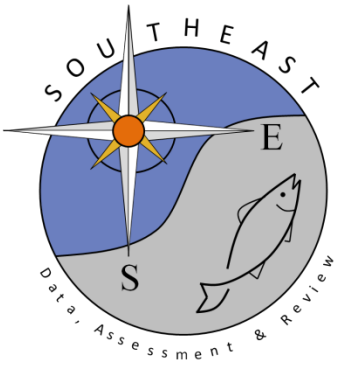
SEDAR 74-DW36: Best practices for standardized reproductive data and methodology to estimate reproductive parameters for Red Snapper in the Gulf of Mexico

Susan Lowerre-Barbieri, Claudia Friess, Nancy Brown-Peterson, Heather Moncrief-Cox, and Beverly Barnett

SEDAR90-RD-27

April 2025



Best practices for standardized reproductive data and methodology to estimate reproductive parameters for Red Snapper in the Gulf of Mexico

Susan Lowerre-Barbieri, Claudia Friess, Nancy Brown-Peterson, Heather Moncrief-Cox, and Beverly Barnett

SEDAR74-DW-36

30 June 2022
Updated: 5 July 2022
Updated: 25 July 2022

Please cite this document as:

Lowerre-Barbieri, Susan, Claudia Friess, Nancy Brown-Peterson, Heather Moncrief-Cox, and Beverly Barnett. 2022. Best practices for standardized reproductive data and methodology to estimate reproductive parameters for Red Snapper in the Gulf of Mexico. SEDAR74-DW-36. SEDAR, North Charleston, SC. 43 pp.

Best practices for standardized reproductive data and methodology to estimate reproductive parameters for Red Snapper in the Gulf of Mexico

By Susan Lowerre-Barbieri[1], Claudia Friess[2], Nancy Brown-Peterson[3], Heather Moncrief-Cox[4,1], and Beverly Barnett[5]

[1]Fisheries and Aquatic Sciences Program, School of Forest Resources and Conservation, University of Florida, Gainesville, FL, USA
[2]Fish and Wildlife Research Institute, Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL, USA
[3]Center for Fisheries Research and Development, University of Southern Mississippi, Ocean Springs, MS, USA
[4]Cooperative Institute for Marine and Atmospheric Studies, Rosenstiel School, University of Miami, Miami, FL, USA
[5]NOAA Fisheries, SEFSC, Panama City Facility, FATES Division, Biology and Life History Branch, Panama City, FL, USA

Introduction

Reproductive potential, defined as the "annual variation in a stock's ability to produce viable eggs and larvae that may eventually recruit to the adult population or fishery" (Trippel 1999) plays an important role in stock assessments and biological reference points (Lowerre-Barbieri et al., 2011a). Common measures of reproductive potential are female spawning stock biomass (SSB) and total egg production (TEP), with varying data needs and associated uncertainties. Methodological issues that affect uncertainty in stock assessment measures of reproductive potential include a lack of standardized data and methods, as well as potential biases due to sampling (especially fisheries-dependent samples) and the age and size range over which reproductive data is available. In particular, females with oocytes in the appropriate stage for estimating batch fecundity are ephemeral and typically have the smallest sample sizes over wide size ranges. Standardizing the data and methods is especially important in assessments, particularly if there is evidence that reproductive parameters are not invariant over time or space, as reported for the Gulf of Mexico Red Snapper stock (i.e., Kulaw et al. 2017, Brown-Peterson et al. 2019, Brown-Peterson et al. 2022).

Stock assessments and recent publications both have reported decreased reproductive productivity in the region west of the Mississippi River and throughout the Gulf of Mexico (GOM or Gulf) in recent years as the stock recovers. In SEDAR7, SEDAR31, and SEDAR 52 fish in the eastern Gulf (east of the Mississippi River) were reported to be younger and to mature earlier than those from the western Gulf (SEDAR 2005; SEDAR 2013; SEDAR 2018). More recently, decreased reproductive output at age has been reported, although with varying intensity depending on region (SEDAR 52). New publications and data since SEDAR 52 support these patterns and include: Brown-Peterson et al. (2019, 2021), Leontiou et al. (2021a, b), Froelich et al. (2021), Millender and Brown-Peterson (2022), and Brown-Peterson and Millender (2022). Brown-Peterson et al. (2019) conducted a meta-analysis on Red Snapper reproductive data collected from 1991-2017 throughout the GOM. Using the gonadosomatic index (GSI) as an indicator of spawning activity, they reported peak spawning months of June through August, with a high probability of spawning in May. For recent years, they report increased spawning in September and decreased spawning frequency and batch fecundity, especially in the western Gulf. Red Snapper spawning activity also has been reported to increase with depth (Glenn et al., 2017; Brown-Peterson et al., 2021; Froehlich et al. 2021; Millender and Brown-Peterson 2022). In contrast, structure type does not appear to greatly influence Red Snapper reproductive parameters in either the eastern (Brown-Peterson et al. 2021) or western (Downey et al. 2018) GOM. However, to fully assess the apparent spatio-temporal patterns in GOM Red Snapper reproduction, we need to first address if methodological differences could have affected results.

The reproductive data needed to estimate reproductive potential differs with reproductive strategy and data availability. Red Snapper are gonochoristic and reproductive potential is based on females. For SSB, the parameters needed are a sex ratio and a maturity at age estimate to calculate the proportion of the biomass which should be assigned to mature females. The assumption when using SSB as a proxy for reproductive potential is that egg

production is proportional to weight. For TEP there is a need to develop a fecundity at age matrix. For batch spawners, like Red Snapper, this includes estimating batch fecundity, spawning interval, and spawning seasonality. Data needed to estimate these parameters includes gonad weight (and type of gonad preservation), total weight, length, age, date, time, capture location, form of fish capture, and histological or macroscopic indicators used to assign reproductive phase and state. Here, we review data used in SEDAR 7, 31 and 52, and the data available for SEDAR 74 for estimating both SSB and TEP. We evaluate best practices for standardizing reproductive data and methods that affect estimates of these reproductive parameters and conclude with a discussion of pros and cons of SSB vs TEP.

Materials and Methods

Reproductive compensation

Recent stock assessments have indicated that Red Snapper are increasing in abundance and that there is a need to assess if reproductive compensation occurs as the stock recovers (Porch et al., 2015). To assess this, we assign stock status time periods as follows: (1) from 1991-2008, when the stock was severely overfished; (2) from 2009-2016, when the stock was rapidly recovering; and (3) from 2017-2019 as stock abundance has been stabilizing. Past stock assessments broke the GOM Red Snapper stock into two regions based on whether fish were sampled east or west of the Mississippi River, and we conducted our spatial analysis on these same two regions. This was necessary as the spatial reproductive data was not sufficient to divide the eastern region into separate central and east regions.

Reproductive data summary for previous and current assessments

Reproductive analysis for SEDAR 7 utilized data collected from 1991 to 2003, including 1,956 female histological samples and 563 batch fecundity estimates. Data came from the NMFS Panama City laboratory as well as a study in the northern Gulf of Mexico (Cowan et al. 2002; Woods 2003). Results on reproductive parameters are also published in Jackson et al. (2006) and Porch (2007).

The 2009 update assessment included new data on size and age at maturity due to evidence that Red Snapper sexual maturity might occur earlier than estimates reflected in SEDAR 7. Targeted sampling occurred during 2008 SEAMAP cruises to collect smaller Red Snapper during peak spawning months (June through August) and to more fully sample immature fish (Cook et al., 2009; n=270 females, n=56 immature).

SEDAR 31 included new data collected from 2004 to 2011, and a data set from collections in 1999 that had not been previously submitted. The largest provider of new data was the 2011 Congressional Supplemental Sampling Program (CSSP), which allowed Gulf-wide, synoptic sampling of Red Snapper during the April through October reproductive season. The CSSP survey provided 1,002 ovarian histology samples, 992 with ages, and 50 additional batch fecundity estimates. Data from outside data providers came from: Florida, mainly in 2009 (Lowerre-Barbieri et al. 2012 SEDAR31-DW15, n=237 females) and oil platforms in the northern GOM from 2009 and 2010 (Cowan et al. 2012 SEDAR31-DW03, n=337 females). Additional

fecundity data (n=35) included: fish from 2004 in the Tortugas (n=6; Brown-Peterson et al. 2009), from 2009 in the northern GOM (n=8; Cowan et al., 2012), and fish collected in 1999 in the northern GOM (n=21; Szedlmayer and Furman 2000). A total of 648 fecundity samples, 592 with ages, were analyzed for SEDAR31.

SEDAR 52 included new data collected from 2012 to 2016, as well as data collected in previous years but not previously submitted. A total of 949 female histological records by age and 1,008 records by length were collected from 2012 to 2016 by the NMFS Panama City Laboratory, SEFSC fishery independent surveys (reef fish vertical line and bottom longline), and observer programs (reef fish and shark bottom long line). New batch fecundity data included 252 records by age and 256 records by length. Most batch fecundity estimates came from 2012-2016 (n=231). However, 26 batch fecundity estimates came from fish collected in 2007-2011 that were not previously submitted. Large, older females (n=53; Lang and Falterman 2017, SEDAR52-WP-07) were collected from fishing tournaments in LA. Debra Murie at the University of Florida provided 73 batch fecundity estimates from FL (n=40) and LA (n=33) with samples collected from tournaments and scientific surveys that were not submitted through NMFS data. The Panama City Lab provided an additional 131 batch fecundity estimates, for a total of 844 batch fecundity estimates by age for SEDAR52 (n=904 with length).

SEDAR 74 has a total of 11,532 records with reproductive data. Primary data providers for new histological data were NMFS Panama City (n=1,740), Brown-Peterson and Millender 2022 (S74-DW-09; years 2016-2019, n=917), Downey et al. 2018 (SEDAR74-RD24; years 2013-2015, n=526), Glenn et al. 2017 (SEDAR74-RD42; years 2011-2013, n=161), Lowerre-Barbieri (integrated into analysis with this working paper, n=608, years 2009-2018), and Kulaw et al. 2017 (SEDAR74-RD-43; years 2009-2010, n=269). An additional 325 batch fecundities with age were added for SEDAR74, with primary data providers being NMFS Panama City (years 2016-2019, n=131), Brown-Peterson and Millender (S74-DW-09; years 2016-2019, n=90), Downey et al. 2018 (SEDAR74-RD24; years 2013-2015, n=71), Glenn et al. 2017 (SEDAR74-RD42; years 2011-2013, n=6), and Kulaw et al. 2017 (SEDAR74-RD-43; years 2009-2010, n=27). This resulted in a total of 1,212 batch fecundity estimates analyzed for SEDAR74.

Standardizing reproductive data

Gonadal development occurs over multiple temporal scales: lifetime, reproductive cycle, seasonal and diel. All fish reach sexual maturity once in life, participate in one or more reproductive cycles, release gametes or offspring once or more within a given reproductive cycle, have a maximum reproductive age (often synonymous with maximum age), and die often before reaching that age (Figure 1). A reproductive cycle represents the gonadal development needed for mature fish to spawn at the appropriate time for offspring survival. Reproductive cycles are most commonly annual. In iteroparous species, which go through multiple reproductive cycles in a lifetime, part of the cycle is the removal of residual oocytes by atresia and regeneration of oocytes for the next spawning season. Within each reproductive cycle there is a period of time associated with spawning or the spawning season. Batch spawners, like Red Snapper, will spawn multiple times within the spawning season and their annual fecundity is estimated based on the number of spawns in a season (or spawning frequency)

multiplied by the number of eggs released in a batch. For group or aggregate spawners, part of the reproductive strategy is to synchronize the release of gametes into the water column, and these fish will exhibit diel periodicity to their spawn times. In species with diel periodicity, it is possible to estimate the age of post-ovulatory follicles (POF, what is left after an egg is ovulated) on field samples. For other species, in-captivity experiments are needed.

Standardizing the terms used to describe reproductive timing and the assignment of reproductive state and phase is critical to stock assessments, which draw on multiple data providers. Brown-Peterson et al. (2011) address universal terminology, and a recent series of webinars built on this initial effort to develop best practices for standardizing reproductive parameters for stock assessments in the Southeast. This resulted in a draft table of field names and acceptable values. We use this analysis to build on these initial efforts to develop best practices for reproductive phase assignment, data and methodological standardization, and refining the draft table for standardized reproductive data needed.

Sex ratio

Sex ratio was estimated based on the original full database sent to us, which included all fish which had been either macroscopically or histologically assigned a sex.

Spawning seasonality

Spawning seasonality affects reproductive success and resilience, and because it is often exogenously triggered by water temperature, it can be affected by climate change. Estimates of spawning season duration play a role in temporal filters to increase accuracy in maturity assignments (Hunter and Macewicz 2003) and in annual fecundity estimates for fish with indeterminate fecundity. Most species in the southeastern US do not have determinate fecundity as seen in cold water species and total spawners (i.e., species which ovulate and spawn all their eggs in one event or over a very short time). For species with indeterminate fecundity, the number of spawning events in a season needs to be estimated and will be greatly affected by the estimated season duration (see results).

At the population level, spawning seasonality varies in terms of its duration (restricted or extended); the degree of synchronization among individual spawning periods; and the season of occurrence (e.g., fall–winter or spring–summer). Temporal filters work best in species with synchronized or restricted spawning seasons, as in these species development amongst individuals is more synchronized and there will be a time period when there is little overlap between regenerating and immature females (Hunter and Macewicz 1985, 2003).

There is no standardized method to assign spawning season or peak spawning periods, although a number of emerging methods were presented in Lowerre-Barbieri et al. (2011b). We further develop these methods here. The maximum spawning season duration was estimated based on the time period between the first and last dates that spawning females were observed. The core spawning season was estimated using a binomial regression to model calendar date associated with 50% spawning (Lowerre-Barbieri et al., 2020). We selected developing and spawning females to determine the mid-point for the beginning of the

spawning season and spawning and regenerating females were used to estimate the mid-point for the end of the spawning season. Typically, we would use the regressing rather than regenerating phase (Lowerre-Barbieri et al., 2011b; 2020). However, regressing was not a phase identified in the NMFS Panama City historic classification scheme. Peak spawning months were determined based on those months within the core spawning season which had a spawning fraction (the proportion of spawning females out of all mature females, see below) greater than that of the core spawning season as a whole.

Maturity

The timing of sexual maturity plays an important role in population dynamics and life history theory. Age at first maturity affects generation time (e.g., the average age of mature females in a population with a stable age distribution), and it is often used as a de facto biological reference point in an effort to allow fish to reproduce at least once before they are harvested (Beverton and Holt 1957; Caddy and Agnew 2004). When SSB is used as the measure of reproductive potential, maturity is the only reproductive metric integrated into stock assessments. However, size and age at maturity are not invariant, with changes in fishing mortality affecting them in one of two ways, (1) a density-dependent compensatory response wherein fish reach a higher average nutritional state (i.e., condition) with decreased relative population size which results in earlier maturation (Marshall and McAdam 2007); and (2) fisheries-induced evolution (Dieckmann and Heino 2007).

Size and age at 50% maturity are typically calculated from logistic models. However, a number of sampling issues, including where and when fish are sampled, if they come from fishery-dependent sampling with a minimum size limit, as well the histological indicator used to assign maturity, affect these results (Lowerre-Barbieri et al., 2011b). In addition, maturity is often accompanied by ontogenetic habitat shifts, resulting in recruitment to the spawning population occurring when fish are on the spawning grounds (Lowerre-Barbieri et al., 2016). Because of this, reproductive studies focused only on adult, spawning fish may not adequately sample for maturity. In addition, scientific surveys focused on adult fish, in conjunction with harvest regulations affecting fishery-dependent samples, can result in data that does not include the range of sizes and ages associated with immature, maturing, and mature fish.

Physiologically, the maturation process is a complex, continuous process that begins in the brain and pituitary and is finalized through gonadal development and fish participating in their first spawning event (Figure 1). Secondary growth oocytes (SG) include cortical alveolar (CA), vitellogenic (Vtg), and oocytes undergoing oocyte maturation (OM), and fish with this level of development are considered to have received the physiological cue to develop oocytes for the coming spawning season (Lowerre-Barbieri et al., 2011b). However, gonadal development does not always correspond to functional maturity (i.e., females that will definitely spawn during the current season), and determining functional maturity is complex given that the most advanced gamete stage (MAGS) cannot be used to distinguish between immature and mature females. This is because both immature and reproductively inactive mature females (i.e., regenerating) have primary growth (PG) oocytes as their MAGS, and fish maturing for the first time as well as repeat spawners developing for their next spawning season both will develop CA and Vtg

oocytes (Figure 1). However, because maturity is a process and ovaries in fish that spawned in previous seasons will have been stretched to accommodate hydrated oocytes, additional histological indicators can help identify young immature females from old regenerating females (Tables 1 & 2). These include small ovarian cross sections, increased interstitial tissue, well-organized lamellar structure, a lack of muscle bundles and/or small blood vessels, and thin ovarian walls.

However, the only histological markers with 100% accuracy in assigning functionally mature females are spawning markers (i.e., OM oocytes or POFs), as these confirm the fish matured and was part of the spawning population in the year it was sampled. Physiological maturity is indicated when fish have received the cue to develop secondary growth oocytes, i.e., CA and Vtg. Because fish recruiting to spawn for the first time often join the spawning population later in the season than repeat spawners (Lowerre-Barbieri et al., 2011b; Lowerre-Barbieri et al., 2018), fish sampled with CA oocytes during peak spawning months have been hypothesized to not have had enough time to fully develop and spawn. Whereas, for most warm-water fish, once they have developed vitellogenic oocytes they are either capable or very close to being capable of spawning.

To evaluate best practices for estimating size and age at maturity for Gulf of Mexico Red Snapper, we test several concepts associated with the above processes. First, we evaluate the temporal distribution of immature fish to see if there is a period of the year when few are sampled, suggesting a temporal filter could be used. We then calculate the size and age range containing both immature and mature females, the maturation window. This is calculated based on the smallest/youngest spawning female and the largest/oldest immature female. We use the maturation window to assess if secondary growth MAGS (CA and Vtg) sampled during peak spawning months are representative of immature and mature females, respectively. Past SEDARs based maturity estimates on the peak spawning months of June through August. We use this same time period to assess how this temporal filter affects sample sizes of immature females and the maturation window and the efficacy of CA, Vtg, and spawning markers to assign maturity. In SEDAR 7, immature fish were considered to be those assigned with an immature reproductive phase based on PG as their MAGS and additional histological indicators as outlined above. However, in SEDAR 31 and 52, females sampled during historic peak spawning months with MAGS of CA (equivalent to the early developing reproductive phase used here) were also assigned as immature. This was based on the assumption that fish this undeveloped in peak spawning months had never spawned before and would not have time to spawn within the year they were sampled. To test this, we assessed whether early developing females sampled in these months fell within the maturation window, or whether some were larger than the 100% mature size and age limits.

We first use data and models similar to those used in past SEDARs to compare results and determine the best methods of maturity assignment. Binomial generalized linear models (GLMs) were used with different link functions (logit, probit, cloglog and cauchit) and the best model was chosen via Akaike Information Criterion with Correction factor for small samples (AICc). Models were fitted in R (version 4.1.3) and model comparison was performed using the

R package 'MuMIn' (Bartoń K (2022). Estimated parameters were the intercept and slope. The inflection point (age or length at 50% maturity) was calculated by dividing the negative value of the model intercept by the slope. Immature fish were scored as 0 and mature fish as 1. For all initial models, data were selected for historic peak spawning months (June through August) to be comparable to past estimates. Models were run with two maturity assignments reflecting those used in SEDAR 7 (e.g., fish with a reproductive phase of immature were scored as 0 and all other females as 1) and SEDAR 31 and 52 (immature and early developing phases were scored as 0). Two additional models were run with reproductive phases of uncertain maturity removed from the data set. The first of these censored only early developing females, while the second censored all phases other than immature and functionally mature females, i.e. those with spawning markers (OM oocytes or POF). AICc scores were compared for different link functions and data definitions to determine the best approach.

Results from these initial analyses informed the data used to model whether maturation schedules varied by region (west and east of the Mississippi River) or stock status time period as defined above. Results showed an extended and asynchronous Red Snapper spawning season, and that peak spawning months included September. Because of this, the temporal filter did not improve estimates but did decrease sample sizes and was removed. Instead, we used the reproductive phase filter (retaining immature and functionally mature only) to ensure reproductive phases with uncertain maturity did not bias model results. Age and length at maturity were modeled as binomial regressions, including period and region as covariates. All models were first fitted using frequentist inference and additive covariate terms under different link functions (probit, logit, clog-log, and cauchit), then covariates were modeled as interactive terms and random effects using the link function with the highest AIC support, and those models were further compared using AIC. All models were fit in R and model comparisons were performed using the 'MuMIn' R package. The logit link had the highest support for both age and length, and in both cases, the models where both slope and intercept were treated as random effects had higher AIC support than models with additive or interactions terms for region and period. Because the frequentist models resulted in singular fits for the random effects models due to insufficient data availability for some period and region combinations, the models were refitted using Bayesian inference in the 'rstanarm' package (Goodrich et al., 2022), using the logit link function only. The response variables were mean-standardized and scaled to improve numerical stability. Fractional age rather than calendar age was used as the response variable for the age model. All models were run with default settings, including default, weakly informative priors and allowing internal coefficient autoscaling. Model fit was evaluated using the Rhat diagnostic (which compares between- and within-MCMC chain estimates to ensure proper mixing of the chains) as well as effective sample size and visual inspection of parameter trace plots.

The best model was chosen based on a combination of model comparison using k-fold cross validation (Vehtari and Lampinen, 2002), comparison of Bayesian R^2 values, and biological realism of the resulting predictions. Briefly, k-fold cross validation involves separating the data into chunks or folds, then refitting the model while holding out a fold at a time and evaluating the probability density of the held-out data based on parameter estimates. This was done using

the 'loo' R package (Vehtari et al., 2022) using 10 subsets. The inflection points (age and length at 50 percent maturity) were determined from tables of model predictions-at-age and -length, period and region.

Batch fecundity

We address here methodological issues that affect batch fecundity results to help inform parameters to be included in the full batch fecundity model (Lowerre-Barbieri and Friess, 2022), including the method of ovarian preservation and the stage of oocyte maturation at which the hydrated batch can be clearly separated from yolked oocytes. An analysis of covariance was used to assess the effect of non-formalin preservation (i.e, Gilson's and/or frozen) on the relationship between batch fecundity and somatic weight. To improve linearity, these variables were log-transformed.

Spawning frequency

Spawning frequency is the number of spawning events within a spawning period (for an individual) or the spawning season (for the population). For batch spawners with indeterminate fecundity, such as Red Snapper and most fish in the southeastern US, fecundity at age matrices and TEP cannot be estimated without this quantity. The data traditionally used to estimate spawning frequency includes spawning fraction and spawning season duration (Hunter and Macewicz 1985; Lowerre-Barbieri et al., 2011b). The spawning fraction is defined as the proportion of mature females spawning daily (Hunter and Macewicz 1985; Murua et al. 2003, 2010; Stratoudakis et al. 2006; Ganias 2009). The inverse of the spawning fraction is called the spawning interval (Lowerre-Barbieri et al., 2011b), but at the population scale this is a misnomer as it is not comparable to what is observed when individual spawning behavior is tracked over time (Lowerre-Barbieri et al., 2013).

Because spawning fraction is estimated at the daily scale, traditional measures are based on hydrated females (imminent and active spawners, Table 1) expected to spawn the day they are sampled or fish with day one POFs. These are the percent hydrated and POF methods, respectively (Hunter and Macewicz 1985). When spawning markers of longer duration are used, a correction factor is needed to standardize to 24 h. The accuracy of these estimates are affected by: (1) the spatial distribution of spawning versus sampling; (2) potential gear or spatial selectivity of spawning or recently spawned females (i.e. those with hydrated oocytes or day one POFs); (3) asynchronous spawn times affecting our ability to accurately age POFs from fish sampled in the wild, needed to calculate spawning marker duration; (3) choice of spawning marker (i.e., % hydrated or % POF) and how the mature population is defined; and (4) spawning season duration.

Although evaluating the spatial overlap between spawning and sampling was beyond the scope of this analysis, we address the other issues to help inform models used in Lowerre-Barbieri and Friess (2022). Catch times were not in the data but were available for the data provided by Brown-Peterson and Millender (2022 S74-DW-09) and used to assess time of day when Red Snapper spawn, if spawn times are synchronized, and to assess if markers of recent spawning (i.e., hydrated vs fresh POFS) occur at similar times. The full data set did include histological

markers associated with imminent spawning (hydrated, late hydrated, or late hydrated and fresh POFs) and recent spawning (POFs < 4 h old). However, this data was not provided for all records. These were compared to assess potential selectivity associated with sampling females just prior to spawning versus after recently completing it.

To better understand factors affecting traditional estimates of spawning frequency to both inform and gain insight into results from our model (Lowerre-Barbieri and Friess, 2022), we estimate spawning fraction, spawning interval, and spawning frequency using different spawning markers, definitions of the mature population, and estimates of the spawning season. Spawning markers include hydrating oocytes, day one POFs, and both combined. To select the mature population, we removed (1) immature females; (2) immature and early developing females; or (3) immature and early developing females smaller than the size at 50% mature. Two measures of spawning season (the core season and the season based on first and last occurrence of spawning females) were evaluated. For estimates of spawning fraction and frequency using all spawning markers, a correction factor was used to standardize results to daily spawning (i.e., 24 h/spawning marker duration). Following Porch et al. (2015), we used a spawning duration time of 34 h and a correction factor of 0.71.

Results and Discussion

Standardizing reproductive data best practices

Histological indicators

Reproductive phases, based on histological indicators, need data on MAGS, atresia, and POFs (Table 1, Figure 1). Fish with a developed brain-pituitary-gonad axis and which have reached a species-specific energetic threshold within the correct environmental context, will develop secondary growth oocytes, which include CA and later vitellogenic oocytes (Lowerre-Barbieri et al., 2011a). Prior to spawning, fish need to receive an additional cue to initiate OM (Figure 1). Most fished species in the Gulf of Mexico have pelagic eggs which undergo hydration as part of OM, resulting in the oocyte approximately doubling in size and becoming transparent. Fish in the late stages of OM, where hydrated oocytes are macroscopically identifiable, but no POFs are identified in histological slides are those needed for batch fecundity estimates (Table 1).

Brown-Peterson et al. (2011) presented standardized terminology for describing reproductive development in fishes. Here we slightly modify the reproductive phases described in their previous paper (immature, developing, spawning capable, regressing and regenerating). The phases we use here are: immature, early developing, late developing, spawning, regressing and regenerating (Table 1). The early developing phase has CA as the MAGS, late developing has Vtg oocytes (all stages of vitellogenesis), and spawning females have spawning markers (OM oocytes and/or POFs). Regressing fish are defined based on a high degree of atretic secondary growth oocytes and thus their MAGS can vary (Figure 1). These refinements were needed because some data providers did not assign vitellogenic oocyte stages (Vtg1, Vtg2 and Vtg3), but rather assigned a V for all vitellogenic oocytes. This is not surprising, as differentiating

between vitellogenic oocyte stages is difficult and can be somewhat subjective if the reader does not have extensive experience. We also needed a spawning phase to include all females with spawning markers for maturity and spawning frequency analyses. The immature phase uses the additional histological indicators outlined in the methods, but it is worth noting that these indicators work best for females which are very immature and have not yet developed a full PG population (e.g., Table 2.1). As immature fish develop a full PG population, these indicators are more difficult to observe (Table 2.1 H&E stain) and there is no conclusive histological indicator that can distinguish these phases.

Data synthesis

Fully compiled reproductive data has not typically been included in the standard SEDAR database. This, in conjunction with Panama City Laboratory personnel turnover, and a large amount of historic histological data, resulted in extensive time spent determining what data had been used in previous SEDARS but was not in our data set, as well as compiling and standardizing the data. To improve this process for future SEDARS, the workflow developed is described here and diagrammed in Figure 2. Individual data providers (including the NMFS Panama City Laboratory) contributed life history files and the NMFS Panama City Laboratory's database administrator merged these files based on field names. All field names were included, which resulted in a reproductive data set with many fields (Table 3), some for the same data type, but with different names, and no way to select for females (multiple fields with sex and varying designations) with reproductive data (no unique identifier). The largest challenge was the integration of historic and current data with varying classification schemes. For example, reproductive phase assignment was divided amongst three fields: 'histo_class', 'spawning_state', and 'repro_phase', as was the most advanced gamete stage. When there were data in multiple fields for the same variable, it often did not agree.

To make the data set useable we first standardized sex assignment, selected for females, standardized MAGS, and then assigned/confirmed reproductive phases. Records with a reproductive phase retained that phase, while those without, had one assigned using oocyte stage (i.e., PG, CA, V, OM) and presence of POFs (0-4 h, <= 24 h, > 24 h). This allowed for the assignment of all phases, with the exception of regressing, which is based on atresia. A series of checks were used to confirm reproductive phase assignment. Cases where new POFs were present and/or where MAGS were in stages of OM and/or where batch fecundity estimates were conducted and Reproductive Phase was not set to Spawning were assigned as Spawning. Batch Fecundity Estimates of 0 were changed to NA.

In past assessments (Lowerre-Barbieri et al., 2020; 2021) we have cross-referenced reproductive phases with the gonadosomatic index (GSI). However, this was difficult to do with this data set as Red Snapper exhibit greater variability in gonad weight with reproductive phase than most species, and also because ovaries were preserved with multiple methods (fresh, formalin, frozen) affecting ovarian weight and thus GSI value. Given the large, multi-species reproductive data sets that the Panama City Laboratory oversees, updating historic databases

to agree with current field names and assignments will be a priority. The R code developed here was shared and hopefully will help with this challenge.

Data

In the final data set used for this report, there were 11,527 females with a reproductive phase assigned. Of these, 11,334 had a fork length and 10,527 had both a length and a calendar age, referred to as simply age through the rest of this report. A total of 344 immature females were sampled, all with length but three are missing age. Most immature females were sampled either in targeted sampling of smaller females (2008) or in the most recent time period, as abundance stabilized (n=200; Figure 3A). Of the batch fecundity estimates with length, 1,138 also had age. Most reproductive data came from relatively young fish, 15 y or younger (Figure 3).

Sex ratio

The sex ratio, similar to past assessments, was approximately 1:1, with 52% female and 48% male.

Spawning seasonality

Sampling was not equally distributed throughout the year, with the greatest number of samples collected from May through September (Figure 4A). GOM Red Snapper have an extended and asynchronous spawning season. The earliest observed spawning activity was on January 16th and the latest was on December 18th, a duration of 337 d. A core spawning season of 218 days from March 17th to October 21st was estimated using the 50% spawning method (Figure 4B). Within the core spawning season, the overall spawning fraction was 48%. However, monthly spawning fractions within that time period greatly varied. Monthly spawning fraction was < 10% in March and April, increasing to 28% in May. Peak spawning months with a spawning fraction > 48% were June (60%), July (54%), August (49%), and September (59%). By October, the spawning fraction had decreased to 19%. Previous peak spawning months were reported as June through August (Kulaw et al., 2017, Glenn et al., 2017; SEDAR 52, 2018), and Brown-Peterson et al. (2019) suggested May exhibited peak spawning since 1995. Based on the standardized method of assigning the core spawning season and peak spawning months developed and applied here to the full SEDAR 74 data set, May was not a peak spawning month. However, results could vary depending on spatial scale and location, as well as potential gear selectivity.

Maturity

Immature females were sampled in all months, with the exception of February. Histological samples (all phases) came primarily from hook and line, handline, and long-line gear (92%). Roughly half of these (64%) were collected in scientific studies. However, sampling was often biased due to location or gear towards larger fish. In the full data set, the maturation size range was 196 mm to 542 mm FL based on the smallest spawning female and largest immature female. Most samples (65%) fell within this size range (n=7,415), with 34% larger than the maturation window (n=3,852) and only 1% (n=75) smaller than the smallest spawning female (Figure 5A). Of the fish smaller than the maturation window, 75% came from the 2008 SEAMAP

that targeted small fish for the 2009 update assessment. The maturation age range for all samples was ages 1 to 8 years and 88% of the samples fell within this range (Figure 5B).

The method of using a temporal filter and assigning early developing females as immature was not considered best practices due to decreased sample sizes and an inconsistent indicator of maturity. Selecting fish for historic peak spawning months (June through August) reduced the sample size of reproductive phases by 56% (n=6,476) and the number of immature females by 42% (n=146). Using the temporal filter also decreased the maximum observed length and age of immature fish from 542 mm FL to 473 mm FL and from 8 to 5 years old. Early developing females in peak spawning months ranged in size from 158 to 877 mm FL and in age from 1 to 10 years old, falling both within and above the maturation window (Table 4). The minimum size of early developing females was similar to that of late developing females (168 mm FL). Both early and late developing females had a minimum size larger than that of immature females (132 mm FL) but less than that of spawning females (196 mm FL). However, the mean size and age of late developing and spawning females was greater than that of early developing, suggesting that the early developing reproductive phase included both mature and immature fish.

Estimated L50s were similar when the temporal filter was used for the four maturation assignments, but models differed in the preferred link function and model fit (Figure 6). Four maturation assignments were used: (1) immature scored as 0, all other phases were scored as 1); (2) immature and early developing phases scored as 0, all other phases as 1; (3) immature scored as 0, early developing females removed, other phases scored as 1; and (4) immature scored as 0, spawning as 1, and all other reproductive phases removed. The logit model was the best fit for all but the second maturation assignment, where early developing individuals were considered immature, resulting in an extended size range for immature fish. For this maturation assignment, the best fit model was the cauchit. However, the AICc was an order of magnitude larger than the other models. The model with the best fit was maturation assignment four, with only immature and spawning females. The AICc was 497.5 and the L50 was 255 mm FL. Based on these results, models to assess spatio-temporal effects in maturity did not use a temporal filter and were based on only immature and spawning phase females.

Age-at-maturity – The models supported a period-and-region effect on maturity at age (the model without covariates had the lowest R^2 value and the lowest expected log pointwise density, elpd; Table 5). The model with both the highest elpd and Bayesian R^2 was the interaction model, but this model produced biologically unrealistic estimates of age at 50% maturity for period 1 in the East and period 2 in the West (Table 5). The model with the second highest R^2 value was the full random effects model (parameter estimates and mcmc fit diagnostics shown in Table 6). This model produced biologically plausible A50 values and we therefore chose to use the random effects model for further inference. The results from this model suggest that age at 50% maturity increased over time in both regions, and that fish in the Western Gulf consistently had higher age at maturity than fish in the Eastern Gulf (Table 5). Age at 50% maturity in the Eastern Gulf was estimated to increase from 1.36 y (fractional age) in the early period to 1.44 y in the mid period and finally 1.93 y in the late period. In the Western Gulf, age at maturity increased from 1.52 y in the early period to 1.71 y in the mid period to 2.46 y in

the final period. Furthermore, the shape of the estimated maturity-at-age relationship is less knife-edged over time in both regions (Figure 7). The A50 estimate for the time-and-space-aggregated model was 1.64 y (Table 5).

Length-at-maturity – As with age-at-maturity, the length-at-maturity models supported the existence of the period-and-region effect, and the interaction model had the highest R^2 value and the highest elpd. The R^2 value for the model without covariates was 0.43 while that for the interaction model was 0.57. A close second was the full random effects model with an R^2 of 0.56 (Table 7). As with age, the random effects length model suggested an increase in length at 50% maturity by period, but unlike the age model, estimated length-at-maturity was higher in the East than the West for all but the additive model (Table 7). Generally, the L50 estimates were similar between the additive, interaction, and random effects model, with the random effects model estimating a higher L50 for the period/region combinations that the models generally had a hard time fitting (i.e., the early period in the East and the mid period in the West). To be consistent with the age model, we show the random effects model diagnostics in Table 8. As with the age model, the predicted relationship of length at maturity became less steep with time (Figure 8). Length at 50% maturity in the East was estimated to be 25.6 cm in the early period, 28 cm in the mid period, and 32.8 cm in the late period. In the West, the estimates were 22 cm in the early period, 23.8 cm in the mid period, and 31.5 cm in the late period (Table 7). The L50 estimate for the time-and-space-aggregated model was 28.3 cm fork length (Table 7).

Batch fecundity

Preliminary data visualization of batch fecundity at age suggested differences with stock status periods (i.e., overfished, rapidly recovering and stabilizing), with lower batch fecundity at age observed in the most recent period, as stock abundance stabilizes (Figure 9). However, ovarian preservation type can affect batch fecundity estimates. Of the 1,212 batch fecundity estimates with age, 138 were preserved either in Gilson's or were frozen. Gilson's is known to break down hydrated oocytes over time (Lowerre-Barbieri et al., 1993) and freezing ovaries is reported to change ovarian weight and oocyte size (Ganias et al., 2015). There was a significant difference in the batch fecundity to size relationship (Figure 10) for ovaries that were preserved in formalin versus in Gilson's or frozen [$F(2, 1064) = 31.11, = < 0.001$] after adjusting for somatic weight. This preservation effect was integrated into the final batch fecundity model (Lowerre-Barbieri and Friess, 2022).

Spawning frequency

Spawn times (i.e., the time of day that spawning events occur) are not synchronized in Red Snapper. Females undergoing the different stages of oocyte maturation were observed throughout daylight hours from 0700 to 1900 h. In Red Snapper collected from Mississippi waters, the greatest number of females with hydrated oocytes were captured between 1100 and 1400 h (Figure 11), but fully hydrated oocytes were seen as early as 0700 h and as late as 1500 h. Newly collapsed POFs first appeared at 1400 h and were most common at 1900 h. This is similar to results reported in Jackson et al. (2006), who report hydrated oocytes in Red

Snapper between 0900 and 1700 h. They suggested peak spawning occurs at 1600 h based on the occurrence of fresh POFs. In Red Snapper sampled along the east coast of Florida, Lowerre-Barbieri et al. (2015) found newly collapsed POFs as early as 0700 h and throughout the day. The time period with the greatest number of fresh POFs was 1600 h, similar to the results from Jackson et al. (2006). However, similar to the pattern in Red Snapper collected from Mississippi waters, the peak of fresh POFs was seven hours after the peak in fully hydrated females (11:00; Jackson et al. 2006). This lag between imminent and recent spawners is surprising, imminent and recent spawners typically overlap in time. In the full database, 45% of females with OM oocytes were imminent spawners (n=1,630). In contrast, of the females that had age categories assigned to POFs (n=2,703), only 4% were 0-4 hours old, suggesting fish which had recently spawned were not equally sampled.

Traditional estimates of annual spawning frequency ranged from ~37 to 109 spawning events, depending on the choice of spawning marker, definition of the mature population, and method to assign spawning season (Table 9). Spawning intervals ranged from ~ 2 d to 6 d. However, as mentioned, this does not represent the real time between individual spawning events, which varies between individuals and over time. For example, 5% of females had both hydrated oocytes and day 1 POFs, indicating daily spawning. The mature spawning population for spawning frequency typically uses all but immature fish in the denominator. Not surprisingly, when non-spawning reproductive phases were not included, spawning frequency increased, as also seen in Brown-Peterson and Millender (2022, S74-DW-09). Although filtering out early developing females smaller than the size at 50% maturity would seem intuitively to address potential immature females in the denominator, it resulted in a slightly decreased spawning fraction. Spawning frequency also varied with spawning marker. Using all mature females and the core spawning season, there was a wide range in spawning frequency depending on spawning marker used. Spawning frequency varied with spawning marker, from: (1) 39 spawns for % hydrated; (2) 46 spawns for % POFs; and (3) 70 spawns for all markers after applying the marker duration correction factor. The number of spawns for the latter increased to 109 if the spawning season was based on the first and last occurrence of spawning fish, which is common in most discussions of annual spawning frequency for Red Snapper.

Within the core spawning season, the proportion of spawning females (all markers) varied with age. Only 44% of the youngest fish (< age 8) were spawning, 65% of fish between ages 8 and 15 were spawning, and 65% of fish older than age 15 were spawning (Table 9). These differences were significant ($\chi 2=255.7$, $P< 0.0001$, n=9660), and resulted in fish younger than age 8 having an estimated spawning frequency of 67 compared to older fish, which were estimated to spawn 99 times (Table 9). In addition, Brown-Peterson and Millender (2022, S74-DW-09) showed that daily spawning increased in older females.

These results illustrate the uncertainty associated with estimating spawning frequency for fish with indeterminate fecundity. The effect of this uncertainty on estimates of annual fecundity using traditional methods is large and is obvious when looking at annual fecundity. Taking the mean batch fecundity for all females of 270,927 eggs and the range of observed spawning frequency estimates (37 to 109 spawning events), mean annual fecundity varies from ~10

million eggs to ~29 million eggs. Best practices for identifying what spawning markers to use and how to select for the mature population can help decrease uncertainty in spawning frequency estimates. Improved modeling approaches to estimate spawning frequency will also decrease uncertainty (Porch et al. 2015). The Porch et al. (2015) model was adapted by Lowerre-Barbieri and Friess (2022) to integrate multiple years of data and to assess the effects of region and stock status period. This model moves beyond traditional measures of spawning frequency by modeling the probability of a fish having spawning markers based on its length or age and relevant covariates. In addition, it addresses two key areas of uncertainty: the difficulty in estimating mature females and how best to define the spawning season, as neither of these variables are needed for these models. Spawning frequency is modeled using only presence/absence of spawning markers, which only occur in mature fish. Rather than a spawning season, spawning fraction is estimated for the full year and monthly differences are addressed with a gamma function (Lowerre-Barbieri and Friess, 2022; Porch et al., 2015).

Both batch fecundity and spawning frequency are necessary for TEP estimates. However, there remain a number of data limitations for using TEP, which result in uncertainty. These include that most stock assessments do not have fecundity data for the lifespan of the fish being assessed due to age truncation. For example, Red Snapper is an extremely data rich species, yet 98% of the batch fecundity estimates are for fish younger than 15 years old, despite an estimated life span of 57 years. The spawning marker used, potential selectivity issues associated with sampling spawning females, and a poor understanding of spawning marker duration and thus the appropriate correction factor also contribute to uncertainty in TEP estimates used as the measure of reproductive potential in stock assessments.

Recommendations for Best Practices for Standardizing Reproductive Methodology

Based on our experience working through this analysis as a group, we make the following best practices recommendations for future reproductive studies and stock assessments:

1. **For the SEDAR reproductive data template,** we recommend simplifying it to address the most important data needs. Specifically, rather than developing a template that can be used for all species we recommend the development of a template for gonochoristic females, which is the data most commonly used in stock assessments, with the recognition that hermaphroditic species will use a more complex template. To be able to assess diel periodicitiy, spawn times, and potential selectivity for spawning females, we recommend adding a catch time field and the need for POF ages and OM sub-stages.

2. To improve the ease of assigning **reproductive phase** and its use in analysis, we recommend the following refinements to Brown-Peterson et al. (2011): Changing Early Developing with CA MAGS, from a subphase to a phase; replacing Spawning Capable with Spawning for females with all spawning markers; and using a Late Developing phase for fish with any stage of vitellogenic oocytes but no spawning markers.

3. **QA/QC protocols** for reproductive data: ensuring that each data provider has standardized their own reproductive data before providing it, character variables having the same capitalization scheme, spelling mistakes corrected, and ensuring values from Comments fields are in their correct location. All fish with reproductive data should have a provider-derived unique identifier and sex assigned as 'M', 'F'. or 'U'. Data providers should be instructed prior to submitting data to ensure that they do not have multiple fields for the same thing. If the reproductive template is not yet in place, data providers should provide a data dictionary, which defines what each variable represents and acceptable responses. Lastly, the compiled data should be checked against that used in previous assessments to ensure there is not missing data.

4. To standardize methodology used to determine the **spawning season** duration and peak spawning months we recommend: using the first and last occurrence of spawning females to identify the maximum duration of spawning for a population. We recommend the core spawning period be based on a binomial regression to model calendar date associated with 50% spawning (Lowerre-Barbieri et al., 2020) and the appropriate developing phase for the start date and regressing or regenerating phase for the end date. Peak spawning months should be determined based on those months with a higher spawning fraction than that observed throughout the core spawning season.

5. To standardize data used for **maturity models**, we recommend that phases indicative of physiological maturity (i.e., fish with secondary growth oocytes, either CA or V) be evaluated for their size and age range versus that of the maturation window and that best practices, if sample sizes allow, is to only use reproductive phases indicative of immature females and functionally mature females (i.e, fish with spawning markers). We suggest that this reproductive phase filtering approach may increase accuracy more than temporal filters for fish with extended spawning seasons, which are common in warm waters.

6. We recommend as best practices for estimating **batch fecundity** to use only fish which are in late OM whose "batch" of hydrating oocytes has clearly separated from less developed oocytes. We also recommend conducting batch fecundities on fresh ovaries where possible and formalin-preserved ovaries when needed, such as with relatively deep-water reef fish like Red Snapper. The washing process presented in Lowerre-Barbieri et al. (1993), which works equally well on fresh or preserved samples, is recommended for separating out the OM oocytes for fecundity estimates. Lastly, we recommend that all ovaries used for batch fecundity estimates also be analyzed histologically to confirm they do not have POFs <4 h, i.e., have not started to ovulate.

7. To improve traditional estimates of **spawning frequency** we recommend that spawning fraction be estimated with all females other than those assigned as immature in the denominator. To improve estimates of spawning frequency, we recommend additional research into understanding factors driving spawning marker prevalence and spawning

marker duration, as both of these will affect spawning frequency estimates. We also recommend that research assessing selectivity of imminent and recent spawners is needed, and lastly that models with the necessary covariates be developed following Porch et al. (2015) and Lowerre-Barbieri and Friess (2022).

Acknowledgements

We would like to thank Erik Lang, who participated in the workshop and several discussions afterwards, providing important insights. We'd also like to acknowledge all of the data providers and the technicians who conduct the time-consuming batch fecundity estimates and histological analyses. This report would not have been possible without your efforts! A special thanks to Hayden Menendez, Ashley Pacicco, Michelle Duncan, and Anna Millender.

Table 1. Reproductive state, reproductive phase, histological indicators associated with each phase, and importance of each phase to reproductive dynamics. PG—primary growth; CA—cortical alveolar; Vtg—vitellogenic; OM—oocyte maturation; GVM—germinal vesicle migration; GVBD—germinal vesicle breakdown; POF—postovulatory follicle

Reproductive state		Phase	Histological indicators	Significance
Immature	Nonspawn-ing	Immature	Oogonia and PG oocytes, no muscle bundles or large blood vessels. Lamellae are well-organized.	Virgin that has not yet recruited to the spawning population.
Mature	Preparing for the spawning season	Early Developing	PG and CA oocytes. No evidence of POFs. Some atresia may be present.	Environment conducive to secondary oocyte growth.
Mature	Close to or in the spawning season	Late Developing	Females with vitellogenic oocytes in any stage (Vtg1, Vtg2, Vtg3) and no spawning markers. Can have low levels of atresia.	Secondary growth oocytes are well developed
	Spawning season	Spawning	OM hydration or POFs.	Fish with indicators of spawning activity.
		Imminent	Early OM (lipid coalescence and GVM with little yolk coalescence)	Will spawn in 14 h. Too early for batch fecundity estimates
		Active	Late OM (hydrated oocytes can be seen without a microscope), late-stage GVM or GVBD with yolk coalescence and partial to full hydration), ovulation, or newly-collapsed POFs	Spawning +/- 2 h. Ovaries with late OM and no POFs are used for batch fecundity estimates.
		Recent	POFs typically 12 to 24 h old, in some fish can be identified to 48 h	Spawned within the past 1-2 days
Mature	Ending the season	Regressing	50% or more of yolked oocytes are undergoing atresia (alpha and beta).	Cessation of spawning.
	Between spawning seasons	Regenerat-ing	Only PG growth oocytes present. Muscle bundles, enlarged blood vessels, thick and/ or convoluted ovarian wall, and gamma or delta atresia may be present.	Sexually mature, reproductively inactive.

Table 2. Red Snapper, *Lutjanus campechanus* reproductive phases (1=immature; 2=early developing; 3=late developing; 4=spawning; 5=regressing; 6=regenerating).

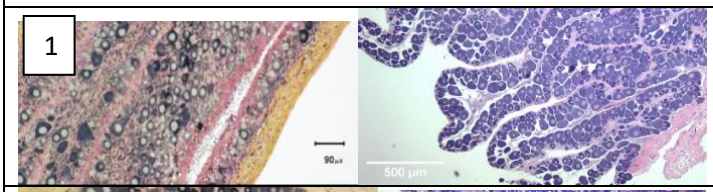
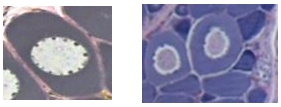
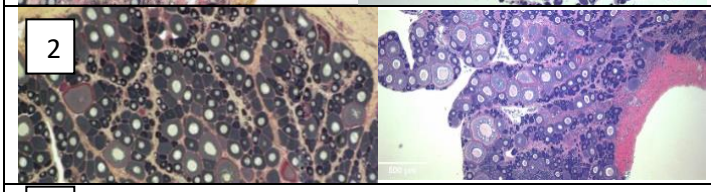
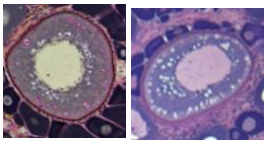
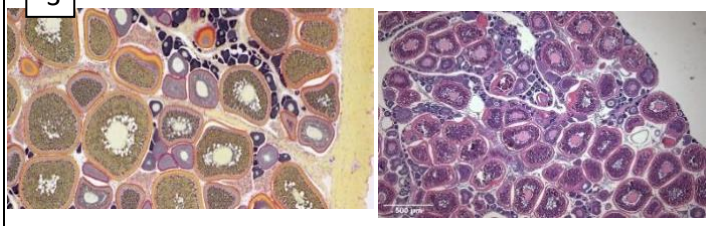
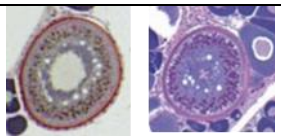
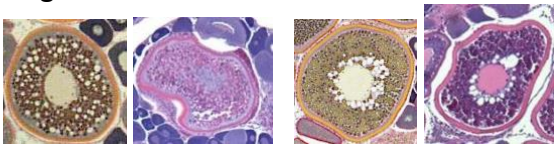
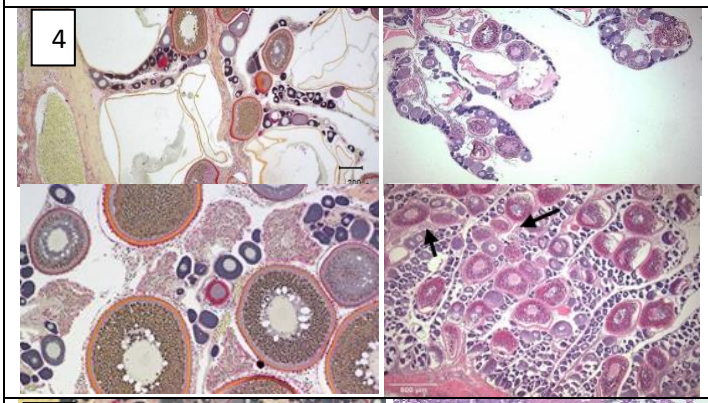
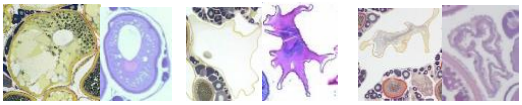
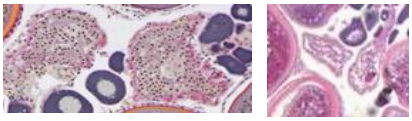
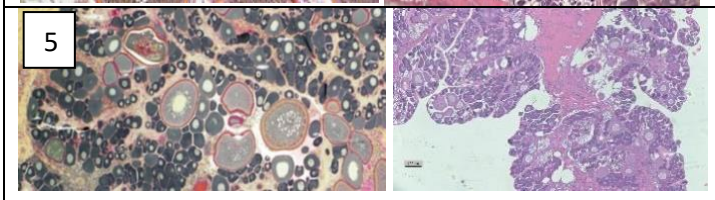
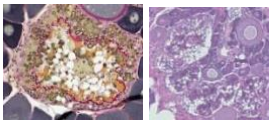
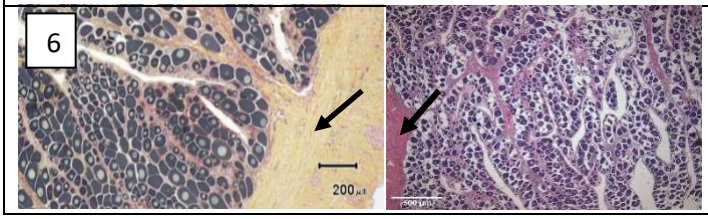
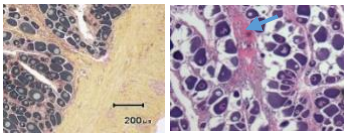
Ovarian Cross Section		**Most advanced oocyte or key histological indicator**	
PAS stain	**H&E stain**	**PAS**	**H&E**
1 		 Perinucleolar	
2 		 Cortical alveolar	
3 		 Vtg1  Vtg2 Vtg3	
4 		 GVM Hydrated Ovulated  24 hour POFs	
5 		 Alpha atresia	
6 		 Thick ovarian wall Blood Vessels	

Table 3. Reproductive and demographic/sampling variables needed to estimate parameters for reproductive potential, reproductive variables identified as important in best practices webinars, and reproductive variables in the current data set.

Reproductive variables needed	**Variables from best practices**	**Variables in data set**
Sex	Gonad_Observed	atresia
Ovarian preservation method	Histo_Taken	average_HO_diameter
Macroscopic or Histological assessment	Macro_Sex	Batch_fecundity_estimate
Batch fecundity estimate	Secondary_Sex	BFE_comments
Gonad weight	Secondary_Sex_Attribute	BFE_date_read
Most advanced gamete stage (MAGS)	Macro_Repro_Phase	BFE_reader_initials
POFs	Histo_Sex	blocking comments
Reproductive phase	Historic_Data	bug_6249_BFE_notes
Reproductive comments	Histo_Repro_Phase	gonad_comments
Transitioning (for sequential hermaphrodites)	Histo_Repro_Sub_Phase	gonad_condition
Indicators of prior spawning	Most_Advanced_Gamete_Stage	gonad_percentage
	POF	gonad_region
Additional data needed	Histological_Indicator_1	gonad_status_code
Length	Histological_Indicator_2	gonad_weight_fresh_g
Weight	Histological_Indicator_3	gonad_weight_formalin_g
Age	Parasites	gonad_weight_frozen_g
Date of capture	Melanomacrophages	***histo_class*****
Time of capture		histo_date_read
Location of capture		histo_maturity
Survey type (SS or FDM)		histo_maturity_impression
Gear		histo_nbr
		histo_reader_comments
		histo_reader_initials
		histo_sex
		ind_prior_spwn_state_nbr
		leading_gamete_stage*
		long_term_atresia
		macro_class
		macro_maturity
		macro_sex
		MAGS*
		MaxOD
		micro_stage
		NBR_HOs_Portion_1_Sample_A
		(these have 6 portions and sample A

	and B)
	oocyte_stage*
	outlier_and_Notes
	Peak_spawning
	POFs**
	post_ovul_foll_state_nbr**
	preservation_type
	repro_phase*
	repro_notes
	short_term_atresia_code
	spawner
	spawning_state*
	UF_fecundity_estimated
	UF_samples_provided_by
	UF_source_fecundity_estimate
	whole_weight_g
	*These are all the same thing
	**These are all the same thing
	***These are the same thing

Table 4. Size (mm FL) and age of female Red Snapper sampled in historic peak spawning months (June-August) by reproductive phase, demonstrating the overlap in both size and age among phases. Spawning females are considered the best indicator of mature females and immature females the best indicator of immature females. Most advanced gamete stage (MAGS) indicated for each phase. PG—primary growth; CA—cortical alveolar; Vtg—vitellogenic; OM—oocyte maturation; POF—postovulatory follicle

Reproductive phase (MAGS)	**Sample size**	**Minimum size**	**Maximum size**	**Mean size**	**Minimum age**	**Maximum age**	**Mean age**
Immature (PG)	146	132	473	248	1	5	1.7
Early developing (CA)	387	158	877	407	1	10	3.6
Late developing/ Spawning capable (Vtg)	387	168	919	493	1	34	5.3
Spawning (OM or POFs)	3,376	196	925	510	1	40	5.5
Regenerating (PG)	236	222	737	415	1	16	1.7

Table 5. Select age-at-maturity model comparison results. Covariate terms were period and region. The interaction model is the preferred mode with the highest expected log pointwise density (elpd) based on 10-fold cross-validation, but it produced biologically unrealistic inflection point estimates for some period-region combinations. The random effects model where group-specific intercepts and slopes for region and period were estimated was chosen as the preferred model. 1– overfished (1991-2008; 2– rapidly recovering (2009-2016); 3–stabilizing (2017-2019).

Model	**elpd_kfold**	**R^2**	**a50**					
No covariates	-700.9	0.32	1.64					
			East			*West*		
			1	*2*	*3*	*1*	*2*	*3*
Interaction	-574.6	0.43	0.57	1.63	2.00	1.71	0.76	2.06
Additive terms	-619.9	0.40	0.77	1.11	2.00	1.41	1.76	2.64
Random effects	-597.9	0.42	1.36	1.44	1.93	1.52	1.71	2.46

Table 6. Random effects age-at-maturity model parameter estimates and mcmc fit diagnostics (note: age was mean-standardized and scaled (divided by 10) to improve numerical stability).

	mean	**sd**	**10%**	**50%**	**90%**	**mcse**	**Rhat**	**n_eff**
(Intercept)	2.9	2.2	0	2.9	5.6	0	1	2016
age_cent	11	4.4	5.4	11.3	16.3	0.1	1	1769
b[(Intercept) period:1]	10.6	3.1	6.6	10.6	14.7	0.1	1	1429
b[age_cent period:1]	19.5	6.3	11.5	19.1	27.8	0.2	1	1678
b[(Intercept) period:2]	5.3	2.6	2.1	5.2	8.8	0.1	1	1357
b[age_cent period:2]	8.6	5	2.5	8.2	15.1	0.1	1	1487
b[(Intercept) period:3]	1.2	2.5	-1.9	1.1	4.5	0.1	1	1295
b[age_cent period:3]	1.2	4.5	-4.4	0.9	7.2	0.1	1	1447
b[(Intercept) region:E]	2.1	2	0.3	1.6	4.9	0.1	1	1324
b[age_cent region:E]	2.8	2.9	0	2.1	6.6	0.1	1	1470
b[(Intercept) region:W]	0.3	1.8	-1.3	-0.1	2.8	0	1	1497
b[age_cent region:W]	0.1	2.3	-2.2	-0.3	2.8	0.1	1	1771
Sigma[period:(Intercept),(Intercept)]	24.2	18.3	7.5	19.5	46	0.4	1	1809
Sigma[period:age_cent,(Intercept)]	29.6	20.8	8.7	25.4	56.7	0.4	1	2276
Sigma[period:age_cent,age_cent]	63.2	41.1	21.2	53.7	117.2	0.9	1	2194
Sigma[region:(Intercept),(Intercept)]	5	8	0.3	2.2	12.4	0.2	1	2172
Sigma[region:age_cent,(Intercept)]	2.5	6	-0.5	0.9	7.7	0.1	1	2259
Sigma[region:age_cent,age_cent]	7.2	11.8	0.3	3.3	18	0.3	1	2231
mean_PPD						0	1	4083
log-posterior						0.1	1	1159

Table 7. Select length-at-maturity model comparison results. Covariate terms were period and region. The interaction model is the preferred mode with the highest expected log pointwise density (elpd) based on 10-fold cross-validation. We chose the random effects model as the best model to be consistent with age model results. Period 1– overfished (1991-2008; 2– rapidly recovering (2009-2016); 3–stabilizing (2017-2019).

Model	**elpd_kfold**	**R^2**	**l50**					
No covariates	-626.5	0.43	28.3					
			East			*West*		
			1	*2*	*3*	*1*	*2*	*3*
Interaction	-463.5	0.57	23.7	28.5	32.9	21.9	21.3	31.0
Additive terms	-489.3	0.54	22.3	26.5	32.7	22.7	26.9	33.1
Random effects	-473.9	0.56	25.6	28.0	32.8	22.0	23.8	31.5

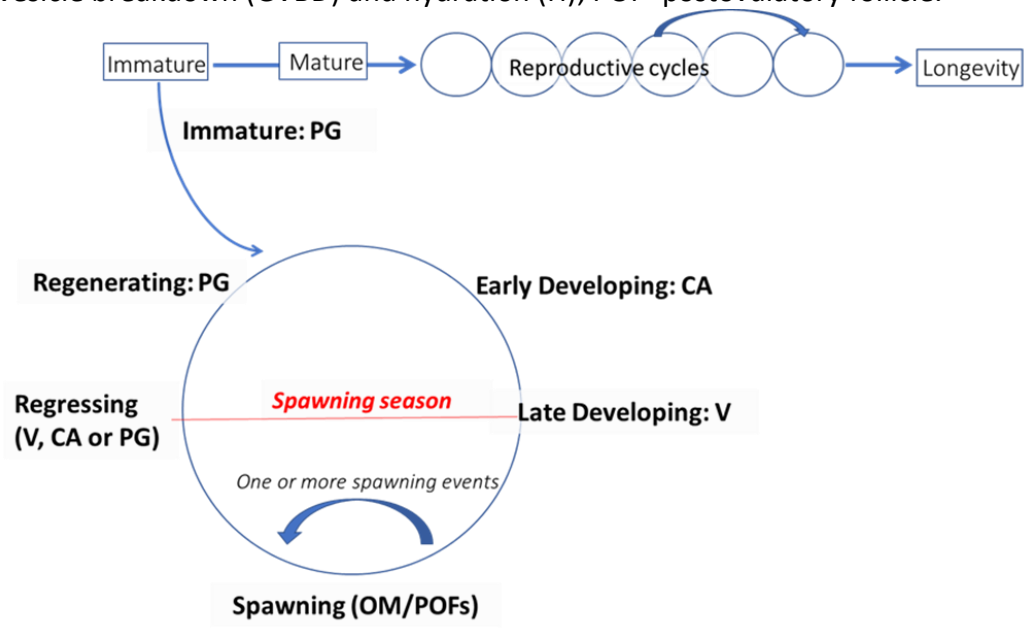
Table 8. Random effects length-at-maturity model parameter estimates and mcmc fit diagnostics (note: length was mean-standardized and scaled (divided by 10) to improve numerical stability).

	mean	**sd**	**10%**	**50%**	**90%**	**mcse**	**Rhat**	**n_eff**
(Intercept)	3.6	2.2	0.7	3.6	6.4	0	1	2576
fl_cent	1.3	1.3	-0.5	1.3	2.9	0	1	2350
b[(Intercept) period:1]	8.2	3.1	4.5	8	12.4	0.1	1	1670
b[fl_cent period:1]	2.5	1.3	1	2.3	4.2	0	1	1659
b[(Intercept) period:2]	2.8	2.6	-0.3	2.5	6.3	0.1	1	1763
b[fl_cent period:2]	0.8	1.2	-0.5	0.6	2.3	0	1	1721
b[(Intercept) period:3]	-0.3	2.5	-3.4	-0.5	3.1	0.1	1	1669
b[fl_cent period:3]	0.3	1.2	-1	0.1	1.8	0	1	1593
b[(Intercept) region:E]	4.1	2.5	1.4	3.6	7.6	0.1	1	1579
b[fl_cent region:E]	2.3	1.5	0.7	2.1	4.4	0	1	1719
b[(Intercept) region:W]	1	2.4	-1.6	0.5	4.3	0.1	1	1554
b[fl_cent region:W]	0.6	1.5	-1.1	0.3	2.6	0	1	1707
Sigma[period:(Intercept),(Intercept)]	19.1	16	5.4	14.4	38.6	0.4	1	2029
Sigma[period:fl_cent,(Intercept)]	4.8	5.5	0.5	3.3	11	0.1	1	2091
Sigma[period:fl_cent,fl_cent]	3.8	5.5	0.5	2	8.5	0.1	1	1899
Sigma[region:(Intercept),(Intercept)]	9.7	12.5	1.4	5.3	22.3	0.3	1	2275
Sigma[region:fl_cent,(Intercept)]	3.1	5.5	-0.4	1.6	8.6	0.1	1	1910
Sigma[region:fl_cent,fl_cent]	4.8	6.2	0.6	2.7	11	0.1	1	2420
mean_PPD						0	1	4043
log-posterior						0.1	1	1296

Table 9. Data choices affecting estimates of spawning fraction, interval and frequency (top) and spawning frequency by age group (bottom). Changes in parameters are in bold. A correction factor of 0.7 (Porch et al. 2015) was used in estimates based on all spawning markers

Data used for mature population	Spawning marker	Spawning season	Spawning fraction	Spawning interval (days between spawns	Spawning frequency (# spawns in season)
no immature	Hydrated	core (218 d)	18%	5.6	39.2
no immature; early developing FL > L50	Hydrated	core (218 d)	17%	5.9	37.1
no immature or early developing	Hydrated	core (218 d)	20%	5.0	43.6
equivalent to spawning capable (i.e., late developing and spawning)	Hydrated	core (218 d)	22%	4.5	48.0
no immature	**Day 1 POFs**	core (218 d)	21%	4.8	45.8
no immature	**All markers**	core (218 d)	32%	3.1	69.8
no immature	All markers	**1st & last (337 d)**	32%	3.1	108.7
Differences with age groups					
no immature; females < age 8	All markers	core (218 d)	44%	3.2	67.1
no immature; females ages 7 to 15 y	All markers	core (218 d)	65%	2.2	99.2
no immature; females > 15 y	All markers	core (218 d)	65%	2.2	99.2

Figure 1. Fish mature once in a lifetime and iteroparous species participate in multiple reproductive cycles within their lifetime (top). The reproductive cycle (middle) is associated with the needed ovarian development to spawn at a time and place conducive to offspring survival. Batch spawners, like Red Snapper, spawn multiple times within a cycle. Reproductive phases and most advanced gamete stages (MAGS) are used to define the cycle. Oocyte development needed to result in a spawning event (bottom). PG–primary growth; CA–cortical alveolar; V–vitellogenic (including primary (Vtg1), secondary (Vtg2), and tertiary (Vtg3); OM–oocyte maturation stages (germinal vesicle migration (GVM), yolk coalescence (YC), germinal vesicle breakdown (GVBD) and hydration (H); POF–postovulatory follicle.



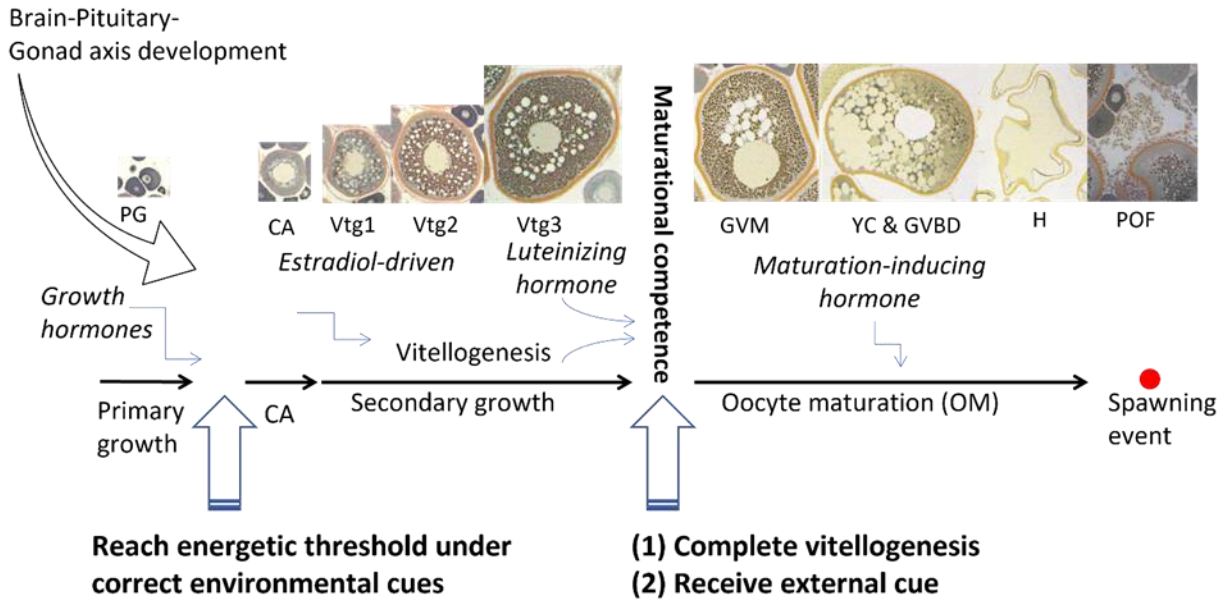


Figure 2. Reproductive data collection, QC, and standardization processes.

Figure 3. Red Snapper reproductive phase and batch fecundity data by age and region sampled. C=Central, E=East, W=West. Due to low sample sizes from the East, this was combined with the Central region, resulting in an East and West region for consequent analyses.

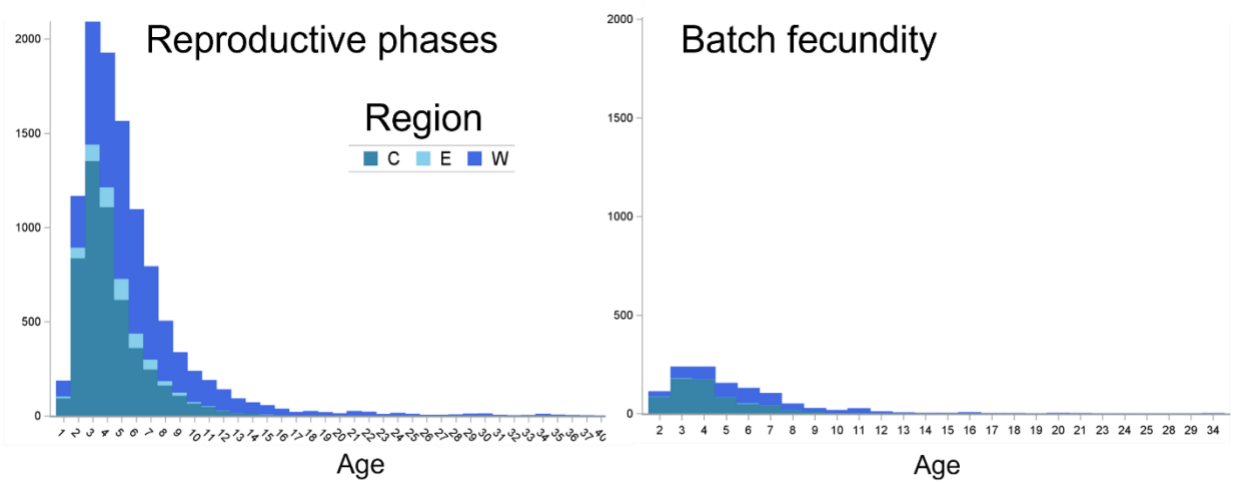


Figure 4. Determination of Red Snapper spawning seasonality. A. Number of females captured each month in six reproductive phases (years and locations combined). 1=immature, 2=early developing, 3=late developing, 4=spawning, 5=regressing and 6=regenerating. B. Determination of the core spawning season based on 50% of early developing, spawning and regenerating fish.

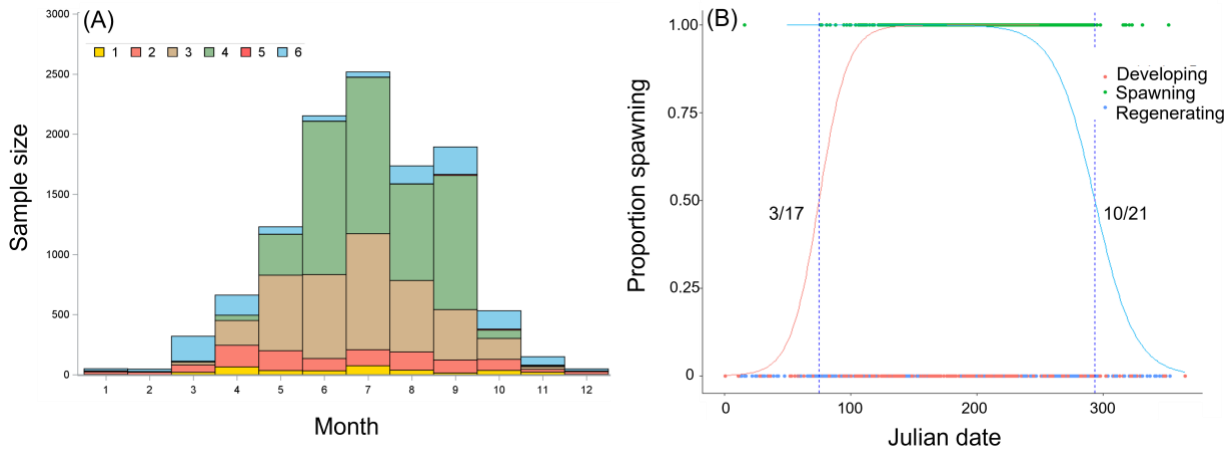


Figure 5. (A) Annual size (mm FL) and (B) age ranges of female Red Snapper in the SEDAR 74 reproductive data file. Dashed lines represent the maturation window, i.e., the smallest/youngest and largest/oldest immature females collected.

Figure 6. Maturity at length observations and ogives from binomial generalized linear models with different link functions (logit, probit, cloglog and cauchit) and different data and maturity assignments. These were used to be comparable to past SEDARs, utilizing two ways to assign immature fish (1 and 2) and two reproductive phase data filters (3 and 4). Only samples from historic peak spawning months (June-August) were used. The preferred link function determined via AICc was the logit in all cases except when early developing females were considered immature.

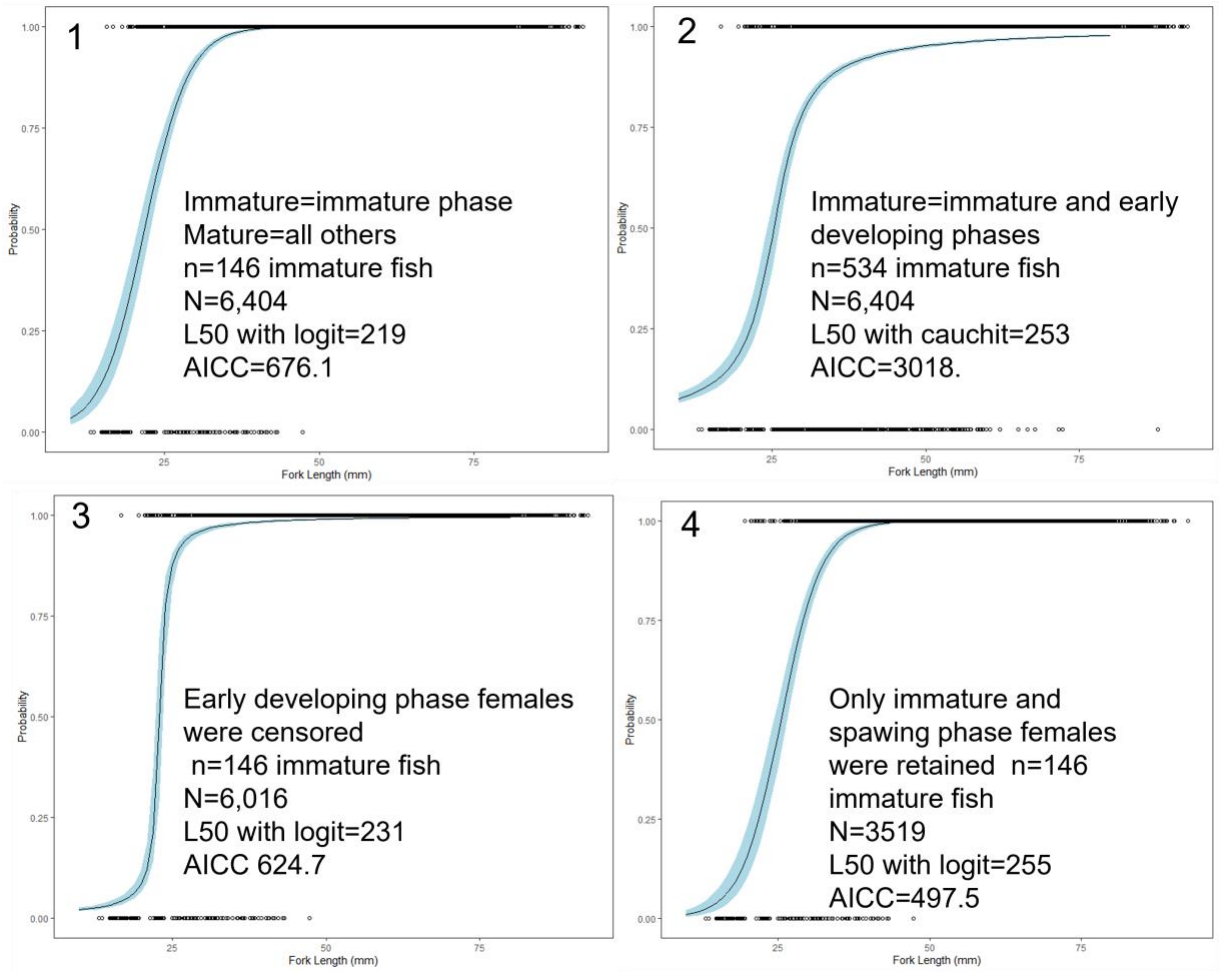


Figure 7. Observed and predicted age at maturity, from a logistic binomial regression that estimated period-and-region-specific slopes and intercepts in a Bayesian modeling framework. The blue shaded area represents the upper and lower 2.5% quantiles from the posterior distribution of parameter estimates. Period 1– overfished (1991-2008); 2– rapidly recovering (2009-2016); 3–stabilizing (2017-2019).

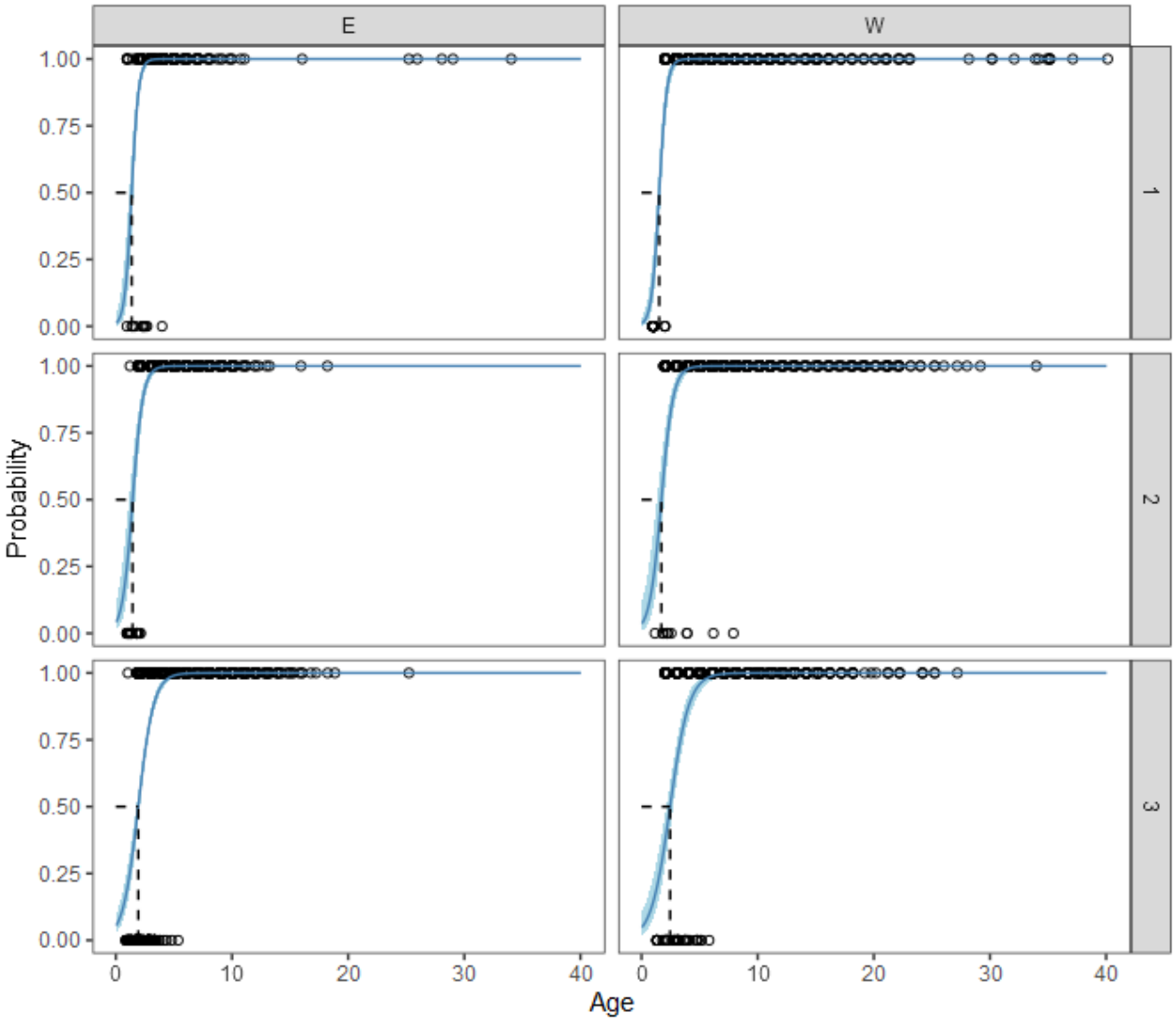


Figure 8. Observed and predicted size at maturity results from a logistic binomial regression that estimated period-and-region-specific slopes and intercepts in a Bayesian modeling framework. These models used data collected from throughout the year but only immature and spawning reproductive phases. The blue shaded area represents the upper and lower 2.5% quantiles from the posterior distribution of parameter estimates. Period 1– overfished (1991-2008); 2– rapidly recovering (2009-2016); 3–stabilizing (2017-2019).

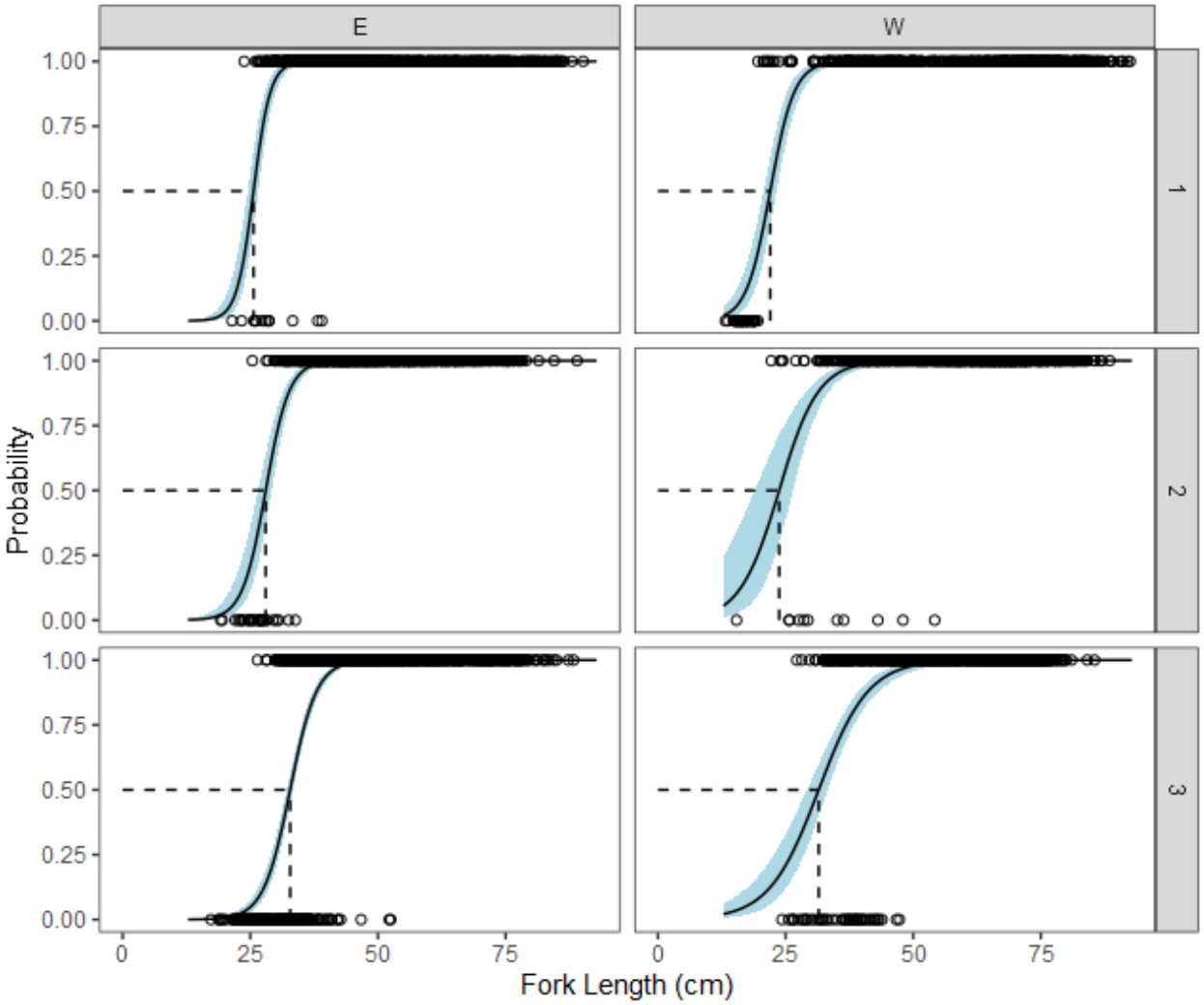


Figure 9. Data visualization of Gulf of Mexico Red Snapper batch fecundity at age estimates for three time periods based on fishing history of the stock. 1– overfished (1991-2008); 2– rapidly recovering (2009-2016); 3–stabilizing (2017-2019). Regions and all ovarian preservation methods are combined. Circle=the mean and filled bars represent the interquartile range (25% to 75%).

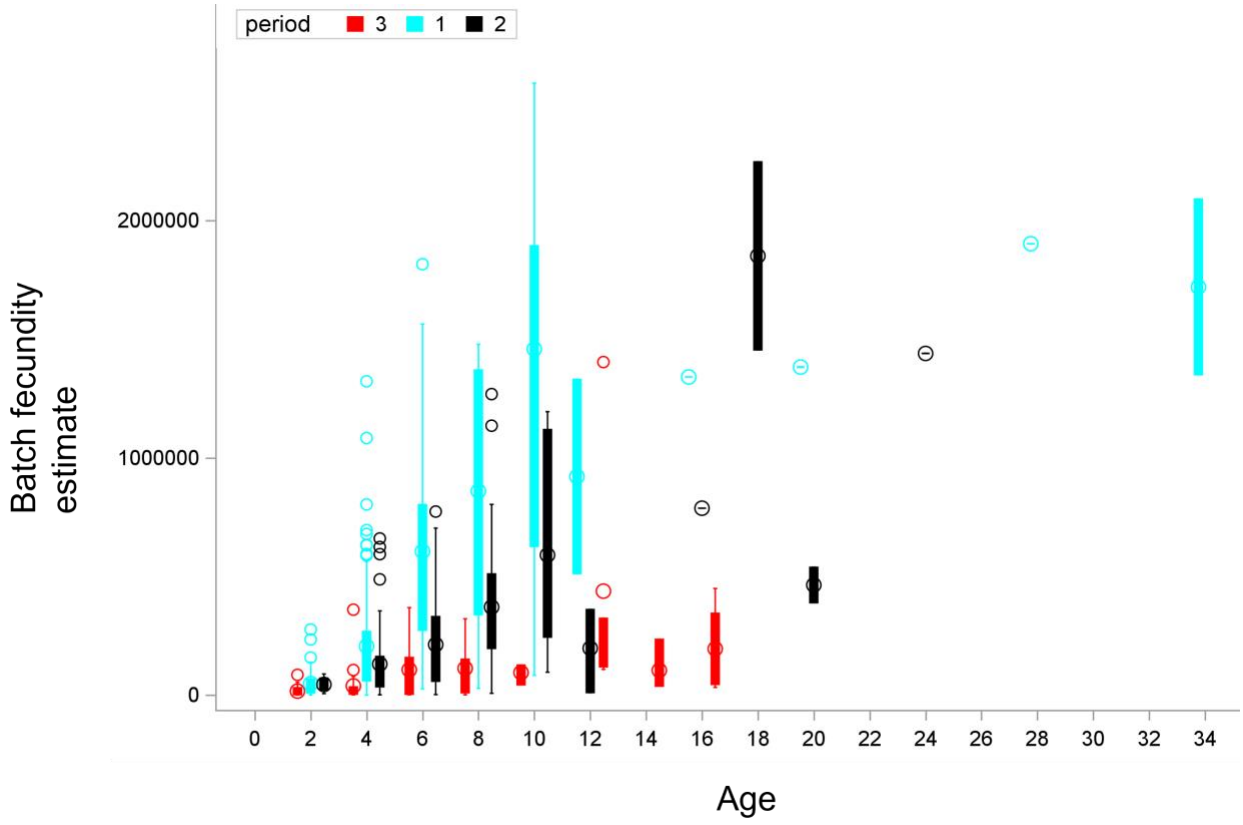


Figure 10. Effect of preservation method on batch fecundity. Ovaries not preserved in formalin (1) exhibited a lower fecundity to weight relationship than those preserved in formalin (2). Those not preserved in formalin were either frozen or in Gilson's.

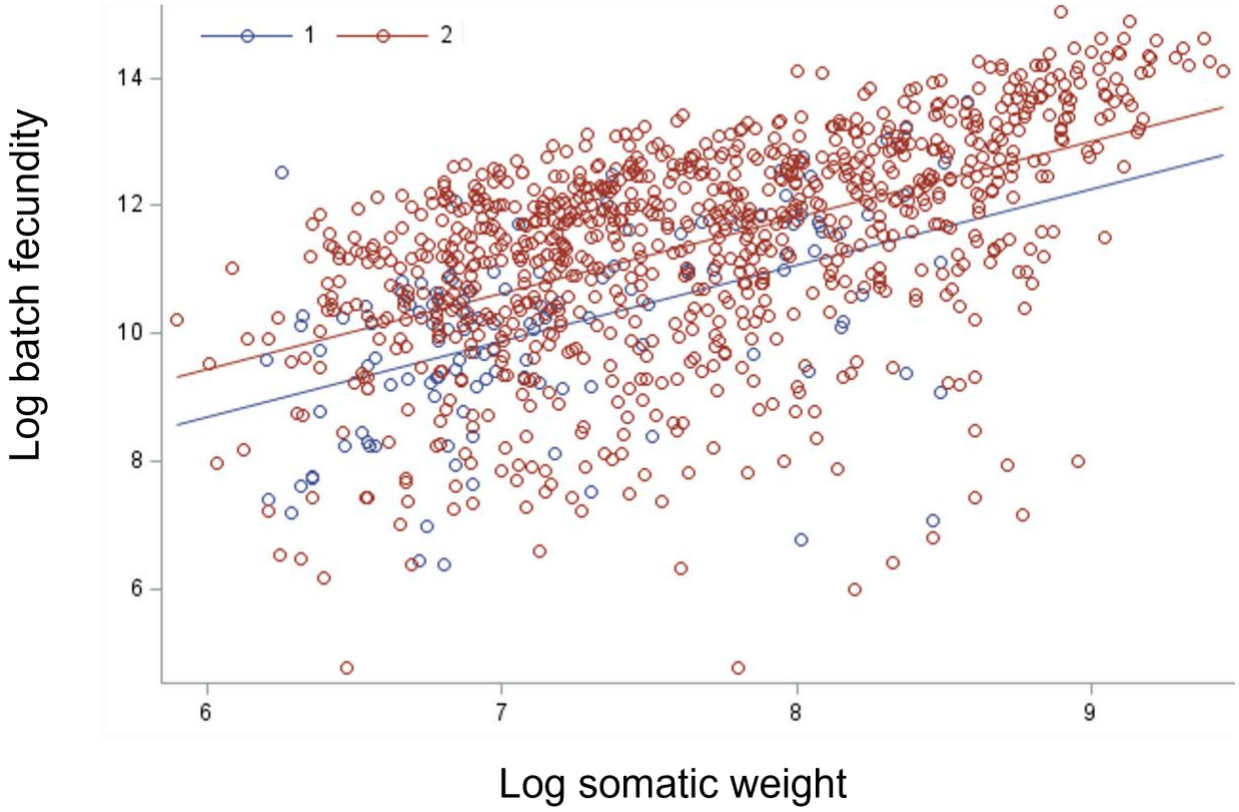
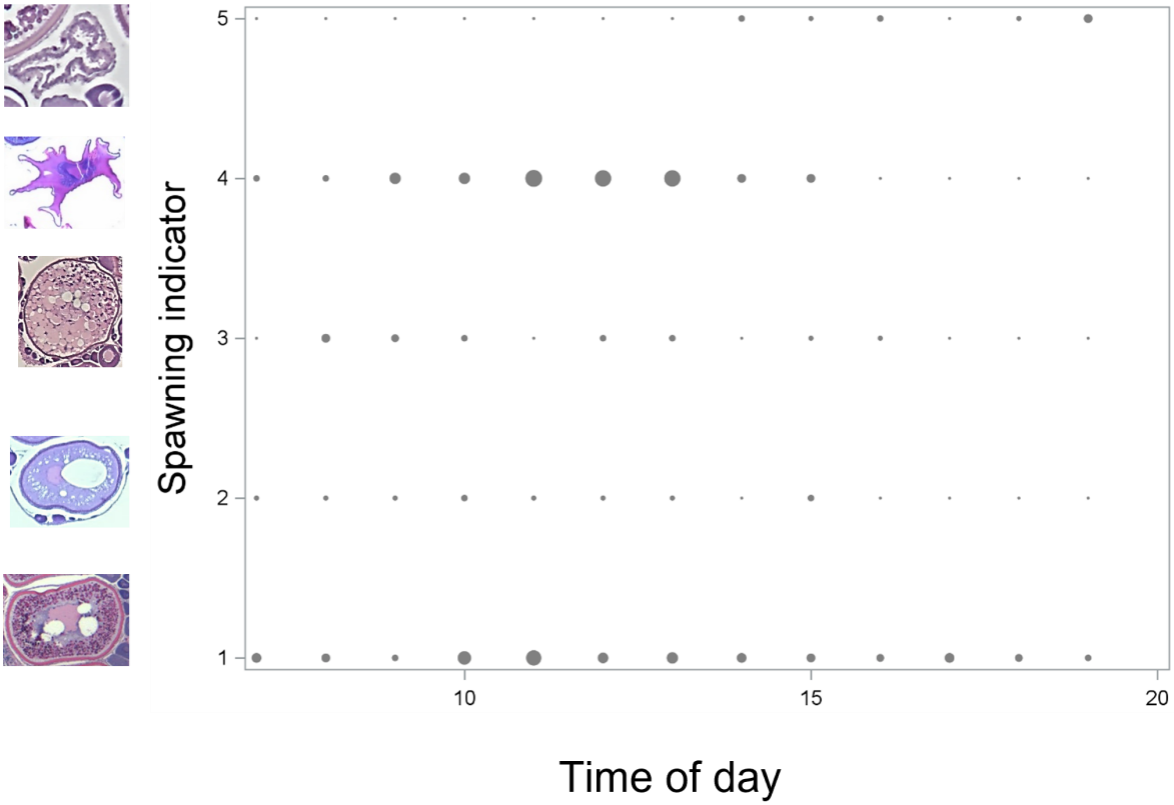


Figure 11**.** Diel periodicity of spawning in red snapper from Mississippi waters based on progression of oocyte maturation. Size of dots corresponds to the number of fish at each time point, ranging from a low of 1 to a high of 16; 0 fish indicated by small gray dot. Spawning indicators defined from bottom to top as 1–lipid coalescence, 2–germinal vesicle migration, 3–yolk coalescence and germinal vesicle breakdown, 4–hydration, 5–new (< 12 h) post ovulatory follicle, with histological micrographs of each indicator to the left.



Literature Cited

Bartoń K (2022). _MuMIn: Multi-Model Inference_. R package version 1.46.0, https://CRAN.R-project.org/package=MuMIn.

Beverton, R.J.H. and S.J.Holt. (1957). On the dynamics of exploited fish population. Fisheries Investigations, 19, 1-553.

Brown-Peterson, N.J. and A.K. Millender. (2022). The Reproductive Biology of Red Snapper in Mississippi Waters. SEDAR74-DW09. SEDAR, North Charleston, SC. 34 p.

Brown-Peterson, N., K.M. Burns, and R.M. Overstreet. (2009). Regional differences in Florida Red Snapper reproduction. Proceedings of the Gulf and Caribbean Fisheries Institute 61:149-155.

Brown-Peterson, N.J., D. Wyanski, F. Saborido-Rey, B. Macewicz, and SK. Lowerre-Barbieri. (2011). A standardized terminology for describing reproductive development in fishes. Marine and Coastal Fisheries: Dynamics. Management, and Ecosystem Science 3:52-70.

Brown-Peterson, N.J., C.R. Peterson, and G.R. Fitzhugh. (2019). Multidecadal meta-analysis of reproductive parameters of Red Snapper (*Lutjanus campechanus*) in the northern Gulf of Mexico. Fishery Bulletin 117:37-49. https://doi.org/10.7755/FB.117.1.5

Brown-Peterson, N.J., R.T. Leaf, and A.J. Leontiou. (2021). Importance of depth and artificial structure as predictors of female Red Snapper reproductive parameters. Transactions of the American Fisheries Society. 150(1):115-129. https://doi.org/10.1002/tafs.10277.

Brown-Peterson, N.J., W. Wu, C. Slife, K.S. Dillon, and A.J. Leontiou. (2022). Variations in Red Snapper oocyte development and spawning in relation to environmental and habitat parameters. Environmental Biology of Fishes 105:in press. https://doi.org/10.1007/s10641-022-01287-9

Cook, M., B.K. Barnett, M.S. Duncan, R.J. Allman, C.E Porch, and G.R. Fitzhugh. (2009). Characterization of Red Snapper (*Lutjanus campechanus*) size and age at sexual maturity for the 2009 Gulf of Mexico SEDAR update. National Marine Fisheries Service, Southeast Fisheries Science Center, Panama City Laboratory Contribution Series 09-16, Panama City, Florida.

Cowan, J.H. Jr., M. Woods, W. Patterson, and D. Nieland. (2002). Otolith microchemistry (and reproductive biology) portion – stock structure of Red Snapper in the northern Gulf of Mexico: Is their management as a single stock justified based on spatial and temporal patterns of genetic variation, otolith microchemistry, and growth rates? Final report to the U. S. Department of Commerce, National Marine Fisheries Service, Marine Fisheries Initiative (MARFIN) Cooperative Agreement NA87FF0425.

Cowan, J.H. Jr., K.M. Boswell, K.A. Simonsen, C.R. Saari, and D. Kulaw. (2012). Working Paper for Red Snapper Data Workshop (SEDAR 31). SEDAR31-DW03. SEDAR, North Charleston, SC. 49 p.

Caddy, J.F. and D.J. Agnew. (2004). An overview of recent global experience with recovery plans for depleted marine resources and suggested guidelines for recovery planning. Reviews in Fishery Biology and Fisheries 14:43-112.

Dieckmann, U. and M. Heino. (2007). Probabalistic maturation reaction norms: Their history, strengths, and limitations. Marine Ecolology Progress Series 335:253-269.

Downey, C.H., M.K. Streich, R.A.Brewton, M.J. Ajemian, J.J. Wetz, and G.W. Stunz. (2018) Habitat-specific reproductive potential of Red Snapper: A comparison of natural and artificial reefs in the

western Gulf of Mexico. Transactions of the American Fisheries Society 147:1030-1041. https://doi.org/ 10.1002/tafs.10104

Fitzhugh, G.R., M.S. Duncan, L.A. Collins, W.T. Walling and D.W. Oliver. (2004). Characterization of Red Snapper (*Lutjanus campechanus*) reproduction: For the 2004 Gulf of Mexico SEDAR. SEDAR7-DW-35. SEDAR, North Charleston, SC, 67 p.

Froehlich C.Y.M., A.M. Lee, R. Oquita, C.E. Cintra-Buenrostro, and J.D. Shivley. (2021). Reproductive characteristics of Red Snapper *Lutjanus campechanus* on artificial reefs in different jurisdictions. Regional Studies in Marine Science 47:101936. https://doi.org/10.1016/j.rsma.2021.101936

Ganias, K. (2009). Linking sardine spawning dynamics to environmental variability. Estuarine, Coastal, and Shelf Science 84:402–408.

Ganias K., G. Claramunt, R. Dominguez-Petit, P. Gonçalves, F. Juanes, J. Keneddy, N. Klibansky, M. Korta, Y. Kurita, S. Lowerre-Barbieri, G. Macchi, M. Matsuyama, A. Medina, C. Nunes, G. Plaza, R. Rideout, S. Somarakis, A. Thorsen, A. Uriarte, and M. Yoneda. (2015). Chapter 4: Egg production. In Handbook of applied fisheries reproductive biology for stock assessment and management, ed. R. Domínguez-Petit, H. Murua, F. Saborido-Rey and E. Trippel. Vigo, Spain. Digital CSIC. http://hdl.handle.net/10261/87768.

Glenn H.D, J.H. Cowan, Jr., and J.E. Powers. (2017) A comparison of Red Snapper reproductive potential in the northwestern Gulf of Mexico: Natural versus artificial habitats. Marine and Coastal Fisheries 9:139–148. https://doi.org/10.1080/19425120.2017.1282896.

Goodrich B, Gabry J, Ali I & Brilleman S. (2022). Rstanarm: Bayesian applied regression modeling via Stan. R package version 2.21.3 https://mc-stan.org/rstanarm.

Hunter, J.R. and B.J. Macewicz. (1985). Measurement of spawning frequency in multiple spawning fishes. NOAA Technical Report NMFS 36:79–94.

Hunter, J.R. and B.J. Macewicz. (2003). Improving the accuracy and precision of reproductive information used in fisheries. *In* Report of the working group on modern approaches to assess maturity and fecundity of warm- and cold-water fish and squids. O.S. Kjesbu, J.R. Hunter, and P.R. Witthames, eds. Institute of Marine Research, Bergen, Norway, p. 57-68.

Jackson, M.W., D.L Nieland, and J.H. Cowan, Jr. (2006). Diel spawning periodicity of Red Snapper *Lutjanus campechanus* in the northern Gulf of Mexico. Journal of Fish Biology 68:695-706. https://doi.org/10.1111/j.1095-8649.2006.00951.x

Kulaw, D.H., J.H. Cowan, Jr., and M.W. Jackson. (2017) Temporal and spatial comparisons of the reproductive biology of northern Gulf of Mexico (USA) Red Snapper (*Lutjanus campechanus*) collected a decade apart. PLoS One 12:1–39. https://doi.org/10.1371/journal.pone.0172360.

Lang, ET. and B. J. Falterman. (2017). A Comparison of Sampling Methods and Continuation of Red Snapper Life History Metrics. SEDAR52-WP-07. SEDAR, North Charleston, SC. 10 p.

Leontiou, A.J., W. Wu and N.J. Brown-Peterson. (2021a). Immature and mature female Red Snapper habitat use in the north-central Gulf of Mexico. Regional Studies in Marine Science 44:101715, 8 p. https://doi.org/10.1016/j.rsma.2021.101715.

Leontiou, A.J., W. Wu, and N.J Brown-Peterson. (2021b). The role of maturity in artificial habitat selection by female Red Snapper. Marine and Coastal Fisheries 13:332-344. https://doi.org/10.1002/mcf2.10160.

Lowerre-Barbieri, S.K. and L.R. Barbieri. (1993). A new method of oocyte separation and preservation for fish reproduction studies. U S National Marine Fisheries Service Fishery Bulletin 91:165-170.

Lowerre-Barbieri, S.K., N.J. Brown-Peterson, H. Murua, J. Tomkiewicz, D. Wyanski, and F. Saborido-Rey. (2011a). Emerging issues and methodological advances in fisheries reproductive biology. Marine and Coastal Fisheries: Dynamics. Management, and Ecosystem Science 3:32-51.

Lowerre-Barbieri, S.K., K. Ganias, F. Saborido-Rey, H. Murua, and J.R. Hunter. (2011b). Reproductive timing in marine fishes: variability, temporal scales, and methods. Marine and Coastal Fisheries: Dynamics. Management, and Ecosystem Science 3:71-91.

Lowerre-Barbieri, S., L. Crabtree, T.S. Switzer, and R.H. McMichael. (2012). Spatio-temporal dynamics in Red Snapper reproduction on the West Florida Shelf, 2008-2011. SEDAR31-DW15. SEDAR, North Charleston, SC. 12 p.

Lowerre-Barbieri, S.K., S. Walters, J. Bickford, W. Cooper, and R. Muller. (2013). Site fidelity and reproductive timing at a Spotted Seatrout spawning aggregation site: Individual versus population scale behavior. Marine Ecology Progress Series 481:181-197.

Lowerre-Barbieri S.K., L. Crabtree, T. Switzer, S.W. Burnsed, and C. Guenther. (2015) Assessing reproductive resilience: An example with South Atlantic Red Snapper *Lutjanus campechanus*. Marine Ecology Progress Series 526:125–141. https://doi.org/ 10.3354/meps11212.

Lowerre-Barbieri, S.K., S.L. Walters Burnsed, and J.W. Bickford. (2016). Assessing reproductive behavior important to fisheries management: A case study with red drum, *Sciaenops ocellatus*. Ecological Applications 26:979-995.

Lowerre-Barbieri, S., V. Beech, and C. Friess. (2020). Scamp grouper reproduction in the Gulf of Mexico. SEDAR68-DW-28. SEDAR, North Charleston, SC. 30 p.

Lowerre-Barbieri, S.K., C. Friess, L.P. Griffin, D. Morley, G.B. Skomal, J.W. Bickford, N. Hammerschlag, M.J. Rider, M.J. Smukall, van Zinnicq, M.P.M. Bergmann, et al. (2021). Movescapes and eco-evolutionary movement strategies in marine fish: Assessing a connectivity hotspot. Fish and Fisheries 22, 1321– 1344. https://doi.org/10.1111/faf.12589.

Lowerre-Barbieri, S., H. Menendez, and C. Friess. (2021). Gag grouper reproduction in the Gulf of Mexico. SEDAR72-DW-08. SEDAR, North Charleston, SC. 26 p.

Lowerre-Barbieri, S. and C. Friess. 2022. Modeling fecundity at age in Gulf of Mexico Red Snapper to help evaluate the best measure of reproductive potential. SEDAR74-DW-40. SEDAR, North Charleston, SC. 31 pp.

Marshall, C.T. and B.J. McAdam. (2007). Integrated perspectives on genetic and environmental effects on maturation can reduce potential for errors of inference. Marine Ecology Progress Series 335:301-310.

Millender, A.K. and N.J. Brown-Peterson. (2022). Reproductive parameters of female Red Snapper differ across depth. Proceedings of the Gulf and Caribbean Fisheries Institute 74:in press.

Murua, H., G. Kraus, F. Saborido-Rey, A. Thorsen, P. Witthames, and S. Junquera. (2003). Procedures to estimate fecundity of wild collected marine fish in relation to fish reproductive strategy. Journal of Northwest Atlantic Fishery Science 33:33–54.

Murua, H., L. Ibaibarriaga, M. Alvarez, M. Santos, M. Korta, M. Santurtun, and L. Motos. (2010). The daily egg production method: A valid tool for application to European hake in the Bay of Biscay? Fisheries Research 104:100–110.

Porch, C.E. (2007). An assessment of the Red Snapper fishery in the U.S. Gulf of Mexico using a spatially-explicit age-structured model. American Fisheries Society Symposium 60:355-384.

Porch, C.E., G.R. Fitzhugh, E.T. Lang, H.M. Lyon, and B.C. Linton. (2015). Estimating the dependence of spawning frequency on size and age in Gulf of Mexico Red Snapper. Marine and Coastal Fisheries 7: 233-245.

SEDAR7 (2005). Stock Assessment Report of SEDAR 7 Gulf of Mexico Red Snapper (SEDAR One Southpark Circle #306 Charleston, SC 29414 Southeast Data, Assessment, and Review).

SEDAR31 (2013). - Gulf of Mexico Red Snapper Stock Assessment Report. SEDAR, North Charleston SC. 1103 pp

SEDAR 52 (2018) SEDAR 52: Stock assessment report Gulf of Mexico Red Snapper. North Charleston, SC 435 p.

Stratoudakis, Y., M. Bernal, K. Ganias, and A. Uriarte. (2006). The daily egg production method: Recent advances, current applications and future challenges. Fish and Fisheries 7:35–57.

Szedlmayer, S.T. and C. Furman. (2000). Estimation of abundance, mortality, fecundity, age frequency, and growth rates of Red Snapper, *Lutjanus campechanus*, from a fishery independent stratified random survey. Report to the Gulf and South Atlantic Fisheries Foundation, Inc. National Oceanographic and Atmospheric Administration, Department of Commerce Cooperative agreement NA87FM0221.

Trippel, E. (1999). Estimation of stock reproductive potential: History and challenges for Canadian Atlantic gadoid stock assessments. Journal of Northwest Atlantic Fishery Science 25:61-82.

Vehtari A, Gabry J, Magnusson M, Yao Y, Bürkner P, Paananen T, Gelman A (2022). "loo: Efficient leave-one-out cross-validation and WAIC for Bayesian models." R package version 2.5.1, https://mc-stan.org/loo/.

Woods, M.K. (2003). Demographic Differences in Reproductive Biology of Female Red Snapper (*Lutjanus campechanus*) in the Northern Gulf of Mexico. Masters Thesis. The University of South Alabama, Mobile, AL. 148 p.