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ARTICLE

Age, growth, maturity, and mortality of an understudied Gray Snapper fishery from the north-central Gulf of Mexico

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Abstract

Objective: Gray Snapper *Lutjanus griseus* constitute a significant recreational fishery and minor commercial fishery throughout the Gulf of Mexico. The overall stock appears healthy based on the results of the most recent assessment; in fact, shifting climate conditions have led to range expansions and subsequent population growth in the north-central Gulf of Mexico, a region for which the full suite of basic biological data is currently lacking for this species. This work presents the results of a comprehensive study on the age, growth, maturity, and mortality of Gray Snapper in Alabama and Mississippi waters.

Methods: From 2011 to 2021, otoliths ($n=886$) and gonads ($n=364$) were sampled and processed according to standard microscopic techniques. Age data were used to fit three separate growth functions and derive estimates of total, natural, and fishing mortality, while testes and ovaries were categorized by reproductive phase to determine maturity at length and age.

Result: Ages ranged from 0 to 27 years, representing one of the most comprehensive collections across published studies to date. Sex-specific growth curves constructed using the von Bertalanffy growth function were preferred over the Gompertz and logistic models based on Akaike information criterion and suggest that males reach a higher mean asymptotic length $\left(L_t = 731.52\left[1 - e^{-0.15\{t+1.34\}}\right]\right)$ than females $\left(L_t = 704.28\left[1 - e^{-0.14\{t+1.62\}}\right]\right)$. Based on histological analyses, we estimate total length at 50% maturity to be 181 mm for males and 273 mm for females and total length at 90% maturity to be 215 mm for males and 354 mm for females. We estimate the age at 50% maturity to be <1.0 year for males and 2.0 years for females and the age at 90% maturity to be 1.4 years for males and 3.6 years for females. Mortality rates calculated using preferred estimators ($Z=0.30$–0.38; $M=0.26$; $F=0.04$–0.12) indicate relatively low levels of exploitation in the north-central Gulf of Mexico, with full recruitment to the fishery occurring at age 4.

Conclusion: Based on these results, the Gray Snapper population in the north-central Gulf of Mexico is characterized by a relatively unexploited age structure with moderate longevity that has been subject to minimal fishing pressure. The findings from this study introduce new regional data for incorporation into assessments and provide an informed basis for future management decisions in this fishery.

KEYWORDS
age and growth, fisheries, management, reproduction, Gray Snapper

INTRODUCTION

Gray Snapper *Lutjanus griseus* is a lutjanid whose range extends from the southeastern United States and Gulf of Mexico to South America (Burton 2001; Fischer et al. 2005). Larvae disperse through a planktonic phase in which they can drift into temperate waters of the northeastern United States via the Gulf Stream, an area well outside their effective adult range (Sumner et al. 1911; Denit and Sponaugle 2004; Schwartz 2007). This planktonic phase typically lasts from 20 to 33 days (Allman and Grimes 2002; Denit and Sponaugle 2004), after which recent settlers occupy sea grass beds and mangroves in coastal estuaries (Chester and Thayer 1990; Faunce and Serafy 2007). Juveniles recruit to hard structures in deeper water as they grow, eventually migrating to offshore reefs as adults, where they aggregate to spawn during the summer months (Starck and Schroeder 1971; Domeier et al. 1996). In areas with a preponderance of natural hard bottom, such as the west coast of Florida, Gray Snapper seek patch reefs and complex rocky substrate (Starck and Schroeder 1971; Smith 1976). Elsewhere in the Gulf of Mexico, they reside on artificial reef structures (Dance et al. 2011; Ajemian et al. 2015; Streich et al. 2017).

Recent studies suggest that Gray Snapper are expanding geographically due to warming of coastal waters in response to climate change. In the Gulf of Mexico, this species is most abundant off Florida (Morley et al. 2018), but comparative inshore surveys across several decades in the north-central Gulf of Mexico have revealed a marked proliferation in juvenile abundance correlated to regional increases in air and sea surface temperature of as much as 3°C (Fodrie et al. 2010) that could be connected to the magnitude of adult recruitment to artificial reefs off Alabama (Fodrie et al. 2020). Increased juvenile winter survivorship is thought to play a key role in allowing populations to establish and propagate in areas where they have previously been limited (Tolan and Fisher 2009) by protracted water temperatures below approximately 17°C, according to both experimental and empirical observations (Wuenschel et al. 2004, 2012). Furthermore, Gray Snapper are expected to continue to increase in abundance in the northern and western portions of their range expansion under current warming scenarios (Morley et al. 2018).

Impact Statement

Investigations into the life history of Gray Snapper in the Mississippi Bight (Alabama and Mississippi coastal waters) fill important regional gaps in various biological parameters, supplementing estimates from recent Gulf of Mexico stock assessments. The environment in this region is likely changing and becoming more suitable for Gray Snapper.

Regulation of Gray Snapper was initiated in 1990 under Amendment 1 to the Reef Fish Fishery Management Plan, which allowed harvest with a 10-fish bag limit (all snapper species in aggregate) and a 305-mm (12-inch) minimum total length (Gulf of Mexico Fishery Management Council [GMFMC] 1989) that has been maintained to the present day (GMFMC 2019b). Since 2001, gulfwide catch estimates of Gray Snapper have typically fluctuated between 680,000 and 1,040,000 kg (1,500,000 and 2,300,000 lb), primarily from the recreational sector. Although Florida is responsible for much of this catch, states in the northern Gulf of Mexico have developed small yet growing, recreational fisheries (GMFMC 2019b). Recent inquiries into the status of the Gulf of Mexico Gray Snapper fishery have led to updates in both regulations and previously undefined reference points. The first stock assessment for this species in the Gulf of Mexico, conducted by the SouthEast Data, Assessment, and Review (SEDAR) in 2018, determined that the stock was not overfished despite overfishing since the mid-1970s (SEDAR 2018), and Amendment 51 was proposed, approved, and implemented in 2020, which preserved existing bag and size limits while reducing the annual catch limit and setting new reference point benchmarks (GMFMC 2019b). A follow-up operational assessment conducted in 2022 declared that the stock is neither overfished nor undergoing underfishing (SEDAR 2022).

Gray Snapper have seen a dramatic increase in popularity among recreational anglers, with directed fishing trips increasing by 30% over the past two decades in the Gulf of Mexico. This increase is particularly notable in the Mississippi Bight (Mississippi and Alabama coastal waters), where trips have doubled during the same span of time (National Marine Fisheries Service Marine Recreational Information Program, data query) in an environment that has become more suitable for this species with the effects of global warming. Historically, recreational harvest in the northern Gulf of Mexico has been low (SEDAR 2018), suggesting that these latest projections could have implications for development of a more viable fishery in the area. Because the majority of life history information on Gray Snapper is derived from Florida and Louisiana, adding biological information throughout its exploitable range is important for future management decisions.

Gray Snapper growth dynamics have been examined across their geographic distribution. In the Gulf of Mexico, the longest-lived individuals were 28 years old from Louisiana (Fischer et al. 2005) and 26 years old from Florida (Allman and Goetz 2009). Additionally, a single specimen aged from collections throughout the northern Gulf of Mexico was estimated to be 32 years old (Thornton et al. 2017). Estimates of theoretical maximum length (L_∞) range from 506 to 673 mm total length for pooled-sex models (Johnson et al. 1994; Burton 2001; Allman and Goetz 2009). However, there has been disagreement regarding the significance of dimorphic growth among studies of both length–age and weight–length relationships (Burton 2001; Fischer et al. 2005; Allman and Goetz 2009; Andrade and Santos 2019). At the southernmost extent of their range, Andrade and Santos (2019) report markedly abbreviated growth, with longevity estimated at just 10 years and an L_∞ of 350 mm despite minimal fishing mortality. In all studies, parameters were reported solely for the von Bertalanffy growth function, leaving the possibility that other models may provide better fits to the length–age relationship (Katsanevakis and Maravelias 2008). It is presumed that these variations in population structure are geographically influenced by a combination of climate (Andrade and Santos 2019) and fishing pressure (Burton 2001; Fischer et al. 2005; Allman and Goetz 2009), suggesting that other regional populations could be locally sensitive to these conditions as well.

There remains a critical need for contemporary information on Gray Snapper reproduction that reflects regional population demographics, especially given that there is genetic evidence of disparate stocks throughout the Gulf of Mexico (Gold et al. 2009). Of particular importance are updated estimates of spawning interval, spawning frequency, fecundity, and length and age at maturity (SEDAR 2018). Of the histological samples used to generate data for the 2018 and 2022 assessments, most samples were collected from either the west coast of Florida or Louisiana (Fitzhugh et al. 2017; Garner et al. 2022). Female mean estimates of maturity from these samples have been reported as 2.3 years and 253 mm fork length by Fitzhugh et al. (2017) and 2.5 years and 270 mm fork length by Garner et al. (2022). The most recent estimate of male sexual maturity using histology occurred in 1996 (Domeier et al. 1996). Other studies, including more recent ones, have relied on macroscopic evaluation of gonads (Starck and Schroeder 1971; Andrade and Santos 2019), which is more subjective and increases the likelihood of misclassifying developmental stages (Vitale et al. 2006; Midway and Scharf 2012).

The conclusions drawn from the recent assessments are based on data collected from extensive investigations throughout the Gulf of Mexico. However, no specific studies to date have been performed on the north-central population residing primarily in Alabama and Mississippi coastal waters, a latitudinal terminus where a distinct temperature regime and differences in fishing pressure may influence growth and reproductive patterns. Prospectively, deciphering the size-selective effects of a developing fishery in tandem with possible climate-driven shifts in life history traits may be a potential forthcoming issue in monitoring, especially as warming trends are known to favor Gray Snapper growth in this area (Black et al. 2011). Thus, despite a currently diminutive fishery, the expected growth of this northernmost segment calls for heightened consideration of its importance to future assessments, especially given recent movement towards regional management of federal fisheries (GMFMC 2019a). As such, the initial management of this stock will require a comprehensive survey of various life history parameters to facilitate an understanding of local population characteristics and life history adaptations. The present study examines multiple growth models and sex-specific growth, provides estimates of mortality, and introduces histology-based length and age at maturity for this species in the north-central Gulf of Mexico.

METHODS

Specimen collection and processing

Gray Snapper samples were collected from a variety of sources between 2011 and 2021. Adult specimens for this study were primarily sampled at offshore hook-and-line and spearfishing tournaments that occur along the coast of Alabama and Mississippi. Fish were also periodically provided by recreational for-hire charter vessels and local fishermen. Juvenile specimens were captured through hook-and-line efforts and fishery-independent inshore surveys in Mobile Bay and Orange Beach, Alabama, while young of the year representing the age-0 class were obtained from benthic sled sampling of sea grass beds in the Chandeleur Islands through the Gulf Coast Research Laboratory in 2018.

Meristics and biological samples were collected from all fish. Standard length, fork length, and stretched total length were recorded in millimeters. Body weight was measured with a spring scale in increments of 0.05 kg for larger fish, while smaller fish were measured to the nearest gram. Sagittal otoliths were extracted from the otic capsule through the operculum, and gonads were examined to determine sex. Intraperitoneal fat, if present, was trimmed from the gonads, and both intraperitoneal fat and gonads were weighed to the nearest 0.001 g. When possible, processing occurred within 24 h of capture. For tournament sampling, all gonads were bagged, stored on ice, and processed at the laboratory on the same day.

Histological sampling occurred from April to November of 2019 and May to October of 2020. Approximately 1 cm^3 of tissue was cut from the middle of the right gonad and submerged in a cassette in 10% histological grade formalin (Bennetts et al. 2019). Smaller gonads were fixed whole in biopsy bags to ensure that sufficient tissue was available for processing. For maturity analyses, sublegal fish in 20-mm size bins from 140 to 304 mm total length, centered around previous size at 50% maturity estimates (Fitzhugh et al. 2017), were targeted inshore under a state-issued permit. Sampling occurred solely during presumed peak spawning months of June, July, and August to verify that individuals were capable of attaining maturity at a given length (Woods et al. 2003).

Aging

Otoliths were prepared following VanderKooy et al. (2020) and aged independently by two readers following completion of the Gray Snapper reference set from the Gulf States Marine Fisheries Commission. Using a Hillquist Thin Section Machine, the left otolith was ground along the transverse plane to the core, mounted on a slide, and then ground again down to 0.5-mm thickness. The right otolith was substituted if needed, and small otoliths were left intact to be aged whole. Prepared slides were placed under a microscope and aged by counting opaque rings (i.e., annuli) along the sulcus from the core towards the dorsal margin. Whole otoliths were placed in a shallow dish with water and tilted by the concave face to view opaque rings. Gray Snapper have previously been age-validated via marginal increment analysis (Burton 2001) and bomb radiocarbon analysis (Fischer et al. 2005) and determined to deposit one annulus per year. A margin code of 1 was designated for an opaque margin, and margin codes of 2, 3, and 4 were used to denote translucent zone growth measured past the last annuli by increments of one-third. Otoliths with margin codes of 3 or 4 and catch dates between January 1 and June 30 were promoted to the next age-group to sort fish by cohorts (VanderKooy et al. 2020). Upon completion of aging, the precision of each reader's age estimates were measured by the average percent error (Beamish and Fournier 1981). Individual discrepancies were then reviewed to reach a consensus final age or margin code.

Growth modeling

Age and length measurements were used to derive growth functions. Fractional ages were used to obtain more accurate estimates of individual ages by adding the time difference between the catch date and an assumed birth date of August 1, specifying any additional growth in decimal form (VanderKooy et al. 2020; Jefferson et al. 2021). Although VanderKooy et al. (2020) proposes July 1 as the accepted birth date for Gulf of Mexico Gray Snapper, analyses of female condition indices and monthly reproductive phase distribution indicate that August 1 is a more appropriate approximation of peak spawning in this area (Kim 2022). Growth parameters were then estimated by fitting models of total length against fractional age using the Gompertz, logistic, and von Bertalanffy (VBGF) growth functions (Gompertz 1825; von Bertalanffy 1938; Ricker 1975). Model fitting was carried out using the FSA package version 0.8.31 (Ogle et al. 2020) in R version 4.0.3 (R Core Team 2020). These growth functions are given as follows:

$$L_t = L_\infty \left[e^{-e^{-g_i (t - t_i)}} \right]$$

for the Gompertz growth model, where L_∞ is the mean hypothetical asymptotic length and g_i and t_i are the growth rate and age at the inflection point, respectively;

$$L_t = \frac{L_\infty}{1 + e^{-g_{-\infty} (t - t_i)}}$$

for the logistic growth model, where $g_{-\infty}$ is the growth rate at negative infinity; and

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

for the VBGF, where k is the Brody growth coefficient and t_0 is the theoretical age when length is equal to 0.

Model selection was based on Akaike information criterion (AIC) (Akaike 1973; Katsanevakis and Maravelias 2008). The best fitting model was then selected for further sex-specific analysis. Individuals of unknown sex were included for the multimodel comparisons but omitted from the subsequent sex-specific models. Separate growth curves were then fit to male and female data, and confidence intervals (CIs) for growth parameters were obtained through bootstrapping. To determine whether models with sex-specific parameters provided better fits than a model with shared parameters, a series of likelihood ratio tests (Kimura 1980; Cerrato 1990; Ogle 2013b) were used to compare a full model (all three parameters allowed to vary by sex) to a set of nested models with different parameters held constant and others allowed to vary by sex.

The weight–length relationship for Gray Snapper was defined by the power function given by the following equation:

$$W = aL^b,$$

where W is the weight in kilograms, L is the total length in millimeters, a is a constant, and b is an exponent indicating the scaling of isometric versus allometric growth (Le Cren 1951; Froese 2006). A linear model was used to regress the natural logarithm of weight against the natural logarithm of total length to obtain estimates of a as e raised to the power of the intercept value and b as the slope (Brodziak 2012; Ogle 2013a). Parameters with confidence intervals were calculated for both pooled and sex-specific models, and an additional interaction term between length and sex was specified to detect any difference between sexes.

Marginal increment analysis

Marginal increment analysis was performed to identify the time of year when opaque zones are formed on the edge of the otolith. The number of otoliths with opaque margins was divided by the total number of otoliths by month, yielding the proportion of opaque margins across time. A peak in this value indicates the timing of annulus formation and the corresponding translucent zone development throughout the rest of the year.

Histological processing and maturity analysis

Following preservation in 10% neutral buffered formalin, histological sample cassettes were dehydrated in ethanol (Bennetts et al. 2019) and sent to the Texas A&M College of Veterinary Medicine and Biomedical Sciences Histology Laboratory for slide preparation. Two to three cross sections per sample were cut to 4 μm thickness, mounted on a slide, and stained with Harris hematoxylin and eosin. Slides were returned to the University of South Alabama, viewed under a Leica DM2000 microscope by two trained readers, and classified by the most advanced reproductive phase present in the tissue according to standardized terminology (Brown-Peterson et al. 2011). In males, these phases are categorized as immature, early developing, developing, spawning capable, regressing, and regenerating. The spawning capable phase was separated into three subphases when possible: early germinal epithelium, mid germinal epithelium, and late germinal epithelium, which are progressive indicators of the spawning season. Females were categorized into the same main phases, plus an actively spawning subphase. Sexual maturity was defined as the presence of primary spermatocytes in males and cortical alveoli in females (Brown-Peterson et al. 2011; Lowerre-Barbieri et al. 2011), and hydrated oocytes and ≤24-h-postovulatory follicles in ovarian tissue were noted as spawning markers (Fitzhugh et al. 2017). Estimates of length at 50% maturity (L_{50}) and 90% maturity (L_{90}) were generated using a binary logistic regression, with fish coded as either immature or mature and bootstrapped confidence intervals (Fitzhugh et al. 2017). Estimates of age at 50% maturity (A_{50}) and 90% maturity (A_{90}) were generated in similar fashion. All maturity analyses were conducted in R version 4.0.3 (R Core Team 2020) with the package FSA version 0.8.31 (Ogle et al. 2020).

Mortality estimation

Methods for mortality estimation were based on a fishery-dependent catch curve constructed by plotting the natural logarithm of catch (i.e., the number of individuals caught) pooled across years against age-class (Burton 2001). Because one of the assumptions inherent in catch curve analysis is an unbiased sample with respect to the distribution of age-classes (Robson and Chapman 1961; Nelson 2019a), any fish from sampling efforts that may not be representative of the population, such as sublegal fish targeted in length bins for histological examination, were removed from the data set prior to analysis. The remaining data were composed exclusively of hook-and-line and spearfishing gears. Due to selectivity concerns associated with tournament sampling, nontournament samples were isolated as a separate data set alongside the complete data set. Mortality was also estimated from Gray Snapper length measurements collected during fishery-independent remotely operated vehicle (ROV) surveys of reefs in the Alabama artificial reef zone and adjacent waters from 2011 to 2019 (see Powers et al. 2018 for a full description of survey).

The instantaneous total mortality rate (Z) was estimated through the slope of the fishery-dependent catch curves using both unweighted and weighted linear regressions (Maceina and Bettoli 1998). The initial age-group specifying full recruitment occurs at the peak abundance, or the apex of the catch curve (Smith et al. 2012). While Smith et al. (2012) recommends against the use of unweighted linear regression due to better alternatives that reduce underestimation of Z, this method was included here for comparison to previous studies (Burton 2001; Fischer et al. 2005; Allman and Goetz 2009; Andrade and Santos 2019). The instantaneous total mortality rate was also estimated separately using the Chapman–Robson estimator (Chapman and Robson 1960), with modifications to account for overestimation of Z (Hoenig et al. 1983) and variance inflation (Smith et al. 2012). For the ROV data, the equilibrium Beverton–Holt length-based mortality estimator (Beverton and Holt 1956) was used to calculate Z from samples following the peak abundance of the length frequency distribution. The annual mortality rate (A) corresponding to Z for all methods was estimated using the following formula:

$$A = 1 - e^{-Z}$$

Several methods were used to estimate the instantaneous natural mortality rate M based on life history and environmental parameters. The Hoenig longevity–mortality relationship (Hoenig 1983) and Hoenig nonlinear least squares (Hoenig$_{\text{nls}}$) estimator (Then et al. 2015) both require a maximum age $t_{\max}$ obtained from the oldest fish aged in the datasets, whereas the Pauly method (Pauly 1980) requires the growth parameters L_∞ and k as well as the mean annual water temperature, which was computed from sea surface data recorded by National Data Buoy Center Station 42012 south of Orange Beach, Alabama. Estimates of fishing mortality (F) were derived from the calculated values of Z and M using the formula $Z=F+M$. Mortality estimates for all methods were calculated in R version 4.0.3 (R Core Team 2020) with the packages FSA version 0.8.31 (Ogle et al. 2020) and fishmethods version 1.11-1 (Nelson 2019b).

RESULTS

Sample distributions

A total of 886 Gray Snapper (Figure 1) were collected from ports ranging from Orange Beach, Alabama, to Gulfport, Mississippi, between 2011 and 2021, with the majority of sampling beginning in 2018 and occurring during the summer months, when fishing efforts tend to be highest. Sampling was extended to the spring and fall months (March through November) and opportunistically in January to better capture trends in annulus formation. Fishery-dependent samples, comprised solely of recreational hook-and-line and spearfishing gears, represented 61.6% of all fish sampled, whereas scientific and collection surveys that additionally used benthic sleds, traps, trawls, and vertical longlines accounted for the remaining 38.4%. Benthic sleds were successful in sampling 98 fish in the smallest size-class (<100 mm total length) present in the data set that rarely recruited to the other gear types. Most fishery-dependent samples are known or presumed to have been caught in the Alabama artificial reef zone or waters directly offshore of Alabama, with a small subset originating in Mississippi waters.

Otoliths and length data were collected from 353 females, 362 males, and 171 individuals of unknown sex. Body weight was measured for all but 35 fish. The data provided no evidence that the population sex ratio differs from 1:1 ($X^2=0.113$, df $=1$, $p=0.736$) according to a Pearson's chi-square test. Gonads and intraperitoneal fat were obtained from 600 and 521 fish, respectively; intraperitoneal fat was weighed only when gonads were weighed.

Sizes ranged from 29 to 774 mm total length and were greatest in frequency in the 351–400-mm size-class for both males and females. Difficulty in sexing smaller fish without the use of histological techniques was apparent given the prevalence of indeterminate samples under 300 mm. A significant difference in sex-specific length frequency distributions was detected with a Kolmogorov–Smirnov test ($D=0.13$, $p=0.004$), with greater numbers of males in the largest size-classes (Figure 1).

Aging

Gray Snapper otoliths produced distinct annuli beginning with an initial ring proximal to the core and subsequent annuli forming closer together towards the dorsal margin, which facilitated precision in annuli counts. Readers agreed on 94.1% of ages and differed by 1 year on 5.7% of ages and 2 years on 0.2% of ages, resulting in an average percent error of 0.6%. One set of otoliths was removed due to structural deformities that prevented an age consensus from being reached. Final assigned ages ranged from 1 to 27 years for females, 1 to 25 years for males, and 0 to 3 years for individuals of unknown sex. No evidence of a difference in sex-specific age frequency distributions was detected with a Kolmogorov–Smirnov test ($D=0.07$, $p=0.273$).

Growth modeling

Among the three models fit to the pooled data, the VBGF ranked first based on its AIC score and was followed by the Gompertz model (ΔAIC $=208.10$) and the logistic

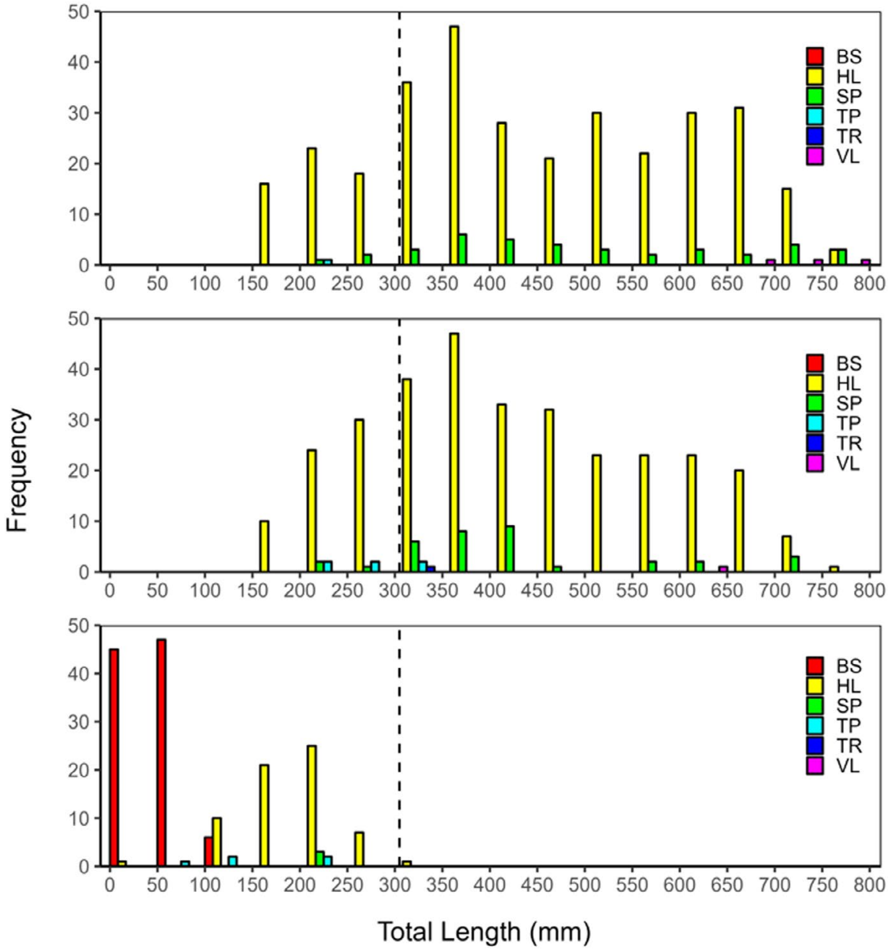

FIGURE 1 Length frequency distributions in 50-mm size-classes for all sampled male (top panel), female (middle panel), and unknown-sex (bottom panel) north-central Gulf of Mexico Gray Snapper ($n = 886$) by gear type (BS = benthic sled, HL = hook and line, SP = spearfishing, TP = trap, TR = trawl, VL = vertical longline). Dashed lines indicate the 305-mm (12-inch) total length size limit in both state (Alabama–Mississippi) and federal waters.

TABLE 1 Multimodel length–age growth comparisons of north-central Gulf of Mexico Gray Snapper ranked by Akaike information criterion (AIC). CI = confidence interval.

Model	Parameter	Estimate	95% CI	ΔAIC
von Bertalanffy	L_∞	687.43	676.45–698.84	0.00
	k	0.18	0.17–0.19	
	t_0	−0.66	−0.75 to −0.58	
Gompertz	L_∞	655.14	645.76–664.53	208.10
	g_i	0.30	0.29–0.31	
	t_i	1.84	1.75–1.92	
Logistic	L_∞	640.46	631.69–649.49	362.79
	$g_{-\infty}$	0.42	0.40–0.44	
	t_i	3.09	2.98–3.20	

model (ΔAIC = 362.79) (Table 1). The VBGF was consequently selected as the best model and was used for sex-specific modeling. The pooled VBGF equation is given by

$$L_t = 687.43\left[1 - e^{-0.18(t+0.66)}\right]$$

Compared to the other candidate models, the VBGF exhibited a pattern of more rapid early growth and a more gradual decline in growth rate with age (Figure 2), resulting in a significantly higher estimate of L_∞ as evidenced by nonoverlapping 95% confidence intervals (Table 1).

The VBGF was subsequently fit to male and female data, allowing all three parameters to differ between the sexes (Figure 3; Table 2):

$$\text{Male}: L_t = 731.52\left[1 - e^{-0.15(t+1.34)}\right]$$

$$\text{Female}: L_t = 704.28\left[1 - e^{-0.14(t+1.62)}\right]$$

In order to determine whether growth differed between males and females in the population, this full model was compared, using likelihood ratio tests, to a set of nested models with some parameters allowed to vary between the sexes and others held constant (Table 3). The most parsimonious of these candidate models allowed L_∞ to vary but held both k and t_0 constant. While the data set did not provide evidence that k and t_0 differ between the sexes, it did provide evidence that males achieve a larger L_∞ than females in this population.

Age-0 Gray Snapper were not sampled for histology and were therefore unavailable to anchor the sex-specific growth curves. To compensate for this, an abundance of Gray Snapper spanning the youngest age-classes down to age 1 were sampled to ensure that the curves represented the earliest segment of growth as accurately as possible (Figure 3).

The weight–length relationships between males and females were not significantly different based on the interaction term of length and sex ($p = 0.430$). Thus, the data were aggregated for the pooled model given by

$$W = 2.13 \times 10^{-8} \times L^{2.93}$$

This additionally allowed the model to incorporate a greater number of small individuals of unknown sex that would otherwise have been censored from the sex-specific relationships.

Marginal increment analysis

Marginal increment analysis revealed annulus formation beginning in April, peaking in May, and ending abruptly before the start of June (Figure 4). Samples were taken contiguously between the months of March and November. No otoliths were available in February or December. However, opaque margins were not present in the otoliths of six fish caught in January, suggesting a single maximum in May.

Histological processing and maturity analysis

Gonadal histology samples were taken from 182 females, 176 males, and 6 individuals that were later microscopically examined as undifferentiated. Histological data were censored from the same fish that was removed from growth modeling due to otolith quality. Readers agreed on sex for 98.9% of all samples. The four disagreements occurred over juvenile fish that had just begun to differentiate and were therefore difficult to sex. Readers agreed on reproductive phase for 94.9% of male samples and 95.1% of female samples. Immature males ($n = 8$) ranged from 1

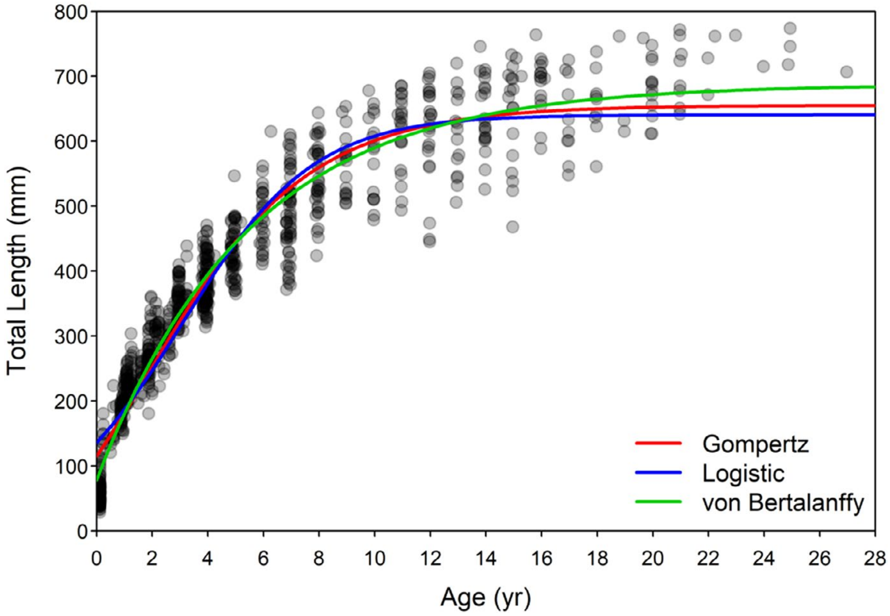

FIGURE 2 Multimodel length–age growth comparisons of north-central Gulf of Mexico Gray Snapper using Gompertz, logistic, and von Bertalanffy growth functions. Areas of darker shading indicate overlapping points.

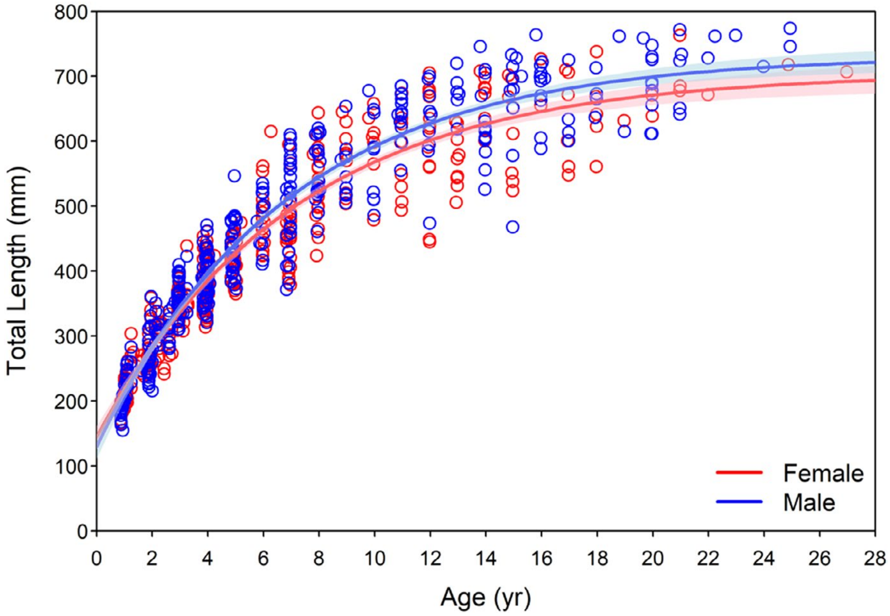

FIGURE 3 Sex-specific von Bertalanffy growth models of north-central Gulf of Mexico Gray Snapper; shaded regions surrounding the curves represent 95% confidence intervals.

TABLE 2 Sex-specific von Bertalanffy growth model parameter estimates of north-central Gulf of Mexico Gray Snapper. CI = confidence interval.

Sex	Parameter	Estimate	95% CI	*p*-value
Male	L_∞	731.52	712.01–753.68	$<2\times10^{-16}$
	k	0.15	0.13–0.16	$<2\times10^{-16}$
	t_0	−1.34	−1.65 to −1.06	$<2\times10^{-16}$
Female	L_∞	704.28	679.81–732.96	$<2\times10^{-16}$
	k	0.14	0.12–0.16	$<2\times10^{-16}$
	t_0	−1.62	−2.00 to −1.29	$<2\times10^{-16}$

TABLE 3 Nested likelihood ratio tests to determine significance of L_∞, k, and t_0 between sexes of north-central Gulf of Mexico Gray Snapper. (Residual df = residual degrees of freedom, RSS = residual sum of squares).

Model parameters	Subset parameters	Residual df	RSS	*p*-value
All	L_∞, k	709	1,485,775	0.236
	L_∞, t_0	709	1,483,200	0.675
	k, t_0	709	1,487,730	0.126
L_∞, t_0	L_∞	710	1,489,947	0.073
	t_0	710	1,526,567	6.13×10^{-6}
L_∞	None	711	1,534,690	4.54×10^{-6}

to 2 years in age and 155 to 216 mm total length, whereas mature males ($n=168$) ranged from 1 to 25 years in age and 164 to 774 mm total length. Immature females ($n=42$) ranged from 1 to 7 years in age and 166 to 457 mm total length, whereas mature females ($n=140$) ranged from 1 to 25 years in age and 240 to 763 mm total length. No postovulatory follicles were observed within females in the actively spawning subphase, indicating that Gray Snapper do not spawn daily.

Sexual differentiation that is microscopically observable likely takes place at some point between late in the first year and early in the second year of growth. Six age-1 individuals (156–193 mm total length) were undifferentiated, while others had just begun to develop signs of spermatogonia

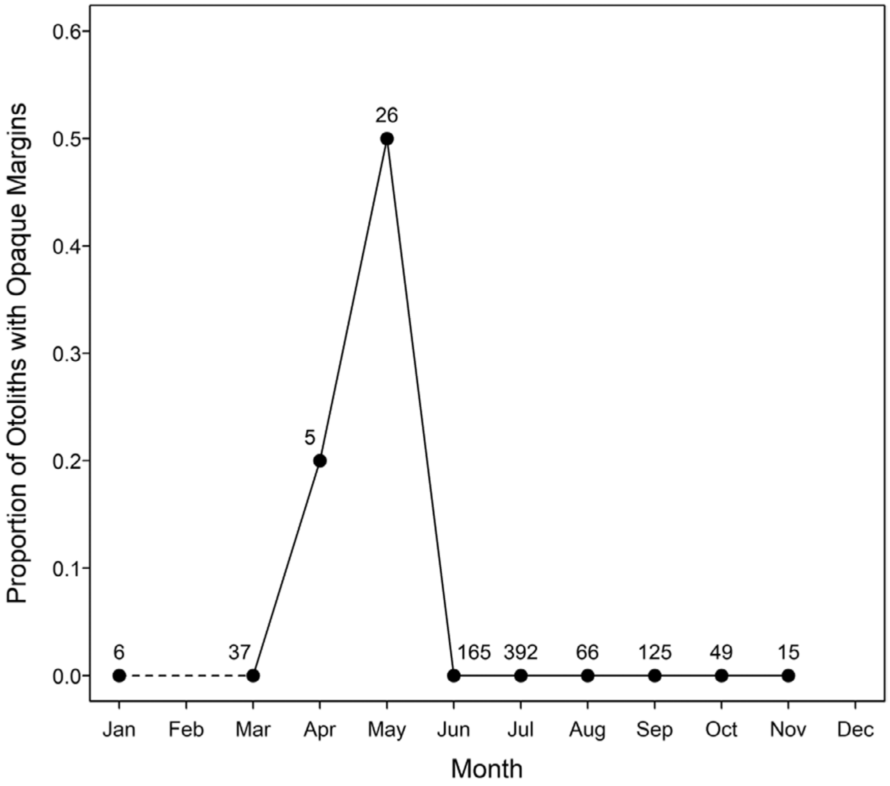

FIGURE 4 Marginal increment analysis of otoliths from north-central Gulf of Mexico Gray Snapper. Sample sizes are included at each point; no otoliths were available in February or December.

or oogonia among undifferentiated cells. Estimates of maturity illustrate earlier maturation in males than females (Figure 5; Table 4). Male L_{50} and L_{90} were determined to be 181 mm (95% CI = 155–196) and 215 mm (193–229), respectively, whereas female L_{50} and L_{90} were 273 mm (255–292) and 354 mm (312–390). Male A_{50} and A_{90} were determined to be <1.0 and 1.4 years (95% CI = 1.0–1.9), respectively, whereas female A_{50} and A_{90} were 2.0 years (1.7–2.4) and 3.6 years (2.5–4.6). Because no Gray Snapper younger than 1 year old were sampled for histology, the male A_{50} estimate was not extrapolated below this age limit. Furthermore, the male age estimates could not be modeled precisely because spermatozoa were present in the majority of age-1 individuals, and only eight males in total were classified as immature. Comparisons of the maturity estimates against length and age frequency distributions by catch location display nearly complete male maturation inshore compared with females, which continue to mature throughout the transition to offshore habitat (Figure 6).

Mortality estimation

The complete fishery-dependent data set for mortality estimation consisted of 546 Gray Snapper, of which 366 originated from tournament sources and 180 originated from nontournament sources, while the ROV (fishery-independent) data set consisted of 413 measured Gray Snapper. Length frequency distributions among these three sources (Figure 7) clearly demonstrate the effect of tournament sampling, with greater numbers persisting in higher size-classes in the tournament data compared with the gradual decline in frequency with size in both the nontournament and ROV data. Distributions of the nontournament and ROV lengths were proportionally similar in size-classes above the legal length limit for harvest.

Due to the length distribution bias associated with tournament sampling, only nontournament fishery-dependent catch data were used to estimate mortality. Peak abundance of the catch curve occurred at age 4 and decreased to the terminal age in the distribution at 25 (Figure 8). Unweighted linear regression yielded a low Z estimate equal to 0.16 ($A = 0.15$). With the weighted linear regression and Chapman–Robson estimator, Z equaled 0.30 and 0.38, respectively ($A = 0.26$ and 0.32) (Table 5). Estimates of M ranged from 0.17 to 0.43 (Table 6). Based on the latter two methods and the fact that M cannot be greater than Z, F was calculated as 0.04 to 0.21. For comparative purposes, the Beverton–Holt estimator produced $Z = 0.41$ ($A = 0.34$) for the ROV lengths, and calculations using the same methods above applied to the complete fishery-dependent data set

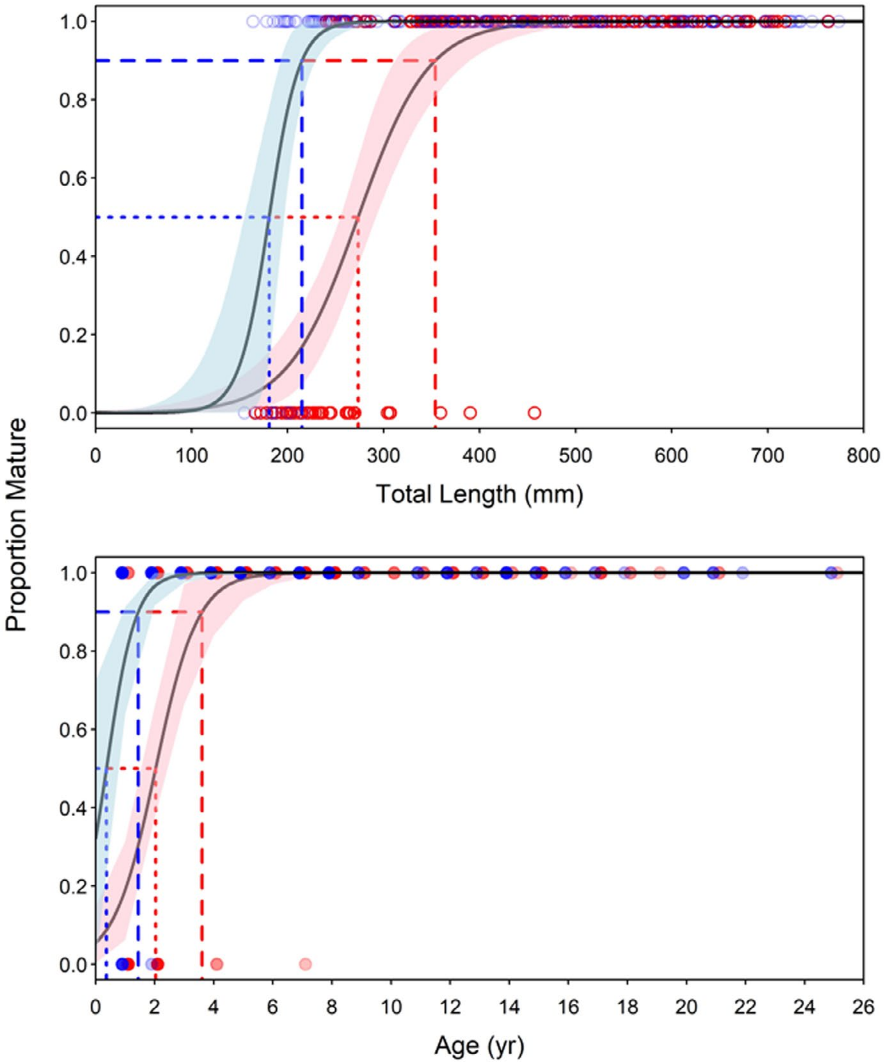

FIGURE 5 Maturity at total length (top panel) and age (bottom panel) of north-central Gulf of Mexico Gray Snapper; male estimates are colored in blue, and female estimates are colored in red. The intersections of segmented lines with each curve indicate values at 50% maturity (dotted lines) and 90% maturity (dashed lines), and shaded regions surrounding the curves represent 95% confidence intervals. Points with darker shades in the age-at-maturity plot represent greater sample sizes.

TABLE 4 Sex-specific estimates for total length (in millimeters) at 50% (L_{50}) and 90% (L_{90}) maturity and age (in years) at 50% (A_{50}) and 90% (A_{90}) maturity of north-central Gulf of Mexico Gray Snapper (95% confidence intervals are shown in parentheses).

Sex	n	L_{50}	L_{90}	A_{50}	A_{90}
Male	176	181 (155–196)	215 (193–229)	<1.0 (<1.0–1.0)	1.4 (1.0–1.9)
Female	182	273 (255–292)	354 (312–390)	2.0 (1.7–2.4)	3.6 (2.5–4.6)

resulted in $Z = 0.16–0.17$ ($A = 0.15–0.16$), $M = 0.15–0.43$, and $F = 0.01–0.02$.

DISCUSSION

Little is known about the Gray Snapper fishery in Alabama and Mississippi coastal waters despite the species' increasing popularity as a target for recreational anglers, and as such, investigation of this population was previously recommended in a federal assessment. Here, we model age and growth of Gray Snapper using the VBGF, which has been used exclusively in previous studies of this species as the optimum model in the north-central Gulf of Mexico. Our work adds to the body of evidence that growth appears to vary among distinct geographic populations.

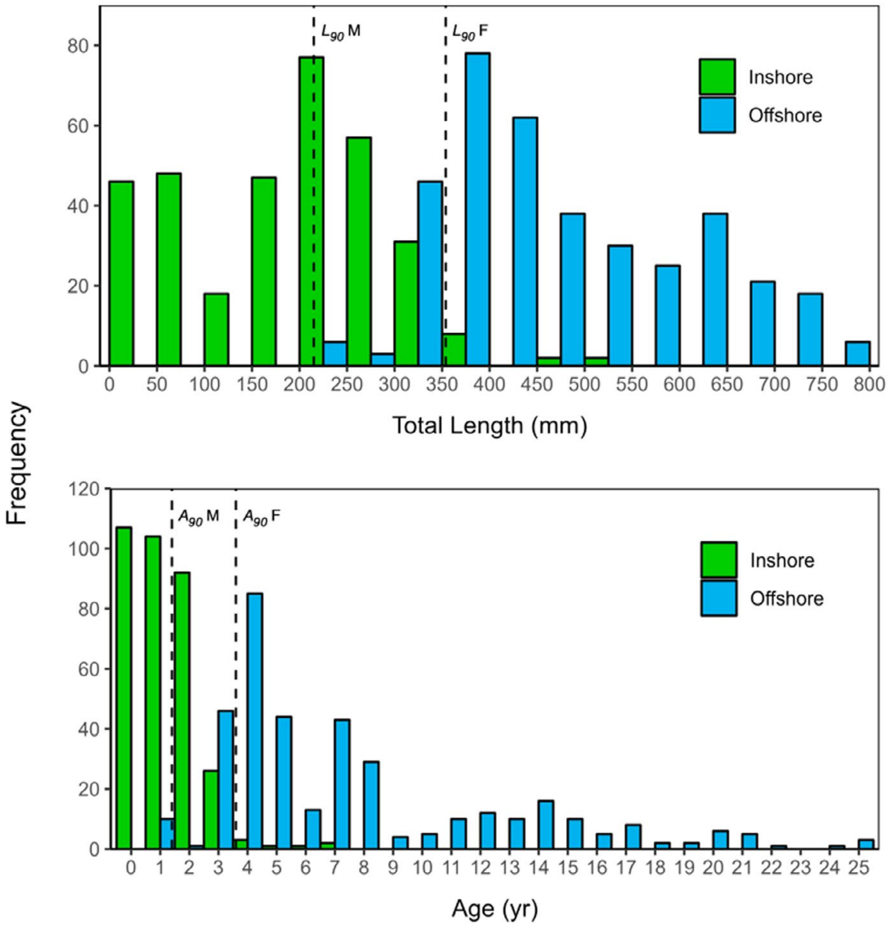

FIGURE 6 Length (top panel) and age (bottom panel) frequency distributions for north-central Gulf of Mexico Gray Snapper collected by location inshore or offshore ($n = 707$). Sex-specific 90% maturity estimates (length: L_{90}; age: A_{90}) are indicated by the dashed lines (M = male, F = female).

Estimates from Guatemala (Andrade and Santos 2019) represent one end of a spectrum in which early growth rates are high, but the growth trajectory appears to flatten out relatively quickly, resulting in comparatively small, older fish, while estimates from Louisiana (Fischer et al. 2005) and the northeastern coast of Florida (Burton 2001) represent the other end of the spectrum, in which fish grow slower initially but reach larger sizes at age. The L_∞ in this study falls in the upper portion of these values and k falls in the lower portion, suggesting that, for the north-central Gulf region, Gray Snapper achieve greater size at age following a more prolonged growth trajectory. However, it is important to note that the parameterization of the VBGF results in a correlation of L_∞ and k that trends inversely (Pilling et al. 2002), so care must be taken in extrapolations regarding growth rates and maximum size across populations. While the latter two studies from Louisiana and Florida occurred in the early 2000s and may be outdated with respect to current population demographics, the results still indicate that Gray Snapper in this area are among the largest described throughout its geographic range.

The large L_∞ observed in this study was a product of extensive sampling at tournaments, which reward anglers for obtaining the largest (and thus the most uncommon) specimens. Interestingly, direct anecdotes from the anglers indicate that many Gray Snapper entered into these tournaments are rare bycatch events that occur while targeting other reef fish and not the result of concerted efforts to capture trophy individuals of this species. Despite this, the persistence of this "tournament selectivity effect" was still noticeable in the sample distributions. Spearfishing presents the same phenomenon in that it is highly selective and can more efficiently sample larger individuals (Frisch et al. 2008) that may not be as susceptible to hook-and-line fishing. However, other studies report similar findings of sizable fish in the Gulf of Mexico. Gray Snapper are known to differ morphologically at the fringes of their distribution, with larger, longer-lived specimens characteristic in more temperate climates (Burton 2001; Fischer et al. 2005; Andrade and Santos 2019). Increasing size with latitude has been documented in other marine fish populations (Blanck and Lamouroux 2007; Fisher et al. 2010)

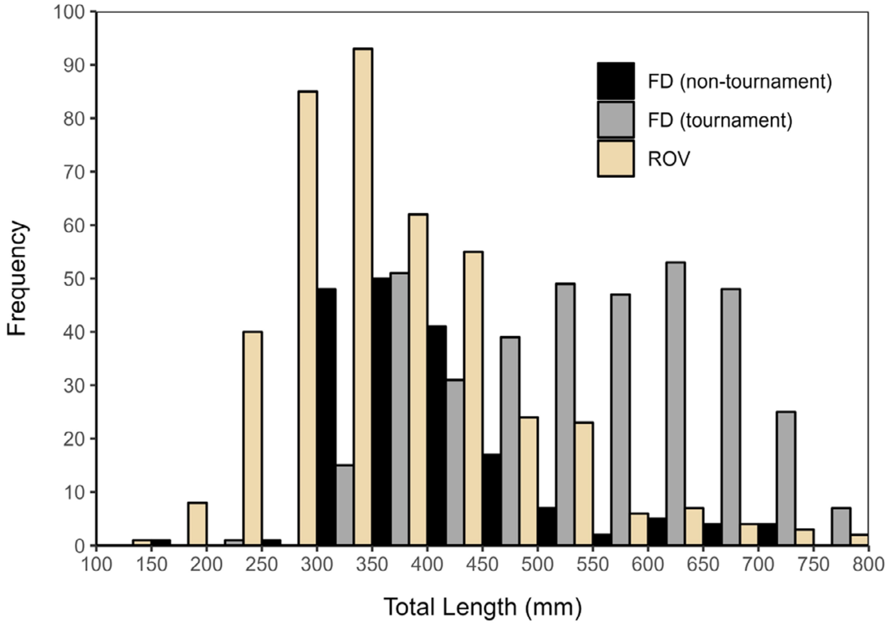

FIGURE 7 Length frequency distributions for mortality estimation of north-central Gulf of Mexico Gray Snapper. Abbreviations are as follows: FD (nontournament) = fishery-dependent data with only nontournament data, FD (tournament) = fishery-dependent data with only tournament data, and ROV = remotely operated vehicle.

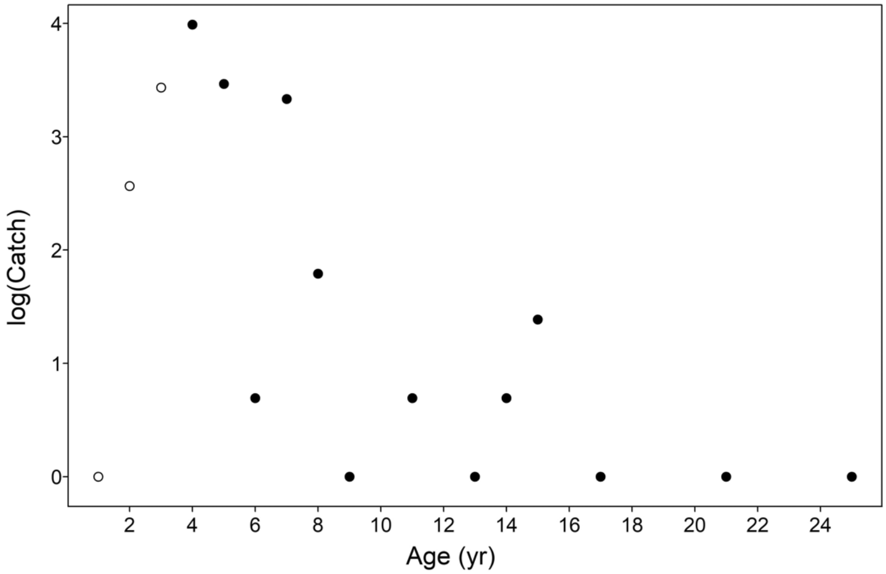

FIGURE 8 Nontournament fishery-dependent catch curve of north-central Gulf of Mexico Gray Snapper with peak abundance at age 4. Filled and unfilled circles represent age-classes that have and have not fully recruited to the fishery, respectively.

and appears to be an adaptation rooted in energetic advantages conferred from heightened thermal tolerance, most notably over the winter (Cargnelli and Gross 1997). The considerable size and age attained in this study are therefore likely intrinsic to the north-central Gulf of Mexico population. In this case, the abundance of large Gray Snapper that were sampled allowed for more accurate estimation of the true population L_∞.

Male Gray Snapper were found to have a significantly greater L_∞ than females based on the sex-specific VBGF curves, which showed growth trajectories that begin to diverge at approximately 3 to 4 years of age. However, this statistical difference could be driven by bias stemming from the large sample sizes obtained for both sexes and is probably not biologically meaningful, given that the difference of 27 mm between asymptotes is relatively minute.

TABLE 5 Instantaneous total mortality rate (Z) and annual mortality rate (A) estimates of north-central Gulf of Mexico Gray Snapper. Abbreviations are as follows: FD (nontournament) = fishery-dependent data with only nontournament data, and ROV = remotely operated vehicle. CI = confidence interval.

Data set	n	Method	Parameter	Estimate	95% CI
FD (nontournament)	180	Unweighted linear regression	Z	0.16	0.05–0.27
	180	Unweighted linear regression	A	0.15	0.05–0.24
	180	Weighted linear regression	Z	0.30	0.07–0.53
	180	Weighted linear regression	A	0.26	0.07–0.41
	180	Chapman–Robson	Z	0.38	0.20–0.57
	180	Chapman–Robson	A	0.32	0.18–0.43
ROV	413	Beverton–Holt	Z	0.41	0.35–0.48
	413	Beverton–Holt	A	0.34	0.29–0.38

TABLE 6 Instantaneous natural mortality rate (M) estimates of north-central Gulf of Mexico Gray Snapper.

Method	Input parameter	Input value	M
Hoenig longevity–mortality	$t_{\max}$	25	0.17
Hoenig nonlinear least squares	$t_{\max}$	25	0.26
Pauly	L_{∞}	68.74	0.43
	k	0.18	
	T (°C)	23.8	

There is little consensus regarding sex-specific growth in the existing literature (Burton 2001; Fischer et al. 2005; Allman and Goetz 2009; Andrade and Santos 2019), and growth differences have not been seen in other common snapper species endemic to the Gulf of Mexico (Saari et al. 2014; Moncrief et al. 2018) and are not generally characteristic of the family Lutjanidae (Carter and Perrine 1994). Sexual dimorphism in Gray Snapper, if it exists, may consequently be region-specific.

Gray Snapper are known to lay down a single annulus per year, but the timing of this event varies broadly by location. In the present study, annulus formation begins in April and peaks in May. Annulus formation is a result of alternating periods of slow growth laying rings close together (seen as narrow opaque bands) and fast growth laying rings spaced farther apart (seen as broad translucent bands), a pattern thought to be connected to energetic factors such as reproduction or temperature (Pilling et al. 2007; Wakefield et al. 2017; Irgens et al. 2020). Gray Snapper appear to lay opaque zones around the onset of the reproductive season (Burton 2001; Allman and Goetz 2009; Andrade and Santos 2019), usually late spring through early summer (Domeier et al. 1996; Denit and Sponaugle 2004; Fitzhugh et al. 2017), throughout much of their range. Commencement of spawning is a likely explanation for this deposition schedule, as proportionally more energy is diverted from somatic growth and dedicated to gonadal development at this time. Annulus formation in Louisiana, which is the most similar in latitude to this study, may be an outlier based on a limited number of individuals ($n=3$) sampled in January and February by Fischer et al. (2005) that exhibited opaque zone formation, suggesting that seasonal temperatures could also have a metabolic influence in some northern populations, although these results are inconclusive due to low sample sizes and monthly gaps in the data.

This study presents the first concurrent sex-specific maturity estimates known for Gray Snapper, which show that maturity is dimorphic and attained sooner in males. According to comparisons of these estimates against sample frequency distributions, most males and a portion of females are technically mature prior to their ontogenetic migration to offshore waters at the ages of 2 to 3 years to join the adult component of the population that comprises the spawning stock. However, these fish are unlikely to be reproductively active, as there are no contingents known to spawn inshore even as adults (Rutherford et al. 1989; Domeier et al. 1996; Luo et al. 2009; Anderson et al. 2022). Earlier maturation is one sign of fishery-induced evolution, especially in long-lived species that mature late (Enberg et al. 2009), but the negligible fishing mortality in this area indicates that the observed schedule is inherent to the regional life history of this population. Furthermore, because full recruitment to the fishery occurs at the age of 4, by which time virtually all fish have transitioned to offshore waters, the female A_{90} estimate of 3.6 years marks the beginning of susceptibility to harvest as each cohort approaches complete maturity and most fish enter either their first or second spawning cycle. Understanding this timing relative to harvest regulations is vital in calculating stock metrics that are fundamental to management (Vaughan and Carmichael 2002). Additionally, the importance of these maturity estimates is especially pronounced because they are based on standardized methods and terminology (Brown-Peterson et al. 2011), whereas the few existing studies on Gray Snapper maturity (Domeier et al. 1996; Andrade and Santos 2019) differ procedurally and do not yield reliable comparisons to the current study. The recent assessments provide the only comparable results for female conspecifics (Fitzhugh et al. 2017; Garner et al. 2022) and are largely encompassed by the confidence intervals for the size and age estimates here.

Using unweighted linear regression, the fishery-dependent estimate of Z without tournament data was among the lowest recorded in the Gulf of Mexico, where Gray Snapper are subject to varying degrees of fishing pressure and age truncation ensuing from the removal of larger individuals. In Florida, the effects of a high intensity fishery in southern areas versus northern areas is reflected in mortality as high as 0.94 and a difference in maximum ages of as much as 9 years (Burton 2001; Allman and Goetz 2009). Fishing pressure of this magnitude can induce evolutionarily selected shifts in demographic structure and growth, namely smaller fish that mature earlier (Kuparinen and Merilä 2007), that can ultimately have ramifications in altering reference points for management (Heino et al. 2013). By contrast, data from the Gray Snapper population in Louisiana (Fischer et al. 2005), which is only mildly exploited, reflect those of the population in the north-central Gulf of Mexico, with respective maximum ages of 28 and 27 and nearly identical values of Z. It is readily apparent from this low mortality that Gray Snapper here are capable of surviving to the known extent of the species' longevity. Overall, these findings are in concordance with long-term historical landings in Alabama and Mississippi that document consistently sparse harvests (SEDAR 2018) and support numerous anecdotes that Gray Snapper are, at least for now, predominantly a sporadic and incidental catch, as opposed to a targeted species, in this area. Similar parallels may occur in the recreational fishery in Texas, where despite decadal increases in abundance and expansion of age structure, angler intercept data have shown that 68% of the catch resulted from anglers targeting other species (Anderson et al. 2022), which could be attributed to the difficulty in directly targeting Gray Snapper.

The use of certain mortality estimators may lead to greater bias in mortality rates. Improved methods in the weighted linear regression and Chapman–Robson estimators for Z (Dunn et al. 2002; Smith et al. 2012) and the Hoenig$_{\text{nls}}$ estimator for M (Then et al. 2015) yielded higher fishery-dependent estimates of F while still providing evidence of a nominal exploitation rate (<0.12) and should be given more weight for management purposes. These methods also reveal substantial disparities between Z derived from data sets with and without tournament-sampled fish that illustrate the consequences of selectivity at these events. The length-based estimator for the ROV data set, intended as a contrast without fishery-dependent bias, aligned most closely with the Z estimated without tournament samples, supporting the exclusion of these data. Tournament events are nevertheless beneficial for sampling the largest individuals for specific objectives in growth modeling (Wilson et al. 2015) or reproductive analyses (Lowerre-Barbieri et al. 2015), especially for species like Gray Snapper that are not normally susceptible to physical sampling methods (Gregalis et al. 2012; Bacheler et al. 2013). However, overrepresentation in the final distribution remains a concern and must be reviewed and partitioned appropriately to prevent underestimation of mortality. That the ROV Z estimate is higher than the range of values from the improved methods may still indicate some bias in these data and is likely due to the heavy exploitation of artificial reefs in this area; thus, the true population Z is probably between those of the nontournament fishery-dependent data and the ROV data.

The findings from this study form the first characterization of this species' life history in the north-central Gulf of Mexico and introduce data for management and inclusion in future assessments. Current population dynamics indicate that Gray Snapper here are a robust, underexploited resource and run counter to more depleted stocks elsewhere throughout the Gulf of Mexico, suggesting that the most effective decisions regarding the fishery should be applied on an individual, regional basis. While recreational harvest is low, the presence of an established population that may grow with rising temperatures may generate more attention to this species in the near future, particularly in the Alabama artificial reef zone, where the dense assemblage of artificial reefs provides both ample habitat (Dance et al. 2011; Gregalis et al. 2012; Ajemian et al. 2015) and angling opportunities. Greater fishing pressure will clearly necessitate further monitoring to optimize management, but efforts to do so may be obfuscated by the possibility that warming could simultaneously alter length–age distributions by favoring growth to a smaller adult size (Atkinson 1994; Lindmark et al. 2022), diminishing the proportion of larger fish that are currently present. Although outside the scope of this study, collection of additional data and subsequent analysis of these patterns and their intersection could hold some predictive utility in interpreting population demographics affected to different degrees by both anthropogenic and environmental factors and may have the added benefit of informing management of analogous fisheries. In light of this, continued monitoring of the north-central population will likely become increasingly important considering a potentially emergent fishery and the development of any climate-driven shifts in life history.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data that support the findings of this study are available from the corresponding author (ekim@neaq.org) and Dr. Sean Powers (spowers@disl.org) upon reasonable request.

ETHICS STATEMENT

Research activities were conducted following protocol 1562086 approved by the University of South Alabama Institutional Animal Care and Use Committee. Specimens were collected under permits issued by the National Marine Fisheries Service and the ADCNR MRD.

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