



Endangered Green Turtles (*Chelonia mydas*) of the Northern Mariana Islands: Nesting Ecology, Poaching, and Climate Concerns

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Marine turtles in the western Pacific remain threatened by anthropogenic impacts, but the region lacks long-term biological data for assessing conservation status and trends. The Central West Pacific (CWP) population of green turtles (*Chelonia mydas*) was listed as Endangered by the U.S. in 2016, highlighting a need to fill existing data gaps. This study focuses on the subset of this population nesting in the Commonwealth of the Northern Mariana Islands (CNMI). Using 11 years of nesting data, we (i) estimate reproductive demographic parameters, (ii) quantify abundance and trends, and (iii) estimate the impacts of anthropogenic threats, such as poaching of nesting females and increasing sand temperatures. In 2006–2016, nesting beach surveys, identification tagging, and nest excavations were conducted on Saipan, and rapid assessments of nesting activity were conducted on Tinian and Rota. On Saipan, temperature data-loggers were deployed inside nests and evidence of poaching (adults and eggs) was recorded. This study documents year-round nesting with a peak in March–July. Nester abundance for the three islands combined was 11.9 ± 5.7 (mean \pm standard deviation) females annually, with at least 62.8 ± 35.1 nests observed per year. For 39 tagged individuals, straight carapace length was 95.6 ± 4.5 cm, remigration interval was 4.6 ± 1.3 years, and somatic growth was 0.3 ± 0.2 cm/yr. Reproductive parameter estimates included clutch frequency of 7.0 ± 1.3 nests per female, inter-nesting interval of 11.4 ± 1.0 days, clutch size of 93.5 ± 21.4 eggs, incubation period of 56.7 ± 6.4 days, hatching success of $77.9 \pm 27.0\%$, and emergence success of $69.6 \pm 30.3\%$. Mean nest temperature of $30.9 \pm 1.5^\circ\text{C}$ was above the pivotal threshold of 29.0°C for temperature dependent sex determination, suggesting a female bias may already exist. Model results suggest (i) hatching success decreases and embryonic death increases when nests experience maximum temperatures beyond 34.4°C and 33.8°C , respectively, and (ii) embryonic death increases in nests with mean temperatures beyond 31.1°C . On Saipan, 32% of nesters were poached, reducing the annual population growth rate from 11.4 to 7.4%. This study provides the first comprehensive assessment of a nesting green turtle population in the Mariana

Archipelago, as well as Micronesia, providing baseline data for the endangered CWP population. Our reproductive demographic data, abundance trends, and anthropogenic threat impact analyses are critical for endangered species management, including assessments of population status and fisheries impacts.

Keywords: Central West Pacific, sea turtles, population assessment, nesting demographic data, nest temperature, climate change, embryonic death

INTRODUCTION

Green sea turtles (*Chelonia mydas*) are ubiquitous throughout tropical and sub-tropical waters and have been of conservation concern for decades (Witherington and Ehrhart, 1989; Jackson et al., 2001; Broderick et al., 2006; Chaloupka et al., 2008; Wallace et al., 2011). Their life-history traits (e.g., long-lived, late maturation, highly migratory) make them vulnerable to anthropogenic impacts on land and at sea (Lutcavage et al., 1997; Jackson et al., 2001; Lewison et al., 2004; McClenachan et al., 2006). While many populations of green turtles have seen remarkable post-exploitation recoveries in recent decades (e.g., 285% increase at Ascension Island and 417% in Costa Rica; Troëng and Rankin, 2005; Broderick et al., 2006) some regions have sub-populations that are still in decline or are too data-limited to assess (McClenachan et al., 2006; Seminoff et al., 2015). A global review of green turtle populations (IUCN 2017, ongoing), recommendations to implement regional management units (Wallace et al., 2010), and a U.S. status review of green turtles (Seminoff et al., 2015) all suggest that distinct populations (e.g., geographically separated, genetically distinct) exist and have differing conservation status and trends based on nesting numbers. Specifically, the recent status review under the U.S. Endangered Species Act suggested that eleven distinct population segments (DPS) exist for green turtles worldwide (Seminoff et al., 2015). Several regions, such as the North Atlantic (i.e., Florida, Gulf of Mexico, and Caribbean) and Central North Pacific (i.e., Hawaii) have populations with recovering trajectories that are listed as Threatened; however, populations in a few regions, including the Central West Pacific (CWP; i.e., Micronesia to the Ogasawara Islands, Japan) are listed as Endangered and have declining or data-limited populations (Seminoff et al., 2015).

Like all marine turtles, green turtles are tied to land for ovipositioning, making them more readily accessible to observation on land than at sea. Counts of nesting turtles and the associated demographic parameters (e.g., remigration interval, clutch frequency, hatching success) are therefore particularly important in assessments of population status and trends. Nesting demographic parameters vary by region and population, but adult females typically return to their natal beach to nest every 2–6 years (Witherington and Ehrhart, 1989; Trono, 1991; Limpus, 2009; Balazs et al., 2015), replenishing energy stores at distant foraging grounds in non-nesting years. In one nesting season, they typically deposit three to six nests (Mortimer and Carr, 1987; Witherington and Ehrhart, 1989; Suganuma et al., 1996) over 2–3 months, returning to the water for 10–20 day inter-nesting intervals (Balazs et al., 2015) to rest and mate between nesting events. Nests contain roughly 80–120

eggs (Pilcher and Basintal, 2000; Limpus, 2009) and take 50–90 days to incubate (Balazs et al., 2015). Ovipositioning on land makes marine turtles highly susceptible to poaching and introduced predators (e.g., pigs, dogs; Lutcavage et al., 1997). The nest environment and sex-determination (i.e., temperature-dependence) makes them vulnerable to climate impacts through population feminization and embryonic death with increasing temperatures (Packard et al., 1977; Miller, 1985; Standora and Spotila, 1985; Mrosovsky, 1994; Ackerman, 1997; Fuentes et al., 2010). Understanding the nesting demographics and threats for each population facilitates assessment of its reproductive output, conservation status, and resilience to anthropogenic impacts.

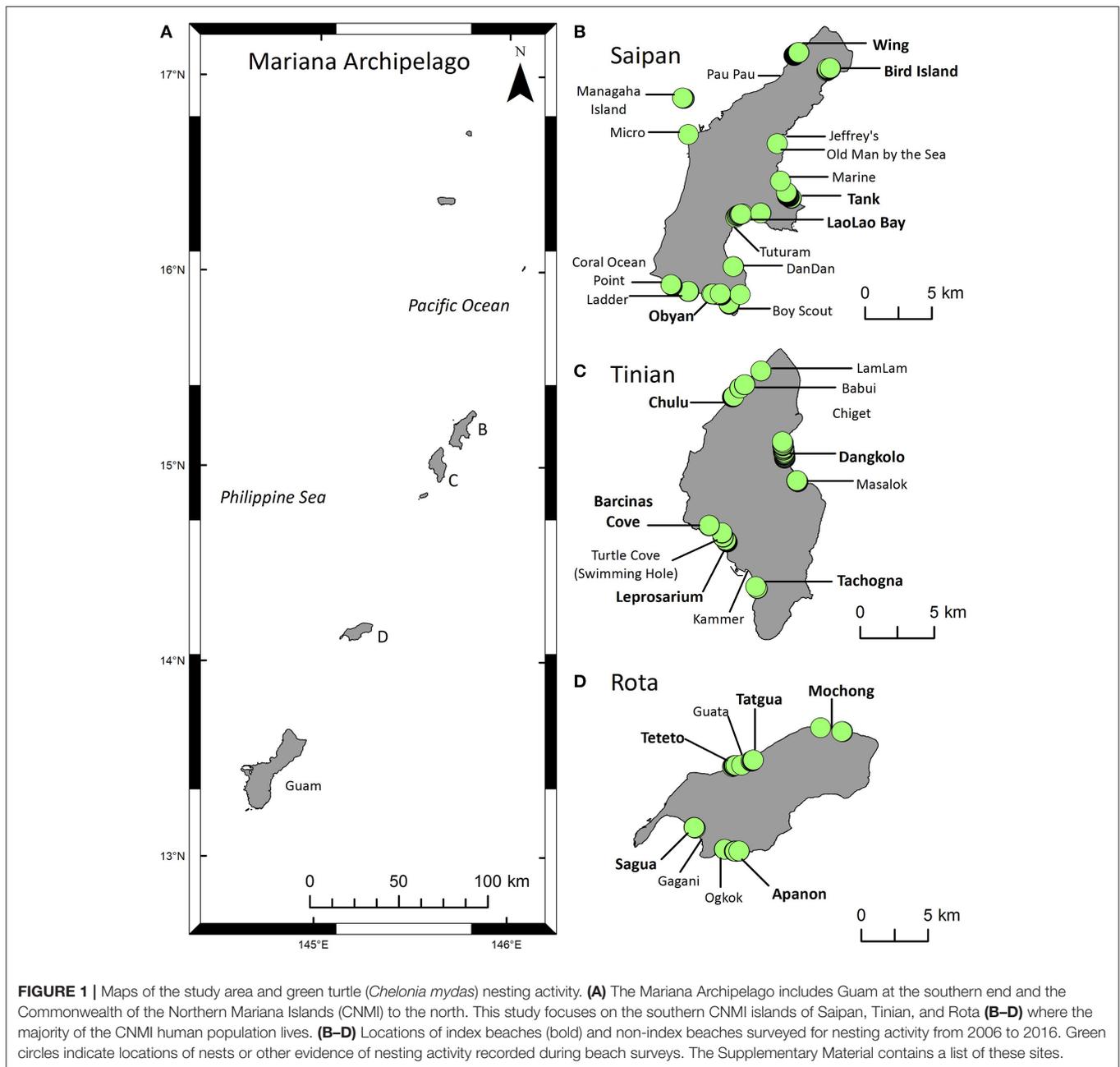
Green turtles in the insular western Pacific remain impacted by anthropogenic threats (Seminoff et al., 2015), yet a lack of long-term ecological data in the region makes it difficult to assess conservation status and trends (Martin et al., 2016). The CWP population of green turtles was listed as Endangered under the U.S. Endangered Species Act (ESA) because it was data deficient in large portions of its range and exploitation of green turtles in the region was well-known (Seminoff et al., 2015). Prior to this study, the extent to which sea turtles used CNMI terrestrial habitats was based on short-term surveys conducted over 1 year or less (Pultz et al., 1999; Kolinski et al., 2001). Here, we summarize an 11-year research effort to characterize the nesting ecology of green turtles in the Commonwealth of the Northern Mariana Islands (CNMI).

The primary goals of this study were to (i) estimate reproductive demographic parameters of this nesting population (e.g., clutch frequency, remigration interval, and hatching success), (ii) quantify abundance and trends of nesting females, (iii) estimate the impacts of anthropogenic threats, such as poaching and increasing sand temperatures. This study provides the first comprehensive characterization of a nesting green turtle population in the Mariana Archipelago, as well as Micronesia more broadly, and provides a baseline for a portion of the Endangered CWP population. These demographic data serve a critical role in endangered species conservation and management, including assessments of population status, trends, and fisheries impacts.

METHODS

Study Area

The CNMI comprises 14 islands of the Mariana Archipelago, located in the western Pacific Ocean along the eastern boundary of the Philippine Sea (Figure 1). This study focuses on the southernmost islands of the CNMI (Saipan, Tinian, and Rota), comprising 6% of the nesting sites for the CWP DPS. These



tropical islands are located approximately 2,200 km east of the Philippines and 2,300 km southeast of Japan. Saipan (15.25°N, 145.75°E) is 122 km² and hosts 89% of CNMI residents (48,220 people; CNMI Dept. Of Commerce 2010). Tinian (15.00°N, 145.62°E) hosts the next largest population of 3,136 residents (CNMI Dept. Of Commerce 2010) on 102 km². Rota (14.15°N, 145.21°E) is 85 km² and supports 2,527 residents (CNMI Dept. Of Commerce 2010).

These islands have a distinct rainy (typhoon) season in July–November and a dry season in January–May (Carruth, 2003). Mean rainfall is 200 cm/yr and mean temperature is 20–32°C (Stafford et al., 2002). The beaches are primarily made of medium to coarse-grained calcareous sand, gravel,

and coral rubble (Eldredge and Randall, 1980). In a few places, streams flow from high, interior lands to the coastline, where they deposit volcanic material (Eldredge, 1983) and create finer, darker beach sediments (e.g., Apanon beach on Rota). Beach length ranges from 0.01 to 3.35 km, and beaches are often narrow and segmented into small pockets by raised limestone (Eldredge, 1983). Saipan has 26 beaches of various sizes including the largest beaches of the three islands, Tinian has 13 beaches all < 0.5 km in length (Pultz et al., 1999), and Rota has 16 small pocket beaches. This study included five index beaches on each island, plus various non-index beaches per island (**Figure 1**, Supplementary Table 1).

Nesting Surveys

Surveys to monitor nesting activity and nester abundance were conducted by local biologists at index and non-index beaches (Figure 1). A “survey” includes monitoring effort conducted on a single beach in a single day (or overnight); five beaches surveyed in 1 day represents five surveys. Non-index beaches were surveyed intermittently, primarily when there were public reports of nesting activity. On Saipan, where the field team was located, index beaches were surveyed as regularly as possible from 2006 to 2016, both diurnally to record all nesting activity and nocturnally to tag nesting females. Survey effort fluctuated annually, with diurnal surveys typically conducted 2–5 days per week over 6–12 months per year. Surveys on Rota and Tinian (2009–2016) were limited to diurnal rapid assessments (1–5 days each) conducted 1–2 times per year toward the end of the nesting season, and rare nocturnal tagging surveys. See Supplementary Table 1 for a summary of the years and locations of data collection incorporated into each metric described below.

Diurnal surveys were performed on foot during morning hours (06:00–11:30) along the edge of vegetation and high tide lines. All turtle crawls from the previous night(s) were recorded. Species and crawl identification followed Pritchard and Mortimer (1999) and the “Sea Turtle Identification Key” (www.seaturtle.org 2005). Nesting and non-nesting emergences were differentiated by examining crawl signs (e.g., presence/absence of escarpment, primary/secondary body pits, and thrown sand) and verifying the presence of eggs in suspected nests (Schroeder and Murphy, 1999). On Saipan index beaches, body pits and abandoned egg chambers were recorded as non-nesting emergences only if there were fresh tracks accompanying them. On Rota and Tinian, signs of non-nesting emergence were recorded even when fresh tracks were not present, as tracks become weathered over time and surveys were infrequent. Locations of nests and non-nesting emergences were recorded using a handheld GPS device.

Nocturnal tagging surveys were conducted during anticipated emergence periods. Nesters were tagged and measured after they completed oviposition and began backfilling the nest with sand. Turtles were double-marked with either titanium (Stockbrands Co. Pty Ltd, large size) or Inconel tags (National Band & Tag Co, 681C), with one tag attached proximally and adjacent to the first large scale on the posterior edge of each front flipper (Balazs, 1999). Passive integrated transponder (PIT) tags were applied from March 2009 onward. Turtles’ flippers were scanned for the presence of PIT tags with a Biomark Pocket Reader[®] PIT tag scanner. If no PIT tags were found, then a single PIT tag was injected subcutaneously into one of the hind flippers using a 12-gauge disposable hypodermic needle and applicator.

Standard measurements were recorded. 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) were measured at the widest point (Bolten, 1999). Measurements were taken to the nearest millimeter using forester calipers (S-882 00 Haglof, Sweden) for straight measurements and a flexible tape measure for curved measurements. Prior to March 2009, only the curved measurements were taken. We converted CCLs to SCLs using

a conversion equation specified for CNMI green turtles in Summers et al. (2017).

Nesting season length and peak were estimated on Saipan. Season length was determined through consistent survey effort on index beaches 2–3 days per week for 1 year (January 2012–January 2013). Dates of the first and last nests were recorded, along with the date of the last nest inventoried (see methods below). Season peak was evaluated using the mean number of nests laid per month across all years (except 2008 due to reduced effort during peak months).

Nesting periodicity was estimated at inter- and intra-annual scales on Saipan. Remigration interval, the number of years between nesting seasons, was calculated for recaptured turtles. Inter-nesting interval was estimated as the number of days between one successful nesting event and the start of the next nesting attempt within a season, even if the next landing was a non-nesting emergence (Alvarado and Murphy, 1999). This calculation only included data from 2011 to 2013, as monitoring effort during that period was intensified to ensure that nesters were directly observed each time they emerged.

Clutch frequency (number of nests per female within a season) was estimated using Saipan data from 2011 to 2016, when emergence schedules were tracked closely enough to attribute specific nests to individual nesters, even if the nester was not directly observed each time. Females included in this calculation were physically encountered at least twice in the season to confirm their emergence schedule and ensure particular nests were attributed correctly to specific individuals (Alvarado and Murphy, 1999). Turtles that were poached prior to their final nesting attempt were not included in this calculation.

Threats were assessed during surveys and nest excavations by quantifying: (1) nesters and nests poached (or nearly poached) by humans (details below), (2) nests depredated by predators (details below), (3) nests inundated by water caused by tropical storms, typhoons, and storm-water drainage from beach erosion, (4) nests with hatchling emergence success negatively impacted by roots of invasive vegetation and large pieces of coral rubble, and (5) human disturbance activities. We counted turtles as poached if at least one of the following lines of evidence were present: (1) crawl tracks emerging from the water but not returning, (2) human activity at the nest, such as digging, foot prints, and/or vehicle tracks, (3) a drag mark (indentation in the sand/vegetation) from flipping the turtle over at the nest and dragging it to the nearest parking lot or foot path, (4) discarded tools at the nesting site, including ropes and pallets, or (5) emergence tracks wiped away by humans, presumably to disguise a poaching event, typically in conjunction with missing return tracks and cessation of future nesting by a female that was expected to have additional nesting events in the season. Nests were considered poached if they were confirmed to be present and had evidence of human removal of eggs (e.g., digging and broken shells), sometimes accompanied by signs that the nester was also poached. For depredated nests, we determined predator type as follows: (1) monitor lizards on Rota left evidence of digging (or were observed digging), drag marks from their tails, large holes into nest chambers, egg shells strewn about on top of the nest, and/or eggs eaten within the chamber, (2) crabs left crab

sized holes into the chamber and shells outside/on top of the nest, and (3) ants left tiny holes in the eggs, but the eggs remained in the chamber, and ants were sometimes observed in the nest.

Nest Excavations

Nests were marked for post-incubation triangulation and excavation by attaching labeled aluminum tags (Forestry Suppliers, 79260) and survey flagging to vegetation in two locations a measured distance away. Aluminum tags and triangulation methods began in 2012; prior to that, nests were marked using natural landmarks. Cryptic nest marking techniques are necessary in the CNMI due to the threat of egg poaching.

Nests were excavated 3 days after the first evidence of hatching was observed on diurnal surveys (except in rare cases when there was a 2–3 week logistics delay). When no hatching was evident, nests were inventoried on the 70th day after the original observation date. Only nests which showed obvious signs of hatching were inventoried during rapid assessments of Tinian and Rota. Incubation periods were estimated as the number of days between oviposition and hatching (the date primary hatching evidence was observed), using data from 2012 to 2013 on Saipan.

We examined and categorized the contents of each nest following Miller (1999). Categories included: (i) E = emerged hatchlings (departed/departing from nest); (ii) S = shells (empty shells counted if >50% intact); (iii) L = live hatchlings (remaining among shells; assumed to have missed the window for successful emergence); (iv) D = dead hatchlings (outside shell but dead); (v) UD = undeveloped eggs (unhatched with no obvious embryo); (vi) UH = unhatched eggs (with obvious embryo); (vii) UHT = unhatched term eggs (fully developed in egg shell or pipped); (viii) P = depredated eggs (open, nearly complete shell with egg residue). Reproductive output metrics were calculated as:

$$\text{Total clutch size} = E + L + D + UD + UH + UHT + P$$

$$E = S - (L + D)$$

$$\text{Hatching success (\%)} = [S / (S + UD + UH + UHT + P)] \times 100$$

$$\text{Emergence Success (\%)} = [(S - (L + D)) / (S + UD + UH + UHT + P)] \times 100$$

Nester Abundance and Trends

We estimated annual nester abundance for Saipan using the nocturnal tagging survey data, as every nester was either tagged or identified through nesting activity. For Tinian and Rota, where only diurnal rapid assessments were feasible, we divided total observed nests by mean clutch frequency to estimate the number of nesters (Alvarado and Murphy, 1999). We summed these island-specific estimates for each year (except 2008 due to a lack of survey effort during peak nesting months) to estimate annual nester abundance for all three islands combined.

For Saipan, we estimated the population growth rate (PGR) using a log linear regression of annual nester counts ($\ln[\text{nesters}]$) as a function of untransformed year. We used the total number

of nesters observed each year, regardless of whether they were eventually poached that year. Data from 2008 were excluded here as well (see above comment). We estimated the 95% confidence interval, *p*-value ($\alpha = 0.05$), and R-squared goodness-of-fit.

Recognizing that poaching of nesters occurred throughout the study period, we let the analysis above represent the population trend with poaching and conducted a second analysis to estimate PGR without poaching. For nesters that were poached in a given year, we added them back into the annual counts for subsequent years as if they had not been poached, and ran the regression on the increased annual counts. Our analysis (i) assumes the poached nesters had the mean remigration interval determined by this study, (ii) ignores natural mortality, as annual survivorship for adult green turtles in the Pacific can be as high as 0.95–0.98 (Chaloupka, 2002; Seminoff et al., 2003) and the analysis only pertains to a short 10-year period, and (iii) assumes 100% of poaching was detected, which is likely true for this study period based on the overall low numbers, limited nesting habitat, small island community, and consistent monitoring efforts. We interpret the difference between the PGR estimates for the two scenarios—“with poaching” and “without poaching”—to represent the estimated impact of poaching on the nester abundance trend.

Climate Impacts

Nest temperatures were measured using HOBO temperature data loggers (Onset Computer Corporation, Pocasset, MA) on Saipan beaches (primarily index beaches) between mid-November 2012 and mid-September 2016. Loggers were set to record temperature every hour and deployed inside the egg chamber, with an identification tag attached by monofilament line or parachute cord (Layton, 2011). They were retrieved during nest excavations and transported back to the office, where the data were downloaded using HOBOWare Pro software version 3.2.2 (Onset Computer Corp. 2002–2011). We removed the first and last 7 days of temperature data from each logger due to uncertainty associated with logistical field challenges (e.g., possible time lags between the logger being switched on and deployment, or retrieval and the logger being switched off after transport). This conservative decision minimizes the influence of temperature fluctuations associated with deployment and retrieval, and retains the most relevant incubation data.

We developed generalized additive models (GAMs; Hastie and Tibshirani, 1990) to explore the influence of nest temperature on reproductive success. We constructed several models, each with Hatching Success or Embryonic Death (proportion of eggs that were unhatched, UH, or unhatched term, UHT) as the response variable and combinations of Nest Temperature (mean and maximum), Beach, Year, and Month as predictor variables. All predictor variables were ordinal, except Beach was categorical. Although we were interested exclusively in Nest Temperature as a known mechanistic driver of reproductive success, the other predictors served to control other sources of variation in the response variables to isolate the influence of temperature as much as possible. We estimated the models using data from Saipan nests for which we had both temperature

logger data (nest temperatures throughout incubation) and excavation data (hatching success and embryonic death).

We constructed and compared models in a forward step-wise manner in three stages, adding one predictor variable to the best model at each stage and selecting a new model to carry forward, similar to Ortiz et al. (2016). We included Beach in all models to capture inherent but unmeasured differences across sites (e.g., beach slope, length and width, sand grain size, rainfall, moisture, vegetation, shade, etc.) that may influence Hatching Success and Embryonic Death. We used standard selection criteria—Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC)—to evaluate competing models within each stage (Ortiz et al., 2016). In general, models with low AIC and BIC values and high Deviance Explained are considered the best. We selected the model with the lowest AIC and BIC values within each stage, without comparing it to previous stages. In the final stage, we confirmed that the selected model both included a Nest Temperature predictor and had higher Deviance Explained than models from previous stages with the same Nest Temperature predictor if the AIC/BIC values were similar (within 3 points for AIC and 7 points for BIC). We used this selection process because our intention was to examine the functional form of the relationship between Nest Temperature predictors and Hatching Success or Embryonic Death, not to develop the absolute best model for either response variable. We used the “mgcv” (mixed GAM computation vehicle) package in R for this analysis; “mgcv” is a routine that optimizes the degrees of freedom of the fitted GAM (Wood, 2017). We defined the models with the beta regression family of data distributions (“betar”), a “logit” link function appropriate for data in which the response is a proportion (0–1), and a cubic smoothing spline limited to 4 knots. We performed these analyses and produced figures in the R statistical computing environment (R Core Team, 2014; Version 3.1.2).

RESULTS

Nesting Ecology

Over 11 years (2006–2016), there were 5,427 diurnal surveys on index beaches on Saipan, 102 on Tinian, and 64 on Rota (Table 1). On Saipan, where effort was most intense, there was a mean of 493 diurnal surveys per year ($sd = 217$; range = 59–782), or 99 surveys per beach per year ($sd = 43$; range = 3–161). Nocturnal tagging surveys on index beaches totaled 467 on Saipan, 9 on Tinian, and 10 on Rota (Table 1). See Supplementary Table 2 for additional details on survey effort, including a summary by island, index beach, and year.

Green turtles nest year-round in the CNMI, as documented by observations of nests, hatchlings, and nesting females. Peak nesting occurred between March and July (91% of Saipan nests) with a mean of 6.5 nests laid per month ($sd = 4.5$; range = 1–18) during peak months. Nest deposition starts in mid-November of one calendar year and ends late August of the next, with hatchlings emerging into early November.

There were 364 total nests observed on Saipan (mean of 36 nests per year; $sd = 15$; range = 18–64; excludes 2008 due to missing survey effort in peak months), 156 nests on Tinian (22 nests per year; $sd = 15$; range = 1–42), and 113 on Rota (16 nests per year; $sd = 12$; range = 4–36) (Table 1). A total of 199 non-nesting emergences (NNEs) were observed on Saipan (22 NNEs per year; $sd = 16$; range = 2–48), 47 on Tinian (8 NNEs per year; $sd = 6$; range = 1–14), and 31 on Rota (6 NNEs per year; $sd = 3$; range = 4–11) (Table 1). Numbers for Tinian and Rota are likely biased low compared to Saipan due to lower levels of survey effort. For example, in years with frequent or intense tropical storms/typhoons we found little to no evidence of nesting on Tinian or Rota, as most signs of nesting had been inundated by high water by the time beaches were surveyed.

We tagged and measured a total of 39 nesters combined on Saipan ($n = 34$), Tinian ($n = 3$), and Rota ($n = 2$). Mean SCL was 95.6 cm ($sd = 4.5$; range = 81.0–103.6 cm; $n = 39$), mean SCW was 75.0 cm ($sd = 4.6$; range = 59.2–85.0; $n = 29$), mean CCL was 102.2 cm ($sd = 4.7$; range = 87.1–111.3; $n = 38$), and mean CCW was 92.5 cm ($sd = 4.9$; range = 76.7–103.2; $n = 38$) (Table 2). Ten nesters recaptured on Saipan in 2010–2016 (initial SCL: mean = 95.6 cm; $sd = 2.6$; range = 91.2–99.8) exhibited a mean absolute growth rate of 0.3 cm/yr ($sd = 0.2$; range = 0–0.7) (Table 2).

Remigration interval for the 10 recaptured nesters was 1.9–5.9 years (mean = 4.6; $sd = 1.3$) (Table 2). One turtle tagged on Obyan Beach in May 2012 was recaptured only 8.5 months later during in-water reef surveys at Balisa (west coast of Saipan) in January 2013, and then again during nocturnal nesting surveys in March 2014 (1.9 years from initial capture). These encounters suggest this turtle may be a resident forager. The short remigration interval may be explained by the lack of a long-range migration between nesting years and the associated conservation of energy.

Inter-nesting interval was 11.4 days (median = 11 days; $sd = 1.0$; range = 10–13; $n = 16$ nesters) (Table 2). Turtles whose normal nesting periodicity was disturbed by human activities (examples below) re-emerged post-disturbance 14–18 days after their last nesting event.

Mean clutch frequency was 7.0 nests per female per season ($sd = 1.3$; range = 5–10) observed across a mean 5 nesters per year on Saipan ($sd = 2$; range = 3–7; $n = 28$ nesters) for 2011–2016 (Table 2). Mean incubation duration was 56.7 days ($sd = 6.4$; range = 46–70; $n = 41$ nests); this estimate may be biased high since diurnal surveys were not performed 7 days a week.

We excavated 396 nests combined on Saipan ($n = 291$), Tinian ($n = 49$), and Rota ($n = 56$) and estimated a mean clutch size of 93.5 eggs ($sd = 21.4$; range = 32–186; Table 2). Hatching success was 77.9% ($sd = 27.0$; range 0–100) across the three islands but lower on Saipan (74.8%) where the sample size was highest (Table 2 and Supplementary Table 3). Saipan also had a lower emergence success (64.0%) than the three-island mean of 69.6% ($sd = 30.3$; range = 0–100; Table 2 and Supplementary Table 3). High variation in hatching success is possibly attributed to inundation and accompanying erosion from storms, depredation by crabs, ants, and monitor lizards, and temperature variations, as described below.

TABLE 1 | Summary of annual green turtle (*Chelonia mydas*) nesting activity on the islands of Saipan, Tinian, and Rota in the Commonwealth of the Northern Mariana Islands (CNMI), 2006–2016.

Year	2006	2007	2008	2009	2010	2011	2012	2013	2014	2015	2016	Total
SAIPAN												
Diurnal surveys	59	316	782	505	309	404	425	645	692	726	564	5,427
Nocturnal surveys	4	13	2	29	15	49	79	68	74	54	80	467
Nests	24	29	*5	19	18	31	41	40	39	54	64	364
NNEs	0	2	*2	7	11	12	28	44	24	21	48	199
Nesters	8	4	*1	6	5	6	9	8	8	12	11	78
Poached nesters	4	1	1	4	2	1	6	2	1	1	2	25
Poaching attempt	0	1	0	0	0	0	0	0	1	0	0	2
New nesters	8	4	1	6	2	4	5	7	4	6	7	54
% New nesters	100%	100%	100%	100%	40%	67%	56%	88%	50%	50%	64%	69%
TINIAN												
Diurnal surveys	0	0	0	5	3	4	2	9	22	42	15	102
Nocturnal surveys	0	0	0	0	0	0	0	0	0	5	4	9
Nests	nd	nd	nd	38	0	1	22	16	10	27	42	156
NNEs	nd	nd	nd	1	0	0	8	13	1	10	14	47
Nesters	^1	nd	nd	5	0	1	3	2	2	5	6	25
Poached nesters	nd	nd	nd	2	0	0	0	0	0	0	1	3
Poaching attempt	nd	nd	nd	0	0	0	0	0	1	0	0	1
ROTA												
Diurnal surveys	0	0	0	3	3	10	8	12	8	14	6	64
Nocturnal surveys	0	0	0	0	0	0	0	0	0	10	0	10
Nests	nd	nd	nd	13	4	5	27	36	0	15	13	113
NNEs	nd	nd	nd	4	0	0	6	11	0	5	5	31
Nesters	nd	nd	nd	2	0	1	3	5	0	3	3	14

Diurnal and nocturnal survey effort from index beaches is summarized for context. Survey, monitoring effort conducted on a single beach in a single day (or overnight); NNEs, non-nesting emergencies (e.g., false crawls, body pits, and abandoned egg chambers); New nesters, neophyte nesters (untagged or first time observed nesting; Saipan only); % New nesters, percentage of annual nesters that were neophytes; Poaching attempt, harvest thwarted by researchers or enforcement; nd, no data collected. ^no surveys between May 20, 2008 and July 13, 2008. ^nester reported by Tinian wildlife enforcement officials.

Nest excavations revealed low levels of egg predation. Crabs depredated 5% of nests, destroying a mean of 3 eggs per nest ($sd = 3$; range = 0–13). Ants impacted 3% of nests, consuming a mean of 16 eggs per nest ($sd = 32$; range = 0–94). Monitor lizards depredated 2% of nests, devouring a mean of 17 eggs per nest ($sd = 22$; range = 0–57). One percent of nests showed evidence of egg predation by an unknown source, with 4 eggs lost per nest ($sd = 6$; range = 1–13).

Egg poaching accounted for the loss or partial loss of at least 8% of nests on Saipan, 4% on Tinian, and 2% on Rota. Direct take of a hatchling was also documented when a juvenile green turtle (CCL = 17.5 cm) was surrendered to wildlife enforcement by a Saipan resident in 2008. The turtle had been taken from a Saipan beach and raised as a family pet from hatchling size. These poaching observations should be interpreted as minimum values.

Inundation and accompanying erosion from tropical storms, typhoons, and storm-water drainage impacted 9% of nests excavated on Saipan, resulting in a low mean emergence success of 37% ($sd = 34$; range = 0–96). Inundation of excavated nests was not characterized on Tinian and Rota. Nests completely washed out by storms comprised 2% of observed nests on Saipan, 3% on Rota, and 8% on Tinian.

On Saipan, we observed hatchlings trapped inside the nest under introduced vegetation (i.e., *Leucaena leucocephala*, *Cassytha filiformis*, *Casuarina equisetifolia*, and *Cynodon nlemfuensis*) or coral rubble in 10% of excavated nests. This problem affected a mean 26 hatchlings per nest ($sd = 24$; range = 1–101) or 28% of the clutch ($sd = 23$; range = 1–92). Emergence success for these nests was low at 53% ($sd = 26$; range = 3–90). Entrapment observations were not typically possible on Tinian or Rota due to the lower survey frequency, but there was one documented case on Tinian.

Coral rubble, rocky substrate, and roots also impacted nesters by impeding their excavation of egg chambers. Abandoned egg chambers accounted for 29% of NNEs on Saipan, 40% on Tinian, and 32% on Rota. Two extreme cases were observed on Babui Beach, Tinian and Obyan Beach, Saipan where seven and eleven abandoned egg chambers (respectively) were documented within a single crawl each.

Human disturbance of nesters was observed in association with several activities, including camping, building bonfires, driving on the beach, using flashlights, and fishing nearshore with submersible lights. At least one type of disturbance was recorded during 8% of nocturnal surveys on Saipan. Typically, these disturbances prevented nesters from emerging on their

TABLE 2 | Reproductive parameters for green turtles (*Chelonia mydas*) nesting in the Commonwealth of the Northern Mariana Islands (CNMI) on Saipan, Tinian, and Rota islands.

	CNMI	Hawaii, USA	Rose Atoll, Am. Samoa	Turtle Islands, Philippines	Great Barrier Reef, Australia	Ogasawara, Japan	Malaysia
References	This study	Balazs et al., 2015	NMFS unpub. 2013	[1] Trono, 1991 [2] Burton, 2012	[1] Limpus, 2009 [2] Limpus et al., 2003 [3] Fuentes et al., 2010 [4] Limpus and Chaloupka, 1997	[1] Suganuma et al., 1996 [2] Abe et al., 2003	Pilcher and Basintal, 2000
SCL (cm)	$n = 39$ 95.6 ± 4.5 (81.0–103.6)	90.7 (75–106)	94.7	NR	NR	95.2 ± 4.5 (83–108) [1]	NR
CCL (cm)	$n = 38$ 102.2 ± 4.7 (87.1–111)	97.0 (78–113)	NR	99.5 [1]	107 ± 5.5 (91–124) [1]	NR	98.5 ± 6.0 (68–121)
Remig. interval (yr)	$n = 10^\dagger$ 4.6 ± 1.3 (1.9–5.9)	4 (2–9)	NR	2.5 [1]	5.8 ± 1.5 (1–9) [1]	3.7 ± 0.6 (max 6) [2]	2.4 ± 0.8 (1.0–4.3)
Clutch freq. (nests per year)	$n = 28^\dagger$ 7.0 ± 1.3 (5–10)	4 (1–9)	NR	5 [2]	5.1 ± 2.0 (1–9) [1]	4.1 (max 6) [1]	2.7 ± 0.8
Inter-nesting Int. (days)	$n = 16^\dagger$ 11.4 ± 1.0 (10–13)	13.2 (11–18)	NR	14.5 [1]	14.1 ± 1.7 (9–21) [1]	(11–12) [2]	15.5 ± 6.2 (5–30)
Incubation (days)	$n = 41^\dagger$ 56.7 ± 6.4 (46–70)	64.5 (54–88)	NR	54.3 [1]	64.5 ± 6.1 (54–87) [1]	NR	53.1 ± 4.2 (40–69)
Clutch size (eggs)	$n = 396$ 93.5 ± 21.4 (32–186)	104 (38–145)	NR	95.6 [1]	115.2 ± 27.9 (42–195) [1]	102 ± 26.2 (4–183) [1]	87.3 ± 21.9 (4–164)
Hatching success (%)	$n = 396$ 77.9 ± 27.0 (0–100)	76.7 (0–100)	NR	87.1 [1]	79.6 ± 15.0 (20.4–100) [2]	NR	NR
Emergence succ. (%)	$n = 396$ 69.6 ± 30.3 (0–100)	70.8 (0–97.6)	NR	85.7 [1]	78.6 ± 15.2 (19.4–100) [2]	NR	NR
Nest temperature (°C)	$n = 184^\dagger$ 30.9 ± 1.5 (27.6–34.9)	(23.2–29.8)	NR	NR	$29.0 \pm 0.04^*$ [3]	NR	NR
Somat. growth (cm/yr)	$n = 10^\dagger$ 0.3 ± 0.2 (0–0.7) SCL	NR	NR	NR	0.12 ± 0.04 (SE) CCL [4]	NR	0.8 CCL

Values are Mean \pm SD (range). Values from other sites within the western Pacific are provided for context. Relevant regional locations include Hawaii (Balazs et al., 2015), American Samoa (NMFS unpub. data 2013), Philippines (Trono, 1991; Burton, 2012), Australia (Limpus and Chaloupka, 1997; Limpus et al., 2003; Limpus, 2009; Fuentes et al., 2010), Japan (Suganuma et al., 1996; Abe et al., 2003), and Malaysia (Pilcher and Basintal, 2000). SCL, straight carapace length; CCL, curved carapace length; Somat. growth, somatic growth rate observed or modeled from recaptured nesters; † samples were collected on Saipan only (vs. on all three islands for other parameters); NR, not reported by the study. *Fuentes et al. (2010) sand temperature value (measured at nest depth) for Raine Island, with 0.5°C increase added for metabolic heating in nests.

expected return dates and caused them to nest after the activity was no longer a threat or to nest on adjacent (smaller) pocket beaches with sub-optimal habitat. On a few occasions, a nester was disturbed on the beach or could not find suitable habitat during nesting attempts (i.e., impedance by rocks or roots) and switched to a different nesting beach within a season. Most nesters, however, were only observed to nest on a single nesting beach.

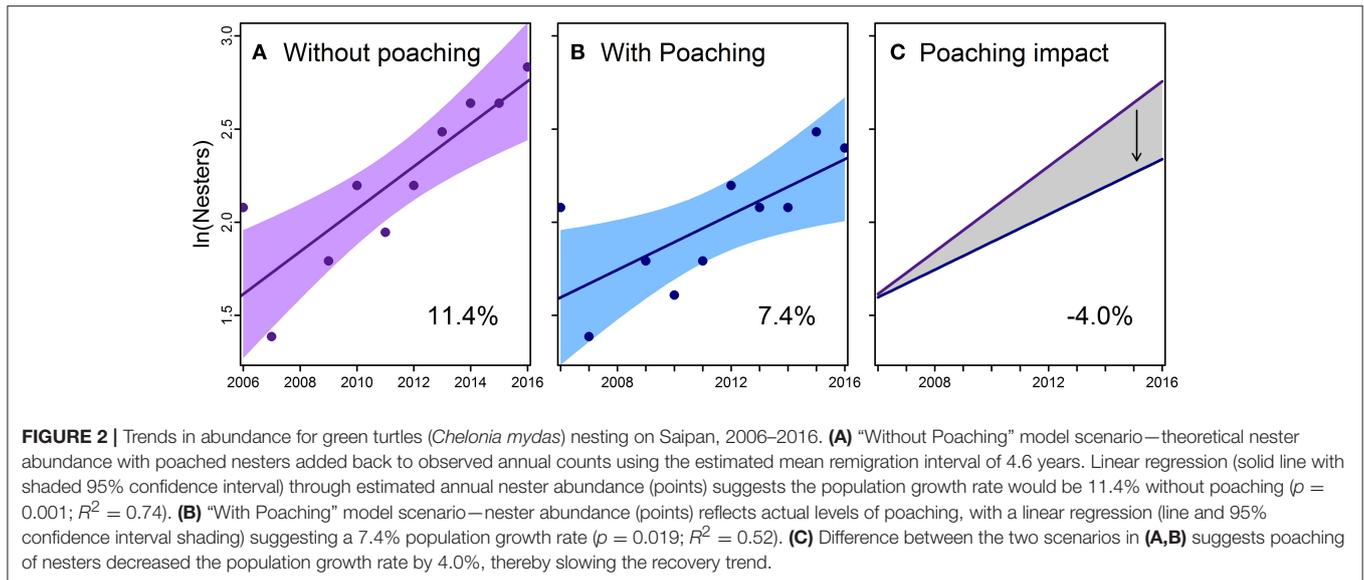
Nester Abundance and Trends

Over 11 years, we recorded 78 nesters on Saipan (7.7 ± 2.5 annual nesters; range = 4–12), 25 on Tinian (3.1 ± 1.9 annual nesters; range = 1–6), and 14 on Rota (2.8 ± 1.3 annual nesters; range = 1–5) for a combined total of 117 nesters (11.9 ± 5.7 annual nesters; range = 4–20) (Table 1). Similar to the numbers of nests and non-nesting emergences, nester abundance estimates for Tinian and Rota are likely biased low due to the relative infrequency of survey effort. Poachers removed 25 females from Saipan (32%) and at least 3 from Tinian (12%); no poaching of nesters was documented on Rota (Table 1). Attempts to

poach at least 2 additional nesters from Saipan and 1 from Tinian were thwarted (Table 1). Neophyte nesters (previously untagged) comprised 40 to 100% of annual nesters, with an overall mean of 69.2% across all years and 59.1% for 2010–2016 only, the period after one remigration interval had passed and thus remigrants could be expected. The estimated PGR for Saipan's nesting population was 11.4% when adding the poached nesters back into the population at the mean remigration interval of 4.6 years ($p = 0.001$; $R^2 = 0.74$) (Figure 2A). However, PGR decreased to 7.4% per year when accounting for observed levels of poaching for 2006–2016 ($p = 0.019$; $R^2 = 0.52$) (Figure 2B).

Climate Impacts

We deployed a total of 246 temperature loggers in Saipan nests in 2012–2016 and successfully retrieved 184 loggers that had at least 7 days of data each. This included 174 loggers from index beaches (Table 3) plus 10 loggers from non-index beaches (Supplementary Table 4). Mean nest temperature was $30.9 \pm 1.5^\circ\text{C}$ (index beach range = 27.6–34.2; non-index beach range =



29.1–34.9; **Table 3** and Supplementary Material). Maximum nest temperature was $33.5 \pm 2.0^\circ\text{C}$ (range = 29.2–42.6).

For our modeling exercise, there were 89 nest temperature loggers with corresponding data on hatching success and embryonic death that were suitable for use. Results from our model selection process are summarized in **Table 4** and the smoothed responses to the predictors in the best models are illustrated in **Figure 3**.

For Hatching Success, the model with the lowest AIC and BIC was in Stage I with Beach and Year as predictors; however, adding Month to that model in Stage II increased Deviance Explained by 2% for a negligible increase in AIC and BIC (**Table 4**). In Stage III, adding Maximum Nest Temperature was better than adding Mean Nest Temperature, as evidenced by a 10% higher increase in Deviance Explained along with clearly lower AIC/BIC scores (**Table 4**). Although some models in Stages I and II had lower AIC/BIC values, we selected the model with Maximum Nest Temperature in Stage III as the best model because it had the overall highest Deviance Explained (57%) and included temperature, our variable of interest (**Table 4**; **Figures 3A–C**). This model (“Model 1”) suggests (i) an annual decrease in hatching success until 2015 and a subtle increase thereafter, (ii) a slight maximum in hatching success in May–July, and (iii) hatching success increases with maximum nest temperature up to 34.4°C , after which it decreases (**Figures 3A–C**).

For Embryonic Death, in Stage I the model with the lowest AIC and BIC included Beach and Year as predictors; however, this model had the lowest Deviance Explained (**Table 4**). Adding Month in Stage II increased the Deviance Explained by 3% while maintaining similar values for AIC/BIC (**Table 4**). In Stage III, adding Mean Nest Temperature or Maximum Nest Temperature yielded similar results, with Mean Nest Temperature offering 1% higher Deviance Explained (29%) but almost identical values for AIC/BIC. For this reason, we considered both models as the best. The model with Mean Nest Temperature (“Model 2”) suggests (i) a steady increase in

embryonic death over the years, (ii) lowest embryonic death between May and July, and (iii) a pronounced increase in embryonic death with mean nest temperatures beyond 31.1°C (**Figures 3D–F**). The model with Maximum Nest Temperature (“Model 3”) suggests (i) embryonic death has increased annually since 2012, (ii) highest embryonic death in February through April, and (iii) embryonic death decreases with maximum nest temperatures up to 33.8°C , and increases sharply beyond that (**Figures 3G–I**).

DISCUSSION

Nesting green turtles in the CNMI are part of the Endangered CWP DPS for which a major knowledge gap exists (Seminoff et al., 2015). Data on nesting ecology, population abundance and trends, direct human impacts, and climate impacts are critical for conducting population status assessments. Understanding these aspects of the population will facilitate science-based management and help direct conservation efforts both locally and regionally. Our 11-year study provides the first comprehensive characterization of this nesting population, filling in those major data gaps in demographic parameters and providing quantitative evidence of the current impact of poaching and the looming threat of rising temperatures.

Nesting Ecology

The reproductive demographic parameters estimated in this study fall within the ranges established for other green turtle populations in the western and central Pacific. Parameter estimates (mean \pm *sd* and range) for several other nesting locations in the region (Hawaii, American Samoa, Australia, Philippines, and Malaysia) are provided in **Table 2** for context. Relative to those populations, CNMI nesters appear to be medium-sized with an intermediate remigration interval. Their SCL of 95.6 ± 4.5 cm and CCL of 102.2 ± 4.7 cm fall between low values observed in Hawaii (Balazs et al., 2015) and high ones

TABLE 3 | Temperature logger data (°C) from green turtle (*Chelonia mydas*) nests on Saipan index beaches, 2012–2016 (*n* = 174 loggers).

		2012	2013	2014	2015	2016	All years
Tank Beach	Mean	30.8	32.0	31.6	31.4	31.8	31.7
	<i>sd</i>	1.9	2.1	1.7	2.1	2.0	1.4
	Range	27.2–36.2	24.8–42.6	26.8–35.9	28.0–36.8	26.8–36.5	24.8–42.6
	N = loggers	7	24	14	3	24	72
	D = points	9,020	24,977	15,949	2,877	25,911	78,734
Obyan Beach	Mean	30.2	–	31.0	29.7	31.2	30.7
	<i>sd</i>	1.5	–	1.7	1.5	1.4	1.2
	Range	27.4–35.3	–	28.2–36.3	26.8–35.4	25.5–34.9	25.5–36.3
	N = loggers	10	–	15	5	3	33
	D = points	8,626	–	15,081	6,512	2,777	32,996
Bird Island	Mean	31.4	30.5	–	29.8	–	30.4
	<i>sd</i>	1.6	1.0	–	1.4	–	1.1
	Range	27.7–34.6	28.5–34.3	–	26.2–34.7	–	26.2–34.7
	N = loggers	7	4	–	14	–	25
	D = points	5,000	3,979	–	16,837	–	25,816
LaoLao Bay	Mean	–	–	29.5	30.0	31.5	30.7
	<i>sd</i>	–	–	0.7	1.3	1.8	1.2
	Range	–	–	25.5–30.3	26.7–35.1	24.5–36.2	24.5–36.2
	N = loggers	–	–	1	4	5	10
	D = points	–	–	1,179	4,194	5,077	10,450
Wing Beach	Mean	29.8	–	30.0	29.1	30.3	29.9
	<i>sd</i>	1.9	–	1.1	1.8	2.2	1.4
	Range	26.4–36.8	–	27.6–31.8	25.2–34.0	25.9–36.0	25.2–36.8
	N = loggers	11	–	2	9	12	34
	D = points	12,123	–	2,589	11,798	13,099	39,609
All Index Beaches	Mean	30.6	31.8	31.3	29.9	31.3	30.9
	<i>sd</i>	1.4	1.5	1.1	1.1	1.4	1.5
	Range	27.9–33.4	27.8–34.1	29.2–32.9	27.7–33.4	27.6–34.2	27.6–34.2
	N = loggers	35	28	32	35	44	174
	D = points	34,769	28,956	34,798	42,218	46,864	187,605

“–”, no data; either no loggers deployed or loggers were lost or washed out by storms or tidal inundation. Summary data for loggers include (i) mean hourly nest temperature (standard deviation), (ii) range of nest temperatures, (iii) N = number of loggers, and (iv) D = number of hourly temperature data points. Mean and standard deviation values for “All Years” and “All Index Beaches” were calculated from the mean temperatures of individual loggers. See Supplementary Material for additional data from non-index beach nests and from loggers placed in the sand at nest depth to characterize ambient temperatures.

from the Great Barrier Reef in Australia (Limpus, 2009). Their remigration interval of 4.6 ± 1.3 yr falls between shorter intervals from the Philippines and Japan (Trono, 1991; Abe et al., 2003) and longer ones from Australia (Limpus, 2009).

Within one season, CNMI nesters lay a relatively high number of nests, deposit a low number of eggs in each nest, and spend a short period of time in the water between nesting events. Clutch frequency of 7.0 ± 1.3 nests per year for CNMI is the highest observed mean for the region (Suganuma et al., 1996; Limpus et al., 2003; Limpus, 2009; Burton, 2012; Balazs et al., 2015), but it falls within the ranges observed in Hawaii and Australia (Limpus, 2009; Balazs et al., 2015). Inter-nesting interval of 11.4 ± 1.0 days is on the short end of observed intervals from the other locations, and is most similar to Japan (Abe et al., 2003). Clutch size of 93.5

± 21.4 eggs falls between smaller clutches observed in Malaysia (Pilcher and Basintal, 2000) and larger ones in Australia (Limpus, 2009).

Nests in the CNMI incubate relatively quickly and have hatching and emergence success comparable to other locations. The incubation period of 56.7 ± 6.4 days is low, similar to values observed in the warm climates of the Philippines and Malaysia (Trono 1991; Pilcher and Basintal, 2000), and shorter than those in the cooler climates in Hawaii and Australia (Limpus, 2009; Balazs et al., 2015). Hatching success of $77.9 \pm 27.0\%$ and emergence success of $69.6 \pm 30.3\%$ are within the ranges for the region (Trono, 1991; Limpus et al., 2003; Balazs et al., 2015), but potentially on the low end. Future studies could test whether these parameters are negatively impacted by (i) higher frequency

TABLE 4 | Generalized additive models (GAMs) exploring the influence of nest temperatures (mean and maximum during incubation) on hatching success and embryonic death for green turtle (*Chelonia mydas*) nests in Saipan, CNMI.

Model stage	Model	DE (%)	AIC	BIC
Hatching success				
Stage I	Beach + TempC.mean	40	-81.6	-57.7
	Beach + TempC.max	51	-98.4	-71.8
	Beach + Month.Exca	39	-169.5	-136.1
	Beach + Year.Exca	42	-173.8	-138.9
Stage II	Beach + Year.Exca + TempC.mean	45	-85.6	-56.9
	Beach + Year.Exca + TempC.max	56	-101.9	-69.1
	Beach + Year.Exca + Month.Exca	44	-173.1	-132.4
Stage III	Beach + Year.Exca + Month.Exca + TempC.mean	47	-85.6	-51.6
	Beach + Year.Exca + Month.Exca + TempC.max	57	-101.7	-64.9
Embryonic death				
Stage I	Beach + TempC.mean	27	-298.6	-271.3
	Beach + TempC.max	24	-295.2	-268.2
	Beach + Month.Exca	14	-389.6	-355.3
	Beach + Year.Exca	13	-391.2	-360.5
Stage II	Beach + Year.Exca + TempC.mean	28	-297.2	-267.5
	Beach + Year.Exca + TempC.max	26	-296.0	-266.4
	Beach + Year.Exca + Month.Exca	16	-390.8	-353.6
Stage III	Beach + Year.Exca + Month.Exca + TempC.mean	29	-294.9	-260.7
	Beach + Year.Exca + Month.Exca + TempC.max	28	-294.1	-259.4

DE, Deviance Explained, the amount of variation in the response variable explained by the predictor variables; higher values indicate better model fits to the data. AIC, Akaike Information Criterion; BIC, Bayesian Information Criterion. "Month.Exca" and "Year.Exca" are the month and year of nest excavation. AIC and BIC are goodness-of-fit performance metrics for which lower values are most ideal. Gray highlighting indicates models that were selected as final models.

and intensity of tropical storms and typhoons inundating nests in the CNMI (Shaw, 2013), (ii) warm temperatures experienced at low latitudes (Matsuzawa et al., 2002), and (iii) habitat factors, such as high instances of coral rubble and roots from non-native vegetation trapping hatchlings in nests (Zárate et al., 2013).

This population of nesting turtles exhibits a relatively low somatic growth rate. Although our recapture sample size was low (10 turtles), we documented a growth rate of 0.26 cm/yr for nesting green turtles in the CNMI. This is relatively low compared to a growth rate of 0.8 cm/yr from Malaysia (Pilcher and Basintal, 2000), the closest comparison in the region, and 0.5 cm/yr for nesters in Florida (Witherington and Ehrhart, 1989). High reproductive output during nesting seasons, combined with long-distance post-nesting migrations to foraging grounds, could potentially explain the low observed growth rate; growth rates of juveniles in this population range from 0.3 to 7.8 cm/yr (Summers et al., 2017).

Nester Abundance and Trends

Our results suggest that poaching is currently the greatest threat to this nesting population. The 32% harvest rate of Saipan's 7.7 ± 2.5 annual nesters potentially would be

higher without the research efforts described in this study. Consistent monitoring often prevented or interrupted poaching and triggered enforcement efforts. Although we document other anthropogenic threats, adult females have a high reproductive value when compared to eggs and hatchlings, and thus their loss has the greatest impact to the population. For example, beach driving is one threat that impacts nests, hatchlings, and adults. The threat has largely been eliminated through beach barricades and a "walk it, don't drive it" campaign led by the CNMI Bureau of Environmental and Coastal Quality; however, on a few non-barricaded nesting beaches on Tinian and Rota and on Saipan beaches where barricades have been removed or recently washed away by super typhoons, there remains a "drive in" poaching opportunity to exploit nesting turtles.

The 4.0% difference between PGR estimates for the scenarios "with poaching" and "without poaching" represents the impact poaching has had on this population. In other words, the removal of nesting females from this small population has slowed its positive population growth trend. However, despite continued removal of reproductive females, this population is experiencing a positive trend in nester abundance with an annual PGR of 7.4%. This rate of increase is relatively high in comparison with the 6.8% estimate for green turtles in the Ogasawara Islands in Japan (Chaloupka et al., 2008; Seminoff et al., 2015), which belong to the same DPS. This rate is also steeper than the 5.4% observed in Hawaii (Balazs et al., 2015; Seminoff et al., 2015) and the 3.8% at Heron Island on the Great Barrier Reef (Chaloupka et al., 2008). While the CNMI nesting population is a small fraction of the larger DPS, the observed increase is a positive sign and suggests potential for recovery of this Endangered DPS.

We estimated a mean abundance of 11.9 nesters per year on Saipan, Tinian, and Rota combined. With a remigration interval of 4.6 years, this yields a total of 55 adult females. Total nester abundance for the CWP DPS is currently 6,518 individuals (Seminoff et al., 2015). While the CNMI portion represents < 1% of the total at present, a population growth rate of 7.4% suggests this population has not reached its carrying capacity. Observing a high percentage of neophyte nesters is expected at the start of any study as new individuals are tagged; however, our annual mean of 59% neophytes for 2010–2016 after one remigration interval had passed supports a hypothesis that newly mature adults continue to recruit into the breeding population. Alternative explanations may include much longer remigration intervals than estimated here, nesting at other sites (e.g., most likely within the Mariana Islands), or less than 100% detection of nesters during the study period. However, given the remigration intervals known for other green turtle populations, extreme nesting site fidelity, local knowledge and monitoring of nesting activity on Saipan, and a 20–40 year age at first reproduction, we find the neophyte hypothesis most plausible. New recruits are generally a good sign for the population, as long as they remain in the population and successfully reproduce. On beaches with saturation monitoring/tagging, the percentage of neophytes would be expected to stabilize at lower levels, assuming the previously tagged nesters are not being removed from the population through anthropogenic activities, such as poaching or bycatch.

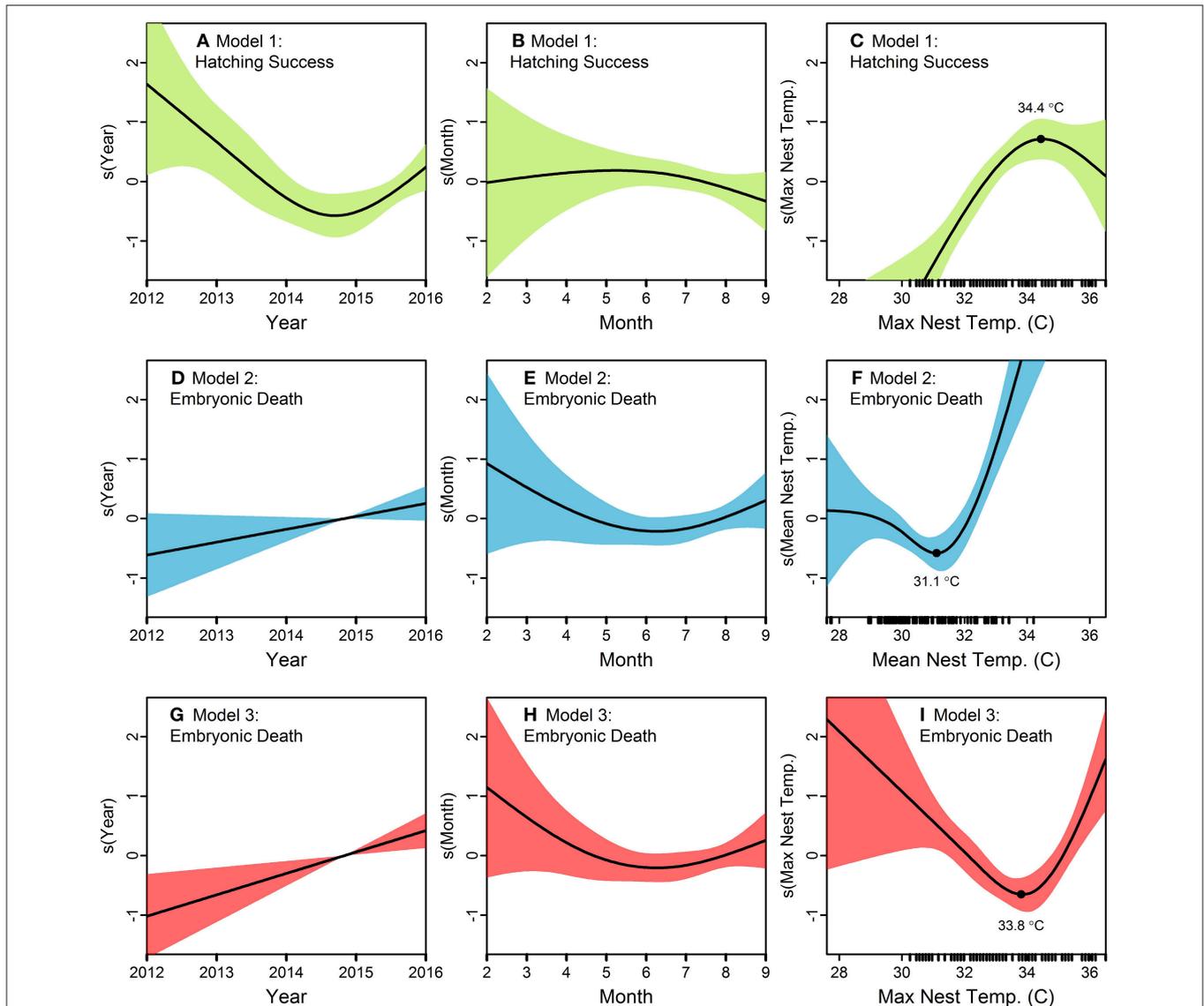


FIGURE 3 | Generalized additive models (GAMs) exploring the influence of year, month, and nest temperature (mean or maximum) on green turtle (*Chelonia mydas*) hatching success (Model 1) and embryonic death (Models 2 and 3) on Saipan beaches in 2012–2016. Nest temperature ($n = 89$ data loggers) is the predictor variable of primary interest, while beach (categorical variable; not shown here), year, and month are included to control other sources of variation in the response variables. Smoothed responses to individual predictors are shown on the y-axis of (A–I). Rug plots along the x-axis of (C, F, I) show the distribution of raw data for the temperature variables. Model 1 suggests (A) an annual decrease in hatching success until 2015, (B) a slight maximum in hatching success in May–July, and (C) hatching success increases with maximum nest temperature up to 34.4°C, after which it decreases. Model 2, which uses mean nest temperature rather than the maximum, suggests (D) a steady increase in embryonic death over the years, (E) lowest embryonic death between May and July, and (F) a pronounced increase in embryonic death with mean nest temperatures beyond 31.1°C. Model 3 suggests (G) embryonic death has increased annually (H) highest embryonic death in February through April, and (I) embryonic death decreases with maximum nest temperatures up to 33.8°C, and increases sharply beyond that.

Climate Impacts

Our finding that the mean nest temperature of green turtles in the CNMI is $30.9 \pm 1.5^\circ\text{C}$ is concerning when compared to known pivotal temperatures for sex determination and embryonic death. This mean is above 29.0°C , the threshold beyond which a clutch becomes female biased (Standora and Spotila, 1985; Mrosovsky, 1994; Ackerman, 1997; Godfrey and Mrosovsky, 2006). Furthermore, it is above 30.3°C , a temperature

which produces a minimum of 90% females in green turtle nests (Standora and Spotila, 1985; Spotila et al., 1987). Our results provide strong evidence that the current generation of green turtles produced in the CNMI is already female biased. This idea could be tested by determining sex for a sample of juvenile turtles on their foraging grounds (Allen et al., 2015). And while the expected female bias could boost the nesting population initially, this could become a problem if there are

eventually too few males to sustain the breeding population (Layton, 2011).

The mean nest temperature of 30.9°C for CNMI green turtle nests currently falls below the pivotal threshold of 33.0°C for embryonic death (Packard et al., 1977; Miller, 1985). However, the maximum temperature of 33.5 ± 2.0°C across all nests in this study creates cause for concern and further investigation. Generally, it is the prolonged exposure to temperatures above 33.0°C that leads to increased hatchling mortality, but the exact critical temperature and exposure time needed to induce mortality in the CNMI is unknown. Projected increases in temperatures could lead to higher rates of embryonic death in the near future.

Our modeling results suggest a decrease in hatching success and corresponding increase in embryonic death beyond maximum nest temperatures of 34.4 and 33.8°C, respectively. Additionally, embryonic death appears to be triggered beyond a mean nest temperature of 31.1°C, which is only slightly higher than the mean nest temperature we measured. Warm temperatures resulting in embryonic death likely played a role in lowering hatching success from 100 to 77.9%. With rising global temperatures leading to rising sand temperatures, we can expect the hatching success of CNMI green turtle nests to continue declining.

CONCLUSION

This study provides the first comprehensive assessment of nesting demographic parameters and abundance trends for nesting green turtles in the Mariana Archipelago specifically, and Micronesia more broadly. Furthermore, it quantifies major threats to the survival of the population. The CNMI nesting data suggest an annual increase in nesting females of 7.4% per year, which is corroborated by a 10% increase in foraging green turtles (mostly juveniles) estimated from aerial surveys in the southern portion of the archipelago (Martin et al., 2016). These positive trends are promising in light of the previous exploitation of nesting and foraging turtles throughout the region (Groombridge and Luxmoore, 1989; Seminoff et al., 2015); however, the trends may be slowed by continued poaching or offset by warming temperatures.

ETHICS STATEMENT

This research was performed under the Commonwealth of the Northern Mariana Islands Department of Lands and Natural Resources. This is a governmental institution which does not require an Institutional Animal Care and Use Committee (IACUC) protocol but does require that endangered species research is permitted through US Federal agencies: US Fish and Wildlife Service (USFWS) and National Marine Fisheries Service (NMFS). The work presented in this paper

was performed under this US territorial government agency under the auspices of a US Endangered Species Act (ESA) valid permit issued by USFWS (permit no. TE-017352-17). All work was done under the USFWS ESA guidelines, permits, and certifications with experienced permitted personnel.

AUTHOR CONTRIBUTIONS

TS, JH, and JR designed the study and collected and maintained nesting data. TS, SM, and TJ quality-checked and analyzed data. TS, SM, and TJ prepared figures and tables and wrote the manuscript. All authors reviewed the manuscript.

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SUPPLEMENTARY MATERIAL

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fmars.2017.00428/full#supplementary-material>

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Conflict of Interest Statement: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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