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Somatic growth rates of green turtles (*Chelonia mydas*) in foraging habitats of northwestern and southeastern of Mexico

J. Adán Avilés-Chávez [a], Elena Solana-Arellano [a], Eduardo Cuevas [b], Vicente Guzmán-Hernández [c], Patricia Huerta-Rodríguez [c], Jeffrey A. Seminoff [d]

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Highlights

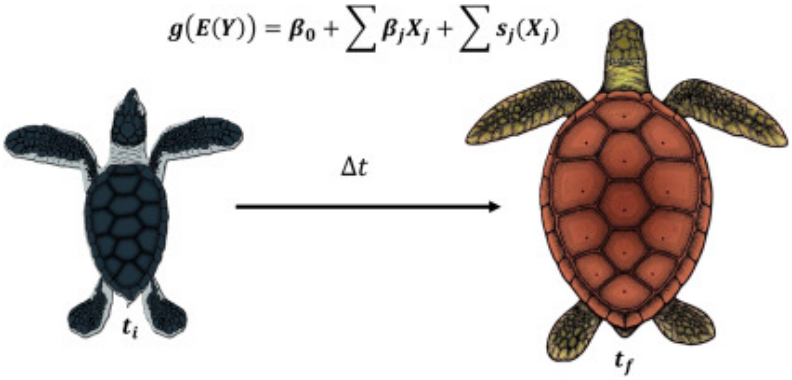
- Models show somatic growth variation across foraging habitats.
- Interannual shifts with sharp somatic growth rate changes are revealed.
- This work offers a comparative framework to understand *Chelonia mydas* growth dynamics.

Abstract

Somatic growth rate estimates contribute to elucidating vital population parameters; therefore, it is imperative to understand green turtle growth dynamics to develop effective management policies/strategies. Here we present the results of statistical modeling of the growth dynamics of green turtle populations assembled at four foraging habitats in Mexico. Size-based growth rates for green turtles at each site were obtained using a mixed longitudinal sampling design from mark-

recapture data (12–17 years). Overall, 239 growth increments from turtles recaptured at intervals ≥10.5 months were recorded. The initial size of turtles ranged from 25.39 to 93.80 cm, and most corresponded to juvenile-size classes (~83.54%; n = 193). Growth rates ranged from 0.08 to 11.25 cm y^{-1} (n = 231) across the four foraging populations. The mean annual growth rates were variable, with the lowest mean growth rate found for turtles at Laguna San Ignacio (2.03 ± 0.318 cm y^{-1}; n = 15) and the highest for turtles at Laguna de Términos (6.45 ± 1.143 cm y^{-1}; n = 10). The size-specific growth rate function was non-monotonic for the four populations, with some being inconsistent with the established regional growth pattern. Based on GAM predictions, we estimated that—once recruiting to their neritic foraging habitats—turtles would take about 12–18 years to reach sexual maturity for the Pacific coast of Baja California Sur populations; 13 years for the Gulf of California; and 12 years for the Gulf of Mexico. The demographic information presented here provides a comparative framework and greater context of the variability of somatic growth across geographic regions and foraging populations, which is crucial for understanding the species' life history patterns and population dynamics.

Graphical abstract



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Keywords

Foraging populations; *Chelonia mydas*; Demography; Somatic growth; Generalized additive models; Eastern Pacific; Gulf of Mexico

1. Introduction

The growth process is a key trait of species life history and demography. In the context of chelonian management and conservation, empirical somatic growth rate estimates contribute to elucidating vital population parameters such as size-at-age, age at first reproduction, size-at-maturity, and neritic habitat recruitment size for a given population (Labrada-Martagón et al., 2017; Lemons et al., 2026). Similarly, such estimates allow the assessment of population demographic changes in response to intrinsic (e.g., pathological, physiological, nutritional, behavioral) and extrinsic factors (i.e., natural and/or anthropogenic) (Heppell et al., 2003). Also, by being intrinsically associated with the habitats where turtles reside, somatic growth rate estimates in critical habitats such as foraging areas may function as an indicator of the habitat quality (e.g., ecological and nutritional habitat quality) and provide valuable context about the life history and conservation status of focal populations (Diez and van Dam, 2002; Kubis et al., 2009; Zárate et al., 2015). Moreover, as the somatic growth process is one of the main drivers of population fluctuations (Heppell et al., 2003), the enhancement of population viability models may rely on empirical somatic growth estimates within and among species and populations, as well as over time and space (Chaloupka and Musick, 1997; National Research Council, 2010). Therefore, to develop effective management policies and restoration strategies, it is imperative to understand sea turtle somatic growth dynamics, including the comparison of growth rates across regions and ontogenetic stages (National Research Council, 2010).

Green turtles (*Chelonia mydas*) have a complex life history characterized by long lifespans, delayed sexual maturity, and cyclical migrations between nesting rookeries and foraging habitats (Hirt, 1997). This life history includes several developmental stages: hatchling, post-hatchling, pelagic juvenile, neritic juvenile, subadult, and adult. Throughout development, it has been documented that *C. mydas* utilizes a variety of habitats; that is, turtles undergo ontogenetic shifts in location and habitat usage (e.g., Howell et al., 2016; Turner Tomaszewicz et al., 2018; Vanderklift et al., 2023). One of the major ontogenetic habitat shifts is the one that demarcates the end of the 'lost years', namely the transition from pelagic zones, which are occupied during the first years of life, toward neritic foraging habitats as juveniles (Bolten, 2003). Although this pattern is evident for several populations, it is increasingly clear that green turtles have a non-homogeneous lifestyle and may exhibit plasticity in behavior, diet and habitat use among individuals, populations, and regions (Hays et al., 2002; Burkholder et al., 2011; Hamabata et al., 2015; Chambault et al., 2020). Those variations in lifestyle suggest that green turtle populations may have differential demographic trajectories that vary depending on the local environment where the population resides.

Foraging habitats, where green turtles aggregate and spend most of their lifespans, are some of the most critical habitats for understanding the species' ecology and demography (Hamann et al., 2010). In the context of green turtle growth, it is well-documented that this parameter is highly variable across populations. While growth variability may result from several factors, such as differences in habitat quality and/or resource availability (Sampson et al., 2015), much of the variation is not well understood (Bjorndal et al., 2017, 2019). In this light, studies centered on understanding the potential drivers that shape growth are fundamental as they contribute to a better understanding of

population dynamics and improve the capacity for managing wild populations (Chaloupka and Musick, 1997; Colman et al., 2015).

For over 40 years, many green turtle populations were considered relictual; nowadays, because of steady conservation efforts, apparent recoveries of several populations have been observed worldwide (Broderick et al., 2006; Chaloupka et al., 2008; Mazaris et al., 2017). Such is the case of the Mexican eastern Pacific (EP) and western Atlantic (WA) populations, as they appear to be rebounding (Delgado-Trejo and Alvarado-Díaz, 2012; Guzmán-Hernández et al., 2022; López-Castro et al., 2022). Nonetheless, it is speculated that they remain below their historical levels (*sensu* McClenachan et al., 2006; Early-Capistrán et al., 2020, 2022). These upward population trends have led to *C. mydas* being downlisted from endangered to vulnerable status on the IUCN Red List (Seminoff, 2023a); however, under Mexican legislation, it is still listed as endangered (SEMARNAT, 2018). There is still much work to do for improving the conservation actions around the world, specifically in Mexico—where despite federal law safeguarding green turtles (DOF, 1990)—their foraging populations remain susceptible to anthropic pressures (Senko et al., 2014; Hart et al., 2015).

As described before, the remarkable recovery of green turtle populations in Mexico has brought an outstanding increase in sea turtle abundance at neritic foraging habitats of northwestern Mexico (Early-Capistrán et al., 2022). This population growth—and the associated changes in green turtle density—may reduce prey availability and induce density-dependent impacts that would be reflected in somatic growth rates (e.g., Bjorndal et al., 2000, 2017, 2019; Labrada-Martagón et al., 2017; Mortimer et al., 2025). The demographic implications of potential shifts in somatic growth rates, then, highlight the need to assess and monitor the growth dynamics of green turtles over time and across a range of foraging habitats in Mexico.

In this study, we present a comprehensive quantitative analysis of the geographic growth dynamics of green turtle populations inhabiting the EP and southeastern Gulf of Mexico (Fig. 1). Particularly, we offer an update and expanded knowledge on previous efforts in understanding the green turtle growth process from several foraging populations along the Baja California Peninsula (e.g., Seminoff et al., 2002; Koch et al., 2007; López-Castro et al., 2010; Mancini et al., unpublished results) and at the Laguna de Términos, Campeche. The growth data presented herein also provide a comparative framework and a greater context of the variability of this parameter across geographic regions and foraging populations, which is crucial for developing effective management and conservation strategies for the species. This is especially so considering the current scenario of recovering populations (increasing the density-dependent effects), and ongoing habitat degradation due to climate change (Bjorndal et al., 2019).

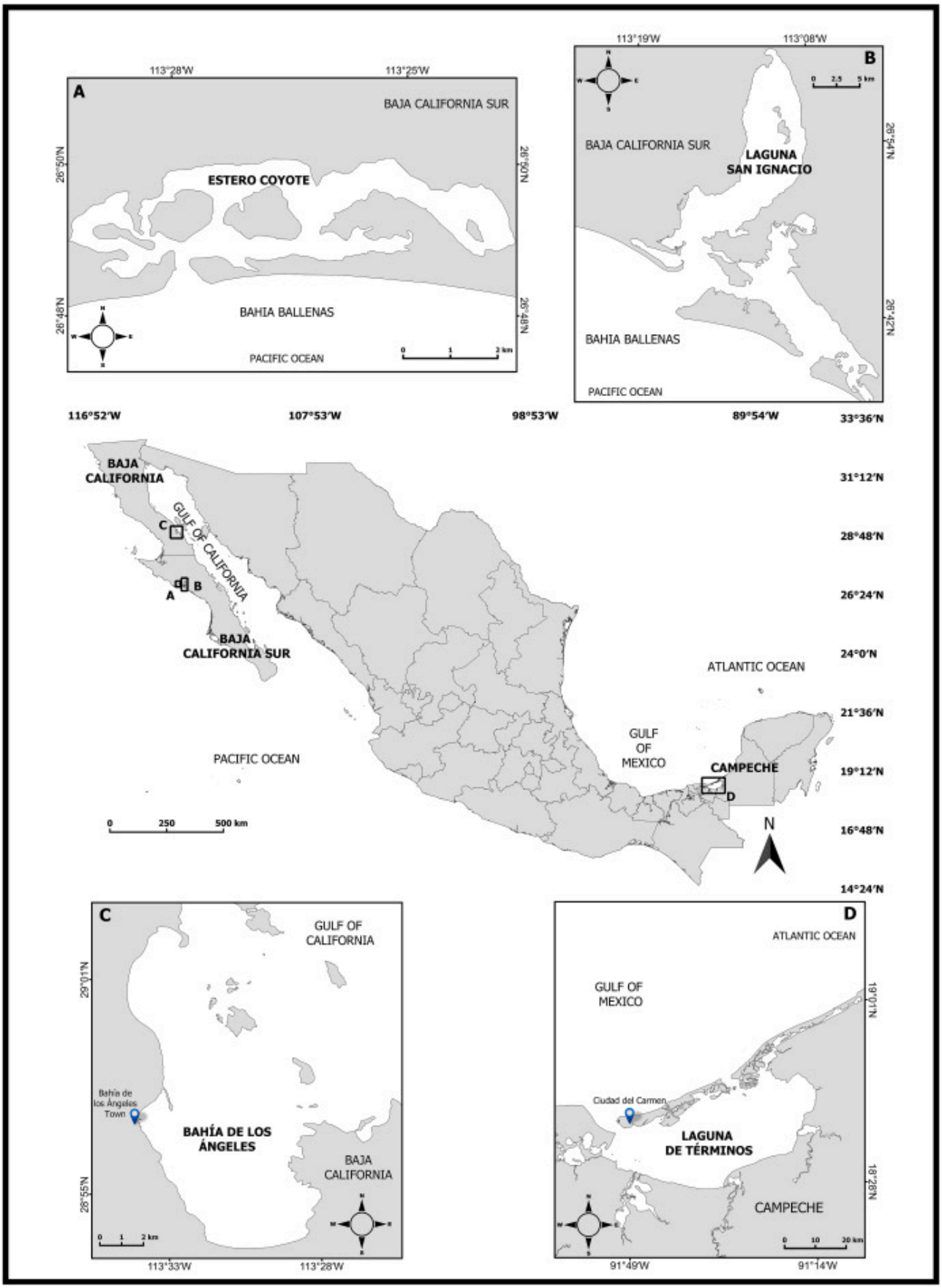

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Fig. 1. Geographic location of the four *Chelonia mydas* foraging habitats included in this study: Estero Coyote (A); Laguna San Ignacio (B); Bahía de los Ángeles (C); and Laguna de Términos (D). The blue marker represents the approximate town or city location (QGIS, 2018). (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

2. Materials and methods

2.1. Study areas

2.1.1. Estero Coyote

(EC; 26°49′ N–113°24’ W) is a small coastal lagoon of ~20 km^2 located on the Pacific coast of Baja California Sur (Fig. 1).This site is part of the El Vizcaino Biosphere Reserve (VBR) and is considered a relatively pristine lagoon due to its lack of urban development (Ward et al., 2022). The sea surface temperature (SST) at EC is variable with an average ~20–26 °C in summer and ~12–18 °C in winter (López-Castro et al., 2010; Koch, 2013). The marine substrate is mainly composed of sand, mud, and clay (Pedrín-Avilés and Padilla-Arredondo, 1999) with the presence of large beds of seagrass (*Zostera marina*; coverage ~17%), widgeon grass (*Ruppia maritima*; coverage ~11%), and sand bars covered by mangrove (*Rhizophora mangle*; coverage ~33%) (Ward et al., 2022).

2.1.2. Laguna San Ignacio

(LSI; 26°58′ N–114°05’ W)—laying within the VBR—is a coastal lagoon of ~175 km^2 located to the northeast of EC (~18.5 km) on the Pacific coast of Baja California Sur (Fig. 1).The SST at LSI exhibits monthly mean values of ~22.5–26 °C in summer and from ~16 to 18 °C in winter (Sicard-González et al., 2012). The marine substrate mainly comprises sand and mud (Kurth, 2007 in Senko et al., 2010) and presents predominantly extensive-patchy beds of *Z. marina* (coverage ~63%) and *R. maritima* (coverage ~33%) as well as *R. mangle* vegetation (coverage ~6%) (Ward et al., 2022).

2.1.3. Bahía de los Ángeles

(BLA; 28°58′ N–113°33’ W) is a semi-closed bay of ~60 km^2 located in Baja California on the western shores of the Gulf of California (Fig. 1).BLA belongs to the Biosphere Reserve Marine Zone Bahía de los Ángeles, Canales de Ballenas y de Salsipuedes, and is protected by 17 islands that separate it from the offshore waters of the Canal de Ballenas (CONANP, 2014). BLA is characterized by high nutrient concentration, high primary productivity, and strong tidal mixing (Delgadillo-Hinojosa et al., 1997). The mean SSTs at BLA range from ~23.5 to 27.3 °C during summer and from ~13.6 to 18.8 °C in winter (Martínez-Fuentes et al., 2022). Marine macroalgae are abundant within the area, dominated by *Sargassum johnstonii*, *Gracilariopsis lemaneiformis* and *Ulva lactuca* (Pacheco-Ruíz et al., 1998, 1999, 2002).

2.1.4. Laguna de Términos

(LDT; 18°01′–19°13′ N and 92°32′–90°59′ W) is a coastal lagoon of ~2500 km^2 located on the southeastern Gulf of Mexico along the west corner of the Yucatán Peninsula and it is the largest coastal lagoon in this oceanic basin (Yáñez-Arancibia et al., 1993) (Fig. 1).In contrast with the EP study sites, this region is characterized by four climatic seasons: dry (February–April), a transitional month (May), rainy (June–September), and storm season (October–March) (Guerra-Santos and Kahl, 2018). The mean SST at LDT ranges from ~28 to 30 °C in summer and from ~23 to 27 °C in winter (Cuevas et al., 2021). The marine substrate is comprised of mud and sand (Yáñez-Arancibia et al., 1993) and is covered by extensive seagrass meadows of the dominant *Thalassia testudinum* along with *Syringodium filiforme* and *Halodule wrightii* (Ávila et al., 2015; Cuevas et al., 2021).

2.2. Field work

2.2.1. Turtle capture and morphometrics

Green turtle monitoring was carried out from 2001 to 2014 in EC (14 years); 2001–2012 in LSI (12 years); 1995–2005/2009–2014 in BLA (17 years); and 2001–2015 in LDT (15 years).In EP study sites (i.e., EC, LSI and BLA), green turtles were caught with entanglement nets of ~100 × 8 m (mesh size = 50 cm stretched) set in shallow water areas (~2–27 m depth) and monitored at 0.5–2-h intervals. The green turtles at LDT were captured in collaboration with local fishermen during their fishing sets (lasting ca. 30 min) using entanglement nets of ~600–1000 × 4.5 m (mesh size 25.4–30.48 cm) in waters of 1 to 4-m depth (Cuevas et al., 2018). Upon capture, the individuals were transported to shore, where they were measured, weighed, tagged, tissue sampled, and evaluated for body condition.

Green turtle carapace length was measured as straight carapace length (SCL) or curved carapace length (CCL). For turtles captured in EP, SCL was measured from the nuchal notch (i.e., nuchal scute) to the posterior tip of the rear marginal scutes (i.e., supracaudal scute) with a forester caliper (precision ± 0.1 cm). For turtles captured at LDT, CCL was measured from the nuchal notch to the posterior tip of the supracaudal scute with a flexible measuring tape (precision ± 0.1 cm). Green turtles were weighed using a 150-kg spring balance (±0.5 kg). Each turtle captured was tagged—usually between the first and second proximal scale of a posterior flipper—with Inconel tags (Style 681, National Band and Tag Company, Newport Kentucky). All turtles were released at their original capture site within 12 h.

2.3. Data analysis

In mark-recapture studies, encounter histories are crucial in estimating demographic parameters such as somatic growth rate. Encounter histories at each study site included a (1) turtle ID, (2) date of capture, (3) SCL or CCL at each capture, and (4) time-at-large for each recapture. Given the mixed longitudinal sampling design (i.e., sampling with a partial replacement), size-based growth rate

estimates included repeated measures for individuals that were recaptured more than once (e.g., Bjorndal et al., 2019; Lemons et al., 2026). For further discussion of the mixed longitudinal sampling method in growth studies of sea turtles see Chaloupka and Musick (1997). To avoid potential seasonal effects and to minimize the estimate error, only turtles with recapture intervals ≥ 0.87 years (10.5 months) were considered in the analyses (López-Castro et al., 2010; Labrada-Martagón et al., 2017). Lastly, to facilitate comparisons among foraging habitats, SCL measurements were used in all analyses. Since in LDT only CCL was measured, we converted the records to SCL using the equation derived from green turtles of the western North Atlantic (Goshe et al., 2010):

$$SCL = -0.0515 + 0.9426CCL \quad \text{(Equation 1)}$$

Putative maturity length for turtles of the Pacific coast of Baja California Sur (i.e., EC and LSI) and the Gulf of California (i.e., BLA) was based on the average SCL of nesting females in Colola, Michoacán (~ 76.50 cm; Delgado-Trejo and Alvarado-Díaz, 2012), whereas putative maturity size for individuals from the Gulf of Mexico (i.e., LDT) was inferred from the average CCL of nesting females in Campeche, Mexico ($\sim 103 - 105$ cm; Méndez Matos et al., 2019). The analyses were performed with the R language (R Core Team, 2020) via the RStudio integrated development environment (Posit team, 2022).

2.3.1. Absolute growth rates

Absolute growth rate for each individual was approximated as a function of the mean initial and recapture size. The prior was made because when the initial or final SCL is used, it often results in biased/misleading interpretations (Bjorndal and Bolten, 1988; Chaloupka and Musick, 1997). The absolute growth rate was calculated for SCL mean sizes based on equation (2).

$$Growth_{Absolute} = (SCL_f - SCL_i)/t \quad \text{(Equation 2)}$$

Where SLC_f and SLC_i are—respectively—the final and initial straight carapace length, and t is the recapture interval in years. Once annual growth rates were calculated, and due to the paucity of repeated measures to obtain a mean and standard error of the averaged sizes, we grouped the turtles in 10–cm SCL size class intervals (see Supplementary Table S1).

2.3.2. Modeling somatic growth rates

In this study—for each foraging area—generalized additive models (GAMs) were used to evaluate the non-linear relationship between the somatic growth rate (i.e., the response) and a series of explanatory features (i.e., size, time[year], recapture interval); which ultimately allowed the estimation of size-specific somatic growth rates. Among the features considered in our GAMs, the year feature—defined as the calendar year when growth was recorded (i.e., year of final recapture)—was included to account for the inherent time-dependent effect that is circumscribed to the sampling design used in the mark-recapture experiments (Bjorndal et al., 2000). The year feature accounts for changes in growth rate attributed to environmental effects and/or age (cohort) effects.

However, as is common in sea turtle research, the age of the individuals was unknown; consequently, environmental and age effects remained confounded. Furthermore, because growth records did not always correspond to precise one-year durations, the year effect may be imprecise (Chaloupka and Musick, 1997; Seminoff et al., 2002). Nonetheless, the inclusion of year effect as defined here provided a useful proxy for the temporal variation in somatic growth. The size feature —defined as the mean of the initial and recapture size—was incorporated as a mean function because it has been established that it is the appropriate metric for describing the size-specific growth in this biological group (see Chaloupka and Musick, 1997). Lastly, because the recapture intervals of the captured turtles ranged from 0.88 to 12.41 years ($\mathbf{10.61 - 148.93}$ months), the recapture interval—defined as the time at large since the last capture—was also included as a feature to account for the potential bias due to the variation in recapture intervals (Bjorndal et al., 2000; Seminoff et al., 2002).

A GAM is defined as follows:

$$g\left(E\left(Y\right)\right) = \beta_0 + \sum \beta_j X_j + \sum s_j\left(X_j\right) \quad \text{(Equation 3)}$$

Where, Y is the response variable; $g\left(\cdot\right)$ is the link function used to associate the predictors X_j to the expected value of the response; β_0 is the intercept; $\sum \beta_j X_j$ represent the linear parametric terms and $\sum s_j\left(X_j\right)$ denote the smooth non-parametric linear functions. Based on its general structure, the GAM is constituted by three main components: 1) a random component, which refers to the distribution of the response Y; 2) a systematic component, representing the set of features $\left(X_1, X_2, \ldots, X_j\right)$ that are related to $E\left(Y\right)$; and 3) a link function $g\left(\cdot\right)$, which associates the random and systematic components (Hastie and Tibshirani, 1990).

Prior to GAMs fitting, for each foraging area, it was necessary to define the random component (i.e., identify the distribution of the response). This was achieved using the Cullen and Frey (1999) procedure. Subsequently, the Akaike Information Criterion (Akaike, 1973) was employed to validate the goodness-of-fit of the underlying distributions. Once the response distribution was identified—and given it approximated a Weibull distribution (i.e., $e \sim W\left(\alpha, \lambda\right)$)—a logarithmic link function was used during GAMs fitting to associate the expected value $E\left[Y\right]$ to the models' systematic component. This component was constituted by a sum of reasonably stiff cubic smoothing splines of the explanatory features defined above. For further details on GAM modeling procedure, see Hastie and Tibshirani (1990). Once the models were fitted, the underlying assumptions were assessed based on the residuals analysis protocol described in Zuur et al. (2009), and the Nagelkerke (1991) Pseudo-R-squared was used as a measure of model performance and explanatory power. It should be noted that for some sites, certain features were excluded from modeling due to insufficient independent repeated measurements across factor levels. All models were fitted via 'gamlss' package (Rigby and Stasinopoulos, 2005) by using R language (R Core Team, 2020).

3. Results

3.1. Growth data

The mark-recapture dataset analyzed for each of the four sites ranged from 12 to 17 years (Table 1). Overall, the monitoring efforts yielded 2920 captures of 2448 marked turtles. From the 2448 marked turtles, 415 were recaptured, resulting in a global recapture rate of ~16.95%. At the regional level, recapture rates were 17.39% for the Pacific Coast of Baja California Sur, 17.20% for the Gulf of California, and 15.10% for the Gulf of Mexico. Among the 415 recaptured turtles, 335 were recaptured at least once; however, only 239 had a recapture interval $\geq$ **10.5 months**. Of these 239 individuals, 195 (81.58%) were recaptured once; 34 (14.22%) twice; 8 (3.34%) three; and 2 (0.83%) up to four occasions (Table 2). Repeated measurements accounted for 18.41% ($\mathbf{n = 44}$) of growth data, as these records were derived from turtles recaptured on multiple occasions. The mean **SCL** per foraging habitat was variable across sites, ranging from **34.36 ± 7.49 cm SCL** (LDT) to **74.85 ± 9.49 cm SCL** (BLA) (Table 2). The time-at-large (interval between the first and last capture) ranged from **15.32 ± 3.87** months (LDT) to **48.08 ± 35.41** months (EC) (Table 2).

Table 1. Summary of green turtles (*Chelonia mydas*) captured in this study (EC: Estero Coyote; LSI: Laguna San Ignacio; BLA: Bahía de los Ángeles; LDT: Laguna de Términos). Numbers inside the brackets indicate the turtles that were recaptured at least once. SCL: straight carapace length; SD: standard deviation.

Site	Year	Recapture ratio (%)	Number of turtles				Descriptive Statistics		
			Captured	Marked	Recaptured	Recaptures (≥10.5 months)	SCL (cm)		Weigl
							Mean ± SD	Range	Mean
EC	2001-2014	19.67	1333	1108	218 (174)	157	58.54 ± 11.09	24.30 – 100.00	29.88
LSI	2001-2012	10.26	426	341	35 (32)	15	55.44 ± 9.81	34.00 – 97.40	24.67
BLA	1995-2005/2009-2014	17.20	620	529	91 (68)	56	73.55 ± 10.75	41.00 – 110.90	58.32
LDT	2001-2015	15.10	541	470	71 (61)	11	36.48 ± 8.28	14.08 – 68.75	07.53

Site	Year	Recapture ratio (%)	Number of turtles				Descriptive Statistics	
			Captured	Marked	Recaptured	Recaptures (≥10.5 months)	SCL (cm)	Weigl
	Total		2920	2448	415 (335)	239		

Note: Descriptive Statistics were calculated based on the number of turtles captured for each study site.

Table 2. Summary of green turtle (*Chelonia mydas*) growth data with recapture intervals ≥ 10.5 months that were analyzed via generalized additive models (GAMs) in this study. Site codes are defined in Table 1. Numbers inside the brackets indicate the proportion relative to the total growth increments. SCL_i: initial straight carapace length; SD: standard deviation.

Site	Growth increments	Number of recapture occassions				SCL_i (cm)		Time-at-large (months)	
		One	Two	Three	Four	Mean ± SD	Range	Mean ± SD	Range
EC	157	133	20	4	-	56.00 ± 9.12	40.11—87.70	48.32 ± 35.40	10.61—136.80
LSI	15	14	1	-	-	53.74 ± 8.96	43.00—74.60	24.53 ± 15.40	11.14—63.35
BLA	56	38	12	4	2	74.85 ± 9.49	58.00—93.80	26.34 ± 23.70	10.78—124.04
LDT	11	10	1	-	-	34.36 ± 7.49	25.39—45.66	15.32 ± 3.87	11.14—22.78
Total	239	195 (81.58%)	34 (14.22%)	8 (3.34%)	2 (0.83%)				

3.2. Absolute growth rates

Annual growth rates ranged from $0.08 - 11.25\ \mathrm{cm\ y^{-1}}$ ($n = 231$) across the four foraging habitats, and the initial size of most turtles ($\sim 83.54\ \%, n = 193$; Table 2) corresponded to juvenile-size classes (see Supplementary Table S1). The mean annual growth rates varied among study sites, with the lowest mean annual growth rates at LSI ($2.03 \pm 0.318\ \mathrm{cm\ y^{-1}}, n = 15$) and BLA (

$2.11 \pm 0.104\ cm\ y^{-1}, n = 53$), followed by EC ($2.34 \pm 0.099\ cm\ y^{-1}, n = 153$), while the highest mean growth rate was recorded at LDT ($6.45 \pm 1.143\ cm\ y^{-1}, n = 10$).

3.3. Growth models

The GAM regression analysis showed variation in the features that described the somatic growth at each site (Table 3; Fig. 2). In EC, both SCL and year features exhibited non-linear and significant effects on growth rate (Table 3; Fig. 2). Similarly, in BLA, the GAM displayed a non-linear relationship both for SCL and year; however, only the year feature showed a significant effect (Table 3; Fig. 2). Regarding LSI, SCL exerted a significant non-linear influence on growth (Table 3; Fig. 2). Lastly, the GAM for green turtles in LDT showed a non-linear and significant effect of SCL on somatic growth rate (Table 3; Fig. 2). In sites where the recapture interval could be incorporated (i.e., EC and BLA) it did not show a significant effect (Table 3; Fig. 2). Overall, the GAMs fitting remained relatively low across the four foraging areas (see Ps-Rsq, Table 3).

Table 3. Summary of the generalized additive models (GAMs) fitted to the growth rates ($cm\ y^{-1}$) of green turtles (*Chelonia mydas*) captured in foraging habitats from Mexico. Abbreviations: Gr, growth rate; SCL, straight carapace length; R Int, recapture interval; Rdf, residual degrees of freedom; Ps-Rsq, Pseudo-R-squared; SE, standard error; p, probabilities at α = 0.05. A significant non-parametric t indicates that the feature is nonlinear. When the asymptotic t-test for a feature is not significant ($p > 0.05$) the non-parametric t-test for nonlinearity is trivial.

		Region							
		Pacific coast of Baja California Sur						**Gulf of Califo**	
		Estero Coyote						**Bahía de los**	
			Asymptotic				**non-parametric**		**Asym**
Model	Rdf		Estimate	SE	t	p	t	p	Estim
Gr~Intercept+SCL+Year+R Int	Deviance Ps-Rsq	Feature							
		Intercept	118.30	0.60	197.56	<0.001			−104.
		SCL					2.27	<0.01	
		Year					−196.40	<0.001	
		R Int	0.00	0.01	0.32	>0.05			−0.02
		142.00						39.00	
		433.30						132.80	
		0.29						0.41	

		Region							
		Pacific coast of Baja California Sur						**Gulf of Califo**	
		Estero Coyote						**Bahía de los**	
			Asymptotic				**non-parametric**		**Asym**
		Pacific coast of Baja California Sur						Gulf of Mexic	
		Laguna San Ignacio						Laguna de Té	
			Asymptotic				non-parametric		Asym
Gr~Intercept+SCL	Rdf		Estimate	SE	*t*	*p*	*t*	*p*	Estim
	Deviance	Intercept	1.21	0.88	1.37	>0.05			1.12
	Ps-Rsq	SCL					5.60	<0.001	
		10.00							5.00
		43.18							46.00
		0.13							0.44

Note: Some model terms were excluded for certain sites due to insufficient independent repeated measurements across feature levels.

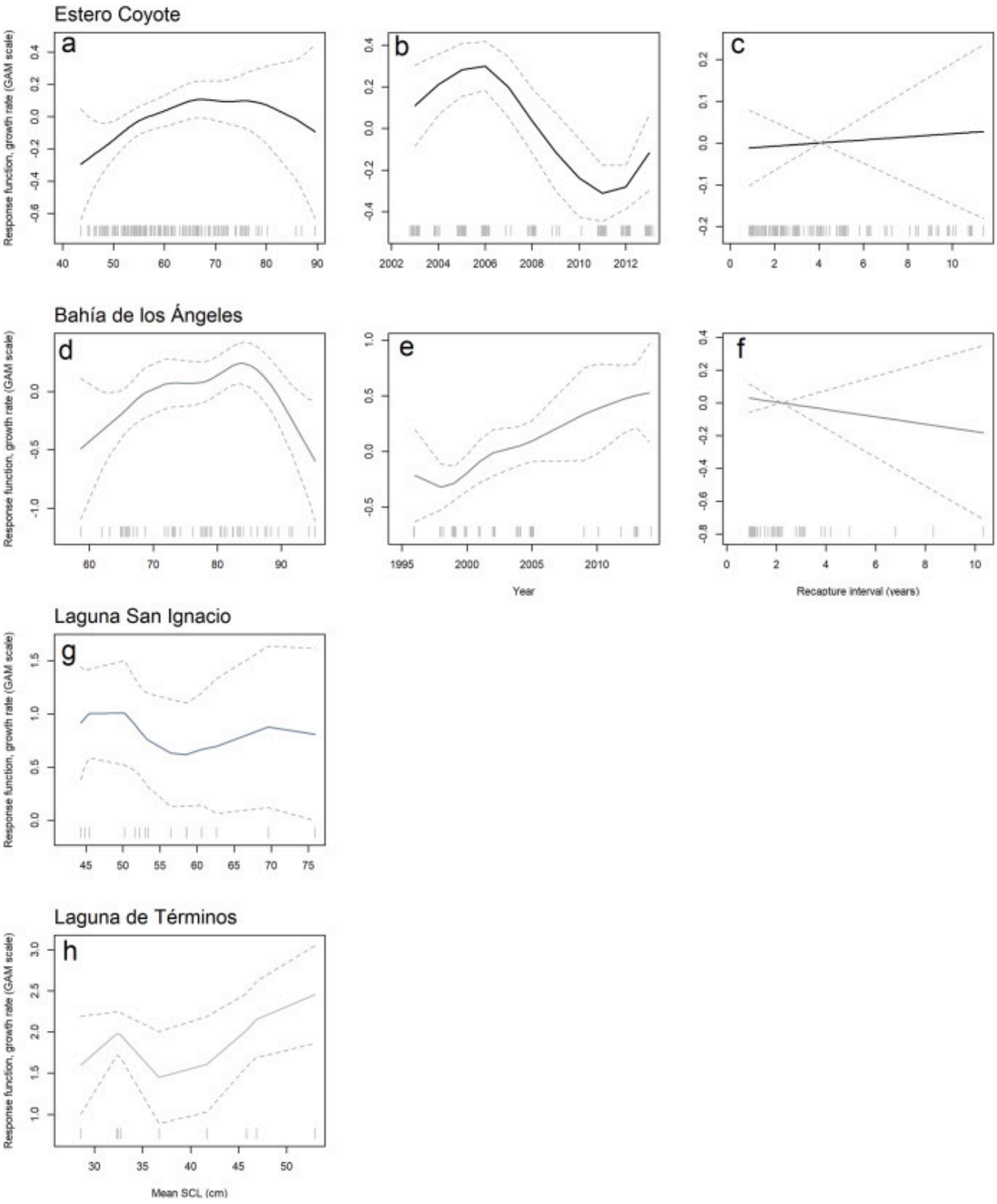

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Fig. 2. Graphical summary of the generalized additive models (GAMs) fitted to the growth rates ($\mathbf{cm\ y^{-1}}$) of green turtles (*Chelonia mydas*) captured in foraging habitats from Mexico that are summarized in Table 3: (a-c) Estero Coyote; (d-f) Bahía de los Ángeles; (g) Laguna San Ignacio; and (h) Laguna de Términos. The response variable (i.e., mean annual growth rate) is shown on the y-

axis as a centered smoothed function scale to ensure a valid pointwise 95% confidence interval. The features shown on the x-axis include (a, d, g, h) mean size between prior or first capture and recapture; (b, e) year of capture (when growth was recorded); and (c, f) recapture interval (time-at-large since the last recapture). Solid curves (a, b, d, e, g, h) are the cubic smoothing spline fitted for each continuous feature when conditioned on all other features in the GAM model (see Table 3). Straight lines (c, f) are the linear function for the continuous feature when conditioned on all other features in the GAM model (see Table 3). Gray-dashed curves are pointwise 95% confidence curves around the fits. Gray-vertical lines along x-axis indicate the punctual values of features. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

The significant effect of the year feature indicated substantial interannual variation in growth rates at both EC and BLA (Table 3; Fig. 2). In the case of EC, the growth function showed fluctuating temporal shifts: growth rates rose steadily from 2003 to 2006—then declined until 2010—before increasing again through 2013 (Fig. 2). Conversely, growth function for turtles from BLA displayed a sustained upward trend throughout the years (Fig. 2). It should be noted, however, since the year feature confounded cohort effects, it was not possible to discern whether the effect was attributable to environmental and/or genetic factors. Moreover, because growth records were not based on precise 1yr durations, the year effect was imprecise. Therefore, our interpretations regarding this feature should be considered conservative.

The GAM-derived plots between the feature and the response are centered on the response scale by subtracting a weighted mean to ensure a valid pointwise 95% confidence interval (Fig. 2) (Hastie and Tibshirani, 1990). While fundamental for analytical purposes, these plots are challenging to interpret at the original scale of the response (i.e., growth rate). To enhance the understanding of the size-specific growth rates, in each foraging area, we extracted the cubic smoothing spline for the SCL feature derived from the GAM and re-plotted on the uncentered growth rate scale to highlight the underlying non-linear function on the original growth rate scale (Fig. 3). Clear differences in growth rate functions among the four study sites were observed. For example, the growth function for EC (Fig. 3) exhibited a nonmonotonic pattern and a monophasic behavior, namely a single growth peak. EC growth function started to rise steadily from $\mathbf{2\ cm\ y^{-1}}$ for sizes $\leq \mathbf{65\ cm}$ SCL until the maximum growth rate of $\mathbf{2.9\ cm\ y^{-1}}$ at about $\mathbf{65-67}$ cm SCL; and then decreased to growth rates over $\mathbf{2.1\ cm\ y^{-1}}$ for turtles above the putative maturity length. In the case of LSI, its growth function was also nonmonotonic with two apparent growth peaks, one around $\mathbf{45-50}$ cm SCL and the other $\sim \mathbf{69}$ cm SCL. The growth function of LSI displayed an irregular monophasic behavior, suggestive of polyphasic growth (Fig. 3). Similarly, the growth function in LDT was nonmonotonic and described by a polyphasic behavior, showing at least two growth peaks: a first spurt at the smallest sizes around $\mathbf{30-35}$ cm SCL and the second spurt at the largest sizes $\sim \mathbf{53}$ cm SCL (Fig. 3). Lastly, the growth function in BLA was nonmonotonic, and it began to rise rapidly from more than $\mathbf{1\ cm\ y^{-1}}$ to $\mathbf{2.2\ cm\ y^{-1}}$, where it remained stable (from $\sim \mathbf{73\ to\ 77}$ cm SCL) before abruptly increasing up to $\mathbf{2.6\ cm\ y^{-1}}$ and then starting to decline to rates slightly under $\mathbf{1\ cm\ y^{-1}}$. The latter

suggests a polyphasic behavior with two growth peaks, an initial peak around $73 - 75$ cm SCL and a final peak at $\sim 82 - 84$cm SCL (Fig. 3).

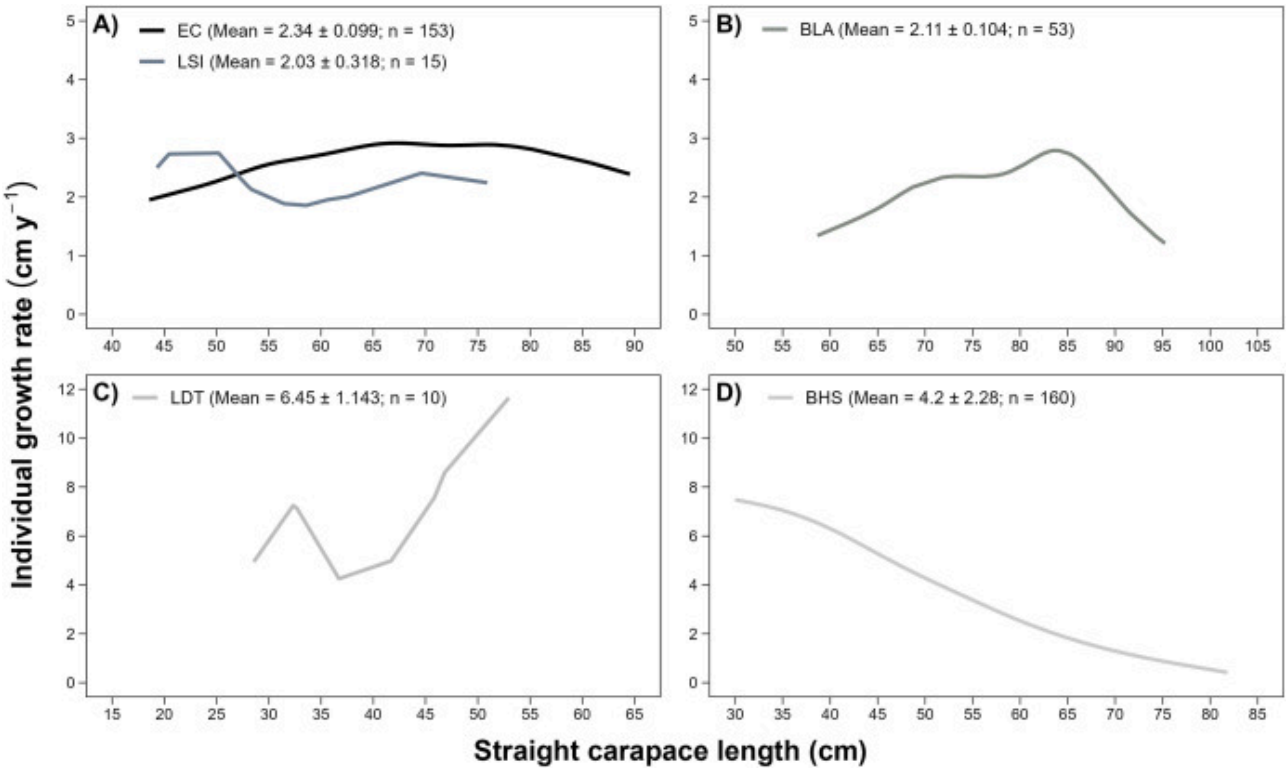

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Fig. 3. Comparison of the estimated size-specific growth rate functions for straight carapace length growth of *Chelonia mydas* in foraging habitats of the (A) Pacific coast of Baja California Sur, (B) Gulf of California, and (C) Gulf of Mexico derived from the fitted GAMs that are summarized in Table 3. Site codes are defined in Table 1. Additionally, to exemplify the characteristic *C. mydas* Atlantic growth pattern, we portray the (D) monotonic size-specific growth function for green turtles in the Union Creek foraging habitat, Bahamas (BHS: Bahamas; adapted from Bjorndal et al., 2000). Note that x-axis scales vary across panels to optimize the visual representation of the somatic growth functions. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4. Discussion

The major findings from this long-term study of green turtle growth dynamics around the Mexican Republic include (1) local and regional variability in growth rates, possibly derived from the differences in ecology and/or oceanographic conditions across foraging habitats; (2) declines in growth rates for EC (from 2006 to 2011) and growth rate increases for BLA population since around 1999 until 2010 approximately, probably as a consequence of effects from climatic phenomena; and (3) a potential deviation of the LDT size-specific growth function from the regional monotonic growth pattern typically observed in the Atlantic.

4.1. Geographic variability in somatic growth

In this study, we found spatial variation in absolute growth rates across populations and marine regions. Although variable, growth rates of foraging populations in the Pacific coast of Baja California Sur (i.e., EC and LSI) were similar to each other and with the BLA population in the Gulf of California; we also found similarities in both the Pacific coast of Baja California Sur and the Gulf of California growth rates with the preliminary results of a growth study (Mancini et al., unpublished results) that is being conducted in Laguna Ojo de Liebre (LOL), a site that also harbors a foraging population in the Pacific coast of Baja California Sur. Contrastingly, the growth rate for the Gulf of Mexico population (i.e., LDT) was substantially higher than the Pacific coast of Baja California Sur and the Gulf of California populations. Possible reasons for population and regional dissimilarities in growth include differences in the ecological and nutritional quality of the sites (Kubis et al., 2009; Sampson et al., 2015; Labrada-Martagón et al., 2017), as well as the oceanographic conditions (Koch et al., 2007; Eguchi et al., 2012); however, such variability could also be influenced by differences in the turtles' mean body sizes and sample sizes across the study areas.

Similarities in growth rates among populations in the Pacific coast of Baja California Sur (i.e., EC, LSI and LOL) may be due to the areas' resemblance in their seagrass coverage (Ward et al., 2022); such consistent food availability may drive a similar foraging behavior and consequently an alike growth. Conversely, growth variation among the Pacific coast of Baja California Sur populations may be associated to the individual dietary preferences of the turtles (López-Mendilaharsu et al., 2008). Although the EC, LSI, and LOL marine substrates are dominated by seagrasses, gut content analysis conducted for *C. mydas* by Rodríguez-Barón (2010) in these foraging habitats revealed that turtles in LSI consume primarily the red macroalgae *Gracilaria textorii*. Similarly, patterns of macroalgae dominance in green turtle diet for Bahía Magdalena and adjacent foraging habitats of Baja California peninsula have been reported (e.g., López-Mendilaharsu et al., 2008). Furthermore, Rodríguez-Barón (2010) documented that animal protein constitutes an important component in turtles' diet in LSI and LOL. The differences in nutrient quality and the digestive efficiency of dietary components (for a review see Bjorndal, 1997; Jones and Seminoff, 2013) could be contributing to the observed growth variations across the Pacific coast of Baja California Sur foraging habitats. This premise could be partially supported by the findings of Amorocho and Reina (2008), who measured the digestibilities of protein, plant, and mixed-food supplied to the EP green turtles' diet, finding the highest digestibility for proteins (85%–91%) followed by mixed-diet (77%) and plants (67%). Turtles' dietary preferences from the Gulf of California and the Gulf of Mexico may also explain variations in growth rates respecting the Pacific coast of Baja California Sur foraging habitats, as the diet of turtles in BLA is based primarily on marine algae (e.g., *Gracilariopsis lemaneiformis*) and invertebrates (Seminoff et al., 2002), whereas LDT presumably is based on seagrasses (Guzmán-Hernández, pers. comm.).

Another explanation of growth variations could be the contrasting oceanographic conditions among regions. Generally, the Gulf of Mexico basin is warmer than the EP basin (Talley et al., 2011). As ectothermic organisms, sea turtles rely on environmental temperature to perform physiological

processes such as digestion and growth (Avery et al., 1993 in Eguchi et al., 2012). In *Chelonia mydas*, it has been documented that warm temperatures appear to benefit growth performance (Eguchi et al., 2012), while low temperatures seem to slow it down (e.g., Koch et al., 2007). Therefore, the accelerated growth of turtles in LDT could be attributed to the physical water conditions of the lagoon; nevertheless, it is necessary to increase the sample size for more robust results. Following the concomitant temperature effect, it also would be expected that growth performance in the Gulf of California would be higher than in the Pacific coast of Baja California Sur as the Gulf of California is warmer (Bray and Robles, 1991). Paradoxically, growth at BLA was lower than at EC and LOL. Although the causes are unclear, this could be associated to the differences in population structures. The BLA population primarily comprises sub-adults and adults, whereas juveniles dominate both EC and LOL. Typically—because of changes in resource allocation toward reproduction—there is a reduction in growth rate prior to reaching sexual maturity, and once it is attained, growth decreases even further (Kozłowski, 1996; Omeyer et al., 2018). An additional cause that could explain the low growth performance at BLA is the hydrodynamics differences between the Gulf of California and the Pacific coast of Baja California Sur foraging habitats. The foraging habitats in the Gulf of California tend to be of high energy compared with the Pacific coast of Baja California Sur: turtles at BLA may be experiencing more net energy expenditure during their foraging activities, thus resulting in slower growth.

Alternative variation sources in growth rates might be partly due to the differences in the size distribution of the study populations. While for the Pacific coast of Baja California Sur and the Gulf of California populations, we analyzed the entire post-recruitment phase; for turtles in the Gulf of Mexico (mean nesting size ~99.5 cm SCL; Goshe et al., 2010), it was only possible to examine the juvenile stage (LDT size range: 14.08–68.75 cm SCL). The latter may explain the highest growth rates recorded at LDT as typically exists an accelerated growth during the juvenile life stage. Similarly, it is highly likely that differences in the representativeness of the size classes (see Supplementary Table S1) might be adding growth variability and, consequently, into the growth performance. Therefore, due to limitations in SCL ranges among study sites, our interpretations about geographic variability in turtle growth must be taken with appropriate caution.

4.2. Interannual variability in somatic growth

Growth models from foraging areas—where it was possible to incorporate the year feature (i.e., EC and BLA)—showed a significant effect of years on the expected somatic growth rates (Table 3). A significant year effect suggests that the interannual growth variability was probably induced by environmental influences (Chaloupka and Musick, 1997). This year effect on the growth behavior of populations is intriguing, as declines in growth rates were found for the Estero Coyote (Fig. 2b) and Laguna Ojo de Liebre (Mancini et al., unpublished results) foraging populations of the Pacific coast of Baja California Sur, whereas an upward trend was observed for green turtles in Bahia de los Ángeles (Fig. 2e) in the Gulf of California over the years. A possible driver of these trends may relate to effects from climatic phenomena such as the El Niño-Southern Oscillation (ENSO). Relationships

between growth increases and decreases with ENSO events have been previously suggested by Limpus and Chaloupka (1997) and Chaloupka et al. (2004) for Australian green turtles. In our study, interestingly, the growth rate declines observed for the Pacific coast of Baja California Sur populations coincide with years when the Oceanic Niño Index (ONI) exhibited positive sea surface temperature (SST) anomalies (e.g., EC = 2006–2007, 2009–2010; LOL = 2014–2015, Mancini et al., unpublished results) (Golden Gate Weather Services, 2024). The declining growth rates for EC (Fig. 2b) and LOL (Mancini et al., unpublished results) are probably a direct consequence of the warmer-than-average SST exhibited in the region during ENSO events. In the same way, as reported by Chaloupka et al. (2004) for western Pacific green turtles, warmer SST temperatures probably caused declines in primary productivity (Venegas et al., 2023), leading to lower food availability and, consequently, reducing growth rates. Contrastingly, during La Niña ENSO phases—given the cooler-than-average SST—primary productivity tends to increase (González-Silvera et al., 2020), which can lead to greater seagrass biomass (Lin et al., 2018). These increases in food availability might explain the somatic growth increase for BLA population (Fig. 2e) as growth peaks coincided with years when ONI presented negative SST anomalies (e.g., BLA = 1998–2001, 2010–2012) (Golden Gate Weather Services, 2024).

Despite variations in SST anomalies during ENSO events that may help explain the interannual growth response, interpreting such patterns is challenging, as there were years where we observed an opposite growth response in the face of SST anomalies, growth rate increases during warm phases and/or decreased during cool phases (e.g., EC = 2002–2005; BLA = 2002–2003, 2009–2010). Such contradictory behaviors may be a consequence of changes that turtles undergo in habitat usage and foraging strategies during ENSO events (Quiñones et al., 2010, 2022). For example, Quiñones et al. (2010) have documented that—during the ENSO warm phase—green turtles shift from a primarily herbivorous diet to consume mainly the scyphozoan jellyfish *Chrysaora plocamia*. Such dietary changes are likely to increase turtle caloric intake, which may, in turn, contribute positively to growth variations. Given that the opposing responses in growth remain unclear, we recommend conducting additional studies to unravel the effects of the ENSO driver on the change in green turtle somatic growth rate.

Declines in growth rates of EC and LOL green turtle (Mancini et al., unpublished results) populations could also reflect intrinsic density-dependent effects (e.g., Bjorndal et al., 2000). These foraging populations are comprised primarily of the Michoacán stock (Arce-Jiménez et al., 2026). According to Delgado-Trejo (2016), the nesting rates in Michoacán increased from 3383 to 17,196 nests y^{-1} between 1982 and 2015, which represents a nesting increment of ~508%. The ongoing Michoacan stock recovery is likely leading to substantial increases in juvenile recruitment and, thus, a higher turtle density at the EC and LOL foraging habitats. Such increases in population density may be inducing interspecific competition, reducing food availability, and ultimately resulting in lower somatic growth rates. Nonetheless, it is puzzling that this density-dependent effect was not observed for BLA, as this population is increasing (Early-Capistrán et al., 2020, 2022) and is also comprised primarily of the Michoacán stock (Dutton, 2003; Arce-Jiménez et al., 2026). It is worth

noting, however, that since the age and genetic stock (cohort) of the turtles were unknown, this interpretation should be considered conservative.

4.3. Size-specific growth function

The mean size-specific growth rate function conditioned on informative features (i.e., SCL, year, recapture interval) was non-monotonic for the four foraging habitats (Fig. 2a–d, g, h). Interestingly, however, the Mancini et al. (unpublished data) preliminary results seem to indicate that LOL growth function is monotonically decreasing. Typically, there is a tendency for green turtle populations in the Pacific to exhibit "dome-shaped" or non-monotonic growth (growth spurt in mid-size classes), while in the Atlantic, it is monotonic (declining growth rate with size; Fig. 3D) (Seminoff et al., 2015). However, such patterns are not met for LOL (Mancini et al., unpublished results) and LDT (Fig. 3C) populations; nonetheless, the limited SCL size ranges at LDT may be obscuring its underlying growth trajectory. Although unusual, discrepancies in general growth patterns have also been reported for other Pacific and Atlantic populations. For example, Koch et al. (2007) reported that the Bahía Magdalena population appears to follow a monotonically decreasing growth pattern. Another example of inconsistency was documented by Kubis et al. (2009), who found that the growth function for three foraging populations along the central coast of Florida is non-monotonic. The reasons for discrepancies in growth patterns (Fig. 3) are unknown but may be related to habitat selection, abundance-quality of food, turtle density and/or population genetic composition.

The data on growth and the inferior tail (quantile ≤0.05) of SCL distribution allowed us to estimate the approximate duration of the neritic juvenile stage (since recruitment) of each foraging population (i.e., after recruiting to these neritic study areas). The estimated age-at-maturity reported for EP and WA green turtles is 33.3 years (77.3 cm SCL, mean nesting size; Seminoff, 2023b) and 42 years (99.5 cm SCL, mean nesting size; Goshe et al., 2010), respectively. Assuming that (1) post-pelagic juveniles recruit at the average of the inferior tail 0.05 quantile of SCL distribution recorded in each foraging area and (2) considering a constant growth rate (estimated average growth rate per area), after recruiting to neritic habitats turtles would take about 12.39–18.39 years ($\mathbf{14.53 \pm 2.06}$) to reach sexual maturity in the foraging habitats of the Pacific coast of Baja California Sur (EC, LSI, and LOL [Mancini et al., unpublished results]); 11.32–13.75 years ($\mathbf{12.42 \pm 0.61}$) in the Gulf of California (BLA); and 8.75–18.07 years ($\mathbf{11.79 \pm 2.09}$) in the Gulf of Mexico (LDT). Notably, our putative time intervals in which turtles reach maturity (since recruitment) both on the Pacific coast of Baja California Sur and in the Gulf of California were shorter than those previously reported for the Pacific region; the time interval for the Gulf of Mexico population (Atlantic), however, appeared to be consistent. In the EP, for example, Koch et al. (2007) estimated a time interval of ca. 24 years for the Bahía Magdalena population. Similarly—based on the growth data presented by Eguchi et al. (2012)—the time required for the San Diego Bay population to reach maturity is ca. 31 years. In the Gulf of California, Seminoff et al. (2002) reported a time interval of 16–27 years for the Bahía de los Ángeles population. While in the Atlantic, Labrada-Martagón et al. (2017) estimated a time interval of ca. 13–14 years for the Akumal

population, and Bjorndal et al. (2000) estimated ca. 12–13 years for the Union Creek population. It should be emphasized, however, that age at sexual maturity in this taxon is a demographic trait characterized by high plasticity across individuals, populations and regions; given such intrinsic heterogeneity, caution is warranted when interpreting our time interval estimations to maturity, as they represent focal growth dynamics subject to the environmental stochasticity when the study was yielded.

Data statement

The data that support the findings of this study are available from the corresponding author, ESA, upon reasonable request.

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CRediT authorship contribution statement

J. Adán Avilés-Chávez: Conceptualization, Data curation, Formal analysis, Investigation, Writing – original draft, Writing – review & editing. **Elena Solana-Arellano:** Conceptualization, Data curation, Formal analysis, Investigation, Supervision, Writing – review & editing. **Eduardo Cuevas:** Investigation, Writing – review & editing. **Vicente Guzmán-Hernández:** Investigation, Writing – review & editing. **Patricia Huerta-Rodríguez:** Investigation, Writing – review & editing. **Jeffrey A. Seminoff:** Conceptualization, Data curation, Investigation, Supervision, Writing – review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

The following is the supplementary data to this article:

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Multimedia component 1.

Recommended articles

Data availability

Data will be made available on request.

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