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Misspecifying Sex-Structured Dynamics in Stock Assessment Models

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ABSTRACT

Sex-specific variation in population demography and life-history traits (e.g., growth, natural mortality) is common in many fish populations. Differences in these processes by sex can dictate population dynamics and influence how harvesters interact with the resource. Across various fisheries management systems, stock assessment models (SAMs), which mathematically represent population age and/or size structure, are widely utilised to estimate fish population status and provide sustainable harvest recommendations. However, few studies have examined the implications of alternative modelling assumptions when incorporating sex-specific dynamics in SAMs. For instance, the impacts of simultaneously ignoring sex-specific variations in growth, selectivity, and natural mortality on SAM performance have not been explored. In this study, a simulation-estimation framework was developed for a sexually dimorphic fish population to: (1) assess the consequences of ignoring sexual dimorphism (i.e., growth, natural mortality, and selectivity) and the benefits of using sex-specific catch data to inform the estimation of these processes, (2) evaluate the implications of incorrect modelling assumptions regarding sex ratio at birth, and (3) develop advice for parameterising observation likelihoods to describe sex-specific composition data. Correctly parameterising sex-specific variation in life-history traits led to more robust population estimates and catch advice. Conversely, SAMs ignoring these variations yielded biased estimates of biomass and harvest recommendations. Collectively, our results underscore that oversimplified assumptions about sex-specific variations in SAMs can lead to poor management advice. Moreover, results emphasise the need for routine collection of sex-specific data to support the development of biologically realistic models.

1 | Introduction

Sex-specific differences in demographic processes are widespread among fish species (Hanson et al. 2008) and are evident in various life-history traits like growth (Parker 1992), species distributions (Bartolino et al. 2011), and natural mortality (Gislason et al. 2010). These dynamics occur in many species that are of commercial, cultural, and subsistence importance, including gadoids (Keyl et al. 2015), rockfishes (Echeverria 1986), flatfishes (Luckenbach et al. 2009), elasmobranchs (Gayford and

Sternes 2024), crustaceans (Ogburn 2019), salmon (Gislason et al. 2017), and highly migratory species (e.g., tunas; Farley et al. 2014). Such differences in demographic processes can influence harvest patterns and population dynamics, with ecological and evolutionary consequences. For instance, sexual size dimorphism in Alaska sockeye salmon (*Oncorhynchus nerka*) can interact with size-selective harvest practices, which have been hypothesized to result in increased harvest of males due to their larger size, potentially altering population sex ratios and breeding ground dynamics (Kendall and Quinn 2013).

Similarly, natural mortality, which can scale with body size (Gislason et al. 2010; Lorenzen et al. 2022) or with increased foraging activity (Ahrens et al. 2012), may vary between sexes in species with sexual size dimorphism, subsequently influencing population sex ratios and reproductive dynamics (Conrad and Kindsvater 2024). Therefore, it is likely important to explicitly account for these biological aspects in the management frameworks of sexually dimorphic species when developing sustainable harvest recommendations.

Maintaining the reproductive biomass of a population at levels that do not impair future recruitment is a primary goal of most contemporary fisheries management systems and decision-making (Kvamsdal et al. 2016). However, for species exhibiting sex variation in life-history traits and harvest patterns (e.g., natural mortality, growth, fishery selection patterns) achieving this goal presents additional complications. For instance, in Alaskan Arrowtooth flounder (*Atheresthes stomias*), where females outnumber males due to lower natural mortality rates, simulation analyses have demonstrated that reproductive potential (measured by egg fertilization rates) depends on a combination of mating behaviour (i.e., males are not considered surplus), population sex ratios, and the level of recommended harvest (Wilderbuer and Turnock 2009). In both Southern flounder (*Paralichthys lethostigma*) and Summer flounder (*P. dentatus*), Conrad and Kindsvater (2024) found that increasing male proportions at birth, as driven by temperature-dependent sex determination mechanisms, has the potential to reduce total egg production, abundance, and biomass. Additionally, for many reef species, such as groupers (*Epinephelidae*), which exhibit protogynous hermaphroditism (i.e., transitioning from females to males), studies indicate that disproportionate harvest of males can reduce fertilisation rates (Alonzo and Mangel 2004). Targeting sub-mature individuals in these hermaphroditic species can also impair egg production through truncation of population age structure and earlier transitions from females to males (Kindsvater et al. 2017). Considering these factors, monitoring sex-specific population dynamics and understanding how sex-specific life-history traits influence population processes are essential for the sustainable management of sexually dimorphic species.

Across various fisheries management systems, recommendations for sustainable harvest levels often rely on stock assessment models (SAMs). SAMs provide a cohesive framework for combining various data sources (e.g., counts, compositions and time-series) into a single analysis and allow the estimation of unknown parameters using a combined statistical function (Maunder and Punt 2013). Typically, SAMs include several sub-models that describe both population processes and observation processes and directly relate observations to population-level parameters. Within fisheries, SAMs commonly incorporate age and/or size-structured dynamics, where the primary objective is to estimate population biomass and project sustainable harvest levels (Maunder and Punt 2013). However, for species exhibiting sex-specific life-history traits, SAMs need to account for age and/or size-structure and sex-structured dynamics (Hamel et al. 2013; Rudd et al. 2021). As such, additional flexibility is required to describe sex-specific population productivity (e.g., natural mortality, growth, population sex-ratios at birth) and harvest patterns (e.g., fishery selectivity).

Additionally, sex-specific data are needed to inform the estimation of these processes. When compared to SAMs that are solely age- or size-structured, those incorporating sex-structure often involve greater complexity and reduced sample sizes to inform parameter estimation.

Considering trade-offs between model complexity and parsimony, and constraints on data availability, simplifying assumptions are often necessary when parameterising SAMs. In some cases, a lack of sex-specific data can impede the implementation of a sex-structured SAM, necessitating the assumption of identical dynamics for both sexes (Terceiro 2024). Even in scenarios where significant sexual dimorphism exists and sex-specific data are available, simplifying assumptions may still be required to describe population processes. Such simplifications are partly due to challenges in modelling sex-specific demographic rates and harvest patterns simultaneously. For example, while sexual size dimorphism likely results in sex-specific natural mortality rates (Gislason et al. 2010; Lorenzen et al. 2022), it is common practice to assume sex-invariant natural mortality rates due to parameter confounding and uncertainty in estimation processes (Wang et al. 2007; Lee et al. 2011; Maunder et al. 2023). Additionally, a prevailing modelling assumption employed in many sex-structured SAMs involves assuming known and equal population sex ratios at birth (hereafter, recruitment sex-ratios) due to parameter confounding with selectivity and natural mortality (Wilberg et al. 2005; Hamel et al. 2013). However, evidence suggests that genetic or environmental factors can result in skewed recruitment sex ratios (Luckenbach et al. 2009; Ospina-Álvarez and Piferrer 2008).

Incorporating sex structure into SAMs for sexually dimorphic species has generally been shown to improve model performance and produce different estimates of population biomass and sustainable harvest levels when compared to SAMs assuming single-sex dynamics. Lee et al. (2014) demonstrated these improvements with their application of a sex-structured SAM for Blue marlin (*Makaira nigricans*), which resulted in improved fits to composition data due to increased model flexibility in representing sex-specific mortality processes. In an application of a sex-structured SAM for swordfish (*Xiphias gladius*), Wang et al. (2007) demonstrated differences in spawning stock biomass (SSB) and sustainable harvest levels between sex-structured and single-sex SAMs. These differences are likely due to the explicit consideration of sex-specific growth and selectivity. Utilising simulation analysis, both Wang et al. (2005) and Su et al. (2011) found that estimates of biomass and management advice were significantly biased in SAMs when sexual dimorphism was ignored. However, in the case of Summer flounder, arguments persist about whether sex-structured SAMs more accurately depict stock status, largely focusing on the modelling assumptions necessitated in the absence of comprehensive sex-specific data (Maunder and Wong 2011; Terceiro 2024).

Despite the demonstrated benefits of incorporating sex structure into SAMs for sexually dimorphic species, several uncertainties remain when parameterising sex-structure in these models, which have yet to be thoroughly examined. In particular, two general approaches have been described for parameterising sex-composition likelihoods. The first approach

assumes sex-specific composition data arise from a single statistical model describing the probability of sampling across all sex and age categories within a given year. By contrast, the second approach assumes that sex-specific composition data are derived from separate statistical models: one describing the probability of sampling ages within a specific sex category, and another describing the probability of sampling a particular sex (Francis 2014; Cheng et al. 2025). However, the benefits and drawbacks of either approach remain relatively unexplored. Moreover, some simulation studies have indicated that sex-specific natural mortality rates can be estimated with reasonable accuracy and precision when informative sex-specific compositional data are available (Lee et al. 2011; Maunder and Wong 2011). Although there are studies on the estimability of sex-specific natural mortality rates, the implications of ignoring these sex-specific rates generally remain uncertain. Furthermore, for some fisheries, sex-specific catch information can be obtained through external inspection of sex-specific characteristics, internal examination of gonads, and the use of novel genetic techniques (Galindo et al. 2011). In theory, sex-specific catch information has the potential to enhance the performance of sex-structured SAMs and improve the precision of model estimates, although its overall utility and associated considerations for its use have not been thoroughly assessed. Finally, while assuming known and equal recruitment sex ratios is common across many sex-structured SAMs (Wilberg et al. 2005; Johnson et al. 2023), the implications of misspecification are also not well understood.

In this study, we utilise a simulation-estimation framework to: (1) understand the consequences of ignoring sexual dimorphism and the utility of incorporating sex-specific catch data, (2) assess the implications of misspecification of recruitment sex ratios, and (3) develop advice for parameterising sex-composition likelihoods. Together, results from this study enhance understanding of the implications of structural decisions regarding the incorporation of sex structure in SAMs for sexually dimorphic fish species, providing valuable insights into the consequences of model misspecification for management advice.

2 | Methods

Under the simulation-estimation framework, an operating model (OM) loosely based on the life-history characteristics of Alaska sablefish (*Anoplopoma fimbria*) was developed to represent the true population dynamics of a sexually dimorphic species and generate simulated data. Alaska sablefish exhibit low natural mortality rates, sex-specific growth patterns (females larger than males), and sex-specific selectivity patterns (females are selected at an earlier age than males) (Goethel et al. 2023). While the OM was loosely based on Alaska sablefish, additional OM scenarios were implemented to explore variations in sex-specific growth, selectivity, natural mortality, and recruitment sex ratio to further generalise simulation results. Corresponding SAMs were developed with varying assumptions about sex-structured dynamics to reflect common modelling choices (e.g., single-sex dynamics; sex-aggregated natural mortality, equal recruitment sex-ratios), when confronted with species exhibiting sexual dimorphism

in population dynamics. These SAMs were applied to each OM scenario to understand the implications of these assumptions on biases in quantities relevant to fisheries management (e.g., spawning stock biomass (SSB), harvest recommendations). All analyses were conducted in the R statistical environment, and SAMs were configured using Template Model Builder (TMB; Kristensen et al. 2016).

2.1 | General Configuration of Operating Models

2.1.1 | Model Structure

The general configuration of OMs in this study was parameterised as a single-area, two-sex (females and males), age-structured population. Over a span of 35 years, a single fishery fleet represented removals from the population, while a single survey fleet provided an index of population abundance. The population was initialized under unfished conditions, and annual abundance was projected forward using an exponential mortality model:

$$N_{y+1,a+1,s} = \begin{cases} N_{y,a,s} e^{-(F_y * FshSel_{a,s} + M_s)} & 1 < a < 30 \\ N_{y+1,a,s} e^{-(F_y * FshSel_{a-1,s} + M_s)} + N_{y,a,s} e^{-(F_y * FishSel_{a,s} + M_s)} & a = 30 \end{cases} \quad (1)$$

Here, subscripts y , a , and s denote year, age, and sex, respectively. N represents abundance, F is the annual instantaneous fishing mortality rate, $FshSel$ denotes fishery selectivity, and M is the instantaneous natural mortality rate. Annual recruitment of individuals into the population occurred at age one following a Beverton-Holt stock recruitment relationship using the parameterisation of Mace and Doonan (1988):

$$N_{y,1,s} = \frac{4hR_0 SSB_{y-1}}{SSB_0(1-h) + SSB_{y-1}(5h-1)} e^{\epsilon_y - \frac{\sigma^2}{2}} \chi_s \quad (2)$$

where, h represents the steepness (0.85) of the stock-recruit function, R_0 is the expected recruitment at unfished equilibrium, and SSB_0 is the SSB at an unfished equilibrium. ϵ_y are annual recruitment deviations from the stock-recruit function constrained by $\epsilon_y \sim N(0, \sigma^2)$ ($\sigma^2 = 0.64$), with a lognormal bias correction of $\frac{\sigma^2}{2}$, and χ describes the sex-ratio at recruitment. These recruitment deviations introduce stochasticity into the simulation framework (i.e., process error), resulting in distinct population trajectories for each simulation run. Recruitment to age one was then related to SSB from the previous year:

$$SSB_y = \sum_{a=1}^A N_{y,a,s=1} W_{a,s=1} \gamma_{a,s=1} \quad (3)$$

where, $W_{a,s=1}$ and $\gamma_{a,s=1}$ were the weight and maturity-at-age for females, respectively. Throughout, subscript $s = 1$ denotes females and subscript $s = 2$ represents males. Sex-specific weight-at-age was determined by combining a von Bertalanffy length-at-age relationship (Equation 4) with an allometric length-weight relationship (Equation 5):

$$L_{a,s} = L_s^\infty \left[1 - e^{(-k_s(a - t_s^0))} \right] \quad (4)$$

$$W_{a,s} = \alpha L_{a,s}^\beta \quad (5)$$

In Equation (4), L_s^∞ , k_s and t_s^0 are parameters describing the sex-specific length-at-age relationship, representing the asymptotic length, the Brody growth coefficient, and the theoretical length defined at $a = 0$, respectively. In Equation (5), α represents a parameter that scales length to weight and β is the allometric scaling parameter. Maturity-at-age for females was defined using a logistic function, following Goethel et al. (2023):

$$\gamma_{a,s=1} = \frac{e^{(-15+0.73a)}}{1 + e^{(-15+0.73a)}} \quad (6)$$

Fishery removals from the population occurred continuously across time following Baranov's catch equation:

$$C_{y,a,s} = \frac{F_y * FshSel_{a,s}}{F_y * FshSel_{a,s} + M_s} N_{y,a,s} \left[1 - e^{-(F_y * FshSel_{a,s} + M_s)} \right] \quad (7)$$

Here, the total fishing mortality-at-age assumed separability and was represented as the product of F and $FshSel$. To aid parameter estimation in SAMs, the annual fishing mortality rate pattern was depicted as a two-way trip, which has been shown to generally improve estimation performance by introducing contrast in the population dynamics (Conn et al. 2010). As such, F_y increased linearly to the F that would achieve maximum sustainable yield ($FMSY$) from years 1–18 and declined linearly to 50% of $FMSY$ for the remainder of the time. The abundance ($I_{y,a,s}$) observed by the survey fleet was calculated as follows:

$$I_{y,a,s} = q * SrvSel_{a,s} N_{y,a,s} \quad (8)$$

$$I_y = \sum_{(a,s)} I_{y,a,s}$$

where, q is a scalar quantity representing survey catchability, $SrvSel$ denotes survey selectivity, and the annual abundance index (in units of numbers; I_y) observed by the survey fleet was obtained by summing across all ages and sexes.

In this study, we assumed that both fishery and survey fleets had length-based logistic selectivity functions. The choice to represent selectivity as length-based, rather than age-based, aligns with a common assumption utilised in many SAMs (Wilberg et al. 2005; Methot and Wetzel 2013). However, there are cases where sex-specific differences in fishing mortality rates-at-age may arise from other processes besides growth, especially when sex-specific differences in spatial distributions influence how fisheries or surveys encounter the resource (e.g., females are located offshore, while males are inshore). This consideration was not addressed in the present study, but should be explored in future research. Therefore, a single length-based selectivity pattern was defined to represent both sexes, which was then converted into ages using a von Bertalanffy length-at-age relationship through a sex-specific age-length conversion matrix ($\varphi_{l,a,s}$), allowing for differential removals to be based on sex-specific differences in growth. The age-length conversion matrix represents the proportion of age a fish that are in length bin l and was formulated as:

$$\varphi_{l,a,s} = \begin{cases} \Phi\left(\frac{L'_{min,s} - L_{a,s}}{\psi_{a,s}}\right) & \text{for } l=1 \\ \Phi\left(\frac{L'_{l+1,s} - L_{a,s}}{\psi_{a,s}}\right) - \Phi\left(\frac{L'_{l,s} - L_{a,s}}{\psi_{a,s}}\right) & \text{for } 1 < l < 30 \\ 1 - \Phi\left(\frac{L'_{max,s} - L_{a,s}}{\psi_{a,s}}\right) & \text{for } l=30 \end{cases} \quad (9)$$

Here, Φ represents the standard normal cumulative density function, $L'_{min,s}$ is the lower limit of length bin l , $L'_{max,s}$ is the lower limit of the largest length bin, and n_L is the total number of length bins modelled. $L_{a,s}$ represents the length-at-age relationship and $\psi_{a,s}$ determines the variability of this relationship. Given that selectivity-at-length was modeled as logistic before being converted to selectivity-at-age, the maximum fishery and survey selectivity may not equal one for one of the sexes (Figure 1). Selectivity-at-length for the fishery and the survey were then converted into selectivity-at-age using the following:

$$Sel_{a,s} = \sum_{l=1}^{n_L} Sel_l * \varphi_{l,a,s} \quad (10)$$

where, Sel represents the selectivity pattern for either the fishery or the survey.

2.1.2 | General Sex-Structured Dynamics

Unless stated otherwise, the configuration of sex-structured dynamics across most OMs in this study assumed that the L^∞ parameter describing the length-at-age relationship for males was approximately 15% lower than females (Female $L^\infty = 81.2$ cm, Male $L^\infty = 66.5$ cm). This resulted in males being smaller and weighing less than females, a pattern consistent with the life-history of Alaska sablefish (Sasaki 1985). Given the assumption of length-based selectivity, these growth disparities led to greater fishery and survey selection of females compared to males across ages. Such preferential selection for a given sex could theoretically arise due to numerous factors (e.g., mesh-or hook-size of gear, high-grading, gape limitation, differences in fish behaviour). Natural mortality for males was also 15% lower than females (Female $M = 0.108$, Male $M = 0.0918$), which aligns with predictions from foraging arena theory (Ahrens et al. 2012). Moreover, the recruitment sex-ratio (χ) was assumed to be equal. While the recruitment sex-ratio was equal, differences in selectivity and natural mortality between sexes led to unequal population sex-ratios at later life stages. An illustration of these general dynamics are depicted in Figure 1.

2.1.3 | Simulating Data

Six data sources were simulated annually with observation error, which were all utilised to inform SAM estimation. These included: (1) survey age-composition, (2) survey length-composition, (3) fishery age-composition, (4) fishery length-composition, (5) a survey abundance index and (6) fishery catches. All compositional data (age and length) simulated were sex-specific and assumed a

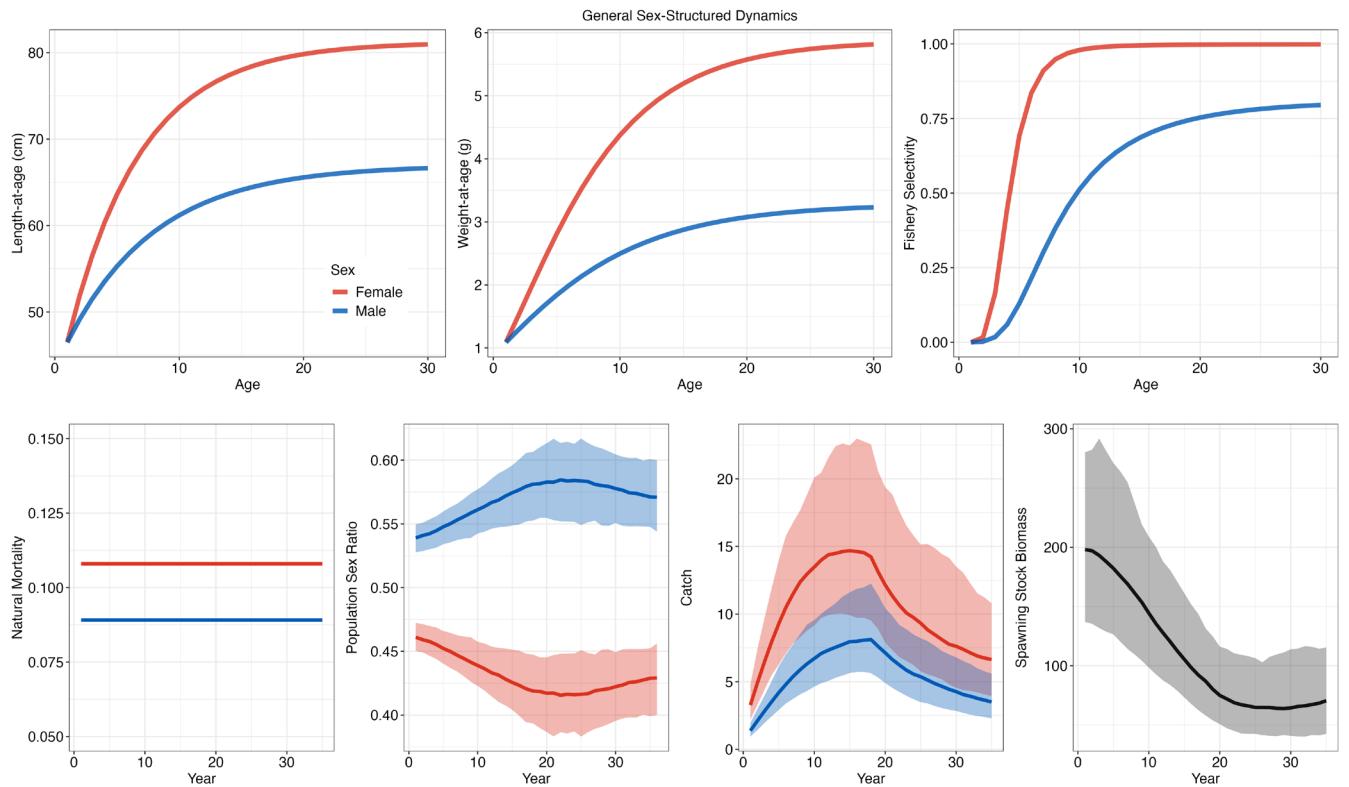


FIGURE 1 | Graphical representation of the general sex-structured dynamics described in Section 2.1.2. Most operating models developed in this study generally replicated these dynamics. The upper row illustrates length, weight, and fishery selectivity across ages and sexes. The bottom row illustrates natural mortality, population sex-ratios, catch, and spawning stock biomass over a 35-year period (generated from OM ‘Grwth15_Mort15’ in Experiment 2), with shaded areas indicating 95% simulation intervals (solid lines within these shaded areas represents the median across 500 simulation replicates). Sex-specific growth parameters for these general sex-structured dynamics are defined as follows: Female $L^\infty = 81.2$ cm, Female $k = 0.17 t^{-1}$, Female $t^0 = -4$; Male $L^\infty = 66.5$ cm, Male $k = 0.23 t^{-1}$, Male $t^0 = -4$. Sex-specific natural mortality rates are defined as: Female $M = 0.108$, Male $M = 0.0918$.

multinomial distribution, with a total sample size (Tot^{Samp}) of 100 shared across both sexes (i.e., the 100 samples were distributed according to the population sex-ratio and selectivity patterns defined in the OM). The survey abundance index was sex-aggregated and simulated following a lognormal distribution with a coefficient of variation (CV) of 0.25. Fishery catches were similarly generated following a lognormal distribution, assuming negligible error (CV = 0.025). While fishery catches were generally aggregated across sexes (i.e., summed across ages and sexes in Equation (7)), they were simulated for both sexes in some cases (i.e., only summed across ages in Equation (7)), with differences in sex-specific catch attributed to primarily due to sex-specific fishery selectivity and abundance, and some differences due to sex-specific natural mortality. These data were also assumed to follow a lognormal distribution with negligible error (CV = 0.025). Although such precision in sex-specific catch information is unlikely in the real-world, its use aimed to illustrate the potential utility of sex-specific catch information under an ideal scenario. A total of 500 replicate datasets were simulated to reflect observation error and process error.

2.2 | General Configuration of Stock Assessment Models

The majority of SAMs were configured similarly to OMs and were generally sex-and age-structured population models.

Furthermore, identical likelihood distributions and associated variance terms were used to parameterise SAMs as were used to generate simulated data. However, differences in model structure were introduced for certain simulation experiments, which are described in subsequent sections. Parameter estimation followed a penalized maximum likelihood framework, estimating several key parameters, including recruitment at unfished equilibrium (R_0), annual recruitment deviations (ϵ_y), annual fishing mortality rates (F_y), and survey catchability (q). Following the OMs, fishery and survey selectivity were length-based and estimated sex-invariant parameters describing the length-at-50% selection and the slope of a logistic function (converted into sex-specific selectivity-at-age using Equations (9) and (10)). We note that assuming length-based selectivity in SAMs when sex-specific growth is known (i.e., treated as a fixed input in this study) likely improves the estimability of selectivity. However, this assumption was made to maintain consistency with OMs and better isolate how biases emerge. Natural mortality rate (M) was freely estimated, with their specification as either aggregated or sex-specific contingent on the experiment. Weight-at-age values and the age-length conversion matrices were estimated external to the assessment model using simulated age-length pairs independently for each sex, following Equations (4), (5) and (9). Additionally, maturity-at-age values (γ), steepness (h), recruitment variance (σ^2), and observation errors (i.e., CV for abundance indices and catch, and Tot^{Samp} for

compositional data) were set at their true values. The parameter representing sex-ratio at recruitment (χ) was also set at its true value (i.e., equal ratio) across most simulation scenarios.

2.3 | Simulation Experiments

We conducted three distinct experiments to evaluate the effect of different representations of sex-structured dynamics on model performance. Each experiment followed a full-factorial design, wherein each SAM was applied to the 500 replicate datasets generated by each OM scenario. Model estimates from SAMs were then compared to the true dynamics generated by each OM scenario. A summary of the simulation experiments can be found in Tables 1 and 2.

2.3.1 | Experiment 1: Parameterisation of Sex-Composition Likelihoods

Sex-specific age- and length-composition data are integral for SAMs that consider sex structure, providing information on population sex ratios and selectivity. In Experiment 1, we aimed to develop advice on the parameterisation of sex-compositional likelihoods by formulating two distinct OM scenarios (Figure 2a, Table 1) and two corresponding SAMs (Table 2).

2.3.1.1 | Operating Models in Experiment 1. Both OM scenarios in Experiment 1 maintained identical model structure and sex-structured dynamics outlined in Section 2.1. For brevity, we use notation from catch-at-age ($C_{y,a,s}$) to highlight differences among these OMs, although the same process is also used for observations generated from the survey. In the first scenario

(OM ‘Joint’), sex-specific composition data were simulated using a multinomial distribution by normalizing proportions across both ages and sexes (vectors ordered by females then males):

$$P_{y,s}^{Joint} = \frac{C_{y,a,s}}{\sum_{(a,s)} C_{y,a,s}}, \quad \sum_{(a,s)} P_{y,s}^{Joint} = 1 \quad (11)$$

$$X_{y,s}^{Joint} \sim \text{Multinomial}\left(\text{Tot}^{\text{Samp}}, P_{y,s}^{Joint}\right)$$

where $X_{y,s}^{Joint}$ represents samples drawn from a multinomial distribution via the ‘Joint’ approach, with probabilities of $P_{y,s}^{Joint}$, which summed to 1 across all ages and sexes for a given year.

In the second scenario (OM ‘Split’), sex-specific composition data were simulated following a two-step process. Here, the sex-ratio for females ($\phi_{y,s=1}$) observed by the fishery or survey fleet was computed and conditioned on a binomial process, where Tot^{Samp} was shared across sexes to determine sex-specific sample sizes ($S_{y,s}^{\text{Samp}}$):

$$\phi_{y,s=1} = \frac{\sum_a C_{y,a,s=1}}{\sum_{(a,s)} C_{y,a,s}} \quad (12)$$

$$S_{y,s=1}^{\text{Samp}} \sim \text{Binomial}\left(\text{Tot}^{\text{Samp}}, \phi_{y,s=1}\right), \quad S_{y,s=2}^{\text{Samp}} = \text{Tot}^{\text{Samp}} - S_{y,s=1}^{\text{Samp}}$$

Sample sizes for males ($S_{y,s=2}^{\text{Samp}}$) was Tot^{Samp} subtracted by the number of samples drawn for females. Catch proportions were subsequently normalized within a given sex (summed to 1 within a sex for a given year), with probabilities $P_{y,s}^{Split}$:

TABLE 1 | Summary of operating models (OMs) developed this study, separated into three distinct experiments. The column ‘Composition Parameterisation’ describes whether sex-specific composition data summed to one split between sexes (Split) or jointly across sexes (Joint). The columns ‘Male Growth Deviation from Female (%)’ and ‘Male Natural Mortality Deviation from Female (%)’ indicate the percent difference of growth and natural mortality of males compared to females, respectively. The last column ‘Recruitment Sex-Ratio (Female, Male) (%)’ denotes the specified recruitment sex-ratio.

Operating model name	Composition parameterisation	Male growth deviation from female (%)	Male natural mortality deviation from female (%)	Recruitment sex-ratio (female, male) (%)
Experiment 1				
Split	Split	15%	15%	50, 50
Joint	Joint	15%	15	50, 50
Experiment 2				
Grwth0_Mort0	Joint	0	0%	50, 50
Grwth0_Mort15	Joint	0%	15	50, 50
Grwth15_Mort0	Joint	15	0	50, 50
Grwth15_Mort15	Joint	15	15	50, 50
Experiment 3				
Fem40_Mal60	Joint	15	15	40, 60
Fem50_Mal50	Joint	15	15	50, 50
Fem60_Mal40	Joint	15	15	60, 40

TABLE 2 | Summary of stock assessment models utilised in this study. Stock assessment models described in each experiment are applied to all operating models (OMs) outlined in corresponding experiments (Table 1), following a full-factorial experimental design. ‘Composition Parameterisation’ indicates whether sex-specific composition data summed to 1 within a given sex (Split) or jointly across sexes (Joint). The columns ‘Growth and Selectivity’ and ‘Natural Mortality’ represents whether these components were estimated as sex-specific or aggregated. The column ‘Catch Data’ indicates whether sex-specific or aggregated catch was utilised in corresponding stock assessment models, and the column ‘Recruitment Sex-Ratio’ denotes the parameterisation of recruitment sex-ratios. ‘General Description’ describes the general parameterisation of a given stock assessment model. ‘Convergence Rates (%)’ denotes the mean convergence rate of a stock assessment model within a given simulation experiment.

Stock assessment model name	Composition parameterisation	Growth and selectivity	Natural mortality	Catch data	Recruitment sex-ratio	General description	Convergence rates (%)
Experiment 1							
Split	Split	Sex-specific	Sex-specific	Aggregated	Fixed at 50, 50	Multi-sex model with compositions summing to one split between sexes	98.6%
	Joint	Sex-specific	Sex-specific	Aggregated	Fixed at 50, 50	Multi-sex model with compositions summing to one jointly across sexes	98.8%
Experiment 2							
<i>SgSx</i>	Joint	Aggregated	Aggregated	Aggregated	Fixed at 50, 50	Single-sex model	98.4%
	<i>MtSx_AggM_AggC</i>	Joint	Aggregated	Sex-specific	Aggregated	Multi-sex model assuming aggregated natural mortality and utilising aggregated catch	98.7%
<i>MtSx_AggM_SxC</i>	Joint	Sex-specific	Aggregated	Sex-specific	Fixed at 50, 50	Multi-sex model assuming aggregated natural mortality and utilising sex-specific catch	81.8%
	<i>MtSx_SxM_AggC</i>	Joint	Sex-specific	Aggregated	Fixed at 50, 50	Multi-sex model assuming sex-specific natural mortality and utilising aggregated catch	98.2%
<i>MtSx_SxM_SxC</i>	Joint	Sex-specific	Sex-specific	Sex-specific	Fixed at 50, 50	Multi-sex model assuming sex-specific natural mortality and utilising sex-specific catch	96.8%
Experiment 3							
<i>EstSxRat</i>	Joint	Sex-specific	Sex-specific	Aggregated	Estimated in logit space	Multi-sex model estimating initial recruitment sex-ratio	98.1%
<i>FixSxRat</i>	Joint	Sex-specific	Sex-specific	Aggregated	Fixed at 50, 50	Multi-sex model assuming a 50:50 recruitment sex-ratio	97.4%

$$P_{y,s=1}^{Split} = \frac{C_{y,a,s=1}}{\sum_a C_{y,a,s=1}}, \quad P_{y,s=2}^{Split} = \frac{C_{y,a,s=2}}{\sum_a C_{y,a,s=2}} \quad (13)$$

$$\sum_a P_{y,s=1}^{Split} = 1, \quad \sum_a P_{y,s=2}^{Split} = 1$$

and assumed that sex-specific composition data ($X_{y,s}^{Split}$) arose from two multinomial processes:

$$X_{y,s=1}^{Split} \sim \text{Multinomial}\left(S_{y,s=1}^{\text{Samp}}, P_{y,s=1}^{Split}\right), X_{y,s=2}^{Split} \sim \text{Multinomial}\left(S_{y,s=2}^{\text{Samp}}, P_{y,s=2}^{Split}\right) \quad (14)$$

2.3.1.2 | Stock Assessment Models in Experiment 1. Similar to the OM scenarios discussed above, both SAMs in Experiment 1 maintained identical model structure (Section 2.2), differing only in the likelihood structure for sex-specific composition data. The

first SAM was parameterised (*Joint*) following the assumptions of OM ‘Joint’, where proportions for sex-specific compositional data summed to 1 across both ages and sexes, and these proportions arose from a single multinomial process (as in Equation 11). The second SAM (*Split*) followed the assumptions of OM ‘Split’, where proportions for sex-specific compositional data summed to 1 within each sex. Here, the sex ratios for composition data were assumed to arise from a binomial process (as in Equation 12), with subsequent composition data arising from two multinomial processes for each sex (as in Equations 13 and 14). These SAMs were applied to OM scenarios in a full-factorial design to assess whether the distributional assumptions in SAMs and the data generating process OMs influenced model performance. The OM and SAM combination that demonstrated the best model performance (i.e., lowest relative error; see Section 2.4) was utilised for parameterising the likelihoods of sex-specific composition data in subsequent simulation experiments.

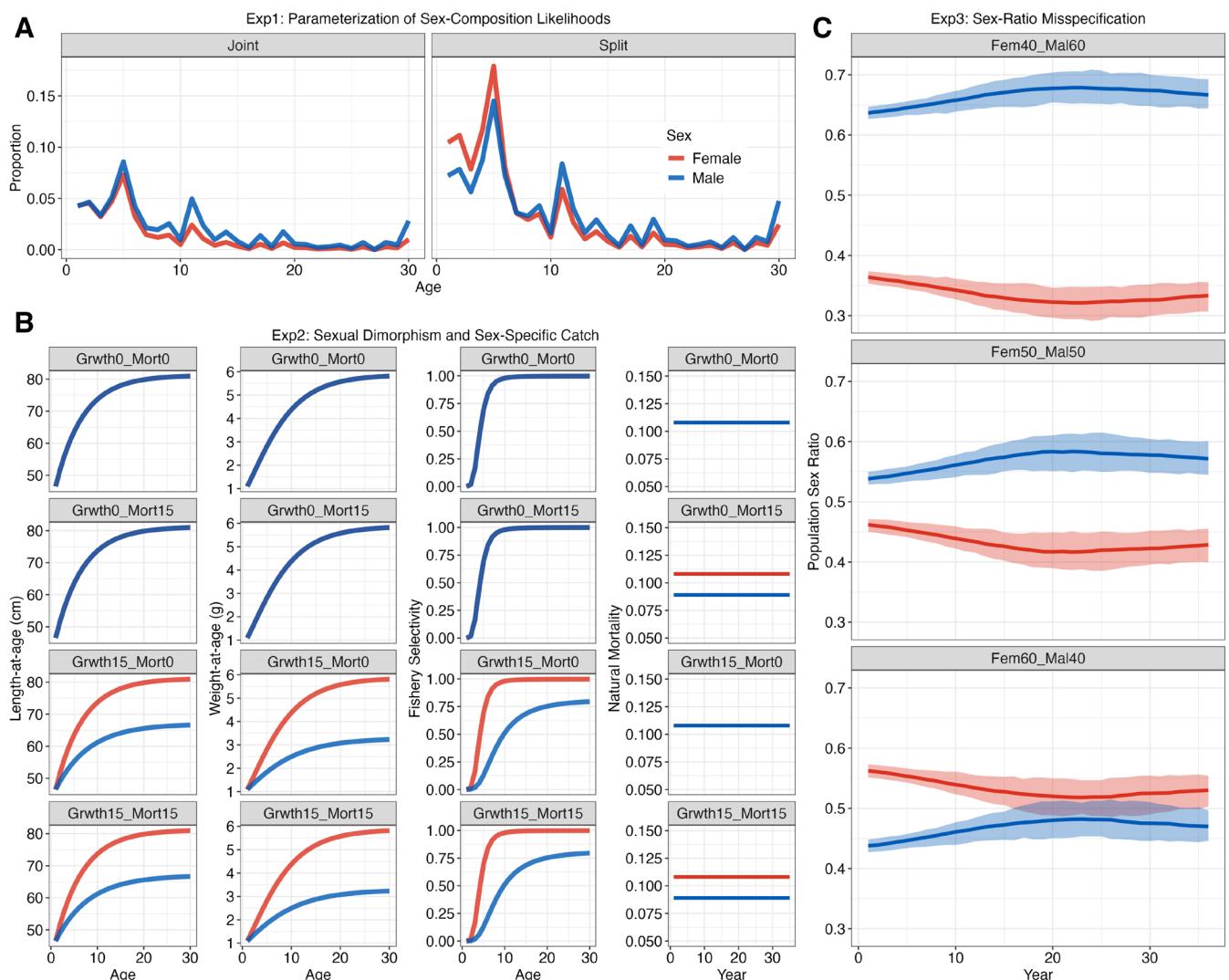


FIGURE 2 | Graphical representation of the three simulation experiments explored in this study, which are also described in Section 2.3. Panel A illustrates the two operating models (OMs) utilised in Experiment 1, which aimed to evaluate the implications of alternative parametrizations of sex-specific composition data (proportions sum to 1 across all ages and sexes for OM ‘Joint’, while proportions sum to 1 across ages within a given sex for OM ‘Split’). Panel B depicts key differences in growth (length and weight), selectivity, and natural mortality among the four OMs utilised in Experiment 2, which assessed the consequences of ignoring sex-structure and the utility of sex-specific catch. Panel C shows changes in population sex-ratios for the three OMs developed in Experiment 3, which evaluated the consequences of recruitment sex-ratio misspecification. Solid lines in Panel C indicate the median across simulation replicates, while shading represents 95% simulation intervals.

2.3.2 | Experiment 2: Sexual Dimorphism and Sex-Specific Catch

To investigate the implications of ignoring sexual dimorphism and the utility of sex-specific catch for improving the estimation of sex-specific processes (e.g., selectivity and natural mortality), we formulated four OM scenarios for Experiment 2. Here, each OM represented variations in sex-specific growth and natural mortality (Figure 2b, Table 1). Five distinct SAMs (Table 2) were then developed, each with differing modelling assumptions regarding sex-structured dynamics and the use of sex-specific catch data.

2.3.2.1 | Operating Models in Experiment 2. OM scenarios formulated in Experiment 2 followed the same model structure described in Section 2.1.1, differing only in the values specified for growth and natural mortality rates (Figure 2b). The first scenario (Grwth0_Mort0) had identical growth patterns and natural mortality rates ($M=0.108$) for both sexes, resulting in identical sex-specific dynamics. In the second scenario (Grwth0_Mort15), growth patterns remained consistent between sexes, while male individuals experienced a 15% reduction in natural mortality (Female $M=0.108$, Male $M=0.0918$) compared to females, leading to a higher proportion of males in the population. The third OM scenario (Grwth15_Mort0) introduced sex-specific differences in length and weight, with males approximately 15% smaller than females (Female $L^\infty = 81.2\text{ cm}$, Male $L^\infty = 66.5\text{ cm}$), while maintaining the same natural mortality rate for both sexes ($M=0.108$). Considering that growth disparities manifest as sex-specific age-based selectivity, males were removed at a lower rate than females, resulting in a population sex-ratio skewed towards males (due to male selectivity not reaching a maximum of one, even for the oldest individuals; Figure 2b). Lastly, the fourth scenario (Grwth15_Mort15) incorporated growth and natural mortality rate differences between sexes. Here, males were also approximately 15% smaller and experienced a 15% reduction in natural mortality compared to females (common in many sexually dimorphic species such as flatfishes and tunas; Luckenbach et al. 2009; Farley et al. 2014), which similarly resulted in a higher proportion of males remaining in the population (Figure 2b).

2.3.2.2 | Stock Assessment Models in Experiment 2. To evaluate the consequences of ignoring sexual dimorphism, we developed a single-sex SAM that only considered age structure (denoted as $SglSx$ to reflect single-sex dynamics). This SAM closely followed the model structure outlined in Section 2.2, with the exception that all operations were aggregated across sexes (i.e., subscript s was removed). Additionally, compositional and catch data were combined across both sexes. Single-sex growth dynamics were estimated by combining simulated age-length pairs from both sexes using Equations (4) and (5), resulting in growth and selectivity misspecification (because selectivity is length-based). Within Experiment 2, SAM $SglSx$ was the only model with mis-specified growth and selectivity. Comparisons of model outputs from SAM $SglSx$ were conducted assuming equal sex ratios (i.e., 50% females and males) for SSB, which is common across assessment models that are solely age-structured.

The remaining SAMs developed for Experiment 2 incorporated both sex- and age-structure, explicitly addressing sexual dimorphism in growth by utilising externally estimated sex-specific growth curves (as in Section 2.2; these SAMs are labeled to begin with $MltSx$ to reflect multi-sex dynamics). However, these SAMs differed depending on whether sex-specific natural mortality rates were estimated and if sex-specific catch data were utilised. Specifically, we developed two SAMs that assumed an aggregated natural mortality rate across sexes while utilising either aggregated catch ($MltSx_AggM_AggC$) or sex-specific catch ($MltSx_AggM_SxC$). Two additional SAMs were developed, assuming sex-specific natural mortality rates and also utilised either aggregated catch ($MltSx_SxM_AggC$) or sex-specific catch ($MltSx_SxM_SxC$).

2.3.3 | Experiment 3: Sex-Ratio Misspecification

In many sex-structured SAMs, the sex ratio at recruitment is typically assumed to be known and equal across sexes. However, various ecological and environmental processes (e.g., temperature, genetic basis of sex-determination) can lead to skewed recruitment sex ratios. Thus, in Experiment 3, we developed three OM scenarios (Figure 2c, Table 1) and two SAMs (Table 2) to evaluate the potential benefits of estimating a recruitment sex ratio and the consequences of its misspecification.

2.3.3.1 | Operating Models in Experiment 3. With the exception of values specified for the recruitment sex-ratio, the three OM scenarios developed in Experiment 3 adhered to the general model structure and sex-structured dynamics described in Section 2.1, where males were approximately 15% smaller in size and had natural mortality rates that were also 15% lower than females. These OMs were: (1) Fem40_Mal60, with a time-invariant recruitment sex-ratio of 40% females and 60% males, (2) Fem50_Mal50, with an equal time-invariant recruitment sex-ratio across sexes and (3) Fem60_Mal40, with a time-invariant recruitment sex-ratio of 60% females and 40% males (Figure 2c, Table 1).

2.3.3.2 | Stock Assessment Models in Experiment 3. The two SAMs evaluated in Experiment 3 maintained identical model structure (Section 2.2), differing only in whether the sex-ratio at recruitment was estimated. To determine the value of estimating the sex-ratio at recruitment, an SAM estimating this ratio ($EstSxRat$) was developed. For SAM $EstSxRat$, an additional time-invariant parameter for the proportion of females at recruitment (χ) was estimated in logit space to ensure that parameter estimates were between 0 and 1. The proportion of male recruits were then defined as $1-\chi$. Additionally, the consequences of misspecifying the recruitment sex-ratio was evaluated by developing an SAM that assumed an equal recruitment sex-ratio ($FixSxRat$). Unlike Experiment 2, none of the SAMs here utilised sex-specific catch data to inform parameter estimation. This was done because sex-specific catch information is not a common data source, and our goal was to develop advice that applies broadly across various fisheries systems. Furthermore, survey compositional data alone are likely able to inform the estimation of the recruitment sex-ratio, when an informative time-series exists.

2.4 | Model Evaluation

During model development, SAMs that produced positive definite Hessian matrices, maximum absolute gradients <0.01 , and parameter standard errors <100 consistently produced reliable results without parameters estimated on bounds. Consequently, we used these criteria to determine model convergence and only evaluated model runs that converged. For each simulation experiment, we computed relative error for quantities of interest to evaluate model bias. Relative error was then summarized by computing the median and the 75% and 95% quantiles across 500 replicates (hereafter, simulation intervals). The quantities of interest assessed were: R_0 , $BMSY$ (the SSB that would achieve maximum sustainable yield), $\frac{SSB_{cur}}{BMSY}$ (the SSB estimated in the terminal year relative to $BMSY$), Female M , Male M , recommended catch advice (catch advice from a sloping harvest control rule; Kvamisdal et al. 2016), female recruitment sex-ratio (only computed for Experiment 3), time series of SSB , time series of depletion (SSB in a given year divided by the SSB in the first year, $(\frac{SSB_y}{SSB_1})$), and the time series of total biomass. Biases in catch advice were further examined to evaluate the potential for loss yield (negative biases) or overharvest (positive biases) associated with each source of model misspecification in sex-structured dynamics. Details on calculations for $BMSY$ and development of catch advice can be found in Data S1.

3 | Results

3.1 | Experiment 1: Parameterisation of Sex-Composition Likelihoods

Despite differences in the data generating process for sex-specific composition data, models *Joint* and *Split* exhibited minimal biases across all metrics, demonstrating exceedingly similar simulation intervals (i.e., the distribution of relative errors in biomass and depletion across replicate simulations), when compared within a given OM scenario (Figure 3, Figures S1 and S2). Given that negligible differences were observed, sex-composition likelihoods were parameterised following the 'Joint' approach in all subsequent simulation experiments, due to considerations of model parsimony (i.e., no additional likelihood component needed).

3.2 | Experiment 2: Sexual Dimorphism and Sex-Specific Catch

Overall, when sex-structured dynamics were absent from the population ('Grwth0_Mort0'), all SAMs explored in Experiment 2 demonstrated comparable model performance, with minimal biases and negligible differences in simulation intervals (Figures 4 and 5, Figures S3 and S4). However, biases in several metrics emerged when sex-structured dynamics were present within the population but were ignored within SAMs. When only natural mortality rates varied among sexes ('Grwth0_Mort15'), SAMs that assumed an aggregated natural mortality rate developed some biases. Specifically, these SAMs were *SglSx*, *MltSx_AggM_AggC* and *MltSx_AggM_SxC*, all of which displayed a consistent positive bias in SSB (~15% on average;

Figure 4), negative biases in $\frac{SSB_{cur}}{BMSY}$ (~10%), and negative biases in catch advice, resulting in potential lost yield (~16% on average; Table 3). Interestingly, despite moderate biases in SSB , total biomass and depletion estimates only exhibited small biases (~5% on average; Figures S3 and S4). Comparisons of aggregated natural mortality rate estimates for these SAMs revealed negative biases of approximately 10% for females and a positive bias of similar magnitude for males (Figure 5).

When only growth and selectivity differed between sexes ('Grwth15_Mort0'), the single-sex SAM (*SglSx*) was the only approach that demonstrated biases. In particular, *SglSx* initially exhibited negative biases in SSB (~20%), which trended towards unbiased towards the latter half of the time-series (Figure 4). While total biomass estimates (Figure S3) generally demonstrated minimal biases, notable positive biases in depletion (~25%, Figure S4), $\frac{SSB_{cur}}{BMSY}$ (~30%), catch advice (~70%, indicating potential overharvest) and negative biases (~20%) in $BMSY$ were detected for *SglSx* (Figure 5, Table 3). These large biases likely resulted from the misspecification of growth and selectivity processes, which was estimated approximately as the average of the two sexes (Figure S5). Overall, all sex-structured SAMs explored under scenario 'Grwth15_Mort0' displayed negligible biases, where those utilising sex-specific catch information (*MltSx_AggM_SxC* and *MltSx_SxM_SxC*; Figure 4) exhibited considerably narrower simulation intervals (i.e., reduced uncertainty).

In the OM scenario where growth, selectivity, and natural mortality all varied between sexes ('Grwth15_Mort15'), *SglSx* exhibited similar bias patterns to those observed in the scenario where only growth and selectivity differed ('Grwth15_Mort0'). For instance, initial biases in SSB were also negative, although they transitioned towards positive biases towards the latter half of the time series (Figure 4). Additionally, *SglSx* similarly demonstrated minor biases in total biomass estimates (<5%; Figure S3) but large positive biases in depletion estimates (~25%, Figure S4) and catch advice (~90%, with a potential for overharvest; Table 3). For sex-structured SAMs that estimated aggregated natural mortality rates (*MltSx_AggM_AggC*, and *MltSx_AggM_SxC*), negative biases in both SSB and total biomass were observed (Figure 4, Figure S3), which were accompanied by positive biases in depletion (~25%, Figure S4). Moreover, these SAMs also demonstrated similar negative biases in various quantities of interest. Notably, R_0 , $\frac{SSB_{cur}}{BMSY}$, and catch advice (~83%, with potential yield loss; Table 3) were both frequently underestimated. Likewise, estimated aggregated natural mortality values were consistently lower than the true values for both females and males. In line with the scenario where only growth and selectivity differed between sexes, SAMs utilising sex-specific catch information (*MltSx_AggM_SxC* and *MltSx_SxM_SxC*) exhibited narrowed simulation intervals (Figure 4). Although reduced uncertainty was observed, assuming aggregated natural mortality rates while using sex-specific catch information led to large biases (~|25%). Overall, when sex-specific processes were present in growth, selectivity, and natural mortality, SAMs that correctly accounted for these processes were unbiased across the timeseries, independent of whether catch data were aggregated across sexes.

3.3 | Experiment 3: Sex-Ratio Misspecification

Sex-ratio at recruitment was consistently estimated with high accuracy and precision in *EstSxRat*. Furthermore, *EstSxRat* displayed minimal biases across all metrics of interest, regardless of whether this ratio was skewed towards males or females (Figure 6). By contrast, misspecifying the recruitment sex-ratio in *FixSxRat* resulted in substantial biases across all metrics assessed. Counterintuitively, incorrectly assuming an equal recruitment sex-ratio when the population was skewed towards males (i.e., SAM assumes females are more abundant at recruitment compared to the OM; ‘Fem40_Mal60’) led to negative biases in both SSB and total biomass (~30%; Figure 6, Figure S6), and in quantities describing population scale (R_0 , Female M , and Male M). Resulting catch advice from *FixSxRat* demonstrated large negative biases (~80%), suggesting the potential for losses in yield (Table 3). Depletion, however, demonstrated a dome-shaped relationship, with initial positive biases, followed by negative biases (~20% across the time series; Figure S7). Conversely, assuming an equal recruitment sex-ratio when the population was skewed towards females (i.e., SAM assumes females are less abundant at recruitment;

‘Fem60_Mal40’) resulted in relatively large positive biases in SSB, total biomass, and the same parameters related to population scale (~50%; Figure 6, Figure S6). Likewise, catch advice demonstrated large positive biases (~94%), which could potentially result in overharvest of the population (Table 3). Under this scenario, estimates of depletion exhibited a concave up relationship, with negative biases initially observed, which then trended in the positive direction (~15% across the time series; Figure S7).

4 | Discussion

Sexually dimorphic demographic processes are found in many fish populations of commercial, cultural, and subsistence importance, with sex-and age-structured models commonly employed to assess these populations (e.g., ~70% of groundfish assessments in the Pacific Fishery Management Council and ~50% in the North Pacific Fishery Management Council, (NPFMC 2024a, 2024b; PFMC 2024)). While these models are commonly applied, this study provides a unique perspective on the impacts of multiple misspecifications in sex-structured

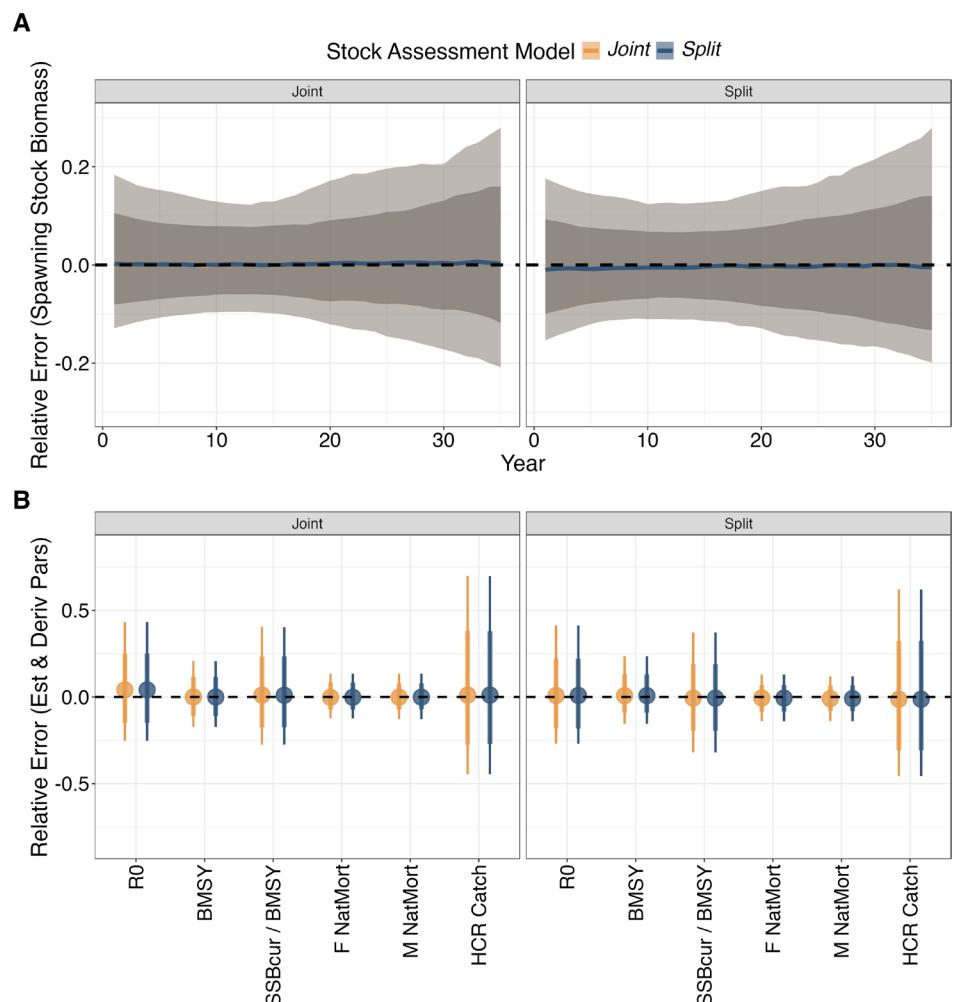


FIGURE 3 | Relative error in quantities of interest for Experiment 1. In both panels, columns denote operating models, colors represent stock assessment models, and the black dotted horizontal line indicates 0% relative error. Panel A shows the relative error in spawning stock biomass, where solid lines depict the median relative error and shading are the 75% and 95% simulation intervals. Note that the appearance of grey in Panel A indicates near complete overlap in relative error between stock assessment models. Panel B illustrates the relative error in estimated and derived quantities, with median relative error depicted as points and 75% and 95% simulation intervals represented as line ranges.

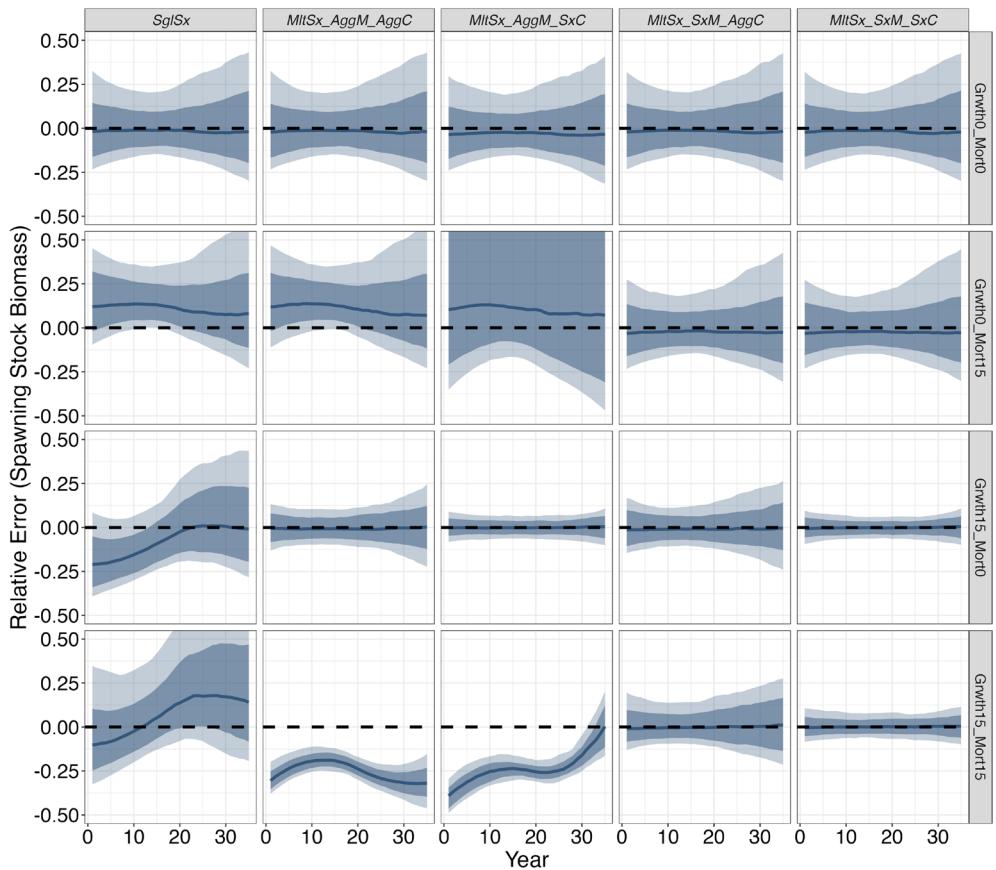


FIGURE 4 | Relative error in spawning stock biomass for Experiment 2. Row panels denote operating models (see Table 1), while column panels are stock assessment models (see Table 2). The black dotted horizontal line represents 0% relative error. Blue solid lines are the median relative error and shaded areas correspond to the 75% and 95% simulation intervals.

models, underscoring that effective management of sexually dimorphic species requires robust and biologically valid assumptions in sex-structured SAMs. In general, effectively managing species that exhibit sexual dimorphism requires careful monitoring and understanding of sex-specific dynamics to ensure the implementation of appropriate management strategies (Hanson et al. 2008). Suitably parameterised sex-structured SAMs can facilitate accurate monitoring of population sex ratios, which can be crucial for hermaphroditic species and male-only fisheries (e.g., many crustacean populations), where sperm limitation and the maintenance of optimal sex ratios can influence social structure, breeding dynamics, and resultant reproductive output (Brooks et al. 2008). In fisheries with minimum size limits or spatial closures, the use of sex-structured SAMs can evaluate whether these strategies result in disproportionate harvest impacts on one sex, as influenced by sexual growth dimorphism or spatial sex segregation (Alonzo and Mangel 2004). Moreover, in the face of climate change, sex-structured SAMs will be imperative for developing novel management strategies that effectively address climate-driven changes in recruitment sex ratios (i.e., temperature sex-determination; Conrad and Kindsvater 2024). Therefore, the efficacy of sustainable management practices for sexually dimorphic species will depend upon adopting sex-structured SAMs with reasonable biological assumptions, complemented by continued research and investments in sampling programs that collect sex-specific information.

4.1 | Interpretation of Bias Trends Across Experiments

Overall, the choice of parameterisation for sex-composition likelihoods had minimal impacts on model performance in Experiment 1, when assuming a multinomial sampling process (Figure 3). In fact, this occurred because both approaches ultimately result in the same distribution (Cheng et al. 2025). Cheng et al. (2025) also demonstrated that when sampling composition data follow a Dirichlet-Multinomial distribution, the ‘Joint’ parameterisation is able to accommodate greater sampling variability. In light of these findings, we generally recommend the ‘Joint’ parameterisation for sex-composition likelihoods due to its relative simplicity in implementation and its ability to accommodate overdispersion and covariances across sexes. However, the ‘Split’ approach also has the potential to occur in some sampling schemes. For instance, if individuals can be visually separated by sex, they might first be separated by sex and then randomly sampled within each sex. Therefore, practitioners should also carefully consider how composition data arise from existing sampling schemes employed in their systems.

For species exhibiting sexual dimorphism, modelling all aspects of sex-specific variations (e.g., growth, selectivity and natural mortality) was generally necessary to achieve unbiased model results and management advice (Experiment 2). Consistent

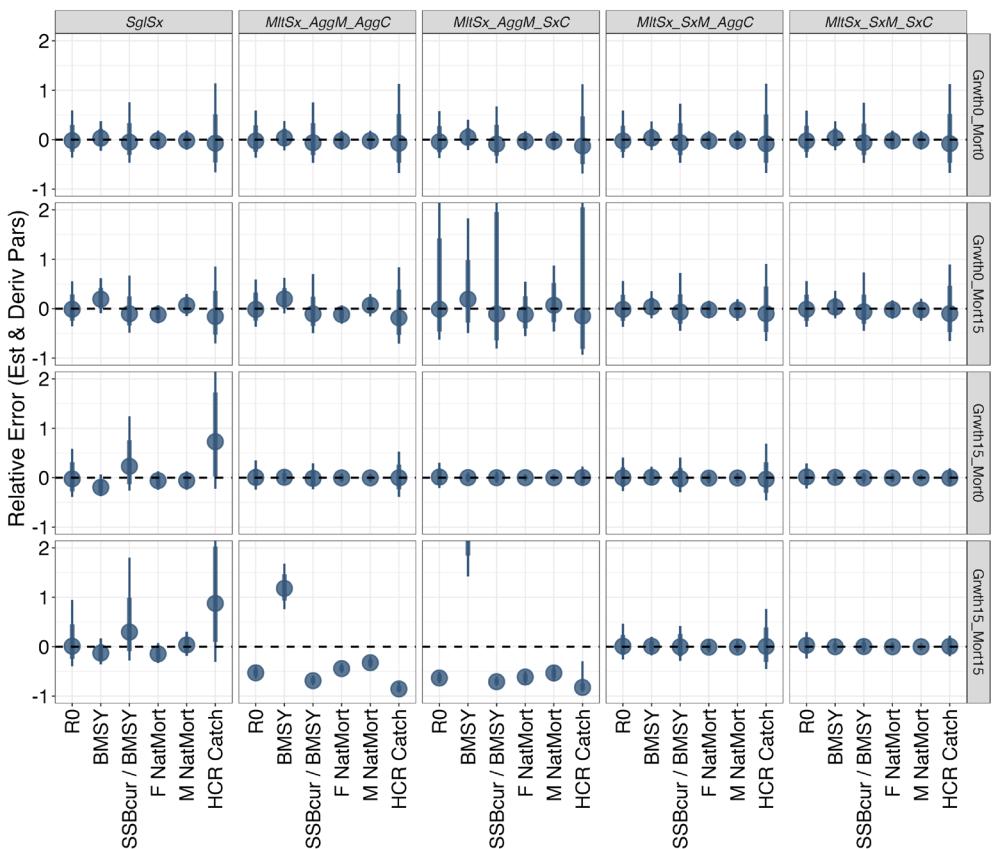


FIGURE 5 | Relative error in estimated and derived quantities for Experiment 2. Row panels are operating models, while column panels are stock assessment models. The black horizontal dotted line represents 0% relative error. Blue points represent the median relative error and line ranges correspond to the 75% and 95% simulation intervals.

TABLE 3 | Relative biases in recommended catch advice (HCR Catch) derived from a sloping harvest control (HCR Catch) across the three experiments evaluated in this study. Results presented here focus on stock assessment models with severe model misspecifications (e.g., ignoring key sex-specific dynamics) and their corresponding operating models. Negative biases in HCR Catch reflect potential yield loss, while positive biases suggest a risk of overharvest.

Operating model name	Stock assessment model name	Bias in HCR catch (%)	Type of misspecification
Experiment 1			
Joint	Split	1.10	Mis-specified parameterisation of composition likelihood
Split	Joint	-1.13	Mis-specified parameterisation of composition likelihood
Experiment 2			
Grwth0_Mort15	SglSx	-16.00	Ignored sex-specific natural mortality
Grwth0_Mort15	MltSx_AggM_AggC	-18.40%	Ignored sex-specific natural mortality
Grwth0_Mort15	MltSx_AggM_SxC	-15.00	Ignored sex-specific natural mortality
Grwth15_Mort0	SglSx	72.90%	Ignored sex-specific growth
Grwth15_Mort15	SglSx	87.77%	Ignored sex-specific growth and natural mortality
Grwth15_Mort15	MltSx_AggM_AggC	-85.60	Ignored sex-specific natural mortality
Grwth15_Mort15	MltSx_AggM_SxC	-82.60%	Ignored sex-specific natural mortality
Experiment 3			
Fem40_Mal60	FixSR	-81.30%	Mis-specified initial recruitment sex-ratio
Fem60_Mal40	FixSR	93.90%	Mis-specified initial recruitment sex-ratio

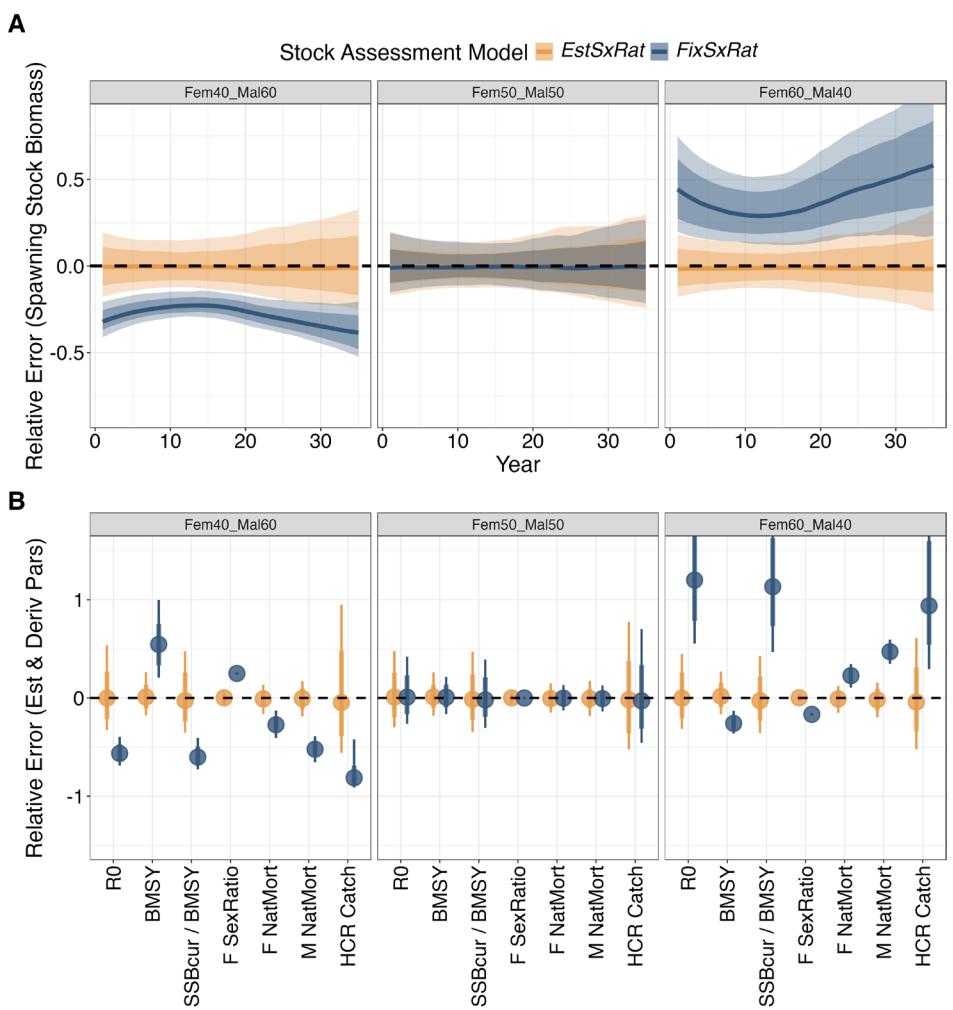


FIGURE 6 | Relative error in quantities of interest assessed for Experiment 3. For both panels, columns denote operating models, colors represent stock assessment models, and the black horizontal line indicates 0% relative error. Panel A shows the relative error in spawning stock biomass, where solid lines are the median relative error and shaded areas represent the 75% and 95% simulation intervals. Panel B illustrates the relative error in estimated and derived quantities. Here, points depict the median relative error and line ranges correspond to the 75% and 95% simulation intervals.

with previous simulation studies, we found that SAMs assuming single-sex dynamics demonstrated biased model estimates (Wang et al. 2005; Su et al. 2011). Surprisingly, total biomass estimates for these SAMs remained minimally biased across all OM scenarios examined (Figure S3). However, we caution against basing management advice on total biomass, as it neglects the key role of females in governing reproductive dynamics (Figure 4, Figure S4).

Even when sex-specific dynamics were partly addressed by accounting for growth and selectivity differences, sex-structured SAMs assuming aggregated natural mortality rates demonstrated large negative biases in population scale (Figures 4 and 5). These results uniquely underscore that ignoring some elements of sex-specific dynamics (i.e., natural mortality) can be as detrimental as ignoring them entirely. We hypothesize that these large negative biases stem from composition data indicating that population sex ratios should reflect fewer females (Figure 1). However, by estimating an aggregated natural mortality rate, female natural mortality will be underestimated relative to males (in the context of this study), given that the estimate should reflect an average of both rates. This underestimation results in an overestimation of female abundance in

the modeled population, leading to conflicting signals with the available composition data and poor fits to catch data. As such, SAMs assuming aggregated natural mortality rates must underestimate the overall population scale (i.e., reduce the number of individuals in the modeled population) to reconcile these inconsistencies (Punt et al. 2021).

The utility of sex-specific catch information was evident only when growth differences were present, greatly reducing model uncertainty (Figures 4 and 5). However, improved model performance and management advice required a correctly specified model. Incorrectly assuming aggregated natural mortality rates decreased model stability and performance by limiting flexibility to describe sex-specific catch patterns (evidenced by lower convergence rates; Table 2). Given the assumption of sex-invariant fishing mortality rates in this study, SAMs relied primarily on selectivity to represent sex-specific removals, resulting in fewer parameters to describe sex-specific removals and exacerbating parameter confounding. Therefore, ensuring sufficient model flexibility to accommodate sex-specific catch differences and a well-specified model aligned with the species life-history is imperative to fully leverage the potential of these data.

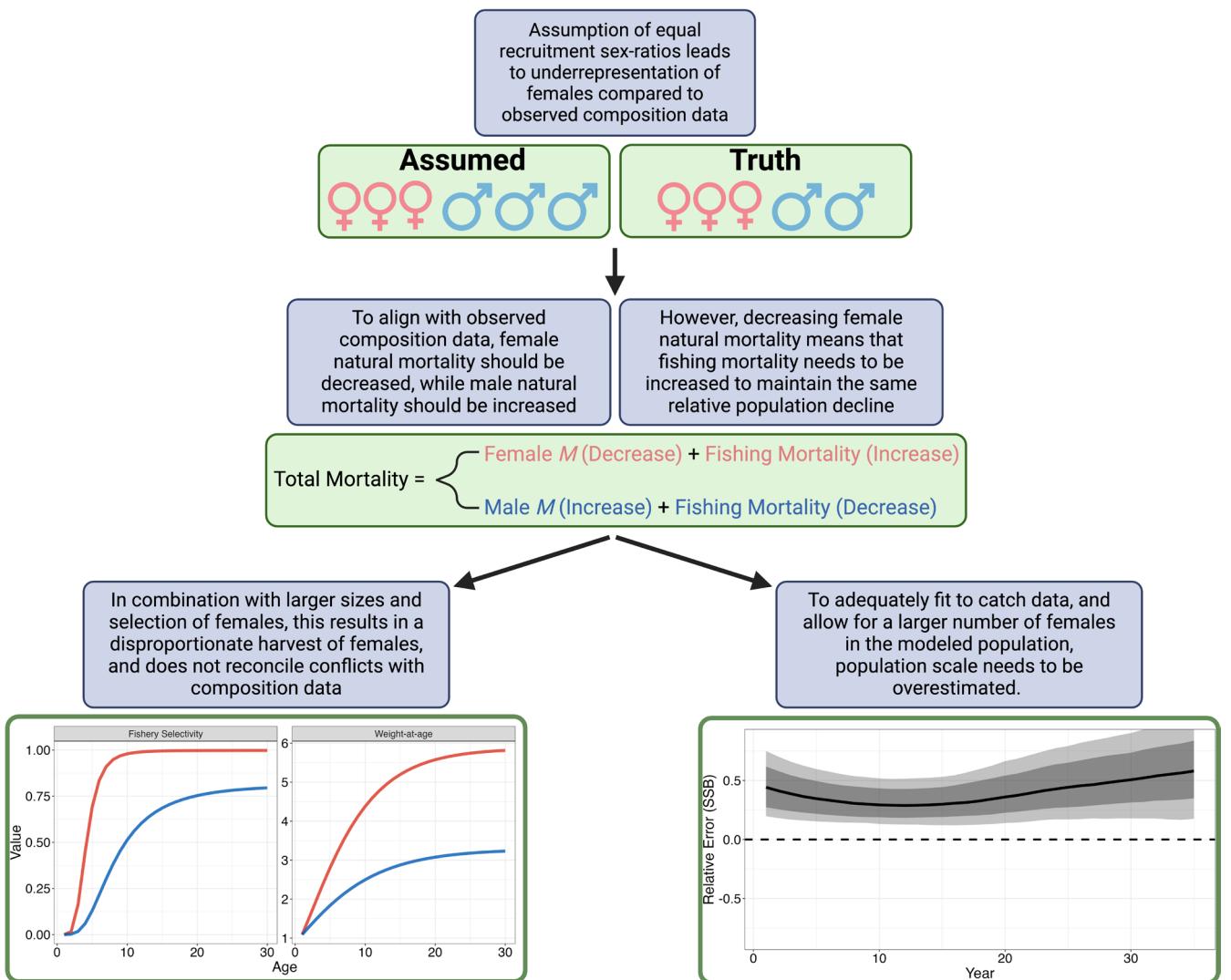


FIGURE 7 | A conceptual diagram illustrating how biases in population scale and spawning stock biomass (SSB) arise when operating models (OMs) reflect a recruitment sex ratio of 60% females and 40% males (OM: Fem60_Mal40), but are incorrectly assumed to be equal and known (SAM: FixSxRat).

While assuming known and equal recruitment sex ratios is common in many sex-structured SAMs, findings from Experiment 3 underscore the value of estimating recruitment sex ratios and understanding species life history to ensure reasonable assumptions in population modelling. Notably, we detected significant biases in biomass estimates and management advice when recruitment sex ratios were incorrectly assumed to be equal. To illustrate how these biases may have developed, we consider a SAM assuming an equal recruitment sex ratio in a scenario where the true ratio is skewed towards females ('Fem60_Mal40'; Figure 7). In this case, incorrectly assuming an equal recruitment sex ratio results in fewer females being present in the model than are observed in compositional data. Thus, several parameter estimates must be adjusted within the SAM to address these discrepancies. Firstly, female natural mortality estimates must be reduced at a greater relative rate compared to males (Figures 6 and 7), which in turn requires a higher total fishing mortality rate to achieve the same relative population decline for females. However, combining higher fishing mortality rates with sex-specific growth and selectivity differences (females are larger

and more heavily selected) disproportionately removes females from the population, leading to poor fits to catch data. Considering the small, assumed variances associated with catch data, the SAM has to accommodate these factors by overestimating parameters related to population scale (i.e., increase the number of individuals in the modeled population), leading to positive biases in biomass estimates. Conversely, if assuming an equal recruitment sex ratio results in more males being present in the model, a similar process occurs, albeit in the opposite direction. External investigations suggest that these biases were likely driven by growth disparities rather than natural mortality, given that population scale was adequately characterised when growth differences were absent (Figure S9).

Although not examined in this study, the impact of misspecifying the recruitment sex-ratio may be further compounded by the modeled age at recruitment. In particular, many fishery SAMs begin with the youngest age in the population that can be reliably observed in fishery or survey catches. For example, the youngest age modeled in the New Zealand Mid-East Coast

orange roughy (*Hoplostethus atlanticus*) assessment is age 10 (Dunn et al. 2022). In these cases, if differences in natural mortality in the intermediate ages between the age-at-hatching and modeled recruitment ages are present, biases from incorrectly assuming an equal recruitment sex-ratio can potentially be more pronounced. Therefore, results from Experiment 3 question the routine assumption of a known and equal recruitment sex ratio within sex-structured SAMs, suggesting that estimating a time-invariant sex ratio at recruitment could be beneficial when informative sex-specific composition data are available.

4.2 | Caveats and Future Work

Various aspects of this simulation study were limited due to computational constraints and to maintain focus and interpretability of these results. To maintain focus, only one life history was explored in these simulations. Moreover, several values (e.g., maturity-at-age, steepness) were set at their true values within SAMs, which likely resulted in overly optimistic model performance. Additionally, although growth was estimated outside of the assessment model, there is potential for these dynamics to interact with other components of the stock assessment model (e.g., natural mortality; Lee et al. 2024). Therefore, future research evaluating the potential implications of model misspecification, while estimating sex-specific growth within a stock assessment model, would be a fruitful endeavor. Furthermore, several components of OMs likely facilitated the estimation of sex-specific natural mortality in this study, a parameter typically challenging to estimate. For instance, the specification of time-invariant asymptotic fishery and survey selectivity, the presence of age-composition data at the beginning of the fishery, contrast in the fishing mortality pattern, and good data quality likely aided in its estimation (Lee et al. 2011; Maunder and Wong 2011; Punt et al. 2021). While these factors are not necessarily common across many fisheries, the goal of these analyses was not to determine the estimability of sex-specific natural mortality, but to illustrate the consequences of misspecification. Similarly, we utilised estimates of recommended catch advice from a sloping harvest control rule to illustrate the potential for losses in yield or overharvest when sex-specific dynamics are mis-specified (e.g., Table 3). However, future research using closed-loop management strategy evaluations may be better suited to fully quantify the effect of such misspecifications on harvest recommendations and population dynamics.

The use of a multinomial distribution to simulate compositional data also likely limited some of our findings from Experiment 1. Specifically, the correlation structure of a multinomial distribution does not depend on the ordering of categories and can only accommodate negative correlations (Francis 2014), which is generally not reflective of real-world sampling variation. Therefore, future studies should evaluate the implications of parameterising sex-composition likelihoods using a ‘Joint’ or ‘Split’ approach, while employing models capable of accommodating alternative correlation structures (e.g., logistic-normal). Furthermore, we recognise that sex-specific catch was simulated with low uncertainty in Experiment 2, achieving a level of precision generally unrealistic in real-world sampling programs. However, the aim was to depict a best-case scenario and illustrate the utility of these data, while maintaining comparability

with aggregated catch data. Findings from Experiment 3, which assumed a time-invariant recruitment sex-ratio in both OMs and SAMs, could also be expanded upon in several ways. For instance, certain species may exhibit environmentally dependent sex-determination (Ospina-Álvarez and Piferrer 2008; Luckenbach et al. 2009), which could potentially lead to non-stationarity and the potential for temporal variation in recruitment sex ratios, underscoring an additional layer of biological complexity that merits further exploration.

Across simulation scenarios, we assumed selectivity was a length-based process, with sex-specific patterns in selectivity arising from growth differences. Although this is common in many fishery stock assessments, sex-specific selectivity can also occur due to differences in sex-specific distributions, which may be better represented with age-based selectivity or independent fishing mortality rates for each sex. However, the utility of these approaches should be assessed using a spatially explicit simulation framework capable of simulating data at a high resolution (e.g., Goethel et al. 2024), which was outside the scope of this study. Thus, we encourage future investigations to evaluate model performance by comparing spatially explicit models and single-area models incorporating age-based sex-specific selectivity or fishing mortality rates to account for heterogeneity in sex and spatial dimensions.

Evaluating methods to address sexual dimorphism when sex-composition data are historically unavailable or absent for a specific fishery also remains an important area of research. Theoretically, if sexual dimorphism results from differences in size or spatial distributions, predictive models could be developed to establish relationships between sexes and relevant variables (e.g., length, space, depth), enabling the assignment of sexes to historical unsexed composition data. Additionally, in cases where sex-composition data are only available for specific fishery fleets, it may be reasonable to assume that the relative difference in selectivity between sexes is similar to that observed in another fishery with sex-composition data (Maunder 2013). If new, sex-specific data are collected, models may be fitted to sex-specific data for the period they are available, but sex-aggregated data when they are not available. However, the relative merits of these methods will require further evaluation, and their performance likely depends on the stationarity of the relationships over time.

4.3 | General Recommendations

Despite the widespread occurrence of sex-specific dynamics in numerous fisheries (Wilderbuer et al. 2005; Gislason et al. 2017), there remains a lack of comprehensive guidance on their integration into SAMs utilised in fisheries. Herein, we provide general recommendations for integrating sex-structured dynamics into SAMs utilised in fisheries. Our results indicate the need to explore the estimation of all aspects of sex-structured dynamics (growth, selectivity, natural mortality, and recruitment sex-ratio), given the potential for significant biases to manifest if ignored. However, simplifications and assumptions will often be necessary, depending on the quality and quantity of data available. In particular, while limited sex-specific composition data have sometimes precluded

the adoption of sex-structured SAMs in some fisheries (Terceiro 2024), we suggest that sex-structured SAMs can still be formulated with the appropriate assumptions. For instance, growth, natural mortality, recruitment sex ratio, and selectivity values from similar species and/or fisheries can be utilised as fixed values or priors to inform the estimation processes. Priors for sex-specific natural mortality rates and recruitment sex ratio may also be formulated utilising life-history information (Thorson et al. 2017; Maunder et al. 2023). Targeted studies that develop relationships between sex and relevant variables (length, space, depth) can potentially be utilised to convert unsexed data into sex-specific composition data to support sex-structured SAMs, depending on the life history of the species (Morson et al. 2015). Although additional modelling assumptions are required, a sex-structured SAM enables an explicit evaluation of these assumptions (Maunder 2013). Moreover, we also recommend conducting exploratory analyses to aid in prioritising the incorporation of particular sex-specific processes. For example, catch curves and comparing sex ratio data can aid in determining the magnitude of sex-specific mortality processes (Hoenig and Hewitt 2005; Su et al. 2013; Cerviño 2014), while comparing sex-specific composition data can indicate the need for modelling sex-specific selectivity. The development of robust management strategies and stock assessments critically depends on sustained investments in sampling programmes, which facilitate enhanced understanding of species biology and life-history characteristics. Expanding the collection of sex-specific data is strongly recommended to support these efforts.

As a unifying theme to these general recommendations for sexually dimorphic species, we encourage: (1) continued and sustained collection of sex-specific data, (2) conducting external analyses to determine the relative importance of modelling certain sex-specific processes (e.g., data exploration of sex-specific data) and (3) utilising a priori considerations and ecological knowledge of species life-history to ensure plausible estimates from SAMs (Duplisea 2018). Ultimately, explicitly considering all aspects of sex-structured dynamics is required to achieve accurate population estimates. However, simplifying assumptions in population models will always be necessary, requiring thoughtful consideration and justification of population processes that can be appropriately simplified.

5 | Conclusions

We showed that sex-structured SAMs can provide improved management advice for species that exhibit sexually dimorphic traits, which are common across many fish populations. Our study represents one of the few that comprehensively evaluated the consequences of multiple misspecifications in sex-structured SAMs, offering pragmatic recommendations and revealing important considerations for population modelling, fisheries management, and data collection protocols when sex-structured dynamics are present. Collectively, results from this study suggest the critical need to carefully consider sexual dimorphism in growth, selectivity, natural mortality, and the recruitment sex ratio, coupled with simplifying modelling assumptions when appropriate, to mitigate biases in population model estimates and ensure the provision of robust management advice.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

All analyses and simulated data associated with this study can be found at [10.5281/zenodo.14851219](#).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.