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

Steven L. H. Teo

NOAA Fisheries

Southwest Fisheries Science Center

8901 La Jolla Shores Drive

La Jolla, CA 92037, USA

Email: steve.teo@noaa.gov

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ABSTRACT

The instantaneous rate of natural mortality (M) parameter was identified by the albacore working group (ALBWG) as a key source of uncertainty in the 2014 stock assessment of north Pacific albacore tuna (NPA). A previous study (Kinney and Teo 2016) developed a probability distribution of M for NPA based on meta-analyses of several empirical relationships between life history parameters and adult M. After reviewing results from that study, the ALBWG recommended 4 potential base case assumptions for the 2017 assessment: 1) a constant M of 0.3 for all ages and sexes (i.e., base case for 2014 assessment); 2) age-specific M based on the meta-analyses in Kinney and Teo (2016), with a constant adult M starting at age-6+ ; 3) same as #2 but with a constant adult M starting at age-3+; and 4) sex-specific M based on meta-analyses similar to Kinney and Teo (2016). The aim of this study is to develop M values and/or priors that are consistent with these four options. The data sources and analytical methods used in this study are the same as Kinney and Teo (2016), albeit with minor differences. Meta-analyses of three empirical relationships between life history factors (i.e., maximum age, age at maturity, and growth) and M were used to calculate prediction intervals and priors for M of NPA. These multiple M priors were combined into a single M distribution using weights based on the degree of overlap in the data sets used for the meta-analyses (data independence weights). Age-specific M values were developed using the Lorenzen relationship between size and M. Overall, I recommend that the ALBWG use one of these four options for the 2017 NPA assessment: 1) constant M of 0.3 for all ages and sexes; 2) age-specific M from 1.67 at age-0 to 0.38 at age-6+; 3) age-specific M from 1.32 at age-0 to 0.38 at age-3+; and 4) constant M of 0.48 for all ages of female NPA and 0.39 for all ages of male NPA. Based on discussions during the 2017 assessment meeting, the ALBWG developed a fifth option, which was a combination of options #3 and #4 resulting in age and sex specific M from 1.36 at age-0 for both sexes to 0.48 and 0.39 for females and males at age-3+ respectively. Option #5 was used in the base case model in the 2017 NPA stock assessment.

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 2014, the Albacore Working Group (ALBWG) of the International Scientific Committee for Tuna and Tuna-like Species in the North Pacific Ocean (ISC), assumed that the instantaneous rate of natural mortality (M) of north Pacific albacore tuna (NPA) was similar to north Atlantic albacore tuna based previous assessment results, and used an M of 0.3 for all ages (ALBWG 2014). This value for M is consistent with the current assessments for various stocks of albacore tuna (Kinney and Teo 2016).

Kinney and Teo (2016) developed a probability distribution of M for NPA based on meta-analyses of several empirical relationships between life history parameters and adult M. The resulting M distribution was relatively wide, with 95% of the distribution ranging from 0.16 to 0.95, and a point estimate of 0.39 (median of the lognormal distribution). In addition, Kinney and Teo (2016) assumed that the resulting M distribution represented the M of adult NPA (age-6+), and the age-specific natural mortality of younger age classes (ages-0 to 5) were size dependent according to the Lorenzen (1996) relationship between body weight and M. The age-specific M ranged from 1.71 at age-0 to 0.39 at age-6+.

After reviewing the results of Kinney and Teo (2016), the ALBWG agreed that the meta-analysis was a significant improvement (ALBWG 2016). However, the ALBWG interpreted the results as being supportive of assuming an M of 0.3 in the 2017 assessment because the meta-analysis showed a relatively wide distribution of M, and an M of 0.3 is within the 50% intervals of the resulting M distribution. The ALBWG recommended 4 potential base case assumptions for the 2017 assessment: 1) a constant M of 0.3 for all ages and sexes (i.e., base case for 2014 assessment); 2) age-specific M based on the meta-analyses in Kinney and Teo (2016), with a constant adult M starting at age-6+ ; 3) same as #2 but with a constant adult M starting at age-3+; and 4) sex-specific M based on meta-analyses similar to Kinney and Teo (2016). During the 2017 assessment meeting, the ALBWG developed a fifth option. Option #5 was a combination of options #3 and #4, with a constant sex-specific M starting at age-3+ but age-specific M at age-0 to age-2. The basis for option #5 was that male and female tunas are thought to have the same M as juveniles but female tunas exhibit higher M upon maturity due to the much higher energetic cost of female reproduction.

The aim of this study is to develop M values and/or priors that are consistent with the four options listed above by the ALBWG. For option #1, there is no need for any analysis because a constant M of 0.3 is assumed. For option #2, this study will update the age-specific M provided by Kinney and Teo (2016) because there was an accidental omission of some data used in the meta-analysis of the relationship between M and the age of maturity (AgeMat). For options #3, #4 and #5, this study will perform new analyses to derive M values for NPA.

METHODS

The data sources and analytical methods used in this study are the same as Kinney and Teo (2016), albeit with minor differences. Interested readers should refer to Kinney and Teo (2016), Hamel (2015), and Then et al. (2015) for details on the data sources and methods used. In short, I 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. Three empirical relationships between life history and M were examined in this study: 1) Hoenig (1983), 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); and 3) Charnov and Berrigan (1990), based on age at maturity (AgeMat) (Table 1). Kinney and Teo (2016) had also analyzed the relationship between M and gonadosomatic index (GSI) in their study but the M distributions derived from GSI appeared to be outliers, and were therefore not used in their final analysis. As with Kinney and Teo (2016), the AgeMax and Lk meta-analyses were based on data from Then et al. (2015). However, Kinney and Teo (2016) used data from three studies (Beverton and Holt 1959, Beverton 1963, Gunderson 1997) for the AgeMat meta-analysis but accidentally omitted data from 7 fish stocks in the Gunderson (1997) study. In this study, I included data from these 7 fish stocks and performed the regression of AgeMat vs M again (Figure 1).

Life history parameter values of NPA used to predict M were based on published literature and/or used in the 2014 stock assessment. The age of maturity for both male and female NPA were set at 5 (Ueyanagi 1957). The maximum age, k and L_∞ parameters were based on two age and growth studies with different sampling regions and designs (Chen et al. 2012, Wells et al. 2013). 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 different estimates of M based on combined sex (AgeMax_1 and Lk_1), female (AgeMax_2 and Lk_2), and male (AgeMax_3 and Lk_3) values for AgeMax, k and L_∞ (Table 1).

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 (Kinney and Teo 2016). Three weighting schemes were used in this study (Table 2). Weighting A is identical to the recommended weighting (Weighting B) in Kinney and Teo (2016), and the resulting M was used to calculate the age-specific M for options #2 and #3. For options #4 and #5, Weightings B and C were used to calculate the sex-specific M for female and male NPA respectively (Table 2).

The age-specific M for younger ages 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 (option #2) or age-3 (option #3). For option #4, sex-specific weights-at-age were used instead of the sex-averaged weights-at-age for options #2 and #3. For option #5, the M_W was the median of the estimated male adult M distribution and *W* were the age-specific sex-averaged weights. At age-3+, it was assumed for option #5 that the female and male M became constant and were the medians of the estimated female and male adult M distributions respectively. 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 0.532 when the slope was fixed at -1 (Figure 1). Regression values for each empirical relationship can be seen in Table 1, along with parameters used for NPA and the resulting prediction intervals for M.

Combining the M priors using Weighting A resulted in an adult M distribution with a median of 0.38 (Table 3 and Figure 2), which is very similar to that found in Kinney and Teo (2016) (M = 0.39). The combined M distribution for female NPA (median = 0.48; weighting B) was higher than for male NPA (median M = 0.39) (Table 3 and Figure 2).

Age-specific M estimates for option #2 ranged from 0.38 at age-6+ to 1.67 at age-0 (Table 4), which is similar to that found in Kinney and Teo (2016). Shifting the age when M plateaus from age-6 to age-3 (i.e., option #3), resulted in M becoming lower at younger ages (e.g., M = 1.32 at age-0) (Table 4). For option #4, the age-specific M for female NPA ranged from 2.11 at age-0 to 0.48 at age-6+, while the age-specific M for male NPA ranged from 1.66 at age-0 to 0.39 at age-6 (Table 4). However, it is unclear if option #4 was meant to be age-specific. For option #5, the age-specific M for female and male NPA were the same from age-0 (1.36) to age-2 (0.45), before increasing to 0.48 at age-3+ for female NPA but decreasing to 0.39 for male NPA (Table 5).

Overall, I originally recommended that the ALBWG use one of these four options for the 2017 NPA assessment: 1) constant M of 0.3 for all ages and sexes; 2) age-specific M from 1.67 at age-0 to 0.38 at age-6+; 3) age-specific M from 1.32 at age-0 to 0.38 at age-3+; and 4) constant M of 0.48 for all ages of female NPA and 0.39 for all ages of male NPA. However, during the 2017 NPA stock assessment meeting, option #5 was developed and accepted by the ALBWG as the M schedule for the base case model in the 2017 NPA assessment.

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Table 1. 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).

Empirical relationship	Equation	Regression type	Parameter value	Parameter source	log M	SD of log M
AgeMat	$M = \frac{1.703}{AgeMat}$	log-log regression (fixed slope = -1)	5	Ueyanagi 1957	-1.077	0.839
AgeMax_1	$M = \frac{5.410}{AgeMax}$	log-log regression (fixed slope = -1)	15	Wells et al. 2013 (unsexed)	-1.020	0.433
AgeMax_2	$M = \frac{5.410}{AgeMax}$	log-log regression (fixed slope = -1)	10.25	Chen et al. 2012 (female)	-0.639	0.433
AgeMax_3	$M = \frac{5.410}{AgeMax}$	log-log regression (fixed slope = -1)	14.25	Chen et al. 2012 (male)	-0.969	0.433
Lk_1	$M = 6.497 L_{inf}^{-0.348} k^{0.557}$	log-log regression	L_{inf}=124.1 k=0.164	Wells et al. 2013 (unsexed)	-0.815	0.845
Lk_2	$M = 6.497 L_{inf}^{-0.348} k^{0.557}$	log-log regression	L_{inf}=103.5 k=0.34	Chen et al. 2012 (female)	-0.345	0.843
Lk_3	$M = 6.497 L_{inf}^{-0.348} k^{0.557}$	log-log regression	L_{inf}=114 k=0.253	Chen et al. 2012 (male)	-0.544	0.843

Table 2. Data independence weights used for alternative weighting schemes to combine multiple priors: 1) identical to Weighting B in Kinney & Teo, 2016 (Weighting A); 2) female (Weighting B); and 3) male (Weighting C).

Empirical relationship	Weighting A (combined sex)	Weighting B (female)	Weighting C (male)
AgeMat	1.0	1.0	1.0
AgeMax_1	0.5	0.0	0.0
AgeMax_2	0.0	0.5	0.0
AgeMax_3	0.0	0.0	0.5
Lk_1	0.25	0.0	0.0
Lk_2	0.125	0.5	0.0
Lk_3	0.125	0.0	0.5

Table 3. Estimated probability distribution of north Pacific albacore tuna natural mortality (M) using the weightings in Table 2. Point estimate of M is the median of the distribution in normal space.

M distribution	Weighting A (combined sex)	Weighting B (female)	Weighting C (male)
M	0.38	0.48	0.39
2.5%	0.15	0.20	0.16
25%	0.28	0.36	0.29
75%	0.51	0.66	0.53
97.5%	0.92	1.19	0.96

Table 4. Age-specific natural mortality (M) of north Pacific albacore tuna from age-0 to age-6+. The age-specific M for Weighting A (combined sex) with adult M at age-6+ and 3+ correspond to options 2 and 3 respectively that were proposed by the ALBWG. The age-specific versions of option 4.

Age	Weighting A (combined sex) adult M at age-6+ [Option #2]	Weighting A (combined sex) adult M at age-3+ [Option #3]	Weighting B (female) [Option #4]	Weighting C (male) [Option #4]
0	1.67	1.32	2.11	1.66
1	0.70	0.55	0.88	0.69
2	0.54	0.44	0.69	0.56
3	0.47	0.38	0.59	0.49
4	0.42	0.38	0.54	0.44
5	0.40	0.38	0.50	0.41
6+	0.38	0.38	0.48	0.39

Table 5. Age-specific natural mortality (M) of north Pacific albacore tuna from age-0 to age-3+, corresponding to option #5. This M schedule was used in the base case model of the 2017 north Pacific albacore stock assessment.

Age	Weighting B (female) [Option #5]	Weighting C (male) [Option #5]
0	1.36	1.36
1	0.56	0.56
2	0.45	0.45
3	0.48	0.39

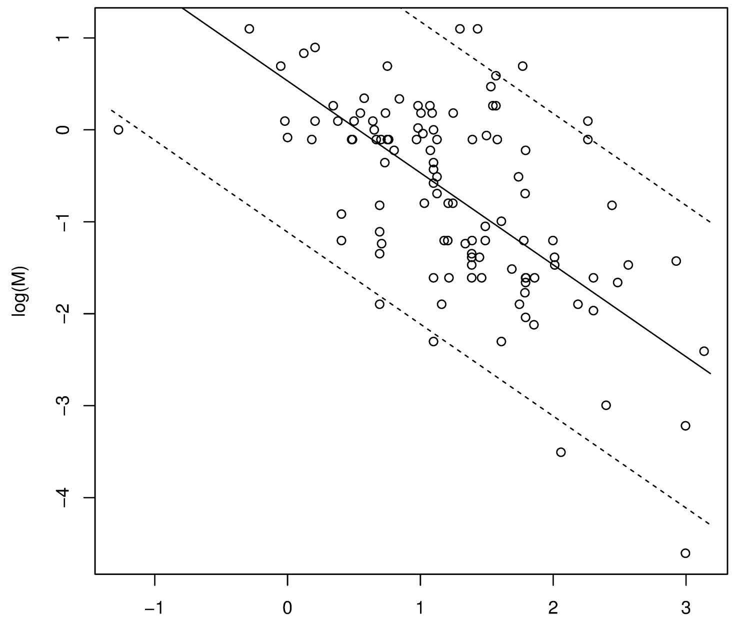

Figure 1. Regression of age of maturity and natural mortality (both in log space). Slope was fixed at -1. Dashed lines indicate the 95% prediction intervals. Residual standard error is 0.836, N = 115.

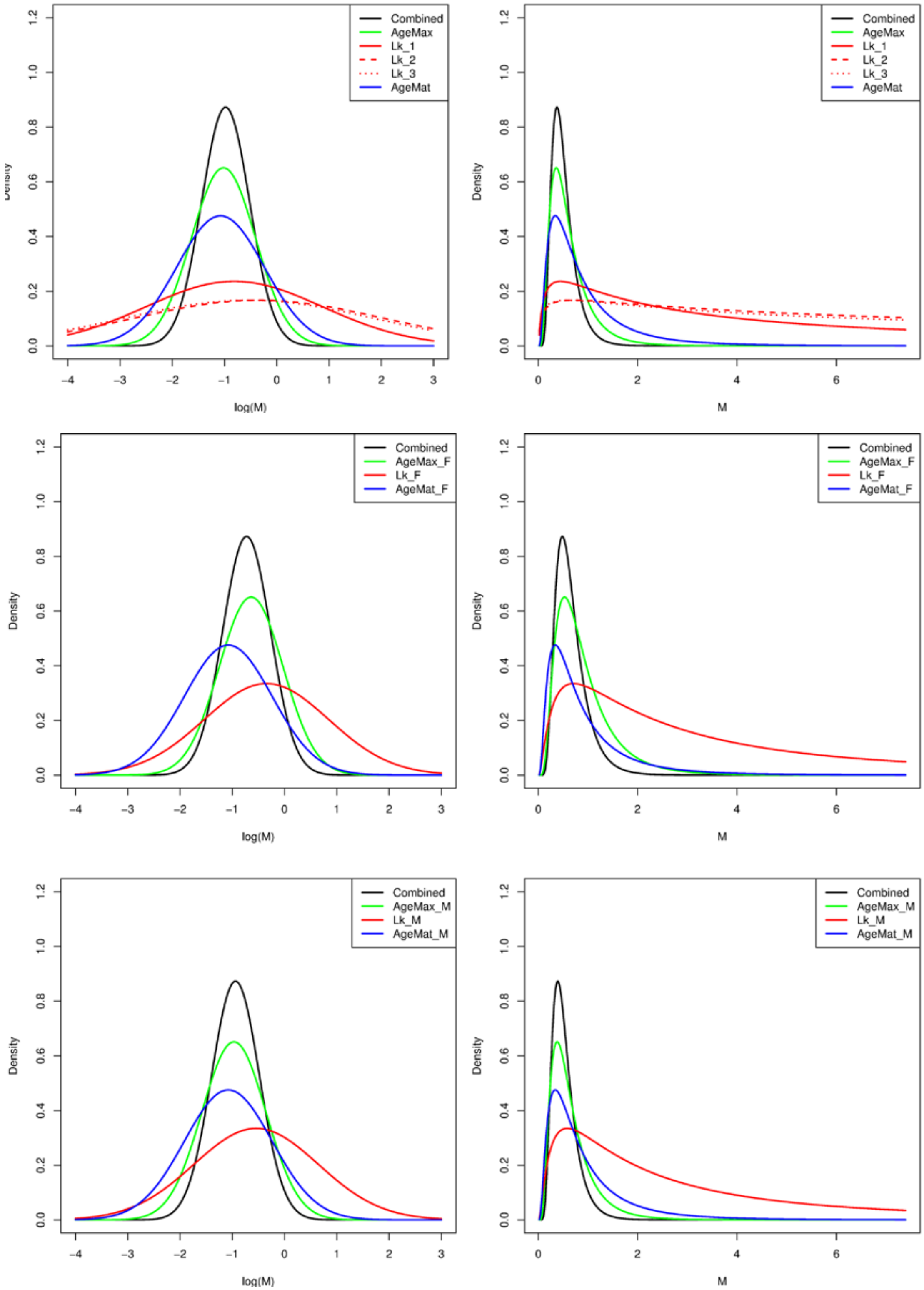

Figure 2. Probability distributions of natural mortality in log space (left panels) and normal space (right panels) for Weightings A (upper panels), B (middle panels), and C (lower panels). Colored lines show weighted distributions for each empirical relationship described in Table 1.