

# Development and considerations for application of a longevity-based prior for the natural mortality rate

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## ABSTRACT

The natural mortality rate  $M$  is a key parameter in estimating the productivity of a fish stock. However, it is quite difficult to estimate given its correlation with other parameters, variation in processes governing population dynamics and data acquisition, as well as other factors such as ageing error. Meta-analytical approaches relating  $M$  to other life history parameters are often used to provide an estimate and/or Bayesian prior for  $M$ . Longevity is the one of these life history parameters most directly related to  $M$ . The maximum observed or estimated age serves as a proxy for longevity in predicting, or developing a prior for,  $M$  to be used within a stock assessment or other population model. Consideration of the age data and factors that might influence its quality for determining a maximum age is important in using a meta-analytically derived relationship between maximum age and  $M$ , though these factors are not completely absent from the data used to develop that relationship. Here, we discuss these issues, propose a relationship between maximum age and  $M$ , and develop an updated prior for  $M$  based upon maximum age.

## 1. Introduction

The natural mortality rate  $M$  associated with a fish stock is an important parameter in characterizing its productivity and dynamics, and errors in its estimation can have substantial effects on stock assessment and management (Punt et al., 2021). However, estimating the value of  $M$  is a consistently difficult proposition, as monitoring a fish cohort for its lifetime, especially when the species is long-lived, is impractical.  $M$  can be estimated within an assessment (Lee et al., 2011), directly from demographic (e.g. catch curve; Beverton and Holt, 1956; Quinn and Deriso, 1999) or tagging (or mark-recapture) data (Seber, 1982; Brownie et al., 1985), or indirectly from life-history parameters such as longevity or growth (e.g. Pauly, 1980; Hoenig, 1983; Kenchington, 2014; Hamel, 2015; Then et al., 2015; Hoenig et al., 2016; Maunder et al., in this issue; Cope and Hamel, in this issue). Here we consider meta-analytical methods using life history parameters that correlate with  $M$  to develop an approach to provide a point estimate and prior distribution (Hamel, 2015) for  $M$  that has broad applicability across animal taxa. While some approaches (e.g. Lorenzen, 2000; Gislason et al., 2010) attempt to provide estimates of  $M$  that can vary at age and/or size, the majority of stock assessments use the simplifying

assumption of a single value of  $M$  or one value for each sex, representing the average mortality across time and ages beyond some minimum age (the youngest, smallest fish likely have higher  $M$  values but for many species are not seen in substantial numbers in fishery catches, and thus early mortality can be accounted for by estimating “recruitment” to a stock at a more advanced age). Confounding of trends in  $M$  with age and variability in  $M$  across time with other life-history and fishery processes leads to the necessary use of simplifying assumptions, including, often, a single value of  $M$  (Punt et al., 2021).

A wide variety of direct, indirect and theoretical approaches for estimating  $M$  have been developed and employed over the years (see reviews in Kenchington, 2014; Maunder et al., in this issue). Among these are those based on meta-analyses of observed relationships between other estimated life history parameters and  $M$  (e.g. Cope and Hamel, in this issue). These life history parameters include size and growth parameters (e.g. von Bertalanffy  $k$  (growth rate coefficient),  $t_0$  (theoretical age at length = 0), and  $L_\infty$  (asymptotic size)) and those related to maturity, reproduction, and longevity. Estimates from these relationships can be used to fix  $M$  in a base model or sensitivity analysis within an assessment, or to provide a prior distribution of  $M$  (Hamel, 2015; Cope and Hamel, in this issue).

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Analysis of the relationship of  $M$  to various other life history parameters has been applied to particular taxonomic groups (e.g. [Beverton, 1992](#)), fish in general, or even to a combination of fish and other species (e.g. [Hoenig, 1983](#)). It has been argued that each of these relationships is dependent on taxonomy to a greater or lesser extent. For example, [Beverton \(1992\)](#) argued that the  $M/k$  relationship varied over an order of magnitude across differing taxa.

The longevity of, or maximum age achieved by, a species should be related closely to the natural mortality rate. Theoretically, given an exponential decay in population numbers, the probability of continued existence at any age is non-zero. In reality, older individuals experience senescence and increased  $M$ . Thus, while the relative timing and severity of senescence varies, the impact of this variability is small relative to the impact of  $M$  itself, and thus  $M$  is a good predictor of maximum age ([Dureuil and Froese, 2021](#)). Other factors such as the impacts of fishing, as modified by selectivity and refugia, and ageing error can affect the observed or estimated maximum age, and should be considered ([Hoenig, 2017](#)). However, compared to other life history parameters, maximum age is expected to have a more consistent relationship with  $M$  across taxa, and therefore is a better predictor of  $M$  ([Beverton, 1992](#); [Then et al., 2015](#)). Here we provide an updated estimator that applies a previous method of constructing priors ([Hamel, 2015](#)) with a corrected application of a valuable database ([Then et al., 2015](#); based on careful review of the origin of literature values as well as new analyses, substantially revising previous databases from [Pauly, 1980](#); [Hoenig, 1982](#); and others) on maximum observed or estimated age ( $A_{max}$ ; closely related to, but not identical, to “longevity” being the actual lifespan, which is unobservable) and  $M$  estimates to build a better relationship (both in central tendency and variability) between maximum age and  $M$ .

## 2. Theory of $M$ to maximum age relationship

To develop the theoretical relationship between  $A_{max}$  and  $M$ , certain consistent assumptions are necessary. These include the assumptions that  $A_{max}$  represents longevity,  $M$  is constant from some relatively early age,  $A_{init}$ , until the age at which senescence causes a rapid increase in that parameter, and that, across species, senescence, leading to a substantial increase in the natural mortality rate, occurs at an age,  $A_{sen}$ , when  $M$  would lead to the same proportion ( $C_a$ ) of a cohort size (at  $A_{init}$ ) remaining. With the additional assumption that the maximum age observed,  $A_{max}$ , is a constant multiplier (by a factor of just over 1.0) of  $A_{sen}$  (i.e.  $A_{max} = \beta_1 A_{sen}$ ), and  $A_{init}$  is also a constant proportion of  $A_{max}$  (i.e.,  $A_{init} = \beta_2 A_{max}$ ),

$$C_a = e^{-(A_{sen}-A_{init})M} \quad (1)$$

or, with substitution:

$$C_a = e^{-\left(\frac{1}{\beta_1} - \beta_2\right)A_{max}M} \quad (2)$$

and, equivalently:

$$C_b = e^{-A_{max}M} \quad (3)$$

from which follows:

$$C = MA_{max} \quad (4)$$

and, rearranging:

$$M = \frac{C}{A_{max}} \quad (5)$$

where  $\beta_1$ ,  $\beta_2$ ,  $C_a$ ,  $C_b$  ( $= C_a e^{\left(\frac{1}{\beta_1} - \beta_2\right)A_{max}M}$ ), and  $C$  ( $= -\ln(C_b)$ ) are constants. Eq. (5) is referred to as the one-parameter  $A_{max}$  equation for  $M$ . Eq. (5) can also be written as:

$$\ln(M) = c - \ln(A_{max}) \quad (6)$$

Of course, all of the assumptions in the theoretical relationship are not strictly met in all cases, leading to variation in the relationship between  $M$  and  $A_{max}$  across species and stocks.

### 2.1. Estimating the relationship between maximum age and $M$ requires log-transformed values

It is very common to build relationships between  $A_{max}$  and  $M$  by regressing the two values across many taxa. It is also common to estimate  $M$  using the slope of log-transformed numbers at age. In a basic age-structured population dynamics model, it is shown that  $M$  is an exponential rate parameter. Another way to think of this is not that  $M$  changes but that the time scale to which it applies changes with longevity. Thus rate parameters scale with time, as does their variability, and log-transformation eliminates the heteroscedasticity that occurs in real space. While minor heteroscedasticity may not cause substantial issues with regression analyses, in this case the heteroscedasticity is severe, as seen in [Fig. 1](#). In addition, [Eq. \(6\)](#) implies a linear relationship between  $\ln(M)$  and  $\ln(A_{max})$ . We therefore recommend assuming geometric error and to log-transform both  $A_{max}$  and  $M$  prior to any regression analysis.

[Then et al. \(2015\)](#) provided estimates of  $M$  and related life history parameters across a large number of fish species as an update to the original [Hoenig \(1983\)](#) analysis that developed an  $M$  estimator for fish species in general. After conducting a number of regression analyses relating  $M$  to covariates, in real and log-transformed space, [Then et al. \(2015\)](#) recommended  $M$  estimates be based on maximum age alone (assuming maximum age is known). Their recommended relationship is based on an updated non-linear least squares (NLS) estimator,  $M = 4.899A_{max}^{-.916}$  (Using  $A_{max}$  here for consistency, rather than  $t_{max}$ , which was used in [Then et al., 2015](#)).

There are two issues with the analyses conducted by [Then et al. \(2015\)](#). In fitting the alternative model forms relating  $M$  to  $A_{max}$ , they did not consistently apply the lognormal transformation. In particular, in real space, one would expect substantial heteroscedasticity in both the observation and process error associated with the observed relationship of  $M$  to  $A_{max}$  (see [Fig. 1](#)). Both the one-parameter  $A_{max}$  ([Eq. \(5\)](#)) and Then NLS models are fit in real space, giving too much weight to short-lived species and very little weight to long-lived species. The consequence of this is that, given limited flexibility, the shape of the relationship will be driven by data from species with high  $M$  and short lifespans. The model fit comparisons made by [Then et al. \(2015\)](#), and in particular the Cross Validation Prediction Error (CVPE), were made in real space, essentially ignoring poor relative fits to small  $M$  values and giving too much weight to absolute fits to large  $M$  values. Whether viewed in log space ([Fig. 2](#)) or real space ([Fig. 3](#)), the fit to the data is clearly biased high (whether considering the mean or the median of the data) for longevities greater than 50, and somewhat for ages between 20 and 50. This is due to the fact that the shape of the curve is driven the high number of data points with longevities between 5 and 10 years ([Fig. 3](#)) rather than being an intrinsic property of their approach. To evaluate the fits of the alternative methods using CPVE, one should compare the CPVE in log space rather than in real space, so that each point is given equal weight in properly considering relative error.

### 2.2. An updated approach to construct an estimate and prior for the natural mortality rate

[Hamel \(2015\)](#) developed a method for constructing a prior on  $M$  by combining a suite of estimators, and demonstrated the method using relationships to life history parameters such as longevity, size, growth rate and reproductive effort. Using the analytical approach shown in that paper to reevaluate the data used in [Then et al. \(2015\)](#) through

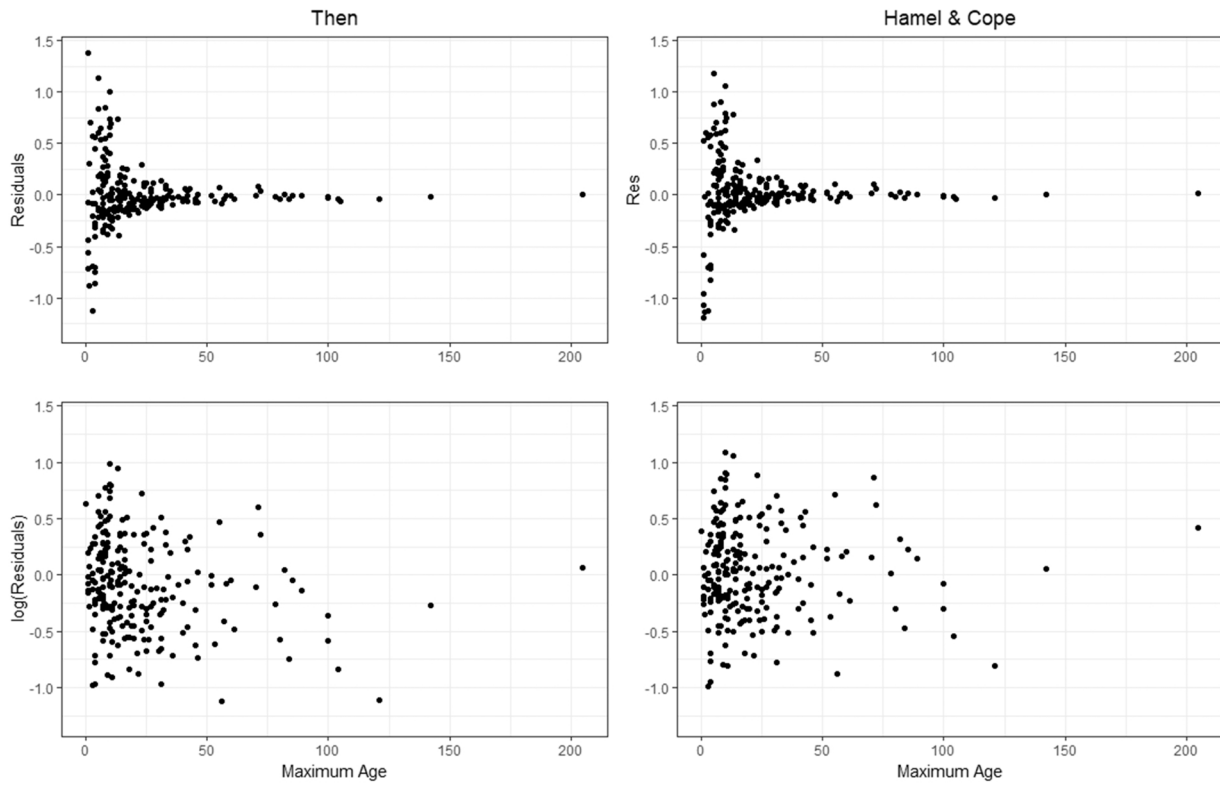


Fig. 1. Residuals between  $M$  values from database and those predicted from the Then NLS and Hamel & Cope models in real space (top) and natural log space (bottom).

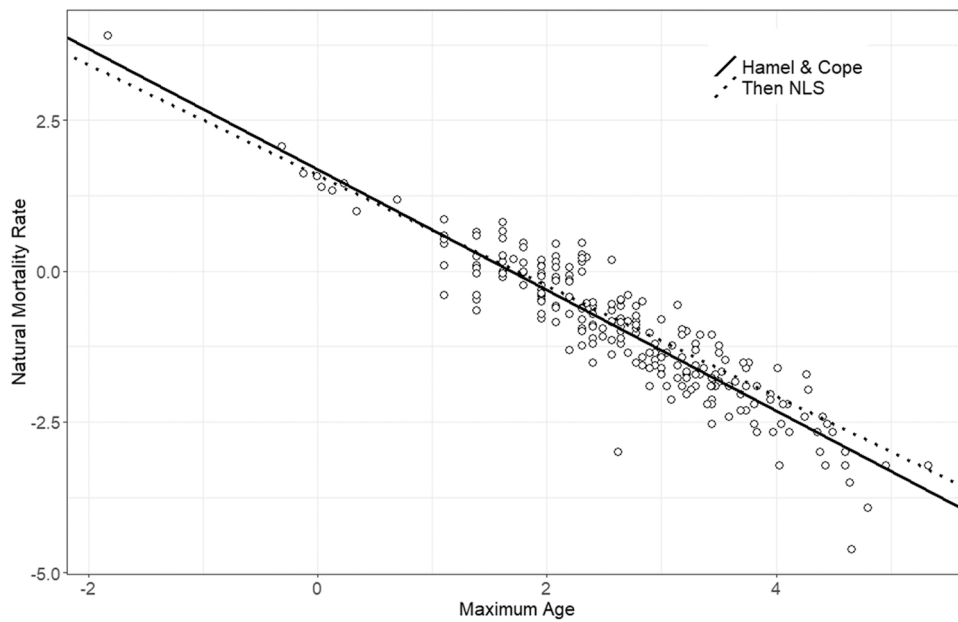


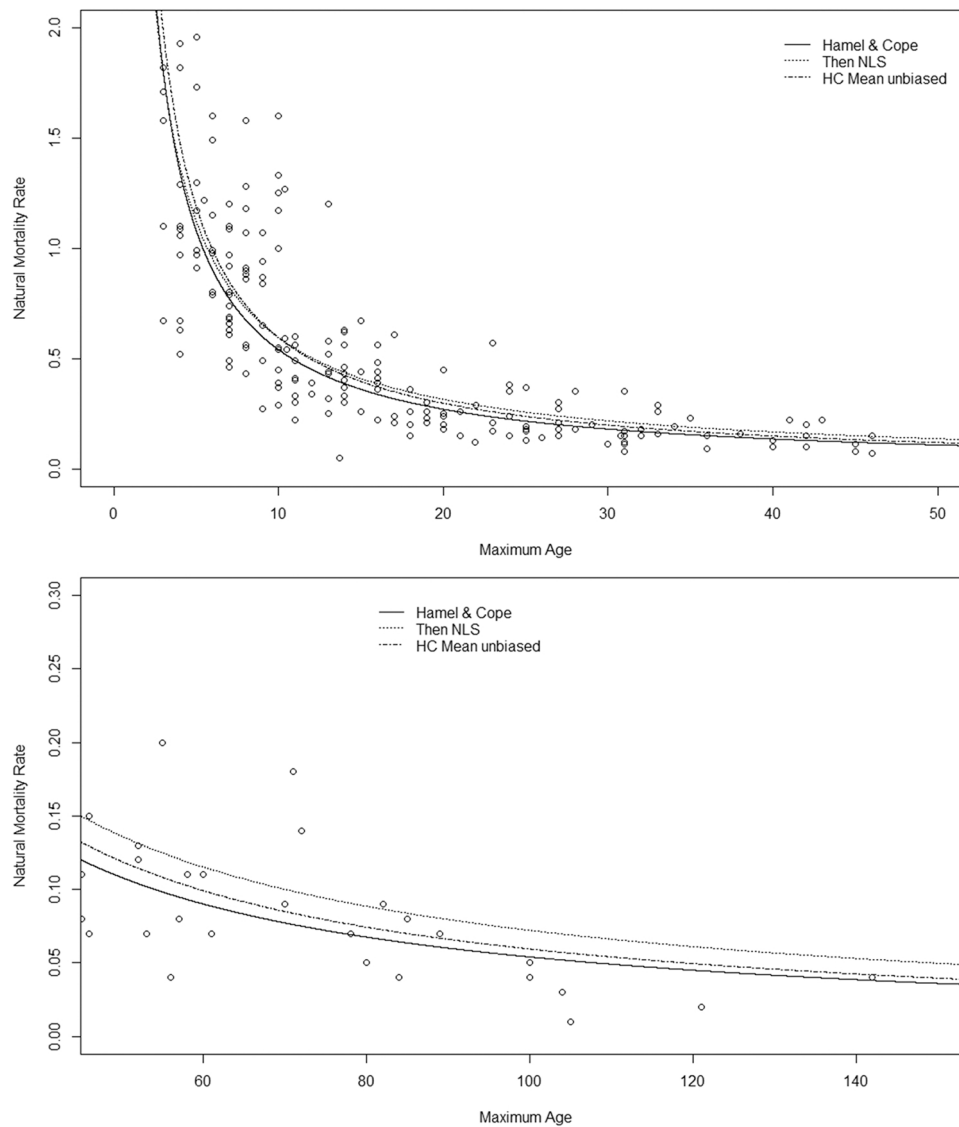
Fig. 2. Comparison of NLS model from [Then et al. \(2015\)](#) and the Hamel & Cope model fit to the same data, displayed in log-log space.

fitting the one-parameter  $A_{max}$  model under a log-log transformation, which requires forcing the slope to be  $-1$  in the transformed space (Eq. (6)); The analytical approach used in [Hamel, 2015; Figs. 2 and 3](#), the point estimate for  $M$  is:

$$M = \frac{5.40}{A_{max}} \tag{7}$$

The coefficient of 5.40 is larger than the value of 5.109 found in [Then](#)

[et al. \(2015\)](#) when using untransformed data or that found by [Hamel \(2015\)](#) of 4.37 using the much older and smaller data set from [Hoenig \(1983\)](#), under log transformation. It is also larger than either the rule of thumb value of 3.0 (e.g., [Rugolo et al., 1998](#); which involves rather arbitrarily setting  $C_b = 0.05$  (which can be thought of as having 5% of the cohort remaining at  $A_{max}$ )) or the 4.22 suggested by [Hewitt and Hoenig \(2005\)](#) by simply setting the not quite unitary exponent from [Hoenig \(1983\)](#) to 1.0, without refitting. The value of  $M$  in Eq. (7) is the



**Fig. 3.** Comparison of NLS model from [Then et al. \(2015\)](#) and the Hamel & Cope model (both in its original median-unbiased form, and in a mean-unbiased form (“HC mean unbiased”)) fit to the same data, plotted in real space across two ranges of maximum age.

median of the proposed prior on  $M$ . The point estimate represents the median instead of the mean of the prior in order to provide a risk neutral estimate for stock assessment, such that half of the probability density is above, and half below, the point estimate.

The residuals (in log space) around this new one-parameter relationship (Eq. (7)) are far closer to being homoscedastic than the real-space residuals around the Then NLS formulation (Fig. 1). The distribution of log-space residuals around Eq. (7) appear reasonably close to normal (Fig. 4), while the log-space residuals around the Then NLS formulation appear similarly close to normal but not centered around zero.

The prediction interval is typically defined using the standard deviation of the data around the regression line in log-transformed space (see [Hamel, 2015](#) for equations). Recall, however, that the regression is not relating longevity to  $M$ , but rather an estimate of longevity to an estimate of  $M$ . What we want to have for both prediction intervals and priors is the expected range of actual  $M$  given  $A_{max}$ , which is an estimate of longevity. Therefore, it is necessary to take into account the error in the estimates of  $M$  used in the meta-analysis. That is to say, in order to predict  $M$ , and given that we do not have perfect estimates of longevity, we need to evaluate the relationship between the estimate of longevity and the “true”  $M$  (admitting even this represents some average over time

and age). In other words, we would like to remove the variance due to error in the values of  $M$  used in the meta-analysis.

The natural log-space standard deviation around the relationship defined in Eq. (7) is 0.44, which combines sources of error in both  $A_{max}$  and  $M$ . Since we do not know the error due to estimates of  $M$  used in the [Then et al. \(2015\)](#) meta-analysis nor that due to errors in estimates of  $A_{max}$  or due to the actual variation in the longevity to  $M$  relationship among species and stocks, we make the assumption that half of the observed variance is due to errors in estimating the values of  $M$  in the database. We chose half of the variance given that  $M$  is more difficult to estimate than  $A_{max}$  (otherwise we would not need or use the meta-analytical approach), while we expect both errors in  $M$  estimation and variation in the actual relationship to be substantial. This assumption results in a prior defined as a lognormal distribution with median (or mean in log-space) =  $5.40/A_{max}$ , with a standard deviation in log-space = 0.31 (i.e. 0.44 divided by  $\sqrt{2}$ ; this is equivalent to a log-space variance of 0.097). This prior replaces previously published priors based upon maximum age, including that from [Hamel \(2015\)](#), which, when using maximum age alone, provided a lognormal prior with a median =  $4.37/A_{max}$  and a standard deviation in log-space = 0.51. Thus the refined prior is both tighter and shifted higher (Fig. 5).

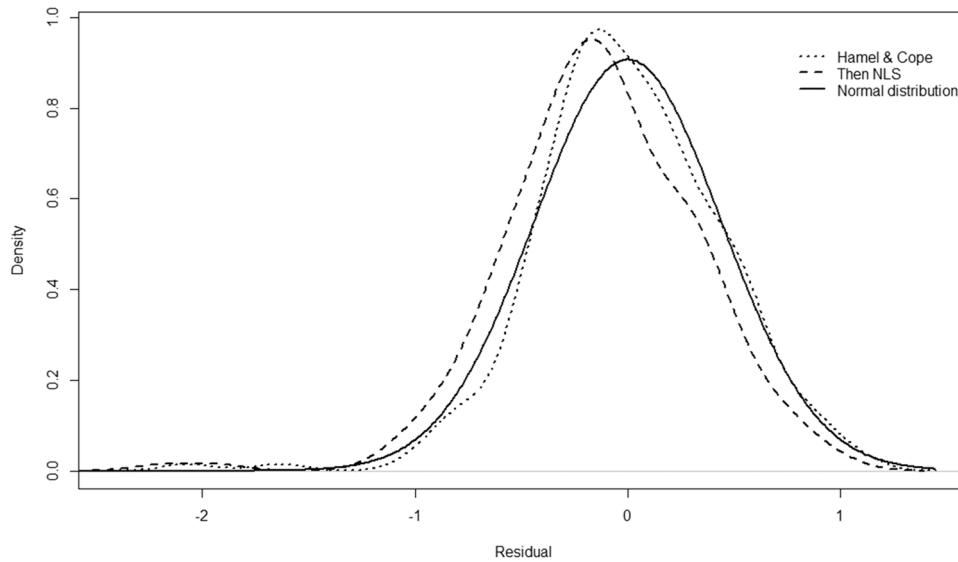


Fig. 4. Residuals in log-space for Hamel & Cope and Then NLS formulations. A normal ( $\mu = 0$ ,  $sd = 0.44$ ) distribution, matching the observed  $sd$  for the Hamel & Cope analysis, is shown for comparison.

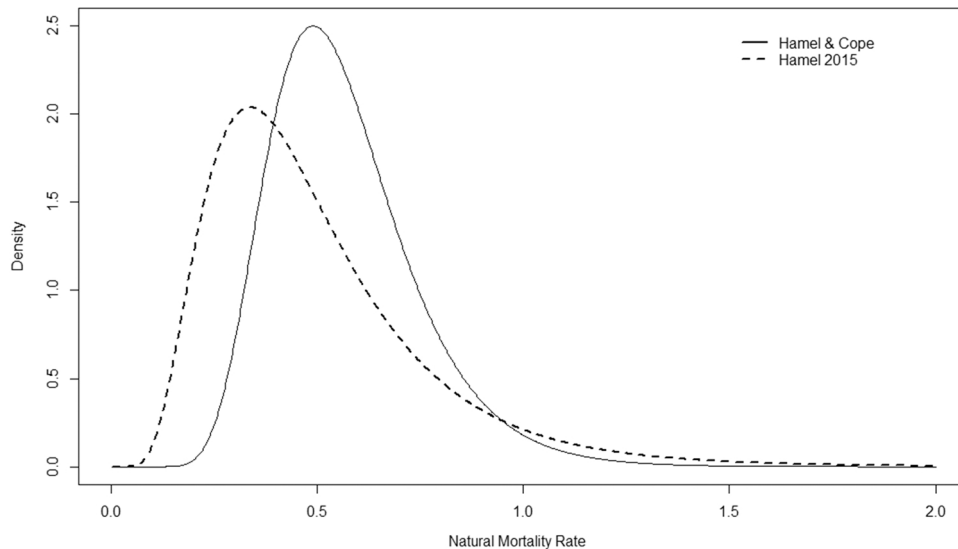


Fig. 5. Example of Hamel & Cope and Hamel (2015) Bayesian prior forms for a maximum age value of 10 (median  $M$  values of 0.54 and 0.44 respectively). The Hamel and Cope formulation eliminates unrealistically small and large values of  $M$  (95% interval of (0.29, 0.99) vs. (0.16, 1.19) for the Hamel, 2015 formulation).

### 3. Does sample size of aged individuals matter?

Obtaining an accurate estimate of maximum age is not a simple undertaking. The idea of relating  $M$  to longevity dates to at least the middle of the 20th century (e.g. Beverton, 1963), while the debate around including sample size in relating  $M$  to  $A_{max}$  has been around just as long. Holt (1965) developed a relationship between constant age-invariant mortality rate, constant recruitment size, and expected maximum age (with the notation used here):

$$A_{max} = \frac{\ln(n) + 0.577}{Z} + A_{init} \tag{8}$$

with  $Z$  = total mortality rate and  $n$  = number of individuals at  $A_{init}$ . Hoenig (1983) developed an approximation to expected maximum age given a sample size  $n$  and constant mortality rate and knife-edged selectivity (i.e. assuming all ages that are caught in the fishery are equally likely to be caught; other selectivity assumptions would require a modification to the equation, but not change its general form), and

arrived at an equation:

$$A_{max} \approx \frac{\ln(2n + 1)}{Z} + A_{init} \tag{9}$$

that provides results similar to those of Holt (1965) given equivalent samples sizes, particularly when those sample sizes are large. Kenchington (2014) challenged the validity of these formulations, and came up with an alternative relationship

$$A_{max} = \frac{\ln(2Zn_e + 1)}{Z} + A_{init} \tag{10}$$

(replacing  $n$  by  $n_e$  to represent effective sample size, though that caveat would apply to Hoenig's equation as well). However, Kenchington's calculation was based upon flawed logic. In his formulation,  $N_t$  represents the expected number observed at any age  $t$  given a sample size  $n$ , constant  $M$  among selected ages, and knife-edged selectivity. In particular, he states that the expected maximum observed age "can be approximated as the age at which  $N_t = 0.5$ , as about half of all trials

should return higher values and half lower.” However, his statement is clearly false. The correct formulation would state that the expected maximum observed age can be approximated as the first age beyond which the sum of  $N_t$  is less than or equal to 0.5, or:  $\sum_{i=t+1}^{\infty} N_i \leq 0.5$ . Using this formulation, one recovers the equation found by Hoening (1983). Hoening (2017) provided numeric evidence of this, though using the simple analytical approach we describe above allows one to arrive at the same conclusion using nothing but pencil and paper.

Observed longevity should occur when one expects about half a fish to be older than that age. This is under the assumption of constant  $M$  across ages, when, in fact, we know that  $M$  does increase at some point due to senescence (Dureuil and Froese, 2021), and therefore the number of older fish is more limited than that formula would suggest, and the impact of more samples is likely to be small in terms of finding older fish.

Hoening (2017) went on to suggest that sample sizes (beyond some minimum) need not be considered, since (1) expressions including sample size “may not be robust to failures of the parametric assumptions, (2) it is often difficult or impossible to determine the effective sample size, and (3) new estimators may not be needed because of the insensitivity of the maximum age to sample size”. A number of factors are problematic in assuming a strict sample size relationship to  $A_{max}$  given  $M$ , including fishery selectivity, increased  $M$  due to senescence, recruitment variability, ageing error and fishing history (Hoening, 2017). Subpopulations with different fishing (and/or recruitment) histories and fishery selectivity, refugia including protected areas, and migratory patterns among subpopulations could all lead to non-homogeneity by sampling location and method in expected observed  $A_{max}$  in any year. Thus including sample size in the relationship between  $A_{max}$  and  $M$  is not seen as useful in general.

### 3.1. How to measure/estimate maximum age for use in estimating $M$ through the meta-analysis

It is important to recognize that the data used for the meta-analyses suffers from the same issues of ageing error, selectivity, recruitment variability, and error in estimates of covariates, including  $A_{max}$ . If we had perfect data on each of these things, then we could estimate  $M$  within the assessment model (e.g. Lee et al., 2011). Since we do not, the approach of using the results of meta-analyses to provide a point estimate and/or prior for  $M$  is appropriate. A question remains, however, about when to reject the observed maximum age and use an alternate estimate of  $A_{max}$  for estimation of  $M$  and when to turn to other methods or life-history covariates altogether. There do exist situations, such as where there has been an ongoing period of sustained heavy fishing pressure and inadequate or no age sample estimates from prior to that period (Barnett et al., 2017; Berkeley et al., 2004), sampling that only targets younger/smaller fish, unvalidated ageing structures (Bishop et al., 2006), or where ageing error or bias is severe and unresolvable (e.g. Taylor et al., 2013) such that a reasonable estimate of  $A_{max}$  may not be achievable. While some of the maximum age values in Then et al. (2015) data set may have been impacted by fishing, one expects the vetting process to have removed those where fishing had a large impact. Therefore the relationship found here may be most appropriate in cases where there has been a small impact of fishing, while also being well suited for cases with no fishing impact to moderate fishing impact.

Errors in estimates of  $A_{max}$  can occur due to errors in species identification and data entry, as well as ageing error, and therefore it is important to consider whether there are obvious outliers in the data, as well as if ageing error may be biasing the ages. One approach would be to use some consistent percentile of the aged sample in an attempt to address both outliers and ageing error, however this could result in a substantial shift in the perceived maximum age, and was not a procedure generally used for the  $A_{max}$  values used in the meta-analysis itself (though what the procedures were, exactly, is not documented). It would be better to evaluate the data and look for obvious outliers, as

well as consider if ageing error is unusual for the species or stock under consideration.

Ageing error undoubtedly occurred in the data used for estimating  $A_{max}$  in meta-analyses, including the Then et al. (2015) data set used here. Therefore, this should not be an issue to consider, except in the case of extreme ageing error or obvious outliers, and especially if an age cannot be reconfirmed.

Note that while ageing error tends to increase for the oldest fish, it is also more likely that the estimated ages for the oldest fish would be biased low due to the greater difficulty in discerning individual bands for older fish that are no longer growing or growing very slowly. Thus we recommend removing only clear outliers that would not be expected given the other observed ages, while more commonly the oldest estimates may be influenced by ageing error but no more so than the oldest estimates in the data set used to develop the meta-analytical relationship. While double-reading of age structures can identify variability (or imprecision) in age estimates, and relate this to age, validation methods can identify bias in ageing (Campana, 2001). In particular, bomb radiocarbon ageing validation can measure bias in ageing of older fish by evaluating those with estimated birth years in or near the 1960s (Hamel et al., 2008).

In order to determine whether and which value of  $A_{max}$  to use to estimate  $M$  (or a prior for  $M$ ), one should: 1) consider whether there is sampling bias or fishing impacts that would preclude collecting individuals representative of the longevity of a stock, or require larger sample sizes; 2) consider whether there are adequate ages available to represent the ages in the sampled population (hundreds of samples or more (Hoening, 2017)); 3) check for outliers that could be due to species misidentification or data entry errors, including ones that appear out of the distribution of ages; 4) consider if there is evidence of unusual ageing error or bias, consulting or conducting age validations if available.

We do not generally recommend 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.

### 3.2. How does estimating $M$ from $A_{max}$ compare to using other life history parameters?

Meta-analyses have been undertaken for a wide variety of life-history parameters to predict  $M$  (see reviews in Kenchington, 2014; Maunder et al., this issue). For example, the relationship between the von Bertalanffy growth parameter  $k$  and  $M$  has been analyzed multiple times. Beverton (1992) suggested that the relationship would vary greatly across taxa. Jensen (1996) used Pauly’s (1980) data set to provide an estimate of  $M = 1.6k$  by regressing the untransformed data, while making the incorrect assertion that R-squared values are comparable across transformations. Then et al. (2015) made the same error of conducting the meta-analysis of their data without transformation, arriving at a value of  $M = 1.692k$ . Hamel (2015) log-transformed Pauly’s data and found  $M = 1.753k$ . Here, we reanalyze the larger dataset from Then et al. (2015) under transformation and find:

$$M = 1.55k \quad (11)$$

Here, the log-space standard deviation is around the estimate = 0.90. In order to develop prediction intervals and priors for  $M$  itself, we need to decompose the variance to remove that due to errors in the estimation of  $M$  values used in the meta-analysis, as we did for the  $A_{max}$  to  $M$  relationship above. Having already calculated variance due to estimation of  $M$  in the  $A_{max}$  relationship from the same data set, we use that same value of variance associated with errors in those  $M$  values calculated above (0.097). Accounting for this results in a modified log-space standard deviation of 0.85 to be used for prediction intervals or priors

for  $M$  given  $k$ . Therefore, while the raw log-scale standard deviation for the  $k$  to  $M$  relationship is over twice that for the  $A_{max}$  to  $M$  relationship, the values remaining after correcting for the estimation errors in  $M$ , making the same correction to each standard deviation, differ by a factor of nearly three (0.85/0.31). The resultant prediction intervals and prior for  $M$  using  $k$  are therefore far wider than the prior using longevity. A 95% prediction interval for  $M$  given  $A_{max}$  would be bounded by the point estimate multiplied and divided by 1.8, whereas for  $M$  given  $k$ , the factor would be 5.3. This is as expected, given body growth is at least a degree removed from  $M$  compared to longevity, thus resulting in a larger expected and observed variation among taxa in the relationship between these two parameters (e.g. [Beverton, 1992](#)) and the actual variation in the observed relationship between estimated  $k$  and estimated  $M$ .

If we compare variances around relationships using log-transformed  $M$ , we see that most meta-analytical approaches, whether using a single or multiple covariates, lead to high variances (e.g. [Peterson and Wroblewski, 1984](#); [Jensen, 1996](#) (0.90\*); [Gunderson, 1997](#) (0.43\*); [Gislason et al., 2010](#) (0.72); \* as calculated in [Hamel, 2015](#)) with raw standard deviation values generally being greater than the 0.44 for the relationship derived here for the relationship between  $A_{max}$  and  $M$  (with an exception for Gunderson's gonadosomatic index, which provides a similar variance). This is likely due to greater variability in the relationship of most other covariates and  $M$ , including greater variability across and within taxa ([Beverton, 1992](#)) and ecosystems ([Lorenzen, 1996](#)), as well as more difficulty in estimating other covariates compared to longevity.

[Kenchington \(2014\)](#) suggested that his estimator was better than others, since for 10 of the 11 finfish he considered, estimates from his estimator were roughly within half to double of "true" value. However, that was, in fact, also the case for [Hoenig's \(1983\)](#) estimator. If one chooses a more restrictive, and therefore informative, geometric range, only 4 of 11 estimates using Kenchington's method were within two-thirds and three-halves of the "true" values, while 8 of 11 estimates were within that range for Hoenig's method. Moreover, estimates based upon the longevity-based method presented here are within that narrower range for 10 of 11 species considered by Kenchington. By this measure, then, the estimator presented here performs by far the best.

#### 4. Conclusions

[Then et al. \(2015\)](#) provided a valuable updated dataset of  $M$  and  $A_{max}$  and other life history values, but misapplied the variance form in constructing the predictive relationships. Here we correct those relationships. In theory, maximum age and  $M$  should be closely and inversely related, more so than other commonly measured life history values, and our analysis shows that the data support this conclusion ([Figs. 2 and 3](#)). These updated relationships provide point estimates and priors for  $M$  for use in stock assessment and other uses, emphasizing the importance of log-transformation of the data prior to analysis. We recommend using this approach whenever reasonable estimates of  $A_{max}$  are available, though we also note the challenges in obtaining maximum age estimates. We also present an updated relationship for  $k$  and  $M$  when maximum age is not obtainable, though note the larger expected variance in that relationship when constructing  $M$  priors for modeling application. See [Maunder et al. \(in this issue\)](#) for additional review and recommended approaches and Cope and Hamel (in this issue) for an estimation tool that includes the new formulations.

#### CRedit authorship contribution statement

**Owen S. Hamel:** Conceptualization, Methodology, Software, Validation, Formal analysis, Writing – original draft, Writing – review & editing, Visualization. **Jason M. Cope:** Software, Validation, Writing – original draft, Writing – review & editing, Visualization.

#### Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

#### Data Availability

Data has previously been made public by the authors of [Then et al. \(2015\)](#) cited in the manuscript.

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#### References

- Barnett, L.A.K., Branch, T.A., Ranasinghe, R.A., Essington, T.E., 2017. Old-growth fishes become scarce under fishing. *Curr. Biol.* 27 (2843–2848), e2 <https://doi.org/10.1016/j.cub.2017.07.069>.
- Berkeley, S.A., Hixon, M.A., Larson, R.J., Love, M.S., 2004. Fisheries sustainability via protection of age structure and spatial distribution of fish populations. *Fisheries* 29, 23–32. [https://doi.org/10.1577/1548-8446\(2004\)29\[23:FSVPOA\]2.0.CO;2](https://doi.org/10.1577/1548-8446(2004)29[23:FSVPOA]2.0.CO;2).
- Beverton, R.J.H., 1963. Maturation, growth and mortality of clupeid and engraulid stocks in relation to fishing. *J. Cons. Int. Explor. Mer.* 154, 44–67.
- Beverton, R.J.H., 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *J. Fish. Biol.* 41, 137–160.
- Beverton, R.J.H., Holt, S.J., 1956. A review of methods for estimating mortality rates in exploited fish populations, with special reference to sources of bias in catch sampling. *J. Cons. Int. Explor. Mer.* 14, 67–83.
- Bishop, S.D.H., Francis, M.P., Duffy, C., Montgomery, J.C., 2006. Age, growth, maturity, longevity and natural mortality of the shortfin mako shark (*Isurus oxyrinchus*) in New Zealand waters. *Mar. Freshw. Res.* 57, 143–154. <https://doi.org/10.1071/MF05077>.
- Brownie, C., Anderson, D.R., Burnham, K.P., Robson, D.S., 1985. *Statistical Inference From Band-Recovery Data—A Handbook*, second ed. U.S. Fish and Wildlife Service Resource Publication, p. 156.
- Campana, S.E., 2001. Accuracy, precision and quality control in age determination, including a review of the use and abuse of age validation methods. *J. Fish. Biol.* 59, 197–242.
- Cope, J.M., Hamel, O.S., in this issue. Upgrading from M version 0.2: an application-based method for practical estimation, evaluation and uncertainty characterization of natural mortality. *Fish. Res.* <https://doi.org/10.1016/j.fishres.2022.106493>.
- Dureuil, M., Froese, R., 2021. A natural constant predicts survival to maximum age. *Commun. Biol.* 4, 1–6. <https://doi.org/10.1038/s42003-021-02172-4>.
- Gislason, H., Daan, N., Rice, J.C., Pope, J.G., 2010. Size, growth, temperature and the natural mortality of marine fish. *Fish. Fish.* 11, 149–158.
- Gunders, D.R., 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. *Can. J. Fish. Aquat. Sci.* 54, 990–998.
- Hamel, O.S., 2015. A method for calculating a meta-analytical prior for the natural mortality rate using multiple life history correlates. *ICES J. Mar. Sci.* 72, 62–69.
- Hamel, O.S., Piner, K.R., Wallace, J.R., 2008. A robust deterministic model describing the bomb radiocarbon signal for use in fish age validation. *Trans. Am. Fish. Soc.* 137, 852–859.
- Hewitt, D.A., Hoenig, J.M., 2005. Comparison of two approaches for estimating natural mortality based on longevity. *Fish. Bull.* 103, 433–437.
- Hoenig, J.M., 1983. Empirical use of longevity data to estimate mortality rates. *Fish. Bull.* 82, 898–903.
- Hoenig, J.M., 2017. Should natural mortality estimators based on maximum age also consider sample size? *Trans. Am. Fish. Soc.* 146, 136–146.
- Hoenig, J.M., Then, A.Y.-H., Babcock, E.A., Hall, N.G., Hewitt, D.A., Hesp, S.A., 2016. The logic of comparative life history studies for estimating key parameters, with a focus on natural mortality rate. *ICES J. Mar. Sci.* 73, 2453–2467.
- Hoenig, J.M., 1982. *Compilation of Mortality and Longevity Estimates for Fish, Mollusks, and Cetaceans with a Bibliography of Comparative Life History Studies*. University of Rhode Island, Graduate School of Oceanography, Technical Report Reference No. 82–2, p. 14.
- Holt, S.J., 1965. A note on the relationship between the mortality rate and the duration of life in an exploited fish population. *Int. Comm. N. Atl. Fish. Res. Bull.* 2, 73–75.
- Jensen, A.L., 1996. Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. *Can. J. Fish. Aquat. Sci.* 53, 820–822.
- Kenchington, T.J., 2014. Natural mortality estimators for information-limited fisheries. *Fish. Fish.* 15, 533–562. <https://doi.org/10.1111/faf.12027>.
- Lee, H.-H., Maunder, M.N., Piner, K.R., Methot, R.D., 2011. Estimating natural mortality within a fisheries stock assessment model: an evaluation using simulation analysis based on twelve stock assessments. *Fish. Res.* 109, 89–94.
- Lorenzen, K., 1996. The relationship between body weight and natural mortality in juvenile and adult fish: a comparison of natural ecosystems and aquaculture. *J. Fish. Biol.* 49, 627–647.

- Lorenzen, K., 2000. Allometry of natural mortality as a basis for assessing optimal release size in fish-stocking programmes. *Can. J. Fish. Aquat. Sci.* 57, 2374–2381.
- Maunder, M.N., Hamel, O.S., Lee, H.-H., Piner, K.R., Cope, J.M., Punt, A.E., Ianelli, J.N., Castillo-Jordán, C., Kapur, M., Methot, R.D., in this issue. A review of estimation methods for natural mortality and their performance in the context of fishery stock assessment. *Fish. Res.* <https://doi.org/10.1016/j.fishres.2022.106489>.
- Pauly, D., 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. *J. Cons. int. Explor. Mer* 39 (2), 175–192.
- Peterson, I., Wroblewski, J.S., 1984. Mortality rate of fishes in the pelagic ecosystem. *Can. J. Fish. Aquat. Sci.* 41, 1117–1120.
- Punt, A.E., Castillo-Jordán, C., Hamel, O.S., Cope, J.M., Maunder, M.N., Ianelli, J.N., 2021. Consequences of error in natural mortality and its estimation in stock assessment models. *Fish. Res.* 233, 105759.
- Quinn II, T.J., Deriso, R.B., 1999. *Quantitative Fish Dynamics*. Oxford University Press, New York.
- Rugolo, L.J., Knotts, K.S., Lange, A.M., Crecco, V.A., 1998. Stock assessment of Chesapeake Bay blue crab (*Callinectes sapidus* Rathbun). *J. Shellfish Res.* 17, 493–517.
- Seber, G.A.F., 1982. *The Estimation of Animal Abundance and Related Parameters*. Griffin, London.
- Taylor, I.G., Gertseva, V., Matson, S.E., 2013. Spine-based ageing methods in the spiny dogfish shark, *Squalus suckleyi*: how they measure up. *Fish. Res.* 147, 83–92.
- Then, A.Y., Hoenig, J.M., Hall, N.G., Hewitt, D.A., 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on 201 fish species. *ICES J. Mar. Sci.* 72, 82–92.