SEDAR 74-DW40: Modeling fecundity at age in Gulf of Mexico Red Snapper to evaluate the best measure of reproductive potential

Susan Lowerre-Barbieri and Claudia Friess

SEDAR90-RD-13

April 2025

This information is distributed solely for the purpose of pre-dissemination peer review. It does not represent and should not be construed to represent any agency determination or policy.

Modeling fecundity at age in Gulf of Mexico Red Snapper to help evaluate the best measure of reproductive potential

Susan Lowerre-Barbieri and Claudia Friess

SEDAR74-DW-40

18 July 2022

This information is distributed solely for the purpose of pre-dissemination peer review. It does not represent and should not be construed to represent any agency determination or policy.

Please cite this document as:

Lowerre-Barbieri, Susan and Claudia 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.

Modeling fecundity at age in Gulf of Mexico Red Snapper to help evaluate the best measure of reproductive potential

By Susan Lowerre-Barbieri[1] and Claudia Friess[2]

[1] Fisheries and Aquatic Sciences Program, School of Forest, Fisheries, and Geomatic Sciences, University of Florida, Gainesville, FL, USA

[2] Florida Fish and Wildlife Conservation Commission, Fish and Wildlife Research Institute, 100 8th Avenue SE, St. Petersburg, FL, USA

SEDAR 74

July 15, 2022

Introduction

Although conserving sufficient reproductive or spawning potential for a stock to maintain or rebuild itself is a fundamental goal of fisheries management (Goodyear, 1993), accurately estimating a stock's reproductive potential is challenging. Due to the difficulty in reliably estimating the parameters of the purported stock-recruitment relationship which is needed to develop maximum sustainable yield (MSY)-based reference points, the spawning potential ratio (SPR) is widely used as an MSY proxy. SPR is defined as the ratio of potential lifetime reproductive output in the fished condition and that in the unfished condition (Goodyear, 1993). Potential recruit fecundity is defined as the number of eggs that could be produced by an average recruit in the absence of density dependence (Goodyear, 1993). Theoretically, "potential" fecundity should be estimated from a period when density-dependent effects are negligible (Goodyear, 1993). Unfortunately, we do not have the means to document if or when a stock has been fished to a new equilibrium or even if this happens, as reproductive potential varies temporally and with fishing pressure (Marshall et al., 2006). In practice, lifetime reproductive potential is often calculated as spawning stock biomass (SSB). SSB is calculated based on abundance of mature females at age, mean weight at age, the proportion of females that are mature at a given age and estimates of natural mortality and fishing mortality to predict survivorship in any given year. Recently, it has been suggested that mature weight-at-age should be replaced with fecundity-at-age to estimate total egg production (TEP), as a better means of measuring reproductive potential and valuing older females (Marshal et al., 2021). TEP is the reproductive measure used for Red Snapper in SEDAR 31 and 52.

However, both SSB and TEP have pros and cons as measures of reproductive potential. Using SSB as a proxy for egg production assumes that fecundity-at-age and mass-at-age are proportional, whereas fecundity-at-age often increases more rapidly (Marshal et al., 2021). Additional factors affecting increased reproductive value with age (i.e., the ability to produce offspring which survive to maturity) include energetics, differences in reproductive timing, egg quality, or spawning site selection (Lowerre-Barbieri et al., 2017). This has resulted in a general acceptance that BOFFFFs, i.e., Big Old Fat Fecund Female Fish are essential for the successful maintenance of long-lived fish populations (Marteinsdottir and Steinarsson, 1998; Scott et al., 1999; Longhurst 2002; Berkeley et al., 2004; Palumbi, 2004; Scott et al., 2006; Field et al., 2008; Wright and Trippel, 2009; Cooper et al., 2013; Hixon et al., 2014). Because TEP more accurately measures fecundity of older females it is typically considered better able to protect BOFFFFs and a more sensitive index of reproductive potential (Marshall, 2009; Morgan et al., 2009; Mehault et al., 2010; Murua et al., 2010).

However, there are a number of uncertainties with TEP which have not been fully explored, associated with sample size, age truncation, and methodological challenges. Fecundity-at-age samples are not as abundant as maturity-at-age or weight-at-age samples. For example, for SEDAR 74 fecundity samples were only 0.5% (n=1,136) of the records with size and age for Red Snapper (n=239,409). In addition, estimating annual fecundity at age is both more complicated and associated with greater uncertainty than size-at-age, especially in warm water species with indeterminate fecundity, like Red Snapper. Species with indeterminate fecundity participate in

multiple spawning events within a spawning season and their annual fecundity is estimated as the product of the number of eggs released in one spawning event (batch fecundity) and spawning frequency (the expected number of spawning events in a season). The methods to estimate batch fecundity are not yet standardized and can affect results (Ganias et al., 2015; Lowerre-Barbieri et al., 2022). Also, fecundity often varies with condition (Brooks, 2011; Kell et al., 2016), and in Red Snapper, batch fecundity varies with sampling region and time (Brown-Peterson et al., 2019). However, the greatest uncertainty with estimating fecundity for species with indeterminate fecundity is the need to estimate spawning frequency. Spawning fraction (the ratio of females with spawning markers to that of mature females) is the foundation of spawning frequency estimates. It is affected by sample size at age, catchability of females with spawning markers, the duration of spawning markers, and how accurately the spawning season reflects the average time over which individuals spawn (Lowerre-Barbieri et al., 2022). The assumption of no immigration/emigration from the sampling sites underlying this spawning fraction method means that if it is violated resulting spawning fractions can differ significantly from the population's spawning frequency (Lowerre-Barbieri et al., 2013; Zarada et al., 2019). In Red Snapper, spawning fraction is reported to vary by month within the spawning season, size, and age (Porch et al., 2015; Lowerre-Barbieri et al., 2015; Lowerre-Barbieri et al., 2022).

Thus, when evaluating SSB vs TEP as the best measure of reproductive potential one must consider tradeoffs between accuracy and uncertainty. Ideally, the measure of reproductive potential would: (1) improve the stock-recruitment relationship and predictions of future productivity; (2) effectively track changes in productivity with fishing mortality and external stressors over space and time; (3) protect old age growth structure in long-lived species; and (4) be based on sufficient data quantity and quality to represent the stock. There is relatively little literature on assessing whether TEP improves stock-recruitment relationships, but publications-to-date suggest it does not (Cerviño et al., 2013; Kell et al., 2016). However, this may also not be a reasonable expectation given emerging knowledge that density dependence in stock recruitment relationships is not limited to only survival from egg to recruit, but also occurs in the spawning population, affecting body size and fecundity. For the remaining three indicators of a successful measure of reproductive potential, TEP is a more sensitive indicator of changes in egg production (Morgan et al., 2009; Kell et al., 2016). However, the data quantity and quality for TEP in exploited stocks is rarely evaluated. Due to age truncation, it is often difficult or impossible to collect fecundity samples for fish in the second half of their reproductive lifespan, exactly those which are most critical for evaluating productivity. To a certain extent, this is also true for estimates of size-at-age needed for SSB. However, the combination of larger sample sizes and numerous studies to test the accuracy of ageing methodology and standardize it across laboratories has resulted in representative size-at-age data for many exploited stocks.

Red Snapper have been overfished since the 1960s in the Gulf of Mexico (SEDAR52; Figure 1) as well as in the South Atlantic (SEDAR 73). Red Snapper reproductive traits suggest that they adapted to this long-term increased mortality. For example, maturation schedules occur at much younger ages than expected based on their longevity and individuals can mobilize very small batches of eggs resulting in higher variability in batch fecundity-at-age than in other batch spawners (Lowerre-Barbieri et al., 2015). Red Snapper in recent SEDARs are reported to mature

by age 2, with a reproductive lifespan of at least 48 y. The mean reported age at maturity for lutjanids is 3.5 y with a mean reproductive lifespan of 11.7 y (Martinez-Andrade, 2003). Assuming these changes are not due to fisheries-induced evolution (Wright, 2007), the Gulf Red Snapper stock is expected to exhibit reproductive compensation as it recovers, with size- and age-at-maturity increasing and fecundity-at-age decreasing. Stock assessments and recent publications suggest this process is occurring (SEDAR 31, SEDAR 52, Brown-Peterson et al., 2019). However, it is unknown if decreased fecundity is similar across all age groups. Increased abundance and density-dependent feedback loops are expected to be greatest in young fish and thus changes in fecundity-at-age may be greater for relatively young fish (< 20 y) versus older fish.

Reproductive dynamics vary over time, space, abundance, and age composition (Goodyear, 1993; Kell et al., 2015; Vert-pre et al., 2013; Klaer et al., 2015, 2016; Lowerre-Barbieri et al., 2017). Given that Red Snapper is long-lived, has undergone periods of large fluctuating abundance, and its relative fecundity (eggs per g body weight) increases with age indicating hypoallometry (Lowerre-Barbieri et al., 2015; Brown-Peterson et al., 2019), there is a need to assess the efficacy of TEP vs SSB as the best measure of reproductive potential for the Gulf stock. This necessitates estimates of fecundity-at-age over time and over sufficient contrasts of stock abundance and spatial distributions. SEDAR 74 has extensive reproductive data dating from 1991. This data encompasses three time periods with varying stock status: 1991-2008, when the stock was severely overfished, 2009-2016, when the stock was rapidly recovering, and 2017-2019, when stock abundance had begun to stabilize (Figure 1). We extend previously developed models assessing Red Snapper batch fecundity (Porch et al., 2007) and spawning fraction (Porch et al., 2015) to predict annual fecundity-at-size and -age. The mature weight-at-age (the basis for SSB) and fecundity-at-age (the basis for TEP) vectors are estimated and compared by region and stock status time periods. Due to data limitations, only two regions are assessed, West of the Mississippi River (W) and East of the Mississippi River (E).

Methods

Batch fecundity

We analyzed batch fecundity using regression on length and a number of covariates in a generalized log-linear modeling framework following that of Porch et al., (2007). Additional covariates included: stock recovery period (three levels, 1991-2008, 2009-2015, 2016-2019), region (Eastern or Western Gulf), month, ovarian preservation method (formalin vs. 'other'), and condition. Relative condition was estimated as weight divided by the predicted length-specific mean weight and is referred to as simply condition for the remainder of this report.

We excluded BF samples from the analysis that had fresh post-ovulatory follicles (POFs), so as to not negatively bias egg counts when some of the batch may have already been released. However, POF data were missing for over half of all batch fecundity samples, suggesting that some of these fish may have begun to spawn but were not filtered out, which would lead to under-estimated batch fecundities. Most (98%) batch fecundity estimates with length and age

(n=1,211) were age 15 or less. Period and region sample sizes ranged from n=87 (period 3, W) to 432 (period 1, E).

Due to low sample sizes for some covariate level combinations, all models were estimated within a Bayesian framework using Stan as the backend through the 'rstanarm' R package. All priors were weakly informative: the default specifications with mean = 0 and sd = 2.5 were used, and the model was allowed to internally adjust each prior's scale to generate the weakly informative priors to provide model regularization and computation stability. Model comparison was conducted using leave-one-out cross-validation via the 'loo' package. The method calculates the expected log pointwise predictive density and the LOO information criterion (which has the same purpose as AIC).

The final model included a three-way interaction between fork length, period, and region and additive terms for the remaining covariates (method, month, and condition). Model fit was confirmed by checking convergence diagnostics (Table 1) and by visually inspecting parameter trace plots and conducting posterior predictive checks.

Covariate effects on BF estimates were evaluated using probability of direction (pd) and the percent of the posterior samples that fall within the region of practical equivalence (ROPE). These are measures of certainty regarding effect direction (positive or negative) and statistical significance. A pd of greater than 97.5% was considered strong evidence for effect direction. To compute percent in ROPE, we used the 95% equal-tailed interval, and we considered a percentage of the posterior within the ROPE < 0.025 to be significant. The ROPE range was set to -0.1 to +0.1. To evaluate the effects of period and region, we computed and generated contrasts between estimated marginal means for the interaction between length, period, and region using the 'emmeans' package.

Spawning fraction

Spawning fraction is the proportion of mature females spawning daily (Hunter and Macewicz, 1985; Lowerre-Barbieri et al., 2011). Its inverse is the spawning interval, or estimated time between spawns for a population of batch spawners, which can vary within the spawning season. Spawning frequency is estimated based on spawning season duration divided by the spawning interval.

We followed the approach of Porch et al., (2015) for estimating spawning fraction. This model differs from traditional approaches to estimating spawning fraction in that it is, at its core, a logistic binomial regression of (individual) spawning markers against length or age and relevant covariates, while the traditional method calculates the fraction from pooled raw data. The traditional approach cannot easily account for sampling effects affecting the proportion of females with spawning markers such as the interaction effect between sampling date and within-season differences in spawning fraction affecting results. The Porch et al., (2015) model includes time of year, but rather than including it in the linear predictor of the binomial model,

it is expressed as a gamma function that models the dependence of spawning fraction on time of year, and the full model (Porch et al., 2015, Eqn. 6) is the product of the logistic and gamma probabilities. We added region and period to the linear predictor of this model and implemented it in the 'rjags' package in a Bayesian inference framework. Models with region-and-period specific slopes and intercepts were tested. The final model was chosen based on convergence statistics (Rhat, effective sample size, and visual checks of trace plots) as well as posterior predictive checks.

Spawning fraction (at length and age) at peak season was calculated from the slope and intercept parameters of the spawning fraction model. This was then converted to average daily spawning fraction by correcting for the length of time that spawning markers are observable (set to 34 hours, as per Porch et al., 2015) and multiplying by the integral of the season effect.

Annual fecundity

Annual fecundity-at-age was estimated as the product of batch fecundity and spawning frequency following Porch et al., (2015). Spawning frequency was calculated as daily spawning fraction times 365 d, rather than using a specific spawning season, due to the extended duration of Red Snapper spawning.

Mature biomass and fecundity at age vectors

Region- and period-specific mature biomass-at-age was calculated using region and period-specific weight-at-age and maturity-at-age estimates from Garner et al., (2022) and Lowerre-Barbieri et al., (2022). Region and period-specific fecundity-at-age vectors were calculated using the average spawning frequency-at-age times the predicted batch fecundity-at-age for each combination. The relationship described in Porch et al., (2007) integrating batch fecundity-at-length and length-at-age was used to estimate batch fecundity-at-age, following the approach of SEDAR 31 and 52.

Results

Batch fecundity

Sample sizes for batch fecundity estimates (BF) were unevenly distributed across months, with most samples (840 out of 1092) coming from June through August. Only 8 samples each came from April and October, corresponding to the month before and after peak spawning months. The model-estimated month effect showed reduced BF in April, September and October, and increased BF in May-July (Figure 2). There was substantial evidence for effect existence for May-July and October (pd was 99.95% in October to 100% for the other months), and this effect was significant (percent in ROPE 0%). Ovarian preservation other than formalin produced smaller BF estimates but the effect was not significant (pd = 95%, % in ROPE = 28).

BF increased with length and condition (pd = 100% and %in ROPE = 0, table 1). However, the effects of region and period are not easily summarized due to the interaction between region, period, and length. One way to look at it is by comparing marginal means between factor pairs (table 2). For small (25 cm FL bin) fish BF was lower in the early period than the mid period and higher in the mid period than the late period. Between the East and the West, BF for small fish was always higher in the East than the West. All those comparisons were certain (pd = 1) and significant (percent in ROPE = 0). For large fish (90 cm FL bin), BF was larger in the early period than the mid period and this was certain (pd > 0.975) and significant (percent in ROPE < 0.025). It was also larger in the mid period than the late for each region, but this was not certain or significant.

The fit to the log-transformed values of batch fecundity and fork length was good (Figure 3). The fit to the back-transformed values was also good, but higher values of BF tended to be underestimated, especially for the West in the early period (Figure 4). This underestimate becomes somewhat exaggerated when converting length to age, (Figure 5) but the nature of this model is to allow larger variance for larger values, as per the multiplicative error structure.

Spawning frequency

The smallest fish in the data set was 13.2 cm FL, and the smallest fish observed with spawning markers was 19.6 cm FL. The youngest fish in the data set was 0.85 years old, and the youngest fish with spawning markers was 0.95 years old. The best models included a single slope and region-and period-specific intercepts (parameter estimates and convergence statistics shown in tables 3 and 4). Models where both slope and intercept were allowed to vary had trouble converging. Predicted spawning fraction was generally similar to observed, but proportions of fish with spawning markers at age were better estimated than at length (Figures 6-9). Both models had higher uncertainty when samples were sparce, i.e., older ages and smaller and larger sizes. This can be seen in the older ages when due to small sample sizes, predictive capacity is lost as spawning fraction often alternates between 0% and 100% (Figure 9). The length models had trouble fitting the lower proportions with spawning markers at smaller sizes in the East in the middle and later periods, overestimated proportion with spawning markers at larger sizes in the early period in the East, and underestimated proportions with spawning markers at larger sizes in the West in the middle and later period (Figure 7). The models predicted a smaller average daily spawning fraction in the West than the East, for both length and age, particularly at smaller lengths and ages (tables 5 and 6, respectively). No clear pattern in proportion of spawning markers within region between periods was apparent. The age models indicate a slight progressively declining trend in spawning fraction by age within period, while the length models do not; the mid period was the highest (tables 5 and 6).

Annual fecundity

Both estimated fecundity-at-length and fecundity-at-age show a trend of decreasing fecundity over time within region. Fecundity-at-length and age were greater in the E than the W (Figure 10, tables 7 and 8). Annual fecundity at length was similar to the results of Porch et al. (2015)

and used in SEDAR 31 and 52. However, annual fecundity-at-age was consistently lower in our models than the results of Porch et al., (2015).

Mature biomass and fecundity at age vectors

Estimated annual fecundity-at-age decreased in both regions as the stock recovered. For length and age relationships, results from Porch et al (2015) for older ages compared most closely with those in the overfished period (1991-2008). Predicted fecundity-at-age relationships for older fish (ages 20-40 y) decreased by ~50% in the rapidly recovering period and by ~60% in the stabilizing period (Figure 10).

Comparing the relationships underlying SSB and TEP over space and time (Figure 11) indicates that mature-biomass-at age remains fairly constant over space and time, while fecundity-at-age greatly decreases as the stock recovers (Figure 11).

Discussion

Although reproductive dynamics are known to vary temporally and spatially, this variability is often not integrated into stock assessments. We provide evidence in this analysis for the existence of spatio-temporal patterns in reproductive output in line with what one would expect with reproductive compensation as the stock recovers (Porch et al., 2015). Total age-specific fecundity was estimated to be highest in the Eastern Gulf in the early period (1991 - 2008), in the time and place where the population was most depressed. Fecundity was estimated to be lower in the Western Gulf, where the population has consistently been estimated to be in better condition than in the East (SEDAR 52, 2018). In recent years, the difference between the Eastern and Western Gulf has gotten smaller as the population in both areas is recovering.

Selectively harvesting of fish can lead to plastic and/or evolutionary changes in fish life histories (Heino et al., 2015), with one of the most commonly reported changes being decreased size and age at maturity in highly exploited stocks (Marshall and Browman, 2007; Rochet, 2009; Dunlop et al., 2009). Overfishing led to severe declines in GOM red snapper biomass during the 1960s-1990s (Figure 1), estimated to have fallen below an SPR of 26% in 1964. It had an estimated SPR of only 2% from 1983 to 1991. Estimated SPR rapidly increased from 2009 to 2016 (from 0.07 to 0.18) but was not predicted to reach 26% by 2032 (SEDAR52). Given both the magnitude and duration of overfishing, it has been hypothesized that life history traits adapted to the change in mortality. Using the Lester biphasic growth curve model and back-calculated size at age data, Honsey (2018) evaluated changes in Gulf Red Snapper maturation schedules. Although his sample size was rather small (n=166 GOM Red Snapper otoliths age 10 or older sampled from 1941 to 2005), his results suggested that Gulf Red Snapper adapted their maturation schedules from an estimated age-at-maturity of 7.5 y in 1940 to 3.06 y in 2001-2005.

As the stock recovers, it is expected to demonstrate the opposite trend. Lowerre-Barbieri et al., (2022) estimated maturation schedules for the same three stock status periods as used here

and report a 1.6-fold increase in age at maturity from 1.52 y to 2.46 y in the West and age-at-maturity was larger in the West than the East. They also report, as do prior SEDARs, that in the years before 2008 sampling did not fully cover the younger sizes and ages when fish were maturing.

Clearly if maturity-at-age is increasing fecundity-at-age for the youngest fish must decrease. However, without fecundity data for fish ages 20 and older, there is no easy way to evaluate what the effect should be on these older ages. Given that abundance at younger ages is expected to show the greatest change and thus density-dependent feedback loops, fish which were born starting with the first year of the rapidly recovering period (birth year of 2009 or later) are expected to be most impacted. This would translate to fish ages 1 through 11 in the current assessment. However, our models predicted consistently decreasing fecundity-at-age vectors as the stock recovered, including for fish ages 20 to 40 y.

For fecundity in those older ages to decrease at the rate of younger fish, density would have to have also increased at the same rate. Given reports of older Red Snapper being less gregarious and moving to deeper water this seems unlikely. An alternative explanation is that the lack of fecundity for older age fish, combined with our use of the asymptotic batch fecundity-to-age relationship, led to biased results. Again, unfortunately, we have no way of knowing the shape of the fecundity-at-age relationship over the Red Snapper reproductive lifespan as we only have data on the first third of it. Based on energetics, it does not seem reasonable to assume it increases throughout life, but it could be asymptotic, or dome shaped, as seen in many other species.

Our analysis highlights the additional uncertainties associated with estimating annual fecundity for species with indeterminate fecundity. These include a lack of standardized methodology and the assumption that capture-based samples accurately reflect the proportion of spawning females and that the proportion of spawning females over time is comparable to the number of times an individual would spawn over a spawning season (Lowerre-Barbieri et al., 2022). In addition, we often do not have good data to inform the spawning marker duration correction factor. Following Porch et al., (2015), we used 24/34 (0.71), but further research is needed to resolve this. Given the asynchronous spawning times reported for Red Snapper (Lowerre-Barbieri et al., 2022), the correction factor could be as low as 24/48 (0.5) which would reduce the estimated fecundity-at-age vectors by about 30 percent. Ideally, this uncertainty would be incorporated in stock assessment model runs. The final major source of uncertainty we want to highlight pertains to the nature of the modeling approach used here. Due to the hierarchical nature of the models, future data additions affect all estimated parameters and would thus be expected to produce slightly different fecundity-at-age estimates in the future. This is demonstrated by the predicted fecundity-at-age vectors with stock status period. Our models predict the same fecundity-at-age vector as Porch et al., (2015) when we filter for the same time period.

Given the uncertainties and major data gaps associated with TEP, we recommend SSB as the best measure of reproductive potential for Gulf Red Snapper. This differs from the past two

assessments, and from the general perception that TEP is a better measure of reproductive potential than SSB. However, past SEDARs did not have the data to assess changes in the fecundity-at-age vector over differing stock status time periods. TEP does appear to be more sensitive at tracking changes in reproductive output over space and time than SSB. However, this sensitivity is driving the lower fecundity-at-age vectors presented here, compared to SEDAR 31 and 52. Our concern is that there is high uncertainty in these estimates, given that we are predicting fecundity well beyond the age range we have data for and that they have the potential to result in a lower estimate of stock productivity in recent years. However, this can only be fully assessed once we have the estimated abundance-at-age vectors.

Fish reproductive strategies adapt to fishing mortality. Optimal age-at-maturity is driven by an animal's mortality environment, with higher mortality rates resulting in fish maturing earlier either due to a compensatory response wherein fish reach a higher average nutritional state (condition) at a younger age (Marshall and McAdam, 2007) or fisheries induced evolution (Dieckmann and Heino, 2007). These same factors can affect fecundity-at-age. Recognizing these time-varying changes is important as they can indicate opposite stock status compared to assumptions of equilibrium. For example, under the assumption of equilibrium, earlier maturity leads to greater estimated spawning biomass and egg production, a higher SPR, and the conclusion that the stock can withstand a greater level of fishing mortality, when in fact a decreased age-at-maturity is often an indicator of a stressed and over-fished stock.

In conclusion, when the mortality environment of a stock significantly changes from that under which the species evolved, outcomes range along a continuum from relatively easily reversed density-dependent adaptation to extinction of population components, or whole species. In the middle of this continuum are adaptations to alternate states (productivity regime shifts). Red Snapper are one of the most reproductively resilient stocks in the Southeast US, with large phenotypic plasticity in reproductive cues, and widely distributed spawning and nursery habitat (Lowerre-Barbieri et al., 2015). Their resilience, even though they are long-lived, is further indicated here as they shift their reproductive effort back towards older ages, indicative of a healthier stock.

Table 1. Model parameter estimates and mcmc fit diagnostics for the batch fecundity-at-length model. The mean of the posterior predictive distribution (11.3) was nearly identical to the mean of the observed log batch fecundities (11.34). Rhat values (all less than 1.1) and effective sample size (n_eff) values (all greater than 1000) suggest convergence and a large enough sample size for analysis, respectively. mcse = Monte Carlo standard error. Parameter estimates with certain direction (pd > 0.975) and significant (% in ROPE < 0.025) are highlighted.

	mean	sd	10%	50%	90%	mcse	Rhat	n_eff	pd	% in ROPE
(Intercept)	**-12.60**	**1.90**	**-15.10**	**-12.60**	**-10.20**	**0**	**1**	**3429**	**1.00**	**0.00**
log_fl	**3.90**	**0.30**	**3.60**	**3.90**	**4.20**	**0**	**1**	**2192**	**1.00**	**0.00**
period1	**6.60**	**1.70**	**4.50**	**6.70**	**8.80**	**0**	**1**	**1888**	**1.00**	**0.00**
period2	-0.20	2.10	-2.90	-0.30	2.50	0	1	1824	0.55	0.06
region1	**-6.70**	**1.60**	**-8.80**	**-6.60**	**-4.60**	**0**	**1**	**1643**	**1.00**	**0.00**
method1	-0.30	0.20	-0.50	-0.30	0.00	0	1	4442	0.95	0.28
month5	**1.30**	**0.40**	**0.70**	**1.30**	**1.80**	**0**	**1**	**1279**	**1.00**	**0.00**
month6	**1.30**	**0.40**	**0.80**	**1.40**	**1.90**	**0**	**1**	**1221**	**1.00**	**0.00**
month7	**1.00**	**0.40**	**0.40**	**1.00**	**1.50**	**0**	**1**	**1238**	**0.99**	**0.00**
month8	0.60	0.40	0.10	0.60	1.20	0	1	1243	0.93	0.12
month9	0.20	0.40	-0.30	0.20	0.80	0	1	1234	0.71	0.28
month10	-0.80	0.60	-1.50	-0.80	0.00	0	1	1910	0.90	0.10
log_rw	**1.80**	**0.30**	**1.40**	**1.80**	**2.20**	**0**	**1**	**5851**	**1.00**	**0.00**
log_fl:period1	**-1.70**	**0.40**	**-2.20**	**-1.70**	**-1.10**	**0**	**1**	**1884**	**1.00**	**0.00**
log_fl:period2	-0.20	0.50	-0.90	-0.20	0.50	0	1	1833	0.65	0.24
log_fl:region1	**1.50**	**0.40**	**0.90**	**1.50**	**2.00**	**0**	**1**	**1627**	**1.00**	**0.00**
period1:region1	-1.70	2.50	-4.90	-1.80	1.40	0.1	1	1730	0.76	0.05
period2:region1	0.20	3.10	-3.60	0.20	4.20	0.1	1	1741	0.52	0.05
log_fl:period1:region1	0.50	0.60	-0.30	0.50	1.20	0	1	1721	0.77	0.17
log_fl:period2:region1	0.00	0.80	-1.00	0.10	1.00	0	1	1731	0.53	0.19
sigma	**1.20**	**0.00**	**1.10**	**1.20**	**1.20**	**0**	**1**	**5416**	**1.00**	**0.00**
mean_PPD						0.0	1	4250		
log-posterior						0.1	1	1401		

Table 2. Marginal means comparisons of select factor levels. The 'median' column is the difference in log-scale predicted batch fecundity between the specified factors, averaging over the levels of the other factors. For small (25 cm FL bin) fish, all comparisons were certain (pd = 1) and significant (percent in ROPE = 0): within the East and West, BF was lower in the early period than the mid period and higher in the mid period than the late period. Between the East and the West, BF for small fish was always higher in the East than the West. For large fish (90 cm FL bin), only the early to mid period comparisons within the East and West were significant: BF was larger in the early period. It was also larger in the mid period than the late for each region, but this was not certain or significant.

Length Bin	Comparison	Median	CI_low	CI_high	pd	ROPE Percentage	Rope Equivalence
				East			
	Early vs Mid	**-1.247**	**-1.810**	**-0.654**	**1.000**	**0.000**	**Rejected**
	Mid vs Late	**2.126**	**1.247**	**2.992**	**1.000**	**0.000**	**Rejected**
				West			
25 cm	***Early vs Mid***	**-0.977**	**-1.766**	**-0.203**	**0.995**	**0.000**	**Rejected**
	Mid vs Late	**1.485**	**0.506**	**2.438**	**0.997**	**0.000**	**Rejected**
				East vs West			
	Early	**1.944**	**1.289**	**2.563**	**1.000**	**0.000**	**Rejected**
	Mid	**2.204**	**1.483**	**2.941**	**1.000**	**0.000**	**Rejected**
	Late	**1.559**	**0.515**	**2.589**	**0.997**	**0.000**	**Rejected**
				East			
	Early vs Mid	**0.895**	**0.291**	**1.456**	**0.998**	**0.000**	**Rejected**
	Mid vs Late	0.234	-0.613	1.119	0.714	0.161	Undecided
				West			
90 cm	***Early vs Mid***	**0.557**	**0.026**	**1.069**	**0.979**	**0.019**	**Rejected**
	Mid vs Late	0.215	-0.485	0.950	0.716	0.195	Undecided
				East vs West			
	Early	0.118	-0.355	0.599	0.682	0.290	Undecided
	Mid	-0.223	-0.829	0.406	0.748	0.203	Undecided
	Late	-0.250	-1.117	0.656	0.706	0.161	Undecided

Table 3. Spawning frequency at age estimated parameters. Season_b and season_mode are parameters of the gamma probability that describes the effect of time of year on spawning fraction. Period-and-region-specific intercepts and one common slope were estimated. Period 1 is the overfished period (1991 to 2008), period 2 is the rapidly recovering period (2009-2016), period 3 is the stabilizing period (2016-2019). Region 1 is the East and region 2 is the West.

	mean	**sd**	**0.025**	**0.50**	**0.975**	**Rhat**	**n.eff**
intercept	-2.235	0.161	-2.566	-2.231	-1.934	1.000	837
intercept_period[1]	0.000	0.000	0.000	0.000	0.000	NaN	0
intercept_period[2]	0.411	0.100	0.215	0.409	0.602	1.000	1769
intercept_period[3]	0.691	0.098	0.500	0.690	0.887	1.000	1402
intercept_region[1]	0.000	0.000	0.000	0.000	0.000	NaN	0
intercept_region[2]	1.614	0.095	1.432	1.612	1.811	1.000	1247
scale	0.933	0.015	0.903	0.933	0.963	1.000	1557
season_b	0.056	0.002	0.052	0.056	0.061	1.000	4126
season_mode	0.564	0.003	0.558	0.564	0.570	1.000	4392
slope	-0.421	0.026	-0.473	-0.420	-0.373	1.000	1353

Table 4. Spawning frequency at length estimated parameters. Period-and-region-specific intercepts and one common slope were estimated. Period 1 is the overfished period (1991 to 2008), period 2 is the rapidly recovering period (2009-2016), period 3 is the stabilizing period (2016-2019). Region 1 is the East and region 2 is the West.

	mean	**sd**	**0.025**	**0.50**	**0.975**	**Rhat**	**n.eff**
intercept	-0.713	0.190	-1.073	-0.715	-0.332	1.010	885
intercept_period[1]	0.000	0.000	0.000	0.000	0.000	NaN	0
intercept_period[2]	-0.982	0.082	-1.144	-0.982	-0.822	1.000	3809
intercept_period[3]	-0.807	0.079	-0.958	-0.807	-0.648	1.000	3234
intercept_region[1]	0.000	0.000	0.000	0.000	0.000	NaN	0
intercept_region[2]	1.291	0.127	1.037	1.292	1.530	1.010	990
scale	0.861	0.030	0.810	0.858	0.927	1.000	939
season_b	0.062	0.003	0.057	0.061	0.067	1.000	4170
season_mode	0.568	0.004	0.561	0.568	0.575	1.000	4000
slope	-0.065	0.006	-0.077	-0.065	-0.053	1.010	924

Table 5. Predicted average daily spawning fraction by fork length, period and region.

FL (cm)	East, Early	East, Mid	East, Late	West, Early	West, Mid	West, Late
10	0.042	0.090	0.080	0.013	0.032	0.027
20	0.071	0.136	0.123	0.023	0.055	0.048
30	0.111	0.184	0.172	0.042	0.090	0.080
40	0.159	0.227	0.217	0.071	0.136	0.123
50	0.206	0.258	0.251	0.111	0.184	0.172
60	0.244	0.278	0.274	0.160	0.227	0.217
70	0.269	0.290	0.288	0.206	0.258	0.251
80	0.285	0.297	0.295	0.244	0.278	0.274
90	0.294	0.300	0.300	0.269	0.290	0.288

Table 6. Predicted average daily spawning fraction by age, period and region.

Age	East, Early	East, Mid	East, Late	West, Early	West, Mid	West, Late
2	0.213	0.184	0.162	0.093	0.069	0.055
4	0.261	0.241	0.223	0.155	0.124	0.103
6	0.290	0.278	0.268	0.218	0.189	0.167
8	0.304	0.298	0.293	0.264	0.245	0.228
10	0.310	0.308	0.305	0.291	0.280	0.271
12	0.313	0.312	0.311	0.304	0.299	0.294
14	0.314	0.314	0.313	0.311	0.308	0.306
16	0.315	0.315	0.315	0.313	0.312	0.311
18	0.315	0.315	0.315	0.315	0.314	0.314
20	0.315	0.315	0.315	0.315	0.315	0.315

Table 7. Predicted total fecundity (in millions of eggs) by fork length, period and region.

FL (cm)	East, Early	East, Mid	East, Late	West, Early	West, Mid	West, Late
10	0.004	0.146	0.004	0.000	0.001	0.000
20	0.104	1.019	0.076	0.003	0.029	0.004
30	0.794	3.391	0.471	0.054	0.253	0.060
40	3.495	7.910	1.716	0.432	1.252	0.406
50	10.782	14.746	4.535	2.245	4.266	1.807
60	25.898	23.820	9.687	8.526	11.152	5.869
70	52.159	34.958	17.899	25.144	23.942	15.176
80	93.026	48.033	30.191	60.686	44.781	33.225
90	151.863	63.130	47.160	126.036	75.840	64.220

Table 8. Predicted total fecundity (in millions of eggs) by age, period and region.

Age	East, Early	East, Mid	East, Late	West, Early	West, Mid	West, Late
5	17.587	15.076	4.151	2.142	2.857	1.233
10	64.049	36.293	17.221	21.489	19.052	9.503
15	96.432	48.974	29.155	47.548	35.551	20.285
20	112.081	55.582	36.779	66.264	45.575	28.438
25	118.957	58.900	41.176	77.150	51.070	33.883
30	121.875	60.587	43.509	83.020	53.916	37.198
35	123.067	61.399	44.695	86.070	55.350	39.189
40	123.546	61.807	45.316	87.611	56.069	40.335

Table 9. Comparison of total fecundity at age (in millions of eggs) for ages 1-20 from the current report to that reported by Porch et al. (2015) for the Eastern and Western Gulf combined, for the 2011 supplementary survey data.

	West			**East**			**Porch et al., 2015**
Age	1991-2008	2009-2015	2016-2019	1991-2008	2009-2015	2016-2019	
1	0.0	0.0	0.0	0.2	1.3	0.1	0.0
2	0.0	0.2	0.1	1.5	3.4	0.4	0.0
3	0.3	0.5	0.3	4.7	6.6	1.1	0.3
4	0.9	1.4	0.6	10.2	10.6	2.4	2.6
5	2.1	2.8	1.2	17.6	15.1	4.2	9.1
6	4.3	5.1	2.2	26.4	19.7	6.4	20.3
7	7.5	8.0	3.6	36.0	24.3	8.9	34.7
8	11.5	11.4	5.3	45.8	28.6	11.7	50.0
9	16.3	15.2	7.3	55.2	32.7	14.5	64.3
10	21.5	19.0	9.5	64.0	36.3	17.2	76.8
11	26.9	22.8	11.8	72.1	39.5	19.9	87.2
12	32.4	26.4	14.0	79.4	42.3	22.5	95.5
13	37.6	29.7	16.2	85.8	44.8	24.9	102.1
14	42.7	32.8	18.3	91.5	47.0	27.1	107.3
15	47.5	35.5	20.3	96.4	49.0	29.2	111.3
16	52.0	38.0	22.2	100.6	50.7	31.0	114.3
17	56.1	40.3	23.9	104.2	52.2	32.7	116.6
18	59.8	42.2	25.5	107.2	53.5	34.2	118.4
19	63.2	44.0	27.0	109.8	54.6	35.5	119.7
20	66.3	45.6	28.4	112.1	55.6	36.8	120.7

Figure 1. Based on SEDAR52, tables 5.3 and 5.4. The annual proportion of target SPR is measured as annual $SSB/SSB_{SPR26\%}$ (dashed line=SPR of 26%). The stock first fell below this target in 1964, reaching an SPR of only 2% for the years of 1983 to 1991. Because the reproductive data starts in 1991, the over-fished period used here is from 1991 to 2008 (SPR range: 0.02 to 0.05). The rapidly recovering period included 2009-2016 (SPR range: 0.07 to 0.18). Data from 2017 onwards is predicted based on the SEDAR52 stock assessment. The terminal year of data is 2019. Vertical lines mark annual milestones and our stock status periods.

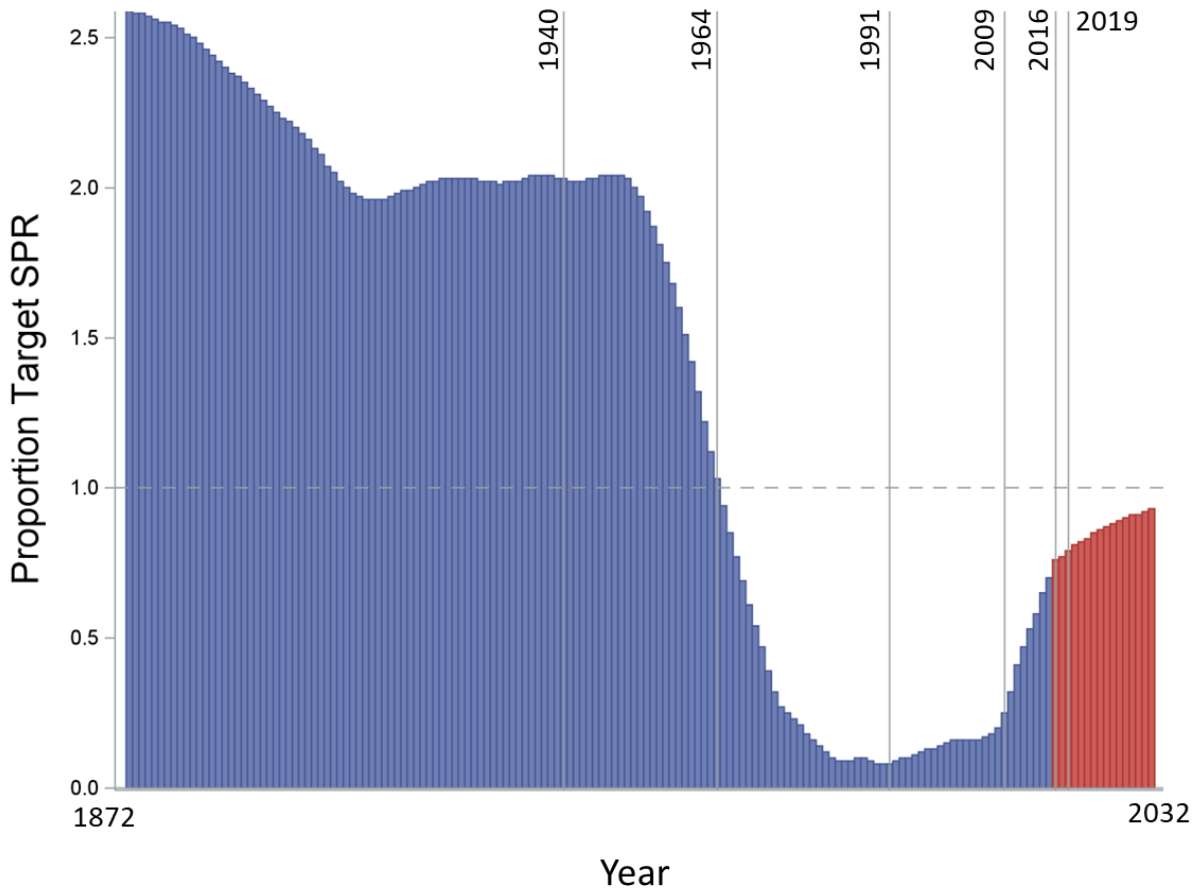


Figure 2. Estimated marginal means of log-batch fecundity by month from the fitted model, showing lower BF estimates in months 4 (April) and 10 (October).

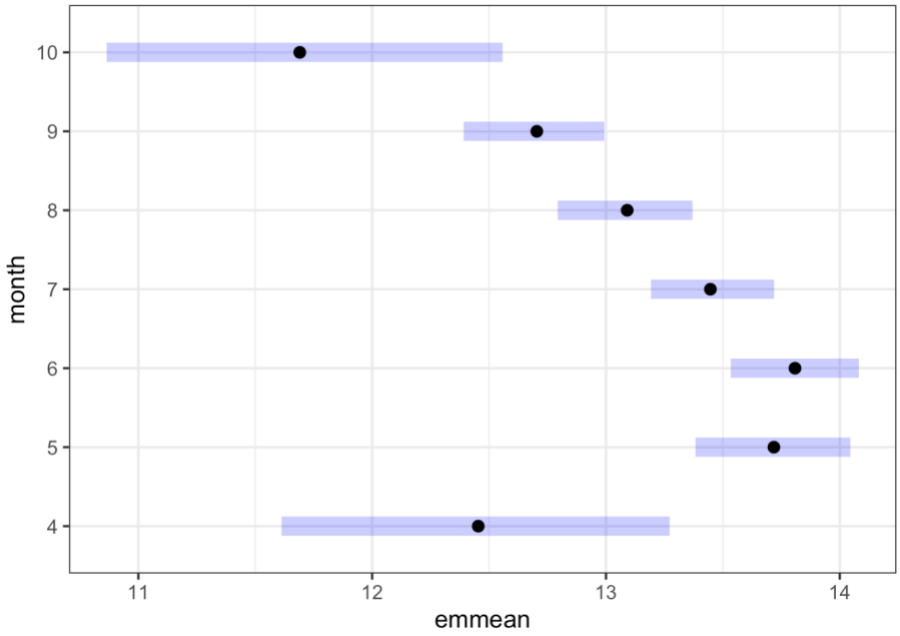


Figure 3. Observed (black points) and predicted (red lines) batch fecundity model fits by region and period of log-transformed batch fecundity to log-transformed fork length. The shaded blue areas are the 2.5% and 97.5% quantiles of predicted values from the posterior draws.

Figure 4. Observed (black points) and predicted (red lines) batch fecundity model fits by region and period to back-transformed batch fecundity and fork length. The shaded blue areas are the 2.5% and 97.5% quantiles of predicted values from the posterior draws.

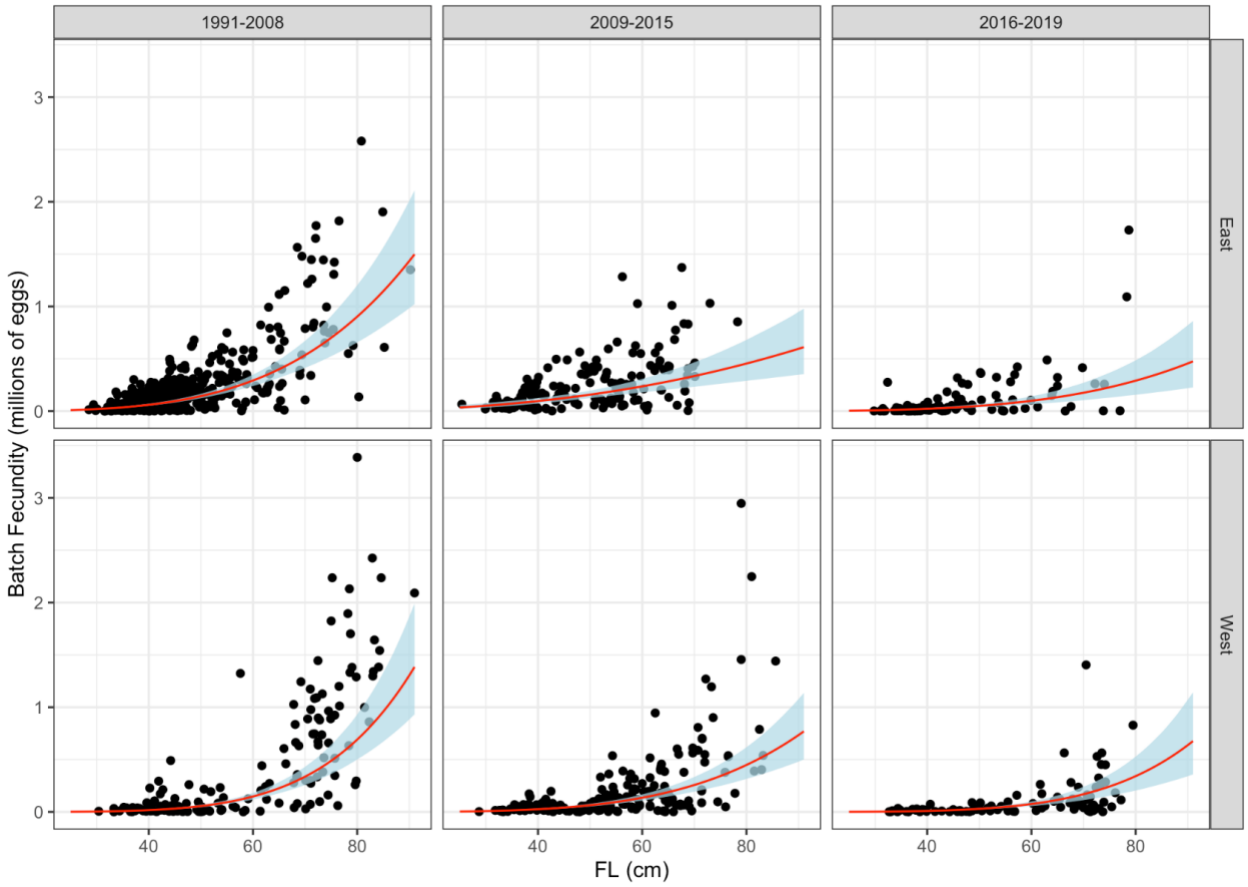


Figure 5. Observed (black points) and predicted (red lines) batch fecundity model fits by region and period to back-transformed batch fecundity and age. Period-and-region-specific von Bertalanffy growth parameters were used to obtain BF at age from BF at length. Red Snapper exhibit high variation of length at age. To reflect the uncertainty due to that variation, VB growth models were fitted to the 1st and 99th quantile of fork length at age and used to predict BF at those lower and upper ranges of length at age; these are reflected in the blue shaded area. Observed points are drawn transparently to better illustrate that the majority of observations occurred at young ages and low BF values which the model is fitting fairly well in all cases.

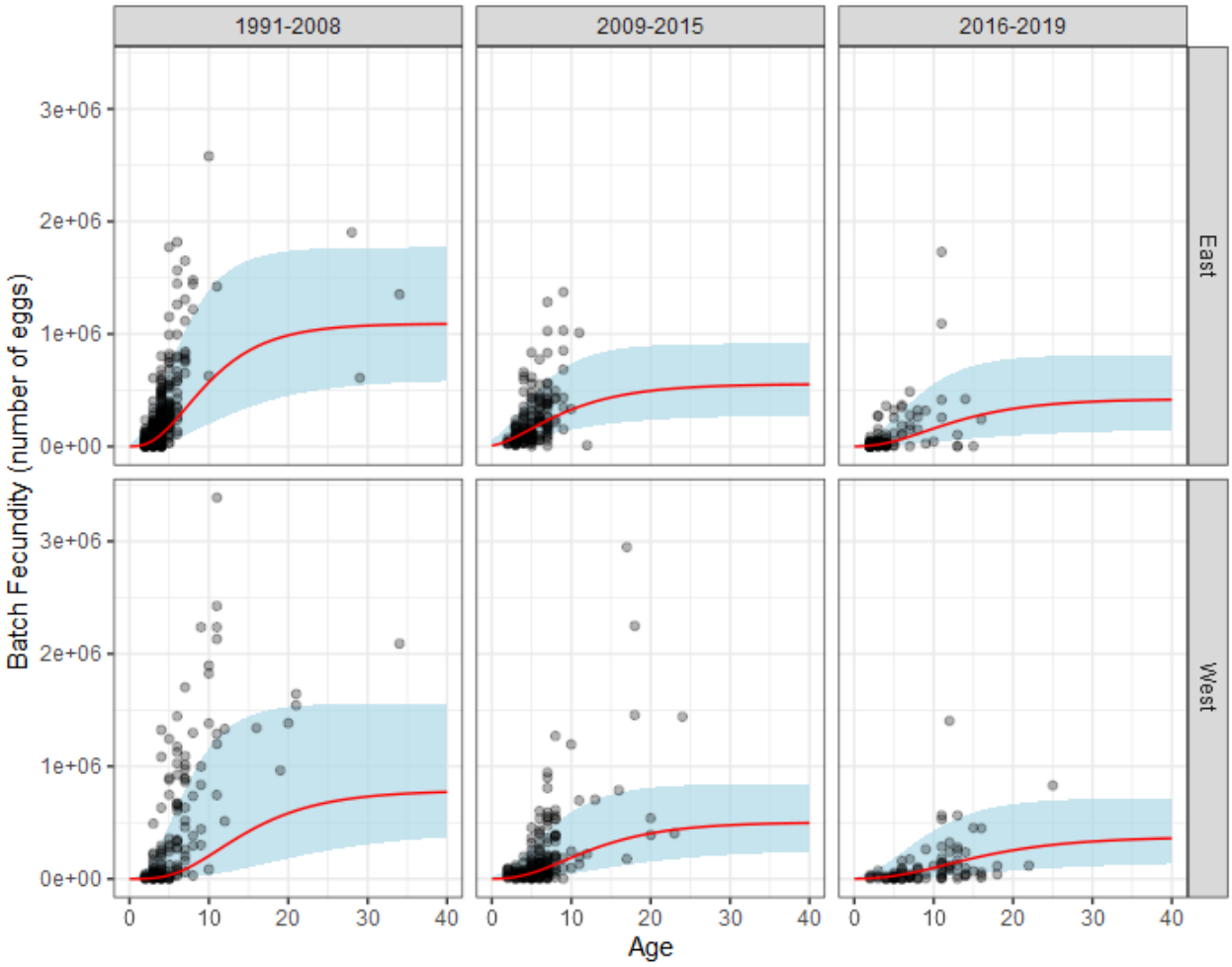


Figure 6. Observed (open circles) and estimated (closed circles) number with spawning markers by 25 mm length bin. Closed circles represent mean values from posterior draws, and vertical lines indicate the 95th quantile of estimated values.

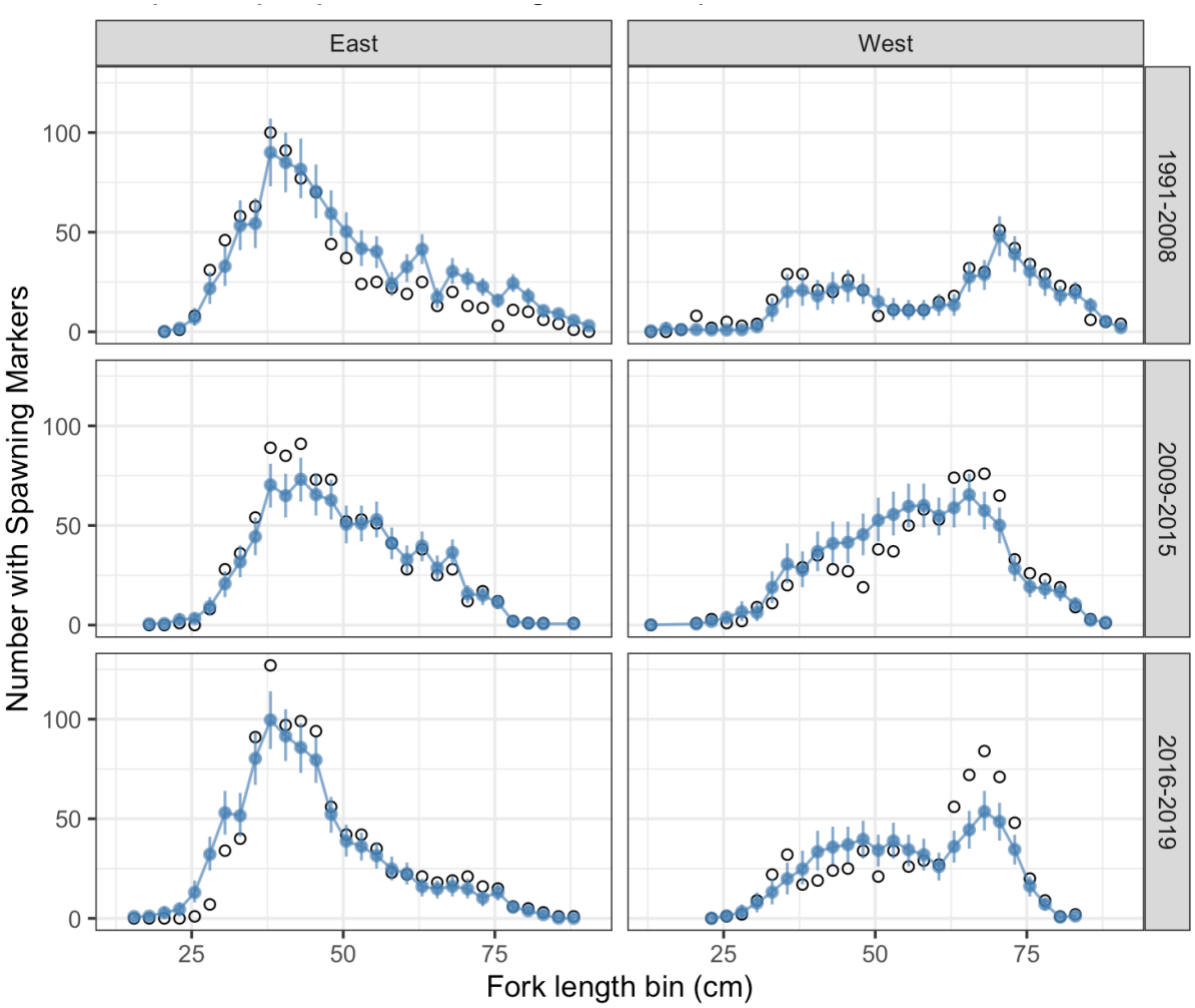


Figure 7. Observed (open circles) and estimated (closed circles) proportion with spawning markers by 25 mm length bin. Closed circles represent mean values from posterior draws, and vertical lines indicate the 95th quantile of estimated values

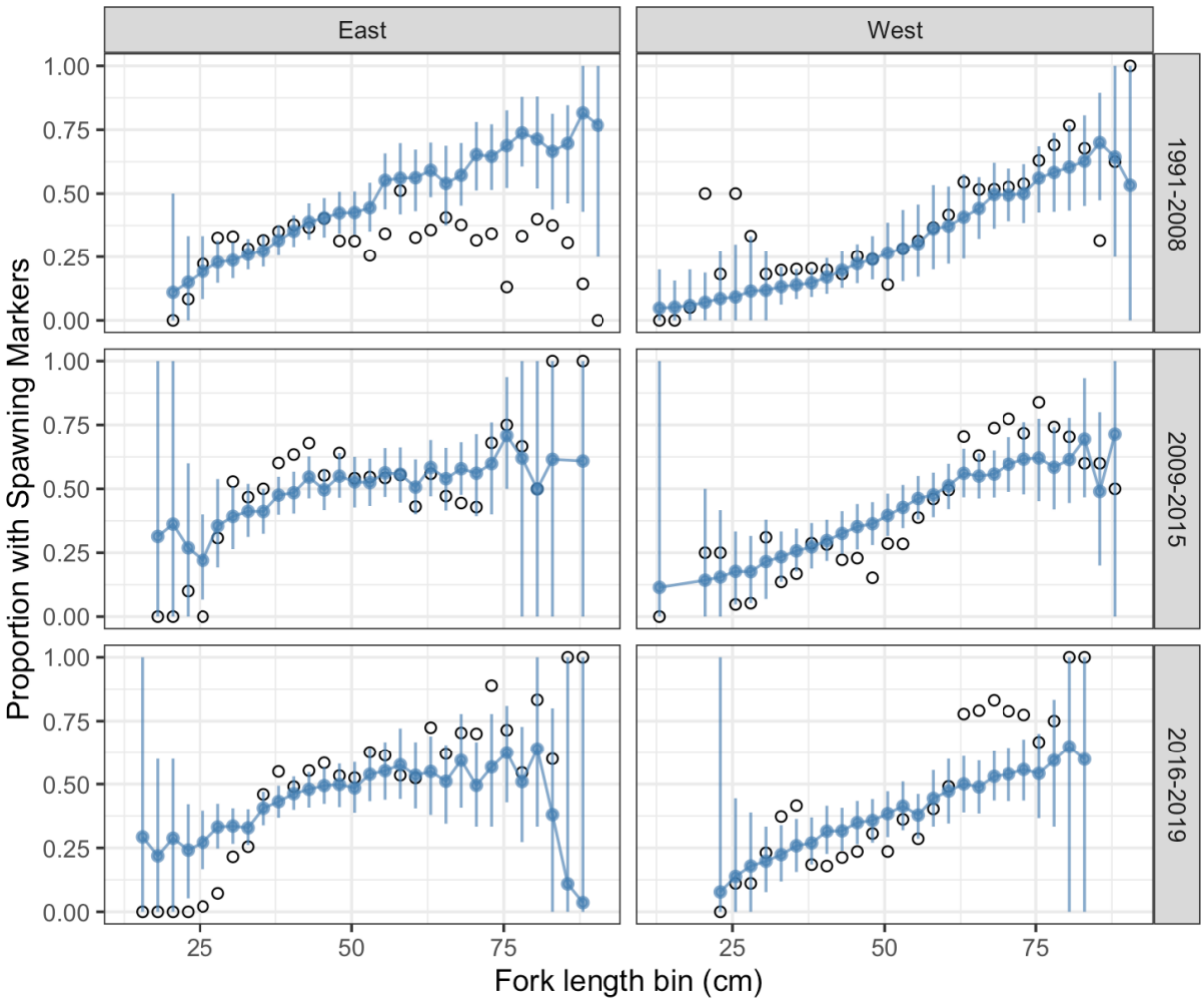


Figure 8. Observed (open circles) and estimated (closed circles) numbers with spawning markers by age. Closed circles represent mean values from posterior draws, and vertical lines indicate the 95th quantile of estimated values

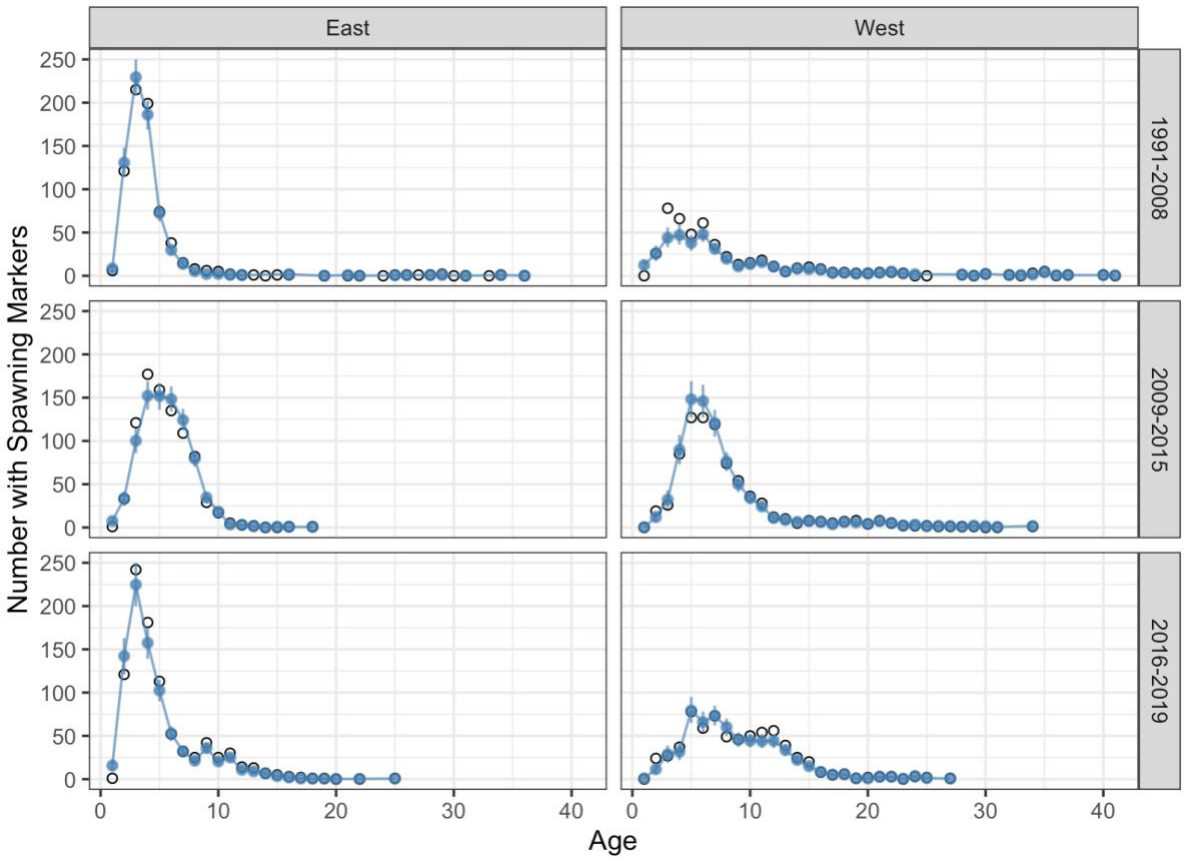


Figure 9. Observed (open circles) and estimated (closed circles) proportion with spawning markers by age. Closed circles represent mean values from posterior draws, and vertical lines indicate the 95th quantile of estimated values

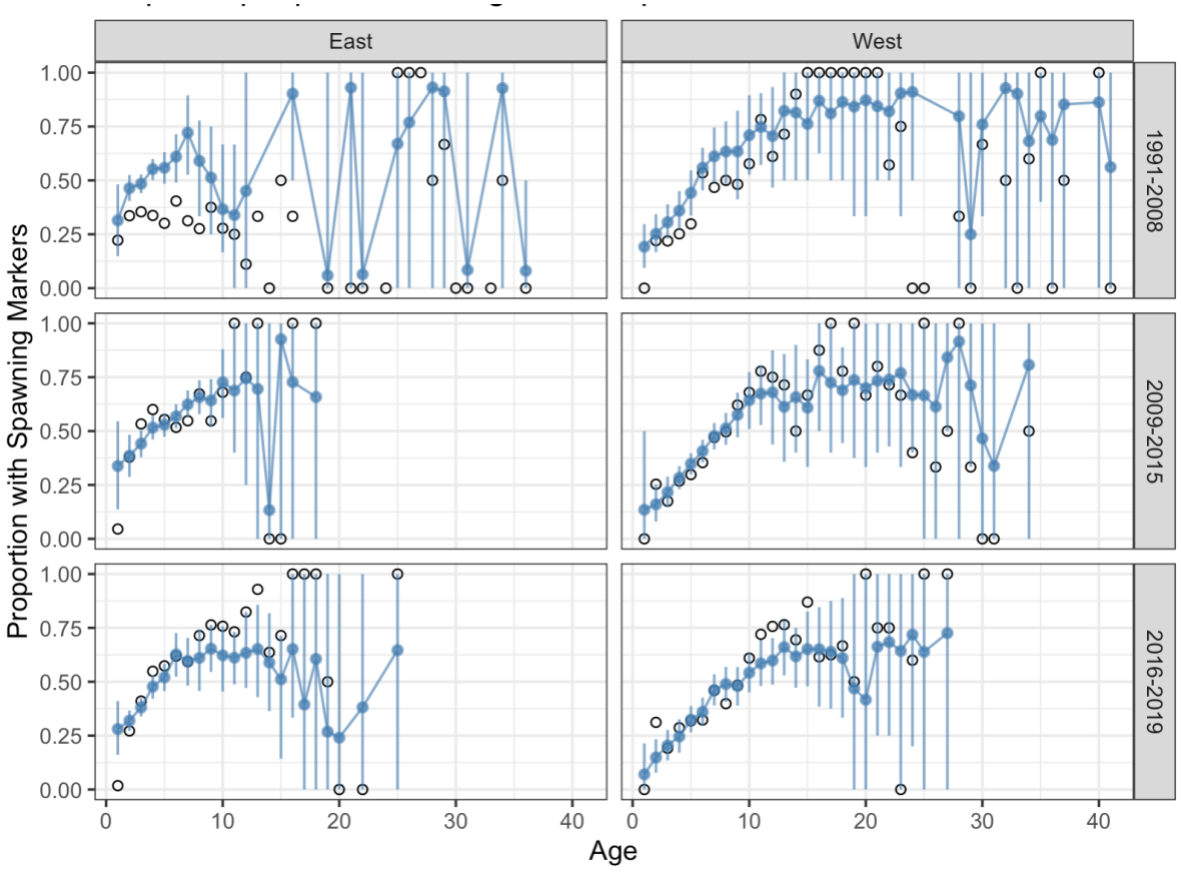
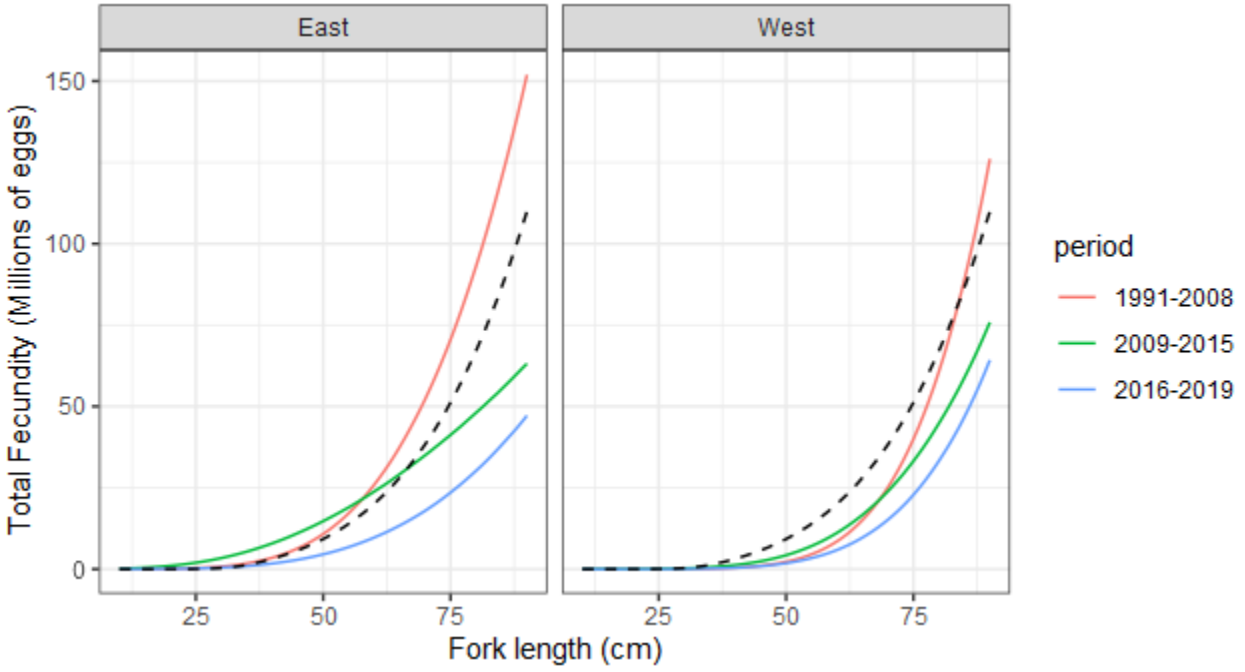


Figure 10. Estimated annual fecundity at length (top panels) and age (bottom panels), obtained by combining results from the batch fecundity and spawning fraction models. For comparison, the annual fecundity calculated by Porch et al. (2015) is shown as dashed black lines (note: the 2015 fecundity at length relationship was for total length rather than fork length and spawning frequency was based on data from the Congressional supplemental Red Snapper survey conducted in 2011 (n=1,002).



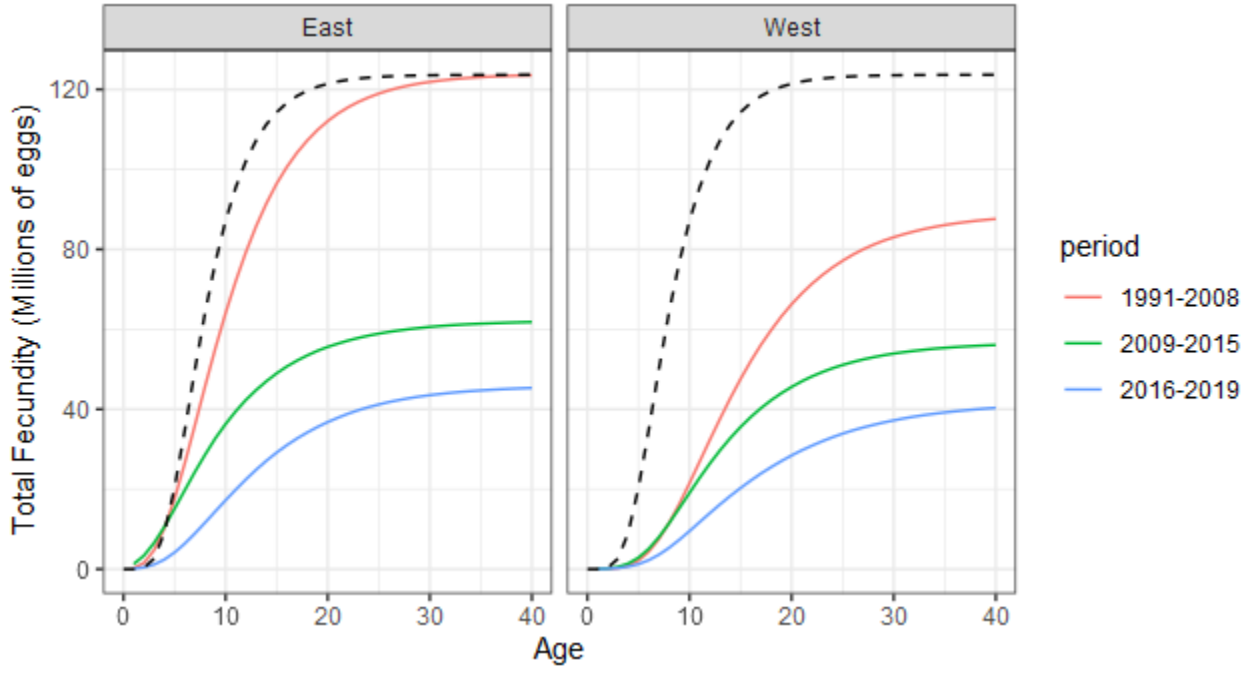
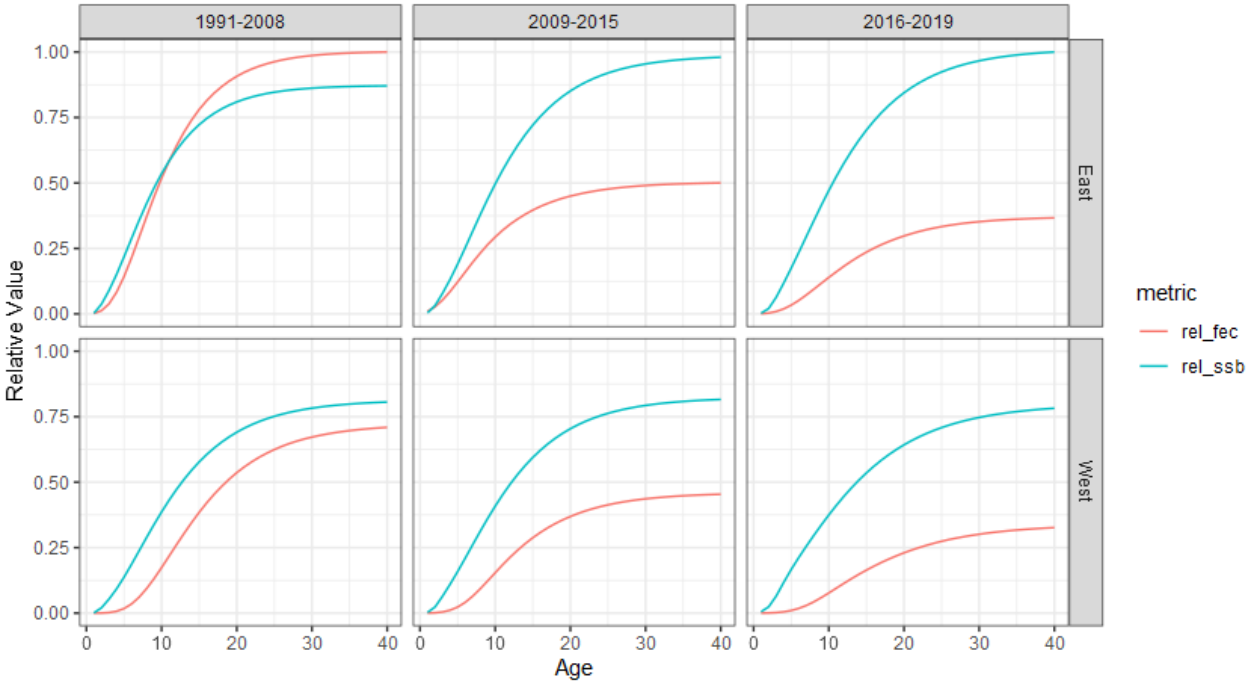


Figure 11. Region-and-period specific relative reproductive potential according to the SSB approach (maturity-at-age * weight-at-age) and TEP. Both SSB and TEP were standardized by their maximum values across space and time. Weight-at-age was calculated from region-and-period specific von Bertalanffy growth curve parameters developed for SEDAR 74 (Garner et al., 2022), and maturity-at-age is from maturity estimates for SEDAR 74 (Lowerre-Barbieri et al., 2022).



References

Berkeley, S. A., M. A. Hixon, R. J. Larson, and M. S. Love. Aug. 2004. Fisheries Sustainability via Protection of Age Structure and Spatial Distribution of Fish Populations. Fisheries 29:23-32.

Brooks, E.N. (2013). Effects of variable reproductive potential on reference points for fisheries management. Fisheries Research 138, 152-158.

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

Cerviño, S., Domínguez-Petit, R., Jardim, E., Mehault, S., Piñeiro, C. and Saborido-Rey, F. (2013) Impact of egg production and stock structure on MSY reference points and its management implications for southern hake Merluccius merluccius. Fisheries Research 138, 168– 178.

Cooper, W.T., Barbieri, L.R., Murphy, M.D., and Lowerre-Barbieri, S.K. (2013). Assessing stock reproductive potential in species with indeterminate fecundity: Effects of age truncation and size-dependent reproductive timing. Fisheries Research 138, 31-41.

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

Dunlop, E.S., Enberg, K., Jorgensen, C., and Heino, M. (2009). Toward Darwinian fisheries management. Evolutionary applications 2, 246-259.

Field, J.G., Jarre, A., Moloney, C.L., Stroemme, T., Buisson, L.d., Lipinski, M.R., and Kainge, a.P. (2008). Exploring the BOFFFF Hypothesis Using a Model of Southern African Deepwater Hake (Merluccius paradoxus). Paper presented at: Fisheries for Global Welfare and Environment, 5th World Fisheries Congress (Terapub).

Garner, S., Allman, R., Barnett, B. and Willett, N. 2022. Description of age, growth, and natural mortality of Red Snapper from the northern Gulf of Mexico 1980 and 1986-2019. SEDAR74-DW-34. SEDAR, North Charleston, SC. 33 pp.

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.

Goodyear, C. P. 1993. Spawning stock biomass per recruit in fisheries management: foundation and current use. p. 67-81. In S. J. Smith, J. J. Hunt and D. Rivard [ed.] Risk evaluation and biological reference points for fisheries management. Can. Spec. Publ. Fish. Aquat. Sci. 120.

Heino, M., Díaz Pauli, B., and Dieckmann, U. (2015). Fisheries-Induced Evolution. Annual Review of Ecology, Evolution, and Systematics 46, 461-480.

Hixon, M.A., Johnson, D.W., and Sogard, S.M. (2014). BOFFFFs: on the importance of conserving old-growth age structure in fishery populations. ICES Journal of Marine Science 71 2171-2185.

Honsey, A.E. (2018). Fish growth, temperature, and life history: applying theory to improve fisheries research and management. University of Minnesota Digital Conservancy, https://hdl.handle.net/11299/202191.

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

Kell L.T., Nash R.D., Dickey-Collas M., Mosqueira I., and Szuwalski C. 2016. Is spawning stock biomass a robust proxy for reproductive potential? Fish Fish. 17(3): 596–616.

Klaer, N.L., O'Boyle, R.N., Deroba, J.J. et al. (2015) How much evidence is required for acceptance of productivity regime shifts in fish stock assessments: are we letting managers off the hook? Fisheries Research 168, 49–55.

Longhurst, A. (2002). Murphy's law revisited: longevity as a factor in recruitment to fish populations. Fisheries Research 56, 125-131.

Lowerre-Barbieri, S.K. (2009). Reproduction in relation to conservation and exploitation of marine fishes. In Reproductive biology and phylogeny of fishes (Agnathans and bony fishes) B.G.M. Jamieson, ed. (Enfield, New Hampshire: Science Publishers), pp. 371-394.

Lowerre-Barbieri, S.K., N.J. Brown-Peterson, H. Murua, J. Tomkiewicz, D. Wyanski, and F. Saborido-Rey. (2011). 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., Walters, S., Bickford, J., Cooper, W., and Muller, R. (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., Crabtree, L., Switzer, T., Walters Burnsed, S., and Guenther, C. (2015). Assessing reproductive resilience: an example with South Atlantic red snapper Lutjanus campechanus. Marine Ecology Progress Series 526, 125-141.

Lowerre-Barbieri, S., DeCelles, G., Pepin, P., Catalán, I.A., Muhling, B., Erisman, B., Cadrin, S.X., Alós, J., Ospina-Alvarez, A., Stachura, M.M., et al. (2017). Reproductive resilience: a paradigm shift in understanding spawner-recruit systems in exploited marine fish. Fish and Fisheries 18, 285–312.

Lowerre-Barbieri et al., (2022) Best practices for standardized reproductive data and methodology to estimate reproductive parameters for red snapper in the Gulf of Mexico. SEDAR74-DWxx. SEDAR, North Charleston, SC.

Marshall, C.T., Needle, C.L., Thorsen, A., Kjesbu, O.S., and Yaragina, N.A. (2006). Systematic bias in estimates of reproductive potential of an Atlantic cod (*Gadus morhua)* stock: implications for stock recruit theory and management. Canadian Journal of Fisheries and Aquatic Sciences 63, 980-994.

Marshall, C.T., and Browman, H.I. (2007). Disentangling the causes of maturation trends in exploited fish populations. Marine Ecology Progress Series 335, 249-251.
Marshall, C.T., and McAdam, B.J. (2007). Integrated perspectives on genetic and environmental effects on maturation can reduce potential for errors of inference. Marine Ecology Progress Series 335, 301-310.

Marshall, C.T. (2009) Implementing information on stock reproductive potential in fisheries management: the motivation, challenges and opportunities. In: Fish Reproductive Biology: Implications for Assessment and Management (eds T. Jakobsen, M.J. Fogarty, B.A. Megrey and E. Moksness). Wiley-Blackwell, Chichester, UK, pp. 395– 420.

Marshall D.J., Bode M., Mangel M., Arlinghaus R., and Dick E.J. (2021) Reproductive hyperallometry and managing the world's fisheries. Proc. Natl. Acad. Sci. U.S.A. 118(34): e2100695118.

Marteinsdottir, G., and Steinarsson, A. (1998). Maternal influence on the size and viability of Iceland cod Gadus morhua eggs and larvae. Journal of Fish Biology 52, 1241-1258.

Martinez-Andrade F (2003) A comparison of life histories and ecological aspects among snappers (Pisces: Lutjanidae). PhD dissertation, Louisiana State University and Agricultural and Mechanical College, Baton Rouge, LA.

Mehault, S., Domínguez-Petit, R., Cerviño, S. and Saborido-Rey, F. (2010) Variability in total egg production and implications for management of the southern stock of European hake. Fisheries Research 104, 111– 122.

Morgan, M.J., Murua, H., Kraus, G. et al. (2009) The evaluation of reference points and stock productivity in the context of alternative indices of stock reproductive potential. Canadian Journal of Fisheries and Aquatic Sciences 66, 404– 414.

Murua , H., Quincoces, I., Garcia, D., and Korta, M. (2010) Is the Northern European hake, Merluccius merluccius, management procedure robust to the exclusion of reproductive dynamics? Fisheries Research 104: 123–135.

Palumbi, S.R. (2004). Why mothers matter. Nature 430, 621-622.

Porch, C. E., G. R. Fitzhugh, M. S. Duncan, L. A. Collins, and M. W. Jackson. (2007) Modeling the dependence of batch fecundity on size and age for use in stock assessments of Red Snapper in U.S. Gulf of Mexico waters. Pages 229–244 in W. F. Patterson III, J. H. Cowan Jr., G. R. Fitzhugh, and D. L. Nieland, editors. Red Snapper ecology and fisheries in the U.S. Gulf of Mexico. American Fisheries Society, Symposium 60, Bethesda, Maryland.

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: Dynamics, Management, and Ecosystem Science [online serial] 7:233–245.

Rochet, M.-J. (2009). Effects of Fishing on the Population. In Fish Reproductive Biology, T. Jakobsen, M.J. Fogarty, B.A. Megrey, and E. Moksness, eds. (West Sussex: Wiley-Blackwell), pp. 172-206.

Scott, B., Marteinsdottir, G., and Wright, P. (1999). Potential effects of maternal factors on spawning stock-recruitment relationships under varying fishing pressure. Can J Fish Aquat Sci 56, 1882-1890.

Scott, B.E., Marteinsdottir, G., Begg, G.A., Wright, P.J., and Kjesbu, O.S. (2006). Effects of population size/age structure, condition and temporal dynamics of spawning on reproductive output in Atlantic cod (Gadus morhua). Ecological Modelling 191, 383-415.

SEDAR31 (2013). Gulf of Mexico Red Snapper Stock Assessment Report. SEDAR, North Charleston SC. 1103 pp
SEDAR 52 (2018). Stock assessment report Gulf of Mexico Red Snapper. North Charleston, SC 435 p.

SEDAR52 (2018). Stock Assessment Report Gulf of Mexico Red Snapper SECTION I - INTRODUCTION UPDATED 9 MAY 2018.

SEDAR73 (2021). South Atlantic Red Snapper Stock Assessment Report. SEDAR, North Charleston SC. 194 pp.

Trippel EA (1999) Estimation of stock reproductive potential: history and challenges for Canadian Atlantic gadoid stock assessments. Journal of Northwest Atlantic Fisheries Science 25:61–81.

Vert-pre, K.A., Amoroso, R.O., Jensen, O.P. and Hilborn, R. (2013) Frequency and intensity of productivity regime shifts in marine fish stocks. Proceedings of the National Academy of Sciences of the United States of America 110, 1779–1784.

Wright, P.J. (2007). Understanding the maturation process for field investigations of fisheries-induced evolution. Marine Ecology Progress Series 335, 279-283.

Wright, P.J., and Trippel, E.A. (2009). Fishery-induced demographic changes in the timing of spawning: consequences for reproductive success. Fish and Fisheries 10, 283-304.

Zarada, K., Walters Burnsed, S., Bickford, J., Ducharme-Barth, N., Ahrens, R.N.M., and Lowerre-Barbieri, S. (2019). Estimating site-specific spawning parameters for a spawning aggregation: an example with spotted seatrout. Marine Ecology Progress Series 624, 117-129.