral species of the bank-barrier reef and the patch reefs include *Montastria annularis, Porities astreoides, Diploria* sp., *Porites porites,* and *Acropora cervicornis*. Other dominant organisms include various algae, *Zoanthus* sp., *Briarium, Millepora* sp., and seagrasses. The waters of BIRNM provide foraging habitat for all four species of sea turtle that nest on Buck Island.

The current boundary of BIRNM was expanded in 2001 from the original 1961 designation, adding 73.4 km^2 of submerged lands. Our study took place from 1994 to 1999, while the original boundary was in place and all activities occurred within that area. This included 0.71 km^2 of land and 2.9 km^2 of water and coral reef system. For all surveys, we entered the lagoon via motor boat, and either moored the boat near dive locations (i.e., Underwater Trail or SCUBA Cut) or anchored it in sand at other locations, depending on weather, sea conditions, or location of in-water surveys (see Fig. 1).

Turtle distribution surveys

We conducted daily turtle distribution surveys, weather permitting, from May to August 1998 (summer) and from December 1998 through March 1999 (winter). To define

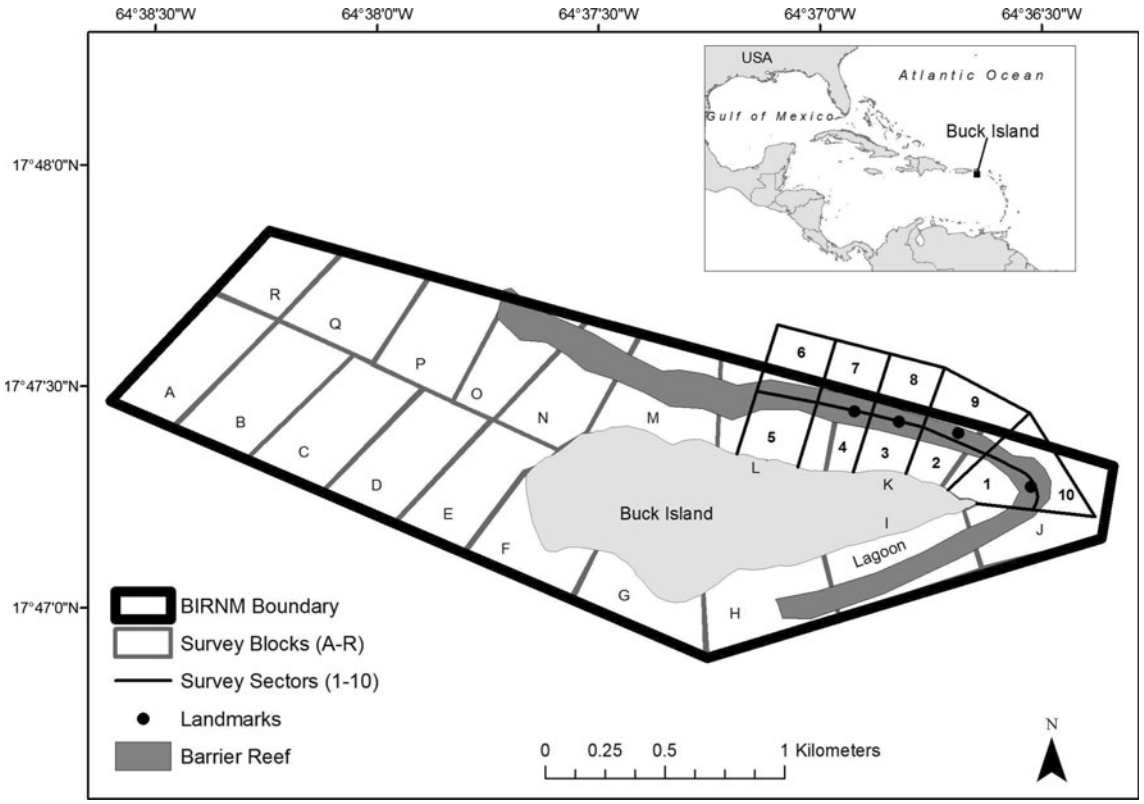

Fig. 1 The original boundary of BIRNM with survey blocks (A–R) and sectors (1–10). The landmarks from west to east include Boat Cut, SCUBA Cut 2, SCUBA Cut 1 and Underwater Trail

the relative distribution of sea turtles throughout BIRNM, we divided the area within the Monument into 18 blocks of approximately 0.15 km^2 each (range 0.09–0.19 km^2, for a total of 2.85 km^2; Fig. 1), with the exception of block J, which was extended out to the east and measured approximately 0.26 km^2. Blocks generally contained four habitat types from the island out to open water: (1) shoreline reef—the reef system directly adjacent to Buck Island's shoreline, (2) lagoon—a shallow (<4 m) limestone pavement with scattered live coral heads, coral rubble, sand, and sparse seagrass patches, (3) backreef—the landward side of the bank-barrier reef, and (4) the forereef—the seaward side of the bank-barrier reef including the contiguous reef and the bank patch reefs or haystacks (Anderson 1985). We recorded sea turtle sightings (location, time, and number of turtles) and dominant habitat characteristics for each block during summer surveys. During winter surveys, we recorded sea turtle sighting data.

We completed turtle distribution surveys with manta tows where possible, otherwise we surveyed by snorkel. We towed a life ring approximately 5–6 m behind the boat at 1–3 knot speed; a snorkel swimmer held onto it as the boat traveled across the block. All surveys began in near-shore areas and zig-zagged across blocks until reaching the forereef areas. We completed un-towed snorkel swims in areas of the reef not accessible by small boat. Surveys ran parallel to the prevailing current when possible, in order to stay on the survey line. Surveyors swam on a line parallel and within submerged sight of each other from one side of a block to the other; an average of 15 lines were surveyed per block, depending on sea conditions and visibility. Visual coverage for each observer ranged from approximately 2–6 m on each side and was dependent on the visibility and depth of the water column.

Zoanthid distribution

During the summer turtle distribution surveys, we also completed habitat surveys; these revealed that Zoanthids (*Zoanthus* sp.) were present in blocks I–O (Fig. 1). We subsequently sampled along transect lines in these blocks to compare the abundance of Zoanthids to the presence of hawksbills. Transects ran down the middle of the block from the shore to forereef, and we completed 3 random 1 m^2 quadrats along each transect per habitat zone, recording the percent of Zoanthids in each.

Capture surveys

We concentrated capture activities near the east-south-eastern tip of Buck Island, to the north-western end of the patch reef system. We divided the eastern section into 10 sectors ranging in size from approximately 0.05–0.08 km^2 (1–10; Fig. 1) to identify capture locations on a finer scale. We conducted captures from May to December 1994, January–November 1995, May–September 1996, January–December 1997, and January–October 1998. For each capture, we recorded the sector in which each turtle was originally sighted. For each hawksbill sighting and capture event, we recorded location, water depth, turtle depth, time, sea conditions, and visibility. Whenever possible, we captured turtles for individual work-up and standard data collection. However, a non-captured turtle (and the accompanying data, e.g., water depth) was considered "recaptured" for data summary purposes if the flipper tags were successfully read while under water.

Turtle capture

We free-dove and hand-captured hawksbill juveniles in BIRNM. After anchoring the boat, snorkelers would swim alongside each other, spreading out to maximize the area surveyed while also maintaining visual contact (approximately 4.5 m apart). Once a snorkeler sighted a turtle, they would secure the attention of at least one other snorkeler to assist with capture. Captures were made by grabbing the carapace, with one hand placed at the nuchal scute and the other on the post-marginal region. Turtles were then pointed head up and carefully brought to the surface. Once captured, turtles were brought on board the boat for workup.

Standard turtle workup

Upon reaching the boat, we carefully lifted each turtle by taking hold under the front flippers to bring it onto the boat. While on the boat, we covered the head and body of the turtles with a wet towel to keep them moist and cool. Workup consisted of collecting biological samples (i.e., blood, tissue), taking standard straight carapace length (SCL), curved carapace length (CCL), straight plastron length (SPL), curved plastron length (CPL), as well as tail measurements, and identification photos. Measurements of minimum CCL (to the notch) were used for all analyses. Each turtle was weighed on an Ohaus electronic scale (model I5S; Forestry Suppliers, Jackson, Mississippi) suspended from a pole and was measured to the nearest 0.1 kg.

Each turtle over 20 cm CCL was tagged with two National Marine Fisheries Service Inconel tags (National Band & Tag Co., Newport, Kentucky) and one AVID Passive Integrated Transponder (PIT) tag/chip (Norco, California). One Inconel tag was placed on the scale closest to the body on the left front flipper and another on either the scale tab or tissue of a hind flipper. These tags were placed with certain considerations in mind: to avoid the tag catching on marginal scutes by placing the tag closer to the body than the hind flipper scale, to leave space for growth, and to avoid interference with future nest digging. PIT tags were placed in the right shoulder. All turtles were released within an hour near the site of capture; we carefully released them over the side of the boat into the water, observing each turtle until it swam away.

Gastric lavages

We performed gastric lavages on juvenile hawksbills captured in 1996 (July, August, and September) and 1998 (January). We captured turtles on the northeast section of the island and referenced captures to the same block numbers as in the distribution surveys. If gastric lavage was performed, turtle workup took up to an hour and a half. The flushing during the lavage procedure took 3 min or less.

Gastric lavage techniques generally followed Mendonça (1983) and were performed by a trained veterinary technician (B. Phillips). We placed the turtles with their carapace down and posterior end slightly elevated. We opened the jaws by hand and placed a bite block with protective padding inside the mouth to prevent closure. We used a single lavage tube ranging from 12.7/9.5 to 9.0/7.0 mm (outer/inner tube dimensions) based on the turtle's size. All tubes had rounded tips to prevent damage to the esophagus upon insertion. Once the single tube was inserted approximately 5 cm into the esophagus, we started the flow of salt water and collected water and food particles expelled from the mouth. We stored lavage samples in vials containing formalin (Fisher Scientific Formalde-Fresh solution diluted with filtered sea water to 4 %) to later identify food particles to genus, or species when possible.

In 1996, we combined specimens from all the samples to collect a total wet weight value, weighed with an Acculab Pocket-Pro scale Model PP-250-B (250 g × 0.1 g capacity/readability; Forestry Suppliers, Jackson, Mississippi). In 1998, we identified species consumed per turtle. For both sampling periods, we divided the samples into four groups based on CCL ranges (30–39, 40–49, 50–59, 60–69 cm) and compared dominant food types across groups. We assessed diversity within samples in two ways: (1) distinct food items: the number of species (or genera if species was unavailable) in each sample per turtle, and (2) the prevalence of an individual food item across all samples, provided as a range from a species occurring in one sample within the group to all samples. We also classified food

items into separate groups based on taxonomy (i.e., red algae, green algae, brown algae, Cnidaria, *Zonathus*, *Lebrunia danae*, and non-food). We summed these groups across all samples by size class for both years.

Hawksbill high-use areas

We compared juvenile hawksbill sightings to the percent abundance of Zoanthids for each block using linear regression analysis; samples from each block were assumed to be independent, and the variances were found to be homogenous using Levene's Test. We also used an analysis of variance (ANOVA) to compare the sightings of juvenile hawksbills to the concentrations of Zoanthids. The Zoanthid concentrations ("Zoanthid Cover") were classified as either Low (0–0.3 %) or High (10–34.8 %), and the corresponding number of juvenile hawksbills served as the response (dependent) variable. We used the statistical program SAS (1997) v. 6 for all analyses, with an alpha <0.05 to signify statistical significance.

To determine habitat characteristics of hawksbill high-use areas, we compared areas with high numbers of turtle sightings to both a 3 m LIDAR bathymetry layer collected by the National Oceanic and Atmospheric Administration (NOAA) in 2011 (http://ccma.nos.noaa.gov/products/biogrography/usvi_nps/data/; accessed 11 May 2012) and a hardbottom habitat layer published in 2012 by NOAA (http://ccma.nos.noaa.gov/ecosystems/coralreef/stcroix_data.aspx; accessed April 10, 2012). Using these layers in ArcGIS 9.3 (ESRI 2007), we extracted the range of depths and dominant habitat types per high-use blocks. Finally, we determined length of time between recapture events for individual turtles, or minimum presumed site residency, by calculating the difference in days between first and last in-water capture events at BIRNM.

Growth rates

We summed all captures and recaptures by sector and size class. For recaptured turtles, we calculated the days between first and last capture event and the yearly growth rates for both length (CCL) and mass if the turtles had more than one measurement. We calculated change in CCL following Bjorndal et al. (2000) and included zero growth rates. We did not, however, constrain the data to only recaptures with >11-month intervals. For growth rates by size class, we included measurements from within a given size class; if an individual turtle had more than one growth rate estimation, it had multiple measurements over the years and changed size classes.

An earlier radioimmunoassay study was conducted on juveniles caught at Buck Island for an independent analysis from 1995 to 1999 (Geis et al. 2003); we incorporated these sex results for applicable turtles in this study for use in comparing growth rates of the different sexes.

Results

Turtle distribution surveys and high-use areas

We sighted a total of 85 turtles including 66 hawksbills and 19 green turtles (data not shown) during the distribution surveys. Turtles from 30 to 39 and 40 to 49 cm CCL were the most frequently observed size classes. Hawksbill turtles were observed in blocks A, D, E, and H–R, but primarily in blocks J through N (Fig. 2). Linear regression revealed that the number of juvenile hawksbills per block was positively correlated to the percent cover of Zoanthid per block ($R^2 = 0.848$, $p < 0.0001$). Additionally, the number of hawksbills sighted in areas of High Zoanthid cover was significantly higher than the number of hawksbills sighted in areas of Low Zoanthid cover (ANOVA, $F_{(1,16)} = 39.92$, $p < 0.0005$).

Data from the NOAA depth layer showed the blocks with the highest number of hawksbill sightings (J–N) ranged in depths from 0.0 to 15.2 m (J: 0.0–15.2 m, K:0.0–13.1 m, L:0.0–9.7 m, M:0.0–9.4 m, N:0.0–8.9 m). Blocks J–N were the most structurally diverse in habitat (see Fig. 2). In the high-use blocks, hardbottom cover ranged from 56 to 92 % within blocks J–N (J: 92 %; K: 69 %; L: 72 %; M: 56 %; N: 57 %). Dominant habitat types as a percentage of total block area were aggregate reef (AR), aggregated patch reef (APR), and lagoon "pavement" (LP) (J: APR 38 %, AR 30 %, LP 18 %; K: AR 33 %, APR 15 %; L: AR 35 %, APR 22 %; M: AR 29 %, APR 18 %; N: AR 25 %, APR 16 %, LP 16 %).

Capture study

Primary capture summary

From May to December 1994, we captured and tagged 12 juvenile hawksbills. In the four following years, we captured and tagged an additional 6, 23, 16, and 18 new individuals, respectively, for a total of 75 individual hawksbills (Table 1). For all primary captures (first capture of an individual turtle), individuals ranged in size from 23.2 to 77.7 cm CCL (mean 42.1 ± 12.3 cm SD; $n = 75$). Mass ranged from 1.5 to 49.5 kg (mean 11.5 ± 9.6 kg SD; $n = 74$).

Water depths at initial sightings ranged from 0.3 to 12.2 m (mean 5.2 ± 3.3 m SD; $n = 61$), Over all years, more primary captures were made in sectors 1 ($n = 18$), 6 ($n = 10$), 2 ($n = 9$), and 10 ($n = 9$; Table 2; Fig. 3). Captures made in backreef sectors (1–5) included turtles

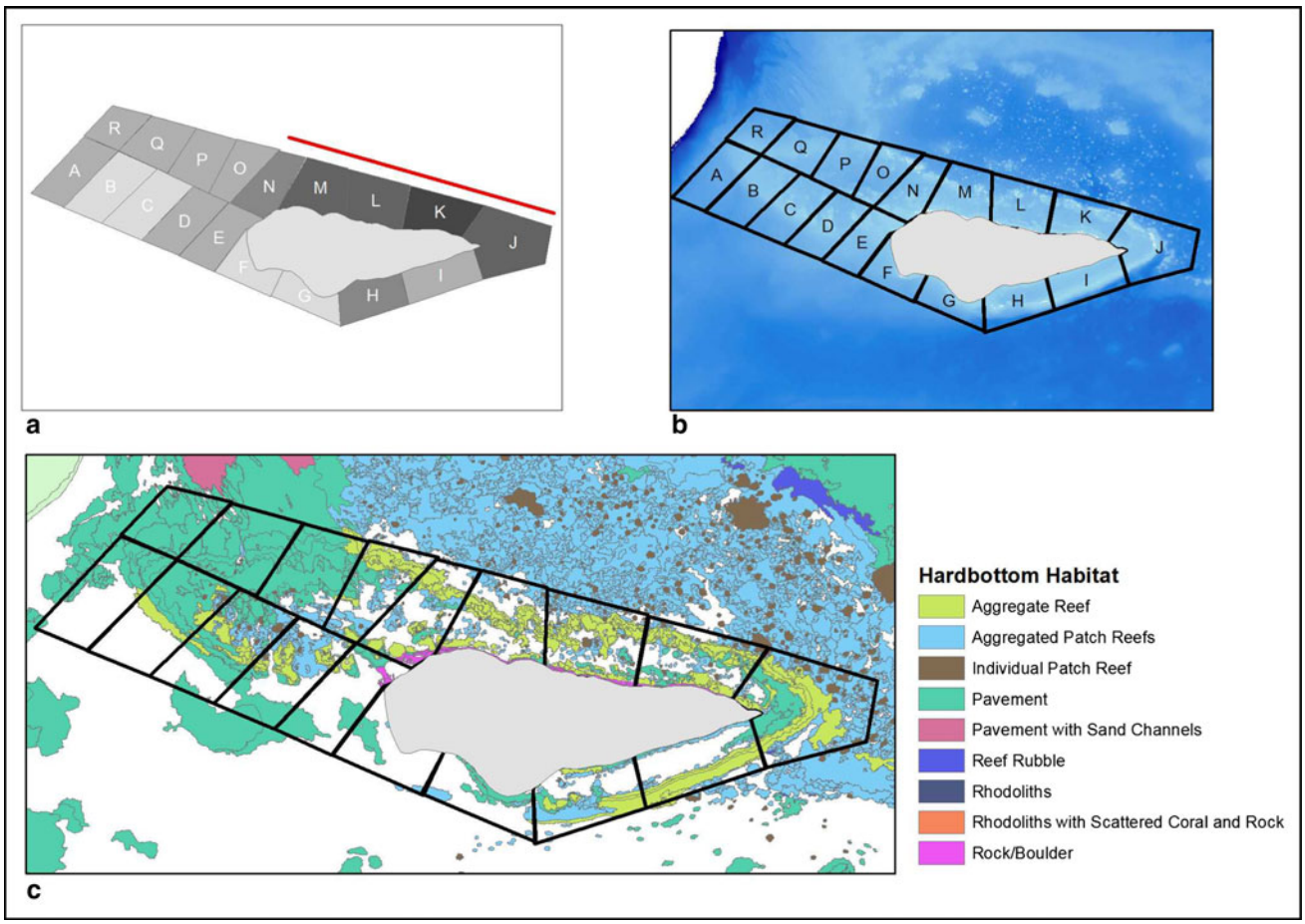

Fig. 2 Hawksbill distribution survey. **a** Hawksbill sightings by block. The red line runs along blocks with the highest percent cover of Zoanthid (J–N). *Darker shading* denotes a larger number of sightings. **b** 3 m bathymetry of sectors (data from http://ccma.nos.noaa.gov/products/biogeography/usvi_nps/data/). **c** Hardbottom habitat (data from NOAA at http://ccma.nos.noaa.gov/ecosystems/coralreef/stcroix_data.aspx)

Table 1 Hawksbill capture summary across all years

	1994	1995	1996[a]	1997[a]	1998[a]	Total over all years
Unique captures						
Total	**12**	**14**	**30**	**28**	**36**	**120**
Primary captures	12	6	23	16	18	**75**
Recaptures, previous years[b]	0	8	7	12	18	**45**
% Recaps of total captures	N/A	57 %	23 %	43 %	50 %	
All capture events						
Total	**25**	**38**	**57**	**46**	**74**	**240**
Recaptures, (both in and across seasons)[c]	13	32	33	30	54	**162**
% Recaps of total captures	52.0 %	84.2 %	57.9 %	65.2 %	73 %	

Bold values denote totals

[a] Park service staff increased/increased effort for captures

[b] These recaptures include the number of individual turtles recaptured in that year that were tagged in a previous year

[c] These recaptures include all recapture events: in-season, across seasons, and recaptures even if <1 week had passed

that ranged in size from 23.2 to 63.0 cm CCL (mean 41.0 ± 13.3 cm SD; $n = 37$) and 1.5–35.0 kg (mean 11.1 ± 9.7 kg SD; $n = 36$). Turtles captured in the forereef (sectors 6–10) were slightly larger and ranged in size from 30.6 to 77.7 cm CCL (mean 43.4 ± 11.3 cm SD; $n = 31$) and 3.5–49.5 kg (mean 12.0 ± 10.0 kg SD;

$n = 31$). One turtle (49.3 cm CCL at initial capture) was caught and recaptured outside sectors 1–10, in blocks D, M, N, and O (see Fig. 2a) between June 12, 1998, and August 10, 1998.

Recapture summary

We recaptured 33 of the 75 turtles (44 %) throughout the study period. However, three turtles were recaptured within

Table 2 Number of hawksbill captures (of 68 total) by sector with mean, min, and max curved carapace length (CCL) and mass. n/a not applicable

Sector	Block[a]	#Captures	Mean CCL (cm)	Min CCL (cm)	Max CCL (cm)	Mean mass (kg)	Min mass (kg)	Max mass (kg)
1	J	18	41.6	23.2	63.0	11.7	1.5	35
2	K	9	38.7	25.3	62.4	9.9[b]	2[b]	26.5[b]
3	K	4	43.6	24.5	56.1	10.8	1.5	24
4	K	1	29.2[c]	n/a	n/a	3[c]	n/a	n/a
5	L	5	43.8	37	50.2	10.8	6	15.5
6	L	10	48.6	37.6	67	14.9	6	34.5
7	K	3	54.5	32.8	77.7	24.3	4.5	49.5
8	K	3	37.4	35.5	39.5	7.0	8	6.5
9	K	6	38.5	32.1	51.1	8.25	4	17.0
10	J	9	39.4	30.6	62	8.7	3.5	27.5

[a] Blocks and sectors do not line up exactly. The block number here is given for reference only and is the block with the most area within a sector (see Fig. 1)

[b] N = 8 for these values, although there were 9 captures in sector 2

[c] The measurements of the single capture are given here

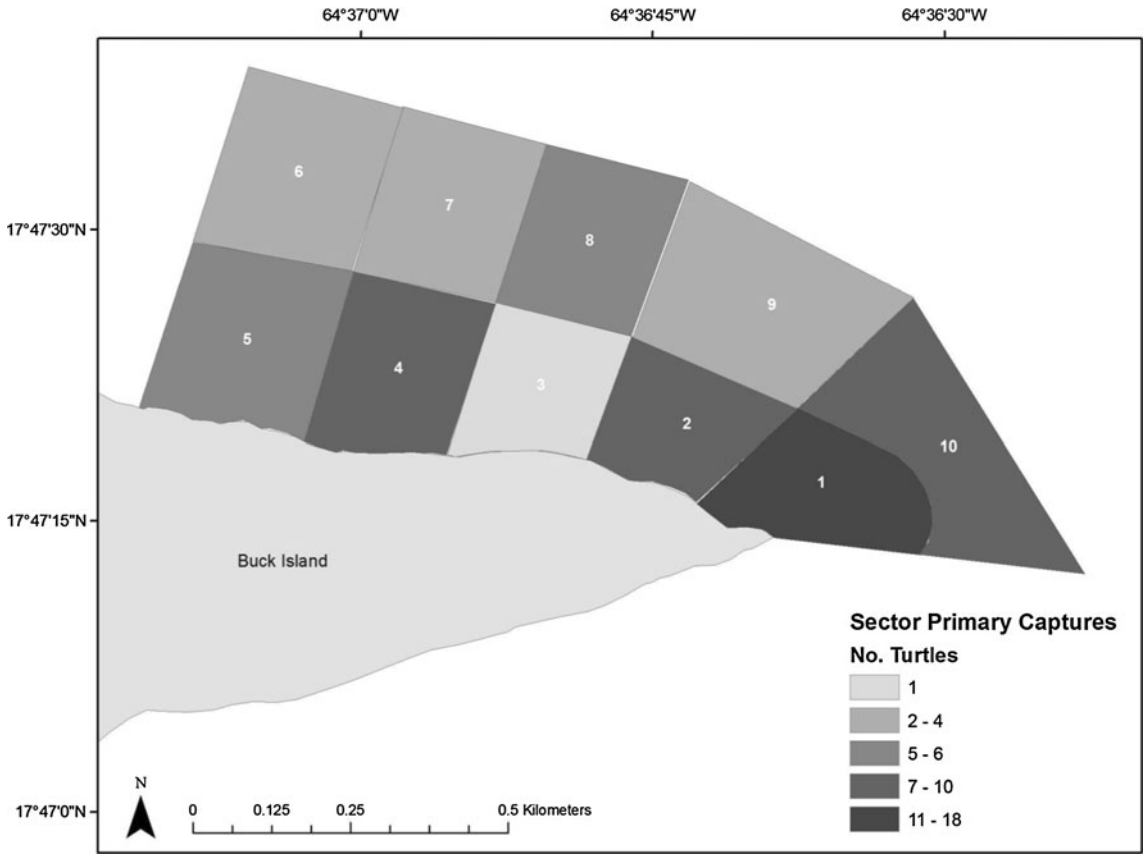

Fig. 3 Hawksbill captures by sector; primary captures shown ($n = 68$; sector information unavailable for $n = 7$ primary captures). *Darker shading* denotes a larger number of captures. Sampling effort was biased to areas of high hawksbill concentration

1 week of primary capture and were excluded from analysis. For the 30 remaining recaptured individuals, we had 162 recapture events from June 27, 1994, to October 9, 1998. Turtles were recaptured both within the same year and across years (Table 1). The length of time between recaptures, or presumed minimum residency, for these 30 turtles ranged from 59 to 1,396 days (mean 620.8 ± 402.4 days SD; $n = 30$); none of the turtles had tracking devices affixed to them so even though we presume site residency based on their juvenile life stage, turtles may not have remained in the area between capture events. Of these 30 recaptured turtles, 25 were measured for primary capture CCL. Size class comparisons (based on the primary CCL) showed similar ranges for minimum residency times: 20–29 cm CCL was 225–1,276 days, 30–39 cm CCL was 237–1,396 days, 40–49 cm CCL was 143–1,359 days, 50–59 cm CCL was 101–1,177 days, and 60–69 cm CCL was 280–1,233 days (Fig. 4).

Recapture location (sector) was predominantly in the same sector as original capture location; 18 of 29 turtles (62 %) were recaptured in their primary capture sector or in sectors immediately adjacent to their primary capture sector. Of the remaining turtles, the number of sectors in which they were captured ranged from 1 to 6 (mean 2.6 ± 1.3 sectors SD; $n = 29$).

Growth rates

A total of 23 turtles had measurements taken after an in-water recapture. Recapture events ranged 101–1,276 days from initial capture events (mean 646.0 ± 337.7 days; $n = 23$). The measured change in CCL ranged from 0.0 to 24.1 cm CCL (mean 7.5 ± 5.9 cm SD; $n = 23$). The measured change in mass ranged from 0.0 to 21.0 kg (mean 5.1 ± 5.2 kg; $n = 23$). Thus, growth rates for these turtles ranged from 0.0 to 9.5 cm year^{-1} CCL (mean 4.1 ± 2.4 cm SD; $n = 23$) and 0.0–6.9 kg year^{-1} (mean 2.4 ± 1.7 kg SD; $n = 23$; Table 3).

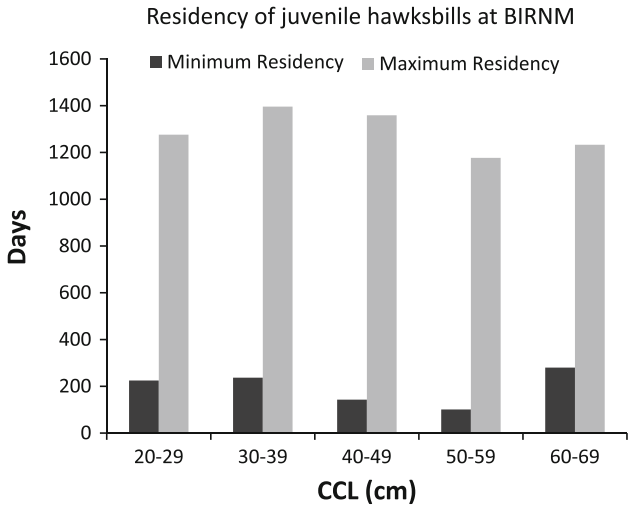

Fig. 4 Numbers of days between first and last recapture events (if greater than 1 week) for all in-water recaptured turtles by size class. Size class (cm CCL) 20–29 ranged 225–1,276 days, 30–39 ranged 237–1,396 days, 40–49 ranged 143–1,359 days, 50–59 ranged 101–1,177 days, and 60–69 ranged 280–1,233 days

Annual mean growth rates differed by size class, with the largest mean growth rate occurring in the 30–39 cm CCL size class and otherwise decreasing with increasing turtle size (Fig. 5): 4.7 cm year^{-1} CCL for 20–29 cm CCL ($n = 2$), 7.9 cm year^{-1} for 30–39 cm CCL ($n = 1$), 4.0 cm year^{-1} CCL for 40–49 cm CCL ($n = 6$), 2.9 cm year^{-1} CCL for 50–59 cm CCL ($n = 8$) and 1.9 cm year^{-1} CCL for 60–69 cm CCL ($n = 4$).

One hawksbill was not recaptured in-water but instead 7 years later while nesting at BIRNM. Upon primary capture in-water, this female was 49.9 cm CCL and 16 kg (July 28, 1997) and 2,547 days later (~7 years) when this turtle nested on Buck Island she was 72.9 cm CCL (Z. Hillis-Starr, pers. observ.; mass not recorded, July 18, 2004; Table 3). Over this period, she showed a 23.0 cm increase in CCL.

We calculated growth rates for 18 females and four males (sex determination from Geis et al. 2003), including 21 of the 23 in-water recaptures (that had measurements and determined sex). Growth rates for females (24.5–63.0 cm CCL first capture size) ranged from 0.0 to 7.8 cm year^{-1} (mean 4.2 ± 2.2 cm SD year^{-1}; $n = 18$). For males (46.8–61.5 cm CCL first capture size), growth rates ranged from 1.7 to 4.9 cm year^{-1} (mean 2.7 ± 1.5 cm SD; $n = 4$). As a comparison to the male growth rates, which were only available in the 40–49, 50–59, and 60–69 size classes, female growth rates for the same classes ranged from 0.0 to 5.5 cm year^{-1} (mean 2.6 ± 1.5 cm year^{-1} SD; $n = 10$).

Gastric lavages

In 1996, we attempted gastric lavages on 25 turtles captured during summer months, yielding 18 samples (72 %). Successfully lavaged turtles ranged in size from 31.0 to 67.0 cm CCL (mean 49.5 ± 10.7 cm SD, $n = 18$) and were captured in blocks J, K, and L (see Fig. 2a) at water depths of approximately 2–12 m (mean 6.3 ± 3.3 m SD; $n = 16$). Stomach contents included primarily Zoanthids (*Zoanthus sociatus*), which constituted 85.7 % of the total wet weight of all samples (present in 11 samples; Fig. 6). We found various algae (e.g., red, brown, and green species) in 17 samples; however, they comprised only 5.6 % of the total wet weight of all samples (Fig. 6; Table 4). Various red macroalgae, not identified to species or genus, occurred in 16 of the 18 samples. Further, each individual sample contained 1–12 distinct food items (identified to genus or species; mean 6.9 ± 3.2 items SD; $n = 18$). Across all samples, particular food items (identified to

Table 3 Hawksbill growth measured for recaptures by change in curved carapace length nuchal to notch (CCL) and mass for turtles with recapture events >1 week ($n = 23$) and for turtle 809 which did not have an in-water recapture, but was found nesting at BIRNM

Turtle	Orig. CCL	Recapture interval (days)	Change in CCL (cm)	Change in mass (kg)	Sex	Growth cm year^{-1}	Growth kg year^{-1}
410	45.4	413	2.8	1.0	F	2.482	0.88
603	54.5	709	2.0	1.0	F	1.022	0.51
605	61.5	1,222	7.0	12.0	M	2.0805	3.58
607	63.0	280	0.0	0.0	F	n/c	n/c
610	34.8	816	12.2	8.5	F	5.475	3.8
611	57.0	1,177	5.4	5.0	M	1.679	1.53
613	46.5	1,118	16.8	21.0	F	5.475	6.86
615	46.8	801	10.8	11.5	M	4.9275	5.26
617	29.0	1,276	24.1	13.0	F	6.8985	3.72
622	43.8	922	8.5	3.0	I	3.358	1.2
629	27.4	851	12.9	7.0	F	5.548	2.99
630	25.5	621	16.2	7.0	I	9.5265	4.12
631	54.4	607	6.0	5.0	F	3.6135	2.99
633	25.5	537	6.7	1.5	F	4.5625	1.02
637	31.0	358	7.7	3.0	F	7.8475	3.07
643	53.0	532	2.9	0.5	M	2.0075	0.33
652	51.2	412	3.0	2.5	F	2.6645	2.23
665	37.0	516	8.0	5.0	F	5.6575	3.54
672	46.7	587	4.6	5.0	F	2.847	3.1
683	24.5	635	8.4	2.5	F	4.818	1.42
822	59.1	101	0.5	0.5	F	1.825	1.83
832	27.7	225	4.7	1.0	F	7.6285	1.61
839	44.8	143	1.2	0.0	F	3.066	n/c
809[a]	49.9	2,547	23.0	n/a	F	3.285	n/a
				X ± SD, cm		4.1 ± 2.4 cm	
				X ± SD, mass		2.4 ± 1.7 kg	

[a] not included in mean values

Orig. CCL is the curved carapace length at first measurement. Recapture interval was between the first and last recapture if the turtle was recaptured multiple times. Sex determination from Geis et al. (2003): *M* male, *F* female, *I* intermediate testosterone levels (sex unknown). n/a not applicable, n/c no change

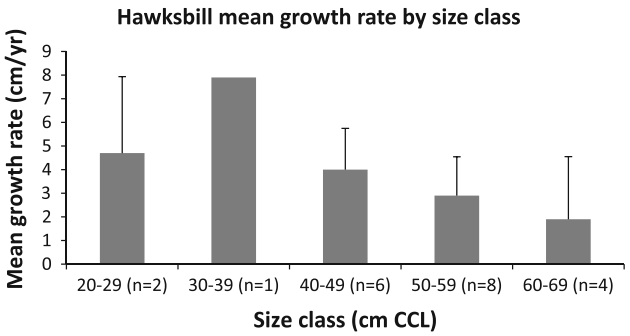

Fig. 5 Hawksbill mean growth rate by size class. The number of hawksbills (n) used in calculation of mean is given for each size class. The SD for each size class is as follows: 20–29 cm CCL (3.2); 30–39 cm CCL (none); 40–49 cm CCL (1.7); 50–59 cm CCL (1.6); 60–69 cm CCL (2.6)

genus or species) were found in 1–11 of the 18 samples (mean 4.8 ± 3.2 samples SD; $n = 18$) with the species *Z. sociatus* occurring most often in samples.

In 1998, we attempted gastric lavages during winter on 17 turtles captured in water depths of approximately 1–8 m (mean 3.1 ± 1.7 m SD; $n = 17$) within blocks J, K, and L (see Fig. 2a). We collected samples from all 17 of these turtles, including two repeat samples from two different turtles (Turtle QQD-605 on January 7, 1998, and January 16, 1998; and turtle QQD-617 on January 8, 1998, and January 21, 1998), resulting in 19 total samples. However, only the first sample from each turtle was used for the summary. Turtles lavaged in 1998 ranged in size from 32.2 to 68.5 cm CCL (mean 47.6 ± 10.8 cm SD; $n = 17$). The number of distinct food items (identified to genus or species) in each sample ranged from 1 to 6 (mean 3.2 ± 1.6 items SD; $n = 17$; Table 5). Across all samples, particular food items were found in 1–17 samples (mean 1.5 ± 3.1 items SD; $n = 17$). The most common food item was *Z. sociatus*, which occurred in all 17 samples. Various red macroalgae species occurred in 13 samples. Small amounts of plastic and fiber (non-food) were found in two samples. In summary, *Zoanthus* and red algae were found in the majority of samples for all size classes (Fig. 7). However, in 1996, the total wet weight of *Zoanthus* (85.7 %) as compared to red algae (3.8 %) showed that *Zoanthus* was the most abundant species in the samples. A similar pattern was observed in the 1998 samples.

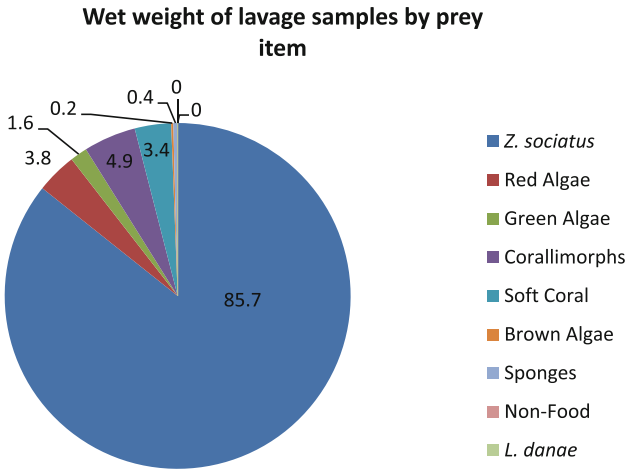

Fig. 6 Hawksbill lavages. Numbers given are percent total wet weight of all samples combined from 1996 by prey item

Table 4 Wet weights of gastric lavage samples collected in 1996

Organism	No of samples (total 18)	Total wet weight (g)	Percent total wet weight
Z. sociatus	11	43.1	85.7
Red Algae	16	1.9	3.8
Green Algae	10	0.8	1.6
Corallimorphs	3	2.5	4.9
Soft Coral	3	1.7	3.4
Brown Algae	12	0.1	0.2
Sponges	5	0.2	0.4
Non-Food	n/m	n/m	n/m
L. danae	0	0	0

No. of samples: number of samples in which the organism was found. *Z. sociatus*: *Zoanthus sociatus*. *L. danae: Lebruniadanae*. n/m not measured

Additionally, one species (*L. danae*) was only found in lavage samples from hawksbills in the 30–39 cm CCL size class, and it was present in 4 of 8 total samples from that size class (all from 1998). Also, four juvenile turtles were sampled both in 1996 and 1998 (QQD-605, QQD-617, QQD-643, and QQD-665). All four turtles had a higher number of discrete food items in the 1996 summer lavages (12, 5, 7, 9) as compared to the 1998 winter lavages (4, 3, 5, 1). For the two turtles lavaged twice in 1998, the second sample for QQD-605 contained plastic, *Zoanthus sociatus*, *Jania adherens* (red algae), *Hypnea cervicornis* (red algae), and *C. testudinaria*. The second sample for QQD-617 contained *C. testudinaria*, plastic, and *Halimeda* sp. (green algae).

Lastly, in 1996, we lavaged an adult male (79.3 cm CCL, QQD-678) originally captured in block L (see Fig. 2a); stomach contents included *Syringodium filiforme*

Table 5 Food item diversity across size classes and years

Time of year	Size class	No. samples	# Food items per sample	X ± 1 SD
Summer (1996)	30–39	4	1–9	4.5 ± 3.3
	40–49	4	5–11	7.5 ± 3.0
	50–59	7	4–12	7.0 ± 2.5
	60–69	3	4–12	9.0 ± 4.4
Winter (1998)	30–39	4	1–4	2.5 ± 1.3
	40–49	5	1–6	4.0 ± 2.3
	50–59	5	2–5	3.2 ± 1.1
	60–69	3	1–4	2.7 ± 1.5
Combined years	30–39	8	1–9	3.5 ± 2.6
	40–49	9	1–11	5.5 ± 3.1
	50–59	12	2–12	5.4 ± 2.8
	60–69	6	1–12	5.8 ± 4.5
9/20/1996	79.3	1	7	n/a

n/a not applicable

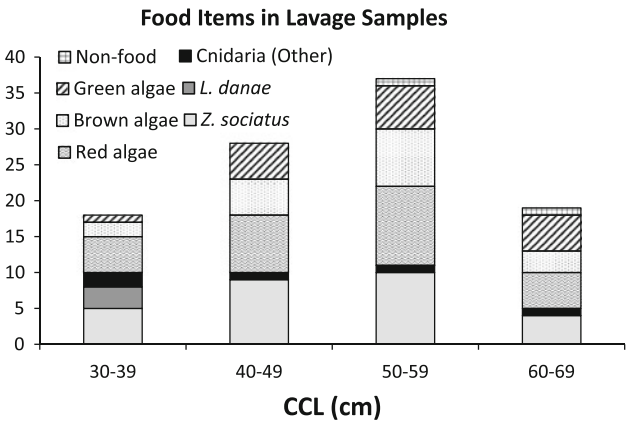

Fig. 7 Number of lavage samples containing various groups of food items. Data are combined for both years of lavage (1996 and 1998). Note only the 30–39 cm CCL group contained *L. danae*, and only the two larger groups contained any non-food items

(manatee grass), *Ceramium* sp. (red algae), *Gelidiella* sp. (red algae), *Herposiphonia* sp. (red algae), *Dictyota* sp. (brown algae), *Laurencia* sp. (red algae), and *Cyanophyta* (blue-green algae). All of these items were also seen in juvenile samples, except for manatee grass. All species from lavage samples in both 1996 and 1998 are listed in Table 6.

Discussion

Near-shore foraging habitats offer researchers and conservation managers the most practical marine habitats in which to census sea turtles in the water. In some areas, these coastal habitats serve as key developmental areas for

Table 6 All species from lavage samples in 1996([1]) and 1998([2]) (* = both)

Chlorophyta (green algae)
Dictyosphaeria cavernosa[1]
Codium sp.[1]
Halimeda opuntia[1]
Halimeda incrassata[2]
Bryopsis sp.[1]
Bryopsis pennata[2]
Cladophoropsis macromeres[2]
Caulerpa racemosa var peltata[2]
Phaeophyta (brown algae)
Dictyota sp.[1]
Dictyota ciliolata[2]
Dictyota cervicornis[2]
Dictyopteris sp.[1]
Giffordia sp.[1]
Lobophora variegata[2]
Rhodophyta (red algae)
Laurencia sp.[1]
Laurencia intricata[2]
Herposiphonia sp.[1]
Heterosiphonia sp[1]
Martensia pavonia[1]
Spermothamnion sp.[1]
Ceramium sp.[1]
Gelidiella sp.[1]
Amphiroa sp.[1]
Amphiroa brasiliana[2]
Jania sp[1]
Jania adherens[2]
Kallymenia sp.[1]
Botryocladia sp.[1]
Gracilaria curtissiae[2]
Gracilaria damaecornis[2]
Hypnea cervicornis[2]
Flahaultia tegetiformis[2]
Cyanophyta (blue-green algae)[1]
Cnidaria
Zoanthus sociatus (zoanthid)[*]
Ricordea florida (corallimorph)[1]
Scleractinia (stony coral)[1]
Lebrunia danae[2]
Arthropoda
Cirripedia (barnacles)[1]
Chelonibia testudinaria[2]
Mollusca
Fissurellidae (limpets)[1]
Porifera (sponge)
Tethya sp.[1]
Protista
Homotrema rubrum (foraminifera)[1]

juvenile turtles, but these habitats are also the most susceptible to anthropogenic influence, with a high probability of sea turtle—human interactions. Thus, identification of sea turtle habitats may serve as a first step in designing practical guidelines to regulate human activities that may affect turtles (i.e., boating, anchoring, fishing) at specific times of the year and in certain locations.

Here, we present results of baseline surveys of the abundance and distribution of juvenile hawksbills in the BIRNM developmental habitat, which can be utilized for management plans and comparison to future studies and inventories. We also identified benthic composition in foraging areas, determined diet through lavages, gathered data on growth rates for juvenile male and female turtles, and calculated presumed minimum residency for recaptured turtles. This study therefore contributes to the general understanding of juvenile hawksbill ecology at BIRNM.

Distribution surveys showed that hawksbills were primarily present in blocks J–N on the north side of the island, and hawksbills were found in the most structurally diverse habitat blocks around Buck Island. Opportunistic capture surveys in this area resulted in 75 individual hawksbills captured over 4 years; captures occurred where effort was concentrated. Thus, these data were not intended to assess abundance or evaluate quantitative turtle numbers due to the lack of effort-corrected data. Instead, these data are most useful for planning future ecological assessments. In particular, future effort-corrected data with equivalent effort per zone could reveal whether juvenile hawksbills at BIRNM show a true habitat preference for zones within the north area of the island.

Individual hawksbills were recaptured in 1–6 different sectors over the 4 year survey. The small area in which we consistently recaptured the majority of turtles over several years may indicate turtle home ranges were small with considerable site fidelity, as seen in previous studies (Van Dam and Diez 1997, 1998; Scales et al. 2011; see also Cuevas et al. 2007). However, this is indeterminate from our data. Future tracking studies of juveniles would be ideal to elucidate home range size of hawksbills at BIRNM.

For recaptured turtles, we found growth rates for turtles measuring 24.5–63.0 cm CCL ranged from 1.0 to 9.5 cm $year^{-1}$ CCL. Other studies have directly compared CCL and SCL for hawksbills, asserting there is a minimal difference in CCL and SCL growth rates, which has been shown for green turtles (Bjorndal and Bolten 1988; see Bjorndal and Bolten 2010). Other hawksbill growth rates in the Caribbean region (Cayman Islands, USVI, Barbados and Puerto Rico) reportedly range from negligible up to 9.1 cm $year^{-1}$ for sizes ranging from 19.5 to 84.5 cm SCL (Boulon 1994; Diez and Van Dam 2002; Blumenthal et al. 2009a; Krueger et al. 2011), except for hawksbills in the

Bahamas, for which growth rates of up to 15.7 cm year^{-1} SCL have been measured (Bjorndal and Bolten 1988, 2010). Our growth rate estimates for juvenile hawksbills fall within previous estimates, with a slightly higher growth rate as compared to juveniles from non-Bahamian Caribbean sites.

We found that the growth rates of these turtles generally decreased with turtle size, but peaked at the 30–39 cm CCL size class. These results should be considered with caution, as our peak growth rate came from a size class with only one measurable growth rate; however, previous studies on growth rates of hawksbills have found both monotonic and non-monotonic growth rates. Monotonic growth rates, showing a decrease in growth rates with increasing turtle size, from the Bahamas, St Thomas USVI, and Cayman Islands were found for turtles measuring 20.5–71.3 SCL (Bjorndal and Bolten 1988; Boulon 1994; Blumenthal et al. 2009a; Bjorndal and Bolten 2010). Non-monotonic growth rates from various locations showed peaks within two different brackets of size classes, including the 30–35 or 50–60 cm SCL size class (Puerto Rico: 34–35 cm SCL, Diez and Van Dam 2002; Souther Great Barrier Reef: 60 cm CCL, Chaloupka and Limpus 1997; Barbados: 30–35 cm SCL, Krueger et al. 2011; Aldabra: 50–60 cm CCL, Mortimer et al. 2003). A slower growth rate for smaller hawksbills may reflect a period of adjustment to new habitat for newly recruited juveniles (Bjorndal and Bolten 2010) and increased growth rates that follow (for non-monotonic growth rates) may represent a compensatory phase (see Krueger et al. 2011). The lack of smaller size classes in growth rate studies may contribute to an inability to detect a non-monotonic growth rate (see Krueger et al. 2011). Variable growth rates across the Caribbean indicate either density-dependent or habitat quality factors may affect growth rates (Diez and Van Dam 2002; Krueger et al. 2011, and see Kubis et al. 2009 [green turtles]). Reported growth rates for hawksbills in the Caribbean are higher than those reported from Australia or Aldabra, further suggesting that growth rates may be affected by local conditions.

There have been three previous studies that evaluated differences in growth rates of hawksbills based on sex; only one occurred in the Caribbean region. Chaloupka and Limpus (1997) found females from the Southern Great Barrier Reef had a faster growth rate than males (turtles from 39.0 to 85.0 cm CCL), but Bell and Pike (2012) found no difference in growth rates by sex for turtles 61.3–91.4 cm CCL at a site in the Northern Great Barrier Reef. Similarly, Krueger et al. (2011) found no difference in growth rates by sex for turtles 23.7–80.0 cm CCL in Barbados. Due to small sample size, we were unable to statistically compare the male and female growth rates in our study; however, mean growth rates across size classes from 40–69 cm CCL appear similar at BIRNM (females: 0.0–5.5 cm year^{-1}, males: 1.7–4.9 cm year^{-1}).

Habitat use studies rarely characterize the forage resources simultaneously with captures, and there are few hawksbill lavage studies in the literature for comparison. Generally considered spongivores (Meylan 1988), hawksbills consume other species such as corallimorphs, hydroids, sea urchins, and jellyfish (Carr et al. 1966; Leon and Bjorndal 2002; Blumenthal et al. 2009a; Rincon-Diaz et al. 2011). Cnidarians have therefore been reported in hawksbill diets (corallimorphs, hydroids and jellyfish), as well as the consumption of another Zoanthid species, *Palythoa caribaeorum* (Stampar et al. 2007), but the genus *Zoanthus* has not previously been documented as a high proportion of the hawksbill diet. Thus, our lavage results shed new light on hawksbill prey items in the Caribbean. Further, only the two largest size classes (50–59 and 60–69 cm CCL) had non-food items in their lavage samples (e.g., plastic and fibers). We speculate that these larger individuals may consume food items near where human activities occur at BIRNM (i.e., at recreational use areas near beaches).

Rincon-Diaz et al. (2011) were first to report the presence of *L. danae* in the diet of a juvenile hawksbill. This species contains highly venomous nematocysts with a potent neurotoxin (Sánchez-Rodriguez and Cruz-Vázquez 2006). We also found this species in our samples ($n = 3$), but only in the smallest size class (30–39 cm CCL). It is possible these specific toxins do not harm the turtles. However, toxicity analyses of some sponges commonly consumed by hawksbills have shown low or variable chemical defenses (Pawlik et al. 1995; Swearington and Pawlik 1998) suggesting the species may avoid highly toxic prey. The absence of this item from the diets of older turtles and other lavage studies suggests learning or competition with larger hawksbills for particular food items may be involved.

Recent studies suggest that hawksbill prey selection results from the interaction between preference and local abundance, with positive selectivity sometimes occurring for rare items and low preferences sometimes occurring for items abundant in lavages (Leon and Bjorndal 2002; Rincon-Diaz et al. 2011). Habitat surveys of BIRNM in the late 1980s and early 1990s revealed very little sponge at the site, whereas *Zoanthus* occurred in dense mats (Gladfelter et al. 1977; Bythell 1992). Additionally, the number of prey items per lavage sample at BIRNM ranged from 1 to 12. Previous lavage studies in other Caribbean locations have only reported up to three or four prey items per sample (Leon and Bjorndal 2002; Rincon-Diaz et al. 2011). The higher amount of prey items per sample observed at BIRNM, and the high percent of Zoanthids, may be due in part to the lack of sponges at the site, perhaps signifying

compensatory behavior as they attempt to obtain necessary nutrients without sponges in their diet. Future studies at BIRNM investigating the abundance of other prey species in benthic surveys, in conjunction with lavages, could elucidate prey selectivity.

Studies at other foraging grounds have shown juvenile hawksbill residency for at least several years in small home ranges (Mona and Monito Islands, Puerto Rico; Van Dam and Diez 1998). Thus, we presumed continued residency of immature hawksbills between capture–recapture events. Our results showed presumed minimum residency up to almost 4 years, with similar residency periods for all size classes. However, we are uncertain that turtles remained within the BIRNM boundaries between captures; future tracking studies should aim to confirm site residency for juveniles at this site.

The time required to grow to given sizes is key information for stage-based population models (Kendall and Bjorkland 2001; Heppell et al. 2003). The growth rates presented here will contribute toward creating and improving hawksbill population models and our general understanding of variation in these rates from one site to another. Moreover, the basic biological data presented here can be used to determine size structure and growth rates; these data will ultimately help determine which conservation methods will be most effective (i.e., through elasticity analyses, see de Kroon et al. 1986). In the short term, georeferenced sighting and capture rate information can be used by managers to identify locations where human–turtle interactions may be possible, as well as where resources used by turtles may warrant additional protection. As well, additional studies on turtle use of deeper regions of BIRNM are warranted. The condition of the foraging resources at BIRNM will be important for sustaining juvenile hawksbills in this developmental habitat over many years. Our results support the growing body of evidence that hawksbill diet may be much more plastic than previously believed.

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References

Anderson MH, Lund D, Gladfelter E, Davis M (1985) Ecological community type maps and biological community descriptions for Buck Island Reef National Monument and proposed marine sites in the British Virgin Islands. In: Virgin Islands Resource management cooperative biosphere reserve research report 4. National park service technical report: 214–229

Bass AL, Good DA, Bjorndal KA, Richardson JI, Hillis Z-M, Horrocks JA, Bowen BW (1996) Testing models of female reproductive migratory behaviour and population structure in the Caribbean hawksbill turtle, *Eretmochelys imbricata*, with mtDNA sequences. Mol Ecol 5:321–328

Bell I, Pike DA (2012) Somatic growth rates of hawkbsill turtles *Eretmochelys imbricata* in a northern great barrier reef foraging area. Mar Ecol Prog Ser 446:275–283

Berube MD, Dunbar SG, Rützler K, Hayes WK (2012) Homes range and foraging ecology of juvenile hawksbill sea turtles (*Eretmochelys imbricata*) on inshore reefs of Honduras. Chelonian Conserv Biol 11(1):33–43

Bjorndal KA, Bolten AB (1988) Growth rates of immature green turtles, *Chelonia mydas,* on feeding grounds in the southern Bahamas. Copeia 3:555–564

Bjorndal KA, Bolten AB (2010) Hawksbill sea turtles in seagrass pastures: success in a peripheral habitat. Mar Biol 157:135–145

Bjorndal KA, Bolten AB, Chaloupka MY (2000) Green turtle somatic growth model: evidence for density dependence. Ecol Appl 10(1):269–282

Blumenthal JM, Austin TJ, Bell CDL, Bothwell JB, Broderick AC, Ebanks-Petrie G, Gibb JA, Luke KE, Olynik JR, Orr MF, Solomon JL, Godley BJ (2009a) Ecology of hawksbill turtles, *Eretmochelys imbricata*, on a western Caribbean foraging ground. Chelonian Conserv Biol 8(1):1–10

Blumenthal JM, Austin TJ, Bothwell JB, Broderick AC, Ebanks-Petrie G, Olynik JR, Orr MF, Solomon JL, Witt MJ, Godley BJ (2009b) Diving behavior and movements of juvenile hawksbill turtles *Eretmochelys imbricata* on a Caribbean coral reef. Coral Reefs 28:55–65

Boulon RH (1994) Growth rates of wild juvenile hawksbill turtles, *Eretmochelys imbricata*, in St. Thomas. United States Virgin Islands. Copeia 3:811–814

Bythell JC, Gladfelter EH, Bythell M (1992) Ecological studies of Buck Island Reef National Monument. A quantitative assessment of selected components of the coral reef ecosystem and establishment of long-term monitoring sites. Part II. US National Park Service, Cruz Bay, St. John, US Virgin Islands, St. Croix, p 72

Bythell JC, Bythell M, Gladfelter EH (1993) Initial results of a long-term coral-reef monitoring program—impact of hurricane Hugo at Buck Island Reef National Monument, St Croix, U.S. Virgin Islands. J Exp Mar Biol Ecol 172:17–18

Carr A, Hirth H, Ogren L (1966) The ecology and migrations of sea turtles, 6. The hawskbill turtle in the Caribbean Sea. Am Mus Novit 2248:1–29

Chaloupka MY, Limpus CJ (1997) Robust statistical modeling of hawksbill sea turtle growth rates (southern Great Barrier Reef). Mar Ecol Prog Ser 146:1–8

Cuevas E, Liceaga-Correa MA, Garduno-Andrade M (2007) Spatial characterization of a foraging area for immature hawksbill turtles (*Eretmochelys imbricata*) in Yucatan, Mexico. Amphibia-Reptilia 28:337–346

de Kroon, Hans, Anton Plaisier, Jan van Groenendael, and Hal Caswell. 1986. Elasticity: the relative contribution of demographic parameters to population growth rate. Ecology 67:1427–1431. http://dx.doi.org/10.2307/1938700

Diez CE, Van Dam RP (2002) Habitat effect on hawksbill turtle growth rates on feeding grounds at Mona and Monito Islands, Puerto Rico. Mar Ecol Prog Ser 234:301–309

Dunbar SG, Salinas L, Stevenson L (2008) In-water observations of recently released juvenile hawksbills *Eretmochelys imbricata*. Mar Turt Newsl 121:5–9

ESRI (2007) ArcGIS 9.3 GIS, Redlands, CA

Gaos AR, Lewison RL, Yañez IL, Wallace BP, Liles MJ, Nichols WJ, Baquero A, Hasbún CR, Vasquez M, Urteaga J, Seminoff JA (2012) Shifting the life-history paradigm: discovery of novel habitat use by hawksbill turtles. Biol Lett 8(1):54–56

Geis A, Wibbels T, Phillips B, Hillis-Starr Z, Meylan A, Meylan P, Diez C, Van Dam R (2003) Predicted sex ratio of juvenile hawksbill sea turtles inhabiting Buck Island Reef National Monument, US Virgin Islands. J Herpetol 37:400–404

Gladfelter WB (1982) White-band disease in *Acropora palmata*: implications for the structure and growth of shallow reefs. Bull Mar Sci 32(2):639–643

Gladfelter WB, Gladfelter EH, Monahan RK, Ogden JC, Dill RF (1977) Environmental studies of Buck Island Reef National Monument, St. Croix, VI. West Indies Laboratory, St. Croix, USVI. 136 pp

Heppell SS, Crowder LB, Crouse DT, Epperly SP, Frazer NB (2003) Population models for Atlantic loggerheads: past, present, and future. In: Bolten AB, Witherington BE (eds) Loggerhead sea turtles. Smithsonian Institution Press, Washington, pp 255–273

Kendall WL, Bjorkland R (2001) Using open robust design models to estimate temporary emigration from capture—recapture data. Biometrics 57:1113–1122

Krueger BH, Chaloupka MY, Leighton PA, Dunn JA, Horrocks JA (2011) Somatic growth rates for a hawksbill turtle population in coral reef habitat around Barbados. Mar Ecol Prog Ser 432:269–276

Kubis S, Chaloupka M, Ehrhart L, Bresete M (2009) Growth rates of juvenile green turtles *Chelonia mydas* from three ecologically distinct foraging habitats along the east central coast of Florida, USA. Mar Ecol Prog Ser 389:257–269. doi:10.3354/meps08206

Leon YM, Bjorndal KA (2002) Selective feeding in the hawksbill turtle, an important predator in coral reef ecosystems. Mar Ecol Prog Ser 245:249–258

Leon YM, Diez CE (1999) Population structure of hawksbill turtles on a foraging ground in the Dominican Republic. Chelonian Conserv Biol 3(2):230–236

Limpus CJ (1994) The hawksbill turtle, Eretmochelys imbricate, in Queensland: population structure within a southern Great Barrier Reef feeding ground. Wildl Res 19(4):489–505

Mendonça MT (1983) Movements and feeding ecology of immature green turtles (*Chelonia mydas*) in a Florida lagoon. Copeia 1983(4):1013–1023

Meylan A (1988) Spongivory in hawksbill turtles: a diet of glass. Science 239:393–395

Meylan PA, Meylan AB, Gray JA (2011) The ecology and migrations of sea turtles. 8. Tests of the developmental habitat hypothesis. B Am Mus Nat Hist. Number 357. 70

Mortimer JA, Donnelly M (IUCN SSC Marine Turtle Specialist Group) (2008) *Eretmochelys imbricata*. In: IUCN 2012. IUCN Red List of Threatened Species. Version 2012.1. www.iucnredlist.org. Downloaded on 30 July 2012

Mortimer JA, Collie J, Jupiter T, Chapman R, Liljevik A, Betsy B (2003) Growth rates of immature hawksbills *(Eretmochelys imbricata)* at Aldabra Atoll, Seychelles (Western Indian Ocean). In: Seminoff JA (ed) Proceedings of the 22nd annual symposium on sea turtle biology and conservation. NOAA Technical Memorandum NMFS-SEFSC-503. US Department of Commerce, Miami, FL, pp 247–248

National Marine Fisheries Service (NMFS) and United States fish and wildlife service (USFWS) (1993) Recovery plan for hawksbill turtles in the U.S. Caribbean Sea, Atlantic Ocean, and Gulf of Mexico. St. Petersburg, FL

NMFS & USFWS (1998) Recovery plan for U.S. Pacific populations of the hawksbill turtle (*Eretmochelys imbricata*). NMFS Silver Spring, MD

Pawlik JR, Chanas B, Toonen RJ, Fenical W (1995) Defenses of Caribbean sponges against predatory reef fish. I. Chemical deterrency. Mar Ecol Prog Ser 127:183–194

Pemberton RA Jr (2001) The Habitat Utilization of Hawksbill Sea Turtles *Eretmochelys imbricata* at Buck Island Reef National Monument St. Croix U.S. Virgin Islands, MS Thesis, Virginia Institute of Marine Science, Gloucester Point, VA 111 pp

Rincon-Diaz MP, Diez CE, Van Dam RP, Sabat AM (2011) Foraging selectivity of the hawksbill sea turtle (*Eretmochelys imbricata)* in the Culebra Archipelago, Puerto Rico. J Herpetol 45:277–282

Sánchez-Rodríguez J, Cruz-Vázquez K (2006) Isolation and biological characterization of neurotoxic compounds from the sea anemone *Lebrunia danae* (Duchassaing and Michelotti 1860). Arch Toxicol 80:436–441

SAS (1997) SAS version 6. SAS Institute Inc, Cary

Scales KL, Lewis JA, Lewis JP, Castellanos D, Godley BJ, Graham RT (2011) Insights into habitat utilisation of the hawksbill turtle, *Eretmochelys imbricata* (Linnaeus 1766), using acoustic telemetry. J Exp Mar Biol Ecol 407:122–129

Stampar SN, da Silva PF, Luiz OJ Jr (2007) Predation on the Zoanthid *Palythoa caribaerum* (Anthozoa, Cnidaria) by a hawksbill turtle (*Eretmochelys imbricata)* in southeastern Brazil. Mar Turtle Newsl 117:3–5

Swearington DC, Pawlik JR (1998) Variability in the chemical defense of the sponge *Chondrilla nucula* against predatory reef fishes. Mar Biol 131:619–627

Van Dam RP, Diez CE (1997) Diving behavior of immature hawksbill turtles (*Eretmochelys imbricata*) in a Caribbean reef habitat. Coral Reefs 16:133–138

Van Dam RP, Diez CE (1998) Home range of immature hawksbill turtles (*Eretmochelys imbricata* (Linnaeus)) at two Caribbean islands. J Exp Mar Biol Ecol 220:15–24

Velez-Zuazo X, Ramos WD, Van Dam RP, Diez CE, Abreu-Groboiss A, McMillan WO (2008) Dispersal, recruitment and migratory behaviour in a hawksbill sea turtle aggregation. Mol Ecol 17:839–853

Witzell WN (1983) Synopsis of biological data on the hawksbill turtle *Eretmochelys imbricata* Linnaeus, 1766). FAO Fisheries Synopsis 137:1–78