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Geographic variation in the life history of lane snapper *Lutjanus synagris*, with new insights from the warm edge of its distribution

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Abstract

Research on life-history variations in widely distributed fish species is needed to understand global warming impacts on populations and to improve fisheries management advice. The lane snapper *Lutjanus synagris* (Linnaeus, 1758) is commercially important to fisheries in the Western Central Atlantic, where spread information on its life-history traits is available. We studied growth, age, reproduction and mortality of lane snapper in the Guatemalan Caribbean, the warmest part of its distribution range, and collated the new information with published data in a latitudinal analysis extending between 18°S and 30°N. Longevity was estimated at 11 years, and von Bertalanffy growth parameters were asymptotic length (Linf) 45.6 and 42.2 cm for females and males, respectively, the growth coefficient (K) was 0.1 year^{-1} and the theoretical age at zero length (t_0) was −4.4 years. Lane snapper grew slowest in April, prior to the rainy season, and at the onset of the reproductive season, which lasted from May to October. Fifty percent of female and male lane snappers matured at 23 and 17 cm, corresponding to 3.5 and 2.4 years of age respectively. A regional multivariate analysis found seawater temperature to be an important driver of life-history variation. Lane snapper lifespan was shorter at the warm edge of its distribution range, and maximum size and peak reproductive investment were negatively related to sea surface temperature. The trade-offs in lane snapper life-history traits and phenology likely enhance its fitness to differing environments. Interpolation from the present regional estimates to less-studied regions of the Caribbean is useful for preliminary understanding of reaction norms and harvest potentials.

KEYWORDS
biogeography, data-limited fisheries, latitudinal gradient, Mesoamerican reef, otolith, reproduction

1 | INTRODUCTION

Variation of life-history traits (*e.g.*, asymptotic length, growth rate, reproductive effort, sex change, longevity) and demographic rates (*e.g.*, recruitment and mortality) is common in widely distributed sub-populations of marine fish (King & McFarlane, 2003; Lowe *et al.*, 2021; Munch & Salinas, 2009; Planque *et al.*, 2010; Trip *et al.*, 2014). These divergences arise from genetic and possible epigenetic

differentiation between populations, including fishery-induced evolution, and metabolic adaptations to local environmental conditions, occurring under different climate and harvest regimes (Audzijonyte et al., 2016; Jonsson & Jonsson, 2019; Lowe et al., 2021; McKenzie et al., 2021; Munch & Salinas, 2009; Scheuffele et al., 2021; Wang et al., 2020).

There is now evidence that rises in global temperatures have prompted poleward shifts in the distributions of several marine species (Clarke et al., 2021; Fodrie et al., 2010; Marshak & Heck, 2019; Morley et al., 2018). At poleward range extremes, populations have become more abundant in increasingly favourable conditions, compared to populations at the equatorward side, which may decline as a consequence of warming (Hastings et al., 2020). Tropical fish are vulnerable to warming temperatures as they have a narrow thermal range, with equatorial species living close to their upper thermal limits (Booth et al., 2017; Cereja, 2020; Jones & Cheung, 2014; Lam et al., 2020). Empirical evidence supports the idea that tropical species adapt to local warming conditions using different mechanisms (Booth & Beretta, 2021; Lowe et al., 2021; Maharaj et al., 2018; Munday et al., 2017; Robitzch et al., 2023; Wang et al., 2020). There is a clear need for more field research on climate adaption in the wild (Hastings et al., 2020) because increases in habitat temperature have been associated with higher natural mortalities and decreases in fecundity (Thorson et al., 2023), which may modulate responses to other factors, such as fishing. Populations of marine ectotherms with wide geographical distributions are good models for investigating life-history plasticity under climate change.

The lane snapper Lutjanus synagris (Linnaeus, 1758) is caught in commercial and recreational fisheries in the Western Central Atlantic, with yearly landings varying between 3000 and 4000 t since 2000, but these are underestimates as only a few countries report catches (FAO, 2023). The IUCN Red List of Threatened Species considers lane snapper as "Near threatened" due to decreasing population trends (Lindeman et al., 2016). Lane snapper is widely distributed, from the Atlantic coasts of North to South America, and from Bermuda and North Carolina to south-eastern Brazil, including the West Indies, the Gulf of Mexico and the Caribbean Sea (Lindeman et al., 2016), with potential northwards range expansion owing to climate warming (Fodrie et al., 2010; Marshak & Heck, 2019). This makes it a good candidate for biogeographical trend studies.

Aspects of the growth, age and reproduction of lane snapper from different locations have been compiled (Aschenbrenner et al., 2017; Claro & Lindeman, 2008), but fisheries and life-history data are still deficient across a temperature range (Lindeman et al., 2016). The available data suggest divergent longevity, growth and reproduction patterns, but no formal biogeographic analysis has yet been conducted. Understanding fish life history and the drivers of variation is key to sustainable fisheries management (Audzijonyte et al., 2016; Wang et al., 2020; Wootton et al., 2020).

Little is known about lane snapper life history at the Mesoamerican Reef (MAR), a 1000 km barrier reef system extending along the coastlines of Mexico, Belize, Guatemala and Honduras. The MAR is a biological hotspot with conflicting conservation and human livelihood interests. It is a priority region for conservation in the world as well as a critical fishing ground for thousands of small-scale fishers (Chollett

et al., 2017; Heyman & Granados-Dieseldorff, 2012; Olson & Dinerstein, 2002). The MAR encompasses some of the warmest marine physicochemical provinces of the Caribbean and is currently in a state of increasing heat stress (Chollett et al., 2017; Muñiz-Castillo et al., 2019). To circumvent the lack of local life-history studies, data from other areas of lane snapper distribution have been incorporated into the fishery assessment models (Babcock et al., 2018; Sierra Castillo et al., 2020; Sierra Castillo & Fujiwara, 2021). The need for research on local life-history parameters to improve the reliability of fisheries assessments and management has been highlighted (Babcock et al., 2013, 2018). Life-history data from a warm area can inform conservation and exploitation management by suggesting processes of biological adaptation or rupture, or show gradients across latitudes. Such information is important for the management of species with a wide distribution in the neo-tropics.

We investigated the life history and phenological traits of lane snapper at the warm edge range limit of its distribution. Commercial catches were sampled at Amatique Bay and Punta de Manabique, two sites in Guatemala located in the warmest Caribbean region (Chollett et al., 2012). Seasonal patterns of growth and reproduction, and their relation to meteorological and hydrographic cycles were studied during a 13-month period. The life history, phenology and processes that influence the ecology of lane snapper in the present thermal regime are described. The new information was combined with data from the literature to undertake a large-scale geographical analysis (18°S–30°N) of lane snapper life-history variation and environmental drivers that potentially influence the parameters.

2 | MATERIALS AND METHODS

2.1 | Ethics statement

The fish sampled in this study originated from conventional commercial catches, hence no extra harm was caused to fish during this research.

2.2 | Study site

The Caribbean coast of Guatemala extends along 150 km of the Gulf of Honduras (Figure 1). Punta de Manabique is a 50 km long sandy barrier that separates the estuarine waters of Amatique Bay from the open sea (Fonseca & Arrivillaga, 2003; Yanez-Arancibia et al., 1999). The bay has an average depth of <10 m and comprises a 542 km^2 area, with an additional 200 km^2 of associated wetlands. Habitats in the bay include coastal lagoons, seagrass meadows, reefs, mangroves and marshes, all of which are influenced by terrestrial runoff (Yanez-Arancibia et al., 1999). The reefs around Punta de Manabique comprise continental carbonate banks, where up to 29 species of scleractinian corals have been identified (Fonseca & Arrivillaga, 2003). Precipitation, runoff and wind regimes are important drivers of the ecosystem, and are associated with reproduction and movements of marine, catadromous and estuarine fish (Andrade et al., 2013, 2015;
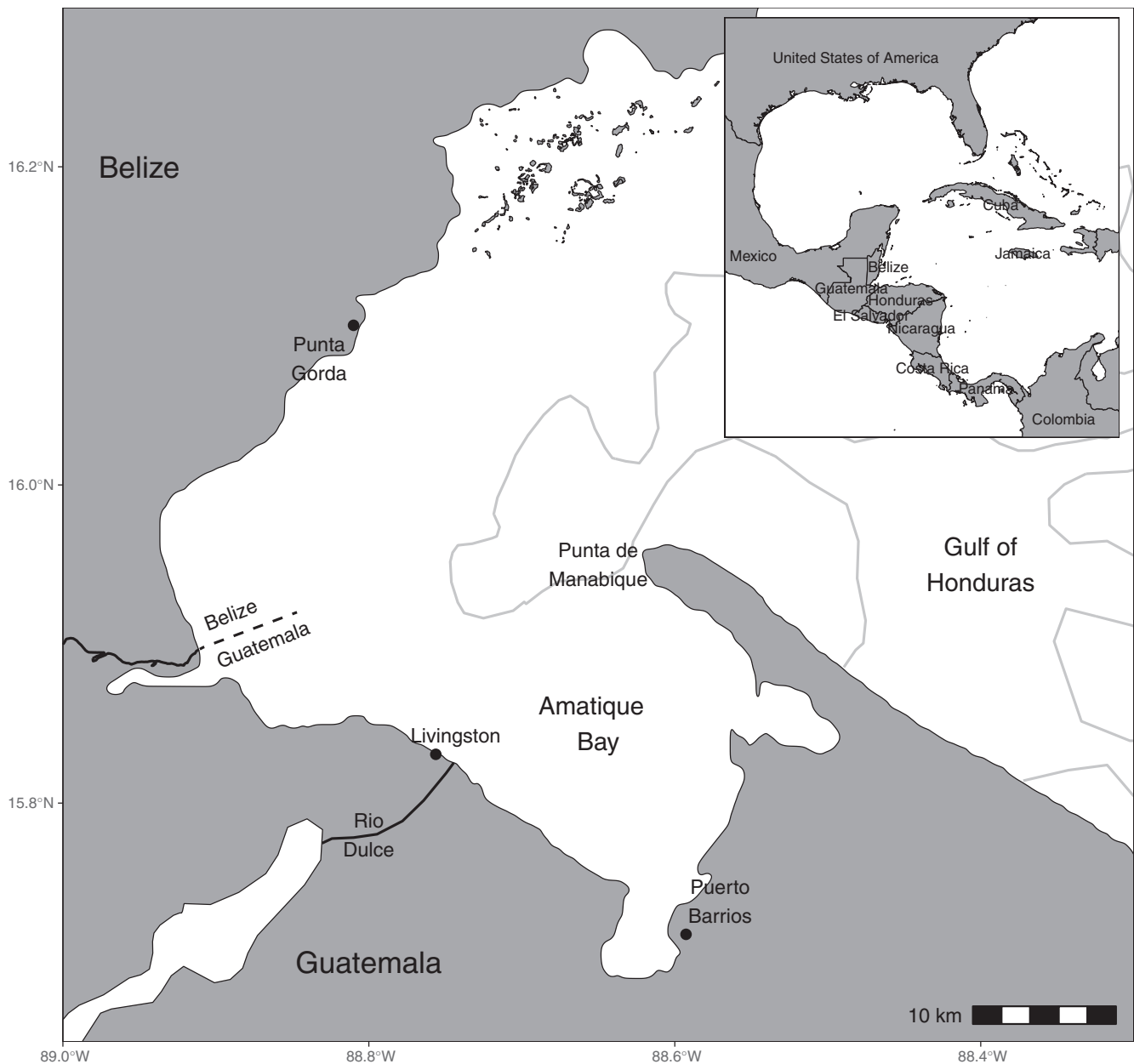
FIGURE 1   Study area on the Atlantic coast of Guatemala. Grey lines indicate 20 m depth contours

Andrade & Santos, 2019). Sea surface temperature (SST) ranges from about 27°C in May–November to 30°C in September (Andrade et al., 2015). Small-scale fisheries operate in Amatique Bay and around Punta de Manabique, and occasionally enter Belizean waters (Andrade & Midré, 2011; Heyman & Granados-Dieseldorff, 2012; Perez, 2009; Sabbagh & Hickey, 2020).

2.3 | Field sampling and laboratory analyses

Biological sampling of lane snapper was done over a 13-month period, from March 2006 to March 2007, in Livingston and Puerto Barrios, the two main fishing harbours along the Guatemalan Caribbean coast. Artisanal fishers using different gears that include hooks and lines, baited traps and nets, land fish intact. In Livingston, the catch is sold from boats operating mainly with hooks and lines. In Puerto Barrios, fish are caught with multiple fishing gears and stored on ice until sale in the markets. Between 30 and 50 snappers were sampled monthly from these fish markets except in March 2007, when only five fish were sampled. To obtain smaller fish, sporadic samples were obtained from shrimp trawlers, as small lane snappers are a common by-catch of this fishery.

The total (TL), fork (FL) and standard (SL) lengths of 492 lane snappers were measured, and linear regressions between length variables constructed to aid conversions. Total weight (WT; $n = 389$) and gonadal weight (WG; $n = 304$) (±0.1 g) were recorded, and the body mass (WT, g) distribution of individual fish investigated by means of the power relationship $WT = aTL^b$ and Fulton's $K = 100 \times WT/TL^3$ (Froese, 2006). The gonadosomatic index (GSI) was computed as

TABLE 1 Macroscopic stages employed to study the reproductive cycle of *Lutjanus synagris* in Amatique Bay, based on (Brown-Peterson *et al.*, 2011), except that in the Amatique study, only four stages were employed to classify resting/regenerating individuals

Stage	Macroscopic characteristics	
	Female	Male
I, immature	Small ovaries, often clear, blood vessels indistinct	Small testes, often clear and threadlike
II, maturing	Enlarging ovaries, blood vessels becoming more distinct	Small testes but easily identified
III, capable of spawning	Large ovaries, blood vessels prominent	Large and firm testes, milt released with gentle pressure on abdomen
IV, regenerating	Flaccid ovaries, blood vessels prominent	Small and flaccid testes, no milt release with pressure

GSI = 100% × (WG/(WT − WG)) (n males = 54, n females = 238). Fresh gonads were inspected macroscopically and scored for sex and maturity class (n = 458, males = 159, females = 299). Maturity classes were defined based on gonadal appearance using a key (I, immature; II, developing; III, spawning capable; IV, regenerating) based on Brown-Peterson *et al.* (2011) except that the stages 'regressing' and 'regenerating' were not differentiated and thus were grouped as stage IV (Table 1). The maturity classes I and II were considered immature and the classes III and IV mature in the consequent binary maturity analyses.

The left sagittal otolith was collected for age determination and three thin sections were prepared using a low-speed saw (Taylor *et al.*, 2000). The section with the clearest otolith core was photographed under a compound microscope with transmitted light. Annual increments in the otoliths were counted twice by a single reader to learn the deposition patterns following Vanderkooy *et al.* (2020), and data from a third count (n = 426) were used for the growth analysis. Fish <1 year old were assigned an age of 0.5 years. An edge-type analysis of the monthly frequency of otoliths with a terminal opaque zone was conducted to assess the seasonal deposition of increments (Manickchand-Heileman & Phillip 2000; Rhodes *et al.*, 2011), which has been reported to occur annually for this species (Aiken, 2001; Luckhurst *et al.*, 2000).

2.4 | Data analysis

We used von Bertalanffy growth functions (VBGF) to investigate whether there was a difference in average growth between the sexes:

$$L_t = L_{inf}\left(1 - e^{-K(t - t_0)}\right),$$

where L_{inf} is the asymptotic average length, K is the Brody growth coefficient and t_0 is the age with an average length of zero (generally

considered as a model artefact). We first fitted a general model using all data and the nonlinear least-squares method (nls function in *R*) to visually examine the model assumptions of residual homoscedasticity and normality. Once the assumptions were confirmed, we formulated all possible model variations, separating each parameter by sex. We used the Akaike information criterion (AIC) to select the best supported by the evidence.

Generalized linear models with a binomial logit link function were used to estimate the length (L_{50}) and age (A_{50}) at 50% maturity for both sexes using the glm function in *R*. Small males and females (< 10 cm) were poorly represented in the sample, so we augmented the datasets by adding immature 0 cm, 0 age fish to help the models converge without undue shrinking of parameter variance. The number of added fish was estimated using the total mortality equations for each sex (explained below) leading to the addition of 256 (86% of observed for L_{50}) and 174 (109% of observed for L_{50}) females and males, respectively. Confidence intervals for the 50% maturity values were estimated by resampling with replacement (*i.e.*, bootstrapping) as many values from the datasets with added 0 age juveniles as observations in the dataset (299 females and 159 males for L_{50}). We used 1000 bootstrap repetitions in the routine using the plot maturity function from the ggFishPlots package (Vihtakari, 2023).

An age-based catch-curve (Ricker, 1975) was used to estimate instantaneous total mortality (Z), using an unweighted regression between ages 3 and 8, assuming constant mortality and flat selectivity for the age range. We did not have enough age data to estimate Z for a specific time point, which is one of the assumptions of the method. Consequently, the Z estimates can be biased due to selectivity and collating age data throughout the year. The observed maximum age was used as an approximation to longevity (t_{max}, years), following Hewitt and Hoenig (2005).

The natural mortality rate (M) was determined using the Natural Mortality Tool (Cope & Hamel, 2022), which employs various empirical estimators of natural mortality. Longevity, VBGF and length parameters from our study as well as average water temperature in the Amatique Bay (28.3°C) were provided as inputs for calculations (see Supporting Information Table S2). A composite M with inverse variance, which uses the variance of each method to weight the composite prior of M, was employed to calculate the final M (Cope & Hamel, 2022; Hamel, 2014).

To study the variation in life-history traits across the species' distribution, published peer-reviewed and 'grey' literature was reviewed to extract data on the maximum size, longevity and reproduction (female GSI) (Table 2). Estimates of longevity and maximum length were determined as the oldest and largest individuals sampled from each area (Lowe *et al.*, 2021). Much of the life-history data from the years 1980–2000 have been reviewed by Claro *et al.* (2001) and Claro and Lindeman (2008), and from more recent years by other authors (*e.g.*, Aschenbrenner *et al.*, 2017; Trejo-Martíinez *et al.*, 2021). These authors have employed different methods to age the fish (*e.g.*, reading of scales, whole otoliths or sectioned otoliths) and to calculate longevity and GSI (*e.g.*, monthly GSI from only mature fish). To avoid methodological biases in longevity, we included only studies based on sectioned otoliths, as these are considered superior to whole otoliths for

TABLE 2 Data for the analysis of geographic variation in the life-history traits

Location		Traits			SST			Chl a			Reference
Country	Place	TL (cm)	Longevity (years)	Maximum GSIf (%)	Average	Minimum	Maximum	Average	Minimum	Maximum	
Belize	Glover's Reef	44.00			27.99	26.26	29.58	0.33	0.10	0.62	Babcock et al. (2018)
Bermuda	Bermuda	38.31	19		23.06	18.80	28.24	0.33	0.26	0.39	Luckhurst et al. (2000)
Brazil	Abrolhos Bank	56.00	18	1.58	26.14	24.61	27.85	0.21	0.14	0.35	Aschenbrenner et al. (2017); Freitas et al. (2014)
	Maranhão	53.00		4.00	27.95	27.19	28.67	1.22	0.27	3.71	Fernandes et al. (2022)
	Pernambuco	44.00			27.42	26.09	28.78	0.43	0.12	0.97	Viana et al. (2015)
Colombia	Central Guajira	56.00			26.73	24.26	28.86	1.17	0.53	2.45	Ramírez et al. (2017)
	Magdalena north	41.00		2.41	26.83	24.45	28.78	0.69	0.30	1.50	Gómez Cubillos (2010)
	Magdalena south	40.00		2.21	27.69	25.40	29.43	2.26	0.61	5.37	Restrepo Gómez (2010)
	San Bernardo	37.20		2.81	29.18	27.86	30.63	1.07	0.49	2.06	Jaimes Rodríguez (2011)
Cuba	Batabano	44.52		6.40	27.63	23.69	30.95	4.09	3.04	5.70	Claro and Lindeman (2008)
Guatemala	Amatique	40.40	11	1.17	28.23	25.62	30.28	5.00	1.29	13.51	This study
Honduras	Tela	43.32			28.22	26.16	30.06	1.26	0.35	3.30	Sierra Castillo & Fujiwara (2021)
Jamaica	Jamaica south	44.88	14		28.24	26.64	29.72	0.55	0.23	1.00	Aiken (2001)
Mexico	Yucatan	44.52		3.09	26.25	23.59	28.76	0.84	0.50	1.37	Trejo-Martínez et al. (2021)
Trinidad	Gulf of Paria West	45.00			27.63	26.20	29.09	10.65	2.23	30.05	Manickchand-Dass (1987)
USA	Florida Keys	36.80	10	3.19	27.12	23.91	30.25	0.62	0.34	0.91	Acosta & Dixon (2003)
	Panhandle–South Florida		15	24.50	18.32	30.04	2.10	1.55	2.82	24.50	Carrol, pers. comm.
	Florida–Tequesta	45.00	11	5.15	26.07	22.75	29.12	0.59	0.25	1.46	Barbieri & Colvocoresses (2003)
	Jacksonville–Key West	51.20	10		27.31	24.70	29.84	0.15	0.10	0.23	Manooch & Mason (1984)
	Northern Gulf of Mexico	67.30	17		24.30	18.06	29.97	2.69	1.98	3.76	Johnson et al. (1995)
	Puerto Rico	42.29			27.76	26.15	29.22	0.24	0.15	0.36	Acosta & Appeldoorn (1992)
Venezuela	Gulf of Paria East	46.7			26.5	26.5	28.4	2.0	0.8	4.5	Gómez et al. (2001)

Note: Traits include maximum total length (TL), longevity (maximum age in years) and maximum female gonadosomatic index (GSIf). Selected environmental parameters derived from Giovanni web services include sea surface temperature (SST) and chlorophyll *a* (Chl *a*).

the determination of age (Manooch & Mason, 1984). Size reported as fork length (FL) was converted to total length (TL) using the formula $TL = 1.0344FL + 0.3963$, which was derived from our data ($n = 237$, $R^2 = 0.997$). To analyse GSI trends, we employed studies reporting monthly average GSI female data. In some studies, GSI was calculated as $GSIa = 100\% \times (WG/WT)$ while in others, including ours, as $GSIb = 100\% \times (WG/(WT - WG))$. We converted these values to a general GSI formula using the formula $GSIb = 1.035 \times GSIa - 0.0149$, based on our data, which we assumed universal. This secondary relationship was derived after calculating the two GSI indices from our own observations ($n = 298$, $r = 0.997$). For Batabano Cuba, GSI values were available at each maturity stage (*e.g.*, average GSI immature, average GSI mature, *etc.*) (Claro, 1982). We recalculated the monthly values by employing a weighted average, using the data reported in the study.

To retrieve estimates of environmental variables for the different regions of the tropical ocean, SST (average, minimum and maximum) and chlorophyll *a* (Chl *a*) for locations where the previous studies took place, we used Giovanni web services (https://giovanni.gsfc.nasa.gov/giovanni/). Giovanni is an online environment for the display and analysis of geophysical data retrieved from the NASA Earth observation satellites (Acker & Leptoukh, 2007). We used Aqua MODIS Global Mapped 11 μm Nighttime Sea Surface Temperature. Area-averaged SST, average minimum SST and Chl *a* time series were produced using monthly values from January 2003 to December 2020 in approximate locations (see Supporting Information Table S1 for exact coordinates). Ideally, the environmental parameter time series and sampling periods should correspond in time for the different sites to reflect prevailing environmental conditions when the studies were conducted. However, remote-sense data are not available to match the older biological studies, therefore the 2003–2020 period was chosen arbitrarily and we assumed that the relative differences across areas remained relatively stable. To investigate large-scale relationships between environmental variables and the life-history traits across the distribution of lane snapper, correlation matrixes and principal component analysis (PCA) were utilized with pair-wise deletion of samples when necessary. Correlations were considered low ($0.25 \le r \le 0.4$), moderate ($0.4 < r < 0.6$) or strong ($r \ge 0.6$) and the statistical significance between paired variables was assessed at $P < 0.05$. Statistical analyses were conducted using the R statistical programming language (Team, 2022). Figures were created using the ggplot2 package (Wickham, 2009) for R and Microsoft Excel. The map was made using ggOceanMaps (Vihtakari, 2022). Detailed map data originate from University of Florida, the Paseo Pantera Consortium and the US Agency for International Development (https://hub.arcgis.com/datasets/ucsb::bathymetry-mayaforestgis-1/about), and the overview map shapes from Natural Earth Data.

3 | RESULTS

3.1 | Size and sex distribution

In total, 492 fish were sampled in Livingston ($n = 414$) and Puerto Barrios ($n = 78$). The average TL was 23 cm (range 13.3–40.4 cm, standard deviation 4.6 cm) throughout the year, with females typically larger than males (Figure 2). Small snappers were scarce in the samples and therefore sporadic sampling from shrimp trawlers contributed young fish (TL 13.3–18.3 cm, $n = 20$). Although regulations on the size limits of the species are nonexistent, small fish are hard to find in the local markets. Our perception is that the harvest made by the compound set of fishing gear is relatively size-unselective for large fish, as fishers adapt their gear to the available fish. Female fish ($n = 301$) were more common than males ($n = 176$) on most occasions. The female-to-male ratio for the whole sampling period was 1.71. The sex ratio only approached 1:1 in the month of August, when smaller fish were sampled (Figure 2).

3.2 | Age and growth

Annuli were visible in otolith sections (Figure 3), but these were not as well defend as for *Lutjanus griseus* (Linnaeus, 1758) collected from the same area (Andrade & Santos, 2019). The distance between the core and the first annulus varied greatly among individuals, a reflection of the long spawning season of this species (Vanderkooy et al., 2020). The age distributions of females and males were similar and ranged from young-of-the-year to 11 years, but most fish were between 1 and 5 years old (Figures 4 and S1). Longevity was established at 11 years, the oldest age determined in our samples. A submodel with separate L_{inf} but common K and t_0 parameters for both sexes had the lowest AIC value of the VBGF alternatives (Table 3). The model indicated that females had a slightly higher asymptotic average length (L_{inf}) than males (Table 4 and Figure 4). The wide confidence intervals for the VBGF parameters indicated a considerable uncertainty in the model fitting, possibly due to the lack of small (<10 cm) and large (>40 cm) individuals in the dataset as our maximum sampled length was 40.4 cm. Deposition of an opaque edge in otoliths, an indication of slower growth periods (Fowler, 2009), followed a clear seasonal pattern. More than 50% of the otoliths sampled between April and June had opaque edges in 2006, as well as in March 2007 (three out of five otoliths) (Figure 5a). This pattern corresponds to the end of the dry season in Amatique (Andrade et al., 2015). From September onwards, less than 25% of the otoliths showed an opaque edge and they finally disappeared in October. In contrast, the condition factor of the fish presented little monthly variation (Figure 5b).

3.3 | Reproduction and mortality

The GSI peaked in May to July and fell to its lowest level in November to December (Figure 6a,c). This pattern lagged peak opaque zone formation in otoliths (April–May) by a month (Figure 5). Although size-dependent, the overall GSI remained at modest levels (0.2%–1.2% females, 0.1%–1.1% males, on average). Frequent occurrence of mature female fish (stage III and IV gonads) was observed between May and October (>50%), with a peak of regressing females (>50%) in September–October. Mature males were frequent throughout the year, but were more prominent between September and October (Figure 6). The spawning season thus seemed to be prolonged, lasting 6 months, from May to October.
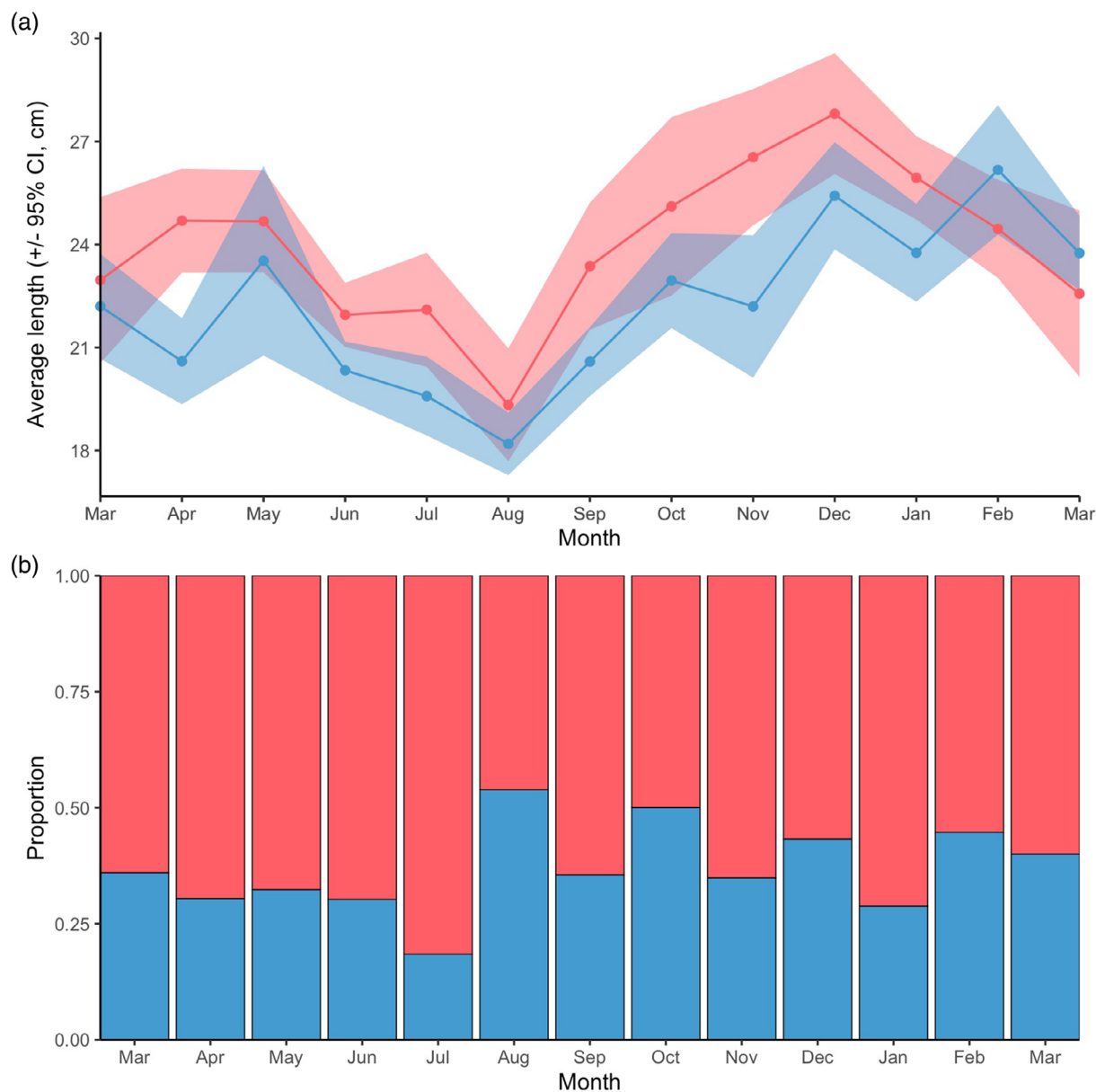
FIGURE 2 Average length (*a*, ±CI) and sex ratio (b) of *Lutjanus synagris* samples by month and sex (red = females, blue = males) sampled in the Guatemalan Caribbean (2006–2007). Sex: ▪, F; ●, M; CI, confidence interval

Males matured at a smaller size than females, and the minimum size at maturity was 15.4 cm for males and 16.6 cm for females. The logistic regression models did not converge without forcing the sigmoid through the origin (immature, 0 cm length fish), indicating that the dataset did not contain enough immature fish to reliably calculate L_{50} values (Supporting Information Figure S2). However, addition of immature 0 cm fish calculated from the catch curves (Figure 7) led to length at 50% maturity (L_{50}) of 17.1 cm [15.2–19.1, 95% confidence interval (CI)] for males and 22.9 cm (20.8–25.5, 95% CI) for females, respectively (Figure 8). Similar values for age at 50% maturity were 2.4 years (1.8–3.1, 95% CI) for males and 3.5 years (2.8–4.2, 95% CI) for females. The addition of immature fish increased the L_{50} estimates depending on the percentage of fish added but seemed to
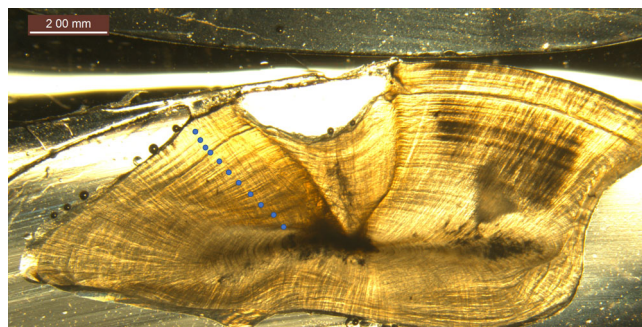
FIGURE 3 Transverse section of a sagittal otolith from a 11-year-old female *Lutjanus synagris* sampled in the Guatemalan Caribbean. Blue dots indicate the opaque zones that were used in determining age

converge to relatively stable levels after 50%. The percentages of added individuals were 86% and 109% of observations for females and males, respectively.
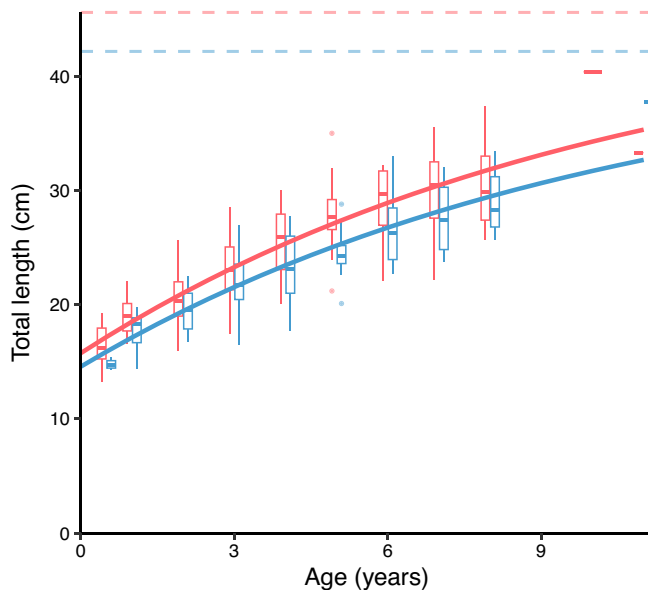
FIGURE 4 The von Bertalanffy growth function separated by sexes and fitted to the age–length observations using the nonlinear least-squares method. Red indicates females and blue males. The underlying boxplots show the raw data, solid lines the growth models and dashed lines L_{inf} values for the models. The K and t_0 parameters are common for both models

TABLE 3 Selection of the best-fitting von Bertanlanffy growth model

Hypothesis	N	AIC
$L_{inf}(F) \neq L_{inf}(M)$	4	2075.5
$K(F) \neq K(M)$	4	2076.5
$L_{inf}(F) = L_{inf}(M)$	5	2076.6
$K(F) = K(M)$	5	2077.1
$t_0(F) = t_0(M)$	5	2077.4
All separate	6	2078.1
$t_0(F) \neq t_0(M)$	4	2082
All common	3	2121.7

Note: Hypothesis column indicates the model parametrization (F = female, M = male, $\neq$ means that only these parameters were separate, while = that all except these parameters were separate), N, number of model parameters; AIC, Akaike information criterion.

TABLE 4 Parameters for the best fitting growth model ranked by AIC (Linf(F) ≠ Linf(M))

Parameter	Estimate	CI low	CI high	SE	t value	P value
$L_{inf}(F)$	45.58	33.70	57.46	6.04	7.54	0.000
$L_{inf}(M)$	42.17	31.15	53.17	5.60	7.53	0.000
K	0.10	0.04	0.15	0.03	3.36	0.001
t_0	−4.38	−5.88	−2.87	0.77	−5.72	0.000

Note: The estimate and CI columns give the parameter values together with *t*-based 95% confidence intervals, SE the standard error, *t* value the test parameter, and the corresponding *P* value for each parameter. F = female, M = male.

The average composite instantaneous rate of natural mortality was 0.27 (lower and upper CI 0.25 and 0.28, respectively). The estimate of total mortality by catch-curve analysis was $Z = 0.44$, assuming full recruitment to the gears at the age of 3–8 years (Figure 7a). The value of F was thus 0.17.

3.4 | Geographic trends in life-history patterns

The major patterns observed in the regional data were the trend for fishes to live longer and grow to larger maximum lengths in areas where the winter temperature and the average temperature were lowest (Table 2). The major axis of the PCA summarizes these trends and explains about 51% of the variance in the data (Figure 9). Longevity was also partially related to low summer temperatures. The longest and shortest maximum longevity were reported for, respectively, the coldest waters of Bermuda fish (19 years at average SST = 23.1°C) and in south Florida (10 years at average SST = 27.1). The relationship between longevity and average SST was clear across the region ($n = 9$, $r = -0.72$, $P = 0.03$). The relationship between minimum and average seawater temperature and maximum size, which was related to longevity, was, however, weaker ($n = 21$, $r = -0.34$ to -0.35, $P = 0.13$). The highest and lowest maximum lengths were reported for the Northern Gulf of Mexico and the Florida Keys (67.3 and 36.8 cm, respectively), where average SST and winter SST were 24.3 and 18.1°C for the Gulf, and 27.1 and 23.9°C for Florida, respectively. Bermuda and San Bernardo presented among the lowest recorded maximum lengths across opposing temperature extremes (38.1 and 37.2 cm at average SST = 23.06 and 29.18°C, respectively). There was a trend for declining maximum female reproductive effort (GSIf) with increasing temperatures. The major pattern disclosed in axis 2 of the PCA (explaining 27% of the variance) relates to the relationship between GSIf and productivity (Chl a). However, this can be a spurious relationship introduced by the present study in Amatique where very high productivity levels (Chl a average = 5 mg m^{-3}) were related to low gonad size (GSI$_f$ = 1.17), and to the Cuba study (Claro, 1982) where GSI$_f$ values were the highest (GSI$_f$ = 6.4). Removal of the observations reported for Amatique and Cuba resulted in an apparent random association between productivity and reproductive effort.
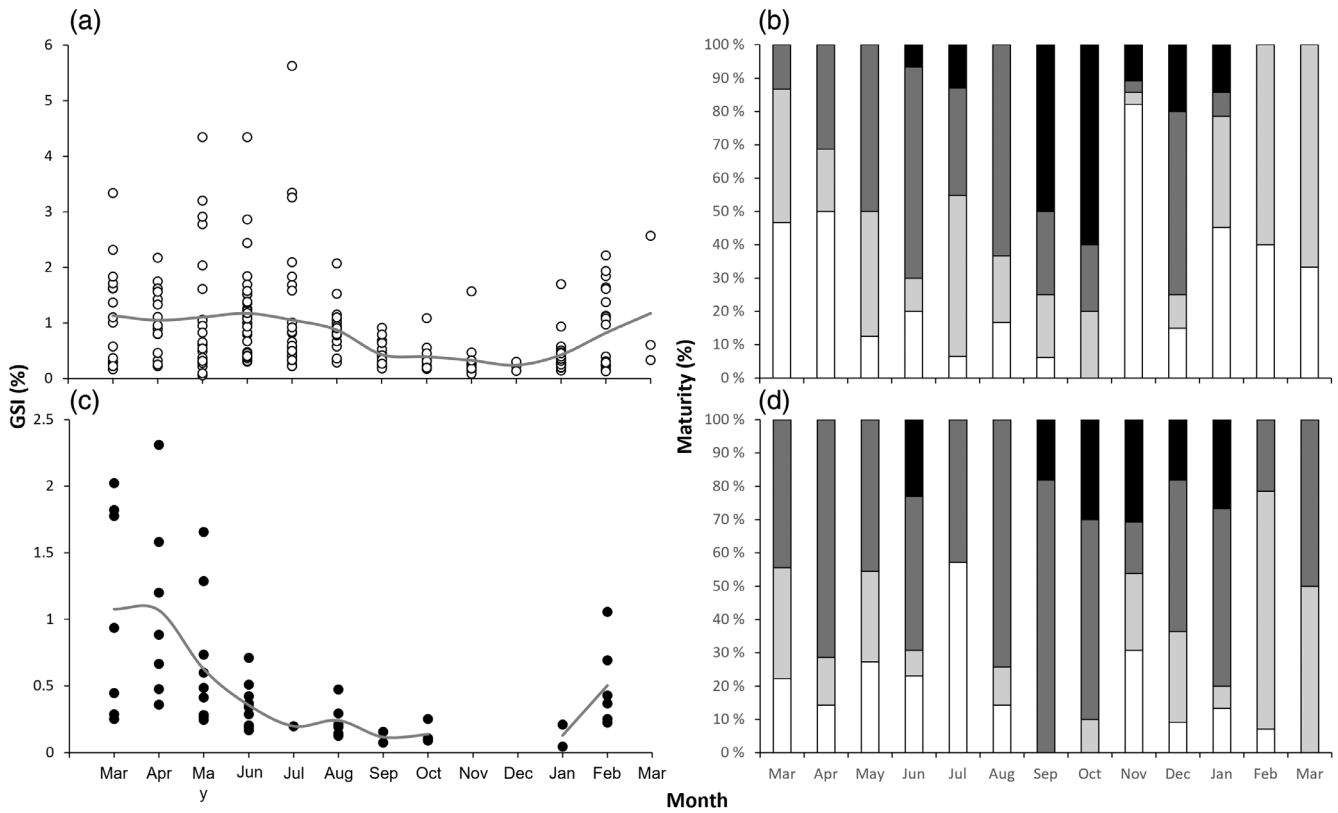
4 | DISCUSSION

We studied the phenology and life history of lane snapper in the Guatemalan Caribbean, a rarely studied tropical environment. This is
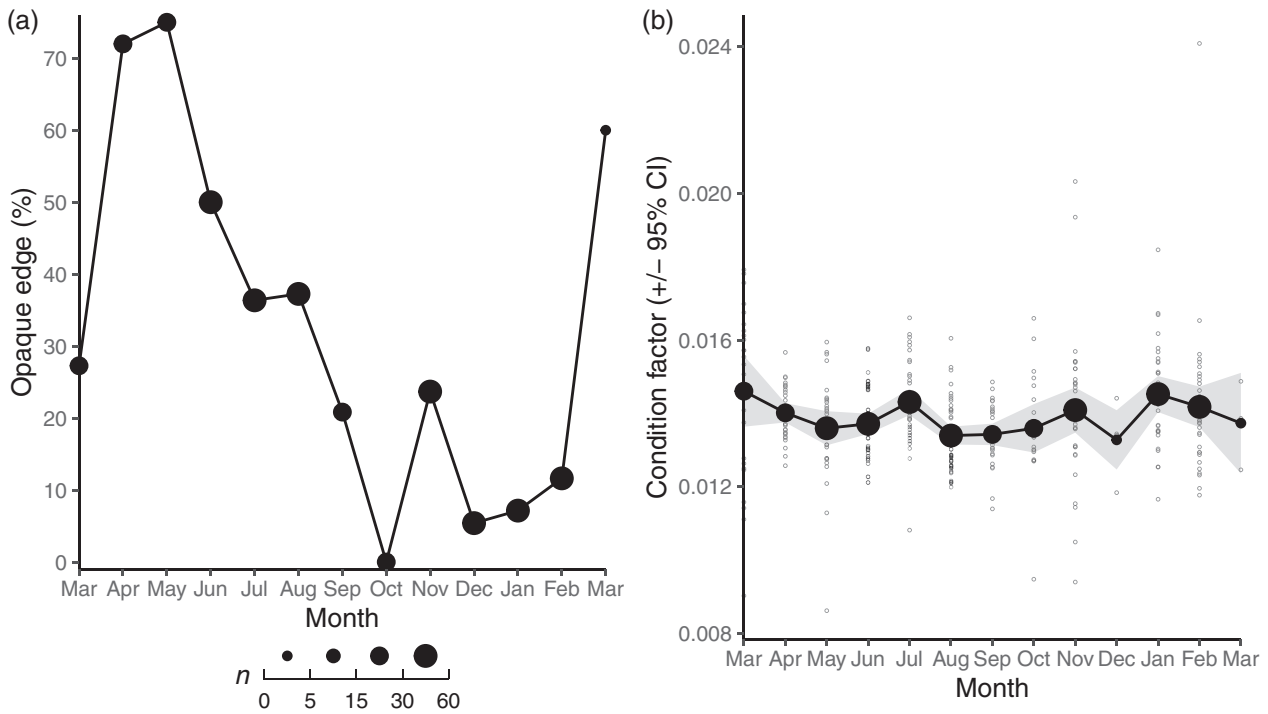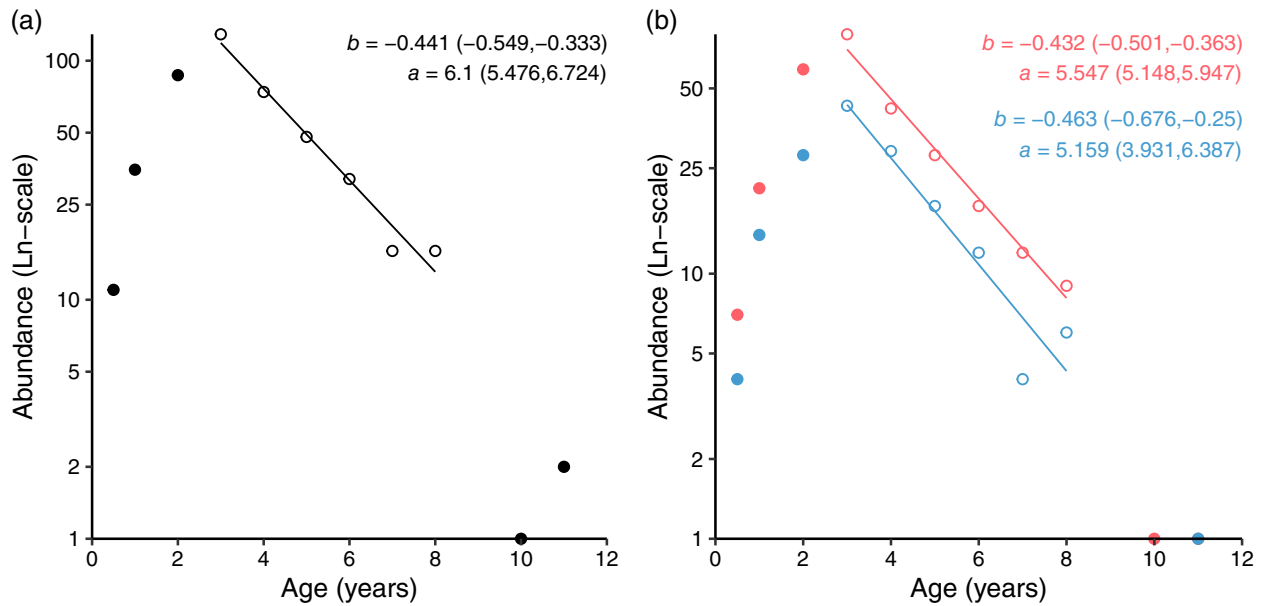
FIGURE 5 Frequency of occurrence of opaque edges and condition factor for *Lutjanus synagris* from March 2006 to March 2007 in the Guatemalan Caribbean. CI, confidence interval

FIGURE 6 Monthly gonadosomatic index (GSI) and observed maturation cycle, respectively, for female (a, b) and (c, d) male *Lutjanus synagris* in the Guatemalan Caribbean from March 2006 to March 2007. I, immature; II, developing; III, spawning capable; IV, regenerating. Lines denote average GSI. □, I; ▨, II; ▩, III; ■, IV

(a)

$$b = -0.441 \; (-0.549, -0.333)$$
$$a = 6.1 \; (5.476, 6.724)$$

(b)

$$b = -0.432 \; (-0.501, -0.363)$$
$$a = 5.547 \; (5.148, 5.947)$$
$$b = -0.463 \; (-0.676, -0.25)$$
$$a = 5.159 \; (3.931, 6.387)$$

FIGURE 7   Age-structured catch curve for the estimation of total mortality (Z) for *Lutjanus synagris* in the Guatemalan Caribbean. (a) All data used to estimate Z and (b) sex split data used to estimate the number of 0 length/age juveniles added to the maturity data. Empty circles indicate ages used in the calculations. Sex: ⚬, F; ⚬, M

(a)

17.1 cm
($n = 333$)

23 cm
($n = 555$)

(b)
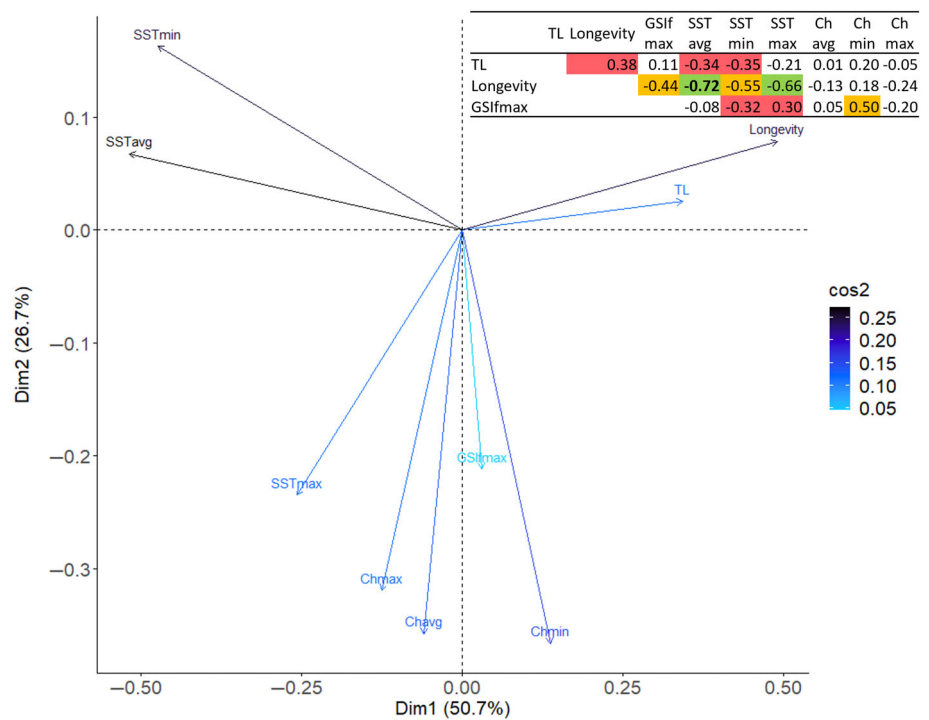
2.4 years
($n = 316$)

3.5 years
($n = 533$)
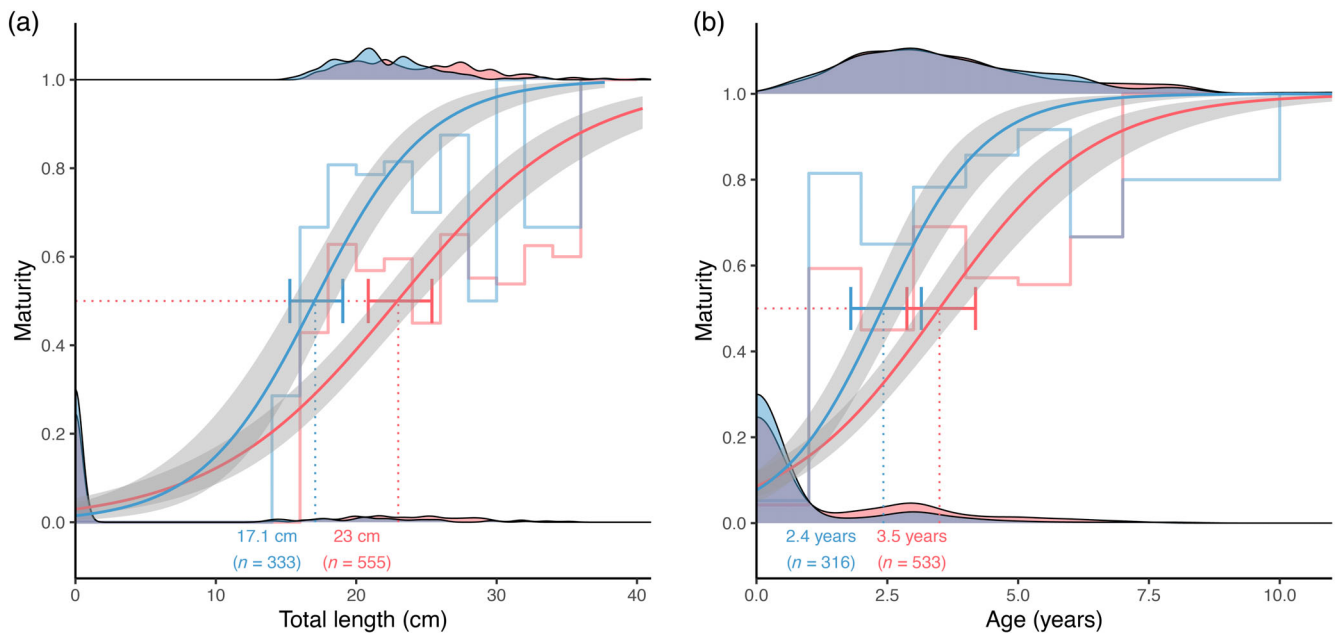
FIGURE 8   Maturity ogive by length (left) and age (right). Red and blue refer to males and females, respectively. Distributions at 1 and 0 show the distribution of mature (1) and immature (0) fish. Solid lines with shading indicate the logistic general linear models and their standard error. Dotted lines show the L_{50} values from these models. Horizontal error bars indicate the confidence intervals of L_{50} estimates. Stepwise solid lines indicate the proportion of observations between 1 and 0 binned to 2 cm groups. As many immature 0 cm fish as males and females in the dataset have been added to make the logistic models converge

one of the warmest areas in the Caribbean Sea and western Atlantic (Chollett et al., 2012; Muñiz-Castillo et al., 2019). Our goal was twofold: to provide biological data for local fisheries assessment purposes and to explain the regional variation in life-history traits of lane snapper to describe possible reaction norms. This was the first formal

biogeographical analysis of life-history traits, covering the full range of the species' distribution. The series of SST and life-history parameter data do not match exactly in time but represent averages over a period when warming may have taken place. However, the interval of temperatures in the wide geographical

FIGURE 9 Large-scale relations between sea surface temperature (SST average, min) and available *Lutjanus synagris* life-history traits (total length, longevity and average maximum female GSI) in the Western Atlantic. The table in the insert shows *r* values between environmental and life-history values with colours denoting the strength of the linear relationship (0.25–0.39 red, 0.4–0.59 yellow and >6 green in absolute values). Cos2 indicates the quality of representation of the variables on a factor map. See Table 1 for values and Supporting Information Table S1 for coordinates.

	TL	Longevity	GSIf max	SST avg	SST min	SST max	Ch avg	Ch min	Ch max
TL		0.38	0.11	-0.34	-0.35	-0.21	0.01	0.20	-0.05
Longevity			-0.44	-0.72	-0.55	-0.66	-0.13	0.18	-0.24
GSIfmax				-0.08	-0.32	0.30	0.05	0.50	-0.20

range is large and the analysis is probably robust to smaller deviations in local or regional patterns.

Our results showed that seawater temperature is an important driver of life-history variation as (i) life span was shorter at the warm edge of lane snapper distribution compared to temperate climates and (ii) weak negative relationships were found between maximum size, peak reproductive investment and SST. In Amatique, the seasonal variation in seawater temperatures is low (26–30°C), and snappers in this area inhabit the warmest edge of their thermal range. Despite the low temperature variation in Amatique, we observed marked seasonal biological patterns for lane snapper. The seasonal cycle of growth in the otoliths (opaque zone) was closely related to the gonadal cycle (GSI), lagging by approximately 1 month.

4.1 | Variations in size distribution

In our lane snapper samples, size distributions varied little throughout the year, with snappers in most reproductive stages occurring throughout the year. Seasonal ontogenetic movements are well described elsewhere for lane snapper, which is a habitat generalist, capable of successful settlement across a variety of habitats (Mikulas & Rooker, 2008; Reis-Filho et al., 2019). In an estuary-bay-continental shelf gradient, Reis-Filho et al. (2019) reported that the smallest individuals (5–10 cm) were exclusively found in sea-grass habitats, medium-sized fish (10–20 cm) were more frequent over sandy and rhodolith bottoms, and larger individuals (20–40 cm) were found predominantly over muddy and reef habitats. Except for rhodolith bottoms, all these habitats have been reported in the Guatemalan

Caribbean (reviewed in Andrade et al. (2015), and thus could potentially support all life stages locally. Our lack of sampling in sea-grass habitats and low sampling effort from shrimp trawler catches can explain the low juvenile numbers in our analyses.

4.2 | Seasonal cycles and life-history traits

The rain season and peak freshwater runoff are the main drivers of ecosystem functioning in Amatique Bay (Andrade et al., 2015) and probably the rest of the Guatemalan Caribbean and the Gulf of Honduras (Thattai et al., 2003). The peak runoff period is potentially linked to the formation of opaque edges in otoliths (lower growth rates) and the onset of the reproductive season. Opaque edges formed predominantly before the start of the rainy season (April–June) followed by spawning in May to October. Most fish capable of spawning were observed in May to August, just prior to and during the peak runoff period. From July, terrestrial nutrient supply and primary productivity are elevated, possibly creating favourable conditions for egg and larval development (Andrade et al., 2015). Our results corroborate that opaque zones in otoliths are formed just before or at the start of the spawning season, which appears ubiquitous across the species distribution (Aiken, 2001; Aschenbrenner et al., 2017; Claro & García-Arteaga, 2001; Luckhurst et al., 2000; Manickchand-Dass, 1987), despite differences in spawning months. For example, at Abrolhos Bank, Brazil, annulus formation occurs in June to October followed by the main spawning event in September and October (Aschenbrenner et al., 2017; Freitas et al., 2014). In Cuba, the opaque edge formation peaks in March to April and peak reproduction follows from April to May (Claro & García-Arteaga, 2001).

A synchronism between the rainy season and occurrence of mature females or maximum GSI have also been reported in Brazil (Fernandes *et al.*, 2022) and Colombia (Jaimes Rodríguez, 2011).

The timing of the spawning season for the Guatemalan Caribbean coincided with the timing reported for other Central Caribbean areas, where temperatures seem to be suitable for spawning throughout the year. In contrast, the onset of the spawning season in Bermuda and north-central Cuba is delayed by 1 month and is concentrated in a period of 3 and 5 months, respectively, around the warmer summer and fall months (Claro & Lindeman, 2003; Luckhurst *et al.*, 2000). This pattern generally displayed by fish species in Bermuda is related to the lower winter temperatures experienced at higher latitudes (Eddy *et al.*, 2019; Smith *et al.*, 2013). In Cuba, the demographic variation in the timing and duration of spawning has been attributed to tempera-ture differences between shelf areas where spawning aggregations form (Claro & Lindeman, 2003). Similarly, in southern Brazil, reproduc-tion occurs from September to April during the austral spring–summer months when waters become warmer (Freitas *et al.*, 2011, 2014; Viana *et al.*, 2015). In general, seasonality seems to be stronger at the species cold edge. While temperature may be a structuring variable of life history at larger scales, the modulation of growth and reproduc-tion seems to be primarily related to runoff and production in the warmer areas, where temperature is nearly constant throughout the year. This is a recurrent pattern for fish species with wide distribu-tion in the neo-tropics (Andrade & Santos, 2019; Andrade *et al.*, 2013; Trindade-Santos & Freire, 2015).

4.3 | Growth, age, maturation and mortality

Some geographical patterns in the maximum size and age of fish were observed. The maximum observed size of lane snapper in Guatemala (40 cm) was within the maximum length range in the Central Carib-bean (40–44 cm), including Belize, Cuba, Puerto Rico and Jamaica (Acosta & Appeldoorn, 1992; Aiken, 2001; Babcock *et al.*, 2018; Claro & Lindeman, 2008). Considerably larger sizes (50–68 cm) are attained at the northern and southern range of the species' distribution, including the Gulf of Mexico, Florida, Colombia and Brazil (Aschenbrenner *et al.*, 2017; Johnson *et al.*, 1995; Manooch & Mason, 1984; Ramírez *et al.*, 2017), where temperatures are normally lower and more variable than in the Caribbean. Longevity in the Guatemalan Caribbean (11 years) was also shorter than at the northern (Gulf of Mexico, Bermuda) and southern (Abrolhos, Brazil) species range, where estimates range between 17 and 19 years (Aschenbrenner *et al.*, 2017; Johnson *et al.*, 1995; Luckhurst *et al.*, 2000).

4.4 | Geographic trends in life-history patterns

The decreased longevity and maximum sizes reported across the spe-cies distribution followed the postulated temperature-size gradient, with ectotherms attaining larger sizes and greater longevity in colder regions (Angilletta *et al.*, 2004; Atkinson, 1994; Munch & Salinas, 2009). A smaller maximum body length (39 or 37 cm fork

length; Luckhurst *et al.*, 2000) was an exception. The occurrence of smaller body sizes at both the warm and cold edges of distribution is in accordance with the gill-oxygen limitation theory. As spontaneous protein denaturation may limit growth at both warm and cold temper-atures, this theory postulates that the relationship between maximum length and temperature might be parabolic (Bigman *et al.*, 2023; Lavin *et al.*, 2022; Pauly, 2021). Such relationship could explain the weak negative linear relationship found in our analysis, but more data are required to test this hypothesis in lane snapper. The smaller body sizes observed in warmer waters potentially lead to a negative feed-back in reproductive output because for fish, fertility increases dispro-portionately with body size (Barneche *et al.*, 2018). However, shorter body size and generation time maintain population turnover (Wang *et al.*, 2020) and may be compensatory mechanisms.

With respect to reproductive patterns, our regional dataset was sparse in GSI records and did not allow a meaningful comparison across the species distribution. Furthermore, female L_{50} is highly variable in this species, with values ranging from 17 cm in Pernambuco, Brazil, to 30 cm in the Gulf of Paria, Trinidad (Manickchand-Dass, 1987; Viana *et al.*, 2015). At a larger geographical scale, the discrepancy in reported female L_{50} values [reviewed by Claro and Lindeman (2008)] may be related to the dif-ferent methods employed in the parameter's calculations, use of different gonad maturation scales and/or the fish size sampled (Wootton *et al.*, 2020). As we have experienced in the present work, failure to include the whole size spectrum results in highly uncertain estimates. Nev-ertheless, male and female lane snapper in Guatemala reached maturity (A_{50}) at comparable ages (2.4 ± 1.5–3.7 years for males and 3.5 ± 2.5–4.9 for females) to those from Abrolhos, Brazil (2.8 years, pooled sexes) (Aschenbrenner *et al.*, 2017). This is the only other study known to us where age data were obtained from sectioned otoliths and maturity at age derived from direct age-maturity logistic regressions.

The discrepancy in life-history traits and phenology across lane snapper range is likely an adaptation to enhance fitness across differ-ent environmental gradients. These interactions have been suggested for other tropical species undergoing range expansions (Taylor *et al.*, 2019; Zarco-Perello *et al.*, 2022). Different fishing regimes across the lane snapper range may further affect life-history estimates (Allman & Goetz, 2009; Audzijonyte *et al.*, 2016) to an unknown extent. Historical fishing pressure data across the region is limited. Pioneering efforts to assess the fisheries of the MAR have relied on data-limited methods, utilizing length frequency data coupled with life-history parameters. Where local length frequency data were una-vailable, information from other areas of lane snapper distribution have been incorporated into models, thus blurring stock-dependent variables (Babcock *et al.*, 2018; Sierra Castillo *et al.*, 2020; Sierra Castillo & Fujiwara, 2021). In the present study, we provided indepen-dent point-estimates of life-history parameters for lane snapper to allow mapping across regional scales (see Babcock *et al.*, 2013, 2018).

To conclude, we found plasticity in lane snapper life-history parameters, with a reduced maximum size, longevity and peak repro-ductive investment, compensated by a protracted spawning season and reproductive life span at the warm edge of its distribution range. The geographical gradients in life history can be used to predict

responses across the latitudinal (temperature) range of the species. These patterns are relevant for an ecological and evolutionary understanding of marine fish species affected by climate change and should be accounted for in fisheries assessments.

AUTHOR CONTRIBUTIONS

Hector Andrade and Jorge Santos: Project idea, funding, fieldwork and data generation. Hector Andrade, Mikko Vihtakari, Jorge Santos: Data analysis and manuscript preparation.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.