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A MULTIVARIATE MODEL FOR ESTIMATING LIFE HISTORY PARAMETERS FOR NORTH AND SOUTH ATLANTIC OCEAN BLUE SHARK STOCKS

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SUMMARY

We obtain estimates of life history parameters and steepness from the FishLife database that contains the metanalytical information from Fishbase and from Myers Legacy data. The first stage in the estimation process was to conduct the analysis using the existing records in the FishLife database. The second stage was to update the analysis with most recent life-history parameters being applied in the 2023 ICCAT Blue Shark assessment. Finally, we compare the results of the parameters derived using FishLife with those using Leslie Matrix approaches. The set of life-history parameters and steepness can form the basis for priors in assessments and Operating Models for Management Strategy Evaluation.

RÉSUMÉ

Nous avons obtenu des estimations des paramètres du cycle de vie et de la pente à partir de la base de données FishLife qui contient les informations méta-analytiques de Fishbase et des données de Myers Legacy. La première étape du processus d'estimation a consisté à effectuer l'analyse en utilisant les registres existants dans la base de données FishLife. La deuxième étape a consisté à mettre à jour l'analyse avec les paramètres du cycle de vie les plus récents appliqués dans l'évaluation du requin peau bleue de l'ICCAT de 2023. Enfin, nous avons comparé les résultats des paramètres obtenus avec FishLife avec ceux obtenus avec les approches de la matrice de Leslie. L'ensemble des paramètres du cycle de vie et de la pente peuvent constituer la base des distributions a priori dans les évaluations et des modèles opérationnels pour l'évaluation de la stratégie de gestion.

RESUMEN

Obtenemos estimaciones de los parámetros del ciclo vital y de la inclinación a partir de la base de datos FishLife que contiene la información metanalítica de FishBase y de los datos de Myers Legacy. La primera etapa del proceso de estimación consistió en realizar el análisis a partir de los registros existentes en la base de datos FishLife. La segunda etapa consistió en actualizar el análisis con los parámetros más recientes del ciclo vital aplicados en la evaluación del tiburón azul de 2023 de ICCAT. Por último, comparamos los resultados de los parámetros derivados utilizando FishLife con los obtenidos mediante los enfoques de la matriz de Leslie. El conjunto de parámetros del ciclo vital y la inclinación puede constituir la base para las distribuciones previas en evaluaciones y los modelos operativos para la evaluación de estrategias de ordenación.

KEYWORDS

Natural mortality, Productivity, Steepness, Lifespan, Generation time, Stochastic models, Life history, Blue shark, meta-analysis, phylogenetic regression

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1. Introduction

Life history parameters including von Bertalanffy growth, natural mortality, age at maturity, and steepness form some of the basic ingredients for many stock assessment models. But it can be challenging to determine such age-specific demographic parameters. These difficulties can be due to data being unavailable, the data being unrepresentative, or ageing uncertainty. Another challenge is that in some cases, the statistical methods used to estimate these parameters are unreliable. Consider the von Bertalanffy growth parameters: the difficulties in estimating growth parameters and particularly the effects of historical fishing mortality and of size-selective sampling have long been known (Lee 1912; Ricker 1969; Parma and Deriso 1988) yet statistical methods that attempt to address these effects have not been very successful at estimating the underlying "true" parameters from simulated data (Taylor *et al.* 2005, Goodyear 2019). Given that any given point estimate of a life history parameter can be wrong, it is useful to define distributions for all life history parameters of interest. While it is difficult to include such distributions in stock assessments that rely on non-linear minimizers like AD Model Builder (Fournier *et al*. 2012), these distributions can be used for stock assessment with Bayesian methods like Sampling Importance Resampling (Hilborn *et al*. 1994, Walters *et al*. 2006). A second option is to use such parameter distributions in Operating Models for Management Strategy Evaluation (Punt *et al*. 2016). In MSE, having a multi-variate distribution of life-history parameters and steepness means avoiding some of the problems of having arbitrary grids of fixed parameters for natural mortality and steepness; by using the whole matrix of uncertainty for life-history and productivity parameters, there is an appropriate correlation structure. This therefore avoids unrealistic combinations of life history parameters and steepness (Taylor *et al.* 2022a, Taylor *et al.* 2022b).

Cortés (2016) documented several methods for deriving productivity parameters, one of which was based on multi-variate distributions of some life-history parameters. Multiple methods have been used to derive intrinsic rates of growth for stock assessment (McCallister *et al.* 2001) and similar methods relying on life history parameters have been developed to determine steepness (Mangel *et al*. 2011). These have been applied in stock assessment for scombrid fishes (Mangel *et al.* 2011), Xiphiidae (Brodziac and Mangel 2012, Taylor *et al*. 2022), and chondrichthyan fish (e.g., Cortés and Semba. 2020). Given the relationships between the life history and productivity parameters, Cortés (2016) argued for obtaining estimates of all required vital rates simultaneously, so the resulting productivity parameters are consistent with the life-history parameters that determine them.

Thorson *et al.* (2020) defined a new method for jointly estimating life history parameters and steepness. Thorson *et al.* (2017) used a multivariate model for trait evolution along a taxonomic tree, while using replicated samples for each individual species to distinguish trait evolution from residual covariance. This method generates multivariate distributions for life-history parameters and the productivity parameter steepness, h, (Mace and Doonan 1988). This model, available in the R package FishLife allows users to extract a set of life-history parameters by taxonomic group. Fishlife combined data from both the Fishbase database and the RAM Legacy Stock Assessment Database that is the descendant of Myers *et al.* (1999) meta-analysis of recruitment steepness (Mace and Doonan 1988) and/or Goodyear Compensation Ration (Goodyear 1980). Fishlife allows users to obtain matrices of life-history parameters including steepness at varying degrees of taxonomic resolution.

Here we apply the FishLife method to blue sharks and compare its results to those obtained using vital rates and the Leslie matrix methods (SCRS/2023/115).

2. Materials and Methods

Thorson *et al.* (2023) used a data-integrated life-history model, which extends a simple model of evolutionary dynamics to field-measurements of life-history parameters (Thorson *et al.* 2017) as well as historical records of spawning output and subsequent recruitment from the meta-analytical results of Myers and Mertz (1998). The approach is a modification of the evolutionary model used by Thorson *et al*. (2017) to fit both adult life-history parameters as well as stock-recruit measurements for over 150 fish populations worldwide. Thorson *et al* (2017) assumed that life-history parameters x_g for taxon g evolve to deviate from the parameters $x_{p(g)}$ for their taxonomic parent *p(g)*, where this deviation follows a multivariate normal distribution. Thorson *et al*. (2023) extended the Thorson *et al.* (2017) model to predict stock-recruit parameters by fitting to records of 225 spawning stock size and subsequent recruitment estimates from the RAM Legacy Stock Assessment Database. Each stock-recruit study with a corresponding vector of life-history and steepness estimates. This evolutionary model predicts recruitment productivity (the intrinsic rate of growth *r* and steepness, h) and recruitment variability (sigma_R) as well as life history parameters including natural mortality, maturity, growth, and size (see **Table 1** for a list of symbols). It uses these to predict intrinsic growth rates for all described fishes.

We apply this model to blue shark stock in the Atlantic Ocean. For illustrative purposes, we show the distribution of life history parameters for blue shark ancestors (i.e., class Chondrichthyes, order Carcharhiniformes, and family Carcharhinidae) but only consider the data at species-level resolution for the purpose of estimating the distribution of life-history parameters and productivity parameters steepness, h and the intrinsic rate of population growth, *r*. We focus on presenting eight key life-history parameters and h (**Table 1**). To visualize the resulting distribution for the FishLife model, we approximate it with a multivariate normal distribution (MVN) as

$$MVN=\mu\sum \quad (1)$$

where μ is the vector of means and ∑ is the covariance matrix. We drew 10000 samples from the MVN to visualize the parameter densities. To view the correlations between key life-history parameters in the FishLife MVN analysis, we solved for the correlation matrix τ as:

$$\tau = D^{-1}\sum D^{-1} \quad (2)$$

where D is the diagonal of ∑.

FishLife has the capacity to update life-history parameters with user-specified data. We did not explore this option because while the life-history parameters can be updated, productivity parameters cannot be associated with the update. Having separate sets of life-history parameters and productivity parameters would have been contrary to our objective of producing a joint distribution for productivity and life-history parameters.

Comparison with demographic parameter estimates

We explore the differences between the Fishlife's MVN parameter estimates, and the values used in SCRS/2023/115's Leslie matrix estimates for both the northern and southern Atlantic stocks.

We explore a third option for developing a multivariate distribution of life-history parameters for blue shark. The SPMpriors R package can generate demographic parameters with tuning from FishLife. The package operates by searching for the life history parameter set in FishLife and then updating these estimates with prior probability distributions for the *Loo, K, tmax, tm*, length at maturity *Lm* and *h*. Apart from h, which takes a uniform distribution, the other parameters' prior distributions are assumed to be normal. For *h*, we use the 95% upper and lower confidence limit on h (see Cortés and Taylor Table 3) to define the parameters of the normal distribution Cortés and Taylor 2023's Table 5. For *Loo*, *K*, *tmax*, *tm* we use values described in Cortés and Taylor's Table 1 and Table 2 for northern and southern stock respectively. For *M*, we use the mean and CV from the Leslie Matrix model estimates. For length at maturity, Anonymous 2015 report ranges of 192-208 and 168-188, respectively. Given that the SPMpriors package requires that the input be priors with normal distributions, we assume that

$$L_{m,n} \sim N(200,4)$$

for the northern *n* stock and

$$L_{m,s} \sim N(178,5)$$

for the southern *s* stock.

3. Results and Discussion

Fishlife Results

Figure 1 shows the Fishlife's predictive MVN distribution for 12 life-history variables of blue shark (*Prionace glauca*) as well as the predictive distribution for genus *Prionace* and its ancestral taxa. The shape and size of the ellipses represent the correlation and the covariance of each parameter pair at each ancestral taxonomic level. This figure represents some expected patterns, namely that as the analysis is conducted at higher degrees of taxonomic resolution the covariance (the area of the ellipses in **Figure 1**) gets smaller. At the coarsest taxonomic resolution i.e., the subclass Elasmobranchii, there is a large spread of parameter values. For most combination of parameters such as M, K, L_∞, W_∞, the covariance shrinks markedly as taxonomic level increases in resolution, but for recruitment autocorrelation (rho) and the variation in recruitment (Sigma_R), it remains high. This is likely because these parameters are usually poorly determined in most fisheries stock assessments.

Similarly, covariance in the productivity parameters (h and r) remains uncertain at the species level. In stock assessments, productivity and the unfished biomass or recruitment are often poorly determined because the data lack contrast to estimate them reliably (Ludwig and Walters, 1985; Magnusson and Hilborn 2007). Barring the unusual situation where the data stock was depleted and allowed to recover, estimates of productivity and the unfished state are confounded because there is not enough information in the data to distinguish between a stock that had a high unfished state but low productivity (i.e., low h) and vice versa. Accordingly, it is reasonable to expect a wide range of steepness or r values for a given taxon in the RAM legacy database. These expectations were realized: the range of credible values for h ranges from 0.2 to about 0.83 and rmax from about 0.003 to 0.45; this is a huge variability. It would encompass the h for the SA stock (0.78) and the rmax values for both stocks (0.39 and 0.30) obtained with the stochastic Leslie matrix approach SCRS/2023/115.

Figure 2 is the correlation matrix of the Fishlife MVN parameters. They correlated in expected ways but at different magnitudes. For example, *tm* was positively correlated with *Lm* and *tmax* as expected: age at maturity increases as maximum age increases and is also associated with longer length at maturity; and M was negatively correlated with *tm*, *tmax*, and *Lm*. But the magnitude of the correlation coefficient for other combinations was much smaller than expected. Whereas the predictive distribution's correlation coefficient between Linf and K was -0.06 (**Figure 2**). Other analyses have shown that the correlation between K and $L\infty$ can be much higher: Cummings *et al.* (2016) showed these parameters having a median correlation coefficient of -0.69 and Helser *et al.* (2007) showed that for Pacific rockfishes this correlation coefficient is -0.85. Most importantly this correlation coefficient differs from the correlation coefficient estimated in SCRS/2023/115 where the correlation coefficient for North Atlantic blue shark was 0.98.

Figure 3 shows the density of log parameter estimates for blue shark estimated using FishLife and **Figure 4** shows the exponentiated values log parameter estimates of h, K, L_∞, M, t_m, and t_{max}. Summary statistics for h, M and r are shown in **Table 3** and their corresponding density estimates in **Figure 5**.

Comparison between Fishlife estimates and demographic methods

The Fishlife MVN normal method and the methods used to h and r from life history parameters (Cortés and Taylor 2023, SCRS/2023/115) represent different hypotheses about how productivity parameters like h and r can be predicted. Fishlife determines h and r by estimating correlations between stock-recruit parameters either across related taxa or with life-history parameters (Thorson *et al.* 2019). In addition to being fundamentally different hypotheses, the data sources are also different. The FishLife MVN method uses life-history values from Fishbase and Myers and Mertz (1998) whereas SCRS/2023/115 uses a set of life-history parameter estimates agreed-upon at Anonymous 2023 (BSH DP reference). Accordingly, we expected results would be different.

The prediction that h estimates would differ between the two methods was realized. Values for h are very different for both methods. While the mean estimates of h for northern and southern stocks are similar at 0.84 and 0.78, respectively, the mean MVN h estimate was 0.36 (**Table 3**). The density of the Lesley matrix estimates for northern and southern stocks' steepness are not monotonic. Both have bimodal shapes. Densities of the MVN estimates for M and those generated using the Leslie matrix methods are shown in **Figure 5** (center). Estimates of M were more similar between the methods that they were for h (**Table 3**) with means of approximately 0.2 for all. The standard deviations of M for the MVN method were higher than for the Leslie matrix method estimates (**Table 3**).

As expected, differences between values of r determined using the different methods resemble the differences between the h estimates, with the FishLife MVN distribution having a much smaller mean (0.04) than the means estimated in Cortés and Taylor, 2023 using the Lesley matrix (**Table 3** and **Figure 5**, bottom) with means of 0.40 and 0.29 for North (NA) and South Atlantic (SA) stocks respectively. Taylor and Cortés 2023 (Table 4) mean estimates of r using multiple methods other than the Leslie matrix/Euler-Lotka equation were in the order of 0.22 and 0.13 for NA and SA stocks, respectively. While taking means across multiple methods presents a wide range of uncertainty, the Leslie matrix method is the most complete because it uses all the life history information available whereas the other methods make simplifying assumptions; the Lesley matrix mean estimates were 0.39 and 0.29 for the north and south Atlantic, respectively (Taylor and Cortés 2023, Table 5). Even using the most conservative length-based method to compute M with the Leslie matrix approach, r estimates are well above the mean FishLife MVN estimate at 0.28 and 0.14 for the NA and SA respectively.

The dramatic differences between the FishLife MVN estimates cast some doubt on the veracity of the Fishlife results for sharks. The mean value of rmax=0.04 (a value of 0.019 is obtained using Fishlife for *P. glauca* with no ancestors) makes little sense because this is one of the most productive shark species. In addition, it is also difficult to understand how that the family carcharhinidae with multiple less productive species would have mean values almost 3 times the rmax value of blue sharks **(Table 2**). The inconsistencies are not limited to the Carcharhinidae either, Thorson's (2020) Table 4 reports r values of 0.02 for both carcharhiniformes and lamniformes, species.

Updating the FishLife MVN estimates with the demographic parameters inputs and outputs (*M* and *h*) resulted in more defensible parameter estimates than the MVN estimates or obtained directly from Fishlife. The updated marginal posterior distribution of the multivariate normal distribution MVN* are shown in **Figure 6** and **Figure 7** for the southern and northern stocks, respectively. For *r*, the posterior distributions were updated substantially by using priors. The updated means and standard deviations for MVN* are in **Table 4** and **Table 5** for the North and South respectively. While the mean *r* value (standard deviations in parentheses) from the original MVN estimate for blue sharks generally was 0.06(0.04) (**Table 3**) the mean MVN* estimate was 0.33 (0.35) and for the southern stock the MVN* estimate was stock 0.175(0.37) (**Table 5**). There were similarly large updates for *h* (**Figure 6** and **Figure 7**). Other than for *h* and *r*, updates to other parameter estimates were relatively small.

The results of this analysis suggest that for at least the shark taxa, Fishlife should be used with caution. They depart significantly from other analyses conducted estimating the productivity (as determined by *h* and *r*). While the addition of prior distributions helped bring these analyses into more realistic ranges, the fact that the posteriors were updated so much by the addition of the priors suggests that the FishLife database data are not very informative for these parameters. For immediate use in any application such as stock assessment, we would suggest that results from **Table 4** and **Table 5** or the demographic estimates in Cortés and Taylor 2023 be used.

References

Cortés, E. and Taylor N.G. 2023. Estimates of Vital Rates and Population Dynamics Parameters of Interest for Blue Sharks in the North and South Atlantic Ocean. SCRS/2023/115

Cortés, E. 2016. Perspectives on the intrinsic rate of population growth. Methods in Ecology and Evolution. 7(10), 1136–1145. https://doi.org/10.1111/2041-210X.12592

Cortés, E and Y. Semba. 2020. Preliminary estimates of vital rates and population dynamics parameters of interest for Porbeagle Shark in the Western North Atlantic and South Atlantic oceans. *Collect. Vol. Sci. Pap. ICCAT*, *76*:0 164–172.

Cummings, N., Sagarese, S., & Harford, B. (2016). Synthesis of Literature on vonBertalanffy Growth Parameter Correlations SEDAR49-AW-07.

Fournier, D. A., Skaug, H. J., Ancheta, J., Ianelli, J., Magnusson, A., Maunder, M. N., Nielsen, A., & Sibert, J. 2012. AD Model Builder: using automatic differentiation for statistical inference of highly parameterized complex nonlinear models. Optimization Methods and Software, 27, 233–249. https://doi.org/10.1080/10556788.2011.597854

Goodyear, C. 1980. Compensation in fish populations.

Goodyear, C. P. 2019. Modeling Growth: Consequences from Selecting Samples by Size. *Transactions of the American Fisheries Society*, *148*: 528–551. https://doi.org/10.1002/tafs.10152

Hilborn, Mcallister, M. K., Pikitch, E. K., Punt, A. E., & Hilborn, R. (1994). A Bayesian approach to stock assessment and harvest decisions using the sampling importance resampling algorithm. Can. J. Fish. Aquat. Sci, 51, 2673–2687.

Helser, T. E., Stewart, I. J., and Lai, H.-L. L. 2007. A Bayesian hierarchical meta-analysis of growth for the genus Sebastes in the eastern Pacific Ocean. Canadian Journal of Fisheries and Aquatic Sciences, 64: 470–485. https://doi.org/10.1139/f07-024

Lee, R. M. 1912. An Investigation into the Methods of Growth Determination in Fishes by Means of Scales. ICES Journal of Marine Science, S1: 3–34. https://doi.org/doi.org/10.1093/icesjms/s1.63.3

Ludwig, D., & Walters, C. J. 1985. Are Age-structured Models Appropriate for catch and Effort Data? Canadian Journal of Fisheries and Aquatic Sciences, 42: 1066–1072.

Mace, P. M., & Doonan, I. J. 1988. A generalized bioeconomic simulation model for fish population dynamics. New Zealand Fisheries Assessment Research Documents, 88/4.

Magnusson, A., & Hilborn, R. (2007). What makes fisheries data informative? Fish and Fisheries, 8: 337–358. https://doi.org/10.1111/j.1467-2979.2007.00258.x

Mangel, M., Brodziak, J., & DiNardo, G. 2010. Reproductive ecology and scientific inference of steepness: A fundamental metric of population dynamics and strategic fisheries management. *Fish and Fisheries*, *11*: 89–104. https://doi.org/10.1111/j.1467-2979.2009.00345.x

A. Myers, R., & Mertz, G. (1998). Reducing uncertainty in the biological basis of fisheries management by meta-analysis of data from many populations: a synthesis. Fisheries Research, 37(1), 51–60. https://doi.org/https://doi.org/10.1016/S0165-7836(98)00126-X

Myers, R. A., Bowen, K. G., & Barrowman, N. J. 1999. Maximum reproductive rate of fish at low population sizes. *Can. J. Fish. Aquat. Sci.*, *56*:2404–2419

McAllister, M. K. K., Pikitch, E. K. K., & Babcock, E. A. A. 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. *Canadian Journal of Fisheries and Aquatic Sciences*, *58*: 1871–1890. https://doi.org/10.1139/cjfas-58-9-1871

Punt, A. E., Butterworth, D. S., de Moor, C. L., De Oliveira, J. A. A., & Haddon, M. 2016. Management strategy evaluation: Best practices. Fish and Fisheries, 17: 303–334. https://doi.org/10.1111/faf.12104

Ricker, W. E. 1969. Effects of size-selective mortality and sampling bias on estimates of growth, mortality, production and yield. Journal of the Fisheries Research Board of Canada, 26: 479–541.

Sinclair, A. F., Swain, D. P., & Hanson, J. M. 2002. Measuring changes in the direction and magnitude of size-selective mortality in a commercial fish population. Can. J. Fish. Aquat. Sci, 59: 361–371.

Taylor, N. G., Walters, C. J., & 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: 215–223. https://doi.org/10.1139/f2011-100

Taylor, N. G., Ortiz, M., Kimoto, A., & Coelho, R. 2022a. Preliminary Closed-Loop Simulations for Northeast Porbeagle: Illustrating the Efficacy of Alternative Management Procedures and Assessment Frequency. Collect. Vol. Sci. Pap. ICCAT, 79: 216–230.

Taylor, N. G., Sharma, R., & Arocha, F. 2022b. A Stochastic Prior on steepness for Atlantic Swordfish derived from life history information. *Collect. Vol. Sci. Pap. ICCAT*, *79*: 693–704.

Thorson, J. T., Munch, S. B., Cope, J. M., & Gao, J. 2017. Predicting life history parameters for all fishes worldwide. Ecological Applications, 38(27), 2262–2276. https://doi.org/https://doi.org/10.1002/eap.1606

Thorson, J. T. 2020. Predicting recruitment density dependence and intrinsic growth rate for all fishes worldwide using a data-integrated life-history model. Fish and Fisheries, 21(2), 237–251. https://doi.org/10.1111/faf.12427

Thorson, J. T., Maureaud, A. A., Frelat, R., Mérigot, B., Bigman, J. S., Friedman, S. T., Palomares, M. L. D., Pinsky, M. L., Price, S. A., & Wainwright, P. (2023). Identifying direct and indirect associations among traits by merging phylogenetic comparative methods and structural equation models. Methods in Ecology and Evolution, 2023(June 2022), 1259–1275. https://doi.org/10.1111/2041-210X.14076

Walters, C. J., Martell, S. J. D., & Korman, J. 2006. A stochastic approach to stock reduction analysis. Canadian Journal of Fisheries and Aquatic Sciences, 63, 212–223.

Table 1. Key life history parameters

Parameter	*Symbol*
Asymptotic weight	Winf
Temperature	-
Age at maturity	Tm
Maximum age	tmax
Natural mortality	M
vonBertalanffy K	K
Length at maturity	Lm
Asymptotic length	L_∞
Beverton-holt steepness	h

Table 2. Summary of productivity parameter extracts from FishLife by taxonomic resolution including steepness *h*, and intrinsic rate of growth (*r*), and their corresponding standard deviations (sd) by taxonomic level (rows).

	mean h	*sd h*	*r*	*sd r*
Carcharhiniformes	0.36	0.19	0.11	0.21
Carcharinidae	0.35	0.18	0.11	0.17
Prionace glauca	0.31	0.13	0.04	0.05

Table 3. Summary statistics for natural mortality, steepness and intrinsic rate of growth for Leslie Matrix estimates and MNV summaries.

Description	*name*	*mean*	*median*	*sd*
Fishlife MNV Natural Mortality	M	0.20	0.20	0.04
Leslie matrix natural mortality N	M.N	0.18	0.18	0.02
Leslie matrix natural mortality S	M_S	0.20	0.20	0.02
Fishlife MNV steepness	h	0.36	0.35	0.10
Leslie matrix steepness N	h.N	0.84	0.86	0.11
Leslie matrix steepness S	h.S	0.78	0.80	0.13
Fishlife MNV instrinsic rate of growth	r	0.06	0.05	0.04
Leslie matrix intrinsic rate of growth N	r.N	0.40	0.39	0.14
Leslie matrix intrinsic rate of growth S	r.S	0.29	0.30	0.06

Table 4. Summary statistics of the updated marginal posterior densities for life history parameters MVN* for northern blue shark

Parameter	*mean*	*sd*
G	15.58	2.39
K	0.12	0.01
Lm	211.53	23.23
Loo	332.80	20.22
M	0.19	0.04
h	0.72	0.14
r	0.36	0.38
rho	0.71	0.21
sigR	0.36	0.17
tm	9.59	3.00
tmax	20.00	4.66

Table 5. Summary statistics of the updated marginal posterior densities for life history parameters MVN* for southern blue shark

key	*mean*	*sd*
G	14.76952	2.144897
K	0.12568	0.012903
Lm	212.0238	22.76178
Loo	333.308	17.92035
M	0.204985	0.037461
h	0.552287	0.164321
r	0.189709	0.26628
rho	0.598457	0.222734
sigR	0.381533	0.165158
tm	9.062892	3.243581
tmax	19.56061	4.244346

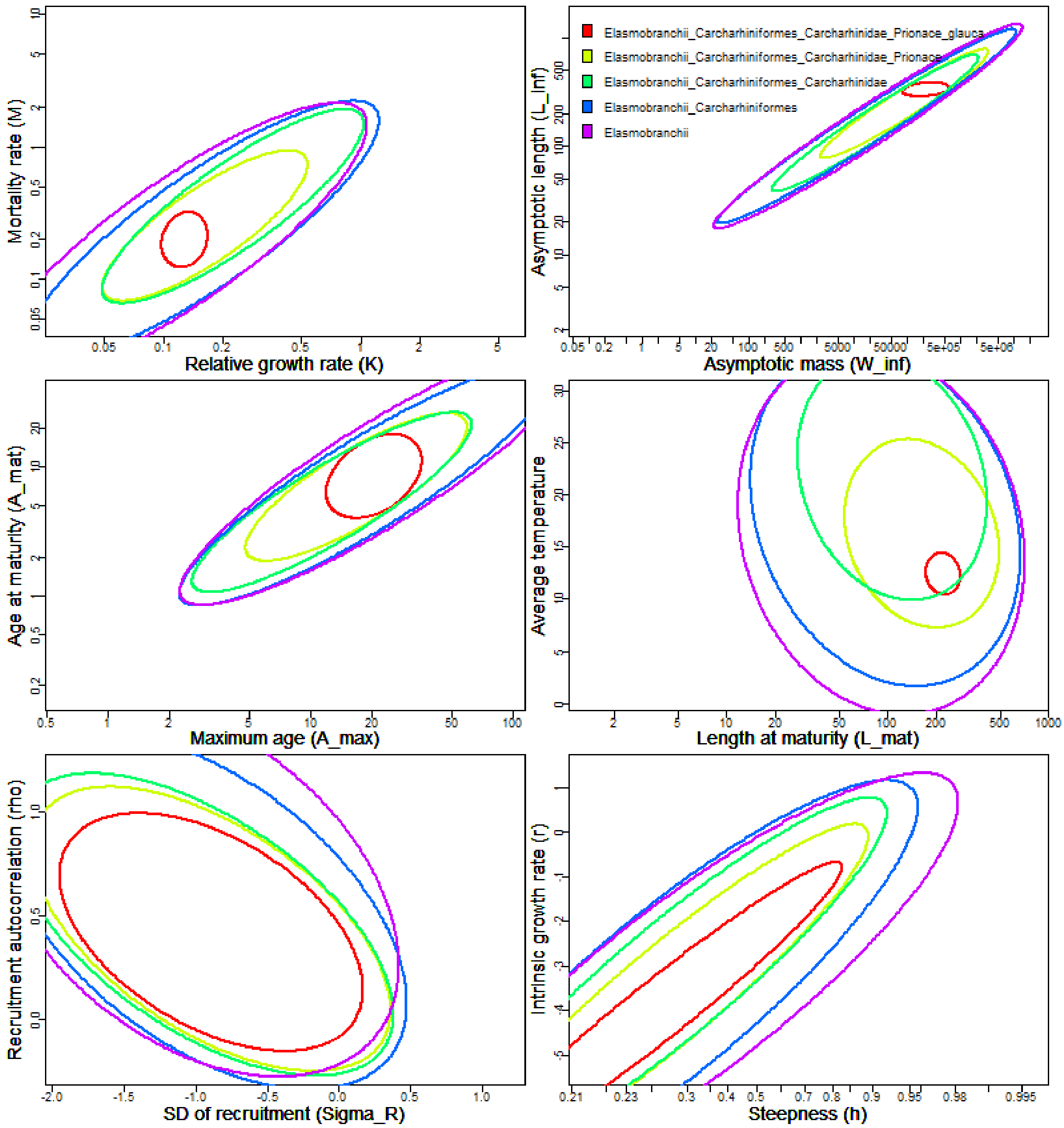

Figure 1. Predictive distribution for 12 life-history variables of blue shark (*Prionace glauca*) as well as the predictive distribution for genus *Prionace* and its ancestral taxa (Class, Chondrichthye, Order Carcharhiniformes and family Carcharhinidae). Panels show the 95% predictive distribution for all life-history variables in the Fishlife database: individual growth (x-axis) and natural mortality rate (y-axis; top-left right); asymptotic maximum weight (x-axis) and asymptotic maximum length (y-axis; top-right panel); maximum age (x-axis, middle left panel) and age at maturity (y-axis; middle-left panel); length at maturity (x-axis, middle right) and average temperature for the species' spatial distribution (y-axis; middle-right panel); as well as standard deviation in recruitment, Sigma_R (x-axis) and recruitment autocorrelation (y axis; bottom left panel).

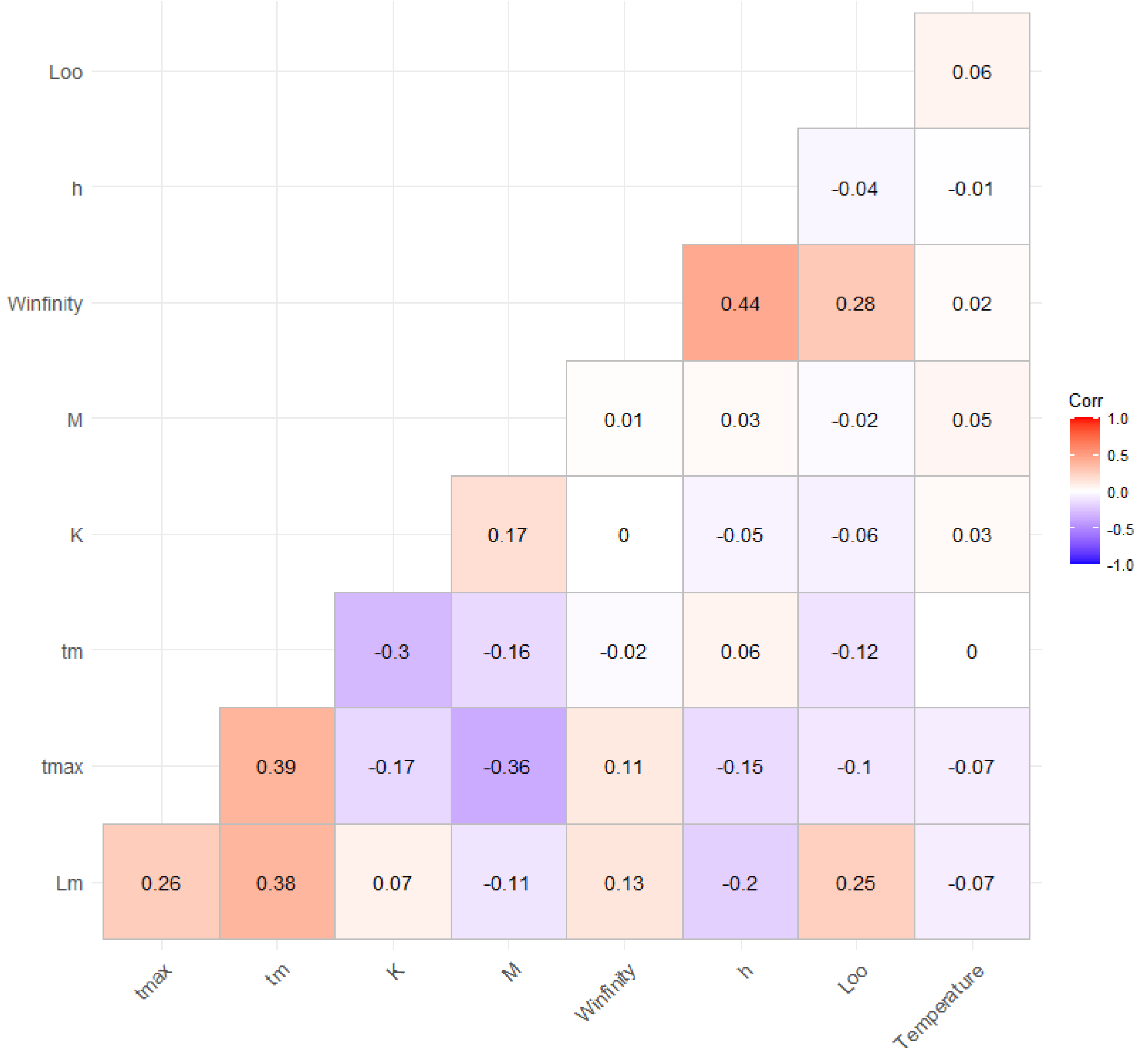

Figure 2. Correlation between the key life-history parameters and steepness h. Parameter symbols are listed in **Table 1**.

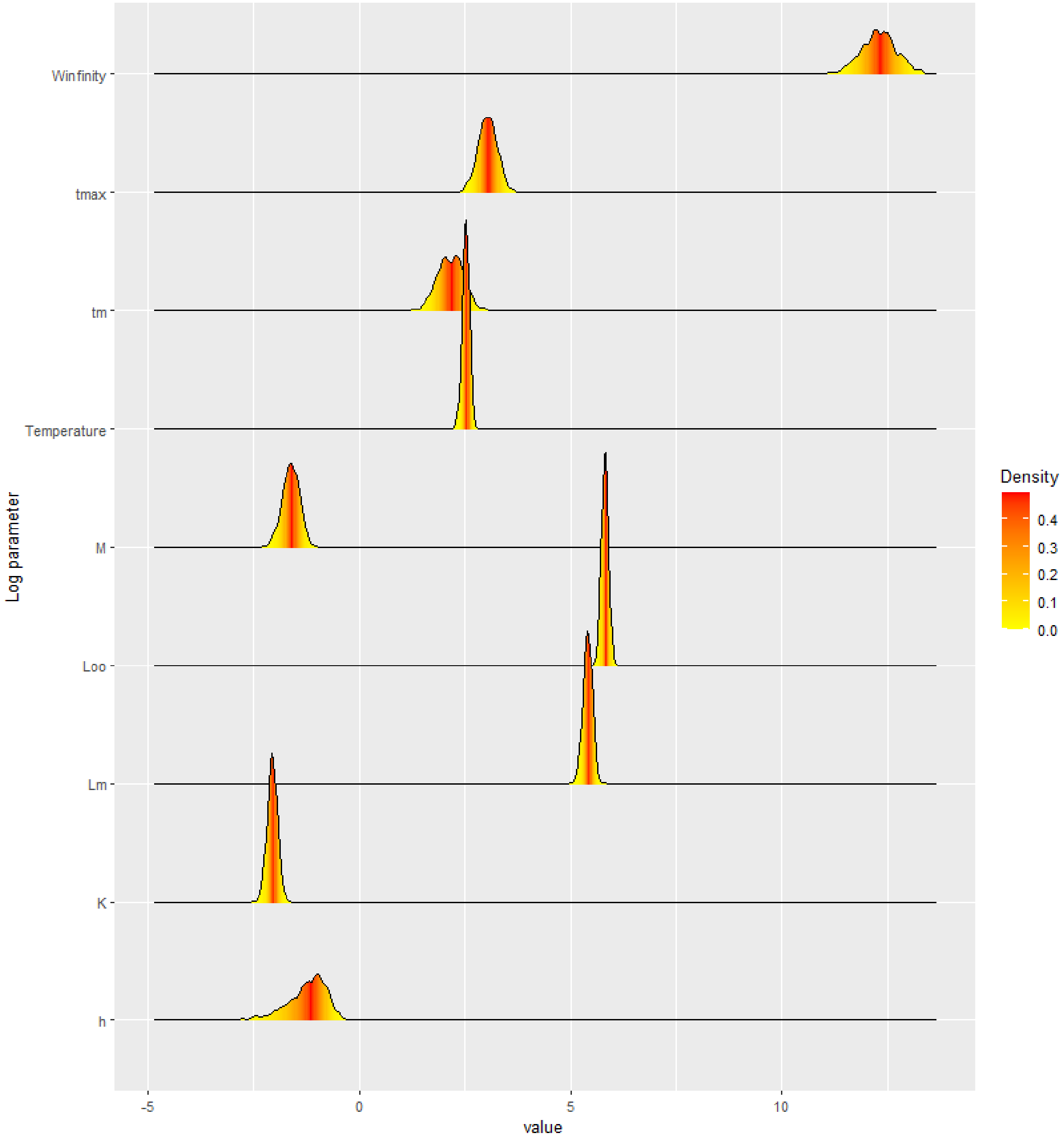

Figure 3. Log density of FishLife parameter densities

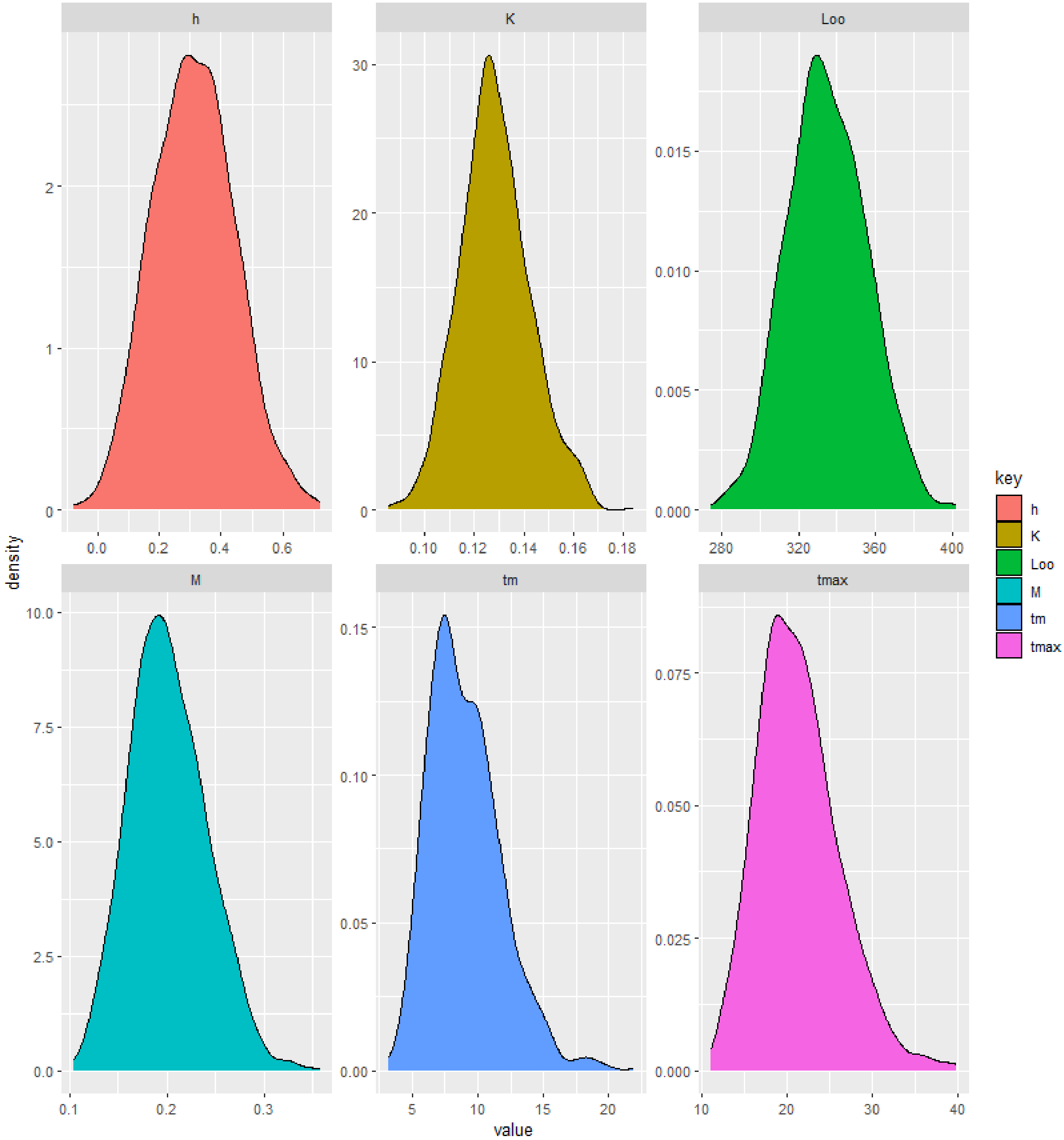

Figure 4. Density plots of steepness (h), vonBertalanffy metabolic growth parameter (K), asymptotic size (L_∞), natural mortality (M), age at maturity (tm), and maximum age (tmax).

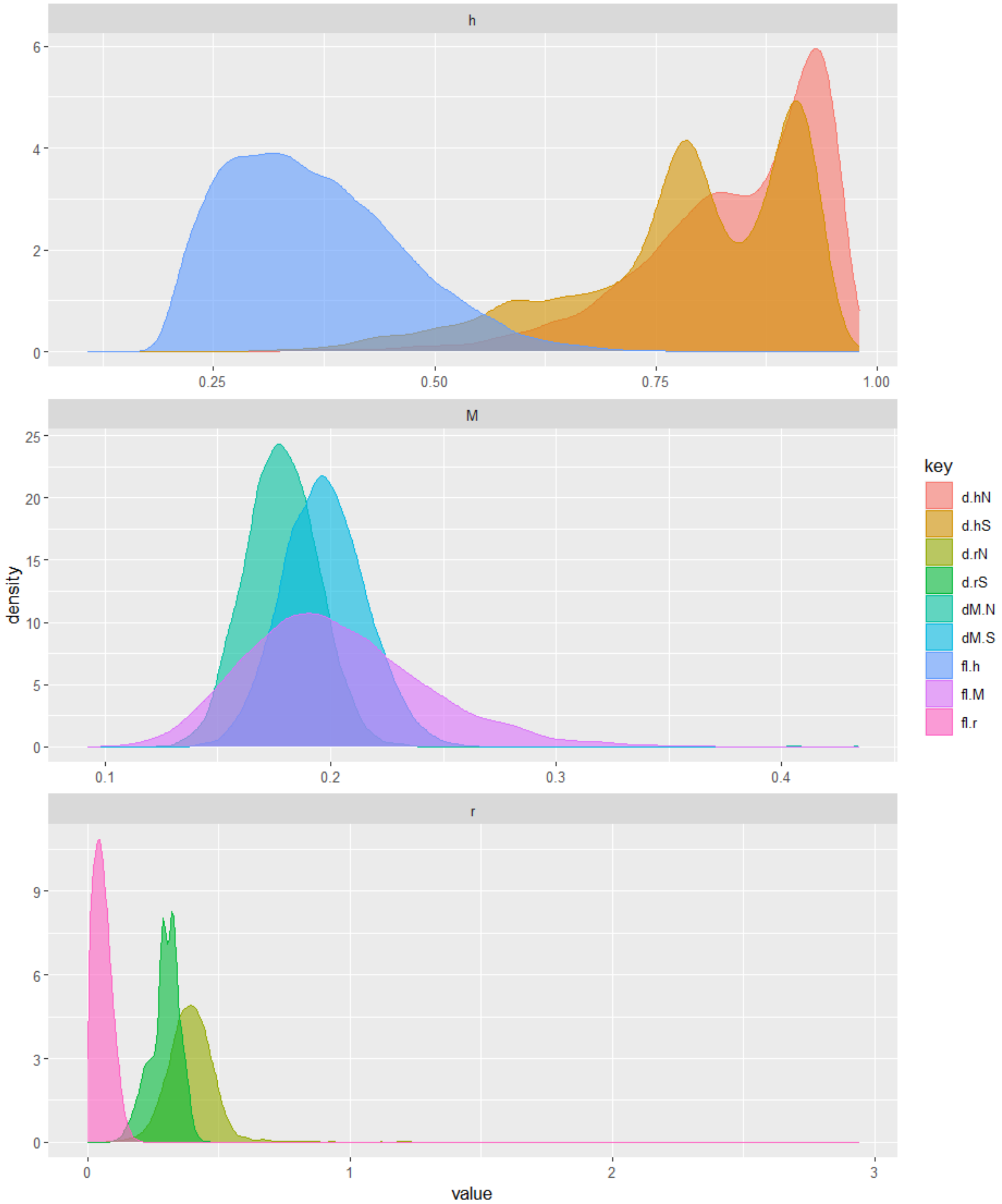

Figure 5. Comparison of density estimates for MVN and Leslie matrix estimates of steepness *h*, natural mortality *M*, and intrinsic rate of growth *r* (x, value). d.hN and d.hS are the Leslie matrix densities of steepness for northern and southern stocks. d.rN, d.rS are the Leslie matrix estimates for the intrinsic rate of growth for northern and southern stocks. dM.N and dM.S are the Leslie matrix estimates of the densities for natural mortality. fl.h, fl.M, and fl.r are the MVN estimate for steepness h, natural mortality M, and intrinsic rate of growth r.

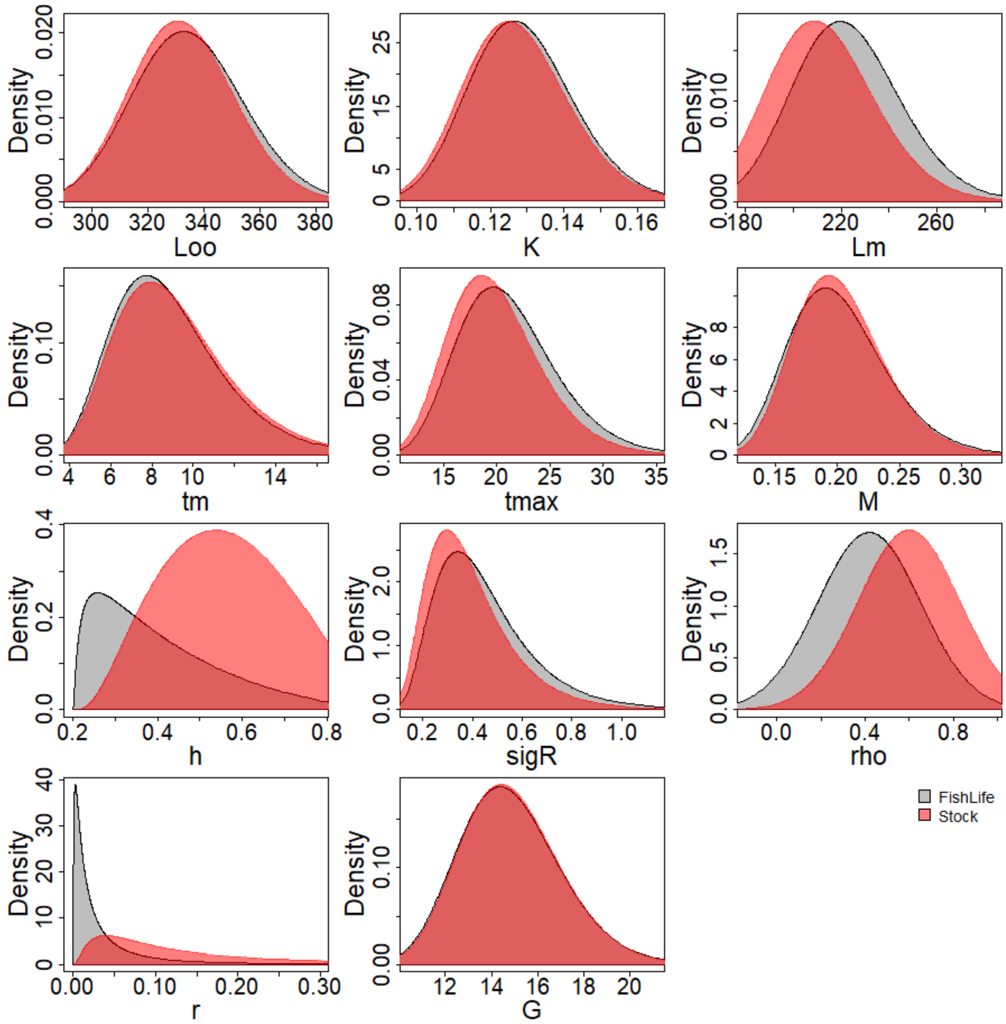

Figure 6. Updated posterior distributions for life history and productivity parameters for the southern blue shark stock. L∞ is the asymptotic size, K is the vonBertalanffy growth parameter, Lm is the length at maturity, h is the Beverton-Holt steepness, sigR is marginal standard deviation of recruitment variability, rho is the autocorrelation of recruitment variability, r is the intrinsic rate of growth and G is the generation time.

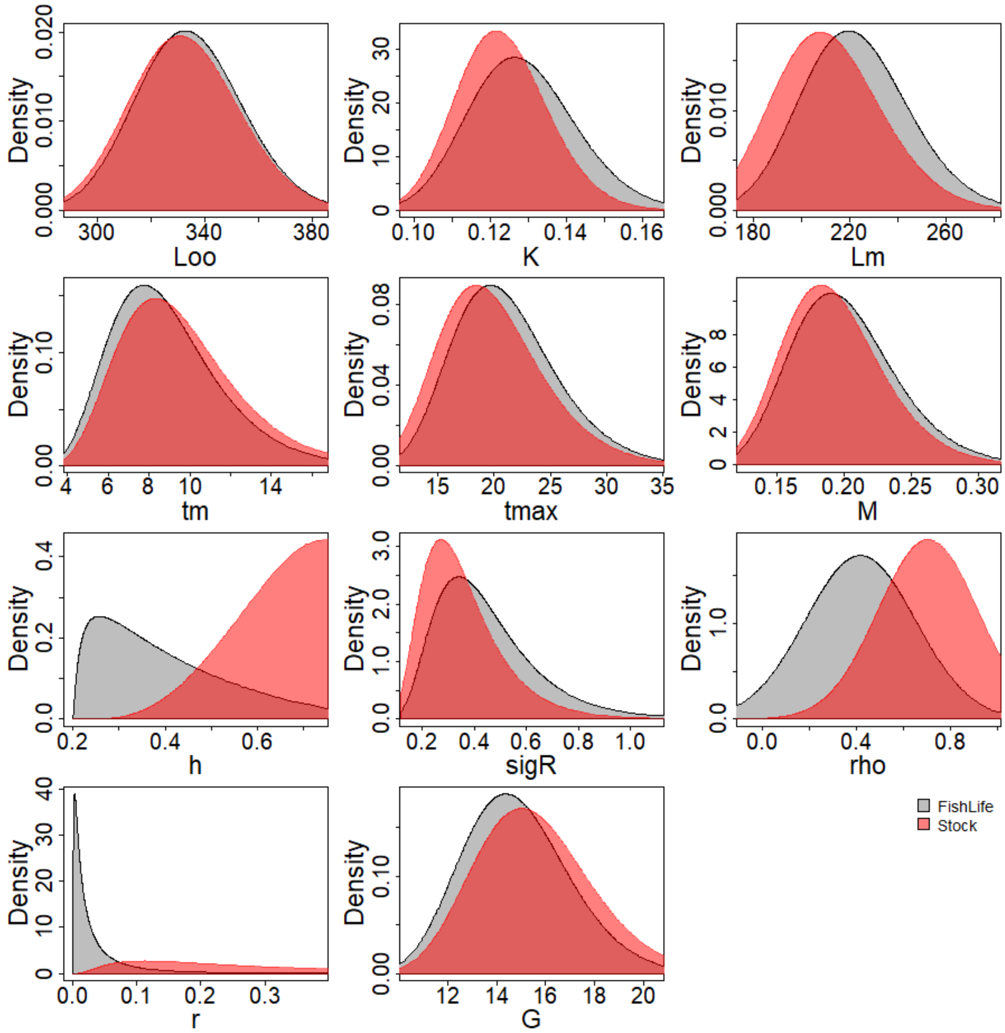

Figure 7. Updated posterior distributions for life history and productivity parameters for the northern blue shark stock. L∞ is the asymptotic size, K is the vonBertalanffy growth parameter, Lm is the length at maturity, h is the Beverton-Holt steepness, sigR is marginal standard deviation of recruitment variability, rho is the autocorrelation of recruitment variability, r is the intrinsic rate of growth and G is the generation time.