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Meta-analysis of north Pacific albacore tuna natural mortality [1]

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ABSTRACT

The instantaneous rate of natural mortality (M) parameter was identified as a key source of uncertainty in the 2014 stock assessment of north Pacific albacore tuna (NPA), and was identified by the albacore working group (ALBWG) as being in need of updating prior to the next assessment in 2017. Meta-analyses of four empirical relationships between life history factors (i.e., maximum age, age at maturity, growth, and gonadosomatic index [GSI]) and M were used to calculate prediction intervals and priors for M of NPA. These multiple M priors were combined using weights based on the degree of overlap in the data sets used for the meta-analyses (data independence weights). Preliminary results indicated that M priors produced using GSI as the predictor variable were inconsistent with the results from other meta-analyses. The methods used to estimate GSI values for NPA may also have been inconsistent with the methods used in the study examining the relationship between M and GSI. Without the influence of the GSI prior, the estimated adult M (age 6+) distribution for NPA had a median of 0.39 (95%: 0.16 - 0.95). Age-specific M for juvenile NPA (ages 0-5) were estimated using the Lorenzen relationship between size and M, and an adult M of 0.39 for NPA at age 6, and ranged from 1.71 at age-0 to 0.39 at age-6+. Overall, we recommend using the age-specific M estimates from this study in the next albacore stock assessment. With a higher M, it would indicate that the NPA stock may be more productive than previously assumed. Although this analysis is still based on some subjective decisions and the influence of life history variability between different geographic regions and substocks was not explored thoroughly, the resulting M estimates are likely more appropriate than previous estimates. In addition, the derived M distribution should also suggest the appropriate bounds for sensitivity analyses or M priors in future assessments. Although the derived M distribution is wide, we consider this to be a realistic representation of our uncertainty in the M estimates of NPA, due to the large uncertainty in the relationships between M and various life history parameters.

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 & Lee 2011). The assumed instantaneous rate of natural mortality (M) used in current stock assessments for various stocks of albacore tuna is 0.3 yr^{-1} (ICCAT 2011, ALBWG 2014, Harley et al. 2015, ICCAT 2016). However, south Pacific albacore tuna assessments had used M values of 0.4 yr^{-1} up until the most recent assessment (Table 1). Despite the consistency in the M values used in current albacore tuna assessments, different approaches used to estimate M have produced values ranging from 0.24 to 0.46, a range often tested in sensitivity analyses of these assessments (ICCAT 2011, ICCAT 2014).

In spite of its importance, past assessments of north Pacific albacore (NPA) did not attempt to estimate M. Tag return rates from the north Pacific were deemed too low, especially in the western Pacific (Bertignac et al. 1999), to produce a reliable estimate of M. Instead, M for the NPA was assumed to be the same as for north Atlantic albacore, since productivities of the north Atlantic and north Pacific albacore stocks were similar based on previous assessment results (ALBWG 2014). Therefore, M was fixed at 0.3 yr^{-1} for both sexes and all ages in previous assessments. Sensitivity analyses were run on values of M ranging from 0.25 to 0.40.

The assumed rate of M was highly influential on the estimated scale of the 2014 NPA stock assessment. A higher M resulted in higher spawning stock biomass, higher depletion ratio, and lower fishing intensity estimates (ALBWG 2014). Due to its influence on the stock assessment results, M was identified as a key source of uncertainty in need of updating prior to the next assessment of NPA.

METHODS

In this study, we applied meta-analytical methods to a range of empirical relationships between M and life history parameters to obtain a range of prior probability distributions of M for NPA (Hamel 2015), which were subsequently combined into a single probability distribution. Four empirical relationships between life history and M were examined in this study: 1) Hoenig (1982), based on maximum age (AgeMax); 2) modified Pauly (1980), based on maximum size and k (Pauly 1980 originally included water temperature as a variable but Then et al. (2015) found that water temperature was unimportant) (Lk); 3) Charnov and Berrigan (1990), based on age at maturity (AgeMat); and 4) Gunderson (1997), based on the gonadosomatic index (GSI) (Table 2). Table 2 shows equations for the relationships, parameter data sources, and regressions.

Following Hamel (2015), log–log regressions were used for all four meta-analyses, and prediction intervals were calculated for each estimated M using appropriate empirical data sets and life history parameters for NPA (Table 2). Importantly, prediction intervals contain both the actual variability in the dependent variable around the regression line and estimation error in the original data (Hamel 2015). The prediction interval is therefore often wider than the actual variation in the dependent variable around the regression line and corresponding confidence interval. Both prediction and confidence intervals are imperfect representations of the uncertainty in a new M estimate, with the truth likely to be somewhere in the middle. However, the prediction interval was favored here because there was likely to be some bias in the original data of the empirical relationships, and the prediction interval is wide enough to compensate for that (Hamel 2015).

The AgeMax and Lk meta-analyses in this study were updated from those in Hamel (2015) to use data from Then et al. (2014), who reviewed and updated the data used in the original Hoenig (1982) and Pauly (1980) studies. There was no recent published meta-analysis of the AgeMat empirical relationship, so we performed a new meta-analysis (i.e., regression of M and age at maturity) using data from three studies representing results from 78 different fish stocks or species (Beverton & Holt 1959, Beverton 1963, Gunderson 1997) (Figure 1). The meta-analysis for GSI was the same as Hamel (2015), which was based on data from Gunderson (1997).

Life history parameter values of NPA used to predict M were based on published literature and/or used in the 2014 stock assessment. Maximum age was considered to be 15 years based on Wells et al. (2013), age at 50% maturity was set at 5 based on Ueyanagi (1957), and a GSI value for NPA was taken from Chen et al. (2010). Values for k and L_∞ were taken from Chen et al. (2012) and Wells et al. (2013). With different sampling regions and designs, Chen et al. (2012) focused mostly on the western Pacific and estimated sex-specific growth curves for both males and females, while Wells et al. (2013) only estimated a sex-combined growth curve using data from primarily the eastern Pacific. This resulted in three different estimates of M based on the male (Lk_1), female (Lk_2), and combined sex (Lk_3) values for k and L_∞ (Table 2), which allowed us to examine potential geographical differences in M.

Besides prediction intervals, log-normal probability distributions were also produced from the meta-analyses. These probability distributions were considered to be priors for the M of

NPA. As in Hamel (2015), we combined the multiple priors using weights based on the degree of overlap in the data sets used for the meta-analyses (data independence weights). The mean μ_c and variance σ_c^2 of the combined distribution were calculated as, $\mu_c = \sum_i (\frac{w_i \mu_i}{\sigma_i^2}) / \sum_i (\frac{w_i}{\sigma_i^2})$, and $\sigma_c^2 = 1/\sum_i (\frac{w_i}{\sigma_i^2})$, where w_i is the assigned data independence weight for prior *i*. 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 the entire GSI data set and two other data sets (Beverton & Holt 1959, Beverton 1963). The AgeMat-based prior was therefore assigned a data independence weight of 0.75 while the GSI-based prior was assigned a weight of 0.5. In addition, the Lk meta-analysis resulted in three priors (Lk_1, Lk_2, and Lk_3 based on three growth curves), and the 0.5 weight for the Lk meta-analysis was subdivided among the three priors. The Lk_1 and Lk_2 priors were assigned weights of 0.125 each, while the Lk_3 prior was assigned to a weight of 0.25, in order to give equal weight to the western and eastern Pacific.

Preliminary results indicated that the M priors produced from using GSI as the predictor variable were inconsistent with the other methods. In addition, Chen et al. (2010) might have estimated GSI values using methods that were inconsistent with the methods used in the Gunderson (1997) study. Two alternative weighting schemes for the data independence weights were therefore developed, with Weightings A and B including and excluding the GSI-based prior, respectively (Table 3). With the removal of the GSI-based prior, the weighting scheme was altered to reflect the independence of data used in the AgeMat meta-analysis (Table 3).

The resulting M distribution was assumed to represent adult M (age-6+). The age-specific natural mortality estimates for younger ages (ages 0-5) were assumed to be size dependent (Lorenzen 1996, Lorenzen 2000). Using age-specific average weights from the 2014 NPA stock assessment, the M at a specific weight *W*, M_W was calculated by (Lorenzen 1996), $M_W = M_u W^b$, where M_u was the natural mortality rate at unit weight, and *b* was the allometric scaling factor. M_u was calculated as M_W / W^b where M_W was the median of the estimated adult M distribution and *W* was the average weight at age-6. The parameter *b* was set to -0.305, which was estimated by Lorenzen (1996) as the value for *b* in the ocean.

RESULTS AND DISCUSSION

The regression for age at maturity and M had an estimated intercept of 0.57 when slope was fixed at -1, with an adjusted R-squared value of 0.2908 (Figure 1). Regression values for each method can be seen in Table 2, along with parameters used for NPA and the resultant estimates of M.

Results from all the meta-analyses were assessed for the plausibility of their median estimated M value, as well as their overall variance and comparability. The M prior based on using GSI as the predictor variable (Gunderson 1997) appeared to be an outlier (much higher than other estimates) (Table 2; Figure 2). In addition, we were unsure if the methods used to estimate GSI for NPA were consistent with the methods used by Gunderson (1997). We therefore only used the combined M prior using Weighting B (i.e., zero weight for the GSI-based prior) for further analyses. Using Weighting B, the median of adult M (age-6+) of NPA was estimated to be 0.39 (95%: 0.16 - 0.95) (Figure 3; Table 4).

Age-specific M estimates, derived from the relative size-dependent relationship (Lorenzen 1996) ranged from 1.71 at age-0 to 0.39 at age-6+ (Table 5). The distribution of age-specific M was not calculated because the prediction intervals for the empirical relationship between size and changes in M were not evaluated. However, the uncertainty for these age-specific M estimates are undoubtedly very large.

Although previous assessments of NPA have used a single M value for all ages, the ALBWG have recommended exploring the use of age-specific M in future assessments. This approach is also consistent with recommendations from past NOAA workshops on M, and with the approaches used in the Billfish (BILLWG) and Pacific Bluefin Tuna (PBFWG) Working Groups of the ISC. This paper does not explicitly consider increasing M at older ages due to senescence (Siler 1979) or maturation (Lehodey et al. 2008). Although M may increase at older ages, we assumed that the meta-analyses used in this paper produced an average adult M (age-6+). We also did not explore sex-specific M estimates. Nevertheless, the M estimates in this study are likely an improvement over the assumed M used in previous assessments.

Overall, we recommend using the age-specific M estimates from this study in the next albacore stock assessment. With a higher M, it would indicate that the NPA stock may be more productive than previously assumed. Although this analysis is still based on some subjective decisions and the influence of life history variability between different geographic regions and substocks was not explored thoroughly, the resulting M estimates are likely more appropriate than previous estimates. In addition, the derived M distribution should also suggest the appropriate bounds for sensitivity analyses or M priors in future assessments. Although the derived M distribution is wide, we consider this to be a realistic representation of our uncertainty in the M estimates of NPA, due to the large uncertainty in the relationships between M and various life history parameters.

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Table 1. Natural mortality values used in other assessments for albacore in the Atlantic, Pacific, and Mediterranean. Each assessment used a single value for all ages and both sexes.

Region	M	Assessment	Method
North Atlantic	0.3	ICCAT 2016	Assumed
South Atlantic	0.3	ICCAT 2011	Assumed
Mediterranean	0.3	ICCAT 2011	Assumed, however analyses using Pauly (1990) and Froese and Pauly (1997) produced values of 0.456 and 0.420 respectively.
North Pacific	0.3	ISC 2014	Assumed to be the same as Atlantic
South Pacific	0.3	WCPFC 2015	Modified from 0.4 to 0.3 to match values from ISC 2014

Table 2. Empirical relationships (method) used to estimate M along with parameter values for north Pacific albacore tuna and estimated prediction intervals (log M and SD of log M).

Method	Equation	Regression Type	Log Intercept	Parameter Value	Parameter Source	log M	SD of log M
AgeMat	M = 1.775 /AgeMat	log–log regression (fixed slope = -1)	0.5739	5	Ueyanagi 1957	-1.036	0.842
AgeMax	M = 5.40/AgeMax	log–log regression (fixed slope = -1)	1.68642	15	Wells et al. 2013	-1.022	0.433
Lk_1	M = 6.4967 * Linf^-0.3481 * k^0.5575	log–log regression	1.8713	Linf=124.1; k=0.164	Wells et al. 2013	-0.815	0.845
Lk_2	M = 6.4967 * Linf^-0.3481 * k^0.5575	log–log regression	1.8713	Linf=103.5; k=0.34	Chen et al. 2012 (female)	-0.345	0.843
Lk_3	M = 6.4967 * Linf^-0.3481 * k^0.5575	log–log regression	1.8713	Linf=114; k=0.253	Chen et al. 2012 (male)	-0.544	0.843
GSI	M = 1.817 * GSI	log–log regression (fixed slope = 1)	0.5973	0.6	Chen et al. 2010	0.086	0.439

Table 3. Data independence weights used for alternative weighting schemes to combine multiple priors, with (Weighting A) and without (Weighting B) the GSI-based prior.

	AgeMat	**AgeMax**	**Lk_1**	**Lk_2**	**Lk_3**	**GSI**
Weighting A	0.75	0.50	0.25	0.125	0.125	0.50
Weighting B	1.00	0.50	0.25	0.125	0.125	0.00

Table 4. Estimated probability distribution of north Pacific albacore tuna natural mortality (M) using the weightings in Table 3. Point estimate of M is the median of the distribution.

	M	**2.50%**	**25%**	**75%**	**97.50%**
Weighting A	0.57	0.27	0.44	0.74	1.20
Weighting B	0.39	0.16	0.29	0.53	0.95

Table 5. Age-specific natural mortality (M) of north Pacific albacore tuna from age-0 to age-6+. The Lorenzen (1996) equation was applied to the median of the estimated M distribution for adults (age-6+) using Weighting B, and extrapolated to ages 0 - 5 with average weights-at-age from the 2014 stock assessment.

Age	**0**	**1**	**2**	**3**	**4**	**5**	**6+**
M	1.71	0.71	0.55	0.48	0.43	0.41	0.39

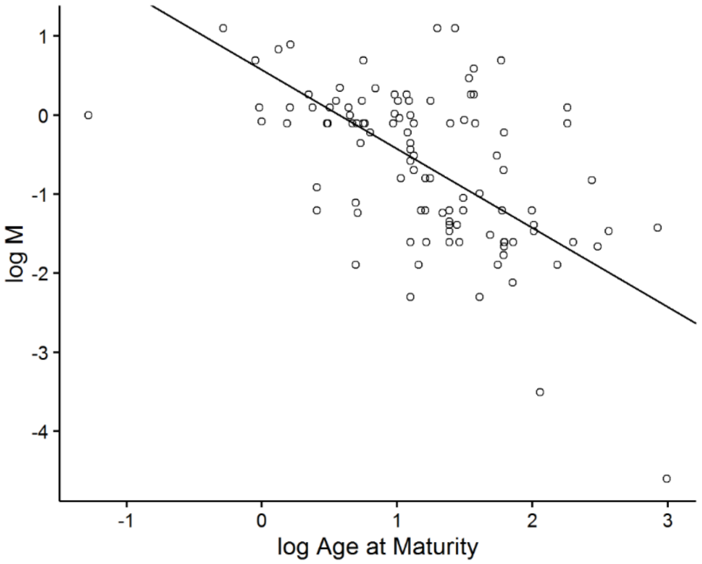

Figure 1. Regression of age at maturity and natural mortality (both in log space). Slope was fixed at -1. Adjusted R^2 = 0.2908, N= 78. See Table 2 for parameter estimates.

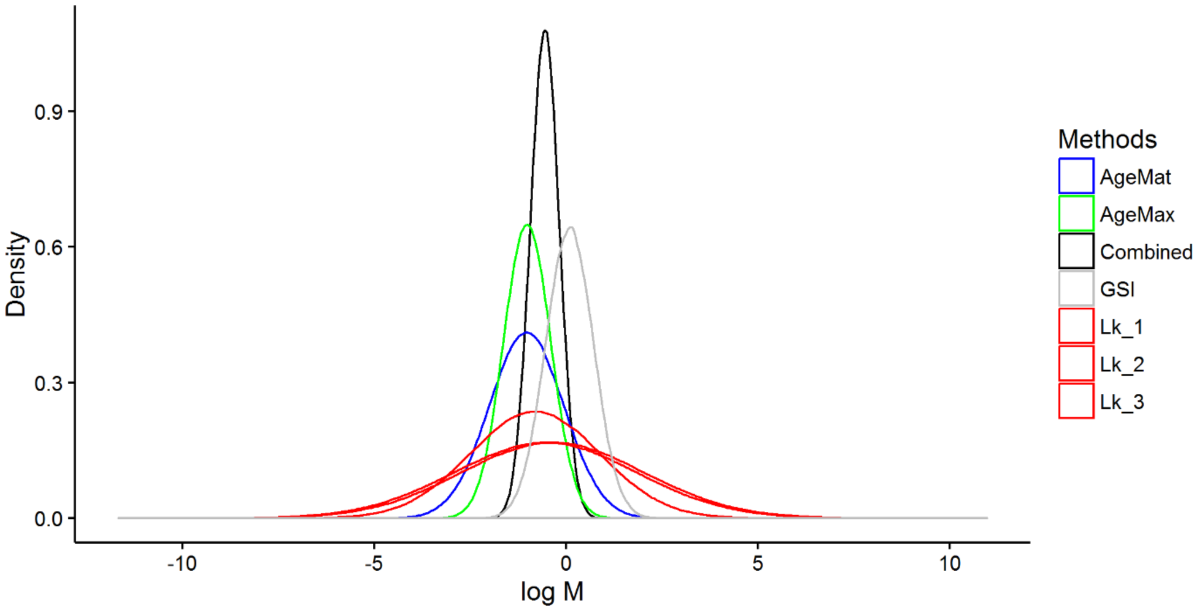

Figure 2: Estimated M probability distributions in log space for each meta-analysis (method) after weighting using Weighting A (with GSI; see Table 3 for weighting details). The colored lines are the priors from each individual method (including three versions of the Lk method based on different growth parameters; sex combined=Lk_1, males=Lk_2, females=Lk=3), after the weighting described in the text and Table 3. The black line is the combined prior. Note that the GSI meta-analysis resulted in an M prior much higher than all other methods.

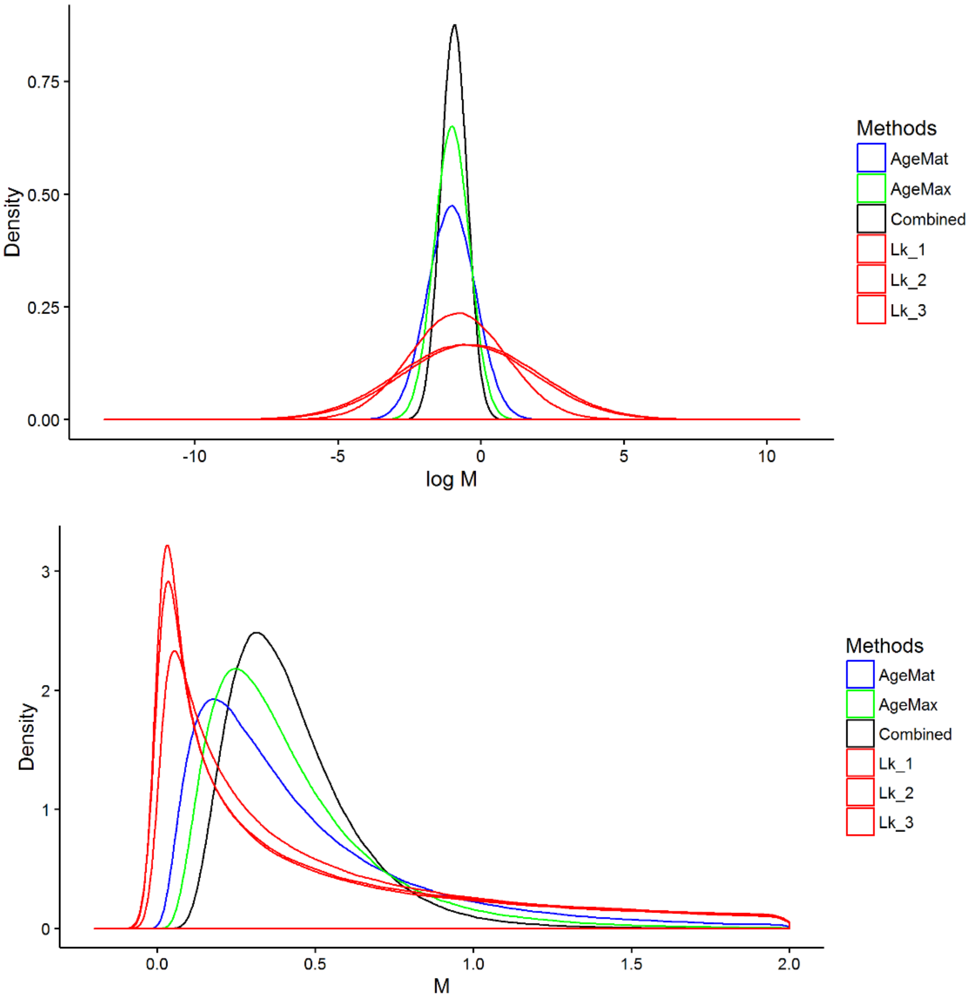

Figure 3. Estimated M probability distributions in log space (upper panel) and normal space (lower panel) for each meta-analysis (method) after weighting using Weighting B (without GSI; see Table 3 for weighting details). The colored lines are the distributions for each individual method (including three versions of the Lk method based on different growth parameters; sex combined=Lk_1, males=Lk_2, females=Lk=3), after the weighting described in the text and Table 3. The black line is the combined posterior.