A method for calculating a meta-analytical prior for the natural mortality rate using multiple life-history correlates

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Abstract

The natural mortality rate *M* is an extraordinarily difficult parameter to estimate for many fish species. The uncertainty associated with *M* translates into increased uncertainty in fishery stock assessments. Estimation of *M* within a stock assessment model is complicated by the confounding of this parameter with other life history and fishery parameters which are also uncertain, some of which are typically estimated within the model. Ageing error and variation in growth, which may not be fully modeled, can also affect estimation of *M*, as can various assumptions, including the assumed form of the stock recruitment function (e.g., Beverton-Holt, Ricker) and the level of compensation (or steepness), which may be fixed (or limited by a prior) in the model. To avoid these difficulties, stock assessors often assume point estimates for *M* derived from meta-analytical relationships between *M* and more easily measured life history characteristics. However, these relationships depend upon estimates of *M* for a great number of species, and those estimates are also subject to errors and biases (as are, to a lesser extent, the

other life history parameters). Therefore, at the very least, some measure of uncertainty in *M* should be calculated and used for evaluating uncertainty in stock assessments as well as in management strategy evaluations. Given error-free data on *M* and the covariate(s) for the meta-analysis, prediction intervals would provide the appropriate measure of uncertainty in *M*. In contrast, if the relationship between the covariate(s) and *M* is exact and the only error is in the estimates of *M* used for the meta-analysis, confidence intervals would appropriate. Using multiple published meta-analyses of *M*'s relationship to various life history correlates, and beginning with the uncertainty interval calculations, I develop a method for creating combined priors for *M* for use in stock assessment.

Key Words: Natural mortality rate, meta-analysis, prediction interval, prior distribution, fisheries stock assessment, Hoenig, Pauly, Jensen, Gunderson, McCoy and Gillooly.

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Introduction

The majority of models commonly used for stock assessment, with the exception of surplus production models, require (or produce) an estimate of the instantaneous natural mortality rate (*M*). However, *M* is a particularly difficult parameter to estimate for many commercially important fish species. The high degree of uncertainty in the value of this parameter is a problem that can greatly affect the accuracy and precision of the stock assessment results. Yet most stock assessments use a point estimate for *M* and, at best, include sensitivity analyses across a range of values which are considered plausible for *M*. Management strategy evaluations (MSEs), which are used to evaluate how well management strategies work given uncertainty in and estimation errors for population and fisheries parameters within a stock assessment framework, rarely consider misspecification of *M* (e.g. Punt, 2003; Kraak et al., 2008; Punt et. al. 2008).

The single value of *M* used in many stock assessment models must be taken to represent an averaging of the natural mortality rates for individuals of a species above a minimum age. The averaging occurs over variations with age and time, across space and between the sexes. The reality that *M* varies with time, age, sex and cohort, and due to environmental conditions, predation, and inter- and intra-specific competition, makes estimation even more difficult. However, the data rarely exist to estimate the variation in even some of these directions (Vetter 1988). Thus, most statistical catch-at-age stock assessments assume a constant *M*, or, at most, include some variability across age or length and/or differences between the sexes. While Lorenzen (2000) and Gislason et al.

(2010) provide compelling arguments for having *M* vary with age, the data available to estimate even a single, time- and age-invariant *M* are subject to a number of errors and uncertainties. These include ageing error and bias, which can lead to quite poor estimates of *M* (e.g. Beamish, 1979), uncertainty in fishery and survey selectivity (particularly in the case of dome-shaped selectivity, for which the estimate of the drop-off in selectivity with age can be highly correlated with the estimate of *M*), and uncertainty in catch levels and the fishing mortality rate (*F*) over time. Variance and bias in otolith-based ageing tends to increase with fish age, especially for those fish that essentially stop growing past a certain age or size, resulting in annuli which are extremely narrow and difficult to identify (Chilton and Beamish, 1982; Campana, 2001). Bias in ageing can lead to poor understanding of fish population dynamics (Yule et al. 2008). Fishery and survey selectivity can peak at an intermediate size or age, decreasing afterwards due to ontogenetic movement into areas that are more difficult to fish, or due to physiological changes allowing larger fish to escape capture. However, estimating the degree of reduced (dome-shaped) selectivity is also difficult due to correlation of the rate of decline in selectivity with age with *M* and other parameters (including steepness (*h*), catchability (*q*) and *F*), and the fact that selectivity itself is often time-varying. Finally, it can be difficult to decompose the total mortality rate into its natural and fishing-related components (Aenes et al., 2007).

Estimating *M* within stock assessment models is difficult and often ill-advised due to the issues raised above. Simulation analyses using a statistical catch-at-age model found that estimation of *M* was relatively accurate when age data and index data were available

from the beginning of significant fishing, *h* and selectivity parameters were known, and the stock was fished down to a relatively low level during the period of the data (Magnusson and Hilborn 2007). However, these are considerable and generally unachievable caveats. Similarly, Thompson (1994) found that right-hand selectivity is more accurately estimated when *M* is known. Simulation analyses for MSEs, in contrast, often assume that *M* is known exactly (e.g. Magnusson and Hilborn, 2007; Punt et al., 2008). However, getting *M* wrong in a full age-structured forward projection model can result in quite incorrect impressions of stock status (Clark, 1999). Misspecification of *M* can also lead to large biases and spurious time trends when using cohort analysis or virtual population analysis (VPA) (Mertz and Myers, 1997).

To avoid the pitfalls of trying to estimate *M* either directly from data or within a model, a number of meta-analytical approaches have been developed over the years. These methods use relationships between *M* and other life-history parameters which are ostensibly easier to estimate. While the methods are generally empirical, they are rooted in life history and evolutionary theory (e.g. Roff, 1984; Charnov, 1991; Charnov and Gillooly, 2004; Charnov et al., 2013). Often these approaches use a single independent parameter in the meta-analysis, although multiple regression analysis has been applied as well (e.g. Pauly, 1980). Meta-analyses have found relationships between *M* and maximum age (A_{max}; Hoenig, 1983; Beverton, 1992), age at maturity (A_m; Jensen, 1997), von Bertalanffy growth parameter *k* (Beverton and Holt, 1959; Jensen, 1996), and Gonadosomatic index (GSI), a measure of reproductive effort (Gunderson, 1997; Gunderson and Dygert, 1988), among others. McCoy and Gillooly (2008) developed a

theoretical model across species and taxa based upon the relationship of body size and temperature to the metabolic rate.

Often, single point estimates from these meta-analyses have been used in assessments despite the generally fairly wide scatter of points around the regressions. While this wide scatter is due in part to error in both the particular covariate and in *M*, it is undoubtedly also true that a good deal is due to an imperfect relationship between the parameters in question. Alternative values of *M* are often considered in sensitivity analyses, but it is unlikely that these are capturing the full uncertainty associated with the meta-analysis. While Hewitt et al. (2007) provide ranges for *M* by looking a number of meta-analytical relationships and ranges of estimates of the associated meta-analytical covariates, no formal method of developing statistically based prediction intervals or prior distributions of *M* have been proposed. Here, the extent of uncertainty associated with the various meta-analyses is analyzed and methods of creating prediction intervals and priors on *M* are described.

Gunderson et al. (2003) calculated confidence intervals for meta-analytical estimates of *M* from estimates of von Bertalanffy growth coefficient *k* (Jensen, 1996) and gonadosomatic index (GSI; Gunderson, 1997). They also reported point estimates without confidence intervals for Hoenig's maximum age meta-analysis for predicting *M*, which is the most common method cited in US west coast stock assessments. However, confidence intervals give a range for the mean value of *M* across multiple hypothetical species or stocks with the same values for the covariate, rather than the potential range

for *M* in an individual species or stock. Confidence intervals are only appropriate for describing uncertainty in the dependent variable for a new observation of the independent variable(s) when all the variability about the regression line in the meta-analysis is due to error in the individual estimates of the dependent variable used in the regression – i.e. the relationship is exact. Prediction intervals are more commonly used for delineating the range of values that would be predicted to be observed for the dependent variable for a new observation of the independent variable, in this case for a new species or stock. Prediction intervals give an expected range for a new observation drawn from the same distribution as the original data.

One important caveat regarding prediction intervals is that the original distribution around the regression usually includes both actual variability in the dependent variable around the regression line and estimation error in the original data, and therefore the prediction interval is possibly wider than the actual variation in the dependent variable about the regression line. Neither confidence nor prediction intervals are prefect for describing the uncertainty in a new estimate but here represent the bounds for possible intervals to describe uncertainty in *M*, assuming no bias in the original analysis. If all the variation in points around the regression is due to unbiased error in estimation of *M* in the data used for the meta-analysis, then the confidence interval provides the best estimate of uncertainty in *M* for a new stock given the covariate. If all of the variation around the regression is due to actual variation around the relationship, then the prediction interval is the best representation of that uncertainty. The truth is undoubtedly in between these two extremes, although there is likely some bias in the original data as well, which argues for

the use of a prediction interval which is more likely to be wide enough to compensate for such bias.

This paper describes a method for developing priors from individual or combined meta-analyses, based upon prediction intervals, which implicitly implies the assumption that there is variation in the meta-analytical relationships themselves.. Examples of application to individual species are provided.

Methods

For each of the five meta-analyses considered, I re-analyzed the original data to calculate uncertainty estimates along with point estimates of *M*. In doing so, I reconsidered the form of the regression. In the original analyses, Hoenig (1983), Pauly (1980) and McCoy and Gillooly (2008) used log-log regression, while Gunderson (1997) did not transform the data before regression. Jensen (1996) performed linear regression in both real and log-transformed space and concluded that the higher R^2 for the regression in untransformed space (0.77 vs. 0.65) indicated that the regression in untransformed space was superior. In reality, of course, one cannot make that comparison across transformations as log-log regression has an underlying assumption of the presence of heteroscedasticity in the original data.

For the three meta-analyses based on a single covariate, I performed four regressions for comparison, and to provide analyses similar to the original articles. These include: simple linear regression, simple linear regression forced through the origin, log-log regression,

and log-log regression with slope forced to be 1 (or -1 for Hoenig's method). Given the form of the heteroscedasticity in *M*, log-log regression is clearly more appropriate than regression in untransformed space. For the three univariate meta-analyses, the prior distributions are based upon the log-log regressions with slope forced to be unitary. This makes the relationship linear in real space, which is in line with the theoretical relationships. None of the slopes in the log-log regressions is significantly different from 1 (in absolute value).

For Hoenig's maximum age method, the maximum age and the natural mortality rate data for 82 stocks from Hoenig (1982) were used. I assumed a simple linear relationship in log space (log-log relationship), with a slope (exponent in real space) of -1, since *M* and maximum age should be inversely proportional and in the original analysis (Hoenig, 1983) the values of this exponent were not significantly different from -1 for either fish or all species combined.

For Jensen (1996) and Gunderson (1997), I assumed a log-log relationship as well. Since *M* is positively correlated with both *k* and GSI, this forces the relationship through the origin (in real space), which is desirable. The regressions were forced to have a slope of 1 in log space (making them linear in real space).

For Pauly (1980), the data on growth rate (*k*), temperature and either asymptotic mass or asymptotic length were used, a log-log(-log-log) relationship was assumed, and the full

variance-covariance structure was considered in determining the uncertainty for each predicted point.

For McCoy and Gillooly's (2008) data, the theoretical relationship relates dry mass *m* and temperature *T* (°K) to biological rate process: *M* should be dependent on *m* (dry wt in grams) and *T* (Kelvin). Rearranging and simplifying their resulting equation for fish:

$$M = Cm^{a} e^{\left(\frac{b}{T_{Kelvin}}\right)} \quad (1)$$

, or equivalently, ln*M* = c + a ln*m* + b/T. Thus a log-log(-log) relationship is assumed, and the full variance-covariance structure was considered in determining the uncertainty for each predicted point as with Pauly's method. The parameter a is theoretically near -0.25, and b is near -7,000 (the activation energy of heterotrophic respiration (~0.6 eV) divided by Boltzmann's constant (0.0000862 eV T^{-1}, where, again, T is in degrees Kelvin)). Weight data is converted to dry mass by dividing by 4, as was done in McCoy and Gillooly (2008).

Uncertainty intervals are calculated using the residual mean squared error (MSE) about the regression and the equations for the standard error s_c around the regression line (for confidence interval calculation; Zar, 1996), where:

$$MSE == \frac{\sum (Y_h - \hat{Y})^2}{df} \quad (2)$$

For regular linear regression (in real or transformed space), for any given X_h:

$$s_c^2(\hat{y}_h) = MSE\left[\frac{1}{n} + \frac{(X_h - \bar{X})^2}{\sum (X_i - \bar{X})^2}\right] \quad (3)$$

For linear regression forced through the origin (in real or transformed space);

$$s_c^2(\hat{y}_h) = MSE\left[\frac{(X_h)^2}{\sum(X_i)^2}\right] \quad (4)$$

And for linear regression with fixed slope (in real or transformed space);

$$s_c^2(\hat{y}_h) = MSE\left[\frac{1}{n}\right] \quad (5)$$

For all of the above cases, the standard deviation s_p around regression line (to be used for prediction interval calculation) is:

$$s_p^2(\hat{y}_h) = MSE + s^2(\hat{y}_h) \quad (6)$$

The interval itself is calculated as:

$$\text{interval} = \hat{y} \pm t_{\alpha,df}\, s\,, \quad (7)$$

where α is the confidence level, df = degrees of freedom, and s can be s_c or s_p as appropriate. Here, I calculate confidence and prediction intervals for the five meta-analytical methods described above. Three involve direct use of the above equations, whereas the two multivariate meta-analyses involve variance-covariance matrices. All calculations were conducted using the R programming language (R Development Core Team, 2010).

Priors

Along with prediction intervals, the above analysis provides log-normal distributions which can be taken as priors on *M* for the new species or stock of interest. Strictly speaking, as described above for prediction intervals, the prior is on a new observation of *M*, given all the error and bias in the original sample for the meta-analysis. However, we

will take it to be a prior on *M*, noting that the meta-analyses should be redone with currently available estimates of *M* and the related life-history correlates.

Given multiple such priors, the question is how to combine them. Under the assumption that each prior gives unique and orthogonal information from the others, the normal priors (in log space) could all be multiplied together and standardized to give a new log-normal prior. Combining normal priors results in a prior with the inverse-variance weighted mean of the individual prior means and with variance equal to the inverse of the sum of the inverse variances (which equals the harmonic mean of the variances divided by n). If, on the other hand, the individual meta-analyses are actually providing the same information (for example, due to complete overlap of data sources, and correlation among the different covariates) , they should all be averaged (via multiplying n normal priors together, all to the power n^{-1}) , as one would for multiple observations of a single quantity of interest. This is equivalent to giving a weight of 1/n to each of the priors. The resulting combined mean μ and variance σ^2 can be calculated as follows:

$$\mu_{combined} = \frac{\sum_i \frac{w_i \mu_i}{\sigma_i^2}}{\sum_i \frac{w_i}{\sigma_i^2}} \tag{8}$$

$$\sigma^2_{combined} = \frac{1}{\sum_i \frac{w_i}{\sigma_i^2}}, \tag{9}$$

where the w_is are the assigned weights for each normal prior, as described above (or all 1s when assuming independence).

In any particular case weighting should be done based upon overlap in data and covariates, knowledge about correlation of parameters, and confidence in the application of the prior to the species in question (i.e. does the relationship between the covariate(s) and *M* vary by taxonomic group, and is the meta-analysis representative of the taxon in question).

Here, I make the assumption that the meta-analyses based upon Maximum Age and GSI are independent of each other and the other meta-analyses, as I found no evidence of overlapping data sources. Pauly's meta-analysis (based on *k*, W and T) and Jensen's (based on *k*), however, use the same data set. McCoy and Gillooly (using W and T) use Pauly's 175 data points along with an additional 59 data points. Thus, these cannot be said to be independent – even Jensen and McCoy and Gillooly which use different covariates are not independent given the use of the overlapping data on *M* itself. Additionally, the relationship between *k* and *M* varies by taxon, and is quite different for Pacific *Sebastes* species than for most fish species (Beverton, 1992). Therefore, at least for Pacific *Sebastes*, the meta-analyses using *k* should be downweighted further, or simply not used.

Given that the analysis performed by Pauly (1980) included additional informative covariates, I simply do not use the relationship based upon *k* alone when data on temperature and maximum size are available. Thus Jensen's method is not used if Pauly's method is used. Jensen's method is also not used for Pacific *Sebastes* species. When Jensen's method is used (when data on *k* are available but size and/or temperature data

are not), it is given a weight of 1. Given the different functional forms in the meta-analyses of Pauly (1980) and McCoy and Gillooly (2008) and their incomplete overlap of data, they are each assigned weights of 0.75 if both are used, reflecting an intermediate state between being completely independent (weights of 1 each) and providing identical information (weights of 0.5 each). If data on weight and temperature but not *k* is available, then McCoy and Gillooly's method is given a weight of 1, since Pauly's (and Jensen's) method then lacks the necessary covariate information. The other two methods (Hoenig's and Gunderson's) are always given weights of 1 when used. When both the weight- and length-based Pauly multiple regressions are used, they each get half the weight that just one would be given (i.e. the same total weight as just using one, as really the same information is being produced). Other weighting schemes could be considered.

Examples

In practice, we often do not have all of the information necessary to calculate all of the meta-analytical estimates of *M* described above, along with their related intervals and priors. Three flatfish species from the northeast Pacific Ocean, English sole (*Parophrys vetulus*), rex sole (*Glyptocephalus zachirus*) and Petrale sole (*Eospetta jordani*), are used as examples for developing priors on *M*.

Results

While the results of the alternative regression assumptions for Hoenig's, Jensen's and Gunderson's methods are shown in Table 1, it is only the log-log regressions that are considered appropriate given the form of the heteroscedasticity in the data. The equations

describing the median point estimates for these three methods using the preferred log-log regression with the slope forced to be 1 (or -1, for Hoenig's method) are as follows:

Hoenig's method: $$M = \frac{4.374}{A_{Max}} \quad (10)$$

Jensen's method: $$M = 1.753k \quad (11)$$

Gunderson's method: $$M = 1.817GSI \quad (12)$$

These are similar to the published values in all three cases. For Hoenig's method, the exponent on A_{Max}, estimated in Hoenig (1983) to be -1.01, has here been forced to be -1, but the numerator is similar (4.33 vs. 4.37 here); Gunderson (1997) used linear regression in real space forced through the origin, and found a coefficient of 1.79 vs. 1.82 here; Jensen (1996), also conducting the regression in real space and forced through the origin, reported a coefficient of 1.6 instead of the 1.75 estimated here (though the regression in real space forced through the origin in Table 1 gives the identical value of 1.6).

While the log-log regressions with slope estimated could be used as well, their similarity to those with slope forced to 1 (or -1), the simplicity in interpretation and in calculation of point estimates given the resultant linearity in real space, and the correspondence with the life-history theory makes the use of the log-log regressions with slopes forced to be 1 (or -1) more appealing.

The data used, regression fits (transformed back into real space) and resultant confidence and prediction intervals for the three univariate meta-analyses are show in figures 1, 2 and 3. In Table 1, note that for all three methods, the simple linear regressions provide positive intercepts, so that if these were used, all point estimates from these methods would be larger than those values. This is particularly unrealistic for Hoenig's and Jensen's methods for which the intercepts are above M = 0.2. This is another reason for rejecting the regressions in real space.

For the two meta-analyses relying upon multivariate relationships (Pauly 1990, McCoy and Gillooly 2008), the resultant relationships are as follows (and in Table 2):

Pauly with W_{∞}:
$$M = 0.6117 W_{\infty}^{-0.08202} k^{0.6764} T^{0.4641} \tag{13}$$

Pauly with L_{∞}:
$$M = 0.9766 L_{\infty}^{-0.2775} k^{0.6551} T^{0.4645} \tag{14}$$

In both cases the exponents are nearly identical to those reported in Pauly (1980).

For the meta-analysis based upon the work of McCoy and Gillooly, the estimated relationship is:

$$M = 4.1x10^{9} m^{-0.276} e^{\left(\frac{6,173}{TKelvin}\right)} \tag{15}$$

Or, in their formulation:

$$M = 2.94 m^{-0.276} e^{\left(\frac{-0.532}{K}\left[\frac{1}{T_{Kelvin}} - \frac{1}{293.15}\right]\right)} \tag{16}$$

Where K is Boltzmann's constant and $m = \left(\frac{W_{\infty}}{4}\right)$. This compares to the value from their paper, with E fixed at 0.65:

$$M = 3.2 m^{-0.27} e^{\left(\frac{-0.65}{K}\left[\frac{1}{T_{Kelvin}} - \frac{1}{293.15}\right]\right)} \tag{17}$$

In Equation14, the estimated exponent on dry mass (-0.276) is slightly larger in magnitude from McCoy and Gillooly's (2008) theoretical -0.25 or estimated -0.27, while

E (the average activation energy of heterotrophic respiration) is estimated to be 0.532 eV, slightly below the value of 0.6-0.7 eV suggested by Gillooly et al. (2001, 2005).

The life-history covariates and resultant priors for *M* for the three flatfish species are given in Table 3. Figure 4 shows the individual and combined priors in transformed and real space for petrale sole, for illustration. For both rex and petrale soles, the combined prior is based upon the reanalyzed methods of Hoenig, Pauly and McCoy and Gillooly. For English sole, the combined prior includes the prior based upon Gunderson's method as well.

Discussion

The natural mortality rate *M* is a very important parameter in fisheries stock assessment and management. The subject is expounded upon in Beverton and Holt (1957), and has remained an important issue over the intervening half-century. However, *M* remains a very difficult parameter to estimate. Given the move to account for stock assessment uncertainty in setting harvest limits in the United States (Ralston et al., 2011), it is especially important to incorporate the uncertainty in life-history and harvest parameters in stock assessments through the use of priors or by developing ranges such as prediction intervals to guide sensitivity analysis.

Meta-analytical approaches are simple methods allowing the use of large amounts of related data to predict *M*. While there are many different approaches relate *M* to other parameters in addition to the ones reanalyzed above (Vetter, 1988), none of them are

fundamentally better than the ones explored here. While meta-analytical approaches often provide the only or best estimates of *M* and are based upon life-history theory, these estimates remain highly uncertain. The log-log regressions used here provide linear relationships between *M* and the covariates, while acknowledging the multiplicative nature of *M*, and the reality that the absolute uncertainty in *M* increases with *M*.

While the method for producing priors focuses on a single *M* across ages, space and time, it could be used to calculate priors for multiple *M* values for a single species taking into account some of the factors which induce variability. However, even the reduced complication of a single *M* value does not eliminate the uncertainty in its value. Ideally one could estimate *M* by following year classes moving through the population within a stock assessment. However, the confounding of *M* with *F*, catchability (*q*) selectivity, spawner-recruit steepness (*h*) and ageing error usually makes this extremely difficult. Time varying *q* and selectivity can make this value even more intractable. Unfished areas, such as MPAs, could eventually provide improved data for calculating *M* and other life-history parameters (Garrison et al., 2011).

The prediction intervals and priors developed here are based upon regression analyses which have the underlying assumption that the independent variables are known without error. Uncertainty and variation in the covariates violate this assumption. Since, for example, growth rate varies with environmental conditions (temperature, food availability) and competition, even a perfectly measured value at one time may not reflect the average growth rate nor, therefore, the average *M*. Ageing and age validation methods

have improved greatly over recent years (e.g. Campana, 2001, Hamel et al. 2008), and for some species the estimate of maximum age has changed greatly due to changes in ageing method (e.g. for Pacific ocean perch (*Sebastes alutus*); Chilton and Beamish, 1982). While the large biases in estimates of maximum age have been addressed, the smaller issue of uncertainty in both the "independent" and "dependent" variables could be addressed through an "errors-in-variables" or "functional regression" approach. However, this requires knowing or assuming the level of error (or relative error) in the independent variables, and becomes especially intractable for multiple regression approaches. Here taking that approach for the univariate regressions might provide a slightly better estimate of the slope of the regression, if it were not fixed at 1 or -1, and might provide a better estimate of the prediction interval given perfect knowledge of the covariate value for the stock for which *M* is being estimated. However, since uncertainty in that covariate would have to be accounted for in the final calculation of the prediction interval and prior, this approach would simply add multiple new layers of calculation and uncertainty, without any obvious benefit.

Gunderson et al. (2003) did calculate confidence intervals taking into account the uncertainty in the values of the covariates that they were using to predict *M*, but not for the data in the original regression analysis. These confidence intervals are indeed slightly wider than those that do not consider the error. However, since the regressions they used were not functional regressions, all variability in the covariate would have been accounted for in the standard error about the regression line, and in a sense adding in the

uncertainty in the covariate again is double counting this uncertainty. A larger issue is their use of confidence intervals rather than prediction intervals.

There are many approaches to modeling the process of natural mortality. Simple models have been developed to relate the process of survivorship and mortality to a few parameters that can be related to environmental factors, pressures, etc. (e.g. Anderson, 2000; Salinger et al., 2003). More complex models may address how natural mortality in a species or stock changes adaptively over time given fishing pressure (Mangel et al., 2007). One could question how "natural" *M* is for certain species given adaptive pressure on that and other parameters due to fishing pressure. The main purpose of this paper, however, is to provide prior information *M* for use in stock assessment. This should include current or recent *M*, but could include analyses of data from earlier periods for comparison or even use.

Ageing bias and other factors resulted in some of the data on *M* in the cited meta-analyses being relative far off from what we would now believe, and new methods mean that improvements could be made to the underlying data for the meta-analyses (e.g. Then and Hoenig, *this volume*). The methods developed here can be used with any appropriate data set, and the data used here could certainly be improved. Another issue that should be further addressed is which of these meta-analyses apply to which taxa, and how to limit the data to make it applicable to various groups of taxa (as in Beverton, 1992).

The ability to create priors on *M* and use them to conduct full Bayesian assessments allows one to more fully quantify the uncertainty in stock assessments associated with *M* (and other parameters). Even using prediction intervals to define the range of *M* for sensitivity analyses is an improvement over using ad-hoc values for that range. A combined prediction interval can be calculated from the combined prior for that purpose. In producing these priors and prediction intervals, one can use as many meta-analyses as for which you have good estimates of the covariates and for which the meta-analyses are deemed appropriate for the species in question.

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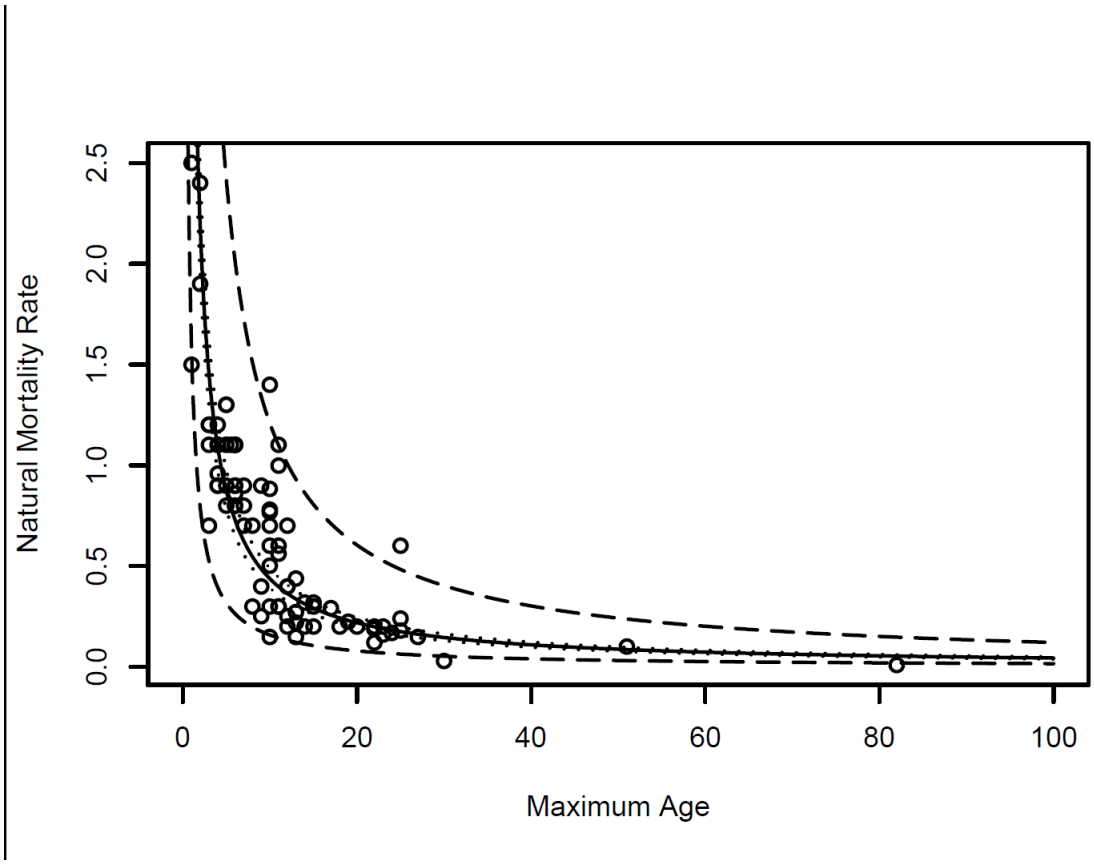

Figure 1. Hoenig's maximum age and *M* data with 95% confidence and prediction envelopes.

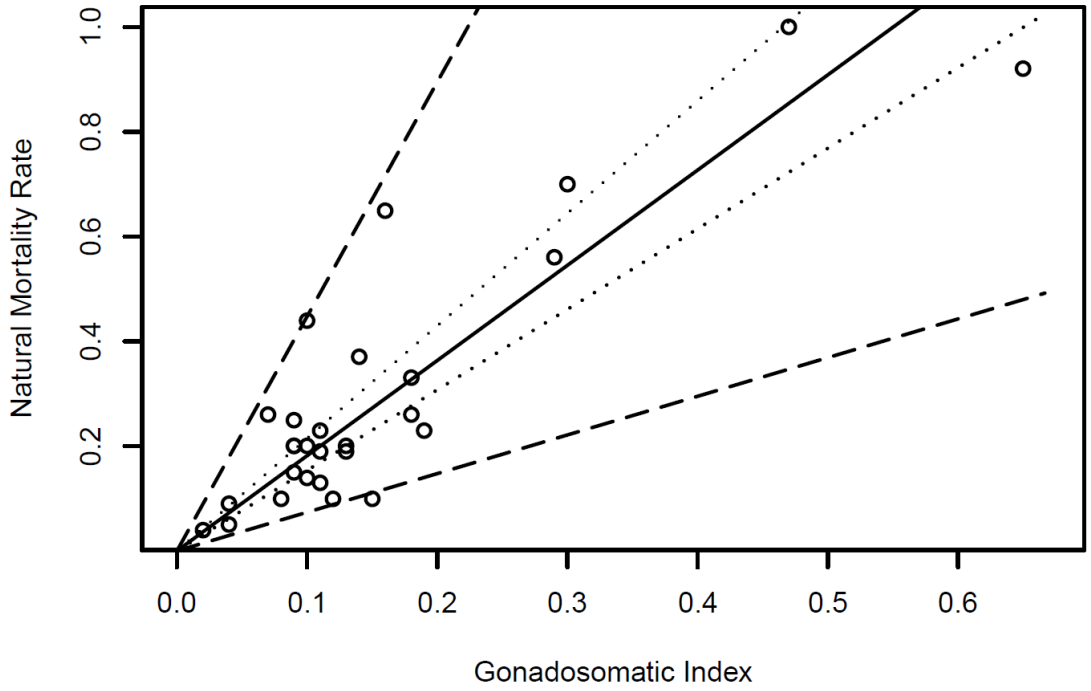

Figure 2. Gunderson's GSI and *M* data with 95% confidence and prediction envelopes.

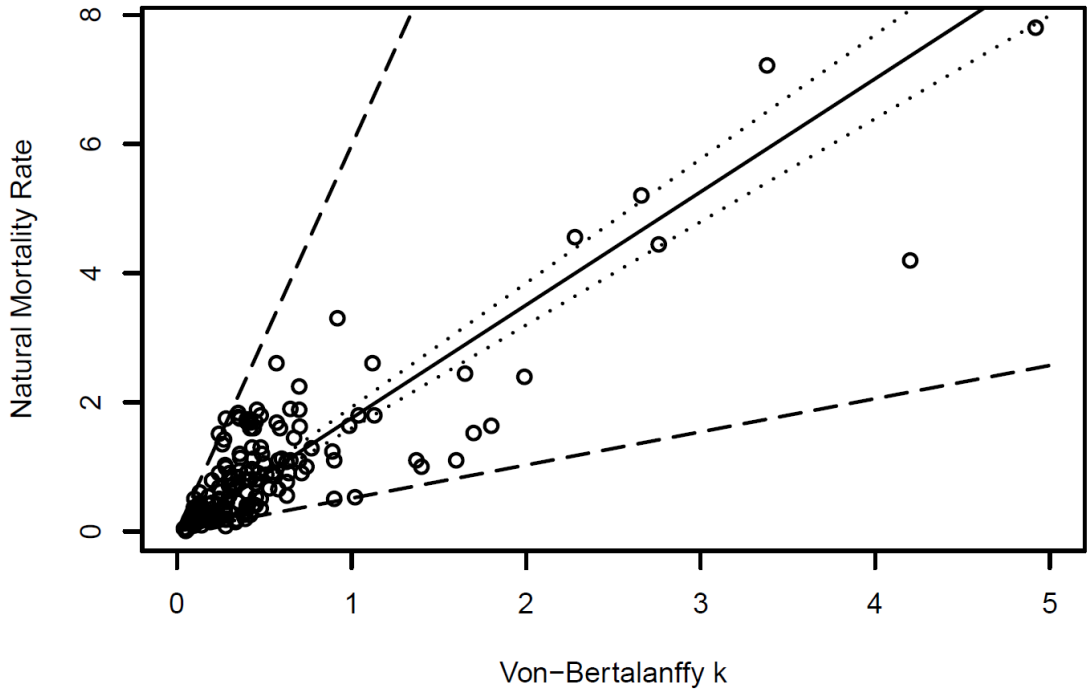

Figure 3. Jensen's *k* and *M* data with 95% confidence and prediction envelopes.

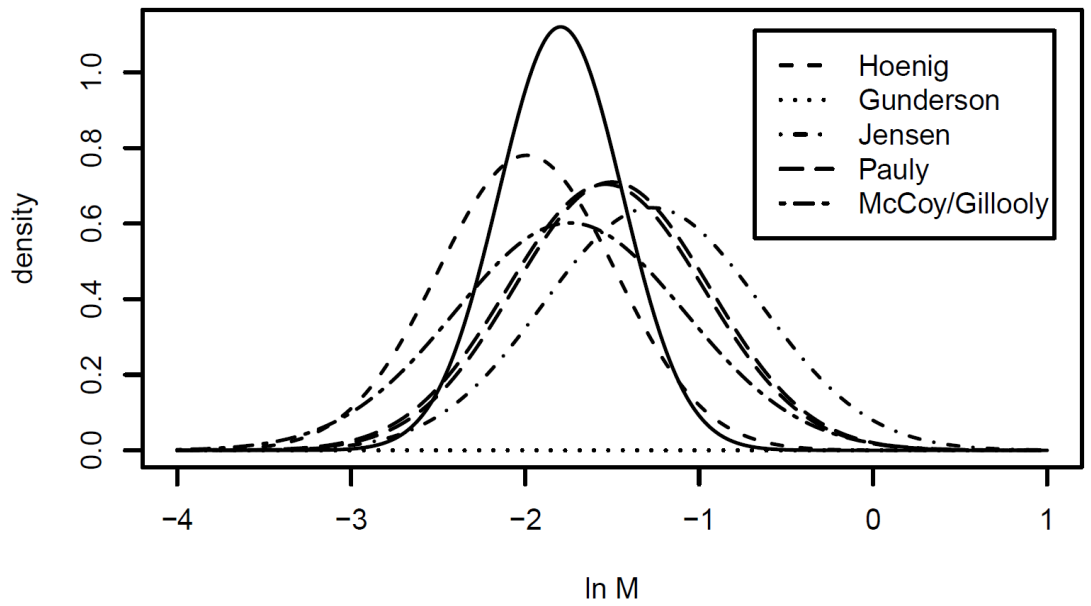

Figure 4. Priors and combined prior in log space and their equivalents in real space for petrale sole (*Eopsetta jordani*), using the inputs in Table 3. The dotted and dashed lines are the priors for each individual meta-analysis (including the two versions for Pauly's method), while the solid line is the combined prior, based upon weighting the individual priors as described in the text. There is no GSI data for petrale sole, so there is no prior for Gunderson's method. Jensen's prior is shown although it is given no weight in the combined prior.

Table 1. Coefficients (and standard errors) from linear, linear forced through the origin, log-log (LL), and log-log with slopes forced to be 1 (or -1) regressions for the three meta-analyses based upon a single life-history covariate. “Log inter” and “Log slope” refer to the intercept and slope for the log-transformed variables.

Method	Regression	Log inter	Log slope	Intercept	slope
Hoenig *M* vs. Max Age*; n = 82	Linear	-	-	0.31 (0.05)	2.35 (0.21)
	Linear origin	-	-	0	3.30 (0.19)
	LL	1.52 (0.17)	-1.02 (0.07)	-	-
	LL slope=-1	1.48 (0.06)	-1	0	4.37 (*0.25*)
Jensen *M* vs. von Bertalanffy *k*; n = 175	Linear	-	-	0.21 (0.05)	1.45 (0.06)
	Linear origin	-	-	0	1.60 (0.05)
	LL	0.50 (0.08)	0.95 (0.05)	-	-
	LLslope=1	0.56 (0.05)	1	0	1.75 (*0.08*)
Gunderson *M* vs. GSI; n = 28	Linear	-	-	0.041 (0.036)	1.64 (0.18)
	Linear origin	-	-	0	1.80 (0.12)
	LL	0.49 (0.27)	0.95 (0.12)	-	-
	LLslope=1	0.60 (0.08)	1	0	1.82 (*0.15*)

* The linear regressions for Hoenig’s method are M vs. 1/MaxAge, as is the reported transformation for the log-log regression with slope -1.

Table 2. Results of multiple log-log regression for meta-analyses based upon 2 or 3 covariates. Coefficients (and standard errors) are all in natural log space except for McCoy and Gilloly Temperature, parameterized as 1/°K rather than as °C as in Pauly.

Method	Intercept	Weight, Length or Mass	von Bertalanffy *k*	Temperature
Pauly (weight)	-0.49 (0.24)	-0.082 (0.022)	0.676 (0.072)	0.464 (0.083)
Pauly (length)	-0.02 (0.26)	-0.277 (0.066)	0.655 (0.072)	0.465 (0.081)
McCoy and Gillooly (mass)	22.1 (1.5)	-0.276 (0.015)		-6,173* (427)

*Linear in real space, and parameterized as 1/°K rather than °C

Table 3. Results of analyses for English sole (*Parophrys vetulus*), rex sole (*Glyptocephalus zachirus*) and petrale sole (*Eopsetta jordani*). Log mean M and Log sd refer to the average and standard deviation of ln M.

Species	Amax	GSI	*k*	L_∞	W_∞	T	Log mean *M*	Log sd	Median *M*	Mean *M*
English	23	0.18	0.36	40.56	596	8	-1.22	0.28	0.295	0.307
Rex	29		0.39	41.82	489	7	-1.41	0.36	0.245	0.261
Petrale	32		0.16	54.31	2400	6	-1.80	0.36	0.166	0.177