
CHARACTERIZATION OF A HAWKSBILL TURTLE (*ERETMOCHELYS IMBRICATA*) FORAGING AGGREGATION IN A HIGH-LATITUDE REEF COMMUNITY IN SOUTHEASTERN FLORIDA, USA

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Abstract.—A foraging aggregation of Hawksbill Turtles (*Eretmochelys imbricata*) on the Southeast Florida Continental Reef Tract off Palm Beach County, Florida, is the first described within the waters of the continental United States. The aggregation is the second most northerly known in the western Atlantic; its existence may be due in part to the proximity of the Florida Current. We captured 146 individual hawksbills 181 times at 44 dive sites over 5.5 y. We captured turtles on five benthic habitat types. Individuals varied from 35.7 to 83.9 cm SCL_{n-t} and > 95% were likely to be immature; thus the site serves primarily as developmental habitat. Captures and observations of tagged turtles indicate year-round presence; average observed residency was 24.9 mo (up to 73 mo). The average distance between researcher dive initiation sites associated with sequential observations of individual turtles was 1345 m, indicating a high degree of site fidelity. Control region (mtDNA) sequences for 112 individuals showed a predominance (> 65%) of haplotypes associated with Mexican nesting beaches. The minimum size of hawksbills captured at the study site suggests that the turtles have already spent time in benthic developmental habitat elsewhere. Observation rates and growth rates were comparable to those at several Caribbean sites, indicating that this high-latitude reef system constitutes primary habitat for this species.

Key Words.—coral reef; developmental habitat; endangered; haplotypes; size; Southeast Florida Continental Reef Tract

INTRODUCTION

The Hawksbill Turtle (*Eretmochelys imbricata*) is a highly specialized marine turtle associated with coral reefs and other hard-bottom habitats in tropical and subtropical seas world-wide. It is listed as Critically Endangered by IUCN (2009; see also Mortimer and Donnelly 2007). In the western Atlantic Ocean, hawksbills occur from the southern United States to Brazil and throughout the Greater and Lesser Antilles. In the continental USA, nesting is rare; only one nest has been documented in Texas, and four or fewer were recorded annually in Florida between 1979 and 2003 (Meylan and Redlow 2006). However, hawksbills occur with regularity in Florida waters, particularly along the southeastern and central Gulf of Mexico coasts and in the Florida Keys (Meylan and Redlow 2006). These authors confirmed the presence of all life stages in the state and described their distributions based on observations of live turtles at sea, in-water capture programs, incidental captures, museum records, and stranding data. However, few studies have focused on this species in Florida waters (Eaton et al. 2008), and

relatively little is known about its biology or habitat use in continental U.S. waters.

In this study Hawksbill Turtles were observed and captured on reefs off Palm Beach County, Florida (26°45'N, 80°01'W), which represent one of the most northerly sites in the western Atlantic Ocean at which a hawksbill foraging aggregation has been identified. The existence of hawksbills at this site may be due, in part, to the proximity of the Florida Current, a branch of the Gulf Stream Current (Fig. 1). The current passes near the southeastern Florida coastline and brings warm tropical water from the Gulf of Mexico and Caribbean. It continues northeast towards Bermuda and may similarly account for the presence of a hawksbill foraging aggregation there (Meylan et al. 2011). Meylan and Redlow (2006) hypothesized that the convergence of currents from a wide area of the Gulf of Mexico and the Caribbean into the Florida Current may serve to concentrate pelagic-sized hawksbills along the coast of southeastern Florida and would help to explain observed stranding patterns. The hypothesis of a dispersal corridor in this area was supported by the results of Blumenthal et al. (2009b), who used ocean current data

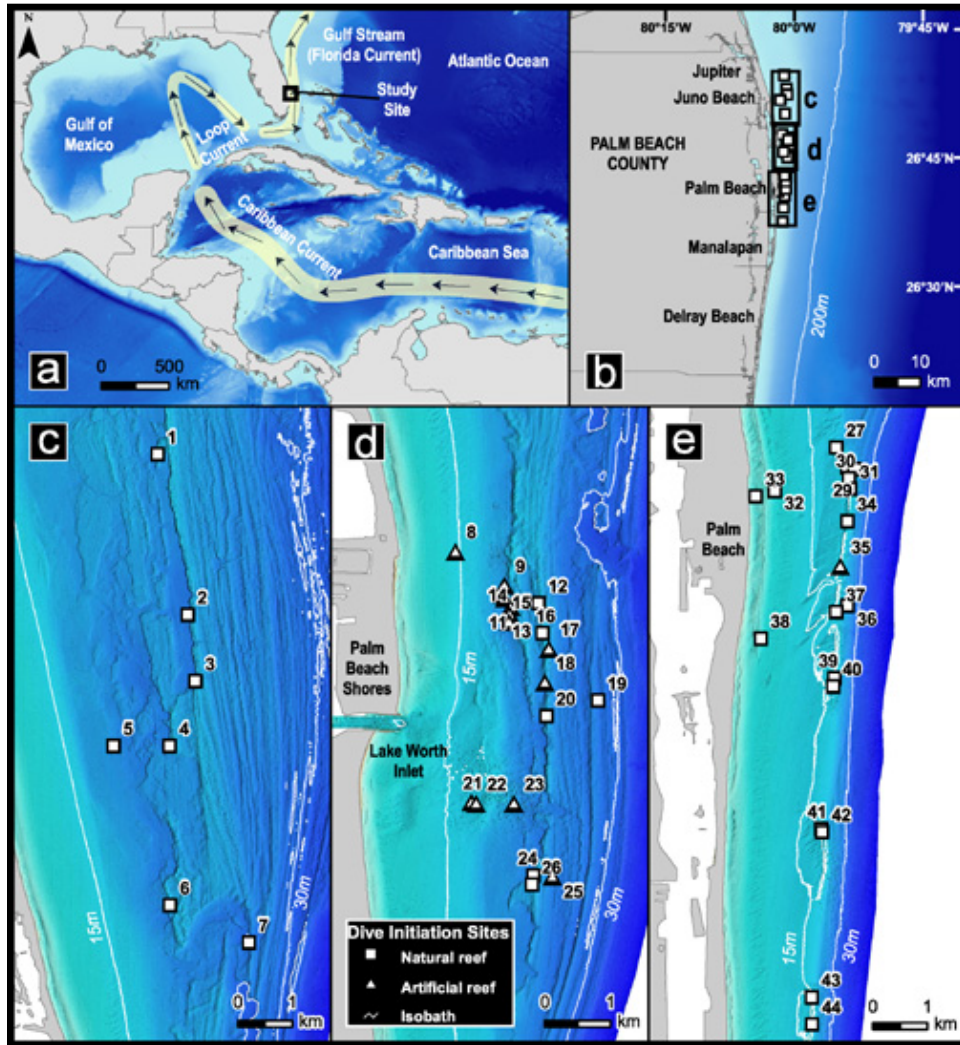


FIGURE 1. Palm Beach County, Florida, USA, study area. (a) At regional scale showing proximity to Gulf Stream Current. (b–e) Locations of dive initiation sites described in Table 1 and shown in Fig. 2. Figure uses Laser Airborne Depth Sounding data collected for Palm Beach County, Environmental Resources Management, by Tenix LADS, Inc. under contract to Coastal Planning and Engineering.

and models of passively drifting particles to predict the dispersal patterns of Caribbean hawksbills.

The reefs off Palm Beach County are part of the Southeast Florida Continental Reef Tract, which has been described as a high-latitude reef system (Moyer et al. 2003; Banks et al. 2007, 2008; Riegl et al. 2007). The reef supports a fauna similar to that of the Florida Keys, Bahamas, and Caribbean but with a different community structure, lacking the major reef-building coral, *Acropora palmata*; it is characterized by low coral cover (1–13%) and a dominance of sponges and octocorals (Jaap and Hallock 1990; Moyer et al. 2003; Banks et al. 2008).

The discovery of a foraging aggregation of hawksbills at this high-latitude site broadens the understanding of habitat use of this Critically Endangered species. Coral

reefs appear to be its primary habitat, although the use of other rocky, high-energy environments such as cliff walls, shoals, and limestone and volcanic outcrops has also been documented (Meylan and Redlow 2006 and references therein). These observations are consistent with the spongivorous feeding habits of the species (Meylan 1988). Seagrass beds are also used to some extent (Diez et al. 2003; Bjorndal and Bolten 2010) as are mangrove-fringed bays, lagoons, and estuaries in the eastern Pacific (Carr 1952).

To characterize the Palm Beach County hawksbill foraging aggregation, we provide a description of size structure, maturity status, habitat use, relative abundance, residency, site fidelity, and nesting beach origins. The female-biased sex ratio of this aggregation has been treated elsewhere (Blanvillain et al. 2008). Data

Wood et al.—A Hawksbill Turtle Aggregation.

TABLE 1. Sampling effort and Hawksbill Turtle (*Eretmochelys imbricata*) capture and sighting results for 435 SCUBA dives at 44 dive initiation sites off Palm Beach County, Florida, USA. Sites are mapped by number in Fig. 1. Habitat type for each site is shown in Fig. 2. Abbreviations are SC = sum of captures, SR= sum of recaptures, SST = sum of sightings of tagged turtles, SSU = sum of sightings of untagged turtles.

Site number	Dive initiation site	Distance to shore (m)	Number of dives	Latitude °N	Longitude °W	SC	SR	SST	SSU
1	Drum Stick	4070	3	26.911	80.020	2	0	0	0
2	Juno Ball	3733	1	26.884	80.015	1	0	0	0
3	Juno Ledge	3528	21	26.873	80.013	12	1	8	3
4	Snapper Reef	2849	1	26.862	80.018	0	0	0	0
5	Shark Canyon	1942	15	26.862	80.027	4	0	1	1
6	Jolly Jack's	2269	5	26.836	80.018	2	1	0	0
7	Larry's Ledge	3428	1	26.830	80.005	1	0	0	0
8	Tug Boat Barge	790	1	26.796	80.024	1	0	0	1
9	Playground	1527	1	26.791	80.017	0	1	0	0
10	Brazilian Docks	1506	1	26.790	80.017	0	1	0	0
11	China Barge	1535	3	26.789	80.017	2	1	2	0
12	Larson's Valley	1996	2	26.789	80.012	2	0	0	0
13	Amaryllis	1624	15	26.788	80.016	8	0	12	1
14	PC1174	1599	3	26.787	80.016	1	0	2	0
15	Mizpah	1579	13	26.786	80.016	7	1	12	0
16	Yellowtail	2019	8	26.785	80.012	5	1	1	0
17	Spearman's Barge	2087	10	26.783	80.011	5	1	4	1
18	Mid-Reef (to Spearman's)	2001	8	26.778	80.011	3	0	5	1
19	Nun's Ledge	2715	6	26.775	80.004	3	0	0	1
20	Mid-Reef	2027	28	26.773	80.011	14	1	20	5
21	Toybox/Playpen	1533	2	26.762	80.021	1	0	0	2
22	60 ft. barge	1595	8	26.761	80.021	2	2	1	0
23	60 ft. rocks	2107	1	26.761	80.016	0	0	0	0
24	South Double Ledges	2285	25	26.752	80.013	8	2	0	1
25	Governor's Riverwalk	2548	5	26.751	80.010	1	0	0	0
26	North Double Ledges	2261	2	26.750	80.013	0	0	0	0
27	Turtle Mound	1477	4	26.716	80.018	0	0	2	0
28	Breakers 2nd	1631	4	26.713	80.017	0	1	2	0
29	Window	1746	6	26.713	80.015	0	1	4	0
30	Breakers Backside	1659	17	26.711	80.016	3	1	11	1
31	Breakers 4th	1697	17	26.710	80.016	4	0	5	1
32	Elevator Shaft	456	4	26.709	80.029	0	0	0	0
33	Cable Crossing	138	12	26.708	80.032	2	0	0	0
34	Breakers Nearshore	1624	56	26.704	80.017	18	3	20	2
35	Trench	1544	34	26.697	80.018	9	5	8	1
36	Flower Garden	1695	4	26.690	80.017	1	0	0	0
37	Teardrop	1526	21	26.689	80.018	5	6	3	2
38	Ron's Reef	367	3	26.685	80.031	1	0	0	0
39	Pink House	1654	23	26.678	80.019	5	2	6	0
40	Bath and Tennis	1645	13	26.677	80.019	5	1	2	0
41	Janine's Ravine	1585	1	26.6533	80.0208	0	0	0	0
42	Sloan's Curve	1599	21	26.6528	80.0207	6	1	2	1
43	Paul's Reef	1453	5	26.625	80.022	2	0	0	0
44	Horseshoe	1437	1	26.621	80.022	0	1	1	0
44	Casino	1437	1	26.621	80.022	0	1	1	0
			435			146	35	134	25

from this foraging aggregation are relevant to conservation efforts on behalf of hawksbills and the reef ecosystems they occupy. These habitats face numerous threats in Florida (Collier et al. 2008) and world-wide (Jackson et al. 2001; Wilkinson 2004).

MATERIALS AND METHODS

Study site.—This study was conducted within a 30-km stretch (26°55'N to 26°37'N) of the Southeast Florida Continental Reef Tract off Palm Beach County, Florida, USA (Fig. 1). Drift dives began at 44 dive initiation sites with associated GPS coordinates (Table 1; Fig. 1).

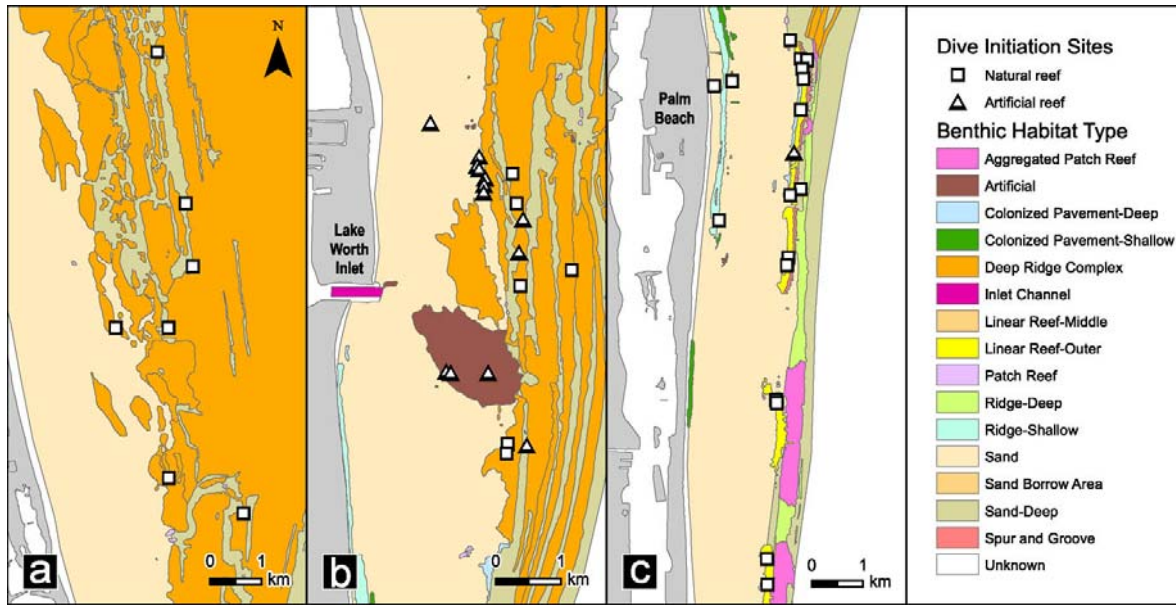


FIGURE 2. Benthic habitat type at 44 dive initiation sites that were the starting points for 435 dive transects used in this study. Habitat types are from Banks et al. (2007, 2008) and Riegl et al. (2007).

Surveys focused on hard-bottom habitat types in waters 367–4070 m (mean 1917) from shore, in depths ranging 2–26 m (Table 1; Fig. 2).

The southern portion of the study site consisted of both “nearshore colonized pavement” and, farther offshore, the northernmost section of the relict acroporid-based southeastern Florida outer reef tract (Jaap and Hallock 1990; Banks et al. 2007, 2008; Riegl et al. 2007; Fig. 2). Both reefs are roughly shore-parallel and separated by approximately 1.5 km of uncolonized sandy seafloor. The nearshore reef is of very low relief and subject to considerable wave energy and sand dispersal, resulting in highly variable benthic cover that is typically macroalgae-dominated. The deeper reefs “linear reef outer” are well defined, 0.1 km-wide ridge-like structures. They typically feature steep, undercut shoreward ledges that rise 2–3 m from the seafloor, then rise to a crest at approximately 16 m below sea level. The fore-reef slopes gradually eastward to a sandy seafloor where it is common to encounter shore-perpendicular finger-like ridges and valleys known as “spur and groove” formations (Banks et al. 2007). The southern portion of the study area also contains several artificial reefs that include sunken vessels, limestone boulders, and concrete debris.

The northern portion of the study area consists of a series of shore-parallel, deep-water (20–35 m) ridges that form a “deep ridge complex” of distinct origin (possibly cemented beach dunes; Riegl et al. 2007; Banks et al. 2008). These ridges result in a highly variable and non-uniform seascape containing

discontinuous ledges, outcroppings, craters, and mounds separated by areas of exposed rock and sandy seafloor. This habitat has low cover (except near areas of higher relief) that is dominated by small gorgonians, sponges, and macroalgae.

The Florida Current flows northward along the coast with its axis approximately 30 km offshore. Based on daily sea surface temperature imagery data, the western boundary of the current ranged 2–20 km from the hawksbill study site (US Navy Oceanographic Office 2005). Average speeds ranged from 1.0 m s⁻¹ in November to 2.3 m s⁻¹ in July with a yearly average of 1.3 m s⁻¹ (Banks et al. 2007, 2008).

Sampling.—We made 435 dives beginning at one of 44 dive initiation sites between 5 April 2004 and 22 October 2010. Total dive time was 234.3 h. A commercial dive charter provided dive logistics. Utilizing the dive charter method precluded the possibility of following a standardized sampling design and may have biased the results. The destinations on each day were chosen by the charter operator based on depth, distance from shore, ocean conditions, diver experience, and scheduling limitations. Sampling sessions consisted of two to three drift dives that averaged 32.3 min. Dive times varied widely because dives that resulted in a turtle capture were terminated as soon as the turtle was brought to the surface. Dives traversed the majority of hard-bottom habitat types found between 15 to 30 m. In the southern part of the study area, the dive path often followed ridges that

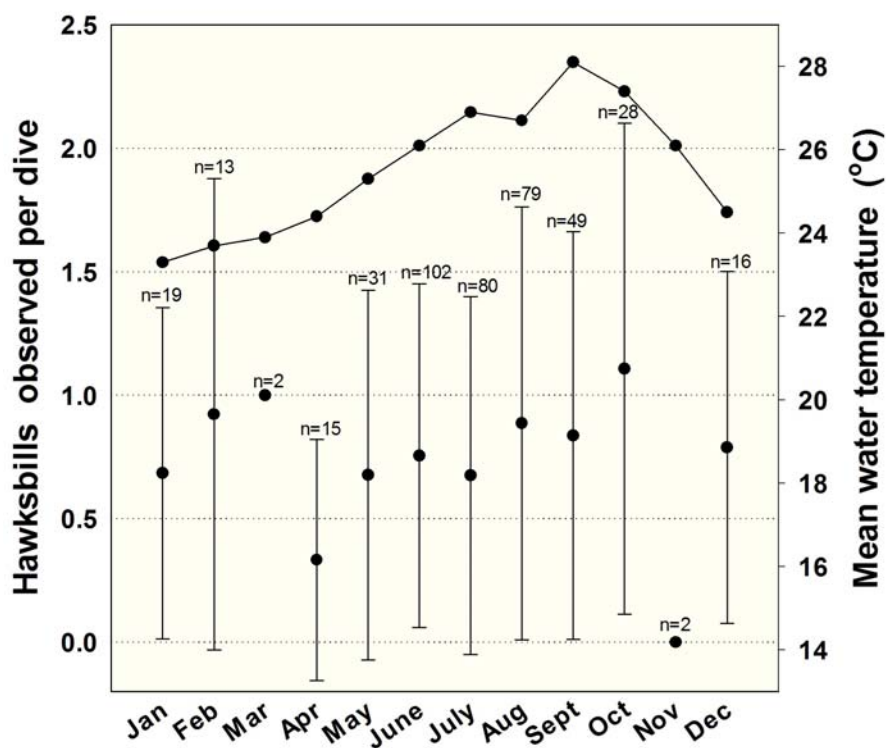


FIGURE 3. Sampling effort, mean monthly temperature, and frequency of observation of Hawksbill Turtles (*Eretmochelys imbricata*), April 2004 to October 2010, Palm Beach County, Florida. Figure shows mean number (and one standard deviation) of observations of hawksbills per dive (bar) and mean of monthly water temperatures at dive sites (line). Observations include captures, recaptures, and sightings of both tagged and untagged *Eretmochelys* by project staff. Number of dives per month is indicated (n).

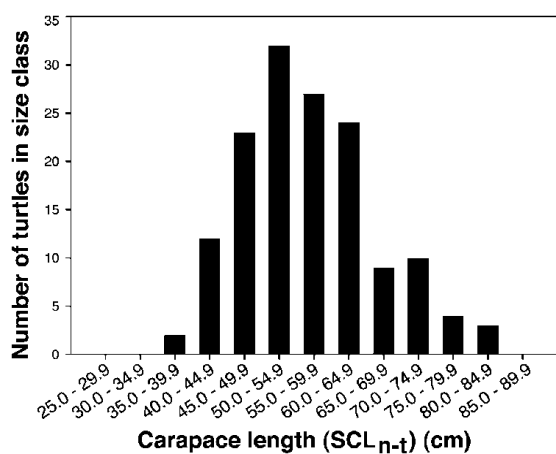


FIGURE 4. Size distribution of 146 Hawksbill Turtles (*Eretmochelys imbricata*) captured between April 2004 and October 2010 on reefs off Palm Beach County, Florida. Size at first capture is shown.

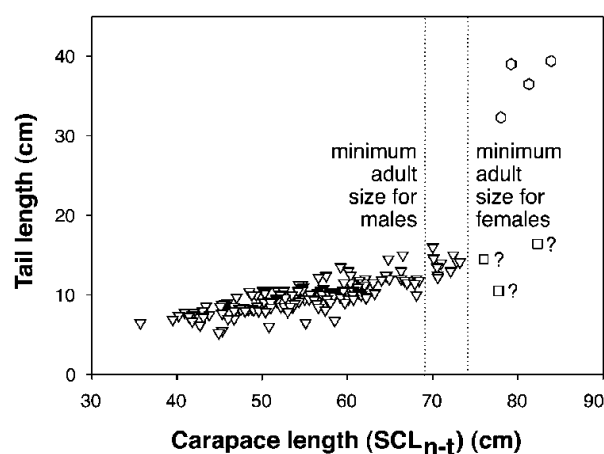


FIGURE 5. Tail length (plastron-to-tail-tip) as a function of carapace length (SCL_{n-t}) at first capture for 146 Hawksbill Turtles (*Eretmochelys imbricata*) captured on reefs off Palm Beach County, Florida. Triangles represent assumed immatures, hexagons adult males, and squares possibly mature females. Minimum carapace length for adult males (69.1 cm SCL_{n-t}) and adult females (74.1 cm SCL_{n-t}) converted from SCL_{min} from Meylan et al. (2011).

served as landmarks to orient the recreational-client divers. These biases in sampling were a necessary compromise in order to use the commercial diving firm for logistical support.

The research team began dives adjacent to or downstream from the client group to minimize interference with study animals. The course taken and distance traveled by the team were determined by current direction and velocity, with adjustments made to avoid high turbidity. Based on 16 dives for which dive times and GPS coordinates for start and stop points were available, the average speed of travel of the divers was 0.42 m s^{-1} (range 0.1–1.3, $SD \pm 0.329$). Thus, a typical drift dive traversed approximately 816 m of reef (estimated total linear distance 355 km).

At least two but usually three to four survey-dedicated divers swam close enough to maintain visual contact 3–5 m above the bottom to maximize the area surveyed. Upon sighting a hawksbill, team members signaled to each other its location. Water temperature and depth were recorded with a Sherwood Scuba, LLC (Santa Ana, California, USA) “Wisdom 2” dive computer. We assigned benthic habitat type following the terminology of Banks et al. (2008: 190; see also Riegl et al. 2007; Walker et al. 2008). If the turtle was untagged, flipper tags were unreadable, or at least 1 y had elapsed since the previous capture, we captured the turtle. We recorded but did not recapture tagged turtles that did not fit these criteria. We also recorded observations of turtles other than hawksbills seen during the dive.

Each turtle captured was brought to the surface at a safe ascent rate by a pair of divers. In some cases, GPS coordinates of the point at which the diver/turtle group surfaced were recorded by an observer on the boat. Recording precise surface positions for each capture was not possible because client diver recovery was the first priority of the dive vessel crew. In lieu of an exact position, we associated turtle capture locations with the dive initiation site for which GPS coordinates were always available. The average maximum location error was estimated to be 816 m, the average distance traversed during a complete dive. However, depending on when a turtle was captured during a dive, the distance from the dive initiation site was often much less.

Data collection.—Captured turtles were transferred to the dive boat for data collection. We collected morphometrics as described by van Dam and Diez (1998b) using calipers for straight measurements and a flexible tape for curved measurements. The primary size measurement used in this paper is straight carapace length (SCL) in cm from the nuchal notch to the tip of the longer pygal scute (SCL_{n-t}). We attached Inconel tags to the trailing edge of each front flipper in the second scale distal to the axilla, and we injected a PIT tag into the muscles at the base of the right front flipper.

We obtained a tissue sample for genetic analysis with a sterile 4 mm biopsy punch and placed in NaCl-saturated buffer (SED). Photographs (dorsal, ventral, right and left lateral head, head-on, epibionts, anomalies) were taken and notes were made of anomalies. We released turtles at the surface near the capture site.

We gave instructions to cooperating divers to photograph tags and/or record tag numbers and corresponding dates and locations of turtles bearing tags. All parties were instructed to avoid pursuing or harassing the turtles and to read tag numbers of only those turtles that permitted close approach. We accepted re-sighting data only if a valid tag number was recorded or if a photograph showed diagnostic features.

Data analysis.—We categorized observations of hawksbills as captures, recaptures, or sightings (with or without tag identification). In the case of both captures and recaptures, we took the turtles to the dive platform for data collection. To facilitate comparisons among studies, we used the equation of van Dam and Diez (1998b), $SCL_{min} = 1.0217 SCL_{n-t}^{0.9876}$ to convert midline measurements to notch-to-tip measurements. We calculated catch-per-unit-effort (CPUE) as all observations (including captures) per unit effort. The duration of individual dives was not always recorded, but total dive time was recorded daily and represented surface-to-surface time. Hence, we calculated CPUE as total observations per total dive time. Regression was used to explore the predictive value of some variables ($\alpha = 0.05$). Growth was plotted using midpoints between size at first and last capture for the longest recapture interval for turtles recaptured after > 1 y. We included zero and negative growth rates (Chaloupka and Limpus 1997). We calculated the amount of time that transpired between first and last observation of a turtle and distance between sightings for observations by both project personnel and third parties supporting the project. Because it was difficult to take GPS coordinates at the exact location of turtle captures during drift dives, we calculated distances between observations using dive initiation site locations. However, depth and habitat type correspond to point-of-capture and not to the dive initiation site. We performed site fidelity analyses using the Animal Movement Analysis Extension within ArcView 3.3 (Hooge and Eichenlaub 1997) and in ArcGIS 9.3.

Sequence data were generated by the ICBR Genetic Analysis Core, University of Florida, USA. We extracted DNA using Qiagen DNeasy Tissue Kits and manufacturer’s protocols. A 740 base pair segment of mtDNA control region was amplified using primers LTEi9 and H950 (Abreu-Grobois et al. 2006; Browne et al. 2010) and sequenced on an Applied Biosystems model AB3730xl sequencer at the ICBR DNA Sequencing Core, University of Florida, USA.



FIGURE 6. (a) Hawksbill Turtle (*Eretmochelys imbricata*) on linear reef-outer habitat of the Southeast Florida Continental Reef Tract, Palm Beach County. (b) The deep ridge complex of Southeast Florida Continental Reef Tract provides resting sites for *E. imbricata*. (Photograph 6b color corrected. Both photographed by Terri Roberts)

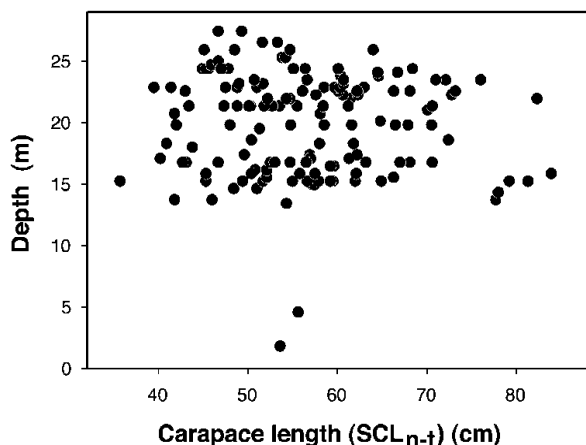


FIGURE 7. Depth of capture as a function of size (SCL_{n-t}) for all first captures of Hawksbill Turtles (*Eretmochelys imbricata*) made during this study. There was no correlation between turtle size and depth at capture site ($r^2 = 0.003$, $P = 0.524$).

Sequences were aligned with published Atlantic and Caribbean 380–480 bp (short) sequences (Bass et al. 1996; Bowen et al. 1996, 2007; Díaz-Fernández et al. 1999) and longer (740 bp), unpublished sequences

(Abreu-Grobois et al. 2006; Vélez-Zuazo et al. 2008) using MULTALIN (Corpet 1988) and assigned a three-part haplotype name following Vélez-Zuazo et al. (2008) and Browne et al. (2010); e.g., Q/MX1 (EiA41). To compare foraging aggregations for which long (740 bp) sequence data are available (Palm Beach, Mona Island, and Cayman Islands), we performed an AMOVA in Arlequin 3.01 (Excoffier et al. 2005). To estimate source populations for the Palm Beach foraging aggregation, it was necessary for us to truncate sequences to the 384 bp segment used by Bass et al. (1996), Bowen et al. (2007), Blumenthal et al. (2009b), and Browne et al. (2010) because data on the frequencies of the longer sequence are not yet available from most nesting beaches. An estimate of the sources for the Palm Beach aggregation was generated using SPAM 3.7b (Alaska Department of Fish and Game 2003) with baseline nesting data from Bass et al. (1996), Díaz-Fernández et al. (1999), Troëng et al. (2005), Bowen et al. (2007), Vélez-Zuazo et al. (2008), and Browne et al. (2010). We removed seven presumed adults ($> 74.1 SCL_{n-t}$) from the Palm Beach sample before this estimate was generated.

RESULTS

We observed Hawksbill Turtles 340 times during 435 dives (Table 1; Fig. 3). We conducted dives during all months with greatest effort during June through August. Water temperatures at initiation sites varied in monthly mean from 23.3 °C in January to 28.1 °C in September. We captured turtles in all months except November (two dives). Sightings of tagged turtles by third parties did occur during November. Neither month ($F_{1,10} = 0.201$, $P = 0.664$) nor mean monthly temperature ($F_{1,10} = 0.058$, $P = 0.815$) was a good predictor of observation rate.

Hawksbills were observed by the research team (no third-party sightings) at the rate of 1.45 h^{-1} or one observation for every 41.4 minutes. Using the estimate that researchers were transported by currents at an average speed of 0.42 $m s^{-1}$, one hawksbill was observed for every 1.04 km of survey. We captured 146 hawksbills 181 times (35 recaptures). Straight carapace lengths at first capture ranged from 35.7–83.9 cm SCL_{n-t} (mean = 56.6, SD = 9.7; Fig. 4). We considered the majority (95.2%) to be immature based on tail length (males) and carapace length (females; Fig. 5). Of 17 turtles judged to be possibly mature on the basis of size, four showed the elongated tail typical of adult males (> 30 cm plastron-to-tip-of-tail, van Dam and Diez 1998b) and three had carapace lengths large enough to be mature females. The remaining 10 over the minimum size of maturity were too small to be mature females and their tails were too short to be mature males and thus we considered them to be immature.

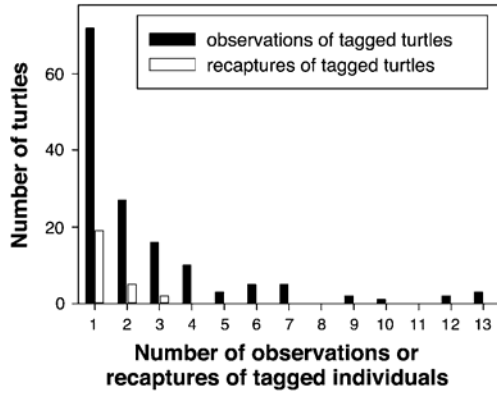


FIGURE 8. Number of observations and recaptures of individual tagged Hawksbill Turtles (*Eretmochelys imbricata*) made during this study. Observations include those made by project personnel and third parties (see Methods).

Habitat use.—The 146 first captures occurred in five habitat types (Riegl et al. 2007; Banks et al. 2008; Walker et al. 2008). Fifty-nine (40.4%) were on the deep ridge complex (14.9–27.5 m), 55 (37.7%) on the linear reef-outer (reef crest of outer reef; 13.4–25.9 m), 25 (17.1%) on artificial bottom-types (13.7–24.4 m), five (3.4%) in spur-and-groove habitat (15.3–19.5 m), and two (1.4%) turtles were on nearshore colonized pavement (1.8–4.6 m). We found hawksbills in linear reef-outer and deep ridge complex habitats (Fig. 6).

Turtles were found at depths of 1.8–27.5 m; but size was not dependent upon depth at capture site ($F_{1,141} = 0.408, P = 0.524$; Fig. 7). Two individuals were captured at shallow inshore sites; both were of average size for this study. The distance from shore at dive initiation sites was 138–4,070 m (Table 1). Distance from shore was not a good predictor of average number of turtles observed per dive ($F_{1,42} = 0.001, P = 0.977$).

Recaptures and resightings.—Seventy-four (50.7%) of the 146 turtles we tagged in the study were subsequently recaptured or resighted at least once (Fig. 8). Nineteen were recaptured once, five twice, and two three times. Project personnel sighted but did not recapture tagged turtles 134 times; they read tag numbers for 87 of these. In addition, 118 third-party sightings of project turtles were made in which tag numbers were recorded or diagnostic photographs taken. No reports of hawksbills tagged by this project were received from divers on reefs adjacent to the study site, although sightings were requested from these areas. No hawksbills tagged by other in-water projects were encountered.

Residency and site fidelity.—The average interval of observation for the 74 hawksbills that were seen more than once (Fig. 9) was 24.9 mo (SD = 20.6, range 0.2–

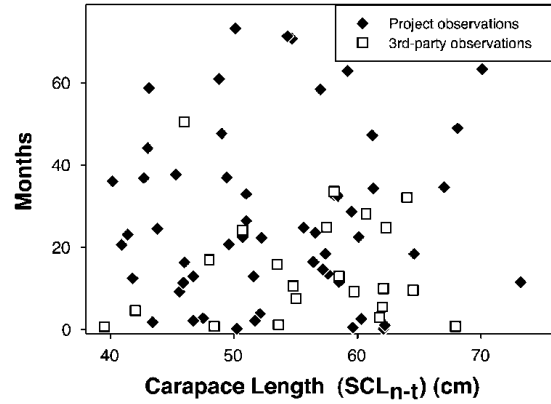


FIGURE 9. Longest interval of observation of flipper-tagged Hawksbill Turtles (*Eretmochelys imbricata*) captured on reefs off Palm Beach County, Florida, as a function of carapace length. Carapace length is initial size (SCL_{n-t}).

73.1 mo). The average time between visits to individual dive sites was 127.7 d (median = 30.0 d, range 0–1,844 d). The length of time between first and last observations was not a function of turtle size ($F_{1,72} = 0.025, P = 0.875$).

The average distance between researcher dive initiation sites associated with sequential observations of individual turtles (Fig. 10A) was 1,345 m (SD = 2,302, range 0–9,308 m, n = 73). Turtle size was not a good predictor of this distance ($F_{1,71} = 0.919, P = 0.341$), that is, large turtles did not move further. The farthest distance between dive initiation sites associated with sequential observations of 73 individual hawksbills was 11.1 km. (Fig. 10B). Furthest distance between observations was not found to be a function total time of observation ($F_{1,71} = 1.883, P = 0.174$).

Growth.—Growth rates for 24 turtles averaged 2.88 cm/y (range -0.7–5.9 cm/y SCL_{n-t} , SD = 1.72). Growth rates decreased significantly with respect to carapace length ($F_{1,22} = 13.26, P = 0.001, r^2 = 0.376$) with an approximate reduction of 1 cm y^{-1} in growth rate for each 10 cm increment in SCL_{n-t} from 50 to 80 cm (Fig. 11).

Genetic identity.—A 740 bp sequence was generated for 112 individuals (Table 2). Seventeen “long sequences” were represented, all assignable to known haplotypes (Abreu-Grobois et al. 2006). Mexican haplotypes (P and Q) made up 65.1% of the sample. One haplotype, n (Ei-A36), currently known only from foraging grounds in Cuba, is represented by the largest of three possible adult females captured during the study. The genetic diversity of the Palm Beach aggregation is comparable to that at Mona and Cayman (Table 2), but these sites differ significantly in haplotype frequencies (Table 3). The

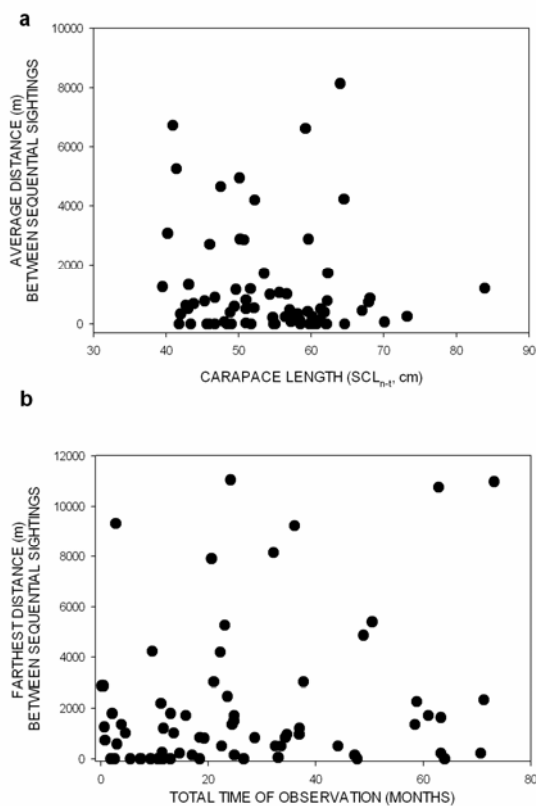


FIGURE 10. (a) Average distance between researcher dive initiation sites associated with sequential observations of turtles as a function of size (SCL_{n-t}). Coordinates for turtle capture locations are based on dive initiation sites (see Methods); (b) Farthest distance between researcher dive initiation sites associated with sequential observations of 73 individual Hawksbill Turtles (*Eretmochelys imbricata*) during the total observation period.

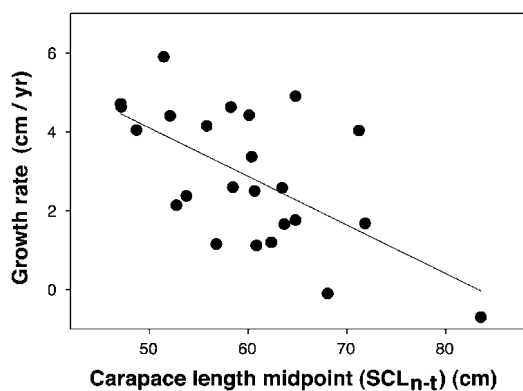


FIGURE 11. Growth rate as a function of size (SCL_{n-t}) in Hawksbill Turtles (*Eretmochelys imbricata*) captured on reefs off Palm Beach County, Florida. Growth rate over the longest recapture interval is shown for 24 individuals captured after more than 12 months.

baseline data set for the 384 bp sequences used in the maximum likelihood estimate of possible sources of the Palm Beach includes data from nine nesting beaches (Table 4). The preliminary estimate of source areas (Table 5) suggests that Mexican beaches are the predominant source and that other likely contributors from most to least important include the leeward side of Barbados, Costa Rica, Mona Island, Antigua, and the US Virgin Islands.

DISCUSSION

This study provides the first description of a significant foraging aggregation of the Critically Endangered Hawksbill Turtle within the waters of the continental United States. Hawksbills were observed on the Southeast Florida Continental Reef Tract off Palm Beach County at rates comparable to those reported at several sites in the wider Caribbean (Table 6). However, comparisons must take into account the differences in methodologies and sampling strategies. Other foraging aggregations within US waters in the Caribbean region have been described in Puerto Rico (van Dam and Diez 1998a; Vélez-Zuazo et al. 2008; Rincón-Díaz et al. 2011) and the US Virgin Islands (Boulon 1994; Mayor et al. 1998). Foraging areas for hawksbills also exist within the Florida Keys (Meylan and Redlow 2006, Eaton et al. 2008).

The size range of hawksbills captured in this study was similar to that observed for several other foraging aggregations in the western Atlantic that represent benthic developmental habitat (Meylan et al. 2011). However, unlike sites in Puerto Rico (van Dam and Diez 1998b), the Dominican Republic (León and Diez 1999), Cayman Islands (Blumenthal et al. 2009a), and Bermuda (Meylan et al. 2011), there were very few hawksbills smaller than 40 cm SCL ($n = 4$, 2.7%) in this study. Hawksbills in the western Atlantic appear to leave the epipelagic environment when they reach 20–26 cm SCL (Meylan and Redlow 2006: 109; Meylan et al. 2011), which suggests either that small, post-pelagic hawksbills along this stretch of Florida coastline frequent unsurveyed areas or that this study site is not an initial post-pelagic settlement site. The presence of numerous divers in the area cooperating with the study increased the likelihood that these small turtles were not simply overlooked.

Large subadults (65–75 cm SCL) were not well represented. These large subadults are approaching the minimum size of sexual maturity of hawksbills observed in the Caribbean and may be pubescent. Pubescence has been associated with a shift from developmental habitat to adult foraging range (Meylan et al. 2011). Only seven turtles captured during the study were judged to be mature or possibly mature. All four with elongated tails

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TABLE 2. Long (740 bp) haplotypes for Hawksbill Turtles (*Eretmochelys imbricata*) from three foraging grounds in the western Atlantic. Data for Mona are from Vélez-Zuazo et al. (2008) and data from Cayman Islands are from Blumenthal et al. (2009b).

380–480 bp haplotype	740 bp haplotype	Palm Beach Co. FL (all)	Palm Beach Co. (all) proportion	Palm Beach Co. FL (juveniles)	Palm Beach Co. juvenile proportion	Mona "juveniles" only	Mona juvenile proportion	Cayman (juveniles)	Cayman proportion
A/Cu1	Ei-A01	3	0.027	2	0.019	15	0.268	44	0.478
alpha/g	Ei-A02	1	0.009	1	0.010	1	0.018	2	0.022
B/e	Ei-A03	1	0.009	1	0.010	1	0.018	1	0.011
F/c	Ei-A09	4	0.036	4	0.038	6	0.107	8	0.087
F/PR1	Ei-A11	14	0.126	12	0.114	17	0.304	17	0.185
G/i	Ei-A12	1	0.009	1	0.010				
L	Ei-A18							1	0.011
N/PR2	Ei-A20	1	0.009	1	0.010	2	0.036	1	0.011
P/MX3	Ei-A22	6	0.054	6	0.057	1	0.018		
Q/MX1	Ei-A23	50	0.450	48	0.457	2	0.036		
Q/MX2	Ei-A24							11	0.120
a	Ei-A27	1	0.009	1	0.010				
	Ei-A28							4	0.043
CU3	Ei-A29					2	0.036	1	0.011
m	Ei-A35	1	0.009	1	0.010				
n	Ei-A36	1	0.009			1	0.018		
q	Ei-A39	10	0.090	10	0.095				
Q/MX1	Ei-A41	12	0.108	12	0.114	1	0.018		
Q/MX2	Ei-A43	3	0.027	3	0.029	1	0.018		
F/PR1	Ei-A45					2	0.036		
A/CU1	Ei-A51					1	0.018		
	Ei-A59					1	0.018		
	Ei-A60					1	0.018		
F/PR1	Ei-A63	1	0.009	1	0.010				
A	Ei-A68					1	0.018		
	Ei-A72							2	0.022
Q/MX2	Ei-A83	2	0.018	2	0.019				
Total sample		110		104		56		92	

also had wrinkled and softened plastra (Fig. 12), which can be interpreted as an indication of reproductive readiness in adult male cheloniids (Wibbels et al. 1991; Meylan et al. 2011). These animals were almost certainly mature males. Three individuals without elongated tails were larger than the minimum size for maturity in females (74.1 cm SCL_{n-r}; Meylan et al. 2011) and could have been mature females. However, this cannot be verified without additional data such as laparoscopic examination or observation of the turtle on a nesting beach.

All seven of these large individuals were seen between June and August, which is the reproductive season for hawksbills in Florida (Meylan and Redlow 2006); an adult male was seen twice, in June of two consecutive years. Meylan and Redlow (2006) reported that hawksbill nesting occurs rarely in Florida (0–4 nests/y); the known nesting distribution includes Palm Beach and adjacent southeastern Florida counties. Adult hawksbills

made up only a small proportion of the statewide strandings in Florida (12 individuals > 75 cm from 1980 to 2003; Meylan and Redlow 2006).

Habitat use.—Multiple habitats within the Southeast Florida Continental Reef Tract were used by hawksbills, with the highest proportion (40.4%) of first captures made on the deep ridge complex. This habitat type occurs only in the Palm Beach County portion of the reef tract (Riegl et al. 2007). A nearly equal proportion (37.7%) of first captures was made on the linear reef-outer. Banks et al. (2008) describe the outer reef as extending southward almost without interruption to Biscayne Bay, a distance of 125 km. These authors report that at a lower sea level stand, this would have been one of the best-developed fringing reefs in the western Atlantic, especially if combined with the Florida Keys reefs. Thus, historically, southeast Florida may have provided extensive foraging areas for this species. Further investigation of this extensive reef tract is

TABLE 3. Pairwise comparisons of haplotype frequencies (FST values) among three foraging aggregations of Hawksbill Turtles (*Eretmochelys imbricata*) for which 740 bp haplotypes are available. Conventional F-statistics from haplotype frequencies are shown at and below the diagonal; FST P values are shown above the diagonal. The Palm Beach foraging aggregation is included as all samples and juveniles only. Data for Mona are from Vélez-Zuazo et al. (2008); data from Cayman Islands are from Blumenthal et al. (2009b).

	Palm Beach (all)	Palm Beach (juveniles)	Mona (juveniles)	Cayman (juveniles)
Palm Beach (all)	0.00000	0.99967	0.00000	0.00000
Palm Beach (juv.)	-0.00897	0.00000	0.00000	0.00000
Mona (juv.)	0.14517	0.15281	0.00000	0.00529
Cayman (juv.)	0.22715	0.23468	0.03794	0.00000

warranted to quantify the current level of usage by hawksbills. Hawksbills are known to occur off Broward County on the nearshore reefs off Galt Ocean Mile and Hillsboro Beach, as well as on the reefs farther from shore (Meylan and Redlow 2006). Data on habitat associations represent minimum usage and are biased by the charter dive method; i.e., guest divers are typically taken to attractive reef dive sites, and ridges may be followed to provide landmarks (affecting depth and distance-to-shore data), etc. However, it is clear that hard-bottom habitats of this reef tract are used by hawksbills in this area.

No pattern was discerned regarding turtle size and water depth. Blumenthal et al. (2009a) found a weak but significant correlation between these parameters in the Cayman Islands, with larger turtles occupying deeper water. A large body size was correlated with longer and

deeper foraging dives, but not resting dives, in studies of hawksbills in Puerto Rico (van Dam and Diez 1997). We made 25 (17.1%) first captures in artificial habitats, including sunken vessels. Hawksbills were seen feeding on encrusted surfaces of wrecks and emerging from the interiors; divers who entered wrecks regularly reported seeing hawksbills. Hawksbills were also frequently encountered on or near natural ledges, resting under the ledges or in shallow caves. We also identified areas with vertical relief as important habitat for hawksbills in the Cayman Islands (Blumenthal et al. 2009a). Van Dam and Diez (1997) reported that immature hawksbills sighted at night via SCUBA at Mona Island were associated with ledges and crevices. In the Palm Beach study, turtles were occasionally found sheltered during the daytime in dense pastures of soft corals. Hawksbills were also commonly observed in areas of featureless and/or sparsely colonized hard-bottom that did not offer



FIGURE 12. Adult male Hawksbill Turtles (*Eretmochelys imbricata*; 83.9 cm SCL_{n-t}), showing an elongated tail (39.4 mm) and softened area of the plastron (lighter color on both sides of midline) that is characteristic of reproductively active male cheloniid sea turtles (Wibbels et al. 1991; Meylan et al. 2011). (Photographed by Larry Wood).

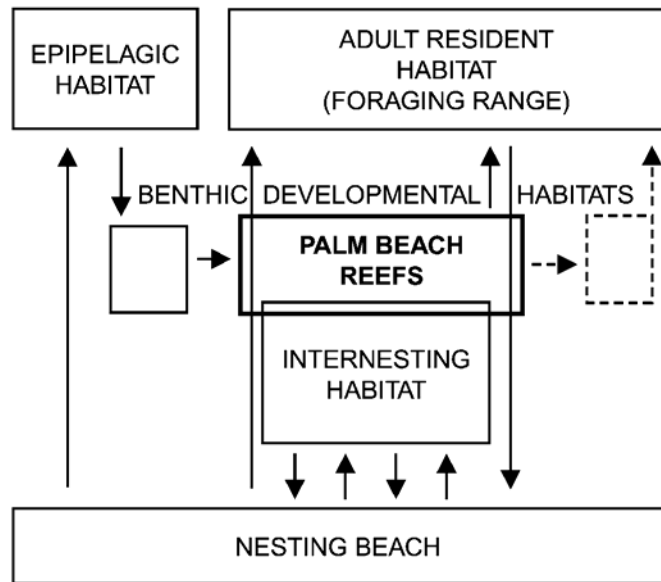


FIGURE 13. Life-stage model for cheloniid turtles from Carr et al. (1978), modified to show proposed role of Palm Beach reefs in the life cycle of the majority of hawksbills that use this site. The possible overlap between a benthic developmental stage and either or both reproductive migratory corridor and interesting habitat is shown.

TABLE 4. Distributions of short (384 bp) haplotypes for known Caribbean nesting beaches and the Palm Beach, Florida, foraging aggregation used in mixed stock analysis. Baseline data for the maximum likelihood estimate (MLE) are from Bowen et al. (2007: Table 1) with additions from Browne et al. (2010) and Vélez-Zuazo et al. (2008). Nesting beach population size (N§) is updated on the basis of Mortimer and Donnelly (2007). Haplotypes D and E of Bass et al. (1996) were not reproducible in Browne et al. (2010) and are not included here. Similarly, haplotypes K and M of Bass et al. (1996) have not been reproduced in subsequent studies and were not included in our analysis. Brazilian hybrid haplotypes R, S, T, U have not been found at other nesting beaches or in our foraging aggregation and are not included. Rookery size is given as the number of nesting females per year following Mortimer and Donnelly (2007).

Nesting areas	n	A	B	C	F	G	H	I	J	L	N	O	P	Q	BII	α	β	γ	Reference for haplotypes					N§	Source for rookery size ¹	
																			Cu3	Cu4	Cum	DR1	DR2			EATL
Antiqua, Jumby Bay	15	9	4	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	52	7	
Barbados (leeward side)	54	54	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	400-667*	8*	
Barbados (windward side)	30	3	0	0	27	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	--	--	
Belize, Gales Point	14	0	0	0	11	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	3	40	1	
Costa Rica, Tortuguero,	57	0	0	0	33	6	0	0	4	0	0	0	0	0	0	10	0	0	4	0	0	0	4	10	7	
Cuba, Doce Leguas,	70	62	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	5	1	1	0	0	5	400 – 833	7
Mexico, Yucatán,	68	0	0	0	0	0	0	0	0	0	0	0	3	64	1	0	0	0	0	0	0	0	0	1	534 – 891	7
Puerto Rico, Mona Island	113	1	0	0	71	0	0	0	1	32	6	0	2	0	0	0	0	0	0	0	0	0	0	6	148 – 247	7
US Virgin Islands, Buck Island	50	5	1	0	43	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	1	56	7
Florida, Palm Beach County juvenile foraging aggregation	94	2	1	0	17	1	0	0	0	1	0	6	65	0	1	0	0	0	0	0	0	0	0	0	**	

¹ Bowen et al. (2007), ² Browne et al. (2010), ³ Bass et al. (1996), ⁴ Troëng et al. (2005), ⁵ Diaz-Fernández et al. (1999), ⁶ Vélez-Zuazo et al. (2008), ⁷ Mortimer and Donnelly (2007), ⁸ Beggs et al. (2007).

*All of Barbados

** This study

protective cover.

Residency.—Hawksbills were present in the study area year-round. The lack of seasonality in the observation rate may be due, in part, to the effects of the Florida Current (Gulf Stream) which contributes to the consistently warm water temperatures. Mean monthly water temperature varied only 4.8 °C during the study. With the exception of Bermuda (Meylan et al. 2011), which also receives warm Gulf Stream water, known foraging areas for hawksbills in the Caribbean and western Atlantic exist only at latitudes lower than Palm Beach County. At the St. Lucie Nuclear Power Plant hawksbills (1976–2003, $n = 39$) were captured in the cooling water intake structure in all months except January and February (Eaton et al. 2008).

Several lines of evidence suggest that at least some hawksbills were resident in the study area for extended periods. The average interval of observation for turtles seen more than once was over 2 y, with the maximum interval (73 mo) approaching the time span of the study (79 mo). Although the possibility exists that individuals left the area between sightings, this seems unlikely given the frequency of re-sightings and their temporal distribution.

The length of time over which the same individual was observed was not correlated with turtle size, but the largest turtles tended not to be seen more than once. Only one of the seven animals larger than the minimum size at sexual maturity was seen more than once. Given the average growth rate of 2.88 cm/y at the study site, turtles that reside within the study area while they grow from 35 to 75 cm SCL could be resident for as long as 14 y. Residency appears to be a common behavior for several species of sea turtles in developmental habitat (Meylan et al. 2011). Repeated observations of individually tagged hawksbills at the same site over

intervals of many years have been reported in Florida (Meylan and Redlow 2006) and throughout the Caribbean (Boulon 1994; León and Diez 1999; Diez and van Dam 2002; Blumenthal et al. 2009a; Krueger et al. 2011).

Site fidelity.—The researcher dive initiation sites associated with most (79.5%) observations of turtles that were seen again after their first capture were less than 2 km from the initiation sites where they were last observed, even after periods of more than 5 y. For more than one-third (38.4%) of the sample, the first and last observation sites (dive initiation sites) were the same. This is consistent with the pattern reported by van Dam and Diez (1998a) in which 87 hawksbills in benthic developmental habitat moved an average of 0.45 km between sightings. In our study, the lack of correlation between average distance between researcher dive initiation sites associated with sequential sightings of individual turtles and turtle size suggests that site fidelity remains relatively constant with increase in size. However, there was a positive relationship between the farthest distance between dive initiation sites associated with sequential sightings and the total time of observation. Blumenthal et al. (2009a) reported a lack of correlation between distance moved between capture and recapture points in the Cayman Islands, as well as between distance and time at large. No hawksbill tagged during this study was reported at another foraging area, and no hawksbill tagged at a different foraging area was observed during this study. This is consistent with the hypothesis that hawksbills of the 40–75 cm SCL size that make up the majority of this sample may not be moving between foraging areas. However, the presence of only a few adults seen during the reproductive season suggests that hawksbills in this aggregation go elsewhere to mature.

Growth.—Growth rate and changes in growth rate with size in hawksbills from Palm Beach reefs were comparable to observations at Caribbean sites. As at other sites, there was a monotonic decrease in size-specific growth rate from about 4 cm y^{-1} to 0 cm y^{-1} across the size range of about 40 to 84 cm. The two most comprehensive studies of hawksbill growth in the Caribbean (Diez and van Dam 2002; Krueger et al. 2011) argue for a non-monotonic trend when individuals smaller than 35 cm are included. But both of these studies, and those of Boulon (1994), León and Diez (1999), Blumenthal et al. (2009a), Bjørndal and Bolten (2010), and this study showed a decreasing trend in growth rate from about 40 cm to the size at which individuals departed the developmental foraging ground. The average rate for this study (2.88, $SD \pm 1.72$ cm y^{-1}) was comparable to that of slightly smaller hawksbills in the Cayman Islands (3.0, $SD \pm 0.9$ cm y^{-1} ; Blumenthal et

TABLE 5. Maximum likelihood estimate for nesting beach origin of juvenile Hawksbill Turtles (*Eretmochelys imbricata*) from Palm Beach County, Florida, based on 94 of 106 available sequences (12 juveniles had haplotypes that have not been reported from any nesting beach). Estimate is based on 384 bp of control region sequence and was generated using SPAM 3.7b (Alaska Department of Fish and Game, 2003).

Population	Estimate	90% Confidence Intervals	
		Lower	Upper
Mexico, Yucatán	0.7547	0.677	0.822
Barbados – Leeward side	0.1351	0.000	0.228
Costa Rica, Tortuguero	0.0521	0.008	0.134
Puerto Rico, Mona Island	0.0320	0.003	0.112
Antigua, Jumby Bay	0.0201	0.000	0.059
U.S. Virgin Island, Buck Island	0.0061	—	—
Barbados – Windward side	0.0000	—	—
Belize, Gales Point	0.0000	—	—
Cuba, Doce Leguas	0.0000	—	—

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al. 2009a), but the growth rate appeared to be more variable; the higher variance may have resulted from seasonal growth.

Ecological geography of the aggregation.—The aggregation of hawksbills that uses the Palm Beach reefs as benthic developmental habitat represents a temporary assemblage of individuals from multiple nesting beach populations. The concept of “mixed stocks” on foraging grounds is well established for sea turtles in general (Bowen 1995) and for hawksbills specifically (Blumenthal 2009b and references therein). Our results suggest that this foraging aggregation is a mixture of contributions from three to six nesting areas. However, it is unusual in that it is largely derived from a single source, Mexican nesting beaches on the Yucatan Peninsula (75.5%, 90% CI = 67.7–82.2%).

At least one haplotype, q (EiA-39), which could not be included in the Maximum Likelihood Analysis (MLA), is known only from Mexican beaches (F. Alberto Abreu-Grobois, pers. comm.). It represents about 9% of the foraging sample and suggests that the Mexican

contribution to the Palm Beach aggregation is actually greater (close to 85%) than our preliminary estimate. Thus, this aggregation was similar to that reported from Río Lagartos, Mexico, in being dominated by Mexican haplotypes (at least 71% in the case of Río Lagartos; Díaz-Fernández et al. 1999). The Texas aggregation reported by Bowen et al. (2007) was also dominated by Mexican haplotypes, but it represented individuals stranded from the epipelagic stage and not from a benthic foraging aggregation. One other foraging area, Cuba A of Bowen et al. (2007), was dominated by a single source (72% Cuba). For other benthic foraging aggregations, no single nesting area is the source for more than 50% of the individuals observed (Bowen et al. 2007; Vélez-Zuazo et al. 2008; Blumenthal et al. 2009b). This aggregation of immature hawksbills represents a later benthic developmental stage (Fig. 13). Based on an average recruitment size of 20–26 cm SCL for Atlantic benthic developmental sites (Meylan and Redlow 2006; Meylan et al. 2011), it is likely that the hawksbills that recruit to the Palm Beach reefs have already spent time in benthic developmental habitat elsewhere. The work

TABLE 6. Observation rates (CPUE) of Hawksbill Turtles (*Eretmochelys imbricata*) at foraging grounds in Florida and the Caribbean using different capture methodologies. Sampling strategies also varied and were not stated in some references.

Location	Method	Observations/h			Reference	Notes
		Average	SD	Range		
USA, US Virgin Islands, Buck Island	snorkel	0.40			Mayor et al. 1998	total sightings and captures /total snorkel time
Venezuela, Los Roques Archipelago	snorkel	0.51			Hunt 2009	total sightings /total snorkel time
Venezuela, Los Roques Archipelago	tow	0.53			Hunt 2009	total sightings /total tow time
Belize, Lighthouse Reef Atoll	snorkel	1.41		0 – 7.7	Scales et al. 2011	observations/snorkel time
USA, Florida, Palm Beach County	scuba	1.45			This study	total sightings and captures/total dive time
USA, Puerto Rico, Culebra Archipelago (5 sites)	snorkel	1.53 ¹	± 0.86	0.53 – 3.07 ²	Rincón-Díaz et al. 2011	sightings and captures
Cayman Islands, Grand Cayman	snorkel/ tow	1.60	± 0.45		Blumenthal et al. 2009a	sightings and captures
Dominican Republic (11 sites)	snorkel	1.77 ³	± 1.00	0.08 – 3.43 ⁴	León and Diez 1999	sightings and captures
Cayman Islands, Little Cayman	snorkel/ tow	3.15	± 0.98		Blumenthal et al. 2009a	sightings and captures
USA, Puerto Rico, Mona Island	snorkel	3.86			Rincón-Díaz et al. 2011	sightings and captures
USA, Puerto Rico, Monito Island	snorkel	19.33			Rincón-Díaz et al. 2011	sightings and captures

¹average across five sites; ²range across five sites; ³average across 11 sites; ⁴range across 11 sites

of Blumenthal et al. (2009b) suggests that for the majority of individuals (those from Mexican nesting beaches), this site or sites should be in the Gulf of Mexico or more southerly parts of the Southeast Florida Continental Reef Tract. Arrival at the Palm Beach reefs is almost certainly facilitated by the prevailing surface currents, including the Yucatan, Loop and Florida Currents.

The Palm Beach developmental aggregation appears to overlap with adults in the internesting habitat and/or migratory corridor. The rarity of adults at the site, their infrequent subsequent observation, and occurrence only during the reproductive season suggest that they were not resident but rather were involved in some aspect of reproductive behavior. Overlap of this nature has been described for Barbados (Horrocks et al. 2011) and Panama (Meylan et al. 2011) and likely occurs at several other benthic developmental sites (Meylan et al. 2011). The largest of three possible adult females had haplotype n (Ei-A36), which is not yet known from any nesting beach. This haplotype has only been identified from foraging areas in Cuba and Puerto Rico (Díaz-Fernández 1999; Vélez-Zuazo et al. 2008).

With the exception of Bermuda, Palm Beach County is the northernmost location in the greater Atlantic known to serve as benthic developmental habitat for hawksbills. It appears that the presence of the Florida Current allows densities and growth rates that are comparable to sites in the Caribbean. This reef system extends north at least as far as northern Palm Beach County and south to the Florida Keys, and thus the possibility exists that Florida's east coast supports large numbers of immature hawksbills. Furthermore, the turtles in the Palm Beach aggregation are in the later part of their benthic developmental stage and have survived the earliest stages of the life cycle during which survivorship is expected to be low. They are thus of high demographic value, and the reef system off southeastern Florida that supports them merits consideration as critical habitat. Appropriate management of these reefs will be important to the long-term survival of this critically endangered species.

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