Effects of sex-specific fishing mortality on sex ratio and population dynamics of Gulf of Mexico greater amberjack

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Abstract

The US Gulf of Mexico stock assessment of greater amberjack *Seriola dumerili* assumes a 1:1 male:female sex ratio. However, the observed sex ratio in the landed catch is 1:1.8, and for fish >1 m fork length is 1:2.4. To theoretically explore whether this female-skewed sex ratio may arise due to differential fishing mortality between the sexes, we used a sex-specific age- and size-based model to investigate how different fishing mortality rates could create a female-skew in the landed catch as well as its subsequent effects on reproductive potential. When fishing mortality rates in the model were equal between the sexes, the sex ratio of the landed catch was approximately 1:1 for all legal-sized fish, and approximately 1:2.4 for fish >1 m FL. However, reproductive potential decreased in comparison to the corresponding scenario with equal fishing mortality rates when fishing mortality rates between the sexes were changed to create the 1:1.8 sex ratio observed in the landed catch. This modeling study demonstrates one possible route that could explain the female-skewed sex ratios observed in the landed catch, and indicates that sex ratio values other than 1:1 should be considered in future stock assessments for Gulf of Mexico greater amberjack.

Keywords: *Seriola*, greater amberjack, sex ratio, population dynamics

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1. Introduction

Traditionally, fisheries models tend to focus on growth, female reproductive output, and survival of a population, with little consideration of behavior, life history strategies, and reproductive patterns (e.g., sex change, skip spawning, sex ratios, and size, type, and location of spawning aggregations) (Ricker, 1950; Beverton and Holt, 1957; Schnute, 1987). However, effective management often requires an understanding of many of these factors (Alonzo and Mangel, 2004, 2005; Calduch-Verdiell et al., 2014). Gonochoristic as well as sex-changing populations tend to have a reduced reproductive capacity as fishing increases due to a decrease in spawning stock biomass. This results in reduced egg production from a decrease in reproductive individuals (Huntsman and Schaaf, 1994; Calduch-Verdiell et al., 2014). Although there is still considerable uncertainty in the relationship between stock size and recruitment in many species (Maunder and Piner, 2015), information regarding reproduction and recruitment are often among the most common future research recommendations in stock assessments (NMFS, 2014A, 2014B). In sex-changing species that undergo size-selective fishing there tends to be a large reduction in the individuals of the larger sex, especially species that form large spawning aggregations, such as gag *Mycteroperca microlepis* (Heppell et al., 2006). Non-aggregating spawners, such a red grouper *Epinephelus morio*, may not experience such reductions (NMFS, 2017). However, in some species that do not form spawning aggregations, characteristics of the spawning behavior and fishery can still lead to reductions in the larger sex, as is the case with common hogfish *Lachnolaimus maximus* (Cooper et al., 2013) and California sheephead *Semicossyphus pulcher* (Alonzo et al., 2004). Such sex-specific fishing mortality can lead to an altered sex ratio and a theoretical reduction in reproductive potential either through egg (protandrous species) or sperm (protogynous species) limitation, which is often greater than that seen in gonochoristic species if there is no compensation mechanism (Huntsman and Schaaf, 1994; Armsworth, 2001; Alonzo and Mangel, 2004, 2005; Heppell et al., 2006; Molloy et al., 2007; Alonzo et al., 2008; Brooks et al., 2008).

The need to understand the effect of sex-specific harvest rates on reproductive output is not limited to sex-changing species, as any species in which fishing imposes greater mortality on one sex compared to the other may result in potential sperm or egg limitation (Alonzo et al., 2008; Heupel et al., 2010; Kelly-Stormer et al., 2017; Williams et al. 2017). In the Gulf of Mexico (hereafter "Gulf"), there is evidence of potential sex-skewing in greater amberjack *Seriola dumerili*, which is not a sex-changing species. Individual spawning events in this species appear to occur in pairs, but relatively large aggregations form in association with spawning (Graham and Castellanos, 2005). Sex ratios of greater amberjack in the landed catch from commercial and recreational fisheries are female-skewed, with an annual mean male to female sex ratio of 1:1.8 (Smith, 2011; Smith et al., 2014). This indicates that there is either a pre-existing female-skewed sex ratio (i.e., the sex ratio of the entire population from birth is female skewed) or that females are being selectively exploited by the fisheries. This latter scenario would ultimately lead to a male-skewed sex ratio in the remaining unharvested population.

Greater amberjack are gonochoristic but show sexual dimorphism in growth with females generally having a greater size at age (Harris et al., 2007; Murie and Parkyn, 2008), as well as dominating the largest size classes (Burch, 1979; Beasley, 1993; Thompson et al., 1999; Harris et al., 2007; Smith et al., 2014). The greater growth of females compared to males appears to be less significant in the Gulf stock (Murie and Parkyn, 2008) compared to the US South Atlantic stock (Harris et al., 2007), but may still play some role in creating a sex-selective fishery due to size regulations. A minimum size limit of 30 in (762 mm) fork length (FL), which was increased to 34 in (864 mm) FL as of January 4, 2016, is enforced in the recreational fishery, and 36 in (914 mm) FL in the commercial fishery in the Gulf (NMFS, 2016). Larger fish are typically landed in the commercial fishery (Fig. 1). but this figure is aggregated across time from the early 1980s to present and, in more recent years, the number of fish over 1 m FL landed in both the commercial and recreational fisheries has increased. The landing of these large individuals may result in selectivity towards females because landed fish greater than 1 m FL are comprised of approximately 70% females in both the Gulf and US South Atlantic stocks (Beasley, 1993; Thompson et al., 1999; Harris et al., 2007; Smith et al., 2014).

The most recent stock assessment of greater amberjack in the Gulf found it to be overfished and potentially undergoing overfishing, despite continued increases in regulations over the last two decades (i.e., higher minimum size limits, smaller bag limits/quotas, closed season) (NMFS, 2014A). This stock assessment assumed that the sex ratio of the Gulf stock was 1:1. However, the sex ratio of the landed catch, and especially fish over 1 m, is known to be skewed towards females (Beasley, 1993; Thompson et al., 1999; Harris et al., 2007; Smith et al., 2014).

The goal of this study was to use simulation modelling to: 1) determine if theoretical sex-specific mortality rates could create sex ratios observed in the landed catch; 2) examine how these theoretical sex-specific mortality rates may influence the reproductive potential of the simulated population of Gulf greater amberjack; and 3) examine how the sex ratio of the modeled population (i.e., the sex ratio of unharvested fish) changes based on the fishing mortality scenario being modeled. This study is not meant to serve as a stock assessment for this species, but rather to highlight how sex-specific mortality and altered sex ratios could influence the population dynamics of greater amberjack.

2. Methods

2.1 Model structure and parameterization

An age-structured model, as outlined in Hilborn and Walters (1992) and Walters and Martell (2004), was constructed to examine the potential impacts of sex-specific fishing mortality rates on the sex ratios and reproductive potential of the Gulf greater amberjack stock. Age-structured models are forward-projection models based on estimates of initial unfished population numbers and annual recruitment. The number of fish from a particular cohort surviving to the following year is determined by the initial size of that cohort less any catch occurring during that year multiplied by a survival rate (number alive = survival x (initial number – catch). The catch applied to a particular cohort within a given year is based on a fishing mortality rate and selectivity of that cohort by a particular fishery based on size. Growth curves are used to determine the size of fish at a particular age, and length-weight relationships combined with maturity schedules are used to determine the reproductive output within a particular year. This reproductive output is used in a recruitment function to estimate the number of new recruits entering the population the following year. Additional parameters, such as discard mortality, can be added to age-structured models to provide greater detail, and to examine various model scenarios. This model incorporated sex, size, and age structure and examined several outputs. To ensure the model had reached equilibria, it was run for 50 years both prior to and after the onset of fishing.

The number of fish at age-*A* and time-*t* in the unfished condition for each sex was determined as:

$$N_{A,t,s} = N_{(A-1),(t-1),s}(e^{-M}) \qquad (1)$$

where: $N_{A,t,s}$ is number fish at age-A and time-t for each sex (s), $N_{(A-1),(t-1),s}$ is the number of fish of the previous age in the previous year for each sex, and M is the instantaneous natural mortality rate. A value of M equal to 0.25 yr^{-1} was used based on the baseline value used in the 2006 Gulf Stock Assessment and its 2010 update (NMFS, 2006, 2011) (Table 1). The instantaneous natural mortality rate used in this model was assumed to be the same between the sexes and over time, as it was in these stock assessments.

The number of fish at age-A and time-t in the fished condition for each sex was calculated as:

$$N_{A,t,s} = N_{(A-1),(t-1),s}(e^{-M})\{[1 - U_s \cdot CMHL_{(A-1)} \cdot [PCL_{(A-1),s} + (1 - PCL_{(A-1,s)})D]\} \cdot \{1 - U_s \cdot CMLL_{(A-1)} \cdot [PCL_{(A-1),s} + (1 - PCL_{(A-1),s})D]\} \cdot \{1 - U_s \cdot HB_{(A-1)} \cdot [PRL_{(A-1),s} + (1 - PRL_{(A-1),s})D]\} \cdot \{1 - U_s \cdot RCP_{(A-1)} \cdot [PRL_{(A-1),s} + (1 - PRL_{(A-1),s})D]\} \tag{2}$$

where: U_s is the annual exploitation rate for each sex ($U_s = [F_s\,(1 - e^{-Z})]/Z_s$), where F_s is the instantaneous fishing mortality rate for each sex and Z is the instantaneous total mortality rate for each sex, and $Z_s = F_s + M$; $CMHL$, $CMLL$, HB, and RCP are the respective gear selectivities at age (based on Diaz et al., 2005) for commercial handline gear (CMHL), commercial longline gear (CMLL), recreational headboat fishery (HB), and the combined charter and private boat recreational fishery (RCP) (Table 2). D is the discard mortality applied to both sexes across all ages and fisheries (Table 1) and PCL and PRL are the proportions of fish at age that are of legal size for the commercial and recreational (including headboat) fisheries, respectively, for each sex. The proportion of legal sized fish at age for each sex was calculated as: ($PCL_{A,s} = \{1 + e^{[-(L_{A,s} - LCL)/\sigma]}\}^{-1}$ and ($PRL_{A,s} = \{1 + e^{[-(L_{A,s} - LRL)/\sigma]}\}^{-1}$, where L is the FL (mm) at age for each sex, LCL and LRL are the commercial and recreational size limits in place during the time of this study, and σ is a parameter that incorporates the variability in length-at-age (Table 1). Discard mortality was set at 0.2 based on the baseline value used on the 2014 stock assessment (NMFS, 2014A), and was applied across all ages for all fisheries because there are discards both above and below the minimum size limits due to size and bag limits, closed seasons, trip limits, and early closures due to quotas being met (GMFMC, 2013; Johnson, 2013; Sauls and Cernak, 2013). The value of σ is often set at 10% of a particular length of interest, such as a length limit (Coggins et al., 2007; Pine et al., 2008; Tetzlaff et al., 2011). The ratios of the difference in the upper and lower estimates of length-at-age estimates and mean length-at-age estimates for Gulf of Mexico greater amberjack, which were calculated from mean values and standard errors of von Bertalanffy growth parameters from Murie and Parkyn (2008), ranged from approximately 0.05 to 0.13. Based on this information, σ was set at 10% of LCL and LRL.

To incorporate the sex-specific growth rates of Gulf greater amberjack, the von Bertalanffy growth parameters for each sex (Table 1) were used to determine length-at-age for each sex ($L_{A,s}$). The growth model was parameterized as:

$$L_{A,s} = L_{\infty_s}[1 - e^{-k_s(A - t_{0_s})}] \tag{3}$$

where L_∞ is the asymptotic FL (mm), k is the Brody growth coefficient, and t_o is the hypothetical age at zero length, for each sex (s).

The weight-at-age relationship for males and females was described by:

$$W_{A,s} = aL_{A,s}^{\,b} \tag{4}$$

where W is the whole weight (kg), and a and b are constants in the length-weight relationship and $L_{A,s}$ is the FL in mm for each sex at a particular age (Table 1).

The spawning stock biomass (SSB_t) of each sex (s) for each year was calculated as:

$$SSB_{t,s} = \sum_A N_{A,t,s} \cdot PM_{A,s} \cdot W_{A,s} \tag{5}$$

where $PM_{A,s}$ is the proportion mature at age-A for each sex based on Table 3.

Batch fecundity at age-A (BF_A) was calculated as: $BF_A = af + (bf \cdot A)$, where af and bf are constants in the fecundity-age relationship (Table 1). Annual fecundity at age-A (AF_A) was calculated as $AF_A = n(BF_A)$, where n = number of batch spawns per season (Table 1). Batch fecundity and number of batches per season are currently unknown for the Gulf of Mexico stock and therefore were estimated using data from the Atlantic stock of greater amberjack from Harris et al. (2007). The total number of eggs produced each year (E_t) was determined by:

$$E_t = \sum_A (N_{A,t,fem}\, AF_A) \tag{6}$$

where $N_{A,t,fem}$ = number of females at age-A for each year.

The proportion of fertilized eggs (PFE_t), a function of the fertilization rate and the proportion of mature males in the spawning stock, was calculated as:

$$PFE_t = f[1 - e^{(-\theta \cdot PMSS_t)}] \quad \text{(from Heppell et al., 2006)} \tag{7}$$

where: f is the maximum fertilization rate; θ is a fertility parameter that determines the steepness of the curve; and $PMSS_t$ is the proportion of mature males in the spawning stock, calculated as:

$$PMSS_t = \frac{(\sum_A (N_{A,t,male} \cdot PM_{A,male}))}{(\sum_A (N_{A,t,male} \cdot PM_{A,male}) + \sum_A (N_{A,t,female} \cdot PM_{A,female}))} \tag{8}$$

The maximum fertilization rate (f) was set at 0.8 based on data from captive spawning experiments with greater amberjack by Jerez et al. (2006). This was the highest average monthly fertilization rate observed in their study. There is currently no empirical data on fertility functions for greater amberjack, so a theoretical value for θ was selected based on Heppell et al. (2006). A value for $\theta = 20$ was chosen for θ to represent a "low fertility" function as described by Heppell et al. (2006), which could produce at least minor changes in fertilization rate to investigate potential sperm limitation when model parameters are changed. A "high fertility" ($\theta = 80$) function would show virtually no change in fertilization rate with the sex ratios observed in greater amberjack. Total annual production of fertilized eggs (FE_t) was calculated as: $FE_t = E_t(PFE_t)$.

Recruitment (R_t) was calculated using the compensation form of the Beverton and Holt model (Walters and Martell, 2004), which was also used in the most recent stock assessment of greater amberjack (NMFS, 2014A). This recruitment function was calculated as:

$$R_t = \frac{\frac{K}{EPR_0} E_t}{1 + \left\{\frac{(K-1)}{R_0 \cdot EPR_0}\right\} E_t} \tag{9}$$

where K is the recruitment compensation ratio, which represents the ratio of juvenile survival in the unfished condition to juvenile survival in a state where egg have been fished down to near zero, R_0 is the average recruitment in an unfished condition (Table 1), and EPR_0 is the average unfished lifetime egg production per recruit. Because recruitment in this model was being dictated by fertilized egg production to incorporate male and female contributions, $FEPR_0$ (average unfished lifetime fertilized egg production per recruit) was used in place of EPR_0 , and FE_t was used in place of E_t. $FEPR_0$ was calculated as:

$$FEPR_0 = \sum_A l_A(AF_A)(PM_{A,female})(FP) \quad (10)$$

where l_A is the unfished survivorship at age-A, and FP is the proportion of females in the population in the unfished condition. The unfished survivorship was calculated as the proportion of fish surviving from the previous year (starting at 1 for the first age modeled) multiplied by the unfished survival rate, S, where $S = e^{-M}$. The sex ratio of new recruits was assumed to be 1:1. To incorporate uncertainty in recruitment, a lognormal deviation was applied to Equation 9 with a mean of 1 and coefficient of variation of 0.4 (Turner et al., 2000). A K value of 10 was selected based on values from species with similar life histories (Myers et al., 1999) and from Goodwin et al. (2006) as:

$$\log_e(K) = 4.69 + 0.32\log_e(W_\infty) + 0.72\log_e(TM) - 0.25\log_e(FM) \quad (11)$$

where W_∞ is the asymptotic total weight (calculated from Equation 4 for the maximum age modeled, age-10), TM is the age where female maturity was 50% (calculated as 3.5 from Table 3), and FM is the fecundity at TM (estimated by AF_A at TM).

Spawning potential ratio is the ratio of some measure of productivity on a per recruit basis in the fished to the unfished condition (Goodyear, 1990). For this study SPR was measured as the ratio of fertilized eggs per recruit in the fished condition to the number of fertilized eggs per recruit in the unfished condition to incorporate both male and female contributions to the productivity of the stock.

2.2 Fishing mortality scenarios

2.2.1 Fishing mortality rate equal for both sexes

Currently, stock assessments of Gulf of Mexico greater amberjack assume that the fishing mortality rate is equivalent between the sexes and that the sex ratio of the landed catch is 1:1. However. it is possible that fishing mortality may vary between sexes. Estimates of the instantaneous fishing mortality rate (F) for greater amberjack in the Gulf of Mexico have been variable and cover a range of approximately 0.2-0.6 yr^{-1} (NMFS, 2006, 2011, 2014A). To cover this range of values without exceeding it, a base case scenario F-value of 0.4 yr^{-1} was selected and F-values 20% in either direction (0.2yr^{-1} and 0.6 yr^{-1}) were selected as alternative values. Preliminary modeling exercises also showed that all of these F-values produced a male to female sex ratio of 1:1 (± 0.1) in the landed catch. The baseline model conditions thus consisted of a single F-value of 0.4 yr^{-1} for both sexes, which produced a sex ratio in the landed catch of approximately 1:1.

2.2.2 Fishing mortality rate varied by sex

This scenario is based on evidence that the sex ratio of the landed catch is actually female-skewed, with an annual mean (± SE) male to female sex ratio of 1:1.8 (± 0.14) (Smith, 2011, Smith et al., 2014). An even more female-skewed sex ratio has been noted by a number of studies for fish ≥ 1 m FL (Beasley, 1993; Thompson et al., 1999, Smith et al., 2014). The annual mean sex ratio (± SE) for landed fish ≥ 1 m FL was calculated to be 1:2.4 ± (0.74) (based on data from Murie and Parkyn, 2008, Smith et al., 2014). A what-if analysis was performed to determine what combinations of separate male and female fishing mortality rates (0.05 yr^{-1} increments from 0 to 1 yr^{-1}) would produce these sex ratios in the landed catch. To perform the what-if analysis, recruitment variability was set to 1. The target cell for the what-if analysis of the sex ratio for the entire catch was the ratio of all males to all females harvested in the final year of the model. The target cell for the what-if analysis of the sex ratio for the landed catch >1 m FL was the ratio of males >1 m FL (determined to be age-6+ by Equation 3 for males) to the ratio of females >1 m FL (determined to be age-5+ by Equation 3 for females) in the final year of the model. The number of fish harvested for each sex in a particular year was calculated as:

$$U_s\left(\sum\nolimits_{A,t,s} N_{A,t,s} \cdot PCL_{A,s} \cdot HL_A\right) + U_s\left(\sum\nolimits_{A,t,s} N_{A,t,s} \cdot PCL_{A,s} \cdot LL_A\right) + U_s\left(\sum\nolimits_{A,t,s} N_{A,t,s} \cdot PRL_{A,s} \cdot RCP_A\right) + U_s\left(\sum\nolimits_{A,t,s} N_{A,t,s} \cdot PRL_{A,s} \cdot HB_A\right) \tag{12}$$

Equation 12 was also used to calculate the number of fish >1 m FL for each sex in a particular year with the ages being restricted to age-6+ for males and age-5+ for females. The median value of all *F*-value combinations that produced a sex ratio within the desired ranges (1:1.8 ± 0.14 for all landed fish and 1:2.4± 0.74 for landed fish >1 m FL) was selected for model analysis. To incorporate the range of potential effects on reproductive output, the median value of the lower and upper quartile of all *F*-value combinations were also selected as scenarios to investigate.

2.3 Model outputs and data analysis

Several model outputs were assessed to determine the potential effects of varying the fishing mortality rate between the sexes. All scenarios were run through 100 stochastic simulations to incorporate recruitment variability (Equation 9). Effects of *F* between males and females on reproductive potential were assessed by graphically comparing the mean values of female spawning stock biomass (*FSSB*), *FE,* and *SPR* from these 100 simulations. *SPR* values were compared with reference values, including 0.2 and 0.3 (Mace and Sissenwine, 1993) and 0.4 (Clark, 2002) to determine if recruitment-overfishing was occurring. If the spawning potential ratio was less than the reference value then the stock was considered to be recruitment-overfished. The effect of varying fishing mortality rate between males and females on sex ratio was assessed by graphically comparing the ratio of males to females in the landed catch for both all landed fish and fish >1 m FL. In addition, the ratio of males to females remaining in the unharvested model population (fish predicted to be above the recreational size limit (age-3+) and fish >1 m FL (age-6+ for males and age-5+ for females) were graphically compared.

3. Results

3.1 Fishing mortality rate equal for both sexes

Scenarios in which fishing mortality was equivalent between the sexes generally produced the expected model outputs; the reproductive potential of the stock declined as fishing mortality rate increased (Fig. 2A and B) and the potential for recruitment overfishing increased (Fig. 2C). In addition to the landed catch having a 1:1 sex ratio, the sex ratio of legal-sized fish (i.e., ≥ 3 years of age) remaining in the unharvested population also had a sex ratio of approximately 1:1 (Figs. 3A and B). There is a brief spike in both the number of females in the landed catch as well as those remaining in the unharvested population. However, the male to female sex ratio of fish >1 m FL in the landed catch and the remaining unharvested population ranged from 1:1.8 to 1:3.3 after a brief spike in the number of females at the onset of fishing (Figs. 3C and D). In addition, the sex ratio of fish >1 m FL, both in the landed catch and the modeled unharvested population became more female-skewed as the fishing mortality rate increased

3.2 Fishing mortality rate varied by sex

A wide range of male and female fishing mortality rate (*F*) combinations produced a male to female sex ratio of 1:1.8 (±0.14) (i.e., range of 1:1.66-1:1.94) in the landed catch (Fig. 4A). In all cases, the female *F*-value was greater than that of males. The median combination of *F*-values that produced a sex ratio within this range was F = 0.15 yr^{-1} for males and F = 0.70 yr^{-1} for females, and the median combinations of the lower and upper quartiles were F_{male} = 0.10 yr^{-1}/F_{female} = 0.30 yr^{-1}, and F_{male} = 0.15 yr^{-1}/F_{female} = 0.95 yr^{-1}, respectively.

Overall, reproductive output decreased as the female fishing mortality rate increased (Figs. 5A and B). The mean value of the male and female F-values for all three of these scenarios corresponded (± 0.05 yr^{-1}) to one of the scenarios with an equivalent F-value for both sexes (e.g., the mean F-value of the F_{male} = 0.10 yr^{-1}/F_{female} = 0.30 yr^{-1} is equal to 0.20yr^{-1} and corresponds to the single F-value scenario of 0.2yr^{-1}). Unlike scenarios in which F was equal between the sexes (Figs. 2A and B), scenarios that varied F between the sexes did not produce sex ratios in the landed catch that were similar to the sex ratio of legal-sized fish remaining in the unharvested population (Figs. 6A and B). In all cases, the sex ratio of the modeled population became male-skewed after the onset of fishing, becoming more male-skewed as the female fishing mortality rate increased (Fig. 6B)). This occurred to an even greater degree in the scenarios with F-values varied to produce the sex ratio observed in landed fish >1 m FL (Figs. 6C and D).

A different set of male and female F-value combinations produced a sex ratio of 1:2.4 (±0.74) (i.e., range of 1:1.66-1:3.14) in the landed catch of fish >1 m FL (Fig. 4B). These combinations generally had male and female fishing mortality rates equal or nearly equal (F_{male}=F_{female} ± 0.1 yr^{-1} for F_{male}<0.55 yr^{-1}; F_{male}=F_{female} ± 0.25 yr^{-1} for F_{male}≥55 yr^{-1}) (Fig. 4B). The median combination of F-values that produced a sex ratio in this range was F = 0.5 for males and F = 0.6 yr^{-1} for females, and the median combinations of the lower and upper quartiles were F_{male} = 0.25 yr^{-1}/F_{female} = 0.2 yr^{-1}, and F_{male} = 0.75 yr^{-1}/F_{female} = 0.9 yr^{-1}, respectively. Similar to the scenarios with a single F-value, these scenarios produced sex ratios in the landed catch that were similar to the sex ratio of legal-sized fish remaining in the modeled unharvested population (Figs. 3A, 3B, 7A, and 7B). This was also the case with fish > 1 m FL (Figs. 3C, 3D, 7C, and 7D). The main difference was that as the male and female fishing mortality rates increased, the sex ratio of the legal-sized fish in the population became slightly male skewed (Fig. 7B).

4. Discussion

Varying fishing mortality rates between the sexes can theoretically have pronounced effects on the reproductive potential and sex ratios of the Gulf stock of greater amberjack. The main concern with such scenarios is potential egg limitation, as only minimal potential sperm limitation in greater amberjack has been noted (Smith, 2011). This is despite selecting a value of θ that would theoretically represent a low fertility scenario (Heppell et al., 2006). Unless the maximum fertilization rate is much lower than estimated based on captive studies, or the sex ratios of greater amberjack become highly female-skewed across all mature individuals, this parameter will have little bearing on the model outcome for various scenarios.

When F-values are equivalent between the sexes, as is assumed in current stock assessments (NMFS, 2014A), reproductive potential decreases as F increases, and the potential for recruitment overfishing increases. These scenarios produce an approximate 1:1 sex ratio in both the landed catch and legal-sized fish remaining in the unharvested population. This 1:1 sex ratio is also what is currently assumed to occur within the Gulf stock. However, actual male to female sex ratio estimates of the landed catch point towards a female-skew of approximately 1:1.8 (Smith et al., 2014). Interestingly, these scenarios do produce the approximately 1:2.4 sex ratio in fish >1 m FL that have been noted in several previous studies (Beasley, 1993; Thompson et al., 1999; Smith et al., 2014). Based on the model structure, the initial spike in the number of females (Figs. 3A-D) and the persistent female-skew in fish >1 m FL (Figs. 3C and D) appears to occur because the females grow faster than males, enter the fishery sooner, but also quickly grow out of the full selectivity of some fleets (e.g., recreation headboats). Landings data based on fleet and fish size generally supports this possibility (Fig. 1). Conversely, males take longer to grow into the fishery but are exposed to the full selectivity of all fleets for a greater period of time leading to fewer males reaching a meter in length.

Several male and female fishing mortality rates could produce either the approximate 1:1.8 sex ratio observed in the landed catch or the approximate 1:2.4 sex ratio in the landed catch of fish >1 m FL (Figs. 4A and B). Male and female fishing mortality rates in the upper quartile of combinations that produced the observed sex ratios were often greater than the highest *F*-value that was equivalent for both sexes (i.e., $F= 0.6$ yr^{-1} for both males and females) that was modelled in this study, and represent more extreme scenarios. However, certain scenarios in previous assessments of this stock have pointed to fishing mortality rates as high as 0.86 yr^{-1} (NMFS, 2006), which does not completely rule out the more extreme separate sex *F*-value scenarios.

Most of the combinations that produced the 1:2.4 sex ratio had equal or nearly equal male and female fishing mortality rates (Fig. 4B). This generally produced the same outputs as the closest scenario with a single fishing mortality rate for both sexes, namely decreased reproductive potential (Figs. 2A, 2B, 5D, and 5E) and greater potential for recruitment overfishing (Figs. 2C and 5F) as *F* increased. Conversely, to produce the 1:1.8 sex ratio in the landed catch, female fishing mortality rates were always considerably higher than male fishing mortality rates (Fig. 4A). This greater harvest intensity on females leads to male-skewed sex ratios within the remaining unharvested population of legal-sized fish, particularly for those over a meter in length, which leads to lower reproductive potential than the corresponding scenario with a single *F*-value for both sexes (Figs. 2A, 2B, 5A, and 5B). In all but one instance, these scenarios lead to situations that would be indicative of recruitment overfishing, even at the least conservative reference value (Fig. 5C). Despite the overall landed catch being female-skewed (Fig. 6A), the landed catch of fish >1 m FL quickly declines and becomes male-skewed in two of the scenarios, as nearly all of the large females are quickly fished out (Fig. 6C).

This study was not meant to serve as an assessment of the Gulf of Mexico greater amberjack stock. However, the equal sex *F*-value scenarios and the less extreme cases of differing fishing mortality rates by sex did produce similar results as recent assessments of this stock (NMFS, 2011, 2014A). This in general indicated a low but stable or slowly declining (toward the end of the time series) stock that was indicative of being overfished and undergoing overfishing. Landings from this stock show that many fish >1 m are harvested (Fig. 1) and a large portion of greater amberjack over 1 m FL are skewed toward females (Burch, 1979; Beasley, 1993; Thompson et al., 1999; Harris et al., 2007; Smith et al., 2014). This information, as well as the simulations in this study, suggests that these large females could be experiencing a high degree of fishing mortality, which may be a contributing factor to the continued designation of being overfished, despite increasing size limits and reduced quotas.

It should be noted that none of the scenarios modeled produced both the 1:1.8 sex ratio in the landed catch and the 1:2.4 sex ratio in the landed catch of fish >1 m that were observed in Smith et al. 2014 (Fig. 5), and in fact none of the possible male and female fishing mortality rate combinations would produce both of these sex ratios at the same time (Fig. 4). There are a number of possible explanations why this may have occurred. It may simply be that the sexes only experience differential fishing mortality rates at certain ages or during certain times of the year. Site-specific sex ratios of greater amberjack can also be highly skewed to one sex or the other (Smith, 2011), which could influence the differential fishing mortality between the sex and overall sex ratios. However, there is not enough consistent site-specific sex data to discern any clear trends in sex ratio based on geographic location, distance from shore, or season. It is also possible that the sex ratio of new recruits (i.e., the sex ratio at birth) is not actually 1:1 as is currently assumed. Although the data are limited, it has been demonstrated that fish below the current minimum size limits may have sex ratios differing from 1:1 in some regions of the Gulf (Smith et al., 2014). Fisheries-independent sampling, where the entire catch was either retained or non-lethally sexed (i.e., population sex ratio), also indicated that there was either a slight male- or slight female-skew depending on the dataset analyzed (Smith, 2011; Smith et al., 2014). The fisheries-independent estimates of sex ratio may be more representative of the actual population's sex ratio because the minimum size limits used in the fisheries were not applied. Additionally, the mechanism (genetic, environmental, etc.) controlling sex determination in this species also has not yet been determined, although some sex-linked genetic markers have been found in closely related species (Sola et al., 1997; Fugi et al., 2010). Another possibility is that males and females have different natural mortality rates, which could have a greater effect depending on how much natural mortality differs at size/age within this species, since females tend to grow faster (i.e., may have a lower natural mortality after a certain age). This model and earlier assessments of the Gulf stock of greater amberjack assumed natural mortality was equal across all sizes/ages. However, more recent assessments have begun to use size-based natural mortality estimates (NMFS, 2014A) and could potentially investigate how this parameter varied by age between the sexes and the subsequent influence on the stock status.

There are several factors to consider that could improve the model used in this study. The selectivities and fishing mortality rates were directly applied, but a gradually changing set of selectivities and *F*-values may more accurately simulate changes within the Gulf of Mexico stock over time. It was assumed that the number of spawnings per year was equivalent for all mature females. This may not be the case, and further research in this area is still needed. It was also assumed that all females spawn every year. However, personal observations of the authors suggest that skipped spawning may occur at least to some degree in this species. This model could, however, be adapted to simulate the effects of both varying spawning frequency based on fish size/age and varying the proportion of mature females that spawn each year. A prior sensitivity analysis showed that several parameters related to mortality and recruitment can cause substantial changes in the model's output, but the trends between different scenarios were maintained (Smith, 2011).

Ever increasing pressure on fisheries resources requires finer scale detail on biological information of fish species to build resiliency into management strategies. Understanding the influences of differential sex ratios and how they vary regionally and seasonally could be employed to impose geographic or temporal management, such as designated closures, as well as limitations on landings, aimed at protecting aggregations of female fish, particularly those in the largest size classes. Currently the Gulf stock is assumed to have a 1:1 sex ratio in the landed catch, although data sources document female-skewing in the landings, particularly in fish >1 m. Simulation modeling suggests that sex-specific harvest rates could potentially result in negative impacts on population dynamics of the stock. Therefore, consideration should be given to sex ratios other than 1:1, or over a range of possibilities, in future greater amberjack stock assessments.

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References

Alonzo, S. H., Mangel, M. 2004. The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. Fish. Bull., 102, 1-13.

Alonzo, S. H., Mangel, M. 2005. Sex-change rules, stock dynamics, and the performance of spawning-per-recruit measures in protogynous stocks. Fish. Bull., 103, 229-245.

Alonzo, S. H., Key, M., Ish, T., MacCall, A. D. 2004. Status of the California sheepshead (*Semicossyphus pulcher*) stock. California Department of Fish and Game. https://www.wildlife.ca.gov/Conservation/Marine/Sheephead.

Alonzo, S. H., Ish, T., Key, M., MacCall, A. D., Mangel, M. 2008. The importance of incorporating protogynous sex change into stock assessments. Bull. Mar. Sci., 83(1), 163-179.

Armsworth, P. R. 2001. Effects of fishing on a protogynous hermaphrodite. Can. J. Fish. Aquat. Sci., 58, 568-578.

Beasley, M. L. 1993. Age and growth of greater amberjack, *Seriola dumerili*, from the northern Gulf of Mexico. M.S. thesis. Louisiana State University, Baton Rouge, Louisiana.

Beverton, R.J.H., Holt, S. J. 1957. On the dynamics of exploited fish populations. Fisheries Investigations, Series 2, Volume 19. U.K. Ministry of Agriculture and Fisheries, London.

Brooks, E. N., Shertzer, K. W., Gedamke, T., Vaughan, D. S. 2008. Stock assessment of protogynous fish: evaluating measures of spawning biomass used to estimate biological reference points. Fish. Bull., 106, 12-23.

Burch, R. K. 1979. The greater amberjack, *Seriola dumerili*: its biology and fishery off southeastern Florida. M.S. thesis. University of Miami, Coral Gables, FL.

Calduch-Verdielli, N., McKenzie, B. R., Vaupel, J. W. 2014. A life-history evaluation of the impact of maternal effects on recruitment and fisheries reference points. Can. J. Fish. Aquat. Sci., 71(7), 1113-1120.

Clark, W. G. 2002. $F_{35\%}$ revisited ten years later. N. Am. J. Fish. Manage., 22, 251-257.

Coggins, L. G., Catalano, M. J., Allen, M. S., Pine, W. E., Walters, C. J. 2007. Effects of cryptic mortality and the hidden costs of using length limits in fishery management. Fish Fish., 8, 196-210.

Cooper, W., Collins, A., O'Hop, J., Addis, D. The 2013 stock assessment report for hogfish in the south Atlantic and Gulf of Mexico. Florida Fish and Wildlife Conservation Commission, St. Petersburg, FL. http://sedarweb.org/sedar-37-final-stock-assessment-report-southeastern-us-hogfish.

Diaz, G. A., Brooks, E. N. Porch, C. E. 2005. Gulf of Mexico greater amberjack stock assessment. National Marine Fisheries Service, Southeast Fisheries Science Center. SEDAR9-AW-05-REV, Miami, Florida. http://sedarweb.org/s9aw05-gulf-mexico-greater-amberjack-stock-assessment.

Fugi, K., Yoshida, K., Hattori, K., Ozaki, A., Araki, K., Okauchi, M., Kubota, S., Okamoto, N., Sakamota, T. 2010. Identification of the sex-linked locus in yellowtail, *Seriola quinqueradiata*. Aquac., 308(S1), S51-S55.

Goodwin, N. B., Grant, A., Perry, A. L., Dulvy, N. K., Reynolds, J. D. 2006. Life history correlates of density-dependent recruitment in marine fishes. Can. J. Fish. Aquat. Sci., 63(3), 494-509.

Goodyear, C. P. 1990. Spawning stock biomass per recruit: the biological basis for a fisheries management tool. Collective Volume of Scientific Papers, ICCAT (International Commission for the Conservation of Atlantic Tunas), 32(2), 487-497.

GMFMC (Gulf of Mexico Fishery Management Council). 2013. Gulf of Mexico Greater Amberjack management history. SEDAR33-RD05. North Charleston, SC. http://sedarweb.org/s33rd05-gulf-mexico-greater-amberjack-management-history.

Graham, R. T. & Castellanos, D. W. 2005. Courtship and spawning behaviors of carangid species in Belize. Fish. Bull., 103, 426-432.

Harris, P. J., Wyansky, D. M., White, D. B., Mikell, P. P., Eyo P. B. 2007. Age, growth, and reproduction of greater amberjack off the southeastern U.S. Atlantic coast. Trans. Am, Fish. Soc., 136, 1534-1545.

Heppell, S. S., Heppell, S. A., Coleman, F., Koenig C. C. 2006. Models to compare management options for a protogynous fish. Ecol. Appl., 16(1), 238-249.

Heupel, M. R., Williams, A. J., Welch, D. J., Davies, C. R., Penny, A., Kritzer, J. P., Marriot, R. J., Mapstone, B. D. 2010. Demographic characteristics of exploited tropical lutjanids: a comparative analysis. Fish. Bull., 108, 420-432.

Hilborn, R., Walters C. J. 1992. Quantitative fisheries stock assessment: choice, dymanics, and uncertainty. Springer Science and Business Media B.V., Dordrecht, Netherlands.

Huntsman, G. R., Schaaf, W. E. 1994. Simulation of the impact of fishing on reproduction of a protogynous grouper, the Graysby. N. Am. J. Fish. Manage., 14, 41-52.

Jerez, S., Samper, M., Santamaría, F. J., Villamandos, J. E., Cejas, J. R., Felipe, B. C. 2006. Natural spawning of greater amberjack (*Seriola dumerili*) kept in captivity in the Canary Islands. Aquac., 252, 199-207.

Johnson, D. R. 2013. Observer reported size distribution and discard characteristics of Gulf of Mexico Greater Amberjack from the commercial vertical line and bottom longline fisheries. SEDAR33-DW14. North Charleston, SC. http://sedarweb.org/s33dw14-observer-reported-size-distribution-and-discard-characteristics-gulf-mexico-greater.

Kelly-Stormer, A., Shervette, V., Komos, K., Wyanski, D., Smart, T., McDonough, C., Reichert, M. J. M. 2017. Gray triggerfish reproductive biology, age, and growth off the Atlantic Coast of the southeaster USA. Trans. Am. Fish. Soc., 146, 523-538.

Mace, P. M., Sissenwine, M. P. 1993. How much spawning per recruit is enough? Pages 101-118 *in* S. J. Smith, J. J. Hunt, and D. Rivard, Eds. Risk evaluation and biological reference points for fisheries management. Canadian Special Publication of Fisheries and Aquatic Science 120. National Research Council of Canada, Ottawa, Canada.

Maunder, M. N., Piner, K. R. Contemporary fisheries stock assessment: many issues still remain. ICES J. Mar. Sci., 72(1), 7–18.

Molloy, P. P., Goodwin, N. B., Côté, I. M., Gage, J. G., Reynolds J. D. 2007. Predicting the effects of exploitation on male-first sex-changing fish. Anim. Cons., 10, 30-38.

Murie, D. J., & Parkyn, D. C. 2008. Age, Growth, and Sex Maturity of greater amberjack (*Seriola dumerili*) in the Gulf of Mexico. SEDAR33-RD13. North Charleston, SC. http://sedarweb.org/s33rd13-age-growth-and-sex-maturity-greater-amberjack-seriola-dumerili-gulf-mexico.

Myers, R. A., Bowen, K. G., Barrowman, N. J. 1999. Maximum reproductive rate of fish at low population sizes. Can. J. Fish. Aquat. Sci., 56(2), 2404-2419.

NMFS (National Marine Fisheries Service), Southeast Fisheries Science Center, Sustainable Fisheries Division. 2006. SEDAR9 (Southeast Data, Assessment, and Review), Gulf of Mexico Greater Amberjack. SEDAR, Stock Assessment Report 2, Charleston, SC. http://sedarweb.org/sedar-09-stock-assessment-report-gulf-mexico-greater-amberjack.

NMFS (National Marine Fisheries Service), Southeast Fisheries Science Center, Sustainable Fisheries Division. 2011. SEDAR9 (Southeast Data, Assessment, and Review): Gulf of Mexico Greater Amberjack, Stock Assessment Update Report, North Charleston, SC. http://sedarweb.org/2010-update-sedar-09-gulf-mexico-greater-amberjack.

NMFS (National Marine Fisheries Service), Southeast Fisheries Science Center, Sustainable Fisheries Division. 2014A. SEDAR33 (Southeast Data, Assessment, and Review): Gulf of Mexico Greater Amberjack, Stock Assessment Report, North Charleston, SC. http://sedarweb.org/2016-update-sedar-33-gulf-mexico-greater-amberjack-report.

NMFS (National Marine Fisheries Service), Southeast Fisheries Science Center, Sustainable Fisheries Division. 2014B. SEDAR33 (Southeast Data, Assessment, and Review): Gulf of Mexico Gag, Stock Assessment Report, North Charleston, SC. http://sedarweb.org/sedar-33-stock-assessment-report-gulf-mexico-gag-grouper.

NMFS (National Marine Fisheries Service). 2016. Southeast Fishery Bulletin: NOAA fisheries announces greater amberjack allowable harvest and management measured in the Gulf of Mexico for 2016 and beyond. FB15-089. St. Petersburg, FL. http://sero.nmfs.noaa.gov/fishery_bulletins/bulletin_archives/2015/index.html.

NMFS (National Marine Fisheries Service), Southeast Fisheries Science Center, Sustainable Fisheries Division. 2017. SEDAR53 (Southeast Data, Assessment, and Review): South Atlantic Red Grouper, Stock Assessment Report, North Charleston, SC. http://sedarweb.org/sedar-53-stock-assessment-report-south-atlantic-red-grouper.

Pine, W. E., Martell, S. J. D., Jensen, O. P., Walters, C. J., Kitchell, J. F. 2007. Catch-and-release and size limit regulations for blue, white, and striped marlin: the role of post-release survival in effective policy design. Can. J. Fish. Aquat. Sci., 65, 975-988.

Ricker, W. E. 1954. Stock and recruitment. J. Fish. Res. Board Can., 11(5), 559-623.

Sauls, B. & Cernack, B. 2013. Characterization of greater amberjack discards in recreational for-hire fisheries. SEDAR33-DW04. North Charleston, SC. http://sedarweb.org/s33dw04-characterization-greater-amberjack-discards-recreational-hire-fisheries.

Schnute, J. 1987. A general fishery model for a size-structured fish population. Can. J. Fish. Aquat. Sci., 44(5), 924-940.

Smith, G.H. 2011. Field based non-lethal sex determination and effects of sex ratio on population dynamics of greater amberjack, *Seriola dumerili*. Master's thesis. University of Florida, Gainesville, Florida.

Smith, G. H., Murie, D. J., Parkyn, D. C. 2014. Nonlethal sex determination of greater amberjack, with direct application to sex ratio analysis of the Gulf of Mexico stock. Mar. Coast. Fish., 6, 200-210.

Sola, L. Cipelli, O., Gornung, E., Rossi, A. R., Andaloro, F., Crosetti, D. 1997. Cytogenetic characterization of the greater amberjack, *Seriola dumerili* (Pisces: Carangidae), by different staining techniques and fluorescence in situ hybridization. Mar. Biol., 128(4), 573-577.

Tetzlaff, J. C., Catalano, M. J., Allen, M. S., Pine W. E. 2011. Evaluation of two methods for indexing fish year-class strength: catch-curve residuals and cohort method. Fish. Res., 109, 303-310.

Thompson, B. A., Beasley, M., Wilson, C. A. 1999. Age distribution and growth of greater amberjack, *Seriola dumerili*, from the north-central Gulf of Mexico. Fish. Bull., 97, 362-371.

Turner, S. C., Cummings, N. J., Porch, C. E. 2000. Stock assessment of Gulf of Mexico greater amberjack using data through 1998. National Marine Fisheries Service, Southeast Fisheries Science Center, Sustainable Fisheries Division, Document: SFD 99/00 – 100. http://sedarweb.org/s9rd06-stock-assessments-gulf-mexico-greater-amberjack-using-data-through-1998.

Walters, C. J., Martel, S. J. D. 2004. Fisheries ecology and management. Princeton University Press, Princeton, New Jersey.

Williams, A. J., Wakefield, C. B., Newman, S. J., Vourey, E., Abascal, F. J., Halafihi, T., Kaltavara, J., Nicol, S. J. 2017. Oceanic, latitudinal, and sex-specific variation in demography of a tropical deepwater snapper across the Indo-Pacific region. Front. Mar. Sci., 4, 1-15.

TABLE 1

Input parameters for sex-, size-, and age-specific model for greater amberjack in the Gulf of Mexico.

Parameter	Value	Source
von Bertalanffy growth parameters		
L_∞ (mm)		
Male	1196.6	Murie and Parkyn, 2008
Female	1279.6	Murie and Parkyn, 2008
Combined	1240.5	Murie and Parkyn, 2008
K (yr^{-1})		
Male	0.29	Murie and Parkyn, 2008
Female	0.26	Murie and Parkyn, 2008
Combined	0.28	Murie and Parkyn, 2008
t_0 (yr)		
Male	-0.92	Murie and Parkyn, 2008
Female	-1.12	Murie and Parkyn, 2008
Combined	-1.01	Murie and Parkyn, 2008
Weight-length parameters		
A	6.7×10^{-8}	Murie and Parkyn, 2008
b	2.765	Murie and Parkyn, 2008
Mortality		
M	0.25	NMFS, 2011
D	0.2	NMFS, 2014A
Proportion Legal		
LCL (mm)	762	GMFMC, 2013
RCL (mm)	914.4	GMFMC, 2013
σ	LCL·0.1 / RCL·0.1	Mure and Parkyn, 2008; Tetzlaff et al., 2011
Fecundity		
af	655746	Harris et al., 2007
bf	387.897	Harris et al., 2007
N	14	Harris et al., 2007
Fertility		
f	0.8	Jerez et al., 2006
Θ	20	Heppell et al., 2006
Recruitment		
K	10	Myers et al., 1999; Goodwin et al., 2006
R_0	3.5×10^5	Diaz et al., 2005

TABLE 2

Gear selectivities for Gulf of Mexico greater amberjack. CMHL = commercial handline, CMLL = commercial longline, HB = headboat, RCP = combined recreational charter and private fisheries. Values from Diaz et al. (2005).

Gear	Age									
	1	2	3	4	5	6	7	8	9	10+
CMHL	0.0	0.0	0.2	0.8	1.0	1.0	1.0	1.0	1.0	1.0
CMLL	0.0	0.0	0.0	0.5	0.9	1.0	1.0	1.0	1.0	1.0
HB	0.0	1.0	0.9	0.4	0.0	0.0	0.0	0.0	0.0	0.0
RCP	0.0	0.9	1.0	1.0	1.0	1.0	1.0	1.0	1.0	1.0

TABLE 3

Proportion of mature male and female Gulf of Mexico greater amberjack by age. Female values from Murie and Parkyn (2008), and male values from D. Murie and D. Parkyn (University of Florida, unpublished data).

Sex	Age									
	1	2	3	4	5	6	7	8	9	10+
Male	0.103	0.103	0.597	0.804	0.806	1.000	1.000	1.000	1.000	1.000
Female	0.029	0.067	0.225	0.844	0.857	0.900	1.000	1.000	1.000	1.000

FIGURE 1: Proportion of numbers at length aggregated across time for Gulf of Mexico greater amberjack landings in the recreational and commercial fisheries: commercial handline gear, commercial longline gear, recreational charter and private fisheries, and the recreational headboat fishery. (Modified from data in NMFS 2014A).

FIGURE 2. Reproductive potential outputs and SPR values for Gulf of Mexico greater amberjack produced by model scenarios where *F*-values were equivalent for males and females: A) female spawning stock biomass (FSSB); B) fertilized egg production (FE); and C) spawning potential ratio (SPR). Dashed lines represent SPR reference values of 0.2, 0.3, and 0.4. Note that all *F*-value combinations in the legend are plotted but may be stacked on output plots due to equivalent values.

FIGURE 3. Number of female to male Gulf of Mexico greater amberjack produced by model scenarios where *F*-values were equivalent for males and females: A) male to female sex ratio of the landed catch; B) sex ratio of legal sized (age 3+) fish remaining in the modeled population; C) sex ratio of the landed catch of fish >1 m FL; D) sex ratio of fish >1 m FL remaining in the modeled population.

FIGURE 4. Male to female sex ratio in the final year of the model with recruitment variability set to 1 across all possible combinations of male and female fishing mortality rates from 0 to 1 yr^{-1} (in 0.05 yr^{-1} increments): A) sex ratio of the landed catch, M indicates the median value of *F*-value combinations that produce a sex ratio of 1:1.8 ± 0.14, Q1 and Q3 indicates the median value of the upper and lower quartiles that produce a sex ratio of 1:1.8 ± 0.14; and B) sex ratio of the landed catch of fish >1 m FL, M indicates the median value of *F*-value combinations that produce a sex ratio of 1:2.4 ± 0.74, Q1 and Q3 indicates the median value of the upper and lower quartiles that produce a sex ratio of 1:2.4 ± 0.74.

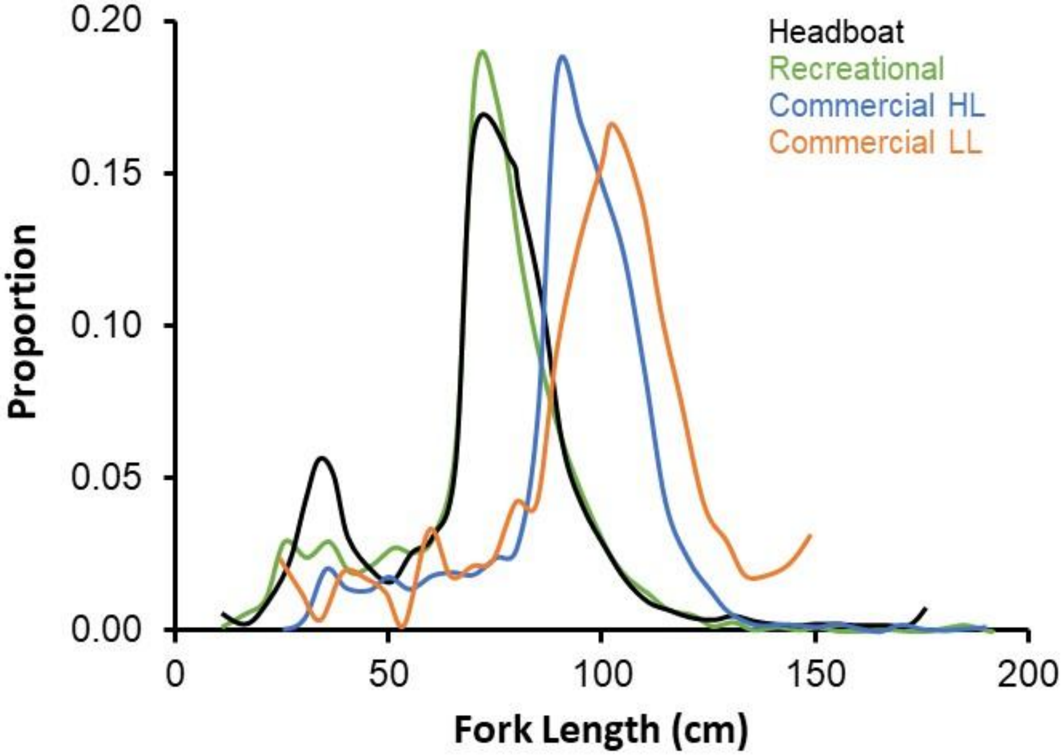
FIGURE 5: Reproductive potential outputs and SPR values for Gulf of Mexico greater amberjack produced by model scenarios where *F*-values varied by sex. Scenarios include separate male and female *F*-values (F_{male}/F_{female}) that produced a 1:1.8 ± 0.14 male to female sex ratio in the landed catch (A-C), and separate male and female *F*-values (F_{male}/F_{female}) that produced a 1:2.4 ± 0.74 male to female sex ratio in the landed catch of fish >1m FL(D-F): A and D) female spawning stock biomass (FSSB); B and E) fertilized egg production (FE); and C and F) spawning potential ratio (SPR). Dashed lines represent SPR reference values of 0.2, 0.3, and 0.4. Note that all *F*-value combinations in the legend are plotted but may be stacked on output plots due to equivalent values.

FIGURE 6: Number of female to male Gulf of Mexico greater amberjack produced by model scenarios where *F*-values were varied by sex to produce a 1:1.8 ± 0.14 male to female sex ratio in the landed catch; A) male to female sex ratio of the landed catch; B) sex ratio of legal sized (age 3+) fish remaining in the modeled population; C) sex ratio of the landed catch of fish >1 m FL; D) sex ratio of fish >1 m FL remaining in the modeled population.

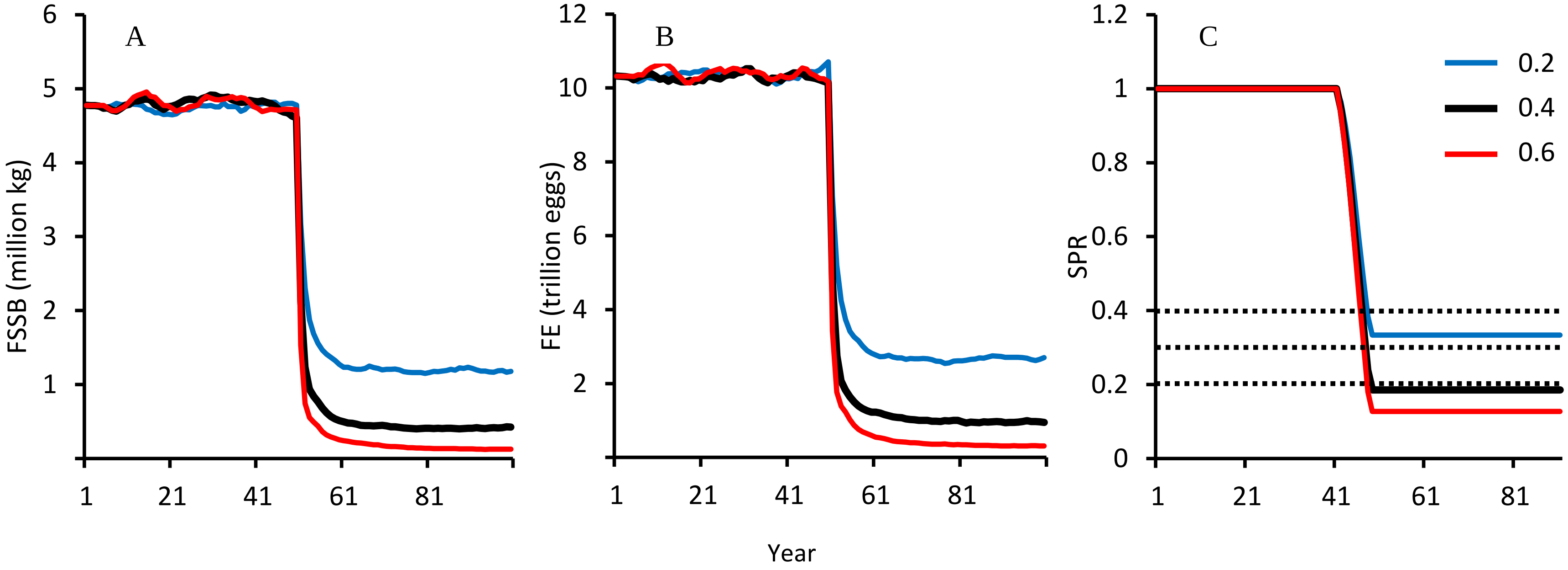
FIGURE 7: Number of female to male Gulf of Mexico greater amberjack produced by model scenarios where *F*-values were varied by sex to produce a 1:2.4 ± 0.74 male to female sex ratio in the landed catch; A) male to female sex ratio of the landed catch; B) sex ratio of legal sized

(age 3+) fish remaining in the modeled population; C) sex ratio of the landed catch of fish >1 m FL; D) sex ratio of fish >1 m FL remaining in the modeled population.

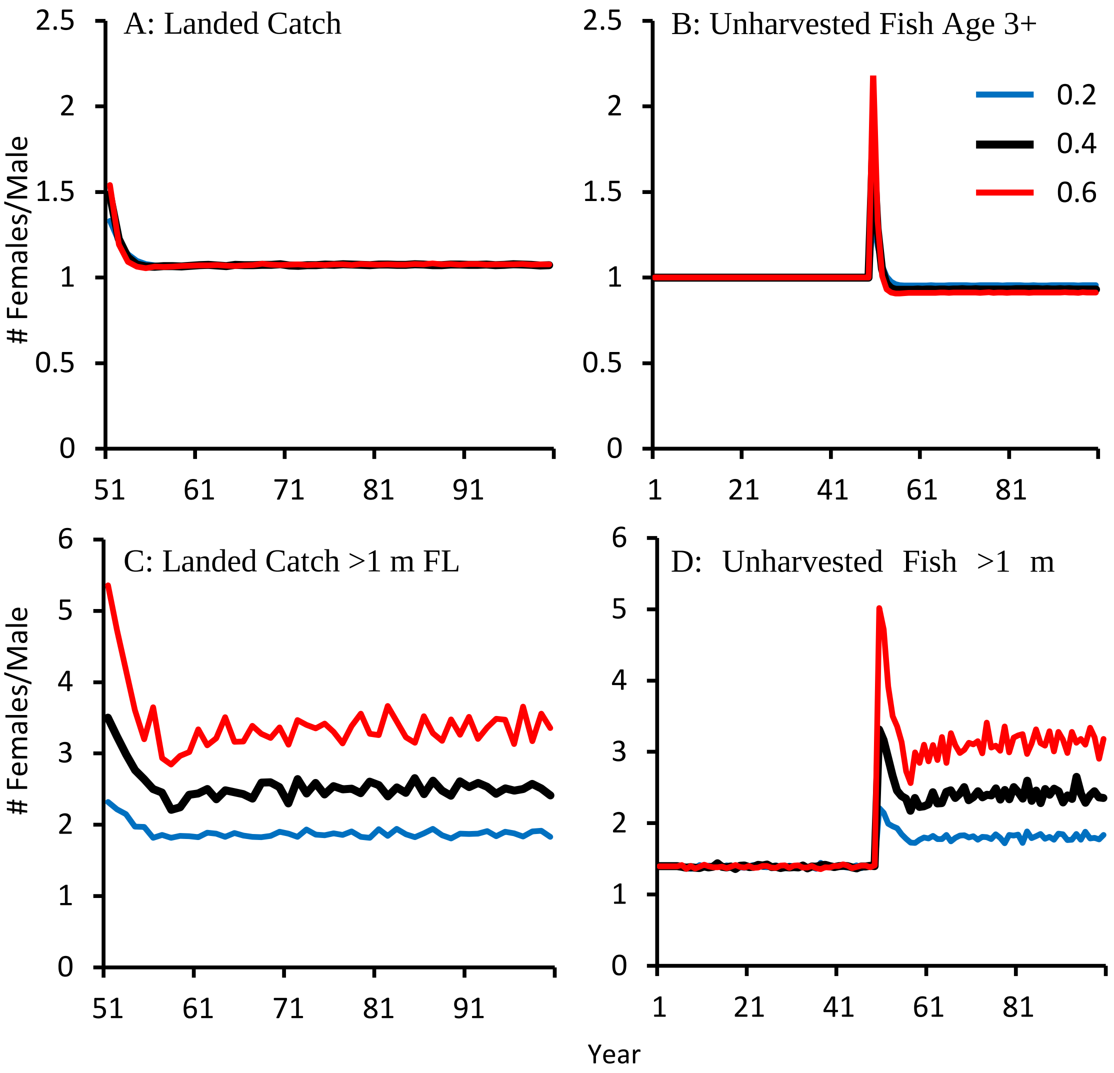
Figure


0.20
0.15
0.10
0.05
0.00
Proportion
0
50
100
150
200
Fork Length (cm)
Headboat
Recreational
Commercial HL
Commercial LL

Figure

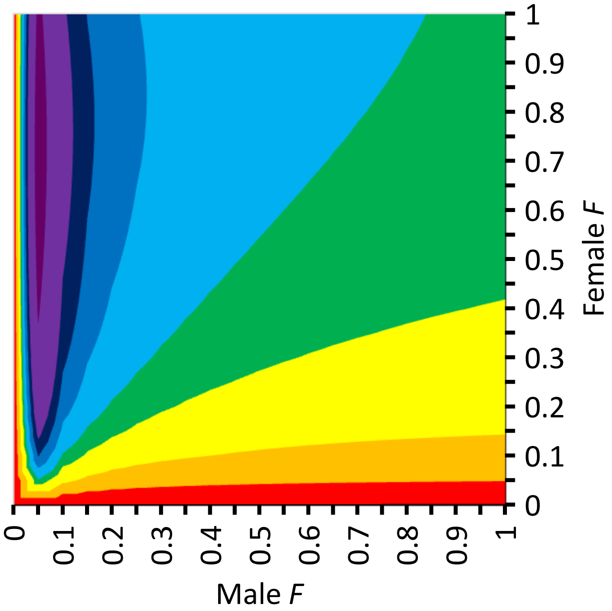

A
B
C
FSSB (million kg)
FE (trillion eggs)
SPR
6
5
4
3
2
1
12
10
8
6
4
2
1.2
1
0.8
0.6
0.4
0.2
0
1
21
41
61
81
Year
0.2
0.4
0.6

Figure

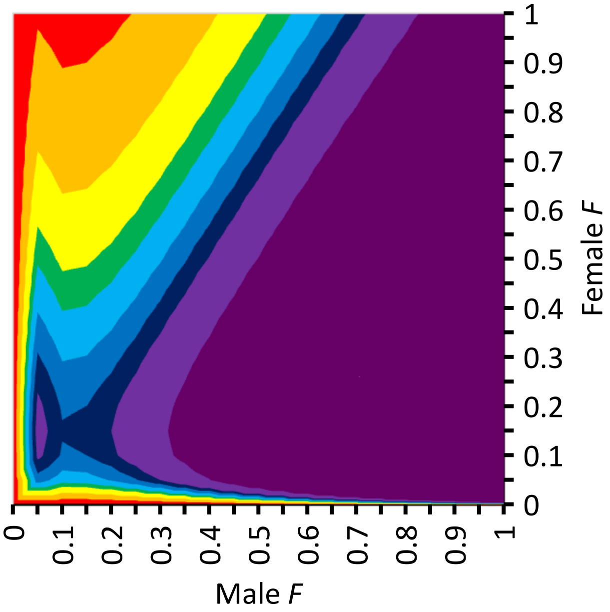

A: Landed Catch
B: Unharvested Fish Age 3+
C: Landed Catch >1 m FL
D: Unharvested Fish >1 m
Females/Male
Females/Male
0.2
0.4
0.6
2.5
2
1.5
1
0.5
0
6
5
4
3
2
1
0
51
61
71
81
91
1
21
41
61
81
Year

Figure

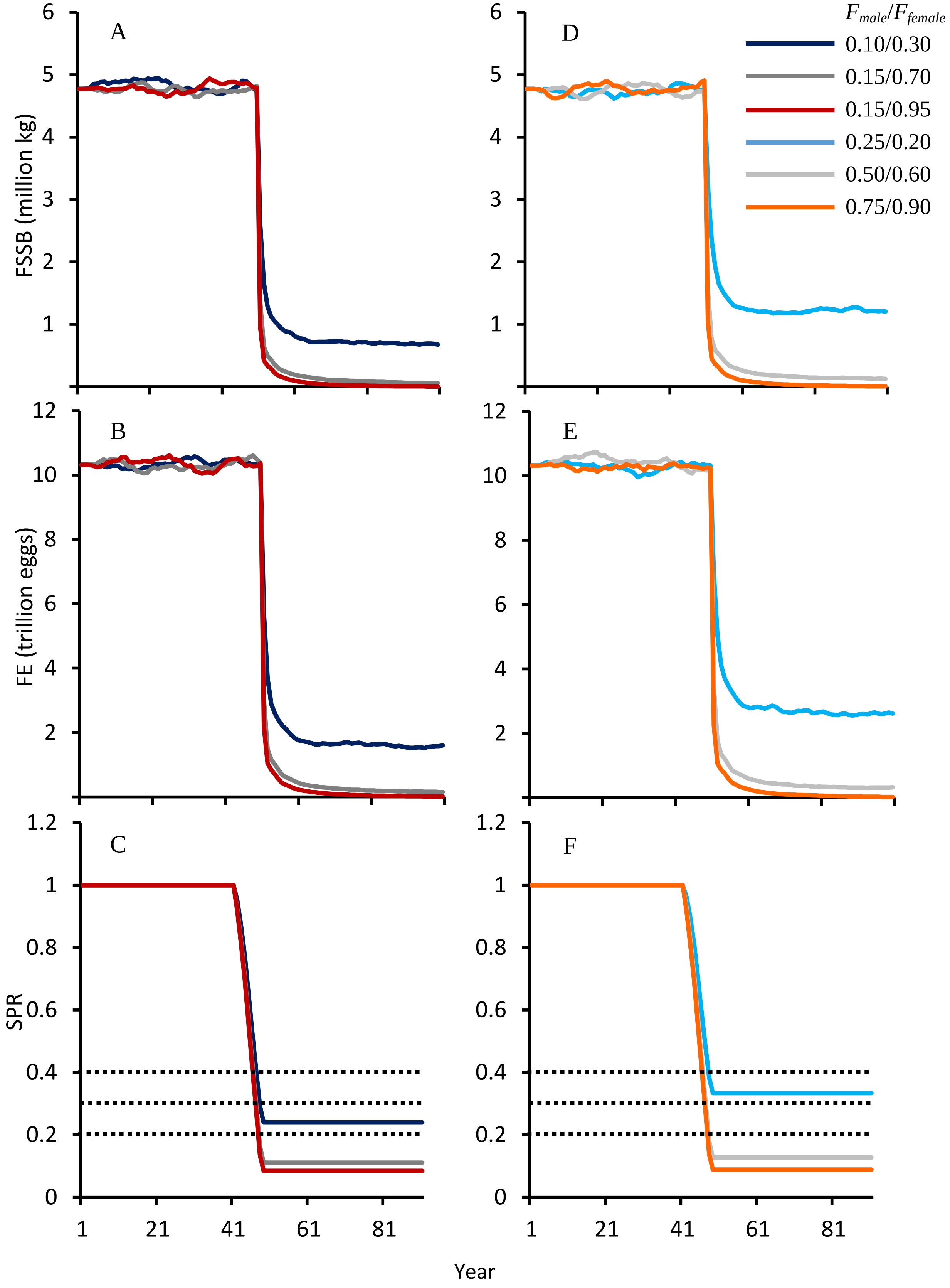
A:


Female F
Male F
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

B:

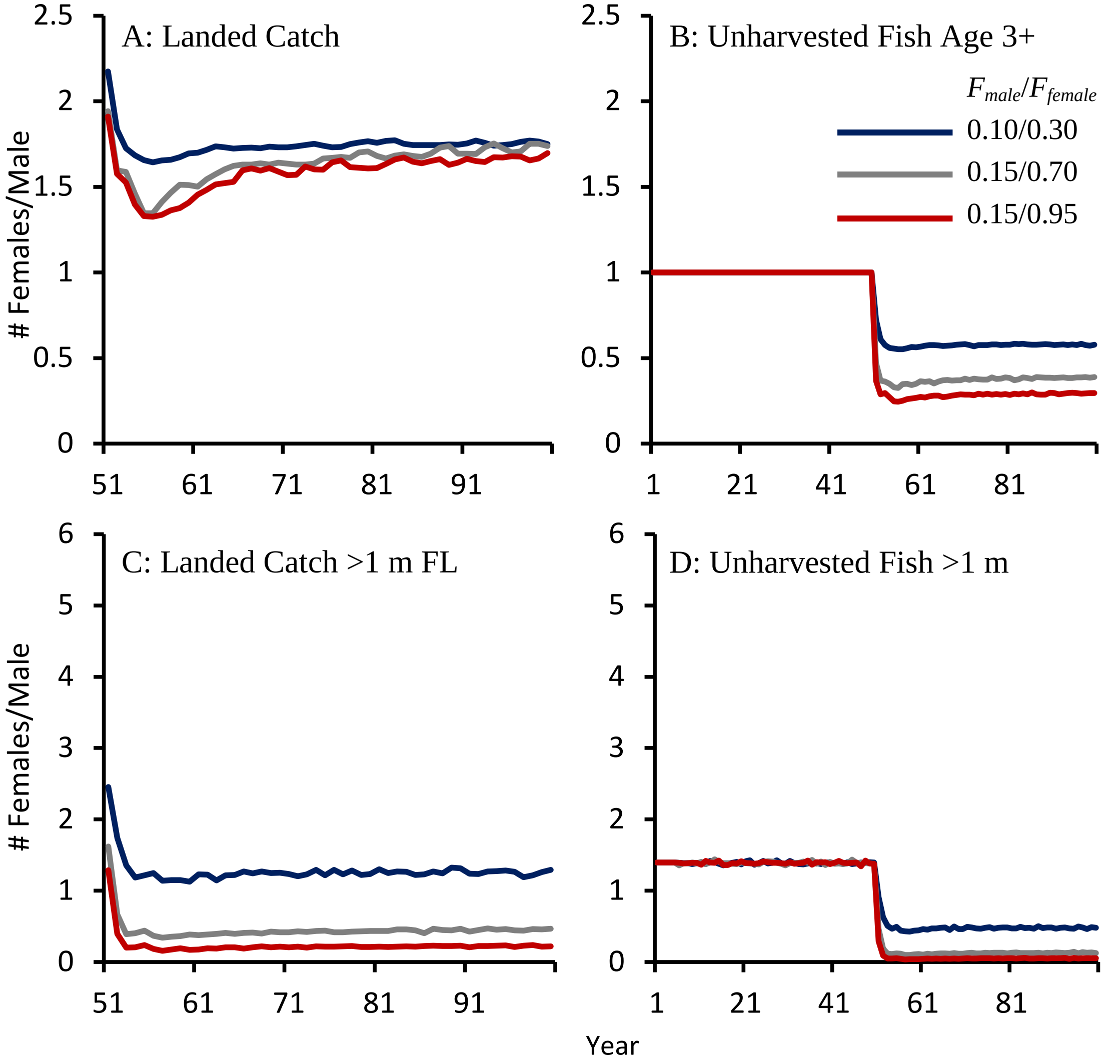

Female F
Male F
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0.8
0.9
1

Figure

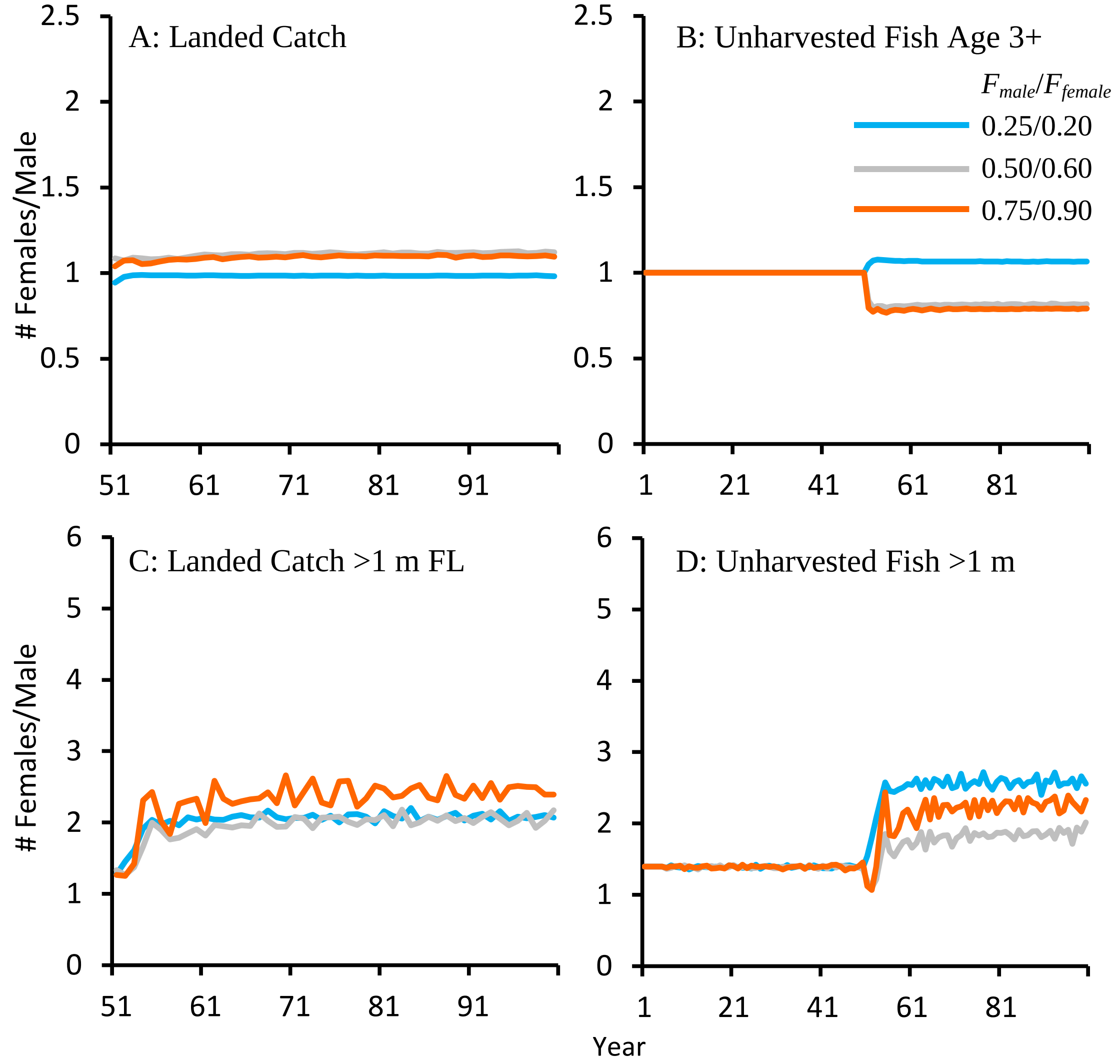


A
B
C
D
E
F
FSSB (million kg)
FE (trillion eggs)
SPR
Year
0
0.2
0.4
0.6
0.8
1
1.2
2
4
6
8
10
12
1
2
3
4
5
6
1
21
41
61
81
F_{male}/F_{female}
0.10/0.30
0.15/0.70
0.15/0.95
0.25/0.20
0.50/0.60
0.75/0.90

Figure


A: Landed Catch
B: Unharvested Fish Age 3+
C: Landed Catch >1 m FL
D: Unharvested Fish >1 m
F_{male}/F_{female}
0.10/0.30
0.15/0.70
0.15/0.95
Females/Male
Females/Male
2.5
2
1.5
1
0.5
0
6
5
4
3
2
1
0
51
61
71
81
91
1
21
41
61
81
Year

Figure



A: Landed Catch
B: Unharvested Fish Age 3+
C: Landed Catch >1 m FL
D: Unharvested Fish >1 m
Females/Male
Females/Male
Year
F_{male}/F_{female}
0.25/0.20
0.50/0.60
0.75/0.90
2.5
2
1.5
1
0.5
0
6
5
4
3
2
1
0
51
61
71
81
91
1
21
41
61
81