UNIFYING PARAMETERIZATIONS BETWEEN AGE-STRUCTURED AND SURPLUS PRODUCTION MODELS: AN APPLICATION TO ATLANTIC WHITE MARLIN (*KAJIKIA ALBIDA*) WITH SIMULATION TESTING

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SUMMARY

*Integrated age-structured models (Stock Synthesis), and surplus production models (JABBA) are increasingly run in parallel during stock assessments of tuna and tuna-like species. Yet, the choice of parameterization for the two different model types may not always be chosen to be compatible. Here, we use age-structured simulation testing to evaluate an approach to translate life history parameters into the intrinsic rate of population increase r and the shape parameter of the surplus production curve. We apply this approach using the stock parameters for Atlantic white marlin (*Kajikia albida) *and approximate the functional form of a 16-parameter yield curve for an age- and sex-structured stock to approximate by the 3-parameter Pella surplus production curve. Our simulation results show that a correctly specified JABBA model enables fairly accurate estimation of the true stock status quantities SB/SB$_{MSY}$ and F/F$_{MSY}$ with satisfactory confidence interval coverage, suggesting that here presented surplus production model parameterization provides, in principle, a parsimonious framework for billfish assessments with comparable population dynamics.*

RÉSUMÉ

*Les modèles intégrés structurés par âge (Stock Synthèse) et les modèles de production excédentaire (JABBA) sont de plus en plus utilisés en parallèle lors des évaluations des stocks de thonidés et d'espèces apparentées. Cependant, le choix du paramétrage pour les deux types différents de modèles pourrait ne pas toujours être réalisé de façon à être compatible. Ici, nous utilisons des tests de simulation structurés par âge pour évaluer une approche permettant de traduire les paramètres du cycle vital en taux intrinsèque d'augmentation r de la population et en paramètre de forme de la courbe de production excédentaire. Nous appliquons cette approche en utilisant les paramètres de stock pour le makaire blanc de l'Atlantique (*Kajikia albida*) et la forme fonctionnelle d'une courbe de production à 16 paramètres pour un stock structuré par âge et par sexe afin de la rapprocher de la courbe de production excédentaire Pella à 3 paramètres. Nos résultats de simulation montrent qu'un modèle JABBA correctement spécifié permet une estimation assez précise des quantités réelles de l'état des stocks SB/SB$_{PME}$ et F/F$_{PME}$ avec un intervalle de confiance satisfaisant, ce qui suggère que le paramétrage du modèle de production excédentaire présenté ici fournit, en principe, un cadre moins strict pour les évaluations des istiophoridés avec une dynamique de population comparable.*

RESUMEN

*Los modelos integrados estructurados por edad (Stock Synthesis), y los modelos de producción excedente (JABBA) se ejecutan cada vez más en paralelo durante las evaluaciones de stock de túnidos y especies afines. Sin embargo, la elección de la parametrización para los dos tipos de modelos diferentes no siempre se puede realizar de tal modo que sea compatible. Aquí, usamos pruebas de simulación estructuradas por edad para evaluar un enfoque que traduzca los parámetros del ciclo vital en la tasa intrínseca de crecimiento de la población r y el parámetro de forma de la curva de producción excedente. Aplicamos este enfoque utilizando los parámetros de stock para la aguja blanca del Atlántico (*Kajikia albida*) y la forma funcional de una curva de rendimiento de 16 parámetros para un stock estructurado por edad y sexo para*

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aproximarla a la curva de producción excedente de Pella de 3 parámetros. Nuestros resultados de la simulación muestran que un modelo JABBA correctamente especificado permite una estimación bastante precisa de las cantidades reales del estado del stock SB/SB_{RMS} y F/F_{RMS} con una cobertura satisfactoria del intervalo de confianza, lo que sugiere que la parametrización del modelo de producción excedente aquí presentado proporciona, en principio, un marco menos estricto para las evaluaciones de marlines con una dinámica de población comparable.

1. Introduction

Surplus Production Models (SPMs) are one of the least data demanding and parsimonious population dynamic models that can be used to provide estimates of stock status, and fisheries reference points (FRPs) such as the Maximum Sustainable Yield (MSY). Despite the increased application of age-structured models (ASMs) within tuna Regional Management Fisheries Organizations (tRFMOs), SPMs have remained an integral part of the assessment toolbox for large pelagic tuna and billfish (Brodziak and Ishimura, 2012; Chang et al., 2014; Punt et al., 2015). In particular, billfish assessments are commonly conducted with SPMs (Chang et al., 2014; Punt et al., 2015), due to paucity of stock-specific biological information and reliable size structure data.

SPMs are age- and size aggregated models that approximate changes in biomass as a function of the biomass of the preceding year, the surplus production in biomass and the removal by the fishery in the form of catch. Somatic growth, reproduction, natural mortality and associated density-dependent processes are inseparably captured in the estimated surplus production function that is governed by three parameters: (1) the intrinsic rate of population increase r (2) the shape parameter m and (3) the unfished equilibrium biomass K. In contrast to SPMs, age-structured models (ASMs) allow separating between spawning-biomass (SB) and exploitable biomass (EB), where SB is the biomass fraction of mature fish (or females) in the population, and EB is the exploitable (vulnerable) biomass fraction of the total biomass that is selected by the fishery. ASMs therefore explicitly account for the lag-effect of the biomass response of EB, which is related to the observed abundance index, as well as the differential impact of selectivity by multiple fisheries. This comes with the trade-off of approximately ten (and often more) stock parameters to model the population dynamics. In particular, the form and steepness (h) of the SRR and estimates of M are highly uncertain. Because it is rarely possible to reliably estimate h and M from the data, scientists often fix values for one or both parameters in age-structured stock assessments (Lee et al., 2012; Mangel et al., 2013) , thereby making strong presumptions about the stock's resilience and stock status reference points.

The number of ASM-based assessments of tuna and tuna-like species has been continuous increasing over the last three decades (Thorson et al., 2019), with stock synthesis having been playing a leading role in this development in recent years. However, due to their low data requirements, SPMs persist as a routine assessment tool within their traditional realm of large pelagic tuna, billfish and shark assessments (Carvalho et al., 2014; Punt et al., 2015; Winker et al., 2018a). As a result, ASMs, such as stock synthesis (ss3) (Methot and Wetzel, 2013) , and SPMs, such as JABBA (Winker et al., 2018a) are increasingly run in parallel during stock assessments conducted by tuna Regional Management Organizations .

For SPMs, structural and biological uncertainty is typical represented in the form of alternative values of r and the shape m of the production function, where Schaefer and Fox formulations are probably the most common choices. However, the choice SPM parameterization may not necessarily be compatible with the input parameters considered in the ASM assessment runs, where it is common practice to formulate alternative scenarios by varying h and M over a range of plausible values. Selecting non-compatible sets of parameters for the two different model types can violate the validity model comparison and consequently inference about the stock status.

Here, we apply an approach that aims to unify the model parameterization between ASMs and SPMs. To do this, we first revisit the functional links between the ASEM and Pella-Tomlinson SPM, which we then apply to translate input parameters of ASMs into the key SPM parameters r and the shape parameter m. We implement this approach using the age- and sex-structured stock parameters for Atlantic white marlin (*Kajikia albida*) with the specific objective to develop surplus production functions formulations as a function of r and the shape m that matches the implications of age-structured parameter scenarios put forward for the 2019 ICCAT white marlin assessment.

2. Material and Methods

2.1. Deriving r priors and shape for surplus production from stock parameters

The following concepts build on previous work by Winker et al. (Winker et al., 2018a, 2018b, 2017). Central to their idea of linking age-structured stock parameters and the surplus production function is the application of age-structured spawning biomass- and yield-per-recruit models with integrated stock-recruitment relationship (SRR), which we subsequently refer to as age-structured equilibrium model (ASEM). This type of model is widely used for ASMs to derive MSY-based fisheries reference points (FRPs) from estimated stock parameters by searching iteratively for the fishing mortality that produces *MSY*, F_{MSY}, from the corresponding biomass B_{MSY} at MSY (Punt et al., 2013). Typical ASEM inputs are the stock parameters describing length-at-age (L_a), weight-at-age (w_a), maturity-at-age (ψ_a) and selectivity-at-age (s_a), natural mortality M and the steepness parameter h of the of the assumed Beverton and Holt SSR (Punt et al., 2013).

To illustrate the link between the generalized three parameter SPM by Pella and Tomlinson (1969) and the ASEM, we first revisit the surplus production function form:

$$SP = \frac{r}{m} B \left(1 - \left(\frac{B}{B_0} \right)^{m-1} \right) \qquad (1)$$

where r is the intrinsic rate of population increase at time t, B_0 is the unfished biomass and m is a shape parameter that determines at which B/B_0 ratio maximum surplus production is attained. If the shape parameter $m = 2$, the model reduces to the Schaefer form, with the surplus production (SP) attaining MSY at exactly $B_0/2$. If $0 < m < 2$, SP attains MSY at biomass levels smaller than $K/2$; the converse applies for values of m greater than 2. The Pella-Tomlinson model reduces to a Fox model (Fox, 1970) if m approaches one, resulting in maximum surplus production at $\sim 0.37 SB_0$, but there is no solution for the exact Fox surplus production with $m = 1$.

The shape parameter m can be directly translated into the biomass level where MSY is achieved, B_{MSY}, via the ratio B_{MSY}/K:

$$\frac{B_{MSY}}{B_0} = m^{\left(-\frac{1}{m-1} \right)} \qquad (2)$$

and the corresponding harvest rate at MSY (H_{MSY}) is:

$$H_{MSY} = \frac{r}{m-1} \left(1 - \frac{1}{m} \right) \qquad (3)$$

where the harvest rate defined here as the ratio of catch to biomass ($H = C/B$). Correspondingly, MSY can be expressed by:

$$MSY = H_{MSY} B_{MSY} \qquad (4)$$

Combing and re-arranging equations 2, 3, and 4, it follows that r in equation (1) can be expressed as:

$$r = \frac{MSY}{B_{MSY}} \frac{m-1}{1-m^{-1}} \qquad (5)$$

Equation 2 together with the re-rearranged Equation 5 emphasizes the potential of translating estimates of MSY/B_{MSY} and B_{MSY}/K into r and m, respectively (Maunder, 2003; Thorson et al., 2012; Wang et al., 2014; Winker et al., 2018a). In terms of Bayesian model formulations, this lends itself to deriving informative priors for r and m from Monte-Carlo Simulations to produce a distribution of likely values for MSY/B_{MSY} and B_{MSY}/B_0 (Mangel et al., 2013; McAllister et al., 2001). However, it remains unclear if B_{MSY} and B_0 should be best substituted by EB_{MSY} and EB_0 (EB-model) or SB_{MSY} and SB_0 (SB-model). This will be addressed in the following sections.

2.1.1 Age-structured equilibrium model (ASEM)

Assuming deterministic, sex-structured population dynamics, the numbers at age a and sex s per-recruit ($\widetilde{N}_a^s$) at equilibrium are given by:

$$\widetilde{N}_a^s = \begin{cases} 1 & if\ a = 0 \\ \widetilde{N}_{a-1}^s \exp(-s_a^s F - M) & if\ a > 0 \end{cases} \tag{6}$$

where s_a^s is the selectivity at age a and sex s, F is the instantaneous rate of fishing mortality and M instantaneous rate of natural mortality. For ease of presentation, we assumed a constant M and omitted the plus group.

The Spawning-biomass-per-recruit ($\tilde{S}$) is obtained as function of F, such that:

$$\tilde{S}(F) = \sum_a w_a^f \psi_a \widetilde{N}_a^f \tag{7}$$

where w_a^f is the weight at age for females f, ψ_a is the proportion of mature females in the population and $\widetilde{N}_a^f$ is the number of females per recruit, assuming an equal sex ratio at birth.

The corresponding exploitable-biomass-per-recruit ($\tilde{E}$) is obtained as function of F, such that:

$$\tilde{E}(F) = \sum_s \sum_a w_a^s s_a^s \widetilde{N}_a^s \tag{8}$$

The yield-per-recruit of a sex-structured population is given by:

$$\tilde{Y}(F) = \sum_s \sum_a \frac{w_a^s s_a^s F}{s_a^s F + M} \widetilde{N}_a (1 - e^{-s_a^s F - M}) \tag{9}$$

Under steady state conditions, the yield (Y) can then be expressed as a function of equilibrium recruitment $\widetilde{R}$ and yield-per-recruit (YPR)

$$Y(F) = \tilde{Y}(F) \times \tilde{R}(F) \tag{10}$$

The corresponding equilibrium spawner-biomass SB is:

$$SB(F) = \tilde{S}(F) \times \tilde{R}(F) \tag{11}$$

and the equilibrium exploitable-biomass is:

$$EB(F) = \tilde{E}(F) \times \tilde{R}(F) \tag{12}$$

Assuming a Beverton and Holt SSR, the equilibrium recruitment at F is given by:

$$\tilde{R}(F) = R_0 \frac{4h\tilde{S} - (1-h)\tilde{S}_0}{\tilde{S}(5h-1)} \tag{13}$$

where the steepness parameter h is defined as the ratio of recruitment of average unfished recruitment R_0 when spawner biomass is reduced to 20% of unfished levels, SB_0, i.e., $hR_0 = R(0.2SB_0)$ (Mace and Doonan, 1988) and $\widetilde{S}_0$ is unfished spawner-biomass-per-recruit when $F=0$.

The quantity MSY and the corresponding fishing mortality at MSY, F_{MSY}, is obtained through iterative maximization of Eq. 10 over a range of plausible F values, which then allows calculating SB_{MSY} and EB_{MSY} by inputting F_{MSY} into Eq. 11 and 12, respectively.

2.1.2 Prior generation for white marlin surplus production parameters

Prior distributions for r and m were obtained as a function of random deviates of MSY/B_{MSY} and B_{MSY}/B_0 that were generated from Monte-Carlo simulation based on 5000 iterations, where B_{MSY} and B_0 were either substituted by EB_{MSY} and EB_0 (*EB-model*) or SB_{MSY} and SB_0 (*SB-model*). However, we noted that ignoring the missing males in cases where SB_{MSY} is calculated from mature females would inherently over-estimate the productivity per unit biomass and thus r as function of MSY/ B_{MSY}, because in SPMs the modelled quantity B_{MSY} would be an aggregated biomass proxy that comprises both sexes. To compensate for this specific case, we therefore modified Eq. 5 for approximating r as a function of female-specific SB by:

$$r = \frac{MSY}{2SB_{MSY}} \frac{m-1}{1-m^{-1}} \tag{14}$$

The prior distributions were generated using the following of steps: (1) randomly generate permutations of *M'* from the assumed lognormal distribution ($\mu = \log(0.2)$, CV = 0.3) and input the steepness h given of the three considered scenarios (h = 0.5, $h = 0.6$ or $h = 0.7$), (2) iteratively maximize Equation 10 over a range of F values to obtain deviates of MSY' and the corresponding F'_{MSY}, (3) input the resulting F'_{MSY} into the ASME to obtain the associated B'_{MSY} through either Eq. 11 or Eq. 12, (4) set $F = 0$ to obtain B_0 through Equations 11 or 12, (5) calculate ratios MSY'/B'_{MSY} and B'_{MSY}/B'_0 and (5) iteratively solve Eq. 2 for B'_{MSY}/B'_0 to derive *m'* and input *m'* and the ratio MSY'/B'_{MSY} into Equation 2 to obtain *r'*. Note that ratios of MSY'/B'_{MSY} and B'_{MSY}/B'_0 are insensitive to the choice of R_0 (in Equation 13) and thus the absolute quantity of SB_0, that there is not loss of generality by setting $R_0 = 1$.

2.1.3. ASEM parameterization for white marlin surplus production parameters

Stock parameters estimates were broadly based on those used in the 2012 ICCAT Stock Synthesis model, which were further refined based discussions during the white marlin Data Preparatory Meeting (2019), including an initial range the range of plausible natural mortality and steepness values (**Table 1**). Three possible values for steepness of $h = 0.5$, 0.6 and 0.7. The central value of $h = 0.6$ steepness value was adopted as the reference case value. Natural mortality was assumed to be $M = 0.2$, which is consistent with a maximum age $t_{max} = 20$ (Hoenig, 1983). The three alternative steepness values were treated as fixed input into ASPM, whereas uncertainty about M was accounted for by assuming a gamma distribution with a fairly large CV of 30% and the central value mean value of 0.2 (**Figure 1a**).

Sex-specific weight-at-age is described as function of the weight to length conversion parameters ω and δ and length-at-age for sex s, L_a^s (**Figure 1b**), such that

$$w_a^s = \omega L_a^{s\,\delta} \tag{15}$$

where the two length-weight relationship parameters ω and δ were in this case assumed to be the same for both sexes (**Table 1**). The corresponding L_a^s was calculated based on the Bertalanffy growth function parameters as:

$$L_a^s = L_\infty^s(1 - e^{-\kappa^s(a-a_0^s)})$$ (16)

where L_∞^s is the asymptotic length, κ^s is the growth coefficient and a_0^s is the theoretical age at zero length for sex s, respectively (**Figure 1c**).

The fraction of mature females at age t was calculated as:

$$\psi_a = \frac{1}{1+e^{-(l_a-L_{m50})/\delta_\psi}}$$ (17)

where $L_{m_{50}}$ is the estimated length-at-50%-maturity (**Figure 1d**), which was assumed to be 160.4 cm LJFL (**Table 1**) and δ_ψ is the inverse slope of the ogive fixed a 5% of .

Selectivity-at-age was calculated as a function of length-at-age, L_a, using a two parameter logistic model of the form (**Figure 1f**):

$$s_a^s = \frac{1}{1+e^{-(L_a^s-L_{s50})/\delta_s}}$$ (18)

where s_a^s is the proportion of fish selected in the age a and sex s, L_{s50} is the length at which 50% of the fish are retained and δ_S is the inverse slope of the logistic ogive. The parameters L_{s50} and δ_S were chosen the approximate the selectivity of the long-line fishery (**Fig. 3e**), which is representative of the majority of blue marlin landings (Schirripa and Goodyear, 2018).

2.2 Age-structured Simulation experiment

We conducted a simulation experiment to evaluate the performance of the *EB*-model and *SB*-model, which we implemented as estimation models (EMs) in JABBA (Winker et al., 2018). The simulation procedure first creates a true population dynamics from an stochastic age-structured operating model (OM). The OM is used to generate typical data moderate fisheries data (catch and indices of abundance). The EMs are fitted to the data and estimate the population dynamics and resulting quantities of interest. These results are then compared to the true values from the OM.

For the purpose of this study we considered two EMs both implemented in JABBA (Winker et al., 2018). The first EM is the *EB*-model, which parameterized using the r prior and shape m approximated as function of *EB*. The second *EM* is identical only that we use the r prior and shape m approximated as function of *SB*. For both *EMs* and *OM* , we assume $h = 0.6$. Detailed descriptions of the OM and EM are given below.

2.2.1 Operating Model

As the operating model (OM) we used the age-structured simulation model by Thorson and Cope (2015). This OM has been used for comparisons of stock assessment model performances in a number of previous studies (Thorson et al., 2019; Thorson and Cope, 2015; Thorson and Kristensen, 2016) and forms part of the age-structured simulation-estimation tool that is implement in the open-source package CCSRA (Thorson and Cope, 2015) within the R statistical software. The population dynamic equations of the OM correspond to the ASEM formulation (Section 2.1) and are provided in Appendix A. Growth, maturation, natural mortality, and the BH-SSR function were described by the stock parameters for white marlin (see **Table 1**). Stochastic variation in recruitment was introduced by treating recruitment as lognormally distributed variable with the expected annual means derived from the BH-SSR function and a log-recruitment standard deviation of $\sigma_R = 0.5$. The unfished mean recruitment R_0 was set to 100 so as to attain a large enough SB_0 that was similar to real world assessment.

Compared to the real-world dynamics of white marlin, the simulation experiment is idealized and simplified by (1) ignoring the sex-structure and basing the life history on females only and (2) by only generating one CPUE index based on a logistic selectivity function that is of the same form as used to generate priors.

A simulation horizon of 50 years was adopted (**Figure 2**) under the assumption that both catch and abundance indices for a single fishery over this time period were available as input into the EMs (c.f. Thorson et al., in press). The observed abundance index was generated as the product of EB_y and a constant catchability coefficient ($q = 0.05$) with an associated constant, fairly large lognormal observation error of $\sigma_\varepsilon = 0.3$.

We used the effort-dynamics model by (Thorson et al., 2013) to generate unique stochastic realizations of fishing mortality trajectories that determine the population dynamics and resultant catch data. Accordingly, the instantaneous rate of fishing mortality (F_y) for year y was randomly generated based on a Markovian process:

$$\ln(F_y) \sim Normal\left(\ln\left(F_{y-1}\left(\frac{SB_{y-1}}{\delta SB_0}\right)^\lambda\right) - 0.5\sigma_F^2, \sigma_F^2\right) \tag{16}$$

where F_1 determines the initial fishing mortality at the start of the time series, λ is the rate of increase in F_y, σ_F introduces process noise around the underlying trend, and δ determines the spawning biomass depletion level to a 'bioeconomic' equilibrium around which that is approached by F_y (see Thorson et al. 2013 for further details). We conditioned the simulation model so that stock biomass decreased to low levels ranging between 15% and 20% at around year 30, followed by varying strength of none to slight stock rebuilding (**Figure 2**). This was achieved by setting $F_1 = 0.01$, $\lambda = 0.12$, $\delta = 0.15$, and $\sigma_F = 0.1$.

2.2.2 JABBA estimation models

The two JABBA EMs were fitted to the simulated abundance index I_y, and annual catch C_y (in weight) time series, where C_y was assumed to be known without error. Catchability q and (additional) observation variance σ_{est}^2 was estimated for the CPUE time series. The fixed observation error was set to $\sigma_{fix} = 0.1$ to mimic a constant $\hat{\sigma}_{SE_i} = 0.1$ for the input time series, so that the total observation is given by $\sigma_\varepsilon^2 = \sigma_{est}^2 + \sigma_{fix}^2$. The r priors and shape m were those derived from the ASEM according to the *EB-model* and *SB-model*, respectively. To match the OM, we used the life history parameters of females to generate the r prior and shape m, assuming sex-aggregated population dynamics. Note that because of the sex-aggregated population dynamic assumption SB_{MSY} correction for missing males (Eq. 15) was not necessary for the simulation experiment. For B_0, we used a vaguely informative priors with a mean set to the average of the "true" EB_0 and SB_0 and a CV = 200%. The prior for q had a uninformative uniform distribution over a wide range of values. Process and observation variance were treated the uninformative inverse-gamma priors $x \sim 1/gamma(0.001, 0.001)$.

2.2.3 Performance metrics

We recorded the relative errors in estimates relative to the 'true' value for the stock status $SB_{y=50}/SB_{MSY}$, $EB_{y=50}/EB_{MSY}$ and $F_{y=50}/F_{MSY}$ of the final assessment year 50, as well as MSY. We recorded relative errors $RE_{j,k}$ for EM j and replicate k as:

$$RE_{j,k} = \frac{(\hat{X}_{j,k} - X_{j,k})}{X_{j,k}} \tag{19}$$

where $\hat{X}_{j,k}$ is the estimated quantity of interest and $X_{j,k}$ is the corresponding 'true' value. The accuracy of the estimates compared to the 'true' values was evaluated using the Median Absolute Relative Error (MARE). To assess if the models accurately capture uncertainty, we also computed the 'confidence interval coverage' (CIC), by calculating the proportion of iterations out of 100 where the true value of a population parameter in the terminal year is within the 50%, 80% and 95% confidence intervals (Rudd and Thorson, 2017).

3. Results and Discussion

We applied our ASEM approach to transform a total of 16 input parameters, describing the age- and structured demographics of white marlin, into the surplus production function parameters r and m, which we approximated as function of either EB_{MSY} or SB_{MSY} (**Figure 3**). Our results confirmed that the functional form of the 16-parameter age-structured yield curve can be closely approximated by the ASEM-derived parameterization equivalent surplus production curves (**Figure 3**).

The smaller length-50%-selectivity (140 cm) relative to length-at-maturity for females (160.2 cm) resulted in an EB_{MSY} that was on average 4.7 times larger than female SB_{MSY} and 2.35 larger than $2 \times SB_{MSY}$. The latter was considered here to compensate for the 'missing' males. The difference between EB_{MSY} and SB_{MSY} has notable effects on the derived r and m quantities (**Figure 3**). Given that MSY is the denominator in Equation 5 (and remains the same irrespectively of whether EB_{MSY} or SB_{MSY} is taken as a proxy for B_{MSY}), the range of simulated r' values comprised substantially smaller values when using EB_{MSY} instead of SB_{MSY} (**Figure 2; Table 2**). The range of inflection points at MSY was higher for $EB_{MSY}/EB_0 = 0.36 - 0.42$ than for $SB_{MSY}/SB_0 = 0.26 - 0.34$ (**Figure 3**). In general, the inflection points and thus m decreased with increasing steepness h input values (**Table 2**). In the case of white marlin with $L_{m_{50}} > L_{s_{50}}$ and assuming logistic selectivity, the larger ratios of EB_{MSY}/EB_0 also imply that EB behaves hyper-stable relative to SB as biomass is declining.

Randomly generated deviates of EB'_{MSY}/EB'_0 and SB'_{MSY}/SB'_0 were substantial less variable than the generated r' values for fixed input values of h and given the assumed uncertainty about M (CV = 30%), with EB'_{MSY}/EB'_0 showing the least variation (**Figure 3**). Whereas steepness and thus m are mainly governed by the choice of the h (Equation 2), our results suggest that r is strongly influenced by both M and h. The effect of h on r can be inferred from the notable change in central r values for three alternative steepness assumptions (**Figure 3**).

For our simulation experiment, we generated a total of 100 simulation replicates for each of the two EMs. On visual inspection of the first four simulation replicates, the EM-predicted B/B_{MSY} and F_{MSY} trajectories indicated some notable differences between *EB-model* and *SB-model* (**Figure 4**). The *EB-model* tended to approximate the 'true' SB_y/SB_{MSY} more closely than the 'true' EB_y/EB_{MSY} at the start of the time series, when biomass was close to unfished levels. However, at biomass levels at and below B_{MSY}, the differences between EB_y/EB_{MSY} and SB_y/SB_{MSY} became smaller and were increasingly difficult to discern visually. As a result both quantities could be could be equally approximated by the estimated B_y/B_{MSY} from the *EB-model* for the second half of the time series (**Figure 4**). Similarly, the estimated H_y/H_{MSY} from the *EB-model* closely approximated 'true' F_y/F_{MSY} with the exception of replicate 3, where F_y/F_{MSY} was underestimated. In contrast to the *EB-model*, the *SB-model* showed a general tendency to over-estimate B_y/B_{MSY} and underestimate H_y/H_{MSY} relative to the 'true' reference values in three out of the first four simulation replicates (**Figure 4**).

Performance evaluation across the 100 simulation replicates confirmed that the *EB-model* produced close to unbiased estimates of the 'true' quantities of $SB_{y=50}/SB_{MSY}$, $EB_{y=50}/EB_{MSY}$ and $F_{y=50}/F_{MSY}$ for the final assessment year. By comparison, the *SB-model* produced positively biased stock status estimates by systematically overestimating $SB_{y=50}/SB_{MSY}$ and $EB_{y=50}/EB_{MSY}$, while underestimating $F_{y=50}/F_{MSY}$. The MARE values suggested that the *EB-model* was able to estimate $SB_{y=50}/SB_{MSY}$ four times more accurately than the *SB-model*. The MSY estimates from both EMs showed a slight negative bias, but were again more accurate for the *EB-model*.

The *EB-model* also performed well in terms of the confidence interval coverage (CIC) for the stock status quantities $SB_{y=50}/SB_{MSY}$ and $F_{y=50}/F_{MSY}$ (**Table 3**), with exactly 95% of true values $SB_{y=50}/SB_{MSY}$ falling within the 95% CIs of the estimated $B_{y=50}/B_{msy}$ and CICs generally exceeding the estimated 50% and 85% CIs. The CICs for $F_{y=50}/F_{MSY}$ were even better with 100% of the 'true' values $F_{y=50}/F_{MSY}$ falling within the 95% CIs of the estimated $H_{y=50}/H_{MSY}$ (**Table 3**).

The satisfactory CICs of the true stock status quantities SB/SB_{MSY} and F/F_{MSY} for the *EB-model* suggest that a correctly specified JABBA model provides, in principle, a parsimonious framework for billfish assessments with comparable population dynamics. Considering three alternative steepness h scenarios ($h = 0.5$, $h = 0.6$ and $h = 0.7$) and admitting reasonable uncertainty about M, we propose three sets steepness-specific priors for r and m input values derived from the *EB-model* (**Table 2)** for consideration in 2019 JABBA assessments scenarios for Atlantic white marlin.

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Table 1. Summary of life history parameters for Atlantic white blue marlin used as input for the ASEM to generate for Bayesian Surplus Production Model assessments.

Parameter	Females	Males	Unit
L_∞	172.0	160.6	cm
κ	0.32	0.54	year^{-1}
t_0	-1	-1	years
a	5.21×10^{-6}	5.21×10^{-6}	cm/g
b	3.2842	3.2243	kg cm^{-1}
L_{m50}	160.4		years
δ_ψ	8.2		year^{-1}
a_{min}	0	0	years
a_{max}	20	37	years
S_L	140	140	cm
δ_S	7	7	cm^{-1}
M	0.2 (CV=0.3)		year^{-1}
h	0.5, 0.6, 0.7		

Table 2. Mean and standard deviation (log.sd) for a lognormal r prior specifications and associated input values for the inflection point BMSY/B0 (~ SBMSY/SB0) as determined by the shape m, derived for three alternative steepness h parameters for the EB-model and SB-model

	EB-Model			*SB-Model*		
Parameters	$h = 0.5$	$h = 0.6$	$h = 0.7$	$h = 0.5$	$h = 0.6$	$h = 0.7$
prior mean r	0.158	0.183	0.201	0.256	0.285	0.305
log.sd r	0.162	0.172	0.183	0.271	0.278	0.288
B_{MSY}/B_0	0.42	0.39	0.36	0.34	0.3	0.26
shape m	1.3	1.12	0.95	0.88	0.69	0.53

Table 3. Confidence interval coverage (CIC) for the *EB-model* and *SBmodel* denoting the proportion of iterations where the 'true' values $SB_{y=50}/SB_{MSY}$ and $F_{y=50}/F_{MSY}$ for the final assessment year ($y = 50$) fell within the JABBA predicted 50%, 80% and 95% confidence intervals (CIs) for $B_{y=50}/B_{MSY}$ and $H_{y=50}/H_{MSY}$, respectively.

	SB/SB_{MSY}			F/F_{MSY}		
Model	CI50%	CI80%	CI95%	CI50%	CI80%	CI95%
EB	0.67	0.86	0.95	0.95	0.99	1
SB	0.58	0.81	0.91	0.08	0.31	0.58
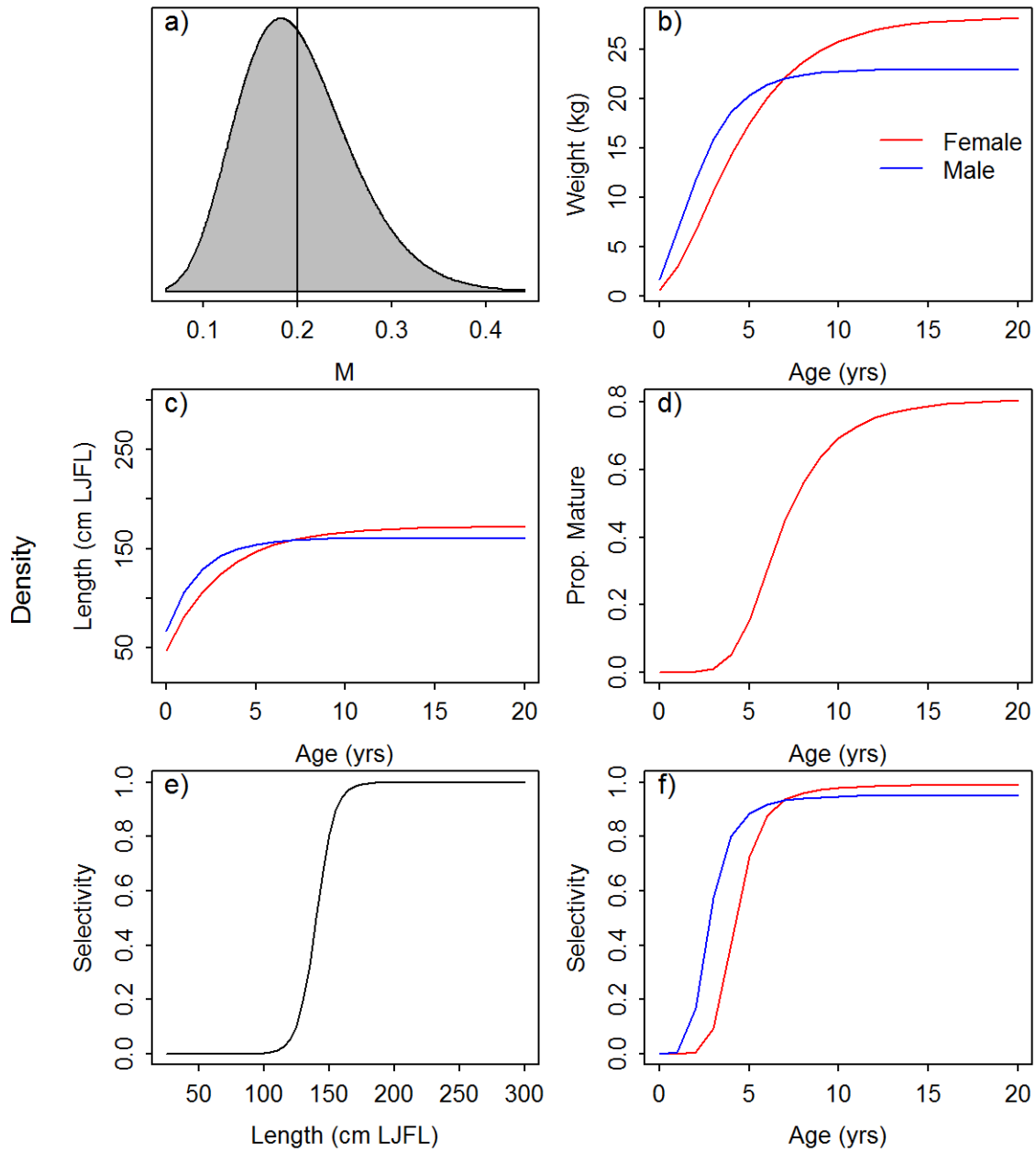
**Figure 1.** Basic population dynamic functions for Atlantic white marlin showing (a) central value of *M* (solid line) and assumed uncertainty (CV = 30%) , (b) sex-specific weight-at-age functions, (c) sex-specific length-at-age functions, (d) assumed proportion mature females at age, (e) selectivity-at-length and (f) sex-specific selectivity-at-age as a function of sex-specific length-at-age and selectivity-at-length.
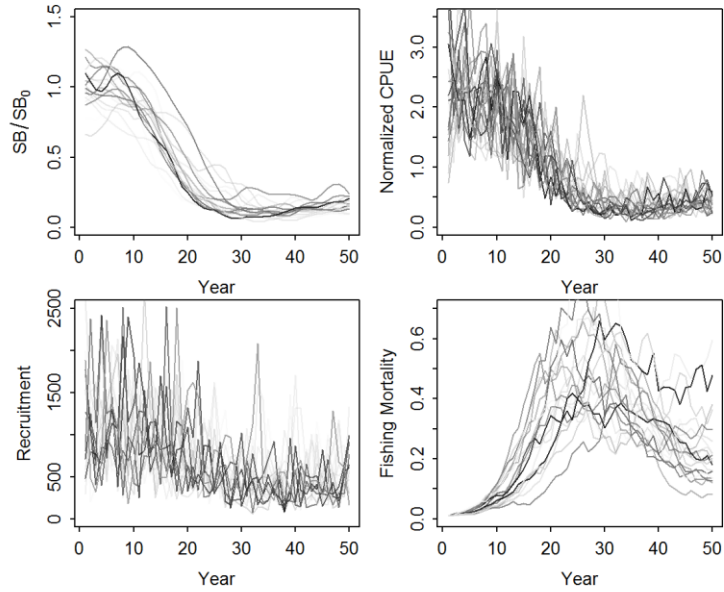
Figure 2. Simulated age-structured population dynamics for Atlantic white marlin, showing the trajectories of SB_y/SB_0, normalized abundance indices (CPUE; CV = 30%), recruitment deviates ($\sigma_R = 0.5$) and fishing mortality F for the first 20 simulation replicates over 50 year time horizon.
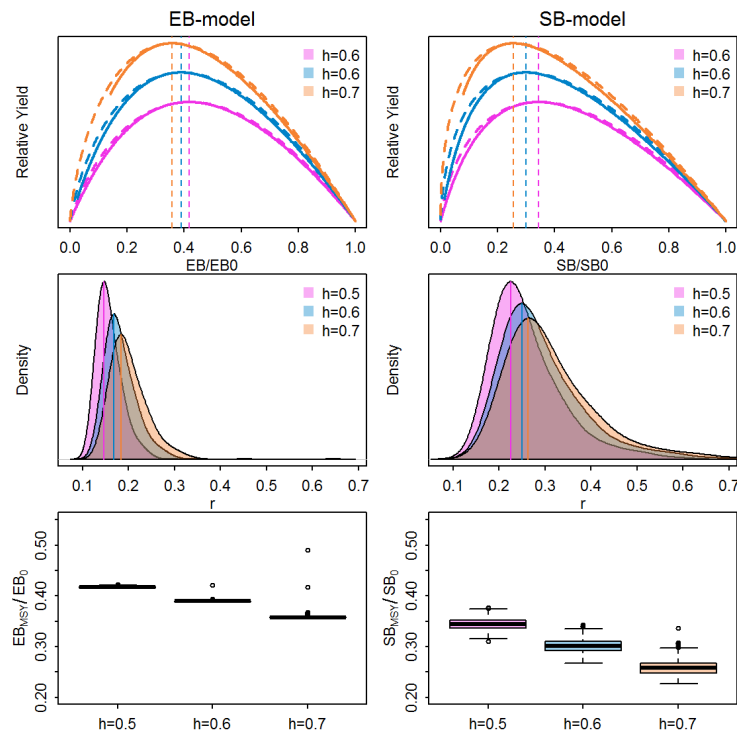
Figure 3. (Top Panel) Showing the functional from of the yield curves produced from the Age-Structured Equilibrium Model (ASME; solid line) and the JABBA formulation of the Surplus Production function (solid) as a function of EB/EB_0 and SB/SB_0 for a range of fixed steepness values of the spawning recruitment relationship ($h = 0.4$, $h = 0.5$, $h = 0.6$) (top panel); (Middle Panel) density distributions of simulated r values from Monte-Carlo simulations based on the *EB-model* and *SB-model;* and (Lower Panel) boxplot generated inflection points of EB_{MSY}/EB_0 and SB_{MSY}/SB_0 for each of the fixed steepness h input values.
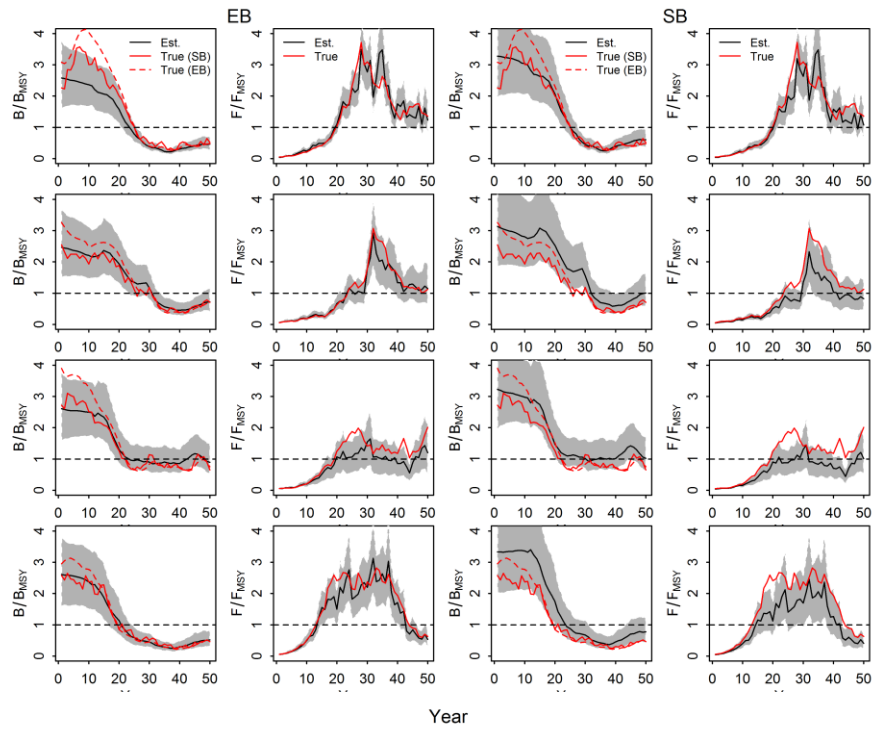
Figure 4. Simulated 'true' trajectories of *EB/EB_MSY* and *SB/SB_MSY* relative to the estimated *B/B_MSY* with associated 95% Confidence Intervals (CIs); and 'true' *F/F_MSY* trajectories relative to estimated *H/H_MSY* for the first 4 of 100 simulation runs (top to bottom), comparing the JABBA estimates from the *EB-model* (left) and *SB-model* (right).
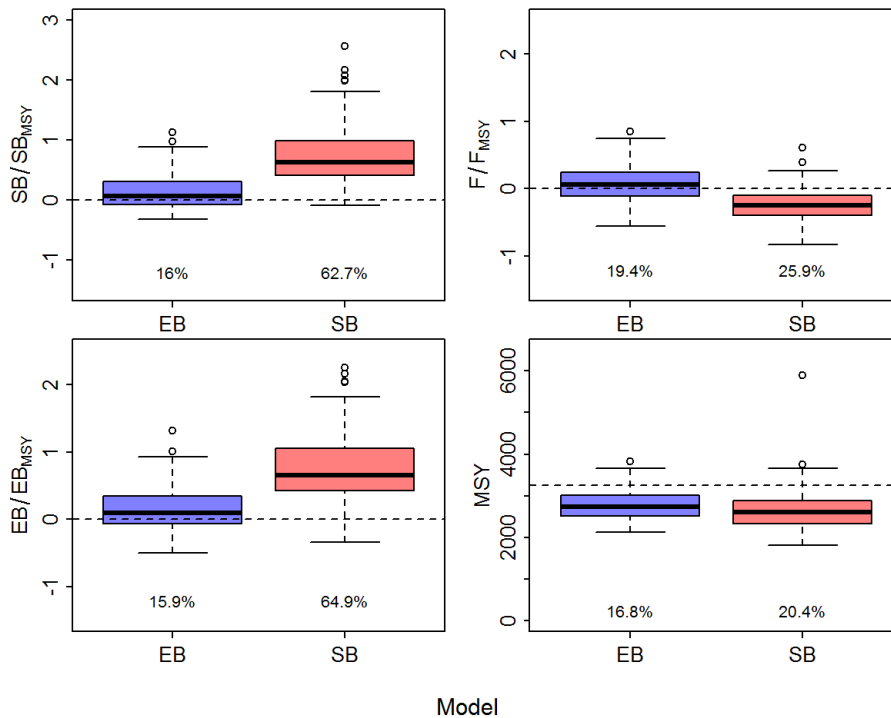
Figure 5. Boxplots illustrating the relative errors calculated from 100 simulation replicates for JABBA estimates of *B/B_MSY* compared to the 'true' *SB/SB_MSY* and *EB/EB_MSY*, *H/H_MSY* estimates compare to the 'true' *H/H_MSY* and MSY for the *EB-model* and *SB-model*. Median-Absolute-Relative-Error (MARE%) are displayed in each box.

Age-structured dynamics

The age-structured simulation and estimation models were formulated building on the age-structured simulation-estimation framework employed in previous studies (Thorson and Cope, 2015). Numbers-at-age a and year y, $N_{a,y}$, are governed by:

$$N_{a,y} = \begin{cases} R_y & for\ a = 0 \\ N_{a-1,y-1}e^{-s_{a,s}-F_{y-1}M} & for\ a > 0 \end{cases} \tag{A5}$$

where R_y is recruitment in year y, $s_{a,s}$ is fishery selectivity at age under selectivity regime s, M is the instantaneous rate of natural mortality, and F_y in year y.
Spawning biomass SB_y is expressed as:

$$SB_y = \sum_a w_a \psi_a N_{a,y} \tag{A6}$$

where w_a is the weight at age, ψ_a is the proportion of mature fish in the population.

Stochastic recruitment is introduced as a lognormally distributed random variable with the expected mean derived from the Beverton-Holt SSR function:

$$\ln(R_t) \sim Normal\left(ln\left(\frac{4hR_0 SB_y}{SB_0(1-h)+SB_y(5h-1)}\right) - 0.5\sigma_R^2, \sigma_R^2\right) \tag{A7}$$

where R_0 is the unfished average recruitment and σ_R^2 is the variance is recruitment.

To initiate the age structure in the first year of the available catch time series, it is assumed that the stock is in an unfished stated, so that $N_{a,y=1}$ can be approximated by a stochastic age-structured as result of recruitment variation in previous years:

$$\ln(N_{a,y=1}) \sim Normal(\ln(R_0 e^{-aM}) - 0.5\sigma_R^2, \sigma_R^2) \tag{A8}$$

Catch-at-age $c_{a,t}$ (in numbers) was calculated from the Baranov catch equation:

$$c_{a,y} = N_{a,y}\frac{s_{a,s}F_y}{s_a F_a + M}(1 - e^{-s_{a,s}F_y - M}) \tag{A9}$$

and total yield C_y (in weight) in year y the summed product of catch at age and weight at age, such that:

$$C_y = \sum_a c_{a,y} w_a \tag{A10}$$

The abundance index I_y (CPUE) for year y was assumed to be proportional to the exploitable portion of the biomass (EB_y) and associated with a lognormally distributed observation error ε_y:

$$\log(I_y) \sim Normal(\ln(qEB_y), \sigma_\varepsilon^2) \tag{A11}$$

where q is the catchability coefficient and EB_y is a function of selectivity-at-age, such that:

$$EB_y = \sum_a N_{a,y} w_a s_{a,s} . \tag{A12}$$