


Mixed-stock aging analysis reveals variable sea turtle maturity rates in a recovering population

Calandra N. Turner Tomaszewicz^{1,2}  | Larisa Avens³ |
Erin L. LaCasella² | Tomoharu Eguchi² | Peter H. Dutton² |
Robin A. LeRoux² | Jeffrey A. Seminoff²

¹National Research Council, NOAA
Southwest Fisheries Science Center, La Jolla,
CA 92037, USA

²NOAA Southwest Fisheries Science Center,
La Jolla, CA 92037, USA

³NOAA Southeast Fisheries Science Center,
Beaufort, NC 28516, USA

Correspondence

Calandra N. Turner Tomaszewicz, NOAA
National Marine Fisheries Service, Southwest
Fisheries Science Center, 8901 La Jolla
Shores Drive, La Jolla, CA 92037, USA.
Email: Cali.Turner@noaa.gov

Funding information

National Oceanic and Atmospheric
Administration, Grant/Award Number: Sea
Turtle Stock Assessment Award FY18-19

Abstract

Quantifying demographic parameters and variable vital rates, such as somatic growth rates, time to maturity, and reproductive longevity, is important for effective management of threatened and endangered populations such as sea turtles (Cheloniidae). To address these knowledge gaps, we applied skeletochronology to analyze and compare somatic growth rates and variation in life-history traits such as age and size at sexual maturity for 65 green turtles (*Chelonia mydas*) in the eastern Pacific Ocean (EP), along the west coast of the United States; turtles belonged to ≥ 2 nesting subpopulations that differed in body size (mean nesting size). Green turtles in the EP spend approximately 5 years in the oceanic stage before recruiting to nearshore habitats, males may be smaller and younger than females at maturation ($\bar{x} = 17.7 \pm 5.5$ yr vs. 28.0 ± 8.2 yr), and younger age at sexual maturity was associated with smaller size at sexual maturity, suggesting that mean nesting body size may be reflective of maturation timing for subpopulations. Smaller body sizes for females nesting at Michoacán, Mexico (continental) rookeries, yielded a younger predicted age at sexual maturity ($\bar{x} = \sim 17$ yr) compared to females from Revillagigedo Islands, Mexico rookeries, which displayed larger body sizes and older age at sexual maturity ($\bar{x} = \sim 30$ yr). We consider possible mechanisms driving the observed divergence in life-history traits, including the possibility

that earlier maturation (reduced generation length) for turtles in the Michoacán nesting subpopulation may be a response to intense harvesting in the past 50 years, and consideration of such anthropogenic impacts is warranted by population managers. Finally, our results indicate green turtles moved into nearshore neritic habitats at a young age (4–6 yr), emphasize the importance of protecting neritic habitats along the southwestern United States and northwestern Mexican coasts, and encourage the incorporation of variable maturation time in population recovery assessments.

KEYWORDS

age at sexual maturity, *Chelonia mydas*, demography, endangered species management, green sea turtle, growth, life history

Sea turtles (Cheloniidae) are an ancient lineage, proven resilient over time as climate fluctuated, and direct (e.g., harvesting, consumption) and indirect (e.g., pollution, fishery bycatch, habitat destruction) human pressures expanded. Long-term collaborative monitoring and emerging techniques have yielded novel insights into sea turtles' life histories, habitat use, somatic growth rates, diets, population structure, and movements (National Research Council 2010, Avens and Snover 2013, Komoroske et al. 2017, Wyneken and Salmon 2020). Yet for all sea turtle species, as for many long-lived and migratory animals occupying remote habitats, significant gaps remain about basic biological information, especially those related to life history and vital rates (Hamann et al. 2010, National Research Council 2010, Godley et al. 2020). Understanding the intrinsic variability in life-history traits and the impact of extrinsic drivers that affect the timing of sea turtle ontogenetic transitions, such as oceanic juvenile development (age at settlement), age at sexual maturation (ASM), and the duration of resulting stages (e.g., reproductive longevity, life span), is fundamental for assessing population recovery (Bjorndal et al. 2013, 2014; Avens et al. 2015; Bailey et al. 2018). Recovery potential is an especially important metric to evaluate, yet it remains poorly quantified in many conservation-dependent populations, including marine mega-vertebrate taxa such as sea turtles (National Research Council 2010, Bailey et al. 2018).

In the eastern Pacific Ocean, green turtles (*Chelonia mydas*) range from the United States to Chile, and in the northern-most portion of their range, they nest on mainland Mexico beaches, centered in the state of Michoacán (MI), and at a collection of insular sites, including the uninhabited Revillagigedo Islands (RI) and Tres Mariás Islands (TM; Delgado-Trejo and Alvarado-Figueroa 2012, National Marine Fisheries Service [NMFS] and United States Fish and Wildlife Service [USFWS] 2015, Fonseca et al. 2018; Figure 1). Green turtles from these separate nesting locations forage together in mixed-stock groups in bays and lagoons along the northwestern coast of Mexico and southern California, USA, and belong to the East Pacific (EP) population (NMFS and USFWS 2015, Dutton et al. 2019; Figure 1). At the 2 main Mexican rookeries (i.e., nesting colonies), RI (insular) and MI (continental), nesting female green turtles differ in body size and coloration (Juárez-Cerón et al. 2003, Delgado-Trejo and Alvarado-Figueroa 2012), and at the molecular level, the MI and RI rookeries each have some unique mitochondrial DNA (mtDNA) haplotypes, making it possible to distinguish these nesting subpopulations (Dutton et al. 2014, 2019; Jensen et al. 2019).

The EP green turtle population had been targeted for harvest since the 1800s, and even earlier by local inhabitants (Early-Capistrán et al. 2018). In the twentieth century, green turtles in northwest Mexico, from the state of Michoacán to the northern edge of Baja California Sur and including the Gulf of California, incurred high levels of harvesting, decimating the population (Delgado-Trejo and Alvarado-Figueroa 2012, NMFS and USFWS 2015, Early-Capistrán et al. 2018). At the mixed-stock foraging grounds, juveniles and adults were targeted, and large

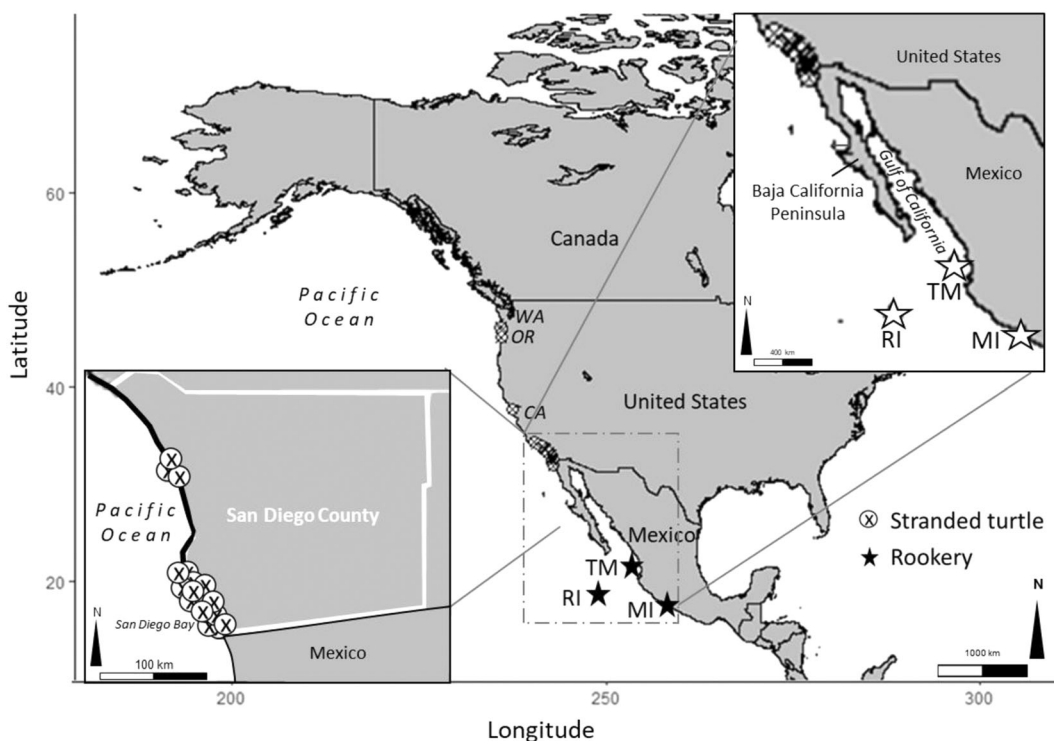


FIGURE 1 The East Pacific study site for green sea turtles showing stranding locations along the United States west coast (CA, OR, WA) from 1990–2018. Map also shows known key northern rookeries for the East Pacific green turtle population: RI = Revillagigedo Islands, Mexico; MI = Michoacán, Mexico; TM = Tres Marias Islands, Mexico

numbers of adult female and male turtles were taken at the MI rookeries, along with nearly 100% of the eggs (Cliffton et al. 1982, Delgado-Trejo and Alvarado-Figueroa 2012, Early-Capistrán et al. 2018, Dutton et al. 2019; Figure 1). In contrast, geographically isolated insular nesting beaches, such as the RI, remained largely untouched during this intense harvesting period (Alvarado-Díaz and Figueroa 1990; Figure 1). Between the 1960s and 1980s, green turtle take-levels were an order of magnitude greater than during any other time period, and the impact on the turtles breeding at MI was greater than on the turtles breeding at insular rookeries (Delgado-Trejo and Alvarado-Figueroa 2012, Early-Capistrán et al. 2018). Prior to the 1960s, an estimated 25,000 female green turtles nested at a single beach in MI, and by 1988, there were only 170 nesting females (Delgado-Trejo 2018). Since the late 1980s, green turtles in the EP and their habitats have been protected, and today the population continues to grow and recover, with an estimated 10,000 to 15,000 female green turtles nesting annually at the MI beaches; similar data do not exist for the RI rookeries (Delgado-Trejo 2018).

Because more regular monitoring of these rookeries began in the 1980s, we know that the nesting females at the insular RI rookeries tend to be larger than green turtles nesting at the mainland MI rookeries (94 ± 6.8 cm curved carapace length [CCL], $n = 42$ vs. 82 ± 6.6 cm CCL, $n = 200$, respectively; Juárez-Cerón et al. 2003, Delgado-Trejo and Alvarado-Figueroa 2012). The adult males are also typically larger at RI versus MI (78.5 ± 5.9 cm CCL, $n = 20$, vs. 72.5 ± 5.5 cm CCL, $n = \text{unknown}$, respectively), and mature males are typically smaller than nesting females, although sample sizes are small (Juárez-Cerón et al. 2003, Delgado-Trejo and Alvarado-Figueroa 2012). Further, no other green turtle population in the world has small nesting turtles in the 60-cm CCL size range at the frequency found at the MI breeding grounds, making these some of the smallest nesting green turtles globally (nesting range = 60–102 cm CCL; Figure S1, available in Supporting Information; Hirth 1971, 1997; NMFS and USFWS 2015).

For this recovering northern foraging mixed-stock with a history of heavy exploitation, a comparison of somatic growth rates and maturation timing of sympatric foragers from different nesting subpopulations should prove useful in elucidating the mechanisms and scope of population growth and recovery. Specifically, understanding what external factors may affect growth and maturation rates of species, how growth rates vary, and how species may respond to changing environmental conditions are top priorities for sea turtle population managers assessing recovery (National Research Council 2010).

Current estimates for time to maturity for green turtles in the eastern North Pacific is based on mark-recapture-derived growth rates from foraging turtles and values ranged from 24 to 38 years (Seminoff et al. 2002, Koch et al. 2007, Delgado-Trejo and Alvarado-Figueroa 2012), and 1 study of bone growth layers (skeletalochronology) with values that ranged from 17 to 30 years old and size at maturity that ranged from 75 to 95 cm CCL (Turner Tomaszewicz et al. 2018), raising questions about what drives maturation rates.

Novel methods are required to further understand these life-history traits, and accretionary tissues have particular value for tracking changes in animals' demographic parameters and growth patterns over time. Skeletochronology can be applied to estimate the age of individuals in the wild, which when paired with body size measurements, can pinpoint somatic growth rates and maturity status (Avens and Snover 2013; Avens et al. 2015, 2020; Ramirez et al. 2015; Turner Tomaszewicz et al. 2017). This method generates age-specific demographic parameters that can illuminate otherwise-undetected life-history trends and provides an approach to compare population demographic parameters, including growth and maturation rates (i.e., age at sexual maturation) among different groups (e.g., breeding, foraging populations), and could help illuminate possible population-level recovery mechanisms.

In the current study, we examined somatic growth and maturation timing (age and size at sexual maturation) for a mixed stock of green turtles in the EP found foraging along the United States west coast to characterize the demographic parameters of this foraging population. Based on the different body size of turtles at the 2 main northern nesting subpopulations, we expected that the larger turtles at RI may be older at maturation in comparison to the smaller turtles at MI. We explored these demographic parameters of the green turtle population in the EP to examine the possibility of a species' capability to recover, perhaps more quickly, if there is variation within the population's life-history traits (e.g., maturation age, reproductive longevity, reproductive output).

STUDY AREA

We collected green turtle bone samples on beaches along coastlines from San Diego, California, to the Oregon-Washington border (12,785 km, at sea level) between 1990 and 2018 (Figure 1). Topography along the Pacific Ocean coasts was primarily sandy beaches, with some areas of rocky shores, including bays and estuaries with mudflats and marshes. Dominate vegetation included eelgrass (*Zostera marina*, *Z. pacifica*), saltwort (*Batis maritima*), and California cordgrass (*Sporobolus foliosus*). Shoreline fauna include several species of birds (e.g., western gull [*Larus occidentalis*], marbled godwit [*Limosa fedoa*], brant [*Branta bernicla*], western sandpiper [*Calidris mauri*]) and intertidal invertebrates (e.g., California horn snail [*Cerithideopsis californica*], Pacific acorn barnacle [*Balanus glandula*], and striped shore crab [*Pachygrapsus crassipes*]). The climate in these areas is variable, ranging from Mediterranean dry coastal climates in southern California (mean monthly temperature and precipitation summer: 22.2°C, 0 cm; winter: 14.4°C, 2.0 cm; National Weather Service 2021), to cooler temperate coastal forests in Oregon (mean temperature and precipitation summer: 15.6°C, 4.0 cm; winter: 7.8°C, 19.3 cm; National Weather Service 2021). We collected samples year-round, from open public spaces along the coast. The land use in some areas are highly urbanized, such as the San Diego Bay, which is a major shipping port and is also home to a United States Naval base at Coronado Island, while in other areas, recreational activities are the dominate human use, as is the case for Mission Bay, also in San Diego, with a year-round presence of boaters and jet skiers. Most of the open coastline is adjacent to human development but with sandy beaches or rocky shores providing a buffer between the ocean and

development (roads, homes, and businesses). Upon collection, we transferred samples to the Southwest Fisheries Science Center in La Jolla, California for storage until laboratory processing conducted in 2019.

METHODS

Sample collection and processing

Members of the United States West Coast Marine Mammal and Turtle Stranding Network routinely respond to and collect samples from dead sea turtles from along the entire United States Pacific coastline. We did not handle or use live turtles in this project. For this study, we used humeri and skin samples collected from 65 dead green sea turtles that stranded along the United States west coast. Turtles were stranded in Clatsop County in Oregon ($n = 4$) and in California: San Diego County ($n = 43$), Orange County ($n = 5$), Los Angeles County ($n = 10$), Ventura County ($n = 1$), Santa Barbara County ($n = 1$), and San Francisco County ($n = 1$; Figure 1). Most turtles were recovered between 2010 and 2018 ($n = 60$), with the remaining recovered between 1990 and 2009 ($n = 5$). Upon finding the carcasses, we measured body size (CCL or straight carapace length [SCL]). For any sample where we measured only SCL, we estimated CCL using the SCL-to-CCL conversion equation for green turtles in the EP from Eguchi et al. (2012): $CCL = 0.64 + 1.06 \times SCL$ ($n = 211$, $r^2 = 0.99$). We collected samples directly in the field via removal of the humerus and using a scalpel to retrieve a small skin sample, and stored the sample frozen until processed, or we froze the entire carcass and collected samples later during necropsy. When possible, we inferred sex based on gonadal examination during necropsy, or using tail length of large turtles (Wibbels 1999). We collected and analyzed skin for mitochondrial DNA (mtDNA) haplotype identification for a separate study (Dutton et al. 2019).

One author (CTT) prepared and processed all humeri for skeletochronological analysis, and age and growth estimation as described elsewhere (Snover et al. 2007, Avens and Snover 2013, Avens et al. 2015, Turner Tomaszewicz et al. 2018, Goshe et al. 2020). Briefly, we cut 2 3-mm cross sections from each humeri; 1 was fixed in 10% formalin, decalcified using a rapid histological decalcifier (RDO Decalcifier; Electron Microscopy Sciences, Hatfield, PA, USA), sectioned into 0.2- μm slices, stained with hematoxylin, mounted to a slide, and imaged to produce a digitized record of the bone revealing lines of arrested growth (LAGs). We assumed LAGs form annually (Snover et al. 2011, Goshe et al. 2016), which has been preliminarily demonstrated for green sea turtles in the EP using oxytetracycline mark-recapture (Turner Tomaszewicz et al. 2018). Two authors (CTT and LA) independently examined and determined the location and count of LAGs and reached a final consensus, and CTT measured LAG diameters along the antero-posterior axis (Goshe et al. 2009, Avens and Snover 2013) and used these measurements for age, size, and growth estimation.

To explore potential differences in growth rates between the 2 nesting subpopulations, we assigned each turtle to a nesting subpopulation based first on satellite tracking between the foraging area and the nesting beach if available from a previously published study (Dutton et al. 2019), then using endemic nesting mtDNA haplotypes (Dutton et al. 2019) known from each of the nesting assemblages (RI and MI). We assigned green turtle samples with the following mtDNA haplotypes to RI: CmP4.2, CmP6.1, CmP6.2, CmP1.1, and CmP3.1. We assigned those with CmP4.8, CmP5.1, and CmP7.1 to MI. We classified any sample with a shared green turtle haplotype (CmP4.1, CmP4.6, CmP25.1, CmP92.1, CmP100.1) or with a null or new haplotype as unknown.

Age, size, and growth estimation

For all samples, we applied standard skeletochronology analysis for age, somatic growth, and size estimation (Snover et al. 2007, Goshe et al. 2009, Avens and Snover 2013). Briefly, we first evaluated the relationship between humeri section diameter and turtle body size (CCL; Avens et al. 2015). Next, for age and size estimation, we used

LAG measurements to group bones based on the minimum LAG diameters measured (Avens et al. 2012, Turner Tomaszewicz et al. 2018). We used the LAG diameter and corresponding LAG numbers to generate stepwise correction factors for each preceding group of larger bones until we estimated the number of LAGs lost because of resorption for all bones (see Additional Details for Age Estimation, available in Supporting Information). Next, we back-calculated body size (CCL) at each measured LAG to produce estimated size and incremental growth, following standard skeletochronology analytical methods (Snover et al. 2007; Avens et al. 2012, 2015). We also referenced any live-capture body-size histories, when possible, to help validate estimated ages and sizes using data from Dutton et al. (2019) for turtles captured and marked with flipper tags in San Diego Bay, California, a green turtle foraging site monitored since 1990. We then analyzed annual somatic growth rates among individual turtles, size and age classes, and between nesting origin subpopulations using the incremental growth results. To create a multi-year record of size, age, and growth for each individual turtle, we paired the estimated size and annual growth values with estimated age for each LAG. We determined estimated age and size at maturation (SSM) for any individual turtle where we observed compression of the LAGs at the lateral edge of the bone (i.e., rapprochement), which is associated with sexual maturity (Francillon-Vieillot et al. 1990; Avens et al. 2012, 2015; Avens and Snover 2013).

We modeled the size-at-age relationship for all turtles combined using the paired size, age, and growth data from each individual turtle bone applied to a generalized additive mixed model (GAMM) and a von Bertalanffy growth model. We then repeated modeling for each of the designated nesting subpopulations, RI and MI, when sample sizes permitted, similar to the process conducted by Avens et al. (2015, 2017). The GAMM accounted for individual variation and repeated observations by including individual identity as a random effect (Chaloupka and Musick 1997; Avens et al. 2013, 2015; Turner Tomaszewicz et al. 2018). We conducted the analysis using the *mgcv* package and the *gamm* function in R version 4.0.1 (Wood 2017, R Core Team 2020). After converting all measurable LAG diameters to CCL estimates, we used that size-at-age data to fit a smoothing spline model to characterize the size-at-age relationship. We also generated the predicted fit for the same data, with 95% confidence intervals, using the *smooth.spline* function in the *stats* package in R (Hastie and Tibshirani 1990, R Core Team 2020). Next, we generated von Bertalanffy growth models using a bootstrapped method, as described in Avens et al. (2015, 2017) for loggerhead (*Caretta caretta*) and Kemp's ridley sea turtles (*Lepidochelys kempii*), respectively. We repeatedly sampled the back-calculated somatic growth rate data in the model to extract a single growth-at-length data point for each individual turtle in the sample and then used these nonparametric bootstrap samples to estimate the growth parameter, k , and estimate upper size limit, L_{inf} , for Fabens modification of the von Bertalanffy growth curve. For this growth model, we conducted randomized re-sampling of the growth rate data 1,000 times to describe uncertainty in the von Bertalanffy parameters (Avens et al. 2015, 2017). For all analysis, we evaluated significance as $\alpha = 0.05$, and present results as mean \pm standard deviation unless otherwise noted.

RESULTS

Nesting subpopulation assignment

Of the 65 turtles with paired bone and skin samples, we assigned 37 to 1 of 2 nesting subpopulations based on mtDNA haplotypes unique to RI or MI and 1 turtle to a subpopulation based on satellite-tracked movements (Dutton et al. 2019). We assigned 34 turtles to the RI subpopulation group (33 by haplotype, 1 by satellite track), 4 turtles to the MI subpopulation group, and the remainder to the unknown group ($n = 27$). The observed dominance of RI-origin turtles in our study aligns with previous stock origin and mixed stock analysis conducted by Dutton et al. (2019) who reported that 71% (95% CI = 55–87%) of turtles sampled in San Diego Bay, California were assigned to RI rookeries, and only 24% (95% CI = 7–40%) to MI rookeries.

Age and growth estimation

We analyzed humeri from 65 green turtles, with individual CCL ranging from 43–110.2 cm ($\bar{x} \pm SE = 67 \pm 1.9$ cm). We determined sex for 26 turtles; 6 were male and 20 were female. The female-to-male sex ratio (3.35 females:1 male) reflects similar female bias reported in a previous study from San Diego, California (2.83 females:1 male for all turtles, 3.5 females:1 male for only putative immature turtles; Allen et al. 2015). There was a linear relationship between humeri section diameter and turtle size (CCL = $2.70 \times$ humeri section diameter - 4.92, $P < 0.001$, adjusted $r^2 = 0.922$; Figure 2). For age and size estimation, we identified and measured 533 LAGs from among the 65 humeri; individual turtles retained 3–27 (8.4 ± 4.6) LAGs. Ten humeri retained an annulus (the LAG formed during the first year of a turtle's life), which allowed us to directly age these individuals (group 1, $n = 10$, CCL 55.6 ± 5.1 cm) following standard protocols (Goshe et al. 2010, Avens et al. 2013). The remaining 55 bones did not retain an annulus; thus, ≥ 1 LAG had been lost (resorbed) during bone growth. We assigned these bones to different groups based on increasing humeri diameter: group 2 ($n = 42$), group 3 ($n = 10$), and group 4 ($n = 3$; see Additional Details for Age Estimation, available in Supporting Information). We estimated ages using each group's correction factor equation, estimated the number of LAGs lost, and then summed this value with the number of LAGs retained to obtain estimated age at stranding (Figure S2, available in Supporting Information). The number of estimated lost (resorbed) LAGs from individual bones ranged from 1 to 34 (4.1 ± 5.9 , $n = 55$ bones). We adjusted final estimated age (LAGs retained + LAGs resorbed) to account for date of stranding relative to mean hatch date for the population as fully described in Turner Tomaszewicz et al. (2018), with all ages rounded to the nearest whole number. From the skeletochronological analysis, estimated ages ranged from 5 to 50 years (Figure 2), and mean age ($\pm SE$) was 12.4 ± 1.1 years. The majority (58%) of the recovered turtles were young; estimated age was ≤ 10 years (median age = 9 yr; Figure 2).

Back-calculated body sizes (CCL) estimated at each measurable LAG yielded 536 CCL-at-age estimates, and we calculated 481 annual somatic growth estimates from these growth increments (Figures 3 and 4). Annual CCL growth ranged from 0 to 14.8 cm/year; this does not include the rapid growth estimated in the first year of life (age 0–1). Ten turtles retained a measurable annulus and had estimated body sizes ranging between 24 to 33 cm CCL by age 1 (Figures 3 and 4). Estimated annual growth was greatest for age 0 to 3 ($n = 24$), where the mean was 11.4 cm/year (Figure 3). The mean annual growth rates for age classes (10-year increments) and for size classes (10-cm increments) were not different among turtles assigned to RI, MI, and unknown, except for the 31–40 age class, where turtles from RI had a greater average growth rate than the unknown group ($P < 0.001$; Figure 4).

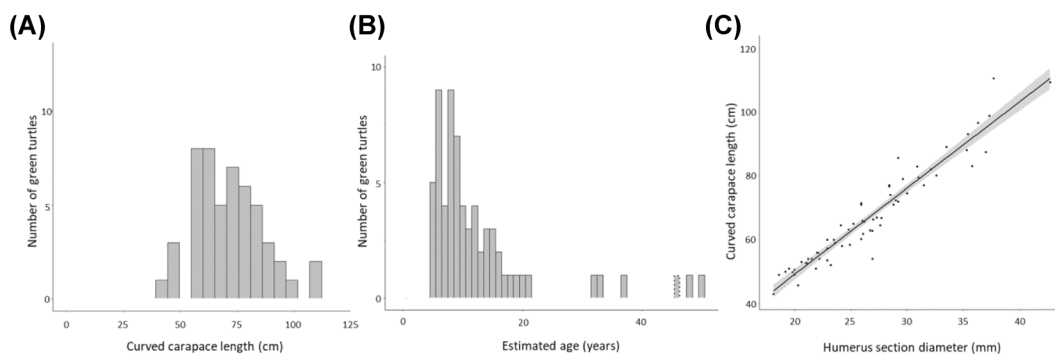


FIGURE 2 Frequency of A) final size as measured by curved carapace length (cm), and B) estimated age (years) of the 65 green turtles recovered along the United States west coast, 1990–2018. C) Relationship between curved carapace length (cm) and the total humerus diameter (mm) for the 65 green turtle bones processed for skeletochronology

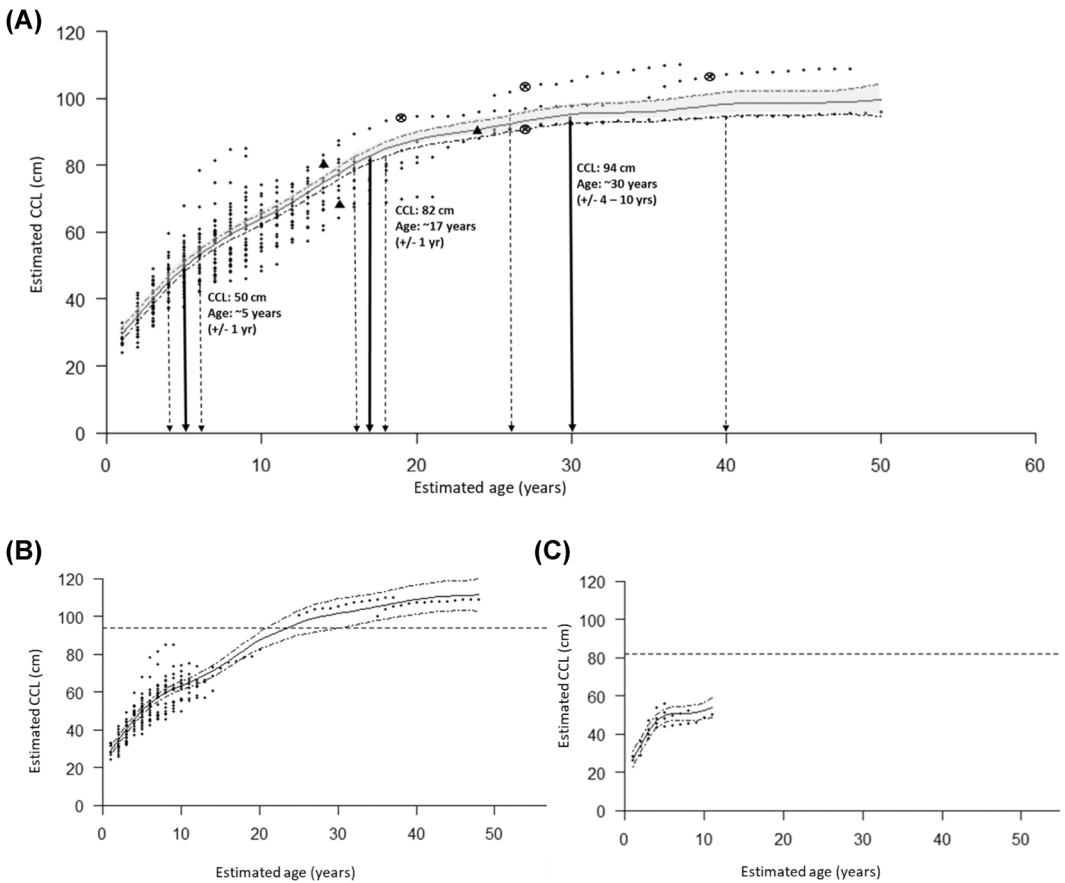


FIGURE 3 Generalized additive mixed model smoothing splines fit to the size-at-age relationship for A) the paired size and age values ($n = 533$) from all green turtles ($n = 65$ green turtles) recovered along the United States west coast, 1990–2018, and those assigned to B) Revillagigedo Islands, Mexico (RI; $n = 34$ green turtles), and C) Michoacán, Mexico (MI; $n = 4$ green turtles). Predicted estimates are in black solid line and double-dashed lines mark the 95% confidence intervals. Frame A shows key green turtle life-history body size estimates and the corresponding estimated age for 1) age at settlement predicted at a curved carapace length (CCL) of 50 cm, 2) age at maturity for a mean nesting size for MI of 82 cm CCL, and 3) age at maturity for a mean nesting size for RI of 94 cm CCL. Vertical black lines show the estimated age and dashed lines show the full range of ages at each size (50, 82, 94 cm CCL). In frame B and C, we show the mean of observed nesting sizes (CCL) in horizontal dashed lines for RI (mean \pm SE, 94 cm \pm 1.0) and MI (82 cm \pm 0.5). We show age and size at sexual maturity for the 7 mature turtles, 3 males (triangles) and 4 females (circles with \times)

The GAMM spline fit to the paired CCL and estimated ages, for all of the turtles combined, was significant ($P < 0.001$, estimated degrees of freedom [edf] = 7.993, adjusted $r^2 = 0.88$) and characterized by relatively constant growth from age 0 to approximately 10, with some variability to age 17 or so. Growth approached an asymptote at approximately age 30 years at approximately 95 cm CCL (Figure 3). When we included nesting subpopulation in this model as another fixed effect, it was not a significant parametric term ($P = 0.342$). Referencing each nesting subpopulation's mean nesting size published in the literature, the GAMM-predicted age for turtles from MI (mean nesting size = 82 cm CCL) was approximately 17 ± 1 years, and for turtles from RI (mean nesting size = 94 cm CCL) was approximately 30 ± 4 years (Figure 3A). Similarly, there was a significant positive non-linear relationship

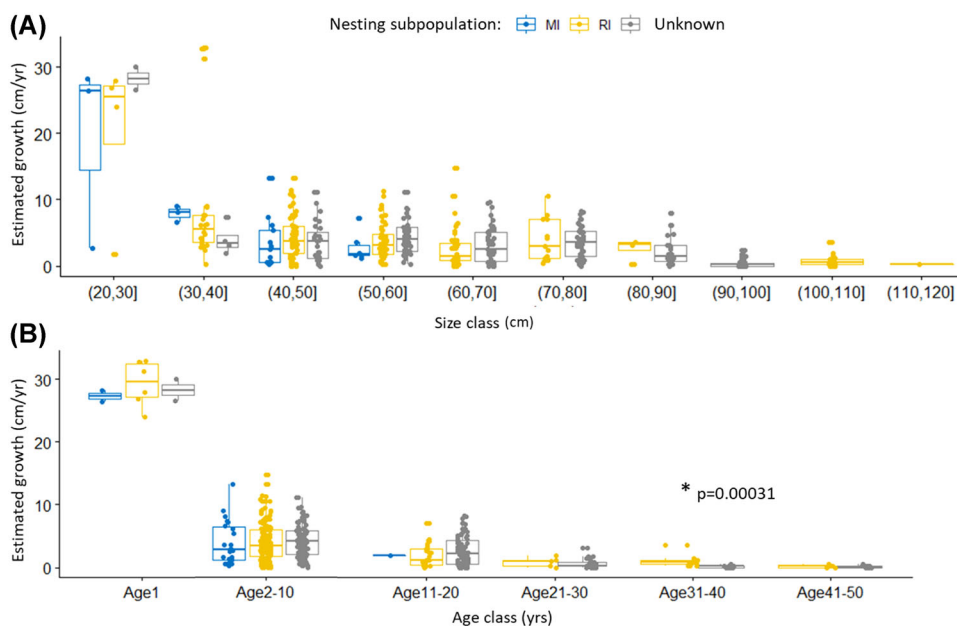


FIGURE 4 Comparison of estimated annual growth (cm/yr) for green turtles recovered along the United States west coast, 1990–2018 and assigned to Revillagigedo Islands, Mexico (RI) and Michoacán, Mexico (MI) nesting subpopulations. A) Green turtle growth increments grouped by 10-cm size classes. B) Growth increments grouped by age classes. The main boxes in the plot show the 25th–75th percentile, the bold line in the middle of the box shows the median value, the whiskers represent the minimum and maximum value, and any outliers are represented as standalone points

between CCL and estimated age for the GAMM splines fit to each of the RI and MI subpopulations ($P < 0.001$, $\text{edf} = 8.321$, adjusted $r^2 = 0.89$; $P < 0.001$, $\text{edf} = 6.331$, adjusted $r^2 = 0.82$, respectively; Figure 3B, C).

The von Bertalanffy growth models for all turtles and the RI, MI, and unknown groups individually showed similar growth patterns until about age 5 and approximately 60 cm CCL, then patterns began to diverge (Figure S3, available in Supporting Information). The calculated asymptotes (L_{inf}), representing upper CCL for mature turtles, were >100 cm CCL for all turtles combined ($\bar{x} \pm \text{SE} = 103.5 \pm 0.61$ cm, $n = 65$), RI (112.2 ± 2.40 cm, $n = 34$), and unknown (123.1 ± 13.7 cm, $n = 27$; Figures S3 and S4). The MI group included only 4 juvenile turtles, all <60 cm CCL, and therefore results were not robust enough to obtain an L_{inf} estimate. The intrinsic growth rate parameters (k) for the groups in the current study ($\bar{x} \pm \text{SE}$) were all = 0.12 ± 0.0013 , RI = 0.12 ± 0.0018 , unknown = 0.09 ± 0.0021 , and 0.34 ± 0.0205 for the group of 4 juveniles from MI (Figure S3).

Age and size at sexual maturity

We identified 7 turtles with rapprochement growth patterns, indicating the timing of the onset of sexual maturity. Estimates for ASM ranged from 14 to 39 years (23.6 ± 8.6 yr, $\text{CV} = 0.37$), and SSM ranged from 68 to 107 cm CCL (91.0 ± 13.3 cm, $\text{CV} = 0.15$; Figure 3; Table 1). Estimating the coefficient of variation is useful for comparing range of age and size at maturity with other sea turtle populations. The sex of all 7 mature turtles was known, with the male turtles ($n = 3$) reaching maturity (SSM) at 79.8 ± 11.1 cm CCL and the females ($n = 4$) maturing at 99.3 ± 7.3 cm CCL (Welch 2-sample t -test $P = 0.070$, $t_{3,2} = -2.64$). Of the 4 largest turtles, all females, the 2 largest were confirmed RI nesters (1 by satellite track and 1 by haplotype). Both of these females from RI reached SSM above the mean

TABLE 1 For the 7 mature green turtles recovered along the United States west coast, 1990–2018, identification and subpopulation if known, estimated age at sexual maturity (ASM), estimated size at sexual maturity, post-sexual-maturity annual growth rates beyond onset of maturity, sex, final estimated age, final size measured as curved carapace length, and reproductive longevity (the number of years beyond ASM)

Turtle identification	Age at sexual maturity (yr)	Size at sexual maturity (cm)	Post-maturity annual growth (cm/yr)	Sex	Final estimated age (yr)	Final size (cm)	Reproductive longevity (yr)
21_EPCm (RI)	39	107.0	0.3	F	48	109.2	10
23_EPCm (RI)	27	103.9	0.3	F	46	110.5	20
15_EPCm	19	94.7	0.0	F	33	98.7	14
22_EPCm	27	91.6	0.3	F	32	93.0	16
19_EPCm	24	90.5	0.3	M	50	96.5	27
76_EPCm	14	80.6	0.3	M	17	82.0	4
17_EPCm	15	68.4	0.2	M	21	71.0	7

nesting body size of 94 cm CCL for RI, and had a final CCL of approximately 110 cm (Table 1). The mean ASM of the 3 males was 17.7 ± 5.5 years versus 28.0 ± 8.2 years for the 4 females (Welch 2-sample *t*-test $P = 0.104$, $t_{4,98} = 1.99$; Figure 3; Table 1). Finally, the number of LAGs observed beyond the onset of maturity (at the rapprochement LAG) represents the observed minimum reproductive longevity (Avens et al. 2020). For the 7 mature turtles, minimum reproductive longevity ranged from 4 to 27 years (Figure 4; Table 1; see Using Capture History to Inform Skeletochronology Age Estimates, available in Supporting Information). These findings document the reproductive longevity of 1 male green turtle from the EP at 27 years, a unique observation because estimates of this parameter are commonly limited to female turtles that have been tagged at nesting beaches during long-term monitoring.

DISCUSSION

The estimated ages, growth patterns, and vital rates represent age-specific demographic characterizations of green turtles along the United States west coast and are some of the only such data for green turtles in the entire EP region. The findings complement and build upon previous growth analyses using mark-recapture for green turtles in San Diego Bay, California (Eguchi et al. 2012), estimating demographic parameters essential for effective species management and recovery planning.

Life-history events

The age and size of the youngest and smallest turtles observed nearshore is the best available proxy of the age and size at settlement for green turtles recruiting from their oceanic juvenile stage into neritic habitats (Seminoff et al. 2003, Arthur et al. 2008, Avens et al. 2013). Settlement from the oceanic habitat is one of the first important life-history transitions, and estimating the duration of the oceanic developmental stage is important for population assessments and modeling. Most of the green turtles recovered dead along the United States west coast and analyzed in this study were juveniles (min. age = 5 yr, median age = 9 yr; Figure 3). Typical settlement size for turtles from EP observed recruiting to San Diego Bay was approximately 40–50 cm CCL (Eguchi et al. 2012), which is similar to the size and estimated ages of turtles observed recruiting to northwestern Mexico foraging sites

(50 cm CCL, Seminoff et al. 2003; ~3–5 yr, Turner Tomaszewicz et al. 2018), and agrees with estimated values of 4–6 years (range = 3–11 yr; Figure 3) in the current study.

Maturity size and age, and reproductive longevity, are also important life-history parameters required for population assessments. Estimated age at maturity spanned 25 years (14–39 yr), and the coefficient of variation around ASM (0.37) was larger than what has been reported for green (CV = 0.11), loggerhead (CV = 0.22), and Kemp's ridley (CV = 0.29) sea turtles in the Atlantic (Avens et al. 2015, 2017). The ASM in this study for the 2 smallest male turtles (14 yr, 15 yr), although based on a small sample size, is notable as being among the youngest reported thus far for any sea turtle species, with the exception of the small-bodied Kemp's ridley sea turtle (min. ASM = 6.8 yr, SSM = 53.3 cm SCL; Avens and Snover 2013, Avens et al. 2017). The younger ASM of these 2 male turtles introduces empirical evidence suggesting that males may mature earlier than females (the youngest female ASM was 19 yr; Figure 3; Table 1). Clearly the sample size here is very small, yet the potential implications of earlier maturation for males are important for sea turtle conservation and biology, and future studies should focus on exploring this possible difference in maturation timing. Lastly, the young ASM for the 3 males (17.7 ± 5.5 years) and the 27-year reproductive longevity for 1 male green turtle, provides hopeful evidence for the ability of male turtles to contribute to population growth for several decades. This is promising as emerging evidence suggests that climate change is warming nests and producing female-skewed sea turtle populations (Hays et al. 2014, Jensen et al. 2018). Continued research documenting and sharing such examples of decades-long reproductive longevity are important now, especially when considering survivorship rates for adult sea turtles.

In comparison to the other life stages of sea turtles, adults have a relatively high annual survivorship rate (i.e., $\bar{x} = 84.1\%$, range = 77–92.5%, Warden et al. 2017; 70–90% for females, Schofield et al. 2020). When survival over a long period (i.e., 20–30 yr) is calculated (\bar{x} annual survival rate of 84.1% for 25 yr, or $0.841^{25} = 0.0133$), there is a 1.33% chance of an adult turtle having a 25-year reproductive longevity. Given these low estimated rates of approximately 1 in 100 adult turtles having such a long reproductive period, it is encouraging to know that there are numerous examples from around the world of individual sea turtles at nesting and foraging sites being recorded for >30 years (Schofield et al. 2020) and monitoring programs should continue to share records documenting adult turtle longevity to help better refine these important demographic rates.

The mean body size of nesters at MI (82 cm CCL) is the smallest of all documented green turtle populations in the world (Figure S1; Hirth 1997, NMFS and USFWS 2015), and corresponded with an estimated ASM of approximately 17 years, at the low end of the ASM range known for any sea turtle species (Avens and Snover 2013). Future skeletochronology analysis of MI-origin turtles will help refine these estimates, given that no mature turtles from here have yet to be recovered and analyzed. Our results also provide evidence of possible sexual size dimorphism, as has been previously noted in sea turtles, with some males maturing smaller than females (Table 1; Limpus and Chaloupka 1997, Godley et al. 2002, Goshe et al. 2010, Avens and Snover 2013). The 2 smallest mature male turtles (both of unknown origin) plateaued at approximately 68 and 80 cm (SSM), within the range of adult males observed at MI (71–85 cm CCL, $n =$ not known; Fuentes-Farias et al. 2010) and RI (72–93.5 cm CCL, $n = 20$; Juárez-Cerón et al. 2003). The third male (also of unknown origin) had an estimated SSM of 90.5 cm CCL, well above the range of males thus far observed at MI, and therefore was most likely from RI or another insular EP nesting subpopulation. Similarly, the distribution and mean nesting size of females from MI (82 ± 6.6 cm CCL, $n = 200$; Delgado-Trejo 2012) suggests that the 2 unknown-origin mature females (SSM > 90 cm CCL), were likely from RI or other insular nesting subpopulations. Potential differences in the demographics of these 2 subpopulations deserve continued research.

Finally, estimated growth coefficients confirmed that the green turtles we examined had higher growth rates than reported for any other green turtle population (Eguchi et al. 2012, Velez-Zuazo et al. 2014, Ramirez et al. 2021). The asymptote (L_{inf}) for all 65 turtles in the current study (103.5 cm CCL) was similar to that predicted for green turtles foraging in San Diego Bay (Eguchi et al. 2012; $L_{inf} = 102$ cm CCL, median range = 91.3–112.0 cm CCL). The intrinsic growth rate parameters (k) calculated for the 3 groups in the current study (mean \pm SE:

all = 0.12 ± 0.0013 , RI = 0.12 ± 0.0018 , unknown = 0.09 ± 0.0021) were lower than the estimated value of 0.2 (95% posterior interval = 0.19–0.23) reported by Eguchi et al. (2012) based on mark-recapture data (Figure S3).

Fully understanding the impact of variable life-history parameters, such as age to maturity, on reproductive output and ultimately, population growth rates, both among and within sea turtle populations, is a top priority for effective management and for assessing population status (National Research Council 2010, Mazaris et al. 2017). Based on the current study, SSM appears to be correlated with ASM and could provide insight to potential differences in maturity rate among different sea turtle populations. For the green turtle population in the EP, this could mean that the smaller-bodied MI nesting subpopulation could potentially enjoy a quicker recovery rate than the larger-bodied RI subpopulation, assuming other reproductive parameters are comparable (e.g., remigration interval, clutch frequency, clutch size), and mortality rates. For green turtles in the EP, and all sea turtle populations, differences in maturation patterns among subpopulations could potentially lead to changes in the population's genetic diversity with unknown ramifications for the genetic health of the stock (Chassin Noria et al. 2004, Dutton et al. 2014).

Potential drivers of variable life-history traits

For sea turtles, there is documented variation in life-history traits within populations. Bjørndal et al. (2013, 2014) reported a wide range of age and size at sexual maturation among green turtles hatched and raised in a controlled, captive setting, and variation has also been described for wild populations (Avens and Snover 2013, Avens et al. 2017). This variation is often attributed to individuals having subtly different habitat-use patterns or foraging behaviors (Goshe et al. 2010, Piovano et al. 2011, Avens et al. 2017). In the current study, if observed differences in mean nesting body sizes between RI and MI nesting subpopulations were due to accelerated growth primarily driven by environmental conditions, then incremental growth analysis would be expected to show differing growth patterns between each group, but such differences were absent. As a final consideration, Avens et al. (2015) compared growth trajectories of loggerhead sea turtles in the western North Atlantic to loggerheads in the Mediterranean and reported that both groups followed the same growth trajectory, but the turtles in the Mediterranean were maturing earlier and at a smaller size than their Atlantic counterparts. In Avens et al. (2015), the authors proposed that decreasing size at sexual maturity for Mediterranean turtles could reflect “the outcome of prolonged, high mortality pressures, as seen in heavily exploited fish populations (Trippel 1995)” (Avens et al. 2015:1762). This possibility also exists for green turtles in the EP population and the extreme intensity of harvesting during the past century may have resulted in divergence of mean nesting size and timing to maturity across breeding groups, particularly given the high harvest rates of nesting and mating adult turtles at MI.

Is smaller nesting size a response to intense harvesting?

While the occurrence of earlier maturation is a ubiquitous example of fishery-induced evolution within fish species (Borisov 1978, Trippel 1995, Jørgensen et al. 2007, Sharpe et al. 2009, Heino et al. 2015), it is not easily documented for larger, long-lived, non-fish marine species. For the green turtle population in the EP, harvesting during the 1960s–1980s stands out as the most profound anthropogenic pressure of the past century (Alvarado-Díaz and Figueroa 1990, Delgado-Trejo and Alvarado-Figueroa 2012, Early-Capistrán et al. 2018). Differential mortality of all life stages (eggs to adults) across subpopulations could influence age and size distributions in the remaining reproducing stocks. If this were to be the case in the eastern North Pacific, the more intensely harvested turtle nesting subpopulation (stock) in MI may have shifted toward an earlier mean maturation age, relative to its former mean age of maturation, as has been reported for heavily harvested fish populations following the removal of older

and larger fish (e.g., Atlantic cod [*Gadus morhua*], Jørgensen 1990; haddock [*Melanogrammus aeglefinus*], and other stocks; Borisov 1978, Trippel 1995, Lomolino 2005, Jørgensen et al. 2007, Heino et al. 2015).

To the best of our knowledge, complete data documenting the size of green sea turtles nesting at the MI or RI beaches before the 1980s or the body sizes (CCL) of the turtles harvested do not exist. But research by Early-Capistrán et al. (2018, 2020) used ethnographic methods to document and quantify local ecological knowledge and reported anecdotal evidence that the median size of green turtles in this region did decrease as harvesting continued. From interviews with fishers and former turtle harvesters in northwestern Mexico, Early-Capistrán et al. (2018, 2020) documented that harpooners preferentially tried to catch the largest turtles first, and while set nets were less selective, turtles smaller than the minimum size (65 cm CCL) were released, and fishers stated that larger turtles (>100 kg) were depleted first, and that over time, the captures of large turtles decreased.

We encourage future studies, of all exploited sea turtle populations, to investigate possible changes in patterns of maturation and to document the distribution of body sizes and genetic diversity in nesting turtles. Currently such data are noticeably absent (Nalovic et al. 2020). Future studies that apply and integrate results of different techniques (e.g., mark-recapture, genetic fingerprinting, stable isotope analysis of skeletal growth layers, satellite tracking, diet analysis) will help elucidate drivers of variable maturation rates for green turtles in the EP and other regional mixed-stock foraging sea turtle populations.

MANAGEMENT IMPLICATIONS

Two main lessons for managers emerge from our research. First, juvenile green turtles in the EP recruit to nearshore neritic habitats after 4–6 years at approximately 50 cm CCL, and thus display an oceanic pelagic stage shorter than many other sea turtle populations (Avens and Snover 2013). This pattern heightens the importance of protecting neritic habitats along the southwestern United States and northwestern Mexican coasts. Second, the variable maturation time documented here should alert population managers that application of a singular maturation rate (age and size) in population recovery assessments may not capture the full story. Maturation time for sea turtles may have the potential to shift in response to mortality pressures, similar to exploited fish stocks, which suggests that evolution of life-history traits may occur in these long-lived megavertebrates relatively rapidly and can be documented by monitoring adult body sizes, and lessons learned from fisheries management might be applied to their populations. At present, the green turtles in the EP are in a recovery phase, representing one of the greatest success stories for an endangered population in recent history. We recommend adaptive management policies and actions that account for previously underappreciated and unforeseen effects that historical harvest may have had on this and other sea turtle populations.

ACKNOWLEDGMENTS

We thank the numerous folks who contributed to making this research possible. Bone collection and necropsies, essential to this work, were conducted by the United States West Coast Marine Mammal and Turtle Stranding Network and dedicated members at National Oceanic and Atmospheric Administration National Marine Fisheries Service Southwest Fisheries Science Center's Marine Mammal and Turtle Division. Special thanks goes to J. O. Schumacher, G. E. Lemons, G. Serra-Valente, S. E. Roden, A. K. J. Lanci, E. L. Wurster, B. C. Groom, and A. B. Johnson. We thank M. E. Hanna, A. R. Gaos, and M. M. Early-Capistrán for reviewing and contributing to the improvement of this work. Funding provided by the National Oceanic and Atmospheric Administration's National Marine Fisheries Service Stock Assessment Improvement Plan/Stock Assessment Review programs and a National Research Council Research Associateship.

CONFLICT OF INTEREST

The authors declare that there are no conflicts of interest.

ETHICS STATEMENT

All samples were collected and processed under USFWS-NMFS Memorandum of understanding 50 CFR17.21(c)(3).

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in InPort at <https://www.fisheries.noaa.gov/inport>, at ID number 1370.

ORCID

Calandra N. Turner Tomaszewicz  <http://orcid.org/0000-0002-0889-8877>

REFERENCES

- Allen, C. D., M. N. Robbins, T. Eguchi, D. W. Owens, A. B. Meylan, P. A. Meylan, N. M. Kellar, J. A. Schwenter, H. N. Nollens, R. A. LeRoux, et al. 2015. First assessment of the sex ratio for an East Pacific green sea turtle foraging aggregation: validation and application of a testosterone ELISA. *PLoS ONE* 10:e0138861.
- Alvarado-Díaz, J., and A. Figueroa. 1990. The ecological recovery of sea turtles of Michoacán, Mexico. Special attention: black turtle (*Chelonia agassizii*). Final report. USFWS, Washington, D.C., USA.
- Arthur, K. E., M. C. Boyle, and C. J. Limpus. 2008. Ontogenetic changes in diet and habitat use in green sea turtle (*Chelonia mydas*) life history. *Marine Ecology Progress Series* 362:303–311.
- Avens, L., L. R. Goshe, L. Coggins, D. J. Shaver, B. Higgins, A. M. Landry, and R. Bailey. 2017. Variability in age and size at maturation, reproductive longevity, and long-term growth dynamics for Kemp's ridley sea turtles in the Gulf of Mexico. *PLoS ONE* 12:1–24.
- Avens, L., L. R. Goshe, L. Coggins, M. L. Snover, M. Pajuelo, K. A. Bjorndal, and A. B. Bolten. 2015. Age and size at maturation- and adult-stage duration for loggerhead sea turtles in the western North Atlantic. *Marine Biology* 162: 1749–1767.
- Avens, L., L. R. Goshe, C. A. Harms, E. T. Anderson, A. Goodman Hall, W. M. Cluse, M. H. Godfrey, J. Braun-McNeill, B. Stacy, R. Bailey, and M. M. Lamont. 2012. Population characteristics, age structure, and growth dynamics of neritic juvenile green turtles in the northeastern Gulf of Mexico. *Marine Ecology Progress Series* 458:213–229.
- Avens, L., L. R. Goshe, M. Pajuelo, K. A. Bjorndal, B. D. MacDonald, G. E. Lemons, A. B. Bolten, and J. A. Seminoff. 2013. Complementary skeletochronology and stable isotope analyses offer new insight into juvenile loggerhead sea turtle oceanic stage duration and growth dynamics. *Marine Ecology Progress Series* 491:235–251.
- Avens, L., L. R. Goshe, G. R. Zug, G. H. Balazs, S. R. Benson, and H. Harris. 2020. Regional comparison of leatherback sea turtle maturation attributes and reproductive longevity. *Marine Biology* 167:4.
- Avens, L., and M. L. Snover. 2013. Age and age estimation in sea turtles. Pages 97–134 in J. Wyneken, K. J. Lohmann, and J. A. Musick, editors. *Biology of sea turtles volume III*. CRC Press, Boca Raton, Florida, USA.
- Bailey, C. J., D. C. Braun, D. McCubbing, J. D. Reynolds, B. Ward, T. D. Davies, and J. W. Moore. 2018. The roles of extrinsic and intrinsic factors in the freshwater life-history dynamics of a migratory salmonid. *Ecosphere* 9:e02397.
- Bjorndal, K. A., J. Parsons, W. Mustin, and A. B. Bolten. 2013. Threshold to maturity in a long-lived reptile: interactions of age, size, and growth. *Marine Biology* 160:607–616.
- Bjorndal, K. A., J. Parsons, W. Mustin, and A. B. Bolten. 2014. Variation in age and size at sexual maturity in Kemp's ridley sea turtles. *Endangered Species Research* 25:57–67.
- Borisov, V. O. 1978. The selective effect of fishing on the population structure of species with a long life cycle. *Journal of Ichthyology* 18:896–904.
- Chaloupka, M. Y., and J. A. Musick. 1997. Age, growth, and population dynamics. Pages 233–276 in P. L. Lutz and J. A. Musick, editors. *The biology of sea turtles*. CRC Press, Boca Raton, Florida, USA.
- Chassin Noria, O., A. Abreu-Grobois, P. H. Dutton, and K. Oyama. 2004. Conservation genetics of the East Pacific green turtle (*Chelonia mydas*) in Michoacán, Mexico. *Genetica* 121:195–206.
- Cliffton, K., D. O. Comejo, and R. S. Felger. 1982. Sea turtles of the Pacific coast of Mexico. Pages 199–209 in K. A. Bjorndal, editor. *Biology and conservation of sea turtles*. Smithsonian Institution Press, Washington, D.C., USA.
- Delgado-Trejo, C. 2012. Recovery of the black sea turtle (*Chelonia agassizii*) of Michoacán, Mexico: 30 years (1982–2012) in black sea turtle conservation. U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Delgado-Trejo, C. 2018. Michoacán's black turtle: back from the brink. Pages 44–45 in R. B. Mast, B. J. Hutchinson, P. E. Villegas, editors. *State of the world's sea turtles report volume 13*. SWOT, Ross, California, USA.
- Delgado-Trejo, C., and J. Alvarado-Figueroa. 2012. Current conservation status of the black sea turtle in Michoacán, Mexico. Pages 236–278 in J. A. Seminoff and B. P. Wallace, editors. *Sea turtles of the Eastern Pacific: advances in research and conservation*. University of Arizona Press, Tucson, USA.

- Dutton, P. H., M. P. Jensen, A. Frey, E. L. LaCasella, G. H. Balazs, P. Zarate, O. Chassin Noria, A. L. Sarti-Martinez, and E. Velez. 2014. Population structure and phylogeography reveal pathways of colonization by a migratory marine reptile (*Chelonia mydas*) in the central and eastern Pacific. *Ecology and Evolution* 4:4317–4331.
- Dutton, P. H., R. A. LeRoux, E. L. LaCasella, J. A. Seminoff, T. Eguchi, and D. L. Dutton. 2019. Genetic analysis and satellite tracking reveal origin of the green turtles in San Diego Bay. *Marine Biology* 166:3.
- Early-Capistrán, M. M., A. Sáenz-Arroyo, J. G. Cardoso-Mohedano, G. Garibay-Melo, S. H. Peckham, and V. Koch. 2018. Reconstructing 290 years of a data-poor fishery through ethnographic and archival research: the East Pacific green turtle (*Chelonia mydas*) in Baja California, Mexico. *Fish and Fisheries* 19:57–77.
- Early-Capistrán, M. M., E. Solana-Arellano, F. A. Abreu-Grobois, N. E. Narchi, G. Garibay-Melo, J. A. Seminoff, V. Koch, and A. Saenz-Arroyo. 2020. Quantifying local ecological knowledge to model historical abundance of long-lived, heavily-exploited fauna. *PeerJ* 8:e9494.
- Eguchi, T., J. A. Seminoff, R. A. Leroux, D. L. Dutton, and P. H. Dutton. 2012. Morphology and growth rates of the green sea turtle (*Chelonia mydas*) in a northern-most temperate foraging ground. *Herpetologica* 68:76–87.
- Fonseca, L. G., P. S. Tomillo, W. N. Villachica, W. M. Quirós, M. Pesquero, M. Heidemeyer, F. Joyce, P. T. Plotkin, J. A. Seminoff, E. R. Matarrita, and R. A. Valverde. 2018. Discovery of a major East Pacific green turtle (*Chelonia mydas*) nesting population in northwest Costa Rica. *Chelonian Conservation and Biology* 17:169–176.
- Francillon-Vieillot, H., J. W. Arntzen, and J. Géraudie. 1990. Age, growth and longevity of sympatric *Triturus cristatus*, *T. marmoratus* and their hybrids (Amphibia, Urodela): a skeletochronological comparison. *Journal of Herpetology* 24: 13–22.
- Fuentes-Farías, A. L., V. H. Garduno-Monrow, G. Guierrez-Ospina, L. Perez-Cruz, E. Melendez-Herrera, and J. Urrutia-Fucugauchi. 2010. Reconnaissance study of Colola and Maruata, the nesting beaches of marine turtles along the Michoacán coast in southern Mexico. *Geofísica Internacional* 49:201–212.
- Godley, B. J., A. C. Broderick, L. P. Colman, A. Formia, M. H. Godfrey, M. Hamann, A. Nuno, L. C. M. Omeyer, A. R. Patricio, A. D. Phillott, A. F. Rees, and K. Shanker. 2020. Reflections on sea turtle conservation. *Oryx* 54(3):287–298.
- Godley, B. J., A. C. Broderick, R. Frauenstein, and F. Glen. 2002. Reproductive seasonality and sexual dimorphism in green turtles. *Marine Ecology Progress Series* 226:125–133.
- Goshe, L. R., L. Avens, J. Bybee, and A. A. Hohn. 2009. An evaluation of histological techniques used in skeletochronological age estimation of sea turtles. *Chelonian Conservation and Biology* 8:217–222.
- Goshe, L. R., L. Avens, F. S. Scharf, and A. L. Southwood. 2010. Estimation of age at maturation and growth of Atlantic green turtles (*Chelonia mydas*) using skeletochronology. *Marine Biology* 157:1725–1740.
- Goshe, L.R., L. Avens, M. L. Snover, and A. A. Hohn. 2020. Protocol for processing sea turtle bones for age estimation. NOAA Technical Memo NMFS-SEFSC-746. U.S. Department of Commerce, NOAA, Washington, D.C., USA.
- Goshe, L. R., M. L. Snover, A. A. Hohn, G. H. Balazs. 2016. Validation of back-calculated body lengths and timing of growth mark deposition in Hawaiian green sea turtles. *Ecology and Evolution* 6:3208–3215.
- Hamann, M., M. Godfrey, J. Seminoff, K. Arthur, P. Barata, K. Bjørndal, A. Bolten, A. Broderick, L. Campbell, C. Carreras, et al. 2010. Global research priorities for sea turtles: informing management and conservation in the 21st century. *Endangered Species Research* 11:245–269.
- Hastie, R. J., and T. J. Tibshirani. 1990. Generalized additive models. CRC Monographs on Statistics & Applied Probability. Chapman & Hall, New York, USA.
- Hays, G. C., A. D. Mazaris, and G. Schofield. 2014. Different male and female breeding periodicity helps mitigate offspring sex ratio skews in sea turtles. *Frontiers in Marine Science* 1:43.
- Heino, M., B. Díaz Pauli, and U. Dieckmann. 2015. Fisheries-induced evolution. *Annual Review of Ecology, Evolution, and Systematics* 46:461–480.
- Hirth, H. F. 1971. Synopsis of biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). FAO Fisheries Synopsis No. 85:1.1–8.19.
- Hirth, H. F. 1997. Synopsis of the biological data on the green turtle *Chelonia mydas* (Linnaeus 1758). Fish and Wildlife Service, Washington, D.C., USA.
- Jensen, M. P., C. D. Allen, T. Eguchi, I. P. Bell, E. L. LaCasella, W. A. Hilton, C. A. M. Hof, and P. H. Dutton. 2018. Environmental warming and feminization of one of the largest sea turtle populations in the world. *Current Biology* 28: 154–159.
- Jensen, M. P., N. N. FitzSimmons, J. Bourjea, T. Hamabata, J. S. Reece, and P. H. Dutton. 2019. The evolutionary history and global phylogeography of the green turtle (*Chelonia mydas*). *Journal of Biogeography* 46:860–870.
- Jørgensen, C., K. Enberg, E. S. Dunlop, R. Arlinghaus, D. S. Boukal, K. Brander, B. Ernande, A. Gårdmark, F. Johnston, S. Matsumura, et al. 2007. Managing evolving fish stocks. *Science* (80)318:1247–1248.
- Jørgensen, T. 1990. Long-term changes in age at sexual maturity of Northeast Arctic cod (*Gadus morhua*). *ICES Journal of Marine Science* 46:235–248.

- Juárez-Cerón, J. A., A. L. Sarti-Martínez, and P. H. Dutton. 2003. First study of the green/black turtles of the Revillagigedo Archipelago: a unique nesting stock in the Eastern Pacific. Page 70 in J. A. Seminoff, editor. Proceedings of the twenty-second international sea turtle symposium. NOAA Technical Memorandum NMFS-SEFSC-503, Miami, Florida, USA.
- Koch, V., L. B. Brooks, and W. J. Nichols. 2007. Population ecology of the green/black turtle (*Chelonia mydas*) in Bahía Magdalena, Mexico. *Marine Biology* 153:35–46.
- Komoroske, L. M., M. P. Jensen, K. R. Stewart, B. M. Shamblin, and P. H. Dutton. 2017. Advances in the application of genetics in marine turtle biology and conservation. *Frontiers in Marine Science* 4:156.
- Limpus, C., and M. Chaloupka. 1997. Nonparametric regression modelling of green sea turtle growth rates (southern Great Barrier Reef). *Marine Ecology Progress Series* 149:23–34.
- Lomolino, M. V. 2005. Body size evolution in insular vertebrates: generality of the island rule. *Journal of Biogeography* 32: 1683–1699.
- Mazaris, D. A., G. Schofield, C. Gkazinou, V. Almpnidou, and G. C. Hays. 2017. Global sea turtle conservation successes. *Science Advances* 3:e1600730.
- Nalovic, M. A., S. A. Ceriani, M. M. P. B. Fuentes, J. B. Pfaller, N. E. Wildermann, and E. Cuevas, editors. 2020. Sea turtles in the North Atlantic & wider Caribbean region. MTSG Regional Report 2020. IUCN-SSC Marine Turtle Specialist Group, Ross, California, USA.
- National Marine Fisheries Service [NMFS] and United States Fish and Wildlife Service [USFWS]. 2015. Green turtle (*Chelonia mydas*) status review under the U.S. Endangered Species Act. Green Turtle Status Review Team, Washington, D.C., USA.
- National Research Council. 2010. Assessment of sea-turtle status and trends: integrating demography and abundance. National Academies Press, Washington, D.C., USA.
- National Weather Service. 2021. Past weather. <https://www.weather.gov/>. Accessed 22 Dec 2021.
- Piovano, S., M. Clusa, C. Carreras, C. Giacomini, M. Pascual, and L. Cardona. 2011. Different growth rates between loggerhead sea turtles (*Caretta caretta*) of Mediterranean and Atlantic origin in the Mediterranean Sea. *Marine Biology* 158:2577–2587.
- R Core Team. 2020. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
- Ramírez, M. D., L. Avens, J. A. Seminoff, L. Goshe, and S. Heppell. 2015. Patterns of loggerhead turtle ontogenetic shifts revealed through isotopic analysis of annual skeletal growth increments. *Ecosphere* 6(11):1–17.
- Ramírez, M. D., T. Popovska, and E. A. Babcock. 2021. Global synthesis of sea turtle von Bertalanffy growth parameters through Bayesian hierarchical modeling. *Marine Ecology Progress Series* 657:191–207.
- Schofield, G., M. Klaassen, K. Papafitsoros, M. K. S. Lilley, K. A. Katselidis, and G. C. Hays. 2020. Long-term photo-id and satellite tracking reveal sex-biased survival linked to movements in an endangered species. *Ecology* 101(7):e03072.
- Seminoff, J. A., T. T. Jones, A. Resendiz, W. J. Nichols, and M. Y. Chaloupka. 2003. Monitoring green turtles (*Chelonia mydas*) at a coastal foraging area in Baja California, Mexico: multiple indices to describe population status. *Journal of the Marine Biological Association of the United Kingdom* 83:1355–1362.
- Seminoff, J. A., A. Resendiz, W. J. Nichols and T. T. Jones. 2002. Growth rates of wild green turtles (*Chelonia mydas*) at a temperate foraging area in the Gulf of California, Mexico. *Copeia* 3:610–617.
- Sharpe, D. M. T., and A. P. Hendry. 2009. Life history change in commercially exploited fish stocks: an analysis of trends across studies. *Evolutionary Applications* 2:260–275.
- Snover, M., L. Avens, and A. Hohn. 2007. Back-calculating length from skeletal growth marks in loggerhead sea turtles *Caretta caretta*. *Endangered Species Research* 3:95–104.
- Snover, M. L., A. A. Hohn, L. R. Goshe, G. H. Balazs. 2011. Validation of annual skeletal marks in green sea turtles *Chelonia mydas* using tetracycline labeling. *Aquatic Biology* 12:197–204.
- Trippel, E. A. 1995. Age at maturity as a stress indicator in fisheries. *Bioscience* 45:759–771.
- Turner Tomaszewicz, C. N., J. A. Seminoff, L. Avens, L. R. Goshe, J. M. Riguez-Baron, S. Hoyt Peckham, and C. M. Kurlle. 2018. Expanding the coastal forager paradigm: long-term pelagic habitat use by green turtles *Chelonia mydas* in the eastern Pacific Ocean. *Marine Ecology Progress Series* 587:217–234.
- Turner Tomaszewicz, C. N., J. A. Seminoff, S. H. Peckham, L. Avens and C. M. Kurlle. 2017. Intrapopulation variability in the timing of ontogenetic habitat shifts in sea turtles revealed using $\delta^{15}\text{N}$ values from bone growth rings. *Journal of Animal Ecology* 86:694–704.
- Velez-Zuazo, X., J. Quiñones, A. S. Pacheco, L. Klinge, E. Paredes, S. Quispe, and S. Kelez. 2014. Fast growing, healthy and resident green turtles (*Chelonia mydas*) at two neritic sites in the central and northern coast of Peru: implications for conservation. *PLoS ONE* 9(11):e113068.
- Warden, M. L., H. L. Haas, P. M. Richards, K. A. Rose, and J. M. Hatch. 2017. Monitoring trends in sea turtle populations: walk or fly? *Endangered Species Research* 34:323–337.

- Wibbels, T. 1999. Diagnosing the sex of sea turtles in foraging habitats. Pages 139–143 in K. L. Eckert, K. A. Bjorndal, F. A. Abreu-Grobois, and M. Donnelly, editors. Research and management techniques for the conservation of sea turtles. IUCN/SSC Marine Turtle Specialist Group Publication Number 4, Ross, California, USA.
- Wood, S. 2017. Generalized additive models: an introduction with R. Chapman and Hall/CRC, New York, New York, USA.
- Wyneken, J., and M. Salmon. 2020. Linking ecology, morphology and behavior to conservation: lessons learned from studies of sea turtles. *Integrative and Comparative Biology* 60:440–455.

Associate Editor: Cynthia Paszkowski.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of the article at the publisher's website.

How to cite this article: Turner Tomaszewicz, C. N., L. Avens, E. L. LaCasella, T. Eguchi, P. H. Dutton, R. A. LeRoux, and J. A. Seminoff. 2022. Mixed-stock aging analysis reveals variable sea turtle maturity rates in a recovering population. *Journal of Wildlife Management* e22217. <https://doi.org/10.1002/jwmg.22217>