A STOCHASTIC PRIOR ON STEEPNESS FOR ATLANTIC SWORDFISH DERIVED FROM LIFE-HISTORY INFORMATION

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SUMMARY

We expanded the derivation of the Beverton and Holt steepness parameter h by Sharma and Arocha 2017 by simulating steepness values for a range of input parameters, including natural mortality, von Bertalanffy growth, maturity and early life history information. We derived or assumed standard deviations for the 15 quantities used for this derivation to simulate the resultant distribution of steepness. We present it with the corresponding distributions of lifehistory parameter distributions used to derive it. The former could be improved by developing a correlation matrix for the parameters so that a multivariate distribution could be fitted. This could be used to draw parameter combinations for deriving the distribution of steepness as input to MSE or to weight existing scenarios. Having a distribution for steepness and the associated life-history parameters used to derive it means that it is possible to input distributions of steepness, growth and mortality parameters as custom parameters in Operating Models for swordfish and others MSE so that combinations of such parameters can be appropriately weighted in Operating Models.

RÉSUMÉ

Nous avons étendu la dérivation du paramètre de pente h (steepness) de Beverton et Holt par Sharma et Arocha 2017 en simulant les valeurs de pente pour une gamme de paramètres d'entrée, y compris la mortalité naturelle, la croissance de von Bertalanffy, la maturité et les informations sur le début du cycle vital. Nous avons dérivé ou postulé des écarts types pour les 15 quantités utilisées pour cette dérivation afin de simuler la distribution de la pente qui en résulte. Nous la présentons avec les distributions correspondantes des distributions des paramètres du cycle vital utilisées pour la dériver. La première pourrait être améliorée en développant une matrice de corrélation pour les paramètres, de sorte qu'une distribution multivariée puisse être ajustée. Celle-ci pourrait être utilisée pour établir des combinaisons de paramètres afin de dériver la distribution de la pente en tant qu'entrée de MSE ou pour pondérer les scénarios existants. Le fait de disposer d'une distribution de la pente et des paramètres associés du cycle vital utilisés pour la dériver signifie qu'il est possible de saisir les distributions des paramètres de pente, de croissance et de mortalité en tant que paramètres personnalisés dans les modèles opérationnels pour la MSE de l'espadon et d'autres espèces afin que les combinaisons de ces paramètres puissent être pondérées de manière appropriée dans les modèles opérationnels.

RESUMEN

Ampliamos la derivación del parámetro h de inclinación de Beverton y Holt h por Sharma y Arocha 2017 mediante la simulación de los valores de inclinación para una serie de parámetros de entrada, incluyendo la mortalidad natural, el crecimiento de von Bertalanffy, la madurez y la información sobre la fase temprana del ciclo de vida. Derivamos o asumimos desviaciones estándar para las 15 cantidades utilizadas para esta derivación para simular la distribución resultante de la inclinación. Lo presentamos con las correspondientes distribuciones de los parámetros del ciclo vital utilizadas para derivarlo. El primero podría mejorarse elaborando una matriz de correlación para los parámetros, de modo que pudiera ajustarse una distribución multivariante. Esto podría utilizarse para extraer combinaciones de parámetros para derivar la distribución de la inclinación como entrada para la MSE o para ponderar los escenarios existentes. Disponer de una distribución para la inclinación y los parámetros asociados del ciclo

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vital utilizados para derivarla significa que es posible introducir las distribuciones de los parámetros de inclinación, crecimiento y mortalidad como parámetros personalizados en los modelos operativos para el pez espada y otras MSE, de modo que las combinaciones de dichos parámetros puedan ponderarse adecuadamente en los modelos operativos.

KEYWORDS

Mathematical models, Yield predictions, Computer programs, Tuna fisheries, Age at recruitment, Life history, Recruitment rate

1. Introduction

Recruitment steepness (Mace and Doonan 1988), commonly represented as h in age-structured stock assessment models is one of the key parameters that determines a stock's productivity and resilience. Indeed, it is a key component in determining the fishing mortality F that produces maximum sustained yield, *MSY*, or F_{MSY} . In practice however, steepness is difficult to estimate with typical fisheries data (Walters and Ludwig 1981; Ludwig and Walters 1985; Magnusson and Hilborn 2007). As a result of these difficulties, steepness is often fixed in stock assessment models and Operating Models (OMs) for Management Strategy Evaluation (MSE). In such cases uncertainty is often represented by integrating across a grid (Merino *et al.* 2017) of (typically) equally weighted alternatives (Sharma *et al.* 2020).

Some authors have been critical of fixing both steepness and natural mortality in stock assessment models. Mangel *et al.* 2010 shoes that steepness is a function of natural mortality so they cannot be considered independent. With respect to the practice of fisheries stock assessment generally, Mangel *et al.* 2013 noted that when a Beverton and Holt Stock Recruitment relationship is used and natural mortality and steepness are fixed, there is not much flexibility that remains for learning about reference points and the state of the stock from the data. Mangel *et al.* 2013 were especially critical of fishing steepness at unity or nearly so, stating that it amounted to assuming that there were an infinite number of age classes or assuming that the F_{MSY} is infinity. Mangel *et al.* 2013, are not the only authors who have been critical of fixing steepness see also (Brodziak *et al.* 2001, 2002; Martell *et al.* 2008; Mangel *et al.* 2010). Debate about how to properly model productivity parameters for fish stocks is not limited to steepness alone: Cortés 2016 argues for obtaining all vital rates simultaneously. While grids of steepness allow capturing some uncertainty in steepness and other parameters that is lost when steepness is fixed in a single stock assessment, the grid comes with some problems, and in particular how to weight each scenario in the grid. Given the difficulties in estimating steepness and on the other hand the problems of fixing it, the question to address is how to get sensible values for it in stock assessment and OMs?

Fortunately, Mangel *et al.* 2013 proposed some remedies to the fixing-steepness problem. Among them, they showed that with life-history information, it is possible to build a prior for steepness (Mangel *et al.* 2010). While the mathematics of the prior are slightly different, such priors are used in stock assessment for sharks but using the method described by (Cortes 2016, 2020). Such methods have also been applied to northern swordfish stock specifically (Sharma, R., Arocha 2017) but in this instance they did not explore a stochastic set of input values. Here we expand on the Sharma and Arocha 2017's analysis to develop a distribution of steepness and the relevant life-history parameters used to define them. After some additional work, this distribution could be input as a prior for fitting stock assessment models, custom parameters for MSE simulations, or used to weight existing OMs *post hoc*.

2. Methods

We expand on the work done by Sharma and Arocha 17 by adding variance each of the terms used to determine a distribution of steepness values. The derivation follows the method described by (Mangel *et al.* 2010). The derivation assumes that reproduction is not limited by males and that males and females have similar patterns of growth and mortality. Here steepness h is given as

$$h = \frac{\alpha_S SPR_0}{4 + \alpha_S SPR_0}$$

(1)

Where the slope at the origin (α_s), as per Brodziac *et al.* (2015) as the product of larval survival and the spawning biomass, calculated by using life history data from SWO north, and is expressed as:

$$\alpha_S = \frac{l_S \sum_a N_S F_a}{\sum_a F_a} \tag{2}$$

Where, *ls* is larval survival to the expected weight at age-0 under a von Bertalanffy growth function; Ns is the number of spawning events (days); F(a), expected egg production in a single spawning event for an age *a* fish; W(a) the weight of fish.

Spawning Biomass per Recruit (SPR₀) is:

$$SPR_0 = \sum_a l_a m_a w_a \tag{3}$$

Where *l* is the survivorship at age *a*, given as $l_a = e^{-M(a-1)}$ where M is the natural mortality of fish ages $a \ge 1$. *m* is the maturity at *a* and *w* is the weight at age *a* given as:

$$M_a = \frac{1}{1 + e^{-\Upsilon(L_a - l_{50})}}$$

Predicted weight at age a is given by:

$$w_a = \alpha L_a{}^\beta \tag{4}$$

Where α and β and the length to weight conversion parameters. Length at age La is given by the von Bertalanffy growth equation (von Bertalanffy 1938):

$$L_a = L_{\infty} (1 - e^{-k(a - t_0)}) \tag{5}$$

Batch fecundity at age is:

$$f = \alpha^* + \beta^* a^{\psi} \tag{6}$$

So that the realized fecundity F at age

$$F_a = \sum_a \rho f_a \, m_a \tag{7}$$

This analysis takes the key input parameters from Sharm and Arocha 2017 and determines or assumes a standard deviation for each so that a distribution of input variables can be generated. The means and standard deviations for each input parameter are described in **Table 1**. As an initial attempt to simulate these distributions we simulated variance about these parameters as being uncorrelated, i.e., from a set of independent distributions.

3. Results

The combined simulated distributions for the key input parameters for the derivation of steepness and of the steepness itself are presented in **Figure 1**.

Importantly **Figure 1** shows that while the input distributions for the derivation of steepness are normal (by design), the resulting distribution of steepness is highly non normal. **Table 2** shows that 50% of the density is above 0.88.

As is expected from Mangel's 2010 derivation and equations 1 and 2, the derived values of steepness depend on the parameters used to derived it. These follow from equations 1 to 5 but we illustrate them with the results of the simulations. First, assumptions about M constitute assumptions about steepness. Figure 2 illustrates how steepness changes with changes in M (assuming all other parameters held equal). But M is not the only parameter that has a significant effect on steepness. While there is a non-linear negative relationship between h and M, there is a positive nonlinear relationship between S_e and h (Figure 3); in this case, we vary values of egg to larval survival from values of half the mean input value to double the mean value.

But *M* and S_e are not the only input parameters that have a large effect on the resultant *h*. We illustrate the correlations between all the input parameters and the resulting steepness in a pairs plot of the simulated values (**Figure 4**). Input parameters with relatively large effect (i.e., correlations greater than 0.1) include: *M* and L_{50} that are negatively correlated with *h*; as well as β^* , δ , parchange, the number of spawning days v, and the daily larval survival *Se* that are positively correlated (**Table 3**).

Discussion

Here we have derived a prior for the distribution of steepness and other key parameters that determine it. The distribution of steepness is highly non normal. This resembles other priors that have been derived using this method (Mangel *et al.* 2010; Brodziak and Mangel 2012) in that its distribution is skewed left leading these investigators to represent these distributions with Beta distributions.

The skewed nature of the distribution for h means that analysts should consider fixed values of M and the resulting h to ensure that there are consistent because they are not independent. Given how steepness is determined, assumptions about M imply corresponding values of h. Therefore, how grids of OMs with different values of h and M should be weighted requires careful consideration: given the shape of this prior, it is improbable that values of steepness that are uniformly distributed should be equally weighted. Values of steepness in grids of OMs or stock assessment models should be inversely proportional to values of M.

This multivariate distribution is potentially useful for a variety of situations. First, the distributions of steepness and M could be used as a prior for stock assessment: this would alleviate some of the problems identified by Mangel *et al.* 2013 that by fixing steepness and natural mortality stock assessment scientists essentially limit how much the data used in model fitting can actually inform reference points (Mangel *et al.* 2013). Secondly, a multivariate distribution of steepness, natural mortality, and the von Bertalanffy growth parameters could be input into Operating models for MSE directly as custom parameters (Carruthers and Hordyk 2018); in this way scenarios that incorporate and variability in M and h could be consistent and avoid choosing combination of parameters in scenarios that given the life history, are highly unlikely. Indeed, in an analogous situation, i.e., estimating the intrinsic rate of population increase (Cortés 2016) it has been recommended that all the vital rates be obtained simultaneously to provide estimates of the r_{max} that are plausible given other vital rates. Finally, by fitting a multivariate distribution function to the data, one could estimate a multi-variate density function that could be used for determining the relative weight of existing MSE OMs that could not otherwise be weighted by their fits to the data.

Additional work is needed on how characterizing the uncertainty of the parameters underlying the estimates of steepness. One thing that is notable about the correlogram in **Figure 3** is what it is missing. The von Bertalanffy growth parameters (von Bertalanffy 1938) and natural mortality are typically correlated (Andersen *et al.* 2009; Gislason *et al.* 2010) as are correlations between the von Bertalanffy parameters themselves. L_{∞} and *K* are typically negatively correlated (Pilling *et al.* 2002; Taylor *et al.* 2005). But there it is not just correlation between the input parameters that requires some closer examination: some of the early life history parameters, for example larval survival rates have large effects on the resulting steepness but are potentially not well known.

References

- Andersen, K.H., Farnsworth, K.D., Pedersen, M., Gislason, H., and Beyer, J.E. 2009. How community ecology links natural mortality, growth, and production of fish populations. ICES J. Mar. Sci. 66(9): 1978–1984. doi:10.1093/icesjms/fsp161.
- von Bertalanffy, L. 1938. A Quantitative Theory of Organic Growth (Inquiries On Growth Laws. II). Hum. Biol. **10**(2): 181–213. Wayne State University Press. Available from http://www.jstor.org/stable/41447359.
- Brodziak, J., and Mangel, M. 2012. Probable Values of Stock-Recruitment Steepness for North Pacific Striped Marlin. : 1–13.
- Brodziak, J.K.T., Overholtz, W.J., and Rago, P.J. 2001. Does spawning stock affect recruitment of New England groundfish? Can. J. Fish. Aquat. Sci. **58**(2): 306–318. doi:10.1139/cjfas-58-2-306.
- Carruthers, T.R., and Hordyk, A.R. 2018. The Data-Limited Methods Toolkit (DLMtool): An R package for informing management of data-limited populations. Methods Ecol. Evol. 9(12): 2388–2395. doi:10.1111/2041-210X.13081.
- Cortes, E. 2016. Estimates of Maximum Population Growth Rate and Steepness for Blue Sharks. Collect. Vol. Sci. Pap. ICCAT **74**(4): 1822–1929.
- Cortes, E. 2020. Preliminary Estimates of Vital Rates and Population Dynamics Parameters of Porbeagle Shark in the Northwest Atlantic Ocean. Collect. Vol. Sci. Pap. ICCAT **76**(10): 164–172.
- Cortés, E. 2016. Perspectives on the intrinsic rate of population growth. Methods Ecol. Evol. 7(10): 1136–1145. doi:10.1111/2041-210X.12592.
- Gislason, H., Daan, N., Rice, J.C., and Pope, J.G. 2010. Size, growth, temperature and the natural mortality of marine fish. Fish Fish. **11**(2): 149–158. doi:10.1111/j.1467-2979.2009.00350.x.
- Ludwig, D., and Walters, C.I.J. 1985. Are Age-structured Models Appropriate for catch and Effort Data? Can. J. Fish. Aquat. Sci. **42**(6): 1066–1072.
- Mace, P.M., and Doonan, I.J. 1988. A Generalised Bioeconomic Simulation Model for Fish Population Dynamics. New Zealand Fishery Assessment Research Document 88/4. New Zeal. Fish. Assess. Res. Doc. 88/04.
- Magnusson, A., and Hilborn, R. 2007. What makes fisheries data informative? Fish Fish. **8**(4): 337–358. doi:10.1111/j.1467-2979.2007.00258.x.
- Mangel, M., Brodziak, J., and DiNardo, G. 2010. Reproductive ecology and scientific inference of steepness: A fundamental metric of population dynamics and strategic fisheries management. Fish Fish. 11(1): 89–104. doi:10.1111/j.1467-2979.2009.00345.x.
- Mangel, M., MacCall, A.D., Brodziak, J., Dick, E.J., Forrest, R.E., Pourzand, R., and Ralston, S. 2013. A perspective on steepness, reference points, and stock assessment. Can. J. Fish. Aquat. Sci. 70(6): 930– 940. doi:10.1139/cjfas-2012-0372.
- Martell, S.J.D.D., Walters, C.J., and Hilborn, R. 2008. Retrospective analysis of harvest management performance for Bristol Bay and Fraser River sockeye salmon (Oncorhynchus nerka). Can. J. Fish. Aquat. Sci. 65(3): 409–424. doi:10.1139/f07-170.
- Merino, G., Arrizabalaga, H., Santiago, J., and Sharma, R. 2017. Uncertainty grid for north Atlantic albacore management strategy evaluation: conditioning operating models. Collect. Vol. Sci. Pap. ICCAT 74(2): 432–456.
- Pilling, G.M., Kirkwood, G.P., Walker, S.G., and Mangel, M. 2002. An improved method for estimating individual growth variability in fish, and the correlation between von Bertalanffy growth parameters. Can. J. Fish. Aquat. Sci. 59: 424–432.
- Serafy, J.E., Cooke, S.J., Diaz, G.A., Graves, J.E., Hall, M., Shivji, M., and Swimmer, Y. 2012. Circle hooks in commercial, recreational, and artisanal fisheries: Research status and needs for improved conservation and management. Bull. Mar. Sci. 88(3): 371–391. doi:10.5343/bms.2012.1038.

- Sharma, R., Arocha, F. 2017. Resiliency for North Atlantic Swordfish. Collect. Vol. Sci. Pap. ICCAT, **74**(3): 1306–1321.
- Sharma, R., Levontin, P., Kitakado, T., Kell, L., Mosqueira, I., Kimoto, A., Scott, R., Minte-Vera, C., Bruyn, P., Ye, Y., Kleineberg, J., Walton, J., Miller, S., and Magnusson, A. 2020. Operating model design in tuna Regional Fishery Management Organizations: Current practice, issues and implications. Fish Fish. doi:10.1111/faf.12480.
- Taylor, N.G., Walters, C.J., and Martell, S.J.D. 2005. A new likelihood for simultaneously estimating von Bertalanffy growth parameters, gear selectivity, and natural and fishing mortality. Can. J. Fish. Aquat. Sci 62(1): 215–223. doi:10.1139/f2011-100.
- Walters, C.J., and Ludwig, D. 1981. Effects of measurement errors on the assessment of stock-recruitment relationships. Can. J. Fish. Aquat. Sci. **38**: 704–710.

Parameter	Symbol	Name	Mean	SD	Description		
Natural mortality for ages a>1	m	mort	0.245	0.0495	Estimated from mean of Honig's method estimated from max age 15 and max age 20		
Slope of the maturity ogive	Υ	mat.slope	1.24	0.248	Assumed to be 20% of the mean		
Length at 50% maturity	L ₅₀	mat.50	5.01	1.337	Derived from the reported percentiles		
Length weight coefficient	α	length.weight.alpha	7.16E-06	1.43E-06	Assumed to be 20% of the mean		
Length weight exponent	β	length.weight.beta	3.10	0.621	Assumed to be 20% of the mean		
Asymtotic size	L∞	vLinf	336	33.9	Estimated from the mean female growth parameter estimates from Sharma and Arocha 2017		
vonBertalanffy growth parameter	К	vonK	0.0632	0.0484	Estimated from the mean female growth parameter estimates from Sharma and Arocha 2017		
theoretical time at length=0	tO	vtto	-2.51	2.172	Estimated from the mean female growth parameter estimates from Sharma and Arocha 2017		
Batch fecundity constant	α*	BFConstant	1850000	369000	Assumed to be 20% of the mean		
Batch fecundity coefficient	β*	Bfa	77.4	15.5	Assumed to be 20% of the mean		
Batch fecundity exponent	Ψ	BFb	4.64	0.927	Assumed to be 20% of the mean		
Realized fecundity factor	ρ	RealizedFecFactor	2.6	0.52	Assumed to be 20% of the mean		
Number of spawning days	ν	NS	212	42.4	Assumed to be 20% of the mean		
Daily survival rate from egg to age 1	Se	Se	5.7E-09	1.14E-09	Assumed to be 20% of the mean		

Table 1. Summary of the mean and standard deviation values for life-history parameters used to derive steepness.

Probability	Quantile
0%	0.203663
10%	0.551689
20%	0.660099
30%	0.746024
40%	0.819011
50%	0.882329
60%	0.938938
70%	0.974879
80%	0.992004
90%	0.998646
100%	1

Table 2. Percentiles for the distribution of steepness.

Table 3. Correlations between the derived steepness (h) and the input parameters. Red colors indicate negative correlations and green correlations indicate positive ones.

h	1
М	-0.30147
Linf	-0.00847
Κ	0.069608
t0	-0.02495
mat.50	-0.13761
mat.slope	-0.02773
lw.alpha	0.012327
lw.beta	-0.07673
BFCons	0.093292
Bfa	0.060901
BFb	0.566376
ParChange	0.542352
RealFFact	0.062638
NS	0.102194
Se	0.152083



Figure 1. Distribution of resulting steepness (h) and corresponding vonBertalanffy K, L_{∞} , t_0 , and natural mortality M used to derive it. Vertical solid lines represent the median.



Figure 2. The relationship between natural mortality *M* and the derived value of steepness.

Figure 3. The relationship between the egg to larval survival (*Se*) and steepness (*h*).

	h	М	Linf	к	t0	mat.50	mat.slope	lw.alpha	lw.beta	BFCons	Bfa	BFb	ParChange	RealFFact	NS	Se	
a constant		Corr: -0.301***	Corr: -0.008	Corr: 0.070*	Corr: -0.025	Corr: -0.138***	Corr: -0.028	Corr: 0.012	Corr: -0.077*	Corr: 0.093**	Corr: 0.061.	Corr: 0.566***	Corr: 0.542***	Corr: 0.063.	Corr: 0.102**	Corr: 0.152***	7
0.4		\wedge	Corr: 0.015	Corr: 0.010	Corr: -0.016	Corr: 0.007	Corr: -0.026	Corr: -0.001	Corr: 0.048	Corr: 0.066.	Corr: -0.001	Corr: -0.023	Corr: -0.039	Corr: 0.017	Corr: 0.018	Corr: 0.022	м
400 350 300		-	A	Corr: -0.030	Corr: -0.050	Corr: -0.027	Corr: 0.016	Corr: 0.045	Corr: -0.003	Corr: -0.012	Corr: -0.069.	Corr: -0.023	Corr: -0.018	Corr: -0.045	Corr: 0.009	Corr: -0.027	Linf
821	15000			\frown	Corr: 0.004	Corr: -0.033	Corr: 0.041	Corr: 0.077*	Corr: -0.036	Corr: 0.037	Corr: 0.002	Corr: 0.020	Corr: -0.004	Corr: 0.014	Corr: 0.024	Corr: -0.045	×
0257		-	-		$ \land $	Corr: 0.012	Corr: -0.036	Corr: 0.022	Corr: -0.011	Corr: -0.069.	Corr: 0.007	Corr: 0.004	Corr: 0.029	Corr: 0.024	Corr: -0.033	Corr: -0.067.	8
10.0	Million	-			-	\wedge	Corr: 0.028	Corr: -0.024	Corr: 0.073*	Corr: 0.008	Corr: -0.057	Corr: -0.011	Corr: 0.035	Corr: 0.001	Corr: 0.006	Corr: -0.038	mat.50
2.0 1.5 1.0		-				-	\wedge	Corr: -0.054	Corr: 0.012	Corr: 0.002	Corr: -0.051	Corr: -0.026	Corr: -0.014	Corr: -0.041	Corr: -0.001	Corr: -0.002	nat.slop-
1e-06								$ \land $	Corr: 0.027	Corr: -0.012	Corr: -0.006	Corr: -0.009	Corr: 0.017	Corr: 0.092**	Corr: -0.042	Corr: -0.028	hv.alpha
The state of the s	-	-				-		-	\wedge	Corr: -0.027	Corr: -0.017	Corr: -0.057	Corr: 0.017	Corr: 0.050	Corr: 0.029	Corr: 0.047	hv.beta
351388	-	-	NOR			-		-		N	Corr: 0.006	Corr: 0.054	Corr: 0.003	Corr: 0.060.	Corr: 0.024	Corr: 0.014	BFCons
185			-							-	$ \land $	Corr: -0.033	Corr: 0.038	Corr: -0.008	Corr: -0.033	Corr: 0.008	Bfa
0041	-	-				-						\wedge	Corr: 0.012	Corr: -0.088*	Corr: -0.048	Corr: 0.025	BFb
1.5	-	-					-			-	-		A	Corr: -0.019	Corr: 0.000	Corr: 0.052	arChang
4004		-								-				\wedge	Corr: 0.068.	Corr: -0.020	ealFFac
300 200 100	-				-			-		*			*		\wedge	Corr: -0.051	NS
8e-09 6e-09 4e-09 2e-09			4350300350400					-		-		-			10. 200. 200.2	\bigwedge	Se

Figure 4. Correlogram of steepness and key life history parameters. The upper right triangle displays correlations between the input parameters and with the resulting steepness. *** indicates that correlation is significant with p-value is < 0.001, ** if the p-value is < 0.01 and * if the p-value is < 0.05, "." if the p-value is < 0.10.