1 Upgrading from *M* version 0.2: An application-based method for practical
2 estimation, evaluation and uncertainty characterization of natural mortality
3
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11 ABSTRACT

12 Natural morality (*M*) is a notoriously difficult population parameter to estimate, yet it is also one

13 of the most important measures of life history that sets, as Beverton and Holt called it, "the

14 course of events". Stock assessments that include this parameter often show great sensitivity to

15 its value, reflecting the need to not only define its value, but also the uncertainty inherent in its

16 estimation. Direct measurement of natural mortality is often limited to resource intensive tag-

17 recapture studies. Indirect measures are more often used, and are built on life history theory,

18 relating natural mortality to traits such as age, size, maturity and reproductive condition (or just

19 assuming 0.2). The Natural Mortality Tool attempts to accumulate several empirical estimators

20 of *M* into one application. Users simply input life history values to obtain estimates of natural

21 mortality. These estimates can be taken individually or can be combined into a weighted density

22 function that can be used to develop an *M* prior that integrates uncertainty across several

23 estimates. Comparing estimators can also reveal inconsistencies in life history values that may

24 lead to further refining of basic biological understanding. Two examples are used to demonstrate

25 tool functionality and highlight general recommendations on implementation. Making these

26 estimators and the development of uncertainty in estimating natural mortality more widely

27 available hopefully supports transparent and defensible decision-making on the treatment of this

28 important population parameter.

30

1. Introduction

Life and death are binary moments for organisms. While the individual is considered either dead or alive (if questionably useful; Du et al. 2018), mortality is a population process over a given time period (e.g., 10% of the population has died over a year). The causes of mortality are numerous and intertwined, and include starvation/malnutrition (Fey et al. 2015; Hill et al. 2020), disease (Cigler et al. 2020; Stenkat et al. 2013), predation (Hill et al. 2020), competition or defense (Lenting et al. 2019; Stenkat et al. 2013), environmental conditions (Fey et al. 2015), senescence (Reznick et al. 2002), poor decision-making (Lendrem et al. 2014) and/or bad luck (e.g., black swan events; Hoag 2003; Anderson et al. 2017).

Mortality is a key component of basic population modelling, as births minus deaths defines population growth (in a closed population) for a given time period (Ebert 1999). While mortality can be expressed as a finite or discrete rate (i.e., a percentage), it is often expressed as an exponential instantaneous (i.e., continuous) rate of change. Using instantaneous rates provides mathematical convenience and flexibility to express at what point mortality occurs (Ebert 1999).

When modelling marine fish populations, it is common to distinguish mortality due to human extraction (i.e. fishing) from other sources. This quantification is possible when fishing removals (landings plus dead discards) are monitored, and results in the following common treatment: total mortality (Z) = natural mortality (M) + fishing mortality (F), where natural mortality is the remaining predation combined with any other sources of mortality (Sparre and Venema 1989). This separation of mortality components is particularly useful for fisheries management, as the F contribution can be compared to a reference level of fishing (F_{ref}) that indicates whether overfishing is occurring (e.g., $F > F_{ref}$ indicates overfishing: Cordue 2012).

53 While there are advanced treatments to remove other predation sources from M (often called M2

54 (Pope et al. 2021)), M in this paper includes all sources of mortality excluding fishing mortality.

55   In many of the analytical approaches used to estimate stock status and other important

56 fisheries management metrics under conditions of varying data and resource availability (Cope et

57 al. in prep), M is an essential input parameter. In those models, M is widely recognized as both a

58 highly influential parameter in stock assessment modelling and in defining stock productivity

59 and subsequent fishery reference points, but is difficult to directly measure in marine organisms

60 (Maunder et al., this issue; Punt et al. 2021). This is particularly true for populations with

61 individuals that move around, do not stay in the sampling area and/or are in habitats that make

62 routine monitoring a challenge. Direct estimation in age-structured models is possible, but

63 requires adequate biological composition data and an understanding of the functional form of

64 fishery selectivity (Lee et al. 2011). Mark-recapture studies (Chapman 1961; Seber 1982) or age-

65 based sampling of cohorts through time (Chapman and Robson 1960; Schnute and Haigh 2007;

66 Thorson and Prager 2011) are other direct ways to measure mortality. In some instances, M can

67 be directly estimated separate from Z (Hoenig et al. 1998; Jiang 2005; Jiang et al. 2007), though

68 it is common that Z rather than M is estimated, thus F would be required to derive M from Z

69 (i.e., M= Z-F).

70   In one of the most famous and cheeky derivations of M, John Pope in 1975 showed the

71 evolution of a question mark into an often assumed value of $M = 0.2$ (Figure 1 of Anderson 2015

72 and Pope et al. 2021). Sadly, 0.2 was indeed a commonly used default value when no other M

73 value was available. Since then, a host of empirical approaches have been developed to allow the

74 indirect estimation of M. These approaches have been well described and evaluated elsewhere

75 (Kenchington 2014; Maunder et al. this issue; Then et al. 2015; Vetter 2008), and while there are

76 some approaches that are favored over others, having ready access to the many empirical

77 estimators of M allows for more examination and comparison of these estimators under a variety

78 of situations. This paper describes a free software application with a graphical user interface

79 (GUI), the Natural Mortality Tool, designed to be a practical, user-friendly way to explore a wide

80 variety of empirical M estimators. Available methods, tool features, and suggested rules for use

81 are provided herein to demonstrate the range of tool functionality and how it can support both

82 point estimation and uncertainty analysis in this critical model parameter.

83 **2. The Natural Mortality Tool (NMT)**

84 The NMT[1] is written in the Shiny (Chang et al. 2021) package for R (R Core Team 2021), which

85 allows for the creation of interactive graphical user interface (GUI) web-based applications. The

86 GUI is a key feature of this tool, as it allows for user interaction and real-time response based on

87 user input. It also allows for saving output objects and images. It does not require the user to

88 know how to formally use R. The code can also be downloaded from the GitHub repository[2] for

89 running the tool offline, where user installation instructions are found. The NMT currently has

90 23 different estimators of M based on 14 possible inputs (all of which can be expanded as new

91 methods develop), with an additional input available for unlimited user supplied M values (e.g.,

92 0.2). This provides a plaform to compare M values generated from each estimator and/or user

93 supplied value. Not all inputs need to be entered, only those that are available to the user, and

94 thus outputs will only be provided for those methods fully specified by those inputs. The NMT

95 has links that open windows to show associated references and a table (Table 1) of the inputs

96 needed for each method. Of the 23 estimators (22 provide a constant M across ages and 3

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[1] https://connect.fisheries.noaa.gov/natural-mortality-tool/
[2] https://github.com/shcaba/Natural-Mortality-Tool

97   (including two that also provide a constant *M* value) provide age-specific *M* estimates), one is

98   based on the R library FishLife (Thorson et al. 2017; Thorson 2019), six are based on the

99   fishmethods R library (using the function *M.empirical*(); Nelson 2021), and the remaining are

100   coded within the NMT. The latest version of each of these estimators are used, with updates and

101   additions to the *M* estimators an ongoing point of tool maintenance. The authors welcome further

102   recommendations of additional *M* estimators to include, as well as comments on the usefulness

103   of those estimators currently available, via issues reporting on the GitHub repository.

104   *2.2 Empirical Estimators in the NMT*

105   Empirical estimation of *M* is generally based on relationships between other, easier to measure

106   life history parameters. Beverton and Holt (1959) were early investigators on building

107   relationships between *M* and growth parameters, maximum age, and reproductive biology

108   (Beverton 1992; Prince et al. 2015). Subsequent work has built on those relationships and

109   developed multi-parameter relationships to estimate *M* (Charnov et al. 2013; Chen and Watanabe

110   1989). By entering just the scientific name of the species, one can access the estimate of *M* from

111   the FishLife library that applies a taxonomically-structured multivariate model to information

112   found in the FishBase database (Thorson et al. 2017; Froese and Pauly 2021).

113   Maximum age is one of the most commonly used values to build relationships to *M*, as it

114   makes intuitive sense that higher life expectancies must mean a lower population mortality rate

115   (Hamel and Cope, this issue; Maunder et al., this issue; Then et al. 2015). While using maximum

116   age tends to be preferred, establishing the maximum age (not necessarily the maximum age ever

117   recorded) of a population is not always straightforward or available (Hamel and Cope, this issue;

118   Maunder et al., this issue). Maximum age can be affected by ageing error and/or sampling age-

119   truncated populations (Hamel and Cope, this issue; Hoenig 2017). Thus, while possibly easier to

120   measure than *M*, maximum age-- and the meta-analytical estimators based on them-- still suffers

121   from uncertainty that needs careful consideration. There are currently six methods in the NMT

122   that can use longevity in the estimation of *M* (the Chen and Watanabe (1989) method can take

123   any age, as it provides age-specific *M* estimates, but longevity is recommended when using one

124   age value), with three combining maximum age with other parameters in the estimator (Table 1).

125   Parameters of the Beverton-Holt (1959) version of the von Bertalanffy growth function

126   ($L\infty$, *k* and t_0) are also commonly used in empirical *M* estimators. The process of accounting for

127   metabolism and its allocation to maintenance, growth, reproduction, and mortality links these

128   processes and are foundational to life history theory (Boukal et al. 2014; Enberg et al. 2012;

129   Essington 2001). The individual growth coefficient *k* is most directly related to *M* (even forming

130   what is considered a dimensionless ratio within or across taxa, *M/k*; Beverton and Holt 1959;

131   Charnov et al. 1993; Jenning and Dulvy 2008; Prince et al. 2015), though several methods (Table

132   1) also require either the theoretical age at size 0 (t_0) or the average maximum size ($L\infty$). While

133   less directly related to *M* than maximum age, the von Bertalanffy growth parameters tend to be

134   easier to estimate than maximum age (though issues of ageing error, fishery selectivity and

135   sampling, along with the correlation among the three parameters, can also make this difficult,

136   especially for *k* and t_0), thus providing, in some cases, a more accessible method when maximum

137   age is poorly understood. There are currently 11 methods in the NMT that use von Bertalanffy

138   growth parameters, three of which use only *k*, three of which use both *k* and $L\infty$ on their own or

139   with length information, and five that use other parameters, including three of which combine

140   with age (Table 1). One of the growth-based methods also includes water temperature as it may

141   affect metabolism and behavior thus indirectly influencing *M* (Pauly 1980).

142   The original von Bertalanffy growth function was derived using weight (W) (von

143 Bertalanffy 1938; Essington 2001), but is converted to length using the common power weight-

144 length relationship of $W=aL^b$. Thus, weight (either wet or dry) can also be related to M carrying

145 over the logic used in those relationships derived from length (Pauly 1980). The NMT contains

146 four weight-based M estimators, two of which use weight only, two of which include

147 temperature, and one that uses the weight-based von Bertalanffy equation (W_∞, k_w; Table 1).

148   Reproduction is also part of the energy allocation equation, and the onset of reproductive

149 years usually dictates when growth begins to slow (Enberg et al. 2012). This interplay between

150 growth and reproduction also makes the length or age at maturity another candidate as an

151 estimator of M (Jensen 1996). There are three estimators that use age at maturity as an input,

152 with only one of them adding an additional parameter (k) in the equation (Table 1).

153   The remaining method uses the allometric concept of growth and reproduction as related

154 to mortality and interprets the M relationship through the ratio of reproduction (measured by the

155 gonad weight) and fish weight to express reproductive effort (Gunderson 1997; Hamel 2015).

156 The gonadosomatic index (GSI) is a metric not often sampled, thus represents a unique, often

157 unavailable, but relatively easy to measure value as an option to estimate M.

158   The tool responds to user inputs as they are included, producing both a figure of outputs

159 across the different methods and a simple table to see the actual quantities illustrated in the plot.

160 Both the table (as a .csv file) and the figure are downloadable with a click of the button, as is an

161 R object that contains all user inputs and the resulting M values. This object is especially notable

162 as it reserves a record of the exact inputs used to produce the M values, in addition to an object

163 that can be imported into R.

164   *2.3. Accounting for uncertainty in the NMT*

165   Sources of uncertainty in M can be expressed in at least two main ways: among estimators and

166   within estimators. The default is to assume each estimator produces a point estimate, though

167   there is an option to include either lognormally or normally distributed error with a user-

168   specified amount of error. Lognormally distributed error is more appropriate for most estimators,

169   as M itself is a rate parameter that occurs in the exponent when relating to population size.

170   Estimated uncertainty is only empirically available for some methods and requires the initial

171   dataset for calculation (Hamel 2015). Instead, an option for user input uncertainty is included and

172   assumed the same for each estimate for tool simplicity. Future modifications to the tool could

173   consider method-specific uncertainty, but may also overly complicate the tool. One could also go

174   back and attempt to calculate uncertainty from the original data set used to create a given

175   empirical relationship and input that value into the NMT. Further uncertainty can also be

176   explored through changing input values (e.g., what if longevity is 60 instead of 50?).

177   Once the estimators are activated via parameter inputs and additional variance included,

178   the user can navigate to the second tab ("Composite M: User weighted") to create a custom

179   distribution of M that combines all M estimators and associated uncertainty into a composite

180   distribution (Figures 2 and 3). A user-specified method-weighted (i.e., percent contribution)

181   approach is used to construct the composite distribution of M. This composite can then be used

182   in a Monte Carlo approach for resampling or used to specify a prior on M. Allowing for user-

183   based weighting of each method addresses multiple issues:

184   1. Input influence: Multiple methods may use the same input (e.g., longevity), thus causing

185   unequal input influence when comparing M estimates across methods if all methods are

186   equally weighted. For instance, if there are three methods that use only longevity and one

187   that uses GSI, weighting each method equally upweights the influence of the longevity

188   input purely based on the number of estimators used. One solution is to downweight each

189   longevity-based estimator by two-thirds so the overall weighting of each adds up to one.

190   The user gets to determine the combination of weightings based on their preferences. The

191   default weightings in the NMT are a mix of applying the above rational to avoid outsized

192   input influence and starting some estimators at a weight of 0 as they often produce

193   outliers (see next issue).

194 2. Method removal: Included in the user decision of how to weight each method is whether

195   to include each method at all. There are many reasons why some methods may produce

196   highly questionable values (e.g., extreme outliers) when applied in certain situations. The

197   user may decide to ignore that method by setting the weighting to 0. Recommendations

198   of using some estimators over others (e.g., longevity-based estimators are preferred over

199   growth-based estimators; Then et al. 2015) may also be a reason to omit certain

200   estimators.

201 3. Custom priors: The custom combination of weightings across all M estimators and any

202   additional uncertainty the user may have included creates the composite M distribution.

203   The construction of the composite is first done by setting X number of total composite

204   samples (user defined, but the default is one million). The individual method weightings

205   are then turned into standardized weights (individual method weight/sum of all method

206   weightings) to give the Y_i number of samples from the total number of X samples for each

207   estimator, where i is the estimator (e.g., 200000 out of 1000000 samples for estimator 1)

208   and $X = \Sigma Y_i$. If there is no additional uncertainty added to the methods, then the point

209   estimate is replicated Y_i times for each method i. If there is a specified error distribution

210   (either lognormal or normal), then a Y_i random sample is taken for each distribution. A

211   final option to tune the bandwidth, with values greater than 1 causing more diffuse

212   distributions, is offered for further M distribution customization.

213

214   Once the user specifies the composite weightings, number of samples, and choice of density

215   bandwidth (which smooths out the density distribution and allows the user to make more diffuse

216   priors if they so choose), a plot of both the component points (left column plots in Figure 2) or

217   distributions (left column plots in Figure 3) and the overall density distribution (right column

218   plots in Figures 2 and 3) are provided for download and examination. R objects that contain the

219   details of the sampling of each method and the final composite M values by methods are also

220   provided for download.

221   A second approach to characterizing uncertainty (third tab: "Composite M: Inverse

222   variance") that develops a lognormal Bayesian prior distribution from multiple methods is also

223   available (Hamel, 2015). This approach essentially multiplies the individual distributions

224   together, and thus weights the alternative methods based upon the inverse of the variance (or 1

225   divided by the square of the input standard deviation). Additional user-specified weights, as

226   presented previously, can also be included. Where individual distributions are bimodal, this

227   approach will provide a single central mode, in contrast to the treatment of biomodal results for

228   the first approach. Thus the two approaches to characterizing uncertainty represent distinct views

229   of the information each distribution provides relative to the other distributions included. The tool

230   offers users their choice of either or both.

231   Overall, the point estimates (from the first tab) and/or the composite distributions and

232   priors (from the second and third tabs) offer different ways of processing the estimates from each

233   method. Each can then be used to parameterize the variety of stock assessment methods that

234   require natural mortality as an input, specify operating models used in simulation testing, or any

235   other application that needs a value or distribution of M values.

236   **3. Benefits of and best practices when using the NMT**

237   The intent of the NMT goes beyond just easy access to the numerous M estimators. When

238   considering the vagaries of inputs available for any given method, and the life history theory that

239   underpins these methods, it is advantageous to be able to look across multiple M estimators and

240   consider how they can be applied collectively to reflect uncertainty in M for a given population.

241   To demonstrate and highlight some of the recommended uses of the tool, applications are

242   presented using two rockfish (genus *Sebastes*) species, yelloweye (*Sebastes ruberrimus*) and

243   gopher (*S. carnatus*) rockfishes (Table 2).

244   Comparing life history inputs across methods often results in a variety of possible M

245   values, including the potential for large discrepancies in estimates (Figure 1). But which should

246   be used? Considering the yelloweye rockfish example (Figure 1A), the method-specific estimates

247   group roughly by those using longevity and those using either growth or maturity, with the latter

248   group estimating higher M values. These groups result in a bimodal composite distribution of M

249   under default method weightings (Figure 3A).

250   Given the previously stated difficulties in defining a representative longevity estimate,

251   uncertainties in growth parameters, and potential variability in parameter relationships across

252   taxa, seeing such discrepancies offers an avenue to explore these differences. One could ask the

253   question "how much do I need to change the longevity input to achieve M values near the

254   estimators using growth and maturity?" In this example, longevity needs to be lowered to a value

255   of ~50 years to match the growth and maturity estimates of M. This is well outside the

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256 uncertainty envelope of longevity for yelloweye rockfish. One could do a similar exploration

257 with the von Bertalanffy values, which would take a 50% reduction in the k value to achieve M

258 values as low as the longevity estimators. The differences in the estimators may be due to

259 departures in the generalized life history relationships for a given taxa or species. For example,

260 some *Sebastes* species tend to grow to near maximum size (L_∞) quickly relative to their

261 lifespans, and therefore, as noted in Beverton (1992), the standard cross-taxa relationship

262 between k and M may be expected to be biased high for species, like some *Sebastes*, that grow

263 quickly to asymptotic size. In contrast to the yelloweye rockfish results, there is less difference

264 among the estimates of M for gopher rockfish among estimator groups, but still notable

265 variability among individual methods that results in a bimodal distribution (Figure 3B).

266   The treatment of the resultant bimodal distributions should depend on the source of the

267 bimodality. For the yelloweye example, there are two modes comprised of different estimators:

268 one from longevity estimators and the other from growth and maturity (left plot of Figure 3A).

269 Given neither could be resolved through initial confirmation of poor estimations of any of the

270 inputs, one perspective is the two modes represent distinct distributions of M that represent

271 alternative hypotheses. The expression of alternative hypotheses in life history parameters is a

272 standard approach to characterize uncertainty in population modelling and defining "states of

273 nature" for decision analysis (Punt and Hilborn 1997). In this approach, there is no requirement

274 to assume equal probability of these alternative hypotheses, and requires separating out methods

275 into each hypothesis to construct each distribution. For the case of yelloweye rockfish, the higher

276 M mode consists of growth and maturity-based estimators, but as previously stated, clearly

277 incompatible with realistic longevity expectations. Figure 3A (right plot) shows a treatment that

278 uses the methods weighting approach (second tab in the NMT) to downweight to zero all

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279 estimators except the longevity-based estimators, isolating the lower M mode. For the gopher

280 rockfish example, there is no grouping distinction or obvious reasoning to exclude certain

281 estimators, so one may choose to use the overall bimodal composite distribution (Figure 3B,

282 right plot), or either downweight the growth based estimators (as done with yelloweye rockfish)

283 or the longevity based estimators (if there is concern with the maximum age estimate) to use a

284 single mode.

285   Some general recommendations on estimating natural mortality emerge from using the

286 NMT:

287   1. Enter all available inputs (including other available estimates of M entered as user input)

288   into the NMT. Critical evaluation of inputs should occur both before inclusion in the tool

289   and once M values are generated (as it may become clearer some inputs are questionable

290   upon seeing the estimated M) to gain some sense of potential reliability in methods based

291   on that input.

292   2. Consider adding uncertainty to the M estimates rather than just using point estimates. A

293   lognormal distribution is typically assumed, and Hamel and Cope (*this issue*) recommend

294   a standard deviation of 0.31.

295   3. Initially consider the longevity (if available) estimators of M as most informative (Then

296   et al. 2015), but compare them to the other estimators. If there is low overlap between

297   longevity and other estimators (or between estimators in general), consider again the

298   quality of the life history inputs and observe deviations in well-known life history

299   correlations (e.g., fast growing and quick to mature, but long-lived) at the species or other

300   taxonomic level. If the major differences are by groups of estimators, investigate what it

301   takes to change input values to achieve the estimates of M from other estimators (e.g.,

302   changing longevity for yelloweye rockfish to match *M* estimates from the growth- and/or

303   maturity-based *M* estimators), and determine whether these input changes are realistic

304   (e.g., yelloweye rockfish longevity needed to change to unreasonably low values to

305   obtain *M* estimates similar to growth-based methods)

306 4. 'If multiple modes are present and there are no obvious errors in the life history inputs or

307   notable bias in estimators for the particular taxon, but uncertainty remains in the

308   reliability of the longevity estimate,

309   a. Consider the multiple modes as different hypotheses of *M* and create separate

310   distributions. Altering the weighting of methods (e.g., downweighting certain

311   estimators to isolate others) is one way to do this. These alternative hypotheses of

312   *M* do not need to be treated equally, and in some cases, some modes may be

313   deemed unrealistic (e.g., *M* values that seem much too high; see *M* values from

314   growth and maturity estimators in yelloweye rockfish) and can be ignored (Figure

315   3A, right panel). Prior distributions can be developed using the prior distribution

316   portion of the tool, with appropriate consideration of intra-input weighting (e.g. if

317   two estimators use longevity, weight each by 0.5 so they are not unintentionally

318   upweighted).

319   b. 'If there are no evident natural groupings of the M estimates based on methods,

320   but still multiple modes, one can either use a distribution inclusive of all methods

321   (e.g., Figure 3B, right panel) or choose to break them out into multiple

322   distributions as in (3a).

323   5. The resultant prior distributions can either be specified using summary statistics (e.g.,

324   median and variance) or as a vector with a user-specified number of random draws (with

325   the default being 1 million draws).

326   Additionally, it may also be appropriate to consider the age-specific estimates that also are

327   provided by the NMT, if the required inputs are available.

328   The ultimate formulation of a value or distribution of M is up to the user, but the *in situ*

329   ability to compare across methods offers the potential for building an ongoing understanding of

330   how these methods relate to one another under a variety of data conditions and life history

331   configurations. These types of comparisons may eventually reveal inherent patterns and

332   sensitivities in certain methods under different life history types. For instance, the revised

333   versions of the Alverson and Carney (1975) method (Zhang and Megrey 2006) often result in

334   extremely low estimates of natural mortality (Figure 1A, left panel, ZM_AC_dem and

335   ZM_AC_pel; see Zhang and Megrey 2006 results that also show this tendency), but in some

336   cases can show more reasonable values (Figure 1B, left value,, ZM_CA_dem and ZM_CA_pel).

337   Understanding such individual vagaries on top of the already complicated evaluation of input

338   value quality and life history types on M estimators benefits from extensive applications and

339   comparisons. The Natural Mortality Tool, while making these methods accessible, provides the

340   space to grow intuition on applying M estimators. The tool is also open to further estimator

341   inclusion and additional diagnostics and functionality improvements, offering an adaptable

342   interface and utility as options change and grow.

343   We are well beyond the default days of $M = 0.2$. May we now instead turn 0.2 back into a

344   question mark (Figure 4) and use the power of empirical analysis and accessible, transparent

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345 tools to promote investigation and construction of M values that embrace uncertainty and are

346 situation-specific.

347

348 ## Acknowledgements

357

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521

522 # Tables

523

524   Table 1. List of empirical *M* estimators and the inputs needed to apply the method. A link
525   to references for each method is found in the NMT app.

Method	Inputs
FishLife	Scientific name
Then_nls	longevity
Then_lm	longevity
Hamel_Amax	longevity
ZM_CA_pel	longevity, k, t_0
ZM_CA_dem	longevity, k, t_0
Chen-Wat	Age, k, t_0
Then_VBGF	$L\infty$, k
Hamel_k	k
Jensen_k 1	k
Jensen_k 2	k
Gislason	$L\infty$, k, length
Charnov	$L\infty$, k, length
Pauly_lt	$L\infty$, k, Temp
Roff	k, age at maturity

Jensen_Amat	age at maturity
Ri_Ef_Amat	age at maturity
Pauly_wt	$W\infty$, k_w, Temp
McC&Gil	dry weight, Temp
PnW	dry weight
Lorenzen	wet weight
GSI	GSI

Table 2. Life history inputs for the two rockfish species used as example applications of the NMT. Values are taken from the U.S. west coast stock assessment for each species (Gertseva and Cope 2017; Monk and He 2019).

	Yelloweye	Gopher
Longevity (years)	123	28
$L\infty$ (cm)	64.1	30.6
K	0.65	0.1
t_0 (years)	-1.22	-2.89
$A_{maturity}$ (years)	15.5	9
Temperature (C$^\circ$)	7	10
Wet wt. (g)	5000	500

Figures

534   A) Yelloweye rockfish
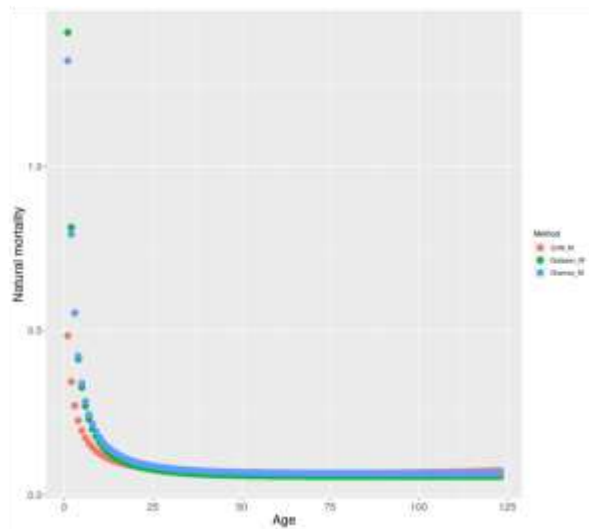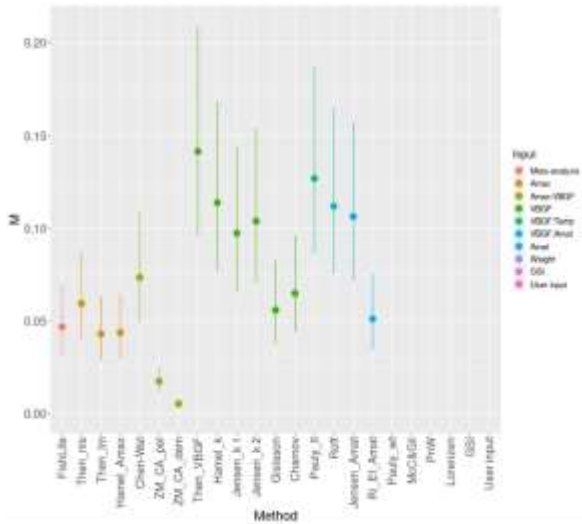
535
536   B) Gopher rockfish

537
538
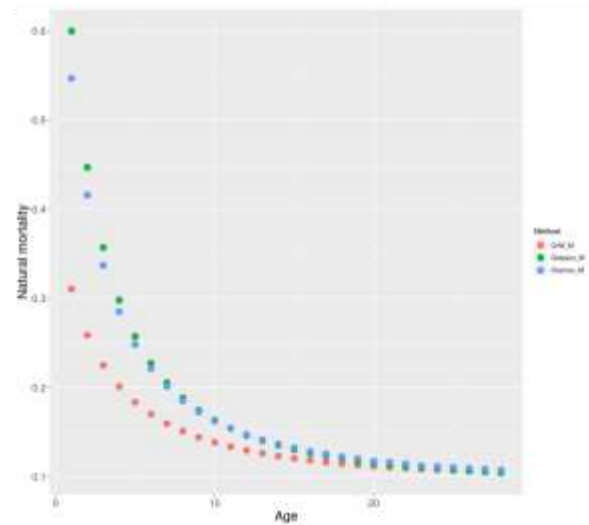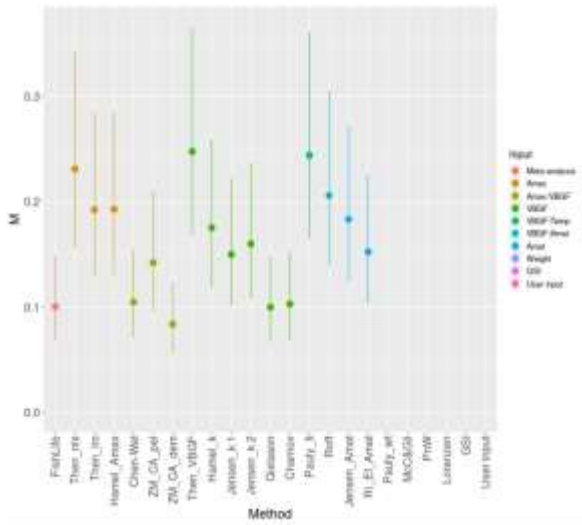
Figure 1. Point (with 95% lognormal error bars; left column panels) and age-specific (right top and right bottom panels) estimates of M by method for yelloweye (top row) and gopher (bottom row) rockfishes. Colors in the point estimate panels refer to the life history parameters used in each estimator.
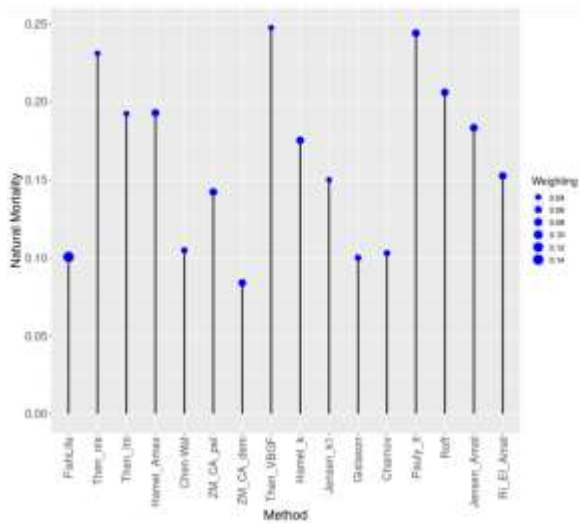
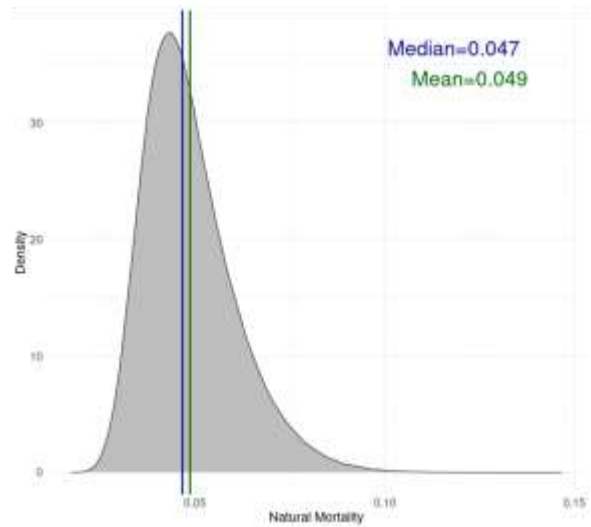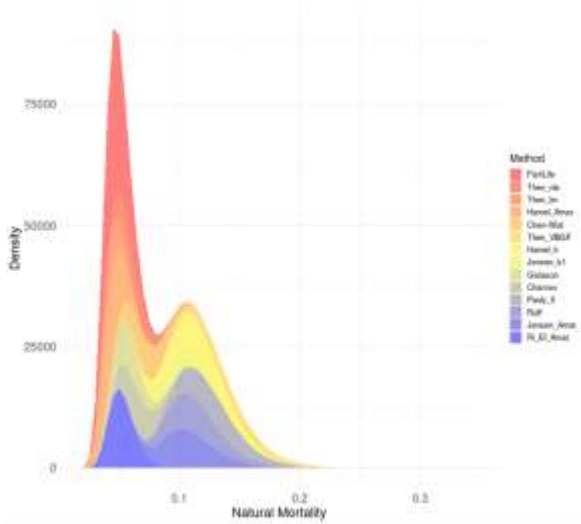544   A) Yelloweye rockfish
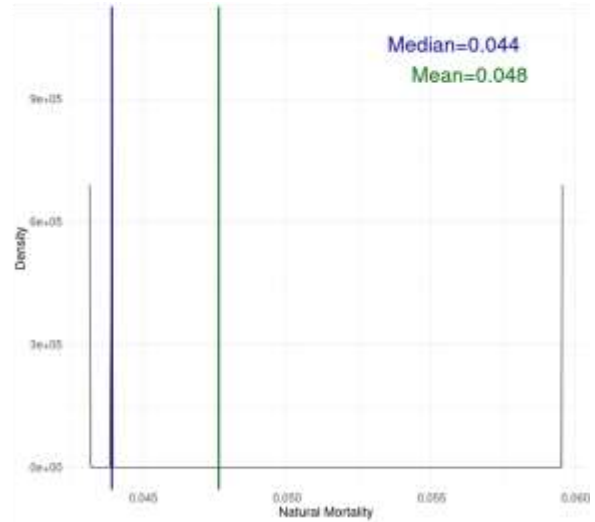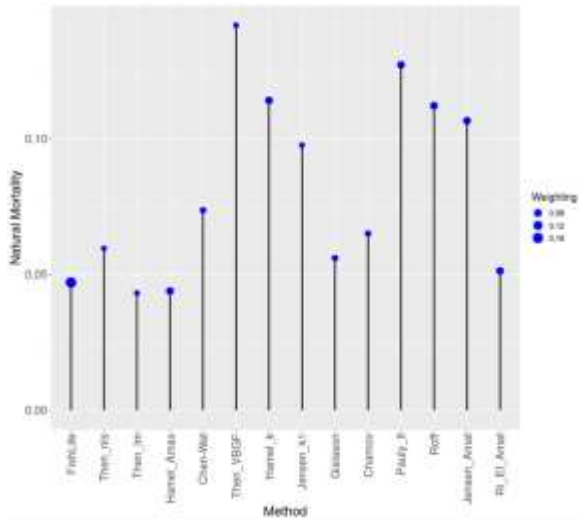
545
546   B) Gopher rockfish

547
548
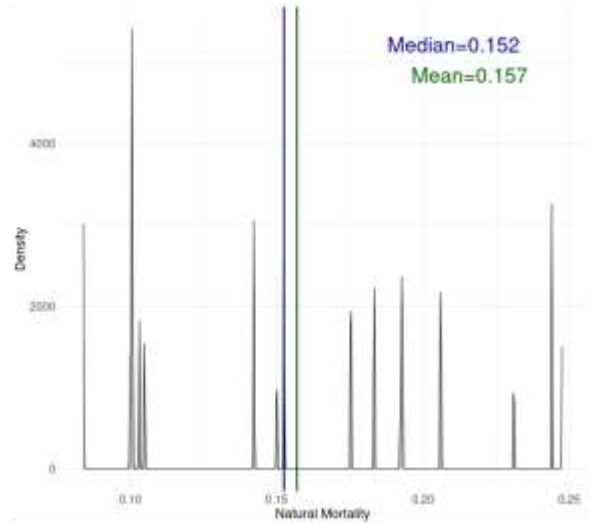
Figure 2. Weighted empirical *M* estimators with no additional variance using the default weightings (left column panels) and the final distribution with central tendency measures (right column panels) of *M* for yelloweye (top row) and gopher (bottom row) rockfishes. In the yelloweye rockfish example, the final distribution is composed of estimators applying longevity only; all other estimators are downweighted to 0.

554
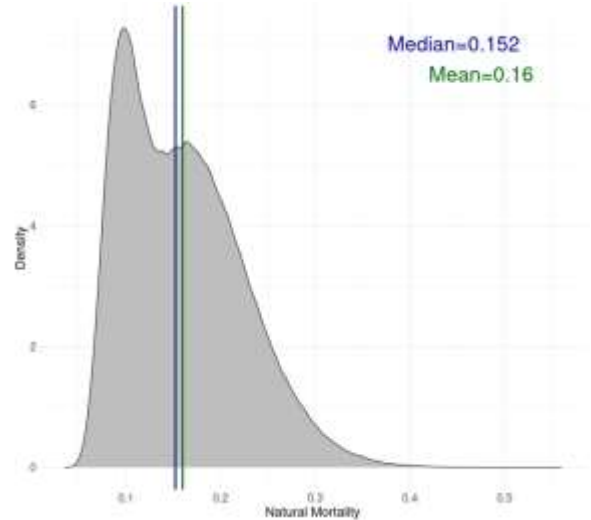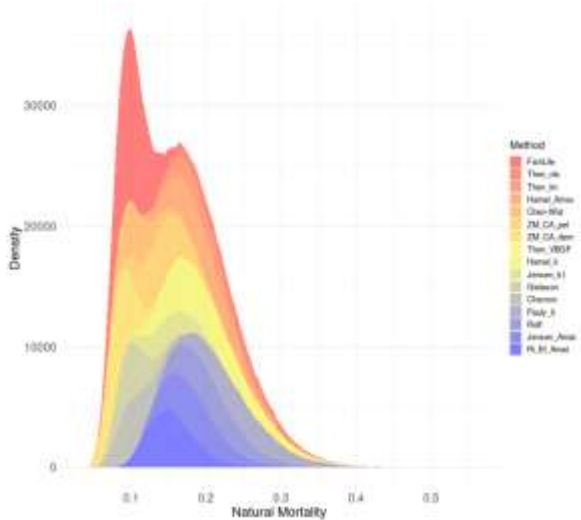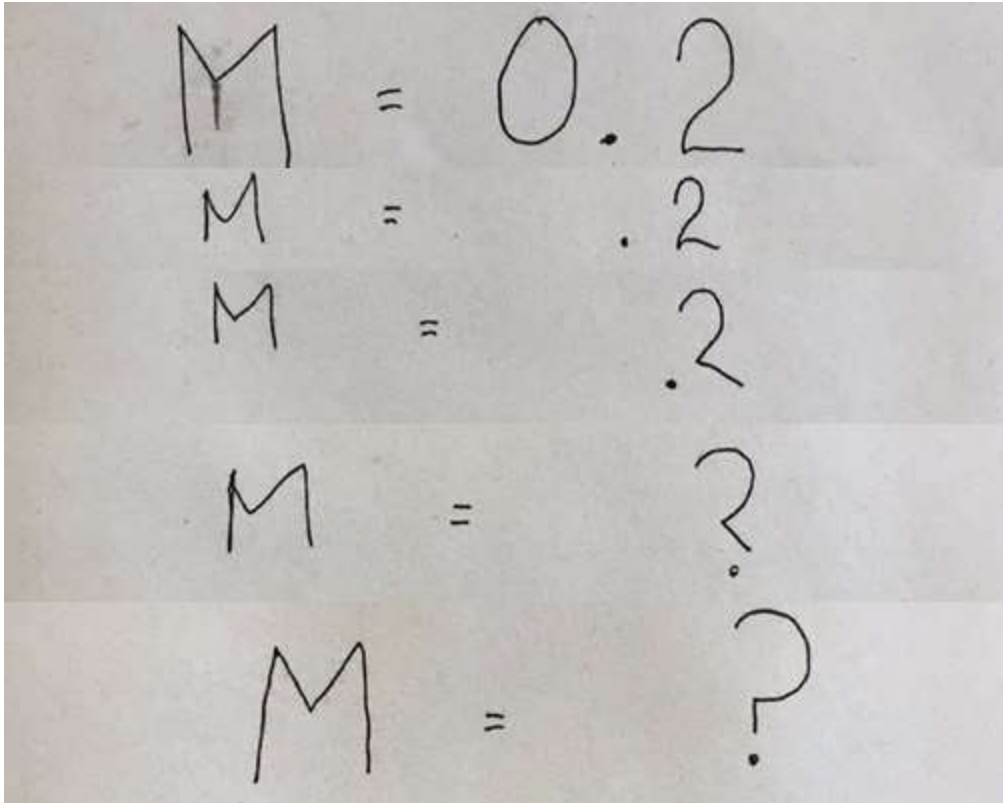
555   A) Yelloweye rockfish

556
557   B) Gopher rockfish

558
559   Figure 3. Weighted empirical *M* estimators with additional variance (CV = 0.2) using the default
560   weightings (left column panels) and the final distribution with central tendency measures (right
561   column panels) of *M* for yelloweye (top row) and gopher (bottom row) rockfishes. In the
562   yelloweye rockfish example, the final distribution is composed of estimators applying longevity
563   only; all other estimators are downweighted to 0.
564

Figure 4. The reversion of *M* that invites inquiry. Using a tool like the NMT can turn the question mark into a species-specific estimate of *M*.