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Expanding the coastal forager paradigm: long-term pelagic habitat use by green turtles *Chelonia mydas* in the eastern Pacific Ocean

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ABSTRACT: The East Pacific green turtle *Chelonia mydas* population is gradually recovering, yet much remains unknown about their long-term demographics and habitat use due to their inaccessibility for study. We present the first detailed characterization of age-at-settlement (~3–5 yr), age-at-maturity (~17–30 yr), and long-term resource use patterns for these turtles by combining skeletochronology with stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis of annual bone growth layers. We studied dead green turtles stranding along the Baja California Peninsula at Playa San Lázaro in Mexico, where their deaths are presumed to be a result of regional fisheries bycatch. Our stable isotope results indicate that these turtles utilize resources differently than other regional, lagoon-foraging green turtle aggregations. Based on stable isotope values from multiple years for individual turtles, we propose these green turtles are long-term pelagic foragers in the coastal shelf habitat of the Gulf of Ulloa and consume a more carnivorous diet from the epipelagic zone, likely including fishery discards, similar to a sympatric group of foraging North Pacific loggerhead turtles. Thus, green turtles use the Gulf of Ulloa as more than a transit area between benthic lagoon foraging and/or breeding locations. This unexpected and prolonged use of a pelagic foraging area could benefit the turtles by facilitating increased somatic growth, but may be of conservation concern as this area also experiences high fisheries turtle bycatch rates. Our findings expand the current paradigm of green turtle life history and habitat use by demonstrating an unexpected exploitation of habitat and prey for post-oceanic stage turtles.

KEY WORDS: ^{13}C · ^{15}N · Sea turtle · Foraging ecology · Habitat use · Age

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INTRODUCTION

Elucidating variation in foraging behavior among individuals and populations is important for understanding the basic biology and ecology of organisms and is essential for effective management of species of conservation concern. Foraging ecology affects life

history and demographic parameters such as growth rates, age-at-maturity, life-stage duration, and, ultimately, fecundity (Weimerskirch et al. 1997, Bradshaw et al. 2004, Boyce et al. 2006, Hatase et al. 2013, Jones & Seminoff 2013). Unfortunately, elucidating inter- and intrapopulation variation in foraging strategies is difficult for many species with cryptic migra-

tory behavior that occupy remote habitats, and is especially problematic for many long-lived marine vertebrates (National Research Council 2010, Silber et al. 2016).

Despite these difficulties, recent advances in biogeochemistry, satellite telemetry, and remote sensing have revealed more complete behaviors and widespread distributions for many marine species (e.g. Halpin et al. 2006, Block et al. 2011, Crossin et al. 2014, Pendoley et al. 2014, Smolowitz et al. 2015), including revealing new biological paradigms for some populations of sea turtles, a globally distributed and long-lived migratory taxon (e.g. Turner Tomaszewicz et al. 2017a). For example, satellite tracking of hawksbill turtles *Eretmochelys imbricata* in the eastern Pacific demonstrated their unexpected utilization of inshore estuary and mangrove habitats (Gaos et al. 2011) and, in the Caribbean, demonstrated their dependence on seagrass pastures (Bjorndal & Bolten 2010) as opposed to their previously assumed primary specialization on coral reefs (Jones & Seminoff 2013). Here, we focus on the foraging ecology and demographics of a group of green sea turtles *Chelonia mydas* in the eastern Pacific Ocean to determine the degree to which they utilize a foraging hotspot off the Baja California Peninsula (BCP) in Mexico, where high rates of loggerhead turtle *Caretta caretta* mortality, likely due to fisheries bycatch, also occur (Peckham et al. 2007).

High productivity caused by wind-driven upwelling along coastal regions of the eastern Pacific Ocean creates foraging hotspots for numerous migratory and resident marine species (Ballance et al. 1997, Olson & Dinerstein 1998, Block et al. 2011). One of these areas off the west coast of North America and Mexico is the California Current Large Marine Ecosystem (CCLME), the southern range of which supports the recovering East Pacific (EP) population of threatened green turtles (Seminoff et al. 2015). This population nests along mainland Mexico and on 2 groups of Mexican Pacific oceanic islands. Once the target of a large regional fishery, the abundance of the EP green turtle population remains well below historic levels, but has experienced continued growth in recent decades, owing in large part to international protection of marine turtles (Delgado-Trejo & Alvarado-Figueroa 2012, Seminoff et al. 2015).

Green turtles are generally the most herbivorous of marine turtles and their life history begins with an omnivorous juvenile oceanic stage post-hatching, followed by settlement as juveniles in neritic coastal habitats, where they become resident foragers, often

in bays and lagoons, consuming predominantly seagrasses and algae (Bjorndal 1980, 1997, Arthur et al. 2008, Vander Zanden et al. 2012). However, numerous populations, including the EP population, remain omnivorous even after settling in neritic foraging grounds and developing to their adult stage (i.e. EP: Seminoff et al. 2002a, Carrión-Cortez et al. 2010, Parker et al. 2011, reviewed in Vélez-Rubio et al. 2016; NW Africa: Cardona et al. 2009; Japan: Hatase et al. 2006; Australia: Heithaus et al. 2002; the Mediterranean: Godley et al. 1998). In addition to seagrass and algae, EP green turtles consume benthic and plant-associated invertebrates (e.g. anemones, tube worms, sea pens) and pelagic invertebrates (e.g. sea jellies, pelagic red crabs, squid; Seminoff et al. 2002a, 2006, López-Mendilaharsu et al. 2005, Rguez-Baron 2010, UABCS 2014, Vélez-Rubio et al. 2016).

Post-oceanic stage EP green turtles generally settle in neritic habitats and forage benthically in near-shore lagoon areas, but have also been observed foraging in epipelagic zones of more open coastal shelf areas, such as the Gulf of Ulloa (López-Castro et al. 2010, Senko et al. 2010, UABCS 2014). For EP green turtles, size-at-settlement into neritic lagoon habitats has been observed to occur between ~33 to 50 cm curved carapace length (CCL) (Seminoff et al. 2002b, Koch et al. 2007, López-Castro et al. 2010, Eguchi et al. 2012). However, age-at-settlement analysis has not been conducted and the importance of the Gulf of Ulloa habitat for green turtles remains unclear. Traditional study methods, such as direct observation and flipper and satellite tagging, are limited by the duration of time that individual turtles may be continually observed. Better methods for characterizing resource use by long-lived species with complex life histories, such as sea turtles, include recently developed techniques to recreate sequential, multi-year habitat use and foraging patterns (Ramirez et al. 2015, Turner Tomaszewicz et al. 2016, 2017a). We linked skeletochronology with stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope analysis of annual bone growth layer and skin samples from dead-stranded EP green turtles collected along the BCP to describe their size, age, and long-term habitat use and foraging behaviors in the Gulf of Ulloa. The combination of skin and bone stable isotope (SI) data allowed us to better link relationships in the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from more commonly collected skin samples to those from bone, facilitating comparison with previous studies. We reconstructed multi-year resource and habitat use patterns for green turtles in this area of the eastern Pacific to better understand how residency in this coastal habitat may drive their demo-

graphics and overall population ecology. Our results offer new insights about the life history of green sea turtles in this region and have strong applications to the conservation, management, and ongoing recovery of this endangered population.

MATERIALS AND METHODS

Study area and sample collection

We collected humerus bone ($n = 62$) and skin ($n = 25$) samples (25 of which were paired skin and bone from the same turtles) from dead-stranded EP green turtles recovered during shoreline surveys along 45 km of Playa San Lázaro (PSL; Fig. 1) on the west coast of Baja California Sur, Mexico, between 2009 and 2012 as part of an ongoing monitoring project.



Fig. 1. Regional map of study site and sampling location, Playa San Lázaro (PSL), adjacent to the Gulf of Ulloa on the west coast of Baja California Sur (BCS), Mexico. Other eastern Pacific green turtle foraging sites are numbered: (1) San Diego Bay, CA, USA; and in BCS, Mexico: (2) Laguna Ojo de Liebre, (3) Punta Abreojos, (4) Laguna San Ignacio, and (5) Bahía Magdalena. Shading shows the depth (bathymetry) in meters

Most of the bones (20 in 2011 and 36 in 2012) were collected after shoreline surveys began targeting green turtle carcasses in August 2011. Skin samples were collected with a 6-mm biopsy punch from the upper shoulder region and humerus bones were removed manually. We cleaned and dried all tissues in the field and stored skin in salt and bones at room temperature until further analysis. During bone collection, if turtles were adequately intact, we measured their body size to the nearest 1 cm as CCL from the nuchal notch to the posterior marginal tip (Wyneken 2001). For samples lacking associated CCL, we estimated turtle sizes based on the relationship between CCL and humerus diameter measured from bones collected from turtles with known CCLs (following Goshe et al. 2010, Avens et al. 2012, Turner Tomaszewicz et al. 2015a): estimated CCL = $1.996 \times \text{humerus diameter} + 14.263$ (adj. $r^2 = 0.80$, $F = 220$, $p < 0.0001$; Fig. S1 in the Supplement at www.int-res.com/articles/suppl/m587p217_supp.pdf).

Skeletochronology — size and age estimation

We prepared a subset of collected turtle humerus bones for skeletochronological analysis and sequential SI analysis ($n = 35$, 8 of which were paired with skin samples), similar to Avens et al. (2013), Ramirez et al. (2015), and fully described in Turner Tomaszewicz et al. (2016, 2017a). We used skeletochronology to identify and measure annual growth layers that are distinguished by visible lines of arrested growth (LAGs; Goshe et al. 2009, Avens & Snover 2013). We then used the identified LAGs to guide sequential sampling of annual growth layers for SI analysis (Turner Tomaszewicz et al. 2016).

We first cross-sectioned humerus bones using a slow-speed Isomet saw and removed 2 adjacent 3 mm sections at the site on the bone proximal to the deltopectoral insertion scar. We set one section aside for future SI analysis (described below), and processed the other section for skeletochronology by fixing it in formalin (10% formalin, Fisher Scientific) and treating it with RDO Rapid Decalcifier (Apex Engineering). We then sliced a 25 μm section from the treated, 3 mm section and stained, mounted, and digitally imaged the subsection. As described in Goshe et al. (2009) and Avens et al. (2012), 3 independent readers (C.N.T.T., L.A., L.R.G.) identified LAGs, reaching a consensus on the number and location of all LAGs retained in each bone. We assigned each annual growth layer a date (year) based on the observed stranding date for each turtle, and esti-

mated age and back-calculated body size following Snover et al. (2007), Avens et al. (2012, 2013), and Turner Tomaszewicz et al. (2017a).

To estimate the age of each turtle using the standard skeletochronology protocol as described in Goshe et al. (2010), Avens et al. (2012), and Avens & Snover (2013), we summed the total number of observed LAGs and the total number of estimated LAGs that had been lost due to resorption. To estimate the number of LAGs lost for each bone, we applied the following commonly used correction factor approach. We first used bones that retained a distinct mark called an annulus that represents the end of the first year of growth (Snover & Hohn 2004, Goshe et al. 2010, Avens et al. 2012). We directly aged this group of turtles (Group 1) and generated a first-order correction factor, based on the best-fit model (selected by highest r^2 value) characterizing the relationship of LAG diameter and LAG number (Zug et al. 1986, Goshe et al. 2010). We used this first-order equation to estimate the LAGs lost from a second group of bones that retained at least one LAG with a diameter less than the largest LAG of Group 1 bones (Group 2). Finally, this second-order correction factor was applied to estimate LAGs lost from the remaining bones (Group 3). To estimate the ages of all Group 2 and Group 3 bones, we used these equations, and then summed the estimated number of LAGs lost from each bone with the number of LAGs retained in each bone.

Depending on the date (month) a turtle stranded relative to its hatching date (month), turtles we sampled were likely in the middle of their growth for the year. Thus, their final growth layer would reflect only a partial year and the age estimates required adjustments to account for this (Avens et al. 2012). We did this by applying population-specific peak hatching months to (1) the estimated time of LAG formation and (2) the stranding month for each individual turtle (fully described in the Supplement at www.int-res.com/articles/suppl/m587p217_supp.pdf; also see Avens et al. 2012, Turner Tomaszewicz et al. 2015a). We then rounded all ages to the nearest whole number (as per Avens et al. 2012 and Turner Tomaszewicz et al. 2015a), assigned the final estimated age-at-stranding to the outer-most growth layer for each turtle, and assigned sequential preceding ages to each sequential interior growth layer.

To back-calculate body size estimates for each turtle at each LAG, we applied the body proportional hypothesis (BPH)-corrected allometric equation as recommended in Snover et al. (2007) and commonly applied in skeletochronology studies:

$$L_i = [L_{op} + 4.85 (D_i - D_{op})^{0.8}] (L_{final}) [L_{op} + 4.85 (D_{final} - D_{op})^{0.8}]^{-1} \quad (1)$$

where L_i is CCL (cm) of the turtle at LAG i , D_i is the diameter (mm) of LAG i , L_{op} is the minimum hatchling CCL, D_{op} is the minimum hatchling diameter (1.6 mm), L_{final} is the final carapace length (cm), and D_{final} is the final humerus diameter (mm). This method allows for conversion of the LAG diameter measurements (mm) into an estimate of body size (CCL, cm) at each LAG, but requires the minimum hatchling carapace length and humerus diameter measurements from EP green turtle hatchlings. We collected these measurements from fully developed but deceased hatchlings excavated from nests at a hatchery near San Pancho, Nayarit, Mexico, in September and October 2015. To estimate incremental growth for each individual turtle, we used the difference between pairs of subsequent LAG measurements and converted these to body size estimates (CCL) (as per Snover et al. 2007 and Turner Tomaszewicz et al. 2017a). We rounded all body size and growth measurements to the nearest whole centimeter.

We evaluated and described the size-at-age relationship using a generalized additive mixed model (GAMM), as conducted and fully discussed in other skeletochronology and growth studies (e.g. Chaloupka & Limpus 1997, Chaloupka & Musick 1997, Avens et al. 2012, 2013). In this analysis, we used the gamm function in the package 'mgcv' in R (Wood 2011, R Core Team 2013) to best describe estimated body size at given ages for this sample group of EP green turtles. Within this model, we accounted for inherent individual variability and growth biases by including individual turtles as a random effect (Chaloupka & Balazs 2005, Avens et al. 2012). We then used the 'smooth.spline' in the package 'stats' (Hastie & Tibshirani 1990, R Core Team 2013) to fit a cubic smoothing spline function to the relationship between the estimated age data and the predicted fit with 95 % confidence intervals.

Stable isotope analysis

We rinsed, homogenized, and freeze-dried the skin samples, then weighed and placed ~1.0 mg of skin tissue in tin capsules for SI analysis. The effect of lipid extraction on the isotope values of skin samples, including samples from this study, has been tested elsewhere (Vander Zanden et al. 2012, Turner Tomaszewicz et al. 2017b) and found to be unneces-

sary, so we report the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ from intact samples. As described above, a second, 3-mm cross-section of turtle humerus bone was utilized for sequential SI analysis. We created a skeletochronology-derived annual layer guide to direct a computer-guided micromill to sequentially sample the individual annual growth layers of the collected humerus bones (see complete description of this process in Turner Tomaszewicz et al. 2016). We extracted ~1.5 mg of bone powder from each individual growth layer, then loaded and weighed the powder into tin capsules for SI analysis. Additional chemical treatment was not required for lipid extraction or the removal of inorganic carbonate (Post et al. 2007, Turner Tomaszewicz et al. 2015b). However, all untreated bone $\delta^{13}\text{C}$ values were mathematically adjusted to reflect bone collagen values as recommended by Turner Tomaszewicz et al. (2015b), using the linear equation specific to EP green turtles: $\delta^{13}\text{C}_{\text{corrected}} = 1.2 \times \delta^{13}\text{C}_{\text{bulk}} + 2.1$ and applied in Ramirez et al. (2015) and Turner Tomaszewicz et al. (2017b). No correction is required for $\delta^{15}\text{N}$ values (Turner Tomaszewicz et al. 2015b). We present the corrected $\delta^{13}\text{C}$ values from the turtle bones here, but all data are available in the Supplement (Table S1).

To facilitate comparison of the SI values from EP green turtle bones in this study with those from skin tissues more commonly collected in previous EP green turtle studies, we compared the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from our bone data with those from skin samples that we collected and from previous studies. We then applied the bone-to-skin relationship, experimentally determined in Turner Tomaszewicz et al. (2017b) for EP green turtles, and calculated skin-equivalent bone SI values for the present study ($\delta X_{\text{bone-to-skin}}$) using the following equations from our previous research (Turner Tomaszewicz et al. 2017b):

$$\delta^{13}\text{C}_{\text{bone-to-skin}} = 0.54 \times \delta^{13}\text{C}_{\text{bone}} - 8.31 \quad (2)$$

(adj. $r^2 = 0.2119$, $p = 0.0137$)

$$\delta^{15}\text{N}_{\text{bone-to-skin}} = 0.89 \times \delta^{15}\text{N}_{\text{bone}} + 2.55 \quad (3)$$

(adj. $r^2 = 0.6116$, $p < 0.0001$)

We recognize these relationships are not perfect correlations and other factors requiring further study are affecting the relationships in isotope ratios between bone and skin. But despite this, we applied these conversion equations because these are the best data available from which to make informed comparisons of SI ratios from different tissues presented in other turtle studies.

We analyzed all samples for their $\delta^{13}\text{C}$, $\delta^{15}\text{N}$, %C, and %N values via combustion in a Carlo Erba NA

1500 CNS elemental analyzer interfaced via a Con-Flow II device to a Thermo Electron DeltaV Advantage isotope ratio mass spectrometer at the Stable Isotope Geochemistry Lab at the University of Florida, Gainesville, FL, USA. Stable isotope ratios of the samples, relative to isotope standards, was expressed using conventional delta (δ) notation in parts per thousand or permil (‰):

$$\delta X = \left(\frac{R_{\text{sample}}}{R_{\text{standard}}} - 1 \right) \times 1000 \quad (4)$$

where the corresponding ratios of heavy to light isotopes ($^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$) in the sample and standard are represented by R_{sample} and R_{standard} , respectively. Here, R_{standard} for $\delta^{13}\text{C}$ was Vienna Pee Dee Belemnite and R_{standard} for $\delta^{15}\text{N}$ was atmospheric N_2 , and laboratory reference materials (USGS40) were calibrated at regular intervals against the standards. We determined the average precision for the isotope data as the SD of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from a set of standards (L-glutamic acid), and these values were 0.04‰ and 0.07‰, respectively.

Identifying resource use patterns

To characterize long-term resource use patterns for this group of EP green turtles compared to other neritic EP green turtle foraging aggregations, we first isotopically categorized EP lagoon foraging areas using the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values measured from green sea turtle skin samples collected in southern California, USA, and the BCP, Mexico, and reported in previous studies detailed below. Turtles in these sites are presumed to be resident foragers (e.g. López-Castro et al. 2010), and any variation among individuals (i.e. movement between other locations, prey preference, size, age, growth, etc.) is captured using the mean (\pm SD) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from multiple turtles at each location to characterize each site. From north to south, lagoon foraging sites included San Diego Bay (Lemons et al. 2011), Laguna Ojo de Liebre (Rguez-Baron 2010), Punta Abreojos (Santos Baca 2008), Laguna San Ignacio (Lewis 2009, Rguez-Baron 2010), and Bahia Magdalena (Santos Baca 2008, Rguez-Baron 2010; Fig. 1). The mean (\pm SD) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values from the 4 BCP lagoon foraging sites ranged from 10.4 to 15.0‰ and -18.4 to -12.1 ‰, respectively (Lewis 2009, Rguez-Baron 2010; Table 1, Fig. 2).

The mean values from all but one of the BCP lagoon foraging sites had $\delta^{13}\text{C}$ values greater than -16 ‰; only turtles from Bahia Magdalena had mean $\delta^{13}\text{C}$ values lower than -16 ‰ (Santos Baca 2008, Lewis 2009, Rguez-Baron 2010; Fig. 2). Therefore, we

Table 1. Mean stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values (‰; \pm SD) from skin sampled from eastern Pacific green turtles collected from different foraging sites in the USA and Baja California Sur, Mexico. The isotope values from both skin and the adjusted bone-to-skin values from this study are also shown, as well as the differences in the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the bone-to-skin values from turtles collected at Playa San Lazaro (PSL) in this study, and those from the skin values at each regional site

Location	$\delta^{13}\text{C}$ (‰)	$\delta^{15}\text{N}$ (‰)	$\delta^{13}\text{C}$ Difference (‰) from PSL bone- to-skin means	$\delta^{15}\text{N}$ Difference (‰) from PSL bone- to-skin means	Reference
San Diego Bay, CA, USA	-15.9 ± 1.1	17.1 ± 1.3	-1.1	-1.7	Lemons et al. (2011)
Laguna Ojo Liebre, Mexico	-14.0 ± 0.6	10.7 ± 0.3	5.3	-3.6	Rguez-Baron (2010)
Punta Abreojos, Mexico	-14.7 ± 2.4	12.1 ± 2.2	3.9	-2.9	Santos-Baca (2008)
Laguna San Ignacio, Mexico	-15.7 ± 3.7	9.7 ± 2.6	6.3	-2.0	Santos-Baca (2008)
	-14.5 ± 1.9	12.8 ± 2.2	3.2	-3.1	Lewis (2009)
	-12.5 ± 0.5	12.3 ± 0.5	3.7	-5.1	Rguez-Baron (2010)
Bahia Magdalena, Mexico	-16.6 ± 3.9	9.9 ± 2.9	6.1	-1.0	Santos-Baca (2008)
	-18.1 ± 0.3	11.2 ± 0.3	4.8	0.5	Rguez-Baron (2010)
Playa San Lazaro, Mexico	16.6 ± 0.8	16.2 ± 1.2	-0.2	-1.0	Present study; Turner Tomaszewicz et al. (2017b)
Playa San Lazaro, Mexico — bone-to-skin	-17.6 ± 1.2	16.0 ± 2.1	-	-	Present study

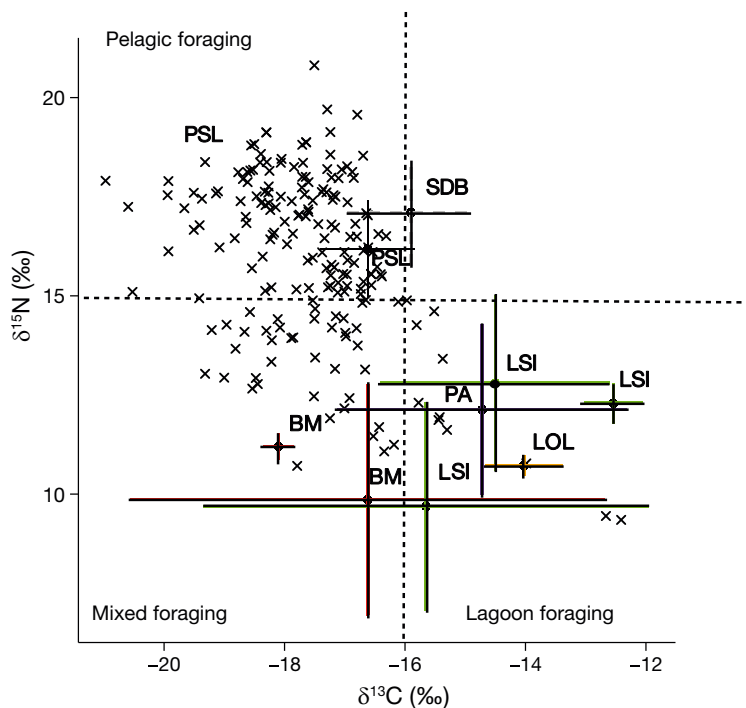


Fig. 2. Mean (\pm SD) stable carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) isotope values of skin from east Pacific (EP) green turtles from foraging sites in Baja California Peninsula (BCP) lagoons and bays and one Southern California bay, coded by letter. Black \times symbols show isotope values converted from bone to skin from the 189 annual growth layer samples taken from 35 dead-stranded turtles at Playa San Lázaro (PSL) for this study. Isotopic thresholds (dashed lines) at 15‰ for $\delta^{15}\text{N}$ and -16 ‰ for $\delta^{13}\text{C}$ distinguish between likely pelagic coastal, benthic lagoon, or mixed foraging. Sampling locations: BM: Bahia Magdalena, Baja California Sur (BCS), Mexico (Santos-Baca 2008; Rguez-Baron 2010); LOL: Laguna Ojo de Liebre, Mexico (Rguez-Baron 2010); PA: Punta Abreojos, BCS, Mexico (Santos-Baca 2008); PSL: Playa San Lázaro, BCS, Mexico (Turner Tomaszewicz et al. 2017b, present study); SDB: San Diego Bay, CA, USA (Lemons et al. 2011); LSI: Laguna San Ignacio, BCS, Mexico (Santos-Baca 2008, Lewis 2009, Rguez-Baron 2010)

used the $\delta^{15}\text{N}$ value of 15‰ and the $\delta^{13}\text{C}$ value of -16 ‰ as threshold values to isotopically characterize lagoon and pelagic coastal shelf foraging areas along the Pacific coast of the BCP (Fig. 2). SI values from turtle bone growth layers that did not match up as described above (e.g. $\delta^{15}\text{N} > 15$ ‰ and $\delta^{13}\text{C} > -16.0$ ‰) indicate possible mixed use of lagoons and coastal pelagic habitats, and we could not definitively assign turtles in those years to a foraging region. The 2 types of foraging habitats described above are hereafter referred to as 'benthic lagoon' and 'pelagic coastal'.

We are confident in our isotopic characterizations of benthic lagoon versus pelagic coastal regions in the EP because the underlying mechanisms driving the differences we observed are clearly understood and described in previous studies (Clementz & Koch 2001, Clementz et al. 2006, Arthur et al. 2008, Snover et al. 2010, Lemons et al. 2011, Avens et al. 2013, Ramirez et al. 2015). Higher $\delta^{15}\text{N}$ values from EP green turtles foraging in the epipelagic zone of the coastal Gulf of Ulloa habitat (pelagic coastal) versus those foraging benthically in a lagoon habitat are expected

to be primarily caused by the differing diets between the 2 groups. Turtles foraging in the coastal pelagic Gulf of Ulloa commonly consume higher trophic level prey, such as pelagic red crabs, cephalopods, fish that have been discarded from local fisheries (Peckham et al. 2011, UABCS 2014), and minimal amounts, if any, of algae or seagrass. This higher trophic level, pelagic-based diet would result in higher $\delta^{15}\text{N}$ values in their tissues than turtles foraging more herbivorously in lagoons (DeNiro & Epstein 1981, Turner Tomaszewicz et al. 2017a). Further, the $\delta^{13}\text{C}$ values in marine systems are typically higher in nearshore (i.e. lagoon) than offshore (i.e. coastal shelf) areas (Clementz & Koch 2001, Clementz et al. 2006), underscoring their utility for differentiating between benthic and pelagic foraging. This underlying natural gradation of $\delta^{13}\text{C}$ values is magnified for green turtles, as those foraging in lagoons typically consume high $\delta^{13}\text{C}$ -value seagrass ($\sim -10\text{‰}$) (Clementz et al. 2006, Santos Baca 2008, Arthur et al. 2008, Lewis 2009, Lemons et al. 2011), to which turtles foraging exclusively offshore in coastal shelf pelagic waters have no access.

Finally, we combined the sequential bone growth layer SI results with our skeletochronology-derived size and age estimates to examine life history and long-term habitat use patterns of this group of EP turtles. To assess their habitat use and foraging patterns, and how these may change over time with age and/or size, we assigned individual turtles to an isotopically characterized habitat (benthic lagoon versus pelagic coastal), based on the SI values of individual growth layers, and matched those data to specific years and the corresponding turtle ages and sizes (as per Ramirez et al. 2015 and Turner Tomaszewicz et al. 2017a). Significance for statistical analyses was tested at the $\alpha = 0.05$ level and all means are reported \pm SD.

RESULTS

Size distribution and size and age estimates

Body sizes (CCL) for the 62 dead-stranded green turtles we collected, and the subset of 35 bones selected for skeletochronology, ranged from 42 to 95 cm (means 59.6 ± 10.2 and 60.3 ± 12.7 cm, respectively; Figs. S1 & S2 in the Supplement). The CCL values from 3 of the turtles for which we had bones were missing, so we estimated them based on previously established relationships between humerus bone diameters and CCL measures (see 'Materials and

methods'; Fig. S1). For age and size estimation, we identified and measured a total of 276 LAGs from the 35 individual turtles. The number of retained LAGs from an individual turtle ranged from 2 to 22. Bones that retained an annulus (the LAG from the first year of a turtle's life) and were therefore directly aged (Group 1, $n = 5$, mean CCL 49 ± 6.9 cm), with age ranging from 3 to 5 yr old (Fig. 3). The 15 LAG diameters and LAG numbers retained in Group 1 bones were positively correlated ($p < 0.001$, adj. $r^2 = 0.71$) and were used to generate the first-order correction factor equation (Fig. S3 in the Supplement):

$$\text{LAG diameter (mm)} = 2.1199 \times \text{LAG number} + 10.006 \quad (5)$$

The maximum measured LAG diameter from Group 1 was 18.73 mm. Following the skeletochronology age estimation protocol (see 'Materials and methods'), the first-order equation was applied to estimate the number of LAGs lost due to resorption for Group 2 bones (those with at least one LAG with a diameter less than 18.73 mm, $n = 23$, mean CCL 58 ± 7.6 cm). The LAG diameters and LAG numbers from these Group 2 bones were also positively correlated ($p < 0.001$, adj. $r^2 = 0.78$). We then generated the second-order correction equation using all the retained LAGs from both Group 1 ($n = 5$ bones, 15 LAGs) and Group 2 ($n = 23$ bones, 113 LAGs) to estimate the number of LAGs lost for the remaining Group 3 bones ($n = 8$, mean CCL 77 ± 14.4 cm), which were those that did not retain at least one LAG less than 18.73 mm ($n = 7$ bones, 65 LAGs; Fig. S3):

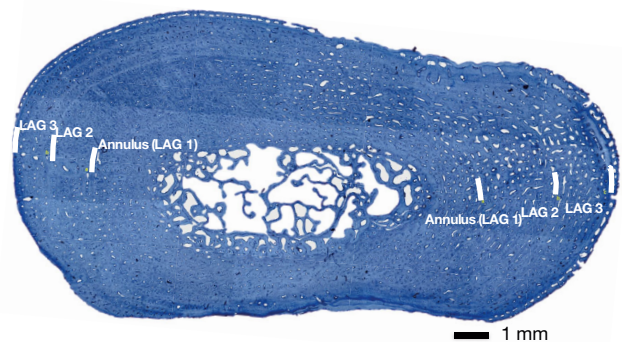


Fig. 3. Image of a stained cross-section cut from a humerus bone collected from a 44 cm curved carapace length green turtle stranded in July 2012. This bone retained its annulus layer of arrested growth (LAG), which is the LAG from the first year of a turtle's life. Age was determined to be 4 yr by counting the 3 retained LAGs, adding 0.5 yr to account for partial growth that occurred over ~ 6 mo from January (peak hatching for east Pacific green turtles) to the stranding month of July, and rounding to the nearest whole number. See 'Materials and methods' for details

$$\text{LAG diameter (mm)} = 1.2562 \times \text{LAG number} + 11.444 \quad (6)$$

The estimated age, adjusted for stranding date and partial growth, and rounded to the nearest whole number, for all 35 turtles used in our skeletochronology analysis ranged from 3 to 32 yr old at stranding (mean 9.8 ± 7.2). The 2 oldest turtles (~32 yr) were similar in both body size and bone diameter, yet the spacing of the growth layers varied, which could affect final age estimates, with one turtle being omitted for age-at-maturation estimates (see Discussion and the supplement). Estimated body sizes (CCL, cm), converted from measured LAG diameters (mm), ranged from 31 to 95 cm. For this conversion, the minimum EP green turtle hatchling ($n = 6$) carapace length was 4.3 cm (mean 4.8 ± 0.35 cm) and minimum hatchling humerus diameter was 1.6 mm (mean 1.8 ± 0.25 mm):

$$L_i = [4.3 + 4.85 (D_i - 1.6)^{0.8}] (L_{\text{final}})[4.3 + 4.85 (D_{\text{final}} - 1.6)^{0.8}]^{-1} \quad (7)$$

The relationship between CCL and humerus diameter at stranding for the 35 bones was allometric, with slope (b) = 4.85 and the proportionality coefficient (c) = 0.8002.

Estimated length-at-age for young turtles (<5 yr) ranged from ~30 to 65 cm CCL, whereas older turtles (>15 yr) ranged from ~60 to 95 cm CCL (Fig. 4). For

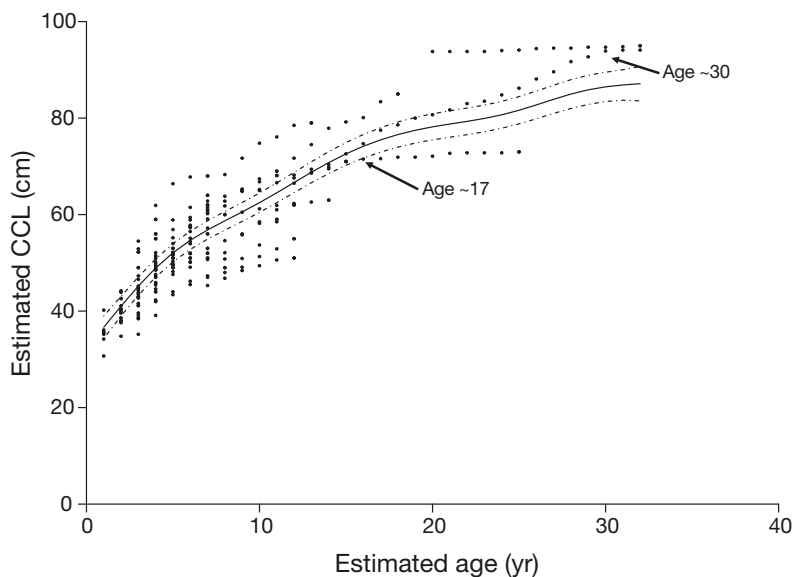


Fig. 4. Estimated body sizes (curved carapace length [CCL], cm) and estimated ages for individual turtles ($n = 35$), and predicted length-at-age relationship (black line; dashed lines mark the 95% confidence intervals). We estimated age-at-settlement based on the estimated age for turtles at 50 cm CCL (46 cm straight carapace length; Seminoff et al. 2003). We estimated the range for age-at-maturity using the CCL growth plateaus observed for the 3 largest individuals. See 'Materials and methods' for details

individual turtles, the length-at-age record indicates age at maturation when an observable plateau in CCL occurs. The growth of the 3 oldest turtles plateaued at 2 distinct size classes—a smaller size at ~75 to 85 cm CCL, and a larger size at ~95 cm CCL—and the corresponding ages at onset of these plateaus were ~17 and ~30 yr of age, respectively (Fig. 4, Fig. S4 in the Supplement). Based on our 95% CI for size-at-age from the GAMM (Fig. 4, Fig. S4), when aligned to previously reported size-at-settlement for EP green turtles in this region (Pacific coast, 33 cm, López-Castro et al. 2010; Gulf of California, 50 cm, Seminoff et al. 2003), the estimated age-at-settlement for this population, when the transition from the oceanic to the neritic stage occurred, was ~3 to 5 yr. The oldest age for a turtle corresponding to the maximum reported size-at-settlement range (50 cm CCL, Seminoff et al. 2003) was 10 yr old, and this represents a maximum range estimate for age-at-settlement. Finally, annual somatic growth, estimated from incremental growth, ranged from 0 to 11.1 cm yr^{-1} , and the mean was $2.7 \pm 2.3 \text{ cm yr}^{-1}$ (Fig. S5). The mean annual growth decreased with increasing size class; it was highest at $3.9 \pm 2.1 \text{ cm yr}^{-1}$ for the 30–40 cm size class, and lowest at $0.4 \pm 0.6 \text{ cm yr}^{-1}$ for the 90–100 cm size class (Fig. S5 in the Supplement). The maximum amount of estimated CCL growth recorded within a single bone was ca. 29 cm, which was represented by over 22 annual growth layers measured in the humerus bone from a 94 cm CCL turtle.

Stable isotope analysis

We identified 276 LAGs in the turtle humerus bones, and 189 growth layers, which are separated by LAGs, were wide enough to permit sequential isotopic sampling. We observed high variation in SI patterns and values within individual turtles (Fig. 5, Fig. S6 in the Supplement) and the $\delta^{15}\text{N}$ and corrected $\delta^{13}\text{C}$ (see 'Materials and methods') values ranged from 7.6 to 20.5‰ (mean 15.1 ± 2.4 ‰) and -23.5 to -7.6 ‰ (mean -17.2 ± 2.2 ‰), respectively. The $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were negatively and positively correlated, respectively, with both increasing body size and age (size: N slope = -0.03 , $p = 0.01$, adj. $r^2 = 0.03$; C slope =

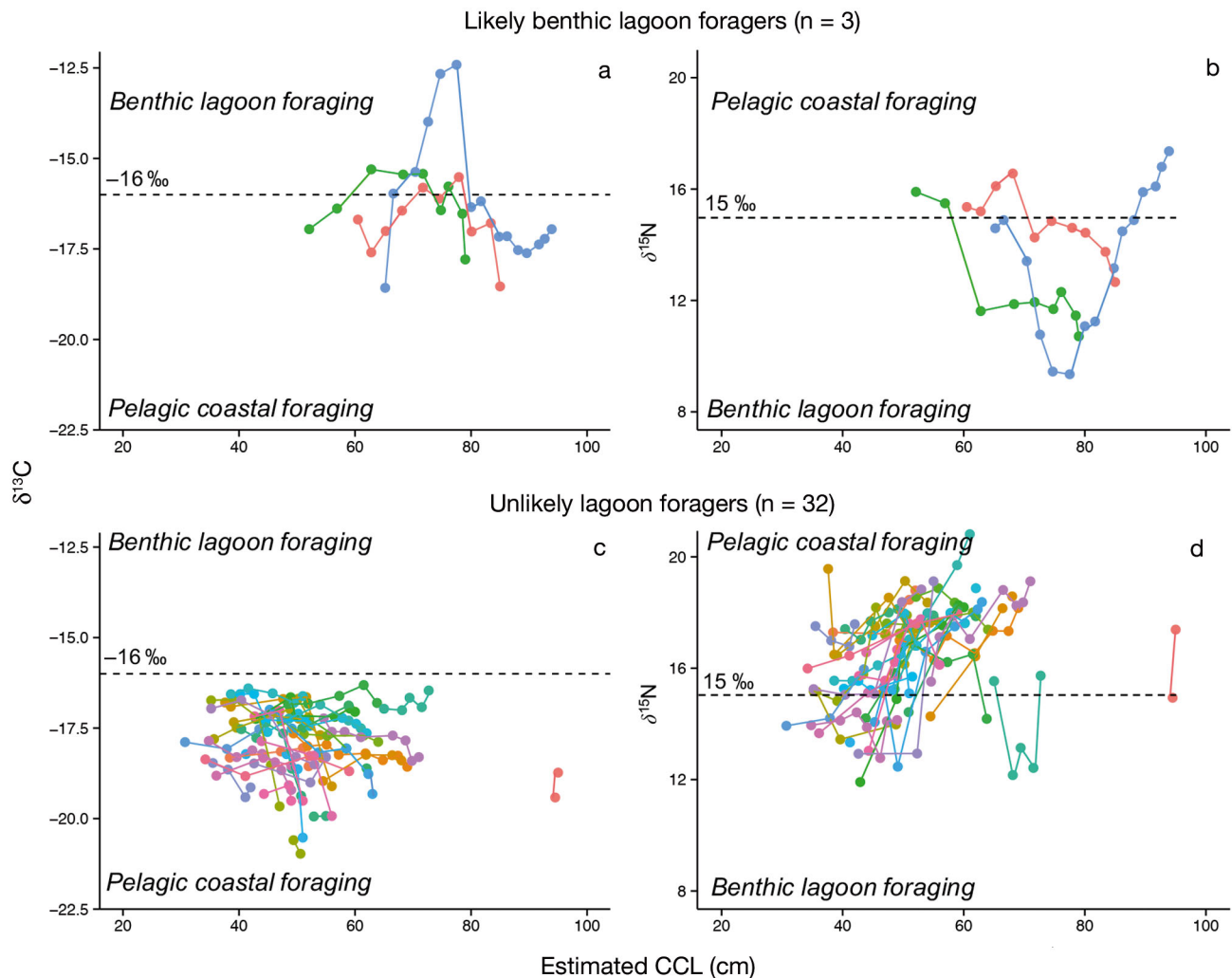


Fig. 5. Bone-to-skin stable isotope values from humerus bone growth layers from $n = 35$ individual turtles, shown in different colors, and aligned to corresponding estimated body sizes (cm, curved carapace length [CCL]). Dashed lines at the 15.0‰ ($\delta^{15}\text{N}$) and -16.0 ‰ ($\delta^{13}\text{C}$) thresholds distinguish likely pelagic coastal (>15 ‰, <-16.0 ‰) versus benthic lagoon (<15 ‰, >-16.0 ‰) foraging. Turtles sorted into 2 groups based on their isotope values: (a,b) those indicating likely use of benthic lagoon foraging habitats ($n = 3$), and (c,d) those indicating unlikely use of benthic lagoon foraging habitats ($n = 32$), based on $\delta^{13}\text{C}$ values and -16 ‰ threshold (see 'Materials and methods'). The $\delta^{13}\text{C}$ (a,c) and $\delta^{15}\text{N}$ (b,d) values from the 2 groups of turtles were significantly different between likely and unlikely benthic lagoon foragers (Welch 2-sample t -test, $p < 0.0001$, $t = -7.0631$, $df = 43$, means: 13.7 ‰ versus 16.5 ‰)

0.04; age: N slope = -0.07 , $p = 0.02$, $r^2 = 0.02$; C slope = 0.05 , $p = 0.04$, adj. $r^2 = 0.02$, respectively).

The mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values from the skin samples were -16.6 ± 0.8 ‰ and 16.2 ± 1.2 ‰, respectively (Table 1, Fig. 2). The converted bone-to-skin mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were -17.6 ± 1.2 ‰ and 16.0 ± 2.1 ‰, respectively (Table 1, Fig. 2). A total of 135 of the 189 annual layers (71.4%; from 34 of the 35 turtles) had SI values indicating pelagic coastal foraging ($\delta^{13}\text{C} < -16$ ‰ and $\delta^{15}\text{N} > 15$ ‰; Figs. 2 & 5). Only 11 of the 189 annual layers (5.8%; from 3 turtles) had $\delta^{13}\text{C}$ greater than -16 ‰ and $\delta^{15}\text{N}$ values less than 15‰,

suggesting benthic lagoon foraging (Figs. 2 & 5). The remaining 43 annual layers (22.8%; from 18 turtles) had SI values indicating mixed (and therefore unassignable) foraging for at least one annual growth layer, with $\delta^{13}\text{C}$ values suggesting pelagic coastal foraging, and $\delta^{15}\text{N}$ values suggesting benthic lagoon and/or lower trophic level foraging (Figs. 2 & 5). For the 3 individual turtles with SI values indicative of at least some benthic lagoon foraging, the annual layers with higher $\delta^{13}\text{C}$ values also had corresponding lower $\delta^{15}\text{N}$ values, as expected with some benthic lagoon foraging that would include consumption of

eelgrass *Zostera marina* and macroalgae (Fig. 5). Similarly, for the 32 turtles that did not have $\delta^{13}\text{C}$ values above -16‰ , their annual layers with lower $\delta^{13}\text{C}$ values corresponded to higher $\delta^{15}\text{N}$ values, as expected from more carnivorous foraging in the pelagic coastal habitat (Fig. 5). The $\delta^{15}\text{N}$ values from the 3 turtles indicating some benthic lagoon foraging were significantly lower than the $\delta^{15}\text{N}$ values from the other 32 turtles (Welch 2-sample *t*-test, $p < 0.0001$; Fig. 5).

Finally, the likely timing of isotope-indicated ontogenetic shift between oceanic and neritic habitats, based on changes in $\delta^{15}\text{N}$ values, was observed in several individual turtles. Fourteen individuals showed pronounced increases in $\delta^{15}\text{N}$ values of more than 3‰ before the age of ~ 10 yr, and at sizes smaller than ~ 60 cm CCL (Fig. 5, Fig. S6).

DISCUSSION

Here we present the first detailed characterizations of the age, size, and multiple, sequential-year life histories and resource-use patterns of EP green turtles, along with the first empirical estimates of their age-at-settlement to coastal waters along the BCP and age-at-maturation. Our data also expand the array of life history paradigms for green turtles, providing evidence for long-term, pelagic coastal foraging by some individuals, and highlighting potential conservation and management implications.

While the size distribution of green turtles using the pelagic coastal Gulf of Ulloa habitat is comparable to the size distribution of green turtles observed foraging regionally in benthic lagoon and bay habitats (López-Castro et al. 2010, Eguchi et al. 2012), the SI values suggest that this group of turtles stranding at PSL uses resources differently. Turtles in the present study had both higher $\delta^{15}\text{N}$ values and lower $\delta^{13}\text{C}$ values (Figs. 2 & 5) than would be expected from turtles foraging primarily in a lagoon habitat, even in comparison to other omnivorous foraging aggregations of EP green turtles in the region (Santos Baca 2008, Rguez-Baron 2010).

Tens of thousands of North Pacific loggerhead turtles use the productive waters of the Gulf of Ulloa (Wingfield et al. 2011, Seminoff et al. 2014), and based on the distinct SI values recorded over several years from multiple green turtles, our annual bone growth layer data indicate that at least some green turtles may be foraging long-term in this pelagic coastal area as well. These green turtles consume a more carnivorous diet, similar to the long-term habi-

tat use demonstrated for the carnivorous, sympatric group of loggerheads (Peckham et al. 2011, Turner Tomaszewicz et al. 2015a, 2017a). This unexpected habitat use of a pelagic coastal foraging area by green turtles is important for future conservation of this population as it could expand the regional management scope beyond the previously assumed lagoon neritic foraging regions and nesting sites.

Identifying ontogenetic shifts

Sea turtle ontogenetic shifts, from oceanic to more neritic habitats, based on SI data have been identified in other studies (Arthur et al. 2008, Cardona et al. 2009, Snover et al. 2010, Ramirez et al. 2015, Turner Tomaszewicz et al. 2017a). This includes studies comparing SI values from green and loggerhead turtle tissues with those of prey items consumed by turtles in each distinct habitat (oceanic offshore versus neritic nearshore) (Arthur et al. 2008, Lewis 2009, Rguez-Baron 2010, Snover et al. 2010, Lemons et al. 2011, Ramirez et al. 2015). We observed distinct isotope-indicated ontogenetic shifts in several individual turtles in our study, especially for those in the early life stages, when juvenile green turtles are thought to shift from an oceanic to a neritic stage (Bjorndal 1997). First, individuals with biologically meaningful changes in their $\delta^{15}\text{N}$ values (i.e. $>3\text{‰}$) and before the age of 10 yr, and smaller than 60 cm CCL (Fig. 5, Fig. S6), likely underwent an ontogenetic shift in resource use, moving from an oceanic juvenile to a neritic juvenile stage. The small variability observed in the $\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$ values ($<3\text{‰}$ and $<2\text{‰}$, respectively) from larger juvenile turtles (40 to 60 cm CCL) suggests more consistent resource use by turtles once they have already shifted from oceanic to neritic habitats (Fig. 5). Finally, regarding shifts in habitat at later life stages, some of the older and larger turtles showed variable patterns in their $\delta^{15}\text{N}$ and/or $\delta^{13}\text{C}$ values, suggesting mixed resource use during these large juvenile and adult life stages (Fig. 5, Fig. S6).

Among green turtles that have settled to neritic habitats, we expected fluctuations in $\delta^{13}\text{C}$ values to reflect significant changes in resource use between benthic lagoon and pelagic coastal foraging areas (Clementz & Koch 2001, Clementz et al. 2006, Arthur et al. 2008). The $\delta^{13}\text{C}$ values from the bones of our EP green turtles at PSL showed changes $>2\text{‰}$ (Fig. 5, Fig. S6) and, similar to the skin from PSL turtles (Turner Tomaszewicz et al. 2017b), were lower than the $\delta^{13}\text{C}$ values from other benthic lagoon EP turtle

foraging sites. This is indicative of pelagic coastal habitat use by PSL turtles (Figs. 2 & 5). Interestingly, the mean $\delta^{13}\text{C}$ values of PSL turtles aligned with the mean $\delta^{13}\text{C}$ values of turtles from Bahia Magdalena, which is immediately south of PSL (Figs. 1 & 2), suggesting that the $\delta^{13}\text{C}$ values in this region are similar, and resource use between these 2 groups of turtles could be comparable. Related to year-round foraging for turtles stranding at PSL, most of the $\delta^{13}\text{C}$ values from the annual bone growth layers (converted to skin equivalent values) were lower than those from PSL skin. Isotope values from bone reflect an entire year's worth of resource use, whereas those from skin reflect diet ingested ~4 to 6 mo previous and up to the time of tissue collection (Reich et al. 2008). The lower $\delta^{13}\text{C}$ values of the PSL bone suggests increased use of pelagic coastal habitats throughout the entire year, rather than over the shorter ~4 to 6 mo reflected in the PSL skin samples. Finally, lipids, which are known to have lower $\delta^{13}\text{C}$ values than proteinaceous material, and are present in whole bone (Post et al. 2007, Medeiros et al. 2015), may lower the $\delta^{13}\text{C}$ from the bone samples. However, we are confident that lipids were not influencing the $\delta^{13}\text{C}$ values from our samples because we (1) corrected the $\delta^{13}\text{C}$ values as recommended in Turner Tomaszewicz et al. (2015b), and (2) only sampled cortical bone for SI analysis. The cortical bone has low lipid content (Turner Tomaszewicz et al. 2015b) and our precise sampling method allowed us to avoid the inclusion of the more lipid rich medullary cavity (as included and tested by Medeiros et al. 2015).

We also expected an overall pattern of increasing $\delta^{15}\text{N}$ values as turtles made an ontogenetic shift from their oceanic juvenile stage to a neritic juvenile stage and continued to increase in body size. This is because the $\delta^{15}\text{N}$ values would reflect both trophic and baseline changes in diet and habitat. First, $\delta^{15}\text{N}$ values would increase due to the higher trophic level of prey as turtles increase in size (DeNiro & Epstein 1981, Minagawa & Wada 1984, Post 2002) and move into more productive neritic regions, which include both lagoons and the pelagic coastal Gulf of Ulloa. Second, higher baseline $\delta^{15}\text{N}$ values are characteristic of more nearshore neritic environments, especially areas of upwelling that introduce denitrified waters with higher $\delta^{15}\text{N}$ values (Rau et al. 2003, Somes et al. 2010). The mean $\delta^{15}\text{N}$ values from the PSL turtles were much higher (3.4 to 5.5‰) than the mean values from turtles sampled at other BCP lagoon foraging sites (Table 1, Figs. 2 & 5), and were nearly as high as those observed in green turtles from San Diego Bay. Turtles in San Diego Bay are omnivo-

rous, and further, the habitat is likely affected by nutrient loading from urban runoff, which may result in higher baseline $\delta^{15}\text{N}$ values (Lemons et al. 2011; Fig. 2). Therefore, the high $\delta^{15}\text{N}$ values observed in turtles in our study suggest a high degree of carnivory, likely including surface and midwater invertebrates, as well as consumption of fish that have been discarded by regional benthic fisheries. These values may also be a reflection of the upwelled, denitrified, nearshore isotopic signature driving the $\delta^{15}\text{N}$ values at the base of the food web that are distinct from the lower $\delta^{15}\text{N}$ values measured in oceanic areas.

These patterns support previously observed behavior and habitat use patterns for this turtle population. EP turtles have been observed consuming benthic and vegetative-associated invertebrates, and gut content, lavage, and SI analysis of skin has confirmed these patterns (e.g. Seminoff et al. 2002a, López-Mendilaharsu et al. 2005, Rguez-Baron 2010, Lemons et al. 2011). Video-time-depth recorders have also recorded turtles consuming benthic as well as pelagic animal prey (Seminoff et al. 2006).

Long-term resource use of EP green turtles

Despite the historic presumption that green turtles are largely herbivorous and occupy neritic benthic foraging habitats following their oceanic juvenile stage (Bjorndal 1997, Bolten 2003), green turtles in the EP have been shown to behave differently (e.g. Carrión-Cortez et al. 2010, Rguez-Baron 2010, Lemons et al. 2011, Seminoff et al. 2015). We expected 2 potential scenarios for the long-term resource use and foraging behavior of EP green turtles dead-stranding at PSL: (1) turtles transit across the coastal continental shelf of the Gulf of Ulloa and forage in benthic lagoon sites, as established life-history paradigms would suggest; or (2) turtles actively forage in the epipelagic waters of the Gulf of Ulloa, a behavior atypical of green turtles. For the first scenario, we would expect the turtles to exhibit characteristic benthic lagoon and low trophic level SI values (high $\delta^{13}\text{C}$ and low $\delta^{15}\text{N}$ values, respectively), particularly in the most recent annual bone growth layers, which reflect their most recent foraging habitat. These skin-equivalent SI values would be similar to those observed in previous BCP studies of lagoon-foraging EP green turtles. This may include 'newly settled' turtles that recently shifted from the oceanic to neritic habitats, and this shift would be detectable in their annual bone growth layers. In contrast, if scenario 2 were

true and turtles actively forage within the pelagic Gulf of Ulloa, then we expect the observed skin-equivalent SI values of the more recent growth layers to be different from the benthic lagoon foraging turtles (lower $\delta^{13}\text{C}$ and higher $\delta^{15}\text{N}$ values). Pelagic coastal foraging in the Gulf of Ulloa would be represented by lower $\delta^{13}\text{C}$ values due to the lack of ^{13}C -depleted benthic eelgrass consumption. Higher $\delta^{15}\text{N}$ values would reflect continental shelf habitat use and potential consumption of higher trophic level prey including pelagic invertebrates (e.g. jellies, pyrosomes, gastropods, cephalopods) as well as fish commonly discarded by fisheries in this habitat. Most of the fisheries in the Gulf of Ulloa are bottom-set gill-nets and long-lines; therefore, the discarded fish are likely benthic species that are further enriched in ^{15}N (Peckham et al. 2011, McMahon et al. 2013).

The PSL green turtle samples from the present study and from Turner Tomaszewicz et al. (2017b) had lower and higher mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values, respectively, as well as larger ranges in both values, than those from most other green turtle studies in the region (Fig. 2), supporting scenario 2 outlined above. Our data suggest these turtles rely less on benthic lagoon areas, if at all, and that these turtles may be successfully exploiting food resources in the pelagic shelf habitat of the Gulf of Ulloa, without settling into lagoons or bays. Thus, this group of EP green turtles is likely not utilizing sheltered lagoon-type areas as expected for post-settlement juvenile and adult turtles. If they had exhibited higher $\delta^{13}\text{C}$ values, like those reported for turtles from nearby lagoon foraging sites such as Laguna Ojo de Liebre and Punta Abreojos, then they would likely be consuming at least some seagrass, which is confined to coastal, shallow waters, and macroalgae. Both seagrass and macroalgae have distinctly high $\delta^{13}\text{C}$ values of \sim –10‰, in comparison to more ^{13}C -enriched marine algae (Clementz et al. 2006, Arthur et al. 2008, Santos Baca 2008, Rguez-Baron 2010).

Very few turtles in our study (3 of 35) had SI values indicative of herbivorous benthic lagoon foraging ($\delta^{15}\text{N} < 15\text{‰}$, $\delta^{13}\text{C} > -16\text{‰}$) and each of these turtles appear to have occupied lagoon habitats for a short period (\sim 1 to 2 yr), then switched habitats, exhibiting plasticity in resource use. This type of movement between lagoon and coastal (more offshore) habitats has also been documented for Northwest Atlantic loggerheads (McClellan et al. 2010, Ramirez et al. 2015).

Our hypothesis that some EP green turtles do not forage benthically in lagoons, but instead use the epipelagic zone of the Gulf of Ulloa, is also supported

by previous studies reporting stomach contents of green turtles stranded in the Gulf of Ulloa and in coastal waters outside Bahia Magdalena near PSL. For example, López-Mendilaharsu et al. (2005) reported a green turtle (59 cm CCL) with stomach contents containing 82% pelagic red crabs (*Pleuroncodes planipes*). While red crabs are frequently observed as a common food item for sympatric North Pacific loggerheads, their importance in the diet of green turtles is less well documented. In addition, the UABCS (2014) report on the Gulf of Ulloa described a dead green turtle (43 cm CCL) killed by fisheries entanglement, with stomach contents of primarily pelagic red crabs, cephalopods (squid and octopus), and trace remains of fish (bones). Similar findings have been reported in oceanic, pelagic, and mostly carnivorous green turtles (sized 30 to 70 cm CCL) collected as bycatch mortalities both north and south of Hawaii (Parker et al. 2011). In that study, various crustaceans, gelatinous zooplankton, and mollusks dominated the turtles' stomach contents (Parker et al. 2011). Interestingly, genetic analysis by Parker et al. (2011) showed the green turtles foraging south of Hawaii were of EP origin, and EP turtles have also been found in Japan and the Australasia region, further confirming their widespread distribution, ability to exploit pelagic prey, and high degree of plasticity in resource and habitat use (Seminoff et al. 2015). Beyond the Pacific, green turtles in Northwest Africa have been observed remaining more omnivorous after their neritic settlement (Cardona et al. 2009). Our findings add to the growing body of literature demonstrating that post-oceanic stage green turtles may exploit omnivorous food sources in pelagic foraging habitats.

The wide range of size and age reflected in the 189 growth layer samples from our 35 turtles assigned to the pelagic habitat suggests turtles use this foraging strategy in this hotspot through multiple life stages, from the neritic juvenile through the adult stage. In addition, because the SI values from the bone growth layers reflect a composite of a turtle's diet and habitat use over an entire year, this suggests that pelagic foraging is the primary and long-term foraging strategy of these turtles. If the turtles in our study were only transiting through the pelagic Gulf of Ulloa as they moved between benthic lagoon foraging sites (i.e. Magdalena Bay to the south, San Ignacio to the north), then the SI values reflecting the pelagic waters would be masked by those reflecting the benthic foraging. This would result in more of our samples having the higher $\delta^{13}\text{C}$ and lower $\delta^{15}\text{N}$ values characteristic of herbivorous

foraging in these lagoon habitats, and this was not the case. Finally, the high somatic growth rates observed in this study could be facilitated by long-term use of this pelagic coastal habitat in the Gulf of Ulloa, where turtles have access to a high protein, largely carnivorous diet—likely including fishery discards. Our findings that this group of turtles exploits pelagic coastal habitats and prey items, contrary to expectations for post-oceanic stage green turtles, expand the current paradigm of green turtle life history and habitat use.

Age-at-maturity and age-at-settlement estimates

Size plateaus can indicate the onset of maturity for turtles when resource allocation begins to shift from somatic growth to reproduction, thereby greatly slowing body growth. The growth of the 3 largest turtles in this study either was at, or reached, a plateau over deposition of their final LAGs. The haplotypes of most turtles from our study are unknown; however, turtles stranded at PSL are known to originate from one of 2 main rookeries, Revillagigedos Archipelago or Michoacán (P. Dutton unpubl. data). The CCL of 2 of the largest turtles in the present study converged near 95 cm CCL, which is the mean nesting size for turtles at the Revillagigedos Archipelago rookery (Juarez-Ceron et al. 2003), whereas the third turtle plateaued at ~73 cm CCL, and was more similar to the mean nesting size (~82 cm CCL, minimum ~61 cm CCL) for turtles at the Michoacán rookery (Alvarado-Díaz & Figueroa 1990).

Further, we estimated the age-at-maturation for 2 of these turtles at 17 and 30 yr (CCL of 73 and 95 cm, respectively). These are the first empirically estimated ages-at-maturation for EP green turtles. The findings are near previous estimates, ~15 to 25 yr, for this population based on growth rates of green turtles in the Gulf of California (Seminoff et al. 2002b), and are similar to the range of maturity for other green turtle populations (Avens & Snover 2013, Seminoff et al. 2015). Our data support that turtles at the 2 main EP green turtle rookeries reach maturity at different sizes, and, critical to conservation and population recovery, suggest that this size difference could also translate to different ages-at-maturation. The Michoacán rookeries have experienced continued population growth in recent decades, and this could be in part due to the younger age-at-maturity results reported here, together with effective nesting-habitat protection efforts (Delgado-Trejo & Alva-

rado-Figueroa 2012). Much less is known about the Revillagigedos rookery (Seminoff et al. 2015). Because of this rookery's much larger mean nesting size (95 versus 82 cm CCL), and the older age-at-maturity for these turtles as estimated in this study, more research is required. It is important to better understand these turtles' life history and foraging patterns at this nesting site, and their contribution to the recovering EP population, especially as population recovery from this later-maturing group will presumably occur more slowly in response to conservation efforts.

Our estimated age-at-settlement of 3 to 5 yr is within range of those from previous green turtle studies that also estimated relatively low ages-at-settlement [Northwest Atlantic green turtles: mean 3 yr, range 1 to 7 yr (Goshe et al. 2010), 3 to 6 yr (Zug & Glor 1998), and 3 to 5 yr (Reich et al. 2007); Hawaiian green turtles: 4 to 10 yr, (Zug et al. 2002)], especially in comparison to other hard-shelled marine turtle species, which can range up to 24 yr (reviewed in Avens & Snover 2013). The timing of settlement is expected to vary by individual and environmental conditions, but settlement for this population likely occurs prior to age 10, given that no turtles <50 cm CCL (the maximum estimated size-at-settlement for EP green turtles; Seminoff et al. 2003) were over 10 yr old (Fig. 4). Finally, for a more robust estimation of average age-at-settlement for the entire EP green turtle population, and not only those turtles stranding at PSL, future studies should apply our approach linking skeletochronology with SI analysis to turtle bones collected within benthic lagoon habitats.

Size at age and growth

The small body size class (30 to 50 cm CCL) included estimated ages of 1 to 4 yr old, suggesting EP green turtles have the potential for rapid somatic growth, especially in the early years (other populations and species reviewed in Avens & Snover 2013). EP turtles settle at ~33 to 50 cm CCL (~30 to 46 cm SCL), but other populations' settlement sizes range from 30 cm SCL in the Northwest Atlantic (Mendonça 1981) and the Caribbean (Bjørndal et al. 1995, 2000), to ~35 cm SCL in Hawaii (Zug et al. 2002, Balazs & Chaloupka 2004) and Australia (Limpus & Chaloupka 1997). With similar settlement ages, the slightly larger settlement size of the EP green turtles supports the hypothesis that this population may experience higher growth rates during their first few oceanic juvenile years.

Our length-at-age estimates (~30 to 50 cm CCL at ~1 to 4 yr old) may seem extreme for characteristically slow-growing marine turtles, but rapid growth in the first few years has been observed in captive EP green turtles maintained on a relatively high protein diet (Turner Tomaszewicz et al. 2017b, C. N. Turner Tomaszewicz et al. unpubl. data). These captive turtles reached CCLs of 46 to 53 cm by age 3, corresponding to the estimated length-at-age estimated by our GAMM and observed in our CCL and age estimates, and translates to annual growth of $>15 \text{ cm yr}^{-1}$ (Fig. S4). Other studies have also found high growth rates ($>10 \text{ cm yr}^{-1}$) in captive green turtles, such as those raised at the Cayman Turtle Farm (Wood & Wood 1980, reviewed in Avens & Snover 2013). High growth rates, up to 11.4 cm yr^{-1} , have also been observed in wild juvenile and adult EP green turtles at a northern foraging site in San Diego Bay, California (Eguchi et al. 2012). However, at least some of the accelerated somatic growth of this aggregation was attributed to warmer water temperatures facilitated by a once-through cooling power plant (Eguchi et al. 2012, Turner Tomaszewicz & Seminoff 2012). In the present study, the mean incremental growth of the smallest sizes class (mean $3.9 \pm 2.11 \text{ cm}$ for 30 to 40 cm CCL size class) was within the range of other growth studies, as were our incremental growth estimates for the larger size classes, which all decreased with increasing size class (Table 2, Fig. S5; e.g. Bjorndal et al. 1995, Seminoff et al. 2002b, Balazs & Chaloupka 2004, Eguchi et al. 2012). Finally, we acknowledge that increasing sample size would improve growth rate and length-at-age analyses and modeling, which could refine these initial estimations for this population.

Limitations of skeletochronology could affect the length-at-age relationships observed in this study. Namely, skeletochronology of marine turtles is pred-

icated on the assumption that one year's worth of growth is marked by a LAG (Zug et al. 1986, Goshe et al. 2009). LAGs form during periods of slower growth assumed to occur during seasons of cooler water temperatures and/or low food availability (Snover & Hohn 2004, Snover et al. 2010, Goshe et al. 2016). Annual LAG formation has been validated for green turtles in Hawaii, USA (Snover et al. 2011, Goshe et al. 2016), but it has not yet been empirically shown for this EP population. Despite these potential limitations, skeletochronology currently provides the best estimation of length-at-age for this early life stage, and we recommend future research to further validate the annual formation of LAGs for EP green turtles.

Additionally, estimating the age of some of the oldest turtles can be limited when using skeletochronology, due to bone remodeling and compression of LAGs at the bone periphery, a phenomenon termed 'rapprochement' (Francillon-Vieillot et al. 1990). For large bones, such as humeri from large mature marine turtles, compressed LAGs are typically still identifiable (Snover & Hohn 2004), but the correction factors applied might not be as accurate. This could result in an underestimation of the turtle's age. In the present study, we applied our second-order correction factor to 7 turtles, including the 2 largest turtles in our sample, both estimated at age ~32 yr (Fig. 4). This age estimate is reasonable given that the CCL of each of the 2 large turtles was similar (94 and 95 cm). However, if we assumed for one of these turtles that some of the visible, yet incomplete lines were true LAGs, and the innermost of these potential LAGs were extrapolated through the rest of the bone (Fig. 6), the new age estimate for this individual would be ~46 yr. (For further discussion on age estimations in this study and skeletochronology, see the Supplement.) Estimated age-at-maturation for marine turtles is typically ~25 to 35 yr, but range from 10 to 50 yr (reviewed in Avens & Snover 2013, Seminoff et al. 2015). Turtles can then breed for 20 to 40 yr (Chaloupka & Limpus 2005, Humburg & Balazs 2014, Avens et al. 2015, Seminoff et al. 2015), making a life expectancy of 50 to 60 yr likely in the absence of anthropogenic pressures. Despite these various limitations of skeletochronology, it is one of the best tools currently available to age and estimate life history parameters for marine turtles. Resolution of the types of challenges described here requires future studies using larger sample sizes of large, mature turtles. Continuing analysis of wild and captive known-age turtles will also help refine the process and likely add a third correction factor specific to mature adults.

Table 2. Summary of estimated mean incremental annual growth (cm yr^{-1}) from paired layers of arrested growth (LAG) measurements and grouped by 10-cm size class bins. Sample size (n) represents the number of LAG pairs used to calculate estimated growth. CCL: curved carapace length

Size class bin (cm, CCL)	n	Mean	SD	SE
30–40	6	3.9	2.11	0.86
40–50	40	3.5	2.21	0.35
50–60	41	3.6	2.74	0.43
60–70	32	2.6	1.90	0.34
70–80	23	1.5	1.27	0.26
80–90	11	1.4	0.74	0.22
90–100	15	0.4	0.60	0.16

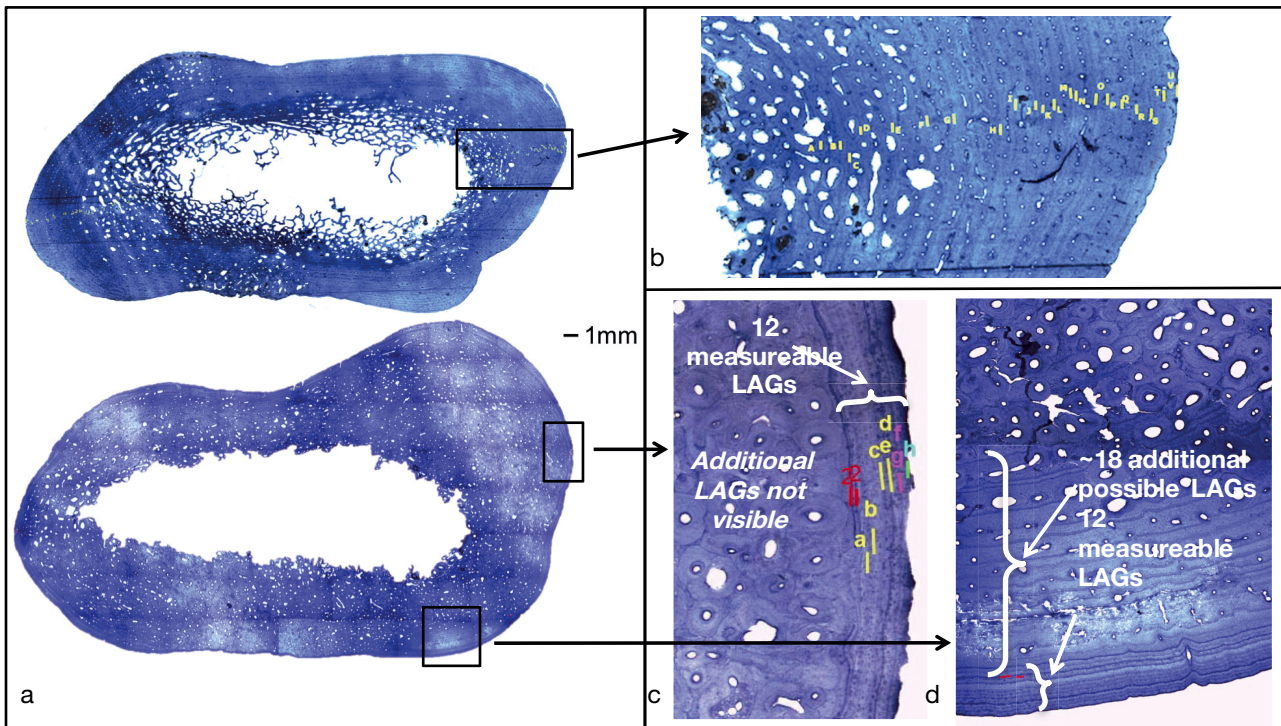


Fig. 6. Histological images showing the morphology and identified layers of arrested growth (LAGs) for the 2 largest turtles analyzed in this study. (a) Size and shape of the 2 bones with the magnified sections (b–d) outlined in black, (b) the 22 identifiable LAGs spanning the entire portion of the cortical bone, (c) the 12 identifiable and measurable LAGs observed, and (d) the same 12 measurable and additional potential LAGs from another section of bone. Most of the cortical bone did not retain visible LAGs, but one small section (pictured in d) showed ~18 additional possible LAGs, which, if they are true LAGs, could have a significant impact on the age estimation of this individual (see 'Results' and the Supplement for details on the potential complications involved with using skeletochronology to estimate turtle age)

Management implications

While much attention has recently tried to address the impact of fishery bycatch on the sympatric group of foraging North Pacific loggerheads in the Gulf of Ulloa (Peckham et al. 2007, UABCS 2014, Senko et al. 2017), less management focus has been given to the impact these same fisheries have on EP green turtles. This is largely due to (1) higher numbers of loggerheads aggregating and therefore being affected by the bycatch in the Gulf of Ulloa and stranding at PSL (Koch et al. 2006, Mancini & Koch 2009, Seminoff et al. 2014); and (2) the continuing population growth and recovery of the EP green turtle population (Seminoff et al. 2015). However, our findings underscore the unique ecology of this particular group of EP green turtles. The long-term and unusual foraging and habitat-use behavior of these turtles in the Gulf of Ulloa subjects them to increased impacts from the local artisanal fishing. Management efforts focused on their protection will help to conserve this portion of the population, thus preserving

additional behavioral plasticity within the entire EP green turtle population. The ongoing efforts to minimize bycatch of loggerheads in the Gulf of Ulloa (Senko et al. 2017) are likely to reduce the bycatch impact on these EP green turtles as well; however, continued monitoring of bycatch rates at this location, specifically for EP green turtles, is important.

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