ARTICLE

Life History of the Gray Snapper at the Warm Edge of Its Distribution Range in the Caribbean

Hector Andrade* (ID)

Akvaplan-niva AS, Fram Centre, Post Office Box 6606, Langnes, 9296 Tromsø, Norway; and
Faculty for Biosciences, Fisheries, and Economics, Norwegian College of Fishery Science, University of Tromsø,
9037 Tromsø, Norway

Jorge Santos (ID)

Faculty for Biosciences, Fisheries, and Economics, Norwegian College of Fishery Science, University of Tromsø,
9037 Tromsø, Norway

Abstract

Knowledge of the life history of populations at the warm edge of their distributional range can provide a better understanding of how they will adapt to climate warming, including potential poleward redistribution. The range of Gray Snapper *Lutjanus griseus* has the potential to expand along its northern temperate fringe, but little is known about this species in the warmest portion of its range. We studied the age, growth, reproduction, and mortality of commercially caught Gray Snapper in the Guatemalan Caribbean, where sea surface temperature consistently exceeds 26°C. Longevity was estimated as 10 years, and von Bertalanffy growth parameters that were consolidated through Bayesian estimation incorporating earlier estimates from the Caribbean region were as follows: asymptotic length (L_∞) was 35 cm, the growth coefficient (K) was 0.56 year^{-1}, and the theoretical age at zero length (t_0) was −0.7 year. Gray Snapper grew slowest in April, prior to the rainy season, and at the onset of the reproductive season, which lasted to September. Fifty percent of the Gray Snapper matured at 31 cm and at 3.5 years of age. Gray Snapper had a lower maximum size, longevity, and peak reproductive investment, a protracted spawning season and reproductive life span, and elevated natural mortality at the warm edge of their distribution relative to temperate climates. Despite the plasticity in life history of Gray Snapper observed in this study, their potential to further adapt to warming remains unknown.

There is an increasing interest in the life history of animal populations at the warm edge of their distributional range, not only because climate warming may lead to poleward displacements but also because it provides information on the adaptive potential of populations in cooler areas (Rehm et al. 2015). A longstanding north–south hypothesis suggests that the equatorward range of a species is determined by biotic interactions and the poleward range is determined by abiotic factors (reviewed by Schemske et al. 2009; Cunningham et al. 2016). A contrasting hypothesis suggests that because of a narrow seasonal temperature range, tropical species are poorly

adapted to changes in the climate regime (Janzen 1967; Chejanovski and Wiens 2014). Empirical evidence supports different mechanisms of adaptation in terrestrial and marine species (Cahill et al. 2014). In marine ectotherms, range limits correspond more closely to thermal boundaries; thus, ocean warming may lead to more predictable range shifts (Sunday et al. 2012). Marine ectotherms with wide geographical distributions are good models to investigate adaptation under climate change.

The Gray Snapper *Lutjanus griseus* is caught by commercial and recreational fishers in the western central Atlantic (FAO 2016; Lindeman et al. 2016). Its distribution expands over two warm (temperate and tropical) biogeographical regions in the eastern Atlantic (sensu Briggs and Bowen 2012). Although juveniles have been collected in Massachusetts, the species is more prominent southwards along the United States coast, Bermuda, the Bahamas, Gulf of Mexico, the Caribbean, and Venezuela (Denit and Sponaugle 2004; Lindeman et al. 2016). A thermal tolerance model has been used to predict northward range expansion of tropical species (Hare et al. 2012; Morley et al. 2018), but forecasts did not consider potential life history adaptations.

The age, growth, and reproduction of Gray Snapper have been studied in Florida and the northern Gulf of Mexico (e.g., Manooch and Matheson 1981; Domeier et al. 1996; Burton 2001; Barbieri and Colvocoresses 2003; Fischer et al. 2005; Allman and Goetz 2009; Black et al. 2011; Dzaugis et al. 2017). Information from the Caribbean province mainly pre-dates the 1990s (Claro et al. 2001; Claro and Lindeman 2008). Similar data are available from Cuba (e.g., Báez Hidalgo et al. 1980; Claro 1983a, 1983b) and Venezuela (Guerra Campos and Bashirullah 1975), and additional growth estimates are available from Yucatán (Alfaro and López 1986) and Jamaica (Munro 1999).

The life history of Gray Snapper suggests divergent longevity, growth, and reproduction patterns potentially arising from adaptation to environmental conditions or the influence of fishing regimes (Allman and Goetz 2009). In the cooler areas of the northern Gulf of Mexico, increasing sea temperature, warm spring temperatures, and onshore winds favor Gray Snapper growth and recruitment (Black et al. 2011; Wuenschel et al. 2012; Muller-Karger et al. 2015), resulting in increased abundance and potentially a further poleward range expansion (Tolan and Fisher 2009; Fodrie et al. 2010; Hare et al. 2012; Gericke et al. 2014; Morley et al. 2018). In contrast, the effects of warming on Gray Snapper life history at the more tropical warm edge of its range in the south is less well known. Most ectotherms within their normal thermal range demonstrate higher growth and maturation rates after small temperature increases, but above a threshold temperature metabolic costs increase, leading to lower productivity and contracted geographical distribution

ranges (Neuheimer et al. 2011; Neuheimer and MacKenzie 2014). Demographic changes may affect community structure and function but also have practical implications for fisheries management and conservation (Gray 2015; Audzijonyte et al. 2016).

We investigated the life history and phenological traits of Gray Snapper at the warm edge of its distributional range in the Guatemalan Caribbean by sampling commercial catches from Amatique Bay and Punta de Manabique, two sites located within the warmest physicochemical province in the Caribbean and Neotropics (Chollett et al. 2012). Seasonal patterns of growth and reproduction and their relation to meteorological and hydrographic cycles were studied during a 12-month period. Data from commercial catches were augmented with information available from previous studies in the region. The life history, phenology, and processes that influence Gray Snapper ecology in the present thermal regime were described, and the potential effects of climate change on its biogeography were inferred.

METHODS

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 (Yañez-Arancibia et al. 1999; Fonseca and Arrivillaga 2003). The bay has an average depth of less than 10 m and comprises a 542-km^2 area, with an additional 200 km^2 of associated wetlands. Sea surface temperature ranges from about 26°C in May–November to 30°C in September (Andrade et al. 2015). Habitats in the bay include coastal lagoons, seagrass meadows, reefs, mangroves, and marshes, all of which are influenced by terrestrial runoff (Yañez-Arancibia et al. 1999). Reefs around Punta de Manabique comprise continental carbonate banks, where up to 29 species of scleractinian corals have been identified (Fonseca and Arrivillaga 2003). Precipitation and wind regimes are important drivers of the ecosystem and are associated with reproduction and movements of marine, catadromous, and estuarine fish species (Andrade et al. 2013, 2015). Small-scale fisheries in sheltered areas of Amatique, including Punta de Manabique, contribute to the economy and food security of coastal communities (Andrade and Midré 2011; Heyman and Granados-Dieseldorff 2012).

Field sampling and laboratory analyses.— Biological sampling of Gray Snapper was undertaken from March 2006 to February 2007 in Livingston and Puerto Barrios, the two main fishing harbors along the Guatemalan Caribbean coast. Artisanal fishers deploy hooks and lines, baited traps, and nets, and they land fish intact. In Livingston, the catch is sold from the boat, but at markets
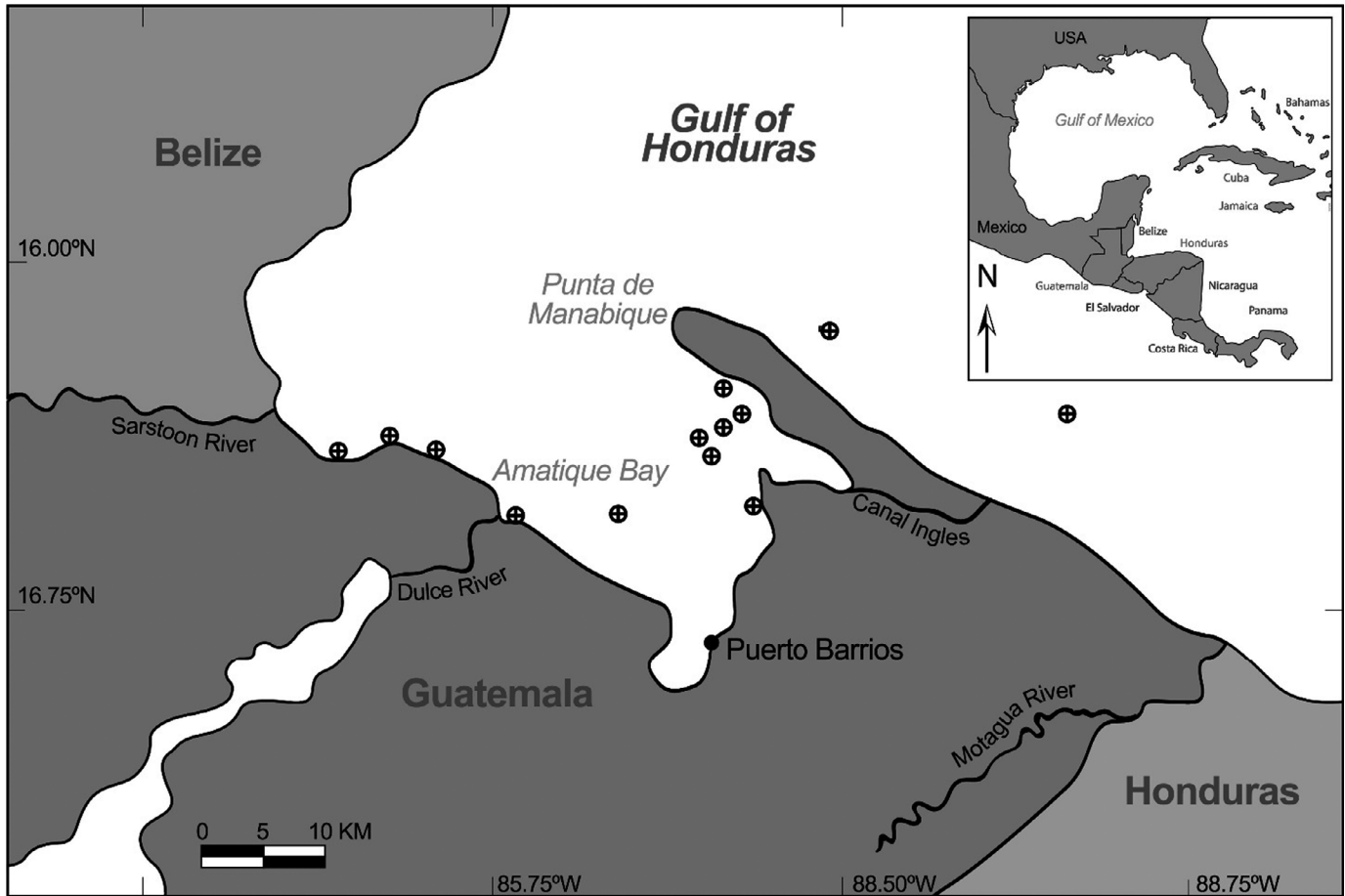
FIGURE 1. Location of the study area with identified reefs and hard-bottom habitats (circled crosses) on the Atlantic coast of Guatemala (modified from Fonseca and Arrivillaga 2003).

in Puerto Barrios the fish are stored on ice until sold. About 30–40 snappers were sampled each month, except in May 2006, when only 12 snappers were sampled. Total lengths, FLs, and SLs of 390 Gray Snapper were measured, and linear regressions between length variables were constructed to aid conversions. Total weight (WT; $n = 320$) and gonadal weight (WG; $n = 244$; ± 0.1 g) were recorded, and the body mass (WT, g) distribution of individual fish was investigated by means of the linearized power relationship $W = a\text{TL}^b$ and Fulton's condition factor (K; Froese 2006). The gonadosomatic index (GSI) was computed as $\text{GSI} = 100 \times [\text{WT}/(\text{WT} - \text{WG})]$ (males: $n = 100$; females: $n = 137$). Fresh gonads were inspected macroscopically and scored for sex and maturity determination ($n = 340$). Maturity classes were defined based on gonadal appearance using a key (I = immature, II = developing, III = spawning, and IV = regenerating; Domeier et al. 1996; Brown-Peterson et al. 2011).

The left sagittal otolith was collected for age determination, and three thin sections were prepared using a low-speed saw. The section with the clearest otolith core was photographed under a compound microscope with transmitted light (Taylor et al. 2000). Bands were counted thrice by a single reader to learn snapper otolith deposition patterns, and data from the third count ($n = 357$) were used for the growth analysis. Fish less than 1 year old were assigned an age of 0.5 years. An edge-type analysis of the monthly frequency of otoliths with an opaque zone at the edge was conducted to assess the seasonal and annual deposition of increments (Manickchand-Heileman and Phillip 2000; Rhodes et al. 2011).

Data analysis.— Linear models (LMs), generalized linear models (GLMs), and generalized linear mixed models (GLMMs; Venables and Dichmont 2004) were used to assess the different morphometric relationships and life history parameters and their dependencies on sex, size, season, and growth rate (growth index [GI]). Binomial regressions (logit) were performed when response variables consisted of binary outcomes (e.g., sexual maturity), but beta regressions (logit) were utilized for proportions, such as the GSI. The size and age at 50% maturity (L_{50} and A_{50}) were estimated using binomial regression and

represent the size or age at which a randomly chosen specimen would have a 50% chance of being mature. To describe the periodic oscillation of edge marks on the otoliths as well as the proportion of mature fish in the samples collected over a year, sinusoidal waves with the form

$$y(t) = \sin\left(t \cdot \frac{2\pi}{12}\right) + \cos\left(t \cdot \frac{2\pi}{12}\right)$$

were fitted, making use of the error distributions and links described above (t = month [1, 12]). For continuous response variables, Gaussian or gamma regression was utilized, depending on the visual fit and strength of evidence for the model. All of the generalized models were ranked by their improvement in Akaike's information criterion (ΔAIC; Burnham and Anderson 2004), and tests of goodness of fit were performed using the likelihood ratio test. No correction was attempted for missing data other than the TL, and listwise deletion was performed in the different regression analyses.

To investigate whether fish of different sex had similar growth patterns, the unconstrained von Bertalanffy growth function (VBGF) with the form

$$L_t = L_\infty \left[1 - e^{-K(t - t_0)}\right]$$

was first fitted to the age–length data (years, cm) using generalized nonlinear regression (L_t = length at age t; L_∞ = asymptotic length; K = growth coefficient; t_0 = theoretical age at zero length). The VBGF was then fitted in its constrained form ($t_0 = 0$) to compensate for the scarcity of small fish in the samples. Finally, the full VBGF was fitted with a Bayesian approach to estimate the joint posterior distribution of growth curve parameters based on the present study and four past studies on Gray Snapper growth at warm edge locations in Yucatán, Cuba, and Jamaica (Báez Hidalgo et al. 1980, cited by Claro and Lindeman 2008; Claro 1983b; Alfaro and López 1986; cited by Torres-Lara et al. 1991; Munro 1999, cited by Claro and Lindeman 2008). The studies relied on different aging techniques, such as age readings from whole otoliths, size-frequency analyses, and tagging. To cope with increased uncertainty, flat priors that incorporated all previous parameter estimates were used: $L_\infty \sim$ U(35, 60), $K \sim$ U(0.1, 0.8), and $t_0 \sim$ U(−0.7, 0.7), in addition to a vague precision parameter with a gamma distribution ($G \sim$ [0.001, 0.001]). Three Markov chains were simulated with a total of 20,000 iterations, burn-in of 10,000, and thinning of 10, using pooled sex data. Convergence in the Bayesian model was evaluated through visual inspection of autocorrelation to ensure independence of values within each chain. The deviance information criterion was also calculated. The SD of the posterior distributions was calculated to allow comparison

with the analogous SE approximation provided by default by other statistical software. For each individual fish, the GI (or studentized residual between the fish's observed size and its Bayesian predicted size) was calculated.

An age-based catch curve (Ricker 1975) was used to estimate instantaneous total mortality (Z) using an unweighted regression and assuming constant mortality. Longevity (t_{max}; years) was derived from the catch-curve intercept, and the natural mortality rate (M) was determined from the updated Hoenig nonlinear least-squares estimator (Then et al. 2015). Statistical propagation of estimation and predictive errors was calculated as recommended by Taylor (1997) for uncorrelated variables. For example, if $f = CA$ is the product of a constant C and a variable A (measured with error σA), then its SD is $\sigma f = C\sigma A$. Statistical analyses were conducted using the R statistical programming language (R Development Core Team 2017), including the software packages betareg (Cribari-Neto and Zeileis 2010), lmtest (Zeileis and Hothorn 2002), mass (Venables and Ripley 2002), nlme (Pinheiro et al. 2012), and rjags (Plummer 2016).

RESULTS

Size, Sex Distribution, and Condition

In total, 391 fish were sampled in Livingston ($n = 323$) and Puerto Barrios ($n = 68$). Meristic relations and all modeled life history parameters with their variances are provided in Table 1, grouped under different headings, including those relative to morphometric (length and weight), growth, and reproduction relationships. The sampled fish did not significantly deviate from the 1:1 sex ratio, with an excess of males only noticeable in November and December (Table 1). The average TL remained constant at 27 cm (range = 19–55 cm) throughout the year, with females usually being larger than males (Figure 2). Small Gray Snapper were scarce in the samples. Although there are no restrictions regarding size limits of the fish, 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. No marked changes in body condition, measured as either the weight–length relationship or Fulton's K, were detected over a year or between sexes (Table 1).

Age and Growth

Clear annuli were visible in otolith sections (Figure 3), making them easier to read than those of several other species from the same area (e.g., Snook *Centropomus undecimalis* and Lane Snapper *Lutjanus synagris*; Andrade et al. 2013, and unpublished data). The age distributions of females and males were similar and ranged from young of the year to 10 years, but most fish were between 1 and 5

TABLE 1. Coefficients of predictors in regression analyses of morphometric, growth, life history, and reproductive traits of Gray Snapper in the Guatemalan Caribbean. Also indicated are predictors that were excluded in more complex but less parsimonious models and statistics of fit. Lengths are given in centimeters, weights are given in grams, and time is expressed in years or months (Adj. R^2 = adjusted R^2; LM = linear model; GLM = generalized linear model; GLMM = generalized linear mixed model; GNLS = generalized nonlinear least squares; M = instantaneous rate of natural mortality; Z = instantaneous rate of total mortality; Fulton's K = Fulton's condition factor; GSI = gonadosomatic index; L_∞ = asymptotic length; K = growth coefficient; t_0 = theoretical age at zero length; DIC = deviance information criterion; AIC = Akaike's information criterion; MSE = mean square error; GI = growth index; LR = likelihood ratio test; probability levels: nonsignificant [ns], *$P < 0.05$, and ***$P < 0.001$).

Variable	Model, distribution (link)	N	Constant (SE)	Predictor (SE)	Predictors excluded	Fit
Morphometric						
FL	LM, Gaussian	190	0.51 (0.109)	SL: 1.13 (0.005)		Adj. $R^2 = 0.997$
TL	LM, Gaussian	297	1.05 (0.106)	SL: 1.14 (0.004)		Adj. $R^2 = 0.996$
TL	LM, Gaussian	189	0.67 (0.090)	FL: 1.01 (0.003)		Adj. $R^2 = 0.998$
TL	GLM, gamma (identity)	370	27.0 (0.8)	Sex male: −2.0 (0.6) Apr–Aug: >2.0 (1.2) Dec, Feb: >2.0 (1.2)		ΔAIC = 30 (LR***)
Weight ($\log_e$)	LM, Gaussian	305	−4.44 (0.101)	$\log_e$TL: 3.04 (0.030)		Adj. $R^2 = 0.971$ (MSE = 0.01)
Weight ($\log_e$)	GLM, Gaussian (identity)	305	−4.44 (0.101)	$\log_e$TL: 3.04 (0.030)	Month, Sex	ΔAIC: 2 (LR*)
Fulton's K	GLM, gamma (identity)	305	1.37 (0.008)		Month, Sex	ΔAIC = 28 (LR*)
Growth and von Bertalanffy growth function						
TL	GNLS (power of variance)	357		L_∞: 59 (47) K: 0.07 (0.096) t_0: −6.0 (3.2)	Sex	ΔAIC = 317 (LR***)
TL	GNLS (power of variance)	358		L_∞: 28 (0.31) K: 3.1 (0.26) t_0: 0 (constrained)	Sex	AIC = 2,185
TL	Bayesian NL	357		L_∞: 35 (3.4) K: 0.56 (0.40) t_0: −0.7 (0.38)		DIC = 2,268
Opaque zone on edge$_{\{0,1\}}$	GLM, binomial (logit)	357	−2.2 (0.20)	$\sin(\pi t/6)$: 1.1 (0.28) $\cos(\pi t/6)$: −1.0 (0.27)		AIC = 225
Life history						
Sex ratio	GLM, binomial (logit)	341	0.09 (0.11)		Month, TL	ΔAIC = 13 (LR***)
Z (catch curve) M	GLM, Gaussian Hoenig nonlinear least squares	8	6.3 (0.37) M: 0.6 (0.42)	$-Z$: −0.7 (0.06)	Sex	ΔAIC = 2 (LR ns)
Reproduction						
Maturation$_{\{0,1\}}$	GLM, binomial (logit)	215	−4.8 (0.71)	Age: 0.94 (0.185) Sex male: 3.5 (0.47) GI: 1.1 (0.25)		AIC = 169
Maturation$_{\{0,1\}}$	GLM, binomial (logit)	215	−13.3 (2.35)	TL: 0.39 (0.076) Sex male: 3.5 (0.47) GI: −1.0 (0.39)		AIC = 168

TABLE 1. Continued.

Variable	Model, distribution (link)	N	Constant (SE)	Predictor (SE)	Predictors excluded	Fit
Maturation$_{\{0,1\}}$	GLM, binomial (logit)	232	−4.4 (0.87)	TL: 0.14 (0.030)	Sex, GI	AIC = 292
Maturation$_{\{0,1\}}$	GLM, binomial (logit)	215	−2.4 (0.41)	Age: 0.66 (0.124)	Sex, GI	AIC = 260
GSI$_{\{0,1\}}$	Beta regression (logit)	237	−7.5 (0.21)	TL: 0.06 (0.005)	Sex	ΔAIC = 1 (LR ns)
GSI$_{\{0,1\}}$	Beta regression (logit)	237	−5.3 (0.05)	Mar, Jul, Aug: 0.6 (0.19) Apr, May: 1.0 (0.20) Jun: 1.4 (0.18) $\sin(\pi t/6)$: 0.16 (0.06) $\cos(\pi t/6)$: −0.56 (0.07)		

FIGURE 2. Size composition of Gray Snapper samples given as mean TL (±95% confidence interval) by month and sex.
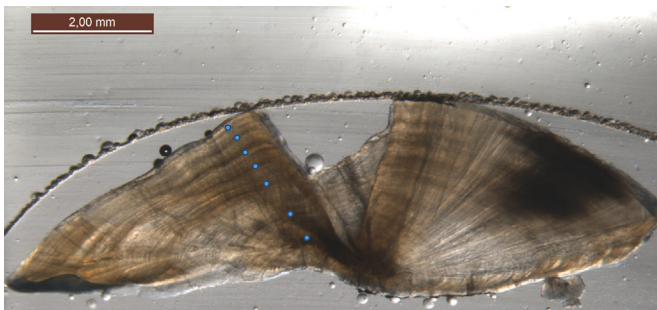

FIGURE 3. Transverse section of a sagittal otolith from a 7-year-old female Gray Snapper collected in the Guatemalan Caribbean. Blue dots indicate the opaque bands that were used in determinig age.

years old (Figure 4). Size at age varied considerably over the most frequent range of ages (Figure 5). The preliminary unconstrained VBGF fit revealed no differences between male and female growth parameters (Table 1). The fit of the constrained VBGF ($t_0 = 0$) provided very high estimates of K and very low L_∞ (Table 1), which reflected the poor representation of the youngest year-classes in samples. The Bayesian fit to the pooled data, using priors from other warm areas of the Gray Snapper's range, resulted in a lower L_∞ and higher K than the unconstrained fit (Table 1). This trend was correlated with an estimate of t_0 closer to zero, as expected from this population parameter for teleosts.

Deposition of an opaque edge in otoliths, an indication of slower growth periods (Fowler 2009), followed a clear seasonal pattern, with over 25% of the otoliths sampled
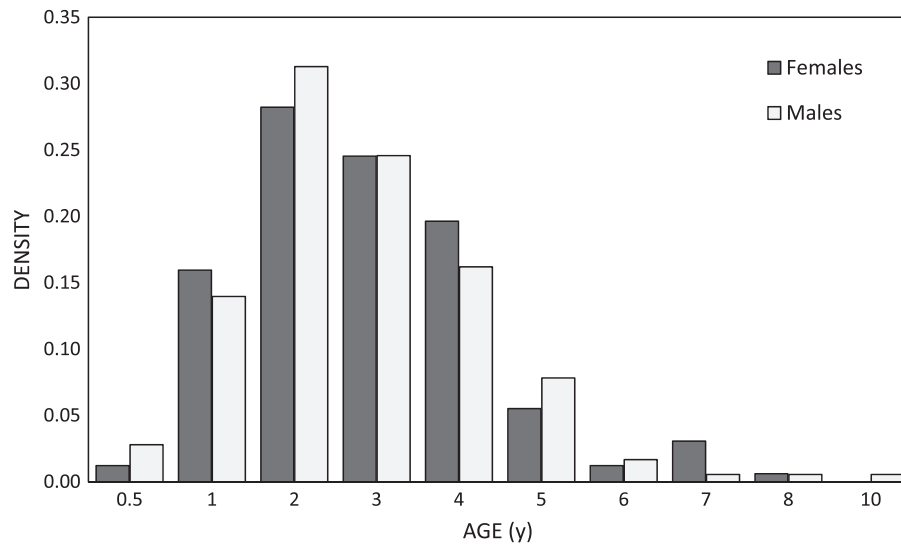
FIGURE 4. Age distribution (y = years) of Gray Snapper in the samples. Data represent 342 aged and sexed fish, of which 173 were males and 169 were females.
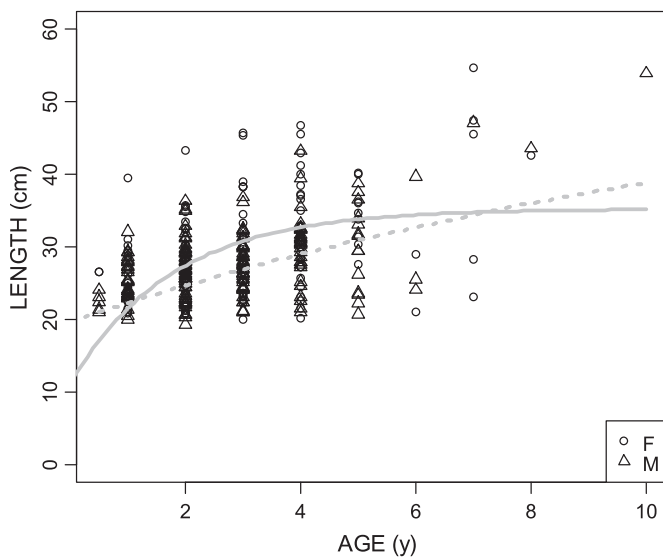

FIGURE 5. The von Bertalanffy growth function fitted to the age–length observations (y = years) of Gray Snapper by means of the generalized nonlinear least-squares method (dashed line) and the Bayesian approach (solid line) using the pooled data for females (circles) and males (triangles). Statistics of fit are given in Table 1.

between March and June showing its presence (Table 1; Figure 6). In April, 40% of otoliths had an opaque edge, but few or no otoliths showed such an edge in September–January.

Reproduction and Mortality

The onset of sexual maturity was related to the sex, size, and GI of Gray Snapper. The GSI peaked in May–July and fell to its lowest level in October–February (Table 1; Figure 7). This lagged the peak opaque zone formation in otoliths (i.e., April) by a month. Although size-dependent, the overall GSI remained at a modest level (0.8–1.0%, on average). Frequent occurrence of mature fish (stage III gonads) was observed between April and September (>30%), with a peak (70%) in June–July (Table 1; Figure 7). Few fish were mature between December and March, when most stage I gonads were sampled, suggesting a period of recruitment to the fishery. Stronger evidence supported the sigmoid (logistic) maturation model expressed in terms of TL rather than age (ΔAIC = 1.6; likelihood ratio test: $P < 0.001$). Additionally, fish that grew fast were more frequently mature than other fish of the same size (Table 1). Males matured at a smaller size than females (Table 1), and the minimum size at maturity was 20.6 cm for males and 27.5 cm for females. However, there was some uncertainty about sex staging of young males, and the pooled sex data gave a more consistent fit, resulting in an L_{50} of 31.1 $\pm$ 1.10 cm (mean $\pm$ SE) at an A_{50} of 3.6 $\pm$ 0.24 years (Table 1; Figure 8).

The value of M estimated from longevity (t_{max}) was relatively high ($M = 0.6$; Table 1). The estimate of Z obtained by catch-curve analysis was 0.7, assuming full recruitment to the gears at age 2. Thus, the value of M was close to the value of Z, indicating a relatively low exploitation rate.

DISCUSSION

Sea surface temperatures have increased in the Caribbean, affecting the structure of marine communities (Hayes and Goreau 2008; Maharaj et al. 2018). Tropical
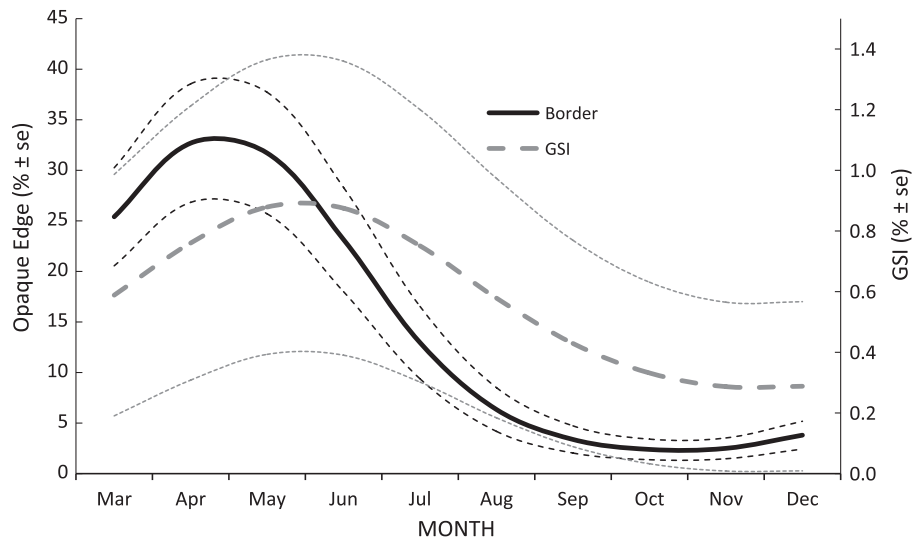
FIGURE 6. Sinusoidal curve fit to data on the occurrence of opaque otolith edge and the gonadosomatic index (GSI) with a monthly time step for Gray Snapper. Statistics of fit are given in Table 1.

fish at the warm edge have limitations in oxygen metabolism at increasing temperatures that may put them at a higher risk than core range populations (Wuenschel et al. 2004, 2005; Rummer et al. 2014; Maharaj et al. 2018; Pauly and Cheung 2018). Simple climate models based on different temperature scenarios in the Northern Hemisphere and based on the present thermal range of the species predict increased dispersal and recruitment along the leading northern edge—changes that may already be taking place (Tolan and Fisher 2009; Fodrie et al. 2010; Hare et al. 2012; Gericke et al. 2014). However, an understanding of the adaptations in life history is also called for (Pauly and Cheung 2018).

We studied the biology and life history of Gray Snapper in the Guatemalan Caribbean, a little-studied tropical environment classified as one of the warmest physicochemical provinces in the Caribbean Sea (Chollett et al. 2012). As elsewhere in the tropics, the seasonal gradient in seawater temperature is shallow (26–30°C) and snappers in this area inhabit the warmest edge of their thermal range. Despite the narrow temperature variation, there were marked biological rhythms in Gray Snapper. The seasonal cycles of growth and reproduction observed were closely related, with the gonadal cycle (i.e., GSI) lagging the growth cycle (opaque zone) by about 1 month. These cycles were consistently linked in the sampled Gray Snapper, despite the relatively small number of monthly observations.

Variations in Size Distribution

Size distribution varied little throughout the year, with snappers in all reproductive stages occurring in samples throughout the period. Seasonal ontogenetic movements are well described elsewhere for Gray Snapper, which inhabit estuaries mostly during their nursery and subadult grow-out phases. Larger individuals are most often found in deep channels and further offshore, associated with hard-bottom habitats (Flaherty et al. 2014 and references therein). However, a diverse range of habitats in the Guatemalan Caribbean, including seagrass meadows, mangroves, reefs, and hard bottoms, potentially supports all of the snapper life stages locally. Nevertheless, a prevalence of subadults throughout the year suggests that it is also a grow-out area for late juveniles (>1 year).

Environmental Cycles and Life History Traits

The rainy season and peak freshwater runoff are the main drivers of ecosystem functioning in Amatique Bay (Andrade et al. 2015) and probably for 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 (March–June) followed by spawning in May–July, with most spawners observed in June, around the peak runoff period. At this time, terrestrial nutrient supply and primary productivity are elevated, providing favorable conditions for egg and larval development (Andrade et al. 2015). This observation corroborates the findings of Claro and Lindeman (2008) that opaque zones in otoliths are formed during this period in marine fishes in Cuba. Further north, in Florida, opaque edges form 1–2 months later (Burton 2001;
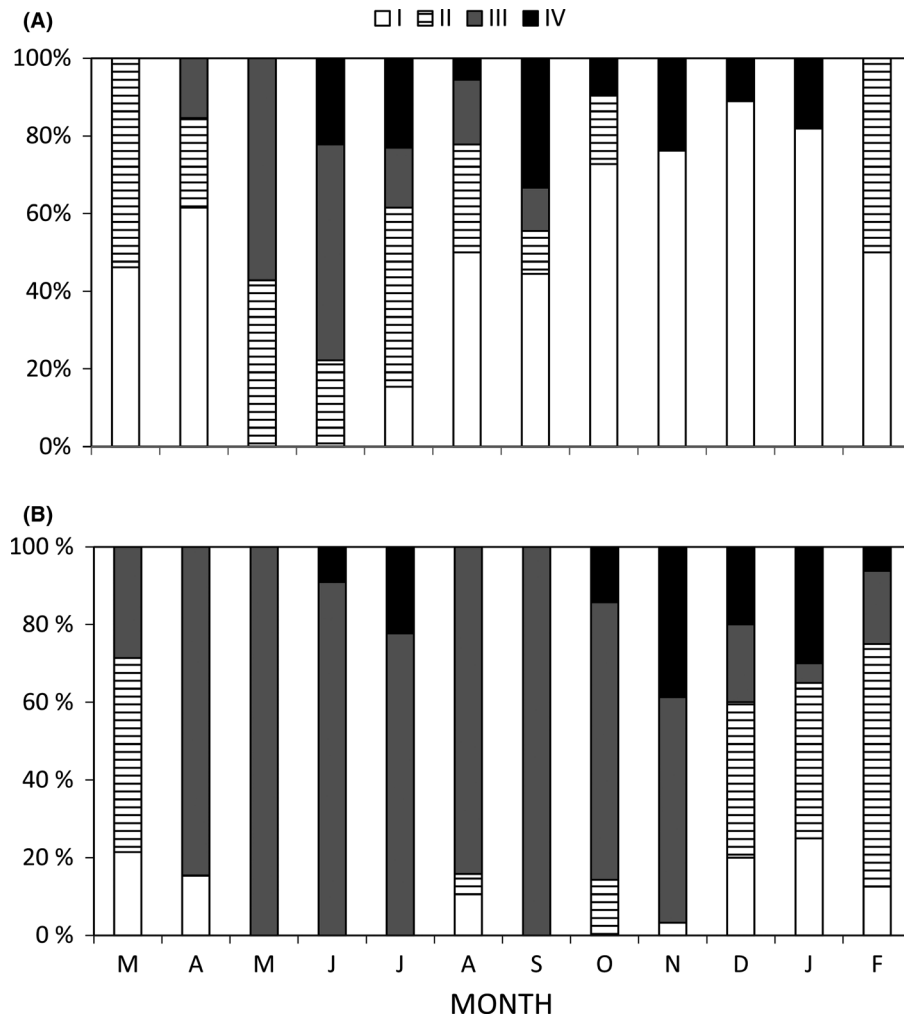
FIGURE 7. Observed maturation cycle of **(A)** female and **(B)** male Gray Snapper in the Guatemalan Caribbean from March 2006 to February 2007 (I = immature; II = developing; III = spawning; IV = regenerating).

Allman and Goetz 2009), and they form even later in Louisiana, where growth subsides only in December–May (Fischer et al. 2005). Similarly, spawning occurred at least 1 month earlier in the Guatemalan Caribbean than in south Florida, Cuba, and Venezuela (Guerra Campos and Bashirullah 1975; Domeier et al. 1996; García-Cagide et al. 2001 and references therein). Given the wealth of studies available across the latitudinal range occupied by Gray Snapper, it should now be possible to derive phenological hypotheses and models relative to the influences of abiotic drivers.

Growth, Age, Maturation, and Mortality

The individual variability in growth rate was pronounced in Gray Snapper in the Guatemalan Caribbean and elsewhere. Our sampling secured a limited number of fish under 19 cm TL, and these were often young of the year, to which we assigned an arbitrary age of 0.5 years. Together, these limitations may have contributed to uncertainty in the estimates of the VBGF parameters, particularly t_0. To consolidate estimates, a Bayesian framework was used to incorporate growth parameters obtained in Cuba and Jamaica using fishery-independent methodology (Claro 1983b; Munro 1999, cited by Claro and Lindeman 2008). The resultant maximum observed size of Gray Snapper in Guatemala and the western Caribbean was approximately 55 cm, considerably smaller than at sites in Louisiana, Florida, and Venezuela (62–76 cm; Guerra Campos and Bashirullah 1975; Burton 2001; Fischer et al. 2005; Allman and Goetz 2009). Our findings are supported by extensive observations by divers across reefs in Mesoamerica, where Gray Snapper length seldom exceeds 30 cm (A. Giro, Healthy Reefs, personal communication; www.healthyreefs.org/cms/).
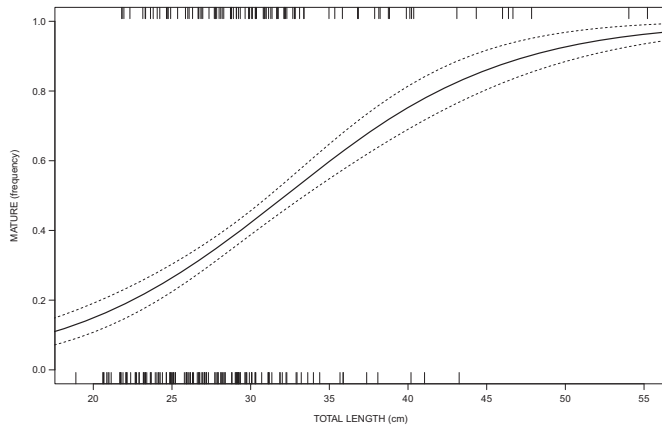
FIGURE 8. Maturation ogives of Gray Snapper for both sexes combined, presented with SEs (dashed lines). Vertical hash marks along the size axes denote the individual fish classified as mature (top) or immature (bottom).

Although most growth studies have been performed in temperate regions, often using different methodology (Claro and Lindeman 2008), they support the present findings of large individual variability in length at age. In the Guatemalan Caribbean, we found no differences in growth between sexes, but a trend toward earlier maturation of male fish may exist. Furthermore, much of the variability in maturation could be attributed to growth rate variability. Interactions between growth rate and sexual maturation are not uncommon (e.g., Gunnarsson 2014; Kodama et al. 2018), and factors that affect growth rate, such as warming temperatures and sea climate, may thereby also affect sexual traits (Wuenschel et al. 2004; Neuheimer et al. 2011; Neuheimer and MacKenzie 2014).

The longevity of Gray Snapper in the Guatemalan Caribbean ($t_{max} = 10$ years) was lower than at northern latitudes, where most estimates were between 14 and 28 years. The exceptionally short life span of 6 years reported from Venezuela (Guerra Campos and Bashirullah 1975) has been attributed to an artifact caused by the scale-reading methodology used (Manooch and Matheson 1981). The present estimate of M (0.6) was relatively high compared to previous estimates from the Gulf of Mexico (0.15–0.50; Fischer et al. 2005), north Florida (0.14–0.43), and southeast Florida (0.29–0.38; Burton 2001). However, the present M-estimate is similar to those obtained in the warm waters of Cuba (0.53–0.58; Claro and Lindeman 2008). These convert to an identical M (0.6) if Hoenig's method is used together with the assumed t_{max} of 10 years (Claro and Lindeman 2008). The fact that the present estimate of M was only marginally lower than Z (i.e., $Z = 0.7$), implying low instantaneous fishing mortality ($F = 0.1$), may be related to an influx of migrants from the Mesoamerican Barrier Reef System. This occurrence is frequently mentioned by Guatemalan fishers (Andrade and Midré 2011).

Thus, relatively low t_{max} and high M may well be true characteristics of Gray Snapper at the warm edge of its distribution.

A conspicuous difference between Gray Snapper in tropical and warm-temperate areas is related to the allocation of reproductive effort. The L_{50} observed in the Guatemalan Caribbean (31 cm) was slightly larger than earlier observations (26–28 cm) from Cuba but was well below the L_{50} in Venezuela (>46 cm; Claro 1983b; Claro and Lindeman 2008), where water is cooler. We have presented one of the first maturation curves for this species. Whilst there were clear trends for earlier maturation in males than in females, this issue deserves further investigation. Particularly for the young males, it is difficult to stage maturity without histological sampling. Few other estimates of L_{50} are available for this species in the literature, hindering further comparative analysis. In Guatemala, the average GSI peaked in June at 1.3%, but this ratio is over 3.0% elsewhere, including Key West, Florida (Domeier et al. 1996); Batabanó Gulf, Cuba (Claro 1983a; García-Cagide et al. 2001); and Cubagua Island, Venezuela (Guerra Campos and Bashirullah 1975). This supports earlier suggestions (Andrade et al. 2013) of the existence of latitudinal gradients or clines in reproductive output, as measured by GSI, which can be compensated for by protracted spawning and reproductive activity in tropical climates.

Our findings suggest plasticity in life history parameters in a fish species at the warm edge of its distribution range, extending to a reduced maximum size, longevity, and peak reproductive investment; a protracted spawning season and reproductive life span; and elevated natural mortality. Plasticity in life history traits can now be taken into account in spatial models of future adaptation to climate warming and fisheries management. A study of reaction norms of Gray Snapper along its latitudinal and thermal distribution ranges can bring a new level of sophistication to models of redistribution, adaptation, and management of the trailing edge of fish populations in the neotropics.

ORCID

Hector Andrade https://orcid.org/0000-0001-5334-7022
Jorge Santos https://orcid.org/0000-0001-8532-9240

REFERENCES

Alfaro, G. L. A., and M. López. 1986. Contribución al estudio de la pesquería del pargo criollo *Lutjanus analis*, Cuvier) y pargo mulato (*Lutjanus griseus*, Linneo) en el litoral del Estado de Yucatán. Universidad Nacional Autónoma de México, Mexico City.

Allman, R. J., and L. A. Goetz. 2009. Regional variation in the population structure of Gray Snapper, *Lutjanus griseus*, along the West Florida Shelf. Bulletin of Marine Science 84:315–330.

Andrade, H., and G. Midré. 2011. The merits of consensus: small-scale fisheries as a livelihood buffer in Livingston, Guatemala. Pages 427–448 *in* S. Jentoft and A. Eide, editors. Poverty mosaics: realities and prospects in small-scale fisheries. Springer, Dordrecht, The Netherlands.

Andrade, H., J. Santos, and M. J. Ixquiac. 2015. Ecological linkages in a Caribbean estuary bay. Marine Ecology Progress Series 533:29–46.

Andrade, H., J. Santos, and R. Taylor. 2013. Life-history traits of the Common Snook *Centropomus undecimalis* in a Caribbean estuary and large-scale biogeographic patterns relevant to management. Journal of Fish Biology 82:1951–1974.

Audzijonyte, A., E. Fulton, M. Haddon, F. Helidoniotis, A. J. Hobday, A. Kuparinen, J. Morrongiello, A. D. M. Smith, J. Upston, and R. S. Waples. 2016. Trends and management implications of human-influenced life-history changes in marine ectotherms. Fish and Fisheries 17:1005–1028.

Báez Hidalgo, M., L. Alvarez-Lajonchere, and B. Pedrosa Tabio. 1980. Edad y crecimiento del caballerote *Lutjanus griseus* (Linné), en Tunas de Zaza, Cuba. Revista de Investigaciones Marinas 1:135–150.

Barbieri, L. R., and J. A. Colvocoresses. 2003. Southeast Florida reef fish abundance and biology: five year performance report. Florida Fish and Wildlife Conservation Commission, Florida Marine Research Institute, St. Petersburg.

Black, B. A., R. J. Allman, I. D. Schroeder, and M. J. Schirripa. 2011. Multidecadal otolith growth histories for Red and Gray snapper (*Lutjanus* spp.) in the northern Gulf of Mexico, USA. Fisheries Oceanography 20:347–356.

Briggs, J. C., and B. W. Bowen. 2012. A realignment of marine biogeographic provinces with particular reference to fish distributions. Journal of Biogeography 39:12–30.

Brown-Peterson, N. J., D. M. Wyanski, F. Saborido-Rey, B. J. Macewicz, and S. K. Lowerre-Barbier. 2011. A standardized terminology for describing reproductive development in fishes. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science [online serial] 3:52–70.

Burnham, K. P., and D. R. Anderson. 2004. Multimodel inference: understanding AIC and BIC in model selection. Sociological Methods and Research 33:261–304.

Burton, M. L. 2001. Age, growth, and mortality of Gray Snapper, *Lutjanus griseus*, from the east coast of Florida. U.S. National Marine Fisheries Service Fishery Bulletin 99:254–265.

Cahill, A. E., M. E. Aiello-Lammens, M. C. Fisher-Reid, X. Hua, C. J. Karanewsky, H. Y. Ryu, G. C. Sbeglia, F. Spagnolo, J. B. Waldron, and J. J. Wiens. 2014. Causes of warm-edge range limits: systematic review, proximate factors and implications for climate change. Journal of Biogeography 41:429–442.

Chejanovski, Z. A., and J. J. Wiens. 2014. Climatic niche breadth and species richness in temperate treefrogs. Journal of Biogeography 41:1936–1946.

Chollett, I., P. J. Mumby, F. E. Müller-Karger, and C. Hu. 2012. Physical environments of the Caribbean Sea. Limnology and Oceanography 57:1233–1244.

Claro, R. 1983a. Ecología y ciclo de vida del caballerote, *Lutjanus griseus* (Linnaeus), en la plataforma cubana. I. Identidad, distribución y hábitat, nutrición y reproducción. Reporte de Investigación del Instituto de Oceanología Academia de Ciencias de Cuba 7:30.

Claro, R. 1983b. Ecología y ciclo de vida del caballerote, *Lutjanus griseus* (Linnaeus), en la plataforma cubana. II. Edad y crecimiento, estructura de las poblaciones y pesquerías. Reporte de Investigación del Instituto de Oceanología Academia de Ciencias de Cuba 8:26.

Claro, R., and K. C. Lindeman. 2008. Biología y manejo de los pargos (Lutjanidae) en el Atlántico occidental. Instituto de Oceanología, Ministerio De Ciencia, Tecnología y Medio Ambiente, Cuba.

Claro, R., K. C. Lindeman, and L. R. Parenti, editors. 2001. Ecology of the marine fishes of Cuba. Smithsonian Institution Press, Washington, D.C.

Cribari-Neto, F., and A. Zeileis. 2010. Beta regression in R. Journal of Statistical Software [online serial] 34(2).

Cunningham, H. R., L. J. Rissler, L. B. Buckley, and M. C. Urban. 2016. Abiotic and biotic constraints across reptile and amphibian ranges. Ecography 39:1–8.

Denit, K., and S. Sponaugle. 2004. Growth variation, settlement, and spawning of Gray Snapper across a latitudinal gradient. Transactions of the American Fisheries Society 133:1339–1355.

Domeier, M. L., C. C. Koenig, and F. C. Coleman. 1996. Biology and culture of tropical groupers and snappers. Pages 189–201 *in* F. Arreguín-Sánchez, J. L. Munro, M. Balgos, and D. Pauly, editors. Biology, fisheries and culture of tropical groupers and snappers. International Center for Living Aquatic Resources Management, Conference Proceedings 48, Makati City, Philippines.

Dzaugis, M. P., R. J. Allman, and B. A. Black. 2017. Importance of the spring transition in the northern Gulf of Mexico as inferred from marine fish biochronologies. Marine Ecology Progress Series 565:149–162.

FAO (Food and Agriculture Organization of the United Nations). 2016. FAO yearbook: fishery and aquaculture statistics 2014. FAO, Rome.

Fischer, A. J., M. S. Baker, C. A. Wilson, and D. L. Nieland. 2005. Age, growth, mortality, and radiometric age validation of Gray Snapper (*Lutjanus griseus*) from Louisiana. U.S. National Marine Fisheries Service Fishery Bulletin 103:307–319.

Flaherty, K. E., T. S. Switzer, B. L. Winner, and S. F. Keenan. 2014. Regional correspondence in habitat occupancy by Gray Snapper (*Lutjanus griseus*) in estuaries of the southeastern United States. Estuaries and Coasts 37:206–228.

Fodrie, F. J., K. L. Heck, S. P. Powers, W. M. Graham, and K. L. Robinson. 2010. Climate-related, decadal-scale assemblage changes of seagrass-associated fishes in the northern Gulf of Mexico. Global Change Biology 16:48–59.

Fonseca, A. C., and A. Arrivillaga. 2003. Coral reefs of Guatemala. Pages 159–169 *in* J. Cortés, editor. Latin American coral reefs. Elsevier Science B.V., Amsterdam.

Fowler, A. J. 2009. Age in years from otoliths of adult tropical fish. Pages 55–92 *in* B. S. Green, B. D. Mapstone, G. Carlos, and G. A.

Begg, editors. Tropical fish otoliths: information for assessment, management and ecology. Springer, Dordrecht, The Netherlands.

Froese, R. 2006. Cube law, condition factor and weight–length relationships: history, meta-analysis and recommendations. Journal of Applied Ichthyology 22:241–253.

García-Cagide, A., R. Claro, and B. V. Koshelev. 2001. Reproductive patterns of fishes of the Cuban shelf. Pages 71–102 in R. Claro, K. C. Lindeman, and L. R. Parenti, editors. Ecology of the marine fishes of Cuba. Smithsonian Institution Press, Washington, D.C.

Gericke, R. L., K. L. Heck, and F. J. Fodrie. 2014. Interactions between northern-shifting tropical species and native species in the northern Gulf of Mexico. Estuaries and Coasts 37:952–961.

Gray, C. A. 2015. Spatial variation in demography of an estuarine teleost: implications for population and fishery assessments. Aquatic Biology 23:209–223.

Guerra Campos, A., and A. K. M. Bashirullah. 1975. Biología del pargo Lutjanus griseus (Linn.) de la Isla de Cubagua, Venezuela. II. Maduración sexual y fecundidad. Boletín del Instituto Oceanográfico de la Universidad de Oriente 14:190–116.

Gunnarsson, A. 2014. Atlantic Wolf-fish Anarhichas lupus population diversity: growth and maturation. Journal of Fish Biology 84: 339–353.

Hare, J. A., M. J. Wuenschel, and M. E. Kimball. 2012. Projecting range limits with coupled thermal tolerance–climate change models: an example based on Gray Snapper (Lutjanus griseus) along the U.S. East Coast. PLoS (Public Library of Science) ONE [online serial] 7 (12):e52294.

Hayes, R. L., and T. J. Goreau. 2008. Satellite-derived sea surface temperature from Caribbean and Atlantic coral reef sites, 1984–2003. Revista de Biologia Tropical 56:97–118.

Heyman, W. D., and P. Granados-Dieseldorff. 2012. The voice of the fishermen of the Gulf of Honduras: improving regional fisheries management through fisher participation. Fisheries Research 125–126: 129–148.

Janzen, D. H. 1967. Why mountain passes are higher in the tropics. American Naturalist 101:233–249.

Kodama, M., J. J. Hard, and K. A. Naish. 2018. Mapping of quantitative trait loci for temporal growth and age at maturity in Coho Salmon: evidence for genotype-by-sex interactions. Marine Genomics 38:33–44.

Lindeman, K., W. Anderson, K. E. Carpenter, R. Claro, J. Cowan, B. Padovani-Ferreira, L. A. Rocha, G. Sedberry, and M. Zapp-Sluis. 2016. Lutjanus griseus. The IUCN Red List of Threatened Species 2016: E.T192941a2180367. Available: http://www.iucnredlist.org/details/192941/0. (July 2019).

Maharaj, R. R., V. W. Y. Lam, D. Pauly, and W. W. L. Cheung. 2018. Regional variability in the sensitivity of Caribbean reef fish assemblages to ocean warming. Marine Ecology Progress Series 590:201–209.

Manickchand-Heileman, S. C., and D. A. T. Phillip. 2000. Age and growth of the Yellowedge Grouper, Epinephelus flavolimbatus, and the Yellowmouth Grouper, Mycteroperca interstitialis, off Trinidad and Tobago. U.S. National Marine Fisheries Service Fishery Bulletin 98:290–298.

Manooch, C. S. III, and R. H. Matheson. 1981. Age, growth and mortality of Gray Snapper collected from Florida waters. Proceedings of the Annual Conference Southeastern Association of Fish and Wildlife Agencies 35:331–344.

Morley, J. W., R. L. Selden, R. J. Latour, T. L. Frölicher, R. J. Seagraves, and M. L. Pinsky. 2018. Projecting shifts in thermal habitat for 686 species on the North American continental shelf. PLoS (Public Library of Science) ONE [online serial] 13(5):e0196127.

Muller-Karger, F. E., J. P. Smith, S. Werner, R. Chen, M. Roffer, Y Liu, B. Muhling, D. Lindo-Atichati, J. Lamkin, S. Cerdeira-Estrada, and D. B. Enfield. 2015. Natural variability of surface oceanographic conditions in the offshore Gulf of Mexico. Progress in Oceanography 134:54–76.

Munro, J. L. 1999. Marine protected areas and the management of coral reef fisheries. International Center of Living Aquatic Resources Management, Caribbean and Eastern Pacific Office, Technical Report, Tortola, British Virgin Islands.

Neuheimer, A. B., and B. R. MacKenzie. 2014. Explaining life history variation in a changing climate across a species' range. Ecology 95:3364–3375.

Neuheimer, A. B., R. E. Thresher, J. M. Lyle, and J. M. Semmens. 2011. Tolerance limit for fish growth exceeded by warming waters. Nature Climate Change 1:110.

Pauly, D., and W. W. L. Cheung. 2018. Sound physiological knowledge and principles in modeling shrinking of fishes under climate change. Global Change Biology 24:e15–e26.

Pinheiro, J. C., D. M. Bates, S. D. DebRoy, and D. Sarkar. 2012. The nlme package: linear and nonlinear mixed effects models. R package version 3. Available: https://CRAN.R-project.org/package=nlme. (July 2019).

Plummer, M. 2016. Bayesian graphical models using MCMC. R package version 4-6. Available: https://cran.r-project.org/web/packages/rjags/rjags.pdf. (July 2019).

R Development Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. Available: https://www.r-project.org/. (July 2019).

Rehm, E. M., P. Olivas, J. Stroud, and K. J. Feeley. 2015. Losing your edge: climate change and the conservation value of range-edge populations. Ecology and Evolution 5:4315–4326.

Rhodes, K. L., B. M. Taylor, and J. L. McIlwain. 2011. Detailed demographic analysis of an Epinephelus polyphekadion spawning aggregation and fishery. Marine Ecology Progress Series 421:183–198.

Ricker, W. E. 1975. Computation and interpretation of biological statistics of fish populations. Fisheries Research Board of Canada Bulletin 191.

Rummer, J. L., C. S. Couturier, J. A. W. Stecyk, N. M. Gardiner, J. P. Kinch, G. E. Nilsson, and P. L. Munday. 2014. Life on the edge: thermal optima for aerobic scope of equatorial reef fishes are close to current day temperatures. Global Change Biology 20:1055–1066.

Schemske, D., G. Mittelbach, H. Cornell, J. M. Sobel, and K. Roy. 2009. Is there a latitudinal gradient in the importance of biotic interactions? Annual Review of Ecology, Evolution, and Systematics 40:245–269.

Sunday, J. M., A. E. Bates, and N. K. Dulvy. 2012. Thermal tolerance and the global redistribution of animals. Nature Climate Change 2:686–690.

Taylor, J. 1997. Introduction to error analysis, the study of uncertainties in physical measurements. University Science Books, New York.

Taylor, R. G., J. A. Whittington, H. J. Grier, and R. E. Crabtree. 2000. Age, growth, maturation, and protandric sex reversal in Common Snook, Centropomus undecimalis, from the east and west coasts of south Florida. U.S. National Marine Fisheries Service Fishery Bulletin 98:612–624.

Thattai, D., B. Kjerfve, and W. D. Heyman. 2003. Hydrometeorology and variability of water discharge and sediment load in the inner Gulf of Honduras, western Caribbean. Journal of Hydrometeorology 4:985–995.

Then, A. Y., J. M. Hoenig, N. G. Hall, and D. A. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES Journal of Marine Science 72:82–92.

Tolan, J. M., and M. Fisher. 2009. Biological response to changes in climate patterns: population increases of Gray Snapper (Lutjanus griseus) in Texas bays and estuaries. U.S. National Marine Fisheries Service Fishery Bulletin 107:36–44.

Torres-Lara, R., S. Salas-Márquez, G. Mexicano-Cíntora, and M. A. Cabrera-Vázquez. 1991. Sinopsis de la dinámica poblacional de cinco especies de la familia Lutjanidae en la costa de Yucatán. Anales del Instituto de Ciencias del Mar y Limnología 18:189–198.

Venables, W. N., and C. M. Dichmont. 2004. GLMs, GAMs and GLMMs: an overview of theory for applications in fisheries research. Fisheries Research 70:319–337.

Venables, W. N., and B. D. Ripley. 2002. Modern applied statistics with S. Springer, New York.

Wuenschel, M. J., J. A. Hare, M. E. Kimball, and K. W. Able. 2012. Evaluating juvenile thermal tolerance as a constraint on adult range of Gray Snapper (*Lutjanus griseus*): a combined laboratory, field and modeling approach. Journal of Experimental Marine Biology and Ecology 436–437:19–27.

Wuenschel, M. J., A. R. Jugovich, and J. A. Hare. 2004. Effect of temperature and salinity on the energetics of juvenile Gray Snapper (*Lutjanus griseus*): implications for nursery habitat value. Journal of Experimental Marine Biology and Ecology 312:333–347.

Wuenschel, M. J., A. R. Jugovich, and J. A. Hare. 2005. Metabolic response of juvenile Gray Snapper (*Lutjanus griseus*) to temperature and salinity: physiological cost of different environments. Journal of Experimental Marine Biology and Ecology 321:145–154.

Yañez-Arancibia, A., D. Z. Lomeli, M. G. Cruz, R. G. Orantes, and V. S. Fandino. 1999. The ecosystem framework for planning and management the Atlantic coast of Guatemala. Ocean Coastal Management 42:283–317.

Zeileis, A., and T. Hothorn. 2002. Diagnostic checking in regression relationships. R News 2(3):7–10