

## Developing surplus production model priors from a multivariate life history prediction model for IOTC billfish assessments with limited biological information

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### ABSTRACT

Production Model remain widely used to assess stock status and can represent a parsimonious alternative to age-structured assessment models, in particular in the absence of reliable size and/or age structure information and in cases where life history parameters are uncertain. Here we present an approach to objectively incorporate available life history parameters into Bayesian surplus production model priors for the intrinsic rate of population increase  $r$ . First we use the R package *FishLife* to determine probable life history parameters from *FishBase*. The model is then updated with stock-specific estimates of the asymptotic length ( $L_{\infty}$ ), as derived by fitting the recently proposed Length-based Bayesian estimator (*LBB*) to available size data for the Indian Ocean region. The resulting *FishLife* predictions of parameter means and their covariance are then used to propagate parameter uncertainty and correlation structure into the formulation of the  $r$  prior. In addition, *LBB* was applied to estimate a logistic selectivity function for each stock, which is required to parameterize the age-structured model. The approach is illustrated by its application to Indian Ocean striped marlin and black marlin with the aim to develop objective priors for  $r$  for a range of steepness assumptions about the stock-recruitment relationship. The results demonstrate that the functional form of a 14-parameter yield curve for an age-stock stock can be well approximated by the 3-parameter Pella-Tomlinson surplus production curve. To adequately account for the uncertainty about the productivity of each stock, we propose three steepness-specific sets of priors for  $r$  and  $B_{MSY}/K$  values for consideration in the 2018 IOTC assessments based on the Bayesian Surplus Production Modelling software *JABBA*.

### KEYWORDS

*Bayesian priors, Monte-Carlo simulation, life history traits, JABBA, Marlin*

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## INTRODUCTION

Surplus Production Models (SPMs) are one of the least data demanding population dynamic models to provide estimates of stock status and fisheries reference points (FRPs) such as the Maximum Sustainable Yield (MSY). Despite the increased application of more complex age-structured models (ASMs) within tuna Regional Management Fisheries Organizations (RFMOs), 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 and the removal by the fishery. Somatic growth, reproduction, natural mortality and associated density-dependent processes are inseparably captured in the estimated surplus production function that is governed by the intrinsic rate of population increase  $r$ , the shape parameter  $m$  and the unfished biomass  $K$  (Winker et al., 2018a). In contrast, it typically requires at least 14 parameters to approximate the surplus production function within an age-structured assessment framework (Winker et al., 2018a, 2018b, 2017). Most of these parameters are rarely estimable within the ASM framework and therefore typically assumed without error, especially in data-poor to -moderate assessments. The parameterization of ASM strongly relies on externally estimated parameters describing growth, maturity, natural mortality and the spawning- recruitment relationship of the stock. Misspecification of one or several parameters can introduce severe bias in the stock status estimates or cause data conflict between abundance indices and size data (Henriquez et al., 2016). In the absence of reliable data to infer life history and stock parameter estimates SPMs may provide a more parsimonious alternative to estimate stock status.

Here, we apply an age-structured Monte-Carlo simulation approach to convert life history parameters into Bayesian surplus production model priors for  $r$  (Winker et al. 2017; Winker et al. 2018b). We make use of the multivariate hierarchical life history tool *FishLife* (Thorson et al., 2017; <https://github.com/James-Thorson/FishLife>) to source life history parameters from *FishBase* ([www.fishbase.org](http://www.fishbase.org)). The *FishLife* model estimates plausible combinations of species-specific life history parameters nested within taxonomic relationships by employing hierarchical multivariate statistics on available data. To obtain stock-specific estimates, we then update the *FishLife* predictions with stock-specific estimates of the asymptotic length ( $L_{\infty}$ ), which we derived by fitting the Length-based Bayesian estimator (LLB; Froese et al., 2018) to available size data for the Indian

Ocean region. These updated model results are used to propagate parameter uncertainty and correlation structure into the formulation of the  $r$  prior. In addition, LBB was applied to estimate a logistic selectivity function for each stock, which is required for parameterizing the age-structured model. We implement this approach for Indian Ocean striped marlin (MLS) and black marlin (BLM) with the aim to develop objective priors for  $r$  for a range of steepness assumptions about the stock-recruitment relationship.

## 1. MATERIALS AND METHODS

### 1.1 Linking Age-Structured and Surplus Production Model

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 from estimated stock parameters by searching iteratively for the fishing mortality that produces  $MSY$ ,  $F_{MSY}$ , from the corresponding spawning biomass  $SB_{MSY}$  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 ( $\psi_a$ ) and selectivity-at-age ( $s_a$ ), natural mortality  $M$  and the steepness parameter  $h$  of the of the assumed SSR (Punt et al., 2013).

To illustrate the link between the generalized three parameter SPM by Pella and Tomlinson (1969) and an ASEM, we make the assumption that surplus production is a function of spawning biomass (Thorson et al., 2012), so that:

$$SP = \frac{r}{m-1} SB \left( 1 - \left( \frac{SB}{SB_0} \right)^{m-1} \right) \quad (1)$$

where  $r$  is the intrinsic rate of population increase,  $SB_0$  is the unfished biomass and  $m$  is a shape parameter that determines at which  $SB/SB_0$  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  $SB_0/2$ . 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  $\sim 0.37SB_0$ , but there is no exact solution for the Fox surplus production with  $m = 1$  (Figure 1)

The functional link between the Pella-Tomlinson SPM and the ASEM is illustrated in Figure 2. Accordingly, it is possible to first generate  $MSY/SB_{MSY}$  and  $SB_{MSY}/SB_0$  from the ASEM and translate those into surplus production parameter  $r$  and  $m$  from typical input parameters for age-structured assessment models, where  $m$  is directly related to the inflection point  $SB_{MSY}/SB_0$  of the surplus production curve:

$$\frac{SB_{MSY}}{SB_0} = m^{\left(-\frac{1}{m-1}\right)} \quad (2)$$

and  $r$  can be expressed as a function of  $MSY/SB_{MSY}$  and  $m$  such that:

$$r = \frac{MSY}{SB_{MSY}} \frac{m-1}{1-m^{-1}} \quad (3)$$

## 1.2 Age-structured equilibrium model (ASEM)

Assuming deterministic, age-structured population dynamics, the numbers at age per-recruit ( $\tilde{N}_a$ ) at equilibrium are given by:

$$\tilde{N}_a = \begin{cases} 1 & \text{if } a = 0 \\ \tilde{N}_{a-1} \exp(-s_a F - M) & \text{if } a > 0 \end{cases} \quad (4)$$

where  $s_a$  is the selectivity at age  $a$ ,  $F$  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 ( $S'$ ) is obtained as function of  $F$ , such that:

$$\tilde{S}(F) = \sum_a w_a \psi_a \tilde{N}_a \quad (5)$$

where  $w_a$  is the weight at age,  $\psi_a$  is the proportion of mature fish in the population and  $\tilde{N}_a$  is the number survivors-at-age per recruit. The corresponding yield-per-recruit is given by:

$$\tilde{Y}(F) = \sum_a \frac{w_a s_a F}{Z_a} \tilde{N}_a (1 - \exp(-Z_a)) \quad (6)$$

where  $Z_a$  is the age- and sex-specific total mortality given by:

$$Z_a = M + s_a F \quad (7)$$

and  $s_a$  is the selectivity-at-age.

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

$$Y(F) = \tilde{Y}(F) \times \tilde{R}(F) \quad (8)$$

The corresponding equilibrium spawner-biomass  $SB$  is:

$$SB(F) = \tilde{S}(F) \times \tilde{R} \quad (9)$$

where  $\tilde{S}(F)$  denotes the spawning-biomass-per-recruit for a given fishing mortality  $F$ .

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

$$\tilde{R}(F) = R_0 \frac{4h\tilde{S} - (1-h)\tilde{S}_0}{\tilde{S}(5h-1)} \quad (10)$$

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.,  $hR_0 = \tilde{R}(0.2SB_0)$  (Mace and Doonan, 1988) and  $\tilde{S}_0$  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. 8 over a range of plausible  $F$  values, which then allows calculating  $SB_{MSY}$  by inputting  $F_{MSY}$  into Eq. 9.

Weight-at-age is described as function of the weight to length conversion parameters  $\omega$  and  $\delta$  and length-at-age for sex  $s$ ,  $L_a$ , such that

$$w_a = \omega L_a^\delta \quad (11)$$

The corresponding  $L_a$  was calculated based on the Bertalanffy growth function parameters as:

$$L_a = L_\infty(1 - \exp(-k(a - a_0))) \quad (12)$$

where  $L_\infty$  is the asymptotic length,  $k$  is the growth coefficient and  $a_0$  is the theoretical age at zero length.

The fraction of mature fish at age  $a$  was calculated as:

$$\psi_a = \frac{1}{1 + \exp(-(a - a_{mat})/\delta_\psi)} \quad (13)$$

where  $a_{mat}$  is the estimated age-at-50%-maturity and  $\delta_\psi$  is the inverse slope of the ogive.

Selectivity-at-age was calculated as a function of length-at-age,  $L_a$ , using a two parameter logistic model of the form

$$s_a = \frac{1}{1 + \exp(-(L_a - L_c)/\delta_s)} \quad (14)$$

where  $s_a$  is the proportion of fish selected in the age  $a$  and sex  $s$ ,  $L_c$  is the length at which 50% of the fish are retained and  $\delta_s$  is the inverse slope of the logistic ogive.

### 1.3 Generating life history input parameters

A general overview of the approach to generate stock parameters as input for the ASEM is illustrated in Figure 2.

First, we derived approximations of stock-specific asymptotic length ( $L_\infty$ ) estimates and fisheries selectivity parameters by applying the Bayesian length-frequency analysis tool LBB (Froese et al. 2018) to combined size frequency data for the period 2000-2016 from the Taiwanese longline fleet. The size data for MLS ( $n = 85,898$ ) and BLM ( $n = 12,676$ ) were made available for the 2017 meeting of the IOTC Working Party on Billfish (WPB). LBB provides a Bayesian estimation framework to simultaneously estimate  $L_\infty$ , the length-at-50%-selectivity ( $L_c$ ), the slope parameter of the logistic selectivity function ( $\alpha$ ), relative natural mortality and relative fishing mortality from length frequency

data (Froese et al. 2018). In LBB, selectivity is assumed to follow a logistic function of length classes  $L_i$  relative to  $L_\infty$ , such that:

$$S_{L_i} = \frac{1}{1 + \exp\left(-\alpha_s \left(\frac{L_i - L_c}{L_\infty}\right)\right)} \quad (15)$$

where  $S_{L_i}$  is the probability of fish in length class  $i$  (here 3 cm) are vulnerable to the fishery and  $\alpha_s$  is the slope of the selectivity curve. Here, we only focus on the LBB estimates of  $L_\infty$  and the selectivity parameter estimates  $L_c/L_\infty$  and  $\alpha_s$  for MLS and BLM.

Next, we made use of the R package *FishLife* (Thorson et al. 2017) to generate random deviates of the ASEM input parameters  $L'_\infty, k', a'_{mat}, a'_{max}$  and  $M'$ . This R package allows predicting life history traits for marine fishes based on a multivariate prediction model, which draws inferences from life history information for more 32,000 marine fishes available in FishBase, while accounting for taxonomic structure in residuals with five levels for class, order, family, genus, and species. On species level, the multivariate prediction model produces the expected mean values ( $\hat{y}_{spec}$ ) and covariance matrix ( $Cov_{spec}$ ) for the following seven life history parameters and, in addition, temperature:

$$\hat{y}_{spec} = \{\log(L_\infty), \log(k), \log(W_\infty), \log(a_{max}), \log(a_{mat}), \log(M), \log(L_{mat}), \log(T)\} \quad (16)$$

$$Cov_{spec} = \{\log(L_\infty), \log(k), \log(W_\infty), \log(a_{max}), \log(a_{mat}), \log(M), \log(L_{mat}), \log(T)\} \quad (17)$$

where  $L_{mat}$  is the length-at-50% maturity and  $T$  is the temperature. *FishLife* also provides a function to update predictions of life history parameters for a given species based on user-supplied data. Here, we only updated the predictions with the  $L_\infty$  estimate from *LBB* to tune the predictions to more stock-specific estimates  $\hat{y}_{stock}$  and  $Cov_{stock}$  for MLS and BLM in the Indian Ocean. We then applied a multivariate random generator in R to obtain a large number ( $n_{sim} = 1000 \times 1000$ ) of random deviates  $y'_{stock}$ , such that:

$$y'_{stock} \sim MVN(\hat{y}_{stock}, Cov_{stock}) \quad (18)$$

To further exclude implausible sets of history parameters given the stock specific size information (e.g. observed mean length  $> L_{oo}$ ), we extracted a random subset of 1000 generated life history

parameters, based on the condition that  $L'_{\infty}$  falls within the 2.5<sup>th</sup> and 97.5<sup>th</sup> percentile of lognormal distribution with a CV of 15% around the log of the LBB-based  $L_{oo}$  estimate. From this subset, we extracted the vectors random deviates of  $L'_{\infty}$ ,  $k'$ ,  $a'_{mat}$ ,  $a'_{max}$  and  $M'$  as input for the ASEM.

The remainder of required ASEM input parameters were parameterized as follows. The theoretical age at zero length was set to  $a_0 = -1$  (Eq. 12) and the weight-length parameters were set to  $\omega = 0.01$  and  $\beta = 3$  (Eq. 11). In both cases, the choice of parameter is predicted to have little influence on the results as these are expressed in the form of relative quantities. The slope of the maturity ogive was set to  $\delta_{\psi} = 0.01 a_{mat}$  (Eq. 13) to approximate knife-edge maturation. Finally, we generated random selectivity input parameters (Eq. 14) as function of:

$$L'_c = L'_{\infty} \frac{L_c}{L_{\infty}} \quad \text{and} \quad \delta'_s = L'_{\infty} / \alpha_s \quad (19)$$

where  $L_c/L_{\infty}$  and  $\alpha_s$  are the LBB estimates and  $L'_{\infty}$  is the vector randomly generated  $L_{oo}$  deviates from the stock-specific *FishLife* model predictions

#### 2.4 Monte-Carlo procedure for prior generation

Prior distributions for  $r$  and corresponding proxies for  $B_{MSY}/K$  (and  $m$ ) were obtained as a function of random deviates of  $MSY/SB_{MSY}$  and  $SB_{MSY}/SB_0$  that were generated from Monte-Carlo simulation based on 1000 iterations. This was done using the following of steps: (1) iteratively input the 1000 stock parameters deviates into the ASEM, (2) iteratively maximize Eq. 6 over a range of  $F$  values to obtain deviates of  $MSY'$  and the corresponding  $F'_{MSY}$ , (3) input the resulting  $F'_{MSY}$  into the ASEM to obtain the associated  $SB'_{MSY}$  through Eq. 9, (4) set  $F = 0$  to obtain  $SB'_0$  through Eq. 9, (5) calculate ratios  $MSY'/SB'_{MSY}$  and  $SB'_{MSY}/SB'_0$  and (5) iteratively solve Eq. 2 for  $SB'_{MSY}/SB'_0$  to derive  $m'$  and input  $m'$  and the ratio  $MSY'/SB'_{MSY}$  into Eq. 2 to obtain  $r'$ . Note that ratios of  $MSY'/SB'_{MSY}$  and  $SB'_{MSY}/SB'_0$  are insensitive to the choice of  $R_0$  (in Eq. 10) and thus the absolute quantity of  $SB_0$ , hence there is not loss of generality by setting  $R_0 = 1$ .

The Monte-Carlo simulation was repeated of the range of fixed input values of  $h = 0.4-0.8$  in steps of 0.1. In addition, we added  $h = 0.86$  so as to match the stock-recruitment assumption for the stock synthesis (SS3; Methot and Wetzel, 2013) reference run for the 2017 IOTC striped marlin assessment (Wang, 2017).

### 3. Results and Discussion

The *LBB* approximations of  $L_{oo}$  were 331.5 cm for MLS and 363.3 cm for BLM and the size-at-50%-selectivity was estimated as ratios of  $L_c/L_{oo} = 0.46$  and 0.37, respectively (Figure 4). The pairwise predictions of six selected variables ( $L_{oo}$ ,  $k$ ,  $L_{mat}$ ,  $a_{mat}$ ,  $a_{max}$  and  $M$ ) highlight the interrelations among life traits, which are represented in *FishLife* by the covariance (Figs. 5-6). The MLS life history predictions mostly overlapped between species and stock level, suggesting that the model-update based on  $L_{oo}$  estimate from *LBB* had little influence on the predictions (Fig. 5). This was notably different for BLM, where the predictions on species level initially produced a large proportion of surprisingly small  $L_{oo}$  deviates (Fig. 6). In particular,  $L_{oo}$  values below 190 cm appear implausible for the Indian Ocean stock when compared the observed size data shown in Fig. 4. The reason for this discrepancy is likely related to limited, highly variable life history records for BLM in FishBase. Updating *FishLife* and subsetting the generated sets parameters based on the  $L_{oo}$  estimate from *LBB* seemingly produced more realistic stock-specific life history estimates for BLM (Fig. 6). Kernel density distributions of the subsets of stock-specific ASEM input parameters are shown in Figs. 7-8. The resulting relationships of length-at-age, maturity-at-age, unfished numbers-at-age and selectivity-at-age provide an illustration of the ranges of uncertainty that are propagated into the  $r$  priors for MLS (Fig. 9) and BLM (Fig. 10).

The results from ASEM demonstrate that the iterative ( $F$ ) solution of a 14-parameter yield curve of an age-structured stock can be closely approximated by the closed-form solution of the 3-parameter Pella surplus production curve over a wide range of steepness  $h$  assumptions for both stocks (Figs. 11-12). The larger  $r$  priors for MLS (Fig. 11) suggest that the stock is more resilient to exploitation than BLM (Fig. 12), with minimal overlap between expected mean  $r$  values of 0.21-0.31 for MLS and 0.15-0.22 for BLM over the same range of steepness  $h$  input values (Table 1). In addition, the precision of the  $r$  priors was substantially higher for MLS (CV  $\sim$  15%) than for BLM (CV  $\sim$  30%), which is probably an adequate reflection of the quality and quantity of available biological information for the two species.

Our results also revealed an approximately linear relationship between steepness  $h$  and  $B_{MSY}/K$ , which was comparable between the stocks. For example, a steepness value of  $h=0.5$  closely approximated a Fox-type surplus production function with an inflection points at about  $B_{MSY}/K \sim 0.37$  for MLS and BLM; and the same was found in the case of Atlantic blue marlin (Winker et al., 2018b). This agrees previous findings by Forrest et al. (2010) and Mangel et al. (2013), who showed that steepness is a strong predictor for  $SB_{MSY}/SB_0$  in general. Whereas the inflection point  $B_{MSY}/K$  and thus the shape  $m$  of the surplus production function appear to be mainly governed by the choice of the

the steepness parameter  $h$ , we found that  $r$  is influenced by all key life history traits including growth, longevity, natural mortality and  $h$ . In addition,  $r$  is inherently impacted by the selectivity function, a fact that is widely ignored in approaches for predicting  $r$  (McAllister et al., 2001). The effect of  $h$  on  $r$  can be inferred from the notable change in central  $r$  values over the range steepness assumptions (Figs. 11-12). However, this also implies that  $r$  and  $m$  are interdependent and it follows that, for example, the biologically inferred  $r$  prior for a Schaefer SPM is not directly transferrable to a Fox SPM without incurring misspecifications between these two widely used SPM formulations.

As is common practice, the Schaefer ( $B_{MSY}/K = 0.5$ ) and the Fox model ( $B_{MSY}/K = 0.37$ ) were also considered as alternative scenarios in previous SPM-based assessments of Indian Ocean MLS and BLM (Andrade, 2017; Yokoi and Nishida, 2016). For both stocks, we could closely approximate the Fox model based on a steepness input value of  $h = 0.5$ , whereas the lowest considered steepness value  $h = 0.4$  resulted in  $B_{MSY}/K = 0.40-0.41$  and thus still well below the Schaefer model assumption of  $B_{MSY}/K = 0.5$ . The derived lognormal  $r$  priors of 0.253 (CV = 0.15) for MLS and 0.184 (CV = 0.3) for BLM, corresponding to  $h = 0.5$  (Table 1), therefore appear to be a natural choice for a reference case consistent with previous SPM-based assessment. The inflection point of  $B_{MSY}/K = 0.4$  ( $h = 0.4$ ) matches the mean estimate of  $B_{MSY}/K$  derived by meta-analysis of 147 fish stock (Thorson et al., 2012) and is widely considered as a reference point for  $B_{MSY}$  that is fairly robust to recruitment overfishing (Clark, 1991; Punt et al., 2013). As such, the  $r$  priors for  $r$  for  $h = 0.4$  (Table 1) would provide a plausible option for sensitivity runs based on a lower resilience assumption. The high  $h = 0.86$  was included here to match the stock-recruitment assumption for the SS3 reference model for 2017 IOTC striped marlin assessment (Wang, 2017). While perhaps reasonable for striped marlin, the here inferred life history traits for black marlin rather point towards more similarity to the less productive Atlantic blue marlin stock, for which a steepness of  $h = 0.6$  was considered the upper plausible limit by the ICCAT Billfish Working Group (Mourato et al., 2018; Winker et al., 2018b). We therefore propose to only consider the  $r$  prior specific to  $h = 0.86$  for striped marlin, but choose the more conservative  $h = 0.4$  input to specify the  $r$  prior for black marlin.

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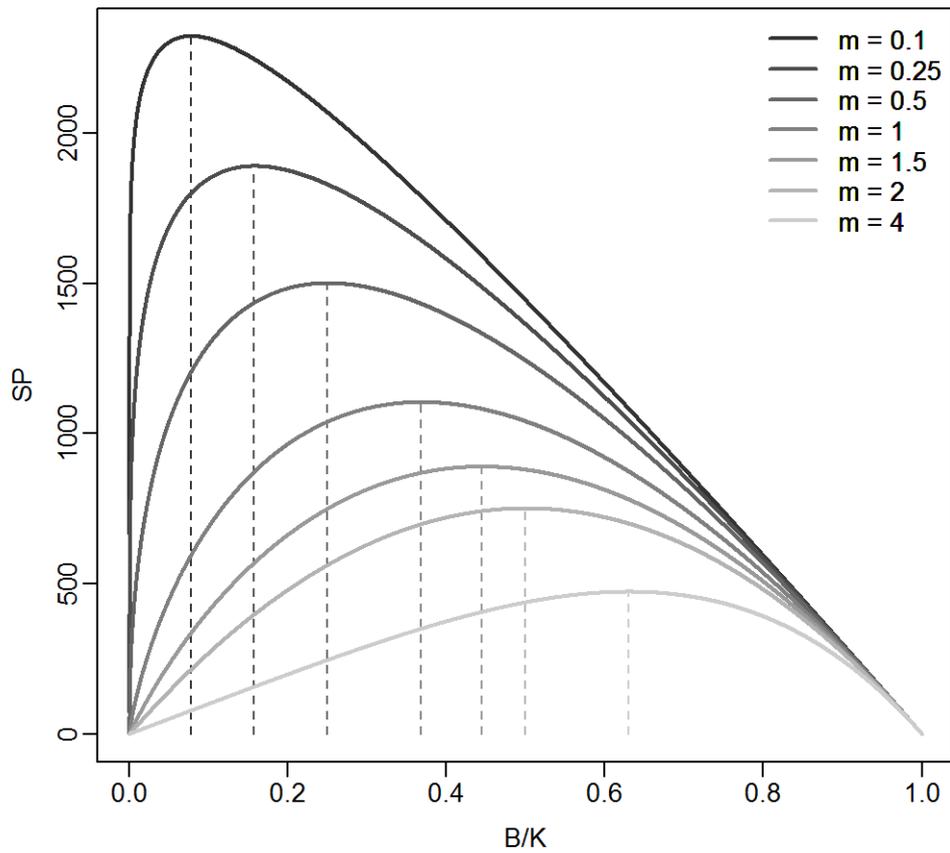
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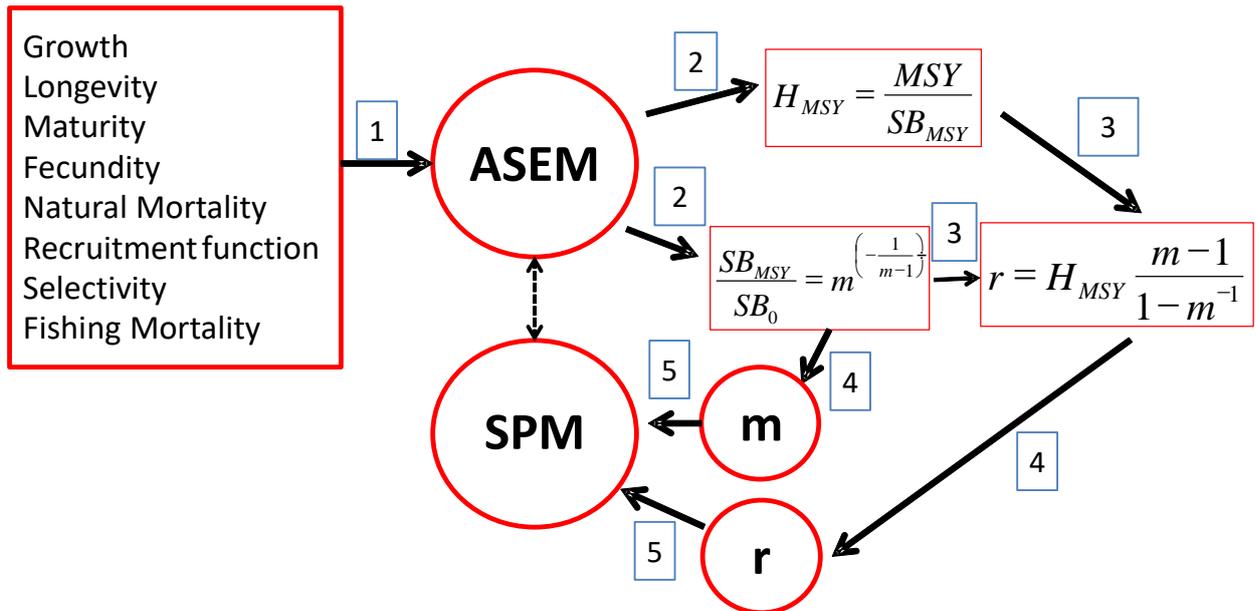
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**Table 1.** Mean and standard deviation (log.sd) for lognormal  $r$  prior approximations and associated input values for the inflection point  $B_{MSY}/B_0$  as determined by the shape  $m$ , derived for each of steepness parameter input scenarios for (a) striped marlin (MLS) and (b) black marlin.

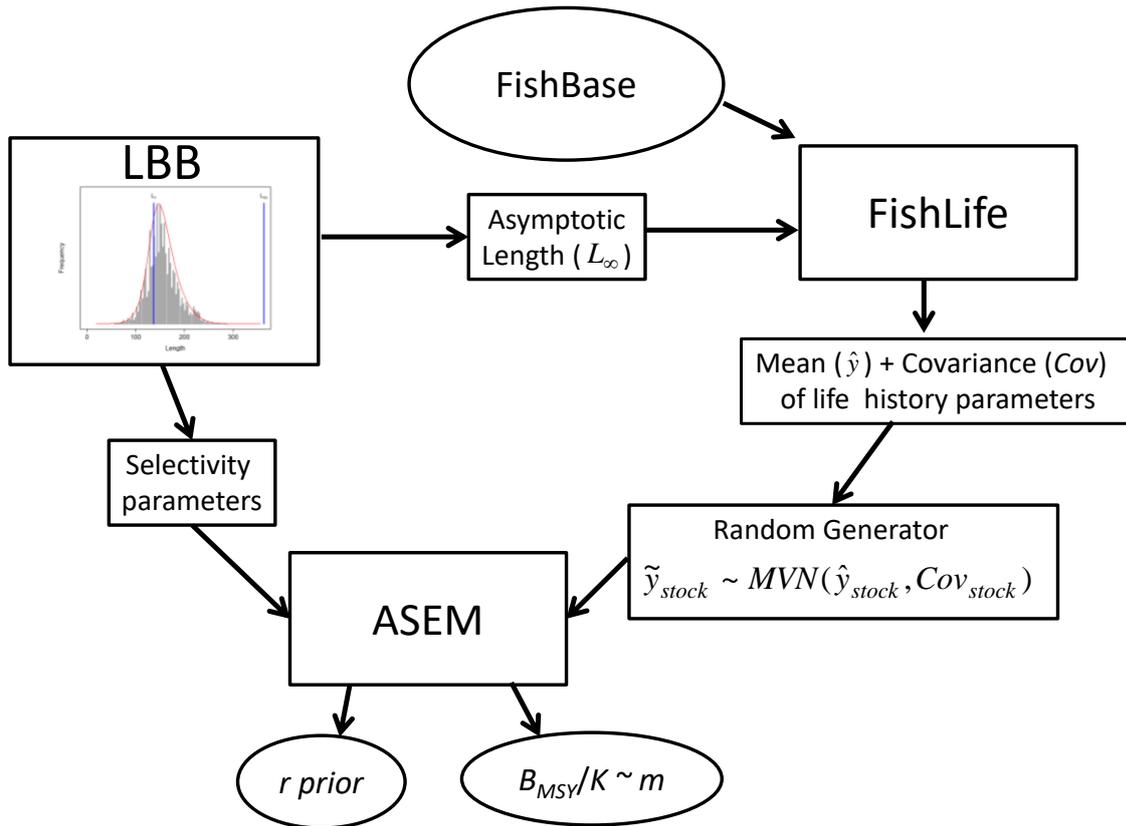
a) Striped marlin (MLS)						
Parameters	$h=0.4$	$h=0.5$	$h=0.6$	$h=0.7$	$h=0.8$	$h=0.86$
prior mean $r$	0.209	0.252	0.28	0.297	0.307	0.308
log.sd $r$	0.14	0.15	0.15	0.15	0.15	0.16
$B_{MSY}/B_0$	0.4	0.36	0.32	0.28	0.24	0.21
shape $m$	1.18	0.95	0.76	0.61	0.46	0.38
b) Black marlin (BLM)						
Parameters	$h=0.4$	$h=0.5$	$h=0.6$	$h=0.7$	$h=0.8$	$h=0.86$
prior mean $r$	0.145	0.174	0.193	0.204	0.21	0.211
log.sd $r$	0.29	0.30	0.30	0.30	0.30	0.31
$B_{MSY}/B_0$	0.41	0.37	0.34	0.3	0.26	0.24
shape $m$	1.23	1.01	0.84	0.69	0.55	0.47



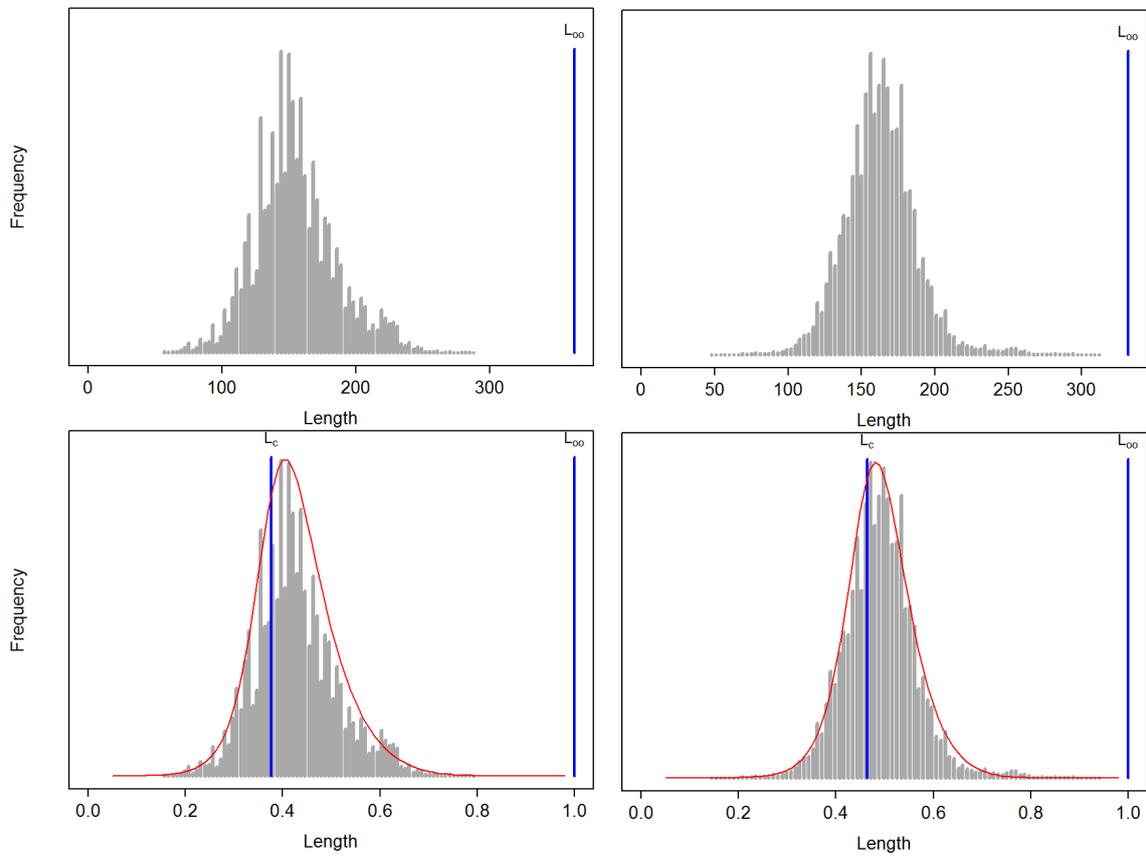
**Figure 1.** Surplus production as a function of biomass for different values of the shape parameter  $m = 0.1 - 4$  (from left to right) based the JABBA Pella–Tomlinson model formulation (Winker et al. 2018a)



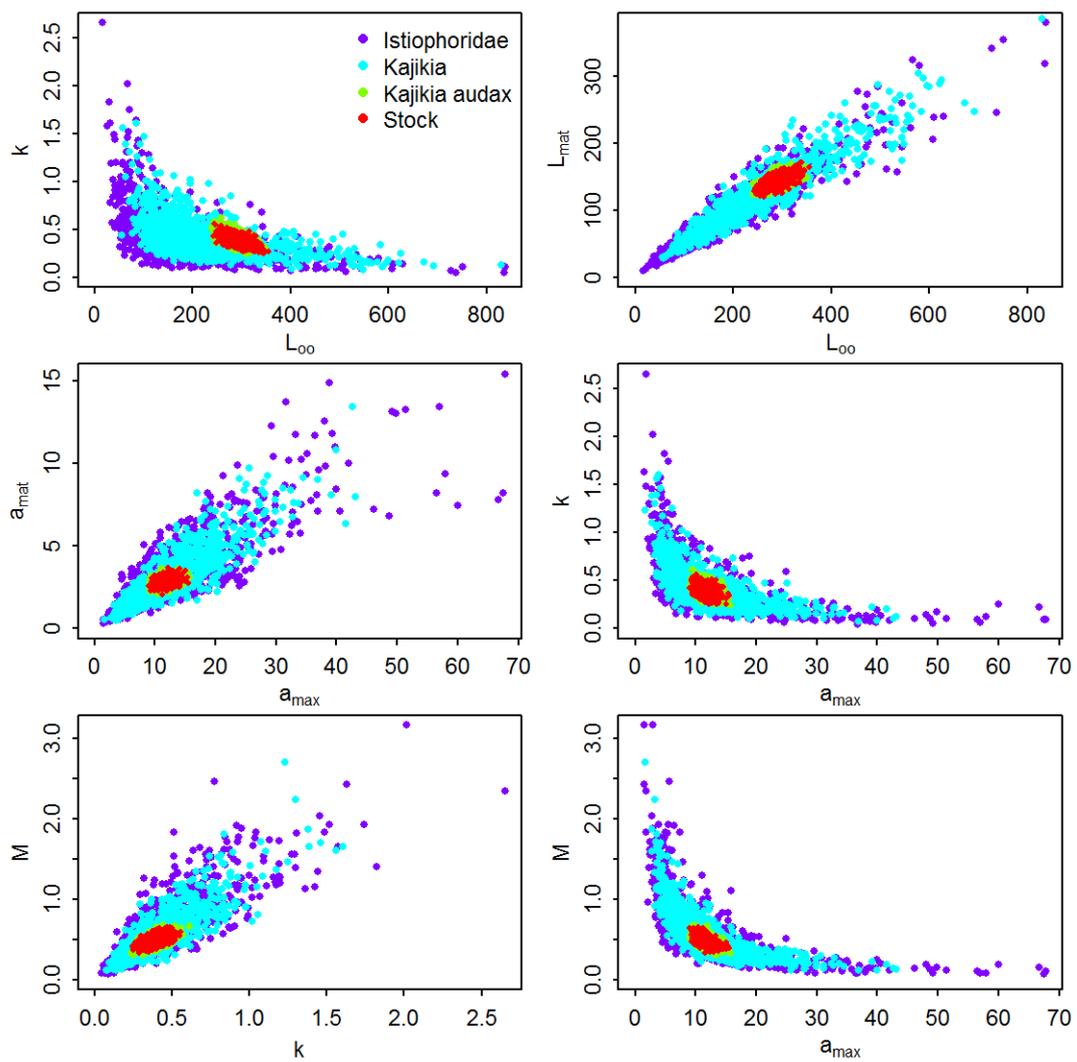
**Fig. 2.** Schematic of functional relationships between the productivity parameter  $r$  and the shape parameter of the surplus production function and the Age-Structured Equilibrium Model (ASEM; i.e. yield- and spawning biomass-per-recruit models with integrated spawner recruitment relationship). Numbers in boxes denote the sequence of deriving deviates of  $r$  and  $m$  from life history and selectivity parameter inputs into the ASEM.



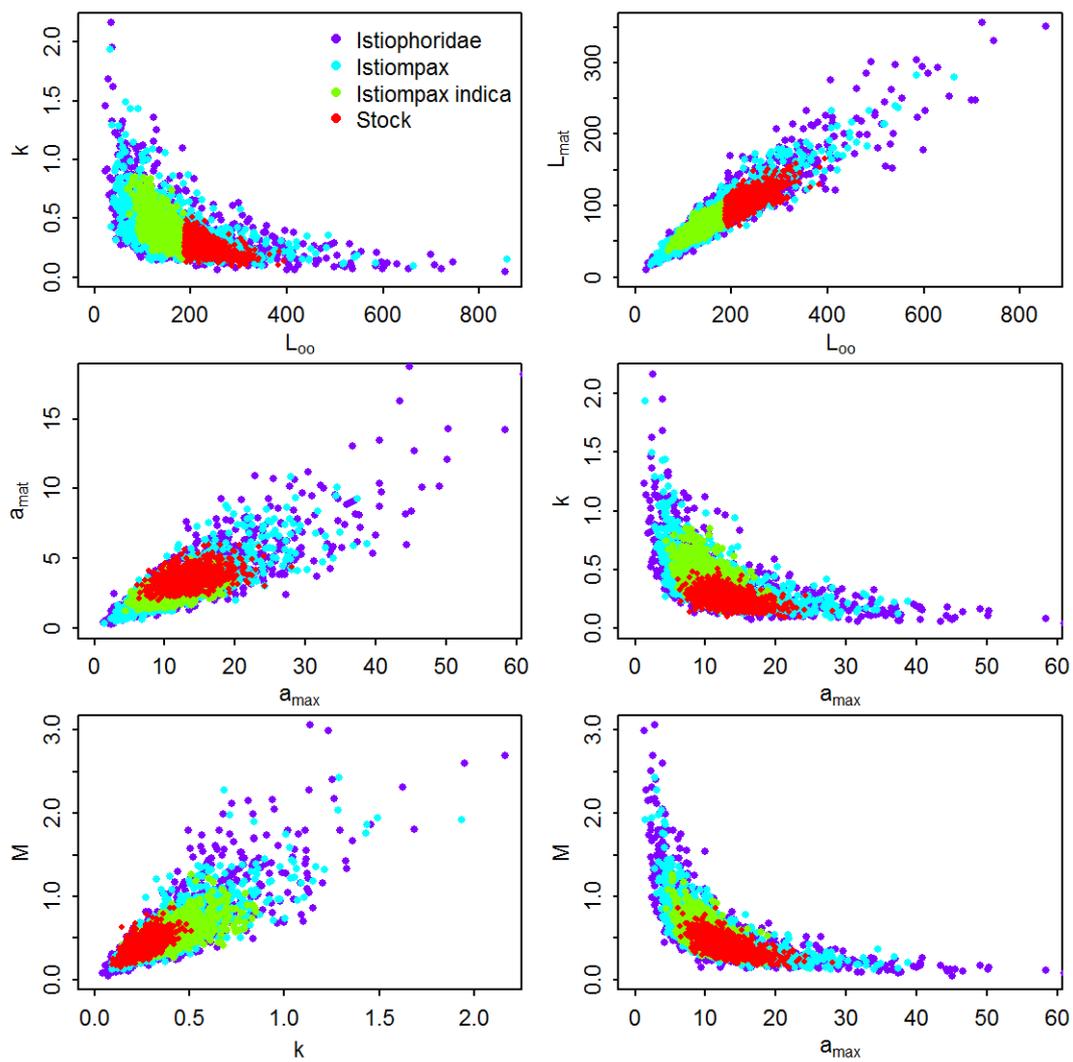
**Fig. 3.** Schematic illustrating the steps for objectively deriving informative  $r$  priors and associated input values of  $B_{MSY}/K$  as a function (“ $\sim$ ”) of the shape parameter  $m$  of Pella-Tomlinson surplus function. ASEM: Age-Structured Equilibrium Model; LBB: Length-based Bayesian length frequency analysis (Froese et al., 2018); *FishLife*: Multivariate life history prediction model (Thorson et al. in press);  $\hat{y}_{stock}$ : Expected stock-specific means of life history parameters predicted by the *FishLife* multivariate model,  $Cov_{stock}$ : Covariance matrix for  $\hat{y}_{stock}$  predicted by *FishLife*; MVN: random Multivariate Normal number generator applied to generate random deviates of life history as input for the ASEM.



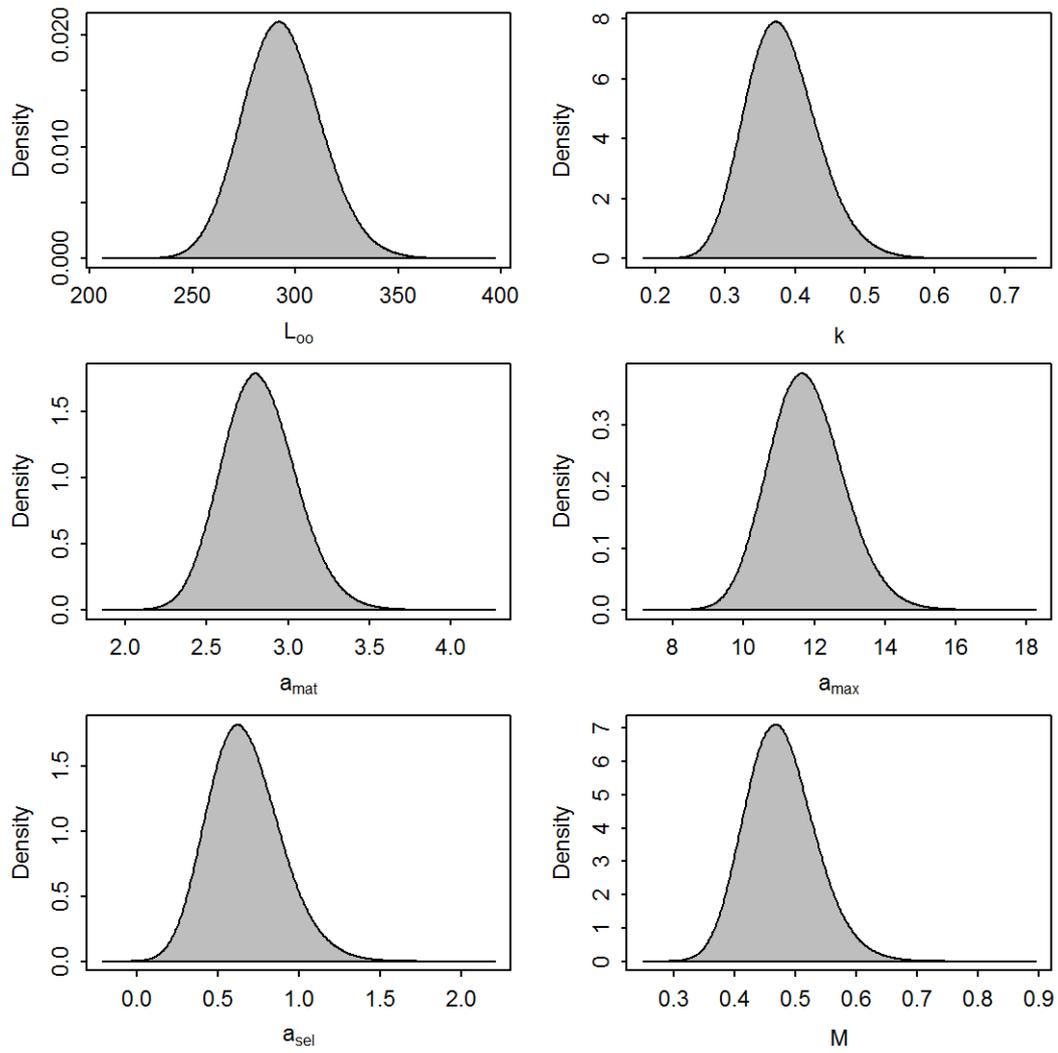
**Fig. 4** Observed length (cm) frequency data from longline fleet of Taiwan, China (upper panel), which were binned into 3 cm length interval ( $L_i$ ) and pooled for the period 2000-2016 for striped marlin (MLS; left) and black marlin (BLM; right). The lower panel shows the LBB fits (red line) to ratios of  $L_i/L_{50}$ , denoting the estimated relative length-at-50%-selectivity  $L_c/L_{50}$  for MLS (left) and BLM (right).



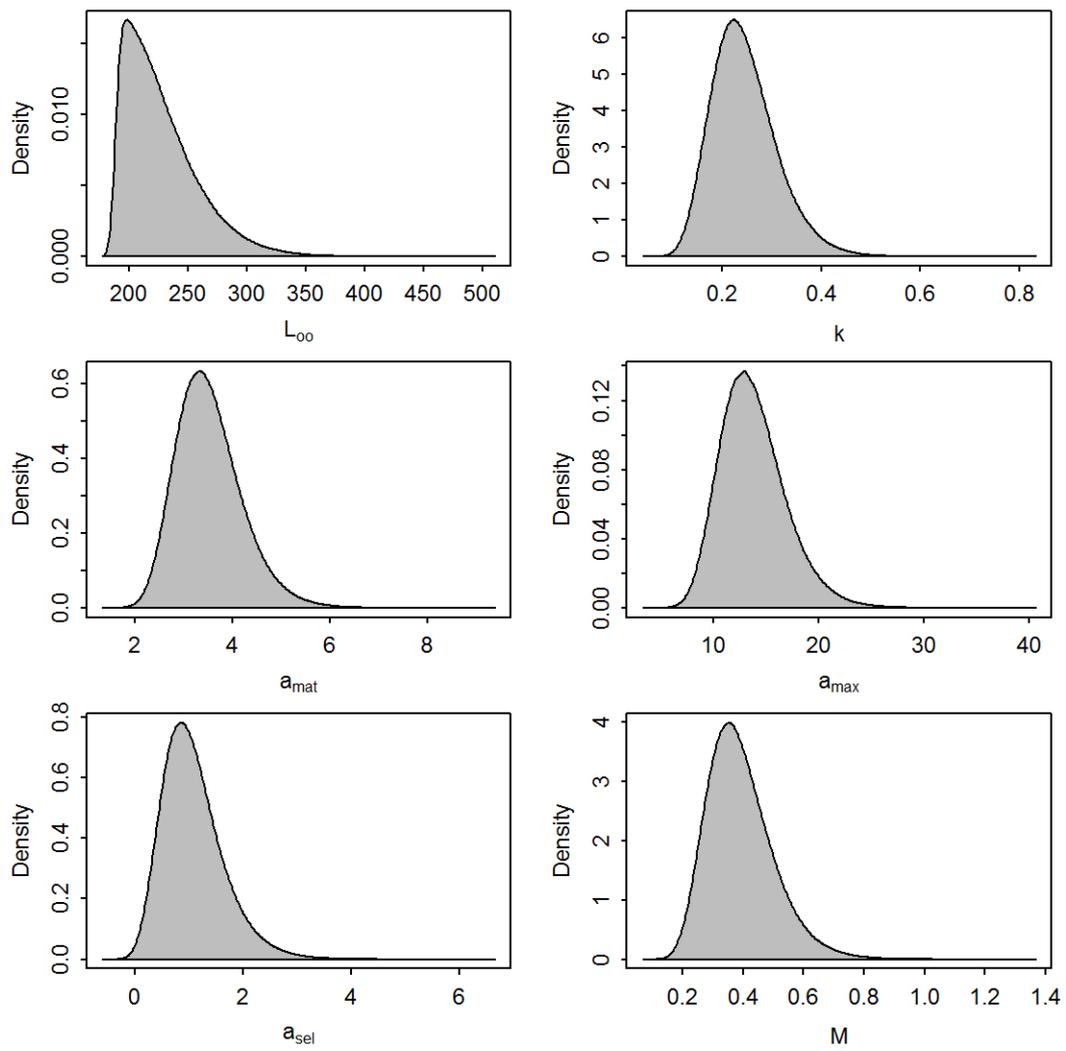
**Fig. 5.** Predictive distribution for six selected life-history variables on stock, species, genus and family level for Indian Ocean striped marlin, illustrating the parameter space and correlation for different combination of life parameters. The distributions were generated from a Multivariate Normal random generator based on predicted means and covariance matrices derived from the R package *FishLife*.



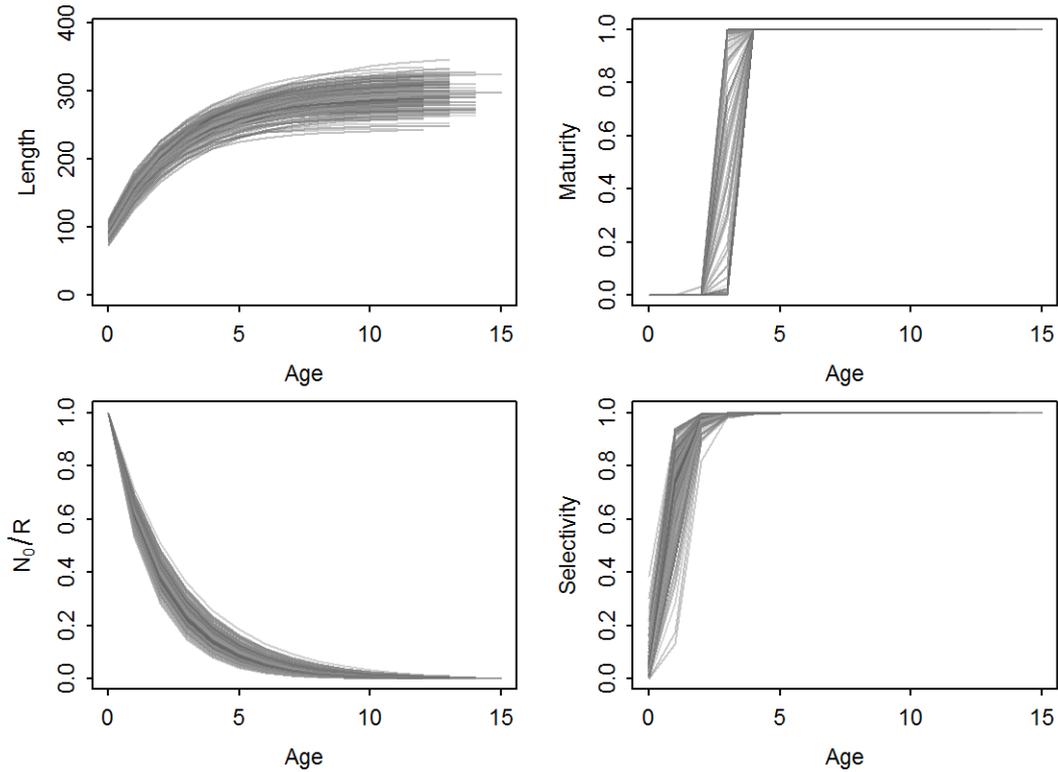
**Fig. 6.** Predictive distribution for six selected life-history variables on stock, species, genus and family level for Indian Ocean black marlin, illustrating the parameter space and correlation for different combination of life parameters. The distributions were generated from a Multivariate Normal random generator based on predicted means and covariance matrices derived from the R package *FishLife*.



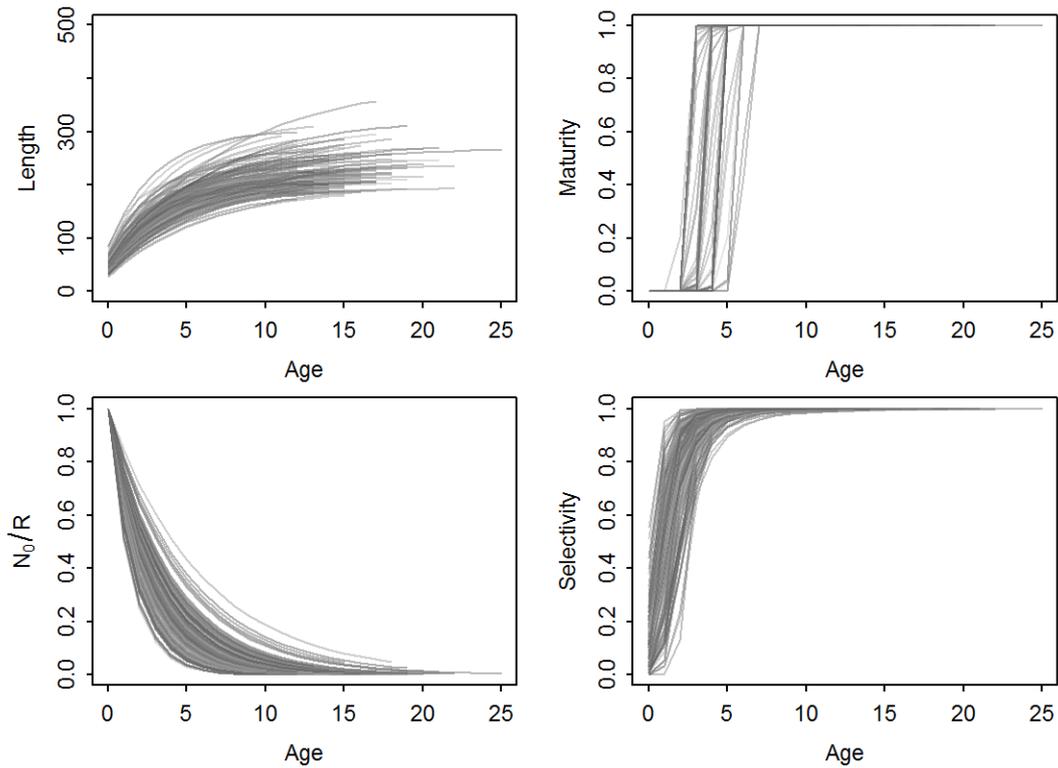
**Fig. 7.** Stock-specific kernel density distributions of generated life history parameter form a multivariate normal distribution for striped marlin (MLS).



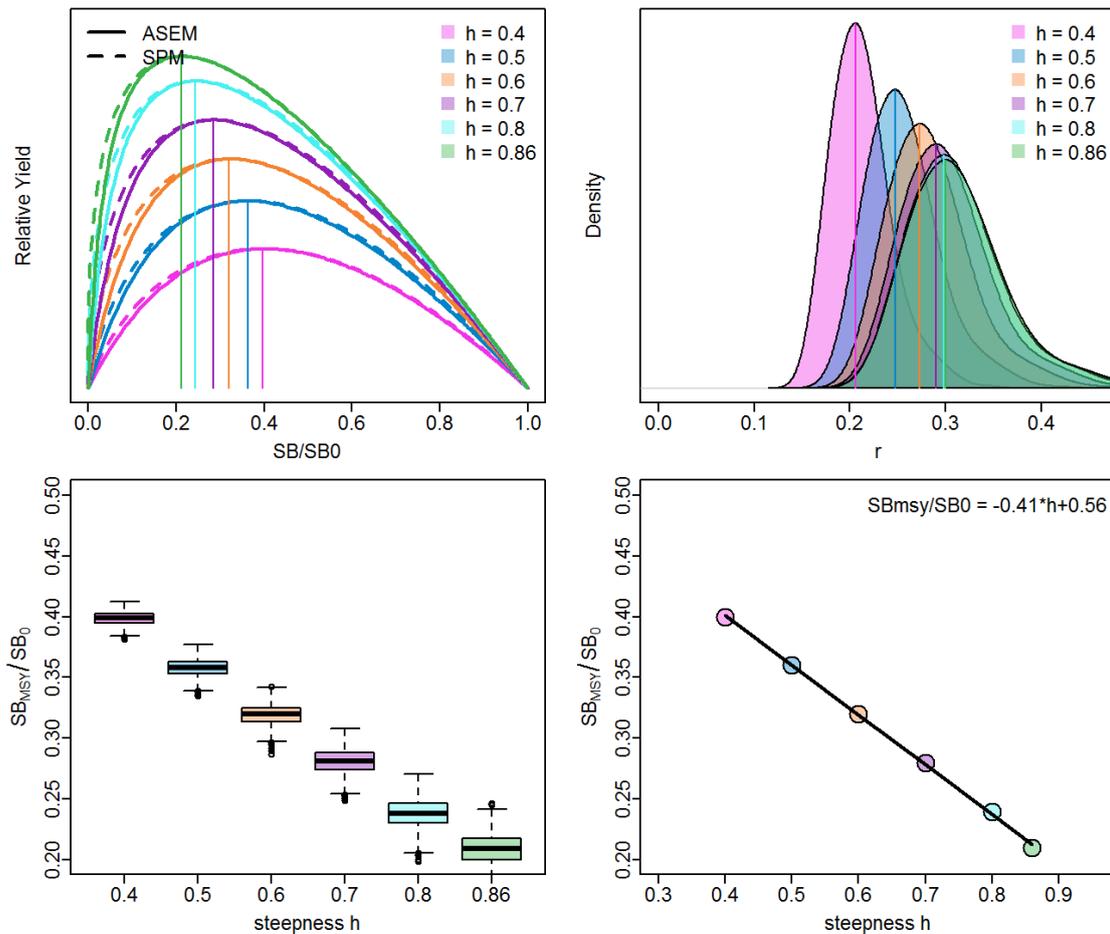
**Fig. 8.** Stock-specific kernel density distributions of generated life history parameter form a multivariate normal distribution for black marlin (BLM).



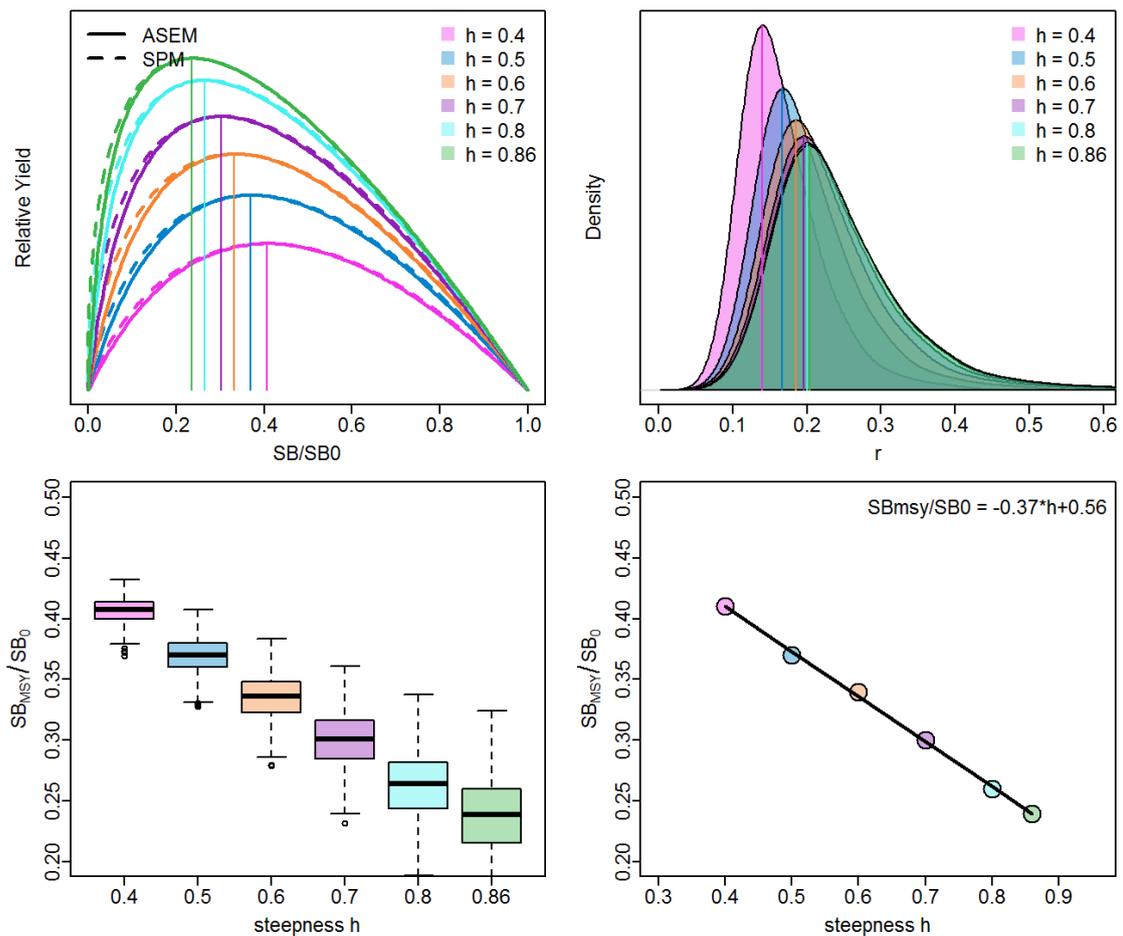
**Fig. 9.** Basic population dynamic functions for striped marlin (MLS) showing generated variations in length-at-age, maturity-at-age, unfished numbers-per-recruit as a function of natural mortality  $M$  and selectivity-age.



**Fig. 10.** Basic population dynamic functions for striped marlin (BLM) showing generated variations in length-at-age, maturity-at-age, unfished numbers-per-recruit as a function of natural mortality  $M$  and selectivity-age.



**Fig. 11.** Monte-Carlo simulation results from the Age-Structured Equilibrium Model (ASEM) for striped marlin (MLS), showing comparisons of the 14-parameter ASEM yield curve and 3-parameter Pella-Tomlinson surplus production over a range of steepness  $h$  values (upper left), the corresponding density distributions of simulated  $r$  values (upper right), boxplots of randomly generated ratios of  $SB_{MSY}/SB_0$  for each of the fixed steepness  $h$  input (low left) and the approximately linear relationship between of the steepness  $h$  and the means of the means of the generated  $SB_{MSY}/SB_0$  ratios.



**Figure 12.** Monte-Carlo simulation results from the Age-Structured Equilibrium Model (ASEM) for black marlin (BLM), showing comparisons of the 14-parameter ASEM yield curve and 3-parameter Pella-Tomlinson surplus production over a range of steepness  $h$  values (upper left), the corresponding density distributions of simulated  $r$  values (upper right), boxplots of randomly generated ratios of  $SB_{MSY}/SB_0$  for each of the fixed steepness  $h$  input (low left) and the approximately linear relationship between of the steepness  $h$  and the means of the means of the generated  $SB_{MSY}/SB_0$  ratios.