# Natural Mortality Rates of Pacific Blue Marlin

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## Abstract

In this working paper, we use a meta-analytical approach to estimate the natural mortality rates of Pacific blue marlin (*Makaira nigricans*) by gender and age. The meta-analyses applied both theoretical and empirical models to predict natural mortality rate as a function of life history parameters or observed mortality rates. Life history parameters from two growth models were used to estimate natural mortality rates of female and male Pacific blue marlin in two separate scenarios. The two sex-specific growth models were the old growth model from Chang et al. (2013) and the new growth model from Chang et al. (2020). We evaluated the relative plausibility of fourteen potential models to estimate natural mortality under the old growth model scenario, which was the best scientific information available in the most recent benchmark assessment of Pacific blue marlin (ISC 2013). Of these, seven models were eliminated because they produced implausible parameter estimates or because they were redundant with a more recent model analysis. We used the seven remaining plausible models to estimate sex-specific natural mortality rates under both growth model scenarios. Fixed-effects, random effects, and unweighted-average analyses were applied to the seven methods to estimate natural mortality rates. These analyses to combine natural mortality estimates across models were similar to those conducted by Lee and Chang (2013). They included identical assumptions about the precision of life history parameters for Pacific blue marlin that were applied to weight the various estimates of adult natural mortality rates. We scaled the estimates of adult natural mortality rates of female and male blue marlin to estimate juvenile natural mortality rates using an allometric relationship between natural mortality and body weight due to Lorenzen (1996). This rescaling approach to calculate juvenile natural mortality was similar to that used by Lee and Chang (2013). Under the old growth model scenario, the results of the meta-analysis indicated that there was no detectable heterogeneity in effect sizes among the seven estimators for both genders. In comparison under the new growth model scenario, some heterogeneity in effects sizes was found but the point estimate of adult female natural mortality based on a random effects analysis was implausibly high. As a result, the fixed-effects meta-analyses were used to predict the adult natural mortality rates of Pacific blue marlin under both growth model scenarios.

Under the old growth model scenario based on growth parameters from Chang et al. (2013), the results indicated that the combined estimates of adult natural mortality rates for females and males were $M_{F,4+} = 0.20$ and $M_{M,1+} = 0.38$, which corresponded to adult ages of age-4 and older for females and age-1 and older for males with 95% prediction intervals of $(0.17, 0.22)$ and $(0.34, 0.43)$, respectively. The scaled estimates of juvenile natural mortality rates at ages 0 to 3 for females were $M_{F,0} = 0.44$, $M_{F,1} = 0.38$, $M_{F,2} = 0.32$, and $M_{F,3} = 0.26$, respectively, while for males, the scaled estimate of the natural mortality rate at age-0 was $M_M = 0.44$. The coefficients of variation for the adult female and male natural mortality rates based on the old growth model were 5.5% and 4.4%, respectively.

Under the new growth model scenario based on growth parameters from Chang et al. (2020), the results indicated that the combined estimates of adult natural mortality rates for females and males were $M_{F,4+} = 0.30$ and $M_{M,1+} = 0.35$, which corresponded to adult ages of age-

4 and older for females and age-1 and older for males with 95% prediction intervals of (0.28,0.32) and (0.31,0.40), respectively. The scaled estimates of juvenile natural mortality rates at ages 0 to 3 for females were $M_{F,0} = 0.41$, $M_{F,1} = 0.35$, $M_{F,2} = 0.33$, and $M_{F,3} = 0.32$, respectively, while for males, the scaled estimate of the natural mortality rate at age-0 was $M_M = 0.41$. The coefficients of variation for the adult female and male natural mortality rates based on the new growth model were 2.5% and 4.9%, respectively.

## Introduction

At the November virtual meeting of the ISC Billfish Working Group (WG), the WG considered several sources of life history information for Pacific blue marlin (*Makaira nigricans*) for the upcoming benchmark stock assessment. The WG noted that it would be useful to revisit the estimation of natural mortality rates at age by gender for this sexually dimorphic species. In this working paper, we used a meta-analytical approach to estimate the natural mortality rates of Pacific blue marlin by gender and age. The meta-analysis applied both theoretical and empirical models to predict natural mortality rate as a function of life history parameters or observed mortality rates. Life history parameters from two growth models were used to estimate natural mortality rates of female and male Pacific blue marlin in two separate scenarios. The two sex-specific growth models were the old growth model from Chang et al. (2013) and the new growth model from Chang et al. (2020). We evaluated the relative plausibility of fourteen potential models to estimate natural mortality under the old growth model scenario, which was the best scientific information available in the most recent benchmark assessment of Pacific blue marlin (ISC 2013). Of these, seven predictive models were considered to be non-credible and were eliminated because they produced implausible parameter estimates or because they were redundant with a more recent model analysis. We used the seven remaining plausible models to estimate sex-specific natural mortality rates under both growth model scenarios.

Fixed-effects, random effects, and unweighted-average analyses were applied to the seven methods to estimate natural mortality rates. These analyses were used to combine natural mortality estimates across the set of credible models. The overall approach was similar to that used by Lee and Chang (2013) and included identical assumptions about the precision of life history parameters for Pacific blue marlin that were applied to weight the various estimates of adult natural mortality rates. We scaled the estimates of adult natural mortality rates of female and male blue marlin to estimate juvenile natural mortality rates using an allometric relationship between natural mortality and body weight due to Lorenzen (1996). This rescaling approach was similar to that used by Lee and Chang (2013). Overall, this working paper provides updated estimates of adult and juvenile natural mortality rates of female and male Pacific blue marlin along with their associated prediction intervals.

## Methods

The set of potential methods to estimate adult natural mortality for the meta-analyses were taken from Lee and Chang (2013) and other sources (Brodziak et al. 2011, Charnov et al. 2013, Kenchington 2014, Hamel 2015). There were a total of 14 potential methods chosen for the meta-analyses of the adult natural mortality rate for Pacific blue marlin (Table 1). These included age-based models that related natural mortality to maximum expected age (Hoenig 1983, Hamel 2015) or age at maturity (Charnov and Berrigan 1990, Charnov et al. 2013, Jensen 1996, Roff 1984). The methods also included models that related natural mortality to length at maturity (Roff 1984), the Brody growth coefficient (Jensen 1996, Roff 1984, Pauly 1980, Alverson and Carney 1975, Zhang and Megrey 2006, Hamel 2015, Charnov et al. 2013), and asymptotic length (Roff 1984, Pauly 1980, Charnov et al. 2013).

We assessed the relative credibility of the potential methods based on several criteria. The first criterion was based on whether two or more methods used the same data set. In this case, a decision was made as to which method would be expected to provide the best estimator, all else being equal. This criterion was applied to estimators (1) and (11) which were based on a data set of maximum observed age and natural mortality analyzed in Hoenig (1983) and was applied to estimators (4) and (12) which were based on a data set analyzed in Jensen (1996). In both cases, it was expected that the log-log regressions applied in Hamel (2015) were more appropriate given the heteroscedasticity in observed $M$ values and as a result, estimators (11) and (12) were selected for use in our the meta-analyses. This criterion was also applied to estimators (9) and (10) which were both based on estimates of the age at which a cohort achieves its maximum expected biomass in the absence of fishing. In this case, estimator (9) was judged more appropriate because it did not include an assumption that expected fish length at age-0 was non-zero.

The second criterion was based on whether two or more estimators were consistent or would be expected to produce the same mean value. In this case, estimators (3) and (12) were both based on the Brody growth parameter ($k$) but had different coefficients of 1.5 and 1.753, respectively. Here we selected estimator (12) over (3) because this estimator was based on a re-analysis of Jensen's empirical data set (Jensen 1996) in comparison to the basis in life history theory used to develop estimator (3).

The third criterion for assessing the credibility of an estimator was whether it was consistent with expectations based on previous studies of Pacific blue marlin or based on the probable survival of females to maximum age. In this context, we chose to eliminate methods that did not make biological sense from the set of candidate models used to infer natural mortality (i.e., Burnham and Anderson 2002, Jardim et al. 2021). Previous studies of blue marlin natural mortality rates reported in Lee and Chang (2013, Table 5) indicated that the unweighted mean adult natural mortality rate for female blue marlin was about $M$=0.17 with a standard error of about $SE$=0.06. Given this information, we calculated the mean $M$ plus or minus five standard errors as credible upper and lower bounds for female natural mortality. This gave a maximum value of adult female $M$ of about $M$=0.45. Given that adult female blue marlin have a maximum age of at least 20 years based on recent bomb radiocarbon ageing results (Andrews et al. 2018), this maximum value of $M$=0.45 would produce a probability of survival to maximum age of about 1 in 10,000. This survival probability is about 100-fold smaller than used in ad hoc calculations of $M$ based on expected maximum age (e.g., Hoenig 1983, Kenchington 2014) and as a result, we judged a predicted female value of $M$=0.45 to be a cutoff value for a credible natural mortality estimator. When we applied this criterion to the set of potential estimators under the old growth scenario that was the best scientific information available on growth from the most recent benchmark assessment, we found that estimators (2), (5), and (6) were non-credible with predicted female $M$ values of 0.60, 0.73, and 0.93, respectively. After applying the three criteria, there were seven candidate methods to predict natural mortality (Table 1); these were estimators (7), (8), (9), (11), (12), (13), and

(14).

Both fixed effects and random effects meta-analysis models (Borenstein et al. 2009) were initially applied to calculate expected values of the adult rates of natural mortality for female and male blue marlin. We also calculated the unweighted mean value of the predicted natural mortality rates across models for comparison with the meta-analysis results. Under the fixed effects model, the observed effect size was assumed the same for each natural mortality estimator. Under this approach, the observed effect, or natural mortality prediction, for any study ($Y_i$) was the sum of the grand mean ($\mu$) and the deviation of the study's true effect from the grand mean ($\zeta_i$):

(1) $$Y_i = \mu + \zeta_i$$

Here the fixed effects weight assigned to each estimator ($W_i$) was the inverse of the within-estimator variance ($V_{Y_i}$) where the within-estimator weight was $W_i = \frac{1}{V_{Y_i}}$.

Under the random effects model, the observed effect size was assumed to vary from one model to another due to the different true effect sizes underlying each method and due to random sampling error that was inherent in each estimator. Under this approach, the observed dispersion reflected both sampling error and the variance of the distribution of the true effects across estimators. The observed effect from the i$^{th}$ estimator ($Y_i$) was the sum of the grand mean ($\mu$), the deviation of the estimator's true effect from the grand mean ($\zeta_i$), and the deviation of the estimator's observed effect from the estimator's true effect size ($\varepsilon_i$):

(2) $$Y_i = \mu + \zeta_i + \varepsilon_i$$

To compute an estimator's variance for the random effects model, one needs to have estimates of both the within-estimator variance ($V_{Y_i}$) and the variance of the distribution of true effect sizes across studies ($\tau^2$). The weight assigned to each estimator (indexed by i) was $W_i^*$ where $V_{Y_i}^*$was the within-estimator variance plus the sample estimate of the between-studies variance ($T^2$):

(3) $$W_i^* = \frac{1}{V_{Y_i}^*} = \frac{1}{V_{Y_i} + T^2}$$

In the absence of new information, we used the same levels of variability in life history parameters by gender that were assumed in Lee and Chang (2013) to set within-estimator variances. The ranges of growth parameters of asymptotic length, Brody growth coefficient, and age-0 length were set by at their mean parameter values ± one standard error (Tables 2.1 and 2.2) using parameter estimates from Chang et al. (2013) for the old growth scenario and using estimates from Chang et al. (2020) for the new growth scenario. The range of maturity at length was derived from Shimose et al. (2009) and Sun et al. (2009) while the range of maturity at age was calculated from the growth and maturity at length curves by gender (Tables 2.1 and 2.2). The value of the exponent for the sex-specific length-weight relationships were taken from Brodziak (2013) while the range of maximum age (Tables 2.1 and 2.2) was derived from the growth curve and bomb radiocarbon ageing (Chang et el. 2013, Andrews et al. 2018). Last, the range of temperature for primary blue marlin habitat (Tables 2.1 and 2.2) was based on three studies (Nakamura 1985, Molony 2005, Su et al. 2008). Overall, these choices determined the set of weights for the fixed effects and random effects analyses of adult natural mortality by gender.

To estimate the juvenile natural mortality rate by gender, we used the same scaling approach as Lee and Chang (2013). This scaling approach involved calculating the relative ratio of juvenile natural mortality at age 0 to age 1 from Lorenzen's allometric scaling of natural mortality at age ($y^{-1}$) to body weight ($g$) at age in natural systems (Lorenzen 1996, Table I) where $M(age) = 3.0 \cdot W(age)^{-0.288}$. Here it was assumed that male and female age-0 and age-1 fish did not exhibit sexual dimorphism (Shimose 2008, unpublished PhD dissertation) and had the same natural mortality rate. This ratio was approximately $s = 1.14$ under the old growth scenario and $s = 1.15$ under the new growth scenario. These ratios were then used to calculate the age-0 natural mortality rate as the product of the ratio and the male adult natural mortality rate as estimated from the fixed or random effects analyses for each scenario. For female juvenile blue marlin, it was assumed that there was a linear decrease from natural mortality at age 1 to the age at full maturity to account for size-dependent mortality.

Given the within-estimator variances, a sample estimate of the between-estimator variance was computed using the method of DerSimonian and Laird (1986) as:

(4) $$T^2 = \frac{Q-(K-1)}{C}$$

where $K$ was the number of studies. Here $Q$ and $C$ were constants that depend on the within-estimator weights and effect sizes (c.f., Borenstein et al. 2009) where:

(5) $$Q = \sum_{i=1}^{K} W_i Y_i^2 - \frac{\left(\sum_{i=1}^{K} W_i Y_i\right)^2}{\sum_{i=1}^{K} W_i} \text{ and } C = \sum_{i=1}^{K} W_i - \frac{\sum_{i=1}^{K} W_i^2}{\sum_{i=1}^{K} W_i}$$

Here also we note that if Q < K-1, then there is no empirical support for using a random effects weights and the between-estimator variance is set to be $T^2 = 0$. Given the random effects weightings, the mean effect size denoted by $M^*$, is computed as a weighted mean of the individual estimator effects as:

(6) $$M^* = \frac{\sum_{i=1}^{K} W_i^* Y_i}{\sum_{i=1}^{K} W_i^*}$$

A fixed-effect meta-analysis was also conducted for comparison. Under the fixed-effect model, the assumption that the within-estimator variance per sample was equal across studies implied that the mean natural mortality rate $M$, or common effect, was simply the average of the estimator effects weighted by the inverse within-estimator variances across studies:

(7) $$M = \frac{\sum_{i=1}^{K} W_i Y_i}{\sum_{i=1}^{K} W_i}$$

## Results

Old Growth Scenario

Under the old growth model scenario, the fixed and random effects meta-analysis results were found to be identical for the candidate set of estimators as applied to Pacific blue marlin by gender (Tables 3.1 and 4.1). In particular, the sample estimate of the between-estimator variance was zero because the weighted sum of squares of the effect size minus the mean effect ($Q$) was smaller than the degrees of freedom ($K$-1) for both female and male blue marlin in this study. This indicated that there was no support for heterogeneous true effects among the seven estimators used to predict natural mortality. This contrasts the results of the meta-analytic study of Lee and Chang (2013) which included several estimators with higher variability in their predictions of adult natural mortality.

For female blue marlin, the fixed effects meta-analysis indicated that the predicted adult natural mortality rate was $M_F = 0.20$ with a standard error of $SE_F = 0.01$ and a 95% prediction interval of $(0.17, 0.22)$ and a coefficient of variation ($CV$) of 6% (Table 3.1). The seven estimators of adult female natural mortality had point estimates ranging from 0.19 to 0.26 with a median value of 0.20. In comparison, the unweighted average of the seven credible estimators produced a mean effect size of $\overline{M}_F = 0.22$ with a $CV$ of about 12%.

For male blue marlin, the fixed effects meta-analysis indicated that the predicted adult natural mortality rate was $M_M = 0.38$ with a standard error of $SE_F = 0.02$ and a 95% prediction interval of $(0.34, 0.43)$ and a coefficient of variation ($CV$) of 4% (Table 4.1). The seven estimators of adult male natural mortality had point estimates ranging from 0.36 to 0.43 with a median value of 0.39. Similarly, the unweighted average of the seven credible estimators produced a mean effect size of $\overline{M}_M = 0.39$ with a $CV$ of about 7%. Thus, the meta-analytic estimates of adult natural mortality for both females and males were slightly lower and less variable than the unweighted averages of the seven credible estimators.

For juvenile female and male blue marlin, the point estimates of natural mortality at age 0 and age 1 were $M_{F,0} = M_{M,0} = 0.44$ and $M_{F,1} = M_{M,1} = 0.38$. The scaled estimates of juvenile natural mortality for females younger than the age at full maturity, or ages 2 and 3, were $M_{F,2} = 0.32$ and $M_{F,3} = 0.26$, respectively. Overall, the best point estimates of natural mortality rates at age for female ($M_{F,age}$) and male ($M_{M,age}$) Pacific blue marlin under the old growth scenario were:

- Female natural mortality at age: $M_{F,0} = 0.44$, $M_{F,1} = 0.38$, $M_{F,2} = 0.32$, $M_{F,3} = 0.26$, and $M_{F,4+} = 0.20$

- Male natural mortality at age: $M_{F,0} = 0.44$ and $M_{F,1+} = 0.38$

New Growth Scenario
Under the new growth model scenario, the fixed and random effects meta-analysis results differed substantially for female blue marlin (Table 3.2). The point estimate of female adult natural mortality was $M_{F,4+} = 0.50$using random effects, or about 67% higher than the estimate using fixed effects and outside the plausible range of female natural mortality based on previous studies. As a result, the random effects meta-analysis results were not considered reliable for female or male blue marlin under the new growth scenario. For female blue marlin, the fixed effects meta-analysis indicated that the predicted adult natural mortality rate was $M_F = 0.30$ with a standard error of $SE_F = 0.01$ and a 95% prediction interval of $(0.28, 0.32)$ and a coefficient of variation ($CV$) of about 3% (Table 3.2). The seven estimators of adult female natural mortality had point estimates ranging from 0.07 to 0.57 with a median value of 0.44. In comparison, the unweighted average of the seven credible estimators produced a mean effect size of $\overline{M}_F = 0.38$with a $CV$ of 50%. Overall, the meta-analytic estimate of adult natural mortality for females was lower and much less variable than the unweighted average of the seven credible estimators.

For male blue marlin, the fixed effects meta-analysis indicated that the predicted adult natural mortality rate was $M_M = 0.35$with a standard error of $SE_F = 0.02$and a 95% prediction interval of $(0.31, 0.40)$ and a coefficient of variation ($CV$) of 5% (Table 4.2). The seven estimators of adult male natural mortality had point estimates ranging from 0.28 to 0.45 with a median value of 0.33. In comparison, the unweighted average of the seven credible estimators produced a mean effect size of $\overline{M}_M = 0.35$ with a $CV$ of about 14%. Overall, the meta-analytic estimate of adult natural mortality for males was equal to the unweighted average of the seven credible estimators and was less variable.

For juvenile female and male blue marlin, the point estimates of natural mortality at age 0 and age 1 were $M_{F,0} = M_{M,0} = 0.41$ and $M_{F,1} = M_{M,1} = 0.35$. The scaled estimates of juvenile natural mortality for age-2 and age-3 females were similar with $M_{F,2} = 0.33$ and$M_{F,3} = 0.32$, respectively. Overall, the best point estimates of natural mortality rates at age for female ($M_{F,age}$) and male ($M_{M,age}$) Pacific blue marlin under the new growth scenario were:

- Female natural mortality at age: $M_{F,0} = 0.41$, $M_{F,1} = 0.35$, $M_{F,2} = 0.33$, $M_{F,3} = 0.32$ and $M_{F,4+} = 0.30$
- Male natural mortality at age: $M_{M,0} = 0.41$ and $M_{M,1+} = 0.35$

## Discussion

Under the old growth scenario, the results of this meta-analysis were robust to the selection of either a random effects or a fixed-effect model for this analysis because there was limited heterogeneity among the credible estimators of adult natural mortality for

Pacific blue marlin. This was in part due to the selection of credible predictive models from the set of potential models considered in this study. In this context, the exclusion of redundant estimators based on the same data and the exclusion of estimators that produced inconsistent results or that led to non-credible probabilities of survival to maximum age can be generally expected to have reduced the bias and the variability of the model-averaged predictions of natural mortality rate (e.g., Burnham and Anderson 2002, Dormann et l. 2018). In comparison under the new growth model scenario, some heterogeneity in effects sizes was found but the point estimate of adult female natural mortality based on a random effects analysis was implausibly high. As a result, the fixed-effects meta-analyses were used to predict the adult natural mortality rates of Pacific blue marlin under both growth model scenarios.

We also note that when we reviewed the details of the computations in Lee and Chang (2013, Table 1), there appeared to be some discrepancies in the application of the Pauly (1980) and Hoenig (1983) estimators to predict natural mortality. These discrepancies may have biased their numerical results based on the relative weights of 13% and 18% that were calculated for these estimators, respectively. However, we also note that under the old growth scenario, the percent differences in the estimates of female and male adult natural mortality ($M_F = 0.22$ and $M_M = 0.37$) from the study of Lee and Chang relative to this study ($M_F = 0.20$ and $M_M = 0.38$) were minor and differed by only 10% and -3%, respectively. Thus, the two studies produced consistent results when life history parameters from the old growth scenario were used, despite using somewhat different approaches for averaging model results to predict natural mortality rates of blue marlin. In contrast, the percent differences in adult mortality estimates were -27% and 6% for female and male blue marlin under the new growth scenario. Overall, the selection of the growth model scenario has an important impact on the predicted natural mortality rate of adult female blue marlin, and it is recommended that this uncertainty be accounted for in any assessment of the Pacific blue marlin stock.

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Table 1. The fourteen potential models to estimate adult natural mortality rates ($M$) of Pacific blue marlin based on life history parameters of maximum expected age ($A_{max}$), age at maturity ($A_{mat}$), Brody growth coefficient ($k$), length at maturity ($L_{mat}$), asymptotic length ($L_{\infty}$), temperature ($T$), and theoretical length at age zero ($t_0$) that were considered in this study with the set of seven candidate models are listed in boldface.

| | Method | Natural Mortality Estimator | Source |
|---|---|---|---|
| (1) | Hoenig $A_{max}$ | $M = 4.31 \cdot A_{max}^{-1.01}$ | Hoenig (1983, Table - fish) |
| (2) | Jensen $A_{mat}$ | $M = \frac{1.65}{A_{mat}}$ | Jensen (1996, eqn 7) |
| (3) | Jensen $k$ | $M = 1.5 \cdot k$ | Jensen (1996, eqn 8) |
| (4) | Empirical $k$ | $M = 0.21 + 1.45 \cdot k$ | Jensen (1996, Table 1) |
| (5) | Empirical $A_{mat}$ | $M = \frac{2}{A_{mat}}$ | Charnov and Berrigan (1990, Table 1) |
| (6) | Roff $A_{mat}$ | $M = \frac{3k}{exp(A_{mat} \cdot k) - 1}$ | Roff (1984, eqn 36) |
| **(7)** | **Roff $L_{mat}$** | $M = \frac{3k \cdot L_{\infty}\left(1 - \frac{L_{mat}}{L_{\infty}}\right)}{L_{mat}}$ | Roff (1984, eqn 39) |
| **(8)** | **Pauly empirical length** | $ln(M) = -0.0066 - 0.279 \cdot ln(L_{\infty})$ $+0.6543 \cdot ln(k) + 0.4634 \cdot ln(T)$ | Pauly (1980, eqn 11) |
| **(9)** | **Empirical max biomass** | $M = \frac{3 \cdot k}{exp(0.38 \cdot k \cdot A_{max}) - 1}$ | Alverson and Carney (1975) |
| (10) | Empirical max biomass $A_0$ | $M = \frac{\beta \cdot k}{exp\left(k(0.302 \cdot A_{max} - A_0)\right) - 1}$ | Zhang and Megrey (2006) |

| | Method | Natural Mortality Estimator | Source |
|---|---|---|---|
| **(11)** | **Hamel – Hoenig $A_{max}$** | $M = \frac{4.374}{A_{max}}$ | Hamel (2015, eqn 10) |
| **(12)** | **Hamel – Jensen *k*** | $M = 1.753 \cdot k$ | Hamel (2015, eqn 11) |
| **(13)** | **Charnov et al. – length** | $M = k \cdot \left(\frac{L}{L_\infty}\right)^{-1.5}$ | Charnov et al. (2013, eqn 3) |
| **(14)** | **Charnov et al. – adult M** | $M(A_{mat}) \approx 1.84 \cdot k$ | Charnov et al. (2013) |

Table 2.1. Ranges of life history parameters used to set within-estimator variances to estimate adult natural mortality rates ($M$) of Pacific blue marlin by gender for the old growth scenario.

| | | Female | | | Male | | |
|---|---|---|---|---|---|---|---|
| Name | Symbol | Mean Value | Lower Range | Upper Range | Mean Value | Lower Range | Upper Range |
| Brody growth coefficient | *k* | 0.11 | 0.05 | 0.16 | 0.21 | 0.15 | 0.28 |
| Asymptotic length | *Linf* | 316 | 267 | 365 | 211 | 194 | 215 |
| Maturation length | *Lmat* | 180 | 180 | 194 | 130 | 130 | 140 |
| Maximum age | *Amax* | 23.0 | 20.0 | 26.0 | 11.5 | 10.0 | 13.0 |
| Maturation age | *Amat* | 2.8 | 2.0 | 4.0 | 1.4 | 1.0 | 2.0 |
| Age-0 length | *A0* | -4.7 | -5.8 | -3.6 | -3.5 | -3.9 | -2.2 |
| Temperature | *T* | 25.5 | 24.0 | 27.0 | 25.5 | 24.0 | 27.0 |
| Length-weight exponent | *Beta* | 2.956 | 2.956 | 2.956 | 2.975 | 2.975 | 2.975 |

Table 2.2. Ranges of life history parameters used to set within-estimator variances to estimate adult natural mortality rates ($M$) of Pacific blue marlin by gender for the new growth scenario.

| | | Female | | | Male | | |
|---|---|---|---|---|---|---|---|
| Name | Symbol | Mean Value | Lower Range | Upper Range | Mean Value | Lower Range | Upper Range |
| Brody growth coefficient | *k* | 0.31 | 0.27 | 0.35 | 0.18 | 0.11 | 0.25 |
| Asymptotic length | *Linf* | 249 | 241 | 257 | 198 | 190 | 205 |
| Maturation length | *Lmat* | 180 | 180 | 194 | 130 | 130 | 140 |
| Maximum age | *Amax* | 23.0 | 20.0 | 26.0 | 11.5 | 10.0 | 13.0 |
| Maturation age | *Amat* | 2.8 | 2.0 | 4.0 | 1.4 | 1.0 | 2.0 |
| Age-0 length | *A0* | -4.7 | -5.8 | -3.6 | -3.5 | -3.9 | -2.2 |
| Temperature | *T* | 25.5 | 24.0 | 27.0 | 25.5 | 24.0 | 27.0 |
| Length-weight exponent | *Beta* | 2.956 | 2.956 | 2.956 | 2.975 | 2.975 | 2.975 |

Table 3.1. Results of the unweighted, fixed effects, and random effects analyses under the old growth scenario to predict the adult natural mortality rate of female Pacific blue marlin based on seven estimators, where "Average(M)", "M", and "M*" are the unweighted average, fixed effects, and random effects estimates of natural mortality, respectively, with lower and upper 95% prediction intervals given by "PI_L95%" and "PI_U95%", respectively.

**Female Natural Mortality Estimators**

| Estimator | Natural Mortality Estimate | Lower Range of Parmeters | Upper Range of Parameters | Standard Error | Within Estimator Variance | W | WY | $WY^2$ | $W^2$ | Between Estimator Variance | Total Estimator Variance | $W^*$ | $W^*Y$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Roff Lmat | 0.25 | 0.07 | 0.42 | 0.09 | 7.671E-03 | 130.4 | 32.6 | 8.2 | 16992.4 | 0.000E+00 | 7.671E-03 | 130.4 | 32.6 |
| Pauly empirical length | 0.21 | 0.13 | 0.27 | 0.03 | 1.183E-03 | 845.3 | 178.3 | 37.6 | 714477.6 | 0.000E+00 | 1.183E-03 | 845.3 | 178.3 |
| Empirical max biomass | 0.20 | 0.32 | 0.12 | 0.05 | 2.502E-03 | 399.7 | 81.6 | 16.7 | 159725.8 | 0.000E+00 | 2.502E-03 | 399.7 | 81.6 |
| Hamel-Hoenig Amax | 0.19 | 0.22 | 0.17 | 0.01 | 1.592E-04 | 6281.5 | 1194.6 | 227.2 | 39457832.4 | 0.000E+00 | 1.592E-04 | 6281.5 | 1194.6 |
| Hamel-Jensen k | 0.19 | 0.09 | 0.28 | 0.05 | 2.324E-03 | 430.3 | 83.0 | 16.0 | 185157.6 | 0.000E+00 | 2.324E-03 | 430.3 | 83.0 |
| CGP M at Lmat | 0.26 | 0.09 | 0.41 | 0.08 | 6.498E-03 | 153.9 | 39.5 | 10.1 | 23686.0 | 0.000E+00 | 6.498E-03 | 153.9 | 39.5 |
| CGP M at Amat | 0.20 | 0.09 | 0.29 | 0.05 | 2.560E-03 | 390.6 | 79.1 | 16.0 | 152545.0 | 0.000E+00 | 2.560E-03 | 390.6 | 79.1 |
| | | | | | Total | 8631.6 | 1688.7 | 331.8 | 40710416.7 | | Total | 8631.6 | 1688.7 |

| | | | | | |
|---|---|---|---|---|---|
| **Female Unweighted Estimate** | | **L95%** | **U95%** | | |
| **Average(M) =** | **0.22** | **0.16** | **0.27** | | |
| SE(M) = | 0.03 | | | | |
| **Female Fixed Effects Estimate** | | **L95%** | **U95%** | **Term** | **Total** |
| **M =** | **0.20** | **0.17** | **0.22** | W | 8631.6 |
| Var(M) = 1/W = | 1.159E-04 | **PI_L95%** | **PI_U95%** | WY | 1688.7 |
| SE(M) = sqrt(Var(M) = | 0.01 | **0.17** | **0.22** | $WY^2$ | 331.8 |
| | | **CV =** | **5.5%** | $W^2$ | 40710416.7 |
| **Between Estimator Variance** | | | | | |
| $Q = WY^2 - (WY)^2/W =$ | 1.4 | | | | |
| DF = K - 1 = | 6 | | | | |
| $C = W - (W^2/W) =$ | 3915.2 | | | | |
| $T^2 = (Q - DF)/C =$ | 0.0 | | | | |
| **Female Random Effects Estimate** | | **L95%** | **U95%** | **Term** | **Total** |
| $\mathbf{M^* =}$ | **0.20** | **0.17** | **0.22** | $W^*$ | 8631.6 |
| $Var(M^*) = 1/W^* =$ | 1.159E-04 | **PI_L95%** | **PI_U95%** | $W^*Y$ | 1688.7 |
| $SE(M^*) = sqrt(Var(M^*) =$ | 0.01 | **0.17** | **0.22** | | |

Table 3.2. Results of the unweighted, fixed effects, and random effects analyses under the new growth scenario to predict the adult natural mortality rate of female Pacific blue marlin based on seven estimators, where “Average(M)”, “M”, and “M*” are the unweighted average, fixed effects, and random effects estimates of natural mortality, respectively, with lower and upper 95% prediction intervals given by “PI_L95%” and “PI_U95%”, respectively.

**Female Natural Mortality Estimators**

| Estimator | Natural Mortality Estimate | Lower Range of Parmeters | Upper Range of Parameters | Standard Error | Within Estimator Variance | W | WY | $WY^2$ | $W^2$ | Between Estimator Variance | Total Estimator Variance | $W^*$ | $W^*Y$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Roff Lmat* | *0.36* | 0.28 | 0.34 | 0.02 | 0.000237 | 4217.2 | 1511.7 | 541.9 | 17784972.8 | 2.962E-02 | 2.986E-02 | 33.5 | 12.0 |
| *Pauly empirical length* | *0.44* | 0.40 | 0.49 | 0.02 | 0.000525 | 1903.9 | 845.6 | 375.6 | 3624696.9 | 2.962E-02 | 3.014E-02 | 33.2 | 14.7 |
| *Empirical max biomass* | *0.07* | 0.12 | 0.03 | 0.02 | 0.000454 | 2200.8 | 146.0 | 9.7 | 4843321.2 | 2.962E-02 | 3.007E-02 | 33.3 | 2.2 |
| Hamel-Hoenig Amax | 0.19 | 0.22 | 0.17 | 0.01 | 0.000159 | 6281.5 | 1194.6 | 227.2 | 39457832.4 | 2.962E-02 | 2.978E-02 | 33.6 | 6.4 |
| *Hamel-Jensen k* | *0.54* | 0.47 | 0.61 | 0.04 | 0.001229 | 813.5 | 442.1 | 240.3 | 661839.0 | 2.962E-02 | 3.085E-02 | 32.4 | 17.6 |
| *CGP M at Lmat* | *0.51* | 0.42 | 0.53 | 0.03 | 0.000792 | 1263.2 | 638.6 | 322.8 | 1595628.3 | 2.962E-02 | 3.041E-02 | 32.9 | 16.6 |
| *CGP M at Amat* | *0.57* | 0.50 | 0.64 | 0.04 | 0.001354 | 738.4 | 421.2 | 240.3 | 545266.4 | 2.962E-02 | 2.560E-03 | 390.6 | 222.8 |
| | | | | | Total | 17418.5 | 5199.7 | 1957.6 | 68513557.0 | | Total | 589.4 | 292.4 |

| **Female Unweighted Estimate** | | **L95%** | **U95%** |
|---|---|---|---|
| **Average(M) =** | **0.38** | **0.01** | **0.76** |
| SE(M) = | 0.19 | | |

| **Female Fixed Effects Estimate** | | **L95%** | **U95%** | **Term** | **Total** |
|---|---|---|---|---|---|
| **M =** | **0.30** | **0.28** | **0.31** | W | 17418.5 |
| Var(M) = 1/W = | 5.741E-05 | **PI_L95%** | **PI_U95%** | WY | 5199.7 |
| SE(M) = sqrt(Var(M) = | 0.01 | **0.28** | **0.32** | $WY^2$ | 1957.6 |
| | | **CV =** | **2.5%** | $W^2$ | 68513557.0 |

| **Between Estimator Variance** | |
|---|---|
| $Q = WY^2 - (WY)^2/W =$ | 405.4 |
| DF = K - 1 = | 6 |
| $C = W - (W^2/W) =$ | 13485.2 |
| $T^2 = (Q - DF)/C =$ | 0.030 |

| **Female Random Effects Estimate** | | **L95%** | **U95%** | **Term** | **Total** |
|---|---|---|---|---|---|
| **$M^*$ =** | **0.50** | **0.42** | **0.58** | $W^*$ | 589.4 |
| $Var(M^*) = 1/W^* =$ | 1.697E-03 | **PI_L95%** | **PI_U95%** | $W^*Y$ | 292.4 |
| $SE(M^*) = sqrt(Var(M^*) =$ | 0.04 | **0.39** | **0.60** | | |

Table 4.1. Results of the unweighted, fixed effects, and random effects analyses <u>under the old growth scenario</u> to predict the adult natural mortality rate of male Pacific blue marlin based on seven estimators, where “Average(M)”, “M”, and “M*” are the unweighted average, fixed effects, and random effects estimates of natural mortality, respectively, with lower and upper 95% prediction intervals given by “PI_L95%” and “PI_U95%”, respectively.

**Male Natural Mortality Estimators**

| Estimator | Natural Mortality Estimate | Lower Range of Parmeters | Upper Range of Parameters | Standard Error | Within Estimator Variance | W | WY | $WY^2$ | $W^2$ | Between Estimator Variance | Total Estimator Variance | $W^*$ | $W^*Y$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Roff Lmat | 0.39 | 0.22 | 0.45 | 0.06 | 3.262E-03 | 306.5 | 119.6 | 46.7 | 93969.6 | 0.000E+00 | 3.262E-03 | 306.5 | 119.6 |
| Pauly empirical length | 0.36 | 0.29 | 0.44 | 0.04 | 1.533E-03 | 652.3 | 235.3 | 84.9 | 425501.3 | 0.000E+00 | 1.533E-03 | 652.3 | 235.3 |
| Empirical max biomass | 0.42 | 0.59 | 0.28 | 0.08 | 5.798E-03 | 172.5 | 72.3 | 30.3 | 29748.1 | 0.000E+00 | 5.798E-03 | 172.5 | 72.3 |
| Hamel-Hoenig Amax | 0.38 | 0.44 | 0.34 | 0.03 | 6.368E-04 | 1570.4 | 597.3 | 227.2 | 2466114.5 | 0.000E+00 | 6.368E-04 | 1570.4 | 597.3 |
| Hamel-Jensen k | 0.37 | 0.26 | 0.49 | 0.06 | 3.246E-03 | 308.1 | 113.4 | 41.8 | 94915.9 | 0.000E+00 | 3.246E-03 | 308.1 | 113.4 |
| CGP M at Lmat | 0.43 | 0.27 | 0.53 | 0.06 | 4.206E-03 | 237.7 | 102.9 | 44.5 | 56521.1 | 0.000E+00 | 4.206E-03 | 237.7 | 102.9 |
| CGP M at Amat | 0.39 | 0.28 | 0.52 | 0.06 | 3.576E-03 | 279.6 | 108.1 | 41.8 | 78197.9 | 0.000E+00 | 3.576E-03 | 279.6 | 108.1 |
| | | | | | Total | 3527.2 | 1348.9 | 517.1 | 3244968.5 | | Total | 3527.2 | 1348.9 |

| **Male Unweighted Estimator** | | **L95%** | **U95%** |
|---|---|---|---|
| **Average(M) =** | **0.39** | **0.34** | **0.44** |
| SE(M) = | 0.03 | | |

| **Male Fixed Effects Estimator** | | **L95%** | **U95%** | **Term** | **Total** |
|---|---|---|---|---|---|
| **M =** | **0.38** | **0.35** | **0.42** | W | 3527.2 |
| Var(M) = 1/W = | 2.835E-04 | **PI_L95%** | **PI_U95%** | WY | 1348.9 |
| SE(M) = sqrt(Var(M) = | 0.02 | **0.34** | **0.43** | $WY^2$ | 517.1 |
| | | | | $W^2$ | 3244968.5 |

| **Between Estimator Variance** | |
|---|---|
| $Q = WY^2 - (WY)^2/W =$ | 1.2 |
| DF = K - 1 = | 6 |
| $C = W - (W^2/W) =$ | 2607.2 |
| $T^2 = (Q - DF)/C =$ | 0.0 |

| **Male Random Effects Estimator** | | **L95%** | **U95%** | **Term** | **Total** |
|---|---|---|---|---|---|
| **$M^*$ =** | **0.38** | **0.35** | **0.42** | $W^*$ | 3527.2 |
| $Var(M^*) = 1/W^* =$ | 2.835E-04 | **PI_L95%** | **PI_U95%** | $W^*Y$ | 1348.9 |
| $SE(M^*) = sqrt(Var(M^*) =$ | 0.02 | **0.34** | **0.43** | | |

Table 4.2. Results of the unweighted, fixed effects, and random effects analyses <u>under the new growth scenario</u> to predict the adult natural mortality rate of male Pacific blue marlin based on seven estimators, where "Average(M)", "M", and "M*" are the unweighted average, fixed effects, and random effects estimates of natural mortality, respectively, with lower and upper 95% prediction intervals given by "PI_L95%" and "PI_U95%", respectively.

**Male Natural Mortality Estimators**

| Estimator | Natural Mortality Estimate | Lower Range of Parmeters | Upper Range of Parameters | Standard Error | Within Estimator Variance | W | WY | $WY^2$ | $W^2$ | Between Estimator Variance | Total Estimator Variance | $W^*$ | $W^*Y$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Roff Lmat* | *0.28* | 0.15 | 0.35 | 0.05 | 0.002366 | 422.6 | 118.8 | 33.4 | 178602.8 | 0.000E+00 | 2.366E-03 | 422.6 | 118.8 |
| *Pauly empirical length* | *0.33* | 0.24 | 0.42 | 0.05 | 0.002072 | 482.7 | 160.2 | 53.2 | 233017.4 | 0.000E+00 | 2.072E-03 | 482.7 | 160.2 |
| *Empirical max biomass* | *0.45* | 0.64 | 0.31 | 0.08 | 0.006739 | 148.4 | 67.0 | 30.3 | 22022.7 | 0.000E+00 | 6.739E-03 | 148.4 | 67.0 |
| Hamel-Hoenig Amax | 0.38 | 0.44 | 0.34 | 0.03 | 0.000637 | 1570.4 | 597.3 | 227.2 | 2466114.5 | 0.000E+00 | 6.368E-04 | 1570.4 | 597.3 |
| *Hamel-Jensen k* | *0.32* | 0.19 | 0.44 | 0.06 | 0.003764 | 265.6 | 83.8 | 26.4 | 70566.8 | 0.000E+00 | 3.764E-03 | 265.6 | 83.8 |
| *CGP M at Lmat* | *0.34* | 0.20 | 0.44 | 0.06 | 0.003838 | 260.5 | 88.0 | 29.7 | 67884.9 | 0.000E+00 | 3.838E-03 | 260.5 | 88.0 |
| *CGP M at Amat* | *0.33* | 0.20 | 0.46 | 0.06 | 0.004147 | 241.1 | 79.9 | 26.4 | 58137.5 | 0.000E+00 | 4.147E-03 | 241.1 | 79.9 |
| | | | | | Total | 3391.4 | 1195.0 | 426.6 | 3096346.7 | | Total | 3391.4 | 1195.0 |

| **Male Unweighted Estimator** | | **L95%** | **U95%** |
|---|---|---|---|
| **Average(M) =** | **0.35** | **0.24** | **0.45** |
| SE(M) = | 0.05 | | |

| **Male Fixed Effects Estimator** | | **L95%** | **U95%** | **Term** | **Total** |
|---|---|---|---|---|---|
| **M =** | **0.35** | **0.32** | **0.39** | W | 3391.4 |
| Var(M) = 1/W = | 2.949E-04 | **PI_L95%** | **PI_U95%** | WY | 1195.0 |
| SE(M) = sqrt(Var(M) = | 0.02 | **0.31** | **0.40** | $WY^2$ | 426.6 |
| | | **CV =** | **4.9%** | $W^2$ | 3096346.7 |

| **Between Estimator Variance** | |
|---|---|
| $Q = WY^2 - (WY)^2/W =$ | 5.6 |
| DF = K - 1 = | 6 |
| $C = W - (W^2/W) =$ | 2478.4 |
| $T^2 = (Q - DF)/C =$ | 0.000 |

| **Male Random Effects Estimator** | | **L95%** | **U95%** | **Term** | **Total** |
|---|---|---|---|---|---|
| **$M^*$ =** | **0.35** | **0.32** | **0.39** | $W^*$ | 3391.4 |
| $Var(M^*) = 1/W^*$ = | 2.949E-04 | **PI_L95%** | **PI_U95%** | $W^*Y$ | 1195.0 |
| $SE(M^*) = sqrt(Var(M^*)$ = | 0.02 | **0.31** | **0.40** | | |