

Abstract—In stock assessments, recruitment is typically modeled as a function of females only. For protogynous stocks, however, disproportionate fishing on males increases the possibility of reduced fertilization rates. To incorporate the importance of males in protogynous stocks, assessment models have been used to predict recruitment not just from female spawning biomass (S^f), but also from that of males (S^m) or both sexes (S^b). We conducted a simulation study to evaluate the ability of these three measures to estimate biological reference points used in fishery management. Of the three, S^f provides best estimates if the potential for decreased fertilization is weak, whereas S^m is best only if the potential is very strong. In general, S^b estimates the true reference points most closely, which indicates that if the potential for decreased fertilization is moderate or unknown, S^b should be used in assessments of protogynous stocks. Moreover, for a broad range of scenarios, relative errors from S^f and S^b occur in opposite directions, indicating that estimates from these measures could be used to bound uncertainty.

Stock assessment of protogynous fish: evaluating measures of spawning biomass used to estimate biological reference points

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Populations persistence requires that losses from mortality must at least be matched by gains from the production of new individuals (i.e., recruitment). The theory of stock reproduction relates recruitment to total egg production (Beverton and Holt, 1957). In practice, however, stock assessment often relates recruitment to the biomass of mature females rather than to total egg production. The two predictors are functionally similar if egg production of a mature female is highly correlated to body mass (Rothschild and Fogarty, 1989), as observed or assumed for many stocks.

With the use of either predictor—biomass of mature females or total

egg production—the proportion of eggs fertilized is assumed to be constant. This assumption is believed to be valid for stocks with little fluctuation in sex ratio, as in most gonochoristic stocks (fish that remain the same sex throughout life). However, this assumption may be inappropriate for protogynous stocks (fish that begin life as female and later become male). Under natural mortality alone, sex ratios of protogynous stocks are expected to be skewed toward females (Allsop and West, 2004). The addition of fishing mortality could skew the ratio even further (Coleman et al., 1996; McGovern et al., 1998; Armsworth, 2001), particularly

if fishing preferentially removes males by targeting larger (older) individuals, for example through gear selectivity or management regulations. A disproportionate reduction of males could lower fertilization rates if not enough males are available to fertilize the eggs of mature females (i.e., the reduction could result in sperm limitation).

The possibility of reduced fertilization rates raises the question of whether protogynous stocks are more susceptible than gonochoristic stocks to overexploitation. Several studies have concluded that protogynous stocks are more susceptible, based on hypothesized patterns of reproduction, sexual transition, and fishing (Huntsman and Schaaf, 1994; Alonzo and Mangel, 2004, 2005). At least one study (Bannerot et al., 1987) indicates that, under some conditions, protogynous stocks are more resilient to exploitation. Either way, management of protogynous stocks merits the consideration of unconventional techniques (Shepherd and Idoine, 1993; Armsworth, 2001; Heppell et al., 2006).

In the United States, fishery management under the Magnuson-Stevens Fishery Conservation and Management Reauthorization Act of 2006 emphasizes the concept of maximum sustainable yield (MSY). Internationally, the use of MSY as a reference point for evaluating sustainable development is well established (FAO, 1999). Standard MSY-based biological reference points—the benchmarks used to gauge stock status—include fishing mortality rate at MSY (F_{MSY}), spawning biomass at MSY (S_{MSY}), and MSY itself. All depend fundamentally on the spawner-recruit relationship, which is typically a function of spawning biomass (S).

In conventional stock assessments, S is computed from females only (S^f), and fertilization rate is implicitly assumed to be constant. Some assessments of protogynous stocks have emphasized the importance of males, by computing S from spawning biomass of males alone (S^m) or from the sum of both sexes (S^b) (Punt et al., 1993; Vaughan et al., 1995). Early use of S^b was in per-recruit analyses (Vaughan et al., 1992; Punt et al., 1993; Vaughan et al., 1995), and later, in spawner-recruit relationships (Vaughan and Prager, 2001).

The measure of spawning biomass— S^f , S^m , or S^b —used in an assessment plays a key role in estimates of biological reference points, and thus in subsequent management advice. For example, in U.S. fishery management, a stock is considered to be overfished if the most recent estimate of S is sufficiently less than S_{MSY} . (The level associated with “sufficiently” varies by stock, but the criterion to determine that level often takes natural mortality into account.) Declaring a stock overfished triggers development of a rebuilding plan to increase the stock to S_{MSY} . In general, the choice of measure used to represent spawning biomass influences analyses on which management is based, including any estimate of stock status. Although various measures are used in assessments, the properties of reference points estimated from S^f , S^m , or S^b have not been examined comprehensively.

We use simulations to evaluate the performance of each measure of spawning biomass. To begin, we simulate a protogynous stock over an array of biological and fishery characteristics and calculate biological reference points for each case. Then we apply an assessment model to estimate those same reference points using each of the three S measures. The estimated reference points are compared to their simulated counterparts to quantify estimation error. These results are intended to help stock assessment biologists identify a robust measure of spawning biomass that is appropriate for the protogynous stock being modeled.

Materials and methods

Two deterministic models were constructed, both structured by age and sex, to describe a protogynous stock. The first, referred to as the simulation model, was considered a representation of the real world. It was used to compute true values of MSY-based biological reference points (BRPs), which determine stock status. The second, the assessment model, was used to estimate those same reference points. Both models included age-specific values of maturity, mortality, sex ratio, and size. They differed only in computation of recruitment: the simulation model derived recruits directly from fertilized eggs, and the assessment model derived recruits indirectly from the spawning biomass of males, females, or both. Thus, with the assessment model the common assumption is that fertilization rates are static. Because that assumption creates the only structural difference between the simulation and assessment models, the source of any estimation error of computed quantities (BRPs) could be isolated and the most robust measure of spawning biomass could be identified. In this sense, estimation error refers to error caused by model misspecification, rather than from fitting data. To quantify error systematically, BRPs were computed and estimated under many combinations of biological parameters and fishery conditions, as described below.

Simulation model

This study used an age-structured population model to compute the number of individuals at age (N_a),

$$N_a = \begin{cases} N_{a-1}e^{-(M+F_{a-1})} & 2 \leq a < 50 \\ N_{a-1}e^{-(M+F_{a-1})} / (1 - e^{-(M+F_a)}) & a = 50 \end{cases}, \quad (1)$$

where N_1 represents the number of recruits (described below), and the maximum age (50) was treated as a plus group. The parameter M is natural mortality rate (constant across age), and F_a is fishing mortality rate at age, equal to the product of total fishing mortality rate (F) and selectivity at age (s_a). Selectivity was assumed to be knife-edge, that is, $s_a = 0$ for all ages younger than the first vulnerable age class (α_s) and $s_a = 1$ otherwise.

Length at age (l_a) was modeled with the von Bertalanffy equation (von Bertalanffy, 1938), $l_a = L_\infty(1 - e^{-K(a-t_0)})$, in which L_∞ is the asymptotic length, K is the growth coefficient, and t_0 is the theoretical age at which length is zero ($t_0=0$ assumed arbitrarily). Length at age was converted to weight at age (w_a) by the allometric relationship

$$w_a = v_1 l_a^{v_2}, \quad (2)$$

where v_1 and v_2 are constants under the assumption of isometric growth. This relationship was also used to model fecundity at age (e_a , eggs per mature female),

$$e_a = \varepsilon_1 l_a^{\varepsilon_2}, \quad (3)$$

where ε_1 and ε_2 are constants. Fecundity often scales nearly linearly with weight, such that $\varepsilon_2 \approx v_2 \approx 3$.

Transition from female to male was modeled as a logistic function of age,

$$p_a = \frac{1}{1 + e^{-\beta_p(a-\alpha_p)}} \quad (4)$$

with p_a the proportion male at age, β_p the slope of sexual transition, and α_p the age at 50:50 sex ratio. The same function was used to model female maturity at age (g_a), with parameter β_g = the slope, and α_g = the age at 50% maturity. All males were considered to be mature on the basis of low numbers of transitional fish observed in the field and the apparent ability to complete sex transition between spawning seasons (Collins et al., 1987).

Total egg production (E) was determined by the product of mature females and eggs per female, summed across ages,

$$E = \sum_a N_a (1 - p_a) g_a e_a. \quad (5)$$

Because fertilization may become limited by sperm availability, fertilization rate (f) was modeled as a function of sex ratio,

$$f(x_F) = \frac{4\kappa x_F}{(1-\kappa) + (5\kappa-1)x_F}. \quad (6)$$

In Equation 6, x_F is the ratio of the proportion of males in the population (in numbers) under fishing rate F to the proportion males at the unfished level, a measure of male depletion ($x_F \in [0,1]$). The fertilization rate function f is a form of the Beverton-Holt recruitment model scaled to one for $x_F = 1$. It has similar shape to the fertilization function of Heppell et al. (2006) and has the following desirable properties. In the absence of males, f takes its minimum value of 0.0, and at the unfished sex ratio, f takes its maximum value, which is set arbitrarily to 1.0. In between these extrema, fertilization rate depends on the steepness parameter

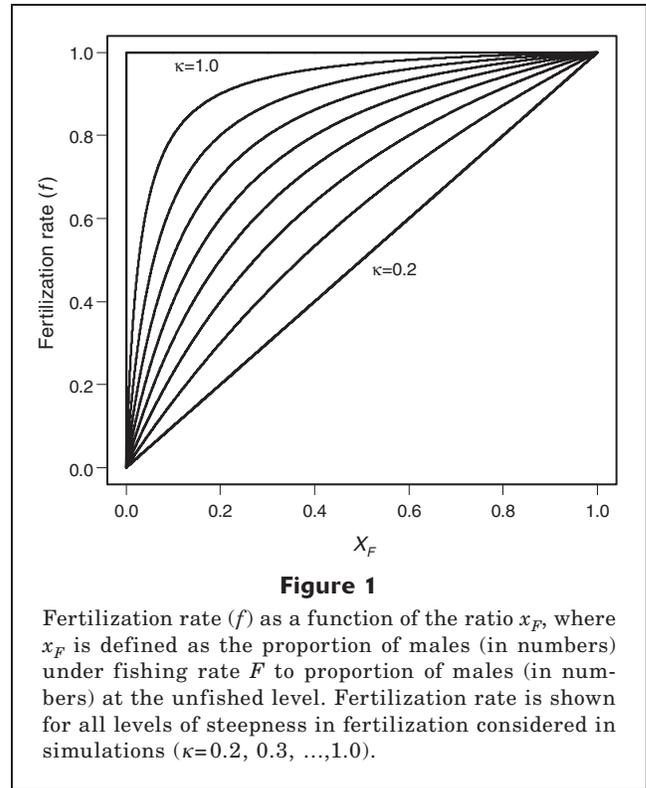


Figure 1

Fertilization rate (f) as a function of the ratio x_F , where x_F is defined as the proportion of males (in numbers) under fishing rate F to proportion of males (in numbers) at the unfished level. Fertilization rate is shown for all levels of steepness in fertilization considered in simulations ($\kappa=0.2, 0.3, \dots, 1.0$).

κ , which can range from 0.2 to 1.0 (Fig. 1). A high value of κ corresponds to a stock that can maintain its fertilization rate when males are scarce. In terms of life histories, one might expect group spawners to have higher κ than pair spawners. The number of fertilized eggs (ψ) under fishing rate F was computed as the product of fertilization rate and total egg production ($\psi = f(x_F)E$).

Recruitment was computed from fertilized eggs ($R(\psi)$) with the Beverton-Holt spawner-recruit model,

$$R(\psi) = \frac{4hR_0\psi}{R_0\phi_0(1-h) + (5h-1)\psi}. \quad (7)$$

In this parameterization (Mace and Doonan, 1988), ϕ_0 is the unfished level of fertilized eggs per recruit, R_0 is unfished recruitment, and h is steepness (analogous to κ in the fertilization function).

Parameter values

Based on life-history theory and empirical study of protogynous fish, values of several parameters were related to natural mortality rate in order to avoid untenable parameter combinations and to maintain generality of results. Gardner et al. (2005) reported relationships between growth rate and natural mortality ($\bar{K}=0.64M$), age at 50% maturity and natural mortality ($\bar{\alpha}_g=0.96/M$), and size at 50:50 sex ratio and asymptotic length ($\bar{L}_{50}=0.77L_\infty$). The results from Gardner et al. (2005)

Table 1

Model parameters. Values in braces are levels used for the primary analysis, where the assessment model did not account for dynamics of fertilization.

| Parameter | Value(s) | Description |
|------------------|---------------------------------|---|
| M | {0.1, 0.2, 0.3} | Natural mortality rate |
| L_∞ | 1000 | Asymptotic maximum length |
| K | 0.64M | Growth coefficient (Gardner et al., 2005) |
| $\bar{\alpha}_g$ | 0.96/M | Mean age at 50% maturity (Gardner et al., 2005) |
| c_g | {0.75, 1.0, 1.25} | Age at 50% maturity relative to the mean |
| α_g | $\alpha_g = c_g \bar{\alpha}_g$ | Age at 50% maturity |
| β_g | {0.2, 0.4, 0.8, 1.6} | Slope of logistic maturity function |
| α_p | 2.3/M | Age at 50:50 sex ratio (Gardner et al., 2005) |
| β_p | {0.2, 0.4, 0.8, 1.6} | Slope of logistic sex-transition function |
| c_s | {0.75, 1.0, 1.25} | Age at selection relative to maturity |
| α_s | $\alpha_s = c_s \alpha_g$ | Age at selection |
| v_1 | 1×10^{-8} | Weight-at-age coefficient |
| v_2 | 3.0 | Weight-at-age exponent |
| ε_1 | 1.0 | Fecundity-at-age coefficient |
| ε_2 | 3.0 | Fecundity-at-age exponent |
| κ | {0.2, 0.3, ..., 1.0} | Steepness of fertilization function (f) |
| h | {0.4, 0.6, 0.8} | Steepness of spawner-recruit function |
| R_0 | 1×10^6 | Unfished recruitment |

were used to describe K and α_g , and to derive the age at 50:50 sex ratio by substituting \bar{K} and \bar{L}_{50} into the von Bertalanffy model and solving for a ($\alpha_p = 2.3/M$). Remaining parameters were set to values or ranges considered reasonable (Table 1). Note that results will be independent of ε_1 , v_1 , and L_∞ because these parameters are merely scalars.

Biological reference points (BRPs)

This study focused on four BRPs: maximum sustainable yield (MSY) and the associated fishing mortality rate (F_{MSY}), spawning biomass (S_{MSY}), and spawning potential ratio (SPR_{MSY}), defined as fertilized eggs per recruit in relation to that at the unfished level. True values of BRPs were computed numerically from the simulation model by maximizing equilibrium yield computed over a range of F at intervals of 0.01. For each F , equilibrium yield (Y_F) was calculated from the Baranov catch equation (Baranov, 1918)

$$Y_F = \sum_a \frac{F_a}{Z_a} N_a w_a (1 - e^{-Z_a}). \quad (8)$$

The MSY was defined as maximum Y_F , F_{MSY} as the F resulting in MSY , and SPR_{MSY} as the corresponding spawning potential ratio (SPR). Unlike those three reference points, the value of S_{MSY} is specific to the measure of spawning biomass (f , m , and b) and was therefore computed as such,

$$\begin{aligned} S_{MSY}^f &= \sum_a \tilde{N}_a (1 - p_a) g_a w_a \\ S_{MSY}^m &= \sum_a \tilde{N}_a p_a g_a w_a \\ S_{MSY}^b &= \sum_a \tilde{N}_a g_a w_a \end{aligned} \quad (9)$$

where \tilde{N}_a = the equilibrium number at age at MSY . Although fertilized eggs, rather than spawning biomass, determined recruitment in the simulation model, values of $S_{MSY}^{f,m,b}$ were computed because of the key role that S_{MSY} plays in determining whether a stock is overfished. Equation 9 provided values in units comparable to estimates from the assessment model, where spawning biomass did determine recruitment.

Assessment model and estimation of biological reference points

The assessment model was structurally identical to the simulation model with the single exception that recruits were computed from a measure of spawning biomass (mature females, males, or both), rather than from fertilized eggs. This difference represents a simplifying assumption common to almost all assessment models. Its inclusion allowed examination of how that assumption affects estimates of BRPs and identification of a robust measure of spawning biomass.

In the assessment model, recruitment (R) was computed from spawning biomass ($S = S^f$, S^m , or S^b) by using the same functional form as Equation 7,

$$R(S) = \frac{4hR_0S}{R_0\phi_0(1-h) + (5h-1)S}, \quad (10)$$

where R_0 = unfished recruitment;
 h = steepness; and
 ϕ_0 = unfished spawning biomass per recruit.

Because fertilization rate is not considered in the assessment model, it is assumed that $\kappa=1.0$ always. Given the spawner-recruit relationship of Equation 10, we computed catch per F assuming equilibrium population structure. The estimate of MSY (\hat{MSY}) was taken to be maximum catch, and \hat{F}_{MSY} was the F that produced that maximum. Also estimated were the associated spawning biomass (\hat{S}_{MSY}) and SPR (\hat{SPR}_{MSY}). These four estimates of BRPs were computed by using each measure of spawning biomass and compared to the true values from the simulation model.

Scope of analyses

These analyses were designed to quantify systematically the magnitude and direction of error of estimated BRPs. Initially, only model misspecification was considered. This part of the study is described as the primary analysis, because it addresses the main goal of isolating error associated with predicting recruits from spawning biomass. Subsequently, additional sources of error were introduced into the assessment model, described as the secondary analysis. Primary and secondary analyses are detailed below.

Primary analysis—model misspecification

The assessment model was misspecified in the sense that it did not explicitly account for dynamics of fertilization. Otherwise, the simulation and assessment models were identical, both in structure and in parameter values. These values were assigned according to a factorial design that included seven factors at various levels (Table 1). The factors were natural mortality rate (M , 3 levels), steepness of spawner-recruit function (h , 3 levels), steepness of fertilization function (κ , 9 levels), slope of sex-transition function (β_p , 4 levels), age at 50% maturity in relation to its mean (c_g , 3 levels), slope of maturity function (β_g , 4 levels), and age at selection by the fishery in relation to maturity (c_s , 3 levels). Thus, the simulations covered a wide array of biological and fishery conditions, with $n = 11,664$ factor-level combinations. At each combination, BRPs were computed with the simulation model, and then estimated with the assessment model by using each of the three measures of spawning biomass (S^f , S^m , S^b).

Secondary analysis—additional misspecifications

Further analysis included additional sources of misspecification. One subset of this analysis examined misspecification of the parameter controlling age at

Table 2

Factors (model parameters) and levels (parameter values) of the secondary analysis, where an incorrect value of age at 50:50 sex ratio was assumed in the assessment model or where fecundity was assumed to scale linearly with weight.

| Factor | Levels | Description |
|-----------|----------------------|---|
| M | {0.1, 0.2, 0.3} | Natural mortality rate |
| κ | {0.2, 0.3, ..., 1.0} | Steepness of fertilization function (f) |
| h | {0.4, 0.6, 0.8} | Steepness of spawner-recruit function |
| β_p | {0.2, 0.4, 0.8, 1.6} | Slope of logistic sex-transition function |
| χ_p | {0.75, 1.0, 1.25} | Multiple of age at 50:50 sex ratio ($\alpha_p=2.3\chi_p/M$) |
| χ_f | {0.75, 1.0, 1.25} | Multiple of fecundity-at-age exponent ($\varepsilon_2=3\chi_f$) |

50:50 sex ratio (α_p). Estimates of this parameter used in an assessment model may be inaccurate because of sampling error or adaptations in response to fishing mortality (Goodyear, 1980; Harris and McGovern, 1997; Barot et al., 2004). Sex transition in the assessment model remained the same ($\alpha_p=2.3/M$; Eq. 4) but was adjusted in the simulation model by a scalar multiple χ_p ($\alpha_p=2.3\chi_p/M$). In a second subset of this analysis we examined violation in the assessment assumption that fecundity scales linearly with weight. This was accomplished by redefining the fecundity exponent in the simulation model ($\varepsilon_2=3$; Eq. 3) by a scalar multiple χ_e ($\varepsilon_2=3\chi_e$), without adjusting the assessment model. For the secondary analysis (Table 2), the remaining model parameter values were as in the primary analysis (Table 1), with the following three exceptions: the slope of maturation was set to a moderate value ($\beta_g=0.8$), age at 50% maturity was set to its mean ($c_g=1$), and age at selection was set to age at 50% maturity ($c_s=1$). As before, the intent was to characterize error of estimated BRPs and thereby identify robust measures of spawning biomass.

Evaluation of assessment results

Assessment results were evaluated in terms of relative error, i.e., the relative difference between reference points known from the simulation model (Eqs. 8 and 9) and the corresponding estimates from the assessment model. At each combination of factor and level, relative error (RE) was computed as

$$\text{RE}(\hat{BRP}^i) = \frac{\hat{BRP}^i - BRP}{BRP} \quad (11)$$

$$\text{RE}(\hat{S}_{MSY}^i) = \frac{\hat{S}_{MSY}^i - S_{MSY}^i}{S_{MSY}^i}$$

Table 3

Summary statistics of relative error (RE) in biological reference points (BRPs) estimated by each measure of spawning biomass. BRPs are maximum sustainable yield (MSY) and the corresponding fishing mortality rate (F_{MSY}), spawning biomass ($S_{MSY}^{f,m,b}$), and spawning potential ratio (SPR_{MSY}). Statistics are 25th quantile, 50th quantile (median), 75th quantile, distance covered by interquartile range (IQD), proportion of model runs with relative error greater than zero (RE>0), mean, and standard deviation (SD). Bold font designates for each BRP the median error closest to zero, mean error closest to zero, proportion of positive RE closest to 0.5, smallest IQD, and smallest SD.

| BRP | Spawning biomass | 25 th quantile | 50 th quantile | 75 th quantile | IQD | RE>0 | Mean | SD |
|-------------|------------------|---------------------------|---------------------------|---------------------------|-------------|-------------|--------------|-------------|
| MSY | female | 0.02 | 0.09 | 0.25 | 0.23 | 0.99 | 0.19 | 0.25 |
| | male | -0.34 | -0.23 | -0.14 | 0.20 | 0.05 | -0.24 | 0.14 |
| | both | -0.15 | -0.07 | 0.01 | 0.16 | 0.27 | -0.05 | 0.16 |
| F_{MSY} | female | 0.06 | 0.26 | 0.68 | 0.62 | 0.82 | 0.50 | 0.63 |
| | male | -0.50 | -0.37 | -0.25 | 0.25 | 0.02 | -0.36 | 0.19 |
| | both | -0.22 | -0.10 | 0.11 | 0.33 | 0.3 | -0.01 | 0.33 |
| S_{MSY}^f | female | -0.11 | -0.05 | -0.01 | 0.10 | 0.12 | -0.07 | 0.07 |
| S_{MSY}^m | male | 0.15 | 0.33 | 0.66 | 0.51 | 0.94 | 0.54 | 1.05 |
| S_{MSY}^b | both | -0.09 | 0.01 | 0.08 | 0.17 | 0.54 | 0.01 | 0.12 |
| SPR_{MSY} | female | 0.01 | 0.06 | 0.18 | 0.17 | 0.93 | 0.14 | 0.19 |
| | male | -0.24 | -0.13 | -0.07 | 0.17 | 0.06 | -0.16 | 0.13 |
| | both | -0.14 | -0.08 | -0.03 | 0.11 | 0.17 | -0.08 | 0.11 |

where $i \in \{f, m, b\}$ indicates female, male, or both, and BRP represents MSY , F_{MSY} , or SPR_{MSY} .

When interpreting relative error, one should be aware that RE has no upper bound but has a lower bound of -1 because the BRPs and estimates are always non-negative. The distribution of relative errors was used to evaluate estimated reference points and thus to provide a general picture of which measure of spawning biomass is most robust.

Analysis of variance (ANOVA) of relative errors was conducted as a form of sensitivity analysis. Factors that explained a significant proportion of total variation represent biological or fishery parameters to which estimates were sensitive. Factors found to be important were then examined in greater detail.

Results

Primary analysis—model misspecification

Aggregated across model runs, variability in estimation error, as indicated by distance covered by interquartile ranges and standard deviations of relative errors, was similar among the three measures of spawning biomass (Table 3). Two exceptions occurred: variability was relatively large when \hat{F}_{MSY} was computed from females only (S^f) and when \hat{S}_{MSY} was computed from males only (S^m).

Estimates of BRPs were closest to the true values (from simulations) when the assessment model counted both males and females (S^b), as indicated by mean and median relative error near zero (Table 3). The assess-

ment model based on females only tended to overestimate F_{MSY} , MSY , and SPR_{MSY} , and it tended to underestimate S_{MSY}^f slightly. The assessment model based on males only showed the opposite pattern; more than 90% of relative errors in \hat{F}_{MSY} , \hat{MSY}^m , and \hat{SPR}_{MSY}^m were negative, and more than 90% in \hat{S}_{MSY}^m were positive. Relative error in \hat{S}_{MSY}^m could be quite large when fertilization rates were independent of male availability ($\kappa=1$). In those cases, males could be almost completely removed from the simulation model without detriment to the population's persistence, but not from the assessment model based on males only. Consequently, the computation of relative error of \hat{S}_{MSY}^m (Eq. 11) included a denominator that approached zero, which magnified the relative error to values much greater than one. The interquartile range of relative error from S^f and from S^m did not include the value of zero for any reference point, where a relative error of zero would correspond to a perfect estimate (Table 3). These relative errors, with opposite signs, were mediated when both sexes (S^b) defined spawning biomass in the assessment model.

For all measures of spawning biomass, the steepness of the fertilization function (κ) explained more of the variation in estimated BRPs than any other model factor (Table 4). The slope of sex transition (β_p) and steepness of the spawner-recruit function (h) explained much of the remaining variation. The remaining factors explained very little. The residual or unexplained error (Table 4) is attributable to interaction terms, which were not included in the ANOVA.

Relative errors of estimated BRPs were further examined by levels of κ and β_p (Fig. 2, A and B). These two parameters were chosen for related reasons: because es-

Table 4

Sensitivity of relative errors in estimated biological reference points to each model factor in the primary analysis, where the assessment model did not account for dynamics of fertilization. For each reference point (F_{MSY} , $S_{MSY}^{f,m,b}$, MSY , and SPR_{MSY}), the measure of spawning biomass (female, male, or both) with the smallest total model error (total SS) demonstrated the least variability (values in italics). Table cells give the proportion of total SS explained by each factor. Values ≥ 0.1 are indicated by bold font and values ≤ 0.01 , by dashes. The term “Residual” is variation explained by all possible interaction terms. Factors (model parameters) are defined in Table 1.

| Factor | F_{MSY} | | | S_{MSY}^f Female | S_{MSY}^m Male | S_{MSY}^b Both | MSY | | | SPR_{MSY} | | |
|-----------|-------------|-------------|-------------|-----------------------|---------------------|---------------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | Female | Male | Both | | | | Female | Male | Both | Female | Male | Both |
| M | 0.03 | — | 0.02 | 0.08 | — | 0.02 | 0.03 | — | — | — | — | — |
| κ | 0.42 | 0.60 | 0.56 | 0.23 | 0.17 | 0.46 | 0.49 | 0.47 | 0.64 | 0.33 | 0.32 | 0.54 |
| h | — | 0.05 | 0.07 | 0.07 | 0.02 | 0.05 | 0.09 | 0.28 | 0.08 | 0.23 | 0.41 | 0.06 |
| β_p | 0.16 | 0.02 | 0.08 | 0.16 | 0.04 | 0.10 | 0.11 | 0.03 | 0.02 | 0.08 | — | — |
| β_g | — | — | — | — | — | — | — | — | — | — | — | — |
| c_g | 0.03 | 0.03 | — | — | 0.02 | — | — | — | — | — | — | 0.02 |
| c_s | 0.05 | 0.09 | — | — | 0.03 | — | — | 0.04 | — | — | 0.02 | 0.02 |
| Residual | 0.31 | 0.22 | 0.27 | 0.45 | 0.72 | 0.36 | 0.27 | 0.15 | 0.23 | 0.34 | 0.23 | 0.36 |
| Total SS | 4624 | 441 | 1283 | 57 | 12,894 | 179 | 728 | 240 | 307 | 423 | 183 | 144 |

estimates were sensitive to them (Table 4) and because of their influences on the dynamics of fertilization (Fig. 1). Examining relative error by steepness of fertilization revealed that the most appropriate measure of spawning biomass depended on the level of κ . If male depletion had little effect on fertilization success (κ in the range 0.8–1.0), the conventional measure, S^f , produced estimates with the least error. However, as fertilization became more limited by male depletion ($0.2 < \kappa < 0.8$), error in estimates from S^f became increasingly more variable and further from the true values. At intermediate values of κ (~0.4–0.7), S^b produced the best estimates. Only for the most limiting values of κ (0.2, 0.3) did S^m appear to be appropriate.

The influence of β_p on fertilization success was perhaps more subtle than that of κ . A shallower slope of sex transition (smaller β_p) provided a broader range of age classes where both males and females were present. This decreased the propensity for fishing-induced male depletion, thereby allowing sex ratio to remain in the range where fertilization rates were relatively high. Conversely, if sex transition occurred across only a few ages (large β_p), disproportionate fishing on males was more likely. The tendency for the depletion of males with a steeper slope of sex transition explains why the assessment model based on S^f performed progressively worse as β_p increased (Fig. 2, A and B). In general, our examination of relative error by slope of sex transition revealed that S^b provided the best estimates.

A consistent pattern in relative errors was that BRPs based on S^f had the opposite sign from those based on S^m , and in most cases ($\kappa > 0.4$), from those based on S^b as well (Table 3, Fig. 2, A and B). Specifically, S_{MSY} tended to be underestimated by S^f and overestimated by S^b , and the other three reference points (MSY , F_{MSY} , and SPR_{MSY}) tended to show the reverse. This result

indicates that, in most cases, estimates from S^f and from S^b could be used to bound uncertainty.

Secondary analysis—additional misspecifications

When the true age at 50:50 sex ratio (α_g) was younger than the age used in the assessment model, S^f provided the best estimates of BRPs; when the true age used in the simulation model was older than the age used in the assessment model, S^b provided the best estimates (Fig. 3). When it was assumed incorrectly with the assessment model that fecundity increased linearly with weight, whether too quickly or too slowly, S^b generally provided the best results (Fig. 3).

As was seen in the primary analysis, resilience of fertilization to male depletion (κ) explained the most variation in relative errors of estimated BRPs, followed closely by the parameter (χ_p) defining misspecification in the age at 50:50 sex ratio (Table 5). Steepness of the spawner-recruit function (h) and slope of sex transition (β_p) also explained some variation. Neither natural mortality (M) nor the parameter (χ_f) defining misspecification of the fecundity exponent explained much variation.

Discussion

We used simulations to investigate the performance of three measures of spawning biomass—females only (S^f), males only (S^m), and both sexes combined (S^b)—for their ability to estimate BRPs. Performance was quantified in terms of relative errors, which were computed across many sets of values of biological and fishery parameters. In the primary analysis, with misspecification in the spawner-recruit relationship only, an

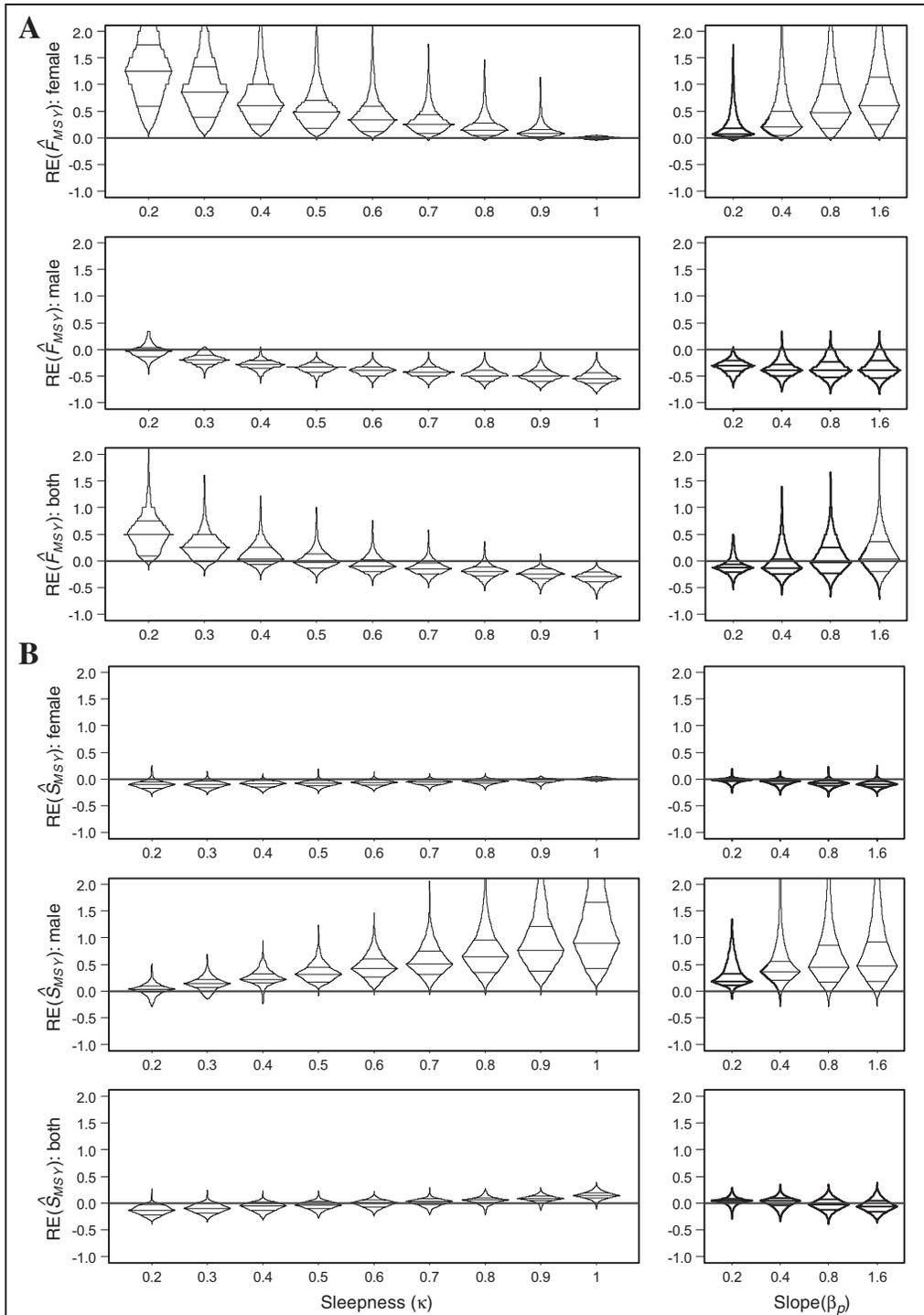


Figure 2

Box-percentile plots of relative error (RE) in estimates of biological reference points, shown across levels of steepness in fertilization (κ) and slope of sex transition (β_p). Rows correspond to the measure of spawning biomass (female, male, or both) used in the assessment model. (A) RE in \hat{F}_{MSY} , (B) RE in \hat{S}_{MSY} . Values of S_{MSY} were calculated separately for each measure of spawning biomass as in Equation 9. Width at each percentile is proportional to the percent of observations more extreme than that percentile. The 25th, 50th, and 75th percentiles are indicated by horizontal lines within each box-percentile plot. Distributions of RE in MSY and SPR_{MSY} were qualitatively similar to \hat{F}_{MSY} , but were less variable (typically ± 0.5).

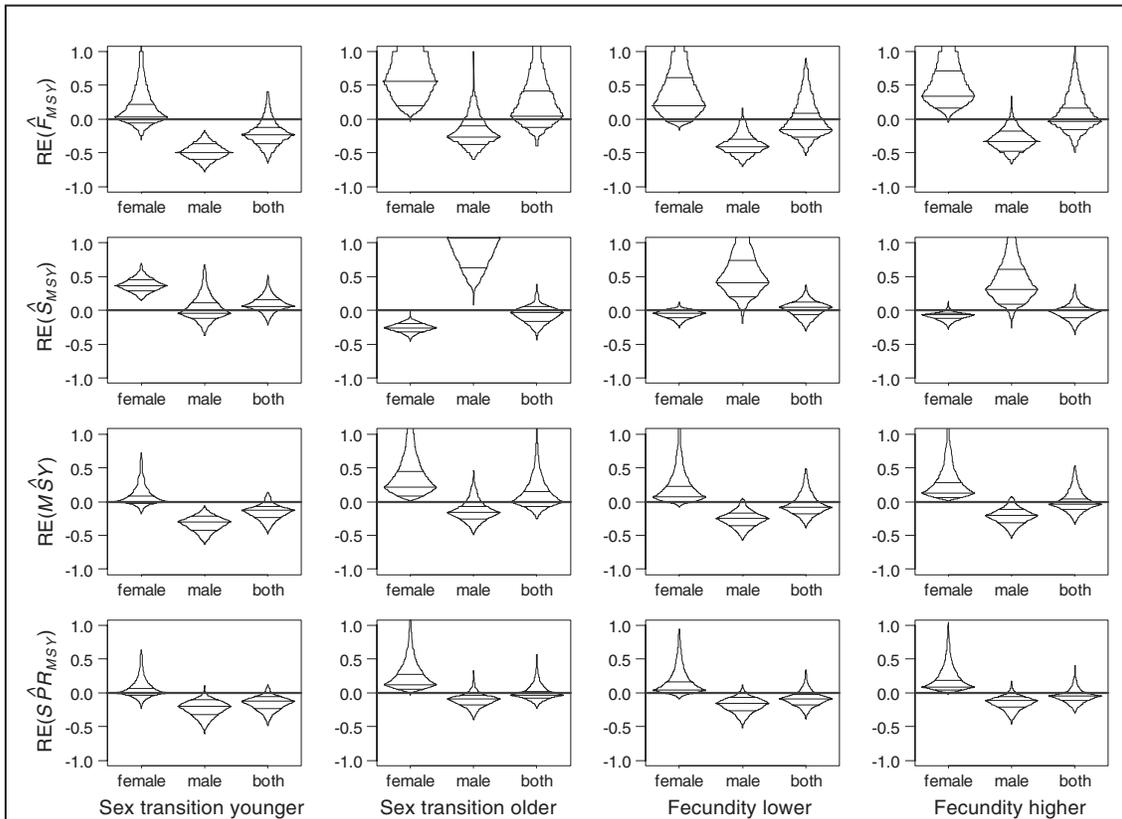


Figure 3

Box-percentile plots of relative error (RE) in estimates of biological reference points from each measure of spawning biomass (female, male, and both), computed in secondary analyses, where an incorrect value of age at 50:50 sex ratio was assumed in the assessment model or where fecundity was incorrectly assumed to scale linearly with weight. Values of S_{MSY} were calculated separately for each measure of spawning biomass as in Equation 9. The first column of panels corresponds to sex transition occurring at a younger age than that assumed in the assessment ($\chi_p=0.75$), the second column to sex transition occurring at an older age than that assumed in the assessment ($\chi_p=1.25$), the third column to fecundity at age being lower than that assumed in the assessment ($\chi_f=0.75$), and the fourth column to fecundity at age being higher than that assumed in the assessment ($\chi_f=1.25$). Width at each percentile is proportional to the percent of observations more extreme than that percentile. The 25th, 50th, and 75th percentiles are indicated by horizontal lines within each box-percentile plot.

assessment model using spawning biomass of both sexes generally provided the best results. When we incorporated additional misspecifications, the assessment model based on both sexes still performed best, with the exception of cases where the age of sex transition in the assessment model was biased towards an older age. Such bias could occur if sex change is adaptive (i.e., if fish alter the timing of sex transition). However, if the age of sex transition is derived from an exploited population, we would expect an estimate used in the assessment to already reflect any adaptation, and thus it seems more likely that any bias in the estimate would be towards a younger age.

Of all the parameters in the factorial design, resilience of fertilization to male depletion, quantified by κ , explains the most variation in relative error of estimates. When $\kappa \geq 0.8$, an assessment model based on

females only provides the best estimates of BRPs. This result is logical, because for the largest values of κ , the proportion of males can be driven quite low before fertilization is limited, and therefore, the number of fertilized eggs will be exactly ($\kappa=1$) or approximately ($\kappa=0.8$ or 0.9) proportional to S^f (given that the exponents of weight at age and fecundity at age are equal). A value of $\kappa=1$ is a limiting case because it implies fertilization can occur even in the absence of males ($x_F=0$). When κ is in the range of about $0.4-0.7$, an assessment model based on both sexes provides the best results. For these levels of κ , fertilization rates decline moderately with depletion of males—an effect that is captured by the use of S^b . Only at the most limiting values of κ ($0.2, 0.3$), where fertilization rates decline dramatically with depletion of males, did an assessment model based on males provide the best estimates.

Table 5

Sensitivity of relative errors in estimated biological reference points to each model factor in secondary analysis, where an incorrect value of age at 50:50 sex ratio was assumed in the assessment model or where fecundity was incorrectly assumed to scale linearly with weight. For each reference point (F_{MSY} , $S_{MSY}^{f,m,b}$, MSY , and SPR_{MSY}), the measure of spawning biomass (female, male, or both) with the smallest total model error (total SS) demonstrated the least variability (values in italics). Table cells give proportion of total SS explained by each factor. Values ≥ 0.1 are indicated by bold font and values ≤ 0.01 , by dashes. The term “Residual” is variation explained by all possible interaction terms. Factors (model parameters) are defined in Table 2.

| Factor | F_{MSY} | | | S_{MSY}^f Female | S_{MSY}^m Male | S_{MSY}^b Both | MSY | | | SPR_{MSY} | | |
|-----------|-------------|-------------|-------------|-----------------------|---------------------|---------------------|-------------|-------------|-------------|-------------|-------------|-------------|
| | Female | Male | Both | | | | Female | Male | Both | Female | Male | Both |
| M | 0.02 | — | — | — | — | — | 0.02 | — | — | — | — | — |
| κ | 0.38 | 0.45 | 0.41 | — | 0.19 | 0.32 | 0.37 | 0.38 | 0.45 | 0.29 | 0.26 | 0.39 |
| h | — | 0.05 | 0.07 | 0.02 | 0.02 | 0.12 | 0.06 | 0.21 | 0.05 | 0.16 | 0.39 | 0.08 |
| β_p | 0.13 | 0.02 | 0.05 | — | 0.05 | 0.05 | 0.08 | 0.03 | 0.02 | 0.05 | — | — |
| χ_p | 0.20 | 0.24 | 0.22 | 0.89 | 0.34 | 0.14 | 0.16 | 0.17 | 0.20 | 0.13 | 0.12 | 0.18 |
| χ_e | — | — | — | — | — | 0.02 | — | — | — | — | — | — |
| Residual | 0.25 | 0.22 | 0.24 | 0.08 | 0.39 | 0.35 | 0.30 | 0.20 | 0.27 | 0.34 | 0.22 | 0.33 |
| Total SS | 1044 | 148 | 419 | 226 | 2869 | 64 | 248 | 78 | 116 | 112 | 55 | 48 |

Sensitivity of results to κ may indicate that estimates of fertilization success, if obtainable, would be quite valuable. Although κ itself may be difficult to estimate directly, fertilization success could be assessed qualitatively if it shifts, for example from high to low, with a change in sex ratio. Such information would make it possible to infer a likely range for steepness of the fertilization function, and hence, to select the measure of spawning biomass most appropriate for that range.

In addition to influencing assessment error, κ influences the values of BRPs themselves, and lower κ results in higher S_{MSY} and lower F_{MSY} and MSY . Comparing the BRPs of these simulated protogynous stocks with those of gonochoristic equivalents, we found that, on average, protogynous stocks could support higher F_{MSY} and MSY when $\kappa \geq 0.5$. This finding resulted from the condition that if age structures are equivalent, protogynous stocks are not inherently more vulnerable to exploitation than gonochoristic stocks, at least over moderate ranges of fishing mortality (Bannerot et al., 1987). It indicates that protogynous stocks are not inherently more vulnerable to exploitation than gonochoristic stocks, at least over moderate ranges of fishing mortality. We caution, however, that higher F_{MSY} does not imply more resilience to all levels of F . If fertilization rate depends on sex ratio, some level of $F > F_{MSY}$ is still likely to be more detrimental to a protogynous stock, where that level would depend on characteristics of the stock in question. For example, if sex transition is rapid, and occurs across only a few ages, fishing could more readily deplete males, leading to fertilization failure and thus recruitment failure.

Reproductive behavior could also affect a stock's vulnerability to exploitation. Spawning aggregations can make a species easier to target but probably better able to adapt to changes in sex ratios. Pair spawners,

on the other hand, may be less easy to target, but more susceptible to effects of male depletion.

Without any information on fertilization rates, a likely range of κ could be postulated from evolutionary considerations. We expect that nature would select against values of κ near its limits (0.2 and 1.0). At the lower bound of $\kappa=0.2$, any decline in the proportion of males would lead to a relatively steep reduction in fertilization success. Individual fitness could be increased by greater sperm production per male, thereby increasing fertilization success and driving κ above 0.2. However, greater sperm production would likely be associated with an energetic cost. Thus, a tradeoff should exist between energy allocated toward sperm production versus other functions, such as somatic maintenance, foraging, or reproductive behavior (Alonzo and Warner, 2000; Scagianti et al., 2005). The tradeoff may be worth the cost, but only to the extent that an increase in fertilization success improves fitness. At the upper range of κ , the marginal gains in fertilization success are only realized if males are extremely depleted (i.e., as $x_F \rightarrow 0$ in Fig. 1). Furthermore, the value of $\kappa=1.0$ implies that a single male can fertilize the eggs of every female in the population, which is obviously not realistic. We therefore hypothesize that moderate values of κ should be most prevalent. Theoretical predictions, and several field experiments, indicate that fertilization is less than 100% and may decline as less sperm is released per spawning event (Petersen et al., 1992; Petersen and Warner, 2002).

Moderate values of κ correspond to the range where BRPs are best estimated from spawning biomass of both sexes, and we therefore recommend a default choice of S^b when the degree of sperm limitation is unknown. The direction and degree of relative error indicate that S^b would produce nearly perfect estimates of S_{MSY} and risk-averse estimates of F_{MSY} , and only a

small loss in potential MSY (negative relative error was slight).

Results of this study are insensitive to the assumption that fecundity is linearly related to body weight, most likely because there are few females remaining at ages where curves of fecundity at age and weight at age would diverge if $\varepsilon_2 \neq 3$. This finding provides support for using spawning biomass as a proxy for total egg production, which is reassuring given that this assumption is commonplace in assessments. However, it does not support the conventional proxy (S^f) unless fertilization rates are nearly constant over a wide range of sex ratios. Furthermore, this finding does not address whether total egg production itself represents reproductive potential adequately. As discussed by Murawski et al. (2001), total egg production does not include potentially important influences such as spawning experience or effects of maternal age and size on offspring quality.

For simplicity, the simulations considered only knife-edge selectivity. In some fisheries, selectivity is dome shaped, as a result of regulations (e.g., slot limits), gear type (e.g., traps), or migration patterns (e.g., if larger fish leave the fishing grounds). In protogynous fish, dome-shaped selectivity would reduce fishing pressure mainly on males. If enough fish can survive the ages of full exploitation, dome-shaped selectivity could allow the proportion of males to remain sufficiently high to avoid severe decline in fertilization success. This effect should maintain sex ratio in the range where S^f and S^b would perform comparatively well. Indeed, this expectation was confirmed by additional simulations where we repeated our primary analysis but with dome-shaped rather than knife-edge selectivity.

Although this simulation study focuses on protogynous fish, we expect the results to hold for any stock that experiences preferential fishing on males. This may occur in gonochoristic stocks, for example, if sexually dimorphic growth or spatial segregation renders males more vulnerable to fishing gear.

This investigation was deterministic by design, so that error from model misspecification could be isolated. A useful extension would be to include other sources of error—observation, process, or both. Data sets that incorporate these additional sources could be generated with the simulation model, and then fitted with the assessment model. This type of approach would make it possible to evaluate the effect of additional error sources on estimates of key population parameters (for example, unfished recruitment [R_0] or steepness [h] in the spawner-recruit relationship) and on management advice.

Although S^b performs best in general, no measure of spawning biomass is best in all cases. One consistent finding is that the relative errors of S^f and S^b tend to have opposite signs over the range of κ that we consider probable; therefore, the use of S^f and S^b in assessments should bound uncertainty in estimates of BRPs. This pattern of relative errors tending to have opposite signs occurred because S^f never accounts for reduction in fertilization success and S^b always does. As a result, S^f

tends to overestimate the ability of a stock to support exploitation, and S^b tends to provide more conservative reference points.

This consistent pattern in the relative errors of S^f and S^b indicates that error in reference points could be reduced by creating a measure of spawning biomass that counts both sexes, but with a heavier weight on females (the measure S^b counted both sexes equally). Alternatively, error could be reduced by combining estimates through model averaging (e.g., Brodziak and Legault, 2005). Either way, estimates from S^f and S^b could be used to bound uncertainty in biological reference points for managing protogynous fish.

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