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Demography of Marine Turtles in the Nearshore Environments of the Northern Mariana Islands[1]

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Abstract: In the western Pacific, green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) sea turtles are listed as Endangered under the U.S. Endangered Species Act (ESA). Population data are limited for both species throughout the entire region and particularly in the Philippine Sea. This study characterizes size class distribution, growth rates, habitat use, behavior, diet, and site fidelity of foraging aggregations of green and hawksbill turtles in nearshore habitats of Saipan, Tinian, and Rota in the Commonwealth of the Northern Mariana Islands (CNMI). Between August 2006 and February 2014, we captured 642 turtles (493 green and 36 hawksbill turtles). Straight carapace length (SCL) ranged from 32.5 to 91.6 cm, with juveniles composing the majority of captures (mean SCL = 50.7 cm). Four of the green turtles were adults (SCL ≥ 81 cm), with SCLs of 84.2 to 91.6 cm. All 36 hawksbill turtles were juveniles (SCL < 78.6 cm). Most captures occurred in coral habitats where turtles were foraging and resting. Diet samples from 47 green turtles included *Amansia* sp., *Gelidiella* sp., *Hypnea* sp., and *Ceramium* sp. Green turtle growth rates ranged from 0.3 to 7.8 cm yr^{-1}. Estimated mean residency time was 17 yr. This is the first study within the CNMI to report on morphometric data and diet composition of marine turtles. These results provide an assessment of green and hawksbill turtle population demographics and habitat use in the CNMI.

Population data are limited for endangered green (*Chelonia mydas*) and hawksbill (*Eretmochelys imbricata*) sea turtles throughout the western Pacific Ocean. In the Philippine Sea region, the Commonwealth of the Northern Mariana Islands (CNMI) provides important foraging grounds for both species (Kolinski et al. 2001, 2004, 2006). Although harvesting turtles is illegal in the CNMI under local (CNMI Public Law 02-51, 1981) and federal (ESA, 16 U.S.C. § 1531 et seq.) laws, hunting continues today (CNMI Department of Land and Natural Resources 2006, 2009, 2011, 2013*a*, 2013*b*). Recovery of these exploited species will require conservation actions guided by population assessments and rely heavily on demographic parameters. Previous studies in the CNMI have used towed-diver and shoreline surveys to estimate the abundance of nearshore foraging turtles (Pultz et al. 1999, Kolinski et al. 2001, 2004, 2005, 2006); however, these methods do not provide demographic data on the size structure,

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growth rates, and residency times for the local population.

In this study, we used mark-recapture methods to assess population demographics and nearshore ecology of green and hawksbill turtles of the southern CNMI region. Our objectives were to characterize the size class distribution, growth rates, habitat use, behavior, diet, and site fidelity of turtles foraging in nearshore habitats. This is the first study to report on morphometric data and diet composition of sea turtles in the CNMI. Our results provide a characterization of green and hawksbill turtle population demographics and habitat use in the CNMI. Further, our results will directly inform turtle management and conservation under the U.S. Endangered Species Act because the CNMI populations of both species are listed as "Endangered" (Federal Register 1970:35 FR 8491, 2016:50 CFR 17, Seminoff et al. 2015).

MATERIALS AND METHODS

This study was conducted on the islands of Saipan, Tinian, and Rota in the CNMI (14.11°N–15.29°N and 145.12°E–145.83°E), which are bordered by the Philippine Sea to the west and the western Pacific Ocean to the east (Figure 1). Study sites included the following: (1) on Saipan: Laguna Garapan (Balisa) in the southwest and Lao Lao Bay in the southeast, (2) on Tinian: Barcinas Cove, Tachungnya Bay, Tinian Harbor, Dumpcoke, Turtle Cove, and Fleming Point along the west coast, and (3) on Rota: Sasanlagu and Teteto along the northwest coast and Sasanhaya Bay (includes Jerry's Reef) and Puntan Poña in the southwest (Figure 2*A–C*). These areas are nearshore foraging grounds for both green and hawksbill turtles. The benthic habitat is characterized by a mixture of coral, uncolonized hard bottom, macroalgae, and coralline algae [National Oceanic and Atmospheric Administration (NOAA) 2004*a*], with depth ranging from 1 m near reef crests to 30 m near reef slope bottoms. Over 30 species of cyanophytes, algae, and sea grass (green turtle diet items) have been identified during nearshore benthic surveys of Saipan, Tinian, and Rota (summarized in Kolinski et al. 2001, 2004, 2006).

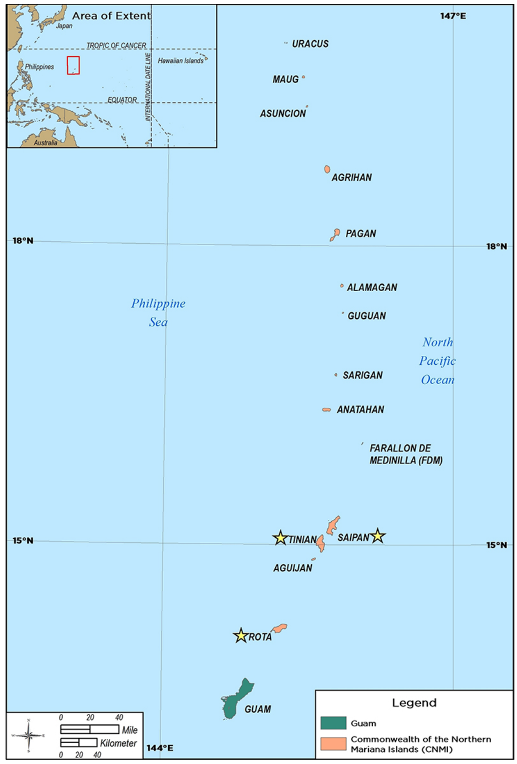

FIGURE 1. Map of the Mariana Archipelago showing the location of the nearshore mark-recapture sites of Saipan, Tinian, and Rota.

Turtles were hand captured by a single free diver (Figure 2*D*) whose technique is part of a cultural knowledge base from Micronesia (i.e., traditional ecological knowledge passed down from elders) (Summers and Kinan-Kelly 2010). The use of nets, diving with active watercraft pursuit, and SCUBA (Ehrhart and Ogren 1999) was precluded by the skittish nature of CNMI turtles combined with the presence of deep waters and other physical and biotic habitat attributes (i.e., currents and patch reef formations). The technique described here involves only free diving (with the use of mask, snorkel, fins, wet suit, and weight belt) and hand capture. The free diver targeted turtles based on behavior regardless

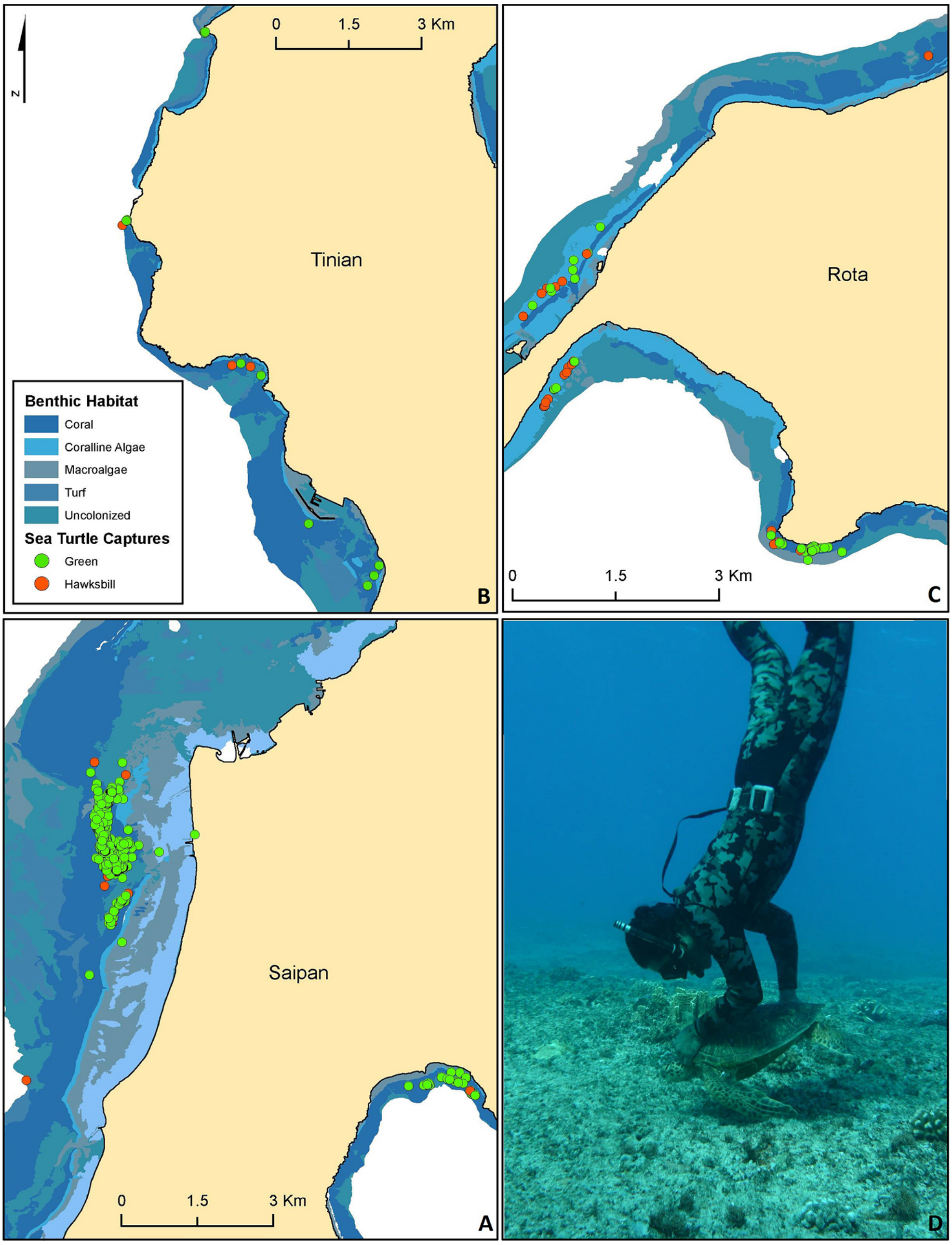

Figure 2. Clockwise from bottom left: nearshore capture locations in relation to benthic habitat of (*A*) Saipan, (*B*) Tinian, and (*C*) Rota, and (*D*) an image of the free diver hand capturing a juvenile green turtle. Green and orange dots depict capture locations for green and hawksbill turtles, respectively. Shading indicates benthic habitat.

of length (i.e., juvenile, subadult, and adult). Foraging and resting turtles are less likely to evade capture than swimming or cognizant turtles; however, the diver captured turtles from all size classes exhibiting all behaviors.

The diver approached turtles from behind, grasping them by the nuchal and posterior marginal scutes and guiding them to the surface for recovery in a McKee Craft 4.88 m (16 ft) skiff (Ehrhart and Ogren 1999). Upon retrieval, capture site depth was recorded using a handheld depth finder. Geographic coordinates were documented using a handheld unit (Garmin GPSMAP 76). The observed habitat (e.g., coral reef) and the turtle's activity at time of capture (e.g., resting or foraging) were also recorded. Turtles were then measured, tagged (see later in this section), weighed, photographed, and released.

Most captures were performed during daylight hours; however, one or two surveys on each island occurred during nighttime hours. Capture rate was calculated as the number of turtles caught per hour of dive time (or per survey day) for each year and species. Survey dive start and end times were not documented consistently between August 2006 and July 2008; thus we did not calculate hourly capture rates for that period. The relative abundance of hawksbill turtles was compared across islands using two metrics: (1) the proportion of total captures made up of hawksbill turtles, and (2) the capture rate of hawksbills.

All captured turtles were double-marked with Inconel (National Band & Tag Co., 681C) or Titanium (Stockbrands Co. Pty Ltd., large size) flipper tags; one tag was attached proximally and adjacent to the first large scale on the posterior edge of each front flipper (Balazs 1999). In addition, most turtles were tagged with Passive Integrated Transponder (PIT) tags. All flippers were scanned for the presence of PIT tags with a Biomark Pocket Reader (Boise, Idaho) PIT tag scanner. If no PIT tags were present, then a single PIT tag was injected subcutaneously into one of the hind flippers using a 12-gauge disposable hypodermic needle and applicator. Inconel, titanium, and PIT tag retention was calculated according to the equation $P_i = b_i/(a_i + b_i)$, where i is the elapsed time in years since initial tag application, P_i is the probability of tag loss i years after attachment, a_i is the number of tags present i years after attachment, and b_i is the number of tags lost i years after attachment (Bellini 2001).

Straight carapace length (SCL) and curved carapace length (CCL) were measured from the anterior point at the midline (nuchal scute) to the longest posterior tip of the supracaudal scutes. Likewise, straight and curved carapace widths (SCW and CCW, respectively) were measured at the widest point (Bolten 1999). SCL and SCW were measured using a forester's caliper (S-882 00 Haglof, Sweden), and CCL and CCW were taken using a flexible tape measure, both to the nearest tenth of a centimeter (cm). Total tail length was taken with a flexible tape measure from the midline of the posterior margin of the plastron to the end of the tail following the curvature of the tail (Bolten 1999). Body mass was measured to the nearest tenth of a kilogram (kg) using a digital scale (Salter Brecknell PS 400).

SCL and SCW measurements were recorded from August 2008 to February 2014; before August 2008 only curved measurements were taken. Thus, for the early sampling period (August 2006 to July 2008), CCLs were converted to SCLs for size classification using simple linear regressions of paired SCL and CCL data points from CNMI turtles for both species (this study). SCL was calculated using a species-specific conversion factor: for green turtles: SCL = 1.57 + (0.91 × CCL) ($n = 384$, $r^2 = 0.99$, $P < .001$), and for hawksbill turtles: SCL = 1.27 + (0.92 × CCL) ($n = 27$, $r^2 = 0.99$, $P < .001$). In this study, we define size at maturity for green turtles as SCL ≥ 81 cm based on the CNMI adult nesting population (CNMI Department of Lands and Natural Resources 2006, 2009, 2011, 2013*a*, 2013*b*) and for hawksbill turtles as SCL ≥ 78.6 cm based on the mean carapace lengths of 17 populations worldwide (van Buskirk and Crowder 1994). When adult turtles were observed during dives but eluded capture, the species, sex, and estimated size class were recorded.

Differences in mean SCL and mass between turtles from Saipan and Rota were tested using Student *t* tests for both green and hawksbill turtles. Recaptures were excluded from these analyses. Fifteen green turtles were captured on Tinian, but these were not included in the analysis due to small sample size. Results are presented as a mean ± standard deviation, unless otherwise noted, with $P < .05$ considered significant.

To estimate growth rates, the SCL measurements of recaptured turtles were compared over time. Absolute growth rates (GR) were calculated using: $GR = (L_R - L_C)/T$ where L_R is the length at recapture, L_C is the length at initial capture, and T is the time between captures (van Dam 1999). Growth rates were assigned to 10 cm length bins based on the midlength, defined as $(L_C + L_R)/2$ (Jones et al. 2011). To minimize potential bias from seasonal effects on growth rate, growth values resulting from capture intervals less than 10 months were not included in the analysis (Kubis et al. 2009). For turtles recaptured more than once, the first capture length and the last capture length were used to calculate growth rates. There were no recaptured turtles documented for Tinian; therefore, Tinian is excluded from the following analyses.

A Welch's *t* test was used to compare growth rates between green turtles captured on Saipan and Rota using the 50–60 cm length bin, because this was the only bin with multiple recaptures on Rota. Significant differences in growth rates among length bins within Saipan (the only island with multiple recaptures in multiple length bins) were determined using a one-way analysis of variance (ANOVA), and a Tukey-Kramer HSD test was used to identify where the significant differences fell among the length bins. For all tests, alpha was set to .05.

Growth rate (cm/yr) for green turtles was modeled using a generalized additive modeling approach (GAM) (Hastie and Tibshirani 1990) as applied by Seminoff et al. (2002) following earlier sea turtle growth studies (Chaloupka and Limpus 1997, Limpus and Chaloupka 1997, Bjorndal and Chaloupka 2000). Detailed methods of the GAM approach for this purpose were outlined by Seminoff et al. (2002). The analyses were conducted in the R statistical environment using the *gam* function in the *mgcv* package and the *smooth.spline* function in the *stats* package (R Core Team 2014). Briefly, the model was specified with annual growth rate (SCL cm/yr) as the response variable and year (calendar year of recapture), mean size (SCL midlength in cm), and time at large (recapture interval in years) as continuous covariates. To estimate nonlinear relationships between the covariates and the response variable, the model included a robust quasi-likelihood error function, an identity link, and a fairly stiff cubic smoothing spline (4 knots or 3 degrees of freedom). The model was estimated to fit all green turtle recapture data from Saipan and Rota. To estimate the size-specific growth rate curve, we followed Seminoff et al. (2002) in fitting a cubic B-spline smooth to the fitted values from the GAM model (fitted growth rate values were produced using the estimated GAM to predict back on the original data). We allowed the smoothing function to optimize the degrees of freedom and confirmed that this specification produced the best fit by comparing the generalized cross validation score to variations of the model forced with different degrees of freedom (e.g., df = 2 produces a linear fit). To generate a confidence interval for the size-specific growth rate curve, we fit cubic B-spline smooths through the 95% confidence limits for each fitted value (calculated from the standard errors). Residency time (number of years in nearshore habitat) was calculated by simulating the growth of a single turtle from its recruitment at 35 cm to its departure at SCL > 81 cm (size at maturity). The fitted cubic B-spline smooths were used to determine the growth rate corresponding to the size of the turtle for each simulated year. To produce a range of residency time estimates, we performed the simulation on each of the fitted smooths (mean, lower 95%, and upper 95%).

Captured turtles with food fragments in their mouth were sampled opportunistically and the samples identified under a dissecting microscope. Each diet item was identified to the lowest possible taxon. Algae were identified in accordance with Abbott (1999) and Abbott and Huisman (2004).

GPS points of capture locations were mapped using ESRI ArcGIS v. 10.1 and overlaid on benthic habitat maps of each island to reveal turtle-habitat associations. Shapefiles were downloaded from the NOAA Benthic Habitat Mapping Web site (NOAA 2004*a*). Benthic habitat maps were prepared by visual interpretation from IKONOS satellite imagery procured by NOAA from 2001 to 2003 (NOAA 2004*a*). Shallow-water benthic habitats were delineated using a hierarchical classification scheme that included biological cover, geomorphological structure, and zone type (NOAA 2004*b*). For each capture location plotted on the maps, a benthic habitat description was generated listing the biological cover (e.g., coral reef, hard bottom), geomorphological structure (e.g., pavement), cover type (e.g., coral), percentage cover (e.g., 10–<50%), and zone type (e.g., fore reef).

RESULTS

Annual effort varied greatly between August 2006 and February 2014. Between August 2008 and February 2014, a total of 341 hr was dedicated to nearshore surveys in the CNMI, with 275 hr on Saipan, 46 hr on Rota, and 20 hr on Tinian (Table 1). Capture rate averaged 2.2 turtles (range, 0–5 turtles) for every 1 hr dive interval (Table 1) for all turtles. A progressive increase in captures over time is explained by increased sampling in succeeding years. A total of 493 green (447 on Saipan, 34 on Rota, and 12 on Tinian) and 36 hawksbill turtles (15 on Saipan, 18 on Rota, and 3 on Tinian) was captured (Table 1). Recaptures included 107 green (100 on Saipan, 7 on Rota, and 0 on Tinian) and 6 hawksbill turtles (3 on Saipan, 3 on Rota, and 0 on Tinian) (Table 1). The proportion of captures that were hawksbill turtles varied widely across islands, ranging from 3.2% on Saipan to 20.0% on Tinian and 34.6% on Rota. In addition, the maximum capture rate for hawksbill turtles in turtles per hour of dive time ranged from <0.1 on Saipan to 0.3 on Tinian and 1.1 on Rota. Comparatively, the maximum capture rate for green turtles was 4.2 turtles per hour on Saipan, 0.7 on Tinian, and 1.2 on Rota (Table 1).

For green turtles, the mean SCL was 51.6 cm ± 9.1 (range, 33.6–91.6 cm; $n = 493$) (Figure 3). The juvenile size class (SCL < 81 cm) accounted for 99.4% of captured turtles ($n = 638$); the remaining 0.6% consisted of four adults (SCL > 81 cm). The mean SCL for hawksbill turtles was 49.7 cm ± 9.6 (range, 32.5–74.3 cm; $n = 36$) (Figure 3). All 36 hawksbill turtles were juveniles (SCL < 78.6 cm). Sea turtles do not display sexually dimorphic traits until sexual maturity (Limpus 1985, Wibbels 1988), thus sex was recorded as unknown for the 638 juveniles.

A total of 19 adults (16 green and 3 hawksbill turtles) was captured or observed between 2008 and 2014. On Saipan, two captured green turtles were identified as males based on tail length (37.0 and 40.4 cm) (Limpus and Reed 1985, Wibbels 1999), and two were identified as females based on tail length (17.0 and 19.0 cm) and nesting behavior observed 8 months prior. Four more captured adults were released by the diver at the surface before boat retrieval due to personal safety considerations; one was estimated to be male based on the observed tail length. The diver observed but did not capture an additional 10 adults (visual estimation of size): seven green (including two males) and three hawksbill turtles (including one male). Observing but not capturing juveniles also occurred (more commonly than with adults) and depended on their behavior rather than size. On Rota (Puntan Poña site) there were four observations of an adult male on different sample days; however, the turtle was identified to be a single resident male from distinctive carapace markings. Collectively, these observations indicate that adults are (1) sometimes present in the areas surveyed, (2) observed in much lower numbers than juveniles, and (3) as likely (if not more) to be caught by the diver as juveniles.

Mean SCLs of green and hawksbill turtles on Saipan (green: 50.9 cm ± 9.2, $n = 447$; hawksbill: 50.7 cm ± 10.1, $n = 15$) and Rota (green: 51.1 cm ± 7.0, $n = 34$; hawksbill: 46.5 cm ± 7.9, $n = 18$) did not differ significantly (green: $t = -0.15$, df = 479, $P = .879$; hawksbill: $t = 1.32$, df = 31, $P = .197$). There was also no significant difference in body mass

TABLE 1

Nearshore In-Water Survey Effort, Turtle Captures, and Capture Rates (Turtles per Hour of Diving or Turtles per Survey Day) on Saipan, Tinian, and Rota, CNMI

Island	Effort/Captures	2006	2007	2008	2009	2010	2011	2012	2013	2014[a]
Saipan										
	Sample days[b]	9	11	24	20	22	40	38	42	4
	Sample hours	—	—	41.3	32.2	27.3	51.2	59.1	57.9	5.9
	No. of green turtles	14(0)	12(0)	40(1)	31(4)	35(5)	99(12)	123(29)	168(45)	25(4)
	No. of hawksbill turtles	3(0)	4(1)	3(0)	0(0)	0(0)	2(1)	2(0)	4(1)	0(0)
	No. of turtles, total	17(0)	16(1)	43(1)	31(4)	35(5)	101(13)	125(29)	172(46)	25(4)
	Capture rate, CM (days)	1.6	1.1	1.7	1.6	1.6	2.5	3.2	4.0	6.3
	Capture rate, EI (days)	0.3	0.4	0.1	0	0	<0.1	<0.1	0.1	0
	Capture rate, total (days)	1.9	1.5	1.8	1.6	1.6	2.5	3.3	4.1	6.3
	Capture rate, CM (hours)	—	—	1.0	1.0	1.3	1.9	2.1	2.9	4.2
	Capture rate, EI (hours)	—	—	<0.1	0	0	<0.1	<0.1	<0.1	0
	Capture rate, total (hours)	—	—	1.0	1.0	1.3	2.0	2.1	3.0	4.2
Tinian										
	Sample days[b]	0	0	0	2	0	0	0	3	0
	Sample hours	0	0	0	7.7	0	0	0	12.2	0
	No. of green turtles	0(0)	0(0)	0(0)	3(0)	0(0)	0(0)	0(0)	9(0)	0(0)
	No. of hawksbill turtles	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	0(0)	3(0)	0(0)
	No. of turtles, total	0(0)	0(0)	0(0)	3(0)	0(0)	0(0)	0(0)	12(0)	0(0)
	Capture rate, CM (days)	—	—	—	1.5	—	—	—	3.0	—
	Capture rate, EI (days)	—	—	—	0	—	—	—	1.0	—
	Capture rate, total (days)	—	—	—	1.5	—	—	—	4.0	—
	Capture rate, CM (hours)	—	—	—	0.4	—	—	—	0.7	—
	Capture rate, EI (hours)	—	—	—	0	—	—	—	0.3	—
	Capture rate, total (hours)	—	—	—	0.4	—	—	—	1.0	—
Rota										
	Sample days[b]	0	0	0	2	5	5	4	3	0
	Sample hours	0	0	0	9.5	12.2	11.4	7.5	5.8	0
	No. of green turtles	0(0)	0(0)	0(0)	11(0)	12(6)	10(1)	4(0)	4(0)	0(0)
	No. of hawksbill turtles	0(0)	0(0)	0(0)	0(0)	3(1)	7(0)	8(1)	3(1)	0(0)
	No. of turtles, total	0(0)	0(0)	0(0)	11(0)	15(7)	17(1)	12(1)	7(1)	0(0)
	Capture rate, CM (days)	—	—	—	5.5	2.4	2.0	1.0	1.3	—
	Capture rate, EI (days)	—	—	—	0	0.6	1.4	2.0	1.0	—
	Capture rate, total (days)	—	—	—	5.5	3.0	3.4	3.0	2.3	—
	Capture rate, CM (hours)	—	—	—	1.2	1.0	0.9	0.5	0.7	—
	Capture rate, EI (hours)	—	—	—	0	0.2	0.6	1.1	0.5	—
	Capture rate, total (hours)	—	—	—	1.2	1.2	1.5	1.6	1.2	—
All islands combined										
	Sample days[b]	9	11	24	24	27	45	42	48	4
	Sample hours	—	—	—	49.4	39.5	62.6	66.6	75.9	5.9
	No. of green turtles	14(0)	12(0)	40(1)	45(4)	47(11)	109(13)	127(29)	181(45)	25(4)
	No. of hawksbill turtles	3(0)	4(1)	3(0)	0(0)	3(1)	9(1)	10(1)	10(2)	0(0)
	No. of turtles, total	17(0)	16(0)	43(1)	45(4)	50(12)	118(14)	137(30)	191(46)	25(4)
	Capture rate, CM (days)	1.6	1.1	1.7	1.9	1.8	2.4	3.0	3.8	6.3
	Capture rate, EI (days)	0.3	0.4	0.1	0	0.1	0.2	0.3	0.2	0
	Capture rate, total (days)	1.9	1.5	1.8	1.9	1.9	2.6	3.3	4.0	6.3
	Capture rate, CM (hours)	—	—	—	0.9	1.2	1.7	1.9	2.4	4.2
	Capture rate, EI (hours)	—	—	—	0	0.1	0.2	0.2	0.1	0
	Capture rate, total (hours)	—	—	—	0.9	1.3	1.9	2.1	2.5	4.2

Note: Numbers without parentheses are total captures, inclusive of recaptures; numbers in parentheses are recaptures. CM, *Chelonia mydas*, green turtle; EI, *Eretmochelys imbricata*, hawksbill turtle). Capture rates include recaptured turtles. Survey dive start and end times were not documented consistently between August 2006 and July 2008; thus hourly capture rates are not available for that period.

[a] Partial year (2-month period).

[b] Sample day is defined as a single day on the water (or at least 1 hr but not exceeding 4 hr total dive time in a single day).

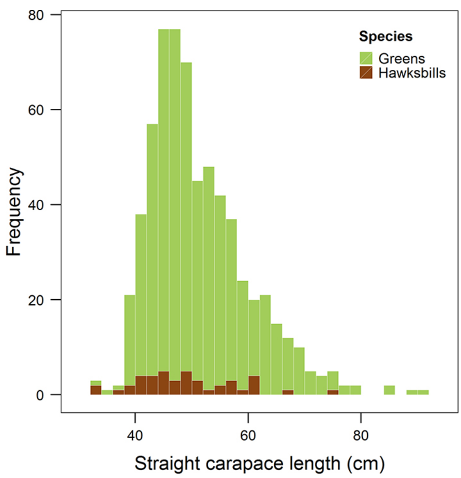

FIGURE 3. Frequency (number of turtles) distribution of straight carapace length for green and hawksbill turtles captured in the CNMI from August 2006 to February 2014. Data for Saipan, Tinian, and Rota were combined (recaptures excluded). For green turtles, the mean straight carapace length (SCL) was 51.6 cm ± 9.1 (range, 33.6–91.6 cm; $n = 493$). For hawksbill turtles, the mean SCL was 49.7 cm ± 9.6 (range, 32.5–74.3 cm; $n = 36$).

between Saipan and Rota for green or hawksbill turtles. Green turtle body mass values were 19.8 kg ± 12.1 ($n = 407$) for Saipan and 17.9 kg ± 7.7 ($n = 34$) for Rota ($t = 1.32$, df = 48, $P = .193$). Hawksbill turtle mean mass values were 19.2 kg ± 14.1 ($n = 8$) for Saipan and 11.8 ± 6.6 ($n = 17$) for Rota ($t = 1.40$, df = 8, $P = .198$). The sample sizes used in these tests were smaller than those used for SCL, because weight measurements were not taken from August 2006 to August 2008.

Recapture intervals ranged from 10 months to 6.1 yr, with median recapture intervals for Rota and Saipan ranging from 1.3 to 2.3 yr, respectively. Within the 50–60 cm length bin, green turtle growth rates were significantly greater on Saipan than they were on Rota (Welch's t test: $t = -10.43$, df = 29, $P < .01$). Therefore, we did not include the Rota recaptures in our analysis of growth rate across length bins. Saipan turtles had a significant difference in growth rates across the different length bins (one-way ANOVA: $F = 4.61$, df = 2, $P = .014$). The Tukey-Kramer HSD suggested that growth rates in the 50–60 cm length bin were significantly higher than those in the 40–50 cm bin on Saipan (q-stat = 1.281, df = 56).

Results from the GAM model of annual growth rate and the cubic B-spline smooths for size-specific growth rate are summarized in Figure 4. For the GAM model: deviance explained = 37.7%; generalized cross validation score = 1.75; R-squared (adjusted) = 0.325; intercept term = 3.11 (standard error = 0.16; significant); estimated degrees of freedom = 2.0, 1.9, and 1.0 for the smooth terms for recapture interval, recapture year, and SCL midlength, respectively; the smooth terms for recapture interval and SCL midlength were significant. For the cubic B-spline smooth when allowing *smooth.spline* to optimize parameters: degrees of freedom = 3.6; generalized cross validation score = 0.62. Model variations forced with fewer degrees of freedom were confirmed to have higher cross validation scores (providing a poorer fit) and were therefore disregarded as suboptimal. From the cubic B-spline smooth for size-specific growth rate (Figure 4*A*), mean residency time for CNMI juvenile green turtles was estimated to be 17 yr with a 95% confidence interval of 13 to 24 yr.

Throughout the 7.6 yr study, tag retention was nearly 100% (Inconel, 98%; Titanium, 100%; PIT 99%), confirming that double- and triple-tagged turtles would remain individually identifiable for extended periods. Recapture intervals for 55 green turtles at Balisa, Saipan, ranged from 10 months to 6.1 yr, and absolute growth increments ranged from 0.9 cm/yr to 5.8 cm/yr (average midlength = 51.3 ± 6.0 cm SCL) (Table 2). Three hawksbill turtles were recaptured: one at Balisa, Saipan, with a recapture interval of 4.3 yr and absolute growth rate of 4.4 cm/yr (average midlength = 51.5 cm SCL); and two on Rota (Jerry's Reef and Sasanlagu), with recapture intervals of 10.5 months to 1.3 yr and growth rates of 2.9 cm/yr to 5.6 cm/yr (average midlength = 52.6 ± 10.8 cm SCL). Recapture intervals for six green turtles at Puntan Poña, Rota, ranged from 1.0 to 2.2 yr and absolute growth increments ranged from 0.3 cm/yr to 1.1 cm/yr (average midlength = 54.6 ± 4.2 cm SCL), respectively. An adult

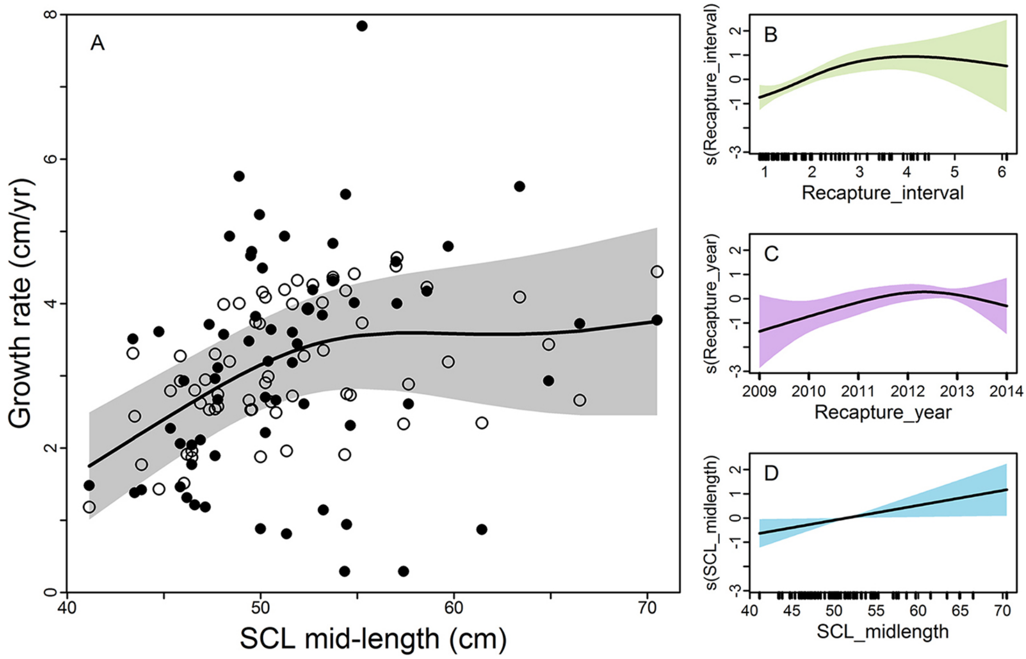

Figure 4. Estimated size-specific growth rate function for green turtles in the CNMI, based on 64 turtles recaptured on Saipan and Rota from July 2007 to September 2014. (*A*) The solid curve is a cubic B-spline smooth fitted to the fitted GAM model values for annual growth rate (○), with the estimated 95% confidence band shaded; observed data (●) are shown for comparison. [GAM methods for growth rates as applied by Seminoff et al. (2002)]. A graphical summary of the fitted GAM model is shown in *B*–*D*; the *y*-axis shows annual growth rate (response variable) on a centered smoothed function scale with 95% confidence bands. Covariates on the *x*-axis are (*B*) recapture interval in years, (*C*) calendar year of recapture, and (*D*) mean straight carapace length (SCL) between first capture and recapture. Deviance explained, 37.7%; generalized cross validation score, 1.75; R-squared (adjusted) = 0.325; intercept term = 3.11 (standard error = 0.16; significant); estimated degrees of freedom = 2.0, 1.9, and 1.0 for the smooth terms in *B*–*D*, respectively; the smooth terms in *B* and *D* were significant. From the fitted smooths in *A*, mean residency time for CNMI juvenile green turtles was estimated at 17 yr (13–24 yr, 95% confidence interval).

green turtle originally tagged by CNMI Department of Lands and Natural Resources (DLNR) Sea Turtle Program staff during nesting surveys was recaptured during near-shore surveys. This female was last observed on her sixth and final nesting event for the season at Obyan beach, Saipan, on 14 June 2012 and was recaptured 215 days later at Balisa, Saipan, only 15.8 km from the nest (following an estimated path along coastline reef systems from nesting site to foraging site). Because this adult was recaptured less than 10 months from the primary tagging date, it was not included in growth rate calculations, but its absolute growth was 0.4 cm/yr (91.6 cm SCL).

Algae samples recovered from three foraging green turtles captured on Saipan were identified as *Amansia rhodantha*. This species of marine algae has not previously been identified as a food source for turtles within the nearshore waters of Saipan, Tinian, or Rota (Kolinski et al. 2001, 2004, 2006) or as a representative green turtle diet item (Hirth 1997, Russell and Balazs 2000, Arthur and Balazs 2008). Algae sampled from 43 other green turtles from Saipan and Rota were identified as *Amansia glomerata*, Order Gelidiales, *Gelidiella acerosa*, *Gelidiella myrioclada*, *Hypnea spinella*, and *Ceramium* sp. One hawksbill turtle on Rota was captured with food in its mouth; however, the sample was extremely small and

TABLE 2

Growth Rate (ΔL/Δt) and Midlength $(L_1 + L_2)/2$ Calculated from Green Turtle Growth Data Divided into 10 cm Straight Carapace Length (SCL) Data Bins

Length Bin (Island)	Avg. Midlength (cm SCL)	SD	Avg. Growth Rate (cm yr^{-1})	SD	*n*
40–50 (Saipan)	46.8	2.2	2.87	1.35	28
40–50 (Rota)	50.0	—	0.88	—	1
50–60 (Saipan)	53.5	2.8	3.79	1.32	26
50–60 (Rota)	54.1	2.5	0.63	0.42	3
60–70 (Saipan)	65.0	1.6	4.09	1.38	4
60–70 (Rota)	61.5	—	0.87	—	1
70–80 (Saipan)	70.5	—	3.77	—	1
All recaptures	51.5	5.7	3.11	1.53	64

Note: For each group (length bin) the standard deviations (SD) and total number of measurements (*n*) are given. Data are from recaptures on Saipan and Rota; no recaptures occurred on Tinian. In the 50–60 cm length bin, the growth rate was significantly higher on Saipan than it was on Rota (Welch's *t* test: $t = -10.43$, df = 29, $P < .01$). Saipan turtles had a significant difference in growth rates across the different length bins (one-way ANOVA: $F = 4.61$, df = 2, $P = .014$). A Tukey-Kramer HSD test suggested that growth rates in the 50–60 cm length bin were significantly higher than those in the 40–50 cm bin (*q*-stat = 1.28, df = 56).

could be identified only as Rhodophyta. In addition, hawksbill turtles were directly observed foraging on sponges (unidentified species) before capture.

Capture sites were characterized by water depths of 4–30 m and distances from shore of 30–2,000 m. Turtles captured on Saipan ($n = 548$) were primarily associated with coral habitat (93%), followed by uncolonized sandy substrate (5%), coralline algae (0.4%), macroalgae (0.7%), sea grass (0.2%), and turf (0.2%) (Table 3, Figure 2). Turtles captured on Tinian ($n = 15$) were also mostly associated with coral habitat (60%), followed by coralline algae (20%), turf (13%), and unknown substrate (7%) (Table 3, Figure 2). Turtle-habitat associations on Rota ($n = 62$) differed, with 47% of captures associated with coralline algae, 45% with coral, and 8% with macroalgae habitat (Table 3, Figure 2). Benthic habitat results are biased for effort, because surveys were performed largely over coral patch reefs where turtles were historically known by local fishermen and divers to be present.

Turtles were observed resting (60.7%), foraging (26.3%), swimming (12.3%), and hovering at cleaning stations (0.7%) ($n = 537$ observations). Cleaning stations are defined as specific locations where turtles hover to receive symbiotic cleaning services of fish such as the bluestreak cleaner wrasse (*Labroides dimidiatus*), which rid the turtles of parasites (Losey et al. 1994). A broad assessment of turtle activity according to habitat (e.g., turtles feeding in coral habitats; $n = 342$) is provided in Figure 5. The dominant activities were resting (47%), foraging (28%), and swimming (13%) over coral.

Data from 85 recaptured turtles (75 on Saipan and 10 on Rota), all of which were green turtles except two hawksbill turtles on Saipan and three on Rota, suggest foraging site fidelity. The mean distance between first and last capture position of individual green turtles was 0.48 km (SD = 0.31; range, 0.09–1.35 km) on Saipan and 0.12 km (SD = 0.14; range, 0.02–0.44 km) on Rota. The mean time interval between capture and recapture of green turtles was 614 days (SD = 491; range, 22–2,224 days) on Saipan and 452 days (SD = 203; range, 120–799 days) on Rota. The mean distance between first and last capture position of two hawksbill turtles on Saipan was 0.30 km (SD = 0.09; range, 0.23–0.36 km); for three hawksbill turtles in Rota waters it was 0.23 km (SD = 0.17; range, 0.07–0.42 km). The mean time interval between captures for Saipan hawksbill turtles was 886 days (SD = 1006; range, 175–1,597 days); for Rota hawksbill turtles it was 226 days (SD = 100; range, 117–314 days).

TABLE 3

Summary of Benthic Habitats Used by Foraging and Resting Turtles on Saipan, Tinian, and Rota, CNMI

Location	Biological Cover	Geomorphological Structure	Cover Type	% Cover	Zone Type	Number and Species of Turtles[a]
Balisa, Saipan	Coral reef and hard bottom	Aggregated patch reef	Coral	10%–<50%	Bank/shelf	249 CM, 10 EI
	Coral reef and hard bottom	Aggregate reef	Coral	10%–<50%	Bank/shelf and fore reef	32 CM, 1 EI
	Coral and hard bottom	Aggregate reef	Macroalgae	10%–<50%	Lagoon	1 CM, 1 EI
	Coral reef and hard bottom	Pavement	Coral	10%–<50%	Bank/shelf and fore reef	8 CM, 2 EI
	Unconsolidated sediment	Sand	Uncolonized	90%–100%	Bank/shelf	22 CM, 0 EI
	Unconsolidated sediment	Sand	Sea grass	90%–100%	Lagoon	2 CM, 0 EI
Lao Lao Bay, Saipan	Coral reef and hard bottom	Spur and groove	Coral	10%–<50%	Bank/shelf	9 CM, 0 EI
	Coral reef and hard bottom	Pavement	Coral	10%–<50%	Bank/shelf	11 CM, 1 EI
	Coral reef and hard bottom	Pavement	Coralline algae	10%–<50%	Reef crest	1 CM, 0 EI
	Coral reef and hard bottom	Aggregate reef	Coral	10%–<50%	Bank/shelf	8 CM, 0 EI
	Unconsolidated sediment	Sand	Uncolonized	90%–100%	Bank/shelf	1 CM, 0 EI
Puntan Poña, Rota	Coral reef and hard bottom	Pavement	Coral	10%–<50%	Bank/shelf	23 CM, 2 EI
	Coral reef and hard bottom	Pavement	Macroalgae	10%–<50%	Bank/shelf	4 CM, 2 EI
Sasanhaya Bay, Rota	Coral reef and hard bottom	Spur and groove	Coralline algae	10%–<50%	Bank/shelf	3 CM, 7 EI
Sasanlagu, Rota	Coral reef and hard bottom	Aggregated patch reef	Coralline algae	10%–<50%	Bank/shelf	3 CM, 3 EI
	Coral reef and hard bottom	Pavement	Coralline algae	10%–<50%	Bank/shelf	3 CM, 3 EI
Teteto, Rota	Coral reef and hard bottom	Spur and groove	Coral	10%–<50%	Bank/shelf	0 CM, 1 EI
Tachungnya Bay, Tinian	Coral reef and hard bottom	Aggregate reef	Coral	10%–<50%	Bank/shelf	2 CM, 0 EI
Barcinas Cove, Tinian	Coral reef and hard bottom	Spur and groove	Coral	10%–<50%	Bank/shelf	1 CM, 0 EI

[a] CM, *Chelonia mydas*, green turtle; EI, *Eretmochelys imbricata*, hawksbill turtle.

DISCUSSION

A Nearshore Foraging Population Dominated by Juveniles

Size distributions of captured green and hawksbill turtles suggest that the nearshore waters of the CNMI provide developmental and foraging habitat for these species. SCL ranged from 32.5 to 91.6 cm (both species combined), with juveniles (mean SCL = 50.7 cm) composing the majority (99%) of captures. Regional comparisons can be made with the southern Great Barrier Reef (Limpus and Reed 1985, Limpus 1992), Sabah, Malaysia (Pilcher 2010), and the Hawaiian Archipelago (Balazs 1982), where 78% to 100% of nearshore populations consist of juvenile turtles. The results of this mark-recapture study also corroborate findings from previous towed-diver surveys around Saipan, Tinian, and

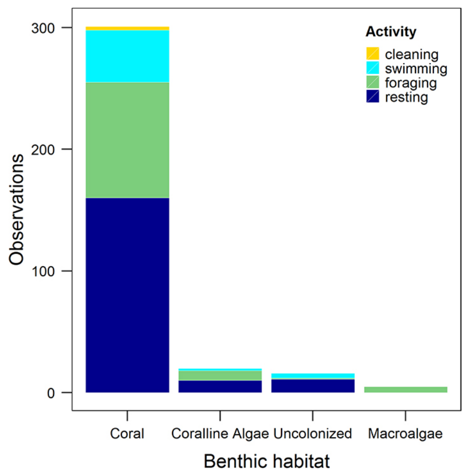

Figure 5. Turtle activity in relation to benthic habitat ($n = 342$ observations). Data for Saipan, Tinian, and Rota were combined.

Rota, where juvenile turtles dominated observations (Kolinski et al. 2001, 2004, 2006). Regionally, the preferred developmental habitat for this size class has been described as shallow (<20 m) coral reefs, which provide abundant food sources (macroalgae and sponges) and structured cover from predators (Musick and Limpus 1997). Shallow lagoon and barrier/patch reef systems are encountered most often along leeward sides of Saipan (with the exception of Lao Lao Bay), Tinian, and Rota and provide suitable developmental habitat for juveniles.

The capture of hawksbill turtles in this study documents their presence in the southern islands of the CNMI, because past aquatic surveys reported only green turtles (Pultz et al. 1999, Kolinski et al. 2001, 2004, 2006). Although Kolinski et al. (2006) questioned the importance of Rota as turtle habitat, this study suggests that Rota is indeed important, particularly for hawksbill turtles. A turtle captured on Rota was 10 times more likely to be a hawksbill turtle than a turtle captured on Saipan; likewise, the capture rate (turtles per dive hour) for hawksbill turtles was 10 times greater on Rota than it was on Saipan. These findings suggest that Rota's relative contribution to supporting foraging turtles, particularly critically endangered hawksbill turtles, may be important and distinct for the region. Future studies could investigate the relative abundance of hawksbill diet items across islands to determine whether Rota provides preferred foraging habitat.

The overall low numbers of adult observations ($n = 19$) suggest that the free-diving technique did not inherently bias or limit adult capture rates within the areas surveyed. The juvenile-dominated captures ($n = 638$) in this nearshore study are not surprising. We would expect to observe this population size structure on a nearshore reef because (1) juvenile turtles experience an ontogenetic shift from open-ocean habitats to coastal habitats at approximately SCL ≥ 35 cm, and (2) late-stage subadults migrate out of coastal foraging habitats and return to nesting rookeries at approximately SCL ≥ 74–78 cm. In addition, the results from this study are similar to those of previous surveys conducted in the CNMI (Kolinski et al. 2001, 2004, 2006) in that juvenile turtle observations were predominant.

Life History of CNMI Foraging Turtles

Juvenile green and hawksbill turtles recruit to benthic foraging habitats in the Pacific region at a minimum CCL of approximately 35 cm (Bjorndal 1997, Musick and Limpus 1997, Seminoff et al. 2002, Arthur et al. 2008, Jones and Seminoff 2013). In this study, capture of newly recruited juvenile green turtles in the nearshore waters of Saipan totaled six individuals with sizes ranging from 36.1 to 40.0 cm (CCL). The three smallest hawksbill turtles captured on Saipan and Rota (34.1, 34.9, and 40.0 cm CCL) were also within the established recruitment size range. These captures demonstrate that the CNMI is an important region for settlement and recruitment of juvenile green and hawksbill turtles; ongoing efforts to capture newly recruited turtles (<40 cm CCL) will provide further support for this finding.

The life history of these foraging turtles before arrival and postdeparture from CNMI waters is poorly understood. The natal origins of CNMI recruits remain largely unknown, but recent genetic analysis suggests that the green turtles may originate from nesting beaches in the Marshall Islands and the Federated States of Micronesia (Dutton et al. 2014). The study reported here found that green and hawksbill turtles typically depart the nearshore environment at ≥78.3 cm and ≥74.3 cm SCL, respectively; however, a small portion of nesting turtles may use the nearshore habitats as postnesting foraging grounds. Previous biotelemetry studies revealed that postnesting green turtles migrate from Saipan to the Philippines (total distance traveled = 2,391 km) and Okinawa, Japan (total distance traveled = 2,441 km) (Summers 2011). Recapture of an adult female in Saipan nearshore waters 8 months after it was originally flipper tagged on a Saipan nesting beach suggests that Saipan may also serve as one of several different foraging grounds for green turtles.

Growth Rates and Residency Times

Growth rates of sea turtles are largely influenced by age, sex, diet, physiology, geographic location, and temperature of their feeding habitat (Hirth 1997, Balazs and Chaloupka 2004). Green and hawksbill turtles foraging in the nearshore waters of Saipan maintained mean growth rates of 3.35 cm/yr ($n = 55$) and 4.41 cm/yr ($n = 1$), respectively. For green turtles, the observed rates were consistent with those observed in central Hawaiian waters (Balazs and Chaloupka 2004, Van Houtan et al. 2014). Mean growth rates of juvenile Hawaiian green turtles ranged from 0.96 cm/yr to 5.28 cm/yr in SCL (Balazs and Chaloupka 2004, Van Houtan et al. 2014), and those of juvenile Saipan green turtles ranged from 0.94 cm/yr (average midlength 54.5 cm SCL; at large 11.5 months) to 5.76 cm/yr (average midlength 48.9 cm SCL; at large 3.2 yr). The single hawksbill turtle recaptured at Balisa, Saipan, had an absolute growth rate of 4.41 cm/yr (average midlength 51.5 cm SCL; at large 4.4 yr). Although the sample size was limited, this growth rate falls within the average range (2.24 to 4.77 cm/yr SCL) estimated for Hawaiian hawksbill turtles using skeletochronology (Snover et al. 2013) and is comparable with those of the same size class on Monito Island, Puerto Rico (Diez and van Dam 2002). A greater number of recaptures will provide better insight into CNMI hawksbill turtle growth rates and foraging site fidelity.

Green turtles grew three to four times faster on Saipan than they did on Rota. Growth rates of six green turtles recaptured on Rota ranged from 0.29 cm/yr (average midlength 54.4 cm SCL; at large 1.4 yr) to 1.14 cm/yr (average midlength 53.3 cm SCL; at large 2.2 yr). The slower growth rates from Rota more closely resembled those for similarly sized juvenile green turtles in the Northwestern Hawaiian Islands (1.1–1.4 cm/yr SCL), Galápagos Islands (0.29–1.60 cm/yr SCL), and Australia (0.75–0.95 cm/yr CCL) (Limpus and Walter 1980, Balazs 1982, Green 1993). In Puerto Rico, growth rates are affected by substantial differences in habitat quality across islands, with rates varying an average of 2.1 times between neighboring island aggregations (Diez and van Dam 2002). In our study, faster growth rates observed for green turtles on Saipan versus Rota, coupled with greater hawksbill turtle abundance on Rota versus Saipan, may suggest substantial differences in habitat quality between islands. Further examination of the quality of foraging habitat among the three CNMI islands will allow for a more complete comparison.

Sea-surface temperatures around the main inhabited islands of the CNMI (27°C–30°C) provide a developmental habitat where green turtles can reside year-round. This is evident from the occurrence of multiple recaptures in the same localized feeding area of Balisa, Saipan, spanning nearly a decade. Based on predicted growth rates, green turtles recruiting to Saipan at 35 cm SCL are estimated to reach maturity 17 yr later (13–24 yr; 95% confidence). Seminoff et al. (2002, 2003) found a similar maturation age for green turtles (nearly 20 yr) in Baja, Mexico. Using growth rates and survival estimates that included mortality from human impacts, Seminoff et al. (2003) found the likelihood of turtles reaching adulthood and reproducing to be low. Juvenile turtles in the CNMI may face a similar outlook. CNMI stranding and salvage recovery data indicate that juveniles compose the majority (91%) of targeted take

(CNMI Department of Lands and Natural Resources 2006, 2009, 2011, 2013*a*, 2013*b*) with a mean SCL of 55.4 cm (min: 37.3 cm, max: 102 cm, $n = 44$) (CNMI Department of Lands and Natural Resources 2006, 2009, 2011, 2013*a*, 2013*b*). The long juvenile life stage estimated here may have implications for fecundity, exposure to harvest, and ultimately recovery of the population.

Habitat Associations and Diet Items

Captured turtles were most commonly associated with coral habitat when total captures across the three islands were examined, but the strength of this association decreased from north to south (Saipan to Rota). In contrast, association of captures with coralline algae habitat increased from Saipan to Rota. This either reflects differences in habitats that were accessible for sampling or suggests differences in habitat quality across the islands, which may be related to the differences in green turtle growth rates and hawksbill turtle abundances observed between Saipan and Rota.

The diet samples ($n = 44$) were solely from the oral cavity at the time of capture. The bulk of samples (95.7%) contained *Amansia* sp., and 12.8% of samples contained *Gelidiella* sp. Both *Amansia* sp. and *Gelidiella* sp. macroalgae have been shown to have high nutritional quality (Rubenstein and Wikelski 2003, McDermid et al. 2007) for marine reptiles. As important sources of energy and protein, CNMI turtles may be selecting these particular macroalgae over other diet items that are abundant in the region (Kolinski et al. 2001, 2004, 2006). However, 99% of diet samples were taken from turtles captured at the Balisa, Saipan, site. Sampling from multiple feeding grounds, coupled with gastric lavage techniques, could provide greater insight into CNMI turtle diets. Additional information on nutritional resources around Rota could also help explain the slower green turtle growth rate observed in this study. Continued diet studies throughout the CNMI will be important for determining the ecological roles and carrying capacities of green and hawksbill juvenile turtles.

CONCLUSIONS

In this study, we analyzed 7.6 yr of hand-capture survey data from the CNMI to understand population demographics and habitat use for green and hawksbill turtles, both of which are endangered in this region. We showed that CNMI green turtles may remain resident for 17 yr (13–24 yr; 95% confidence) and that the local populations of both species are juvenile-dominated with high site fidelity, which could lead to repeated exposure to anthropogenic threats. Unfortunately, populations with delayed maturation and long residency times could take many years to recover, despite complete protection (Seminoff et al. 2003). However, within the Mariana Archipelago there is evidence for potential recovery of once-exploited sea turtle populations given adequate protections and enforcement, with localized increases observed on Guam (Martin et al. 2016). Diurnal enforcement and youth education efforts have been prevalent in the CNMI since 2006, and future efforts should focus on nocturnal/holiday enforcement patrols and long-term conservation outreach strategies that target adult communities in local villages.

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