5-2022

# Characterizing Gray Snapper (Lutjanus Griseus) Life History in the Northcentral Gulf of Mexico: Age and Growth, Mortality, and Reproduction

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### Recommended Citation

CHARACTERIZING GRAY SNAPPER (*LUTJANUS GRISEUS*) LIFE HISTORY IN
THE NORTHCENTRAL GULF OF MEXICO: AGE AND GROWTH, MORTALITY,
AND REPRODUCTION


A Thesis

Submitted to the Graduate Faculty of the
University of South Alabama
in partial fulfillment of the
requirements for the degree of


Master of Science

in

Marine Sciences


by
Edward S. M. Kim
B.A., University of Pennsylvania, 2016
May 2022

## ACKNOWLEDGEMENTS

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# LIST OF ABBREVIATIONS

Akaike information criterion: AIC

Alabama Artificial Reef Zone: AARZ

Alabama Deep Sea Fishing Rodeo: ADSFR

Annual catch limit: ACL

Average percent error: APE

Germinal epithelium: GE

Gulf of Mexico Fishery Management Council: GMFMC

Gulf of Mexico: GoM

Maximum fishing mortality threshold: MFMT

Minimum stock size threshold: MSST

Postovulatory follicle: POF

Remotely operated vehicle: ROV

Scientific and Statistical Committee: SSC

SouthEast Data, Assessment, and Review: SEDAR

von Bertalanffy growth function: VBGF

# ABSTRACT

Kim, Edward S. M., M.S., University of South Alabama, May 2022. Characterizing Gray Snapper (*Lutjanus griseus*) Life History in the Northcentral Gulf of Mexico: Age and Growth, Mortality, and Reproduction. Chair of committee: Sean P. Powers, Ph.D.

Gray Snapper (*Lutjanus griseus*) constitute a significant recreational fishery and minor commercial fishery throughout the Gulf of Mexico, and review of the recent assessment determined that the stock is overfished and has been undergoing overfishing. The absence of regional baseline data in the northcentral Gulf of Mexico, combined with projections of range expansion and subsequent population growth due to climatic warming, highlight the need for the present investigation into the age and growth, mortality, and reproduction of this species in Alabama and Mississippi. Sex-specific growth curves constructed using the von Bertalanffy growth function demonstrated a significantly greater mean asymptotic length achieved by males ($L_t = 731.52(1 - e^{-0.15(t+1.34)})$) than females ($L_t = 704.28(1 - e^{-0.14(t+1.62)})$). Mortality rates ($Z = 0.30 - 0.38$; $F = 0.04 - 0.12$) indicate relatively low levels of exploitation. Histological analyses determined estimates of total length at 50% maturity ($L_{50M} = 181$ mm; $L_{50F} = 273$ mm) and age at 50% maturity ($A_{50M} < 1.0$ yr; $A_{50F} = 2.0$ yr), spawning seasonality (May – August/September), and spawning interval and frequency (3.9 – 4.5 d; 28.7 – 33.4 events/season). The findings from this study will introduce new data for incorporation in future assessments and provide guidance for informed management decisions.

# INTRODUCTION

The Gray Snapper (*Lutjanus griseus*) is a lutjanid species whose range extends from the southeastern United States and Gulf of Mexico (GoM) down to South America (Burton 2001; Fischer et al. 2005). Larvae disperse through a planktonic phase in which they can drift into the temperate waters of the northeastern United States via the Gulf Stream, an area well outside of 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 the settlement stage larvae occupy seagrass 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 (Domeier et al. 1996; Starck II and Schroeder 1971). 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 II and Schroeder 1971; Smith 1976). Elsewhere in the GoM, 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 GoM, this species is most abundant off Florida (Morley et al. 2018), but comparative inshore surveys across several

decades in the northcentral GoM have revealed a marked increase in juvenile abundance (Fodrie et al. 2010) that could be connected to the magnitude of adult recruitment to artificial reefs off of 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 by thermal stress (Wuenschel et al. 2004; Tolan and Fisher 2009; Wuenschel et al. 2012). Furthermore, Gray Snapper are expected to continue this range shift under current warming scenarios, becoming more abundant while also spreading westward (Morley et al. 2018). While recreational harvest in the northern GoM has historically been low (SEDAR 2018), these projections could have implications for future development of a more viable fishery in the area.

The snapper family Lutjanidae comprises a valuable group of fisheries in the GoM. Perhaps the most iconic of these, the Red Snapper (*Lutjanus campechanus*) fishery, has been subject to repeated, severe reductions in season length and bag limit since the 1990s (GMFMC 2019a). These restrictions may have led to a concomitant rise in the Gray Snapper fishery in parts of the northern GoM (Fischer et al. 2005). Since 2001, Gulf-wide catch estimates have typically fluctuated between 1.5 million and 2.3 million pounds, with the recreational sector predominating over the commercial sector (GMFMC 2019c; Figure 1). Although Florida is responsible for much of this catch, states in the northern GoM have developed small, yet growing, recreational fisheries (GMFMC 2019c; Figure 2). Larger Gray Snapper also compose a greater proportion of the catch distribution in these areas compared to Florida (Chih 2017).

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 12-inch minimum total length (GMFMC 1989) that has been maintained to the present day (GMFMC 2019c). In 1999, the Generic Sustainable Fisheries Act Amendment collectively established a standardized maximum fishing mortality threshold (MFMT) value – equal to the fishing mortality rate at a spawning potential ratio of 30% ($F_{30\% \text{ SPR}}$) – for many reef fish, including Gray Snapper (GMFMC 1999), but did not define reference points for several other stock determination criteria (SEDAR 2018). Additionally, no annual catch limit (ACL) existed through 2012, when a combined recreational and commercial cap of 2.42 million pounds was instituted through the Generic Annual Catch Limits/Accountability Measures Amendment (GMFMC 2011). However, insufficient catches have led to an essentially year-round season for Gray Snapper that is especially favorable to recreational anglers given frequent regulation changes and intermittent closures for many other reef fish species (Jefferson et al. 2019; Powers and Anson 2019).

Recent inquiries into the status of the GoM Gray Snapper fishery have led to updated regulations and better-informed reference points. The first stock assessment for this species in the GoM, conducted by the SouthEast Data, Assessment, and Review (SEDAR) in 2018, determined, based on the standardized MFMT as well as a minimum stock size threshold (MSST) of 50% of spawning stock biomass at a spawning potential ratio of 30% ($SSB_{30\% \text{ SPR}}$), that the stock was not overfished despite overfishing since the mid-1970s (SEDAR 2018). Conversely, a follow-up review by the Gulf of Mexico Fishery Management Council (GMFMC) Scientific and Statistical Committee (SSC) found the stock to be overfished according to:

$$MSST = (1 - M) \cdot B_{30\% \text{ SPR}}$$

where $M$ is the instantaneous natural mortality rate (equal to 0.15) and $B_{30\% \text{ SPR}}$ is the stock biomass at a spawning potential ratio of 30% (GMFMC 2018). As a result, Amendment 51 was proposed, approved, and implemented beginning in December 2020, which preserved existing bag and size limits while reducing the ACL to 2.23 million pounds and setting new benchmarks for MFMT equal to $F_{26\% \text{ SPR}}$ and MSST equal to 50% of the stock biomass corresponding to the maximum sustainable yield proxy ($B_{\text{MSY proxy}}$) (GMFMC 2019c).

Accurate estimates of life history parameters are critical to assessing the status of fisheries stocks. These parameters require extensive biological data across birth, growth, maturation, reproduction, and death and are ultimately used to inform models that indicate the exploitation of the stock and appropriate benchmarks for management (Maunder and Piner 2015). At its core, the length-age relationship serves as the foundation of age-structured models in many stock assessments (Kimura 1977; Heery and Berkson 2009), while age composition, growth dynamics, and mortality estimates can be used to further assess demographic structure and infer external pressures on the population (Burton 2001; Fischer et al. 2005; Andrade and Santos 2019). Reproductive characteristics are closely interconnected because they provide information on the annual generation of cohorts that enter the population as new biomass and eventually recruit to the fishery. The spawning population demography of long-lived fishes is tied to reproductive capacity such that truncated age distributions can lead to diminished productivity (Murawski et al. 2001; Cooper et al. 2013) and reduced resilience to disturbance (Lowerre-Barbieri et al. 2015). For species like Gray Snapper, protracted longevity (Fischer et al. 2005), known residency on artificial reefs as adults (Ajemian et

al. 2015), and presumptive high site fidelity (Bortone and Williams 1986; Dance et al. 2011) are qualities that are conducive to over-exploitation (Beamish et al. 2006; Stewart 2011; Addis et al. 2016). These characteristics suggest that collection of reliable growth and reproduction data will be necessary for successful monitoring of Gray Snapper stocks.

Gray Snapper growth dynamics have been examined across their geographic range (Table 1). In the GoM, 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 GoM was estimated to be 32 years old (Thornton et al. 2017). Estimates of theoretical maximum length $L_\infty$ 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 $L_\infty$ 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. To

date, no specific studies on Gray Snapper growth dynamics have been performed to investigate the northcentral segment of the GoM population residing primarily in Alabama and Mississippi coastal waters.

Methodology may account for additional variation or potential error in growth parameters. Specifically, the inclusion of juveniles in length-age models is important because characterization of early growth can improve the overall curve fit (Berumen 2005). For Gray Snapper, juvenile growth has previously been modeled separately on a daily time scale (Allman and Grimes 2002; Denit and Sponaugle 2004; Lounder 2009), but no age and growth studies other than Burton (2001) and Andrade and Santos (2019) incorporate appreciable numbers of age-0 to age-1 individuals to anchor sex-specific growth curves (Burton 2001; Barbieri and Colvocoresses 2003; Fischer et al. 2005; Allman and Goetz 2009), which may lead to better model estimates of the growth coefficient $k$ (Grebel and Cailliet 2010). To account for the absence of sublegal fish in their data, Fischer et al. (2005) and Allman and Goetz (2009) set $t_0$ (the theoretical age at which the fish's length is 0) equal to 0. This constraint is a pragmatic approximation of early growth given a dearth of juvenile samples (Berumen 2005) but remains imperfect, as it still imparts some bias in parameter estimates (Gwinn et al. 2010) which can be exacerbated in ensuing stock-level calculations (Ricker 1969). More complete sampling across younger age classes could mitigate these issues and aid in refining growth descriptions.

Gray Snapper show spatial variability from north to south in their reproductive life history (Table 2). In the Florida Keys (Barbieri and Colvocoresses 2003) and the Caribbean (Andrade and Santos 2019), gonadosomatic index (GSI) values delineate a

spawning season from April through September with a peak in June, although an earlier

account by Domeier et al. (1996) in the Florida Keys noted that spawning began in May

and peaked in August. Samples taken from a broader population across the west coast of

Florida exhibited a later spawning start in May with a peak in July (Allman and Grimes

2002; Fitzhugh et al. 2017), and two studies along the Atlantic coast indicate a similar

schedule using back-calculation from juvenile otoliths (Tzeng et al. 2003; Denit and

Sponaugle 2004). Based on this variability, the expanding range of this species (Hare et

al. 2012; Morley et al. 2018) may feasibly come with the capacity for altered life history

attributes. Other species are known to display shifts in spawning due to phenotypic

plasticity across their distribution (Abookire and Macewicz 2003; Vinagre et al. 2008) as

well as interannual fluctuations in climate (Rogers and Dougherty 2018). The

characterization of these responses across environmental regimes may therefore yield

important insight into reproductive patterns in unstudied populations elsewhere in the

GoM.

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 GoM (Gold et al. 2009). Of particular

importance are up-to-date 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 current stock assessment, approximately two-thirds originated in the

1990s, and virtually all were represented from the west coast of Florida (Fitzhugh et al.

2017). Female mean estimates of maturity from these samples have been reported as 2.3

years and 253 mm fork length. The most recent estimate of male sexual maturity using

histology occurred in 1996 (Domeier et al. 1996), while other studies have relied on macroscopic evaluation of gonads (Starck II 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 proposed work will serve to fill in some of these gaps using condition indices and histological methods to update historical and incomplete estimates and improve our understanding of spawning dynamics and other reproductive characteristics particular to Gray Snapper at its northern boundary in the GoM.

The conclusions drawn from the recent assessment are based on data collected from extensive investigations throughout the GoM. However, no specific studies to date have been performed on the northcentral segment of the 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. Thus, despite a currently diminutive fishery, the expected growth of this northernmost segment of the population calls for heightened consideration of its importance to future assessments, especially given recent movement towards regional management of federal fisheries (GMFMC 2019b). As such, the initial management of this stock will require a comprehensive survey of various life history parameters. Examining these parameters will facilitate an understanding of local population characteristics and life history adaptations and inform proper management of this species and its fishery.

## OBJECTIVES AND HYPOTHESES

Data deficiencies in the northcentral GoM Gray Snapper population will be resolved via the following objectives:

Objective 1: Determine the best fit growth model and describe pooled and sex-specific growth parameters for the length-age relationship of Gray Snapper in the northcentral GoM.

$H_{01}$: Male and female growth models do not differ significantly.

$H_{A1}$: Differential male and female growth rates produce distinct sex-specific growth models.

Objective 2: Describe power function parameters for the weight-length relationship of Gray Snapper in the northcentral GoM.

Objective 3: Determine the timing of annulus deposition via marginal increment analysis of Gray Snapper in the northcentral GoM.

Objective 4: Generate total, natural, and fishing mortality estimates of Gray Snapper in the northcentral GoM.

Objective 5: Assess length and age at maturity, seasonal spawning dynamics, and spawning fraction estimates of Gray Snapper in the northcentral GoM.

Objective 6: Compare northcentral GoM Gray Snapper life history parameters against those from population studies throughout the geographic distribution of the species.

$H_{06}$: Northcentral GoM Gray Snapper life history parameters reflect underlying patterns in climate and mortality among studies.

$H_{A6}$: Northcentral GoM Gray Snapper life history parameters do not appear to be influenced by spatial patterns present among studies.

**METHODS**

**Specimen Collection and Processing**

Gray Snapper samples were previously collected between 2011 and 2017 at the Alabama Deep Sea Fishing Rodeo (ADSFR). To supplement these existing samples, additional fish were collected from a variety of sources beginning in the fall of 2018. Adult specimens for this study were primarily obtained from various hook-and-line and spearfishing tournaments that occur along the coast of Alabama and Mississippi from spring through fall, with fish periodically provided by recreational for-hire charter vessels and local fishermen. Juvenile and sub-adult specimens were obtained through hook-and-line efforts and fishery-independent inshore surveys in Mobile Bay and Orange Beach, Alabama. Particularly small individuals likely to be young-of-the-year representing the age-0 class were obtained from benthic sled sampling of seagrass beds in the Chandeleur Islands through the Gulf Coast Research Laboratory.

Standard length, fork length, natural total length, and total length were recorded in millimeters for each fish. Body weight was measured with a spring scale in increments of 0.05 kilograms 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 gram.

When possible, processing occurred within 24 hours of capture. For tournament sampling, all gonads were bagged, stored on ice, and processed at the laboratory within the same day.

Histological samples approximately 1 cm$^3$ in size were 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 the 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).

**<u>Aging</u>**

Otoliths were prepared consistent with procedures published by VanderKooy et al. (2020) and aged 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 by hand along the transverse plane to the core. The flat edge was mounted on a slide using Loctite 349 and cured with ultraviolet light. The otolith was then ground again down to 0.5 mm thickness in the arm of the precision grinder, coated with Cytoseal 280, and allowed to dry. 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 in order 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 (APE), where a smaller APE signifies greater precision (Beamish and Fournier 1981). Individual discrepancies were then reviewed to reach a consensus final age or margin code.

## **<u>Growth Modeling</u>**

Prior to running Gray Snapper growth models, fractional ages were used to obtain more accurate estimates of individual ages. Assigned age groups represent integer values rounded depending on the margin code relative to the catch date. Fractional ages can then be calculated by adding on the time difference between the catch date and an assumed birthdate of August 1 (based on the timing of peak spawning from female condition indices and monthly reproductive phase distribution), which specifies any additional growth in decimal form (VanderKooy et al. 2020; Jefferson et al. 2021). 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

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1825; von Bertalanffy 1938; Ricker 1975) run in R version 4.0.3 (R Core Team 2020)

with the package FSA version 0.8.31 (Ogle et al. 2020). These growth functions are given

as:

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

for the Gompertz growth model, where $L_\infty$ 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 $L_\infty$ is the mean hypothetical asymptotic length, $g_{-\infty}$ is

the growth rate at negative infinity, and $t_i$ is the age at the inflection point; and

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

for the VBGF, where $L_\infty$ is the mean hypothetical asymptotic length, $k$ is the Brody

growth coefficient, and $t_0$ is the theoretical age when length is equal to 0.

The resulting models were compared using Akaike information criterion (AIC)

values (Akaike 1973; Katsanevakis and Maravelias 2008), and the leading model (i.e. the

VBGF) was selected for further sex-specific analysis. Individuals of unknown sex were

included for these multi-model comparisons but omitted from the subsequent sex-specific

models. Separate growth curves were then fit to male and female data, and confidence

intervals for growth parameters were obtained through bootstrapping. To determine

whether the sex-specific models provided better fits than a model with shared parameters,

a series of likelihood ratio tests (Cerrato 1990; Ogle 2013b) was implemented on all

subsets of a full model with distinct parameters by sex down to the most constrained

subset model with all parameters shared by sex.

The weight-length relationship for Gray Snapper was defined by the power

function given by the 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.

In order to facilitate growth comparisons against previous studies that did not use

total length, conversions among standard length, fork length, and total length were

produced by fitting paired linear regressions for all combinations of lengths (Bennetts

2018).

**Marginal Increment Analysis**

Marginal increment analysis is used to identify the time of year when opaque

zones are formed on the edge of the otolith, which, in Gray Snapper, may be related to

decreased growth associated with spawning or temperature (Fischer et al. 2005; Andrade

and Santos 2019). 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.

**<u>Mortality Estimation</u>**

Methods for mortality estimation were based on a fishery-dependent catch curve,

which was 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 dataset prior

to analysis. The remaining data were composed exclusively of hook-and-line and

spearfishing gears. Due to selectivity concerns associated with tournament sampling,

non-tournament samples were isolated as a separate dataset alongside the complete

dataset. Mortality was also estimated from Gray Snapper laser length measurements

collected during fishery-independent remotely operated vehicle (ROV) surveys of reefs in

the Alabama Artificial Reef Zone (AARZ) and adjacent waters from 2011 to 2019. Fork

lengths were converted to total lengths with the linear conversion formula denoted above.

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). $Z$ 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 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 non-linear least squares (Hoenig$_{nls}$) 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 $L_\infty$ and $k$ as well as the mean annual water temperature, which was computed from sea surface data recorded by the National Data Buoy Center Station 42012 south of Orange Beach, AL. Additionally, because $Z = F + M$, where $F$ is equivalent to fishing mortality, estimates of $F$ were derived from the calculated values of $Z$ and $M$. 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).

## **Principal Component Analysis**

Relationships in spatial variation of Gray Snapper life history were explored with

principal component analysis (King and McFarlane 2003; Matson and Gertseva 2020;

Brooks 2021) among the current study and previous studies occupying discrete

geographic areas between the northern GoM and the Caribbean (Burton 2001; Fischer et

al. 2005; Allman and Goetz 2009; Andrade and Santos 2019). Five common life history

parameters were selected: maximum age ($t_{max}$), $L_\infty$, $k$, $Z$, and $F$. In order to maintain

methodological consistency, unweighted linear regression was used for $Z$ with the non-

tournament fishery-dependent dataset, and $F$ was based on $M$ estimated with the Hoenig

longevity-mortality relationship. Data were scaled to standardize the contributions of

each variable to the principal components.

## **Condition Indices**

Reproductive and somatic condition indices were used to track the development

and peak of spawning for each sex by month (Powers et al. 2012; Corey et al. 2017).

Only individuals determined to be sexually mature by histological analysis or greater than

or equal to the length at 90% maturity were included in the analyses. Samples caught

inshore were excluded from the analyses because Gray Snapper are not known to spawn

inshore. Samples with unknown or missing body weights were also excluded.

The physical status of the population was calculated with the Le Cren relative

condition factor given by:

$$K_{rel} = \frac{W}{aL^b}$$

where $K_{rel}$ is a measure of departure from the mean weight at length and is derived directly from the empirical weigh-length relationship fit to the power function (Le Cren 1951; Froese 2006). A linear model was fit to sex-specific data which was then used to predict and plot monthly mean $K_{rel}$ values and associated confidence intervals. In order to examine pairwise differences among months, a Kruskal-Wallis test was performed and followed by a post hoc Dunn's test with a Bonferroni correction to adjust the type I error rate (Bennetts et al. 2019).

The gonadosomatic index (GSI) and intraperitoneal fat index (IPFI) are proxies for energetic investment and expenditure surrounding spawning and are given by:

$$GSI = \frac{Gonad\ weight}{Gonad\ free\ body\ weight} \cdot 100$$

$$IPFI = \frac{Intraperitoneal\ fat\ weight}{Intraperitoneal\ fat\ free\ body\ weight} \cdot 100$$

where weights are recorded in grams (Powers et al. 2012). In both cases, linear models fit to sex-specific data returned residuals that did not adhere to normality. For GSI, a generalized linear model with a gamma distribution and log link was subsequently tested (Jefferson 2017) and confirmed via AIC to provide a better fit over the linear model. Monthly median GSI values and associated confidence intervals were predicted and plotted, and a Kruskal-Wallis test was performed and followed by a post hoc Dunn's test with a Bonferroni correction (Bennetts et al. 2019). For IPFI, various generalized linear model distributions were unable to approximate normality in the residuals, presumably due to a high incidence of zeros during spawning months. Therefore, a loess smoother (Jacoby 2000) was used to aid in evaluation of changes in mean IPFI values across months. Because GSI and IPFI are correlated as measures of spawning (Powers et al.

2012), they were also plotted simultaneously to observe trends across the reproductive season.

### **Histological Processing and Phase Distributions**

Following preservation in formalin, histological sample cassettes were transferred to an open container with drainage holes and placed under running tap water for 24 hours. The samples were then dehydrated by a 2-hour soak in 60% denatured ethanol followed by an additional 2 hour soak in 70% denatured ethanol and then final storage in 70% denatured ethanol (Bennetts 2018). Samples were sent to the Texas A&M College of Veterinary Medicine & Biomedical Sciences Histology Laboratory to be processed further. Two to three cross-sections per sample were cut to 4 µm thickness, mounted on a slide, and stained with hematoxylin and eosin. Slides were viewed under a 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 (early GE), mid germinal epithelium (mid GE), and late germinal epithelium (late GE), which are progressive indicators of the spawning season. Females were categorized into the same main phases, plus an actively spawning subphase. The proportions of fish in each reproductive phase were then calculated and plotted to show monthly distributions. Additionally, 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 hour postovulatory follicles (POFs) in ovarian tissue were noted as spawning markers (Fitzhugh et al. 2017).

## Maturity

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 (0) or mature (1) 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).

## Female Spawning Dynamics

Spawning fractions were examined for temporal variability by month as well as by size and age. For the latter, fish were separated into intervals of 100 mm total length and 5 years. Ages 1 through 5 were truncated to 3 through 5 due to the absence of mature females, and ages 16 through 25 were aggregated to increase sample size and because this range of ages represent a homogeneous stage of growth where $L_\infty$ is largely achieved according to the VBGF. Calculations followed the method outlined in Porch et al. (2015), where the number of females exhibiting spawning markers was divided by all spawning-capable females. A binary logistic regression was used to model this process according to the presence/absence of spawning markers and predict raw spawning fraction values with confidence intervals. These values were subsequently converted to a daily value using the equation:

$$P = \frac{24}{T_M} \cdot p$$

where $T_M$ is the spawning marker longevity adapted from Red Snapper [equivalent to 10 hours for hydrated oocytes, 24 hours for ≤24 hour POFs, and 34 hours for both according to Fitzhugh et al. (2012) and Porch et al. (2013)] and $p$ is the raw spawning fraction. Similar to the condition indices, the data for this analysis were subset to include only mature females and exclude fish caught inshore. Samples that were unable to be scored for spawning markers due to low sample quality were also excluded.

The spawning interval, or the number of days between spawning events, was calculated as the reciprocal of the mean daily spawning fraction across months with positive daily spawning fraction values (Lowerre-Barbieri et al. 2011). Spawning frequency was calculated by dividing the spawning season length by the spawning interval (Lowerre-Barbieri et al. 2011), where season length is the time difference in days between the first and last females histologically confirmed to be in the actively spawning subphase in a given year (Moncrief et al. 2018). Due to the lack of samples collected in September, the probable end of the spawning season assumed from the available data, lower and upper end estimates of spawning interval and spawning frequency were calculated based on the confidence interval surrounding the daily spawning fraction for July and an end date of September 30, respectively.

# RESULTS

## Sample Distributions

A total of 886 Gray Snapper were collected for various growth and reproductive samples from ports ranging from Orange Beach, AL to Gulfport, MS between 2011 and 2021, with the majority of sampling beginning in 2018 and during summer months when fishery-dependent efforts tend to be highest (Table 3). Sampling was extended to the spring and fall months (March through November) and opportunistically in January to better capture trends in annulus formation as well as reproductive dynamics related to the onset and decline of the spawning season. 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 utilized benthic sleds, traps, trawls, and vertical longlines accounted for the remaining 38.6% (Table 4). Benthic sleds were successful in sampling 98 fish in the smallest size class (<100 mm total length) present in the dataset that rarely recruited to the other gear types. Most fishery-dependent samples are known or presumed to have been caught in the AARZ 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 provide no evidence that the population sex ratio differs from 1:1 ($X^2 = 0.113$, d.f. = 1, $p$

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= 0.736). Gonads and intraperitoneal fat were weighed from 600 and 521 fish,

respectively (intraperitoneal fat weight was only measured when gonad weight was also

measured).

Sizes ranged from 29 to 774 mm total length and were greatest in frequency in the

351-400 mm size class. Likewise, both males and females were caught in the greatest

frequencies in the 351-400 mm size class (Figure 3). 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. Conversion formulas

among different length types are found in Table 5; all conversions displayed high

goodness of fit ($r^2 > 0.996$).


## Aging

Gray Snapper otoliths produced distinct annuli beginning with an initial ring

proximal to the core and subsequent annuli formed closer together towards the dorsal

margin (Figure 4), which facilitated precision in annuli counts. Readers agreed on 94.1%

of ages and differed by one year on 5.7% of ages and two years on 0.2% of ages,

resulting in an APE of 0.6% which is in line with previous aging work (Fischer et al.

2005). 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

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 ($\Delta$AIC = 208.10) and the logistic model ($\Delta$AIC = 362.79) (Table 6). The VBGF was consequently selected as the best model and was used to proceed with sex-specific modeling. The pooled VBGF equation is given by:

$$L_t = 687.43(1 - e^{-0.18(t+0.66)})$$

The VBGF exhibited a pattern of accelerated growth at birth but began tapering off to the asymptotic length at a later age (Figure 5), resulting in a significantly higher estimate of $L_\infty$ as evidenced by non-overlapping 95% confidence intervals.

The VBGF was subsequently fit to separate male and female data (Figure 6; Table 7), which produced the following models:

$$Male: L_t = 731.52(1 - e^{-0.15(t+1.34)})$$

$$Female: L_t = 704.28(1 - e^{-0.14(t+1.62)})$$

No age-0 Gray Snapper were 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.

In order to determine whether growth differed between males and females in the population, a set of subset models were fit which differed in terms of whether or not each

parameter was allowed to vary based on sex. The full model allowed all parameter estimates to vary based on sex, while the most constrained subset did not allow any parameter estimates to vary based on sex. The most parsimonious of the candidate models was selected based on likelihood ratio tests and residual sums of squares. The best fitting model based on these criteria allowed $L_\infty$ to vary but held both $k$ and $t_0$ constant (Table 8). While the dataset did not provide evidence that $k$ and $t_0$ differ between the sexes, it did provide evidence that males achieve a larger $L_\infty$ than females in this population.

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:

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

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. 95% prediction intervals were plotted alongside the fitted line and 95% confidence intervals (Figure 7; Table 9).

### Marginal Increment Analysis

Marginal increment analysis revealed annulus formation beginning in April, peaking in May, and ending abruptly before the start of June (Figure 8). 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. The timing

of annulus formation in the northcentral GoM Gray Snapper population largely aligns with previous studies in other regions that documented annulus formation at times from winter through early summer (Burton 2001; Fischer et al. 2005; Allman and Goetz 2009; Andrade and Santos 2019).

## **Mortality Estimation**

The complete fishery-dependent dataset for mortality estimation consisted of 546 Gray Snapper, of which 366 originated from tournament sources and 180 originated from non-tournament sources, while the ROV dataset consisted of 413 measured Gray Snapper. Length frequency distributions among these sources (Figure 9) clearly demonstrate the effect of tournament sampling, with greater numbers of these samples persisting into higher size classes compared to the gradual decline in the frequency of non-tournament and ROV samples with increasing size. Significant differences in the length frequency distributions were detected with Kolmogorov-Smirnov tests among the complete fishery-dependent and non-tournament fishery-dependent datasets ($D = 0.36$, $p < 0.001$), the complete fishery-dependent and ROV datasets ($D = 0.44$, $p < 0.001$), and the non-tournament fishery-dependent and ROV datasets ($D = 0.36$, $p < 0.001$).

Peak abundance of the complete fishery-dependent and non-tournament fishery-dependent catch curves occurred at age 4 and decreased to the terminal ages in the distribution at 27 for the former and 25 for the latter (Figures 10 and 11). Unweighted linear regression yielded low $Z$ estimates equal to 0.17 ($A = 0.16$) for the complete fishery-dependent dataset and 0.16 ($A = 0.15$) for the non-tournament fishery-dependent dataset. With the weighted linear regression and Chapman-Robson estimator, the

complete fishery-dependent $Z$ fell in a narrow range between 0.16 and 0.17 ($A = 0.15 -$ 0.16), while the non-tournament fishery-dependent $Z$ ranged between 0.30 and 0.38 ($A =$ 0.26 – 0.32) (Table 10). Estimates of $M$ were similarly spread from 0.15 to 0.43 for the complete fishery-dependent $M$ and 0.17 to 0.43 for the non-tournament fishery-dependent $M$ (Table 11), although the upper ends of both ranges were calculated with the same VBGF parameters in the Pauly method. Based on the weighted linear regression and Chapman-Robson values and the fact that $M$ cannot be greater than $Z$, the complete fishery-dependent $F$ was calculated as 0.01 to 0.02, and the non-tournament fishery-dependent $F$ was calculated as 0.04 to 0.21. The Beverton-Holt estimator produced $Z$ equal to 0.41 ($A = 0.34$) for the ROV lengths. Assuming the same non-tournament fishery-dependent $M$ range, $F$ was calculated as 0.15 to 0.24.

**Principal Component Analysis**

The chosen parameters ($t_{max}$, $L_\infty$, $k$, $Z$, and $F$) were reduced down to two principal components encompassing 98.0% of all variation. Positive vectors for $t_{max}$ and $L_\infty$ and a negative vector for $Z$ characterized the first principal component, which comprised 58.5% of variation, whereas negative vectors for $k$ and $F$ characterized the second principal component, which comprised 39.5% of variation. Vectors for $L_\infty$ and $k$ as well as $t_{max}$ and $Z$ were nearly diametrically opposed, which was expected due to their negative correlations. In general, previous studies investigating Gray Snapper life history aspects were separated geographically on the biplot (Figure 12). Populations to the north, consisting of Alabama/Mississippi, the Atlantic coast of northern Florida, and Louisiana, were clustered together and composed of large, long-lived fish with low to moderate

mortality. Conversely, the population along the Atlantic coast of southern Florida appeared to be driven primarily by the presence of exceptionally high fishing mortality, and far to the south, Gray Snapper in Guatemala were characterized as small with an accompanying high $k$ value. Lastly, the variation in the population along the GoM coast of Florida was mostly explained by low fishing mortality.

## Condition Indices

Monthly values for the condition indices were generally available from March through November for males and May through November for females, although sample sizes were limited in the spring and fall compared to the summer and no intraperitoneal fat samples were taken in September for females and March and November for males. No significant differences were found for either sex among monthly pairwise comparisons for $K_{rel}$ (Figures 13 and 14; Table 12). Among monthly pairwise comparisons for male GSI, the greatest values occurred in June and July and were generally greater in the summer months (June, July, August) than in the spring (May) and fall (October) (Figure 15). Female GSI increased from June through August, with an overall peak in August, and declined from August through November (Figure 16; Table 13). A model could not be fit to male and female IPFI, and general trends were therefore observed over the raw monthly mean values. As expected, IPFI trended in the opposite direction compared to GSI, decreasing from spring to summer and increasing from summer to fall (Figures 17 and 18). Overlaid plots of GSI and IPFI by sex displayed these diverging trends in the summer, suggesting support for the height of the spawning season between July and August (Figures 19 and 20).

## Histological Processing and Phase Distributions

Gonadal histology samples were taken from 182 females, 176 males, and 6

individuals that were later microscopically examined as undifferentiated (Table 14).

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. GE subphases could only be assessed for 126 of

153 male gonads in the spawning capable phase, and 20 of 119 females were removed

from daily spawning fraction calculations because the presence of POFs was

indeterminable. Additionally, no POFs were observed within females in the actively

spawning subphase, indicating that Gray Snapper do not spawn daily.

Further delineation of the spawning season was conducted by partitioning

histology samples by reproductive phase each month. The progression of gonadal

development could be tracked by the sequential appearance of phases as well as their

proportions relative to each other. The single male Gray Snapper captured in April was

developing (Figure 21). Spawning capable males dominated the months of May through

September, although only one fish each was sampled in May and September. The

regressing phase was detected, albeit at low levels, in July and August. Regressing and

regenerating males became more prevalent in the month of October accompanied by a

decline in spawning capable males. Closer examination of the GE subphases highlights a

peak in spawning in July based on the rise of the mid GE and late GE subphases (Figure

22). Males in the early GE subphase make up a majority (54.5%) of the samples in

August and both lone fish sampled in September and October, suggesting that at least some portion of the male spawning population continues to develop past the July peak.

The four female Gray Snapper caught in May were split evenly between the developing and spawning capable phases (Figure 23), with one fish exhibiting POFs. Early developing, developing, and spawning capable females were found in June, along with the first actively spawning fish. By July and August, virtually all females were spawning capable or actively spawning, and active spawners composed a majority in August. No data were collected in September. A transition to the regressing and regeneration phases occurred in October and November; three immature females were also captured in October, although these were sublegal fish that had not yet recruited to the fishery but were spearfished as part of a general collection survey. The results from both sexes, similar to supporting data from the GSI and IPFI, indicate that Gray Snapper spawning activity begins in May, reaches its apex between July and August, and largely ceases by October. Gonadal development appears slightly asynchronous between sexes as evidenced by the temporal discrepancy in the maxima of their spawning capable and actively spawning phases, with males reaching reproductively active status earlier and remaining spawning capable longer as well. Accordingly, for the purpose of comparisons to past studies and because female data are predominantly used in the calculation of spawning metrics, the peak in August was adopted as the overall spawning peak.

## Maturity

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

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individuals were undifferentiated, while others had just begun to develop signs of spermatogonia or oogonia among undifferentiated cells. Estimates of maturity illustrate earlier maturation in males than females. Male $L_{50}$ and $L_{90}$ were determined to be 181 (155 – 196; 95% CI) and 215 (193 – 229; 95% CI) mm, respectively, whereas female $L_{50}$ and $L_{90}$ were 273 (255 – 292; 95% CI) and 354 (312 – 390; 95% CI) mm (Figures 24 and 25; Table 15). Male $A_{50}$ and $A_{90}$ were determined to be <1.0 and 1.4 (1.0 – 1.9; 95% CI) years, respectively, whereas female $A_{50}$ and $A_{90}$ were 2.0 (1.7 – 2.4; 95% CI) and 3.6 (2.5 – 4.6; 95% CI) years (Figures 26 and 27; Table 16). 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 to females, which continue to mature throughout the transition to offshore habitat (Figures 28 and 29).

**Female Spawning Dynamics**

Females with spawning markers were present in May, July, and August, but not in June. Daily spawning fractions for these three months were 0.18 (0.02 – 0.54; 95% CI), 0.25 (0.17 – 0.35; 95% CI), and 0.50 (0.31 – 0.63; 95% CI), respectively (Figure 30; Table 17). Because no data were collected for September, two assumptions were made in substituting the July daily spawning fraction confidence interval to generate lower and upper end estimates of spawning interval and spawning frequency. First, based on

Fitzhugh et al. (2017), it was assumed that spawning activity decreased but still persisted in the month following peak spawning, with peak spawning found here to occur in August based on female condition indices and reproductive phase distributions. Second, it was assumed that all spawning concluded at the end of September due to the absence of spawning capable and actively spawning females in October. Given these points, the spawning interval was estimated to be 3.9 to 4.5 days, and the spawning frequency was estimated to be 28.7 to 33.4 events across 130 days, beginning on May 24 and ending on September 30.

The effects of age and length on daily spawning fraction were also explored. Daily spawning fraction was found to increase from 0.14 (0.06 – 0.27; 95% CI) for females in the initial 300-399 mm size class to 0.30 when the 500-599 (0.17 – 0.45; 95% CI) and 600-699 (0.14 – 0.48; 95% CI) mm size classes were attained, after which a decline was seen in larger fish (Figure 31; Table 18). Only five fish were sampled in the 700-799 mm size class, leading to considerable uncertainty surrounding this estimate. Daily spawning fraction increased continually with age, from 0.17 (0.09 – 0.27; 95% CI) for females ages 3 through 5 to 0.31 (0.12 – 0.53; 95% CI) for females ages 16 through 25 (Figure 32; Table 19). However, statistically significant differences were not found in any of these comparisons between age or length intervals (Tables 20 and 21).

# DISCUSSION

Little is known about the Gray Snapper fishery in Alabama and Mississippi despite the species' popularity as a gamefish throughout other states in the vicinity, and insight into this population has been recommended in a federal assessment (GMFMC 2019c). In addition to supplementing management data, the unique environmental conditions surrounding this area afford the opportunity to evaluate the context behind patterns in growth, mortality, and reproduction. By introducing the first comprehensive life history survey of this species in the northcentral GoM, this study will assist in the interpretation of life history characteristics at the population level and improve our ability to manage the stock.

Age and growth were defined using the VBGF, which has been used exclusively in previous studies of this species but has not been compared to other models that are also relevant in describing the growth of fishes. Using pooled sex data, the Gompertz and logistic functions were outperformed by the VBGF in terms of ΔAIC, supporting the VBGF as the optimum model in the northcentral GoM. Among distinct geographic populations, estimates from Guatemala (Andrade and Santos 2019) represent one end of the extreme in which growth is elevated but fish are comparatively small, while estimates from Louisiana (Fischer et al. 2005) and the northeastern coast of Florida (Burton 2001) represent the other end in which fish grow to be much larger. Here, $L_\infty$ falls in the upper

portion of these values and *k* falls in the lower portion, suggesting that a greater size is achieved following prolonged growth. However, it is important to note that the parameterization of the VBGF results in a correlation of $L_\infty$ 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.

Environmental differences in the northcentral GoM, particularly habitat quality, may be conducive to this enhanced growth. Gray Snapper are known to inhabit a variety of artificial structures in the AARZ (Gregalis et al. 2012), which is consistent with previous characterizations that demonstrate artificial reef usage (Dance et al. 2011; Ajemian et al. 2015) and an association with vertical relief (Campbell et al. 2017; Bacheler et al. 2020). The dense assemblage of artificial reefs in the AARZ may also be related to growth via additional pathways such as prey composition and availability (Szedlmayer and Lee 2004; Simonsen et al. 2015). The presence of large fish in this study was likely also facilitated by the sampling methods that were employed. Tournaments, particularly the ADSFR, were advantageous in obtaining the largest, and thus the most uncommon, size class in the population, potentially leading to an increased estimate of $L_\infty$ and decreased estimate of *k* in relation to the true population parameters with overrepresentation of this size class in the data. 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 issue 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.

Male Gray Snapper were found to have a significantly greater $L_\infty$ than females based on the sex-specific VBGF curves, which showed growth trajectories that begin to diverge at approximately three to four years of age, although no such difference was seen in the weight-length relationship. 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 GoM (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 site-specific. Further improvements in successive modeling of sex-specific growth should be pursued in anchoring the curves with age-0 juveniles sexed through histology. Because $k$ measures the rate of convergence to $L_\infty$ (Schnute and Fournier 1980), the absence of the age-0 class in the sex-specific curves flattened the earliest segment of growth, resulting in smaller values of $k$ and larger estimates of $L_\infty$ due to their correlation. Additionally, modeling the earliest stages of life is likely to become increasingly important over time. Warmer water temperatures may stimulate faster growth of juveniles at lower latitudes (Denit and Sponaugle 2004), a finding that has been corroborated by manipulative laboratory experiments (Wuenschel et al. 2004). Given the expanse of the GoM, differential growth

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inshore extrapolated over several years prior to adult recruitment to more stable water temperatures offshore could potentially alter growth curve trajectories and may become more pronounced with projected warming.

It has been previously demonstrated that Gray Snapper lay down a single annulus per year, but the timing of this event varies broadly by location. In the present study, annulus formation was found to begin in April and peak 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. However, annulus formation in Louisiana, which is the most similar in latitude to this study, stands as an outlier in that it occurs in the winter (Fischer et al. 2005) and suggests that seasonal temperatures could also have a metabolic influence in some northern populations, although these results may be inconclusive due to low sample sizes and monthly gaps in the data.

Fishery-dependent estimates of $Z$ based on unweighted linear regression were among the lowest in the GoM. This resulted in low values of $F$ in conjunction with $M$

from the Hoenig longevity-mortality relationship. Generally, it appears that $Z$ for Gray

Snapper is greatly associated with the degree of fishing pressure and potential 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 shifting 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 northcentral GoM, with maximum ages of 28 and 27,

respectively, and nearly identical values of $Z$. The relatively large $L_\infty$ from the VBGF

compared to regional populations with younger maximum ages and higher pressure can

also be interpreted in this context, although this could again possibly be due to the

aforementioned tournament selectivity effect. 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

predominantly a sporadic and incidental catch, as opposed to a targeted species, in this

area.

The use of unweighted linear regression and the Hoenig longevity-mortality

relationship 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$_{nls}$ estimator for $M$ (Then et al. 2015) yield higher non-

tournament 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 the complete fishery-dependent $Z$ and the non-tournament fishery-dependent $Z$ that illustrate the consequences of tournament selectivity. The length-based estimator for the ROV dataset, intended as a contrast without fishery-dependent bias, produced the greatest $Z$ and aligned most closely with the non-tournament fishery-dependent $Z$, supporting exclusion of the tournament data. These 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.

Variation in Gray Snapper life history is frequently attributed to spatial differences in fishing pressure and climate, which was generally seen in the principal component analysis. Such comparisons are important because they provide opportunities to inspect multiple causal mechanisms that may be driving this variation. Due to low mortality, Gray Snapper in Alabama and Mississippi are capable of surviving to their full demographic potential and do not display signs of age truncation as shown in the Atlantic coast of south Florida (Burton 2001), where fishing is recognized to play a large role in diminishing population structure. The uninhibited size and age attained by the population in this study, as well as others in Louisiana (Fischer et al. 2005) and the Atlantic coast of north Florida (Burton 2001), are therefore probably more similar to more northerly

populations of Gray Snapper. The opposite can be seen in the Caribbean, where small fish abound and demonstrate the intrinsic plasticity of this species in a warmer environment with minimal confounding effects of fishing on growth (Andrade and Santos 2019). Conclusions for the GoM coast of Florida were more ambiguous because Gray Snapper were collected across three different regions with distinct demographics (Allman and Goetz 2009). Increasing size with latitude has been documented in other marine fish populations (Blanck and Lamouroux 2007; Fisher et al. 2010) and appears to be rooted in energetic advantages conferred from enhanced thermal tolerance, most notably over the winter (Cargnelli and Gross 1997). Overall, analysis of these patterns could hold some predictive utility in interpreting the demography of populations affected by more moderate environmental factors. Prospectively for the northcentral GoM, 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).

This study presents the first concurrent sex-specific maturity estimates known for Gray Snapper. Maturity appears dimorphic and is attained sooner in males than in females. Although most males and a portion of females are technically mature prior to moving offshore based on comparisons of these estimates against sample frequency distributions, 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). 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 may be inherent to the regional life history of this population. Because full recruitment to the fishery occurs at the age of 4, 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 such as SPR 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 stock assessment provides the only comparable results and estimated female 50% maturity at 253 mm fork length and 2.3 years in Florida (Fitzhugh et al. 2017), which lie within the confidence intervals for the size and age estimates here. However, no males were included in this study. Therefore, these results comprise the most thorough and up-to-date information on Gray Snapper maturity and can be used as a comparative baseline moving forward.

The beginning and end of the spawning season were outlined using various condition indices and refined by examining the distribution of reproductive phases. Monthly $K_{rel}$ observations did not display any noticeable patterns, while GSI and IPFI were more informative and roughly indicate a summer spawning season between May and August/September that fall within previous estimates that begin in April through June and end in September (Barbieri and Colvocoresses 2003; Denit and Sponaugle 2004; Fitzhugh et al. 2017). However, it should be noted that the abrupt drop in female GSI

from August to September is a possible artifact of low sample size since there is typically a prolonged drawdown in spawning as opposed to immediate cessation (Fitzhugh et al. 2017). While no active spawners were found among females sampled in May through June, POFs were identified in one spawning capable female in May, confirming very recent spawning. Thus, while late spring is characterized more by the early stages of ovarian development, there is some evidence that spawning can still take place at this time. In both sexes, the presence of the regressing and regenerating phases in October marked the discontinuation of spawning for the year. In general, limited sample sizes at the earliest and latest months of the dataset warrant further collection efforts to fully substantiate these findings.

For both male and female Gray Snapper, the middle of the summer corresponded to a simultaneous elevation in GSI and reduction in IPFI as well as the rise of the spawning capable phase, signaling the consumption of energy reserves allocated to gonadal development with the progression of spawning. The female spawning peak is assumed to occur in August and lagged the male spawning peak by at least one month, although the lack of samples in September precludes a definitive conclusion and necessitates further sampling. Similar discrepancies in timing have been documented at two separate locations in Florida (Barbieri and Colvocoresses 2003) and may be explained by the higher energy requirements attached to female spawning activity (Schwartzkopf and Cowan Jr. 2017), especially compared to the relatively rapid and complete development seen in males. The August spawning peak in females is also among the latest seen temporally and could possibly be a result of a latitudinal correlation with temperature. Other spawning peaks, albeit predicted via a range of methods, have

been seen as early as June in warmer waters (Barbieri and Colvocoresses 2003; Andrade and Santos 2019) and as late as July in more temperate waters (Allman and Grimes 2002; Denit and Sponaugle 2004; Fitzhugh et al. 2017). Domeier et al. (1996) also recorded a maximum in August in the Florida Keys but remains the oldest study in comparison, when sea surface temperatures were historically cooler on average (Banzon et al. 2016). This correlation is not surprising given that many snapper species also reproduce in the summer (Grimes 1987) and presumably react to temperature as a significant environmental cue (Arnold et al. 1978).

Monthly daily spawning fraction values were irregular but still supported a spawning peak in August. Although no significance was detected in spawning fraction by size or age, both analyses still exhibited general upward trends in magnitude. It is well-established that reproductive output typically increases throughout the lifetime of females. Specifically, the reproductive value of progressively older fish is disproportionate due to the nonlinear increase in fecundity as well as improved egg quality that promotes larval survival (Hixon et al. 2014). The abundance of these females at the terminal end of the distribution is critical in the sustained maintenance of the stock because their enhanced reproductive capabilities allow the stock to better weather through and rebound from adverse conditions (Hixon et al. 2014; Lowerre-Barbieri et al. 2015). Interestingly, a dip in spawning fraction was observed after the penultimate length interval and could imply a decline at the extremities of size, although this is a limited conjecture considering only five females were captured in the last interval. No such decline was seen with age, suggesting that this effect, if legitimate, could be connected to somatic growth more so than longevity.

The resultant spawning interval of 3.9 to 4.5 days and spawning frequency of 28.7 to 33.4 batches per season reflect reduced spawning compared to the estimates of 3.8 days and 37.0 batches per season in Florida for the stock assessment (Fitzhugh et al. 2017). As seen across many species worldwide, the difference in these metrics may be part of a geographic cline in which reproductive adaptations have led to the poleward evolution of larger fish with less frequent, yet more prolific, spawning events throughout a contracted season (Vila-Gispert et al. 2002). Andrade and Santos (2019) noted greater maximum values of GSI in Gray Snapper to the north, a pattern that is consistent with the present study and further supports the concept of latitudinally divergent reproductive strategies that balance spawning interval and frequency, season length, and productivity. The uncertainty around these calculations of spawning dynamics is due in part to the absence of a spawning fraction in September, but other factors may contribute to this as well. For example, past work has distinguished proliferation in spawning activity centering around certain lunar phases (Domeier et al. 1996; Denit and Sponaugle 2004), which could bias the distribution of spawning markers depending on the timing of sampling. Thus, the inclusion of lower and upper limits to these estimates should be viewed as approximate guidelines in management pending clarification of the accuracy of these measurements.

# CONCLUSIONS AND RECOMMENDATIONS

Current population dynamics and low harvest levels indicate that Gray Snapper in the northcentral GoM are relatively underexploited and can tolerate additional fishing without undue detriment to the fishery. Therefore, the present regulations are likely sufficient for promoting continued sustainability. However, given that the stock is essentially in its virgin state, and knowing the effects of intensive pressure in other neighboring stocks, any signs of population-level change should be followed by closer monitoring and precautionary management. This study is imperative in this regard because it provides baseline data for comparisons in understanding when changes to the fishery necessitate subsequent actions. My findings of a locally robust resource also run counter to the conclusion by the GMFMC SSC that the overall GoM stock is overfished following the inaugural assessment of this species in 2018 and suggest that the most effective decisions regarding the fishery should be applied on an individual, regional basis. The underrepresentation of Gray Snapper outside of the eastern GoM in the assessment will become an increasingly important issue as populations are expected to expand and grow throughout the GoM with rising temperatures. Continued monitoring is recommended considering this potentially emergent fishery to ensure the sustainable harvest of this resource and for inclusion of data in future evaluations of the GoM stock.

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**APPENDICES**

**Appendix A: Tables**

Table 1. Reported estimates of von Bertalanffy growth parameters and mortality from Gray Snapper otolith-based age and growth studies (Sex: P = pooled, M = male, F = female).

*Study uses back-calculated lengths for growth parameter estimates; length ranges are given from empirical data.

**Pooled growth parameter estimates use recreational and commercial data, sex-specific growth parameters estimates use only recreational data. All estimates are reported for $t_0$ constrained and unconstrained through 0.

| Study | Area | Age Range (yr) | Length Range (mm TL) | n | Sex | $L_\infty$ (mm) | $k$ (yr⁻¹) | $t_0$ | Dimorphic Growth? | Z | M |
|---|---|---|---|---|---|---|---|---|---|---|---|
| Johnson et al. 1994* | East FL, south FL, LA | 1-25 | 236-764 | 432 | P | 673.33 | 0.1552 | -1.0655 | | 0.17-0.26 | 0.20-0.32 |
| | South FL to LA | 1-23 | --- | 107 | M | 687.99 | 0.1695 | -1.0088 | --- | --- | --- |
| | South FL to LA | 1-25 | --- | 164 | F | 662.28 | 0.1665 | -1.1986 | | --- | --- |
| Burton 2001* | East FL – north | 1-24 | 181-760 | 528 | P | 717 | 0.17 | -0.001 | | 0.35 | 0.18-0.43 |
| | East FL – south | 2-15 | 167-644 | 729 | P | 625 | 0.13 | -1.33 | No difference | 0.94 | 0.29-0.38 |
| | East FL | --- | --- | --- | M | 697 | 0.18 | 0.49 | | --- | --- |
| | East FL | --- | --- | --- | F | 768 | 0.15 | 0.16 | | --- | --- |
| Barbieri and Colvocoresses 2003 | East FL, south FL | 1-14 | 71-670 | 2062 | P | 441.6 | 0.35 | -0.41 | --- | --- | --- |
| Fischer et al. 2005 | LA | 1-28 | 222-756 | 833 | P | 656.4 | 0.22 | --- | | 0.16-0.17 | 0.15-0.51 |
| | LA | 1-28 | 222-732 | 441 | M | 655.4 | 0.23 | --- | F > M | --- | --- |
| | LA | 1-28 | 254-756 | 387 | F | 657.3 | 0.21 | --- | | --- | --- |
| Allman and Goetz 2009** | South FL to northwest FL | 2-26 | 254-724 | 1096 | P | 559 | 0.17 | -2.23 | | 0.22 | 0.17-0.36 |
| | South FL to northwest FL | 2-26 | 254-724 | 1096 | P | 506 | 0.33 | 0 | | 0.22 | 0.17-0.36 |
| | South FL to northwest FL | 26 | --- | 286 | M | 683 | 0.11 | -2.63 | M > F (rec. only) | --- | --- |
| | South FL to northwest FL | 26 | --- | 286 | M | 557 | 0.26 | 0 | | --- | --- |
| | South FL to northwest FL | 19 | --- | 297 | F | 605 | 0.12 | -3.40 | | --- | --- |
| | South FL to northwest FL | 19 | --- | 297 | F | 497 | 0.31 | 0 | | --- | --- |
| Andrade and Santos 2019 | Caribbean - Guatemala | 0-10 | 190-550 | 357 | P | 350 | 0.56 | -0.7 | No difference | 0.7 | 0.6 |
| Kim 2022 | AL, MS | 0-27 | 29-774 | 886 | P | 687.43 | 0.18 | -0.66 | | 0.16-0.38 | 0.17-0.43 |
| | AL, MS | 1-25 | 155-774 | 362 | M | 731.52 | 0.15 | -1.34 | M > F | --- | --- |
| | AL, MS | 1-27 | 166-763 | 353 | F | 704.28 | 0.14 | -1.62 | | --- | --- |

Table 2. Reported estimates of Gray Snapper spawning and maturity (Sex: P = pooled, M = male, F = female).

| Study | Area | Length | Sex | $L_{50}$ | $L_{90}$ | $A_{50}$ | $A_{90}$ | Spawning Period | Methods |
|-------|------|--------|-----|-----|-----|-----|-----|-----------------|---------|
| **Domeier et al. 1996** | South FL | Standard | P | --- | 200 | --- | --- | Late May – early September | GSI, histology |
| **Allman and Grimes 2002** | Southwest FL to northwest FL | --- | P | --- | --- | --- | --- | May – September | Histology, juvenile back-calculation |
| **Barbieri and Colvocoresses 2003** | East FL, south FL | --- | P | --- | --- | --- | --- | ~April – September | GSI |
| **Tzeng et al. 2003** | NC | --- | --- | --- | --- | --- | --- | ~May – September | Juvenile back-calculation |
| **Denit and Sponaugle 2004** | South FL to NC | --- | --- | --- | --- | --- | --- | Late June – early October | Juvenile back-calculation |
| **Fitzhugh et al. 2017** | FL Gulf waters | Fork | F | 253 | 362 | 2.3 | 5.2 | May – September | GSI, histology |
| **Andrade and Santos 2019** | Caribbean - Guatemala | Total | P | 311 | --- | 3.6 | --- | April – September | GSI, macroscopic observation |
| **Kim 2022** | AL, MS | Total | M<br>F | 181<br>273 | 215<br>354 | <1.0<br>2.0 | 1.4<br>3.6 | ~May – August/September | GSI, IPF, histology |

Table 3. Total Gray Snapper sampled by month and year.

| Year | Jan | Feb | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct | Nov | Dec | Total *n* |
|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----------|
| 2011 | 0 | 0 | 0 | 0 | 0 | 0 | 15 | 0 | 0 | 0 | 0 | 0 | 15 |
| 2012 | 0 | 0 | 0 | 0 | 0 | 0 | 8 | 0 | 0 | 0 | 0 | 0 | 8 |
| 2013 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2014 | 0 | 0 | 0 | 0 | 0 | 0 | 31 | 0 | 1 | 0 | 0 | 0 | 32 |
| 2015 | 0 | 0 | 0 | 0 | 0 | 0 | 27 | 0 | 0 | 0 | 0 | 0 | 27 |
| 2016 | 0 | 0 | 0 | 0 | 0 | 0 | 43 | 0 | 0 | 0 | 0 | 0 | 43 |
| 2017 | 0 | 0 | 1 | 0 | 0 | 0 | 20 | 0 | 0 | 0 | 2 | 0 | 23 |
| 2018 | 0 | 0 | 0 | 0 | 2 | 2 | 49 | 5 | 98 | 28 | 8 | 0 | 192 |
| 2019 | 6 | 0 | 36 | 5 | 5 | 108 | 107 | 26 | 26 | 19 | 5 | 0 | 343 |
| 2020 | 0 | 0 | 0 | 0 | 10 | 55 | 92 | 35 | 0 | 2 | 0 | 0 | 194 |
| 2021 | 0 | 0 | 0 | 0 | 9 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 9 |
| **Total *n*** | 6 | 0 | 37 | 5 | 26 | 165 | 392 | 66 | 125 | 49 | 15 | 0 | 886 |

Table 4. Total Gray Snapper sampled by gear type and survey type (BS = benthic sled, HL = hook-and-line, SP = spearfishing, TP = trap, TR = trawl, VL = vertical longline).

| Gear Type | Fishery-dependent | Scientific/Collection Surveys | Total $n$ |
|-----------|-------------------|-------------------------------|-----------|
| BS | 0 | 98 | 98 |
| HL | 492 | 204 | 696 |
| SP | 54 | 21 | 75 |
| TP | 0 | 12 | 12 |
| TR | 0 | 1 | 1 |
| VL | 0 | 4 | 4 |
| **Total $n$** | 546 | 340 | 886 |

Table 5. Linear regression conversion formulas among standard, fork, and total lengths.

| Regression Conversion ($y = ax + b$) | $n$ | Standard Error (a) | Standard Error (b) | $r^2$ |
|---|---|---|---|---|
| SL = 0.86FL - 7.32 | 880 | 1.50E-03 | 0.61 | 0.9973 |
| SL = 0.81TL - 6.45 | 886 | 1.53E-03 | 0.65 | 0.9969 |
| FL = 1.16SL + 9.44 | 880 | 2.02E-03 | 0.69 | 0.9973 |
| FL = 0.94TL + 0.86 | 880 | 6.81E-04 | 0.29 | 0.9995 |
| TL = 1.23SL + 9.10 | 886 | 2.31E-03 | 0.79 | 0.9969 |
| TL = 1.06FL - 0.74 | 880 | 7.67E-04 | 0.31 | 0.9995 |

Table 6. Multi-model length-age growth comparisons ranked by AIC.

| Model | Parameter | Estimate | 95% LCI | 95% UCI | AIC | ΔAIC |
|---|---|---|---|---|---|---|
| von Bertalanffy | $L_\infty$ | 687.43 | 676.45 | 698.84 | 9321.82 | 0.00 |
| | $k$ | 0.18 | 0.17 | 0.19 | | |
| | $t_0$ | -0.66 | -0.75 | -0.58 | | |
| Gompertz | $L_\infty$ | 655.14 | 645.76 | 664.53 | 9529.92 | 208.10 |
| | $g_i$ | 0.30 | 0.29 | 0.31 | | |
| | $t_i$ | 1.84 | 1.75 | 1.92 | | |
| Logistic | $L_\infty$ | 640.46 | 631.69 | 649.49 | 9684.61 | 362.79 |
| | $g_{-\infty}$ | 0.42 | 0.40 | 0.44 | | |
| | $t_i$ | 3.09 | 2.98 | 3.20 | | |

Table 7. Sex-specific von Bertalanffy growth model parameter estimates.

| Sex | Parameter | Estimate | 95% LCI | 95% UCI | *p*-value |
|---|---|---|---|---|---|
| Male | $L_\infty$ | 731.52 | 712.01 | 753.68 | <2E-16 |
| | $k$ | 0.15 | 0.13 | 0.16 | <2E-16 |
| | $t_0$ | -1.34 | -1.65 | -1.06 | <2E-16 |
| Female | $L_\infty$ | 704.28 | 679.81 | 732.96 | <2E-16 |
| | $k$ | 0.14 | 0.12 | 0.16 | <2E-16 |
| | $t_0$ | -1.62 | -2.00 | -1.29 | <2E-16 |

Table 8. Nested likelihood ratio tests to determine significance of $L_\infty$, $k$, and $t_0$ between sexes.

| Model Sex-specific Parameters | Subset Sex-specific Parameters | Residual d.f. | RSS | *p*-value |
|---|---|---|---|---|
| All | $L_\infty, k$ | 709 | 1485775 | 0.236 |
| | $L_\infty, t_0$ | 709 | 1483200 | 0.675 |
| | $k, t_0$ | 709 | 1487730 | 0.126 |
| $L_\infty, t_0$ | $L_\infty$ | 710 | 1489947 | 0.073 |
| | $t_0$ | 710 | 1526567 | 6.13E-06 |
| $L_\infty$ | None | 711 | 1534690 | 4.54E-06 |

Table 9. Weight-length growth model parameter estimates.

| Model | Parameter | Estimate | 95% LCI | 95% UCI |
|---|---|---|---|---|
| Pooled | $a$ | 2.13E-08 | 2.02E-08 | 2.24E-08 |
| | $b$ | 2.93 | 2.92 | 2.93 |
| Male | $a$ | 1.45E-08 | 1.26E-08 | 1.66E-08 |
| | $b$ | 2.99 | 2.97 | 3.01 |
| Female | $a$ | 1.60E-08 | 1.34E-08 | 1.91E-08 |
| | $b$ | 2.97 | 2.94 | 3.00 |

Table 10. Instantaneous total mortality rate and annual mortality rate estimates (FD (complete) = fishery-dependent with combined tournament and non-tournament data, FD (non-tournament) = fishery-dependent with only non-tournament data, ROV = remotely operated vehicle).

| Dataset | n | Method | Parameter | Estimate | 95% LCI | 95% UCI |
|---|---|---|---|---|---|---|
| FD (complete) | 546 | Unweighted linear regression | $Z$ | 0.17 | 0.14 | 0.21 |
| | | | $A$ | 0.16 | 0.13 | 0.19 |
| | | Weighted linear regression | $Z$ | 0.16 | 0.13 | 0.19 |
| | | | $A$ | 0.15 | 0.12 | 0.18 |
| | | Chapman-Robson | $Z$ | 0.17 | 0.15 | 0.20 |
| | | | $A$ | 0.16 | 0.14 | 0.18 |
| FD (non-tournament) | 180 | Unweighted linear regression | $Z$ | 0.16 | 0.05 | 0.27 |
| | | | $A$ | 0.15 | 0.05 | 0.24 |
| | | Weighted linear regression | $Z$ | 0.30 | 0.07 | 0.53 |
| | | | $A$ | 0.26 | 0.07 | 0.41 |
| | | Chapman-Robson | $Z$ | 0.38 | 0.20 | 0.57 |
| | | | $A$ | 0.32 | 0.18 | 0.43 |
| ROV | 413 | Beverton-Holt | $Z$ | 0.41 | 0.35 | 0.48 |
| | | | $A$ | 0.34 | 0.29 | 0.38 |

Table 11. Instantaneous natural mortality rate estimates (FD (complete) = fishery-dependent with combined tournament and non-tournament data, FD (non-tournament) = fishery-dependent with only non-tournament data).

| Dataset | $n$ | Method | Input Parameter | Input Parameter Value | $M$ |
|---|---|---|---|---|---|
| FD (complete) | 546 | Hoenig longevity-mortality | $t_{max}$ | 27 | 0.15 |
| | | Hoenig non-linear least squares | $t_{max}$ | 27 | 0.24 |
| | | Pauly | $L_\infty$ | 68.74 | 0.43 |
| | | | $k$ | 0.18 | |
| | | | $T$ (°C) | 23.8 | |
| FD (non-tournament) | 180 | Hoenig longevity-mortality | $t_{max}$ | 25 | 0.17 |
| | | Hoenig non-linear least squares | $t_{max}$ | 25 | 0.26 |
| | | Pauly | $L_\infty$ | 68.74 | 0.43 |
| | | | $k$ | 0.18 | |
| | | | $T$ (°C) | 23.8 | |

Table 12. Monthly male and female Le Cren relative condition factor pairwise comparisons matrix of *p*-values, respectively, using Kruskal-Wallis test and post hoc Dunn's test.

|  | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct |
|---|---|---|---|---|---|---|---|---|
| **Apr** | 1.000 |  |  |  |  |  |  |  |
| **May** | 1.000 | 1.000 |  |  |  |  |  |  |
| **Jun** | 1.000 | 1.000 | 1.000 |  |  |  |  |  |
| **Jul** | 1.000 | 1.000 | 1.000 | 0.103 |  |  |  |  |
| **Aug** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |  |  |  |
| **Sep** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |  |  |
| **Oct** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |  |
| **Nov** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |

|  | May | Jun | Jul | Aug | Sep | Oct |
|---|---|---|---|---|---|---|
| **Jun** | 1.000 |  |  |  |  |  |
| **Jul** | 1.000 | 0.266 |  |  |  |  |
| **Aug** | 1.000 | 0.207 | 1.000 |  |  |  |
| **Sep** | 1.000 | 1.000 | 1.000 | 1.000 |  |  |
| **Oct** | 1.000 | 1.000 | 1.000 | 0.400 | 1.000 |  |
| **Nov** | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |

Table 13. Monthly male and female gonadosomatic index pairwise comparisons matrix of *p*-values, respectively, using Kruskal-Wallis test and post hoc Dunn's test; significant *p*-values are highlighted.

|  | Mar | Apr | May | Jun | Jul | Aug | Sep | Oct |
|---|---|---|---|---|---|---|---|---|
| Apr | 1.000 |  |  |  |  |  |  |  |
| May | 1.000 | 1.000 |  |  |  |  |  |  |
| Jun | 1.000 | 1.000 | 0.046 |  |  |  |  |  |
| Jul | 1.000 | 1.000 | 4.13E-03 | 1.000 |  |  |  |  |
| Aug | 1.000 | 1.000 | 1.000 | 1.000 | 0.406 |  |  |  |
| Sep | 1.000 | 1.000 | 1.000 | 0.850 | 0.262 | 1.000 |  |  |
| Oct | 1.000 | 1.000 | 1.000 | 2.36E-05 | 2.99E-07 | 0.049 | 1.000 |  |
| Nov | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 | 1.000 |

|  | May | Jun | Jul | Aug | Sep | Oct |
|---|---|---|---|---|---|---|
| Jun | 1.000 |  |  |  |  |  |
| Jul | 0.767 | 2.92E-03 |  |  |  |  |
| Aug | 0.151 | 5.22E-03 | 1.000 |  |  |  |
| Sep | 1.000 | 1.000 | 1.000 | 0.475 |  |  |
| Oct | 1.000 | 0.200 | 3.54E-04 | 8.98E-05 | 1.000 |  |
| Nov | 1.000 | 0.697 | 0.018 | 3.68E-03 | 1.000 | 1.000 |

Table 14. Total Gray Snapper sampled for histology by month and sex, pooled across all years.

| Month | Male | Female | Undifferentiated | Total *n* |
|:---:|:---:|:---:|:---:|:---:|
| Jan | 0 | 0 | 0 | 0 |
| Feb | 0 | 0 | 0 | 0 |
| Mar | 0 | 0 | 0 | 0 |
| Apr | 1 | 0 | 0 | 1 |
| May | 4 | 6 | 0 | 10 |
| Jun | 52 | 45 | 4 | 101 |
| Jul | 77 | 87 | 2 | 166 |
| Aug | 29 | 27 | 0 | 56 |
| Sep | 3 | 8 | 0 | 11 |
| Oct | 10 | 7 | 0 | 17 |
| Nov | 0 | 2 | 0 | 2 |
| Dec | 0 | 0 | 0 | 0 |
| **Total *n*** | 176 | 182 | 6 | 364 |

Table 15. Sex-specific estimates for lengths at 50% maturity and 90% maturity.

| Sex | $n$ | $L_{50}$ | $L_{50}$ 95% LCI | $L_{50}$ 95% UCI | $L_{90}$ | $L_{90}$ 95% LCI | $L_{90}$ 95% UCI |
|---|---|---|---|---|---|---|---|
| Male | 176 | 181 | 155 | 196 | 215 | 193 | 229 |
| Female | 182 | 273 | 255 | 292 | 354 | 312 | 390 |

Table 16. Sex-specific estimates for ages at 50% maturity and 90% maturity.

| Sex | $n$ | $A_{50}$ | $A_{50}$ 95% LCI | $A_{50}$ 95% UCI | $A_{90}$ | $A_{90}$ 95% LCI | $A_{90}$ 95% UCI |
|---|---|---|---|---|---|---|---|
| Male | 176 | <1.0 | <1.0 | 1.0 | 1.4 | 1.0 | 1.9 |
| Female | 182 | 2.0 | 1.7 | 2.4 | 3.6 | 2.5 | 4.6 |

Table 17. Raw and daily spawning fraction estimates by month.

| Month | n | Total H | Total POF | Total Spawning Markers | Raw Spawning Fraction | Daily Spawning Fraction | Daily 95% LCI | Daily 95% UCI |
|---|---|---|---|---|---|---|---|---|
| May | 4 | 0 | 1 | 1 | 0.25 | 0.18 | 0.02 | 0.54 |
| Jun | 22 | 0 | 0 | 0 | 0.00 | 0.00 | 0.00 | --- |
| Jul | 53 | 4 | 15 | 19 | 0.36 | 0.25 | 0.17 | 0.35 |
| Aug | 14 | 7 | 3 | 10 | 0.71 | 0.50 | 0.31 | 0.63 |
| Sep | 0 | --- | --- | --- | --- | --- | --- | --- |
| Oct | 4 | 0 | 0 | 0 | 0.00 | 0.00 | 0.00 | --- |
| Nov | 2 | 0 | 0 | 0 | 0.00 | 0.00 | 0.00 | --- |

Table 18. Raw and daily spawning fraction estimates by length interval.

| Length Interval (mm TL) | n | Total H | Total POF | Total Spawning Markers | Raw Spawning Fraction | Daily Spawning Fraction | Daily 95% LCI | Daily 95% UCI |
|---|---|---|---|---|---|---|---|---|
| 300-399 | 30 | 3 | 3 | 6 | 0.20 | 0.14 | 0.06 | 0.27 |
| 400-499 | 29 | 4 | 4 | 8 | 0.28 | 0.19 | 0.10 | 0.33 |
| 500-599 | 21 | 2 | 7 | 9 | 0.43 | 0.30 | 0.17 | 0.45 |
| 600-699 | 14 | 2 | 4 | 6 | 0.43 | 0.30 | 0.14 | 0.48 |
| 700-799 | 5 | 0 | 1 | 1 | 0.20 | 0.14 | 0.02 | 0.49 |

Table 19. Raw and daily spawning fraction estimates by age interval.

| Age Interval (yr) | n | Total H | Total POF | Total Spawning Markers | Raw Spawning Fraction | Daily Spawning Fraction | Daily 95% LCI | Daily 95% UCI |
|---|---|---|---|---|---|---|---|---|
| 3-5 | 47 | 6 | 5 | 11 | 0.23 | 0.17 | 0.09 | 0.27 |
| 6-10 | 24 | 3 | 4 | 7 | 0.29 | 0.21 | 0.10 | 0.35 |
| 11-15 | 19 | 1 | 7 | 8 | 0.42 | 0.30 | 0.16 | 0.46 |
| 16-25 | 9 | 1 | 3 | 4 | 0.44 | 0.31 | 0.12 | 0.53 |

Table 20. Odds ratios of daily spawning fraction estimates between length intervals.

| Reference (mm TL) | Comparison (mm TL) | Odds Ratios | 95% LCI | 95% UCI | *p*-value |
|---|---|---|---|---|---|
| 300-399 | 400-499 | 1.52 | 0.46 | 5.32 | 0.495 |
| | 500-599 | 3.00 | 0.88 | 10.92 | 0.083 |
| | 600-699 | 3.00 | 0.75 | 12.45 | 0.120 |
| | 700-799 | 1.00 | 0.05 | 8.50 | 1.000 |
| 400-499 | 500-599 | 1.97 | 0.60 | 6.62 | 0.264 |
| | 600-699 | 1.97 | 0.51 | 7.62 | 0.320 |
| | 700-799 | 0.66 | 0.03 | 5.34 | 0.724 |
| 500-599 | 600-699 | 1.00 | 0.25 | 3.95 | 1.000 |
| | 700-799 | 0.33 | 0.02 | 2.76 | 0.361 |
| 600-699 | 700-799 | 0.33 | 0.01 | 3.04 | 0.376 |

Table 21. Odds ratios of daily spawning fraction estimates between age intervals.

| Reference (yr) | Comparison (yr) | Odds Ratios | 95% LCI | 95% UCI | p-value |
|---|---|---|---|---|---|
| 3-5 | 6-10 | 1.35 | 0.43 | 4.06 | 0.598 |
|  | 11-15 | 2.38 | 0.76 | 7.48 | 0.134 |
|  | 16-25 | 2.62 | 0.56 | 11.67 | 0.202 |
| 6-10 | 11-15 | 1.77 | 0.50 | 6.45 | 0.379 |
|  | 16-25 | 1.94 | 0.38 | 9.69 | 0.411 |
| 11-15 | 16-25 | 1.10 | 0.21 | 5.52 | 0.907 |

**Appendix B: Figures**
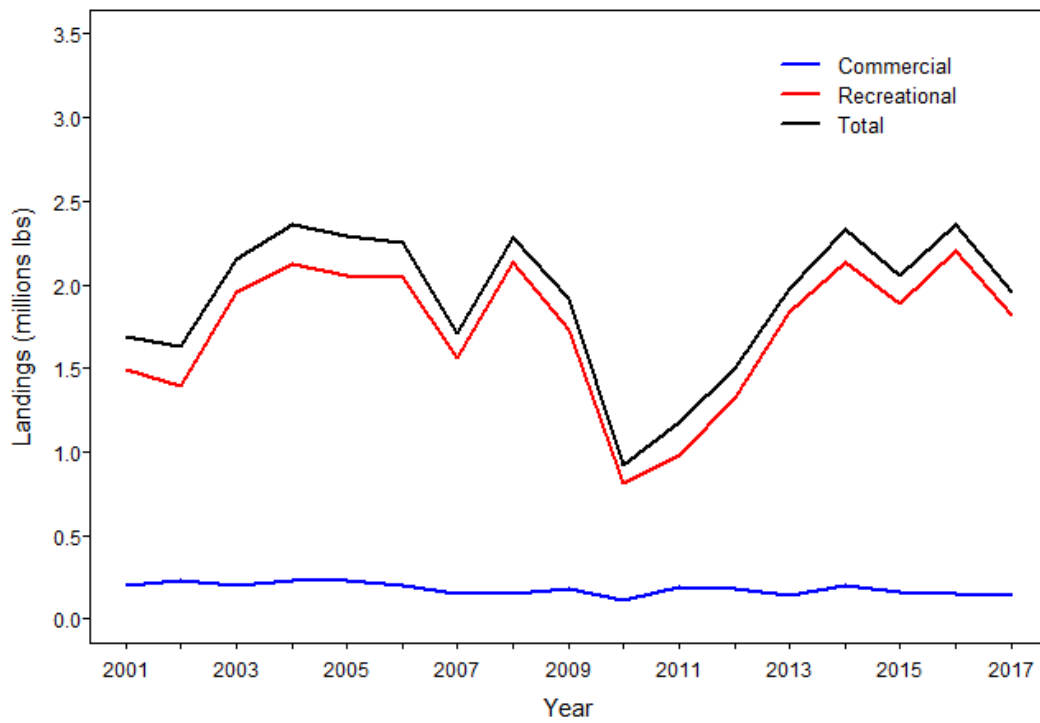
Figure 1. Gulf of Mexico Gray Snapper commercial and recreational landings. Source: SEFSC Recreational MRFSS ACL Data and Commercial ACL Data (via GMFMC 2019c).
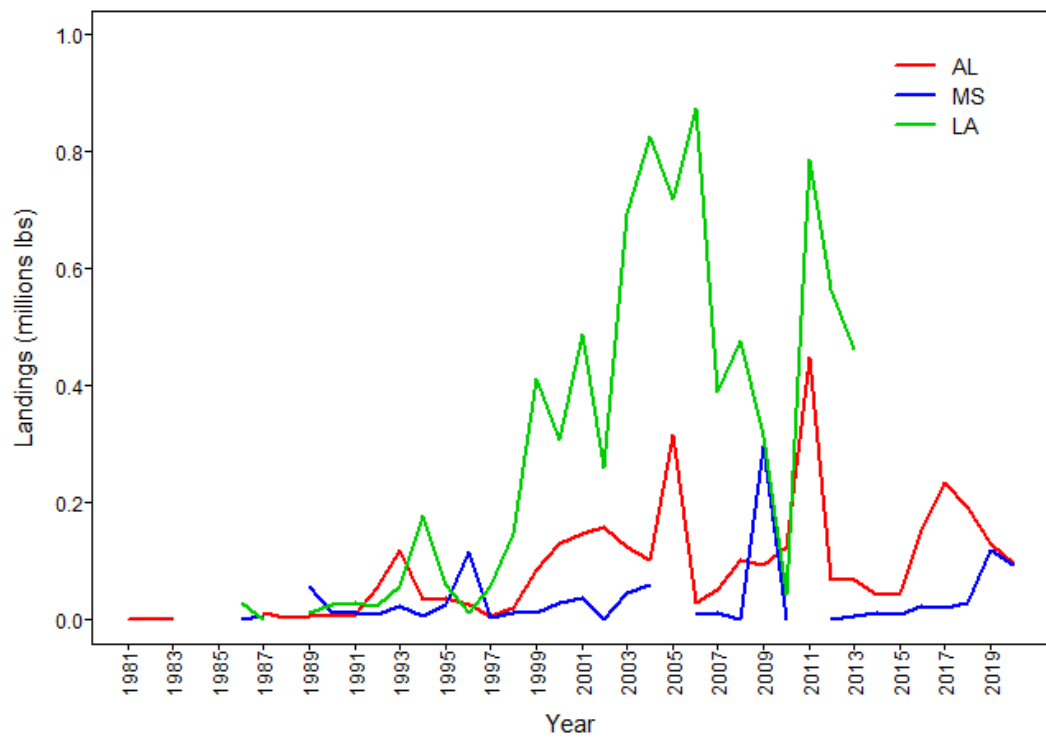
Figure 2. Northern Gulf of Mexico Gray Snapper recreational landings by state. Source: NOAA MRIP.
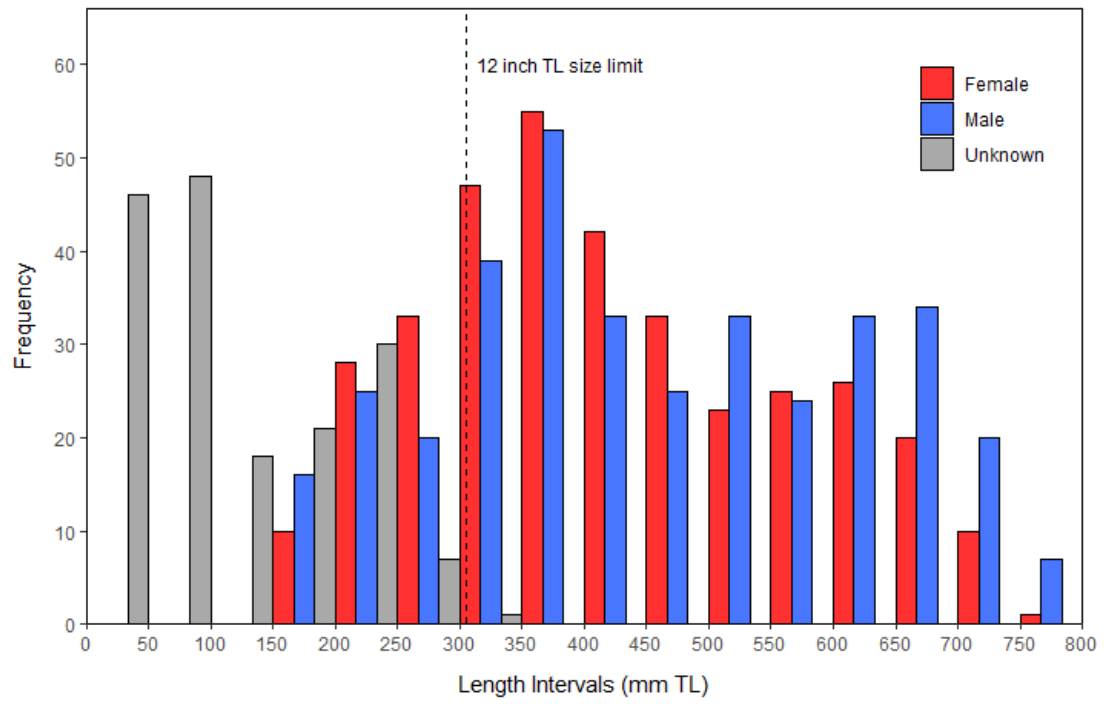
Figure 3. Sex-specific length frequency distribution.
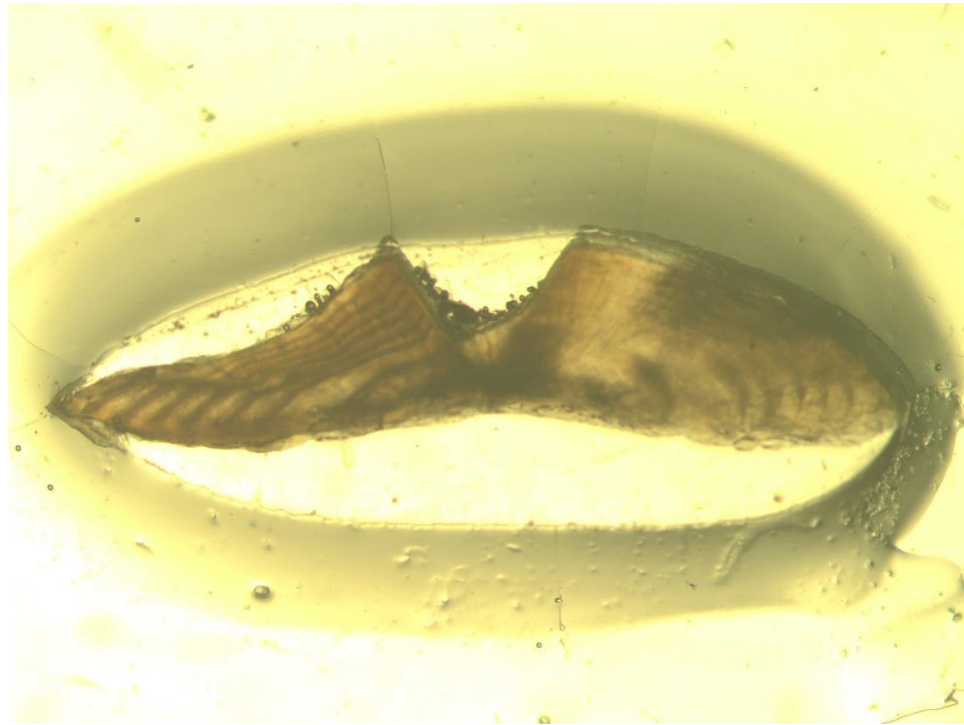
Figure 4. Sagittal otolith from an age-8 Gray Snapper; annuli are clearly visible on the left side of the otolith.
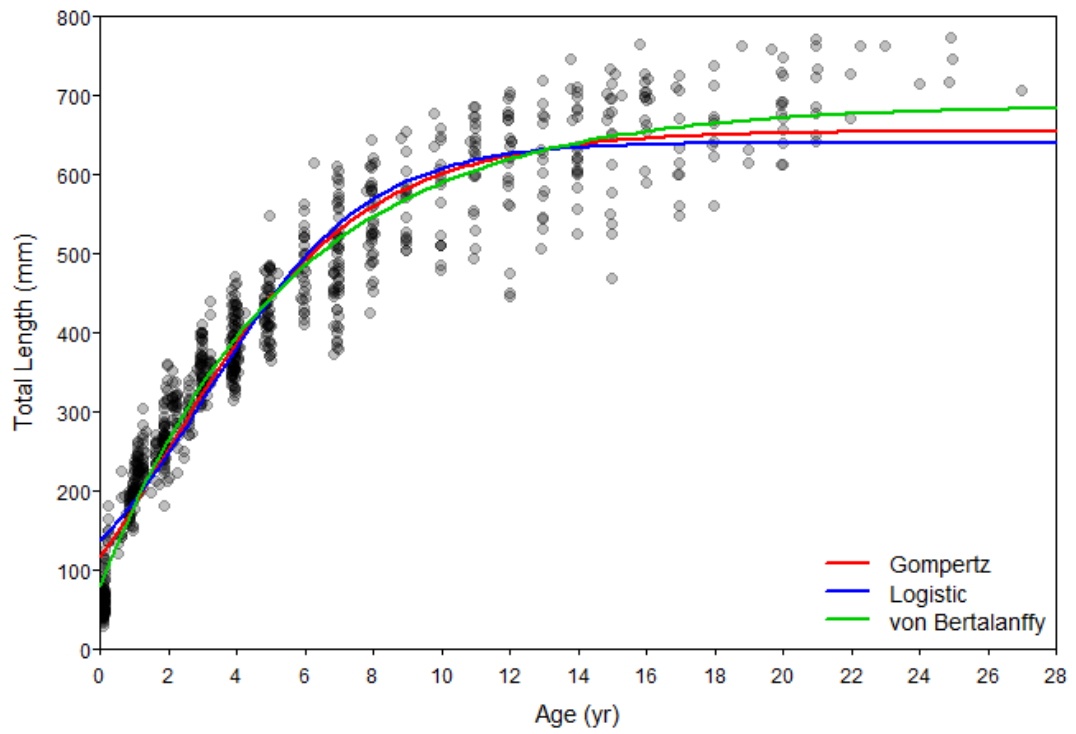
Figure 5. Multi-model length-age growth comparisons using Gompertz, logistic, and von Bertalanffy growth functions.
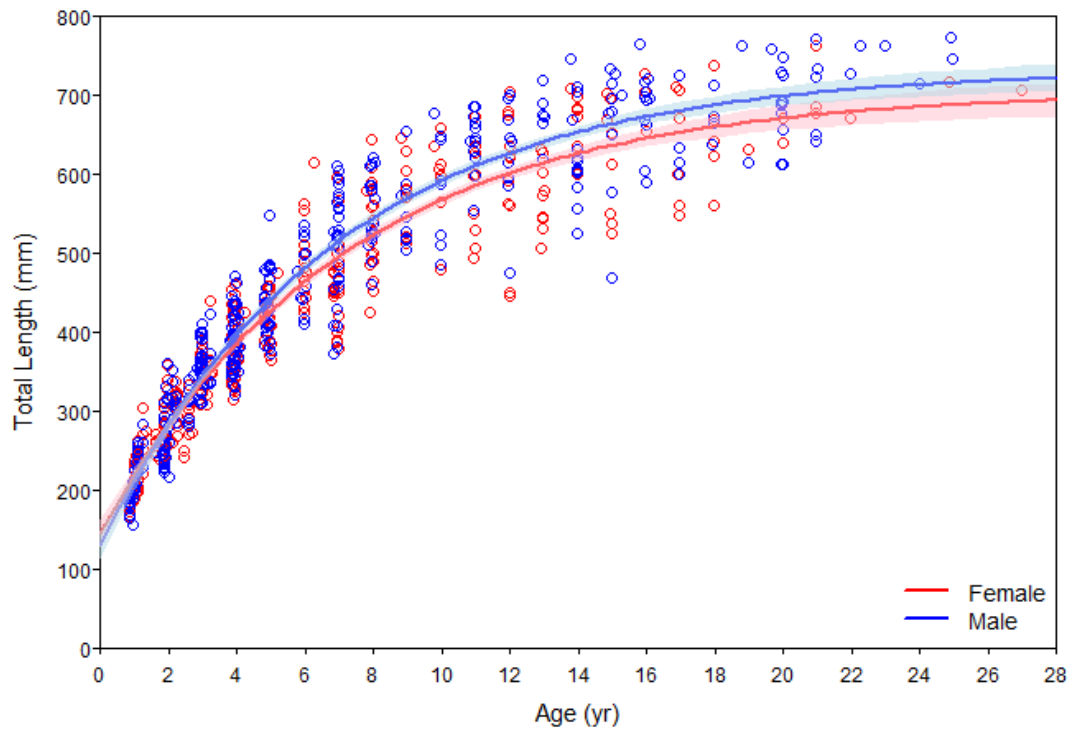
Figure 6. Sex-specific von Bertalanffy growth models.
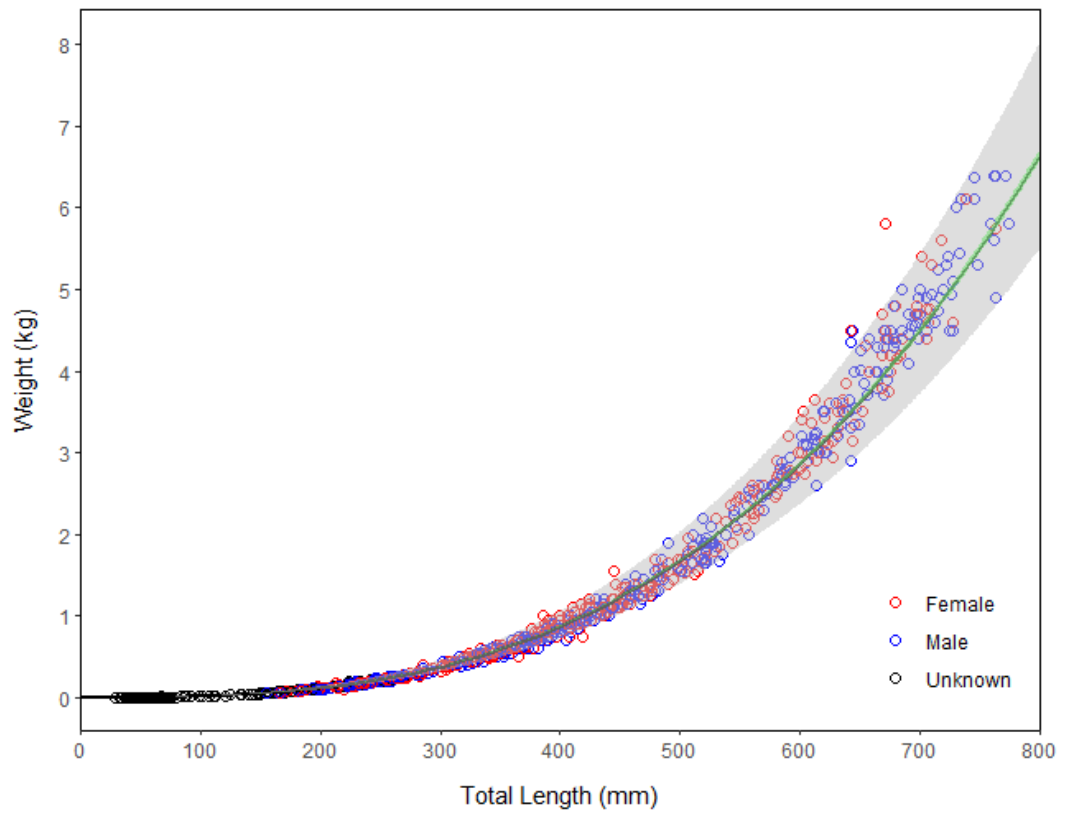
Figure 7. Weight-length relationship.
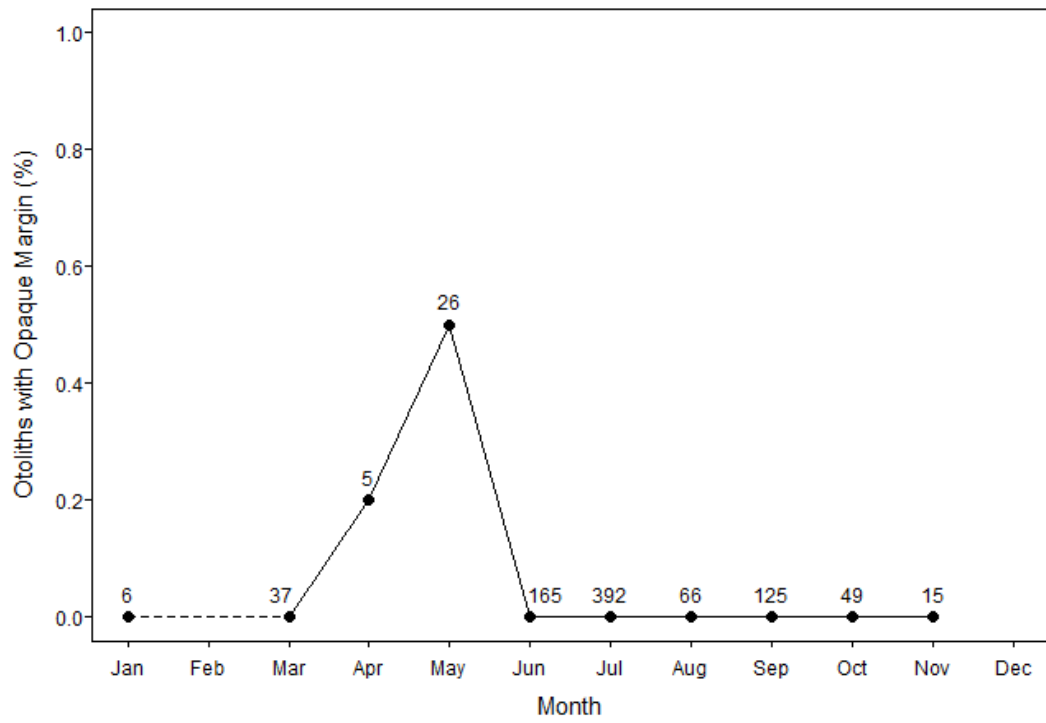
Figure 8. Marginal increment analysis, sample sizes included at each point.
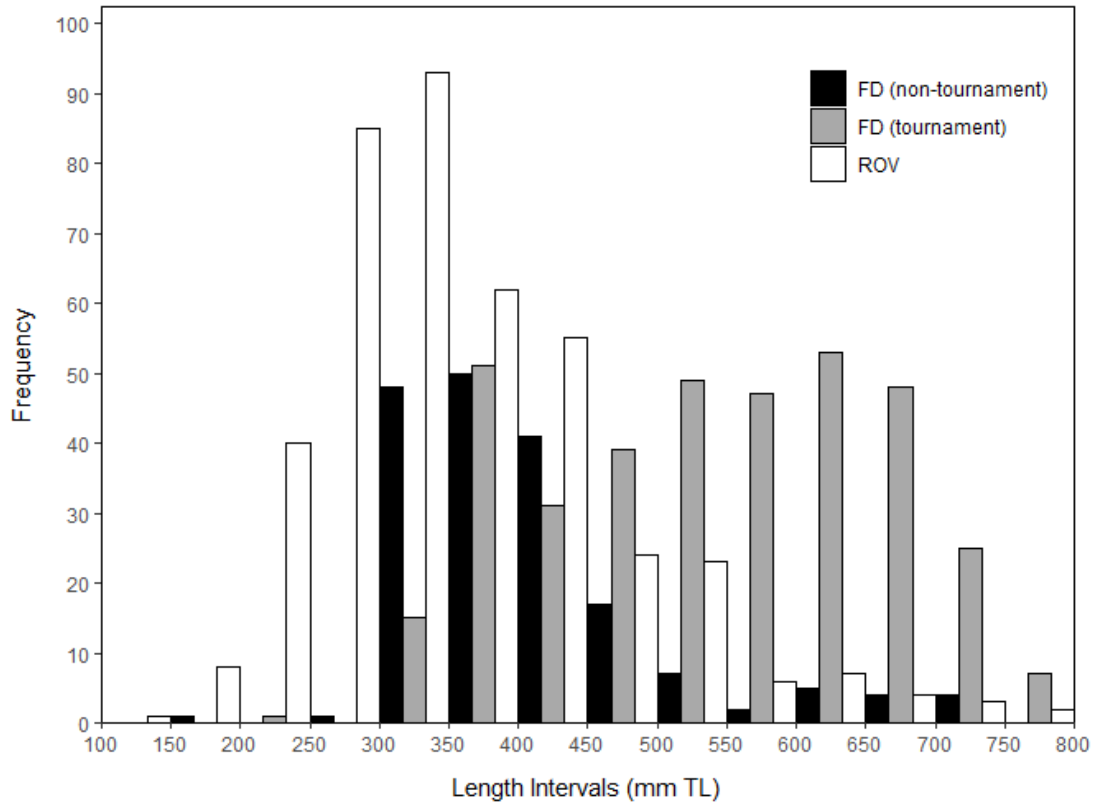
Figure 9. Length frequency distributions for mortality estimation (FD (non-tournament) = fishery-dependent with only non-tournament data, FD (tournament) = fishery-dependent with only tournament data, ROV = remotely operated vehicle).
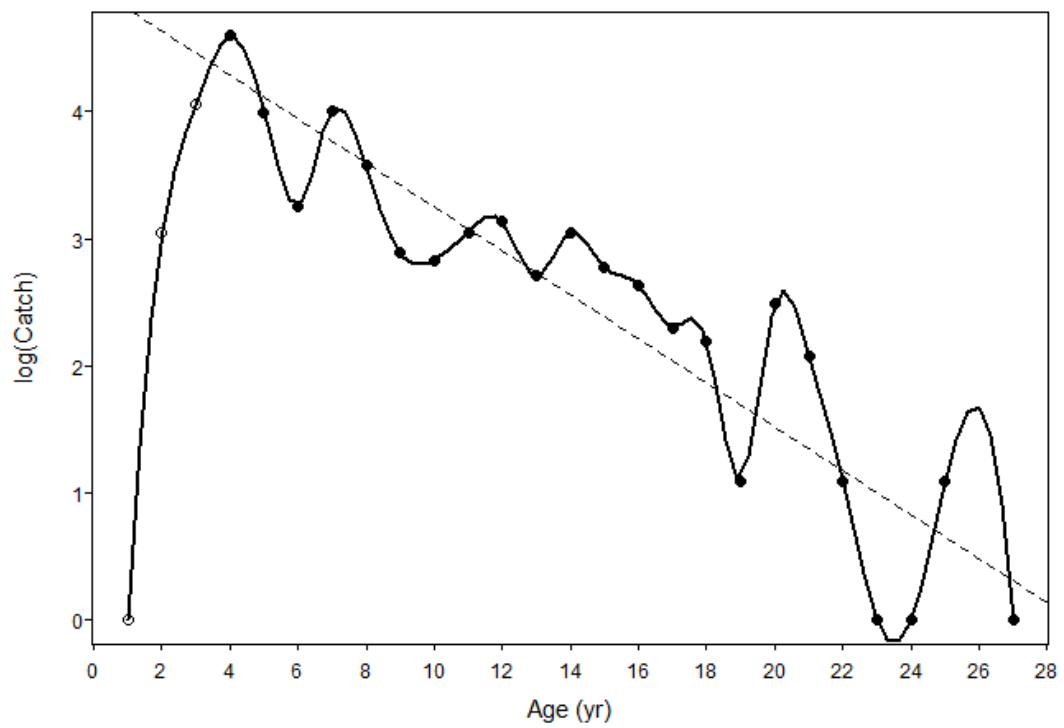
Figure 10. Complete fishery-dependent catch curve with peak abundance at age 4.
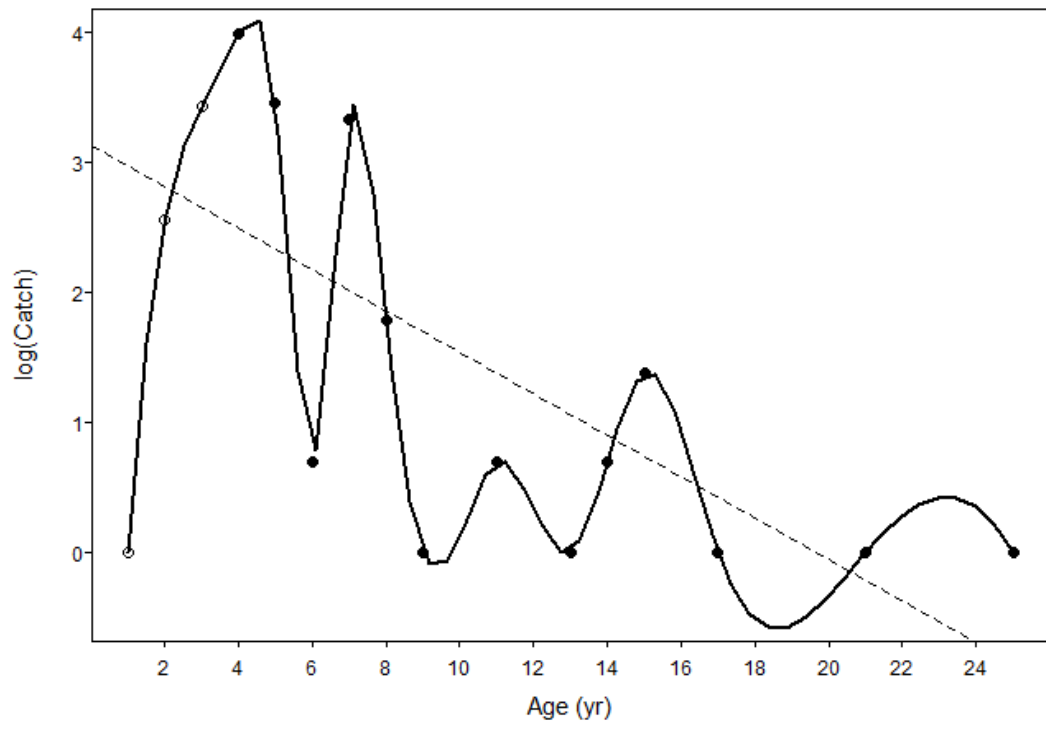
Figure 11. Non-tournament fishery-dependent catch curve with peak abundance at age 4.
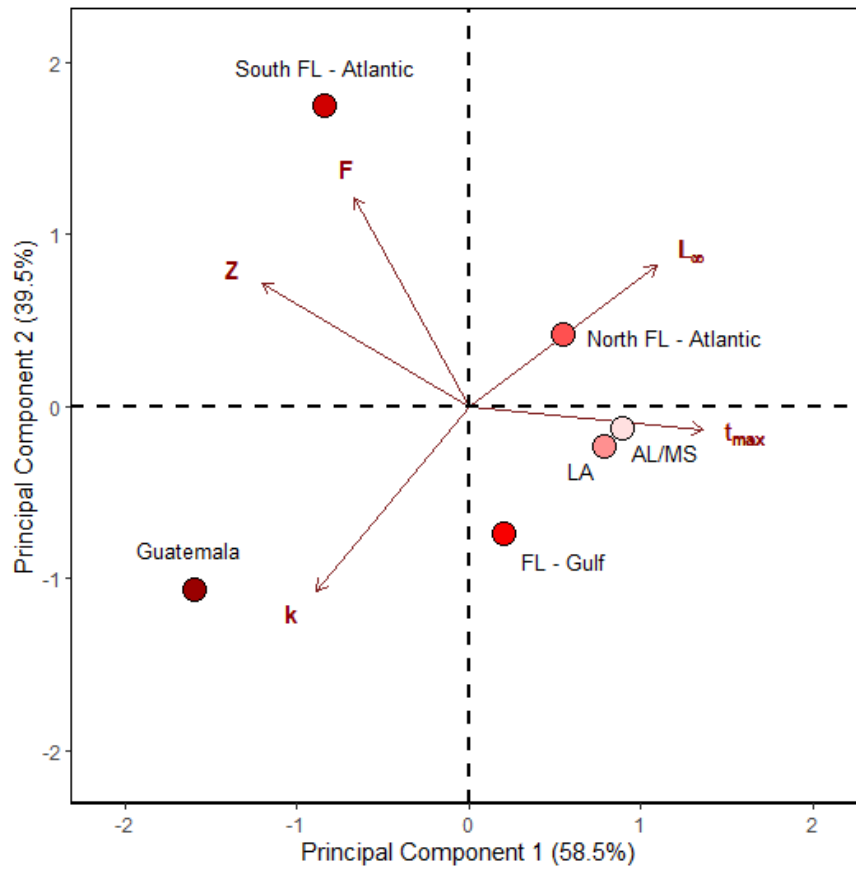
Figure 12. Principal component analysis biplot of regional Gray Snapper life history parameters. Points are shaded according to relative latitudinal position, with lighter points further north and darker points further south.
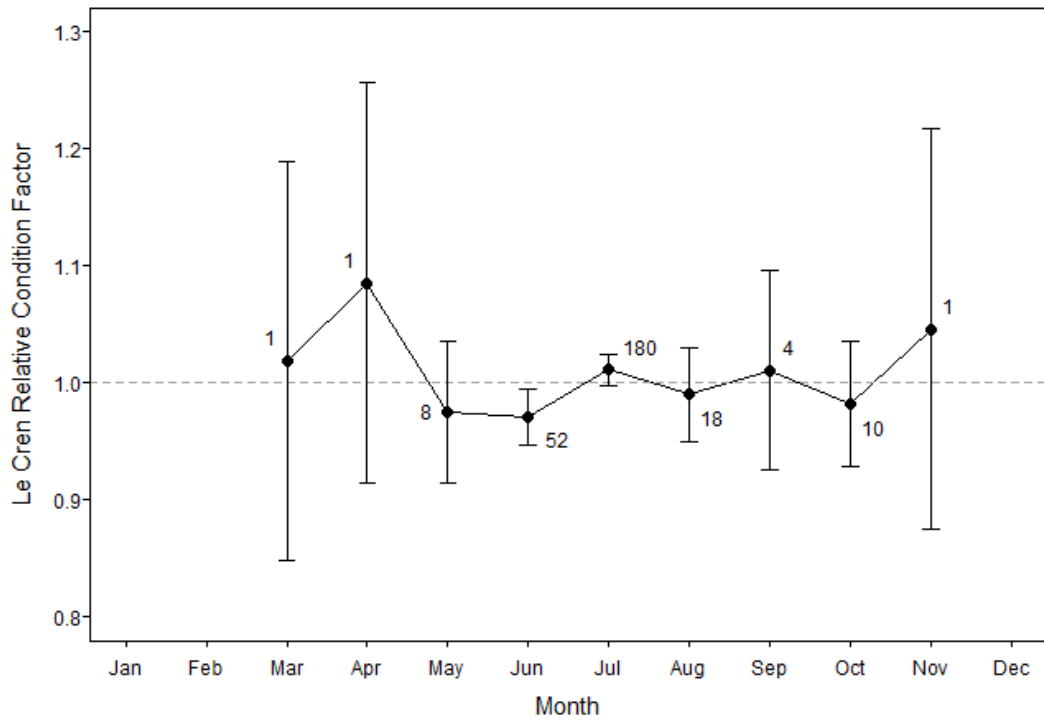
Figure 13. Monthly mean male Le Cren relative condition factor estimates, sample sizes included at each point. Values above and below the dotted line indicate fish that are heavier and lighter on average relative to a given length, respectively.
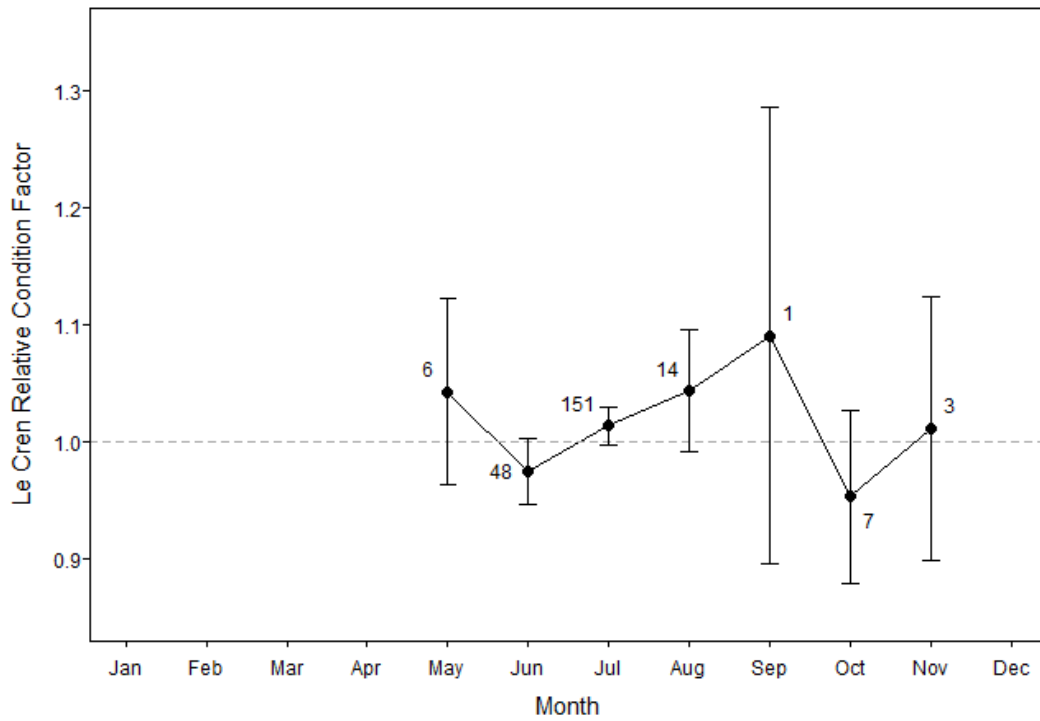
Figure 14. Monthly mean female Le Cren relative condition factor estimates, sample sizes included at each point. Values above and below the dotted line indicate fish that are heavier and lighter on average relative to a given length, respectively.
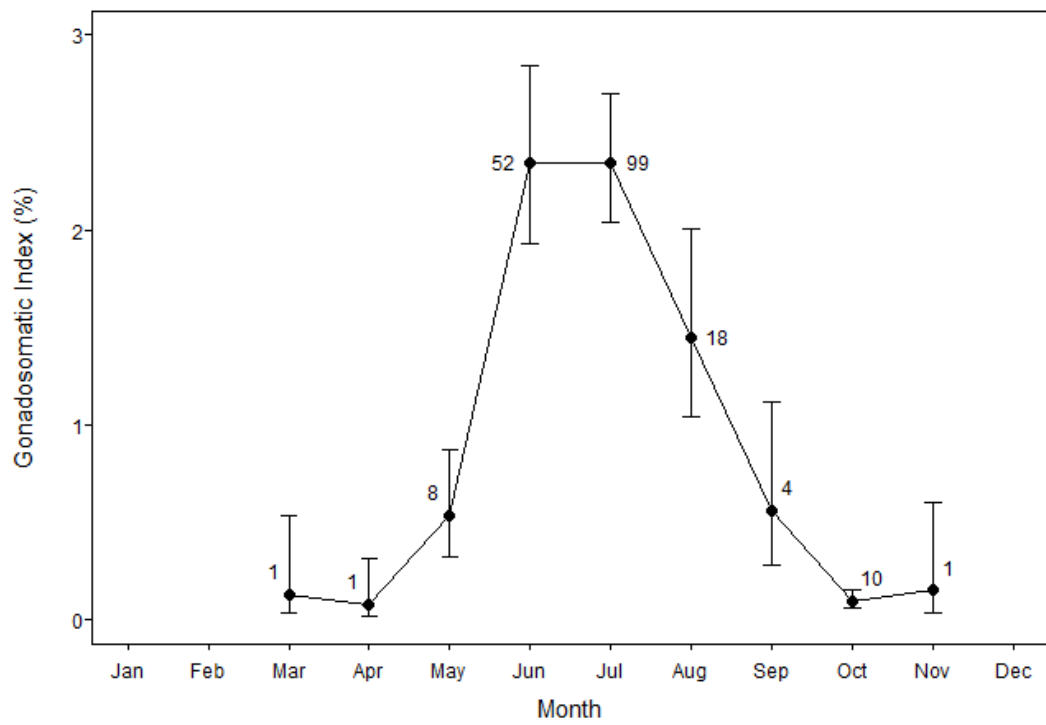
Figure 15. Monthly median male gonadosomatic index estimates, sample sizes included at each point.
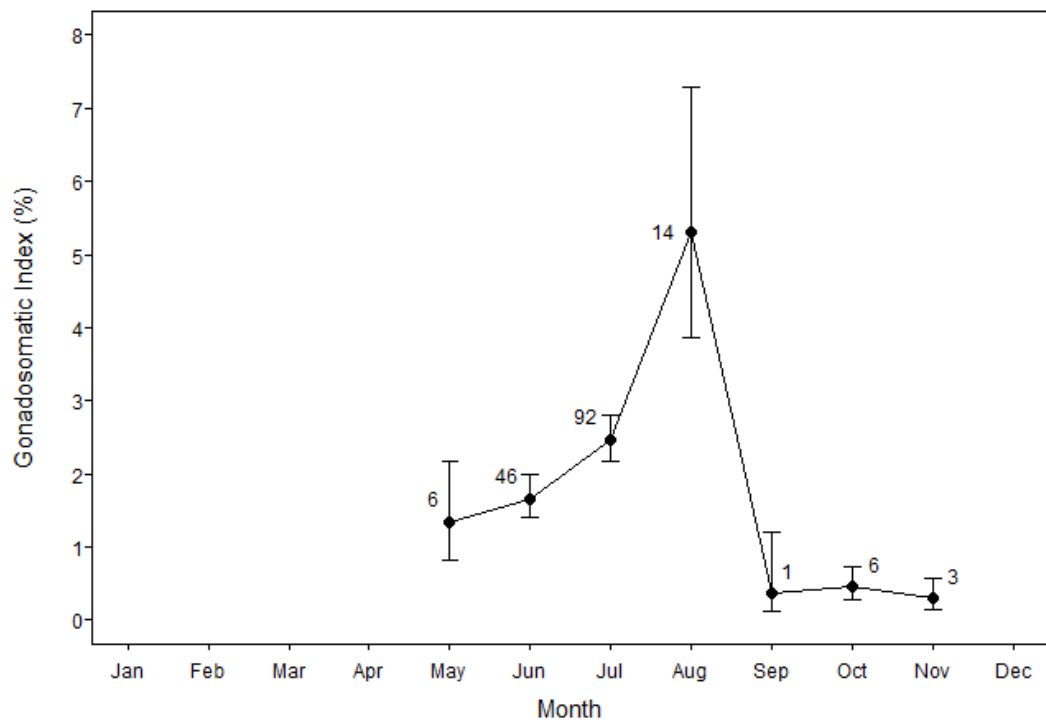
Figure 16. Monthly median female gonadosomatic index estimates, sample sizes included at each point.
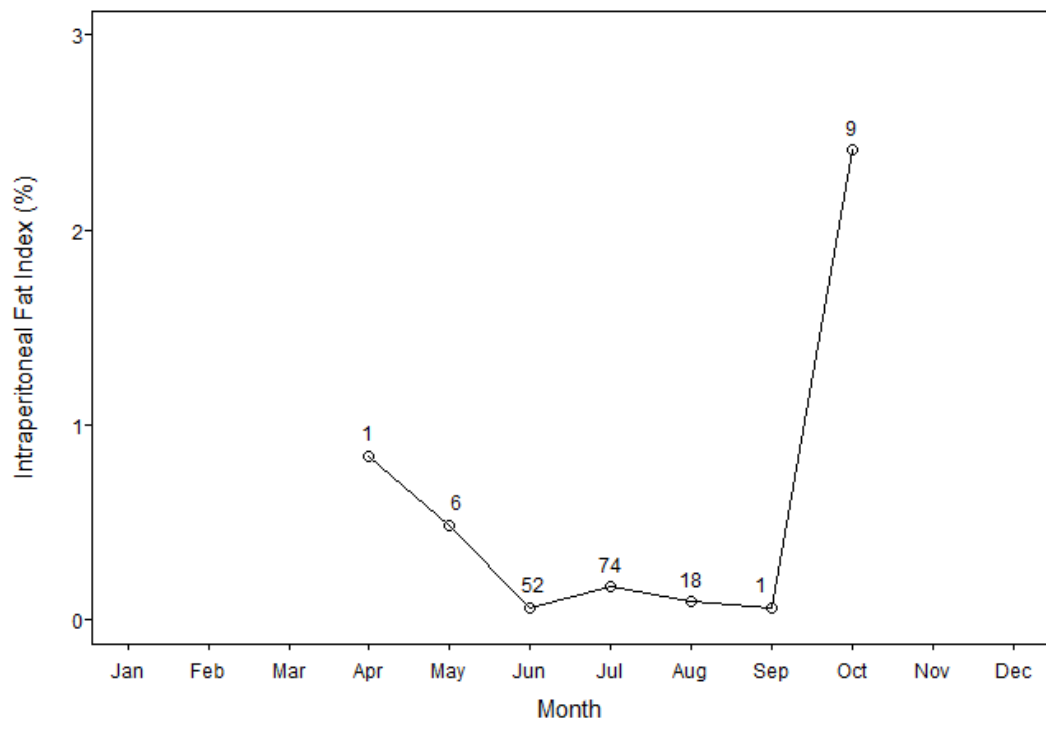
Figure 17. Loess curve fit to monthly mean male IPFI values, sample sizes included at each point.
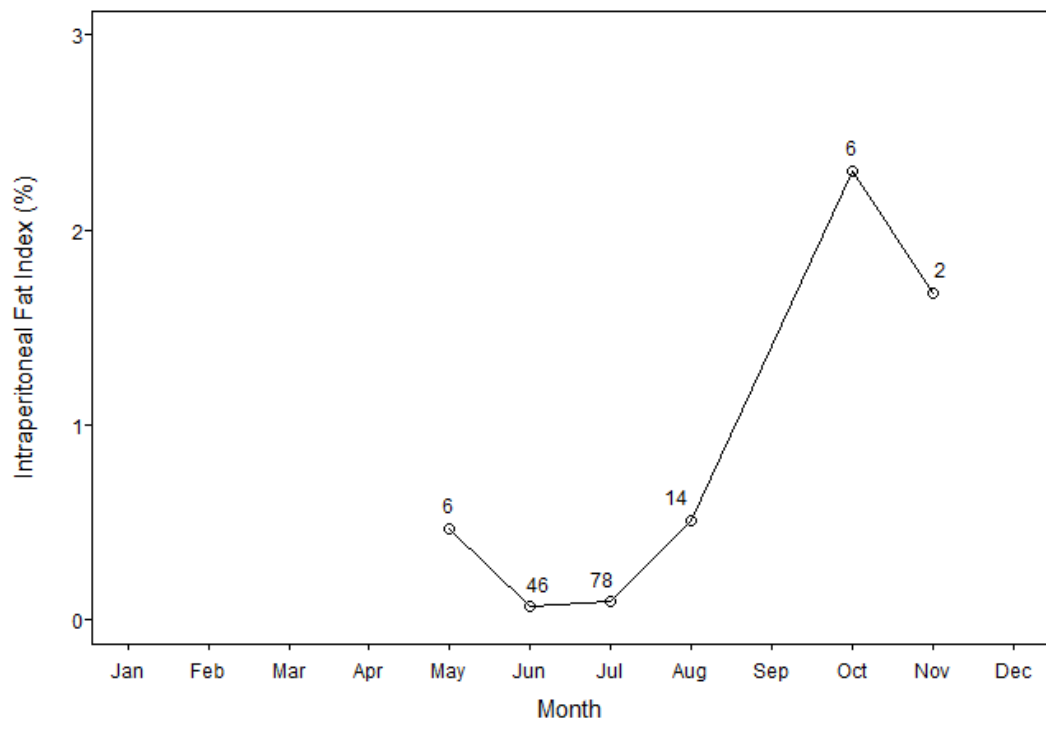
Figure 18. Loess curve fit to monthly mean female IPFI values, sample sizes included at each point.
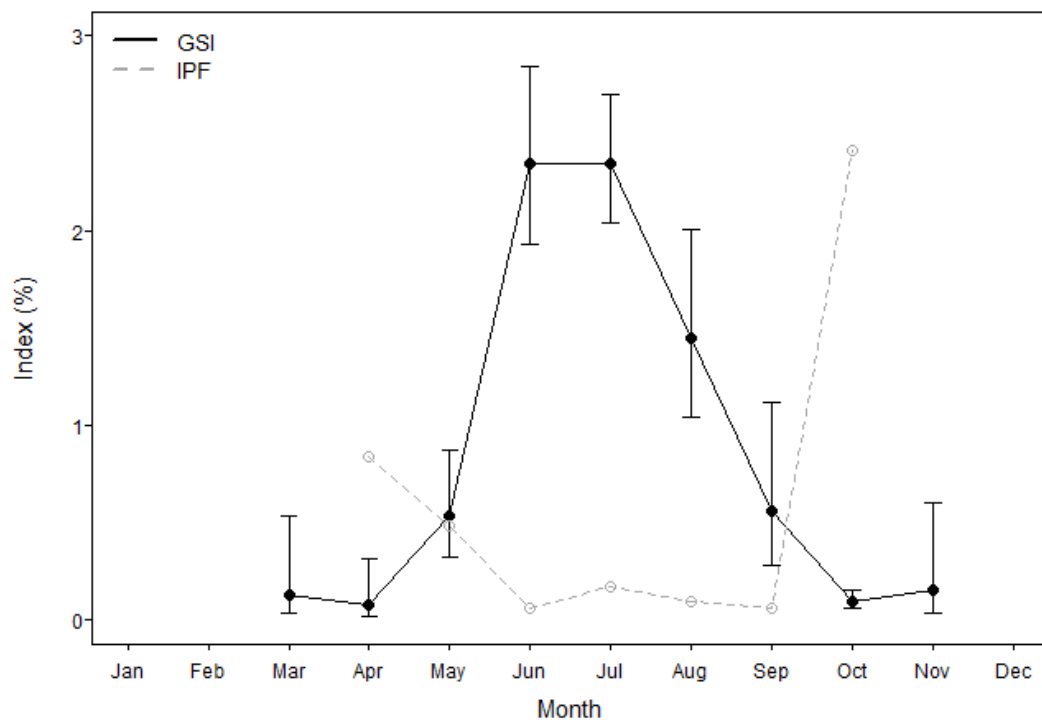
Figure 19. Monthly male gonadosomatic index and intraperitoneal fat index comparison.
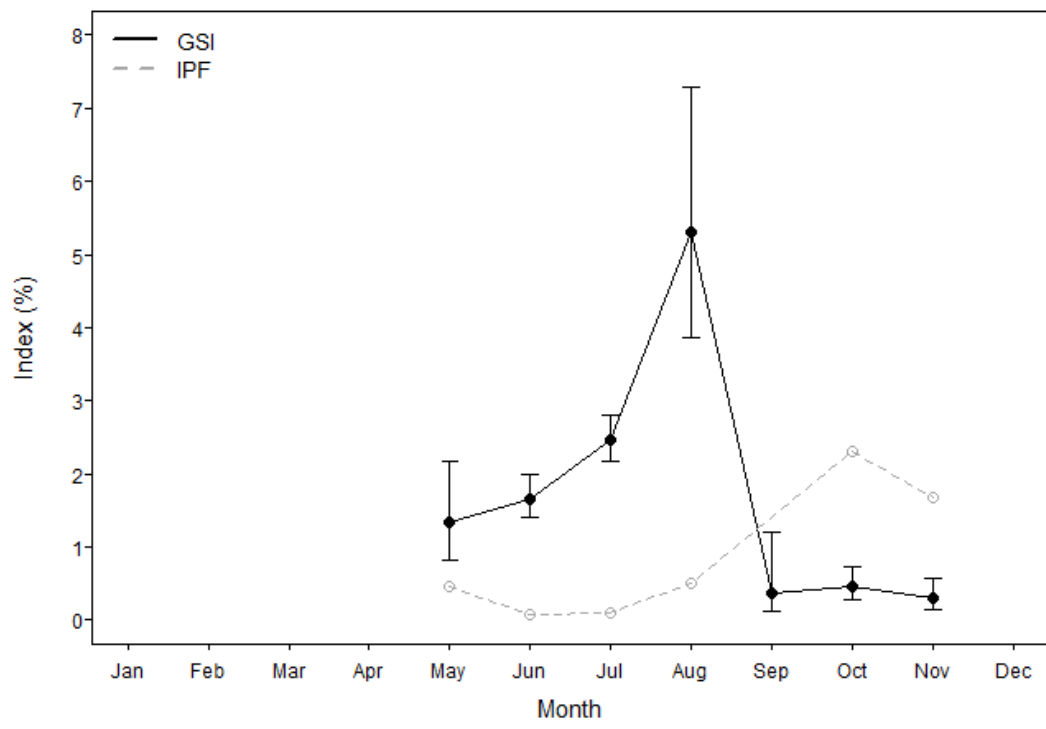
Figure 20. Monthly female gonadosomatic index and intraperitoneal fat index comparison.
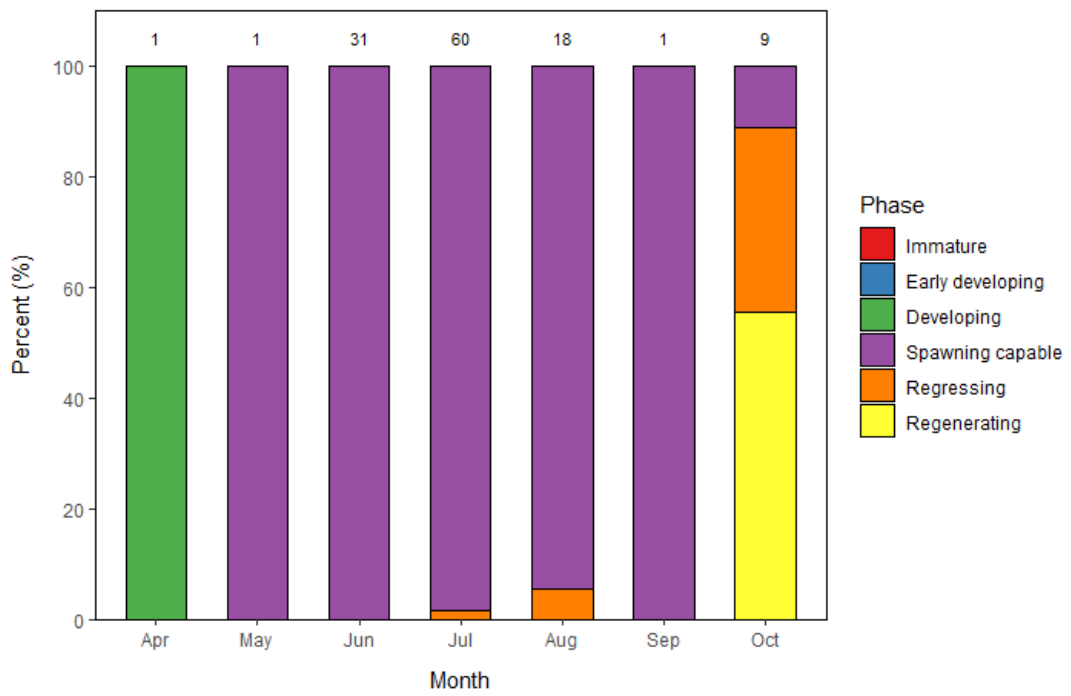
Figure 21. Monthly male reproductive phase distribution, sample sizes included above each bar.
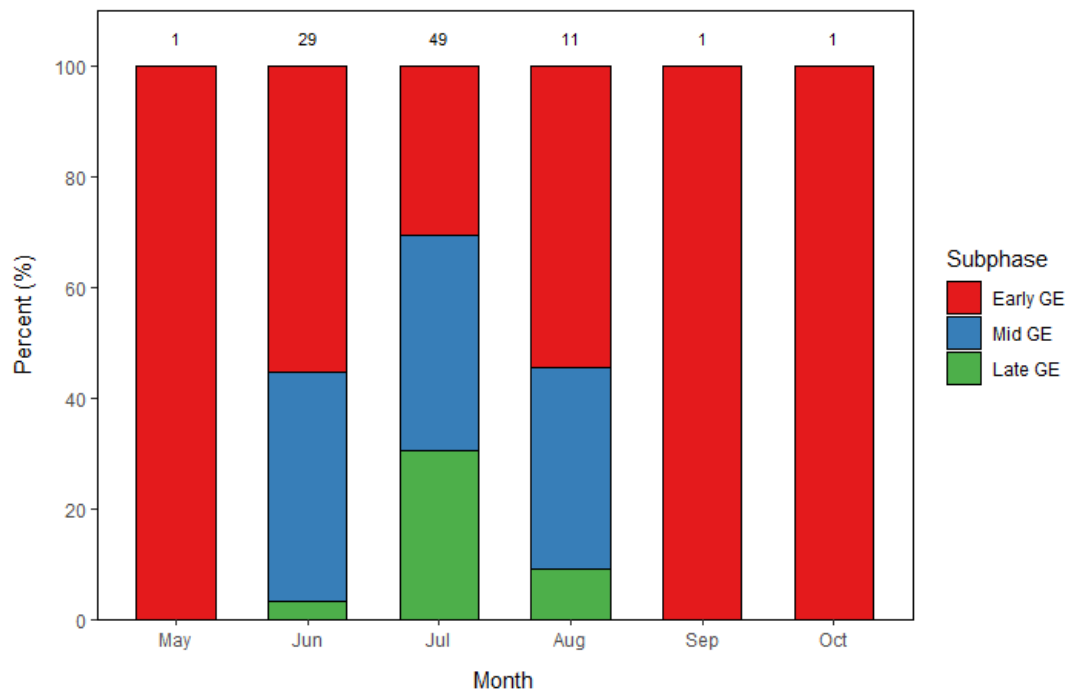
Figure 22. Monthly male GE subphase distribution, sample sizes included above each bar.
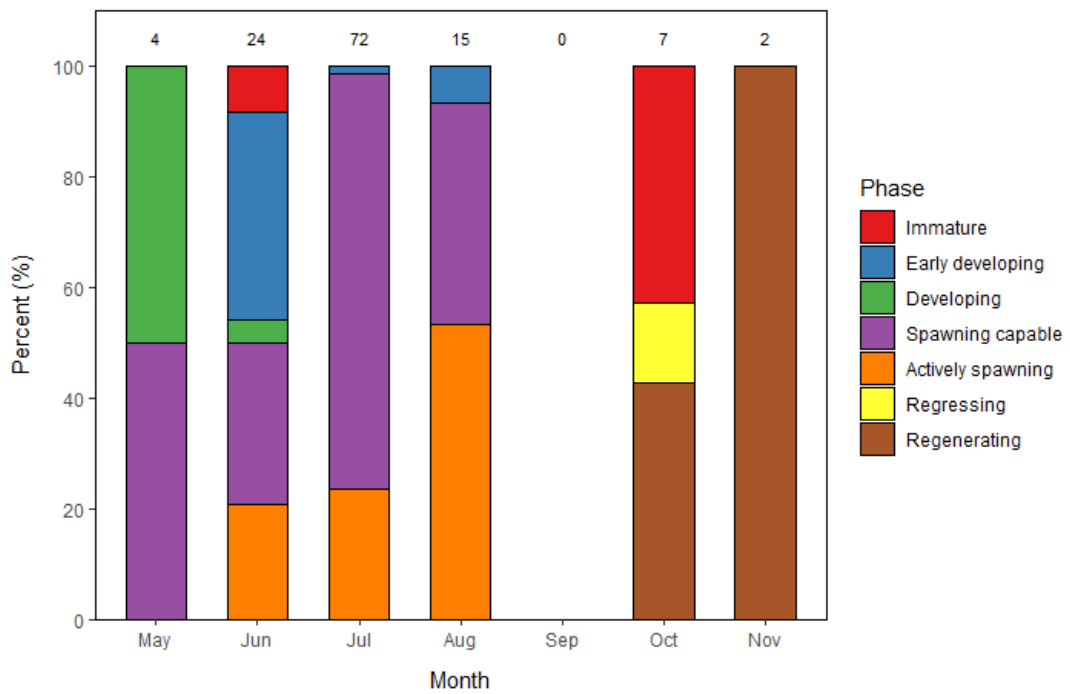
Figure 23. Monthly female reproductive phase distribution, sample sizes included above each bar.
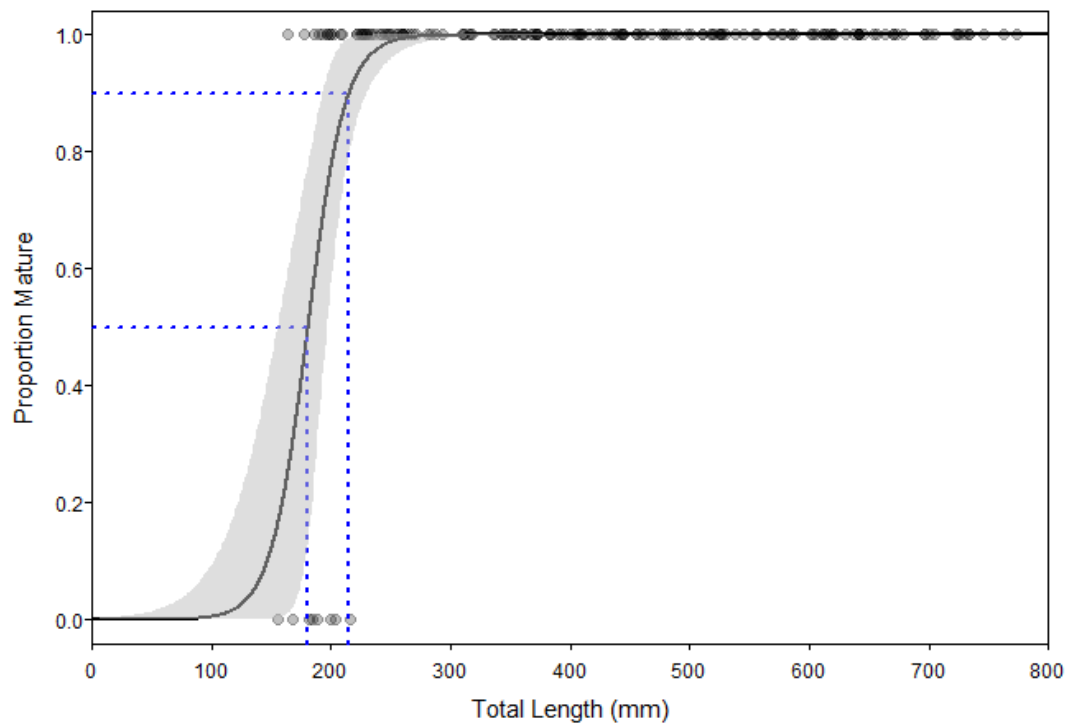
Figure 24. Male maturity at length curve; dotted blue lines indicate lengths at 50% maturity and 90% maturity.
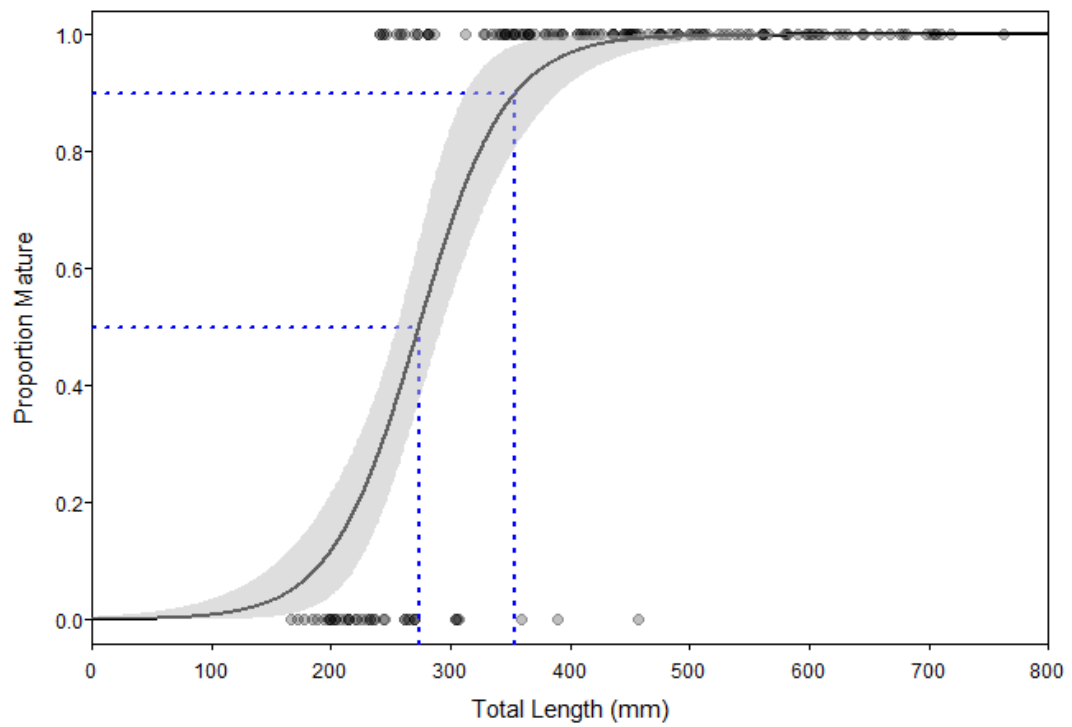
Figure 25. Female maturity at length curve; dotted blue lines indicate lengths at 50% maturity and 90% maturity.
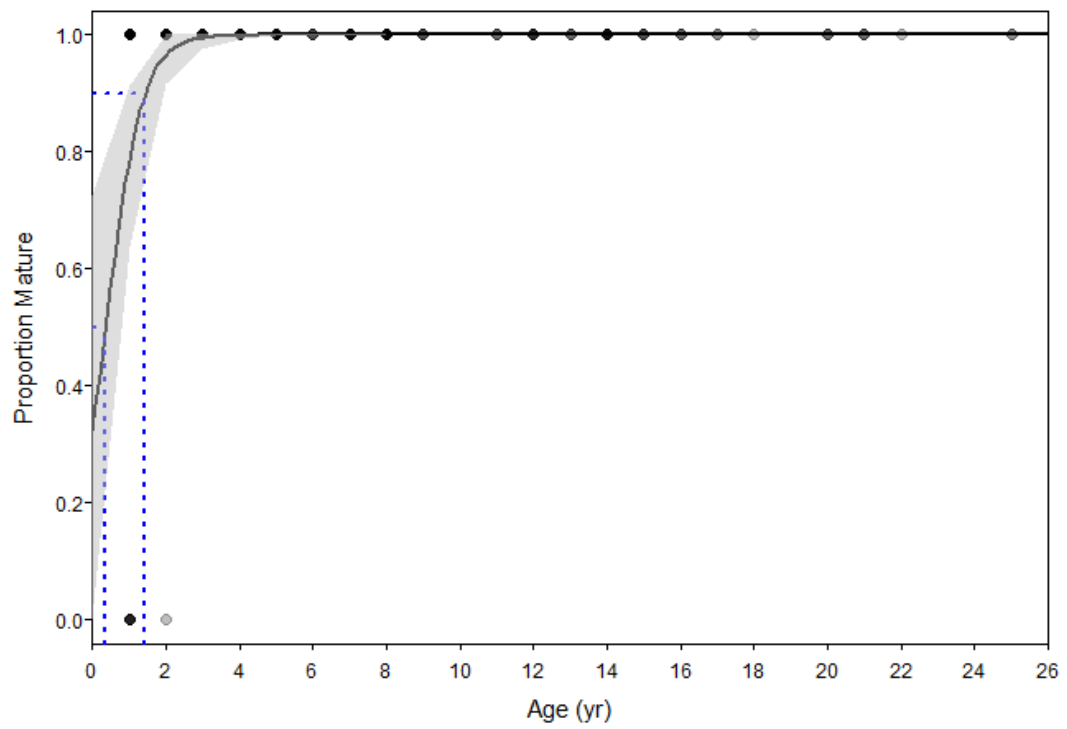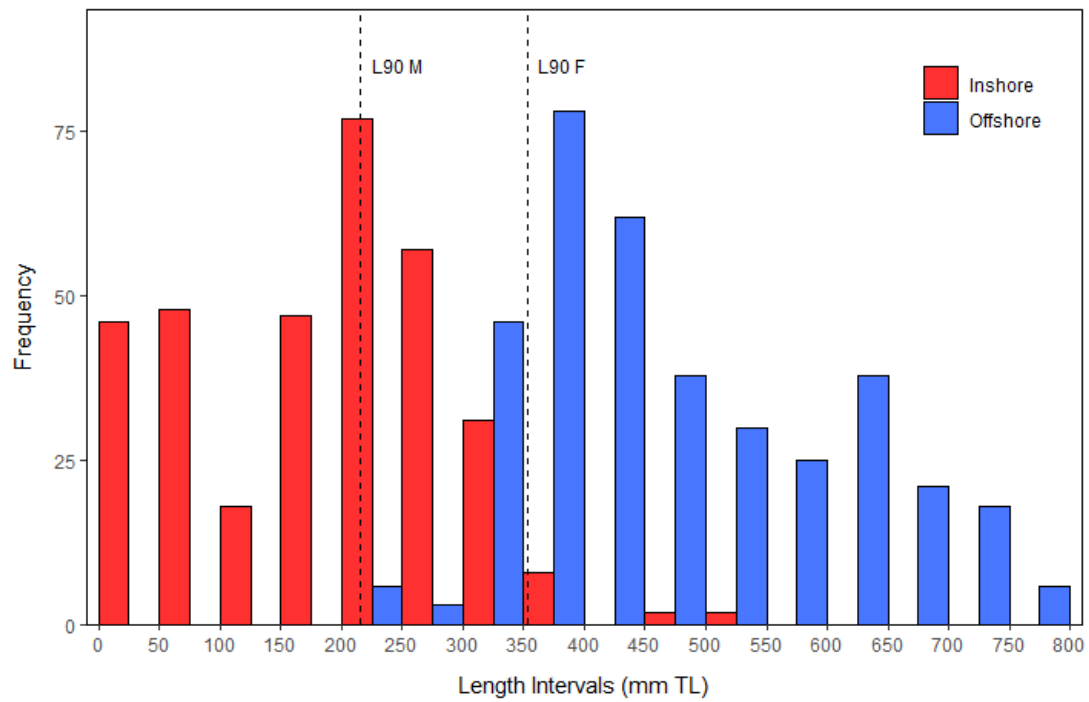
Figure 26. Male maturity at age curve; dotted blue lines indicate ages at 50% maturity and 90% maturity.
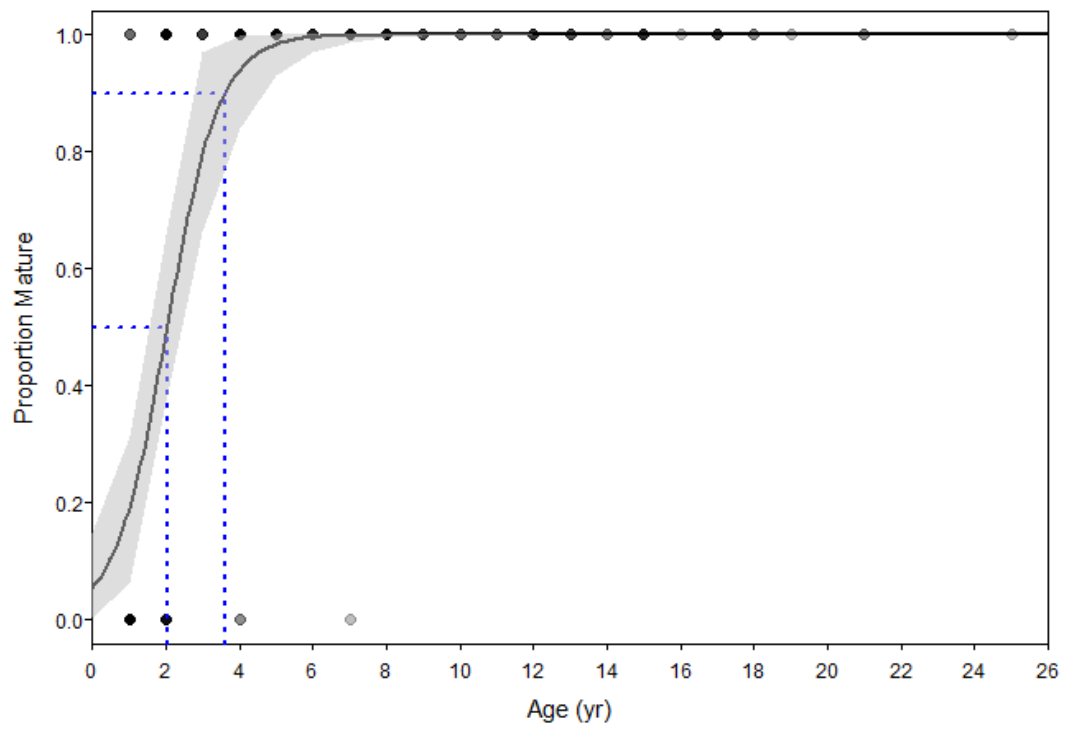
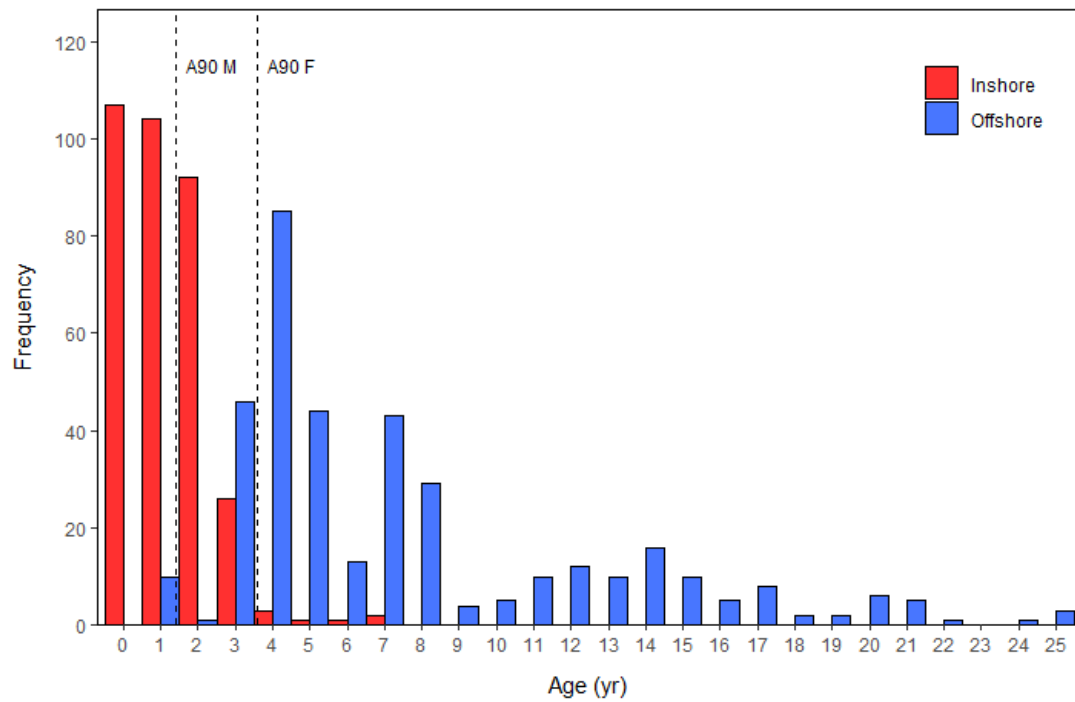Figure 27. Female maturity at age curve; dotted blue lines indicate ages at 50% maturity and 90% maturity.

Figure 28. Length frequency distribution for Gray Snapper collected by location inshore or offshore; sex-specific length at 90% maturity estimates indicated by dotted lines.

Figure 29. Age frequency distribution for Gray Snapper collected by location inshore or offshore; sex-specific age at 90% maturity estimates indicated by dotted lines.
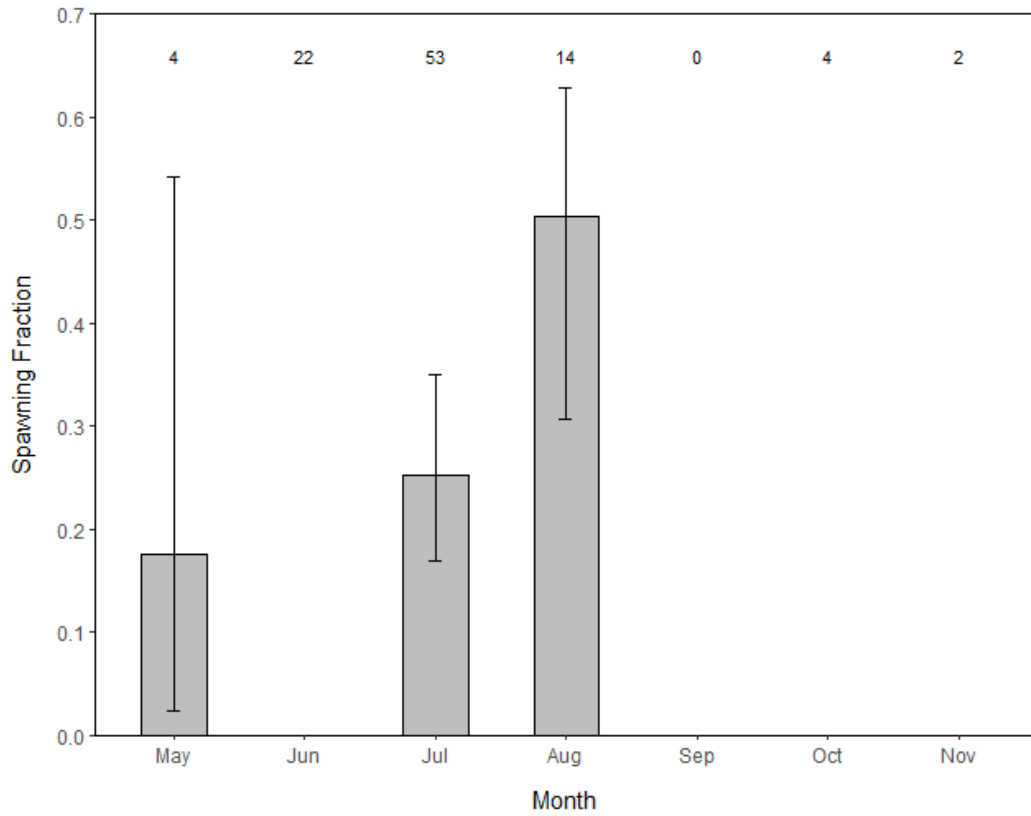
Figure 30. Monthly daily spawning fraction estimates, sample sizes included above each bar.
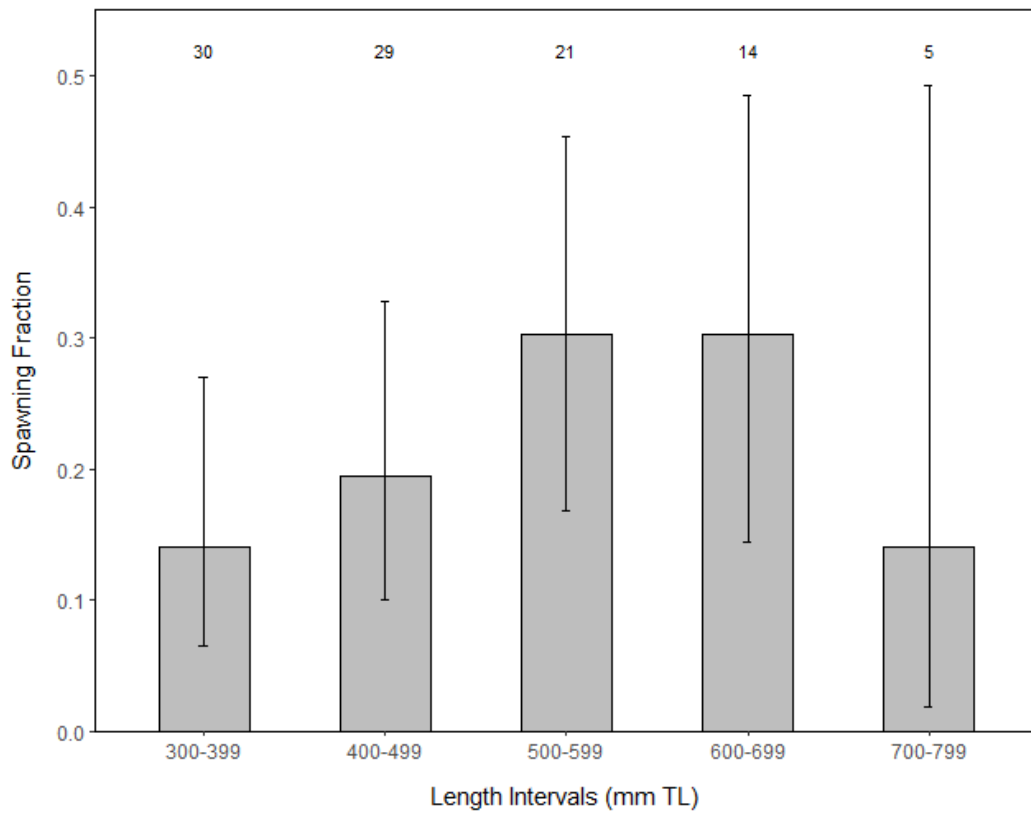
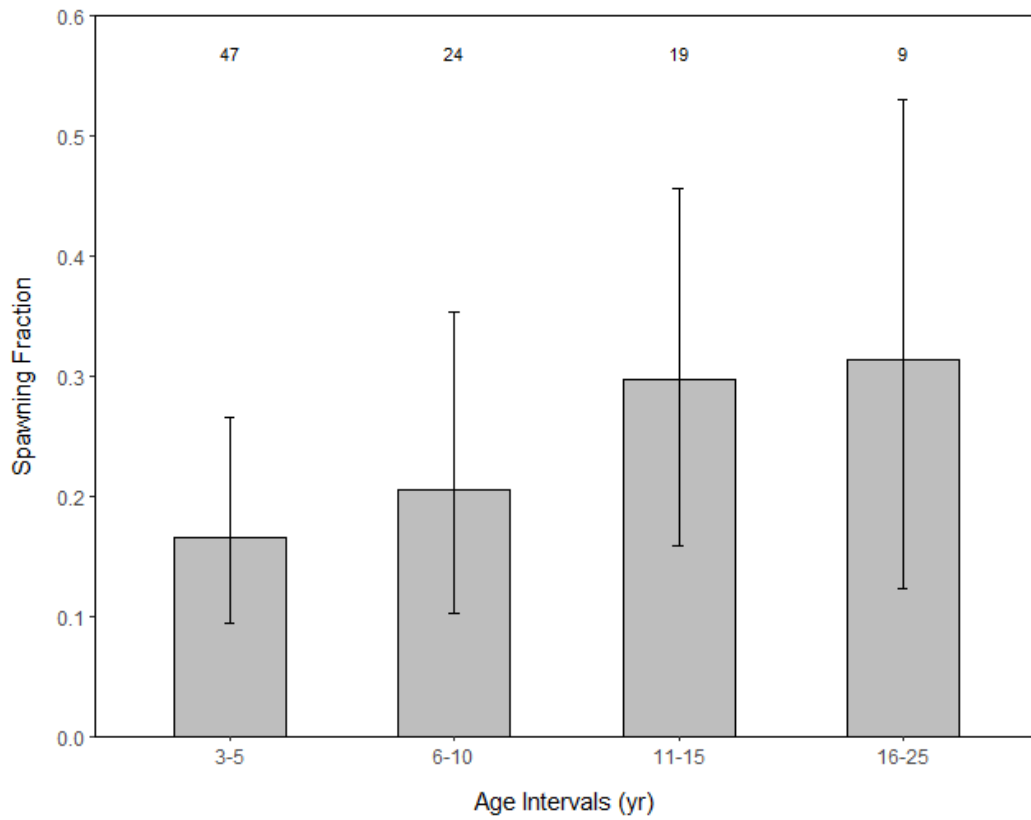Figure 31. Daily spawning fraction estimates by length interval, sample sizes included above each bar.

Figure 32. Daily spawning fraction estimates by age interval, sample sizes included above each bar.

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