
SEA TURTLE ABUNDANCE AND DEMOGRAPHIC MEASUREMENTS IN A MARINE PROTECTED AREA IN THE FLORIDA KEYS, USA

RICHARD M. HERREN^{1,2,4}, DEAN A. BAGLEY¹, MICHAEL J. BRESSETTE¹,
KAREN G. HOLLOWAY-ADKINS³, DAVE CLARK¹, AND BLAIR E. WITHERINGTON¹

¹Inwater Research Group, Inc., 4160 NE Hyline Drive, Jensen Beach, Florida 34957, USA

²Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall,
Gainesville, Florida, 32611, USA

³East Coast Biologists, Inc., 141 Atlantic Avenue, Indialantic, Florida 32903, USA

⁴Corresponding author, e-mail: rherren@ufl.edu

Abstract.—We used vessel-based surveys to estimate sea turtle abundance and capture them in a 129 km² area within the Key West National Wildlife Refuge, USA, and adjacent waters. We measured captured turtles, externally examined them for disease and injuries, and analyzed diet in 62 Green Turtles (*Chelonia mydas*). Between 2003–2012, we sighted 1,087 Green Turtles, 789 Loggerheads (*Caretta caretta*), 65 Hawksbills (*Eretmochelys imbricata*), one Kemp’s Ridley (*Lepidochelys kempii*), and 12 unidentified turtles. We fitted the sighting data to a probability of detection model, which gave us an estimate of 46.4 turtles km⁻². Most sightings were clustered in four distinct areas that were in the lee of islands. Captured Loggerheads were significantly larger (mean straight carapace length [SCL ± SD], 74.2 ± 9.3 cm) than Green Turtles (54.3 ± 21.8 cm) which were significantly larger than Hawksbills (46.7 ± 11.3 cm). However, Green Turtles were a mixture of three size classes and exhibited significant size class partitioning with larger turtles found in deeper water (> 3 m) and smaller turtles found in shallower water (< 3 m). The majority of recaptures (79%) were found < 1 km from their initial location suggesting a high degree of site fidelity. The proportion of Green Turtles with fibropapillomatosis was 6%, while 13% of all species had boat propeller injuries. Green Turtles primarily consumed Turtle Grass, *Thalassia testudinum* (62%). Our results highlight the importance of this area and the return of Green Turtles to a place where they were once commercially harvested.

Key Words.—diet; density; detectability; fibropapillomas; Green Turtle; injuries; Loggerhead; sightings

INTRODUCTION

Effective species management requires knowledge of demographic parameters such as abundance, spatial distribution, disease rates, and human impacts (Roessig et al. 2004). These data are particularly necessary in Marine Protected Areas (MPAs) where populations need to be adequately monitored so managers can set conservation priorities and evaluate the effects of management actions (Arcos et al. 2012). For more than a decade, U.S. wildlife managers have emphasized the need for in-water sea turtle demographic studies to evaluate recovery efforts and manage anthropogenic threats (National Marine Fisheries Service [NMFS] 2013; National Research Council 2010; U.S. Fish and Wildlife Service [USFWS] 2009). In this study, we addressed this need by describing the distribution and abundance of sea turtles in a MPA in the Florida Keys with a long history of human exploitation.

Sea turtle population declines in the U.S. in the 19th and 20th Centuries were largely the result of commercial harvest and nowhere was this more apparent than in Key West, Florida (National Research Council 1990;

Witzell 1994; Jackson et al. 2001). Key West was the site of the largest sea turtle fishery in the country and acted as a holding and processing facility for Green Turtles (*Chelonia mydas*; Schroeder 1924). By the 1920s, locally caught turtles became scarce from fishing pressure, and most of the landings came from as far away as the western Caribbean (Loennberg 1894; Schroeder 1924; Carr and Ingle 1959; Witzell 1994). Loggerheads (*Caretta caretta*), Hawksbills (*Eretmochelys imbricata*), and Kemp’s Ridleys (*Lepidochelys kempii*) were also harvested in Florida, though they were usually captured incidentally and classified as less palatable (Schroeder 1924; Witzell 1994). Today, populations of all species in the northwest Atlantic are considered to be much smaller than their historical size (Jackson et al. 2001; McClenachan et al. 2006; Witherington et al. 2006a). While abundance estimates have traditionally come from nesting beaches (Heppell et al. 2003; Stewart et al. 2011), a more recent focus has been in-water surveys (National Research Council 2010).

Sea turtles exhibit complex life cycles and the methods used to study them at sea have taken place on vastly different spatial scales and levels of detail (Carr

1986; Musick and Limpus 1997; Bjørndal et al. 2000). Published accounts of stage-specific turtle abundance have come from captures in recreational and commercial fisheries (Bolten et al. 1993; Braun-McNeill and Epperly 2002; Avens et al. 2003; Grazette et al. 2007), stranding events (Witherington and Ehrhart 1989; Foley et al. 2007), independent trawl surveys (Butler et al. 1987; Arendt et al. 2012), aerial surveys (Fritts et al. 1983; Epperly et al. 1995; Coles and Musick 2000; Cardona et al. 2005), and discrete netting sites (Ehrhart et al. 2007; Eguchi et al. 2010). Aerial surveys for sea turtles are carried out over a broad area, but suffer from species misidentification, unknown values for sex, and completely missing smaller juveniles (Fritts et al. 1983; Epperly et al. 1994; Cardona et al. 2005; Seminoff et al. 2014). Captures allow identification and sampling of individual animals, but commonly take place at a single geographic location, which may not be representative of the broader population (Eaton et al. 2008). Bjørndal et al. (2005) suggested the best approach for providing information on both sexes and multiple life stages would be a combination of expansive surveys and discrete capture methods.

In its Comprehensive Management Plan for the Lower Florida Keys, the USFWS prioritized sea turtle population monitoring and the collection of demographic data in the Key West National Wildlife Refuge (Key West NWR), yet acknowledged it had few resources to accomplish the task (USFWS 2009). The refuge is comprised of mostly open water and was designated as a MPA in 2000. Fewer than 100 Loggerhead and Green Turtle nests are deposited each year on the small mangrove islands. In contrast, the refuge contains hundreds of square kilometers of seagrass beds, which are thought to be important foraging habitat for sea turtles (USFWS 2009). In 1986, the USFWS attempted vessel surveys and capture attempts over several days. They reported nine sightings of juvenile Green Turtles and one capture near the Marquesas Keys (Barbara Schroeder, pers. comm.). Over a decade later, Loggerheads and Green Turtles were satellite tracked from Florida and Mexico nesting beaches to the shallow waters of the refuge (Girard et al. 2009; Foley et al. 2013; Mauricio Garduño, unpubl. data; Barbara Schroeder, unpubl. data). These findings combined with the historical significance of the Key West turtle fishery suggested the Key West NWR might be an important foraging ground for juvenile and adult sea turtles.

The overarching objective of ours was to survey and capture sea turtles in the Key West NWR to describe their distribution and demographic composition. We expected to find sea turtles, but had no preconceptions regarding their abundance, species composition, and specific locations. In addition to estimating sea turtle abundance from vessel surveys, we sought to quantify

the injury and disease rates that might be useful in wildlife management decisions. Our specific objectives were to assess the species composition, density, habitat use, size class, sex ratio, diet, and external condition of captured turtles. We used non-linear surveys using vessels over expansive shallow water habitat combined with hand capture methods to describe the community of sea turtles in the Key West NWR.

MATERIALS AND METHODS

Study site.—The Key West NWR lies within the Florida Keys National Marine Sanctuary (FKNMS) and contains approximately 835 km² of open water and 8 km² of land. The area includes the Marquesas Keys and 13 other Keys with surrounding shallow water basins stretching 3–36 km west of Key West, Florida, USA (Fig. 1). A variety of in-water habitats are found in the refuge including expansive seagrass beds containing mostly Turtle Grass, *Thalassia testudinum*, tidal channels, sponge dominated hard-bottom, intertidal flats, and patch reefs containing gorgonians and hard corals (USFWS 2009). In 2004, we expanded our study to include the Eastern Quicksands, which is a deeper water sand and seagrass flat stretching 2–12 km west of the Marquesas Keys and the Key West NWR boundary (Bresette et al. 2010; Figs. 1, 2).

Study period.—We conducted 27 survey and capture trips over a 10-y period from September 2003 through September 2012 for a total of 139 days on the water. We planned our survey trips for 6-d periods based on our budget and crew availability, with the summer months being the highest priority because of favorable weather. Weather or mechanical delays occurred on 14% of the planned days. We conducted six trips in the spring months (22%), 10 in the summer (37%), seven in the fall (26%), and four in the winter (15%).

Distribution and abundance surveys.—We used Haphazard, Unmarked, Nonlinear Transects (HUNTs) to sight turtles and capture them in relatively shallow water (0.2–6.0 m; Bresette et al. 2010). HUNTs were near haphazard with respect to course decisions and were biased by weather conditions, access opportunity, and water depths where visibility was top-to-bottom. Using a Garmin Global Positioning System (GPS) Map 182 (Garmin, Olathe, Kansas, USA), we were able to avoid overlapping previous vessel paths within a survey day. HUNTs gave us the ability to explore new areas, maneuver around obstacles (e.g., reefs, shoals, grass flats), and, when possible, capture turtles. During sighting transects, two experienced observers stood atop a 2 m elevated central tower installed on a 7 m flat-bottomed skiff. Observers scanned the water

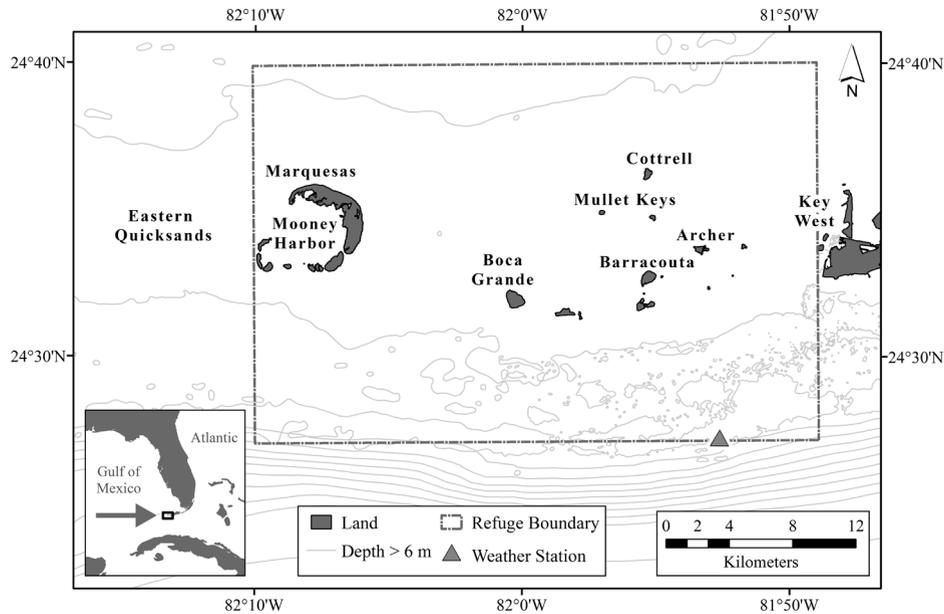


FIGURE 1. Map of the Key West National Wildlife Refuge located just west of Key West, Florida, USA, between the Atlantic Ocean and the Gulf of Mexico (inset).

from the vessel track line to approximately 300 m away, depending on sea state. We recorded transect start points, end points, turtle sightings, water depth, and continuous vessel tracks (20-m resolution) using GPS. We maintained a speed of 9 km h⁻¹ during transects and ended HUNTs when we attempted a hand capture or when a combination of water depth (too shallow or too deep), poor visibility, or bad weather forced us to move to a new location.

We identified sightings of turtles during HUNTs to species and life stage. Experienced observers estimated life stage based on head size and/or a complete view of the turtle. We assigned the term juvenile to Loggerheads and Green Turtles that were < 65 cm in estimated straight carapace length (SCL); the term subadult to turtles that were approximately 65–90 cm SCL; and the term adults to turtles > 90 cm SCL (Witherington et al. 2006a; Witherington et al. 2006b). We calculated the observer error in life-stage categories by comparing initial sighting categories with capture measurements in 31 randomly selected Loggerheads and Green Turtles (Bresette et al. 2010). Observers recorded the GPS location of each turtle at the point perpendicular to the vessel path. Beginning in 2006, we recorded the estimated perpendicular distance (m) from the vessel path to the turtle (Beavers and Ramsey 1998) and whether turtles were at the surface or below the surface. Observers used the vessel length (7 m) to calibrate their distance estimates.

Captures.—We opportunistically captured sighted turtles using the rodeo method (Ehrhart and Ogren

1999). We attempted to hand capture turtles we could clearly follow in safe conditions (e.g., clear top-to-bottom visibility and surface waves no larger than 0.5 m). We classified captured turtles as either in good, fair, or poor body condition based on external appearance. Good turtles had convex plastrons, fair turtles had flat plastrons, and poor turtles had concave plastrons (Thomson et al. 2009). We transferred turtles in poor condition to the Florida Fish and Wildlife Conservation Commission (FWC) for veterinary care. We tagged, measured, and released all other turtles. We inserted inconel metal tags (No. 681; National Band & Tag Company, Newport, Kentucky, USA) with pliers in the first or second proximal scale of each front flipper and a passive integrated transponder (PIT) tag in the right front flipper, medial to the second proximal scale and in the soft tissue. We weighed turtles using a digital scale and took carapace measurements with aluminum forestry calipers and graduated fiberglass tape as described by Bolten (1999). We measured tail length from the terminus of the anal scutes to the tip of the tail and used this measure to determine sex in turtles > 90 cm SCL (Bresette et al. 2010).

We used an esophageal flushing technique (lavage) to collect diet samples from Green Turtles in good condition (Balazs 1980). We carefully inserted a lubricated surgical tube that was 9 mm outside diameter (OD) for smaller turtles (< 35 cm SCL) or 13 mm OD for larger turtles (> 35 cm SCL) into the mouth and esophagus. We manually pumped fresh seawater through the tube for approximately 30 sec and collected the diet samples in a receiving bucket. We strained the

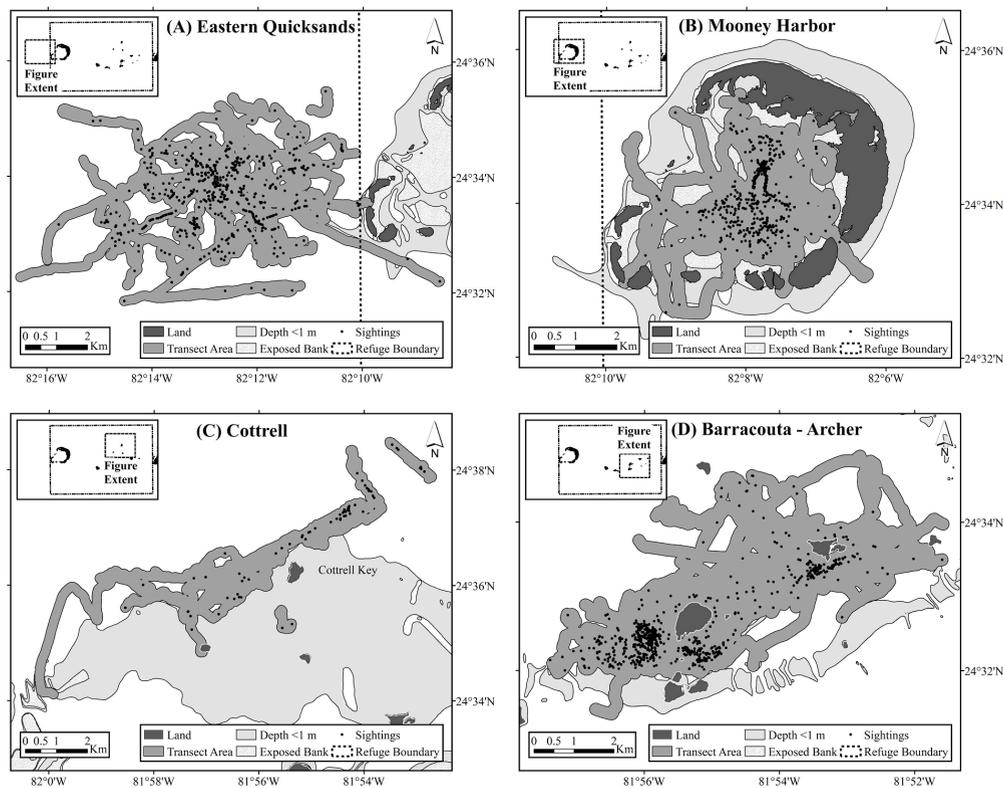


FIGURE 2. Transects and turtle sightings at four core use areas: (A) Eastern Quicksands, (B) Mooney Harbor, (C) Cottrell Key, and (D) Barracouta and Archer Keys. Transect lines were buffered to 150 m and dissolved into a single polygon.

samples through a 0.5 mm mesh cloth and transferred them into a jar containing a 4% formalin-seawater solution.

We carefully examined turtles for the presence of fibropapilloma tumors (FP) and scored them using the standards described by Work and Balazs (1999). We determined FP severity by counting the number of tumors in each size category (< 1 cm, 1–4 cm, 4–10 cm, and > 10 cm) and assigning each turtle a score of either light, moderate, or severe affliction. We photographed significant injuries ($\geq 10\%$ loss of the body part) to the head, flippers, carapace, and plastron, and we carefully described them. We assigned injuries to obvious causes when possible (e.g., propeller strikes, entanglements). Prior to release, we painted turtles with a sequential number on the carapace (avoiding the scute seams) using a two-part white marine epoxy paint. This allowed us to identify previously captured turtles within the same sampling period. We treated re-sightings of turtles after 24 h as independent observations.

Data analyses.—We pooled vessel tracks and sightings for all years and converted them into shapefiles using ArcGIS 10.1 (Esri, Redlands, California, USA). We then generated transect lengths (km) and calculated encounter rates (turtles km^{-1}) from the shapefiles. We

buffered transect lines to 150 m, which is the distance we truncated the sightings for detection analysis (see below), dissolved them into polygons, and then used the polygons to analyze sightings for a random, uniform, or clustered distribution pattern using ArcGIS 10.1 Average Nearest Neighbor Tool. We downloaded average hourly weather observations (wind direction, wind speed, air pressure, and air temperature) from the Sand Key Weather Station (SANF1) of the National Data Buoy Center, which is located near the southeast corner of the Key West NWR (Fig. 1). We averaged weather data for 0800–1600 h during transect days and calculated sea state (Beaufort Scale) from average wind speeds (km h^{-1}).

We determined the probability of detection, effective strip width (ESW) and density estimate using the perpendicular sighting distances and the program DISTANCE 6.0 (Thomas et al. 2010). We binned the distance data at 10 m intervals to account for rounding errors and truncated the distance measurements at 150 m because we considered data beyond that point (1%) outliers (Eguchi et al. 2007; Thomas et al. 2010). We ran hazard, half-normal, and uniform models with no stratification, no model constraints, and an automatic selection of adjustment terms set at a maximum of 5 in DISTANCE 6.0. We selected the best fit model based

on an examination of the probability detection curve, χ^2 Goodness of Fit test, and Akaike's Information Criterion (AIC) value. We estimated the density (D) and abundance (N) of turtles using the standard line-transect formula (Buckland et al. 2001):

$$D_j = \frac{n_j f(0)}{2L_j g(0)},$$

$$N_j = D_j A_j,$$

Where n_j = the total number of turtles observed during surveys, $f(0)$ = the probability density function evaluated at zero perpendicular distance, L_j = the distance surveyed in km, $g(0)$ = the probability of detection at zero distance, and A_j = the area surveyed in km².

The area surveyed (A) was based on the distance traveled and the width of the observations (150 m) on either side of the transect line (Beavers and Ramsey 1998). We used the best-fit model to calculate density estimates and examined the effect of seven factors on the detection function using a multiple covariate analysis in DISTANCE 6.0. The factors were species, turtle size (large = subadult and adult, small = juvenile), at or below the surface, water depth (shallow = 0.2–3.0 m; deep = 3.1–6.0 m), Beaufort sea state, season, and year. We ranked delta AIC values from smallest to largest in the order of influence and considered factors with the best fit to the model to have the most influence.

For captured turtles, we created a boxplot of SCL for Loggerheads, Green Turtles, and Hawksbills and then analyzed SCL means between species and across four core use areas that had the highest concentration of turtles using the program R. We analyzed the mean distances from first capture to recapture for each species using ArcGIS 10.1 Point Distance Analysis Tool (Esri, Redlands, California, USA). We analyzed the overall SCL data in R, but the data were not normal (Shapiro-Wilk, $W = 0.973$, $P < 0.001$). Therefore, we analyzed these data using non-parametric tests in R (Kruskal-Wallis) with post-hoc multiple comparisons (Dunn's). Other data were normally distributed and we conducted tests in R using either ANOVA or t tests with Welch's correction for data with unequal variances. We used $\alpha = 0.05$ for all tests.

We placed each lavage sample into a Petri dish marked with 16 1-cm² gridlines (Forbes 1999; Arthur and Balazs 2008). We then spread the sample to a thin layer and quantified diet content using a stereoscope fitted with a 100-square 10 mm graticule in the ocular. We aligned one of the 16 squares on the Petri dish within the graticule and identified the foraging item located in the top left corner to the lowest taxonomic level for all odd-numbered squares. We then aligned the Petri dish with the next square until the foraging items that

covered all the squares were counted. We calculated the mean percent composition (based on counts of each foraging type in a lavage sample divided by the total counts in the sample) and standard deviation (\pm SD) for individual foraging samples. We also determined how many of the lavage samples out of the total number of samples contained a foraging type (i.e., frequency of occurrence; FO). We used PRIMER-E to run an Analysis of Similarities (ANOSIM; Clarke and Warwick 2001) to examine differences in foraging samples among four size classes (30.0–40.0 cm, 40.1–50.0 cm, 50.1–70.0 cm, and > 70.1 cm SCL) and turtles captured in three core use areas (Barracouta-Archer, Mooney Harbor, and Eastern Quicksands).

RESULTS

Sightings and encounter rates.—We recorded 1,954 sea turtle observations from 1,089 HUNTs covering a distance of 2,102 km and an area of 128.6 km². Green Turtles were the most common turtle observed with 1,087 sightings (56%), followed by 789 Loggerheads (41%), 65 Hawksbills (3%), one Kemp's Ridley (0.05%), and 12 unidentified turtles (0.6%; Table 1). The overall encounter rate was 0.93 turtles km⁻¹. Encounter rates varied across species and mirrored the overall composition of sightings with Green Turtles having the highest encounter rates, followed by Loggerheads, and then Hawksbills (Table 1). We did not see any turtles on 168 transects (15%). The majority of sightings were classified as subadult or adult animals (73%), below the surface (75%), and in shallow water 3 m or less (85%). We placed 68% of the Loggerheads and Green Turtles initially sighted and then captured in their correct life-stage category. We overestimated size in 32% of the turtles, however, they were all within 8 cm of the next larger size class.

We conducted 94% of the HUNTs in four core use areas: (a) Eastern Quicksands (35.7 km²), (b) Mooney Harbor (16.3 km²), (c) Cottrell Key (14.6 km²), and (d) Barracouta-Archer Keys (26.7 km²; Fig. 2). Sightings were significantly clustered within each of these areas (Eastern Quicksands, $Z = -23.45$, $P < 0.001$; Mooney Harbor, $Z = -20.35$, $P < 0.001$; Cottrell, $Z = -8.87$, $P < 0.001$; Barracouta-Archer, $Z = -26.02$, $P < 0.001$). The Eastern Quicksands differed from other locations by having deeper water (3.1–6.0 m) with a bottom containing a series of large shifting sand areas interspersed with seagrass beds of *Thalassia testudinum* and *Syringodium filiforme* (Manatee Grass). Mooney Harbor and the Barracouta-Archer Keys were both similar in habitat with shallow water (0.2–3.0 m) and a mixture of continuous and patchy *Thalassia* beds with a smaller proportion of mixed hard-bottom habitat comprised of sand patches, sponges, and calcareous macroalgae. The

TABLE 1. Sightings, encounter rates, and density estimates by site and species. Species abbreviations are GT = Green Turtle (*Chelonia mydas*), L = Loggerhead (*Caretta caretta*), and H = Hawksbill (*Eretmochelys imbricata*). An asterisk (*) indicates insufficient data for analysis. Sites correspond to the core use areas shown in Figure 2.

Site	Transects	Depth (m)	Distance (km)	Species	Sightings	Encounter Rate (turtles km ⁻¹)	Density (turtles km ⁻²)	Density 95% CI (turtles km ⁻²)
All Sites	1,089	1.9	2,102.2	GT	1,087	0.52	29.1	19.1–44.3
				L	789	0.38	18.1	14.4–22.8
				H	65	0.03	1.8	0.6–5.3
Eastern Quicksands	155	4.1	314.1	GT	552	1.76	58.5	33.0–103.8
				L	44	0.14	2.4	1.2–4.8
				H	3	0.01	*	*
Mooney Harbor	248	1.5	427.4	GT	251	0.59	31.5	19.2–51.6
				L	231	0.54	23.8	17.3–32.7
				H	25	0.06	1.4	0.4–4.3
Cottrell	72	2.5	147.0	GT	13	0.09	3.8	1.8–8.0
				L	30	0.20	5.4	2.7–11.0
				H	24	0.16	8.2	2.0–32.5
Barracouta-Archer	545	1.3	968.6	GT	241	0.25	17.0	7.9–36.8
				L	410	0.42	27.0	17.7–41.1
				H	13	0.01	*	*

area around Cottrell Key was more variable in both depth (0.2–6.0 m) and habitat. It was comprised of a mixture of patchy *Thalassia*, fringing reef, hard-bottom, and, on its eastern edge, two submerged rock jetties. All of the core use areas were located in the lee of islands, exposed banks, or reefs (Fig. 2).

Detection probability and density estimates.—The sighting data fit a hazard-rate cosine series expansion model where $k(y) = 1 - \exp(-(y/A(1))^{-A(2)})$, and $A(I) = i$ -th parameter in the estimated probability density function (Fig. 3). The model estimated the effective strip width (ESW) for all sightings at 9.1 m on either side of the vessel with a density of 46.4 turtles km⁻². The detection function revealed a steep decline in the probability of observing turtles beyond 10 m and, indeed, over one-

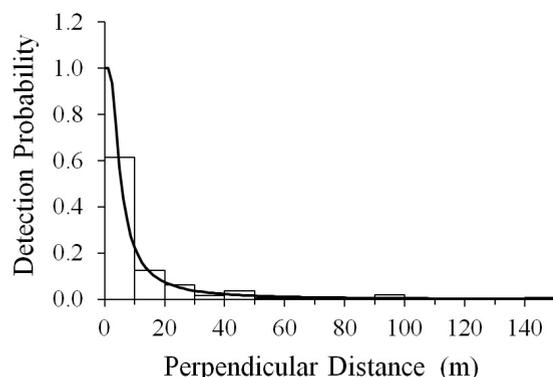


FIGURE 3. The detection probability versus the perpendicular distance of turtles from the survey vessel (m) grouped in 10 m bins and truncated at 150 m for the 2006–2012 sighting data.

third (35%) of our observations were within 3 m of the vessel transect line. Green Turtles had the highest estimated density at 29.1 turtles km⁻² followed by Loggerheads (18.1 turtles km⁻²) and Hawksbills (1.8 turtles km⁻²). Based on these densities and the area covered, we estimated there were 6,299 sea turtles (95% CI = 4,384–9,308) in the Key West NWR during the study period (Table 1). The total includes an estimated 3,741 Green Turtles (95% CI = 2,455–5,695), 2,327 Loggerheads (95% CI = 1,851–2,931), and 231 Hawksbills (95% CI = 77–681).

Multi-factor detection probability.—Multiple covariate analyses revealed that sea state was the variable that most influenced the probability of detection (Table 2). Turtle size and whether they were observed at or below the surface also affected the model, and these two factors, when combined with sea state, produced the lowest AIC value or best fit of the model. Water depth, season, species, and year had less of an influence on the probability of detection. The detection probability was higher for larger turtles and lower sea states and most of the turtles we observed at the surface were seen farther from the vessel. The average sea state for all surveys was 3.3 (range, 1-7 Beaufort Scale) and averaged 2.4 during surveys in the Eastern Quicksands and 3.8 during Barracouta-Archer surveys. The predominant wind direction during all surveys was from the east with 70% of the transect days having an easterly wind component.

Captures.—From 2003–2012, we captured 623 turtles during HUNT surveys (Table 3). Loggerheads

TABLE 2. Multiple co-variate analysis of the influence of seven factors on the hazard-rate cosine detectability function. Factors were ranked based on the lowest Akaike's Information Criterion (AIC) value.

Factor	Rank	Observations	Samples	Parameters	AIC Value	Δ AIC
Sea State + Size + At-Below Surface	1	1,016	772	9	2914.9	0.0
Sea State + Turtle Size	2	1,033	772	8	2963.3	48.4
Sea State	3	1,050	772	7	3054.5	139.6
Size	4	1,234	772	3	3548.6	633.7
At-Below Surface	5	1,231	772	3	3558.0	643.1
Water Depth	6	1,251	772	3	3641.5	726.6
Season	7	1,251	772	5	3645.2	730.3
Species	8	1,251	772	6	3647.1	732.2
Year	9	1,251	772	8	3651.1	736.2

(63%) were the most captured species, followed by Green Turtles (32%), Hawksbills (5%), and one Kemp's Ridley. The size of turtles varied significantly by species ($H = 173.16$, $df = 2$, $P < 0.001$). Loggerheads were significantly larger than Green Turtles (Dunn's; $P < 0.001$), which were significantly larger than Hawksbills (Dunn's; $P = 0.027$). However, large variances in the size distribution of Green Turtles (range, 23.1–108.5 cm SCL) revealed they were a mixture of three size classes: juvenile, subadult, and adult (Fig. 4). In contrast, Loggerheads were almost entirely subadults and adults (range, 52.4–102.6 cm SCL) while Hawksbills were mostly juveniles with a small percentage of subadults (range, 26.4–69.0 cm SCL). Based on the tail length of 22 Loggerheads > 90 cm SCL, 73% were likely male (95% CI = 54–92%) resulting in a male:female sex ratio of 2.66. For Green Turtles, 29% were likely male (95% CI = 11–47%) for a male:female sex ratio of 0.41.

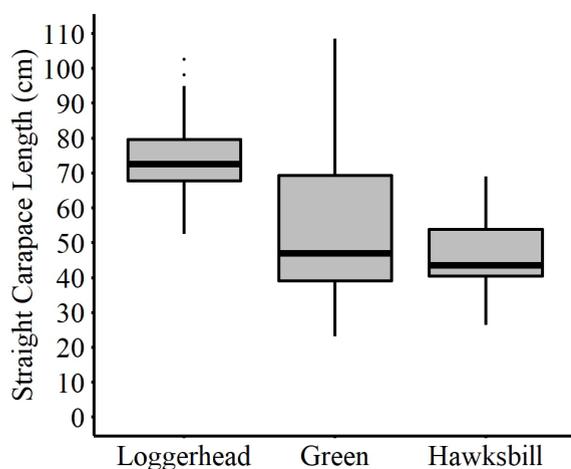


FIGURE 4. Boxplots of straight carapace lengths (SCL cm) for Loggerheads, Green Turtles, and Hawksbills captured during Haphazard, Unmarked, Nonlinear Transects (HUNTs) from 2003–2012. The boxes contain the first quartile, median (thick black line), and third quartile while the vertical bars describe the range and the small circles are outliers.

Differences among areas.—Species and size classes varied between core use areas (Table 1). Captured Green Turtles were significantly larger (mean SCL) at the Eastern Quicksands than those captured at either Mooney Harbor or Barracouta-Archer Keys ($F_{2,194} = 503.15$, $P < 0.001$; Table 3). However, there were no significant size differences among study areas for Loggerhead ($F_{3,376} = 1.80$, $P = 0.147$) or Hawksbill captures ($F_{2,24} = 2.27$, $P = 0.125$).

Recaptures.—We captured 70 turtles 166 times (mean = 2.4 captures per turtle, range, 2–5 captures per turtle) with a mean period between capture and recapture of 839 d (range, 48–2,943 d). We captured 23% more than twice. Hawksbills and Loggerheads were the most frequently recaptured species (25% and 23%, respectively). In contrast, relatively few Green Turtles were recaptured (Table 3). The highest proportion of recaptures was in Mooney Harbor and the Barracouta-Archer Keys. There was evidence of strong site fidelity for recaptured individuals in all three species, most of which were sighted and recaptured < 1 km from their previous location (79% of recaptures). The mean distance from first capture to recapture for Loggerheads was 872 m ($n = 81$, 95% CI = 658–1,087 m), which was significantly farther than the mean distance of 451 m for Green Turtles ($t = 2.78$, $df = 35$, $P = 0.009$, 95% CI = 246–657 m), and 353 m for Hawksbills ($t = 2.90$, $df = 10$, $P = 0.016$, 95% CI = 74–632 m). However, there was no significant difference in the mean distance between Green Turtles and Hawksbills ($t = 0.56$, $df = 8$, $P = 0.591$). The shortest measured distance was a juvenile Hawksbill recaptured after 98 d only 8 m away from its initial location. There were five Loggerheads and three Green Turtles tagged on this project that were observed on nesting beaches (Dry Tortugas, Florida, Melbourne Beach, Florida, Quintana Roo, Mexico), captured in in-water projects (St. Lucie Power Plant, Hutchinson Island, Florida, USA) or hit by a vessel in the Key West NWR. Conversely, we observed five

TABLE 3. The mean (\pm SD) straight carapace length (SCL, in cm), weight (kg), percent recaptured, and size of species by site in the Key West National Wildlife Refuge from 2003–2012. Species abbreviations are GT = Green Turtle (*Chelonia mydas*), L = Loggerhead (*Caretta caretta*), and H = Hawksbill (*Eretmochelys imbricata*). Sites correspond to the core use areas shown in Figure 2. An asterisk (*) indicates insufficient data for analysis.

Site	Species	Captures	SCL (cm)	Weight (kg)	Recapture (%)	Percent Large (> 65 cm SCL)
All Sites	GT	201	54.3 \pm 21.8	31.0 \pm 42.4	5.0	25.4
	L	393	74.2 \pm 9.3	60.8 \pm 22.7	23.2	83.7
	H	28	46.7 \pm 11.3	14.8 \pm 10.0	25.0	7.1
Eastern Quicksands	GT	51	88.3 \pm 11.0	101.3 \pm 41.3	0.0	100.0
	L	9	67.2 \pm 12.0	41.2 \pm 15.2	0.0	44.4
	H	1	*	*	*	*
Mooney Harbor	GT	66	44.5 \pm 8.3	12.7 \pm 6.6	1.5	0.0
	L	93	74.3 \pm 7.8	60.3 \pm 20.2	32.3	92.5
	H	13	48.3 \pm 9.9	14.9 \pm 8.7	30.8	0.0
Cottrell	GT	2	*	*	*	*
	L	13	73.3 \pm 8.3	59.1 \pm 20.3	7.7	84.6
	H	6	49.3 \pm 11.7	17.1 \pm 12.9	16.7	16.7
Barracouta-Archer	GT	80	41.4 \pm 7.7	9.9 \pm 5.6	11.3	0.0
	L	265	74.5 \pm 9.7	61.7 \pm 23.8	22.6	81.5
	H	8	39.6 \pm 9.3	9.7 \pm 6.4	25.0	0.0

Loggerheads and two Green Turtles in this study that were originally tagged by other researchers on nesting beaches in Florida and Costa Rica, commercial fishing vessels off the mid-Atlantic, and in-water projects in Florida. A subadult Loggerhead that was originally tagged in the Azores was at large 2,563 d and travelled a minimum distance of 6,625 km.

FP and injuries.—We found fibropapilloma tumors on 6% of the Green Turtles and 0.5% of the Loggerheads (Table 4). We did not observe any FP tumors on Hawksbills. The Green Turtle FP rate ranged between 5% (Mooney Harbor) and 8% (Eastern Quicksands) with afflicted turtles ranging in size from 39.6–103.6 cm SCL. However, most turtles were in the 40–60 cm size range (67%). Analysis of tumor score showed 58% of the Green Turtles captured with FP were lightly afflicted by the disease, 42% were moderately afflicted, and none were severely afflicted. The vast majority of captured turtles were in good condition based on field evaluations (97%). Three percent of the turtles were in fair or poor condition due to recent injuries and/or underweight appearance. We found 22% of all captures had evidence of carapace, flipper, or head injuries. Most of these injuries were from an unknown source; however, boat propeller wounds were the most common identifiable injury and most of these were found on Loggerheads (Table 4). Shark bite and fishing gear interactions were found less often although the latter was observed on Green Turtles in the Eastern Quicksands (Table 4). Fishing gear interactions included trap line entanglement

from the commercial spiny lobster fishery, and we documented a dead adult Green Turtle found entangled in trap line.

Green Turtle diet.—We collected foraging samples from 62 Green Turtles ranging in size from 31.6–100.0 cm SCL (mean 49.4 cm SCL \pm 13.9 SD). We identified 23 unique food or substrate/debris types collected by lavage with 1–5 types per sample (mean 2.1 \pm 1.0). Types included seagrass, red macroalgae, mobile invertebrates (e.g., isopods, arthropods, and polychaetes), sessile invertebrates (e.g., tunicates and sponges), and substrate/debris (e.g., sand, pieces of wood; Table 5). We found seagrass and/or seagrass rhizomes in all the samples (FO = 100%) and red macroalgae were present in 25.8% (16 of 62) of the samples. While *Syringodium filiforme* and *Halophila decipiens* (Paddle Grass) were identified in samples, *Thalassia testudinum* and *Halodule wrightii* (Shoal Grass) were the most abundant species. Invertebrates were in 22.6% of the samples and comprised mostly of tunicates. Substrate (sand, calcium carbonate) was in 12.9% of samples. The percent compositions of foraging types in lavage samples were similar for turtles across size classes and locations (ANOSIM, Size R = 0.02, $P = 0.328$; Location R = 0.03, $P = 0.182$).

DISCUSSION

This study is the first comprehensive assessment of sea turtle aggregations over a relatively broad protected area in the Florida Keys. Over a 10-y period, we

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TABLE 4. The proportion of turtles with fibropapillomatosis (FP) and significant injuries ($\geq 10\%$ loss) in the Key West National Wildlife Refuge from 2003–2012. The sample number (n) does not include recaptured turtles. Species abbreviations are GT = Green Turtle (*Chelonia mydas*), L = Loggerhead (*Caretta caretta*), and H = Hawksbill (*Eretmochelys imbricata*). Sites correspond to the core use areas shown in Fig. 2. An asterisk (*) indicates insufficient data for analysis.

Site	Species	n	FP (%)	Injuries (%)				Total
				Shark	Boat Prop	Fishing Gear	Unknown Source	
All	GT	191	6.0	2.1	0.5	1.0	11.5	15.1
	L	302	0.5	2.3	7.7	0.6	16.2	26.8
	H	21	0.0	0.0	4.8	0.0	14.3	19.1
Eastern Quicksands	GT	51	7.8	0.0	0.0	3.9	15.7	19.6
	L	9	0.0	0.0	0.0	0.0	33.3	33.3
	H	1	*	*	*	*	*	*
Mooney Harbor	GT	65	4.5	3.1	0.0	0.0	15.4	18.5
	L	63	0.0	1.6	11.1	0.0	23.8	36.5
	H	9	0.0	0.0	11.1	0.0	11.1	22.2
Cottrell	GT	2	*	*	*	*	*	*
	L	12	0.0	0.0	0.0	8.3	0.0	8.3
	H	5	0.0	0.0	0.0	0.0	20.0	20.0
Barracouta-Archer	GT	71	6.3	2.8	1.4	0.0	5.6	9.8
	L	205	0.7	2.9	7.8	0.5	13.7	24.9
	H	6	0.0	0.0	0.0	0.0	0.0	0.0

observed thousands of sea turtles in patchy seagrass beds, mixed hard-bottom, sponge dominated hard-bottom, and fringing reefs representing four species and three life stages (juvenile, subadult, and adult). The

TABLE 5. Frequency of occurrence and mean percent composition (\pm SD) of foraging types found in Green Turtle (*Chelonia mydas*) lavage samples (n = 62).

Foraging item	Frequency (n)	Composition (%)
Seagrass		
<i>Thalassia testudinum</i>	53	61.5 \pm 41.4
<i>Halodule wrightii</i>	15	9.8 \pm 24.3
<i>Syringodium filiforme</i>	11	5.7 \pm 18.7
<i>Halophila decipiens</i>	7	2.8 \pm 13.5
seagrass rhizome	7	0.9 \pm 3.4
Rhodophyta		
<i>Gracilaria</i> spp.	3	2.8 \pm 14.1
<i>Gelidium</i> spp.	5	2.3 \pm 9.7
<i>Chondria dasyphyllus</i>	1	1.5 \pm 11.6
<i>Lomentaria</i> sp.	1	1.3 \pm 10.5
<i>Chondria littoralis</i>	1	0.9 \pm 7.4
<i>Polysiphonia</i> sp.	1	0.1 \pm 0.9
unidentified alga	4	2.2 \pm 11.2
Invertebrates		
sessile (tunicate, sponge)	6	4.8 \pm 17.8
mobile (isopod, arthropod)	9	0.7 \pm 3.1
Substrate		
debris (sand, calcium carbonate)	8	1.91 \pm 9.6

current abundance of sea turtles on this foraging ground may be attributed to the protection of the habitat through the establishment of the Key West NWR, but more broadly to the protection of sea turtle populations by the U.S. Endangered Species Act of 1973 (ESA). Historical reports of decimated Green Turtle populations due to the Key West turtle fishery (Witzell 1994) contrast sharply with the turtle densities found during this study and provide further evidence that Green Turtles are recovering in the northwest Atlantic after centuries of commercial exploitation (Ehrhart et al. 2007; Chaloupka et al. 2008; Metz and Landry 2013).

Florida is known to have a mixture of Green Turtles, Loggerheads, Hawksbills, and Kemp's Ridleys in its waters (Mendonça and Ehrhart 1982; Schmid 1998; Makowski et al. 2005; Ehrhart et al. 2007; Gorham et al. 2014). Seasonal migrations (Schmid 1998), breeding migrations (Arendt et al. 2012; Ceriani et al. 2012), and ontogenetic habitat shifts (Witherington et al. 2006a) occur with some juvenile turtles showing strong site fidelity to foraging areas (Mendonça and Ehrhart 1982; Makowski et al. 2006; Hart and Fujisaki 2010). While juvenile Loggerheads and Green Turtles are found foraging in nearshore waters of Florida throughout the year (Ehrhart et al. 2007; Kubis et al. 2009; Hart and Fujisaki 2010), adults are almost exclusively observed from April through September during the nesting season. The exception to this appears to be the extreme southern part of the peninsula and Florida Keys (Witherington et al. 2006a; Foley et al. 2013). The Loggerheads and

Green Turtles observed in this study place the Key West NWR and Eastern Quicksands as an important year-round adult foraging ground.

We estimated abundance using a relatively low survey platform in shallow water with top-to-bottom visibility. In contrast, observers using large vessels and aircraft have had challenges identifying species and size classes due to the much higher platform, deeper water, and/or poor visibility (Beavers and Ramsey 1998; McDaniel et al. 2000). Encounter rates using aircraft and large vessels have ranged from 0.09 Loggerheads km⁻¹ in the Columbretes Islands, Spain (Gomez de Segura et al. 2003), to 0.24 Olive Ridley's km⁻¹ (*Lepidochelys olivacea*) in the eastern tropical Pacific (Eguchi et al. 2007). While these encounter rates appear to fall between the 0.03 to 0.56 turtles km⁻¹ reported here, they are not comparable because of the higher platform height (typically 150–250 m for manned aircraft surveys) and the larger proportion of missed underwater turtles. Because of these issues, our density measurements were more comparable to those of Roos et al. (2005), who surveyed shallow water off Mayotte Island in the western Indian Ocean using a paramotor and found that densities at 12 sites ranged from 13–297 Green Turtles km⁻². In comparison, the highest densities we found were 59 Green Turtles km⁻² in the Eastern Quicksands.

Sea turtles were aggregated in core use areas containing patchy seagrass interspersed with mixed hard-bottom and located in shallow basins in the lee of islands, exposed banks, or reefs. Examples of this included the Barracouta flats (west of Barracouta Key), Man Key basin (south of Barracouta Key), Archer Key basin, and central Mooney Harbor. This preference may be a function of food availability (Mendonça and Ehrhart 1982) and predator avoidance (Heithaus et al. 2007; Bresette et al. 2010). Resource competition could have been driving turtles towards more structurally complex habitats that can be used for shelter and rest (Thomson et al. 2015). However, because most of the habitat we observed was patchy seagrass, we are unsure as to why some seagrass areas had higher turtle densities than others. Rigorous habitat measurements may be able to answer this question in the future. While we found Loggerheads equally represented in the shallow basins mentioned above, Green Turtles were separated by size class and preferred deeper water at larger sizes (Koch et al. 2007; Bresette et al. 2010). Hawksbills were strongly associated with fringing reefs, yet smaller juveniles were also found on the edge of seagrass beds, which supports the assertion of a dietary shift from omnivory to carnivory as they mature (Bjorndal and Bolten 2010; Hart et al. 2012; Gorham et al. 2014). This ontogenetic habitat shift has also been observed in Barracuda (*Sphyræna barracuda*), Gray Angelfish (*Pomacanthus*

arcuatus), and Yellowfin Mojarra (*Gerres cinereus*) in the Key West NWR (Eggleston et al. 2004).

Green Turtles are known to feed on red macroalgae and seagrass (Bjorndal 1985; Bjorndal et al. 2005; Makowski et al. 2006; Williams et al. 2014; Holloway-Adkins and Hanisak 2017). However, throughout the tropics, *Thalassia testudinum* appears to be the most prevalent food item (Mortimer 1981; Fuentes et al. 2006). While size-class partitioning between shallow and deeper water habitats occurred, our diet analysis indicated Green Turtles are not partitioned by food resources in the Key West NWR. The robust body condition, abundance, and range of size-classes suggests this area has plenty of available food. Along the east coast of central Florida, juvenile Green Turtles also demonstrate size-class partitioning between habitats, but the turtles in this region primarily feed on red macroalgae, even in areas that contain seagrass (Holloway-Adkins 2001). A comparison of Green Turtle health and foraging resources in heavily developed parts of the state compared to the Key West NWR could highlight differences in habitat quality, resource abundance, and/or nutritional needs.

The sea turtles in the Key West NWR appeared relatively healthy with some evidence of vessel and predator interactions. Fibropapillomatosis is common in Florida Green Turtles even though its etiology remains in question (Page-Karjian et al. 2014), yet juvenile Green Turtles in this study had much lower FP rates than reported for the Indian River Lagoon along the east coast of Florida (6% vs. 53%; Ehrhart et al. 2007). Offshore waters, which are further from urban and agricultural development, seem to have lower proportions of turtles with FP (Foley et al. 2005; Kubis et al. 2009). In addition, many of the FP Green Turtles in this study were mildly afflicted and larger on average than those found along the east coast of Florida (Ehrhart et al. 2007). These larger turtles may have recruited to the Key West NWR from locations further north where FP is more prevalent and were recovering from the disease (Witherington et al. 2006a; Patricio et al. 2016). The injuries we observed reflected a combination of threats, turtle size and responsiveness to approaching vessels in shallow water. For example, we found Green Turtles to be much quicker than Loggerheads when pursued by our vessel (juvenile Green Turtles were recorded swimming at 19 km h⁻¹). In contrast, slower and, on average, larger Loggerheads appear to be susceptible to a higher proportion of boat propeller injuries in shallow water (Norem 2005). Shark attack injuries were equally represented in both Green Turtles and Loggerheads. However, this may have been the result of size differences because the avoidance of sharks in similarly sized healthy turtles favors the more responsive Green Turtle (Heithaus et al. 2002).

We may have violated several assumptions in our distance sampling methodology. In this study, the assumptions were: (1) turtle movements were independent of the platform; (2) all turtles on the transect line were detected; and (3) sighting distance measurements were exact. The turtles we observed appeared to be unaffected by our presence until we were within 7 m of them. However, without concurrent comparisons with other survey platforms (e.g., aerial), we cannot know for certain if unobserved turtles were negatively affected by our vessel and missed. The proportion of turtles on our transect line that were not detected was also unknown, but, due to the top-to-bottom visibility and shallow water, it was likely negligible. Observers estimated sighting distances at 50 and 100 m more frequently than expected in the model because they tended to round their estimates at those distances (Eguchi et al. 2007). While the distance estimates were not precise, binning the data smoothed out the variation. Lastly, our HUNTS were biased toward areas where we could observe turtles under a variety of weather conditions and, ultimately, capture them. Because of this, our effort was not uniform throughout the refuge. However, we estimated abundance using a probability of detection model and not raw count data.

The Eastern Quicksands is unique and contains relatively high densities of subadult and adult Green Turtles (range, 69.3–108.5 cm SCL). However, the area is greatly affected by wind, waves, and strong currents, so whenever possible, we took advantage of calm weather to work there. In 2008, five subadult and adult Green Turtles outfitted with GPS transmitters in the Eastern Quicksands were found foraging in distinct core areas (50% Kernel density estimates) that averaged 6.35 km² (Dean Bagley, unpubl. data). Bresette et al. (2010) provided evidence that Green Turtles in this area forage in herds. Possibilities for future research include the rare opportunity to collect behavioral data on adults. While there may be deeper sites in the region that also contain adults, access to them would be more restricted and include constrained survey methods (e.g., SCUBA surveys). Because the Eastern Quicksands contains one of the few known adult Green Turtle foraging sites in North America, wildlife managers should consider adding it to the boundaries of the Key West NWR.

Several aspects of this study offer an opportunity for wildlife management. The proportion of vessel strike injuries on stranded sea turtles in Florida from 1980–2014 was 21% (Allen Foley et al., unpubl. report), and a recent examination of 200 turtles with vessel strike injuries in Florida concluded that vessel strikes were the most likely cause of death (Brian Stacy, pers. comm.). This issue has the potential to cause increased mortality as turtle populations recover and the human population continues to expand into the marine environment

(Shimada et al. 2017). Additionally, derelict lobster traps in the Florida Keys are accumulating faster than they can be removed and this problem is expected to increase with more intense tropical storms (Uhrin 2016). We noted dozens of derelict lobster trap lines on surveys in deeper water and suggest the focus on derelict trap removal be in the areas where the likelihood of interactions with adult turtles and other large marine life is high, particularly in the Boca Grande Channel and Eastern Quicksands. Based on the results of this study, we strongly recommend the USFWS and NMFS designate the Key West NWR and Eastern Quicksands as critical habitat for Green Turtles, Hawksbills, and Loggerheads under the ESA. Among other things, this could lead to the establishment of idle speed, no motor, or no access zones in Mooney Harbor, Cottrell, and Barracouta-Archer Keys (USFWS 2009).

This study provides sea turtle abundance estimates and identification of core use areas for multiple species and size classes in a Marine Protected Area for which in-water population estimates were previously unknown. The Key West NWR and surrounding waters may be pivotal in the recovery of Green Turtles, Loggerheads, and Hawksbills in the U.S. because the area is relatively large, undeveloped, and contains turtles that appear to be relatively healthy. Future work might include comparisons with populations living along the Florida peninsula, which face more anthropogenic threats than those in the refuge. Based on tag returns and satellite telemetry, turtles that use the Key West NWR spend significant portions of their lives outside of U.S. waters (Foley et al. 2013). This means the status of sea turtles in other countries in the northwest Atlantic may be detected in the turtles that frequent this area. Regional networks that connect nesting beaches, migratory corridors, and foraging grounds may be the most effective tools in future sea turtle conservation planning (Hays et al. 2014). Because of its relative importance, we expect the Key West NWR to be included in these critical efforts.

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RICHARD HERREN (Rick) received his M.S. in Biology from the University of Central Florida, Orlando, USA. He has been working in sea turtle biology since 1992 and currently manages several conservation and research projects for the Sea Turtle Conservancy. Rick co-founded and is on the Board of Directors of Inwater Research Group, Inc. and Coastal Biology, Inc. He is currently working on his Ph.D. at the University of Florida, Gainesville, USA, where he is studying the spatial distribution and habitat selection of juvenile sea turtles in Florida's waters. (Photographed by Chris Koeppel).



DEAN BAGLEY has been working with the Marine Turtle Research Group (UCFMTRG) at the University of Central Florida (UCF), Orlando, USA, since 1989. Her extensive nesting beach experience was gained while working in the globally important Archie Carr National Wildlife Refuge in Melbourne Beach, Florida, USA. Between UCF and Inwater Research Group, she has worked regularly in developmental habitats throughout Florida. She is Vice President of the Southeast Regional Sea Turtle Network and continues to work at the Archie Carr NWR and in various inwater projects around the state. (Photographed by Jim Stevenson).



MICHAEL BRESSETTE's love for the marine environment began in his early teens during a summer course with Dr. Peter Auger studying diamondback terrapins in Cape Cod, Massachusetts, USA. Michael went on to attend Florida Institute of Technology in Jensen Beach, majoring in Oceanographic Technology. His interest in the status of sea turtles in the southern Indian River Lagoon was the impetus for the creation of Inwater Research Group and he has been the President and Executive Director of the non-profit since its incorporation in 2001. (Photographed by Carrie Keske).



KAREN HOLLOWAY-ADKINS's research interests center on the ecology of sea turtles, assessing characteristics of inwater developmental habitat, and the role sea turtle foraging plays in marine systems. Her special interests include macroalgae identification, impacts of foraging on aquatic vegetation, consumer-prey relationships among herbivores, resource competition vs. partitioning, and the function of these processes in marine ecosystems. Karen is a scientist working within the Kennedy Space Center Ecological Program and she also conducts sea turtle research on Florida nearshore reefs as a primary investigator for East Coast Biologists, Inc. (Photographed by Chris Koeppel).



DAVE CLARK worked as a Biologist at Inwater Research Group from 2007 to 2015 where he captured thousands of sea turtles entrained in the intake canal at the St. Lucie Nuclear Power Plant on Hutchinson Island, Florida, USA. He helped plan in-water sea turtle projects throughout the state and was involved in the rescue of sea turtles in the Gulf of Mexico in the wake of the Deep Water Horizon Oil Spill. (Photographed by Dean Bagley).



BLAIR WITHERINGTON is a Senior Sea Turtle Conservation Biologist with Disney's Wildlife Conservation Program and the Archie Carr Center for Sea Turtle Research at the University of Florida, Gainesville, USA. Blair has a doctorate in Zoology from the University of Florida. In 30 y of research, he has contributed more than 50 scientific articles and book chapters on sea turtle biology. He is on the Board of Directors of Inwater Research Group and a member of the Marine Turtle Specialist Group of the International Union for Conservation of Nature. (Photographed by Dawn Witherington).