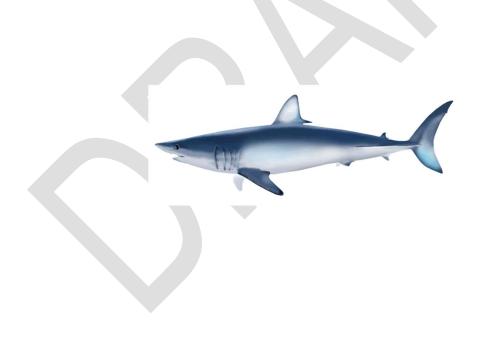
Developing natural mortality priors for North Pacific shortfin make sharks ¹

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ABSTRACT

In the previous stock assessment of north Pacific shortfin make sharks in 2018, the instantaneous natural mortality rate (M) was assumed to be 0.128 y⁻¹ for both sexes and all ages. This study re-examined the assumptions for M of this stock in preparation for the next assessment in 2024. Following the recommendations for "best" practices, this study developed probability distributions for M that could be used as priors for the assessment. Meta-analytical methods were first used to estimate a range of probability distributions of M for this stock, based on empirical relationships between M and life history parameters. These probability distributions were subsequently combined into a single probability distribution that could be used as a prior for M in the upcoming assessment. We used three empirical relationships between life history and M: 1) Maximum age (AgeMax); 2) Growth (Lk); and Age at maturity (AgeMat). This study found severe problems with a publicly available data with Ms and life history parameters with sharks and instead focused on another dataset with primarily teleosts, which may result in M priors that would be biased high for sharks. This study used the results from previous studies to calculate prediction intervals for each estimated M (in log-scale), using appropriate empirical data sets and life history parameters for this stock. We combined the priors from each empirical relationship using weights based on the variance of the logM distribution (i.e., inverse variance weighting) and the degree of overlap in the data sets used for the meta-analyses (data independence weights). In general, the predicted Ms from the AgeMax relationship was relatively high compared to the Lk and AgeMat relationships. The exception appeared to be the predicted Ms from the AgeMat relationship or male make sharks, which was due to the young AgeMax for male sharks. It was noted that the results from the two growth curve methodologies were relatively similar, and averaging all three growth curves may have overweighted the US-based growth methodologies. The overall predicted M distributions also appear to be similar to the range of M point estimates from shark-based relationships. It would be recommended that these M distributions be used as priors for the upcoming stock assessment, if possible. Even if a fixed M point estimate is preferred due to model specification problems, it would be recommended to use the priors to specify the limits of sensitivity runs. This would allow the upcoming assessment to follow current "best" practices to the extent possible. However, it is noted that these predicted M distributions are based on datasets largely derived from teleosts but these datasets appear to be the currently best available datasets for this work.

INTRODUCTION

Natural mortality is a measure of stock productivity and is important in the calculation of population dynamics and biological reference points (e.g. MSY (Piner and Lee 2011). In the

previous assessment of shortfin make sharks in the North Pacific (NPSFM) (SHARKWG 2018), the instantaneous natural mortality rate (M) was assumed to be 0.128 y⁻¹ for both sexes and all ages, based on the empirical relationship between M and maximum age (AgeMax) for cetaceans (Hoenig 1983). However, given our improved understanding of the biology of the stock, it would be appropriate to re-examine the assumptions for M in the upcoming assessment in 2024.

The primary objective of this study was to develop sex-specific M priors based on the SHARKWG's current understanding of NPSFM biology. Most importantly, the growth, and age at 50% maturity (AgeMat) of male and female NPSFM appear to be quite different (Semba et al. 2009, 2011), and it would be reasonable to expect sex-specific M as well. The SHARKWG has also re-examined the ageing data for the stock and has developed new growth curves, which can be used to estimate M. In addition, it is important to develop M estimates as priors rather than point estimates, especially if empirical life-history relationships are used (Hamel 2015). A recent review on best practices for M in stock assessments (Maunder et al. 2023) highlighted the importance of "capturing estimation uncertainty to maximum extent possible, e.g. by estimating M with a prior and hence representing uncertainty in M in the posteriors for model outputs or including M as an axis of uncertainty in ensembles". Including a M prior for a stock assessment allows the SHARKWG to explicitly express the uncertainty of the M used in the assessment based on the methods used to obtain that estimate. This is important because the M values used in assessments are inherently uncertain and typically based on uncertain relationships. This also improves the ability to estimate M within the assessment model because the model is starting with an informative prior based on empirical relationships. Even if a fixed point estimate is used for a base case model in an assessment, the M prior is still useful because it can be used to inform the range of M in sensitivity model runs (ALBWG 2017) or an ensemble of model scenarios.

In previous meetings, the SHARKWG had recommended the use of M estimates or estimation approaches in Zhou et al. (2022) because these estimates were specific to sharks. The original objective for this study was to use the approaches described in Zhou et al. (2022) with updated biological parameters for the upcoming assessment. An initial examination of the approaches reviewed in Zhou et al. (2022) indicated that the machine learning approach described in Liu et al. (2020) may be useful for developing a M prior for this stock because it was the only study where the uncertainties of the empirical relationship were included. However, upon closer examination, it was found that the metadata used in Liu et al. (2020), which are publicly available as supplementary information, were seriously flawed and it would not be appropriate to use the results from that study. The metadata in Liu et al. (2020) consisted of metadata from Then et al. (2015) and 60 additional M and life-history estimates from previous studies on shark species. Out of the 60 additional estimates, 27 were from Cortes (2002), 10 were

from Simpfendorfer et al. (2008), and 8 were from NOAA (2008). The M estimates from the first two studies were from empirical life-history relationships (Cortés 2002; Simpfendorfer et al. 2008) while third study (NOAA 2008) was a report to the US Congress without any substantive details. It is inappropriate to use M estimates from empirical life-history relationships as metadata to estimate a new empirical life-history relationship. In addition, Liu et al. misclassified 5 shark species in the Then et al. (2015) dataset as teleosts and mistakenly used cm instead of mm (which were the units used in Then et al. 2015) for the units of Linf.

Given the problems with the Liu et al. (2020) dataset, this study instead focused primarily on using meta-analytical approaches (Hamel 2015; Kinney and Teo 2016; Hamel and Cope 2022) with the Then et al. (2015) dataset to estimate M priors for north Pacific shortfin make sharks from empirical life-history approaches. An important drawback of using only this data is that the data are dominated by teleosts and may result in M priors that would be biased high for sharks. It would therefore be important to compare the estimates from this study with other life-history empirical relationships for sharks (Chen and Watanabe 1989; Frisk et al. 2001; Hisano et al. 2011). While comparing these results, it would be important to note that the estimated M priors from this study are distributions rather than point estimates.

MATERIALS AND METHODS

In this study, meta-analytical methods (Hamel 2015) were first used to estimate a range of probability distributions of M for NPSFM, based on empirical relationships between M and life history parameters. These probability distributions were subsequently combined into a single probability distribution that could be used as a prior for M in the upcoming NPSFM assessment. We used three empirical relationships between life history and M that were examined by previous studies: 1) Hamel and Cope (2022), which was a modification of previous studies (Hoenig 1983; Hamel 2015) based on maximum age (AgeMax); 2) Kinney and Teo (2016) modified Pauly (1980), based on Linf and k (Pauly 1980 originally included water temperature as a variable but Then et al. (2015) found that water temperature was unimportant) (Lk); and 3) Kinney and Teo (2016) modified Charnov and Berrigan (1990), based on age at maturity (AgeMat). Table 1 shows equations for the relationships, parameter data sources, and regressions.

This study used the results from previous studies (Kinney and Teo 2016; Teo 2017; Hamel and Cope 2022) to calculate prediction intervals for each estimated M (in log-scale), using appropriate empirical data sets and life history parameters for NPSFM (Semba et al. 2011; Kinney et al. 2024). This study also followed the assumption of Hamel and Cope (2022) that half the observed variances in the estimated empirical relationships are due to errors in the observed Ms, and hence divided the SD of the estimated prediction intervals by $\sqrt{2}$. The AgeMax

empirical relationship was taken directly from the results of Hamel and Cope (2022), with M=5.40/AgeMax and a SD of 0.31 for logM, which was the same as that found in Kinney and Teo (2016) and Teo (2017), albeit with different assumptions for SD. The Lk empirical relationship was from Kinney and Teo (2016), who updated the meta-analyses in Hamel (2015) to use data from Then et al. (2014), and estimated that $M = 6.4967 Linf^{-0.3481}k^{0.5575}$. This study re-estimated the SD of logM from the Lk relationship to be 0.60. This study modified the AgeMat meta-analysis in Kinney and Teo (2016) by including viviparous species from the Charnov and Berrigan (1990) data and estimated that M = 1.703 /AgeMat and a SD of logM of 0.59.

Life history parameter values of NPSFM used to predict M were based on published literature (Natanson et al. 2006; Semba et al. 2011) or recently developed by the WG (Kinney et al. 2024). AgeMax for female and male NPSFM were considered to be 32 and 29 years, respectively, based on the oldest directly aged samples in Natanson et al. (2006). These AgeMax values were consistent with the non sex-specific AgeMax used in the previous NPSFM assessment from a bomb radiocarbon study (Ardizzone et al. 2006). Natanson et al. (2006) also estimated sex-specific AgeMax values by calculating the number of years need for a shark to reach a length equivalent to 95% of Linf. However, this study did not consider these AgeMax values because Hamel and Cope (2022) recommended against "attempting to extrapolate maximum age, or to use a proxy, or otherwise discern maximum age from some other method, unless this modifies the highest observed age only modestly. Rather, it is generally better to use the data available to more directly estimate M and its uncertainty, whether through alternative meta-analyses, within a stock assessment, or directly observing relative numbers-at-age". In addition, these extrapolated AgeMax values were sensitive to growth function used and were inconsistent (Natanson et al. 2006). However, there was a concern that direct observations of AgeMax in fished populations may be underestimates because the original relationship are based on unfished or lightly fished populations. It is also unclear if vertebral band-pairs reliably record the ages of sharks because they are structural and could be influenced by changes in the stress loads exerted on the body column (Natanson et al. 2018).

The Linf and k parameters were taken from a recent meta-analysis of NPSFM aging and length composition data (Kinney et al. 2024). Three plausible combinations of band-pair counts per year (2 vs 1 band-pairs/year), base case aging methodologies (base case using: US or Japan (JP) aging methodologies), and incorporating length frequency (LF) data into the estimation, were developed by Kinney et al. (2024): 1) US_2_LF (Table 8 in Kinney et al. 2024); 2) US_2_noLF (Table 3 in Kinney et al. 2024); and 3) JP_1_noLF (Table 4 in Kinney et al. 2024). Given the substantial sex-specific differences in Linf and k, this study also assumed sex-specific differences in predicted M from the Lk relationship. It should be noted that the Linf values in

Then et al (2015) metadata were in mm and were a mixture of fork lengths (FLs), total lengths (TLs), and unspecified length types. Therefore, the Linf parameters from Kinney et al. (2024) were converted from post-caudal length into mm FL and mm TL using length-length relationships used by the WG (Joung and Hsu 2005; Wells et al. 2013). The combination of the abovementioned factors resulted in 12 predicted M distributions for the Lk relationship (3 bandpair and methodology combinations * 2 length types * 2 sexes) (see Table 1). For each of these combinations, we extracted 1000 draws from the Linf and k posteriors of the meta-analysis by Kinney et al. (2024) and used them to predict a distribution for logM. The 1000 logM distributions were averaged using inverse-variance weighting, which resulted in a single distribution for each of the 12 combinations (Table 1). It should be noted that the estimated variances of the 1000 draws were essentially identical and the inverse variance weighting did not change the resulting SD of the logM distribution. Sex-specific logM distributions were subsequently developed by averaging the six logM distributions for each sex (Table 1).

The AgeMat parameters used in this study were based on the lengths at 50% maturity from Semba et al. (2011) for female and male NPSFM. Given the abovementioned uncertainties in the growth of this stock, we developed six combinations for AgeMax (3 band-pair and methodology combinations * 2 sexes) and developed six logM distributions (Table 1). Sexspecific logM distributions were subsequently developed by averaging the three logM distributions for each sex (Table 1).

As in Hamel (2015), we combined the priors from each empirical relationship using weights based on the variance of the logM distribution (i.e., inverse variance weighting) and the degree of overlap in the data sets used for the meta-analyses (data independence weights). If the priors were based on independent data sets, all weights would be 1, which would result in a combined prior with a mean equal to the inverse variance weighted mean of the means of all the priors. If n priors from completely overlapping data sets were combined, the weights would be 1/n. Variances of the priors were obtained from the meta-analyses, while data independence weights were assigned based on the degrees of overlap between the data sets. For example, the AgeMax and Lk meta-analyses used the same data set (Then et al. 2015) and these priors were therefore assigned a data independence weight of 0.5 each. In comparison, the AgeMat data set consisted of a combination of data sets from three studies (Beverton and Holt 1959; Beverton 1963; 1997) and was considered to be independent from the AgeMax and Lk meta-analyses.

In addition, we also combined the sex-specific priors from each empirical relationship, using only the growth parameters that were consistent between empirical relationships. The Lk and AgeMat relationships are dependent on the growth parameters either directly (Lk) or indirectly (AgeMat because that is derived from the length at 50% maturity using a growth curve). Here, for each set of growth parameters (US_2_LF; US_2_noLF; and JP_1_noLF), we

derive and combine the sex-specific logM priors for the Lk and AgeMat relationships for that set of growth parameters, together with the same AgexMax logM prior. This will allow the use of M priors in an assessment that is consistent with the growth parameters for that model.

Lastly, we calculated point estimates of predicted M from several shark-based empirical life-history relationships recommended by Zhou et al (2022), except for Liu et al. (2020) for the abovementioned reasons: 1) $\ln(M) = 0.42\ln(k) - 0.83$ (Frisk et al. 2001) (Frisk1); 2) M = 1/(0.44*AgeMat + 1.87) (Frisk et al. 2001) (Frisk2); and 3) M=1.65/(AgeMat – t0) (Hisano et al. 2011) (Hisano); 4) M=K/(1-exp(k(t-t0))), when t<ts and M=K/(a0 + a1(t-ts)+a2(t-ts)^2), when t≥ts (Chen and Watanabe 1989) (Chen). See Zhou et al. (2022) for detailed equations and definitions.

RESULTS AND DISCUSSION

In general, the predicted M from the AgeMax relationship was relatively high compared to the the Lk and AgeMat relationships (Table 1). The exception appeared to be the predicted Ms from the AgeMat relationship or male NPSFM, which was due to the young AgeMax for male NPSFM. As explained above, it is important to consider these M predictions as a probability distribution rather than point estimates because of the uncertainty in the estimated empirical relationships.

This study averaged the predicted sex-specific M distributions for the Lk and AgeMat relationships using the biological parameters from three growth curve types (US_2_LF, US_2_noLF, and JP_1_noLF). However, it was noted that the results from the US_2_no_LF and US_2_noLF growth curves were relatively similar, and averaging all three growth curves may have overweighted the US-based growth methodologies. Therefore, it is recommended to use the M priors in Table 3, with sex-specific M priors that are based on consistent growth parameters. Interestingly, the sex-specific M priors were relatively similar for all three growth models. This was because even though the Lk relationship resulted in lower predicted Ms for the JP_1_noLF growth model compared to the US_2_noLF and US_2_LF growth models, the JP 1 noLF growth model resulted in a lower AgeMax and hence higher predicted Ms.

The overall predicted M distributions also appear to be similar to the range of M point estimates from shark-based relationships (Table 2 and 4). It would be recommended that these M distributions be used as priors for the upcoming stock assessment, if possible. Even if a fixed M point estimate is preferred due to model specification problems, it would be recommended to use the priors to specify the limits of sensitivity runs or an ensemble of model scenarios. This would allow the upcoming assessment to follow current "best" practices to the extent possible. However, it is noted that these predicted M distributions are based on datasets largely derived from teleosts but these datasets appear to be the currently best available datasets for this work. In

addition, there were several decisions (e.g., growth curves included, parameter sources) that the WG may want to discuss and decide upon.

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Table 1. Empirical relationships (method) used to estimate M, log M and SD of log M along with parameter values for north Pacific shortfin make sharks, assuming that half the variance in the prediction intervals was due to errors in the observed M in the empirical relationships (Hamel and Cope 2022). †Growth parameters were 1000 random draws from posterior of specific growth curve from Kinney et al. (2024). IDs with US_2_LF, US_2_noLF, and JP_1_noLF are based on Tables 8, 3, and 4 in Kinney et al (2024). §AgeMat parameters were converted from length at 50% maturity estimates from Semba et al. (2011) into age at 50% maturity based on specific growth curves from Kinney et al. (2024). ¶AgeMat relationship modified from Kinney and Teo (2016) to include viviparous fish.

ID	Method	Equation	Regression Source	Parm Value	Parm Source	log M	SD of log M	M (y ⁻¹)
AgeMax_fem	AgeMax	M = 5.40/AgeMax	Hamel & Cope (2022)	32 y	Natanson et al. (2006)	-1.78	0.31	0.169
AgeMax_mal			ij	29 y	Natanson et al. (2006)	-1.68	0.31	0.186
Lk_US_2_LF_TL_fem	Lk	M = 6.4967 * Linf^- 0.3481 * k^0.5575	Kinney & Teo (2016)	†Linf=3343 mm TL; k=0.129	Kinney et al (2024)	-2.10	0.60	0.123
Lk_US_2_LF_TL_mal				†Linf=2764 mm TL; k=0.141	Kinney et al (2024)	-1.98	0.60	0.138
Lk_US_2_LF_FL_fem				†Linf=3048 mm FL; k=0.129	Kinney et al (2024)	-2.07	0.60	0.127
Lk_US_2_LF_FL_mal		···		†Linf=2520 mm FL; k=0.141	Kinney et al (2024)	-1.95	0.60	0.142
Lk_US_2_noLF_TL_fem				†Linf=3377 mm TL; k=0.129	Kinney et al (2024)	-2.10	0.60	0.123
Lk_US_2_noLF_TL_mal				†Linf=2762 mm TL; k=0.137	Kinney et al (2024)	-2.00	0.60	0.135
Lk_US_2_noLF_FL_fem				†Linf=3079 mm	Kinney et al (2024)	-2.07	0.60	0.127

ID	Method	Equation	Regression Source	Parm Value	Parm Source	log M	SD of log	M (y ⁻¹)
				FL; k=0.129				
Lk_US_2_noLF_FL_mal				†Linf=2517 mm FL; k=0.137	Kinney et al (2024)	-1.97	0.60	0.140
Lk_JP_1_noLF_TL_fem				†Linf=3768 mm TL; k=0.102	Kinney et al (2024)	-2.28	0.60	0.102
Lk_JP_1_noLF_TL_mal				†Linf=2929 mm TL; k=0.120	Kinney et al (2024)	-2.09	0.60	0.123
Lk_JP_1_noLF_FL_fem				†Linf=3436 mm FL; k=0.102	Kinney et al (2024)	-2.25	0.60	0.106
Lk_JP_1_noLF_FL_mal				†Linf=2670 mm FL; k=0.120	Kinney et al (2024)	-2.06	0.60	0.127
Lk_fem_avg				NA	NA	-2.14	0.60	0.117
Lk_mal_avg		,		NA	NA	-2.01	0.60	0.134
AgeMat_US_2_LF_fem	AgeMat	M = 1.703 /AgeMat	Kinney & Teo (2016)¶	§19.3 y	Semba et al. (2011)	-2.43	0.59	0.088
AgeMat_US_2_LF_mal				§5.9 y	Semba et al. (2011)	-1.24	0.59	0.289
AgeMat_US_2_noLF_fem	,			§18.0 y	Semba et al. (2011)	-2.36	0.59	0.095
AgeMat_US_2_noLF_mal				§6.0 y	Semba et al. (2011)	-1.26	0.59	0.283
AgeMat_JP_1_noLF_fem				§15.1 y	Semba et al. (2011)	-2.19	0.59	0.112
AgeMat_JP_1_noLF_mal			•••	§6.2 y	Semba et al. (2011)	-1.30	0.59	0.273
AgeMat_fem_avg				NA	NA	-2.32	0.59	0.098
AgeMat_mal_avg		.,.		NA	NA	-1.27	0.59	0.282

Table 2. Data independence weights and combined distributions of log M and SD of log M for north Pacific shortfin make sharks. See Table 1 for individual distributions and biological parameter values.

ID	Data independence weights	log M	SD of log M	M (y ⁻¹)
AgeMax_fem	0.5	-1.78	0.31	0.169
AgeMax_mal	0.5	-1.68	0.31	0.186
Lk_fem_avg	0.5	-2.14	0.60	0.117
Lk_mal_avg	0.5	-2.01	0.60	0.134
AgeMat_fem_avg	1.0	-2.32	0.59	0.098
AgeMat_mal_avg	1.0	-1.27	0.59	0.282
Combined_fem	NA	-2.00	0.33	0.136
Combined_mal	NA	-1.60	0.33	0.201

Table 3. Combined distributions of log M and SD of log M for north Pacific shortfin make sharks, using consistent growth parameters. See Table 1 for individual distributions and biological parameter values, and Table 2 for data independence weights.

			log M	SD of	M (y-1)
AgeMax ID	Lk ID	AgeMat ID	log M	log M	
AgeMax_fem	Lk_JP_1_noLF_avgFLTL_fem	AgeMat_JP_1_noLF_fem	-1.972	0.326	0.139
AgeMax_fem	Lk_US_2_noLF_avgFLTL_fem	AgeMat_US_2_noLF_fem	-1.998	0.326	0.136
AgeMax_fem	Lk_US_2_LF_avgFLTL_fem	AgeMat_US_2_LF_fem	-2.019	0.326	0.133
AgeMax_mal	Lk_JP_1_noLF_avgFLTL_mal	AgeMat_JP_1_noLF_mal	-1.624	0.326	0.197
AgeMax_mal	Lk_US_2_noLF_avgFLTL_mal	AgeMat_US_2_noLF_mal	-1.600	0.326	0.202
AgeMax_mal	Lk_US_2_LF_avgFLTL_mal	AgeMat_US_2_LF_mal	-1.591	0.326	0.204

Table 4. Predicted M values for four shark-based empirical life-history relationships recommended by Zhou et al.(2022).

ID	Relationship	Biological Parameters	Predicted M
Frisk1_US_2_LF_fem	Frisk1	K=0.129	0.184
Frisk1_US_2_LF_mal		K=0.141	0.192
Frisk1_JP_1_noLF_fem		K=0.102	0.167
Frisk1_JP_1_noLF_mal		K=0.120	0.179
Frisk2_US_2_LF_fem	Frisk2	AgeMat=19.3 y	0.097
Frisk2_US_2_LF_mal		AgeMat=5.9 y	0.224
Frisk2_JP_1_noLF_fem		AgeMat=15.1 y	0.117
Frisk2_JP_1_noLF_mal		AgeMat=6.2 y	0.217
Hisano_US_2_LF_fem	Hisano	AgeMat=19.3y, t0=-2.13y	0.077
Hisano _US_2_LF_mal		AgeMat=5.9y, t0=-2.41y	0.199
Hisano _JP_1_noLF_fem		AgeMat=15.1y, t0=-2.33y	0.095
Hisano _JP_1_noLF_mal		AgeMat=6.2 y, t0=-2.70y	0.185
Chen_US_2_LF_fem	Chen	K=0.129, t0=-2.13y	Age1=0.388,, Age10=0.163,
Chen _US_2_LF_mal		K=0.141, t0=-2.41y	Age1=0.369,, Age10=0.172,
Chen _JP_1_noLF_fem		K=0.102, t0=-2.33y	Age1=0.354,, Age10=0.146,
Chen _JP_1_noLF_mal		K=0.120, t0=-2.70y	Age1=0.335,, Age10=0.154,